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Tools and Technology

Contrasting Aerial Moose Population Estimation Methods and Evaluating Sightability in West-Central Alberta, Canada

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ABSTRACT Population assessment is a primary component of ungulate management, but managers are continuously under pressure to reduce survey cost. Another concern in aerial surveys is accounting for undetected animals (i.e., visibility bias). Currently, a stratified random block-survey design (hereafter, block-surveys) is used to develop moose (*Alces alces*) population estimates in several regions of North America. In this case study, we evaluated the application of distance sampling as an alternative to block-surveys in Alberta, Canada. We conducted distance-sampling surveys in 2010 and 2012 and compared density estimates, precision (coeff. of variation) and flight effort (hr/100 km^2 of survey area) to block-surveys flown in 2002, 2007, 2009, and 2012. To assess sightability bias and subsequently correct for moose missed on the transect line, we developed a predictive sightability model using 41 sightability trials with 21 radiocollared moose in 2009 and 2010. Without correcting for visibility bias on the transect line, distance sampling was more efficient in terms of flight-hours than block-surveys, while providing population estimates with similar or higher precision. Estimated sightability on the transect line was 67% in 2010 and 46% in 2012, which was used to re-scale the detection functions. Considering that population estimates from block-surveys as applied in Alberta are based on observable moose, distance sampling with a sightability correction likely provided more accurate estimates. Our results support the application of distance sampling as an alternative to block-surveys, but we suggest further investigation of methods for correcting visibility bias on the transect line.

KEY WORDS Alberta, *Alces alces*, distance sampling, moose, sightability correction, stratified random block-surveys.

Population assessment is one of the primary components of moose (*Alces alces*) management, and aerial surveys are the most practical tool for estimating moose population size in North America. Accounting for missed animals without adding substantial cost remains a fundamental concern (Ward et al. 2000). The magnitude of visibility bias, the sum of the underlying causes for incomplete detection, is especially underestimated in heterogeneous landscapes (Pollock et al. 2006). Visibility bias is a function of perception bias and availability bias. The former occurs when observers miss potentially visible animals, while the later occurs when animals are not available to be detected (e.g., they may be covered by vegetation; Marsh and Sinclair 1989). Distinction between both sources of visibility

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bias can be difficult and methods to account for visibility bias will often only correct for bias from one source (Buckland et al. 2004). For example, using dual observers only corrects for perception bias, not availability bias (Marsh and Sinclair 1989, Buckland et al. 2004). In general, studies correcting for both types of visibility bias simultaneously are rare, even though availability bias may be much larger than perception bias.

Ideally, moose populations should be estimated in small survey areas with complete survey coverage and high certainty of detection or survey-specific detection estimates based on known (i.e., marked) animals (e.g., Keech et al. 2011). However, such surveys are rarely feasible because of high costs of complete coverage in larger survey units, necessitating statistical sampling approaches. Among the most common techniques in aerial population estimation are plot or strip-based methods (Buckland et al. 2001) and for moose, either individual animals or their tracks are counted (Gasaway et al. 1986, Ver Hoef 2008). In our study area in Alberta, Canada, and several other regions in North America a stratified random block-survey design (hereafter, block-surveys) developed by Gasaway et al. (1986) is used. This method uses preliminary stratification flights to classify the survey area into survey units based on moose counts, tracks, or habitat characteristics. Upon stratification, survey units are resurveyed at random with increased effort. Similar to other block or strip-based methods, this moose block-survey design is very flight-intensive, especially for low-density moose populations, and these high costs often limit their frequency and spatial extent (Ward et al. 2000). With respect to visibility bias, block-surveys can be corrected with a sightability correction factor, traditionally developed by resurveying smaller portions of the general survey units with higher search effort (intensive survey) and estimating the proportion of moose missed during the general survey (Gasaway et al. 1986). However, sightability of moose can be low, especially in regions with dense vegetation cover where availability bias may be underestimated. Therefore, even during a very intensive search it is unlikely that all moose will be observed and moose population estimates from block-surveys will still be biased low (Quayle et al. 2001). In addition, in our study area moose densities can be below the recommended threshold of 0.39 moose/km^2 where estimating a sightability correction factor is economically feasible (Gasaway et al. 1986). Thus, usually no sightability correction factor is estimated in Alberta and results from block-surveys can only be considered minimum estimates of observable moose.

Distance sampling is gaining popularity for estimating animal abundance across many taxa, but it has been rarely used to estimate moose densities (Nielson et al. 2006). In contrast to block-surveys, where the probability of detecting a moose ($g(y)$) is assumed to be constant for all distances (y) within a fixed transect width (e.g., in Alberta commonly 200 m), distance sampling uses the perpendicular distances to estimate detection probability as a function of distance (Buckland et al. 2001, Laake et al. 2008). The most critical assumption for distance sampling is that animals on the transect center line are detected with certainty ($g(0) = 1$; Buckland et al. 2001). Double-observer approaches are commonly used to correct for perception bias on the transect line during distance sampling surveys (Manly et al. 1996), but this technique cannot account for availability bias. Sightability models that can correct for both types of visibility bias can be developed using known, marked animals by relating the probability of detection to covariates that influence sightability (Anderson and Lindzey 1996).

In this case study, we first evaluated the potential of distance sampling for moose population estimation in a survey area with moderate moose densities in west-central Alberta relative to traditionally used block-survey methodology. In general, survey methods can be compared in terms of accuracy of the estimate (i.e., moose density), precision (coeff. of variation [CV]) and survey effort. Complete census data were not available in our study area and block-survey and distance-sampling results overlapped only during 1 year. Therefore, we focused our comparison between the 2 methods mainly to flight time efficiency (hr/100 km^2) and the CV of density estimates. We also discuss density estimates for the simultaneously flown block- and distance-sampling surveys in 2012. We hypothesized that distance sampling would provide more precise moose population estimates, while requiring less survey effort. Additionally, to assess whether $g(0) = 1$, we surveyed radiocollared moose at known locations independent of distance or block-surveys. We hypothesized that $g(0) < 1$ because of visibility bias, in which case we would rescale the detection function to the estimated probability of detecting moose using a predictive sightability model for $\hat{g}(0)$. Based on previous studies, we expected canopy closure and/or group size to affect visibility of moose on the transect line (e.g., Gasaway et al. 1986, Anderson and Lindzey 1996, Quayle et al. 2001).

