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We executed four mark-resight helicopter surveys during the winter months January-February for each of the three years 1999-2001 at 7-10 day intervals to estimate population size of a wintering elk *Cervus elaphus canadensis* herd in northern New Mexico. We counted numbers of radio-collared and uncollared elk on a simple random sample of quadrats from the study area. Because we were unable to survey the entire study area, we adopted a superpopulation approach to estimating population size, in which the total number of collared animals within and proximate to the entire study area was determined from an independent fixed-wing aircraft. The total number of collared animals available on the quadrats surveyed was also determined and facilitated detectability estimation. We executed superpopulation estimation via the joint hypergeometric estimator using the ratio of marked elk counted to the known number extant as an estimate of effective detectability. Superpopulation size estimates were approximately four times larger than previously suspected in the vicinity of the study area. Despite consistent survey methodology, actual detection rates varied within winter periods, indicating that multiple resight flights are important for improved estimator performance. Variable detectability also suggests that reliance on mere counts of observed individuals in our area may not accurately reflect abundance.

Key words: aerial surveys, Cervus elaphus canadensis, detection, elk, helicopter, mark-resight, population estimation, superpopulation

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Mark-resight techniques have been used to estimate abundance for a wide variety of animal populations including mammals (Hein & Andelt 1995, McCullough et al. 2000, Focardi et al. 2002), birds (Collazo & Bonilla-Martinez 2001, Ganter & Madsen 2001), and fish (Young & Hayes 2001). In addition, population size estimates from mark-resight studies have been used in a comparative manner to assess the reliability of indices (Fuller et al. 2001, Young & Hayes 2001) and other estimation methods (Casagrande & Beissinger 1997, Bender & Spencer 1999, Fisher et al. 2000). Estimator developments in which individual animals must be identifiable (Minta & Mangel 1989, Arnason et al. 1991, Bowden & Kufeld 1995, Gardner & Mangel 1996), and Bayesian estimation approaches (Ananda 1997) have also received attention.

The Lincoln-Petersen estimator (Petersen 1896, Lincoln 1930) or Chapman's (1951) estimator, which is a less-biased version of the former, are typically used for estimating population size on the individual surveys. Rather than simply averaging individual estimates from multiple resighting events, Bartmann et al. (1987) concluded that the joint hypergeometric estimator (JHE) was more efficient. The JHE is found by maximizing (numerically) the likelihood,

$$\pounds\left(\hat{N} \mid M_i, n_i, m_i\right) = \prod_{i=1}^{k} \frac{\binom{M_i}{m_i}\binom{\hat{N}-M_i}{n_i-m_i}}{\binom{\hat{N}}{n_i}} \quad (1),$$

where $\hat{N}$ is the estimated abundance, M_i is the number of marked individuals in the population on the i^{th} occasion, n_i is the number of sighted individuals (marked and unmarked) on the i^{th} occasion and m_i is the number of marked animals sighted during the i^{th} occasion.

The JHE assumes that 1) the population is closed demographically and geographically, 2) all animals have equal, independent detection probabilities on a given survey occasion, 3) marks are not lost and all are reported, and 4) animals are sampled without replacement. Neal et al. (1993) estimated relative bias, precision and confidence interval coverage via simulation when the second assumption was violated. When sighting probabilities were not independent, bias for estimated population size was negligible, although confidence interval coverage was lowered. Heterogeneous sighting probabilities were more likely to bias population estimates and lower confidence interval coverage, but in general the bias was small and obviated the need for using the Minta & Mangel (1989) estimator that allows for unequal sighting probabilities.

In most capture-recapture studies, recapture events are conducted over the entire area of interest. Due to the large size of our study area (~1,750 km^2), we were not able to resight animals over the entire study area. We randomly sampled the study area on which to conduct helicopter surveys. Skalski (1994) presented a framework for combining finite sampling theory and density estimation techniques for making statistical inference when the study area is sampled. Skalski's (1994) approach relied on combining population estimates from the individually sampled area units. Bowden et al. (2003) extended Skalski's work by developing estimators that allowed correlated quadrat-specific estimates, primarily motivated by a need to pool information across quadrats.

Our present study differs from these approaches in two ways. First, quadrat-specific abundance estimates for use in traditional finite sampling approaches (e.g. see Thompson 2002) were not feasible due to low numbers of marked animals within quadrats. Secondly, we adopted a 'superpopulation' approach (Kendall 1999) to abundance estimation via mark-resight techniques in which individuals were not individually identifiable in our resight surveys. The superpopulation refers to the group of animals that have a non-zero probability of being located and detected on the study area during the wintering survey periods. Thus, geographic closure of the wintering population was not assumed.

