

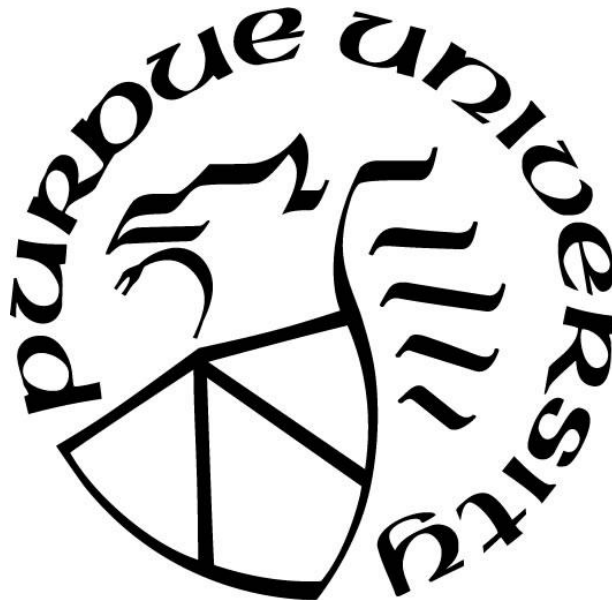
**MODELING DENSITY AND GROUP SIZE OF WHITE-
TAILED DEER (*ODOCOILEUS VIRGINIANUS*) WITH
DISTANCE SAMPLING**

by
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A Dissertation

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Dedicated to my late papa, J. Kenneth Bastin, who always encouraged me to do the right thing. I miss you papa. I am excited to finally hear your last dying thoughts about me. And to my daughter, Juliette A. Pelletier, who has unknowingly motivated me with her smiles.

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ABSTRACT

Management of white-tailed deer (*Odocoileus virginianus*) remains a high priority for wildlife agencies, and principally sound and current science is a foundation of effective wildlife management. To ensure that deer management in Indiana is grounded in sound and current science, my dissertation aims to: (1) improve components of density estimators for deer management; (2) compare candidate deer density estimators; (3) examine how spatially explicit density of demographic classes of deer change across Indiana and test for differences between demographic ratios of density; and (4) examine how deer group sizes change across space and time in Indiana. I accomplish these goals with data from fecal-pellet, camera-trap, and aerial sampling collected in Deer Regional Management Units 3, 4, and 9 within Indiana.

Two issues when estimating persistence time, $\hat{t}$, of dung piles frequently occur in deer management: (i) differences between observers on what constitutes a dung pile; and (ii) substituting the number of days between the date in which 98% of deciduous trees shed leaves in autumn and field sampling for $\hat{t}$. I therefore developed and implemented a new method for estimating $\hat{t}$, which produced density estimates that were larger than previous leaf-off methods and accounted for variation attributable to interobserver classification discrepancies. Similarly, density estimates from aerial sampling often suffers from sources of error. I showcased the importance of accounting for common types of error in aerial sampling by using a simple double-observer approach with infrared and visible cameras. My results stressed the significance of pairing red-green-blue sensors with infrared thermal sensors, choosing appropriate sampling altitudes, and using specific criteria to classify thermal signatures.

To aid decision making, I then extended cost-effectiveness analysis to choose between density-estimation methods, and simultaneously integrated precision and per-area cost of sampling, allowed for situation weighting of factors, and annualized capital cost across a single or multiple applications of capital equipment. I found aerial sampling to be the most cost-effective method for long-term deer monitoring in Indiana.

I next developed a density surface model that utilized camera-trap distance sampling within a hierarchical generalized additive model to estimate spatially explicit densities of bucks, does, and fawns. I found that deer density was influenced by landscape fragmentation, wetlands, and

anthropogenic development. By extending simple statistical theory to test for differences in two ratios of density, I found strong evidence that recruitment was tied to agriculture.

Finally, I used camera traps, detectability estimates from distance sampling, and hierarchical Bayesian modelling to index group size and test multiple group-formation hypotheses in deer. I found a strong relationship between group size and several interactive predictors. I documented the largest groups in areas near anthropogenic development, in areas with high predator use intensity, and during times of day when predators were active. Additionally, groups were larger in locations with concealment when the area of concealment within the surrounding landscape was small, and larger in open areas when the amount of concealment within the surrounding landscape was large.

I lastly concluded my dissertation by encouraging future deer management in Indiana to carefully consider their goals for population estimation, and recognize and address sources of bias in common sampling protocols for population data.

