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DEVELOPMENT AND EVALUATION OF SIGHTABILITY MODELS FOR SUMMER ELK SURVEYS

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Abstract: We developed 2 sightability models from summer helicopter surveys of radiocollared elk (*Cervus elaphus*) in Grand Teton National Park, Wyoming. Significant variables ($P < 0.05$) included elk group size, activity, and percent vegetation cover for Model A, and elk group size and percent vegetation cover for Model B. We compared these 2 summer models and a winter elk sightability model developed in Idaho that incorporates group size, percent vegetation cover, and percent snow cover. We based model comparisons on predicted detection rates and model performance when applied to well-documented elk populations at Starkey Experimental Forest and Range, Oregon (SEF), and Wind Cave National Park, South Dakota (WCNP). Predicted sightability was similar from summer Models A and B for active elk in <60% vegetation cover, but was lower from Model A for bedded elk. Model estimates of elk abundance (WCNP, SEF) and composition (SEF) usually were more accurate and consistently more precise from Model B, suggesting elk activity had little influence on estimates of summer elk population characteristics. Comparisons between Model B and the Idaho model indicated predicted sightability of small groups (≤10 elk) was similar; the Idaho model provided better accuracy and precision for validation tests of populations consisting of predominantly small elk groups (WCNP: = 4.7 elk/group; SEF: = 6.3 elk/group). The Idaho model, however, overestimated detection of large elk groups (30–45 elk/group) in moderate–dense vegetation (>30% vegetation cover), but this overestimation was accounted for by Model B. Thus, we recommend application of the Idaho model during summer surveys where elk are less gregarious (<20 elk) and recommend application of summer Model B to high-density elk populations where elk occur in larger groups.

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Key words: accuracy, aerial survey, *Cervus elaphus*, elk, population estimate, precision, sightability model.

Elk harvest in northwestern Wyoming has historically consisted of harvesting animals as they congregated and migrated to winter ranges in Grand Teton National Park (GTNP), the Gros Ventre River Valley, Buffalo Valley, and the National Elk Refuge. This approach maintained the population near objective through 1986. However, various segments of the Jackson Elk Herd were harvested unequally (Smith and Robbins 1994), which prompted more conser-

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vative seasons and the subsequent expansion of the herd by 3,000–5,000 animals above the management objective (Smith 1994).

Herd segments share common winter ranges and often mix during later stages of the fall migration. Hence, management agencies need to know the size and composition of discrete herd segments to design hunting seasons that equitably harvest elk from various summer ranges. Population modeling of herd segments and a better understanding of timing of migrations from each summer–fall range will promote control of the Jackson Elk Herd's size.

Samuel et al. (1987) developed an elk sightability model in Idaho to account for sightability bias during winter aerial surveys. This method attempts to standardize survey conditions that are controllable (e.g., air speed, number and experience level of observers, aircraft type) and develop correction factors, via logistic regression, for the behavioral and environmental factors found to influence detection rates (e.g., group size, vegetation cover). Correction factors from the resulting sightability model are then applied to animals seen during surveys on a group-by-group basis. The major advantage of this approach is that variable sightability (e.g., year-to-year variation, changes in group size distribution, sex and age segregation) can be accounted for to produce more reliable estimates of population size and sex and age composition.

The initial elk sightability model developed in Idaho (Samuel et al. 1987) was validated against elk drive counts in Montana (Unsworth et al. 1990) and provided reliable estimates of elk abundance. This area represented relatively open habitats with complete snow cover; however, model deficiencies were suspected under variable snow conditions in dense canopy habitats. Thus, additional data were later added to the model to account for these deficiencies (Leptich and Zager 1992). This enhanced sightability model was validated against a well-documented elk population at the SEF, Oregon (under variable snow conditions in dense vegetation), and provided reliable estimates of population size and sex and age composition (Leptich and Zager 1993). Leptich and Zager (1993), however, cautioned against using the Idaho model during seasons other than winter, because factors influencing sightability probably differ seasonally.

Although the elk sightability model developed for winter conditions appears to provide valid estimates of elk population size and composition, the adequacy of this technique during summer has not been evaluated. Our objectives were (1) determine factors that influence elk sightability during summer helicopter surveys and develop predictive sightability models to estimate elk population size and sex–age composition, (2) evaluate summer and winter elk sightability models with aerial survey data collected under summer–fall survey conditions to determine model adequacy and robustness, and (3) compare the summer models we developed to the Idaho winter model to determine if differences exist between summer and winter elk sightability from helicopters.

STUDY AREA

Sightability surveys took place in and adjacent to GTNP, north of Jackson, Wyoming. Elevations ranged from 1,890 m in the Snake River Valley to 3,600 m in the mountains. Plant communities included cottonwood–willow (*Populus angustifolia–Salix* spp.) riparian areas, sagebrush (*Artemisia* spp.) grasslands, aspen (*Populus tremuloides*), Douglas-fir (*Pseudotsuga menziesii*), and lodgepole pine (*Pinus contorta*), with some spruce–fir (*Picea engelmannii–Abies lasiocarpa*) forests at higher elevations (Smith and Robbins 1994).

