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Population Ecology

Using Distance Sampling and Hierarchical Models to Improve Estimates of Dall's Sheep Abundance

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ABSTRACT Management of large mammal populations has often been based on aerial minimum count surveys that are uncorrected for incomplete detection and lack estimates of precision. These limitations can be particularly problematic for Dall's sheep (*Ovis dalli dalli*) due to the high cost of surveys and variation in detection probability across time and space. The limitations of these methods have been recognized for some time, but previously proposed alternatives for sheep surveys proved to be too costly and logistically unfeasible in most circumstances (Udevitz et al. 2006). We assessed the potential for a combination of distance sampling surveys and a hierarchical modeling approach to provide a more efficient means for estimating Dall's sheep abundance by conducting aerial contour transect surveys over all sheep habitat in Gates of the Arctic National Park and Preserve (GAAR), Alaska in 2009 and 2010. We estimated the population of Dall's sheep was 8,412 (95% CI: 6,517–11,090) and 10,072 (95% CI: 8,081–12,520) in 2009 and 2010, respectively. Abundance within the Itkillik Preserve area within GAAR was 1,898 (95% CI: 1,421–2,578) and 1,854 (95% CI: 1,342–2,488) in 2009 and 2010, respectively. Estimates of lamb abundance in 2010 were more than double those of 2009 after correcting for detection bias related to group size, suggesting that the apparent estimate of lambs in the population may be biased in some years depending on the degree of aggregation. Overall, the contour transect surveys were feasible logistically, cost 70–80% less than minimum count surveys, and produced precise estimates of abundance, indicating that the application of these methods could be used effectively to increase the statistical rigor and spatial extent of Dall's sheep abundance surveys throughout Alaska. These methods could be used to improve the assessment of long-term trends in populations and productivity and provide valuable information for harvest management at both local and landscape scales at reduced costs in comparison to traditional minimum count surveys. © 2011 The Wildlife Society.

KEY WORDS abundance, aerial survey, Alaska, Dall's sheep, distance sampling, hierarchical spatial modeling, *Ovis dalli*.

Management of large mammal populations often depends on minimum count index surveys for population assessment (e.g., Wehausen 1996, Udevitz et al. 2006, Poole 2007, Seip et al. 2007), which are typically interpreted either as actual abundance or as indices of true population abundance (Williams et al. 2002). The basic assumptions of this type of survey are that all, or a constant proportion, of the individuals in the survey area are detected during each survey and changes in counts between surveys represent temporal variation in abundance. In many situations this assumption is tenuous at best, and variation in detection probability across time, space, and habitat can lead to misleading conclusions about population abundance and trends (Williams et al. 2002). These methods can also be quite inefficient due to the amount of time necessary to complete counts when conducted over large areas, suggesting that less intensive sampling approaches providing abundance estimates adjusted for incomplete detection, would be useful in most instances (Williams et al. 2002). Reduction in cost and improved estimation may be of particular importance for Dall's sheep (*Ovis dalli dalli*) management, which is currently based almost exclusively on aerial minimum count surveys (e.g., Singer 1984*a*, Udevitz et al. 2006, Alaska Department of Fish and Game 2008, Arthur and Prugh 2010). These counts are known to be affected by survey intensity, weather conditions, terrain ruggedness, and other factors, complicating comparisons between years and areas, and the intensity of the methods limits spatial coverage to localized survey areas.

Dall's sheep are an important game species and populations are monitored throughout Alaska to provide continued har-

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vest opportunities (Alaska Department of Fish and Game 2008). Sheep have also been identified for long-term monitoring as part of the National Park Service's (NPS) Inventory and Monitoring program in both the Central Alaska and Arctic Networks (MacCluskie et al. 2005, Lawler et al. 2009). The Arctic Network encompasses Gates of the Arctic National Park and Preserve (GAAR), Noatak National Preserve (NOAT), Kobuk Valley National Park, Cape Krusenstern National Monument, and Bering Land Bridge National Preserve; and the Central Alaska Network encompasses Denali National Park and Preserve, Wrangell-St. Elias National Park and Preserve, and Yukon-Charley Rivers National Preserve. Total available Dall's sheep habitat within these units is extensive, with estimates of over 41,000 km^2 and 29,700 km^2 within the Arctic and Central Alaska Networks, respectively. These areas combined have been estimated to contain as much as 40% of the entire Alaskan population of Dall's sheep (Heimer 1980). Gates of the Arctic National Park and Preserve alone is thought to contain >10% (Singer 1984*a*, *b*; Lawler et al. 2009) of the world's population (approx. 100,000; Valdez and Krausman 1999). Estimates of Dall's sheep abundance within GAAR are of particular interest because this species is valued by both subsistence and sport hunters, as well as non-consumptive park visitors seeking wildlife viewing opportunities.

Sheep habitat within and bordering GAAR has only been surveyed in its entirety once in the early 1980s using minimum count methods, and at that time the population was estimated to be approximately 11,000–12,000 sheep (Singer 1984*a*, *b*). During the 1990s, drastic declines in Dall's sheep numbers were reported across Alaska following several winters with higher than average snowfall and icing events that likely reduced access to forage and increased mortality (Ayers 1996, Whitten 1997, Brubaker and Whitten 1998). Although the population in the western Baird Mountains in NOAT adjacent to GAAR appears to be recovering (Shults 2004), the degree to which Dall's sheep numbers have changed in GAAR since the early 1980s is unknown. Localized areas have been surveyed subsequently using a combination of minimum counts and double-sampling (Adams 1988, Brubaker and Whitten 1998, Lawler 2004, Rattenbury and Lawler 2010), but surveys over the entire area were not attempted. Between 2005 and 2007, portions of GAAR were surveyed using minimum counts combined with stratified random sampling methods, but these surveys yielded imprecise abundance estimates. This was due to a lack of recent density data, sheep movement, and aggregation that affected sample unit stratification, as well as inadequate sample sizes and post hoc sightability estimation (K. L. Rattenbury and J. P. Lawler, National Park Service, unpublished data). The varying methods and success among these previous surveys makes trend analysis or comparisons among population estimates difficult, warranting the investigation of alternate methods of population estimation.