CHAPTER 1. INTRODUCTION

Wildlife agencies and landowners have consistently prioritized the management of cervids in nearly all regions of North America. Of the North American cervids, many regions including the Midwestern USA give precedence to population management of white-tailed deer (henceforth deer; *Odocoileus virginianus*; Wallmo 1981, Waller and Alverson 1997). The pre-eminence given to deer management in wildlife agencies is likely attributable to the unique, intrinsic, and comparatively intense economical (Conover 1997, Bissonette et al. 2008), ecological (Gill and Beardall 2001, Horsley et al. 2003, Côté et al. 2004), and societal (Conover 1994, Conover et al. 1995, Conover 2011) impacts of deer.

Economic costs attributable to deer stem mainly from deer-vehicle collisions and property damage. Rue (1989) reported 726,000 nationwide deer collisions, and Romin and Bissonette (1996) reported 500,000 deer road mortalities within only 35 states. More recently, State Farm's 16th annual deer-vehicle collision study that projects deer-vehicle collisions across the entire insurance industry (includes elk [*Cervus canadensis*], moose [*Alces alces*], and caribou [*Rangifer tarandus*], but deer likely comprise the majority of this cost) reported 1.33 million deer-vehicle collisions between 1 July 2017 and 10 June 2018 in the USA. This report found the average cost per deer collision to be \$4,341, with a total cost exceeding \$5.75 billion; however, this total is likely a conservative estimate, as Marcoux and Riley (2010) noted that only 52% of drivers report deer-vehicle incidents to their insurance company. Thus, 2.56 million deer-vehicle collisions that accumulated \$11.1 billion in damage over the approximately 1-year period may be more accurate. Similar to deer-vehicle collisions, deer-induced property damage has a steep cumulative cost to land owners across the USA. In an economic synopsis of the available literature at the time, Conover (1997) estimated deer-related agricultural damage at \$100 million, silvicultural damage at \$750 million, and household damage at \$251 million.

Contrasting with economic cost, activities related to hunting of deer generate considerable economic revenue (Conover 2011). In 2006, 10.7 million people hunted elk and deer in the USA (U.S. Fish and Wildlife Service 2006). In so doing, the average hunter spent \$1121 in their pursuits, resulting in nearly \$12 billion spent on elk and deer hunting in the USA during 2006 (U.S. Fish and Wildlife Service 2006).

Ecological impacts of deer are well documented in natural settings. Abundant deer herds can drastically alter the natural successional trajectory of inhabited areas because of their cumulative browse intensity (Horsley et al. 2003, Conover 2011). Successional shifts can alter the growth of preferred flora and can cause ecological strife and logistical hardships for property management (Horsley et al. 2003, Conover 2011). For instance, Rooney and Waller (2003) observed a decline in *Quercus* and *Betula* regeneration and herb diversity that was linked to high deer abundance in northern Wisconsin. Similarly, Horsley et al. (2003) found a decline in species richness of flora with increasing deer abundance that resulted in a prolonged fern-, grass-, and sedge-dominated community. Such deer-induced ecological shifts are hard to reverse, and the effects can be extremely expensive for management and landowners (Côté et al. 2004).

In addition to direct effects on plants, the feeding intensity of abundant deer herds can cause cascading effects for other fauna. Specifically, deer browsing can impact small mammal, avian, and invertebrate populations (reviewed by Côté et al. 2004). Over-abundant deer herds are also subject to subsequent density-dependent feedback effects because of increased competition for limited resources (Fowler, 1987). For instance, Kilpatrick et al. (2001) reported a positive relationship between deer density and size of home range, and other studies also found negative relationships between deer abundance and individual fecundity, body mass, and fat index (Swihart et al. 1998, Kie and Bowyer 1999, Kilpatrick et al. 2001).

Although the economic revenue that deer accumulate is undeniable, deer also have a unique intrinsic value unrelated to hunting. Many people enjoy watching deer, while others are pleased simply by knowing that deer herds are doing well (Conover 2011). Conversely, other individuals are active proponents for herd reductions (Conover 1994, VerCauteren et al. 2006). Such proponents of herd reductions often include victims of deer-vehicle collisions, agricultural crop damage, damage to households, or silvicultural damage.

