

NAVIGATING UNCERTAINTY IN WILDLIFE MANAGEMENT:
AN EMPIRICAL EVALUATION OF A REGULATION CHANGE AND SUBSEQUENT IMPACTS ON
MICHIGAN WHITE-TAILED DEER POPULATIONS

By

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ABSTRACT

Assessing changes in population abundance is important when evaluating the effectiveness of conservation and management for wildlife. However, both observational and structural uncertainty affect the reliability of abundance estimates and may limit the ability to assess temporal or spatial differences in abundance. Further, evaluating a conservation or management action on a free-ranging population presents challenges with partial controllability. Recently, wildlife managers in Michigan sought to understand whether a specific harvest regulation had the intended consequences on a white-tailed deer (*Odocoileus virginianus*) population. I used a camera-trap study design to evaluate the effects of an antler point restriction (APR) regulation change on a white-tailed deer population in the south-central Lower Peninsula of Michigan, USA, 2019–2022. In my first chapter, I used a subset of camera-trap data to evaluate the sensitivity of abundance estimates to alternative sampling strategies that modified sampling frequency, sampling duration, and camera distribution. Results indicated that an N-mixture model generated reasonably reliable estimates (i.e., precise and accurate), irrespective of data modifications, and that precision was sensitive to modifications. My results emphasized the importance of sampling relevant to animal activity and highlighted viable ways to improve sampling efficiency. In my second chapter, I evaluated potential population-level changes over time and space following an APR change in a before-after-control-impact design. I found weak evidence for APRs affecting the relative abundance by sex-and-age classes. In both APR and Non-APR treatment areas, I consistently observed increasing trends in Legal and Sub-legal Male deer relative abundance over time and found no evidence supporting change in Female and Fawn relative abundance.

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GENERAL INTRODUCTION

Chronic wasting disease (CWD) is a fatal disease caused by a prion that infects cervids (family Cervidae), including white-tailed deer (*Odocoileus virginianus*; Williams 2005). The disease is a major management challenge as CWD is transmissible through animal-to-animal contact and acts as an environmental contaminant. Shed prions can remain infectious for years in the environment and further contribute to the maintenance of the disease (Miller et al. 2004). Described as the most important disease threatening North American cervids, CWD poses a serious threat to both the sustainability of free-ranging and captive cervids and conservation nationwide (Gillin and Mawdsley 2018). In areas where CWD is established, it has emerged as a major threat, reducing the health of wild cervid populations, and potentially causing long-term population decline (Gross and Miller 2001, Manjerovic et al. 2014, Edmunds et al. 2016, DeVivo et al. 2017). In addition to population-level impacts, CWD can discourage hunters from harvesting deer in and around affected areas (Needham et al. 2004, Vaske and Lyon 2011). This is problematic because funding for state wildlife agencies comes from hunting-related expenditures and license sales (Jacobson et al. 2010). Deer hunters account for the largest portion of the hunting public and generate a substantial portion of conservation dollars (Hewitt et al. 2015). Consequently, CWD-driven declines in deer hunting and deer-hunting revenue can destabilize the overall economic well-being of wildlife conservation.

Deer hunting regulations and hunter harvest are the primary levers used by state wildlife agencies for managing deer populations and disease. Management actions are often intended to manipulate the total abundance or sex-and-age composition of targeted deer populations (Demarais et al. 2000). As it relates to disease, some studies have shown that

reducing deer densities has been successful at maintaining low prevalence of CWD (~1–2%; Manjerovic et al. 2014, Mateus-Pinilla et al. 2013), whereas other research has established that different sex-and-age classes of free-ranging deer have different prevalence rates of the disease (Miller and Conner 2005, Grear et al. 2006, Osnas et al. 2009, Rees et al. 2012, Jennelle et al. 2014). Due to changes in the sex-and-age composition, harvest strategies that target specific sex-and-age classes may be useful for CWD management (Mysterud and Edmunds 2019).

Wildlife management agencies often alter harvest regulations to change the composition and structure of harvests with the expectation that the alteration will result in population-level changes in abundance, composition, and structure (Carpenter 2000, Demarais et al. 2000). For example, mortality from hunting antlerless deer (including females) is a common approach for managing white-tailed deer abundance (Woolf and Rosenberry 1998, Diefenbach et al. 2021). Harvest can provide an effective tool for managing populations, and management decisions can greatly influence the targeted population. For example, sex- and age-specific hunting can alter the composition and structure of targeted populations, which in turn can affect various demographic processes (Ginsberg and Milner-Gulland 1994, Milner et al. 2007). Historically, male-biased harvesting regimes have been applied to North American cervids (McCullough 2001). This type of harvest strategy can lead to a female-biased sex ratios in populations (Noyes et al. 1996, Nilsen and Solberg 2006). With regards to age, disproportionate harvests of young animals can limit animals from advancing to older age classes and skew a population's age structure (Milner et al. 2007).

Mandatory antler-point restrictions (APRs) are an example of a deer harvest regulation intended to change the sex-and-age composition of harvests. Antler point restrictions are based

on antler size (i.e., number of antler points), and antler size generally increases with the age of the animal (Strickland and Demarais 2000). Specifically, APRs are designed to limit the harvest of younger antlered deer and thus increase recruitment of male deer into older age classes (Carpenter and Gill 1987, Frawley 2017, Hansen et al. 2017, Wallingford et al. 2017). APRs may also decrease deer abundance in an APR area which could reduce contact rates and thus overall spread of CWD. These decreases can result from indirect effects of APRs on harvest, like shifting harvest pressure to antlerless deer (Cornicelli et al. 2011, Hansen et al. 2017, Wallingford et al. 2017, Hansen et al. 2018), although this has not been observed in all places with APRs (Hansen et al. 2017, Cain et al. 2022). Overall, natural resource agencies have limited information on how deer harvest regulations affect the abundance and sex-and-age composition of the true state of the population (as opposed to the harvested segment; Brown et al. 2000, Carpenter 2000, Riley et al. 2003, Giles and Findlay 2004, Morina et al. 2021). This limitation is relevant because CWD transmission rates are related to the sex-and-age composition of the population, thus different harvest regulations could have different implications for CWD transmission.

White-tailed deer are an important game species, and the accurate estimation of population parameters is essential for the evaluation of management actions (Ludbow et al. 1996, Gibbs 2000, Furnas et al. 2018). Further, precise abundance estimates by sex-and-age class can offer a more rigorous assessment needed for relevant disease management. This need is especially relevant in areas where population-management actions are aimed at mediating the spread of CWD in free-ranging deer. However, estimating abundance and composition can be logistically difficult, with traditional methods often involving live capture and marking animals (O'Connell et al. 2011, Burton et al. 2015, Wearn and Glover-Kapfer 2019). Most state

agencies instead rely on estimated or enumerated harvest for population monitoring efforts (Roseberry and Woolf 1991, Skalski et al. 2005, Hansen 2011, Ryder 2018, Diefenbach et al. 2021). Although useful, sex-and-age data of the harvested population may be nonrepresentative of the true state of the population (Carpenter 2000, Demarais et al. 2005, Collier and Krementz 2007).

Camera trapping has become an increasingly common method for monitoring wildlife over large spatial scales and represents an alternative to more intensive methods (O'Connell et al. 2011, Burton et al. 2015, Parsons et al. 2017, Wearn and Glover-Kapfer 2019). Likewise, camera trapping has emerged as a valuable tool for gathering count data for monitoring cervid populations (DeYoung 2011). Camera-trap data have been used to estimate population parameters for numerous cervids (Furnas et al. 2018, Moeller et al. 2018, Furnas et al. 2020), including white-tailed deer (Jacobson et al. 1997, Roberts et al. 2006, Petroelje et al. 2014, Haus et al. 2019). Camera-trap based population estimates can be compared across time and space to monitor changes in populations and, by extension, can be used to test hypotheses about the effects of management actions. However, one major challenge with camera-trap approaches is the labor required to review high numbers of photographs (DeYoung 2011, Pierce et al. 2012), and it is not uncommon to collect large quantities of camera-trap data. This often forces wildlife managers to compromise between the quality of data and the sampling strategies used (Marcon et al. 2019). Solutions to the photo-reviewing issue include increasing efficiency of data management (Price Tack et al. 2016) or decreasing survey intensity, such as reducing the survey duration or number of camera sites. However, these modifications may also influence the precision and accuracy of abundance estimators and thus need to be critically evaluated

before formal application. Therefore, methodological assessments for data collection and parameter estimation are needed to maximize the utility of camera-trap approaches.

In Michigan, CWD was first identified in free-ranging deer in 2015 (Stewart et al. 2016) and has now been detected in 3 primary areas (southwest Upper Peninsula, and south-central and southeast Lower Peninsula). The south-central Lower Peninsula area is considered a CWD hotspot, where the disease is established in Kent and Montcalm County. In addition to changes in state and peninsula-wide deer harvest regulations designed to mediate potential spread of disease, the Natural Resource Commission implemented APRs in select counties in the south-central Lower Peninsula as part of experimental management. This action was coupled with research aimed to evaluate the efficacy of APRs as a tool for managing CWD (hereafter, APR study). To address this, camera traps were used to collect data on white-tailed deer populations over 4 consecutive years (2019–2022) within a 5-county area (Ionia, Kent, Mecosta, Montcalm, and Newaygo counties).

The overarching goals of my thesis are to evaluate the consequences of camera-trap sampling design and estimate potential population-level changes following the implementation of an APR in an area with CWD. The first goal was developed to identify sampling strategies that minimize financial and human resources to attain precise and reliable estimations of deer abundance using N-mixture models (Royle 2004). The second goal was developed to help fill critical knowledge gaps about the effects of APRs on deer abundance by sex-and-age.

In Chapter 1, I leveraged a subset of camera-trap data from the APR study to conduct a *post hoc* methodological assessment focusing on survey design and abundance estimation. My objectives were to evaluate the sensitivity of abundance estimation to modifications in 1)

sampling frequency, 2) sampling duration, and 3) camera distribution. Specifically, for these three vital aspects of camera-trap study design, I investigated how modifications affected estimates of abundance, detection probability, and model performance. Further, the development of reliable sampling strategies and statistical techniques in Chapter 1 were critical to informing abundance-estimation efforts in Chapter 2.

In Chapter 2, I used the APR study's 2019–2022 camera-trap data to estimate annual white-tailed deer abundance by sex-and-age class in areas with varying harvest treatment (APR and Non-APR). My objectives were to empirically evaluate two, prevalent APR hypotheses: 1) that APRs increase the abundance of adult males, and 2) that APRs decrease overall deer abundance. Finally, the conclusion section at the end of my thesis provides a summary of my findings and general conclusions, including recommendations for practitioners modeling abundance with N-mixture models and camera-trap count data, and for managers considering alternative harvest regulations to achieve management goals.

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CHAPTER 1: CAMERA-TRAP SAMPLING STRATEGIES AFFECT ABUNDANCE ESTIMATION FOR AN UNMARKED DEER POPULATION

INTRODUCTION

Population abundance measures are crucial to ecological studies and form the foundation of effective wildlife-monitoring programs. Whether studying threatened species, invasive species, or game species, an understanding of abundance is important for evaluating the impact of conservation and management efforts (Kidwai et al. 2019, Schlichting et al. 2020, Christensen et al. 2021). However, meaningful assessments are only realized when the methodology is sensitive enough to detect population trends. Suboptimal sampling strategies can limit precision, accuracy, and the ability to identify temporal or spatial differences in abundance, which can then lead managers to incorrect inference and flawed decisions. Obtaining precise estimates of animal abundance can be logistically difficult, time-consuming, and costly (Pierce et al. 2012), requiring wildlife managers to balance the quality of results and the sampling strategy implemented (Marcon et al. 2019). Given the limited resources available for monitoring wildlife populations, there is a need for reliable and cost-effective methods sensitive enough to detect population trends needed by wildlife management agencies.

Remote cameras, also known as camera traps, have become a standard non-invasive method for monitoring wildlife populations. Their ease of use, cost-effectiveness, and capability to survey large geographic areas have made them a valuable and powerful tool in wildlife research (O'Connell et al. 2011, Burton et al. 2015, Parsons et al. 2017). Camera-trap data are typically categorized based on number of individuals and sometimes by physically distinguishable characteristics like sex and age. Once characterized, camera-trap data can be used to estimate population parameters, including density, abundance, and relative abundance

indices (Burton et al. 2015). These estimates can be compared over time and space to monitor population changes and test hypotheses about the effects of conservation and management actions. Most camera-trap studies to date have focused on estimating population abundance using individually recognizable, or "marked," animals (Gilbert et al. 2021). Consequently, abundance estimation of unmarked populations remains a significant frontier in camera trapping.

The application of camera traps as a wildlife population monitoring tool offers a myriad of advantages, albeit accompanied by the challenge of managing and processing image data (DeYoung 2011). With the surge in popularity of camera trapping and advancements in technology and data management, large quantities of image data (e.g., millions of images) are becoming more common, requiring time-consuming and labor-intensive efforts to process. To address this challenge, several potential solutions have been proposed, including improving data management efficiency (Price Tack et al. 2016), using artificial intelligence for photo processing (Vélez et al. 2022), and altering sampling strategies. Different sampling strategies that vary the survey duration or number of camera sites can have different travel and field-labor costs, but they may also affect precision and accuracy of abundance estimators. Sampling strategies must therefore be critically evaluated before formal application. Ultimately, understanding how sampling strategies influence abundance estimation is important for designing effective and efficient monitoring programs (Si et al. 2014).

A suite of models are available to estimate the abundance of unmarked animals based on camera-trap data, including site-structured models (see review by Gilbert et al. 2021). These analytical frameworks offer a unique advantage in that they incorporate ecological and

observational processes (Kéry and Royle 2015). By accounting for imperfect detection, these models can provide a more accurate picture of wildlife populations. Site-structured models are subject to critical assumptions, including population closure (i.e., no individuals leave or enter the population via birth, immigration, death, or emigration), detection probability is equal for all individuals, absence of false-positive detections (i.e., no misidentifications or double counting of individuals), and detections of individuals are independent of one another (Royle 2004). Deviations from these assumptions can affect the validity of the estimates produced by these models (Barker et al. 2018, Link et al. 2018). Consequently, if the underlying assumptions are not satisfied, it is advisable to interpret estimates as relative abundance indices instead of absolute values (Barker et al. 2018, Gilbert et al. 2021).

N-mixture models (Royle 2004) are site-structured models and have been successfully applied to numerous species, including birds (Lyons et al. 2012, Jakob et al. 2014, McCaffery et al. 2016, Zou et al. 2019), amphibians (Ficetola et al. 2018, Costa et al. 2020), reptiles (Ward et al. 2017, Barão-Nóbrega et al. 2022), and large mammals (Belant et al. 2016, Haus et al. 2019, Kidwai et al. 2019, Christensen et al. 2021, Brack et al. 2023). N-mixture models can be used to estimate site abundance and thus produce relative abundance indices (Burton et al. 2015). Implementing N-mixture models with camera-trap data has been found to be an effective approach for estimating size of unmarked white-tailed deer (*Odocoileus virginianus*) populations (Keever et al. 2017, Haus et al. 2019). Haus et al. (2019) found that this approach achieved greater precision compared to road-based distance sampling techniques that used spotlight or forward-looking infrared surveys. Keever et al. (2017) conducted a study using a known population of enclosed white-tailed deer and demonstrated that N-mixture models

accurately estimated population size. Additionally, the authors identified strategies for resource optimization by minimizing the necessary number of survey days. Although shorter surveys may reflect lower costs and reduced data-processing, estimates of free-ranging populations may be sensitive to such manipulations in sampling design (Haus et al. 2019). Further, the required sampling intensity may vary over the species' range, highlighting study-area specificity of camera-trap approaches (DeYoung 2011). Although N-mixture modeling has been applied successfully to camera-trap studies of white-tailed deer, there is still limited information on how different sampling strategies can affect abundance estimation of free-ranging populations.

An important consideration when applying N-mixture models to camera-trap surveys is the designation of sampling frequency, survey duration, and number of camera sites for survey design and abundance estimation. To address this matter, I used an existing camera-trap dataset from a Michigan study aimed to assess potential changes of a white-tailed deer (hereafter, deer) population following a harvest regulation change. That study generated a high volume of images (>2.6 million) that I leveraged and subset to conduct a *post hoc* methodological assessment. The goal of my study was to evaluate the consequences of sampling design and provide methodological recommendations to researchers and practitioners. My objectives were to evaluate the sensitivity of abundance estimation to modifications in sampling frequency, sampling duration, and camera distribution. For these three vital aspects of camera-trap study design, I investigated how modifications affected estimates of relative abundance, detection probability, and model performance. In the absence of knowledge about the true state of the deer population, I used a data-simulation approach to evaluate the robustness of my statistical inferences. I hypothesized there would be sampling

strategies that balanced precision of relative abundance estimates with high detection probability and model performance. The outcomes of my study allowed me to offer methodological recommendations for camera-trap survey design. More specifically, my results identified sampling strategies that minimize financial and human resources to attain precise and reliable estimations of deer relative abundance using N-mixture models and highlight the importance of sampling relevant to animal activity.

STUDY AREA

The study took place in the south-central Lower Peninsula of Michigan in a 5-county area (Newaygo, Kent, Mecosta, Montcalm, and Ionia County; hereafter, 5-County Area) that included a known chronic-wasting-disease hotspot (Kent and Montcalm County; Figure 1.1). In 2019, an antler point restriction (APR) was implemented in a portion of the 5-County Area and a study was designed to evaluate its effect on the abundance and sex-and-age composition of deer populations in the area. Specifically, the APR prohibited hunters from harvesting antlered deer that did not have at least 4 antler points on one side. A paired-comparison study design was implemented to monitor deer populations in APR and non-APR areas (i.e., experimental and control areas, respectively). A robust before-after-control-impact (BACI) study design (Green 1979) was employed to monitor potential population-level changes, over 3 consecutive years (2020–2022), following the regulation change. This design was intended to allow researchers to identify changes in population abundance and composition in the treatment area (APR Zone) relative to the control area (Non-APR Zone) over the course of the study.

The study implemented a camera-trap sampling design restricted to 8 townships within the 5-County Area, encompassing an area of approximately 749 km² (Figure 1.1). In the APR

Zone (4,845-km²), antlered deer with at least four points on one antler could be taken with a valid license (a legal point was defined as ≥ 2.54 cm [1 inch] long as measured from its tip to the nearest edge of antler beam). In the Non-APR Zone (4,488-km²), any antlered deer with an antler ≥ 7.62 cm (3 inches) in length could be taken. Apart from the APR regulation, all other deer-hunting regulations were comparable between the APR and Non-APR Zones (Frawley 2020, 2021, 2022). Deer hunting occurred every fall and regulations were similar between zones prior to the 2019 APR-regulation change. Natural predators included coyote (*Canis latrans*) with the addition of bobcat (*Lynx rufus*) and American black bear (*Ursus americanus*) in the northernmost stretches of the study area.

The 5-County Area spanned a floristic tension zone and multiple ecoregions, including the Lansing loamy plain ecoregion in the south and Newaygo barrens and Cadillac hummocky moraines ecoregions in the north (Barnes and Wagner 2004, EPA 2010). Consequently, the study area was a fragmented mosaic composed of different land-use and land-cover types. The southern region was flat and dominated by large expanses of agricultural land (primarily corn, soybeans, wheat, alfalfa), fragmented woodlots, and development (Albert 1995). The southern region was distinguished from the northern by warmer annual temperatures and a longer, less variable growing season (Barnes and Wagner 2004). At higher latitudes, the landscape transitions to sandy rolling hills, greater forest cover (Albert 1995), and an increased conifer presence in uplands and wetlands (Barnes and Wagner 2004). Across the study area, average elevation is approximately 268 m with a range of 182–411 m. Overstory vegetation in the study area varied by ecoregion but included northern hardwood (dominated by maple [*Acer spp.*], oak [*Quercus spp.*], and hickory [*Carya spp.*]) and pine (*Pinus spp.*) with scattered hardwood-conifer

swamps (Albert 1995). The 5-County Area was approximately 9,332 km² and 40% was used for agriculture, 30% was forested, 15% wetland, and 12% was developed (Dewitz and USGS 2021). Monthly mean temperatures ranged from -6.1–21.1 °C, with a mean annual precipitation of 84 cm, including 165 cm of snowfall (NOAA 2021).

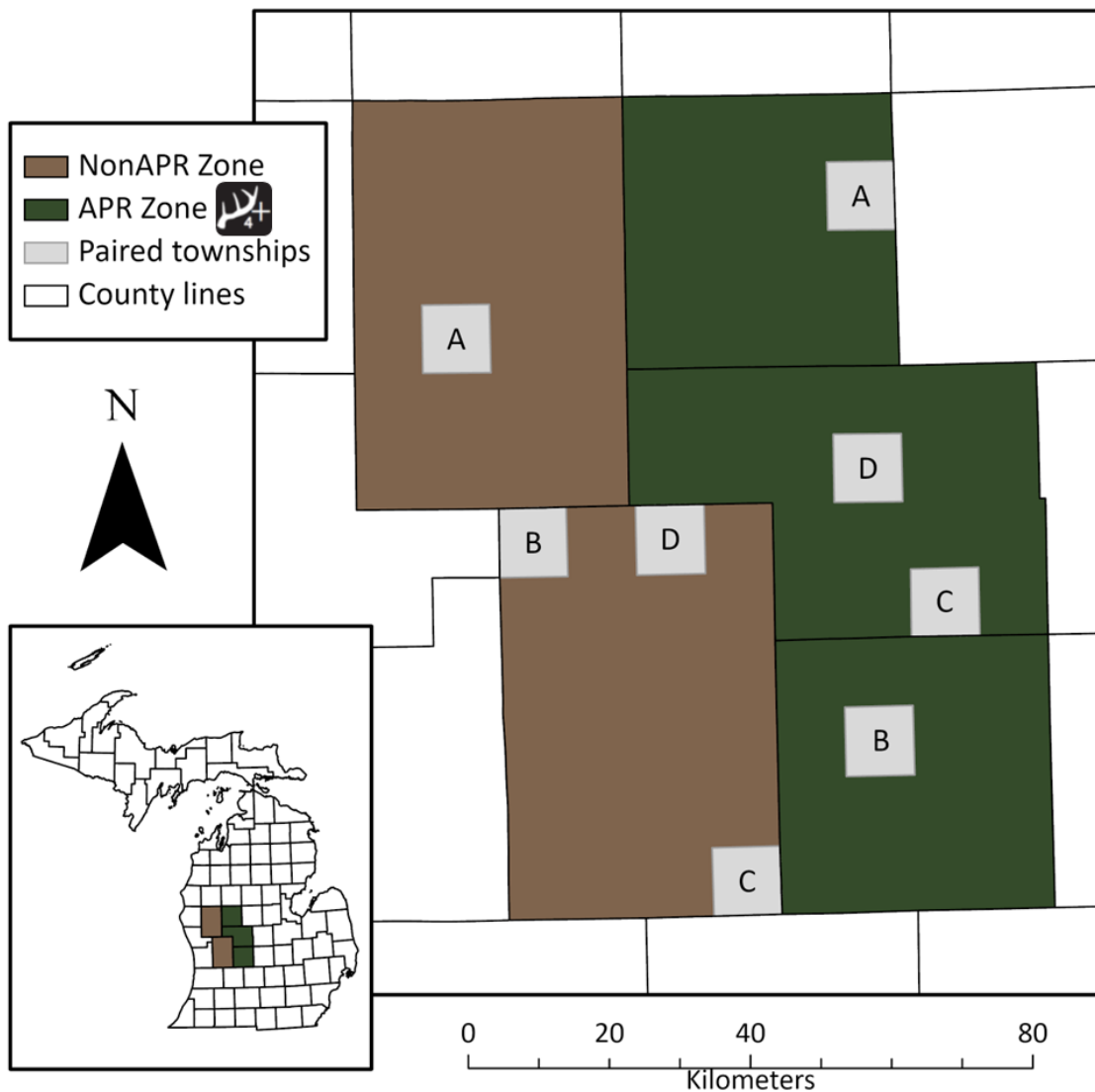


Figure 1.1. Study area in the south-central Lower Peninsula of Michigan, USA, in a designated 5-county area that included a known chronic-wasting-disease hotspot. Mandatory antler point restrictions (APRs) were implemented in 2019 in the experimental area (APR Zone) and not in the control area (Non-APR Zone). Townships were paired (A–D) between zones, and remote cameras were placed in each township to monitor white-tailed deer (*Odocoileus virginianus*) populations over a duration of four years (2019–2022). Maps created in ArcGIS Pro (version 2.7.1; ESRI 2020).

METHODS

Site selection

The study area was longitudinally divided instead of latitudinally to minimize the effects, other than APRs (e.g., land-use and land-cover types), on deer populations. Landscape compositional analyses (e.g., % forest, % public hunting land) were completed for each township in the 5-County Area to identify similar townships for pairing. Additional pairing criteria included geological features (e.g., rivers), human density, and apparent CWD presence (Table 1.1). Eight townships were systematically selected and paired between the APR Zone and Non-APR Zone to compare deer populations over time at a scale that was achievable with camera-traps while also reflecting the variation within the 5-county study area (Figure 1). A stratified-random design (at the township-section scale) was used to select 144 camera sites evenly across the 8 townships using generalized random-tessellation stratification (GRTS; Stevens and Olsen 2004). The GRTS sampling design is advantageous because it maintains statistical qualities of a random draw when removing intractable samples (i.e., no land access), while yielding a spatially balanced set of points (Stevens and Olson 2004). Random camera placement was selected with the intent of providing the least biased approximation of population structure. Sample sites were located on both public and private land, the latter necessitating landowner permission.

Table 1.1. Criteria used to determine township pairings (A, B, C, D) between experimental and control areas zones (APR and Non-APR Zones, respectively) for a before-after-control-impact study design. Eight townships were paired based on similarities including land-cover features, geographic features, and apparent presence of chronic wasting disease. Pairings were applied to a camera-trap study design in the south-central Lower Peninsula of Michigan, USA, 2019.

Pairing	APR Zone township	Non-APR Zone township	Pairing criteria
A	Sheridan	Sherman	Heavily forested, public lands
B	Easton	Tyrone	Mixed cover, large rivers, public lands
C	Bushnell	Bowne	Agriculturally dominated
D	Douglass	Nelson	Agriculture-forest mix, CWD detected

Camera-trap setup and data collection

Eighteen infrared cameras (Strike Force HD Pro X®, Browning Trail Cameras, Birmingham, AL) were deployed in each of the 8 selected townships. Camera make and model were selected to balance cost and trigger speed. To minimize potential bias, camera sites were nonbaited (Koerth and Kroll 2000, McCoy et al. 2011, Newbolt et al. 2017) and placed as close to the generated GRTS sample locations as possible (Kays et al. 2009). In exceptional circumstances cameras were placed within 100 m of the point. In such situations, exact camera location was selected to avoid locations with a high risk of theft, open water, road rights-of-way, close proximity to human dwellings, and to maintain a clear field of view. Cameras were oriented north to minimize direct sunlight exposure, false triggers caused by exposure to the sun's rays (Wilton 2021), and observer bias in placement. Cameras were placed on a straight tree and secured with a security box, cable, and lock. If no suitable trees were available, a steel T-post was used to mount the camera. Cameras were mounted so that the center of the lens was 36–41 cm (14–16 inches) above the ground and the horizon was centered in the field of view (guidance provided by Moll et al. 2018). The selected camera height was intended to detect all age groups of deer and allow overhanging vegetation (e.g., branches) to be reached and removed from the field of view. Ground vegetation and debris were cleared 5 m in front of the camera to minimize false triggering and allow for an unobstructed field of view.

Cameras were active for 63 days on 24-hour capture mode with a 5-sec delay, taking a burst of 3 photographs per motion-triggered event. Since camera sites were not baited, cameras were programmed to rapid fire (0.3 sec between each image within a burst) and fast-motion infrared flash to maximize clear images of mobile deer. Photo data were collected

during what was considered a 9-week closure period (i.e., no immigration or emigration) from 15 July to 15 September for four consecutive years (2019–2022). Each camera site was visited for maintenance (e.g., check batteries, change memory cards, clear vegetation) approximately every two weeks over the duration of the data-collection period. Camera surveys were used to create detection histories for each site. If a camera was not functional for some time, these occurrences were treated as missing data in the detection history (Furnas et al. 2020).

All photos were entered into Colorado Parks and Wildlife Photo Warehouse, a Microsoft Access application designed to facilitate camera-trap photo processing (Newkirk 2016). Deer were counted in each image and classified as Fawns, Does (yearling and adult females), Sub-legal Males (antlered deer that did not meet the APR criteria), Legal Males (antlered deer that met the APR criteria), or Unknown Deer. Deer were classified as Unknown when it was impossible to determine the sex and age of an individual (e.g., unable to see head). To minimize misidentifications, all photos were processed by two independent observers that received species-specific image training (Newbolt and Ditchkoff 2019, Elliot et al. 2022). Photo data was considered validated when photo classifications matched between the two observers (e.g., 1 Doe and 2 Fawns in the photo). If there was a discrepancy on the identification of a deer in an image, then a third observer served as a referee. Discrepancies were judged by an experienced referee to maintain consistent and accurate classification of photographs (Newbolt and Ditchkoff 2019, Elliot et al. 2022). See the Appendix for detailed camera-trap and photo-review protocols (Appendix 1A, Appendix 1B, respectively).

Abundance modeling

In this study, I used relative abundance of deer as an index, assuming it was functionally related to population size. Specifically, I summed site-level abundances to derive an estimated total study-area abundance, where total abundance related to the number of deer within the total area of all 1.24-km² effective sampling areas in the study area (e.g., 144 camera sites = 179 km² [69 mi²]; Figure 1.2). Hence, my abundance estimates reflect relative abundance, not absolute, as I did not infer site-level abundances for areas beyond the total surveyed area (i.e., total effective sampling area). Since the larger study included baseline data, and intended to look at change over time, the use of relative abundance as an index was deemed sufficient.

To account for imperfect detection, I estimated population parameters with a closed N-mixture model (Royle 2004) applied to camera surveys of unmarked deer. As described by Kéry and Schaub (2012), I implemented a Bayesian hierarchical framework using software program JAGS (Plummer 2003) in program R (version 4.1.2; R Core Team 2021) with the jagsUI package (Kellner 2015). I chose this Bayesian approach because of its ease of use for fitting hierarchical models and it allowed me to build a custom model that embodied complex ecological processes while accounting for uncertainty of population parameters. Essentially, the N-mixture model consists of two linked generalized linear models. The first generalized linear model is the ecological process. The ecological process yields the latent state and the spatial variation of abundance at site i , N_i , for a group of sites with a mean λ (Kéry and Schaub 2012). Since properly modeling error maximizes the utility of N-mixture models (Joseph et al. 2009), it was important to select a mixing distribution that best fit the underlying data. An exploratory data analysis was conducted using data from this study and included an evaluation of N-mixture

models with alternative mixing distributions, including Poisson, zero-inflated Poisson, negative binomial, and Poisson lognormal (Appendix 1C). Results from those explorations indicated that the Poisson mixing distribution best fit the data (Appendix 1C). Using these results as guidance, I opted to use the Poisson distribution in my ecological-process model. To extract more information from the data and better allocate variance, I built on the ecological model to include township as a random effect on abundance, thus λ was described as $\mu\lambda$ (i.e., a distribution of distributions):

$$N_i \sim \text{Poisson}(\mu\lambda_i)$$

I assumed site abundances reflected the number of deer within a 1.24-km² (0.48-mi²) circular buffer around each camera-trap site, which represents an effective sampling area (Figure 1.2) equivalent to the average summer home range size of a rural female deer ($n = 22$) in the south-central region of the Lower Peninsula, Michigan (Trudeau et al., unpublished data). Agriculture was the dominant land-cover class in the study area and is considered an important driver of demographic variation in abundance (Nixon et al. 1991, Nixon et al. 1994, Nixon et al. 2001) and antler growth (Felix et al. 2002, Strickland and Demarais 2008). Further, exploratory data analyses identified agricultural cover as a valuable predictor of abundance (Appendix 1C). For these reasons, I included agriculture cover as a covariate in the ecological-process model. I calculated the proportion of agricultural cover using effective sampling areas and the National Land Cover Database (Dewitz and USGS 2021) land-cover classification layer (30-m² resolution) in ArcPro (ESRI 2020). This approach allowed me to extract values and collapse 3 NLCD land-cover types (herbaceous, hay/pasture, cultivated crops) into a single agriculture classification. I incorporated the effects of the agriculture covariate into the ecological model, associated with

abundance through a log-link function, and described by a nonlinear relationship with percent agricultural cover as a site-specific covariate. Additionally, I included a random intercept κ into the log-link function, which allowed township to act as a random effect on abundance:

$$\log(\mu\lambda_i) = \kappa(\text{Township}_i) + \beta_2(\%Agriculture)^2$$

The second generalized linear model of the N-mixture framework is the observational process. The observational process yields the observed counts $y_{i,j}$ (given N_i) at site i and during replicate survey j , and are described by a binomial distribution with sample size N_i and detection probability p (Kéry and Schaub 2012):

$$y_{i,j} | N_i \sim \text{Binomial}(N_i, p[\text{Cover}_i])$$

Cover data were collected during camera-trap setup and was defined as far cover or the majority of cover in a 100-m radius of the camera (open or closed). Note that I included cover in the observational-process model as it may be important to the presence and detectability components of detection probability. Further, an exploratory data analysis evaluated the value of alternative covariates and identified cover (far cover) as important to the detection process (Appendix 1C). To incorporate this covariate on detection probability, I used a logit-link function, described by a linear relationship with site-specific cover:

$$\text{logit}(p_i) = \alpha + \beta_1(\text{Cover}_i)$$

With regards to the Bayesian framework, I assumed vague prior distributions for all analyses to express the absence of prior information about estimated parameters. For my Markov Chain – Monte Carlo (MCMC) approach, I ran 3 parallel chains for 50,000 iterations, discarded the first 3,000 iterations as burn-in, and thinned the remaining iterations by 1 in 5, resulting in 28,200 draws of the posterior distribution for inference. Parameters monitored

included total N , p , α , β values, and κ values. I monitored model convergence by evaluating posterior distributions, visual inspection of MCMC trace plots, and using the Gelman-Rubin convergence diagnostic (R-hat or $\hat{R}$; Gelman 2006).

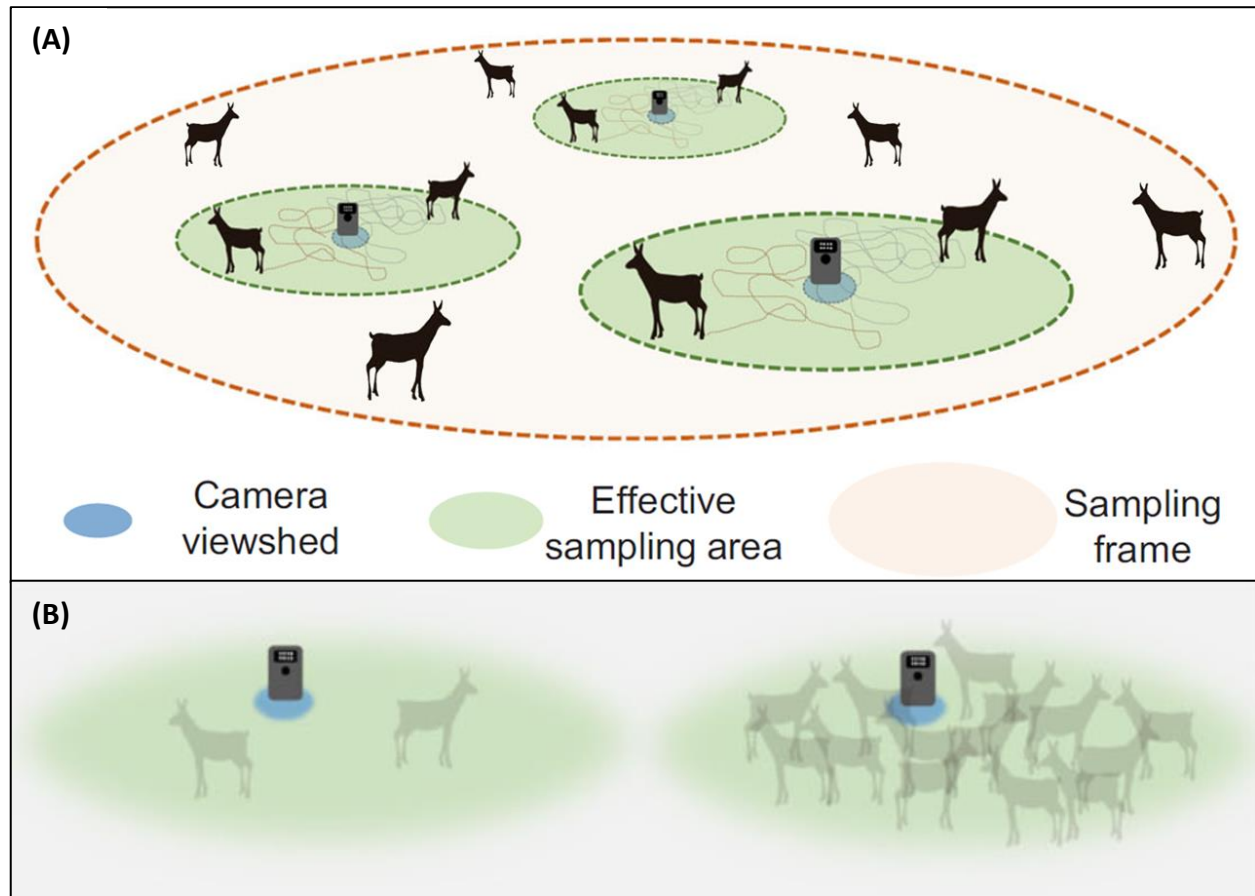


Figure 1.2. Camera-trap study design used to estimate relative abundance of unmarked white-tailed deer (*Odocoileus virginianus*) where (A) the effective sampling areas for individual cameras are functions of animal movement and survey length, and (B) relative abundance measures the number of deer at one camera site compared with another. Relative abundance was used as an index assumed to be functionally related to population size. This study produces relative abundance estimates for the effective sampling area (green) of independent cameras and aggregations of cameras ($n = 18$) within each township (orange). Township abundances were aggregated to produce a single population estimate. Revised images from Gilbert et al. 2021.

Sensitivity analyses

I conducted a *post hoc* sensitivity analysis to evaluate the sensitivity of parameter estimates to sampling strategies that modified daily-sampling frequency (i.e., counts per day), sampling duration (i.e., number of days in sampling period), and the distribution of camera sites (i.e., number of camera sites per township). I simulated these scenarios using my N-mixture modeling approach and evaluated the sensitivity of relative abundance, detection probability, and model performance to alternative sampling strategies. Sensitivity was calculated as the relative change of the output quantity (e.g., relative change of precision). To standardize precision of abundance estimates for meaningful comparisons across treatments, I calculated the percent coefficient of variation (%CV) by multiplying the quotient of standard deviation (SD) divided by the mean ($\bar{x}$) by 100:

$$\%CV = \left(\frac{SD}{\bar{x}} \right) * 100$$

For my sensitivity analyses I used a subset of validated photo data from the 2019 field season. Since I was interested in using the product of this research to detect potential population-level changes over time, final sampling approaches recommended will maximize precision of relative abundance estimates while considering detection probability and model performance.

Data simulation and model diagnostics

Since truth was unknown for the deer population in my study, I used a modeling approach to explicitly simulate ‘true’ scenarios of deer abundance (i.e., scenarios of known abundance). To supplement my sensitivity analysis, simulations allowed me to investigate the performance and accuracy of my N-mixture model under alternative-sampling strategies (i.e.,

sampling frequency, sampling duration, camera distribution). For each sampling strategy, I generated 50 unique datasets per scenario to capture variability in random draws and produce a comparable number of data points. Using program R (version 4.1.2; R Core Team 2021), I simulated ‘true’ scenarios of deer abundance as Poisson distributed. The Poisson distribution was selected based on recommendations provided by an exploratory data analysis (Appendix 1C). I also incorporated parameters estimated from empirical data into simulations, including mean site abundance by township (random effect), coefficient values for the percent-agriculture covariate on abundance (β_2, β_3), and mean detection probability. For each set of simulations, I defined the scenario-specific number of camera sites and counts (e.g., 9 camera sites per township and 63 counts per site).

To enable comparisons among sampling strategies, I used root-mean-square error (RMSE) as a metric to evaluate model performance, complemented by relative bias (RB) analysis (Duarte et al. 2018). Specifically, I used RMSE as a measure of overall accuracy and RB to assess the directionality of biases in model output. I calculated RMSE as the average distance between simulated truth and predicted data values by taking the square root of the mean-squared difference between simulated abundance and predicted abundance (i.e., the square root of the variance of the residuals):

$$RMSE = \sqrt{\frac{\sum_{i=1}^n (N_i - \hat{N}_i)^2}{n}}$$

Using RMSE as a model-performance metric allowed me to aggregate the magnitudes of errors in predictions into a single measure of predictive power on the same scale as the unit being predicted (i.e., site abundance). RMSE values are always non-negative and although unlikely, a

value of zero indicates a perfect fit of the data. Thus, I considered scenarios with lower RMSE values as having more predictive power.

I calculated RB by subtracting simulated abundance (N) from predicted abundance ($\hat{N}$) divided by simulated truth (Doser et al. 2022), for each camera site (i), summed across the total number of camera sites (n):

$$RB = \frac{\sum_{i=1}^n (N_i - \hat{N}_i)}{\sum_{i=1}^n (N_i)}$$

Relative bias values that approximated and were centered around zero represented no bias between simulated truth and predicted abundance. Negative and positive RB values indicated an under and over estimation of abundance, respectively.

I estimated parameters for each simulated dataset using my N-mixture modeling approach, but since model convergence improved under simulated scenarios, I reduced MCMC settings to 12,000 iterations and a burn-in of 2,000 (resulting in 6,000 draws total) to accelerate simulations. To further reduce computation time, I used supercomputing resources at Michigan State University's High Performance Computing Center. For each sampling scenario, I obtained parameter (β_2 , β_3 , RMSE, RB) summary statistics by integrating the 50 distinct posterior distributions and calculating mean and 95% quantile values (Q95%; Doser et al. 2022) from the associated 300,000 data points. Sensitivity analyses also incorporated these model-performance metrics. I monitored coefficient (β_2 , β_3) and quantile values to determine if results were reasonable given the 'true' parameter values (i.e., overlapping error).

Daily-sampling frequency

I evaluated how population parameters were affected by different daily-sampling frequencies (i.e., counts per day), including 1, 2, 3, and 4 times per day and at crepuscular hours. I accomplished this by systematically sampling within distinct daily time intervals throughout the sampling period. Counts were restricted to the maximum number of individuals (aggregated by class) observed in a single image, per unit of time (Haus et al. 2019, Zou et al. 2019). To better align with deer activity, standard time was rescaled to local solar time. For daily sampling frequencies 1, 2, 3 or 4 times per day, I divided the day into 1–4 even time intervals and sampled within each interval. For example, a daily frequency of 2 generated 2 samples per day (2 counts), one for the first half of the day and another for the second half of the day (solar noon = midday). Crepuscular sampling generated 2 samples per day (2 counts) using 2-hr intervals around sunrise and sunset (i.e., 1 hour before and after sunrise and sunset). I estimated parameters using my N-mixture abundance modeling approach and summarized parameters by mean and 95% Bayesian credible intervals (95% BCI). I concluded that scenarios generated different estimates if there was no 95% BCI overlap.

Sampling duration and camera distribution

I simulated reductions in sampling intensity by reducing the number of days in the sampling period and the number of camera sites distributed. The sampling-duration and camera-distribution scenarios were modeled independently from one another. I evaluated the sensitivities of these reductions on parameter estimation to determine if subsampling could produce sufficient precision. My approach included comparing parameter estimates from reduced datasets to parameter estimates from the full dataset. For the sampling-duration

scenario, I reduced days from the full sampling period (63 days) by 7-day steps to simulate sampling durations of 56, 49, 42, and 35 days. Sampling durations did not specifically include sequential blocks of days, but instead days were selected at random within the 63-day window of the full sampling period (15 July to 15 September). My intent of this random approach was to identify sampling durations (i.e., total number of days) that performed well regardless of calendar date. For distribution of camera sites, the number of camera sites corresponded to the number distributed in each of the 8 townships surveyed (1 township = 93 km² [36 mi²]). I reduced the number of camera sites from 18 by steps of 3 to simulate camera distributions of 15, 12, and 9 per township. Individual camera sites were randomly selected from the 18 pre-established sites within each township. I opted to choose camera sites randomly rather than relying on specific data metrics (e.g., land cover) to capture an unbiased snapshot of populations and ensure alignment with model assumptions (e.g., equal detectability). To capture variability in random-sampling approaches, I generated 10 unique datasets for each sampling-duration and camera-distribution scenario (e.g., 10 random datasets for the 35-day treatment). Additionally, I replicated the 100%-data scenario (63 days with 18 sites per township) 10 times to produce a comparable number of datapoints to the treatments ($n = 282,000$). I simulated random datasets and estimated parameters using my N-mixture abundance modeling approach. Final count data were determined using the best performing daily-sampling frequency identified during my initial analysis. For each sampling scenario, I obtained parameter summary statistics by integrating the 10 distinct posterior distributions and calculating mean and 95% quantiles (Q95%; Doser et al. 2022) from the associated 282,000

datapoints. I concluded that scenarios generated different estimates if there was no Q95% overlap.

RESULTS

Data collection and processing

The data subset from 2019 included photo data from 144 camera traps deployed for 63 days, which resulted in a total survey effort of 8,772 trap days. Including camera operation failures, average camera deployment period was 61 days (SD = 5.9; range = 27–63 days). Twenty-four cameras were not fully operational during deployment due to memory cards filling up (from false triggering), camera malfunctioning, and vandalism. Camera density was approximately 1 per 5.2 km² (1 per 2.0 mi²) within each township and cameras averaged 1.4 km (SD = 0.7) between nearest neighbor camera sites.

Camera traps collected 797,407 images during the 2019 survey period, including 275,794 images with deer in the field of view (≥ 1 deer in each image). The APR Zone accounted for 414,626 images, including 155,111 with deer. The Non-APR Zone accounted for 382,781 images, including 120,683 with deer. All but 5 cameras detected deer throughout the sampling period. Most deer photos included Does in the field of view ($n = 146,145$; Table 1.2). With the exception of Unknown Deer ($n = 16,161$), Legal Males were photographed the least ($n = 20,039$; Table 1.2). Deer were photographed most frequently around sunrise and sunset, with most detections occurring between 0.2 and 0.35 (24-hr time rescaled 0–1; Figure 1.3).

Table 1.2. Summary of white-tailed deer (*Odocoileus virginianus*) image classifications by sex and age class, zone, and study area. Note that a single image could include multiple classifications (e.g., doe and fawn in image). Images were collected using a camera-trap study design in the south-central Lower Peninsula of Michigan, USA, 2019.

Photo classification	APR Zone	Non-APR Zone	Study area total
Doe	84,205	61,940	146,145
Fawn	57,416	54,456	111,872
Sub-legal Male	24,649	15,392	40,041
Legal Male	14,404	5,635	20,039
Unknown Deer	9,627	6,534	16,161



Figure 1.3. White-tailed deer (*Odocoileus virginianus*) diel activity pattern of each sex-age class (Doe, Fawn, Legal Male, Sub-legal Male, Unknown Deer) during 15 July–15 September 2019 camera-trap surveys in the south-central Lower Peninsula, Michigan. Deer detected (≥ 1 individual) in photographs were used as an index for activity. Standard time was rescaled to local solar time (0–1). Dashed vertical lines indicate sunrise and sunset times.

Abundance modeling

For all sampling scenarios with empirical data, N-mixture models converged with $\hat{R}$ values <1.1 (Gelman and Rubin 1992) and adequate mixing based on visual inspection (Gelman 2006). Similarly, successful convergence was achieved with simulated datasets. Simulated datasets also yielded estimates of β_2 and β_3 coefficients comparable (i.e., overlapping error) to those estimated with the empirical data. Collectively, these results indicated that the MCMC sampler reached stationary distributions and that the predictor of abundance (% agriculture) performed consistently among sampling scenarios.

Daily-sampling frequency

The sensitivity analysis indicated that selected daily-sampling frequency had a significant effect on most parameter estimates. For frequencies 1, 2, 3, and 4 per day, I found that mean relative abundance increased as daily-sampling frequency increased (Figure 1.4). Crepuscular sampling produced significantly lower relative abundance estimates than all other frequencies ($\bar{x} = 1,374$; 95% BCI = 1,286–1,471; Figure 1.4). The precision of abundance estimates were relatively insensitive to changes in sampling frequency with CVs approximating 3% for all scenarios (Figure 1.4). I found a negative relationship between daily-sampling frequency and mean detection probability, with detection probability decreasing as sampling frequency increased (Figure 1.5). The 1-per-day frequency produced significantly higher detection probabilities than all other scenarios ($\bar{x} = 0.073$; 95% BCI = 0.062–0.085; Figure 1.5). Apart from the 1-per-day frequency, crepuscular sampling produced detection probabilities ($\bar{x} = 0.028$; 95% BCI = 0.023–0.034) similar to all other scenarios (Figure 1.5).

My sensitivity analysis also indicated that selected daily-sampling frequency influenced model performance. The accuracy of the abundance estimator was highest (lowest RMSE) with the 1-per-day ($\bar{x} = 3.07$; 95% BCI = 2.02–5.91) and crepuscular ($\bar{x} = 2.54$; 95% BCI = 1.83–4.69) sampling strategies and lowest (highest RMSE) with 3 per day ($\bar{x} = 3.60$; 95% BCI = 2.12–8.48; Figure 1.6). On average, all sampling frequencies produced relatively unbiased abundance estimates (i.e., RB approximated and centered around 0; Figure 1.6). However, error intervals (Q95%) suggested slight underestimation, especially with the 3-per-day sampling frequency (Figure 1.6).

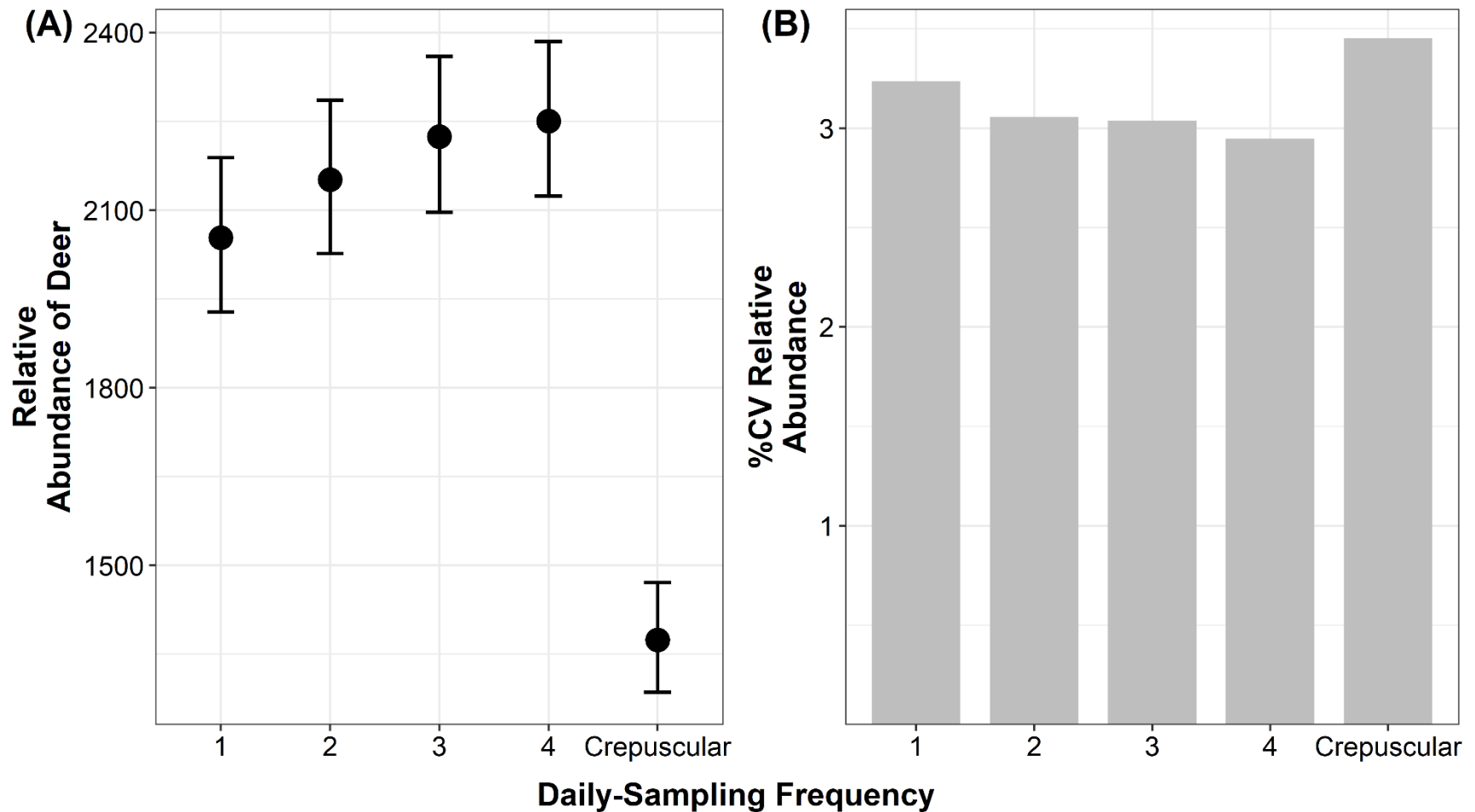


Figure 1.4. Estimates of (A) relative white-tailed deer (*Odocoileus virginianus*) abundance and (B) associated percent coefficient of variation (%CV) by alternative daily-sampling frequencies (i.e., counts per day). Relative abundance was used as an index and assumed to be functionally related to population size. Crepuscular sampling generated 2 counts per day using 2-hr intervals around sunrise and sunset. Error bars indicate a 95% Bayesian credible interval. Estimates were obtained using an N-mixture modeling approach applied to a camera-trap study design in the south-central Lower Peninsula of Michigan, USA, 2019.

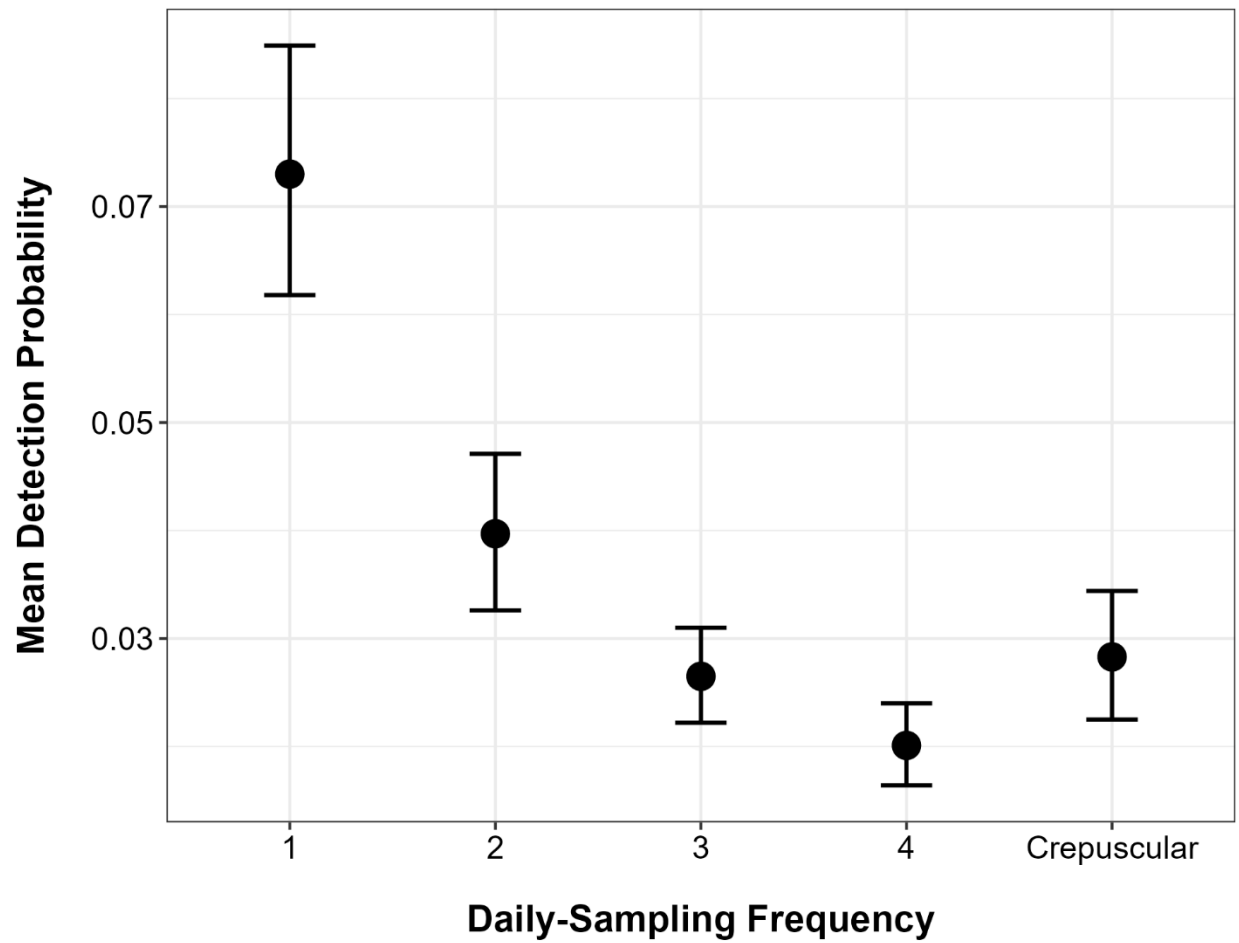


Figure 1.5. Mean white-tailed deer (*Odocoileus virginianus*) detection probability by alternative daily-sampling frequencies (i.e., counts per day). Crepuscular sampling generated 2 counts per day using 2-hr intervals around sunrise and sunset. Error bars indicate a 95% quantile interval. Estimates were obtained using an N-mixture modeling approach applied to a camera-trap study design in the south-central Lower Peninsula of Michigan, USA, 2019.