The weaknesses of standard minimum counts have been recognized for some time, and over the last several decades attempts have been made to estimate the proportion of sheep missed during standard fixed-wing surveys. Four alternatives have been considered: double-sampling (Gasaway et al. 1986, McDonald et al. 1990, Whitten 1997), sight-resight (Strickland et al. 1992), mark-resight (Neal et al. 1993, Udevitz et al. 2006, McClintock and White 2007), and the sightability-model approach (Bodie and Oldenburg 1995, Bodie et al. 1995, Udevitz et al. 2006). These methods all provide potential improvements over the minimum count approach, however, double-sampling and sight-resight models require repeated surveys of each unit, and mark-resight and sightability-model approaches require a marked population, increasing cost substantially. The assumptions of these survey methods can be difficult to meet under field conditions, and logistical requirements and financial restraints have limited their implementation (see Udevitz et al. 2006). Because of these limitations, landscape-scale surveys (e.g., >2,500 km^2) have been rare and often do not include corrections for sightability. Also, due to cost and logistical limitations (e.g., weather, aircraft availability), survey extent often fluctuates between years. The combined effects of incomplete detection, annual variability in search intensity, annual changes in sheep distribution, and differences in survey extent often result in population estimates that are highly variable with limited interpretability.

Distance sampling (Burnham et al. 1980; Buckland et al. 2001, 2004) is one potential alternative that has been used successfully to estimate density and abundance of a variety of species including:bears (*Ursus spp.*; Quang and Becker 1999, Becker and Quang 2009, Walsh et al. 2010), sika deer (*Cervus nippon*; Marques et al. 2001), wild turkeys (*Meleagris gallopavo*; Butler et al. 2007), and killer whales (*Orcinus orca*; Williams and Thomas 2009), among many others. In its most basic form, as transects are surveyed and individuals or groups are detected, the perpendicular distance to the transect line is recorded along with group attribute information. Detection probability generally declines with distance from the center-line and the shape of this decline, the detection function, can then be used to estimate the proportion of groups missed during the survey (Buckland et al. 2001, 2004). Covariates expected to affect detection probability (e.g., group size, habitat type) can also be added to the model for the detection function to help account for heterogeneity in the detection process, which improves local estimates (Marques et al. 2007). The basic assumptions of distance sampling are: 1) all groups on the line are detected, 2) distance measurements are accurate, 3) animals do not move away from the line in response to the observer prior to detection, and 4) detections are independent of one another. If these assumptions are met, estimates tend to be unbiased, even in the presence of heterogeneity in detection probability. Analytical methods for data collected using distance sampling have recently been incorporated into a Bayesian hierarchical modeling framework, allowing covariates to be included on both the detection and abundance processes (Royle et al. 2004, Royle and Dorazio 2008). These analytical tools tend to be more efficient and can be formulated to allow abundance to vary spatially, providing unbiased local abundance estimates.

In 2009 and 2010, we conducted separate aerial distance sampling surveys over all sheep habitat within GAAR with the goals of providing unbiased abundance estimates, with associated measures of precision, while reducing survey costs. Our primary objectives for this project were: 1) to assess the potential of aerial distance sampling surveys to provide theoretically sound estimates of Dall's sheep abundance over large areas, 2) to develop a Bayesian hierarchical modeling approach providing precise estimates of abundance across time and space, and 3) to provide design and analysis recommendations for future surveys of Dall's sheep.

STUDY AREA

Our study area included all Dall's sheep habitat within GAAR as well as small areas contiguous with the southern and eastern border of GAAR containing historically surveyed areas (67°03′–68°40′N and 149°22′–156°52′W; Fig. 1). This area covered most of the central Brooks Range and is characterized by the rugged Schwatka and Endicott Mountains and the headwater catchments for the Noatak, Alatna, Killik, Chandler, Anaktuvuk, John, North Fork of the Koyukuk, and Itkillik Rivers. These mountains reach 2,500 m and are characterized by steep spires, cirques, and arêtes sculpted by Pleistocene glaciers (Lawler et al. 2009). Mean maximum temperatures for July ranged spatially across GAAR from 10° C to 22° C (Davey et al. 2007). The predominant vegetation communities at higher elevations across the central Brooks Range were *Dryas*-sedge-lichen tundra and *Dryas*-mixed herb-lichen tundra on well-drained ridges and mountain sides.

METHODS

Survey Design

We conducted surveys across the entire study area during 2009 and 2010, although transect spacing and survey area were reduced in 2010 based on preliminary findings from the previous year. In 2009, we included all areas (31,452 km^2) that encompassed historic Dall's sheep survey units in GAAR based on Singer (1984*a*) and Brubaker and Whitten (1998; Fig. 1). We removed all non-sheep habitat in 2010, defined as areas below 600 m that were classified as spruce-dominated boreal forest based on Jorgenson et al. (2009), resulting in a reduced total survey area of 26,921 km^2 (Fig. 1). In 2009, we generated transect center points using a systematic 10 km grid to provide uniform coverage throughout the study area and to minimize transect overlap. We created transects ($n = 316$) approximately 20 km in length centered on each grid point using ArcMap 9.3 (Environmental Systems Research Institute, Inc. [ESRI], Redlands, CA). Transects followed contours at the elevation of their respective center points, although straight transects were used when points occurred in areas with slopes $\leq 7°$ based on a 60-m digital elevation model (USGS National Elevation Dataset [NED]). When full 20-km transects could not be generated due to limited terrain at the original elevation, we moved the center point slightly until a transect $\geq$15 km could be generated. In 2010, we generated transects ($n = 321$) using a 9-km grid and the same 60-m digital elevation model used in 2009. Where transects $\geq$15 km could not be generated due to limited terrain at the selected elevation, we continued the remaining portion as an additional segment at the same elevation on the

