Management and Conservation

Incorporating Detection Probability Into Northern Great Plains Pronghorn Population Estimates

CHRISTOPHER N. JACQUES,[1,2] *Department of Natural Resource Management, South Dakota State University, Brookings, SD 57007, USA*

JONATHAN A. JENKS, *Department of Natural Resource Management, South Dakota State University, Brookings, SD 57007, USA*

TROY W. GROVENBURG, *Department of Natural Resource Management, South Dakota State University, Brookings, SD 57007, USA*

ROBERT W. KLAVER, *U.S. Geological Survey, Iowa Cooperative Fish and Wildlife Research Unit, Iowa State University, Ames, IA 50011, USA*

CHRISTOPHER S. DEPERNO, *Fisheries and Wildlife Sciences Program, North Carolina State University, Raleigh, NC 27695, USA*

ABSTRACT Pronghorn (*Antilocapra americana*) abundances commonly are estimated using fixed-wing surveys, but these estimates are likely to be negatively biased because of violations of key assumptions underpinning line-transect methodology. Reducing bias and improving precision of abundance estimates through use of detection probability and mark-resight models may allow for more responsive pronghorn management actions. Given their potential application in population estimation, we evaluated detection probability and mark-resight models for use in estimating pronghorn population abundance. We used logistic regression to quantify probabilities that detecting pronghorn might be influenced by group size, animal activity, percent vegetation, cover type, and topography. We estimated pronghorn population size by study area and year using mixed logit-normal mark-resight (MLNM) models. Pronghorn detection probability increased with group size, animal activity, and percent vegetation; overall detection probability was 0.639 (95% CI = 0.612–0.667) with 396 of 620 pronghorn groups detected. Despite model selection uncertainty, the best detection probability models were 44% (range = 8–79%) and 180% (range = 139–217%) greater than traditional pronghorn population estimates. Similarly, the best MLNM models were 28% (range = 3–58%) and 147% (range = 124–180%) greater than traditional population estimates. Detection probability of pronghorn was not constant but depended on both intrinsic and extrinsic factors. When pronghorn detection probability is a function of animal group size, animal activity, landscape complexity, and percent vegetation, traditional aerial survey techniques will result in biased pronghorn abundance estimates. Standardizing survey conditions, increasing resighting occasions, or accounting for variation in individual heterogeneity in mark-resight models will increase the accuracy and precision of pronghorn population estimates. © 2013 The Wildlife Society.

KEY WORDS aerial survey, *Antilocapra americana*, detection probability, mark-resight models, northern great plains, pronghorn, South Dakota, visibility bias.

The management of ungulates (e.g., for hunting) requires accurate and precise estimates of population size (Skalski et al. 2005). The ability to achieve large ungulate management strategies and harvest quotas requires accurate knowledge of abundance. Pronghorn (*Antilocapra americana*) population size commonly is estimated using data collected in fixed-wing surveys (Firchow et al. 1990, Johnson et al. 1991, Pojar et al. 1995, Guenzel 1997). Attempts to conduct total population counts of all pronghorn in a given area have had limited success in most situations because of prohibitive time and financial constraints (Guenzel 1997) and potential

biases associated with unequal detection probabilities in different survey conditions (Skalski et al. 2005). To overcome potential detection biases in total count surveys, Guenzel (1997) suggested the use of trend counts to quantify relative changes in abundance between surveys (i.e., increasing, decreasing, or stable population). Despite rigorous attempts to standardize survey conditions, unpredictable proportions of pronghorn populations often were undetected between surveys, and quantifying accuracy and precision of population estimates using trend counts were unreliable (Guenzel 1997).

Aerial strip transect surveys (hereafter traditional surveys) have been conducted annually since the 1940s to determine population status, distribution, and productivity of pronghorn populations throughout western South Dakota (West 1969, Jacques 2006). This method assumes that all pronghorn within a specified distance of the aircraft are detected. However, sampling variance (e.g., spatial variability of the species of interest as influenced by landscape

heterogeneity; Steinhorst and Samuel 1989) and visibility bias (e.g., the failure to observe all individuals or groups of animals in survey areas; Caughley 1974, Samuel et al. 1987) often contribute to negatively biased population estimates and thus, they have been identified as primary sources of inaccuracy in aerial surveys (Caughley 1974, 1977).

Line transect sampling is a type of distance sampling that offers an alternative to trend or total counts by correcting population estimates for animals that should have been detected during surveys (Gates 1979, Burnham et al. 1980, Buckland et al. 1993, Guenzel 1997). Although line transect sampling has been adapted to aerial surveys of many species of wildlife (Beasom et al. 1981, White et al. 1989, Johnson et al. 1991, Buckland et al. 1993), Guenzel (1986) first evaluated the feasibility of applying line transect sampling to aerial surveys of pronghorn and Johnson et al. (1991) later refined the technique. Despite widespread use in pronghorn abundance estimation, Pojar and Guenzel (1999) suggested that line transect abundance estimates were negatively biased because of the inability of observers to detect all groups of pronghorn within the nearest distance band. Relative to other aerial survey techniques, line transect sampling also requires a high level of quality control and specially equipped aircraft, and may lead to negatively biased population estimates because of poor survey design, improperly trained personnel, and when used on low density pronghorn populations (Guenzel 1997). Smyser (2005) suggested that pronghorn detection during aerial line transect monitoring was primarily influenced by the distance from the aircraft and that incorporation of additional explanatory variables into traditional line transect survey designs was of limited value. Despite limitations of the method, line transect sampling has been integrated into routine pronghorn management across Wyoming (Guenzel 1997).

Mark-resight methods for estimating closed population abundance have received considerable attention in recent years (McClintock et al. 2008, 2009). Compared to traditional mark-recapture, mark-resight often can be a less-invasive alternative by minimizing capture-related stress because animals can be detected at a distance with minimal disturbance following initial capture events (McClintock et al. 2009). Thus, the primary advantage of these methods is that physical capture and marking of animals is limited to a single capture event, and subsequent data from marked and unmarked individuals are used for estimating population abundance (McClintock et al. 2009). Limitations of mark-resight estimators include sampling without replacement and that the number of marked animals available for resighting typically is not precisely known (McClintock et al. 2009). Despite recent use in estimating population abundance of several North American ungulates (Bartmann et al. 1987, Neal et al. 1993, Bowden and Kufeld 1995), mark-resight methods have not previously been used to estimate pronghorn abundance.

A common method of accounting for animals missed during aerial surveys because of visibility bias is detection probability (e.g., sightability) modeling (Caughley 1974, 1977) through the use of logistic regression; the technique estimates the probability that a group of animals are either detected or undetected during aerial surveys (Samuel et al. 1987). Detection probability models are likely to be particularly well suited in regions with variable topographic relief where line-transect sampling is impractical, and when animals occur in large groups (Bodie et al. 1995). Detection probability models are efficient because they require only capture and marking of animals to develop the model, though survey conditions must be representative of field conditions during the time of model development (Samuel et al. 1987, Samuel and Garton 1994, White and Shenk 2001). With the use of radio telemetry, the exact number of marked animals in the survey area can be determined precisely prior to and at the time of aerial surveys (Grassel 2000).

Detection probability models have been used widely when estimating abundance of numerous North American ungulates (Samuel et al. 1987, Ackerman 1988, Bodie et al. 1995, Anderson and Lindzey 1996, Rice et al. 2009). To our knowledge the only previous documented evaluation of pronghorn detection probability was presented by Firchow et al. (1990), who reported detection probability rates of 0.55–0.65 associated with quadrat and standard strip transect census techniques in short-grass prairie habitats. However, quantitative data on potential effects of intrinsic (groups size, animal activity) and extrinsic (topography, percent vegetation, cover type) factors on pronghorn detection probability was not evaluated during their study.

