



## AN ABSTRACT OF THE THESIS OF

Jennifer E. Nelson for the degree of Master of Science in Wildlife Science presented on September 9, 2020.

Title: Using Spatial Capture Recapture to Estimate Density of Roosevelt Elk in Western Oregon

Abstract approved:

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Clinton W. Epps

Spatial capture-recapture (SCR) is employed for estimating abundance and density of species, particularly those that are cryptic or solitary, and evaluating how population density varies with habitat. However, it is uncertain whether estimates are biased when applied to species that aggregate, such as elk (*Cervus canadensis*). Wildlife managers in the Pacific Northwest lack a reliable method to estimate abundance and density of Roosevelt elk (*C. c. roosevelti*), as that subspecies frequents dense forests and occurs singly or in groups sometimes exceeding 100 individuals. Hitherto, decision-making in elk management has relied on visual counts as population indices, yet such counts are potentially biased because group size influences detection and observers are unlikely to detect individuals in forests. We employed non-invasive sampling and spatial capture-recapture (SCR) modeling to estimate Roosevelt elk population density in two Oregon wildlife management units (WMUs), Tioga and McKenzie, and examined how density varied with habitat or land ownership type. We imposed a grid across both WMUs, basing cell size on elk home ranges that we estimated in these habitats from existing telemetry data, and stratified sampling by land ownership and nutrition quality, calculated from U.S. Forest Service Westside Elk Nutrition models. We randomly selected cells in each stratum and placed three, 2-km transects within each to facilitate recaptures. We sampled transects once in March

to June 2018 and again in 2019 by walking a pre-determined bearing and searching for elk feces, tracking distance to control for variation in effort. We genotyped samples at 9 microsatellite loci and one sex-determining marker to identify individuals, then created a capture history for each individual. We evaluated a suite of SCR models to assess the effects of covariates relating to habitat type, terrain, precipitation, human activity, and sampling effort on elk population density and probability of detection. We applied the models to the capture histories, tested for the influence of aggregation on density estimates, and estimated mean elk population density for 2018 and 2019 at 0.80 and 0.20 individuals/km<sup>2</sup> in Tioga and McKenzie, respectively. Our models performed well in areas with high elk density, deviating from true density 16% of the time. In contrast, our models deviated from true density 54% of the time when applied to areas with low elk density, indicating sampling intensity would need to be increased to obtain adequate recaptures. We did not find evidence that aggregation of individuals influenced our estimates of density in this system. Our results indicate that effort and precipitation influenced the probability of detecting an individual, and distance to forage/cover edge, distance to roads, percent slope, distance to crops, and precipitation influenced our estimates of elk population density. Overall, our models predicted fewer elk on federal lands, indicating that public recreational opportunities involving elk such as hunting and wildlife viewing may be more limited on public lands. Our methodology provides a framework for managers to develop and implement surveys to reliably estimate elk density in forested landscapes.

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Using Spatial Capture-Recapture to Estimate Density of Roosevelt Elk in Western  
Oregon

by  
Jennifer E. Nelson

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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

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Jennifer E. Nelson, Author

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## CONTRIBUTION OF AUTHORS

Jennifer E. Nelson developed the research questions presented here, created the study, performed field work and data collection, conducted the analysis, and drafted this manuscript. Clinton W. Epps assisted in developing research questions. DeWaine H. Jackson provided data and field equipment, obtained funding, and with Clinton W. Epps, conceived the study. Rachel S. Crowhurst conducted all laboratory work. Tabitha A. Graves assisted in analysis. All authors assisted in writing this manuscript.



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## Chapter 1

### GENERAL INTRODUCTION

Jennifer Nelson

## GENERAL INTRODUCTION

Prior to human settlement, elk occupied much of North America. Over exploitation and loss of habitat resulted in the loss of most elk populations in the eastern United States, and reduced population sizes in the west (Bryant and Maser 1982, Boyd 1978). From 1892-1939 a recovery effort involved the translocation of over 5,000 elk from Yellowstone National Park to much of their historic range. This effort, which sought to establish new populations and aid recovery of existing populations, failed in most eastern states but succeeded in regions such as the Pacific Northwest (Schmidt 1978, Witmer 1990).

Three subspecies of elk occur in the Pacific Northwest: Roosevelt (*Cervus canadensis roosevelti*), Rocky Mountain (*Cervus canadensis nelsonii*) and Tule elk (*Cervus canadensis nannodes*); two of which occur in Oregon: Roosevelt (*Cervus canadensis roosevelti*) and Rocky Mountain (*Cervus canadensis nelsoni*) elk. In the 1880s, Oregon elk populations had declined to a few small and scattered herds after a period of exploitation (ODFW 2003). Elk hunting was prohibited from 1909 to 1932, during and after which translocations and other population recovery efforts resulted in the reestablishment of elk in much of their former range. In 2003, when Oregon Department of Fish and Wildlife (ODFW) published the Oregon Elk Management plan still in effect, they concluded that both subspecies of elk were still increasing and expanding in much of their range or had stabilized or slightly decreased in small parts of Oregon (ODFW 2003).

ODFW attempts to maintain elk populations at levels that maximize hunting while retaining ecosystem health and resolving complaints of interaction with livestock through monitoring and harvest quotas (ODFW 2003). Hunting Roosevelt and Rocky Mountain elk in Oregon is popular and benefits Oregon's economy. In 2011, hunters in Oregon spent approximately \$83 million in trip expenditures, 88% of which comes from big game hunting (e.g., deer, elk, bear; USFWS et al. 2011). ODFW controls hunting opportunities by establishing management objectives (MOs) for each wildlife management unit (WMU) in the state (ODFW 2003). Currently, ODFW assesses whether populations of both subspecies meet MOs with helicopter surveys in late winter and early spring when elk are more likely to occupy open areas.

However, these efforts are difficult to translate into population estimates (McCorquodale et al. 2013) and therefore, provide little information for managers when determining appropriate harvest limits.

Using methods that cannot accurately estimate abundance can lead to a perpetual reduction in ODFW's ability to meet MOs (Hagen et al. 2014), which could cause poor population and ecosystem health. Roosevelt elk inhabit much of the Oregon Coast Range and western slope of the Oregon Cascade Range. Those regions are comprised of forests with dense structure, resulting in a substantial reduction in the ability to detect elk directly from the ground and air (McCorquodale et al. 2013). Thus, a technique is desired that would allow generation of accurate and cost-effective population estimates for elk, even in dense habitat. The goal of this study is to determine whether sampling fecal DNA in a spatial capture-recapture framework could meet this need.



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## Chapter 2

### USING SPATIAL-CAPTURE RECAPTURE TO ESTIMATE DENSITY OF ROOSEVELT ELK IN WESTERN OREGON

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## INTRODUCTION

Wildlife managers often use abundance and density estimates to assess whether they are meeting management goals established to aid rare species recovery, control nuisance species, increase ecosystem function, or promote sustainable hunting (Dice 1938, Williams et al. 2002, Groom et al. 2005). Animal abundance and density are fundamental population attributes, but are difficult to measure, particularly for species that are hard to observe directly. For species that are solitary with large home ranges, live in dense habitats, or exhibit cryptic or nocturnal behavior, methods such as mark-resight, distance sampling, or direct counts are often infeasible for estimating abundance (Durant et al. 2011, McCorquodale et al. 2013). In these cases, capture-recapture methods that utilize counts from indirect observations (e.g., photographic images, Karanth 1995; eDNA, Lacoursière-Roussel et al. 2019; or feces, Eggert et al. 2003) of animals may be more efficient in estimating population characteristics (Morin and Woodruff 1996, Kohn and Wayne 1997, Waits and Paetkau 2005).

Capture-recapture methods that estimate population density require reliable identification of individual animals across multiple surveys. Individual capture histories can then be constructed and used in mark-recapture models to estimate abundance and identify covariates that influence detectability and abundance (Pollock 2002, Royle 2009). If individuals are visually or audibly unique, camera traps or acoustic recordings can be used to generate capture histories (e.g., jaguar spots, Sollmann et al. 2011; zebra stripes, Petersen 1972; tiger roars, Ji et al. 2013). Alternatively, when observers cannot reliably distinguish individuals of a species, capture histories can be created by genotyping non-invasively (e.g., hair snares or

feces) or semi-invasively (e.g., biopsy darts) collected samples (Waits and Paetkau 2005). Genotypes using 5 to 15 variable neutral microsatellites, or a larger number of single-nucleotide polymorphisms (SNPs), typically allow reliable distinction among even closely-related individuals (Taberlet et al. 1996, Waits et al. 2001). Non-invasively collected genotypes have been widely used for estimating abundance of cryptic species such as bears (*Ursus spp.*; Gardner et al. 2010, Kendall et al. 2016, Molina et al. 2017), eagles (*Aquila heliaca*; Rudnick et al. 2008), bats (*Rhinolophus hipposideros*; Puechmaille and Petit 2007), and seahorses (*Hippocampus guttulatus*; Correia et al. 2014).

Translating abundance estimates to density with capture-recapture methods, however, poses additional challenges. Density estimates allow comparisons across sites or habitats (e.g., Miller et al. 1997, Beausoleil et al. 2016) and are thus more desirable for management decision-making. As density is the quotient of abundance and area, calculating density requires an accurate estimate of the area sampled. Researchers applying capture-recapture methods often attempt to do this in an ad-hoc approach such as by buffering the study area using estimates of animal movement and home range size (e.g., Trolle and Kéry 2005). The metric typically used to describe an animal's scale of movement is the mean maximum distance moved (Otis et al. 1978, Wilson and Anderson 1985), which is based on distance between redetections of individuals. Alternatively, spatial capture-recapture (SCR) methods (Efford 2004) allow for precise estimates of density and the area sampled as well as parameters describing movement, resource selection, and connectivity (Royle et al. 2018). SCR methods can be used to estimate density of a species using a single survey and infer

how density varies with environmental or other covariates. SCR analyses incorporate spatial location (i.e., X and Y coordinates) directly into capture histories and estimate an activity center (i.e., center of home range) for each individual in the sampled population. The estimated activity centers are formalized into a statistical point process, a class of models that describe patterns and distributions of points, with the assumption in the simplest SCR models that the points (i.e., activity centers for individuals) are distributed uniformly across landscapes (Royle et al. 2018).