METHODS

Sightability Trials

We used radiocollared elk from a concurrent study (Smith et al. 1997) to determine factors that influenced elk sightability during summer helicopter surveys. Prior to sightability trials, we used fixed-wing aircraft (Maule M5) to locate radiocollared elk and determine locations of search units. The pilot randomly assigned a 4.6-km^2 circular plot around each elk location and radioed the coordinates to the helicopter survey crew; circular search units were used because of navigational simplicity. We used a Global Positioning System (GPS) Apollo 820 receiver (II Morrow, Salem, Oregon, USA) to determine elk locations during presurvey flights, and we used a GPS Pathfinder TransPak II receiver (Trimble Navigation, Sunnyvale, California, USA) to navigate the helicopter and delineate search-unit boundaries during surveys. Survey crews were typically directed to search units containing $\geq$1 radiocollared elk, although search units without radiocollared elk were also surveyed to assure observers did not expect radiocollared elk to be present.

Sightability surveys were flown in a Hiller-Soloy or a Hiller-12E helicopter. Both helicopters were structurally identical, except for engine type, and afforded good visibility with 3 seats abreast. The helicopter crew consisted of a pilot, a primary observer (experienced in aerial elk surveys and familiar with the survey area), and a secondary observer (at least some aerial survey experience). Seating arrangement was pilot in the middle and observers on either side. All 3 crew members assisted in spotting and classifying elk. Observers were limited to $\leq$4 hr/day in the helicopter to minimize the influence of observer fatigue on survey results. Elk sightability during summer deteriorates by midday as groups disperse into denser canopy as temperatures increase. Angle of the sun during summer also creates heavier shadows in timbered areas by late morning (Lanka et al. 1993. Validation of the Idaho elk sightability model for use in the Black Hills of Wyoming and South Dakota, unpublished. Wyoming Cooperative Fish and Wildlife Research Unit, Laramie, Wyoming, USA). Therefore, surveys were flown between sunrise and 1200.

Survey protocol followed J. W. Unsworth et al., 1994 (Aerial Survey: user's manual. Second edition, unpublished. Idaho Department of Fish and Game, Boise, Idaho, USA). We recorded group size, elk activity, topography (flat, moderate, steep), cover type, percent vegetation cover, light intensity (flat or bright), and sex and age of each group member (yearling or ad M, ad F $\geq$1 yr old, calves) for each radiocollared group seen or missed during surveys. We located radiocollared elk missed during surveys with helicopter-mounted telemetry equipment (164–167 MHz; Telonics, Mesa, Arizona, USA) immediately after we surveyed a search unit. To maintain independent samples, groups containing $>$1 radiocollared elk were treated as a single observation. We recorded elk activity as bedded or active (standing or moving) for the first group member seen during or after the survey. We classified cover type where the group was first seen into categories based on dominant plant species and structure. Percent vegetation cover (recorded in 5% increments) was estimated within a 9-m perimeter around the group where it was first observed. Vegetation that obscured elk obliquely from view was considered vegetation cover (Unsworth et al. 1994:8). Survey time was also recorded for each search unit.

Sightability Analyses

We used univariate analyses to determine appropriate groupings for the discrete independent variables. We examined discrete variables (time of day, sex and age groupings, elk activity, light intensity, topography, cover type, year) via chi-square contingency analyses (PROC FREQ; SAS Institute 1988). We combined categories for discrete variables if the likelihood ratio chi-square score improved and biological interpretation remained intact.

The assumption that continuous variables (vegetation cover, group size) were linear in the logit was examined by placing continuous data into categories and plotting the odds-ratio versus the midpoint of each category (Hosmer and Lemeshow 1989:90). Nonlinear relations were adjusted with linear transformations and were maintained during multivariate analyses.

Multivariate analysis of data from elk groups seen or missed during helicopter sightability trials were analyzed with forward stepwise logistic regression (BMDP–LR: Dixon et al. 1988; Hosmer and Lemeshow 1989; PROC LOGIST: SAS Institute 1990) where the dependant variable was coded as 1 for groups seen or zero for groups missed during surveys. To predict model parameters, we used maximum likelihood estimation when possible or conditional exact estimation if categorical data were highly imbalanced (LogXact–Turbo; Mehta and Patel 1993). Variables not included ($P \geq 0.05$) during stepwise analysis were individually forced into the logistic model to determine if their influence became statistically important when considered with previously selected variables. We also considered 2-way interactions of all independent variables for inclusion in the model. To determine adequate fit of our data to the logistic regression model ($P \geq 0.05$), we examined Brown's, Hosmer-Lemeshow, and maximum likelihood goodness-of-fit chi-square tests, and the proportion of observations correctly classified as seen or missed by the selected model (cutpoint = 0.50; Hosmer and Lemeshow 1989).

Model Selection.—We evaluated 2 nested summer models based on (1) significant improvement in the chi-square score from the likelihood ratio test for variable addition, (2) biological interpretation, (3) relative change in the model coefficients after removal of potentially important variables (Hosmer and Lemeshow 1989:88), and (4) model performance when validated against well-documented elk populations.

Model Comparisons

Predictions of elk sightability from the summer models we developed and the Idaho sightability model that accounts for group size, vegetation cover, and snow cover (Unsworth et al. 1994:41) were plotted to compare model predictions. We also evaluated the utility of the Idaho model for use during summer by assessing goodness-of-fit to the summer sightability data we collected. Goodness-of-fit was evaluated for observed and predicted sightability across 10 groupings (i.e., deciles) of the predicted values (Hosmer and Lemeshow 1989:140).

