1-2020

Evaluation of an elk detection probability model in the Black Hills, South Dakota

Evan C. Phillips
South Dakota State University

Chadwick P. Lehman
South Dakota Game, Fish and Parks

Robert W. Klaver
U.S. Geological Survey, bklaver@iastate.edu

Angela R. Jarding
National Park Service

Susan P. Rupp
South Dakota State University

See next page for additional authors

Abstract

Since 1993, elk (*Cervus canadensis nelsoni*) abundance in the Black Hills of South Dakota has been estimated using a detection probability model previously developed in Idaho, though it is likely biased because of a failure to account for visibility biases under local conditions. To correct for this bias, we evaluated the current detection probability across the Black Hills during January and February 2009–2011 using radio-collared elk. We used logistic regression to evaluate topographic features, habitat characteristics, and group characteristics relative to their influence on detection probability of elk. Elk detection probability increased with less vegetation cover (%), increased group size, and more snow cover (%); overall detection probability was 0.60 (95% CI 0.52–0.68), with 91 of 152 elk groups detected. Predictive capability of the selected model was excellent (ROC = 0.807), and prediction accuracy ranged from 70.2% to 73.7%. Cross-validation of the selected model with other population estimation methods resulted in comparable estimates. Future applications of our model should be applied cautiously if characteristics of the area (e.g., vegetation cover >50%, snow cover >90%, group sizes >16 elk) differ notably from the range of variability in these factors under which the model was developed.

Evaluation of an Elk Detection Probability Model in the Black Hills, South Dakota

Authors: Phillips, Evan C., Lehman, Chadwick P., Klaver, Robert W., Jarding, Angela R., Rupp, Susan P., et. al.

Source: Western North American Naturalist, 79(4) : 551-565

Published By: Monte L. Bean Life Science Museum, Brigham Young University

URL: https://doi.org/10.3398/064.079.0408

Western North American Naturalist 79(4), © 2019, pp. 551–565

Evaluation of an elk detection probability model in the Black Hills, South Dakota

Evan C. Phillips[1,6], Chadwick P. Lehman[2], Robert W. Klaver[3], Angela R. Jarding[1,4], Susan P. Rupp[1,7], Jonathan A. Jenks[1], and Christopher N. Jacques[5,*]

[1]*Department of Natural Resource Management, South Dakota State University, Brookings, SD 57007*
[2]*Custer State Park, South Dakota Game, Fish and Parks, Custer, SD 57730*
[3]*U.S. Geological Survey, Iowa Cooperative Fish and Wildlife Research Unit, Iowa State University, Ames, IA 50011*
[4]*Wind Cave National Park, National Park Service, Hot Springs, SD 57747*
[5]*Department of Biological Sciences, Western Illinois University, Macomb, IL 61455*
[6]*Present address: Colorado Parks and Wildlife, Department of Natural Resources, Montrose, CO 81401*
[7]*Present address: Enviroscapes Ecological Consulting LLC, Gavette, AR 72736*

Abstract.—Since 1993, elk (*Cervus canadensis nelsoni*) abundance in the Black Hills of South Dakota has been estimated using a detection probability model previously developed in Idaho, though it is likely biased because of a failure to account for visibility biases under local conditions. To correct for this bias, we evaluated the current detection probability across the Black Hills during January and February 2009–2011 using radio-collared elk. We used logistic regression to evaluate topographic features, habitat characteristics, and group characteristics relative to their influence on detection probability of elk. Elk detection probability increased with less vegetation cover (%), increased group size, and more snow cover (%); overall detection probability was 0.60 (95% CI 0.52–0.68), with 91 of 152 elk groups detected. Predictive capability of the selected model was excellent (ROC = 0.807), and prediction accuracy ranged from 70.2% to 73.7%. Cross-validation of the selected model with other population estimation methods resulted in comparable estimates. Future applications of our model should be applied cautiously if characteristics of the area (e.g., vegetation cover >50%, snow cover >90%, group sizes >16 elk) differ notably from the range of variability in these factors under which the model was developed.

Resumen.—Desde 1993, la abundancia de uapitíes (*Cervus canadensis nelsoni*) en las Black Hills del Sur de Dakota ha sido estimada usando un modelo de probabilidad de detección desarrollado en Idaho, aunque es probable que este modelo esté sesgado dada su incapacidad para dar cuenta de los sesgos visibles en condiciones locales. Para corregir el sesgo, evaluamos la probabilidad de detección actual en las Black Hills durante enero y febrero de 2009–2011 utilizando ciervos con radio collares. Empleamos regresión logística para evaluar las características topográficas, del hábitat y del grupo, relativas a su influencia en la probabilidad de detección de ciervos. La probabilidad de detección aumentó cuando la cobertura vegetal disminuyó (%) y cuando el tamaño del grupo y la capa de nieve aumentaron (%). En general, la probabilidad de detección fue de 0.60 (IC 95% 0.52–0.68) con 91 de 152 grupos de ciervos detectados. La capacidad predictiva del modelo seleccionado fue excelente (ROC = 0.807) y la precisión de la predicción varió de 70.2% a 73.7%. La validación cruzada del modelo seleccionado con otros métodos de estimación de la población, dio como resultado estimaciones comparables. Las futuras aplicaciones de nuestro modelo deben realizarse con cautela siempre que las características del área (e.g., cobertura vegetal >50%, capa de nieve >90% y tamaño del grupo >16 ciervos) difieran notablemente del rango de variabilidad de los factores bajo los cuales se desarrolló este modelo.

Management of harvested ungulates benefits from periodic assessment of population size (Skalski et al. 2005). Accordingly, aerial surveys often are used to monitor population abundance of ungulates across most of North America (Gilbert and Moeller 2008, Rice et al. 2009, Jacques et al. 2014, Smyser et al. 2016). However, these surveys often yield biased abundance estimates and only permit detection of population-level changes under specific survey conditions (Gilbert and Moeller 2008, McCorquodale et al. 2013). To aid in promoting sound management decisions, ideal survey estimators should be accurate, precise,

*Corresponding author: cn-jacques@wiu.edu

RWK orcid.org/0000-0002-3263-9701 SPR orcid.org/0000-0002-1427-653X JAJ orcid.org/0000-0002-8630-8385
CNJ orcid.org/0000-0001-5225-457X

repeatable, and cost-effective (Gasaway et al. 1986). A primary goal for the improvement of aerial survey estimates is to account for the number of undetected animals during surveys (McCorquodale et al. 2013). Detection of all animals in a given area is seldom, if ever, achieved during aerial surveys, in part due to potential biases associated with unequal detection probabilities in different survey conditions (Skalski et al. 2005). Two potential sources of error in aerial surveys that can induce bias in population estimates are the variability of animals across the landscape (sampling variance; Steinhorst and Samuel 1989) and the inability to detect all animals during surveys (visibility bias; Allen 2005, Gilbert and Moeller 2008). These sources of bias led to recent advances in aerial survey techniques to correct for undetected animals, including line-transect sampling (Buckland et al. 1993), mark-resight methods (McClintock et al. 2008, 2009, McCorquodale et al. 2013), and detection probability models (Rice et al. 2009, Jacques et al. 2014).

