The Journal of Wildlife Management 82(7):1429–1441; 2018; DOI: 10.1002/jwmg.21507

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Research Article

Integrated Modeling to Estimate Population Size and Composition of Mule Deer

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ABSTRACT Estimating population size, age composition, and sex ratio of mule deer (*Odocoileus hemionus*) is important to conservation and managed hunting of this species in the western United States. Increasingly, wildlife agencies are estimating abundance of deer using fecal DNA (fDNA), especially in forested habitats where aerial surveys are not feasible. These same data can be used to estimate overall sex ratio but require additional data on age structure to quantify adult- and fawn-specific sex ratios, which are expected to differ substantially. We demonstrate an integrated modeling approach to estimating population sizes of adult females, adult males, and fawns from 3 sources of data: fDNA, camera stations, and global positioning system (GPS) telemetry. We conducted the study on an 11,500-km^2 forested region in northern California, USA, corresponding to 3 hunt management zones. Within a Bayesian framework, we used spatial capture–recapture (SCR) modeling of fDNA samples and prior information on home range sizes from telemetry to estimate sex-specific densities, and N-mixture modeling of camera detections to separate adult and fawn densities. We estimated 29,317 adult females (90% CI = 24,550–34,592), 10,845 adult males (90% CI = 7,778–14,858), and 19,587 fawns (90% CI = 15,340–24,430) within the study area. The inclusion of telemetry increased precision of our results, and cameras provided comparable estimates of density when we calibrated them on the SCR results. Based on these results, we recommend a monitoring program of fDNA transects repeated once every 5 years, camera stations repeated at half of transects every year, and telemetry data from 1 deer for every 2 transects on average. We estimated an average annual cost of $1,316 (U.S.) per transect to sustain this endeavor. The integration of cameras with fDNA to combine age structure data with sex-specific abundance data represents a novel and significant step forward in the capacity to estimate deer population parameters. © 2018 The Authors. *Journal of Wildlife Management* published by Wiley Periodicals, Inc. on behalf of The Wildlife Society.

KEY WORDS cameras, costs, density, fecal DNA, monitoring, N-mixture model, spatial capture–recapture, telemetry.

Precise estimates of population size of mule deer (*Odocoileus hemionus*) are essential to conservation and managed hunting of this species in the western United States. Although a variety of methods exist to survey deer, state wildlife agencies have struggled to obtain credible population estimates over large geographical regions for which planning information is required (Rabe et al. 2002, Freddy et al. 2004, Mason et al. 2006). Researchers have devoted attention to improvement of aerial survey methods in open habitats. For example, aerial surveys can be used to obtain robust estimates of deer density, through distance sampling, sightability models, and capture–recapture techniques (Keegan et al. 2011). However, aerial surveys are less useful for deer in montane forests, in other densely vegetated habitats, and in rugged terrain where direct observation is consistently low or variable.

For this reason, wildlife agencies have increasingly turned to fecal DNA (fDNA) surveys and capture–recapture modeling of these data (Brinkman et al. 2011, Lounsberry et al. 2015, Brazeal et al. 2017). Molecular genetic techniques allow researchers to identify individual-specific genotypes from epithelial cells on the surfaces of fecal pellets of ungulates (Waits and Leberg 2000, Lukacs and Burnham

Received: 17 August 2017; Accepted: 19 April 2018

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2005). These same methods can be used to determine the sex of individuals (Ebert et al. 2012). Use of fDNA data and capture–recapture modeling for population estimates is more reliable than abundance indices based on pellet counts (Brinkman et al. 2013).

The value of the fDNA studies is enhanced through combination with other sources of data. First, although fDNA can be used to accurately identify individual deer and their sex, DNA alone cannot be used to distinguish adults from fawns. Therefore, independent methods are needed to estimate age structure. A promising approach for addressing this data gap is N-mixture modeling of deer counts by age and sex class from camera stations (Royle 2004, O'Connell et al. 2011, Keever et al. 2017). Second, traditional (i.e., non-spatial) capture–recapture modeling of fDNA data only estimates abundances along transects, requiring additional information about effective survey area to get estimates of density and population size. Spatial capture–recapture (SCR) modeling can be used to directly estimate density and is less vulnerable to biases stemming from incorrect assumptions about effective sampling area. However, because SCR entails estimation of a parameter additional to abundance (individual movement scale), it may yield lower precision for a given sample size (Brazeal et al. 2017). Independent home range size estimates or raw location data from global positioning system (GPS) telemetry can be used to inform individual movement scale, which can be integrated into the modeling process to increase the precision of SCR estimates (Dice 1938, Ivan et al. 2013).

Integrated modeling methods, in general, facilitate the combination of different information sources of varying quality to fill data gaps (White and Lubow 2002, Pacifici et al. 2017). Recently, this approach has been adapted to combine abundance estimates from unmarked animals with independent telemetry data to estimate density for carnivores (Furnas et al. 2017, Popescu et al. 2017). Alternatively, modeling of replicated samples from different survey methods can increase robustness of results (Dennis et al. 2010). For example, calibrating lower-cost but less accurate estimates (e.g., from camera stations) on higher-cost but more accurate estimates (e.g., from fDNA) can facilitate broader spatiotemporal sampling that relies more on the lower-cost method. Bayesian models are particularly flexible for integrating different sources of data and computing derived quantities such as population size, home range size, and demographic ratios (Link et al. 2002).

We combined modeling of data from fDNA, camera stations, and GPS telemetry to obtain mule deer population size estimates for adult females, adult males, and fawns on an 11,500-km^2 forested region of summer range for migratory deer in northern California, USA. To evaluate the accuracy and precision of our results from this descriptive and methodological study, we compared them to modeling without telemetry data. Finally, we provide recommendations for adapting our methods to monitor population size and inform deer management across California including an assessment of costs.

STUDY AREA

The study area encompassed a 11,500-km^2 area in the Southern Cascades and Sierra Nevada Mountains, California, USA, during the late spring and early summer of 2015 and 2016 (Fig. 1). We selected 3 deer management zones (C3, C4, X4) and truncated them to potential summer range habitat, which we defined as all areas >500 m in elevation. The deer in this area are predominantly migratory. The study area spans 39.7–41.0°N in latitude and 120.4–122.1°N in longitude. Elevations range from 159–3,175 m across mountainous terrain punctuated by valleys and old lava flows. Average annual precipitation varied from 242–3,132 mm ($\bar{x}$ = 1,098 mm), most of which came as snow and rain during winter (Dec–Mar). Conifer- or oak (*Quercus* spp.)-dominated forests covering 92% of the area were primarily Sierran mixed conifer, Douglas-fir (*Pseudotsuga menziesii*), white fir (*Abies concolor*), red fir (*Abies magnifica*), lodgepole pine (*Pinus contorta*), ponderosa pine (*Pinus ponderosa*), Jeffrey pine (*Pinus jeffreyi*), eastside pine, montane hardwood-conifer, and juniper (*Juniperus* spp.) forest types interspersed by wet meadows, pockets of chaparral, and alpine areas (Mayer and Laudenslayer 1988). Private lands actively managed for timber covered 47% of the study area. Public lands that were less intensely managed covered 50% of study area. Designated wildernesses on public lands summed to 643 km^2. Wildlife using the area