Studies show the uniformity assumption is robust in SCR modeling (Borchers and Efford 2008), but it is unclear if density estimates are biased when applied to individuals distributed non-independently (Royle et al. 2016). Social predators such as wolves (*Canis lupus*) or gregarious ungulates such as elk (*Cervus canadensis*) aggregate routinely, but group size and cohesion (i.e., the degree of dependence among individual movements within a group) varies depending on season or other factors (Jenkins and Starkey 1982). Few studies have attempted to address this problem. López-Bao et al. (2018) used simulations to evaluate how grouping behavior by wolves influenced spatial capture-recapture estimates, and concluded that grouping resulted in only a slight negative bias to density estimates. However, López-Bao et al. (2018) only considered group sizes of up to 8 individuals. Granjon et al. (2017) likewise found that some spatial capture-recapture models underestimated group and population size of eastern chimpanzees (*Pan troglodytes schweinfurthii*). In contrast, simulations conducted by Bischof et al. (2020) found high levels of aggregation (group sizes > 8 individuals) positively biased density estimates, particularly if group cohesion was low. For herd-living species such as elk, group

sizes can routinely exceed 100 individuals (Proffitt et al. 2012), suggesting that an assessment on the effects of aggregation on density is necessary when applying this method to social ungulates.

Along much of the Pacific coast in the northwestern United States, Roosevelt elk (*C. c. roosevelti*) exemplify the challenge of population estimation for species that are difficult to directly observe and aggregate socially. Direct counts are employed at small scales and in relatively open habitat where this approach is feasible (e.g., meadows in northern California; Starns et al. 2014). However, many Roosevelt elk occupy dense coniferous forests and travel in groups ranging from 1 to >100 individuals depending on sex, habitat, and time of year, making it difficult to develop reliable density estimates or even indices of population size. Managing agencies in this region rely on composition (sex, age) counts, harvest statistics, and telemetry data as indices of elk abundance to meet their management objectives (Oregon Department of Fish & Wildlife 2003, McCorquodale et al. 2013, Washington Department of Fish and Wildlife 2014). However, such counts are achieved by locating elk from the air while they are using open areas such as clear cuts, which may bias results if use of open habitats varies seasonally, temporally, or on the basis of sex, age, or individual preference. Mark-resight models have been developed for many elk habitats (Unsworth et al. 1990, Leptich and Zager 1993, McIntosh et al. 2009), but the ability to verify the accuracy of those models wanes without true abundance estimates, and those approaches rely on large numbers of animals with marks visible from the air.

Elk in the Pacific Northwest provide public wildlife viewing and hunting opportunities, but cause substantial human-wildlife conflicts through depredation on timber and agricultural crops (Walter et al. 2010), underscoring the need to accurately estimate both abundance and density at scales applicable to harvest regulation. In western Oregon, where land ownership often follows the “checkerboard” pattern of interspersed publicly and privately-owned sections (Figure 1), elk also use habitats with considerable variation in land management practices such as intensity of timber harvest. Current timber management practices create early-seral habitat at scales up to 120 acres (48.6 ha), the maximum legal size of a clear cut defined by the Oregon Forest Practices Act (OAR 629). Elk are thought to use early-seral habitat extensively because of the increased availability of suitable forage (Cook et al. 2016), but aerial surveys currently used to locate elk are largely ineffective in areas with dense forest canopy, leading to population undercounts and bias towards animals using early-seral habitats.

In this study, we employ spatial capture-recapture and non-invasive genetic sampling to estimate elk population abundance and density in two wildlife management units in western Oregon. Our method was based on walking transects, where we collected elk fecal pellets to identify individuals. We developed a sampling design intended to maximize encounters with elk fecal pellets and facilitate adequate recaptures of individuals using one sampling occasion. We implemented the method over two consecutive spring seasons in two study areas that represented different types of Roosevelt elk habitat in western Oregon, with expected population densities ranging from low to high. Our objectives were to 1) assess whether our method could

produce precise estimates of Roosevelt elk density for management decision-making, as indicated by an established threshold for relative standard error in SCR modeling (Evans and Boulanger 2019), and 2) evaluate the differences in elk density in areas subject to different land management practices which we depict by land ownership type.

## **METHODS**

### **Study Area**

In Oregon, Roosevelt elk frequent the closed-canopy forest types of the Coast Range and western slope of the Cascade Range. The Oregon Coast Range is characterized by rugged terrain and a mosaic of western red cedar (*Thuja plicata*), western hemlock (*Tsuga heterophylla*), and Douglas-fir (*Pseudotsuga menziesii*) forests. This area is highly productive due in part to high annual precipitation occurring primarily from fall to spring (Thorson et al. 2003). The west side of Oregon's Cascade Range maintains a moist, temperate climate supporting highly productive conifer forests. At low elevations, western hemlock and Douglas-fir forests dominate and transition, from west-east, into steep-sloped forests comprised of western hemlock, Douglas-fir, noble fir (*Abies procera*), and Pacific silver fir (*Abies amabilis*) at mid-elevations. Near the Cascade crest, high elevation subalpine meadows persist and forests consist of mountain hemlock (*Tsuga mertensiana*) and Pacific silver fir (Thorson et al. 2003).

Our study took place in two wildlife management units (WMUs) in western Oregon, Tioga and McKenzie (Figure 1). The Oregon Department of Fish & Wildlife (ODFW) monitors elk population trends and sets hunting limits and management



objectives in each of Oregon's 67 WMUs (Oregon Department of Fish & Wildlife 2003). Thus, our method would be most practical to use if it produced density estimates at the same WMU scale. The Tioga and McKenzie WMUs differ in climate, geology, terrain, and land practices, allowing us to assess the relevance of this method to Roosevelt elk across a wider range of their Pacific Northwest habitats.

Land ownership and uses in McKenzie and Tioga differ sharply (Figure 1) and may influence the amount of early-seral habitat available in these WMUs (Phalan et al. 2019). Located within the Oregon Coast Range, the Tioga WMU comprises primarily of private lands, followed by Bureau of Land Management (BLM) land, Elliott State Forest, and Oregon Dunes National Recreation Area. With the exception of the Oregon Dunes National Recreation Area, land owners and managers primarily use Tioga lands for high-intensity timber production, although silvicultural practices differ by landowner. Within the Oregon Cascade Range, ownership in the McKenzie WMU consists primarily of the U.S. Forest Service, followed by owners conducting commercial agricultural and timber operations, and the BLM. The east side of the McKenzie WMU is comprised of three wilderness areas totaling 1,518 km<sup>2</sup>: Mt. Washington Wilderness, Three Sisters Wilderness, and Lake Waldo Wilderness, where roads, aircraft, and extraction of natural resources are prohibited. While commercial timber operations continue to harvest at high intensity, the U.S. Forest Service and BLM reduced timber operations on public lands in 1994 with the adoption of the Northwest Forest Plan, largely reducing the amount of early-seral forage habitat by 18% on federal land and 30% on private industrial land (Phalan et al. 2019).

## General Workflow

We designed our study based on a systematic stratified sampling approach employed at the scale of each wildlife management unit. We used ~2 km walking transects, clustered in groups of 3 at a spatial scale intended to allow recapture of individuals across transects. We established transect cluster locations using a stratified grid-based design and based grid cell size on home range estimates from telemetered elk near the study areas. Transect clusters were placed in selected cells, which were stratified and randomly chosen to evenly sample across habitat types expected to influence elk density and to avoid sampling adjacent grid cells when possible. On the walking transects, we collected elk fecal pellets and genotyped them using microsatellite loci to identify individuals and assess recaptures across transect segments. We used the R-package *secr* (Efford 2020) to create capture histories and study area masks, build SCR models, and compute parameter estimates using maximum-likelihood estimation techniques. We used covariates describing habitat and sampling effort to model variation in density and detectability and employed elk location data from telemetered animals in each study area to inform the spatial scale parameter,  $\sigma$ , of the SCR analysis. Next, we projected our models to map elk population density across both WMUs. Finally, we used our projections to evaluate how elk population density varied by land ownership. Each step is described in detail below. Unless indicated otherwise, all analyses and formatting were conducted in ArcGIS version 10.3.1 (ArcGIS 2015) and R-version 3.6.3 (R Core Team 2020).

## Sampling Design

To facilitate adequate detections of unique and redetected individuals for SCR analysis using one sampling occasion, we adopted a clustered sampling design informed by estimates of sigma. Sigma ( $\sigma$ ) is the spatial scale parameter and describes the spatial scale over which the probability of detecting a given individual in a particular location declines (Efford 2004). In SCR modeling,  $\sigma$  can be estimated directly from the capture-recapture data (Efford 2004), or can be informed by other data on animal movement such as telemetry or home range estimates (Paterson et al. 2019). With unlimited resources (i.e., technician time, equipment), it is ideal to sample for individuals with a detection device (e.g., live trap, camera trap, transect, or hair snare, referred to hereafter as a trap) in every potential home range within the study area. However, wildlife management resources are usually limited. Sun et al. (2014) found that a clustered design, where two or more traps are grouped in strategically selected home ranges, requires less resources and produces accurate estimates of abundance. Ideally, clusters are spaced  $2\sigma$  apart. When spacing exceeds  $2\sigma$ , clusters require additional traps as the distances between clusters increase.

