

NORTHERN BOBWHITE DENSITY ESTIMATION: APPLICATIONS OF NOVEL
METHODS AND ANALYSES

by

NATHAN GARRET WILHITE

(Under the Direction of James Alan Martin)

ABSTRACT

Population monitoring is a valuable facet of managing sustainable Northern Bobwhite populations. I built upon current survey methodologies by incorporating novel technology and analyses to bolster Northern Bobwhite monitoring capabilities. I field-tested a commercially-available acoustic recording device to record play-back bobwhite covey calls. I detected 47.5% of projected covey calls from 0-400 m with the furthest detection being 241 m. I evaluated an automated recognition software which only successfully detected 31.5% of manually-identified covey calls. Additionally, I applied spatial capture-recapture density estimation methods to bobwhite conservation. I estimated densities with and without supplemental telemetry data and produced relative standard errors of 13.8% and 13.4%, respectively. Top combined capture history models produced density estimates of 0.25 birds/ha (95% CL = 0.18, 0.36) across the study site. These results lay the foundation for further expansion of Northern Bobwhite population monitoring procedures through passive acoustics and intensive spatial capture-recapture trapping.

INDEX WORDS: acoustics, acoustic recording devices, density estimation, Northern Bobwhite, spatial capture-recapture

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CHAPTER 1

INTRODUCTION

Understanding the status and trends of wildlife populations is important on local, landscape, and sometimes global scales. The International Union for Conservation of Nature (2012) issues globally-recognized wildlife conservation statuses, and considers population size to be a key factor in identifying conservation priorities. On a more local level, landowners and cooperatives may have simplified goals such as achieving target white-tailed deer (*Odocoileus virginianus*) buck to doe ratios or desirable Northern Bobwhite (*Colinus virginianus*) densities. Regardless of scale, the ability to assess and quantify population size of target species is of utmost importance.

Methods for abundance estimation can vary drastically between different taxonomic groups. Visual observation or physical capture techniques are common methodologies applied to a wide variety of taxa from large mammals, to reptiles, rodents, waterfowl, and many others (Lefebvre et al. 1982, Nomani et al. 2008, Hooker et al. 2015, Zimmerman et al. 2015). For many species, physical mark-recapture of a population is not convenient or financially feasible. Life history traits such as crepuscular or nocturnal movement, secretive activity patterns, and habitat selection can make detecting or trapping individuals very difficult (Marques et al. 2013). Species that vocalize provide an alternative avenue for detection and monitoring.

The most common forms of avian population surveys are some variation of a point or line transect (Gregory et al. 2004). Observers proceed along defined paths or to specified locations and document relevant information: species heard or seen, number of individuals detected, time of detection, distance to detected individuals, etc. As with any survey, there are numerous

limitations and sources of uncertainty. Oftentimes, the greatest source of error in point count data is due to observer abilities, bias, and experience (Simons et al. 2007). Alldredge et al. (2007) used speaker-projected calls, and documented significant observer error in signal localization and distance estimation. Despite differences in training background, Alldredge et al. (2007) documented substantial error in distance estimation with both trained and untrained observers. Additionally, ambient noise, such as birds calling in the background or breezy conditions can produce sizable discrepancies in detection and estimated distances to vocalizing individuals (Simons et al. 2007). Error estimates from studies on detection probability of bird vocalizations are likely conservative due to lack of temporal and spatial replication, variations in species' calls, use of standardized song directionality and volume, and other key factors (Hansen and Guthrey 2001, Alldredge et al. 2007). There are numerous ways to address individual aspects of uncertainty in aural surveys, and advancements in acoustic recording technology grant these opportunities to biologists and managers.

As technology continues to progress, many standard operating procedures in the wildlife profession will be altered in an attempt to increase accuracy and precision in abundance estimation. One area in which this potential exists is in passive acoustics technology utilizing acoustic recording devices (henceforth ARDs). These are programmable recording units that are designed to be deployed for extended periods of time to survey species or areas of interest. The use of ARDs to identify wildlife vocalizations and estimate species abundances is a developing field with a recent influx in projects studying birds (Dawson and Efford 2009, Cragg et al. 2015), anurans (Stevenson et al. 2015, Brauer et al. 2016, Measey et al. 2016), cetaceans (Martin et al. 2013), and a host of other wildlife taxa. These devices may assist or substitute for standard auditory surveys by allowing areas to be observed repeatedly, providing permanently stored

records that allow multiple analyses, and minimizing observer error (Dawson and Efford 2009, Venier et al. 2012, Marques et al. 2013).

The fusion of acoustic recording technology and avian monitoring may be the next step to better managing bird populations. Abundance estimation using ARDs has not yet been applied to a gamebird species. Fall covey call surveys have been a common method of choice for bobwhite population monitoring throughout their range. Generally, covey call surveys are conducted by a combination of inexperienced and experienced observers, often lack spatial and temporal replication, and assume observers can localize calling coveys up to 500 meters away (Wellendorf and Palmer 2005) or more (DeMaso et al. 1992). These concerns paired with ubiquitous environmental factors such as cloud cover, wind speed, and background noise that affect survey estimates (Wellendorf et al. 2004) bolster the argument to standardize as much of the survey process as possible. I investigated ARDs as tools to monitor bobwhite populations by testing the efficacy of the Wildlife Acoustics Song Meter 3 to detect bobwhite covey calls. Future research could aim to develop acoustic sampling protocols using ARDs that can either substitute or complement current survey methods.

Developments and modifications to population surveys require consistent evaluation of the precision and accuracy of the estimates produced. Generally, for most wildlife taxa, there is not a consensus standardized means for evaluating the numerous methods of abundance estimation. This holds true in bobwhite abundance estimation as well. As efforts to implement novel technologies for bobwhite population monitoring are underway, proper assessment of these innovative techniques is paramount. Spatial capture-recapture analyses offer a potential avenue for developing a universal, standardized density estimation approach for evaluating current and future wildlife population monitoring techniques.

Spatial capture-recapture, also known as SCR, is a modification to capture-mark-recapture (CMR) methods that model detection as a function of a baseline capture probability that declines with distance from a trap or detector (Efford 2004, Borchers and Efford 2008). Incorporating the spatial arrangements of detections and implicit non-detections of individuals in a population, allows SCR methods to estimate density through a spatial point process and draw inferences about the effective sampling area (Borchers and Efford 2008, Royle et al. 2013). Bobwhite present an opportunity to apply SCR methods to an upland gamebird in hopes of providing more robust estimates of density for a prized game species.

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CHAPTER 2

EVALUATION OF ACOUSTIC RECORDING DEVICES TO SURVEY NORTHERN BOBWHITE POPULATIONS

Population monitoring and density estimation are central aims in ecology and conservation. Advances in statistical modelling have greatly improved our ability to monitor population trends and to more accurately and precisely estimate spatial and temporal variation in population density (e.g., Royle et al. 2013). The development of these statistical methods has been spurred on by technological advances in non-invasive wildlife monitoring techniques. For example, acoustic recording devices (ARDs) have provided opportunities to improve avian research and monitoring (Hobson et al. 2002, Acevedo and Villanueva-Rivera 2006, Venier et al. 2012, Holmes et al. 2014, Cragg et al. 2015). This technology has been used to identify trends in avian population declines, understand community assemblages along environmental gradients, produce reliable evaluations of species richness, and serve as phenological indicators of birds arriving to breeding grounds (Celis-Murillo et al. 2009, Furnas and Callas 2015, Buxton et al. 2016, Leach et al. 2016). Spatial capture-recapture models have recently been extended to estimate spatial variation in density from acoustic detections (Dawson and Efford 2009, Royle 2018). However, prior to designing and implementing an acoustic monitoring program, it is important to consider several key factors, such as effective survey radius, the effects of background noise on detection probability, and the influence of distance, landscape structure, and background noise on signal strength decay of target vocalizations (Yip et al. 2017, Royle 2018). Furthermore, the amount of

recorded data generated from acoustic surveys could be a constraint unless software is evaluated and proven capable of processing these data.

Determining the size of the sampling area is fundamental to estimating density. Several studies have determined the effective survey area of an ARD by comparing detection probability across distance bins (Venier et al. 2012, Stiffler et al. 2018). In another study, Colbert et al. (2015) demonstrated that playback gobblers of wild turkey (*Meleagris gallopavo*) could be detected at a maximum of 207 meters using an ARD. Understanding the amount of area being surveyed offers direct insight into local densities and provides further information for future survey designs (Dawson and Efford 2009). Several factors may impact acoustic survey area including background noise levels and how rapidly calls of interest attenuate based on landscape features (e.g., dense forest vs. open pasture) and distance between a calling individual and ARDs. Furnas and Callas (2015) estimated the survey radius to be the distance at which call power of a bird species attenuates below the average background noise level. Background noise (e.g., wind, rain, non-target species vocalizations, and anthropogenic noise) has been shown to negatively affect avian species detections during point count surveys as well as ARD surveys (Simons et al. 2007, Rempel et al. 2013). Individual call types (encounter calls, flight calls, assembly calls, warning calls, etc.) within species may vary in detectability as well (Cragg et al. 2015). Detection probability has also been shown to decline with distance and to be affected by the habitat types between the receiver and the source of sound (Selby et al. 2016). Therefore, proper evaluation of sampling area should consider the effects of distance, background noise, and landscape structure on attenuation of target species vocalizations.

One benefit of ARD data collection is the ability to passively record large volumes of data that can be subsequently reviewed. A potential disadvantage lies in the time-consuming

processing and formatting of these data, prior to statistical analysis. Several studies have explored analyzing various proportions of large volume recordings with mixed results (Venier et al. 2012, Wimmer et al. 2013). There are numerous software programs designed to automatically process sound recordings by developing recognizers of target species vocalizations (Knight et al. 2017). However, the efficacy of automatic recognizers is dependent on the species of interest and specific project goals. Studies seeking to identify presence/absence or occupancy may not need to detect every call (Goyette et al. 2011), whereas surveys for rare species or density estimation may require higher detection rates (Swiston and Mennill 2009). Efficacy of automatic recognizers should be evaluated on a species by species basis, with consideration for the research objectives.

We evaluated the efficacy of ARDs for detecting northern bobwhite (*Colinus virginianus*) covey calls and offer a proof-of-concept that can be used for designing acoustic monitoring programs. Bobwhite represent a species of concern because of cultural interests as a game species and their associated range-wide population declines (Hernández et al. 2013). Assessing local bobwhite densities often provides insight into effects of habitat management and hunting harvest. Should ARDs prove to be useful tools in detecting fall covey calls, further methodologies could be developed to estimate fall densities. We estimated the effective sampling radius for a commonly used ARD by projecting a recording of a bobwhite covey call at various distances from the ARD. We developed an automatic recognizer and evaluated its performance on known detections from manually analyzed recordings of projected covey calls. Additionally, we sought to assess the attenuation of projected bobwhite covey calls in relation to distance, landscape structure, and background noise levels in the recordings. This study provides the foundation for assessing bobwhite densities using acoustic recording devices.

STUDY AREA

Our research took place at Di-Lane Plantation Wildlife Management Area located in the Southeastern Plains eco-region in Burke County, Georgia (Griffith et al. 2001). Di-Lane is a 3,280-ha property owned by the United States Army Corps of Engineers and managed by the Georgia Department of Natural Resources. Bobwhite is the priority species for management, but other species are managed, including wild turkey, white-tailed deer (*Odocoileus virginianus*), and mourning dove (*Zenaida macrura*). Managers use prescribed fire, herbicide application, timber management, mowing and discing, supplemental feeding, and meso-mammal trapping to meet site-specific objectives for bobwhite density and hunter satisfaction. Approximately 2000 ha constituted bobwhite habitat; with a large proportion of this area receiving a heavy timber thinning from the summer of 2017 to the spring of 2018. Pine savannas consisted primarily of longleaf (*Pinus palustris*) and loblolly pine (*Pinus taeda*). The old field grass and forb component consisted primarily of splitbeard bluestem (*Andropogon ternarius*), broomsedge bluestem (*Andropogon virginicus*), common ragweed (*Ambrosia artemisifolia*), camphorweed (*Heterotheca subaxillaris*), *Rubus* spp., and showy partridge pea (*Chamaecrista fasciculata*). The predominate woody species in the old fields and hedgerows was Chickasaw plum (*Prunus angustifolia*) and bicolor lespedeza (*Lespedeza bicolor*). Average annual rainfall for the area was 121.6 cm (National Climate Data Center, National Oceanic and Atmospheric Administration).

