A POPULATION ASSESSMENT FOR THE NORTH CASCADES ELK HERD: 2006-2011

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EXECUTIVE SUMMARY

The North Cascades (Nooksack) elk herd declined during the 1980s, prompting a closure to recreational and subsistence harvest by state and tribal hunters in 1997. The Washington Department of Fish and Wildlife (WDFW) and the Pt. Elliot Treaty Tribes initiated collaboration in the late 1990s to promote herd recovery. The principal strategies used were the temporary recreational / subsistence harvest moratorium and 2 translocations of elk from the Mt. St. Helens (MSH) elk herd (fall 2003 and fall 2005).

In 2005, WDFW and the Pt. Elliot Treaty Tribes initiated a joint study to evaluate the size and demographics of the current Nooksack elk herd, judge the effectiveness of the recovery strategy, and develop a rigorous monitoring strategy. Two principal monitoring approaches were concurrently evaluated: sightability-correction modeling and mark-resight modeling. We report the results from work conducted during the fall of 2005 through the spring of 2011 (winters 2005-2006 through 2010-2011).

We collected data during intensive late winter helicopter surveys (2 total area surveys per year). We used data from Feb-Apr flights, 2006-2007 to fit a logistic regression model to predict the sightability of elk groups based on group and environmental covariates. Several covariates influenced sightability in univariate logistic regression models. We then used multi-model inference and an information-theoretic criterion (AIC_c) to compare several alternative multivariate models of varying complexity; our results indicated the best multivariate model predicted sightability of elk groups based on: 1) group size, 2) forest canopy cover (%), and 3) a categorical activity covariate (active vs. bedded). Predicted sightability increased with increasing group size, with decreasing cover, and when elk were active. The final logistic regression model was effective at correctly discriminating sighted and unsighted groups from the model building dataset, and we applied it to the full aerial survey datatset (2006-2011). The sightability model indicated relatively steady and modest herd growth during 2006-2011, but model estimates for years we had good *minimum-known-alive* estimates were negatively biased. The sightability model estimated the

Nooksack elk population was about 350 elk in the spring of 2006, rising to about 550 elk by the spring of 2011.

Among available mark-resight models, we principally used the recently developed logit-normal mixed effects (LNME) model to generate estimates of total elk population size and the sizes of the cow and branch-antlered bull subpopulations. We explored 15 a priori LNME models to predict total population size and 12 models to predict subpopulation sizes. We again used multi-model inference and AIC_c to evaluate the evidence in our data for the various models in the *a priori* model sets. Our results supported evidence for individual heterogeneity in resighting probabilities and variation in resighting probabilities across some years. The LNME model estimates suggested growth in the total elk population and the gender-based subpopulations during 2006-2011. Estimates of total population size increased from 644 (95% CI = 570-706) in spring 2006 to 1,248 (95% CI = 1,094-1,401) in 2011. The cow subpopulation was estimated to have increased from 381 (95% CI = 338-424) in spring 2006 to 573 (95% CI = 507-639) in 2011. The branch-antlered bull subpopulation estimates increased from 87 (95% CI = 54-119) to 180 (95% CI = 118-241) from spring 2006 to spring 2011.

The LNME model estimates were consistently and substantially higher than the sightability model estimates across years. The LNME model estimates were higher than minimum-known-alive estimates, but seemed reasonable in comparison. The trends among total population size (sightability model and LNME model derived) and cow elk subpopulation size (LNME model) were very similar and suggested a finite growth rate of $\lambda \approx 1.07$-1.12 or an exponential growth rate of $r \approx 0.07$-0.11. The mean estimates of λ and r from an age-structured stochastic population model using empirical estimates of vital rates were 1.10 and 0.10, very similar to the trends estimated from both sightability modeling and mark-resight modeling. Collectively, these results provided considerable evidence that the core Nooksack elk population (GMU 418) grew modestly during 2006-2011.

We also used radiomarked elk to estimate survival rates and explore possible sources of variation in survival. We explored 16 *a priori* survival models with known-fate models implemented in Program MARK, using AIC_c and model weights to draw conclusions about Nooksack elk survival during 2000-2008. Based on early results from the population assessment work, limited bull harvest had been reinitiated in the fall of 2007. Our results suggested bull elk survival was high during the harvest moratorium (0.92; 95% CI = 0.76-0.99), but declined after the resumption of limited-entry bull harvest (0.68; 95% CI = 0.50-0.82). Cow survival was high under the best supported model (0.93; 95% CI = 0.90-0.95), except adult cows translocated from MSH in fall 2003 had lower survival for the first year post-translocation (0.68; 95% CI = 0.51-0.82). There was little evidence of any early post-translocation effect on adult cow survival for cows moved from MSH in the fall of 2005.

Our results suggested that the strategy jointly pursued by WDFW and the Pt. Elliot Treaty Tribes was effective in promoting recovery of the Nooksack elk herd and that the recent trajectory for the population has been consistently positive. Recent levels of limited bull harvesting have reduced bull survival, as expected, but survival seems high enough to protect the bull subpopulation from over-exploitation and meet management objectives. Despite the conservation closure since 1997, adult cow elk were regularly harvested under damage permits and seasons in the agricultural valleys of the Nooksack herd area during 2005-2011. We documented at least 270 elk deaths and 91 cow elk deaths during 2005-2011. Losses of adult cows were principally from damage hunts and roadkills along local highways.

We suggest mark-resight is the best approach for monitoring the population, but the use of this approach will require periodic remarking of elk. Both the scales of the landscape and of the elk population make mark-resight a viable management option. We offer further suggestions regarding monitoring strategies and overall herd management in light of our results.

INTRODUCTION

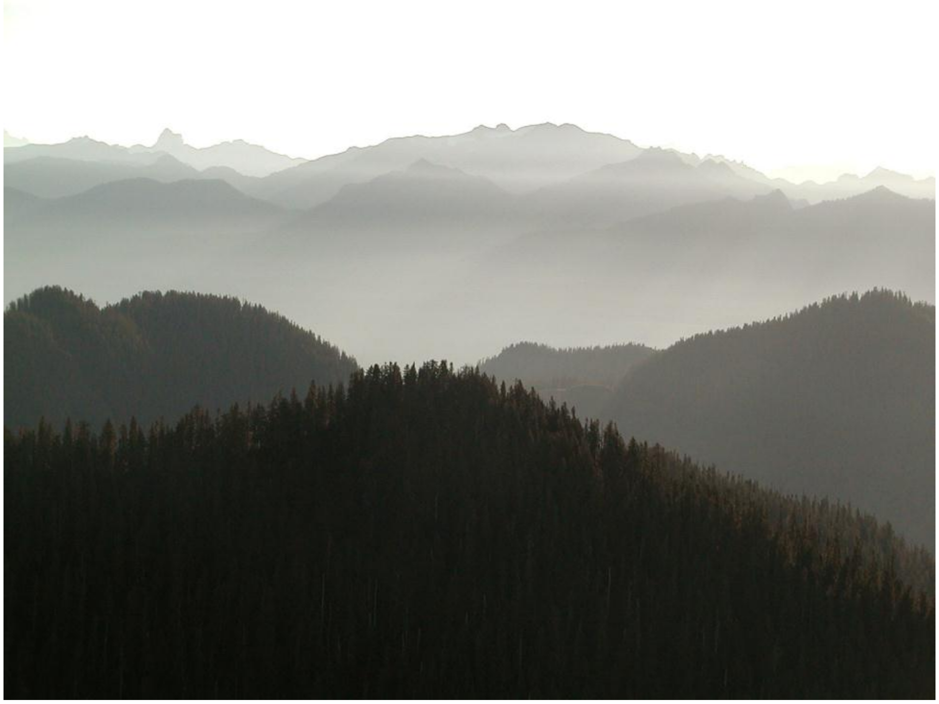
The North Cascades elk (*Cervus elaphus*) herd, commonly known as the *Nooksack* herd, is the smallest of 10 major elk herds in Washington (WDFW 2002). The herd inhabits a heterogeneous mosaic of managed forest uplands and valley floodplains in the northwestern part of the state. In recent decades the population was believed to have declined from a peak population of approximately 1,700 elk in 1984 to perhaps as few as ≈300 elk by the early 1990’s. A variety of factors, including possibly excessive human harvest, apparently led to this decline. In a concerted effort to rebuild the Nooksack elk population, the Washington Department of Fish and Wildlife (WDFW) and the Pt. Elliot Treaty Tribes jointly invoked a harvest moratorium in the core Nooksack elk range in 1997. Additionally, elk were translocated from the Mount St. Helens (MSH) elk herd in southwestern Washington in 2003 and 2005 to increase the Nooksack population and promote recovery.

Because of the lack of formal population estimates needed to track recovery and support management decisions, we initiated an investigation in fall 2005 to explore approaches to population monitoring and to generate an updated formal population assessment. We were fortunate that radiocollared elk were already present in the population in 2005, stemming from past research on the native herd and from the translocated elk from MSH. In 2005, it was generally believed that the combination of a harvest moratorium and translocation efforts had effectively reversed the population decline and that the population was likely approaching benchmarks established to define when controlled harvest could be reinitiated (WDFW 2002). However, enough uncertainty existed about herd size, composition, and trend in 2005 to preclude reinitiating harvest, pending better data.

Aerial surveys represent a basic fundamental tool for monitoring elk populations, but raw data from aerial surveys are known to be plagued by substantial biases (Caughley 1974, Routledge 1981, Samuel and Pollock 1981, McCorquodale 2001). Methods, such as sightability correction models have been developed to reduce biases in aerial survey data (Pollock and Kendall 1987, Samuel et al. 1987, Steinhorst and Samuel 1989, Otten et al. 1993, McCorquodale 2001, Udevitz et al. 2006). Model developers have cautioned against applying sightability correction models outside of the environmental context in which they were constructed (Samuel et al. 1987, McCorquodale 2001), and no models for Westside Washington or Oregon habitats had been published by 2005. Alternatively, mark-recapture models could potentially be used to generate unbiased population size estimates from aerial survey data (Bear et al. 1989, Eberhardt et al. 1998, White and Shenk 2001, Gould et al. 2005, Tracey et al. 2008) using a mark-resight design, but no mark-resight population estimates were available for the North Cascades elk herd prior to our work. Rigorous population reconstruction methods were not practical, given the harvest moratorium (typically age-at-harvest data are the principal data). Therefore, we undertook a 5-year effort in the fall of 2005 with 3 primary goals:

1) *explore the development of an elk sightability model,*
2) *compare mark-resight and sightability modeling as alternative approaches for monitoring the Nooksack elk herd, and*
3) *estimate the size and composition of the current Nooksack elk herd.*

We believed these goals were achievable because of the existing availability of a large number (>70) of radiocollared elk prior to our work and considerable overlap in the nature of the data required for mark-resight and sightability modeling (*i.e.*, data collected for 1 context, could be applied to the other with only slight modification to sampling protocols). Additionally, we desired to: *1) estimate recent patterns in elk survival, and 2) evaluate the effectiveness of recent elk translocations to the Nooksack elk herd range*.



STUDY AREA DESCRIPTION

Location, Ownership, and Physiography

The Nooksack elk herd area includes part or all of Whatcom, Skagit, Snohomish, and King Counties and comprises Washington State Game Management Units (GMU) 418 (Nooksack), 437 (Sauk), 448 (Stillaguamish), and 450 (Cascade) (Figure 1). The herd's current core area represents about 1,230 km^2 (492 mi^2) of the historic range within GMU 418, and our primary study area was approximately the lower half of this GMU.

About 530 km^2 (43%) of the total Nooksack elk herd range is privately owned, and most of this land is managed as large blocks for commercial timber products. The Washington State Department of Natural Resources manages 420 km^2 (34%), and the U.S. Forest Service manages 280 km^2 (23%). Our study area, mostly the winter landscape used by Nooksack elk, was predominantly corporately owned timberland, except for floodplains and developed areas.

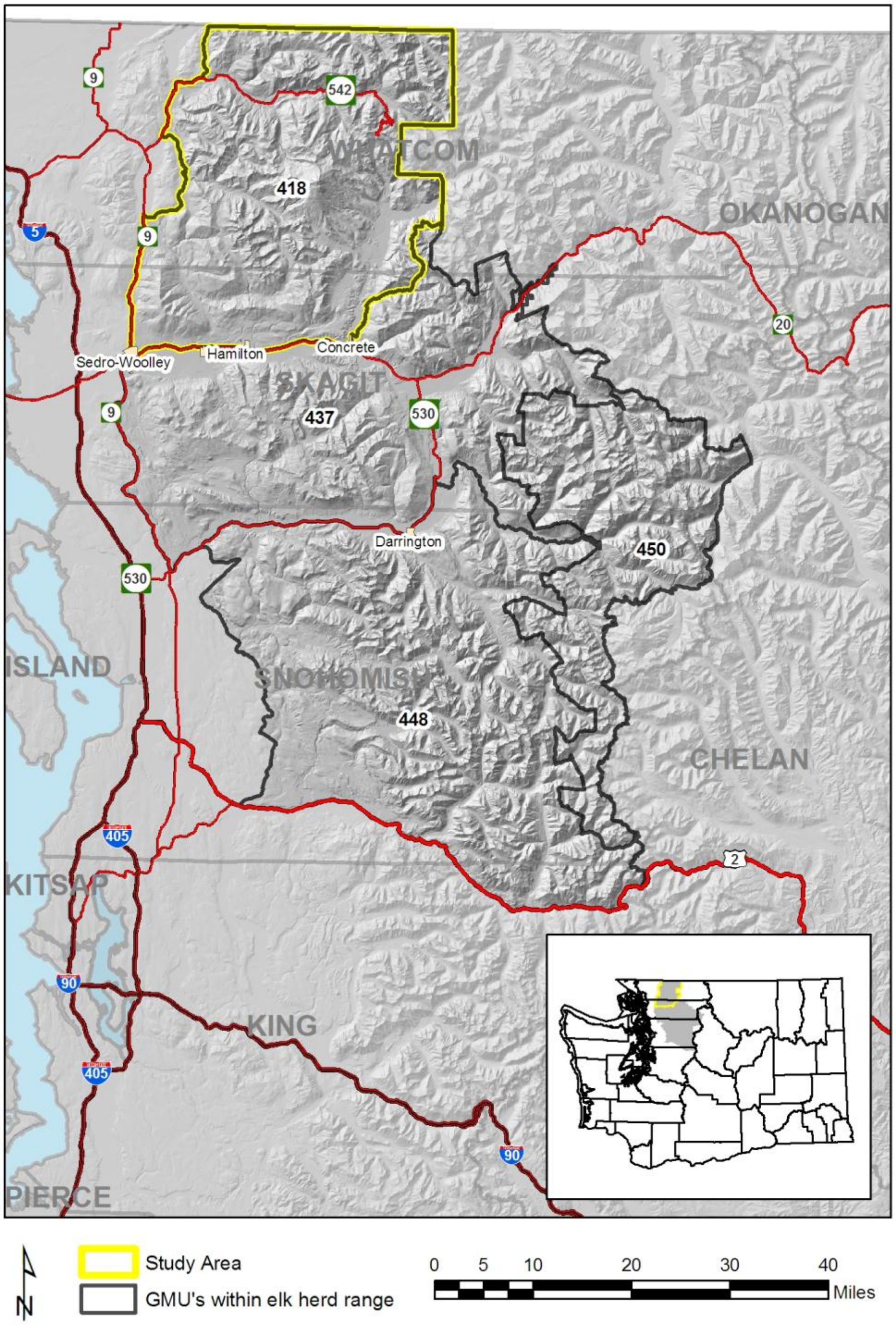


Figure 1. Nooksack Elk Herd Area and primary Study Area location

The study area was within the Northern Cascade physiographic province described by Franklin and Dyrness (1973). Elevations in the study area ranged from 61 meters along Washington State Highway 9 to approximately 1,400 meters at the crest of Bald Mountain. Most of the study area was characterized by mid-elevation mountainous terrain bordered by agricultural lands and rural development to the west and south. The North, Middle, and South Forks of the Nooksack River were prominent features of the core herd range, and our study area encompassed the Middle and South Fork drainages (Fig. 2), plus the foothills south to the Skagit River.

Figure 2. The South Fork of the Nooksack River within the core range of the Nooksack elk herd was one of the focal areas for the winter population assessment work.

Vegetation and Climate

Coniferous forest dominated much of the study area. Three major forest zones occurred along elevation and moisture gradients (Franklin and Dyrness 1973). Lower coniferous forests were dominated by western hemlock *(Tsuga heterophylla)*, mid-elevation forests by Pacific silver fir *(Abies amabilis)*, and mountain hemlock *(Tsuga mertensiana)* dominated the highest elevation conifer stands. The Western Hemlock Zone, generally limited to elevations less than 600 meters, was the most important timber production zone in the study area. Major tree species in this zone were Douglas fir *(Pseudotsuga menziesii)*, western hemlock, and on moist sites, western red cedar *(Thuja plicata)*. Historic forest management had resulted in a mosaic of clearcuts and timber stands of various ages throughout much of the study area (Fig. 3).

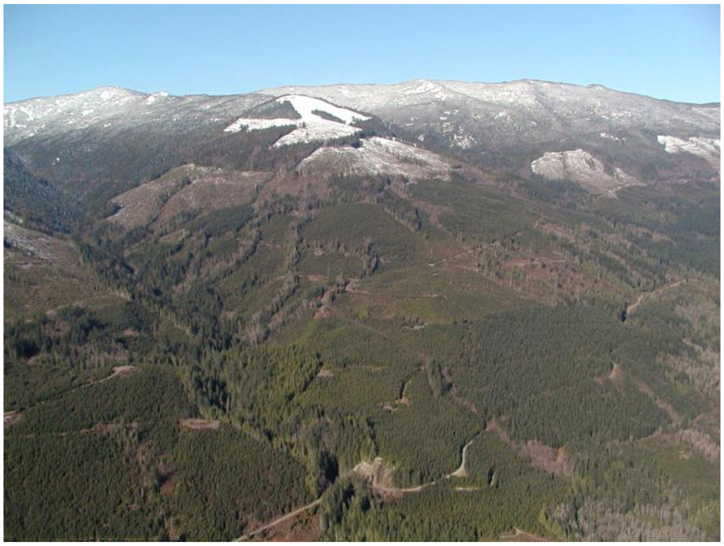


Figure 3. Much of the study area in the Nooksack elk herd core range consisted of a managed forest mosaic of variously aged timber stands and clearcuts.

Hardwood species, such as red alder *(Alnus rubra)* and bigleaf maple *(Acer macrophyllus)*, occurred mainly as pioneers on recently disturbed sites or in floodplains and dominated a considerable portion of our study area. Understory composition varied, depending on site moisture and soil class. Moist sites with more productive soils were often dominated by sword fern *(Polystichum munitum)* and its associates, while poorer, drier soils often supported salal *(Gaultheria shallon)*, an evergreen shrub.