We approximated  $\sigma$  for our sampling design with GPS collar locations and created a grid for each study area. We calculated  $\sigma$  as:

$$\sigma = \sqrt{\frac{95\% \text{ home range estimate}/\pi}{q_{2,\alpha}}},$$

(Eqn. 1)

where  $q_{2,\alpha}$  represents the critical value of a Chi-square with two degrees of freedom ( $\alpha = 0.05$ ,  $q_{2,\alpha} = 5.99$ ; Royle et al. 2014). To determine the 95% home range estimate, we calculated home range sizes from locations of five GPS collared female elk

collected by ODFW in western Oregon from 2015 to 2017. First, we cleaned and clipped data to include locations collected in March - June, the desired sampling period. To estimate home range size (Worton 1989) for each individual elk during that period, we calculated a 95% kernel density estimate (KDE) from points for each collared individual in the Geospatial Modelling Environment (Beyer 2015). Then, we overlaid a grid on the study areas with a cell size equal to the median 95% KDE. Next, we randomly picked an initial cell, then systematically selected additional cells spaced two cells apart to the unit boundary.

To examine whether elk density varied by land ownership type, we adjusted the placement of some cells to better reflect the variation in land ownership and nutrition quality of forage in the study areas. We estimated nutrition quality for each cell by averaging the values of a raster map of predicted dietary digestible energy (DDE) that classified forage quality from 1 (poor) to 6 (excellent). DDE is a nutrition metric informed by structural characteristics (e.g., ecological site potential, canopy cover) that are extracted from a detailed vegetation composition map computed using gradient nearest neighbor (GNN) imputation, which we obtained from Oregon State University's Landscape Ecology, Modeling, Mapping, and Analysis team (see full description below; Cook et al. 2016, LEMMA 2018; Rowland et al. 2018). Land ownership type was determined by the majority land ownership of the cell from a layer compiled by Oregon Department of Forestry (ODF 2017). Finally, we adjusted our cell selection to equally represent each DDE/ownership combination while retaining the spacing from the previous step as much as possible. Within each selected cell we placed our traps: three transects that were 2 km in length and spaced

1 km apart (Figure 2), with the expectation that technicians would spend no more than 3 hours searching on one transect.

### **Implementation and Analysis of Genetic Samples**

We collected fecal samples from transects in late March – June 2018 and 2019, during one sampling occasion each year. We sampled in spring so that density estimates would reflect elk that survived through winter and to avoid collecting pellets from newborn calves, satisfying the demographically closed population assumption of SCR models (Royle et al. 2014). With one to three observers (typically 2), we accessed the most northern or southern endpoint of each transect and followed animal trails and elk sign towards the opposite endpoint while staying within 500 m of the transect line. We searched for pellets for approximately 2 km of search effort or as far as terrain allowed within a 3-hour time limit. We tracked distance by recording where we walked on each transect with the track-logging function on a Garmin GPS inReach Explorer®+ (Part number: 010-01735-10), which recorded our location every minute. When we encountered pellets, we recorded their location and determined whether a mucosal layer was present. We collected samples with a mucosal layer into 50mL falcon tubes and submerged pellets in 95% ethanol. If pellets were dry, we placed them in envelopes. We stored samples at room temperature until processed.

We placed 3 to 4 pellets from each sample into a weigh boat and allowed them to dry overnight before using a razor blade to scrape 0.025-0.03g of exterior material. We extracted DNA from scrapings using a modified version of the Aquagenomics Soil and Stool Kit protocol (MultiTarget Pharmaceuticals LLC,

Colorado Springs, CO). Modifications included the addition of 450  $\mu\text{L}$  of AquaGenomic solution to pellet scrapings, a fifteen minute bead-beating step with 1.0 mm silica/zirconium beads (BioSpec Products Inc., Bartlesville, OK) for cell lysis, and the addition of 12 mAU proteinase K (Qiagen Inc., Valencia, CA). Lastly, we added 150  $\mu\text{L}$  of AquaPrecipi solution (MultiTarget Pharmaceuticals LLC) to cell lysate to remove PCR inhibitors present in fecal samples. We rehydrated DNA samples with 100  $\mu\text{L}$  of 1xTE buffer and did not quantify them before use.

We amplified nine microsatellite primers and one primer for sexing in two 10  $\mu\text{L}$  multiplex PCR reactions. Each reaction consisted of 1x Qiagen Multiplex PCR master mix, 0.2  $\mu\text{M}$  of each primer except for RT1 which had 0.4  $\mu\text{M}$ , 10  $\mu\text{g}$  of bovine serum albumin, and 0.5-1  $\mu\text{L}$  DNA; reactions were brought to volume with nuclease-free water. We added the higher amount of DNA for samples that were clear or light-colored, while samples that were darker colored or opaque were diluted 1:1 to counteract the presence of PCR-inhibitors (i.e., 0.5  $\mu\text{L}$  DNA and 0.5  $\mu\text{L}$  of nuclease-free water). For each locus, we fluorescently tagged one primer on the 5' end with NED, PET, VIC, or 6-FAM (Applied Biosystems, Carlsbad, CA). We replicated samples three times. Because preliminary results showed that a large number of samples did not amplify well, we genotyped samples at one panel initially to reduce costs, and then genotyped successful samples at the second panel. We conducted PCRs on a Bio-Rad C1000 or MyCycler thermocycler with the following cycling conditions: initial denaturation of 15 minutes at 95  $^{\circ}\text{C}$ , followed by 35 cycles of 95  $^{\circ}\text{C}$  for 30 seconds, 59  $^{\circ}\text{C}$  for 90 seconds, 72  $^{\circ}\text{C}$  for 60 seconds, and a final

elongation of 30 minutes at 60 °C. We included one positive and one negative control on each PCR plate to align our calls and monitor for contamination, respectively.

Amplification was verified on a 2% agarose gel with GelRed nucleic acid stain (Biotium; Fremont, CA), and amplicons were diluted depending on band brightness to avoid excessive DNA concentration for genotyping. After dilution, 1  $\mu$ L of PCR product was precipitated to remove unincorporated dNTPs and excess salts, and submitted to the Oregon State University Center for Genome Research and Biocomputing for fragment analysis on an ABI 3730 DNA Analyzer with GeneScan 500LIZ sizing standard (Applied Biosystems, USA). Genotypes were scored manually using GeneMapper™ Software v4.1 (Applied Biosystems, USA). To generate a consensus call, we considered a genotype verified if both alleles in a heterozygote were seen at least twice, and the single allele for a homozygote was seen in all three replicates, otherwise we conducted an additional 3-6 replicate PCR reactions. Any sample with three or more unique alleles at any locus in all three replicates was considered contaminated and removed from the data set.

To distinguish individuals and identify recaptures from sample genotypes in each study area, we used Program CERVUS (Kalinowski et al. 2007) to conduct allele frequency analyses and estimate two metrics that establish confidence in our ability to reliably distinguish individuals: probability of identity ( $P_{ID}$ ) and probability of identity among siblings ( $P_{ID_{sibs}}$ ; Waits et al. 2001). Datasets that contain many genotypes of the same individual result in biased allele frequencies. Therefore, we conducted this analysis in two phases. In the first phase, we identified and removed duplicate genotypes as follows. First, we conducted an allele frequency analysis on all

genotypes from both years and multiplied the resulting  $P_{ID}$  and  $P_{IDSibs}$  estimates from each locus together to calculate the cumulative values of  $P_{ID}$  and  $P_{IDSibs}$ . To sustain confidence in our ability to distinguish individuals in the worst-case scenario that a sample genotypes at loci with the least amount of power to distinguish individuals, we established a threshold of  $P_{ID} < 0.001$  and  $P_{IDSibs} < 0.05$ . We removed the loci with the most power from the product, one at a time, until we determined the minimum number of loci required to meet the threshold. We then removed from the data set any samples that amplified at fewer than this number of loci. We conducted an identity analysis in CERVUS to compare the remaining genotypes, allowing for mismatches at up to 2 loci. We examined pairs of genotypes with mismatches to determine whether a mismatch could be explained by allelic dropout (i.e., if no more than two alleles were present across both samples at the same locus). After we identified and matched individuals, we deleted duplicate individuals from the original genotype file and began the second phase of analysis. There, we conducted an allele frequency analysis on the new dataset and recalculated  $P_{ID}$  and  $P_{IDSibs}$  to confirm that our results from the first phase were not affected by any bias in allele frequency estimates from duplicate genotypes present in the initial dataset. If we determined a different minimum number of loci in the second phase, we removed samples and conducted an identity analysis, again. After the second phase, we assigned individuals a unique identifier.

### **Compiling Data and Estimating Density**

For each year of data collection, we constructed detection histories (typically referred to as capture histories) and a trap file comprised of the traps' identifiers,



spatial locations, and probability of detection covariates. We defined traps by dividing transects into four equal segments and used the median location of each segment as the trap location. For each trap, we created a unique identifier and extracted the probability of detection covariates: Julian day, effort, and average daily precipitation two weeks prior to collection date. We used distance walked on each transect as a measure of effort, which can influence density estimates by positively affecting probability of detection (Russell et al. 2012). We included average daily precipitation over the 14-day period prior to each sample's collection date because high rainfall and humidity may cause DNA in feces to degrade more quickly, thus influencing densities of fecal samples that can be successfully genotyped (Harestad and Bunnell 1987, Barnes et al. 1997, Brinkman et al. 2011). Finally, we calculated Julian day for each collected sample to evaluate potential linear trends in detection, caused by factors such as decreasing precipitation over the course of the study season, or temporary emigration of individuals at the start of the calving period (early May to early July; Jenkins and Starkey 1982, Johnson et al. 2019). To create capture histories, we determined the closest trap to each sample, defined as the trap with the smallest Euclidean distance from the sample, and assigned the trap to the sample's individual ID.