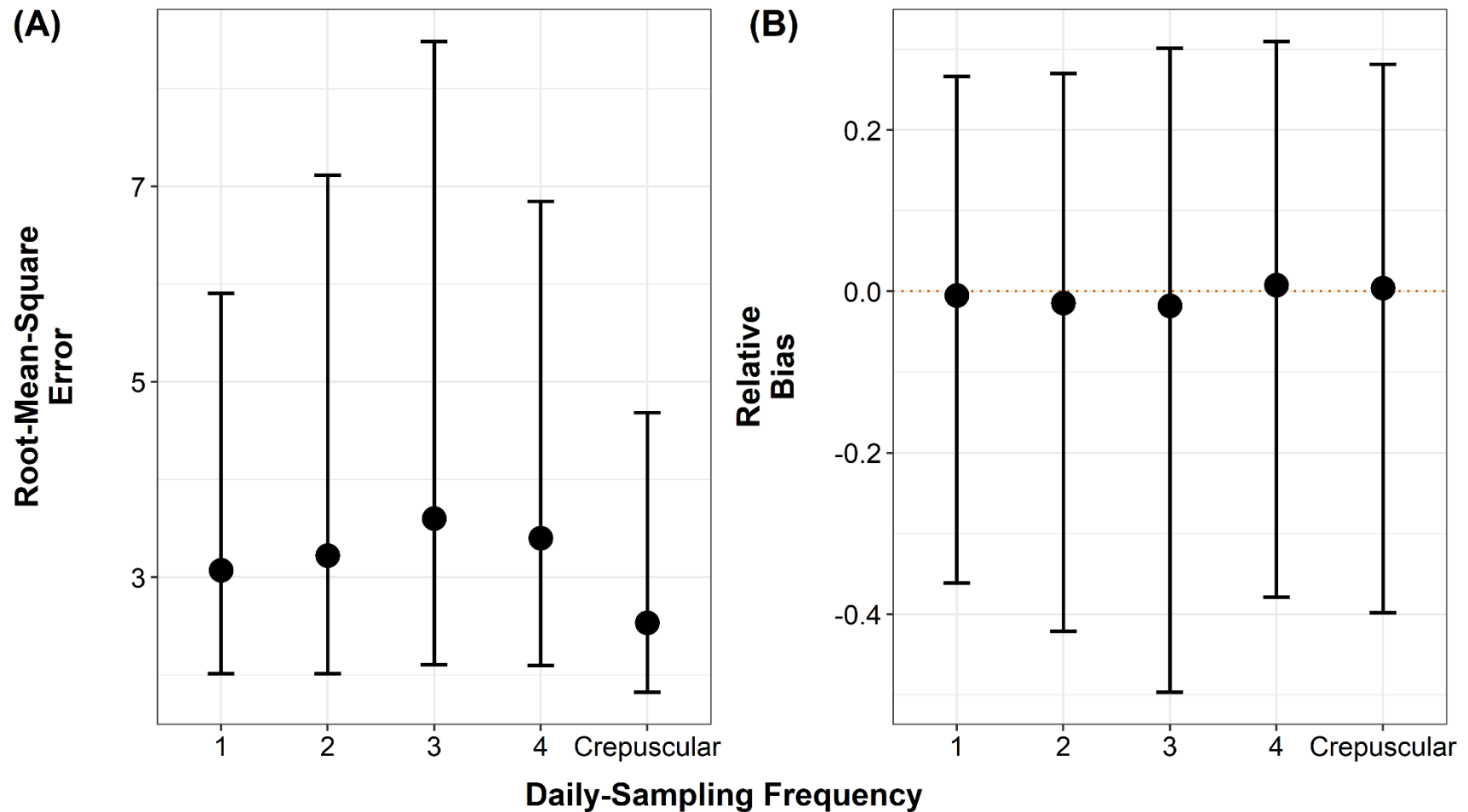


Figure 1.6. (A) Root-mean-square error and (B) relative bias of white-tailed deer (*Odocoileus virginianus*) abundance estimates by alternative daily-sampling frequencies (i.e., counts per day). Error bars indicate a 95% quantile interval. The dashed, orange horizontal line represents zero or no bias between simulated truth and predicted abundance. Crepuscular sampling generated 2 counts per day using 2-hr intervals around sunrise and sunset. Estimates were obtained using empirical and simulated data with an N-mixture modeling approach applied to a camera-trap study design in the south-central Lower Peninsula of Michigan, USA, 2019.

Sampling duration

The sensitivity analysis with the 1-per-day sampling frequency indicated that sampling duration had a significant effect on relative abundance estimates. I found a positive relationship between the number of days in the sampling period and relative abundance (Figure 1.7). Both the 56-day ($\bar{x} = 1,956$; Q95% = 1,828–2,094) and 63-day ($\bar{x} = 2,046$; Q95% = 1,920–2,181) scenarios produced relative abundance estimates significantly higher than the 35-day scenario ($\bar{x} = 1,618$; Q95% = 1,459–1,796; Figure 1.7). Further, I found that precision improved (i.e., %CV decreased) with more days sampled with a CV ranging from 5.41% (35-day scenario) to 3.26% (63-day scenario; Figure 1.7). I found an inverse relationship between the number of days in the sampling period and mean detection probability (Figure 1.8). Mean detection probabilities ranged from 0.074 (63-day scenario; Q95% = 0.062–0.086) to 0.092 (35-day scenario; Q95% = 0.077–0.108) and were comparable among all scenarios (Figure 1.8).

My sensitivity analysis with the 1-per-day sampling frequency also indicated that sampling duration had a slight influence on the accuracy of the abundance estimator. Specifically, I found that model error (RMSE) was the highest with the 56-day scenario ($\bar{x} = 3.13$; Q95% = 2.00–6.63; Figure 1.9). The model produced relatively unbiased abundance estimates across all scenarios (i.e., RB approximated and centered around 0) with some higher underestimation occurring with the 56-day and 63-day scenarios (Figure 1.9).

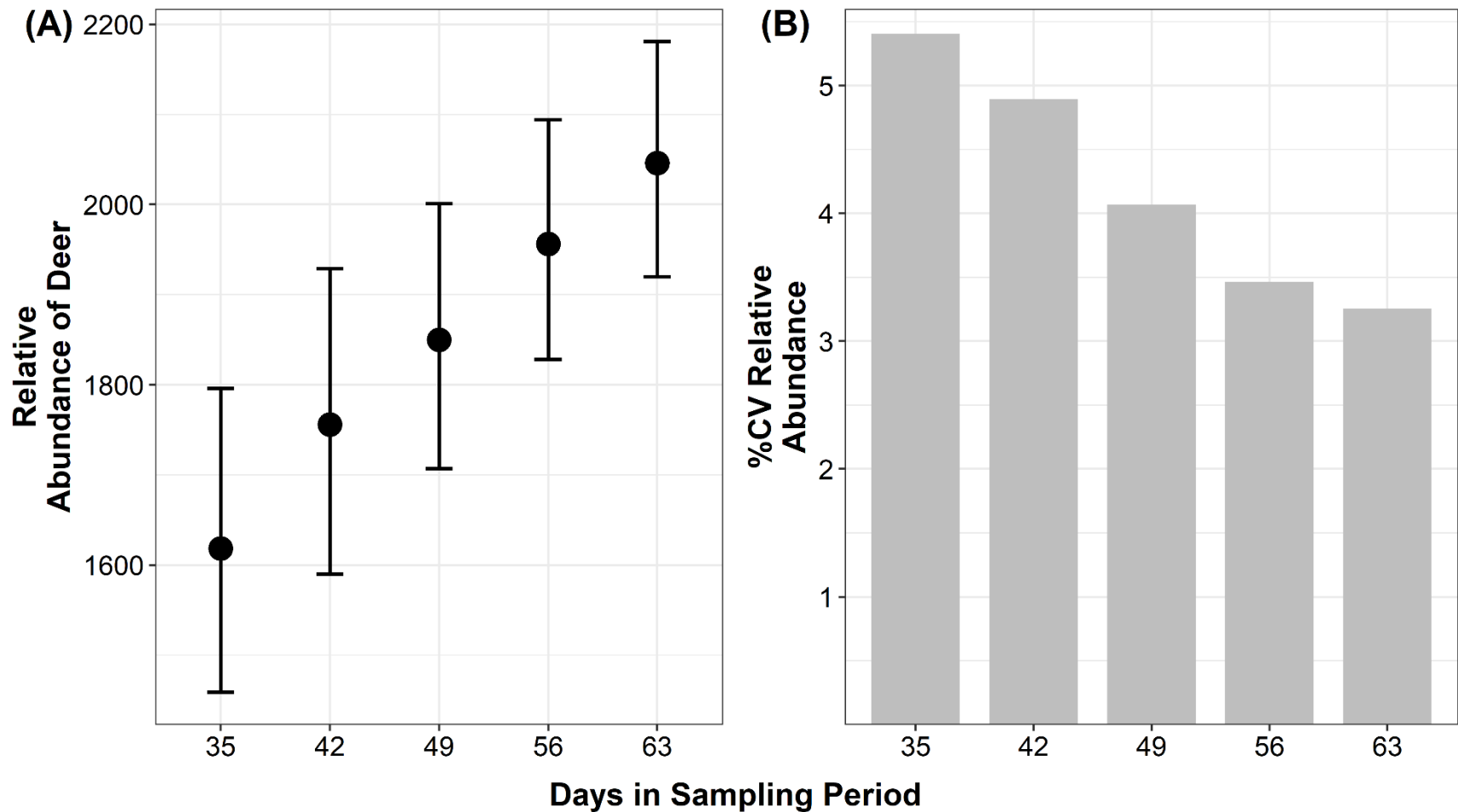


Figure 1.7. Estimates of (A) relative white-tailed deer (*Odocoileus virginianus*) abundance and (B) associated percent coefficient of variation (%CV) by number of days in sampling period. Relative abundance was used as an index and assumed to be functionally related to population size. Counts were restricted to the maximum number of individuals observed in a single image per day (daily-sampling frequency = 1). Error bars indicate a 95% quantile interval. Estimates were obtained using an N-mixture modeling approach applied to a camera-trap study design in the south-central Lower Peninsula of Michigan, USA, 2019.

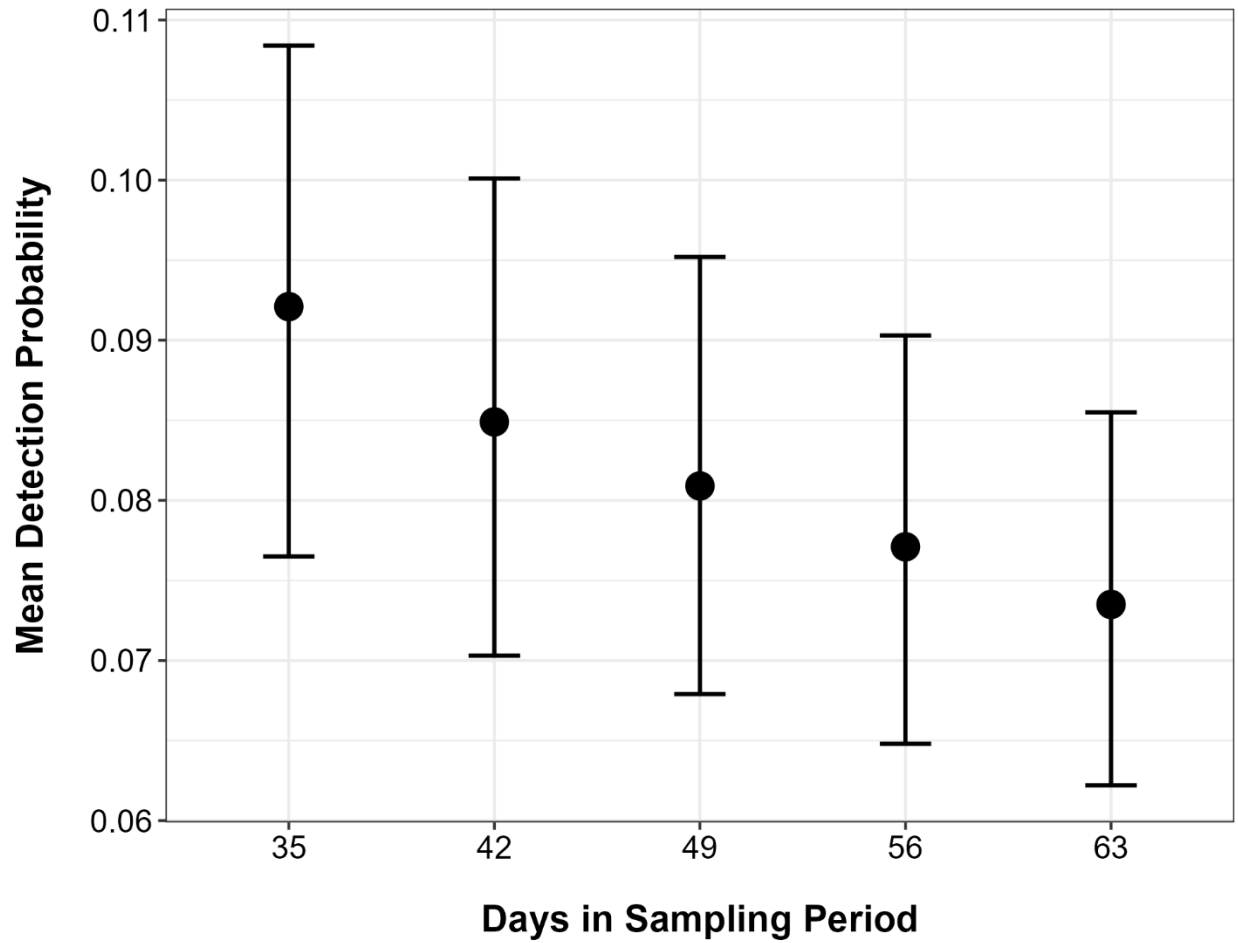


Figure 1.8. Mean white-tailed deer (*Odocoileus virginianus*) detection probability by number of days in sampling period. Counts were restricted to the maximum number of individuals observed in a single image per day (i.e., a daily-sampling frequency of 1). Error bars indicate a 95% quantile interval. Estimates were obtained using an N-mixture modeling approach applied to a camera-trap study design in the south-central Lower Peninsula of Michigan, USA, 2019.

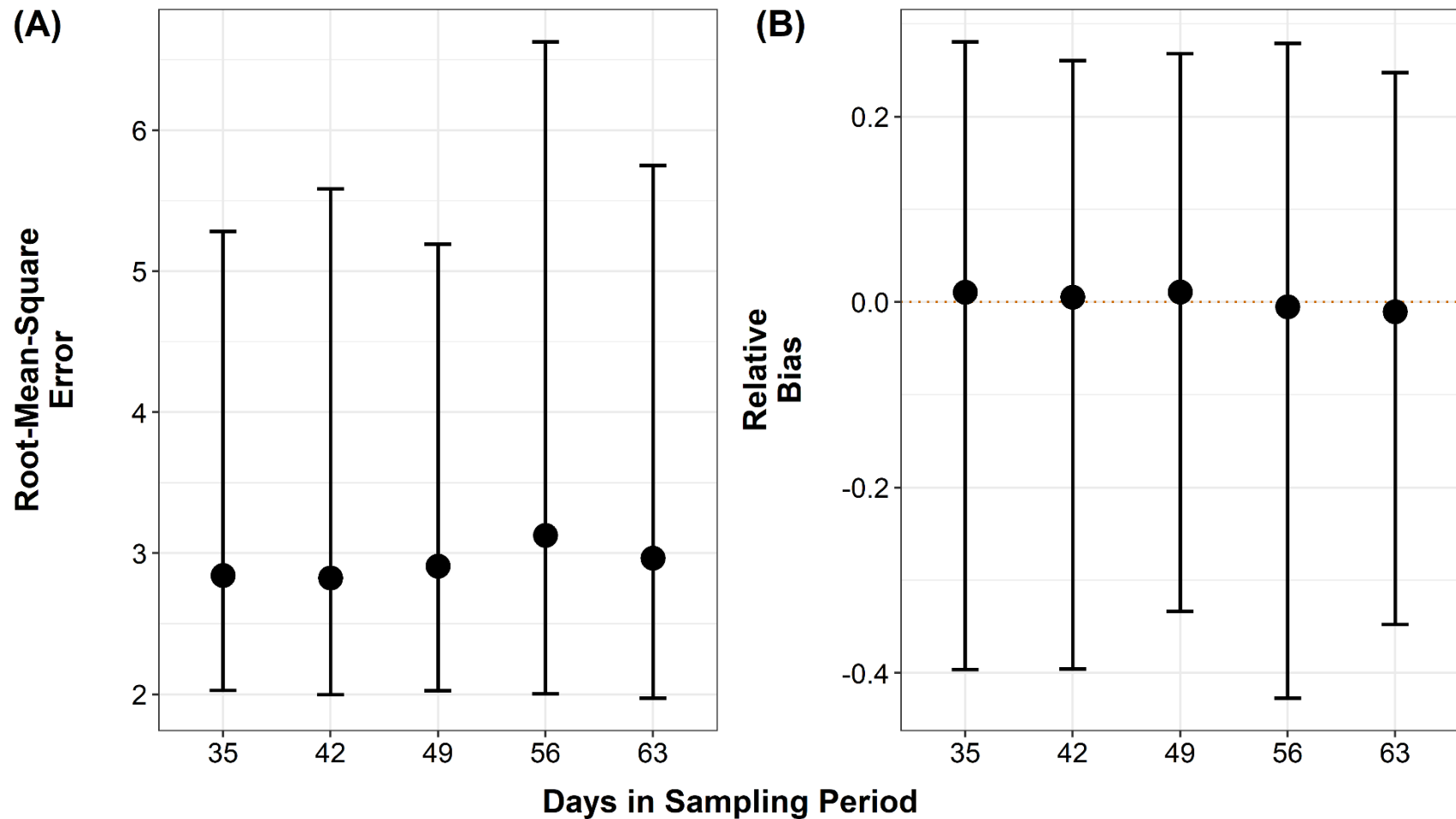


Figure 1.9. (A) Root-mean-square error and (B) relative bias of white-tailed deer (*Odocoileus virginianus*) abundance estimates by number of days in sampling period. Counts were restricted to the maximum number of individuals observed in a single image per day (daily-sampling frequency = 1). Error bars indicate a 95% quantile interval. The dashed, orange horizontal line represents zero or no bias between simulated truth and predicted abundance. Estimates were obtained using empirical and simulated data with an N-mixture modeling approach applied to a camera-trap study design in the south-central Lower Peninsula of Michigan, USA, 2019.

Camera distribution

I used a 1-per-day sampling frequency and found that relative abundance estimates were sensitive to modifications in camera distribution. Relative abundance estimates increased as the number of sites increased, and most scenarios were significantly different from one another (Figure 1.10). The 9-site scenario produced the least precise mean relative abundance estimate (8.53%) with a CV 2.6 times greater than the 18-site scenario (3.26%; Figure 1.10). However, I found that mean detection probability was relatively insensitive to changes of camera distribution and approximated 0.07 for all scenarios (Figure 1.11).

The sensitivity analysis with a 1-per-day sampling frequency also indicated that camera distribution influenced model performance. The accuracy of the abundance estimator grew poorer (i.e., higher RMSE) for camera distributions less than 18 sites ($\bar{x}$ = 2.97; Q95% = 1.97–5.75) and was poorest with the 12-site scenario ($\bar{x}$ = 3.78; Q95% = 2.09–10.68; Figure 1.12). All camera distributions produced relatively unbiased abundance estimates (i.e., RB approximated and centered around 0), but the 18-site scenario had the least variable estimates ($\bar{x}$ = -0.01; Q95% = -0.35–0.25, Figure 1.12).

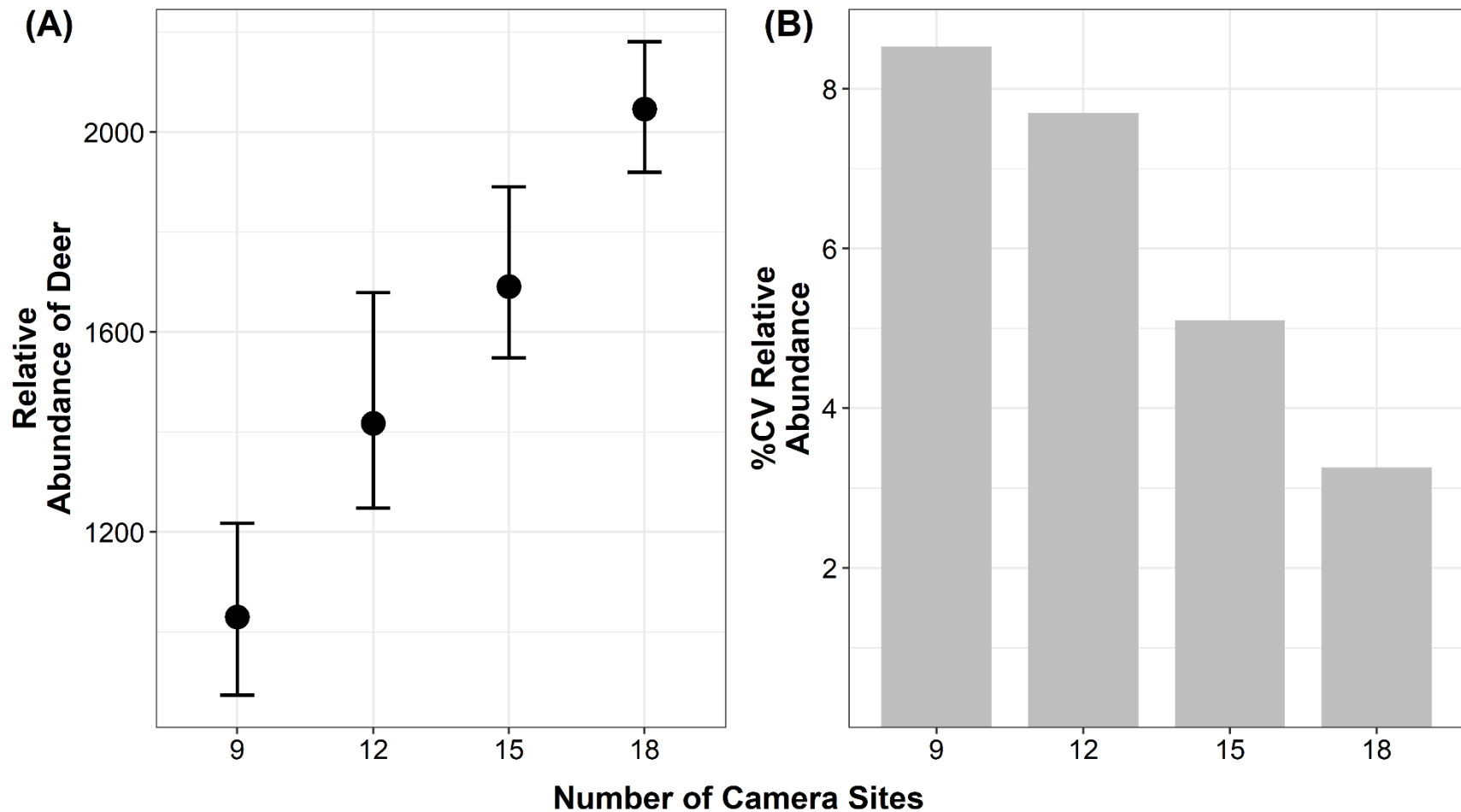


Figure 1.10. Estimates of (A) relative white-tailed deer (*Odocoileus virginianus*) abundance and (B) associated percent coefficient of variation (%CV) by number of camera sites. Relative abundance was used as an index and assumed to be functionally related to population size. The number of camera sites corresponds to the number of camera sites distributed in each of the 8 townships surveyed (1 township = 93 km² [36 mi²]). Counts were restricted to the maximum number of individuals observed in a single image per day (daily-sampling frequency = 1). Error bars indicate a 95% quantile interval. Estimates were obtained using an N-mixture modeling approach applied to a camera-trap study design in the south-central Lower Peninsula of Michigan, USA, 2019.

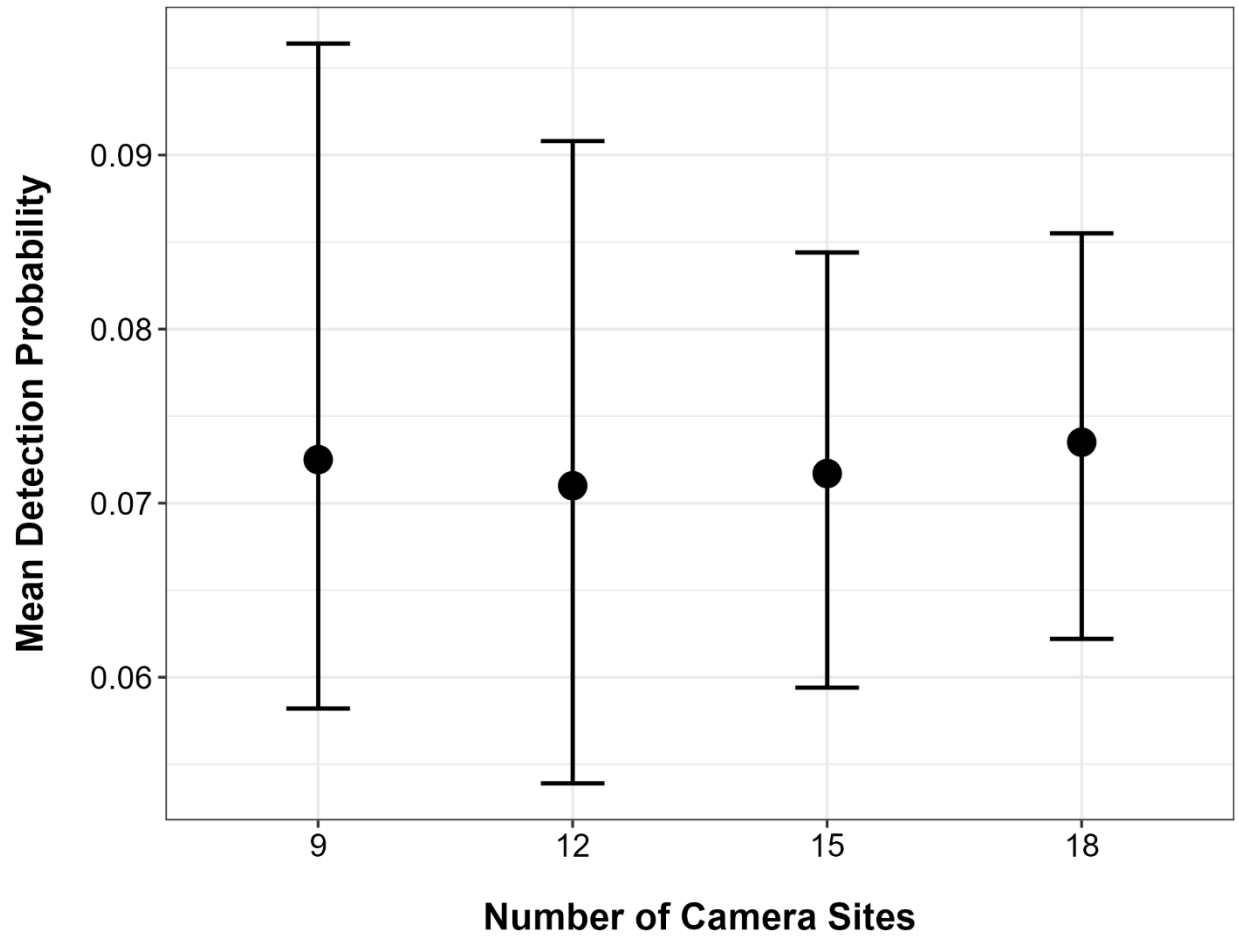


Figure 1.11. Mean white-tailed deer (*Odocoileus virginianus*) detection probability by the number of camera sites used. The number of camera sites corresponds to the number of camera sites in each of the 8 townships surveyed (1 township = 93 km² [36 mi²]). Counts were restricted to the maximum number of individuals observed in a single image per day (i.e., a daily-sampling frequency of 1). Error bars indicate a 95% quantile interval. Estimates were obtained using an N-mixture modeling approach applied to a camera-trap study design in the south-central Lower Peninsula of Michigan, USA, 2019.

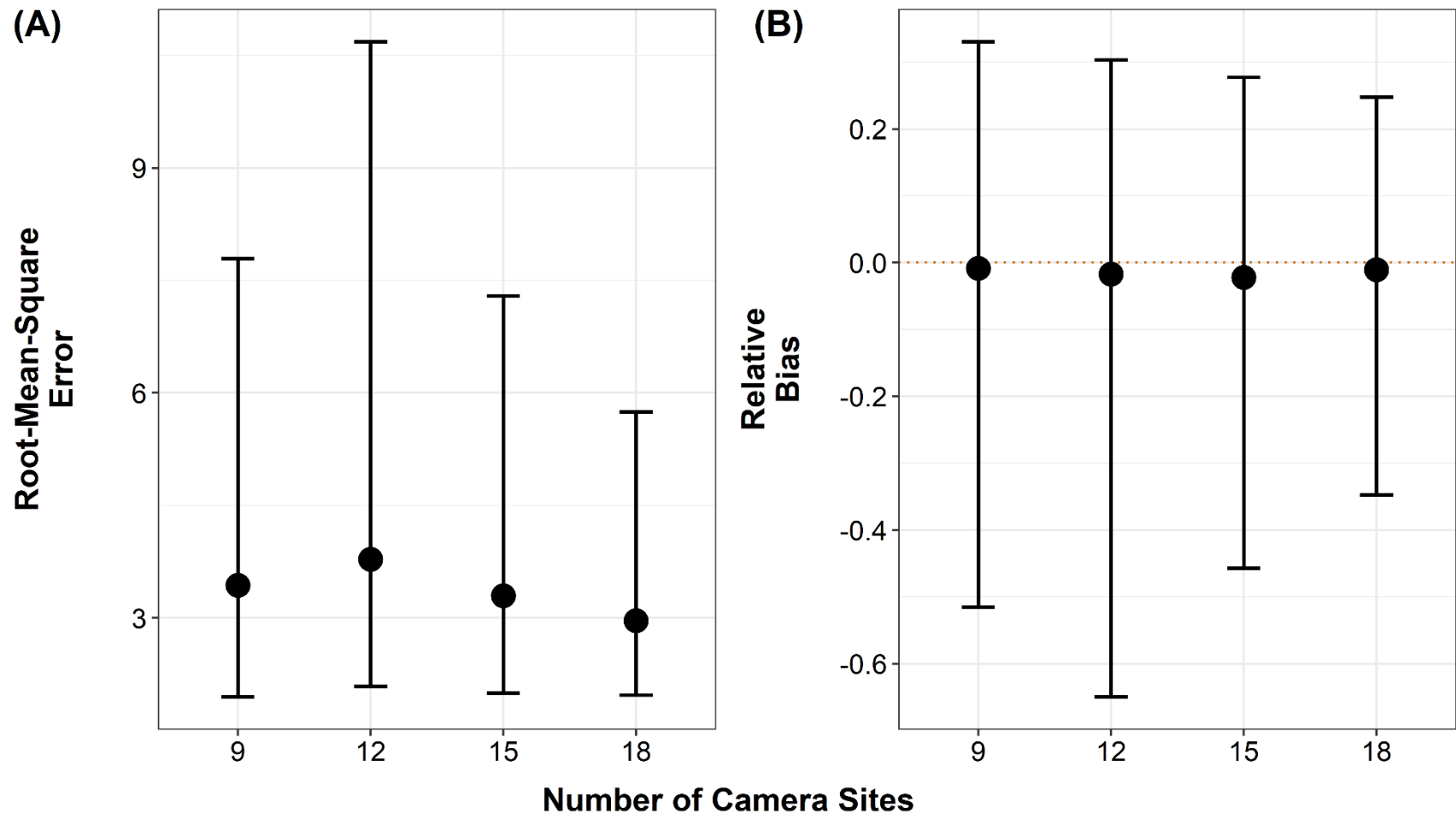


Figure 1.12. (A) Root-mean-square error (RMSE) and (B) relative bias of white-tailed deer (*Odocoileus virginianus*) abundance estimates by number of camera sites. The number of camera sites corresponds to the number of camera sites in each of the 8 townships surveyed (1 township = 93 km² [36 mi²]). Error bars indicate a 95% quantile interval. The dashed, orange horizontal line represents zero or no bias between simulated truth and predicted abundance. Estimates were obtained using empirical and simulated data with an N-mixture modeling approach applied to a camera-trap study design in the south-central Lower Peninsula of Michigan, USA, 2019.

DISCUSSION

In this study, I presented an assessment of sampling strategies for N-mixture models to assist camera-trap study designs for estimating deer abundance. This included a post-hoc methodological assessment of different treatments of sampling frequency, sampling duration, and camera distribution. To my knowledge, this is the first sensitivity analysis of sampling strategies of free-ranging deer with camera traps and an N-mixture model. My results supported my hypothesis that each sampling strategy could balance precision of relative abundance estimates with high detection probability and model performance.

First, I found that the precision of abundance estimates was relatively insensitive to modifications in sampling frequency. However, among scenarios that modified sampling frequency, sampling duration, and camera distribution, I found detection probability was most sensitive to modifications in sampling frequency. The 1-per-day frequency provided relatively precise and accurate abundance estimates with the lowest amount of bias (Figure 1.4, Figure 1.6). Further, the 1-per-day frequency produced detection probabilities significantly higher than other frequency scenarios (Figure 1.5). For these reasons, the 1-per-day sampling strategy was selected as best performing and was used for subsequent analyses as a method for counting deer. Moreover, I found scenarios that decreased the sampling duration or reduced camera distribution compromised the precision of the results, thus were deemed inadequate for the broader scope of my study.

I found that the precision of abundance estimates was more sensitive to modifications in sampling duration than sampling frequency (Figure 1.4, Figure 1.7). Of the sampling-duration scenarios, the 63-day scenario produced the most precise (CV = 3.3%; Figure 1.7) and relatively

accurate abundance estimates with the lowest degree of bias ($\bar{x} = -0.01$, Q95% = -0.35–0.24; Figure 1.10), thus was identified as the best performing sampling duration. Despite having similar detection probabilities among scenarios (Figure 8), the 63-day scenario (maximum duration) produced a significantly different mean relative-abundance estimate 1.26 times higher and 0.40 times more precise than the 35-day scenario (minimum duration; Figure 1.7). These differences were likely attributed to differences in sample size, with shorter sampling durations less likely to detect higher counts of deer and thus not representative of the population of interest over the period of study. Keever et al. (2017) evaluated sampling duration and obtained reliable population estimates of a known, enclosed white-tailed deer population (174 ha) in as little as 5 days. It is worth noting that shorter surveys could help alleviate any privacy concerns the public may have regarding cameras on public land (R. Campa, Michigan State University, personal communication). Shorter surveys can also substantially reduce survey costs, but free-ranging deer with potentially more variable detection probabilities showed that reductions in sampling duration also reduced precision.

As suggested by the 63-day scenario, longer surveys can capture a more representative sample that better reflects characteristics of a free-ranging population during the summer season in the south-central Lower Peninsula of Michigan. However, sampling deer more than 63 days in this system would not be appropriate because of a high likelihood of violating the N-mixture model's population closure assumption. The 63-day sampling duration corresponded to summer months during the post-fawning period when large-scale deer movements are limited (Beier and McCullough 1990, Rosenberry et al. 1999, Nixon et al. 2007, Long et al. 2008, Skuldt et al. 2008, Hiller et al. 2009), which was confirmed by GPS-collar data from deer in the area

(Trudeau et al., unpublished data). Further, shorter sampling periods may lead to small sample sizes of rare animals (e.g., Legal Males in this study system) or fail to detect them altogether (Si et al. 2014, Kays et al. 2020). For long surveys where closure violation is a concern, an extension of the N-mixture model could be implemented to relax the assumption and produce an open population model (e.g., Dail and Madsen 2011).

Among the scenarios that modified sampling frequency, sampling duration, and camera distribution, I found precision of relative abundance estimates were most sensitive to the number of camera sites (Figure 1.4, Figure 1.7, Figure 1.10). These were comparable with previous research by Schlichting et al. (2020), where the authors demonstrated that increasing the number of camera sites used for estimating wild pig populations improved precision of estimates. Also consistent with their findings, the mean detection probability from my analysis was relatively insensitive to changes of camera distribution, and uncertainty grew as sites decreased. As expected, I found that relative abundance estimates decreased as the number of camera sites decreased. This relationship can be explained by a reduced geographic area covered by the effective sampling areas, which led to a corresponding alteration in the population-level of inference (i.e., total abundance associated with a smaller geographic area). Overall, the 18-camera-site scenario produced the most precise abundance estimates of all camera-distribution scenarios (CV = 3.26%; Figure 1.10). Further, the 18-camera-site scenario produced the most accurate abundance estimates with the lowest RMSE ($\bar{x}$ = 2.97; Q95% = 1.97– 5.75) and RB ($\bar{x}$ = -0.01; Q95% = -0.35–0.25, Figure 1.12). Given these results, the 18-camera-site scenario was considered the best performing camera distribution.

Although precision and accuracy increased with more camera sites, I do not recommend camera distributions >18 sites per township (1 per 5.2 km² [1 per 2.0 mi²]) in this study system. Higher camera densities would have a higher chance of violating the assumption of site independence and detection of an individual animal at multiple sites within a sampling period (i.e., violation of the closure assumption; Royle 2004). Violating this assumption could result in double counting individuals and consequently, abundance estimates that are biased high. As a standard practice in camera-trapping studies, I calculated a 1.24-km² (0.48 mi²) effective sampling area based on average home range size (Suwanrat et al. 2015, Wilton 2021) using data from GPS-collared deer in the area ($n = 22$ rural female deer; Trudeau et al., unpublished data). The effective sampling areas for individual cameras are functions of both animal movement and survey length (Gilbert et al. 2021). Spacing among camera traps must be large enough so that the effective sampling areas do not overlap. This issue can be particularly challenging in situations where sites are randomly selected on private lands and camera densities are high. Studies targeting rare animals may also benefit from maximum camera densities, provided that model assumptions are met. This sampling approach may increase animal detections, which is particularly pertinent as N-mixture models can perform poorly with small sample sizes and low detection probabilities (Royle 2004, Couturier et al. 2013, Veech et al. 2016, Barker et al. 2018). Further, reducing the distribution of cameras could affect the abundance estimates of sex-and-age classes due to variations in home range size and susceptibility to photographic capture (Jacobson et al. 1997, Weckel et al. 2011).

Using the best performing sampling strategies (daily-sampling frequency = 1 per day; sampling duration = 63 days; camera distribution = 18 sites per township) I estimated a 3.26%

CV, highlighting the N-mixture model's ability to produce relative abundance estimates with high precision. A CV <25% is often considered sufficient for rough wildlife management decisions and <12.8% for precise management (Skalski et al. 2005). Compared with other similar studies, my results included an estimated precision that was higher than previously recorded in the literature. For example, Haus et al. (2019) estimated a CV as low as 12.3% for a 14-day survey of a free-ranging deer population using camera traps and an N-mixture model; and Keever et al. (2017) estimated a CV consistently around 20% for a 7-day survey of a semi-captive deer population. It is worth noting that both studies utilized bait to improve detectability. Haus et al. (2019) did not evaluate accuracy of their abundance estimates whereas Keever et al. (2017) used number of known, marked individuals to validate the accuracy of their results. The more precise abundance estimates in my study were likely the result of a larger sample size associated with a longer sampling period (63 days). Further, my simulation results validated the abundance estimator's ability to produce relatively accurate and unbiased estimates. Although longer surveys may improve precision, large sample sizes may not be feasible for some studies due to budget or logistical constraints. A potential alternative approach to improving precision of parameter estimates is implementing a multi-species model to leverage shared information (Yamura et al. 2012, Gomez et al. 2017, Moral et al. 2018). Similarly, if multiple years of data are available, a year-stratified approach may also leverage shared information (Kéry and Royle 2021). Although promising, these frameworks may require more data and can be more complex and computationally intensive than single-species or single-season models.

As confirmed in this study, the human effort required to manage and process camera-trap data can be substantial (Price Tack et al. 2016) and even exceeded that of the fieldwork involved (Table 1.3). Altogether, the collection, management, and processing of image data required an estimated 4,700 person-hours of work in a single season (Table 1.3). This is a conservative measure and pertains to the work conducted after the study design phase and before the analysis phase of the study, otherwise considered the photo collection and processing phase. This high level of effort is concerning and may not be sustainable for other camera-trap studies, which should consider novel ways to reduce such labor requirements (e.g., artificial-intelligence approaches for image processing; see Vélez et al. 2023 for review of platforms). A large portion of photo-processing time was spent reviewing irrelevant images, including images without animals (i.e., empty images). Excluding time periods when target species are least active would reduce irrelevant or empty images. Interestingly, I found a bulk of non-deer photos (comprised of mostly empty images) occurring midday and peaking at solar noon (Figure 1.13). Field records indicated a pattern of vegetation movement or the interaction of solar radiation and shadow movement triggering cameras midday (Wilton 2021), although it is worth noting that these phenomena would be dependent on the local conditions of a site (Welbourne et al. 2016). For example, more false-trigger events may occur when vegetation is growing or when there is a lack of canopy cover and an interaction between isolation and shadow movement (Iannarilli et al. 2021). Excluding the midday period when deer are least active (an hour past sunrise to an hour before sunset) from data collection would translate to an estimated 61% reduction in images (~490,000 images) and an associated 57% reduction in data management and processing labor (~1,500 person-hours). Although this approach has

promise for labor reduction, the sensitivity of parameter estimates still need to be critically evaluated before application. Alternatively, while computationally intensive, all images could be initially reviewed by machine-learning applications designed to remove empty images (e.g., MegaDetector; Beery et al. 2019).

My findings also highlighted the importance of sampling relevant to animal activity and its potential for photo processing reduction. Given knowledge of white-tailed deer diel activity patterns (Beier and McCullough 1990, Rouleau et al. 2002, Webb et al. 2010), it was not surprising that deer detections peaked during crepuscular hours (Figure 1.3). My intentions of the crepuscular-sampling frequency were to capture peak activity (i.e., maximize detection probability), minimize the possibility of double counting individuals, and reduce the amount of photo data. It was surprising to find that the crepuscular-sampling frequency produced similar detection probabilities to most scenarios (2, 3, and 4 per day) but significantly lower relative abundance estimates (Figure 1.4). The later result was likely due to missed counts occurring outside of the crepuscular sampling windows (Appendix 1C). Although deer were most active at crepuscular hours, larger aggregations of deer may be detected during other periods. This notion is further supported by the abundance estimator's lowest error (RMSE) with crepuscular sampling (RMSE is sensitive to outliers; Figure 1.6). One suggestion to capture these higher counts would be to increase the length of the crepuscular periods subsampled. For example, increasing the crepuscular period to sunrise $\pm$ 2 hrs and sunset $\pm$ 2 hours. Keever et al. (2017) found that using only nighttime data resulted in accurate estimates of a known population size. However, studies seeking to characterize animals by distinctive features (e.g., sex, age, antler

points) should consider potential limitations of using photo data from low-light periods (Newbolt and Ditchkoff 2019).

This study aimed to disentangle strengths and weaknesses of alternative camera-trap sampling strategies, and low detectability was recognized as a common limitation among scenarios evaluated. Specifically, mean detection probability was <0.10 among all scenarios for all 3 sampling strategies. As demonstrated by my results (Figure 1.4; Figure 1.5), lower detection probabilities can inflate abundance estimates when using N-mixture models (Dénes et al 2015, Dennis et al. 2015). Low detection probabilities were likely driven by a high occurrence of zero counts, with datasets becoming more saturated with zeros at higher sampling frequencies and longer sampling durations. Many studies estimate detection probabilities <0.5 (Kellner and Swihart 2014), but Duarte et al. (2018) found that their Poisson N-mixture model performed best when detection probability was ≥ 0.30 (and statistical assumptions were met). My observed increase in detectability when decreasing daily-sampling frequency from 2 to 1 per day supports a coarser sampling frequency as a viable option for increasing detection probability. However, the empirical data raises some concern regarding the detectability of deer when using unbaited, randomly placed camera traps, even when the target species is considered highly visible and relatively abundant (MDNR 2016). Adequate detection probabilities are important as they increase the chances of capturing all individuals in the population, providing a more representative sample and a stronger foundation for inference. Further, relatively high detection probabilities may allow for decreased sampling intensity and resource savings. For example, higher detectability may reduce the number of camera sites required to produce reliable estimates (MacKenzie and Royle 2005, Maffei et al.

2011, Guillera-Aroita and Lahoz-Monfort 2012). To achieve higher detection probabilities, future work should consider the application of a weekly or monthly sampling frequency. For example, Zou et al. (2019) addressed the issue of low detectability of pheasants by using month as a replicate (i.e., monthly sampling frequency). An alternative and common approach to increasing detection probability in camera-trap surveys is the use of bait or non-random camera placement (e.g., on trails). However, behavioral responses to baiting (Koerth and Kroll 2000, McCoy et al. 2011, Newbolt et al. 2017) and potential differences of animal activity on trails (Kayes et al. 2009) may violate the N-mixture model's assumption of equal detectability.

Another potential limitation of this study was the possible violation of the N-mixture model's assumption of equal detectability. Past camera-trap studies have shown that detection probability can vary among sex-and-age classes of deer (Jacobson et al. 1997, Koerth and Kroll 2000, McCoy et al. 2011, Weckel et al. 2011, Keever et al. 2017). By modeling abundance with counts aggregated by sex-and-age class, it was likely that I masked variations in detectability among classes. Failure to meet the equal-detectability assumption can result in biased parameter estimates. In such cases, it is advisable to interpret the estimates as relative abundance measures (Barker et al. 2018, Gilbert et al. 2021), however this aligns with the original intent of my abundance modeling efforts.

To conclude, this study demonstrates that N-mixture models can perform well for the precise relative abundance estimation of white-tailed deer in the south-central Lower Peninsula of Michigan, based on the modeling of camera-trap count data. However, N-mixture models should be paired with careful consideration of assumptions and sampling strategies as large uncertainty in parameter estimates can obscure signals of change in abundance over time.

Although this study focused on white-tailed deer, the general approach could be applied to many terrestrial wildlife species, providing an explicit method to test for the required sampling frequency, camera duration, and camera distribution for N-mixture modeling. More specifically, I encourage study-specific sensitivity analyses to identify efficient and effective sampling strategies for long-term monitoring projects from pilot or initial datasets. Shorter sampling durations and lower camera distributions can facilitate resource savings, but they can also compromise the precision of relative abundance estimates, with the latter being most sensitive to manipulation. Precise and reliable abundance estimates may require a high amount of financial and human resources, but there are viable ways to improve efficiency. For example, surveys could exclude time periods when animals are least active (e.g., midday for deer) or machine-learning platforms could be used to accelerate processing of photo data (e.g., MegaDetector; Beery et al. 2019). For studies seeking to improve detection probability, coarser sampling frequencies (e.g., weeks, months) are recommended. Lastly, simulations are integral to understanding a hierarchical model's ability to produce accurate and unbiased parameter estimates (Kéry and Schaub 2012, Kéry and Royle 2016, 2021). My diagnostic results were encouraging as they highlighted the N-mixture model's ability to generate reasonably reliable estimates, irrespective of data modifications. Despite the value of diagnostic tests, many studies fail to report any validation of their hierarchical models, thus potentially undermining their statistical inference, reliability, and compatibility with open science practices (DiRenzo et al. 2023). Therefore, practitioners are strongly encouraged to implement simulation-based validation of their models before results are used to inform management and conservation decision making.

Table 1.3. A breakdown of estimated person-hours required to collect, manage, and process a single season of white-tailed deer (*Odocoileus virginianus*) camera-trap data. Camera-trapping included 144 cameras that collected 797,407 images over a 63-day sampling period in the south-central Lower Peninsula of Michigan, USA, 2019. Estimates do not include person-hours associated with study-design labor or analyses.

Labor	Employees	Person-hours
Fieldwork ^a	4	2,000
Data management ^b	2	800
Photo processing ^c	14	1,900

^aFieldwork includes obtaining landowner permission, deploying cameras, biweekly camera checks, and camera retrieval.

^bData management includes uploading images from SD cards, transferring files, reformatting files, backing up data, and deleting data files.

^cPhoto processing includes classifying images (each image reviewed by 2 employees) and verifying discrepancies between classifications. Photo reviewers spent approximately 1 hour to review 1,000 photos and 1 hour to judge 300 discrepancies.

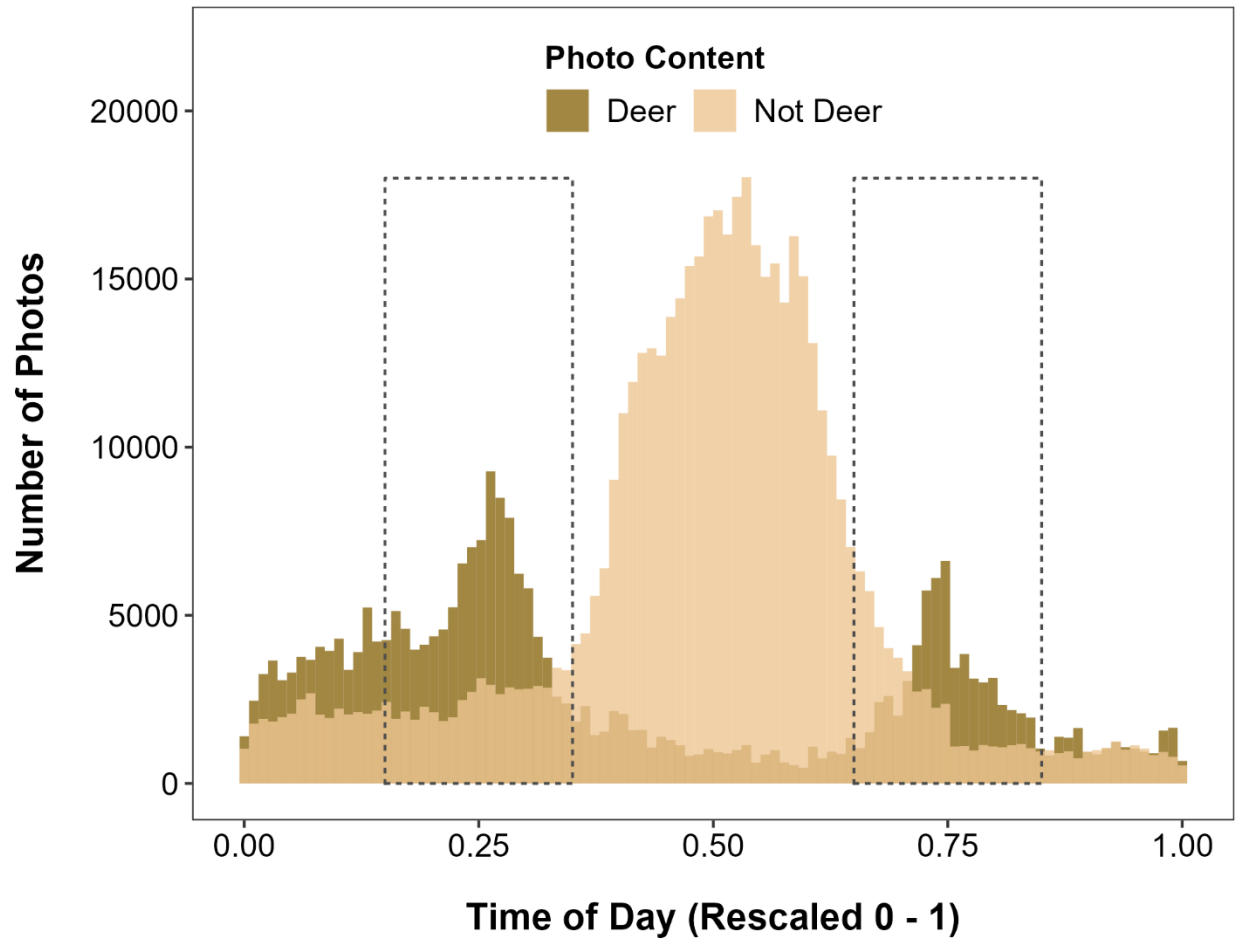


Figure 1.13. Distribution of images that included white-tailed deer (*Odocoileus virginianus*; Deer) in and images that did not (Not Deer) by time of day. Standard time was rescaled to local solar time (0–1). Images were collected during 15 July–15 September 2019 camera-trap surveys in the south-central Lower Peninsula, Michigan. Brown bins correspond to images with deer and tan bins to images without deer; and distributions overlay one another with transparency. Dashed boxes indicate defined crepuscular periods (sunrise $\pm$ 1 hr and sunset $\pm$ 1 hr).

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CHAPTER 2: ASSESSING THE EFFECT OF A DEER HARVEST REGULATION CHANGE ON RELATIVE ABUNDANCE: AN EXPERIMENTAL APPROACH

INTRODUCTION

Assessing changes in population abundance is important when evaluating the effectiveness of conservation and management for wildlife. However, evaluating a single regulation change on a free-ranging population is considerably challenging. Given partial controllability limitations (Fackler and Pacifici 2014), robust evaluations generally require coupling the regulation change with before and after population monitoring within treatment and control areas (Green 1979, Christie et al. 2019). For game species, many agencies (i.e., federal, state, or provincial wildlife management organizations) instead rely on estimated or enumerated harvest for population monitoring efforts (Roseberry and Woolf 1991, Skalski et al. 2005, Hansen 2011, Ryder 2018). Although useful, sex and age data of the harvested population may be nonrepresentative of the true state of the population (Carpenter 2000, Demarais et al. 2005, Collier and Krementz 2007). For example, changes in harvest trends may reflect changes in harvest regulations and hunter effort rather than population-level changes. Ultimately, wildlife management actions cannot be thoroughly assessed without reliable data on population parameters (Lubow et al. 1996, Lancia et al. 2000).

Selective-harvest regulations involve the differential protection or harvest of animals based on specific criteria like phenotypic traits, sex, and age. Agencies generally implement selective-harvest regulations because of 1) hunter preferences for sex, age, or size, and 2) the expectation that the regulation will exert a desired population effect (Carpenter 2000, Demarais et al. 2000). For species where hunter harvest is a large source of mortality, sex- and age-specific harvest can affect population composition, structure, and demographic processes

(Ginsberg and Milner-Gulland 1994, Milner et al. 2007). For example, density reduction programs may focus on female harvest as a conventional means to reduce a population's reproductive potential (Woolf and Rosenberry 1998, Brown et al. 2000). Further, male-biased harvest can lead to female-biased sex ratios in a population (Noyes et al. 1996, Nilsen and Solberg 2006) whereas disproportionate harvests of young animals can limit animals from advancing to older age classes and skew the age composition of a population (Milner et al. 2007).

Antler-based regulations are a common form of selective harvest applied to cervid (family *Cervidae*) management programs. In practice, antler-based regulations are designed to limit harvest of antlered animals, especially younger individuals, allowing these age classes a greater likelihood of survival and thus entering older age classes (Carpenter and Gill 1987, Frawley 2017, Hansen et al. 2017, Wallingford et al. 2017). These types of regulations are based on age-specific antler growth and vary by species, population attributes, and management objectives. Agencies have used various criteria to define antler-based regulations, including minimum main beam length, spread width, number of antler points (i.e., antler point restrictions), or some combination thereof (Demarais and Strickland 2011, Morina et al. 2021). Over time, antler-based regulations have been widely adapted for the management of elk (*Cervus canadensis*; Boyd and Lipscomb 1976, Bender and Miller 1999, Biederbeck 2001, Bender et al. 2002), moose (*Alces alces*; Schwartz et al. 1992, Young and Boertje 2008, Child et al. 2010), mule deer (*Odocoileus hemionus*; Erickson et al. 2003, Kuzyk et al. 2011), and more recently white-tailed deer (*Odocoileus virginianus*; Cohen et al. 2016, Wallingford et al. 2017, Kellner et al. 2021, Cain et al. 2022). Many U.S. states have, or currently use, some form of

antler-based regulation to achieve management goals, including increasing the number of older males in the population or harvest (Boyd and Lipscomb 1976, Bender et al. 2002, Frawley 2017, Wallingford et al. 2017, Hansen et al. 2017), managing sex ratios (Schwartz et al. 1992, Bender and Miller 1999, Young and Boertje 2008), influencing population size or increasing antlerless harvest (Schroeder et al. 2014, Hansen et al. 2017, Wallingford et al. 2017), and responding to stakeholder requests or increasing hunter satisfaction (Frawley 2017, Hansen et al. 2017). Antler point restrictions (APRs) are the most common form of antler-based regulations and are frequently applied to white-tailed deer (hereafter, deer) harvest programs—typically in response to the preference among some hunters for harvesting older male deer with larger antler growth (Adams and Hamilton 2011, Cohen et al. 2016, Frawley 2017, Hansen et al. 2017, Cain et al. 2022).

It is hypothesized that APRs advance the age structure of male deer in a population (Wallingford et al. 2017). Given the direct relationship between antler growth, age-specific male survival and male age structure, this hypothesis has foundations in logic. In theory, implementing a mandatory APR that protects most yearling males from harvest will result in increased yearling-male survival and thus increased recruitment of yearling males into the adult age class (Carpenter and Gill 1987, Hansen et al. 2017, Wallingford et al. 2017). Further substantiating this hypothesis is the widely held consensus that APRs reduce the proportion of yearlings in the antlered harvest as yearlings are largely protected (Demarais et al. 2005, Hansen et al. 2017, Wallingford et al. 2017, Kellner et al. 2021, Cain et al. 2022). APRs have been implemented and evaluated under a diversity of conditions (e.g., motivations, type of APR, pre-existing conditions) resulting in a diversity of outcomes among studies. For example, Kellner et

al. (2021) evaluated the effect of APR treatments in 2 study areas in New York and found that the proportion of yearlings in the antlered harvest declined from 51% and 58% to 13% and 19% after 5 years, respectively. In 2 study areas in Missouri, Hansen et al. (2017) found that the proportion of yearling males in the antlered harvest decreased from 58% and 60% to 26% and 22% after 4 years of APR treatments, respectively. Numerous studies have also observed increased proportions of older male deer harvested following APR implementation (Strickland et al. 2001, Hansen et al. 2017, Wallingford et al. 2017, Kellner et al. 2021, Cain et al. 2022), but these increased proportions may be explained in part by lower proportions of yearling harvest (Demarais et al. 2005, Collier and Krementz 2007). Regardless, these studies lacked estimates of male abundance by age, thus it was not possible to evaluate the magnitude of effect APRs had on adult male abundance.

Although APRs focus on age-structure management of antlered deer, an indirect outcome is also hypothesized. Specifically, APRs are hypothesized to reduce the overall abundance of deer in a population. The theory underlining this hypothesis is that hunters will voluntarily shift harvest pressure to antlerless deer when APRs reduce the availability of harvestable yearling males (Hamilton et al. 1995, Hansen et al. 2017, Wallingford et al. 2017, Hansen et al. 2018). The additional compensatory harvest pressure on antlerless deer can translate to increased female mortality and a subsequent reduction in a population's reproductive potential (Woolf and Rosenberry 1998, Brown et al. 2000, Diefenbach et al. 2021). For example, Wallingford et al. (2017) concluded that the combination of APR-regulation changes and increased antlerless harvest were effective in reducing deer abundance in Pennsylvania over a 5-year period. Under APR regulations, Hansen et al. (2017) found different

antlerless harvest outcomes in different regions of Missouri. Antlerless harvest increased in a region with better-quality deer habitat (northern Missouri) but did not increase in a region with poorer-quality deer habitat and a relatively lower deer population density (central Missouri; Hansen et al. 2017). In contrast, APR studies in New York (Kellner et al. 2021) and northern Michigan (Cain et al. 2022) evaluated harvest data and failed to find definitive empirical support for any increases in antlerless harvest. To my knowledge, Wallingford et al. (2017) were the only authors to evaluate the effects of APRs on overall deer abundance. To better understand the relationship between APRs and deer abundance, there is a critical need for additional population-level assessments.

Hunter harvest accounts for a significant proportion of deer mortality in the United States (Ditchkoff et al. 2001, Nixon et al. 2001). Therefore, selective harvest has the potential to influence population size and sex-age composition (Milner et al. 2007), which in turn can influence disease dynamics (Cross et al. 2009). These concepts are particularly relevant to emergence in wildlife health issues because changing the selectivity of harvest over sex and age classes has implications for disease spread and growth. Therefore, knowing the true demographic features (e.g., sex-age composition) of affected deer populations is more pertinent and useful to management than harvest data alone.