We present an example of superpopulation estimation for a Rocky Mountain elk *Cervus elaphus canadensis* herd in northern New Mexico. In previous years, aerial surveys of our study area had been conducted by the New Mexico Department of Game and Fish (NMDGF), but these surveys assumed 100% detectability in surveyed units (e.g. see Kufeld et al. 1980). The advantage of having known numbers of marked elk in the population is that we were able to estimate the effective detection probability, thus achieving less-biased abundance estimates than those based on unadjusted counts. Additionally, we consider model assumptions and evaluate the impact of assumption violations on our population estimates.

Study area

San Antonio Mountain (3,325 m a.s.l.) lies in north-central New Mexico approximately 30 km equidistant northwest of Tres Piedras, New Mexico and southwest of Antonito, Colorado. Our study area is largely east of the Continental Divide and is defined in part by the New Mexico-Colorado border to the north and the Rio Grande to the east (Fig. 1). Specifically, the original winter range

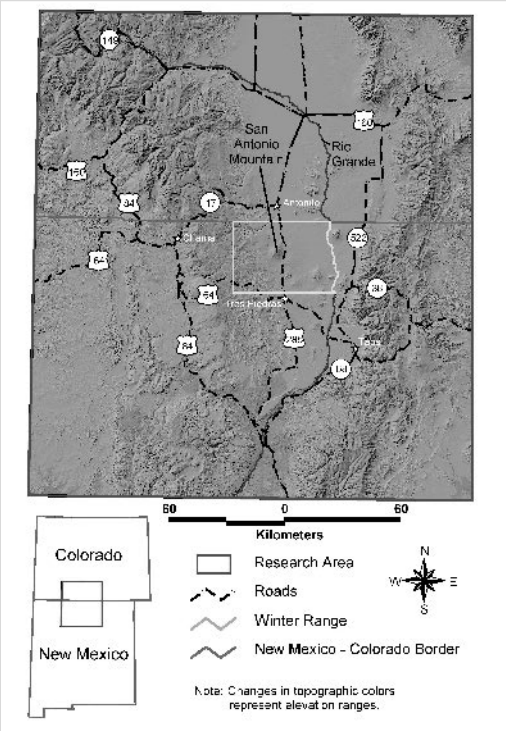

Figure 1. Geographic location of San Antonio Mountain, New Mexico, where elk research was conducted from December 1998 to December 2001.

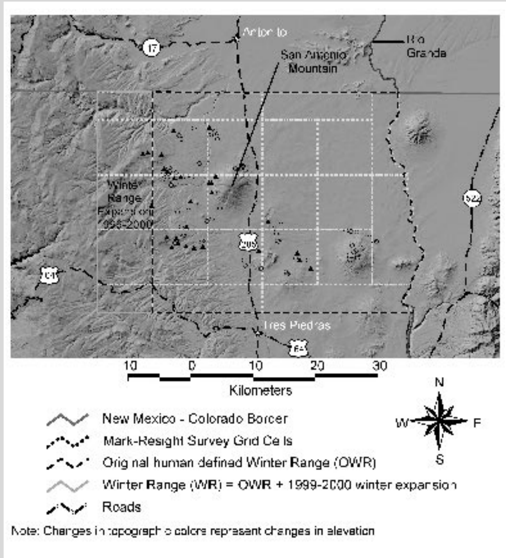

Figure 2. Mark-resight grid cells used to conduct aerial surveys of elk wintering near San Antonio Mountain, New Mexico, during the winters of 1998/99, 1999/2000, 2000/01. Circles indicate initial radio collar distribution and triangles indicate placement of additional radio collars during the second year.

(OWR) that we investigated encompassed a 1,437 km^2 area in NMDGF Game Management Units 4, 50, and 52 in the counties of Rio Arriba and Taos that was expanded to 1,748 km^2 in the 1999-2000 winter to accommodate a western shift in wintering elk location likely due to lower snow levels (Fig. 2). The OWR and expanded winter range (WR) is primarily comprised of federal and state administered lands with only 18 and 13%, respectively, in private ownership.