Logistic regression models have been developed for estimating abundance of several ungulates, including elk (Samuel et al. 1987, Walsh 2007, Gilbert and Moeller 2008, McCorquodale et al. 2013), mule deer (*Odocoileus hemionus;* Ackerman 1988), moose (*Alces alces;* Anderson and Lindzey 1996, Quayle et al. 2001), pronghorn (*Antilocapra americana;* Jacques et al. 2014), bighorn sheep (*Ovis canadensis;* Bodie et al. 1995), and mountain goats (*Oreamnos americanus;* Rice et al. 2009). These detection probability models predict the probability of a dichotomous response variable (animal groups detected or undetected) from aerial surveys using logistic regression analysis (Anderson and Lindzey 1996). Among abundance estimation methods that use radio-collared animals to correct for visibility bias, a key assumption is that collared individuals have similar detection probabilities to uncollared animals (Fieberg et al. 2015). In Washington, detection rates did not statistically differ for collared and uncollared elk, but they did differ for other species such as moose (Fieberg et al. 2015). Correction factors are developed from variables that influence the probability of detecting radio-collared animals and are subsequently applied to each animal group detected during surveys (Anderson and Lindzey 1996). Detection probability models are advantageous in rugged mountainous terrain, where line transects are not practical, and when animals occur in groups (Phillips 2011). Furthermore, detection probability models are efficient because they only require capturing and marking animals one time to develop the model (McCorquodale et al. 2013).

Elk are native to South Dakota. They once ranged over the entire state but were extirpated by the late 1800s due to unregulated harvest and market hunting. In the early 1900s, western state and federal agencies began cooperative transplant efforts to reintroduce elk into the Black Hills of South Dakota (SDGFP 2015). Elk abundance has varied considerably since the reintroduction, and the Black Hills elk population was estimated to be around 1000 elk during the 1960s through the late 1980s (Turner 1974, Rice 1988). During the 1990s, the elk population began to increase, and by the year 2000, the total population had increased to approximately 4600 (Halseth and Benzon 2001).

Expanding elk populations led to a growing number of complaints from landowners; they reported crop depredation and damage to private property, which prompted the SDGFP to reduce population densities by increasing harvest quotas (SDGFP 2011). Elk's importance as a native game species demands that fluctuations in population size have accurate monitoring and that managers need improved abundance estimation for elk in the Black Hills.

In 1993, SDGFP biologists implemented an elk detection probability model that was developed in Idaho (Unsworth et al. 1991) to estimate elk abundance in the Black Hills of South Dakota. Following more than a decade of using the model, wildlife managers concluded that the unique vegetation and habitat conditions in the Black Hills were contributing to biased abundance estimates (Phillips 2011). Despite rigorous attempts to standardize survey conditions, unpredictable proportions of elk populations went undetected between surveys, and using detection models to quantify the accuracy and precision of population estimates gave unreasonable results. Thus, an evaluation of elk detection probability models in the Black Hills of South Dakota was initiated in 2008 to refine elk abundance estimation techniques and correct former inaccuracies in the elk detection probability model. Our specific study objectives were to (1) determine the topographic features, habitat characteristics,

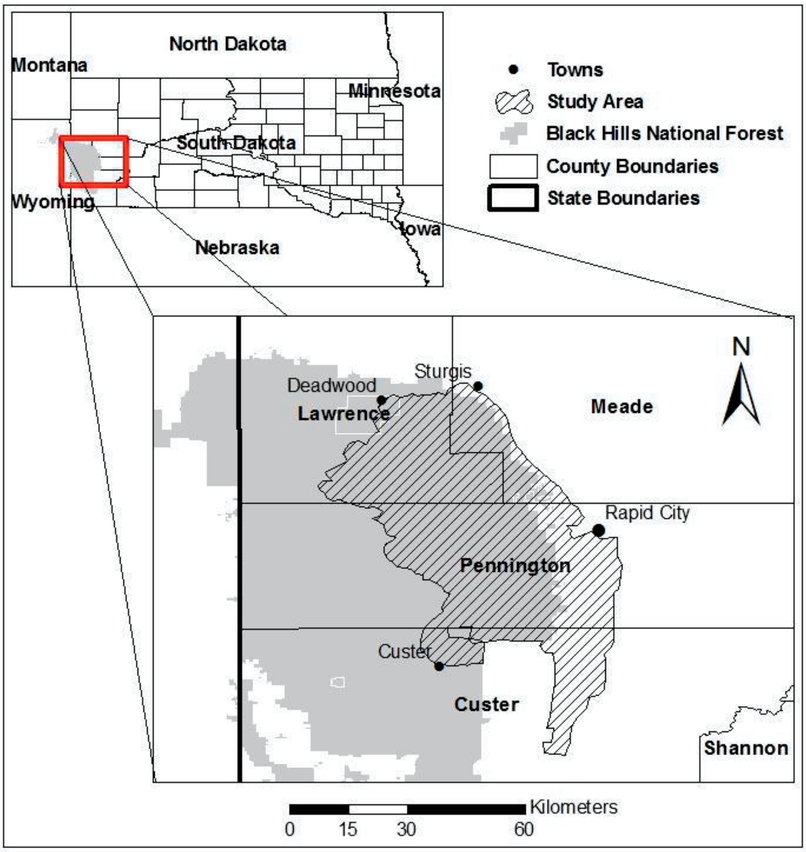

Fig. 1. The Black Hills elk detection probability study area (hatched area) included parts of Lawrence, Meade, Pennington, and Custer Counties in western South Dakota, 2009–2011. Counties are bound by thin black lines; states are delineated by thick black lines; and the Black Hills National Forest is shaded in grey.

and group characteristics that influence elk detection probability in the Black Hills of South Dakota, (2) estimate population abundance, and (3) evaluate detection probability model performance by comparing population estimates with alternative approaches to population estimation.

METHODS

Study Area

Our study was conducted throughout the Black Hills of western South Dakota, on 2418 km^2 of U.S. Forest Service and private land located in portions of Custer, Pennington, Lawrence, and Meade Counties north of Custer State Park and Wind Cave National Monument (Figs. 1, 2). The Black Hills are characterized by an isolated mountainous outcrop surrounded by the nonglaciated Missouri Plateau section of the northern Great Plains Physiographic Province (Turner 1974). Average temperatures ranged from 5.5 °C in the higher elevations to 7.4 °C in the lower elevations. Average annual precipitation ranged from 47.0 cm to 53.6 cm in lower and higher elevations, respectively. Snow cover during winter months was variable; higher elevations typically average 11.43 cm in January and 18.8 cm in February, whereas lower elevations average 10.2 cm and 13.97 cm in January and February, respectively (South Dakota Office of Climatology 2011). Elevation ranged from 915 m to 2207 m above mean sea level. Vegetation consisted primarily of forested areas with ponderosa pine (*Pinus ponderosa*) dominant over 84% of the land area (Hoffman and Alexander 1987). Quaking aspen (*Populus tremuloides*) and paper birch (*Betula papyrifera*) were present in isolated patches and accounted for 4% of forest cover (Hoffman

