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Development of an Aerial Survey Population Estimation Technique for Mountain Goats in Alaska

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Cover Photo: An adult female mountain goat with twins accompanied by another adult female, Copper Mountain, Cleveland Peninsula, Alaska, July 2016. Photo by Kevin White.

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Abstract

Acquisition of precise and reliable information about population abundance and productivity is critical for understanding population dynamics and devising effective conservation strategies. Mountain goats are an iconic species of northern ecosystems and are highly valued for their human and aesthetic value, yet routine monitoring of populations is hampered by limited technical capabilities for assessing sources of variability in raw survey data. We addressed this problem by developing a regression-based fixed-wing aerial survey estimator using Bayesian statistical methods. We used mark-resight data with associated covariates collected from 558 observations of radio-marked mountain goats during 2008–2015 in 4 different study areas in Southeast Alaska to parameterize models. Our top model indicated that mountain goat aerial survey sighting probabilities varied with respect to cloud cover, group size, habitat, and terrain type. When statistically accounting for these covariates our model produced reliable results when compared to independent estimates for 25 different surveys. We also determined that our estimator was capable of deriving precise (i.e., CV ≤ 0.20) estimates when the average number of individuals seen on a given survey was greater than 26 animals, or 13 groups. We recommend broad use of our model to derive population estimates in routine monitoring of mountain goat populations, and to assist in development of conservation strategies.

Key words: aerial survey, Alaska, Bayesian statistics, mountain goat, *Oreamnos americanus*, population estimation, sightability modeling

Introduction

Mountain goats (*Oreamnos americanus*) are an iconic species of northern ecosystems and are highly valued for their human and aesthetic values. Compared to other North American ungulate species, mountain goats are particularly sensitive to human activities, including hunting (Hamel et al. 2006, Rice and Gay 2010), industrial disturbance (Joslin 1986, Côté 1996, Côté et al. 2013, White and Gregovich 2016), and recreational activities (Richard and Cote 2015, Hurley 2004, Goldstein et al. 2005, Cadsand 2012, St-Louis et al. 2013). Consequently, acquisition of precise and reliable information about population abundance and productivity is critical for understanding population dynamics and devising effective conservation strategies.

Estimating mountain goat population size presents a technical challenge due to the remote and rugged mountain environments they inhabit. In most cases, mountain goats are enumerated during aerial surveys in order to derive inference over large, management-relevant landscapes (Poole 2007, Rice et al. 2009); though ground-based estimates are possible in some settings (Gonzalez-Voyer et al. 2001, Belt and Krausman 2012). Survey counts can be of limited utility for conservation because not all animals in the survey area will be seen and counted during the survey (Caughley 1974), and the unknown proportions of animals not seen varies among surveys. This problem can be rectified by estimating the number of animals missed during surveys, often using marked animals and mark-resight (e.g., Lincoln-Petersen or Chapman) or logistic regression-based statistical estimators (Williams et al. 2001). Mark-resight estimators are capable of providing very accurate and precise population estimates but can have limited spatial and temporal utility due to the requirement of having an adequate sample of marked animals in a given area at the time of survey. Regression-based estimators are designed to have broader utility and, while based on mark-resight data, do not require marked animals in order to produce population estimates for a given area.

Rice et al. (2009) developed a regression-based “sightability” model for mountain goats in the Cascade and Olympic ranges in Washington based on mark-resight data using a helicopter-based aerial survey approach. This model has broad utility throughout many areas in mountain goat range but cannot be directly applied in regions where fixed-wing aerial surveys are routinely used. In Alaska and other large, remote jurisdictions, slow flying fixed-wing aircraft (e.g., Piper PA-18 Supercub) are commonly used to conduct mountain goat aerial surveys due to their extended flight service range (6–7 hours), cost efficiency and more limited noise disturbance, relative to helicopters. An apparent disadvantage of fixed-wing aircraft relates to reduced visibility due to higher travel speed and limitations on the number of observers, relative to helicopters. Sightability models (and associated coefficient estimates) derived from helicopter-based survey data may not be applicable with data collected from fixed-wing aircraft. Consequently, a need exists to develop a regression-based aerial survey estimator applicable to fixed-wing aerial surveys for broad utility across Alaskan and other comparable landscapes.

Rice et al. (2009) employed a design-based approach to population size estimation through a logistic regression analysis applied to sightability data collected from mountain goats fitted with GPS collars. This analysis modeled the detection probability as a function of group size, terrain obstruction, and overstory vegetation. They then estimated abundance by applying a modified Horvitz-Thompson (mHT) sightability adjustment to groups observed during operational surveys by dividing counts by their estimated detection probability. The mHT estimator has been shown to be right-skewed when operational surveys involve few sampling units (Fieberg et al. 2013) and to be inefficient when detection probabilities are low (Little 2009). The standard variance estimator developed by Steinhorst and Samuel (1989) for this type of model also underestimates the variance when the number of sightability trials is small (Fieberg and Giudice 2008).

The goal of this study was to develop a model-based estimator from fixed-wing aerial surveys using a Bayesian framework, similar to that developed by Fieberg et al. (2013), that could be widely used to produce population estimates of mountain goats from data collected during routine aerial surveys conducted in Alaska (and elsewhere). The use of a model-based estimator developed within a Bayesian framework provides an intuitive approach for handling survey non-response (i.e., non-detection of a marked animal that is known to be present within the bounds of the survey area) and missing covariate data, as well as having the potential for improved inference when sample sizes are small (Little 2009). Use of a Bayesian statistical framework was also intended to enable easy integration of future analytical advancements, specifically as it relates to using multiple sources of information (i.e., Johnson et al. 2010).

Study Area and Methods

Study Area

Mountain goats were studied in 4 separate study areas in Southeast Alaska (White et al. 2010, 2012a, 2012b, 2012c, 2012d; Fig. 1a). In general, the overall area has a maritime climate characterized by cool, wet summers and relatively warm, snowy winters. Annual precipitation at sea level averages 140–400 cm and winter temperatures are rarely less than -15º C and average 0º C. Elevations above 800 m can receive ca. 635 cm of snowfall annually (Eaglecrest Ski Area, Juneau, AK, unpublished data). Predominant vegetative communities occurring at low to moderate elevations (<750 m) include Sitka spruce (*Picea sitchensis*)-western hemlock (*Tsuga heterophylla*) coniferous forest, mixed-conifer muskeg, and deciduous riparian forests. Mountain hemlock (*Tsuga mertensiana*) dominated 'krummholtz" forest comprises a subalpine, timberline band occupying elevations between 750 and 1000 m. Alpine plant communities are a mosaic of relatively dry ericaceous heathlands, moist meadows dominated by grasses and forbs and wet fens, rocky unvegetated areas, and snowfields. Avalanche chutes are common in the study area, bisect all plant community types, and often terminate at sea level.

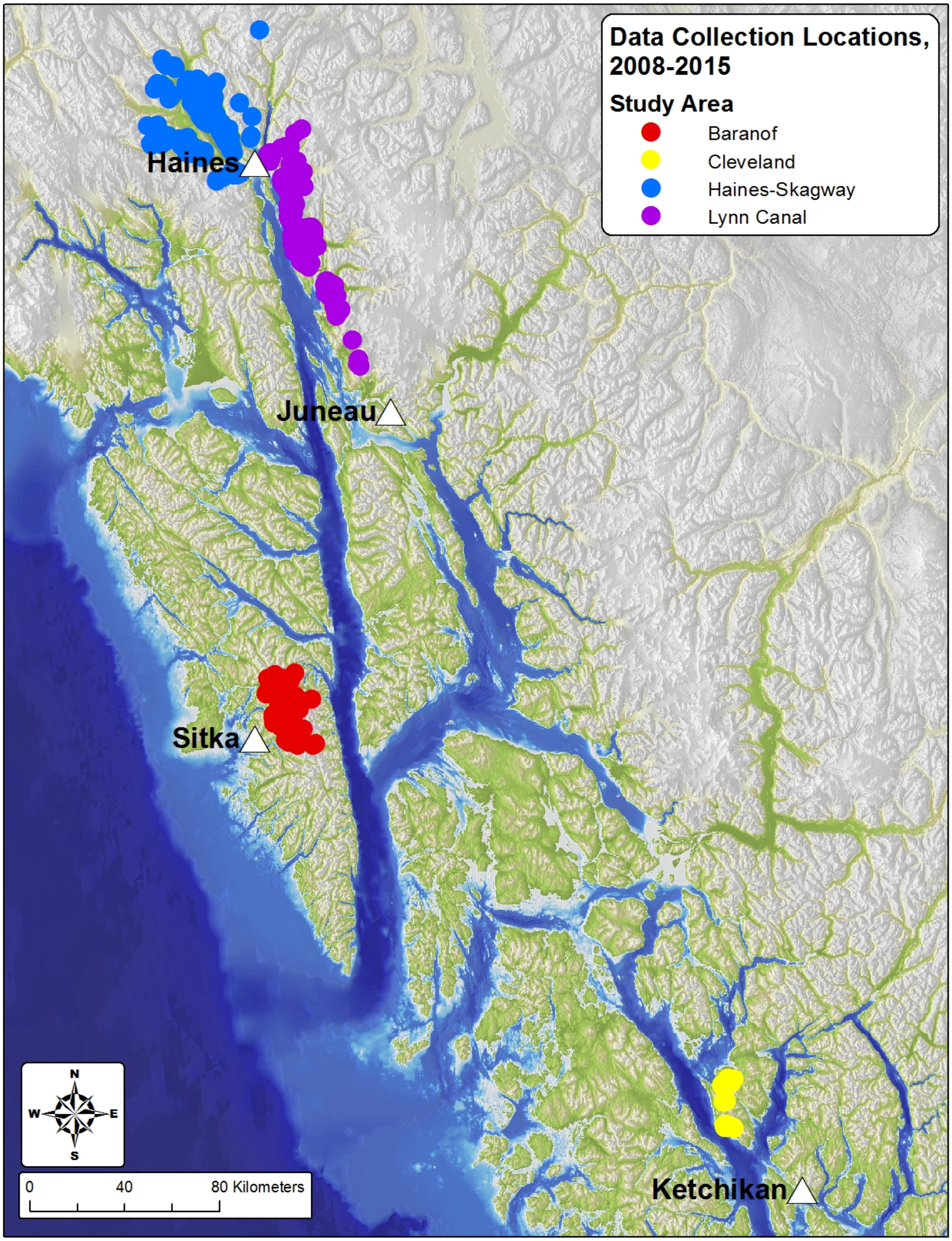

Figure 1. Mountain goat study areas, Southeast Alaska, 2008–2015.

During summer and fall mountain goats use relatively open subalpine and alpine habitats between 900 and 1,500 m in elevation (White et al. 2012b).

Mountain Goat Capture

Mountain goats were captured using standard helicopter darting techniques and immobilized by injecting 3.0–2.4 mg of carfentanil citrate, depending on sex and time of year (Taylor 2000, White et al. 2012a-d), via projectile syringe fired from a Palmer dart gun (Cap-Chur, Douglasville, GA). During handling, all animals were carefully examined and monitored following standard veterinary procedures (Taylor 2000) and routine biological samples and morphological data collected. All animals were equipped with red or orange GPS (Telonics TGW-3590; Telonics Inc., Mesa, AZ) and/or VHF radio collars (Telonics MOD-500, MOD-410) and ear tags (Allflex, Dallas, TX). Following handling procedures, the effects of the immobilizing agent were reversed with 100 mg of naltrexone hydrochloride per 1 mg of carfentanil citrate (Taylor 2000). All capture procedures were approved by the State of Alaska Animal Care and Use Committee.

Aerial Survey Data Collection

Aerial Surveys—Population abundance and composition surveys were conducted using fixed-wing aircraft (Heliocourier and PA-18 Super Cub) during August–October 2008–2015. Aerial surveys were conducted when conditions met the following requirements: 1) flight ceiling >1,524 m above sea level, 2) wind speed <37 km/hr, and 3) sea level temperature <18.8^{o} C. Surveys were flown at speeds between 110 and 130 km/hr along established flight paths between 760 m and 1,060 m above sea level (i.e., alpine mountain goat summer range habitat) and followed a single geographic contour. Mountain goats were typically observed from 500 m to 1,500 m away. The pilot and experienced observers enumerated and classified all mountain goats seen as either adults (includes adults and sub-adults) or kids. In addition, each mountain goat group observed was checked (via 14× image-stabilizing binoculars) to determine whether radiocollared animals were present.

Sightability Data Collection—During aerial surveys, data were simultaneously collected to evaluate individual-based and survey-level sightability. For accomplishing survey-level objectives, we enumerated the number of radiocollared animals seen during surveys and compared this value to the total number of radiocollared animals present in the area surveyed to produce “current survey” population estimates for a given area using the Chapman estimator (1954), a modified Lincoln-Peterson estimator with reduced bias for low sample sizes (Williams et al. 2001). To gather individual-based sightability data, we characterized behavioral, environmental, and climatic conditions for each radiocollared animal seen and not seen (i.e., missed) during surveys (see Table 1, Figs. 2a, and 2b). When radiocollared animals were missed during the initial survey, we back-tracked and used radiotelemetry to locate animals and

Table 1. Description of categories for each variable used to predict mountain goat aerial survey sighting probabilities.

