FINAL RESULTS FROM THE EAST TEHAMA DEER ABUNDANCE STUDY

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Draft Version: 6 March 2017

EXECUTIVE SUMMARY

For an 11,500 km^2 study area comprising 14% of deer summer range in California, we demonstrate how the combined use of fecal DNA surveys, camera stations, and GPS collars can be implemented to efficiently estimate deer population size. For the mostly forested, 3-zone area, we found an average density of 2.82 does per km^2 (7.30 per mi^2) and 1.11 bucks per km^2 (2.87 per mi^2) summing to a total of 12,718 bucks (90%CI: 10,534–15,302) available for hunting. Besides establishing a baseline against which to monitor population trends, our methods can be readily applied to answer a variety of other questions of conservation and management interest. For example, we demonstrated an association between relative density of bears (and other deer predators) at survey sites and the abundance of fawns.

INTRODUCTION

As part of an effort to develop methods that better measure and monitor mule deer (*Odocoileus hemionus*) population size for hunt zones and conservation units, the California Department of Fish and Wildlife (CDFW) tested the use of fecal DNA (fDNA) transects as a survey method. In 2015 and 2016, we surveyed at random locations throughout summer range in zones C3, C4, and X4 for the East Tehama Deer Abundance Study (ETDA). This area includes deer from the East Tehama and Cow Creek herds. We used non-spatial capture-recapture modeling to estimate deer abundance at these sites (Kéry and Schaub 2012). We combined the modeling of the fDNA data with modeling of home range and camera station data in an integrated model to estimate density and population size for does, bucks, and fawns.

METHODS

Sampling Design and Surveys

Our field and laboratory methods were adapted from those of Lounsberry et al (2015). We randomly selected and surveyed 30 sites in 2015 and 50 additional sites in 2016 throughout an 11,500 km^2 study area defined as all portions of deer hunt zones C3, C4, and X4 above 500 m in elevation (Figure 1). An approximately 1-km transect generally following deer trails was established at each site. It was visited on up to 4 occasions one week apart during late June through early August when does were assumed to be on fawning grounds. During each visit deer pellet groups were collected and cleared from a swath extending 1 m either side of the transect. These pellets were preserved in vials containing 95% ethanol. The physical condition of all pellet groups collected was noted. Un-baited camera stations were set up along a deer path near each end of the transect during the 3-week period when the transects were surveyed.

Figure 1. ETDA study area and locations of 80 fecal DNA transects and camera stations in summer range (>500 m elevation) of deer hunt zones C3, C4, and X4.

Genetic Analysis

The pellet samples were transferred to Ben Sack's laboratory at UC Davis where DNA was extracted to identify unique individuals and gender. We restricted analysis to "good condition" pellet categories likely to have usable DNA. Those categories included pellet groups that when collected were slimy, wet, or dry but with a shiny, un-cracked surface. We used these data to create detection histories of all individuals for each survey at each transect for use in capture-recapture modeling.

Non-spatial Capture Recapture Modeling of fDNA data

We used a non-spatial capture-recapture model on the fNDA detection history of individual deer. We adapted the approach of Royle et al (2014, Chapter 14) using a stratified, multinomial model structure to address the constraint that transects were far enough apart that each individual could only be recaptured along a single transect. We used data augmentation in a Bayesian modeling framework to estimate the total number of deer expected along transects after correcting for detection probability. We modeled females and males in separate model components. Our detection probability model component included date of first survey and survey year as covariates. The covariates in our abundance model component included average tree canopy cover (Toney et al. 2009) in the transect buffer area, average elevation in the transect buffer area, and survey year. The buffer distance was 400 m approximately corresponding to the radius of a circle given the average median home range size for does from our analysis of GPS collar data.

