TARGETING SOCIAL COHESION IN FEMALE ROOSEVELT ELK (CERVUS CANADENSIS ROOSEVELTI) GROUPS MINIMIZES SURVEY EFFORTS FOR FECAL DNA CAPTURE-RECAPTURE ESTIMATES OF ABUNDANCE

By

Rudolph Gabriel Mena

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Committee Membership

Dr. Micaela Szykman Gunther, Committee Chair

Dr. Daniel Barton, Committee Member

Dr. William Bean, Committee Member

Dr. Andrew Stubblefield, Graduate Coordinator

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ABSTRACT

TARGETING SOCIAL COHESION IN FEMALE ROOSEVELT ELK (CERVUS CANADENSIS ROOSEVELTI) GROUPS MINIMIZES SURVEY EFFORTS FOR FECAL DNA CAPTURE-RECAPTURE ESTIMATES OF ABUNDANCE

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Group size abundance estimates of Roosevelt elk (*Cervus canadensis roosevelti*) in Humboldt and Del Norte counties, California have largely been inferred through visual counts. However immigration and emigration, the inability to sight elk behind viewing obstructions, and a lack of individual identifiers makes precise and accurate estimates difficult to obtain. Using DNA collected through fecal samples left by elk groups can aid in addressing these difficulties. I tested the hypothesis that GPS (Global Positioning System) collar data from adult female elk could indicate discrete site use locations of their social groups, which in turn yield sufficient sample sizes for use in a capture-recapture framework of abundance estimates of group size. I also evaluated the relationship between increased site use and the rate of capturing individual elk through fecal DNA by analyzing GPS collar data in Local Convex Hull (LoCoH). I found that GPS location data from female elk were sufficient in delineating discrete fecal DNA sampling sites that could be used to calculate group size estimates within 2-4 sampling occasions. I also found that more intensely used sites indicated by LoCoH yielded more unique genotypes when compared to lesser used locations for 2 of the 3 elk groups in this

study. Abundance estimates were confounded by shifting elk social dynamics during the rutting season, indicating that sampling during times of increased social cohesion and increased site use (i.e., January and February) could be more efficient for estimating group size.

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INTRODUCTION

Roosevelt elk (*Cervus canadensis roosevelti*) have long been a species of interest to several native tribal groups, wildlife management agencies, tourism industries, and private landowners (Raedeke et al. 2002). However, little about this species' demography and distribution within its present range is known. Population estimates for these elk have largely been inferred through opportunistic visual counts (Weckerly and Kovacs 1998, Weckerly 2007, Julian et al. 2013). By necessity, these observations have generally occurred in open meadows, areas where elk are more readily observable, due to the logistical difficulties of collecting count data in alternative habitat types (e.g., forests and areas of varying topography) (Weckerly 2007). For these reasons, traditional methods of identifying individuals for sight-resight estimates are confounded by the inaccessibility of groups that tend to utilize areas not readily visible during visual counts (Jenkins and Starkey 1982, Pollock et al. 2002). This, in turn, results in heterogeneous detection rates, which are biased high towards individuals more readily observed in open habitats (Weaver and Weckerly 2011).

Similar challenges to visually counting wildlife have inspired techniques that estimate abundance in a capture-recapture framework using genetic material left behind by a species of interest (Eggert et al. 2003, Lukacs and Burnham 2005, Ebert et al. 2012). Known as genetic capture-recapture, this technique uses DNA from individuals of a target species (usually obtained through hair or fecal samples), to estimate abundance with greater precision and less invasiveness than traditional mark-recapture efforts. This

technique reduces the risk of negative behavioral responses or injuries that are inherent in physically interacting with an animal for marking (Murray and Fuller 2000).

Originally developed to estimate population sizes of elusive animals such as coyotes (*Canis latrans*) (Kohn et al. 1999), wolves (*Canis lupus*) (Stenglein et al. 2010), and badgers (*Meles meles*) (Wilson et al. 2003), genetic capture-recapture has since been used to estimate abundances of grouping animals such as argali (*Ovis ammon*) (Harris et al. 2010), wild boar (*Sus scrofa*) (Ebert et al. 2012), and Sonoran pronghorn (*Antilocapra americana sonoriensis*) (Woodruff et al. 2016). However, creating sampling schemes that maximize capture rates of individuals is often a challenge due to the differences in ways species utilize space (Thompson 1990, Lukacs and Burnham 2005). In addition, large scale abundance monitoring of wildlife populations can become unmanageable as sufficient sample sizes for accurate population estimates cannot be obtained effectively (Pollock et al. 2002).

Obtaining high capture rates for a target population during sampling occasions has been found to greatly increase the accuracy of capture-recapture estimates (Lukacs and Burnham 2005, Petit and Valiere 2006). Without prior knowledge of how many individual animals or groups deposited the samples collected, surveys that optimize capture rates based on a species' known behavioral ecology, habitat use, and interactions with the environment become necessary. In addition, assessing demographic closure during a sampling interval is also necessary when using mark-recapture methods because emigration and immigration in a target population can negatively or positively bias point estimates of abundance (Harris et al. 2010, Hettinga et al. 2012).

Seasonal reproductive cycles and forage availability act as the primary drivers of elk movement and social cohesion of female groups (Weckerly 2005, Kolbe and Weckerly 2015), which in non-migratory populations is defined by the constant association between adult females (Bender and Haufler 1999). Through spring and early summer, adult females become solitary during calving (Bowyer 2004). During this period, social cohesion of adult females is at its lowest point of the year (Jenkins and Starkey 1982, Weckerly 1999). As their newborn calves become more resilient, adult females begin to congregate in late summer (Bowyer 2004). During the fall rutting period, dominant males will follow and push female groups (mainly composed of adult females and their young) into large harems to maximize breeding opportunities, while warding off other potential adult male suitors and preventing adult females from leaving the group (Bowyer 1981, 2004). As a result, relative closure of a female group is maintained as long as rutting bulls can persist in their rut, which is largely determined by their physical condition during this period. Entering the winter months, males become less territorial and the species clusters into even larger groups at low elevations (Weckerly 1999, Bowyer 2004, Kolbe and Weckerly 2015). During this time resource availability is at its lowest and group cohesion is at its highest, resulting in large groups utilizing more discrete patches of space.

This typical seasonal ecology has been found to vary in coastal non-migratory Roosevelt elk groups in California (Bowyer 1981, Jenkins and Starkey 1982, Weckerly 2005). Snow-free grazing habitats promote increased social cohesion and bonding in some groups throughout the year (Jenkins and Starkey 1982), whereas elk that utilize

silviculturally managed forests exhibit less social cohesion and have a higher rate of movement of individuals between groups. However, despite this variation in their ecology, groups of elk in Humboldt and Del Norte counties in northern California display the behaviors of sexual segregation during summer months and clustering during the fall and winter seasons that are typical of migratory populations (Franklin et al. 1975, Bowyer 1981, Bliss and Weckerly 2016).

The phenomenon of increased social cohesion and concentrated space use in the winter months has been exploited in traditional methods of counting elk such as aerial (Anderson et al. 1998, Weckerly and Kovacs 1998) and road surveys (Weckerly 2007, Starns et al. 2015). It also facilitates targeting locations frequented by grouping ungulates for collecting fecal DNA samples (Hettinga et al. 2012, Woodruff et al. 2016). Unfortunately, rainfall in Humboldt and Del Norte counties is at its highest during this time of year, which may decrease the likelihood of successfully amplifying DNA from fecal samples (Goode et al. 2014, NOAA 2018). For ungulate species, the rate of successful amplification of genetic samples decreases as exposure to rainfall increases, which in turn can decrease the probability of capturing a group during the rainy season (Brinkman et al. 2009).

As a result, sampling fecal DNA during the fall months when group cohesion increases from the summer months due to the rutting season, and when successful fecal DNA amplification is less likely to be affected by the frequent precipitation that is typical of the winter season, may be the most viable alternative to sampling during the winter. During this time, the vast majority of behavioral activity exhibited by established

dominant adult males (i.e., master bulls) is targeted toward the possession of adult female groups (Bowyer 1981). Far less activity is spent towards warding off bulls seeking to possess females, resulting in master bulls often maintaining cohesion of female groups in excess of a month. The movements of a single adult female may likely be indicative of those of her respective group during this time suggesting that using the spatial positions of one female is likely to represent those of her respective group.

Monitoring Global Positioning System (GPS) collared animals has provided wildlife managers with efficient methods for understanding the ecology of grouping species (Thirgood et al. 2004, Ensing et al. 2014). However, without the ability to continuously observe collared individuals, objectively determining how representative GPS collar data is of a group's space use can be difficult. Sampling for fecal DNA at a site used by a GPS collared cow offers the potential to capture a segment of all individuals in her group, particularly during periods of high social cohesion. Furthermore, capturing individual elk in a group through fecal DNA at one location used by a collared cow can be supplemented by subsequent captures of additional individuals in the same group at another location used by the same cow. Using these sampling locations as occasions in a capture-recapture framework can promote the ability to obtain estimates of abundance for the entire group of interest.

The objective of this study was to determine how social cohesion and GPS collar data from adult female Roosevelt elk could inform estimates of group abundance through fecal DNA capture-recapture (FCR) analysis. Using the GPS locations of 4 elk cows from 3 distinct groups, I aimed to test two hypotheses: (1) the discrete locations used by GPS-

collared elk cows are indicative of the space-use of their respective female social groups and (2) using individual genetic profiles of elk identified through fecal DNA at these locations can be used to determine accurate and precise estimates of group sizes.

I predicted that (1) sampling within survey plots at recently utilized sites by GPS collared cows would yield fecal DNA samples that contained individual genetic markers of their respective social group and (2) these locations would yield sufficient sample sizes to delineate capture-recapture occasions for estimates of female elk group size. By examining the relationship between space use and capture probability through fecal DNA, this study can aid in future assessments of elk population abundance.

MATERIALS AND METHODS

Study Area

This study focused on approximately 24.4 km^2 in Humboldt and Del Norte counties in northwestern California (Figure 1). The study area comprised a variety of habitats utilized by Roosevelt elk that span multiple land management areas including National and State Parks, National Forests, and private land (Jenkins and Starkey 1982, Kolbe and Weckerly 2015). The maritime climate is characterized by a rainy season from October to April that can exceed 200 cm of precipitation (NOAA 2018). This is contrasted by a dry season from May to September that experiences less than 21 cm of precipitation. Elevations of the study area range from 15-934 m.

Visual counts and fecal DNA collection were concentrated on 3 elk groups. Two of these groups were previously defined and utilized habitat typical of elk in Humboldt County (Starns et al. 2015). The third group, defined in this study, contained 2 GPS-collared elk originally collared near Rowdy Creek and Hastings Tree Farm near the town of Smith River, California. Together, these 2 cows will be referred to as part of the Rowdy/Hastings group. An elk group was defined as individual elk seen within 50 m of one another (Weckerly 1999). Visual observations suggested these groups moved together throughout their home ranges (Starns et al. 2015).

