Use of aerial distance sampling to estimate abundance of tule elk across a gradient of canopy cover and comparison to a concurrent fecal DNA spatial capture-recapture survey

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FULL RESEARCH ARTICLE

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Abstract

Historically, aerial surveys have been used widely to monitor abundance of large mammals in the western United States. In California, such surveys have typically served as minimum count indices rather than true abundance estimates. Here, we evaluated the utility of aerial multiple covariate distance sampling (MCDS) to estimate abundance of three populations of tule elk (*Cervus canadensis nannodes*) in northern California. We also compared estimates and costs with published results from a concurrent fecal DNA spatial capture-recapture (SCR) survey. During December 2018 and 2019, we flew line transects for distance sampling of tule elk in Colusa and Lake counties. We modeled detection functions and evaluated effects of group size, canopy cover, and survey year. We averaged the top models comprising ≥0.95 of Akaike Model Weight and estimated abundance of both total and discrete populations. Detection probability increased with increasing group size and decreasing canopy cover. We estimated a two-year average total population size of $\hat{N}$ = 674 elk (90% CI = 501–907) in our survey area which was similar to $\hat{N}$ = 653 elk (90% CI = 573–745) from SCR estimates. Overall precision was greater (CV = 0.08; range = 0.11–0.30 by population) for SCR than for MCDS (CV = 0.18; range = 0.22–0.43 by population). Although estimates differed somewhat between methods for the individual populations, the combined estimate across the study region compared favorably. Total cost of SCR and MCDS surveys was $98,326 and $147,324, respectively. While SCR efforts were more precise and less expensive overall, our MCDS approach reduced staff time by 64% (587 person-hours) and the number of survey days by 87% (64 days). Our results suggest MCDS methods can produce reliable abundance estimates across a gradient of canopy cover, particularly when observations can be pooled across populations to decrease variance. We recommend future research to assess use of hybrid models, such as mark-recapture distance sampling or hierarchical distance sampling, to improve precision and estimation of detection probability.

Key words: abundance estimation, *Cervus canadensis nannodes*, density, fecal DNA, method comparison, line transect, multiple-covariate distance sampling, population assessment, spatial capture-recapture, survey design

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Introduction

Reliable estimates of population abundance are essential to assess demographic status, understand factors related to population persistence, and advance conservation and management strategies (Pollock et al. 1990; Lancia et al. 2005). However, large mammal population monitoring in much of the western United States has conventionally relied upon indices of abundance (e.g., minimum counts, sex ratios), rather than true estimates, to inform conservation and management activities (Mason et al. 2006; Falcy et al. 2016). Indices assume constant spatial and temporal detection (Williams et al. 2002), have variable relationships to true abundance, and frequently are unassociated with any measure of uncertainty (Pollock et al. 2002; White 2005). Understanding uncertainty associated with sampling, for example the probability of detecting the target species during the survey period, is a critical component for reducing bias and improving precision of abundance estimates (Williams et al. 2004). Further, the absence of associated uncertainty, and thus, a lack of bounded statistical estimates, precludes inference of a population’s trajectory over time. Therefore, the overall value of indices to applied management is generally limited (McCullough et al. 1996; Bleich et al. 2001; Schoenecker and Lubow 2016) with some exceptions (Johnson 2008; Stephens et al. 2015).

Over the last few decades, state and federal wildlife agencies have increased efforts to incorporate statistically robust survey methods that account for imperfect detection and quantify uncertainty into population monitoring programs (e.g., Williams et al. 2002; Lancia et al. 2005; Mason et al. 2006; Trausch et al. 2020). These methods include mark-resight (White and Shenk 2001; McCorquodale et al. 2013), sightability correction (Bleich et al. 2001; Dyal et al. 2021), and distance sampling (Burnham and

Anderson 1984; Buckland et al. 2001, 2004, 2005; Oyster et al. 2018). For large mammals, these methods often are employed during aerial sampling of spatial units (e.g., plots, quadrats, transects) and documenting occurrences of target species and covariates that may influence detections (e.g., group size, habitat type, weather conditions, etc.). However, each method uses a different approach to estimate detection probability: mark-resight models detection based on encounter histories of individually marked and unmarked animals observed (Bristof et al. 2018); sightability correction uses a cohort of marked animals to compute detection heterogeneity based on covariates that influence detection, but only during an initial calibration period (Griffin et al. 2013; Schoenecker and Lubow 2016); distance sampling measures the perpendicular distance of individual or group detections from the centerline of the sample transect which is then fitted with a detection function (Buckland et al. 2004, 2005; Crum et al. 2021). Once detection probability is estimated, users can produce a bounded statistical estimate of population abundance that can be used to monitor populations and rigorously assess change over time.

Although mark-resight, sightability correction, and distance sampling can adequately estimate abundance statistics, distance sampling may be more feasible to implement than mark-resight or sightability correction in many circumstances. For example, mark-resight and sightability correction require a portion of the population to be marked (i.e., ear-tagged, GPS collared, etc.) prior to surveys, which is not always practical due to time, cost, and access constraints. Further, distance sampling has more relaxed assumptions than mark-resight (e.g., equal detection probability among marks; McCorquodale et al. 2013; Bristow et al. 2018, but see McClintock et al. 2006 and McClintock and White 2010 for options for dealing with heterogeneity) or sightability correction (e.g., estimated covariate relationships are constant over time; Williams et al. 2002). The primary assumptions of line transect distance sampling are that animals on the transect are perfectly detected, that distances to detected animals are measured accurately prior to any movement in response to the observer, and that all attributes (i.e., group sizes, canopy cover) are recorded without bias (Buckland et al. 2001, 2004, 2005; Crum et al. 2021). As with mark-resight and sightability correction methods, distance sampling allows for modeling detection probabilities as a function of covariates (in addition to distance from the transect) (Buckland et al. 2004). Aerial distance sampling can thus be readily applied across a variety of settings (Williams et al. 2002; Buckland et al. 2004) and has been applied to estimate abundance of marine mammals (e.g., Bonnell and Ford 1987; Evans et al. 2003; Andriolo et al. 2006; Bröker et al. 2019), seabirds (e.g., Heinänen et al. 2017), and terrestrial herbivores (e.g., White et al. 1989, Johnson et al. 1991, Whittaker et al. 2003, Cairns et al. 2008, Lethbridge et al. 2019). Distance sampling, however, has never been evaluated for utility in monitoring populations of tule elk (*Cervus canadensis nannodes*), a subspecies of elk endemic to California, which occupy a suite of habitats that differ greatly from those occupied by other elk subspecies (McCullough 1969; Bleich et al. 2001; CDFW 2018). The utility of distance sampling to estimate tule elk populations may, however, be hindered by their gregarious nature (i.e., large group sizes and a small number of group detections) and by habitat heterogeneity within areas occupied by discrete populations (CDFW 2018; Batter 2020). Given these potential constraints, efforts to evaluate the utility of distance sampling for tule elk would be enhanced with a comparison of an independent population estimate using other methods. Recently, non-invasive fecal DNA spatial capture-recapture (SCR) has proven to effectively estimate tule elk density and abundance in both captive and free-ranging populations (Brazeal and Sacks 2021; Batter et al. 2022).

