



Abundance and Distribution of White-tailed Deer on First State National Historical Park and Surrounding Lands



White-tailed deer (*Odocoileus virginianus*) at First State National Historical Park, Delaware, USA.
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Abundance and distribution of white-tailed deer on First State National Historical Park and surrounding lands

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Abstract

We estimated both abundance and distribution of white-tailed deer (*Odocoileus virginianus*) on the Brandywine Valley unit of First State National Historical Park (FRST) and the Brandywine Creek State Park (BCSP) during 2020 and 2021 with two widely used field methods — a road-based count and a network of camera traps. We conducted 24 road-based counts, covering 260 km of roadway, and deployed up to 16 camera traps, processing over 82,000 images representing over 5,000 independent observations.

In both years, we identified bucks based on their body and antler characteristics, tracking their movements between baited camera trap locations. We tested seven estimators commonly reported in the literature, comparing the relative merits for managers of small, protected natural areas like FRST.

Deer densities estimated from conventional road-based distance sampling were approximately 10 deer/km² lower than densities estimated from camera-trapping surveys. We attribute the bias in road-based distance sampling to the difficulty of recording the precise effort expended to obtain the counts. Modifying the distance sampling method addressed many of the issues associated with the conventional approach. Despite little substantive differences in land cover types between the two methods, a clear spatial segregation of male and female deer at camera trap locations could bias road-based counts if the sexes are not encountered in proportion to their abundances. There was a distinct gradient in deer distribution across the study area, with higher proportions of deer recorded in camera traps at FRST than BCSP, which harvests 20–60 deer annually during a regulated, hunting season.

The most reliable (i.e., low bias, acceptable precision) methods, Spatial Capture Recapture (SCR) and Density Surface Modeling (DSM), produced deer densities of approximately 50 deer/km² in each year — a number which is consistent with previous estimates for New Castle County, Delaware, and our experience in similar, un hunted natural areas. Across both FRST and BCSP, these densities translated into area-wide (~1000 ha) population sizes between 650–1000 deer, with about one-half to two-thirds comprising the FRST population.

Density surface modeling of mapped locations of deer detected during surveys, combined with camera-trapping and a time-to-event data analysis might be the only practical means of reliably assessing white-tailed deer abundance in small (<2000 ha), protected natural areas like FRST. Most other approaches are either too time-consuming, require identification and tracking of individual deer, the use of bait, or require intervention by a subject-area expert.

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Introduction

There exists a need for a relatively simple, inexpensive, and reliable tool for estimating white-tailed deer (*Odocoileus virginianus*; hereafter deer) population density and abundance on small (<2000 ha), protected natural areas. For many parks, for example, the land area is too small to justify the expense of a replicated aerial survey, or the effort to capture and mark a large sample of animals. Yet, despite their small size, most protected natural areas are mandated by policy or law to manage wildlife resources using sound and justifiable methods. These policies and laws are deemed prudent in the face of legal challenges that may be associated with deer management (Porter and Underwood 2001). Estimated population density often defines specific management concerns with hyperabundant deer herds (e.g., deleterious effects on natural or cultural resources), while abundance determines the scope of management action required and costs of implementation. Moreover, population size continues to be the currency of wildlife management (Williams et al. 2002, Kéry and Royle 2016, Kéry and Royle 2021) and is used frequently in the development of wildlife management plans throughout North America. It also represents the most intuitive metric to convey to lay audiences.

Counts conducted along roads have long been the conventional method for monitoring relative abundance of deer populations (Progulske and Duerre 1964; Sage et al. 1983), especially at night (McCullough 1982). Night-spotlighting is the most common method due to its simplicity and low implementation costs (Underwood and Knutson 2011). Reflected light from specialized organs in the eyes of deer makes for high but variable detection rates (Collier et al. 2013). However, the assumption that all deer within the illumination range of the light are detected is false and invariably leads to undercounts (Begier 1996). Underwood et al. (2003) introduced conventional distance sampling (CDS) methodology (Buckland et al. 2001) into the night-spotlighting protocol to address the issue of false-negative detection. The revised protocol was implemented in dozens of small, protected natural areas for monitoring white-tailed deer populations in the national park system (Underwood and Knutson 2011).

A frequent criticism of night-spotlighting is that the sample of animals within the vicinity of the road may not be representative of the entire population (Ruelle et al. 2003). Non-representation can occur due to poor survey coverage (Strindberg and Buckland 2004), exclusion of important land cover-types (McCullough 1982), or differential cover-type utilization by deer (McShea et al. 2011, Beaver et al. 2014) which can lead to bias in abundance estimation (Buckland et al. 2001). Consequently, a method that does not rely on counting animals along roads should be used in conjunction with road-based surveys. Stationary, infrared-triggered game cameras (i.e., camera traps) are ideally suited for this purpose (e.g., Curtis et al. 2009, Macaulay et al. 2020). Alternatively, fully model-based alternatives to CDS like density surface modeling (DSM) or hierarchical distance sampling may mitigate most of the problems associated with counting animals along roads (Kéry and Royle 2021).

The overarching goal of this project is to recommend a strategy for assessing the abundance and distribution of white-tailed deer in small (<2000 ha), protected natural areas. Our purpose is to generate estimates of population size and density and map the distribution of deer across the

landscape. We use two field methods, and several analytical approaches to achieve the following objectives for August–October of 2020 and 2021:

Estimate deer density/abundance/distribution using:

1. road-based, conventional distance sampling along a pre-determined night-spotlighting route (density),
2. two conventional, mark-recapture methods based on natural marks of deer in camera trap images (abundance),
3. two hierarchical approaches using capture histories of identifiable deer (density, abundance),
4. a Poisson/Poisson N-mixture model with auxiliary abundance (distribution), and
5. density surface modeling (DSM), a model-based alternative to conventional distance sampling (CDS) (density, distribution).

Compare land cover-types along the distance sampling route with those surrounding camera traps and map the distribution of independent visits of deer across the camera-trapping network.

Study Area Description

The First State National Historical Park (FRST) was designated in Delaware from a 445-ha parcel of land donated to the National Park Service (NPS) in 2013 by the Conservation Fund. In 2020, an additional 109 ha of land was donated extending FRST northward into Delaware County, Pennsylvania. It is visited (>140,000 visits per year; <https://irma.nps.gov/Stats/Reports/Park/FRST>) for its recreational activities such as hiking, horseback riding, biking, and water sports (Figure 1).

To the south, Brandywine Creek State Park (BCSP) shares a coterminous boundary with FRST. It was originally part of the General Henry du Pont estate, but was purchased by the State of Delaware and designated a state park in 1965. Like FRST, a significant donation of land increased the area of BCSP to its present-day 380 hectares. Together, the two parks represent a significant protected natural area in an otherwise developed, urbanizing landscape.

Both FRST and BCSP are in the Piedmont physiographic province of Delaware and southern Pennsylvania. The landscape is characterized by relatively fertile plateaus cut by steep ravines from the area's many tributaries of the Christina River, including Brandywine Creek. The parks contain six major upland forest types relevant to this study. The most common is the Northern Piedmont Mesic Oak-Beech forest (PAQ 2011), which corresponds closely to the Central Appalachian Dry-Mesic Chestnut Oak-Northern Red Oak Forest (National Vegetation Classification Code: CEG006057) and the Northern Coast Plain/Piedmont Oak-Beech-Heath/Forest (National Vegetation Classification Code: CEG006919) of the National Vegetation Classification Standard (Coxe 2014).

Unique among both parks are forest patches of high ecological integrity (PAQ 2011). Many forest patch configurations have not changed in nearly nine decades and, as of 2011, possess old-growth characteristics including mature trees and relatively intact understories. From the National Land Cover Database (NLCD) (Dewitz 2021), predominant land cover categories across the two properties includes Deciduous Forest (49.0%), Hay/Pasture (22.4%), Developed (15.6%), and Cultivated Crops (10.9%). Deer hunting was once a cultural tradition on lands comprising FRST but has been prohibited since its designation as a National Historical Park (Stewart Ramsey, personal communication). Deer hunting has been conducted on BCSP since 1994, and is now an archery/crossbow only season (unpublished data, Delaware Division of Fish and Wildlife). Annual take ranges between 20–60 deer with alternating years of higher and lower harvest (Figure 2).

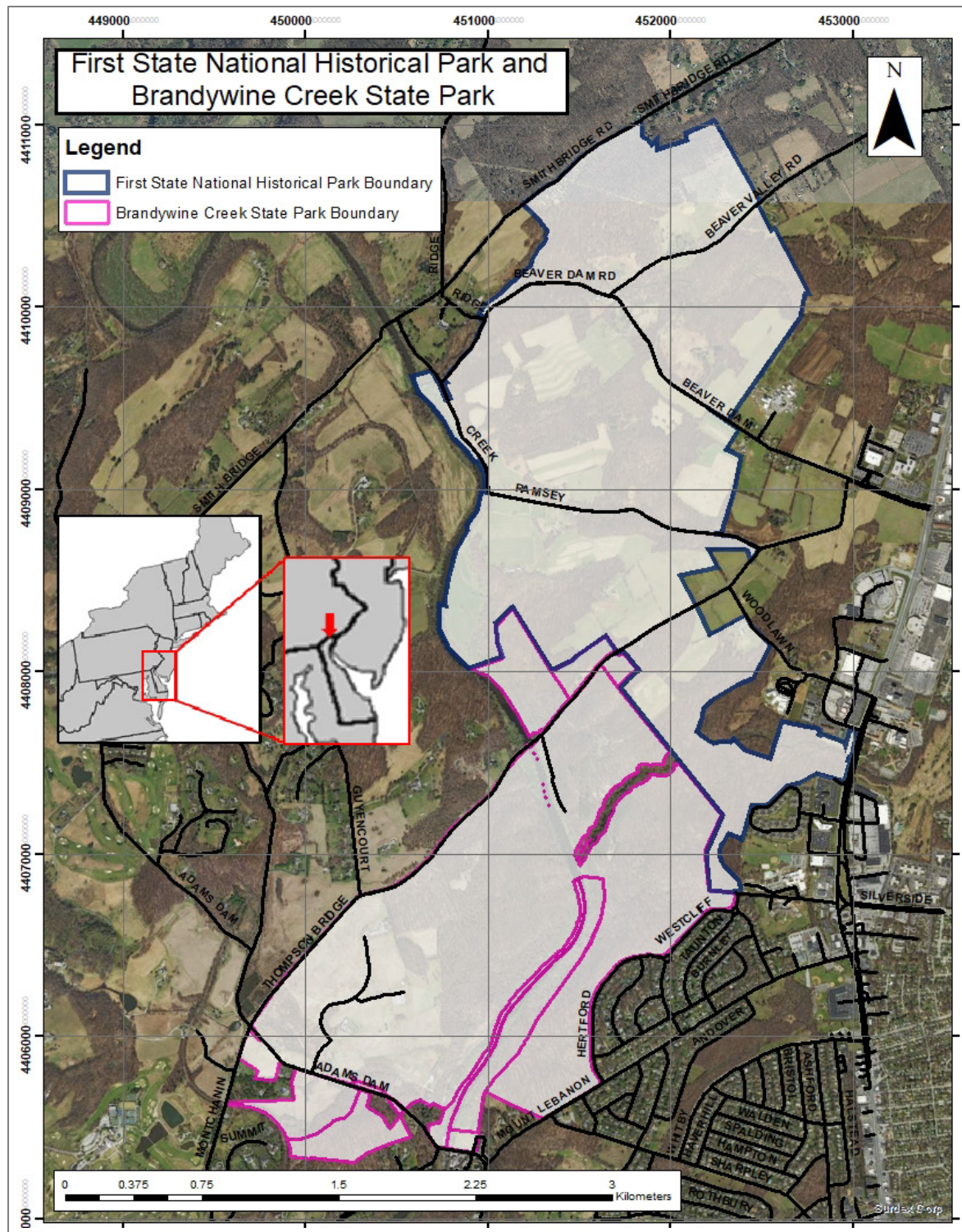


Figure 1. Brandywine Valley unit of First State National Historical Park and Brandywine Creek State Park located in Chester County, Pennsylvania and New Castle County, Delaware, USA.

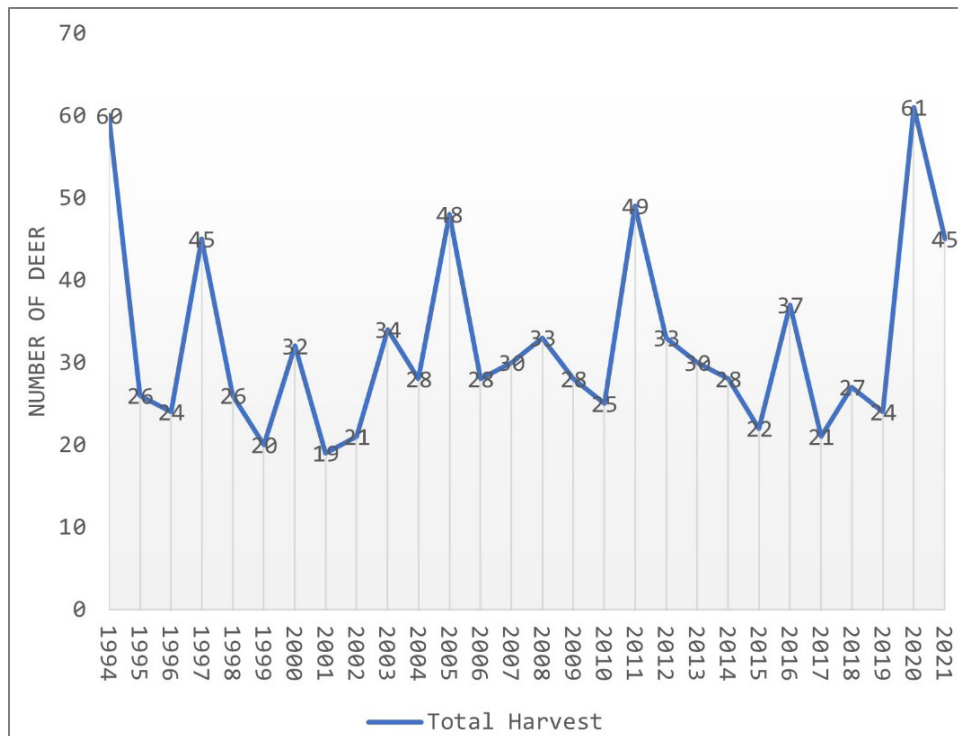


Figure 2. Annual white-tailed deer (*Odocoileus virginianus*) harvest on Brandywine Creek State Park located in New Castle County, Delaware, 1994–2021.

Background

Distance sampling is a hybrid inference method that includes both design and model components. The design component focuses on where the counts are to be conducted and how much effort should be expended to achieve a desired level of precision. The design goal is to achieve adequate coverage for unbiased density estimation with acceptable precision (Thomas et al. 2010). However, adequate coverage is challenging with road-based surveys because it is difficult to select roads that are independent of the distribution of animals (Marques et al. 2010), thus introducing bias in estimation (Roberts et al. 2006). In addition, there is evidence that deer may utilize certain land cover-types disproportionately along roads (McShea et al. 2011). Finally, the distribution of roads is not uniform across most landscapes, which limits the achievement of equal coverage probability and the potential for bias in abundance estimation (Strindberg and Buckland 2004). Consequently, additional tools, such as aerial surveys or camera traps, that do not rely on access from roads are desirable as a hedge against bias (Haus et al. 2019).

We used camera-trapping to assess deer abundance in areas not accessible by roads. Camera-trapping has evolved as a useful wildlife study tool since its introduction in the early 1990s (O'Brien 2011). Today camera-trapping is used extensively in the estimation of occupancy and abundance of many species of wildlife including deer (Desile et al. 2021). Camera traps do not physically trap animals but record their transient presence and are considered proximity count detectors (Efford et al. 2009). For adequate detection rates, cameras need to be placed in areas or along features known to be used by the organism of interest.

Where camera-trapping has been most frequently applied is in situations where individual animals can be identified either through natural or applied marks (Curtis et al. 2009, Macaulay et al. 2020). The whole compliment of closed-capture recapture models can be used in that instance to estimate a variety of population parameters including abundance (Borchers et al. 2002). Unfortunately, ignoring the spatial nature of detection is problematic for two reasons. First, the spatial aspect of the detection process contains useful information relative to abundance estimation. Second, without the spatial detection information, the effective area sampled (i.e., the denominator in the formula for density) cannot be objectively estimated.

Alternatively, spatial capture-recapture (SCR) is a type of individual covariate model with spatial location as the covariate. It describes the detection process in terms of a function that depends on unobserved distances of some measure of an animal's average location and the camera trap network (Borchers 2012, Schaub and Kéry 2021). SCR operates on the capture histories of uniquely identifiable individuals and accounts for heterogeneity in capture probability due to variable exposure to traps (Otis et al. 1978). SCR includes a spatial model for encounters and estimates density through specification of a point-process model for the population (Royle et al. 2014, Sutherland et al. 2019). Like CDS, a key advantage of SCR is an explicit accounting of the effective sampling area leading directly to the estimation of density (Tenan et al. 2017).

Other developments affecting the analysis of camera-trapping data include the estimation of abundance from spatially replicated counts of unmarked individuals (Royle 2004, Royle and Gardner 2011, Kéry and Royle 2016). These approaches are appealing because they circumvent the need to capture, handle and mark a sample of wild animals, which is usually expensive and risky for animals and handlers. Several versions of the N-mixture model of Royle (2004) have been applied to counts of animals acquired at multiple sites and occasions (i.e., meta-population approach; Kéry and Royle 2016). However, these models cannot be applied indiscriminately to camera-trapping data — an appropriate observation model must first be selected (Nakashima 2019).

Primary challenges with camera-trapping include: (1) encompassing meaningful spatial scope, (2) the cost and labor associated with using bait to increase encounter rates, and (3) managing and manipulating the large volume of images collected during a typical study. The first challenge is not easily overcome for most small, protected natural areas like FRST when the home-range of the study organism is large relative to the size of the natural area (Keiter et al. 2017). The second challenge is equally difficult because sufficient encounters at camera traps without bait take much longer to obtain, increasing the likelihood of violating the population closure assumption. The third challenge is partially alleviated by software specifically developed to manage and manipulate camera-trapping data (e.g., Sanderson and Harris 2013).

Finally, hierarchical distance sampling or DSM may mitigate many of the problems associated with CDS because they are fully model-based solutions to density/abundance estimation (Miller et al. 2013, Kéry and Royle 2016, Kéry and Royle 2021). The primary advantage of these methods is that they are flexible and can be tailored to specific applications. However, flexibility comes with an added cost of requiring bespoke coding and a level of sophistication that could be challenging to casual users.

Approach

We approached the challenges of estimating deer abundance in places like FRST by designing a study that allowed us to address the primary concerns with two of the most popular methodologies: road-based distance sampling and camera-trapping (Figure 3). The design has two surveillance periods: passive and active — the latter distinguished by the use of bait while camera-trapping. We explore the use of conventional meta-population deployment (i.e., site by occasion) of camera traps for estimating abundance from a version of the N-Mixture model of Royle et al. (2014). During the active surveillance period, we compare two conventional (i.e., aspatial) mark-recapture estimators of abundance with a multinomial, spatially implicit mixture model. We also compare density estimated from road-based distance sampling, SCR and DSM. We compare differences in land cover between the distance sampling survey route and the network of camera traps, examine the spatial distribution of encounters with deer among camera traps relative to the roads surveyed in FRST, and explore the implications of baiting deer at camera trap locations for abundance estimation. For comparison, Table 1 presents a roundup of relevant studies conducted between 1997 and 2020 of either free-ranging or captive deer populations where >1 analytical method was used for estimating population size.