N-mixture modeling of Camera Station data

Two separate technicians reviewed all images from the cameras placed at each end of each transect. They enumerated the minimum number of unique does, bucks, and fawns observed during each 24-hour period at each station. After this review work was completed, both technicians discussed and resolved any differences between their 2 interpretations. We fit a

multi-species N-mixture model (Royle 2004) to the final detection history. Every parameter was specified as a hyper-parameter varying among does, bucks, and fawns as a random effect. Abundance was modeled to follow a Poisson distribution where the covariates were average tree canopy cover and average elevation in the 400-m-radius circle surrounding each station and survey year. The observation process was modeled to follow a beta binomial distribution without any covariates on the shape parameters (α, β) for the beta distribution.

To evaluate the potential impacts of predators on fawns, we fit a separate integrated model including does, bucks, fawns, and 4 species of carnivores detected at the camera traps. These species were black bear (*Ursus americanus*), coyote (*Canis latrans*), bobcat (*Lynx rufus*), and mountain lion (*Puma concolor*). The deer and predator data were fit in separate model components with separate hyperparameters. There were no covariates in the model component for carnivores. We transformed the model estimates of abundance of each predator species at each site into indices of relative density among species by exploiting a theoretical power law relationship between density and body size that is supported by empirical research (Brown et al. 2004). In particular, we multiplied abundances by $M^{-0.75}$ to get relative densities where M was the average mass of each predator species (bear: 69 kg, coyote: 15 kg, bobcat: 8 kg, mountain lion: 52 kg). We used the relative density estimate of each predator species at each station as covariates in the abundance model component for deer.

Home Range Size and Effective Area of Surveys

We aggregated data from does collared with GPS units in (or within the vicinity of) the study area during 2010–2016. We used this information to estimate the median home range size of does on summer range by clipping the data to the months of June, July, and August. We grouped GPS data by individual, month, and year. We calculated 95% kernel density estimates of home range size for each of these groups. We limited home ranges to groups of $\geq$ 30 points. As the distribution of these home ranges was right-skewed, we used bootstrapping (100,000 samples, Efron 1982) to estimate median home range size and the uncertainty associated with this estimate.

We used our estimate of doe home range size to calculate the effective areas of fDNA and camera surveys for does. We did this by calculating the radius of a circle with area equal to our home range estimate. Effective area for fNDA surveys was the area when each transect was buffered by the radius. Effective area for camera surveys was simply the home range estimate. We assumed fawns had the same home ranges and effective survey area as does. We were unable to estimate the effective area for bucks, because we did not have access to any local data on home range size of bucks. Therefore, we were unable to convert our modeled estimates of buck abundance to density.

Additional Data Sources

As we were unable to estimate the effective survey area for bucks, we used an estimate of bucks per doe (BPD) to scale our density estimate for does to a density estimate for bucks. We used data from 11 camera stations placed along fall migration routes within the study area in 2015 and 2016 to estimate BPD. We assumed that all deer observed moving downslope were

unique individuals. Therefore, we used the average of the ratio of bucks to does at each station as a BPD estimate in the fall representing conditions after most harvest mortality was likely to occur. We also used the average estimate of total buck harvest in 2015 and 2016 to adjust BPD to represent a higher ratio in the summer when the fDNA surveys occurred. Harvest was estimated for zones C3, C4, and X4 from mandatory harvest reports submitted by hunters. For hunting tags where the required report was not submitted, we estimated the kill using hunt-specific kill rates obtained from the database of submitted reports.

Integrated Modeling

The capture-recapture and N-mixture modeling components were combined in a single integrated model as summarized in Figure 2. We used the home range estimate for does to convert the fDNA abundance estimate of females to density. We then converted to an estimate of doe density by multiplying female density by 1–FPD/2, where FPD was our estimate of fawns per doe from camera traps and assuming an equal gender ratio in fawns. We used this estimate of doe density as the central parameter for scaling densities and population sizes for does, bucks, and fawns. In particular, we converted BPD estimated from migration trails to BPD during the summer by adding in harvested bucks. We then estimated buck density by multiplying doe density by BPD_{summer}.