As part of a broader effort to establish repeatable and statistically rigorous long-term population monitoring protocols for tule elk, we initiated aerial surveys using distance sampling to estimate abundance of tule elk in three EMUs in north-central California and compared population estimates from distance sampling to population estimates from SCR generated for the same populations in the same areas (Batter et al. 2022). Our objectives were to: 1) use line-transect distance sampling with multiple covariates to estimate abundance of tule elk populations in northern California; 2) test hypotheses that distance, group size, canopy cover, and survey year affect detection probabilities; and 3) compare abundance estimates, cost, and efficiency of distance sampling with those from a concurrent fecal DNA study (Batter et al. 2022). We expected detection probabilities to decrease with increasing perpendicular distance from the transect, increase with increasing group size, decrease with increasing canopy cover, and be unaffected by year. We also predicted that estimates of abundance from aerial distance sampling would be comparable to estimates published from a concurrent fecal DNA capture-recapture study. Finally, we predicted aerial surveys would be more costly, but also more efficient in terms of personnel hours.

Methods

Study Area

Tule elk are the smallest subspecies of extant North American elk and are the least genetically diverse, owing to a severe genetic bottleneck that occurred when tule elk were nearly extirpated in the late 1800s—being reduced to as few as 3 animals (McCullough 1969; Meredith et al. 2007; Sacks et al. 2016). Through intensive management, tule elk have grown to number ~5,700+ across 22 Elk Management Units (EMUs) (CDFW 2018). The 5,723 km^2 study area lies within three EMUs located in the Northern California Interior Coast Range in Colusa and Lake Counties (**Fig. 1**). Our study populations included the oldest free-ranging elk population (Bear Valley/Cache Creek [BV/CC] EMUs) in north-central California (re-established in 1922) and two additional free-ranging populations at Lake Pillsbury (LPB; re-established 1978) and East Park Reservoir (EPR; re-established 1992; CDFW 2018). All three populations have gradually increased in number and spatial distribution since their re-establishment, and limited harvest of each herd occurs annually (CDFW 2018; Batter et al. 2021).

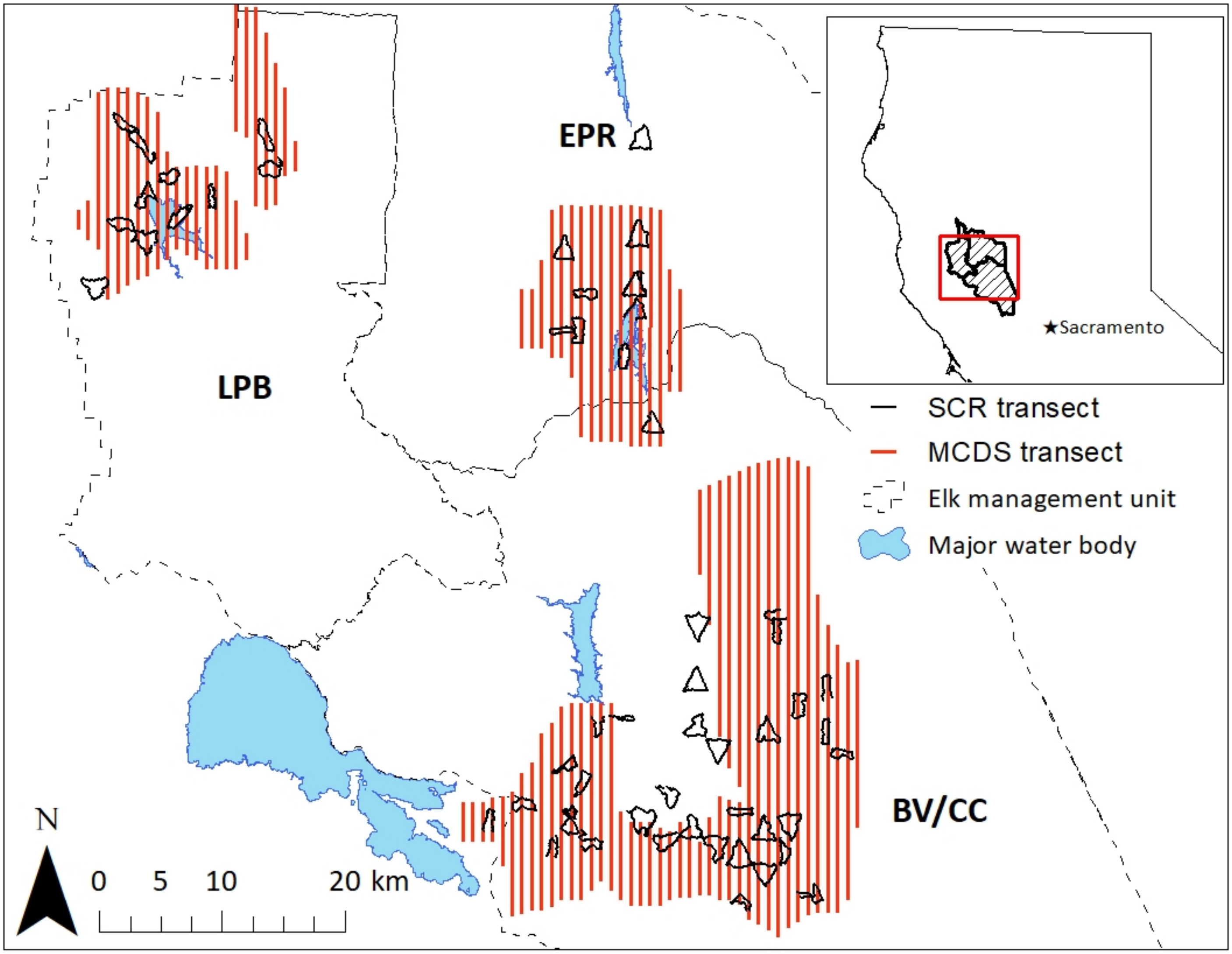

Figure 1. Survey area for tule elk in the Interior Coast Range of north-central California in Colusa and Lake counties. The Lake Pillsbury (LPB), East Park Reservoir (EPR), and Bear Valley/Cache Creek (BV/CC) Elk Management Units (EMUs) contain both helicopter survey (MCDS) transects spaced at 800 m intervals, flown in 2018 and 2019 to gather observation data for abundance estimation following line-transect distance sampling methodology as well as fecal DNA spatial capture-recapture (SCR) transects sampled in Jun–Aug 2017–2019 (Batter et al. 2022). Blue polygons signify major water bodies.

The climate is Mediterranean and characterized by hot, dry summers and mild, wet winters (Kauffman 2003). Average annual precipitation is ~76 cm, mostly occurring as rain from October through May. The landscape is rugged, with rolling foothills and grassy flats interspersed through broken peaks and ridges descending into narrow valleys; elevations range from 30–2,094 m. The dominant habitat types include blue oak (*Quercus douglasii*) woodland, annual grassland, chamise (*Adenostoma fasciculatum*) chaparral, chamise and redshank (*A. sparsifolium*) chaparral, montane hardwood conifer, blue oak–foothill pine (*Pinus sabiniana*) and agricultural lands (CDFW 2018). The landscape is made up of a mosaic of these habitat types, with private property predominantly made up of oak and open grassland in larger valleys and favorable upper slopes which grade into mixed grasslands and oak woodlands; public-administered lands are primarily composed of chaparral communities along dry, steep slopes, with smaller patches of oak woodland and mixed hardwood occurring intermittently. The primary private land uses are cattle ranching and crop production with public lands reserved for outdoor recreation including hunting, fishing, hiking, horseback riding, and wildlife viewing.