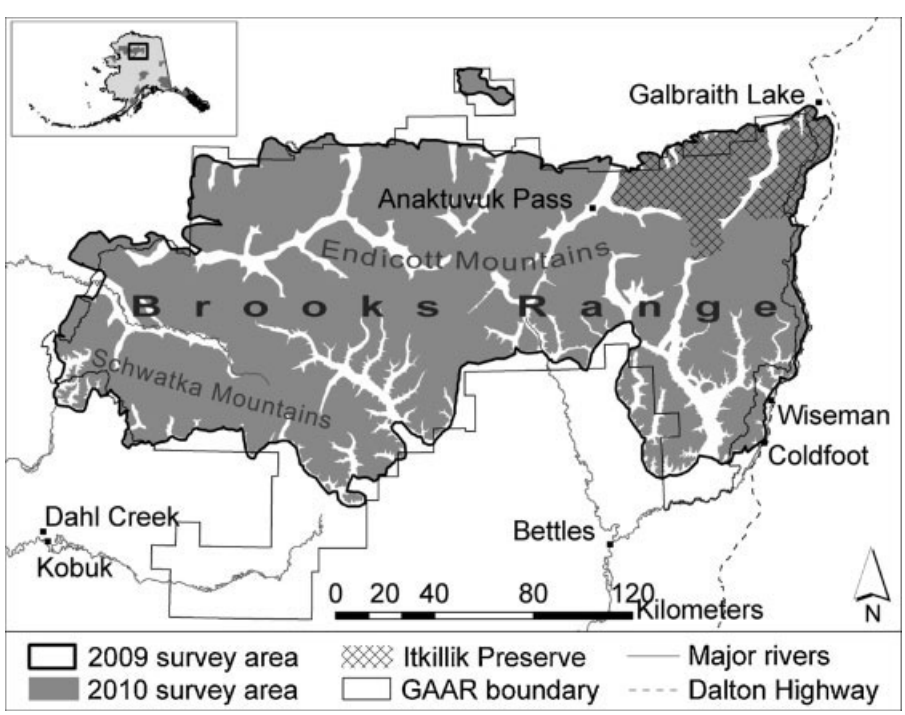

Figure 1. Areas surveyed for Dall's sheep in 2009 and 2010, including the Itkillik Preserve sub-region in Gates of the Arctic National Park and Preserve (GAAR), central Brooks Range, Alaska, USA.

nearest mountain to ensure that all elevations were sampled in proportion to availability (Walsh et al. 2010).

Field Procedures

We conducted surveys in late June and early July after the spring snowmelt, but as close as possible to the post-lambing season when sheep are highly visible. Previous aerial surveys of Dall's sheep in GAAR have also been conducted in late June and early July for similar reasons (Singer 1984*a*, Brubaker and Whitten 1998, Lawler 2004, Rattenbury and Lawler 2010). We conducted surveys using tandem aircraft (Piper Supercub; Piper Aircraft, Inc., Vero Beach, FL and Aviat Husky; Aviat Aircraft, Inc., Afton, WY) flown at roughly 90 m above ground level at approximately 100–120 km/hr. The pilot and observer (team) worked together searching for sheep on the uphill side of the line only (Fig. 2). We directed teams to thoroughly search areas nearest the line first to ensure that the assumption of complete detection on the line was met. Upon detecting a group of sheep (≥1 individual), the aircraft would deviate from the transect line recording the initial location of the group with a global positioning system (GPS). If groups were large and/or diffuse, we recorded the center of the group and considered sheep >100 m apart to belong to separate groups. Before leaving the line to collect information, the team continued past the group a short distance searching upcoming habitat to ensure that additional sheep were not detected after leaving the transect. We did not include additional detections while flying off the transect in the analysis because they would have violated the assumption of independence among detections.

After marking locations, the aircraft circled each group as necessary to confirm the count and composition (Fig. 3). Under certain habitat and terrain conditions, sheep can be difficult to count and classify, so we took digital photographs of most groups of >4 sheep to assist with this step. The team classified all sheep into 5 main sex and age composition classes: lambs, ewe-like (ewes, yearlings, and <1/4-curl rams), sub-curl rams (>1/4-curl and <full-curl), ≥full-curl rams, and unclassified.

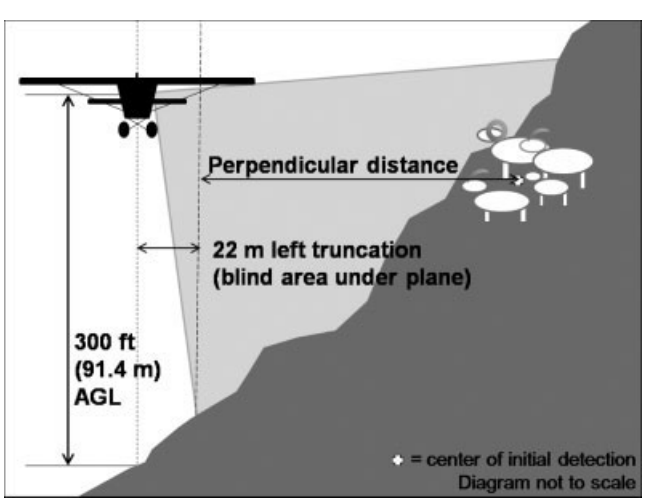

Figure 2. Aerial survey procedures for distance sampling of Dall's sheep in Gates of the Arctic National Park and Preserve, Alaska, USA, 2009 and 2010. Surveys were conducted at approximately 91 m above ground level (AGL), and the uphill search area (light gray area) was bounded by the wing tip and the 22 m unobservable area below the plane.

We recorded all data electronically on laptop computers running an ArcPad 7.1.1 (ESRI) application developed to facilitate data entry. This application displayed real-time GPS locations on a topographic map while automatically recording flight-lines and facilitating electronic data entry. The observer marked the start and end points of transects and because the aircraft could not always follow the transect lines exactly due to terrain, the on-effort flight line replaced the generated transect for analysis (see Becker and Quang 2009, Walsh et al. 2010). We processed all data prior to data analysis to reduce the potential for errors using methods similar to those described by Walsh et al. (2010).