For each study area, we combined 2018 and 2019 data, entered the capture histories and trap file into *secr* to create *capthist* objects, and added telemetry data to inform  $\sigma$  while estimating density. To improve precision in our density estimates, we combined data from both years by specifying each year as a separate session in the trap file and capture histories (Royle and Converse 2014, Morin et al. 2018). This

yielded separate density estimates for each of the two years but using both years together increased power to estimate the probability of detection,  $\sigma$ , and the influence of covariates on density. We used `secr`'s `read.caphist()` function to create a `caphist` object from the trap file and capture histories, specifying the detector type as "count." To further inform the estimates of  $\sigma$  while estimating density, we included telemetry data from female elk in our study areas. Informing  $\sigma$  with spatial locations such as telemetry data can allow SCR models to estimate density more accurately and precisely (Sollmann et al. 2013, Ruprecht et al. 2020). We obtained the spatial data from GPS collars affixed to 18 and 8 female elk by ODFW in Tioga and McKenzie, respectively, in early 2019. Although male and female elk have different home range sizes and movement patterns (Long et al. 2009, Bliss and Weckerly 2016), we chose not to estimate  $\sigma$  separately for males and females, because our genetic data did not allow us to distinguish yearling males traveling in female groups from bulls traveling alone or in bachelor herds, which presumably have different movement patterns and distances. We included locations collected during the sampling period only. To make the file size `secr` compatible, we reduced the number of locations by selecting 150 points each across all individuals for 2018 and 2019 and added them to the `caphist` object, using the `read.telemetry()` and `addTelemetry()` functions, specifying `type = 'independent'`, indicating the data were not collected simultaneously with our study.

We created a habitat boundary layer and generated a habitat mask for each study area by removing portions of the study area we deemed unlikely to be a Roosevelt elk activity center: bays and estuaries, cultivated crops, lava, open water, pasture or hay, suburban, and urban (2018 Oregon Statewide Habitat Map). Then, we

made the habitat mask, a spatial grid of squares containing the density covariate values. When creating the habitat mask, we specified a 1,500 m buffer around trap coordinates because we assumed elk are no longer detectable from a trap beyond this distance. Subsequently, we extracted the values of the density covariates to the mask.

We identified six environmental covariates to include as predictors of spatial variation in elk density. We used four covariates identified by Rowland et al. (2018) as predicting summer habitat use by elk in western Washington and northwest and west-central Oregon: dietary digestible energy (DDE), percent slope, distance to nearest road with public motorized access, and distance to cover/forage edge. We used a toolbox developed by Rowland et al. (2018) to compute rasters of each of the four covariates. We did not have access to a roads layer that adequately classified roads with public motorized access so we used a roads layer from Oregon Department of Transportation (ODOT 2017), likewise included in the Rowland et al. (2018) toolbox. Our fifth covariate was average daily precipitation throughout the sampling period. We included this variable because we predicted that rainfall might be linked to productivity of spring vegetation consumed by elk, because DDE is predicted for summer usage, not spring. We obtained daily 4 km resolution precipitation maps from Oregon State University's PRISM Climate Group (PRISM 2020) to calculate average precipitation over the sampling periods. Because elk are commonly persecuted because of their damage to crops, we included a final covariate, distance to crops, using CropScape (USDA 2020). We clipped the layer to only include crops that wildlife managers identified as most commonly depredated by elk: spring and winter wheat, other hay/non-alfalfa, sod/grass seed, other tree crops, grassland/pasture. This

covariate was not applied to the Tioga analysis as commercial agriculture was not a prominent land use in that WMU.

We fit models in stages to estimate and assess covariate relationships with density. All models were fit using maximum likelihood estimation in the *secr.fit()* function and assumed detections between transect segments were independent (Royle et al. 2014). Further, to compare results on the same scale, we centered and scaled all covariate values with their mean and standard deviation values. When we included telemetry data, we were constrained to fit a hazard half-normal detection function; otherwise, we fit a half-normal detection function and assumed constant density. For each study area, we identified the best covariates for the probability of detection function using Akaike's Information Criteria (AIC; Akaike 1973) with the small-sample bias adjustment ( $AIC_c$ ; Hurvich 1989) and Akaike weights (Burnham et al. 2002) before identifying the best covariates for the density component of the model. We identified a candidate top model when it had the lowest  $AIC_c$  and highest weight; models within two  $\Delta AIC_c$  of the candidate top model were regarded as competing. To identify the top detection model, we first fit a univariate model for each probability of detection covariate, and selected the best model as the candidate top model. Next, we created a new set of models by adding one covariate to the candidate top model. In a stepwise fashion, we repeated the selection process to select the new candidate top model at that step. We continued this process until adding covariates to the final model did not result in a different candidate top model from the previous step. In the second stage, we used the best detection model and conducted the same selection process for the density component of the model.

To quantify and adjust for the effects of aggregation among individuals biasing our density estimates, we calculated Fletcher's  $\hat{c}$  and applied an adjustment when we detected overdispersion in our data. We used outputs from the *derived()* function on the top model to calculate  $\hat{c}$  and apply the adjustment as described by Bischof et al. (2020). A  $\hat{c}$  close to 1 indicate the data are not overdispersed and an adjustment is not needed.

To assess the differences in elk density on different land ownership types, we estimated and predicted density across the study areas. We generated the top model's prediction of realized abundance and 95% confidence intervals with the *region.N()* function. Next, we created a density surface using *predictDsurface()* on the top models and associated habitat masks. In ArcGIS, we summed the predicted density by landownership type and multiplied them by the cell size of the density surface to get predicted elk abundance in each WMU. Finally, to assess the performance of our models we calculated the relative standard error (RSE) of each density estimate. RSE is a metric used to assess how likely our density estimate will deviate from the true population density, where a RSE value above a given threshold indicates poor model performance. When evaluating the performance of SCR models, a threshold of 0.2 is adequate (Efford and Boulanger 2019).

## **RESULTS**

Home range estimates from GPS collar locations of five female elk ranging from 9.33 km<sup>2</sup> to 214.28 km<sup>2</sup> yielded a median home range size of 15.48 km<sup>2</sup>. Therefore, we used a grid with cell size 15.48 km<sup>2</sup> for our sampling design (Figure 2).

We collected 1,084 (542 in 2018; 542 in 2019) fecal samples from 200 (96 in 2018; 104 in 2019) transects in the Tioga WMU, and 168 (82 in 2018; 86 in 2019) fecal samples from 234 (119 in 2018; 115 in 2019) transects in the McKenzie WMU (Table 1). Unbiased  $P_{ID}$  and  $P_{IDSibs}$  were  $5.0 \times 10^{-6}$  and  $3.7 \times 10^{-3}$  in Tioga and  $5.8 \times 10^{-7}$  and  $1.7 \times 10^{-3}$  in McKenzie, respectively (Table A2). In both study areas, we determined that amplification at four loci was required to meet our thresholds of  $P_{ID} < 0.001$  and  $P_{IDSibs} < 0.05$  for reliable distinction of individuals. In Tioga, the four least informative loci (T193, TE167, NVHRT01, C143) yielded cumulative  $P_{ID}$  and  $P_{IDSibs}$  estimates of  $8.1 \times 10^{-4}$  and  $4.6 \times 10^{-2}$ , respectively (Table A2). In McKenzie, cumulative estimates of  $P_{ID}$  and  $P_{IDSibs}$  were  $2.8 \times 10^{-4}$  and  $3.3 \times 10^{-2}$  from the four least informative loci (T193, TE167, TE182, C143; Table A2). We genotyped 41% (506) of 1,252 total samples genotyped at 4 or more loci (Table 1; Table 2). We identified 289 (122 in 2018; 167 in 2019) and 38 (24 in 2018; 14 in 2019) individuals and redetected 96 (41 in 2018; 55 in 2019) and 12 (8 in 2018; 4 in 2019) individuals in Tioga and McKenzie, respectively (Table 2). Redetections occurred on the same transect or between neighboring transects within a cell, with the exception of one individual that we detected in two cells in Tioga. We censored that individual because the large distance between its detections was an outlier and artificially inflated sigma, causing model misbehavior.

We used GPS collar locations from 17 and 4 female elk in Tioga and McKenzie respectively to inform  $\sigma$  in our SCR analyses (Figure 3). McKenzie models that included telemetry data failed to converge. However, in the Tioga models, estimates of  $\sigma$  increased from 637 m (95% CI: 562 - 721) to 1,059 m (95%

CI: 1003 - 1117) when telemetry data were included. We detected little to no signs of overdispersion in our data sets: in Tioga, we estimated Fletcher's  $\hat{c} = 1.01$  in 2018 and Fletcher's  $\hat{c} = 1.01$  in 2019; in McKenzie, we estimated Fletcher's  $\hat{c} = 1.04$  in 2018 and Fletcher's  $\hat{c} = 1.00$  in 2019. We calculated the RSE of the best Tioga model to be 0.16 (2018) and 0.15 (2019) and 0.54 (2018; 2019) for the best McKenzie model.

In both WMUs, the best models suggested probability of detecting and successfully genotyping a sample was negatively associated with effort ( $\beta$ : -0.50 95% CI: -0.65 to -0.34 in Tioga;  $\beta$ : -0.59 95% CI: -1.01 to -0.17 in McKenzie; Table 5; Table 6) but positively associated with average daily precipitation two weeks prior to collection date ( $\beta$ : 0.19 95% CI: 0.08.01 to 0.31 in Tioga;  $\beta$ : 0.26 95% CI: -0.05 to 0.57 in McKenzie; Table 5; Table 6). The best Tioga model suggested distance to nearest road ( $\beta$ : -11.81 95% CI: -19.97 to -3.65) and distance to cover/forage edge ( $\beta$ : -0.49 95% CI: -0.75 to -0.22) were negatively associated with density, while average daily precipitation, which ranged from 2.4 to 5.7 mm/day in 2018 and 5.5 to 15.8 mm/day in 2019, was positively associated with density ( $\beta$ : 0.22 95% CI: 0.10 to 0.33; Table 7). We estimated elk density to be 0.80 individuals/km<sup>2</sup> (95% CI: 0.61 – 1.05), resulting in abundance estimates of 3,023 (95% CI: 2317 – 3958) and 3,005 (95% CI: 2302 – 3941) individuals in 2018 and 2019, respectively. The best model predicted lower elk density on federal lands (0.63 individuals/km<sup>2</sup> in 2018; 0.64 individuals/km<sup>2</sup> in 2019; 1,011 km<sup>2</sup>), followed by private (0.84 individuals/km<sup>2</sup> in 2018; 0.82 individuals/km<sup>2</sup> in 2019; 2,385 km<sup>2</sup>) then state (0.91 individuals/km<sup>2</sup> in 2018; 0.96 individuals/km<sup>2</sup> in 2019; 361 km<sup>2</sup>) lands. The best McKenzie model

suggested distance to crops ( $\beta$ : -87.98 95% CI: -152.14 to -23.83) and percent slope ( $\beta$ : -0.89 95% CI: -1.50 to -0.27) were negatively associated with density (Table 8). We estimated elk density to be 0.2 individuals/km<sup>2</sup> (95% CI: 0.08 – 0.52), resulting in abundance estimates of 1,224 (95% CI: 481 to 3172) and 1,214 (95% CI: 471 to 3162) individuals in 2018 and 2019, respectively. The best model predicted few elk on state lands (0 individuals/km<sup>2</sup> in 2018 and 2019; 7 km<sup>2</sup>), followed by federal (0.04 individuals/km<sup>2</sup> in 2018 and 2019; 3,953 km<sup>2</sup>) then private (0.51 individuals/km<sup>2</sup> in 2018 and 2019; 2,138 km<sup>2</sup>) lands.

