VISIBILITY OF MOOSE IN A TEMPERATE RAINFOREST

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ABSTRACT: Aerial surveys are the principal methods used to estimate populations of moose (*Alces alces gigas*) in Alaska. Accounting for missed animals during aerial surveys is problematical, especially in forested habitats; incorporation of a visibility correction factor to account for the proportion of animals missed is known to improve accuracy of population estimates. Our purpose was to study factors affecting visibility of radio-collared moose during aerial surveys in a temperate rainforest on the Yakutat Foreland, Alaska, USA. Wildlife managers in the area typically assume they observe only 50% of moose during surveys regardless of widely varying conditions. We used logistic regression to examine factors that influenced visibility including vegetation, light conditions, snow cover, and sex, age, and group size of moose. We then used logistic regression to develop a simpler model that only contained variables easily measured during aerial surveys: forest cover, snow cover, light, open versus vegetated habitat, and group size. We used that model to estimate a visibility correction factor. The mean correction factor was 1.304, ranging from1.005-2.138, yielding a population estimate of 699 (90% CI = 671-724) moose from a survey count of 595 animals. Our correction factor was within the range reported for other populations of moose, and lower than the correction factor (2.0) currently used in this area. We conclude that application of site and time-specific visibility models is critical when estimating populations of large ungulates, especially in forested habitats.

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Population estimates of ungulates based on aerial surveys are subject to error associated with the inability to detect animals that are present (visibility bias; Timmerman 1993, Anderson and Lindzey 1996). Environmental factors such as rugged terrain or dense cover may obscure visibility of animals, and differences in habitat selection and morphology by sex and age groups may make some animals more difficult to observe, thereby biasing their visibility (Peek et al. 1974, Thompson and Veukelich 1981, Bowyer et al. 2002, Bowyer 2004). Grouping behavior, activity of individuals (i.e., lying or standing), weather, and ground conditions (e.g., snow cover) can measurably affect visibility of animals. Many of these problems are manifest in aerial surveys of moose (*Alces alces gigas*) in temperate rainforests on the Yakutat Foreland of southeast Alaska, USA where snow conditions that facilitate detecting moose can be intermittent, weather conditions for flying are frequently poor, and forest cover is dense and widespread. Ideally, population surveys should be conducted during the mating season when moose are more active and sexes aggregated (Miquelle et al. 1992, Oehlers et al. 2011). Because Yakutat does not generally receive sufficient snowfall to enhance visibility before sexes spatially segregate after mating and males cast antlers, identification of sex is difficult.

Sightability (also referred to as detectability or visibility) is the probability that an animal within the field of search for an observer will be seen by that observer (Caughley 1974). That probability can be expressed as a scalar, or correction factor for visibility bias, which is then multiplied by the number of moose observed to obtain a more accurate population estimate than an uncorrected count (Steinhorst and Samuel 1989). Correction factors for visibility bias (commonly referred to as Sightability Correction Factors or SCFs, and hereafter referred to as correction factors) that account for the proportion of animals undetected during aerial surveys are known to improve the accuracy of population estimates (Timmerman 1993), particularly for areas with extensive forest cover and variable weather conditions that occur on the Yakutat Foreland. Survey precision incorporates both the variance of total moose sighted and the variance of the correction factor (Timmerman 1993). Logistic regression is commonly used to develop correction factors for ungulates (McCorquodale 2001, Quayle et al. 2001, McIntosh et al. 2009); this method is designed for use with binomial dependent variables (observed or not), and can accommodate continuous and categorical independent variables (Hosmer and Lemeshow 2000).

We studied factors affecting visibility of moose on the Yakutat Foreland to improve population estimates from aerial surveys. We derived a series of models predicting correction factors using data from visibility trials from aerial surveys involving radio-collared moose. We examined the influence of temporal and weather-related variables such as month, time of day, cloud cover, light intensity, precipitation, and wind speed on visibility. We considered effects of environmental variables such as snow, forest, and vegetation cover on visibility of moose. In addition, we investigated the influence of sex, age, group size, sex and age composition of groups, activity, and intensity of site use on visibility. Logically, we expected that forest cover and lack of snow cover would reduce the probability of moose being observed, and that visibility would increase with increasing snow cover. We also hypothesized that visibility would decline with smaller group size or if moose were bedded. Further, we postulated that age or sex would affect visibility, because of morphological differences or if age groups and sexes used different habitats.