Because of the magnitude of ecological and economic impacts, along with the diversity of attitudes of affected parties, population management of deer remains one of the highest priorities for land managers and wildlife agencies. Thus, nearly all states implement a deer management plan and have at least one designated cervid biologist (Waller and Alverson 1997, Urbanek et al. 2011). To ensure that deer management in Indiana is grounded in sound and current science, in 2018 the Indiana Department of Natural Resources initiated a state-wide integrative project to address the challenges involved with management of white-tailed deer. This integrative project

seeks to investigate the relationships between: (1) societal perceptions of the deer herd in Indiana; (2) ecological effects deer have on forests in Indiana; and (3) densities of deer in Indiana. Findings from the project will inform management of deer in Indiana. My dissertation is focused on the third component in the list above.

Throughout my dissertation, I specifically investigated how different components of density estimators can be improved for deer management (Chapters 2 and 3). I then compared candidate methods for estimating deer density and make methodological recommendations for population monitoring of deer conducted by the Indiana Department of Natural Resources going forward (Chapter 4). Following this, I further examined how density of demographic classes of deer change across the landscape of Indiana and tested for differences between demographic ratios of density in different regions of Indiana (Chapter 5). Lastly, I examined how deer group sizes change across space and time in Indiana (Chapter 6). The results within all of my chapters are based on field work conducted within Deer Regional Management Units 3, 4, and 9 within Indiana during the winters of 2019 – 2021 (Figure 1.1; Swihart et al. 2020). These regions were selected because: (1) they span the gradient of landscape compositions in Indiana in terms of row-crop agriculture, wetland, and forest; and (2) putative deer densities in these regions ranged from extremely dense to sparse.