Wildlife-management agencies need to also consider other biological ramifications associated with APRs, like potential influence on disease dynamics (Miller and Fischer 2016, Morina et al. 2021). For example, both bovine tuberculosis (*Mycobacterium bovis*) and chronic wasting disease affect sex-and-age classes disproportionately (O'Brien et al. 2002, Jennelle et al. 2014). Chronic wasting disease (CWD) is a fatal prion disease that infects cervids (Williams 2005)

and is a major threat to the sustainability of free-ranging cervids and conservation (Gillin and Mawdsley 2018). Notably, the prevalence of CWD in deer is estimated to be about twice as high in adult males compared to females, with age-specific prevalence generally increasing with age (Gear et al. 2006, Osnas et al. 2009, Heisey et al. 2010, Rees et al. 2012, Samuel and Storm 2016). The observed higher prevalence in males is likely attributed to differences in behavior. For example, yearling males tend to disperse at the greatest frequency within white-tailed deer populations (Nelson 1993, Long et al. 2005, Nixon et al. 2007, Skuldt et al. 2008) and mature males increase their movements and expand their home ranges seasonally (Beier and McCullough 1990). These life-history traits are important because they can facilitate increased contact rates and thus increased disease spread (Gross and Miller 2001, Skuldt et al. 2008, Cross et al. 2009). Further, the observed increase in disease prevalence with age can be a consequence of an increase in the length of potential cumulative infection risk (Wobeser 2006, Cross et al. 2009).

Following the detection of CWD, agencies generally alter deer harvest regulations or initiate management practices in an attempt to reduce disease transmission (Thompson et al. 2023). Some studies have shown that reducing deer densities has been successful at maintaining low prevalence of CWD (Manjerovic et al. 2014, Mateus-Pinilla et al. 2013). Harvest strategies that target specific, high-risk sex-and-age classes have also been considered useful for CWD management (Skuldt et al. 2008, Jennelle et al. 2014, Potapov et al. 2016, Gillin and Mawdsley 2018, Mysterud and Edmunds 2019, Belsare and Stewart 2020). For example, a simulation study by Belsare and Stewart (2020) found lower probabilities of CWD outbreak associated with higher harvest rates of yearling male deer (i.e., a non-APR harvest scenario).

Most APR studies to date have focused on evaluating harvest in response to APR regulation changes. Consequently, population-level effects of APRs remain unclear, particularly on sex-and-age distribution (Morina et al. 2021). Given the widespread application of and increasing interest in APRs (Adams and Hamilton 2011, Connelly et al. 2012, Frawley 2019), and the seemingly inexorable geographic spread of CWD (Miller and Fisher 2016, Uehlinger et al. 2016, Belsare et al. 2021), empirical investigations are warranted. In 2019, Michigan's Natural Resources Commission implemented an experimental APR in a portion of a 5-county study area that included a known CWD hotspot. This action was coupled with this research designed to evaluate the subsequent effects on white-tailed deer abundance by sex-and-age class. Pairing the regulation change with research provided me a unique opportunity to empirically evaluate two common, independent APR hypotheses: (H_1) antler point restrictions increase the abundance of adult males, and (H_2) antler point restrictions decrease overall deer abundance (Figure 2.1). I predicted that the abundance of adult males would only increase in APR-treatment areas, given the pattern of decreased yearling- and increased adult-male harvest observed in other APR studies (Hansen et al. 2017, Wallingford et al. 2017, Kellner et al. 2021, Cain et al. 2022). I also predicted that, irrespective of harvest treatment, the abundance of other sex-and-age classes would not decline. This prediction was based on the absence of elevated antlerless harvest in a recent APR study in northern Michigan (Cain et al. 2022), as well as the historically low levels of antlerless harvests in the broader context of Michigan (Stewart 2023). A camera-trap sampling design was used to survey deer populations 1 year prior to APR implementation and 3 consecutive years after APR implementation. Using these data, I estimated deer relative abundance by sex-and-age class over time and compared trends

between APR and non-APR areas. By linking field-based population estimates with a before-after-control-impact design in response to APR regulation changes, I quantify and thoroughly evaluate subsequent population-level effects. My findings highlight potential limitations of APRs as a management tool and the importance of developing harvest regulations specific to the targeted deer population, area, and management goals.

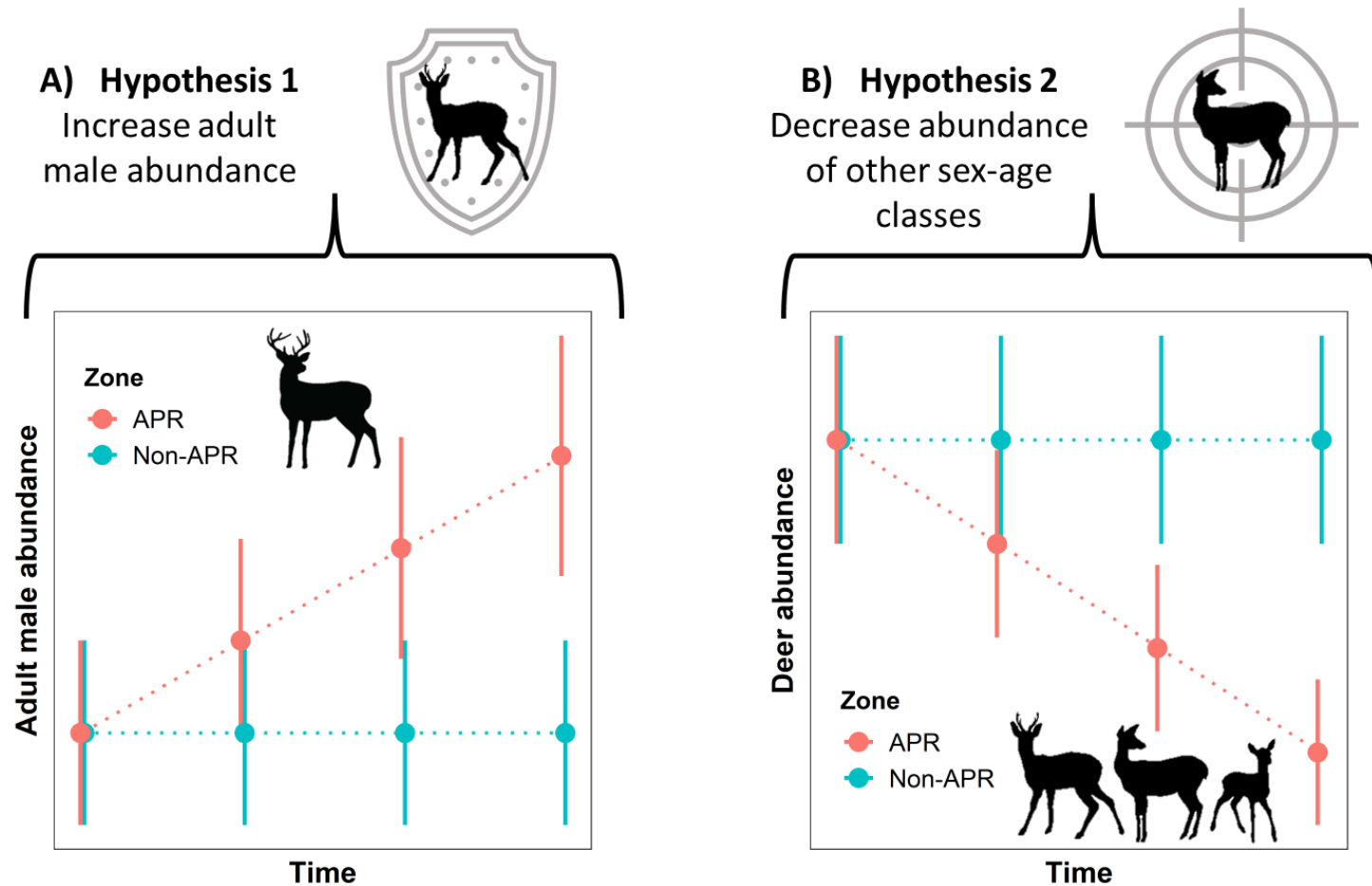


Figure 2.1. Conceptual diagrams of hypotheses regarding white-tailed deer (*Odocoileus virginianus*) population-level changes following the implementation of antler point restrictions (APRs). In (A), young males are protected from harvest in an area with APRs (APR Zone), resulting in Legal Antlered abundance increasing over time. In (B), the reduced availability of harvestable yearling males in the APR Zone translate to increased antlerless harvest and subsequent declines in the abundance of females (yearling and adult), yearling males, and fawns. No changes occur under the *status quo* harvest regime in the Non-APR Zone.

STUDY AREA

The study took place in the south-central Lower Peninsula of Michigan in a 5-county area (Newaygo, Kent, Mecosta, Montcalm, and Ionia County; hereafter, 5-County Area) that included a known chronic-wasting-disease hotspot (Kent and Montcalm County; Figure 2.2). In 2019, there was an APR change in the 5-County Area and a study was designed to evaluate its effect on the abundance and sex-and-age composition of deer populations in the area. A paired-comparison study design was implemented to monitor deer populations in APR and non-APR areas (i.e., experimental and control areas, respectively). A robust before-after-control-impact (BACI) study design (Green 1979) was employed to monitor potential population-level changes, over 3 consecutive years (2020–2022), following the 2019 regulation change. This design was intended to allow researchers to identify potential changes in population abundance and composition in the treatment area (APR Zone) relative to the control area (Non-APR Zone) over the course of the study (Figure 2.2).

Given north-south differences in land-use and land-cover types, the study area was longitudinally divided instead of latitudinally to minimize the effects, other than APRs, on deer populations (see Chapter 1 for detailed description of study area). The study implemented a camera-trap sampling design restricted to 8 townships within the 5-County Area, encompassing an area of approximately 749 km² (Figure 2.2). Landscape analyses (e.g., land-cover composition, proportion of public hunting land) were completed for each township in the 5-County Area to identify similar townships for pairing between APR and Non-APR Zones (Table 2.1). Additional pairing considerations included geological features (e.g., rivers), human density, and apparent CWD prevalence. Eight townships were systematically selected and paired

between the APR Zone and Non-APR Zone to compare deer populations over time at a scale that was achievable with camera traps while also reflecting the variation within the 5-County Area. In the APR Zone (Mecosta, Montcalm, and Ionia County; 4,845-km²), antlered deer with at least four points on one antler could be taken with a valid license (a legal point was defined as ≥ 2.54 cm [1 inch] long as measured from its tip to the nearest edge of antler beam). In the Non-APR Zone (Newaygo and Kent County; 4,488-km²), any antlered deer with an antler ≥ 7.62 cm (3 inches) in length could be taken. Deer hunting occurred annually every fall in Michigan.

Since 1991, Michigan's statewide hunting regulations have limited hunters to a maximum harvest of 2 antlered deer annually (Rudolph 2012, Cain et al. 2022). These antlered deer were defined as those with at least one antler measuring ≥ 7.62 cm (3 inches) in length (MDNR 2016). In 1997, Michigan enacted its first mandatory APR specific to the second antlered hunting license (Rudolph 2012, Cain et al. 2022). According to this regulation, if hunters harvested 2 antlered deer annually, at least one of the deer was required to have ≥ 4 antler points on a side (Rudolph 2012, Cain et al. 2022). In Michigan, a legal antler point was defined as ≥ 2.54 cm (1 inch) long as measured from its tip to the nearest edge of antler beam. Hunters who purchased a single antlered hunting license were permitted to harvest any legal antlered deer without limitations on antler-point count (Cain et al. 2022). Historically, there has never been a limit on the number of hunters pursuing antlered deer or quotas on antlered licenses (Rudolph 2012). In contrast, antlerless-deer harvests have been limited through license quotas specific to Michigan's deer management units. However, in more recent years Michigan began increasing the allocation of antlerless licenses and increasing opportunity to harvest antlerless deer to manage population sizes (Rudolph 2012, MDNR 2016). Antlerless deer are defined as

deer without antlers and deer with antlers <7.62 cm (3 inches) in length. Today, Michigan's deer-harvest regulations vary by management unit, select federal lands (e.g., wildlife refuges), and disease management zone (Frawley 2023, MDNR 2023).

In Michigan, CWD was first identified in free-ranging deer in 2015 (Stewart et al. 2016). Following CWD detection, Michigan's regulatory responses to CWD included increased harvest opportunities by increasing quotas or licenses, extending preexisting hunting seasons, and adding additional hunting seasons (Thompson et al. 2023). In addition to changes in state and peninsula-wide deer harvest regulations designed to mediate potential CWD transmission, the Natural Resource Commission implemented a 4-point APR in a portion of the 5-County Area in 2019 as part of experimental management. The APR prohibited hunters from harvesting antlered deer that did not have at least 4 antler points on one side. This action was expected to protect approximately 70% of yearling males from harvest (B. Rudolph, Michigan Department of Natural Resources, unpublished data). Youth hunters (<17 years of age) and disabled hunters were exempt from the APR during select seasons.

The APRs in the 5-County Area (APRs in 2 counties) were based on a request by the Natural Resource Commission for the Michigan Department of Natural Resources to evaluate the effects of APRs on deer abundance and sex-and-age composition, with the anticipation that the data would better inform management and regulation decisions in CWD management areas (Frawley 2019). It is important to note that Michigan's guidelines for evaluating APR proposals (QDMWG 2013) did not apply in this situation because the APRs were not requested by a local group, but instead directly by the Natural Resource Commission (Frawley 2019). The Natural Resources Commission maintained consistent APR regulations in the study area for a full 3-year

harvest regulation cycle (2019–2021). Apart from the APR regulation, all other deer hunting regulations were comparable between the APR and Non-APR Zones throughout the duration of the study (Frawley 2020, 2021, 2022) and in the years preceding it.

Table 2.1. Land-cover composition and total public land for each township pairing (A–D) in areas without antler point restrictions (the control area or Non-APR Zone) and areas with antler point restrictions (the experimental area or APR Zone). Land-cover composition and percent public land were the main criteria used for pairing townships with a before-after-control-impact study design. Land composition was calculated using the National Land Cover Database (Dewitz 2019) land-cover classification layer (30-m² resolution) in ArcPro (ESRI 2020). Landcover reclassifications included Agriculture (Cultivated crop, Hay-pasture, Grassland-herbaceous), Forested (Deciduous forest, Coniferous forest, Mixed forest), Wetland (Palustrine forested wetland, Palustrine scrub-shrub wetland, Palustrine emergent wetland, unconsolidated shore, Palustrine aquatic bed), and Developed (Highly developed, Moderately developed, Low development, Developed open space). Total public land included public lands open to hunting and was calculated using in the Protected Areas Database of the United States (USGS 2022) in ArcPro (ESRI 2020).

Township by zone	% Agriculture	% Forested	% Wetland	% Scrub-shrub	% Open water	% Developed	% Barren land	Total public land (%)
Non-APR								
A	32.56	34.60	22.47	4.14	3.39	2.67	0.18	19.38
B	49.77	24.45	17.16	2.68	0.51	4.84	0.59	19.61
C	67.61	11.46	15.28	1.22	0.66	3.61	0.17	0.00
D	48.13	21.28	20.40	2.83	1.14	5.98	0.24	0.00
APR								
A	37.71	31.72	20.60	5.90	2.00	2.03	0.04	3.74
B	63.73	16.65	14.08	1.83	0.37	3.23	0.11	10.23
C	66.44	6.68	22.72	1.81	0.84	1.44	0.07	0.00
D	58.46	10.91	23.33	1.94	2.59	2.73	0.05	0.00

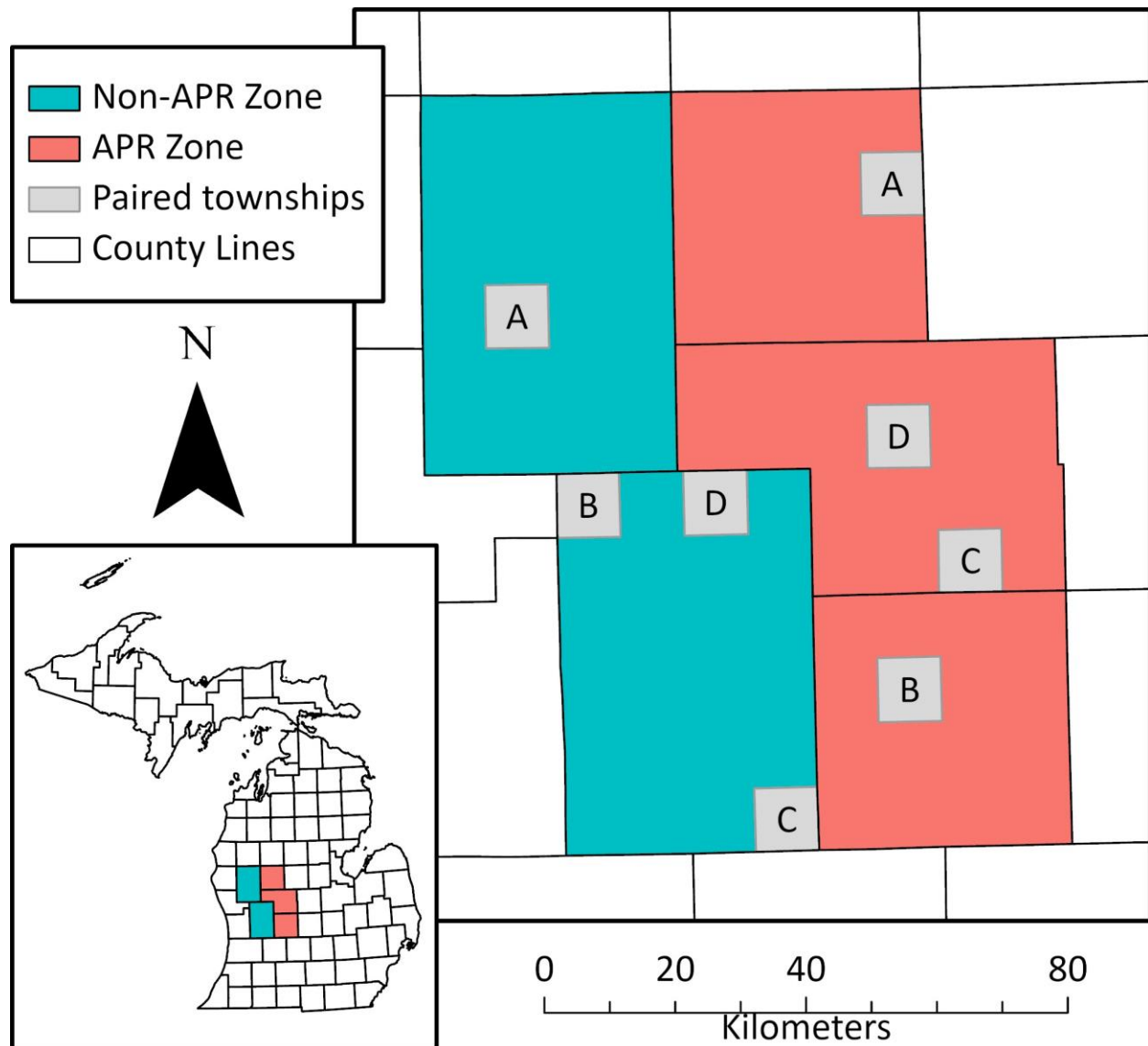


Figure 2.2. Study area in the south-central Lower Peninsula of Michigan, USA, in a designated 5-county area. Mandatory antler point restrictions (APRs) were implemented in 2019 in the experimental area (APR Zone) and not in the control area (Non-APR Zone). Townships were paired (A–D) between zones, and remote cameras were placed in each township to monitor white-tailed deer (*Odocoileus virginianus*) populations over a duration of four years (2019–2022). Maps created in ArcGIS Pro (version 2.7.1; ESRI 2020).

METHODS

Field sampling and site selection

A stratified-random design (at the township-section scale) was used to select 144 camera sites evenly distributed across the 8 townships using generalized random-tessellation stratification (GRTS; Stevens and Olsen 2004). The GRTS sampling design is advantageous because it maintains statistical qualities of a random draw when removing intractable samples (i.e., no land access), while yielding a spatially balanced set of points (Stevens and Olson 2004). Random camera placement was selected with the intent of providing the least biased approximation of population structure. Sample sites were located on both public and private land, the latter necessitating annual landowner permission. Note that only half of the township pairs (C and B; Figure 2.2) were surveyed in 2020 due to COVID-19 pandemic-related constraints.

Camera-trap setup and data collection

Eighteen infrared cameras (Strike Force HD Pro X®, Browning Trail Cameras, Birmingham, AL) were deployed in each of the 8 selected townships. To minimize potential bias, camera sites were nonbaited (Koerth and Kroll 2000, McCoy et al. 2011, Newbolt et al. 2017) and placed as close to the generated GRTS sample locations as possible (Kays et al. 2009). In exceptional circumstances cameras were placed within 100 m of the point. In such situations, exact camera location was selected to avoid locations with a high risk of theft, open water, road rights-of-way, and to maintain a clear field of view. Cameras were oriented north to minimize direct sunlight exposure, false triggers caused by exposure to the sun's rays (Wilton 2021), and observer bias in placement. Cameras were placed on a straight tree and secured with a security box, cable, and

lock. If no suitable trees were available, a steel T-post was used to mount the camera. Cameras were mounted so that the center of the lens was 36–41 cm (14–16 inches) above the ground and the horizon was centered in the field of view (guidance provided by Moll et al. 2018). The selected camera height was intended to detect all age groups of deer and allow overhanging vegetation (e.g., branches) to be reached and removed from the field of view. Ground vegetation and debris were cleared 5 m in front of the camera to minimize false triggering and allow for an unobstructed field of view.

Cameras were active for 63 days on 24-hour capture mode with a 5-sec delay, taking a burst of 3 photographs per motion-triggered event. Since camera sites were not baited, cameras were programmed to rapid fire (0.3 sec between each image within a burst) and fast-motion infrared flash to maximize clear images of mobile deer. Photo data were collected during what was considered a 9-week closure period (i.e., no immigration or emigration) from 15 July to 15 September for four consecutive years (2019–2022). Each camera site was visited for maintenance (e.g., check batteries, change memory cards, clear vegetation) approximately every two weeks over the duration of the data-collection period. Camera surveys were used to create detection histories for each site. If a camera was not functional for some time, these occurrences were treated as missing data in the detection history (Furnas et al. 2020).

All photos were entered into Colorado Parks and Wildlife Photo Warehouse, a custom Microsoft Access application designed to facilitate archiving, managing, and processing camera-trap data (Newkirk 2016). Deer were counted in each image and classified as Legal Antlered (antlered deer that met the APR criteria), Female (yearling and adult females, i.e., does), Sub-legal Antlered (antlered deer that did not meet the APR criteria), Fawn, or Unknown Deer. Legal

Antlered are assumed to be adult males and Sub-legal Antlered are assumed to be yearling males. Deer were classified as Unknown when it was impossible to determine the sex and age of an individual (e.g., unable to see head). To minimize misidentifications, all photos were processed by two observers that received species-specific image training (Newbolt and Ditchkoff 2019, Elliot et al. 2022). If there was a discrepancy on the identification of a deer in an image, then a third observer served as a referee. Discrepancies were judged by trained referees (with years of professional experience reviewing deer images) to maintain consistent and accurate classification of photographs (Newbolt and Ditchkoff 2019, Elliot et al. 2022). See Chapter 1 appendices for detailed camera-trap and photo-review protocols (Appendix 1A, Appendix 1B).

Image processing

Images were downloaded from memory cards after each camera check and organized into a folder hierarchy by zone, township, camera-check number, and unique site ID (e.g., NonAPR/Sherman/Check1/11001). This folder structure facilitated a multi-step method for filtering and manually classifying images. Given the concerning high level of human effort required to process the 2019 camera-trap data and the surplus of false positive images (i.e., empty images with no animals in frame; see Chapter 1 Discussion), it was critical to improve efficiency in subsequent years of the study. This need motivated change in the existing workflow to integrate machine learning for animal detection while continuing manual classification of species. I implemented MegaDetector, an open-source, generalizable, object-detection model designed to expedite camera-trap image processing (version 3; Beery et al. 2019, Microsoft 2020). I used this automated model to determine whether animals (not species) were present in

images—thus it was implicitly used as a coarse filter to screen out empty images. Before implementing it into the workflow, it was important to first evaluate the platform’s performance with a test dataset (Christin et al. 2021). A total of 52,232 validated photos from 2019 were leveraged to evaluate MegaDetector’s accuracy for detecting deer and determine a desired confidence threshold (see Appendix 2E for more details).

All images from 2020–2022 seasons were initially reviewed by MegaDetector to remove empty images and improve efficiency of the manual species-classification process. To produce image-recognition data in real-time during sampling periods, a set of local modern computers (e.g., in-office agency laptops) executed MegaDetector in tandem. Timelapse software (version 2.2.2.4; Greenburg 2019) was used to inspect MegaDetector’s image-recognition data and organize detections based on a desired confidence threshold. An intermediary database was used to transfer data from Timelapse to CPW Photo Warehouse. CPW Photo Warehouse was used to manually classify species within images containing animals (i.e., animals detected by MegaDetector). A detailed description of the MegaDetector workflow is provided in Appendix 2A.

General abundance-modeling approach

In this study, I used relative abundance of deer as an index, assuming it was functionally related to population size. When modeling abundance, I assumed site-level abundance reflected the number of deer within the effective sampling area surrounding a camera site (see Chapter 1 for details on effective sampling area). I used these site-level abundances to derive estimated abundance by township, where abundance related to the number of deer within the total area of all effective sampling areas in a specified township (18 sites per township = 22 km²

[9 mi²]). Hence, my abundance estimates reflect relative abundance, not absolute, as I did not infer site-level abundances for areas beyond the total surveyed area (i.e., total effective sampling area). Given the incorporation of baseline data and the study's focus on examining changes over time, the use of relative abundance as an index was considered adequate. To interpret the potential effects of harvest treatment on deer abundance, I compared 2019 baseline abundance estimates (i.e., the system before the APR implementation) to estimates from subsequent years (i.e., the system after the APR implementation).

I investigated changes in deer abundance over 3 consecutive years using two separate hierarchical modeling approaches. Model development is an iterative undertaking, exemplified by my use of two distinct frameworks. I modeled relative abundance first using a static binomial N-mixture model (Royle 2004) and then extended it to develop a year-stratified N-mixture model (Kéry and Royle 2021). The static model is described in detail in the Appendix (Appendix 2B). For both the static and year-stratified N-mixture approaches, I modeled the abundance of sex-and-age classes individually (Legal Antlered, Female, Sub-legal Antlered, Fawn). I followed recommendations from Chapter 1 and used data associated with a weekly sampling frequency (i.e., weekly counts), a 63-day sampling duration (15 July–15 September), and a camera distribution of 18 sites per township. Both N-mixture models included similar covariates, in which agriculture cover (% of land cover) affected abundance and landscape cover (open or closed) affected detection probability (see Chapter 1 for details on deriving covariates). Prior to building my models, I standardized all covariates (mean = 0) to improve interpretation and reduce potential multicollinearity. With regards to the Bayesian implementation, Markov chain Monte Carlo (MCMC) settings and model-convergence assessments were similar between

modeling approaches (described in detail in Chapter 1). I assumed vague prior distributions for all analyses.

N-mixture models are subject to critical assumptions, including population closure (i.e., no individuals leave or enter the population via birth, immigration, death, or emigration), detection probability is equal for all individuals, absence of false-positive detections (i.e., no misidentifications or double counting of individuals), and detections of individuals are independent of one another (Royle 2004). Deviations from these assumptions can affect the validity of the estimates produced by these models (Barker et al. 2018, Link et al. 2018). Consequently, if the underlying assumptions are not satisfied, it is advisable to interpret estimates as measures of relative abundance indices instead of absolute values (Barker et al. 2018, Gilbert et al. 2021).

I considered a minimum of 3 years post-harvest regulation change was needed to observe and evaluate potential population-level changes. Multiple years of data are important to recognizing natural, annual variation in deer abundance. Delayed population-level effects from the APR regulation change were also expected. For example, the males (including fawns) that remain after harvest need time to mature and advance to older age classes (Figure 2.3). Further, any change in antlerless hunting pressure needs time to affect the female population, fawn production, and maturing of males (Figure 2.3). Therefore, I considered comparisons between 2019 and 2022 abundance estimates within townships important and comparisons among paired townships as most meaningful. A significant change in one of the paired townships, but not the other, implied that different harvest treatment may influence abundance.

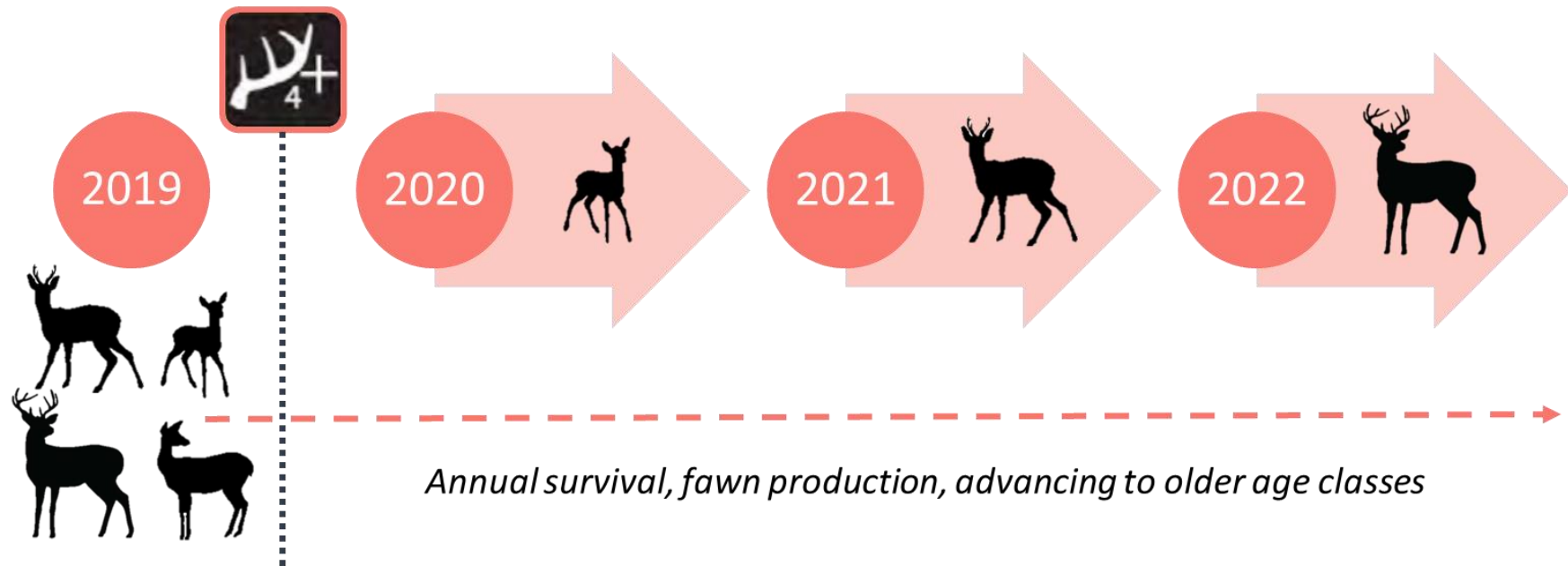


Figure 2.3. Conceptual diagram of the timeframe needed to evaluate potential population-level changes of white-tailed deer (*Odocoileus virginianus*) populations following the implementation of antler point restrictions (APRs). Pink circles indicate annual, summer population surveys. Deer hunting occurred every fall following the summer surveys. Black vertical dashed line indicates that the APR was implemented and effective following the 2019 survey. Delayed population-level effects from the APR regulation change were expected. The males (including fawns) that remain after harvest need time to mature and advance to older age classes. Further, any change in antlerless hunting pressure needs time to affect the female population, fawn production, and maturing of antlered males (pink horizontal dashed line). Three years of data post-harvest regulation change was needed to observe and evaluate potential population-level changes (4 years of data total, including 2019 baseline data).

Year-stratified N-mixture model

To accommodate the open-population structure that arose from sampling across multiple years, I fit all the T years (4) jointly using a year-stratified framework (Kéry and Royle 2021). The year-stratified N-mixture model is a class of hierarchical models for open populations (i.e., populations subject to change over time via addition or subtraction of individuals) that can be used to estimate trends or covariate effects, when dynamics are not of interest (Kéry and Royle 2021). By analyzing the entire data set in a model where every parameter is year-specific, it allows the user to impose explicit constraints on the parameters and to share parameters among the datasets (Kéry and Royle 2021). This approach is like fitting T separate static models (e.g., Appendix 2B), except with the data pooled into a single dataset (also referred to as stacking the data) and analyzed jointly (Kéry and Royle 2021). Stacking successive years of data yields distinct site-year combinations, enabling the estimation of abundance based on these combinations. This approach also satisfies the model's closure assumption, which denotes closure during survey periods and openness between them.

To account for imperfect detection and spatiotemporal differences in the data (Kellner and Swihart 2014), I fit a year-stratified N-mixture model as described by Kéry and Royle (2021). For this modeling approach, I converted from JAGS to NIMBLE (Nimble Development Team 2023a) for increased modeling flexibility (Kéry and Royle 2021) and efficiency (Ponisio et al. 2020). I fit the model using NIMBLE (de Valpine et al. 2017) in program R (version 4.1.2; R Core Team 2021) with the `nimble` package (version 0.13.1; NIMBLE Development Team 2023b). My year-stratified model was much like my static model (Appendix 2B), but with an additional index t for year (i.e., an additional loop). To accommodate this new looping structure, I reformatted

the count data from wide to long format (i.e., stacked) and stored data in a 3-dimensional array by site (i), replicate count (j), and year (t).

Using a year-stratified N-mixture modeling approach, I modeled sex-and-age classes independently to estimate township-level abundances. My township-abundance model was as follows, for each site $i = 1, 2, \dots, M$:

$$N_{i,t} \sim \text{Poisson}(\lambda_{i,t})$$

$$\log(\lambda_{i,t}) = \beta_1(\text{Treatment}_{i,t}) + \beta_2(\text{Treatment}_{i,t}) * \text{Year}_{i,t}$$

$$+ \beta_3 * (\%Agriculture_{i,t})^2 + \varepsilon(\text{Township}_{i,t})$$

In addition to the extra level of hierarchy (t), my year-stratified model differed from my static model in other ways. Harvest treatment and year were hypothesized to influence abundance, therefore I incorporated both into the year-stratified model. To account for changes across years (i.e., the openness of the system), I included a year effect in the abundance model's log-link function as a set of T year-specific intercepts by harvest treatment (β_1) and as a set of T year-specific interactions between year and harvest treatment (β_2). Note that harvest treatment (APR or Non-APR) was not included as a binary covariate via categorical indicator variables, but instead as categorical index variables (analogous to ID numbers). Simply put, I had 2 values for the intercept (β_1) and 2 values for the interaction term (β_2) which the model accessed by referencing the specified index variable (APR or Non-APR). This mechanism was advantageous over common indicator variables (e.g., using 1s and 0s as on-off switches) which can introduce unwanted asymmetric uncertainty between treatment groups. I used a similar indexing structure to introduce a township random effect in the abundance model. More specifically, I gave the model latitude to account for variation in lambda (λ) among township and year

combinations by adding the residual-error term epsilon (ε) to the model's log-link function. I assigned epsilon an exponential prior to ensure positive values (i.e., drawn from a mean-zero normal distribution).

The year-stratified observational model differed from my static model (Appendix 2B), with the additional index t for year and the addition of a random effect. My year-stratified observation model specified in algebra, was as follows, for sites $i = 1, 2, \dots, M$:

$$y_{i,j,t} \sim \text{Binomial}(N_{i,t}, p_{i,t})$$

$$\text{logit}(p_{i,t}) = \alpha_0 + \alpha_1(\text{Cover}_{i,t}) + \varepsilon_{i,t}$$

Here, I included a site-by-year random effect in the observation model's logit-link function, with the standard deviation among site and year combinations modeled as the residual-error epsilon (ε). This approach gave the model latitude to account for heterogeneity in detection probability among sites and years, which if not addressed, could confound trend estimates. I assigned epsilon an exponential prior to ensure positive values. Parameters monitored included α , β , and ε values. The R code for the year-stratified N-mixture model is available in the Appendix (Appendix 2C).

Change in site-abundance

As models grow in complexity, it can be increasingly difficult to interpret coefficients. This is particularly relevant when models include quadratic or interaction terms. In such cases, visualizing marginal effects can help interpret the relationship between predictors and outcome. To interpret the effects of harvest treatment, year, and interaction of the two on deer abundance, I plotted the marginal effects derived from the year-stratified N-mixture model. I used the estimated model to interpret these effects by township and sex-and-age class,

enabling a more intuitive interpretation expressed in terms of mean site-abundance. Put differently, I used model predictions for interpretation. This analysis was informed by the N-mixture model's intercept, error, and coefficient estimates, with the agriculture covariate excluded as it was held constant at the standardized mean (i.e., 0). To preserve uncertainty, I used full posterior distributions (28,200 datapoints) for summarizing means and 95% BCIs of parameter estimates. I visually inspected marginal-effects plots to interpret relationships between the predictors and abundance. Marginal-effect visualization in this context helped determine whether the implementation of an APR would produce a negative or positive impact on deer abundance in the years following. Note that for township pairs A and D, marginal effects were visualized without 2020 data (missing data due to COVID-19 pandemic-related constraints).

Using the year-stratified model, I quantified mean change in site-abundance ($\bar{x}$) by summing differences between 2019 abundance estimates (i.e., the system before the APR implementation; $\widehat{NB}$) and 2022 abundance estimates (i.e., the system 3 years after the APR implementation; $\widehat{NA}$), for each MCMC iteration (i), divided by the total number of datapoints ($n = 28,200$):

$$\bar{x} = \frac{\sum_{i=1}^n (\widehat{NA}_i - \widehat{NB}_i)}{n}$$

I calculated mean change and determined the magnitude of change to differ between APR and Non-APR townships if 95% BCIs did not overlap. Further, I concluded there was a significant change in site-abundance if 95% BCIs did not overlap zero. Code for quantifying change in abundance and evaluating marginal effects is provided in the Appendix (Appendix 2D).

RESULTS

Field sampling

From 2019–2022, 144 or 72 camera traps were deployed annually for 63 days, which resulted in a total survey effort of 31,227 trap days (Table 2.2). Including camera operation failures, the mean camera deployment period was 62 days (SD = 4.2; range = 27–63 days; Table 2.2). Across years, an average of 11 cameras (SD = 8.8; range = 5–24) experienced partial operation issues throughout the deployment period (e.g., full memory cards, camera malfunctions, vandalism; Table 2.2). Camera density was approximately 1 per 5.2 km² (1 per 2.0 mi²) within each township and cameras averaged 1.3 km (SD = 0.7) between nearest neighbor camera sites. Approximately 83% of camera sites were on private lands, an outcome of the random site-selection process and partnership with 160 landowners. Under rare circumstances (e.g., land-use changes, change in landownership, landowner ceasing to participate in study), alternative camera sites had to be secured in later years of the study. In total, 185 distinct camera sites were used during this study, resulting in a site similarity of 72% between 2019 and 2022.

Table 2.2. Annual summaries of the total number of camera traps deployed, the number of cameras not fully operational during the deployment period, the mean, SD, and range of camera deployment period (days), and total survey effort (trap days). Camera traps were deployed during summer months (15 July–15 September) in the south-central Lower Peninsula of Michigan, USA, 2019–2022.

Year	Camera traps	Cameras not fully operational	Average camera deployment	SD of camera deployment	Range of camera deployment	Survey effort
2019	144	24	60.9	5.9	27–63	8,772
2020	72	6	61.9	4.1	42–63	4,457
2021	144	5	62.5	3.2	32–63	9,002
2022	144	10	62.5	2.4	43–63	8,996

Image processing

Camera traps collected 2,644,590 images during the 4 years of the study, with the APR Zone accounting for 1,489,730 images and the Non-APR Zone 1,154,860 (Table 2.3). To expedite photo processing after year one of the study (2019), 1,847,183 images from 2020–2022 were processed using the MegaDetector object-detection model. A 90+ confidence threshold setting was selected for MegaDetector for its ability to minimize the number of irrelevant images needing manual review while having little effect on the number of false-negative deer images (Appendix 2E). MegaDetector classified 56% of images (1,039,972) as “Animal” and 44% as “Empty” (807,211; Figure 2.4).

All Animal images were manually reviewed to classify species in the field of view. Altogether, ≥ 1 deer were detected in 906,792 photos (Table 2.4). Cameras detected deer at 97% of site-year combinations (496/509) throughout the sampling periods (2019–2022), resulting in a total of 1,118,757 verified deer detections. Most deer photos included Females in the field of view (510,486 detections; Table 2.5). Apart from Unknown Deer (45,606 detections), Legal Antlered were detected the least (83,407 detections; Table 2.5).

Table 2.3. Summary of total images collected by year, zone, and study area total (zones combined). Images were collected during summer months (15 July–15 September) using a camera-trap study design in the south-central Lower Peninsula of Michigan, USA.

Year	APR Zone	NonAPR Zone	Study area total
2019	414,626	382,781	797,407
2020	249,972	198,014	447,986
2021	390,693	271,439	662,132
2022	434,439	302,626	737,065

Table 2.4. Summary of total deer images by year, zone, and study area total. Deer images included ≥ 1 deer detected in the field of view, verified by dual observers. Images were collected during summer months (15 July–15 September) using a camera-trap study design in the south-central Lower Peninsula of Michigan, USA.

Year	APR Zone	NonAPR Zone	Study area total
2019	155,111	120,683	275,794
2020	72,184	46,441	118,625
2021	140,816	85,463	226,279
2022	185,383	100,711	286,094

Table 2.5. Summary of yearly white-tailed deer (*Odocoileus virginianus*) image classifications by sex-and-age class, zone, and total study area. Deer classifications included ≥ 1 deer detected in the field of view, verified by dual observers. Images were collected during summer months (15 July–15 September) using a camera-trap study design in the south-central Lower Peninsula of Michigan, USA.

Photo classification by year	APR Zone	Non-APR Zone	Study area total
2019			
Female ^a	84,205	61,940	146,145
Fawn ^b	57,416	54,456	111,872
Sub-legal Male ^c	24,649	15,392	40,041
Legal Male ^d	14,404	5,635	20,039
Unknown Deer ^e	9,627	6,534	16,161
2020			
Female ^a	43,518	28,248	71,766
Fawn ^b	22,805	21,824	44,629
Sub-legal Male ^c	10,830	4,004	14,834
Legal Male ^d	5,559	3,839	9,398
Unknown Deer ^e	3,694	2,587	6,281
2021			
Female ^a	75,854	47,995	123,849
Fawn ^b	42,700	34,404	77,104
Sub-legal Male ^c	20,480	13,500	33,980
Legal Male ^d	25,805	7,188	32,993
Unknown Deer ^e	7,111	5,434	12,545
2022			
Female ^a	107,675	61,051	168,726
Fawn ^b	73,480	39,573	113,053
Sub-legal Male ^c	30,313	13,657	43,970
Legal Male ^d	12,584	8,393	20,977
Unknown Deer ^e	7,011	3,608	10,619

^aFemale classifications include yearling and adult female deer.

^bFawn classifications include male and female fawns.

^cSub-legal Male classifications include antlered deer that did not meet the antler point restriction criteria.

^dLegal Male classifications include antlered deer that met the antler point restriction criteria.

^eDeer were classified as Unknown Deer when it was impossible to determine the sex or age of the deer (e.g., unable to see head).

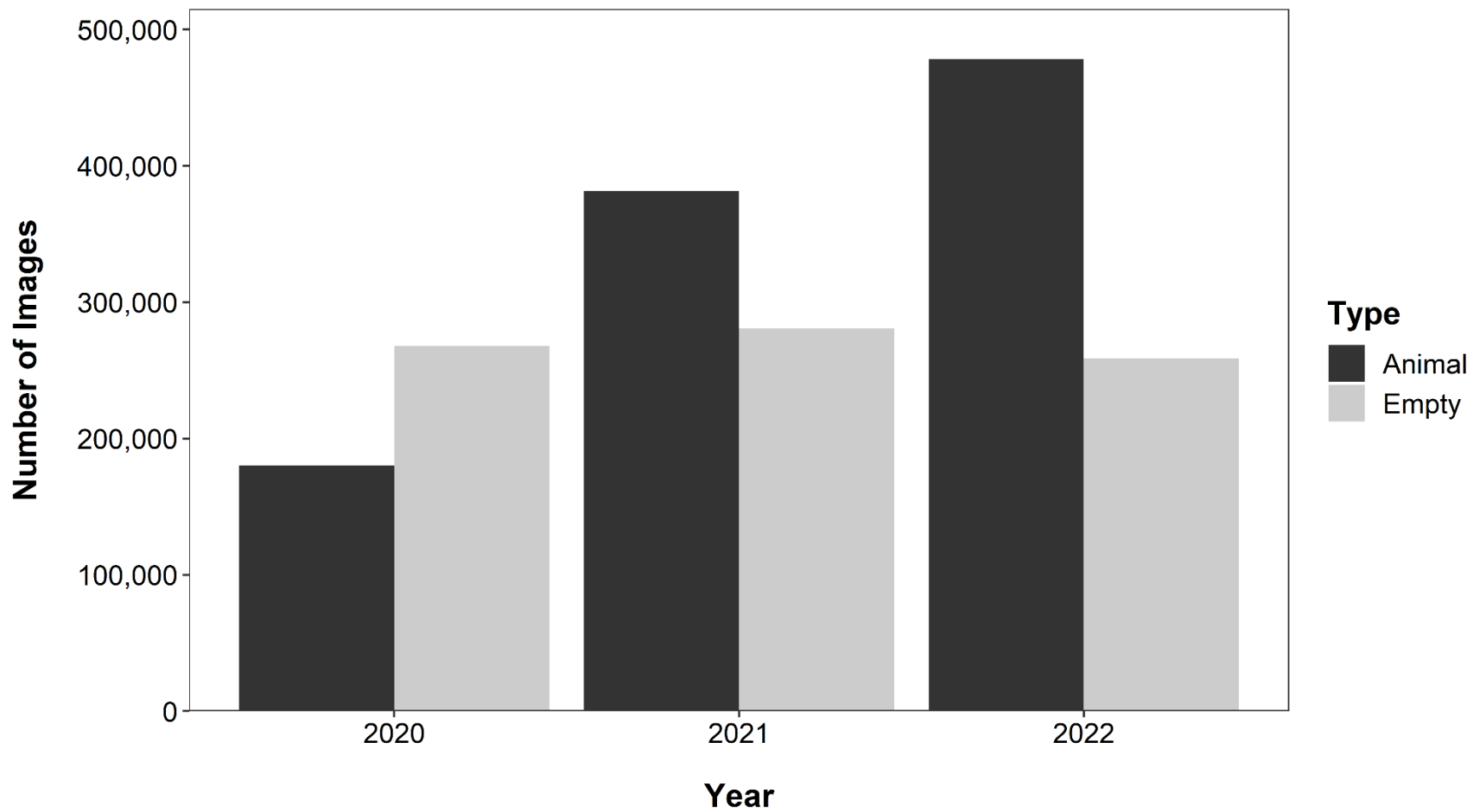


Figure 2.4. Classification results produced by MegaDetector, a machine-learning model designed to detect and classify objects in images. Images analyzed were collected using a camera-trap study design in the south-central Lower Peninsula of Michigan, USA, 2020–2022.

Static binomial N-mixture model

I used the static binomial N-mixture model to estimate deer abundance one-year-at-a-time. Although there are applications for this closed-population model, I did not consider it appropriate for this study—based on model limitations and the objectives of the state wildlife agency. Outcomes from this modeling effort are described in detail in the Appendix (Appendix 2B).

Year-stratified N-mixture model

Using my year-stratified N-mixture model, I fit all 4 years of data jointly to estimate annual deer abundance. I did not detect any significant changes in Legal Antlered abundance in APR or Non-APR townships (Figure 2.5). Relative to its corresponding baseline estimate in 2019, I detected a single increase in Female abundance in the Non-APR Zone's B Township (2019: $\bar{x}$ = 29.4 [95% BCI = 26–35]; 2021: $\bar{x}$ = 42.1 [95% BCI = 37–48]; Figure 2.6). Relative to 2019 baseline estimates, I detected significant increases in Sub-legal Antlered abundance in the Non-APR Zone's Township A (2019: $\bar{x}$ = 21.2 [95% BCI = 17–27]; 2022: $\bar{x}$ = 37.7 [95% BCI = 31–47]) and Township D (2019: $\bar{x}$ = 21.6 [95% BCI = 17–28]; 2022: $\bar{x}$ = 41.4 [95% BCI = 34–51]; Figure 2.7). I failed to detect any significant changes in Fawn abundance in APR or Non-APR townships (Figure 2.8).

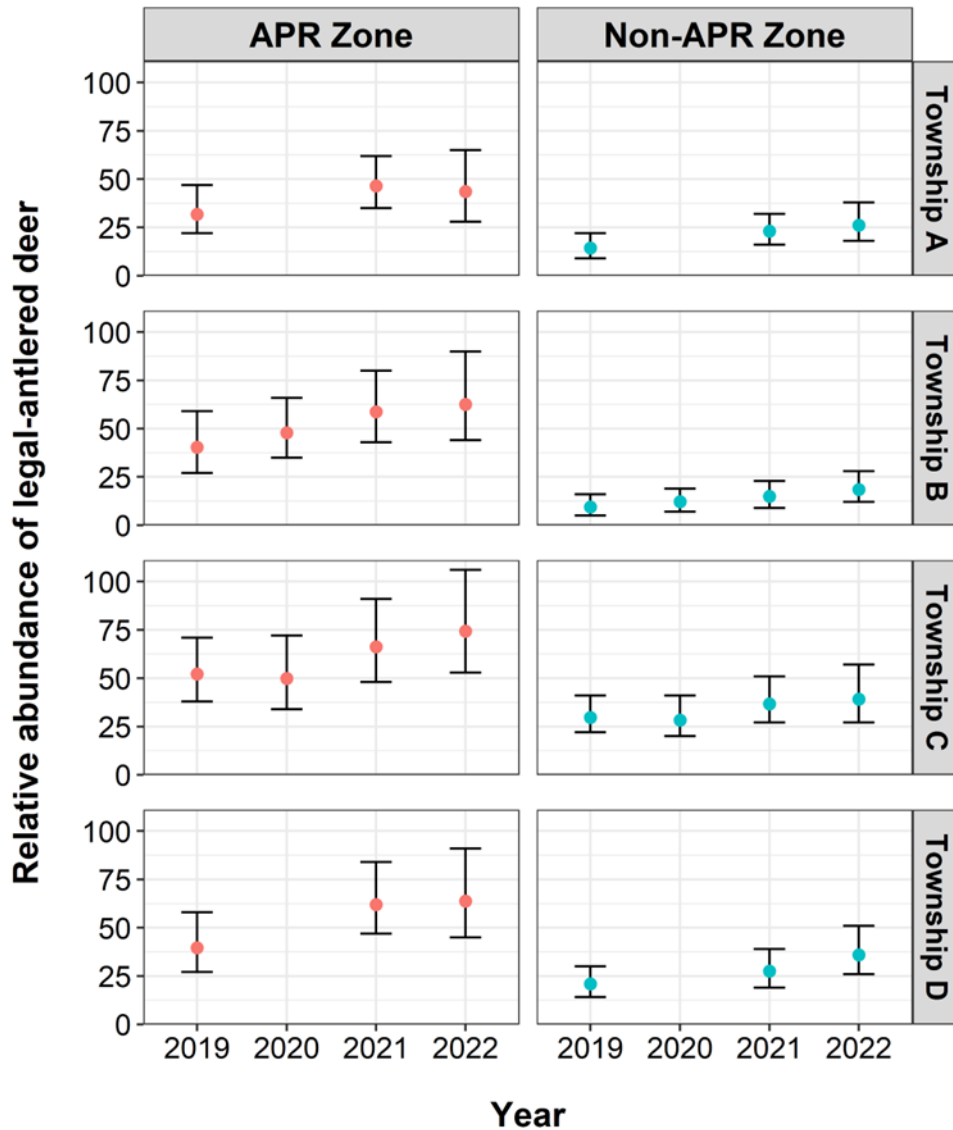


Figure 2.5. Pre-harvest mean abundance of legal antlered white-tailed deer (*Odocoileus virginianus*) in the south-central Lower Peninsula of Michigan, USA, 2019–2022. Relative abundance was used as an index and assumed to be functionally related to population size. Beginning in 2019, antlered deer harvest was limited by a 4-point antler point restriction (APR) in the APR Zone, but not in the Non-APR Zone. Legal-antlered deer are defined by the APR criteria in the APR Zone. Zones are displayed in the grid columns and township pairs (A–D) in the grid rows. Abundance relates to the number of deer within the effective sampling area (i.e., area surveyed) of a specified township. Error bars indicate 95% Bayesian credible intervals. Only half of the townships were surveyed in 2020 due to pandemic-related constraints. Relative to 2019 baseline estimates (i.e., the system before APR implementation), no significant changes were detected.

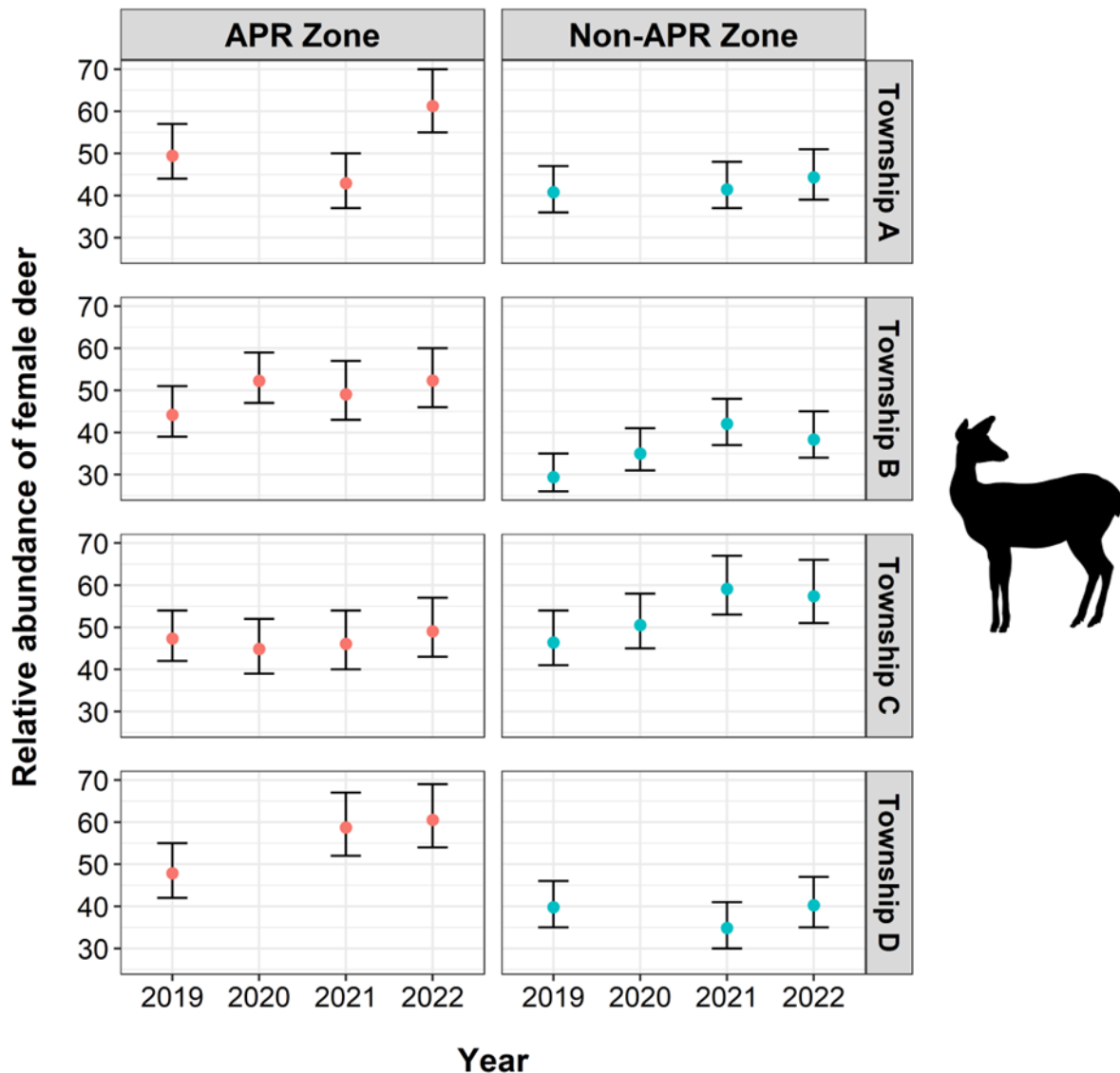


Figure 2.6. Pre-harvest mean abundance estimates of female (subadult and adult, i.e., does) white-tailed deer (*Odocoileus virginianus*) in the south-central Lower Peninsula of Michigan, USA, 2019–2022. Relative abundance was used as an index and assumed to be functionally related to population size. Beginning in 2019, antlered deer harvest was limited by a 4-point antler point restriction (APR) in the APR Zone, but not in the Non-APR Zone. Zones are displayed in the grid columns and township pairs (A–D) in the grid rows. Abundance relates to the number of deer within the effective sampling area (i.e., area surveyed) of a specified township. Error bars indicate 95% Bayesian credible intervals. Only half of the townships were surveyed in 2020 due to pandemic-related constraints. Relative to baseline estimates in 2019 (i.e., the system before APR implementation), a significant increase was detected in the Non-APR Zone (Township B 2021).

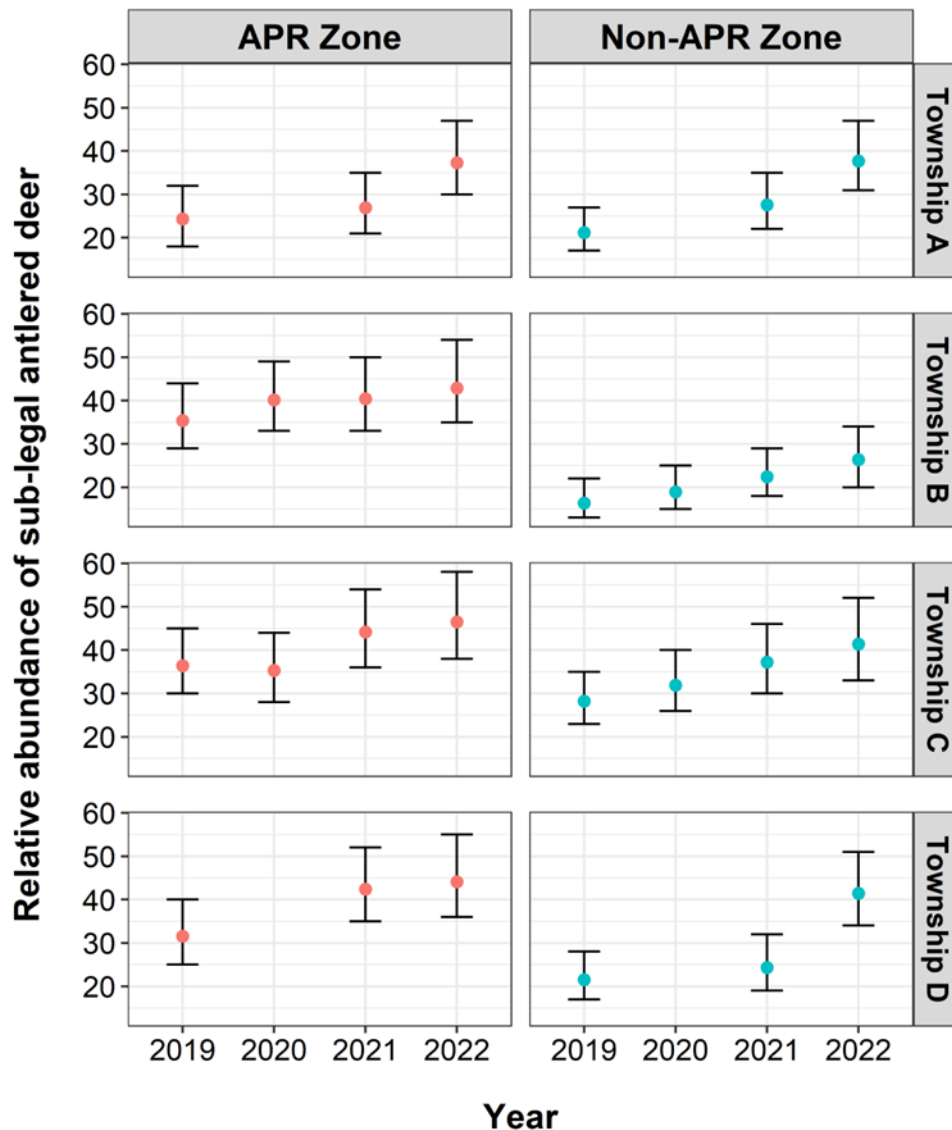


Figure 2.7. Pre-harvest relative abundance estimates of sub-legal antlered white-tailed deer (*Odocoileus virginianus*) in the south-central Lower Peninsula of Michigan, USA, 2019–2022. Relative abundance was used as an index and assumed to be functionally related to population size. Beginning in 2019, antlered deer harvest was limited by a 4-point antler point restriction (APR) in the APR Zone, but not in the Non-APR Zone. Sub-legal antlered deer are defined by not meeting the APR criteria in the APR Zone. Zones are displayed in the grid columns and township pairs (A–D) in the grid rows. Abundance relates to the number of deer within the effective sampling area (i.e., area surveyed) of a specified township. Error bars indicate 95% Bayesian credible intervals. Only half of the townships were surveyed in 2020 due to pandemic-related constraints. Relative to baseline estimates in 2019 (i.e., the system before APR implementation), a significant increase was detected in the Non-APR Zone (Township A 2022; Township D 2022).