Precision of pronghorn abundance estimates may be improved by incorporating additional intrinsic and extrinsic variables that influence detectability into current population estimation techniques (Smyser 2005). Reducing bias and improving precision of line-transect-derived abundance estimates through use of detection probability or mark-resight models may allow for more responsive pronghorn management actions (Smyser 2005). Thus, given the potential application of detection probability and mark-resight models in population estimation, our objectives were to 1) develop and evaluate a pronghorn detection probability model for subsequent use in estimating population abundance and 2) compare our detection probability model-derived estimates with pronghorn population estimates from mark-resight analysis within an eastward extension of sagebrush steppe communities of the northern Great Plains.

STUDY AREA

Our study was conducted in a 6,940-km^2 area of northwestern (e.g., Harding County) and a 5,071-km^2 area of southwestern (e.g., Fall River County) South Dakota (Fig. 1). Topography of western South Dakota was flat to gently rolling. Landscape in western South Dakota was characterized by a mosaic of mixed-grass prairie interspersed with sagebrush (*Artemisia* sp.) and limited stands of ponderosa pine (*Pinus ponderosa*; Jacques et al. 2009*a, b*). Distribution of pronghorns in western South Dakota was within an eastward extension of sagebrush-steppe communities, including both big sagebrush (*Artemisia tridentata*)
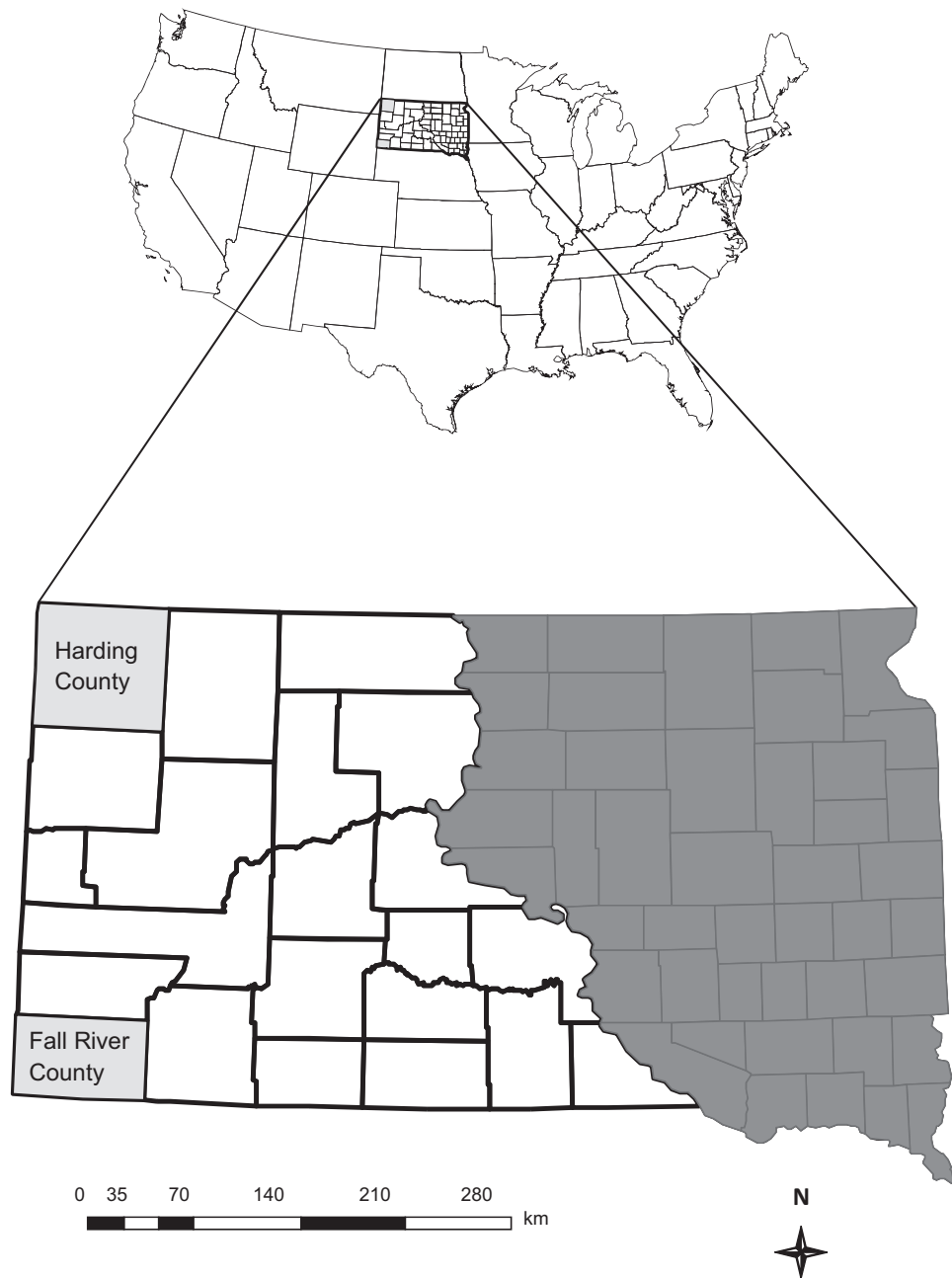
Figure 1. Pronghorn (*Antilocapra americana*) aerial survey areas were located in Harding and Fall River counties (shaded light gray) of western South Dakota, 2003–2005. Thick black lines delineated county boundaries in western South Dakota and the dark gray shaded area encompassing eastern South Dakota represented the area outside the current pronghorn range.

and silver sagebrush (*A. cana*; Schroeder et al. 1999, Smith et al. 2004).

Fall River County was situated in the southwest corner of South Dakota (Fig. 1). Of the total land area in Fall River County, approximately 125 km² were federal lands administered by the United States Department of Agriculture Forest Service (Kalvels 1982). Land elevation ranged between 914 m and 1,478 m above mean sea level; approximately 83% of farm and ranch land in Fall River County was grazed by livestock and 17% was used for cultivated crops, tame pasture (e.g., pastures planted primarily to cool season exotic or introduced grass and/or legume species), or hay (Kalvels

1982). Fall River County was located within the mixed grass prairie region of western South Dakota and dominant grasses on the landscape included western wheatgrass (*Agropyron smithii*), buffalograss (*Buchloe dactyloides*), green needlegrass (*Stipa viridula*), needle-and-thread (*S. comata*), side oats grama (*Bouteloua curtipendula*), blue grama (*B. gracilis*), and prairie junegrass (*Koeleria pyramidata*). Dominant overstory woody vegetation consisted of limited stands of ponderosa pine interspersed with small stands of quaking aspen (*Populus tremuloides*) and paper birch (*Betula papyrifera*; Kalvels 1982). Silver sagebrush and big sagebrush were limited in distribution throughout Fall River County. Plant nomen-

clature followed Larson and Johnson (1999) and Johnson and Larson (1999).

Harding County was situated in the northwest corner of South Dakota (Fig. 1). Most of the land area in Harding County was treeless, semi-arid rolling plains. Land elevation ranged between 817 m and 1,224 m above sea level and the majority of farm or ranch acreage (88%) in Harding County was used as grazing land, whereas 12% was used for cultivated crops, pasture, or hay. Dominant grasses on the landscape included western wheatgrass, prairie junegrass, buffalograss, green needlegrass, and blue grama. Silver sagebrush and big sagebrush were the dominant shrubs on the landscape (Johnson 1988).