## **DISCUSSION**

We demonstrated that SCR methods can be used to estimate density of gregarious ungulates in closed-canopy forests, although the precision of estimation varied. We estimated density of Roosevelt elk populations in two Oregon wildlife management units representing different habitats and expected densities of elk, but only achieved an acceptable level of precision in one of the two areas, suggesting this method is most applicable for management in areas that support moderate or higher densities of elk at this level of sampling. In both study areas, we predicted lower elk densities on federal lands relative to predicted elk density on lands in private or state ownership.

As demonstrated by the RSE estimates, our sampling achieved good precision in the Tioga WMU where higher elk densities led to numerous spatial recaptures (Table 4). In the McKenzie WMU, however, low elk density resulted in few (2018) or no (2019) spatial recaptures. This may have occurred because the number of transects placed per cell was insufficient for this density of elk. To increase redetections in



areas of low density, sampling intensity could be increased by using multiple sampling occasions or placing more transects per selected cell (Efford and Boulanger 2019). However, greatly increasing sampling effort in areas where samples are unlikely to be encountered may be inefficient. Eliminating sampling in areas where elk are very unlikely to occur may be more appropriate and cost effective. Such an approach would, however, confine estimates of density to the sampled area, such that density estimates could not be applied to the entire WMU.

In Tioga, models with distance to nearest road, distance to cover/forage edge, and precipitation best explained density. In contrast to findings by Rowland et al. (2018), our analysis predicted more elk near roads. However, we expect that relationship would change if we classified our roads layer by human use levels. In the field, we commonly observed elk sign on rarely-used, logging roads on public land, particularly in steep areas. However, many studies have observed elk avoiding roads open to the public (Witmer and deCalesta 1985, Cole et al. 1997, Rowland et al. 2018). Therefore, separately considering distance to roads open to the public and distance to roads closed to the public likely would improve modeled estimates. In agreement with Rowland et al. (2018), we predicted more elk in close proximity to cover/forage edges. We expect that the relationship with distance to cover/forage edge in our analysis might strengthen once remote sensing imagery from 2018 and 2019 become available: in this landscape, distance to cover/forage edges in a given location can change quickly due to high rates of timber harvest, suggesting that the data available for this study (2016 and 2017) could be less representative of actual conditions during the study. Our top model predicted high elk density in areas with

higher precipitation rates. We suggest that higher elk densities in areas with higher precipitation in the two weeks prior to sampling reflects the influence of precipitation on availability of green forage in spring, when elk transition from conifers to grass as a major food source (Leslie 1982, Jenkins and Starkey 1991).

In the McKenzie WMU, our best density model predicted lower elk density on steep slopes and higher density close to fields planted with crops commonly depredated by elk (e.g., wheat, hay, and grass of various types). We expected a negative relationship between percent slope and density, but suggest that this relationship was amplified because most steep slopes occurred on the Willamette National Forest, where low levels of early seral habitat remain after the implementation of the Northwest Forest Plan (Phalan et al. 2019). In the McKenzie WMU, flat areas consisted of commercial agricultural fields, timberlands, high-alpine meadows, and high-alpine forests, which provide more foraging opportunities. We also predicted higher elk density close to habitats classified by CropScape as spring and winter wheat, other hay/non alfalfa, sod/grass seed, other tree crops, or grassland/pasture, of which 82% was classified as sod/grass seed and grassland/pasture in McKenzie. Our model predicted elk in the wilderness portion of McKenzie WMU, an area that ODFW has been unable to monitor due to aircraft restrictions. We found few viable samples in our transects there, although older samples were observed; therefore, density predictions in this region were largely influenced by covariate relationships described in areas with higher elk densities farther to the west in the WMU. To improve density estimates for wilderness areas,

we recommend further investigation into relationships between elk densities and covariates in high-alpine habitats.

In both WMUs, recent precipitation and transect length influenced our probability of detecting an individual. We expected an increase in average daily precipitation would decrease the density of viable samples as observed by Barnes et al. (1997), thus reducing our probability of detecting a sample with a mucosal layer for genetic analysis. However, we suspect that the positive relationship we observed occurred because rain quickly degrades signs of freshness (e.g., smell, temperature, color, texture), making samples that were recently defecated, and more likely to have a mucosal layer, easier to detect. Moreover, although we expected a positive relationship between transect length and probability of detecting an individual, we observed the opposite. A possible explanation for this results from the aggregation of individuals into herds: when we encountered elk sign, we often encountered sign from many individuals, and therefore walked shorter distances because of the increased time spent examining pellets and collecting viable samples.

While the aggregation of individuals may affect the probability of detecting elk, our calculations of Fletcher's  $\hat{c}$  suggest that aggregation was not high enough to influence our density estimates. Bischof et al. (2020) found instances of bias when simulated groups were greater than 8 individuals and cohesion among individuals was low. Aerial surveys conducted in our study areas indicate average herd size is above 8 individuals (ODFW, unpublished data); however, detections in such visual surveys are biased towards larger herds (McCorquodale et al. 2013), suggesting that true average herd size could be lower. Additionally, the simulations conducted by Bischof

et al. (2020) used equal group sizes, and did not explore the effects of variation in group size on density estimates and Fletcher's  $\hat{c}$ . Although SCR analyses have been used to estimate density of gregarious species that display different levels of aggregation and cohesion of individuals, including wolves (López-Bao et al. 2018), giraffes (*Giraffa camelopardalis*; Muneza et al. 2017), chimpanzees (Granjon et al. 2017) and now elk, the effects on density estimates of aggregation of individuals and non-independence among redetections requires further exploration.

As predicted, we estimated fewer elk on federal lands and more elk on lands where commercial timber harvest occurs. Previous studies in this region recognize that elk can access herbaceous forages more easily in meadows and clear cuts, particularly in deep snow, and indicate elk select early-seral habitats, which active timberlands consistently provide (Harper et al. 1967, Harper 1985, Cook et al. 2016). Although our estimates vary in precision, we observed clear differences in elk density between public and private land, presumably due to their timber harvest practices. Further research that investigates how different land practices or logging methods affect available early-seral habitat, elk habitat use, and elk vital rates could elucidate the mechanisms behind this difference.

Previous studies that have attempted to monitor forest-dwelling ungulate populations face a variety of biases and limitations. Fecal pellet surveys (i.e., counts or estimates of pellet density) could detect whether a population is increasing or decreasing over time and are inexpensive and feasible in the Pacific Northwest (Lehmkuhl et al. 1994, Plumtree and Harris 1995, Rowland et al. 2006), but it is difficult to assess whether the assumptions required to translate those estimates to

abundance are met when true density is unknown (Mills et al. 2005). Mark-resight methods reveal population trends and are less time-intensive, but their detections are biased toward large group sizes, use invasive capture methods, increase safety risks, and are expensive (McCorquodale et al. 2013). Capture-recapture analyses on individuals identified from fecal samples (Eggert et al. 2003, Brinkman et al. 2011) produce abundance estimates successfully but do not reliably translate to density if SCR methods are not employed. Our non-invasive method, at the level of sampling effort described, produced density estimates at an acceptable level of precision for management in areas with moderate to high elk density. However, our method required intensive sampling on lands with restricted access and challenging terrain, and incurred additional costs for genotyping and field time compared to costs of a helicopter survey.

## **MANAGEMENT IMPLICATIONS**

In the Pacific Northwest, management of Roosevelt elk populations is tied to a variety of financial and recreational interests and generates high public attention. Attempts to maximize hunting opportunities and reduce human-wildlife conflict would be aided by accurate and precise estimates of elk population density. However, individual elk are visually indistinguishable and frequent dense habitats, making most methods for estimating abundance and density of cryptic species infeasible. Spatial capture-recapture using non-invasive collection and genotyping of fecal pellets allowed us to estimate elk density and identify spatial and non-spatial factors that influenced density, probability of detection, and movement. Employing this method in areas with low elk density would require greater sampling intensity to achieve

adequate numbers of spatial recaptures or stronger assumptions about which areas are not possible activity centers. We consistently estimated higher elk density on lands with more timber harvest, most of which occurs on private property. This suggests that public recreational opportunities involving elk (hunting, wildlife viewing) may be more limited on public lands due to lower elk density.

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**Table 1** Summary of fecal samples collected from walking transects in 2018 and 2019 to estimate Roosevelt elk density in two western Oregon wildlife management units, Tioga and McKenzie. Genotyping success indicates the percent of samples that genotyped at the minimum number of loci required to be included in SCR analyses.

Year	Tioga			McKenzie		
	Transects Sampled	Samples Collected	Genotyping success	Transects Sampled	Samples Collected	Genotyping success
2018	96	542	37%	119	82	46%
2019	104	542	46%	115	86	23%
<b>Total</b>	<b>200</b>	<b>1084</b>	<b>41%</b>	<b>234</b>	<b>168</b>	<b>35%</b>

**Table 2** Summary of unique and redetected individuals that were detected after genotyping fecal samples of Roosevelt elk. Samples were collected in 2018 and 2019 from two western Oregon wildlife management units, Tioga and McKenzie, to estimate Roosevelt elk density. Samples were sexed using a sex-determining marker. The number of samples sexed female (F), male (M), and unknown (U) are indicated. In 2019, one male was censored to eliminate inflation of sigma.

