Coyotes, deer, and hunters: applied ecology for informing deer and hunter management

by

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Abstract

My research was conducted to provide new methods and analyses to better inform management of white-tailed deer, coyotes, and hunters in Al In particular, my research will support efforts of the Alabama Deer Management Steering Committee, a committee comprised of individuals from the Alabama Department of Conservation and Natural Resources, U.S.G.S. Fish and Wildlife Cooperative Research Unit and Auburn University researchers, with the objective of managing white-tailed deer to meet multiple herd, hunter, and economic objectives. My first chapter introduces and tests AnimalFinder, a program that reduces the cost and time associated with camera surveys by semi-automating the presence-absence identification of animals in time-lapse camera trap images. I then explore the relationship between predators and competitors, and white-tailed deer fawn recruitment. My second chapter estimates coyote density and the influence of land cover at multiple sites across Alabama using spatial capture-recapture. In my third chapter, I use the coyote density estimates, along with camera survey data of wild pigs and deer, to examine factors influencing fawn recruitment across 16 management areas in Alabama. Finally, in my fourth chapter, I introduce a novel approach for evaluating actions that wildlife management agencies can take to influence hunter recruitment, retention, reactivation, and ultimately, hunting license sale profits that are crucial for state agency-led wildlife conservation efforts. These research contributions have the potential to help state agencies better manage and monitor wildlife populations, understand community dynamics, and anticipate changes in hunter-generated conservation funds.

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Table of Contents

List of Tables

List of Illustrations

Chapter 1: AnimalFinder: A semi-automated system for animal detection in time-lapse camera trap images

INTRODUCTION

Camera trap surveys have become increasingly popular for monitoring elusive wildlife in recent years and can provide a way to reduce the cost of monitoring programs relative to many traditionally invasive and labor-intensive methods. Rowcliffe and Carbone (2008) documented a 50% annual growth in publications using cameras or assessing camera survey methodologies between 1998 and 2008; a trend that has persisted (Burton et al., 2015; Rovero et al., 2013), and will likely to continue due to ever-improving camera technology and the popularity of camera traps for citizen science projects (Cohn, 2008). Monitoring with camera traps is potentially advantageous because surveys are non-invasive, capture data on elusive animals, reduce field hours, and provide high quality data. Among other applications, camera trap data, along with relevant quantitative methods, have been used by researchers to estimate demographic parameters and inventory species, for both marked and unmarked populations (e. g. Giman et al., 2007; Karanth et al., 2006; Keever, 2014). However, there are issues associated with camera traps surveys, including equipment failures, data management requirements, observer errors when manually reviewing photos, and heterogeneity in the detection probability of individuals within a population (Meek et al., 2015; Newey et al., 2015; Rovero et al., 2013; Swann et al., 2011).

Another issue with camera traps is the variability in detection probability as a result of camera equipment. Most cameras use motion sensing (passive infrared) to detect animals and take photographs, or use time-lapse photography to take photos at a specified interval regardless of animal presence (Meek et al., 2015; Rovero et al., 2013; Swann et al., 2011). Motion sensing

results in fewer empty photos (photos without an animal), but greater sampling variability due to variation in trigger sensitivity and detection probabilities of individuals and species (Hamel et al., 2013; Newey et al., 2015; O'Connell et al., 2010; Rovero et al., 2013). These differences are apparent between camera makes and models for detection between and among species (Hamel et al., 2013; Newey et al., 2015), and even within the same camera model (Damm et al., 2010; Newey et al., 2015). It is advised that practitioners fully understand the factors that affect camera trap limitations: make and model quality and the resultant limitations they exhibit (Meek et al., 2015; Newey et al., 2015). Many different factors contribute to whether or not a picture is taken, including environmental conditions at the camera site, size of the object moving in the frame, and sensitivities of the triggers themselves (Damm, 2010; Meek et al., 2015; Swann et al., 2004). In contrast, the time-lapse setting takes photos at specified intervals; thus reducing sampling error. Newey et al. (2015) reported that motion detection cameras failed to detect 49 – 68% of animals captured at the same time by time-lapse data. Hamel et al. (2013) found that raw error rates in daily presence varied between 30 and 70% among seven artic/subarctic species (hooded crow, *Corvus cornix*, common raven, *Corvus corax*, white-tailed eagle, *Haliaeetus albicilla*, golden eagle, *Aquila chrysaetos*, arctic fox, *Vulpes lagopus*, red fox, *Vulpes vulpes,* and wolverine, *Gulo gulo*) using a motion-trigger survey design, while a 5-minute time-lapse setting varied between 5 and 30% among species. However, time-lapse camera surveys also possess drawbacks, and can generate a staggering number of uninformative images that must be manually processed to extract relevant data – adding time and overall cost to the monitoring program (Harris et al., 2010; Newey et al., 2015). Time-lapse surveys may also miss capturing events that occur during the time intervals between images, and potentially inappropriate for species occurring at low densities and when sites are not baited (Hamel et al., 2013; Newey et

al., 2015). Ultimately, when designing a camera survey, researchers and managers must weigh

tradeoffs between greater survey cost and greater sampling variability, considering both methods

risk losing informative images (Hamel et al., 2013; Meek et al., 2015; Newey et al., 2015; Swann

et al., 2011; Weingarth et al., 2012).

Significant strides have been made to streamline processing of camera trap images.

Harris et al. (2010), Fegraus et al. (2011), Krishnappa and Turner (2014), He et al. (2016),

Niedballa et al. (2016), and Bubnicki et al. (2016), among others, have developed software

packages for managing large quantities of camera trap images. These programs offer a wide

array of features, including standardization procedures for retrieval and storage of images,

cataloguing options for tagging species and individuals, and methods for extracting data into a

useable format for further analysis. Species-specific recognition software has also been

developed to assist in identifying individuals of numerous species, including elephants (Ardovini

et al., 2008), tigers (Raj et al., 2015), and marine mammals (Adams et al., 2006; Gope et al.,

2005). These methods utilize unique individual characteristics and compare images to a

catalogue of known individuals. Bolger et al. (2012) developed an open source software package

for pattern extraction and matching in a variety of species, which performed very well on Masai

giraffe (*Giraffa camelopardalis tippelskirchi*).

Despite these advancements, there are few automated tools available to identify animal

presence/absence in photos. eMammal is a subscription-based service for camera trap image

collection and analysis that employs a method that identifies animals and species from image

sequences collected triggered by a motion sensor (He et al., 2016). However, this program

analyses sequences of images with multiple pictures of the same animal within a short span of

time and was not developed for time-lapse images, which frequently only contain a one or two

images per animal encounter. Alternatively, methods to detect motion in videos captured by camera traps may also be applicable animal identification in images if sequences of image files converted into a video file (Swinnen et al., 2014; Weinstein, 2015). These approaches were not optimized for images and have not been tested for this application. Similar to eMammal, images captured using a time-lapse survey may not provide enough images per animal visit and/or changes between images may be too drastic relative to changes between video frames. To address this need, we developed AnimalFinder in MATLAB ® (2012b, The MathWorks, Inc., Natick, Massachusetts, United States) to classify animal presence/absence in time-lapse photographs. The AnimalFinder source code is freely available for download (Appendix 1), and was developed to analyze time-lapse photos by site and survey, producing a directory of photos likely to contain a medium- to large-bodied animal. Thereafter, some manual review is required to remove false positives and collect relevant data (number of animals, sex, etc.). In this paper we describe the program and test it on a set of camera trap photos obtained from a white-tailed deer (*Odocoileus virginianus*) survey. We estimate population abundance using results from our semi-automated program vs. manual-only image review and examine differences in resulting parameter estimates, coefficient estimates, and model rankings and weights. We also consider the potential of the program to detect wild pigs (*Sus scrofa*) and raccoons (*Procyon lotor*), two non-target mammals who frequently visited the baited sites, in addition to white-tailed deer.

METHODS

How the program works

We developed AnimalFinder to identify animal presence/absence in time-lapse camera trap photos and tested it on white-tailed deer in Alabama; however, the system could be applied to other medium- or large-bodied species that are relatively monotone (we did not directly test

4

the program on species with stripes or spots). First, the program takes a set of pictures from one survey location and separates day and night photos. Due to the different nature of daytime (full color and shadows) and nighttime (grayscale) pictures, the respective subsets are processed using different methods. These photos are first converted to grayscale, and an edge-detection algorithm, called a canny edge detector, is applied to identify lines in the images. Since deer are inherently smooth, AnimalFinder identifies large areas with low line density and applies a color saturation mask. The result is a single binary "blob" which is analyzed in size and shape. Nighttime pictures are first filtered with a median filter of pixel size 40, and then a canny edge detector is applied. The result is a binary image of lines.

From this point, the classification of deer presence is the same for day and night photos. Because the pictures may have common features that may trigger a false positive classification (i.e. large rocks, bushes, logs), we use a threshold value that will ignore pixels that appear in a given frequency throughout the data set (a threshold value of 0.5 will ignore pixels that are seen in half of images). Finally, the line pixels, excluding ignored pixels, are counted for each image and those with a count of line pixels greater than two standard deviations of the respective subsets are classified as positive animal presence.

Evaluation of program performance

We tested our program on a dataset of images obtained from a camera survey that was conducted by Keever (2014) at Fort Rucker, Alabama during February and March of 2012. Fort Rucker is a U.S. Army post located in southeastern Alabama in Dale and Coffee Counties and is predominantly comprised of pine (*Pinus* spp.) and mixed pine-hardwood forests (Keever, 2014). Twenty camera sites, spaced 2.42 km apart, were cleared and baited with 11 kg of whole corn for one week. Then cameras were deployed 4 m away from the bait pile and set to take an image

every 4 minutes for 7 days. Bait was refreshed with up to 11 kg as necessary every 3-4 days for the duration of the survey. These images were reviewed manually by Keever (2014), who recorded raw counts of deer and non-target animals (i.e. pigs, raccoons) observed in each image. See Keever (2014) for further information regarding study design.

We ran AnimalFinder on the images collected from the 20 camera sites using a range of pixel frequency threshold values between 0.01 and 0.95. For each threshold value we compared AnimalFinder performance with results obtained from Keever (2014) by counting the number of images in which both methods classified an image as containing a deer (deer presence), both methods classified an image as not containing a deer (deer absence), AnimalFinder flagged an image classified as deer absence by the manual method (type I error), and AnimalFinder missed an image classified as deer presence by the manual method (type II error).

We selected one frequency threshold value to further test AnimalFinder by assessing the tradeoff between type II errors and total number of images flagged. We calculated the change in the proportion of type II errors relative to deer images classified by manual review and the change in proportion of flagged images relative to the total number of images reviewed for each incremental increase in the threshold value, and used the threshold value at the equilibrium point between those two measurements to further test the performance of our semi-automated approach. We conducted a concordance analysis to estimate Cohen's kappa, which measures the normalized difference between the rate of agreement between the two methods that is observed and the rate of agreement that would be expected by chance (Cohen, 1960). We used the presence/absence data obtained from both methods to estimate Cohen's kappa, replacing AnimalFinder type I errors with zeros to simulate the final dataset (assuming further manual review would remove all false positive).

Using the selected threshold value, we constructed count histories for all deer counted from the manual review-only results and from the AnimalFinder semi-automated results. Following Keever (2014), we reduced the survey occasions to every 12 minutes and used only images between 15:36 to 8:12; two hours before mean sunset time until two hours after mean sunrise time [i.e., we eliminated "day time" photographs because white-tailed deer are inactive during day time hours (Keever 2014)]. We used the count data from the manual-only method for all images flagged by AnimalFinder; this eliminated potential observer bias that could arise from another observer reviewing the images. Thus, all correctly classified images and false positives had the same count data recorded as the observer-only method. When AnimalFinder committed a Type II error (missed a deer image) the deer count was recorded as zero for that occasion.

We further tested the utility of AnimalFinder for use in time-lapse camera monitoring programs aimed at estimating demographic parameters and covariate effects, and to demonstrate a method for practitioners to conduct their own pilot study to assess the performance of AnimalFinder with their own images. We used the AnimalFinder results to estimate deer abundance, and compared the results to estimates using counts obtained by manual-only review. Some low levels of overlooked deer (Type II errors) might be acceptable if the goal is to estimate demographic parameters and those estimates are relatively unaffected by using AnimalFinder compared to the manual-only method. We estimated total deer abundance, covariate effects on abundance and detection, and ranked models with AnimalFinder-derived count histories and manual-only derived count histories from Keever (2014) using the maximum likelihood, single season N-mixture model developed by Royle (Royle, 2004) and implemented in function pCount of the 'unmarked' package (Fiske and Chandler, 2011) in R (R Core Team, 2015) . Royle's (2004) N-mixture model is a hierarchical abundance estimate model that uses spatially or

temporally replicated counts of unmarked individuals in which spatial replicates are achieved by deploying multiple cameras across space and temporal replicates are obtained using images captured at given time increments. The N-mixture model is comprised of a binomial model for detection probability (p) and a Poisson model for abundance (λ) and allows for covariates to be incorporated for both parameters.

Our study estimated mean abundance and detection probability of white-tailed deer on Fort Rucker using the combined counts of mature bucks, immature bucks, does, and fawns. We included covariate data from Keever (2014), including habitat covariates with our abundance parameter (% of habitat type), and time and precipitation for our detection parameter. We excluded wild pigs as a covariate because we did not have the original covariate data, and further, we did not want to confound performance of AnimalFinder for use on deer with its performance with wild pigs. Our single-season analysis also necessitated the elimination of the covariate for season. We selected a subset of the models developed by Keever (2014), comprised of a null model and the highest-ranked abundance models with each combination of detection covariates excluding covariates relating to wild pig or season.

To assess the efficacy of using AnimalFinder for research applications, in which models with covariates are examined to address competing hypotheses about the ecological system, we compared model rankings and weights from 20 models using manual-only and AnimalFinder-derived count histories. We ranked an identical suite of models for each method using Akaike's information-theoretic criterion (AIC) and estimated coefficient estimates, model weights, and parameter estimates (Burnham and Anderson, 2002). We then estimated total abundance and 95% confidence intervals for each method using a parametric bootstrap analysis with 1,000 iterations.

The original survey by Keever (2014) was intended for white-tailed deer; however, wild pigs and raccoons were also detected at camera sites. We examined the ability of the program to correctly identify images containing these species and considered potential utility to use AnimalFinder in an occupancy or abundance framework. We determined the type II error rates for AnimalFinder's detection of an animal over a range of threshold values when a pig or raccoon was manually identified. We also calculated the number of days that each species was correctly detected at each camera site at least once to determine potential utility of the program in an occupancy framework. Daily presence data would allow researchers to create occupancy capture histories with sampling occasions on each day of the survey, and estimate species occupancy probability in relation to environmental covariates and estimate detection probability. Finally, we estimated the time savings achieved by using AnimalFinder relative to the traditional manual-only method. We estimated the rate of images reviewed per hour by recording the time required for an observer to classify animal presence/absence in a subset of images and extrapolated the review rate to estimate time required to review the full set of images and the images flagged by AnimalFinder. We also recorded the time it took to run the images through AnimalFinder, but did not include it in the time comparison between methods because it is inactive time for the observer.

RESULTS

A total of 65,291 images were collected from 20 cameras, and Keever (2014) classified 1,577 images as containing deer (deer presence), 590 as containing wild pigs, and 2,108 as containing raccoons. Increasing the threshold value of AnimalFinder increased the total number of images flagged; which varied from 2,174 images (3% of total) at a threshold of 0.001, to 21,147 images (63%) when the threshold value was set to 0.95. At a threshold value of 0.005,

AnimalFinder correctly classified 45% of deer images, 23% of wild pig images, and 18% of raccoon images, and these numbers increased to 95% of deer images, 97% of wild pig images, and 94% of raccoon images at a threshold of 0.95 (Figure 1.1). If using the data to apply an occupancy analysis, AnimalFinder correctly detected at least one individual present on 95% of days with a threshold of ≥0.25 for deer and wild pigs and a threshold of ≥0.55 for raccoons (Figure 1.2).

The threshold value that represented the best tradeoff between type II errors and total images flagged for deer was 0.35. At this threshold value and for night images, there were 1,098 images correctly classified as deer presence, 28,937 images correctly classified as deer absence, 6,144 type I errors, and 367 type II errors (Table 1.1). At the same threshold for the day images, there were 46 images correctly classified as deer presence, 26,250 images correctly classified as deer absence, 2,382 type I errors, and 66 type II errors. Cohen's kappa, estimating observer agreement, for the adjusted presence/absence dataset was 0.838.

The manual-only and AnimalFinder-derived count histories contained 756 observations per site (15,120 observations in total). For each image review method, deer were detected at 17 of the 20 sites. The manual-only count history contained 436 observations with one deer counted, 63 with two deer, 11 with three deer, and 1 with four deer. The AnimalFinder count history contained 317 observations with one deer counted, 48 with two deer, 11 with three deer, and 1 with four deer.

Using the N-mixture modeling analysis for manual-only and AnimalFinder data, each method resulted in the same model rankings for all model weights of 0.01 or greater; however there were slight differences in model weights between equivalent models (Table 1.2). Results from both methods ranked three models as competitive based on delta 2 AIC. However the

second and third-ranked models contained only one additional parameter relative to the highest-ranked model, indicating weak, if any, evidence that their addition improved model fit (Burnham and Anderson, 2002). The highest-ranked model included time of day as a detection covariate (manual-only model weight [w] = 0.43; AnimalFinder w = 0.36), followed by the model with % pine forest and time of day (manual-only w = 0.17; AnimalFinder w = 0.20), and the model with rain and time of day (manual-only w = 0.16; AnimalFinder w = 0.14). These models accounted for 0.76 of the cumulative model weight for the manual-only method and 0.70 for the AnimalFinder method.

The model-averaged deer abundance across all sites was estimated to be 78 deer (confidence interval (CI): 47, 211) using the manual-only method and 77 (CI: 46, 220) for the AnimalFinder method. The model-averaged detection was 0.0101 (SE = 0.0011) for manual-only review and 0.0078 (SE = 0.0010) for AnimalFinder. Model-averaged beta estimates and 95% confidence intervals were similar between both methods (Figure 1.3).

The manual-only method required 16.84 hours for four observers to classify animal presence/absence in 62,288 images with an average review rate of 4,274 images per hour. AnimalFinder required <5 minutes of manual prep and 2.5 hours of unassisted processing time to analyze the same set of images using three threshold values, exceeding 26,000 images reviewed per hour. We estimated that the average review rate for AnimalFinder saved between 99.5% and 45.3% of presence-absence manual review time for the same set of images, depending on the threshold value applied (Figure 1.4). At a threshold value of 0.35, AnimalFinder saved 14.8 hours (~1 hour per 4,400 images) of manual review time compared to the manual-only method.

DISCUSSION

   We demonstrated that our semi-automated approach for processing time-lapse camera trap photos has the capacity to reduce effort and overall monitoring costs for deer and other animals by reducing the number of images from our data set requiring manual review. While our dataset was relatively small (one season and twenty cameras), we amassed over 60,000 images and realized a reduction of >70% of images that required manual review due to AnimalFinder. The benefits of this program could be significant for larger datasets that are the result of long-term and large-scale surveys. For example, Alabama's Department of Conservation and Natural Resources recently completed a 6-season time-lapse camera survey at 256 camera sites each season generating >3 million images (Price et al. unpublished data). Based on our results in this study, the application of AnimalFinder could save up to 600 hours (15, 40-hour weeks) of presence/absence classification. This time savings may reduce lag time between data collection and project results, which could translate to increased speed with which managers can utilize results to inform decision-making. Financially, our program could save the agency $5,400 compared to employing a technician at a rate pf $9 per hour to manually review images. These benefits may make large-scale surveys and monitoring programs more cost and time effective to implement.