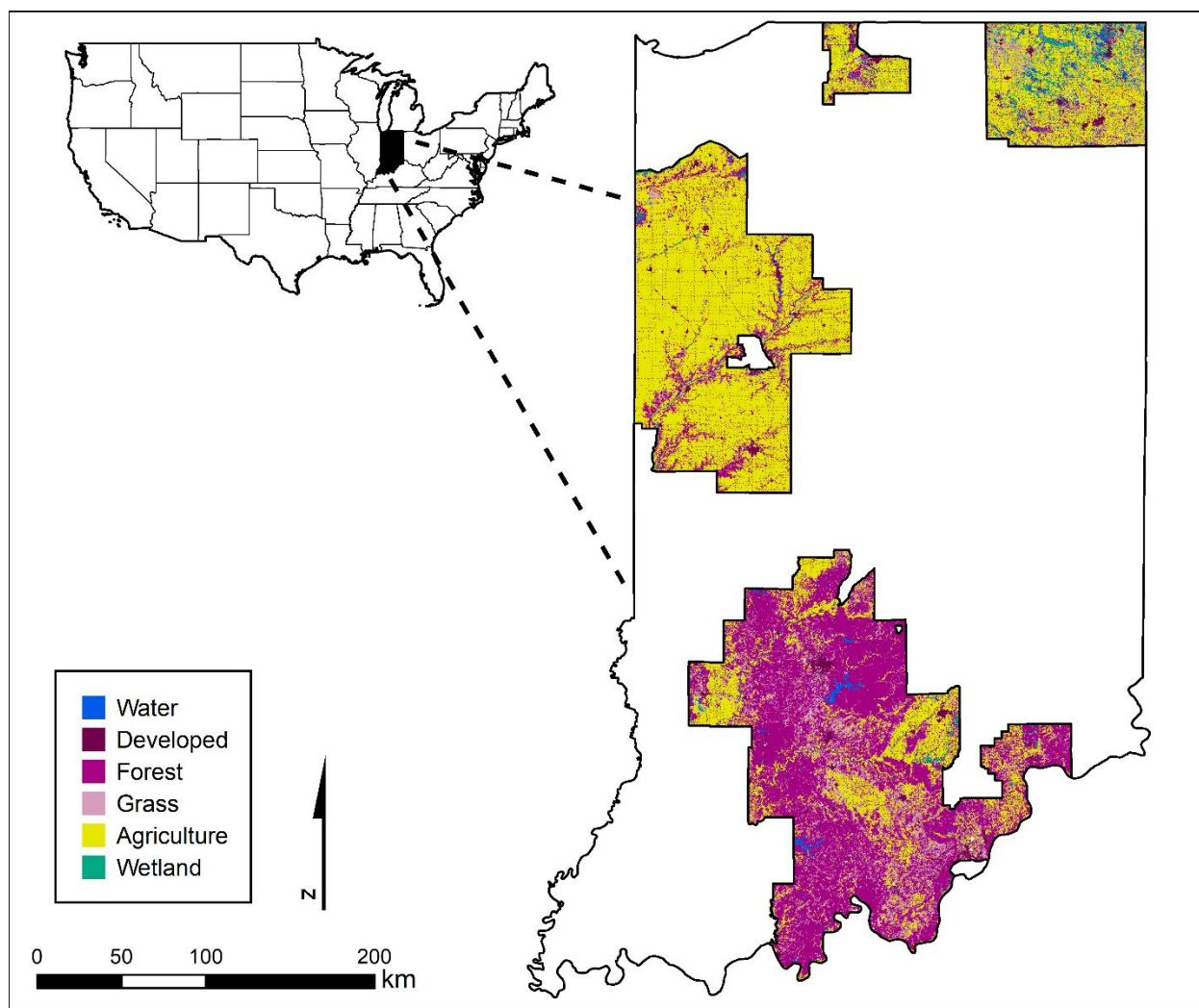


Figure 1.1. Land cover types within Deer Regional Management Units 3 (west central), 4 (southern), and 9 (northeastern; two parcels) of Indiana, USA.

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CHAPTER 2. DENSITY FROM PELLET GROUPS: COMPARING METHODS FOR ESTIMATING DUNG PERSISTENCE TIME

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2.1 Abstract

Effective wildlife management often relies on estimates of animal density, and cue counting is a viable estimation strategy. A key component of density estimation from dung, a form of cue counting, is estimation of the persistence time, $\hat{t}$, of dung piles. However, differences between observers on what constitutes a dung pile may alter subsequent density estimates. Additionally, many researchers studying white-tailed deer (*Odocoileus virginianus*) have substituted for $\hat{t}$ the number of days between the date in which 98% of deciduous trees shed leaves in autumn and field sampling. To address these 2 concerns, I compared 3 methods for estimating $\hat{t}$ of white-tailed deer pellet groups: (1) a common modelling approach based on observations from a single observer (single-observer method), (2) a method that accommodates interobserver variation on the status of dung during field surveys (interobserver method), and (3) the days elapsed since 98% of deciduous trees shed autumn leaves (leaf-off method). I then applied these 3 $\hat{t}$ estimates to distance-sampling data on pellet groups from white-tailed deer that I collected along transects during 3 sampling seasons from 2019–2021 in west-central Indiana. I estimated habitat- and year-specific deer densities. Persistence probability of pellet groups varied across habitats and years, positively with age and number of pellets, and negatively with precipitation and temperature. In several instances, I found strong or marginal differences between densities estimated using the leaf-off method and the other 2 methods. The densities using the interobserver and single-observer methods were similar, with the latter being larger by an average of 8.0% (SE = 1.71). The latter also yielded coefficients of variation (CV) that averaged 16.6% (SE = 4.8) larger, attributable to interobserver discrepancies in scoring dung persistence. Density estimates from the leaf-off method were 32.6% (SE = 15.3) and 37.8% (SE = 13.0) less than the density estimates from the interobserver and single-observer method, respectively. I encourage future researchers estimating density using multiple observers and dung sampling techniques to incorporate interobserver

variation. I advocate that biologists relying on dung-based estimation of density for white-tailed deer abandon the conventional leaf-off method and adopt other modelling approaches.

2.2 Introduction

Understanding the population density of wildlife species is critical for the effective application of management strategies (Williams et al. 2002). Density estimation from cue counting is a viable method to estimate the density of many wildlife species that produce cues such as calls (Marques et al. 2011), burrows (Nomani et al. 2008), dung (Wood 1988), or nests (Hashimoto 1995). Cue counting estimates the density of cues that a population produces and subsequently converts to animal density by use of a cue production rate (Buckland et al. 2001). Dung sampling is a form of cue counting that estimates the density of dung piles produced by a population, from which animal density is estimated by use of the daily defecation rate and number of days that dung piles persist before degrading beyond recognition (Marques et al. 2001). Commonly, dung sampling uses a distance-sampling framework under the following formula (Marques et al. 2001):

$$\hat{D} = \frac{\left(\frac{n}{L}\right) * \hat{f}(0) * 0.5}{\hat{t} * \hat{s}} \quad (1)$$

where $\hat{D}$ = the density estimate of the animal population, n = the number of dung piles detected, L = transect length, $\hat{f}(0)$ = the estimated probability density function of perpendicular distances measured from the transect line to detected dung piles evaluated at distance 0, $\hat{s}$ = the estimated defecation rate of the animal, and $\hat{t}$ = the estimated persistence time for dung piles deposited during the study period.