Data Analysis

We used a spatially-explicit Bayesian modeling approach for analysis, allowing us to include covariates and random effects thought to influence detection probability, group abundance, and group size, while also allowing unbiased abundance estimation for smaller areas of specific management importance (Royle et al. 2004, Royle and Dorazio 2008, Johnson et al. 2010). This model-based approach is an extension of multiple covariate distance sampling (Buckland et al. 2004, Marques et al. 2007), and has been shown to be more efficient for non-random (e.g., systematic) sampling schemes (Johnson et al. 2010). The complete model we used consisted of 3 sub-models: 1) a model describing detection probability relative to distance, 2) a model for presence on the transect by a series of individual sheep groups (using a data augmentation approach for unobserved groups; see Royle and Dorazio 2008), and 3) a model for the size of each group present on a given transect. The observed group detection data are assumed to be the product of the probability of presence and the probability of detection for each potential group on each transect. To obtain estimates of abundance at the transect level, the estimates of group-specific probability of presence are multiplied by the estimated group size for each group and summed within transects. This is similar to the occupancy-abundance mixture models described by Royle (2004) and Kery et al. (2005) except that a detection function based on distance replaces repeated surveys for estimating detection probability, making subsequent visits unnecessary.

This approach required several data processing steps prior to abundance estimation. First we right-truncated the distance data from both years combined by removing the largest 5% of observed distances because the relatively few detections at large distances added little information for the estimation of the detection function and could complicate model fitting (Buckland et al. 2001). Second, standard line transect distance sampling theory assumes detection probability (P) = 1.0 on the transect line, but because of the configuration of the windows and landing gear, a small strip directly beneath the aircraft is blocked from view. We accounted for this unobservable area by left-truncating observed distances by 22 m, which is the width of this area on the uphill side of the aircraft (Walsh et al. 2010). Finally, we reduced the measured distances by the width of the unobserved strip

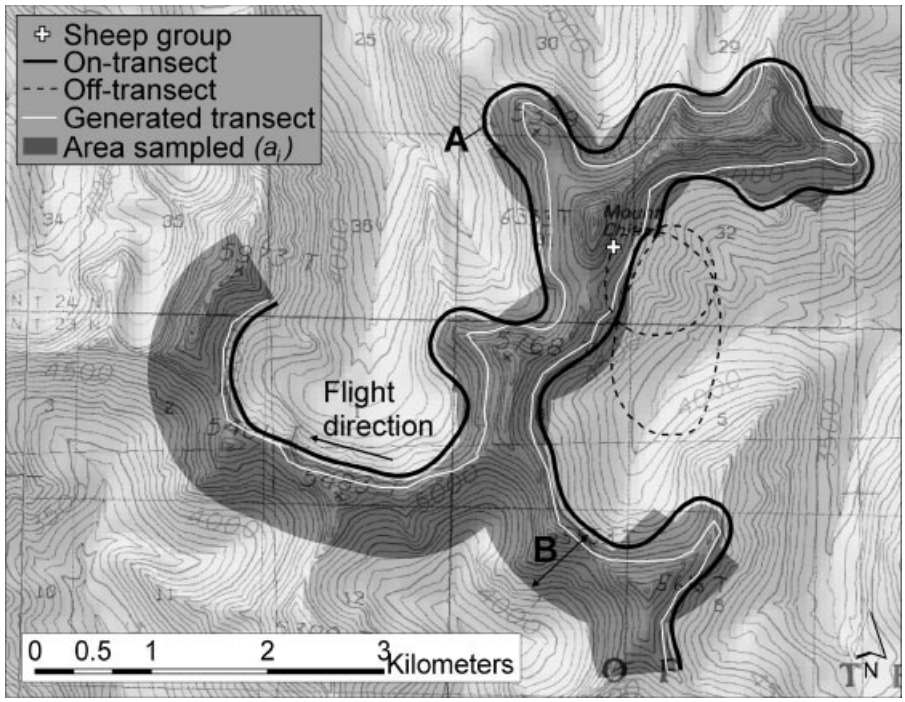

Figure 3. Example of a contour transect flown during Dall's sheep surveys in Gates of the Arctic National Park and Preserve, Alaska, USA in 2009 and 2010 showing the effective area sampled (a_i). Note the actual flight line (A) differs from the computer generated transect line. We estimated the effective strip width (B) from the smallest 95% of observed distances.

(Buckland et al. 2001). After these steps, the maximum remaining distance became the strip width estimate, w, which we used to calculate the area searched.

After we had an estimate of w, we then calculated the area searched on each transect, a_i. Conventional line transect theory for 1-sided transects assumes that density, D, can be estimated by

$$\hat{D} = \frac{n}{wL\hat{P}}$$

where n is the total number of animals, w and L are the width and total length of all transects, respectively, and $\hat{P}$ is the estimate of detection probability. In the case of single-sided contour transects, the value of the denominator is no longer simply $w \times L$ because portions of the surveyed strip may overlap (Quang and Becker 1999, Buckland et al. 2001, Walsh et al. 2010). Overlapping areas must be combined to create a polygon representing the total area surveyed, a_i, for each transect, and transect specific density, D_i, can now be estimated by

$$\hat{D} = \frac{n_i}{a_i\hat{P}_i}$$

where $\hat{P}_i$ is the transect-specific detection probability. To calculate a_i, we used the buffer tool in ArcMap 9.3 (ESRI) to create a buffer of width w beginning at 22 m from the flight line on the uphill side of each transect. The area of the polygon for each transect i represents the sampled area per transect, or a_i (Fig. 3). Once these measurements were complete, model fitting could begin.

