ESTIMATING MOOSE ABUNDANCE IN LINEAR SUBARCTIC HABITATS IN LOW SNOW CONDITIONS WITH DISTANCE SAMPLING AND A KERNEL ESTIMATOR

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ABSTRACT: Moose (*Alces alces*) are colonizing previously unoccupied habitat along the tributaries of the lower Kuskokwim River within the Yukon Delta National Wildlife Refuge (YDNWR) of western Alaska. We delineated a new survey area to encompass these narrow (0.7–4.3 km) riparian corridors that are bounded by open tundra and routinely experience winter conditions that limit snow cover and depth necessary for traditional moose surveys. We tested a line-transect distance sampling approach as an alternative to estimate moose abundance in this region. Additionally, we compared standard semi-parametric detection functions available in the program Distance to a nonparametric kernel-based estimator not previously used for moose distance data. A double-observer technique was used to verify that the probability of detection at the minimum sighting distance was 1.0 (standard assumption). Average moose group size was 2.03 and not correlated with distance from the transect line. The top semi-parametric model in the program Distance was a hazard-rate key function with no expansion terms. This model estimated average probability of detection as 0.70 with an estimated abundance of 352 moose (95% CI = 237–540). The CV for the semi-parametric model was 20% and had an estimated bias of 1.4%. The nonparametric kernel-based model had an average probability of detection of 0.73 and an estimated abundance of 340 (95% CI = 238–472) moose. The CV for the kernel method was 18% and the estimated bias was <0.001%. Line-transect distance sampling with a helicopter worked well in the narrow riparian corridors with low snow conditions, and survey costs were similar to traditional surveys with fixed-wing aircraft. The kernel estimator also performed well compared to the standard semi-parametric models used in program Distance. Our technique provides a viable approach for surveying moose in similar areas that have restrictive conditions for standard aerial surveys.

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The Yukon Delta National Wildlife Refuge (YDNWR) is divided into 4 primary moose (*Alces alces*) survey units along the Yukon and Kuskokwim Rivers. Surveys in these units are typically conducted using the GeoSpatial Population Estimator (GSPE) technique (Ver Hoef 2002, DeLong 2006, Kellie and DeLong 2006, Ver Hoef 2008), which is the preferred method adopted by the Alaska Department of Fish and Game (ADFG) and several other federal agencies including other National Wildlife Refuges in Alaska. Only one survey unit is on the lower Kuskokwim River within YDNWR, and encompasses nearly 2250 km^2 of contiguous habitat along the

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relatively wide riparian corridor. The GSPE technique overlays a grid of sample blocks on the study area where each block is stratified into high or low moose density based on a previous stratification flight. A random selection of survey blocks in each strata are surveyed using a fixed-wing aircraft to completely search each selected block. The analysis uses the block's spatial correlation to increase the estimate's precision based on finite population block kriging (Ver Hoef 2002). Complete and adequate depth of snow cover is essential for this type of survey. Ideally surveys are conducted approximately every 3–5 years to monitor trends in moose abundance. However, the Yukon-Kuskokwim Delta and other coastal areas of western Alaska experience moderating climatic effects from the Bering Sea and have frequent thaw-refreeze events (1–9 events/winter; Wilson et al. 2013). As a result, weather and snow conditions may preclude survey initiation or completion, extending the typical period between surveys.

Despite adequate habitat to sustain a higher moose population, the lower Kuskokwim River has historically had a low moose density (0.03 moose/km^2 in 2004; Perry 2010) because of extensive hunting pressure (Coady 1980). Therefore, a moratorium was implemented on the lower Kuskokwim River watershed between 2004 and 2009 when the population increased substantially (0.23 moose/km^2 in 2008; Perry 2010) and expanded into previously unoccupied, or occasionally occupied habitat making it necessary to create an expanded survey unit. The new survey unit was developed to include the major tributaries of the lower Kuskokwim River within the YDNWR, which are narrow riparian corridors that originate from the adjacent mountains (Fig. 1). These tributaries can support a substantial population and are important wildlife corridors to other parts of YDNWR and neighboring conservation units (i.e., Togiak National Wildlife Refuge; Aderman and Woolington 2006). The Kuskokwim tributary survey unit was first proposed, designed, and partially surveyed in the winters of 2009 and 2010 using the GSPE technique; weather and lack of snow cover prevented completion of both surveys.

Environmental conditions such as snow cover are among the most influential variables that affect survey quality (LeResche and Rausch 1974, Gasaway et al. 1986, Quayle et al. 2001, Oehlers et al. 2012). The GSPE technique recommends that surveys occur after fresh or moderately fresh snow with complete ground coverage (Gasaway et al. 1986, Kellie and DeLong 2006), typically ≥20 cm in this area. Retrospectively, we questioned the suitability of the GSPE technique for these tributaries because of the time and cost required to conduct the survey given the unreliable weather and snow conditions. In addition, we sought to evaluate whether this technique is ideal for use in the narrow linear habitats given that large portions of many survey blocks (~3.7 km × 4.5 km) included non-moose habitat (i.e., open tundra). The stratified random block design of the GSPE is better suited for larger and more contiguous blocks of similar habitat (Kellie and DeLong 2006).

A minimum count (termed complete count, a non-sampling approach) survey is used in adjacent areas (Aderman 2008) with a fixed-wing aircraft flown throughout the entire area, counting all moose observed; the count is the population estimate (Lancia et al. 2005). This method requires more flying time to search all areas completely and the minimum count has neither an estimate of precision (i.e., confidence interval) nor typically a sightability correction factor (Gasaway and DuBois 1987). Simple aerial strip-transect surveys require less flying than minimum counts and incorporate an estimate of precision (Timmermann 1974, Timmermann and Buss 2007, Jung et al.