Multiple Covariate Distance Sampling Survey Design

We adapted and applied aerial line-transect distance sampling (Buckland et al. 2001, 2004) to survey for elk. To guide survey efforts, we referenced spatial data from past aerial surveys, ground-based fecal DNA monitoring surveys (Batter et al. 2020, 2022), and 63,727 location data points from 78 collared elk (39 bull; 39 cow, Feb 2017–Nov 2018). Within the study area, we mapped flight polygons and placed north-south oriented line transects at 800-meter intervals from east to west within the boundaries of the survey polygon (**Fig. 1**). Survey polygons bounded all location data points, buffered by an additional 1.6–8 km on the periphery of these locations, intended to increase the likelihood of detecting elk expanding from their historic and known range (e.g., transient males). Given tule elk life-history traits (i.e., preference for open habitat; McCullough 1969), we excluded large tracts of conifer-dominated plant communities from survey polygons, where elk use is presumed limited and aerial visibility low, to increase survey efficiency (Weckerly and Kovacs 1998; CDFW 2018).

Data Collection

We flew surveys from 3–6 December 2018 and 3–16 December 2019. We performed a single survey in 2018 and two replicate surveys in 2019 to increase precision in estimates of detection probability and abundance while allowing sufficient time between surveys to maintain independence of detection. Within each survey polygon, a Bell 407 helicopter was flown approximately 40 m above ground level with airspeed maintained at 30–40 knots and followed the topography of the landscape along transects. Flight crew consisted of three observers in addition to the pilot. Observers visually scanned the landscape for elk on either side of the aircraft. When elk were located, the pilot deviated the aircraft from the transect and flew to the location of the observed elk. Observers then counted the number of elk in a group and recorded group composition, that is we tallied the numbers of bulls, cows, and calves. We collected a waypoint at the center of locations where we detected groups of elk and we visually estimated percent canopy cover (COVER), in the location where elk were first detected (plus a 10-m radius buffer). Percent canopy cover was estimated in 5% increments from 0–100%, based on a reference schematic (**Supplementary Fig. 1**). The aircraft then returned to the transect at the point of deviation and we continued the survey. We determined the distance from the transect to the elk using rangefinders for 24 observations in 2018 but owing to difficulties in getting accurate ranges through helicopter windows in rugged terrain, we abandoned rangefinders and measured distance from the transect to GPS locations of elk groups after completing surveys. To do so, we measured the perpendicular distance in meters from the transect to the waypoint for each detection using the “Ruler” tool in Google Earth (Google, Inc. 2005).

Data Analysis

We estimated population size using multiple covariate distance sampling (MCDS; Buckland et al. 2001, Buckland et al. 2004). In MCDS, the detection probability of an object is modeled as a monotonically decreasing function of the perpendicular distance from the survey transect to the object. In clustered populations such as elk, the objects consist of groups of animals detected together. Recommended model forms for MCDS are the half-normal and hazard-rate models each with a scale parameter σ (> 0) governing how rapidly detection declines with distance. The hazard-rate model has an additional parameter determining shape as well. To incorporate the effects of covariates such as tree cover on detection probability, $\log \sigma$ is modeled as a linear combination of covariates associated with detection of the object (Buckland et al. 2004; Miller et al. 2019). Based on preliminary modeling without covariates we found that the half-normal model was more predictive for our distance data and used this model form in subsequent modeling.

We selected covariates for potentially explaining variation in the scale parameter. For concealing cover, we considered two covariates. COVER was our ocular estimate of concealing cover recorded during surveys. We also calculated COVER50, an estimate of the mean tree canopy cover over a 50-m radius of detection waypoints, from the LANDFIRE Existing Vegetation Cover database (LANDFIRE 2013). In preliminary modeling, we found COVER was more predictive than COVER50 and used COVER for subsequent modeling. To account for potential effects of group size on detection, we included the covariate SIZE equal to the number of elk in a group and scaled by the mean and standard deviation. To account for potential differences in detection probability between years of the survey, we included the covariate YEAR.

We fit covariate detection probability models to ungrouped detection distance data pooled from all three replicate surveys. We fit 8 candidate models for detection probability representing all combinations of the COVER, SIZE and YEAR covariates including the null model ($\sigma \sim 1$) using maximum likelihood estimation via R statistical software (version 3.5.2, R Core Team 2019) and the Distance package (Miller 2017). We tested each fitted model for goodness-of-fit using an unweighted Cramer-von Mises test of the hypothesis that distance data were generated by the fitted model and discarded any models with significant fit test statistics ($P < 0.1$; Buckland et al. 2004). For each fitted model, we also calculated Akaike's Information Criterion (AIC) and Akaike model weights indicating the degree of support for each model explaining the data relative to the other candidate models. We then selected the models with the lowest AIC and comprising at least 0.95 of cumulative model weight (Burnham and Anderson 2002).

Following the methods of MCDS, we used each selected detection probability model to estimate the individual probabilities of all observations. We then summed group sizes divided by their respective detection probabilities in a Horvitz-Thompson-Like estimator to obtain EMU-replicate-specific population estimates of the covered area for each detection probability model (Buckland et al. 2015; Miller et al. 2019). Because we were interested in establishing a method useful for assessing long-term population trends (rather than inter-year fluctuations), we combined replicates within model and EMU using a weighted average with weights 0.5 for 2018 and 0.25 for each of the two 2019 replicates. We then combined these into EMU-specific and total population estimates using model-averaging based on the AIC weights. Additionally, we model-averaged model-specific predictions of mean group size and mean detection probability from the selected detection probability models to obtain estimates of mean group size and detection probability for the study area. We computed standard errors for population estimates using the R2 estimator of Fewster et al. (2009) with the variation of Innes et al. (2002). We did not use a finite population correction for estimates of population size (Buckland et al. 2001) because we were interested in the precision of our methods irrespective of the relative sizes of the sampled area and study area. Using the standard errors we calculated 90% confidence intervals for all estimates consistent with a long-term monitoring objective (Gibbs et al. 1998; Bart et al. 2004; Nielson et al. 2009).