We derived a model containing all of the covariates that we determined were important predictors of visibility, and a second model that included only those variables for which information could be obtained from routine aerial surveys. The full model was needed to consider all variables, including life-history characteristics such as sex and age and their potential influence on visibility, and would be useful in areas where sex and age composition is known or could be determined during surveys. We considered the second model to be more appropriate for management purposes in our study area, because it did not require data that could only be obtained reliably from radio-collared animals, and is more appropriate for late-winter surveys when sex cannot be accurately determined. Finally, we applied the management model to a sample data set to estimate the density of moose within our study area. Ours is one of few studies to examine factors influencing visibility of ungulates in a northern temperate rainforest, and our results should be useful to biologists managing ungulates throughout the northern coastal forests of the Pacific Northwest.

STUDY AREA

We conducted research on the Yakutat Foreland of the Tongass National Forest, located along the southeast coastline of Alaska (Fig. 1). Our study area of approximately 1,280 km^2 encompassed most of the Foreland, and included ~80 km of coastline extending from

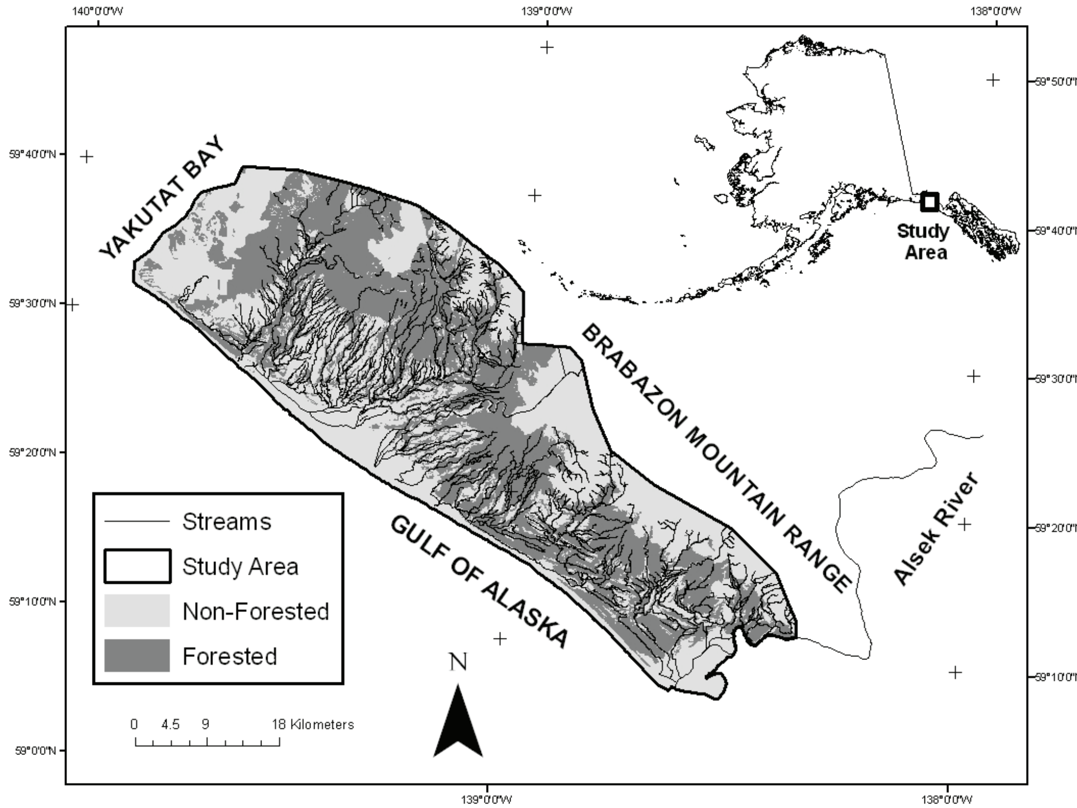

Fig. 1. Study area for developing a visibility model for moose on the Yakutat Foreland, Alaska, USA, 2003-2004.

Yakutat Bay to Dry Bay. Distance between the coast and mountain ranges varies from 8-24 km. There are several large rivers as well as numerous smaller streams distributed throughout the study area (Fig 1).

The Yakutat Foreland (Lat. 59°20' N, Long. 139°0' W) falls within the humid temperate domain, characterized by year-round cloudy, cool, and wet conditions (Shephard 1995). The mean annual temperature was 4.1° C and the mean total precipitation was 381 cm (combined snow and rain) from 1971-2000 (NOAA 2005). The mean temperature during this same time period was -3.4° C during January (the coldest month) and 12° C during July (the warmest month). Total snowfall during the study was 345 cm; mean daily snowfall was 3.0 cm and the mean snow depth was 20 cm.