The Davison Meadows group occupied approximately 3.1 km^2 of the southern extent of the Prairie Creek drainage north of the town of Orick, California during data

collection for this study (Figure 1). This area is bisected by the major US Highway 101 and consists of open meadows frequented by tourists (Starns et al. 2015). The Davison Meadows study area consisted of secondary and old-growth redwood-conifer forests that also contain Sitka spruce (*Picea sitchensis*), and Douglas fir (*Pseudotsuga menziesii*) with an understory of bracken fern (*Pteridium aquilinum*), willow (*Salix* sp.), red alder (*Alnus rubra*), Himalayan blackberry (*Rubus discolor*), horsetail (*Equisetum* sp.), and wax myrtle (*Myrica californica*). Small meadows were dispersed throughout the area, towards which elk in the region display strong site fidelity (Starns et al. 2015).

The Bald Hills group occupied approximately 8.9 km^2 of aggregate meadows near forest edge on the south/southwest facing ridgeline of Redwood Creek (Starns et al. 2015) during this study. The study area consisted largely of Douglas fir with meadows interlaced with tanoak (*Lithocarpus densiflorus*), madrone (*Arbutus menziesii*), big-leaf maple (*Acer macrophyllum*), California bay (*Umbellularia californica*) and red alder (Starns et al. 2015). Roosevelt elk in the Bald Hills region display seasonal affinity towards areas where forage is available (Kolbe and Weckerly 2015). The Davison Meadows and Bald Hills groups' home ranges encompassed areas within Redwood National and State Parks and privately-owned land.

The Rowdy Creek and Hastings Tree Farm groups primarily utilized approximately 12.4 km^2 of silviculturally-managed forests (Figure 1) during this study. The majority of this land was adjacent to privately owned grass fields, which elk in this group frequented on the eastern side of US Highway 101 south of the town of Smith River, CA. The study area consisted of an aggregate of timber stands and clear cuts,

which largely consisted of coast redwood (*Sequoia sempervirens*), Douglas fir, and western hemlock (*Tsuga heterophylla*). Adjacent meadows contained annual grasses (*Festuca* sp.), perennial grasses (*Lolium* sp.) and forbs (*Ranunculus* sp., *Trifolium* sp., *Lupinus* sp.) (Weckerly and Ricca 2000).

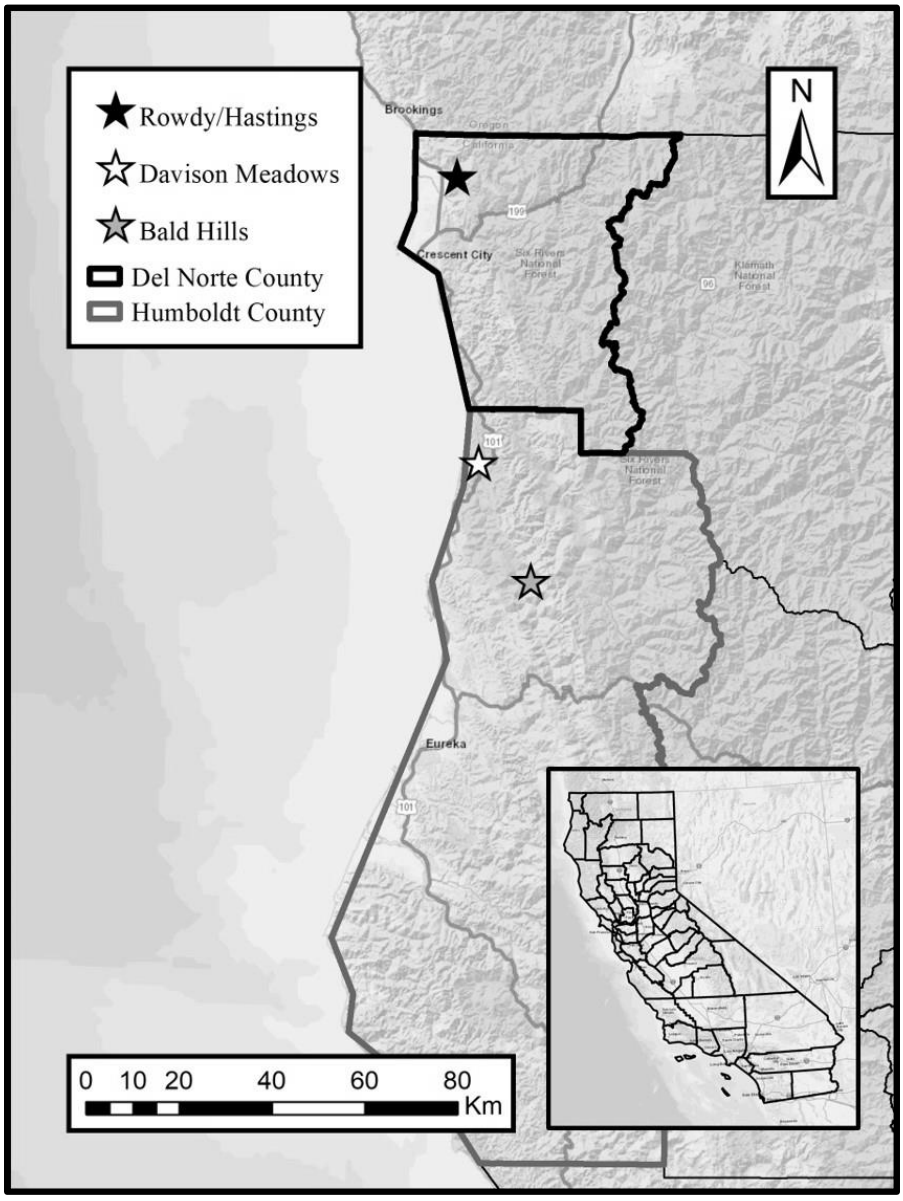

Figure 1. The Davison Meadows, Bald Hills, and Rowdy/Hastings study areas in Humboldt and Del Norte counties California, USA for use in fecal DNA capture-recapture abundance estimates of female elk groups during Sep - Nov 2017.

GPS Collaring

I used the locations of 4 female GPS-collared Roosevelt elk as proxies to the movements and space use of their respective social groups. Each of these elk were GPS-collared and monitored in a larger effort by the California Department of Fish and Wildlife to monitor elk populations in northwestern California. The Humboldt State University's Institutional Animal Care and Use Committee approved all capture efforts (Protocol #15/16.W.96-A). Throughout each fecal DNA sampling period, the locations of these elk cows were collected hourly.

Visual Counts

To acquire baseline data with which the precision of FCR estimates of abundance could be compared, I conducted visual counts of elk groups by driving across each collared cow's previously determined home range (Jenkins and Starkey 1982, Weckerly and Ricca 2000, Starns et al. 2015) throughout each fecal DNA sampling interval. When the group was difficult to locate, I used Very High Frequency (VHF) homing techniques (Edge and Marcum 1989), starting at the most recently recorded GPS location for each collared elk, to find the group. I defined an elk group as elk within 50 m of one another (Weckerly 1999). Upon sighting elk, I documented the number of individuals in the group and classified each elk as either cow (adult female), calf (young elk born within the year), bull (adult male with branched antlers), or spike (juvenile) male with un-branched

antlers) (Weckerly 1999, Starns et al. 2015). I also documented all other instances of elk sighted within each home range that weren't within the collared cow's group.

Elk in the Davison Meadows area exhibited strong habituation to the presence of humans (Starns et al. 2015). Therefore, when possible, I remained close and recounted the group when previously uncounted elk became visible. I used the highest count of each elk classification when multiple counts were conducted during a survey as an estimate of the total number of elk within the group at the time.

I used the total number of elk observed with the Bald Hills cow as my estimate of group size rather than attempting to classify individuals. This was due to the group's relatively large size, and its tendency to flee upon sighting me, making assessments of sex and age difficult. For the Rowdy/Hastings elk, which were also less habituated yet were a smaller group than the Bald Hills elk, I classified individuals in the same manner as the Davison Meadows group. When possible, I observed all elk from a distance greater than 50 m using a pair of binoculars or a spotting scope in order to minimize behavioral changes due to my presence (Bowyer 1981).

Rutting Behavior

For the Davison Meadows group, I documented the presence of rutting behavior by bulls because such activities can alter the social cohesion in adult female groups (Bowyer 1981, Bowyer 2004). I defined rut as the time period when adult bulls possessed and defended harems of cows which generally occurs annually between August and November (Bowyer 1981). This included instances of mating, bugling, harem holding,

and aggressiveness towards other male elk. Unique antler configurations on bulls were also noted to more accurately identify individuals on subsequent visual count occasions.

Fecal DNA Collection and Individual Genotyping

Fecal DNA sampling areas were largely determined by navigable topography, accessibility, and permission by private landowners and state agencies. I targeted such areas that met these criteria using recent GPS locations (< 2 weeks) of each collared elk, giving preference to sites used for at least several hours. I averaged all GPS locations within these discrete sample areas to determine a center for fecal DNA sampling plots.

Upon arriving at this center in the field, a 50.8 m diameter plot (2.03 km^2) for sampling fecal DNA was established. Based on preliminary data on the average distance between scat piles by walking transects in the summer of 2017, this diameter was chosen to be sufficient for sampling discrete site use locations by elk groups while being manageable for 1-2 technicians. Plots were created using a flagged 2 m piece of PVC tubing staked at the center. Two 25.4 m lengths of paracord were then tied to the PVC tubing and laid out to the plot's perimeter to delineate a "wedge" of the plot's area.

Beginning at the plot's center, I walked to the plot's perimeter along a length of paracord while scanning the ground for fecal groupings within both arm's length and continued until the perimeter of the wedge was completely surveyed. I then surveyed the interior of the wedge using the same pattern. Upon completely surveying a wedge, a new wedge was delineated and surveyed until the entire plot was completed. All plots were

sampled once, and each plot was created in a different area of discrete space used by the GPS collared elk.

Upon encountering each fecal grouping within a plot, 4-6 pellets were collected and placed in a 50 mL conical tube (Sachs 2016). Only recently deposited fecal groupings that were moist, odorous, and free of insect activity were sampled to reflect recent use of the site (Weckerly and Ricca 2000) and to avoid low DNA amplification rates due to rain and weathering (Lukacs and Burnham 2005, Brinkman et al. 2009). In addition, samples which met these criteria were targeted to better reflect the recent demography of each elk group (Brinkman et al. 2009), which visual observations indicate changes throughout the year.

Only groupings of 10 or more pellets that were adjacent to one other (no more than 0.1 m from the center of the grouping) were sampled to reduce the likelihood of mixing pellets from different individuals (Goode et al. 2014). After surveying a pile, it was subsequently covered with the surrounding substrate (e.g., dirt, grass, or sticks) or was destroyed in a manner that it could be easily identified as sampled if encountered again. All conical tubes were filled with 95% ethanol for subsequent individual genotyping (Sacks 2016).

Piles that were amorphous or not well-pelleted were sampled by scraping the exterior of the pile with the flat end of a toothpick to collect as many epithelial cells as possible (Sacks 2016). The toothpick was then placed into a small manila coin envelope, sealed, and labeled with a unique identification. All pelleted and amorphous groupings were collected with a fresh pair of nitrile examination gloves for each sample to reduce

risk of contamination. All methods described here for fecal DNA collection were approved by Humboldt State University's Institutional Animal Care and Use Committee (Protocol # 16/17.W.46-E).