STUDY AREA

We conducted distance sampling and block-surveys in the 4,606-km^2 Wildlife Management Unit 353 (54°N/117°W), which was representative (i.e., vegetation composition and elevation) of a broader study area in which sightability trials were flown (Fig. 1). We flew sightability trials on radiocollared moose in the region surrounding unit 353 in west-central Alberta and east-central British Columbia, Canada. Climate in the study area is subarctic with short, wet, cool summers and long, dry, and cool winters (Smith et al. 2000). Vegetation was characterized by pure lodgepole pine (*Pinus contorta*) or lodgepole pine and black spruce (*Picea mariana*) forests on drier, low-elevation sites, and mixed balsam fir (*Abies lasiocarpa*), spruce (*Picea* spp.), and lodgepole pine forests on more mesic, higher elevation sites. Along drainages, willow (*Salix* spp.), birch (*Betula* spp.), and some aspen (*Populus tremuloides*) were interspersed with dry grassy benches. The study area experienced substantial levels of human disturbance and was characterized by high densities of forest harvests and linear developments (e.g., roads, pipelines, seismic lines; Smith et al. 2000). Elevations in unit 353 ranged from 650 m to 1,600 m, similar to elevations of the whole study area (650–1,880 m).

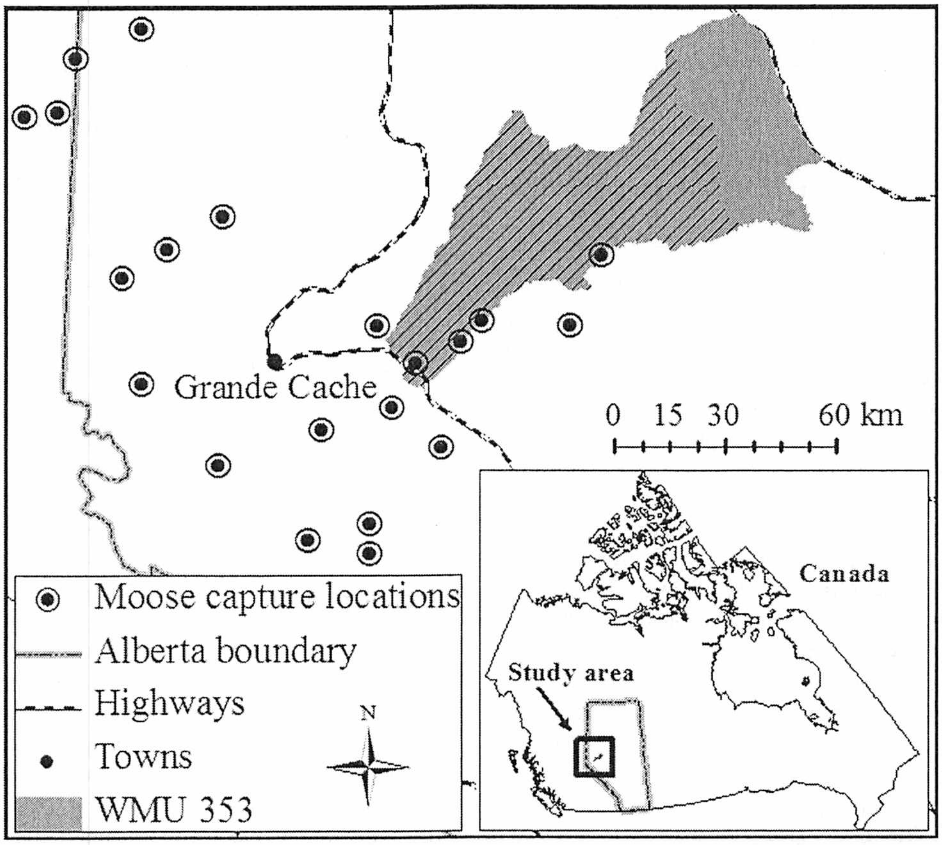

Figure 1. Study area located in west-central Alberta and east-central British Columbia, Canada. Stratified random block-surveys to estimate moose population size were conducted in 2002, 2007, 2009, and 2012 in wildlife management unit (WMU) 353 (2009 only shaded area was surveyed). For comparison of precision and flight effort, distance-sampling surveys were conducted in 2010 and 2012 in WMU 353. Sightability data were collected using radiocollared moose in winters 2009 and 2010 to develop a moose predictive sightability model.

METHODS

Stratified Random Block-surveys

We surveyed unit 353 completely during January or February in 2002, 2007, 2012, and partially in 2009 (about 0.75 of the unit; Fig. 1) using block-surveys. We conducted fixed-wing stratification in 2002, 2007, and 2009 following Gasaway et al. (1986). We flew stratification flights using a Bell 206 Jet Ranger helicopter in 2012 for simultaneous comparison of block- and distance-sampling surveys (see below). The general survey was flown following Gasaway et al. (1986), and modified by Alberta Fish and Wildlife Division following Lynch and Shumaker (1995) and Lynch (1997). Survey units were 5-minute latitude × 5-minute longitude in size and a minimum of 5 survey units from each of 3 density strata were randomly chosen and re-surveyed with a Bell 206 Jet Ranger helicopter at about 80–140 km/hour. Transect line spacing was 400 m and the survey altitude varied between 80 m and 100 m above ground level. Flight crews consisted of 4 experienced observers, including the pilot. We estimated population density and its CV following Gasaway et al. (1986) and recorded survey effort in hour/100 km^2.