Other than a few rolling bedrock hills, most of the Foreland is of low relief (average elevation 20 m; Shephard 1995), and is a mosaic of forests, wetlands, and shrublands (Shephard 1995). Forested areas are dominated by Sitka spruce (*Picea sitchensis*), and a small percentage of the upper canopy is composed of black cottonwood (*Populus trichocarpa*), western hemlock (*Tsuga heterophylla*), and mountain hemlock (*T. mertensiana*). Shephard (1995) documented 20 different forest communities on the Foreland, with canopy cover ranging from 1-80% and averaging 60% for the common forest communities, with stand heights ranging from 15-47 m. Nonforested areas include wetlands and shrublands composed primarily of graminoids, forbs, and shrubs including several species of tall and low willow (*Salix* spp.*)* ranging from 1-6 m in height, and Sitka alder (*Alnus sinuata*) up to 4 m. Nonforested areas dominate the coastal areas on the western half of the study area, with patches of spruce dispersed on the heaths and adjacent to some riparian zones; contiguous forested stands predominate the remainder.

The most recent aerial surveys (2002) conducted in the Forelands by Alaska Department of Fish and Game (ADFG) estimated a density of 0.5 moose/km^2 with a composition ratio of 19 males:100 females:14 young (N. L. Barten, ADFG, pers. comm.). Total count surveys by parallel transects set approximately 0.4-0.5 km apart are conducted in the non-forested portions of the Foreland by ADFG in late autumn as soon as snow covers most of the ground, but often those conditions do not occur until well into winter. The ADFG assumes that 50% of moose along transects are detected; consequently, the observed number of moose is doubled to estimate population size. That correction factor, however, has never been empirically evaluated or assessed. In addition, ADFG does not survey forested portions of the Forelands because of low (unknown) visibility, which constitutes about one-half of the study area.

Other large mammals that occur on the Forelands include brown bear (*Ursus arctos*), black bear (*U. americanus*), and gray wolves (*Canis lupus*). Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) occupy some of the islands offshore but are uncommon on the mainland. In addition, moose are an important part of the subsistence economy (Ballew et al. 2006, Schmidt et al. 2007).

METHODS

Capture and handling

Twenty-two female and 16 male moose were darted from a helicopter by ADFG personnel with Palmer CAP-CHUR equipment with the immobilizing drugs carfentanil and xylazine (Roffe et al. 2001) during March and November 2002, and March and December 2003. Dosages ranged from 3.0-5.0 mg of carfentanil and 100-130 mg of xylazine depending on time of year, sex, and animal condition. All capture and handling methods followed guidelines established by the American Society of Mammalogists Animal Care and Use Committee (1998) for research on wild mammals. Our protocols were approved by independent Institutional Animal Care and Use committees at the University of Alaska Fairbanks (protocol # 04-26) and the ADFG (protocol # 03-0001).

We fitted moose with GPS radio-collars (Model 4000, Lotek Wireless, Ontario, Canada) that recorded locations 4 times daily, or standard VHF radio-collars (Model MP2-MPP4, AVM, Colfax, California and Model 600NH, Telonics, Mesa, Arizona). We programmed both types of collars to release remotely relative to time of deployment (typically 1.5 yr). A lower incisor was removed from each moose to determine age from cementum annuli (Gasaway et al. 1978). Naltrexone (350-1300 mg) and tolazoline (400-800 mg) were subsequently administered and moose were monitored until they recovered from the immediate effects of immobilization. We also monitored each moose by aerial survey for 1 month post-capture to assess capture-related mortality. Three females died or their collars malfunctioned within 1 month of capture, and were not included in the visibility trials.

Visibility trials

We flew surveys to locate collared moose between 24 November 2003 and 18 March 2004 using a Cessna® 185 fixed-wing aircraft. Timing of sampling and type of aircraft were the same used by ADFG when conducting moose surveys. We defined a visibility trial as the effort by the survey crew to count all moose within a 5 km^2 sampling quadrat (square survey block) that included a radio-collared moose on a particular day. The aerial-survey crew was composed of the pilot, the primary observer in the front seat, and a secondary observer in the back seat behind the pilot. We attempted to control as many factors as possible, such as using the same aircraft, pilot, and primary observers for all trials. One pilot and 2 primary observers with >150 h of moose survey experience were used in the trials, with 8 secondary observers ranging in initial experience level of 6-8 (40-150 h of moose survey experience) on a Lickart scale of 1-10.