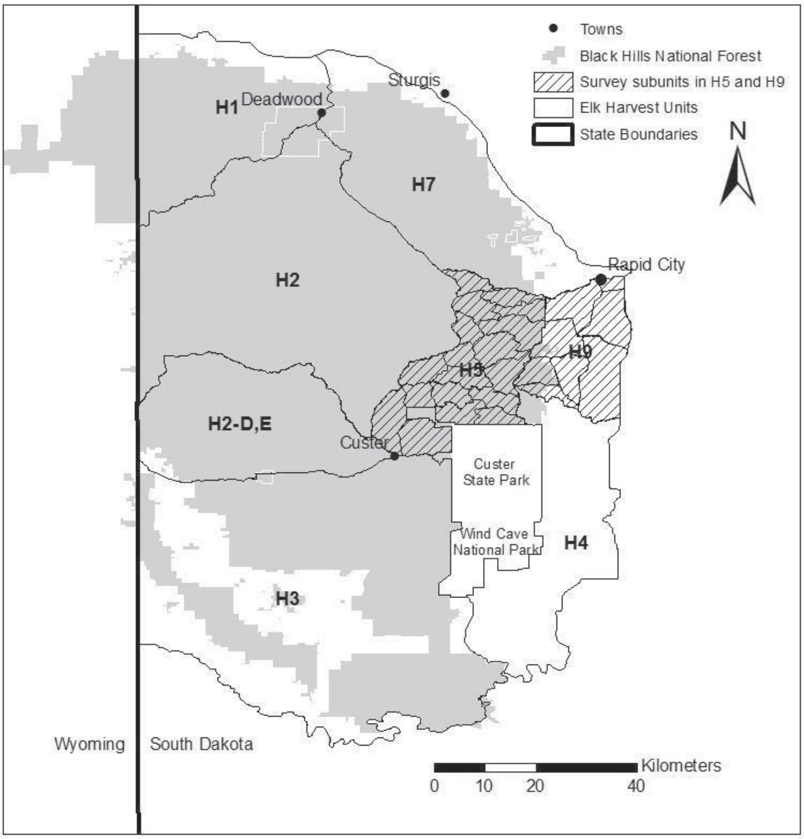

Fig. 2. Complete surveys to evaluate the final developed detection probability models were conducted in harvest units H5 and H9 (hatched area) of the Black Hills, South Dakota, February 2011.

and Alexander 1987). White spruce (*Picea glauca*) occurred at higher elevations and on north-facing slopes, and comprised 2% of forest cover (Hoffman and Alexander 1987). Habitat in the southern Black Hills consisted of open grassland with patches of ponderosa pine. The landscape throughout the northern Black Hills exhibited dense canopy cover interspersed with selective timber harvest and small meadows.

Elk Capture and Monitoring

We net-gunned or darted elk from a helicopter during January–February 2007 and January–April 2008 and 2009. To maintain a sample size of 50 animals per year, we captured additional elk by darting from ground blinds or tree stands set up over bait sites. Elk were processed on site and fitted with one of 3 types of radio collar: standard VHF (n = 83; Mod-601 NH, Telonics, Mesa, AZ), store-on-board GPS (n = 17; Gen. III TGW-3600, Telonics, Mesa, AZ), and live-uplink GPS (n = 5; Model NSG-LD2, North Star Science and Technology, LLC, King George, VA). We equipped GPS and VHF collars with a MS6A mortality sensor (4-h delay) and GPS collars with a CR-2A release mechanism set for February 2010. We used a combination of Butorphanol (6 mL, 50 mg/mL), Azaperone (2 mL, 50 mg/mL), and Medetomidine (3 mL, 40 mg/mL; BAM) to immobilize elk, and reversed using a mixture of Atipamezole (10 mL, 5 mg/mL), Naltrexone (10 mL, 50 mg/mL), and Tolazoline (10 mL, 200 mg/mL; Mich et al. 2008). Animal handling methods were approved by the Institutional Animal Care and Use Committee at South Dakota State University (approval number 10-022A) and followed guidelines for the care and use of animals approved by the American Society of Mammalogists (Sikes and the Animal Care and Use Committee of the American Society of Mammalogists 2016).

Aerial Surveys

We conducted aerial surveys during January and February of 2009, 2010, and 2011, when there was a higher probability of snow cover. We conducted all aerial surveys in a Robinson R44 Raven II (Robinson Helicopter Company, Torrance, CA) helicopter with a pilot in the front right, a primary observer in the front left, and a secondary observer behind the pilot. The primary observer concentrated on searching for elk below and to the left, the secondary observer searched below and to the right, and the pilot flew the helicopter but also assisted in observing elk ahead of and below the helicopter. To standardize training among observers, we required that all primary observers complete a minimum of 8 h of helicopter elk survey training. Our search patterns followed contour intervals that were separated by 200 m to 300 m, starting at lower elevations and working up to higher elevations. We oriented transect surveys in a north-to-south direction to minimize sunrise glare from the east. We maintained an airspeed of approximately 65 km to 80 km per hour and a prescribed height of 30–45 m above ground level (Unsworth et al. 1999).

Detection Probability Model Development

We divided the study area into 80 individual subunits based on topographic (e.g., ridges, streams) and anthropogenic (e.g., roads) features that were easily distinguished from the air; sizes of subunits were designed to ensure that surveys were completed in approximately 1 h (Unsworth et al. 1999, Halseth and Benzon 2001). We located radiocollared elk in the study area by triangulation on the ground, or by fixed-wing aircraft 2–4 h prior to a helicopter survey; all efforts to locate elk were conducted between 06:00 and 08:00. We conducted elk survey observations during two 3-h flights between 08:00 and 16:00. Survey subunits that contained radio-collared elk, and randomly selected survey subunits that did not contain radio-collared elk, were assigned to the helicopter survey crew by the elk location crew via radio without identifying which units contained elk. To survey a subunit, the helicopter pilot maintained approximately 200–300 m transects using GPS (Garmin GPSmap 296; Garmin International Inc., Olathe, KS) until the entire survey subunit was surveyed to within at least 150 m. The primary observer, secondary observer, and pilot scanned the landscape area within at least 150 m in front of and to the sides of the helicopter. We assumed that undetected elk groups within this distance were undetected due to visibility bias (present but not detected) rather than sampling bias (not within survey subunits).

When an elk group was detected and the presence of at least one radio-collared elk was confirmed, we interrupted the search pattern to circle the group and collect information on group size and composition (GS), animal activity (ACT), percent vegetation cover (VEG), percent snow cover (SNOW), light intensity (LI), and location (Universal Transverse Mercator; North American Datum 27, Zone 13). Observers counted the number of elk in the group and classified individuals as mature females, calves, yearling males (spikes), immature males/raghorns ($\leq$4 points per antler), and mature males (males having $\geq$5 points on at least one side). We characterized ACT of the first elk sighted as either bedded, standing, or moving (Unsworth et al. 1999). We qualitatively measured VEG as an ocular estimate to the nearest 10% (Unsworth et al. 1999) at an oblique angle within a 9-m radius enveloping the initial location of each elk group detected (Anderson and Lindzey 1996, Jacques et al. 2014). We estimated SNOW to the nearest 10%, from no snow on the ground (0%) to complete snow cover (100%) when no bare ground was visible within the 9-m radius. We recorded LI as either "flat," with clouds blocking direct sunlight (no shadows), "intermediate" sunlight, or "bright," with direct sunlight that caused shadows and reflected light (Allen 2005). After quantifying habitat and group data, we turned on the telemetry receiver to confirm the identification of each radio-collared individual. We turned the receiver off after each radio-collared elk was identified. Once data were collected, the pilot maneuvered the helicopter to direct moving groups of elk toward previously surveyed areas in order to decrease the chance of double counting. In addition, we monitored postdetection movement and locations of radio-collared elk on adjacent transects; we double counted $\leq$6 of 152 (3.9%) elk groups and censored these observations from our analyses. Thus, we assumed that recounting elk on adjacent surveys was minimal during our study.

If radio-collared elk were not visually detected during the search of a subunit, the elk location crew informed the survey crew and continued aerial surveys uninterrupted until they were completed (Grassel 2000, Jacques et al. 2014). Upon completing individual survey areas (i.e., subunits), we immediately used radiotelemetry to locate collared elk not detected during surveys. Subsequently, we collected information on the same variables as collected for detected groups of elk (Jacques et al. 2014). To maintain statistical independence, we considered groups of elk with more than one collared individual a single observation (Samuel et al. 1987). We posited biologically plausible a priori logistic regression models of how the probability of detecting elk may be influenced by GS, ACT, VEG, SNOW, RUG, and LI (Table 1); all models were additive without interactions.