   There are tradeoffs between cost/time savings and program performance when using AnimalFinder which are important to consider with regards to survey objectives. Employing a greater threshold level decreased the number of photos with animals that are missed (type II errors), but also increased the number of photos with no animal present flagged for review. In our study, the low rate of type II errors in presence/absence image classification experienced when using our semi-automated approach produced a negligible effect on our analysis of a

white-tailed deer population. Slight differences in estimated model weights, covariate effects, and total abundance did not change the ecological and demographic inference resulting from the study and is unlikely to impact management decisions pertaining to the population. We anticipate that, in most cases, a bias of a few individuals will be an acceptable tradeoff given the time and cost savings attributed to the new method. Still, it is important to consider the project objective and the precision and accuracy required to inform decision-making. In some cases, the decreased precision may affect management decisions. For example, decreased precision in estimates of demographic parameters for an endangered species may result in the selection of a different management action relative to the alternative that would have been selected using estimates obtained using manual-only image review and hurt species recovery. We suggest utilizing recent quantitative methods to calculate the value of information for management such as the expected value of perfect information and expected value of sample information to determine whether or not the decreased precision resulting from using AnimalFinder is justifiable (Canessa et al., 2015; Williams and Johnson, 2015).

We observed differences between estimates of detection probability and related covariate effects between the manual-only method and AnimalFinder. Detection probability is a parameter that accounts for the probability of an animal being available for detection (i.e. in the camera frame) and the conditional capture probability that the animal is correctly detected given that it is available (O'Donnell et al., 2015; Pollock et al., 2006, 2004). Both components of detection can affect parameter estimates (O'Donnell et al., 2015). AnimalFinder does not influence the availability of target organisms, but we anecdotally found that several environmental factors, including rain and time of day, have the potential to influence the conditional capture probability of AnimalFinder relative to the manual-only method. While there was little evidence for the

influence of rain on detection probability (and any effect may also be attributed to its effect on animal availability), rain drops on the camera lens sometimes blur the images and have the potential to make animal bodies less likely to be detected. Similarly, the presence of shadows in daytime photos can lead to type II errors by obscuring an animal body. Utilizing methods aimed at sheltering cameras from rain or removing shadows from images prior to analysis (Finlayson et al., 2002; Prati et al., 2003), and/or applying more complex object detection algorithms, may further reduce false absences. However, in most cases, including this study, detection probability is not a focal parameter and differences in estimates or covariate relationships are only a concern if it affects abundance and other demographic estimates of interest to the extent that it alters a management decision (Williams et al., 2002). Future studies may include covariates on availability and conditional capture probabilities and model these components separately. Pollock et al. (2006) and O'Donnell et al. (2015) have developed such models which could lead to improved insights regarding the influence of bias in the conditional capture probability on estimates of parameter values of interest arising from semi-automated image review.

AnimalFinder committed more type II errors for wild pigs and raccoons than deer. A greater threshold value was required for pigs and raccoons to achieve the same low level of type II errors obtained with a deer when using a threshold value of 0.35. We believe that type II errors were produced when animals in a frame were directly in front of the corn pile. Because the corn pile was present in a high frequency of images, those pixels were ignored at low threshold values. Raccoons and pigs were often captured when their bodies were in front of the bait while they were feeding. This was less common with deer whose taller stature kept their bodies above the corn pile. Thus, if the pixels comprising the bait are ignored, animal bodies within that boundary will be missed. Ultimately, the program could be improved by finding a better way to

filter out blobs that remain in a high frequency of the images while still allowing for the detection of new blobs within that same space. For example, an additional layer or image processing could be incorporated that would characterize regions within the image based on color, saturation, texture, or other image traits. Such methods could be utilized as a "bait pile detector" which could help the program determine the orientation of the camera with respect to the bait and our expectation of detecting animals in different regions of the images (i.e. we would not expect animals in sky or treetop portion of the image). In the meantime, studies targeting raccoons, pigs, or animals with similar characteristics (i.e. short-statured) may reduce false absences by positioning cameras lower to the ground to improve the angle of the animals with respect to the bait pile. However, repositioning of the camera in such a way could also negatively affect later manual review where animals in front of the camera block the view of other animals. We may have experienced additional false negatives as a result of the presence of some spotted pigs in our study because AnimalFinder was developed to detect non-patterned animals that create monotone blobs in the image processing. Considering that > 95% of images containing wild pigs were identified when applying a high threshold value, we feel that the program performed better than expected on patterned animals, however, further testing is needed to validate AnimalFinder for such animals. Although we did not estimate demographic parameters for wild pigs or raccoons, our results suggest that AnimalFinder may be used to reduce manual review efforts for count and occupancy based studies for many medium and large bodied animals.

Ultimately, a careful evaluation of AnimalFinder and a range of threshold values for potential target species using a subset of images will be essential to inform users of the tradeoffs between type I and type II errors and lead to the most efficient use of the program. Researchers

may also examine the sensitivity of their decision models to anticipate the level of precision required by the intended analyses. We suggest conducting a pilot study by reviewing a subset of survey images manually and conducting an analysis similar to ours to 1) evaluate efficacy of using AnimalFinder to identify presence/absence and estimate demographic parameters of the target animal, and 2) determine what threshold value to employ given project needs. We also encourage users to consider camera placement to reduce sources of error and natural blobs that may interfere with the ability of the program to identify an animal occupying the same space in the images. For example, placing bait in several small piles instead of one large pile may reduce type II errors related to animals within the bait pile.

AnimalFinder can provide numerous benefits to animal monitoring. Using a semi-automated system to review camera trap images can reduce survey costs, lag time between data collection and data analysis, and potentially reduce observer errors. It can be used in conjunction with other programs and procedures developed in recent years to streamline and reduce costs of time-lapse camera trap surveys (e.g. Harris et al., 2010; He et al., 2016; Krishnappa and Turner, 2014). Increasing the efficiency of data management for such non-invasive survey techniques without significantly sacrificing analytical accuracy may enable researchers and managers to better monitor animal populations and inform natural resource decision-making.

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FIGURES AND TABLES

Figure 1.1. Percent of deer, wild pig, and raccoon images identified by the semi-automated system compared to the manual -only review and the percent of total images flagged under a range of threshold values.
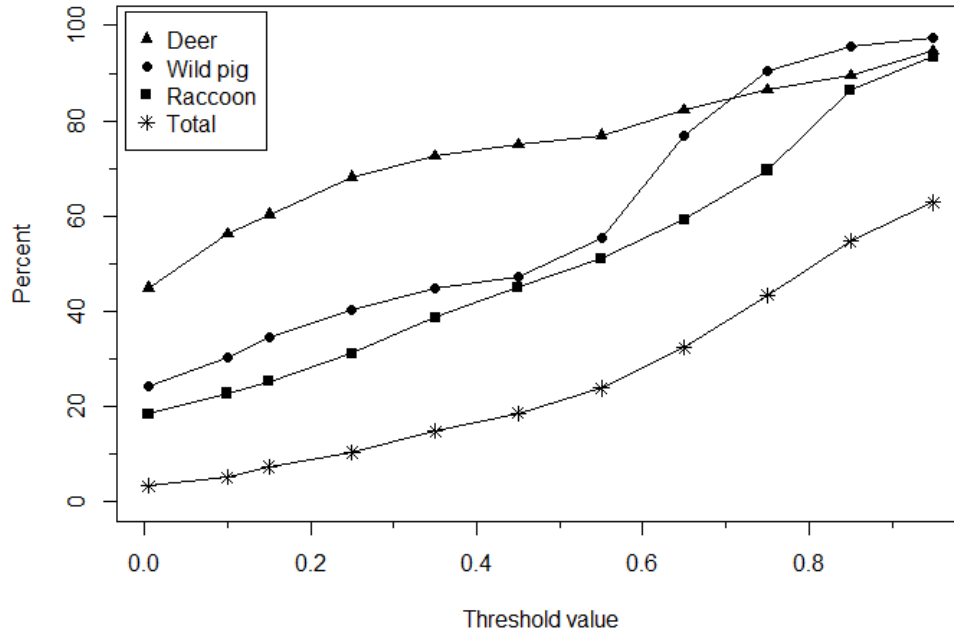
Figure 1.2. Percent of site- days with at least one detection for deer, wild pigs, and raccoons by the automated system compared to the manual-only method and the percent of total images flagged under a range of threshold values.
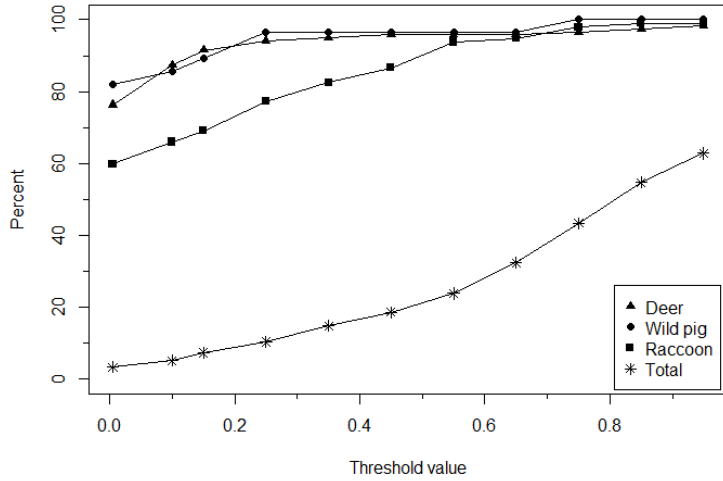
Table 1.1. Concordance tables for white-tailed deer using the semi-automated system using a threshold value of 0.35 for a) night images, b) day images, and c) day and night images.

a) Night

		Manual-Only		
		Deer	Deer	
		Present	Absent	Total
AnimalFinder	Deer Present	1098	6144	7242
	Deer Absent	367	28937	29304
	Total	1465	35081	36546

b) Day

Manual-Only

	Deer Present	Deer Absent	Total
AnimalFinder Deer Present	46	2382	2428
Deer Absent	66	26250	26316
Total	112	28632	28744

c) Night + Day

Manual-Only

	Deer Present	Deer Absent	Total
AnimalFinder Deer Present	1144	8526	9670
Deer Absent	433	55187	55620
Total	1577	63713	65290

Table 1.2. The AIC table including estimates of total abundance and detection probability for
AnimalFinder (AF) and the manual-only method (MO) for models with model weight ≥ 0.01.

Total abundance was estimated by summing the site-specific abundance estimates and

confidence intervals were estimated using parametric bootstrap analyses with 1,000 simulations.

Probability of detection (p) and standard errors were averaged across all sites for each model.

*Standard errors were 0.0011 for all manual models and 0.0010 for all AnimalFinder models.

Model	Par.	AIC		delta AIC		AIC Model Weight		Cumulative Weight		Total Abundance		Mean Detection Probability*	
	-	MO	AF	MO	AF	MO	AF	MO	AF	MO	AF	MO	AF
lam(.)p(time)	3	4639	3811	0.00	0.00	0.43	0.36	0.43	0.36	78 (47, 192)	76 (46, 185)	0.0101	0.0079
lam(Pine)p(time)	4	4641	3812	1.83	1.15	0.17	0.20	0.60	0.56	78 (47, 220)	77 (44, 228)	0.0101	0.0078
lam(.)p(rain+time)	4	4641	3813	2.00	1.90	0.16	0.14	0.76	0.69	78 (46, 190)	76 (44, 206)	0.0101	0.0079
lam(Dev+Pine)p(time)	5	4643	3813	3.83	2.80	0.06	0.09	0.83	0.78	78 (47, 234)	77 (48, 251)	0.0101	0.0077
lam(Pine)p(rain+time)	5	4643	3814	3.83	3.05	0.06	0.08	0.89	0.86	78 (46, 217)	76 (44, 206)	0.0101	0.0078
lam(Hrdwd+Mixed+Pine)p(time)	6	4644	3814	4.64	3.82	0.04	0.05	0.93	0.91	79 (49, 284)	78 (49, 284)	0.0100	0.0077
lam(Dev+Pine)p(rain+time)	6	4645	3815	5.80	4.70	0.02	0.03	0.96	0.95	78 (47, 239)	77 (46, 276)	0.0101	0.0077
lam(Dev+Hrdwd+Mixed+Pine)p(time)	7	4645	3816	6.24	5.52	0.02	0.02	0.98	0.97	79 (48, 314)	78 (48, 356)	0.0100	0.0077
lam(Hrdwd+Mixed+Pine)p(rain+time)	7	4646	3816	6.61	5.80	0.02	0.02	0.99	0.99	79 (48, 298)	78 (50, 288)	0.0100	0.0077
lam(Dev+Hrdwd+Mixed+Pine)p(rain+time)	8	4647	3818	8.21	7.42	0.01	0.01	1.00	1.00	79 (49, 305)	78 (49, 360)	0.0100	0.0077

Figure 1.3. Model-averaged abundance (lambda) and probability of detection (p) beta estimates and 95% confidence intervals using all models with AnimalFinder results in black and manual-only results in gray.
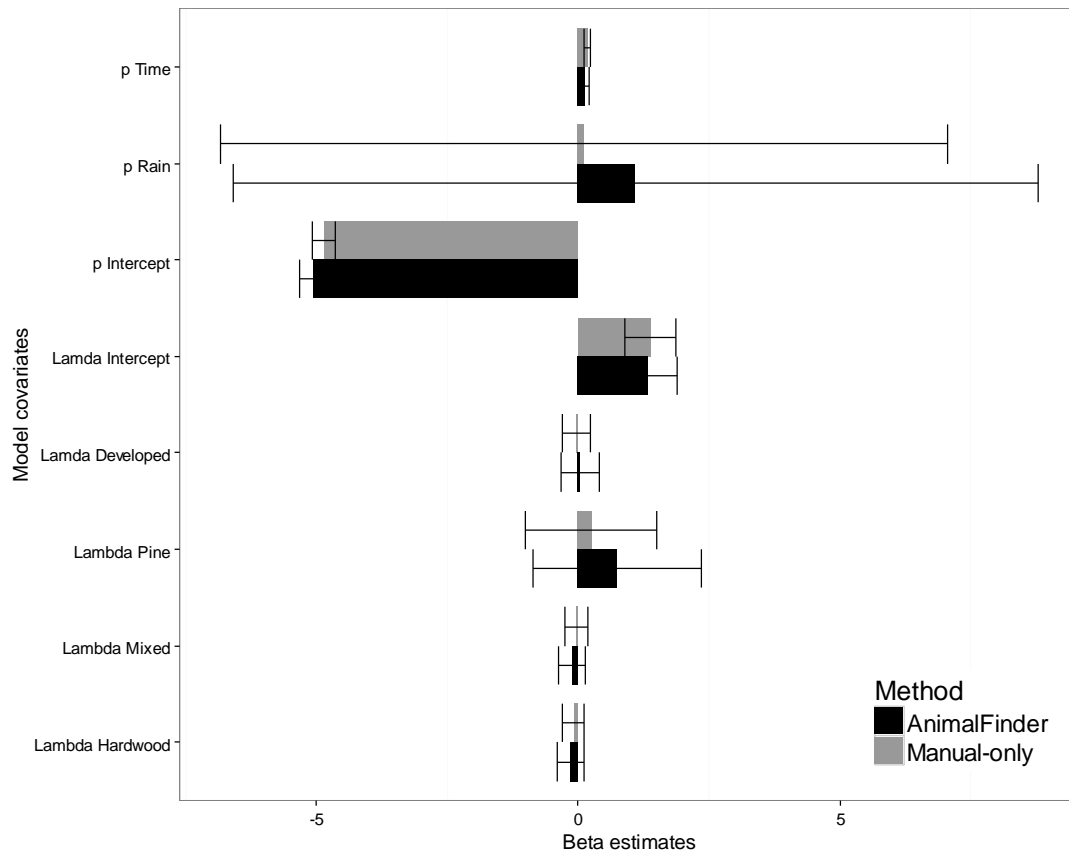
Figure 1.4. Percent time savings for presence-absence review of camera trap images using AnimalFinder relative to manual-only review under a range of threshold values.
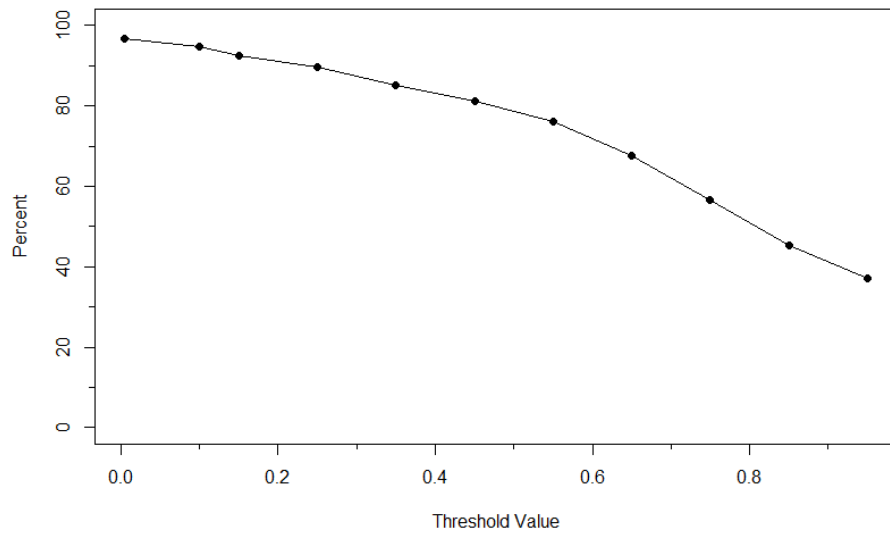
Chapter 2: The effect of landcover on coyote density with a multi-site spatial capture-recapture analysis

INTRODUCTION

Humans directly and indirectly facilitate the spread and colonization of species outside their historical ranges, which can lead to changes in ecological communities and ecosystem functions. If a novel species becomes introduced, established, and naturalized, impacts on native species include, but are not limited to, predation, competition, herbivory, introduction of diseases, and the alteration of habitat. Armadillos (*Dasypus novemcinctus*; Taulman and Robbins 1996) and raccoons (*Procyon lotor;* Zeveloff 2002; Larivière 2004) are examples of species that greatly expanded their range into non-native areas and threaten native species; including organisms with considerable conservation or economic value. Conversely, non-native species can positively affect native species, including the provision of resources (i.e. habitat, food) or ecosystem functions (Schlaepffer et al. 2011 Ultimately, non-native species can cause a wide range of impacts on ecosystems and anticipating/responding to resultant ecosystem perturbations is a challenge for natural resource managers.