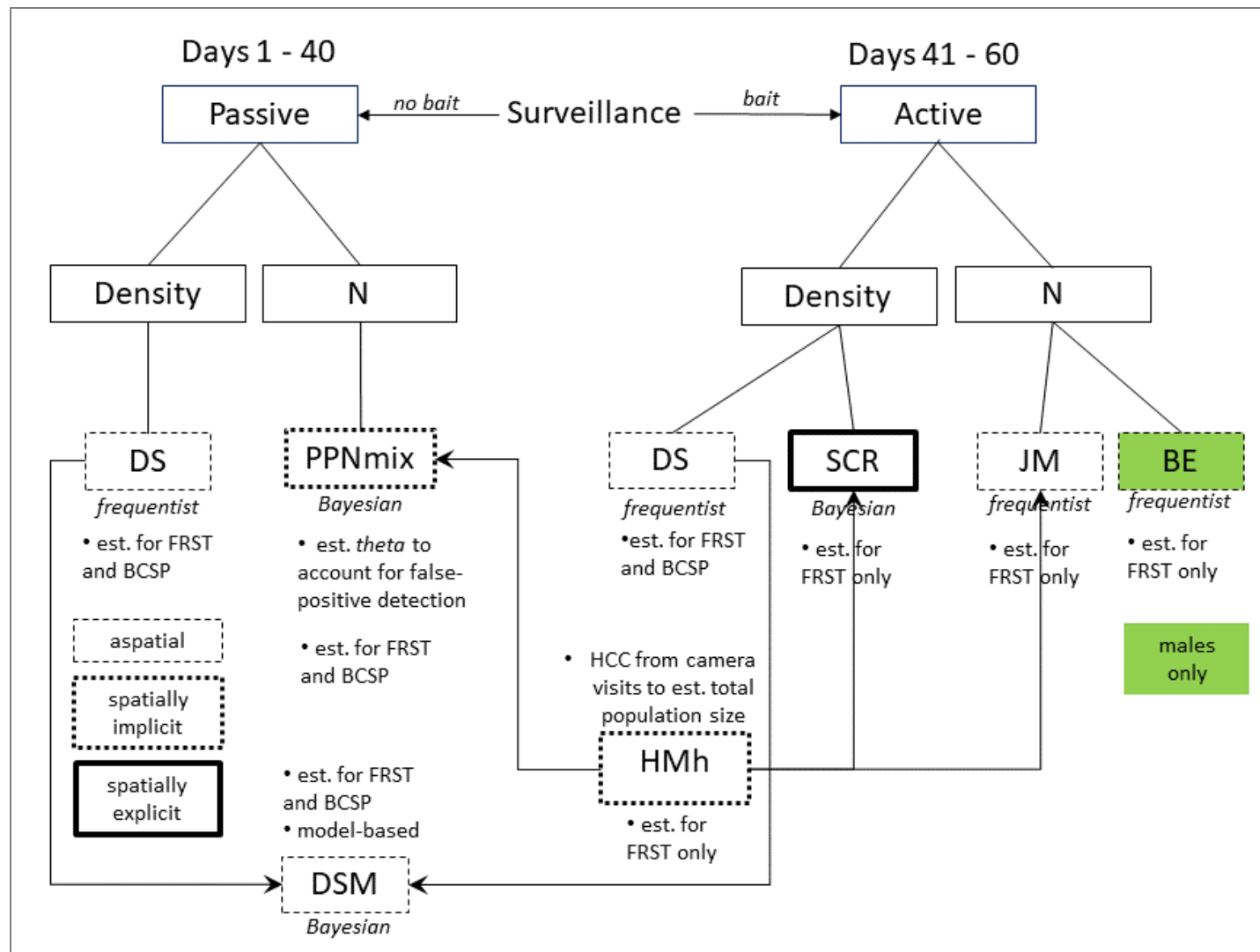


Figure 3. Approaches to the estimation of density and abundance of white-tailed deer (*Odocoileus virginianus*) on small, protected natural areas like First State National Historical Park (FRST) and Brandywine Creek State Park (BCSP), New Castle County, Delaware and Chester County, Pennsylvania, USA. DS = distance sampling; PPNmix = Poisson-Poisson N-mixture model; SCR = spatial capture; JM = Jacobson's Method; BE = Bowden's Estimator, HMh = hierarchical heterogeneity model; DSM = density surface modeling; HCC = herd composition count.

Table 1. Studies of free-ranging or captive deer herds (*Odocoileus virginianus*) where >1 analytical method for estimating abundance or density was compared. An “X” indicates presence.

Source	Known N	LP ^A	JM ^B	BE ^C	CDS ^D	NMIX ^E	SCR ^F	DSM ^G
Jacobson et al. (1997)	X	X	X	–	–	–	–	–
Roberts et al. (2006)	–	X	–	–	X	–	–	–
Curtis et al. (2009)	–	X	X	X	–	–	–	–
McShea et al. (2011)	–	–	–	–	X	–	–	–
Dougherty and Bowman (2012)	–	–	X	X	–	–	–	–
Beaver et al. (2016)	–	–	X	–	–	–	X	–
Keever et al. (2017)	X	–	–	–	–	X	–	–
Haus et al. (2019)	–	–	X	–	X	X	–	–
This study	–	–	X	X	X	X	X	X

^A LP = Lincoln-Peterson Index

^B JM = Jacobson’s Method

^C BE = Bowden’s Estimator

^D CDS = Conventional Distance Sampling

^E NMIX = N-Mixture Modeling

^F SCR = Spatial Capture-Recapture

^G DSM = Density Surface Modeling

Field Methods

Distance Sampling

We conducted road-based distance sampling at approximately bi-weekly intervals from August through October in 2020 and 2021. Surveys were initiated 20 minutes after local sunset to align with peak deer activity levels (Montgomery 1963). Based on reconnaissance, we selected a route of approximately 12 km of roadway in and around FRST and BCSP (Figure 4). BCSP was included so that the route length would minimally meet distance sampling precision requirements (Buckland et al. 2001).

Starting locations, direction of travel and specific roads segments were routinely rotated to maximize variability when possible. Deer were counted from both sides of the vehicle using two spotters (i.e., a driver and front seat passenger), and speed was constrained to <13 km/h. A navigator, who doubled as a data recorder, sat in the rear seat of an extended-cab pickup truck. Because deer are moderately social animals (Hirth 1977), we recorded distances and angles to clusters (i.e., groups of ≥ 1 deer) of deer along with cluster size. We used a nearest neighbor criterion along with social and behavioral cues to define clusters of deer (Underwood et al. 1998). With a GPS unit, laser-rangefinder, and window-mounted protractor, we recorded the following: (1) the position of the vehicle; (2) the range distance from the vehicle to the center-mass of the cluster; and (3) the acute angle between the observer and the deer cluster. The offset (i.e., position) of the deer cluster was calculated using standard trigonometric relationships (Pierce 2000) and stored along with the survey routes as shapefiles (ArcGIS ver. 10.4, Esri, Redlands, CA).

On both sides of the survey route, we mapped the lengths of roadway where visibility was limited due to dense vegetation or road grade below the surrounding terrain. We adjusted the effort for each road-segment by subtracting the length of zones with zero-visibility from each side. We made similar corrections if only one side of a road-segment was counted.

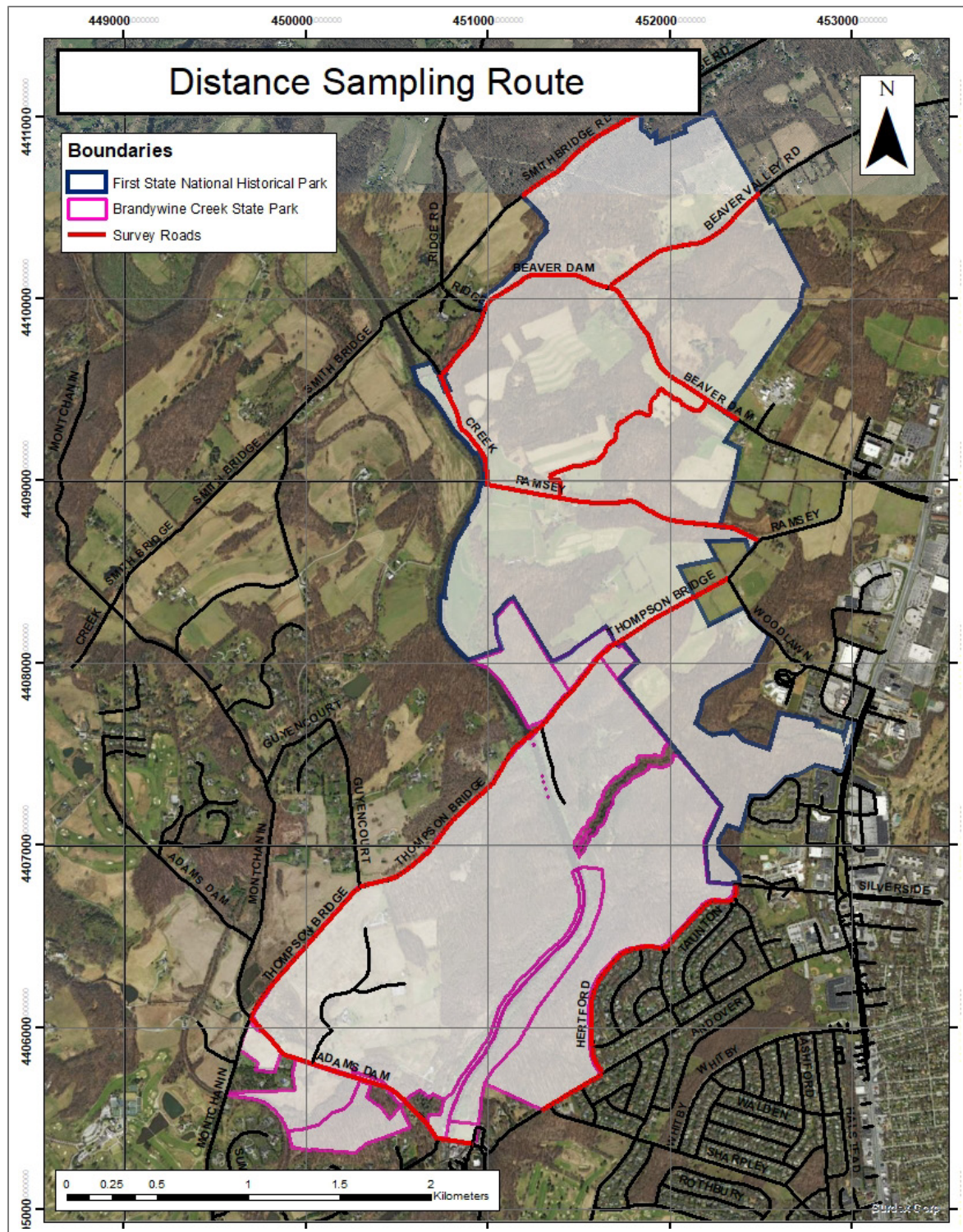


Figure 4. Distance sampling route used during nighttime road-based surveys of white-tailed deer (*Odocoileus virginianus*) conducted from July–August in 2020 and 2021 on First State National Historical Park and Brandywine Creek State Park in Delaware and Pennsylvania, USA.

Camera-trapping

We deployed up to 16, infrared-triggered, game trail cameras (Reconyx HC500 and Reconyx Hyperfire 2, Holmen, Wisconsin) in FRST and BCSP during 2020 and 2021 for the purpose of recording deer numbers in locations not accessible by roads (Figure 5). Camera traps were situated along trails in forested land cover-types, placed on trees approximately 50 cm above ground level, and their positions recorded using a handheld GPS unit. We angled cameras slightly downward and oriented them away from direct sunlight and walk-tested them to ensure a deer within the field-of-view would be recorded. During the passive surveillance period, we placed a single camera trap per 1-km² across FRST and BCSP by using the Universal Trans Mercator (UTM) projection as our reference grid. During the active surveillance period, we relocated cameras from BCSP to FRST for an approximately 20-day period (Dougherty and Bowmen 2012) at the end of September and into the first week of October. We initially selected a camera trap density of 2 per km² based on recommendations in Jacobson et al. (1997) but adjusted where necessary to achieve uniform coverage throughout FRST (Figure 6). We baited each camera site with 22.7 kg of whole corn, placed in a line or V-pattern approximately 5 m in front of the camera, to attract as many deer as possible. Bait was replenished weekly to encourage high encounter rates with deer. Camera traps were programmed to take multiple pictures in 1-second bursts once triggered, and to re-arm after 3–5 minutes to accommodate deer loitering in front of the camera while consuming bait. We increased the re-arm duration from 3 minutes in 2020 to 5 minutes in 2021 to reduce the number of images to be processed. We monitored camera traps weekly and swapped out Secure Digital (SD) cards and batteries as needed. All cameras were removed in early October of each year.

We used a computer program (DataOrganize; vers. 4.5, March 03, 2020 from CAMERASWEET; Small Wild Cat Conservation Foundation) to organize and sort camera images (Sanderson and Harris 2013). The software uses a file directory structure (Microsoft Windows) to sort and store images based on site, camera, species, and number of individuals in the image. We sorted camera images by sex and age-group (i.e., males, females, and fawns) to characterize herd composition during the surveillance periods. Once the timestamps were validated, a master list was created of all images by camera trap, sorted by their respective categories and in order of timestamp.

For the active surveillance period, we modified the directory data structure to store information on identifiable antlered deer (i.e., yearling and older males). Males were identified based on head and antler conformation, body size, and the number of antler points. We used the “Species” label to create a unique identity for each male by the number of antler points (e.g., 0105 was the first identifiable five-point deer, while 0205 was the second identifiable five-point deer). Consequently, we had as many Species as identifiable males in each year. Instead of recording the number of deer in the image, we used Number to record the camera trap location where each identifiable male deer was detected. We included an Unknown category for males that could not be unambiguously identified. Similar to the herd composition sort, a master list of all identifiable and unknown males was created by camera trap location, in order of image timestamp.

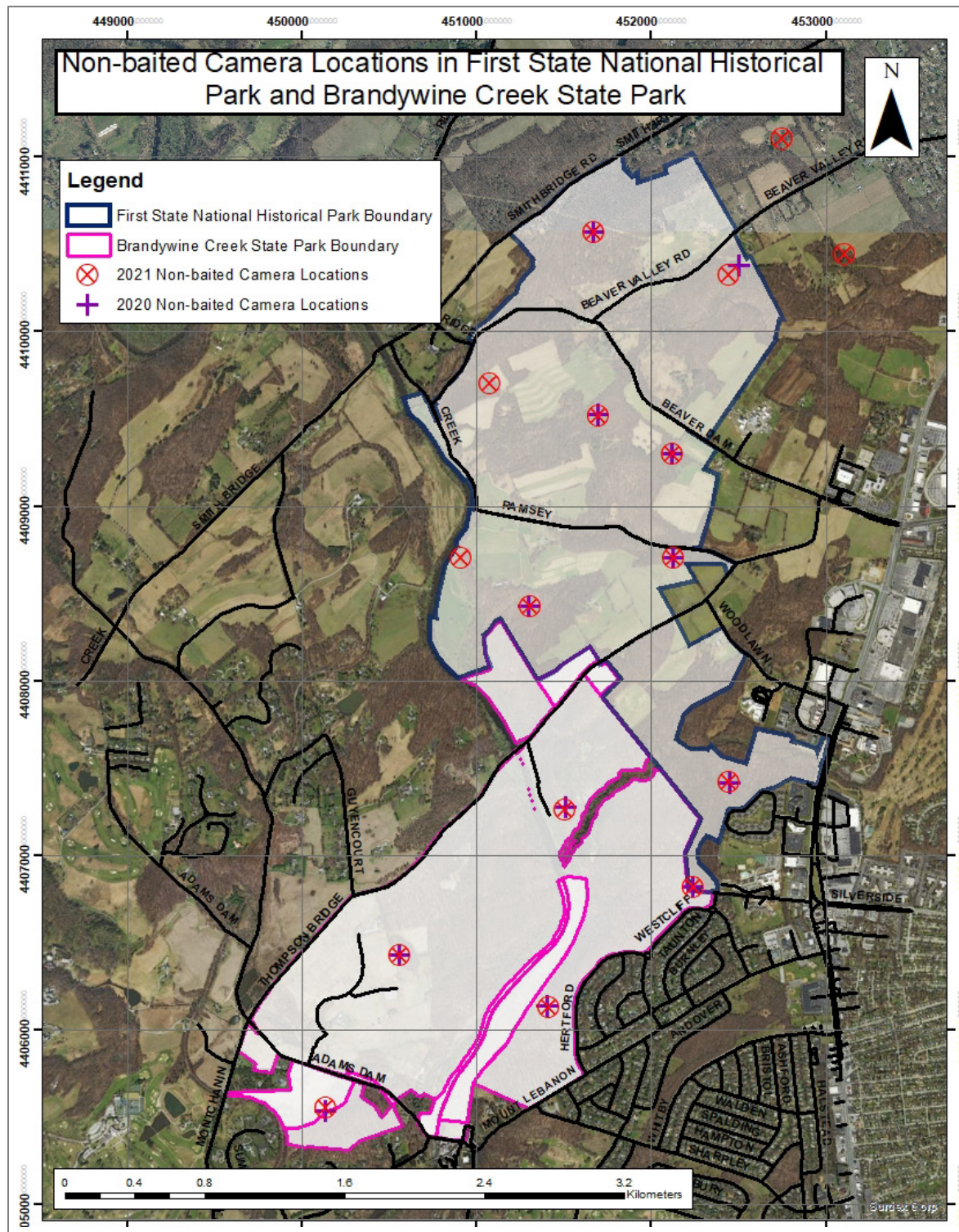


Figure 5. Non-baited camera-trapping locations for white-tailed deer abundance estimation during August–September 2020 and 2021 on First State National Historical Park and Brandywine Creek State Park in Delaware and Pennsylvania, USA.

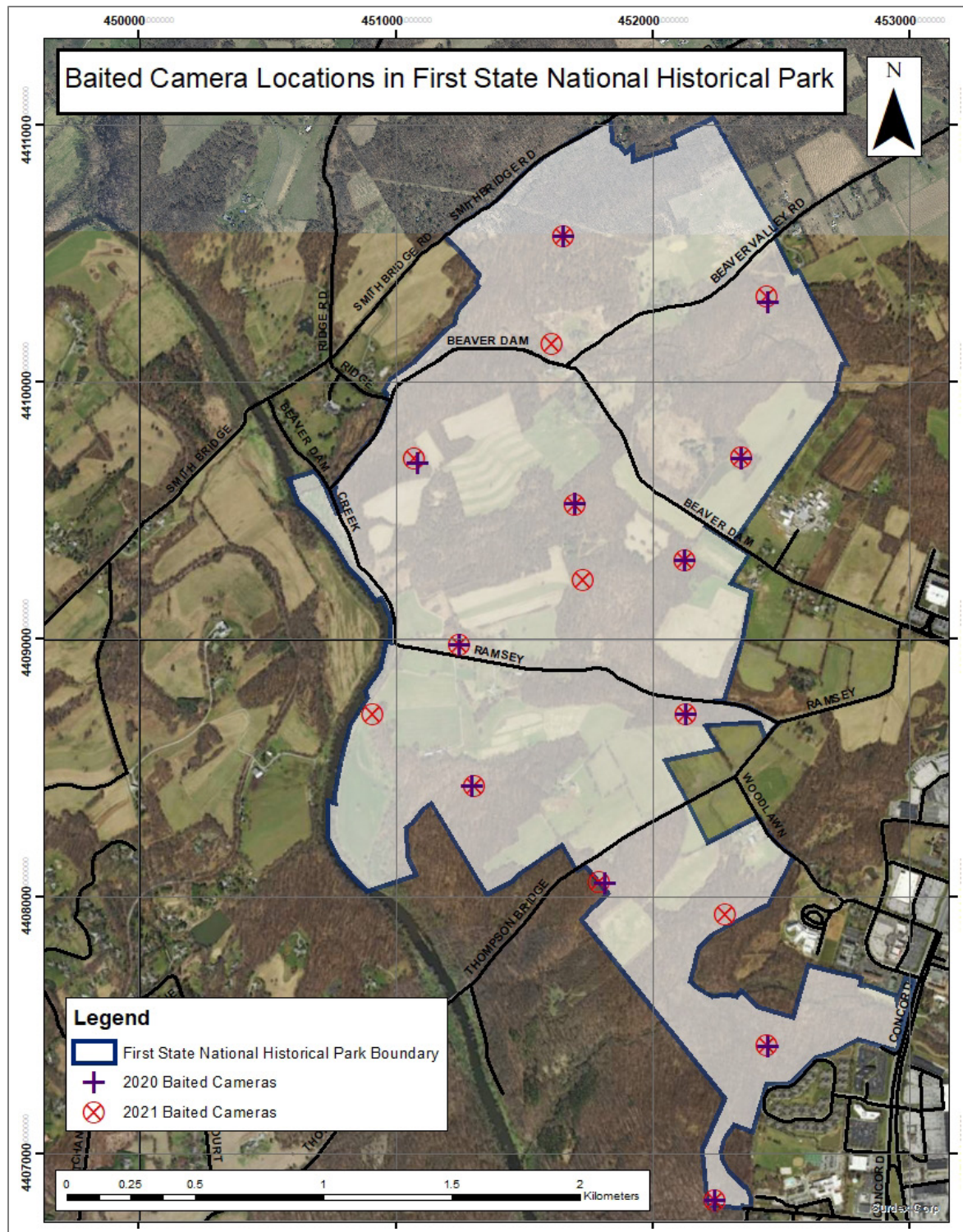


Figure 6. Baited camera-trapping locations used during a study of white-tailed deer abundance conducted from September–October in 2020 and 2021 in First State National Historical Park in Delaware and Pennsylvania, USA.

We used the concept of visits (Macauley et al. 2020) rather than total image occurrences to reduce bias associated with the overrepresentation of deer in front of the baited camera traps. We arbitrarily selected 60 minutes between successive timestamps to indicate an independent visit and wrote R scripts to process the lists for both herd composition and identifiable males. For each set of images included in an independent visit, the median timestamp of the interval and the maximum number of deer in images were recorded for further analysis (Code Book I. Underwood et al., 2024).