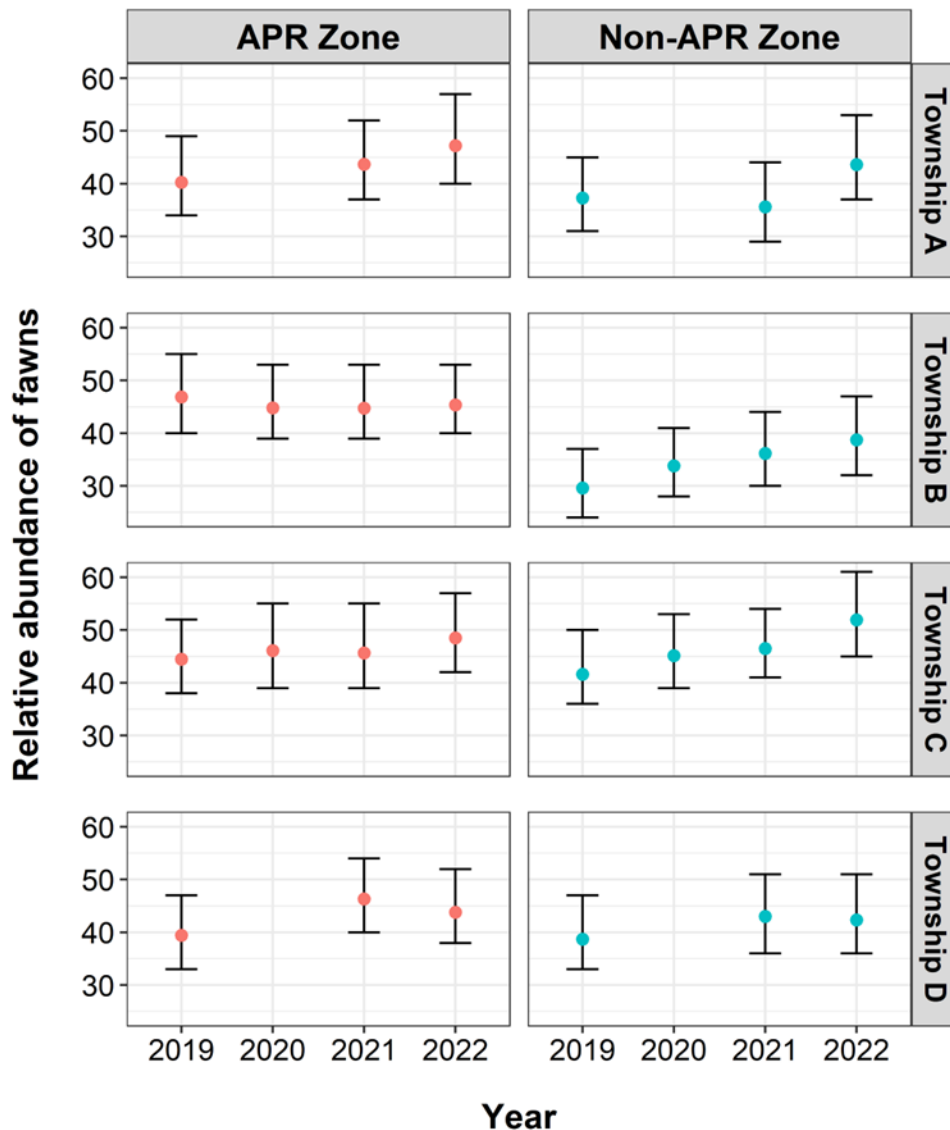


Figure 2.8. Pre-harvest relative abundance estimates of fawn white-tailed deer (*Odocoileus virginianus*) in the south-central Lower Peninsula of Michigan, USA, 2019–2022. Relative abundance was used as an index and assumed to be functionally related to population size. Beginning in 2019, antlered deer harvest was limited by a 4-point antler point restriction (APR) in the APR Zone, but not in the Non-APR Zone. Zones are displayed in the grid columns and township pairs (A–D) in the grid rows. Abundance relates to the number of deer within the effective sampling area (i.e., area surveyed) of a specified township. Error bars indicate 95% Bayesian credible intervals. Only half of the townships were surveyed in 2020 due to pandemic-related constraints. Relative to 2019 baseline estimates (i.e., the system before APR implementation), no significant changes were detected.

Change in site-abundance

To better interpret the year-stratified N-mixture model's predictions, I plotted the marginal effect of explanatory variables (harvest treatment, year, and interaction of the two) on site-abundance by sex-and-age class. These visualizations revealed a pattern of positive trends in marginal effects for all sex-and-age classes across all townships (Figure 2.9, Figure 2.10, Figure 2.11, Figure 2.12). I calculated the difference between 2019 and 2022 site-abundance and determined the magnitude of change to be similar between paired townships for all sex-and-age classes (Figure 2.13, Figure 2.14, Figure 2.15, Figure 2.16). I detected significant changes (i.e., 95% BCIs did not include zero) in site-abundance with Legal Antlered and Sub-legal Antlered increasing in all townships (Figure 2.13, Figure 2.15). I failed to detect significant changes in site-abundance for Females and Fawns (Figure 2.14, Figure 2.16). The largest mean change in site-abundance was estimated with Legal Antlered in the APR Zone's Township B ($\bar{x}$ = 1.35; 95% BCI = 0.39–2.54; Figure 2.13) and smallest with Fawns in the APR Zone's Township D ($\bar{x}$ = 0.18; 95% BCI = -0.42–0.79; Figure 2.16).

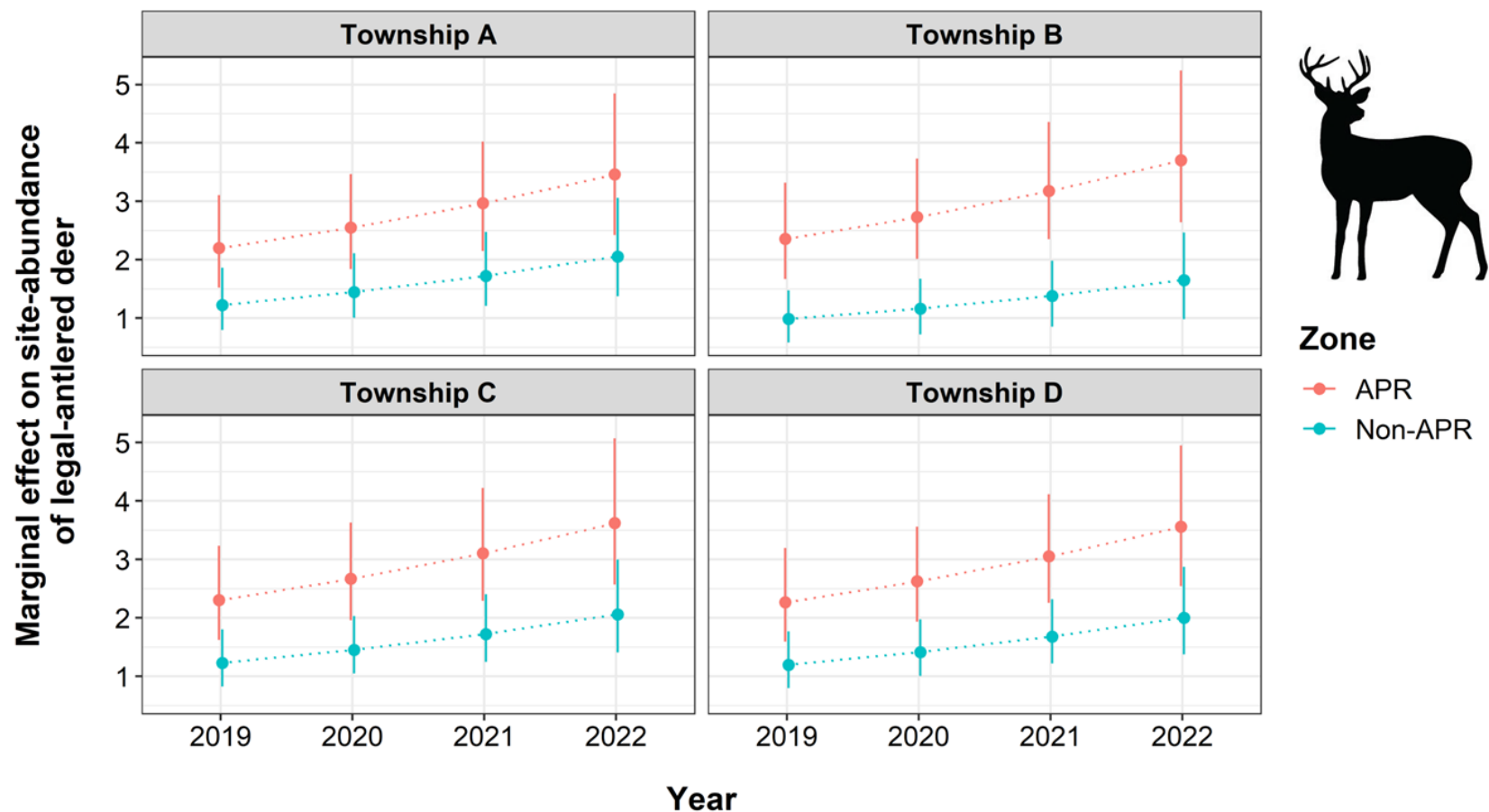


Figure 2.9. Marginal effect of harvest treatment, year, and the interaction of the two on mean site-abundance of legal-antlered white-tailed deer (*Odocoileus virginianus*) in the south-central Lower Peninsula of Michigan, USA, 2019–2022. Beginning in 2019, antlered deer harvest was limited by a 4-point antler point restriction (APR) in the APR Zone, but not in the Non-APR Zone. Legal-antlered deer are defined by the APR criteria in the APR Zone. Zones are differentiated by color and individual township pairs (A–D) are displayed in each panel. Site-abundance relates to the mean number of deer within the effective sampling area at survey sites. Error bars indicate 95% Bayesian credible intervals. Only half of the township pairs were surveyed in 2020 (due to COVID-19 pandemic-related constraints), and consequently, marginal effects were visualized in the absence of 2020 data for township pairs A and D.

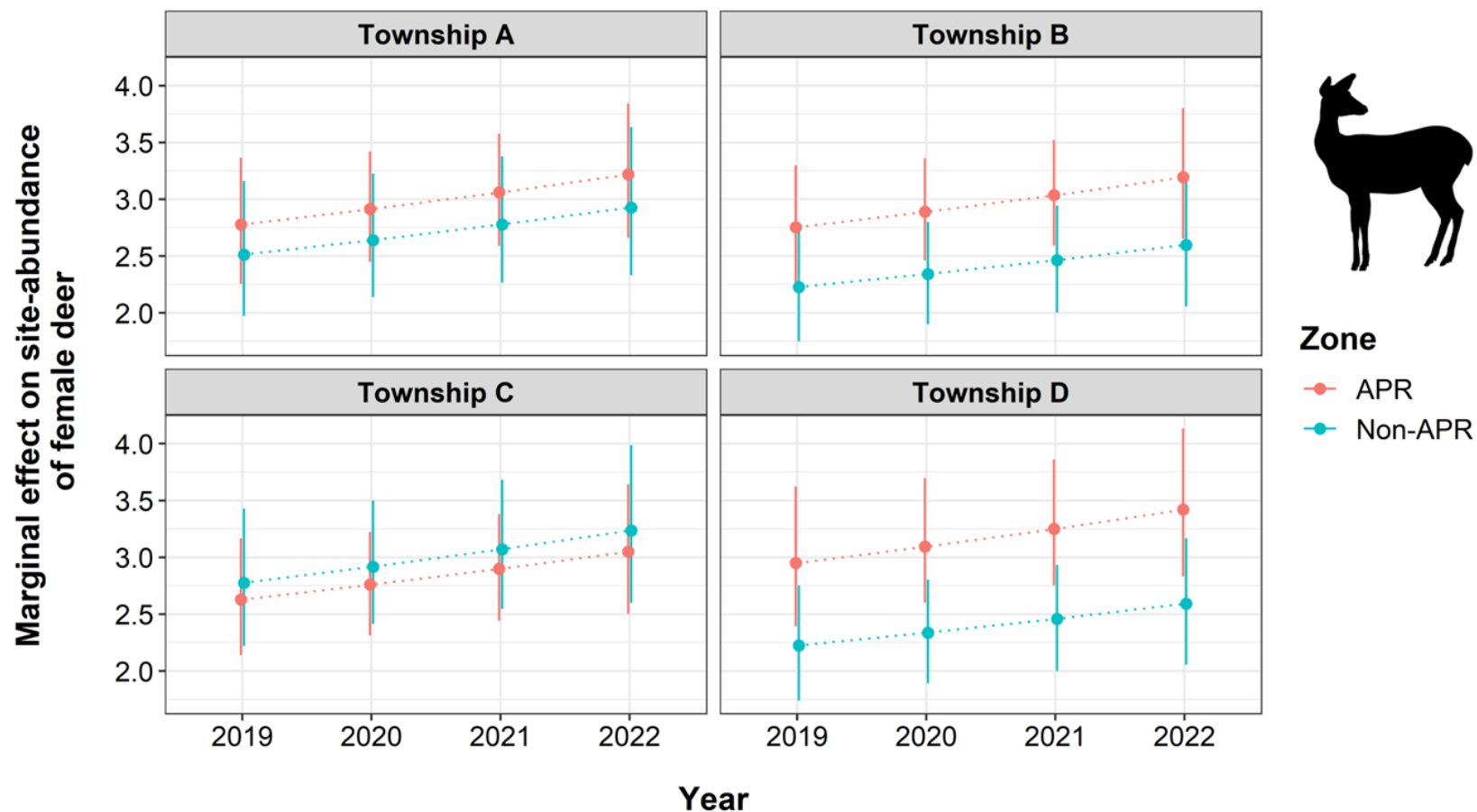


Figure 2.10. Marginal effect of harvest treatment, year, and the interaction of the two on mean site-abundance of female (subadult and adult, i.e., does) white-tailed deer (*Odocoileus virginianus*) in the south-central Lower Peninsula of Michigan, USA, 2019–2022. Beginning in 2019, antlered deer harvest was limited by a 4-point antler point restriction (APR) in the APR Zone, but not in the Non-APR Zone. Zones are differentiated by color and individual township pairs (A–D) are displayed in each panel. Site-abundance relates to the mean number of deer within the effective sampling area at survey sites. Error bars indicate 95% Bayesian credible intervals. Only half of the township pairs were surveyed in 2020 (due to COVID-19 pandemic-related constraints), and consequently, marginal effects were visualized in the absence of 2020 data for township pairs A and D.

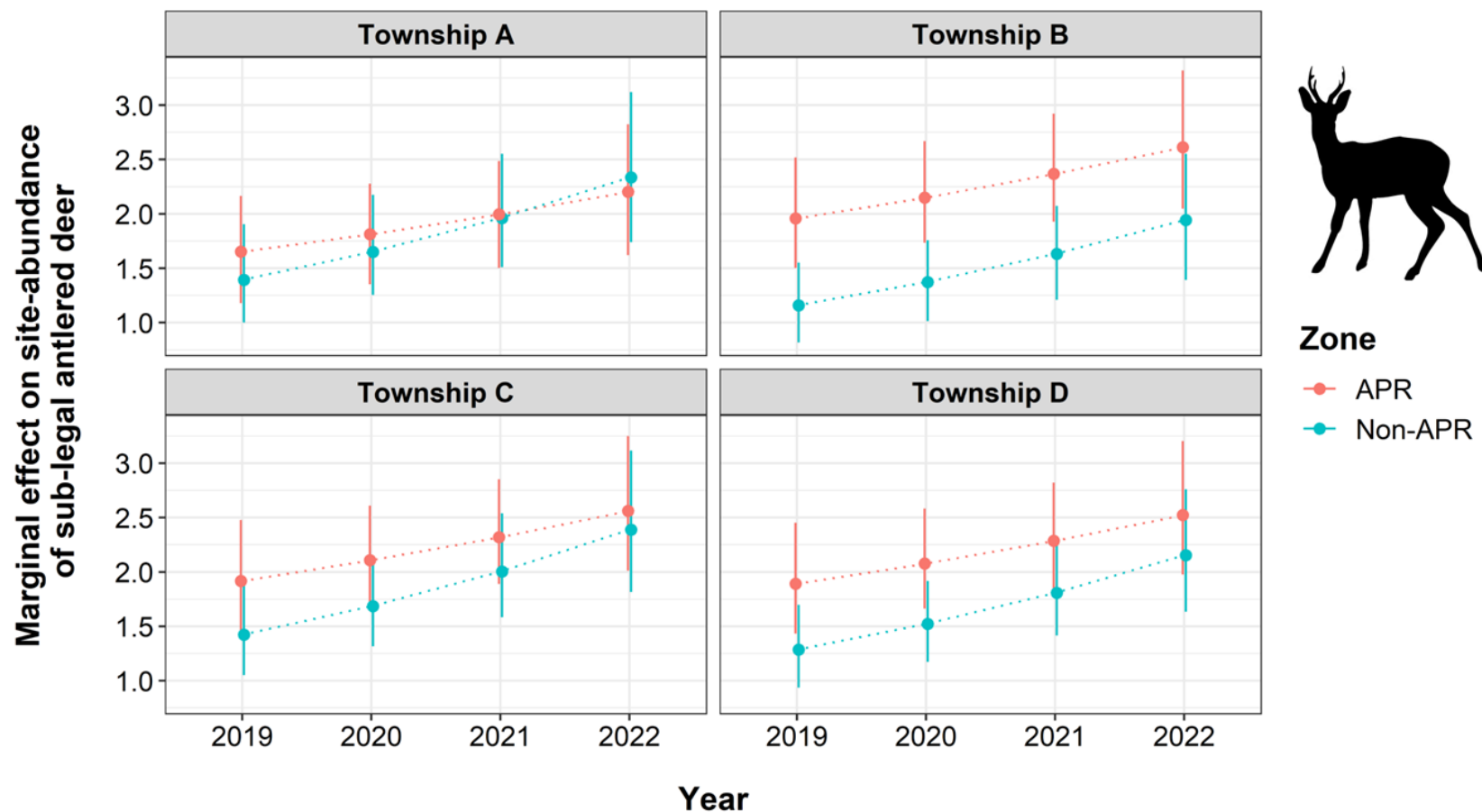


Figure 2.11. Marginal effect of harvest treatment, year, and the interaction of the two on mean site-abundance of sub-legal antlered white-tailed deer (*Odocoileus virginianus*) in the south-central Lower Peninsula of Michigan, USA, 2019–2022. Beginning in 2019, antlered deer harvest was limited by a 4-point antler point restriction (APR) in the APR Zone, but not in the Non-APR Zone. Sub-legal antlered deer are defined by not meeting the APR criteria in the APR Zone. Zones are differentiated by color and individual township pairs (A–D) are displayed in each panel. Site-abundance relates to the mean number of deer within the effective sampling area at survey sites. Error bars indicate 95% Bayesian credible intervals. Only half of the township pairs were surveyed in 2020 (due to COVID-19 pandemic-related constraints), and consequently, marginal effects were visualized in the absence of 2020 data for township pairs A and D.

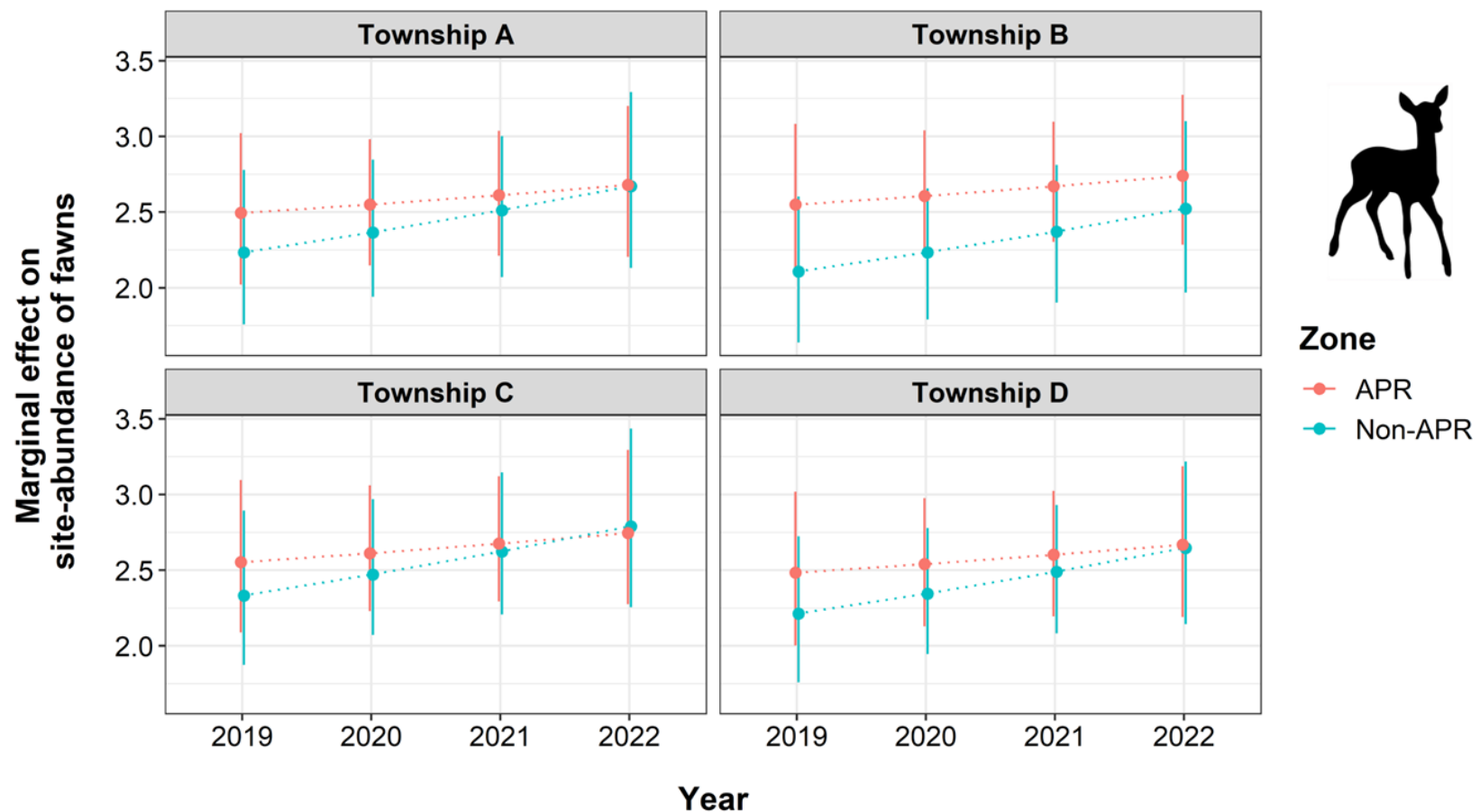


Figure 2.12. Marginal effect of harvest treatment, year, and the interaction of the two on mean site-abundance of fawn white-tailed deer (*Odocoileus virginianus*) in the south-central Lower Peninsula of Michigan, USA, 2019–2022. Beginning in 2019, antlered deer harvest was limited by a 4-point antler point restriction (APR) in the APR Zone, but not in the Non-APR Zone. Zones are differentiated by color and individual township pairs (A–D) are displayed in each panel. Site-abundance relates to the mean number of deer within the effective sampling area at survey sites. Error bars indicate 95% Bayesian credible intervals. Only half of the township pairs were surveyed in 2020 (due to COVID-19 pandemic-related constraints), and consequently, marginal effects were visualized in the absence of 2020 data for township pairs A and D.

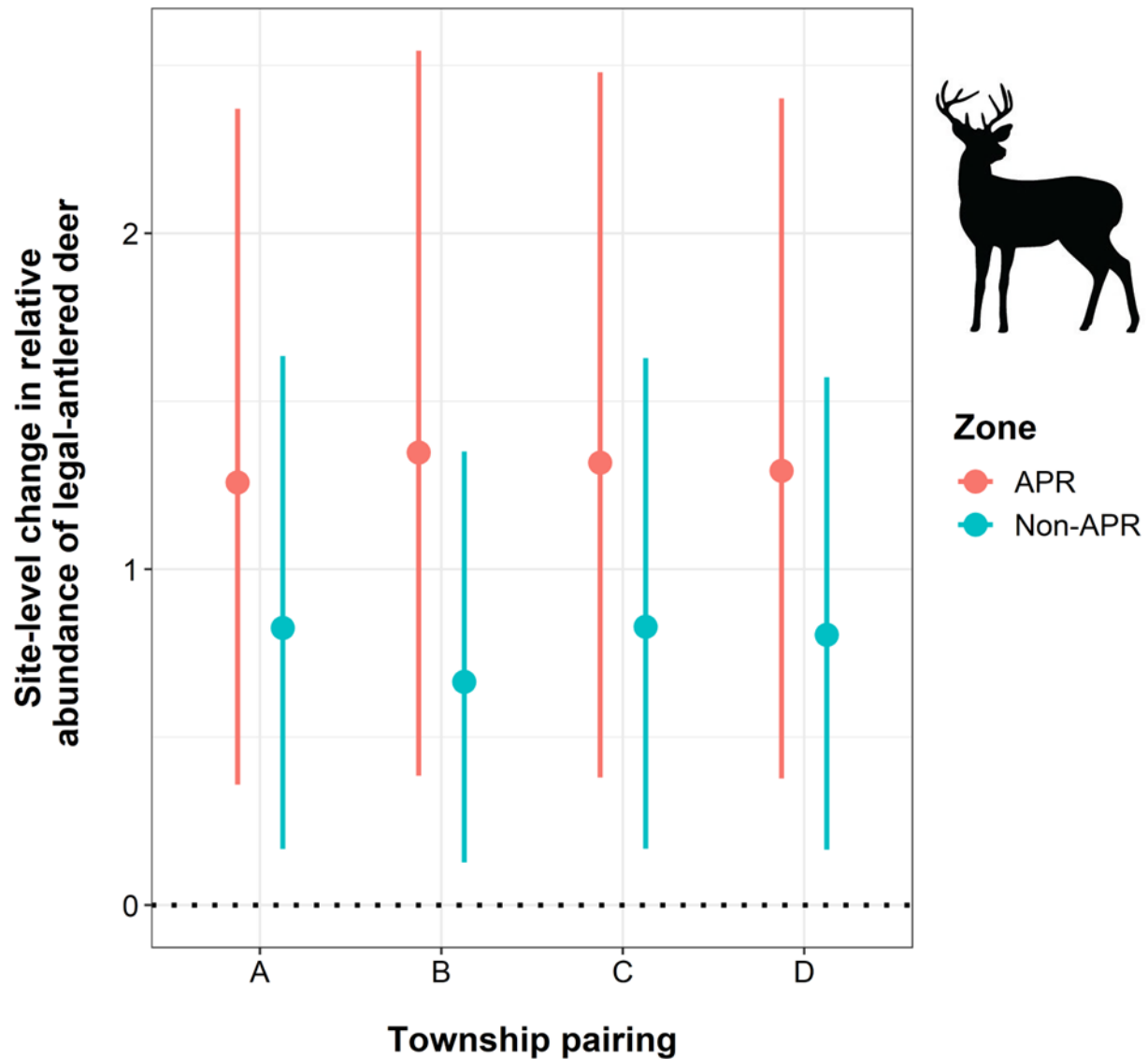


Figure 2.13. Mean change in site-abundance of legal antlered white-tailed deer (*Odocoileus virginianus*) between 2019 and 2022 in the south-central Lower Peninsula of Michigan, USA. Estimates were derived from pre-harvest abundance estimates. Beginning in 2019, antlered deer harvest was limited by a 4-point antler point restriction (APR) in the APR Zone, but not in the Non-APR Zone. Legal-antlered deer are defined by the APR criteria in the APR Zone. Zones are differentiated by color, the horizontal dashed line indicates zero change in site abundance, and error bars indicate 95% Bayesian credible intervals. Similar increases were detected across APR and Non-APR townships.

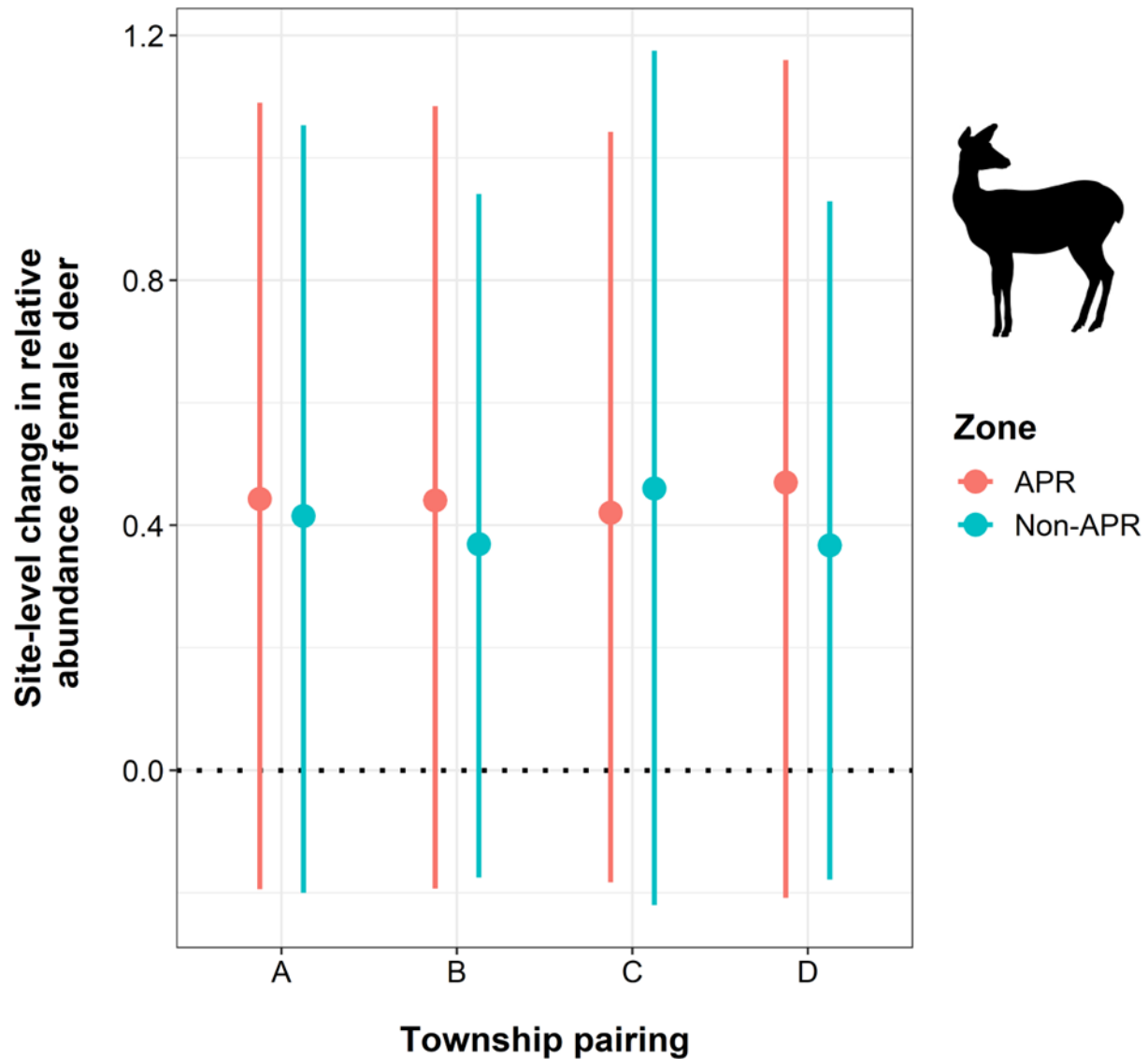


Figure 2.14. Mean change in site-abundance of female (subadult and adult, i.e., does) white-tailed deer (*Odocoileus virginianus*) between 2019 and 2022 in the south-central Lower Peninsula of Michigan, USA. Estimates were derived from pre-harvest abundance estimates. Beginning in 2019, antlered deer harvest was limited by a 4-point antler point restriction (APR) in the APR Zone, but not in the Non-APR Zone. Zones are differentiated by color, the horizontal dashed line indicates zero change in site abundance, and error bars indicate 95% Bayesian credible intervals. Estimates were similar among townships and no changes were detected.

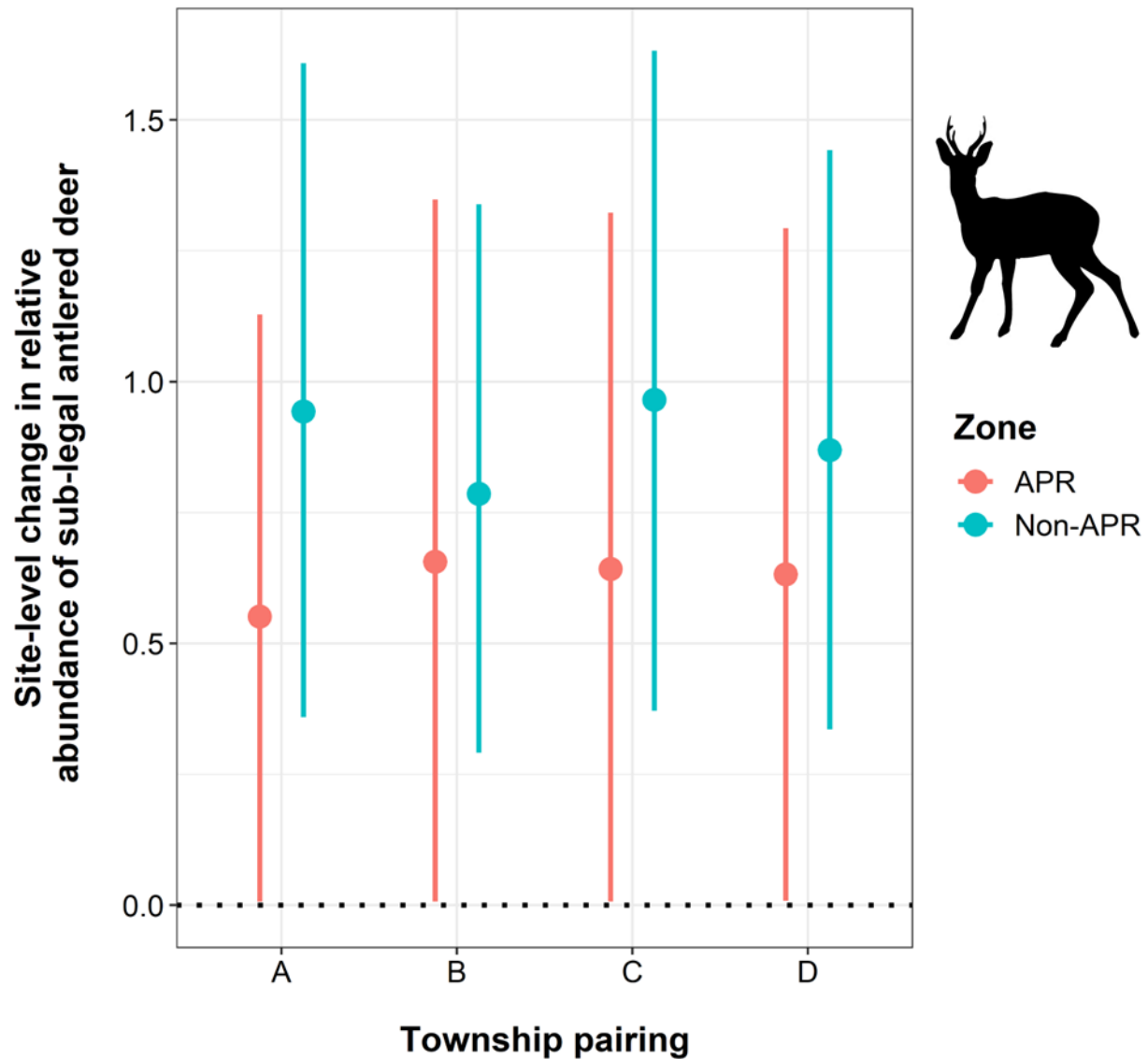


Figure 2.15. Mean change in site-abundance of sub-legal antlered white-tailed deer (*Odocoileus virginianus*) between 2019 and 2022 in the south-central Lower Peninsula of Michigan, USA. Estimates were derived from pre-harvest abundance estimates. Beginning in 2019, antlered deer harvest was limited by a 4-point antler point restriction (APR) in the APR Zone, but not in the Non-APR Zone. Sub-legal antlered deer are defined by not meeting the APR criteria in the APR Zone. Zones are differentiated by color, the horizontal dashed line indicates zero change in site abundance, and error bars indicate 95% Bayesian credible intervals. Similar increases were detected across APR and Non-APR townships.

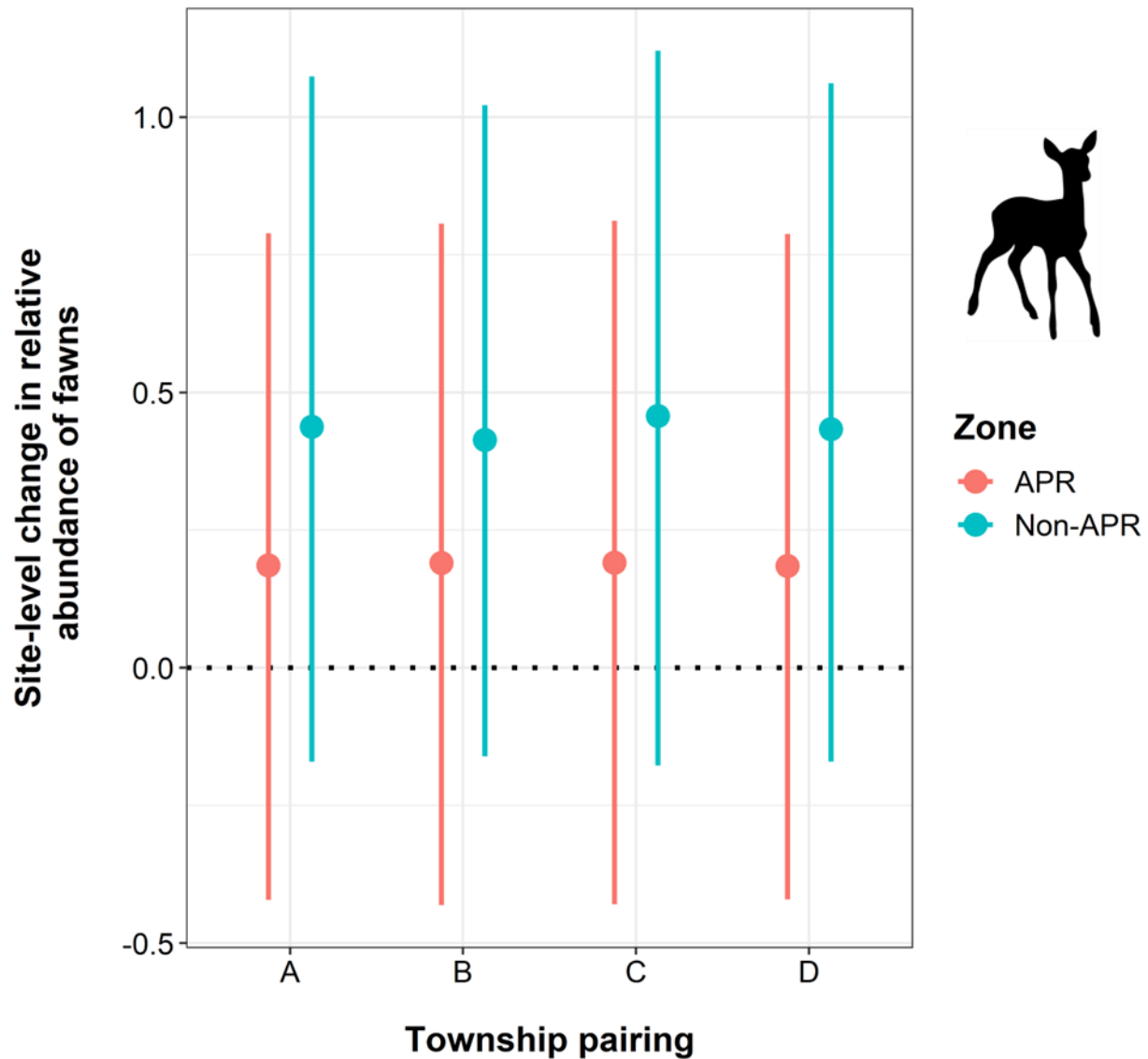


Figure 2.16. Mean change in site-abundance of fawn white-tailed deer (*Odocoileus virginianus*) between 2019 and 2022 in the south-central Lower Peninsula of Michigan, USA. Estimates were derived from pre-harvest abundance estimates. Beginning in 2019, antlered deer harvest was limited by a 4-point antler point restriction (APR) in the APR Zone, but not in the Non-APR Zone. Zones are differentiated by color, the horizontal dashed line indicates zero change in site abundance, and error bars indicate 95% Bayesian credible intervals. Estimates were similar among townships and no changes were detected.

DISCUSSION

In this study, I assessed population-level changes over time and space following a deer harvest regulation implementation in a before-after-control-impact design. I used several analytical approaches to evaluate if APRs affect deer relative abundance by sex-and-age class. To my knowledge, this is the first study paired with an APR regulation change specifically designed to evaluate this question. I found weak evidence for APRs affecting the relative abundance by sex-and-age classes. In both APR and Non-APR areas, I consistently observed increasing trends in the relative abundance of Legal- and Sub-legal Antlered deer. In comparison, there was a lack of evidence supporting change in Female and Fawn relative abundance in APR or Non-APR areas.

My results suggest that the implementation of APRs had an insignificant impact on the Legal-Antlered deer populations in the experimental zone of the 5-County Area. In contrast to my prediction, I found increases in the relative abundance of Legal-Antlered deer in both APR and Non-APR treatment areas. It is important to note that when evaluating results, I considered comparisons between 2019 and 2022 relative abundance estimates within townships important and comparisons among paired townships as most meaningful due to partial controllability in a natural system (i.e., I relied on the BACI study design). Relative to 2019 baseline abundance estimates, I did not detect any significant township-level changes in APR or Non-APR areas, but I did observe a general trend of increasing mean estimates over time (Figure 2.5). Further, I detected similar increases in site-abundance of Legal Antlered deer from 2019–2022 among paired townships. This finding was reinforced by my evaluation of the year-stratified N-mixture model, where I observed similar effects of harvest treatment, year, and the interaction of the

two on Legal-Antlered deer abundance among paired townships (Figure 2.9). It is worth noting that the increases in Legal-Antlered deer were considerably small at the site level (approximately 1 deer for APR and Non-APR areas; Figure 2.13). These small magnitudes of change were likely the reason why I was unable to detect annual changes in abundance at the township scale (Figure 2.5). The APR may have helped with advancing Sub-legal Antlered deer to the next age class, as I observed higher mean estimates of site-level changes in APR areas compared to Non-APR areas.

Despite the increased protection of Sub-legal Antlered deer in APR-treatment areas, my results indicated similar trends in relative abundance of Legal-Antlered deer between APR and Non-APR areas. These results were surprising, as I expected the additional antlered-harvest opportunities in the Non-APR Zone would limit the number of Sub-legal Antlered deer advancing to the Legal-Antlered class. Kellner et al. (2021) evaluated the effects of an APR on deer harvest in New York and observed a decline in the proportion of yearlings in the antlered harvest in Non-APR areas adjacent to APR-treatment areas. However, this phenomenon may have been explained in part by New York's outreach strategies to encourage hunters to voluntarily restrain from harvesting young antlered deer (New York State Department of Environmental Conservation 2011, 2023; Robinson et al. 2016). Michigan's state agency did not encourage hunters to harvest any specific age class of antlered deer. It is possible that there was some sort of linkage effect, where hunter behavior changed in the Non-APR Zone because of the study or implementation of APRs in adjacent counties. Alternatively, the similar increases in Legal-Antlered deer in APR and Non-APR treatment areas may indicate a generalized shift towards yearling male protection among Michigan deer hunters.

It is possible that voluntary (i.e., non-mandatory) APRs played an important role in the results of this study. Partial controllability of hunter harvest (also referred to as implementation uncertainty) can limit the influence of management decisions on realized harvest (Williams 1997, Moa et al. 2017, Dahlgren et al. 2021). My results showed similar trends in relative abundance of Legal-Antlered deer between APR and Non-APR areas, at both the township and site level (Figure 2.5, Figure 2.13). It is important to emphasize that the hypothesis that mandatory APRs increase adult male abundance was dependent on hunters not practicing voluntary APRs. Given it was not feasible to prevent hunters from practicing voluntary APRs before or during this study, it is possible that this accounts for similar trends in the Non-APR Zone. Similarly, it is possible that hunters in the APR Zone were already practicing APRs prior to them becoming mandatory. One of these scenarios on its own could affect the results of this study. Combined, voluntary APRs in these contexts could explain the similar population-level trends for Legal-Antlered deer in APR and Non-APR areas.

Over the past few decades, there has been a growing interest in APRs across the United States (Adams and Hamilton 2011), and the MDNR has received numerous requests to implement mandatory APRs (Frawley 2019). Concurrently, there has been an increasing percentage of Michigan hunters who indicate they voluntarily restrict themselves from harvesting young antlered deer (Frawley and Rudolph 2008, 2014). Further, this hunter behavior has been reflected in trends from MDNR deer check station data. These data have shown a steady decline in the proportion of yearling males harvested in the 5-County Area, declining by approximately 10% in the years leading up to this study (Appendix 2F). Prior to the APR regulation change in this study, opinion surveys indicated that 63% of hunters in the 5-County

Area supported the implementation of mandatory APRs (Frawley 2019). Later, in 2022, Michigan began a mandatory harvest reporting program and found that approximately two-thirds of all antlered deer harvested in the state of Michigan met the 4-point APR described in this study (Stewart 2023). Although this program occurred outside of our study period and included areas with and without mandatory APRs, it does suggest a statewide trend of hunter selection for larger-antlered deer and self-imposed restrictions on yearling male harvest (Appendix 2F).

Hunter selectivity for older deer with larger antler growth has implications for CWD spread and growth. With regards to hunter selectivity, increasing deer populations can translate to more, larger-antlered deer on the landscape, which may facilitate hunters being more selective for these deer (i.e., not harvesting females or younger males). This type of selective behavior may influence the size of the adult-male population on the landscape (Milner et al. 2007), as suggested by this study. From a CWD-management perspective, this is concerning, given that CWD prevalence generally increases with age and is estimated to be higher in adult males than females (Gear et al. 2006, Osnas et al. 2009, Heisey et al. 2010, Rees et al. 2012, Samuel and Storm 2016). Further, APRs (mandatory or voluntary) leave more yearling males on the landscape with larger movement patterns than adults (Nelson 1993, Long et al. 2005, Nixon et al. 2007, Skuldt et al. 2008), which can further contribute to disease spread. Several model-based studies have concluded that harvesting males, without distinguishing among age classes, or intensifying harvest of yearling males, is a viable strategy to mitigate CWD prevalence or lower the likelihood of CWD outbreaks (Potapov et al. 2016, Belsare and Stewart 2020). Further, Michigan-specific agent-based models (Belsare and Stewart 2020) informed and adapted with

empirical data from this study show harvest plays an important role in CWD dynamics, with higher outbreak severity in populations with higher compositions of adult males (Appendix 2G).

My results suggest that deer densities are likely increasing throughout the study area. I found clear support for my prediction that the abundance of Females, Sub-legal Antlered deer, and Fawns would not decline under APR or Non-APR harvest treatments. Survival rates of female deer are important to the extent that they influence population growth (Gaillard et al. 1998). Relative to 2019 baseline abundance estimates, I did not detect any significant declines in township-level relative abundance of Female deer in APR or Non-APR areas. However, I did detect a significant increase in a Non-APR township and observed a general increasing trend in mean abundance estimates over time (Figure 2.6). I did not detect significant changes in Female relative abundance from 2019–2022 at the site level, but most posterior estimates included values greater than zero, suggesting overall increasing trends (Figure 2.14). Model predictions further reinforce these claims, highlighting increasing trends in relative abundance for all sex-and-age classes in APR and Non-APR areas (Figure 2.9, Figure 2.10, Figure 2.11, Figure 2.12).

Harvest data from the MDNR indicated that both antlered and antlerless deer harvest were similar between APR and Non-APR counties in the 5-County Area during the study period (2019–2021 harvest seasons) and in the preceding year (2018 harvest season; Appendix F). While the evaluation of harvest data was not an objective of this study, it is important to consider harvest when interpreting the pre-harvest relative abundance estimates here. This is particularly relevant to the hypothesis that APRs reduce deer abundance, as it depends on augmented antlerless harvest. This effect did not materialize, as the trends in antlerless harvest were comparable between APR and Non-APR counties throughout the 2018–2021 deer harvest

seasons. Although not significant, the highest antlerless harvests were observed in 2020 for both APR and Non-APR counties.

While the scope of this study was limited to measuring deer ecology and abundance in relation to a harvest regulation, I recognize that the human dimensions and social landscape are important to consider. This is especially relevant given that my study sites were predominantly on private land (83%) and the southern Lower Peninsula of Michigan has the highest density of private-land, deer-hunting cooperatives in the state (Kramer et al. 2016). There are several important factors that affect whether hunters on private land support or disapprove of APRs (voluntary or mandatory). One may be the participation in a hunter cooperative, as there were at least 15 deer-hunting cooperatives within the study area (MUCC 2023). These cooperatives voluntarily collaborate to meet common harvest and population management goals, and provide opportunities for hunters to influence deer management across private lands (Mitterling et al. 2021). Close-knit families or social groups that do not belong to cooperatives, but own large or adjacent parcels, may have had a similar influence. For either group, support may be high among hunters pursuing adult males if the APR is intended to increase the abundance of adult male deer. In contrast, deer hunters interested in harvesting any sex-and-age class may feel a loss of opportunity under APR scenarios. In this study, hunters were not required to harvest antlerless deer in Michigan, and antlerless harvest was dependent on hunter willingness. As seen in other regions, hunter willingness to harvest antlerless deer is often limited (Brown et al. 2000, Riley et al. 2003, Giles and Findlay 2004, Van Deelen et al. 2010), and may be a limiting factor in Michigan (Stewart 2023).

It is unlikely that recreational harvest will have the capacity to control deer populations in Michigan. Although undetected in my data, there were statewide increases in hunter participation and antlerless harvest in the 2020 season. From 2019–2020, there was a 5% significant increase in hunters afield and a 26% significant increase in the number of antlerless deer harvested (Frawley 2020). These increases likely reflected the effect of COVID-19 restrictions allowing more individuals more time to hunt (Danks et al. 2022), and that hunters in the Lower Peninsula could harvest an antlerless deer with a combination license beginning in 2020 (Frawley 2020). Further, most counties in the study area accounted for some of the highest antlerless harvest densities in the state (Frawley 2020). Despite the increased mortality of antlerless deer, I failed to detect any significant declines in Female relative abundance in 2021. At the township level, most pre-harvest Female mean abundance estimates were actually higher in 2021 than 2020, including a significant increase in a Non-APR township (Figure 2.6). Together, these findings suggest that deer populations continued to grow despite higher hunter participation and antlerless harvest.

The increasing deer populations may, in part, be attributed to a decline in overall hunter participation or willingness to harvest antlerless deer (Brown et al. 2000, Riley et al. 2003, Giles and Findlay 2004). For example, the number of deer hunting license buyers in Michigan has declined 33% from 1995–2019 and has been projected to decline an additional 26% by 2030 (50% total decline from 1995; B. Frawley, MDNR, unpublished data). Today, approximately 50% of Michigan deer hunters harvest deer, most of which are antlered, and most hunters only harvest a single deer (Frawley 2020, 2021, 2022). To highlight the extent to which hunters favor antlered deer, MDNR data shows that 75% of Michigan hunters do not harvest an antlerless

deer (Stewart 2023). To stabilize or reduce current deer densities, more females would need to be harvested—and my results suggest that APR and Non-APR harvest regimes were not sufficient in achieving these goals. To achieve these goals, it may require the adoption of hunting regulations that incentivize hunters to harvest antlerless deer voluntarily or require them to do so (Brown et al. 2000).

It is possible that other uncontrollable factors influenced deer populations in this study, including natural and anthropogenically driven landscape changes. Resulting deer habitat alterations can impact populations at different spatial scales, depending on the size, shape, frequency, and intensity of the manipulation or disturbance (Hiller et al. 2009). For example, agricultural practices, including annual crop rotations, were a common occurrence at study sites. Evidence of timber harvest was also observed, although these occurrences were infrequent at sites and did not occur at annual intervals. Changes in deer habitat such as these are particularly relevant because deer distribution and abundance is influenced by the amount of forested cover and agricultural food available (VerCauteren and Hygnstorm 1994, Walter et al. 2009). Further, during non-breeding seasons (e.g., the summer survey period), sexual segregation occurs within deer populations (McCullough 1979), defined as the differential use of space or other resources by the sexes (Bowyer 2004). For example, in agro-forested ecosystems, adult males commonly associate with row crops and females with early successional upland forests (Nixon et al. 1991, 1994). Therefore, any deer habitat alterations during this study may have influenced the distribution and abundance of sex-and-age classes across the landscape.

This study highlights the challenge of evaluating regulation changes on free-ranging wildlife populations given inherent structural and observational uncertainty. I found that the APR regulation change in this study had little effect on deer populations and the magnitude of change was unimportant at the deer-management scale (e.g., county, multi-county). Similar studies seeking to improve the ability to identify temporal or spatial differences in abundance could pair the camera-trap study design with marked animals (e.g., ear-tagged or collared deer) to help correct for imperfect detection and address assumptions of closure and independence. A potential alternative approach to improving precision of parameter estimates is implementing a multi-species model to leverage shared information (Yamura et al. 2012, Gomez et al. 2017, Moral et al. 2018). Although promising, these frameworks may require more data and can be more complex and computationally intensive than single-species models. Further, the high level of effort in this study (see Chapter 1 single-season labor estimates) may not be sustainable for other camera-trap studies and additional efforts may challenge the feasibility of such studies altogether.

Here, I assessed potential population-level changes following the implementation of a mandatory APR and examined two prevalent APR hypotheses: (H_1) implementing APRs increases adult male abundance, and (H_2) implementing APRs decreases overall deer abundance. Taking a comprehensive view of my findings, I found little and no support for these two hypotheses, respectively. In areas where deer populations exceed management objectives, declining hunter participation, increased selectivity, and increasing deer populations will likely decrease the effectiveness of recreational harvest as a population-control mechanism under current regulatory systems (Brown et al. 2000, Riley et al. 2003, Giles and Findlay 2004).

Specifically, my results highlight potential limitations of APRs achieving desired effects for population reduction goals and the importance of developing harvest regulations specific to the targeted deer population, area, and management goals, and I recommend careful consideration of the partial controllability of harvest regulations.

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CONCLUSIONS AND MANAGEMENT IMPLICATIONS

By investigating camera-trap sampling strategies that attain precise and reliable estimates of white-tailed deer relative abundance using N-mixture models and applying population-estimation techniques appropriate for population-change assessment, I was able to address uncertainties on population impacts of antler point restrictions (APRs) for white-tailed deer by sex-and-age class. In this final section, I briefly review the findings and contributions from each chapter.

Chapter 1 sought to disentangle strengths and weaknesses of alternative camera-trap sampling strategies. This *post hoc* methodological assessment included a subset of camera-trap data and data-simulation approaches. My results demonstrate that N-mixture models can perform well for the precise relative abundance estimation of white-tailed deer in the south-central Lower Peninsula of Michigan, based on the modeling of camera-trap count data. However, N-mixture models should be paired with careful consideration of assumptions and sampling strategies as large uncertainty in parameter estimates can obscure signals of change in abundance over time. I found that the precision of abundance estimates was relatively insensitive to modifications in sampling frequency, but detection probability was highly sensitive to these manipulations. Shorter sampling durations and lower camera distributions can facilitate resource savings, but my results showed reductions compromised the precision of relative abundance estimates, with the latter being most sensitive to manipulation. My results also highlighted the importance of designing sampling efforts relevant to animal activity and its potential application in improving sampling efficiency. The findings from this chapter can be used to provide general recommendations to researchers and practitioners seeking to identify

sampling strategies that minimize financial and human resources to attain precise and reliable estimations of relative abundance when using N-mixture models with count data from camera-trap surveys.

Chapter 2 sought to assess potential population-level changes over time and space following a deer harvest regulation change in a before-after-control-impact design. More specifically, this chapter aimed to fill knowledge gaps regarding effects of antler point restrictions (APRs) on relative abundance by sex-and-age class. Using sampling recommendations from Chapter 1 and data associated with approximately 3 million camera-trap images, I used several analytical approaches to evaluate if antler point restrictions affect deer relative abundance by sex-and-age class. Looking at all my results holistically, I found weak evidence for APRs affecting the relative abundance by sex-and-age classes. My results suggest that the implementation of APRs had an insignificant impact on the relative abundance of Legal-Antlered deer. Although trends may have suggested increases in the abundance of Legal-Antlered deer, they do not represent significant statistical change in either the APR or Non-APR areas. There was a lack of evidence supporting change in Female and Fawn relative abundance in APR or Non-APR treatment areas. Harvest data from the Michigan Department of Natural Resources further substantiates these outcomes as antlerless deer harvest was similar between APR and Non-APR counties during the study period. Collectively, my results suggested that overall deer densities were increasing in the 5-County Area. My results from Chapter 2 highlight potential limitations of APRs achieving desired effects for population reduction goals and the importance of developing harvest regulations specific to the targeted deer population, area, and management goals. I recommend careful consideration of the partial controllability of

harvest regulations. For example, hunters in a Non-APR area may participate in voluntary APRs, and thus a desired outcome of a regulation change may not be realized. This issue is particularly relevant to emergence of wildlife health issues because selectivity of harvest over sex-and-age classes has implications for disease spread and growth. The finding from this chapter can be used to help managers and hunters alike set reasonable expectations for changes in deer abundance by sex-and-age class under antler point restrictions.