Rather than assuming our 80 survey locations were truly random and representative of the study area, we generated 640 random GIS points throughout the study area and calculated their covariate values to predict abundance at each of those points. We took the average predicted abundance at the points as an estimate of average abundance for the study area based on the female portion of the fDNA model component and then converted or scaled to densities by deer class as previously discussed. We multiplied these densities by study area (11,500 km^2) to get population sizes. We also estimated the proportion of the buck population harvested using the harvest data and our population estimate.

The capture-recapture modeling of fDNA data and N-mixture modeling of camera data were not linked or constrained by each other in the integrated deer population model. Therefore, we were interested to see how similarly each model component estimated deer abundance scaled to density. Although our model was structured to base all final density and population estimates on only the female fDNA abundance estimate, we were also interested to see how well the model would perform if we had instead used the camera abundance estimates to scale density. To make this comparison, we used our estimate of doe abundance from the cameras along fDNA transects to alternatively estimate doe density by dividing it by our estimate of doe home range size. We calculated concordance of camera station and fDNA density estimation, which was simply doe density from cameras divided by doe density from fDNA.

Both integrated models (deer population & predator effects) were solved through a Markov Chain Monte Carlo (MCMC) algorithm (Link et al. 2002) implemented in JAGS (4.2.0, Plummer 2003) accessed via R statistical software (3.3.1, www.r-project.org) with the jagsUI package (Kellner 2015). Uninformative priors were assumed for all parameters. Five independent chains each of 20,000 samples were run with a burn-in period of 10,000 and a thinning rate of three. Effective mixing of these chains was assessed by means of the Gelman–

Rubin convergence statistic (< 1.1; Gelman et al. 2004). We reported 90% credible intervals on parameter estimates and deemed covariates predictive if the credible interval for its effect parameter did not overlap zero.

RESULTS

The Sacks lab was able to produce reliable gentoypes for 69% of the 1,154 "good" condition pellet samples we provided them. They identified 493 captures of 240 females and 265 captures of 139 males. This equated to an average of 2.43 individuals captured per transect visit.

In the fDNA model component (Table 1), detection probability increased with date of first survey for both genders, whereas detection probability was lower in 2016 than in 2015 for females only. Transect abundance increased with tree canopy cover and elevation for females, but neither of these covariates were predictive for males. There were no differences in abundance among years. In the camera model component (Table 2), tree cover was positively associated with abundance for does and fawns, and station abundance was apparently lower for fawns in the 2016. Elevation was not predictive of abundance for any of the 3 deer classes. The non-spatial capture-recapture modeling of the fDNA data provided precise estimates of transect abundance ($CV_{Female} = 0.06$, $CV_{Male} = 0.10$).

In the second model including data on predators, we found that bears were more abundant than other deer predators (Fig. 3) and that the relative density of bears was positively associated with deer abundance at cameras. This effect was strongest for fawns (Fig. 4). The associations for coyotes and mountain lions trended positive, but the effect sizes were smaller with credible intervals that overlapped zero. In contrast, relative density for bobcats was negatively associated with fawn abundance.

We got an estimate of 1-month doe summer home range size of 0.482 km^2 (se = 0.062) based on 56 monthly home range estimates from 26 does. This equated to a buffer radius distance of 391 m (se = 25) such that the average effective survey area for females for our transects was 1.22 km^2 (se =0.11).

Using the migration trail camera data, we got a post-harvest estimate of 0.538 (se = 0.032) fawn per doe and a post-harvest estimate of 0.303 (se = 0.023) buck per doe. This contrasted with a pre-harvest estimate of 0.639 (se=0.089) fawn per doe at the fDNA transects. After adding in an estimated average annual buck harvest of 2,888 (no error information), we got a pre-harvest estimate of 0.393 (se = 0.026) buck per doe.

Using the random GIS points, our final, pre-harvest density estimates were 2.82 does per km^2 (7.30 per mi^2) and 1.11 bucks per km^2 (2.87 per mi^2). For the entire study area, we estimated a population of 32,465 does (90%CI: 26,271–39,779) and 12,718 bucks (90%CI: 10,534–15,302). There was good concordance between the fDNA and the camera station density estimates. There was also close agreement between average density at survey sites and at the random GIS points (Table 3). However, coefficients of variation on our integrated density and

population estimates were approximately twice as large as for our local abundance estimates only using the fDNA data.