Data Analyses

Prior to modeling, we quantified the severity of multicollinearity among covariates using a variance inflation factor (VIF) with a predetermined cutoff value of 3 (Zuur et al. 2010). We screened all predictor variables for collinearity using Pearson's correlation coefficients ($|r| > 0.5$) and used quantile plots to evaluate assumptions of normality; we used only one variable from a set of collinear variables for modeling (Jacques et al. 2014). We used logistic regression models to evaluate potential effects of predictor variables on elk detection probability. We used Akaike's information criterion, adjusted for small sample size (AICc), to select models that best described the data, and we used Akaike weights (w_i) as a measure of relative model support for model fit (Burnham and Anderson 2002). We removed models within 1 ΔAICc with little change in model deviance, indicative of uninformative parameters (Arnold 2010). After we removed models with additional uninformative parameters, we recalculated model weights based on the smaller model set (Burnham and Anderson 2002). We estimated odds ratios for each parameter using the regression coefficients from the logistic regression equation (Keating and Cherry 2004).

We selected 18 models a priori based on factors known to significantly affect detection probability in previous research and prior knowledge of elk in the region. Independent variables used for modeling included VEG, GS, SNOW, LI, RUG, and ACT; we set standing elk as our reference category. Natural logarithm transformation of GS, SNOW, and VEG variables did not result in improved model fit; therefore, we did not use transformed data in our final analyses (Cogan and Diefenbach 1998).

We evaluated model fit using the area under the receiver operating characteristic (ROC) curve (Hosmer and Lemeshow 2000, Sing et al. 2005); we considered values between 0.7 and 0.8 acceptable discrimination and values ≥0.8 excellent discrimination (Hosmer and Lemeshow 2000). We assessed classification accuracy of models using 2 methods. First, we determined predictive capabilities of models with area under the receiver operating characteristic (ROC) curve; we considered ROC values between 0.7 and 0.8 acceptable discrimination and values ≥0.8 excellent discrimination (Hosmer and Lemeshow 2000). Furthermore, ROC values 0.5–0.7 indicated low discrimination, and values ≤0.5 indicated that model predictive capabilities were no better than random (Grzybowski and Younger 1997, Hosmer and Lemeshow 2000). Second, we used 10-fold cross-validation with 200 repetitions by iteratively fitting with one group withheld at a time and assessing performance in predicting withheld data (Efron 2004). To evaluate model performance, we conducted separate, complete surveys in February 2011, independent of model development flights in 2 elk harvest management units, H5 and H9 (Fig. 2), where variability in previous density estimates was traditionally low and biologists had the best knowledge of elk numbers. We conducted elk detection probability modeling using Program R (Version 3.4.3; R Core Team 2015); statistical tests were conducted at $\alpha = 0.05$.

We used a modified Horvitz–Thompson estimator and variances to calculate abundance estimates of detection probability models (Samuel and Garton 1994). Additionally, we used methods developed by Steinhorst and Samuel (1989) in program AERIAL SURVEY (Unsworth et al. 1999) to calculate 95% confidence intervals. Confidence intervals represented detection probability variance (error associated with the correction factor applied

TABLE 1. Effects of independent variables on detection probability of 152 elk groups containing radio-collared individuals in the Black Hills of South Dakota, 2009–2011.

	Number of groups			
Variable	Detected	Undetected	DP[a]	95% CI
Animal activity				
Bedded	18	9	0.67	0.49–0.84
Standing	57	46	0.55	0.36–0.82
Moving	14	8	0.64	0.45–0.82
Light intensity				
Sunny	45	38	0.54	0.35–0.73
Partly cloudy	10	9	0.53	0.33–0.72
Cloudy	34	16	0.68	0.50–0.86
Group size				
1	4	13	0.24	0.07–0.40
2	2	6	0.25	0.14–0.52
3	3	10	0.23	0.07–0.40
4	10	6	0.63	0.44–0.81
5	5	3	0.63	0.43–0.82
6–10	12	10	0.55	0.35–0.74
11–15	18	9	0.67	0.49–0.85
16–20	12	4	0.75	0.58–0.92
21–25	3	2	0.67	0.47–0.86
≥26	20	0	1.00	0.99–1.00
% Vegetation				
0	7	2	0.78	0.61–0.94
10	13	3	0.81	0.66–0.96
20	12	2	0.86	0.72–0.99
30	10	6	0.63	0.44–0.81
40	14	5	0.74	0.57–0.91
50	11	16	0.41	0.22–0.60
60	11	11	0.50	0.31–0.69
70	6	6	0.50	0.30–0.70
80	2	9	0.18	0.03–0.33
≥90	3	3	0.50	0.29–0.71
% Snow				
0	4	3	0.57	0.37–0.77
10	2	4	0.33	0.14–0.53
20	0	2	0.00	
30	0	5	0.00	
40	2	2	0.50	0.28–0.72
50	7	1	0.88	0.74–1.00
60	0	0		
70	2	1	0.67	0.45–0.88
80	3	1	0.75	0.56–0.94
90	4	2	0.67	0.14–0.53
100	67	40	0.63	0.44–0.81
Vector ruggedness				
0–0.0012	14	11	0.56	0.39–0.58
0.0012–0.0028	22	9	0.71	0.51–0.87
0.0028–0.0062	17	14	0.55	0.35–0.74
0.0062–0.0133	21	15	0.58	0.39–0.77
0.0133–0.0600	15	14	0.52	0.31–0.69

[a]DP = detection probability: (no. groups detected)/(no. groups detected + no. groups undetected).

to each group) and model variance (error in estimating the detection probabilities during model development). Singular use of the highest-ranked model for predicting detection probability was not strongly supported because of the low evidence ratio between the highest-ranked and second highest-ranked model ($w14/w15 = 1.67$; Burnham and Anderson 2002); therefore, estimated parameters were averaged across all models in the set. We then incorporated parameter estimates from the 2 models (i.e., the model-averaged parameter estimates [i.e., averaged Black Hills model] and the highest-ranked model [i.e., highest-ranked Black Hills model]) into AERIAL SURVEY to generate abundance estimates. In addition, we generated a population estimate using parameters from the original Hiller 12E (with snow) model that was developed in Idaho using the population estimator previously developed by Steinhorst and Samuel (1989) to obtain abundance estimates. We calculated total variance as the sum of the detection probability error and sampling error (Steinhorst and Samuel 1989). We calculated the minimum number of elk known alive (MNA) for units H5 and H9 by totaling all individuals that were observed during the complete survey, and a Lincoln–Petersen (L–P) estimate corrected for small sample size using resighting events of collared individuals (Seber 1982). We used data collected for the elk detection probability model to calculate 95% confidence intervals by assuming asymptotic normality of the detection probability estimator and generating 2.5 and 97.5 percentiles for 10,000 population estimates from bootstrap model data sets (see Cogan and Diefenbach 1998 for a detailed description of the bootstrap technique for calculating confidence intervals). We compared population estimates or count data using a chi-squared contrast with $\alpha = 0.05$ (Sauer and Williams 1989) among the resulting models: the highest-ranked Black Hills model, the averaged Black Hills model, the Idaho Hiller 12E model, the L–P method, and MNA.