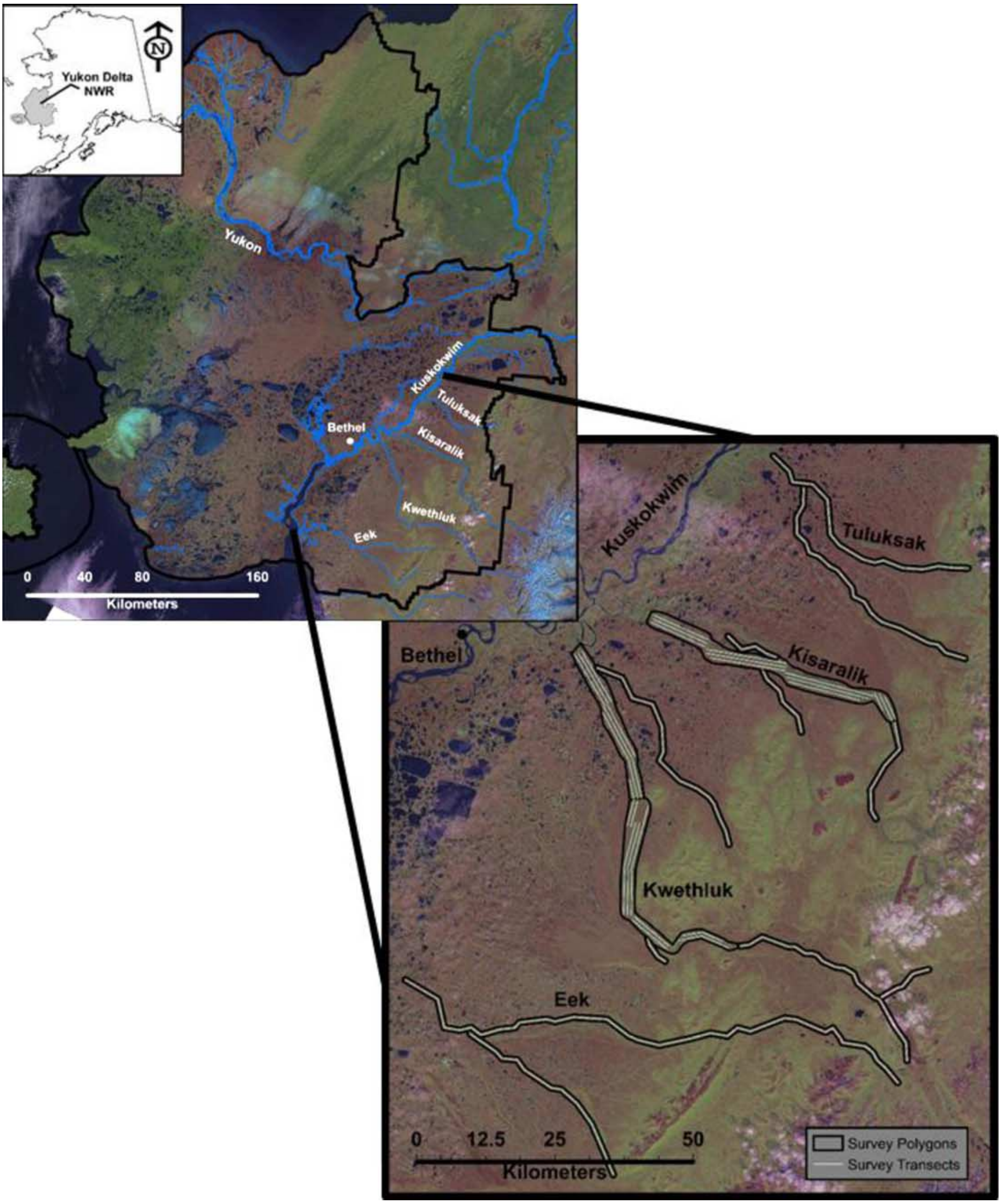

Fig. 1. The Yukon Delta National Wildlife Refuge encompasses the Yukon-Kuskokwim Delta in western Alaska. Bethel is the main community along the Kuskokwim River. The four main tributaries of the lower Kuskokwim River include the Tuluksak, Kisaralik, Kwethluk, and Eek Rivers which form the study area. These rivers are characterized by narrow riparian corridors bounded by open tundra.

2009); however, this method assumes equal detection of animals from the centerline out to the designated strip width (Burnham and Anderson 1984). Typically there is no estimate of sightability with strip transect sampling (Evans et al. 1966, Timmermann

1993), although sightability could be estimated with marked animals (Anderson and Lindsey 1996), or more intensive flying at an increased cost (Gasaway et al. 1986, Gasaway and DuBois 1987).

We determined that a viable survey method was line-transect distance sampling (Burnham et al. 1985, Buckland et al. 2001) using a helicopter for several reasons: 1) the area tends to have marginal snow cover each year making it difficult to complete a GSPE, 2) a helicopter can fly lower and more slowly with better visibility than a fixed-wing aircraft, helping to compensate for minimal snow cover, 3) line-transects can "fit" in the narrow riparian corridors better than GSPE blocks that typically encompass large portions of non-moose habitat, 4) distance sampling incorporates sightability corrections (e.g., weather, lighting, snow conditions, observer experience) provided that probability of detections at some distance is known or assumed and, 5) we expected time, logistics, and costs may be similar compared to a fixed-wing GSPE survey in the same region.

Thompson (1979) initially applied a distance sampling approach to estimate moose abundance in Ontario, Canada, where it was later improved upon by Dalton (1990). Thompson (1979) had problems fitting detection functions, and both surveys had difficulties meeting some of the sampling assumptions (e.g., exact distance measurements, movement of animals before detection, sightings not always independent) and were limited to the technological and statistical challenges of that period (Gasaway and Dubois 1987, Pollock and Kendall 1987, Dalton 1990). Significant advances in distance sampling methodology and statistical analysis have been recognized over the last 30 years (Buckland et al. 2001, 2004; Thomas et al. 2010), and these improvements led to the development of distance sampling protocol for moose in interior Alaska (Nielson et al. 2006). Although distance sampling has been used successfully to estimate moose abundance in relatively large contiguous blocks of boreal forest habitat with adequate snow conditions, no study has demonstrated that this technique works in subarctic tundra along small, narrow riparian corridors.

Distance sampling analyses typically involve estimation of semi-parametric detection functions (Buckland et al. 2001, Thomas et al. 2010). During early development and analyses of line-transect distance data, Burnham et al. (1980) suggested that other nonparametric methods such as kernel estimators or splines might prove "fruitful" for estimating probability of detection, and Mack and Quang (1998) further suggested that kernel methods could be a viable technique in wildlife distance sampling. The nonparametric kernel density estimator does not assume an underlying distribution for the detection function, and thus has more flexibility by allowing the data to "speak for themselves" or dictate the shape of the detection function (Silverman 1986, Wand and Jones 1995). Kernel estimators are considered a robust alternative to other density function estimators (Chen 1996a) and are computationally more efficient than polynomials (Buckland 1992). Both kernel and semi-parametric methods are robust against changing detection functions during a survey (Gerard and Schucany 2002) and are resilient to changing survey conditions such as snow depth/coverage, sun angle and overcast skies, and wind or other environmental conditions that could change during a survey over time and space (Burnham et al. 1980, Chen 1996b); it is assumed that no correlation exists between moose density and these changing conditions. Popular computer programs such as Distance 6.0 do not include a kernel-based detection function (Thomas et al. 2010) for use in analysis of line-transect data, although the kernel method has been used for distance data in other types of surveys (Buckland 1992, Chen 1996a, Mack and Quang 1998, Gerard and Schucany 2002, Jang and Loh 2010, Nielson et al. 2013, Nielson et al. 2014), but not for moose.

The objectives of this study were twofold: 1) evaluate helicopter-based aerial line-transect distance surveys with a double-observer modification to obtain an estimate of moose abundance within narrow riparian corridors during a low snow year, and 2) compare the nonparametric kernel-based detection function to the more traditional semi-parametric models in the program Distance (Thomas et al. 2010). We investigated what we presumed was a viable alternative to traditional moose survey methods for areas with environmental conditions that preclude traditional surveys.

STUDY AREA

The Yukon Delta NWR is located in western Alaska and encompasses the delta formed by the Yukon and Kuskokwim Rivers which empty into the Bering Sea (Fig. 1). The Kuskokwim tributary survey unit includes parts of 4 main lower Kuskokwim River tributaries originating from the mountains to the south and east. These tributaries include the Eek, Kwethluk, Kisaralik, and Tuluksak Rivers and are characterized by narrow (0.7–4.3 km wide) riparian corridors (Fig. 2) running through the foothills and tundra flats that drain the northwest sides of the Eek and Kilbuck Mountains.

Fig. 2. Tributary rivers within the study area are characterized by narrow riparian corridors bounded by open tundra. The relatively open forest and shrub habitat is conducive to sighting moose during a line-transect survey with a helicopter. This corridor is a part of the Kwethluk River and is approximately 800 m wide.

The Eek and upper Kwethluk Rivers are represented by open riparian shrubs (*Salix* spp. and *Alnus* spp.) and scattered clumps of balsam popular (*Populus balsamifera*), whereas the lower Kwethluk River transitions to open forests that include sporadic mixing of spruce (*Picea glauca*), balsam popular, and birch (*Betula papyrifera*) as the overstory with an understory of open willow and alder. The Tuluksak River riparian zone is primarily a narrow corridor of spruce and birch with an understory of willow and alder. The Kisaralik River riparian zone is mostly mixed coniferous open woodland which exhibits a moderate transition between the Kwethluk and Tuluksak riparian habitats. All 4 tributary habitats are bounded by tundra and include variously sized open meadows, old river channels, and beaver ponds.