We assessed the predicted effect of concealing cover on detection probability. For COVER values of 0, 20, 50 and 80%, we computed the distance-detection probability curves as predicted by the COVER model. We also assessed the relative importance of the COVER, SIZE and YEAR covariates by computing relative importance weights. The relative importance weight of a covariate was the sum of the model weight for each of the 8 candidate models containing the covariate (Burnham and Anderson 2002).
We evaluated the power of annual application of our distance sampling survey to detect long-term

population trends. The power (1-Type II error rate) or probability of a population monitoring program to detect a trend depends on the size, shape (e.g., linear vs. precipitous) and duration of the trend, the CV of survey estimates, and the type and significance level (Type I error rate) of the statistical test for the trend. To assess the effect of trend size on power we simulated scenarios of non-random log-linear (exponential) population declines of 25–75% occurring over 10 years. To assess the effects of sample effort, we either matched the current effort of 3 replicates over 2 years or doubled the effort to 3 replicates every year. For each scenario, we simulated 1,000 sets of population estimates with independent normally distributed errors using a constant CV based on the CV from our completed surveys and inversely proportional to the square root of sample size. In each simulation we used linear regression to estimate the population trend and detected the population decline if the two-tailed t-test of no slope was rejected at the 0.1 significance level. The power to detect the decline in each scenario was the proportion of simulations in which the decline was detected. We compared this estimate of power to an 80%-power monitoring standard that has been proposed elsewhere for assessing the adequacy of wildlife monitoring programs (Bart et al. 2004). We noted that the reverse of declines of 25–75% were increases of 33–300% so that it was unnecessary to repeat the power analysis for population increases.

Fecal DNA Spatial Capture-Recapture

We compared abundance estimates derived from aerial MCDS surveys to independent estimates from a fecal DNA SCR study conducted on the same populations from Jun–Aug 2017–2019 (Batter et al. 2022). Methods used in the SCR study were detailed in Batter et al. 2022. Briefly, 98 sample transects (4–6 km each) were established throughout the known range of the BV/CC, LPB, and EPR EMUs based on random selection of 4 km2 grid cells stratified by predictive habitat quality. Fecal pellets were collected and stored in >95% ethanol prior to laboratory analysis and fecal DNA was analyzed using 20 microsatellite markers and a sex marker then genotypes were assigned to individuals (Sacks et al. 2016; Batter et al. 2021). Transect segments were discretized at 75 m intervals and used as “traps”; capture-recapture histories were then constructed for each individual at each trap. For each population, data were modeled using the R package *secr* (v. 4.2) (Efford 2004) and abundance estimates generated using the Region.N function applied to the MCDS sampled area for each population. We computed 90% confidence intervals for the population estimates.

Total Cost, Cost Effectiveness, and Efficiency Comparison

We compared total costs, cost effectiveness, and efficiency of MCDS and SCR survey methods. To compare total costs, we compiled the direct cost associated with field work and analysis for each survey method. Total costs included staff time and travel, contractor work and travel, and sampling associated lab analyses. We calculated the costs for two personnel per transect to perform these surveys. Staff time was recorded to the nearest half hour, and travel times were averaged based on a central location of all staff.

Results

Multiple Covariate Distance Sampling

We flew 272 transects including replicates for a total distance flown of 3,351 km over an area 2,681 km^2. We recorded 156 detections of elk groups, ranging in size from 1–120 animals (median = 4; **Supplementary Fig. 2**), for a total minimum count of 627 elk in 2018 and 516 elk in 2019. In both years and replicates, the highest counts were in Bear Valley followed by Lake Pillsbury, Cache Creek, and East Park Reservoir (**Table 2**). Distances to detected groups ranged from 0–393 m with 49 groups at <100 m, 39 at 100–200 m, 39 at 200–300 m, and 29 at 300–400 m. Cover at detected groups ranged from 0–80% with a mean of 19% (**Supplementary Fig. 3**). The detection probability model with greatest support was σ ~ COVER with 41% of the model weight (**Table 1**). We selected five additional models to contribute to model-averaged estimates of detection probability and population size including all remaining models with the covariate COVER plus the σ ~ SIZE model and the null model (distance alone). Goodness-of-fit tests indicated adequate model fit for all models ($P_{GOF} > 0.1$).

Table 1. Model selection results for detection probability from aerial distance sampling surveys of elk in Colusa and Lake counties, CA, USA, December 2018–2019. Models in the top 0.95 of cumulative AIC weights (Total *w*) are shown here in bold type.

Detection model[a]	**K**[b]	**AIC**	**ΔAIC**	***w***[c]	**Total *w***	**P_{GOF}**[d]	**$\hat{N}$**
COVER	2	–294.8	0.0	0.412	**0.412**	0.987	672
COVER+YEAR	3	–293.8	1.1	0.243	**0.655**	0.987	690
COVER+SIZE	3	–292.9	1.9	0.158	**0.814**	0.988	647
COVER+YEAR+SIZE	4	–291.8	3.0	0.090	**0.904**	0.984	706
SIZE	2	–289.7	5.1	0.032	**0.936**	0.854	606
NULL (distance only)	1	–289.6	5.3	0.030	**0.966**	0.927	693
YEAR	2	–288.9	5.9	0.022	0.987	0.917	713
YEAR+SIZE	3	–287.9	6.9	0.013	1.000	0.853	607

[a] Detection models are named by covariates used to model detection scale parameter σ.
[b] The number of parameters in the model.
[c] The Akaike weight.
[d] P-value for goodness-of-fit test of model fit.

Table 2. Population estimates, standard errors, upper and lower confidence intervals, and coefficients of variation for aerial distance surveys of elk in Colusa and Lake counties, CA, USA, December 2018–2019.

EMU	**Count**[a]	**$\hat{N}$**	**SE**	**CIL90%**	**CIU90%**	**CV**
Bear Valley	214	253	72	160	400	0.28
Cache Creek	108	147	49	87	250	0.33

EMU	Count[a]	$\hat{N}$	SE	CIL90%	CIU90%	CV
Bear Valley+Cache Creek[b]	322	400	87	281	569	0.22
East Park Reservoir	95	109	47	55	215	0.43
Lake Pillsbury	148	165	70	84	323	0.43
Total	564	674	122	501	907	0.18

[a] Mean count observed across replicates.
[b] Bear Valley and Cache Creek EMUs were also modeled as one population to provide for a fair comparison with fecal DNA spatial capture-recapture models (**Fig. 4** and **Supplementary Table 1**).
We estimated a total population size of $\hat{N}$ = 674 elk (90%CI = 501–907; **Table 2**). Based on the top performing models, BV/CC abundance was estimated at $\hat{N}$ = 400 (90% CI = 281–569), followed by LPB at $\hat{N}$ = 165 (90% CI = 84–323), and EPR at $\hat{N}$ = 109 (90% CI = 55–215). Coefficients of variation for population-specific estimates were all ≥ 0.22 (range = 0.22–0.43), while the CV for the total estimate was 0.18. Mean cluster size for the survey was 9.7 elk (90% CI = 7.3–12.0). For elk groups within 400 m of a transect, mean detection probability was 0.79 (90% CI = 0.67–0.87).

The detection probability model σ ~ COVER predicted a significant effect of concealing cover on detection probability (**Fig. 2**). While detection probability decreased with distance from the transect at all levels of COVER, it dropped off more quickly as COVER increased. The average detection probabilities at the minimum (0%), mean (19%) and maximum (80%) levels of COVER were 0.93 (90% CI = 0.72–0.99), 0.85 (0.66–0.95) and 0.33 (0.19–0.56), respectively. Among all models, coefficients for the COVER covariate were significantly different from 0 ($P < 0.05$), while coefficients for the SIZE and YEAR covariates were not ($P > 0.1$; **Supplementary Table 1**). Covariate importance weights using the 8 candidate models were 0.90 for COVER, 0.37 for YEAR and 0.29 for SIZE.