Distance Sampling

Distance-sampling surveys were conducted in unit 353 on 5 days between January and March in 2010 and 6 days in January 2012. We conducted surveys during high-visibility weather conditions and complete snow coverage with a Bell 206 Jet Ranger helicopter with bubble windows. We established systematic transects every 3 minutes of latitude in 2010. In 2012 we collected distance-sampling data during stratification for block-surveys at every minute of latitude, but conditions were less suitable in 2012 than 2010 (see Discussion section). We flew transects following a Global Positioning System (GPS) at 80–100 m above ground level and 80–140 km/hour. Surveys were conducted by 4 experienced observers, including the pilot, similar to block-surveys. In addition to the pilot, the front-left observer was responsible for detecting moose near the transect line through the foot-window of the helicopter and the rear observers recorded moose on each side. The rear-right observer recorded locations of moose with an independent GPS to measure perpendicular distances from the transect line following Marques et al. (2006) in ArcGIS 9.3. Once the helicopter was perpendicular to the initial location of the observed moose, it went off the transect line to record its location. Moose groups were the unit of observation to ensure independence (Buckland et al. 2001) and included closely aggregated moose (i.e., <30 m apart). The rear-left observer recorded covariates including composition (male, female, cow–calf), moose activity (bedded, standing, or moving), light intensity (flat or bright), and topography (flat, moderate, steep). We classified canopy closure in 3 categories at 33% intervals based on figures by Unsworth et al. (1994).

Distance-sampling data were analyzed in Program Distance v. 6.0. release 2 (Thomas et al. 2010). We conducted exploratory analysis to determine a suitable truncation distance improving model fit of the detection functions (Buckland et al. 2001). Modeling the detection function followed a 2-stage approach, where first a key function was selected and then a series expansion (adjustment term) was added (Buckland et al. 2001). We considered robust combinations of key functions and up to 3 adjustment terms following recommendations of Buckland et al. (2001). Our *a priori* candidate models were a half-normal key function with the option of hermite adjustment terms, a uniform key function with the option of cosine or polynomial adjustments, and a hazard-rate key function with cosine adjustments. We further considered multiple-covariate distance sampling by including variables that were significant in the sightability probability model for the transect line (see below) to improve precision and model robustness (Marques et al. 2007). The best detection function was determined using Akaike's Information Criterion (AIC), where the model with the lowest AIC is considered the most parsimonious (Anderson et al. 1998). We examined results from goodness-of-fit tests (χ^2 GOF) and qq-plots, especially at $y = 0$, to detect potential violations to the assumptions of distance sampling (Buckland et al. 2001).

We used a size-bias regression estimator to obtain an unbiased estimate of the expected group size in Program Distance by regressing the log of moose group size against the probability of detection at distance x ($g(x)$; Buckland et al. 2001). Our systematic sampling design permitted the use of the S2 variance estimator in Program Distance, which is a post-stratification sampling scheme to estimate encounter rates for moose with greater precision (Fewster et al. 2009). The total variance of the density estimate was estimated analytically by combining the individual variances of the model components using the delta method (Seber 1982).

Sightability Trials

Moose were captured and radiocollared via helicopter net-gunning (Carpenter and Innes 1995) during winters of 2007 and 2008. Net-gunning protocols followed Alberta Fish and Wildlife Division (2005) guidelines and were approved by the University of Montana Animal Care and Use Protocol 056-56MHECS-010207. We used 7 very-high-frequency (LMRT 4; Lotek Wireless, Inc., Newmarket, ON, Canada) and 14 GPS radiocollars (G2000L; Advanced Telemetry Systems, Inc., Isanti, MN) for sightability trials (Fig. 1) and radiocollars were distributed across a range of representative habitat conditions.

We conducted sightability surveys in February 2009 and February and March 2010 on 3 days under conditions in which aerial moose surveys would be conducted in Alberta. First, we located radiocollared moose from a fixed-wing aircraft (Cessna 336/7 Skymaster) and projected a randomly located sampling block of 1.6 km × 1.6 km (buffered by 300 m to avoid edge effects) over the moose. We then surveyed sampling blocks in accordance to block-survey and distance-sampling protocols described above (e.g., in terms of survey speed, ht above ground level). Transects were spaced 400 m apart, and we recorded every moose detected (regardless of whether it was collared). Also, we assessed the same covariates as for distance sampling (see above) for each moose observation. A missed radiocollared moose was relocated immediately with radiotelemetry equipment mounted to the helicopter. We discarded trials if missed moose were moving once relocated with telemetry, because it was impossible to determine the initial location of a missed moose. We resampled radiocollared moose, but time between survey trials was ≥ 1 day.

To explore the relationship between the independent categorical covariates and the probability of detection, we initially conducted univariate tests using χ^2 contingency tables at an alpha-level of 0.05. The effects of distance on whether a moose group was observed (1) or not (0) was examined using univariate logistic regression and non-linear transformations of distance (Hosmer and Lemeshow 2000). Following univariate analyses, we developed an *a priori* set of multiple logistic regression candidate models. Categorical covariates were estimated using reference cell coding (Hosmer and Lemeshow 2000). We screened all candidate covariates for collinearity based on a Pearson's correlation threshold of $|r| > 0.6$ and included the variable with the lowest log-likelihood and smallest P-value in the model. The logistic regression model predicting moose sightability (Y), can be written as:

$$Y = \exp^U/1 + \exp^U,$$

where $U = \beta_0 + \beta_1 x_1 + \ldots \beta_k x_k$ is the linear equation of the model including the predictor covariates (x_1, ..., x_k) influencing sightability. We selected the top model using ΔAIC_c and evaluated model fit using the Pseudo R^2, Hosmer–Lemeshow's C-statistic, classification tables, and the area under the receiver operating characteristic curve (Hosmer and Lemeshow 2000). We conducted data analysis using Stata v.10.1 (StataCorp LP, College Station, TX).