The first step in the model fitting process was to select a basic model for the detection function. We considered both the hazard-rate

$$1-\exp\left(-\left(\frac{x}{\sigma}\right)^{-b}\right)$$

and half-normal

$$\exp\left(\frac{-x^2}{2\sigma^2}\right)$$

key functions as a model for the detection process where x is distance from the line, σ is the scale parameter, and b is the shape parameter. Preliminary histograms of the data showed that detection declined monotonically out to distance w suggesting 1 of these models could be an appropriate representation of the data without any series expansions. We then fit each of these models to the entire data set (i.e., both years combined) using Program Distance 6.0 (Thomas et al. 2009, 2010) and used differences in the Akaike's Information Criterion (ΔAIC) to select among them (Burnham and Anderson 2002). Once the functional form of the detection function was selected, we conducted all subsequent analyses and interpretation in a Bayesian framework.

For abundance estimation, we used a data-augmentation approach similar to that described by Royle and Dorazio (2008) where the matrix of distances to observed groups on each transect was augmented with a large number of missing values representing potential unobserved groups to be estimated during the updating process. We then derived the

total abundance of groups by summing the posterior inclusion probabilities across all groups, both observed and unobserved. We also needed to estimate the size of the unobserved groups. We assumed the population of group sizes came from a Poisson distribution, although we suspected that the assumption of equal mean and variance for this distribution was not likely to be met. To more accurately represent the uncertainty surrounding these estimates, we modified this estimator to include a mean 0, normally distributed random effect, e_{ij}, for each of the 2 years, creating an over dispersed Poisson model for group size. We assumed that the distribution of group sizes would vary between years, so we fit a model containing separate intercepts and random effects distributions for each year. Our full model for group size is

$$\hat{E}(s_{ij}) = \exp(\alpha_{\text{year}} + e_{ij})$$

where $\hat{E}(s_{ij})$ is expected cluster size on transect i for cluster j (detected or not), and α_{year} is a year-specific intercept.

We modeled variation in detection probability relative to covariates through adjustments to the scale parameter, σ, of the selected detection function (Buckland et al. 2004, Marques et al. 2007). We assumed that detection probability likely differed between the 2 years of the project. Because transects may have been in somewhat less rugged terrain in 2009 due to slight adjustments made to ensure transect generation, and the inclusion of non-habitat that tended to be flatter, we expected that the scale parameter would be larger (i.e., visibility is better in less rugged terrain) than in 2010 when habitat was sampled in direct proportion to availability (i.e., higher proportion of rugged terrain in the sample). We also expected cluster size to influence detection probability with larger clusters having higher detection probabilities at longer distances. This relatively simple model for variation in σ was

$$\sigma = \exp\left(\beta_{\text{year}} + \beta_1 \text{size}_i\right)$$

where β_{year} is the year-specific intercept and β_1 is the adjustment for cluster size. We considered additional covariates such as weather conditions and turbulence severity for each surveyed transect, but we did not record these covariates in 2009 preventing us from investigating these potential effects. Pilot-observer team effects can also be an important source of heterogeneity in detection probability, but these effects were confounded with density because transects were completed in blocks by each team precluding unbiased estimation of this parameter (see Johnson et al. 2010). We minimized this potential problem by using only experienced teams, although we were not able to assess the magnitude of this issue directly.

Finally, we expected variation in the distribution of sheep throughout the study area based on previous work. For example, previous surveys have recorded higher densities of sheep in the Itkillik Preserve than in other areas within GAAR (Singer 1984*a*, K. L. Rattenbury and J. P. Lawler unpublished data), and we expected quality of habitat to vary spatially and temporally in this highly seasonal and heterogeneous environment. We also suspected that densities and distribution could be different between the 2 years. To account for these sources of variation we allowed the intercept to vary between the 2 years and included a quadratic effect of the transect elevation on group presence. Transect elevations were scaled to have a mean = 0 and standard deviation = 1 to improve convergence. Other habitat-specific covariates that may have explained variation in density of groups were unavailable; we therefore included a conditionally autocorrelated (CAR) random effect to account for spatial patterns in unmeasured habitat covariates. We considered transects within each year to be neighbors if their center points were $\leq$11 km apart, corresponding to the 4 neighbors in the 4 cardinal directions. Although transects in similar geographic locations between years were not considered to be neighbors, the variance of the overall random effect was shared under the assumption that the annual spatial autocorrelation process would be similar. Our final model describing variation in the probability of group presence on each transect, Ψ_i, was

$$\text{logit}(\Psi_i) = (\gamma_{\text{year}} + \gamma_1 E_i + \gamma_2 E_i^2 + e_i)$$

where γ_{year} is the year-specific intercept, γ_1 and γ_2 are parameters, E_i is the elevation of transect i, and e_i is the CAR random effect.

We fit the described model using Markov chain Monte Carlo (MCMC) sampling in WinBUGS 1.4 (Spiegelhalter et al. 2004), using program R (R version 2.9.0, www.r-project.org, accessed 25 June 2011) for data processing and as an interface with WinBUGS (see Supporting Information for WinBUGS code and data used for analysis, available online at http://onlinelibrary.wiley.com). We used diffuse normal priors on most parameters with all $\alpha_i \sim N(0,100)$, $\beta_{\text{year}} \sim N(0,100)$, and $\gamma_i \sim N(0,100)$. Because we used a normal CAR distribution for the spatial random effects, we used a flat prior for the year intercepts for cluster presence. The prior for the precision of the spatial random effect was $\tau_{\text{spat}} \sim \text{Gam}(0.5, 0.0005)$, and priors for standard deviation of the random effects on probability of presence were $\sigma \sim \text{UNIF}(0, 100)$. We ran 2 MCMC chains with a burn-in of 40,000 iterations to eliminate any effects of the starting values. We used the next 60,000 iterations for inference, keeping every sixth sample, yielding 20,000 samples from the posterior distribution for each parameter. We assessed convergence through a visual inspection of plots of the chains and by using the Gelman-Rubin diagnostic (Brooks and Gelman 1998). We assumed convergence had been reached when chains were substantially overlapping and the Gelman-Rubin diagnostic was <1.1 for all monitored parameters.