Genetic analysis of elk fecal samples was conducted by the University of California, Davis Mammalian Ecology and Conservation Unit of the Veterinary Genetics Laboratory. Samples were analyzed for individual genetic profiles and sex determination using 12 microsatellites and a sex marker previously developed for tule elk (*Cervus canadensis nannodes*) (Sacks et al. 2016). Replicate genotypes (n = 2 per sample) from elk sampled more than once were combined into consensus genotypes. The allele-matching distribution from these genotypes was then analyzed to decide on a threshold above which differences between genotypes were likely due to genotyping error. All remaining samples were then compared to these consensus genotypes where >92% of allele matches were assigned to the same individual and any discrepancies were assumed to be from genotyping error. Individuals having alleles match at > 80% and mismatch at < 85% were then analyzed based on sex, verifiable heterozygote mismatches, and the original electropherograms of all replicates to assess if they could confidently be determined to be different individuals. Profiles that could not be confidently determined as a unique genotype were assigned a low-confidence ranking and were omitted from the capture-recapture analysis. The allelic dropout rate, defined as the probability of not detecting an allele in all heterozygous individuals (Taberlet et al. 1996), was determined using the weighted average of the frequency of allelic dropout at all heterozygous loci (Broquet and Petit 2004) of consensus genotypes.

Group Size Estimates

Each FCR sampling plot was used as a single capture occasion in capture-recapture estimates of group abundance. For example, the Davison Meadows group had 4 unique fecal DNA sampling plots which were combined to create a 4-occasion capture history for that group. I used Huggins' Heterogeneity “pi and p” closed capture modeling in Program MARK to estimate abundance for each group and to examine how different variables influenced capture probability across each sampling period (Harris et al. 2010, Cooch and White 2018). I tested a finite mixture of 2 capture probabilities within each elk group based on the pre-defined model Mth2 in Program Mark (Otis et al., 1978)

$$\{P_a(.) = C_a(.) + t,\ P_b(.) = C_b(.) + t,\ \pi\}$$

for each sex (s) within each estimated elk group. This was done by adding capture probability by sex as an additional beta parameter. P_a (i.e., π) is defined as the probability of an individual occurring in mixture A and P_b (i.e., 1- π) is the probability of an individual occurring in mixture B. I used the term Het to represent the capture probability of the 2 groups in the finite mixture. All interaction beta parameters where removed as a starting model. Reduced models were tested by systematically removing individual beta parameters.

For the Davison Meadows and Bald Hills groups, I also tested models where each occasion (t) varied in capture probability (Harris et al. 2010). I grouped time steps (i.e., capture occasions), which yielded a similar number of individual captures as having

equal capture probabilities to one another, whereas time steps that yielded a distinctly higher or lower amount of individual captures were assigned a unique parameter.

To rank models, I used Akaike's Information Criterion corrected for small sampling size (AICc),

$$AICc = -2*LL + 2*nPar\ [n/(n-nPar - 1)]$$

where LL is the log likelihood, nPar is the number of parameters in the model and n is the sample size being considered (Burnham and Anderson 2002). More supported models were those that produced lower AICc scores than others and were considered better models. Model weights were also used to compare the relative support of each model and for model averaging point estimates of abundance for each group.

I assumed there was no behavioral responses due to initial capture and only used models where the probability of initial capture was equal to recapture (i.e., $p = c$) (Harris et al. 2010). I chose not to use abundance estimators that took advantage of multiple recaptures within plots. This was because elk were likely traveling together as a group during each sampling interval, and detections of the same individuals within each plot may have been from single or multiple visits to the site, thus providing no new additional information on the capture probability of individuals in each group (Lukacs and Burnham 2005, Petit and Valiere 2006, Harris et al. 2010).

To examine the effect sampling across longer periods of time had on the accuracy and precision of point estimates, I also investigated sets of Huggins' “p and c” closed capture models using only a single subsequent sampling occasion for the Davison Meadows group, which had the longest sampling interval of the three groups. I compared

the model averaged point estimates and variances generated from each of these intervals to the 4-occasion set and also to the estimates of group size from my visual counts.

Effect of Sample Size on Group Size Estimates

To investigate the effects parameterization, model selection, and sample size had on point estimates of group size, I simulated estimates of group abundance using subsets of data (Buckland and Garthwaite 1991) from each capture occasion for the Davison Meadows group in program RMark. This analysis consisted of randomly selecting fecal DNA samples from the full sample of each capture occasion then assembling them into a capture history to estimate group abundance. I ran 1,000 iterations of group size estimates with random subsample sizes of 5, 10, 15, 20 and 25 from each occasion with replacement for each iteration using the model Mth2. This model was chosen to represent capture probability of the Davison Meadows group as a finite mixture and as having full variation in capture probability by occasion, both of which held high support using AICc and allowed for the full parameterization of the (t) term. Models which included the sex term (s) were also excluded as capture by group was more accurately described using finite mixture models. Because individual heterogeneity in capture likely arose from elk entering and leaving the collared cow's social group, I also tested this model to examine how precise finite mixture models were at estimating group abundance at lower sample sizes; that is, to see if a targeted sampling effort was efficient when individual heterogeneity occurred in the group.

For comparison, the reduced model p(.) = c(.) was also analyzed using the same subsets of data. This analysis represented the fully reduced version of all models in the set where capture probability was equal across all occasions and wasn't influenced by any additional parameters. Although this model held low support using the full dataset, it allowed for a more basic model structure when using subsets of data.

Duplicate recaptures of the same individual elk within each occasion were removed if they were selected more than once, thus reducing the number of captures per occasion when this occurred. This was done to reflect the possibility of recapturing the same individuals in a field collection setting where the number of unique genotypes per sampling location is unknown prior to genetic analysis.

Pradel Modeling

I investigated a set of Pradel models using the FCR data from the Davison Meadows group to examine the assumption of closure for by each sex throughout the full sampling interval (Harris et al. 2010, Cooch and White 2018), as rutting behavior was observed to alter group cohesion. This allowed me to determine if the visual observations I made of changing group structure influenced the capture-recapture estimates of group size using closed capture modeling. I did not infer any potential changing group dynamics through Pradel modeling for the two other groups because I did not observe rutting behavior in those groups during my visual observations.

Because support for occasion varying capture probability was found during sampling for the Davison Meadows group, I tested the full time varying model

$$\varphi_{st}p_{st}f_{st}$$

where the subscript st defines variation by sex and time, φ is apparent survival, p is the variability in capture probability, and f is the recruitment of individuals into the group (Cooch and White 2018). Pradel modeling consisted of comparing the fit of a reduced model (i.e., one where the apparent survival term [phi] was constrained to 1 [no subtractions from the group] and where the recruitment term [f] was constrained to 0 [no additions to the group]) to various unconstrained models that tested closure by sex or overall group closure. I ranked models according to likelihood ratio tests (i.e., LRT in Program MARK) and deviance from the reduced model rather than AICc, since AICc values tend to be lower with constrained models due to having fewer parameters (Harris et al. 2010, Cooch and White 2018).

Influence of Space Use on Detection Probability

Fecal pellet grouping counts are indicative of the relative space use of ungulates, whereby a higher number of pellet groupings indicates increased site use (Edge and Marcum 1989, Ripple et al. 2001, Mansson et al. 2011). Using this concept, I conducted a post-hoc analysis on how intensity of site use, as indicated by elk cow GPS collar data, influenced the capture probability of each group at plot locations using Local Convex Hull (LoCoH) in program R. This was done by overlaying the locations of FCR plots for each group on utilization distribution maps created using intensity of site-use isopleths.

Although I aimed to collect samples deposited within the previous week or less, I tested different collar intervals due to varying decay rates and sampling bias in judging

recently deposited scat (Lehmkuhl et al. 1994, Jung and Kukka 2016). These intervals were 1, 2, 3, and 4 weeks of GPS collar data. Isopleth levels created at each of these intervals were used as proxies of intensity of use.

As a starting point to understand overall home range use and to set parameters to be used subsequently in each interval of plot analysis, I used all collar data prior to 1 month of the first sampling occasion to the hour of the final sampling occasion for each collared elk. Using these data, I followed the recommendations of LoCoH for R Tutorial and User Guide for constructing hullsets (Lyons 2014).

To reduce the influence of thin and scattered points that may have caused isopleths to include excess space not utilized by any elk in each group, I created utilization distribution maps using the a-LoCoH method to better represent space use of each group (Getz et al. 2007). The a-LoCoH method determines the construction of hulls by summing up the cumulative distance from a parent point to neighboring points until the value of "a" is reached. As a result, the a-LoCoH method more clearly defines utilization boundaries inaccessible to the animal being researched (e.g., cliff edges and water bodies) when creating utilization distribution maps (Getz et al. 2007).

I selected a value of "a" by using the "aVal" suggested using the "auto.a()" function in RStudio, because it accurately reflected the range of ideal values using the "a vs. isopleth area" and "a vs. isopleth:edge ratio" analyses (Lyons 2014). Using these determined "a" values, I then separated utilization distribution maps for each interval of collar data for all plot sites into 10, 25, 50, 75, and 95 percent intensity of use isopleths as

proxies for space use by each elk group. Lower isopleth values indicated increased site use.

The isopleth value a plot was located on during each collar interval was used to score how intensely the site was used by an elk group. I averaged values when a plot was located on more than one isopleth. Since lower isopleth values indicated increased site use and higher values decreased use, I subtracted each value from 100 for ease of comparison with the actual detection probability at each plot. The detection probability isopleth values predicted through LoCoH were then compared to the estimated detection probability at plots (i.e., the proportion of unique genotypes detected for each group) to assess if sites that yielded the most unique genotypes were also those that were indicated as the most heavily utilized by each collared elk cow.

RESULTS

Visual Counts

I assigned a classification for all individual elk seen during 13 visual counts for the Davison Meadows group (Table 1). Due to the group's habituation to the presence of humans, I was able to wait until counting conditions were ideal to obtain optimal visual estimates of group size and composition. However, between count dates, group size was found to fluctuate with no indication (other than physical markers on some individuals in the group) of which individuals were being re-observed or which may have been new to the group. Separate elk groups within the Davison Meadows were also observed on 2 occasions (Table 1). Using the maximum from all counts of each classification of the collared female's group yielded an estimate of 72 elk, including 49 females and 23 males (assuming a 50:50 sex ratio for calves).

For the Bald Hills group, visual counts ranged from 89 to 188 individuals across 4 counts during the sampling interval. Before fleeing on each count occasion, elk alerted one another, grouped together, and left the count location in a linear fashion allowing me to count them more clearly as they passed a reference point. Individuals obstructed from view by other elk or the landscape during counts weren't added to total counts as I could not accurately determine if they were single or multiple individuals as they passed. Therefore, all surveys resulted in minimum counts for this group.