RESULTS

Accounting for collar failure and mortality, 36 (10 bulls and 26 cows), 31 (8 bulls and 23 cows), and 19 (4 bulls and 15 cows) collared elk were available to be counted in our survey areas during winter 2009, 2010, and 2011, respectively. The number of marked elk available to survey was 40, 31, and 18 during 2009, 2010, and 2011, respectively. We conducted 9, 7, and 7 winter flights during 2009, 2010, and 2011, respectively, which accounted for greater sample sizes of groups than radio-marked elk; marked elk often were detected more than once over multiple flights. Mean number of detections per individual was 3.10 (SE 0.32, range 1–7), 4.26 (SE 0.33, range 1–7) and 2.11 (SE 0.20, range 1–3) during 2009, 2010, and 2011, respectively. In addition, we detected 41 of 63 groups, 37 of 71 groups, and 13 of 22 groups of elk in 2009, 2010 and 2011, respectively. We collected observations on 156 total groups of elk that contained at least one radio-collared individual over those 3 years. After removing 4 observations due to surveyor error, overall detection probability was 0.60 (95% CI 0.52–0.68), with 91 of 152 observations detected without the use of telemetry. Elk groups ranged in size from 1 to 154 individuals with a mean of 14.3 (SD 20.95), a median of 8, and a mode of 1. Our results revealed that probability of detecting elk varied with GS ($F_{1,150} = 17.46$, $P < 0.001$), VEG ($F_{1,150} = 17.30$, $P < 0.001$), and SNOW ($F_{1,150} = 5.28$, $P < 0.007$); detection increased with increasing group size and percent snow, yet declined as percent vegetation increased (Table 1). In contrast, we documented no effects of ACT ($F_{1,150} = 0.10$, $P = 0.76$), RUG ($F_{1,150} = 0.32$, $P = 0.58$), or LI ($F_{1,150} = 2.27$, $P = 0.13$) on elk detection probability (Table 1).

Logistic Regression Model Selection

Variance inflation factors ranged from 1.006 to –1.466, indicating no correlation among model covariates. The highest-ranked model for detecting elk in the Black Hills was VEG + GS + SNOW. Our analysis revealed model selection uncertainty among competing models; weight of evidence (w_i) supporting the highest-ranked model was 0.50 (Table 2), and predictive capability was excellent (ROC = 0.807). Assessment of classification accuracy using ROC resulted in 73.7% of 152 observations correctly classified, whereas 10-fold cross-validation of over 200 repetitions averaged 70.2% (SE 0.047). Using a ROC-calculated optimal classifier performance cutoff of 0.57, the highest-ranked model correctly classified 73.7% of the 152 observations (range 63.8%–75%) (Table 3). Percent of detection probability observations classified correctly by models in the 95% confidence set ranged from 68.2% to 70.5% correct (Table 4). The weight of evidence supporting this model (VEG + GS + SNOW) was 1.7 times greater than the second highest-ranked model (VEG + GS + SNOW + ACT), 5.8 times greater than the global model (VEG + GS + LI + SNOW + ACT + RUG), and 9.1 times greater than the fourth highest-ranked model (VEG + GS + ACT). All other models were noncompetitive ($w_i < 0.053$) and thus were excluded from further

TABLE 2. Akaike information criterion model selection of a priori logistic regression models for 599 elk detections in the Black Hills of South Dakota, 2009–2011; all detection probability models were estimated using 152 observations of radio-collared elk.

Model covariates[a]	K[b]	AICc[c]	ΔAICc[d]	w_i[e]	ROC[f]
VEG + GS + SNOW	4	162.941	0.000	0.502	0.807
VEG + GS+ SNOW + ACT	6	163.960	1.018	0.302	0.817
VEG + GS + LI + SNOW + ACT + RUG	8	166.457	3.516	0.0087	0.825
VEG + GS + ACT	5	167.360	4.419	0.055	0.809
VEG + GS	3	167.618	4.677	0.048	0.792
GS + SNOW	3	172.374	9.433	0.004	0.785
GS	2	176.207	13.266	0.001	0.758
GS + LI + ACT	6	179.230	16.289	0.000	0.771
VEG + SNOW	3	190.921	27.980	0.000	0.701
VEG	2	193.930	30.988	0.000	0.689
SNOW	2	207.117	44.175	0.000	0.566
INTERCEPT-ONLY	1	208.274	45.33	0.000	0.500

[a]VEG = percent vegetation, GS = group size, SNOW = percent snow cover, ACT = animal activity, LI = light intensity, RUG = terrain ruggedness.
[b]Number of parameters.
[c]Akaike's information criterion adjusted for small sample sizes (Burnham and Anderson 2002).
[d]Difference in AICc relative to minimum AICc.
[e]Akaike weight (Burnham and Anderson 2002).
[f]ROC = area under the receiver operating characteristic curve. Values ≥0.8 were considered excellent discrimination; values between 0.7 and 0.8 were considered acceptable discrimination; and values <0.7 were considered low discrimination (Hosmer and Lemeshow 2000).

TABLE 3. Optimal classification cutoff points from ROCR (R Core Team 2015); classification tables where rows were as follows: 0 = classified as undetected, 1 = classified as detected; and percent of elk detection probability observations classified as correct in the Black Hills of South Dakota, 2009–2011.

Model covariates[a]	ROC cutoff point	Classification by model	True observation: Detected	True observation: Undetected	Classified correct (%)[b]
VEG + GS + SNOW	0.57	0	46	17	73.7
			1	23	66
VEG + GS + SNOW + ACT	0.50	0	42	21	75.0
			1	17	72
VEG + GS + LI + SNOW + ACT + RUG	0.42	0	36	27	73.7
			1	13	76
VEG + GS + ACT	0.41	0	34	29	73.7
			1	11	78
VEG + GS	0.39	0	35	28	73.7
			1	12	77
GS + SNOW	0.45	0	37	26	75.0
			1	12	77
GS	0.41	0	29	28	71.7
			1	9	80
GS + LI + ACT	0.42	0	31	32	71.1
			1	12	77
VEG + SNOW	0.40	0	22	41	67.8
			1	8	81
VEG	0.60	0	45	18	66.4
			1	33	56
SNOW	0.50	0	16	47	63.8
			1	8	81

[a]VEG = percent vegetation, GS = group size, SNOW = percent snow cover, ACT = animal activity, LI = light intensity, RUG = terrain ruggedness.
[b]Classified correct (%) = ([# observed missed, classified missed + # observed sighted, classified sighted]/152) * 100.

consideration (Table 2). The 95% confidence intervals for parameter estimates of the VEG (95% CI −0.046 to −0.011), GS (95% CI 0.059–0.173), and SNOW (95% CI 0.004−0.031) covariates did not overlap zero, and P values were significant ($P \leq 0.013$), indicating that these variables were influential predictors for detecting elk. In contrast, 95% confidence

TABLE 4. Average accuracy of correctly classified elk detection probability observations based on 10-fold cross validation over 200 iterations, standard error (SE), and 95% confidence intervals (CI) of the correct classification rate in the 95% confidence model set for elk detection probability in the Black Hills of South Dakota, 2009–2011.

Model covariates[a]	Correct classification (%)	SE	95% CI Lower	95% CI Upper
VEG + GS + SNOW	70.2	0.05	70.1	70.3
VEG + GS + SNOW +ACT	70.5	0.06	70.4	70.6
VEG + GS + LI + SNOW + ACT + RUG	68.2	0.08	68.1	68.4
VEG + GS + ACT	69.4	0.08	69.3	69.6
VEG + GS	70.3	0.08	70.1	70.4

[a]VEG = percent vegetation, GS = group size, SNOW = percent snow cover, ACT = animal activity, LI = light intensity, RUG = terrain ruggedness.

TABLE 5. Model-averaged parameter β estimates ($\hat{\beta}$), standard error (SE), odds ratio, and odds ratio 95% confidence intervals for parameters averaged across models that contained the 3 variables (i.e., percent vegetation cover, group size, and percent snow cover) evaluated for elk detection probability in the Black Hills of South Dakota, 2009–2011.