Observer bias is a well-recognized issue in cue counting and is mentioned in the context of several taxa including large mammals (Neff 1968, Härkönen and Heikkilä 1999, Jenkins and Manly 2008), small mammals (Murray et al. 2002, Prugh and Krebs 2004), and primates (Kuehl et al. 2007). To limit the amount of observer bias, many animal surveys that rely on cue counting have constrained field sampling to a single surveyor (Brodie 2006, Urbanek et al. 2012). However, employing a single surveyor is not feasible for large-scale monitoring, and many cue count surveys employ multiple individuals to collect data across large study areas (Barnes et al. 1995, Barnes 2001, Marques et al. 2001, Ahrestani et al. 2018). The decision for an observer to classify a dung pile as intact (and thus counted) or decayed (and thus ignored) contains a potentially important element of subjectivity in multi-observer surveys (Neff 1968). Concordance between individuals

when classifying dung piles is critical to avoiding spurious fluctuations in density estimates that are solely due to interobserver discrepancies during dung classification. Unfortunately, opinions frequently differ in the field among trained observers (Spaulding et al. 2000), as performance is associated with experience, gender, and motivation (Silvertown et al. 2013). Consequently, interobserver variation represents an additional source of variation in $\hat{t}$. However, few published methods to incorporate interobserver variation into $\hat{D}$ are available (but see Burt et al. 2014).

White-tailed deer (*Odocoileus virginianus*) are an ecologically and economically important species in the eastern U.S. (Conover 1997, Waller and Alverson 1997), and management objectives would be better served if estimates of deer abundance were available (Hewitt 2011). Dung sampling (termed pellet sampling for many ungulates, e.g., Urbanek et al. 2012, Alves et al. 2013) can provide useful density estimates or indices of ungulate abundance (Marques et al. 2001, Forsyth et al. 2007, Alves et al. 2013). Traditionally, researchers estimating white-tailed deer density from pellet sampling have substituted for $\hat{t}$ the estimated number of days between the date when over-story trees shed 98% of leaves in autumn (henceforth referred to as 98% leaf off) and the date when surveyors sample for pellet groups (Eberhardt and Van Etten 1956, Urbanek et al. 2012, Anderson et al. 2013, DeCalesta 2013). The substitution assumes that leaf fall covers all previously deposited pellet groups permanently and all pellet groups defecated after 98% leaf off persist until field sampling. In addition, 98% leaf off typically has been treated as a constant rather than an estimate, with the practical consequence of assuming that $\widehat{var}(\hat{t}) = 0$. Urbanek et al. (2012) reported from analysis of unpublished data that white-tailed deer pellet groups in woodland and prairie habitat persisted without significant decay from September through April in Illinois. However, studies on other ungulates in temperate regions have determined that persistence of pellet groups can vary with habitat conditions (e.g., Smart et al. 2004, Tsaparis et al. 2009), and spatiotemporal variation in dung persistence rates is a well-known issue in tropical regions (Ahrestani et al. 2018).

To address the aforementioned concerns, I present a method to estimate $\hat{t}$ that accommodates interobserver variation on the status of dung during field surveys. I apply this method to monitoring data on pellet groups from white-tailed deer. Additionally, I estimate $\hat{t}$ using 2 existing methods: (1) a common modelling approach based on observations from a single observer following Laing et al. (2003); and (2) the days passed between 98% leaf off and field sampling, as customarily adopted for white-tailed deer in central and northern latitudes. Finally, I

apply estimates of $\hat{t}$ derived from each of these 3 methods in a case study to estimate the density of white-tailed deer in west-central Indiana, USA, and compare density estimates and corresponding measures of precision.

2.2.1 Study Area

I conducted all pellet-group monitoring in west-central Indiana, USA, centrally located in deer management unit 3 (10,233.3 km²; Swihart et al. 2020; Figure 2.1). The management unit is located within the Central and Eastern Corn Belt Plains ecoregions (U.S. Environmental Protection Agency 1997). The primary land use in this area was soybean and corn row-crop agriculture. Natural cover types such as forest and prairie were primarily constrained to intermittent patches. Forest patches primarily contained mesic hardwoods with silty loam soils. Dominant overstory tree species included black cherry (*Prunus serotina*), black oak (*Quercus velutina*), black walnut (*Juglans nigra*), pin oak (*Q. palustris*), sassafras (*Sassafras albidum*), and white oak (*Q. alba*), and dominant herbaceous species included black snakeroot (*Sanicula marilandica*), enchanter's nightshade (*Circaea lutetiana*), garlic mustard (*Alliaria petiolata*), sweet cicely (*Osmorhiza claytonii*), and Virginia knotweed (*Polygonum virginianum*). Weather regimes followed a 4-season temperate pattern. Annually across my study site, the average rainfall was 96.27 cm, and the average minimum and maximum daily temperatures were 6.57° and 16.57° C, respectively.