I obtained one count of the Rowdy/Hastings group during the sampling interval. Due to the difficulty of sighting this group in their forested habitat, classifying individuals during this occasion was largely based on separating the group into antlered and antlerless individuals. I counted 2 antlered and 23 antlerless individuals, although it is possible more individuals were in the group but not visible. On a separate occasion, I also obtained a count of 25 elk along the same survey route that weren't grouped with the collared cow (further supported by her GPS location at the time). In addition, a group of 6 cows and 4 calves were seen on 2 subsequent days along the survey route that did not include the collared cows. Although there was no way of determining if individuals moved between these groups, as all counts were obtained on different occasions, an earlier summer count of a group in open habitat of 13 calves, 26 cows, 2 spikes, and 3 bulls, which included the Rowdy and Hastings collared cows, indicated that more individuals utilized this home range than each of the later fall sampling interval counts suggest. Therefore, for comparison with the number of individuals identified using fecal DNA sampling, I selected this maximum count of 32.5 females and 11.5 males (assuming a 50:50 sex ratio for calves) as representing the estimated size of the Rowdy/Hastings group.

Table 1. Visual count totals of elk groups in the Davison Meadows study area. Counts of elk which were not grouped with the representative GPS-collared cow are indicated by an asterisk (*).

Date	Calves	Cows	Spikes	Bulls	Total
9/12/2017	10	32	4	2	48
9/12/2017*	-	4	-	1	5
9/13/2017	11	20	-	4	35
9/13/2017	11	28	-	1	40
9/14/2017	9	38	1	4	52
9/14/2017	14	36	-	4	54
9/15/2017	8	31	-	5	44
9/15/2017	5	33	2	6	46
9/19/2017	7	38	4	6	55
9/21/2017	17	38	3	7	65
9/21/2017	16	38	4	7	65
9/29/2017	12	38	6	5	61
10/1/2017*	10	12	5	1	28
10/1/2017	7	20	-	3	30
10/5/2017	20	23	4	2	49
10/14/2017	17	33	4	3	57
10/17/2017	17	25	4	3	49
10/18/2017	18	33	5	3	59
10/20/2017	17	39	6	2	64
Highest Count	20	39	6	7	72

Rutting Behavior

Rutting in the Davison Meadows group was first documented on 12 Sept 2017 when 2 adult males were seen holding a harem of elk cows that included the collared female. One of these males had an easily identifiable antler configuration of 4 tines on the right antler with a small distinct hooked tine growing at the base of the right brow tine, and 6 tines on the left antler. I referred to this male as the "4 by 6" bull for brevity. Harem-holding consisted of these 2 bulls pushing wandering females with their antlers back into the Davison Meadows group while chasing away other bulls as they tried to enter the group. During this same visual survey, a second group of 4 adult cows and a single adult bull were observed in the northern portion of the home range (Table 1); however, the bull in this group exhibited no rutting behavior.

One day later on 13 Sept 2017, the "4 by 6" bull was observed defending the Davison Meadows group and successfully mated with a female. This male also aggressively kept 3 additional bulls from staying within the group; however, they were included in one of two counts during this occasion since it was unknown if they spent any time with the group prior or after my observation (Table 1). A few bulls were tolerated within the group by the "4 by 6" bull on subsequent surveys yet were shown aggression towards them when they attempted any mating behaviors.

Harem-holding and aggression towards other adult males by the "4 by 6" bull was continually documented until 1 Oct when he was observed bedding near the group. Another group of 12 cows, 10 calves, 5 spikes, and a bull were seen in the northern

portion of the home range earlier during this same survey (Table 1). This occasion marked the end of observed rutting behavior by any bulls and was the only occasion when the number of elk associated with the collared cow was distinctly lower than previous counts.

Fecal DNA Collection and Individual Genotyping

In total, I collected 523 fecal samples for DNA analysis from 12 unique plots: 193, 245, and 85 fecal samples from the Davison Meadows, Bald Hills, and Rowdy/Hastings groups, respectively (Table 2). Plot 3 for the Rowdy/Hastings group yielded 0 samples and was disregarded in capture-recapture analysis. This was largely due to the site being opportunistically sampled based on only 2 GPS locations from the collared cows in the group.

Genotyping success overall was 82.2% of all collected fecal samples (n = 430) yet varied between plots (63.9 - 100.0%) (Table 2). Of all samples successfully genotyped, only 11 were ranked with a low confidence of identity. Although I excluded these from capture-recapture analysis, 7 had additional medium or high-confidence counterparts within the same plot. Thus, only 4 individual identifications without counterparts within a plot (2 in the Davison Meadows group and 2 in the Bald Hills group) were excluded from capture-recapture analysis in total.

On average, every 1.48 scored samples and every 1.83 collected samples resulted in a unique genotype (Table 2). The allelic dropout rate, using the consensus genotypes of heterozygous individuals, was 5.1%. The toothpick rub method for fecal DNA collection

was not very effective when compared to collecting fecal pellets in conical tubes and immersing them in ethanol. Twenty-five out of 74 toothpick samples (33.8%) failed to amplify. In contrast, only 68 out of 449 fecal pellet samples (15.1%) failed to amplify.

Across all plots, 217 unique genotypes were identified. Individual female genetic profiles for the Davison Meadows, Bald Hills, and Rowdy/Hastings groups were 48, 101, and 23, respectively. Individual male genetic profiles for the Davison Meadows, Bald Hills, and Rowdy/Hastings groups were 12, 25, and 8, respectively. Comparing visual count data from the Davison Meadows group to subsequent sampling at each plot location confirmed that targeted fecal DNA sampling was largely female-centric (Table 3). Across all occasions for the Davison Meadows, Bald Hills, and Rowdy/Hastings groups, 38.0%, 26.7%, and 30.4% of all female unique genotypes were recaptured at other plots, respectively (Figure 2). The time between each sampling occasion for all groups varied between 1 and 19 days due to differing site accessibility.

Newly encountered female genotypes decreased across capture occasions for both the Davison Meadows and Rowdy/Hastings groups (Figure 2). The low recapture rate across plots as well as the increase in newly detected genotypes for the Bald Hills group were largely due to an increase in detection at Plot 4 (n = 87) from previous plots (Table 2). Female recaptures across plots were higher than within plots for both the Davison Meadows and Rowdy/Hastings groups. The opposite was true for the Bald Hills group.

Table 2. Fecal DNA samples collected, successfully scored, and unique genotypes per plot. Sampling effort, based on the number of successfully scored samples needed to achieve a unique genotype, and the percent of successfully scored samples from collected samples are shown for comparison across plots. The Rowdy/Hastings group is indicated as R/H.

Plot ID	Samples collected	Samples Scored	Unique Genotypes Within Plot			Scored per unique genotype	Successfully scored (%)
			All	Females	Males		
Davison 1	65	54	33	29	4	1.6	83.1
Davison 2	37	27	18	15	3	1.5	73.0
Davison 3	47	32	22	20	2	1.5	68.1
Davison 4	44	35	25	19	6	1.4	79.5
Bald Hills 1	10	7	6	5	1	1.7	70.0
Bald Hills 2	58	50	38	34	4	1.3	86.2
Bald Hills 3	48	48	31	25	6	1.5	100.0
Bald Hills 4	129	112	87	69	18	1.3	86.8
R/H 1	36	23	15	12	3	1.5	63.9
R/H 2	20	18	15	10	5	1.2	90.0
R/H 3	-	-	-	-	-	-	-
R/H 4	29	24	13	11	2	1.8	82.8

Table 3. Proportion of females and males in the Davison Meadows elk group indicated by visual counts (assuming a 50:50 sex ratio of calves) and subsequent genotyping of fecal DNA samples at plot sites.

	Females		Males	
Plot	Visual Count	Genotype	Visual Count	Genotype
1	0.84	0.88	0.16	0.12
2	0.80	0.83	0.20	0.17
3	0.61	0.91	0.39	0.09
4	0.67	0.76	0.33	0.24

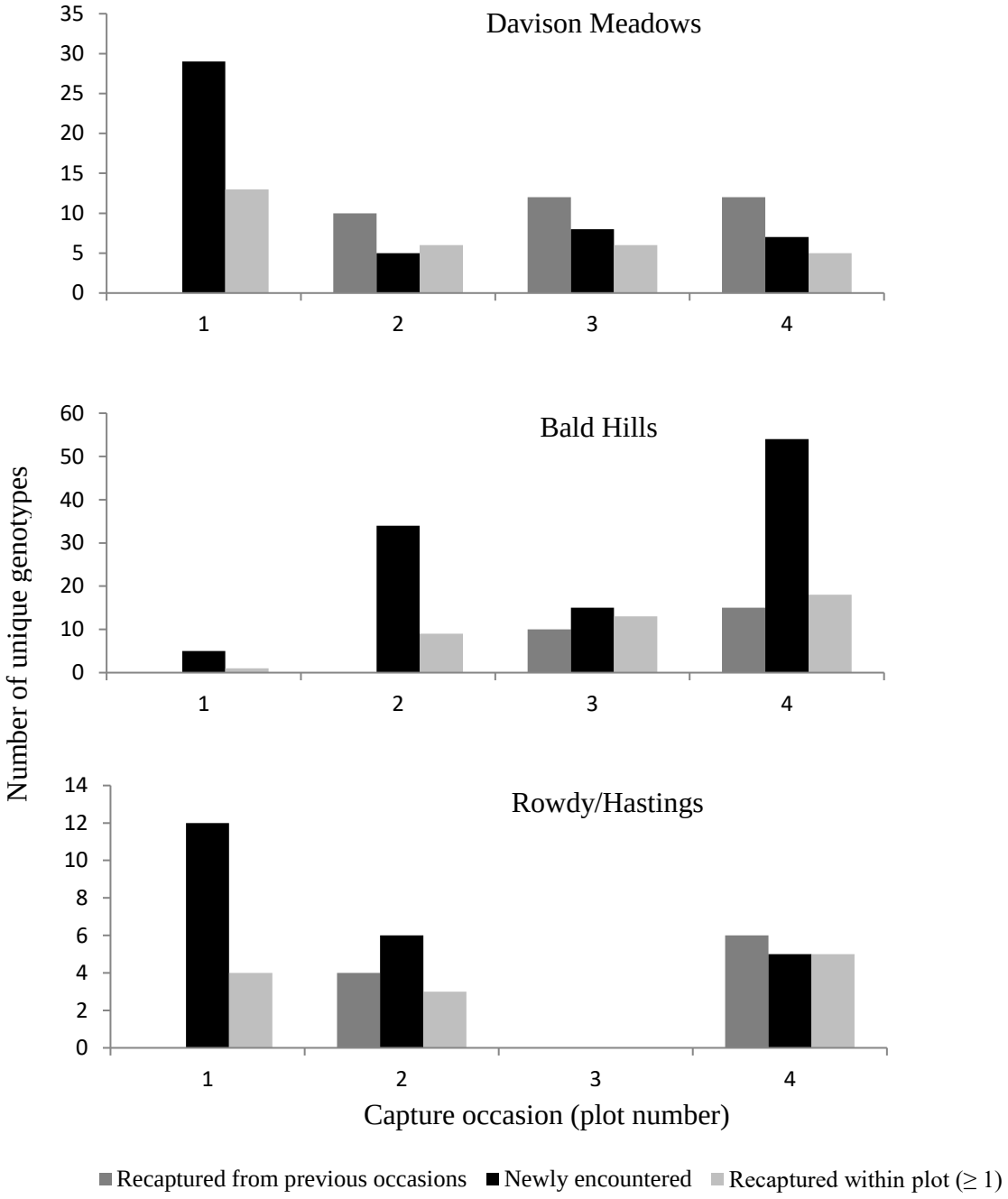

Figure 2. Capture rates of female elk genotypes across sampling occasions using FCR for three female elk groups in Humboldt and Del Norte counties, California. Shown are the number of repeat genotypes from previous occasions, unique genotypes captured for the first time within each capture occasion, and repeat captures within each occasion.