Annual precipitation for the area ranges from 25 to ~ 90 cm. The majority of precipitation accumulation occurs from April through October. Annual snowfall ranges between 50 and ~ 200 cm. Air temperature varies from a mean minimum range of -18˚C to -11˚C in January to a mean maximum range of 24-33˚C in July. The landscape ranges from Great Basin scrub and grassland and pinon-juniper *Pinus-Juniperus* woodland at lower elevation (1,850-2,100 m) to spruce-fir *Picea-Abies* forest and montane grassland at the highest elevation (Dick-Peddie 1993). Landscape features within the area include canyons, elevated plains, simple slopes, scarps, hills, mesas, sub-alpine and alpine meadows, and mountains.

Methods

Aerial survey

We used a helicopter net-gun method (Jessup et al. 1988) to capture and mark 75 elk in December 1998 with highly visible white 3-inch (7.6 cm) wide collars containing Very High Frequency (VHF) radios. We captured and radio-collared 30 supplemental elk in January of 2000 to replace any mortalities and collar failures that had occurred previously. In the first wintering season, collars were distributed throughout the study area (see Fig. 2) with a goal of attaining a 20% bull representation in the collared elk population to obtain a sufficient number of bulls for other purposes (e.g. evaluating migration timing and origin of animals). The wintering elk population consists of an interstate herd from southern Colorado, migrants from surrounding areas in New Mexico, and year round residents. In the second wintering season, animals on and off the OWR (see Fig. 2) were captured and collared due to the change in wintering location of a substantial portion of the population.

We conducted helicopter resight surveys (Bell 206B Jetranger and Bell 206L Longranger) in which a helicopter pilot, a primary and a secondary observer visually detected and counted the number of marked elk (radio-collared) and unmarked elk in areas randomly selected for surveying. Four mark-resight helicopter surveys were conducted during the winters of 1998/99, 1999/2000, 2000/01 at 7-10 day intervals to reduce interdependence of day-to-day locations. Aerial telemetry flights were conducted concurrently via fixed-wing airplane to determine the number of marked elk in areas surveyed (and thus the number of marked elk missed). After completing radio-tracking in the survey area, all other radio-collared elk were located via fixed-wing airplane to determine their proximity to the study area.

Because our study area was too large to survey completely within a day, we partitioned the area into 18 quadrats using latitude and longitude coordinates to define corners. Most quadrats were similar in size (~ 78 km^2), but collectively ranged within 38-120 km^2 (15-46 mi^2) in size (see Fig. 2). We selected a simple random sample of seven quadrats for each mark-resight survey, although we were not able to survey all seven on every occasion. For the winters of 1998/99 and 2000/01, 18 grid cells were available, whereas 23 cells were available for the 1999-2000 winter surveys due to weather-related elk distribution changes. Specifically, elk distribution had shifted decidedly west from the previous year which made it necessary to add five grids cells onto the western boundary of the OWR to contact the majority of elk wintering near San Antonio Mountain (see Fig. 2). Cells were flown in an order that minimized ferry time between adjacent or closely positioned cells and maximized survey time while considering logistics of refueling stops and rest breaks. Marked elk were considered available for detection if they occurred in a grid cell selected for survey on that given day.

Helicopter speeds approximated ≤ 90 $km.h^{-1}$ in dense cover, 55-90 $km.h^{-1}$ in mixed cover, and 90-130 km. h^{-1} over open flat grasslands at about 46 m above ground level (AGL) over heavy and mixed cover and 76 m AGL over open grasslands. We (pilot and observers) attempted complete aerial coverage of each randomly selected survey cell. Wind direction, sun position and logistics influenced cardinal direction of flight path and ensured safety, observer advantage, and fuel and flight time efficiency. Transects were spaced at approximately 350-m intervals in open cover with course and spacing maintained and aided by GPS receiver moving map display, onboard compass, grid cell corner waypoints and geographic features. We decreased transect spacing with increasing cover.

Estimation

We adopted a 'superpopulation' approach to estimation (Kendall 1999) because elk were sampled at two different scales. First, we randomly selected portions of the originally-defined study area for conducting counts of marked and unmarked animals, thus the presence of marked elk in the surveyed area was randomized, in a sense mimicking random emigration from the wintering area. At this smaller spatial scale, not all marked elk present in the study area were available for detection in our surveys, but their presence or absence was a random process resulting from our random sampling of the study area. Knowledge of the number of marked elk available in the study area, M', is necessary for population estimation of the study area.