Analytical Methods

Conventional Distance Sampling for Density

Mapped detections of deer formed the basis for estimating density and population size using CDS. Density, or $(\hat{n} * \hat{s}) / (2 * L * \hat{e}sw)$, is a transcendental metric that expresses the number of animals per unit area, and is often a more ecologically meaningful construct for managers than population size (Buckland et al. 2001). It is formed (in our case) by four parts: (1) $\hat{n}$, the number of deer clusters encountered, (2) $\hat{s}$, the average cluster size, (3) L = the total effort (km), and (4) $\hat{e}sw$ (m), the effective strip half-width. The first two parts represent the numerator (i.e., $\hat{N} = \hat{n} * \hat{s}$) and the third part represents the denominator (i.e., $2L * \hat{e}sw$) in the expression for density.

The method derives its name from the perpendicular distance measured or calculated between each deer cluster and the survey route. We accomplished this step in GIS by calculating the closest approach distance between mapped detections and the survey route. The premise is that the probability of detecting deer from the roadside decreases with increasing distance from the survey route. This phenomenon occurs because the apparent size of the target decreases with distance, while the field of view increases and becomes more cluttered with non-target objects making detection more difficult. These distances are modeled to determine the proportion of targets (i.e., deer) that go undetected. The inverse of that proportion represents a correction factor on $\hat{n}$, the number of deer clusters encountered that when multiplied by the average cluster size, $\hat{s}$, gives the total number of deer in the covered area. The total number of deer in the covered area is then divided by the effective area sampled to yield density. Modeling the effective area sampled is among the more sophisticated aspects of CDS and requires an experienced analyst (Thomas et al. 2010).

In CDS, it is common to pool detection data across surveys to increase the sample size for modeling the effective area sampled, while either pooling or retaining the individual counts as replicates for estimating the uncertainty around encounter rate (Thomas et al. 2010). For each year, we pooled detection data to estimate the effective area sampled (i.e., $\hat{e}sw$). We analyzed CDS data using the R packages *Rdistance* (McDonald et al. 2019), *Distance* (Miller et al. 2019), and *mrds* (Laake et al. 2022). We used the rStudio 2021.09.2+382 graphical user interface for the R programming environment (R Core Team 2022). We left-truncated distance data to satisfy the primary assumption of CDS that objects directly on the transect line are always detected, and to eliminate land area associated with the road that is infrequently used by deer.

Spatial Capture-Recapture for Density

We used *secr*, an R-package for the analysis of SCR models under the classical paradigm (Borchers and Efford 2008) to facilitate building capture histories of identifiable males, defining state-spaces, and verifying that Bayesian models produced sensible results (Appendix A, Code Book III, Underwood et al., 2024). We developed Bayesian hierarchical SCR models (Royle and Dorazio 2008) to estimate the density of deer on FRST. Cameras were located in a way to ensure that one or more identifiable males would use >1 camera site — a prerequisite for SCR to work.

Specifically, we developed two SCR models — one (SCR_b) to test for the behavioral effects of bait on subsequent encounters (see Section 7.2.3 in Royle et al. 2014) with identifiable males (Code Book IV, Underwood et al., 2024), and another incorporating random effects to ameliorate individual heterogeneity (SCR_{Mh}) induced by a strong behavioral response to bait (Code Book V, Underwood et al., 2024). For our Bayesian models, we incorporated the posterior predictive check to assess goodness-of-fit using the Freeman-Tukey discrepancy (Kéry and Royle 2016). In addition, we used the ratios of female:male and fawn:female from camera trap visits classified for herd composition to estimate total population density to compare with CDS. We incorporated uncertainty in sex-age ratios by using the binomial approximation to the hypergeometric distribution as described in Bowden et al. (1984) and passing the variances to the Bayesian SCR models as informed priors.

In Bayesian SCR models developed using JAGS (i.e., Just Another Gibbs Sampler, Appendix B), abundance is modeled using data augmentation (Royle and Dorazio 2012), in which the encounter history matrix of identified individuals is padded by a number of M potential animals (i.e., ghosts). The estimation problem then becomes one of determining the proportion of M that are members of the population exposed to capture. The M individuals are used to generate a distribution of activity centers in a state-space and must be large in number such that the posterior distribution of population size, or N , is not truncated. The distance from each individual's (real or ghost) activity center to a camera trap location is treated as a random effect and used to model the probability of detection. The latent state $z[i]$ takes a value 1 if individual i is known to occur (i.e., was detected at least once), so is automatically 1 for the number of identifiable deer ($n0$) detected one or more times. The $z[i]$ is stochastically assigned values of 0 or 1 for the remaining $M-n0$ individuals, consistent with the updated values of the model parameters for the distance-based detection function (Royle 2009, Chandler and Clark 2014). Abundance is then computed $N = \text{sum}(z[i])$ and density is derived as $D = N/\text{area}$, where area is the area of the state-space. In our case, a discrete state-space was generated by default in *secr* and converted so it could be used in JAGS (makeJAGSmask; Meredith 2021). Appendix B provides details on the development, execution, and analysis of posterior distributions of all Bayesian hierarchical models in this report.

Jacobson's Method (JM) and Bowden's Estimator (BE) for Abundance

A ratio-estimator, JM uses the total occurrences of spike-antlered bucks (SB) to branch-antlered bucks (BA) in camera images to estimate the total buck population (N_b). It does so by multiplying the number of identifiable branch-antlered bucks (IB) by SB:BA, then adding the product to IB. N_b is then used to estimate the number of yearling and adult females, N_d , from their respective frequency of occurrences in camera images relative to BA. Similarly, the number of fawns, N_f , is calculated by multiplying the ratio of fawns to yearling and adult females in camera images by N_d . The sum of the individual herd segments is the estimated total deer population (Jacobson et al. 1997, Matthews and Springer 2019). In our study, we were able to identify a number of spike-antlered bucks and wished to include them in the marked sample of IB. Therefore, we used the total occurrences of unknown antlered bucks (UB) to all bucks (AM) as the ratio for estimating N_b . If each IB visited one or more cameras >1 time, then the sum of independent visits would exceed IB. Consequently, we scaled the calculation for N_b by the quantity: $IB/[\text{sum}(\text{IB visits})]$. All subsequent calculations are as previously described.

In its conventional usage, there is no uncertainty associated with estimated population size using JM limiting its application. Like Weckel et al. (2011), we developed a bootstrapping procedure for estimating the variance around total population size from the frequency of visits by each herd segment at camera traps. Treating the total number of uniquely identifiable and unknown bucks as fixed, we estimated population size from JM calculations after drawing a bootstrap sample (i.e., a sample with replacement) equal in size to the original dataset, from the observed frequency of visits contained in the herd composition list. Each bootstrapped dataset was created in a way that preserved the proportional representation of each camera trap in the overall sample (i.e., it was stratified by camera). This procedure was automated in R with the aid of packages *rsample* (Frick et al. 2022) and *purrr* (Henry and Wickham 2020). We used 10,000 bootstrap samples and computed the 2.5 and 97.5 percentile limits around estimated mean quantities (Code Book VI, Underwood et al., 2024).

We also used Bowden’s Estimator (Bowden and Kufeld 1995) to estimate the size of the antlered buck population on FRST in each year of the study. It uses the mean number of times identifiable bucks are sighted, $\bar{y}_i$, and the total number of sightings of identifiable and un-identifiable bucks, Y , to estimate $N = \frac{Y}{\bar{y}_i}$, the total buck population size. BE is unique in that it allows for sighting probability to vary among individual deer and over time, a major assumption violation of most closed population capture-recapture estimators (Bowden and Kufeld 1995). Because the sighting process need not consist of independent trials, it is acceptable to observe the same deer more than once during a sighting occasion as long as identifiable and un-identifiable males are equally likely to be sighted and recorded (Diefenbach 2009). We used the bias-corrected estimate for N , and computed log-based 95% confidence intervals around population size (Bowden and Kufeld 1995). We did not attempt to incorporate herd composition ratios in BE and so did not estimate total population size. All calculations were programmed in R-scripts (Code Book VII, Underwood et al., 2024).

Hierarchical Multinomial Mixture Model for Abundance

We programmed a Bayesian, multinomial formulation of the heterogeneity model (HM_h) based on a modification of the version presented in Kéry and Royle (2016). Like SCR, it uses full capture histories of identifiable bucks and predicts abundance at each camera site (i.e., it is spatially implicit). As the name implies, it also accounts for heterogeneity in encounter probabilities through the addition of random effects for each identifiable buck. We present it as a more realistic alternative to the conventional JM and BE capture-recapture models due to its hierarchical structure and because it includes more realistic variance components. It also represents an alternative to CDS and SCR because it obviates the need for modelling the effective area sampled (Code Book VIII, Underwood et al., 2024).

We modeled site-specific abundance from principal components of land cover-types in the 1-km² surrounding each camera trap location (Code Book IX, Code Book X, Underwood et al., 2024). Similar to previous models, we incorporated herd composition ratios and their uncertainties in order to estimate total population size and added a Poisson observation process to accommodate independent camera trap visits instead of binary detections. For continuity, we confined analysis to camera locations common between years.

N-Mixture Model for Distribution

We used the N-mixture model of Royle (2004) to assess the abundance and distribution of deer across the entire study area during the passive surveillance period. N-mixture models of animal abundance come in three varieties (Nakashima 2019), differing mainly in how the observations are modeled. They are formed by modeling the state variable, N , and observations separately (Royle and Dorazio 2008). Observations are linked to the state variable through a detection probability, which is estimated from repeat visits to multiple sites. Because camera-trapping allows for some individuals to be detected multiple times during a sampling occasion, we adopted the Poisson observation process where the total number of detections of an individual is the product of N and the expected number of times it is detected, θ (Kéry and Royle 2016, Nakashima 2019). We included principal components of landcover (see NLCD Land Cover Analysis) in the 1-km² UTM grid surrounding each camera as covariates on abundance. We also coded a posterior predictive check to assess goodness-of-fit (Kéry and Royle 2016) using the Freeman-Tukey discrepancy (Code Book XI, Underwood et al., 2024).

Preliminary analyses determined that 12–16 sites and approximately 40 sampling occasions were insufficient to estimate abundance with acceptable precision from passive surveillance data alone. Consequently, we used abundance estimated from *CDS* as auxiliary data on N , and treated it as a normally-distributed, stochastic node with standard deviation equal to the *CDS* standard error. We plotted all estimated site-specific abundances as a proportion of the total abundance to generate distribution maps for each year.

Density Surface Modeling for Abundance & Distribution

We used a pixel-based approach to DSM, a form of hierarchical distance sampling (Kéry and Royle 2021), as an alternative to *CDS* density estimation. DSM differs from *CDS* in several important ways. First, DSM is fully model-based and not subject to many of the design constraints imposed by *CDS*. Second, because it is hierarchical, spatial variation in density across the study area can be estimated. Finally, deer detections are summarized across pixels of a gridded landscape so some details associated with individual detection distances and cluster sizes are not utilized.

To implement DSM, we generated a 100 × 100-m fishnet across the study area in a GIS (ArcGIS; ver. 10.4, Esri, Redlands, CA) and obtained a count of the number of detections in each 1-ha pixel. When formulated in terms of pixel frequencies, the DSM model amounts to a special case of the binomial N-mixture model (Kéry and Royle 2021). Abundance per pixel (i.e., density: no./ha) is treated as a Poisson variable with intensity modeled with a generalized additive model (GAM) of thin-plate splines rather than a habitat covariate. The regression splines are smoothed over a series of knots placed throughout the state-space. With some trial-and-error, we selected 60 knots systematically located across the virtual study area (Kéry and Royle 2021).

In the vernacular of Kéry and Royle (2021), the probability of detection is modeled with a distance-based covariate calculated from the minimum distances between each pixel centroid and the survey route. Because the distances for each individual detection are not used in this formulation, a more accurate description of this metric is a probability of encountering deer as a function of the pixel's

proximity to the survey route. In fact, it is constructed in exactly the same manner as the encounter rate in a SCR problem. We included a baseline encounter probability to the half-normal function provided in Kéry and Royle (2021) to account for land cover-types with inherently higher probabilities of detecting deer (e.g., hay/pasture). Baseline encounter probability (i.e., 0–1) was assigned subjectively to each land-cover type encapsulated in the fishnet based on relative amounts of vegetation impeding the detection of deer. Open land cover-types received lower values (i.e., low clutter) and densely vegetated land cover-types received higher values. We included site random effects to accommodate cells in the fishnet with lower or higher average density across the study area than predicted from the GAM alone. We also incorporated a cluster size model based on the individual detection data in order to prorate the estimated number of clusters per pixel to number of deer per pixel (Code Book XII, Underwood et al., 2024). We estimated the mode of the distribution of cell densities for FRST from kernel density plots.

National Land Cover Database (NLCD) Land Cover Analysis

To assess its influence on deer visits to camera traps, we extracted land cover-type from the NLCD in the 1-km² surrounding each camera trap location. Because land cover percentages are naturally complementary, we subjected them to a principal components analysis (PCA) with R package *factoextra* (Kassambara and Mundt, 2020). Land cover-types associated with the camera-trapping network for each surveillance period and year were analyzed separately. PCA consolidates the correlation among land cover-type percentages onto new, uncorrelated variables (i.e., principal components), which can be used as covariates in statistical models of abundance. In our experience, the PCA weights reveal dipole components with one or more land cover-types opposed to others by virtue of sign and magnitude of each eigenvalue. We interpret these dipoles as gradients in land cover which may have some influence on the abundance and distribution of the organism of interest.

Additionally, we extracted NLCD land cover-type percentages along that portion of the distance sampling survey route corresponding to the camera-trapping network during the active surveillance period. Percentages were obtained from a 250-m buffer zone on either side of the road. We selected 250 m as our buffer zone width because it corresponded to the right-truncation distance specified in CDS analyses. A comparison was made by charting the percentages against each other to determine disparities in the land cover sampled by each method.

Distribution of Deer Visits

Finally, to explore potential bias in encounters with different herd segments, we created point-density maps in a GIS (ArcGIS; ver. 10.4, Esri, Redlands, CA) of independent visits of male and female deer (excluding fawns) across the camera-trapping network and overlaid them on the distance sampling survey route and its buffer zone for comparison.

Left-truncation distances for each year were determined by fitting gamma-shaped detection functions (Becker and Quang 2009) to the detection data and recording that distance where the probability of detection equaled 1. In addition, we right-truncated distance data at 250 m. We constructed detection function models with half-normal and hazard-rate key functions, and with two covariates singly and in combination. The first covariate was cluster size to test for size-biased detection (i.e., larger

clusters are more easily detected), and the second covariate was a binary (i.e., 1 or 0) corresponding to whether or not the detection was made in a cluttered field-of-view.

All models were constructed on the same data with the same truncation distances; consequently, we used Akaike's Information Criterion (AIC) to rank and select the model with the smallest AIC as best supported by the data (Burnham and Anderson 2002). Goodness-of-fit testing on selected detection function models was accomplished with Q-Q plots, Kolmogorov-Smirnov, and Cramér-von Mises tests on exact distances. Finally, because we designated whether each detection was made on FRST or BCSP, the software was instructed to produce density estimates for each jurisdiction treating them as geographical strata (Code Book II, Underwood et al., 2024).

Results

Eleven road-based distance sampling surveys were completed in 2020, from 31 July to 3 October. Over 120 km of roadway was driven and an average of 19 clusters and 47 deer per survey were detected (Table 2). From 8 August to 2 October 2021, 13 road-based distance sampling surveys were completed. Over 140 km of roadway was driven and an average of 26 clusters of deer and 57 total deer were detected per survey (Table 3). Surveys took an average of 2.5 hours to complete. The distribution of closest-approach distances in each year revealed a dearth of detections within 30 m of the road. Gamma-shaped detection functions confirmed a necessary left-truncation distance of 18.4 m in 2020, and 30.9 m in 2021, to meet the main assumption of CDS (Figure 7).

Table 2. Details of conventional road-based distance sampling surveys conducted on First State National Historical Park and Brandywine Creek State Park in Delaware and Pennsylvania, USA, 2020.

Date	Start Time	End Time	Total Time (Hours:Minutes)	Total Detections	Total Deer	Distance Travelled (km)
7/31/2020	21:07	23:47	2:40	7	30	10.0
8/1/2020	20:41	22:49	2:08	22	68	10.0
8/21/2020	20:39	23:57	3:18	23	65	10.0
8/22/2020	20:21	23:09	2:48	22	60	10.0
9/11/2020	20:35	22:52	2:17	21	51	11.4
9/12/2020	20:12	22:21	2:09	18	39	11.4
9/18/2020	20:26	23:41	3:15	26	38	11.4
9/19/2020	20:21	22:56	2:35	12	17	11.4
9/25/2020	20:31	22:58	2:27	18	52	11.4
10/2/2020	20:10	22:38	2:28	20	50	11.4
10/3/2020	19:54	23:11	3:17	22	45	11.4
Sums:	–	–	29:22	211	515	120.2

Table 3. Details of conventional road-based distance sampling surveys conducted on First State National Historical Park and Brandywine Creek State Park in Delaware and Pennsylvania, USA, 2021.

Date	Start Time	End Time	Total Time (Hours:Minutes)	Total Detections	Total Deer	Distance Travelled (km)
8/6/2021	20:48	23:25	2:37	25	72	11.1
8/7/2021	20:27	22:55	2:28	23	43	11.1
8/20/2021	20:25	23:02	2:37	23	47	9.8
8/21/2021	20:26	23:17	2:51	22	45	9.8
8/27/2021	20:00	22:50	2:50	22	57	11.1

Table 3 (continued). Details of conventional road-based distance sampling surveys conducted on First State National Historical Park and Brandywine Creek State Park in Delaware and Pennsylvania, USA, 2021.

Date	Start Time	End Time	Total Time (Hours:Minutes)	Total Detections	Total Deer	Distance Travelled (km)
8/28/2021	20:03	22:55	2:52	27	46	9.8
9/10/2021	20:07	23:09	3:02	23	47	11.1
9/11/2021	19:40	22:12	2:32	27	59	11.1
9/17/2021	19:43	22:42	2:59	33	64	11.1
9/18/2021	19:52	22:29	2:37	26	69	11.1
9/24/2021	19:25	21:38	2:13	18	45	11.1
9/25/2021	19:22	21:39	2:17	28	66	11.1
10/1/2021	19:25	22:21	2:56	31	70	11.1
10/2/2021	19:13	22:00	2:47	33	73	11.1
Sums:	–	–	37:38	361	803	118.0

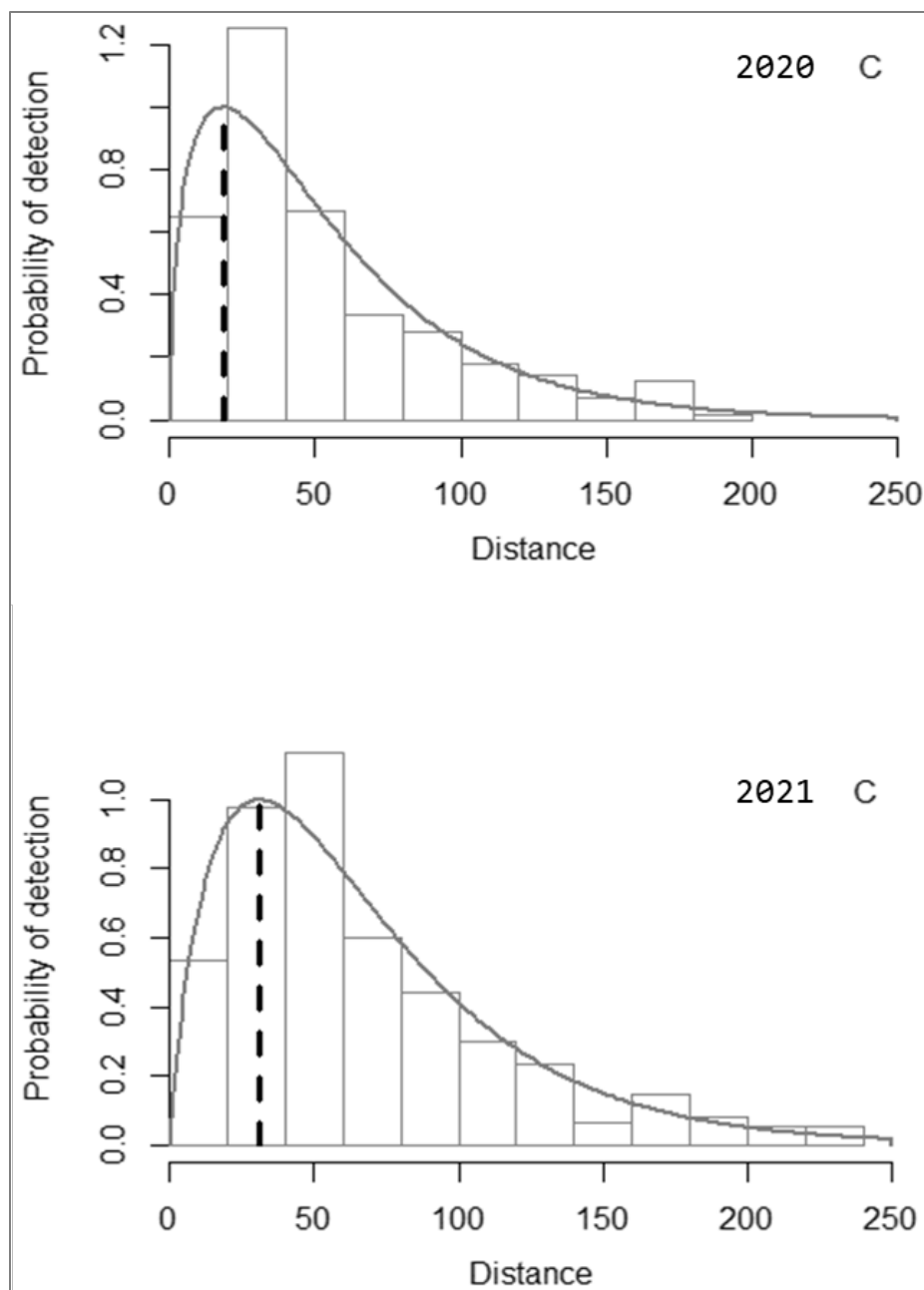


Figure 7. Modeled, gamma-shaped detection functions identifying the left truncation distance required to meet the main assumption of distance sampling (i.e., $g[0] = 1$).