Variable	Category	Description
Group Size	1	All animals (adults and kids) within 100m of each other and feeding/interacting in coordination.
	2–3	
	4–5	
	6–10	
	11–15	
	16–20	
	21–40	
Habitat	Alpine Meadow	>50% vegetated habitats less than 1 m in height
	Rocky	>50% rocky habitats
	Subalpine Conifer	Open timberline conifer forest
	Thicket	Shrubs 1–5m in height
	Snow	<25% snow
	Mature Forest	Mature, closed canopy conifer forest
Terrain	Smooth	0–25% broken, rocky habitat
	Broken	25–75% broken, rocky habitat
	Very Broken	75–100% broken, rocky habitat
Sky Conditions	Overcast	75–100% cloud cover
	Partly Cloudy	25–75% cloud cover
	Clear	0–25% cloud cover

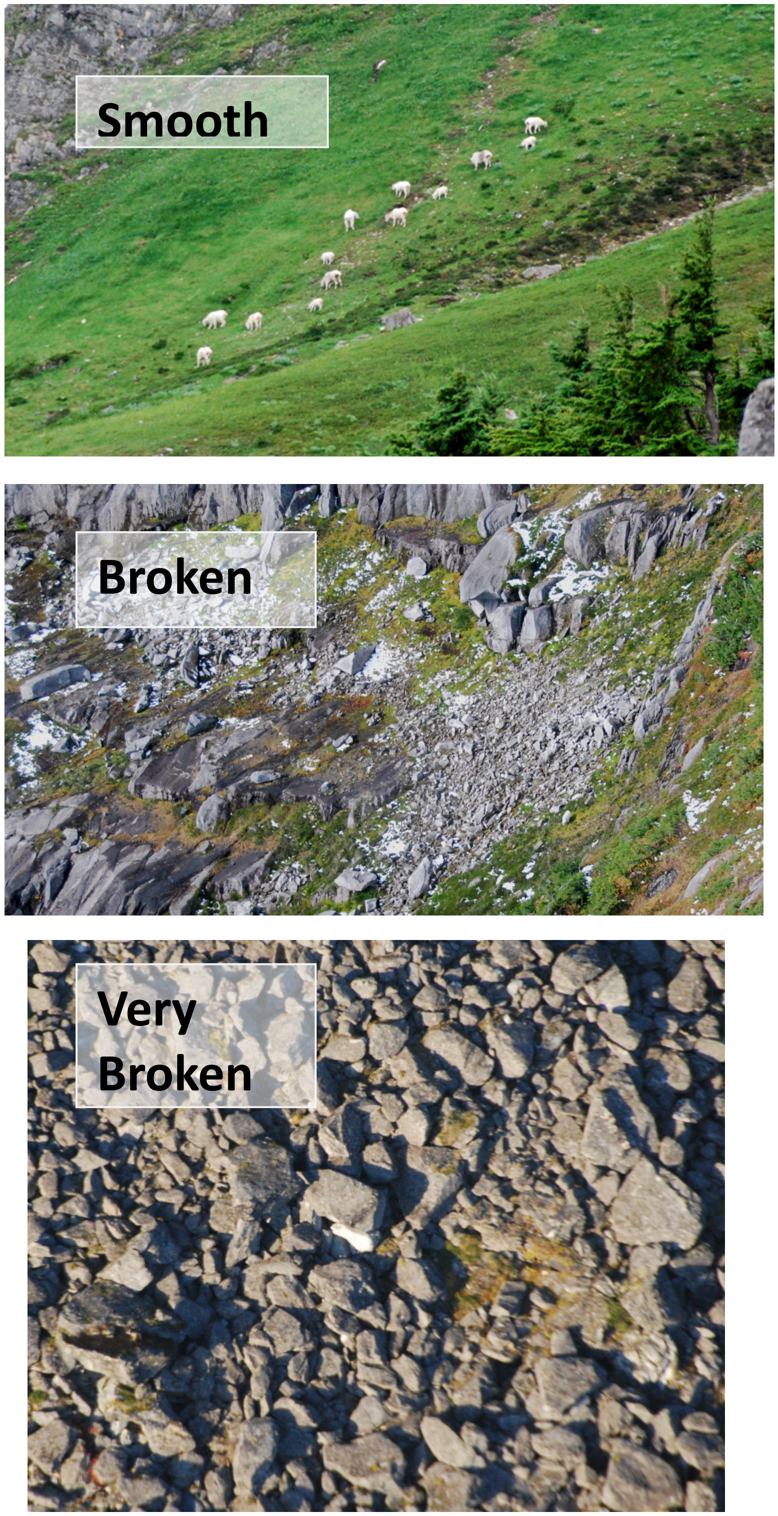

Figure 2a. Illustration of terrain types used for modeling mountain goat aerial survey sighting probabilities, southeastern Alaska, 2008–2015.

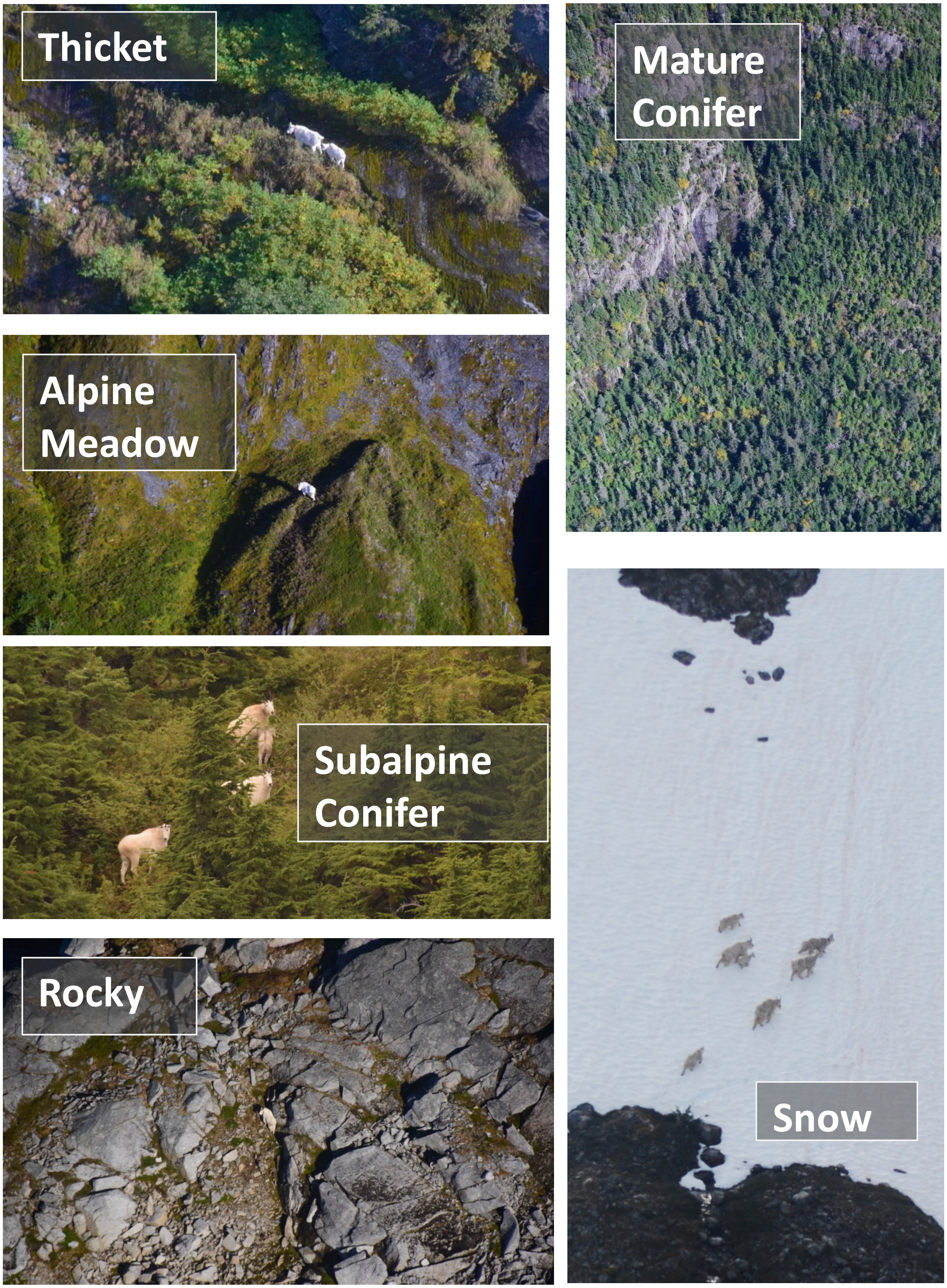

Figure 2b. Illustration of habitat types used for modeling mountain goat aerial survey sighting probabilities, southeastern Alaska, 2008–2015.

gather associated covariate information. Since observers had general knowledge of where individual radiocollared animals were likely to be found (i.e., specific ridge systems, canyon complexes, etc.) based on initial capture location and previous resights, missed animals were typically located within 5–15 minutes after a specific sub-area was originally surveyed. In most cases, it was possible to completely characterize behavioral and site conditions; however, in some cases this was not possible (i.e., animals that were initially missed because they were located in forested habitats, steep ravines, or turbulent canyons) and incomplete covariate information was collected resulting in missing data.

MODELING APPROACH AND METHODS

We modeled the detection process using Bayesian logistic regression on data collected on marked animals during sightability surveys. This resulted in an equation to estimate sighting probabilities. We defined z_i as an indicator variable that takes the value of 1 when the *i*th group containing a marked animal was seen on the survey transect, and 0 when the *i*th group containing a marked animal was missed on the initial transect but subsequently located via radiotelemetry. We assume these detections were independent Bernoulli random variables such that

$$z_i | x_i \sim \text{Bernoulli}(p_i)$$

where p_i is the probability of sighting group *i* conditional on the survey- and group-level covariates x_i (e.g., the air temperature and terrain type and where group *i* was located). This sighting probability was modeled as

$$p_i = \frac{1}{1 + \exp(\beta_0 + \beta_1 x_{1i} + \cdots + \beta_k x_{ki} + \cdots + \beta_K x_{Ki})}$$

where K is the number of covariates retained in the final model. Vague prior distributions for all β_k parameters were specified as $\beta_k \sim$ Normal(0, 100).

To estimate the number of animals in a given area from data collected during operational surveys, we employed a data-augmentation method first demonstrated with abundance estimation by Royle et al. (2007) and later applied to sightability models by Fieberg et al. (2013). To implement this technique, the set of *n* observed groups are augmented with a set of *m* groups whose detection indicator variables Z_i are all set to 0 (unobserved or missed). Based on the size of the survey areas and numbers of groups observed, we set m = 100 such that the total augmented population size *M* was 100 groups greater than the maximum number observed and thus ensuring that the total augmented population size was larger than the true population size in the survey area.

Covariates X_i for the unobserved augmented groups (or observed groups with missing covariate values) were also specified. Categorical group-level covariates *m* augmented groups were assumed to follow

$$X_i \sim \text{multinomial}\left(\frac{Y_1}{\sum_{l=1}^{L} Y_l}, \cdots, \frac{Y_L}{\sum_{l=1}^{L} Y_l}\right)$$

where Y~gamma(1,1) and L are the number of levels for that particular categorical covariate. The probabilities associated with each multinomial category are based on the observed proportions in each category across all surveys in the dataset. Survey-level covariates for the augmented groups were assigned the same values as those for the observed groups. Group size for unobserved groups were assumed to follow a shifted Poisson, such that $g_i - 1 \sim \text{Poisson}(\lambda)$.

We then defined a second Bernoulli indicator variable, *I*, that is set to 1 for all observed groups and left missing for the augmented groups. The probability of detection for each group in the augmented dataset was modeled as $Z_i | X_i \sim \text{Bernoulli}(I_i \times \pi_i)$, where

$$\pi_i = \frac{1}{1 + \exp(\beta_0 + \beta_1 X_{1i} + \cdots + \beta_k X_{ki} + \cdots + \beta_K X_{Ki})}$$

The second indicator variable, *I*, is modeled as $I \sim \text{Bernoulli}(\psi)$, where ψ represents the probability that an augmented group is a real group located within the study area. We used the beta-binomial formulation of Fieberg et al. (2013) and modeled ψ as $\psi \sim \text{beta}(a, b)$, except that we used fixed values of $a = 0.001$ and $b = 1$ rather than specifying diffuse gamma hyperpriors for *a* and *b*. This framework allows for the estimation of *I* for unobserved groups, and the total estimated population size in the survey area, $\hat{N}$, can be derived by as:

$$\hat{N} = \sum_{i=1}^{M} I_i$$

Models were implemented using OpenBUGS version 3.2.3 (Surhone et al. 2010) interfaced by R version 3.2.2 (R Development Core Team 2015) and the R package R2OpenBUGS version 3.2 (Sturtz et al. 2005). Model convergence was assessed inspecting the pattern of the full Markov chain simulations as well as using the Gelman-Rubin statistic computed for three independent chains. All Gelman-Rubin statistics were <1.01 after 15,000 iterations, posterior distributions for model parameters were unimodal, and the distributions for each chain were similar. Model parameters estimates and 95% credible intervals were obtained from the median of 30,000 sampled values from each parameter's posterior distribution. Model selection proceeded in a step-wise fashion, with parameters being retained if the 95% credible intervals of their posterior distributions did not contain 0. All levels within categorical predictors were retained.

Model Assessment

To assess the predictive performance of our model-based estimator, we derived estimates using field data collected during 25 fixed-wing aerial surveys conducted in 4 different areas over multiple years. We then compared our model-based estimates to paired "real-time" Chapman estimates, derived based on "fates" of marked animals, for the same surveys. Since it was not possible to acquire a true census of any of the survey areas, we used the Chapman estimates as baseline from which to compare the performance of the model-based estimator. This approach is imperfect but nonetheless we felt that it would provide meaningful insight into the performance of the model-based estimator. (We constrained our Chapman estimates to include only estimates with greater than 10 marked animals, because we considered estimates derived from smaller samples sizes to be too imprecise).