METHODS

Pronghorn Capture and Monitoring

We captured adult female pronghorns (≥1.5 years old) by net-gun deployed from a helicopter (Jacques et al. 2009a) at sites in Harding and Fall River counties during 22–24 January 2002 and 18–19 February 2003, respectively. We restrained, hobbled, blindfolded, and transported each captured pronghorn to nearby processing sites. We ear-tagged, recorded morphological measurements and assessed body condition of each pronghorn. We monitored rectal temperature continuously throughout the processing period as an indicator of physical stress and released individuals if body temperature exceeded 42°C. We attached radiocollars (151 MHz; Telonics, Inc., Mesa, AZ; Advanced Telemetry Systems [ATS], Isanti, MN) equipped with activity and mortality sensors to each captured pronghorn (Jacques et al. 2009b). We monitored each radiocollared animal for movement and mortality status 2–3 times per week from January 2002 to August 2005, after which time field work was terminated (Jacques et al. 2009b). Animal handling methods were approved by the Institutional Animal Care and Use Committee at South Dakota State University (approval number 02-A001) and followed guidelines for the care and use of animals approved by the American Society of Mammalogists (Sikes et al. 2011).

Aerial Surveys

We conducted 4 aerial surveys per survey area per year (e.g., 24 total flights) from 15 May through 15 June 2003–2005. We conducted all aerial surveys in a Cessna 182 aircraft (Cessna Aircraft Company, Wichita, KS) with a pilot in the left front seat, a primary observer in the right front seat, a secondary observer in the back seat behind the pilot, and a non-observer positioned in the back seat behind the primary observer. We conducted aerial surveys within 4 hours of sunrise or sunset, respectively, to maximize detection rates and minimize observer fatigue (Guenzel 1997, Whittaker et al. 2003). To standardize training among observers prior to conducting surveys, we required that all observers conduct a minimum of 8 hours of pronghorn aerial survey training. Prior to conducting surveys, we followed procedures described by Guenzel (1997) to mark a defined offset (e.g., blind) area from 0 to 65 m and a 250-m strip width on either side of the plane at a prescribed height above ground

level (AGL) of 91.4 m; we placed electrical tape on the struts to denote the start of the survey line (i.e., inside cut point) and to define the outer distance limit (i.e., outside cut point). We validated the placement of our 250-m strip width by positioning objects (e.g., people) at known distances (65 m and 315 m) from the edge of the airport runway and making multiple (e.g., 10) flights down runway edges at a prescribed flight of 91.4 m AGL. During aerial surveys, our observers were careful to maintain similar body postures because large position changes could have affected transect strip width relative to position of tape on plane struts (Beringer et al. 1998). We assumed perfect detection of animals out to 250 m on either side of the plane and ignored all pronghorn groups detected beyond that distance. We systematically searched pronghorn survey areas by flying along established transects that were oriented north to south and separated by 805 m; thus, the margin between transect edges was minimal (i.e., 20 m). Further, we assumed that the probability of animal groups being recounted on adjacent transects also was minimal. We randomly selected starting locations in each survey area and completed all flights in 2–4 hours. We used a global positioning system (GPS; Garmin International, Inc., Olathe, KS) to navigate search unit boundaries and delineate transect endpoints during surveys. We maintained airspeed of approximately 110 km/hr and a prescribed height of 91.4 m AGL (Guenzel 1997).

Evaluating Detection Probability Models

We outfitted the aircraft with a pair of 2-element H-antennas (Telonics, Inc.) and used radiocollared pronghorn to evaluate aerial surveys for visibility biases. We conducted telemetry flights 2–3 hours prior to initiating aerial surveys to confirm that all radiocollared pronghorns were alive and located within each survey area. Prior to conducting aerial surveys, we informed observers that radiocollared pronghorn were located within survey areas but information regarding the number of animals or their precise locations was not provided. Additionally, we instructed observers to notify the non-observer when radiocollared animals were sighted during aerial surveys. We did not inform the pilot of the presence or location of radiocollared pronghorn within survey areas. During aerial surveys, the non-observer scanned frequencies of radiocollared animals using an ATS receiver to determine their precise locations and record whether or not observers detected radiocollared animals (Grassel 2000).

We classified radiocollared pronghorns as detected if the animal was visually observed or by visually observing the pronghorn group the radiocollared animal was associated with. When a radiocollared pronghorn or group of pronghorn to which the radiocollared animal was associated was detected, we interrupted the search pattern and collected information on group size, animal activity, vegetation cover, cover type, topography, and to obtain a Universal Transverse Mercator (UTM) location above the precise location where pronghorn were initially detected (Grassel 2000). We assigned animal activity (bedded, standing, running) based on the activity of the first pronghorn detected in a group of animals (Unsworth et al. 1994). We estimated percent

vegetation cover within a 9-m radius surrounding the initial location of each pronghorn detected (Anderson and Lindzey 1996). Upon detecting pronghorn, we flew a complete circle around the initial location of the animal and subsequently estimated the proportion of the ground that was obscured from view by vegetation (Unsworth et al. 1994, Anderson and Lindzey 1996, Drummer and Aho 1998). We recorded percent vegetation to the nearest 5%; we defined 0% vegetation as bare ground (i.e., dirt) with no vegetation visible, and 100% vegetation as no bare ground visible from the air. Because our study sites were dominated by mixed-grass prairie interspersed with sagebrush, we assumed height of dominant vegetation at pronghorn locations would not be an influential predictor in our detection probability models. Consequently, we did not record or account for vegetation height during aerial surveys. We broadly defined cover type as the dominant landscape characteristic (e.g., grassland, sagebrush, bare ground) within the same 9-m radius surrounding the initial location of each pronghorn detected. We recorded topography (flat or uneven terrain) at the initial location where pronghorn were first detected.

We resumed the search pattern at the location where it was interrupted following data collection on the radiocollared individual or group to which it was associated (Grassel 2000). If a radiocollared pronghorn or its associated group was not detected, observers were not notified and the survey continued uninterrupted until completed (Grassel 2000). We attempted to qualitatively differentiate groups of pronghorn with radiocollared individuals that were unde-tected because of visibility bias (e.g., present but undetected) and sampling bias (e.g., present immediately under the aircraft or in the margins between transects) by recording relative perpendicular locations of animals to the aircraft (i.e., below plane, within 250-m strip width, or outside of strip width) as a function of transmitter signal strength or collar pulse rate. We assumed that transmitters that were the same signal strength on either side of the aircraft were directly below or within the blind area of the aircraft. In contrast, we assumed that transmitters that were notably unequal in signal strength and positioned on 1 side of the aircraft or the other were beyond the outer limit of our 250-m strip width. We also assumed that transmitters that were similar in signal strength on either side of the plane or changed pulse rates between fast (i.e., feeding) and slow (i.e., alert) were in response to approaching aircraft and thus, were within our 250-m strip width. Upon completing individual survey areas, we immediately located individuals not detected during surveys using radiotelemetry and subsequently collected information on the same variables as collected for detected groups of pronghorn. We censored undetected radiocollared animals that were directly below or within the blind area of the plane, or outside of our 250-m strip width from our analyses; therefore, we believe sampling bias during surveys was minimal. We assumed remaining radiocollared individ-uals were undetected because of visibility biases. To maintain statistical independence, we considered groups of pronghorn with more than 1 radiocollared individual a single observa-tion (Samuel et al. 1987).