Parameter[a]	($\hat{\beta}$)	SE	Odds ratio	Odds ratio 95% confidence intervals Lower	Odds ratio 95% confidence intervals Upper
Intercept	−0.951	0.775			
VEG	−0.029	0.009	0.972	0.955	0.989
GS	0.116	0.029	1.123	1.061	1.189
SNOW	0.017	0.007	1.017	1.004	1.031

[a]VEG = percent vegetation, GS = group size, SNOW = percent snow cover.

intervals for parameter estimates of the ACT_bedded (95% CI −0.173 to 1.911), ACT_moving (95% CI −0.537 to 1.738), LI (95% CI −0.183 to 0.671), and RUG (95% CI −26.747 to 46.367) covariates overlapped zero, and P values were not significant ($P \geq 0.103$), indicating that these variables were not statistically important predictors of detecting elk. Thus, we further model-averaged parameter estimates across models that contained only the GS, VEG, and SNOW covariates. The logistic equation for the averaged Black Hills model (Table 5, Fig. 3) was

$$\text{logit}\,(\mu\text{: probability of elk detected}) = 0.952 - 0.029(\text{VEG}) + 0.116(\text{GS}) + 0.017(\text{SNOW})\,.$$

Probability of detecting elk increased by 1.12/1 unit increase in group size and by 1.02/1 unit increase in percent snow. In contrast, probability of detecting elk decreased by 0.03/1 unit increase in percent vegetation (Table 5).

Population Estimation and Evaluation

Complete independent surveys of units H5 and H9 yielded 84 elk (40 cows, 17 calves, 13 adult bulls, 8 immature bulls, and 6 yearling bulls) in 10 groups. Group size ranged from 1 to 29 ($\bar{x}$ = 8.4, SD 7.16). There were 8 collared elk (3 bulls and 5 cows) available during the survey, all of which were detected (i.e., detection probability = 1.0). Within our study area, elk population estimates were relatively consistent across our detection probability models and the original Hiller 12E model (Fig. 3). The minimum number of elk known to be alive (MNA) in harvest units H5 and H9 at the time of the survey was equal to the total individuals counted during the survey (84 individual elk). Because all marked individuals were detected during the complete survey, the bias-corrected L–P estimate was identical to the MNA with a confidence interval of ±0. Population estimates generated by the highest-ranked Black Hills model, the model-averaged Black Hills model, the Idaho Hiller 12E model, and the L–P method were similar at the 95% level (χ^2_3 = 5.935, P = 0.115); 95% CIs of L–P and MNA estimates encompassed model-derived abundance estimates. Nevertheless, our analyses indicated that the most precise abundance estimates were associated with the averaged Black Hills model (Fig. 3).

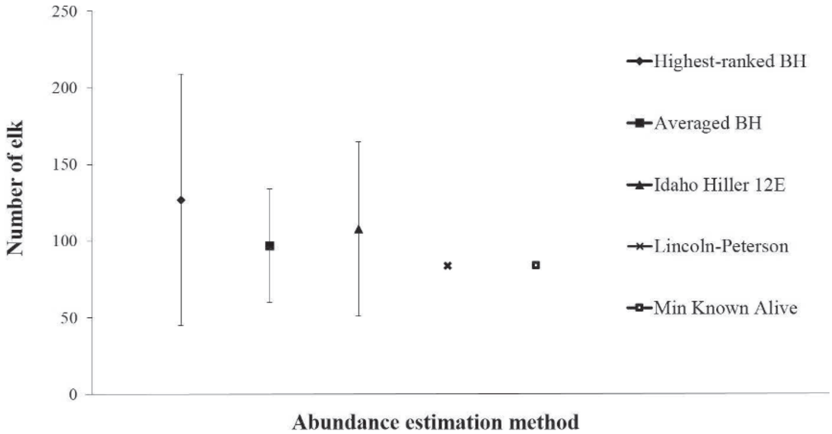

Fig. 3. Elk abundance estimates derived from the highest-ranked Black Hills (BH) model (diamond), averaged Black Hills (BH) model (solid square), Idaho Hiller 12E model (triangle), Lincoln–Petersen model (x), and minimum number known alive (open square) in harvest units H5 and H9 in the Black Hills of South Dakota, February 2011.

Discussion

Logistic Regression Model Selection

Group size of elk in the Black Hills was the dominant variable in the model and positively influenced detection probability (Samuel et al. 1987, McCorquodale et al. 2013). Even at relatively high percentages of vegetation cover (i.e., >60%), all groups >50 individuals were detected. In open areas with lower vegetation cover (i.e., <20%), probability of detecting elk approached 0.9 even at lower group sizes (i.e., <10 individuals). Secondly, the importance of vegetation cover has been quantified in virtually every study that has evaluated ungulate detection probability (Gilbert and Moeller 2008, Walsh et al. 2009, McCorquodale et al. 2013, Jacques et al. 2014). We noted a negative effect of percent vegetation on the probability of detecting elk, which is consistent with results reported previously for elk (Samuel et al. 1987, Cogan and Deifenbach 1998, McCorquodale 2001, Vander Wal et al. 2011) and moose (Anderson and Lindzey 1996). Nevertheless, heterogeneity in landscape characteristics that we encountered during aerial surveys was notable, and it was characterized by reduced overstory vegetation in the outer foothill regions and dense overstory vegetation in the interior regions of the Black Hills. Further research evaluating the range of habitat complexity may broaden the applicability of detection probability models or identify habitats that require alternative statistical approaches (Samuel et al. 1987).

Aerial surveys of ungulates are typically conducted during the winter, when snow is likely present, and when ungulates are concentrated on winter ranges (Rabe et al. 2002). Accordingly, snow cover is generally believed to influence ungulate detection probability by enhancing color contrast between dark-bodied animals and a snow background (Gasaway et al. 1986). Our analyses revealed that snow cover had a positive effect on the probability of detecting elk. However, the relative magnitude of this effect was not as influential as the GS or VEG covariates, which may reflect the limited range of snow cover measured during our study; 74% of elk detected occurred in areas with ≥90% snow cover (Table 1). Further analyses of the potential effects of snow quality and quantity over a wider range of environmental conditions and habitat types may aid in refining ungulate detection probability models across mixed and coniferous forests of North America.

We detected 60% of the 152 groups containing radio-collared elk over a range of group sizes, snow cover, and vegetation cover densities. Our detection rate was similar to rates reported for elk (57%–61%) in similar studies (Samuel et al. 1987, Cogan and Diefenbach 1998, Allen 2005). We selected winter surveys to best represent the range of biological variables expected during implementation because detection probabilities are estimated for each elk group encountered (Anderson et al. 1998). Accordingly, our detection rate should be higher than would be expected outside of winter or early spring, when elk tend to occur in smaller groups and occupy areas of dense vegetation, in which case determination of correction factors for animal groups may not be feasible (Samuel et al. 1987). Our model also may apply to late-winter surveys, because the influence of vegetation cover and elk behavior should be similar (Samuel et al. 1987).

The modified Horvitz–Thompson estimator assumes that groups are counted completely (Samuel and Garton 1994). Group size can frequently be underestimated during helicopter surveys, especially in habitats with high percentages of vegetation cover (Cogan and Diefenbach 1998). The result is that estimates of abundance and variance are biased low. Walsh et al. (2009) developed an estimator for the number of individuals in each group using 3 independent counts by the primary observer, the secondary observer, and the pilot. We initially attempted a similar approach, but the observers and pilot needed to communicate to maneuver the helicopter and facilitate a better view for counting elk and thus negated true independence of observations. Therefore, we addressed the assumption that group sizes were counted correctly by maneuvering the helicopter to completely circle around the group so that observers were satisfied with their final counts.