Group Size Estimates

For the Davison Meadows group, all heterogeneity models tested ranked higher than those that did not include the heterogeneity terms π and Het (Tables 4 and 5). These heterogeneity models also held all the model weight when compared to those without the π and Het terms. However, each of the finite mixture models had much higher standard errors and much larger 95% confidence intervals. Therefore, I separated the finite mixture models from those without the π or Het terms into two different model sets for subsequent model averaging of abundance estimates. Also, this separation was conducted to explore the effects of excluding individual heterogeneity during abundance estimates.

The highest-ranking finite mixture model for the Davison Meadows group held a model weight of 0.564 and produced estimates of 127.68 females and 30.65 males. (Table 4). This model consisted of occasion 1 having a unique capture probability (t_1) and occasions 2, 3, and 4 (t_{234}) being constrained to having equal capture probabilities. This model was tested since occasion 1 yielded a comparatively higher number of unique genotypes than all subsequent occasions. I also explored a model where occasions 1 and 2 had unique capture probabilities, and occasions 3 and 4 had equal capture probabilities; however, this parameterization was less parsimonious than the $t_1 + t_{234}$ version, therefore it was removed from the set. Estimates of the π parameter for all finite mixture models indicated a much higher probability of individual elk being in mixture 1 of the two mixture groups (Table 6).

The highest-ranking model for the Davison Meadows group without the heterogeneity terms was one where capture probability varied by sex (s) and the same occasion-specific parameterization as the top heterogeneity model (Table 5). The same model without the sex term also held high support, as did one that varied by sex alone. Full time variability (i.e., each capture occasion having a different capture probability), the dot model, and sex with full time variability all held less support. Averaging across models gave a point estimate of 63.2 female elk with a 95% confidence interval of 51.5 - 74.8 and 21.2 male elk with a 95% confidence interval of 1.8 - 40.6. Variance due to model uncertainty was 8.7% for females and 43.7% for males.

Each interval point estimate for females (45.6 - 49.2) (Table 7) was considerably lower than the 4-occasion estimates (Tables 4 and 5). No reliable model-averaged estimate for males was obtained for the first two intervals, as several models yielded extremely high point estimates.

All of the finite mixture models for the Bald Hills group performed poorly (i.e., they either resulted in low AICc scores or provided erroneously large point estimates) and were removed from the model set. A model which categorized occasions 1 and 4 with unique capture probabilities, whereas occasions 2 and 3 had equal capture probabilities, held the highest support (Table 5). This categorization was tested since occasion 4 yielded a comparatively high number of unique genotypes and occasion 1 yielded a comparatively lower number of unique genotypes (Table 2). The same model with the sex term (s) included also held high support. Model averaging gave a point estimate of 166.4 females with a confidence interval of 129.5 - 203.3 and 40.5 for males

with a confidence interval of 22.5 - 58.6. Model uncertainty was 1.1% and 31.0%, for females and males respectively.

Finite mixture models all performed poorly for the Rowdy/Hastings group as well and were removed from subsequent analysis. The dot model p = (.) held the highest support in this set (Table 5). Variability in capture probability by sex also held relatively high support. Full-time variability and group plus full-time variability held low support. Occasion specific parameterizations were also tested yet performed poorly since all occasions had relatively equal capture probabilities (Table 2). Model averaging gave an estimate of 33.5 females with a confidence interval of 21.3 - 45.8 and an estimate of 13.1 males with a confidence interval of 2.6 - 23.4. Variance due to model uncertainty was 2.3% and 28.6% for females and males, respectively.

Table 4. Top ranked model using Huggins' Heterogeneity “pi and p” closed capture modeling for measuring group size (N) of the Davison Meadows group between September 2017 and October 2017. Models were ranked based on Akaike’s Information Criterion (AICc) and model weight (*wi*). Number of model parameters (K), and model deviances are shown for comparison.

Model[a]	AICc	ΔAICc	*W*i	K	Deviance	-2LL	$\hat{N}$ F	SE	$\hat{N}$ M	SE
$p = \pi + Het + t_1 + t_{234}$	293.99	0.00	0.564	4	355.98	285.83	127.68	75.03	30.65	18.99
95% C.I.							65.82 - 431.36		15.57 -109.44	

[a]Abbreviations: π = the probability an individual occurs in mixture A assuming a finite mixture of 2 probabilities (1- π being the probability of occurring in mixture B), Het = the capture probability of the two heterogeneity groups, s = sex, with male and females having separate capture probabilities, t = time representing each sampling occasion having a different capture probability or occasions grouped as having equal capture probability, and (.) = constant capture probability across occasions.

Table 5. Top ranked models using Huggins' "p and c" for measuring group size (N) for three distinct Roosevelt elk groups in Humboldt and Del Norte counties, California, between September 2017 and January 2018. Models were ranked based on Akaike's Information Criterion (AICc) and model weight (*wi*). Number of model parameters (*K*) and model deviances are shown for comparison.

Davison Meadows										
Model[a]	AICc	ΔAICc	*W*i	K	Deviance	-2LL	$\hat{N}$ F	SE	$\hat{N}$ M	SE
$p = s + t_1 + t_{234}$	306.93	0.00	0.347	4	368.92	298.76	61.5	5.27	25.5	11.27
$p = t_1 + t_{234}$	307.54	0.61	0.256	2	373.65	303.49	65.02	6.16	15.61	2.40
$p = s + t_1 + t_2 + t_3 + t_4$	308.36	1.43	0.169	5	368.27	298.11	61.65	5.30	24.86	10.83
$p = s$	309.21	2.29	0.111	2	375.32	305.16	62.36	5.52	25.47	11.27
$p = t_1 + t_2 + t_3 + t_4$	310.08	3.15	0.072	4	372.08	301.92	64.87	6.12	15.57	2.38
$p = (.)$	310.95	4.02	0.046	1	379.09	308.93	65.72	6.35	15.78	2.47
Weighted Average							62.96		21.68	
Unconditional SE							5.90		7.88	
95% C.I.							51.4-74.52		1.89-41.48	
Variance due to Model Uncertainty							8.45%		39.08%	

Bald Hills										
Model	AICc	ΔAICc	*W*i	K	Deviance	-2LL	$\hat{N}$ F	SE	$\hat{N}$ M	SE
$p = t_1 + t_{23} + t_4$	438.01	0.00	0.338	3	878.40	431.96	167.15	18.8	39.34	6.23
$p = s + t_1 + t_{23} + t_4$	438.21	0.20	0.306	4	876.57	430.13	158.87	18.76	55.26	20.76
$p = t_1 + t_2 + t_3 + t_4$	439.18	1.18	0.187	4	877.55	431.10	166.98	18.19	39.30	6.23
$p = s + t_1 + t_2 + t_3 + t_4$	439.39	1.39	0.169	5	875.71	429.27	158.71	23.67	55.18	20.71
$p = (.)$	541.36	103.35	0.000	1	985.80	539.35	197.87	25.09	46.61	8.28
$p = s$	541.63	103.62	0.000	2	984.05	537.61	186.34	23.67	68.63	28.68
Weighted Average							163.16		46.88	
Unconditional SE							18.66		16.96	
95% C.I.							126.58-199.74		13.63-80.12	
Variance due to Model Uncertainty							5.02%		40.20%	

Rowdy/Hastings										
Model	AICc	ΔAICc	*W*i	K	Deviance	-2LL	$\hat{N}$ F	SE	$\hat{N}$ M	SE
p = (.)	115.18	0.00	0.590	1	139.80	113.14	34.15	6.34	11.89	2.94
p = s	116.6	1.42	0.290	2	139.13	112.47	32.16	5.82	15.47	7.91
$p = t_1 + t_2 + t_3 + t_4$	119.13	3.95	0.082	3	139.53	112.86	34.09	6.31	11.86	2.92
$p = s + t_1 + t_2 + t_3 + t_4$	120.65	5.47	0.038	4	138.86	112.19	32.11	5.79	15.43	7.88
Weighted Average							33.49		13.06	
Unconditional SE							6.24		5.40	
95% C.I.							21.26-45.72		2.47-23.64	
Variance due to Model Uncertainty							2.40%		28.40%	

[a]Abbreviations: s = sex, with male and females having separate capture probabilities, t = time representing each sampling occasion having a different capture probability or occasions grouped as having equal capture probability, and (.) = constant capture probability across occasions.

Table 6. Estimates of the parameter π from all finite mixture models tested for the Davison Meadows group. This estimate indicated the probability of individuals occurring in mixture 1 of 2 mixture groups. Mixture 2 is estimated as (1- π). Models which included the (s) parameter have two estimates of π for females and males, respectively.

Model	π
$p = \pi + Het + t_1 + t_{234}$	0.90
$p = \pi + Het + t_1 + t_2 + t_3 + t_4$	0.90
$p = \pi + Het$	0.90
$p = \pi + s + Het + + t_1 + t_{234}$	0.88, 0.97
$p = \pi + s + Het + t$	0.88, 0.96
$p = \pi + s + Het$	0.88, 0.96

Table 7. Top ranked models for measuring abundance (N) using only one subsequent capture occasion for the Davison Meadows elk group between September and October 2017. Models were ranked based on Akaike's Information Criterion (AICc) and model weight (*wi*). Number of model parameters (*K*), and model deviances are shown for comparison.