The climate of the study area was strongly affected by the maritime influence of Puget Sound and the Pacific Ocean just west of the Nooksack elk herd range. Mean annual precipitation historically ranged between approximately 100 cm at lower elevations to ~450 cm in the higher mountains. Winter snowfalls are common and occur at all elevations. Snow is usually transitory below 750 meters, but persistent deep snowpacks typically accumulate at elevations above 1,000 meters. Most elk winter habitat for the Nooksack elk herd has historically been in the western hemlock zone, below 650 meters. During our study, winters were fairly typical for the region; however, during the winter of 2008-09 several large winter snowstorms and persistent snowpacks pushed elk into valley bottoms and floodplains in greater numbers than usual.

Human Influences

The cumulative impacts of human activities within the core range of the Nooksack elk herd are believed to have been responsible for historic declines in the elk population. Urban development and agricultural conversion has been common along the western, southwestern, and southern peripheries of the elk range. Residential construction has been widespread in most lowland areas that were once suitable as elk winter range, and this development continues (Fig. 4). Agricultural conversion of low elevation forests has dramatically altered the landscape and elk habitat along the Highway 9 and Highway 20 corridors. Human recreational use has been common on national forest lands to the east of our study area and has included camping, hiking, hunting, fishing, bird watching, photography, mountain climbing, horseback riding, riding motorcycles and All Terrain Vehicles (ATVs), snowmobiling, and cross country skiing.

Figure 4. Residential development in traditional Nooksack elk winter range.

HERD HISTORY

Distribution

The Nooksack elk herd occupies part of the original range of native Roosevelt elk (*C. e. roosevelti*) in western Washington, but the current herd shows considerable genetic evidence of introgression of Rocky Mountain elk (*C. e. nelsoni*) alleles, presumably reflecting translocations of Montana and Yakima area elk into the Nooksack country in the early to mid 1900's.

The majority of the current Nooksack herd occupies lands above 500 meters that drain the Middle and South Forks of the Nooksack River and the northern tributaries of the Skagit River within the core elk range (GMU 418). At lower elevations, elk distribution in GMU 418 is fragmented, with small satellite populations exploiting agricultural, residential, and suburban areas. At the start of our study it was believed that approximately half of the current herd used these lower elevation habitats to some degree. The extent of elk use in the Sauk, Stillaguamish and Cascade GMUs remains relatively unknown. Recently elk emigration appears to have occurred from the Skagit River Valley south into the Sauk. In GMU 418, occupied winter range includes the lowland valleys where elk sometimes cause damage to agriculture and other private property values. During 2006-2007, a few (<15) elk were passively trapped in an agricultural setting just west of GMU 418 by the Pt. Elliot Treaty Tribes and relocated to GMU 437 (Sauk). A more through discussion of the history of the Nooksack elk herd can be found in the *North Cascade Elk Herd Plan* (WDFW 2002).

Management

The Nooksack elk herd was historically managed with a variety of recreational hunting regulations and seasons (WDFW 2002). In recent time, but prior to the conservation closure implemented in 1997, general season bull harvest in GMU 418 was regulated under a 3-pt antler restriction. During 1980-1996, the average antlered bull harvest by licensed hunters across all Nooksack elk herd GMUs was 42 bulls (WDFW 2002). During the same period, the average antlerless elk harvest was 23 elk. Since 1990, antlerless elk general season harvest opportunity has been very limited across the Nooksack GMUs. No general season hunting for antlerless elk has occurred in GMU 418 since 1991.

In 1999, an Elk Area was created along the Skagit River corridor just south of Highway 20 (originally Elk Area 941, but later changed to 4941) to deal with elk damage issues on private property. Legal methods for state licensed hunters in the Elk Area were limited to primitive weapons until 2010 (muzzleloaders and archery), but the season was liberal (generally from Oct 1- Jan 31). The intent of the Elk Area was to use extended hunting pressure, but limited harvests to discourage elk from using these lands. Notably, in the winter of 2008-2009, a series of winter snowstorms pushed elk into Elk Area 4941 in greater numbers than usual, and a substantial number of elk were harvested (22 bulls and 20 antlerless elk; Appendix A). In 2010, hunting in Elk Area 4941 was changed from a general season to permit-only hunting limited to WDFW-certified Master Hunters. Other sporadic hunts have occurred, as needed, to deal with elk damage in other lowland areas, such as near the community of Acme.

During 1997-2006, the core Nooksack herd range was under a conservation closure for state-licensed elk hunters. Most Pt. Elliot Treaty Tribes also implemented a conservation closure during this time, but some unreported ceremonial hunting by the Tribes may have occurred on a limited basis during the closure. In 2007, based on preliminary data collected during this study, limited permit-controlled bull elk hunting was reinitiated in GMU 418 by WDFW and the Tribes by consensus. The preliminary data suggested that the Nooksack elk herd had recovered sufficiently by spring 2006 to meet the criteria previously defined as necessary for reinitiating harvest (WDFW 2002). In the fall of 2007, and again in 2008, state and tribal elk hunters equally shared the 30 bull elk permits that were allocated each year. In the fall of 2009, the total permit number was increased to 40, with half of the permits designated “spike only” and half “any bull”; the state:tribal allocation remained 50:50. This permit strategy was retained for fall 2010.

METHODS

Elk Marking

VHF Radiomarked elk were available for use in our investigation from 2 sources: 1) *native elk marked for research, and 2) elk translocated to the Nooksack for population augmentation*. From 2000-2002, 21 native adult females were helicopter darted with a carfentanil/xylazine mixture and equipped with radiocollars in support of research on cow elk condition and reproductive dynamics (Bender et al. 2006). In October 2003, 34 adult female elk were radiocollared on the Mount St. Helens (MSH) Wildlife Area after they were driven into a large corral trap by helicopter (Fig. 5*a*). These elk were loaded into modified horse trailers and driven to the Nooksack elk herd area and released. Similarly, in October 2005, 27 adult female elk were helicopter drive-trapped at MSH, radiocollared, and translocated to the Nooksack. In addition, 11 adult female elk were also trapped in a passive corral trap at MSH in 2005, radiocollared, and translocated to the Nooksack. We translocated 19 elk calves to the Nooksack from MSH in 2003 (*n* = 5) and 2005 (*n* = 14). We also helicopter darted and radiocollared Nooksack adult bulls in September 2005 (*n* = 7), February 2006 (*n* = 4), October 2006 (*n* = 4), February 2007 (*n* = 5), April 2008 (*n* = 4), April 2009 (*n* = 1), and April 2010 (*n* = 8). We helicopter darted and radiocollared 7 additional adult cows in April 2008, and 3 more in April 2010 (Fig. 5*b*). We conducted all animal handling procedures in compliance with WDFW's Animal Restraint and Chemical Immobilization Policy (POL-M6003).

Figure 5. Radiocollared elk used in the population assessment came from elk captured and translocated from Mt. St. Helens in 2003 and 2005 (a) and native Nooksack elk darted from a helicopter on the Nooksack study area (b).

Sightability-Correction Modeling

We developed and evaluated sightability correction models for late winter-early spring helicopter surveys in the Nooksack herd area by collecting data from sighted and unsighted groups of radiocollared elk, Feb-Mar 2006-2007. We delineated 12 sampling units that were 16.8-62.7 (mean = 31.0) km^2. Larger units included agricultural and rural developments. Sampling unit sizes were selected such that a unit could be sampled in ~20-60 minutes of flight time. We defined unit boundaries such that they were easily identified from the air (roads, streams, distinct topographic features), except that we established the 2,500-ft elevation contour as an upper elevation boundary where appropriate, based on previous data on elk distribution during the period corresponding to our data collection flights. This elevation contour generally reflected the elevation at which snow depth precluded elk use during our Feb-April survey timing.

Prior to each set of data collection flights, we attempted to pre-survey units in a fixed-wing aircraft to determine the distribution of radiocollared elk among the counting units. We purposefully did not locate radiocollared elk precisely during these flights, but only attempted to allocate them properly among the 12 sampling units. When weather or other constraints prevented us from conducting fixed-wing pre-survey flights, we verified the distribution of radiocollared elk among our sampling units prior to a survey by flying just off the perimeter of each unit with the telemetry-equipped survey helicopter, being careful to not gain specific information about the location of elk within the units.

Crews conducted initial visual surveys and telemetry-assisted follow-up in each sampling unit from a *Bell 206 Jet Ranger* helicopter. The crew of the survey helicopter was given information on the distribution of radiocollared elk among counting units, but did not know the exact locations of these elk. We selected sampling units to apportion equivalent sampling effort across the units. We flew adjacent units consecutively where movement of elk across sampling unit boundaries was expected to be common, based on previous telemetry data. The helicopter crew consisted of the pilot and 3 observers. The primary observer sat abreast the pilot and also recorded data; the 2 additional observers sat abreast, in the back seat of the aircraft. One backseat observer assisted in navigation and maintaining flight line protocols by following a GPS track log on a laptop computer. The helicopter was equipped with a single, forward-looking VHF telemetry antenna and a receiver that allowed radiocollared elk to be relocated when needed during the data collection flights, as described below.

We conducted visual surveys of the counting units initially with the helicopter's telemetry system turned off. The counting units were surveyed systematically at an altitude of 40-70 m AGL, flying at 80-110 km/hr, and with transects separated by approximately 150-300 m, depending on terrain and the presence of potentially concealing tree/shrub cover. Generally, units were surveyed with transects paralleling elevation contours, flying progressively from lower contours to upper contours.

The helicopter crew scanned for elk groups within approximately 200 m of transects in open areas and within 75-100 m in areas with extensive tree/shrub cover. When a crewmember sighted an elk group, the pilot deviated from the transect and circled the group while the crew collected the following covariate data: group size (GRP), activity of the first elk sighted (ACT), percent canopy closure typical of the area immediately around the group (CAN), percent snow cover (SNOW), and cover type (COV) as a categorical variable (opening, young clearcut, older clearcut, alder, conifer forest) (Fig. 6). The crew derived canopy closure estimates via crew consensus, and crews had graphical depictions of various canopy closure settings available for reference. We recorded CAN and SNOW as continuous covariates, in increments of 5%. We also recorded GPS waypoints for all elk groups.

Figure 6. Data for covariates potentially useful for modeling detectability of elk during aerial surveys were collected for groups containing radiocollared elk. Data were collected for both seen and missed groups during experimental helicopter surveys.

Crews also scrutinized sighted groups for the presence of radiocollared elk and recorded the composition of the groups (*i.e.*, the numbers of adult females, calves, yearling bulls, subadult bulls [2-3 yr-olds], and mature bulls [≥4 yr-olds]). If radiocollared elk were sighted in a group, the telemetry system was activated, and the crew identified all radiocollared elk present. We took digital photos of larger groups (≥ 30 elk) and later verified group size and composition from these photos. After we collected data for each sighted group, we deactivated the telemetry system if it had been used to identify collared elk, the pilot repositioned the helicopter back onto the original transect, and we resumed the survey protocol.

When we had finished surveying a counting unit and had collected data for all sighted groups, we reactivated the telemetry system aboard the helicopter to facilitate locating elk groups containing radiocollared elk that we had missed during the visual survey. We located all missed radiocollared elk precisely via telemetry and collected the same data for these groups that we had collected for sighted groups. When these missed groups were located in heavy cover, the pilot homed to the radio signal, and maneuvered the aircraft in low concentric circles over the radiocollared elk's location while the crew carefully watched for elk movement for several minutes. Often, the pilot was able to haze these groups into sparser cover where the crew could enumerate and classify them. Sometimes, groups in the heaviest cover could not be completely counted or estimated with confidence, and these instances resulted in *missing data* for the GRP covariate. We also recorded GPS waypoints for all groups that had been missed, but were subsequently located via telemetry.

We modeled the sighting process as a binary outcome (*i.e*., 1 = sighted group, 0 = missed group) using logistic regression (Hosmer and Lemeshow 1989), employing group and environmental covariates as potential predictor variables. Modeling was based only on radiomarked groups (*i.e*., we recorded data from sighted groups that did not contain radiocollared elk, but did not use those data to model sightability). For groups that had missing values for the GRP covariate, we substituted the median group size from all groups we had confidently counted, but limited the data to nonagricultural setting groups for groups missed in natural (*i.e*., forested) habitats (elk groups exploiting agricultural fields tended to be larger than groups observed in natural habitats). For modeling sightability, we derived a covariate reflecting the dominant gender of the group (SEX). We conceptualized 15 alternative models of varying complexity reflecting logical combinations of covariates potentially affecting the sightability of elk groups during helicopter surveys (Table 1). We used Akaike's Information Criterion, adjusted for small samples (AIC_c) for assessing model support and used model averaging to derive final coefficient estimates and their unconditional standard errors (Burnham and Anderson 2002).

Table 1. Candidate model covariates for predicting the sightability of elk groups from a helicopter in the Nooksack Elk Herd Area, 2006-2007.

Candidate Model Covariates	k
GRP	2
CAN	2
GRP , CAN	3
GRP, CAN, SEX	4
GRP, CAN, SNOW	4
GRP, CAN, SNOW, SEX	5
GRP, CAN, COV	4
GRP, CAN, COV, SEX	5
GRP, ACT, CAN	4
GRP, ACT, CAN, SEX	5
GRP, ACT, CAN, SEX, SNOW	6
GRP, CAN, COV, ACT	5
GRP, CAN, COV, ACT, SEX	6
GRP, CAN, COV, ACT, SNOW	6
GRP, CAN, COV, ACT, SNOW, SEX	7

We then used the data collected only for sighted groups each year to generate estimates of population size using the best-supported sightability model. These data included the data used to develop the sightability model (*i.e.*, 2006-2007) and non-model-building data (*i.e.*, 2008-11). We did this by developing an R script (R Development Core Team 2008) that implemented the estimators described by Steinhorst and Samuel (1989).

Mark-Resight

Background

Mark-recapture methods for estimating population sizes have a long history and are based on a well-developed body of theory (Otis et al. 1978, White et al. 1982, Pollock et al. 1990). These methods have been adapted to the application of estimating large mammal population size, wherein the typical approach uses *resightings* of marked animals (*e.g.*, collared deer or elk) as a surrogate for physical *recaptures* (Rice and Harder 1977, Bartmann et al. 1987, Bear et al. 1989). A mark-resight approach to large mammal population estimation provides a mechanism to address sighting biases (*i.e.*, incomplete sightability), but in a fundamentally different way than sightability-correction modeling. Whereas sightability modeling is designed to *predict* group-specific sightability as a function of factors affecting sightability, mark-resight methods commonly ignore the factors that affect sightability. There is no intent to explain why some animals are missed; it is just assumed that some are, and that if marked and unmarked animals have equal resighting (*i.e.*, recapture) probabilities, a resighted sample can yield an unbiased estimate of *N* under some specific assumptions (see below). Each resighting session is usually assumed to be independent, with no inherent assumption that sighting biases remain the same over time.

Historically, the most commonly applied mark-recapture model in big game applications has been the Lincoln-Petersen (LP) model (Chapman 1951). Under this model, population size (N) is commonly estimated as:

$$\boldsymbol{N_i = [(M_i + 1)(n_i + 1) / m_i + 1] - 1,}$$

where N_i = estimated population size at time *i*, M_i = the number of marked animals present at time *i*, n_i = the total number of animals recaptured (*i.e*., resighted) at time *i*, and m_i = the number of marked animals among the sample n_i.

The LP estimator is a *closed* population estimator (see assumption #5 below). The LP estimator has been widely used because it has a *closed form* solution (*i.e*., does not require *numerical* solutions that have become tractable only since the advent of powerful computers), because it is a *batch mark* model (*i.e*., during resighting, animals needn't be identified individually, only as marked animals), and because estimates can be derived from a single resighting survey (*i.e*., k = 1). The LP estimator can yield an unbiased estimate of *N*, but several key assumptions must be met to do so (Otis et al. 1978, Pollock et al. 1990). The major assumptions are:

1) *marked animals do not lose their marks;*
2) *marked and unmarked animals have equal recapture (resighting) probabilities;*
3) *marked animals are never misclassified as unmarked animals (and vice versa);*
4) *marked animals represent an unbiased sample of the population, or random mixing of marked and unmarked animals occurs before the resighting phase of the application, and;*
5) *the population is geographically and demographically closed (i.e., immigration and emigration never occurs, and births and deaths do not occur between marking and recapture).*

The LP model and other simple mark-resight batch models further assume no *individual heterogeneity* in detection probabilities within a resighting session (*i.e*., each animal in the population has an equal chance of detection). This assumption is required in batch-mark models because modeling individual heterogeneity (*i.e*., variation in detection rate across individuals) requires encounter histories for each or most individuals. The closure assumption ensures that there are no unknown changes to the population between marking and recapture (losses of marked animals are particularly problematic, as they lead to errors in M_i, the number of marked animals in the population). Violations of closure can be corrected for if losses from the marked population are known (White et al. 1982). Radiomarks provide a means of addressing closure and correcting for violations of closure, and are therefore superior to visual-only marks (*e.g.*, colored neckbands, ear tags).

In previous applications, the LP model has proven useful for estimating populations of deer and elk at small geographic scales (Rice and Harder 1977, Bartmann et al. 1987, McCorquodale 2000, McCoy 2002). In applications where the true population size was known with relative confidence, estimates were often biased, but the magnitude of bias was typically small (Bartmann et al. 1986, McCullough and Hirth 1988). Biases are generally assumed to result from assumption violations, most likely the assumption that all animals have equal recapture probabilities, and that marked animals are an unbiased sample from the population.

More sophisticated mark-recapture models have been developed that offer improved approaches to mark-resight applications to large mammal surveys. Several of these methods have been summarized, including their strengths and weaknesses, by White and Shenk (2001). When the number of resighting sessions is at least $k = 2$, and individual marked animal identities are obtained during resighting, models are available that allow the assumption of no individual heterogeneity in resighting probabilities to be relaxed (Minta and Mangel 1989, Bowden and Kufeld 1995, Gardner and Mangel 1996, McClintock et al. 2008). These models have potentially great utility in aerial surveys of elk, given the considerable evidence that elk groups do not have equal detection probabilities during such surveys (Samuel et al. 1987, Anderson et al. 1998, McCorquodale 2001). At a minimum, larger elk groups can generally be assumed to have greater detection probabilities.

Mark-Resight Strategy

Among currently available mark-resight estimators that are robust to heterogeneity of resighting probabilities across individuals within resighting occasions, we chose the maximum-likelihood based nonlinear *logit-normal mixed effects* (LNME) model (McClintock et al. 2008). We also generated estimates using the bootstrapping-based *Bowden's Estimator* (BOWE) (Bowden and Kufeld 1995, White and Shenk 2001) and the *Joint Hypergeometric Estimator* (JHE) (Bartmann et al. 1987, White and Shenk 2001). The JHE estimator is a multiple occasion, LP-like batch-mark estimator that assumes no individual heterogeneity in sighting probabilities. However, it is somewhat robust to violations of the heterogeneity assumption. We generated BOWE and JHE estimates to compare these results with those from the newer LNME model.