Weather conditions are highly variable across the survey area. Average temperatures and snow depth at Bethel, Alaska airport (2000–2010; NOAA 2011) during the primary survey months were −21 °C (range −36 to 4 °C) with 23 cm (0–56 cm) of snow in January, −10 °C (−37 to 5 °C) and 23 cm (0–64 cm) of snow in February, and −9 °C (−27 to 4 °C) with 20 cm (0–56 cm) of snow in March. In many years there are freeze-thaw events (Wilson et al. 2013) throughout the winter which ultimately limit total snow accumulation and duration. Our study period (2010) was an El Niño year which affected the winter weather pattern on the Yukon-Kuskokwim Delta from June 2009 to March 2010 (NOAA 2013). Repeated high pressure systems over the Delta kept numerous low pressure systems south and subsequently pushed easterly, resulting in unusually clear and dry conditions with periods of colder temperatures and little snowfall over the study area during winter 2009–2010. A portion of the survey unit experiences a "banana belt" effect, especially along the foothills between the Kwethluk and Kisaralik Rivers. This area is usually affected by a warming trend that typically melts snow more frequently and rapidly than other parts of the area, perhaps resulting from an inversion. These conditions can limit GSPE surveys along the lower Kwethluk and Kisaralik Rivers in any given year.

Nearly 3 cm of new snow accumulated 4 days prior to the survey. Total snow depth was 5 cm (Bethel airport) but was 8–10 cm at 2 snow stakes in the study area (Kwethluk River) during the survey. Snow coverage ranged from 85–100% throughout the survey area with meadow grasses and short vegetation protruding and snow melted off stumps and root wads. Weather conditions during this survey were mostly clear, 9–37 kph winds, and −12 to 2 °C. Day length was nearly 12 h with sunrise at 0900 hr and shadows becoming long at about 1500 hr. Survey times were typically between 0900 and 1700 hr each day and flying conditions were generally favorable during the entire survey.

METHODS

Field Survey

Aerial line-transect distance sampling protocol for moose followed Nielson et al. (2006). The survey area (i.e., sampling universe) was limited to the riparian corridor for the rivers of interest. Polygons were created around rivers to encompass riparian vegetated areas within the floodplain and between the tundra benches on each side of the river (ArcMap 9.2, Environmental Systems Research Institute, Redlands, California, USA; Fig. 1). Satellite imagery was used to facilitate creation of survey areas which encompassed nearly 730 km^2.

Survey transects were created within river corridors and varied by length and number along each river (Fig. 1). Multiple transects were placed in areas wide enough to allow equidistance spacing of 700 m, providing a maximum 350 m search area on each side of a transect centerline. Transect length varied according to stretches of river that allowed straight transects with sections changing direction in a saw-toothed manner as the river corridor meandered (Nielson et al. 2006). Some riparian corridors were sufficiently narrow to allow only a single transect which had a random start point contingent on allowing the minimum half transect width (350 m) to be in moose habitat. The centerline could not be on the edge of the habitat (i.e., one side having a hard boundary of no moose habitat or open tundra and the other side all moose habitat) to avoid extreme asymmetry of g(y), although this source of bias is minimal in most studies (Buckland et al. 2001). Areas with systematic parallel transects had a random start point for the first transect. A total of 46 transects were delineated with a combined length of 698 km (Fig. 1).

We used a Robinson (R-44) helicopter with bubble windows to survey moose during 16–17 March 2010. Helicopters provide a better platform for observing moose because of better sightability, smaller variances, and often comparable cost with fixed-wing surveys (Smits et al. 1994, Gosse et al. 2002). Protocol recommends a flight altitude of 122 m above ground level (AGL) which results in good visibility and minimal disturbance of moose (Nielson et al. 2006). However, snow conditions were poor, so flight altitude was adjusted to 100 m AGL to increase visibility while remaining high enough to minimally affect moose and prevent ground flash, the visual effect of ground zooming by too fast when flying at a lower altitude (Becker and Quang 2009). Our target ground speed was 64 kph (40 mph) depending on terrain and wind.

Four people were onboard during this survey. The pilot was responsible for maintaining desired altitude, speed, and heading on transect centerlines using a preprogramed GPS (Garmin 695). Two observers were seated in the back (one on each side) and were the primary observers for the survey. Their responsibilities were to sight moose groups, count and classify each group, and measure the perpendicular distance from the transect centerline to each group centerpoint. The data recorder sat in the front-left seat and was responsible for recording all data including GPS locations, performing as a double-observer, frequently measuring helicopter AGL, and overall survey coordination. The front observer recorded survey data while flying off transect in order to not interfere with double-observer duties while flying on transect.

The double-observer method was used in conjunction with the line-transect survey to test the assumption that detection was 100% on or near the transect centerline, or at the minimum available sighting distance (Buckland et al. 2001, Laake and Borchers 2004, Borchers et al. 2006). This assumption is sometimes violated (Chen 1999, 2000) and information regarding heterogeneity in observer bias should be modeled (Graham and Bell 1989) because it can produce negatively biased estimates.

The data recorder in the front-left seat was paired with the rear left observer to conduct the double-observer sampling, which is essentially a mark-recapture method (Borchers et al. 2006). The data recorder focused on or near the centerline to detect moose, but recorded all moose observations at any distance. Double-observer data are used to estimate detection rate on or near the centerline by the rear seat observers. This requires that the front and rear seat observers operate independently of each other (Buckland et al. 2010). Data were recorded on the number of moose groups detected by both observers, and groups detected by the front and not the rear observer. To account for observer bias, the 2 rear observers rotated sides each day to be paired with the front-left observer to incorporate biases from both observers into the model (Cook and Jacobson 1979). Thus, we considered the probability of detection estimated for the back-left observer based on the mark-recapture data to be relevant for both backseat observers during analyses. The recorder also worked with the pilot to keep flight speed and altitude within the range of survey protocol. A laser rangefinder (Nikon Forestry 550 Hypsometer) was frequently used to measure true vertical distance from the ground to helicopter every 2–3 min to check flight altitude and recommended adjustments as needed.

Moose groups were defined as one or more moose within a 50 m radius (Molvar and Bowyer 1994). The distance of groups perpendicular to the transect centerline was measured by the rear observer with a laser rangefinder (Leupold RX-1000 TBR) with a built-in clinometer that had maximum range of ~900 m; clinometers allow for accurate horizontal measurements regardless of survey altitude. A group that was hard to laser-range (e.g., trees, helicopter movement, animal movement) required flying back over the group and marking its location with a GPS (Marques et al. 2006). Distance was measured to the center of a group using the laser rangefinder directed at their feet to avoid over-estimating the distance; this measurement was associated with the location of the group when first observed. If moose moved before a distance was acquired, the observer ranged the location of the initial observation. Doubling back to mark GPS locations worked well, but some moose moved after detection because of the aircraft hovering directly overhead; tracks in the snow proved reliable as reference points for these cases. The distances measured with the GPS method (~90% of all groups observed) were calculated in a GIS. Additional moose observed "off transect" while doubling back to obtain GPS locations were not included in any analysis. Observers determined group size, composition (i.e., adults and calves), and classified percent habitat cover for ~50 m radius around each group.