At a larger spatial scale, marked and unmarked elk are variable in their return to the defined wintering area within and among years. Thus, there is a superpopulation of elk that have a potential to reside in the wintering area, but doing so depends on a variety of factors including environmental conditions (e.g. snow depth) and elk behaviour. Thus, the superpopulation is a group of elk that is not associated with a specific land area at any one time; rather it is a group of elk that share a common tie to wintering at some point in the vicinity of San Antonio Mountain. That is to say that the animals that comprise the superpopulation have a non-zero probability of being located and detected on the study area during the wintering survey periods. If one can consider the presence or absence of an individual on the wintering area as a random process, then it is still possible to estimate the superpopulation size. The validity of this assumption is addressed in the discussion.

Under the typical superpopulation scenario (Kendall 1999), the usual estimate of detectability, $\hat{p}$ is confounded with the probability of presence within the study area, τ, thereby resulting in an effective capture probability ($\hat{p}\tau$). However, because all marked individuals were located on each survey flight independently from the helicopter resight flight (hence we knew availability for marked animals), we were able to separately estimate availability and actual detectability in our helicopter resight survey. Superpopulation size for each resight flight can therefore be estimated by

$$\hat{N} = \frac{n_2}{\hat{\tau} \cdot \hat{p}_{detect/available}}.$$

Availability is estimated as $\hat{\tau} = \frac{M_i}{M}$ where M_i is the number of marked animals in the sampled areas from our defined study area and M is the total number of marked animals in the superpopulation. Conditional detectability (detection rate given availability) is esti-

Table 1. Original and expanded winter range (OWR and WR) elk population and superpopulation estimates ($\hat{N}$) for the winter survey periods 1998/99, 1999/2000 and 2000/01, San Antonio Mountain wintering area, New Mexico.

Estimation type	Year	No. Surveys	$\hat{N}$	80% C.I.	90% C.I.
Winter area					
OWR	1998/1999	4	6154	5366 - 7145	5173 - 7471
OWR	1999/2000	2	4984	3906 - 6338	3684 - 6864
WR	1999/2000	2	6974	5487 - 9139	5153 - 9928
OWR	2000/2001	4	7119	6185 - 8305	5956 - 8698
Super population	1998/1999	4	6447	5614 - 7493	5410 - 7837
	1999/2000	4	8611	6906 - 10985	6512 - 11823
	2000/2001	4	8178	7078 - 9572	6808 - 10033

mated as $\hat{p} = \frac{m_2}{M_i}$. The product of these two terms results in the estimator, $\hat{N} = \frac{n_2}{m_2/M}$, the familiar form of the Lincoln-Petersen estimator, (Petersen 1896, Lincoln 1930). Thus, we were able to use the JHE estimator for estimation of $\hat{N}$ where $\hat{N}$ represents the estimated superpopulation size of wintering elk. We used Program NOREMARK (White 1996) to analyze our mark-resight survey data. Population estimates for the OWR were also determined using the known number of marked animals on the OWR, M', in the denominator (as opposed to M) for comparison to previous NMDGF surveys. Note that $\hat{\tau}$ and $\hat{p}$ are not necessary for population estimation, but by estimating these quantities, we were able to consider the reliability of counts as indices to population size for population monitoring (e.g. see Yoccoz et al. 2001).

Results

Superpopulation estimates ranged within 6,400-8,600 for the three winter estimates (Table 1) and were derived by substituting the number of marked animals extant (Table 2) for the number of marked elk available on quadrats of a particular survey. Population estimates for OWR were 6,154 and 7,119 for two of the three winters and 6,974 for the expanded wintering area (WR) in the 1999/2000 winter (see Table 1). The WR estimate for 1999/2000 should be considered analogous to the 1998/99 and 2000/01 estimates for OWR. Considerable overlap among years is evident in 80 and 90% confidence intervals. These intervals are likely biased narrow, so the true overlap will be even greater. Estimates for the 1999/2000 winter survey period were made for OWR and WR separately as necessitated by changing the size of the area to be surveyed. Only two surveys each were performed on OWR and WR in winter 1999/2000 (see Tables 1 and 2).

Detectability, which is often considered a nuisance parameter, ranged from 17 to 69% among surveys (see Table 2). Within a wintering season, we observed up to 5-fold differences in elk numbers in the surveyed areas (see Table 2). Spatial variation in the quadrats selected and elk distribution are both contributing factors to this observed variation (as opposed to actual abundance). Proportions of marked elk available for detection also

Table 2. Mark-resight elk survey data for the winters of 1998/99, 1999/2000 and 2000/01, San Antonio Mountain wintering area (OWR), New Mexico. *: number of elk within quadrats surveyed was not discriminated with respect to entire study area.