Correcting for Sightability Bias at $y = 0$

In Program Distance, a correction factor for $g(0) < 1$ can be incorporated by specifying the point estimate of the detection probability on the transect line as a divisor and its standard error (SE; Buckland et al. 2004). After testing whether $g(0) = 1$ and estimating the shape of the detection function for surveys flown in unit 353 with assuming $g(0) = 1$, we corrected the detection function for $g(0) < 1$ to shift the intercept accordingly. To estimate the average detection probability for the transect line, we used the model parameters from our logistic regression model developed above to predict the probability that an observed moose would be detected at $y = 0$ during the distance-sampling surveys. We used the $\hat{g}(0)$ to predict the probability of detection for observed moose groups within 0–25 m and its SE, estimated with the delta method (Seber 1982).

Table 1. Moose population density estimates ($\hat{D}$) per km^2 from helicopter-based stratified random block (SRB) surveys (uncorrected for sightability bias) and distance sampling (DS) during 5 survey years, the survey area (km^2), upper and lower 90% confidence intervals (CI), coefficient of variation of the density estimate (CV($\hat{D}$)), the fixed-wing aircraft survey effort (hr/100 km^2), and the helicopter survey effort (hr/100 km^2) for wildlife management unit 353 in west-central Alberta, Canada.

Method	Year	Survey area	$\hat{D}$	90% CI Lower	90% CI Upper	CV ($\hat{D}$)	Fixed-wing effort	Helicopter effort
SRB	2002	4606.3	0.28	0.210	0.350	0.156	0.395	0.825
SRB	2007	4579.5	0.51	0.423	0.600	0.106	0.581	0.908
SRB[a]	2009	2772.0	0.32	0.238	0.402	0.160	0.297	0.819
SRB	2012	4606.3	0.44	0.384	0.496	0.128	0.802[c]	0.999
DS[b]	2010	4606.3	0.30	0.233	0.383	0.150	0	0.349
DS_{adj}[b]	2010	4606.3	0.45	0.270	0.735	0.293	0	0.349
DS[b]	2012	4606.3	0.42	0.358	0.485	0.076	0	0.803
DS_{adj}[b]	2012	4606.3	0.90	0.479	1.650	0.322	0	0.803

[a] Only portion of wildlife management unit 353 was surveyed.

[b] DS, the probability of detection on the transect line was assumed to be complete ($g(0) = 1$); DS_{adj}, the probability of detection on the transect line was estimated at 0.671 in 2010 and 0.463 in 2012 and the detection function was adjusted accordingly.

[c] Stratification conducted with helicopter instead of fixed-wing in 2012 (see Methods section).

Comparison of Distance Sampling and Stratified Random Block-surveys

We conducted most block-surveys (2002, 2007, and 2009) and distance-sampling (2010) surveys in different years. Because of promising distance-sampling results in 2010 (see below) we conducted one simultaneous survey trial of both methods in 2012 to standardize conditions. Because absolute moose densities were unknown for all survey years and most surveys did not overlap temporally, we focused our comparison of results on the CV of density estimates and survey effort (hr/100 km^2, including ferry time between survey plots or lines, but excluding ferry time from the airport to the survey region). We compared density estimates from both methods only for data collected simultaneously in 2012. Further, because block-surveys were uncorrected for sightability, we compared effort and precision for both unadjusted (as an approximation for standardization) and adjusted distance-sampling results (including our $\hat{g}(0)$ correction factor).

RESULTS

Stratified Random Block-Surveys

The CV of moose density estimates from block-surveys ranged between 0.106/km^2 (2007) and 0.160/km^2 (2009; Table 1). Helicopter survey effort varied between 0.83 and 1.0 hours/100 km^2 and fixed-wing survey effort varied between 0.30 and 0.58 hour/100 km^2 (no fixed-wing data for 2012; Table 1). We provided density estimates for general information (Table 1).

Distance Sampling

In 2010 we flew 33 transects for a transect length of 777.9 km and observed 124 moose in 76 groups. The observed group size varied between 1 and 4 moose ($\mu = 1.606$, SE = 0.089). Because the estimated expected group size of 1.413 (SE = 0.073) was suggestive of size bias, we used the expected group size to estimate moose density rather than the mean group size (Buckland et al. 2001). The encounter rate of moose groups (n/L) was 0.09 moose/km. We selected a truncation distance of 368 m, which represented the 95th percentile of all distances recorded, corresponding to the distance at which the probability of detection was about 15% (Buckland et al. 2001). This removed 5 data points, leaving 71 moose groups for detection function modeling.

Based on the lowest AIC and model fit close to the transect line, a half-normal model with no adjustment terms was selected (Table 2; Fig. 2). This detection function estimated a moose population density of 0.30 moose/km^2 (CV = 0.150) with a probability of detection of 0.59 (CV = 0.110). We

Table 2. The number of parameters (k), the P-value from the χ^2 goodness-of-fit test (GOF), the estimated average detection probability ($\hat{P}a$) and its coefficient of variation CV($\hat{P}_a$), and the estimated moose density ($\hat{D}$) per km^2 and its CV for all candidate conventional distance-sampling detection functions that fell within 2 Akaike's Information Criterion values (ΔAIC) from the top model to estimate moose density in Program Distance 6.0 release 2. Competing models for helicopter distance sampling in wildlife management unit 353 in west-central Alberta, Canada, are only shown for surveys conducted in 2010 because of high model selection uncertainty that year (in contrast to low model selection uncertainty in 2012).