Sensitivity Analyses

In order to assess the utility of the model-based estimator for routine field survey applications we conducted sensitivity analyses focused on determining the minimum number of individual animals and groups seen that were required to derive a population estimate with precision suitable for routine research and management purposes. Specifically, we derived estimates from 185 different surveys that varied in the minimum number of groups and individual animals seen in each given survey area (Fig. 3). We then calculated the coefficient of variation (CV) of the model-based estimate to determine the minimum and mean sample sizes required to derive population estimates where CV ≤ 0.20, a level of precision considered suitable for most routine management applications. Once the analyses were complete we used the model to calculate population estimates in the Lynn Canal Study Area for small and larger scale areas that might be relevant to routine management applications (Appendices 1 and 2).

Assumptions

There are several general assumptions associated with this model that should be considered prior to model applications. The extent to which these assumptions are violated can influence the reliability of the resulting population estimates. First, the model assumes that all animals in an area during a survey have a non-zero probability of being seen; if there are "invisible" animals (e.g., those in extremely dense forest or in unsurveyed parts of the study area), the resulting estimate does not apply to them; thus, the model only estimates the number of "observable" animals within a given survey area. Next, the model assumes that all animals have a common p_i (i.e., no individual variation in sighting probability), except for what is accounted for by predictor variables. Further, the model assumes that the relationship between p and the predictors does not vary among study areas or across time. For example, the decrease in sighting probability in broken terrain relative to smooth terrain is the same irrespective of study area; yet, this does not imply that the proportions of broken and smooth terrain are the same in all study areas.

Figure 3. Survey areas used for deriving the "small-area" estimates used to determine minimum samples sizes for deriving estimates below the CV < 0.20 threshold, Lynn Canal, Alaska.

Finally, for missing values, the current model imputes categorical predictors and group size based on the distribution of these variables across all surveys in the dataset, irrespective of location or time. If the relative proportions in each category for the categorical predictor variables, or average group size, differ among study areas, potential bias could result. The size of the potential bias effect of this assumption will vary with the number of observations with missing covariates; if there are no missing covariate values, then this assumption will not be important. The effects of violating this assumption would be a function of the severity of the violation (e.g., how different is habitat composition among areas) and the number of missing covariate values, but recall that all covariate values are 'missing' for augmented groups. Whether this assumption is violated can be assessed by comparing variable distributions between the survey area of interest and the overall dataset.

Additional Models and Future Directions

In developing the model described in this report, we also investigated models that dealt with other aspects of mountain goat aerial survey data including: 1) simultaneous estimation of current-survey Lincoln-Petersen-type estimates and logistic regression estimates of population size, 2) inclusion of mountain goat observations where collar status (i.e., with or without a collar) could not be determined, and 3) models that provide a single population estimate for multi-survey data (Appendix 3). These features were either not retained in the current model or have yet to be fully integrated into the current model. We also briefly outline additional generalizations or other improvements that might be developed in future studies (Appendix 4).

Results

Mountain Goat Capture and Handling

Capture Activities—Mountain goats were captured August–October in 2005–2015. Overall, 211 animals were captured using standard helicopter darting methods in 4 different study areas (Baranof Island, n = 38; Cleveland Peninsula, n = 8; Haines-Skagway, n = 57; Lynn Canal, n = 108; Table 2).

Aerial Survey Technique Development Data Collection

Aerial Surveys—Overall, 38 aerial surveys were conducted during September–October 2008–2015 (Table 2). An aerial survey was defined as a day in which aerial survey activities were conducted; however, multiple discrete geographic survey areas (i.e., an area for which population estimate would be calculated) were typically flown in a given day. During surveys, data were collected for the purpose of developing individual-based and survey-level sighting probability models. Aerial surveys were conducted in all 4 study areas (Baranof Island, n = 5; Cleveland Peninsula, n = 6; Haines—Skagway, n = 13; Lynn Canal, n = 14; Table 2).

Sightability Data Collection—During 2008–2015, habitat and behavioral covariate data were collected for 558 radiomarked mountain goat observations during aerial surveys. These data were paired with records of whether animals were seen or not seen during aerial surveys and used to develop models for predicting mountain goat sighting probabilities. The proportion of radiomarked mountain goats seen during aerial surveys varied between study areas. A higher proportion of radiomarked mountain goats was seen in the Baranof Island (0.68 ± 0.05, n = 107) and Haines-Skagway (0.69 ± 0.04, n = 136) study areas as compared to the Lynn Canal (0.55 ± 0.03, n = 273), or Cleveland Peninsula (0.36 ± 0.07, n = 42) study areas (Table 2).

Table 2. Descriptive summary of the number of individual mountain goats radio-marked, surveys and sightability trials flown in each study area in southeastern Alaska during 2008–2015.

Area	No. of marked animals	No. of surveys	Sightability trials			
			Seen	Total	Prop	SE
Baranof	38	5	73	107	0.68	0.05
Cleveland	8	6	15	42	0.36	0.07
Haines-Skagway	57	13	94	136	0.69	0.04
Lynn Canal	108	14	150	273	0.55	0.03
Total	211	38	332	558	0.59	0.02

MODEL PARAMETERS

We considered several potential group-level predictors, including habitat type, terrain type, animal behavior, landform, slope, and group size. We also considered several survey-level predictors, including Julian day, air temperature, mean and maximum wind speed, survey area, and sky conditions. The final model retained group size, habitat type, terrain type, and sky conditions. We defined the most common survey conditions (Meadow, Broken, and Overcast) as the baseline levels for the Habitat, Terrain, and Sky Condition categorical predictors, respectively (Tables 3-4 and Fig. 4).

Sighting probability decreased significantly as the terrain became rougher (Table 4). Sighting probabilities were lowest in very broken terrain, with only a 59.5% probability of sighting a single animal in otherwise optimal conditions (meadow habitat, overcast skies), and increased by 1.3× in broken terrain (78.4%) and over 1.6× in smooth terrain (97.7%).

Table 3. Descriptive summary of the proportion of radio-collared mountain goats seen during aerial survey "sightability" trials for each variable used to predict sighting probabilities.

Variable	Category	Seen	Total	Prop	SE
Group Size	1	133	201	0.66	0.03
	2–3	108	157	0.69	0.04
	4–5	45	54	0.83	0.05
	6–10	36	38	0.95	0.04
	11–15	4	4	1.00	0.00
	16–20	2	2	1.00	0.00
	21–40	3	3	1.00	0.00
	missing values	1	96		
Habitat	Alpine Meadow	173	192	0.90	0.02
	Rocky	109	176	0.62	0.04
	Subalpine Conifer	24	43	0.56	0.08
	Thicket	19	57	0.33	0.06
	Snow	2	21	0.10	0.06
	Mature Forest	0	15	0.00	0.00
	missing values	5	54		
Terrain	Smooth	108	116	0.93	0.02
	Broken	193	307	0.63	0.03
	Very Broken	27	79	0.34	0.05
	missing values	4	56		
Weather	Overcast	216	311	0.69	0.03
	Clear	103	218	0.47	0.03
	Partly Cloudy	13	29	0.45	0.09
	missing values	0	0		

Table 4: Model coefficients used for estimating mountain goat sighting probabilities and population size in Southeast Alaska, 2008–2015.

Parameter	Median	SE	95% Credible Interval
Intercept	0.723	0.245	(0.246, 1.211)
Group Size	0.564	0.108	(0.362, 0.782)
<u>Terrain Type (Baseline = Broken)</u>			
Smooth	2.420	0.498	(1.522, 3.498)
Very Broken	-0.902	0.305	(-1.500, -0.300)
<u>Habitat Type (Baseline = Meadow)</u>			
Rocky	-0.379	0.284	(-0.943, 0.164)
Forest	-1.209	0.381	(-1.971, -0.476)
Thicket	-1.688	0.388	(-2.459, -0.952)
Snow	-4.855	1.099	(-7.324, -3.024)
<u>Sky Conditions (Baseline = Overcast)</u>			
Partly Cloudy	-0.755	0.510	(-1.744, 0.269)
Clear	-0.755	0.250	(-1.246, -0.274)

[a]Sightability in rocky habitat was not significantly different from that in meadows at the baseline terrain type and sky condition

[b]Sightability under partly cloudy skies was not significantly different from that under overcast skies at the baseline habitat and terrain types

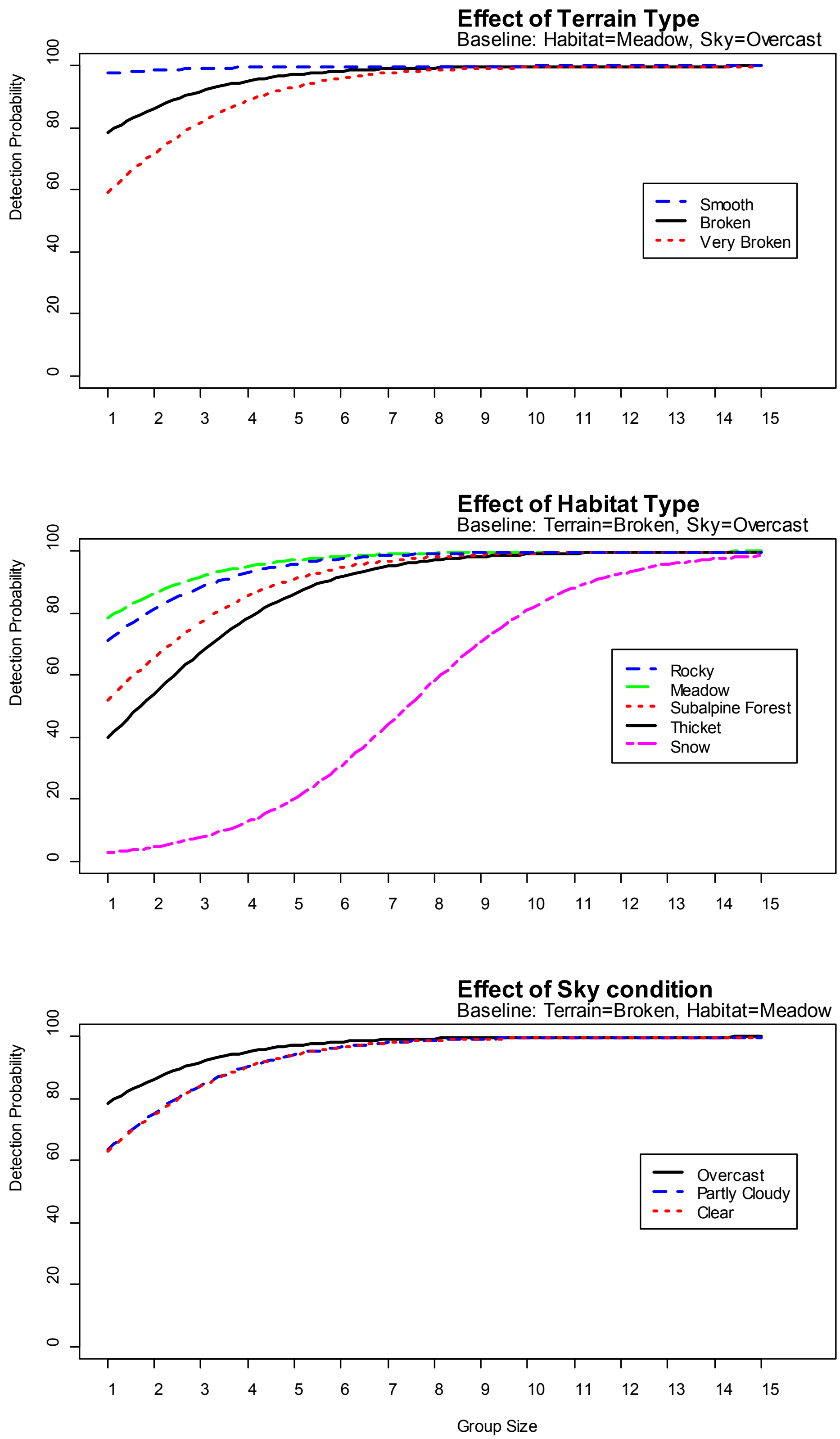

Figure 4. Effects of individual covariates on the sighting probability of mountain goats by group size, Southeast Alaska, 2008–2015.

Habitat type also significantly influenced sighting probability (Table 4). Sighting probabilities were lowest on snow-covered terrain, with only a 1.5% probability of detecting a single animal at the baseline terrain type and sky condition. Sighting probabilities were moderately low in thickets and subalpine forests, with single-animal detection rates of 27.5% and 38.1%, respectively. Detection rates in meadows were as high as 67.4% for single animals. There was not a significant difference between detection probabilities in meadows and rocky habitats at the baseline terrain and sky conditions.

The probability of sighting a group increased substantially with the size of the group across all conditions (Table 4, Fig. 4). The optimal conditions for sighting mountain goats were smooth meadows with overcast skies, with the probability of sighting a single animal at 97.6% and

increasing to over 99% with a group size of only 3. Sighting probabilities were lowest in very-broken, snow-covered terrain on clear, sunny days. Under these conditions, the probability of sighting a group of fewer than 7 animals was less than 1% and increased to only a 1 in 3 chance of sighting a group of 9 animals. The mean group size across the entire region was 2.1 ± 2.2 with a median size of 1. Distribution of group sizes among survey areas was similar, with the exception of the East Berners survey area which had several very large groups of up to 58 goats (Table 5).