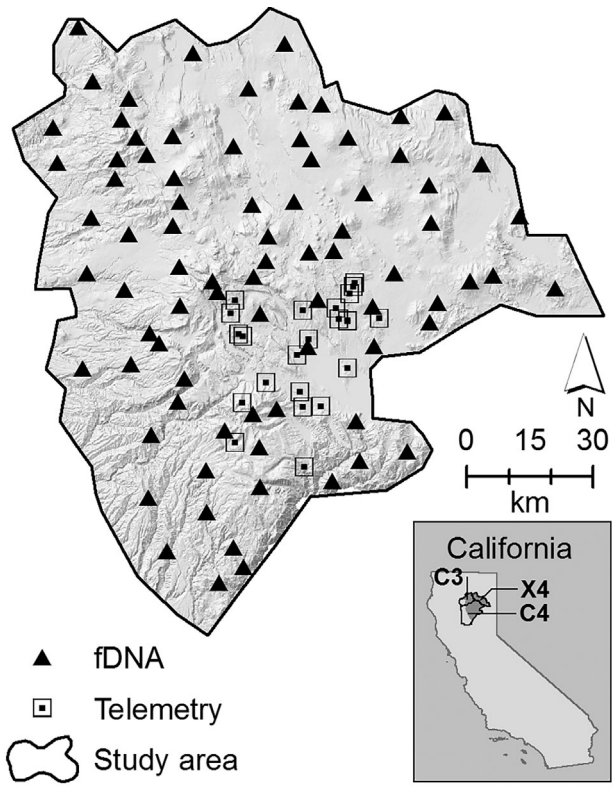

Figure 1. Locations of fecal DNA (fDNA) transect surveys for mule deer and telemetry-monitored deer in an 11,500-km^2 region representing summer range portions of 3 hunt zones (C3, C4, X4) in northern California, USA, June–August 2015 and 2016.

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included numerous species of birds (Furnas and McGrann 2018) and other taxa. Besides mule deer, other common and widespread large mammals included coyote (*Canis latrans*), western gray fox (*Urocyon cinereoargenteus*), American black bear, (*Ursus americanus*), and mountain lion (*Puma concolor*). Elk (*Cervus canadensis*) and fisher (*Pekania pennanti*) were less common, but their populations may be increasing (California Department of Fish and Wildlife [CDFW] 2017, Furnas et al. 2017).

METHODS

Sampling Design and Protocol

Our fDNA surveys were adapted from recent applications in California (Lounsberry et al. 2015, Brazeal et al. 2017). Consistent with our goal to estimate population size over a large geographical area, we used spatially balanced, random sampling to locate survey sites evenly throughout the study area (Stevens and Olsen 2004). We assigned hexagons from the Forest and Inventory Analysis (FIA; Bechtold and Patterson 2005) sampling frame overlaid on the study area to spatially clustered groups of similar size, and then randomly selected sampling hexagons within each group. The starting point for fDNA surveys was usually located at the centroid of a selected hexagon, but private property, steep terrain, and other logistical issues often required relocating survey sites to more accessible locations within selected hexagons.

From the starting point within a selected FIA hexagon, we established an approximately 1,000-m long by 2-m wide belt transect. We started by following a pre-determined compass bearing (PB), switched to deer trails when we encountered them, and reverted to the PB when we lost a trail or a trail began to head more than 90 degrees from the PB. We sampled transects every 6–8 days to allow sufficient time for pellets to accumulate for recapture, while minimizing the time pellets were exposed to the environment. We sampled pellets only from piles that appeared sufficiently fresh for DNA extraction (i.e., with a mucous sheen or no sheen but un-cracked). From each pile, we collected 4–6 pellets in a sample vial. At the end of each day, we placed 95–100% ethanol in each vial to submerge all pellets for DNA preservation. We swept excess pellets off the transect path or buried them to avoid false recaptures on subsequent sampling occasions. We sampled each transect 4 times except if we did not collect pellets during the first 2 visits, we discontinued the transect. We sampled 30 transects in 2015 from 17 June to 25 August, and 50 additional new transects in 2016 from 6 June to 30 August (Fig. 1). The sampled locations included a mix of public and private ownerships.

Concurrent to the fDNA surveys, we placed an unbaited camera station within 50 m of each end of each transect. Where available we aligned cameras to take pictures along deer trails. At each station we affixed a stealth-mode Reconyx PC 90 or PC 900 infrared sensor, motion-activated, digital camera (Reconyx, Holmen, WI, USA) to a tree or a fencepost. We placed the camera 1 m above the ground aimed slightly down ($<20^{\circ}$) and pointed at a 45° angle incident to the trail, if present. We set cameras to trigger with high sensitivity and to take 3 pictures/trigger with 1-second intervals and no delay between consecutive triggers. We reviewed surveys to create a detection history for each site, which indicated the minimum distinguishable count of deer by class (adult female, adult male, fawn) observed for each 24-hour survey day up to 21 days. If the survey duration was <21 days, or if the camera was not functional some of the time, we treated these days as missing data (x) in a full 21-day detection history (e.g., 00000230102000xxxxxxx for a 14-day survey). Two persons independently reviewed all images after which they conferred to resolve any differences in a final detection history. Because we could not usually distinguish individual deer within each class, we considered the minimum count to be the greatest number observed passing the camera from the same direction within the same hour. However, we used antlers, ear notches, body shape, and other distinguishable features to differentiate among individuals where possible, and among age and sex classes (e.g., adult females, adult males, and fawns). We instructed image reviewers to err on the side of caution and not include additional deer in their counts if they were not confident in age and sex determination.

DNA Analysis and Genotyping

We transferred fecal pellets to the Mammalian Ecology and Conservation Unit of the University of California Davis Veterinary Genetics Laboratory for DNA extraction and genotyping; the methods have been described elsewhere (Lounsberry et al. 2015, Brazeal et al. 2017). Briefly, epithelial cells were washed from the surface of pellets with buffer ATL (Qiagen, Valencia, CA, USA), from which the lab extracted DNA using the Qiagen DNeasy Blood and Tissue Kit according to the manufacturer's protocols for blood. Each DNA sample was then genotyped at 10 microsatellite loci and a sex marker ≥ 2 times, combined into a multilocus consensus genotype, and retained only if ≥ 8 microsatellite loci were successfully amplified.