METHODS

Acoustic Recording Device and Projection Speakers

We used the Song Meter SM3; a weatherproof, dual-channel acoustic recording device produced by Wildlife Acoustics Inc. (Massachusetts, U.S.A.) for all sound recordings. The SM3 units were programmed using default factory settings for all auditory factors in the SM3 Configurator

software developed by Wildlife Acoustics. Customized schedules for timing of recordings were the only adjustments made in any of the settings. All recordings from these devices are saved in a .WAV format onto a Secure Digital (SD) card that must be inserted into the device. For deployment, we drove 1.5-meter light duty fence posts several inches into the ground and attached SM3 units using zip-ties and a 2-cm resettable combination padlock.

In order to simulate covey calls, we collaborated with the University of Georgia Instrument Shop to build customized artificial bobwhite playback devices. These devices required a single-board Raspberry Pi computer to initiate playback through an amplifier and subsequently through a 2-way Yamaha outdoor speaker (NS-AW150). All units were powered by two 12-volt, 8 amp-hour, sealed lead-acid batteries with F1 terminals. We uploaded a recording of a bobwhite covey, recorded at a distance of 2-meters, to the Raspberry Pi boards and programmed them to run 1 minute after battery connection occurred. We calibrated the projected covey call at a signal strength of 80 decibels at 2 meters from the speaker based on the average signal strength of a wild calling covey (J. A. Martin, University of Georgia, unpublished data).

Field-Testing

We tested SM3 detection-distance capabilities by projecting covey calls from speakers at random locations. We chose an area of the property that contained vegetation types that were representative of the landscape; old field, hedgerows, pine savannas, and agriculture. The SM3 was stationed at a single location and programmed to record for the duration of the field-testing.

We projected bobwhite covey calls from 0 to 400 meters, using 50-meter bins to establish an understanding of detection distance. We assigned 5 random azimuths and 5 associated random distances to each 50-meter bin. In total, we projected a bobwhite covey call sequence from 40

locations within a 400-meter radius of an SM3 (Figure 1). Additionally, we replicated the same covey call sequence at 10 locations from 150 to 250 meters. We considered this the likely range for drop-offs in detection of covey calls with the SM3 unit.

Sound Analysis

Initially, recordings from field-testing were manually reviewed. Examination of the field-testing data was done in Kaleidoscope Pro Analysis software (Wildlife Acoustics Inc., Massachusetts, USA). Kaleidoscope provides a spectrogram of input recordings as well as a waveform plot of log-linear power. The time in the recording for every projected location was observed multiple times to determine if the covey call sequence could be heard. A covey call was noted as ‘detected’ if any part of the sequence was capable of being seen on the spectrogram plot or audibly heard.

We then used Kaleidoscope Pro software to develop an advanced classifier using “Cluster Analysis In Depth” tutorials provided by Wildlife Acoustics. Training data for these classifiers consisted of recordings ($n = 22$) captured across multiple field sites across parts of the bobwhite historical range. These recordings provided variation in bobwhite covey calls and types of background noise; key factors to building a robust classifier (Wildlife Acoustics 2018). Kaleidoscope advanced classifier analysis operates by searching through specified sound parameters (frequency range, duration, etc.) and sorting individual call syllables into similar groups called clusters. Reviewers are then required to sift through the clusters and train Kaleidoscope by providing manual identification for aural cues of interest. Clusters with large amounts of target vocalizations may also provide reviewers the opportunity to manually identify false positives that have been misclassified within the clusters of interest. Once the manual identification is complete, the input recordings are used to re-train the classifier. This process is

repeated by continually identifying sounds until a desired percentage of recognized target vocalizations is achieved. We initially trained our classifier with 16 one-hour long recordings containing thousands of bobwhite “koi-lee” calls manually identified for training purposes. We retrained the classifier 7 times to maximize the sensitivity of the classifier. We added 6 additional recordings from a new geographical location to build a more robust, flexible classifier. The addition of the 6 complementary recordings from another field site resulted in an error message from the program and failure to incorporate them into the classifier. Because of this, we only used the advanced classifier from the original 16 hours of recordings. Our advanced classifier was then tested against the manual detection analysis in Kaleidoscope for the field-testing recordings.

We measured signal strength and background noise with Raven Pro Interactive Sound Analysis Software (The Cornell Lab of Ornithology, Ithaca, NY, U.S.A.). Raven Pro allows for collection of noise components using a standardized area of sound analysis in a spectrogram (Figure 2). This standardized method for manually collecting noise data is not available in Kaleidoscope Pro. Reviewers are able to draw customized sampling spaces by inputting desired time durations and frequency ranges. Within these sampling spaces, reviewers can then select sound characteristics of interest, which are measured automatically by Raven Pro. We programmed Raven Pro to collect: low frequency (Hz), high frequency (Hz), average power (dB), and maximum power (dB) for every sample taken from the spectrogram. Our noise analysis methods followed Dawson and Efford’s (2009) protocols for measuring sound bursts and background noise levels. We used maximum power as our standardized measure of noise. Our sampling frame consisted of 0.1 second duration by a 200 Hz area (Figure 2). This timeframe and area allowed consistent measurement of individual “koi-lee” calls in a covey call

sequence. Every visible covey call, from field-testing recordings, was sampled by placing a sampling frame in the brightest region of the spectrogram. For every noted call measured, we sampled the identical frequency range of the corresponding call within an offset of 0.5 seconds. This second sample was outside of the signature of the “koi-lee” call, and provided a level of background noise for future statistical analyses. Once the recordings were analyzed, Raven Pro produced a text file of the signal parameters mentioned previously and the time of occurrence for each call signature.

We conducted all data analyses in R version 3.5.1 (R Core Team 2018). We fitted one generalized linear model with a logit link to model the effect of background noise on detection. We fitted a second linear regression model with a normal error term to model the effect of distance on bobwhite covey call power. Furthermore, we used the R package “Distance” (Thomas et al. 2010) to format distance sampling data and model a half-normal detection function for the field-testing data. This provided an estimate of sigma, the decline in detection probability with distance, for the detection curve. We also tested for an influence of landscape structure on sound attenuation and detection probability. To do so, we used the known source sound attenuation model from Royle (2018) to relax the assumption that signal strength (i.e., call power) is a function of Euclidean distance. Rather, we modelled signal strength as a function of cost-weighted distance, which depends on the spatial distribution of habitat features between the source of sound and the sensor. Specifically, we used the least cost path (i.e., the path that has the minimum cost-weighted distance of all possible paths between the source and sensor) as our distance metric (Adriaensen et al. 2003). We used a normalized difference vegetative index (NDVI) produced in Google Earth to represent landscape structure. Values closer to 1 likely

indicate denser vegetation that should impede sound and result in a more rapid sound attenuation (Gorelick et al. 2017).

RESULTS

We were able to manually detect the projected covey call sequence from 19 out of 40 locations (47.5%). A large proportion of detections were heard as well as seen on the spectrogram (84%). Detection was aided by the observer's ability to view spectrograms, and filter out background noise by selecting frequency ranges of interest. The farthest manual detection of a projected call was 241 meters, which was solely identified by aural detection. The Kaleidoscope advanced classifier cluster analysis did not prove to be a reliable solution to automate the analysis of sound recordings as it only successfully identified 6 out of the 19 (31.5%) manual detections from field-testing.

There was no significant effect of landscape structure on sound attenuation (sound attenuation coefficient = -1.38×10^{-5} ; 95% CL = -0.11, 0.11), as illustrated by an example least-cost path deviating very little from a straight line (Figure 3). Therefore, we present results from our model with detection probability and signal strength varying as a function of Euclidean distance. The sigma estimate for the detection curve was 96.23 meters (95% CL = 75.27, 123.02). Probability of detection for the half-normal model declined steadily beyond 50 meters from the ARD. Our results indicated that probability of detection at 200 meters and beyond is less than 20% (Figure 4). Furthermore background noise ($\beta_{\text{BACKGROUND}} = -0.361$; 95% CL = -0.820, -0.041) negatively affected detection probability (Table 1). Signal strength of the bobwhite covey call declined in a linear fashion with a 1.5 dB (β_{DISTANCE} ; 95% CL = -2.2, -0.78) decline in signal strength for every 10 meters of distance ($\beta_0 = 76.45$; 95% CL = 68.68, 84.23; Figure 5). Average background noise level was 51.11 dB (SD = 3.72). Background noise effected detection

probability differently based on the distance of the projected covey call. The estimated detection probability for mean background noise levels of 51 dB was approximately 92% at 100m, 17% at 200m, and 0% at 300m (Figure 6).

DISCUSSION

Passive acoustic surveys offer many advantages over traditional observer survey methods, such as lower relative costs, digitally recorded datasets, opportunity for increased sampling efforts, ability to replicate surveys, and standardization of data collection and analysis (Hobson et al. 2002, Marques et al. 2013, Alquezar and Machado 2015, Colbert et al. 2015, Cragg et al. 2015). Our study provides guidance for researchers interested in applying ARD technology to survey bobwhite. Traditional methods for bobwhite population surveys consist of fall covey call counts and spring male whistling indices; however, these techniques are constrained by the number of human observers available and variation in their experience level. Acoustic sampling may be appropriate under some situations. We found that the survey radius for the ARD was shorter than conventional bobwhite survey techniques. Also, we confirmed that background noise will play an important role in the detection process for ARDs, similarly to traditional observer surveys. We were unable to visually detect several covey call sequences due to background noise. It is likely that we would have missed these aural-only detections had we not known the exact time that the projected call took place. Finally, current algorithms to automatically detect covey calls are not sufficient—this will increase the amount of time necessary to process recordings. Despite these constraints, we believe surveys using ARDs can be developed to assess bobwhite occupancy and density.

Traditional bobwhite covey call surveys assume a radius of 500 meters or more (DeMaso et al. 1992, Wellendorf and Palmer 2005). The SM3 had a 95% survey radius of 228-meters.

Based on a radius of 228 meters, the estimated size of the survey area for a single ARD is approximately 16 hectares. Having the ability to quantify effective survey area allows for density estimates to be compared across space and time. Future bobwhite survey designs using a single ARD would cover less area than traditional observer methods. However, this could be offset by the ability to replicate surveys spatially and temporally. Multiple ARDs can be deployed by a single observer, collecting considerably more survey data than is possible with the equivalent time committed to traditional surveys (Colbert et al. 2015). Background noise, distance to call source, wind, and other environmental factors commonly effect the detection distance for a human observer (Simons et al. 2007). Our results have shown these factors affect surveys conducted with ARDs as well. Traditional bobwhite covey call surveys attempt to negate this variability by sampling during times with little to no wind, minimal cloud cover, and low amounts of background noise (Wellendorf et al. 2004). Similar survey conditions should be targeted when using ARDs.

Contrary to our expectations, landscape structure did not significantly influence sound attenuation. One possible explanation is that NDVI does not adequately characterize the landscape as it pertains to the movement of sound from vocalization to sensor. More detailed datasets, such as Lidar technology (Zolkos et al. 2013), may allow us to better characterize vegetative structure and detect an effect of landscape structure on sound attenuation. In our study, we were only able to deploy a single song meter to detect speakers emitting bobwhite calls. It's possible that our ability to detect an effect of landscape structure was limited by the number of sensors we deployed. Future research should be aimed at exploring a variety of song meter configurations with both known (as in our study) and unknown (as in a field study with real animals) sources to explore the effect of landscape structure on sound attenuation.