Cloud cover also had a significant effect on sighting probability (Table 4). Overcast skies provided the best sighting conditions, with nearly a 67.4% single-animal detection probability. Single-animal detection probabilities decreased under Partly Cloudy and Clear skies to 49.2% and 49.3%, respectively, and were not significantly different from one another. This may have been the result of such a course categorization, with “Partly Cloudy” being any amount of cloud cover between perfectly clear and completely overcast.

Assessment of Model Performance

We assessed the performance of our model by comparing 25 population estimates from our model with corresponding “current survey” Chapman estimates (Table 6 and Fig. 5). There was a strong and significant correlation between estimates ($r = 0.85$, $p < 0.0001$). We assessed the difference between Chapman and Bayesian estimates by examining the bootstrapped confidence intervals of the difference between the 2 estimates and found that the estimates obtained using the 2 different methods were not significantly different from one another in any of the 25 surveys examined. With the exception of a single survey (Sinclair 2008, Julian Day 281) where the Chapman estimate was 104 goats higher than the Bayesian estimate, the estimates from the 2 different methods were within 24 animals of each other, on average. Although the mean values were similar, coefficients of variation of the Chapman estimates were on average 1.7× higher than those produced by the Bayesian model, indicating that the Bayesian model produces more precise estimates of population size.

Table 5. Summary of mountain goat group size based on data collected during aerial surveys in Southeast Alaska, 2008–2015.

Survey area	Sub-Area	Mean ± SD	Median	Maximum
BL Ridge	BL Ridge	1.7 ± 1.3	1	8
E Berners	Total	3.1 ± 4.3	2	58
	Antler Lk	2.2 ± 1.8	2	10
	N Sawmill	3.7 ± 5.6	2	58
	S Davies	1.9 ± 1.1	2	6
	S Sawmill	2.8 ± 2.8	2	17
Kakuhan	Total	2.0 ± 1.6	1	18
	Katzehin Lk	1.9 ± 1.8	1	13
	Kensington	1.8 ± 1.4	1	9
	Met	2.0 ± 1.5	2	12
	S Katzehin	2.0 ± 1.5	1	11
	S Meade	1.7 ± 1.1	1	6
	U Lace	1.9 ± 1.3	1	7
	W Berners	1.5 ± 0.8	1	6
	Yeldagalga	2.2 ± 2.0	2	18
Villard	Total	2.0 ± 1.6	1	18
	Mt Villard	2.0 ± 1.7	1	10
	N Katzehin	2.0 ± 1.6	1	12
	NW Katzehin	1.5 ± 0.8	1	5
	NW Meade	2.3 ± 1.7	2	7
	Snow Top	2.1 ± 1.9	1	17

Table 6. Comparison of population size estimates from the Bayesian sightability model and Chapman estimator. Estimates are shown as ± SE. Numbers in parentheses for the Bayesian model and Chapman estimates are 95% credible intervals and 95% confidence intervals, respectively.

Study area	Year	Julian day	Total seen	Bayesian Estimate	Chapman Estimate
East Berners	2010	254	100	155 ± 16 (135, 201)	184 ± 45 (94, 273)
East Berners	2010	265	93	175 ± 19 (156, 228)	135 ± 20 (95, 176)
East Berners	2011	270	149	205 ± 14 (202, 266)	186 ± 27 (133, 239)
East Berners	2012	263	182	241 ± 15 (225, 283)	259 ± 29 (200, 317)
East Berners	2014	269	157	230 ± 16 (210, 274)	209 ± 39 (133, 286)
Lions Head	2008	281	80	120 ± 12 (119, 172)	168 ± 32 (104, 232)
Lions Head	2009	224	39	71 ± 11 (54, 92)	63 ± 10 (42, 83)
Lions Head	2010	249	65	121 ± 17 (103, 163)	102 ± 14 (74, 130)
Lions Head	2010	264	81	160 ± 19 (136, 200)	149 ± 25 (98, 200)
Lions Head	2011	261	110	166 ± 14 (161, 218)	165 ± 21 (123, 207)
Lions Head	2012	263	80	139 ± 15 (123, 177)	114 ± 12 (90, 138)
Lions Head	2013	266	82	168 ± 23 (119, 183)	130 ± 20 (90, 170)
Lions Head	2014	253	64	104 ± 12 (106, 162)	117 ± 20 (76, 158)
Lions Head	2015	265	31	69 ± 13 (54, 107)	83 ± 19 (45, 120)
Sinclair	2008	281	151	219 ± 15 (211, 268)	323 ± 65 (195, 450)
Sinclair	2010	249	82	158 ± 19 (135, 197)	129 ± 18 (93, 165)
Sinclair	2010	264	89	169 ± 19 (153, 217)	164 ± 28 (107, 220)
Sinclair	2011	261	161	231 ± 15 (233, 293)	242 ± 32 (178, 305)
Sinclair	2012	263	126	178 ± 14 (177, 237)	179 ± 20 (139, 219)
Sinclair	2013	266	81	159 ± 22 (116, 178)	128 ± 20 (89, 168)
Sinclair	2014	253	85	136 ± 13 (131, 187)	155 ± 28 (99, 210)
Sinclair	2015	265	66	135 ± 18 (106, 167)	174 ± 43 (90, 259)
Villard	2011	261	172	251 ± 16 (247, 300)	258 ± 34 (190, 326)
Villard	2013	266	49	111 ± 20 (74, 129)	78 ± 11 (55, 100)
Villard	2014	269	143	214 ± 15 (207, 263)	191 ± 35 (121, 260)

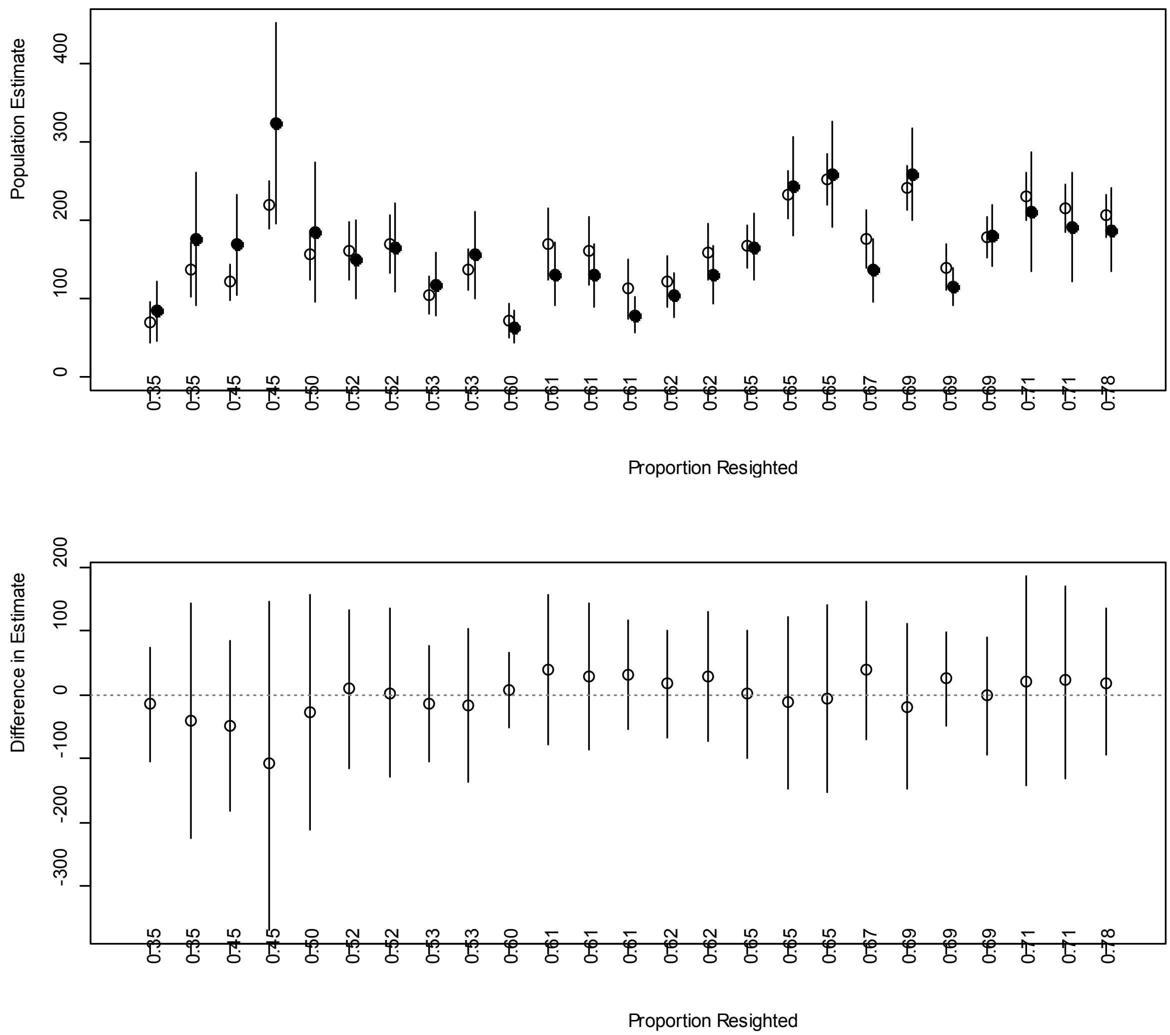

Figure 5. Upper panel: Comparison of Bayesian (open circle) and Chapman (filled circles) population estimates. Error bars represent the 95% credible or 95% confidence intervals, respectively. Lower panel: Absolute difference between the Bayesian and Chapman population estimates with bootstrapped 95% confidence intervals. Proportion of animals resighted on a given survey are shown on the x-axis. Cases where multiple surveys resulted in the same proportion of marked animals resighted are presented in no particular order.

We examined the effect of the number of individuals and groups seen in a survey area on the precision of the population size estimates by plotting the coefficient of variation of the population estimate against the number of individuals and groups seen on 277 different surveys (Fig. 6). The CV decreased in a logarithmic fashion with increasing numbers of individuals and groups seen. We defined 0.20 as the upper threshold for what we considered to be a reasonably precise population estimate. On average, 26 individual animals, or 13 groups, needed to be sighted to obtain a minimum CV of 0.20. All surveys where at least 31 individuals or 17 groups were seen had CVs <0.20. The precision improved at a much lower rate beyond 29 individuals, dropping to an average of 0.09 when between 50 and 175 individual animals were seen in a survey area.

Discussion

Covariate Effects

Individual mountain goat aerial survey sighting probabilities varied with respect to group size, habitat type, terrain, and sky conditions. Similar to previous studies for the species (i.e., Rice et al. 2009) sighting probabilities increased with group size and declined when substrate conditions included habitats with high amounts of vegetative or terrain obstruction. These findings are intuitive in that larger group sizes present more chances of seeing individuals and substrates with physical obstructions prevent easy detection of groups. Our models also indicated that overcast sky conditions resulted in higher sighting probabilities than clear or partly cloudy conditions. Overcast conditions present optimal, low-contrast sighting conditions and alleviate challenging sighting conditions associated with glare, shadows or mottled lighting (i.e., those associated with clear or partly cloudy conditions).

Model Performance

Estimates derived from our Bayesian regression-based estimator were statistically indistinguishable from paired “current survey” Chapman mark-resight estimates in all cases. In this analysis, we considered mark-resight estimates to be the “gold standard” for performance assessment of the Bayesian regression-based estimator. While mark-resight estimates could be more accurate with respect to actual population size, as compared to regression-based estimates (because they are estimated in real-time), they often are imprecise because of the relatively small number of marked animals available within a study area to estimate sighting probability. Ideally, estimates would be compared to true population size via population censuses. Unfortunately, conducting a population census and determining true population size is not feasible in the large, remote, and complex landscapes under consideration. Nonetheless, we consider our assessment to be a useful and informative gauge of model performance. The observed strong correlation between the Bayesian regression-based estimates and mark-resight estimates indicate that the