We applied all models to a summer elk survey dataset collected 2–3 September 1992 at WCNP, South Dakota (Lanka et al. 1993:Appendix C), and another dataset collected 10–11 November 1991 at SEF, Oregon (Leptich and Zager 1993). Although elk survey data from SEF were collected during fall, these data provided a meaningful test for our summer models because snow cover was absent. Aerial surveys during model validation at WCNP and SEF were conducted following guidelines described by Unsworth et al. (1994).

Both elk populations occupied enclosed areas. The SEF population is intensively managed, and elk population estimates from research staff were assumed reliable. Only two-thirds of the area within WCNP was censused during drive counts and aerial surveys by Lanka et al. (1993). Thus, the assumption of population closure between the drive count and aerial surveys (4–5 days) could have been violated. However, elk not censused at WCNP were separated by 3 km of open habitat from surveyed elk in timbered areas.

We used program AERIAL SURVEY, version 4.01 (Unsworth et al. 1994), to calculate population estimates and variances (90% CI) for the SEF and WCNP survey data, applying both summer models (A and B) and the Idaho model. Confidence intervals represented sightability variance (error associated with the correction factor applied to each group) and model variance (error in estimating the sighting probabilities during model development; Steinhorst and Samuel 1989). Sampling variance was not included in these estimates because each survey represented a census. To compare bias and precision of estimates from competing models, we calculated the square root of the mean squared error (RMSE) for each estimate.

We acknowledged that applying the Idaho model to summer surveys required assigning snow cover as a constant (i.e., 0% snow cover). While population estimates will not be affected, the variance and covariance from estimating this coefficient during model development could produce slightly inflated estimates of model variance from summer survey data. Thus, we assigned the variance and covariance values of snow cover to zero to produce consistent variance estimates during summer elk surveys.

RESULTS

During model development, we collected 55 data points from 36 radiocollared elk during 1992 (bulls: 7 calves, 6 yearling, 3 ad; cows: 8 calves, 5 yearling, 7 ad), 40 data points from 24 radiocollared elk during 1993 (bulls: 5 yearling, 5 ad; cows: 3 yearling, 11 ad), and 33 data points from 22 radiocollared elk during 1994 (bulls: 5 ad; cows: 1 yearling, 16 ad). Surveys were conducted during late July and early August. During surveys, we saw 96 elk groups ($\geq$1 elk/group) ($\bar{x}$ = 42.4 elk/group; $\bar{x}$= 39.0% vegetation cover) and missed 32 groups ($\bar{x}$ = 7.4 elk/group; $\bar{x}$ = 63.4% vegetation cover), representing 82% detection of elk groups and 95% detection of all elk surveyed. For surveyed elk groups, mean group size was 33.7 elk/group and mean vegetation cover was 45.1%. Mean search rate for search units completely surveyed was 5.1 min/km^2.

Preliminary and Multivariate Analyses

We reduced the number of topography, time, and cover-type categories to improve their fit to the dependent variable: seen or missed elk groups. Improvement in the likelihood ratio chi-square score for topography (from χ^2_2 = 2.66, P = 0.265 to χ^2_1 = 2.55, P = 0.110) and time (from χ^2_4 = 4.98, P = 0.290 to χ^2_2 = 4.24, P = 0.120) indicated elk sightability was similar in moderate and steep terrain and from 0800–1059. Thus, categories were redefined as flat and broken (moderate to steep) terrain for topography and 0700–0759, 0800–1059, and 1100–1159 for time. The exact conditional scores chi-square also improved (from χ^2_5 =

9.749, P = 0.101 to χ^2_2 = 9.655, P = 0.003) when cover-type categories were combined to deciduous shrub, conifer, and deciduous timber. Additionally, percent vegetation cover was grouped into 12.5% vegetation classes (VC) to reduce the potential of visual estimation errors. Thus, VC values of 1–8 were used in analyses. The plotted odds-ratios for continuous variables indicated VC was approximately linear, but group size was nonlinear. A natural log transformation provided a linear fit for group size and was maintained during model building.

Stepwise logistic regression analysis indicated group size ($P < 0.001$), VC ($P < 0.001$), and elk activity ($P = 0.007$) were statistically important predictors of elk sightability during summer helicopter surveys (Table 1). Other independent variables previously not included during stepwise analysis were not significant ($P \geq 0.125$) when forced into the model containing group size, VC, and elk activity (Table 1); all 2-way interactions also were not significant ($P > 0.05$).

Model Selection

We began model selection procedures by fitting the model containing ln(group size), VC, and elk activity. Our ability to correctly identify the activity of elk missed during surveys from elk observed after the survey was questionable. Anderson and Lindzey (1996) found survey and postsurvey moose (*Alces alces*) activity differed in 23% of the cases they investigated. Radiocollars used in this study were not equipped with activity sensors, and therefore we could not verify the accuracy of activity measured for elk groups missed during surveys. Erroneous activity data could produce biased estimates of elk sightability; thus, we fit a second model containing only ln(group size) and VC. Independent variables other than elk activity were not significant ($P \geq 0.195$) when forced into the second model containing ln(group size) and VC.