After truncation, model selection with two key functions (i.e., half-normal and hazard-rate) and two covariates (i.e., cluster size and presence/absence of clutter) indicated support for the half-normal detection function and the binary covariate indicating clutter in the field of view for the 2020 data (Table 4, Figure 8). For 2021, model selection best supported a hazard-rate key function with the additive effects of cluster size and clutter on probability of detection (Table 5, Figure 8). A map of cluster detections by year is presented in Figure 9. Models for both years demonstrated acceptable goodness-of-fit characteristics (Figure 10). The resulting density for FRST was 30.7 deer/km² (95%

CI: 22.2–42.4) in 2020 and 31.2 deer/km² (95% CI: 19.5–50.1) in 2021. Estimated densities for BCSP and for the combined study areas are provided for comparison (Table 6).

Table 4. Candidate detection function models from road-based distance sampling surveys of white-tailed deer conducted on First State National Historical Park and Brandywine Creek State Park in Delaware and Pennsylvania, USA, 2020. Covariates included cluster size (C_1) and obstruction of the field of view at each detection (C_2).

Model	Covariates	df ^A	AIC ^B	Δ AIC
Half-Normal	C_2	2	1668.7	0.0
Half-Normal	C_1+C_2	3	1670.0	1.3
Hazard Rate	C_2	3	1670.9	2.1
Hazard Rate	C_1+C_2	4	1672.7	4.0
Half-Normal	None	3	1698.3	29.6
Hazard Rate	None	2	1701.1	32.4
Hazard Rate	C_1	3	1702.9	34.2
Half-Normal	C_1	2	1710.3	41.6

^A df = Satterthwaite degrees of freedom

^B AIC = Akaike's Information Criterion

Table 5. Candidate detection function models from road-based distance sampling surveys of white-tailed deer conducted on First State National Historical Park and Brandywine Creek State Park in Delaware and Pennsylvania, USA, 2021. Covariates included cluster size (C_1) and obstruction of the field of view at each detection (C_2).

Model	Covariates	df ^A	AIC ^B	Δ AIC
Hazard Rate	C_1+C_2	4	2564.5	0.0
Hazard Rate	C_2	3	2570.0	5.5
Half-Normal	C_1+C_2	3	2576.3	11.8
Half-Normal	C_2	2	2580.0	15.5
Half-Normal	None	2	2606.3	41.8
Hazard Rate	C_1	3	2606.4	41.9
Half-Normal	None	2	2608.2	43.7
Half-Normal	C_1	2	2616.5	52.0

^A df = Satterthwaite degrees of freedom

^B AIC = Akaike's Information Criterion

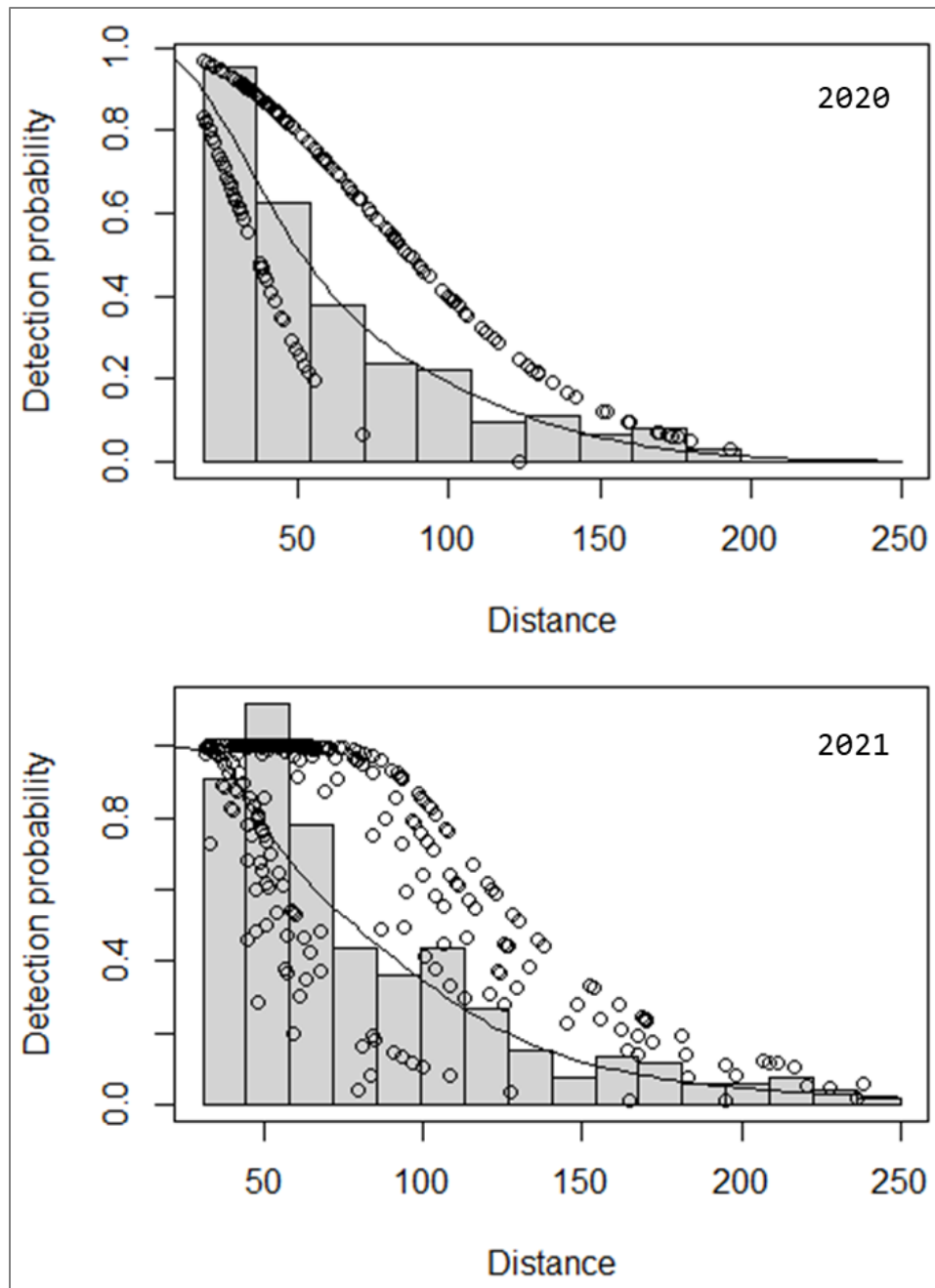


Figure 8. Best-fit detection functions for each year ($\Delta AIC=0$) from road-based distance sampling surveys conducted during 2020 and 2021 for the First State National Historical Park and Brandywine Creek State Park in Delaware and Pennsylvania, USA.

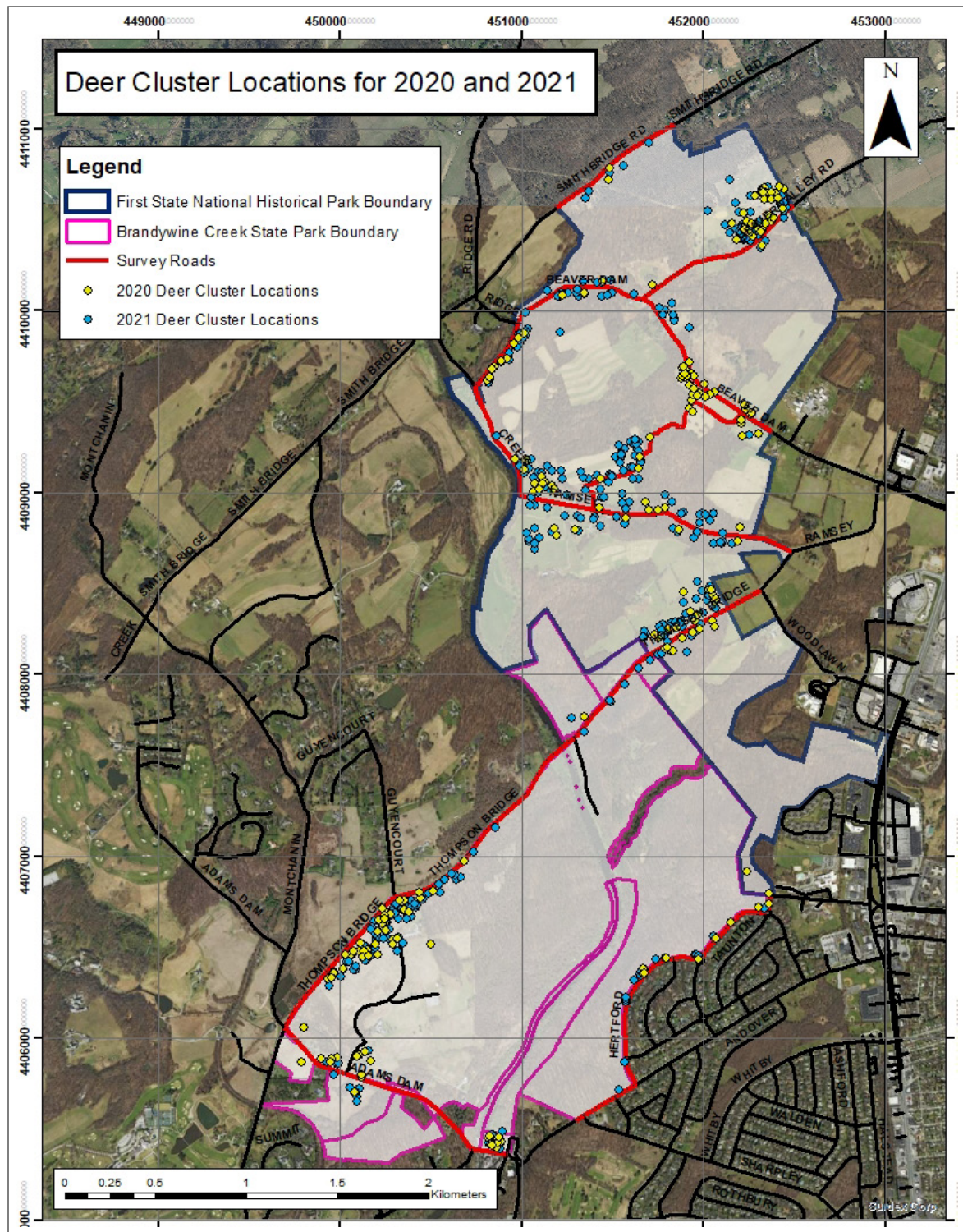


Figure 9. Mapped deer cluster locations from road-based distance sampling surveys conducted during 2020 and 2021 for the First State National Historical Park and Brandywine Creek State Park in Delaware and Pennsylvania, USA.

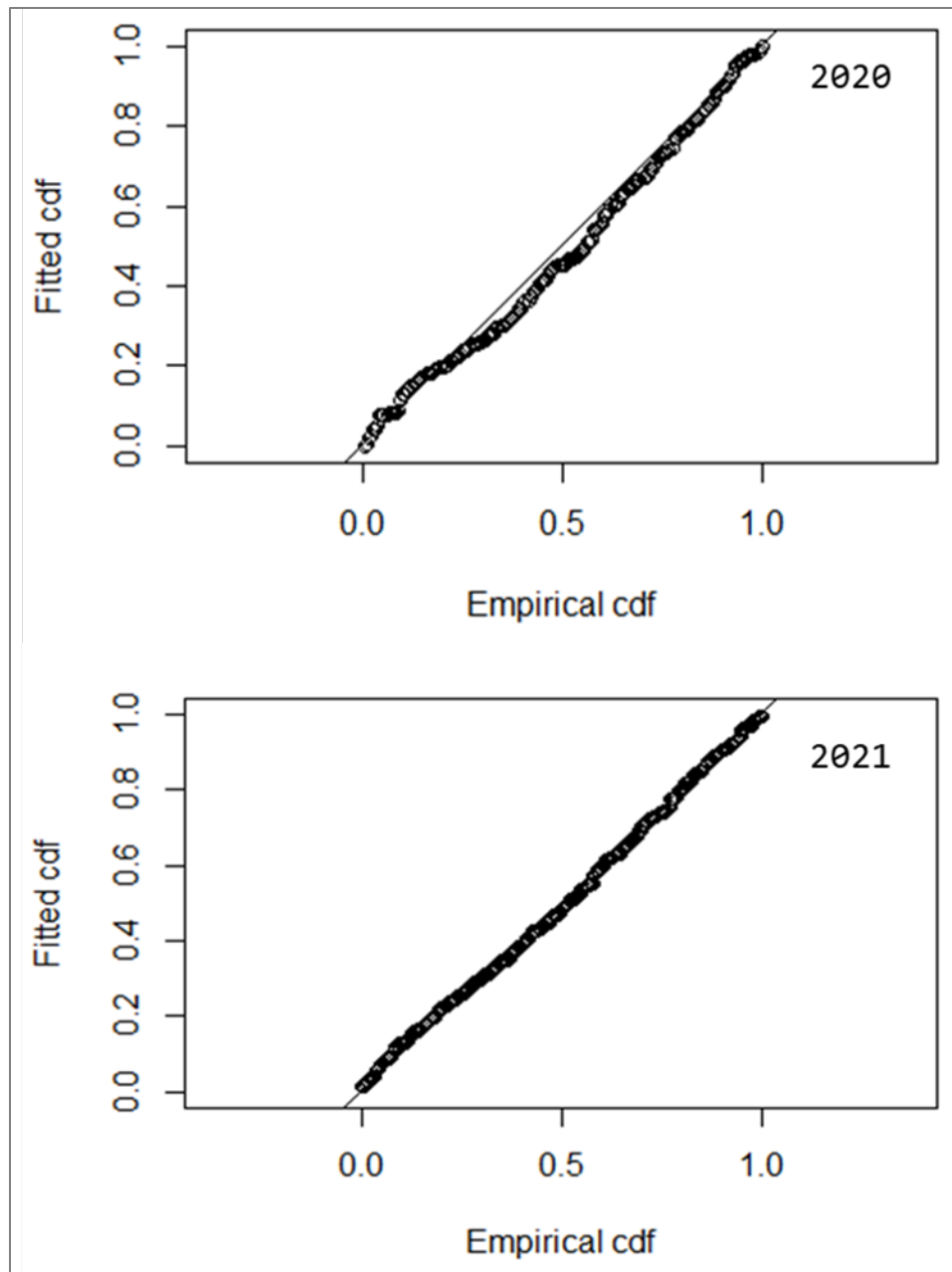


Figure 10. Plots of empirical versus fitted cumulative distribution functions of fitted detection models from road-based distance sampling data collected during 2020 and 2021 for the First State National Historical Park and Brandywine Creek State Park in Delaware and Pennsylvania, USA.

Table 6. White-tailed deer density (No./km²) estimated from road-based distance sampling conducted in 2020 and 2021 on First State National Historical Park (FRST) and Brandywine Creek State Park (BCSP) in Delaware and Pennsylvania, USA.

Year	Jurisdiction	Density	%CV ^A	df ^B	Lower 95% Control Limit	Upper 95% Control Limit
2020	FRST	30.7	16.5	182.4	22.2	42.4
2021	FRST	31.2	24.4	366.2	19.5	50.1
2020	BCSP	30.4	18.3	75.4	21.2	43.6
2021	BCSP	22.9	22.2	90.1	14.8	35.4
2020	Combined	30.6	12.9	278.1	23.7	39.3
2021	Combined	27.7	20.0	386.3	18.7	40.8

^A CV = coefficient of variation

^B df = Satterthwaite degrees of freedom

In 2020, we deployed 12 camera traps, initiating active surveillance on 11 September and finishing on 2 October. We processed 33,600 camera trap images, of which 19,179 contained deer. In 2021, we deployed 16 camera traps, initiating active surveillance on 10 September and finishing on 2 October. With four additional camera traps and the switch from 3 photos per trigger event to 5, we processed 84,346 camera images of which 63,708 contained deer. We recorded 2,112 and 3,364 independent visits to camera traps in 2020 (Table 7) and 2021 (Table 8), respectively.

Table 7. Independent visits recorded during a baited camera-trapping survey conducted from September to October in 2020 in First State National Historical Park in Delaware and Pennsylvania, USA.

Camera	Independent Visits		
	Fawns	Females	Males
1	79	95	43
2	52	64	44
3	51	80	25
4	78	106	22
5	10	17	81
6	16	47	5
7	72	97	29
8	70	130	40
9	44	43	60
10	49	56	91
11	51	108	86
12	80	60	31
Sum:	652	903	557

Table 8. Independent visits recorded during a baited camera-trapping survey conducted from September to October in 2021 in First State National Historical Park in Delaware and Pennsylvania, USA.

Camera	Independent Visits		
	Fawns	Females	Males
1	91	136	47
2	79	105	74
3	41	78	45
4	26	79	39
5	35	50	95
6	44	107	29
7	34	82	89
8	80	147	70
9	52	82	46
10	7	56	114
11	100	124	1
12	108	89	36
13	60	88	128
14	27	78	59
15	81	100	59
16	14	77	76
Sum:	879	1478	1007

During 2020, in the 20 days comprising occasions 2–21, we detected 82 identifiable antlered deer, 13 of which used >1 camera trap. Similarly, in the 20 days comprising occasions 3–22, we detected 108 identifiable antlered deer in 2021, 36 of which used >1 camera trap. The mean maximum distance moved by these deer was 932.4 m in 2020 and 1045.5 m in 2021 (Figure 11). When constrained to common camera trap locations between years, the number of identifiable antlered deer detected in 2021 was reduced to 96, of which 25 were detected at >1 camera trap and exhibited a mean maximum distance moved of 1042.7 m.