The storage of digital recordings allows biologists to review, reanalyze, and confirm detections of vocalizations or background noise components (Haselmayer and Quinn 2000, Celis-Murillo et al. 2009, Venier et al. 2012). Automated recognition of sound files collected from ARDs has been a point of emphasis to increase the utility of this technology (Acevedo and Villanueva-Rivera 2006, Blumstein et al. 2011, Alquezar and Machado 2015, Colbert et al. 2015, Jeliaskov et al. 2016). Methods of sound analysis differ by the program of interests, which leads to variable performance of recognizers across software programs (Knight et al. 2017). We chose Kaleidoscope Pro Software since it was recently released and produced by the same company as the ARDs we selected. For our purposes, Kaleidoscope was not a reliable option for sound analysis. Numerous studies have similarly concluded that various automatic recognition programs are not suitable replacements for manual analyses of recordings (Hutto and Stutzman 2009, Swiston and Mennill 2009, Sidie-Slettedahl et al. 2015). Similarly, we relied upon manual analysis in our study. We have provided an effective, standardized method for call measurements using Raven Pro software, but do encourage further efforts at producing an automatic recognizer for northern bobwhite. We plan to quantify the time required to conduct manual sound analysis for bobwhite covey call recordings to understand tradeoffs in conducting surveys and evaluating recordings.

We have established a foundation for applying acoustic recording technology to survey bobwhite populations by confirming detectability of projected bobwhite covey calls, assessing the impacts of background noise, distance, and landscape structure on detection probability, and identifying an effective sampling radius for an SM3 in relatively noisy conditions. Our evaluation of this ARD provides a blue-print for future researchers seeking to apply this technology to other species and systems. Additionally, governmental agencies, non-

governmental organizations, and private landowners may employ ARDs for surveying bobwhite because of the evidence provided. Applications of ARDs for bobwhite covey calls should target similar conditions (i.e. weather, background noise, time) as traditional surveys. Those planning to use this technology should be aware of the constraints when it comes to spatial coverage of a single unit. However, spatial and temporal replication with multiple units or by repeating surveys is a major advantage of this technology and should not be overlooked. It is important to note that increased sampling effort will result in added time requirements for post-hoc sound analysis. Acoustic recording devices are a viable avenue for detecting bobwhite covey calls, and work is already underway to survey fall bobwhite numbers using ARDs. Future research and monitoring efforts should be able to produce occupancy estimates using ARDs with relative ease. It is also possible that bobwhite density could be estimated given simultaneous detections of calling coveys across multiple ARDs.

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Figure 1. Field-testing locations where Northern Bobwhite covey calls were projected from. Black circles are projected recordings that were detected, white circles are recordings that were not detected by the song meter. The red cross in the center indicates the location of the Wildlife Acoustics SM-3 unit. The Normalized difference vegetation index (NDVI) is depicted in the background.

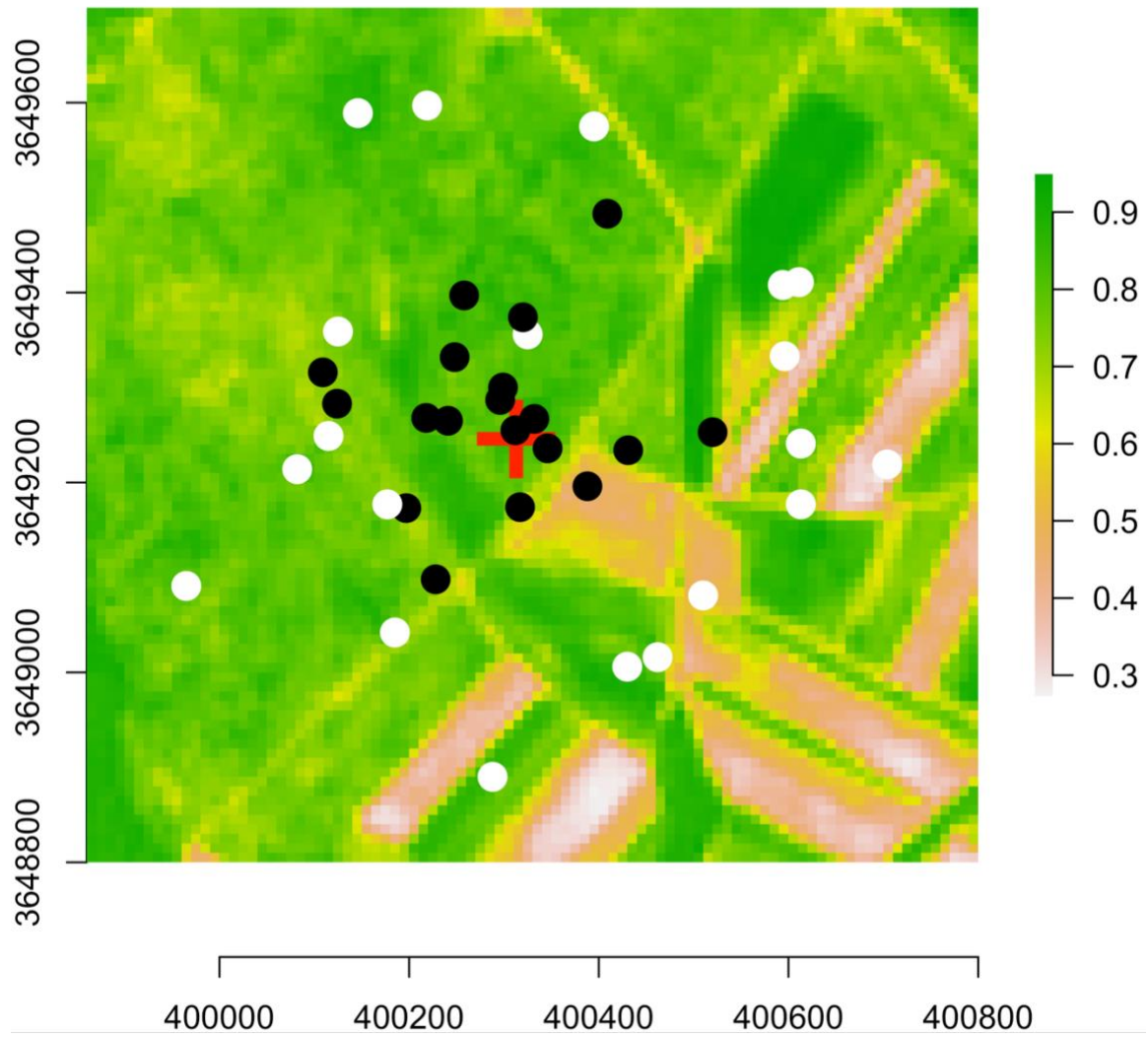
Figure 2. Raven Pro sound analysis methods being used to measure the strength of Northern Bobwhite “koi-lee” calls and associated background noise. Light blue squares indicate sampling frames recording covey call signal strength measurements. Offset red sampling frames are collecting background noise measurements within the same frequency range as the individual “koi-lee” call of interest.

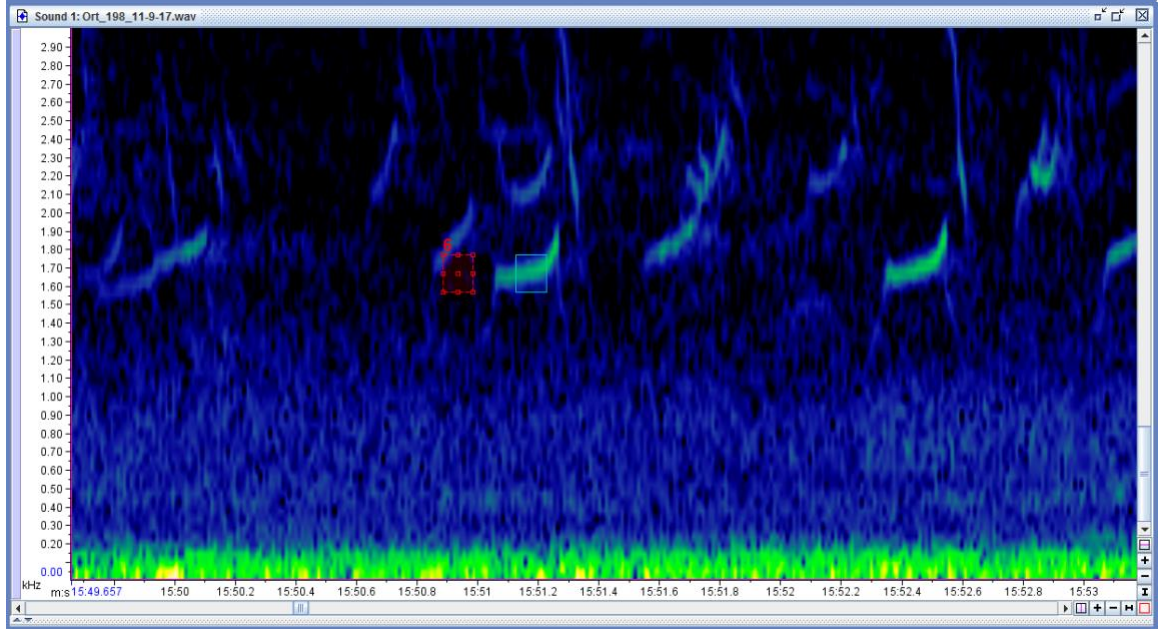
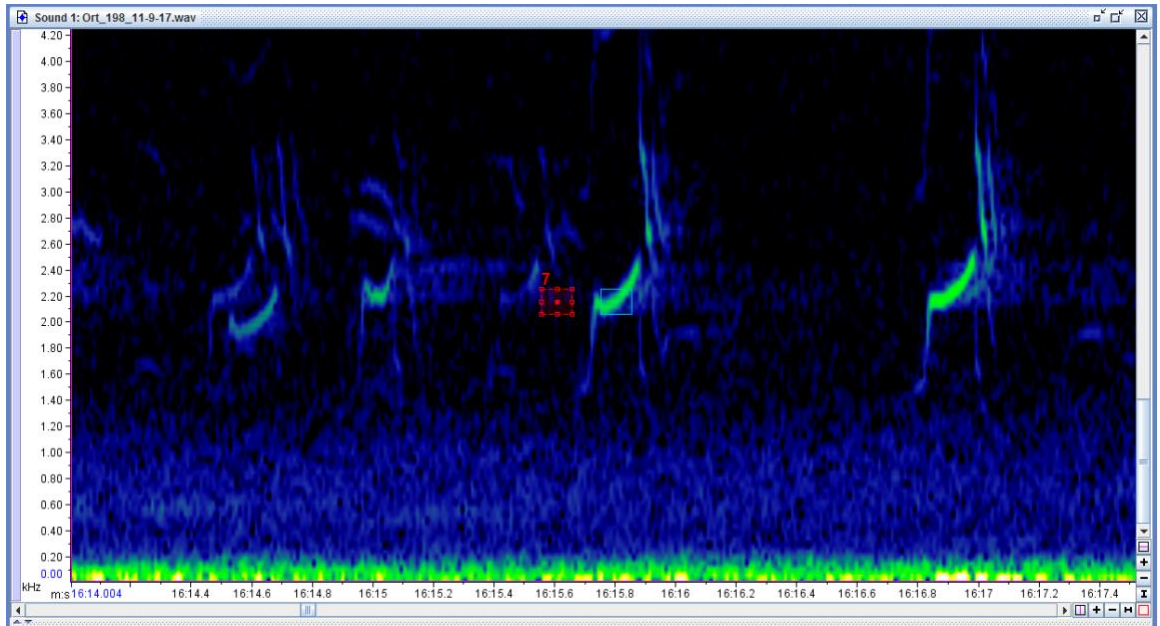
Figure 3. Example of a least-cost path (green line) estimated from our model of sound attenuation as a function of landscape structure (NDVI) between a sensor (red cross) and a speaker (white circle) emitting a bobwhite covey call. Black circles are projected recordings that were detected, white circles are recordings that were not detected by the song meter. The Normalized difference vegetation index (NDVI) is depicted in the background.

Figure 4. Half-normal detection curve of projected Northern Bobwhite covey calls using Wildlife Acoustics SM3 and 95% confidence limits on sigma from ‘Distance’ R package.