Model key	Adjustment term	k	ΔAIC	χ^2 GOF	$\hat{P}_a$	CV($\hat{P}_a$)	$\hat{D}$	CV($\hat{D}$)
Half-normal	None	1	0.00	0.974	0.59	0.110	0.30	0.150
Uniform	Cosine	1	0.27	0.961	0.57	0.080	0.31	0.131
Uniform	Simple polynomial	1	0.28	0.981	0.65	0.040	0.30	0.113
Uniform	Cosine	2	1.40	0.969	0.65	0.160	0.28	0.131
Uniform	Simple polynomial	2	1.48	0.972	0.61	0.110	0.29	0.151
Half-normal	Hermite polynomial	2	1.52	0.967	0.64	0.181	0.28	0.210
Half-normal	Cosine	2	1.68	0.959	0.64	0.190	0.28	0.218
Hazard-rate	None	2	1.98	0.959	0.69	0.094	0.28	0.234

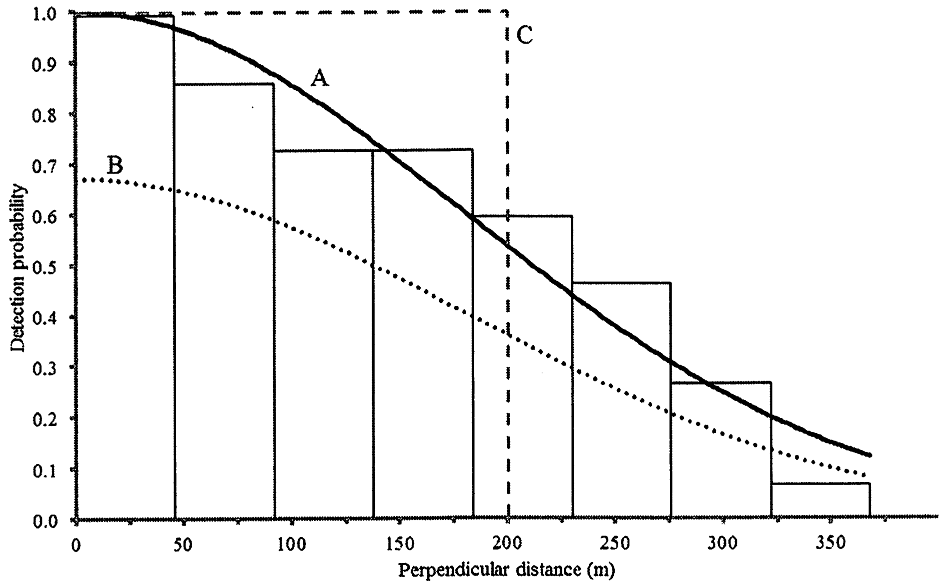

Figure 2. Histogram of moose groups detected as a function of distance from a helicopter line-transect survey in wildlife management unit 353 in west-central Alberta, Canada, during winter 2009–2010. Graph A shows the estimated half-normal detection probability function (no adjustment terms) of moose groups if no animals were left undetected along the transect line ($g(0) = 1$). Graph B shows the rescaled detection function with a probability of detection on the transect line of $\hat{g}(0) = 0.671$, estimated with a sightability model. Rescaling the half-normal detection function shifts the intercept of the function down, which adjusts for the bias of decreased detection along the transect line. Finally, rectangle C shows the area that is assumed to have equal probably of detection during stratified random block-surveys (200 m on each side of the helicopter). In this example, uncorrected stratified random block-surveys following methods outlined by Lynch and Shumaker (1995) and Lynch (1997) underestimate moose densities by the proportion of the area under rectangle C minus the area under graph B out to a distance of 200 m.

observed high model-selection uncertainty (i.e., ΔAIC < 2; Burnham and Anderson 2002) between the top model and other detection functions (Table 2). However, all competing models showed good fit, with *P*-values from χ^2-GOF tests between 0.959 and 0.981, and they yielded similar detection probabilities ($\hat{P}a$; between 0.57 and 0.69) and density estimates (between 0.28 and 0.31) with overlapping confidence intervals (CIs; Table 2 [Buckland et al. 2001]). Finally, using the multiple-covariate distance-sampling framework, the only variable selected based on AIC was moose group size and the ΔAIC to the top conventional distance-sampling model was only 1.23. Given that moose group size was already accounted for using conventional distance sampling with the size bias regression estimator and the small ΔAIC, we selected the conventional distance-sampling model for simplicity. The effective strip width was 210.70 m.

In 2012, our survey effort was higher using simultaneous block-survey stratification and we flew 75 transects totaling a transect length of 2000.7 km. We observed 401 moose in 296 groups and group sizes varied between 1 and 4 moose ($\mu = 1.366$, SE = 0.032). The estimated expected group size (1.362 with SE = 0.030) was not suggestive of size bias and the average group size was used. We selected a truncation distance of 372 m (7%) similar to the distance-sampling survey in 2010 and used the remaining 275 moose observations for detection function modeling. A half-normal key function with no adjustment terms and "canopy closure" as a categorical variable (Fig. 3) was superior by a ΔAIC of 21.36 to the next best conventional distance-sampling model, which was a uniform key model with 3 cosine adjustments terms. Because model selection uncertainty was very low, we do not report results from other models, but overall model parameters compared well between highest ranked models (W. Peters, unpublished data). The encounter rate was 0.137 moose/km. Our top model estimated a moose density of 0.42/km^2 with a CV of 0.076 (Table 1). The probability of detection of 0.60 (CV = 0.040) and the effective strip width of 223.88 m were similar to the 2010 survey.

Sightability Trials

We flew 7 sightability trials in February 2009 and 34 in February and March 2010, with each moose surveyed 1–3 times. During 41 sightability trials, 20 radiocollared moose (49%) were missed within the 200-m strips on either side of the helicopter and there was no difference in sightability by gender ($\chi^2 = 0.93$, $P = 0.628$). Univariate analysis indicated that group size, canopy closure, and terrain significantly affected sightability (Table 3). Building from these univariate relationships, the best-fitting multiple logistic regression model from our candidate model set was a function of group size, terrain, and canopy closure with all predictor covariates being significant at an alpha-level of 0.05. Further, we additionally included "distance" in our top sightability model although the predictor variable was not significant ($P = 0.727$), because our distance-sampling data clearly indicated that detection probability declines with distance from the transect line. Possibly, "distance" was not significant