APPENDIX 1A: CAMERA-TRAPPING PROTOCOL

Protocol for Camera-Trap Set Up and Maintenance

*Supplemental research to:
Influence of deer harvest regulations on antlerless harvest, abundance, and sex and age composition: implications for managing deer in the face of chronic wasting disease*

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Site Selection and Camera Setup

1. You have an ordered list of 108 randomly selected locations for the cameras within each of the 8 townships. Use OnX app (with GRTS sites uploaded) for navigating and identifying landowners. Note that our electronic devices do not have cell service, so consider saving offline OnX maps, or installing OnX on your personal cell phone, or both. Work your way through the list in sequential order and attempt to gain permission from landowners to access 18 points per township (this process may have been started in previous seasons). Leave door hangers when you visit a residence, and nobody is home. Leave contact information on the back of door hangers (do not use personal contact information, use GoogleVoice accounts). If landowners grant permission after all sites are already secured, request to use their property as a back up option (you will likely need it). For new camera sites only, you will have latitude to set the camera within 50 m or 100 m of the randomly selected point (see details below), which may place the camera location on the land of a different landowner. A landowner grants permission for you to access their land by signing the “Landowner Agreement” document annually. For camera sites from previous seasons, given you have permission again, try to place cameras in the exact locations as previous seasons (refer to GPS-coordinate records).
2. Before you go into the field to set up cameras, make sure you have an iPad (or CAT device) with the Survey123 survey Deer Cameras downloaded (and updated). You must also have one hard copy of the “Camera Location Datasheet” for each camera.
3. Once you have permission to access the appropriate land, set up the camera. Remember that some landowners may want a phone call or text before you visit their property. Use your GoogleVoice account for this. Aim to start setting up cameras by mid-June. All cameras must be set up before July 14 (data collection starts on July 15). Ideally, cameras will be set up about 2 weeks before the official data collection period starts. This approach will allow time for an initial camera check and time to address any problematic cameras (e.g., poor field of view, vegetation setting off camera) prior to the start of the data collection period. If site ends up being a poor location altogether, consider any backup points or finding new locations. Place camera within 50 m of the randomly selected point to maintain a clear field of view, but prioritize staying as close to the random point as possible. Be cognizant of property lines, as points may fall near property boundaries. Make sure you are not trespassing. In exceptional circumstances you may select a location within 100 m. Exceptional circumstances include high risk of theft, open water, road right-of-ways, agricultural fields.
4. Record basic site information in Survey123.
 - a. Season Year
 - b. Study Area (APR or Non-APR)
 - c. Township
 - d. Point ID
 - i. 1st digit = 1 for Non-APR Zone; 2 for APR Zone

- ii. 2nd digit = 1-4 corresponding to the paired townships
 - iii. 3rd - 5th digit = 3 digit number based on GRTS sample selection order
- 5. Record specific location information on a “Camera Location Datasheet” (datasheet included at end of document). Note that location data (e.g., coordinates, landowner names) are private to Michigan State University. Save established camera site as a waypoint on the GPS.
- 6. Always check that camera settings, date, and time are correct. Record camera ID, card ID, and SD card set date in Survey 123. Camera settings:
 - a. Mode = Trail
 - b. Capture Delay = 5s
 - c. PicSize – LOW
 - d. MultiShot = RPF-3 SHOT
 - e. Smart IR = On
 - f. Night Exp = Fast Motion
 - g. Temp Units = F
 - h. Info Strip = On
 - i. SD Management = Off
 - i. *If this is accidentally turned on, and the SD card becomes full, the camera will start to delete photos to make room for the new ones. This must be set to “off”.*
- 7. Camera Placement Protocol:
 - a. Remember that some landowners may want a phone call or text before you visit their property. Use your GoogleVoice account for this.
 - b. Cameras will be placed in a northerly direction to minimize direct sunlight exposure to the camera trap. Sunlight can trigger cameras and UV exposure can reduce the sensitivity of the camera’s heat sensor. South-facing bearings between 91 and 269 should be avoided. Record camera direction, in degrees, in Survey123.
 - c. Find the closest straight tree that is not so thin that it will blow in the wind (or so thin that people can easily cut through the tree to remove the camera). Do not place cameras on snags or dead trees.
 - d. If no suitable trees are available, use a steel T-post to mount the camera.
 - e. Mount the camera to the tree (or T-post) using the fabric strap with the center of lens 14 – 16” above ground, but use personal judgement if terrain is uneven. For example, if your camera tree is located on a hill, you should adjust the height of the lens to maximize the detection window and so the horizon is approximately centered in the field of view. Small sticks can be lodged behind the camera to get desired angle, but make sure the sticks are secured tightly because animals can bump the camera and alter the angle (strap slack can be used to secure wedged sticks). Record camera height in inches from ground to center of lens in Survey123.

- f. Clear all vegetation and debris (e.g., branches, logs, large rocks) five meters in front of the camera. Keep in mind that debris, tree trunks, boulders, human-made objects, etc., can trigger cameras due to differences in temperature. Our cameras have an approximate 44-degree horizontal detection angle (22 degrees to the left and 22 degrees to the right). Using a compass, determine the area to be cleared and remove all ground and shrubby vegetation. Overhanging vegetation (e.g., branches) that greatly obstruct the field of view or may trigger the camera on a windy day should be removed from the target viewing area. Ground vegetation and debris (e.g., tall grass, shrubs, large rocks, man-made objects, etc.) should be cleared from the target viewing area to minimize false triggering and allow for an unobstructed field of view. The camera is set very low to the ground so clear all vegetation to a maximum height of 2–3 inches. Cameras are low so they can detect fawns (and mesocarnivores like bobcats). Also, consider how much the vegetation will grow between maintenance visits (e.g., ferns grow very fast). Try to remove branches immediately around and behind the camera to further limit vegetation issues. Any large shrubs or branches cleared should also be removed from the camera's field of view and away from the camera site.
- g. Turn on the camera and use the display screen to check your camera placement. In Survey123, hold the phone directly in front of the camera lens and take a picture of the camera field of view. Note that the camera's field of view is similar to that of a camera phone. Review photo and make sure:
 - i. No vegetation that will easily be moved by wind was in camera view.
 - ii. Horizon is close to the center of the image.
 - iii. Ensure the camera is level (i.e., not crooked) and take a test image to verify orientation and that the intended target area is viewed.
- h. In Survey 123, enter SD card number and the SD card set date and time.
- i. In Survey 123, enter the names of staff that set up the camera.
- j. Legibly record the site name, set date, and set time on the whiteboard. Using the viewing screen on the camera, center the whiteboard in the camera frame so that all information is visible and push "OK" to take a photo of the whiteboard. These photos will be saved on the SD card and provide additional reference.
- k. Check camera to see if photos were taken and recorded on the SD card.
 - i. If you are unable to record photos on the card, switch out the card with one of the extras provided and try again. Sometimes SD cards fail, or their tiny lock gets flipped on.
 - ii. Do not delete whiteboard photos as they will be used to double check that photos are assigned to the correct site.
- l. Check that camera is set to "ON" and close camera. If you are with a partner, both of you are responsible for making sure the camera is on. You can do this by using a double-verbal confirmation (e.g., one of you says "camera is on" and the other person responds with "camera is on").

- m. Wrap cable around tree and secure it to camera with lock. Tuck away camera strap and lock cable.
 - n. Take a photo of the camera in Survey123. Stand 10 ft in front of the camera and take a picture of the camera set-up. Center the camera in the image.
8. Complete the “Land-cover” fields in Survey123.
- a. Near Cover – Select the majority cover in a 1-m radius from the camera (“Open” or “Closed”)
 - b. Landscape Cover – Select the majority cover in a 100-m radius from the camera. (“Open” or “Closed”)
 - c. Landscape Land-cover Type – Select the majority land cover in a 100-m radius from the camera.
 - d. Open Water – Stand next to the camera and look around. Is there open water within sight? (“Yes” or “No”)
 - e. Deer Sign – Meander around within a few meters of the camera. Is there deer sign (scat, tracks, bedding, etc.) within sight? (“Yes” or “No”)
 - f. Wildlife Trail – Stand next to the camera. Is the camera on or within sight of a wildlife trail? (“Yes” or “No”)
9. If there is additional information you would like to capture about the site, use the “Comments” section in Survey123 if it does not relate to the specific location or landowner. Note that location data (e.g., coordinates, landowner names) are private to Michigan State University.
10. If a site is difficult to navigate to, or if it might be difficult for a teammate to navigate to, consider putting some flagging up. However, do not draw too much attention to the actual camera site.

CWD APR Deer Study
CAMERA LOCATION DATASHEET

Point ID: _____

Record the 5-digit unique ID assigned to point.

Staff Name 1:

Staff Name 2:

Landowner Name:

Landowner Agreement Signed:

YES NO

Landowner Phone:

Landowner Email: _____

Date Location Recorded: _____

Latitude: _____

Longitude: _____

Hold the GPS receiver directly over the camera. Record the location in decimal degrees to as many decimal places as possible.

Street Address: _____

Record street address of property, if available.

Directions:

Describe how to access the camera location.

Notes:

CHECKLIST ON BACK

Field Setup Checklist:

- ☐ Marked in GPS
- ☐ SD card checked for recording
- ☐ Camera batteries >80%
- ☐ Camera date checked
- ☐ Camera settings checked
- ☐ Field of view clear of vegetation
- ☐ Photo of whiteboard with Point ID and date taken and saved to the trail camera's SD card
- ☐ Survey123 form completed

Survey123 And Camera Checking

1. Getting started with Survey123
 - a. Connect a CAT phone (or iPad) to a WIFI network. Go to the Play Store and install the “Survey123 for ArcGIS” app (if Survey123 is already installed, update if necessary).
 - b. Open the “Survey123” app. In the “My Surveys” screen, tap the menu icon and sign in using your assigned ArcGIS username and password.
 - i. If the Deer Cameras survey (created by S. Mayhew) is already installed, tap the Updates Available header. Then tap Deer Cameras to download the updated version.
 - ii. If the Deer Cameras survey is not already installed, tap your initials in the upper right corner and select Download Surveys. Find the survey called Deer Cameras and tap to download.
 - c. Tap the left-pointing arrow in the upper left corner to return to “My Surveys” screen.
2. Collecting data with Survey123 during camera setup
 - a. Note, your CAT phone (or iPad) should be offline at the time of data collection.
 - b. When at each camera location, tap “Collect” in Survey 123.
 - c. Complete the entire Survey 123 form (as described in the Site Selection and Camera Setup protocol). Note that you should only enter 1 SD card per camera at the time of set up.
 - d. When the survey form is completed, tap the check mark at the bottom of the screen. Your survey will be saved in the outbox.
3. Submitting Survey123 data
 - a. Whenever possible, preferably at the end of each field day, connect the CAT phone to a WIFI network.
 - b. On the “Deer Cameras” screen in Survey123, open the Outbox and tap the “Send” button at the bottom of the screen. If you do not see the “Send” button, you may need to force close the Survey123 app and restart.
4. Survey123 data collection and SD-card replacement
 - a. Before heading out into the field for camera maintenance (i.e., camera checks), open the Survey123 app on your CAT phone. Open the “Deer Cameras” survey.
 - b. Tap “Inbox.” At the bottom of the “Deer Cameras Inbox” screen, tap the “Refresh” button so you can see all of the available camera locations.
 - c. Once you are at a camera location, tap on the appropriate camera location in the “Deer Cameras Inbox” screen.
 - d. Do not change any of the setup data. Scroll down to the “SD Cards” section. Tap the + button to add another SD card.
 - e. Enter the new SD card ID and the date and time of SD card change.

- f. Tap the check mark at the bottom of the survey screen. Your survey will be saved in the outbox.
 - g. Make sure to follow the “Submitting Data” instructions when possible.
5. Camera maintenance during camera checks
- a. Remember that some landowners may want a phone call or text before you visit their property. Use your GoogleVoice account for this.
 - b. Verify camera is still set up appropriately.
 - i. Confirm field of view and fix any issues or deviations from setup protocol.
 - ii. If cameras record a high volume of images, flip through photos using the camera, and try to diagnose and address problems if they exist (e.g., a branch triggering the camera).
 - c. Change SD cards during every camera check.
 - i. To remove the SD card, push it in so it clicks and unlocks, then remove (to replace it, push it in and make sure it clicks and locks).
 - ii. Sometimes the new SD card (the one brought into the field to replace the SD card in the camera) will still have photos on it. To check, press the D-pad arrows to scroll through any old photos. To delete, press “M” and scroll up or down to the “Delete All” function.
 - iii. To prevent mixing up new and old SD cards, always make sure the camera is off and the old SD card has been removed and put away before inserting a new card and deleting photos. SD card wallets help with this process.
 - iv. SD cards can accidentally become locked if a tiny tab is switched on the actual SD card.
 - d. Take photo of whiteboard with site ID, date and time during every camera check.
 - i. Write legibly.
 - ii. Make sure SD card is recording photos.
 - e. Clear vegetation at every camera check.
 - i. Clear all vegetation to a maximum height of 2 – 3 inches.
 - f. Complete Survey123 form during every camera check (SD card portion).
 - g. Double check camera settings every camera check.
 - h. Replace batteries if <80% battery life.
 - If you change batteries, you may have to reset all the settings (including time and date).
 - i. Make sure the battery pack is locked into place properly because it may back out over time and eventually fail to take pictures.

APPENDIX 1B: PHOTO-REVIEW PROTOCOL

Protocol for Identifying Wildlife in Camera-Trap Photos

*Supplemental research to:
Influence of deer harvest regulations on antlerless harvest, abundance, and sex and age
composition: implications for managing deer in the face of chronic wasting disease*

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Please review this document before beginning to review (i.e., tag) photos, even if you have tagged photos for this project in the past. To improve your understanding and accuracy of photo IDing, you will be provided with comprehensive, species-specific training prior to reviewing photos. We use CPW Photo Warehouse for storing, managing, and reviewing photos (more info here: <https://cpw.state.co.us/learn/Pages/ResearchMammalsSoftware.aspx>).

Getting Started

A designated data-manager (e.g., data-management technician, MDNR staff) will provide you with a flash drive. The main folder on the flash drive will contain subfolders labeled with things like “21003_Check2.” Within this folder will be another folder titled “Photos” and a database file called “PhotoID.accdr.” This database file is a standalone file that is not truly connected to our main photo database (i.e., if something happens to this file while you have access to it will not harm the main database). Each of these folders and databases contains the info for a single camera during a single two-week period. Depending on the site, the folder could contain 5 to over 5000 photos—and our big goal is to identify the deer in each of these photos. Also worth noting, the database you will be working with is a Microsoft Access application and uses an auto-save feature (so you don’t have to worry about hitting a save button before you close the application).

When you open the PhotoID.accdr file you will be asked to select your name. If your name does not appear in the list, just type it in and the database will add your info (we just need your name and initials in the dialog box that pops up). Sometimes it is much quicker to flip through the photos outside of the database (where they will be larger and you can zoom in), and sometimes you will want to look at a series of photos before deciding on an ID.

To assign a species to a photo, select the appropriate species in the drop-down box at the bottom left. You can assign multiple species to the same photo by adding additional rows in the subform. For this project, we have divided deer into multiple “species” – Doe, Fawn, Legal Buck, Sub-legal Buck, and Unknown Deer, then those species are broken down even farther based on the number of antler points on bucks and details (e.g., cannot see head) on Unknown deer. The only other species we are interested in are bear, bobcat, fox, and coyote (fox and coyote new to 2022). Once you have created a row in the subform for each species present in an image, use the “Next” button to move on. Do not just skip photos with nothing or non-focus species in them – specify “None” as the ID otherwise you will not be able to differentiate between photos that have not been looked at yet and those that have been reviewed but do not contain any focal species. We are only identifying deer, bear, bobcat, fox, and coyote. Please do not add other species to the table (e.g., if a photo contains a raccoon, it is still tagged as “None”). Also, do not worry about the number of individuals in a photo tagged as “None” —leave it as the default 1 individual for photos tagged as “None”. For example, if a photo contains 5 raccoons it would be tagged as “None” with the default 1 number of individuals, which basically means we have a single record for an image labeled “None”.

If you spot an interesting photo, a photo that would be good for presentations, a photo of a feral hog, or a photo of an animal that appears ill, please use the “Highlight” checkbox on the right side – tick this box to flag photos to be reviewed by project PIs. If you identify an animal that looks ill, or if you identify a feral hog in any images, share that information with the project PIs immediately. You can also add comments to these photos in the comments column for future reference.

Using Keyboard Shortcuts

Using the mouse to identify species can be unwieldy and time-consuming, so there are keyboard shortcuts available when using the PhotoID form. To see a list of keyboard shortcuts available, click the link below the “Next” and “Previous” buttons. These shortcuts will only work when the “focus” is on the main form, not within the subform where species are listed. This can be tricky to figure out, but if the keyboard shortcuts are not working, try clicking the “Next” button, and then click the “Previous” to return to the record you were on – this ensures that the main form has the focus. In addition to the shortcuts specific to a species or detail, you can use the “Z” key to repeat all of the data recorded from the previous photo.

You can also use the up, down, left, and right arrows to move between records, and pressing the space bar will move to a new line in the subform so you can add an additional ID. Getting this system down can take some practice, but once you learn how to use it you will be able to work through hundreds of photos in no time. There are a couple of situations to note when using the shortcut keys – first, detail shortcuts will only work if the appropriate species has already been assigned. Otherwise, the species shortcut will take precedence if it exists. For example, if “f” is the shortcut for fawn, “b” is the shortcut for bear (both in the Species table), and “b” is also assigned for the detail “Buttonbuck” associated with the species fawn (in the Detection Details table). Pressing “f” then “b” will set the species to Fawn and the detail to “Buttonbuck,” but pressing “b” first will set the species to Bear.

How To ID Photos

Almost all deer should be assigned a species and detail tag. Keyboard shortcuts for all possible combinations are below. See Figure 1B.1 for data-input and keystroke example. See Figure 1B.2 for a photo with data-input example.

Species shortcut table:

Shortcut	Species
B	Bear
C	Bobcat
Y	Coyote
V	Fox
P	Camera Problem
D	Doe
F	Fawn
L	Legal Buck (at least 4 points on one side)
S	Sub-legal buck (does not have 4 points on a side)
U	Unknown Deer
X	Camera Setup/Takedown
r	Remove (photos of humans)

Detection Details List:

Shortcut	Species	Detail
b	Fawn	Buttonbuck
f	Fawn	Female
q	Legal Buck	Four Point
f	Legal Buck	Five Point
s	Legal Buck	Six Point
v	Legal Buck	Seven Point
e	Legal Buck	Eight Point
n	Legal Buck	Nine Point
t	Legal Buck	≥ Ten Point
t	Sub-Legal Buck	Three Point
q	Sub-Legal Buck	Four Point
f	Sub-Legal Buck	Five Point
s	Sub-Legal Buck	Six Point
p	Sub-Legal Buck	Spike
a	Unknown Deer	Antlered
l	Unknown Deer	Antlerless
u	Unknown Deer	Cannot see head

Species	Detail	Individuals	Comments
Doe		1	
Fawn		2	
Sub-legal Buck	Five	1	
		1	

Figure 1B.1. Data input example for an image that includes a doe, two fawns, and a buck with three points on one side and two points on the other. This example has three rows of data. If you were using keyboard shortcuts you would have typed out: “d”, “space bar”, “f”, “2”, “space bar”, “s”, “f” → these keystrokes would indicate “Doe”, next row, “Fawn”, “2 individuals”, next row, “Sublegal buck”, “Five Points”, next photo.



Species	Detail	Individuals
Doe		1
Fawn		2

Figure 1B.2. Photo example and data-input example that includes one doe and two fawns. Note that there are only two rows of data.

Note that the spacebar will allow you to jump to the next row for data entry without having to point and click. Also, there is an option to add comments in the table where you input species. However, you should only add comments when deemed absolutely necessary because adding comments can really slow down the photo-review process for you.

Legal Bucks must have 4 or more points on at least one antler beam. Sub-legal Bucks must have less than 4 points on both antler beams. First determine if the buck is Legal or Sub-legal then move on to the detail category. Count every single point that looks like it would be an inch or greater by November—this can be tricky when antlers are still covered in velvet so use your best judgement. We are recording total points in the detail category, not just the points from one side. Sometimes it is not possible to see every single point. If you can see that a deer has at least four points on one main antler beam but cannot see the other main antler beam, ID the deer as “Legal Buck” with no point description (i.e., provide no detail). If you can only see one main antler beam and there are three or fewer points on that side, ID the deer as “Unknown Deer” with an “Antlered” detail since you cannot be sure the other antler beam does not have four or more points. Sometimes it is obvious that a deer is not a legal buck, but you cannot count all points, in this case it would be okay to ID the deer as “sublegal buck” with no detail, but only use this if you are extremely confident there’s no way the other side has four points. A similar approach can be applied for legal bucks.

Every deer tagged as “Unknown Deer” must also be assigned a detail (antlered, antlerless, cannot see head). It can be very difficult to differentiate between sexes of fawns, so it is okay if you do not assign a detail to fawn photos. However, later in the season many male fawns will start to have antler growth and small buttons will become visible on their heads—so keep an eye out for that and assign the “Buttonbuck” detail to these fawn images.

If a deer walks completely out of the frame, you should no longer tag it. If, however, one deer walks in front of another deer, but you know both deer are still present you should ID both deer. If a deer walks out of the frame and then a deer walks back in the frame, be conservative and do not assume it was the same deer unless you identify similar characteristics (e.g., number of antler points).

Eyeshine without deer confirmation is not enough to ID a deer, photos that contain eyeshine that does not later reveal itself to be a deer should be labeled as “None”. If you see eyeshine in the distance, and a deer slowly reveals itself, then it would be appropriate to tag the early eyeshine photos as that deer. Don’t be afraid to go back and change your IDs if more information presents itself. For example, you did not notice a fawn in some tall grass until it pops out later, but then you go back in the image series and can see movement behind the grass. In this situation, those earlier photos should likely be tagged as fawn. It is a common occurrence to have to go back and change IDs, so make sure to address these issues as they arise because if you do not, they will likely be flagged in the database and result in additional work for the photo judge (i.e., the 3rd observer or referee that resolves discrepancies between IDs).

If you find a photo of a human who is not one of our technicians (i.e., the photo is not a camera maintenance photo at the very beginning or end of the series), please ID it as “Remove” so we

can delete them from our master photo storage. We do not want to keep any photos of humans—we are required by the university to remove all photos of humans (tag as “Remove” and so we can delete in bulk later). If a photo is a white-out due to flash overexposure, and you cannot be sure what is in the photo frame, label the photo as “camera problem.” If there is a white-out photo but you can identify deer, then do not label the photo as “camera problem”, instead provide deer IDs. A similar approach should be applied for our other species of interest defined above.

The “Batch ID” button is a wonderful resource, especially when you are looking at a thousand photos of a bedded deer (or photos of a fawn dawdling in front of the camera also happens often). Flip through the photos outside of the database to find the last photo in the series. Starting with the first photo in the series, click “Batch ID” and navigate to the final photo of the series. Notice you can only add one ID per “Batch ID,” so if you have a doe and a fawn in 100 photos you will have to add them separately using the Batch ID function (i.e., do 2 separate batch ID functions, one for the doe and one for the fawn).

Sometimes you will have a group of deer hang out in front of a camera for a long series of photos and it can be difficult to know what deer are in each photo. In these instances, it can be helpful to copy the photos into a PowerPoint and label each deer; then track one deer through the series of photographs to better tell A) what the deer is (i.e., sometimes you only get one clear shot of antlers out of a series of 100 photographs) and B) to tell when each deer leaves the frame. Once you have tracked each deer throughout the photo series and have triple checked that each deer has been marked, go back to the database and enter all of the information for each photograph.

Adding Boxes to Photos

In some cases, even after photos have been identified it can be difficult to spot the animal in question or figure out exactly what’s going on. These cases can be frustrating when the IDs are reconciled, since the referee needs to repeat the effort of trying to find the animal all over again to determine which ID is correct. To alleviate these issues, you can add “boxes” to photos to highlight specific regions, thereby helping the referee spot the important content. A box is just an orange box that draws attention to a specific part of a photo. They are stored in the database and not added to the image files themselves, so they will not appear if you open the image file externally. They only appear within the database in the PhotoID form, and they are only visible to the observer who created them or when comparing IDs. To add boxes in the PhotoID form, single-click or click and drag on the region you want to highlight. You can add up to 5 boxes per photo. To delete an existing box, click within it. Also, there is an option to add comments in the table where you input species. However, you should only add comments when deemed absolutely necessary because adding comments can really slow down the photo-review process for you.

Exploring Alternative Mixing Distributions, Sampling Frequencies, and Covariates: An N-Mixture Modeling Approach with Empirical Data

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Supplemental research to Michigan's antler-point-restriction study in the south-central Lower Peninsula, October 2023.

SUMMARY

Exploratory data analyses with an N-mixture model show that a Poisson mixing distribution best fit data from an unmarked camera-trap survey of white-tailed deer (*Odocoileus virginianus*; hereafter, deer). Results varied by sampling frequency and further evaluation is recommended to determine its effect on accuracy and bias of the abundance estimator. Of the covariates explored, Far Cover (landscape cover open or closed within 100 m of camera) and Percent Agriculture were identified as important to detection and ecological processes, respectively. When modeling the abundance of deer in the south-central Lower Peninsula of Michigan, it is recommended to carefully consider these findings as they may help produce an appropriate and meaningful model.

INTRODUCTION

White-tailed deer are an important game species, and reliable abundance estimation is essential for the evaluation of management actions. This need is especially relevant in areas where population-management actions are aimed to mediate the spread of chronic wasting disease (CWD) in free-ranging deer. Camera trapping has become an increasingly common method for monitoring deer populations, but poorly designed analytical methods may compromise abundance estimation and lead to flawed management decisions. Using a camera-trap study design, we plan to evaluate the effect of an antler point regulation (APR) change in an area with CWD on a deer population over three consecutive years. Here, we use a subset of data from that study to conduct an exploratory data analysis with an N-mixture model (Royal 2004). The purpose of the exploratory data analysis was threefold and included explorations of mixing distributions, sampling frequencies, and potential covariates.

STUDY GOAL

Use an N-mixture model with empirical data to estimate parameters, explore characteristics of data, and provide recommendations for appropriate and meaningful abundance modeling.

OBJECTIVES

1. Identify a mixing distribution that best fits the underlying data.
2. Explore the use of alternative daily sampling frequencies.
3. Evaluate potential covariates to include in the ecological- and observational-process models.

STUDY AREA

My exploratory data analysis included a subset of camera-trap data from a 5-county area (Newaygo, Kent, Mecosta, Montcalm, and Ionia County) in the south-central Lower Peninsula of Michigan that included a known chronic-wasting-disease hotspot (Kent and Montcalm County; Figure 1C.1). The study area had an experimental and control area (APR Zone and Non-APR Zone, respectively) with townships paired (A–D) between zones.

METHODS

General modeling approach

During the summer of 2019 (15 July to 15 September), randomly placed, unbaited camera traps collected 797,407 photos, including 275,794 photos of deer. We leveraged this high volume of camera images of a highly visible and relatively abundant species (MDNR 2016) to conduct an exploratory data analysis. To account for imperfect detection in the camera survey of unmarked deer, we used a hierarchical modeling approach. Specifically, we used a Bayesian framework to estimate parameters with an N-mixture model (Royal 2004). We used software program JAGS (Plummer et al. 2003) in program R (version 4.1.2; R Core Team 2021) and used the R package *jagsUI* (version 1.5.2; Kellner 2021) to streamline analyses.

We first started modeling abundance with a Poisson model that produced abundance estimates one township at a time (Appendix 1C.1). After some experimentation, it was clear that this approach was inefficient and made poor use of the data. We decided to revise the model so that it would share information across townships and produce estimates for all townships in a single model run (Appendix 1C.2). We used this general modeling framework for all analyses. For Markov chain Monte Carlo (MCMC) settings, we ran 3 parallel chains for 100,000 iterations, discarded the first 5,000 iterations as a burn-in period, and thinned the remaining iterations by 1 in 5, resulting in 57,000 draws of the posterior distribution for inference. We assumed vague prior distributions for all analyses to express the absence of prior information about model parameters. We monitored model convergence via visual inspection of MCMC trace plots and using the Gelman-Rubin convergence diagnostic (R_{hat} or $\hat{R}$; Gelman 2006). To further assess model performance, we evaluated precision of abundance estimates (coefficient of variation [CV]) and effective sampling size. If a model exhibited evidence of autocorrelation (e.g., relatively short effective samples), we increased all MCMC settings (Kéry and Royle 2015) by a multiple of 4, resulting in a comparable 57,000 draws of the posterior distribution. We summarized posterior distributions of abundance and detection probability using means and 95% Bayesian credible intervals (95% BCIs).

We used a multi-step approach to evaluate the ecological realism of abundance estimates (Joesph et al. 2009). First, we calculated a 1.24-km² (0.48 mi²) effective sampling area per camera site based on average home range size (Suwanrat et al. 2015, Wilton 2021) using data from GPS-collared deer in the area ($n = 22$ rural female deer; Trudeau et al., unpublished

data). We summed site-level abundances to derive estimated abundance by township, where abundance related to the number of deer within the total area of all effective sampling areas in a specified township (18 sites per township = 22 km² [9 mi²]). We used mean abundance estimates to calculate deer density within the total area of effective sampling areas per township. Lastly, we compared deer density estimates to historical density estimates for the areas of interest (Michigan Department of Natural Resources; Appendix 1C.3).

Alternative mixing distributions and sampling frequencies

We tested four variants of the simplistic N-mixture model, including Poisson (Appendix 1C.2), zero-inflated Poisson (Appendix 1C.4), negative binomial (Appendix 1C.5), and Poisson lognormal (Appendix 1C.6) to estimate both total abundance and township abundance. Note that these were simplistic models without explanatory variables on model parameters (i.e., no covariates on the ecological or observational process). The Poisson distribution is one of the most common distributions used when analyzing count data, when the probability of a given number of independent events occur in a fixed interval of time and space. Royal (2004) used the Poisson mixing distribution for the development of the N-mixture model, thus was our *a priori* selection when building our base models (Appendix 1C.1, Appendix 1C.2).

In the 2019 dataset, we noticed many zero-counts and at least one camera failing to detect deer altogether (i.e., all zero counts). These observations motivated us to test a zero-inflated Poisson mixing distribution. Zeros are common in count data and often cannot be accompanied properly by a Poisson or negative binomial model, as these count distributions generally under-predict zeros. Excessive zeros can cause overdispersion and ignoring these zeros can lead to biased estimated parameters and standard errors.

Overdispersed data (i.e., variance > mean) are also common for individuals that form groups. White-tailed deer are a gregarious species that can form small groups (DeYoung and Miller 2011), thus overdispersion was a potential concern with the data. In such situations, the negative binomial distribution can be advantageous over the Poisson because it has a parameter (θ) that accounts for overdispersion. The Poisson-lognormal mixing distribution is also used to account for overdispersion in count data. Specifically, the lognormal component of the Poisson-lognormal distribution describes the overdispersion in the Poisson rate parameter due to clustering of some factors and describes how the average of these factors varies across the population. This approach is a common alternative to a negative binomial because the Poisson-lognormal can be more straightforward while producing similar inferences. For these reasons, we tested both the negative binomial and Poisson-lognormal mixing distributions.

Given that sampling frequency was undetermined (i.e., how often to count deer), we tested each of the mixing distributions (i.e., model variants) with alternative daily sampling frequencies. Early data explorations suggested that sampling frequency affected parameter estimation and that sampling efforts needed to be relative to animal activity. To better understand deer activity, we plotted the density of deer photos by time of day (Figure 1C.2) and sex-age-class counts by time of day (Figure 1C.3). We rescaled standard time to local solar time and decided to systematically sample within 1, 2, 3, and 4 even time intervals throughout the day and at crepuscular hours. For example, a daily frequency of 2 generated 2 samples (counts) per day, one for the first half of the day and another for the second half of the day. Crepuscular sampling occurred within 2-hr time intervals, at a frequency of twice per day, 1 hour before and

after sunrise and sunset. The crepuscular-style sampling was intended to minimize the possibility of double counting individuals with repeated visits while still capturing peak activity (Figure 1C.2, Figure 1C.3). Counts were restricted to the maximum number of individuals observed in a single image within a selected time interval (Haus et al. 2019, Zou et al. 2019).

Covariates on detection probability and abundance

We evaluated the effect of covariates on detection probability using the Poisson N-mixture model with a crepuscular sampling strategy. This analysis was conducted independent of our other efforts here. The Poisson mixing distribution and crepuscular sampling frequency were an *a priori* selection. It is important to note that detection probability (p) consists of three components: 1) the probability of presence during survey, 2) the probability of availability given presence, and 3) the probability of detection given availability and presence. To select potential detection covariates for inclusion in the model, we used data collected during camera-trap setup and during sampling occasions. Most potential covariates were selected and defined prior to camera setup (Table 1C.1). After reviewing images, we decided to evaluate Camera Field of View (relative size: low, medium, large) because it was believed to potentially limit ability to identify individuals and limit the maximum number of individuals that can be captured in a single image (Table 1C.1, Figure 1C.4). Other data explorations suggested temporal variation of detectability (Figure 1C.5), so we also explored the importance of time on the detection process. Specifically, we explored the effect of time on detection probability using sampling occasion (j) as an index of time (Appendix 1C.7). It is important to note that modeling the time covariate occurred later in the exploratory data analysis phase and included Far Cover as a predictor in the observational-process model.

Aside from the time covariate, each covariate was modeled independent of one another. Covariates were determined to be important to the detection process if categories differed from one another (i.e., at least one category had BCIs that did not overlap the others) and 95% BCIs did not include a value of zero. We tested correlations among landscape metrics to identify any potential correlations. Using the `psych` package (Revelle 2023) in program R (version 4.1.2; R Core Team 2021), we used a tetrachoric correlation coefficient to measure the correlation (0–1) between two binary variables in a 2-by-2 contingency table, Near Cover and Far Cover (Table 1C.2). Using the package `rcompanion` (Mangiafico 2023) in program R, we used Cramer's V correlation to examine the association (0–1) between two nominal variables with a contingency table larger than a 2-by-2, Far Cover and Cover Type (Table 1C.3). Note that due to small sample sizes, Cover Type was collapsed from eight categories to four: 1) Crops, 2) Open Vegetation (Mowed Grass, Shrub), 3) Upland Forest, and 4) Wetland (Forested Wetland, Open Wetland). The Other Cover Type had a sample size of zero thus was excluded.

We tested covariates on abundance using an alternative Poisson model that included township random effects on abundance and the Far Cover covariate on detection probability (Appendix 1C.8). This analysis was conducted independent of our other efforts here and included a much coarser sampling frequency (week). The study area's two dominant land-cover classes, forest and agriculture, were hypothesized to be important predictors of deer abundance (e.g., forest for cover and agriculture for food). We used a multi-step process to evaluate Percent Forest cover and Percent Agriculture cover as potential covariates on abundance. First, we calculated the proportion of cover (forest or agriculture) for each camera

site using effective sampling areas (1.24-km² circular buffers around camera sites [0.48 mi²]) and the National Land Cover Database land-cover classification layer (30-m² resolution; Dewitz and USGS 2021) in ArcPro (ESRI 2020). This approach allowed us to collapse 3 land-cover types into a single ‘agriculture’ classification (herbaceous, hay/pasture, cultivated crops), collapse 4 cover types into a single ‘forest’ classification (deciduous forest, evergreen forest, mixed forest, woody wetland), and extract associated values. We incorporated these site-specific covariates independently into the ecological model, associated with abundance through a log-link function, and described by a nonlinear relationship with specified cover (forest or agriculture). Therefore, percent agriculture and percent forest were each modeled as quadratic because the two were considered to be in direct competition with another. We plotted relationships using parameters estimated by the models and compared results.

RESULTS

We compared the relative performance of 4 simplistic variants of an N-mixture model (Poisson, zero-inflated Poisson, negative binomial, Poisson lognormal) with 5 alternative sampling frequencies (1, 2, 3, and 4 times per day and at crepuscular times [2 per day]) to identify a suitable mixing distribution. Results varied by sampling frequency for all model variants (Table 1C.4). Most model variants demonstrated successful convergence ($\hat{R}$ values below 1.1; Gelman and Rubin 1992; Table 1C.4). However, the zero-inflated Poisson model failed to converge in every sampling-frequency scenario and the Poisson lognormal failed with crepuscular sampling (Table 1C.4). We observed the lowest $\hat{R}$ values with the Poisson model ($\hat{R} = 1$ for all parameters). The original negative-binomial model failed to successfully run as it produced infinite abundance estimates, but a zero-truncated version of the model successfully ran after increasing MCMC settings. The best mixing was observed with the Poisson model and the worst with Poisson lognormal (see Figure 1C.6 for examples of mixing). We estimated abundance with the highest precision using the Poisson model (CV range = 2.75–3.14%) and with the least using the Poisson lognormal (CV range = 11.22–17.51%; Table 1C.4). The most precise abundance estimates were produced with the Poisson model and a 4-per-day sampling frequency. The Poisson produced the most ecologically realistic abundance and density estimates (total abundance range = 1,195–1,927; township abundance range = 69–349; township density range = 8–39 deer per mi²) and the negative binomial variants produced the most unrealistic (total abundance range = 8,666–13,071; township abundance range = 407–2,467; township density range = 45–274 deer per mi²; Table 1C.4, Table 1C.5, Table 1C.6).

We explored potential covariates on detection probability and determined if landscape metrics were correlated. Results indicated that mean detection probability was similar (i.e., 95% BCIs overlapped) for categories within Open Water (water: $\bar{x} = 0.027$, 95% BCIs = 0.024–0.031; no water: $\bar{x} = 0.033$, 95% BCIs = 0.031–0.035), Wildlife Trails (trail: $\bar{x} = 0.034$, 95% BCIs = 0.031–0.038; no trail: $\bar{x} = 0.030$, 95% BCIs = 0.028–0.033), and Camera Field of View (small: $\bar{x} = 0.029$, 95% BCIs = 0.024–0.034; medium: $\bar{x} = 0.023$, 95% BCIs = 0.020–0.026; large: $\bar{x} = 0.029$, 95% BCIs = 0.023–0.036; Table 1C.7). Far Cover was correlated with Near Cover (0.8; Table 1C.2) and highly correlated with Cover Type (0.96; Table 1C.3). Models failed to run properly (e.g., failed to converge, poor mixing, very low precision, high autocorrelation, extreme parameter estimates) when including time as a covariate on detection probability, thus no results are presented here. We explored potential covariates on abundance and found Percent Forest and Percent

Agriculture produced similar parameter estimates (Table 1C.8). Further, expected abundance was estimated high when Percent Agriculture values were just above average and high when Percent Forest values were just below average (Figure 1C.7).

DISCUSSION

The Poisson mixing distribution was identified as the best performing of the four N-mixture model variants tested. The Poisson model produced the most precise abundance estimates (CV range = 2.75–3.14%; Table 1C.4). The Poisson was also the only converging model to produce ecologically realistic estimates of population size (Table 1C.2, Table 1C.3, Table 1C.4). These ecologically realistic estimates were likely a result of the Poisson's higher detection probabilities (p range = 0.02–0.08) compared to the other model variants ($p \leq 0.02$). At convergence, $\hat{R}$ equals 1 (Gelman and Rubin 1992), but values below 1.1 are usually taken as indicating convergence. However, $\hat{R}$ values closer to 1 (e.g., < 1.01) can be better for producing posterior summaries with lower Monte Carlo error (Kéry and Royle 2015). The Poisson was the only model to produce perfect convergence for all parameters monitored ($\hat{R} = 1$). Further, MCMC trace plots showed that the Poisson model had exceptional mixing (Figure 1C.6).

The results from the zero-inflated Poisson variant were not reliable because the model failed to converge. Specifically, the model failed to converge on the zero-inflation parameter (z), indicating that the chains failed to agree on camera sites (i) with abundance estimates of zero (driven by a Bernoulli process for zero and non-zero values). The negative binomial model produced very low mean detection probabilities ($p \leq 0.02$), which was likely the driver of ecologically unrealistic estimates (e.g., township densities 45–274 deer per mi^2). Ficetola et al. (2018) did not consider evaluating a negative binomial error distribution in their N-mixture model because of its potential to produce infinite abundance estimates, especially when detection probability is limited (Joseph et al. 2009). We considered the negative binomial mixing distribution and ran into this issue, causing our negative-binomial model to fail during most simulations. The slice sampler (used by JAGS) does not work properly when the probability density of the sampled variable is infinite at a point. Specifically, distributions with a Gamma shape parameter (a component of λ) can cause trouble when the shape parameter is less than 1 (i.e., close to zero) and the probability mass gets concentrated into a single point. The cause of the error can be from sampling extremely small values for the shape parameter of a dataset with a particularly large variance and small mean. In these situations, the density function is not bounded but goes to infinity at the boundary of support (0 for the Gamma distribution). We successfully worked around this issue by truncating the Gamma distribution away from its problematic endpoint using the JAGS truncation construct on the stochastic relation. However, the zero-truncated negative binomial variant showed evidence of high autocorrelation in the chains (i.e., it produced low effective sample size values in the hundreds). We increased MCMC settings by a multiple of 4 and successfully reduced autocorrelation (i.e., produced effective sample size values in the thousands). Despite these efforts, this model was the most computationally expensive of the variants and was deemed computationally prohibitive for our future modeling efforts.

Of the model variants that converged, all models but the Poisson-lognormal successfully converged under all sampling frequencies. The Poisson-lognormal failed to converge with a crepuscular sampling frequency (Table 1C.4). After plotting deer activity, we considered

crepuscular sampling important because deer activity and counts were high during these times (Figure 1C.2, Figure 1C.3). We found it concerning that the Poisson-lognormal model failed to converge with data from this important time interval. A visual inspection of trace plots suggested marginal mixing with the Poisson-lognormal model variant. Further, the Poisson-lognormal produced abundance estimates with the lowest precision (CV range = 11.22–17.51%; Table 1C.4). In comparison, the precision was over four times worse than that of the Poisson variant (CV range = 2.75–3.14%; Table 1C.4). Like our results from the negative binomial model, we observed low effective sample sizes with the Poisson-lognormal model variant, which suggested high levels of autocorrelation (Table 1C.4). We considered increasing the MCMC settings to reduce autocorrelation like we did with the negative binomial but decided it too would be computationally prohibitive to our future modeling efforts.

Our results indicated that Open Water, Wildlife Trails, and Camera Field of View were not important to the detection process, thus are not recommended for future modeling efforts of the system. Many important covariates were correlated with one another, including Near Cover and Far Cover (0.8; Table 1C.2). We recommend using Far Cover over Near Cover because Far Cover was considered a more limiting factor on the landscape and a 100-m scale (Far Cover) was likely more important to the detection process than a 1-m scale (Near Cover). There was an even stronger correlation between Far Cover and Cover Type (0.96; Table 1C.3). Further, we found similar detection probabilities between Crops and Open Vegetation Cover Types (Crops: $\bar{x}$ = 0.039, 95% BCIs = 0.036–0.043; Open vegetation: $\bar{x}$ = 0.034, 95% BCIs = 0.030–0.038) and similar detection probabilities between Upland Forest and Wetland Cover Types (Upland Forest: $\bar{x}$ = 0.025, 95% BCIs = 0.022–0.028; Wetland: $\bar{x}$ = 0.024, 95% BCIs = 0.020–0.028). These similarities highlighted a noticeable break point in detection probability between the Crops-Open Vegetation group (95% BCI ranges = 0.030–0.043) and the Upland-Wetland group (95% BCI ranges = 0.020–0.028; Table 1C.7). Notably, the range of estimates for these groups closely reflected that of Far Cover estimates (Open: 95% BCIs = 0.034–0.040; Closed: 95% BCIs = 0.023–0.028; Table 1C.7). Given these results, and the value of simplicity in modeling, we recommend selecting for the more parsimonious Far Cover covariate over Cover Type.

We attempted to model time as a covariate on detection probability, but models failed to run properly (e.g., failed to converge, poor mixing, very low precision, high autocorrelation, extreme parameter estimates). We used sampling occasion (j) as an index for time and as a covariate on detection probability (Appendix 1C.8). After our first failed modeling attempt, we found that sites with all zero counts (i.e., no deer detected) were associated with poor mixing and extreme parameter estimates. We suspected that these zeros were causing problems, so we revised the structure of the model to include a Bernoulli variable (z) on the j parameter in the logit function (Appendix 1C.9). This new revision treated the Bernoulli variable like an on-off switch and allowed the time covariate to be modeled or not depending on patterns (i.e., zero counts at sites). Despite our efforts, however, we found that the model still failed to converge. These results suggested that including j as a covariate overparameterized the model. We suspected that data limitations prevented the model from estimating two parameters for each site, so we tried modeling with other sampling frequencies to increase the amount of data informing the model. The model still failed to converge with the additional data. My final attempt introduced an additional hierarchical level to the model, incorporating weeks (k) into the structure (Appendix 1C.10). However, the model still performed poorly. After many failed

attempts, we abandoned time as a covariate and considered it as unimportant to the detection process.

We explored the effects of Percent Forest and Percent Agriculture as covariates on deer abundance and found similar results (Table 1C.8). It is worth noting that we also explored a week sampling frequency during these analyses and found that the model produced detection probabilities higher than the alternative daily sampling frequencies (e.g., values in the tenths compared to hundredths). Expected site abundance peaked just below average Percent Forest cover and just above average Percent Agriculture cover (Figure 1C.8), which suggested a potential correlation. Further investigation showed the two were highly correlated with one another (0.96; Table 1C.3). This result was not surprising given the agro-forested landscape of the study area. Given the high correlation, we did not consider modeling Percent Forest and Percent Agriculture simultaneously or modeling an interaction between the two. Most parameter estimates were comparable between the two classes, but the Percent Agriculture covariate estimated abundance with slightly more precision (agriculture: CV = 4.6%; forest: CV = 4.7%). Further, past studies in the Midwest have considered agriculture to be an important driver of demographic variation in deer abundance (Nixon et al. 1991, Nixon et al. 1994, Nixon et al. 2001). For these reasons, we recommend using the Percent Agriculture covariate over Percent Forest.

Collectively, our results suggest that the Poisson mixing distribution best fits the underlying count data. All other model variants tested failed to perform well (e.g., lack of convergence, unrealistic abundance estimates). Results varied by sampling frequency, with the Poisson model and a 4-per-day sampling frequency producing the highest precision (CV = 2.75%). However, we found that this sampling frequency also produced the lowest detection probability with the Poisson model ($p = 0.02$), thus coarser sampling frequencies may be a viable option for increasing detection probability. Although explored here, we recommend further evaluation of alternative sampling frequencies to determine levels of accuracy and bias associated with each of the alternatives. Most covariates tested were found to be unimportant to the detection process. However, we recommend the inclusion of Far Cover as a covariate on detection probability. We also recommend including Percent Agriculture as a covariate on abundance. When using an N-mixture model to estimate the abundance of deer in the south-central Lower Peninsula of Michigan, we recommend careful consideration of these findings as they may help produce an appropriate and meaningful model.

TABLES

Table 1C.1. Table listing potential covariates on detection probability of white-tailed deer (*Odocoileus virginianus*), how they were defined, and logic as why they were considered for inclusion in the observational-process model of an N-mixture model.

Potential covariate	Definition	Why consider?
Near cover	The majority cover in a 1-m radius from the camera ("Open" or "Closed")	Deer need cover, cover requirements may vary by sex-age class, and vegetation can limit detection
Far cover	The majority cover in a 100-m radius from the camera ("Open" or "Closed")	Deer need cover, cover requirements may vary by sex-age class, and vegetation can limit detection
Cover type	The majority land cover in a 100-m radius from the camera (Crops, Forested Wetland, Grassland, Mowed Grass, Open Wetland, Other, Shrub, Upland Forest)	Deer use a variety of habitat types, certain sex-age classes may favor certain habitat types, and different vegetation can affect detection differently
Open water	Was there open water within sight of the camera ("Yes" or "No")	Deer frequent water sources
Wildlife trail	Stand next to the camera. Is the camera on or within sight of a wildlife trail? ("Yes" or "No")	Deer may favor the path of least resistance
Camera field of view	The relative field of view for a camera (Small, Medium, Large)	Can limit ability to identify an individual deer, limits the maximum number of deer that can be captured in a single image

Table 1C.2. The 2-by-2 contingency table used to measure the tetrachoric correlation coefficient between two binary variables, Near Cover and Far Cover (open or closed). Near cover was defined as the majority cover in a 1-m radius from the camera. Far cover was defined as the majority cover in a 100-m radius from the camera. Both landscape metrics were considered for inclusion in an N-mixture model as covariates on detection probability.

	Open far cover	Closed far cover
Open near cover	35	3
Closed near cover	37	70

Table 1C.3. The 2-by-4 contingency table used to measure Cramer's V correlation between two categorical variables, Far Cover and Cover Type. Far cover was binary and defined as the majority cover in a 100-m radius from the camera (open or closed). Cover type was defined as the majority of land cover in a 100-m radius from the camera. Both landscape metrics were considered for inclusion in an N-mixture model as covariates on detection probability.

	Crop cover type	Open vegetation cover type	Upland forest cover type	Wetland cover type
Open far cover	43	25	0	4
Closed far cover	0	0	58	15

Table 1C.4. Estimates from an N-mixture model with different combinations of daily sampling frequencies and mixing distributions. Estimates include convergence results ($\hat{R} < 1.1$ = convergence), degree of mixing observed in Markov chain Monte Carlo (MCMC) trace plots, effective sampling size for abundance (N n.eff), total abundance (N), standard deviation of abundance (N SD), and the coefficient of variation for abundance (N CV%). All sampling frequencies with the zero-inflated Poisson and the crepuscular sampling frequency with the Poisson-lognormal failed to converge, thus these estimates were not reliable. NA values indicate that the model failed to run.

Mixing distribution	Sampling frequency	Did it converge?	Degree of mixing	N n.eff	N	N SD	N CV (%)
Poisson	1	Yes	Good	11,129	1,759	53	3.02
	2	Yes	Good	57,000	1,845	52	2.81
	3	Yes	Good	8,785	1,908	53	2.78
	4	Yes	Good	28,663	1,927	53	2.75
	Crepuscular	Yes	Good	23,196	1,195	37	3.14
Zero-inflated Poisson	1	No	Good	9,015	1,870	60	3.23
	2	No	Good	57,000	1,949	58	2.99
	3	No	Good	24,914	2,019	60	2.96
	4	No	Good	4,451	2,036	59	2.91
	Crepuscular	No	Good	25,747	1,355	49	3.61
Negative binomial	1	Yes	Marginal	1,001	9,818	956	9.74
	2	Yes	Marginal	1,610	11,684	1,059	9.06
	3	NA	NA	NA	NA	NA	NA
	4	NA	NA	NA	NA	NA	NA
	Crepuscular	NA	NA	NA	NA	NA	NA
Negative binomial, zero-truncated	1	Yes	Marginal	997	9,901	969	9.79
	2	Yes	Marginal	674	11,772	1,084	9.21
	3	Yes	Marginal	8,178	12,483	1,092	8.75
	4	Yes	Marginal	870	13,071	1,119	8.56
	Crepuscular	Yes	Marginal	2528	8,666	917	10.59

Table 1C.4. (cont'd)

Negative	1	Yes	Marginal	25391	9,904	967	9.76
binomial,	2	Yes	Marginal	2,974	11,715	1,065	9.09
zero-	3	Yes	Marginal	5,223	12,539	1,127	8.99
truncated,	4	Yes	Marginal	12,670	13,029	1,127	8.65
high MCMC	Crepuscular	Yes	Marginal	3,418	8,693	931	10.71
Poisson-	1	Yes	Marginal	1,051	4,473	502	11.22
lognormal	2	Yes	Marginal	778	6,480	790	12.18
	3	Yes	Marginal	832	8,162	1,188	14.55
	4	Yes	Marginal	123	9,066	1,287	14.20
	Crepuscular	No	Marginal	349	4,667	817	17.51

Table 1C.5. Mean abundance estimates by township (e.g., APR-Zone A) by alternative combinations of daily sampling frequencies and mixing distributions. All sampling frequencies with the zero-inflated Poisson and the crepuscular sampling frequency with the Poisson-lognormal failed to converge, thus these estimates were not reliable. NA values indicate that the model failed to run. Note that estimates of error are not included because mean values were used as the key metric for evaluating ecological realism of estimates.

Mixing distribution	Sampling frequency	Non-APR Zone A	Non-APR Zone B	Non-APR Zone C	Non-APR Zone D	APR Zone A	APR Zone B	APR Zone C	APR Zone C
Poisson	1	175	119	230	166	224	260	318	268
	2	182	119	237	170	233	277	334	294
	3	184	122	244	175	244	289	345	305
	4	187	121	248	177	244	288	349	313
	Crepuscular	122	69	147	117	148	173	217	202
Zero-inflated Poisson	1	186	127	244	176	239	276	337	284
	2	192	126	251	180	246	292	352	309
	3	195	130	259	185	259	306	364	322
	4	198	128	262	188	258	304	368	330
	Crepuscular	139	79	166	133	168	196	246	226
Negative binomial	1	915	593	1,266	846	1,244	1,477	1,867	1,609
	2	1,080	666	1,477	981	1,460	1,784	2,213	2,022
	3	NA	NA	NA	NA	NA	NA	NA	NA
	4	NA	NA	NA	NA	NA	NA	NA	NA
	Crepuscular	NA	NA	NA	NA	NA	NA	NA	NA
Negative binomial, zero-truncated	1	922	598	1,277	854	1,254	1,489	1,883	1,623
	2	1,088	672	1,488	988	1,471	1,797	2,229	2,038
	3	1,120	710	1,570	1,039	1,589	1,931	2,355	2,169
	4	1,192	718	1,655	1,100	1,635	1,982	2,467	2,323
	Crepuscular	828	407	1,004	761	1,031	1,295	1,666	1,673

Table 1C.5. (cont'd)

Negative	1	923	599	1,277	854	1,255	1,490	1,884	1,623
binomial,	2	1,083	668	1,481	984	1,464	1,789	2,219	2,027
zero-	3	1,125	714	1,577	1,043	1,596	1,940	2,365	2,179
truncated,	4	1,188	716	1,649	1,096	1,630	1,975	2,459	2,315
high MCMC	Crepuscular	831	409	1,007	763	1,035	1,299	1,671	1,679
	1	487	413	659	488	541	542	697	646
	2	674	526	916	671	793	811	1,096	993
Poisson-	3	854	582	1,133	834	983	1,003	1,406	1,366
lognormal	4	867	639	1,288	882	1,089	1,189	1,554	1,558
	Crepuscular	450	239	595	466	538	558	876	943

Table 1C.6. Density estimates by township (e.g., APR-Zone A) by alternative combinations of daily sampling frequencies and mixing distributions. All sampling frequencies with the zero-inflated Poisson and the crepuscular sampling frequency with the Poisson-lognormal failed to converge, thus these estimates were not reliable. NA values indicate that the model failed to run. Note that estimates of error are not included because mean values were used as the key metric for evaluating ecological realism of estimates. Of the models that converged, only the Poisson variant produced ecologically realistic density estimates.

Mixing distribution	Sampling frequency	Non-APR Zone A	Non-APR Zone B	Non-APR Zone C	Non-APR Zone D	APR Zone A	APR Zone B	APR Zone C	APR Zone C
Poisson	1	19	13	26	18	25	29	35	30
	2	20	13	26	19	26	31	37	33
	3	20	14	27	19	27	32	38	34
	4	21	13	28	20	27	32	39	35
	Crepuscular	14	8	16	13	16	19	24	22
Zero-inflated Poisson	1	21	14	27	20	27	31	37	32
	2	21	9	28	20	27	32	39	34
	3	22	14	29	21	29	34	40	36
	4	22	14	29	21	29	34	41	37
	Crepuscular	15	9	18	15	19	22	27	25
Negative binomial	1	102	66	141	94	138	164	207	179
	2	120	74	164	109	162	198	246	225
	3	NA	NA	NA	NA	NA	NA	NA	NA
	4	NA	NA	NA	NA	NA	NA	NA	NA
	Crepuscular	NA	NA	NA	NA	NA	NA	NA	NA
Negative binomial, zero-truncated)	1	102	66	142	95	139	165	209	180
	2	121	75	165	110	163	200	248	226
	3	124	79	174	115	177	215	262	241
	4	132	80	184	122	182	220	274	258
	Crepuscular	92	45	112	85	115	144	185	186

Table 1C.6. (cont'd)

Negative	1	103	67	142	95	139	166	209	180
binomial,	2	120	74	165	109	163	199	247	225
zero-	3	125	79	175	116	177	216	263	242
truncated,	4	132	80	183	122	181	219	273	257
high MCMC	Crepuscular	92	45	112	85	115	144	186	187
Poisson-	1	54	46	73	54	60	60	77	72
lognormal	2	75	58	102	75	88	90	122	110
	3	95	65	126	93	109	111	156	152
	4	96	71	143	98	121	132	173	173
	Crepuscular	50	27	66	52	60	62	97	105

Table 1C.7. Mean estimates for the effect of potential covariates on detection probability. The 2.5% and 97.5% represent the lower and upper limits of 95% Bayesian credible intervals, respectively.

Potential covariate	Category	Mean	2.5%	97.5%
Far cover	Open	0.037	0.034	0.040
	Closed	0.025	0.023	0.028
Cover type	Crops	0.039	0.036	0.043
	Open vegetation	0.034	0.030	0.038
	Upland forest	0.025	0.022	0.028
	Wetland	0.024	0.020	0.028
Open water	Open water nearby	0.027	0.024	0.031
	No open water nearby	0.033	0.031	0.035
Wildlife trail	Trail nearby	0.034	0.031	0.038
	No trail nearby	0.030	0.028	0.033
Camera field of view	Small	0.029	0.024	0.034
	Medium	0.023	0.020	0.026
	Large	0.029	0.023	0.036

Table 1C.8. Parameter estimates for the effect of potential covariates on abundance, including detection probability in areas with open (p_1) and closed far cover (p_2), and total abundance (N). The 2.5% and 97.5% represent the lower and upper limits of 95% Bayesian credible intervals, respectively. Estimates were comparable between covariates.