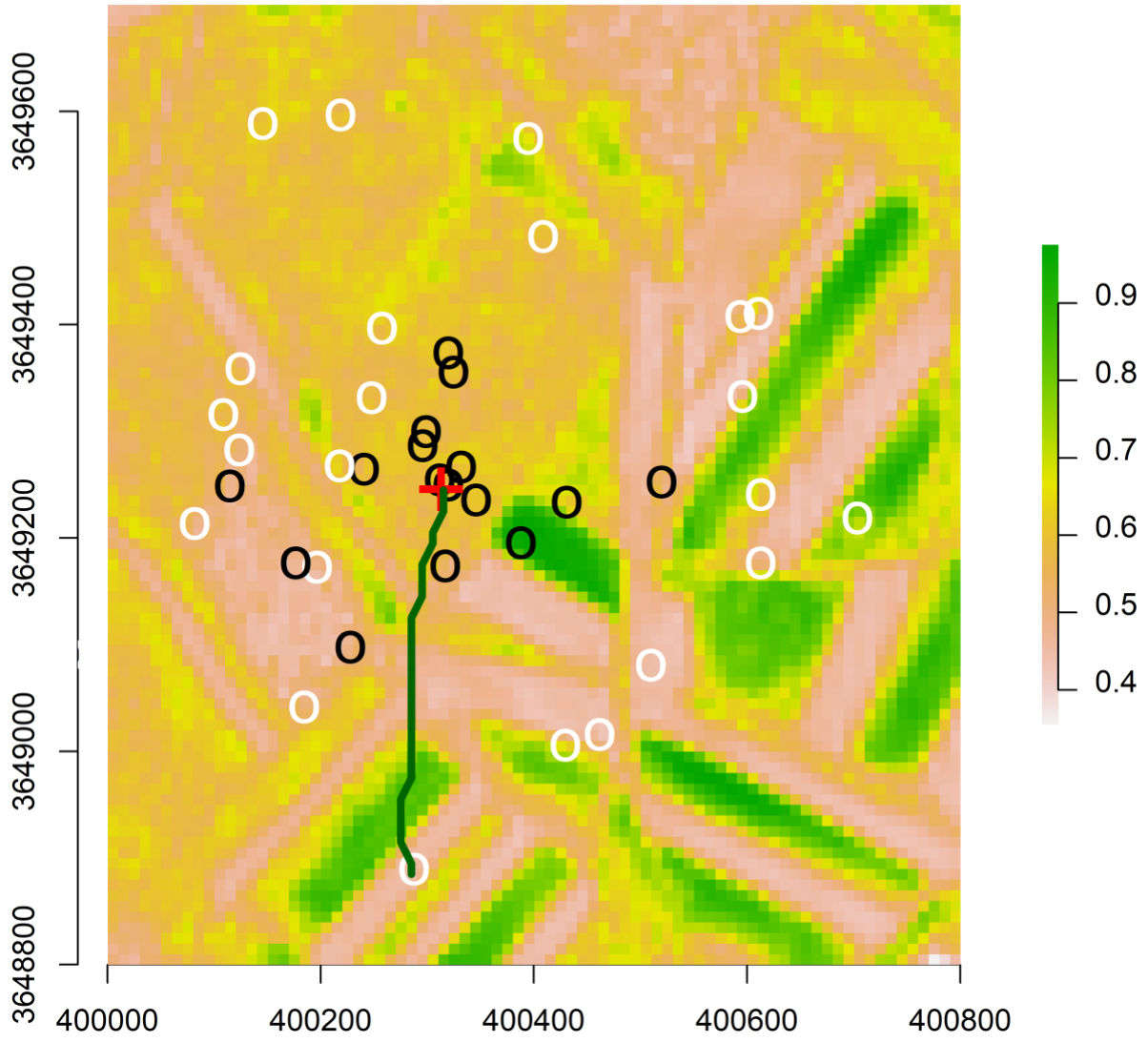
Figure 5. Decline in projected Northern Bobwhite covey call signal strength with distance.

Figure 6. Effects of background noise on detection probability for a speaker-projected Northern Bobwhite covey call.





Estimated attenuation coefficient = -1.76



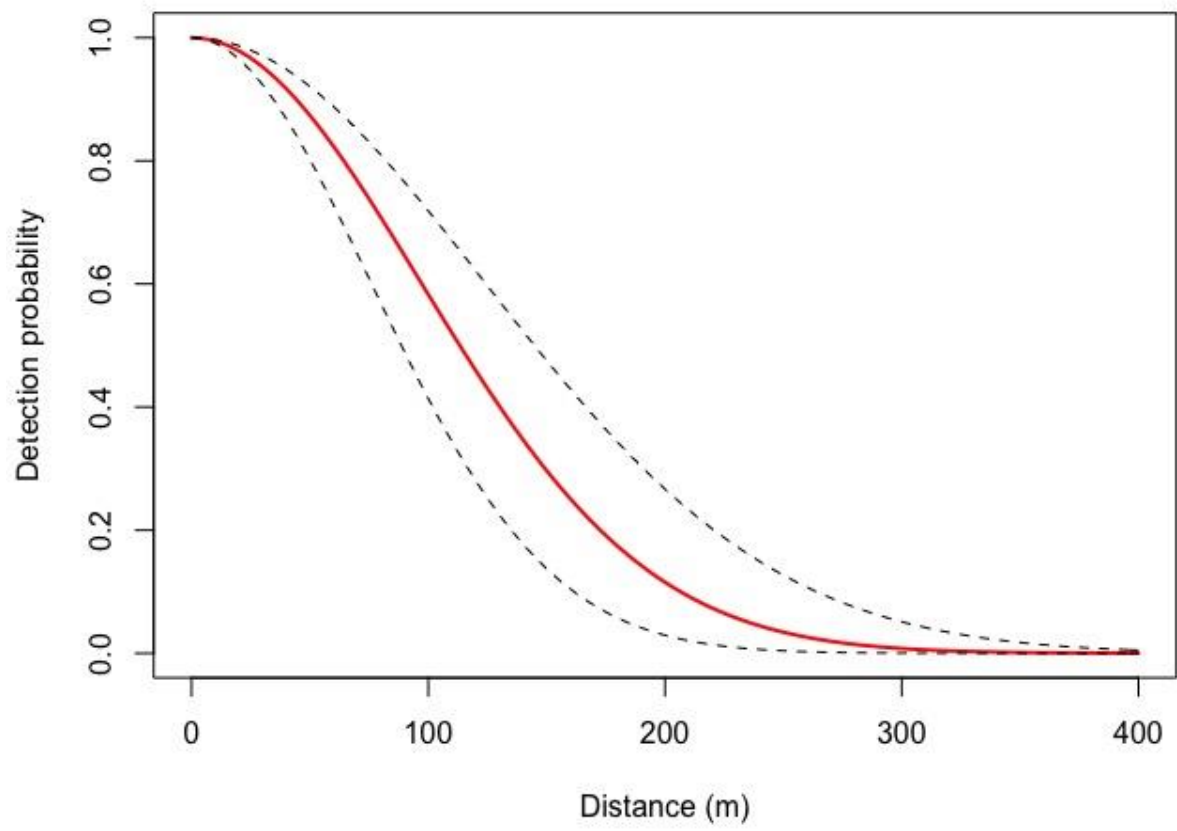
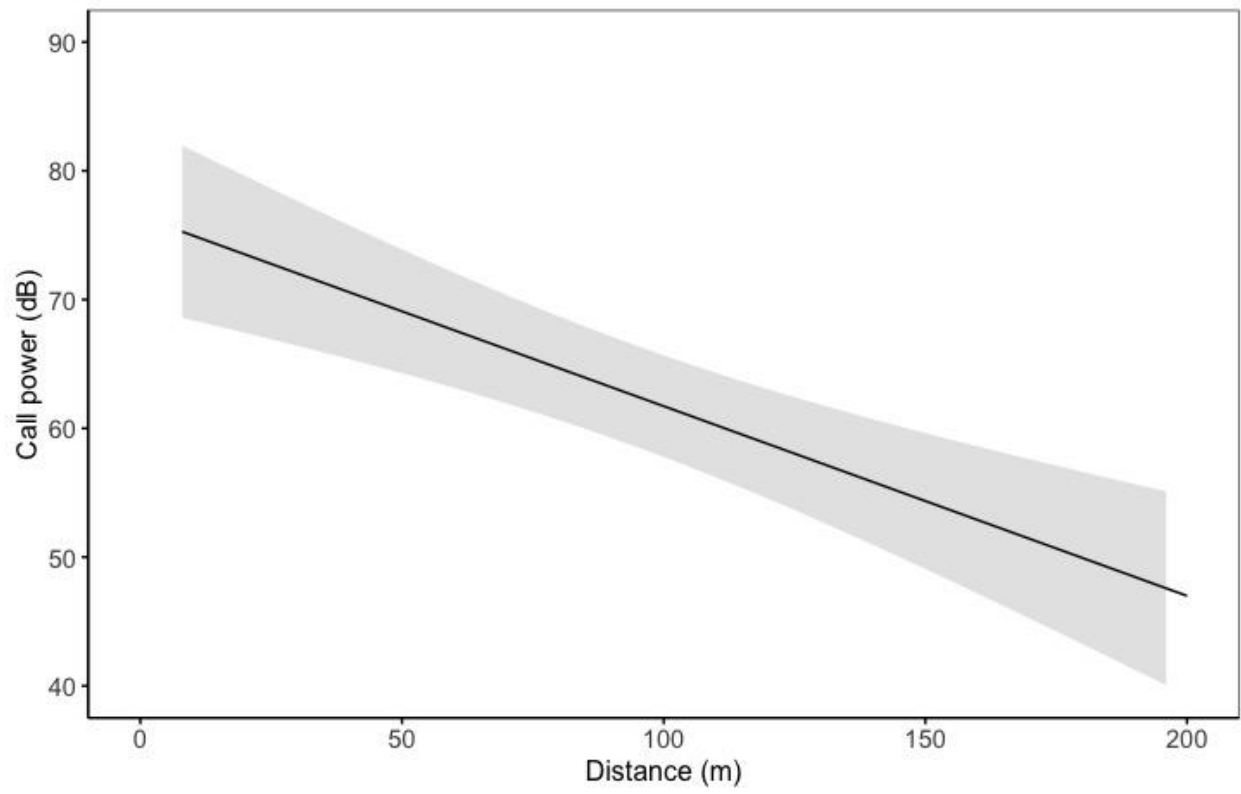
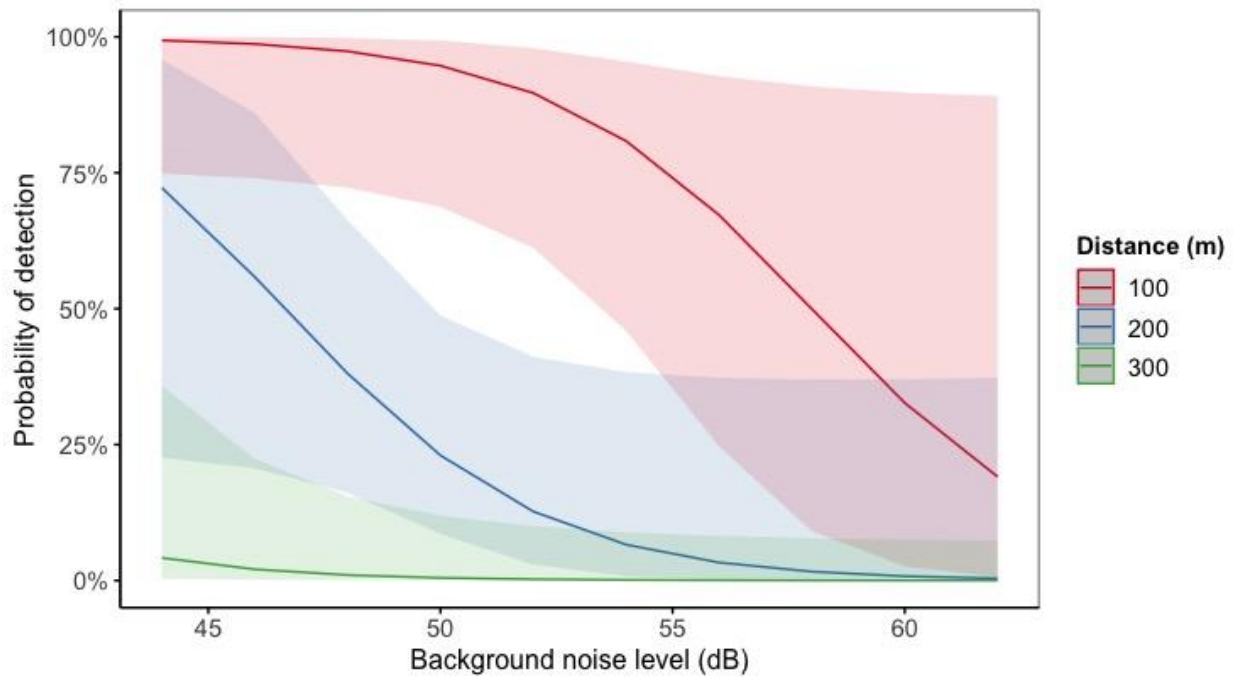


Table 1. Logistic regression parameters for the model {Detection ~ Distance + Background Noise} to understand the effects of background noise on detection probability using Di-Lane WMA field-testing data.