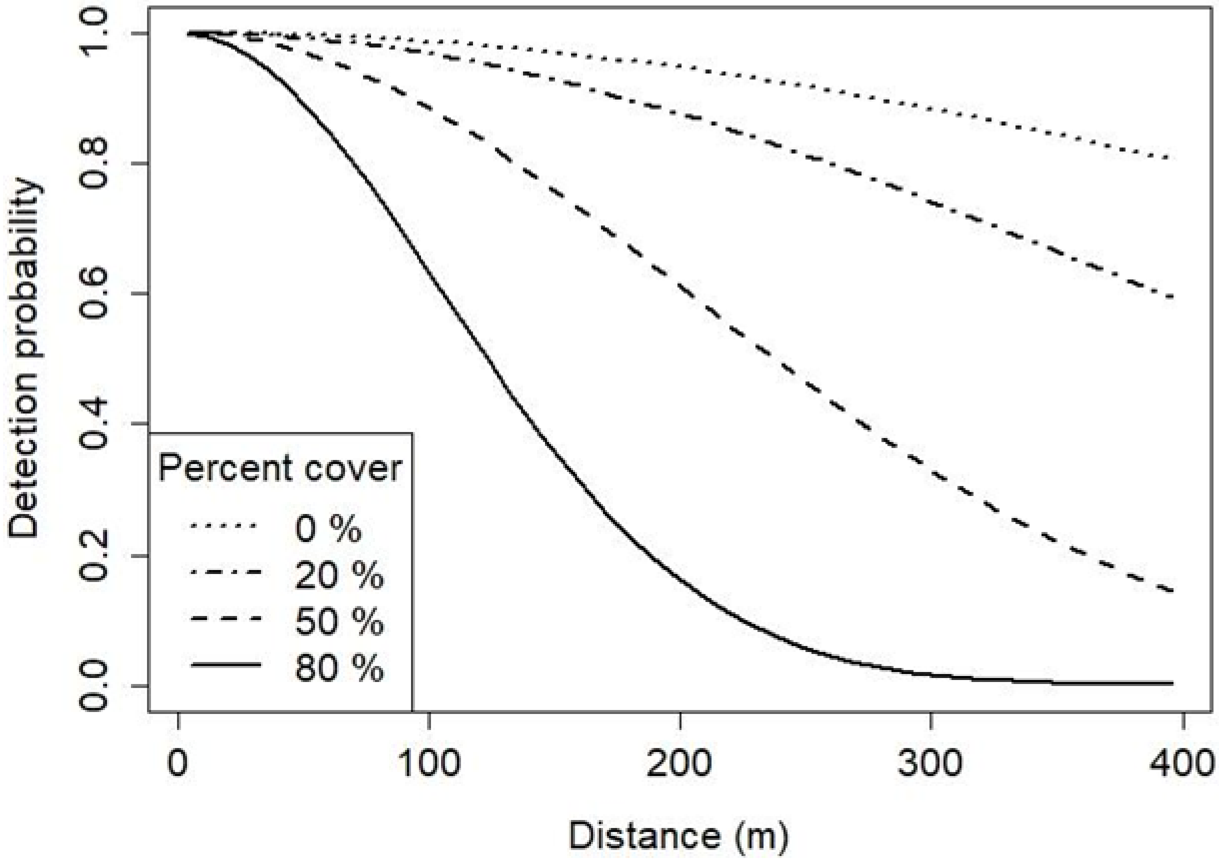

Figure 2. Joint effects of perpendicular distance and percent vegetation cover covariates on detection probability in aerial distance sampling surveys of elk in Colusa and Lake counties, California, USA, December 2018–2019.

The power analysis demonstrated how effectiveness of long-term monitoring with MCDS increased with size of the trend and sample size (**Fig. 3**). With a 10-year MCDS monitoring program at our original sampling effort (3 replicates over every 2 years), declines of $\geq$ 53% and increases of $\geq$ 108% or more were detected with 80% power. With doubled sampling effort (3 replicates per year) smaller trends could be detected with 80% power: declines of $\geq$ 40% and increases of $\geq$ 67%.

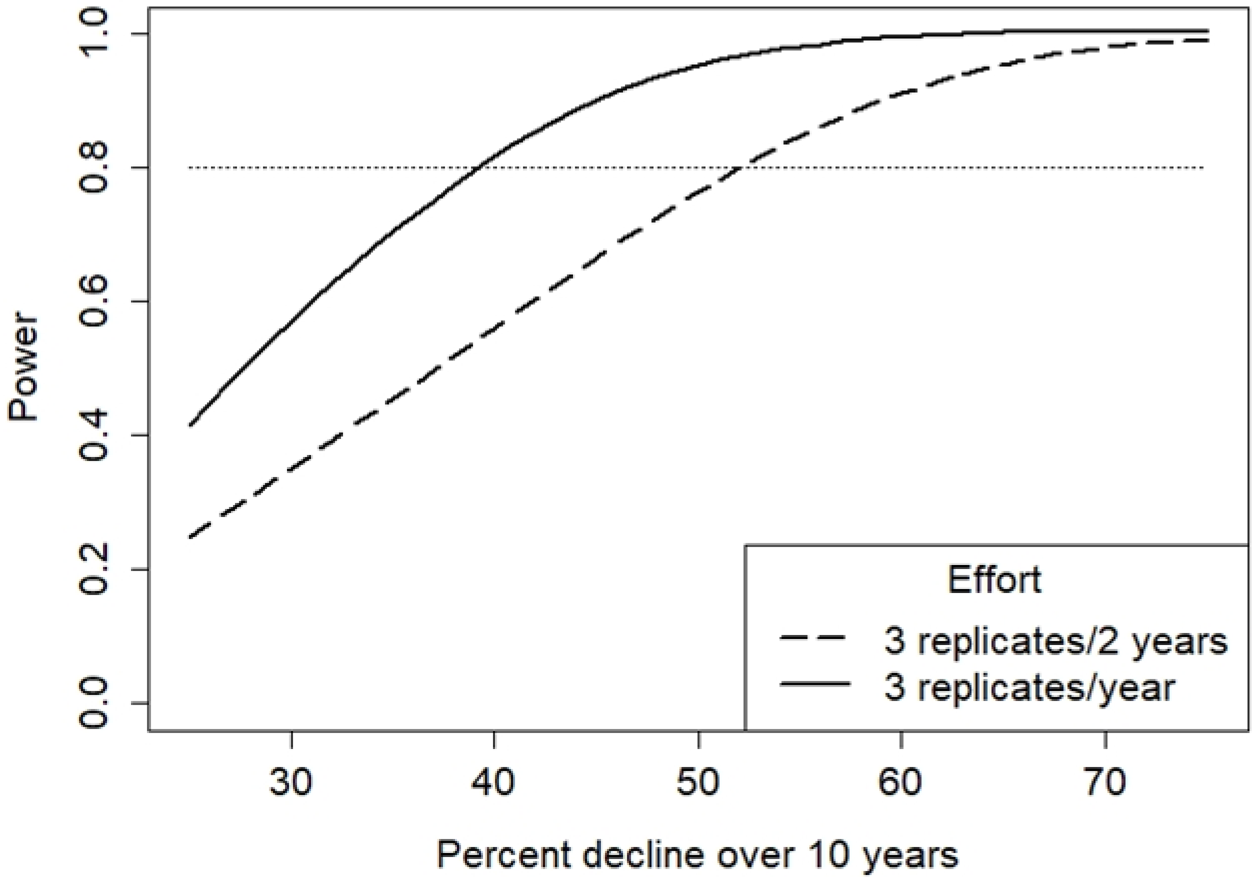

Figure 3. Power to detect declines in population size in aerial distance sampling surveys of elk in Colusa and Lake counties, CA, USA, December 2018–2019. Power to detect declines is shown as a function of decline sizes of 25–75% occurring over 10 years, and of survey effort of 3 replicates every 2 years (as in the current study) and 3 replicates per year (doubled survey effort). Points above the dotted line designate declines and effort that meet the 80%-power wildlife monitoring standard.