Our trial procedure was similar to that of Quayle et al. (2001). Trials to locate individual radio-collared moose were separated by ≥3 days to reduce autocorrelation among locations. The extremely large home ranges of moose on the Foreland (mean seasonal home ranges varied from 24.3-86.3 km^2; Oehlers et al. 2011) made this interval a reasonable choice for attempting to achieve independence among locations. Frequencies for the subset of moose to be sampled during a flight were programmed into a receiver (model R4000, ATS, Isanti, Minnesota) and scanned while flying at an altitude of 245-300 m above ground level. Once a signal was received, the primary observer obtained the general position of the moose without identifying an exact location. We used a laptop computer equipped with Baker Geolink Sketchmapping software (Michael Baker Corporation, Moon Township, PA) to record our location and flight path so that the telemetry operator (primary observer) could identify the approximate location of the collared moose on the map without viewing the ground, thereby minimizing observer bias. The pilot and secondary observer also avoided scanning the ground in the immediate survey area to prevent detection of the target animal before beginning the survey. The survey crew noted if the collared moose was accidentally spotted by either observer while obtaining the general location; those observations were eliminated from analyses.

The primary observer then delineated a 5 km^2 (2.23 km x 2.23 km) quadrat (Quayle et al. 2001) centered around the general location of the identified moose on the laptop computer using a 0.4 km grid overlay on the screen. Because the location of the moose was inexact, the actual location of the moose was not centered within the quadrat. Consequently, observer bias was minimized because none of the observers knew where in the quadrat to expect to find the radio-collared moose. The pilot then flew over the quadrat along transects spaced 0.4 km apart, which were delineated by the grid overlaid on the screen. The laptop screen displayed our flight path, allowing the pilot to navigate and follow the specified transect lines. The pilot flew the aircraft at an altitude of approximately 185 m and speed of about 130 km/h, resulting in a search intensity of approximately 1.0 min/km^2. We circled the location of each moose sighted in the quadrat to identify and record information on all of the variables included in the Appendix, and recorded the location of the moose using the Sketchmapper software. If the targeted moose was not sighted during the survey, we located that animal via telemetry and recorded the same information.

Forest cover was measured at 2 scales and recorded as “0” if the predominant vegetation within both a 10 m and 250 m radius of the radio-collared moose was nonforested, and “1” if this same area was predominantly forested (including a range of canopy covers). Vegetation cover was defined as “0” if the predominant vegetation was open habitat such as muskeg, meadow, sand, or gravel bar, or “1” if there was vegetation such as tall shrubs or forest that could obscure visibility of the moose. Percent vegetation was recorded as a categorical variable (1-3) representing percentage of vegetative cover (shrubs or trees) within a 10 m and 250 m radius of the observed moose that could obscure visibility of that moose.

We defined a “group” as 1 or more moose within 50 m of each other (Siegfried 1979, Molvar and Bowyer 1994, Bowyer et al. 2001) to encompass the complete range of sociality for this species (Monteith et al. 2007). We categorized age of non-collared animals as young (<1 year) or adult (≥1 years old) through visual observation. We expected a high pregnancy rate of yearlings (Boer 1992), because preliminary data indicated a predator-limited population (Bowyer et al. 2005, Oehlers et al. 2011). Consequently, we considered yearling females as adults (Monteith et al. 2007). Moreover, distinguishing between yearlings and adults during aerial surveys in winter was difficult, and further distinguishing of ages beyond yearling or adult was not possible during aerial surveys.

We used ArcView 3.2 geographic information software (ESRI, Redlands, CA, USA) to plot GPS locations for moose and determine elevation and distance to the coast for each moose. Elevation was extracted from a raster data layer provided by the U.S. Forest Service (USFS), which was based on USGS digital elevation model with 20-m resolution. Distance from shore was calculated with the USFS shoreline polygon layer for the study area.

Statistical analyses

Detection of a radio-collared moose during visibility trials was coded 1 if detected and 0 if not observed. We used SAS 9.1 (SAS Institute, Cary, NC) for all statistical tests, and adopted an $\alpha = 0.05$. We used multivariate logistic regression to model visibility. Our suite of potential predictors of detection included parameters such as sex, age, group size, forest cover, snow cover, light conditions, aircraft speed, and experience of observers (Appendix). Group size was squared because the untransformed covariate was not linear in the logit. We included the identification of individual moose as a coded variable to control for making repeated measures of individual moose. We reduced potential multicollinearity among independent variables by testing for strong correlations between pairs of covariates ($|r| \geq 0.7$) and preventing their simultaneous inclusion in logistic regression models. During initial model screening, we also examined variance inflation factors (VIF) and tolerance (Tol) of independent continuous and discrete variables to identify intercorrelated variables. Values of VIF <10 and Tol >0.40 were considered acceptable (Neter et al. 1996, Allison 2001). We ultimately considered 16 variables from the initial set of 27 candidate predictor variables. We then screened these remaining covariates using forward step-wise logistic regression (PROC LOGISTIC; Agresti 1990) with an alpha to enter of 0.15 (Hosmer and Lemeshow 2000, p. 118) and alpha to remove of 0.3, and backward logistic regression with alpha to remove of 0.3, to define a broad initial set of candidate models. We restricted the number of covariates within any candidate model to ≤8, because our sample size of visibility trials was 88; our sample size precluded a global model. Our sample size also precluded an all possible regressions approach. We used Hosmer and Lemeshow tests for goodness-of-fit (Hosmer and Lemeshow 2000) to determine the appropriateness of the logistic models.