Figure 3. Relative densities of deer predators at camera stations .

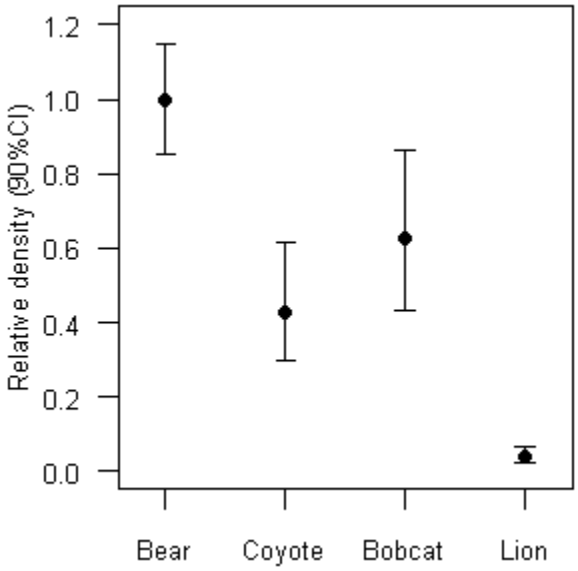
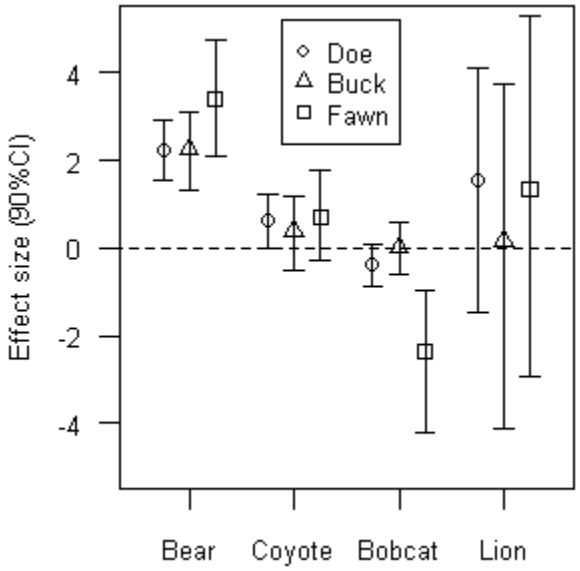


Figure 4. Effect sizes of associations between co-occurrence of deer predators and deer at camera stations.



DISCUSSION

The integrated modeling of data from DNA transects, camera stations, and GPS collars led to reasonably precise estimates of density for does, bucks, and fawns. Concordance between independently estimated abundances from the fDNA and camera data suggests accuracy. We were unable to use the fDNA results for males to estimate buck density, because we had no GPS collars on bucks. Instead, we relied on additional camera station data along migration trails to estimate a buck to doe ratio which we used to scale our female fDNA results to get buck density. Although the precision of our buck and doe density estimates were comparable, the design of the migration camera study was not random, and we are therefore unsure of how representative it may be of conditions throughout the study area. However, as buck home range information based on GPS collars becomes available, we will be able to use the fDNA data to more directly estimate densities of both genders. Given the preponderance of buck-only hunting in California, our estimate of doe population size (32,465) is potentially the most valuable information provided by our surveys. Monitoring doe population size through regular surveys and adapting management decisions accordingly may be the best option to ensure deer conservation while maintaining a conservative and sustainable level of harvest. The CDFW deer program in cooperation with CDFW Regions is currently placing GPS collars on deer throughout the State with a target of at least 25% placed on bucks.

Our estimate of total deer population size (65,818) is 91% larger than the latest available 2-year average Killvary model estimate (34,400) for the area. However, our estimate includes approximately 20,634 young fawns, many of which would not be expected to survive maturation, migration downslope, and over winter. Indeed, we estimated that approximately 14% of those fawns died before fall migration. The Killvary estimate is also probably too low because the survey count data it used was not corrected to address detection probabilities <1.