	Tioga								McKenzie							
	2018				2019				2018				2019			
	Total	F	M	U	Total	F	M	U	Total	F	M	U	Total	F	M	U
Unique	122	81	27	14	167	106	32	29	24	11	11	2	14	9	3	2
Redetected	41	28	12	1	55	39	12 <sup>a</sup>	3	8	2	6	0	4	4	0	0

a- censored individual



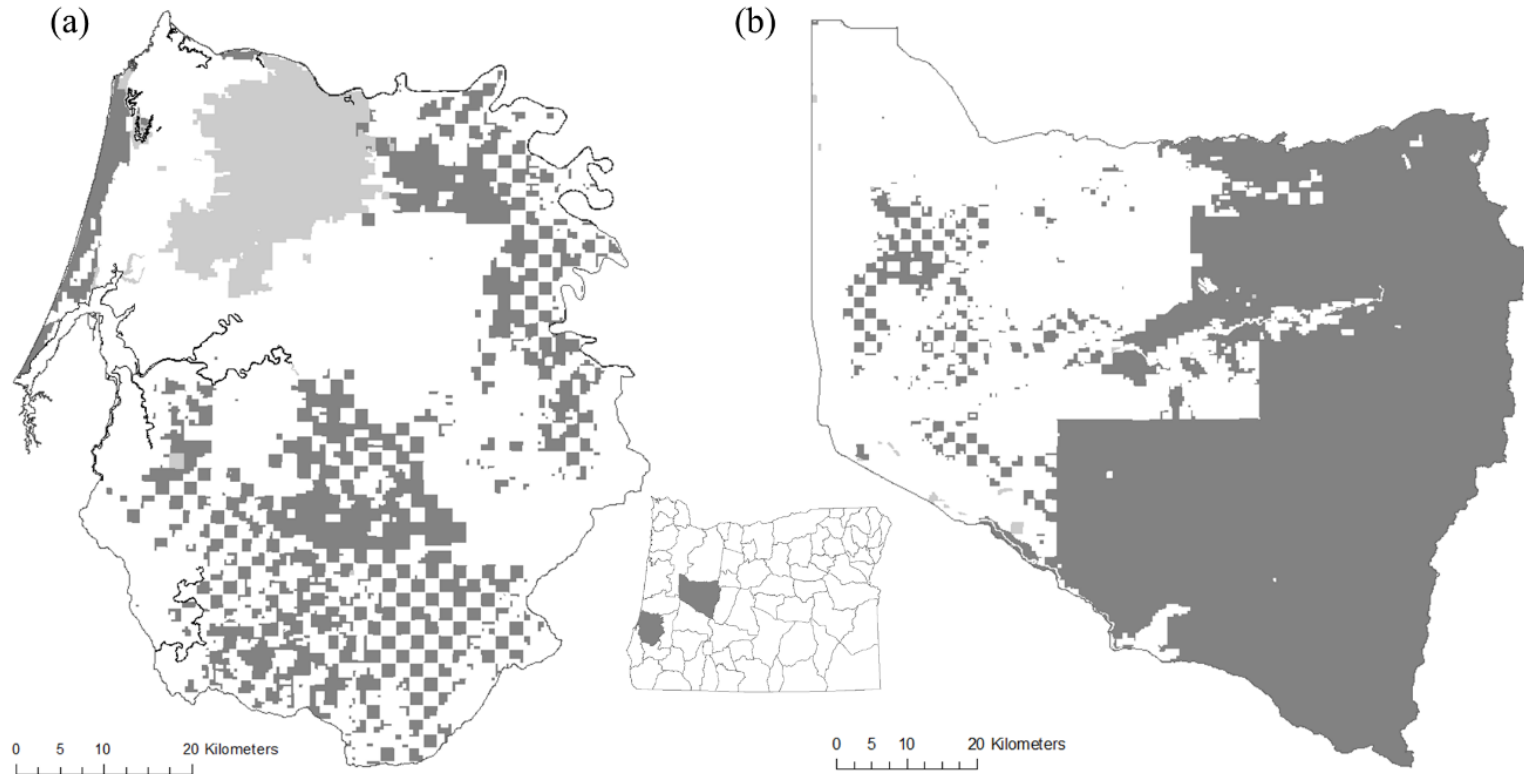
**Table 3** Number of unique Roosevelt elk detected at a given number of transect segments in a study estimating elk density in western Oregon from collected fecal pellets in 2018 and 2019.

# segments detected	Tioga		McKenzie	
	2018	2019	2018	2019
1	90	129	20	19
2	25	31	3	0
3	4	4	1	0
4	1	2	0	0
5	0	0	0	0
6	1	0	0	0

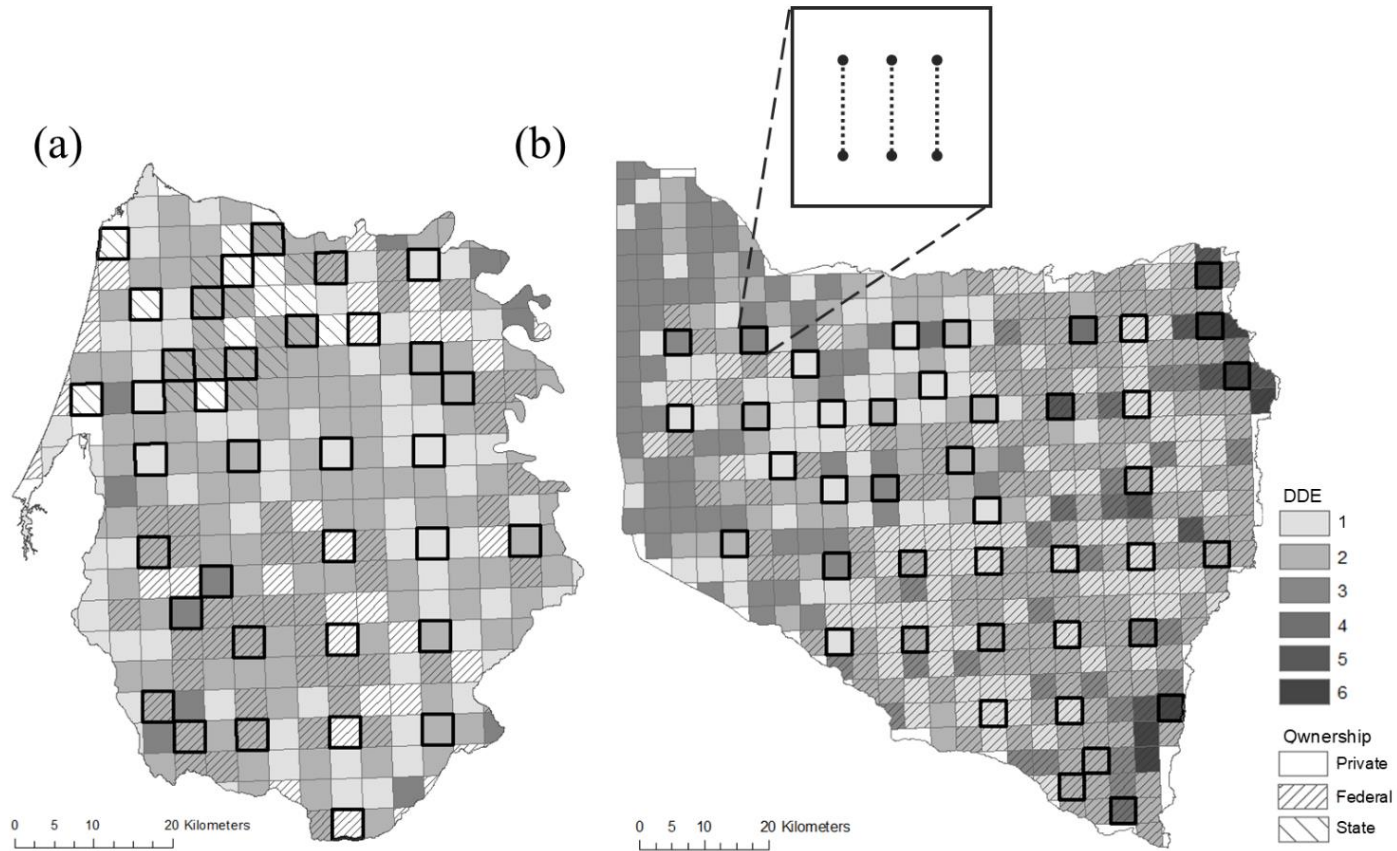
**Table 4** Model selection for probability of detection and density models for spatial capture-recapture analysis fitted to genetic capture-recapture data collected in 2018 and 2019, used to estimate density of Roosevelt elk in western Oregon in the Tioga Wildlife Management Unit, including number of parameters (K),  $\Delta AIC_c$  scores, and  $\Delta AIC_c$  weights. Models were fitted using a hazard half-normal function in the R-package secr (Efford 2020). Average daily precipitation<sub>2 weeks prior</sub> was calculated from daily precipitation maps, obtained from PRISM Climate Group, Oregon State University. Effort was based on the distance technicians searched for fecal pellets on transects. Distance to cover/forage edge and dietary digestible energy (DDE) were calculated using methods described by Rowland et al. (2018) and average DDE and percent slope were calculated with a buffer with a 350 m radius.