Fecal DNA Spatial Capture-Recapture

Independent SCR models yielded similar overall estimates of abundance as the MCDS models, although with greater overall precision (Batter et al. 2022; **Fig. 4**). Based on the top performing models, total abundance was estimated at $\hat{N}$ = 653 (90% CI = 573–745); BV/CC abundance was estimated at $\hat{N}$ = 324 (90% CI = 259–397), followed by LPB at $\hat{N}$ = 264 (90% CI = 199–339), and EPR at $\hat{N}$ = 65 (90% CI = 33–112) (**Supplementary Table 2**). However, differences in methods between the individual population estimates were more variable. All of the 90% CIs associated with MCDS estimates contained SCR point estimates for those same populations, but all MCDS point estimates fell outside the 90% CIs for the corresponding SCR estimates. Coefficients of variation for population-specific estimates for SCR models were ≤ 0.14 in the two populations sampled in two years (BV/CC, LPB) and 0.30 for the EPR population, which was only sampled in 2018 (**Supplementary Table 1**).

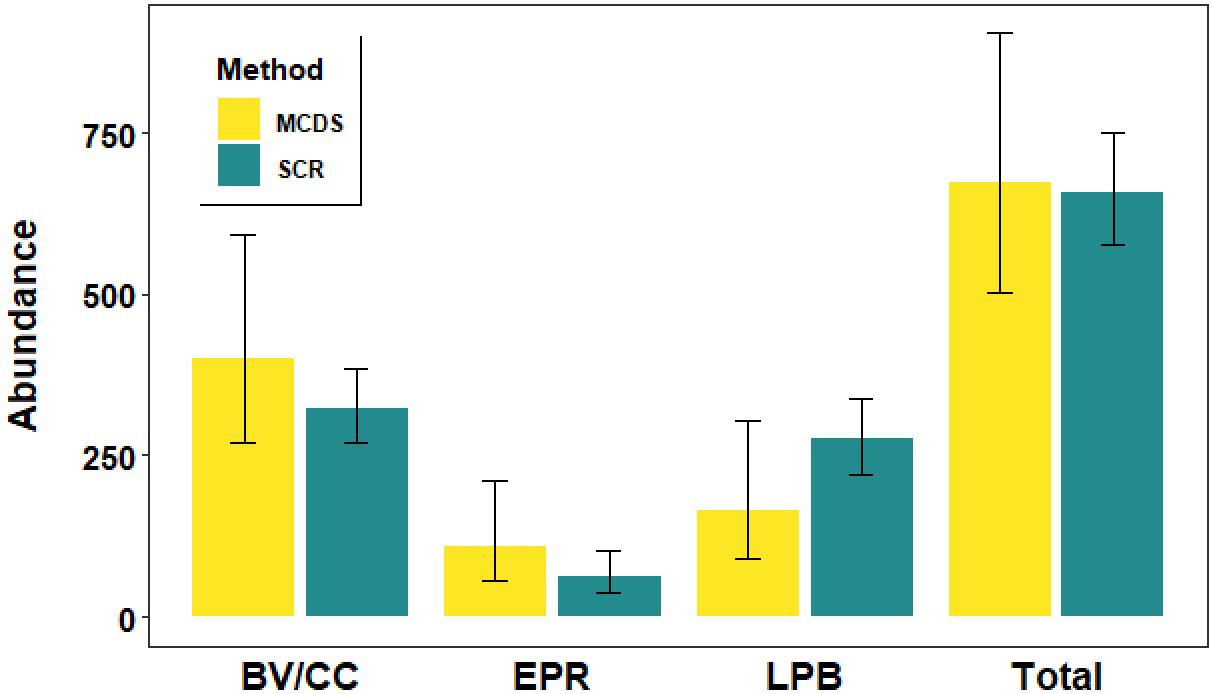

Figure 4. Comparison of two-year averaged fecal DNA spatial capture-recapture (SCR) abundance estimates (+/- 90% CI) to multiple covariate distance sampling (MCDS) abundance estimates (+/- 90% CI) for the Bear Valley/Cache Creek (BV/CC), East Park Reservoir (EPR), and Lake Pillsbury (LPB) Elk Management Units (EMUs) in Colusa and Lake counties, CA, USA 2017–2019 (SCR) and 2018–2019 (MCDS). The estimates for MCDS and SCR are shown in **Table 2** and **Supplementary Table 1**, respectively. The EPR population was only sampled for SCR in 2018.

Total Cost and Efficiency Comparison

Total cost (U.S. dollars summed across years) of obtaining $\hat{N}$ using SCR (2017–2019) and MCDS (2018–2019) was $98,326 and $147,324, respectively (**Table 3**). Lab analysis of fecal samples for SCR models is a set cost per sample and cost reflected the actual number of samples collected (n = 1,573). Field work using SCR totaled 74 survey days and covered 748 km while MCDS totaled 10 survey days and covered 3,336 km.

Table 3. Total cost (U.S. dollars, summed across years) of performing ground-based fecal DNA (fDNA) spatial capture-recapture (SCR) surveys and aerial-based multiple covariate distance sampling (MCDS) in Colusa and Lake counties, CA, USA, 2017–2019.

Table 3a. SCR ’17, ’19

Item	Cost($)/Unit	Units	Cost($)
Transect technician	$15/hr	923.8[a]	$13,857.00
Travel	$15/hr	294[b]	$4,410.00
fDNA processing	$45/sample	1,573	$70,785.00
CDFW employee mileage	$0.52/mile	17,836[c]	$9,274.72

Item	Cost($)/Unit	Units	Cost($)
Total			$98,326.72

Table 3b. MCDS ’18, ’19

Item	Cost($)/Unit	Units	Cost($)
Helicopter flight time	$1,700/hr	67.4	$114,580.00
Helicopter daily rate	$448/day	14[d]	$6,272.00
Per diem	$46/day	26[e]	$1,196.00
Hotel	$112.98/day	20	$2,259.60
Driver OT	$36/hr	28.5	$1,026.000
Pilot OT	$42/hr	23.75	$997.50
Helicopter fuel truck mileage	$2.45/mi	1,990	$4,875.50
CDFW personnel flight time (Env Sci)	$38/hr	202.2[f]	$7,683.60
CDFW personnel flight time (Sci Aid)	$15/hr	134.8[g]	$2,022.00
Travel time (Env Sci)	$38/hr	67.5[4]	$2,565.00
CDFW personnel flight following(Sci Aid)	$15/hr	45[4]	$675.00
Mileage reimbursement	$0.52/mi	6,1000[8]	$3,172.00
Total Cost			$147,624.20