We converted the transect-level estimates of density, $\hat{D}_i$, to local abundance, $\hat{N}_i$, by multiplying $\hat{D}_i$ by the area sampled for each transect (a_i). We then obtained regional abundance estimates, $\hat{N}_{\text{total}}$, by summing all $\hat{N}_i$'s in the region of interest and dividing this by the ratio of the total area sampled (i.e., sum of a_i's within the region) to the total survey area. We calculated group size-adjusted estimates of lamb abundance

by multiplying estimates of individual group size per transect by the year-specific observed mean number of lambs in each group size category during each iteration. We summed these values to obtain the total number of lambs per transect, and estimated total lamb abundance using the same methods as $\hat{N}_{\text{total}}$. We estimated the adult component of the population by subtracting the lamb estimate from $\hat{N}_{\text{total}}$. Because lambs are always found with adults and detection probability was related to group size, it was not possible to directly estimate lamb and adult abundance separately. We calculated all derived estimates as part of the MCMC updating process so that all variances and credible intervals appropriately reflected any co-variation between parameters. We presented all estimates as means and 95% credible intervals (CI).

RESULTS

During 2009 with 4 pilot-observer teams, we completed 287 transects from 23 June to 30 June and an additional 21 transects between 22 July to 25 July for a total of 308 of 316 transects. Lingering snow cover in some areas during June necessitated later completion of the remaining transects in July 2009. During 2010, 5 teams conducted surveys from 6 July to 13 July and completed 318 of 321 transects. Seventeen transects completed in 2010 consisted of multiple segments, and snow cover was minimal. We detected 166 groups, totaling 727 sheep on 73 transects in 2009, and 220 groups, totaling 557 individuals on 86 transects in 2010 (Fig. 4). Flight time per sampled transect averaged approximately 15–20 min. The total amount of aircraft time used to complete the surveys was 170 hr and 110 hr in 2009 and 2010, respectively.

After right-truncating the data to remove approximately 5% of observations at the largest distances, 146 and 214 groups of sheep remained for analysis in 2009 and 2010, respectively. After left truncation, to account for the 22 m unobservable strip beneath the aircraft, we estimated that $w = 663$ m. Using this estimate, approximately 11–12% of the total study area was covered by the surveyed transects in each year. Model-selection results indicated that the hazard-rate function provided a better fit to our combined data than did the half-normal (ΔAIC $= 3.9$), and was used to produce all subsequent abundance estimates. Detections declined monotonically with distance, and the fitted detection function represented the observed data (Fig. 5) suggesting that the basic assumptions of the method were met.

Estimates of total abundance of Dall's sheep in GAAR did not differ substantially between years and were quite precise with approximate coefficient of variations (CVs) of 14% and 11% for 2009 and 2010, respectively (Table 1). Abundance estimates for the 2,542 km^2 Itkillik Preserve area were also similar between years, with approximate CVs of 16% in both years (Table 1). Estimates of the adult component of the population were comparable between years, but estimates of lamb abundance were 57% lower in 2009 than in 2010 (Table 1). This contrasts with the naïve estimate derived from raw counts unadjusted for group size bias, which suggests only a 40% difference in lamb abundance between the 2 years. Based on the adjusted estimates, lambs composed 10% and 19% of the population in 2009 and 2010, respectively. Observed mean group sizes were much higher in 2009 ($\bar{s} = 4.3$) than in 2010 ($\bar{s} = 2.5$), although estimated group sizes, corrected for size-biased detection relative to distance, were much smaller in both years (Table 2). The positive

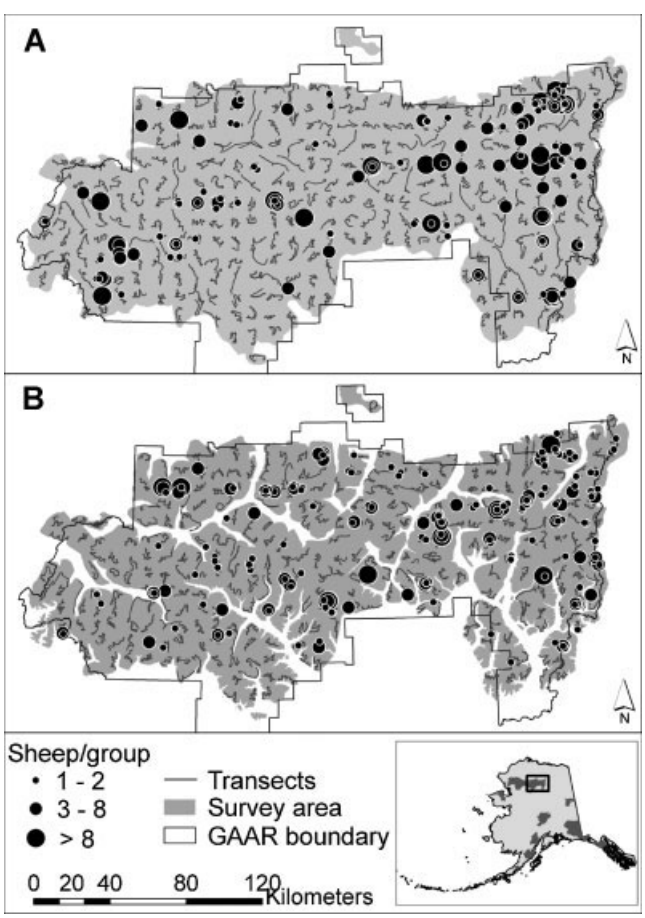

Figure 4. Locations of generated transects and detected groups of Dall's sheep during distance sampling surveys, Gates of the Arctic National Park and Preserve (GAAR), Alaska, USA, 2009 (A) and 2010 (B).