Potential covariate	Parameter	Mean	SD	2.5%	97.5%
Percent forest	p_1	0.323	0.018	0.289	0.358
	p_2	0.313	0.019	0.277	0.351
	N	1,206	56.3	1,102	1,324
Percent agriculture	p_1	0.328	0.018	0.294	0.364
	p_2	0.310	0.019	0.274	0.348
	N	1,200	55.2	1,100	1,317

FIGURES

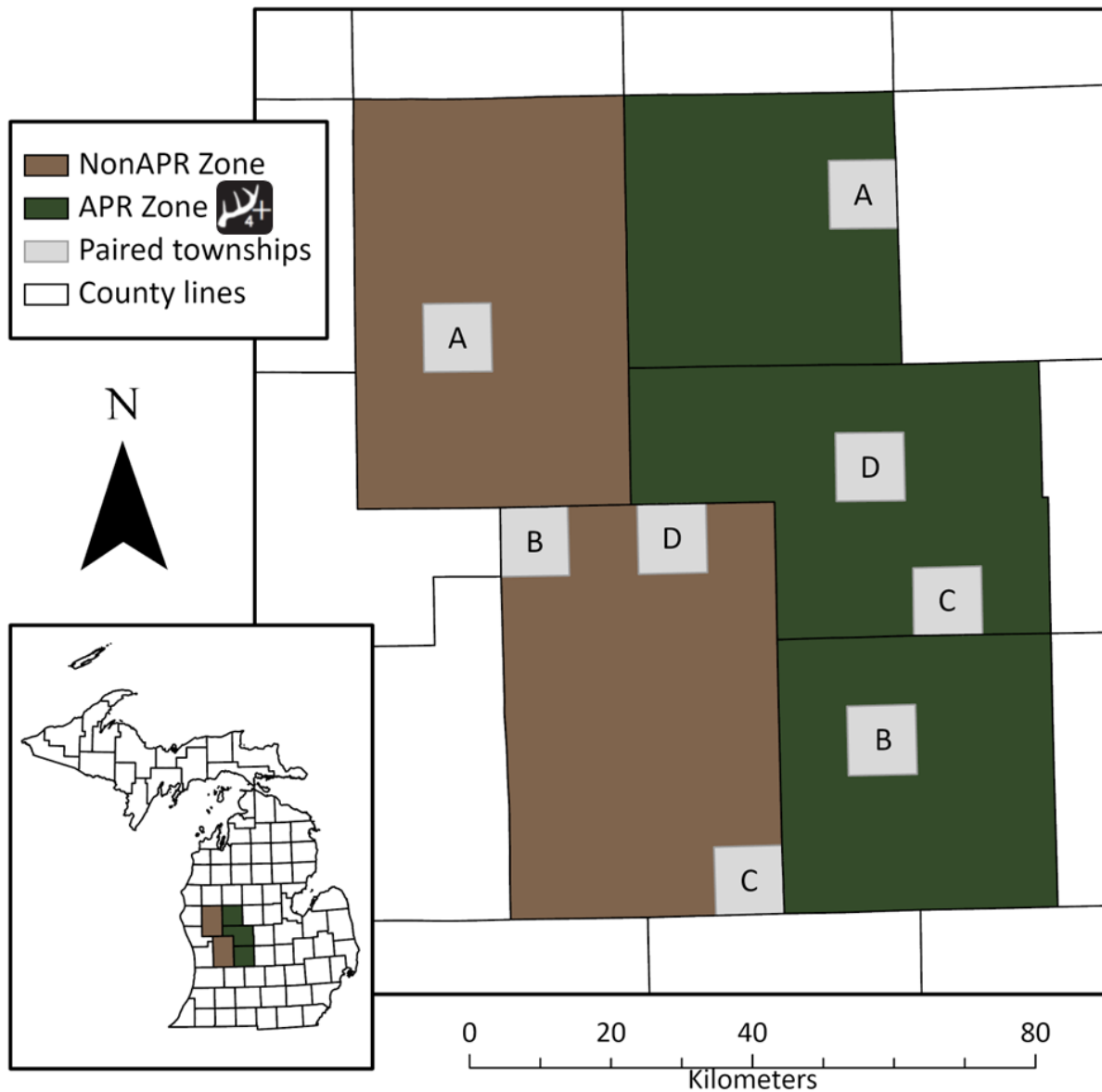


Figure 1C.1. Study area in the south-central Lower Peninsula of Michigan, USA, in a designated 5-county area. Mandatory antler point restrictions (APRs) were implemented in 2019 in the experimental area (APR Zone) and not in the control area (Non-APR Zone). Townships were paired (A–D) between zones, and remote cameras were placed in each township to monitor white-tailed deer (*Odocoileus virginianus*) populations over a duration of four years (2019 – 2022). Maps created in ArcGIS Pro (version 2.7.1; www.esri.com).

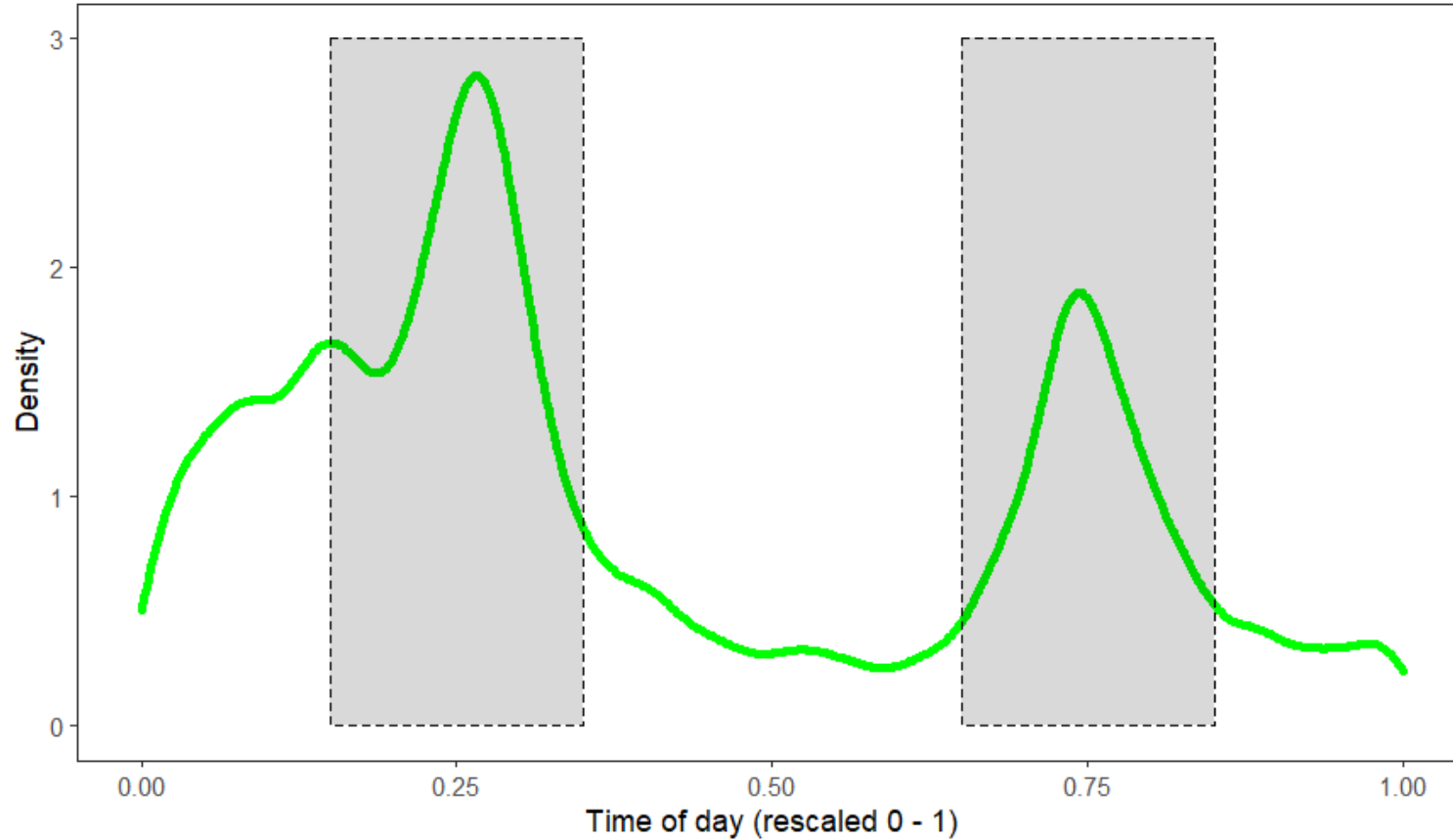


Figure 1C.2. Density of white-tailed deer (*Odocoileus virginianus*) photos by time of day (rescaled 0–1). Using density of photos as an index, peak activity was observed during crepuscular hours. Grey-shaded boxes represent defined crepuscular sampling windows (2 separate 2-hour windows around sunrise and sunset). Photos were collected during a 2019 camera-trap survey in the south-central Lower Peninsula, Michigan, USA.

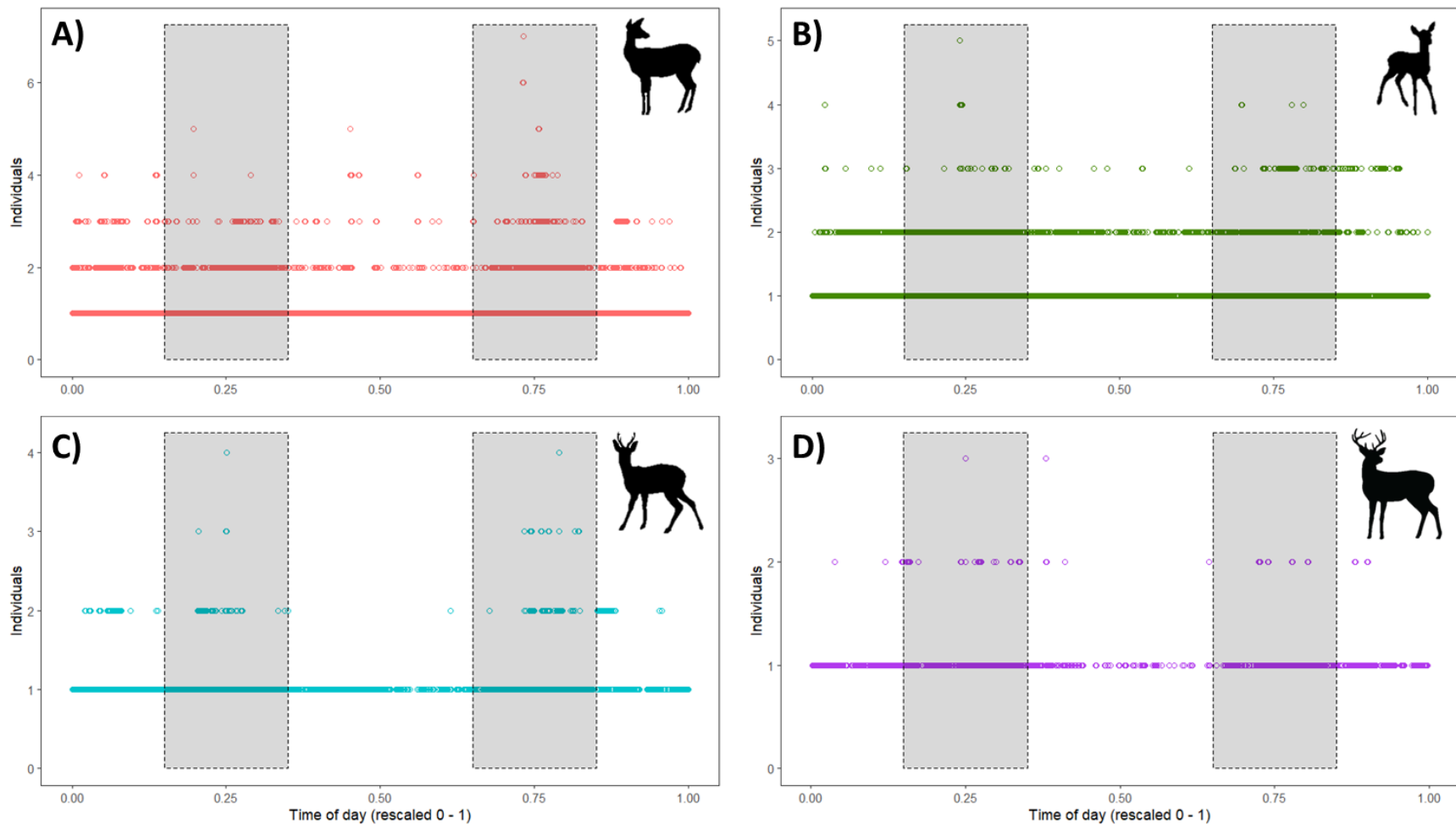


Figure 1C.3. Maximum number of individual white-tailed deer (*Odocoileus virginianus*) detected by time of day (rescaled 0–1) and sex-age class, including A) doe, B) fawn, C) sub-legal male, and D) legal male. Legal males had ≥ 4 antler points on at least one antler and sub-legal males did not. Does included yearling and adult females. Peak deer activity was observed during crepuscular hours for all sex-age classes. Grey-shaded boxes represent defined crepuscular sampling windows (2 separate 2-hour windows around sunrise and sunset). Photos were collected during a 2019 camera-trap survey in the south-central Lower Peninsula, Michigan, USA.

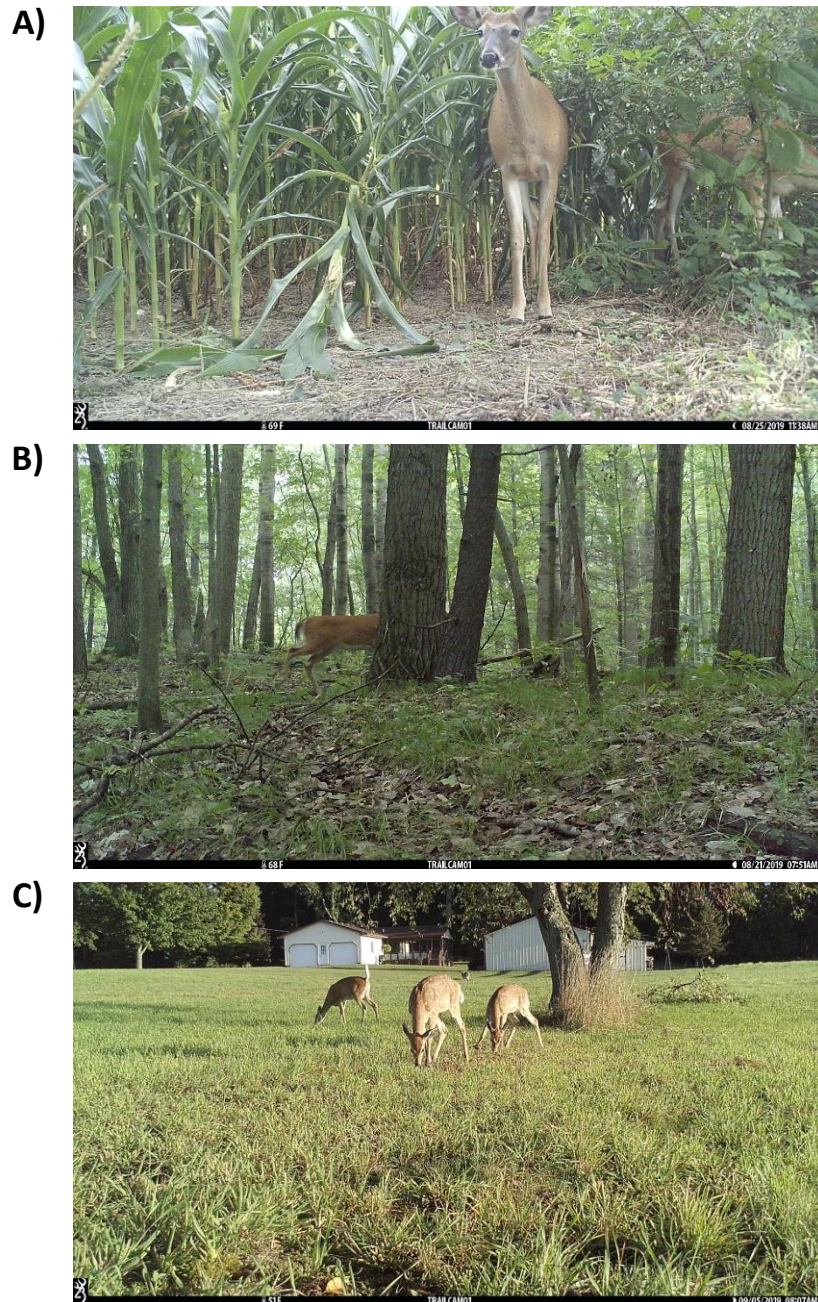


Figure 1C.4. Examples of different classifications of camera-trap field of view. Field of view was classified based on the relative frame size, including A) small, B), medium, or C) large. Field of view was considered as a covariate on detection probability because of its potential to affect ability to identify individuals and could limit the maximum number of individuals captured in a single image.

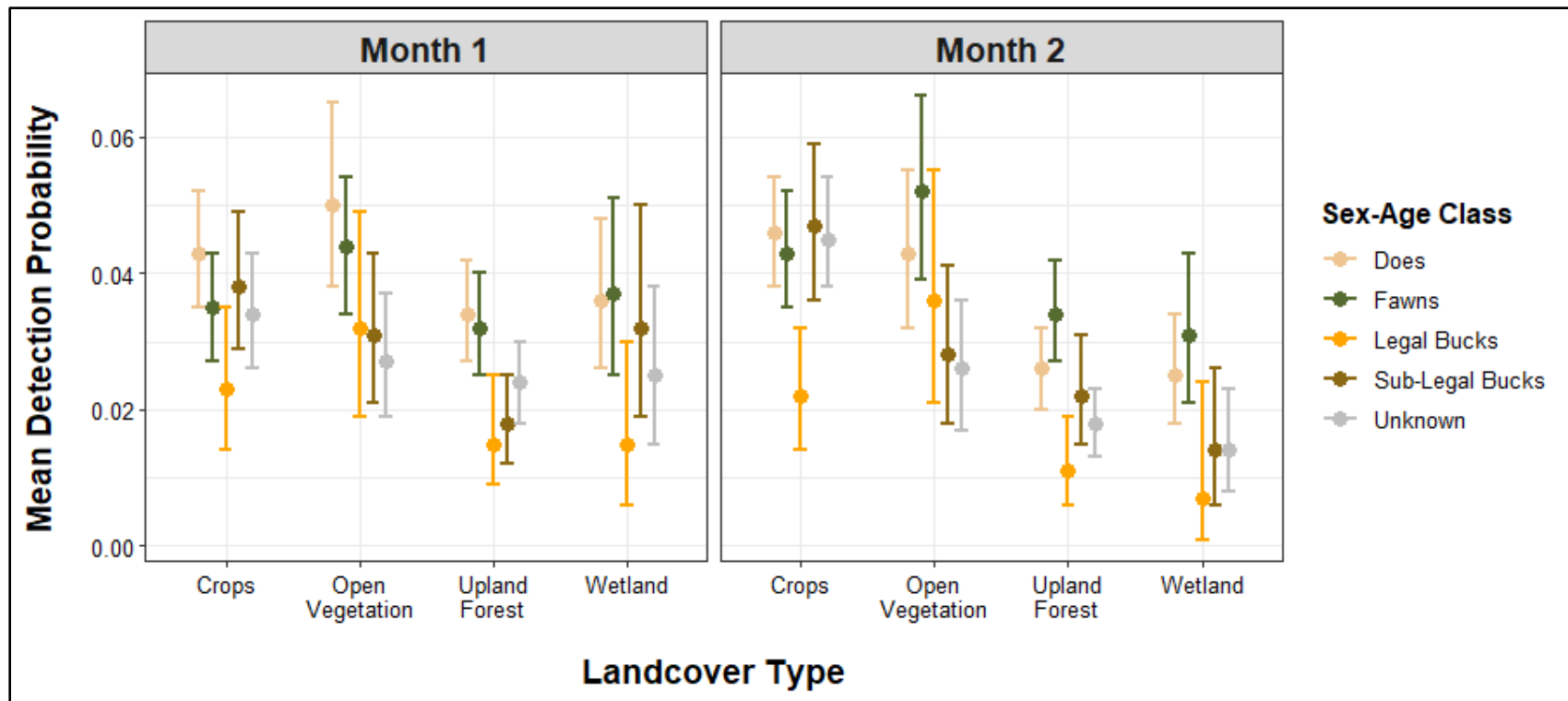


Figure 1C.5. Results from early data explorations with an N-mixture model highlighting monthly variation of detectability among sex-age classes of white-tailed deer (*Odocoileus virginianus*) by land-cover type. Month 1 survey was July 15th–August 14th and Month 2 survey was August 15th–September 14th. Error bars indicate 95% credible intervals. Detection probability of Legal Bucks differed from Does in Month 1 Upland Forest, from both Does and Fawns in Month 2 Upland Forest, and differed from all sex-age classes in Month 2 Crops.

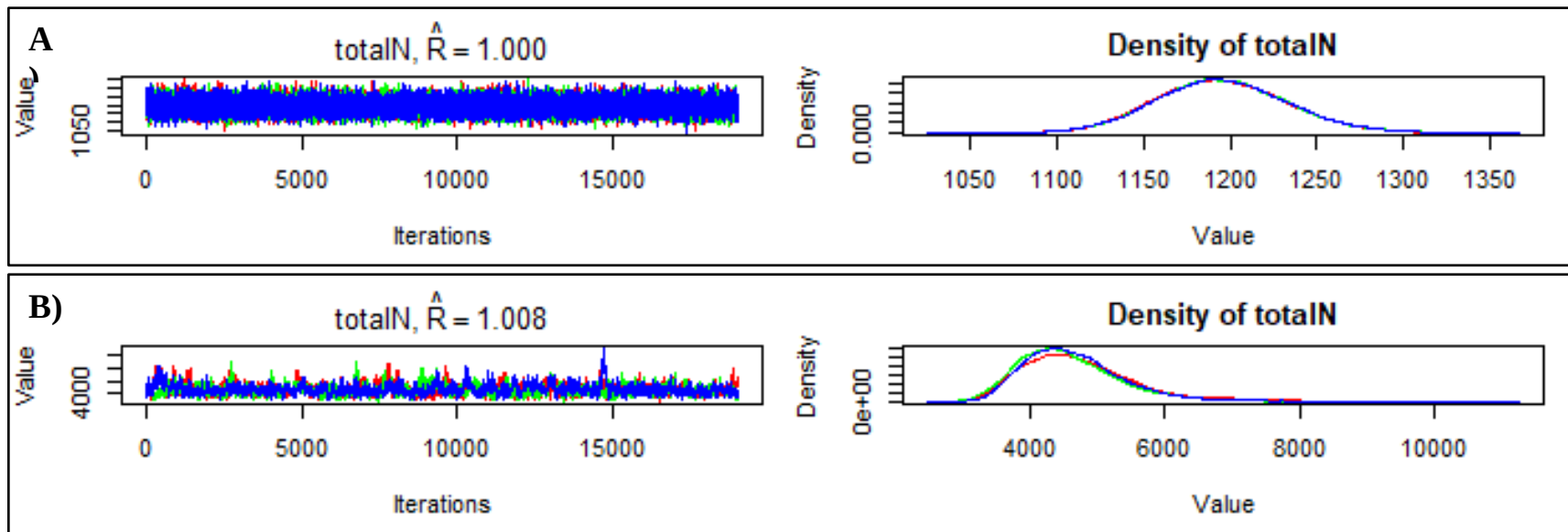


Figure 1C.6. Markov chain Monte Carlo trace plot examples of A) exceptional mixing with the Poisson model and B) marginal mixing with the Poisson lognormal model for total abundance. These examples highlight the best and worse mixing observed in this study. For both scenarios, a simplistic N-mixture model was used for data explorations with white-tailed deer (*Odocoileus virginianus*) count data from a camera-trap study design.

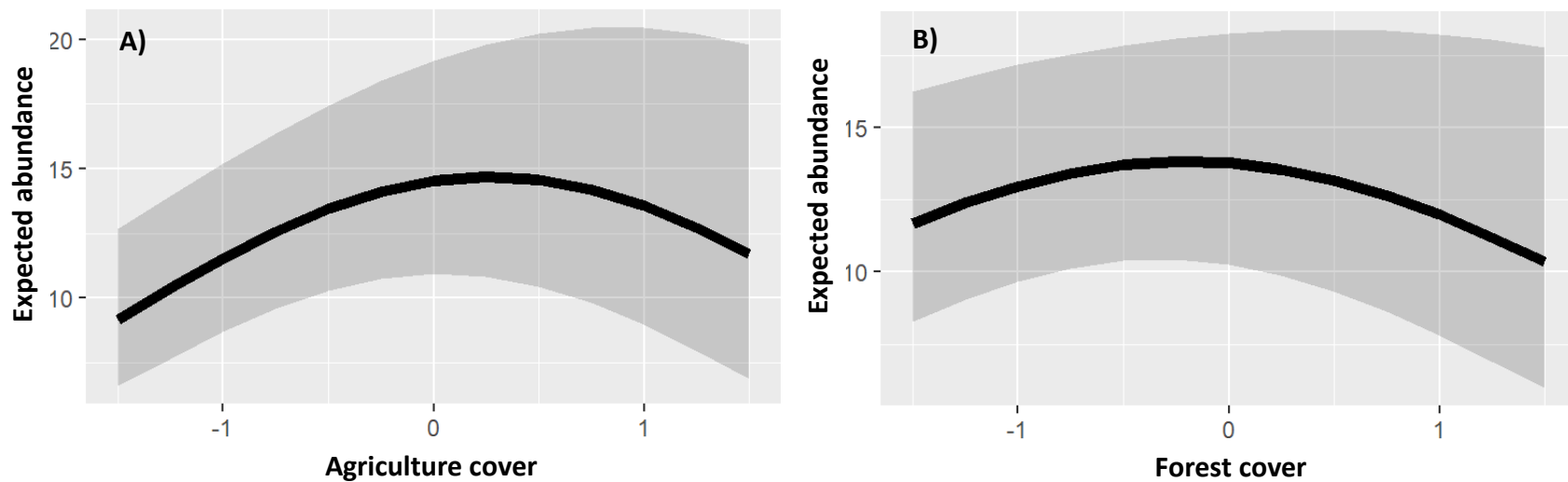


Figure 1C.7. Change in expected deer site abundance as a function of site covariates, including A) percent of agriculture cover and B) percent of forest cover within each camera site's a 1.24-km² [0.48 mi²] effective sampling area. X-axis values are standardized with a mean zero and gray bands represent 95% confidence limits. Expected abundance was high when percent agriculture was slightly higher than average and when percent forest cover was slightly below average.

APPENDIX 1C.1: CODE FOR MODELING ABUNDANCE BY TOWNSHIP WITH A POISSON DISTRIBUTION

```
nmix <- function(twn.final){

  #Data
  max <- ncol(twn.final)
  y <- twn.final[,2:max]
  library("jagsUI")

  # Specify model in JAGS language
  sink("model.txt")
  cat("
  model {

    # Priors
    lambda ~ dgamma(0.005, 0.005) # Standard vague prior for lambda
    p ~ dunif(0, 1)

    # Likelihood
    # Biological model for true abundance
    for (i in 1:R) {
      N[i] ~ dpois(lambda)

      # Observation model for replicated counts
      for (j in 1:T) {
        y[i,j] ~ dbin(p, N[i])
      } #j
    } #i

    # Derived quantities
    totalN <- sum(N[])
  }
  ",fill = TRUE)
  sink()

  # Bundle data
  win.data <- list(y = y, R = nrow(y), T = ncol(y))

  # Initial values
  Nst <- apply(y, 1, max, na.rm = TRUE) + 1 # This line is important
```

```

inits <- function() list(N = Nst)

# Parameters monitored
params <- c("lambda", "p", "totalN")

# MCMC settings
ni <- 100000
nt <- 5
nb <- 5000
nc <- 3

# Call JAGS from R (BRT 0.1 min)
out <-<- jags(win.data, inits, params, "model.txt", n.chains = nc,
n.thin = nt, n.iter = ni, n.burnin = nb)
}

```

APPENDIX 1C.2: CODE FOR MODELING ABUNDANCE FOR ALL TOWNSHIPS WITH A POISSON DISTRIBUTION

```
nmix <- function(twn.final){

  #Data
  max <- ncol(twn.final)
  y <- twn.final[,2:max]
  library("jagsUI")

  # Specify model in JAGS language
  sink("model.txt")
  cat("
  model {

    # Priors
    lambda ~ dgamma(0.005, 0.005) # Standard vague prior for lambda
    p ~ dunif(0, 1)

    # Likelihood
    # Biological model for true abundance
    for (i in 1:R) {
      N[i] ~ dpois(lambda)

      # Observation model for replicated counts
      for (j in 1:T) {
        y[i,j] ~ dbin(p, N[i])
      } #j
    } #i

    # Derived quantities
    totalN <- sum(N[])

    #Relies on input data (rows) being sorted by      site(LocationName)
    shermanN <- sum(N[1:18])
    tyronN <- sum(N[19:36])
    bowneN <- sum(N[37:54])
    nelsonN <- sum(N[55:72])
    sheridanN <- sum(N[73:90])
    eastonN <- sum(N[91:108])
    bushnellN <- sum(N[109:126])
    douglasN <- sum(N[127:144])
```

```

}
",fill = TRUE)
sink()

# Bundle data
win.data <- list(y = y, R = nrow(y), T = ncol(y))

# Initial values
Nst <- apply(y, 1, max, na.rm = TRUE) + 1 # This line is important
inits <- function() list(N = Nst)

# Parameters monitored
params <- c("lambda", "p", "totalN", "shermanN", "tyronN", "bowneN",
"nelsonN", "sheridanN", "eastonN", "bushnellN", "douglasN")

# MCMC settings
ni <- 100000
nt <- 5
nb <- 5000
nc <- 3

# Call JAGS from R (BRT 0.1 min)
out <-<- jags(win.data, inits, params, "model.txt", n.chains = nc,
n.thin = nt, n.iter = ni, n.burnin = nb)
}

```

APPENDIX 1C.3: SUPPLEMENTARY DEER DENSITY MAP PRODUCED BY THE MICHIGAN DEPARTMENT OF NATURAL RESOURCES

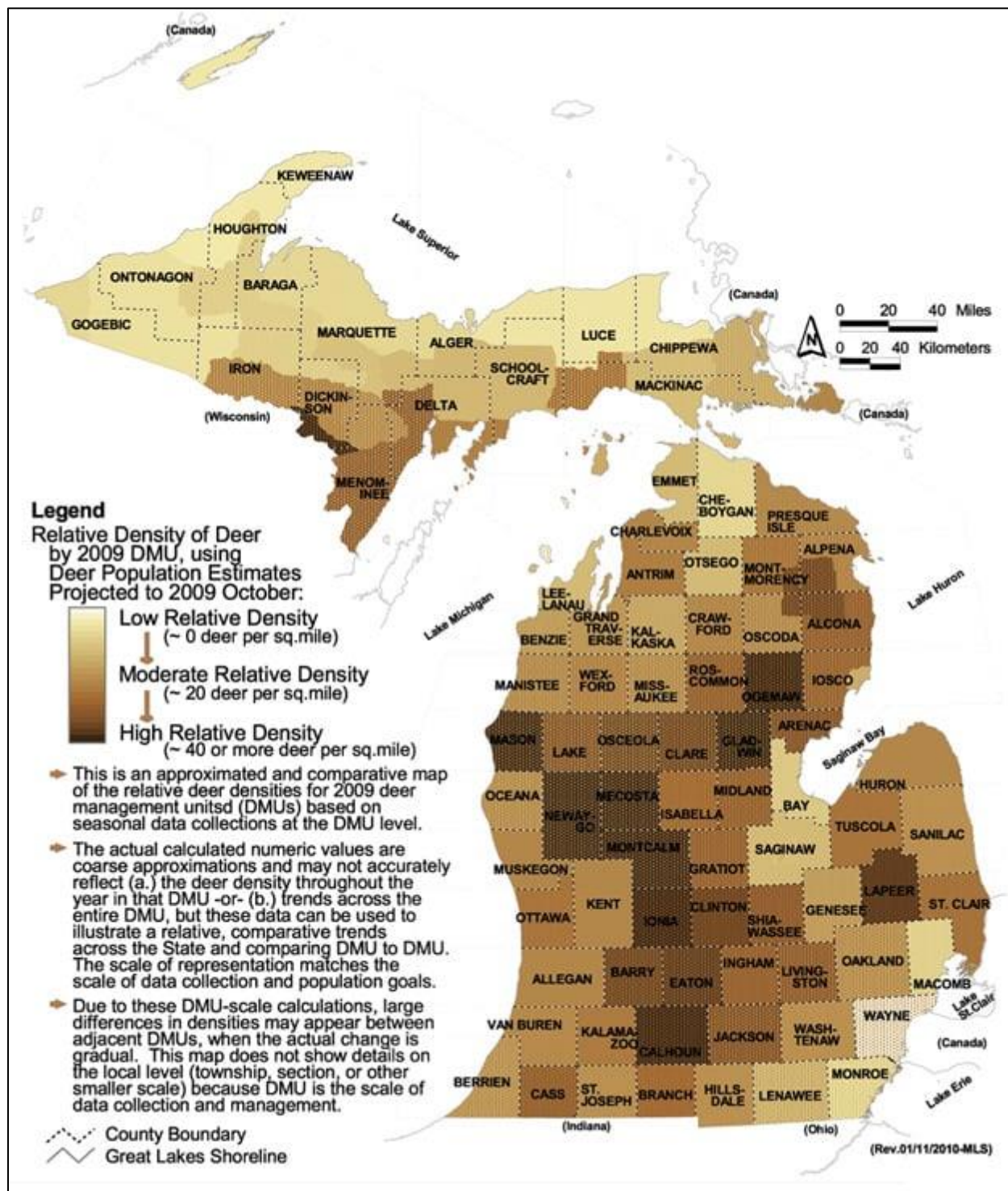


Figure 1C.8. White-tailed deer (*Odocoileus virginianus*) density estimates by deer management unit (DMU) in Michigan, USA, 2009. Estimates and map produced by the Michigan Department of Natural Resources.

APPENDIX 1C.4: CODE FOR MODELING ABUNDANCE FOR ALL TOWNSHIPS WITH A ZERO-INFLATED POISSON DISTRIBUTION

```
zipmix <- function(twn.final){
  max <- ncol(twn.final)
  y <- tw.n.final[,2:max]
  library("jagsUI")

  # Specify model in JAGS language
  sink("model.txt")
  cat("
model {

  # Priors
  p ~ dunif(0, 1)
  lambda ~ dgamma(0.005, 0.005) # Standard vague prior for lambda
  psi ~ dunif(0,1)

  # Likelihood
  # Biological model for true abundance
  for (i in 1:R) {
    N[i] ~ dpois(mu[i])
    mu[i] <- lambda * z[i] + 0.000001
    z[i] ~ dbern(psi)

    # Observation model for replicated counts
    for (j in 1:T) {
      y[i,j] ~ dbin(p, N[i])
    } #j
  } #i

  # Derived quantities
  totalN <- sum(N[])

  #Relies on input data (rows) being sorted by      site(LocationName)
  shermanN <- sum(N[1:18])
  tyronN <- sum(N[19:36])
  bowneN <- sum(N[37:54])
  nelsonN <- sum(N[55:72])
  sheridanN <- sum(N[73:90])
  eastonN <- sum(N[91:108])
  bushnellN <- sum(N[109:126])
```

```

douglasN <- sum(N[127:144])
}
",fill = TRUE)
sink()

# Bundle data
win.data <- list(y = y, R = nrow(y), T = ncol(y))

# Initial values
Nst <- apply(y, 1, max, na.rm = TRUE) + 1 # This line is important
inits <- function() list(N = Nst)

# Parameters monitored
params <- c("lambda", "p", "totalN", "shermanN", "tyronN", "bowneN",
"nelsonN", "sheridanN", "eastonN", "bushnellN", "douglasN")

# MCMC settings
ni <- 100000
nt <- 5
nb <- 5000
nc <- 3

# Call JAGS from R (BRT 0.1 min)
out <- jags(win.data, inits, params, "model.txt", n.chains = nc,
n.thin = nt, n.iter = ni, n.burnin = nb)
}

```


APPENDIX 1C.5: CODE FOR MODELING ABUNDANCE FOR ALL TOWNSHIPS WITH A NEGATIVE BINOMIAL DISTRIBUTION

```
nmix.negbin <- function(twn.final){
  max <- ncol(twn.final)
  y <- twn.final[,2:max]
  library("jagsUI")

  # Specify model in JAGS language
  sink("model.txt")
  cat("
model {

  # Priors
  for (i in 1:R){
    lambda[i] ~ dgamma(0.005, 0.005) # Standard vague prior for lambda
  }
  th ~ dunif(0, 50)
  p ~ dunif(0, 1)

  # Likelihood
  # Biological model for true abundance
  for (i in 1:R) { #sites
    N[i] ~ dnegbin(prob[i], th)
    prob[i] <- th / (th + lambda[i])

    # Observation model for replicated counts
    for (j in 1:T) { #sample occasions
      y[i,j] ~ dbin(p, N[i])
    } #j
  } #i

  # Derived quantities
  totalN <- sum(N[])

  #relies on input data (rows) being sorted by site(LocationName)
  shermanN <- sum(N[1:18])
  tyronN <- sum(N[19:36])
  bowneN <- sum(N[37:54])
  nelsonN <- sum(N[55:72])
  sheridanN <- sum(N[73:90])
  eastonN <- sum(N[91:108])
```

```

bushnellN <- sum(N[109:126])
douglasN <- sum(N[127:144])
}
",fill = TRUE)
sink()

# Bundle data
win.data <- list(y = y, R = nrow(y), T = ncol(y))

# Initial values
Nst <- apply(y, 1, max, na.rm = TRUE) + 1 # This line is important
inits <- function() list(N = Nst)

# Parameters monitored
params <- c("p", "totalN", "shermanN", "tyronN", "bowneN",
"nelsonN", "sheridanN", "eastonN", "bushnellN", "douglasN")

# MCMC settings
ni <- 100000
nt <- 10
nb <- 100000
nc <- 3

# Call JAGS from R (BRT 0.1 min)
out <- jags(win.data, inits, params, "model.txt", n.chains = nc,
n.thin = nt, n.iter = ni, n.burnin = nb)
}

```

APPENDIX 1C.6: CODE FOR MODELING ABUNDANCE FOR ALL TOWNSHIPS WITH A POISSON-LOGNORMAL DISTRIBUTION

```
nmix.poslognorm <- function(twn.final){
  max <- ncol(twn.final)
  y <- twm.final[,2:max]
  library("jagsUI")

  # Specify model in JAGS language
  sink("model.txt")
  cat("
model {
# Priors
for (i in 1:R) {
  p[i] ~ dunif(0, 1)
}
mean.lambda ~ dunif(0, 200)
beta0 <- log(mean.lambda)
tau ~ dgamma(0.1, 0.1) # Excess-Poisson variation (precision)
sigma <- sqrt(1 / tau)

# Likelihood
# Biological model for true abundance
for (i in 1:R) {
  N[i] ~ dpois(lambda[i])
  eta[i] ~ dnorm(0, tau)
  log(lambda[i]) <- beta0 + eta[i]

  # Observation model for replicated counts
  for (j in 1:T) {
    y[i,j] ~ dbin(p[i], N[i])
  } #j
} #i

# Derived quantities
totalN <- sum(N[])

#relies on input data (rows) being sorted by site(LocationName)
shermanN <- sum(N[1:18])
tyronN <- sum(N[19:36])
bowneN <- sum(N[37:54])
nelsonN <- sum(N[55:72])
sheridanN <- sum(N[73:90])
```

```

eastonN <- sum(N[91:108])
bushnellN <- sum(N[109:126])
douglasN <- sum(N[127:144])
}
",fill = TRUE)
sink()

# Bundle data
win.data <- list(y = y, R = nrow(y), T = ncol(y))

# Initial values
Nst <- apply(y, 1, max, na.rm = TRUE) + 1 # This line is important
inits <- function() list(N = Nst)

# Parameters monitored
params <- c("p", "totalN", "shermanN", "tyronN", "bowneN",
"nelsonN", "sheridanN", "eastonN", "bushnellN", "douglasN")

# MCMC settings
ni <- 100000
nt <- 5
nb <- 5000
nc <- 3

# Call JAGS from R (BRT 0.1 min)
out <-<- jags(win.data, inits, params, "model.txt", n.chains = nc,
n.thin = nt, n.iter = ni, n.burnin = nb)
}

```

APPENDIX 1C.7: CODE FOR MODELING SAMPLING OCCASION AS A COVARIATE ON DETECTION

```
nmix.det.newtime <- function(twn.final, cov.table){
  max <- ncol(twn.final)
  y <- twn.final[,2:max]
  NewCover <- cov.table$LandCoverNew
  max.cov <- 2 # Hardcoding solution
  library("jagsUI")

  # Specify model in JAGS language
  sink("model.txt")
  cat("
model {

  # Priors
  lambda ~ dgamma(0.005, 0.005) # Standard vague prior for lambda
  #Landscape cover (far cover) covariate has 2 levels, going to
estimate p for each level
  alpha ~ dunif(-20,20)
  beta1 ~ dunif(-20,20)

  for (i in 1:R) {
    beta3[i] ~ dunif(-20,20)
  }

  #for(i in 1:2){
  # p[i] ~ dunif(0, 1)
  #}

  # Likelihood
  # Biological model for true abundance
  for (i in 1:R) {
    N[i] ~ dpois(lambda)

    # Observation model for replicated counts
    for (j in 1:T) {
      y[i,j] ~ dbin(p[i,j], N[i])
      logit(p[i,j]) <- alpha + beta1 * NewCover[i] + beta3[i] *j
    } #j
  } #i

  # Derived quantities
```

```

totalN <- sum(N[])

#relies on input data (rows) being sorted by site(LocationName)
shermanN <- sum(N[1:18])
tyronN <- sum(N[19:36])
bowneN <- sum(N[37:54])
nelsonN <- sum(N[55:72])
sheridanN <- sum(N[73:90])
eastonN <- sum(N[91:108])
bushnellN <- sum(N[109:126])
douglasN <- sum(N[127:144]) # SG look to see if there's >144 sites
}
",fill = TRUE)
sink()

# Bundle data
win.data <- list(y = y, R = nrow(y), T = ncol(y), NewCover =
as.integer(NewCover))

# Initial values
Nst <- apply(y, 1, max, na.rm = TRUE) + 1 # This line is important
inits <- function() list(N = Nst)

# Parameters monitored, SG included p 09JUL22
params <- c("alpha", "beta1", "beta3", "totalN", "shermanN",
"tyronN", "bowneN", "nelsonN", "sheridanN", "eastonN", "bushnellN",
"douglasN")

# MCMC settings
ni <- 100000
nt <- 5
nb <- 5000
nc <- 3

# Call JAGS from R (BRT 0.1 min)
out <- jags(win.data, inits, params, "model.txt", n.chains = nc,
n.thin = nt, n.iter = ni, n.burnin = nb)
}

```

APPENDIX 1C.8: CODE FOR MODELING COVARIATES ON ABUNDANCE

```
nmix <- function(twn.final, cov.table){
  #Cover (open or closed) covariate on detection process
  #Percent agriculture covariate on abundance process
  #Week counts
  #Township as random effect on abundance process

  #Data
  max <- ncol(twn.final)
  y <- twn.final[,2:max]
  NewCover <- cov.table$LandCoverNew #Open or closed cover covariate on
detection
  AgCover <- cov.table$AgCover #%agriculture covariate on abundance

  #Create group ID for townships; requires all 18 sites in 4 townships
(8 in other years)
  twn <- sort(rep(1:8, 18))

  #Load JAGS package
  library("jagsUI")

  #Specify model in JAGS language
  sink("model.txt")
  cat("
model {
# Priors
alpha ~ dnorm(0,0.25)
beta1 ~ dnorm(0,0.25)
beta4 ~ dnorm(0,0.25)
beta5 ~ dnorm(0,0.25)
mu.kappa ~ dnorm(0,0.25)
sigma.kappa ~ dexp(1)

# Likelihood
# Biological model for true abundance
for (i in 1:R) { # Sites
  N[i] ~ dpois(mu.lambda[i])
  log(mu.lambda[i]) <- kappa[twn[i]] + (beta4 * AgCover[i]) + (beta5
* pow(AgCover[i],2))

  # Observation model for replicated counts
```

```

    for (j in 1:T) { #count reps
      y[i,j] ~ dbin(p[i], N[i])
    } #j
    logit(p[i]) <- alpha + (beta1 * NewCover[i])
  } #i

  for (k in 1:8) { # Townships for random effect on lambda, hard coded
for 8 townships
    kappa[k] ~ dnorm(mu.kappa, tau.kappa)
  }

  # Derived quantities
  tau.kappa <- pow(sigma.kappa,-2)

  totalN <- sum(N[])

  # Relies on input data (rows) being sorted by site (LocationName)
  shermanN <- sum(N[1:18])
  tyronN <- sum(N[19:36])
  bowneN <- sum(N[37:54])
  nelsonN <- sum(N[55:72])
  sheridanN <- sum(N[73:90])
  eastonN <- sum(N[91:108])
  bushnellN <- sum(N[109:126])
  douglasN <- sum(N[127:144]) # 144 camera sites

}
",fill = TRUE)
sink()

#Bundle data
win.data <- list(y = y, R = nrow(y), T = ncol(y[, ,1]), NewCover =
as.integer(NewCover), AgCover = as.numeric(scale(AgCover)), twN = twN)

#Initial values
Nst <- apply(y, 1, max, na.rm = TRUE) + 1 # This line is important
inits <- function() list(N = Nst)

#Parameters monitored

```



```

  params <- c("alpha", "beta1", "beta4", "beta5", "mu.kappa",
"sigma.kappa", "kappa", "p", "totalN", "shermanN", "tyronN", "bowneN",
"nelsonN", "sheridanN", "eastonN", "bushnellN", "douglasN")

# MCMC settings
ni <- 50000
nt <- 5
nb <- 3000
nc <- 3

# Call JAGS from R (BRT 0.1 min)
out <-<- jags(win.data, inits, params, "model.txt", n.chains = nc,
n.thin = nt, n.iter = ni, n.burnin = nb)
}}
```

APPENDIX 1C.9: CODE FOR MODELING SAMPLING OCCASION AS A COVARIATE ON DETECTION WHILE ACCOUNTING FOR ZEROS

```
nmix.det.newtime <- function(twn.final, cov.table){
  max <- ncol(twn.final)
  y <- twn.final[,2:max]
  NewCover <- cov.table$LandCoverNew
  max.cov <- 2 # Hardcoding solution
  library("jagsUI")

  # Specify model in JAGS language
  sink("model.txt")
  cat("
model {

  # Priors
  lambda ~ dgamma(0.005, 0.005) # Standard vague prior for lambda
  #Landscape cover (far cover) covariate has 2 levels, going to
estimate p for each level
  alpha ~ dunif(-20,20)
  beta1 ~ dunif(-20,20)
  psi ~ dunif(0,1)

  for (i in 1:R) {
    beta3[i] ~ dunif(-20,20)
  }
  #for(i in 1:2){
  # p[i] ~ dunif(0, 1)
  #}

  # Likelihood
  # Biological model for true abundance
  for (i in 1:R) {
    N[i] ~ dpois(lambda)
    z[i] ~ dbern(psi)
    # Observation model for replicated counts
    for (j in 1:T) {
      y[i,j] ~ dbin(p[i,j], N[i])
      logit(p[i,j]) <- alpha + (beta1 * NewCover[i]) + (z[i] *
beta3[i] * j)
    } #j
  } #i
}
```

```

# Derived quantities
totalN <- sum(N[])

#relies on input data (rows) being sorted by site(LocationName)
shermanN <- sum(N[1:18])
tyronN <- sum(N[19:36])
bowneN <- sum(N[37:54])
nelsonN <- sum(N[55:72])
sheridanN <- sum(N[73:90])
eastonN <- sum(N[91:108])
bushnellN <- sum(N[109:126])
douglasN <- sum(N[127:144])
sumZ <- sum(z[1:144])
}

",fill = TRUE)
sink()

# Bundle data
win.data <- list(y = y, R = nrow(y), T = ncol(y), NewCover =
as.integer(NewCover))

# Initial values
Nst <- apply(y, 1, max, na.rm = TRUE) + 1 # This line is important
inits <- function() list(N = Nst)

# Parameters monitored, SG included p 09JUL22
params <- c("alpha", "beta1", "beta3", "totalN", "shermanN",
"tyronN", "bowneN", "nelsonN", "sheridanN", "eastonN", "bushnellN",
"douglasN", "sumZ")

# MCMC settings
ni <- 100000
nt <- 5
nb <- 5000
nc <- 3

# Call JAGS from R (BRT 0.1 min)
out <-<- jags(win.data, inits, params, "model.txt", n.chains = nc,
n.thin = nt, n.iter = ni, n.burnin = nb)
}

```

APPENDIX 1C.10: CODE FOR MODELING WEEK AS A COVARIATE ON DETECTION

```
nmix.det.newtime2 <- function(twn.final, cov.table){

  max <- ncol(twn.final)
  y1 <- twn.final[,2:max]
  y <- array(unlist(y1), dim=c(144,14,9)) #restructuring data into 3
dimensions (144 sites, 14 counts per week, 9 weeks)

  NewCover <- cov.table$LandCoverNew
  max.cov <- 2 # Hardcoding
  library("jagsUI")

  # Specify model in JAGS language
  sink("model.txt")
  cat("
model {

  # Priors
  lambda ~ dgamma(0.005, 0.005) # Standard vague prior for lambda
  #Landscape cover (far cover) covariate has 2 levels, going to
estimate p for each level
  alpha ~ dunif(-20,20)
  beta1 ~ dunif(-20,20)
  beta4 ~ dunif(-20,20)

  for (i in 1:R) {
    beta3[i] ~ dunif(-20,20)
  }
  # Likelihood
  # Biological model for true abundance
  for (i in 1:R) {
    N[i] ~ dpois(lambda)
    #z[i] ~ dbern(psi)
    # Observation model for replicated counts
    for (k in 1:9) {
      for (j in 1:T) {
        y[i,j,k] ~ dbin(p[i,k], N[i])
      } #j
      logit(p[i,k]) <- alpha + (beta1 * NewCover[i]) + (beta3[i] * k)
      #logit(p[i,k]) <- alpha + (beta1 * NewCover[i]) + (beta3[i] * k)
+ ((beta4 * NewCover[i] * k))
```

```

    } #k
  } #i

# Derived quantities
totalN <- sum(N[])

#relies on input data (rows) being sorted by site(LocationName)
shermanN <- sum(N[1:18])
tyronN <- sum(N[19:36])
bowneN <- sum(N[37:54])
nelsonN <- sum(N[55:72])
sheridanN <- sum(N[73:90])
eastonN <- sum(N[91:108])
bushnellN <- sum(N[109:126])
douglasN <- sum(N[127:144])
}
",fill = TRUE)
sink()

# Bundle data
win.data <- list(y = y, R = nrow(y), T = ncol(y[, , 1]), NewCover =
as.integer(NewCover), sherman.rows=sherman.rows)

# Initial values
Nst <- apply(y, 1, max, na.rm = TRUE) + 1 # This line is important
inits <- function() list(N = Nst)

# Parameters monitored
params <- c("alpha", "beta1", "beta3", "beta4", "p", "totalN",
"shermanN", "tyronN", "bowneN", "nelsonN", "sheridanN", "eastonN",
"bushnellN", "douglasN")
# MCMC settings
ni <- 10000
nt <- 5
nb <- 1000
nc <- 3

# Call JAGS from R (BRT 0.1 min)
out <- jags(win.data, inits, params, "model.txt", n.chains = nc,
n.thin = nt, n.iter = ni, n.burnin = nb)
}

```

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Protocol for Managing and Processing Camera-Trap Data

Supplemental research to:

Influence of deer harvest regulations on antlerless harvest, abundance, and sex and age composition: implications for managing deer in the face of chronic wasting disease

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MegaDetector Installation and Setup

1. Go to <https://docs.anaconda.com/anaconda/install/windows/> and follow instructions to install Anaconda. You can skip step 2 (verify data integrity) and step 12 (installing PyCharm). The rest of the instructions will assume you have installed to `C:\Workspace\Anaconda` but you can choose a different location, if necessary. It is recommended you choose a location where you know you have write authority and whose address does not contain any spaces (so don't choose `C:\Program Files` or something similar).
2. From your Start menu, Open Anaconda Navigator. Update to latest version, if prompted.
3. In Anaconda Navigator, go to Environments and then Create *cameratraps-detector*. Make sure to select the Python package and select 3.7 from the dropdown (Figure 2A.1).

You may not see an option for 3.7 initially because Anaconda needs time to think, or you need to “update index” first, this might prompt an update too. If 3.7 is not an option try typing it in, otherwise you may need to download a more current version and troubleshoot to downgrade to get the 3.7 version used here.

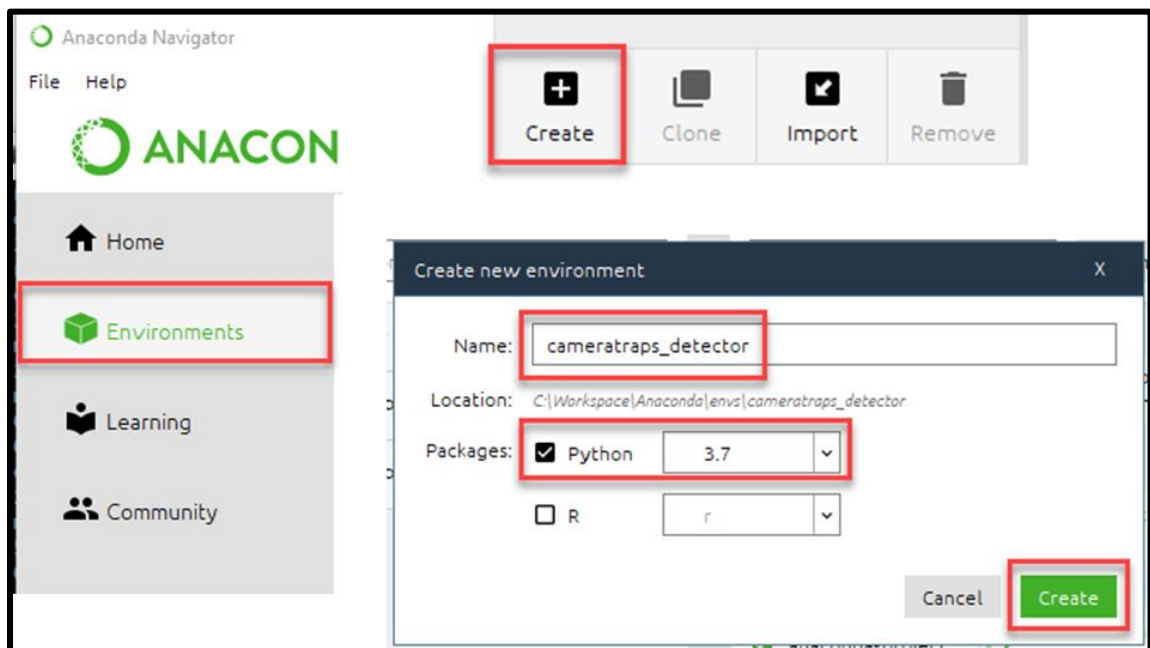


Figure 2A.1 Screenshots from the Anaconda Navigator workflow for installing and setting up MegaDetector. Workflow includes creating a new environment with *cameratraps-detector* and Python version 3.7.

4. Go to Environments, select *cameratraps-detector*, change dropdown to All (Figure 2A.2).

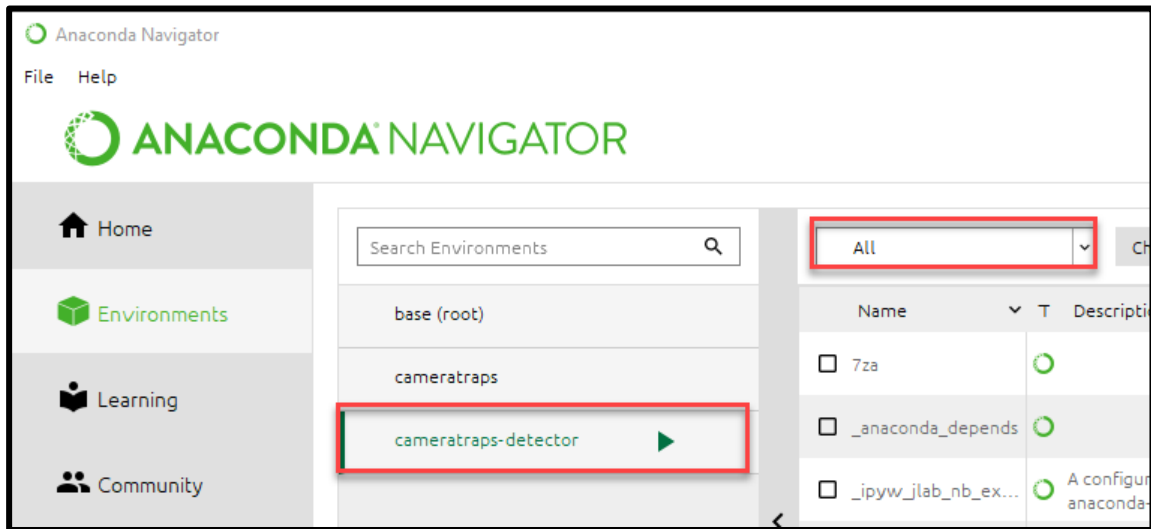


Figure 2A.2. Screenshot from the Anaconda Navigator workflow for installing and setting up MegaDetector. Once the *cameratraps-detector* environment is created, the workflow includes selecting the all-packages option in the index.

- a. Make sure all items listed in <https://github.com/microsoft/CameraTraps/blob/master/environment-detector.yml> as dependencies are selected except *tensorflow*. After selecting each necessary package, click Apply. Dependencies may also need to be installed.
 - i. You may need to Update index to find all the packages (Figure 2A.3).

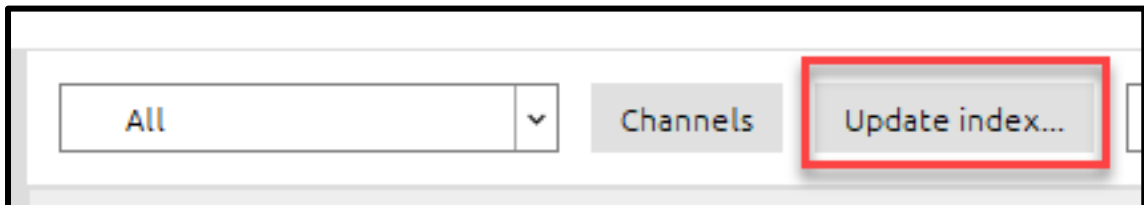


Figure 2A.3. Screenshot from the Anaconda Navigator workflow for installing and setting up MegaDetector. The workflow may require updating the index to find all the required packages for MegaDetector.

- ii. While you are installing packages, if Anaconda seems to get stuck on the *fetching* step, cancel the process, close and restart Anaconda. Then you can start installing the rest of the packages.
 - iii. MegaDetector may require additional downloads, specifications include:

name: cameratraps-detector,
channels:

```

- conda-forge
- pytorch
dependencies:
- python=3.8
- Pillow=9.1.0
- nb_conda_kernels
- ipykernel
- tqdm
- jsonpickle
- humanfriendly
- numpy
- matplotlib
- nb_conda_kernels
- ipykernel
- opencv
- requests
# for running MegaDetector v4
# - tensorflow>=2.0
# for running MegaDetector v5
- pandas
- seaborn>=0.11.0
- PyYAML>=5.3.1
- pytorch::pytorch=1.10.1
- pytorch::torchvision=0.11.2
- conda-forge::cudatoolkit=11.3
- conda-forge::cudnn=8.1
# the `nb_conda_kernels` and `ipykernel` packages are installed so
that we can use Jupyter Notebooks with this environment as a
kernel

```

5. Download MegaDetector
from https://lilablobssc.blob.core.windows.net/models/camera_traps/megadetector/megadetector_v3.pb. The rest of the instructions assume you have installed to `C:\Workspace\MegaDetector` but you can choose a different location, if necessary. It is recommended that you choose a location where you know you have write authority and whose address does not contain any spaces (so don't choose `C:\Program Files` or something similar). Other than that, you should not need to do any special setup with this step.
6. Go to <https://git-scm.com/download/win> and follow the instructions to download and install Git. Install the version called *64-bit Git for Windows Setup*. The rest of the instructions assume you have installed to `C:\Workspace\Git` but you can choose a different location, if necessary. Again, no spaces in the address. Accept all defaults while installing (make sure to open and use all pre-selected options for setup).