We developed Model A to account for the influence of elk group size, VC, and elk activity, and Model B to account for the influence of elk group size and VC during summer helicopter surveys. The probability of detecting elk groups (p) was

$$p = \frac{e^u}{1 + e^u}.$$

The linear portion of the logistic regression equation for Model A was

$$u = 3.651 + 1.140[\ln(\text{group size})] - 0.989(\text{VC}) - 1.475(\text{elk activity}),$$

and for Model B was

$$u = 3.336 + 1.115[\ln(\text{group size})] - 0.996(\text{VC}).$$

Elk activity is 1 if bedded and zero otherwise, and vegetation class (VC) is assigned values 1–8 for each increase of 12.5% vegetation cover. The inverse of p is the correction factor applied to each group observed during surveys. For Model A, estimated standard errors were 1.202 for the intercept, 0.321 for group size, 0.262 for VC, and 0.735 for elk activity. For Model B, estimated standard errors were 1.151 for the intercept, 0.256 for group size, and 0.243 for VC. For both models, the positive coefficients for group size indicated sightability increased for larger groups, and the negative coefficients for VC indicated sightability decreased with increasing vegetation cover (Figs. 1, 2). The negative coefficient for activity in Model A indicated sightability was reduced for bedded elk (Fig. 1). Chi-square goodness-of-fit tests for both models indicated these data were appropriate for the logistic regression model (Model A: Brown's P = 0.668, Hosmer-Lemeshow P = 0.813, maximum likelihood P = 0.999; Model B: Brown's P = 0.467, Hosmer-Lemeshow P = 0.356, maximum likelihood P = 0.999). The proportion of the 128 observations correctly classified as seen or missed was 88.3% for Model A and 87.5% for Model B.

Model Comparisons

We compared predicted elk sightability between Models A and B and the Idaho model under summer survey conditions. Predicted elk sightability from the Idaho model is dependent on group size, vegetation class, and percent snow cover (Unsworth et al. 1994:42). We set snow cover at 0% to represent summer survey conditions (Fig. 3), thus eliminating the coefficient for snow cover from the regression equation.

General trends in predicted elk sightability from the 3 models were similar for groups of ≤10 elk: estimated sightability was moderately higher for these groups from Model B and for active elk from Model A (Figs. 1–3). Model predictions for groups of 20 elk in >55% vegetation cover, however, indicated predicted elk sightability from the Idaho model was higher than predicted by the summer models. Addi-

Table 1. Results of forward stepwise logistic regression and statistical outcome of independent variables forced individually into the model containing ln(group size), vegetation class, and elk activity. Data from 128 elk groups observed during helicopter sightability trials in Grand Teton National Park, summer 1992–94.

Name of discrete or continuous variable	n	% seen	Stepwise[a]		Variables forced[b]	
			χ^2	P	χ^2	P
Discrete						
Time of day			4.22	0.121	0.79	0.674
0700–0759	13	92				
0800–1059	103	80				
1100–1159	12	58				
Sex–age			2.83	0.243	2.83	0.243
All	63	86				
Cow:cow–calf	41	68				
Bull	24	58				
Elk activity			7.26	0.007		
Bedded	34	56				
Standing–moving	94	82				
Light intensity			2.36	0.125	2.36	0.125
Flat	38	84				
Bright	90	71				
Topography			<0.01	0.988	<0.01	0.988
Flat	74	80				
Broken	54	69				
Cover Type			0.61	0.735	0.35	0.838
Deciduous shrub	18	100				
Deciduous timber	24	83				
Conifer	86	67				
Year			1.72	0.424	1.78	0.423
1992	55	80				
1993	40	75				
1994	33	67				
Continuous						
Group size			34.36	<0.001		
1	13	8				
2	11	45				
3	6	83				
4	7	71				
5–7	6	67				
8–15	23	78				
16–30	16	94				
31–50	16	88				
51–100	18	94				
101–197	12	100				
Vegetation class			19.37	<0.001		
1 (0–12%)	11	100				
2 (13–25%)	13	100				
3 (26–37%)	19	89				
4 (38–50%)	40	88				
5 (51–62%)	18	61				
6 (63–75%)	18	44				
7 (76–87%)	9	33				
8 (88–100%)	0					

[a] Significance of independent variables after stepwise logistic regression analysis with ln(group size), vegetation class, and elk activity included in the model ($P < 0.05$).
[b] Significance of independent variables forced into the model containing ln(group size), vegetation class, and elk activity ($P < 0.05$).

tionally, the Idaho model indicated groups of >40 elk were rarely missed during surveys with 0% snow cover, whereas the summer models predicted even large groups may be missed in dense canopy.

The Hosmer-Lemeshow goodness-of-fit test indicated a significant lack-of-fit ($\chi^2_8 = 238.71$, $P < 0.001$) of the Idaho model to the summer sightability data we collected in GTNP. Lack-of-fit primarily occurred within deciles averaging 32 elk/group in vegetation class 4 (43–57% cover) and 43 elk/group in vegetation class 3