The likelihood for the LNME model formally estimated population size (N_j); it also generated MLEs for detection probability (p_{ij}) and the variance (σ_{j}^2) of a random individual heterogeneity effect, where the subscript *j* refers to primary occasions (year) and *i* to secondary occasions (survey) within a primary occasion (McClintock et al. 2008). In the absence of individual heterogeneity, the parameter p_{ij} is interpreted as the overall mean detection probability, but when heterogeneity ≠ 0, overall mean detection probability is estimated under the LNME model as the derived parameter μ (McClintock 2008), which we report. The parameter μ is derived as a function of p_{ij}, σ_{j}^2, and $\varepsilon_{\mathrm{ij}}$ (number of marked animal encounters, where identity was not determined).

We implemented the LNME model in Program MARK (White and Burnham 1999), which allowed us to assess alternative model parameterizations that embodied hypotheses about sources of variability affecting LNME abundance estimates. We coded 2 separate encounter history datasets for the LNME analysis: 1 dataset was coded with a single marked animal group (*i.e.*, marked cows and bulls were lumped), and the second dataset coded marked cows and marked branch-antlered bulls as different groups. The single marked group dataset facilitated estimating total elk abundance, whereas the 2-group dataset supported formal estimates of the subpopulations of total number of adult cows and total number of branch-antlered bulls.

We developed a candidate model set for each analysis that consisted of 15 *a priori* models for the 1-group dataset (Table 2) and 12 models for the 2-group dataset (Table 3). Alternative model parameterizations reflected different model constraints on detection probabilities and individual heterogeneity effects. Our models included possible temporal effects that we believed might be logically related to our survey results (Tables 2, 3). For the recapture (resighting) probability (p_i), we contemplated models with no temporal variation (.), models wherein the first and second survey sessions across years were represented by a different recapture probability, and models where we assumed a different recapture probability for surveys prior to the 3rd week in March and those conducted later (early vs. late). These temporal effects models were based on our field experiences that generally seemed to indicate that detectability of elk was better the later into the spring that we flew. We flew only one February survey (2006), so we also included possible temporal effects stemming from this early session; we parameterized models wherein there was an additional effect on the recapture parameter (as above [early vs. late], but with an additional unique parameter for the Feb survey) and where there was a unique first-year heterogeneity parameter (σ_i) (Tables 2, 3). We used Akaike's Information Criterion, adjusted for small samples (AIC_c) and Akaike model weights (w_i) to support inference about the best supported models among our candidate models (Burnham and Anderson 2002), and we model averaged across models to derive final abundance estimates.

Table 2. Candidate *a priori* LNME mark-resight models for Nooksack elk late winter helicopter surveys, 2006-2011. Data coded for 1 group (*i.e.*, all elk). Model notation denotes parameterization defining modeled sources of variation in parameters ("***p***" = detection probability, "$\boldsymbol{\sigma^2}$ " = variance of individual heterogeneity, "***N***" = estimated population size, "**.**" = no variation modeled, "**yr**" = parameters specific to year, "**11=31=62≠else**" = first session in 2006 and 2008 and last session in 2011 assumed equal and different than a single parameter for all other sessions across years, "**yr1≠else**" = 2006 parameter assumed to be different from all other years, "**sess**" = parameters assumed to vary with survey session and year, "**early≠late**" = different parameters for surveys prior to 3rd week in March and after, "**sess1≠sess2**" = different parameters for first and second sessions across years).

MODEL STRUCTURE	**k**[a]
$p(.),\sigma^2(=0),N(\text{yr})$	7
$p(.),\sigma^2(.),N(\text{yr})$	8
$p(\text{early}\neq\text{late}),\sigma^2(=0),N(\text{yr})$	8
$p(11=31=62\neq\text{else}),\sigma^2(=0),N(\text{yr})$	8
$p(.),\sigma^2(\text{yr1}\neq\text{else}),N(\text{yr})$	9
$p(\text{early}\neq\text{late}),\sigma^2(.),N(\text{yr})$	9
$p(\text{sess1}\neq\text{sess2}),\sigma^2(.),N(\text{yr})$	9
$p(11=31=62\neq\text{else}),\sigma^2(.),N(\text{yr})$	9
$p(\text{sess1}\neq\text{sess2}),\sigma^2(\text{yr1}\neq\text{else}),N(\text{yr})$	10
$p(\text{early}\neq\text{late}),\sigma^2(\text{yr1}\neq\text{else}),N(\text{yr})$	10
$p(11=31=62\neq\text{else}),\sigma^2(\text{yr1}\neq\text{else}),N(\text{yr})$	10
$p(\text{sess}),\sigma^2(=0),N(\text{yr})$	18
$p(\text{sess}),\sigma^2(.),N(\text{yr})$	19
$p(\text{sess}),\sigma^2(\text{yr1}\neq\text{else}),N(\text{yr})$	20
$p(\text{sess}),\sigma^2(\text{yr}),N(\text{yr})$	24

[a] number of model parameters estimated.

Table 3. Candidate *a priori* LNME mark-resight models for Nooksack elk late winter helicopter surveys, 2006-2011. Data coded for 2 groups (*i.e.*, adult cows, branch-antlered bulls). Model notation denotes parameterization defining modeled sources of variation in parameters ("***p***" = detection probability, "$\boldsymbol{\sigma^2}$ " = variance of individual heterogeneity, "***N***" = estimated Ad♀ or Ad♂ population size, "**.**" = *no variation modeled in the parameter*, "**sex**" parameters specific to sex,""**yr**" = parameters specific to year, "**11=31=62≠else**" = first session in 2006 and 2008 and last session in 2011 assumed equal and different than a single parameter for all other sessions across years, "**yr1≠else**" = 2006 parameter assumed to be different from all other years, "**sess**" = parameters assumed to vary with survey session and year, "**early≠late**" = different parameters for surveys prior to 3rd week in March and after, "**Feb≠early≠late**" = different parameters for surveys in Feb, in the first 2 weeks of March, and after, "**sess1≠sess2**" = different parameters for first and second sessions across years).

MODEL STRUCTURE	**k**[a]
$P_{(sex)}$,$\sigma^2_{(0)}$,N(sex,yr)	14
$P_{(sex)}$,$\sigma^2_{♀}$(0),$\sigma^2_{♂}$(.), N(sex,yr)	15
p(sex),σ^2(sex), N(sex,yr)	16
$p_{♀}$(11=31=62≠else), $p_{♂}$(.),σ^2(.), N(sex,yr)	16
$p_{♀}$(11=31=62≠else), $p_{♂}$(.),σ^2(sex), N(sex,yr)	17
$p_{♀}$(early≠late), $p_{♂}$(.),σ^2(sex), N(sex,yr)	17
$p_{♀}$(early≠late), $p_{♂}$(.),$\sigma^2_{♀}$(yr$_1$≠else),$\sigma^2_{♂}$(.), N(sex,yr)	18
$p_{♀}$(Feb≠early≠late), $p_{♂}$(.),$\sigma^2_{♀}$(yr$_1$≠else),$\sigma^2_{♂}$(.), N(sex,yr)	18
p(sex,sess),σ^2(0), N(sex,yr)	36
p(sex,sess),σ^2(.), N(sex,yr)	37
p(sex,sess),$\sigma^2_{♀}$(0),$\sigma^2_{♂}$(.), N(sex,yr)	37
p(sex,sess),σ^2(sex), N(sex,yr)	38

[a] number of model parameters estimated.

We also derived JHE and BOWE model estimates of abundance (*N*) and 95% confidence intervals using Program NOREMARK (White 1996). We generated estimates of abundance under the JHE and BOWE models for: 1) total population size, 2) total cow subpopulation size, and 3) total branch-antlered bull subpopulation size. Whereas the LNME model generated MLEs using data for the full time series (late winter, 2006-2011), the JHE and BOWE model estimates consisted of independent annual estimates based only on each year's data.

The data collection described in the methodology for sightability-correction modeling (above) provided the essential data for our mark-resight analyses. The necessary data elements included the enumeration and classification of all elk within groups encountered during the visual portion of the experimental helicopter surveys and an accounting of the distribution of radiocollared elk among these groups (including identity of radiomarked elk). Our mark-resight analyses were based on replicated full coverage surveys (k = 2) of the core elk range (*i.e*., occupied winter habitat in GMU 418) each winter.

Survival

We estimated annual survival rates for radiocollared elk during 2000-2008 using *maximum-likelihood* methods by invoking known fate models in *Program MARK* (White and Burnham 1999). For this analysis we coded encounter history data using 4 formal groupings: 1) native Nooksack adult females, 2) 2003 MSH-drive-trapped adult females, 3) 2005 MSH-drive-trapped and passively trapped adult females, and 4) adult males. We estimated annual survival for a survival year defined as May 1-Apr 30 and estimated confidence intervals for annual survival using *profile likelihoods*. By using alternative model parameterizations, we tested several *a priori* hypotheses about Nooksack elk survival. We compared 16 candidate survival models (Table 4) using Akaike's Information Criterion, adjusted for small sample sizes (AIC_c) (Burnham and Anderson 2002), and we based our inference principally on a *best models* subset from our candidate model set that comprised 90% of the available Akaike model weight (w_i).

Table 4. Candidate *a priori* survival models for Nooksack elk survival analysis, 2000-2008. Notation denotes parameterization defining modeled sources of variation in survival (“**.**” = *no source of variation*, “**2-*t***” = *Ad M 2000-2006 ≠ Ad M 2007-2008*, “**3-*t***” = *Ad M 2000-2006 ≠ 2007 ≠ 2008*, “**N**” = *native Ad F*, “**MSH**” = *translocated Ad F* (with subscripts for cohorts = 03, 05), “**te**” = translocation effect on survival of Ad F for 1 yr).

MODEL No.	***SURVIVAL MODEL STRUCTURE***	***PARAMETERS***
1	Ad ♀ (.), Ad ♂ (.)	2
2	Ad ♀ (.), Ad ♂ (2-*t*)	3
3	Ad ♀ (.), Ad ♂ (3-*t*)	4
4	Ad ♀ ($\text{N}\neq\text{MSH}_{03=05}$), Ad ♂ (.)	3
5	Ad ♀ ($\text{N}\neq\text{MSH}_{03=05}$), Ad ♂ (2-*t*)	4
6	Ad ♀ ($\text{N}\neq\text{MSH}_{03=05}$), Ad ♂ (3-*t*)	5
7	Ad ♀ ($\text{te}_{03=05}$), Ad ♂ (2-*t*)	4
8	Ad ♀ ($\text{te}_{03=05}$), Ad ♂ (3-*t*)	5
9	Ad ♀ (te_{03}), Ad ♂ (2-*t*)	4
10	Ad ♀ (te_{03}), Ad ♂ (3-*t*)	5
11	Ad ♀ ($\text{te}_{03\neq05}$), Ad ♂ (2-*t*)	5
12	Ad ♀ ($\text{te}_{03\neq05}$), Ad ♂ (3-*t*)	6
13	Ad ♀ ($\text{N}\neq\text{MSH}_{03=05}+\text{te}_{03\neq05}$), Ad ♂ (2-*t*)	6
14	Ad ♀ ($\text{N}\neq\text{MSH}_{03=05}+\text{te}_{03\neq05}$), Ad ♂ (3-*t*)	7
15	Ad ♀ ($\text{N}\neq\text{MSH}_{03\neq05}+\text{te}_{03\neq05}$), Ad ♂ (2-*t*)	7
16	Ad ♀ ($\text{N}\neq\text{MSH}_{03\neq05}+\text{te}_{03\neq05}$), Ad ♂ (3-*t*)	8

We attempted to account for all known elk mortalities by cause, including those of unmarked elk. Outside of the winter-spring season, when we were conducting most of our fieldwork, our monitoring of radiomarked elk was infrequent, so occasionally we could not assign a definitive cause of death. We assumed a negative bias for causes such as illegal kills and natural deaths for unmarked elk. But, given the small size of the Nooksack herd, and its historic vulnerability to overharvest, we wanted to maintain a tally of known elk removals from the population during our study.

RESULTS

Sightability-Correction Modeling

We collected sighting data for 159 radiomarked elk groups for sightability modeling during helicopter surveys, 2006-2007. We saw 57 groups (35.8%) without aid of telemetry and missed 102 groups (64.2%). Of the 159 groups we sampled, 109 groups (68.6%) were classified as cow-calf groups. Of these 109 groups, we saw 46 groups (42.2%) without aid of telemetry and missed 63 groups (57.8%). We collected data from 50 radiomarked bull groups (31.4 % of all groups). We saw 11 bull groups (22.0%) without aid of telemetry and missed 39 groups (78%). Radiomarked elk groups ranged in size from 1 to 77 elk. Summary statistics for group sizes, by group type and sighting class are shown in Table 5 and frequencies of group sizes for bull and cow-calf groups are depicted in Fig. 7 (sighted and unsighted pooled). Of the 109 cow-calf groups sampled, 5 groups (4.6%) included 1 or more adult bulls (range = 1-3), and 9 groups (8.3%) included 1 or more subadult bulls. Of the 50 bull groups sampled, only 1 (2.0%) contained 1 or more adult cows.

Table 5. Summary of group sizes, mean (median), by group and sighting classes for radiomarked Nooksack elk groups, 2006-2007.

CLASS	All Groups	Seen	Missed
All Groups	12.03 (5)	22.74 (12)	6.04 (2.50)
Cow-calf groups	16.92 (8)	29.96 (15)	8.53 (5)
Bull groups	2.68 (1)	5.09 (4)	2.00(1)

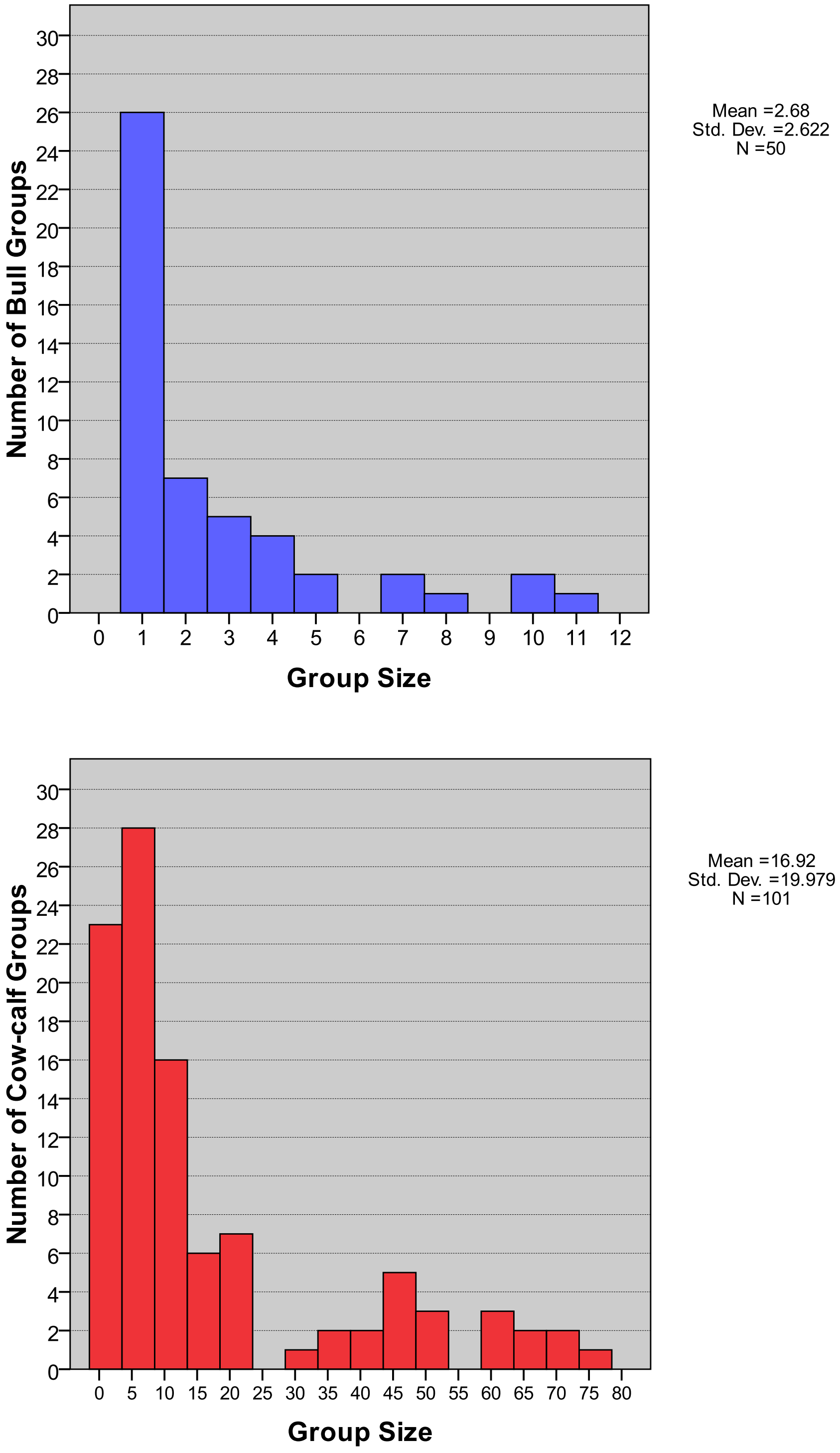


Figure 7. Group size frequencies for Nooksack elk groups counted during helicopter surveys, 2006-2007.

The covariates CAN, SNOW, GRP, and SEX were all related to the probability that an elk group was sighted in univariate tests (Table 6). Because the outcome (*i.e.*, sighted) was unbalanced for at least 1 level of the categorical covariates ACT and COV, MLE estimates did not exist for these covariates. We recoded ACT into a new covariate (ACT2) with 2 levels: 0 = bedded; 1 = active, and we recoded COV into a new covariate (COV2) with 4 levels: 1 = clearcut, field, river, road; 2 = regeneration stand; 3 = conifer; and 4 = alder. These new covariates were related to the probability that an elk group was sighted (Table 6). Systematic effects were apparent in the relationship between levels of the covariates and the percent of elk groups seen (Table 7). Elk groups were clearly more detectable where there was little obscuring forest canopy, when group sizes were larger, when they were active, and in habitat types that were characteristically more open (*e.g.*, clearcuts, fields, leafless alder stands). Cow-calf groups were generally more detectable. Groups were missed more often where snow was extensive on the ground than where snow was minimal or absent.

Table 6. Chi-square tests of univariate significance for covariates potentially affecting sightability of elk groups during helicopter surveys, 2006-2007.