Once we had established a large set of candidate models, we used Akaike's Information Criterion (AICc) (Burnham and Anderson 2002) to select model variables. Age and sex were included in most of the top candidate models. Classifying moose into discrete age classes (i.e., beyond yearling or adult) is not possible from aerial surveys, and correct classification of sex is difficult once males have cast their antlers, so we repeated this same process omitting age and sex to allow development of models that did not rely on data from captured moose. Accordingly, we developed overall explanatory models that included life-history characteristics, as well as management models which included variables that could be measured easily during aerial surveys alone. We used model-averaging procedures to derive composite explanatory and management models (Burnham and Anderson 2002, Giudice et al. 2012). We only considered candidate models with AIC_c Δ values ≤4 for inclusion in composite models. We calculated relative effects (risk ratios) for covariates included in our composite models (Farmer et al. 2006). Relative effects estimate the change in relative probability of detection for an incremental change in magnitude of a predictor variable (Riggs and Pollock 1992). We evaluated relative effects to determine the comparative importance of independent variables in affecting the probability of detection. In general, relative effects >2.0 or <0.5 indicated large effects of covariates on detectability (Riggs and Pollock 1992).

For demonstrative purposes, we applied our composite management model to existing surveys of the moose population that were conducted by ADFG on the Yakutat Foreland from 30 November-4 December 2005 using their survey methodology previously described in Study Area. Model variables were assessed for each individual or group of moose observed during these surveys, and then the corresponding correction factor was calculated for each observation and multiplied by the number of animals in that observation. These corrected estimates were then totaled to derive a mean population estimate and the range of population estimates using the upper and lower correction factor based on the 90% CI (Becker and Reed 1990, Anderson and Lindzey 1996, White 2005). These data included 262 observations of single moose or groups and 595 total moose observed.

RESULTS

The median age for both females (n = 22, range = 3-13 yr) and males (n = 16, range = 1-10yr) was 6 years. We conducted 88 trials involving 55 radio-collared females and 33 males; each was surveyed 1-4 times ($\bar{x}$ = 2.3, SD = 0.70). Snow conditions were generally adequate for aerial surveys from November-January and during the last 20 surveys conducted in March, but comparatively poor during February. We observed 254 groups of moose.

Radio-collared animals were sighted in 71% of the surveys; males were observed in 76% and females in 66% of the trials. Radio-collared animals were detected in 82% of trials in nonforested areas, and in 27% of trials in forested cover. Animals 1-3, 4-6, 7-10, and 11-13 years old were detected in 89, 55, 75, and 100% of trials, respectively. Mean (± SE) group size of collared animals was 3.7 ± 0.4. Radio-collared animals were observed in open (31%), shrub (52%), and forested (17%) habitat during the trials. The location of females and males in nonforested and forested habitat was similar; 82 and 85% and 18 and 15%, respectively.

Logistic regressions

Forest cover, vegetation cover, and percent cover were each correlated ($|r| \geq 0.7$) between the 2 scales of measurement (10 m and 250 m). We considered the 10-m scale more easily estimated and likely to be consistent between observers; consequently, we chose to include the 10-m scale for each of these variables for consideration in our models. Following tests for collinearity, variance inflation factors, and tolerance, candidate models for overall visibility included the parameters age, group size, forest cover, light, snow cover, experience secondary, and wind speed start (Table 1). Age, group size^2, forest cover, and snow cover were included in each of the top 3 candidate models. Visibility increased by 38% for each additional year of the moose aged, and by 75% for each additional (increasing) experience level of the secondary observer (Table 2). Overcast skies (versus sun) increased visibility by 175%. Visibility increased with group size^2 and speed of the plane (flight speed ranged from 129-145 km/h), but effects were small. Visibility declined under forested cover (94%), snow cover of 0-33% (76%) or 34-66% (82%), and for females (23%).

Candidate models derived for management purposes (omitting sex and age) included group size^2, forest cover, snow cover, light conditions, and vegetation cover (Table 3). Similar to the overall model, detectability increased with group size, nonforested and open habitat, overcast skies, and higher snow cover in the composite management model (Table

Table 1. Number of model parameters (k), differences in Akaike's Information Criterion (AIC_c) scores (Δ) and AIC_c weights (*wi*) for candidate visibility models for moose on the Yakutat Foreland, Alaska, 2003-2004.