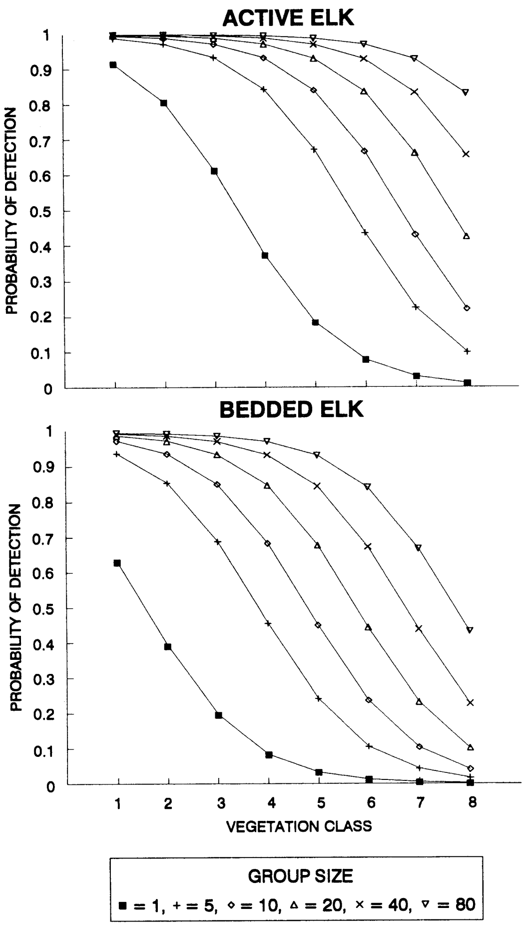

Fig. 1. Predicted elk sightability (Model A) by vegetation class (1 = 0–12%, 2 = 13–25%, 3 = 26–37%, 4 = 38–50%, 5 = 51–62%, 6 = 63–75%, 7 = 76–87%, 8 = 88–100%) for active (top) and bedded elk (bottom) and 6 group sizes. Data from 128 elk groups observed during helicopter sightability trials in Grand Teton National Park, summer 1992–94.

(28–42% cover; Table 2). Excluding these deciles from the chi-square analysis suggested the Idaho model adequately predicted summer elk sightability ($\chi^2_8 = 10.14$, $P = 0.257$) for the other 8 deciles compared (Table 2).

Mean vegetation cover for elk groups seen during surveys was 34.5% at WCNP and 45.7% at SEF; mean group size was 4.7 at WCNP and 6.3 at SEF. For elk groups seen during surveys, mean vegetation cover was 39.0% and mean group size was 42.4 during summer model development; mean vegetation cover was 34.3% and mean group size 10.9 during Idaho model development. For all elk surveyed during summer model development, mean vegetation cover was 45.1% and mean group size was 33.7;

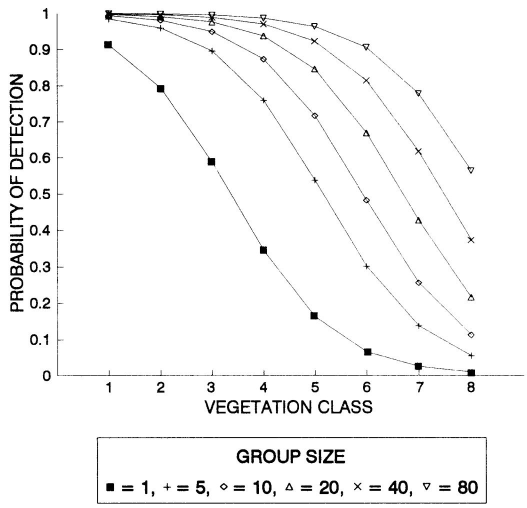

Fig. 2. Predicted elk sightability (Model B) by vegetation class (1 = 0–12%, 2 = 13–25%, 3 = 26–37%, 4 = 38–50%, 5 = 51–62%, 6 = 63–75%, 7 = 76–87%, 8 = 88–100%) for 6 group sizes. Data from 128 elk groups observed during helicopter sightability trials in Grand Teton National Park, summer 1992–94.

during Idaho model development, mean vegetation cover was 51.2% and mean group size was 7.5. When comparing data from elk groups seen during surveys, elk group size was higher at GTNP than WCNP ($t_{104} = -8.08$, $P < 0.001$) and SEF ($t_{111} = -7.62$, $P < 0.001$), but percent vegetation cover did not differ (WCNP: t_{133} =

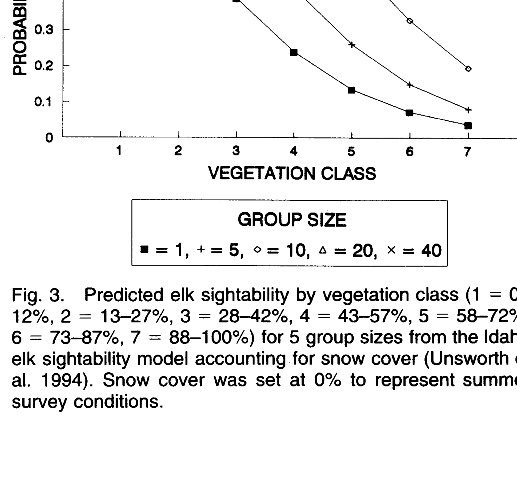

Fig. 3. Predicted elk sightability by vegetation class (1 = 0–12%, 2 = 13–27%, 3 = 28–42%, 4 = 43–57%, 5 = 58–72%, 6 = 73–87%, 7 = 88–100%) for 5 group sizes from the Idaho elk sightability model accounting for snow cover (Unsworth et al. 1994). Snow cover was set at 0% to represent summer survey conditions.