Variable	X^2	***P*-value**
CAN	133.50	<0.001
SNOW	12.77	<0.001
GRP	41.60	<0.001
SEX	6.59	0.010
ACT	***	***
ACT2	98.76	<0.001
COV	***	***
COV2	76.55	<0.001

*** unbalanced outcome, model did not converge; MLE does not exist.

Table 7. Summary of univariate association of independent variable levels and sightability of elk groups during helicopter surveys, 2006-2007.

Variable	Total Groups	Groups Seen	%Seen
Canopy (%)			
0-15	21	21	100.0
20-35	27	20	74.1
40-55	21	13	61.9
60-75	36	3	8.3
>75	54	0	0.0
Snow (%)			
< 50	133	55	41.4
≥ 50	26	2	7.7
Group Size			
1-2	54	3	5.6
3-4	14	3	21.4
5-6	15	6	40.0
7-8	15	6	40.0
9-10	8	5	62.5
>10	45	34	75.6
Group Type			
cow-calf	109	46	42.2
bull	50	11	22.0
Activity			
bedded	107	12	11.2
standing	42	36	85.7
feeding	4	4	100.0
moving	4	4	100.0
Cover Type			
clear cut	10	9	90.0
regeneration	21	5	23.8
conifer	78	8	10.3
alder	36	21	58.3
field	8	8	100.0
river or road	6	6	100.0

Although several continuous independent covariates were significantly correlated ($P < 0.05$), these correlations were small ($|r| < 0.50$). An analysis of variance (ANOVA) suggested that the continuous covariate CAN (% canopy) was collinear with the recoded cover type covariate (COV2) ($r^2 = 0.67$), so we chose to use only the continuous CAN covariate in subsequent multivariate logistic models. That reduced our list of candidate multivariate sightability models (Table 1) from 15 to 9.

Amongst our candidate multivariate sightability models, 2 models accounted for nearly 90% of the available model weight (Table 8). The best model accounted for 64% of the model weight and had 3 explanatory covariates (GRP, ACT2, and CAN) and an intercept. The next best model, which was 1.87 AIC_c units from the best model, incorporated the additional covariate SEX. All of the remaining models were at least 3.5 AIC_c units greater than the best-supported model. Simple (*i.e.*, 1 explanatory covariate) models that predicted sightability based on group size (GRP) or canopy closure (CAN) alone had little support in our data.

Table 8. Results for multivariate models predicting sightability of elk groups during helicopter surveys, Nooksack, 2006-2007.

Model	**k^a**	**-2*LL***	**AIC_c**	**ΔAIC_c**	**w_i^b**
GRP, ACT2, CAN	4	39.65	47.90	0.00	0.64
GRP, ACT2, CAN, SEX	5	39.38	49.77	1.87	0.25
GRP, ACT2, CAN, SEX, SNOW	6	38.95	51.50	3.60	0.11
GRP, CAN	3	57.72	63.87	15.97	<0.001
GRP, CAN, SNOW	4	56.22	64.48	16.57	<0.001
GRP, CAN, SEX	4	57.66	65.92	18.02	<0.0001
GRP, CAN, SNOW, SEX	5	56.21	66.60	18.70	<0.0001
CAN	2	73.12	77.19	29.29	<0.0001
GRP	2	165.01	169.09	121.19	<0.0001

[a] Number of parameters.

[b] Akaike model weight.

Parameter estimates were similar for parameters common to the 2 best-supported sightability models (Table 9). Across all models, coefficient estimates were relatively stable for GRP (0.056-0.089) and very stable for CAN (-0.120 to -0.129), excepting for the poorly supported single covariate model (-0.114).

Table 9. Coefficient estimates and their estimated standard errors (SE) from the 2 best supported sightability models for Nooksack elk, 2006-2007.

Model	w_i	GRP	SE	ACT2	SE	CAN	SE	SEX	SE	INT
1	0.64	0.056	0.025	3.44	0..955	-0.127	0.031	—	—	3.542
2	0.25	0.062	0.028	3.49	0.970	-0.129	0.032	0.504	0.989	3.368

The 2 best models in our candidate model set structurally differed only relative to the inclusion of the indicator covariate SEX. Among the covariates in our models, the estimated coefficients for SEX were relatively unstable, ranging from –0.065 to +0.504 across models in which the SEX covariate occurred. Coefficients with different signs indicate the covariates have opposite effects on the outcome probability, in our case whether an elk group would be sighted or not. The SEX covariate also had a nonsignificant Wald statistic ($W = 0.26$; $P = 0.61$) in the GRP, ACT2, CAN, SEX model. Lastly, although the second ranked model was within 2 AIC_c units of the best model, it differed only by the addition of a single parameter (SEX); based on the formulation of the AICc (or AIC) metric, this model would not be competitive with the best model (Burnham and Anderson 2002, Arnold 2010). Thus, there was little justification for including the SEX covariate in a final model. Therefore, we selected the model GRP, ACT2, CAN as our final model. Model averaging across models to obtain the actual parameter estimates produced a very similar model to the model-specific estimates from the GRP, ACT2, CAN model:

$$\boldsymbol{y = 3.50 + 0.058(\text{GRP}) + 3.45(\text{ACT2}) - 0.128(\text{CAN})}$$

This model fit the data (Hosmer-Lemeshow $\chi^2 = 12.01$, $P = 0.15$) and correctly classified 94.9% of the model building observations; 97 of 101 groups (96.0%) predicted to be missed were missed, and 53 of 57 groups (93.0%) predicted to be seen by the model were seen. A receiver operating characteristic curve (ROC) also suggested the model was effective at correctly discriminating between observed and missed groups in the model building dataset (Fig. 8; Area under the curve [AUC] = 0.989).

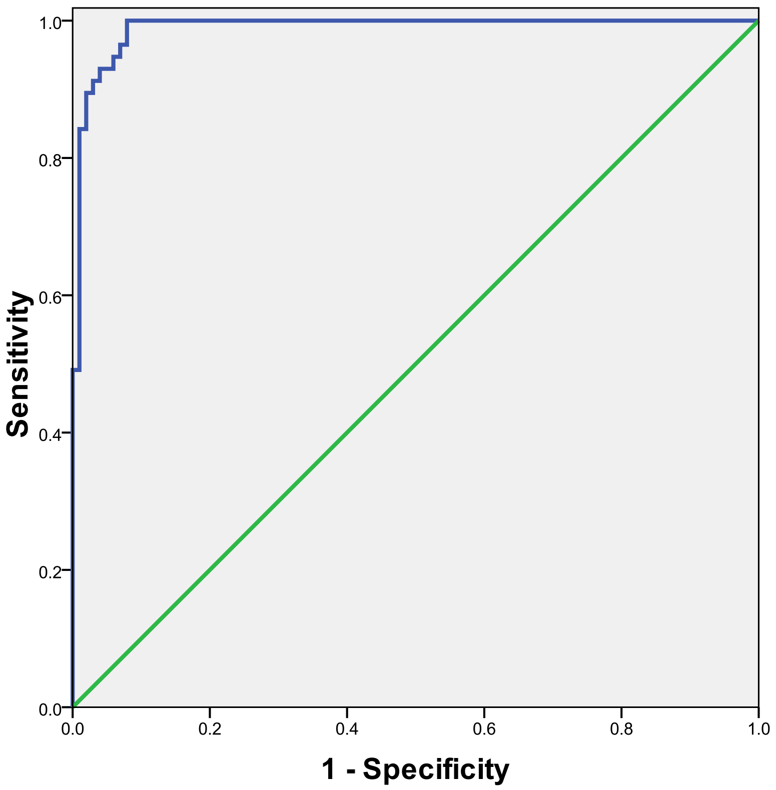


Figure 8. ROC curve for predictions from the GRP, ACT2, CAN sightability model. The blue line represents model performance, and the green horizontal line depicts expected performance for random assignment of the outcome.

The data for sighted groups, 2006-2011 yielded 2 independent model-based estimates of population size each year. The estimates generally indicated an increasing trend (Figure 9). The modeled estimates were lower than the minimum number of elk known to be alive in the springs of 2006 and 2007, obtained by enumerating all elk associated with radiomarked groups (including sighted and missed groups). Minimum known alive estimates were 422 elk in March 2006 and 509 in April 2007. We believe it was very unlikely that all elk groups present on the study area in 2006 and 2007 were radiomarked; missed groups without radiomarked elk were unaccounted for and not included in minimum known alive estimates. In 2009, we observed 5 groups with very low estimated detection probabilities (0.001-0.070) in heavy conifer cover (75-90% canopy closure); these low detection probabilities produced large correction factors and potentially added absurd numbers of missed elk (>1,000 elk). We censored these outliers to obtain the population estimates in Figure 9.

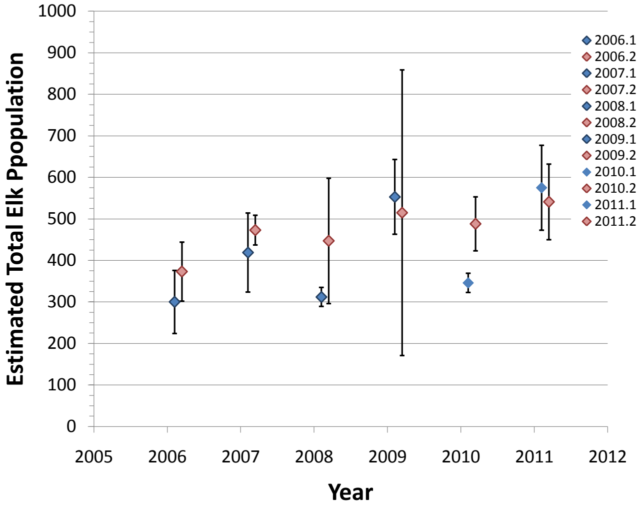


Figure 9. Sightability model population estimates for the Nooksack elk herd, 2006-2011 (2 annual replicates = year.1, year.2).

Based on the sightability model population estimates derived from the 2006-2011 aerial survey data, we estimated the exponential rate of population growth (r) by regressing the natural logs of the population estimates against year. We estimated $r = 0.076$ ($\lambda = e^r = 1.08$).

Mark-Resight

The total number of elk observed during individual resighting sessions ranged 287-535 during 2006-2011 (Table 10). The number of radiomarked cows we observed ranged 9-42 and the number of radiomarked bulls observed ranged 0-8 (Table 10). The average number of elk seen across survey replicates and the maximum number of groups seen in any individual survey generally increased across years (Figure 10). Raw detection rates (no. seen / no. available) averaged 0.54 across survey sessions for radiocollared cows (range = 0.25-0.76; Table 11) and 0.24 for radiocollared bulls (range = 0.0-0.47; Table 11).

Table 10. Results of winter elk survey flights for Nooksack elk (GMU 418) by Survey (k = 2) and Year (n = 6), 2006-2011. The "Week" column is formatted month-week.

Year	Survey	Week	Total	Ad F	Calf	Yg M	S-Ad M	Ad M	Marked F Seen	Marked M Seen
2006	1	2-1	287	188	55	20	2	9	24	1
2006	2	3-2	289	159	59	23	6	29	33	3
2007	1	3-2	375	226	99	24	4	21	42	4
2007	2	4-1	407	252	85	23	15	20	34	8
2008	1	3-2	306	172	71	24	11	28	16	5
2008	2	3-3	391	235	100	33	4	19	29	2
2009	1	3-4	507	294	125	38	23	27	35	2
2009	2	4-1	341	206	54	27	8	29	22	1
2010	1	3-3	340	222	59	21	13	21	34	0
2010	2	4-1	461	302	76	9	12	52	29	2
2011	1	3-3	535	328	118	34	16	27	23	3
2011	2	4-1	503	284	127	26	5	47	9	2

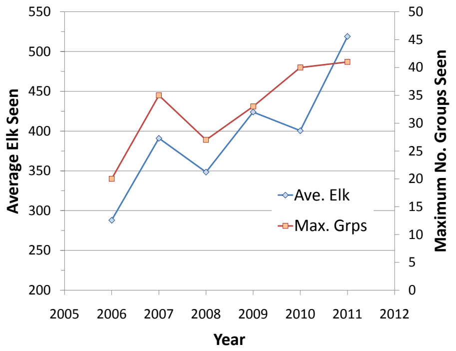


Figure 10. Summary of elk seen (mean total elk and maximum number of groups) for replicated helicopter surveys, 2006-2011.

Table 11. Summary of radiomarked elk available and seen, by gender, during full coverage, winter aerial surveys for the Nooksack elk herd core range, 2006-2011

Year	Survey	Marked F	Marked M	Marked F	Marked M
200	1	66	7	24	1
200	2	67	11	33	3
200	1	62	17	42	4
200	2	60	17	34	8
200	1	51	12	16	5
200	2	51	12	29	2
200	1	46	5	35	2
200	2	45	5	22	1
201	1	47	4	34	0
201	2	48	5	29	2
201	1	34	8	23	3
201	2	36	10	9	2

[a] number seen (% seen).

Among the 15 candidate LNME models we evaluated to predict total Nooksack elk abundance during spring 2006-2011, 1 model accounted for 97% of the available model weight (Table 12). The best supported model assumed 2 different detection probabilities (one for sessions 1-1,3-1,6-2, and one for all other sessions), assumed individual heterogeneity was different for the 2006 surveys than for all other years, and assumed annual variation in population size. The second best model was more than 7 AIC_c units from the best model (Table 12). The remaining models had virtually no support in the data. The models assuming no heterogeneity (σ^2=0) had effectively zero model weight.

Table 12. Model selection results for the 2 best supported LNME models for total population size for the Nooksack elk herd, 2006-2011.

Model	**k**	**AIC_c**	**ΔAIC_c**	**w_i**	**Dev**
p(11=31=62≠else),σ^2(yr1≠else),*N*(yr)	10	1019.82	0.00	0.97	999.21
p(sess),σ^2(yr1≠else),*N*(yr)	20	1027.21	7.39	0.02	984.82

MLEs for mean detection rate (μ) from the best LNME model for total population ranged 0.29-0.55 (Table 13). The coefficient of variation (CV) for detection rate estimates ranged 1.9-13.8%.

Table 13. Mean detection rate (μ) estimates from the best supported LNME model for total population size for the Nooksack elk herd, 2006-2011.

Parameter	**μ**	**SE**	**95% *CI***
2006_1[a]	0.39	0.03	0.33-0.45
2008_1	0.29	0.04	0.22-0.37
2011_2	0.29	0.04	0.22-0.37
2006_2	0.52	0.01	0.50-0.55
Else	0.55	0.02	0.50-0.59

[a] Parameter for: $Year_{(session)}$.

Estimates of total annual population size from the top LNME model ranged 636-1246 (Table 14). Coefficients of variation (CV) for annual LNME total population estimates ranged 4.53-5.98%. Model-averaged population estimates across the full candidate model set were similar to the best model estimates due to the high model weight in the best model (range = 638-1248) (Table 14, Fig. 11).

Table 14. Annual population estimates, 2006-2011, from the best supported LNME model and model-averaged estimates across all 15 candidate models for the Nooksack elk herd. Estimates of N and 95% CIs on N have been rounded to the nearest individual elk.

Year	**Estimated *N***	**SE**	**95% CI**
M_1:2006	636	29.4	581-697
M_1:2007	710	32.2	649-776
M_1:2008	843	50.4	751-949
M_1:2009	771	35.9	704-845
M_1:2010	717	33.7	654-787
M_1:2011	1246	74.3	1109-1401
M_{ave}:2006	639	34.7	570-706
M_{ave}:2007	710	32.9	645-774
M_{ave}:2008	844	51.9	742-945
M_{ave}:2009	772	37.2	699-844
M_{ave}:2010	715	36.0	645-786
M_{ave}:2011	1248	78.4	1094-1401

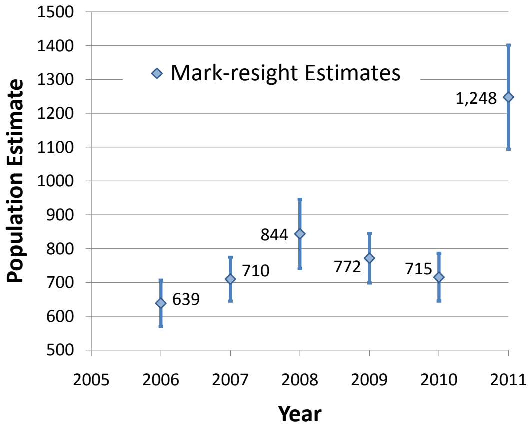


Figure 11. Model-averaged LNME estimates (± 95% unconditional CI) of total elk population size in the Nooksack GMU 418 core study area, from Feb-Apr aerial surveys, 2006-2011.

Among the 12 candidate models we used to generate LNME estimates of adult cow and branch-antlered bull subpopulation sizes, virtually all of the model weight (99%) was accounted for by 2 models (Table 15). The best supported model was the 17 parameter model that used 2 unique parameters for marked cow detection rate ($2006_1 = 2008_1 \neq 2012_2 \neq$ all other sessions [subscripts denote survey session]), had 1 detection parameter for bulls, assumed individual heterogeneity was different for adult cows and for branch-antlered bulls (but was constant across years for both sexes), and assumed annual variation in the numbers of adult cows and branch-antlered bulls (Table 15). The 2nd best supported model was similar, but assumed constant heterogeneity. The next best model was >16 AIC_c units from the best model and was not competitive.

Table 15. Model selection results for the 2 best supported LNME models for estimating subpopulation size for adult cows and branch-antlered bulls in the Nooksack elk herd from helicopter survey data, 2006-2011.

Model	**k**	**AIC_c**	**ΔAIC_c**	**w_i**
$p_{♀}(11=31=62\neq\text{else})$, $p_{♂}(.)$,$\sigma^2(\text{sex})$, $N(\text{sex,yr})$	17	1042.52	0.00	0.77
$p_{♀}(11=31=62\neq\text{else})$, $p_{♂}(.)$,$\sigma^2(.)$, $N(\text{sex,yr})$	16	1044.90	2.38	0.23

*MLE*s for detection rates across the 2 best LNME models for estimating adult cow and branch-antlered bull subpopulation sizes, spring 2006-2011 confirmed that radiomarked cow detection rates were substantially higher than detection rates for radiomarked bulls, excepting for the session estimates for cows in 2006_1 and 2008_1 and 2011_2 (0.32; Table 16). Excepting that estimate, the *MLE* of μ for radiomarked cows during other survey sessions was 0.60. The cow detection rate estimates from these 2 models were precise to modestly precise (*CV* = 3.33-12.50%).

The *MLE* for radiomarked bull detection rates across the 2 best-supported LNME subpopulation models was 0.26 (Table 16). Because of the small annual sample size of radiomarked bulls (4-17) and low estimated detection probability, the *MLE* for bull detection rate was relatively imprecise (*CV* = 15.38%).