The assignment of sample genotypes to individual identities entails some error rate, which, if high, can significantly bias SCR estimates (McKelvey and Schwartz 2004). The magnitude of this problem depends ultimately on genotyping error rates relative to the polymorphism of the marker set in the particular population under study. Based on previous studies of multiple mule deer populations in California using the same marker set and protocols, the genotyping error rate was sufficiently low ($\leq 1.2\%$; Brazeal et al. 2017) relative to the high number of loci used (10, plus a sex marker) and their polymorphism to facilitate identification and differentiation of individuals with high confidence (Lounsberry et al. 2015, Brazeal et al. 2017). We assigned genotypes to individuals based, initially, on a threshold in the number of allelic mismatches between sample genotypes (20% of those compared), below which we considered them to be from the same individual and above which we considered them to reflect 2 distinct individuals (Lounsberry et al. 2015). When the proportion of mismatches between samples was slightly below this threshold (e.g., 10–20%; which was rare), we additionally considered numbers of

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samples and replicates that supported mismatching alleles, particularly at loci for which both putative individuals were heterozygous, occasionally resulting in 2 assigned individuals sharing >80% of their alleles. To characterize the genetic diversity associated with the marker set in the study population, we estimated expected heterozygosity (He_e) and observed heterozygosity (He_o) using Arlequin (version 3.5.1.3; Excoffier and Lischer 2010) and estimated the unbiased probability of identity (PID) and probability of identity of siblings (PID_{sibs}) using equations 2 and 3 from Waits et al. (2001).

We transformed the genotyping results into a detection history for each individual deer. To facilitate SCR at a finite set of detection locations, we converted each transect in to a series of detectors spaced an average of 75 m along transects. The values at each detector represented whether we recovered ≥1 genotyped pellet sample in the vicinity of each detector for each individual deer during each survey visit.

Home Range Size

We used telemetry to augment inferences about effective survey area of the fDNA and camera surveys and to increase precision of our density estimates. We collated data from GPS collars on 19 adult females and 4 adult males located within the study area during 2010–2017. Our objective was to estimate the sampling area within which we used a survey method (fDNA or cameras) to estimate abundance during a 21-day survey period. To do this, we stratified the telemetry data into groups that represented all telemetry from an animal during a single month (May–Aug) with 3–6 locations/day. We included only those groups for which all locations within a month occurred on summer range after spring migration or before fall migration. We did this to ensure that movement associated with migration did not affect estimates of home range size representing summer range use. We calculated 95% kernel density estimates of home range size for these groups using the plug-in method for bandwidth selection. Based on the recommendations of Walter et al. (2011), we chose this method because it conformed best with our purpose of estimating space use of adults (especially females) in a small, concentrated area after fawning. We computed mean home range size by sex and applied bootstrapping (10^5 samples; Efron 1982) to estimate standard errors and used those to represent sex-specific estimates of home range of deer detected in our surveys and their variability prior to the SCR modeling.

It is common practice to use the radius of a circle of area equal to the expected home range to buffer points or transects to approximate the effective sampling area of a survey method (Dice 1938, Furnas et al. 2017, Popescu et al. 2017). However, it was unclear how the radius we derived from kernel estimation methods related to the scale of movement parameter (σ) used in a half normal distribution to model detection probability as a function of distance to a deer home range center in SCR. Therefore, we used simulation to empirically evaluate this relationship. We generated 1,000 simulated monthly telemetry samples of 95–176 points each drawn from a bivariate normal distribution with standard deviation σ uniformly distributed on [100, 1,000]. For each sample we calculated the area (A) of the 95% contour of the kernel density estimate using the plug-in bandwidth, and defined radius as $r = \sqrt{A/\pi}$. We fit the model $\sigma = br$ where b is a constant, using the lm function in the R programming language (3.3.1, www.r-project.org).

One advantage of a Bayesian model is that it allows prior information (e.g., telemetry) and the data at hand (e.g., fDNA used in SCR) to inform a posterior distribution representing current knowledge (Link et al. 2002). Therefore, we used equation $\sigma = br$ to convert our telemetry-based estimate of home range radius to an estimate of σ, which we used as an informative prior in our Bayesian formulation of SCR. In doing so we expected to increase the precision and robustness of our posterior estimates of home range size and density.

The telemetry we used required capture of deer by means of free-range darting and chemical immobilization. All procedures in the capture and fitting of animals with GPS collars followed a capture plan reviewed by CDFW veterinarians and approved by CDFW management. The capture plan complied with the CDFW's Policy on the Use of Pharmaceuticals in Wildlife (CDFW 2004).

Site Covariates

We created site-level covariates for potentially explaining spatial variation in abundance and detection probability in modeling of the fDNA and camera station data. Previous research suggested that mule deer select mesic areas with cover and cooler temperatures on summer range, and that this preference may be stronger for post-parturition females (Nicholson et al. 1997, Long et al. 2009). Therefore, we used average annual precipitation, tree canopy cover, and average maximum daily temperature as proxies for these conditions in our abundance modeling. In particular, we included precipitation as an indicator of forest productivity for providing greater thermal cover. We calculated average annual precipitation in a buffered area surrounding each transect or camera station using an 800-m raster model of 30-year normals (1981–2010) from the Prism Climate Group (http://prism.oregonstate.edu; Daly et al. 2008). For buffering we used different radii for females and males. We chose radii close to those associated with the expected home range size from the telemetry data (500 m for females and 800 m for males). We computed average maximum daily temperature during July 2015 and 2016 within the same buffers using 4-km raster models also from the Prism Climate Group. We created a covariate representing average percent tree canopy cover in the same buffers using land-use and land-cover data derived from the LANDFIRE Existing Vegetation Cover map (Toney et al. 2009). We confirmed that this covariate was not collinear with precipitation ($r = 0.33 - 0.37$ for survey sites). We also created covariates representing the year (2016 [1] vs. 2015 [0]) and start date (number of days since 1 Jan) of surveys for potentially explaining variability in detection probability.

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Integrated Modeling

We combined SCR and N-mixture modeling within an integrated Bayesian modeling framework (Fig. 2). We used fDNA to directly estimate female density using SCR. We used N-mixture modeling of the camera data to compute a ratio of fawns per adult female, which allowed us to get an estimate of adult female density based on the SCR results. Unfortunately, SCR performed poorly for males; therefore, we relied on a ratio of adult males to adult females to estimate male density. We calculated this ratio from 2 separate sources: modeling of the camera data and unmodeled counts of the fDNA pellet samples. Finally, we used telemetry to improve estimates of effective survey area applied during the steps listed above.

We used SCR modeling to estimate densities of females along transects from the fDNA detection histories. In short, SCR behaves like a traditional capture–recapture model (i.e., it estimates the probability of detection of each individual deer for each survey revisit). However, SCR is more complex because it simultaneously estimates the locations of activity centers (i.e., home range centers) of deer within a pre-specified mask area around transects. It does this by modeling how detection probability declines the farther detectors are from latent activity centers (Royle et al. 2014). We fit a Bayesian, state space model using data augmentation to estimate the additional number of deer expected within the mask area but never detected. We did this by adding a large number (i.e., 30) of zeros to the detection history for each site and survey occasion representing additional deer that were potentially present but never detected. We then modeled a data augmentation parameter governed by a Bernoulli distribution representing whether each deer in the augmented data set was present. This approach is analogous to a multi-species occupancy model (Iknayan et al. 2014) with shared hyper-parameters except that species are replaced with individual deer.