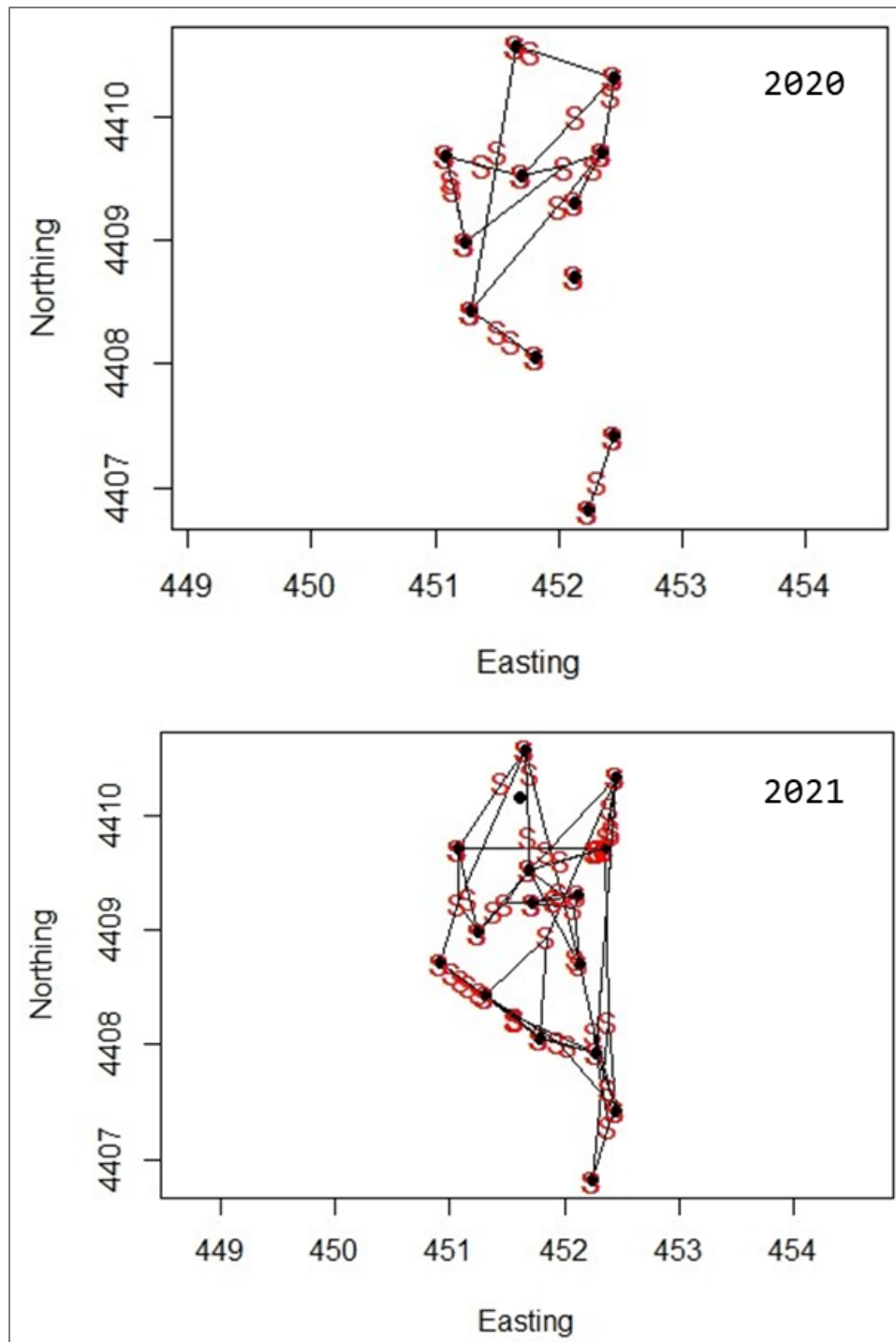


Figure 11. Documented movements of identifiable, male white-tailed deer during a baited camera-trapping survey conducted from September to October in 2020 and 2021, First State National Historical Park in Delaware and Pennsylvania, USA. Filled circles are trap locations. Deer using >1 camera trap shown by connecting lines, and “S” indicates estimated activity center.

Using R-package *secr*, model b_k (i.e., $SECR_b$) was best supported by the data among the three models tested (Table 9), indicating a strong positive, behavioral response of antlered deer to the presence of

bait. The area of the estimated state-space (i.e., the area within which there is a non-zero probability of encountering a male deer) was smaller in 2020 (45.1 km²) than in 2021 (61.3 km²), both many times larger than the size of the administrative boundary of FRST.

The Bayesian model, SCR_b , produced densities of antlered deer in both years similar to those estimated from $SECR_b$, confirming the proper Bayesian model structure (Table 10). However, these models exhibited poor fits to the data (Bayesian p-values >0.9; Appendix C, Appendix D). Models SCR_{Mh} , on the other hand, exhibited acceptable goodness-of-fit characteristics (0.1 < Bayesian p-value < 0.9) once individual-by-trap heterogeneity was accounted for with random effects (Appendix E, Appendix F). In addition, all SCR models produced lower mean buck densities in 2021 than in 2020, though most are not significantly different within the variability of the data (Table 10). Estimated total deer density on FRST from SCR_{Mh} was 48 deer/km² in 2020 and 30 deer/km² in 2021 (Table 11).

Table 9. Candidate *secr* models resulting from data collected during baited camera-trapping surveys in 2020 and 2021 on First State National Historical Park in Delaware and Pennsylvania, USA.

Year	Model ^A			Detection Function	# Parameters	AIC	AICc	$\Delta AICc$	AIC Wt. ^B
	Primary Suffix	Secondary Suffix	Tertiary Suffix						
2020	bucks_bk	D~1 g0~bk	sigma~1	halfnormal	4	2592.5	2593.0	0.0	1
	bucks_b	D~1 g0~b	sigma~1	halfnormal	4	3075.3	3075.9	482.8	0
	bucks_0	D~1 g0~1	sigma~1	halfnormal	3	3123.4	3123.7	530.7	0
2021	bucks_bk	D~1 g0~bk	sigma~1	halfnormal	4	4799.4	4799.8	0.0	1
	bucks_b	D~1 g0~b	sigma~1	halfnormal	4	6309.2	6309.6	1509.7	0
	bucks_0	D~1 g0~1	sigma~1	halfnormal	3	6356.3	6356.6	1556.7	0

^A Model suffixes ending in “b” test for global (b) and local (bk) behavioral responses to the presence of bait; suffix ending in “0” is the null model with no covariates.

^B AIC Wt. is the weight of evidence in favor of the model using Akaike’s Information Criterion. Larger AIC weights indicate better support of the model in the dataset.

Table 10. Buck density and 95% credible intervals estimated using spatial capture-recapture (SCR). Data were collected from baited camera-trapping surveys in 2020 and 2021 on First State National Historical Park in Delaware and Pennsylvania, USA.

Year	Method	Buck Density (deer/km ²)	95% CI	
			Lower Control Limit	Upper Control Limit
2020	SECR _b *	13.0	8.1	20.9
	SCR _b	13.9	8.8	19.3
	SCR _{Mh}	10.1	8.0	12.5
2021	SECR _b *	8.4	6.3	11.1
	SCR _b	7.6	5.8	9.9
	SCR _{Mh}	8.2	6.8	9.8

* Confidence interval for this model. Models using classical paradigms (SECR) help verify Bayesian models (SCR).

Table 11. Total deer density and its uncertainty estimated from conventional distance sampling (CDS), spatial capture-recapture (SCR), and density surface modeling (DSM). Data were collected from road-based distance sampling and baited, camera-trapping surveys in 2020 and 2021 on First State National Historical Park (FRST) and Brandywine Creek State Park (BCSP) in Delaware and Pennsylvania, USA.

Year	Method	Buck Density (deer/km ²)	95% CI	
			Lower Control Limit	Upper Control Limit
2020	CDS _{FRST}	30.7	22.2	42.4
	CDS _{FRST+BCSP}	30.6	23.7	39.3
	SCR _{Mh} *	48.0	37.9	59.8
	DSM	51.2	–	–
2021	CDS _{FRST}	31.2	19.5	50.1
	CDS _{FRST+BCSP}	27.7	18.7	40.8
	SCR _{Mh} *	30.2	25.1	36.2
	DSM	73.1	–	–

* Credible interval for this model.

Visits of unidentifiable antlered deer as a proportion of independent visits of all antlered deer was approximately 18% for both 2020 and 2021, resulting in an estimated total population of 328 (Bootstrap 95% CI: 305–352) deer in 2020 and 381 (Bootstrap 95% CI: 362–401) deer in 2021 with the JM estimator (Table 12). The ratio of females:males in camera visits was 1.37 (Bootstrap 95% CI: 1.25–1.51) in 2020 and 1.24 (Bootstrap 95% CI: 1.16–1.34) in 2021. However, the ratio of fawns to females was significantly lower in 2021 (0.595; 95% Bootstrap CI: 0.547–0.645) than in 2020

(0.722; 95% Bootstrap CI: 0.658–0.802). Using the same data, BE estimated a total buck population of 93 (95% CI: 87–100) for 2020, and 122 (95% CI: 115–130) for 2021 (Table 12).

Modeled site-specific abundance estimated from HM_h was not significantly affected by land cover-type in 2020, but two significant components emerged in 2021 (Appendix G, Appendix H). Estimated total population size exhibited acceptable precision (i.e., $\leq 20\%$ of the mean in each year), and was smaller in 2021 than in 2020 (Table 13). During 2020, mean population size from JM was about 100 deer smaller than estimated from model HM_h ; however, estimates were similar in magnitude during 2021 (Table 13).

Based on the Poisson/Poisson N-mixture models with auxiliary CDS abundance, deer distribution across the forested areas of the study site during the passive surveillance period differed between years (Figure 12). In 2020, the lowest relative abundance occurred on BCSP while the highest occurred on FRST but no clear gradient emerged. However, during 2021 there was a discernable south to north trend in relative abundance with the least in BCSP and the most in FRST. The models exhibited acceptable goodness-of-fit (Appendix I, Appendix J).

There were 14 different land cover-type classes represented in the NLCD for the study area during the active surveillance period. Deciduous Forest and Hay/Pasture composed the vast majority ($\sim 75\%$) of land cover around camera traps and along the distance sampling survey route with Developed Open Space and Agricultural Crops ranking a distant 2nd and 3rd place (Figure 13). Developed land cover-types were slightly more represented in the 1-km² around camera traps than within the distance sampling survey route buffer. Otherwise, there was no discernable difference in land cover around the camera traps compared with the 250-m buffer zone along the distance sampling survey route.

Table 12. Total population size estimated by Jacobson’s Method (JM) and Bowden’s Estimator (BE) from data collected during a baited camera-trapping survey conducted from September to October in First State National Historical Park in Delaware and Pennsylvania, USA. Lower confidence limit (LCL) and upper confidence limit (UCL) are 0.025 and 0.975 percentiles of bootstrapped visit distributions.

Method	Year	Buck			Doe			Fawn			Total Deer		
		Total	LCL	UCL	Total	LCL	UCL	Total	LCL	UCL	Total	LCL	UCL
JM	2020	97	96	98	134	120	148	97	87	108	328	305	352
	2021	127	125	129	159	147	172	94	86	103	381	362	401
BE	2020	93	87	100	–	–	–	–	–	–	–	–	–
	2021	122	115	130	–	–	–	–	–	–	–	–	–

Table 13. White-tailed deer population estimates from Jacobson's Method (JM) and a hierarchical multinomial mixture (HM_h) model. Data were collected during 2020 and 2021 on First State National Historical Park (FRST) in Delaware and Pennsylvania, USA.

Year	Method	Population Size	95% CI	
			Lower Control Limit	Upper Control Limit
2020	JM	328.0	305.0	352.0
	HM _h	452.1	318.3	591.3
2021	JM	381.0	362.0	401.0
	HM _h	370.3	275.5	471.5

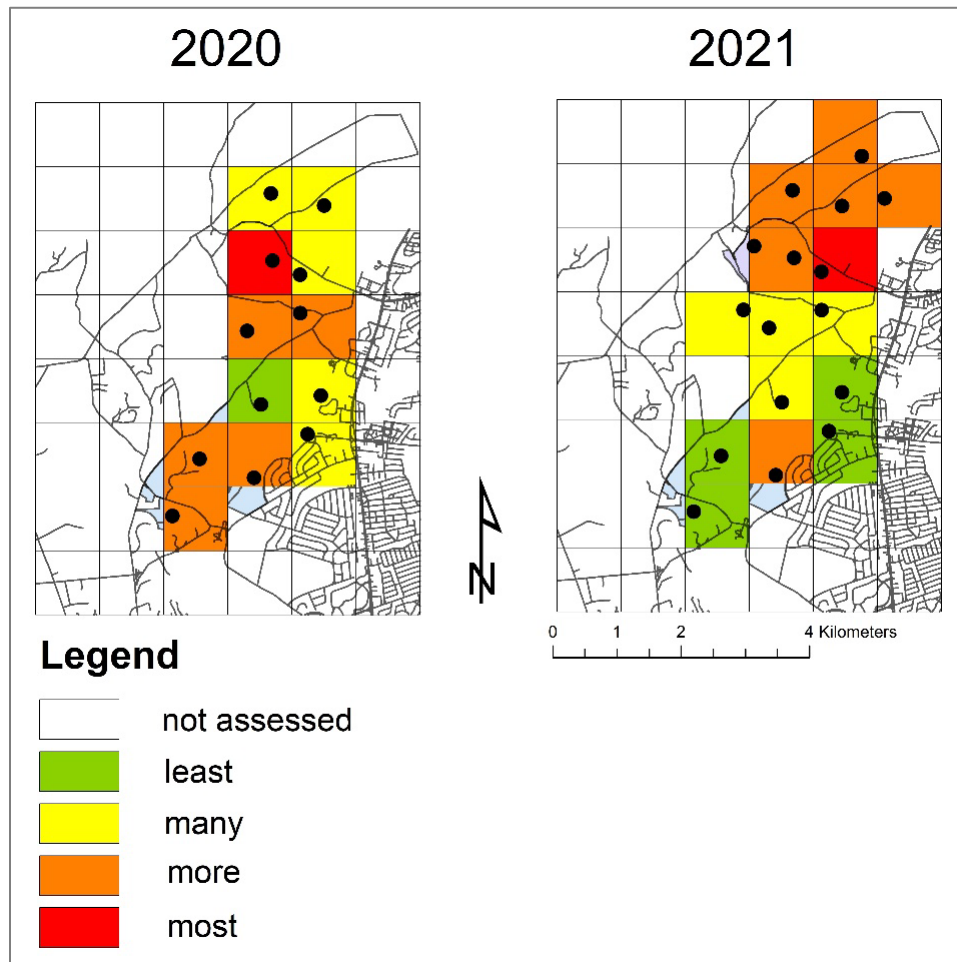


Figure 12. Distribution of white-tailed deer by year derived from a Poisson/Poisson N-mixture model of camera-trapping data collected on First State National Historical Park and Brandywine Creek State Park in Delaware and Pennsylvania, USA. This model uses auxiliary abundance estimated from road-based distance sampling as an informed prior.

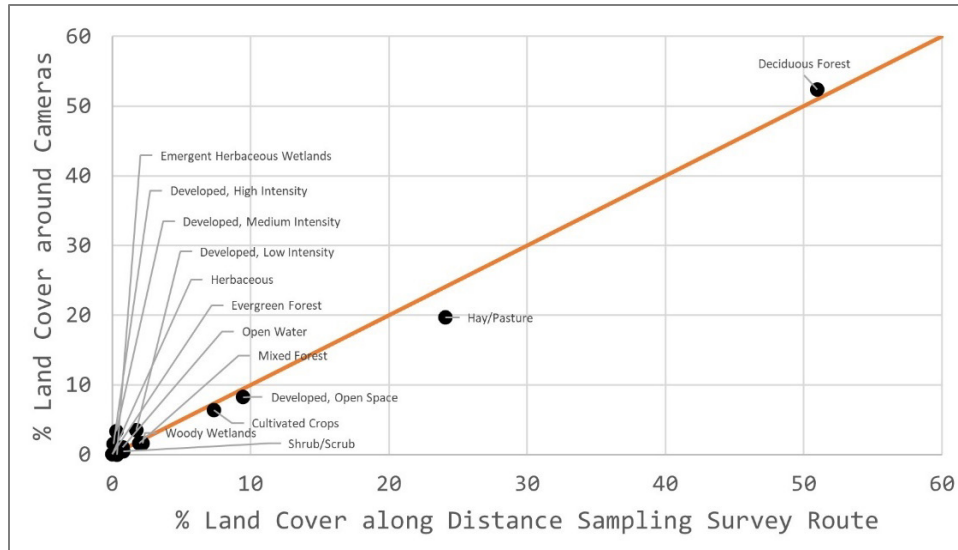


Figure 13. Percent land cover extracted from 1-km² cells surrounding each camera trap and within a 250 m buffer along the distance sampling survey route, First State National Historical Park, Chester County, Pennsylvania and New Castle County, Delaware, USA. Diagonal represents the 1:1 line.

The mode of the distribution of pixel densities on FRST estimated from our version of DSM was 42.2/km² in 2020 and 54.3/km² in 2022. Encounter probabilities associated with 1) proximity of each pixel to the survey route, 2) proportion of vegetation clutter, and 3) overall probability of encounter are shown in Figures 14 and 15. In addition, the spatial distribution of random effects on encounter rate are also shown along with the density surface. Density variation was consistent across FRST, but was substantially higher across BCSP. Mean modeled cluster size was slightly lower in 2021 than in 2020 (2.218 vs. 2.434). Total estimated population size for the combined study areas was 651 deer (591–719) during 2020 (Appendix K) and 1032 (952–1112) during 2021 (Appendix L).

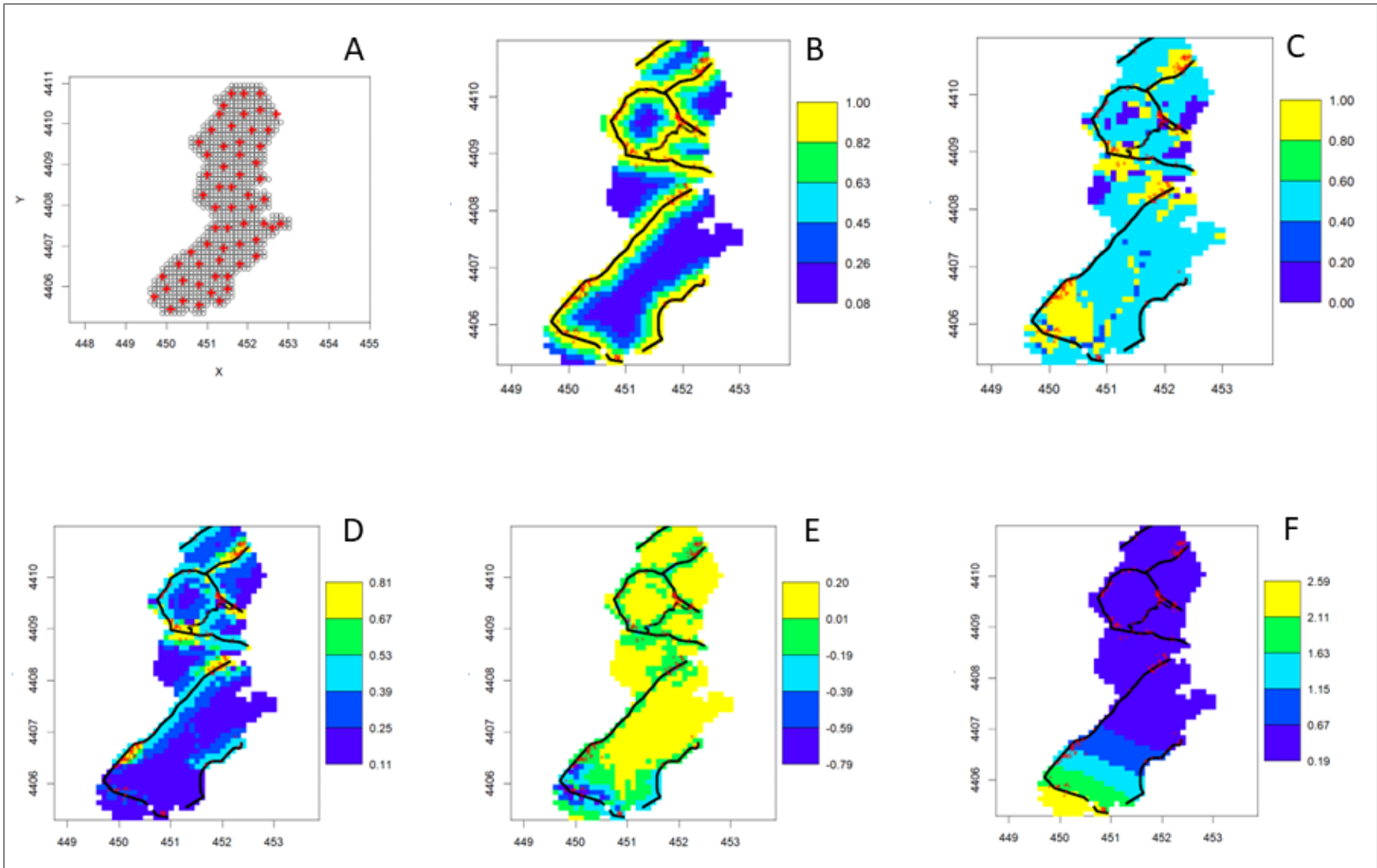


Figure 14. Knot locations (A), deer encounter probability from survey route (B), land cover probability of encounter (C), overall probability of encounter (D), pixel random effect (E), and estimated deer density (No./ha) for 2020 (F), First State National Historical Park and Brandywine Creek State Park, Chester County, Pennsylvania and New Castle County, Delaware, USA.