Prior to analyses, we posited biologically plausible logistic regression models of how observations of pronghorn might be influenced by group size, group behavior, cover type, percent vegetation, and topography (Table 1); all models were additive without interactions. Our justification for inclusion of model covariates under an information theoretic approach to analysis (Burnham and Anderson 2002, Jacques et al. 2011) included:

1. Group size (GS). Group size has been identified as influencing detection probability of moose (*Alces amer-icanus*; Gasaway et al. 1985) and elk (*Cervus elaphus*; Samuel et al. 1987, Cogan and Diefenbach 1998). Pronghorn occupy prairie habitats with a tendency to occur in large social groups (O'Gara 2004a). Despite limited research evaluating pronghorn detection proba-bilities, we predicted that the odds of observing gregarious animals occupying open habitats would increase with increasing group size.
2. Animal activity (ACT). Detection probability has been shown to be greater for moving compared to stationary (or standing) animals (Gasaway et al. 1985, Bodie et al. 1995). We predicted that the odds of observing pronghorns should change with activity status. We treated animal activity as a categorical variable in our analyses (bedded, standing, or running).
3. Cover type (CT). Heterogeneity in cover type as influenced by dynamic landscape features has been suggested as a potential predictor of ungulate detection

Table 1. Effects of independent variables on detection probability of 620 pronghorn groups containing radiocollared individuals in Harding and Fall River counties, South Dakota, 2003–2005.

| | Number of groups | | | |
Variable	Detected	Undetected	DP[a]	95% CI
Animal activity				
Bedded	65	93	0.41	0.29–0.53
Standing	122	121	0.50	0.43–0.61
Running	209	10	0.95	0.94–0.96
Topography				
Flat	257	100	0.72	0.65–0.80
Uneven	139	124	0.53	0.42–0.64
Cover type				
Grass	320	112	0.74	0.71–0.78
Sagebrush	69	100	0.41	0.31–0.50
Bare ground	7	12	0.37	0.16–0.58
Group size				
1	9	56	0.14	0.04–0.23
2	10	62	0.14	0.01–0.27
3	13	45	0.22	0.07–0.38
4	23	23	0.50	0.31–0.69
5	37	17	0.69	0.25–0.95
6–10	167	21	0.89	0.79–0.98
11–19	105	0	1.00	0.99–1.00
≥20	32	0	1.00	0.99–1.00
Percent vegetation				
0–25	7	12	0.37	0.03–0.71
26–50	40	45	0.47	0.33–0.65
51–75	175	88	0.67	0.61–0.73
76–100	174	79	0.69	0.64–0.75

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

probability across the western United States (Bleich et al. 2001). In particular, reduced elk detection probability may be associated with reduced color contrast between study animals and associated cover types (Bleich et al. 2001). We predicted that variation in vegetation characteristics between grassland habitats and sagebrush steppe communities may influence pronghorn detection probability.

4. Percent vegetation (VEG). Percent vegetation cover has been described as a strong predictor of elk detection probability throughout the north-central and western United States (Samuel et al. 1987, Anderson et al. 1998, Bleich et al. 2001). Ackermann (1988) also identified percent vegetative cover as an acceptable predictor of mule deer detection probability in southeastern Idaho. Although pronghorn generally occupy regions of limited vertical structure, detection probability may be influenced by variation in horizontal structure within sagebrush steppe communities of western South Dakota.

5. Topography (TOP). Topographic position has been shown to be related to bighorn sheep (*Ovis canadensis*) detection probability (Bodie et al. 1995). Specifically, bighorn sheep occupying middle and upper slopes were less visible than individuals occupying lower slopes or above canyons (Bodie et al. 1995). We predicted that effects of topography on pronghorn detection probability may be influenced by variation in topographic features between flat terrain and gently rolling hills characteristic of prairie habitats across western South Dakota.

Data Analyses
We used logistic regression to model the probability of observing pronghorn using observations of radiocollared animals. We grouped covariates into pronghorn effects (group size, group behavior) and cover effects (cover type, topography, percent vegetation). Group size data were not normally distributed so we log transformed these data and incorporated the number of pronghorns in a group on a log scale as a covariate in our regression models. We used Akaike's Information Criterion (AIC) to select models that best described the data and used Akaike weights (w_i) as a measure of relative support for model fit (Burnham and Anderson 2002, Jacques et al. 2011). We used model averaging to account for model selection uncertainty (Burnham and Anderson 2002).

Prior to modeling, 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 1 variable from a set of collinear variables for modeling (Jacques et al. 2011). We ranked predictor variables by their summed Akaike model weights ($\sum w_i$). 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, Jacques et al. 2011). We considered ROC values 0.5–0.7 low discrimination, and values ≤ 0.5 indicated that model predictive capabilities were no better than random (Grzybowski and Younger 1997,

Hosmer and Lemeshow 2000). We conducted all statistical analyses using SYSTAT (Wilkinson 1990).

We determined associations between response and predictor variables using odds ratios. The odds ratio for a predictor variable is the relative amount by which the odds of the outcome increase (odds ratio >1.0) or decrease (odds ratio <1.0) with each unit increase in the predictor variable (Hosmer and Lemeshow 2000, Freund and Wilson 2003, Jacques et al. 2011). Thus, odds ratios approximated the likelihood of a predicted outcome among associated variables. The appropriate interpretation of odds ratios obtained from model parameters for continuous (predictor) variables was that multiplicative effects on the odds of a 1-unit increase in the response variable was associated with fixed levels of other predictor variables (Hosmer and Lemeshow 2000, Freund and Wilson 2003, Jacques et al. 2011).

We estimated population size using the overall detection rate of radiocollared pronghorns during annual aerial surveys. We estimated 95% confidence intervals for our model-derived population estimates by calculating mean parameter and standard error estimates for model covariates and incorporating these estimates into standard equations for estimating upper and lower confidence intervals (Zar 1984). Additionally, we estimated pronghorn population size by study area and year using mixed logit-normal mark-resight (MLNM) models (McClintock et al. 2008, 2009) in Program MARK (White and Burnham 1999) for comparison to detection probability model-derived population estimates. Mixed logit-normal mark-resight models account for imperfect detection towards generating reliable abundance estimates (McClintock et al. 2008, 2009). Further, MLNM models assume a proportion of a study population has been marked prior to sampling, and sampling occasions consist of sighting surveys rather than capture periods (McClintock et al. 2008, 2009). Moreover, MLNM models are typically used when sampling is without replacement within secondary sampling occasions and the number of marked individuals in the population for resighting is known exactly (McClintock et al. 2008, 2009). If a known number of marks are in a population, but marks are not individually identifiable, data for MLNM models can be summarized into artificial encounter histories similar to those of the mark-recapture robust design (i.e., individually identifiable marks; McClintock et al. 2008, 2009). Mixed logit-normal mark-resight models with variation in individual heterogeneity (σ) failed to stabilize in our analyses; thus, we set σ to a common parameter for yearly and group (e.g., Harding County and Fall River County) variation and ran models that varied by year and group in mean resighting probability (p_r). Our survey areas for evaluating pronghorn detection probability comprised 1,050 km^2 and 750 km^2 for Harding and Fall River counties, respectively, and encompassed home ranges of all radiocollared animals in our study areas. Our survey areas comprised approximately 15% of the total land area in our study areas; we sampled an equal percentage of land area in each study area. Thus, we generated expanded population estimates (e.g., game management [county] unit

level) by multiplying our model-derived estimates by a factor of 6.67 (e.g., 1/0.15) and used the delta method (Seber 1982, Powell 2007) to estimate standard errors for associated population abundance estimates. The delta method is useful for approximating sampling variance when the desired demographic parameter (i.e., population estimates) is a function of at least 1 other demographic parameter (i.e., game management unit, detection bias; Samuel et al. 1992) or when demographic parameters are averaged across years, in which cases the new demographic parameter (i.e., expanded population estimate) is a function of at least 1 other demographic parameter (Powell 2007). Thus, sampling variance of the new parameter also is a function of the sampling variance of the former parameters (Williams et al. 2002, Powell 2007).