Coyotes, *Canis latrans*, are a native species that has experienced a rapid range expansion, in the past 50-80 years, large part to direct and indirect human facilitation. Historically native to the Great Plains region of the U.S., their range now extends throughout most of North and Central America (Nowak 1978, Gompper 2002). Their success in colonizing new areas stems from anthropogenic factors, including human translocations, human-induced habitat change, and extirpation of predators that previously suppressed or excluded coyote populations (Hill et al. 1987, Gompper 2002). In addition to facilitation by humans, coyotes have successfully colonized

new areas due to their diet plasticity and ability to adapt to diverse habitat types (Parker 1995). Although much of their native range consisted of grasslands, the areas in which they now thrive include Eastern forests and urban/suburban landscapes (Parker 1995, Schrecengost et al. 2009).

In these novel habitats, some have suggested that they may provide a positive benefit in reducing overabundant white-tailed deer (*Odocoileus virginianus*) populations, and increasing nesting success of avian species by suppressing other mesopredators (e.g. raccoons; Crooks and Soulé 1999; Rogers and Caro 1998). However, negative effects of coyote expansion on native wildlife are also frequently cited; including genetic hybridization with the endangered red wolf (*Canis rufus;* Kelly, Miller, and Seal 1999; McCarley 1962) and depredation of white-tailed deer fawns (Kilgo et al. 2012; Jackson and Ditchkoff 2013; Gulsby et al. 2015; Conner et al. 2016).

Coyotes have been extensively studied in the western half of their range in early successional, relatively open, or urban/suburban habitats, however few studies have examined landscape attributes in the eastern United States. Thus, habitat relationships are more uncertain. In the southeastern U.S., Cherry et al. (2017) explored the relationship between landcover and coyotes using N-mixture models and howl survey data collected at 24 sites across a ~330 km^2 area in Georgia. They found that coyotes were positively associated with open habitats, but negatively associated with forests and developed areas. These results are more consistent with studies from the coyote's native range, but varied from those in the northeastern U.S. that found forests are suitable habitat for coyotes (Kays, Gompper, and Ray 2008). Kays et al. (2008) reported that disturbed forests and areas containing edge habitats near water were included in top models predicting abundance. Model results indicated lower coyote densities in heavily human-populated areas and a positive relationship with indices associated with higher deer densities and

predation vulnerability (Kays, Gompper, and Ray 2008). The results of these studies highlight potential differences in southeastern and northeastern states.

Managing coyote populations is a challenging task for wildlife professionals. While, as mentioned above, coyotes are associated with a diverse array of ecological impacts, management is most frequently focused on limiting or reducing their populations. However, removal efforts are costly and typically must be continued annually (Ballard et al. 2001). Ballard (2001) suggested that >70% of coyotes needed to be removed from an area to achieve appreciable increases in fawn recruitment for white-tailed deer in South Carolina. Continued removal efforts are generally required because transients quickly recolonize territories where resident individuals have been removed (Beason et al. 1974, Parker 1995). Further, removal efforts in one year may results in increased reproductive effort by coyotes in the following year as a result of reduced competition (Keever 2014; Knowlton 1972). For public lands and other large areas, wildlife managers can benefit from monitoring and studying coyote populations to better inform management decisions concerning species impacted by coyotes (e.g. deer, mesopredators, nesting birds).

Given the challenges of surveying elusive carnivores, most studies have been restricted to one or few sites, and with diverse methodologies. While such efforts are valuable, state agencies tasked with managing across broad and diverse areas can benefit from studies that survey multiple, diverse areas, using consistent techniques. To better understand how coyote densities vary across the southeastern U.S., we surveyed 13 wildlife management areas across the state of Alabama. We collected scat samples along road transects, which were then identified to individual using non-invasive microsatellite genetic analyses, and used to explore the influence of landcover on coyote density. We estimated density and landcover effects using recent

developments in spatial capture-recapture (Royle and Converse 2014), that pool data across sites to improve parameter estimation, even for sites with few samples. We hypothesized that coyote densities would be highly variable across our sites, and associated with open successional habitats.

METHODS

Site description

We conducted scat collection surveys at 13 areas across Alabama during July and August of 2014. Ten of these sites were public wildlife management areas (WMA). The other three sites were privately-owned; Sedgefield and Westervelt are owned by private companies, and Houston was an area covering multiple adjacent, rural residential/farming properties. The public WMAs were primarily managed for timber (e.g. loblolly pine, *Pinus taeda*, longleaf pine, *Pinus palustris*, and slash pine, *Pinus elliottii*), but also for hunting opportunities. Hunted species included white-tailed deer, eastern wild turkey (*Meleagris gallopavo silvestris*), quail (*Colinus virginianus*), wild pigs (*Sus scrofa*), and dove (*Zenaida* sp.). The main landcover types were hardwood forest (30% average across all sites), pine (24%), mixed pine/hardwood (8%), pasture/herbaceous/young forest (10%), cropland (5%), and developed (3%). Winters in the region are characterized as mild with an annual low temperature of -1–4 °C while summers can exceed an average of 32 °C. Average precipitation is approximately 132 cm.

Scat collection

We overlaid a 5 x 5 km survey grid over each management area. Our cell size reflected mean home range sizes estimated by recent studies on coyotes in the southeastern United States (e.g. Hickman et al. 2015, Morin 2015). We did not survey grid cells that were comprised of <40% of a management area. For study sites with only one or two grid cells, we added additional

sampling area to total four grid cells. This ensured that we would sample enough area to cover

four hypothetical home ranges. Within each cell, we selected 2, 2.5 km transects along unpaved

roads and trails. Transects were randomly-selected from roads identified by area biologists based

on access and perceived ability to see scat (i.e. unpaved, public roads, little road vegetation).

Each transect was divided into 0.5-km transect subunits, and an observer visually inspected each

of these for carnivore scats biweekly over six weeks to collect all potential carnivore scat (three

sampling occasions in total). When a scat was encountered, we collected a small sample from the

surface of each scat using sterile tweezers in the field, and placed it in a DMSO/EDTA/Tris/salt

solution buffer for later processing (Frantzen et al. 1998; Stenglein et al. 2010). The remaining

fecal material was then removed to avoid double counting during subsequent visits.

Genetic analyses

All genetic analyses were conducted at the University of Idaho's Laboratory for

Ecological, Evolutionary and Conservation Genetics. We extracted DNA in a lab designated for

low-quality DNA, using Qiagen QIAmp DNA stool kits (Qiagen, Valencia, CA, USA), which

included batch extraction negatives for assessing reagent contamination. We conducted initial

screening by utilizing a species identification multiplex that analyzes mitochondrial DNA (De

Barba et al 2004). For all coyote samples, nuclear DNA was then extracted and amplified using

PCR amplification and 5-8 loci analyzed to identify individuals based on the methodology of

Stenglein et al. (2010). The microsatellite markers we used were: 2004, CXX119, CXX173,

FH2001, FH2054, FH2088, FH2137, FH2611, FH2670, and FH3725. For each marker, we

required 2 matches to confirm heterozygosity and 3 matches to confirm homozygosity. We

retained all samples with 7 out of 10 loci completed, and required a match at 6 to confirm a

recapture. Each sample was run up to 6 times to meet our thresholds. We used a threshold of

0.01 for our probability of identifying a sibling, indicating that 1 pair out of 100 pairs of siblings could match at 6 loci (Waits, Luikart, and Taberlet 2001). We estimated genotype reliability to better account for, and reduce genotyping errors, such as allelic dropout that resulted in homozygosity with extremely rare alleles.

Spatial capture-recapture

We estimated coyote density at each of the 13 areas using a multi-site spatial capture-recapture analysis (Royle and Converse 2014; Royle, Chandler, Sollmann, et al. 2013). The multi-site SCR model pools data across multiple sites to improve parameter estimation, and utilizes a multinomial model to allocate individuals into strata. We used the 0.5-km transect subunits as our trap locations, and linked each individually-identified coyote sample to the corresponding trap. For example, any scat samples collected between 2.0 and 2.5 km along our 2.5-km transect, were assigned to the fifth subunit, and we recorded the location of the centroid of that subunit as the scat location in our analyses. We constructed an encounter array with dimensions i (individuals) x j (traps) x k (occasions).

Group-level abundances, N_g, for each of the g sites, were modeled assuming they were Poisson-distributed random variables with mean λ_g. We modeled λ_g on the log-scale to allow for the incorporation of model covariates, where x_c are habitat covariates (see below), and β_c are the associated betas:

$$N_g \sim Poisson(\lambda_g), \text{ and}$$

$$\log(\lambda_g) = \beta_0 + \beta_c x_c .$$

We used the multinomial distribution to assign group membership to each individual $g_i \sim Multinomial(\pi)$, given the probability of group membership for each site, $\pi = \pi_1 \dots \pi_G$, is equal to $\frac{\lambda_g}{\sum_G \lambda_g}$.

Spatially explicit capture-recapture analyses assume that individuals use area around their activity center s, and that their probability of detection decreases with distance from s, as described by a detection function. We assumed a bivariate Gaussian (commonly referred to as half-normal) detection function, defined by a scaling parameter, σ, because it can be used to obtain estimates that are robust to most violations of model assumptions (Royle, Chandler, Sollmann, et al. 2013). For example, as discussed by Morin et al. (2016), monotonic decay may not be appropriate for territorial animals that tend to deposit scat near the perimeter of their activity centers, rather than close to their center. Consequently, we do not use estimates of σ to infer home range size.

We applied a standard capture-recapture model for count data, in which the detection of individual i at trap j during sampling occasion k, y_{ijk}, was assumed to be a Poisson random variable with capture probability p_{ijk}:

$$y_{ijk} \sim Poisson(p_{ijk})$$

We modeled p_{ijk} on the logit scale, and included a parameter for each of the k sampling occasions. The Poisson encounter model allows individuals to be detected multiple times at one trap during a single survey, and accommodates parameters to model variation in detection. We expected a greater detection probability for the first occasion because we did not clear the roads of scat prior to the first survey.

$$logit(p0_{ijk}) = \alpha_0[k]$$

The application of data augmentation allow us to account for individuals we did not detect in our surveys, but were a part of the total population, N_T (e.g. Royle, Dorazio, and Link 2007; Royle and Converse 2014). We added all-zero encounter histories to total M individual encounter histories, such that M>>N_T (Royle, Dorazio, and Link 2007). We included an

indicator variable, z_i, which represents whether an individual is part of the population N_T ($z_i = 1$) or a true structural zero ($z_i = 0$), with an imposed prior: $z_i \sim Bernoulli(\psi)$, where ψ is estimated. We selected an M value large enough to ensure that the posterior mass of ψ is not truncated (Kéry and Schaub 2012).

We implemented the multi-site model in JAGS (Plummer 2003), via R (version 3.4.0; R Core Team 2017) using the jagsUI (Kellner 2015), rjags (Plummer 2013), and coda (Plummer et al. 2006) packages. We ran 3 Markov chain Monte Carlo (MCMC) chains in parallel with 1,000 adaptions for the Metropolis algorithm, and used coda to sample 15,000 iterations from the posterior distributions of each parameter with a burn-in of 1,000 iterations and no thinning (Link and Eaton 2012). We examined trace plots and the Gelman-Rubin statistic ($\hat{R} < 1.1$; Gelman and Rubin 1992) to confirm chain convergence and mixing for each monitored parameter (Brooks and Gelman 1998).

Habitat covariates and variable selection

Habitat covariates on λ obtained were from the 2011 National Landcover dataset (NLCD) and processed using ArcMap 10.3 and the Geospatial Modelling Environment (Beyer 2015). We clipped a 5-km buffer around each scat transect centroid, creating 1 polygon per management area. We used the land classifications for deciduous, evergreen, and mixed forests, developed (combining all developed classifications), and agriculture/herbaceous (combining all agriculture and herbaceous categories), and wetlands (combining both wetland categories). We estimated the proportion of each land classification for each management area polygon. To evaluate the influence of our covariates, we follow recommendations by Royle et al. (2013) to use a pragmatic approach considering whether the posterior for each parameter overlaps zero substantially and calculation of posterior probabilities.

RESULTS

We collected 463 scat samples during our survey, and identified 195 samples as coyote. The remaining samples were from bobcat (*Lynx rufus*; n = 77), grey fox (*Urocyon cinereoargenteus*; n = 35), domestic dog (*Canis familiaris*; n = 5), or were unconfirmed due to failure in the mtDNA amplification (151). Our nuclear DNA amplification rate was 54% (106 out of 195 samples), confirmed at 7 out of 9 loci. We dropped one microsatellite markers (CXX119) due to consistent amplification issues. We identified 75 individual coyotes, and 20 of those coyotes had >2 samples collected. Our range of recaptures was 0-6 times, and the individual with the most recaptures was detected on 3 different transects (Table 2.1).

The multi-site model without covariates on N produced density estimates for each of the 13 sites. Density estimates ranged from 0 coyotes per km^2 (posterior mode, 95.5% credible interval = 0 – 0.04 coyotes per km^2) to 1.79 coyotes per km^2 (95.5% credible interval = 0.95 – 2.9 coyotes per km^2; Table 2.2). We classify five sites as low density (<0.2 coyotes per km^2), five as moderate density (0.2 – 0.4 coyotes per km^2), and three as high density (>0.4 coyotes per km^2). The precision in our density estimates was highly variable, and tended to be more imprecise at areas with more samples. The probability of detection was greater during the first survey (p = 0.13; 0.08 – 0.19) than the second (0.03; 0.02 – 0.06), as indicated by the Bayesian credible intervals (Figure 2.1). The credible interval for probability of detection during the third survey (0.06; 0.03 – 0.10) overlapped with the first and second occasion.

Due to issues with convergence for multiple parameters when we added habitat covariates to the spatial capture-recapture model, we removed all sites with fewer than 2 scat samples. We found a positive relationship between coyote density and early successional habitat (pasture/herbaceous/young forests) landcover (6.56 ± 2.2; β ± SD). We also found a positive

relationship between coyote density and both pine (3.58 ± 1.35; β ± SD) and hardwood forests (2.86 ± 0.8; β ± SD; Table 2.3). We did not find a relationship between density and developed areas, mixed forests, or crop landcover.

DISCUSSION

We found that coyote density is highly variable across broad spatial scales. Our moderate density estimates were consistent with the variation we have seen in recent studies in Alabama (0.4 coyotes per km^2; Jackson and Ditchkoff 2013), and generally those reported for suitable habitat across their range (0.2 - 0.4 coyotes per km^2; Knowlton 1972; Windberg 1995). Although most of our sites were low or moderate-density, we did observe several sites with what we consider to be high density. Notably, the site with the greatest density estimate (Scotch WMA; 1.79 coyotes per km^2, 0.95 – 2.90) was similar to, or greater than the highest reported estimate for the southeastern U.S. (0.8–1.5 coyotes per km^2 in South Carolina; Schrecengost 2007), and is only surpassed by densities observed in southern Texas (favorable range = 2.0 - 2.4 coyotes per km^2; Knowlton 1972; max reported = 4 coyotes per km^2; Knowlton et al. 1985), or urban/suburban areas with abundant anthropogenic food sources (2.4 - 4.6 coyotes per km^2; Fedriani, Fuller, and Sauvajot 2001; McClure, Smith, and Shaw 1996). Our findings suggest that there are habitats in the southeastern U.S. that support some of the highest known coyote densities across their current range, but also that such densities are uncommon relative to low and moderate-density areas.

Characteristics associated with landownership may have influenced coyote density at our sites. Three of the low-density sites (Houston, Sedgefield, and Westervelt) were the smallest sites in our study, and the only privately-owned properties. Local biologists reported that they may have experienced increased opportunistic removal of coyotes (i.e. shooting, trapping), relative to

the public management areas. Cherry et al. (2017) suggested that opportunistic removal may affect coyotes in human-occupied areas, at least at finer spatial scales. While adult coyote survival rates are reported to exceed 65%, the primary cause of mortality (~60% adult mortality) is usually attributed to landowner removal efforts (Schrecengost et al. 2009). We do not suggest that removal efforts of private landowners are greatly affecting coyote densities at our sites. But, we agree with Cherry et al. (2017) that coyotes may be avoiding areas with greater potential for opportunistic removal efforts by landowners. Similarly, biologist were actively trapping coyotes at the low-density public management areas (Choccolocco WMA). Fifteen coyotes were removed from the area between May and August. Generally, however, coyote removal efforts have been inconsistent concerning their efficacy at reducing coyote populations (e.g. Conner and Morris 2015, Gulsby et al. 2015), in large part because transient individuals have been shown to quickly fill territories following removal of residents (Hickman et al. 2015; Gulsby et al. 2015). Unfortunately, our survey was only conducted during one summer, and is insufficient to explore temporal dynamics of coyotes.

Anthropogenic land management practices likely supported higher coyote populations at several of our sites by providing early successional habitats. Coyote density in our study was positively associated with open habitat types; namely, pasture, clear-cuts, and young pine stands. The site with the greatest density was an industrial short-rotation pine plantation managed with the intent of maximizing timber harvest, and was characterized by >75% of the areas being clear-cuts and pine sapling stands. The initial impact of clearcutting of temperate North American forests increases abundance of small mammal (Kirkland 1990) and soft mast producing plants (Toweill and Anthony 1988). Studies in South Carolina (Schrecengost et al. 2009) and West Virginia (Crimmins, Edwards, and Houben 2012) reported similar results concerning coyote

39

abundance and early successional habitats.

Although coyote density was most strongly associated with open habitat types, areas that had hardwood or pine forests also supported moderate densities of coyotes. Mature forests were positively associated with coyote abundance in a landscape-scale study in New York (Kays, Gompper, and Ray 2008), but this is the first evidence of an association with forests in the southeastern U.S. However, our results conflict with Cherry et al. (2017), who did not find any evidence that forests were influencing coyote abundance at one site in Georgia. Additionally, some of the mature pine forests in our study areas were comprised of well-managed longleaf pine (*Pinus palustris*) that was characterized by relatively open canopy and herbaceous, grassy understory. Coyotes are not been extensively studied in the open-understory pine ecosystem, but we speculate that this habitat type would be suitable because it provides a diverse array of food items for coyotes (Cherry et al. 2016). We speculate that this habitat is intermediary in preference relative to open habitats and pine stands that lack open canopies and grassy understory. However, we also acknowledge that our estimates may be biased because we did not account for changes in land cover that occurred between the collection of the 2011 NLCD data and our 2014 survey. Areas that were clear-cut during that interval may have skewed our results, and produced a spurious relationship between forest and coyote density.

We demonstrate the utility of multi-site SCR to monitor coyotes at a broad spatial scale, but also demonstrated several important tradeoffs affecting parameter precision and estimation of covariate effects. Despite several areas with few or no samples, the multi-site model enabled us to pool data across sites to obtain density estimates that would have been impossible to obtain using single-site SCR. However, the imprecision of some of our estimates was surprising. Scotch had the greatest sample size, with the greatest number of recaptures, but also the greatest

estimated variance for density. We speculate that this was a consequence of estimating density at sites with few samples. We were also unable to reach convergence for many of our parameters when we included covariates on density. When we removed the areas with <2 scat samples, we were able to estimate covariate effects. Efforts to improve sample sizes, such as adding additional transects, may have reduced parameter uncertainty and enabled us to generate more precise density estimates. Ultimately, our findings highlight tradeoffs between obtaining density estimates across all sites, and the ability to explore more complex models using covariates on density.