We never detected the same individual on >1 transect; thus, we allocated deer to transects in the modeling by means of a multinomial distribution (Royle et al. 2014). We included average annual precipitation, average maximum daily temperature, and tree canopy cover as covariates on abundance. We included survey start date and year as covariates of detection probability. We set the mask area around each transect to include all potential activity centers within 1,000 m of any detector. We chose this limit so that it was $\geq$4 times our expectation for σ in the half normal distance detection model used in SCR (Efford 2017*a*).

We used N-mixture modeling to estimate abundances of adult females, adult males, and fawns at camera stations (Royle 2004, Keever et al. 2017). We fit all 3 classes of deer in the same model component using hyper-parameters that treated differences among classes in all parameters as random effects about community-level means (Yamaura et al. 2012). To address lack of independence among detections, we modeled deer counts to follow a beta-binomial distribution (Martin et al. 2011). Because of the added complexity of this modeling step, we did not attempt to include covariates on the 2 parameters (i.e., α and β) associated with the beta-binomial distribution. We included precipitation, maximum daily temperature, and tree canopy cover, however, as covariates on abundance.

We applied a series of interconnected steps to perform model integration (Fig. 2). First, rather than assuming our 80 transect locations were truly random and representative of

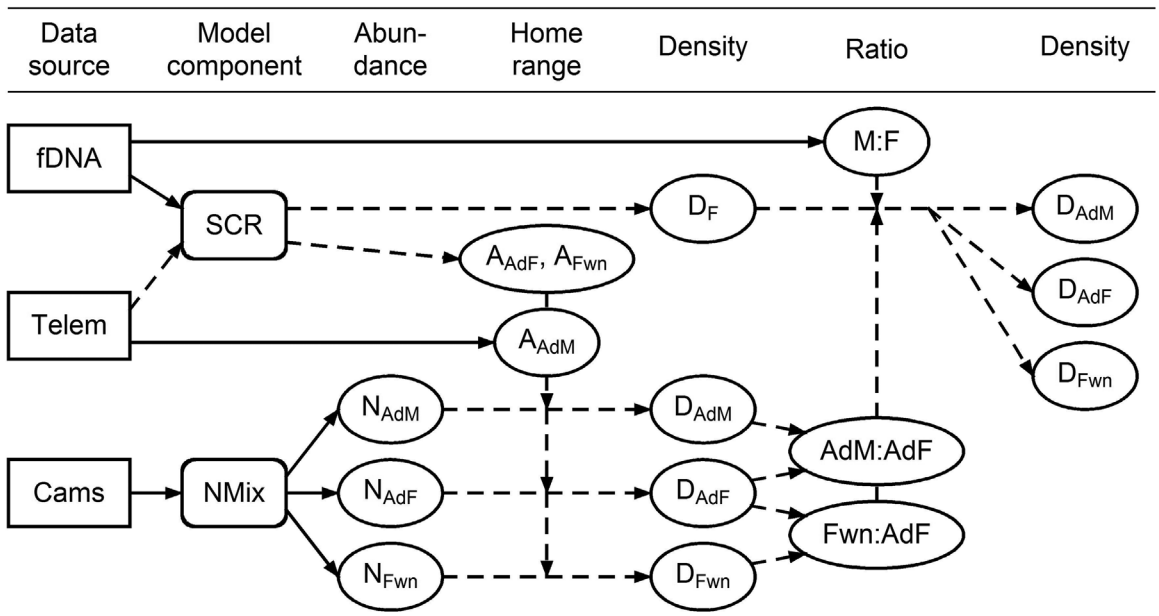

Figure 2. Structure of integrated modeling combining fecal DNA (fDNA), camera stations (cams), and telemetry (telem) to estimate density (D) and composition for mule deer in northern California, USA, June–August 2015 and 2016. Model components are spatial capture–recapture (SCR) and N-mixture (NMix); intermediate parameters are local abundance (N) and home range area (A); population classes are adult male (AdM), adult female (AdF), juvenile of either sex (Fwn), and male and female without regard to age (M and F).

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the study area, we used a geographic information system (GIS) to generate 640 random 1,000-m virtual transects throughout the study area and calculated their site covariate values to predict abundance of females along each virtual transect based on the covariate parameters from SCR. For each iteration of the Markov chain Monte Carlo (MCMC) algorithm used to solve our Bayesian model, we computed the average predicted abundance for a random sample of 80 of the virtual transects, which we divided by mask area to get estimates of average density for the study area. In taking this approach, we based inference about expected density for the study area on covariate effects from modeling instead of a random sampling design for selecting transects (Neyman 1934, Gregoire 1998). Second, assuming similar home ranges for females and their fawns, we estimated a ratio of fawns to adult females (FPD; fawns per doe) using the outputs of the N-mixture model component. We removed female fawns from our estimate of female density ($\text{Density}_{\text{F}}$), which left us with average density of adult females. To do this we assumed an even sex ratio of fawns (Verme 1985, Kucera 1991) such that $\text{Density}_{\text{adult F}} = \text{Density}_{\text{F}}/(0.5 \times \text{FPD} + 1)$. Third, we calculated fawn density by multiplying adult female density by FPD.

We could have repeated the step detailed above to estimate adult male density, but our initial SCR modeling of males provided an imprecise estimate we suspected was biased low. Therefore, we did not include SCR of males in our final integrated model. Instead we used the home range size estimate for males from telemetry to convert adult male abundance from N-mixture modeling to density. We also used the posterior estimate of home range size based on SCR and telemetry to convert female abundance from N-mixture modeling to density. We then used these 2 densities to get a ratio of adult males to adult females (i.e., bucks per doe [BPD]). Because we expected home range sizes to differ for adults by sex, we could not simply compute a ratio of abundances from the N-mixture modeling. To evaluate the robustness of this result, we independently calculated a ratio of males per female (MPF) by computing proportions of male and female samples directly from the genotyping results and estimating their standard errors based on the binomial distribution (Brazeal et al. 2017). We transformed MPF to a ratio of adult males to adult females as follows: $\text{BPD} = \text{MPF} \times (0.5 \times \text{FPD} + 1) - 0.5 \times \text{FPD}$. We calculated average adult male density by multiplying adult female density by an average of BPD calculated using both methods. Finally, we scaled-up density estimates for all 3 classes of deer by multiplying them by the size of the study area (i.e., 11,500 km^2).

Posterior distributions for derived quantities are readily computed in Bayesian models. We used this approach to estimate parameters of interest (e.g., adult male density) that were based on multiple sources of information and incorporated the different levels of error from those sources. To demonstrate how population estimates could contribute towards determination of sustainable harvest levels, we compared our pre-harvest estimate of adult male population size to an estimate of average male deer harvest for 2015 and 2016 ($n = 2{,}873 \pm 28$) based on mandatory reporting of hunter success (CDFW, unpublished data). We report 90% credible intervals on all parameter estimates consistent with the recommendations for monitoring programs (Bart et al. 2004, Purcell et al. 2005). This is because our long-term goal is to monitor deer population trends throughout California, and a Type I error rate of 0.1 is more balanced than 0.05 with respect to a Type II error rate of 0.2 (i.e., 80% power standard to monitor a trend). We report borderline credible effects in cases where the 85% credible interval overlapped zero.