Variable	Estimate	95% CI
INTERCEPT	25.00	6.66 - 52.55
DISTANCE	-0.04	-0.07 - 0.02
BACKGROUND	-0.36	-0.82 - 0.04





CHAPTER 3

APPLYING SPATIAL CAPTURE-RECAPTURE METHODS TO ESTIMATE NORTHERN BOBWHITE DENSITIES

The Northern Bobwhite (*Colinus virginianus*) is a highly sought-after gamebird across much of their range. Despite large-scale population declines due to changing land-use practices, widespread habitat loss, and altered disturbance regimes (Brennan 1991, Hernández et al. 2013), bobwhite remain a valuable economic resource (Burger et al. 1999, Huang 2009). Managers that choose to implement proper management strategies at a sufficient scale are likely to reap the benefits of a recreationally viable population (Martin et al. 2017). There are direct (e.g., sale of hunts) and indirect economic reasons (e.g., jobs for management staff) for bobwhite restoration where maintaining relatively high densities drive local economies (Tall Timbers 2013).

Alternatively, state and federal agencies may want to provide opportunities for the general public to have access to a limited and declining resource. Moreover, researchers may be interested in local bobwhite density or abundance to assess the effects of management strategies or evaluate methods for monitoring bobwhite populations (Norton et al. 1961, Janvrin et al. 1991, Guthery et al. 2001, Wellendorf et al. 2004, Wellendorf and Palmer 2005, Terhune et al. 2009). Regardless of objectives, it is important for managers to be able to properly assess local bobwhite densities.

Bobwhite abundances have been assessed using a variety of methodologies such as flush transects, covey call surveys, spring whistling male surveys, band recoveries, and capture-recapture studies (Norton et al. 1961, O'Brien et al. 1985, Shupe et al. 1987, Guthery 1988, Guthery and Shupe 1989, Janvrin et al. 1991, DeMaso et al. 1992, Hansen and Guthery 2001,

Wellendorf and Palmer 2005, Martin et al. 2013). Fall covey call surveys are a common form of monitoring local populations designed to serve as an index of relative abundance. A tenuous relationship between calling coveys and true densities leave little reliability in extrapolating covey call count data to density estimates (DeMaso et al. 1992). More recently, distance sampling methods have been integrated into covey call survey protocols and determined to be a feasible method for estimating fall densities (Wellendorf and Palmer 2005). Line transects are another common form of distance sampling method readily used on rangeland habitat (Guthery 1988, Guthery and Shupe 1989, Rusk et al. 2007). Additional methods for estimating bobwhite abundances involve more invasive procedures such as capture-mark-recapture (CMR) and capture-removal methods (O'Brien et al. 1985, Guthery and Shupe 1989).

The numerous potential avenues for surveying bobwhite provide researchers and managers many options for assessing local populations. Choosing which survey design to use often comes down to monetary constraints, observer effort required, size of the area of interest, and other important factors. However, each survey method carries its own limitations and assumptions. Covey call point counts (or point transects) and line transect sampling are variations of distance sampling methods commonly used to estimate bobwhite densities (Guthery 1988, DeMaso et al. 1992, Wellendorf and Palmer 2005, Rusk et al. 2007). Extrapolation of these data to a density estimate requires multiplying covey detections by the average observed covey size and then dividing by the area presumed to be surveyed. For example, Rusk et al. (2007), using covey call point counts, assume a survey radius of 900 m (254 ha) while DeMaso et al. (1992) assume an effective survey radius of 700 m (154 ha) for the same sampling approach. Effective survey radius is also a factor in traditional capture-mark-recapture or capture-removal studies. It is common for bobwhite CMR studies to arbitrarily determine survey

area by the study area boundary or by selecting a buffer some distance from the nearest trap (O'Brien et al. 1985, Guthery and Shupe 1989, Borchers and Efford 2008). Because of these key sources of uncertainty, inferences drawn from such surveys should be treated with caution. In hopes of addressing key concerns about effective survey area and inferences about abundances from distance sampling or count data, we conducted a novel application of spatial capture-recapture methods to estimate bobwhite densities.

Spatial capture-recapture (SCR) methods are an advancement of CMR techniques that rely on encounter histories of detected individuals to model density, encounter probability, and space-use of a population (Efford 2004, Borchers and Efford 2008, Royle et al. 2013b). An observation model is governed by a baseline encounter probability, g_0 , that declines with distance from the activity center of an individual. The rate at which detection declines with distance from the nearest trap is a function of the spatial scale parameter, σ . The density sub-model is a spatial point process of the latent activity centers that can vary based on landscape or habitat covariates. These models emphasize the need to capture marked individuals at multiple locations, thus providing insight into their underlying home-range centers (Royle et al. 2013b, Sun et al. 2014). The spatial arrangement of traps, trap density, and temporal replication of trapping has direct implications for the accuracy and precision of density estimates, baseline capture probability, and sigma (Sollmann et al. 2012, Sun et al. 2014, Kristensen and Kovach 2018).

Spatial capture-recapture methods are a fast-growing approach to estimating species' densities. Flexibility in model structures and data inputs have made the approach even more appealing. Royle et al. (2013a) expounded on the basic SCR encounter history datasets by incorporating telemetry locations to model density and resource selection simultaneously. Since

then, additional information in animal locations has led to increased precision of parameter estimates such as density and σ (Ivan et al. 2013, Sollmann et al. 2013, Tenan et al. 2017, Linden et al. 2018). Telemetry data can be used to assess the proportion of a population that is exposed to the trapping area (Ivan et al. 2013), or provide insight into variation in space-use for factors such as sex or habitat preferences (Royle et al. 2013a, Tenan et al. 2017, Linden et al. 2018). Even small sample sizes of telemetered animals can provide valuable insight into model parameter outputs (Royle et al. 2013a, Sollmann et al. 2013, Tenan et al. 2017).

We applied the first SCR models to an upland gamebird species in an effort to precisely estimate density and compare these results to other population monitoring and density estimation methods. We established a trapping scheme designed to optimize recaptures of marked individuals and the likelihood of detecting new individuals. We tested various predictors for baseline encounter probabilities and modeled variations in density due to a key habitat covariate. Additionally, we implemented concurrent telemetry data in hopes of providing more precise parameter estimation. Our research explores the application of spatial capture-recapture methods to a valuable gamebird species by offering novel means for estimating local bobwhite densities.

METHODS

Study Area

Our research took place on Di-Lane Plantation Wildlife Management Area in Burke county, Georgia. This property is owned by the United States Army Corps of Engineers and is managed by the Georgia Department of Natural Resources. Di-Lane is roughly 3300 ha of hardwood bottoms and managed uplands in the form of old fields and pine plantation. Georgia DNR emphasizes upland habitat management to meet demands for bobwhites that occurs through lottery-draw quota hunts. Intensive habitat management through prescribed fire, forest thinning,

disking, and herbicide application produce high densities of bobwhite and provide excellent resources for numerous other game species that are pursued on the property. Average October temperatures for Burke county, Georgia range from 25 to 11 degrees C and average rainfall for the month of October is approximately 9.3 cm (National Climate Data Center, National Oceanic and Atmospheric Administration).

Bobwhite Trapping and Telemetry

We trapped bobwhite from October 6, 2017 to November 2, 2017 for a total of 26 trapping occasions. We used “walk-in” funnel traps (Stoddard 1931) baited with grain sorghum to capture bobwhite. We attempted to sample all available habitat types. We based trap spacing on a winter home-range estimate of radio-tagged Di-Lane bobwhite using a kernel density estimator.

Average winter home-range size was 29.16 ha (unpublished data; range = 5.06, 52.98). Sigma for a 29-ha circular home range area is 305 meters, thus trap spacing for a spatial capture-recapture study should be less than $2*\sigma$ or 610 meters (Sollmann et al. 2012, Sun et al. 2014).

We targeted a trap spacing of no more than 400 meters to optimize spatial coverage across the property and meet operational constraints for checking this number of traps. In total, we set 262 traps to capture bobwhite over a 26-day period. Due to constraints in checking 262 traps nightly, we ran two sequences of traps. We operated half of the traps for the initial 13 days. Once this time period was complete, we flipped the first round of traps and set the remaining trap sites for the second 13-day period.

We checked traps once per day, after dusk. We transported captured bobwhite to an indoor holding facility and held them overnight to be worked up the following morning. We placed aluminum-style leg bands (National Band and Tag Company, Newport, KY) on all captured bobwhite. We aged and sexed all captured individuals, and fit a subset of these captured

birds with VHF, necklace-style radio transmitters (American Wildlife Enterprises, Monticello, FL; Holohil Systems, Carp, Ontario, Canada; Perdix Wildlife Supplies, Warwickshire, UK). Once all birds were worked up, we released them at their respective capture locations the morning after capture.

We sought to deploy 5-6 radio-transmitters per captured covey. Despite recaptures of fully-tagged coveys, we left traps operational for the full 13-day sequence to allow the opportunity for additional captures and spatial recaptures. We closed all traps that had >5 repeated captures to limit detection of the traps and captured bobwhites by predators. We purposefully sacrificed potential spatial recaptures of other bobwhite in order to minimize the possibility of detections and mortalities by predators. We closed all traps that captured bobwhite predators or had signs of predator activity near the trap site (e.g. kill site near the trap). Cooper's hawks (*Accipiter cooperi*), Virginia opossums (*Didelphis virginianus*), Eastern ratsnakes (*Pantherophis alleghaniensis*), and Timber rattlesnakes (*Crotalus horridus*) were all captured inside the funnel traps, resulting in trap closure. Additional avian predation [likely Barred owls (*Strix varia*), Great Horned owls (*Bubo virginianus*), and Red-tailed hawks (*Buteo jamaicensis*)] on captured bobwhites and other bycatch resulted in additional trap closures.

We tracked radio-tagged bobwhite throughout the duration of the trapping schedule; attempting to track marked coveys at least once per week to monitor survival. We used homing methods to track bobwhite coveys to approximately 30 yards. We recorded observer coordinates, azimuth and estimated distance to the tracked covey, as well as covey identification, date and time, and any other pertinent information.

Density Estimation

We used likelihood-based methods in the R version 3.5.1 (R Core Team 2018) ‘secr’ package v. 3.1.6 (Efford 2018) to estimate density. We structured bobwhite capture history into an encounter file fit for integration into ‘secr’. Concurrently, we generated a trapping data file that consisted of trap identification, trap coordinates, and a binary matrix for displaying whether a trap was operated on a given occasion during the 26-day sampling period. This data formed our bobwhite trapping capture history (Figure 1).

Additional bobwhite location information was captured in the form of telemetry data. Current bobwhite research on Di-Lane consists of year-round telemetry that may be used in ‘secr’ data analysis. We indexed all known bobwhite telemetry locations that occurred concurrently to the trapping session. We developed a capture history file for all radio-tagged bobwhite telemetry locations that consisted of individual identification, occasion, and the geographic coordinates of the bird (Figure 1).

Data analysis in ‘secr’ seeks to estimate three parameters: density (D), baseline encounter probability (g_0), and sigma (σ); all of which may be modeled using covariates of interest. The ‘secr’ package contains built-in automatic predictors that are commonly used to model the detection parameters g_0 and σ (Efford 2018). We chose not to model any variation in σ . We fitted 6 models with the bobwhite trapping capture history data that only differed by how we modeled g_0 . We chose the following built-in predictors: a global behavioral response following first capture (b), a behavioral response that varied by each trap location (bk), a time trend (T), a behavioral response that varied by trap location plus a time trend ($bk + T$), and an individual heterogeneity model ($h2$). Additionally, we ran a null model in which g_0 remained constant. Once completed, we combined the trapping capture history file with the telemetry capture history

file to form a combined capture history dataset. We used the combined capture histories with the same automatic predictors described above to compare density estimates with and without telemetry data.