In our study, we were not able to use a model selection approach to test and compare multiple covariate models. While AIC provides a generally accepted method to compare models, Bayesian model selection is still in its infancy, and lacks a generally accepted method (Kery and Royle 2010). We attempted to run our models within a maximum likelihood framework using package 'unmarked' (Fiske and Chandler 2011), but the models would not converge. Given the sensitivity of the unmarked models to the starting values we provided, we suspect that the maximum likelihood approach failed due to our inability to find the global maximum rather than a local maximum. We decided to conduct our analyses within a Bayesian framework that enabled us to estimate density at our sites. We evaluated the influence of our covariates within the global model because our sparse dataset precluded the use of more elegant solutions (i.e. indicator variable selection). These models were already computationally intensive, and required long run times with the parameters we included. The addition of indicator variables resulted in MCMC chains that failed to reach convergence. Indicator variable selection may have been possible if we had removed even more areas with few samples from our study. However, that conflicted with our objective of estimating density and landcover relationships across many sites.

Therefore, we had tradeoffs between our ability to estimate parameters at sites with few samples and the capacity to conduct more elegant model selection within a Bayesian framework.

Multi-site spatial capture-recapture provides a way to estimate density and explore broad-scale population dynamics that can aid wildlife managers in monitoring and managing coyotes and other novel species. The recent increase in coyote studies in the southeastern U.S. has been primarily motivated by evidence that they can limit deer populations through fawn depredation (Kilgo et al. 2010; Saalfeld and Ditchkoff 2007). Most studies have focused on the effects of coyote predation on fawn recruitment at one or two sites, and there may be a bias in research efforts towards surveying areas that have observed declining fawn recruitment or overall deer population declines. Given the variation in coyote-related fawn mortality across the region, sites with high predation may exhibit similar features (e.g. availability of cover, availability of alternate prey). Our study estimated coyote density at multiple sites that were selected to maximize spatial extent rather than to target areas that have exhibited noticeable declines in deer populations. We anticipate that our findings will provide a more accurate portrayal of the variation in coyote densities across the region for researchers and managers interested in understanding complex community dynamics associated with this novel apex predator. In order to improve on our efforts, we suggest adding additional transects to increase sample size. Increasing the number of samples and recaptures can improve our ability to model covariates on density using SCR. Managers can also add additional surveys under robust design to explore more complex population dynamics (e.g. open population models; (Gardner et al. 2010; Royle, Chandler, Sollmann, et al. 2013). In addition to broad scale data, SCR can also tackle finer-scale analyses using inhomogeneous point process models (Royle et al. 2013) that eliminate the assumption that activity centers are randomly distributed across the landscape. Potential future

directions can also employ recent advances in SCR that address landscape connectivity and resource selection (e.g. Royle et al. 2013a, 2013c, Sutherland et al. 2015, Fuller et al. 2016, Morin et al. 2017). The rapid expansion of SCR applications provides many promising avenues for continued investigations into population dynamics and space use that can increase our understanding of coyote ecology.

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FIGURES AND TABLES

Table 2.1. Number of unique encounters (rows) and unique traps (columns) for each individual coyote. The bottom-right column indicates that there was one coyote encounter six times at three different traps.

		Number of unique traps		
		1	2	3
	1	52	0	0
Number	2	4	7	0
of unique	3	0	4	2
encounters	4	0	0	2

5	0	0	0
6	0	0	1

Table 2.2: Density estimates obtained from 13 wildlife management areas in Alabama from a multi-site spatial capture-recapture analysis of individually-identified coyote scat samples during summer 2014.

Site	Total Samples	Unique Individuals	Density (km2)	2.5%	97.5%
Barbour	4	3	0.23	0.08	0.79
Black Warrior	16	14	0.33	0.19	0.55
Choccolocco	0	0	0	0.00	0.04
Coosa	16	10	0.78	0.43	1.54
Freedom Hills	15	9	0.51	0.29	1.08
Houston	0	0	0	0.00	0.14
Lowndes	5	3	0.21	0.08	0.74
Mulberry Fork	8	7	0.35	0.16	0.72

Oakmulgee	3	3	0.11	0.04	0.38
Scotch	18	13	1.79	0.95	2.90
Sedgefield	0	0	0	0.00	0.26
Skyline	20	9	0.27	0.14	0.52
Westervelt	1	1	0.02	0.02	0.65

Figure 2.1. Estimates of detection probability obtained from 13 wildlife management areas in Alabama from a multi-site spatial capture-recapture analysis of individually-identified scat samples during summer 2014.
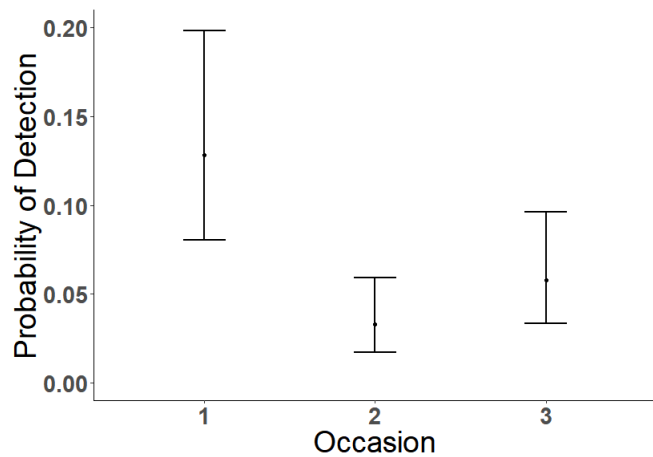
Table 2.3. Estimates total coyote abundance and land cover coefficients from 9 wildlife management areas in Alabama using multi-site spatial capture-recapture analysis of individually-identified scat samples during summer 2014. Early successional land cover combines scrub (including young trees), herbaceous, and grassland classifications from the National Landcover Database.

Parameter	Mean	Standard Deviation
N.total	766	136
b.intercept	2.01	0.68
Hardwood	2.86	0.80
Pine	3.58	1.35
Mixed	0.39	1.95
Developed	-2.59	5.20
Wetland	-5.10	2.73

Early succ.	6.56	2.20
Crop	1.02	5.99
deviance	1258.65	33.14

Chapter 3: Competitors and predators: factors influencing white-tailed deer fawn recruitment

INTRODUCTION

Understanding predator-prey relationships is a complex challenge in ecology and wildlife management, and knowledge regarding effects of predation on prey population dynamics is important for managing economically valuable or endangered prey. Most often, predation does not drive population dynamics and is characterized as compensatory (Bartmann et al. 1992). Conversely, predation can be additive to other sources of mortality and have the capability of limiting populations (Bartmann et al. 1992). Predation as a limiting factor for prey populations can result from direct reductions in prey numbers through predation, or potentially from a "predator pit" – a theory describing an interaction in which prey have two potential equilibrium states; nutritional carrying capacity, K (McNab 1985), and a reduced-abundance equilibrium under which prey populations decline below some threshold and then are maintained by predation (Messier 1991). It is important to note that the original source of prey population

decline may be unrelated to predators, but it is predation that prevents prey population rebound to K (Messier 1991). There is evidence to support that predation can be a limiting factor for prey populations in numerous predator-prey systems including caribou (*Rangifer tarandus*) and wolves (*Canis lupus*; Ballard et al. 1997), moose (*Alces alces*) and wolves (Messier 1994), European rabbits (*Oryctolagus cuniculus*) and red foxes (*Vulpes vulpes*; Fernández de Simón Romero), pronghorn (*Antilocapra americana*) and coyotes (*Canis latrans*; Dunbar et al 1999), bighorn sheep (*Ovis canadensis*) and cougars (*Puma concolor*; Hayes et al 2000, Schaefer et al 2000, Kamler et a. 2002), and white-tailed deer (*Odocoileus virginianus*) and coyotes (Jackson and Ditchkoff 2013; Kilgo et al. 2010). However, little is known about other factors (i.e. habitat) that may influence the functional form of predator-prey relationships and whether predators are regulating a prey population.

A multitude of factors may influence predator-prey dynamics that result in predator-limited prey populations. Prey density relative to habitat carrying capacity has a strong influence on the impact of predation on the prey population. There is a continuum between compensatory mortality dominating when prey populations are near K and additive mortality driving dynamics in prey populations far below K (Bartmann et al. 1992, Ballard 2001). Elevated predator density can also maintain reduced prey populations under a predator pit scenario (Ballard et al. 2001), and if an abundant alternative prey source is maintaining elevated predator densities, the less abundant sympatric species may continue to experience increased predation pressure (e.g. Storaaas et al. 1999, Wegge et al. 2009). Gorini et al. (2012) reviewed current literature regarding the influence of spatial heterogeneity on prey density and distribution, predator density and distribution, and predator kill rates in mammalian predator-prey systems. They suggest that the distribution of hiding or escape cover relative to food supply and other resource needs

influences the amount of movement required by prey and may increase their vulnerability to predation (Gorini et al. 2012). Environmental conditions, such as snow depth and winter severity, can also affect prey vulnerability (e.g. deep snow and moose; Mech et al. 1987; Kunkel and Pletscher 2000; winter severity and deer; Unsworth et al. 1999). Further exacerbating the complex dynamics of predators and prey are disturbances, especially habitat fragmentation (Soele 1991) and other human-induced landscape changes (Van Ballenberge and Ballard 1994). The myriad of potential factors influencing predator-prey dynamics translates to a complex problem for resource managers interested in managing wildlife populations.

Actions available to managers to restore limited prey populations are often costly and fall short of management goals; especially in the long-term (Conner et al. 1998, Ballard 2001, Harding et al. 2002). A common practice is predator control, which aims to reduce predator abundance and allow prey populations to rebound. Ballard et al. (2001) summarized studies that achieved some success at improving deer abundance using predator control and recommended 1) first identifying predation as the limiting factor, 2) removing a significant proportion (~70%) of the predator population, 3) timing removal to just before predator or prey reproduction, and 4) focusing on small scale efforts. Even following these recommendations, removal efforts generally must be repeated every year or for several years to achieve and maintain target prey population numbers (Ballard et al. 2001; Martin et al. 2010), and ultimately the benefits of predator control may not outweigh costs (Conner et al. 1998; Ballard et al. 2001; Robinson, Fefferman, and Lockwood 2013). Habitat management has been suggested as a more feasible approach to restore predator-limited prey populations, however few studies have directly addressed this alternative (Ballard et al. 2001; Gulsby et al. 2017). For game species, such as deer and moose, adjusting harvest regulations are another option to reduce predation mortality

pressure, by reducing pressure on females to improve recruitment rates (Messier 1991). Increasing our understanding of factors associated with potentially predator-limited prey populations may highlight potential management options to inform wildlife decision-making.

Coyotes, formerly restricted to west of Mississippi River, have expanded their range into the southeastern United States. Several studies indicate coyotes are causing high fawn mortality rates in this region (i.e. Saalfeld and Ditchkoff 2007, Kilgo et al. 2012, Jackson and Ditchkoff 2013, McCoy et al. 2013) and other areas of the country (e.g. Cook et al. 1971, Bartush and Lewis 1981, Vreekand et al. 2004). Some studies have concluded that mortality from coyote predation is compensatory (Bartmann et al. 1992, Bishop et al. 2009), and others support the theory that coyotes are limiting deer populations (Messier et al. 1986, Patterson et al. 2002; Kilgo et al. 2010). While efforts to reduce coyote populations have been common practice (i.e. trapping, shooting), research suggests that predator control may result in increased coyote density (Knowlton 1972; Keever 2014). Little is known about the associated factors that influence the capacity of coyotes to limit deer populations, such as habitat structure or hunting pressure.

Habitat is another potential area where managers can influence deer demographics. Deer habitat includes a wide range of factors, such as food resources, hiding cover, and access to water (Hewitt 2011). Hiding and escape cover from predators such as coyotes, who hunt using olfactory and visual cues, are important sources of habitat for survival (Wells and Lehner 1978, Huegel et al. 1986). Neonates, fawns under a month of age, select bed sites within the maternal home range (Huegel et al. 1986, Grovenburg et al. 2010) and typically select a new site daily (Ozoga et al. 1982). Habitat characteristics associated with fawn bed sites are variable, but tend to include vegetation height, (Uresk et al. 1999, Grovenburg et al. 2012), mean vegetation cover,

edge habitat (Rohm, Nielsen, and Woolf 2007; Gulsby et al. 2017), woody cover (Huegel 1986),

vegetation density (Huegel et al. 1986, Hyde et al. 1987), and presence of non-forest patches

(Rohm et al. 2006). As fawns age and increasingly leave their bed sites, proximity to escape

cover influences their ability to evade predators (Grovenburg et al. 2012). Grovenburg et al.

(2012) found that fawns in the Northern Great Plains were less likely to be captured in grasslands

or wetlands in comparison to forests and wheat fields. However, additional research is needed in

the southeastern United States, where coyotes are a novel predator, to determine which habitat

characteristics are the primary drivers of fawn survival.

We surveyed white-tailed deer at 16 management areas across Alabama, and examined

the effect of coyotes, wild pigs, and habitat on fawn abundance. Our study aimed to identify

factors influencing fawn recruitment rates across the state of Alabama. We used open population

N-mixture models (Royle 2004; Dail and Madsen 2011) to estimate site-specific deer abundance

at 314 camera sites across the state and developed models with habitat, harvest, wild pigs, and

coyote density data to determine which factors are associated with fawn recruitment. We

predicted that wild pigs, canopy closure, and coyote density would reduce mean fawn

abundance, while understory cover and doe abundance would be associated with increase mean

fawn abundance.

METHODS

Study Site

This research was conducted in cooperation with Alabama's Department of Conservation

and Natural Resources at 16 state management areas (WMAs) in the state (Figure 3.1). The areas

are widely distributed across the state and represent a range of habitat types and management

regimes (see Site Description in Chapter 2). Each area also experienced some level of deer harvest.

Deer Camera Surveys

We surveyed white-tailed deer at 16 WMAs using camera survey methods outlined by Keever (2014). Surveys were conducted in February and September (pre-and post- breeding) for three years; beginning in September 2012, and ending in February 2015. At each WMA, we designed a survey grid with camera locations spaced 2.41 km apart, as recommended by Keever (2014) to minimize the chance of a deer visiting more than one camera site during the surveys. The number of camera sites identified per area ranged from 5 to 46 sites. For areas with >15 camera sites, we randomly selected 15 per season. We used Reconyx PC800 game cameras (RECONYX, Inc., Holmen, Wisconsin), and placed them facing north or south. We used a 4-minute time-lapse setting rather than the motion-trigger option to reduce potential bias that could be introduced by variation among trigger sensitivities (Hamel et al. 2013; Newey et al. 2015; Rovero et al. 2013; Damm, Grand, and Barnett 2010). We baited each site with ~11 kg of whole corn 4 m away from the camera one week prior to the survey, then refreshed sites as necessary during the survey. We retrieved the cameras after one week, and downloaded the images collected. We reduced the number of images we analyzed to images captured between 17:00 and 5:00 based on the recommendations of Keever et al. (2017). We further reduced the images analyzed to a 12-minute time interval to ensure adherence to the independence assumption of N-mixture models (Royle 2004); which Keever (2013) demonstrated to provide accurate abundance estimates while decreasing data processing requirements versus the use of the full set of photos captured.

We extracted image metadata using Reconyx BuckView, and pre-processed the images to identify images that mostly likely had deer present using AnimalFinder (Price Tack et al. 2016). AnimalFinder is a MATLAB-based program developed specifically for analyzing images with large-bodied, non-patterned animals, and reduces the number of false positive images requiring manual review. We then manually reviewed all images flagged by AnimalFinder as potentially containing a deer, and extracted relevant biological data: number of fawns, does, and wild pigs.

Covariate data

We included data on wild pigs and coyotes in our analyses. We extracted site-specific pig data from our camera surveys to calculate indices of pig visitation and pig abundance. During manual image processing, we counted the number of individual pigs in each image, and used the maximum number seen at each site and survey as an index of pig abundance. We estimated pig visitation as the hourly proportion of images that wild pigs were detected at a site for each site and survey season. We also used the area-specific coyote density estimated in Chapter 2. Coyote density was estimate using individually-identified scat samples collected along roads, and spatial capture-recapture analyses.

We collected site-level vegetation characteristics that potentially influence the ability of fawns to evade predation to use in our fawn recruitment models. In summer 2014, we collect vegetation data around each of our 314 locations. We utilized our grid design from our camera survey, and randomly selected a vegetation sampling point within each grid. We measured horizontal cover using the ball-staff method described by Collins and Becker (2001); which estimates % horizontal cover at predetermined vertical points using binary data that are quicker to obtain and more precise than cover pole or checkerboard methods. An observer marked the center point for each survey site, then walked 50 m in each cardinal direction to mark 4 starting

points for the ball-staff recordings. One ball-staff was placed at the center of the starting point,

then the observer walked a 5-m radius circle around that point with another ball staff. We took

measurements at 0.25 and 0.5 m to determine cover density for bedded fawns, and then at 1 m

for standing deer (Figure 3.2). The observer on the radius of the circle recorded binary

measurements from each of the three points. Using one eye, to avoid parallax bias, the observer

determined if each 1-inch diameter dot on the center pole was visible from each level of the outer

pole; totaling 6 binary cover density readings per radial point. Canopy cover was measured using

a moose-horn densitometer, following the protocol developed for the Alabama Inventory and

Conversation Planning (ICP) Project (Silvano 2013). We recorded 49 binary canopy

measurements (canopy yes/no) in a 25-m radius, circular plot design around the center point, and

used the results to estimate density of canopy cover.

Analysis

We estimated doe abundance to use as a covariate in our fawn models using the Dail-

Madsen (Dail and Madsen 2011). This model is a generalized N-mixture model that was

developed to estimate abundance from repeated counts (Royle 2004) that accommodates robust

design surveys. The model assumes population closure during secondary samplings (i.e. during

each week-long camera survey), but allows for population dynamics between primary survey

periods (i.e. the period between camera surveys). The model cannot differentiate between

emigration and death or immigration and recruitment, so we estimate the number of individuals

recruited into the population (recruitment rate, γ), and the number of individuals that survive and

do not emigrate (apparent survival, ω). We modeled initial abundance (λ) using a Poisson

distribution, $N_{i,t} \sim Poisson(\lambda)$ where N_{it} represents the number of individuals at site i during

primary period t. In subsequent years, we modeled doe abundance using an autoregressive model, such that

$$N_{i,t+1} = G_{i,t} + S_{i,t} \ ,$$

where G_{it} is the number of individuals recruited to the population, modeled as a Poisson-distributed random variable, $G_{it} \sim$ Poisson(γ). S_{it} is the number of individuals that survived and did not emigrate population modeled using a binomial distribution, such that $S_{it} \sim Poisson(\omega)$. The detection process for does was modeled as $y_{i,j,t} \sim Binomial(N_{i,t}, p_{i,t})$, where $y_{i,j,t}$ is the observed count at each site i during secondary sampling occasion j and primary sampling period t.

We included time, precipitation, and the frequency of wild pig visitation as covariates on detection in our doe model. We used Weather Underground to obtain the amount of precipitation recorded taken from the most recent recording (usually within 30 minutes) taken from the nearest weather station to the center of each WMA. We included time as a quartic function (time+time^2+time^3+time^4), as described by Keever (2014) to account for the crepuscular behavior of deer. To address the influence of pigs on the detectability of does, we used the hourly pig visitation index for each site and survey season.