We found a positive association between bear density and deer abundance and this association was heightened for fawns. This finding is consistent with other research in California (Wittmer et al. 2014) and suggests that bears may be partially selecting their summer ranges to coincide with increased availability of fawn prey. Our results suggest that the association between bear and deer was stronger than for other predators. Additionally, bears appear to be the most abundant of the 4 predators. Consequently, more investigation may be warranted to discover whether bears are limiting deer recruitment. Interestingly, bobcats were negatively associated with fawns. This relationship may be the indirect effect of competition among the 2 most abundant predator species leading to avoidance of bears by bobcats. Sweitzer and Furnas (2016) found similar avoidance of competitors by fisher (*Pekania pennanti*). Although, the predator findings were peripheral to our central purpose to monitor deer population size, they demonstrate how population assessment can be readily applied to explore a variety of management and conservation questions.

The limiting factor for further increasing precision appears to be our estimates of home range size from GPS collars (Table 3, CV=0.09) and fawns per doe from cameras (CV = 0.14), not the female abundance estimate from fDNA surveys (CV=0.06). We will investigate other methods for disentangling fawns from the gender-based fDNA data. In theory, spatial capture recapture modeling (SCR, Royle et al. 2014) could reduce reliance on GPS collar data to convert estimates of abundance to those of density and population size. In practice, it may be infeasible and too expensive to implement an effective SCR design over a large geographical area. Nevertheless, SCR projects could be implemented over smaller areas to validate or calibrate non-spatial capture recapture modeling of data from fDNA surveys. Given the concordance we demonstrated between fDNA and camera station results, it may not be necessary to conduct fDNA surveys every year to sustain a monitoring program. For the ETDA study area, we recommend repetition of surveys at the 80 fDNA transects twice a decade (2 out of every 5 years with ½ of the sites surveyed in a single year). Camera stations would occur at all the transects during the fDNA surveys, but camera stations alone would occur at 30 transects (60 stations) every year.

Table 1. Integrated modeling results – Capture-recapture using fNDA component.

Parameters	Model estimates				
	Mean	$CI90_{low}$	$CI90_{up}$	Credible effect	CV
fDNA $_{Female}$					
Detection model parameters					
Intercept	-0.974	-1.176	-0.775		
Survey start date	0.244	0.103	0.385	Yes	
Survey year	-0.372	-0.629	-0.122	Yes	
Abundance model parameters					
Intercept	1.564	1.427	1.702		
Tree canopy cover	0.048	0.003	0.094	Yes	
Elevation	0.060	0.016	0.105	Yes	
Survey year	-0.071	-0.159	0.020	No	
Derived parameters					
Average detection probability per visit	23.6%	20.8%	26.6%		0.08
Average abundance	4.61	4.16	5.11		0.06
fDNA $_{Male}$					
Detection model parameters					
Intercept	-1.470	-1.813	-1.130		
Survey start date	0.348	0.176	0.519	Yes	
Survey year	-0.007	-0.359	0.343	No	
Abundance model parameters					
Intercept	1.118	0.926	1.316		
Tree canopy cover	0.022	-0.024	0.068	No	
Elevation	0.005	-0.040	0.051	No	
Survey year	0.001	-0.092	0.094	No	
Derived parameters					
Average detection probability per visit	19.4%	15.9%	23.1%		0.11
Average abundance	3.09	2.64	3.64		0.10