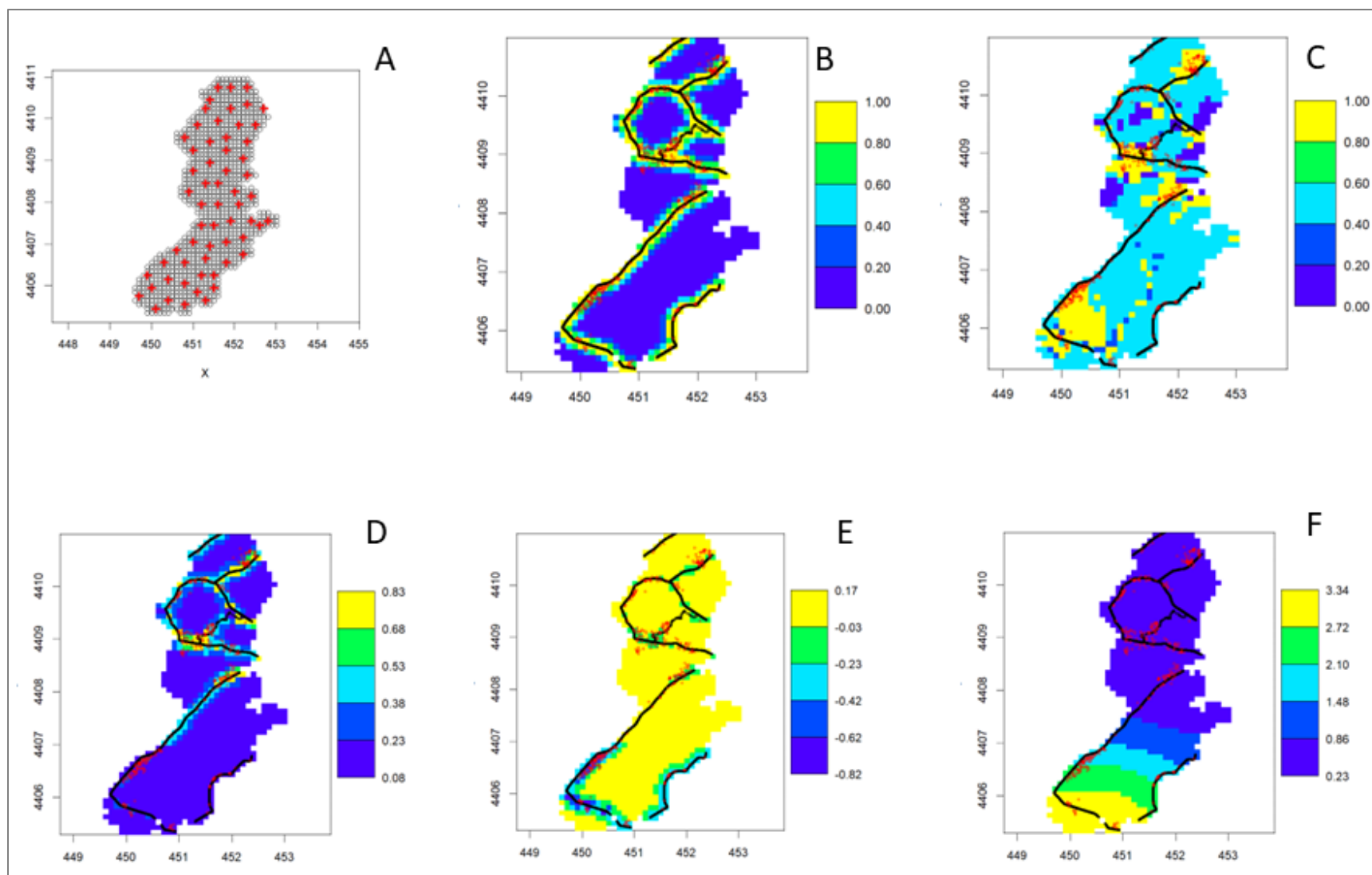


Figure 15. Knot locations (A), deer encounter probability from survey route (B), land cover probability of encounter (C), overall probability of encounter (D), pixel random effect (E), and estimated deer density (No./ha) for 2021 (F), First State National Historical Park and Brandywine Creek State Park, Chester County, Pennsylvania and New Castle County, Delaware, USA.

Point-density (50-m output resolution, 564.2-m search radius, 9 classes of equal intervals) maps derived from independent visits at camera traps revealed pronounced spatial segregation among male and female deer (Figure 16). The pattern of spatial segregation was relatively consistent between years (Figure 17).

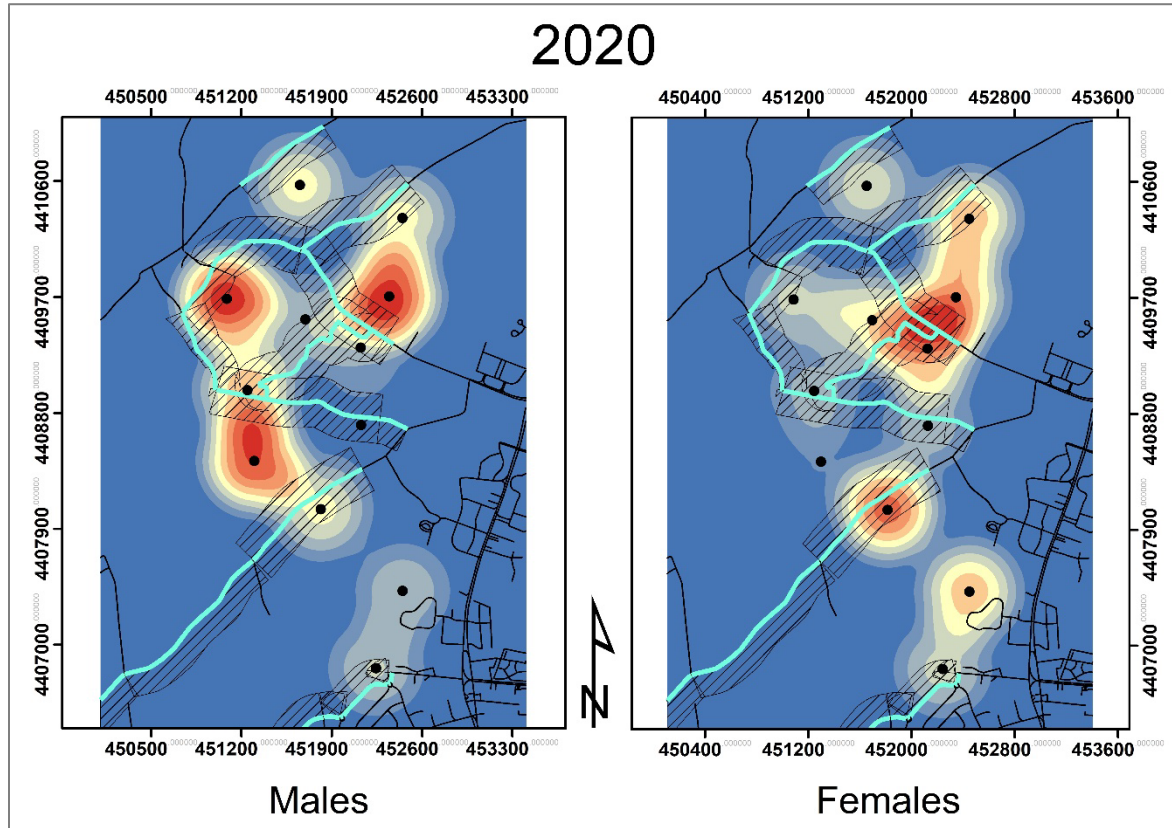


Figure 16. Distribution of camera trap visits by sex relative to the distance sampling survey route (hatched areas) during the active surveillance period on First State National Historical Park during 2020, Chester County, Pennsylvania and New Castle County, Delaware, USA. Distance sampling survey shown (cyan line) for reference.

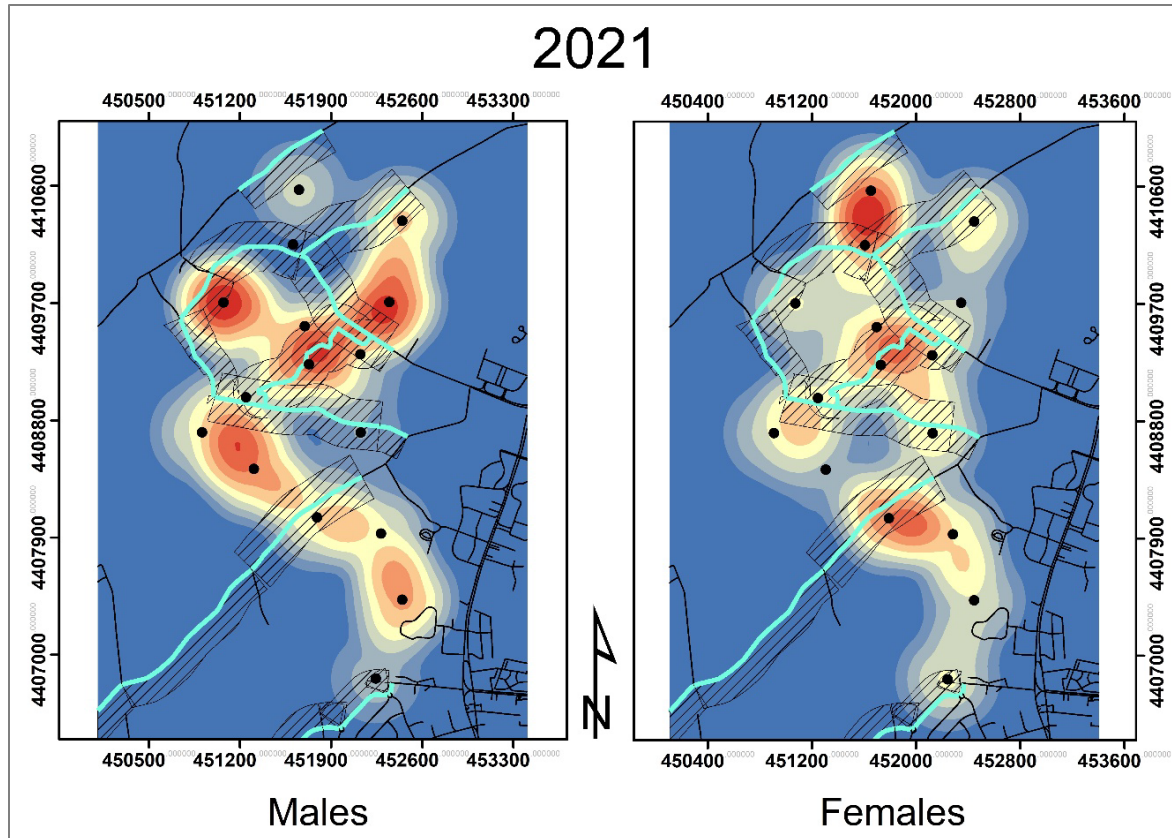


Figure 17. Distribution of camera trap visits by sex relative to the distance sampling survey route (hatched areas) during the active surveillance period on First State National Historical Park during 2021, Chester County, Pennsylvania and New Castle County, Delaware, USA. Distance sampling survey shown (cyan line) for reference.

Discussion

The primary concerns with road-based surveys for deer are that important habitat features of land cover-types may not be adequately represented (McCullough 1982), that deer may be attracted or repelled by land cover-types associated with roads (McShea et al. 2011, Beaver et al. 2014), or that certain herd segments may be underrepresented in counts (McCullough et al. 1989, Johnson et al. 2021). While we found no discernable difference in land cover-types between the distance sampling survey route and the camera-trapping network, our CDS density estimates were 10–20 deer/km² lower than density estimated from either SCR or DSM. By comparison, density estimates from *SCR_{Mh}* and DSM were similar to the 52 deer/km² derived from a forward-looking infrared (FLIR) count of New Castle County in 2005 (Rogerson 2010). The FLIR count was contracted by the Delaware Division of Fish & Wildlife prior to a statewide initiative to reduce overall deer population numbers through more liberal harvest regulations.

The precise causes of downward bias in CDS estimates in our study remain speculative, but we offer some considerations. First, if we overestimated the effort expended during road-based counts, the denominator in the formula for density would be too large resulting in density estimates biased low. We diligently attempted to discount sections of the survey route that could not be adequately surveyed, but over long distance, varied terrain and land cover, this is not an easy task.

Second, while we anticipated a gradient in deer density south (low) to north (high), evidence in support of such a gradient in our study is conflicting. Deer distribution derived from camera trap visits during the passive surveillance period conformed to that expectation, especially for 2021. However, DSM models consistently suggested a gradient of deer density in the opposite direction. We believe the conflict is at least partially resolved by the fact that camera traps were only located in forested land cover, while detections of deer at night were made predominantly in non-forested land cover-types. Deer whose home ranges incorporate both forested and non-forested land cover, often redistribute themselves out of concealment cover and into non-forested land cover-types at night in search of forage (McCullough et al. 1989). Consequently, both gradients could be correct, but because camera traps record visits throughout the diel, we believe the resulting distribution is more realistic.

Third, because land cover-type was similar between the distance sampling survey route and the camera-trapping network, segregation between the sexes and its influence on their encounter rates at night could have contributed to the difference in estimated density between CDS and the other methods. Sexual segregation, both spatial and temporal, during the non-breeding season (approximately January–September) is the rule rather than the exception in deer (Kie and Boyer 1999, Barboza and Boyer 2000). McCullough et al. (1989) reported indices of overlap between the sexes ranging between 45–57% during summer and autumn. The locations of activity centers of males and females relative to the distance sampling survey route could have biased the representation of deer in our night-spotlighting counts if either of the sexes was underrepresented (Johnson et al. 2021).

Though from a distance it was often difficult to discern antlers, we encountered relatively fewer bucks during distance sampling surveys compared with visits recorded at baited camera traps. We typically conducted multiple road-based counts throughout the survey period in an attempt to maximize the probability of encountering all sex- and age-segments of the population. However, travel restrictions imposed early in the SARS-CoV-2 pandemic prevented the conduct of additional surveys.

Finally, because we do not know the true population size, we have to rely on corroborating evidence and our collective experience. Coverage was not an issue with camera-trapping — it was the primary justification for its use. Density and abundance estimates derived from the camera-trapping data were relatively consistent, though the hierarchical methods tended to produce larger estimates with more reasonable uncertainty than the closed-population capture-recapture methods. The pixel-based approach to DSM eliminated the need for accounting for effort — an error-prone but critical exercise for proper CDS density estimation; all that is necessary for DSM is to map the location and record the number of deer in each cluster detected.

Despite criticism, road-based distance sampling has been used successfully to support population management decisions for deer and other wildlife species in protected natural areas across the country and elsewhere (Underwood et al. 2003, Underwood and Knutson 2011, Morelle et al. 2012, Montague et al. 2017, Haus et al. 2019). In our experience, all abundance estimates contain bias. In this study, we presumed that bias was an important consideration, but not the only one, which is why we adopted the approach outlined previously.

Fully model-based solutions like DSM will eventually replace CDS whereby mapped detections of deer are modeled as functions of covariates or thin-plate regression splines in a GAM (Miller et al. 2013, Kéry and Royle 2016). Model-based inference is possible from a survey without depending upon a random sampling design, although a well-designed survey is always preferred (Miller et al. 2013). As the availability of spatially referenced data increases, we expect these kinds of models to play more important roles in population abundance estimation.

Comparison of Methods

In our study, the use of bait resulted in a five-fold increase in visitation rates of deer at camera traps relative to the passive surveillance period. Baiting in camera-trapping studies is primarily used in situations where encounters with the target species are rare (du Preez et al. 2014). However, baiting is necessary when using JM in order to identify as many bucks as possible (Jacobson et al. 1997). In a study of buck resource selection, Johnson et al. (2021) observed that while space-use within the home-range was affected by the short-term presence of bait, the distribution of home-ranges on the landscape was not. Baiting also induces a strong, behavioral response in deer that manifests as unexplained variance in most of the models we applied in this study. Consequently, models need to be robust to this kind of heterogeneity or include random effects to explicitly account for it (Kéry and Royle 2016).

Like Curtis et al. (2009) and Dougherty and Bowman (2012), population sizes estimated from JM and BE agreed closely in our study. But for not entirely clear reasons, they produced larger population estimates for 2021 relative to 2020. Despite their simplicity, JM and BE lack a number of biologically relevant variance components for a camera-trapping application, which results in confidence intervals that are overly precise in our opinion. Other methods we used either explicitly or implicitly embraced spatial aspects of deer encounters and produced more realistic estimates of uncertainty. We believe that addressing key sources of uncertainty in estimation, especially due to individual heterogeneity in visitation (Link 2004) is intellectually honest, important for transparency, and prudent for informed decision-making.

The JM protocol has at least two modifications in the literature that depart from the original proposed in Jacobson et al. (1997). The first computes a *population factor* based on the ratio of unique bucks relative to the total number of images containing bucks, then applies that factor to the other herd segments (Hammerick et al. 2013). Both Haus et al. (2019) and Kilheffer et al. (2019) used this version in their studies of white-tailed deer. We did not use this version of JM because the population factor makes the assumption that all herd segments have the same photographic or visitation rates as antlered bucks, which we believe is unrealistic. Instead, we calculated the buck population from visitation rates relative to unknown bucks, and then used ratios of female:male and fawn:female occurrences in camera visits to compute the size of remaining herd segments. The original formulation of JM assumes that the ratios of total occurrences in camera images are representative of the population, which we believe is a more reasonable assumption to make.

The other variant of JM is the standardized version suggested by Weckel et al. (2011) presumably to account for over/under-representation of certain herd segments in camera trap images. Schmidt et al. (2017) developed a camera-trapping protocol for deer on national wildlife refuges that uses this variant. Compared to the conventional formulation, the standardized variant seemed to erode some precision in their bootstrapped confidence intervals around abundance, but their sample of identifiable males was much smaller than ours. To account for proper representation of herd segments, we used independent visits at camera traps rather than the Weckel et al. (2011) modification.

Only one relevant study compared conventional capture-recapture methods with SCR (Beaver et al. 2016). In order to make the comparison, Beaver et al. (2016) divided abundance from JM into the administrative boundary of their study area. This practice almost always induces a positive bias in calculated density because the state-space tends to include area beyond the administrative boundary, which is not accounted for in the denominator (Foster and Harmsen 2012). This situation is especially true if bait is used to increase encounter rates.

Two studies assessed the N-mixture model with either a known herd size (Keever et al. 2017) or with another method (Haus et al. 2019) and generally reported close agreement. A significant caveat of the N-mixture model is that the effective area surveyed is assumed rather than known or estimated (Kéry and Royle 2016). Implicit in that assumption is that deer visit no more than a single camera trap in a given sampling occasion. We chose a camera density of approximately 1 per square kilometer during

the passive surveillance period, which is consistent with what we know about space-use in suburban and other high-density deer herds (Underwood and Kilheffer 2016). In our study, the mean maximum distance moved by male deer was <1500 m. Given that home-range size in female deer is typically smaller during spring and summer (Tierson et al. 1985, Dechen Quinn et al. 2013), our camera spacing selection seemed appropriate.

Finally, one study compared road-based distance sampling with a conventional capture-recapture method (Haus et al. 2019). Comparing a method that explicitly estimates the effective area sampled (CDS or SCR) with one that does not (JM or BE) requires a conversion to either population size or density, which is rarely satisfactory as previously mentioned. For example, Haus et al. (2019) computed density by dividing their version of JM into an arbitrary area surrounding their camera-trapping network, which resulted in much higher values in two of three survey periods when compared with CDS. In all likelihood, the area selected was too small to accommodate the full extent of movements by identifiable bucks around the camera-trapping network. To our knowledge, ours is the first application of DSM for estimating deer abundance in a small, protected natural area like FRST.

Management Implications

In small protected natural areas, any method used to estimate deer population abundance needs to balance time (i.e., labor), expense (i.e., equipment and supplies) and statistical rigor. Time and expense are always important considerations when staff and budgets are limiting, but some trade-offs may be made between them. The amount of statistical rigor required will often depend on whether management actions are likely to be controversial, or where litigation is anticipated.

Road-based distance sampling is the least expensive method for estimating density of deer in small, protected natural areas like FRST (Underwood and Knutson 2011), but has the highest potential for bias unless density is estimated from DSM (Appendix M). There is minimal investment in equipment and a single survey of 12 km (a minimum requirement) in length can be completed in about 3 hours. In addition, data from multiple surveys can be pooled for efficient parameter estimation. A disadvantage of road-based distance sampling conducted at night is that herd composition counts are challenging to conduct reliably.

With camera-trapping, there is an initial investment in cameras and associated materials, but these costs can be amortized over several years. Camera traps can be placed for very long durations before battery depletion (i.e., up to 1 year), but are typically monitored more frequently for routine maintenance. Passive surveillance (i.e., no baiting) using the meta-population design is straightforward to conduct with camera traps (e.g., Keever et al. 2017). However, sufficient sites and occasions for application of the N-mixture models of Royle (2004) may be challenging to achieve due to a lack of spatial scope as a consequence of the home range size of deer (Keiter et al. 2017). To compensate, a longer study duration will be necessary (Kéry and Royle 2016), but incurs an increased risk of population closure violations. The PPNmix alternative we propose is appealing because it preserves the conventional meta-population application and avoids closure violations by using auxiliary abundance to estimate important model parameters (Clawson et al. 2013) without extending the surveillance period. However, if auxiliary abundance is biased, so too will be the modeled abundance from PPNmix.