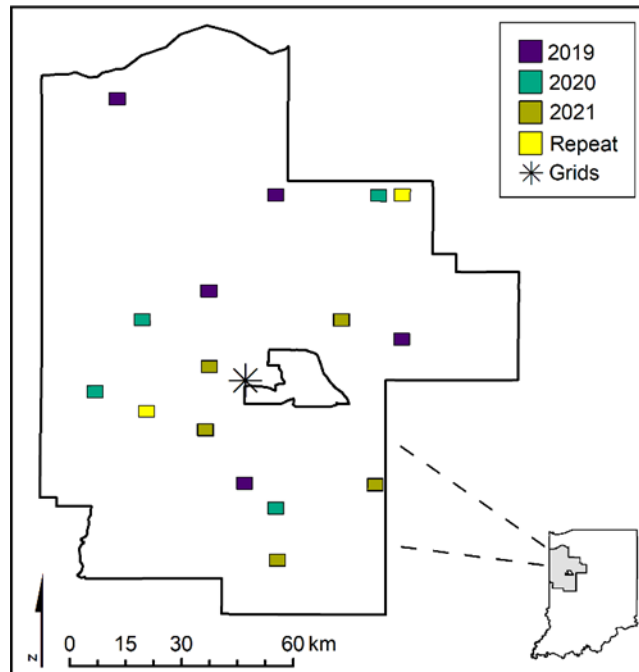


Figure 2.1. Deer management unit 3 located in west-central Indiana, USA. Within deer management unit 3, I depict with a * the immediate area in which grids were located for monitoring of pellet groups to estimate pellet-group persistence (Grids), and 16, 10.36-km² areas in which I conducted line-transect sampling for pellet groups. All 10.36-km² areas are color coded to denote sampling of the area during 2019, 2020, 2021, or during all 3 years (Repeat).

2.3 Methods

2.3.1 Pellet Group Monitoring

I collected, deployed, and monitored freshly deposited pellet groups of white-tailed deer from December to April of 2018–2019, 2019–2020, and 2020–2021, in 6, 1,600-m² grids. Grids were used in lieu of natural deposition sites because the time required to visit the latter in row-crop fields would have been prohibitive. I placed 2 grids in each of 3 different habitat types: forest, prairie, and agricultural fields. The crops in agricultural sites were harvested before my monitoring and were not disturbed by farm equipment during the study period. I systematically separated pellet groups within each grid by 10 m, so that a single grid contained 25 equally spaced stations with pellet groups. I searched for and collected pellet groups in the same search areas. Search areas were located in habitat surrounding the grid locations. Before my first collection, I removed all pellet groups deposited in the search areas. The age of pellet groups from my first collection were then estimated as half the number of days between the removal and first collection. Every 2 weeks, I searched for and collected pellet groups within the search areas, deployed freshly collected pellet groups in the grids, and photographed both freshly deposited pellet groups upon deployment and each previously deployed pellet group. I defined pellet groups as ≥ 6 pellets of the same color, shine, and located within the same immediate vicinity (usually within < 1 m), so each pellet could be assumed to result from the same defecation event. I gently placed pellet groups on the ground to mimic a natural defecation event. I did not fill each station in each grid upon the first sampling occasion in December to allow for future deployment of freshly deposited pellet groups (Laing et al. 2003). In some instances, snow events prevented monitoring. Because it is impossible to determine the exact age of collected pellet groups, I considered the age of each collected pellet group to be half the number of days between searching occasions (Laing et al. 2003).