For ecological inference, we chose to model density as a function of the percent managed upland within a defined area. We used vector land-cover data to define habitat types within the state space of the model. We then converted this data to a binary 30-meter raster of managed uplands versus hardwoods, and performed focal statistics in ArcGIS v. 10.6.1. to determine the mean percent upland within a 210-meter area. This 210 meters represents the radius for an estimated bobwhite home range (13.8 ha) on Di-Lane WMA for the month of October. We then scaled the output raster with a mean of 0 to aid parameter estimation (Figure 2). This scaled raster served as our habitat mask for all fitted models ($n = 12$) and provided a covariate for density at each trap location.

To avoid bias in density estimation, ‘secr’ utilizes a buffer argument to define the area of integration beyond the trap layout. This area delineates the outer limit to which an animal cannot be detected by the trapping grid, thus explicitly defining the area being surveyed. We chose a buffer of 800 meters; approximately $4\sigma_{Half-Normal}$ as suggested in the ‘secr’ R documentation (Efford 2018, <https://www.otago.ac.nz/density/pdfs/secr-habitatmasks.pdf>).

We ranked models using Akaike’s Information Criterion (AIC) according to the capture history data (trapping-only vs. combined capture histories) used in the model call. We identified the models with the lowest AIC value as that which best fits the data. We then compared coefficients and predicted density, encounter probability, and sigma for each model. We generated predicted density surfaces for each point of our model mask using the top trapping-only and combined capture history models. We clipped the density surface rasters by the

boundary of Di-Lane WMA to eliminate inference from the surrounding mask area. We then summed the predicted densities within each raster cell of the clipped area and divided by the number of cells to determine overall density estimates for Di-Lane WMA. We replicated this process for the top trapping-only model and the top combined capture history model. To assess precision of density estimates, we calculated relative standard error (RSE) as standard error divided by density.

RESULTS

We trapped bobwhite over a 26-day period using 262 traps in the fall of 2017. We deployed traps at each site for a maximum of 13 days, with some early closures ($n = 49$) due to disturbance by predators. In total, we accumulated 3,078 total trap nights across Di-Lane WMA. On average, we spaced traps approximately 225 meters apart. This met our goal of spacing traps less than 400 meters apart. We captured 416 bobwhite during this time period, with 279 of those detections being unique individuals. We obtained 26 spatial recaptures of bobwhite (i.e. marked individuals captured in different traps) accounting for 6% of our total detections. The maximum number of spatial recaptures for a marked individual was 3 captures.

We had 20 mortalities of bobwhite during the trapping period (Appendix A). These mortalities were attributed to one captured Cooper's hawk (20%, *Accipiter cooperi*), other unknown avian predation (70%), Virginia opossums (5%, *Didelphis virginianus*), and an Eastern ratsnake (5%, *Pantherophis alleghaniensis*). None of the mortalities were from previously captured individuals. These animals were assigned unique identification and incorporated into the capture histories as both detections and losses. Our telemetry dataset consisted of 82 radio-tagged bobwhite for a total of 171 fixes (Figure 1). We averaged two locations per radio-tagged bobwhite during the 26-day trapping period.

We fitted the same models to both the trapping-only dataset ($n = 6$) and the combined dataset of trapping and telemetry ($n = 6$). Model selection for the trapping-only capture history resulted in 80% support for the top model where g_0 depended on a behavioral response that varied by each trap location (Table 1). Predicted density for the top trapping-only model across the entire study site was 0.34 birds/ha (Figure 3; 95% CL = 0.24, 0.49) with a RSE of 13.8 percent. The average probability of capturing an individual bobwhite, on any single occasion, given its home range center is at a trap site is 0.004 with a recapture probability of 0.125 (Table 2). Overall capture probability for the top trapping-only model was 0.05 (Table 2). The sigma estimate for the top trapping-only model was 346 meters (Table 2; 95% CL = 295.89, 404.24).

When combining the trapping and telemetry capture histories, model selection did not result in the same top model compared to the trapping-only model selection. The fitted model of a behavioral response that varied by trap location carried only 1% of the AIC weight (Table 3). The top model contained an additive effect of a time trend with the behavioral*site predictor and accounted for 98.6% AIC weight. We predicted density across the study area to be 0.25 birds/ha (Figures 3 & 4; 95% CL = 0.18, 0.36) with a RSE of 13.4 percent. Baseline g_0 was 0.01 with a recapture probability of 0.094 (Table 2). Overall capture probability for a single individual over the 13-day trap operation period, given its activity center is at a trap site, was 0.12 (Table 2). The additional 171 telemetry locations positively affected the precision of the sigma estimates compared to the top trapping-only model (95% CL = 207.27, 208.30).

Density increased with the percent managed uplands across the property (Figure 5). The log-transformed beta coefficient for the effect of managed uplands was $\beta = 0.58$ (SE = 0.16) and $\beta = 0.59$ (SE = 0.15) for the top trapping-only and top combined capture history models, respectively. Predictions from the top combined capture history model would produce density

estimates of 0.08 birds/ha (95% CL = 0.06, 0.12) for patches with 100 percent hardwood coverage. The same predictions for 100 percent managed uplands produced density estimates of 0.51 birds/ha (95% CL = 0.36, 0.71).

DISCUSSION

Spatial capture-recapture analyses are a quickly growing approach for estimating wildlife densities. We applied SCR analyses to a heavily-studied upland gamebird, the Northern Bobwhite, and provide an example of trapping procedures and model formulation under an SCR framework. We believe SCR can be a valuable tool for assessing local densities of bobwhite given sufficient commitment to trapping intensity and duration. We provide robust estimates of bobwhite density with relatively high precision. We also offer a blueprint for estimating density along a habitat covariate, and demonstrate the use of supplemental telemetry data to inform parameter estimation. Bobwhite density estimates from SCR analyses can be used for many purposes, such as evaluating population monitoring methods or providing reliable information for setting harvest regulations.

Substantial local populations of bobwhite are commonly subjected to some level of hunting pressure despite numerous dynamics that commonly affect bobwhite survival. The optimal harvest rate for sustaining a bobwhite population may be dependent upon factors such as geographic location, exposure to weather catastrophes, population size (Guthery et al. 2000), predation rates, habitat quality and management, and other relevant considerations (Sisson et al. 2009). Because of these influences on bobwhite survival, imprecise density estimates will likely result in conservative harvest strategies (i.e., fewer hunters, shorter seasons, and lower bag limits) which could have indirect consequences for local and regional conservation efforts. For a property like Di-Lane WMA, hunting access is controlled by a quota system which regulates

hunter numbers, days of access, and bag limits. Ideally, these regulations are dependent on a target harvest rate for a well-defined, precise measure of local abundances. Our SCR models provide noteworthy precision of local quail densities, with and without telemetry data, with relative standard error around 13 percent. Review of the bobwhite literature reveals consistently low precision within survey methods and across studies (Appendix A). Precise, reliable density estimates from SCR results will lead to more informed harvest regulations that seek to optimize hunter access to this valuable resource while also protecting against overharvest.

Applying density estimates to harvest strategies is just one of several key functions SCR estimates can be used for. Another valuable application is in understanding how habitat quality might affect density estimates. The ‘secr’ approach to incorporating a habitat mask or covariate is to extract a value from that mask at the exact pixel of each trap site. We chose to represent habitat as a function of mean percent managed uplands within a 210-m radius from any given mask pixel. Our approach afforded us density measures that varied along a continuous scale from 0 to 100 percent managed uplands across the model state space. Our results displayed a steep increase in density as percent managed uplands increased (Figure 5). Bobwhite are a species that require consistent habitat management (prescribed fire, disking, basal thinning, etc) to maintain valuable herbaceous plant cover. Our SCR estimates provide further evidence of this relationship. The hardwoods on Di-Lane WMA lack sufficient understory vegetation, and oftentimes do not provide suitable conditions for bobwhite foraging habitat or cover. Few detections of bobwhite in these habitat conditions could indicate a selection against these areas during the time of trapping or negative effects on survival when using these areas. Regardless, inferences about the benefits of managed uplands for bobwhite can be used by land managers and biologists to promote additional habitat management practices to maintain target wildlife

densities.

Supplemental telemetry data played a key role in parameter estimation when compared to the trapping-only model sets. Telemetry fixes function as pseudo-captures that provide direct information about sigma. Overall density estimates for our top combined capture history model were lower (0.251 birds/ha) than the top trapping-only capture history model (0.34 birds/ha; Figure 3). Sigma estimates between the two models followed a similar trend as the telemetry data produced lower sigma estimates with increased precision (Table 2). Despite the variation in density estimates, 95% confidence intervals overlapped for the top models despite the difference in data inputs, thus providing evidence that telemetry data is not required to obtain relatively precise density estimates. In our case, telemetry locations bolstered our small number of spatial recaptures ($n = 26$) leading to increased precision. Trapping strategies that successfully produce higher percentages of spatial recaptures can likely afford fewer telemetry fixes.

SCR methods offer many potential advantages over traditional CMR studies. These returns are a product of several key logistical constraints that were overcome by intensive observer-hours. In order to truly optimize the SCR analyses, we needed to capture a sufficient number of unique individuals and recapture marked individuals in multiple traps. Bobwhite trapping is a tedious process where traps are set in thick vegetation (briars, plum thickets, hedgerows, etc.) and checked at least once daily, generally after dusk. We operated 262 traps over 26 days on close to 3000 hectares to achieve the capture rates reported herein. We chose to leave traps open for longer periods of time in order to allow for spatial recaptures. This decision was made despite the risk of trap-happy individuals frequenting traps and possibly alerting predators to their location. With all of this in mind, an SCR trapping protocol is not likely to be a process that can be completed on a yearly basis by state agencies or private landowners due to

the copious amounts of labor and time required to achieve sufficient datasets. However, it can be used to calibrate and compare other less resource-intensive methods aimed at addressing similar questions about local bobwhite populations.

In summary, we successfully generated precise bobwhite density estimates using SCR analyses. We were able to utilize supplemental telemetry data that was already being collected to greater inform parameter estimation. Additionally, we produced density estimates that varied as a function of a key habitat characteristic. Future studies should aim to identify the ideal trap density and trap duration required to generate sufficient amounts of captures and recaptures for precise measures of bobwhite abundance. Those answers will likely depend on several key factors such as home range size, habitat quality, available food resources, weather, etc. Additional research is encouraged to simulate SCR capture histories to test model performance via goodness-of-fit tests.

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Figure 1. Northern Bobwhite capture history data used to model density on Di-Lane Plantation Wildlife Management Area. Separate colors represent individual bobwhite, and lines connecting dots represent the same bird captured or tracked at a different location. Traps are represented by the red symbols in each plot.

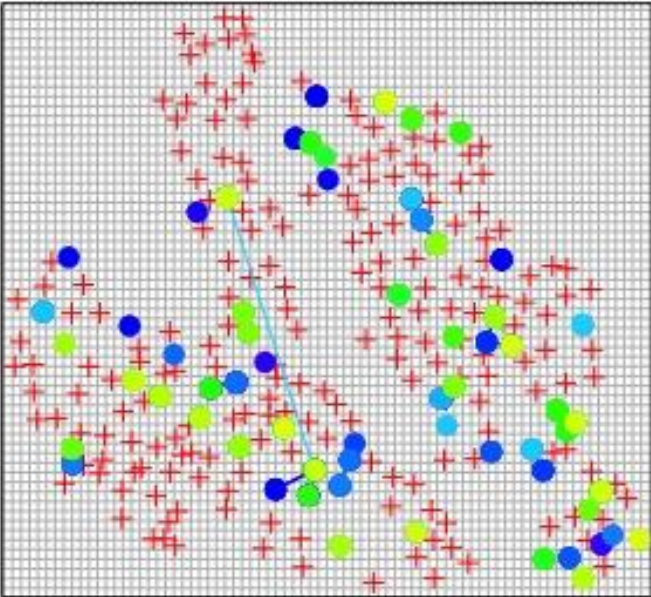
Figure 2. Percent managed upland across Di-Lane Plantation WMA that is used as a habitat covariate to model variation in density for all models.