[a] 282.80 avg minutes per transects/60 min/hr*98 transects*2 techs = 923.80.
[b] 3 hours round trip from Sacramento*98 transects = 294
[c] 182 avg miles round trip*0.52/mile*98 total transect = 17,836
[d] Includes 4 “standby” days (surveys canceled due to weather)
[e] Expected meals and incidental costs for helicopter pilot and fuel truck operator for both survey and “standby” days
[f] 67.4 survey hours*3 staff
[g] 67.4 survey hours*2 staff (1 for automated flight following and 1 for radio following)
[h] 2.5 hours round trip from Sacramento*3 staff*3 days
[i] 122 mi round trip from Sacramento to Colusa*10 survey days*5 people per day

Discussion

Estimates of population abundance and other parameters are critical to conservation and management of harvested populations, but methods to estimate abundance vary widely in their precision, utility, and feasibility. Distance sampling has gained favor as a tool for estimating abundance of populations (Burnham and Anderson 1984; Buckland et al. 2001, 2004, 2005, 2015; Oyster et al. 2018; Schmidt et al. 2022), particularly where marking a large sample of individuals is not feasible. Although distance sampling has been used to estimate abundance or density of many taxa in many ecosystems, it had not been evaluated for utility in surveys of tule elk that occupy habitats characterized by a mixture of oak savannas, grasslands, and chaparral, with different levels of canopy cover. We used multiple covariate distance sampling to estimate population abundance of four populations of tule elk in northern California and evaluated the effect of group size, canopy cover, and survey year on detection probabilities. As predicted, probability of detecting elk decreased with increasing distance from the transect and decreased with increasing canopy cover; survey year had no effect on detection probability. Contrary to our prediction, we found no significant effect of group size on detection probability, but data were highly skewed to small group sizes (**Supplementary Fig. 2**). Additionally, distance sampling with multiple covariates produced estimates of abundance that were comparable to estimates from concurrent fecal DNA SCR. Although distance sampling produced biologically reasonable estimates of abundance, confidence intervals were large and thus precision was moderate at the regional level and low at the EMU/population level. The SCR estimates, on the other hand, produced more precise abundance estimates at both the regional and population levels. Nonetheless, distance sampling represented an improvement over more traditional methods for monitoring tule elk numbers, especially minimum counts, with relatively little additional investment. Collectively, these results suggest that distance sampling can be a useful tool to estimate abundance of elk, producing both abundance estimates and a measure of uncertainty, when faced with administrative and budget constraints, but also highlight important caveats and limitations. Even so, our study demonstrated that distance sampling has utility as a survey method for elk populations in our study area.

Field methods permitted satisfaction of most of the assumptions of MCDS. Observers searched for animals along the transect line immediately below the helicopter and out to a distance of 400 m perpendicular to its path. We measured distances from transects to the initial location of detected elk groups prior to any movement response to the helicopter. Detection probability of elk groups decreased with distance as expected (**Fig. 2**; **Table 1**). Estimates of population in the four EMUs and overall were not significantly different from those obtained by spatial-capture recapture using fecal DNA transects (**Fig. 4**), suggesting these methods were comparable in our study area. Additionally, our use of MCDS rather than conventional distance sampling (which does not include covariates) to analyze data was not necessary for reducing bias or variance of overall population estimates. The half-normal detection function model is “pooling robust” meaning that it has been shown to yield reliable, nearly unbiased estimates, when data are collected under variable conditions affecting detection probability and on animals with heterogeneous detection probabilities (Buckland et al. 2004). Pooling robustness means that a null model (distance only) estimate of population size on the area where data is pooled is as reliable as covariate model estimates. Consistent with pooling robustness, the null model and covariate model estimates were close in our study (**Table 1**).

Although pooling robustness meant covariates were unnecessary for an unbiased estimate of total population, we used covariates to gain information about covariate associations with detection probability in our study system and to reduce potential for bias in population-specific estimates by accounting for heterogeneity in detection among the EMUs. We modeled variation in detection probability due to substantial variation in group size (1 to >100), elk occurring in open and closed-canopy habitats, and any inter-annual differences in the detection process such as change of personnel. MCDS modeling supported our expectations that detection probability would be unaffected by survey year (**Table 1**, **Supplementary Table 2**) and that detection probability would decrease with increasing canopy cover (**Table 1**, **Supplementary Table 2**, **Fig. 3**). Contrary to our expectations, we found no evidence in MCDS modeling that detection probability increased with increasing group size (**Table**

1, Supplementary Table 2). The inability to find a measurable effect of group size on detection probability was probably due to the skewed distribution of group sizes ranging from 1–120 elk, with a median and 75th percentile of 4 and 11 elk respectively (Supplementary Fig. 2).

Previous research has demonstrated that cover likely has the greatest influence on detection probability (Zabransky et al. 2016; Dyal et al. 2021), and our study was no exception. Our MCDS study design was subject to potential bias due to canopy cover that obstructed aerial views of the ground. Line-transect MCDS estimates detection probability of objects in the transect strip relative to the detection probability at distance = 0 ($g(0)$) but does not estimate $g(0)$. Instead, MCDS relies on an assumption of perfect detection along the transect line ($g(0) = 1$). In other words, although MCDS allows for missed groups further away from the transect, it does not allow for missing groups close to the transect. Population estimation with MCDS also requires the assumption that group sizes are counted without bias. When these assumptions are true or nearly true, estimates of detection probability and population size can be made without bias (Buckland et al. 2001). Previous aerial surveys of elk have documented that both imperfect detection and under-counting of groups occur in areas with medium to dense (≥ 40%) canopy cover resulting in under-estimation of population size (McCorquodale et al. 2013, Cogan and Diefenbach 1998). In our survey, 27% of the sampled area was covered by medium to dense tree canopies (LANDFIRE 2013) with the greatest cover occurring in the Lake Pillsbury EMU, suggesting a strong likelihood of failure of these two assumptions. Failure of the first assumption ($g(0) < 1$) yields over-estimation of detection probability, and under-estimation of population size. Under-counting of groups does not bias detection probability but yields under-estimation of population size. This is reflected in a comparison of the MCDS and SCR estimates for the EMU with the highest canopy cover, Lake Pillsbury (Fig. 4); although the confidence intervals are overlapping, the higher SCR point estimate may be attributable to ground access in canopied areas not visible from the air.