Table 2. Hosmer-Lemeshow goodness-of-fit test (Hosmer and Lemeshow 1989:140) indicating significant lack of fit (χ^2_8 = 238.71, $P < 0.001$) of the Idaho sightability model to elk sightability data collected from 128 elk groups at Grand Teton National Park, summer 1992–94.

Decile mean				
Group size	Vegetation class[a]	Detection probability[b]	Proportion detected (n)	Contribution to the χ^2 score
1	6	0.101	0.070 (14)	0.14
3	5	0.229	0.460 (13)	4.02
5	4	0.449	0.750 (12)	4.39
7	4	0.577	0.670 (12)	0.40
11	4	0.764	0.850 (13)	0.49
19	3	0.949	1.000 (13)	0.70
32	4	0.995	0.830 (13)	67.31
43	3	0.999	0.920 (13)	161.26
83	3	1.000	1.000 (13)	0.00
130	3	1.000	1.000 (13)	0.00

[a] Percent vegetation cover within each vegetation class: 1 = 0–12, 2 = 13–27, 3 = 28–42, 4 = 43–57, 5 = 58–72, 6 = 73–87, 7 = 88–100.
[b] Predicted with the Idaho sightability model (Unsworth et al. 1994).

−1.30, P = 0.196; SEF: t_{62} = 1.47, P = 0.146). Similarly, elk group size was higher during Idaho model development than at WCNP (t_{120} = −4.28, $P < 0.001$) and SEF (t_{97} = −2.75, P = 0.007), and percent vegetation cover was similar at WCNP (t_{83} = 0.04, P = 0.968) but was lower than at SEF (t_{194} = 2.53, P = 0.012). For all elk surveyed during model development, higher group sizes (t_{134} = −6.97, $P < 0.001$) and lower vegetation cover (t_{357} = 2.34, P = 0.020) were observed at GTNP than at Idaho.

Model estimates of elk population size from WCNP were similarly precise for all models, but estimates of population size were low from the 2 summer models (Table 3). Accurate estimates of elk abundance and composition at SEF were provided by all 3 models; however, composition estimates were consistently imprecise from summer Model A (Table 3). The RMSE indicated the best population estimates were consistently provided by the Idaho sightability model, while the poorest estimates were typically obtained with the summer model adjusted for elk activity (Model A; Table 3).

DISCUSSION

Factors Influencing Summer Elk Sightability

Our findings that vegetation cover is strongly related to the probability of detecting elk groups during summer surveys are consistent with winter models developed in Idaho (Samuel et al. 1987), Michigan (Otten et al. 1993), and Pennsylvania (Cogan and Diefenbach 1998). Although activity does not appear to influence elk sightability during winter (Samuel et al. 1987), summer elk surveys may be more sensitive to elk activity because the lack of snow cover creates more difficult sighting conditions. Elk group size also influenced sightability, which agrees with the findings of Samuel et al. (1987) and Cogan and Diefenbach (1998) but differs from those of Otten et al. (1993). Otten et al. (1993) reported low variation in group sizes may have reduced importance of this variable during their study. Cogan and Dieffenbach (1998) undercounted elk groups during their study and believed this caused negatively biased elk population estimates. However, they considered all elk within 45 m a group, whereas we defined elk groups as a cohesive unit where behavior and distance rather than distance alone were

Table 3. Number of elk counted during helicopter surveys, elk population estimates with 90% confidence intervals (CI), and the square root of the mean squared error (RMSE) from 3 elk sightability models[a], and comparison estimates from Wind Cave National Park (WCNP), South Dakota, September 1992 (Lanka et al. 1993), and Starkey Experimental Forest and Range (SEF), Oregon, November 1991 (Leptich and Zager 1993).

Parameter for each comparison dataset	No. elk counted	Model A			Model B			Idaho model			
		$\hat{N}$	CI	RMSE	$\hat{N}$	CI	RMSE	$\hat{N}$	CI	RMSE	Estimate[b]
WCNP											
Total	184	257	55	57–112	253	48	58–115	294	54	34–77	303–364
SEF											
Cows	155	303	133	99	329	117	78	351	107	66	360
Calves	64	123	62	44	127	42	32	141	42	26	146
Bulls	56	197	207	156	155	88	73	138	54	47	105
Total	275	623	285	174	611	195	119	631	163	101	611

[a] Predictor variables for each model: Model A = group size, vegetation class, and elk activity; Model B = group size and vegetation class; Idaho model = group size, vegetation class, and snow cover (Unsworth et al. 1994).
[b] WCNP estimate from 29 August 1992 drive count; upper bound represents all elk counted, and lower bound represents elk counted–elk driven from survey area (Lanka et al. 1993). SEF estimate from data collected by SEF research staff (Leptich and Zager 1993).

used to establish elk groups. While we did not verify that elk groups were accurately counted, including elk behavior in defining elk groups may reduce the potential of undercounting elk during model development and application.

Summer Sightability Model Comparisons

Detection probabilities from the 2 summer models (A, B) were generally similar for elk in ≤60% vegetation cover (VC = 1–5) but began to diverge for single, bedded elk and larger groups (>10 elk) in heavy-canopy cover (>60%; VC = 6–8). Models A and B provided similar estimates of elk abundance at WCNP and SEF because most observations were of active elk, and the larger groups were in open-canopy habitats. Models A and B should provide similar estimates for active elk under most survey conditions in northwestern Wyoming because large, dense-canopy timber stands are uncommon, and most large groups of elk should be detected in areas of lower vegetation cover.