1st Two Occasions (15-17 September 2017)										
Model[a]	AICc	ΔAICc	*W*i	K	Deviance	-2LL	$\hat{N}$ F	SE	$\hat{N}$ M	SE
$p = s + t_1 + t_2$	80.75	0.00	0.875	2	195.49	76.60	45.03	6.95	-	-
$p = t_1 + t_2$	85.11	4.46	0.099	2	199.85	80.96	49.26	8.88	10.15	2.64
p = s	88.32	7.57	0.020	2	203.06	84.17	48.40	8.35	-	-
p = (.)	90.58	9.83	0.006	1	207.42	88.53	53.92	10.62	11.11	3.16
Weighted Average							45.57		-	
Unconditional SE							7.37		-	
95% C.I.							31.12-60.03		-	
Variance due to Model Uncertainty							4.86%		-	
2nd Two Occasions (17 September-5 October 2017)										
Model	AICc	ΔAICc	*W*i	K	Deviance	-2LL	$\hat{N}$ F	SE	$\hat{N}$ M	SE
$p = s + t_1 + t_2$	71.11	0.00	0.388	2	146.14	66.92	43.38	9.75	-	-
p = s	71.72	0.62	0.285	2	146.76	67.53	43.75	9.92	-	-
p = (.)	72.21	1.10	0.223	1	149.37	70.15	48.48	12.14	8.66	3.15
$p = t_1 + t_2$	73.72	2.61	0.105	2	148.76	69.53	48.00	11.93	8.57	3.09
Weighted Average							45.11		-	
Unconditional SE							10.85		-	
95% C.I.							23.84-66.37		-	
Variance due to Model Uncertainty							5.29%		-	
3rd Two Occasions (5-10 Oct 2017)										
Model	AICc	ΔAICc	*W*i	K	Deviance	-2LL	$\hat{N}$ F	SE	$\hat{N}$ M	SE
p = (.)	83.86	0.00	0.496	1	176.65	81.81	50.06	10.57	11.31	3.33

3rd Two Occasions (5-10 Oct 2017)										
p = s	85.51	1.65	0.217	2	176.19	81.35	47.53	9.91	16.00	12.00
$p = t_1 + t_2$	85.66	1.80	0.202	2	176.34	81.50	49.85	10.49	11.26	3.30
$p = s + t_1 + t_2$	87.37	3.51	0.086	3	175.88	81.04	47.35	9.83	15.91	11.89
Weighted Average						49.24		12.71		
Unconditional SE						10.42		7.46		
95% C.I.						28.82-69.65		-1.91-27.34		
Variance due to Model Uncertainty						1.33%		36.63%		

[a]Abbreviations: s = sex, with male and females having separate capture probabilities, t = time representing each sampling occasion having a different capture probability or occasions grouped as having equal capture probability, and (.) = constant capture probability across occasions.

Table 8. Estimates of females and males within elk groups from visual counts and closed capture-recapture modeling (excluding finite mixture models) using fecal DNA samples. Visual count estimates were made assuming a 50:50 sex ratio for calves.

	Female		Male	
Elk Group	Visual Count	FCR	Visual Count	FCR
Davison Meadows	49	62.96	23	21.68
Bald Hills	188+*	163.16	188+*	46.88
Rowdy/Hastings	32.5	33.49	11.5	13.06

*Estimate is of males and females combined

Effect of Sample Size on Group Size Estimates

Simulating abundance estimates using the model Mth2 provided no reliable mean estimate at any subsample size; all mean estimates indicated group sizes larger than 1,000 individuals (Figure 3). Ninety-five percent confidence intervals increased as sample sizes grew for both sexes. Despite having high support using the full dataset, this model showed little precision in group size estimates across subsample sizes.

In contrast, conducting the simulation analysis with the reduced model p(.) = c(.) was much more precise in estimating group size across subsample sizes (Table 9). Group size estimates became more precise at 10 subsamples or more with slight increases in estimates occurring as sample size increased. Using only 5 randomly selected samples produced erroneous estimates with much larger confidence intervals.

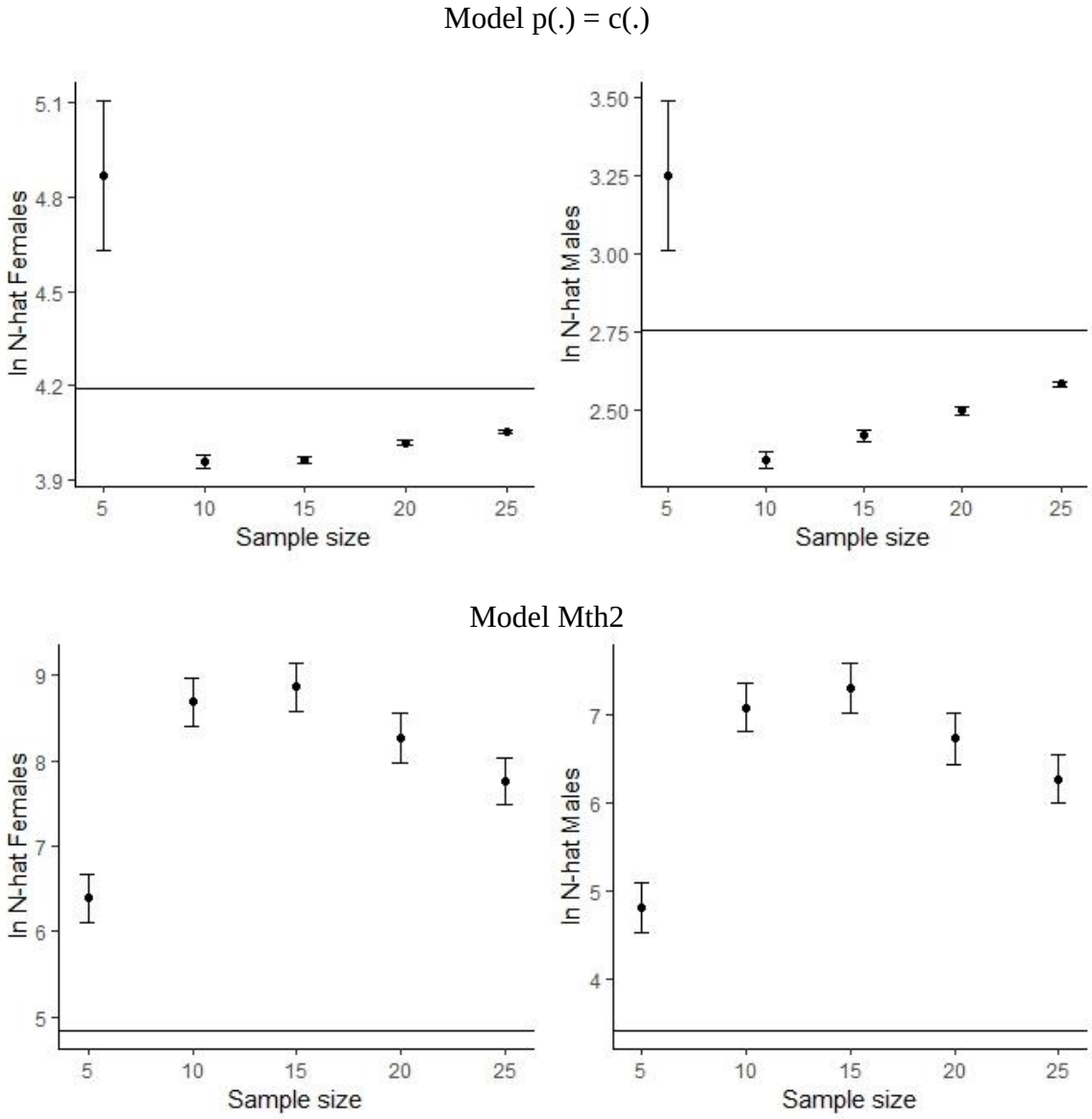

Figure 3. Results of simulation analyses using subsamples from each sampling occasion for the Davison Meadows group. Dots indicate the mean natural log (ln) population size of 1,000 iterations of each subsample size. Error bars indicate 95% confidence intervals. Estimates of N-hat using each model at the full sample are indicated by the reference line on each graph.

Table 9. Range of estimates of group size for females and males within the Davison Meadows elk group using group abundance simulation analysis at various subsample sizes. Group size estimates were obtained running the model p(.) = c(.) at 1,000 iterations of each subsample size.

Sample size	Range $\hat{N}$ Females		Range $\hat{N}$ Males	
	Min	Max	Min	Max
5	12.04	5.89×10^9	1.20	1.54×10^9
10	21.19	208.10	1.89	42.93
15	31.43	96.44	4.29	26.74
20	37.47	89.63	5.32	21.34
25	41.77	83.67	7.66	21.34

Pradel Modeling

Pradel modeling for the Davison Meadows group showed significant support for a fully open model, one where both the apparent survival (φ) and recruitment (*f*) terms were left unconstrained, suggesting that the group size was influenced by individuals entering and leaving the group during the sampling interval (Tables 10 and 11). This was indicated by high deviance compared to the fully closed model and was significant when considering the probability of obtaining its X^2 statistic ($p = 0.04$) (i.e., the probability of obtaining its X^2 if there was no difference in fit between both models) using LRT in Program MARK. A model where the female segment was open and the male segment was closed also showed significant deviance from the reduced model ($p = 0.01$), suggesting that females entered and left the group during the sampling interval. All other parameterizations held less support.

Table 10. Results of Pradel models used to assess the assumption of closure for the Davison Meadows group. Models were ranked based on deviance from the constrained model, $\varphi_t g_t p_t f_t$ where apparent survival (φ) was set to 1 and recruitment (*f*) was set to 0. Models were compared using a likelihood ratio test (LRT) in program MARK. P-values indicate the probability of arriving at the X^2 statistic if there was no difference in model fit. P values are bolded when < 0.05.

Model	AICc	K	Deviance	X^2	DF	P
Both sexes closed	307.19	4	298.76	-	-	-
Both sexes open	306.58	8	288.96	9.80	4	0.04
M (*f*) open, rest closed	306.46	6	293.54	5.22	2	0.07
F (*f*) open, rest closed	307.3	6	294.38	4.38	2	0.11
F φ open, rest closed	311.78	7	296.53	2.23	3	0.53
M open, F closed	311	6	298.07	0.69	2	0.70
M φ open, rest closed	314.01	7	298.76	0	3	-
M closed, F open	302.57	6	302.57	9.11	2	0.01

Table 11. Estimates of apparent survival (φ) and recruitment (*f*) for each sex using the most supported Pradel models for the Davison Meadows group. Apparent survival was used to estimate the probability of elk leaving the group whereas recruitment was used to estimate the probability of elk entering the group.

Model	φ Females	φ Males	*f* Females	*f* Males
Both sexes open	0.76	1.0	0.31	0.27
M closed, F open	0.76	1.0	0.31	0.00

Influence of Space Use on Detection Probability

Using the Davison Meadows cow's GPS collar data, Plot 1 was indicated as the most highly utilized site when compared with other plots for all intervals of collar data (Table 12, Figure 4). This was also the site where the highest number of unique genotypes was identified for the group (Table 2). The remaining plots showed less consistency across collar data intervals with respect to intensity of use.

Similarly, the Bald Hills cow's GPS data indicated that Plot 4 was the most heavily utilized site across all intervals of collar data when compared with other plots (Table 12). This was also the location where the highest proportion of unique genotypes was identified when compared to other plots for this group (Table 2). Plots 1, 2, and 3 for the Bald Hills group fell on much lower intensity of use areas (>75% isopleth values) for all intervals of collar data.

Plot 4 for the Rowdy/Hastings group was indicated as the most heavily used site across all intervals when compared to other plots (Table 12). However, this site yielded the lowest number of unique genotypes per plot where samples were collected (Table 2). Plots 1, 2, and 3 fell on varying isopleth values across all intervals of collar data.