Figure 3. Comparison of density estimates across Di-Lane Plantation WMA from 'secr' density estimation using trapping-only data and combined capture histories of trapping and telemetry data.

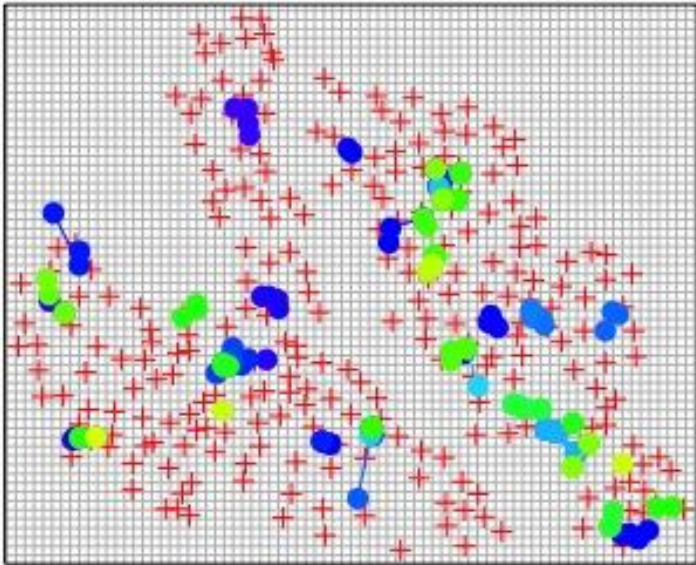
Figure 4. Plotted density surfaces for the top combined capture history model where baseline encounter probability was modeled as a behavioral response that varied by location with the additive effect of a time trend. Plots for lower confidence limits (left), average density estimates (center), and upper confidence limits (right) are shown.

Figure 5. Change in predicted density with an increase in managed uplands from the top combined dataset model where baseline encounter probability functioned as a behavioral response that varied by location with the additive effect of a time trend.

Trapping Capture History



Telemetry Locations



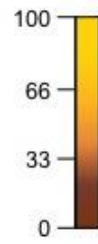
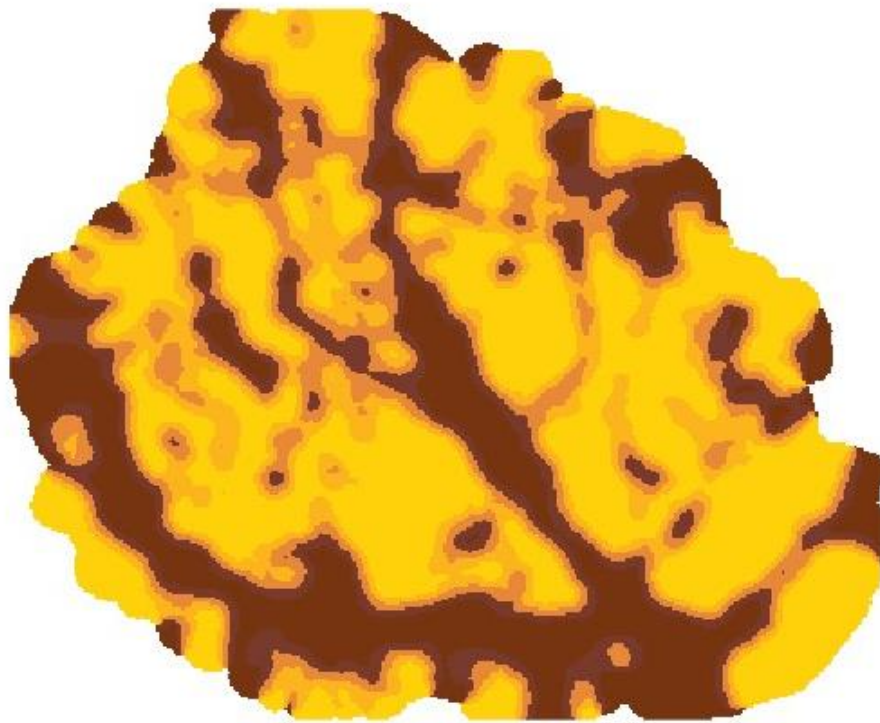


Table 1. AIC model selection results for estimating fall density of Northern Bobwhite on a wildlife management area in Georgia. Data for this consisted of only the trapping capture history for 262 traps over 26 trap nights. All of the capture models were based on a half-normal function with a baseline capture probability and sigma. The baseline encounter probability covariates were; a null model (1), a global behavioral response (b), a behavioral response that varied by trap location (bk), a time trend (Time), and individual heterogeneity (h2).

Model	Density Model	Capture Model	k	AIC	ΔAIC	w_i
M3	D ~ Percent Upland	hn (bk, s)	5	3421.25	0	0.80
M5	D ~ Percent Upland	hn (bk + Time, s)	6	3423.92	2.67	0.20
M2	D ~ Percent Upland	hn (b, s)	5	3650.68	229.42	0
M1	D ~ Percent Upland	hn (1, s)	4	3675.50	254.25	0
M6	D ~ Percent Upland	hn (h2, s)	6	3679.48	258.23	0
M4	D ~ Percent Upland	hn (Time, s)	5	3787.73	366.47	0

Table 2. Model results for estimating fall density of Northern Bobwhite on Di-Lane Plantation WMA (2017). Parameters of interest were: population density (D), baseline detection probability (g0), recapture probability (g1), overall capture probability, and sigma (σ). We only varied the detection parameter g0 for all models. Results show real parameter estimates from models using trapping-only data and combined trapping-telemetry data. Bolded models represent the top model by AIC rank according to the data type used.

	Model	Data	D ¹	g0 ²	g1 ³	Capture Prob ⁴	sigma (m)
M1:	D~ % Upland, g0~ 1, sigma~ 1	Trapping	0.12 (0.10, 0.14)	0.031	--	0.34	205 (204.38 , 205.41)
M2:	D~ % Upland, g0~ b, sigma~ 1	Trapping	0.20 (0.16, 0.26)	0.013	0.038	0.16	207 (207.06, 208.10)
M3:	D~ % Upland, g0~ bk, sigma~ 1	Trapping	0.28 (0.21, 0.40)	0.004	0.125	0.05	346 (295.89 , 404.24)
M4:	D~ % Upland, g0~ Time, sigma~ 1	Trapping	0.11 (0.11, 0.11)	0.08	0.578	0.66	181 (181.64, 181.64)
M5:	D~ % Upland, g0~ bk + T, sigma~ 1	Trapping	0.39 (0.33, 0.47)	0.003	0.072	0.04	277 (273.42, 280.34)
M6:	D~ % Upland, g0~ h2, sigma~ 1	Trapping	0.12 (0.10, 0.15)	0.028	0.032	0.31	205 (204.38, 205.41)
M7:	D~ % Upland, g0~ 1, sigma~ 1	Combined	0.12 (0.12, 0.12)	0.034	--	0.36	183 (182.99, 182.99)
M8:	D~ % Upland, g0~ b, sigma~ 1	Combined	0.24 (0.24, 0.24)	0.018	0.043	0.21	183 (182.91, 182.91)
M9:	D~ % Upland, g0~ bk, sigma~ 1	Combined	0.27 (0.22, 0.33)	0.01	0.117	0.12	221 (214.65, 226.78)
M10:	D~ % Upland, g0~ Time, sigma~ 1	Combined	0.14 (0.14, 0.14)	0.019	0.02	0.22	182 (182.18, 182.18)
M11:	D~ % Upland, g0~ bk + T, sigma~ 1	Combined	0.21 (0.15, 0.29)	0.01	0.094	0.12	208 (207.27, 208.30)
M12:	D~ % Upland, g0~ h2, sigma~ 1	Combined	0.15 (0.15, 0.15)	0.07	0.027	0.61	181 (181.22, 181.22)

¹ Density is shown as birds/hectare when the habitat mask is 50% managed upland and 50% non-upland.

² g0 represents capture probability of an animal, on a single occasion, given its latent home range center is the same location as the trap.

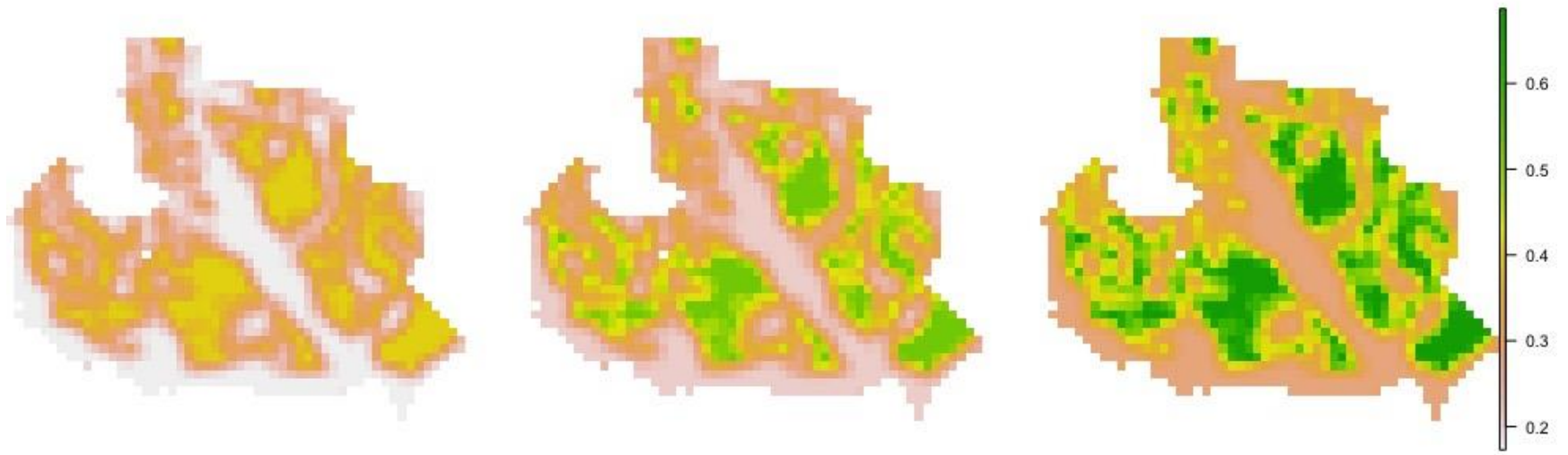
³ g1 is the probability that an individual animal is recaptured given it has been captured previously.

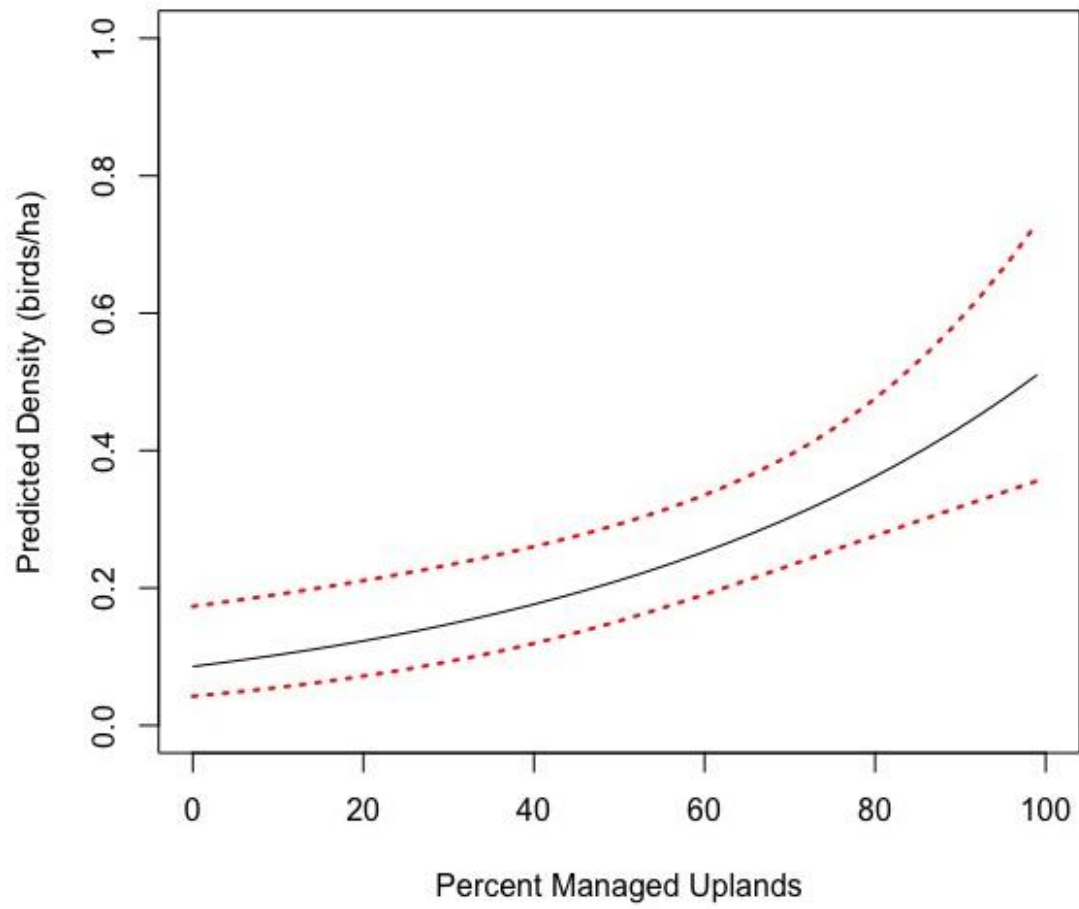
⁴ Capture probability represents the percent chance we have for capturing an individual over the full 13-day operational period of a trap given its latent home range center is the same location as the trap.