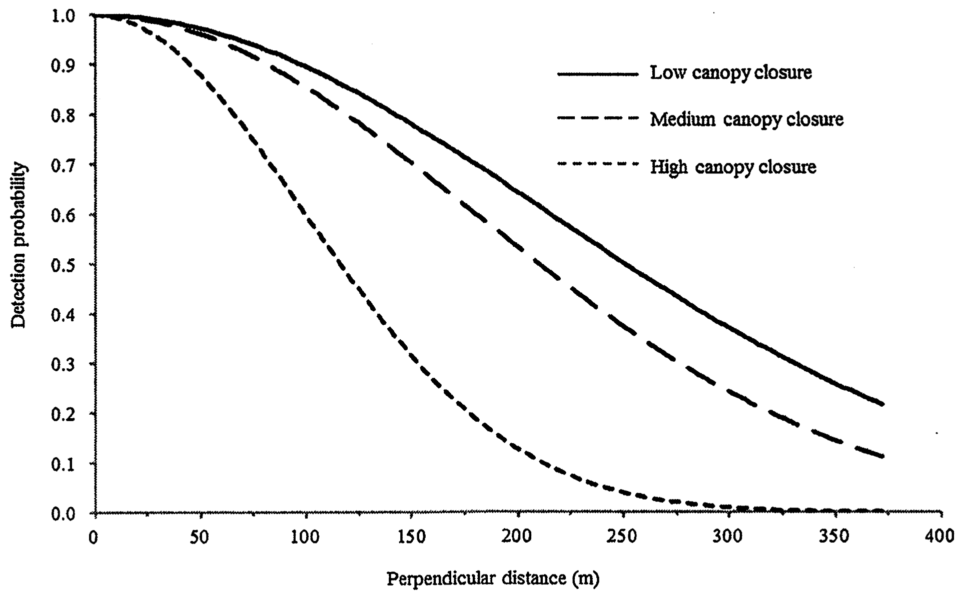

Figure 3. The estimated detection functions for moose in 3 different observed categories of canopy closure modeled in the multiple-covariate distance-sampling analysis engine in Program Distance 6.0 release 2. The helicopter distance-sampling survey was conducted in wildlife management unit 353 in west-central Alberta, Canada, in February 2012.

because of our small sample size, but not including this important variable could lead to an overestimation of sightability bias on the transect line (Buckland et al. 2001). Moose sightability decreased for single moose ($\beta = -3.71$, SE = 1.270) and increasing distance (m; $\beta = -0.004$, SE = 0.012). Sightability increased in flat topography ($\beta = 3.34$, SE = 1.393) and open canopy (0–33%; $\beta = 2.159$, SE = 1.040). The categorical variables for intermediate canopy closure (34–66%), high canopy closure (67–100%), groups of 2 moose, groups of $\geq$3 moose, and uneven terrain were combined in the intercept ($\beta_0 = -1.20$, SE = 1.641). The model predicted moose sightability well according to the Hosmer and Lemeshow χ^2 statistic ($\chi^2 = 4.01$, df = 10, $P = 0.86$). Classification success was good (overall 85.4% at a cut-point probability of 0.5), with high classification of both detected (i.e., sensitivity = 90.5%) and missed (i.e., specificity = 80.0%) moose. The receiver operating characteristic value of 0.93 indicated outstanding

Table 3. Mean (SE) perpendicular distance of detected or missed radiocollared moose from the transect line, and number of detected or missed moose in each group-size category, activity class, canopy-closure category, terrain class, and light-intensity category (on the side where the moose was detected or missed) during helicopter-based sightability surveys in west-central Alberta and east-central British Columbia, Canada, in February 2009 and February and March 2010.

Covariate	Detected	SE	Missed	SE	P
Distance (m)					
$\bar{x}$ (SE)	72.5	59.34	95.3	50.21	0.191[a]
Group size					
1	4		15		>0.001[b]
2	11		4		
>2	6		1		
Canopy closure					
Low (0–33%)	15		5		>0.001[b]
Medium (34–66%)	5		7		
High (67–100%)	1		8		
Activity					
Bedded	10		13		0.262[b]
Standing or moving	11		7		
Terrain					
Flat	19		10		0.004[b]
Uneven	2		10		
Light					
Flat	17		15		0.899[b]
Bright	4		5		

[a] P-value from univariate logistic regression.
[b] P-value from univariate χ^2 contingency analysis.

discrimination ability of the model (Hosmer and Lemeshow 2000).

Correcting for Sightability Bias at $y = 0$

In 2010 the average probability of detection of observations ($n = 10$) on the transect line ($y = 0$, here 0–25 m) was 0.671 and the SE was 0.169 (df = 9). In 2012, the average sightability on the transect line was lower, with 0.462 (SE = 0.145, df = 48) based on 49 observations. Using these values as multipliers in Program Distance changed our density estimate for moose and the associated CV to $\hat{D} = 0.45$ and CV = 0.293 in 2010 and $\hat{D} = 0.90$ and CV = 0.322 in 2012 (Table 1). We illustrated the change in the detection function with the simpler half-normal function for survey data from 2010 in Figure 2. Correcting the population size estimate for decreased probability of detection on the transect line increased the density estimate and its CV by 35.6% and 95.3%, respectively. The correction factor for $\hat{g}(0)$ contributed the most (73.8% in 2010 and 94.4% in 2012) toward the total variance of the density estimate.

Comparison of Distance Sampling and Stratified Random Block-Surveys

The density estimate from the unadjusted distance-sampling survey in 2010 had a comparable CV (0.150) to the block-surveys conducted in previous years (Table 1). In contrast, the CV (0.076) of the uncorrected distance-sampling survey was much lower in 2012 compared with block-surveys. Density estimates of simultaneously conducted distance sampling and block-surveys were similar in 2012 (Table 1). The helicopter flight effort necessary to complete the survey was higher for block-surveys requiring between 0.82 and 1.00 hour/100 km^2 compared with 0.35 hour/100 km^2 for the distance-sampling survey in 2010 and 0.80 hour/100 km^2 in 2012. Furthermore, block-surveys required fixed-wing stratification flights (survey intensity between 0.30 and 0.58 hr/100 km^2), while distance-sampling estimates did not require stratification (Table 1). No fixed-wing stratification results were available for the 2012 block-survey (see Methods section). The CVs of the adjusted distance-sampling estimates (CV = 0.293 in 2010 and CV = 0.332 in 2012) were higher than the CVs from the unadjusted distance sampling and the uncorrected block-surveys (Table 1) because of the added variance from the $\hat{g}(0)$ correction factor. No sightability correction factor was available for the block-surveys. However, correcting block-surveys would similarly increase CVs higher than adjusted distance estimates.