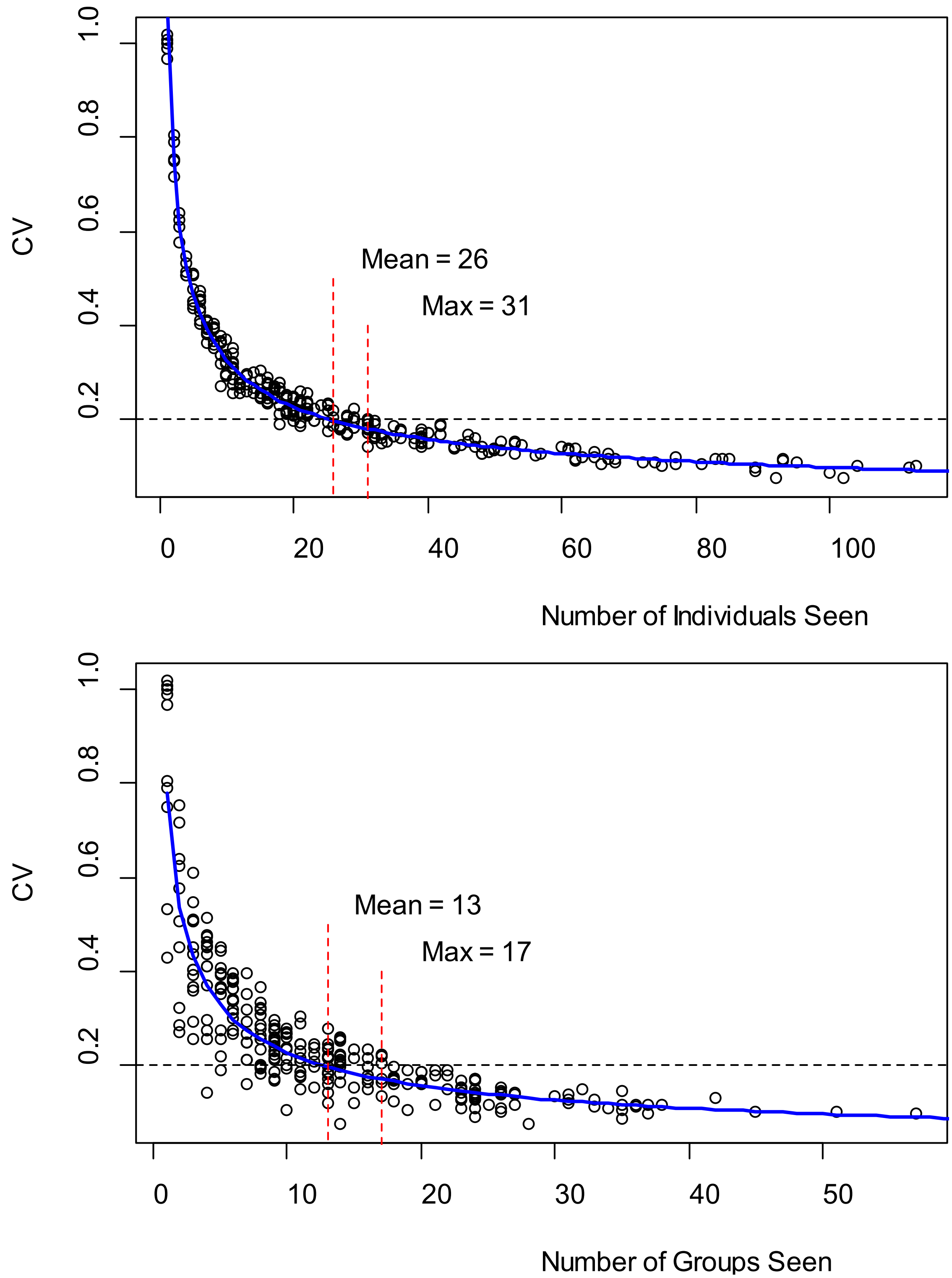

Figure 6. Effect of sample size (i.e., number of individuals or groups) on precision of population estimates (i.e., coefficient of variation, CV) of mountain goats in Southeast Alaska, 2008–2015.

performance of the regression-based estimator is likely to be acceptable for most routine conservation and management applications. This is an encouraging result since field data required for deriving mark-resight estimates is financially costly and logistically difficult, especially for long-term monitoring.

MODEL IMPLEMENTATION AND APPLICATIONS

Routine management and conservation of mountain goats often requires knowledge about the size of small populations, or populations in limited geographic areas. A key goal of our analyses was to determine the minimum number of animals that needed to be observed in a given sampling frame to derive estimates of reasonable precision (i.e., $CV \leq 0.20$). Simulation analyses indicated that our regression-based estimator was capable of deriving reliable estimates based on aerial survey observations ≤ 26 individual animals (or 13 groups). For routine conservation applications, we consider this to be a considerable strength of our modeling approach.

An alternative analysis method applicable to aerial survey data is distance sampling (Williams et al. 2001, Schmidt et al. 2012). Both our approach (logistic regression-based) and distance sampling estimate detection probability for animals in the survey area, can then be used to adjust count data to yield population estimates. Also like our approach, if one assumes that the distance-based detection function is the same across study areas and times (comparable to our assumptions that regression relationships between p and the covariates are constant), then estimates can be produced for small areas that do not have sufficient observations to produce precise estimates. The key differences between the approaches are the required assumptions and the actual quantity estimated. Our key assumptions are listed in the Methods section. Distance methods assume that detection probability declines as animals are farther from the transect line, which is measured as the perpendicular distance from the line, and, typically that animals on the survey line are seen with probability 1 (Williams et al. 2001), but these assumptions can be relaxed (i.e., maximum detectability <1 with the peak not on the transect line) with more complex models (i.e., Becker and Quang 2009). Also, distance models estimate population density that can be converted to a population size estimate by multiplying by the size of the survey area. This conversion (i.e., density to population size) requires the additional assumption that the animal density in the area surveyed from the transect lines is representative of the entire population area (i.e., transect lines approximate a random sample of the area).

Choosing between our regression approach and distance sampling methods will involve considering logistical constraints and which set of model assumptions are more likely met in a given situation. For example, in extremely rugged areas typical of mountain goat habitat, it might be impractical or unsafe to measure the distances from the transect line to observed goats, which often is done by diverting the aircraft from the transect to fly over the observed animals to record location. Also in mountainous terrain, goats far from the transect line but at the same level as the aircraft might be more visible than goats closer to the survey line but far below the aircraft. This combined with cliffs and ridges might result in distance-based detection function that does not decline with distance from the flight line, making use of distance sampling impractical. Again, both approaches are statistically sound and the choice should be based on feasibility and the plausibility of meeting assumptions in any specific situation.

BENEFITS OF BAYESIAN MODELS

Use of a Bayesian modeling framework for estimating population size is desirable for multiple reasons. The Bayesian modeling framework can enable easy integration of future analytical advancements, specifically as it relates to using multiple sources of information (Johnson et al. 2010). For example, it is possible to combine Bayesian regression-based aerial survey estimates of population size, with estimates derived using other techniques (such as matrix population models, mark-resight estimates, ground counts) to derive a final estimate that is more accurate and precise than that derived from any single estimator.

Management Implications

In the absence of statistical models capable of accounting for variability in aerial survey sighting probabilities, routine mountain goat aerial survey data exhibit substantial variability and limit the ability to appropriately manage and conserve mountain goat populations. For example, assigning harvest quotas based on uncorrected minimum counts can result in over- or under-harvest depending on survey conditions associated with a given annual survey. And, if knowledge about how survey conditions influence minimum counts is not available then management impacts on populations are likewise unknown. Statistical models that account for sources of variation enable estimation of actual population size (and credible intervals) and can be input into matrix population models and used to statistically simulate different harvest scenarios. Such methods provide a transparent and informative tool for determining defensible harvest management strategies.

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Appendices

Appendix A: Summary of small-area population estimates, Lynn Canal 2005–2015.

Area	Sub-area	Year	Julian Day	Total Animals Seen	Median Population Estimate	SE	95% Credible Interval
BL Ridge	BL Ridge	2007	245	29	55	11.4	(38, 82)
BL Ridge	BL Ridge	2008	269	22	53	12.7	(33, 82)
BL Ridge	BL Ridge	2011	261	12	17	5.1	(12, 31)
BL Ridge	BL Ridge	2011	269	35	55	9.1	(42, 77)
BL Ridge	BL Ridge	2012	263	27	42	8.0	(31, 62)
BL Ridge	BL Ridge	2013	266	15	37	11.8	(21, 67)
BL Ridge	BL Ridge	2014	253	19	33	7.2	(22, 50)
BL Ridge	BL Ridge	2015	265	22	59	14.0	(37, 91)
E Berners	Antler Lk	2006	240	11	14	4.3	(11, 26)
E Berners	Antler Lk	2006	276	12	23	6.8	(14, 40)
E Berners	Antler Lk	2007	245	11	24	8.8	(13, 47)
E Berners	Antler Lk	2007	265	16	24	5.8	(17, 39)
E Berners	Antler Lk	2007	277	25	36	7.2	(27, 54)
E Berners	Antler Lk	2008	269	21	39	9.7	(25, 63)
E Berners	Antler Lk	2009	222	5	8	3.9	(5, 19)
E Berners	Antler Lk	2009	232	1	1	2.4	(1, 9)
E Berners	Antler Lk	2009	276	11	15	4.4	(11, 27)
E Berners	Antler Lk	2010	254	11	26	8.8	(14, 48)
E Berners	Antler Lk	2010	265	17	39	10.9	(23, 66)
E Berners	Antler Lk	2011	270	38	63	10.3	(47, 87)
E Berners	Antler Lk	2012	263	33	44	6.6	(35, 61)
E Berners	Antler Lk	2013	268	11	22	7.0	(13, 39)
E Berners	Antler Lk	2014	269	49	74	9.8	(59, 97)
E Berners	Antler Lk	2015	275	19	33	8.5	(22, 55)
E Berners	N Sawmill	2006	240	81	102	11.0	(87, 129)
E Berners	N Sawmill	2006	246	93	133	15.7	(109, 171)
E Berners	N Sawmill	2006	276	51	75	10.3	(59, 99)
E Berners	N Sawmill	2007	245	95	144	15.6	(119, 180)
E Berners	N Sawmill	2007	265	89	117	10.7	(100, 142)
E Berners	N Sawmill	2007	277	65	90	10.8	(73, 115)
E Berners	N Sawmill	2008	269	93	166	18.5	(134, 206)
E Berners	N Sawmill	2009	222	92	107	7.9	(96, 126)
E Berners	N Sawmill	2009	232	8	12	4.6	(8, 24)
E Berners	N Sawmill	2009	276	8	15	5.9	(8, 30)
E Berners	N Sawmill	2010	254	77	107	12.8	(88, 138)
E Berners	N Sawmill	2010	265	47	86	13.8	(64, 117)
E Berners	N Sawmill	2011	270	66	88	9.2	(74, 109)
E Berners	N Sawmill	2012	263	102	127	9.4	(112, 149)

Area	Sub-area	Year	Julian Day	Total Animals Seen	Median Population Estimate	SE	95% Credible Interval
E Berners	N Sawmill	2013	268	56	78	9.6	(64, 101)
E Berners	N Sawmill	2014	269	75	103	10.3	(87, 127)
E Berners	N Sawmill	2015	275	31	45	8.3	(34, 66)
E Berners	S Sawmill	2006	240	36	48	7.8	(38, 68)
E Berners	S Sawmill	2006	246	11	14	5.0	(11, 29)
E Berners	S Sawmill	2006	276	26	37	7.1	(28, 55)
E Berners	S Sawmill	2007	245	24	44	10.3	(29, 69)
E Berners	S Sawmill	2007	265	14	24	6.3	(15, 39)
E Berners	S Sawmill	2007	277	29	46	8.5	(33, 66)
E Berners	S Sawmill	2008	269	39	63	10.3	(47, 87)
E Berners	S Sawmill	2009	222	11	14	3.7	(11, 24)
E Berners	S Sawmill	2009	232	20	28	6.3	(20, 44)
E Berners	S Sawmill	2010	254	8	13	5.8	(8, 29)
E Berners	S Sawmill	2010	265	16	35	10.3	(21, 60)
E Berners	S Sawmill	2011	270	32	46	7.5	(35, 64)
E Berners	S Sawmill	2012	263	34	47	7.4	(37, 65)
E Berners	S Sawmill	2013	268	22	36	7.6	(25, 54)
E Berners	S Sawmill	2014	269	21	32	7.3	(23, 51)
E Berners	S Sawmill	2015	275	31	36	5.3	(31, 51)
Lions Head	Kensington	2005	223	26	56	12.6	(37, 86)
Lions Head	Kensington	2005	276	21	46	11.2	(30, 73)
Lions Head	Kensington	2006	240	32	64	12.9	(44, 94)
Lions Head	Kensington	2006	246	29	57	13.1	(38, 89)
Lions Head	Kensington	2006	275	54	137	20.3	(103, 182)
Lions Head	Kensington	2006	289	40	87	15.0	(63, 121)
Lions Head	Kensington	2007	239	16	31	8.0	(20, 51)
Lions Head	Kensington	2007	256	27	42	7.8	(31, 60)
Lions Head	Kensington	2007	271	20	39	10.1	(25, 64)
Lions Head	Kensington	2007	277	27	43	8.0	(31, 62)
Lions Head	Kensington	2008	269	21	44	10.6	(28, 69)
Lions Head	Kensington	2008	281	15	25	6.5	(16, 41)
Lions Head	Kensington	2009	224	19	29	6.3	(20, 44)
Lions Head	Kensington	2009	276	19	30	6.6	(21, 46)
Lions Head	Kensington	2010	249	17	25	6.7	(17, 43)
Lions Head	Kensington	2010	264	25	52	12.4	(34, 82)
Lions Head	Kensington	2011	261	32	50	8.3	(38, 70)
Lions Head	Kensington	2012	263	23	37	7.4	(26, 55)
Lions Head	Kensington	2013	266	22	50	13.2	(31, 83)
Lions Head	Kensington	2014	253	17	32	8.0	(21, 51)
Lions Head	Kensington	2015	265	9	21	8.0	(11, 41)