Annual LNME subpopulation estimates for cow elk varied 381-573, generally increasing from 2006 through 2011(Table 17). The estimates for *N*, *SE(N)*, and the 95% *CI*s for the best-supported model and the model-averaged estimates across the candidate set were very similar to the model-specific estimates because of the high model weight in the best-supported model (Table 17). The model-averaged cow subpopulation estimates were relatively precise (Table 17, Figure 12; *CV* = 4.6-5.9%).

Table 16. Detection rate (μ) estimates from the 2 best supported LNME models for adult cow and branch-antlered bull subpopulation sizes for the Nooksack elk herd, 2006-2011.

Estimate for	μ	SE	95% *CI*
M_1[a]:♀2006_1[b], 2008_1, 2011_2	0.32	0.04	0.26-0.40
M_2:♀2006_1, 2008_1, 2011_2	0.32	0.04	0.25-0.40
$M_{1,2}$:♀$_{\text{else}}$[c]	0.60	0.02	0.55-0.64
M_1:♂(.)	0.26	0.04	0.19-0.35
M_2:♂(.)	0.26	0.04	0.18-0.36

[a] M_i = Model (*i*) from Table 16.

[b] Parameter for: Year$_{\text{(session)}}$.

[c] All sessions except 2006_1, 2008_1, 2011_2.

Table 17. Annual cow elk subpopulation estimates, 2006-2011, from the best supported LNME model and model-averaged estimates across all 13 candidate models for the Nooksack elk herd.

Year	Estimated *N*	SE	95% *CI*
M_1:2006	381	21.8	341-427
M_1:2007	398	18.4	363-436
M_1:2008	452	26.5	403-507
M_1:2009	416	19.8	379-457
M_1:2010	434	20.5	396-476
M_1:2011	573	33.6	511-643
M_{ave}:2006	381	21.8	338-424
M_{ave}:2007	397	18.3	362-433
M_{ave}:2008	452	26.4	400-504
M_{ave}:2009	416	19.7	377-455
M_{ave}:2010	434	20.4	394-474
M_{ave}:2011	573	33.6	507-639

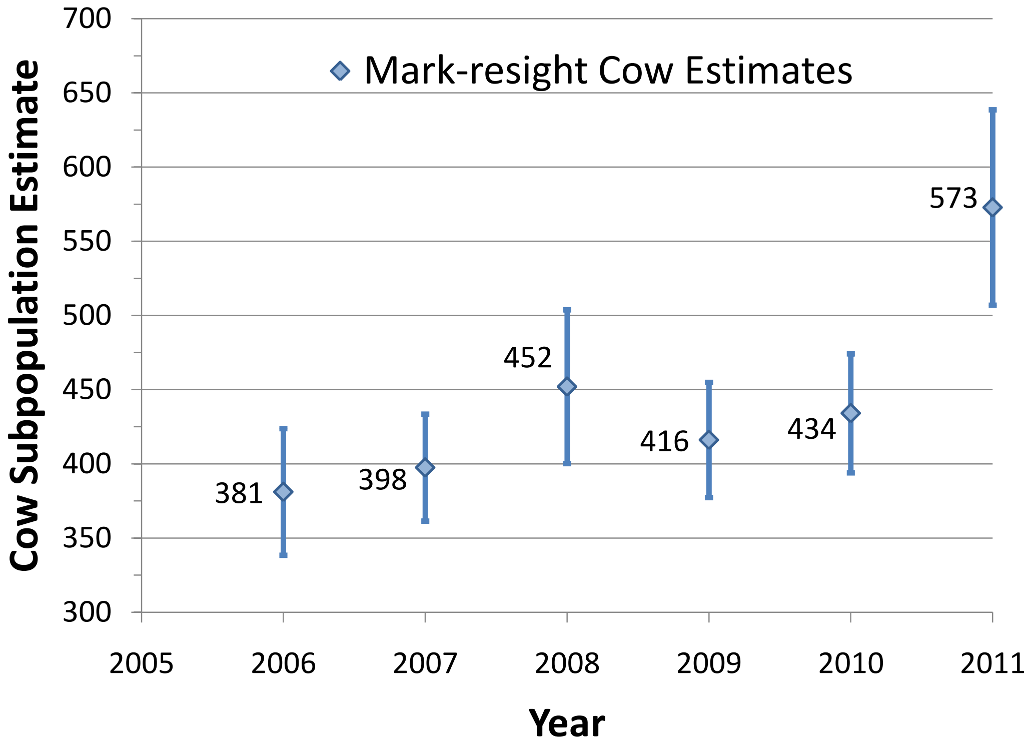


Figure 12. Model-averaged LNME estimates (± 95% unconditional CI) of cow elk subpopulation size in the Nooksack GMU 418 core study area, from Feb-Apr aerial surveys, 2006-2011.

Annual LNME estimates for branch-antlered bulls varied 87-180 annually under the best subpopulation model Table 18). Estimates were relatively similar for 2009-2011. Because of small sample sizes, the estimates were imprecise (*CV* = 17.2-19.2% across all estimates) and confidence intervals were wide. The model-averaged LNME estimates for branch-antlered bulls, 2006-2011 were also very similar to the estimates from the best-supported model due to the high model weight in that model (Table 18). There was an apparent steady increase in the model-averaged branch-antlered bull subpopulation estimates, 2006-2011, but with broadly overlapping confidence intervals (Fig. 13).

Table 18. Branch-antlered bull elk subpopulation estimates, 2006-2011, from the best supported LNME model and model-averaged estimates across all 12 candidate models for the Nooksack elk herd. Estimates of N and 95% CIs on N have been rounded to the nearest individual elk.

Year	Estimated *N*	SE	95% *CI*
M_1:2006	87	16.4	61-126
M_1:2007	108	18.2	79-152
M_1:2008	117	20.4	84-165
M_1:2009	169	29.3	121-238
M_1:2010	178	31.4	126-251
M_1:2011	180	30.8	129-252
M_{ave}:2006	87	16.7	54-119
M_{ave}:2007	108	18.6	72-145
M_{ave}:2008	117	20.8	76-157
M_{ave}:2009	169	29.8	111-227
M_{ave}:2010	178	32.0	115-240
M_{ave}:2011	180	31.3	118-241

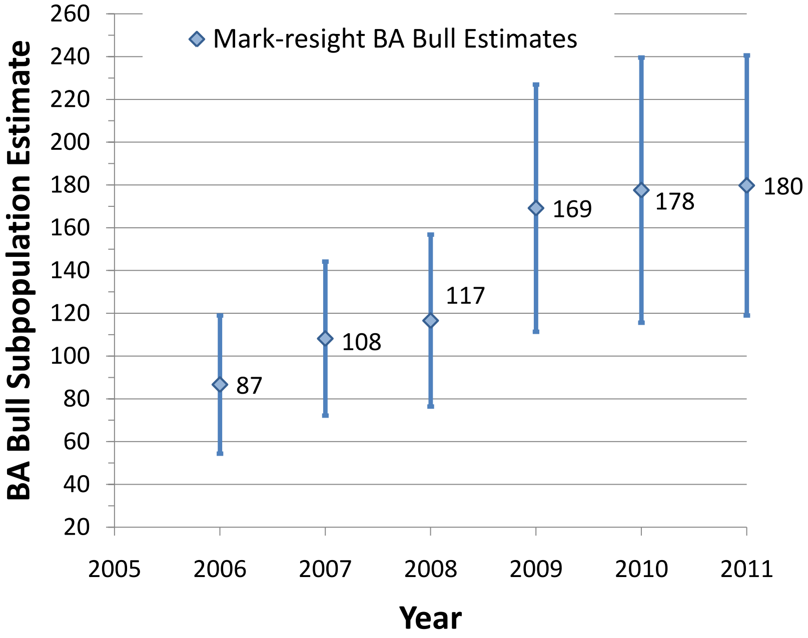


Figure 13. Model-averaged LNME estimates (± 95% unconditional CI) of branch-antlered (BA) bull elk subpopulation size in the Nooksack GMU 418 core study area, from Feb-Apr aerial surveys, 2006-2011.

Estimates for total population size derived from the JHE and BOWE models were relatively similar (Table 19); the BOWE model estimates tended to be slightly higher. Subpopulation estimates from the 2 models for adult cows and branch-antlered bulls were also relatively similar (Table 20). Confidence limits for bull subpopulation estimates were wide. JHE and BOWE bull estimates were not generated for 2009 and 2010 due to extremely limited numbers (≤5) of marked branch-antlered bulls available for resighting each year.

Table 19. Estimates of total elk population size in the GMU 418 core area derived from replicated helicopter survey data, 2006-2011 using the Joint-hypergeometric (JHE) and Bowden's (BOWE) models.

Year	JHE	BOWE
2006	703 (595-856)	741 (585-938)
2007	695 (618-800)	720 (624-832)
2008	839 (700-1042)	841 (669-1058)
2009	709 (626-835)	755 (632-901)
2010	675 (598-788)	648 (549-765)
2011	1224 (986-1598)	1293 (1016-1647)

Total population estimates from the JHE and BOWE models were not appreciably different than those from the LNME model (Fig. 14). Confidence limits for the BOWE total population estimates tended to be slightly wider than those for the JHE model estimates (Fig. 14).

Table 20. Estimates of cow and branch-antlered elk subpopulation sizes in the GMU 418 core area derived from replicated helicopter survey data, 2006-2011 using the Joint-hypergeometric (JHE) and Bowden's (BOWE) models.

Year	JHE	BOWE
Cows		
2006	429 (365-522)	426 (340-535)
2007	397 (356-456)	403 (350-464)
2008	454 (379-567)	463 (367-584)
2009	401 (356-472)	409 (348-480)
2010	321 (378-488)	406 (346-475)
2011	339 (526-864)	595 (462-766)
Branch-antlered Bulls		
2006	118 (64-333)	111 (38-325)
2007	83 (60-135)	88 (59-132)
2008	104 (66-212)	94 (47-188)
2009	—[a]	—
2010	—	—
2011	177 (100-440)	170 (89-328)

[a] Estimates not generated due to small sample of marked bulls (≤5).

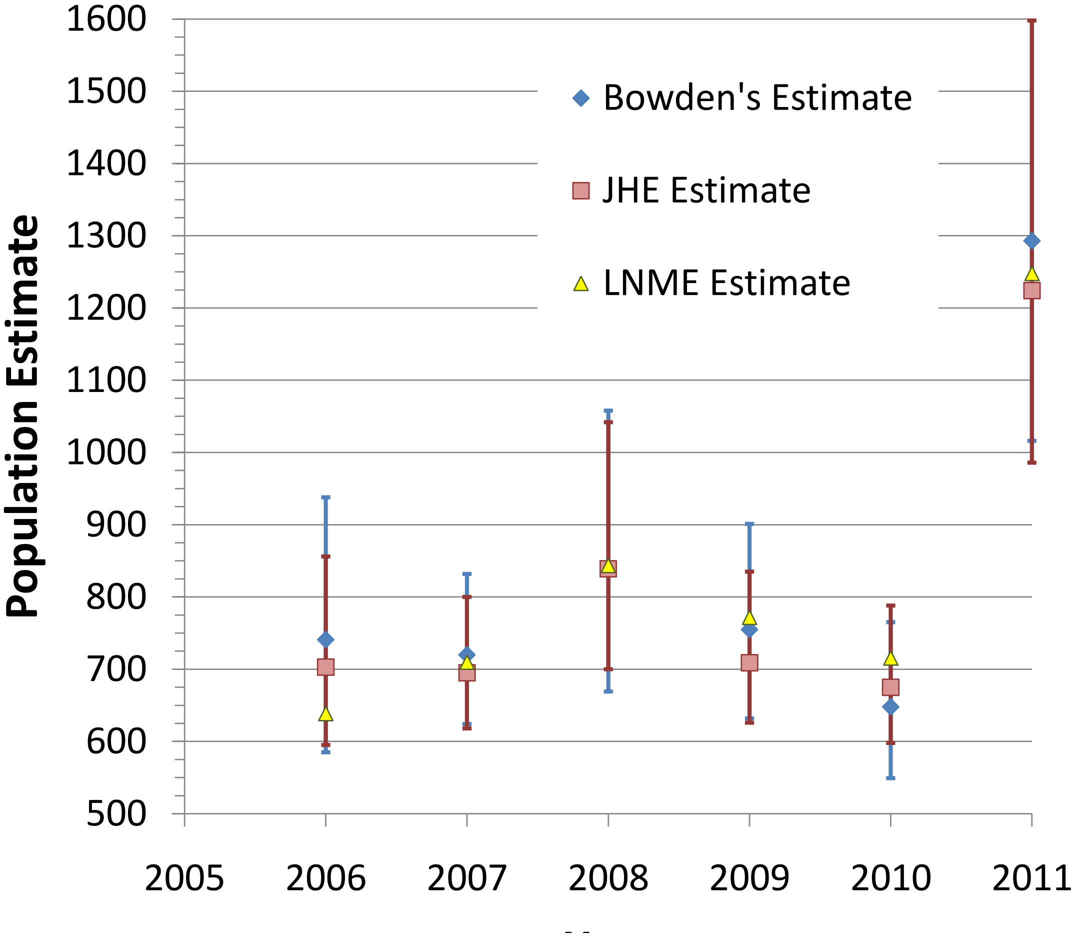


Figure 14. Total elk population estimates from the Joint-hypergeometric mean estimator (JHE) and Bowden's estimator, 2006-2011 (± 95% CI) for the Nooksack GMU 418 core study area. Model-averaged point estimates from the LNME model are also shown for comparison.

Juvenile Recruitment

Estimated recruitment of calves into the Nooksack elk population, indexed during late winter, early spring aerial surveys was typically quite good (Figure 21). Calf:cow ratios (Skalski et al. 2005) exceeded 35:100 in 4 of 6 years (66.7%) and were above 40:100 in 2 years.

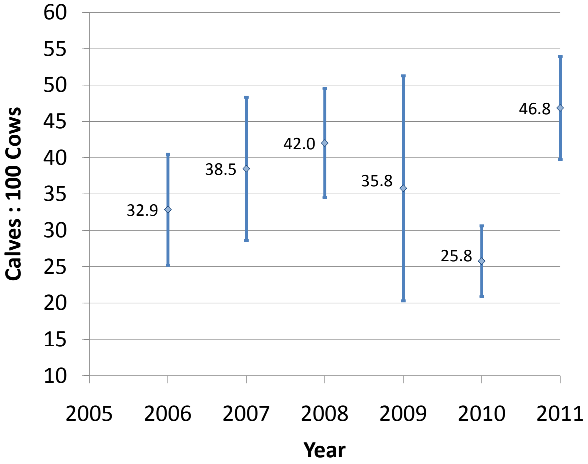


Figure 21. Estimated calf:cow ratios (± 95% CI) for the Nooksack GMU 418 core study area. Data are from annual late winter (Feb-Apr) helicopter surveys, 2006-2011.

Survival

Among the 16 candidate survival models, 5 models accounted for 90% of the available model weight; the best model accounted for 44% of the weight (Table 21). The best model assumed survival was similar among radiomarked adult cow groups, except that there was a 1-year reduction in survival for the elk translocated from MSH in 2003, and branch-antlered bull survival was different prior to 2007 than it was in 2007 and thereafter. All of the models in the 90% confidence set assumed a 1-yr effect on survival for at least some MSH adult cows post-translocation. The top 2 models assumed this effect applied only to the 2003 translocation cohort; the 3rd and 5th best models assumed a cohort-specific effect applied to both translocation cohorts (*i.e.*, 2003 and 2005). The 4th best model invoked more complexity in modeled cow survival; native elk and translocated elk were assumed to have different survival rates, there were unique 1-yr effects for both translocated cohorts, and after the first year post-translocation, the MSH cow elk had similar survival across cohorts. All 5 models in the confidence set presumed branch-antlered bull survival was different pre-2007 than in 2007-08. Although the 4th and 5th best models were in the 90% confidence set, they were clearly not strong competitors with the best model, being >3 AIC$_c$ units from the best model. The simplest (2-3 k) and most complex (7-8 k) models in the candidate set had very little support in the data.

Table 21. Summary of known-fate survival model analysis for Nooksack elk, 2000-08. Models in bold characters collectively account for 90% of the available Akaike model weight (i.e., Σwi = 0.90). ΔAICc = difference in AICc units between modeli and the best supported model.

Model	k[a]	ΔAIC$_c$	w$_i$	Deviance
Ad ♀ (te$_{03}$), Ad ♂ (2-*t*)	**4**	**0.00**	**0.44**	**42.90**
Ad ♀ (te$_{03}$), Ad ♂ (3-*t*)	**5**	**2.02**	**0.16**	**42.88**
Ad ♀ (te$_{03\neq05}$), Ad ♂ (2-*t*)	**5**	**2.03**	**0.16**	**42.89**
Ad ♀ (N≠MSH$_{03=05}$+te$_{03\neq05}$), Ad ♂ (2-*t*)	**6**	**3.35**	**0.08**	**42.16**
Ad ♀ (te$_{03\neq05}$), Ad ♂ (3-*t*)	**6**	**4.06**	**0.06**	**42.87**
Ad ♀ (N≠MSH$_{03\neq05}$+te$_{03\neq05}$), Ad ♂ (2-*t*)	7	5.06	0.04	41.80
Ad ♀ (N≠MSH$_{03=05}$+te$_{03\neq05}$), Ad ♂ (3-*t*)	7	5.39	0.03	42.14
Ad ♀ (N≠MSH$_{03\neq05}$+te$_{03\neq05}$), Ad ♂ (3-*t*)	8	7.11	0.01	41.78
Ad ♀ (te$_{03=05}$), Ad ♂ (2-*t*)	4	7.39	0.01	50.29
Ad ♀ (te$_{03=05}$), Ad ♂ (3-*t*)	5	9.41	<0.01	50.27
Ad ♀ (.), Ad ♂ (2-*t*)	3	14.01	<0.001	58.95
Ad ♀ (N≠MSH$_{03=05}$), Ad ♂ (2-*t*)	4	15.99	<0.001	58.90
Ad ♀ (.), Ad ♂ (3-*t*)	4	16.03	<0.001	58.93
Ad ♀ (.), Ad ♂ (.)	2	16.94	<0.001	63.90
Ad ♀ (N≠MSH$_{03=05}$), Ad ♂ (3-*t*)	5	18.02	<0.001	58.88
Ad ♀ (N≠MSH$_{03=05}$), Ad ♂ (.)	3	18.91	<0.001	63.85

[a] number of survival parameters in model.