Survey Date	Area sampled (km^2)	Unmarked elk counted	Marked elk counted	Marked elk in surveyed plots	Actual detectability	Effective detectability	Marked elk (OWR)	Marked elk extant
22/01/1999	256	424	7	18	39%	10%	68	71
29/01/1999	544	2005	26	43	60%	37%	68	71
12/02/1999	585	1782	20	35	57%	28%	67	71
20/02/1999	508	1051	5	29	17%	7%	69	71
28/01/2000	233	594	3	9	33%	11%		84
09/02/2000	311	247	3	6	50%	7%		84
21/02/2000	311	599	9	-*			74	83
03/03/2000	311	1314	12	-*			75	83
12/01/2001	388	1119	12	29	41%	19%	57	64
22/01/2001	388	2321	20	32	62%	32%	56	63
09/02/2001	430	2352	16	23	69%	25%	52	63
19/02/2001	388	1154	6	17	35%	10%	57	62

varied among surveys within a year and among years. Marked elk were considered available for detection if they occurred in a grid cell selected for survey on that given day. Distribution and activity of marked animals within the survey cells (e.g. lying under a tree or moving in open habitat) as well as the group size in which they existed likely were the greatest contributors to marked elk detection.

Weather, snow cover, animal distribution, helicopter considerations and randomly selected survey polygons influenced the area sampled and the number of elk encountered during surveys (see Table 2). Marked elk distribution was substantially contained in the original winter range (OWR; 1,437 km^2/555 mi^2) defined at the study's initiation and thus served as a reference for 1998/99 and 2000/01 population estimates. During the winter of 1999/2000, a significant portion of elk (marked and unmarked) were located west of the original study area western boundary ($P < 0.001$, 100,000 iterations, multiresponse permutation procedure; see Mielke & Berry 2001). Thus we included an additional expansion area (311 km^2 /120 mi^2) in the latter two mark-resight surveys for 1999/2000 (see Fig. 2). Total number of marked animals known alive remained fairly constant within survey years, but differed among survey years. During the 1998/99 winter survey, 71 marked animals existed in the superpopulation, 83 marked elk were extant in 1999/2000, and 63 marked elk were alive during the 2000/01 survey.

Marked elk moved throughout the OWR during the resighting surveys. This movement suggests that marked and unmarked animals mixed over the survey period, an assumption of mark-recapture methods. Marked animals were also found outside the OWR during winter resight surveys. For example, in the first wintering period (January-March of 1999), the percentage of marked animals on the OWR varied between 80 and 100%. Thus, we suspect that unmarked animals outside the OWR that are considered part of the superpopulation are likely to move onto the OWR during the wintering period and therefore are available to be detected.

Discussion

Our mark-resight population estimates suggested an OWR population approximately 2-3 times greater than that considered by NMDGF personnel (previously estimated at 1,500-3,000) which relied on aerial counts over the entire study area assuming 100% detectability. From a cost perspective, previous survey methods were more efficient because they avoided the time and costs involved with capturing and collaring elk. However, the added benefit derived from marking animals was, in our opinion, worth the additional cost for several reasons. Radio-collared animals allowed us for instance to examine movement patterns (migratory and otherwise) and to determine summer origins of animals on the wintering area. While these components were not the focus of this paper, they were valuable in better understanding the system. Secondly, use of radio collars also allowed us to estimate detectability, that enabled us to assess the potential degree of bias in previous population estimates that assumed 100% detectability. It is possible that our estimates are also biased, but by using mark-resight estimation methods, we are able to assess the degree to which such a bias might occur (see discussion below).

We believe that the precision of our population estimates (see Table 1) is reasonable given the relative size of the population and the biological and logistical complexity associated with estimating a large, mobile population over a large area. The mere fact that our methodology provided measures of precision was an improvement over previous methodology on our study area. Improvements in precision can be made in a variety of ways. The greater the number of resighting events, the greater the precision, although the degree of improvement decreases with successive events. We selected four resight flights on the basis of money available and simulations prior to study initiation via program NOREMARK, which showed variance reduction as a function of number of resight events. Improvements in precision can also be made by increasing detectability. For instance, we could have flown at slower speeds and perhaps used a narrower flight path in our quadrats. However, this may have resulted in less area covered or multiple days of flying which would increase the risk of double counting.