Bayesian models accommodate complex and integrated model structures through an iterative series of simulations (Link et al. 2002). Specifically, we solved our model through an MCMC algorithm implemented in JAGS (4.2.0; Plummer 2003) accessed via R statistical software with the jagsUI package (Kellner 2015). We assumed uninformative priors for all parameters except σ (i.e., for which telemetry data informed the prior). We ran 5 independent chains each of 20,000 samples with a burn-in period of 10,000 and a thinning rate of 5. We assessed the effective mixing of these chains by means of the Gelman-Rubin convergence statistic ($\hat{R} < 1.1$; Gelman et al. 2004). The survey data and R code we used including full technical specification of our modeling and complete model results are provided as an online supplement (Supplemental Material Data S1).

Evaluation of Modeling Performance

To evaluate how well our integrated model estimated deer population size, we compared model outputs based on different data sources. In particular, we ran a second model without any telemetry data. We replaced the informative prior from telemetry on female σ with an uninformative prior. We added a male SCR component also without any informative priors, which we used to directly compute male density instead of relying on the BPD ratio from cameras and pellet counts. However, we continued to use the FPD ratio from cameras to remove fawns from the SCR-based estimates for males and females. We inspected how these changes affected posterior estimates of σ and deer density.

Returning to the first model, we assessed agreement between camera station- and fDNA-based estimates of density. Lastly, we evaluated agreement between density estimates based on our survey sites with those based on the random GIS locations representative of the study area. We made both of these assessments of agreement (or concordance) in terms of female density. In doing so, we computed female density (D_{F}) from cameras as follows: $D_{\text{F}} = D_{\text{adult F}} + 0.5 \times D_{\text{fawn}}$.

Costs

By keeping track of project costs, we were able to estimate average costs on a per-transect basis (i.e., 1 transect/144 km^2). We applied these costs to a monitoring program we recommend based on our surveys. In this program, fDNA surveys at sentinel locations would occur every 1 of 5 years and camera stations would be surveyed at half of these locations every year. To further spread out the sampling

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effort over time we assumed implementation of transects over 2 years in each 5-year cycle (e.g., half in each year). Finally, we assumed deployment of 1 GPS collar for every 2 transects, on average, with a target of 25% of collars on adult males and the remainder on adult females. We reported average annual costs over a 5-year timeframe and separated costs by project component category (e.g., personnel, equipment).

RESULTS

Genotyping and Individual Identification

From 80 transects we collected 1,154 pellet group samples. After eliminating samples with <8 (of 10) amplified loci, we retained genotypes for 758 samples (66%) from 68 of our transects. We identified 493 female captures and 265 male captures, indicating a MPF ratio of 0.538 ± 0.041.

The 758 genotypes were assigned to 379 individuals, including 240 females ($\bar{x}$ number of captures/individual $= 2.1$) and 139 males ($\bar{x}$ number of captures/individual $= 1.9$). The 379 individual genotypes included 97 alleles among the 10 microsatellite loci and the heterozygosities were generally high (Table 1). Correspondingly, the overall (all 10 loci) PID was 2.08×10^{-11} and the overall PID_{sibs} was 1.2×10^{-4}. Although we assigned a small number of individuals contrary to our provisional threshold at 80% alleles shared, most genotype comparisons from samples assigned to a common individual exhibited >0.80 shared alleles and most genotype comparisons from samples assigned to different individuals exhibited <0.80 shared alleles (Fig. 3).

Integrated Modeling

For SCR modeling of the fDNA data, there was limited evidence of habitat selectivity for females (Table 2). Abundance was positively correlated with higher precipitation. There was a borderline credible association for higher abundances at sites with lower temperatures (Table 2). Detection probability increased with survey date (6 Jun–30 Aug). It was lower in 2016 compared to 2015.

From simulation modeling we demonstrated the following relationship between the σ parameter used in SCR and the radius of a circular home range from 95% kernel density estimates using our telemetry data: $\sigma = 0.44\,r \pm 0.0008\,r$. Because precision of this estimate was high, we included 0.44 as a constant in our integrated modeling. From the telemetry we estimated average home range radius-equivalents of 530 ± 24 m ($n = 56$ home ranges) for adult females and 798 ± 112 m ($n = 6$ home ranges) for adult males. Our posterior estimate of the female radius after SCR changed very little (526 ± 21 m).

From N-mixture modeling of the camera station data, we found evidence of habitat selectivity (Table 3). Specifically, abundances of adult females and fawns were positively associated with increasing precipitation and tree canopy cover, but there were no credible associations with temperature. There were no credible abundance associations for adult males. On average, daily detection probability was highest for adult females and lowest for fawns.

Integrating these results we found composition ratios of approximately 67 fawns/100 adult females (FPD = 0.67, 90% CI = 0.53–0.84) and 36 adult males/100 adult females from cameras versus 38 adult males/100 adult females from pellets ($BPD_{cameras} = 0.36$, 90% CI = 0.21–0.59 and $BPD_{pellets} = 0.38$, 90% CI = 0.28–0.48; Table 4). Using the SCR results for females and the demographic ratios, we estimated a population size that included 29,317 adult females (90% CI = 24,550–34,592) and 10,845 adult males (90% CI = 7,778–14,858). We estimated that an average of 27.6% of adult males (90% CI = 19.3–37.0) were harvested in 2015 and 2016.

Evaluation of Modeling Performance

As anticipated, the telemetry data improved precision of our posterior estimates of deer population size compared to the alternative model containing no prior information from the telemetry (Fig. 4). We attribute improved performance to a

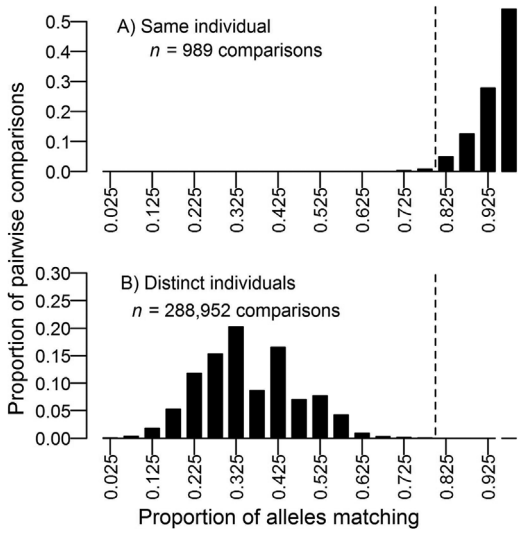

Figure 3. Frequency distributions of allele sharing in pairwise comparisons between fecal DNA genotypes of samples designated as from the same individual (A) and from distinct individuals (B) relative to the provisional threshold (vertical line at 0.80 alleles shared) for mule deer surveys in northern California, USA, June–August 2015 and 2016.