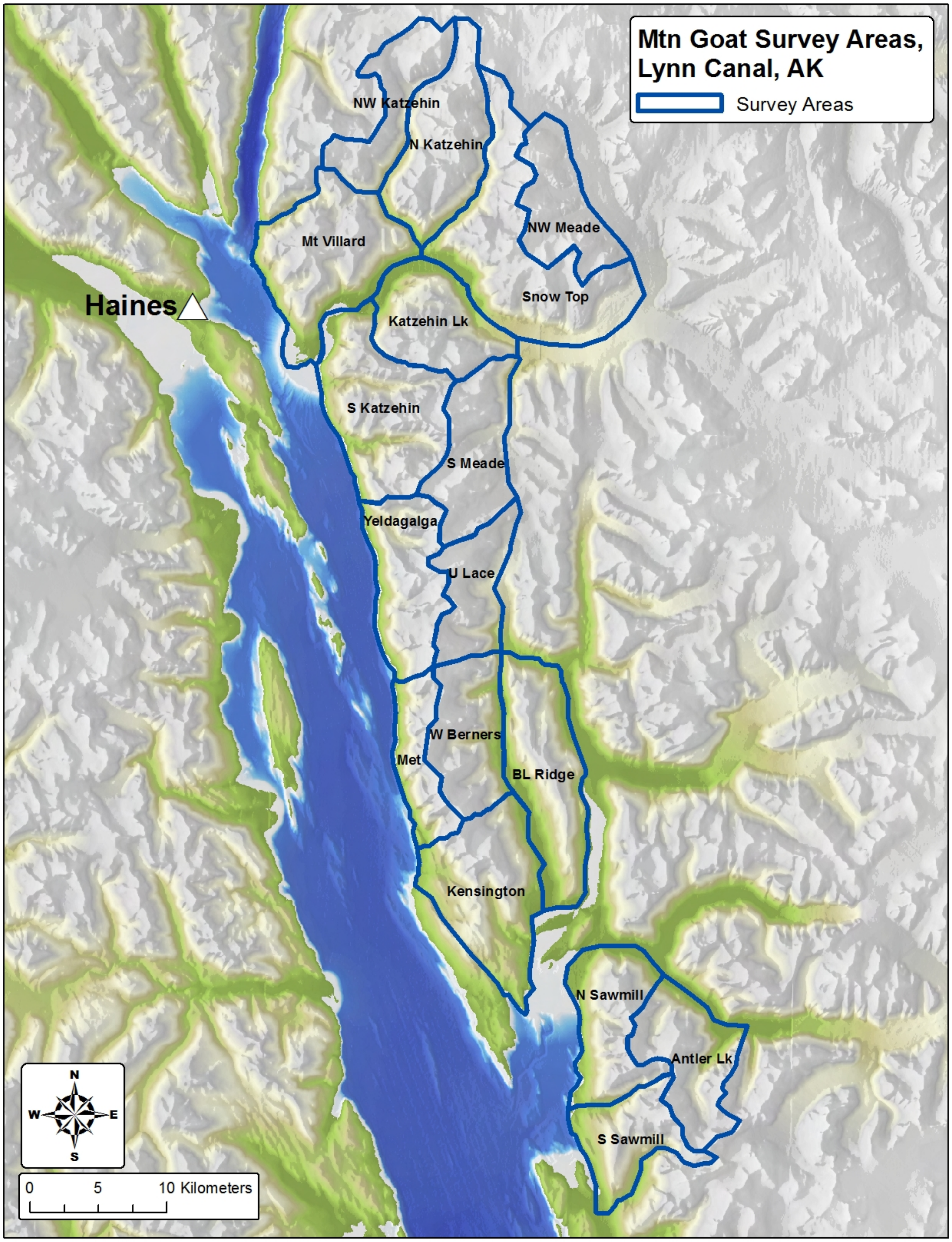
Area	Sub-area	Year	Julian Day	Total Animals Seen	Median Population Estimate	SE	95% Credible Interval
Lions Head	Met	2005	223	5	11	6.3	(5, 28)
Lions Head	Met	2005	276	42	79	13.2	(58, 109)
Lions Head	Met	2006	240	20	40	10.1	(26, 65)
Lions Head	Met	2006	246	21	48	12.8	(30, 79)
Lions Head	Met	2006	266	6	9	4.1	(6, 21)
Lions Head	Met	2006	275	39	84	15.2	(59, 118)
Lions Head	Met	2006	289	61	115	15.6	(89, 150)
Lions Head	Met	2007	239	23	36	7.3	(26, 54)
Lions Head	Met	2007	256	12	21	6.0	(13, 36)
Lions Head	Met	2007	271	53	122	18.4	(91, 162)
Lions Head	Met	2007	277	34	49	7.7	(38, 68)
Lions Head	Met	2008	269	51	100	15.4	(75, 135)
Lions Head	Met	2008	281	49	75	9.8	(60, 98)
Lions Head	Met	2009	224	20	36	8.3	(24, 56)
Lions Head	Met	2009	276	39	54	7.7	(43, 73)
Lions Head	Met	2010	249	42	77	13.2	(57, 108)
Lions Head	Met	2010	264	46	84	13.0	(63, 114)
Lions Head	Met	2011	261	57	87	11.0	(70, 112)
Lions Head	Met	2012	263	44	72	10.1	(56, 95)
Lions Head	Met	2013	266	42	83	16.0	(59, 122)
Lions Head	Met	2014	253	40	67	10.2	(51, 90)
Lions Head	Met	2015	265	16	34	9.7	(20, 58)
Lions Head	W Berners	2005	223	9	17	6.8	(10, 35)
Lions Head	W Berners	2005	276	4	11	6.5	(4, 28)
Lions Head	W Berners	2006	240	6	14	6.9	(6, 32)
Lions Head	W Berners	2006	246	9	25	9.6	(12, 49)
Lions Head	W Berners	2006	275	16	39	10.1	(24, 62)
Lions Head	W Berners	2006	289	15	30	8.9	(18, 52)
Lions Head	W Berners	2007	239	7	12	4.6	(7, 24)
Lions Head	W Berners	2007	256	12	18	5.1	(12, 31)
Lions Head	W Berners	2007	271	25	50	11.0	(33, 76)
Lions Head	W Berners	2007	277	16	28	6.8	(18, 44)
Lions Head	W Berners	2008	269	7	17	7.6	(8, 37)
Lions Head	W Berners	2008	281	16	27	7.2	(18, 45)
Lions Head	W Berners	2009	276	15	23	6.1	(16, 39)
Lions Head	W Berners	2010	249	6	13	6.7	(6, 31)
Lions Head	W Berners	2010	264	10	25	8.9	(13, 47)
Lions Head	W Berners	2011	261	21	36	7.8	(25, 56)
Lions Head	W Berners	2012	263	13	23	6.7	(15, 40)
Lions Head	W Berners	2013	266	18	42	12.1	(25, 71)

Area	Sub-area	Year	Julian Day	Total Animals Seen	Median Population Estimate	SE	95% Credible Interval
Lions Head	W Berners	2014	253	7	14	5.8	(7, 29)
Lions Head	W Berners	2015	265	6	12	6.0	(6, 28)
Sinclair	Katzehin Lk	2005	223	31	49	10.2	(35, 74)
Sinclair	Katzehin Lk	2005	276	13	30	9.3	(17, 53)
Sinclair	Katzehin Lk	2006	240	9	15	5.8	(9, 30)
Sinclair	Katzehin Lk	2006	245	10	14	4.5	(10, 26)
Sinclair	Katzehin Lk	2006	266	27	43	8.0	(31, 62)
Sinclair	Katzehin Lk	2006	289	22	51	11.6	(33, 78)
Sinclair	Katzehin Lk	2007	239	1	1	2.3	(1, 9)
Sinclair	Katzehin Lk	2007	256	2	4	3.9	(2, 16)
Sinclair	Katzehin Lk	2007	271	18	36	9.6	(22, 59)
Sinclair	Katzehin Lk	2008	269	19	39	9.9	(25, 63)
Sinclair	Katzehin Lk	2008	281	9	15	4.9	(9, 28)
Sinclair	Katzehin Lk	2010	249	17	30	8.4	(19, 52)
Sinclair	Katzehin Lk	2010	264	19	37	9.7	(24, 61)
Sinclair	Katzehin Lk	2011	261	9	16	5.7	(9, 31)
Sinclair	Katzehin Lk	2012	263	3	5	3.3	(3, 15)
Sinclair	Katzehin Lk	2013	266	3	6	4.8	(3, 20)
Sinclair	Katzehin Lk	2014	253	4	6	3.5	(4, 16)
Sinclair	Katzehin Lk	2015	265	2	3	3.4	(2, 14)
Sinclair	S Katzehin	2005	223	28	57	12.0	(39, 85)
Sinclair	S Katzehin	2005	276	85	148	17.1	(120, 186)
Sinclair	S Katzehin	2006	240	53	103	16.0	(77, 140)
Sinclair	S Katzehin	2006	245	50	80	11.1	(63, 106)
Sinclair	S Katzehin	2006	266	63	99	12.0	(80, 127)
Sinclair	S Katzehin	2006	289	113	217	21.6	(179, 263)
Sinclair	S Katzehin	2007	239	33	58	9.8	(43, 81)
Sinclair	S Katzehin	2007	256	20	34	7.3	(24, 52)
Sinclair	S Katzehin	2007	271	104	178	18.1	(148, 218)
Sinclair	S Katzehin	2008	269	65	139	18.2	(109, 179)
Sinclair	S Katzehin	2008	281	89	136	13.4	(114, 166)
Sinclair	S Katzehin	2009	224	20	36	7.9	(24, 55)
Sinclair	S Katzehin	2010	249	28	53	11.3	(36, 80)
Sinclair	S Katzehin	2010	264	36	76	13.6	(54, 107)
Sinclair	S Katzehin	2011	261	67	108	12.5	(88, 136)
Sinclair	S Katzehin	2012	263	48	81	11.6	(63, 108)
Sinclair	S Katzehin	2013	266	25	52	12.6	(34, 83)
Sinclair	S Katzehin	2014	253	33	54	8.8	(40, 74)
Sinclair	S Katzehin	2015	265	35	77	14.4	(53, 110)
Sinclair	S Meade	2005	223	6	7	3.6	(6, 18)

Area	Sub-area	Year	Julian Day	Total Animals Seen	Median Population Estimate	SE	95% Credible Interval
Sinclair	S Meade	2005	276	6	9	4.7	(6, 23)
Sinclair	S Meade	2006	266	22	43	9.4	(29, 65)
Sinclair	S Meade	2006	289	16	28	7.9	(17, 48)
Sinclair	S Meade	2007	256	4	7	4.2	(4, 19)
Sinclair	S Meade	2008	269	4	5	3.2	(4, 15)
Sinclair	S Meade	2008	281	5	8	4.2	(5, 20)
Sinclair	S Meade	2010	249	6	15	7.6	(6, 35)
Sinclair	S Meade	2010	264	3	6	4.8	(3, 20)
Sinclair	S Meade	2011	261	13	21	5.7	(14, 36)
Sinclair	S Meade	2012	263	7	15	6.1	(7, 31)
Sinclair	S Meade	2013	266	11	26	9.5	(14, 50)
Sinclair	S Meade	2014	253	8	14	5.3	(8, 28)
Sinclair	S Meade	2015	265	7	15	6.5	(7, 32)
Sinclair	U Lace	2005	276	9	20	7.8	(10, 40)
Sinclair	U Lace	2006	275	1	2	3.0	(1, 11)
Sinclair	U Lace	2007	277	9	16	5.9	(9, 32)
Sinclair	U Lace	2008	269	5	11	6.0	(5, 28)
Sinclair	U Lace	2008	281	6	10	4.6	(6, 23)
Sinclair	U Lace	2010	249	2	3	3.6	(2, 15)
Sinclair	U Lace	2010	264	2	3	2.9	(2, 12)
Sinclair	U Lace	2011	261	10	13	4.1	(10, 25)
Sinclair	U Lace	2012	263	12	16	4.5	(12, 28)
Sinclair	U Lace	2013	266	2	5	4.9	(2, 19)
Sinclair	U Lace	2014	253	9	10	3.1	(9, 20)
Sinclair	U Lace	2015	265	8	19	8.0	(9, 39)
Sinclair	Yeldagalga	2005	223	29	57	11.7	(39, 84)
Sinclair	Yeldagalga	2005	276	83	130	15.1	(105, 164)
Sinclair	Yeldagalga	2006	240	46	87	14.5	(64, 120)
Sinclair	Yeldagalga	2006	245	100	137	11.5	(118, 162)
Sinclair	Yeldagalga	2006	246	6	16	8.4	(7, 38)
Sinclair	Yeldagalga	2006	266	74	114	12.3	(94, 142)
Sinclair	Yeldagalga	2006	275	9	23	9.4	(11, 47)
Sinclair	Yeldagalga	2006	289	112	217	20.8	(179, 260)
Sinclair	Yeldagalga	2007	239	27	44	8.1	(32, 64)
Sinclair	Yeldagalga	2007	256	62	92	10.3	(76, 116)
Sinclair	Yeldagalga	2007	271	84	158	18.4	(127, 199)
Sinclair	Yeldagalga	2008	269	62	115	15.9	(89, 151)
Sinclair	Yeldagalga	2008	281	48	70	8.9	(57, 91)
Sinclair	Yeldagalga	2009	224	35	59	9.7	(44, 81)
Sinclair	Yeldagalga	2009	276	11	19	6.3	(12, 36)