Data Analysis

Standard distance sampling theory assumes all individuals (objects) available to be detected on the centerline, or the minimal available sighting distance, are observed, and that the probability of detection is a function of perpendicular distance from the centerline. There are 3 essential assumptions for accurately estimating density using distance sampling. In order of importance these are: 1) objects at the minimal available sighting distance are detected with certainty, that is $g(W_1) = 1.0$, or can be estimated, 2) objects are detected prior to any movement in response to the survey, and 3) perpendicular measurements to the object are accurate (Buckland and Turnock 1992, Buckland et al. 2001). Other design/analysis assumptions exist but are less stringent, including accurate measurement of group size and that object density is independent of the placement of transects (i.e., uniform distance distributions; Fewster et al. 2008).

Fulfilling these assumptions allow for an accurate density estimate using:

$$\hat{D} = \frac{n\hat{E}(s)}{2(W_2 - W_1)L\hat{P}} \qquad (1)$$

where n is the number of observed groups, $\hat{E}(s)$ is the expected (or average) group size, W_1 and W_2 are the minimum and maximum search distances from a transect, respectively, L is the total length of transects flown, and $\hat{P}$ is the estimated average probability of detection within the area searched (Buckland et al. 2001).

We tested the assumption $g(W_1) = 1.0$, where $g(W_1)$ is the minimum sighting distance with the double-observer technique (Chen 2000, Borchers et al. 2006, Buckland et al. 2010) using observations from the left side of the helicopter. Observations collected independently by individual observers on the left side were used to estimate the probability of detecting a moose group at the minimum available sighting distance. This probability was used to adjust the estimated detection curve starting at that distance (Laake and Borchers 2004).

We used logistic regression (McCullagh and Nelder 1989) in the mark-recapture analysis to estimate the probability of detecting a moose group by the back-left observer given detection by the front-left observer. We considered 3 models that 1) treated the probability that a group was detected by the back-left observer as constant across all distances from the transect line (intercept only model), 2) treated the probability of detection as a function of distance from the transect line, and 3) included both linear and quadratic terms for distance from the transect line. We used Akaike's information criterion for small sample sizes (AICc; Burnham and Anderson 2002) to identify the best model for estimating probability of detection by the backseat observers based on the mark-recapture data. The AICc was calculated as:

$$\mathrm{AICc} = -2\log(\mathit{Likelihood}) + 2kn/(n-k-1) \quad (2)$$

where k was the number of parameters in the model (including intercept term), n was the number of observations used to fit the model, *Likelihood* was the value of the logistic likelihood evaluated at the maximum likelihood estimates, and 'log' was the natural logarithm. The logistic regression model was fit using the program R (R Development Core Team 2010).

We designed transect centerlines to be a minimum of 700 m apart to ensure that moose groups were not counted more than once if they moved during the survey. To meet this assumption, we set the maximum search width, W_2, equal to the maximum distance a moose group was observed within 300 m of the transect centerline. Since the backseat observers had a blind spot underneath the helicopter, we used a laser rangefinder (hypsometer) to determine the minimum sighting distance for the backseat observers. To determine the width of the blind spot at the survey altitude, the backseat observer laser-ranged through the bubble window along their line-of-sight to the ground, just clear of the helicopter skid. The minimum available sighting distance for backseat observers was ~43 m from the centerline. Moose were visible to the front-left observer from 0–43 m through the front helicopter window, but lumping these data into a single distance of "zero", and the fact that the front-right observer (pilot) was not focused on observing moose on that side of the line, precluded using these data in the analyses; therefore, the front-left observer observations in the 0–43 m range were not used. Thus, the minimum available sighting distance, W_1, was set at the minimum distance at which a moose group was detected by a backseat observer.

We evaluated whether correlation existed between expected group size and detection distance because group size can influence detectability, especially at longer distances; larger groups may have a higher probability of detection than smaller groups further from the transect line (Drummer and McDonald 1987, Drummer et al. 1990). We used a Pearson's correlation analysis to estimate the correlation (r) between group size and distance from the transect line, and calculated a 95% confidence interval (CI) for the statistic (Zar 1999). We determined no relationship existed between group size and detection distance if the 95% CI included 0.0. In this situation, we used the average of all observed group sizes for $\hat{E}(s)$ (equation 1). If a correlation was detected, we used the regression method (Buckland et al. 2001) to estimate expected group size. We examined the habitat covariate, percent cover as a potential influence on the probability of detection of groups (i.e., higher percent cover may reduce probability of detection; Anderson and Lindzey 1996, Oehlers et al. 2012).

The underpinning of distance sampling is the detection function g(y) which expresses the probability of detecting a group given that the group was observed at distance (y) from a random transect, and that the assumption g(W_1) = 1.0, or can be estimated, holds true (Buckland et al. 2001). There are many models that can be fitted to distance data in order to estimate the shape of a detection function, and we used the computer program Distance 6.0 release 2 (Thomas et al. 2010) to model semi-parametric detection functions for moose groups. We considered robust key functions with expansion terms as outlined in Buckland et al. (2001), including the half-normal with hermite polynomial and cosine expansion terms, the hazard-rate with a cosine expansion, and the uniform with simple polynomial and cosine expansion terms. Additionally, the half-normal or hazard-rate key functions allow for predictor variables to help model the detection function. We used the half-normal (including hermite polynomial and cosine expansion terms) and hazard-rate (including a cosine expansion term) key functions for modeling the detection function while incorporating the percent cover variable. The number of expansion terms for each key function was allowed to vary from 0–5; the AICc was used to select the number of expansion terms among the various models. The model with the lowest AICc value was selected as the best model to describe the detection function (Burnham and Anderson 2002).

Use of parametric or semi-parametric detection functions may not always be the best approach to fit probability detection curves (Burnham and Anderson 1976, Buckland 1992); instead, a nonparametric kernel density estimator without an assumed probability density function may provide a better fit to the data. We fit a nonparametric kernel estimator (Silverman 1986, Wand and Jones 1995) to our group observations, and used the general univariate kernel density estimator described in Wand and Jones (1995):

$$\hat{f}(x) = (nh)^{-1} \sum_{i=1}^{n} K\left(\frac{x - x_i}{h}\right) \qquad (3)$$

where x is a perpendicular distance within the range of observed distances, x_i is one of the n observed distances, h is a smoothing parameter, or 'bandwidth', and K is a kernel function satisfying the condition $\int K(x)dx = 1$.

Since the bandwidth (h) governs the function smoothness (Chen 1996a, Gerard and Schucany 1999), the choice of bandwidth is more crucial than the choice of kernel (Mack and Quang 1998, Jang and Loh 2010). We used a Gaussian kernel function (Silverman 1986, Chen 1996a) and the direct plug-in bandwidth selection method (Sheather and Jones 1991, Wand and Jones 1995, Sheather 2004) to develop the detection function for groups. The direct plug-in method objectively fits the bandwidth and is considered to be the best compromise between bias and variance among the available methods (Sheather and Jones 1991, Wand and Jones 1995, Venables and Ripley 2002, Sheather 2004).

Kernel estimators inherently do not perform well near sharp boundaries (Jang and Loh 2010). A boundary bias is created, as in our case, when distance observations are not distinguished from the right or left side of the transect line and where all values are non-negative (Buckland 1992, Jang and Loh 2010). In order to model the distances with a kernel estimator, Chen (1996a, 1996b) and Silverman (1986) recommended reflecting the observed distances to both sides of the transect line in order for the kernel density estimator to perform properly. After shifting all observed distances by the left-truncation distance (W_1), we multiplied (reflected) the observed distances by (-1) and added them to the dataset (Buckland 1992, Chen 1996a, 1996b). Once the kernel density function was created from the expanded dataset, the detection function to the right of the zero line (positive) was used for the density estimate. The kernel estimator was fit using the program R (R Development Core Team 2010) and the MASS package in R (Venables and Ripley 2002).