*MLE*s of annual cow elk survival were high (0.90-0.94) across model parameters, excepting for models invoking a 1st-year effect on translocated cow elk survival (Table 22). When the 1-year translocation effect was invoked only for the 2003 MSH cohort, that survival rate was estimated to be 0.68 (95% *CI* = 0.51-0.82). When a common 1st-year translocation effect on both MSH adult cow cohorts was invoked, annual survival was estimated at 0.81 (95% *CI* = 0.71-0.89). Estimates of annual survival for translocated cow elk, from year 2 post-translocation on (0.93-0.95), were actually slightly higher than the estimate specific to native Nooksack cows (0.91). Our *MLE*s for adult cow survival were relatively precise across models; among the 11 unique survival parameters estimated, only 2 had CVs >5%; the CV for the MSH 2003 cohort 1st-year estimate was 11.8% and the CV for the 1st-year survival estimate common to both the 2003 and 2005 MSH cohorts was 5.7%.

Prior to the resumption of bull harvesting (*i.e.*, pre-2007), estimated branch-antlered bull survival was high (*MLE* = 0.92, 95% *CI* = 0.76-0.99) (Table 22), but only 1 bull was radiomarked prior to fall 2005. Branch-antlered bull survival was lower in 2007 (*MLE* = 0.67, 95% *CI* = 0.44-0.85) and 2008 (*MLE* = 0.69, 95 % *CI* = 0.42-0.89). When annual branch-antlered bull survival was estimated with a single parameter for 2007-2008, the *MLE* was 0.68 (95% *CI* = 0.50-0.82). In models that invoked constant bull survival across model years (2000-2008), the *MLE* was 0.78 (95% *CI* = 0.66-0.88), but models with this parameter had very little support in the data (Table 21). Because of the smaller sample of radiomarked branch-antlered bulls, the *MLE*s of annual bull survival were less precise than for adult cows. The 2000-06 *MLE* survival estimate had a CV of 6.1%, and the constant bull survival estimate had a CV of 7.2%. The CVs for estimates of bull survival after the resumption of hunting were 16.4% (2007), 18.8% (2008) and 12.4% (2007-08).

Table 22. Maximum likelihood estimates of survival model parameters for the 16 candidate survival models in the candidate model set. Parameter notation identifies model-specific parameters ("." = no source of variation modeled; "MSH" = translocated elk; "te" = survival specific to a translocation effect on survival for 1 year only; numbers are years and define period-specific survival if not subscripts or identify translocated elk cohorts if subscripts [03 = 2003, 05 = 2005]).

Survival Model Parameter	**$\hat{S}$**	**SE($\hat{S}$)**	**95% *CI***
Adult ♀ (.)	0.91	0.014	0.88-0.93
Adult ♀ (all except MSH$_{03}$ te)	0.93	0.013	0.90-0.95
Adult ♀ (all except MSH$_{03,05}$ te)	0.93	0.014	0.90-0.95
Native Adult ♀ (.)	0.91	0.024	0.86-0.95
MSH Adult ♀ (.)	0.90	0.018	0.87-0.94
MSH$_{03}$ Adult ♀ (03)	0.68	0.080	0.51-0.82
MSH$_{03}$ Adult ♀ (04-08)	0.93	0.026	0.87-0.97
MSH$_{05}$ Adult ♀ (05)	0.92	0.043	0.81-0.98
MSH$_{05}$ Adult ♀ (06-08)	0.95	0.022	0.89-0.98
MSH$_{03,05}$ Adult ♀ (te$_{same}$)	0.81	0.046	0.71-0.89
MSH$_{03,05}$ Adult ♀ (non-te$_{same}$)	0.94	0.017	0.90-0.97
Adult ♂ (.)	0.78	0.056	0.66-0.88
Adult ♂ (2000-06)	0.92	0.056	0.76-0.99
Adult ♂ (2007-08)	0.68	0.084	0.50-0.82
Adult ♂ (2007)	0.67	0.11	0.44-0.85
Adult ♂ (2008)	0.69	0.13	0.42-0.89

During 2005-2011, we accounted for a known minimum loss of 270 elk from the Nooksack elk herd (Fig. 16, Appendix A). Ninety elk were removed under damage permits or damage prevention hunts (*i.e*., Elk Area 4941), including 42 yearling or adult cows. Damage hunts and bull permit hunts during 2007-2010 were the dominant sources of known elk removals (69.3% of all deaths; Fig. 22), but illegal kills and roadkills also were responsible for a substantive loss of elk from the population; roadkills alone removed a minimum of 37 elk (13.7% of all recorded deaths). Almost all of the 270 known removals came from the core range in GMU 418, or that portion of GMU 437 immediately adjacent to the GMU 418 boundary (most from Elk Area 4941) (Appendix A).

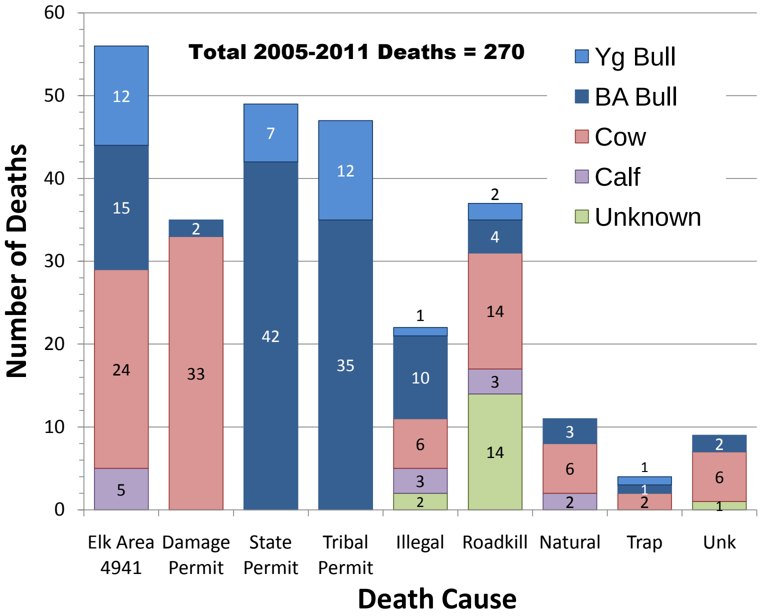


Figure 22. Known elk mortalities, by cause and demographic class, for the Nooksack elk herd, 2005-11.

DISCUSSION

Sightability Modeling

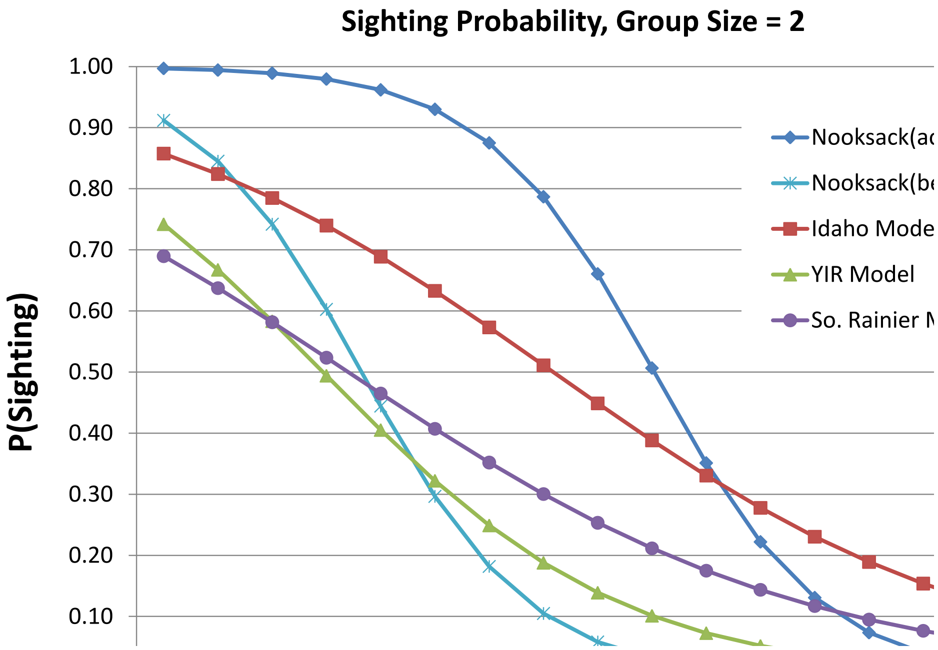
Our work was motivated by the need for a defensible assessment of the current status of the Nooksack elk herd, as well as a need to define a useful strategy for monitoring the herd through time. Regression-based sightability correction models are appealing because they require marked animals only during model development and usually require only slight modifications to data collection methods used in traditional composition surveys. To date, sightability correction models have been derived for aerial surveys of elk in several different regions of North America (Samuel et al. 1987, Otten et al. 1993, Singer and Garton 1994, Anderson et al. 1998, Bleich et al. 2001, McCorquodale 2001, McIntosh et al. 2007, Gilbert and Moeller 2008). Prior to our work, no aerial sightability models for elk had been published for western Washington or Oregon, but during our study, Gilbert and Moeller (2008) published a winter model for the west slopes of the central Washington Cascades. However, substantial landscape differences exist between habitats used by wintering elk in northwest Washington (Nooksack) and those in the central Washington Cascades (South Rainier herd).

Our overall sighting rate for radiomarked elk groups (35.8%) was substantially lower than typical of other sightability model development efforts; sighting rates have generally ranged ≈50-70% on other landscapes during winter (Samuel et al. 1987, Otten et al. 1993, McCorquodale 2001, Gilbert and Moeller 2008), and rates of 58% during fall (Bleich et al. 2001) and 82% during summer (Anderson et al. 1998) have been documented.

That sighting rates were lower in the relatively wet and densely forested northwest Washington landscape occupied by our low density study population does not seem surprising. Coniferous forest types on our study area consisted of dense canopied, multilayered stands of wet series conifers (*e.g.*, western hemlock, Pacific silver fir, Douglas-fir). These settings represented challenging sighting environments, and our radioed elk groups made extensive use of these stands (49% of all sampled groups were in non-regeneration conifer cover). Most elk we detected were in clearcuts, regenerating second-growth stands, leafless alders, wetlands/river bottoms, and agricultural fields.

The final sightability model we developed indicated that elk were more likely to be seen in larger groups and when active; the probability of detection also declined as concealing tree cover (%) increased. These results are intuitive. The logistic coefficient for tree canopy closure (β= -0.128) indicated that with every 5% increase in tree canopy closure, the odds of sighting an elk group declined by almost ½ (odds ratio = $e^{(5 \times -0.128)}$ = 0.53). The strong effect of tree canopy cover in the sightability model we developed was also evident by contrasting the magnitude of our canopy closure coefficient with coefficients in other models with a canopy covariate. This disparity is clearly seen by plotting predicted sighting probabilities as a function of canopy closure while controlling for group size across models (Figure 23). Our model included an effect of activity, so 2 curves are shown in Figure 23, one for active elk and one for bedded elk. In both cases, it is apparent that sighting probabilities decline much more rapidly in our Nooksack elk model as canopy closure increases, relative to other models.

Group size has typically been an important predictor of sighting probabilities for elk during aerial surveys (Samuel et al. 1987, Bleich 2001, McCorquodale 2001, McIntosh et al. 2007, Gilbert and Moeller 2008). Group size had a significant univariate effect on sightability in our dataset and was included in the best multivariate models, but a model with only a group size covariate was not competitive with models that included effects of additional predictors (*e.g*., canopy, activity). Comparing our results with those from other published sightability modeling efforts, there was an apparent disparity in the pattern of detection as a function of group size, with the effect of group size on detectability being more modest on our study area (Table 23). This was also apparent when



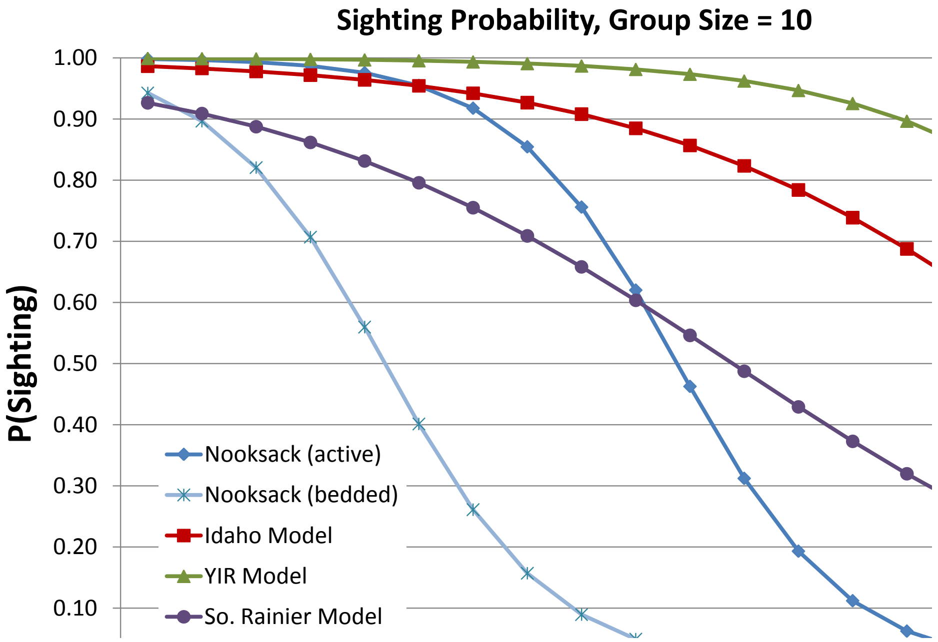


Figure 23. Estimated sightabilities for elk at 2 levels of group size (n = 2 and 10 elk) and different canopy closures for the Nooksack model and other published winter elk sightability models (“Idaho” = Samuel et al. 1987, “YIR” = McCorquodale 2001, “So. Rainier” = Gilbert and Moeller 2008).

contrasting the magnitude of the group size coefficient in our model with those in other models with a group size covariate (Nooksack = 0.058; McCorquodale [2001] = 0.77; McIntosh et al. [2007] = 0.20; Gilbert and Moeller [2008] = 0.22). Thus, our model predicts only modest increases in detectability of elk groups as elk aggregate more; the predicted odds of seeing an elk group increases by a factor of only ~1.8 as group size increases by 10 elk, controlling for other factors.

Table 23. Group size detection patterns (i.e., proportion detected) for winter elk groups (radiomarked) for the Nooksack elk herd, elk in Idaho (Samuel et al. 1987), and elk in the Cascades of Washington (McCorquodale 2001).

Group	Nooksa	Idaho	YIR[a]
1-2	0.06	0.22-0.46	0.07-0.25
3-4	0.21	0.50-0.60	0.50-0.57
5-6	0.40	0.40-0.69	0.80-1.00
7-8	0.40	0.82-1.00[b]	0.75-1.00
>8	0.74	***	1.00

[a] Yakima Indian Reservation, southcentral Washington Cascades.

[b] Groups size detectability summarized for 7-15, 16-30, and >30 in journal article.

Our best model also included an effect of activity. The model of McIntosh et al. (2007) also included an activity covariate similar to ours, but activity was not useful for predicting sightability of elk during winter aerial surveys in several other studies (Samuel et al. 1987, McCorquodale 2001, Gilbert and Moeller 2008). Anderson et al. (1998) found activity was a useful predictor of elk sightability in Wyoming during summer aerial surveys.

Although gender of elk groups (*i.e*., bull groups vs. cow-calf groups) was generally not useful for predicting sightability in the presence of other covariates, we did find a univariate relationship between group gender and the probability a group was detected. The odds ratio associated with gender indicated bull groups were about 0.38 times as likely to be detected as cow groups (or cow groups were 2.63 times more likely to be detected than bull groups), ignoring all other factors affecting sightability. This provides further evidence of a negative sighting bias associated with bull elk groups, similar to the findings of McCorquodale (2001), although the magnitude of the effect was smaller for the Nooksack herd. Multivariate modeling has indicated that the negative sighting bias associated with bull groups is largely driven by group size and affinities for cover, and possibly effects of sex-specific activity patterns (McCorquodale 2001).

Although we were able to develop a sightability model that seemed to effectively discriminate sighted and missed groups from our model building dataset, our results suggested that the model was relatively ineffective at producing unbiased estimates of the size of our study population; estimates appeared to be consistently biased low, based on both mark-resight estimates and minimum known alive estimates. We believe this problem is inherent to how sightability models function. Sightability models apply group-specific correction factors to count data, where the correction factors are the inverse of the group-specific detection probabilities. Missed groups are only accounted for when other groups with similar detection probabilities are observed. Groups associated with covariate patterns predicting very low detection probabilities will only be corrected for if other very low detectability groups are observed, and by definition, low detectability groups are unlikely to be observed. We expect the overall usefulness of a sightability model to be landscape-specific and related to the proportion of the elk population existing in very low detectability settings during surveys. Elk sightability models have validated well where landscapes are relatively open and/or elk use of extremely dense cover is relatively limited (Unsworth et al. 1990, Leptich and Zager 1993, McIntosh et al. 2007).

We also suggest that traditional sightability models will predictably perform erratically where many elk groups have very low detection probabilities, but some are sporadically observed. This results from very large model correction factors associated with very low detection probabilities. Inference regarding real population trends can be complicated and unreliable where few groups are detected overall and where groups that are unlikely to be seen are, on occasion, simply due to stochastic events. This could lead to widely fluctuating estimates wherein most individuals in the estimate may come from large model corrections, rather than observed individuals. For example, if a group of 5 elk were sighted that had a covariate pattern associated with a 10% detection probability, a traditional sightability model would add ≈50 elk to the population estimate. We would expect this could be particularly likely to plague estimates of the adult bull subpopulation in some years in small-to-modest populations and preclude meaningful interpretations of trends. In our cover-rich study area, a substantial proportion of the elk population routinely occupied very low detection probability settings during our surveys (as indicated by radiomarked elk), and we did occasionally observe elk groups with covariate patterns that predicted very low detection probabilities (*e.g.*, 2009).

We are also generally skeptical of sightability model predictions at some extreme levels of predictor variables. For example, both the Idaho model (Samuel at al. 1987) and the Cascades (east slope) model (McCorquodale 2001) predict that more than half the time (*i.e.*, $p_{\text{detection}} \approx 0.60\text{-}0.80$), a group of 10 elk would be sighted under 90% canopy closure (Fig. 16); we think that is highly unlikely to be an empirical result based on our experiences and highlights some of the limitations to this approach.

Mark-resight

Mark-resight modeling represents a fundamentally different approach to imperfect detectability and is based on well-developed theory and a rich literature tradition (Otis et al. 1978, White et al. 1982, Pollock et al. 1990, Schwarz and Seber 1999, Barker 2008). These methods have been widely applied to estimate large mammal population size (and/or density) (Bartmann et al. 1987, Minta and Mangel 1989, Neal et al. 1993, Bowden and Kufeld 1995, Eberhardt et al. 1998, Mahoney et al. 1998, McCorquodale 2000, Gould et al. 2005, McClintock and White 2007, Tracey et al. 2008), with varied success.