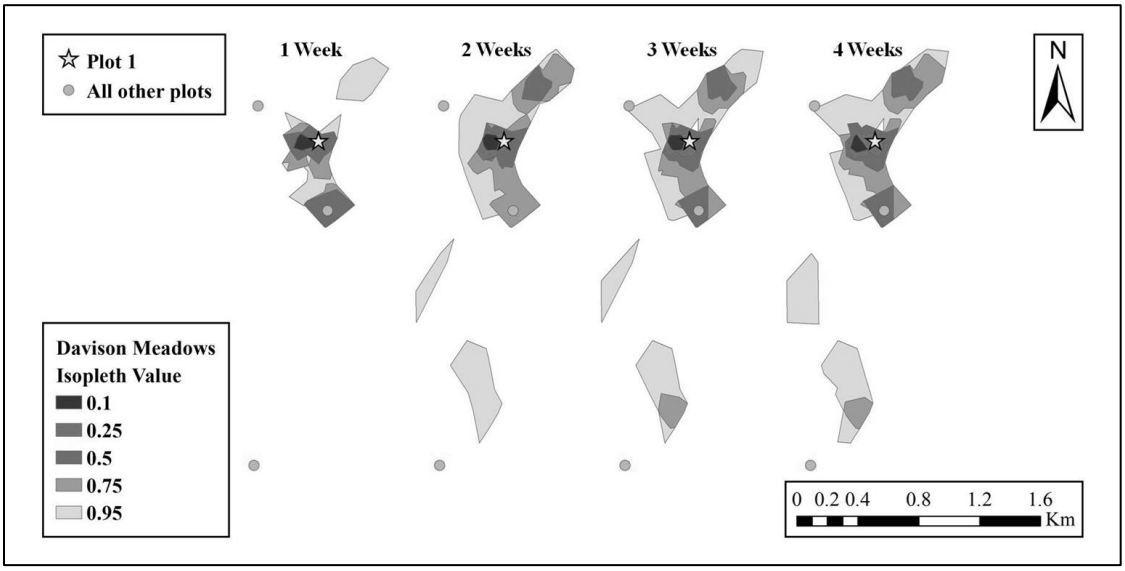

Figure 4. Example of a-LoCoH intensity of site use maps constructed using location data from the GPS-collared elk cow in the Davison Meadows group. Shown are maps using 1, 2, 3, and 4 weeks of location data prior to the hour of fecal DNA sampling at occasion 1. All other occasions were analyzed in the same manner to determine the isopleth values they were located on across the four intervals of collar data.

Table 12. The most heavily utilized plots by the three elk cows as indicated through different intervals of time (1 - 4 weeks of GPS collar data) in LoCoH. Values indicate detection probability (LoCoH $\hat{p}$ as 1 - the isopleth value each plot fell on). Actual detection probabilities (Unique Genotype $\hat{p}$), shown as the proportion of unique genotypes across all plots for the group, are included for comparison. Numbers in parentheses indicate on a scale of 1 (most productive) to 4 (least productive) each plot ranked in capture probability considering unique genotypes detected for the group.

Davison Meadows	LoCoH $\hat{p}$				Unique Genotype $\hat{p}$		
Plot 1	1	2	3	4	Females	Males	Both
	0.63	0.75	0.75	0.75	0.35 (1)	0.27 (2)	0.34 (1)
Bald Hills	LoCoH $\hat{p}$				Unique Genotype $\hat{p}$		
Plot 4	1	2	3	4	Females	Males	Both
	0.50	0.50	0.25	0.25	0.52 (1)	0.62 (1)	0.54 (1)
Rowdy/Hastings	LoCoH $\hat{p}$				Unique Genotype $\hat{p}$		
Plot 4	1	2	3	4	Females	Males	Both
	0.90	0.90	0.90	0.90	0.33 (2)	0.20 (3)	0.30 (2)

DISCUSSION

Using a targeted sampling effort for fecal DNA collection was largely successful in capturing female-centric social groups within each of the home ranges analyzed in this study (Tables 2 and 3). This was largely reflective of the typical ecology of adult females traveling with one another during the fall season (Bowyer 1981, Weckerly 1999). In addition, the high recapture of individuals from prior capture occasions indicates that using GPS-collar data from each representative elk cow was efficient in determining locations where their respective social groups could be captured for FCR estimates of group size (Figure 2) (Hettinga et al. 2012).

Genotyping Roosevelt elk through fecal DNA samples using previously established microsatellite markers from tule elk was successful in distinguishing individual sex and genetic profiles (Sacks et al. 2016) (Table 2). This is the first study to create these profiles in Roosevelt elk using DNA collected from feces, and multiple samples from the same individuals (i.e., consensus genotypes) allowed me to calculate a low allelic dropout rate, indicating a high level of precision when determining unique genotypes (Broquet and Petit 2004). Continued fecal DNA sampling of Roosevelt elk will increase the number and confidence in these unique profiles, further refining the precision of the techniques used in this study.

Areas of increased use were independently consistent with the highest density of unique genotypes at sampling locations for the Davison Meadows and Bald Hills groups (Table 12, Figure 4). These results suggest that utilizing GPS-collar data offers promise

in reducing effort in future fecal DNA sampling. Although I did not sample in the most heavily used areas within the utilization distributions of these groups (i.e., areas indicated by the 0.10 isopleths), I captured over 1/3 of each estimated group size (using models that did not account for individual heterogeneity) through unique genotypes in the most productive plots (Tables 2 and 5). These results suggest that sampling outside of the plot area (2 km^2) or sampling at more heavily utilized locations may reduce the effort needed to arrive at group size estimates through FCR substantially.

Closed capture modeling results for the Bald Hills and Rowdy/Hastings groups were promising, as the high capture rate of genetic profiles increased the accuracy of group size estimates (Woodruff et al. 2016) as compared to visual counts (Table 8). Although it is unlikely these groups were strictly closed populations during the sampling interval, the low support for heterogeneity in capture probability demonstrates that capture probability can more easily be explained by sex or intensity of site use during times of increased group cohesion (i.e., during the winter season). Rut appeared to have ceased for these two groups during this study, suggesting that males were less territorial and that elk in these regions were beginning to amass into the larger congregations typical of the winter season (Weckerly 2017). As a result, emigration from these groups may have been less likely during FCR analysis.

As expected, counting elk during visual surveys for all groups was almost always confounded by imperfect detection of individuals within the group (Weaver and Weckerly 2011). In contrast, the majority of both of these groups was identified through fecal DNA genotyping without the ambiguity of misidentifying or recounting individuals.

The precision between estimates of group size using pairs of capture occasions for the Davison Meadows group also demonstrates the effectiveness of targeted FCR efforts over visual counts (Table 7). Although female abundance may have been underestimated using these occasion pairs due to low sample sizes per occasion (further evidenced by the inability to produce a reliable estimate of males using the first two pairs), each pair of occasions produced point estimates similar to one another. This was despite the support for individual heterogeneity in capture probability using the entire sampling interval, which spanned a much larger time period and may have decreased the accuracy of the closure assumption (Harris et al. 2010) thus allowing more individuals outside the immediate social structure to be counted. As a result, increased sample sizes during occasions spaced closely in time in conjunction with the collection of fresh samples to reflect recent demography is the best option to ensure the accuracy and precision of point estimates of group size as well as avoiding violations of the closure assumption when using closed population models (Brinkman et al. 2009, Harris et al. 2010, Woodruff et al. 2016).

FCR estimates were similar to the estimates obtained through visual counts where individual heterogeneity was excluded (Table 8). However, as expected, the inability to distinguish individuals without markers between occasions during visual counts offered little certainty when making this comparison, especially as group cohesion was observed to change in the most easily observable group (Davison Meadows). Future assessments of group size through FCR can alleviate this ambiguity as unique genotypes can be used to

determine which groups of individuals are being measured across time (Hettinga et al. 2012).

The most supported models for the Bald Hills and Rowdy/Hastings groups were those where the heterogeneity parameters were excluded (Table 5). In contrast, using finite mixture modeling indicated differing capture probabilities of two groups within Davison Meadows (Table 6) (Cooch and White 2018). Comparing the top finite mixture model to the top model without individual heterogeneity for this group suggests that modeling with a mixture of two groups rather than two sexes was more parsimonious with the data collected. Heterogeneity in capture probability among individuals in a target population is the most difficult issue to address during abundance estimation (Lukacs and Burnham 2005). Although discerning the source of heterogeneity is difficult, the large estimates of the π parameter using the full dataset indicate a distinct difference in the proportions of individual elk occurring in each of the two mixtures estimated (Table 6). It is likely that these two proportions were the immediate social group of the collared cow (adult females and young) and adult elk moving into or out of the group due to rutting activities during the time of sampling. This latter group, which had a much lower detection probability and included individuals from adjacent areas, is likely the reason for the large estimates of the Davison Meadows group using heterogeneity models (Table 4).

Sex (s) more accurately described capture probability in the Bald Hills and Rowdy/Hastings groups (Table 5). Treating each of these groups as finite mixtures produced models which held negligible model weights and had erroneously large estimates of group size. Variation in capture probability by sex in these groups was likely

due to low sample size of males overall and the tendency of adult males to take temporary excursions away from the group (Weckerly 2001, 2007). It is less likely that rutting behavior, which appeared to have ceased during the time of data collection for these two groups, had an influence in the same manner as it did for the Davison Meadows group.

Documenting rutting activity from bulls in the Davison Meadows group allowed insight into changing population dynamics during the sampling interval (Bowyer 1981). Group cohesion was determined to be greatly influenced by rutting bulls; however, it was difficult to assess if these activities caused females to emigrate from the main Davison Meadows group based on visual observations alone. The 28 individuals observed elsewhere within the home range prior to sampling at plot 5 (Table 1) may have been due to a temporary split from the main group, which coincided with the end of "4 by 6" bull's rut. Following this occasion, a subsequent visual count of the collared cow's social group indicated an increase in number from 30 to 49 individuals. It is difficult to assess if this was the result of individuals in the observed satellite group later joining the collared cow's group of 30 individuals, or if several individuals with the collared cow were missed during my initial observation. The latter would indicate the satellite group of 28 elk were a completely different group using the Davison Meadows home range.

Adjacent groups have been documented overlapping in site use with the Davison Meadows group in the past (Julian et al. 2013, Weckerly 2017). This phenomenon may in part explain the high support for heterogeneity models as members of adjacent groups would have different capture probabilities than the target group. Fecal DNA sampling in

this study was focused on the site use of the GPS collared cow and didn't attempt to assess overlap with these adjacent groups. Nonetheless, although partitioning of site use by different elk groups will increase the uncertainty of point estimates using fecal DNA, the extent of overlap can be assessed as sampling efforts increase with time (Luikart et al. 2010). Furthermore, targeting fresh scat to reflect recent use can further limit the possibility of sampling adjacent groups, which will use sites at different times than the target group (Weckerly 2017).

Although Pradel models can lack power when the number of sampling occasions is low (Harris et al. 2010), they can nonetheless provide insight into changing group dynamics during mark-recapture analysis (Cooch and White 2018), particularly when supported with additional datasets. Pradel modeling suggested that both sexes of the Davison Meadows group were open to immigration and emigration, likely due to rutting adult males altering female group cohesion (Bowyer 1981) or spatial overlap with adjacent groups (Kolbe and Weckerly 2015, Weckerly 2017). These results indicate that targeted sampling was conducted during a sub-optimal seasonal period for the Davison Meadows group. However, the success of modeling the Bald Hills and Rowdy/Hastings groups, which were more efficiently modeled by sex rather than a finite mixture of two groups, illustrates that group cohesion has an important role in increasing capture rates of a target group or population (Table 5).