Our detection probability model and alternative population abundance estimators demonstrated the importance of quantifying detection probabilities in elk population estimation. We recognize that future use of these techniques requires continued capture and radio collaring of animals across time and space. Consequently, annual capture and radio collaring to maintain adequate samples of animals may not be logistically or economically feasible (Jacques et al. 2014). In such cases, our results could directly incorporate sources of visibility bias into more traditional elk population estimation techniques, thereby enabling wildlife managers to potentially validate our existing model or incorporate additional sources of visibility bias (e.g., observer experience, time of day) into elk population estimation. Our results suggest that improvements in traditional elk aerial survey techniques may be possible by incorporating unique detection functions to account for heterogeneity in animal group size and various habitat features (e.g., percent vegetation, snow cover). Detection probabilities also may vary with different segments of the population. For instance, Jacques et al. (2014) hypothesized that pronghorn detection probabilities may vary between sex and age classes. Such may also be the case with bull elk, who often occur alone and thus have lower detection probabilities relative to cow-calf groups (McCorquodale 2001, Jarding 2010).

Population Estimation and Evaluation

All subunits of the harvest units H5 and H9 were surveyed completely; therefore, error was not associated with sampling nor incorporated into variance or confidence intervals of estimates. This complete survey was flown in as short of a time as possible (3 consecutive days) to minimize elk movement out of the harvest units so the assumption of population closure was met. The number of elk groups recorded during the complete survey of those units was low ($n = 10$), resulting in a small sample size. Larger sample sizes of more groups of elk could result in better evaluation of detection probability estimators. Only one replication was conducted and sample size was small for the initial evaluation; therefore, additional replications of model evaluation should be conducted to ensure satisfaction with model performance. Nevertheless, variance and confidence intervals were smallest for the averaged Black Hills model, followed by the Idaho Hiller 12E and highest-ranked Black Hills models. This was expected because model-averaging parameter estimates reduce bias and increase precision (Burnham and Anderson 2002).

If the assumption was made that the MNA and the L–P estimate were representative of the true number of elk in harvest units H5 and H9 at the time of the survey, then none of our model-derived abundance estimates differed at the 95% confidence level. Despite efforts to standardize factors and reduce their influence on detection probability, it is possible that the open habitat characteristics across subunits H5 and H9 were not representative of the range of habitat complexity encountered in other areas of the Black Hills occupied by elk. Subunits H5 and H9 are some of the more open units with the lowest percent vegetation cover compared to other harvest units in the Black Hills (Phillips 2011). In this open habitat, detection probability may not have resulted in as large of a correction factor as in other units characterized by a higher percentage of canopy cover. Additional information may have been gained on elk detection under more complex habitat conditions (e.g., elk in heavy conifer forests vs. open habitats) and with a larger sample of elk groups detected, particularly given the complexity of our averaged Black Hills detection probability model. Model standard errors may provide information on the relative precision of detection probability models and the influence of model variance on the precision of elk abundance estimates (Samuel et al. 1987, Steinhorst and Samuel 1989).

The previously noted perception of negative bias for the Black Hills held by wildlife managers may have been influenced more by sample size and imperfect sampling than by use of the Idaho methodology (Unsworth et al. 1991) in previous attempts to estimate elk population size. A comparison of elk observations between Idaho (Samuel et al. 1987) and South Dakota (current study) indicated similar detection probabilities in open habitats (58% vs. 65%, respectively) and dense (greater than or equal to approximately 70%) canopy cover (9% and 7%, respectively), suggesting similar performance in detection probability models among study areas. The averaged detection probability model for the Black Hills estimated a population with 95% confidence intervals that encompassed the minimum number of elk known to be alive and the L–P estimates for the area surveyed, indicating favorable performance of the model. Nevertheless, we suggest that this model be further evaluated by using stratification of elk harvest units across a wider range of vegetation density classes (e.g., dense forest cover, open meadows). Improved model performance (i.e., increased accuracy and precision) would also be obtained by increasing the number of elk observations used in future analyses. Future applications of our model should be applied cautiously if characteristics of the area (e.g., vegetation cover >50%, snow cover >90%, group sizes >16 elk) differ notably from the range of variability in these factors under which the model was developed. Finally, if physical capture and marking of individuals are required, data from marked and unmarked individuals could be used for estimating population abundance across the Black Hills using mark-resight methods (McClintock et al. 2009, Jacques et al. 2014) to further validate our model.

ACKNOWLEDGMENTS

Funding was provided by Federal Aid in Wildlife Restoration administered by the South Dakota Department of Game, Fish, and Parks; the Department of Natural Resource Management at South Dakota State University; the South Dakota Agricultural Experiment Station; and the Rocky Mountain Elk Foundation. We are grateful to L. Meduna, L. Jennings, L. Dahl, and L.E. Schmitz for logistical support in organizing aerial surveys and numerous volunteers for assistance with counting elk. We thank South Dakota Civil Air Patrol pilots M. Beason, L.J. Becht, and G. Hewitt for assistance with conducting aerial telemetry flights, and Quicksilver Air pilots B. Lithgow and B. Malo for conducting aerial survey flights. We thank C. Anderson for reviewing an earlier draft of our manuscript. Any use of trade, product, or firm names is for descriptive purposes only, and does not imply endorsement by the United States Government.

LITERATURE CITED

ACKERMAN, B.R. 1988. Visibility bias of mule deer aerial census procedures in southeast Idaho. Doctoral dissertation, University of Idaho, Moscow, ID. 106 pp.

ALLEN, J.R. 2005. Use of sightability models and resource selection functions to enhance aerial population surveys of elk (*Cervus elaphus*) in Alberta. Master's thesis, University of Alberta, Edmonton, Canada.

ANDERSON, C.R., JR., AND F.G. LINDZEY. 1996. Moose sightability model developed from helicopter surveys. Wildlife Society Bulletin 24:247–259.

ARNOLD, T.W. 2010. Uninformative parameters and model selection using Akaike's information criterion. Journal of Wildlife Management 74:1175–1178.

BODIE, W.L., E.O. GARTON, E.R. TAYLOR, AND M. MCCOY. 1995. A sightability model for bighorn sheep in canyon habitats. Journal of Wildlife Management 59: 832–840.

BUCKLAND, S.T., D.R. ANDERSON, K.P. BURNHAM, AND J.L. LAAKE. 1993. Distance sampling: estimating abundance of biological populations. Chapman and Hall, New York, NY. 432 pp.

BURNHAM, K.P., AND D.R. ANDERSON. 2002. Model selection and multi-model inference. Springer-Verlag, New York, NY. 488 pp.

COGAN, R.D., AND D.R. DIEFENBACH. 1998. Effect of undercounting and model selection on sightability-adjustment estimator for elk. Journal of Wildlife Management 62:269–279.

EFRON, B. 2004. The estimation of prediction error: covariance penalties and cross-validation. Journal of the American Statistical Association 99:619–632.

FIEBERG, J.R., K. JENKINS, S. MCCORQUODALE, C.G. RICE, G.C. WHITE, AND K. WHITE. 2015. Do capture and survey methods influence whether marked animals are representative of unmarked animals. Wildlife Society Bulletin 39:713–720.

GASAWAY, W.C., S.D. DUBOIS, D.J. REED, AND S.J. HARBO. 1986. Estimating moose population parameters from aerial surveys. Biological Paper Number 22, University of Alaska, Fairbanks, AK. 108 pp.

GILBERT, B.A., AND B.J. MOELLER. 2008. Modeling elk sightability bias of aerial surveys during winter in the central Cascades. Northwest Science 82:222–228.

GRASSEL, S.M. 2000. Evaluation of methodology used to estimate population size, sex, and age ratios, and mortality of white-tailed deer in the Missouri River Breaks region of South Dakota. Master's thesis, South Dakota State University, Brookings, SD. 88 pp.

GRZYBOWSKI, M., AND J.G. YOUNGER. 1997. Statistical methodology: III. Receiver operating characteristic (ROC) curves. Academic Emergency Medicine 4: 818–826.