Validation tests at WCNP and SEF (Table 3) indicated the activity variable in Model A may actually decrease model performance. Population estimates and 90% confidence intervals at WCNP were similar from the 2 summer models; however, they both appeared biased low. Both models provided accurate elk population estimates at SEF, but abundance and sex–age composition estimates were consistently more accurate and precise from Model B; composition estimates from Model A for cows and bulls proved unreliable (Table 3). Additionally, removing activity from the model did not change the influence of group size and vegetation cover on elk sightability (<2% change for each coefficient), suggesting elk activity exhibited a relatively small and independent influence on model predictions. Thus, the activity variable does not appear beneficial, and, of the 2 summer models, we recommend using Model B to estimate summer elk populations. If the influence of activity is indeed important, differences in predicted sightability by the 2 models should be reduced by conducting surveys early in the day, when elk tend to be active and in larger groups.

Model B and Idaho Model Comparisons

Group size for elk seen during surveys was much higher at GTNP than SEF (GTNP: $\bar{x}$ = 42.4 elk/group; SEF: $\bar{x}$ = 6.3 elk/group). Elk group size was slightly higher during Idaho model development, and vegetation cover was lower than at SEF (Idaho: $\bar{x}$ = 10.9 elk/group, 34.3% vegetation cover; SEF: $\bar{x}$ = 6.3 elk/group, = 45.7% vegetation cover). Based on model predictions of elk abundance and composition (Table 3), both models appear robust to changes in elk grouping behavior, and the Idaho model appears robust to changes in habitat selection. Vegetation cover was similar at GTNP and SEF; thus, we could not evaluate the performance of summer Model B under differing vegetation cover densities.

Elk grouping behavior at WCNP ($\bar{x}$ = 4.7) was lower than during Idaho model development and much lower than during summer model development, but canopy densities for detected groups ($\bar{x}$ = 34.5%) were similar to both models. Model B apparently underestimated elk abundance at WCNP. Lanka et al. (1993) estimated between 303 and 364 elk at WCNP, depending on the number of elk returning to the censused area that were driven out during drive counts. Model B estimated 253 ± 48 elk ($\hat{N}$ and 90% CI), and the Idaho model predicted 294 ± 54 elk. About 34% of the perimeter at WCNP was either unfenced (16%) or the fence was low enough for elk to cross (1.4 m high; 18%), which created potential problems with elk movement back into the censused area during drive counts. If the upper bound of the drive-count estimate (364 elk) was accurate, both models were biased low.

During summer surveys, Lanka et al. (1993) noted that elk moved to dense canopy, forested habitats during midday, where sightability appeared lower than winter surveys because of heavier shadows. Sightability surveys at WCNP were conducted until 1335. Conversely, Model B was primarily developed from data collected before 1100 (91%; Table 1). We developed Model B for summer elk surveys under favorable sighting conditions so that correction factors would be relatively low and resulting population estimates most precise. We suspect Model B would have performed better at WCNP had data been collected during the same time period as model development. Heavy shadows and elk dispersal into dense-canopy habitats during midday summer surveys (Lanka et al. 1993) may also create problems for predictions via the Idaho sightability model. The Idaho model, however, performed better than summer Model B. We suspect the Idaho model may be more robust to these conditions because it was developed from more difficult sighting conditions consisting of denser vegetation and much smaller group sizes.

The summer sightability model, which excludes the influence of elk activity, is similar to the Idaho sightability model (Unsworth et al. 1994) when snow cover is absent. Both models incorporate the influence of group size and vegetation cover, but the relative influence of these variables differs between models. If these models represent summer versus winter survey conditions, the influence of vegetation cover on detection rates appears greater during summer surveys, and the influence of group size appears less. Our summer model predicts even large groups of elk can be missed under dense canopies (Fig. 2), whereas the Idaho model predicts elk groups >40 are rarely missed (Fig. 3). We noted the Idaho model overestimated summer sightability for groups typical of 30–45 elk in 30–60% vegetation cover (Table 2). Only 3.5% of the data used to develop the Idaho model consisted of groups of >30 elk, and only 6.7% consisted of groups of >20 elk (n = 282; P. Zager, Idaho Department of Fish and Game, unpublished data). Conversely, the summer model we developed is more representative of large elk groups during summer surveys (Table 1). Overall, however, the 2 models yielded similar trends in predicted sightability for groups of ≤10 elk. While Leptich and Zager (1993) cautioned the Idaho model might not be appropriate during seasons other than winter, our comparisons suggest this model should provide reliable estimates of summer elk populations when elk occur in small groups, regardless of vegetative cover density.

When both accuracy and precision are considered, better elk population estimates were consistently provided by the Idaho model (lower RMSE; Table 3). Better estimates can be attributed to the Idaho models' development in conditions more representative of SEF and WCNP. Additionally, Idaho model estimates were consistently more precise because it was developed from a much larger dataset (Idaho: n = 282; Model B: n = 128); the relative contribution to confidence intervals (i.e., CV) from sightability error (Steinhorst and Samuel 1989) was similar, while the contribution from model error was typically doubled from summer Model B. However, we caution against applying Idaho's model to high-density populations where elk occur in large groups (≥20 elk) during summer (e.g., GTNP). Using the Idaho model to estimate high-density elk populations may result in negatively biased and overly precise estimates because even large groups can be missed during summer surveys (Table 1). The summer sightability model we developed (Model B) should provide reliable elk population estimates from summer surveys where elk occur in large groups, and it may be robust to populations where elk are less gregarious (Table 3).