Identification of male deer is necessary in order to use conventional closed population capture-recapture models (i.e., JM or BE), SCR or HM_h for estimating deer abundance or density. In high-density deer herds, this is no trivial task and will require a significant investment in time. In addition, tracking individual male deer across multiple camera traps for SCR analysis is a tedious, time-consuming job. Complete capture histories of identifiable deer are not necessary for estimating abundance with JM, which is why the method is so popular despite the fact that it lacks biologically realistic variance components.

The most sophisticated methods for estimating wildlife abundance account explicitly for false-negative (i.e., missed animals) or false-positive (i.e., double counting) detection (Williams et al. 2002). This is accomplished either through replicated counts (e.g., N-mixture modeling) or by directly estimating the effective area sampled using methods like CDS, SPR, or DSM. Conventional or FLIR-based aerial surveys are costly to replicate (Garner et al. 1995, Porter and Underwood

2001), and the use of uncrewed aerial vehicles (UAVs) over small protected natural areas is often restricted by law (e.g., see 36 C.F.R. § 2.12[a][3], 2014 relative to national parks). However, replication is necessary for aerial surveys, including thermal infrared counts, to account for false-negative detection. For example, Underwood and Kilheffer (2016) documented that low-altitude helicopter surveys flown under optimal conditions failed to detect 3-in-10 deer, and Garner et al. (1995) documented concerns related to false-negative detection with thermal infrared technology that may not be addressed in standard practice.

The expertise associated with modeling the effective area sampled is considerable for CDS (Thomas et al. 2010), SCR (Efford and Fewster 2012), and DSM (Kéry and Royle 2021) even for uncomplicated designs. There are many decisions associated with each method that require an experienced analyst. For example, heterogeneity in encounter rates caused by the use of bait in camera-trapping studies will necessarily complicate the analysis of hierarchical models and require bespoke computer codes to mitigate. However, the additional information gained with these kinds of hierarchical models is substantial and may be worth the added investment in effort and time (Macaulay et al. 2020). Table 14 presents important considerations and caveats when selecting among the methods we used for estimating density, abundance, and distribution of deer in small, protected natural areas like FRST.

Density surface modeling of mapped locations of deer detected during road-based surveys, combined with the meta-population deployment of camera traps might be the only practical means of reliably assessing deer abundance on small (<2000 ha), protected natural areas like FRST. All the other approaches we used are either too time-consuming, require identification and tracking of individual deer, require the use of bait, or necessitate the intervention by a subject-area expert.

Recently, methods extending the binomial N-mixture model to estimate abundance from camera traps without individual identification have been proposed. These newer methods focus on the observation process and model the probability of detection as time- or space-dependent variables (see Kéry and Royle 2016, Moeller et al. 2018, Strebel et al. 2021). These time-to-detection (TTD) approaches hold promise for simplifying abundance estimation of deer from camera-trapping data. TTD camera-trapping and road-based DSM may prove to be the most expedient combination for reliable abundance estimation.

Table 14. Approaches and considerations for white-tailed deer abundance/density estimation on small, protected natural areas.

Approach	Logistics Requires				Biological Realism Includes			Sophistication Requires			Comments
	Expense	Time	Marked Sample	Baiting	Herd Composition	Individual Heterogeneity	Covariates on Abundance	Bespoke Code	Capture Histories	Model Effective Area Sampled	
Road-based Distance Sampling (CDS)	low	mod	no	no	no	no	no	no	no	yes	- repeat surveys recommended - subject to bias
Jacobson's Method (JM)	high	high	yes	yes	yes	no	no	no	no	no	partial capture histories
Bowden's Estimator (BE)	high	high	yes	yes	no	yes	no	no	yes	no	- full capture histories - no herd composition
Spatial Capture-Recapture (SCR)	high	high	yes	yes	yes	yes	no	yes	yes	yes	exceedingly time-consuming
Multinomial Heterogeneity Model (HM _h)	high	high	yes	yes	yes	yes	yes	yes	yes	no	alternative to JM or BE, CDS, SCR
Poisson/Poisson N-mixture Model (PPNmix)	mod	mod	no	no	yes	no	yes	yes	no	no	requires auxiliary abundance
Density Surface Modeling (DSM)	low	mod	no	no	no	no	no	yes	no	no	alternative to CDS

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Appendix A. Using *secr* for creating, summarizing, and plotting encounter histories of identifiable male white-tailed deer, as well as establishing an appropriate discrete state-space to be used in SCR analyses.

Creating, manipulating, and summarizing capture histories of marked animals is a fundamental task in SCR (Borchers and Efford 2008). The most expedient manner in which to complete this task is to use R-package *secr* (vers. 4.5.5), which contains a set of functions for analyzing SCR data. Camera traps are considered count detectors in *secr*. By labeling each camera location uniquely, it is simple to match the encounter with the correct location by formatting the capture history by camera trap identity (i.e., *trapID*). The package uses Root Pooled Spatial Variance to obtain an initial value of the *sigma* parameter in SCR models. We used the `esa.plot()` function to gain a first approximation to the buffer needed to create a useable state-space for SCR. While there are rules-of-thumb (e.g., Royle et al. 2014, Efford 2022), *secr* uses `suggest.buffer()`, which operates on a fitted model, to obtain the appropriate buffer size. Once the buffer is correctly specified, the SCR model can be analyzed. A discrete state-space (i.e., mask) is automatically generated by *secr* and stored as an object in the fitted model. We used the `makeJAGSmask` R-package (Meredith 2021) to convert the state-space into a form useable by JAGS, a WinBUGS programming variant (Plummer 2003). The converted state-space masks, one for each year, were stored as R data objects and later restored into the workspace for use in each SCR program. A step-by-step procedure is listed below.

1. Create the encounter data file (EDF) and the trap deployment file (TDF) and store in a spreadsheet (see Royle et al. 2014),
2. Using function `read.traps()`, read the trap locations from the TDF into a *secr* object-class traps with detector type = “count”,
3. Create the capture histories with the *secr*, `make.caphist()` function using the EDF, traps object, and the format type = “*trapID*”,
4. With the *caphist* object, use the `RPSV()` function (i.e., Root Pooled Spatial Variance) to obtain an initial value for the *sigma* parameter of the SCR model,
5. Run `secr.fit()` to fit an initial model from the *caphist* object,
6. Use the `suggest.buffer()` function, along with the fitted model in 5), to identify the appropriate buffer size,
7. Re-run the model with the appropriate buffer size identified in 6),
8. Convert the *secr* mask to a JAGS useable habitat mask with `makeJAGSmask` R package,
9. Save the habitat mask to an R data object to be restored for use in a future Bayesian SCR model,
10. Convert the *caphist* object to a JAGS compatible convention with the `aperm()` function.

Appendix B. The development, execution, and posterior analysis of Bayesian hierarchical models for the estimation of white-tailed deer abundance on First State National Historical Park and Brandywine Creek State Park.

We programmed Bayesian models in *JAGS* (Just Another Gibbs Sampler; Plummer 2003) using the *rjags* (vers. 4.2.0) package (Plummer 2022). This was accomplished in the Windows operating system using the R computing environment (<http://cran.r-project.org>, accessed 5 July 2020) and the RStudio 2021.09.2+382 graphical user interface (RStudio Team 2021). *JAGS* uses Markov Chain Monte Carlo (*MCMC*) simulation from the posterior distribution, which is the product of the conditional likelihood and the distribution of random effects to estimate model parameters (Royle and Gardner 2011). We fitted models using *MCMC* on 1–3 chains generated from $\geq 300,000$ iterations, ≥ 1000 adaptations, and a modest thinning rate. We monitored convergence and mixing of chains visually from their traces, and numerically by virtue of the Gelman-Rubin statistic. We placed emphasis on minimizing *MCMC* error ($\leq 10\%$) and maximizing effective sample size by using diagnostic tools in the *mcmcOutput* package (vers. 0.1.1; Meredith 2020). Summaries of model outputs as well as the posterior predictive checks were facilitated by the *jagsUI* wrapper (Kellner 2022).

Appendix C. Posterior distribution for parameters of model SCR_b for 2020

Posterior distribution for parameters of model SCR_b , which tests for a local behavioral response of male white-tailed deer to the presence of bait during 2020. Alpha2 is the coefficient for the previous capture covariate, which is different from zero. Bayesian p-value = 1; this model does not fit the data based on the Freeman-Tukey discrepancy. MCEpc is the Monte Carlo error as a percentage.

Table 15. Posterior distribution for parameters of model SCR_b for 2020.

Parameter	Mean	SD	Median	I95	u95	MCEpc
alpha0	-4.6	0.3	-4.6	-5.1	-4.0	9.9
alpha2	4.7	0.3	4.7	4.1	5.2	9.8
sigma	7.1	0.8	6.9	5.8	8.8	8.5
psi	0.6	0.1	0.6	0.4	0.9	9.0
NB	627.8	128.4	620.0	398.0	871.0	9.0
ND	1317.4	269.5	1301.3	835.1	1828.5	9.0
NF	1044.1	213.5	1031.5	661.7	1448.8	9.0
TotN	2989.3	611.4	2952.9	1894.8	4151.1	9.0
DB	13.9	2.8	13.7	8.8	19.3	9.0

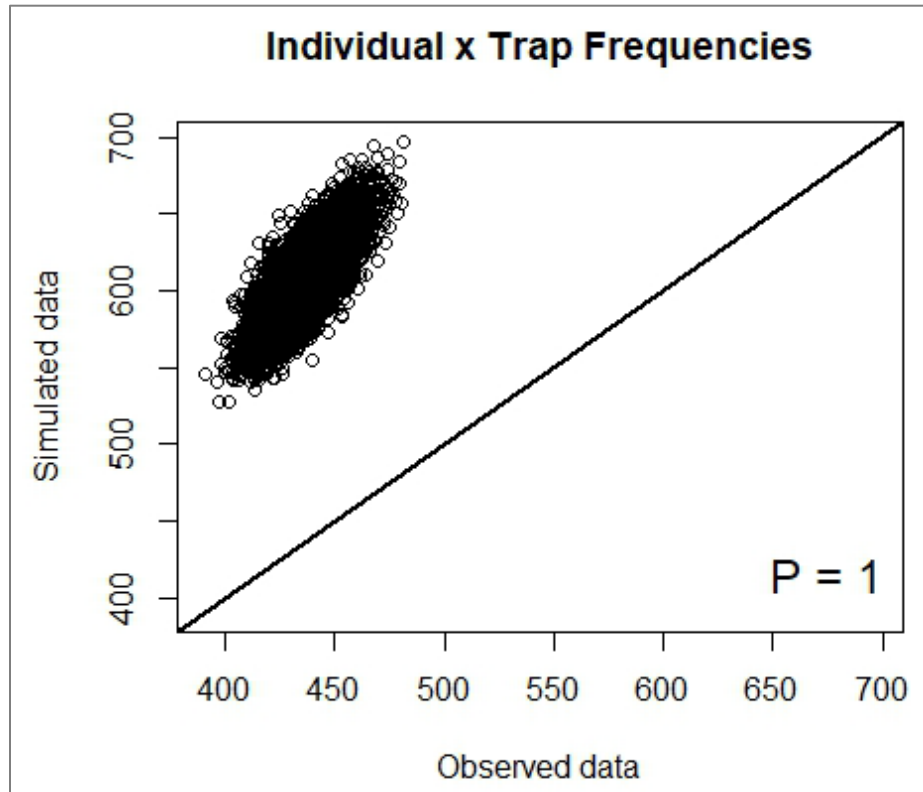


Figure 18. Individual trap frequencies for model SCR_b for 2020.

Appendix D. Posterior distribution for parameters of model SCR_b for 2021

Posterior distribution for parameters of model SCR_b , which tests for a local behavioral response of male white-tailed deer to the presence of bait during 2021. Alpha2 is the coefficient for the previous capture covariate, which is different from zero. Bayesian p-value = 1; this model does not fit the data based on the Freeman-Tukey discrepancy. MCEpc is the Monte Carlo error as a percentage.

Table 16. Posterior distribution for parameters of model SCR_b for 2021.

Parameter	Mean	SD	Median	I95	u95	MCEpc
alpha0	-3.9	0.2	-3.9	-4.2	-3.5	13.0
alpha2	4.3	0.2	4.3	4.0	4.6	12.9
sigma	6.8	0.5	6.8	6.0	7.7	12.4
psi	0.5	0.1	0.5	0.3	0.6	10.0
NB	464.4	66.2	457.0	353.5	604.0	10.3
ND	829.8	118.4	817.5	631.7	1079.7	10.3
NF	414.5	59.1	408.3	315.6	540.3	10.4
TotN	1708.7	243.7	1683.0	1300.9	2224.0	10.4
DB	7.6	1.1	7.5	5.8	9.9	10.3

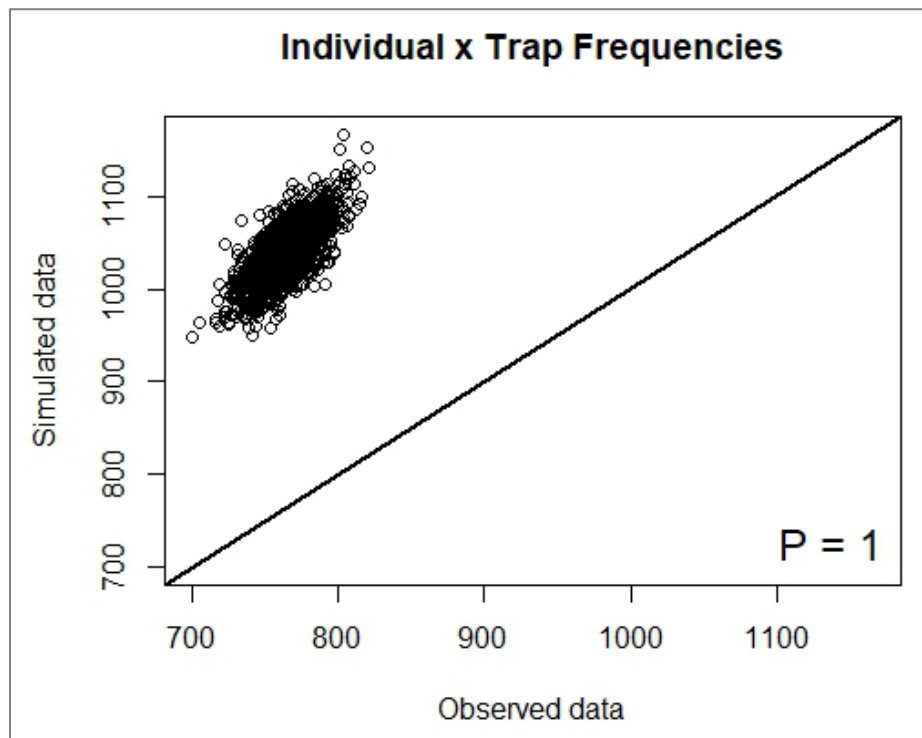


Figure 19. Individual trap frequencies for model SCR_b for 2021.

Appendix E. Posterior distribution for parameters of model SCR_{Mh} for 2020

Posterior distribution for parameters of model SCR_{Mh} , which includes random effects to account for individual by trap heterogeneity in encounter rates of male white-tailed deer in 2020. Bayesian p-value = 0.33; this model fits the data based on the Freeman-Tukey discrepancy. MCEpc is the Monte Carlo error as a percentage.

Table 17. Posterior distribution for parameters of model SCR_{Mh} for 2020.

Parameter	Mean	SD	Median	l95	u95	MCEpc
sigma	2.1	0.1	2.1	1.9	2.3	9.346
psi	0.5	0.1	0.5	0.4	0.6	5.319
mean.t	0.1	0.1	0.0	0.0	0.2	4.420
sig.t	3.3	0.3	3.4	2.6	3.9	9.838
NB	454.9	53.0	452.0	359.0	566.0	5.579
ND	954.6	111.2	947.6	753.1	1187.8	5.580
NF	756.6	88.2	751.1	597.0	942.6	5.580
TotN	2166.1	252.4	2150.4	1708.9	2696.5	5.580
DB	10.1	1.2	10.0	8.0	12.5	5.579

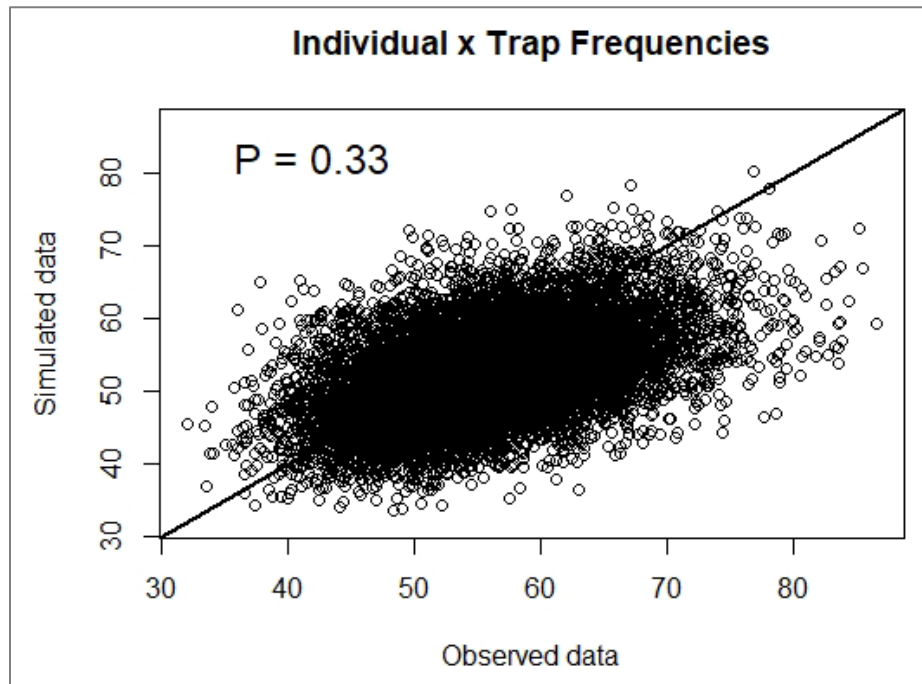


Figure 20. Individual trap frequencies for model SCR_{Mh} for 2020.

Appendix F. Posterior distribution for parameters of model SCR_{Mh} for 2021

Posterior distribution for parameters of model SCR_{Mh} , which includes random effects to account for individual by trap heterogeneity in encounter rates of male white-tailed deer in 2021. Bayesian p-value = 0.24; this model fits the data based on the Freeman-Tukey discrepancy. MCEpc is the Monte Carlo error as a percentage.

Table 18. Posterior distribution for parameters of model SCR_{Mh} for 2021.

Parameter	Mean	SD	Median	I95	u95	MCEpc
sigma	2.6	0.1	2.6	2.4	2.8	13.4
psi	0.4	0.0	0.4	0.4	0.5	9.2
mean.t	0.0	0.0	0.0	0.0	0.2	9.3
sig.t	4.0	0.3	4.0	3.2	4.5	12.8
NB	502.7	47.7	499.6	416.9	602.8	9.5
ND	898.2	85.2	892.9	745.7	1077.2	9.5
NF	448.6	42.5	446.0	372.7	538.3	9.5
TotN	1849.5	175.4	1838.2	1535.3	2217.9	9.5
DB	8.2	0.8	8.2	6.8	9.8	9.5

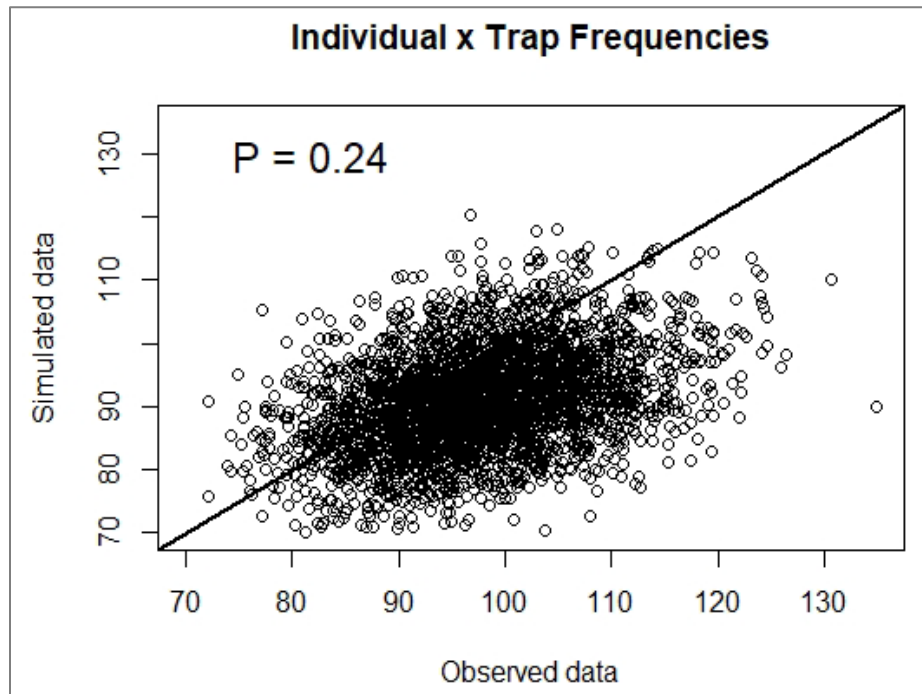


Figure 21. Posterior distribution for parameters of model SCR_{Mh} for 2021.