We used bootstrapping to estimate SEs and 95% CIs for final estimates of moose density and abundance within the sampled region (Efron 1981a, 1981b, Quang 1990, DiCiccio and Efron 1996). Estimates derived from the program Distance 6.0 were bootstrapped within the program, which uses a default of 999 bootstrap re-samplings with replacement (Thomas et al. 2009). Standard errors and confidence intervals for the kernel estimates were derived from bootstrapping 999 resamples (with replacement) to be consistent with program Distance and because the bootstrapped estimates (SE, CI) usually become stable and asymptotic between 500 and 1000 resamples (Efron and Tibshirani 1994). We bootstrapped the 46 line-transects surveyed in which the bootstrap would rerun the analysis for all parameter estimates, including the shape of the detection function and the average probability of detection during each iteration. Additionally, we evaluated bias and precision of the density estimate using the bootstrap (Efron and Tibshirani 1986). We used the percentile method (Efron 1981b, 1982) for calculating the 95% confidence intervals using the 2.5th and 97.5th percentiles of the 1,000 estimates (999 bootstrap estimates + original estimate). The percentile method is the preferred method for calculation of CIs when bootstrapping, because using the standard formula (i.e., estimate ± 1.96[SE]) requires the additional assumption that the bootstrap estimates generally follow a normal distribution (Buckland 1984, Efron and Tibshirani 1994). We estimated relative percent bias of the density estimates as:

$$\%Bias = \left[\frac{\{D_{boot} - D_{orig}\}}{D_{orig}}\right] \times 100 \quad (4)$$

where D_{boot} is the average density estimate from the bootstrap and D_{orig} was the original density estimate. We measured dispersion or the extent of variability in relation to the final density estimate by calculating the coefficient of variation (CV) as $CV = (SE/\hat{D}) \times 100\%$. The standard deviation (SD) of the 1,000 estimates was used as the estimated SE.

In order to estimate the total length (L) of transects needed in future surveys to achieve a certain level of precision (i.e., CV value), we used the formula from Buckland et al. (2001):

$$L = L_0\{cv(D)\}^2 \Big/ \{cv_t(D)\}^2 \quad (5)$$

where L_0 is the total length of transects surveyed, cv (D) is the coefficient of variation of the density estimate from this study and cv_t (D) is the desired target coefficient of variation.

RESULTS

A total of 162 moose (112 adults, 48 calves) in 78 groups were detected on 46 transects along 698 km within a series of polygons encompassing 730 km^2 of riparian moose habitat. There were 37 cow moose with calves including 26 singletons and 11 sets of twins (30% twinning rate). Group size ranged from 1–5 with 73% of groups comprised of 1–2 moose and only 6% with 4–5 moose.

Because the mark-recapture portion of this study was intended to occur only on the left side of the aircraft, a single group observation detected by the front-left observer that was 244 m to the right of the transect line (and not detected by the back-right observer) was excluded from the analysis. Ten of the 78 groups were detected only by the front-left observer and were recorded as seen directly on the transect line (i.e., perpendicular distance = 0). Since these groups could not be seen by the back-left observer and 'lumping' of the perpendicular distances occurred during data recording (i.e., these moose were likely somewhere ± 43 m from the transect line and not all directly on the line), these observations were also excluded from the analysis. Of the remaining observations, the minimum observed distance of a moose group by the backseat observers was 46 m from the transect line, thus W_1 was set to 46 m. We truncated our data to 300 m, which corresponded to a reduction of approximately 8% of the farthest distance observations; Buckland et al. (2001) recommend truncating the farthest 5–10% of distance observations. The maximum observed distance of a group within 300 m of a transect line was 299 m, so W_2 was set at 299 m.

Analysis of moose observations within the defined search width (46–299 m from a transect line) indicated that group size was not correlated with distance from the transect line ($r = 0.048$, 95%, CI = −0.20–0.29). The average group size by the backseat observers within the search strip was 2.03 (95% CI from 1.78–2.32) and was used in the density estimate.

The mark-recapture trials used 34 observations to fit logistic regression equations to estimate the probability of detection by the back-left observer given detection by the front-left observer. Only 3 groups were missed by the back-left observer and these were deleted for the density estimate. The logistic equation with linear and quadratic terms for distance from the transect line had the lowest AICc value (19.8 versus 22.4 and 24 for the intercept only and linear distance function models, respectively). The final estimated logistic regression model was:

$$E[y_i] = \frac{\exp(51.461 - 0.583 distance_i + 0.0012 distance_i^2)}{1 + \exp(51.461 - 0.583 distance_i + 0.0012 distance_i^2)} \tag{6}$$

where $E\,[y_i]$ was the expected probability of detection for mark-recapture observation i.

Based on this final model, the predicted probability of detection of moose at the minimum sighting distance by the back-left observer was 1.0. Therefore, the estimated probability of detection curve was not scaled by a correction factor prior to integration and estimation of $\hat{P}$, and only observations by the rear seat observers were used to estimate moose density.

Comparison of models using AICc values requires that the competing models are all estimated using the same number of observations and the same response (Y) values. Percent cover was not recorded for one observation so this record was not initially included during estimation of the probability of detection curve. In addition, due to the distribution of percent cover values for observations (10–70% in 10% increments) and few observations at the extremes, the original values were collapsed into 3 categories: 1) 10–30, 2) 30–50, and 3) 60–70%.

Comparison of the models with and without the covariate for percent cover indicated that a hazard-rate key function with no expansion terms was the best fit to the data (Table 1). Because the models

Table 1. Estimated semi-parametric detection functions fit to 58 moose group observations using the program Distance (Thomas et al. 2010), including the number of expansion terms, whether the covariate for percent cover was included in the model, the number of parameters (k), AICc value, and estimated average probability of detection ($\hat{P}$), estimated moose density ($\hat{D}$), and coefficient of variation (CV) for each model, Alaska, 2010.

Key Function	Expansion	Expansion Terms	k	% Cover (yes/no)	AICc	$\hat{P}$	$\hat{D}$	% CV
Hazard-rate	Cosine	0	2	N	627.85	0.71	0.480	19.1
Uniform	Cosine	2	2	N	629.26	0.67	0.505	25.3
Uniform	Simple Polynomial	1	1	N	629.47	0.70	0.485	17.3
Half-normal	Cosine/Hermite Polynomial*	0	1	N	629.48	0.62	0.547	21.0
Half-normal	Cosine	1	4	Y	631.40	0.85	0.398	18.2
Hazard-rate	Cosine	0	4	Y	631.42	0.68	0.498	18.4
Half-normal	Hermite Polynomial	1	4	Y	631.68	0.82	0.413	18.4

*No expansion terms were selected using AICc values.

Table 2. Estimated semi-parametric detection functions fit to 59 moose group observations using the program Distance (Thomas et al. 2010), including the number of expansion terms, whether the covariate for percent cover was included in the model, the number of parameters (k), AICc value, and estimated average probability of detection $\hat{P}$, estimated moose density $\hat{D}$, and coefficient of variation (CV) for each model, Alaska, 2010.

Key Function	Expansion	Expansion Terms	k	AICc	$\hat{P}$	$\hat{D}$	% CV
Hazard-rate	Cosine	0	2	643.25	0.70	0.482	20.0
Uniform	Cosine	1	1	643.53	0.60	0.562	19.1
Half-normal	Cosine/Hermite Polynomial*	0	1	643.67	0.64	0.533	20.4
Uniform	Simple Polynomial	1	1	644.47	0.72	0.472	17.4

*No expansion terms were selected using AICc values.

containing the covariate for percent cover ranked last according to AICc values, we refit the models without the predictor variable using all the observations from the rear seat observers within 46–299 m of a transect line, including the single observation where percent cover was not recorded. The results of this analysis were similar to the analysis, minus the missing observation, in that the top model was a hazard-rate key function with no expansion terms (Table 2). We used the goodness of fit (GOF) test statistic to determine if the top model fit the data well (Buckland et al. 2001). There was no evidence of lack of fit for the top model (GOF test; $\chi^2 = 6.07$, df = 4, $P = 0.194$). Based on this final model using 59 groups, the estimated average probability of detection was 0.70 (Fig. 3), and the estimated density was 0.48 moose/km^2 or a population of 352 moose (95% CI = 237–540); this model had a CV of 20% and an estimated bias of ~1.4%.