- a. I renamed my file pathway and workspace to match what I thought would be easier to run on S. Gurney's laptop, "c:\Users\gurneyst\Git"
7. Go to Start menu and open Anaconda prompt.
 - a. In the prompt enter: `conda activate cameratraps-detector`
 - b. At the next prompt, enter: `cd c:\workspace\git`
 - i. Instead of `c:\workspace\git` you should enter the location where you installed Git. I had `c:\Users\gurneyst\Git`. You can move the MegaDetector files to your liking, just make sure that the code matches the pathway where the files are.
 - c. At the next prompt, enter: `git clone https://github.com/microsoft/CameraTraps`
 - d. At the next prompt, enter: `git clone https://github.com/microsoft/ai4eutils/`
 - e. At the next prompt, enter:
`set`
`PYTHONPATH=c:\workspace\git\cameratraps;c:\workspace\git\ai4eutils`
 - i. Instead of `c:\workspace\git` you should enter the location where you installed Git.
 - f. At the next prompt, enter: `pip install tensorflow==1.13.1`
 - g. At the next prompt, enter: `pip install humanfriendly Pillow pandas tqdm`
8. Close all open windows.
9. If the software does not operate, it may require additional troubleshooting. New software updates might require this troubleshooting.

Data Management and Processing with CPW Photo Warehouse and MegaDetector

- A. Create 2 separate CPW Photo Warehouse databases—one for the APR Zone and one for the NonAPR Zone. Dividing the databases this way will prevent the databases from getting too bogged down (and makes it easier when dividing database tasks among technicians). Using CPW Photo Warehouse, you (the data manager) will need to begin by entering all the camera sites using the “Add or Edit Locations” button in the switchboard (the main menu). Do not enter location information here (e.g., coordinates; this information is private to MSU). Once all camera sites for the appropriate study area are listed in the locations table, you can begin adding camera visits. Click on “Add or Edit Visits” in the switchboard then select a location from the dropdown in the visits form. Once you have selected a location click “Add New Visit” (Figure 2A.4).

Visits

Camera Visits

Select a Location:

Visit Type	Date	Comments	Photos
------------	------	----------	--------

[Add New Visit](#)

Access:

Figure 2A.4. Screenshot from the CPW Photo Warehouse workflow for managing camera-trap data. The workflow includes adding new visits and associated data for each camera location.

- B. For each camera you will need to first add the set date. Because we are only collecting data starting July 15 you should make the set date 07/15/YYYY for all cameras.
- C. Pick up SD card from field technicians

- a. Use pocket organizer (i.e., SD wallet) to keep cards organized and to help keep track of when the cameras were checked. A mailbox-type system works well for delivering and returning SD cards (e.g., one mailbox for SD cards that need to be uploaded and one mailbox for SD cards ready to go back into the field).
- D. For the first camera check (which should occur shortly after July 15), start by moving all photos from the SD cards to the correct 1-TB external hard drive (individual 1-TB hard drives should be assigned to individual townships). Next, separate photos into “pre-July 15” and “post-July 15” locations. So, create a folder called “Pre-Post-Jul15” in the Check 1 folder, include a subfolder for each site, like “11001” and then give it subfolders “pre-Jul15” and “post-Jul15” to store photos before renaming them (e.g., “APR_Easton\Check1\Pre-Post-Jul15\Post-Jul15”). We only want to import post July 15 photos into the Photo Warehouse database, and it will be easier to have them presorted. See Figure 2A.4 for an example of a file pathway. None of the folder or file names can have spaces in them. So, you will need to create:
- a. Subfolder for pre-July 15 photos
 - b. Subfolder for first access post-July 15 photos (this is a subfolder needed before manual file renaming happens in CPW Photo Warehouse).
 - i. Subfolder for each township
 1. Subfolder for each site
 - c. Subfolder for each Access (i.e., camera check)
 - i. Subfolder for each township
 1. Subfolder for each site

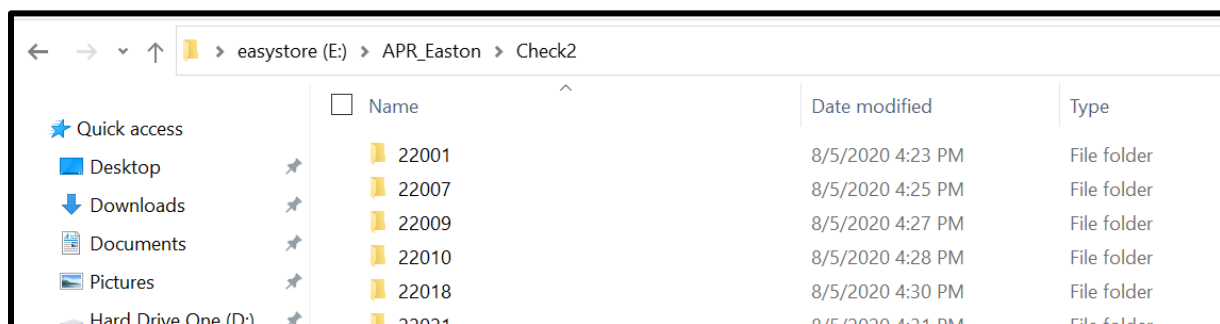


Figure 2A.4. Screenshot from the CPW Photo Warehouse workflow for managing camera-trap data. The workflow includes saving data using a folder hierarchy. This example displays the file pathway for site 22001, Check2, in Easton Township (APR Zone) as “APR_Easton\Check2\22001”. Note that there are individual subfolders for each camera site.

It is very important to have file pathways good from the start; and maintain organizational structure of hard drives throughout seasons).

Since the sampling period ends on September 15th, we will use a similar approach (like D-a and D-b) for separating Pre- and Post-Sep15 photos in the Check 5 folder. Do not forget to separate Pre- and Post-Sep15 photos after the last camera check or it will cause many problems.

- E. Once you have a set date in the database you can add check dates and pull dates using the “Add or Edit Visits” option from Photo Warehouses switchboard (main menu) and clicking the “Add New Visit” button. When you choose “Check” in the Visit Type field, a subform will pop up allowing you to load photos. Do not forget to list the final camera check as “pull.”
- F. Enter the path for the folder containing the photos just for that camera site (for first access, you would choose the path from the “post-July 15 Access 1” subfolder (or at the end of the season “pre-Sep 15 Access 5”), then click the “copy image files”. I know it seems redundant to re-copy the images when they are already stored on the hard drive, but this will allow us to rename all the images in a consistent way. Copy the images into the appropriate subfolder and click the “Rename image files” box. Use the Location ID as the “Prefix option” and Image Number + Date as the “Rename files using” option.
 - a. After the first camera check (except for the final camera check), photos can be imported directly from the SD cards rather than saving them to the external hard drive first, then importing them. Continue uploading photos through the “Visits” subform in the database and copying and renaming the files in the same way as above.
 - b. It is easy to mix up what SD cards have and have not been uploaded, so keep track of what you upload in a notebook (e.g., write Sherman Township Check 3 and list bullet points for each successful upload like, “Card 16/Site 11045, Card 18/Site 11018” and so on). Keeping notes like this allows you to double check that you have uploaded all 18 SD cards per township—and that is important to prevent missing data. You may need to refer to the first few images on the SD card (which show a whiteboard) to identify what the site ID is.
 - c. Make sure that Check 1 and set date are not the same. Camera set = July 15th, Check 1 = any date other than July 15th. When check and set date are the same it creates duplicates of photos that are labeled incorrectly when adding into the database—and this cause serious database problems. Make sure technicians do not check the cameras on July 15th.

- G. The 1-TB hard drives (containing township photos) should be backed up to a 5-TB hard drive weekly (the 5TB hard drive will be stored at the MDNR warehouse). It is good practice to regularly backup the 5-TB hard drive with a separate 5-TB hard drive that is housed at a location off site (e.g., MSU). The 1-TB hard drives must be backed up after each camera check before the SD cards go out in the field again (because photos will be deleted from SD cards in the field). External hard drives can get damaged or ruined during the MegaDetector process (it has happened), so it is critical to back everything up before each round of MegaDetector. For example, after Sherman Check 3 photos have been uploaded to the Sherman external hard drive from the Sherman SD cards, the Sherman hard drive must be backed up before MegaDetector scans the Check 3 photos on Sherman's hard drive.
- H. You will run MegaDetector to screen out the images that do not have any wildlife (i.e., empty or blank images). You will need separate computers, best case scenario is to have one computer designated for each 1-TB hard drive (i.e., township). Repeat the steps below for each computer-hard drive pair. MegaDetector may run for several hours or days (most likely over a week), so the computers you use for MegaDetector should be dedicated to that sole process alone. It is important to change each computer's settings to prevent it from automatically shutting down, going into sleep mode, or doing automatic updates—all of which will disrupt MegaDetector from running continuously. When running MegaDetector, keep computers and drives well ventilated (e.g., create additional space between hardware and surfaces) because days of use and heat can damage hardware (use additional fans if possible).
- a. Connect 1-TB hard drive to the computer. Make sure the hard drive is listed as the "D" drive on your computer, if not it will cause many issues down the road. If the hard drive is listed on the computer as something else, like "E" drive, you will need to change the setting in your computers Disk Management (this issue is very common). You can fix the issue with the computer's "Create and format hard disk partitions" option in the Control Panel. Once you open the Disk Management page, right click the hard drive and select "Change drive letters and paths..." and change the letter to "D." If something else is currently listed as "D" you will need to change it so the hard drive can be labeled "D".
 - b. Go to the Start menu, open Anaconda prompt. These instructions assume you have installed all software to locations recommended in the MegaDetector Installation and Setup instructions (above). You will need to modify the code below according to site, camera check, and zone. The easiest way to do this is by copying and pasting prompts into Anaconda (but remember you need to revise the code first). It can be helpful to save different versions of code below for each township—that way all you need to do is update camera check number. It also

can be helpful to keep the original code below intact. The comment section is a good place to revise the code accordingly—comment on this document by clicking on the “Review” tab and add a “New comment.”

- i. In the prompt, enter:

```
conda activate cameratraps-detector
```

- ii. At the next prompt, enter:

```
cd c:\workspace\git
```

- a. Here is an example pathway for setting the workspace on S. Gurney’s laptop:

```
cd c:\Users\gurneyst\Git
```

- b. In the example above, all program downloads for MegaDetector were in the folder “Git”

- iii. At the next prompt, enter:

```
set PYTHONPATH=c:\workspace\git\CameraTraps;  
c:\workspace\git\ai4eutils
```

- iv. At the next prompt, enter:

```
python  
CameraTraps/detection/run_tf_detector_batch.  
py  
c:/workspace/megadetector/megadetector_v3.pb  
d:/Access1 d:/Access1/Access1_APR.json --  
recursive --output_relative_filenames --  
checkpoint_frequency=50
```

- a. In the command above, instead of **d:/Access1**, use the appropriate path for the access number you are trying to scan (i.e., run MegaDetector on).
- b. In the command above, instead of **d:/Access1/Access1_APR.json**, use the appropriate path and file name to indicate both the

township, access number, and whether the results are for APR or NON.

- c. Here is example code from S. Gurney's laptop (MegaDetector will run this code to analyze each photo in the Easton Check2 folder):

```
python
CameraTraps/detection/run_tf_detector_batch.py
c:/Users/gurneyst/Git/megadetector_V3.py
b d:/APR_Easton/Check2
d:/APR_Easton/Check2/Check2_APR_Easton.json --recursive --
output_relative_filenames --
checkpoint_frequency=50
```

- v. If the scan is interrupted for whatever reason, use the following code to restart from the last checkpoint:

```
python
CameraTraps/detection/run_tf_detector_batch.py
py c:/workspace/megadetector_v3.py
d:/Access1 d:/Access1/Access1_APR.json --
recursive --output_relative_filenames --
checkpoint_frequency=50 --
resume_from_checkpoint=d:/Access1/checkpoint_20200601145050.json
```

- a. In the command above, instead of `checkpoint_20200601145050` you should enter the name of the checkpoint file created during the interrupted run (it will be a .json file automatically saved on the external hard drive; MegaDetector saves output at regular user-defined intervals [50]).

- I. Backup MegaDetector data immediately after it finishes running. You can do this by backing up MegaDetector's .json and .csv output files to our cloud storage (SharePoint). Also, make sure to include MegaDetector output files when backing up data on the 5-TB hard drives. For example, MegaDetector just finished processing Douglass Check 4, now immediately backup the .json and .csv files to the SharePoint cloud storage—then when you go and backup Douglass Check 5 photos on the 5-TB hard drive at the warehouse,

make sure to also backup Douglass Check 4 MegaDetector data at that time.

- J. After MegaDetector has finished running, disconnect the hard drive from the designated MegaDetector computer—do not just unplug drive as it can cause issues—use the computer’s function to safely eject drive (e.g., right click on the drive icon at bottom right of the desktop screen [next to the clock] and select eject). Next, connect the hard drive to a computer not designated for MegaDetector tasks. Make sure the hard drive is listed as the “D” drive on your computer, if not it will cause many issues down the road (refer to section H-a for directions on how to change the drive settings). Copy the file called Mayhew_Test_Template.tbd (custom template for photo and MegaDetector data created by S. Mayhew) from wherever you have installed it and paste into the appropriate Access folder on the 1-TB external hard drive. Open Timelapse2.exe (Timelapse software) from C:\Mayhew on the computer (folder created by S. Mayhew designated to everything Timelapse).

- a. Go to File -> Load template, images, and video files...
- b. Select the template file from the Access folder and open.
- c. When the image set has opened, go to File -> Import image recognition data for this image set.

This option above might be hidden at first. Look at the Timelapse user manual for instructions on how to make it unhidden. Also, if the file path was written wrong in the code, then it will not transfer recognition data—to troubleshoot this, you can save copy of the .json as a .txt and inspect it—to fix issues you can use the “replace” feature to fix the pathway code.

- d. Select the .json file you created above and open it.
- e. Go to Select -> Custom selection...
- f. In the Image Recognition box, select the Use Detections check box. Make sure the Detected entity says “animal.” Adjust the Confidence to 0.90 to 1.00. Click OK (Figure 2A.5).

Image Recognition

☒ Use Detections

Detected entity: animal

Confidence: from 0.90 to 1.00

Figure 2A.5. Timelapse screenshot from the MegaDetector workflow. In this step, the detection confidence is adjusted for the image recognition data.

- g. Back on the image screen, make sure you are at the first image in the set and select the check box next to Animal (Figure 2A.6). Right-click on the check box next to Animal and select Copy forward to end. Click Yes in the message box that appears.

Data entry for Custom selection

File: APR-ASite1_00001_07-15- RelativePath: TownA\Site1 Folder: Access1

DateTime: 15-Jul-2019 19:32:45 ImageQuality: Ok Delete? ☐ Animal ☒

Copy previous values

Instructions Image set Data Table

File: 1 of 560 Select: Custom selection Sorted by: Id1 (the order files were added to Timelapse)

Figure 2A.6. Timelapse screenshot from the MegaDetector workflow. In this step, the “Animal” data is selected and confirmed.

- h. Go to Select -> All Files.

Do not skip this step above, it selects all files that are labeled with and without wildlife. You want to make sure that all files get exported.

- i. Go to File -> Export data for this image set as a .csv file...

The data file will be exported and automatically saved to the Access (i.e., camera check) folder where the images are stored.

- j. Close Timelapse.

- k. Go to the Access folder where Timelapse sent the .csv file (it will still be named "Mayhew_Test_Template"). Rename the .csv file to indicate the appropriate study area, site ID, and camera check number (e.g., "APR_Bushnell_Check2").

- i. Open the CSV file in notepad or excel to make sure in the last column there are "false" and "true" labels, these are MegaDetector's assigned labels for the photos (i.e., animal/no animal).

- l. Copy the .csv and paste it at the root of the hard drive (D:\), and make sure to first delete any previous .csv file you had copied there. Rename the .csv Timelapse.csv. The name of the file must be exactly Timelapse.csv and stored exactly at the root of the hard drive (so the file address is D:\Timelapse.csv) or the next steps will not work.

- i. Make sure to rename that file at the root of the hard drive when you are done with it (e.g., Timelapse_Check3) because you will be putting the .csv file for each camera check here at the root drive and you do not want duplicates, or it will cause issues.

- K. Make sure Photo Warehouse is closed. Open the database called MD_to_CPW.acddb (this is an intermediary database used to move MegaDetector data to Photo Warehouse). Follow the instructions that are displayed on the screen.

- a. When you follow the instructions, know that MegaDetector1 = "1" and MegaDetector2 = "2". These will be the observer IDs (ObsID) Photo Warehouse assigns to MegaDetector 1 and 2 (there are 2 MegaDetectors because MegaDetector uses a dual scan like a dual observer process).

- b. When you import timelapse, there will not be a pop up to indicate a successful import.
 - c. You might need to manually input detection data when you upload data for the first time (it is programmed to remove any previous data but since there is none, the program may not work appropriately). If this is the case, follow this workflow: MD_to_CPW > External Data Source > New Data Source > From File > Text File > Select the Timelapse.csv from external drive's root and keep defaults > select delimited option > Specs (and keep default) > OK > Finish and close. Hit F11 to make sure that it was named Timelapse, if not right click and rename. This whole step can be tricky and may require some expert assistance.
- L. Close the MD_to_CPW database.
- M. To check to see if MegaDetector data successfully imported to Photo Warehouse, open Photo Warehouse, select the "View or Print a Report", and create a "Photo ID Summary" from the dropdown menu. Once the report is produced, check to see if MD1 and MD2 observers are listed as observers at the site(s) of interest for the date(s) of interest.
- N. Once you have successfully imported all photos and MegaDetector information you can create a photo module for photo ID. Go to "View Photos" from the main switchboard then use the filters on the right to determine which photos you would like to ID. You will first select "Photos that haven't been ID'd" in the "Species" section of filters to remove all the photos that MegaDetector determined there were no animals in. When you have selected the appropriate filters, click the "Copy Photos" button. Make sure to click the "Include Runtime Database" option and copy the photos to the appropriate external hard drive (you will probably get a security warning, but just hit "Open" numerous times and it will eventually work). It is important to keep a good organizational structure when saving modules and mirror structure across seasons (e.g., APR_Easton/Check1/Modules/22001_Check1). It is easiest to create and save modules first—then you can drag and drop modules to technician flash drives later. Use spreadsheet journal to stay organized and keep track of what modules have been created (example at bottom of document). See Figure 2A.7 for example screenshots of module file path for Easton Check1 modules and content example for the Easton Check1 Module for site 22001.

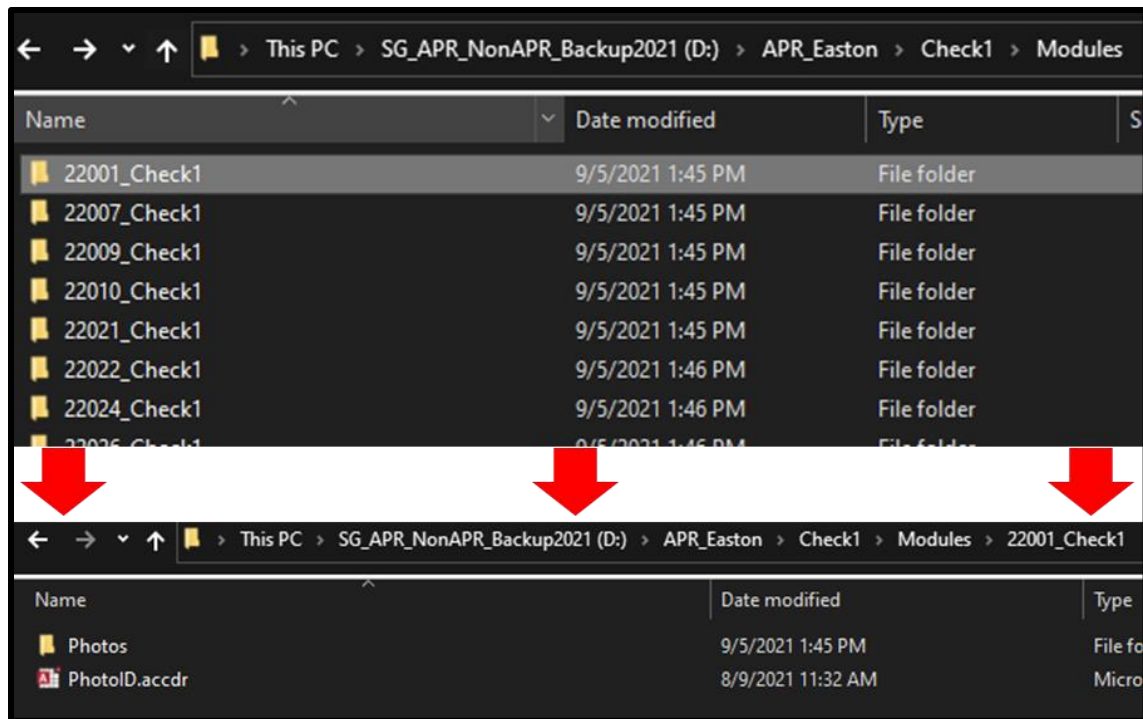


Figure 2A.7. Screenshots from the CPW Photo Warehouse workflow displaying the photo-module file path for Easton Check1 and the post-module creation content for the Easton Check1 module folder for site 22001.

- O. Distribute modules to technicians by copying entire module folders (e.g., 22001_Check1) to a flash drive (via drag and drop from external hard drives). Keep track of who has what modules in the designated spreadsheet journal (example at bottom of document) and keep it updated in real time (e.g., once you load 22001_Check1 on a flash drive for Technician A, immediately record it in the Excel document).
- P. Once technicians have finished their assigned modules, have them give you (the data manager) the flash drive back with many completed modules (.accdr files). Import the technician's modules when they are finished—this will allow you to import data slowly and steadily—and it can prevent both flash drives and work from being lost in the mix.
- Q. To import the IDs, choose the “Import Photo ID Module” option from Photo Warehouse’s main switchboard, then search for the .accdr file you would like to import. Once imported, Photo Warehouse will tell you how many IDs it imported and how many are pending (i.e., not verified with a second observer) and how many were verified (i.e., they match an observation already in the database). Again, keep track of who has sent you what modules and when you have imported them in the spreadsheet journal (example at bottom of document)—and make sure to update it in real time to prevent mistakes (e.g., once you import 22001_Check1 from Technician A’s flash drive, immediately record it in the Excel document).

- R. Often the two photo observers will disagree on an ID. These instances get flagged in Photo Warehouse and someone will need to be the referee (the photo referee should be consistent and should be someone with years of photo-tagging experience). Do this by choosing the “Compare IDs” box from the main switchboard. Choose your name from the dropdown menu and any photos that need to be compared will pop up. If you have many flagged photos, you can filter by location to break them into easier-to-handle chunks.
- View the photo and decide which species, detail and individual count is correct and click the “X” next to IDs that are incorrect. Sometimes all IDs will be correct (i.e., one observer saw a doe and one saw a doe and fawn, the fawn will display in red as it was only marked by one observer), in this case you would click the “Verify All Species” button. If you make a mistake and click the “X” on the wrong line you can click the “Reset” button and all IDs will pop back up.
 - You can use context clues to help you with refereeing by opening the original photo series and looking through surrounding photos. This can help when one observer notices a nose or piece of a leg in a photo that is easy to miss without the context of the deer popping into frame in the previous or next photo.
- S. Once your spreadsheet journal (see Figure 2A.8 for example) indicates all modules have been completed by 2 observers and uploaded, you will need to double check that everything is completed. It is likely that a few (or thousands) of photos will slip through the cracks and go untagged. To check, go to Photo Warehouse’s main switchboard and select “View Photos”. Next, use the species filter options to identify any photos that still need one or multiple observers. If photos still need to be reviewed, take note of the zone, township, date, and site. Next, you will need to share the entire module associated with the unreviewed photos, so the technician has all photos for reference. Repeat steps above to complete the process.

Zone	Township	Point	Access	Created	Sent 1	Sent 2	Received 1	Received 2	Complete	Notes
APR	Easton	22047	1 X	Jazmyn	Veronica	Jazmyn	Veronica	X		
APR	Easton	22047	2 X	Jazmyn	Rachel	Jazmyn	Rachel	X		
APR	Easton	22047	3 X	Jazmyn	Katie	Jazmyn	Katie	X		
APR	Easton	22047	4 X	Katie	Taylor	Katie	Taylor	X		
APR	Easton	22047	5 X	Amber						
APR	Easton	22047 ALL								

Figure 2A.8. Example of spreadsheet journal for tracking the creation and completion of modules by camera site (Point) and camera check number (Access), including the distribution (Sent) and successful upload of completed modules (Received) and record of technicians involved.

A Candid Assessment of the MegaDetector Workflow by S. Gurney

- MegaDetector is a free application and there is value in that. However, MegaDetector required a significant amount of time, energy, and resources to get up and running and to maintain over the years. It first required a test with a validated set of data to confirm MegaDetector's accuracy. It also required an experienced individual to be the main contact point for annual training and regular troubleshooting. Further, every season the technicians needed to set up multiple accounts and download various software packages, which can be a bit cumbersome. However, the MegaDetector approach did provide an educational opportunity for many individuals, including students.
- Once the data managers (i.e., MegaDetector operators) got up to speed, MegaDetector basically worked on its own and required little attention. However, problems would occasionally arise and require additional efforts and intervention (e.g., user mistakes, like using an improper naming convention for files or skipping steps).
- MegaDetector can take a considerably long time to review photos on a basic laptop. For example, it took approximately 30 seconds to review a single image. To put this in perspective, it would take about 35 days to run through 100,000 images. Note that we used up to four laptops at a time to speed up the process and to divide the workload among multiple employees. Given these long runtimes, it was often challenging to review photos throughout the field season (when we had a full team of technicians). More often than not, technicians were reviewing photos from weeks prior, and some camera issues went unnoticed for a while (e.g., poor field of view).

A better use of MegaDetector would probably be to run all photos at the end of a field season on a supercomputer (e.g., using university supercomputing resources), and then have a team of technicians manually review animal photos after the initial MegaDetector review. However, this approach would not allow technicians to review photos during the existing field season. On a side note, the technicians really enjoyed seeing images from the cameras they deployed and took much pride in the data they collected (rightfully so because it required a lot of hard work).

- We did not use MegaDetector during the first field season. It was nice having fewer moving parts on and having fewer technical issues. For some, it was brain-numbing work to review thousands of blank images manually, but technicians were able to do it faster than MegaDetector. For example, if there were 10,000 images of a weeping willow blowing in the wind it would take MegaDetector 3.5 days to review but it would only take a technician maybe an hour or two (as they were able to review blank image sets at a much higher rate than animal photos). However, it is likely that MegaDetector was more accurate when reviewing large blocks of these types of image sets because there is a possibility an animal was present at one point; and it would be easy for a technician to flip past it if they were losing their focus while reviewing images quickly.
- Field records indicated a pattern of vegetation movement or the interaction of solar radiation and shadow movement triggering cameras and resulting in excessive 'blank' photos. Although, it is worth noting that these phenomena would be dependent on the local conditions of a site. For example, more false-trigger events may occur when vegetation is growing or when there is a lack of canopy cover and an interaction between isolation and shadow movement. Also, many cameras were facing agricultural fields and crops (e.g., corn, beans) would trigger cameras.
- In this study, it may have been a better use of time and resources to not use MegaDetector.

Population Snapshots: Estimating Deer Relative Abundance with a Static Binomial N-Mixture Model

Steven M. Gurney

Supplemental research the antler-point-restriction study that took place in the Lower Peninsula of Michigan in an that included a known chronic-wasting-disease hotspot. This study includes preliminary results that were provided to Michigan Department of Natural Resources staff for presentation at the May 2023 meeting of the Natural Resources Commission (<https://www.michigan.gov/dnr/-/media/Project/Websites/dnr/Documents/Boards/NRC/2023/May-2023/APRs.pdf>).

SUMMARY

A static binomial N-mixture model informed by empirical count data produced deer abundance estimates that were highly variable among years. By modeling abundance one-year-at-a-time, the model was considered to make poor use of the available data. Further, the model was considered less than ideal for evaluating population-level changes over time. If a wildlife agency's goal is to compare snapshots among populations within a given year, then the static model is considered suitable. If an agency's goal is to evaluate population trends over time, I recommend using an alternative modeling approach better equipped to test linear relationships, like the year-stratified N-mixture model.

INTRODUCTION

Managing potential spread and localized prevalence of chronic wasting disease (CWD) has proven challenging for wildlife managers nationwide. Whereas some studies have shown that localized intensive harvest of deer has been successful at maintaining low prevalence of CWD (Manjerovic et al. 2014, Mateus-Pinilla et al. 2013), other research has established that different sex-and-age classes of free-ranging deer have different prevalence rates of disease (Gear et al. 2006, Miller and Conner 2005). Consequently, harvest strategies to reduce deer abundance may be more effective if specific demographic segments of the deer population are targeted as well. Unfortunately, detecting change in prevalence of CWD and determining causation for such a change is not feasible given sampling limitations and the multiple factors that can impact wild deer populations. However, it is possible to determine if antler point restrictions (APRs) in an area with CWD result in changes to those demographic segments that contribute the most to the spread and growth of CWD (Gear et al. 2006, Osnas et al. 2009, Heisey et al. 2010, Rees et al. 2012, Samuel and Storm 2016).

STUDY GOAL

The overall goal of this research is to evaluate the effect of an antler point regulation change in an area with chronic wasting disease on a white-tailed deer (*Odocoileus virginianus*) population.

OBJECTIVES

1. Estimate annual deer relative abundance from 2019–2022 for adult males, does, yearling males, and fawns under APR and Non-APR harvest treatments.
2. Evaluate and compare trends in relative abundance by sex-and-age-class for APR and Non-APR harvest-treatment areas.

STUDY AREA

This study uses data collected in the south-central Lower Peninsula of Michigan in a 5-county area (Newaygo, Kent, Mecosta, Montcalm, and Ionia County) that included a known chronic-wasting-disease hotspot (Kent and Montcalm County). That study included a robust before-after-control-impact study design paired with camera-trap surveys to monitor potential population-level changes, over 3 consecutive years (2020–2022), following the 2019 regulation change. This design was intended to make it possible to identify changes in abundance in the treatment area (APR Zone) relative to the control area (Non-APR Zone).

METHODS

Empirical data

This study used a high-volume of camera-trap images collected on public and private lands. A random camera-site-selection process resulted in a partnership with 160 landowners. Data included 2,644,590 verified images collected during the 4 field seasons (2019 to 2022). Of the photos reviewed by artificial intelligence software, 44% were characterized as “Empty” and did not require any further review by personnel. The dataset included a total of 1,118,757 verified images of deer. Count data associated with these images informed my abundance-estimation model here.

Abundance modeling

In this study, I used relative abundance of deer as an index, assuming it was functionally related to population size. When modeling abundance, I assumed site-level abundance reflected the number of deer within the effective sampling area surrounding a camera site (see Chapter 1 for details on effective sampling area). I used these site-level abundances to derive estimated abundance by township, where abundance related to the number of deer within the total area of all effective sampling areas in a specified township (18 sites per township = 22 km² [9 mi²]). Hence, my abundance estimates reflect relative abundance, not absolute, as I did not infer site-level abundances for areas beyond the total surveyed area (i.e., total effective sampling area). Given the incorporation of baseline data and the study’s focus on examining changes over time, the use of relative abundance as an index was considered adequate. To interpret the potential effects of harvest treatment on deer abundance, I compared 2019 baseline abundance estimates (i.e., the system before the APR implementation) to estimates from subsequent years (i.e., the system after the APR implementation).

To account for imperfect detection, I estimated population parameters with a closed N-mixture model (Royle 2004) applied to camera surveys of unmarked deer. As described by Kéry and Schaub (2012), I implemented a Bayesian hierarchical framework using software program JAGS (Plummer 2003) in program R (version 4.1.2; R Core Team 2021) with the jagsUI package (Kellner 2015). Essentially, the N-mixture model consists of two linked generalized linear models. The first generalized linear model is the ecological process. The ecological process yields the latent state and the spatial variation of abundance at site i , N_i , for a group of sites with a mean λ (Kéry and Schaub 2012). Since properly modeling error maximizes the utility of N-mixture models (Joseph et al. 2009), it was important to select a mixing distribution that best fit the underlying data. An exploratory data analysis was conducted using data from this study and included an evaluation of N-mixture models with alternative mixing distributions, including Poisson, zero-inflated Poisson, negative binomial, and Poisson lognormal. Results from those explorations indicated that the Poisson mixing distribution best fit the data. Using these results as guidance, I opted to use the Poisson distribution in my ecological-process model. To extract more information from the data and better allocate variance, I built on the ecological model to include township as a random effect on abundance, thus λ was described as $\mu\lambda$ (i.e., a distribution of distributions):

$$N_i \sim \text{Poisson}(\mu\lambda_i)$$

Agriculture was the most dominant land-cover class in the study area and is considered an important driver of demographic variation in abundance (Nixon et al. 1991, Nixon et al. 1994, Nixon et al. 2001) and antler growth (Felix et al. 2002). Further, exploratory data analyses identified agricultural cover as a valuable predictor of abundance. For these reasons, I included agriculture cover as a covariate in the ecological-process model. I calculated the proportion of agricultural cover using effective sampling areas and the National Land Cover Database (Dewitz and USGS 2021) land-cover classification layer (30-m² resolution) in ArcPro (ESRI 2020). This approach allowed me to extract values and collapse 3 NLCD land-cover types (herbaceous, hay/pasture, cultivated crops) into a single agriculture classification. I incorporated the effects of the agriculture covariate into the ecological model, associated with abundance through a log-link function, and described by a nonlinear relationship with percent agricultural cover as a site-specific covariate. Additionally, I included a random intercept κ into the log-link function, which allowed township to act as a random effect on abundance:

$$\log(\mu\lambda_i) = \kappa(\text{Township}_i) + \beta_2(\%Agriculture)^2$$

The second generalized linear model of the N-mixture framework is the observational process. The observational process yields the observed counts $y_{i,j}$ (given N_i) at site i and during replicate survey j , and are described by a binomial distribution with sample size N_i and detection probability p (Kéry and Schaub 2012):

$$y_{i,j} | N_i \sim \text{Binomial}(N_i, p[\text{Cover}_i])$$

Cover data were collected during camera-trap setup and was defined as far cover or the majority of cover in a 100-m radius of the camera (open or closed). Note that I included cover in the observational-process model as it may be important to both the presence and detectability components of detection probability. Further, an exploratory data analysis evaluated the value of alternative covariates and identified cover (far cover) as important to the detection process. To incorporate this covariate on detection probability, I used a logit-link function, described by a linear relationship with site-specific cover:

$$\text{logit}(p_i) = \alpha + \beta_1(\text{Cover}_i)$$

With regards to the Bayesian framework, I assumed vague prior distributions for all analyses to express the absence of prior information about estimated parameters. For my Markov Chain – Monte Carlo (MCMC) approach, I ran 3 parallel chains for 50,000 iterations, discarded the first 3,000 iterations as burn-in, and thinned the remaining iterations by 1 in 5, resulting in 28,200 draws of the posterior distribution for inference. Parameters monitored included total N , p , α , β values, and κ values. I monitored model convergence by evaluating posterior distributions, visual inspection of MCMC trace plots, and using the Gelman-Rubin convergence diagnostic ($\hat{R}$ or $\hat{R}^*$; Gelman 2006). I summed site-level abundances to derive an estimated total study-area abundance, where total abundance relates to the number of deer within the total area of all 1.24-km² effective sampling areas in the study area (e.g., 144 camera sites = 179 km² [69 mi²]). It is important to note that my total abundance estimates reflect relative abundance, not absolute. Since the larger study included baseline data, and intended to look at change over time, relative abundance was deemed sufficient.

I used the static N-mixture model to estimate relative abundance one-year-at-a-time and compare the number of significant changes detected in the APR and Non-APR townships. I modeled the abundance of sex-and-age classes individually (Legal Males, Does, Sub-legal Males, Fawns). I followed recommendations from an earlier data exploration and used data associated with a weekly sampling frequency (i.e., weekly counts), a 63-day sampling duration (15 July–15 September), and a camera distribution of 18 sites per township. I considered that non-overlapping credible intervals indicated significant differences in abundance between years. I counted and compared the number of significant differences observed in APR and Non-APR townships. When evaluating results, I considered comparisons of abundance estimates within townships from 2019 and subsequent years important, and comparisons among paired townships as most meaningful. Code for the static binomial N-mixture model is provided in the Appendix (APPENDIX 2B.1).

RESULTS

I used a static binomial N-mixture model to estimate relative abundance one-year-at-a-time and compare the number of significant changes detected in the APR and Non-APR townships. Relative to 2019 baseline estimates, I detected increases in Adult Male relative abundance in both APR and Non-APR zones (Figure 2B.1). Most increases in Adult Male abundance were detected in the APR Zone and included Township A (2019: $\bar{x}$ = 22.3 [95% BCI = 17–30]; 2021: $\bar{x}$ = 44.0 [95% BCI = 34–57]), Township B (2019: $\bar{x}$ = 28.0 [95% BCI = 21–37]; 2021: $\bar{x}$ = 53.7 [95% BCI = 41–70]), and Township D (2019: $\bar{x}$ = 28.4 [95% BCI = 22–37]; 2021: $\bar{x}$ = 61.7 [95% BCI = 47–81]; Figure 2B.1). In comparison, I detected a single increase in Adult Male abundance in the Non-APR Zone's A Township (2019: $\bar{x}$ = 11.4 [95% BCI = 8–16]; 2021: $\bar{x}$ = 25.1 [95% BCI = 19–34]; Figure 2B.1).

I detected significant increases in Doe abundance in both the APR and Non-APR zones (Figure 2B.2). Relative to 2019 baseline estimates, most increases in Doe abundance were detected in the Non-APR Zone and included Township B (2019: $\bar{x}$ = 29.4 [95% BCI = 26–34]; 2021: $\bar{x}$ = 43.8 [95% BCI = 39–51]; 2022: $\bar{x}$ = 39.3 [95% BCI = 35–45]) and Township C (2019: $\bar{x}$ = 46.5 [95% BCI = 42–53]; 2021: $\bar{x}$ = 67.0 [95% BCI = 59–78]; Figure 2B.2). Relative to its corresponding baseline estimate in 2019, I detected a single increase in Doe abundance in the

APR Zone's D Township (2019: $\bar{x} = 48.6$ [95% BCI = 44–55]; 2021: $\bar{x} = 68.5$ [95% BCI = 59–80]; Figure 2B.2).

I also detected significant increases in Yearling Male abundance in both the APR and Non-APR zones (Figure 2B.3). Relative to 2019 baseline estimates, most increases in Yearling Male abundance were detected in the Non-APR Zone and included Township A (2019: $\bar{x} = 19.5$ [95% BCI = 16–24]; 2021: $\bar{x} = 32.5$ [95% BCI = 26–41]; 2022: $\bar{x} = 38.2$ [95% BCI = 31–47]), Township B (2019: $\bar{x} = 15.2$ [95% BCI = 12–19]; 2022: $\bar{x} = 25.1$ [95% BCI = 20–31]), and Township D (2019: $\bar{x} = 20.4$ [95% BCI = 17–25]; 2022: $\bar{x} = 43.1$ [95% BCI = 36–52]; Figure 2B.3). In contrast, I detected increases in Yearling Male abundance in 2 of the APR townships, including Township A (2019: $\bar{x} = 21.7$ [95% BCI = 17–27]; 2022: $\bar{x} = 37.7$ [95% BCI = 31–46]) and Township D (2019: $\bar{x} = 31.9$ [95% BCI = 26–39]; 2021: $\bar{x} = 54.2$ [95% BCI = 44–69]; 2022: $\bar{x} = 48.3$ [95% BCI = 40–58]; Figure 2B.3). I failed to detect any significant changes in Fawn abundance in APR or Non-APR zones (Figure 2B.4).

DISCUSSION

It is important to note that the inferences drawn from these results are weak, as the static N-mixture model was considered poorly equipped to address the objectives of this study. I investigated changes in deer abundance over 3 consecutive years and found relative abundance of Adult Males increased in most areas with the APR treatment. In control and treatment areas, I detected no decreases in the relative abundance of Does. Further, I found no evidence that APRs facilitated reductions in overall deer abundance. Most significant increases in Doe abundance were detected in Non-APR Zone townships. Most increases in Yearling Male abundance were detected in the Non-APR Zone. I failed to detect any significant changes in Fawn abundance in APR or Non-APR townships.

Fitting a static N-mixture model to data from each year separately was a simple way to accommodate the open population structure that arose from sampling multiple years in this study (Kéry and Royle 2021). The static N-mixture model provided me with valuable insights (and provided a foundation for future modeling efforts), but there was a lot of noise around the relative abundance estimates. In other words, there was a notable degree of inconsistency in estimates across years. These variable fluctuations were likely the result of unaccounted for spatiotemporal differences in the data (e.g., heterogeneity in detection probability). The noise around estimates made it difficult to identify trends and interpret results. The simplistic static-model approach led to highly parameterized models (e.g., T of each parameter in the model), resulting in statistical inefficiencies (Kéry and Royle 2021). Model development is an iterative undertaking, exemplified by my initial use of this framework here.

A more suitable approach for handling the multiple-year data structure would be to fit all the T years jointly using a year-stratified framework (Kéry and Royle 2021). The year-stratified N-mixture model is a class of hierarchical models for open populations (i.e., populations subject to change over time via addition or subtraction of individuals) that can be used to estimate trends or covariate effects, when dynamics are not of interest (Kéry and Royle 2021). For example, the effect of harvest treatment, year, and the interaction of the two. By analyzing the entire dataset in a model where every parameter is year-specific, it allows the user to impose explicit constraints on the parameters and to share parameters among the datasets (Kéry and Royle 2021). This approach is like fitting T separate static models, except

with the data pooled into a single dataset (also referred to as stacking the data) and analyzed jointly (Kéry and Royle 2021). Stacking successive years of data yields distinct site-year combinations, enabling the estimation of abundance based on these combinations. This approach also satisfies the model's closure assumption, which denotes closure during survey periods and openness between them.

By modeling abundance one-year-at-a-time, the static binomial N-mixture model was considered to make poor use of the available data. Further, the model was considered less than ideal for evaluating population-level changes over time. Although there are applications for this closed-population model, I did not consider it appropriate for this study—based on model limitations and the objectives of the state wildlife agency. If a wildlife agency's goal is to compare snapshots among populations within a given year, then the static model is considered suitable. If an agency's goal is to evaluate population trends over time, I recommend using an alternative modeling approach better equipped to test linear relationships, like the year-stratified N-mixture model.

FIGURES

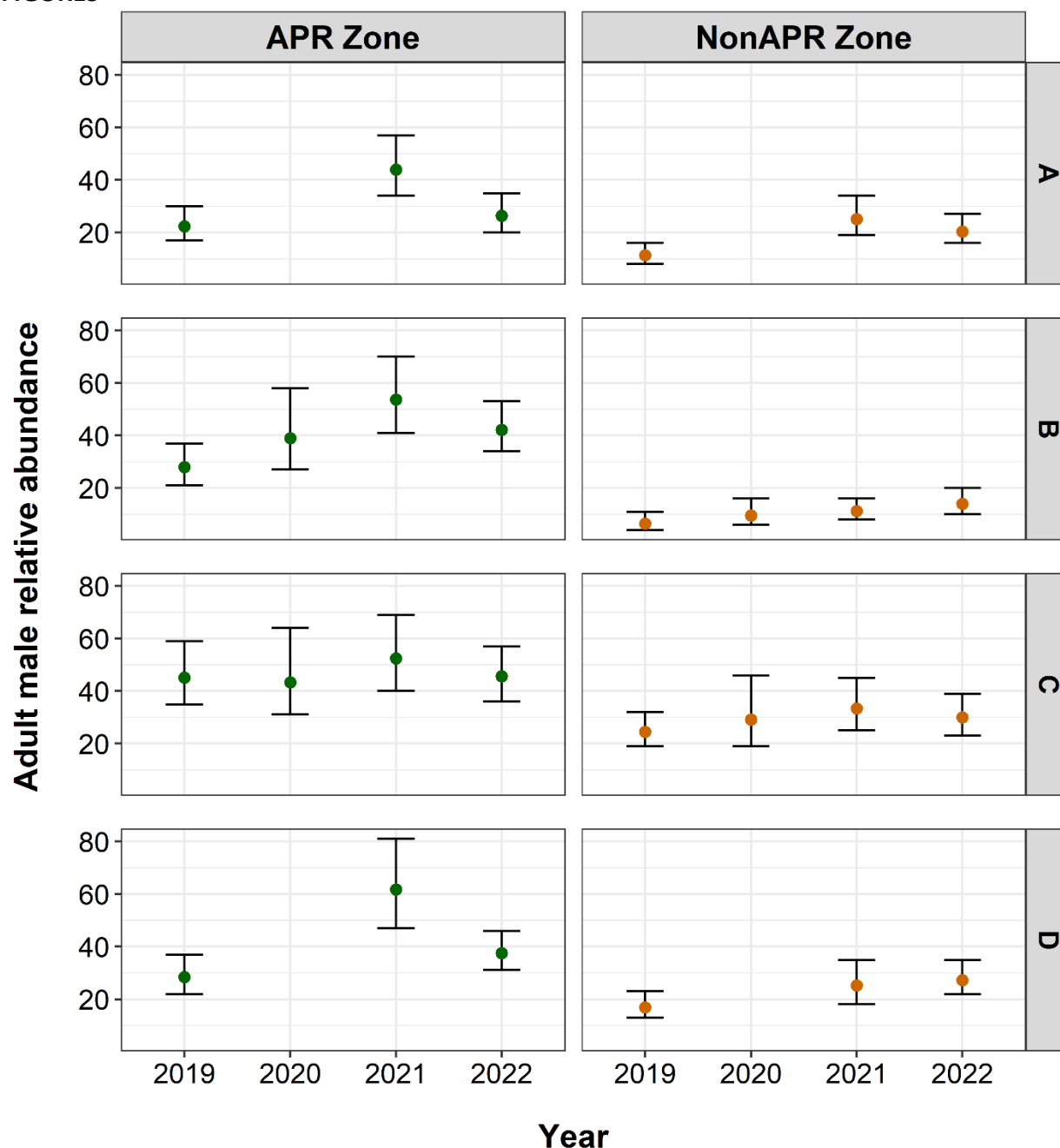


Figure 2B.1. Pre-harvest relative abundance estimates of adult male white-tailed deer (*Odocoileus virginianus*) in the south-central Lower Peninsula of Michigan, USA, 2019–2022. Estimates were produced using a static binomial N-mixture model. Beginning in 2019, antlered deer harvest was limited by a 4-point antler point restriction (APR) in the APR Zone and not in the Non-APR Zone (experimental area and control area, respectively). Zones are displayed in the grid columns and township pairs (Twp A, B, C, and D) in the grid rows. Error bars indicate 95% Bayesian credible intervals. Only half of the townships were surveyed in 2020 due to pandemic-related constraints. Relative to baseline estimates in 2019, we detected significant increases in abundance in both the APR Zone (Twp A, B, and D 2021) and Non-APR Zone (Twp A 2021).

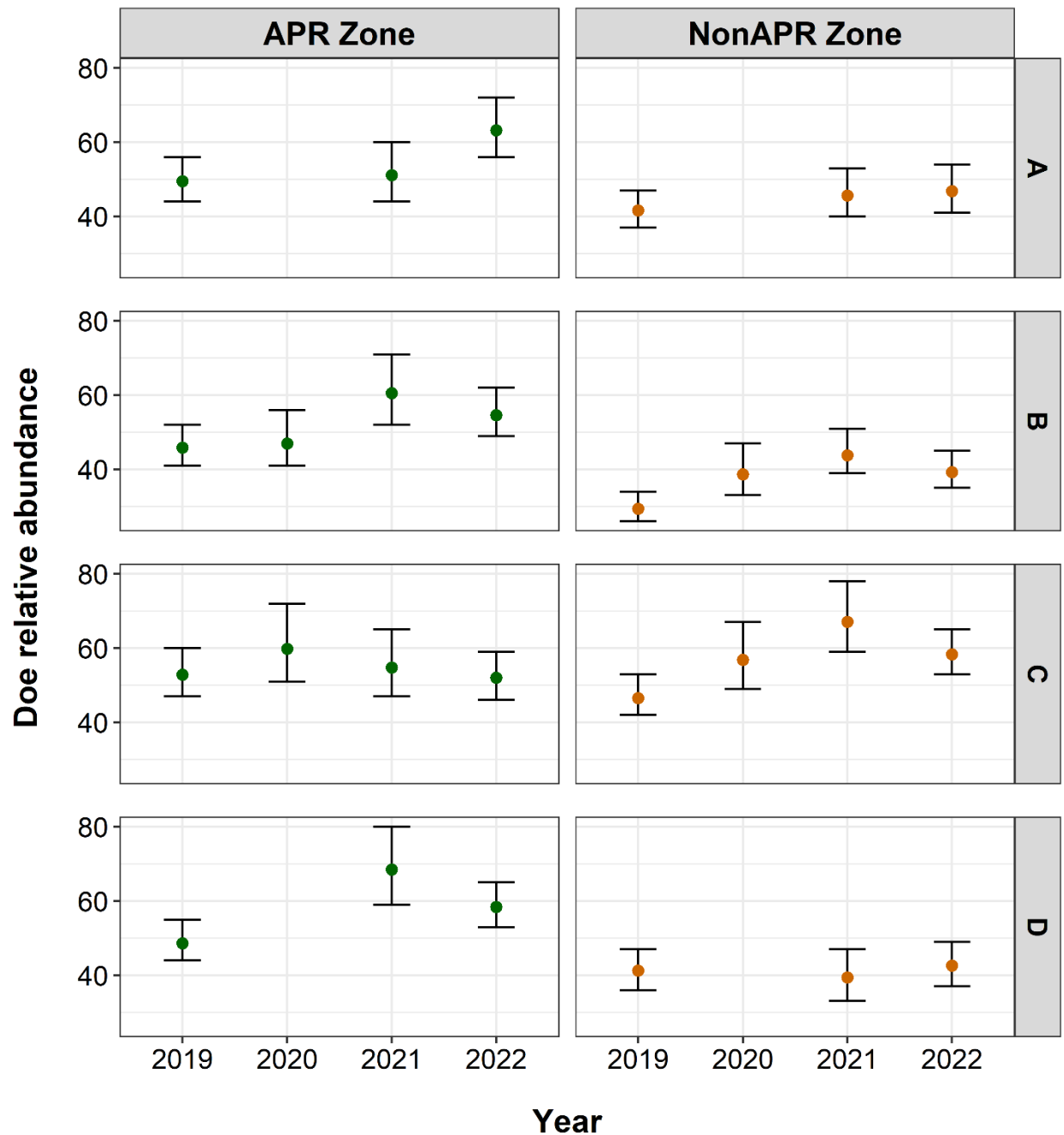


Figure 2B.2. Pre-harvest relative abundance estimates of female (yearlings and adults, i.e., does) white-tailed deer (*Odocoileus virginianus*) in the south-central Lower Peninsula of Michigan, USA, 2019–2022. Estimates were produced using a static binomial N-mixture model. Beginning in 2019, antlered deer harvest was limited by a 4-point antler point restriction (APR) in the APR Zone and not in the Non-APR Zone (experimental area and control area, respectively). Zones are displayed in the grid columns and township pairs (Twp A, B, C, and D) in the grid rows. Error bars indicate 95% Bayesian credible intervals. Only half of the townships were surveyed in 2020 due to pandemic-related constraints. Relative to baseline estimates in 2019, we detected significant increases in abundance in both the APR Zone (Twp D 2021) and Non-APR Zone (Twp B 2021 and 2022, Twp C 2021).

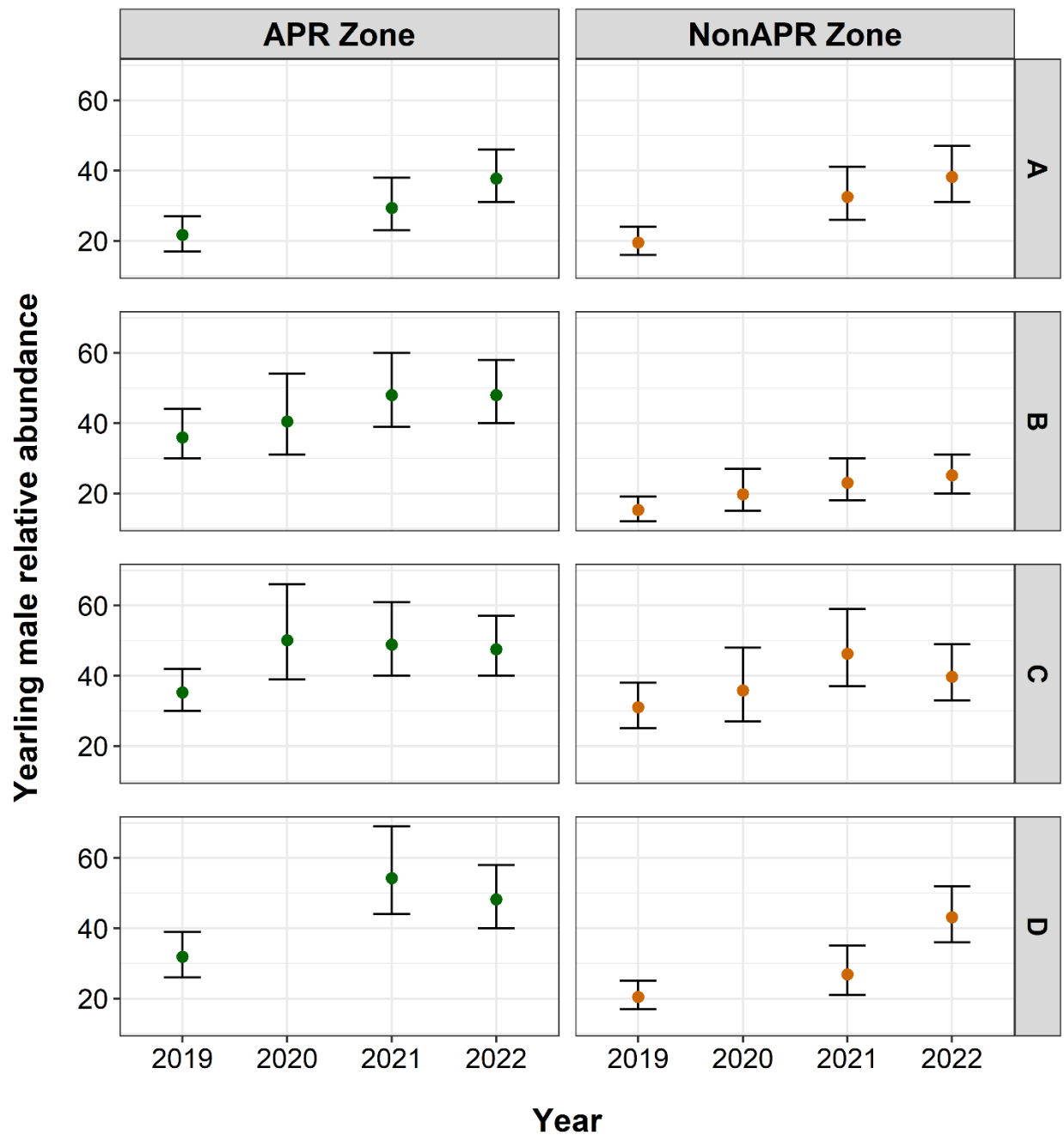


Figure 2B.3. Pre-harvest relative abundance estimates of yearling male white-tailed deer (*Odocoileus virginianus*) in the south-central Lower Peninsula of Michigan, USA, 2019–2022. Estimates were produced using a static binomial N-mixture model. Beginning in 2019, antlered deer harvest was limited by a 4-point antler point restriction (APR) in the APR Zone and not in the Non-APR Zone (experimental area and control area, respectively). Zones are displayed in the grid columns and township pairs (Twp A, B, C, and D) in the grid rows. Error bars indicate 95% Bayesian credible intervals. Only half of the townships were surveyed in 2020 due to pandemic-related constraints. Relative to baseline estimates in 2019, we detected significant increases in abundance in both the APR Zone (Twp A 2022, Twp D 2021 and 2022) and Non-APR Zone (Twp A 2021 and 2022, Twp B 2022, Twp D 2022).

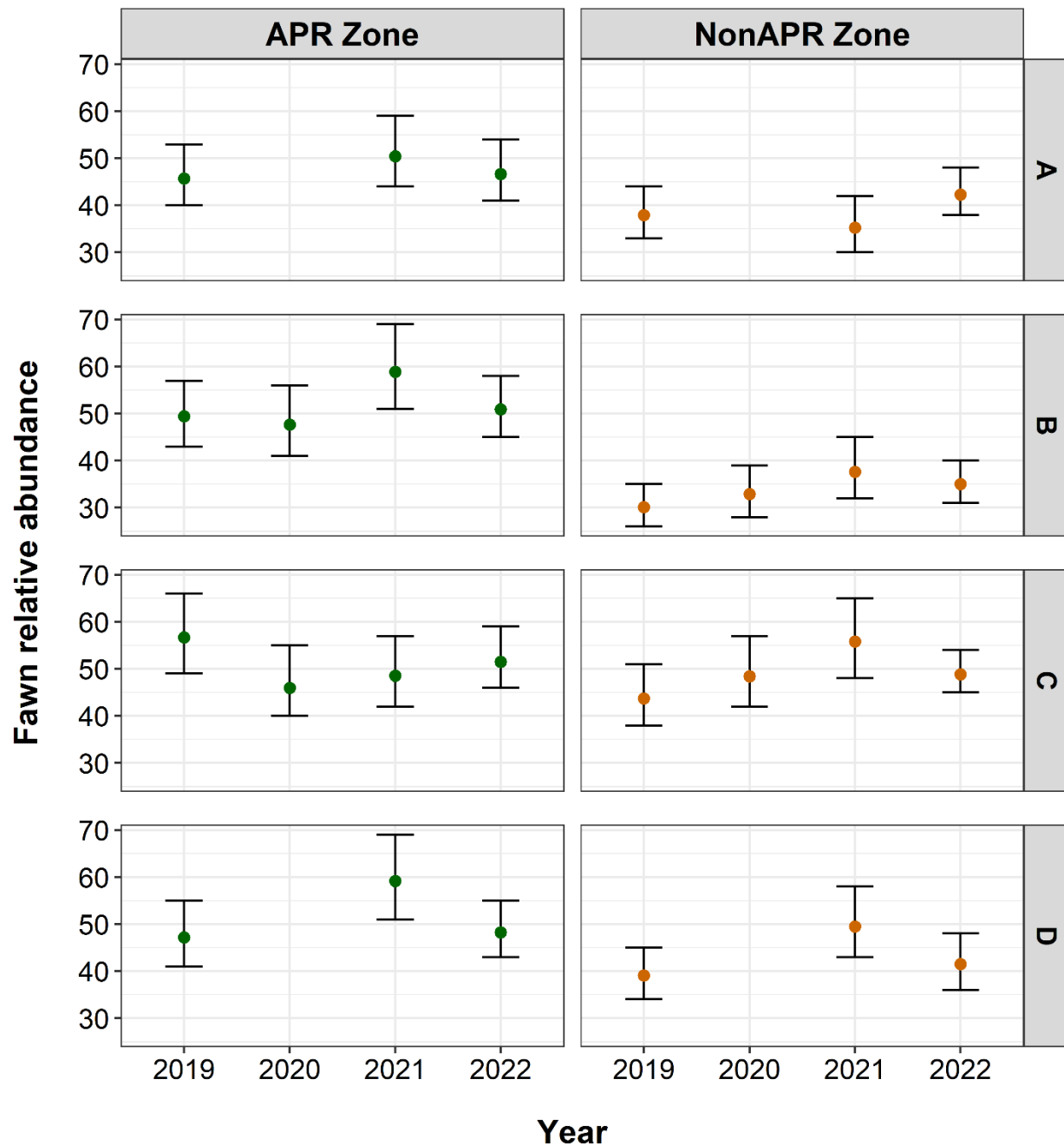


Figure 2B.4. Pre-harvest relative abundance estimates of fawn white-tailed deer (*Odocoileus virginianus*) in the south-central Lower Peninsula of Michigan, USA, 2019–2022. Estimates were produced using a static binomial N-mixture model. Beginning in 2019, antlered deer harvest was limited by a 4-point antler point restriction (APR) in the APR Zone and not in the Non-APR Zone (experimental area and control area, respectively). Zones are displayed in the grid columns and township pairs (Twp A, B, C, and D) in the grid rows. Error bars indicate 95% Bayesian credible intervals. Only half of the townships were surveyed in 2020 due to pandemic-related constraints. Relative to baseline estimates in 2019, we failed to detect any significant changes in abundance.