I compiled all photographs from each monitoring occasion for each pellet group into a single document. Surveyors then independently examined photos and reported a status of decayed (0) or persisted (1) for each pellet group on each monitoring occasion. Surveyors considered pellet groups decayed if < 6 individual pellets were distinguishable (Urbanek et al. 2012). Up to 4 surveyors examined the photos from each year, which were the same surveyors who conducted the line transect sampling in the case study. I extensively trained surveyors in the decay criteria that I used to classify pellet groups during classroom sessions and hands-on field trials. Additionally, all

surveyors received copies of reference photographs of pellet groups and a written protocol that contained the criteria for determining pellet group decay. Because it was infeasible to determine the exact date a pellet group decayed between monitoring occasions, I considered the date when a pellet group decayed as the date midway between the last monitoring occasion I observed the pellet group as intact and the first monitoring occasion I categorized the same pellet group as decayed. This midway point typically was 7 days before the first monitoring occasion that I considered the pellet group decayed, but in some instances snow events delayed photo documentation and led to a corresponding increase. I assessed consistency on the statuses given to pellet groups by surveyors using concordance (i.e., the percentage of pellet-group photos between 2 given surveyors that were assigned the same status) and Somers' D given by $D = \frac{N_c - N_d}{N_t}$, where N_c = the number of concordant pairs, N_d = the number of discordant pairs, and N_t = the total number of pairs.

2.3.2 Estimating Persistence Time for a Single Observer

I estimated the persistence time of pellet groups for a single surveyor using logistic regression and numerical integration (Laing et al. 2003). I fit 9 random-intercept logistic regression models (Table 2.1) to test the effects of year and habitat type on persistence (decayed or not decayed) and used Akaike Information Criterion adjusted for small sample sizes (AIC_c) for model selection (Burnham and Anderson 2002). I used pellet group ID as a random effect. During preliminary analysis, I determined the mean number of pellets in pellet groups monitored during the 2019–2020 season to be less than in the other 2 monitoring seasons. Accordingly, I randomly subsampled pellet groups in the 2019–2020 season using weighted probabilities derived from the other 2 monitoring seasons to ensure that any potential interannual differences in pellet-group persistence resulted from environmental factors and that the size distribution of pellet groups monitored on grids was representative of naturally occurring pellet groups (Figure A1). I also identified a negative relationship between the number of pellets in pellet groups and persistence time. Thus, I included the initial number of pellets in each group as an additive predictor in all regression models of persistence time. Pellet persistence can vary among vegetation types and over seasons (Fernandez-de-Simon et al. 2011, Davis and Coulson 2016). Thus, I included mean daily temperature and mean total daily precipitation, computed over the period from deployment until each unique monitoring occasion, as additive predictors in an effort to enhance the value of my

model to future applications. Due to budget constraints, I did not collect temperature and precipitation data uniquely for each grid, but instead collected these weather variables across all grids. I assessed model goodness of fit using conditional R^2 (Nakagawa and Schielzeth 2013). To facilitate the use of covariates in addition to age of the pellet group, I used the best AIC_c model to predict the probability of persistence $\hat{y}_i$ for each observation i of my monitored pellet groups (Laing et al. 2003). I then fit a logistic curve to the predictions using nonlinear weighted least squares, with weights of $\hat{y}_i = 1/\{\hat{y}_i(1 - \hat{y}_i)\}$ (Buckland et al. 1999), and estimated persistence time using the equation from Laing et al. (2003):

$$\hat{t} = \int_0^{\infty} \frac{-\beta_1 a [1 + \exp(-\beta_0)] \exp(-(\beta_0 + \beta_1 a))}{[1 + \exp(-(\beta_0 + \beta_1 a))]^2} da \quad (2)$$

where $\hat{t}$ = the estimated persistence time, a = the age of a pellet group, and β_0 and β_1 are the coefficients to be estimated from the non-linear weighted least squares logistic model with an asymptote of 1. I approximated $\widehat{var}(\hat{t})$ using the delta method (Eq. 16 in Laing et al. 2003). Henceforth, I will refer to this method as the single-observer method. As the name suggests, when estimating the single-observer persistence time, I only used the photo-observation data from a single observer (ZJD) who examined photographs of all pellet groups from all 3 years.

Table 2.1. Relative support of candidate random-intercept logistic regression models estimating the number of days pellet groups from white-tailed deer persisted before degrading to <6 pellets in west-central Indiana, USA. I obtained the response variable from status of pellet groups (decayed = 0, persisted = 1) given by observers viewing photographs of pellet groups. I photographed pellet groups from December to April in 2018–19, 2019–20, and 2020–21 within prairie, forest and agricultural fields. I present model selection results from the single-observer method. Pellets = number of pellets in each pellet group upon initial deployment. Precipitation = mean daily total of precipitation. Temp = mean daily temperature. Age = the number of days since the estimated data of defecation. Habitat = habitat type the pellet groups was placed in. Year = the year of monitoring. + = additive effect. × = interactive effect.