Area	Sub-area	Year	Julian Day	Total Animals Seen	Median Population Estimate	SE	95% Credible Interval
Sinclair	Yeldagalga	2010	249	31	65	12.5	(46, 95)
Sinclair	Yeldagalga	2010	264	31	66	13.2	(46, 97)
Sinclair	Yeldagalga	2011	261	72	103	11.1	(85, 128)
Sinclair	Yeldagalga	2012	263	68	96	10.6	(79, 120)
Sinclair	Yeldagalga	2013	266	42	81	15.6	(58, 119)
Sinclair	Yeldagalga	2014	253	40	66	10.1	(50, 89)
Sinclair	Yeldagalga	2015	265	22	42	10.3	(28, 67)
Villard	Mt Villard	2005	224	17	32	8.7	(20, 53)
Villard	Mt Villard	2006	245	31	48	8.3	(35, 68)
Villard	Mt Villard	2006	266	7	14	5.8	(7, 29)
Villard	Mt Villard	2006	275	40	89	15.5	(64, 125)
Villard	Mt Villard	2006	290	1	1	2.1	(1, 8)
Villard	Mt Villard	2007	246	29	44	8.9	(32, 66)
Villard	Mt Villard	2007	257	22	32	7.0	(23, 50)
Villard	Mt Villard	2007	265	32	52	9.0	(39, 74)
Villard	Mt Villard	2008	269	29	57	11.6	(40, 85)
Villard	Mt Villard	2009	276	20	28	5.6	(21, 42)
Villard	Mt Villard	2010	255	23	40	9.2	(27, 63)
Villard	Mt Villard	2011	261	32	52	8.9	(38, 73)
Villard	Mt Villard	2012	265	15	27	6.8	(17, 43)
Villard	Mt Villard	2013	266	8	23	9.9	(11, 49)
Villard	Mt Villard	2014	269	18	29	6.8	(20, 46)
Villard	Mt Villard	2015	251	5	11	6.5	(5, 29)
Villard	N Katzehin	2005	224	5	12	6.0	(5, 28)
Villard	N Katzehin	2006	245	39	65	9.8	(49, 87)
Villard	N Katzehin	2006	266	44	71	10.1	(55, 94)
Villard	N Katzehin	2006	275	60	116	16.4	(89, 153)
Villard	N Katzehin	2006	290	77	117	12.3	(97, 145)
Villard	N Katzehin	2007	246	28	50	10.8	(35, 77)
Villard	N Katzehin	2007	257	31	47	8.6	(35, 68)
Villard	N Katzehin	2007	265	45	78	11.3	(59, 103)
Villard	N Katzehin	2008	269	61	115	15.8	(90, 151)
Villard	N Katzehin	2009	276	13	24	6.9	(15, 41)
Villard	N Katzehin	2010	255	10	20	7.2	(11, 39)
Villard	N Katzehin	2011	261	62	91	10.6	(74, 115)
Villard	N Katzehin	2012	265	39	64	9.9	(49, 87)
Villard	N Katzehin	2013	266	16	37	11.1	(22, 64)
Villard	N Katzehin	2014	269	48	70	8.9	(56, 91)
Villard	N Katzehin	2015	251	7	18	7.7	(9, 38)
Villard	NW Katzehin	2005	224	1	2	3.1	(1, 12)

Area	Sub-area	Year	Julian Day	Total Animals Seen	Median Population Estimate	SE	95% Credible Interval
Villard	NW Katzehin	2006	245	19	34	7.8	(23, 53)
Villard	NW Katzehin	2006	266	20	40	9.0	(27, 61)
Villard	NW Katzehin	2006	275	32	74	14.2	(52, 106)
Villard	NW Katzehin	2006	290	28	45	7.8	(33, 63)
Villard	NW Katzehin	2007	246	9	19	7.3	(10, 38)
Villard	NW Katzehin	2007	257	10	19	6.4	(11, 35)
Villard	NW Katzehin	2007	265	21	30	5.8	(22, 44)
Villard	NW Katzehin	2008	269	26	56	11.7	(38, 83)
Villard	NW Katzehin	2009	276	10	20	6.8	(11, 37)
Villard	NW Katzehin	2011	261	22	42	9.1	(28, 63)
Villard	NW Katzehin	2012	265	13	23	7.1	(14, 42)
Villard	NW Katzehin	2013	266	3	9	6.4	(3, 27)
Villard	NW Katzehin	2014	269	14	27	7.4	(17, 45)
Villard	NW Katzehin	2015	251	5	14	6.6	(6, 31)
Villard	NW Meade	2007	246	10	19	7.5	(10, 39)
Villard	NW Meade	2007	257	25	35	6.2	(27, 50)
Villard	NW Meade	2007	265	18	22	4.4	(18, 34)
Villard	NW Meade	2010	255	14	26	8.3	(16, 47)
Villard	NW Meade	2011	261	19	30	6.5	(21, 46)
Villard	NW Meade	2012	265	29	46	8.7	(34, 67)
Villard	NW Meade	2013	266	18	35	9.9	(22, 60)
Villard	NW Meade	2014	269	18	25	5.5	(19, 39)
Villard	NW Meade	2015	251	8	13	5.9	(8, 30)
Villard	Snow Top	2005	224	4	9	5.8	(4, 25)
Villard	Snow Top	2006	245	28	38	6.4	(29, 54)
Villard	Snow Top	2006	266	21	31	6.1	(23, 46)
Villard	Snow Top	2006	275	42	88	14.8	(64, 122)
Villard	Snow Top	2006	290	68	109	12.6	(89, 138)
Villard	Snow Top	2007	246	39	58	10.2	(44, 83)
Villard	Snow Top	2007	257	38	57	8.7	(44, 78)
Villard	Snow Top	2007	265	50	80	10.8	(63, 105)
Villard	Snow Top	2008	269	67	127	16.5	(100, 165)
Villard	Snow Top	2009	276	39	67	10.8	(50, 92)
Villard	Snow Top	2010	255	36	69	12.3	(50, 97)
Villard	Snow Top	2011	261	47	80	11.5	(61, 106)
Villard	Snow Top	2012	265	31	50	8.6	(37, 71)
Villard	Snow Top	2013	266	18	39	11.2	(23, 66)
Villard	Snow Top	2014	269	53	84	10.8	(67, 109)
Villard	Snow Top	2015	251	31	54	11.0	(38, 80)



Appendix A, Figure 1. Mountain goat small survey areas, Lynn Canal, AK

Appendix B: Summary of large-area population estimates, Lynn Canal 2005–2015

Survey Area[1]	Year	Julian Day	Total Animals Seen	Median Population Estimate	SE	95% Credible Interval
BL Ridge	2005	276	10	28	9	(15, 51)
BL Ridge	2007	245	29	55	11	(38, 81)
BL Ridge	2008	269	22	47	11	(31, 74)
BL Ridge	2011	261	12	17	5	(12, 30)
BL Ridge	2011	269	35	52	8	(40, 71)
BL Ridge	2012	263	27	41	8	(31, 60)
BL Ridge	2013	266	15	36	11	(21, 63)
BL Ridge	2014	253	19	32	7	(22, 50)
BL Ridge	2015	265	22	53	12	(34, 81)
East Berners	2006	240	128	166	14	(144, 199)
East Berners	2006	246	104	146	16	(122, 185)
East Berners	2006	276	92	141	14	(117, 173)
East Berners	2007	245	130	200	18	(170, 240)
East Berners	2007	265	125	170	13	(149, 199)
East Berners	2007	277	119	157	12	(137, 184)
East Berners	2008	269	160	274	22	(234, 320)
East Berners	2009	222	113	144	11	(126, 170)
East Berners	2009	232	33	45	7	(35, 62)
East Berners	2009	276	???	30	7	(21, 47)
East Berners	2010	254	100	154	16	(127, 191)
East Berners	2010	265	93	174	19	(142, 215)
East Berners	2011	270	149	204	14	(181, 236)
East Berners	2012	263	182	240	15	(215, 272)
East Berners	2013	268	95	137	12	(117, 165)
East Berners	2014	269	157	229	16	(202, 263)
East Berners	2015	275	85	131	15	(107, 166)
Lions Head	2005	223	40	73	12	(54, 102)
Lions Head	2005	276	67	125	16	(99, 162)
Lions Head	2006	240	58	109	15	(84, 144)
Lions Head	2006	246	59	118	19	(88, 163)
Lions Head	2006	266	6	9	4	(6, 21)
Lions Head	2006	275	109	234	21	(193, 275)
Lions Head	2006	289	116	245	22	(202, 287)
Lions Head	2007	239	46	81	12	(62, 107)
Lions Head	2007	256	51	86	12	(67, 112)
Lions Head	2007	271	98	194	20	(158, 238)
Lions Head	2007	277	77	118	12	(97, 145)
Lions Head	2008	269	79	156	19	(124, 197)
Lions Head	2008	281	80	119	12	(99, 145)
Lions Head	2009	224	39	70	11	(52, 95)
Lions Head	2009	276	73	104	11	(87, 129)
Lions Head	2010	249	65	120	17	(92, 157)
Lions Head	2010	264	81	159	19	(127, 199)
Lions Head	2011	261	110	165	14	(142, 196)
Lions Head	2012	263	80	138	15	(114, 170)
Lions Head	2013	266	82	167	23	(127, 218)
Lions Head	2014	253	64	103	12	(83, 129)
Lions Head	2015	265	31	67	13	(47, 98)

Survey Area[1]	Year	Julian Day	Total Animals Seen	Median Population Estimate	SE	95% Credible Interval
NW Meade	2007	246	10	18	7	(10, 37)
NW Meade	2007	257	25	39	8	(28, 59)
NW Meade	2007	265	18	23	5	(18, 37)
NW Meade	2010	255	14	26	8	(16, 48)
NW Meade	2011	261	19	29	6	(21, 45)
NW Meade	2012	265	25	38	7	(28, 55)
NW Meade	2013	266	18	35	10	(22, 60)
NW Meade	2014	269	18	25	6	(18, 39)
NW Meade	2015	251	8	12	5	(8, 27)
Sinclair	2005	223	94	163	18	(132, 204)
Sinclair	2005	276	187	298	21	(260, 342)
Sinclair	2006	240	108	200	21	(164, 245)
Sinclair	2006	245	160	235	17	(206, 272)
Sinclair	2006	246	6	12	6	(6, 30)
Sinclair	2006	266	186	260	16	(232, 294)
Sinclair	2006	275	9	20	7	(10, 38)
Sinclair	2006	289	266	417	15	(388, 447)
Sinclair	2007	239	61	108	13	(86, 137)
Sinclair	2007	256	88	148	15	(123, 180)
Sinclair	2007	271	206	350	19	(310, 383)
Sinclair	2008	269	150	272	20	(233, 313)
Sinclair	2008	281	151	218	15	(191, 251)
Sinclair	2009	224	55	90	11	(72, 116)
Sinclair	2009	276	11	16	5	(11, 28)
Sinclair	2010	249	82	157	19	(126, 198)
Sinclair	2010	264	89	167	19	(135, 208)
Sinclair	2011	261	161	230	15	(204, 264)
Sinclair	2012	263	126	177	14	(154, 207)
Sinclair	2013	266	81	157	22	(121, 208)
Sinclair	2014	253	85	135	13	(112, 164)
Sinclair	2015	265	66	134	18	(104, 174)
U Lace	2005	276	9	20	8	(11, 40)
U Lace	2006	275	1	2	3	(1, 13)
U Lace	2007	277	9	15	5	(9, 28)
U Lace	2008	269	5	12	6	(5, 29)
U Lace	2008	281	6	10	4	(6, 21)
U Lace	2010	249	2	3	3	(2, 14)
U Lace	2010	264	2	3	3	(2, 14)
U Lace	2011	261	10	13	4	(10, 24)
U Lace	2012	263	12	16	4	(12, 28)
U Lace	2013	266	2	5	5	(2, 19)
U Lace	2014	253	9	11	4	(9, 23)
U Lace	2015	265	8	18	7	(9, 37)
Villard	2005	224	27	61	13	(41, 92)
Villard	2006	245	125	188	15	(163, 219)
Villard	2006	266	92	139	13	(118, 168)
Villard	2006	275	193	354	15	(324, 385)
Villard	2006	290	174	252	16	(224, 286)
Villard	2007	246	115	180	17	(151, 218)

Survey Area[1]	Year	Julian Day	Total Animals Seen	Median Population Estimate	SE	95% Credible Interval
Villard	2007	257	101	151	14	(128, 181)
Villard	2007	265	160	239	16	(211, 275)
Villard	2008	269	194	344	16	(311, 374)
Villard	2009	276	82	127	13	(106, 155)
Villard	2010	255	71	133	17	(105, 171)
Villard	2011	261	172	251	16	(222, 286)
Villard	2012	265	121	187	15	(161, 221)
Villard	2013	266	49	109	20	(78, 155)
Villard	2014	269	143	213	15	(187, 247)
Villard	2015	251	54	102	15	(78, 136)

[1] Survey Area corresponds with Area column in Appendix 1 table. One can consult the Appendix 1 table to find which sub-areas comprise the totals for each Survey Area in this table.

Appendix C. Other topics investigated relating to Bayesian modeling of mountain goat aerial survey data

A. Simultaneous use of Bayesian Lincoln-Petersen-type and regression estimators (group level covariates only) in estimating population size.

The intent of this model was to balance the information from a single survey with marked goats where a Bayesian Lincoln-Petersen-type estimate of p is available and estimates of p from the covariate regression based on survey-level covariates. The regression-based $\hat{p}$ integrates patterns over all available surveys that, in combination, have more data than a single survey, while the survey-specific BLP $\hat{p}$ is more sensitive to specific survey-specific characteristics that might not be captured by the regression part of the model, but is based on fewer data resulting in less precision.

For the regression part of the model, for each survey in the dataset based on all past surveys, the model contains the following quantities and parameters:

n_{ci} = the number of marked goats in survey area i (known)

n_{ui} = the number of unmarked goats in survey area i

c_i = the number of marked goats observed on survey i

u_i = the number of unmarked goats seen on survey i

p_i = the probability of observing a goat present during survey i

b_j = regression coefficients relating the logit of p to j predictor variables, $Y_{ji,}$ for the i^{th} survey; regression coefficients are assumed constant across surveys.