Table 1. Genetic diversity statistics, including number of alleles, expected heterozygosity (H_e), observed heterozygosity (H_o), unbiased probability of identity (PID), and probability of identity for siblings (PID_{sibs}) for the 10 microsatellite loci used to genotype 379 individual mule deer in northern California, USA, June 2015–August 2016.

Locus	Number of alleles	H_e	H_o	PID	PID_{sibs}
ADCYC	2	0.47	0.40	0.394	0.616
BM6506	7	0.74	0.71	0.110	0.410
CELB9	9	0.77	0.48	0.085	0.389
CERVID1	12	0.81	0.63	0.059	0.361
ETH152	13	0.88	0.82	0.028	0.319
SBTD04	20	0.90	0.77	0.020	0.307
SBTD05	10	0.79	0.76	0.070	0.371
SBTD06	6	0.58	0.60	0.229	0.520
SBTD07	14	0.84	0.80	0.046	0.344
TGLA94	4	0.58	0.58	0.232	0.517

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Table 2. Spatial capture–recapture (SCR) portion of integrated modeling results for mule deer using fecal DNA (fDNA) from northern California, USA, June–August 2015 and 2016.

		Model estimate[b]		
Parameter[a]	$\bar{x}$	90% CI_{lower}	90% CI_{upper}	Credible effect[c]
$fDNA_{Female}$[d]				
Detection model parameters				
Intercept	−1.931	−2.161	−1.681	
Survey start date	0.333	0.184	0.488	Yes
Survey year	−0.495	−0.782	−0.218	Yes
Scale of movement (σ)	232 m	217 m	248 m	
Abundance model parameters				
Intercept	3.232	3.072	3.391	
Precipitation	0.038	0.004	0.073	Yes
Temperature	−0.032	−0.065	0.001	Borderline
Tree canopy cover	0.011	−0.024	0.045	No
Data augmentation	0.773	0.656	0.902	

[a] Precipitation, temperature, and tree canopy covariates were standardized. Survey year represents 2016 versus 2015.
[b] Posterior distribution for each parameter estimate on the linear model scale.
[c] We deemed an effect credible if its 90% credible interval did not include zero. Borderline credible effects are reported if the 85% credible interval did not include zero.
[d] We did not use SCR modeling of males to inform our final estimates of population size. We evaluated performance of male SCR in a separate model.

reduction in the coefficient of variation on the scale of movement parameter σ from 0.09 to 0.04 by inclusion of the telemetry. We also confirmed poor estimation of adult male density. This problem became more apparent after subtracting out fawns. The combined uncertainties in male SCR and the FPD ratio led to a credible interval on adult male population size that overlapped zero. Furthermore, the SCR-based estimate of adult male density was 34% lower than what we obtained using the BPD ratios from cameras and pellet counts.

Table 3. Results of N-mixture portion of integrated modeling for mule deer using cameras from northern California, USA, June–August 2015 and 2016.

		Model estimate[b]		
Parameter[a]	$\bar{x}$	90% CI_{lower}	90% CI_{upper}	Credible effect[c]
Adult females				
Detection model parameters[d]				
α (shape parameter)	0.537	0.431	0.634	
β (shape parameter)	4.437	3.530	4.963	
Abundance model parameters				
Intercept	0.194	0.027	0.360	
Precipitation	0.125	−0.005	0.254	Borderline
Temperature	−0.054	−0.184	0.070	No
Tree canopy cover	0.144	0.013	0.281	Yes
Adult males				
Detection model parameters				
α (shape parameter)	0.265	0.206	0.351	
β (shape parameter)	3.593	2.522	4.789	
Abundance model parameters				
Intercept	−0.029	−0.233	0.178	
Precipitation	0.044	−0.134	0.196	No
Temperature	0.026	−0.124	0.194	No
Tree canopy cover	0.058	−0.120	0.215	No
Fawns				
Detection model parameters				
α (shape parameter)	0.211	0.200	0.233	
β (shape parameter)	4.249	3.337	4.937	
Abundance model parameters				
Intercept	−0.225	−0.486	0.024	
Precipitation	0.177	0.009	0.372	Yes
Temperature	−0.095	−0.284	0.067	No
Tree canopy cover	0.211	0.041	0.417	Yes

[a] Precipitation, temperature, and tree canopy covariates were standardized.
[b] Posterior distribution for each parameter estimate on the linear model scale.
[c] We deemed an effect credible if its 90% credible interval did not include zero. Borderline credible effects are reported if the 85% credible interval did not include zero.
[d] The shape parameters pertain to beta-binomial distribution without covariates.

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Table 4. Ratios, density, and population size from integrated modeling of a mule deer population in northern California, USA, June–August 2015 and 2016.

Parameter	Model estimate		
	$\bar{x}$	90% CI_{lower}	90% CI_{upper}
Ratios			
Fawns/adult female	0.672	0.530	0.837
Adult males/adult female			
Cameras	0.359	0.208	0.589
Pellet	0.382	0.283	0.478
Final (cameras and pellets)	0.371	0.279	0.494
Density (deer/km^2)			
Females	3.401	2.886	3.972
Adult females	2.549	2.135	3.008
Adult males	0.943	0.676	1.292
Fawns	1.703	1.334	2.124
Total	5.196	4.392	6.070
Population size (11,500-km^2 study area)			
Adult females	29,317	24,550	34,592
Adult males	10,845	7,778	14,858
Fawns	19,587	15,340	24,430
Total	59,748	50,511	69,803

Concordance among our independent estimates of female density from camera stations and fDNA was 0.58, which reflects a credible difference from unity ($Density_{camera}$/$Density_{fDNA}$, 90% CI = 0.49–0.67). Concordance among our estimates of female density based on survey sites versus random GIS locations was 1.02 ($Density_{survey}$/$Density_{GIS}$, 90% CI = 1.00–1.05).

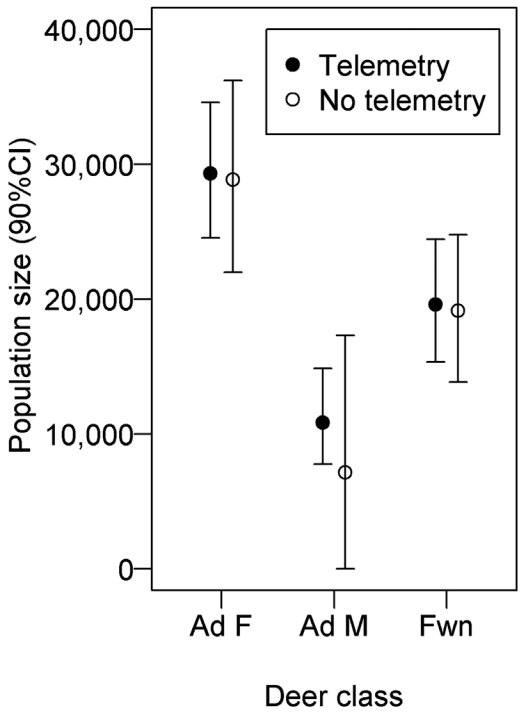

Figure 4. Comparison of mule deer density estimates from integrated modeling of fecal DNA and camera data that was either augmented with telemetry information or not for surveys in northern California, USA, June–August 2015 and 2016. Deer classes include adult females (Ad F), adult males (Ad M), and fawns (Fwn). Results suggest that addition of the telemetry increased precision and accuracy of density estimates, especially for adult males.