RESULTS

During spring aerial surveys, 61, 50, and 44 radiocollared pronghorns were present in our survey areas during 2003, 2004, and 2005, respectively. We collected observations on 620 groups of pronghorn that contained at least 1 radio-collared animal over those 3 years. Pronghorn groups ranged in size from 1 to 30 with a mean of 7.3 (SD = 5.9). We calculated detection probabilities for each category of independent covariates; detection probability increased with increasing group size, animal activity, and percent vegetation (Table 1). Probability of detecting pronghorn was greater on flat (0.72; 95% CI = 0.65–0.80) than uneven (0.53; 95% CI = 0.42–0.64) terrain. Similarly, pronghorn detection probability was greater in grassland habitats than sagebrush dominated habitat or bare ground; overall detection probability was 0.64 (95% CI = 0.61–0.68; Table 1). Probability of detecting large pronghorn groups (≥6 animals) in grassland and sagebrush habitats was 0.96 (95% CI = 0.93–1.00; n = 252 groups) and 0.88 (95% CI = 0.75–0.98; n = 64 groups), respectively. Similarly, probability of detecting small pronghorn groups (1–5 animals) in grassland and sagebrush habitats was 0.42 (95% CI = 0.22–0.62; n = 179 groups) and 0.14 (95% CI = 0.02–0.26; n = 105 groups), respectively.

A Priori Models Predicting Pronghorn Detection Probabilities

The highest-ranked model for detecting pronghorn was group size + activity + percent vegetation (Table 2). Support for this model was substantial ($w_i = 1.00$) and predictive capability of the model was excellent (ROC = 0.915; Table 2); all other models were noncompetitive ($w_i < 0.001$; Table 2). The logistic equation for this model was logit(μ) = −6.450 + 3.281 (lngroup size) − 0.871 (activity_bedded) + 2.796 (activity_running) + 0.014 (percent vegetation; Table 3).

Three variables were most influential in predicting pronghorn detection probability. Group size ($\sum w_i = 1.00$), activity ($\sum w_i = 1.00$), and percent vegetation ($\sum w_i = 0.94$) had the greatest summed AIC weights, whereas summed AIC weights for topography and cover type were 0.05 and 0.00, respectively. Probability of detecting pronghorns

Table 2. Akaike's Information Criterion model selection of a priori logistic regression models for pronghorn detection in western South Dakota, 2003–2005; all detection probability models were estimated using 620 observations of radiocollared pronghorns.

Model covariates	K^a	AIC^b	$\Delta\ AIC^c$	w_i^d	ROC^e
GS + ACT + VEG	6	344.82	0.00	1.00	0.91
GS + ACT + TOP	6	363.87	19.04	0.00	0.68
GS + ACT	5	372.78	27.96	0.00	0.53
GS + ACT + VEG + CT + TOP	8	374.85	30.03	0.00	0.54
GS + CT + TOP	5	427.09	82.27	0.00	0.63
GS + CT	4	431.10	86.27	0.00	0.60
GS + TOP	4	447.60	102.77	0.00	0.80
GS + VEG	4	455.16	110.34	0.00	0.90
GS	3	455.51	110.69	0.00	0.50
ACT + CT	5	604.30	259.48	0.00	0.24
ACT + VEG + TOP	6	606.95	262.13	0.00	0.41
ACT + TOP	5	613.00	268.17	0.00	0.28
ACT + VEG	5	630.34	285.51	0.00	0.44
ACT	4	640.18	295.35	0.00	0.20
VEG + TOP + CT	5	750.55	405.73	0.00	0.43
VEG + TOP	4	785.77	440.94	0.00	0.49
VEG	3	805.22	460.49	0.00	0.59

GS, group size; ACT, animal activity; VEG, percent vegetation; TOP, topography; CT, cover type.
[a] No. of parameters.
[b] Akaike's Information Criterion (Burnham and Anderson 2002).
[c] Difference in AIC relative to minimum AIC.
[d] Akaike weight (Burnham and Anderson 2002).
[e] ROC = area under the receiver operating characteristic curve. Values between 0.7 and 0.8 were considered acceptable discrimination, and values between 0.8 and 1.0 were considered excellent discrimination (Hosmer and Lemeshow 2000).

increased by 26.60 (odds ratio = 26.604, 95% CI = 15.169–46.660) for each per unit increase in lngroup size. Similarly, probability of detecting running pronghorns was 16.38 times greater than detecting standing pronghorns (odds ratio = 16.376, 95% CI = 6.867–39.055). Conversely, we were about half (0.58) as likely to detect bedded pronghorns than standing pronghorns (odds ratio = 0.416, 95% CI = 0.227–0.764; Table 3). Odds of detecting pronghorn increased by 1.014 (odds ratio = 1.014, 95% CI = 1.000–1.029) for each per unit increase in percent vegetation. For continuous variables (group size, percent vegetation) in the highest-ranked model, 95% confidence intervals did not overlap zero,

Table 3. Parameter estimates (β), standard error (SE), odds ratio, and odds ratio 95% confidence intervals for the best approximating model in the set evaluated for pronghorn detection probability in western, South Dakota, 2003–2005.

Parameter[a]	β	SE	Odds ratio[b]	Upper CL	Lower CL
Intercept	−6.450	0.713			
ln(group size)	3.281	0.287	26.604	46.660	15.169
ACT_bedded	−0.877	0.310	0.416	0.764	0.227
ACT_running	2.796	0.443	16.376	39.055	6.867
Percent vegetation	0.014	0.007	1.014	1.029	1.000

[a] ACT_bedded = bedded pronghorns, ACT_running = running pronghorns; standing pronghorn was the reference category.
[b] Odds ratios used to estimate measures of association between variables. A measure of association in which a value near 1 indicates no relationship between variables (Hosmer and Lemeshow 2000).

indicating that these variables were influential predictors of detecting pronghorn. For the categorical variable (animal activity) in the highest-ranked model, 95% confidence intervals did not overlap each other (bedded, standing, running), indicating that activity was an influential predictor of detecting pronghorn.

Pronghorn Population Estimates

Variation in pronghorn population estimates derived from traditional (e.g., uncorrected) surveys, detection probability models, and mark-resight models were notable within and between study areas. For instance, traditional abundance estimates ranged from 5,871–8,634 and 1,545–2,103 in Harding and Fall River counties, respectively (Table 4). Expanded mark-resight abundance estimates ranged from 7,264–10,032 and 3,662–5,863 in Harding and Fall River counties, respectively (Table 4). Similarly, expanded detection probability abundance estimates ranged from 8,544–11,359 and 4,175–6,630 in Harding and Fall River counties, respectively (Table 4). Though variation in pronghorn abundance was evident between years and study areas, mark-resight expanded estimates were comparable to detection probability model expanded estimates; 95% confidence intervals of detection probability model estimates typically encompassed mark-resight abundance estimates (Table 4). Despite model selection uncertainty, the best detection probability and population estimates from the MLNM model were 44% (range = 8–79%) and 28% (range = 3–58%), respectively, greater than traditional (e.g., uncorrected) population estimates in Harding County (Table 4). Similarly, the best detection probability and population estimates from the MLNM model were 180% (range = 139–217%) and 147% (range = 124–180%), respectively, greater than traditional population estimates in Fall River County (Table 4). We found considerable model selection uncertainty among competing MLNM models; support for the best model was not substantial ($w_i = 0.58$; Table 5). Unconditional parameter estimates for pronghorn resighting probabilities ranged from 0.662–0.666 and 0.643–0.647 for Harding and Fall River counties, respectively.