The detection function calculated using the kernel density estimator (without covariates) also had a good fit (GOF test; $\chi^2 = 6.42$, df = 5, $P = 0.73$) with an estimated average probability of detection of 0.73 (Fig. 3). The estimated density was 0.47 moose/km^2 or a population of 340 moose (95% CI =

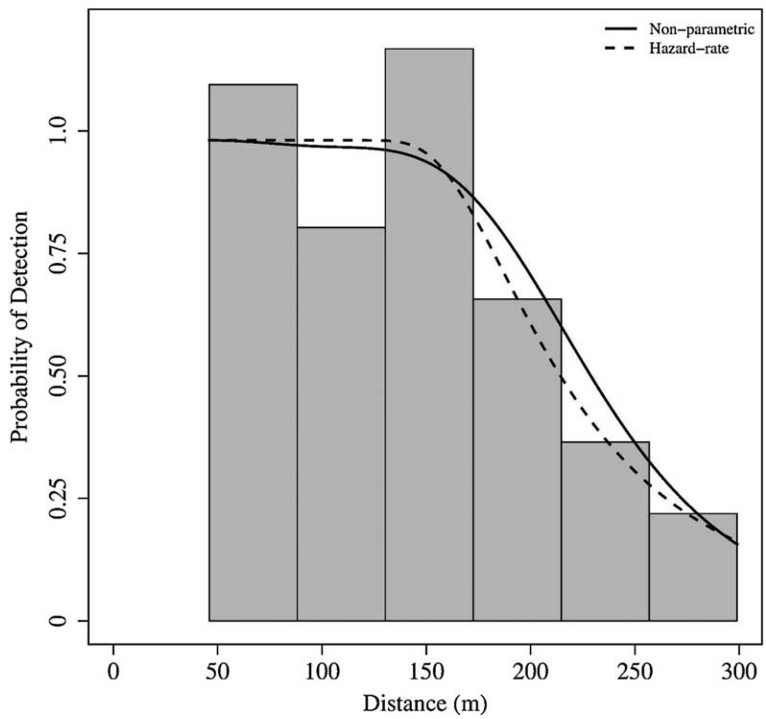

Fig. 3. Histogram of the 59 moose group distance observations with corresponding detection functions superimposed. The final hazard-rate detection function was fit using the program Distance (Thomas et al. 2010). The non-parametric kernel-based detection function was fit using the program R (R Development Core Team 2010). Perpendicular distances were shifted left by 46 m prior to analysis, but shifted back for graphing visual clarity.

238–472); the corresponding CV was 18% and the estimated bias based on bootstrapping was <0.001%.

Based on an encounter rate of 0.085 moose groups/km (59 groups/698 km) and the CV from the kernel estimator (18%), we calculated the total length of transects needed to achieve a targeted CV of 20, 15, and 10%. This analysis indicated that transect lengths of 566, 1006, and 2262 km, respectively, were required to meet these targeted CVs assuming that the encounter rate remains constant.

DISCUSSION

Others have utilized distance sampling with varying degrees of success in model fitting and achieving adequate levels of estimate precision under adequate snow conditions within boreal transition forest of west-central Alaska (Nielson et al. 2006) and central Canadian boreal forest habitats (Thompson 1979, Dalton 1990, Thiessen 2010, Peters et al. 2014). We evaluated this method as an alternative technique for surveying moose in a subarctic tundra ecosystem with variable and often minimal snow conditions, and present an alternative technique for analyzing distance data using a non-parametric kernel density estimator to fit the detection function. Overall, distance sampling proved to be a viable technique to monitor moose along the Kuskokwim tributary rivers in the YDNWR in southwestern Alaska.

Assumptions

Distance sampling depends on 3 main assumptions that need to be met, or nearly so, in order to produce unbiased and reliable estimates (Buckland et al. 2001). Although the assumptions can be relaxed to some degree in certain circumstances and still provide dependable estimates (Buckland et al. 2001), we designed our study in an attempt to meet all assumptions or to estimate our biases if we failed to adequately meet one.

Assumption (1), that objects at the minimum available sighting distance were detected with certainty, is typically addressed by developing a sightability correction factor (SCF) through modeling covariates against mark-recapture data of collared animals (Gasaway et al. 1986, Samuel et al. 1987, Anderson and Lindzey 1996). Distance sampling inherently accounts for, or corrects for, visibility (perception) biases provided that all objects are detected on the transect centerline or at the minimum sighting distance (Buckland et al. 2001, Marques and Buckland 2004). Although many distance sampling studies do not address assumption (1) (Bachler and Liechti 2007), we utilized the double-observer method (Graham and Bell 1989) to test the primary assumption that detection of moose groups on the centerline or at the minimum sighting distance was certain. The mark-recapture logistic regression analysis indicated that we met the assumption with 100% probability of the backseat observer detecting a moose group that was detected by the front-left observer at the minimum sighting distance (g(W_1)). Detection certainty along the transect line in our study was enhanced by several factors including that the survey area was within narrow riparian habitat with a relatively open canopy (range of percent cover data was 10–70% with an average of 39%). Additionally, detection on the centerline was further increased by the fact that we used a helicopter flying at 100 m AGL at a relatively slow speed of 48–88 kph; although snow was shallow, visibility on the centerline was excellent.

Moose in our study area were assumed to be available for detection because of the relatively open habitat (39% canopy closure). One concern was that root-wads of wind-fallen trees could hide an adjacent, bedded moose. However, if we flew directly over a root-wad we detected the moose on the transect line (g(W_1) = 1.0), and it would be accounted for in the detection function at distances off the transect line (Laake et al. 2008). Availability bias could possibly be removed or reduced if the area was surveyed at different times (e.g., hours apart) to allow animals to become available; this is likely dependent on species (Laake and Borchers 2004) and unlikely of concern with moose in most conditions.

Assumption (2), that objects are detected at their initial location, is sometimes difficult to assess (Fewster et al. 2008), and in our case, related to disturbed moose "pushed" by the helicopter some distance before detection. Thompson (1979) reported that moose were not disturbed by circling fixed-wing aircraft and did not move as the airplane approached; however, Cumberland (2012) reported that moose usually initiated some movement from a larger turbine helicopter (Bell 206) at a lower survey altitude (60 m AGL). Random movement is acceptable as long as it is not caused by the observer (Buckland et al. 2001), but failure to meet assumption (2) would bias the density estimate low.

We investigated the validity of this assumption, in part, by reviewing the distance data histogram and identifying whether a bump or peak is evident some distance from the center line. Figure 3 has a slight bump in frequency at ~150 m which might reflect recording bias or movement from the helicopter prior to detection (Dalton 1990). Our front observer was focused on the centerline for the double-observer method, and looking forward of the helicopter to identify any pre-detection movement (Fewster et al. 2008). Few moose were observed moving prior to when the backseat observers detected moose; movement was mainly in response to the helicopter directly overhead. Because these few moose did not move into a zone of detection for the backseat observer, movements were considered moot in our study. Further, observations of moose within the effective search width (46–299 m) did not indicate movement prior to detection by the backseat observer.