Costs

For the monitoring approach we recommend here, we estimated an average annual cost of $1,316 (U.S.) per transect (Table 5). We expect that approximately half of this cost would be associated with personnel expenses. The second largest cost (15%) would be due to equipment purchases (mostly GPS collars), which would be expected to drop by at least half after the first 5 years spent building up telemetry data to support establishment of transects throughout and across the state. We expect this initial information would lead to robust baseline estimates of home range size, migratory patterns, and population size. Assuming a system of 500–1,000 transects under a statewide monitoring program, we estimate an average annual cost of $0.7–1.3 million to establish this network over a 5-year timeframe.

DISCUSSION

Surveying deer using fDNA is an emerging methodology that adds to the toolbox of techniques available to wildlife managers to estimate density and population size (Brinkman et al. 2011, Lounsberry et al. 2015, Brazeal et al. 2017). This is especially important in forested or other densely vegetated habitats where aerial surveys are not practical because of low visibility. To illustrate this point, we note that average tree canopy cover was 39% (SD = 15%) at the locations we surveyed. Our results demonstrate how integrated modeling (Pacifici et al. 2017) can be used to combine fDNA with camera station and telemetry data to get the age- and

Table 5. Projected costs per location to monitor mule deer in California, USA. Monitoring assumes fecal DNA (fDNA) surveys at a location 1 out of every 5 years, camera stations every year at half of locations, and 1 global positioning system (GPS) collar for every 2 transects on average.

Project component	Average annual cost ($U.S.)	% of total
Equipment[a]		
GPS collars	120	
Camera stations	65	
Other supplies	13	
Subtotal	198	15
Personnel[b]		
Field crew	313	
Project management	165	
Design and modeling	96	
GPS collars	134	
Subtotal	708	54
Vehicle miles[c]	91	7
Laboratory[d]	130	10
Indirect costs[e]	190	14
Total	1,316	

[a] Includes GPS collars, cameras, and other supplies including batteries and ethanol.
[b] For 40 locations surveyed in a year, assumes a crew of 4 persons in the field for 3 months and 2 technicians in the office for a month for fDNA and camera surveys, or a single technician in the field for 2 months during years when only camera surveys occur; GPS collar personnel costs assume 38 person-hours for every deer capture on average.
[c] Assumes 3,200 km/month/field crew person at $0.34/km.
[d] $45/sample for DNA analysis.
[e] 30% rate covers administrative and other indirect costs at the California Department of Fish and Wildlife. It excludes laboratory costs, which are contracted out.

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sex-related estimates of density required by managers. We extrapolated our results over a large geographical area corresponding to 3 hunt zones in California to get total population size for adult females, adult males, and fawns. Without the camera station data we would have been unable to separate fawns from adults. This would have been problematic because a substantial but undetermined portion of the population (i.e., fawns) is expected to perish over the summer, fall, and winter. In particular, inability to estimate adult female and adult male portions of the population complicates assessment of recruitment and setting harvest quotas.

We used telemetry data to augment estimation of home range within SCR and N-mixture modeling. In doing so we increased precision of our density and population size estimates (Fig. 4). We incorporated an estimate of average female home range size from telemetry by means of a prior distribution within a Bayesian model. We could have directly incorporated the telemetry locations into SCR (Ivan et al. 2013, Efford 2017*b*), but when we attempted to do so during initial modeling, the estimate of σ based on telemetry did not agree with that derived from the fDNA data (e.g., $\sigma_{\text{Female telemetry}} = 327 \pm 19$ m vs. $\sigma_{\text{Female fDNA}} = 232 \pm 9$ m). We were only able to achieve agreement on estimates of σ from the 2 data sources after computing home range sizes using the plug in kernel density method (Walter et al. 2011) and using simulation to model the relationship between radii from kernel estimation and the scale of movement parameter σ in SCR. We recommend additional investigation into the best use of telemetry in SCR. One approach may be to evaluate the use of alternative scale of movement functions (e.g., hazard rate instead of half normal). In the meantime, we found that the use of prior information in a Bayesian modeling framework provided a straightforward and intuitive means of incorporating telemetry data to improve precision of density estimates from SCR.

The telemetry aided us in evaluating whether our SCR and N-mixture modeling satisfied an assumption of closure (i.e., no change in population state) during surveys along transects and at camera stations. We found that 16% of the telemetered deer arrived on summer ranges in June, and only 2% began fall migration in August. However, none of the late arrivals in June among the telemetered deer occurred during the years our fDNA surveys occurred (i.e., 2015 and 2016, Jun–Aug). Nevertheless, we cannot rule out some violation of the closure assumption, which may explain why we found that detection probability increased with survey date (Table 2). Alternatively, some of this increase in detection probability by date could be explained by survey crews getting better at collecting viable pellet samples over the course of the season. If there was some violation of closure, we expect that it would bias our density estimates high (Royle et al. 2014), but we also expect that any bias would be much smaller than the credible intervals we reported on those estimates.

Model performance using SCR was poor for males. Besides providing lower estimates of population size that did not agree with BPD ratios derived from cameras and pellet counts, we got a population estimate for adult males with a credible interval overlapping zero once we removed fawns from the male population. One reason for this unsatisfactory result may be that the male fDNA data were too sparse to provide enough spatial recaptures of individual deer to properly fit a SCR. Alternatively, our transects could have been too short to adequately survey the larger male home ranges, potentially leading to biased estimates of the scale of movement function. For future surveys in California, we recommend additional spatial sampling substituted in place of as much temporal re-sampling, especially in areas where total deer densities or adult male densities are expected to be lower. A second factor potentially affecting the scale of movement parameter (σ) for males could have been confounding adult and juvenile males. Results suggested that 47% of males were fawns (Table 4). Under this circumstance we expect 2 distinct values of σ instead of a single parameter estimated by SCR. We considered introducing a latent categorical variable assigning fDNA detections to either adult or fawn groups but did not follow through with this approach because our modeling was already very complex.

We took a model-based approach to extrapolation of population size across the study area (Gregoire 1998). Our results suggest that there was little difference in average density estimates from survey sites versus those from the random GIS points used in extrapolation. However, we found relatively weak effects of precipitation and temperature explaining spatial variation in female density from SCR (Table 2). The importance of these covariates was more strongly supported ($P < 0.001$) during initial exploratory modeling when we used a generalized linear model to explain variation in the number of individual deer detected along transects. We suspect that the complexity of SCR may limit the precision of parameters linked to covariate effects on density. We considered switching from the multinomial model component assigning deer to transects to a modeling structure wherein covariates are used to predict the locations of deer activity centers (Royle et al. 2014). We chose not to attempt this approach because it would have further increased model complexity, including a transformation from covariates representing the mask areas about transects to covariates for a discrete set of possible activity centers. As more fDNA data is collected across the state leading to larger sample sizes, we expect it will become more practical to model spatial variation in density with greater precision. As previously noted, we did not trust the accuracy of male density estimates from SCR. We anticipate that additional data from across the state will lead to more robust estimation of male deer density directly from fDNA instead of being inferred through a BPD ratio as we did. We are reasonably confident, however, of our final estimate of adult male population size because our independent estimates of BPD from cameras and pellets differed by <7%. With additional telemetry from across the state, it will also be possible to model how home range varies with covariates and this information could be included in integrated modeling as has been done recently for carnivores (Furnas et al. 2017).