HALSETH, R., AND T. BENZON. 2001. Elk management surveys, 2000. South Dakota Game Report No. 2002–01. 34 pp.

HOFFMAN, G.R., AND R.R. ALEXANDER. 1987. Forest vegetation types of the Black Hills National Forest of South Dakota and Wyoming: a habitat type classification. Research Paper RM-276, U.S. Forest Service, Rocky Mountain Research Station, Fort Collins, CO.

HOSMER, D.W., AND S. LEMESHOW. 2000. Applied logistic regression. 2nd edition. John Wiley & Sons, New York, NY. 375 pp.

JACQUES, C.N., J.A. JENKS, T.W. GROVENBURG, R.W. KLAVER, AND C.S. DEPERNO. 2014. Incorporating detection probability into northern Great Plains pronghorn population estimates. Journal of Wildlife Management 78:164–174.

JARDING, A.R. 2010. Population estimation procedures for elk and deer in the Black Hills: development of a sightability model and spotlight surveys. Master's thesis, South Dakota State University, Brookings, SD. 84 pp.

KEATING, K.A., AND S. CHERRY. 2004. Use and interpretation of logistic regression in habitat selection studies. Journal of Wildlife Management 68:774–789.

MCCLINTOCK, B.T., G.C. WHITE, M.F. ANTOLIN, AND D.W. TRIPP. 2009. Estimating abundance using mark-resight when sampling is with replacement or the number of marked individuals is unknown. Biometrics 65:237–246.

MCCLINTOCK, B.T., G.C. WHITE, K.P. BURNHAM, AND M.A. PRYDE. 2008. A generalized mixed effects model of abundance for mark-resight data when sampling is without replacement. Environmental and Ecological Statistics 3:271–289.

MCCORQUODALE, S.M. 2001. Sex-specific bias in helicopter surveys of elk sightability and dispersion effects. Journal of Wildlife Management 65:216–225.

MCCORQUODALE, S.M., S.M. KNAPP, M.A. DAVISON, J.S. BOHANNON, C.D. DANILSON, AND W.C. MADSEN. 2013. Mark-resight and sightability modeling of a western Washington elk population. Journal of Wildlife Management 77:359–371.

MICH, P.M., L.L. WOLFE, T.M. SIROCHMAN, M.A. SIROCHMAN, T.R. DAVIS, W.R. LANCE, AND M.W. MILLER. 2008. Evaluation of intramuscular butorphanol, azaperone, and medetomidine and nasal oxygen insufflation for the chemical immobilization of white-tailed deer (*Odocoileus virginianus*). Journal of Zoo and Wildlife Medicine 39:480–487.

QUAYLE, J.F., A.G. MACHUTCHON, AND D.N. JURY. 2001. Modeling moose sightability in south-central British Columbia. Alces 37:43–54.

PHILLIPS, E.C. 2011. Development of an elk sightability model for the Black Hills of South Dakota. Master's thesis, South Dakota State University, Brookings, SD. 84 pp.

RABE, J.R., S.S. ROSENSTOCK, AND J.C. DEVOS JR. 2002. Review of big-game survey methods used by wildlife agencies of the western United States. Wildlife Society Bulletin 30:46–52.

R CORE TEAM. 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria; [accessed 4 April 2018]. https://www.R-project.org

RICE, C.G., K.J. JENKINS, AND W. CHANG. 2009. A sightability model for mountain goats. Journal of Wildlife Management 73:468–478.

RICE, L.A. 1988. Evaluation of movements and habitat use of elk in the southern Black Hills, South Dakota, 1980–1988. Completion Report No. 88-05. South Dakota Game, Fish, and Parks, Pierre, SD. 56 pp.

SAMUEL, M.D., AND E.O. GARTON. 1994. Horvitz–Thompson survey sample methods for estimating large-scale animal abundance. Transactions of the North American Wildlife and Natural Resources Conference 59:170–179.

SAMUEL, M.D., E.O. GARTON, M.W. SCHLEGEL, AND R.G. CARSON. 1987. Visibility bias during aerial surveys of elk in northcentral Idaho. Journal of Wildlife Management 51:622–630.

SAUER, J.R., AND B.K. WILLIAMS. 1989. General procedures for testing hypotheses about survival or recovery rates. Journal of Wildlife Management 56:718–725.

SEBER, G.A.F. 1982. The estimation of animal abundance and related parameters. 2nd edition. Macmillan Publishing Company, New York, NY. 654 pp.

SIKES, R.S., AND THE ANIMAL CARE AND USE COMMITTEE OF THE AMERICAN SOCIETY OF MAMMALOGISTS. 2016. 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. Journal of Mammalogy 97:663–688.

SING, T., O. SANDER, N. BEERENWINKEL, AND T. LENGAUER. 2005. ROCR: visualizing classifier performance in R. Bioinformatics 21:3940–3941.

SKALSKI, J.R., J.J. MILLSPAUGH, AND R.D. SPENCER. 2005. Population estimation and biases in paintball, mark-resight surveys of elk. Journal of Wildlife Management 69:1043–1052.

SMYSER, T.J., R.J. GUENZEL, C.N. JACQUES, AND E.O. GARTON. 2016. Double-observer evaluation of pronghorn aerial line-transect surveys. Wildlife Research 43: 474–481

[SDGFP] SOUTH DAKOTA DEPARTMENT OF GAME, FISH AND PARKS. 2011. Big game harvest reports. [Accessed May 2011]. https://gfp.sd.gov/hunting/harvest/reports/BlackHillsPrairieElk.pdf

[SDGFP] SOUTH DAKOTA DEPARTMENT OF GAME, FISH AND PARKS. 2015. South Dakota elk management plan 2015–2019. Completion Report 2015-01. South Dakota Department of Game, Fish and Parks, Pierre, SD.

SOUTH DAKOTA OFFICE OF CLIMATOLOGY. 2011. South Dakota climate and weather. [Accessed March 2011]. https://climate.sdstate.edu

STEINHORST, R.K., AND M.D. SAMUEL. 1989. Sightability adjustment methods for aerial surveys of wildlife populations. Biometrics 45:415–425.

TURNER, R.W. 1974. Mammals of the Black Hills of South Dakota and Wyoming. University of Kansas Press, Lawrence, KS. 178 pp.

UNSWORTH, J.W., F.A. LEBAN, E.O. GARTON, D.J. LEPTICH, AND P. ZAGER. 1999. Aerial survey: user's manual. Electronic edition. Idaho Department of Fish and Game, Boise, ID.

UNSWORTH, J.W., F.A. LEBAN, D.J. LEPTICH, E.O. GARTON, AND P. ZAGER. 1991. Aerial survey: user's manual. 2nd edition. Idaho Department of Fish and Game, Boise, ID.

VANDER WAL, E., P.D. MCLOUGHLIN, AND R.K. BROOK. 2011. Spatial and temporal factors influencing sightability of elk. Journal of Wildlife Management 75: 1521–1526.

WALSH, D.P. 2007. Population estimation and fixed kernel analysis of elk in Michigan. Doctoral dissertation, Michigan State University, East Lansing, MI. 238 pp.

WALSH, D.P., C.F. PAGE, H. CAMPA III, S.R. WINTERSTEIN, AND D.E. BEYER JR. 2009. Incorporating estimates of group size in sightability models for wildlife. Journal of Wildlife Management 73:136–143.

ZUUR, A.F., E.N. IENO, AND C.S. ELPHICK. 2010. A protocol for data exploration to avoid common statistical problems. Methods in Ecology and Evolution 1:3–14.

Received 18 August 2018
Revised 19 April 2019
Accepted 27 June 2019
Published online 9 December 2019