DISCUSSION

Distance Sampling and Sightability at $g(0)$

Previous studies indicated that distance sampling could be a viable alternative to conventional survey techniques to estimate ungulate population densities (Shorrocks et al. 2008, Young et al. 2010, Schmidt et al. 2012), but it has been rarely used to assess moose population size. Our results suggest that distance sampling provides at least equal, if not greater, precision on estimates of density than traditional block-surveys in the forested foothills of Alberta. However, we also show that in forested habitats the critical first assumption of perfect detection on the transect line (i.e., $g(0) = 1$) is likely always violated. It is possible to address this bias with a $\hat{g}(0)$ correction factor derived from a predictive sightability model or with other methods described by Buckland et al. (2004; see below). The second main assumption, that transects should be randomly distributed with respect to moose, can be accommodated with helicopters in the plains, foothills, and even mountains (e.g., Schmidt et al. 2012). Experienced pilots are required to keep the helicopter approximately on the transect line, and very long transect lines should be avoided because they may increase observer fatigue. The third assumption, that moose do not move in response to helicopter noise, appeared to be met because our data did not reflect detection of more moose groups at further distances. Lastly, we were able to ensure that perpendicular distance estimates were precise following Marques et al. (2006). Addressing these four basic assumptions of distance sampling illustrates the applicability of this method for moose population estimation. Moreover, the ease of use of the graphic user interface in Program Distance should encourage more widespread application for moose surveys.

Distance-sampling studies correcting for both types of visibility bias (availability and perception bias) are rare, and separation of both types may be difficult in most study areas (Pollock et al. 2006). For example, depending on the angle of approach, a moose bedded under a tree may be available to be detected or not. Because we used only experienced observers and sightability blocks or transects that were short enough to avoid observer fatigue, we assume that perception bias was a small component of overall visibility bias. Therefore, we reason that availability bias would be the main determinant of the proportion of missed moose in our study. This suggests that double-observer distance sampling would be insufficient to correct for visibility bias, because such methods mainly correct for perception bias (Laake et al. 2008). Thus, the application of a predictive sightability model may improve the accuracy and precision of population estimates over the double-observer approach or the use of a static correction factor.

Methods to estimate correction factors for $g(0) < 1$ with higher robustness such as a Horwitz–Thompson-like estimator (Buckland et al. 2004) are not currently supported in Program Distance and we aimed to account for both components of visibility bias in our distance-sampling population estimates by incorporating a $\hat{g}(0)$ point estimate predicted by the average sighting probability of moose at $y = 0$. Using a point estimate, as in this case study, may be robust only if factors affecting moose detection probability are fairly evenly distributed across the survey area or sample sizes are very large. Especially for 2010, we believe that our estimates for sightability bias on the transect line were reasonable given the relatively dense forest canopies and moose densities in our study area. Our adjusted distance-sampling estimates resulted in different sightability estimates in 2010 (0.671) and 2012 (0.462). We interpret these differences in sightability between the 2 years resulting from differences in survey conditions. In particular, snow conditions were much less suitable in 2012. Snow was not a covariate in our sightability model, because the model was developed with a limited range of snow-cover measurements during our surveys. Further, temperatures were higher and winds much stronger in 2012 and moose may have selected more cover in 2012 than in 2010, decreasing their sightability and introducing more variability (LeResche and Rausch 1974). Overall, we stress that our sightability model is preliminary and suggest that future research should focus on refining methods to correct for $g(0) < 1$.

The detection rate during sightability trials was low (51%), but similar to detection rates from other helicopter sightability surveys of moose in forested ecosystems. For example, sightability was 49% in British Columbia (Quayle et al. 2001), 59% in western Wyoming, USA (Anderson and Lindzey 1996), 57% in northern Ontario (Thompson 1979), and 48% in Minnesota, USA (Giudice et al. 2012). Also, our predictor covariates for sightability were supported by previous studies (LeResche and Rausch 1974, Anderson and Lindzey 1996, Quayle et al. 2001). The classification success of our model (85%), the sensitivity (detected moose, 91%) and specificity (missed moose, 80%) indicated that the model was able to overall correctly classify moose sightability very well. This result supports the potential use of our sightability model in foothills and boreal plains of west-central Alberta under similar survey conditions. In comparison, other moose sightability models correctly classified 83% (Anderson and Lindzey 1996) or 79% (Quayle et al. 2001) of all moose observations as missed or detected.

Finally, precision of distance-sampling estimates could also be improved using a multiple-covariate distance-sampling framework (Marques et al. 2007). Additional covariates in addition to distance can account for un-modeled heterogeneity by modifying the shape and scale of the detection function for different covariate values (but still assume $g(0) = 1$; Buckland et al. 2004). Our 2010 distance-sampling results were not improved, however, by including additional covariates besides group size. Because the AIC value of the model with group size was not significantly different (i.e., within 2 ΔAIC) from our top conventional distance-sampling model, and detection probabilities and population estimates were very similar, we accounted for the effect of group size using size bias regression with conventional distance sampling. However, in 2012 when more observations were collected (72 moose groups in 2010 vs. 275 moose groups in 2012), the model that included canopy closure as a categorical variable was selected by >2 ΔAIC values, indicating low model selection uncertainty. Multiple-covariate distance sampling estimated variation in the detection probability between canopy closure categories, which would have been ignored by conventional distance sampling.