Table 5. Akaike's Information Criterion model selection of mixed logit-normal mark-resight models for estimating pronghorn population sizes (N) in western South Dakota, 2003–2005. Variation in individual sighting heterogeneity (σ_s) was set to a common parameter (.) for yearly (y) and group (g; Harding County and Fall River County) variation in pronghorn resighting probability (p).

Model covariates	K[a]	AIC[b]	ΔAIC[c]	w_i[d]
$\{p(.)\ \sigma_s(.)\ N(g \times y)\}$	8	869.59	0.00	0.58
$\{p(g)\ \sigma_s(.)\ N(g \times y)\}$	9	870.67	1.08	0.34
$\{p(y)\ \sigma_s(.)\ N(g \times y)\}$	10	873.31	3.72	0.09

[a] Number of parameters.
[b] Akaike's Information Criterion.
[c] Difference in AIC relative to minimum AIC.
[d] Akaike weight.

DISCUSSION

Our results indicate that group size influenced detection probability of pronghorns within an eastward extension of sagebrush steppe communities in western South Dakota. Though variation in cover type and percent vegetation cover encountered during aerial surveys were notable, pronghorn groups comprised of ≥ 5 individuals had high (≥ 0.89) probabilities of detection. Despite the paucity of current information describing effects of group size on pronghorn detection probability, the strong relationship between group size and detection probability may be associated, in part, with the tendency of pronghorns to occur in large social groups (O'Gara 2004a).

In contrast to Bleich et al. (2001), our resighting probabilities of small pronghorn groups in grassland (42%) and sagebrush (14%) habitats indicated a complex relationship between group size, percent vegetation, and pronghorn detection probability. We documented a positive relationship between probability of detecting pronghorn and increasing percent vegetation. Heterogeneity in landscape characteristics encountered during aerial surveys was notable and characterized by increasing percentage of vegetation in grassland habitats and reduced vegetation in sagebrush habitats and non-vegetated habitat patches (e.g., bare ground). Although not quantified, we speculate that uniform

Table 4. Comparison of pronghorn abundance estimates derived from traditional spring aerial surveys (N_s), detection probability models (detection probability model estimates), and mark-resight modeling (mark-resight model estimates) in western South Dakota, 2003–2005.

Study area	Year	N_s[a]	Detection probability model estimates				Mark-resight model estimates			
			N[b]	95% CI	N_e[c]	95% CI	N	95% CI	N_e	95% CI
HC	2003	5,871	1,281	1,188–1,374	8,544	7,691–9,204	1,089	983–1,162	7,264	6,584–8,008
	2004	6,381	1,703	1,566–1,840	11,359	10,006–12,324	1,504	1,360–1,581	10,032	9,115–11,038
	2005	8,634	1,388	1,289–1,487	9,258	8,734–9,965	1,330	1,238–1,426	8,871	8,294–9,527
FRC	2003	1,752	626	540–712	4,175	3,615–4,773	587	510–663	3,915	3,517–4,349
	2004	2,103	994	889–1,099	6,630	5,858–7,360	879	813–945	5,863	5,255–6,523
	2005	1,545	657	579–735	4,382	3,877–4,927	549	471–627	3,662	3,276–4,080

HC, Harding County; FRC, Fall River County.
[a] N_s = Pronghorn population estimates determined by independent total count surveys conducted by South Dakota Department of Game, Fish and Parks personnel during May 2003–2005.
[b] Pronghorn population estimates derived using overall pronghorn detection probability rate of radiocollared animals detected (396 of 620 groups) during aerial surveys.
[c] N_e = Pronghorn population estimates expanded to game management units (e.g., county level).

distribution of vegetative cover in grassland habitats may have enhanced color contrast between pronghorns and vegetation, thereby improving detection probability. Conversely, the color signature of pronghorns was less pronounced against relatively more complex sagebrush habitats (e.g., increased vertical structure) and mosaics of vegetated and non-vegetated habitat patches (e.g., bare ground) frequently encountered, thereby providing increased concealment cover for pronghorns and greater challenges for observers to decipher extraneous visual information during aerial surveys. Consequently, variation in resighting probabilities (particularly for small group sizes) may have been associated with the effects of increasing landscape complexity, decreasing percent vegetation, and less conspicuous pelage color contrast between sagebrush and grassland habitats.

Important assumptions regarding effects of animal activity on ungulate detection probability are that animal activity is accurately recorded for animal groups and subsequent recounting of animals on adjacent transects is minimized (Anderson and Lindzey 1996). We qualitatively assessed these potential sources of error during aerial surveys, at which time our back seat observer (CNJ) monitored changes in collar pulse rates between feeding (e.g., fastest pulse rate), alert (e.g., slowest pulse rate), and moving (erratic pulse rates) animals in response to approaching aircraft. Although not quantified, variation in activity level was most often associated with a change from head down (presumably feeding) to head up (e.g., alert) in response to approaching aircraft, and subsequent changes from alert to moving when animals were within 250 m of either side of the aircraft and thus, available for detection by observers. Post-detection activity of radiocollared pronghorn, though not quantified, was most often associated with animal movement away from approaching aircraft, though fleeing distances rarely exceeded 300–400 m and in no instance did the back seat observer (CNJ) recall instances where pronghorn ran more than 500 m before stopping. Further, detection of radiocollared pronghorn on adjacent transects did not occur during aerial surveys. Thus, we assumed that potential errors due to misclassifying animal activity profiles and/or recounting animals on adjacent transects were minimal during or study.

Our analyses indicated that pronghorn detection probability was strongly influenced by animal activity. Probability of observing running pronghorns was greater than observing standing pronghorns, whereas bedded pronghorns were less likely to be observed than standing pronghorns. The strong relationship between group behavior and detection probability was not surprising because intuitively, active animals are more easily detected than bedded or otherwise inactive animals during aerial surveys. Heterogeneity in detection probability between bedded and standing pronghorns is uncertain, but may be attributed, in part, to greater visibility of white hair on the ventral surface of the body (O'Gara 2004b) on standing pronghorns than bedded pronghorns.

Our model-derived estimates of pronghorn population size suggested pronounced heterogeneity between aerial survey techniques. Though uncertain, differences in precision between detection probability and mark-resight estimators may be attributed, in part, to the undercounting of animal groups that biased detection probability estimators. Further, mark-resight estimators tend not to suffer from this bias because both marked and unmarked animals are not observed at the same rates (G. C. White, Colorado State University, personal communication). Nevertheless, model-derived estimates were substantially greater than independent population estimates derived from traditional aerial surveys across our study areas and were concurrent with our detection probability surveys; traditional (e.g., uncorrected) population estimates were negatively biased relative to our model-derived estimates. Although not quantified, marked differences between model-derived and traditional survey population estimates may have been associated with variation in survey conditions (e.g., observer training protocols, above-ground altitude, survey intensity [single vs. repeated flights], different observers, observer experience, strip width, time of day). Consequently, failure to standardize aerial survey conditions has contributed to unreliability in detecting pronghorns between surveys, and the inability to assess accuracy and precision (e.g., repeatability) of abundance estimates (Guenzel 1997).