Detectability estimates were not necessary for the population estimation we performed at two levels, however, we suggest such estimates are valuable when interpreting aerial count data (unadjusted for detectability) used for monitoring purposes. Our observed variability in detection rates violated the constant proportionality assumption that indices rely on when interpreting population trends. Recent debate regarding the value of indices (Anderson 2001, 2003, Engeman 2003) and our results should prompt consideration of the value of aerial counts uncorrected for detectability. Despite using the same personnel, time of year, flight equipment and survey protocol, maintaining a constant proportion of detectability was not achieved. Factors that likely contributed to this variation include, among others, spatial variation in areas surveyed, location of animals with respect to cover and topography.

By randomly sampling our study area, we violated the geographic closure assumption of the JHE estimator. However, because we randomly sampled the study area, we were able to apply the conclusion from Kendall (1999) that random movements in and out of a population do not bias estimates of our study area. In his presentation, Kendall (1999) states that availability and detection probability are confounded unless detectability is determined from the robust design. In our case, however, we were able to estimate availability and detectability separately because we located all marked animals within the study area using a separate radio-telemetry flight. Neal et al. (1993) developed a modified form of the JHE when marked animals move in and out of the study area between surveys, called the immigration/emigration joint hypergeometric estimator (IEJHE). The IEJHE explicitly models presence on the study area as a binomial process and estimates the superpopulation as well as the average number of animals on a study area over the sampling interval. The IEJHE yields equivalent superpopulation estimates to the JHE with negligible differences in confidence interval widths.

Because the elk we radio collared were located on the OWR when captured during the first year, they may have been more likely to be present on the OWR during our aerial surveys that winter, inducing a positive correlation between capture and resight probabilities, thus leading to an underestimate of the superpopulation, which includes animals proximate to the OWR. Such an occurrence may explain the lower estimated superpopulation size in 1999. Examination of marked animal locations reveals that as much as 20% of the marked animals were not located on the OWR at some time during the winter period. Thus, animals are moving on and off the OWR over the winter (i.e. not due to migration).

Original capture on the OWR is less likely to be correlated with resight probability in subsequent years. In the second year, 37-57% of the marked animals were not on the OWR at certain times of the wintering period. That result, coupled with the placement of a few additional radio collars on animals outside the OWR in the second collaring phase, suggests that possible bias in superpopulation estimates may not be substantial. We suggest that when superpopulation estimation is the main research objective, an effort be made to radio-collar animals outside the defined study area, but within a reasonable distance so as to consider those individuals part of the superpopulation. Knowledge of possible or likely traveling distances of the study animal must be considered in such definitions.

Elk are gregarious and thus, animals did not have independent sighting probabilities. However, this should not have caused a bias in our estimates; rather it will have resulted in lower confidence interval coverage (Neal et al. 1993). We eliminated the concern about double counting of individuals by carefully noting the location of detected groups prior to resuming transect flight within our sampled areas. By sampling the study area within a single day as opposed to surveying the area over several days, we eliminated the greater potential for double counting of marked animals under the latter scenario. An alternative scenario might be to fly transects throughout the study area, thereby potentially increasing the number of animals contacted. Given the size of our study area, several days would be required to survey the entire study area, thereby increasing the probability of double counts of marked animals.

Collared animals may have been recorded as unmarked animals. Bear et al. (1989) reported a 36% positive relative bias in mark-resight population size estimates attributed to misclassifying collared elk in one circumstance in which the true population size was known. To investigate the effects of such occurrences on our estimates, we examined the differences between the known number of marked animals on the quadrats surveyed and the number detected. For example, in the 2000/01 survey, there was an average of 12 marked animals that went undetected in the helicopter survey (range: 7-17). Assuming that one-third of this average (4) was misclassified as unmarked animals, estimated population size would be 6,372 elk (90% CI: 5,470-7,554). Thus our estimate assuming no misclassification of marked animals would have a 28.3% positive bias relative to the adjusted population size estimate.

Implicitly, we have also assumed no measurement error in our counts, i.e., all animals seen were recorded once. While we know this to be false based on comparisons of photos and count records, the degree of counting errors observed had negligible effects on our abundance estimates. However, see Linklater & Cameron (2002) in which they reported substantial potential for double counting wild horses *Equus caballus* from helicopter surveys.

Animal behaviour is one of many factors not under researcher control that can greatly affect data retrieved from surveys. We suspect that elk wintering distribution depends greatly on weather conditions that dramatically affect timing and extent of elk movement into the wintering area as well as the actual location on the wintering area. The advantage of our superpopulation approach to estimation is that it provides an indication of potential elk presence during more severe winters. Such an estimate has significant predictive value for management planning and for considering potential severity of resource conflicts with differing stakeholders in and around our study area.

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