Comparison of Distance Sampling and Stratified Random Block-Surveys

Although CVs of unadjusted distance-sampling estimates were similar to the CVs of uncorrected block-surveys, both methods underestimated variance because of un-modeled detection probability heterogeneity (Laake et al. 2008) and population size. We were unable to correct the block-survey density estimates and CVs, but correcting block-survey data for sightability bias would also be possible with a predictive sightability model if covariates were collected during future surveys (Quayle et al. 2001). Other approaches have been suggested, such as counting marked moose in the general survey units and estimating a sightability correction factor based on the proportion of detected tagged moose (Boertje et al. 2009) or using thermal imagery (Millette et al. 2011).

Including the sightability correction factor in the distance-sampling estimates inflated CVs compared with uncorrected block-surveys. However, estimates that adjust for missed animals should be more accurate (Buckland et al. 2001). To increase precision of the density estimate, one could increase the survey effort. Pooling distance data over different years or similar survey areas would also assist in developing a more precise global detection function for moose (Buckland et al. 2001). However most importantly, precision of adjusted distance surveys would decrease if the sightability model can be improved with a larger sample size. This would reduce the high variation resulting from the $g(0)$ correction, which contributed the most toward the total variance of our moose population density estimate. Although collecting more sightability data to improve our model would be costly initially, it would also increase precision and accuracy of the correction factor and decrease survey effort required to achieve desired CVs. A dynamic sightability correction factor based on a robust predictive model in combination with an appropriate sampling protocol could be extended to other regions as long as survey conditions are comparable.

Distance-sampling density estimates should approach true density closer than block-surveys, because assumptions of block-surveys are often not met (as we showed) and because more information is incorporated in the estimator (Dalton 1990). Surprisingly, in 2012, the density estimate derived from the uncorrected block-survey was slightly higher than the unadjusted distance-sampling estimates although we expected higher distance-sampling density estimates because of the inherent sightability correction (Buckland et al. 2001). The 90% CIs of the density estimates of both methods overlapped, but distance sampling produced a density estimate with higher precision. In Alberta, block-surveys use a (half) strip width of 200 m and it is possible that sightability may be relatively constant up to that distance. This is supported by the non-significance of the covariate "distance" in our sightability model, and the effective strip widths of 210–220 m from our distance surveys. Lastly, block-surveys allow departures of the helicopter from the transect line, and more variability in airspeed and height or circling above closed habitat (Gasaway et al. 1986). These variations may increase moose sightability and lead to less biased density estimates than expected.

A comparison of the unadjusted distance sampling and uncorrected block-survey estimates seemed to indicate an increase in moose population size between 2010 and 2012. However, the 90% CIs overlapped between 2010 and 2012, and therefore we can only conclude that the true population parameter lies between the lower and the upper CI.

Although it is troubling that we cannot detect an almost twofold change, we emphasize that our goal was to demonstrate the utility of distance sampling for moose population estimation, and suggest development of a more rigorous sightability estimator. In general, several years of survey data should be collected to determine trends in population size (Boertje et al. 2009). However, moose densities may have actually increased in our study area. First, unit 353 has experienced extensive forest harvest, with the potential to produce higher moose densities (Rempel et al. 1997), especially when predation pressure is low (Boertje et al. 2009). In our study area, wolf (*Canis lupus*) harvests are high in order to recover the declining population of caribou (*Rangifer tarandus*). Concurrently, moose harvest rates declined between 2010 and 2012. In 2010 and 2011, the harvest goal was 35% of antlered and 20% of antlerless moose, but only 36–50% of the harvest quota was met (D. Hervieux, Alberta Sustainable Resource Development, unpublished data). We also observed high moose survival rates, with 1 death out of 33 radiocollared adult moose that were monitored for ≥ 1 year between 2008 and 2011 (W. Peters, unpublished data). Finally, all captured female moose were pregnant ($n = 17$; Haigh et al. 1993). Despite these biological reasons that moose density could have increased, the overlapping 90% CIs emphasize the need to improve the sightability component of distance sampling for moose.

Regardless of discussion of the comparative precision of the different methods, the unadjusted distance-sampling survey was more than twice as efficient (measured in helicopter-hours/100 km^2 of survey area) than uncorrected block-surveys. For example, assuming approximately 780 Canadian Dollars (C$)/helicopter flight-hour, the survey cost of distance-sampling estimates was about 7,000 C$ cheaper than block-survey estimates in 2012. This does not include cost of personnel or stratification. But for example, using the average fixed-wing flight-hour/100 km^2 from 2002, 2007, and 2009 (0.424 hr/100 km^2), stratification of the entire unit 353 (4,606 km^2) required about 19.5 hours. Thus, at an hourly fixed-wing rate of about 275 C$, stratification added approximately 5,400 C$/survey. Consequently, higher efficiency of distance sampling (8,000 C$ + 5,400 C$ savings in unit 353) compared with the block-survey design could allow population surveys to be conducted more frequently. For distance sampling, large or small management units can be surveyed with the same effort given they have the same moose density, because the absolute size of the sample is important, rather than the fraction of the population sampled (Buckland et al. 2001). In contrast, block-survey effort to achieve density estimates with a certain CV is dependent on stratification accuracy and precision, variance among strata, size of strata, or moose density (Gasaway et al. 1986).

MANAGEMENT IMPLICATIONS

In forested survey areas as in Alberta, moose abundance estimates will be biased low without a rigorous sightability estimate. This could lead to under-harvesting moose populations, failing to detect real population changes, and failing to meet harvest potential. We also show that failing to account for sightability <1 also overestimates precision in addition to underestimating population size—both undesirable outcomes for moose managers. Most importantly, if we accept that visibility bias remains without a $g(0) < 1$ correction and distance-sampling estimators are at least as accurate as conventional methods, distance sampling was always more efficient than traditional block-survey methods. Distance sampling will especially outperform traditional block-survey designs in medium- to high-density moose populations because precision of the estimator is dependent on moose encounter rates, not the proportion of the population surveyed.

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