Analysis	WMU	Model Structure	K	$\Delta AIC_c$	$\Delta AIC_c$ weight
Probability of detection	Tioga	Effort + average daily precipitation <sub>2 weeks prior</sub>	5	0	0.65
		Effort + average daily precipitation <sub>2 weeks prior</sub> + Julian day	6	2.07	0.23
		Effort + Julian day	5	3.91	0.09
		Effort	4	6.74	0
		Julian day	4	57.45	0
		Average daily precipitation <sub>2 weeks prior</sub>	4	58.90	0
		Year	4	59.11	0
		Null	3	61.87	0
	McKenzie	Effort + average daily precipitation <sub>2 weeks prior</sub>	5	0	0.66
		Effort + average daily precipitation <sub>2 weeks prior</sub> + Julian day	6	1.63	0.29
		Effort	4	6.50	0.03
		Effort + Julian day	5	7.56	0.02
		Average daily precipitation <sub>2 weeks prior</sub>	4	10.16	0
		Year	4	13.05	0
		Null	3	14.59	0
		Julian Day	4	17.06	0

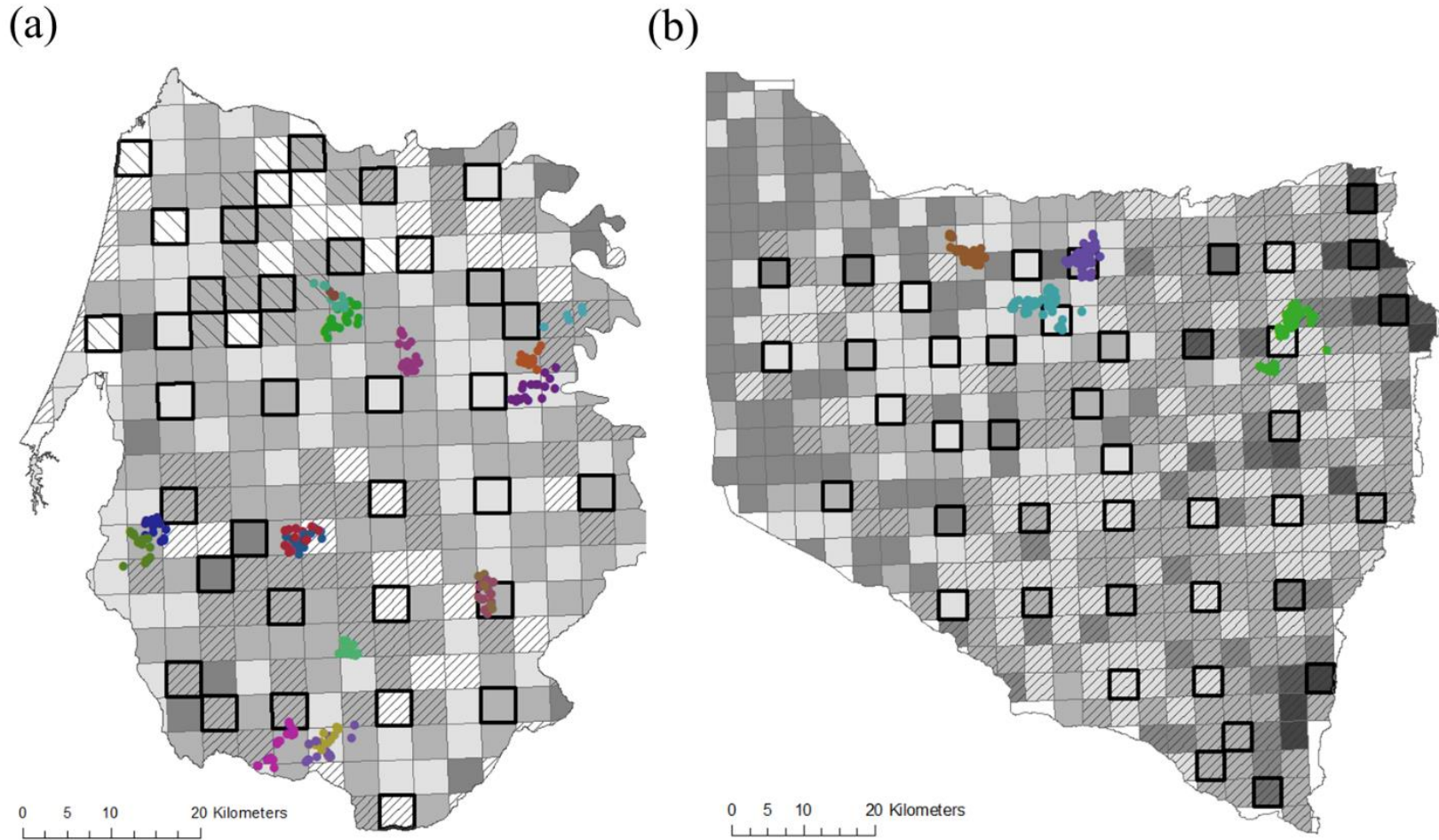
Density	Tioga	Distance to nearest road + Distance to cover/forage edge + average daily precipitation	8	0	0.99
		Distance to cover/forage edge + average daily precipitation	7	9.59	0.01
		Distance to nearest road + Distance to cover/forage edge	7	11.19	0
		Distance to nearest road + average daily precipitation	7	15.65	0
		Distance to nearest road	6	19.63	0
		Distance to nearest road + percent slope	7	20.80	0
		Distance to nearest road + Distance to cover/forage edge	7	21.09	0
		Distance to cover/forage edge	6	30.57	0
		Average daily precipitation	6	37.11	0
		DDE	6	47.55	0
		Percent slope	6	47.63	0
	McKenzie	Distance to crops + percent slope	7	0	0.86
		Distance to crops	6	5.51	0.06
		Distance to crops + percent slope + Distance to cover/forage edge	8	5.80	0.05
		Distance to crops + Distance to cover/forage edge	7	7.30	0.02
		Distance to crops + distance to roads	7	8.36	0.01
		Distance to crops + DDE	7	10.76	0
		Distance to crops + average daily precipitation	7	10.90	0
		Percent slope	6	43.60	0
		Distance to cover/forage edge	6	50.79	0
		Distance to roads	6	56.54	0
		DDE	6	64.77	0



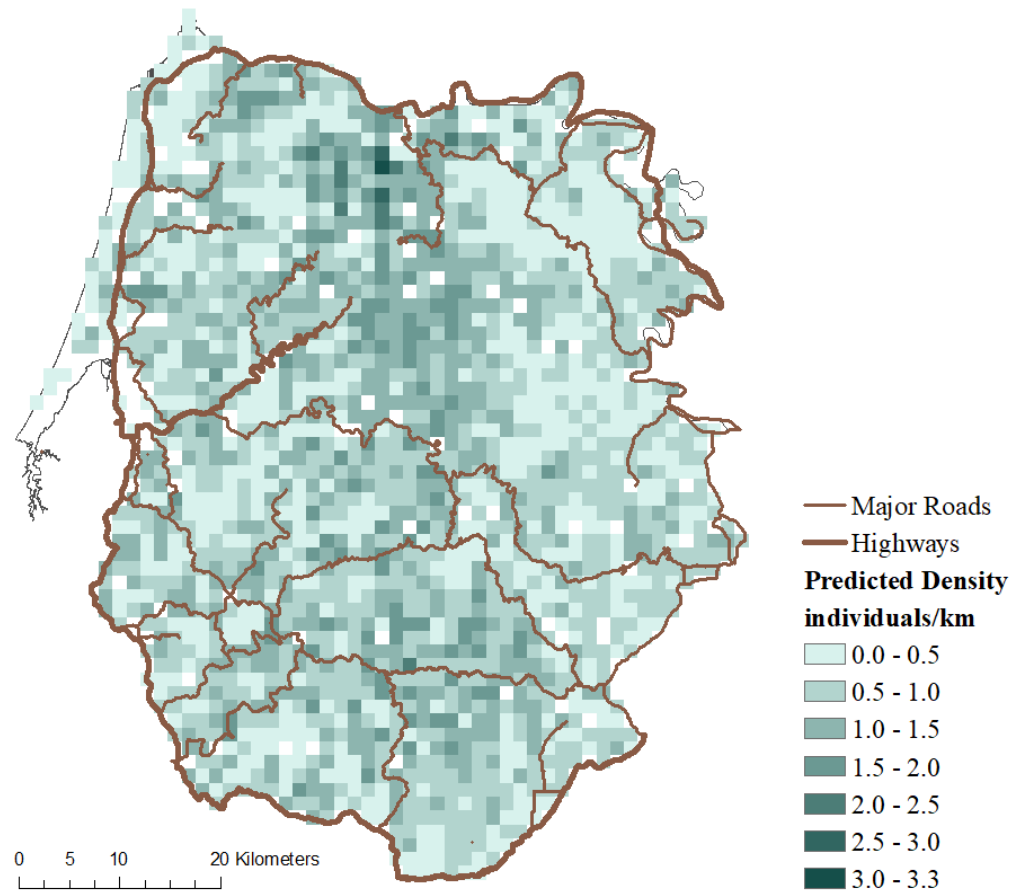
**Figure 1.** Wildlife management units in western Oregon, USA, including (a) Tioga and (b) McKenzie, where population density of Roosevelt elk was estimated in spring 2018 and 2019. Tioga (3,797 km<sup>2</sup>) is managed by private (white; 33%), state (light grey; 10%), and federal (dark grey; 25%). McKenzie (6,847 km<sup>2</sup>) is managed by private (white; 39%), state (light grey; <1%), and federal (dark grey; 61%).