Application of Summer Elk Surveys

Confidence intervals around estimates of elk abundance from all models compared were consistently relatively smaller for estimates from WCNP than estimates from SEF (Table 3). Improved precision from WCNP estimates was not surprising, because sighting conditions were better than at SEF and observers were able to detect a larger proportion of the population during surveys (Table 3). The sightability error component of the variance estimate (Steinhorst and Samuel 1989) is directly related to the proportion of the population that is seen during surveys. As sighting conditions become less difficult (e.g., elk in open habitat, large groups, or both), correction factors decrease and confidence intervals become tighter. To obtain the most precise population estimates, future surveys should be conducted when elk are most observable.

While confidence intervals were relatively wide for elk population estimates from SEF, we expect confidence intervals to be much narrower for estimates from GTNP. Surveys at SEF represented difficult sighting conditions (small elk groups), and only 45% of the elk population was detected (Table 3). In contrast, sighting conditions during model development in GTNP were much simpler (large elk groups), and 95% of the elk in radiocollared groups were observed during surveys (Table 1). Simulated surveys representative of survey conditions encountered in GTNP (1992–94) indicated relative precision may vary from 8–16% of population estimates when stratified sampling is applied (90% coverage of high-density elk areas and 50% coverage of low-density elk areas; C. R. Anderson, unpublished data). Future elk population data collected under similar sighting conditions should provide precise elk population estimates.

MANAGEMENT IMPLICATIONS

We expect that summer Model B will perform well when applied to high-density elk populations consisting of large elk groups and should be robust to changes in elk grouping behavior and possibly habitat selection, if survey protocol are strictly followed. The Idaho model provides superior elk population data for less-gregarious elk populations during summer. When elk groups $\geq$20 are commonly observed during summer surveys, however, summer Model B should be substituted for this model because the Idaho model overestimates summer sightability of larger groups.

The difference in widths of relative confidence intervals at WCNP and SEF suggest estimates become less precise when surveys are applied to elk in dense forest canopy (e.g., >70% vegetation cover). Surveying elk during early morning, when they tend to be in large groups and feeding in open habitats, will provide the most precise estimates of elk abundance and sex and age composition. Surveys applied later in the day (past 1100) or during periods when elk are less gregarious (e.g., calving or rutting season) must be avoided because estimates may be biased and imprecise. If these conditions are unavoidable, the Idaho model may provide the best elk population data. Use of elk behavior patterns to determine the proper time to conduct elk surveys will provide the best management information.

Estimates of summer populations via summer Model B or the Idaho model adjusting for snow cover (depending on survey conditions) will promote the design of management strategies to proportionally harvest migrating elk from various summer ranges. Additionally, application of these models during summer will allow elk population data to be obtained close to the timing of hunting seasons and after most mortality has occurred (i.e., late winter; Smith et al. 1998). Both models should produce reliably accurate and precise population estimates if applied when elk are most observable and surveys are conducted early in the day, before elk disperse into dense cover. Incorporation of additional data points will increase model precision and possibly identify any deficiencies. These data can be inexpensively collected from radiocollared elk in conjunction with summer surveys where radiocollared elk are present. Summer Model B in its current form should function reasonably well over the range of conditions we observed and may be robust to survey conditions encountered on other summer elk range.

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DETECTION OF EARLY PREGNANCY IN CARIBOU: EVIDENCE FOR EMBRYONIC MORTALITY

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Abstract: To investigate relations between body condition and fecundity, we determined pregnancy status of arctic caribou (*Rangifer tarandus granti*) from presence or absence of pregnancy-specific protein B (PSPB) and progesterone concentration in blood sera or plasma. We drew peripheral blood samples from female caribou 3–5 (n = *142*) and 20–23 (n = *44*) weeks after the breeding season. We then weighed and estimated the fat content of each caribou, and we radiocollared 115 of 184 individuals. We verified parturition status for 96 of these radiocollared females in June. In addition, we determined presence of PSPB for captive caribou in autumn and early winter. Progesterone concentration was superior to PSPB as a predictor of pregnancy during early gestation, and a threshold value of 1.5 ng/mL was used to separate pregnant from nonpregnant females in autumn and winter. Pregnancy status was strongly related to body condition in both autumn and winter, and fatter or heavier caribou were more likely to be pregnant. Use of both PSPB and progesterone concentration allowed detection of early embryonic mortality among lactating caribou that were in poor condition.

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Key words: Arctic, body mass, caribou, embryonic mortality, fat, pregnancy, pregnancy-specific protein B, progesterone, *Rangifer tarandus granti,* reindeer.

An accurate technique for detection of pregnancy in free-living mammals is essential to answer questions involving changes in fecundity rate or age at first reproduction. While parturition rates are widely used to estimate fecundity (Festa-Bianchet 1988, Cameron et al. 1993, Festa-Bianchet et al. 1995), birth rates may underestimate conception rates because offspring experiencing early perinatal mortality may not be observed (Whitten et al. 1992), and abortion or resorption of the fetus is not detectable. Also, questions regarding nutritional control of fecundity are best answered with data collected near

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