Given these quantities and parameters, the model contains the following relationships:

$c_i \sim \text{binomial}(p_i, n_{ci})$

$u_i \sim \text{binomial}(p_i, n_{ui})$

$\text{logit}(p_i) = b_1 + b_2 * Y_{2i} + \ldots b_j * Y_{ji}.$

Similarly, the current-survey part of the model is as follows:

N_c = the number of marked goats in the survey area (known)

N_u = the number of unmarked goats in the survey area

C = the number of marked goats observed on the survey

U = the number of unmarked goats seen on the survey

P = the probability of observing a goat present during the survey

b_j = regression coefficients relating the logit of P to the j predictor variables Y_j; regression coefficients are the same as from the multi-survey regression.

Given these quantities and parameters, the model contains the following relationships:

$C \sim \text{binomial}(P, N_c)$

$U \sim \text{binomial}(P, N_u)$

$\text{logit}(P) = b_1 + b_2 * Y_2 + \ldots\ b_j * Y_j.$

$N = N_c + N_u$

Parameter estimates, especially of N, and their posterior distributions are produced via Markov-chain-Monte-Carlo methods (MCMC; cite).

Although this model was intended to balance the effects of both the current survey data and the multi-survey regression, in practice the regression part of the model dominated in all analyses with the current-survey portion of the model have little effect on estimates of *N*. Consequently, this approach was not implemented in the model described in the body of this report, which retains only the regression-part of the model, dropping the current-survey part.

B. Including goats with unknown collar status in population estimation models.

Depending on survey conditions and the equipment available for conducting aerial surveys (e.g., image-stabilizing binoculars unavailable), it is possible that for some goats that are seen, collar status (i.e., "collared" or "not collared") cannot be determined. Goats of unknown collar status are problematic with respect to inclusion in population estimation models. If goats with unknown collar status are treated as if they were not collared, this results in underestimation of sighting probability (p), and consequently because N-hat is of the general form $C/\hat{p}$ (where C is the count of observed animals), N is overestimated, severely if the proportion of goats with unknown collar status is high. A correct strategy to obtain unbiased estimates of N is to drop all observations of goats with unknown collar status from the analyses; this is appropriate because goats with unknown collar status provide no information with respect to p. However, this procedure is inefficient due to the smaller useful sample size, resulting in higher variance for $\hat{p}$ and N-hat.

We will use a Bayesian version of a Lincoln-Petersen type estimator to illustrate a generalized model that accounts for goats with unknown collar status. All goats in a population subject to an aerial survey can be categorized into 6 groups (a-f) based on collar status ("collared" or "not collared"), whether they were seen during a survey ("seen" or "not seen") and, given that they were seen, was their collar status determined (yes or no) (Fig. B1). This also divides the population into 2 subsets, the number of collared goats, n_c, which is known, and the number of uncollared goats, n_u, which is unknown; $N = n_c + n_u$. Two parameters are also defined by this structure, p and π, the probability that an observed goat's collar status is determined (Fig. B1). This structure and parameters leads to a latent multinomial model.

$(a,b,c) \sim \text{multinomial}(n_c,\ \theta)$, where $\theta = (p\pi,\ p\times(1-\pi),\ (1-p))'$

$(d,e,f) \sim \text{multinomial}(n_u,\ \theta)$

The observation vector from the aerial survey is (a, d, b+e), where a are goats seen to be collared, d are goats seen to be uncollared, and b+e are goats that are seen but whose collar status is undetermined. This leads to the following analysis. The joint distribution of the observations can be written as:

$[b+e, a, d] \propto [b+e \mid a, d] \times [a] \times [d]$, where $[a]$ and $[d]$ are independent binomials, binomial(n_c, $p\pi$) and binomial(n_u, $p\pi$), respectively.

Given that:

$(a,b,c)' + (d,e,f)' \sim \text{multinomial}(n_c+n_u,\ \theta)$,

$[b+e \mid a+d] \sim \text{binomial}\{(n_c+n_u-a-d,\ p\times(1-\pi)/(1-p\pi)\}$.

Parameters of the 2 independent binomials and the conditional binomial, most importantly n_u, can be simultaneously estimated using Bayesian modeling, resulting in an estimate of N.

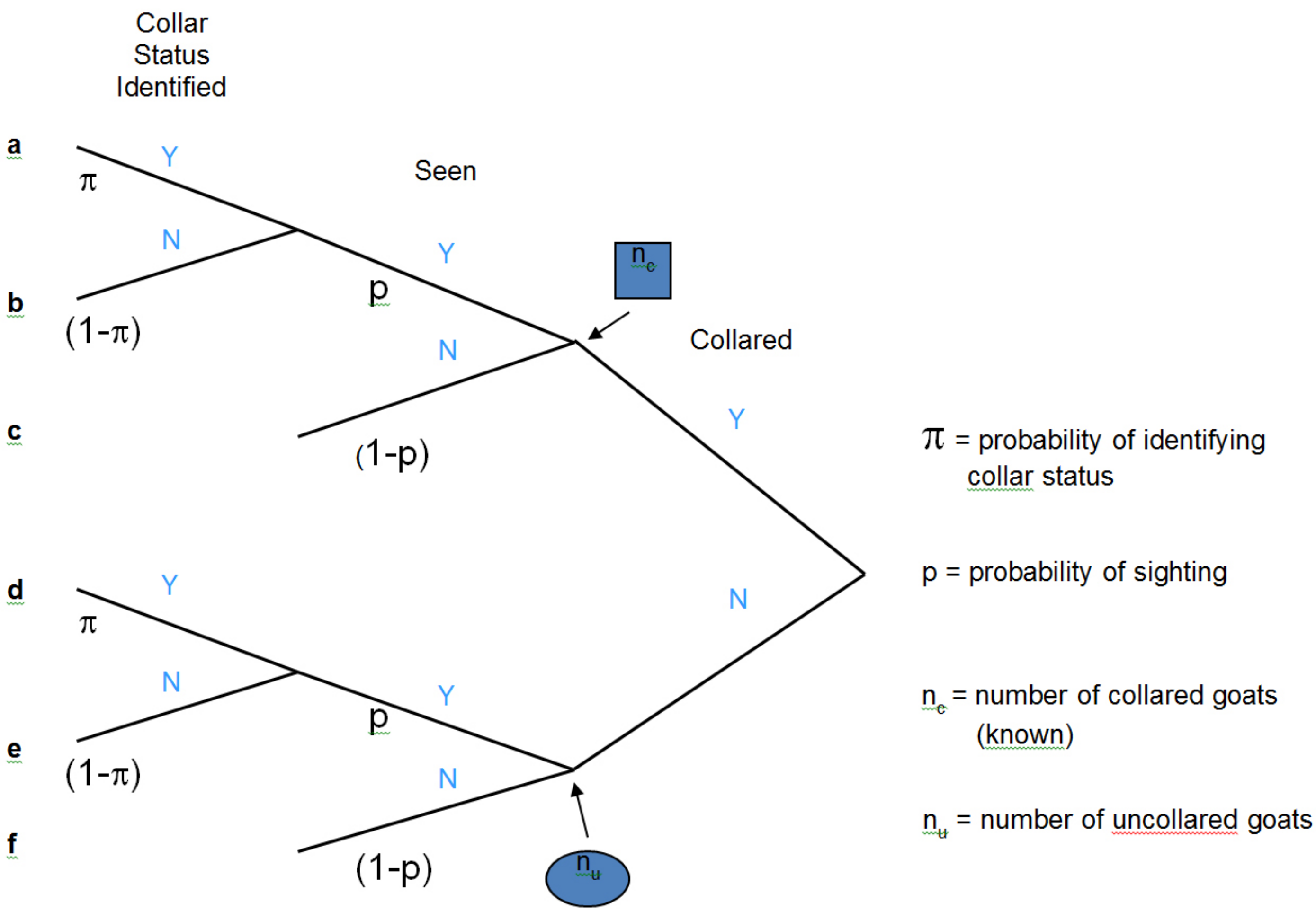
Because observations of goats whose collar status cannot be determined yield no information with respect to p, the model incorporating unknown collar status observation provides little improvement in precision of N-hat, compared to a Bayesian Lincoln-Petersen estimate the drops unknown-status observations from the analysis (ADFG unpublished results). However, there is one advantage to using this model for situations where there are a sizable proportion of unknown-status observations. The lower bound of the credible interval on N-hat under the Bayesian Lincoln-Petersen model (without unknown-status observations) can be less than the number of goats observed during a survey; using the terminology from Fig. B1, the lower bound of the CI < $a+b+d+e$, noting that b and e were not used in the analysis. The admissible (i.e., not < number seen) lower bound (ALB) for an estimated population size is:

$\text{ALB} = n_c + d + \max(b+e-(n_c-c), 0)$

As an example with an extremely high proportion of observations with unknown status:

$n_c = 15$, $a = 2$, $d = 17$, $b+e = 73$; ALB = 15 + 17 + 60 = 92

Using these data in a Bayesian Lincoln-Petersen model results in a lower bound on the 95% credible interval of 65, which is lower than the ALB. Using the model that incorporates the probability of identifying the collar status, the lower CI bound is 96, which is >ALB.



Appendix C, Figure 1. Schematic of a model accounting for sightings of goats with unknown collar status. The 6 possible categories of goats based on collar status, whether seen, and whether collar status was determined are designated a-f (left side of figure).

C. Producing a single estimate of population size for multiple surveys.

In some areas, goat populations are surveyed multiple times in a year. It might be reasonable to assume that the population size (N) is (essentially) the same across all surveys in a year (i.e., no emigration/immigration or mortality), and consequently we would like a model that generates a single population estimate and associated precision rather than separate estimates for each survey occasion. If we were using a model that directly estimated N_i for survey i in a year, we could use data from all surveys in a year in a Bayesian hierarchical model where the N_i were drawn from the distribution for N. However, the covariate regression model described in this report does not estimate N_i directly, but rather estimates the number of goat groups present in the survey area and the average size of these groups from which we estimate N_i-hat. Because N_i-hat is calculated within the model, we cannot also consider it to be generated from the distribution of N under a hierarchical model.

As an alternative, to estimate a single N from multiple within-year surveys we investigated models with estimation based on rejection sampling. For this approach we, we include data from multiple surveys with a single analysis. The regression-part of the model (described in the body of this report) remains unchanged using data from all available surveys. However, the survey specific components, including estimates of group size, are parameterized separately for the data for each survey. Consequently, each N_i is estimated separately. The Markov-chain-Monte-Carlo (MCMC) procedures used to implement the Bayesian models do so with iterative methods. At each iteration, there are estimates for all of the parameters, which, in the case of the multi-survey model, includes the N_i. The estimates of the N_i from the saved MCMC iterations are retained if the N_i estimates are all the same and rejected if the N_i from the iteration differ. In practice to reduce storage requirements, only iterations with all estimated N_i within a predetermined small range need to be saved. The retained N_i, which are estimates of N because all N_i within an iteration are equal, define the posterior distribution of N, from which inferences can be made.

Although this method can produce estimates of N from multiple surveys, this is not guaranteed. If the multiple datasets never produce iterations with the N_i equal, the procedure will fail. This would seem more likely as the number of replicate surveys increase. Additionally, even if replicates with equal N_i do occur, they can be rare, hence requiring large increases in computation time (i.e., many more iterations, most of which will be rejected) to get enough estimates of N to adequately describe the posterior of N.

Appendix D. Future directions in Bayesian sightability modeling for mountain goats.

1. The current model assumes that the effects of the predictors on sighting probability are additive. However, it is possible that interactions between predictors occur. For example, the effect of group size on sighting probability might differ for groups in different habitat types. In an open habitat type (e. g., meadow) group size may have a strong, positive influence on detection probability whereas in mature forest group size may be nearly irrelevant since canopy cover is very thick and largely precludes detectability. Models that account for these differing patterns (e.g., partial interaction models) could be developed and may improve model fit.

2. The current model estimates the distribution of group size based on the observed group sizes across all surveys, irrespective of date or area surveyed. This estimated group-size distribution is used to essentially impute group size when it is missing in survey data. Modeling group size as a function of predictors (e.g., date, habitat) would relax these assumptions with respect to using across-survey estimates of mean group size.

3. In the current model, missing or unobserved categorical predictors (e.g., habitat type, terrain) are essentially imputed from the distribution of the predictors for observed groups of goats across all of the survey datasets. There are several potential issues with this approach, including that the distributions of predictors might vary substantially across survey areas (assuming that data are used from multiple areas) and combinations of predictors might be imputed that do not exist (e.g., maybe very rough meadows do not exist, or snow covered very steep terrain). Area-specific (and survey-specific for snow habitat) predictor distributions based on actual survey area GIS information could possibly be developed and implemented into the model.

4. Mark-resight models have been incorporated into more general matrix population models (e.g., Chilvers et al. 2010, Johnson et al. 2010). In such combined models, the mark-resight and matrix population parts of the model mutually reinforce one another with mark-resight models providing empirical population information and the matrix population dynamics part of the model smoothing estimates over years by accounting for realistic population processes. Our mark-resight models for estimating goat population size are amenable for incorporation into such a combined model.

5. Our model is only for a single survey (or at most multiple surveys of an area in a single year, Appendix 3) and does not account for spatial locations of goats within a survey area. Potentially the model could be extended to a multi-year version of the model that kept track of subarea-specific locations of observed goats. If there were consistent patterns of abundance for subareas (e.g., Fig. 3) of the survey area across years, such a model could be useful for imputing data for subareas that were not surveyed during a specific survey (e.g., due to fog).