Model	k	Parameters	$AIC_c\Delta_i$	$AIC_c w_i$
A	5	Age, group^{2a}, forest cover, light, snow	0.000	0.4428
B	7	Age, sex, observer2[b], speed[c], group^2, forest cover, snow	0.7520	0.3041
C	6	Age, sex, observer2, group^2, forest cover, snow	1.8083	0.1793
D	4	Group^2, forest cover, snow, light	3.5851	0.0738
E	16	Saturated[d]	18.8200	0.0000

[a]Group size^2.

[b]Experience secondary.

[c]Wind speed start.

[d]Includes survey start time, temperature, group, sex, age, experience primary, experience secondary, wind speed start, flight speed, group size^2, forest cover, vegetation cover, percent cover, activity, light, snow cover, and elevation.

4). Application of the composite management model to our sample data yielded a range of correction factors from 1.005-2.138 for each observation. The mean correction factor was 1.304, and mean upper and lower (90% CI) correction factors were 1.215 and 1.390, yielding a population estimate of 671-724 animals (x = 699 moose) from an uncorrected count of 595 animals.

DISCUSSION

Both our overall and management models included group size, forest cover, and snow cover as covariates of visibility. Lack of snow cover strongly reduced visibility of moose and confirmed our hypothesis that visibility would be higher as snow cover increased. Nonetheless, that relationship was not linear because visibility was similar between snow cover of 0-33% and 34-66% (57% and 54%, respectively). We believe that snow cover of 34-66% did not improve visibility because snow was still sufficiently patchy to obscure many moose against a dark background. We hypothesize that no snow cover actually may be preferable to patchy snow because patchy snow conditions may fatigue observers more quickly than uniform coverage.

Table 2. Regression coefficients and risk ratios (RR) for selected composite overall explanatory model for visibility of moose on the Yakutat Foreland, Alaska, 2003-2004. Confidence intervals did not overlap 1 in the individual models.

Variable	β	SE	RR	RR 90% CI
Intercept	-14.284	16.844	n/a	n/a
Age	0.325	0.169	1.384	1.047-1.829
Group size^2	0.074	0.075	1.077	0.951-1.219
Forest cover	-2.849	0.945	0.058	0.012- 0.275
Light	1.010	1.157	2.746	0.407-18.524
Snow cover 1 (0-33%)[a]	-1.419	1.201	0.242	0.033-1.755
Snow cover 2 (34-66%)[a]	-1.661	1.059	0.190	0.033-1.090
Sex[b]	-0.256	0.352	0.774	0.433-1.384
Flight Speed	0.063	0.075	1.065	0.941-1.205
Experience Secondary	0.562	0.693	1.754	0.559-5.504

[a]Snow cover is relative to the reference variable of level 3, 67-100%.

[b]Sex is relative to the reference variable of male.

Forest cover has been included in visibility models for both North American elk (*Cervus elaphus*; Samuel et al. 1987, Bleich et al. 2001) and moose (Peterson and Page 1993, Anderson and Lindzey 1996, Drummer and Aho 1998, Quayle et al. 2001). In our study area, coniferous tree species predominate in the forested areas, obstructing visibility of moose year-round, whereas vegetation in non-forested areas included alders and willows that

Table 3. Number of model parameters (k), differences in Akaike's Information Criterion (AIC_c) scores (Δ), and AICc weights (*wi*) for candidate visibility management models for moose on the Yakutat Foreland, Alaska, 2003-2004.

Model	k	Parameters	$AIC_c\Delta_i$	$AIC_c w_i$
A	4	Group[2a], forest cover, snow, light	0.0000	0.5404
B	5	Group[2], forest cover, vegetation cover, snow, light	1.0609	0.3180
C	3	Group[2], forest cover, snow	2.6844	0.1442
D	14	Saturated[b]	14.4800	0.0004

[a]Group size[2].

[b]Includes survey start time, temperature, group, experience primary, experience secondary, wind speed start, flight speed, group size[2], forest cover, vegetation cover, percent cover, activity, light, snow cover, and elevation.

do not retain leaves during winter and have less effect on visibility.

Group size was less influential on visibility than either forest or snow cover. Group size affects visibility of elk (Samuel et al. 1987, Bleich et al. 2001, McCorquodale 2001), feral horses (*Equus caballus*; Ransom 2012), and mule deer (*Odocoileus hemionus*; Ackerman 1988); logically, larger groups are generally more visible. Moose tend to aggregate in open areas in Alaska during rut (Miquelle et al. 1992, Molvar and Bowyer 1994); therefore, if snow conditions are adequate, visibility would be highest during the peak of rut. Visibility did not differ when moose were standing or bedded. Light condition also was an important predictor of visibility as moose were more visible in overcast conditions when glare and shadows were minimized. Fox (1977) noted similar issues with glare from snowfields during mountain goat (*Oreamnos americana*) surveys conducted in clear weather in southeast Alaska.