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Alternatively, we could generalize σ within SCR by allowing it to vary as a function of site covariates associated with the fDNA and telemetry data.

We observed systematically lower density estimates from N-mixture modeling of the camera trap data versus SCR modeling of the fDNA data. The magnitude of this bias corresponds to the difference between an approximate 75–80% kernel density estimate of the home range and the 95% kernel we used. One interpretation of this discrepancy is that the effective sampling area of camera surveys may be less than an animal's entire home range. Whether or not this is true, unbiased density estimates from N-mixture modeling can be calibrated on SCR results. This could allow wildlife agencies to potentially reduce costs through greater use of cameras relative to fDNA studies, which are more expensive to implement. To increase efficiency, cameras could be placed at a greater number of sites than for fDNA surveys and could be used in years when fDNA surveys do not occur. However, we caution that N-mixture modeling used alone may not be as robust as SCR. Although N-mixture modeling of camera data has been shown to be accurate for estimating density of white-tailed deer (*Odocoileus virginianus*; Keever et al. 2017), our modeling was sensitive to parameterization of detection probability. We believe that our use of the beta-binomial distribution was a good choice because of expected non-independence of detections at cameras (Martin et al. 2011). Another caveat to our use of N-mixture modeling is that simulation studies have demonstrated difficulties in separating inferences about abundance versus detection probability, which has led some to recommend that this modeling approach may be more appropriate for estimating relative abundance (Barker et al. 2018). We agree and have thus used SCR to calibrate our N-mixture modeling results rather than relying on the latter as a robust estimate of abundance.

One possible approach to blending the use of cameras with fDNA surveys would be to increase the sample size of cameras beyond those associated with fDNA transects. This strategy may be useful at locations where placement of transects are infeasible. Alternatively, auxiliary data from other wildlife survey projects using un-baited cameras could be borrowed and added to the integrated model. Camera stations are a widely used survey method that conveniently collect information on multiple species even if those species are not the target of a particular project (Burton et al. 2015).

Our estimate of density (5.20 deer/km^2) was similar to what Brazeal et al. (2017) reported in the central Sierra Nevada Mountains (5.05 deer/km^2). This suggests there may be some level of homogeneity in deer density across summer range in the Sierra Nevada and Southern Cascade Mountains of California. Furthermore, our findings of greater habitat selectivity for female adults and fawns compared to adult males from the camera data are consistent with previous research suggesting that post-parturition females may select areas with greater thermal cover (Nicholson et al. 1997, Long et al. 2009). The CDFW is in the process of expanding implementation of fDNA surveys to other parts of the state including areas occupied by non-migratory populations in the Coast Ranges. As these data become available, it will become increasingly possible to assess how deer density varies throughout the state.

We demonstrated the feasibility of combining fDNA surveys, camera stations, and telemetry studies to efficiently estimate sex- and age-specific components of deer population size over a large geographical area of management interest. We recommend further expansion of this approach across much of California where aerial surveys may be less practical. The precision of the population estimates we provided corresponds to a sampling intensity of 1 transect every 144 km^2, but adjustment of sampling effort in other areas will need to consider differences in expected density and difficulty in accessing survey locations (e.g., wilderness and steep terrain). We estimated that a statewide system of 500–1,000 permanent survey locations each visited once every 5 years for fDNA and half of locations visited every year for camera stations would cost $0.7–1.3 million/year or $1,316/survey location (i.e., 1 transect with 2 camera stations and 1 GPS-collared animal for every 2 transects on average). We anticipate that these data would be used to obtain baseline estimates of deer density in management units throughout the state. Additional information on recruitment and survival would be necessary to add dynamic modeling for projecting the effects of hunting levels on the expected population trajectory (Updike 1990, White and Lubow 2002, Mason et al. 2006). This same approach could be used to assess and adapt to climate, habitat, and species interaction effects on deer carrying capacity (Clements and Young 1997, Monteith et al. 2014). However, there is little information currently available about the rates of long-term population decline that would be of biological or management concern for deer.

A power analysis based on preliminary data from an integrated model that considers population baselines and dynamics would allow refinements of the costs provided above. We expect that the need for telemetry (and associated costs) would decline after the first 5 years of a monitoring program, but telemetry will continue to be important in understanding the migratory patterns of deer and whether they change over time (Monteith et al. 2011). In particular, telemetry data will be important to account for what portion of a population estimated on a summer range is expected to be present on a particular winter range, especially in cases where deer are hunted in areas other than where fDNA surveys occur.

MANAGEMENT IMPLICATIONS

Robust population abundance estimates that include age and sex composition are important for effective deer management and conservation planning. With some additional information on recruitment and natural mortality, a wildlife agency would be able to assess whether harvest levels are sustainable and provide sufficient hunter opportunity. Managers can expect this type of high quality information to become increasingly available as coordinated and robust monitoring methods are expanded throughout California. A combination of fDNA surveys, camera stations, and GPS telemetry can be used to provide much of the necessary data across large

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portions of the state where the use of aerial methods is not practical. Integrated modeling provides an efficient approach to get the most out of the data, but managers will then need to establish thresholds of significance for rates of population change and appropriate measures if those rates are detected.

ACKNOWLEDGMENTS

We thank the many individuals and organizations who facilitated implementation of this project leading to population estimates to be used in management and conservation. In particular, we acknowledge the efforts of L. A. Boswell, N. R. Colbrunn, W. D. Cram, G. C. Harse, T. M. Kash, M. K. Klauer, A. A. Trausch, and C. J. Wise to implement the survey protocol to a high standard of quality despite difficult terrain, hot temperatures, and sometimes thick vegetation including poison oak (*Toxicodendron diversilobum*). R. G. Paiste and J. E. Carlson managed field surveys. C. E. Fust and N. R. Kallman reviewed images from the camera surveys. L. L. Camilo assisted with data management. Z. T. Lounsberry and S. Preckler-Quisquater assisted with laboratory procedures. R. Sollmann and J. L. Brazeal provided advice on SCR analysis. K. E. Converse provided comments on the manuscript. D. M. Mastalir prepared Figure 1. The U.S. Forest Service, Bureau of Land Management, National Park Service, California Department of Fish and Wildlife, Sierra Pacific Industries, Roseburg Forest Products, Fruit Growers Supply Company, W. M. Beaty & Associates, and the Collins Almanor Forest provided access to lands they owned or managed. Surveys, data analysis, and manuscript preparation were funded through revenues from hunting permit sales.

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Associate Editor: Kathryn Schoenecker.

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