We modeled fawn abundance using February surveys due to the difficulty in capturing fawns on camera during February when they are young and relatively immobile (Mccoy, Ditchkoff, and Steury 2011). We estimated abundance using the non-dynamic N-mixture model (Royle 2004) to coincide with the reality that the fawns leave this life stage after one year. Thus, fawn abundance in one year is not influenced by fawn abundance in the previous year. We included time, precipitation, and the frequency of wild pig visitation as covariates on detection. We used Weather Underground to obtain the amount of precipitation recorded taken from the

most recent recording (usually within 30 minutes) taken from the nearest weather station to the center of each WMA. We included time as a quartic function (time+time^2+time^3+time^4), as described by Keever (2014), to account for the crepuscular behavior of deer. To address the influence of pigs on the detectability of fawns, we estimated the hourly proportion of images that wild pigs were detected at a site for each site and survey season. For our site-specific abundance, we incorporated the number of does estimated during September estimated from our Dail-Madsen analysis to eliminate the influence of harvest on the change in doe abundance between September and the following February. We also included site specific pig abundance, area-specific coyote density, and the site-specific canopy and understory cover vegetation data on fawn abundance.

To evaluate the relative influence of our covariates on λ, we used variable selection priors, commonly referred to as "slab and spike" (George and McCulloch 1993; Ishwaran and Rao 2003). This approach essentially combines model averaging and variable selection in one estimation process (Burnham and Anderson 2002). We constructed a prior distribution for each λ coefficient from of a mixture of two prior distributions centered around zero, but with very different variances. Each regression coefficient was given a prior constructed of two Gaussian distributions concentrated around zero, one referred to as the spike and the other, the slab (Ishwaran and Rao 2003). The spike prior represents the absence of a variable from the model, and was modeled as a normal distribution with a narrow peak, such that spike ~ $Normal(\mu,\sigma^2)$ where $\mu = 0$ and $\sigma^2 = 0.01$. The slab prior represents the presence of a variable from the model, and was modeled as a normal distribution with a very large variance, such that slab ~ $Normal(\mu,\sigma^2)$ where $\mu = 0$ and $\sigma^2 = 999999999999$. We included a Bernoulli distribution that represents our prior believe that the model includes the coefficient. We used a starting value of

0.5 for all of our λ coefficients, representing a 50-50 chance of inclusion in the model run. As the MCMC analysis proceeds, the algorithm estimates the probability of inclusion and results in a bimodal posterior distribution that describes the relative support for inclusion or each coefficient in the model (Ishwaran and Rao 2003). Variables that lack strong evidence supporting their inclusion in the model retain the dominate spike in their posterior probability that effectively shrinks the posterior mean towards zero. Coefficients with strong support of inclusion with have posterior densities that are shifted from zero. We examine the posterior distributions for each coefficient and further confirmed our results by considering whether the posterior overlaps zero, and if so, to what extent.

RESULTS

We collected >2 million images during our camera surveys, and used 576,974 in our analyses after reducing the images to every 12 minutes at night. After initial filtering with AnimalFinder (2016) and subsequent manual processing, we identified 35,354 deer in 25,363 (4.4%) of the images. Further classification resulted in 6,083 fawns (17.2% of images with deer), 14,021 does (40.0%), and 12,762 bucks (36.1%). We were unable to classify 2,488 deer (7% of images with deer). Pigs were observed at 12 of our 16 areas with a total of 4,184 pigs counted in 1,745 images of pigs.

Site estimates of does and fawns varied considerably within and among management areas, but much less across years (Figures 3.3 and 3.4). Doe abundance per site ranged from 0.7 to 14.3, with standard deviations ranging from 0.9 to 9.9 does per site. The modes for doe site abundance ranged from 0 to 3 does per site. However, the mean site abundance for 9 of the 16 management areas was between 0 and 3.4 does, with standard deviations ranging from 0.9 and 4.9. There were several outliers with regards to mean doe abundance estimates. Sedgefield (14.3

± 9.9; mean ± SD; mode = 8) and Westervelt (9.9 ± 6.5; mean ± SD; mode = 13) had the greatest

mean site abundance and mode for does. The site abundances at these areas were highly variable,

and included some that exceeded biologically reasonable expectations that further skewed the

estimates of mean site abundance. Fawn abundance trends generally mirrored the doe results.

Mean fawn abundance ranged from 0.8 fawns per site to 8.8, with standard deviations varying

from 0.8 to 6.8 fawns per site. The mode ranged from 0 to 4 fawns per site.

Variable selection supported the inclusion of wild pig (99.6% inclusion) and season

(100%) on doe recruitment, but not coyote density (1%). Wild pigs were positively associated

with doe recruitment (0.10 ± 0.02; standardized β ± SD). Recruitment was greater in February

(0.18 ± 0.03; standardized β ± SD) than September (-0.27 ± 0.05; standardized β ± SD). Coyote

density had no estimable effect (0.00 ± 0.003; standardized β ± SD). Season (46.8%) and harvest

(34.7%) had some support for inclusion on apparent survival. However, the posterior distribution

of the season (-1.24 ± 2.247; standardized β ± SD) and harvest effects (-1.92 ± 2.82; standardized

β ± SD) overlapped zero. Thus, we were unable to ascertain changes in apparent survival among

seasons and due to harvest.

The variables in the fawn model that were supported were doe abundance (100%

inclusion), canopy (96.0% inclusion), and pig abundance (99.6%). Coyote density (0%; Figure

3.5), and cover (0.4%) were not important. Fawn abundance was positively associated with our

estimates of doe abundance from the previous September survey (0.47 ± 0.02; standardized β ±

SD; Figure 3.5). Fawn abundance was also greater with increased canopy closure (0.12 ± .03;

standardized β ± SD). Wild pig abundance was negatively associated with fawn abundance (-

0.16 ± .04; standardized β ± SD; Figure 3.6). Probability of detection was low (~0.01), and

decreased with rain (-1.06 ± 0.03; β ± SD). Pig visitation also resulted in a decrease in detection (-2.70 ± 1.2; β ± SD), although the posterior distribution slightly overlapped zero (Figure 3.7).

DISCUSSION

Our results indicate that recruitment varies across camera sites and among management areas, and demonstrate the utility of N-mixture models as an emerging tool for large-scale monitoring deer populations. The greatest fawn recruitment estimates were consistently at Sedgfield, the areas with the areas with the fewest fawn recruits were Choccolocco and Coosa. We found evidence to suggest that wild pigs and habitat are strongly associated with fawn recruitment and detection, but surprisingly found that fawn abundance was not associated with coyote density. We demonstrate how analyzing deer camera survey data with N-mixture models provide advantages over the traditionally-used Jacobson et al. (1997) method. Relative to the Jacobson et al. (1997) method, N-mixture models provide estimates of precision, eliminate assumptions that antlered bucks can be identified to individual, and assumptions that detectability is equal among all sexes and age classes (Keever et al. 2017). While the Jacobson et al. (1997) method appears to overestimate deer relative to N-mixture models (Haus and Bowman 2015), estimates obtained from N-mixture models were shown to be reliable in a validation study on a marked population (Keever et al. 2017). However, N-mixture models have come under scrutiny due to potential parameter identifiability issues that arise from relying on count data to estimate probability of detection and abundance (Barker et al. 2017). While we agree that the application of these models requires careful consideration, especially with regards to heterogeneity in detection, we feel that this is true with all models, and does not preclude the utility of N-mixture modeling. Keever et al. (2017) showed that N mixture models have considerable potential for accurately estimating ungulate abundance from time-lapse camera-trap

data. Ultimately, we argue that the concerns regarding N-mixture models can be addressed by

taking 3 steps, 1) consider the research or monitoring objectives, 2) carefully consider the model

assumptions relative to the study design and system that is to be modeled, with special attention

to accounting for heterogeneity in detection, and 3) simulate data to better understand how

violations in 2) may bias results. Our study was designed to inform state harvest decisions that

greatly benefit from estimates of abundance rather than relative abundance for setting target

harvest levels and associated regulations. We designed our study to account for heterogeneity in

detection, and previous research (Keever et al. 2017) supports the validity of our methodology.

We found evidence that interspecific competition was occurring between wild pigs and

fawns. Wild pigs were negatively associated with deer abundance and detection; although the tail

of the posterior distribution for pig visitation on detection slightly overlapped zero, indicating

some uncertainty. While there is no evidence that pigs are a significant source of fawn mortality

(Ditchkoff and Mayer 2009), deer have been suggested to exhibit spatial and temporal

avoidance, or resource partitioning with regards to their interactions with wild pigs (Tolleson

1995). Agonistic behavior of wild pigs is common when protecting limited food resources

(Schnebel and Grisworld 1983), and may occur between pigs and deer. Keever (2016) observed

reduced initial deer abundance at sites with greater numbers of pigs, but did not observe an effect

of pigs on deer recruitment. The authors noted that their results may have been due to the low

deer densities on their study site, and may have been further hindered by only sampling a single

site over two years. Our survey included sites with a range of deer abundance, including sites

that were expected *a priori* to have greater deer densities than those reported at Fort Rucker. This

likely increased direct competition for food resources. Although the overlap between the diets of

wild pigs and deer is reportedly minimal in the southeastern U.S (Wood and Roark 1980, Taylor

and Hellgren 1997), numerous studies have suggested competition for food resources between deer and wild pigs in the USA and Argentina (Stegeman 1938; Wood and Barrett 1979, Everitt and Alaniz 1980, Wood and Roark 1980, Graves 1984, Taylor and Hellgren 1997, Pérez Carusi et al. 2009). Competition for limited pulse resources can affect consumer dynamics in terrestrial ecosystems (Ostfeld and Keesing 2000). For example, competition for acorns and other mast crops may affect deer populations during years with poor acorn production (Wood and Lynn 1977). Competition can affect spatial distribution of competitors, and has the potential to reduce survival rates and reproduction of one or both competitors (Begon et al. 2005). Further research is needed to better understand how deer and pigs are competing, what resources are involved, and the spatial and temporal effects of competition on community dynamics.

Fawn abundance was not influenced by coyote density at our sites. Studies have shown that coyotes are a ubiquitous cause of fawn mortality, ranging from ~20% to 80%, in the southeastern U.S (e.g. Saalfeld and Ditchkoff 2007; Kilgo et al. 2012; Jackson and Ditchkoff 2013; Chitwood et al. 2015), but while coyotes prey on fawns, they also utilize a wide range of other food items. If coyotes are consuming food items under optimal foraging theory, the availability of alternate, increased efficiency food items may be driving fawn predation. Evidence suggests that fawns are the most heavily utilized mammalian prey species during summer (Schrecengost 2007; Cherry et al. 2016), but soft mast (e.g. blackberries) were the most frequently occurring food item overall (Schrecengost 2008, Blanton and Hill 1989, Wooding 1984, Hall 1979) Preference has not been well studied in our region, but studies have indicated that availability of soft mast relative to fawn abundance affects predation rates of white-tailed deer fawns (Andelt et al. 1987; Schrecengost et al. 2008). We hypothesize that the sites with greater coyote density and high fawn recruitment, had alternative food items during summer that

resulted in reduced pressure on fawns. Additionally, while coyote populations utilize fawns as a pulse resource, they are omnivorous, generalist predators. Fawn abundance may result in a function response (e.g. cause prey switching in coyotes Holling 1965; Petroelje et al. 2014). However, there is no evidence to suggest that coyote densities are sensitive to deer abundance. Pulse resources have great effects on population densities when they are available during a nutritional bottleneck (e.g. winter food shortages). While fawn predation is hypothesized to increase the survival of coyote pups (Harrison and Harrison 1984), there is no evidence to suggest that the fawning period coincides with a nutritional bottleneck for coyotes. Thus, we hypothesize that coyotes may have an effect of fawn survival, which we did not directly measure, but coyotes are not regulating deer population abundance because coyote populations are themselves regulated by other nutritional limitations in the environment.

The relative benefits of forests and early successional, open habitats on depredation of fawns by coyotes is uncertain. Gulsby et al. (2017) present competing hypothesis concerning cover and predation rates in forests vs. open habitats, and suggest that there are tradeoffs between relative visual concealment and predation risk. The authors posit that visual obstruction is greater in open habitats with dense, early successional vegetation than forests, but that open habitats are also preferred by coyotes relative to forests (Gulsby et al. 2017). Therefore, there is a tradeoff between fawn habitat selection with regards to predation. The positive relationship we found between canopy and fawn abundance supported the hypothesis that predation risk was less in forests; i.e., fawn recruitment was greater and therefore predation was likely less. We predicted that our results would support the opposite conclusion, consistent with (Grovenburg, Klaver, and Jenks 2012; Grovenburg et al. 2012; Gulsby et al. 2017; Watine and Giuliano 2015). However, our results coincide with studies in Illinois (Rohm, Nielsen, and Woolf 2007) and the

69

Red Hills region of Florida and Georgia (Watine and Guiliano 2015) that reported increased survival rates of fawns born near hardwood, natural, and managed pine; which was characteristic of our sites. Further, despite cover affecting multiple aspects of predation (e.g. hiding cover, escape cover, search effort), concealment cover has not been shown to affect coyote-fawn dynamics in the southeastern U.S. Our lack of evidence that understory cover influenced fawn abundance mirrored other studies that were implemented in the region using a variety of metrics and scales (Kilgo et al. 2014; Chitwood et al. 2015; Gulsby et al. 2017). This suggest that spatial avoidance is a more important factor for coyote-fawn dynamics than visual obstruction.

We also recognize that the scale of our study was not ideal for studying habitat factors associated with young fawns. We estimated fawn abundance during our February surveys, due to their low detection probability during September. Our camera traps were spaced to minimize the chance of any deer visiting more than one site during the survey (as recommended by Keever et al. 2017), and would have ideally been spaced closer together to better understand the drivers of young fawn recruitment and abundance. However, the objectives of our study were to better understand fawn recruitment on a larger scale, both temporally and spatially. Further, our study assumed that fawns did not move from one camera site to another during the time between the September and February camera surveys. Movement to another camera survey would bias our estimates of the habitat effects. Hiding cover is the most crucial for fawns in the first 60 days of life (Verme 1977; Huegel 1985; Nelson and Woolf 1985), when they primarily remain in bed sites that they select. They select their bed sites, but do so within the maternal home range. Generally, fawns change bed sites several times a day, moving 100-130 m daily (Ozoga, Verme, and Bienz 1982). However, Kilgo et al. (2014) and Chitwood et al. (2015) examined finer-scale habitat characteristics during summer in southeastern sites, and did not find a relationship

between cover measurements and fawn survival. As discussed above, understory cover does not seem to be a factor driving fawn recruitment in our system.

Given our findings, managers may consider shifting efforts to remove coyotes to increasing alternative prey sources and pig removal. Our data suggest that wild pigs may be affecting deer populations more than previously believed. While coyote removal may be justified in areas that are exhibiting characteristics of a predator pit, our results suggest that the availability of alternative food sources may improve fawn recruitment more than reducing coyote populations. Further, evidence for density-dependent reproduction (Knowlton 1972; Keever 2014) may negate, or even counteract removal efforts. Further, removal efforts are typically short-term in their capacity to reduce fawn depredation, because of the propensity of transient coyotes to fill vacated territories (Hinton, Chamberlain, and van Manen 2012). Gulsby et al. (2017) suggest forests management practices as a management alternative, cautiously suggesting increased interspersion and diversity of stand types and ages. Our findings suggest that mature forests benefit fawns enabling them to spatially avoid coyotes. Ultimately, we agree with our colleagues that in many cases, and unless strategically implemented, coyote removal efforts are unlikely to succeed, and alternate methods may be more fruitful for influencing deer populations.

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FIGURES

Figure 3.1. Wildlife management areas sampled as part of a statewide camera survey for white-tailed deer in Alabama, USA.

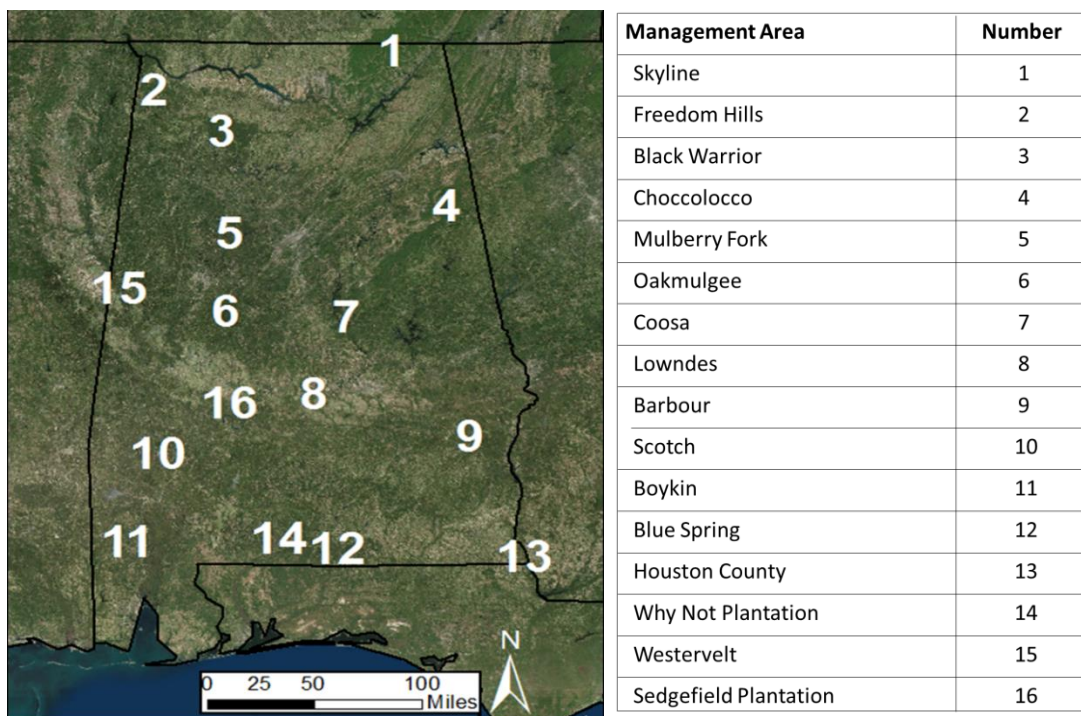| Management Area	Number
Skyline	1
Freedom Hills	2
Black Warrior	3
Choccolocco	4
Mulberry Fork	5
Oakmulgee	6
Coosa	7
Lowndes	8
Barbour	9
Scotch	10
Boykin	11
Blue Spring	12
Houston County	13
Why Not Plantation	14
Westervelt	15
Sedgefield Plantation	16