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APPENDIX 2B.1: CODE FOR MODELING ABUNDANCE WITH A STATIC BINOMIAL N-MIXTURE MODEL

```
nmix <- function(twn.final, cov.table){
  #Cover (open or closed) covariate on detection process
  #Percent agriculture covariate on abundance process
  #Township as random effect on abundance process

  #Data
  max <- ncol(twn.final)
  y <- twn.final[,2:max]
  NewCover <- cov.table$LandCoverNew #Open or closed cover covariate
    on detection
  AgCover <- cov.table$AgCover #%agriculture covariate on abundance

  #Create group ID for townships; requires all 18 sites in 4 townships
    (8 in other years)
  twn <- sort(rep(1:8, 18))

  #Load JAGS package
  library("jagsUI")

  #Specify model in JAGS language
  sink("model.txt")
  cat("
  model {
  # Priors
  alpha ~ dnorm(0,0.25)
  beta1 ~ dnorm(0,0.25)
  beta4 ~ dnorm(0,0.25)
  beta5 ~ dnorm(0,0.25)
  mu.kappa ~ dnorm(0,0.25)
  sigma.kappa ~ dexp(1)

  # Likelihood
  # Biological model for true abundance
  for (i in 1:R) { # Sites
    N[i] ~ dpois(mu.lambda[i])
    log(mu.lambda[i]) <- kappa[twn[i]] + (beta4 * AgCover[i]) + (beta5
    * pow(AgCover[i],2))
```

```

# Observation model for replicated counts
for (j in 1:T) { #count reps
  y[i,j] ~ dbin(p[i], N[i])
} #j
logit(p[i]) <- alpha + (beta1 * NewCover[i])
} #i

for (k in 1:8) { # Townships for random effect on lambda, hard coded
  for 8 townships
    kappa[k] ~ dnorm(mu.kappa, tau.kappa)
}

# Derived quantities
tau.kappa <- pow(sigma.kappa,-2)

totalN <- sum(N[])

# Relies on input data (rows) being sorted by site (LocationName)
shermanN <- sum(N[1:18])
tyronN <- sum(N[19:36])
bowneN <- sum(N[37:54])
nelsonN <- sum(N[55:72])
sheridanN <- sum(N[73:90])
eastonN <- sum(N[91:108])
bushnellN <- sum(N[109:126])
douglasN <- sum(N[127:144]) # 144 camera sites

}
",fill = TRUE)
sink()

#Bundle data
win.data <- list(y = y, R = nrow(y), T = ncol(y[, ,1]), NewCover =
  as.integer(NewCover), AgCover = as.numeric(scale(AgCover)), twN =
  twN)

#Initial values
Nst <- apply(y, 1, max, na.rm = TRUE) + 1 # This line is important

```

```

inits <- function() list(N = Nst)

#Parameters monitored
params <- c("alpha", "beta1", "beta4", "beta5", "mu.kappa",
  "sigma.kappa", "kappa", "p", "totalN", "shermanN", "tyronN",
  "bowneN", "nelsonN", "sheridanN", "eastonN", "bushnellN",
  "douglasN")

# MCMC settings
ni <- 50000
nt <- 5
nb <- 3000
nc <- 3

# Call JAGS from R (BRT 0.1 min)
out <-<- jags(win.data, inits, params, "model.txt", n.chains = nc,
  n.thin = nt, n.iter = ni, n.burnin = nb)
}

```


APPENDIX 2C: CODE FOR YEAR-STRATIFIED N-MIXTURE MODEL

```
# Load package
library(nimble)

# Create constants for model from array
constants <- list(
  nyear = dim(legal_all)[[3]],
  nsite = nsite,
  nreps = dim(legal_all)[[2]],
  trt = trt,
  twn = twn
)

# Bundle data (counts and covariates)
data <- list(
  y = legal_all,
  #trt = trt,
  year = yr,
  ag = ag,
  cover = cover
)

code <- nimbleCode({
  alpha0 ~ dnorm(0, sd = 2)
  alpha1 ~ dnorm(0, sd = 2)

# Standard deviation among site x year combos for the residual error
epsilon, given an exponential prior since it must be positive.
  sd_epsilon ~ dexp(1)

# Use similar approach for lambda.
  sd_epsilon_lambda ~ dexp(1)

# Intercept and slope for year are vectors of length 2 (1 for each
treatment). So, we have beta1, beta2, beta3, & beta4.
  for( i in 1:2){
    beta1[i] ~ dnorm(0, sd = 2)
    beta2[i] ~ dnorm(0, sd = 2)
  }

  for( i in 1:8) {
    epsilon_lambda[i] ~ dnorm(0, sd = sd_epsilon_lambda)
  }
```

```

beta3 ~ dnorm(0, sd = 2)
beta4 ~ dnorm(0, sd = 2)

for( t in 1:nyear ) {

  # loop through only the sites that are surveyed in a given year.
  for( i in 1:nsite[t] ){

    N[i, t] ~ dpois( lambda[ i, t ] )

    # Indexing here
    # We are still treating treatment as a fixed effect
    # but instead of doing the multiply by 0 or 1 hack, we index the
    intercept and slope of year by trt
    # this will "level the playing field" so the two treatments will
    have similar uncertainty. Basically, we extract the current value from
    the "trt" matrix to tell the model which of the two beta1 and beta2s
    to use.

    log( lambda[i, t] ) <- beta1[trt[i,t]] + beta2[trt[i, t]] *
    year[i, t] + beta3 * ag[i,t] + beta4 * ag[i, t] * ag[i, t] +
    epsilon_lambda[tn[i, t]]

    # adding site x year random effect (epsilon) for detection
    probability
    logit( p[i, t] ) <- alpha0 + alpha1 * cover[i, t] + epsilon[i,
    t]

    # epsilon is modeled as a residual - a draw from a zero-mean
    normal distribution
    # we let the model estimate the standard deviation
    epsilon[i, t] ~ dnorm(0, sd = sd_epsilon)

    for( j in 1:nreps ){
      y[i, j, t] ~ dbin( p[i, t], N[i, t] )
    }
  }
}

```

```

}))

# Initial values
Nst <- apply( data$y, c(1, 3), max, na.rm = TRUE)

Nst[Nst == -Inf] <- 0

Nst <- Nst + 1 # This line is important

yst <- data$y

yst[is.na(yst)] <- round( mean( data$y, na.rm = TRUE) )

inits <- function(){
  list(
    alpha0 = rnorm(1, 0, 0.5),
    alpha1 = rnorm(1, 0, 0.5),
    # important
    # beta1 and beta2 get 2 initial values (not 1) since we are
indexing by treatment. Given the indexing structure, initial values
are provided a little differently.
    beta1 = rnorm(2, 0, 0.5),
    beta2 = rnorm(2, 0, 0.5),
    beta3 = rnorm(1, 0, 0.5),
    beta4 = rnorm(1, 0, 0.5),
    N = Nst,
    y = yst,

    # don't forget to provide initial values for epsilon and
sd_epsilon
    epsilon = array( rnorm( constants$nsite[1] * constants$nyear, 0,
0.5),
                    dim = c(constants$nsite[1], constants$nyear)),
    sd_epsilon = rexp(1, 1),
    sd_epsilon_lambda = rexp(1, 1),
    epsilon_lambda = rnorm(8, 0, 0.25)
  )
}

# Good to track sd_epsilon
# to ensure convergence and to get an idea of how much among-site
variation in p there is
params <- c("alpha0", "alpha1", "beta1", "beta2", "beta3", "beta4",
"sd_epsilon", "sd_epsilon_lambda", "N")

```

```
out <- nimbleMCMC(  
  monitors = params,  
  code = code,  
  data = data,  
  constants = constants,  
  inits = inits(),  
  niter = 50000,  
  nburnin = 3000,  
  thin = 5,  
  nchains = 3  
)
```

APPENDIX 2D: CODE FOR MARGINAL EFFECTS AND CHANGE IN ABUNDANCE

```
# Load packages
library(tidyverse)
library(MCMCvis)

#Wrangle betas from the posterior.
legal.betas <- MCMCpstr( out, params = c("beta1"), type =
"chains")[[1]] |>
  as_tibble(rownames = "param") |>
  #Here's a way to avoid hardcoding the number of columns, if you
change the number of iterations.
  pivot_longer(starts_with("V")) |>
  mutate( param = str_remove(param, "beta1")) |>
  mutate( trt = parse_number(param),
          iter = parse_number(name)) |>
  add_column(param_name = "beta1") |>
  dplyr::select(param = param_name, trt, iter, value) |>

#That was all for the intercept, now join up the coefficient for
year.
full_join(
  MCMCpstr( out, params = c("beta2"), type = "chains")[[1]] |>
    as_tibble(rownames = "param") |>
    pivot_longer(starts_with("V")) |>
    mutate( param = str_remove(param, "beta2")) |>
    mutate( trt = parse_number(param),
            iter = parse_number(name)) |>
    add_column(param_name = "beta2") |>
    dplyr::select(param = param_name, trt, iter, value)
)

#Create list of year names to replace standardized years used in
model.
yr_names <- c( 2019, 2020, 2021, 2022)

#Create keys for easier interpretation.
yr_key <- tibble(yr = unique(data$year)[1,], year = yr_names)
trt_key <- tibble( trt_name = c("Non-APR", "APR"),
                  trt = c(1, 2))

#Create dataframe listing the townships and which treatment category
each is in
twm <- tibble(
  twm = 1:8,
```

```

trt = c(rep(1, 4), rep(2, 4))

#Create dataframe with one column with the unique year values (scaled
values)
yr <- tibble(yr = unique(data$year)[1,])

#Merge them together so that you have twm x trt x year combinations
legal.pred_df <- as_tibble( merge( twm, yr, by = NULL))

#Abundance table for treatment and years (i.e., zone estimates)
legal.df <- full_join( legal.betas, legal.pred_df) |>
  as_tibble() |>
  pivot_wider(names_from = param, values_from = value) |>
  mutate( lambda = exp( beta1 + beta2 * yr )) |>
  group_by(twm, trt, yr) |>
  summarise(
    mean = mean(lambda),
    l95 = quantile(lambda, c(0.025)),
    u95 = quantile(lambda, c(0.975))) |>
  full_join(yr_key) |>
  full_join(trt_key)

#Reformat beta data frame.
legal.betas <- legal.betas |>
  pivot_wider(names_from = param, values_from = value)

#Create object for epsilon_lambda estimates (incorporating random
effect by township).
legal.epsilons <- MCMCpstr( out, params = c("epsilon_lambda"), type =
"chains")[[1]] |>
  as_tibble(rownames = "twm") |>
  pivot_longer(starts_with("V")) |>
  mutate( twm = parse_number(twm),
    iter = parse_number(name)) |>
  dplyr::select(-name)

#Create table for plotting marginal effects. "Value" corresponds to
epsilon_lambda estimates.
legal.me <- full_join(legal.betas, legal.epsilons) |>
  right_join(legal.pred_df) |>
  mutate( lambda = exp( beta1 + beta2 * yr + value)) |>
  full_join(yr_key) |>
  dplyr::select( twm, trt, year, iter, lambda) |>
  group_by(twm, trt, year) |>
  summarise( mean = mean(lambda),
    l95 = quantile(lambda, c(0.025)),

```

```

        u95 = quantile(lambda, c(0.975))) |>
full_join(yr_key) |>
full_join(trt_key)

#Save for marginal effects plot.
write.csv(legal.me, "legal.twn.me.csv", row.names = FALSE)

#Create a new table for calculating difference (i.e., the 2019 - 2022
change)
legal.diff <- full_join(legal.betas, legal.epsilons) |>
  right_join(legal.pred_df) |>
  mutate( lambda = exp( beta1 + beta2 * yr + value)) |>
  full_join(yr_key) |>
  dplyr::select( twn, trt, year, iter, lambda) |>
  pivot_wider(names_from = year, values_from = lambda) |>
  mutate(diff = `2022` - `2019`) |>
  group_by(twn, trt) |>
  summarise( mean = mean(diff),
            l95 = quantile(diff, c(0.025)),
            u95 = quantile(diff, c(0.975))) |>
  full_join(trt_key)

#Save for plotting
write.csv(legal.diff, "legal.twn.diff.csv", row.names = FALSE)

```

APPENDIX 2E: MEGADETECTOR ACCURACY

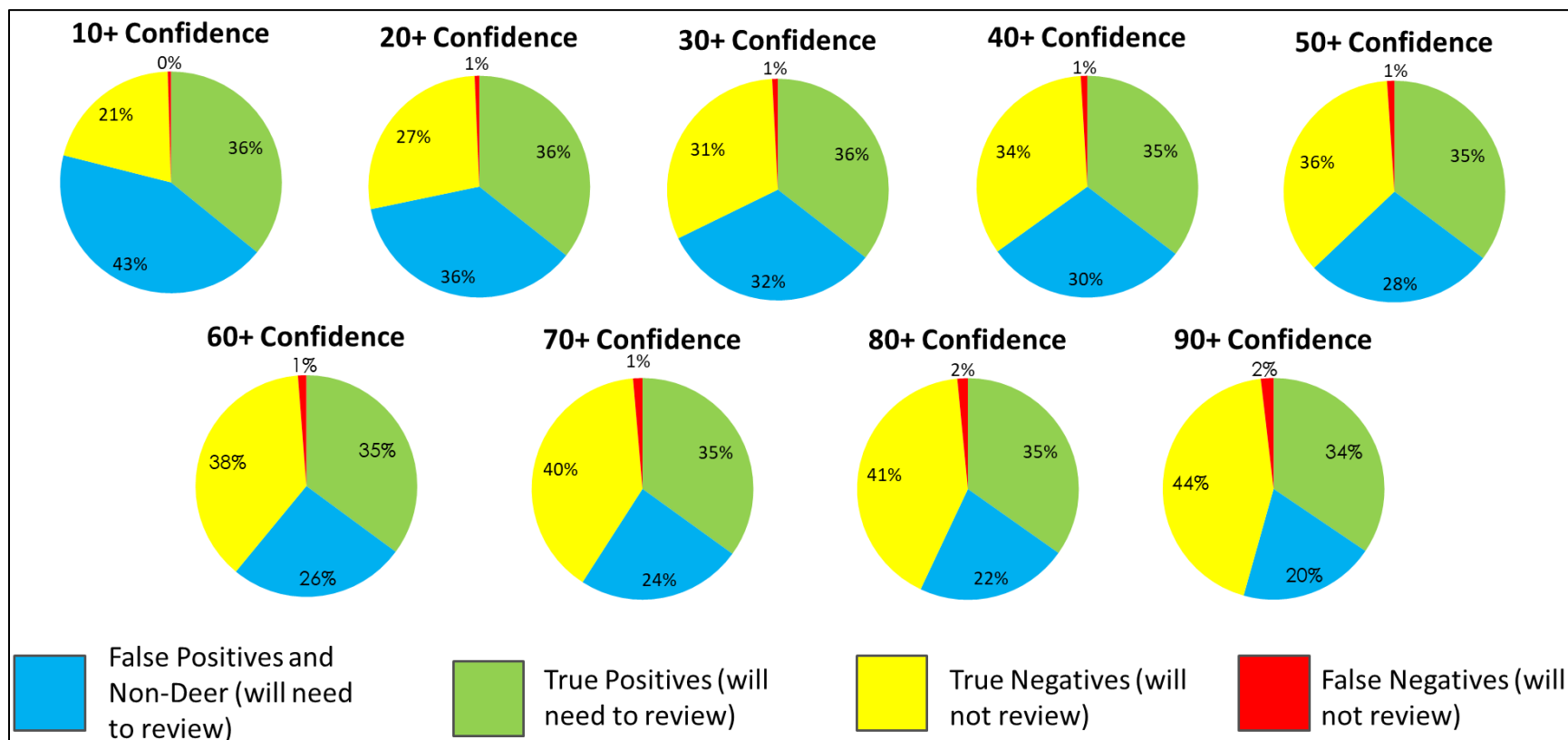


Figure 2E.1. Pie charts showing MegaDetector, a machine-learning model, accuracy for detecting deer when using alternative confidence-threshold settings (10+ to 90+) for general classification of camera-trap images (presence or absence of animal). Analysis conducted by S. Mayhew of the Michigan Department of Natural Resources using a subset of 52,232 validated photos. A 90+ confidence threshold was selected for its ability to minimize the number of irrelevant images needing manual review while having little effect on false-negative deer images. Figures created by S. Mayhew and revised by S. Gurney.

APPENDIX 2F: MICHIGAN DEER-HARVEST TRENDS

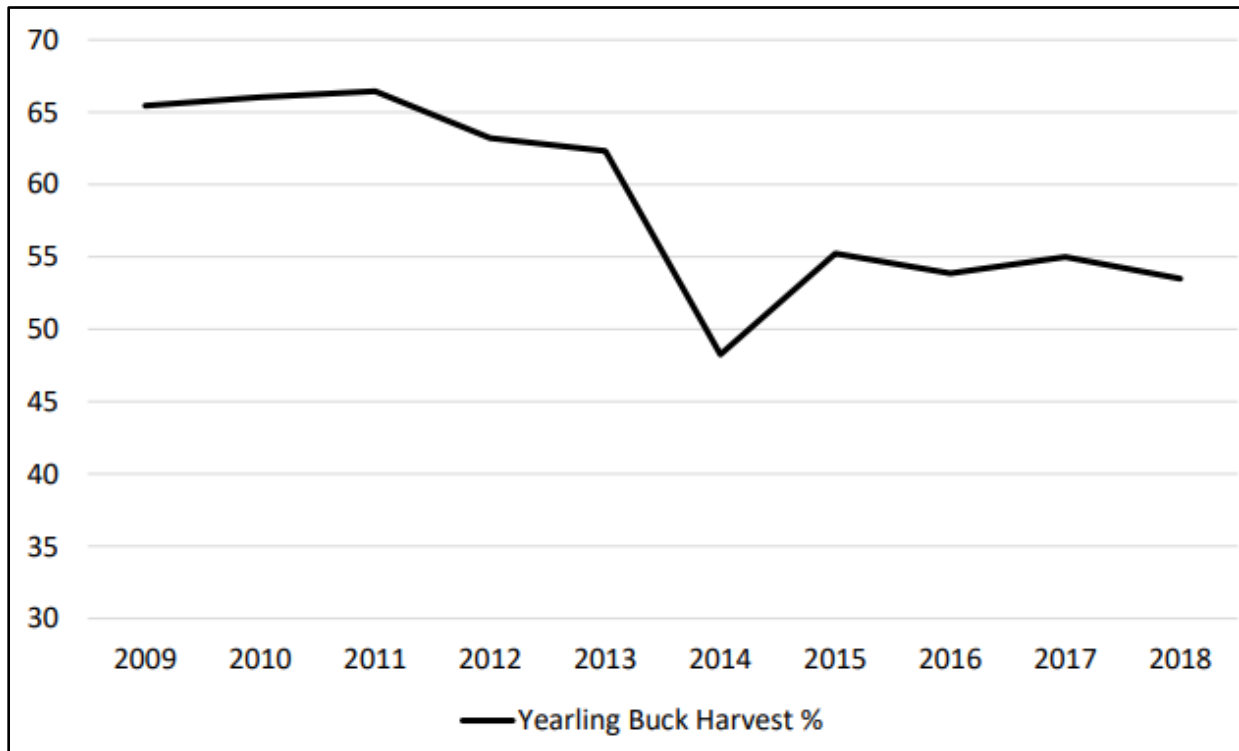


Figure 2F.1. 2009–2018 trends in yearling-male harvest in the south-central Lower Peninsula of Michigan in a 5-county study area (Newaygo, Kent, Mecosta, Montcalm, and Ionia County) that included a known chronic-wasting-disease hotspot (Kent and Montcalm County). Data provided by MDNR deer check station data. These data show a steady decline in the proportion of yearling males in the annual harvest, declining over 10% from 2009–2018. Figure and analysis done by the Michigan Department of Natural Resources. These data below were presented by C. Stewart of the Michigan Department of Natural Resources (MDNR) at the May 2019 meeting of the Natural Resources Commission (https://www.michigan.gov/dnr/-/media/Project/Websites/dnr/Documents/WLD/Deer/apr_field_study_summary_and_presentation.pdf).

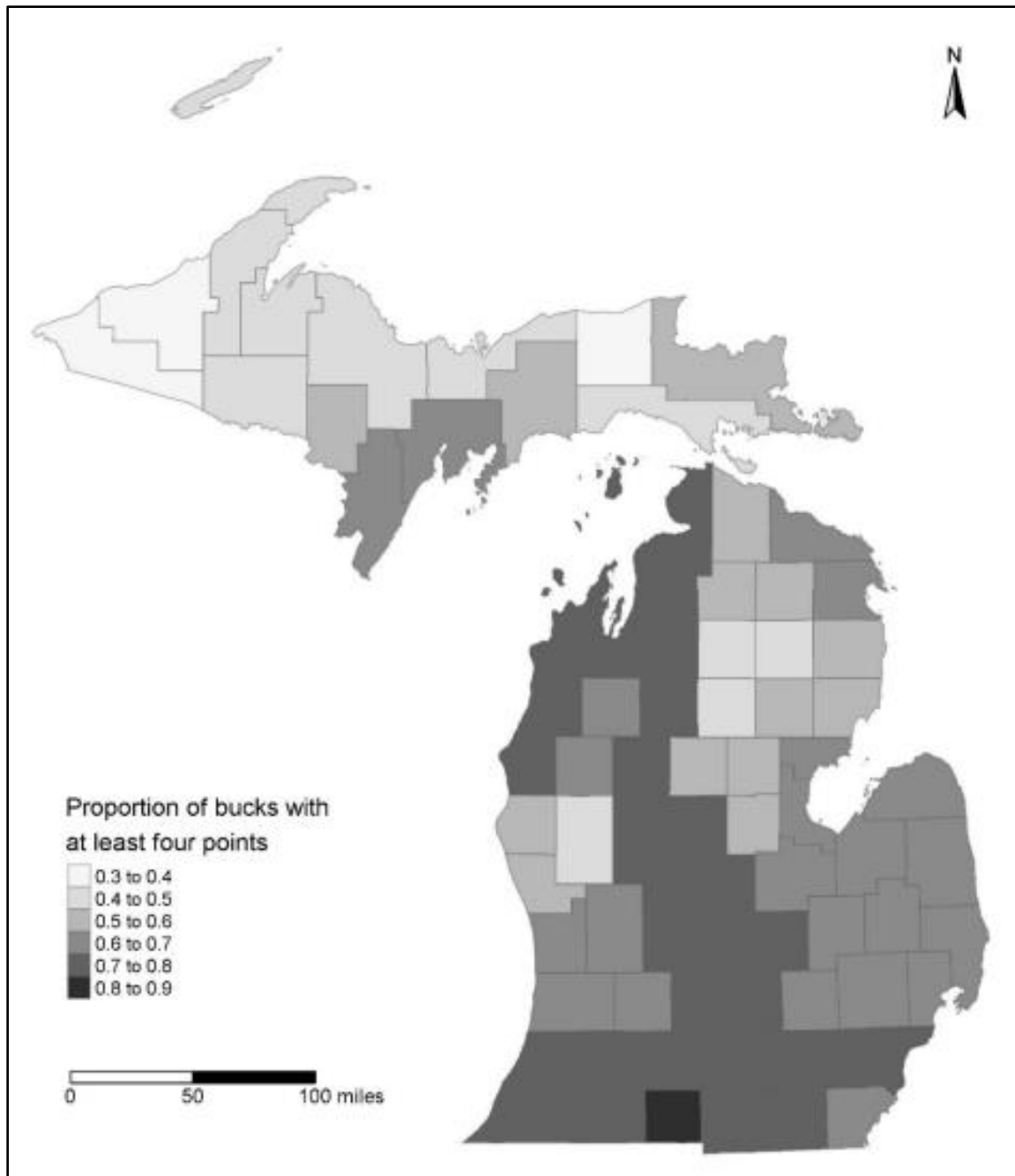


Figure 2F.2. Michigan map showing the proportion of antlered deer harvested in 2022 that had at least 4 antler points on one side. Counties are displayed in different shades of gray depending on harvest results. The analysis and map were conducted and created by the Michigan Department of Natural Resources. These data were presented by C. Stewart of the Michigan Department of Natural Resources (MDNR) at the May 2023 meeting of the Natural Resources Commission (https://www.michigan.gov/dnr/-/media/Project/Websites/dnr/Documents/Boards/NRC/2023/May-2023/Deer_Regulations.pdf).

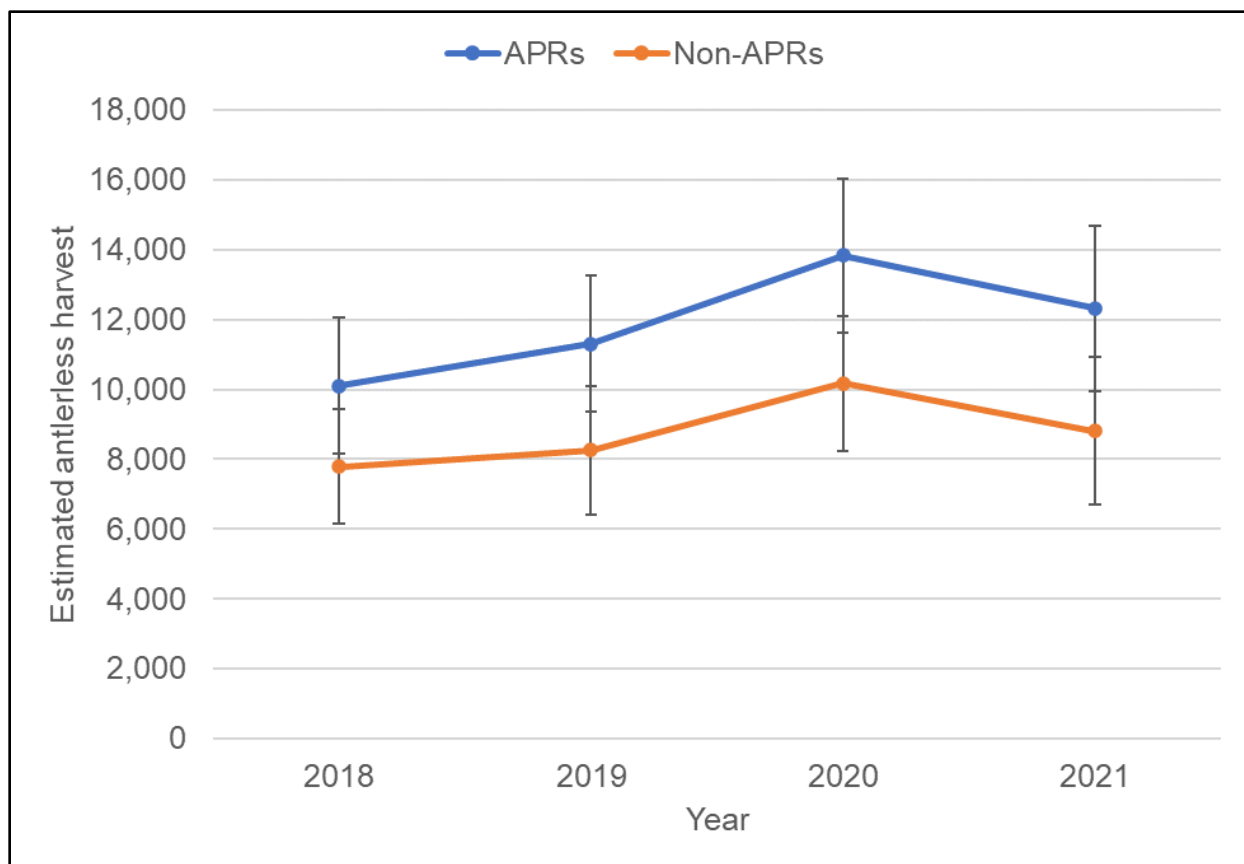


Figure 2F.3. Estimated antlerless deer harvest in counties with antler point restrictions (APRs) and counties without antler point restrictions (Non-APRs) in a 5-county study area, MI, 2018–2021. APR counties included Mecosta, Montcalm, and Ionia County. Non-APR counties included Newaygo and Kent County. Antlerless deer were defined as deer without antlers and deer with antlers <7.62 cm (3 inches) in length. Error bars indicate 95% confidence intervals. Overlapping confidence intervals indicated that antlerless harvest was similar between APR and Non-APR counties during the 2018–2021 deer harvest seasons. Harvest analysis and graph conducted and provided by B. Frawley of the Michigan Department of Natural Resources.

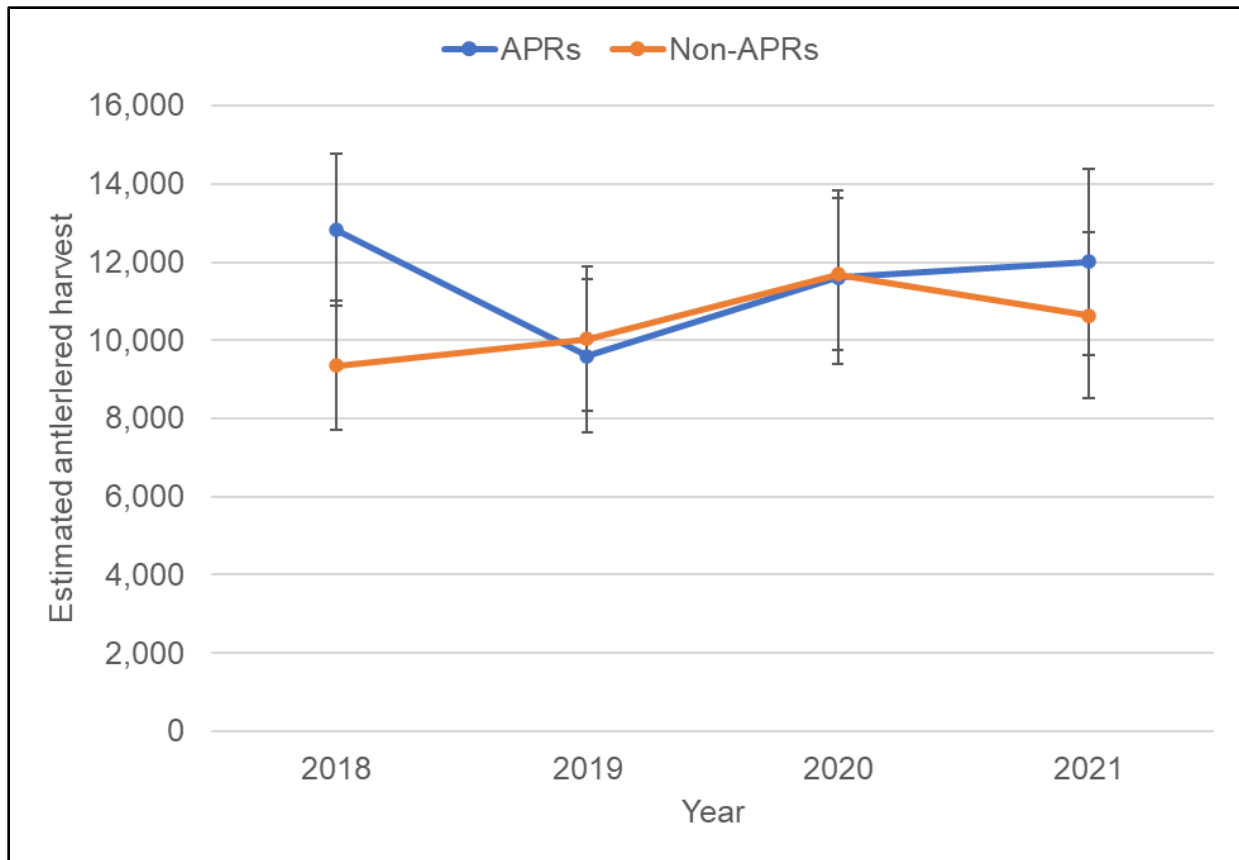


Figure 2F.4. Estimated antlered deer harvest in counties with antler point restrictions (APRs) and counties without antler point restrictions (Non-APRs) in a 5-county study area, MI, 2018–2021. APR counties included Mecosta, Montcalm, and Ionia County. Non-APR counties included Newaygo and Kent County. Antlered deer were defined as deer with at least one antler measuring ≥ 7.62 cm (3 inches) in length. Error bars indicate 95% confidence intervals. Overlapping confidence intervals indicated antlered harvest was similar between APR and Non-APR counties during the 2018–2021 deer harvest seasons. Harvest analysis and graph conducted and provided by B. Frawley of the Michigan Department of Natural Resources.

Linking Antler Point Restrictions to CWD Spread and Growth: An Agent-Based Modeling Approach with Empirical Data

Steven Gurney, Sonja Christensen, Melissa Nichols, Chad Stewart, Sarah Mayhew, Marjorie Liberati, and Dwayne Etter.

Presented at the 4th Annual International Chronic Wasting Disease Conference, June 2023.

SUMMARY

Agent-based models informed by empirical population estimates show harvest regulations play an important role in CWD dynamics, with higher outbreak severity observed under antler point restrictions than without. If a wildlife agency's goal is to reduce the potential severity of an outbreak in a naive population, we recommend harvest strategies that include targeting all age classes of antlered deer.

INTRODUCTION

Wildlife management agencies have limited information on how deer harvest regulations affect deer populations. Chronic wasting disease (CWD) transmission rates are related to sex-and-age composition (Miller and Conner 2005, Gear et al. 2006), thus sex- and age-based harvest regulations could have implications for CWD dynamics. Antler point restrictions (APRs) have become an increasingly popular regulatory action to limit the harvest of younger male deer. However, there is limited information on the realized effect of APRs on sex-age cohort abundance, and by extension, potential outcomes for CWD spread and growth. Agent-based models (ABMs) can simulate disease and population parameters and are useful for understanding emerging properties from complex systems (Belsare and Stewart 2020, Kjær and Schaubert 2022). Though, these models may be improved with validated data from field studies of existing deer populations.

STUDY GOAL

Use empirical white-tailed deer (*Odocoileus virginianus*; hereafter, deer) population estimates with varying harvest-regulation treatment to simulate and investigate CWD spread and growth.

OBJECTIVES

1. Modify an existing ABM to simulate deer populations that reflect empirical population estimates.
2. Evaluate potential CWD spread and growth under APR and Non-APR harvest study treatments.

STUDY AREA

Our ABM simulations were specific to Montcalm County, Michigan (a known CWD hotspot) and included empirical data from the south-central Lower Peninsula of Michigan. These empirical data were associated with a 5-county study area (Newaygo, Kent, Mecosta, Montcalm, and Ionia County; Figure 2G.1).

METHODS

Agent-based modeling framework

We used a published, agent-based modeling framework (OvCWD; Belsare and Stewart 2020) to simulate deer populations and CWD spread and growth under APR and NonAPR harvest treatments (Figure 2G.2). The main components of OvCWD included the landscape, the agents (individual deer), and the decision-making rules and procedures (e.g., deer behavior, CWD transmission; Figure 2G.2). Deer are added to the landscape based on forest-cover data and user-defined deer density. The rules and procedures are the core of the ABM and govern both population and disease dynamics. The OvCWD framework we used comprised of two ABMs adapted to simulate Michigan's deer populations, MIOvPOP (**M**ichigan **O**docoileus **v**irginianus **P**OPulation simulation model; Belsare 2019b) and MIOvCWDdy (**M**ichigan **O**docoileus **v**irginianus **C**hronic **W**asting **D**isease **d**ynamics model; Belsare 2019a). This two-part agent-based modeling framework (OvCWD) was coded in the high-level language NetLogo (version 6.2.2; Wilensky 1999).

Informing model with empirical data

To simulate deer populations, we informed the ABM with data from a Michigan study (S. Gurney, unpublished data) that estimated sex-and-age composition of deer populations in APR and NonAPR treatment areas (townships). In the APR area, antlered deer with at least four points on one antler beam could be harvested with a valid license (a legal point was defined as ≥ 2.54 cm [1 inch] long as measured from its tip to the nearest edge of antler beam). In the Non-APR area, any antlered deer with an antler measuring ≥ 7.62 cm (3 inches) in length could be taken. Given the ABM operated on a county scale, we used township-level data as a proxy for county-level simulations. We used estimated proportions of adults in the antlered class for APR and NonAPR treatment areas, which assumed adult males met the APR criteria and yearlings did not (S. Gurney, Michigan State University, unpublished data; Table 2G.1). From these data, we selected the highest and lowest estimated proportions of adults in the antlered class and then adjusted the ABM's yearling-male harvest rates to produce these values.

Simulations and output evaluated

We simulated APR and NonAPR harvest scenarios independent of one another using the OvCWD modeling framework. We used a stabilized (lambda or population growth rate approximates 1) 10-year population snapshot produced by MIOvPOP, with desired adult-male proportions at year 10, to initialize MIOvCWDdy for CWD simulations. We set each CWD simulation to run for a duration of 25 years and replicated simulations 100 times with model stochasticity. For each simulation, we introduced CWD to a naive system (i.e., no prior disease) via a single dispersing yearling male. We used ABM output to first evaluate the 25-year outbreak probability for each harvest scenario. We characterized an outbreak as a simulation

that resulted in true CWD prevalence (total cases/total deer) ≥ 0.01 at the end of a 25-year simulation. We counted the total number of outbreaks per 100 simulations and divided it by 100 to determine outbreak probability. We plotted outbreak probabilities to visualize results and compare between treatments. To quantify the severity of these outbreaks, we evaluated additional model output including the total number of CWD cases, total CWD area (mi²), and true CWD prevalence at the end of 25-year simulations. Note that total CWD area is reported in mi² to reflect measurement units most used by U.S. wildlife agencies. We summarized outbreak-severity metrics by calculating means from each set of 100 simulations and determined means differed between treatment groups if 95% confidence intervals did not overlap.

RESULTS

We found that estimated proportions of adults in the antlered class varied by APR and Non-APR treatment, with the highest proportion estimated in an APR area (0.49) and lowest in a Non-APR area (0.35; Table 2G.1). We adapted the ABM to reflect these extreme values and found that outbreak probability was comparable between the APR harvest scenario (0.25) and the Non-APR scenario (0.27; Figure 2G.3). Mean number of CWD cases was ~1.6 times higher in the APR scenario ($\bar{x} = 5,410$; 95% CI: 4,535 – 6,284) than the NonAPR scenario ($\bar{x} = 3,480$; 95% CI: 2,828 – 4,132; Figure 2G.4). Mean CWD area was ~1.5 times higher in the APR scenario ($\bar{x} = 1,399$ sq. mi; 95% CI: 1,196 – 1,602 sq. mi) than the NonAPR scenario ($\bar{x} = 930$ sq. mi; 95% CI: 762 – 1,097 sq. mi; Figure 2G.4). Mean CWD prevalence was ~1.6 times higher in the APR scenario ($\bar{x} = 0.11$; 95% CI: 0.09 – 0.14) than the NonAPR scenario ($\bar{x} = 0.07$; 95% CI: 0.05 – 0.08; Figure 2G.4).

DISCUSSION

We found composition of males played an important role in CWD dynamics, and consequently CWD dynamics varied by APR and Non-APR harvest treatments. We found that the proportion of adult males in the antlered class were consistently higher in APR areas compared to Non-APR areas (Table 2G.1). These results suggest that APRs successfully help advance the age structure of antlered deer by limiting harvest of yearling males. Interestingly, the highest proportion of adult males observed in the Non-APR areas was higher than the lowest proportion observed in the APR areas. This is simply an observation, but it does allude to APRs having a different magnitude of effect in different landscape types (e.g., township types) or for the potential for hunters to be practicing non-mandatory APRs in a Non-APR area.

When adapting the ABM to reflect our selected proportions of adult males in the antlered class (highest and lowest proportions), it required us to substantially adjust OvCWD's yearling-male harvest rates. These harvest rates (APR = 0.50; Non-APR = 0.72) were approximately 0.18 – 0.25 higher compared to the harvest rates used by Belsare and Stewart (2020; APR = 0.32; Non-APR = 0.47). These large increases suggest that it requires high levels of yearling harvest to affect population-level changes in the age composition of antlered deer. These results may also suggest potentially limited understanding of the population prior to our study.

Our outbreak probabilities for APR and Non-APR scenarios (APR = 0.25; NonAPR = 0.27; Figure 2G.3) were both more similar to one another and overall lower compared to Belsare and Stewart's (2020) findings (APR = 0.45; Non-APR = 0.37). Our lower outbreak probabilities were

likely driven by our higher harvest rates of yearling males. Replicating our 100-year stochastic simulations could help determine if outbreak probabilities are statistically similar or different between our APR and Non-APR scenarios. At the end of our 25-year simulations, we found that CWD outbreaks were more severe in the APR scenario than the Non-APR scenario. In our APR scenario, the mean number of CWD cases, mean CWD area, and mean CWD prevalence were all > 1.5 times higher than the Non-APR scenario (Figure 2G.4). These results suggest that protecting yearling males from harvest can be counterproductive to CWD-management efforts.

If a wildlife agency's goal is to reduce the potential severity of an outbreak in a naive population, we recommend harvest strategies that include targeting all age classes of antlered deer. Several other model-based studies have reached comparable conclusions, proposing strategies like targeting the harvest of antlered deer (without distinguishing among age classes) or intensifying the harvest of yearling males, to mitigate CWD prevalence or lower the likelihood of CWD outbreaks (Potapov et al. 2016, Belsare and Stewart 2020). The *OvCWD* framework is a unique adaptive management tool that allows users to customize and update the models (Belsare and Stewart 2020), as highlighted in this study. Models like *OvCWD* are invaluable because they can improve our ability to infer unobservable disease processes and improve understanding of disease transmission and our capacity to predict disease dynamics. Future studies should continue to integrate new data and update the ABM's assumptions based on current best knowledge of the system.

TABLES

Table 2G.1. Estimated proportions of adult males in the antlered class of white-tailed deer (*Odocoileus virginianus*) harvest treatment (APR, Non-APR) and township pairing (A–D) in the south-central Lower Peninsula of Michigan, USA, 2022 (S. Gurney, unpublished data). The antler point restriction (APR) harvest treatment limited antlered harvest to deer with ≥ 4 antler points on at least one antler beam. Under the Non-APR harvest treatment, deer with at least one antler measuring ≥ 7.62 cm (3 inches) in length could be taken with an antlered license. Antlered deer were assumed to be adults if they met the APR criteria, otherwise they were assumed to be yearlings.

Township	APR harvest treatment	Non-APR harvest treatment
A	0.41	0.35
B	0.47	0.36
C	0.49	0.43
D	0.44	0.39

FIGURES

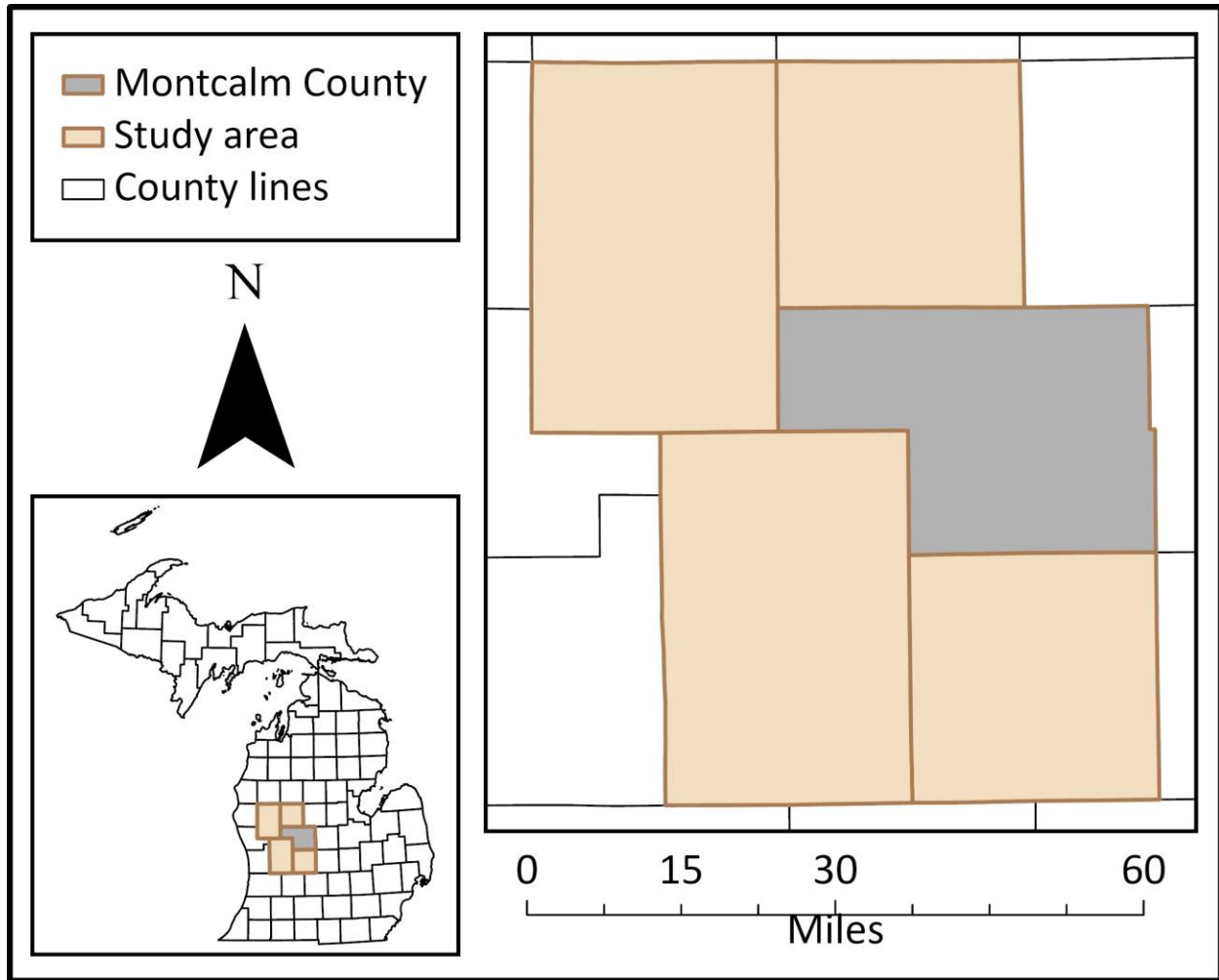


Figure 2G.1. Study area in the south-central Lower Peninsula of Michigan, USA, in a designated 5-county area. Mandatory antler point restrictions (APRs) were implemented in the eastern 3 counties. Agent-based modeling was used to simulate chronic wasting disease spread and growth under alternative deer harvest scenarios in Montcalm County (a known CWD hotspot). Maps created in ArcGIS Pro (version 2.7.1; www.esri.com).

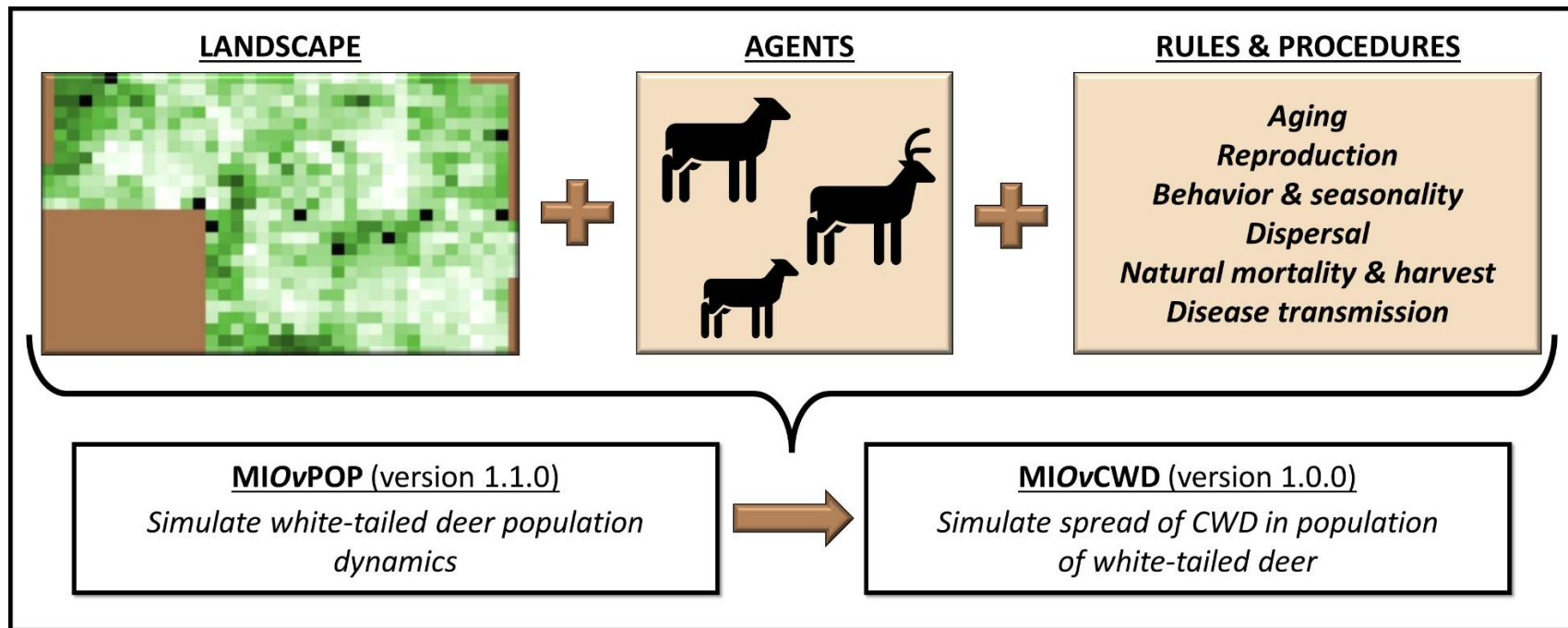


Figure 2G.2. Conceptual diagram of the *OvCWD* agent-based modeling framework (Belsare and Stewart 2020) used to evaluate chronic wasting disease (CWD) spread and growth in a white-tailed deer (*Odocoileus virginianus*) population under alternative deer harvest scenarios. The main components of the ABM include the landscape, the agents (i.e., individual deer), and the decision-making rules and procedures (e.g., deer behavior, transmission of CWD). Deer are added to the landscape based on forest-cover data and user-defined deer density. The rules and procedures are the core of the model and govern both population and disease dynamics. This 2-part ABM (Belsare 2019a, 2019b) was coded in NetLogo (version 6.2.2; Wilensky 1999).

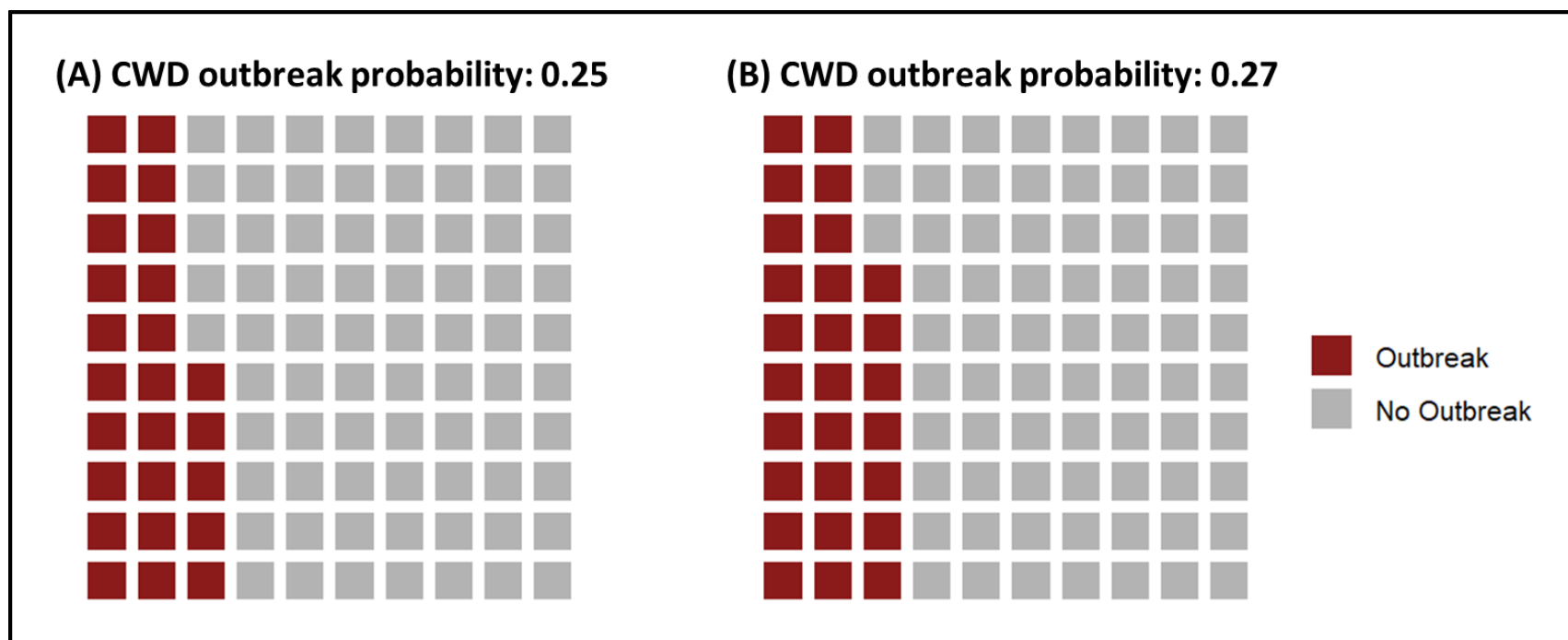


Figure 2G.3. Waffle plots illustrating model-derived CWD outbreak probabilities for two white-tailed deer (*Odocoileus virginianus*) harvest scenarios in Montcalm County, MI, USA. Harvest scenarios include (A) NonAPR and (B) antler point restrictions (APRs). Each square represents one model iteration and red squares indicate iterations that resulted in a chronic wasting disease outbreak at the end of a 25-year simulation. OvCWD, an agent-based modeling framework (Belsare and Stewart 2020), was used for all simulations. Modeling efforts incorporated data from field studies of existing deer populations with APR and NonAPR harvest treatments (S. Gurney, unpublished data). Outbreak probabilities were considered similar between APR and NonAPR harvest scenarios.

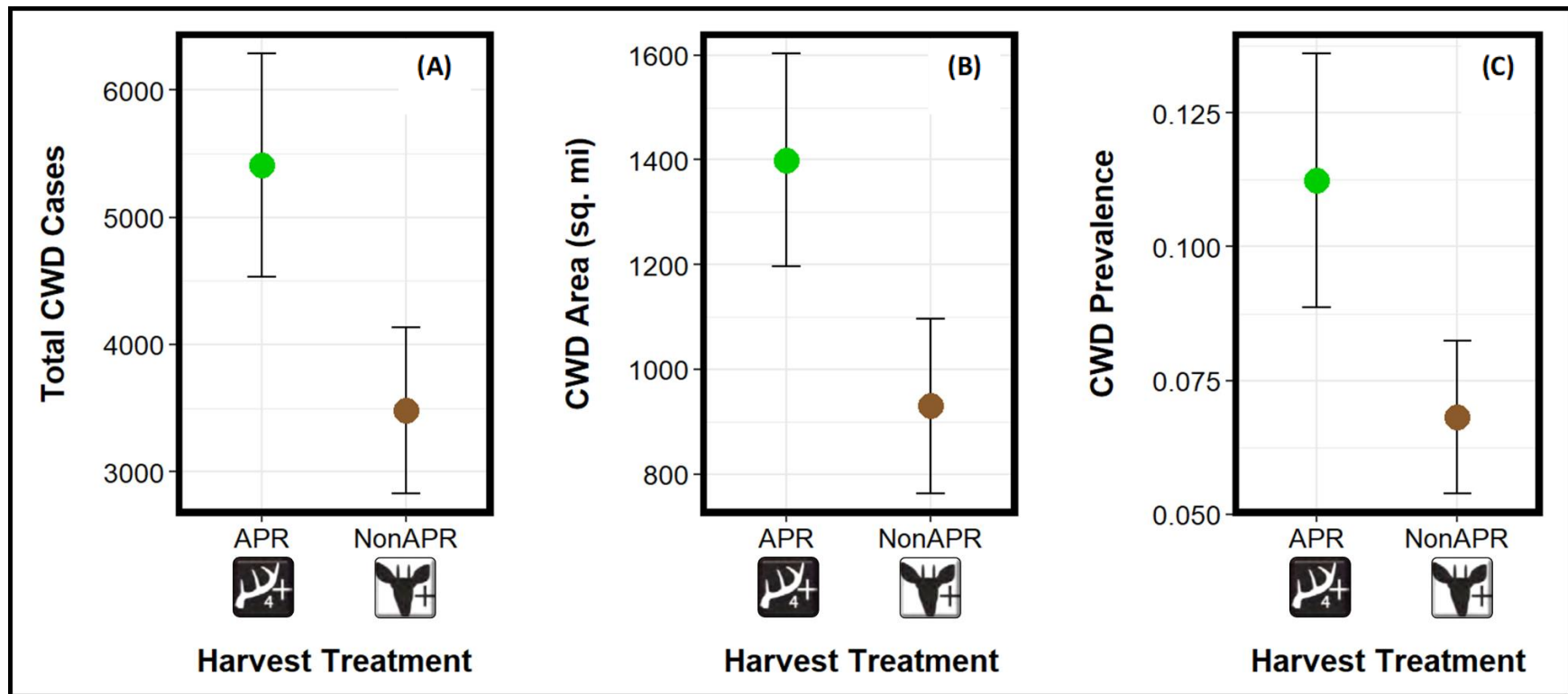


Figure 2G.4. Model-derived estimates for (A) total number of chronic wasting disease (CWD) cases, (B) total CWD area, and (C) true CWD prevalence for antler point restriction (APR) and NonAPR harvest scenarios in Montcalm County, Michigan, USA. Estimates were derived from 25-year simulations using the *OvCWD* agent-based modeling framework (Belsare and Stewart 2020). Modeling efforts incorporated data from field studies of existing deer populations with APR and NonAPR harvest treatments (S. Gurney, unpublished data). Plotted values are means and error bars indicate a $\pm$ 95% confidence interval. The APR scenario resulted in significantly more CWD cases, more CWD area, and higher CWD prevalence compared to the NonAPR scenario.

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