Our LNME modeling results indicated strong evidence in our data for substantial variation in detection rates across some survey sessions. Our models invoked detection rates (μ) of ≥0.50 for all marked elk in more than half of our survey sessions and for marked cows in 8 of 12 surveys sessions. Clearly marked cow detection rates dominated in estimates derived from combined marked cow and marked bull encounter histories. Periodically we experienced reduced detectability, even for marked cows. This occurred notably in the first session of 2006, our only February session, and again in the first session of 2008 and the last session of 2011. Detection rates for marked cows in these surveys were <0.35.

Bull-specific detection rates estimates were consistently and markedly lower than cow-specific detection rates. This provided additional confirmation of the systematic negative sighting bias for adult bulls during late winter aerial surveys, relative to cow elk (McCorquodale 2001). Our small sample of marked adult bulls coupled with low detection rates and our modest level of survey replication resulted in lower confidence in mark-resight point estimates of bull abundance.

We had strong evidence of sighting heterogeneity, which was expected. The models with heterogeneity fixed to 0.0, had virtually undetectable model weight. Our mark-resight estimates, at least for total elk and for adult cows, appeared to be more realistic in light of our minimum known alive tallies, than did sightability modeled estimates. Without knowledge of the true population size, we ultimately do not know if our mark-resight estimates were biased or not, nor the magnitude on any bias that existed. In previous mark-resight applications, population estimates have been variously biased high (McCullough and Hirth 1988) low (Bartmann et al. 1987), and relatively unbiased (Bear et al. 1989, McClintock and White 2007, Curtis et al. 2009).

Many mark-resight applications for big game have employed models that assume no resighting heterogeneity (Rice and Harder 1977, Bartmann et al. 1987, Bear et al. 1989, Eberhardt et al. 1998, Gould et al. 2005; see also summary by White and Shenk 2001). As noted previously, some models have now been developed that allow for heterogeneity (Minta and Mangel 1989, Bowden and Kufeld 1995), but only recently have very flexible, easily-generalized, and maximum likelihood-based models been developed that allow for heterogeneity. The LNME model that we employed (McClintock et al. 2008) is such a model and was well-suited for our purposes. Our estimates were modestly-precise. Precision is generally enhanced by marking a large proportion of the population, obtaining high detection rates, having minimal or modest unexplained heterogeneity, and usually by increasing the number of replicate resighting sessions (Minta and Mangel 1989, White and Garrott 1990, Neal et al. 1993, White and Shenk 2001). Our detection rates for cow elk were variable, but generally acceptable for a mark-resight application, and we had a relatively large number of radiomarked elk available. Our resighting sessions were minimally replicated; adding additional resighting surveys would likely have improved the precision of our estimates and, perhaps, reduced bias, but were precluded by available funding. For future management applications on this landscape, it seems unlikely that additional resighting surveys would be practical without reducing the geographic scale of the survey design. In general, we believe it would be preferable to base inference and management decisions on gender-specific estimates, rather than estimates that combine bull and cow encounter histories (because of the relatively distinct detectability patterns of cows and bulls).

We believe a clear advantage to the use of mark-resight on a landscape such as the Nooksack elk herd area, relative to sightability modeling, is that animals (groups) with relatively low detectability can be accounted for without having to actually detect similarly low detectability groups (necessitated by sightability modeling [see discussion above]). Virtually all low sightability groups could be missed and still be accounted for under mark-resight modeling.

Survival

Among our candidate survival models, only 2 models were within approximately 2 ΔAIC_c units of the best model. However, these models would not be considered truly competitive with the best model, because they differed only by the addition of a single new survival parameter (*i.e.*, resulted from partitioning an existing survival parameter into 2 parameters), with a subsequent change in $\Delta \mathrm{AIC}_c$ of only about 2. Because of the formulation of AIC (*i.e.*, $-2\ \zeta(\Theta \mid x, g) + 2k$), each additional model parameter (k) automatically adds 2 units to the AIC score (Burnham and Anderson 2002, Arnold 2010). The best supported model was a relatively simple model (k = 4) with a single source of variation affecting adult cow survival (translocation; see discussion below) and with survival for branch-antlered bulls varying before and after the end of the harvest moratorium in 2007. Simpler models, as well as several considerably more complex models, had little support in our data.

Our survival modeling indicated adult elk survival on the Nooksack landscape was high (>90%) in the absence of most forms of hunting. Adult female survival ≥90% has commonly been associated with modest to substantial growth rates in wild elk populations (McCorquodale et al. 1988, Ballard et al. 2000, Lubow et al. 2002, Larkin et al. 2003, Lubow and Smith 2004, Sargeant and Oehler 2007). Likewise in our study, adult female survival ≈0.93 (in the best supported model) was associated with apparent population growth, given recent levels of juvenile recruitment. Despite that recreational and tribal subsistence harvest opportunity did not exist on our study area during 2005-2011, adult cow survival was clearly not maximal (*i.e.*, did not solely reflect background natural mortality levels). A substantial number of adult cows were removed via damage control hunts, and radiomarked cows were among those killed.

Our best-supported survival model suggested a first-year effect of reduced survival for translocated cow elk, but only for those translocated in the fall of 2003. It is not clear why the first-year reduced survival was limited to only 1 of the 2 translocation cohorts. Mean fall body fat levels were similar for the 2 groups of cows (5.89 vs. 5.98%), and there was a greater proportion of cows in relatively good condition (>9% body fat) amongst the elk moved in 2003 (10/37 = 27.0%) compared to those moved in 2005 (4/29 = 13.8%); however, there were also relatively more poor condition cows (<5% body fat) moved in 2003 (19/37 =

51.4%) than in 2005 (10/29 = 34.5%) (unpublished WDFW data). SNOTEL climate data collected at a SNOTEL station located at an elevation of 4,970 feet near the Middle Fork of the Nooksack River also indicated a more severe local winter for 2003-04 than for 2005-06; daily accumulated snow water equivalents for the period Nov 1–Mar 31 were 5260.4 inches during 2003-04 and 4249.2 inches during 2005-06 (http://www.wcc.nrcs.usda.gov/nwcc). Initially reduced post-translocation survival has been previously documented for elk (Stussy et al. 1994, Larkin et al. 2003, Nickelson et al. 2003, Merrill et al. 2005), likely due to individuals being naïve regarding resource distribution and threats on landscapes they have no experience on, potentially acerbated by translocation stress.

Adult bull survival appeared to rival cow survival until the resumption of permit-controlled bull hunting in the fall of 2007. Similarly high rates of adult bull survival have been documented elsewhere where hunting is absent or nearly so (Houston 1982, Coughenour and Singer 1996, Larkin et al. 2003). Following the resumption of limited bull hunting in the core Nooksack elk herd range (GMU 418) in 2007, we documented annual bull survival dropping to approximately 0.68 (95% CI = 0.50-0.82). This level of harvest-influenced survival is similar to the level documented elsewhere in western Washington where bull harvest was strictly permit controlled to produce conservative bull harvest mortality (Bender and Miller 1999); a similar rate was also documented in an eastern Washington elk population subjected to modest hunting pressure (McCorquodale et al. 2003). Elsewhere, where bull harvest was by extremely limited permitting (McCorquodale et al. 2011) or where elk occupied very secure landscapes (*i.e.*, roadless) (Unsworth and Kuck 1991), annual bull survival was slightly higher than observed in our study.

Our bull survival estimate under relatively conservative harvesting contrasted with the relatively low bull survival under general season regulations seen elsewhere in western Washington (Smith et al. 1994, Bender and Miller 1999). The Nooksack elk herd remains relatively small, despite recovery; we believe the vulnerability of small populations to overharvest, coupled with statistical uncertainty regarding the actual bull subpopulation size warrant continuing a conservative approach to harvest permitting in Nooksack elk management. Further, we believe that managing for modest bull harvest mortality is essential to reducing the risks of substantially right-truncating the bull age structure, which is a defensible management goal from both the perspectives of conserving high quality hunting opportunity and maintaining a strong component of physiologically mature bulls in the population. The benefits of mature bulls to elk herd reproductive ecology have been previously documented (Prothero et al. 1979, Noyes et al. 1996; see also Mysterud et al. 2002).

Despite that a moratorium on recreational and tribal subsistence hunting was in effect for antlerless elk throughout the study period, and for antlered bulls until fall 2007, people still accounted for a substantial amount of elk mortality during 2005-11. Damage-related hunting, poaching, and roadkills collectively accounted for a considerable number of elk deaths. Clearly, we were less likely to have documentation of natural mortalities, apart from deaths of radiocollared elk, which attests to our dead elk tally being conservative. Even though the management strategy was to conserve adult female elk in order to enhance population recovery, we accounted for nearly 80 human-caused deaths of adult cows in, or near, the core herd range in a 7-year period.

Herd Status and Trend

One of our principal goals was to document the current status of the Nooksack elk population and quantify recent population trend. Both sightability modeling and mark-resight modeling suggested the Nooksack elk population increased during 2006-2011. Qualitatively, the series of point estimates depicted somewhat different patterns. The sightability modeling point estimates followed the raw data closely (*i.e.*, the maximum number of groups observed and the average elk seen). This was not surprising given that the sightability modeling estimates were a direct function of total groups and individuals observed, independent of the actual detection probability for any specific marked elk.

The model averaged mark-resight point estimates for total elk population size increased modestly from 2006 through 2008, decreased during 2009-2010, and increased markedly in 2011. The mark-resight estimates for cow subpopulation size followed a qualitatively similar pattern.

The trends (i.e., rate of increase) depicted by sightability modeling and mark-resight modeling were generally very similar (Table 24). We extended the time series back to 2000 for the core GMU (418) by using a population estimate of 300 elk (WDFW 2002). The indicated finite rate of increase (λ) indicated by mark-resight modeling for total population size was 1.12 for the full time series and 1.10 using only the 2006-2011 estimates. For the cow subpopulation mark-resight estimates, estimated λ was 1.07 for 2006-2011. The sightability model-based estimate was λ = 1.08 for a fitted line through the replicated estimates, 2006-2011.

Table 24. Rate of increase estimates for various model estimates and data subsets, Nooksack elk herd, 2000-11.

Estimate for	Data (ln transformed)	λ	r
All elk, 2000-	LNME $_{\text{point estimates}}$	1.	0.
All elk, 2006-	LNME $_{\text{point estimates}}$	1.	0.
Cows, 2006-	LNME $_{\text{point estimates}}$	1.	0.
All elk, 2006-	Sightability Model $_{\text{fitted line}}$	1.	0.

To examine how realistic the population estimates were, we also developed an Excel spreadsheet population model. The model was built to be very flexible and included stochastic effects on vital rate inputs at each time step and realistic senescence effects. The model tracked numbers of elk in age cohorts through age 25 for cow elk and age 18 for bull elk. We populated the model with fertility and neonatal survival inputs to yield spring calf recruitment levels equivalent to what we observed during 2006-2011, and we used the best estimates for adult cow and bull survival from our survival modeling reported here. Our starting simulated population size was ≈ 300 elk. This model yielded a mean λ value of

1.10 (n = 20 simulation years, measured at April 1), quite similar to our values estimated via mark-resight and sightability correction modeling from aerial survey data. A population growing at approximately this rate would be at approximately 1,211 total elk in spring 2011 (assuming year 1 was 2000; model-averaged LNME estimate = 1,248 elk in spring 2011) and would attain the 1,450 elk population objective (WDFW 2002) by 2013.

Sightability / Mark-resight modeling and population modeling based on data-based estimates of vital rates all indicated a modestly growing elk population. Some concern is perhaps warranted over the level of antlerless elk removals stemming from damage-related hunts near the end of our study. Observed recruitment rates and adult survival rates estimated from radiomarked elk also suggested a demographically healthy population.

MANAGEMENT RECOMMENDATIONS

Because of its history, its recent modest population size, ongoing human-mediated vulnerability (*e.g.*, conflicts with agriculture, highway mortality), complex management issues (*i.e.*, co-harvested by the Pt. Elliot tribes and Washington State, extensive private timberland in the herd range), and a relatively small population objective, the Nooksack elk herd warrants careful monitoring. In recent time, a high level of intergovernmental management coordination has occurred, involving both state and tribal agencies; this coordination is largely responsible for the success achieved in pushing the herd towards recovery, supporting the collection of relevant biological data, and for successfully reinitiating carefully controlled harvest. Undoubtedly, continuing this intergovernmental coordination will be a necessary key to meeting remaining management objectives and sustaining management success through time.

Relevant data collection must be a continuing management priority. Although the authors were hopeful that sightability-correction modeling would be an effective tool for estimating demographics of the Nooksack elk population, the results indicated some substantial limitations, namely, a substantial number of elk groups with very low detection probabilities during most surveys. This prevented estimating elk abundance without bias, and it was also apparent that there was commonly a gender-specific systematic nature to this bias. Sightability modeling could be effective if it were possible to jointly estimate sighting probabilities for elk in modest-to-good detection settings and the probability of elk occupying low detection settings during surveys; however, the latter is technically challenging and no simple or obvious way to do that has been derived for any landscape. Sightability modeling could potentially be used to estimate a redefined metric, such as the “surveyable” population, knowing that this would be an underestimate of the true population. Management objectives would have to be similarly redefined. The principal limitation of this approach would be the inherent assumption of a linear relationship between the surveyable population and the true population across a wide range of abundance. It was encouraging that population trend estimated via sightability modeling was very similar to the trend estimated from mark-resight and an age-structured population model. We suggest that data suitable for generating sightability-corrected estimates continue to be collected in the short-term; this really only requires continuing to record group and environmental covariates. This would facilitate a longer evaluation of sightability model estimates relative to other estimates, such as mark-resight estimates.

Mark-resight appeared to perform better for assessing abundance in this context; the method is relatively robust to the issue of groups with low detectability, given that other key assumptions are met. Typically mark-resight is an impractical tool for longer-term monitoring of ungulate populations due to issues of landscape and population scale and the need for perpetual marking (at least for non-batch-mark models). However, the Nooksack herd core winter range is a relatively small landscape, compared to the ranges of many elk populations. The population objective is also modest relative to other Washington elk populations (i.e., the population will never be large). On this landscape, a mark-resight population monitoring strategy may be relatively feasible, but will require a commitment to periodically mark new individuals. However, the method may be impractical for effective monitoring of adult bull abundance, due to substantial collar attrition associated with harvest, the challenge of marking sufficient numbers of adult bulls, and the relatively low detection rates of collared bulls. Mark-resight, coupled with population modeling and monitoring of harvested bull ages may be the most practical strategy for monitoring the bull subpopulation and harvest effects.

During our study, we captured elk for radiocollaring by helicopter darting. This was a challenging endeavor on the rugged and forested Nooksack landscape; this approach was also expensive and potentially hazardous to capture crews. We believe it would be feasible to develop a ground-based trapping strategy to maintain marked elk for use in a mark-resight monitoring program. Mark-resight would not necessarily require an extensive number of marked elk; rather, the key would be to maintain a good distribution of marks across elk groups present during surveys. A well-distributed array of traps (*e.g.*, semi-permanent corral traps or movable clover traps) could be used to periodically capture and radiomark elk. This approach would require more staff time than helicopter darting, but would likely still be much less expensive and certainly would be safer for biologists/technicians relative to helicopter darting.

For this herd, the application of aerial surveys, such as we explored, should emphasize a strategy to maximize detection rates. Our results suggested late winter / early spring flights were better than mid-winter flights. The ideal timeframe would seem to be late enough that some new forage growth would be occurring in openings, but prior to alder leaf-out. These conditions seem to be associated with maximal use of openings by elk. Some survey units provided a consistently large proportion of the observed groups (*e.g.*, lower South Fork Nooksack units and the Bacus unit), whereas other units yielded few group observations. The survey strategy should prioritize flying the best units during prime sighting windows (*i.e.*, very early morning and evening); flying these units during mid-day, particularly on sunny days is a poor strategy. Replicated surveys–with at least 2 replicates–represent a much better data collection strategy than once yearly flights; replicated flights are also required for the LNME mark-resight model. Replicated flights also help mitigate the effects of occasionally erratic results (very high or low individual session counts).

Radiocollared elk proved very useful for estimating bull elk survival following the resumption of co-harvesting in 2007. The availability of these radiomarked individuals provided a means for directly estimating the rate of mortality under recent permit levels. As the population changes through time, it is anticipated that permit levels will also be dynamic. Maintaining radiocollared elk on this landscape would also continue to be useful for monitoring harvest effects. Assuming the elk population continues to grow, thresholds for reinitiating some level of permit-controlled antlerless elk hunting (recreational and tribal subsistence) may be met in the near future. Monitoring the contribution of harvest to overall antlerless elk mortality would also be facilitated by maintaining a radiocollared elk sample in this herd.

One of the most substantial management challenges ahead is implementing a strategy to meet elk population objectives on a relatively developed landscape. Quality elk habitat exists on public and private forestland, but this core range is surrounded by valleys and foothills with a considerable rural and agricultural development footprint. A substantial elk presence on this developed portion of the landscape will continue to be problematic; effective strategies need to be developed to reduce conflicts between elk and people on this landscape. A variety of tools could be used: habitat improvements (*e.g*., forage enhancements) in the core range, fencing, deterring elk use on private land via hunting and hazing, but some may be counterproductive (*e.g*., damage hunts) to meeting other elk management objectives. This issue is not likely to diminish anytime soon. Success in meeting these challenges will likely require considerable collaboration, sources of adequate long-term funding, and effective communication among stakeholders (*i.e*., municipal and county governments, WDFW, the USFS, tribal governments, conservation groups, and private landowners). Recovery success will necessarily require increasing elk abundance in the core range outside of agricultural / rural development zones while concurrently minimizing chronic or increasing elk use of developed areas.

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Appendix A. Known elk mortalities from the Nooksack herd, 2005-11.