Despite uncertainty in factors contributing to heterogeneity in pronghorn abundance, our population estimates were derived using independent analytical techniques, which also were comparable to independent line-transect (distance) population estimates (13,602; 95% CIs = 11,016–15,743) for Harding County during 2004 (Jacques 2006). Thus, our results support the hypothesis that traditional aerial surveys underestimate pronghorn population size across western South Dakota. Detection probability modeling proved to be an effective technique for incorporating sources of bias into pronghorn abundance estimates, and a viable alternative to traditional line-transect surveys. A key logistical advantage of this approach over traditional line-transect sampling is the ability of game managers to validate our existing model or incorporate additional variables (e.g., habitat heterogeneity, time of day, light conditions, observer experience) encountered during routine management surveys, thereby improving precision of model-derived population estimates (Smyser et al. 2005). Mark-resight (MLNM) models reduced bias and improved precision in pronghorn abundance estimates, though did not incorporate yearly or landscape variation in estimates of resighting probability. Nevertheless, this method seems to be a viable approach for continued population monitoring. Further, our evaluation of pronghorn detection probabilities suggests a compelling need to quantify (and subsequently incorporate) the magnitude of effects of factors contributing to bias into traditional aerial surveys across the northern Great Plains.

Evaluating detection probability is critical for population monitoring (Anderson 2001, 2003). Without this information, it is impossible to determine if heterogeneity in population indices is due to temporal variation in population abundance or variation in detection probability as affected by landscape characteristics (Lancia et al. 2005). We demonstrated that the probability of detecting pronghorn varied

with intrinsic (e.g., group size, animal activity) and extrinsic (e.g., percent vegetation) factors, suggesting that different segments of the population may have different detection probabilities. For instance, territorial males, who are generally alone, may have low detection probability compared to female-offspring groups. Our detection probability and mark-resight analyses demonstrated the importance in estimating detection probabilities in pronghorn population estimation, though future use of these techniques requires maintaining a sample of radiocollared animals across space and time. Capturing and radiocollaring animals across broad geographic regions may impose logistical or financial constraints on wildlife agencies, in which case our findings also could be incorporated into current line transect (i.e., distance) surveys for estimating pronghorn abundance and thus, improve associated estimates of precision. For instance, Smyser et al. (2005) noted that in a distance-sampling framework, application of a single detection function across heterogeneous landscapes failed to account for site-specific differences when estimating pronghorn detection probabilities. Further, their results demonstrated the importance of incorporating a unique site-specific detection function into a distance sampling framework and its effect on pronghorn density estimates. Our results suggest that improvements in current line transect sampling may be possible by incorporating unique detection functions to account for heterogeneity in animal group size and various habitat features (e.g., percent vegetation, topography, cover type).

MANAGEMENT IMPLICATIONS

We provided the first evaluation of potential effects of intrinsic and extrinsic factors on detection probability of pronghorn in the northern Great Plains. When the probability of detecting pronghorn is a function of animal group size (particularly small animal groups), animal activity, and percent vegetation, we have shown that traditional aerial survey techniques will result in biased pronghorn abundance estimates. Similarly, when detection probability is a function of variation in individual, yearly, or group heterogeneity, mark-resight abundance estimates also may result in negatively biased abundance estimates. Standardizing survey conditions, increasing resighting occasions (Wingard et al. 2011), or accounting for variation in individual heterogeneity in mark-resight models (Skalski et al. 2005) will increase the accuracy and precision of pronghorn population estimates.

ACKNOWLEDGMENTS

LITERATURE CITED

Ackerman, B. R. 1988. Visibility bias of mule deer aerial census procedures in southeast Idaho. Dissertation, University of Idaho, Moscow, USA.

Anderson, C. R., and F. G. Lindzey. 1996. Moose sightability model developed from helicopter surveys. Wildlife Society Bulletin 24:247–259.

Anderson, C. R., D. S. Moody, B. L. Smith, F. G. Lindzey, and R. P. Lanka. 1998. Development and evaluation of sightability models for summer elk surveys. Journal of Wildlife Management 62:1055–1066.

Anderson, D. R. 2001. The need to get the basics right in wildlife field studies. Wildlife Society Bulletin 29:129–1297.

Anderson, D. R. 2003. Response to Engeman: index values rarely constitute reliable information. Wildlife Society Bulletin 31:288–291.

Bartmann, R. M., G. C. White, L. H. Carpenter, and R. A. Garrott. 1987. Aerial mark-recapture estimates of confined mule deer in pinyon-juniper woodland. Journal of Wildlife Management 51:41–46.

Beasom, S. J., J. C. Hood, and J. R. Cain. 1981. The effect of strip width on helicopter censusing of deer. Journal of Range Management 34:36–37.

Beringer, J., L.P. Hansen, and O. Sexton. 1998. Detection rates of white-tailed deer with a helicopter over snow. Wildlife Society Bulletin 26:24–28.

Bleich, V. C., C. S. Y. Chun, R. W. Anthes, T. E. Evans, and J. K. Fischer. 2001. Visibility bias and development of a sightability model for tule elk. Alces 37:315–327.

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.

Bowden, D. C., and R. C. Kufeld. 1995. Generalized mark-resight population size estimation applied to Colorado moose. Journal of Wildlife Management 59:840–851.

Buckland, S. T., D. R. Anderson, K. P. Burnham, and J. L. Laake. 1993. Distance sampling: estimating abundance of biological populations. Chapman & Hall, New York, New York, USA.

Burnham, K. P., D. R. Anderson, and J. L. Laake. 1980. Estimation of density from line transect sampling of biological populations. Wildlife Monograph 72:1–202.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York, New York, USA.

Caughley, G. 1974. Bias in aerial survey. Journal of Wildlife Management 38:921–933.

Caughley, G. 1977. Analysis of vertebrate populations. John Wiley & Sons, New York, New York, USA.

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

Drummer, T. D., and R. W. Aho. 1998. A sightability model for moose in upper Michigan. Alces 34:15–19.

Firchow, K. M., M. R. Vaughan, and W. R. Mytton. 1990. Comparison of aerial survey techniques for pronghorns. Wildlife Society Bulletin 18:18–23.

Freund, R. J., and W. J. Wilson. 2003. Statistical methods. Second edition. Academic Press, San Diego, California, USA.

Gasaway, W. C., S. D. Dubois, and S. J. Harbo. 1985. Biases in aerial transect surveys for moose during May and June. Journal of Wildlife Management 49:777–784.

Gates, C. E. 1979. Line transects and related issues. Pages 71–154 in R. M. Cormack, G. P. Patil, and D. S. Robson, editors. Sampling biological populations. International Cooperative Publishing House, Fairland, Maryland, USA.

Grassel, S. M. 2000. Evaluation of methodology used to estimate population size, sex and age ratios, and mortality of white-tailed and mule deer in the

Missouri River Breaks Region of South Dakota. Thesis, South Dakota State University, Brookings, USA.

Grzybowski, M., and J. G. Younger. 1997. Statistical methodology: III. Receiver operating characteristic (ROC) curves. Academic Emergency Medicine 40:818–826.

Guenzel, R. J. 1986. Pronghorn ecology in southcentral Wyoming. Thesis, University of Wyoming, Laramie, USA.

Guenzel, R. J. 1997. Estimating pronghorn abundance using aerial line transect surveys. Wyoming Game and Fish Department, Cheyenne, USA.