Figure 3.2. Ball-staff method for estimating horizontal cover

Figure 3.3. Stacked and smoothed histograms of estimated doe abundance from Dail-Madsen

analysis. Each panel represent a different wildlife management area.
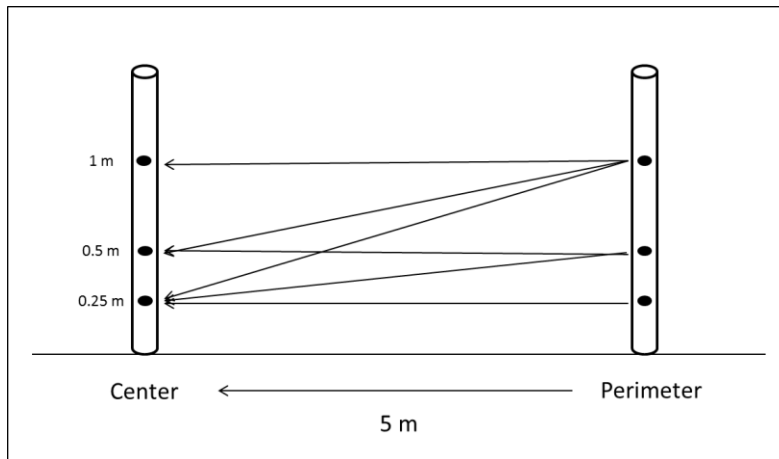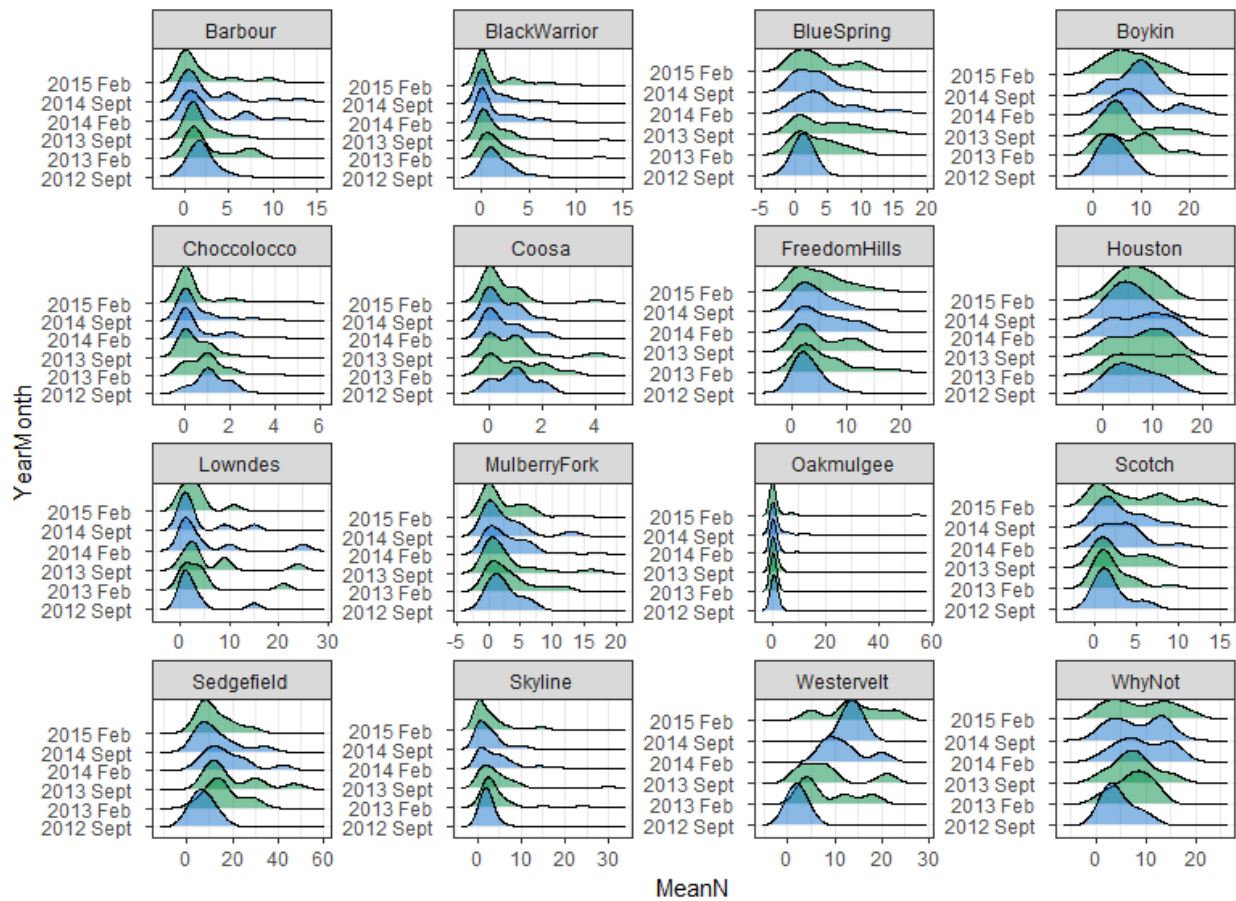
Figure 3.4. Stacked and smoothed histograms of estimated fawn abundance from N-mixture

analysis. Each panel represent a different wildlife management area.
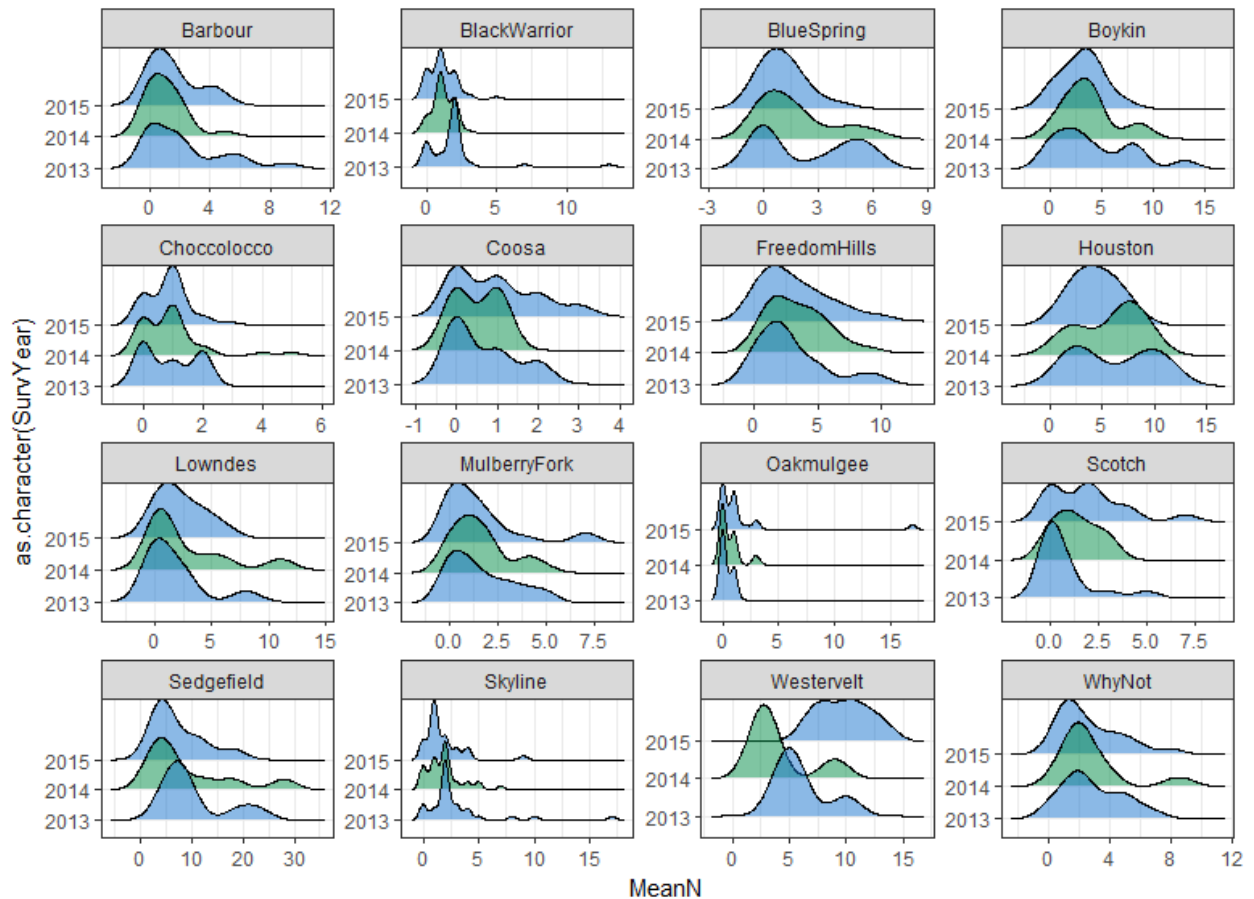
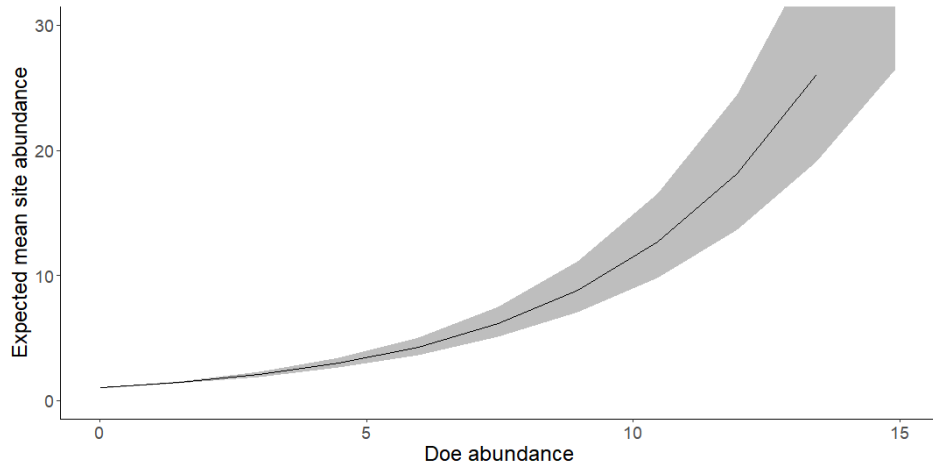Figure 3.5. Relationship between doe abundance and fawn abundance

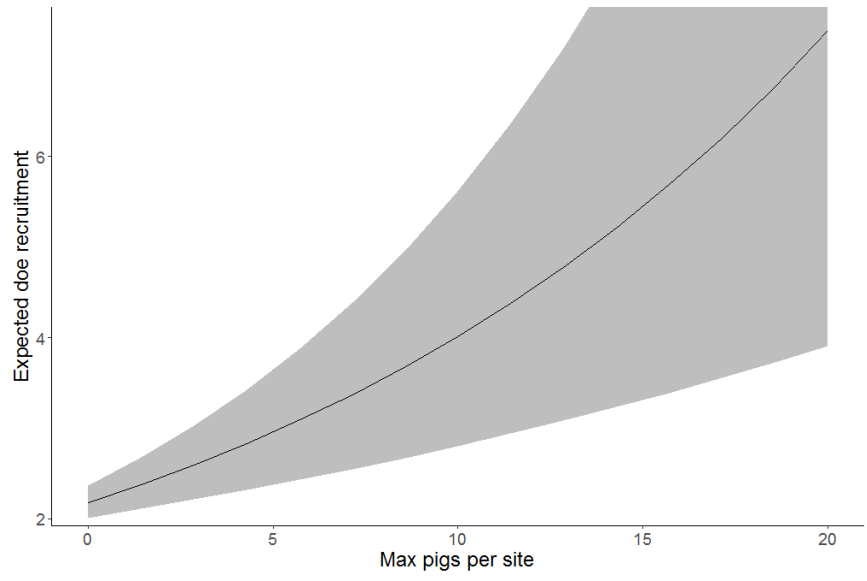Figure 3.6. Relationship between fawn abundance and pig abundance

Figure 3.7. Relationship between detection of fawns and hourly pig visitation
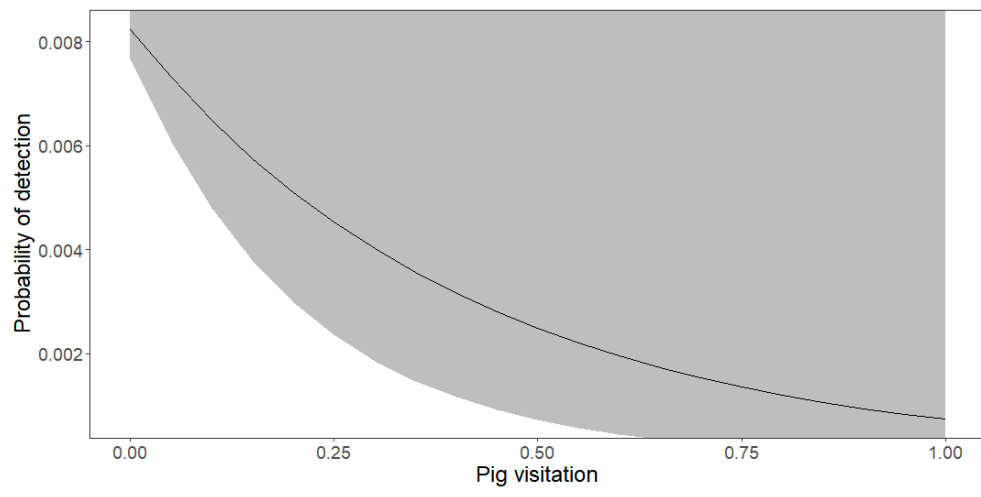
Chapter 4: Managing the endangered North American hunter: a novel framework to address declines in hunters and hunter-generated conservation funds

Hunting has historically been an important aspect of outdoor culture in the United States and a driving force for the conservation of natural resources. Declines over the last 35 years in the number of active hunters (United States Fish and Wildlife Service, 2016), threaten the multitude of societal benefits afforded by hunting (Figure 4.1a). While the total U.S. population continues to rise, the percentage of the population that purchases hunting licenses has fallen (United States Fish and Wildlife Service, 2016; U.S. Census Bureau; Figure 4.1b). Declining hunters are likely to have economic and conservation impacts in the U.S., as hunting is a multibillion dollar industry that benefits local communities and businesses, and generates revenue for state wildlife agencies through license sales and taxes. The economic impact of white-tailed deer hunting alone is massive, with annual gear and license sale revenues exceeding $30 billion; which is more than many companies featured in Forbe's Fortune 500 list (Cambronne, 2013; DeCarlo, 2016). Hunting is a significant driver of the rural real estate market

in many areas of the country (Baen, 1997; Cambronne, 2013; Knoche & Lupi, 2013; Mingie, Poudyal, Bowker, Mengak, & Siry, 2017), and may incentivize landowners to maintain, restore, and/or improve tracts of land for wildlife (Knoche & Lupi, 2007). Another positive ecological impact credited to hunting is derived from the use of wild game as a source of meat (Cawthorn & Hoffman, 2014). If harvested sustainably, game may be more humane and have a reduced environmental impact (i.e. carbon footprint) relative to industrial domesticated alternatives, such as beef and lamb (Cawthorn & Hoffman, 2014), and can help reduce abundant game populations (e.g. Hansen & Beringer, 1997; Kilpatrick, Spohr, & Chasko, 1997; Stedman, Bhandari, Luloff, Diefenbach, & Finley, 2008; S. C. Williams, Denicola, Almendinger, & Maddock, 2013). Beyond economic and ecological benefits, hunting has recreational value (Cordell, Green, & Betz, 2002; Walsh, John, McKean, & Hof, 1992), provides a way for people to connect with nature (Decker, Brown, & Gutiérrez, 1980; Hammitt, McDonald, & Patterson, 1990; Mehmood, Zhang, & Armstrong, 2003; Reis, 2009), and is an integral part of the identity of many participants and communities (Arnett & Southwick, 2015; Chitwood, Peterson, & Deperno, 2011; Marks, 1991; Peterson, Hansen, Peterson, & Peterson, 2010). These benefits of hunting highlight the importance of considering the potential implications of continuing declines in hunter numbers.

Arguably, one of the most important ramifications of declining hunter populations is its threat to the funding mechanism supporting wildlife management in North America. In the U.S., state wildlife agencies have the fiduciary responsibility of managing wildlife resources in the public trust (Geist, 1995; Geist, Mahoney, & Organ, 2001). Historically, the primary mechanism funding wildlife management has been a user-pay system, in which monies are leveraged from consumptive users (i.e. hunters, trappers) to fund state wildlife agency activities (Jacobson,

Organ, Decker, Batcheller, & Carpenter, 2010). Notably, there are other significant sources of funding generated for conservation purposes targeted from local to global scale activities (i.e. by private and non-profit organizations). However, consumptive user-generated funds are the largest contributing source for state-based conservation wildlife (Lueck, 2005; Mahoney, 2009). Hunters generate conservation funds via hunting license sales and permits, in addition to taxes levied under the Federal Aid in Wildlife Restoration Act of 1937 (16 U.S.C. 669-669i; 50 Stat. 917; commonly referred to as the Pittman-Robertson Act), via an excise tax of 11% on firearms, archery equipment, and ammunition, and a 10% tax on handguns. These funds, hereafter PR funds, are then distributed to state agencies via a federal matching program, and are earmarked for wildlife conservation, management, research, and hunter education. The legislation provides funds for game and non-game mammals and birds, while license sale monies can be utilized for any wildlife. Combined, license sales and PR funds sum to over $1.3 billion nationally (Southwick and Associates 2007) and have been estimated to account for approximately 65% of state agency budgets for wildlife (Lueck, 2005; Mahoney, 2009). Reductions in monies levied by these funding mechanisms may limit agency capacity to manage wildlife populations and conserve their habitats.

Concerns regarding the stagnation of hunter numbers are not new (J. R. Miller, 1979; Ryel, 1968), and significant efforts have been extended to better understand hunters and inform management (e.g. Decker & Connelly, 1989; Southwick Associates, 2009). Studies have identified a wide range of factors associated with the decline in hunters, including the presence of competing priorities for an individual's time and money, lack of access to land for hunting, urbanization, changing demographics, and too many regulations (Aiken, 2010; Bissell, Duda, & Young, 1998; Duda, Bissell, & Young, 1995; Gude, Cunningham, Herbert, & Baumeister, 2012;

Karns, Bruskotter, & Gates, 2015; Mehmood et al., 2003; C. Miller & Vaske, 2003; Robison & Ridenour, 2012; Schorr, Lukacs, & Gude, 2014; Winkler & Warnke, 2013). Most of these findings have come from survey-based studies that assess and report patterns in respondents' motivations, values, and preferences. Such surveys are critical for evaluating and garnering support for agency programs. However, predictive capacity of survey results may be limited because hunter survey responses may not match the respondents' actual behavior (Stedman et al., 2004). Studies that have projected hunter populations have generally done so by utilizing national surveys or state license sale data to estimate hunter population parameters, explore the underlying mechanisms driving population dynamics, and then apply their results to forecast the predict the future number of hunters (Bowker, English, & Cordell, 1999; Huck & Winkler, 2008; J. R. Miller & Hay, 1981; Schorr et al., 2014; Walsh et al., 1992; Winkler & Warnke, 2013). While these efforts provide valuable information and guidance regarding which population parameters to target to increase the number of hunters, additional approaches are need to predict the number of hunters under multiple management alternatives that target those population parameters.