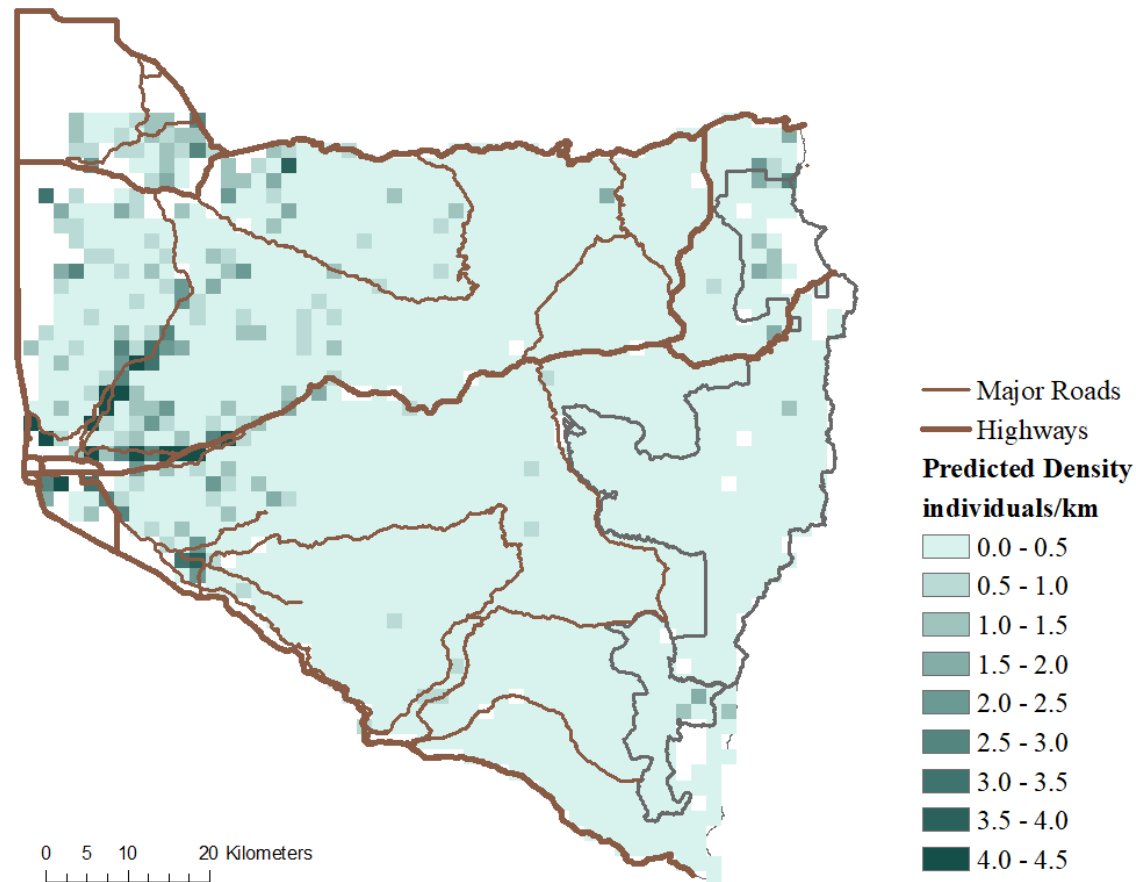
**Figure 2** Sampling schematic for estimating density of Roosevelt elk in two western Oregon wildlife management units, including (a) Tioga and (b) McKenzie. A grid of 15.48 km<sup>2</sup> cells classified by majority land ownership type and average dietary digestible energy (DDE) overlay each unit. An initial cell was randomly identified and cells selected for sampling (outlined in black) were subsequently spaced  $2\sigma$  apart. Selected cells shifted to reflect each combination of ownership type and DDE present while attempting to maintain a spacing of  $2\sigma$ .



**Figure 3** Locations of 17 and 4 female elk in Tioga (a) and McKenzie (b), collected from GPS collars during the 2019 sampling period. Locations were used to inform the spatial scale parameter, sigma ( $\sigma$ ), in spatial capture-recapture analyses.



**Figure 4** Predicted density map of Roosevelt elk in the Tioga wildlife management unit, western Oregon, for 2019. Predictions were produced from spatial capture-recapture models fit to capture histories constructed from non-invasively collected DNA. In 2018 and 2019, 542 and 542 fecal pellets were collected, of which 37% and 46% of samples successfully genotyped. Genotypes considered successful amplified at no less than four loci, the minimum number of loci required to reliably distinguish individuals while satisfying thresholds of  $P_{ID} < 0.001$  and  $P_{IDSibs} < 0.05$



**Figure 5** Predicted density map of Roosevelt elk in the McKenzie wildlife management unit, western Oregon, for 2019. Predictions were produced from spatial capture-recapture models fit to capture histories constructed from non-invasively collected DNA. In 2018 and 2019, 82 and 86 fecal pellets were collected, of which 46% and 23% of samples successfully genotyped. Genotypes considered successful amplified at no less than four loci, the minimum number of loci required to reliably distinguish individuals while satisfying thresholds of  $P_{ID} < 0.001$  and  $P_{IDSibs} < 0.05$ .



Chapter 4

GENERAL CONCLUSION

Jennifer Nelson

## **GENERAL CONCLUSION**

The goal of this study was to determine whether sampling fecal DNA in a spatial capture-recapture framework could provide wildlife managers in the Pacific Northwest with a dependable and precise method to monitor Roosevelt elk populations. The sampling design employed in this study not only produced point estimates of density and 95% confidence intervals for wildlife management units (WMUs), but also identified covariate relationships among density, environmental factors, and land practices. In WMUs where elk are sparsely distributed, sampling intensity must be high to obtain adequate redetection rates to conduct analysis with spatial capture-recapture models.

Agencies such as Oregon Department of Fish and Wildlife and Washington Department of Fish and Wildlife may use this study as a framework to estimate elk density and better assess whether management objectives are being met in dense habitats. However, before implementation, biologists must consider how much sampling needs to occur to obtain a desired level of precision. Both agencies contribute to ongoing research efforts to improve our understanding of how elk use and move through habitats at coarse and fine scales. As demonstrated in this study, such information will help explain the relationships among elk density and covariates when employing spatial capture-recapture models.

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**Appendix 1.** – Supplemental information on genotyping methods.

**Table A.1** Primers used to amplify nine microsatellite loci and one sex-determining marker in a 2018-2018 study to estimate Roosevelt elk density from fecal pellets in western Oregon, USA. The direction (forward, F; revers, R) of each primer is indicated as well as the size range (base pairs; bp) for each amplicon.

<b>Locus</b>	<b>Direction</b>	<b>Primer sequence</b>	<b># alleles</b>	<b>range (bp)</b>	<b>dye</b>	<b>panel</b>	<b>Reference</b>
C143	F	AAGGAGTCTTTCAGTTTTGAGA	4	158-170	vic	1	Meredith et al. (2005)
C143	R	GGTTCTGTCTTTGCTTGTTG					Meredith et al. (2005)
TE83	F	CAGATGCTACAGTGAAGACCA	4	98-108	fam	1	Sacks et al. (2016)
TE83	R	GTTTTTTGTGTCAAACAGAGCGGTGAG					Sacks et al. (2016)
TE167	F	TGCTCCTTGTTTTACATTAAGCTG	7	230-256	pet	1	Sacks et al. (2016)
TE167	R	GTTTCTTAAGCAGAGTCTGTGGAAGACC					Sacks et al. (2016)
TE179	F	TCAGTCCAGGCATTACTTTGC	4	218-224	vic	1	Sacks et al. (2016)
TE179	R	GTTTATTGCAAGTTGTGTGCTTCG					Sacks et al. (2016)
T172	F	AGCATCTCCCCTTTCAACA	6	172-196	pet	2	Jones et al. (2002)
T172	R	GTTTCTTCCCAACCCAAGTATCG					Sacks et al. (2016), pigtailed version of Jones et al. (2002)
T193	F	AGTCCAAGCCTGCTAAATAA	8	177-213	vic	2	Jones et al. (2002)
T193	R	GTTTCTGCTGTTGTCATCATTACC					Sacks et al. (2016), pigtailed version of Jones et al. (2002)
TE182	F	GTCAAAGACCCCTCCGTTTC	4	216-226	pet	2	Sacks et al. (2016)
TE182	R	GTTTCTAGTGCAGATGATCAAGGAGC					Sacks et al. (2016)
NVHRT21	F	GCAGCGGAGAGGAACAAAAG	5	141-153	fam	2	Røed and Midthjell (1998)
NVHRT21	R	GGGGAGGAGCAGGGAAATC					Røed and Midthjell (1998)

RT1	F	TGCCTTCTTTCATCCAACAA	4	215-229	ned	2	Wilson et al. (1997)
RT1	R	CATCTTCCCATCCTCTTTAC					Wilson et al. (1997)
SE47*	F	GTGGATGGCTGCACCACCAA	n/a	206 (Y), 258 (X)	ned	1	Yamamoto et al. (2002)
SE48	R	CCCGCTTGGTCTTGTCTGTTGC					Ennis and Gallager (1994)

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\*Sexing locus

**Table A.2** Locus-specific estimates of probability of identity ( $P_{ID}$ ) and probability of identity among siblings ( $P_{IDSibs}$ ) from genotypes extracted from fecal DNA of Roosevelt elk in two western Oregon wildlife management units (Tioga and McKenzie). Fecal pellets were collected to estimate density of elk populations in 2018 and 2019. The cumulative calculation of  $P_{ID}$  and  $P_{IDSibs}$  represent the probability of incorrectly distinguishing one individual from another and among all individuals and siblings, respectively. The loci are ordered from least informative to most.

<b>Locus</b>	<b>Tioga</b>		<b>Locus</b>	<b>McKenzie</b>	
	<b><math>P_{ID}</math></b>	<b><math>P_{IDSibs}</math></b>		<b><math>P_{ID}</math></b>	<b><math>P_{IDSibs}</math></b>
TE179	0.48	0.71	RT1	0.38	0.60
TE83	0.35	0.71	TE83	0.35	0.58
TE182	0.35	0.61	TE179	0.28	0.56
RT1	0.34	0.58	NVHRT01	0.24	0.52
T172	0.31	0.56	T172	0.23	0.51
C143	0.26	0.52	C143	0.19	0.47
NVHRT01	0.21	0.49	TE182	0.16	0.45
TE167	0.13	0.43	TE167	0.10	0.40
T193	0.11	0.42	TE193	0.10	0.40
<b>Cumulative</b>	<b><math>5.0 \times 10^{-6}</math></b>	<b><math>3.7 \times 10^{-3}</math></b>		<b><math>5.8 \times 10^{-7}</math></b>	<b><math>1.7 \times 10^{-3}</math></b>

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