Visibility increased with increasing age

Table 4. Regression coefficients and risk ratios (RR) for selected composite management model for visibility of moose on the Yakutat Foreland, Alaska, 2003-2004. Confidence intervals did not overlap 1 in the individual models.

Variable	β	SE	RR	RR 90% CI
Intercept	0.048	0.905	n/a	n/a
Group size[2]	0.070	0.038	1.073	1.007-1.142
Forest cover	-2.551	2.190	0.078	0.002-2.894
Light	1.441	0.920	4.225	0.926-19.279
Snow cover 1 (0-33%)[a]	-1.028	0.935	0.358	0.076-1.673
Snow cover 2 (34-66%)[a]	-1.377	0.897	0.252	0.057-1.109
Vegetation cover	-0.284	0.383	0.753	0.400-1.416

[a]Snow cover is relative to the reference variable of level 3, 67-100%.

of moose, and was higher for males than for females, although the relative effect of sex was small. Greater visibility of males could distort male:female ratios and result in the underestimation of the female population, unless a correction for differential visibility is incorporated. Although several other studies of ungulate visibility reported that sex or group composition was accounted for in multivariate models because of correlation with other covariates such as group size or vegetation (Anderson and Lindzey 1996, Bleich et al. 2001, McCorquodale 2001), sex in our model was not correlated with any other variable. The effect of sex on visibility probably occurred because of physical differences between the sexes; larger body size, darker color, and presence of antlers in early winter likely explain the higher visibility of males. Solberg et al. (2010) also reported that male moose were observed by hunters with a 1.26 higher probability than females during the hunting season, and suggested that this difference was reflective of fundamental differences in antipredator behavior, including risk taking (such as use of open habitat), activity level, and space use. Although age was not significantly correlated with other variables, all observations of the oldest animals were in large groups in non-forested habitat; therefore, other covariates besides age were likely more influential on visibility. We did not detect an influence of age and sex composition of groups on visibility.

We attempted to standardize flight speed during surveys, and weather conditions resulted in a minimal range of speeds (130-145 km/h). Remarkably, visibility of moose increased with speed of the plane. Nonetheless, flight speed was in only 1 of the top 4 candidate overall explanatory models, its relative effect was small, and the 90% CI included 0; within the range of speeds we flew, this variable was likely of minimal importance. Experience level (1-10) of the second observer increased visibility by 75% in the explanatory model; however, the effect was highly variable, and was not included in the management model. Although experienced observers have developed a search image, and therefore may be more likely to observe moose, observer experience is difficult to quantify, and experience level changes over the course of visibility trials. Previous studies have documented differences in visibility related to observer experience (LeResche and Rausch 1974, Caughley et al. 1976); however, recent studies have noted little effect on visibility when observers were experienced (Ackerman 1998) or when observer experience correlated with other variables in the model (Samuel et al. 1987, Anderson and Lindzey 1996). All second observers in our study were experienced in moose surveys (i.e., 40-150 h of moose survey experience); consequently, our model will be most effectively applied when using experienced observers, a conclusion also reached by Quayle et al. (2001).

Our overall visibility of moose was 70.5% and similar to that in Quebec (Crête et al.1986; 73%), Alberta (Rolley and Keith 1980; 64%), and Isle Royale, Michigan (Peterson and Page 1993; 78%), and higher than in Minnesota (Giudice et al. 2012; 38-56%), Michigan (Drummer and Aho 1998; 39%), Wyoming (Anderson and Lindzey 1996; 59%), and Alaska (LeResche and Rausch 1974; 43-68%). Correction factors for moose range from 1.03-3.2 (Oosenberg and Ferguson 1992, Timmerman and Buss 1998) and are generally higher in areas of denser cover and higher moose density (Gasaway et al. 1986, Peterson and Page 1993). Comparisons of visibility rates may be tenuous, however, because of differences in aircraft type (Crête et al. 1986), number of observers, search intensity, and habitat (Anderson and Lindzey 1996). Our results are within the range of correction factors reported for moose, but emphasize the variability in visibility and the need to develop correction factors specific to a particular area and time frame.

The use of a dynamic correction factor, such as that developed with a visibility model, is superior to the use of a static correction factor. Our modeled correction factor is offered as an alternative to the use of both a calculated SCF (SCF_c) and an observed SCF (SCF_o) as described by Gasaway et al. (1986). Observed SCFs must be calculated for each survey (preferable daily), and are cost prohibitive in areas dominated by dense coniferous forests and areas of low moose density (Gasaway et al. 1986), both of which occur in our study area. Our results confirm that visibility of moose from aircraft varies with environmental factors and group size. Therefore, application of the visibility model, combined with an appropriate sampling strategy, and with sophisticated analytical methods such as machine learning ('non-linear statistics'; Breiman 2001), may improve the accuracy and precision of population estimates over the use of a static correction factor.