Recent efforts to inform game species harvest management have utilized decision analytical methods, and can be extended to evaluate management alternatives available to agencies to influence hunter populations. In fact, hunter management has long been assimilated into game species harvest decisions using decision analysis frameworks (J D Nichols, F A Johnson, & Williams, 1995; B. K. Williams, 2011), and has expanded to include hunter-specific objectives maximizing hunter satisfaction and minimizing management costs (K. F. Robinson et al., 2016, 2017). Applying these methods to explicitly address questions concerning hunter population dynamics and license sale profit within a decision-making framework could provide

86

additional benefits to wildlife managers allocating resources for managing game species and hunter participation. State wildlife managers have made it a priority to improve hunting participation, and have a wide range of alternatives that could be implement to influence hunters, such as special hunts (e.g. youth dove hunts), hunter education programs, changes to license prices, changes to game harvest regulations, and mentor programs (Responsive Management, 2011). In particular, substantial effort and funding has been used on outreach programs aimed at socializing and training new hunters (Ryan & Shaw, 2011). However, because there has been minimal effort to coordinate and evaluate outreach programs (Frampton & Dunfee, 2016; Kirchner & Seng, 2006; Lamprecht & Seng, 2006), there is a lot of uncertainty around management decisions affecting hunter recruitment, retention, and reactivation. This uncertainty further complicates management decisions concerning hunters, and highlights the need for new approaches to assess options affecting the number of hunters and license profit.

To help state wildlife agencies directly address the declining trend in hunter participation and hunter-generated conservation funds, we applied a modelling approach commonly used in wildlife population management to evaluate management actions aimed at increasing license sales, and demonstrate its utility within a decision-making framework to inform state wildlife agency decisions. We used a matrix population model to simulate a population of hunters in which each matrix element represents a population vital rate (e.g. age- or stage-specific reproduction and survival; Boyce, 1992; Morris & Doak, 2002). We then simulated management actions by perturbing the parameters of the matrix (Mills, Doak, & Wisdom, 1999; Wisdom, Mills, & Doak, 2000; Wootton & Bell, 1992). Population models have been used in variety of contexts including species listing decisions (e.g., Possingham et al., 1993), harvest decisions (e.g., Heinsohn et al., 2004; Taylor et al., 2006), reserve design (e.g., Armbruster and Lande,

1993), and population management decisions (e.g., Forys and Humphrey, 1999; Robinson et al., 2013). However, the application of population modeling within a decision-making framework has not been used to evaluate the impact of management actions on a hunter population or license sale profit. Ultimately, hunters are another population that state agencies are trying to manage, and we demonstrate how extending these methods to hunter management decisions can improve the decision-making capacity of state wildlife agencies interested in influencing hunter and hunting license sales.

METHODS

Decision-making framework

Structured decision-making (SDM) is a values-driven decision-making framework that has been used extensively to guide natural resource decisions (Conroy & Peterson, 2013; Gregory et al., 2012; O. J. Robinson, McGowan, & Apodaca, 2016), and can be applied to hunter management. To address the state wildlife agency hunter management concerns, we utilize SDM's 5-step approach for undertaking a management decision: 1) clearly articulate the problem, 2) define the objectives, 3) determine actions available to managers to address the problem and objectives, 4) predict the consequences of the actions (frequently a modeling exercise), and 5) assess tradeoffs and make a decision given the stated objectives (Gregory et al., 2012). For our hypothetical SDM process, our problem is determining how to increase hunting license sales and hunter-generated revenue over time. We focus on state license sales because, for many state wildlife management agencies, hunting license sales are a primary source of revenue and funding for the agency, and these sales provide a direct link between state agency management and hunter-generated conservation funds. License sale data is collected annually and provides a direct measurement of changes in hunter population dynamics. We excluded

88

Pittman Robertson (PR) funds from our analysis due to the fact that PR taxes are levied from all gun and archery equipment sales; which includes many non-hunting gun owners. Further, PR tax collection and distribution remains under federal jurisdiction, precluding any state agency-directed changes to the system. As states may not directly influence PR funds, modeling state license sales provides a direct link between hunters and hunter management, and state wildlife agency budgets.

We assumed that the objectives of a state wildlife agency would be to maximize state license sale profit by maximizing the license sale revenue and minimizing the cost of management. There are certainly other objectives that influence wildlife management agency decision processes, however, for the purpose of demonstrating the utility of SDM and projection modeling we focused solely on agency hunting license profit. We evaluated state-administered outreach programs to demonstrate the capacity of our approach to predict the outcome of different management scenarios on hunting license sales and profit. We chose to model outreach programs because they are a common practice of state agencies, receiving a significant amount of agency funding and attention (Responsive Management, 2011). Given the lack of empirical evaluations of outreach programs, we chose to model hypothetical 1-day outreach programs for youth and adults. While we focused on one set of potential management actions, our approach could easily incorporate other actions state agencies may consider to increase state license sale profit or address their specific objectives. We examined seven management scenarios comprised of different levels of youth and non-license holding adult participation (hereafter adult) in the programs: 1) no outreach programs, 2) 5% of the youth population participating in an outreach program, 3) 7.5% of youth participating, 4) 10% of youth participating, 5) 5% of non-license holding adults participating in an outreach program, 6) 10% of adults participating, and 7) a

combination of 5% youth and 5% adults participating. We applied a cost to the agency of $100 per youth and $50 per adult for outreach programs, assuming that youth individuals require increased safety measures and heightened liability costs. We then developed a simulation model to predict and evaluate the probable effect of each of these management alternatives on a population of hunting license holders and potential license holders.

Hunter population model

We built a 4-stage hunter population model comprised of stages that reflect the license system in the state of Alabama, where an individual can purchase an annual or lifetime hunting license (Figure 4.2). Several states have similar licensing systems, but the stage structures could be modified to fit a variety of licensure systems (Caswell, 2006). We used a stage-based rather than an age-based model to allow individuals to remain in the same stage for multiple time steps omitted gender in our analysis because we wanted to model gender-neutral management alternatives. Youth (*Y*) represent all individuals under the age of 16 who are not required to purchase a hunting license in Alabama. Once a youth reaches the age of 16, they transition into one of the three adult stages. A potential license holder (*P*) is ≥16 years of age and does not own a hunting license at a given time step. Potential license holders can remain within this stage in any subsequent time step or transition to either hunting stage with the purchase of an annual or lifetime license. An annual license holder (*A*) can remain an annual license holder, transition to a lifetime license holder, or revert to a potential license holder. The lifetime license holder stage (*L*) is an absorbing stage, and individuals remain within this stage regardless of whether they hunt in a given year. New youths are produced by the three adult age classes. We constructed the hunter population as a 4 x 4 matrix and multiplied it by our hunter population vector:

$$\begin{bmatrix} S_{YY} & F_P & F_A & F_L \\ S_{YP} & S_{PP} & S_{AP} & 0 \\ S_{YA} & S_{PA} & S_{AA} & 0 \\ S_{YL} & S_{PL} & S_{AL} & S_{LL} \end{bmatrix} \times \begin{bmatrix} Y_t \\ P_t \\ A_t \\ L_t \end{bmatrix} = \begin{bmatrix} Y_{t+1} \\ P_{t+1} \\ A_{t+1} \\ L_{t+1} \end{bmatrix}$$

where Y, P, A, and L represent individuals in each stage at time t, where each time step is one

year. The subscripts on the F terms indicate the life stage for the reproduction rate, while the

subscripts on the S terms, hereafter q, indicate the stage in the current time step followed by the

stage in the successive time step.

The survival and transition terms (S) for each matrix parameter q, each realization i, at

time t, were modeled as a beta distributed random variable with parameters α_i and β_i derived

from the mean survival rate, $\mu_{q,i}$, and variance, $\sigma_{iq,i}$

$$S_{q,i,t} \sim beta(\alpha_{q,i}, \beta_{q,i})$$

where $\alpha_{q,i}$ and $\beta_{q,i}$ are such that $\mu_{q,i} = \alpha_{q,i}/(\alpha_{q,i} + \beta_{q,i})$ and $\sigma_{q,i} = \mu_{q,i}(1 - \mu_{q,i})/(\alpha_{q,i} + \beta_{q,i} + 1)$.

The reproduction terms (F) were modeled as random variables drawn from a uniform

distribution, such that

$$F_{q,i,t} \sim uniform(\gamma_{q,i}, \rho_{q,i}) \,,$$

where $\gamma_{q,i}$ and $\rho_{q,i}$ represent the minimum and maximum fecundity value. Wildlife population

models frequently use a lognormal or stretched beta distribution, however we used a uniform

distribution that allowed us to include some uncertainty in the values without making

assumptions on the shape of the distribution of reproductive value for humans. Future

applications of the model could apply alternative distributions from which to drawn vital rates.

A simplifying assumption of our model is that no senescence occurred in the breeding

capabilities of adults in the population. However, accounting for decreased fecundity with age

would simply require adding additional adult stages to the population matrix, where P, A and L

no longer have an associated fecundity term.

Modeling outreach

We modeled the effect of outreach on our youth assuming elevated transition rates for youth to annual license holder for outreach participants compared to individuals that did not participate in an outreach program. We calculated an average transition rate from youth to annual license holder (S_{YA}), weighted by the proportion of the youth that participated in an outreach programs (P_{YO})

$$S_{YA} = P_{YO}S_{YA}^{O} + (1 - P_{YO})S_{YA}^{N} \ ,$$

where P_{YO} represents the proportion of youth outreach participants as indicated by the particular management scenario (see above), S_{YA}^{O} is the transition rate from youth to annual license holder for outreach participants, S_{YA}^{N} is the transition rate from youth to annual license holder for non-outreach individuals. We assumed that the rate of transition from youth to annual license holder would increase from 0.001 to 0.6 for outreach participants.

The rate of transition from youth to potential license holder, S_{YP}, is modeled as a function of the transition rate of youth to annual license holders subtracting the difference between S_{YA} and S_{YA}^{N} from the transition rate of youth to the potential license holder stage without youth outreach (S_{YP}^{N})

$$S_{YP} = S_{YP}^{N} - (S_{YA} - S_{YA}^{N}) \ ,$$

where S_{YP} is the transition rate of youth to potential license holder adjusting for outreach. We constrained all youth transition probabilities to sum to 1. We set a ceiling on the rate of youths transitioning into the annual license holder class to represent the maximum rate of youths transitioning into the annual license holder class. This reflects the reality that most youth will not turn 16 and require a hunting license in order hunt in a given year ($S_{YY} \approx 0.928$, $S_{YA} \leq 0.06$).

Similarly, we modeled the effect of outreach on potential license holders using a weighted average and then subtracted the difference in rate from the retention of potential license holders

$$S_{PA} = P_{PO}S_{PA}^{O} + (1 - P_{PO})S_{PA}^{N}$$

and

$$S_{PP} = S_{PP}^{N} - (S_{PA} - S_{PA}^{N}),$$

where P_{PO} represents the proportion of potential license holder outreach participants as indicated by the particular management action (see above), S_{PA}^{O} the transition rate from potential to annual license holder for outreach participants, S_{PA}^{N} the transition rate from potential to annual license holder for non-outreach individuals, S_{PP} the survival/retention rate of potential license holders adjusting for outreach. The superscript, when used, indicates whether the rate is for outreach participants, O, or individuals that did not participate in outreach, N. We assumed that the rate for potential license holders transitioning to the annual license holder stage would increase from 0.02 to 0.8 for individuals participating in outreach.

To demonstrate the capacity for our modeling framework to incorporate additional sources of complexity, we modeled the retention of annual license holders ($S_{AA,t}$) as a density dependent function, assuming that hunter abundance is a surrogate for density given relatively constant land area available for hunting each year. This component reflects evidence that crowded hunting areas are undesirable to hunters (Enck, Swift, & Decker, 1993; Hammitt, McDonald, & Noe, 1989; T. A. Heberlein, 2002; Wright & Kaiser, 1986), and thus crowding in one year may lead to fewer hunters in the successive year. We modeled this overcrowding hypothesis such that the retention of annual license holders is influenced by the number of annual license holders in the previous year (A_t):

$$S_{AA,t} = \frac{e^{(1-(zA_{t-1}))}}{1 + e^{(1-(zA_{t-1}))}},$$

where z is a regression parameter; which controls the slope of the density-dependent interaction, with higher values representing a greater slope. We set z to 0.0005, indicating a weak density-dependent interaction.

We parameterized the model using multiple sources (see Appendix 1), then modeled the influence of each management scenario on the population over 10 years with 10,000 iterations. We incorporated temporal variability to represent environmental stochasticity and parametric uncertainty into our model using the 2-step approach outlined by McGowan, Runge, and Larson (2011) in order to demonstrate the capacity of our model to account uncertainty and stochasticity within the framework of a decision analysis. This approach uses a sequential process for drawing annual parameter values where a set of values for each parameter to shape the distribution is randomly drawn for each simulation replicate. We then draw the parameter values for each year's population matrix from the distribution for that replicate (See McGowan et al. for more detail). For every simulation replicate we drew the shape parameters for survival and transition rates from a beta distribution, and variance shape parameters, σ_i, was drawn from an inverse Gaussian distribution with mean, m_q, and shape parameter, λ_q

$$\sigma_{q,i} \sim IG(m_q, \lambda_q).$$

We ran the model using the parallel simulations method outlined by Robinson, Lockwood, Stringham, & Fefferman (2015), which produces identical values for matrix elements across matrices, except where the modeled management action changes the value of an element. This allows for direct comparison of alternatives as the only source of variation in each realization of each scenario is attributed to the management action itself. For our starting population, we assumed a stable stage distribution, calculated from the "do nothing" alternative in order to avoid unusual dynamics for the first several time steps (Caswell, 2006). However,

assuming stable stage distribution results in each stage remaining at the same proportion of the

population under the do nothing stage, and thus does not reflect the observed decline in hunting.

Using the stable age distribution allowed us to see the influence of each management impact on

the age distribution of the population given the change in parameter values resulting from the

different management actions. For each scenario and across all realizations, we estimated the

mean hunter abundance for each year, the cost of management, revenue from license sales, and

profit, expressed as net present value (NPV). NPV is commonly used in economic analyses to

account for the diminished value of profit in the future relative to the present, such NPV = (Total

revenue from license sales - Total cost of management)/$(1+0.05)^t$), where 0.05 represents a 5%

discount rate (Conrad, 2010). Finally, we evaluated each management scenario using the mean

estimated NPV over 10 years.

RESULTS

Our model predicted that the adult outreach program with 10% participation would result

in the greatest NPV over 10 years, with scenarios results ranging from -$252,417 for 10% youth

outreach and $170,040 for 10% adult outreach (Figure 4.3). The number of annual license sales

increased from 465 in year 1 for all scenarios to 2,026 licenses per year for the 10% adult

outreach scenario (Figure 4.4). While the status quo alternative, assuming the stable stage

distribution, predicted that the percentage of the total population holding a hunting license would

remain around 5%, the 10% adult outreach scenario reach an average of 19.7% in year 10. Adult

outreach cost an average of $18,600 per year for 5% of adult non-license holder participation and

$34,600 for 10% participation.

The scenarios simulating youth outreach were predicted to be poorer alternatives than the

status quo given the objectives. While alternatives employing youth participation increased

license sales and revenue, the cost reduced the total NPV for all youth outreach scenarios relative to the "do nothing" scenario, and resulted in a negative NPV under the 7.5% and 10% youth outreach scenarios. The mean revenue generated per year from license sales under the youth outreach-only scenarios ranged from $166,770 with 5% youth participation to $197,890 with 10% youth participation, (Figure 4.5). The mean annual cost of youth outreach was $16,700 for 5% of youth participating in an outreach program, $33,400 for 7.5% youth participation, and $50,000 for 10% youth participation. The combination of adult and youth participation resulted in an average of $352,000 per year in revenue and cost $16,700 per year.

Transition rates into the lifetime license holder stage were low, resulting in total sales that did not differ greatly among alternatives. The total number of new license sales over the time span ranged from an average of 6 new lifetime license holders under the "do nothing" alternative to 11 for the 10% adult participation scenario. Lifetime license holders accounted for ~0.5% of the total population under each scenario. The percentage of lifetime license holders out of all license holders remained around 9.6% of for the "do nothing" alternative and decreased over the 10 years under the other scenarios due to the increase in annual hunting license holders. In year 10, the percentage of total hunters that held a lifetime license decreased to 7.4% under the 5% youth outreach scenario and 2.7% under the 10% adult outreach scenario.

DISCUSSION

We echo our colleagues (e.g. T. Heberlein, 1991; Jacobson & Decker, 2006) in voicing the need to address declines in hunters and hunter-generated conservation funds, and consider their potential to cripple state agency capacity to manage not only game species, but all wildlife. Our efforts explicitly address this issue and provide a way to aid state agencies in improving their ability to manage hunters. We built a stage-based, stochastic model of a hunter population

and demonstrated its capacity within the context of a decision-making framework to evaluate state wildlife agency management actions aimed at increasing hunting license sales. Though our specific management actions and results are hypothetical, our analysis is potentially useful to managers because we demonstrate the value of population modeling and decision analysis applications to managing hunter populations. Our approach is novel in that it extends methods already heavily in use in wildlife management to the management of human resource users. We directly link changes in a hunter population with economic objectives via hunting license sales. It is a strategy commonly employed to inform the management of game and endangered species, which requires explicit consideration of population dynamics alongside financial constraints. Our model is generally applicable and was designed to enable agencies to parameterize it using state license sale data (Gude et al., 2012; Schorr et al., 2014). State agencies can apply the model to predict the number of hunting license sales, license sale revenue, and overall profit (revenue minus the cost of management with a 5% discount rate) resulting from each management scenario while incorporating temporal and parametric uncertainty. Our results highlight the relationship between population dynamics and cost, demonstrating that evaluating the scenarios based on population size (license sales) alone would imply that all the alternatives increased the number of licenses purchased, and thus were superior to the status quo scenario. However, once the cost of the management alternative was accounted for, the alternatives with youth outreach program resulted in a financial loss to the agency. Thus, any method for informing hunter management necessitates addressing the social and economic aspects of the decision or risks leading to a suboptimal decision. SDM along with predictive modeling enables decision makers to articulate multiple objectives and subsequently evaluate management alternatives with respect to the objectives.

The results of our simulation illustrate the ability of our modeling framework to explore and elucidate complex interactions between management actions, hunters, and objectives. In our example, the results highlight important differences between adult and youth outreach with regards to agency objectives. Youth outreach alternatives were inferior due to the lag time between a youth's participation in a hunter program and the age at which they are required to purchase a hunting license, and the assumed high cost of youth outreach relative to adult outreach. The results also demonstrated the insensitivity of management scenarios on lifetime license holders relative to annual license holders. We learned that because the transition rates for entering the lifetime license holder stage were so low, these license sales resulted in little profit, regardless of the scenario. These results also demonstrate, that while our population parameters were empirically grounded, research is needed to better estimate the cost of management alternatives and their subsequent changes to hunter demographic rates. Such information will benefit wildlife agencies interested in applying the model to their own hunter populations by improving scenario predictions and general understanding of hunter dynamics in their respective states.

The efficacy of our approach will largely rely on the ability of state agencies to clearly define objectives, and we demonstrate how this can be achieved within the structured decision-making framework. The process requires stakeholder participation, a clearly defined problem statement, and fundamental objectives, and uses those objectives to generate potential management actions. Alternatively, an action-focused decision process can reduce the scope of potential alternatives and potentially lead to a suboptimal decision or a decision that does not address the true issue or objectives (Hammond, Keeney, & Raiffa, 1999). The problem and objectives drive the development of the suite of alternatives, and subsequently, the modeling

effort (or other mechanism) for evaluating the alternatives. In our case, we clearly defined the management objective as maximizing license sale profit. This served our problem statement by directly addressing state agency funding concerns. Any changes to the problem statement and/or objectives could have led to a very different suite of management actions and model for evaluating the actions. For example, if one of our objectives had been to include some level of youth hunter outreach (as mandated by many state natural resource agencies), we would have eliminated the adult-only alternatives and included additional youth outreach alternatives. Thus, while our population model is broadly applicable, we anticipate it will be advantageous for state agencies to undergo their own decision-making process to identify their unique objectives and develop their own suite of alternatives.