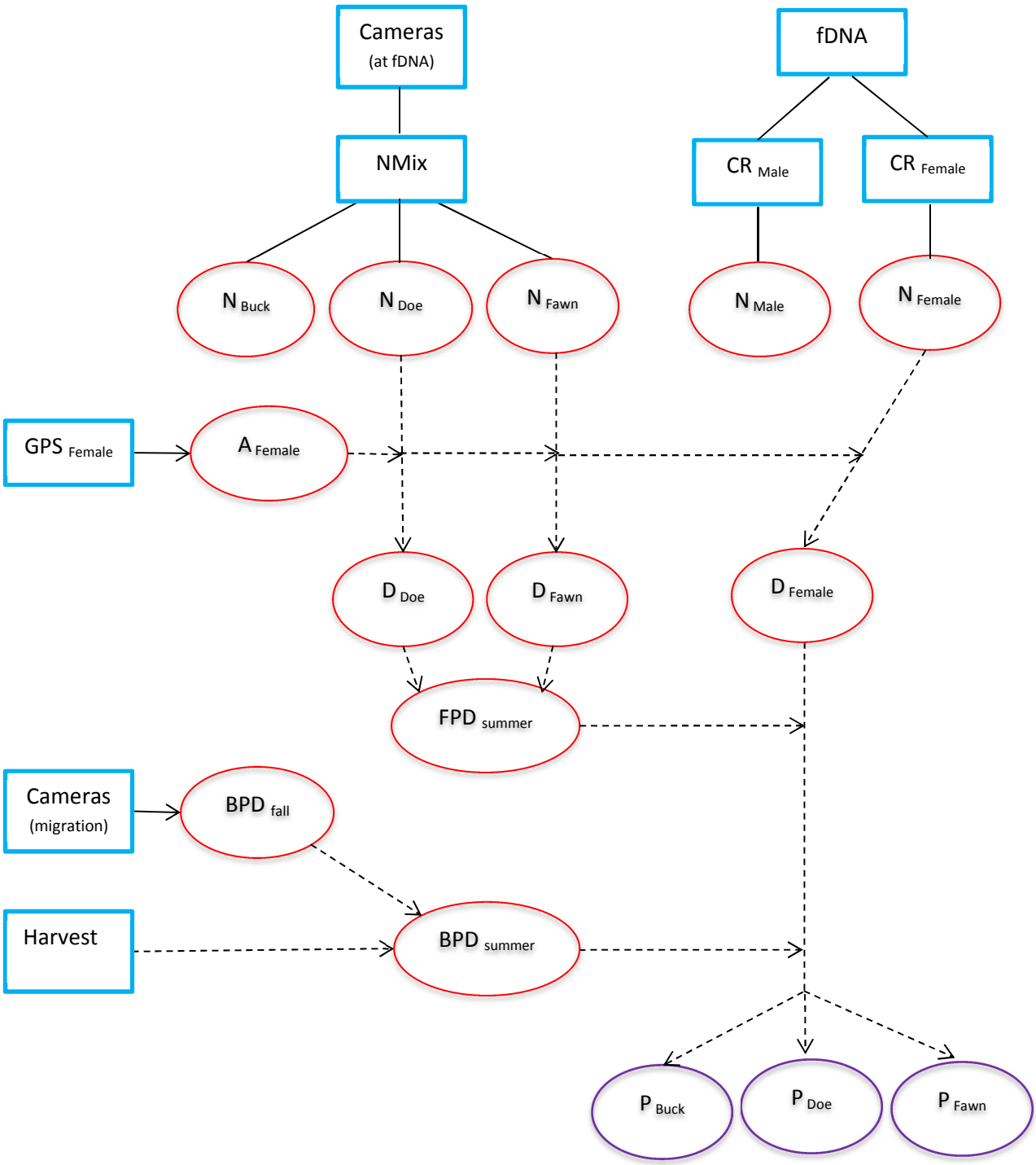
Table 2. Integrated modeling results – N-mixture using cameras component.