Date	Survival Yr	Survey Yr	GMU	Class	Legal	State/ Tribal	Cause	Damage
08/22/2005	2005	2006	418	cow			roadkill	N
09/24/2005	2005	2006	418	calf			predation	N
09/25/2005	2005	2006	418	cow			roadkill	N
10/01/2005	2005	2006	437	5x5	yes	state	archery	N
10/02/2005	2005	2006	418	calf	no		illegal	N
10/08/2005	2005	2006	437	cow	yes	state	archery	Y
10/08/2005	2005	2006	437	calf	yes	state	archery	Y
10/09/2005	2005	2006	437	cow	yes	state	archery	Y
10/11/2005	2005	2006	418	4x5			WDFW	N
10/25/2005	2005	2006	418	cow			predation	N
11/01/2005	2005	2006	437	5x5	yes	state	muzzleloader	Y
11/05/2005	2005	2006	437	1x1	yes	state	muzzleloader	Y
11/05/2005	2005	2006	437	7x8	yes	state	muzzleloader	Y
11/19/2005	2005	2006	418	unknown	no		illegal	N
11/30/2005	2005	2006	437	1x1	yes	state	muzzleloader	Y
11/30/2005	2005	2006	418	cow			roadkill	N
12/09/2005	2005	2006	437	3x4	yes	state	muzzleloader	Y
12/26/2005	2005	2006	437	5x5	yes	tribal	tribal	N
01/04/2006	2005	2006	418	cow			predation	N
01/19/2006	2005	2006	437	cow	yes	state	muzzleloader	Y
01/23/2006	2005	2006	418	cow			unknown	N
03/01/2006	2005	2006	418	6x6			unknown	N
04/18/2006	2005	2007	418	cow	yes	state	damage	Y
04/22/2006	2005	2007	437	cow			roadkill	N
05/03/2006	2006	2007	418	cow			unknown	N
08/18/2006	2006	2007	418	cow			unknown	N
08/20/2006	2006	2007	437	cow			roadkill	N
09/28/2006	2006	2007	437	6x6			natural	N
09/30/2006	2006	2007	418	cow			predation	N
09/30/2006	2006	2007	418	bull	no		illegal	N
10/04/2006	2006	2007	418	bull			natural	N
12/03/2006	2006	2007	437	cow	yes	state	muzzleloader	Y
01/12/2007	2006	2007	437	unknown			roadkill	N
01/18/2007	2006	2007	437	5x5	yes	tribal	tribal	N
01/18/2007	2006	2007	437	6x6	yes	tribal	tribal	N
01/19/2007	2006	2007	418	cow			Trap Mortality	N
02/07/2007	2006	2007	437	cow	yes	state	muzzleloader	Y
02/07/2007	2006	2007	418	cow			unknown	N
02/15/2007	2006	2007	418	calf			natural	N
02/17/2007	2006	2007	437	bull	no		illegal	N
02/20/2007	2006	2007	418	calf	no		illegal	N
02/26/2007	2006	2007	418	1x1			Trap Mortality	N
02/26/2007	2006	2007	418	cow			Trap Mortality	N

Date	Survival Yr	Survey Yr	GMU	Class	Legal	State/ Tribal	Cause	Damage
03/03/2007	2006	2007	418	calf			roadkill	N
03/13/2007	2006	2007	418	7x8			Unknown	N
03/23/2007	2006	2007	418	cow	yes	tribal	tribal	Y
03/23/2007	2006	2007	418	cow	yes	state	modern	Y
03/24/2007	2006	2007	418	cow	yes	tribal	tribal	Y
03/26/2007	2006	2007	418	cow	yes	tribal	tribal	Y
03/28/2007	2006	2007	418	bull	yes	state	modern	Y
03/30/2007	2006	2007	418	cow	yes	state	modern	Y
03/30/2007	2006	2007	418	cow	yes	tribal	tribal	Y
04/03/2007	2006	2007	437	cow			roadkill	N
05/07/2007	2007	2008	418	cow	yes	state	modern	Y
07/07/2007	2007	2008	418	cow			predation	N
08/08/2007	2007	2008	418	cow			unknown	N
08/18/2007	2007	2008	437	cow			roadkill	N
08/18/2007	2007	2008	418	calf	no		illegal	N
08/28/2007	2007	2008	418	6x7	yes	tribal	tribal	N
08/30/2007	2007	2008	418	5x5	yes	tribal	tribal	N
09/01/2007	2007	2008	418	6x7	yes	state	modern	N
09/03/2007	2007	2008	418	8x8	yes	tribal	tribal	N
09/05/2007	2007	2008	418	8x9	yes	state	archery	N
09/07/2007	2007	2008	418	5x5	yes	tribal	tribal	N
09/07/2007	2007	2008	418	unknown	no		illegal	N
09/11/2007	2007	2008	437	7x7			roadkill	N
09/17/2007	2007	2008	418	6x6	yes	state	archery	N
09/17/2007	2007	2008	418	6x7	yes	tribal	tribal	N
09/17/2007	2007	2008	418	cow			unknown	N
09/19/2007	2007	2008	418	bull	no		illegal	N
09/26/2007	2007	2008	437	1x1			roadkill	N
09/30/2007	2007	2008	418	3x3	yes	state	muzzleloader	N
10/01/2007	2007	2008	437	6x7	yes	state	archery	N
10/02/2007	2007	2008	418	4x4	yes	tribal	tribal	N
10/05/2007	2007	2008	418	6x7	yes	state	muzzleloader	N
10/14/2007	2007	2008	418	5x5	yes	state	modern	N
10/14/2007	2007	2008	418	6x8	yes	state	modern	N
10/28/2007	2007	2008	418	6x6	yes	state	muzzleloader	N
10/30/2007	2007	2008	418	7x7	yes	state	modern	N
10/31/2007	2007	2008	418	5x6	yes	state	modern	N
11/04/2007	2007	2008	437	5x5	yes	state	muzzleloader	N
11/04/2007	2007	2008	437	cow	yes	state	muzzleloader	N
11/08/2007	2007	2008	418	5x5	yes	state	modern	N
11/09/2007	2007	2008	418	5x5	yes	tribal	tribal	N
11/16/2007	2007	2008	418	cow			WDFW	N
11/20/2007	2007	2008	418	7x7	yes	tribal	tribal	N
11/20/2007	2007	2008	418	5x5	yes	tribal	tribal	N
12/01/2007	2007	2008	437	cow			roadkill	N
12/06/2007	2007	2008	418	5x5			roadkill	N

Date	Survival Yr	Survey Yr	GMU	Class	Legal	State/ Tribal	Cause	Damage
12/12/2007	2007	2008	418	7x7	yes	state	modern	N
12/15/2007	2007	2008	418	4x5	yes	state	archery	N
12/27/2007	2007	2008	418	4x4	no		illegal	N
12/29/2007	2007	2008	418	cow	no		illegal	N
12/30/2007	2007	2008	437	5x5	yes	state	muzzleloader	Y
12/30/2007	2007	2008	418	3x4	yes	tribal	tribal	N
01/19/2008	2007	2008	418	unknown			unknown	N
01/23/2008	2007	2008	418	unknown			roadkill	N
01/26/2008	2007	2008	418	1x1	yes	tribal	tribal	N
02/18/2008	2007	2008	418	cow	no		illegal	N
03/25/2008	2007	2009	418	cow	yes	tribal	tribal	Y
03/25/2008	2007	2009	418	cow	yes	state	modern	Y
03/26/2008	2007	2009	418	cow	yes	state	modern	Y
03/27/2008	2007	2009	418	cow	yes	tribal	tribal	Y
03/29/2008	2007	2009	418	cow	yes	tribal	tribal	Y
03/30/2008	2007	2009	418	bull	yes	state	modern	Y
04/09/2008	2007	2009	418	bull			capture	N
09/03/2008	2008	2009	418	6x7	yes	state	archery	N
08/31/2008	2008	2009	448	4x4	no		illegal	N
08/31/2008	2008	2009	448	5x5	no		illegal	N
09/05/2008	2008	2009	418	5x5	yes	tribal	tribal	N
09/05/2008	2008	2009	418	6x6	yes	tribal	tribal	N
09/06/2008	2008	2009	418	4x4	yes	tribal	tribal	N
09/06/2008	2008	2009	418	6x6	yes	tribal	tribal	N
09/15/2008	2008	2009	437	calf			roadkill	N
09/15/2008	2008	2009	418	bull	yes	tribal	tribal	N
09/10/2008	2008	2009	418	bull	yes	tribal	tribal	N
09/15/2008	2008	2009	418	bull	yes	tribal	tribal	N
09/20/2008	2008	2009	418	bull	yes	tribal	tribal	N
09/10/2008	2008	2009	418	bull	yes	tribal	tribal	N
09/15/2008	2008	2009	418	bull	yes	tribal	tribal	N
09/17/2008	2008	2009	418	4x4	yes	tribal	tribal	N
09/15/2008	2008	2009	418	bull	yes	tribal	tribal	N
09/28/2008	2008	2009	418	6x6	yes	state	archery	N
09/29/2008	2008	2009	418	6x6	yes	state	muzzleloader	N
10/01/2008	2008	2009	437	6x6	yes	state	archery	Y
10/01/2008	2008	2009	437	6x6	yes	state	archery	Y
10/06/2008	2008	2009	437	calf			roadkill	N
10/06/2008	2008	2009	437	cow	yes	state	archery	Y
10/07/2008	2008	2009	437	4x4	yes	state	archery	Y
10/07/2008	2008	2009	418	6x6	yes	tribal	tribal	N
10/11/2008	2008	2009	418	6x6	yes	state	modern	N
10/11/2008	2008	2009	437	cow	yes	state	archery	Y
10/12/2008	2008	2009	418	5x6	yes	state	modern	N
10/15/2008	2008	2009	418	7x7	yes	state	modern	N
10/17/2008	2008	2009	418	6x6	yes	state	modern	N

Date	Survival Yr	Survey Yr	GMU	Class	Legal	State/ Tribal	Cause	Damage
10/18/2008	2008	2009	448	cow	no		illegal	N
10/18/2008	2008	2009	448	cow	no		illegal	N
10/19/2008	2008	2009	418	6x7	yes	state	modern	N
10/20/2008	2008	2009	437	5x5	yes	state	archery	Y
10/21/2008	2008	2009	437	4x4	yes	state	archery	Y
10/27/2008	2008	2009	437	5x6	yes	state	archery	Y
11/01/2008	2008	2009	418	6x7	yes	state	modern	N
11/01/2008	2008	2009	437	5x6	yes	state	muzzleloader	Y
11/06/2008	2008	2009	418	3x5	yes	state	modern	N
11/22/2008	2008	2009	448	cow	yes	state	modern	Y
11/22/2008	2008	2009	437	5x5	yes	state	muzzleloader	Y
11/24/2008	2008	2009	418	5x5			roadkill	N
11/24/2008	2008	2009	407	5x5	no		illegal	N
11/24/2008	2008	2009	407	3x4	no		illegal	N
11/26/2008	2008	2009	437	1x1	yes	state	muzzleloader	Y
12/03/2008	2008	2009	437	cow	no	state	muzzleloader	Y
12/03/2008	2008	2009	437	6x6	yes	state	muzzleloader	Y
12/04/2008	2008	2009	437	6x6	yes	state	muzzleloader	Y
12/04/2008	2008	2009	437	5x6	yes	state	muzzleloader	Y
12/06/2008	2008	2009	437	cow			roadkill	N
12/08/2008	2008	2009	437	1x1	yes	state	muzzleloader	Y
12/08/2008	2008	2009	437	1x1	yes	state	muzzleloader	Y
12/23/2008	2008	2009	437	2x2	yes	state	muzzleloader	Y
12/28/2008	2008	2009	437	cow	yes	state	muzzleloader	Y
12/28/2008	2008	2009	437	1x1	yes	state	muzzleloader	Y
12/28/2008	2008	2009	437	calf	yes	state	muzzleloader	Y
12/28/2008	2008	2009	437	cow	yes	state	muzzleloader	Y
12/28/2008	2008	2009	437	cow	yes	state	muzzleloader	Y
12/28/2008	2008	2009	437	cow	no	state	muzzleloader	Y
12/28/2008	2008	2009	437	cow	yes	state	muzzleloader	Y
12/29/2008	2008	2009	437	1x1	yes	state	muzzleloader	Y
12/29/2008	2008	2009	437	1x1	yes	state	muzzleloader	Y
12/29/2008	2008	2009	437	1x1	yes	state	muzzleloader	Y
12/29/2008	2008	2009	437	cow	yes	state	muzzleloader	Y
12/29/2008	2008	2009	437	cow	yes	state	muzzleloader	Y
12/29/2008	2008	2009	437	1x1	yes	state	muzzleloader	Y
12/29/2008	2008	2009	437	1x2	yes	state	muzzleloader	Y
12/29/2008	2008	2009	437	cow	yes	state	muzzleloader	Y
12/30/2008	2008	2009	437	cow	yes	state	muzzleloader	Y
12/31/2008	2008	2009	437	cow	yes	state	muzzleloader	Y
12/31/2008	2008	2009	437	cow	yes	state	muzzleloader	Y
01/01/2009	2008	2009	437	1x1	no		illegal	N
01/01/2009	2008	2009	437	calf	yes	state	muzzleloader	Y
01/01/2009	2008	2009	418	cow			roadkill	N
01/04/2009	2008	2009	437	cow	yes	state	muzzleloader	Y
01/04/2009	2008	2009	437	cow	yes	state	muzzleloader	Y

Date	Survival Yr	Survey Yr	GMU	Class	Legal	State/ Tribal	Cause	Damage
01/04/2009	2008	2009	437	calf	yes	state	muzzleloader	Y
01/04/2009	2008	2009	437	cow	yes	state	muzzleloader	Y
01/29/2009	2008	2009	437	cow			roadkill	N
01/29/2009	2008	2009	437	cow			roadkill	N
02/16/2009	2008	2009	418	cow	yes	state	archery	Y
03/24/2009	2008	2009	418	cow	yes	stare	modern	Y
03/30/2009	2008	2009	418	cow	yes	state	modern	Y
03/30/2009	2008	2009	418	cow	yes	tribal	modern	Y
03/31/2009	2008	2009	418	cow	yes	state	modern	Y
04/04/2009	2008	2009	418	cow	no		illegal	Y
04/17/2009	2008	2010	418	cow			predation	N
09/01/2009	2009	2010	418	5x6	yes	tribal	modern	N
09/03/2009	2009	2010	418	6x6	yes	tribal	modern	N
09/05/2009	2009	2010	418	6x6	yes	tribal	modern	N
09/07/2009	2009	2010	418	7x8	no		illegal	N
09/20/2009	2009	2010	418	1x1	yes	tribal	modern	N
09/23/2009	2009	2010	418	6x6	yes	state	archery	N
09/25/2009	2009	2010	418	6x6	yes	state	archery	N
09/26/2009	2009	2010	418	8x8	yes	state	muzzleloader	N
09/26/2009	2009	2010	418	6x6	yes	state	muzzleloader	N
09/27/2009	2009	2010	418	1x1	yes	state	muzzleloader	N
09/30/2009	2009	2010	437	6x7	yes	state	modern	N
10/09/2009	2009	2010	418	unknown			roadkill	N
10/14/2009	2009	2010	418	1x7	yes	state	modern	N
10/15/2009	2009	2010	418	1x1	yes	tribal	modern	N
10/15/2009	2009	2010	418	6x6	yes	tribal	modern	N
10/15/2009	2009	2010	418	1x1	yes	tribal	modern	N
10/15/2009	2009	2010	418	1x1	yes	tribal	modern	N
10/18/2009	2009	2010	418	1x1	yes	state	modern	N
10/24/2009	2009	2010	418	1x1	yes	state	modern	N
11/01/2009	2009	2010	418	1x1	yes	state	modern	N
11/02/2009	2009	2010	437	calf	yes	state	archery	Y
01/18/2010	2009	2010	437	spike			roadkill	N
01/28/2010	2009	2010	437	cow			roadkill	N
01/31/2010	2009	2010	418	cow	yes	state	modern	Y
02/07/2010	2009	2010	418	cow	yes	tribal	modern	Y
02/17/2010	2009	2010	437	cow	yes	state	muzzleloader	Y
02/24/2010	2009	2010	418	cow			roadkill	N
02/25/2010	2009	2010	418	bull	no		illegal	N
02/25/2010	2009	2010	418	cow	no		illegal	N
03/10/2010	2009	2010	418	cow			roadkill	N
03/17/2010	2009	2010	418	unknown			roadkill	N
03/18/2010	2009	2010	437	cow	yes	state	modern	Y
03/25/2010	2009	2010	418	unknown			roadkill	N
04/08/2010	2009	2011	437	unknown			roadkill	N
04/25/2010	2009	2011	418	bull			roadkill	N

Date	Survival Yr	Survey Yr	GMU	Class	Legal	State/ Tribal	Cause	Damage
Fall 2010	2010	2011	418	unknown			roadkill	N
Fall 2010	2010	2011	418	unknown			roadkill	N
Fall 2010	2010	2011	418	unknown			roadkill	N
Fall 2010	2010	2011	418	unknown			roadkill	N
Fall 2010	2010	2011	418	unknown			roadkill	N
Fall 2010	2010	2011	418	1x1	yes	tribal	modern	N
Fall 2010	2010	2011	418	1x1	yes	tribal	modern	N
Fall 2010	2010	2011	418	1x1	yes	tribal	modern	N
Fall 2010	2010	2011	418	1x1	yes	tribal	modern	N
Fall 2010	2010	2011	418	1x1	yes	tribal	modern	N
Fall 2010	2010	2011	418	1x1	yes	tribal	modern	N
Fall 2010	2010	2011	418	1x1	yes	tribal	modern	N
Fall 2010	2010	2011	418	bull	yes	tribal	modern	N
Fall 2010	2010	2011	418	bull	yes	tribal	modern	N
Fall 2010	2010	2011	418	bull	yes	tribal	modern	N
Fall 2010	2010	2011	418	bull	yes	tribal	modern	N
Fall 2010	2010	2011	418	bull	yes	tribal	modern	N
Fall 2010	2010	2011	418	bull	yes	tribal	modern	N
Fall 2010	2010	2011	418	bull	yes	tribal	modern	N
Fall 2010	2010	2011	418	bull	yes	tribal	modern	N
Fall 2010	2010	2011	418	bull	yes	tribal	modern	N
Fall 2010	2010	2011	418	cow	yes	state	modern	N
Fall 2010	2010	2011	418	1x1	yes	state	modern	N
Fall 2010	2010	2011	418	1x1	yes	state	modern	N
Fall 2010	2010	2011	418	1x1	yes	state	muzzleloader	N
Fall 2010	2010	2011	418	6x6	yes	state	archery	N
Fall 2010	2010	2011	418	6x6	yes	state	modern	N
Fall 2010	2010	2011	418	6x6	yes	state	modern	N
Fall 2010	2010	2011	418	6x6	yes	state	modern	N
Fall 2010	2010	2011	418	6x6	yes	state	modern	N
Fall 2010	2010	2011	418	6x6	yes	state	muzzleloader	N
Winter 2011	2010	2011	418	unknown			roadkill	N
Winter 2011	2010	2011	418	unknown			roadkill	N
Winter 2011	2010	2011	418	cow	yes	state	modern	Y
Winter 2011	2010	2011	418	cow	yes	state	unknown	Y
Winter 2011	2010	2011	418	cow	yes	state	unknown	Y
Winter 2011	2010	2011	418	cow	yes	state	unknown	Y
Winter 2011	2010	2011	418	cow	yes	state	unknown	Y
Winter 2011	2010	2011	418	cow	yes	state	unknown	Y
Winter 2011	2010	2011	418	cow	yes	state	unknown	Y
Winter 2011	2010	2011	418	cow	yes	state	unknown	Y
Winter 2011	2010	2011	418	cow	yes	state	unknown	Y
Winter 2011	2010	2011	418	cow	yes	state	unknown	Y