Our method could be extended to other areas of similar environmental conditions such as the remainder of coastal Alaska and British Columbia (and could be tested for applicability to interior Alaska) if protocols associated with the chosen model are followed (McCorquodale 2001). Because visibility may differ among types of aircraft used (Crête et al 1986), surveys should be conducted using a Cessna® 185 or similar fixed-wing aircraft at approximately 185 m above ground elevation, as used in model development (Samuel et al. 1987, Anderson and Lindzey 1996). Additionally, observers should be experienced and their observation skills constantly calibrated in aerial surveys of moose. Conducting surveys when moose are likely to be most visible (i.e., with nearly continuous snow cover and overcast light conditions) will provide the most precise population estimates. Improved population estimates will allow for more knowledge-based and effective management decisions by state and federal managers.

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Appendix

Candidate predictor variables considered during initial modeling for visibility of moose on the Yakutat Foreland, Alaska, 2003-2004.

Variable	Type	Description	Method/Time of Collection
Month	Discrete	Month of visibility trial	Aerial Survey
Age	Discrete	Age of collared moose	Capture
Sex	Discrete	Sex of collared moose	Capture
Group	Indicator	0 = single moose, 1 = ≥ 2 moose	Aerial Survey
Group size	Discrete	Total number of moose seen within 50 m of collared moose	Aerial Survey
Composition	Indicator	0 = single-sex group; 1 = both sexes in group	Aerial Survey
Males	Discrete	Number of adult males in group	Aerial Survey
Females	Discrete	Number of adult females in group	Aerial Survey
Calves	Discrete	Number of calves in group	Aerial Survey
Unknown Sex	Discrete	Number of unknown sex adults in group	Aerial Survey
Forest Cover 10 m	Indicator	0 = nonforested, 1 = forested, within 10 m of moose	Aerial Survey
Forest Cover 250 m	Indicator	0 = nonforested, 1 = forested, within 250 m of moose	Aerial Survey
Vegetation Cover 10 m	Indicator	0 = open habitat such as muskeg, 1= shrub or forested habitat within 10 m of moose	Aerial Survey
Vegetation Cover 250 m	Indicator	0 = open habitat such as muskeg, 1= shrub or forested habitat within 250 m of moose	Aerial Survey
Percent Vegetation 10 m	Indicator	1 = 0-33%, 2 = 34-66%, 3 = 67-100% vegetative cover within 10 m of moose	Aerial Survey
Percent Vegetation 250 m	Indicator	1 = 0-33%, 2 = 34-66%, 3 = 67-100% vegetative cover within 250 m of moose	Aerial Survey
Elevation	Continuous	Elevation above sea level in meters	GIS
Distance from coast	Continuous	Straight-line distance from coastline to center of moose group in meters	GIS
Activity	Indicator	0 = bedded, 1 = active (any moose in group)	Aerial Survey
Site use	Indicator	0 = no beds, few tracks, 1 = beds and multiple tracks	Aerial Survey
Cloud cover	Indicator	0 = clear, 1 = partly cloudy, 2 = overcast	Aerial Survey
Precipitation	Indicator	0 = none, 1 = mist, 2 = light rain, 3 = hard rain, 4 = snow	Aerial Survey
Snow cover	Indicator	1 = 0-33%, 2 = 34-66% ,3 = 67-100%	Aerial Survey
Wind speed start	Continuous	Wind speed (km/h) at beginning of survey	Aerial Survey
Wind speed end	Continuous	Wind speed (km/h) at end of survey	Aerial Survey

Flight speed	Continuous	Average flight speed (km/h) during survey (excludes circling)	Aerial Survey (plane instrumentation)
Temperature	Continuous	Average temperature (Celsius) during survey	Aerial Survey
Start Time	Discrete	Survey start time; military time rounded to hour	Aerial Survey
Light	Indicator	0 = sunny, 2 = flat light/even shadows	Aerial Survey
Experience primary	Continuous	Previous experience level of primary observer, scale of 1-10	Collected from each surveyor prior to visibility trials
Number flights primary	Discrete	Number of previous visibility trials by primary observer	Collected from each surveyor prior to visibility trials
Experience secondary	Continuous	Previous experience level of secondary observer, scale of 1-10	Collected from each surveyor prior to visibility trials
Number flights secondary	Discrete	Number of previous visibility trials by secondary observer	Tabulated throughout visibility trials