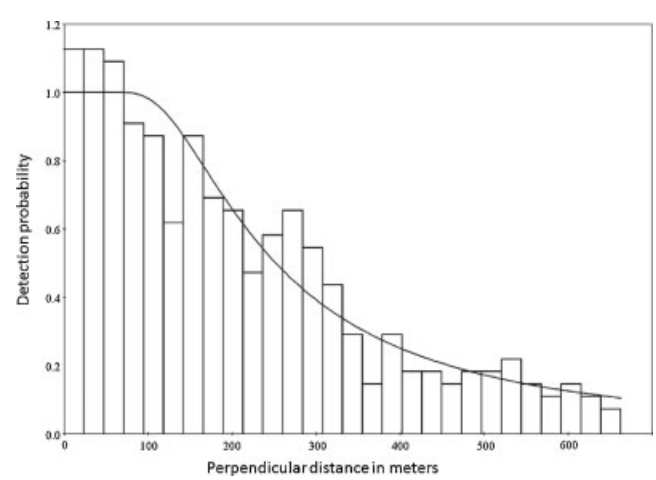

Figure 5. Histogram of observed distances for all Dall's sheep groups observed during 2009 and 2010 in Gates of the Arctic National Park and Preserve, Alaska after right-truncating approximately the largest 5% of observations. The solid line represents the fitted hazard-rate detection function.

Table 1. Estimated Dall's sheep abundance for selected areas and components of the population during 2009 and 2010 in Gates of the Arctic National Park and Preserve, Alaska, USA. Numbers in parentheses indicate 95% Bayesian credible intervals.

Estimate	2009	2010
$\hat{N}_{\text{Total}}$	8,412 (6,517–11,090)	10,072 (8,081–12,520)
$\hat{N}_{\text{AdultTotal}}$	7,571 (5,871–9,975)	8,127 (6,523–10,100)
$\hat{N}_{\text{LambTotal}}$	841 (631–1,126)	1,945 (1,523–2,456)
$\hat{N}_{\text{Itkillik}}$	1,898 (1,421–2,578)	1,854 (1,342–2,488)

group size effect indicated that we saw fewer small groups at larger distances, biasing observed means high in both years. There was strong evidence that the probability of group presence increased with elevation ($\text{logit}[\beta_{\text{elev}}] = 1.28$; 95% CI: 0.94–1.63) and elevation^2 ($\text{logit}[\beta_{\text{elev}}{}^2] = 0.13$; 95% CI: −0.07–0.35) as expected. There was also some evidence that the scale parameter differed between years, although credible intervals overlapped (Table 2).

DISCUSSION

We found distance sampling surveys, using relatively low transect densities, were a viable approach for reducing survey effort while producing precise estimates of Dall's sheep abundance at both regional and landscape scales. We are aware that the adoption and subsequent implementation of a new survey protocol necessitates that any additional complexities are offset by gains in logistical, financial, and analytical efficiency. The distance sampling approach we describe substantially increased the time required for training, data management, and analysis; however, the logistical, financial, and spatial inference advantages were considerable. Because we were able to complete an average transect within approximately 15–20 min, weather conditions were less limiting than in unit-based full coverage surveys, allowing us to complete 2 park-wide surveys in subsequent years. This has never before been possible due to inclement weather and the amount of time required to complete full coverage surveys. The only other total survey of this area took 3 years to complete (Singer 1984*a*), complicating inference due to potential changes in survey conditions, distribution, and abundance. Based on the search intensities used in recent minimum count surveys (Rattenbury and Lawler 2010), our approach reduced total survey costs by 70–80%. These savings dramatically outweighed the increased costs for survey design and analysis, with the added benefit of precise and comparable abundance estimates.

As with any analytical approach, the validity of our estimates depends on meeting the underlying assumptions. The assumption of 100% detection probability on or near the line is probably the most critical for a distance sampling survey of this type, and violation can result in serious negative bias (Buckland et al. 2001). Although we could not directly test this assumption, we did not find any evidence of this in the observed data. The detection function had a characteristic shoulder where detection probability was constant to approximately 100 m (Fig. 5), providing some evidence that teams were not systematically failing to observe sheep near the line (Buckland et al. 2001). It is possible that some small proportion of sheep were unavailable to be sampled because they were in caves, under rock-overhangs, or otherwise not visible. However, sheep are white and occupy largely open habitats making them more visible than other species (Udevitz et al. 2006), suggesting that this potential source of bias was small. However, for these reasons estimates from most sheep surveys, except those based on mark-resight data, should be interpreted as representing the sheep population available for sampling.

The remaining assumptions were less likely to cause problems for estimation due to strict survey protocols. Sheep often move in response to approaching aircraft, therefore, we instructed teams to pay particular attention to and mark the original location of the group. In addition, because sheep move slowly relative to the speed of the aircraft, movement prior to detection was unlikely to cause bias (Buckland et al. 2001). Perpendicular distance measurements were assumed to be accurate, and although the error associated with GPS locations is likely small relative to observed distances, marking of group locations was done while flying parallel to the transect line whenever possible to decrease error. Finally, instructing teams to continue past observed groups to ensure that they did not detect additional sheep after leaving the line helped to meet the assumption of independence. We found that teams were able to follow these instructions, ensuring that we likely met the basic assumptions of the sampling approach. For these reasons, we expected our abundance estimates to reflect true abundance within the study area.

The Bayesian analytical approach we used also provided several advantages. By combining all of the data into a single

Table 2. Parameter estimates and 95% credible intervals from the combined Dall's sheep detection and abundance model during 2009 and 2010 in Gates of the Arctic National Park and Preserve, Alaska. Estimates for group size and detection are on the natural log scale, and estimates for presence are on the logit scale.