A possible explanation for the bump in our data was that the backseat observers had a comfortable scanning level or sight line (i.e., distance) while sitting in the helicopter. Observer fatigue increases as a survey progresses (Briggs et al. 1985, Schroeder and Murphy 1999), possibly contributing to the desire to scan (subconsciously) at a less strained position. For example, Jang and Loh (2010) graphed the classic wooden stake data outline in Burnham et al. (1980) and showed that their histogram had a large bump or spike of detections that clearly was not associated with movement. We believe that we met assumption (2) because the front observer scanned forward of the flight path and there was no change in observation rate moving from the center line (Fig. 3). Flying at a higher altitude (e.g., 122 m instead of 100 m AGL). as suggested by Nielson et al. (2006), would presumably further address assumption (2).

To meet assumption (3), that perpendicular distance measurements are exact, we utilized both rangefinders with built-in clinometers and GPS units to determine perpendicular distances to moose groups. Although both methods can be accurate and efficient, it was difficult to range groups at times, especially when close to the helicopter which required a quick response, and when in cover. Higher quality or industrial-type laser rangefinders should reduce this problem. We eventually adopted the technique used by Marques et al. (2006) and used GPS locations to measure distances. This required more flying time and effort to fly off transect to identify the group location. Because this process caused some moose to move prior to marking the location, we followed tracks in the snow to ascertain the initial location. Increasing flight altitude while off transect may alleviate or reduce disturbance while marking locations. We are confident that movements were minimal and measured adequately, and that groups were not double counted on subsequent transects.

Other assumptions that are not generally discussed in literature, such as the uniformity of the distance distribution and independence of group observations, are typically addressed during the survey design process. The uniformity assumption is addressed by randomly distributing transect lines across the study area, or systematically arranging transects with a random start point, as we did (Fewster et al. 2008, Jang and Loh 2010). The assumption that observations are independent is addressed in the same manner as distance uniformity (Buckland et al. 2001) provided that moose are not clustered together in one part of the survey area. Estimates of density are robust to the independence assumption especially when bootstrapping to obtain confidence intervals (Thomas et al. 2002). Additionally, we did not incorporate "dependent" moose groups observed while flying off transect when obtaining GPS locations for groups that moved.

Detection Functions

Survey design and protocol are paramount for meeting the 3 primary assumptions of distance sampling in order to model detection functions reliably (Thomas et al. 2010). Our survey transects were systematically distributed throughout the riparian corridors with random start points allowing for statistical inference (Fewster et al. 2009). Although transects were spaced 700 m apart and a maximum search width of 350 m could have been used in the analysis, there were few observations beyond 300 m. Restricting the analysis to observations within 300 m reduced the possibility that moose groups were counted more than once. We dropped nearly 8% of the farthest observations which was within the recommended 5–10% range suggested because outliers may have undue influence on the shape and scale of the detection function (Buckland et al. 2001). Our effective search width (W_1 and W_2) was 253 m (46–299 m) which was narrower than the 700 (Dalton 1990) and 800 m (Thiessen 2010) widths used in Canada, and similar to the 250 m search width used by Thompson (1979). Our search width was narrow because of the narrow corridor of habitat, we flew relatively low, and the relatively poor snow conditions which presumably reduces visibility. We recommend using narrow transect search widths during low or poor snow condition years to increase effectiveness of the survey.

We measured percent cover because covariates can improve model precision by accounting for heterogeneity in the data (Buckland et al. 2004, Marques and Buckland 2004), but at an added cost of sample size (Giudice et al. 2012). However, it did not improve the detection function based on the higher AIC values for the models including this covariate. This might reflect the relatively narrow range of values (range = 10–70%, median = 40%) that were lumped into 3 categories. Visual obstruction by vegetation influenced detection of moose in Minnesota where percent cover was higher (range = 0–95%, median = 60%) (Giudice et al. 2012). Buckland et al. (2001) recommend 60–80 observations and at least 10–20 replicate transects to obtain reliable estimates with relatively good precision; we had 58 group observations with percent cover measurements. Seddon et al. (2003) improved their survey precision (i.e., decreased CV values) by increasing observations.

In an analysis of several surveys, Thiessen (2010) found a strong relationship between the number of observations and CVs for those surveys; surveys with 60 observations had a CV of ~20%. Our survey (59 observations) corroborates this relationship as our model without covariates had a CV of 20% (using the hazard-rate key function). Adding covariates or stratifications would require considerably more observations to ensure reliable estimates with a CV of 20%. We examined the possibility of stratifying our study area by each tributary river but moose density was too low to acquire sufficient observations for reliable estimates for all rivers, with the possible exception of the Kwethluk River (~60–80 observation in each strata; Buckland et al. 2001).

Group size influences detection at distance (Drummer et al. 1990), and can be included as a covariate in the program Distance (Laake et al. 2008). We investigated whether a correlation existed between group size and detection distance prior to "penalizing" our analysis with an additional covariate (Giudice et al. 2012). Our analysis indicated that group size was not correlated with detection distance in this study which most likely reflects the group composition in the study area. Most groups were relatively small (73% had 1–2 moose) and most observations were cows with calves. Since there was no correlation between distance and group size, and the composition of groups had a narrow range of sizes (no major outliers), we used the average group size as equivalent to the expected group size in the density estimate (Buckland et al. 2001).

Our model choices were based on recommendations of Buckland et al. (2001) and past experience (Nielson et al. 2006) in order to prevent a "shotgun" approach to modeling. Models that included the percent cover covariate were ranked last and did not contribute to or improve the model according to AICc; we subsequently removed the covariate and analyzed the data without it. Our top model was the hazard-rate key function with no expansion terms. As in our study, several other ungulate studies reported the hazard rate key function with various expansions to be the top models (Focardi et al. 2002, Shorrocks et al. 2008, Young et al. 2010, Schmidt et al. 2011). Other studies with ungulates found the half normal key function with various expansions terms to perform best (Trenkel et al. 1997, Jathanna et al. 2003, Peters 2010, Thiessen 2010).

The kernel estimator used for the probability of detection curve does not use maximum likelihood methods, so AICc values are not available for comparison with models with semi-parametric detection functions in the program Distance. However, the kernel-based estimated probability of detection, animal density, and CV were similar to those obtained from the hazard-rate model in Distance, although the CI was much narrower for the kernel estimator. Based on bootstrapping, all the semi-parametric models estimated that the probability of detection biased low (i.e., lower than the kernel's $\hat{P} = 0.73$), thus estimated densities were biased high. The estimated bias in the hazard-rate model estimate (1.4%) was higher than the estimated bias for the kernel-based estimate (<0.001%). An advantage of the nonparametric estimator is that it is free of parametric assumptions on the detection function. Additionally, using a kernel-based model does not require that detection is a monotonically decreasing function of distance away from the transect centerline, unlike semi-parametric models (Cassey and McArdle 1999). One limitation is that it requires an adequate sample size to produce a reasonable estimate (Chen 2000), but sample size was not a problem in our univariate analysis for the level of precision we achieved. The Hermite polynomial and kernel estimates are very similar with the kernel estimate less intensive to compute (Buckland 1992).

Survey Effectiveness

The study area is characterized by marginal snow conditions during any given year with the most reliable conditions in February (Fig. 4). The daily average snow depth clearly demonstrates that the area does not accumulate deep snow and daily variation is high because of periods of warming and rain causing snowmelt. We considered ~20 cm of snow accumulation as moderate to good conditions, required for the standard GSPE survey method. Conversely, Dalton (1990) considered 20 cm "shallow" for a moose survey in Ontario, Canada.