Hosmer, D. W., and S. Lemeshow. 2000. Applied logistic regression. Second edition. John Wiley & Sons, Inc., New York, New York, USA.

Jacques, C. N. 2006. Evaluation of aerial transect surveys, survival, and movements of pronghorn in western South Dakota. Dissertation, South Dakota State University, Brookings, USA.

Jacques, C. N., J. A. Jenks, C. S. DePerno, J. D. Sievers, T. W. Grovenburg, T. J. Brinkman, C. C. Swanson, and B. A. Stillings. 2009a. Evaluating ungulate mortality associated with helicopter net gun captures in the Northern Great Plains. Journal of Wildlife Management 73:1282–1291.

Jacques, C. N., J. A. Jenks, and R. W. Klaver. 2009b. Seasonal movements and home range use by female pronghorns in sagebrush-steppe communities of western South Dakota. Journal of Mammalogy 90:433–441.

Jacques, C. N., T. R. Van Deelen, W. H. Hall, Jr., K. J. Martin, and K. C. VerCauteren. 2011. Evaluating how hunters see and react to telemetry collars on white-tailed deer. Journal of Wildlife Management 75:221–231.

Johnson, B. K., F. G. Lindzey, and R. J. Guenzel. 1991. Use of aerial line transect surveys to estimate pronghorn populations in Wyoming. Wildlife Society Bulletin 19:315–321.

Johnson, J. R., and G. E. Larson. 1999. Grassland plants of South Dakota and the Northern Great Plains. South Dakota Agricultural Experiment Station, Brookings, USA.

Johnson, W. F. 1988. Soil survey of Harding County, South Dakota. United States Department of Agriculture, Soil, Conservation Service, Washington, D.C., USA.

Kalvels, J. 1982. Soil survey of Fall River County, South Dakota. United States Department of Agriculture, Soil, Conservation Service, Washington, D.C., USA.

Lancia, R. A., W. L. Kendall, K. H. Pollock, and J. D. Nichols. 2005. Estimating the number of animals in wildlife populations. Pages 106–153 in C. E. Braun, editor. Techniques for wildlife investigations and management. The Wildlife Society, Bethesda, Maryland, USA.

Larson, G. E., and J. R. Johnson. 1999. Plants of the Black Hills and Bear Lodge Mountains. South Dakota Agricultural Experiment Station, Brookings, USA.

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.

Neal, A. K., G. C. White, R. B. Gill, D. F. Reed, and H. H. Olterman. 1993. Evaluation of mark-resight model assumptions for estimating mountain sheep numbers. Journal of Wildlife Management 57:436–450.

O'Gara, B. W. 2004a. Behavior. Pages 145–194 in B. W. O'Gara and J. D. Yoakum, editors. Pronghorn ecology and management. Wildlife Management Institute, Washington, D.C., USA.

O'Gara, B. W. 2004b. Physical characteristics. Pages 109–144 in B. W. O'Gara and J. D., Yoakum, editors. Pronghorn ecology and management. Wildlife Management Institute, Washington, D.C., USA.

Pojar, T. M., D. C. Bowden, and R. B. Gill. 1995. Aerial counting experiments to estimate pronghorn density and herd structure. Journal of Wildlife Management 59:117–128.

Pojar, T. M., and R. J. Guenzel. 1999. Comparison of fixed-wing line transect and helicopter quadrat pronghorn surveys. Proceedings of the Biennial Pronghorn Antelope Workshop 18:64–68.

Powell, L. A. 2007. Approximating variance of demographic parameters using the delta method: a reference for avian biologists. Condor 109:949–954.

Rice, C. G., K. J. Jenkins, and W. Chang. 2009. A sightability model for mountain goats. Journal of Wildlife Management 73:468–478.

Samuel, M. D., and E. O. Garton. 1994. Horvitz-Thompson survey sample methods for estimating large-scale animal abundance. Pages 170–179 in Transactions of the 59th North American Wildlife and Natural Resources Conference. Wildlife Management Institute, 18–23 March 1994, Anchorage, Alaska, USA.

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.

Samuel, M. D., R. K. Steinhorst, E. O. Garton, and J. W. Unsworth. 1992. Estimation of wildlife population ratios incorporating survey design and visibility bias. Journal of Wildlife Management 56:718–725.

Schroeder, M. A., J. R. Young, and C. E. Braun. 1999. Sage grouse (Centrocercus urophasianus). Page 425 in A. Poole and F. Gill, editors. The birds of North America. The Birds of North America, Inc., Philadelphia, Pennsylvania, USA.

Seber, G. A. F. 1982. The estimation of animal abundance and related parameters. Second edition. Chapman, London, UK and Macmillan, New York, New York, USA.

Sikes, R. S., W. L. Gannon, and the Animal Care and Use Committee of the American Society of Mammalogists. 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. Journal of Mammalogy 92:235–253.

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.

Smith, J. T., L. D. Flake, K. F. Higgins, and G. D. Kobriger. 2004. History of greater sage-grouse in the Dakotas: distribution and population trends. Prairie Naturalist 36:213–230.

Smyser, T. J. 2005. Response of pronghorn (Antilocapra americana) populations to habitat conditions with modification to survey methods. Thesis, University of Idaho, Moscow, USA.

Smyser, T. J., E. O. Garton, and P. Zager. 2005. The influence of habitat variables on pronghorn recruitment. Idaho Department of Fish and Game, Completion Report, Boise, USA.

Steinhorst, R. K., and M. D. Samuel. 1989. Sightability adjustment methods for aerial surveys of wildlife populations. Biometrics 45:415–425.

Unsworth, J. W., F. A. Leban, D. J. Leptich, E. O. Garton, and P. Zager. 1994. Aerial survey: user's manual with practical tips for designing and conducting aerial big game surveys. Idaho Department of Fish and Game, Boise, USA.

West, D. R. 1969. Spring inventory of antelope in South Dakota 1968. Pittman Robertson Job Progress Report W-95-R-2, J 2-E. South Dakota Department of Game, Fish and, Parks. Pierre, USA.

White, G. C., R. M. Bartmann, L. H. Carpenter, and R. A. Garrott. 1989. Evaluation of aerial line transects for estimating mule deer densities. Journal of Wildlife Management 53:625–635.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46:S120–S139.

White, G. C., and T. M. Shenk. 2001. Population estimation with radio-marked animals. Pages 329–350 in J. J. Millspaugh and J. M. Marzluff, editors. Radio tracking and animal populations. Academic Press, San Diego, California, USA.

Whittaker, D. G., W. A. Van Dyke, and S. L. Love. 2003. Evaluation of aerial line transects for estimating pronghorn antelope abundance in low-density populations. Wildlife Society Bulletin 31:443–453.

Wilkinson, L. 1990. SYSTAT: the system for statistics. SYSTAT, Inc., Evanston, Illinois, USA.

Williams, B. K., J. D. Nichols, and M. J. Conroy. 2002. Analysis and management of animal populations: modeling, estimation, and decision making. Academic Press, San Diego, California, USA.

Wingard, G. J., R. B. Harris, S. Amgalanbaatar, and R. P. Reading. 2011. Estimating abundance of mountain ungulates incorporating imperfect detection: argali Ovis ammon in the Gobi Desert, Mongolia. Wildlife Biology 17:93–101.

Zar, J. H. 1984. Biostatistical analysis. Second edition. Prentice Hall, Inc., Englewood Cliffs, New Jersey, USA.

Associate Editor: David Forsyth.