Parameter	Presence	Group size	Detection
Intercept_{2009}	−4.6 (−5.1 to −4.0)	1.02 (0.80–1.22)	0.56[a] (−0.01 to 1.05)
Intercept_{2010}	−8.0 (−10.6 to −5.7)	0.68 (0.53–0.82)	0.39[a] (−0.09 to 0.78)
Elevation	1.29 (0.96–1.65)		
Elevation^2	0.13 (−0.08 to 0.33)		
Size			0.11 (0.01–0.26)
Tau_{2009}[b]	0.12 (0.08–0.18)	1.88 (1.33–2.57)	
Tau_{2010}[b]		3.19 (2.21–4.54)	
Shape parameter			2.01 (1.40–2.89)

[a] Year specific intercepts for the scale parameter of the detection function.
[b] Precision of the random effect terms. Precision is shared across years for presence.

analysis, we were able to borrow strength for parameter estimation across years and regions. This could help to reduce the sample size requirements for future surveys because information about the detection process is continually collected through time. Covariates can then be included (e.g., year, study area, terrain), reducing bias in local estimates (Royle et al. 2004, Marques et al. 2007) without resorting to stratification, which necessitates larger sample sizes (Buckland et al. 2001). Typically, distance sampling surveys require a minimum of 60–80 detections in order to estimate the detection function and more when populations occur in groups or strata (Buckland et al. 2001). The precision desired for population monitoring and management can increase these requirements substantially (Buckland et al. 2004), but by combining information across surveys in a spatially explicit framework, sample size requirements for individual survey areas may be reduced. The utility of similar techniques for predicting occurrence at individual sample units has recently shown potential for assessing changes in the distribution of animals on the landscape as well (e.g., Gardner et al. 2010) and could be used to identify distributional changes related to harvest management.

We also found Bayesian methods applied in a model-based framework to be more theoretically sound than minimum counts while providing precise estimates (i.e., CVs <15%) useful for management. Our estimates were similar between 2009 and 2010, suggesting that these methods produced repeatable results across years, and we found no evidence that assumption violations occurred. Our point estimates of approximately 8,400 and 10,000 sheep in GAAR in 2009 and 2010, respectively, and approximately 1,900 sheep in the Itkillik Preserve in both years are in line with anecdotal information and the most recent minimum counts for this area (Rattenbury and Lawler 2010). However, a direct comparison of our estimates with past information is not possible due to methodological differences. Despite the lack of a current, comparable estimate of the GAAR sheep population, distance sampling theory is well developed and has been shown to produce unbiased estimates in similar situations when assumptions are met (Buckland et al. 2001, 2004). The correspondence between our results and the available population information, combined with the ability to meet the primary assumptions of the methods, suggests that our estimates reflect true Dall's sheep abundance. We expect this would be the case under similar circumstances in other areas and for other species that occur in open habitats with good sightability.

One result with implications for other aerial survey work was the apparent bias in different age classes due to dependence between group size and detection probability. Our results agreed with past work indicating that larger groups are detected more often than smaller groups (Udevitz et al. 2006), but if certain sex or age classes occur primarily in smaller groups, that component of the population will tend to be underestimated. We found this to be the case when estimating the lamb component of the overall population in GAAR. Single ewes with lambs tended to be undercounted, especially in 2010 due to smaller group sizes overall that year. Our results suggest that using observed ratios as an estimate of lamb abundance can result in negative bias in some years depending on the distribution of group sizes. This problem is likely to occur for other sex and age classes and is especially important if the harvested component of the population tends to occur in smaller groups (i.e., mature rams).

Although we applied these methods solely to Dall's sheep, we expect that similar benefits could be realized across a broad range of other large mammal projects. For example, surveys for other mountain dwelling species, such as mountain goats (*Oreamnos americanus*) that are highly visible, might be improved or expanded using these methods with little or no modification. As long as the primary assumptions of the methods can be met, we expect that the benefits of increased precision and accuracy, as well as a reduction in survey cost, would be realized. For species occupying nonmountainous habitats, such as muskoxen (*Ovibos moschatus*), the use of straight line transects in a similar sampling and analytical framework could be employed with similar benefits. Survey costs often account for a considerable portion of the operating budget for many agencies charged with managing populations of large mammals. A substantial reduction in the amount of effort required to obtain estimates would provide the opportunity to conduct more detailed studies on other aspects of population ecology, complete work on additional populations or species, or simply reduce total operational costs and risk to personnel. Any of these results would benefit population management.

Despite the promising results for Dall's sheep surveys, we caution that distance sampling methods will not be applicable in all settings due to sample size requirements and the limited visibility of some species in some habitats. However, recent advances in sampling methodology (e.g., repeated counts, double observer methods, removal methods) could also be combined in a hierarchical model-based framework to dramatically improve population estimation and monitoring for a variety of large mammals. All of these methods share a common feature, the estimation of and correction for incomplete detection, whereas the primary difference among them is the method used to estimate detection probability. Rather than focusing on a particular field method, we envision a scenario where managers would select the appropriate sampling tool based on the characteristics of the species and population of interest, and then conduct analyses in a hierarchical modeling framework. Many sampling tools, and distance sampling in particular, are backed by well-developed theory, however, researchers should focus more on selecting the appropriate sampling approach for the population of interest and less on the tool itself. Each sampling method has inherent strengths and weaknesses and is unlikely to be ideal in all settings, however, using an adaptive, species-specific approach to sampling and analysis would allow great flexibility, providing managers with many options for population assessment.

MANAGEMENT IMPLICATIONS

The high cost, high variability, and unknown sampling error of minimum count surveys can limit their utility for man-

agement, even within small areas. All survey designs have tradeoffs, and although we did not conduct a detailed power analysis, our results provide some basic guidance for future Dall's sheep surveys with conditions and goals similar to ours. We suggest that approximately 150–200 group detections may represent a reasonable goal for data sets that will be analyzed independently. The assumed sheep density in the area to be sampled should be used to estimate the number of transects necessary to detect this many groups. If variation in group sizes or densities is expected to be higher than in our study, larger sample sizes would be required to realize similar levels of precision. If data from multiple surveys will be combined in a Bayesian framework, sample size requirements for each individual survey would be reduced, suggesting that additional benefits would be gained through a broader coordination of survey and analytical efforts across management units and agencies. This would increase precision and decrease cost due to an overall reduction in effort, although simulations would be required to formally assess the magnitude of this reduction and optimal sample sizes for each survey area. We encourage other agencies to consider using these methods for population monitoring and expect that their implementation would enable managers to survey a much larger proportion of the available Dall's sheep habitat than is currently possible, thereby helping to assess population trends and determine appropriate harvest levels for this desirable game species range-wide.

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