Appendix G. Posterior distribution for parameters of model HM_h for 2020

Posterior distribution for parameters of model HM_h , which includes random effects to account for individual heterogeneity in encounter rates of male white-tailed deer in 2020. MCEpc is the Monte Carlo error as a percentage.

Table 19. Posterior distribution for parameters of model HM_h for 2020.

Parameter	Mean	SD	Median	l95	u95	MCEpc
p0	0.210	0.048	0.210	0.116	0.306	1.000
alpha0	-1.588	0.247	-1.561	-2.078	-1.137	1.000
beta0	-6.564	6.507	-5.071	-20.353	1.554	1.028
beta1	11.276	8.785	9.254	0.376	29.82	1.028
beta2	0.441	0.382	0.353	-0.075	1.268	1.026
beta3	2.781	1.666	2.397	0.667	6.316	1.029
beta4	-7.447	6.032	-6.059	-20.179	0.065	1.027
beta5	-4.782	4.152	-3.828	-13.597	0.451	1.028
beta6	0.205	0.849	0.083	-1.275	2.038	1.002
beta7	-2.195	1.463	-2.248	-5.067	0.831	0.999
beta8	0.001	31.634	0.021	-61.581	62.251	1.000
beta9	-0.031	31.687	-0.053	-62.487	61.601	1.000
beta10	-0.054	31.682	-0.049	-61.781	62.374	1.000
beta11	0.024	31.607	-0.046	-62.127	61.817	1.000
psi	0.190	0.023	0.188	0.148	0.235	1.000
sigma	1.326	0.192	1.304	0.982	1.712	1.000
NB	94.945	14.889	94.000	67.000	124.000	0.991
ND	199.235	31.247	197.391	140.111	260.931	0.996
NF	157.905	24.766	156.479	110.988	206.957	0.997
TotN	452.085	70.901	447.850	318.187	591.913	0.995

Appendix H. Posterior distribution for parameters of model HM_h for 2021

Posterior distribution for parameters of model HM_h , which includes random effects to account for individual heterogeneity in encounter rates of male white-tailed deer in 2021. MCEpc is the Monte Carlo error as a percentage.

Table 20. Posterior distribution for parameters of model HM_h for 2021.

Parameter	Mean	SD	Median	l95	u95	MCEpc
p0	0.358	0.048	0.357	0.264	0.453	0.998
alpha0	-1.035	0.137	-1.030	-1.300	-0.767	0.998
beta0	0.055	1.021	0.154	-1.862	1.699	1.090
beta1	2.743	1.374	2.618	0.521	5.255	1.093
beta2	0.176	0.070	0.172	0.048	0.317	1.042
beta3	0.884	0.264	0.859	0.458	1.390	1.092
beta4	-1.822	0.944	-1.737	-3.526	-0.265	1.096
beta5	-1.229	0.655	-1.166	-2.448	-0.166	1.089
beta6	0.845	0.311	0.844	0.211	1.431	1.004
beta7	1.207	0.483	1.210	0.271	2.166	1.001
beta8	-0.171	31.406	-0.067	-59.42	63.197	1.003
beta9	-0.631	31.610	-0.606	-62.172	61.654	0.999
beta10	0.291	31.885	0.594	-63.545	60.990	0.998
beta11	-0.402	31.450	-0.040	-62.716	59.827	1.000
psi	0.202	0.019	0.201	0.165	0.239	1.001
sigma	1.055	0.114	1.048	0.846	1.280	1.006
NB	100.957	13.968	101.000	73.000	127.000	1.009
ND	180.405	24.958	179.907	133.804	230.333	1.004
NF	90.110	12.467	89.786	66.817	115.082	1.001
TotN	371.473	51.392	370.73	275.814	474.617	1.005

Appendix I. Posterior distribution for parameters of model *PPNmix* for 2020

Posterior distribution for parameters of model *PPNmix*, for exploring the distribution of white-tailed deer on First State National Historical Park and Brandywine Creek State Park, 2020. MCEpc is the Monte Carlo error as a percentage.

Table 21. Posterior distribution for parameters of model *PPNmix* for 2020.

Parameter	Mean	SD	Median	l95	u95	MCEpc
alpha0	-4.182	0.702	-4.276	-4.651	-3.894	0.980
beta0	3.284	0.549	3.366	3.005	3.681	0.979
beta[1]	0.049	0.057	0.047	-0.054	0.157	0.998
beta[2]	-0.027	0.061	-0.026	-0.142	0.084	0.998
beta[3]	-0.057	0.079	-0.058	-0.201	0.086	0.999
beta[4]	-0.140	0.095	-0.142	-0.309	0.019	0.997
beta[5]	-0.030	0.096	-0.030	-0.207	0.146	0.999
beta[6]	-0.056	0.119	-0.060	-0.273	0.162	0.998
beta[7]	-0.079	0.160	-0.078	-0.379	0.219	0.999
beta[8]	-0.159	0.252	-0.156	-0.635	0.299	0.998
beta[9]	-1.357	0.611	-1.340	-2.560	-0.276	0.998
beta[10]	-0.934	0.988	-0.929	-2.878	0.944	0.999
beta[11]	-0.219	2.030	-0.226	-4.220	3.746	1.000
beta[12]	-0.002	3.154	-0.005	-6.218	6.162	1.000
avg.theta	0.027	0.069	0.017	0.012	0.024	0.971
FT.obs	158.258	13.288	158.102	132.989	184.973	0.996
FT.sim	154.793	10.309	154.880	135.175	175.488	0.995

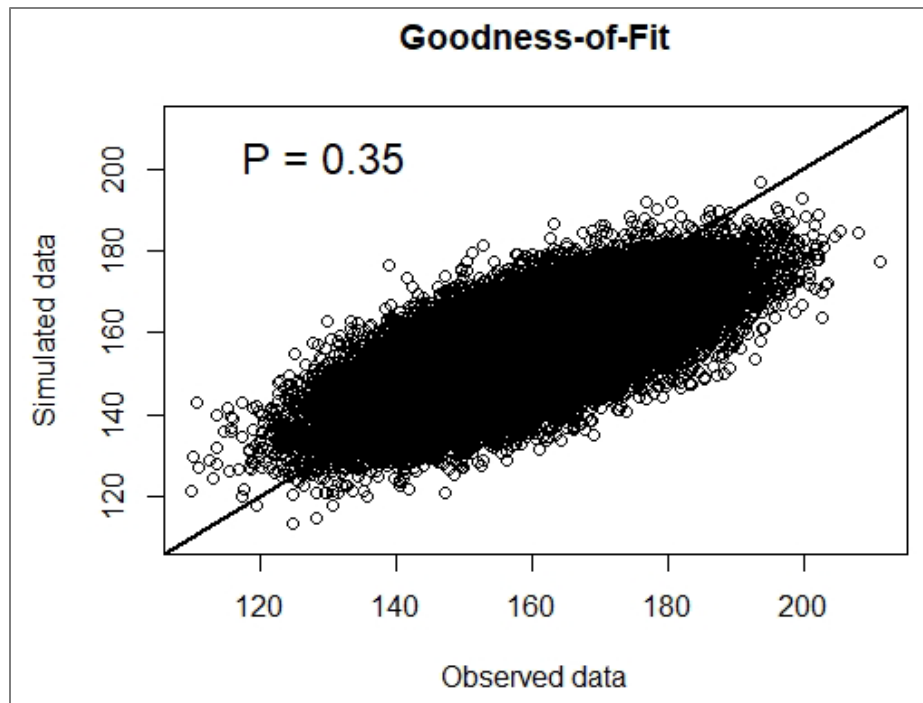


Figure 22. Goodness-of-fit for parameters of model *PPNmix* for 2020.

Appendix J. Posterior distribution for parameters of model *PPNmix* for 2021

Posterior distribution for parameters of model *PPNmix* for exploring the distribution of white-tailed deer on First State National Historical Park and Brandywine Creek State Park, 2021. MCEpc is the Monte Carlo error as a percentage.

Table 22. Posterior distribution for parameters of model *PPNmix* for 2021.

Parameter	Mean	SD	Median	l95	u95	MCEpc
alpha0	-3.273	0.277	-3.295	-3.799	-2.731	5.707
beta0	2.841	0.276	2.870	2.279	3.331	5.478
beta[1]	0.058	0.053	0.056	-0.043	0.166	1.140
beta[2]	0.137	0.055	0.134	0.031	0.244	1.057
beta[3]	-0.021	0.058	-0.022	-0.135	0.093	0.991
beta[4]	-0.185	0.100	-0.179	-0.382	0.009	1.047
beta[5]	0.164	0.111	0.161	-0.053	0.384	1.016
beta[6]	0.204	0.117	0.201	-0.026	0.435	1.011
beta[7]	0.387	0.158	0.379	0.083	0.698	1.061
beta[8]	-0.005	0.272	0.001	-0.558	0.518	1.038
beta[9]	0.184	0.282	0.174	-0.371	0.737	1.058
beta[10]	1.132	0.484	1.124	0.165	2.074	1.022
beta[11]	1.198	0.702	1.187	-0.206	2.541	1.055
beta[12]	-1.326	0.906	-1.320	-3.072	0.496	0.973
beta[13]	-4.060	1.891	-4.059	-7.719	-0.295	0.994
beta[14]	-0.012	3.189	-0.014	-6.357	6.196	0.464
FT.obs	204.106	12.530	204.221	179.882	227.589	4.259
FT.sim	204.254	10.548	204.163	183.806	225.156	2.281

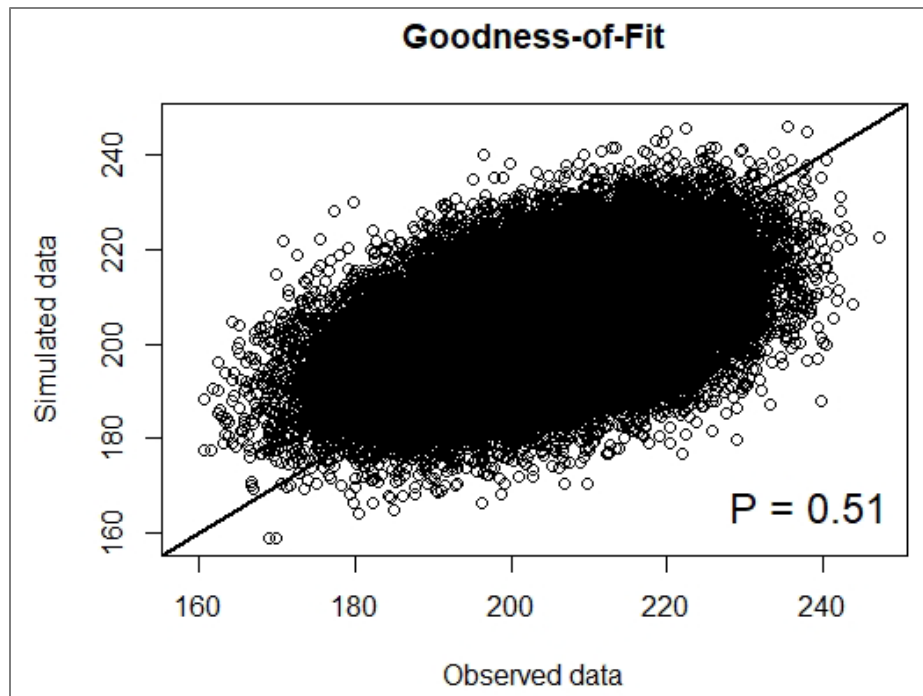


Figure 23. Goodness-of-fit for parameters of model *PPNmix* for 2021.

Appendix K. Posterior distribution for parameters of model *DSM* for 2020

Posterior distribution for parameters of model *DSM* for pixel frequency-based, hierarchical density surface modeling of white-tailed deer on First State National Historical Park and Brandywine Creek State Park, 2020. MCEpc is the Monte Carlo error as a percentage.

Table 23. Posterior distribution for parameters of model *DSM* for 2020.

Parameter	Mean	SD	Median	l95	u95	Rhat	MCEpc
sigma	0.189	0.116	0.157	0.100	0.291	0.832	10.303
b.cs.0	0.357	0.058	0.357	0.244	0.468	1.001	1.193
b.n.0	-1.890	0.151	-1.890	-2.201	-1.609	0.997	5.112
Tot	649.269	35.700	648.020	581.833	721.755	0.996	5.609
ACS	2.432	0.082	2.430	2.276	2.597	1.001	1.195

Appendix L. Posterior distribution for parameters of model *DSM* for 2021

Posterior distribution for parameters of model *DSM* for pixel frequency-based, hierarchical density surface modeling of white-tailed deer on First State National Historical Park and Brandywine Creek State Park, 2021. MCEpc is the Monte Carlo error as a percentage.

Table 24. Posterior distribution for parameters of model *DSM* for 2021.

Parameter	Mean	SD	Median	l95	u95	Rhat	MCEpc
sigma	0.392	0.134	0.363	0.224	0.653	21.155	0.392
b.cs.0	0.190	0.049	0.192	0.105	0.296	4.673	0.190
b.n.0	-1.237	0.112	-1.240	-1.450	-1.012	10.341	-1.237
Tot	1006.425	39.632	1008.832	928.035	1085.510	8.739	1006.425
ACS	2.211	0.059	2.211	2.110	2.344	4.681	2.211

Appendix M. Evidence of bias in road-based surveys for deer and other relevant wildlife studies.

In our experience, road-based surveys have performed adequately for addressing most white-tailed deer management concerns, especially since the addition of distance sampling in the protocol (Underwood et al. 2003). Bias in estimation continues to dominate the dialogue relative to the application of road-based surveys in small, protected natural areas. There are always exceptions, and each natural area must be evaluated independently. Here, we provide an analysis of specific lines of evidence against the use of road-based surveys in deer management contexts. While no study is perfect, evaluating the veracity of specific evidence of road bias in the published literature seems appropriate.

Roberts et al. (2006) published one of the earliest papers offering evidence of bias using road-based surveys for deer abundance estimation. From a sample of marked deer, they compared conventional, capture-recapture abundance estimates between surveys of deer along area roads and those recorded in images from a network of trail cameras. They reported that deer behavior (i.e., an attraction to roads) and an uneven distribution of marked deer (i.e., mostly along roads) in the study area combined to severely bias road-based estimates downward. Note that this occurs with conventional mark-recapture estimators because few encounters with unmarked animals along roads gives the false impression that a high proportion of the population is marked. When relying on a marked sample of deer, it is imperative that it is well-distributed across the study area to avoid such bias. This paper was an excellent example of sample selection bias and how camera-trapping can be used to detect coverage issues.

McShea et al. (2011) published a paper claiming road bias in two protected natural areas that happen to be units of the National Park Service. They compared the average number of deer groups detected in binned intervals of distance relative to the survey route in CDS surveys, and to camera locations relative to a road. Their primary source of evidence was a model predicting higher deer activity at camera traps as a function of distance to the closest paved road, but not distance to the survey route in one of their study areas.

They cited two sources of bias from road-based surveys: (1) deer behavior (i.e., attraction or repulsion from the road), and (2), the position of the road within the landscape, which we have already discussed. In their case, poor study area coverage along the roads in the problematic park was responsible for the bias they documented. However, McShea et al. (2011) made two assertions that are incorrect.

First, they falsely asserted that a fundamental assumption of distance sampling is that a lower percentage of deer should be detected at greater distances. While this is often the case, in some land cover-types the proportion of detections can remain quite high over great distances (Begier 1996). In those land cover-types, a different distribution (e.g., uniform) is used to model the probability of detection. In practical terms, surveys in those land cover-types effectively become strip transects with nearly perfect probability of detection.

Second, they suggest that a low percentage of the study area that is actually covered in the sample is in some way problematic. In CDS, and in most sampling applications of large populations, the absolute size of the sample is most important, not the fraction of the population sampled (Buckland et al. 2001), which is assumed to be proportional to area. We typically strive for a product of $(L * 2 * \widehat{esw})/A$ to meet or exceed 10% as a means of incorporating significant land cover-types.

In our experience, sampling at least 10% of the study area generally incorporates most of the land cover-types in proportion to their availability on the landscape. In addition, for large populations (i.e., >225 animals) a 10% area fraction yields a coefficient of variation around estimated population size of ≤ 0.2 for many plot-based sampling schemes (Seber 1982, pg. 22), which is acceptable precision for most management applications (Robson and Regier 1964). Because the magnitude of bias was not ascertained in McShea et al. (2011), its relevance to abundance estimation in the context of small, protected natural areas remains unclear.

Beaver et al. (2014) published a study comparing two road-based methods with aerial vertical-looking infrared imaging. From the ground, they conducted conventional night-spotlighting counts of deer with and without the aid of a thermal imager, and estimated density using CDS. At a fixed altitude during the aerial surveys, they estimated the width of the strip of ground covered by the thermal imager, and computed density by dividing the number of deer detected by the product of the length and width of the strip. The authors claim bias due to estimated densities from road-based counts that were larger than from aerial infrared, thermal imagery.

We found a number of significant issues with the authors' analyses and claims of bias. First, the aerial, thermal imagery detected 39 clusters of deer, while the two ground-based methods detected easily twice as many clusters from 4 surveys with each method (compare their Figures 1 and 3). The obvious question is where did all those deer counted in the ground surveys go if the aerial thermal imager exhibited a higher detection probability? (Note that the authors went to great lengths to avoid double counting during the ground-based surveys.)

Second, there were no statistics reported for the encounter rate variance component. Encounter rate is the most important variance component of CDS (Buckland et al. 2001, Thomas et al. 2010). These statistics are critical because they detail the effort expended relative to the number of detections made. For example, the authors surveyed alternating transects to minimize spatial dependence, but provided no information on the actual effort expended. In addition, by surveying only the righthand side of the road, the formula for density must be modified to accommodate one-sided transects (Buckland et al. 2001, Section 7.9.3). No information was provided on whether such an accommodation was made in the data or analyses. Without this information, it is impossible for the reader to evaluate the veracity of their claim of road bias.

Third, the detection rate for the aerial thermal imager was assumed to be perfect or nearly so, but the test they present was inadequate to validate that assumption in our view. For example, no land cover-type descriptions were provided for the 10 test sites, nor any indication of how similar test sites were to sites actually flown. Our experience with aerial thermal infrared imaging in wildlife surveys is that

detection of thermal signatures is highly context sensitive. Any obstruction between the animal and the thermal sensor (e.g., tree canopy, rock, etc.), or variability in land cover-types, will invariably lead to missed detections and potentially large undercounts (Garner et al. 1995).

Lastly, the authors presented estimates of density for left-truncated data and for left- and right-truncated data though their justification for so doing was unclear. The analyses with both left- and right-truncation are the correct models for these data (see their Tables 1 and 2), even though they arbitrarily selected the left-truncation distance rather than using an objective criterion like we used in our study. They documented a 35-m difference in the distance of detected and randomly placed clusters of deer relative to the survey route. A doubling of the mean $\widehat{e\hat{S}W}$ they provide in Tables 1 and 2, representing a worst-case scenario, to discount the attraction of deer to roads would decrease density by a factor of 2, not by a factor of 3–8 as they claim. Consequently, we are led to conclude that the aerial vertical-looking, thermal imager failed to detect a large number of deer, consistent with our own experience with the technology.

Green et al. (2021, 2022) published two reports evaluating the effectiveness of road-based distance sampling for estimating deer population density in National Capital Region units of the NPS. They used simulation to generate various distributions of deer numbers across parks and harvested detections in the computer from established routes used by the NPS in their deer surveys. They duplicated a result which was originally discussed in Buckland et al. (2001) — road-based surveys can result in biased density estimates when the samplers are not allocated independently of the (*unknown*, emphasis ours) distribution of animals. Because they also did not know the true distribution of deer across the landscapes in any of these parks, their computer simulations were purely hypothetical.

Chauvenet et al. (2017) used a spatially explicit, individual-based model to evaluate bias in density from both distance sampling and camera-trapping. Within the constraints imposed by their model, they determined that both distance sampling and camera-trapping produced biased density estimates in populations of unmarked animals, but that distance sampling estimates were closer to the simulated quantities when transects were allocated randomly — a finding that remains indisputable.

Our experience using road-based distance sampling supports a general *underestimation* of density, which is most frequently caused by the difficulty of accurately accounting for effort over great distance and variable terrain. Effort is almost always overestimated in these contexts, thus biasing mean density downward. However, it is also our experience that confidence interval coverage will likely include the true (but unknown) density. Consequently, a call for active management based on a selected deer density threshold would be conservative.

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