Comparison of the helicopter line-transect method with the GSPE method considers time, logistics, cost, and the estimate of precision. The GSPE method requires a minimum of 60 units surveyed between 2 moose density strata (30 low and 30 high strata), with preferably more units in high density areas assuming greater variation within that strata (Kellie and DeLong 2006). GSPE survey areas are a minimum of 777 km² because smaller areas have insufficient sample units to generate estimates. These survey units are approximately 16.6 km² and require a minimum search intensity of 40 min/block with cub-like or tandem style fixed-winged aircraft (Kellie and DeLong 2006). The time required to fly the minimum intensity and number of units would be ~40 h. Two aircraft for a minimum

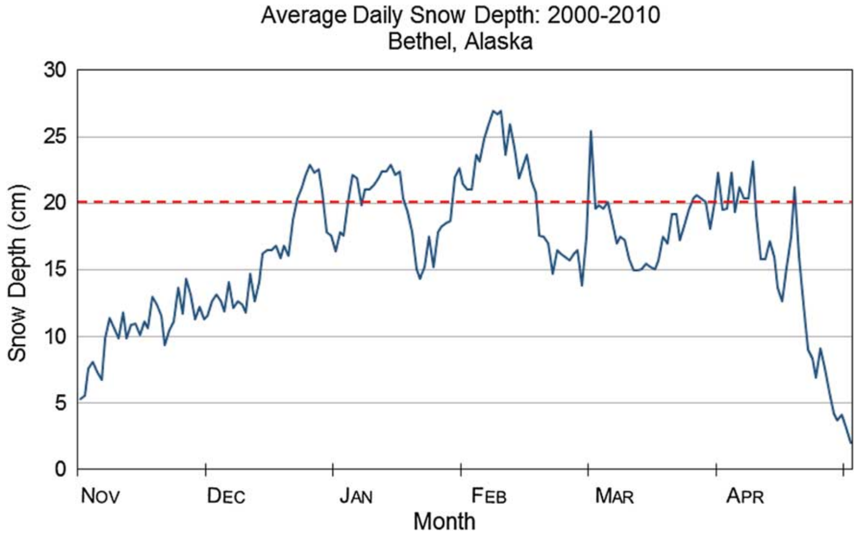

Fig. 4. Average daily snow depth at Bethel, Alaska airport (2000–2010) during typical moose survey months. In this area the minimum snow depth for GSPE type surveys is ~20 cm (dashed line). The variability in snow depth is due to periodic and rapid warming trends (NOAA 2011).

of 5 days would be required to complete the survey given continuous optimal snow conditions, a situation unlikely in the study area.

The helicopter line-transect survey was considerably more efficient in terms of area sampled and flight time than a fixed-wing GSPE. We flew a total of 16 h in one helicopter including about 2.5 h of training prior to the actual survey (training is highly recommended to prepare the survey team for duties and search patterns) and 13.5 h during the actual survey, including ferry times from the base of operation. We accomplished the survey in 2 days which improves the chance of continuous, optimal snow conditions. Cost based solely on flight hours was similar; a fixed-wing survey for the minimum sampling under the GSPE method in this area would be approximately 6% less than the helicopter line-transect technique, a reasonable compromise given the reduction in survey days (2 versus 5). Our helicopter survey had a CV of 18%, a difficult level of precision to obtain with the minimum number of GSPE units required to address potential stratification errors, sample sizes, and high variability of observations between units (Kellie and DeLong 2006).

Management Application

The recent expansion and establishment of moose in the lower Kuskokwim River tributaries prompted our survey efforts. Our survey indicated that moose density is 0.47 moose/km^2 or twice that of the adjacent lower Kuskokwim River survey unit in 2008 (0.23 moose/km^2 without SCF; Perry 2010). The difference can arguably be attributed to better habitat along the Kuskokwim tributaries compared to the main channel of the lower Kuskokwim River, and the 5-year moose hunting moratorium in the lower Kuskokwim drainage that allowed moose to establish a viable population and disperse into unoccupied habitat. The exploitation of underutilized habitat was expressed in population production and is emphasized by the 30% rate of twinning during our March survey, which is high for that time of year.

Comparative twinning rate data are collected in May during the peak calving period and can be used in conjunction with other variables to determine the nutritional status of moose in an area. Density dependence occurs at high moose densities in interior Alaska when May twinning rates are 4–21% indicating nutritional stress, whereas in years of low moose densities and recovery of vegetation, rates are 30–47% (Boertje et al. 2007). The May twinning rate in our study area has recently been estimated as 47–67% (concurrent study; unpublished survey data, YDNWR), corroborating our assumption of a population at high nutritional status. This moose population continues to grow and is an important subsistence resource for local people and a monitoring program is essential for sound management regarding appropriate harvest levels to maintain a healthy, sustainable population. We recommend that surveys occur every 3–5 years to assess population trends and inform management decisions.

Future surveys along the lower Kuskokwim tributaries should follow the same protocol used here (and potentially the same transects; Buckland et al. 2001), with the exception of how moose locations under the aircraft were recorded. Perpendicular distances of moose detected by the front-left observer under the helicopter (i.e., moose groups approximately ± 43 m of the center line) should be estimated and recorded in future surveys. The precision of our density estimates would have increased if we did not lump and remove from analyses the 10 observations directly under the helicopter.

The kernel density estimator was fairly precise (CV = 18%); however, additional transects are required to increase precision in future surveys. Attaining a CV closer to 15% would require an additional 307 km of transects; a precision with CV = 10% would require an additional 1564 km, given the current group encounter rate. Given the narrow riparian corridors, it would be difficult to add transects without greatly increasing the chance of double counting groups. Thus, improved precision is limited by increasing the encounter rate; however, if a CV of 20% is acceptable, transect length could be reduced by ~133 km.

Another consideration is pooling data across years to obtain more robust, and potentially more precise estimates of detection probability (Burnham et al. 1980, Burnham et al. 2004, Fewster et al. 2005). Distance sampling is pooling robust and a common practice in a single study area because each transect typically has too few observations to calculate separate detection functions (Gerard and Schucany 2002). Pooling by year to increase sample size (observations) and to account for various survey conditions (e.g., snow conditions) could improve the global detection function for the area if repeated surveys are in the same area and preferably along the same transects (Nielson et al. 2014).

If the CV ranges from 13–19%, managers should be able to detect at least a 38% change in abundance using a 90% CI with 80% statistical power. Given our density estimate of 0.47 moose/km^2 (340 moose), we should detect a change in density if the population changed by ~0.18 moose/km^2 (129 moose; 38%). Furthermore, if there is a 5-year period between surveys, this would require a finite rate of change ($\lambda = e^{\{(\ln N_t - \ln N_0) / t\}}$, where N_0 is the starting abundance estimate, N_t is the abundance estimate at time *t*, and *t* is the time period between surveys; Skalski et al. 2005: 295) equal to λ = 0.909 annually for a decreasing population, or λ = 1.066 for an increasing population. This is a realistic change for moose in this area since the lower Kuskokwim survey unit showed an extreme growth rate of λ = 1.647 over a 4-year period (from 70 to 515 moose; Perry 2010).

Our research provides a viable alternative method to survey moose in a subarctic tundra ecosystem with marginal snow conditions. Presumably this technique could be applied elsewhere in areas with larger contiguous habitat and variable snow conditions such as portions of moose range within subarctic Alaska, Canada, Scandinavia, and Russia. Areas with dense canopy cover may require accounting for vegetation covariates affecting sightability which would require a larger number of group observations. Nevertheless, as climate change increases the disruption of prevailing weather patterns and causes more atypical and uncertain scenarios such as freeze-thaw or rain-on-snow events, our research and recommendations provide wildlife managers an accurate, efficient, and cost-effective option for surveying moose populations.

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