Parameters	Mean	$CI90_{low}$	$CI90_{up}$	Credible effect	CV
Camera $_{Doe}$					
Detection model parameters					
α (shape parameter)	0.518	0.425	0.608		
β (shape parameter)	4.474	3.611	4.965		
Abundance model parameters					
Intercept	0.394	0.152	0.631		
Tree canopy cover	0.219	0.085	0.360	Yes	
Elevation	-0.083	-0.223	0.047	No	
Survey year	-0.259	-0.524	0.018	No	
Derived parameters					
Average detection probability per day	10.4%	9.1%	11.7%		0.07
Average abundance	1.35	1.21	1.50		0.07
Camera $_{Buck}$					
Detection model parameters					
α (shape parameter)	0.261	0.205	0.340		
β (shape parameter)	3.651	2.525	4.826		
Abundance model parameters					
Intercept	-0.017	-0.374	0.303		
Tree canopy cover	0.089	-0.079	0.251	No	
Elevation	0.045	-0.112	0.223	No	
Survey year	-0.010	-0.365	0.380	No	
Derived parameters					
Average detection probability per day	6.7%	5.4%	8.2%		0.13
Average abundance	0.99	0.83	1.20		0.11
Camera $_{Fawn}$					
Detection model parameters					
α (shape parameter)	0.212	0.201	0.235		
β (shape parameter)	4.202	3.209	4.926		
Abundance model parameters					
Intercept	0.117	-0.211	0.424		
Tree canopy cover	0.265	0.087	0.470	Yes	
Elevation	-0.116	-0.324	0.058	No	
Survey year	-0.616	-1.019	-0.223	Yes	
Derived parameters					
Average detection probability per day	4.8%	4.0%	6.1%		0.14
Average abundance	0.86	0.69	1.03		0.12

Table 3. Integrated modeling results – Density and population size based on scaling of female density estimated from fDNA.

Parameters	Model estimates			
	Mean	$CI90_{low}$	$CI90_{up}$	CV
Effective survey area				
Transect survey area $_{Female}$	1.22 km^2	1.03 km^2	1.39 km^2	0.09
Deer class scaling ratios (summer before harvest)				
Fawns per doe	0.64	0.50	0.79	0.14
Bucks per doe	0.39	0.35	0.44	0.07
Density (summer before harvest, per km^2)				
Female $_{DNA}$	3.72	3.04	4.53	0.12
Doe $_{Scaled\ from\ DNA}$	2.82	2.28	3.46	0.13
Buck $_{Scaled\ from\ DNA}$	1.11	0.92	1.33	0.12
Fawn $_{Scaled\ from\ DNA}$	1.79	1.37	2.31	0.16
Total $_{Scaled\ from\ DNA}$	5.72	4.72	6.93	0.12
Population size (summer before harvest, 11,500 km^2study area)				
Doe	32,465	26,271	39,779	0.13
Buck	12,718	10,534	15,302	0.12
Fawn	20,634	15,705	26,541	0.16
Total	65,818	54,309	79,660	0.12
Doe $_{Zone\ C3}$	6,549	5,272	8,061	0.13
Buck $_{Zone\ C3}$	2,566	2,113	3,100	0.12
Doe $_{Zone\ C4}$	17,464	14,145	21,407	0.13
Buck $_{Zone\ C4}$	6,841	5,658	8,229	0.12
Doe $_{Zone\ X4}$	8,450	6,806	10,390	0.13
Buck $_{Zone\ X4}$	3,310	2,718	3,998	0.12
Mortality				
Harvested bucks $_{(\%\ of\ summer\ population)}$	23.0%	18.9%	27.4%	0.11
Fawn mortality before fall migration $_{(\%\ of\ summer\ population)}$	14.1%	0%	33.6%	0.93
Concordance				
Density $_{Doe\ DNA\ /Doe\ Camera}$	0.98	0.84	1.14	0.09
Density (female DNA) $_{Random\ sites\ /\ Survey\ sites}$	0.97	0.90	1.05	0.05

Figure 2. Integrated modeling of fDNA, camera station, GPS collar, and harvest data to estimate deer density. Boxes represent data inputs and modeling components. Circles represent estimated parameters. Arrows represent inputs used in estimation. Dotted arrows represent links among integrated modeling components. Abbreviations : CR = non-spatial capture-recapture modeling; NMix = N-mixture modeling; N = site abundance; A = effective survey area; D = density; P = population size; BPD = bucks per doe; FPD = fawns per doe.



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