Table 3. AIC model selection results for estimating fall density of Northern Bobwhite on a wildlife management area in Georgia. Data for this consisted of the combined capture histories from trapping data and telemetry data from the fall of 2017. We used a hazard half-normal function to define the capture model with the associated baseline encounter probability covariates and sigma.

Model	Density Model	Capture Model	k	AIC	Δ AIC	w_i
M5	D ~ Percent Upland	hhn (bk + Time, s)	6	7359.446	0	0.9862
M3	D ~ Percent Upland	hhn (bk, s)	5	7368.057	8.611	0.0138
M4	D ~ Percent Upland	hhn (Time, s)	5	7504.667	145.221	0
M2	D ~ Percent Upland	hhn (b, s)	5	7528.464	169.018	0
M6	D ~ Percent Upland	hhn (h2, s)	6	7543.611	184.165	0
M1	D ~ Percent Upland	hhn (1, s)	4	7552.393	192.947	0







CHAPTER 4

CONCLUSION

There are numerous hurdles that accompany Northern Bobwhite abundance estimation. From a species perspective, these hurdles consist of wary behavioral tendencies, cryptic coloration, and preferences for dense overhead cover. Additional observer-based obstacles such as variation in experience, abilities, and bias further complicate attempts at abundance estimation. Despite these variables, researchers and managers must continually reassess bobwhite populations. There are a variety of current methods that are useful for monitoring local population trends and evaluating population responses to habitat or harvest management. Unfortunately, concerns about accuracy and precision are ever-present. I present novel abundance estimation techniques to bobwhite population monitoring with the goal of increasing the accuracy and precision of abundance estimates. I evaluate a passive acoustic recording device for monitoring bobwhite covey calls with the goal of reducing observer error and increasing spatial and temporal survey coverage. I also introduce spatial capture-recapture methods to bobwhite populations in hopes of explicitly defining the effective sampling area of a trap array, thus providing explicit density estimates.

My field test of a commercially-available ARD lays a foundation for bobwhite covey call survey design using passive acoustic technology. My approach provides replicable methods for evaluating ARDs for any novel species or location. I estimated the functional survey radii for the Wildlife Acoustics Song Meter 3, and defined the relationship between detection and distance of a bobwhite covey call. Additionally, I concluded that Kaleidoscope Pro Analysis Software did not suffice to automatically analyze recordings to detect covey calls. In response, I demonstrated

manual sound analysis procedures using Raven Pro Sound Analysis Software. I believe bobwhite passive acoustic surveys are an excellent opportunity to positively affect current population monitoring programs. Efforts to expound on this research are already underway, with intentions of applying acoustic spatial capture-recapture methods to passive acoustic arrays. Acoustic recording devices are a fast-growing tool for numerous wildlife population monitoring programs. Bobwhite managers and researchers should follow suit and employ this technology for assessing occupancy, estimating density, or simply recording raw covey call count data for long-term trend studies.

I further expound on bobwhite density estimation efforts by applying spatial capture-recapture methods to traditional capture-mark-recapture. I modified standard trapping procedures (e.g., trap density and survey duration) to optimize spatial recaptures of marked individuals. I utilized supplemental telemetry data to better inform parameter estimates such as sigma and subsequently derive more informed density estimates. I provide an example for modeling density as a function of a habitat covariate, percent managed uplands, and illustrate SCR's potential for evaluating population responses to habitat management. I used likelihood methods to vary baseline capture probability predictors such as behavioral responses to traps or time trends, and used model selection to determine the top performing models. Top models provided desirable precision with relative standard errors around 13 percent. Limitations to SCR protocols generally involve logistical constraints like intensive trap coverage and prolonged trapping durations. These factors likely limit use of SCR for yearly evaluation of local bobwhite populations, but may yet serve a valuable role in bobwhite conservation. I offer SCR methods as an additional approach for evaluating current and future bobwhite survey protocols. Precise measures of bobwhite densities from spatial capture-recapture analyses can serve as valuable baseline

abundance estimates for the numerous bobwhite surveys being used today as well as those designed in the future.

APPENDIX A: CAUSE-SPECIFIC MORTALITY FOR CAPTURED NORTHERN BOBWHITE DURING SPATIAL CAPTURE-RECAPTURE TRAPPING DURING FALL 2017 ON DI-LANE PLANTATION WILDLIFE MANAGEMENT AREA.

Number of mortalities	Trap ID	Date	Number of days operational	Cause of death
4	25	10/10/17	5	Avian
4	197	10/10/17	5	Avian
1	189	10/13/17	8	Eastern rat snake
2	130	10/16/17	11	Avian
1	75	10/29/17	9	unknown
4	160	10/30/17	10	Cooper's hawk
3	251	10/30/17	10	Avian
1	58	11/1/17	12	Virginia opossum

APPENDIX B: LITERATURE REVIEW OF VARIOUS NORTHERN BOBWHITE DENSITY ESTIMATION PROCEDURES WITH REPORTED DENSITY (BIRDS/HA) AND STANDARD ERRORS (SE). WE CALCULATE RELATIVE STANDARD ERROR (RSE) AS THE QUOTIENT OF SE/DENSITY.

Paper	Methods	Density	SE	RSE
O'Brien et al. 1985	Capture-removal 1979	488 ¹	36.13	0.074
O'Brien et al. 1985	Capture-removal 1980	571 ¹	31.17	0.055
O'Brien et al. 1985	Capture-removal 1981	625 ¹	26.05	0.042
O'Brien et al. 1985	Capture-removal 1982	308 ¹	29.73	0.097
O'Brien et al. 1985	Capture-recapture 1981	338 ¹	3.46	0.010
O'Brien et al. 1985	Capture-recapture 1982	247 ¹	102.80	0.416
Shupe et al. 1987	Helicopter transect	1.78	0.33	0.185
Shupe et al. 1987	Line transect	1.41	0.3	0.213
Shupe et al. 1987	Capture-recapture	1.91	0.2	0.105
Guthery and Shupe 1989	Capture-removal 1984	2.25	0.745	0.331
Guthery and Shupe 1989	Capture-removal 1985	1.81	0.179	0.099
Guthery and Shupe 1989	Capture-removal 1986	2.46	0.258	0.105
Guthery and Shupe 1989	Capture-removal 1987	2.15	0.278	0.129
Guthery and Shupe 1989	Line transect 1984	0.8	0.365	0.456
Guthery and Shupe 1989	Line transect 1985	1.48	0.113	0.076
Guthery and Shupe 1989	Line transect 1986	2.46	0.629	0.256
Guthery and Shupe 1989	Line transect 1987	2.18	0.559	0.256
DeMaso et al. 1992	Covey call point count 1989a	0.06	0.015	0.238
DeMaso et al. 1992	Covey call point count 1989b	0.04	0.006	0.158
DeMaso et al. 1992	Covey call point count 1989c	0.04	0.017	0.405
DeMaso et al. 1992	Covey call point count 1990a	0.06	0.015	0.259
DeMaso et al. 1992	Covey call point count 1990b	0.11	0.02	0.183
DeMaso et al. 1992	Covey call point count 1990c	0.04	0.03	0.714
Wellendorf and Palmer 2005	Covey call grid survey A	4.6	0.29	0.063
Wellendorf and Palmer 2005	Covey call point count A	4.1	0.69	0.168
Wellendorf and Palmer 2005	Covey call grid survey B	2.7	0.44	0.163
Wellendorf and Palmer 2005	Covey call point count B	3.4	0.46	0.135
Rusk et al. 2007	Line transect 2001a	0.39	0.138	0.353
Rusk et al. 2007	Line transect 2001b	0.99	0.238	0.241
Rusk et al. 2007	Line transect 2001c	0.19	0.092	0.486
Rusk et al. 2007	Line transect 2002a	0.56	0.216	0.386

Rusk et al. 2007	Line transect 2002b	0.54	0.167	0.309
Rusk et al. 2007	Line transect 2002c	0.88	0.301	0.343
Rusk et al. 2007	Line transect 2003a	2.29	0.232	0.102
Rusk et al. 2007	Line transect 2003b	1.55	0.271	0.175
Rusk et al. 2007	Line transect 2003c	2.26	0.331	0.146
Rusk et al. 2007	Line transect 2004a	2.5	0.744	0.297
Rusk et al. 2007	Line transect 2004b	3.47	0.698	0.201
Rusk et al. 2007	Line transect 2004c	2.85	0.474	0.166
Rusk et al. 2007	Line transect 2005a	2.55	0.225	0.088
Rusk et al. 2007	Line transect 2005b	2.05	0.208	0.101
Rusk et al. 2007	Line transect 2005c	0.88	0.122	0.139
Rusk et al. 2007	Covey call point survey 2001a	0.3	0.044	0.147
Rusk et al. 2007	Covey call point survey 2001b	0.24	0.064	0.267
Rusk et al. 2007	Covey call point survey 2001c	0.23	0.161	0.700
Rusk et al. 2007	Covey call point survey 2002a	0.32	0.063	0.197
Rusk et al. 2007	Covey call point survey 2002b	0.29	0.032	0.111
Rusk et al. 2007	Covey call point survey 2002c	0.36	0.059	0.165
Rusk et al. 2007	Covey call point survey 2003a	0.78	0.067	0.086
Rusk et al. 2007	Covey call point survey 2003b	0.87	0.044	0.051
Rusk et al. 2007	Covey call point survey 2003c	1.02	0.115	0.113
Rusk et al. 2007	Covey call point survey 2004a	0.53	0.065	0.123
Rusk et al. 2007	Covey call point survey 2004b	0.78	0.104	0.134
Rusk et al. 2007	Covey call point survey 2004c	0.83	0.120	0.145
Rusk et al. 2007	Covey call point survey 2005a	0.5	0.089	0.178
Rusk et al. 2007	Covey call point survey 2005b	0.52	0.063	0.121
Rusk et al. 2007	Covey call point survey 2005c	0.44	0.047	0.108
Rusk et al. 2007	Helicopter transect 2004a	2.02	0.232	0.115
Rusk et al. 2007	Helicopter transect 2004b	1.88	0.190	0.101
Rusk et al. 2007	Helicopter transect 2004c	2.8	0.283	0.101
Rusk et al. 2007	Helicopter transect 2005a	2.44	0.216	0.088
Rusk et al. 2007	Helicopter transect 2005b	1.85	0.177	0.096
Rusk et al. 2007	Helicopter transect 2005c	1.79	0.222	0.124
Martin et al. 2013	Covey call point survey 2004	0.52	0.084	0.161
Martin et al. 2014	Covey call point survey 2005	0.75	0.082	0.110

¹ Estimated population size not converted to measure of density.