The potential applications and extensions of our modeling framework are vast. Additional stages could be added to our population matrix to more accurately describe hunters, such as stages representing sex (Gude et al., 2012; T. A. Heberlein, Serup, & Ericsson, 2008; Metcalf, Graefe, Trauntvein, & Burns, 2015), age or birth cohort (Gude et al., 2012; Schorr et al., 2014; Winkler & Warnke, 2013), or hunter typology (Andersen, Wam, Mysterud, & Kaltenborn, 2014; Kellert & others, 1978; Schroeder, Fulton, & Lawrence, 2006; Ward, Stedman, Luloff, Shortle, & Finley, 2008). Another possible extension could be to explore the influence of game management on hunter dynamics by linking a game population (e.g. deer, turkey) model to our hunter population model. This would facilitate further questions on the influence of prey density and hunting success rates on hunter population dynamics (e.g. Riley et al., 2003). The addition of stages or a game species population model would require the estimation of a greater number of parameters, but would expand the suite of management actions that could be evaluated to influence hunters. We also believe that our framework could easily be extended to anglers or

other natural resource users. Anglers in particular, being consumptive users of natural resources and purchasers of licenses, pose similar issues with regards to management and value to conservation (Quintana, 2015).

An important limitation of our model and approach is the lack of data available to link potential hunter management actions to hunter dynamics. Human dimension surveys of hunters are common, but are typically descriptive and may provide biased estimates of the impact of alternative system states on respondent behavior (Stedman et al., 2004). Still, we anticipate that adding in questions to address functional relationships between management actions and hunter population dynamics can improve predictive models used to evaluate multiple management actions. Models like the one we presented here, with hypothesized relationships and components, can also help to identify research needs. This can in turn help researchers frame survey questions to empirically estimate relationships and reduce uncertainties that were identified as key impediments to decision making. Alternately, increasing our understanding of hunter population dynamics and structural uncertainty in our model could be addressed within a Bayesian framework in which multiple hypotheses, represented by different models, could be evaluated over time to determine the relative support for each hypothesis given empirical evidence. Such an approach could be employed within an adaptive management framework, in which explicit and iterative evaluation of management actions and post-decision data are used to inform subsequent decisions (B. K. Williams, 2011). Hunter management is an excellent candidate for adaptive management: population data are collected annually that can be used to reduce model uncertainty, and there are inherent iterative management decisions affecting the hunter population. Thus, although we have identified key areas lacking data, there are many accessible ways to reduce uncertainty.

Ultimately, we hope that our modeling framework will help managers make better decisions concerning hunters, hunter-generated conservation dollars, and other consumptive natural resource users. We provide a tool to help address the question "is the current user-pay model of wildlife conservation sustainable?" The answer may in fact be that it is not. State agency actions may be insufficient to counter some of the factors driving trends in hunter participation (e.g. increases in urbanization and virtual entertainment; (Robison & Ridenour, 2012)), and consequently do little to bolster agency budgets. It is also important to note that wildlife populations can be over-harvested, and thus it may be ill-advised to endeavor to convert a majority of the total population into hunters. We further acknowledge the fact that our model does not address the question of whether or not the current consumptive user-pay system is reasonable given the small proportion of the total population that pays for state conservation relative to non-consumptive users. Mechanisms to garner financial support from other resource user groups, such as hikers and wildlife viewers, are lacking (Anderson & Loomis, 2006; Hamilton, 1992; Jacobson & Decker, 2006), despite the fact that these non-consumptive users far outnumber hunters and anglers (*National Survey of Fishing, Hunting, and Wildlife-Associated Recreation*, 2011). The skewed balance may cause repercussions when state agencies allocate funds supporting recreational activities (Nie, 2004). Regardless of these larger concerns, our approach can help state agencies address their budgetary concerns and capacity to continue managing wildlife resources.

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FIGURES

Figure 4.1: a) Declining U.S. hunting license holders, and b) declining percentage of U.S. population possessing a hunting license. Data source: U.S. Census Bureau and U.S. Fish and Wildlife Service.
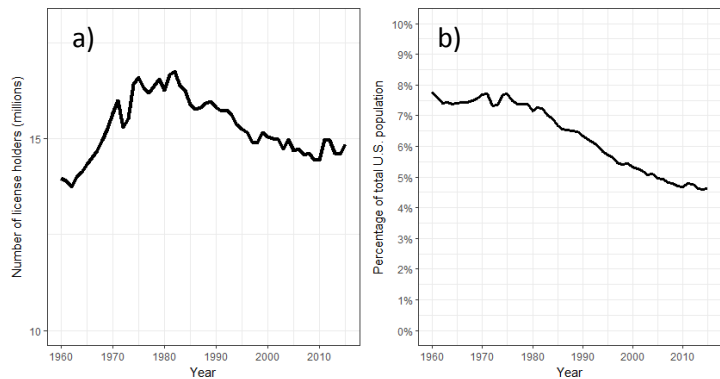

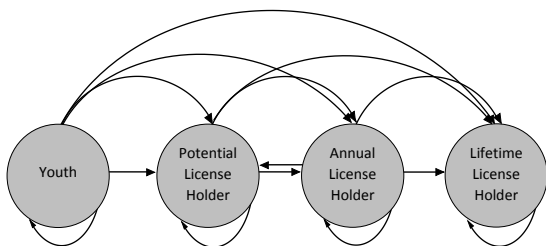Figure 4.2: Conceptual diagram of state hunting license holders.

Figure 4.3 Predicted mean net present value (NPV) generated by each management scenario over 10 years and 10,000 model realizations. The management actions were simulated using a 4-stage matrix population model with youth, potential hunting license holder, annual license holder, and lifetime license holder stages. Management scenarios consisted of a "do nothing" alternative, and varying levels of youth and adult outreach. Adult outreach was targeted at individuals in the potential license holder stage. Net present value represents license sale profit, taking into account a 5% discount rate over time, t, such that NPV = (Total revenue from license sales - Total cost of management)/$(1+0.05)^t$.
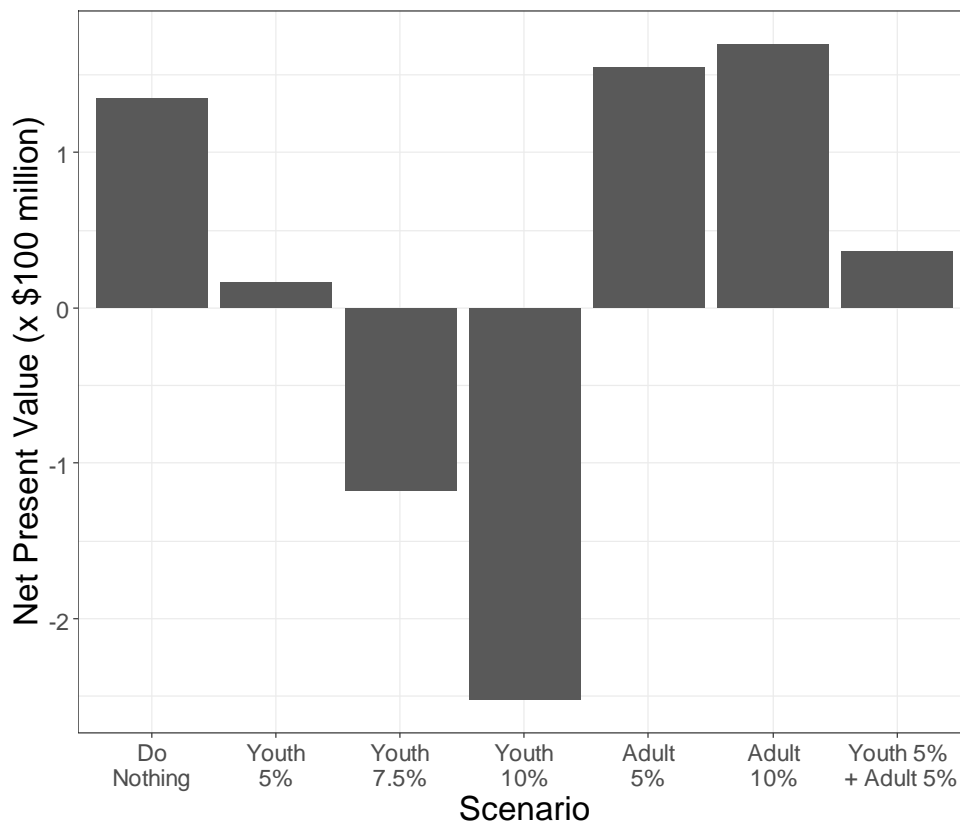
Figure 4.4: Predicted mean revenue generated by each management scenario over 10 years and 10,000 model realizations. The management actions were simulated using a 4-stage matrix population model with youth, potential hunting license holder, annual license holder, and lifetime license holder stages. Management scenarios consisted of a "do nothing" alternative, and varying levels of youth and adult outreach. Adult outreach was targeted at individuals in the potential license holder stage. Revenue is calculated as sum of lifetime and annual license sales.
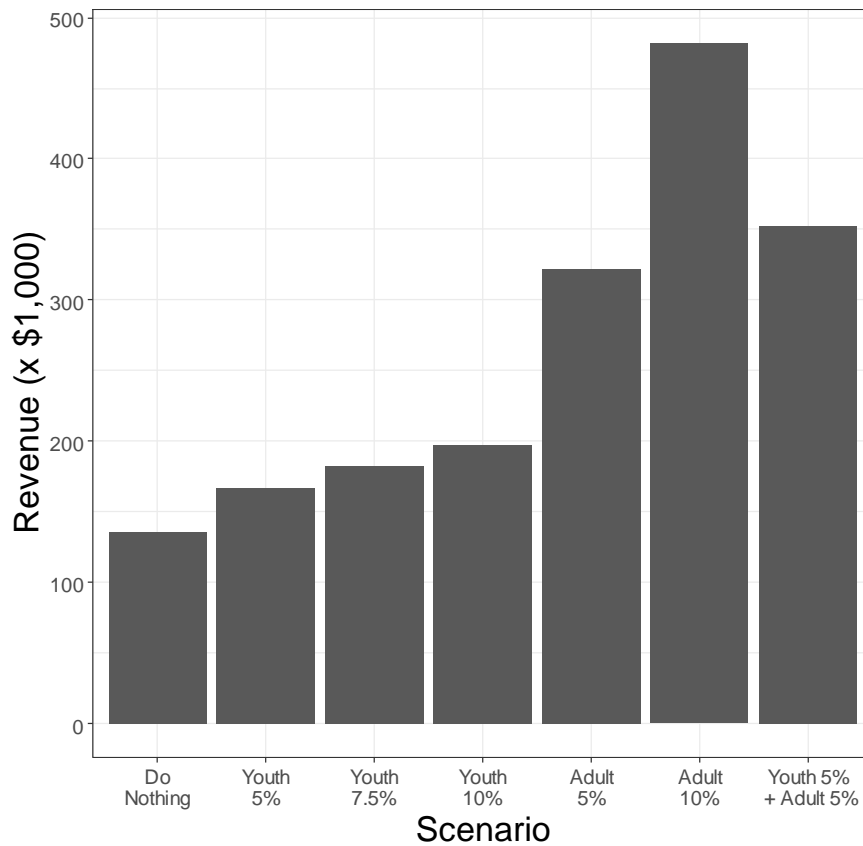
Figure 4.5: Predicted mean number of annual license sales for each management scenario and each year across 10,000 model realizations. The management actions were simulated using a 4-stage matrix population model with youth, potential hunting license holder, annual license holder, and lifetime license holder stages. Management scenarios consisted of a "do nothing" alternative, and varying levels of youth and adult outreach. Adult outreach was targeted at individuals in the potential license holder stage.
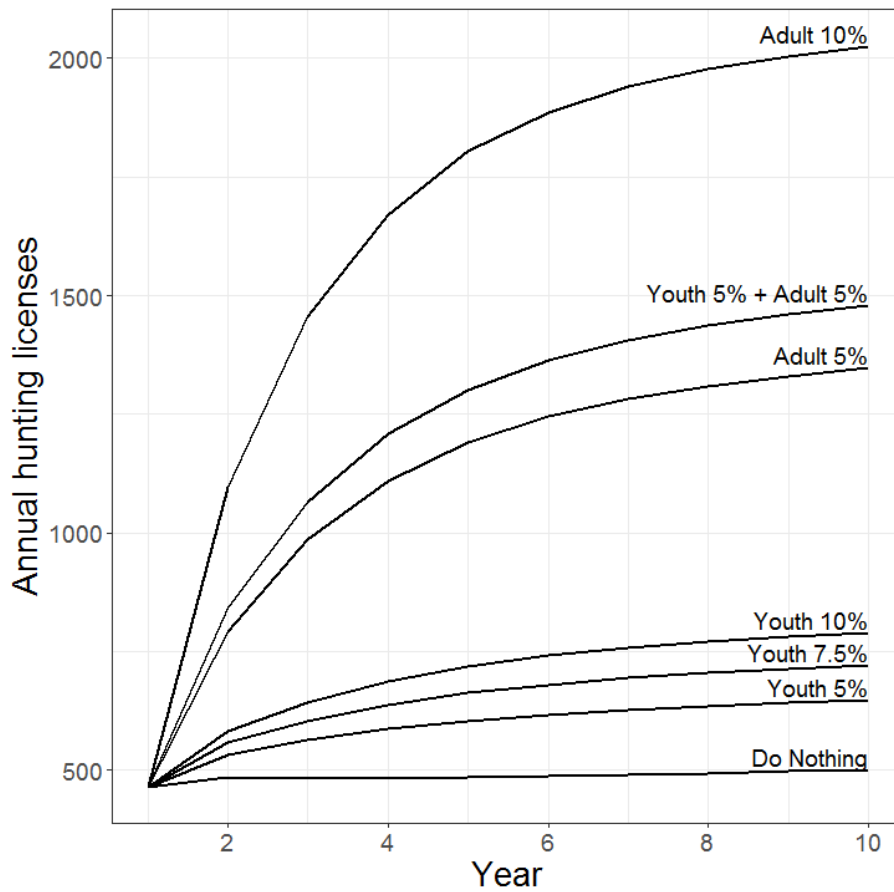
APPENDIX

Appendix 4.1. Mean value of matrix elements were obtained from: a) National Center for Health
Statistics, Center for Disease Control and Prevention, b) KIDS Count Data Center, National
KIDS Count, c) National Shooting Sport Foundation d) Expert opinion and/or assumed given
other transition rates, e) approximated using license sale data from Alabama Department of
Conservation and Natural Resources, f) estimated using other parameter values and assuming
adult mortality given data from a). We assumed values for mean variance and the beta
distribution shape parameters to incorporate parametric uncertainty into the population
simulations.

Hunter Population Simulation Parameters		
Fecundity[a]		
$\gamma_{P,i}$	Minimum fecundity rate of potential license holders	0.01
$\rho_{P,i}$	Maximum fecundity rate of potential license holders	0.02
$\gamma_{A,i}$	Minimum fecundity rate of annual license holders	0.01
$\rho_{A,i}$	Maximum fecundity rate of annual license holders	0.02
$\gamma_{L,i}$	Minimum fecundity rate of lifetime license holders	0.01
$\rho_{L,i}$	Maximum fecundity rate of lifetime license holders	0.02
Youth survival[a]		
$\mu_{YY,i}$	Youth survival	0.92877
$\sigma_{YY,i}$	Variance of $\mu_{YY,i}$	0.0001
m_{YY}	Variance distribution parameter m	0.0001
λ_{YY}	Variance distribution parameter λ	0.00001

Potential license holder survival[b]

$\mu_{PP,i}$	Survival of potential license holders	0.972
$\sigma_{PP,i}$	Variance of $\mu_{PP,i}$	0.001
m_{PP}	Variance distribution parameter m	0.001
λ_{PP}	Variance distribution parameter λ	0.0001

Annual license holder survival[c]

$\mu_{AA,i}$	Survival annual license holders	0.68
$\sigma_{AA,i}$	Variance of $\mu_{AA,i}$	0.01
m_{AA}	Variance distribution parameter m	0.001
λ_{AA}	Variance distribution parameter λ	0.0001

Lifetime license holder survival[a]

$\mu_{LL,i}$	Survival of lifetime license hunters	0.99
$\sigma_{LL,i}$	Variance of $\mu_{LL,i}$	0.0005
m_{LL}	Variance distribution parameter m	0.0001
λ_{LL}	Variance distribution parameter λ	0.00001

Transition from youth to potential license holder[d]

$\mu_{YP,i}$	Transition rate from youth to potential	0.07
$\sigma_{YP,i}$	Variance of $\mu_{YP,i}$	0.0005
m_{YP}	Variance distribution parameter m	0.0001

λ_{YP}	Variance distribution parameter λ	0.00001

Transition from youth to annual license holder[d]

$\mu_{YA,i}$	Transition from youth to annual	0.001
S_{YA}^{O}	Transition from youth to annual for outreach participants	0.6
$\sigma_{YA,i}$	Variance of $\mu_{YA,i}$	0.0001
m_{YA}	Variance distribution parameter m	0.0001
λ_{YA}	Variance distribution parameter λ	0.00004

Transition from youth to lifetime license holder[d]

$\mu_{YL,i}$	Transition from youth to lifetime	0.00001
$\sigma_{YL,i}$	Variance of $\mu_{YL,i}$	0.000005
m_{YL}	Variance distribution parameter m	0.00001
λ_{YL}	Variance distribution parameter λ	0.000001

Transition from potential to annual license holder[e]

$\mu_{PA,i}$	Transition from potential to annual	0.02
S_{PA}^{O}	Transition from potential to annual for outreach participants	0.8
$\sigma_{PA,i}$	Variance of $\mu_{PA,i}$	0.01
m_{PA}	Variance distribution parameter m	0.001
λ_{PA}	Variance distribution parameter λ	0.0001

Transition from potential to lifetime license holder[e]

$\mu_{PL,i}$	Transition from potential to lifetime	0.00002
$\sigma_{PL,i}$	Variance of $\mu_{PL,i}$	0.00001
m_{PL}	Variance distribution parameter m	0.00001
λ_{PL}	Variance distribution parameter λ	0.000001

Transition from annual to potential license holder

$\mu_{AP,i}$	Transition rate from annual to potential	0.3115
$\sigma_{AP,i}$	Variance of $\mu_{AP,i}$	0.01
m_{AP}	Variance distribution parameter m	0.001
λ_{AP}	Variance distribution parameter λ	0.0001

Transition from annual to lifetime license holder

$\mu_{AL,i}$	Transition from annual to lifetime	0.0005
$\sigma_{AL,i}$	Variance of $\mu_{AL,i}$	0.00001
m_{AL}	Variance distribution parameter m	0.00001
λ_{AL}	Variance distribution parameter λ	0.000001

Density dependent survival of annual license holders

z	Density dependence parameter	0.0005