While several newer, non-invasive survey methods, including camera trapping and fecal DNA-SCR, have been successfully applied to estimate abundance for various large mammals (Moeller et al. 2018; Brazeal and Sacks 2021), these methods can be time intensive (Pfeiler et al. 2020: Schoenecker et al. 2021), and impractical where ground access is limited. Tule elk populations in our study system are free-ranging and persist across federal, state-, and privately-owned lands where access may not always be permitted to conduct ground-based surveys (McCullough et al. 1996; CDFW 2018; Batter et al. 2021). Indeed, estimates of abundance for these tule elk populations from fecal DNA in a SCR framework proved robust (Batter et al. 2022). However, surveys were negatively affected by land access. A paucity of samples from one population (EPR) was attributed to a lack of permission to access private property, which influenced our decision to only sample that population a single time leading to imprecise and unreliable estimates (Batter et al. 2022). The lack of access to part of the EPR population also explains that fact that the EPR MCDS point estimate was higher than the respective SCR estimate and outside the 90% CI. Given constraints to ground-based sampling, establishing alternative methods, that transcend socio-political boundaries (e.g., aerial surveys) are necessary for this and other study systems to ensure future routine monitoring of wildlife populations can be achieved.

While mark-resight and sightability correction in aerial surveys are generally considered more robust compared to distance sampling (Barker 2008; McCorquodale et al. 2013; Denes et al. 2015), a combination of cost-prohibitive factors and life-history traits of tule elk influenced our decision to apply distance sampling in northern California. First, both mark-resight and sightability correction require high start-up costs to complete capture and collar efforts, the former requiring long-term investment for maintenance of a suitable quantity of marked individuals for each subsequent survey period (Bristow et al. 2018; Dyal et al. 2021). A previous aerial survey study on mule deer (*Odocoileus hemionus*) recommended that a large proportion (>45%) of the population should be marked to obtain reliable estimates (Bartmann et al. 1986). While 78 elk were collared during the duration of the study period, future monitoring efforts are not guaranteed to have a sufficient number of marked animals available for sampling. Such a long-term investment is unrealistic for our monitoring program, so neither mark-resight nor sightability correction were seriously considered for our purposes. Thus, we elected to assess MCDS as a survey methodology because future application does not require recognition of individually identifiable animals and is broadly applicable (e.g., not site-specific).

Overall, our MCDS abundance estimates compared favorably with estimates generated in a concurrent fecal DNA SCR study supporting accuracy across both methods. While point estimates generated from MCDS were all outside the 90% CI of the SCR estimates, the directionality was inconsistent across populations, suggesting differences were not necessarily due to a systematic cause. For example, in addition to limited ground access, the point estimates were slightly higher for BV/CC and EPR potentially because MCDS methods surveyed a larger area and the time of year was favorable for visibly detecting elk. Importantly, however, point estimates are not statistically different across methods. Our results are similar to other studies comparing aerial surveys with SCR methods for abundance estimation of desert bighorn (*Ovis canadensis nelsoni*; Pfeiler et el. 2020) and North Atlantic right whales (*Eubalaena glacialis*; Crum et al. 2021). Like these other studies, precision of our aerial surveys was generally lower compared to SCR methods (**Fig. 4**). However, acceptable levels of precision and accuracy in survey methods can be informed by management goals (Hone 2008; Lubow and Ransom 2016). Across all populations, the coefficient of variation for our estimate of abundance using MCDS was 0.18, which is at the upper end of the range of CV for reliable scientific studies (CV ≤ 0.20; White et al. 1982). Discrete population CVs using MCDS were outside of this range (> 0.20) but were in the range that may be acceptable for long-term monitoring studies (0.20–0.50; White et al. 1982). To the extent that regional population monitoring is of interest (i.e., multiple EMUs combined), our MCDS methods presented here are adequate to meet monitoring needs for tule elk if issues of bias under the vegetation canopy are mitigated. In fact, at the sampling effort of 3 replicates over 2 years used in our study, we estimated with simulation that long-term monitoring will have 80% power to detect a 53% decline or 108% increase over 10 years. Doubling survey effort to 3 replicates every year yields the same power for 10-year declines of 40% and increases of 67%. In contrast, CVs for individual populations using SCR were much more precise across all populations (CV = 0.08) and for the two populations that were resampled ($CV_{BV/CC}$ = 0.11, CV_{LPB} = 0.13). To achieve goals and objectives at the EMU or population level, application of fecal DNA-SCR as applied in the concurrent study appears to be a more appropriate method. However, larger MCDS sample sizes (i.e., more transects or replicates) may reduce individual population CVs to provide more suitably precise abundance estimates to inform population-level management action (Urbanek et al. 2012).

Survey cost, efficiency, safety, and feasibility must also be considered when determining the most pragmatic survey method to apply to a species within a given system, particularly when management is hindered by administrative, budgetary, and personnel constraints (McClintock et al. 2009; Kilpatrick et al. 2013; Pfeiler et al. 2020). While SCR efforts of the concurrent study were generally more precise and less expensive overall, our MCDS approach reduced dedicated staff time by 64% (SCR = 924 hours; MCDS = 337 hours) and the number of survey days by 87% (SCR = 74; MCDS = 10). Although difficult to quantify, the ground-based SCR approach was much more physically demanding and labor intensive than surveys conducted from helicopter, as it required staff to hike long distances over steep and uneven terrain often in extreme and sometimes hazardous conditions (i.e., temperatures exceeding 100° F). While it is true that aviation accidents are the most common causes of fatalities among wildlife professionals (Sasse

2003), working in outdoor environments also poses inherent risks including environmental, physical, chemical, and biological hazards that must be considered when selecting an appropriate method (Bosch et al. 2013; Taylor and Buttke 2020). If staff time and personnel are limited, or staff cannot reliably and safely meet the physical demands required of field work, aerial surveys present a suitable alternative to gain useful abundance estimates at the regional scale.

Nonetheless, SCR approaches can provide additional benefits over aerial surveys that warrant consideration and may be more appropriate to meet other monitoring program goals. For example, one advantage of a SCR approach is that genetic identification of unique individuals also can support investigations of genetic population structure and landscape connectivity (e.g., Batter et al. 2021) or diet through metabarcoding approaches (Alberdi et al. 2019). While aerial sampling cannot provide the added genetic benefits of SCR, it does have added benefits unachievable through genetic sampling alone, including age-sex structure (Bender 2006, 2012) and visual assessment of animal body condition (e.g., Riney 1960; Meetei et al. 2021).

Overall, aerial distance sampling as applied herein represents an improvement in traditional monitoring of tule elk populations. While aerial distance sampling is not the most robust method, a true estimate rather than minimum count is generated, and it is relatively cost-effective and efficient, as an alternative to more precise ground-based SCR applications. Our aerial survey methods are thus applicable at the regional level to similar tule elk and other large mammal populations that persist across landscapes with varying landownership and habitat types, where long-term investment in marking individuals is unrealistic, and staff personnel and time is limited. We caution that use of MCDS in regions with heavier canopy cover, as may characterize some Roosevelt elk (*C.c. roosevelti*) populations, may be less feasible and entail considerably lower precision and higher bias in resultant estimates (e.g., Weckerly and Kovacs 1998). We thus recommend application of fecal DNA SCR methods in these more extreme cases. Future distance sampling surveys in these elk management units should incorporate one of several distance sampling designs that allow estimation of g(0), for example mark-recapture distance sampling (Buckland et al. 2015), which leverages double observer techniques to generate the required estimate of g(0), and hierarchical distance sampling (Kery and Royle 2016), which employs transect sample repetitions over a short time period to fit hierarchical models. These distance sampling methods should be evaluated for application to reliably estimate abundance at both the regional and population levels for future surveys of elk in these management units and elsewhere.

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