Conducting group size simulation analyses using the time varying finite mixture model produced a large range of abundance estimates at all subsample sizes tested (Figure 3). This was likely due to an increased likelihood of sampling individuals that

were in mixture 1, and a decreased likelihood of sampling the mixture 2 group, resulting in poor model fit at lowered sample sizes (Cooch and White 2018). Running the same analysis using the dot model p(.) = c(.), although not the most parsimonious model given the full dataset, demonstrated that reducing the number of parameters for the Davison Meadows group produced a much smaller range in abundance estimates, which resulted in higher precision as sample sizes increased per occasion (Figure 3, Table 9). Considering the increased group cohesion of the Bald Hills and Rowdy/Hastings groups suggests that sampling periods that avoid heterogeneity in capture probability offer the most accurate estimates of elk group size (Lukacs and Burnham 2005, Harris et al. 2010).

Decreasing home range size and increased group cohesion in late fall and into the winter months may in part explain the sharp increase in detection at plot 4 for the Bald Hills group. Adult female elk within the Bald Hills reduce home range sizes by several thousand hectares moving into the winter months due to declining food resources (Kolbe and Weckerly 2015). It is possible that many elk in this group frequented the plot 4 location as resources began to decline in their home range. Another factor may be the site's remote location. Plot 4 was the furthest of any of the sites from Bald Hills Road, which is the main thoroughfare through the study area. As a result, it may have offered relative security and thus increased utilization from this cautious group.

It is noteworthy that the collared female in the Bald Hills group was originally a representative cow of roughly 25 individuals that occupied an area north of the Bald Hills group’s home range (Kolbe and Weckerly 2015). Her move to the much larger southern Bald Hills group was unexpected yet indicative that the southern group's size is

influenced by adjacent groups at least to some degree. Some home range overlap by these distinct groups has been observed in the past, however, only during periods when food resources were at their highest (April - June). The collared cow in this study emigrated to and remained in the southern population in late October suggesting some other reason for her movements, such as social familiarity (Jenkins and Starkey 1982) or the end of the rutting season for elk in the area, as rutting bulls were observed in the northern group prior to her move. A subsequent count of the northern group, after the collared cow moved south to the Bald Hills range, indicated a decrease by roughly 12 individuals (from 40 down to 28), however the exact number that followed the movements of the collared cow is unknown. Future fecal DNA sampling together with spatially referenced samples of these groups can provide further insight into how much overlap exists between adjacent groups.

Plot 4 for the Rowdy/Hastings group was a location visited almost daily by the collared cow in the week prior to sampling. Subsequent intensity of use analysis indicated this site was in the top 10% of site use for the collared cow during this interval; however, sampling at this site resulted in the opposite of what was expected: the number of unique genotypes was lowest when compared to other plot locations where unique genotypes were found. Group cohesion in elk groups that use silviculturally managed landscapes is relatively low when compared to those that concentrate in meadows (Jenkins and Starkey 1982). It is possible that the plot 4 location wasn't utilized by many elk in the region, which is consistent with visual counts indicating lower cohesion within the Rowdy/Hastings area. Smaller elk groups need less forage, which forested habitats can

sufficiently provide. However, as group size increases to threshold levels, larger groups are required to utilize meadows more intensely (Weckerly 2017). It is noteworthy that association with other elk for these groups is highest in the winter months (Jenkins and Starkey 1982). As a result, it is possible that wintertime fecal DNA sampling may be more efficient for forested groups.

The intensity of use maps constructed for each collared cow were biased towards false commission of space use (i.e., the false inclusion of areas where the elk group never actually was) as opposed to false omission (i.e., not including areas where the elk group actually was) (Getz et al. 2007). However, because my focus was comparing the relative capture rates at each location and because plot locations were focused on areas where GPS data indicated each collared cow's respective group was, bias towards false commission was considered to have less of a negative impact on intensity of use results. Spurious holes in space use (indicative of false omission) are common at lower values of *a* (Lyons 2014) and would have likely resulted in no values for less intensely used areas, which would have produced fewer data to compare the relative use of each site. In addition, higher used areas indicated by LoCoH were more discrete when compared to lesser used areas as a result of setting *s* to 0 (Getz et al. 2007). Therefore, these higher use sites are less likely to contain false commission of space, which is ideal in future efforts if one were to attempt to delineate an effective sampling area.

Using unique genetic identifiers for Roosevelt elk increases our understanding of population dynamics that are obscured by the variables inherent in traditional survey methods. Group size estimates that are confounded by the inability to detect immigration

and emigration are improved when captures of distinctly unique individuals become available. The results in this study will help inform estimates of population trends across years with greater accuracy and precision and will aid in management decision making in regard to harvest, tourism, and the ecology of elk in Humboldt and Del Norte counties in California.

MANAGEMENT RECOMENDATIONS

Identifying individual elk through fecal DNA is an efficient way of determining elk group sizes with an accuracy that exceeds visual counts. Furthermore, this method allows researchers to detect elk in areas that are not directly observable through visual counts (i.e., forested habitats and areas with varying topography). Targeted fecal DNA sampling efforts that take advantage of group cohesion can greatly reduce the time required in the field as a large segment of an elk group can be identified in a relatively small area. Also, targeted sampling allows a researcher to estimate elk group size in a capture-recapture framework, which has several advantages over accumulation curve methods that only utilize the first capture of an animal (Lukacs and Burnham 2005). As a result, the latter of these two methods can render time spent collecting data in the field as being redundant. In contrast, capture-recapture methods make use of subsequent captures of the same individual, which allows one to more fully utilize data collected.

In the absence of GPS collar data, targeted sampling approaches can be utilized to determine elk abundance in a defined survey area, making lengthy transects across a landscape unnecessary. Resource selection functions can easily define probable areas of use (Boyce et al. 2002) by all elk in a region. Targeted sampling at probable areas of use by elk can be translated into a single capture session for the larger study area, reducing field excursions and sampling efforts substantially as it is likely that these sites contain genetic material of the majority of the elk using the study area.

The efficiency of site-specific sampling can further be exploited during the winter months, when group cohesion is at its highest and site use is more concentrated on discrete patches of land (Kolbe and Weckerly 2015). Visual estimates of elk groups are more precise between independent surveyors when group sizes are larger, suggesting that winter season surveys are more indicative of actual abundance of elk in a region (Weckerly 2007). Intensive sampling during this time may increase the capture rate at surveyed locations, which can reduce the number of capture occasions necessary to make an accurate estimate of group size (Hettinga et al. 2012). However, the time needed to obtain a desired number of samples should be considered if the number of occasions is reduced. Using the plot area of 2.03 km^2 in this study required approximately 4 - 6 hours of time by a single surveyor. In addition to travel time to sites and decreased daylight during the fall and winter months, sampling a single location can easily become a full day's effort.

Sampling for multiple groups within a larger population can be treated as a single survey, which can take advantage of grouping behaviors during the winter months (Hettinga et al. 2012). The ability to clearly define areas of use by groups within a population can increase the likelihood of recapturing individuals on subsequent surveys, which can increase the accuracy of abundance estimates. Spatial overlap with adjacent elk groups is less likely during this time (Kolbe and Weckerly 2015) suggesting that targeted sampling will result in less genetic samples from other individuals within the larger population. However, it is unnecessary to maximize capture rates in this manner if

care is given to defining areas of use by groups throughout the entire study area (Hettinga et al. 2012).

Sampling locations were largely determined by site access, topography, and constraints on time. Delineating a manageable survey near clear-cuts in particular was time consuming and care should be given to choosing a location not covered by downed trees or eroding soils, both of which are easily navigated by elk though less so by humans.

Although this study used plots to delineate a sampling area for comparative site use purposes, a less rigid sampling scheme during capture occasions can greatly reduce the time spent in the field. I selected plot centers by averaging GPS locations at desired sampling locations then aimed to sample all piles in a clearly defined radius. However, simply designating this center followed by searching the immediate landscape for the desired number of samples should produce capture occasions sufficient for capture-recapture analysis of each group (Hettinga et al. 2012).

Death, emigration, and immigration can all cloud the assumption of closure during assessments of abundance of wild populations, regardless of the sampling scheme used (Lukacs and Burnham 2005, Cooch and White 2018). However, assessing population trends across years can aid wildlife managers in making responsible decisions regarding harvest and conservation (Hettinga et al. 2012, Woodruff et al. 2016). For elk, this assessment has traditionally been conducted during the winter season due to increased group closure and decreased location use (Weckerly 2017). For these same

reasons, future efforts of using FCR should be conducted during the winter to obtain more precise estimates annually (Hettinga et al. 2012).

The high density of unique genotypes within each plot indicate that sampling more intensely during fewer capture occasions is preferable to sampling extensively across multiple plots. Targeted sampling for population abundance at different locations within a group's home range requires the assumption that all individuals are moving within the study area (Lukacs and Burnham 2005). Although closed capture abundance modeling can increase in accuracy with more capture occasions, the assumption of group closure is less likely as the time between all occasions increases (Harris et al. 2010). In addition, surveying more extensively throughout the landscape invites the potential of sampling adjacent groups on the periphery of the targeted group's home range. As overall space use of elk groups decreases during the winter months, the likelihood of capturing individuals from adjacent groups should be reduced.

Adult male elk tend to utilize forested habitats more often than females and spend less time in social groups (Grenier et al. 1990, Weckerly 2001, Bliss and Weckerly 2016), making population estimates of this class difficult. However, site-specific fecal DNA sampling, such as that conducted in this study, illustrates the potential to detect and count male groups with greater precision than visualizing them in forested areas.

I aimed to avoid sampling fecal DNA during the rainy season in Humboldt and Del Norte counties (rain begins in late October, greatly increases from December to February, and steadily decreases towards May) to avoid low genetic amplification rates (Brinkman et al. 2009). However, despite sampling within a day of a rain event, most of

the fecal samples collected from plot 1 for the Rowdy/Hastings group were scored successfully (Tables 2 and 5). In addition, this site yielded a capture rate comparable to subsequent plots for this group (Table 2). GPS collar data also indicated this was the result of a single visit after the rain event, which lasted < 12 hours. This suggests that a dry spell of a few days or less in the winter is all that is required for obtaining sufficient quantities of amplifiable samples at discrete capture locations.

Samples that didn't amplify may have resulted in additional unique genotypes at survey locations; however, in a capture-recapture context, amplification failure is analogous to never obtaining the sample, as capture probability is assumed to be less than 1 at each location (Lukacs and Burnham 2005). As a result, failed amplifications are absorbed into capture probability. In the context of detection rates, sites with the highest number of unique genotypes successfully amplified corresponded with the highest sampling efforts for the Davison Meadows and Bald Hills groups, indicating failed amplifications had little effect on the detection rate at these sites.

Failed amplifications using the toothpick rub method on amorphous scat were almost exclusively concentrated on the Davison Meadows group. Overall this method performed poorly for amorphous elk scat and shouldn't be used in future analysis. Sampling and preserving pelleted scat, which is a typical consistency of scat deposited in the late fall and winter months (Moskowitz 2010) resulted in more successful amplification rates.

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