Predictors	k ^a	AIC _c ^b	ΔAIC _c ^c	w ^d	Cond R ^{2e}
Pellets + Precipitation + Temp + Age + Habitat × Year	14	600.4	0	0.996	0.665
Pellets + Precipitation + Temp + Age + Habitat + Year	10	611.9	11.55	0.003	0.644
Pellets + Precipitation + Temp + Age × Year + Habitat	12	615.5	15.12	0.001	0.636
Pellets + Precipitation + Temp + Age	12	641.4	40.99	0	0.635
Pellets + Precipitation + Temp + Age + Habitat	8	622.1	21.76	0	0.631
Pellets + Precipitation + Temp + Age + Year	10	634.6	34.18	0	0.644
Pellets + Precipitation + Temp + Age × Habitat	8	626.2	25.85	0	0.631
Pellets + Precipitation + Temp + Age × Year	10	638.2	37.79	0	0.641
Pellets + Precipitation + Temp + Age × Habitat + Year	6	616.1	15.67	0	0.639

^aThe number of parameters estimated.

^bAkaike Information Criterion adjusted for small sample sizes.

^cThe difference between the AIC_c value of the model with the smallest AIC_c value and the AIC_c of the contending model.

^dWeight of evidence suggesting the contending model is the best model.

^eConditional R² values.

2.3.3 Accounting for Interobserver Discrepancies

To account for observer discrepancies on the status of pellet groups, I used a case-wise randomization process to assign a final binary decay status Y ($0 =$ decayed, $1 =$ not decayed) for pellet group i in habitat h and study year j , denoted by Y_{ihj} , where $Y_{ihj} \sim \text{Bernoulli}(P_{ihj})$. Here, P_{ihj} is the fraction of the observers in study year j to classify pellet group ihj as decayed. I conducted $M = 999$ independent Bernoulli trials for all pellet groups. For each m th set of Bernoulli trials, I calculated the persistence time for each habitat and year, denoted by $\hat{t}_{mhj}$, by fitting all possible logistic models in Table 2.1, using an automated model selection procedure with AIC_c, fitting a nonlinear weighted least squares regression model to predictions of observations using the AIC_c-best model, and estimating persistence time with equation 2. As formulated, $\widehat{var}(\hat{t}_{hj})$ is solely attributable to interobserver discrepancies (i.e., if concordance across observers = 100%, $\widehat{var}(\hat{t}_{hj}) = 0$). To incorporate variation due to sampling, I used nonparametric bootstraps to sample pellet observations with replacement for each m th set of Bernoulli trials. Using equation 3.97 from Buckland et al. (2001), a final estimate from the M trials, denoted by $\hat{t}_{hj}$, was estimated by $\hat{t}_{hj} = \frac{\sum_{m=1}^M \hat{t}_{mhj}}{M}$, and $\widehat{var}(\hat{t}_{hj}) = \frac{\sum_{m=1}^M (\hat{t}_{mhj} - \hat{t}_{hj})^2}{M-1}$. Henceforth, I will refer to this method as the interobserver method.

2.3.4 Leaf Off

Within large woodlots (>10 ha), I randomly selected 20 canopy trees and monitored them weekly from October to January 2018–19, 2019–20, and 2020–21. On each monitoring occasion for each tree, I photographed the tree's canopy while standing directly beneath it. Using each photo, I estimated when each tree shed 98% of leaves. During the summer following each tree-monitoring season, I tallied species composition of deciduous canopy trees across the same woodlots sampled in my case study. Specifically, I calculated basal area and species composition with variable radius plots using a $2.296\text{-m}^2/\text{ha}$ basal area factor prism. I sampled 2–9 plots within each woodlot, with sample number dependent on woodlot size, i.e., $A/2p < p$, where A is the area of the woodlot in hectares, and p is the number of plots within the woodlot.

Similar to other studies (Xie et al. 2018), I observed oak (*Quercus* spp.) species shedding leaves after all other tree species during my monitoring. Therefore, I designated the date of 98%

leaf off when φ percent of monitored oaks had shed $\geq 98\%$ of leaves, and $\varphi \cong (Oak - 2)/Oak$, where *Oak* is the percent of the canopy that I identified as oak during my tallying of canopy species composition. Henceforth, I will refer to this method as the leaf-off method.

2.3.5 Case Study: White-Tailed Deer

I applied my estimates of $\hat{t}$ for agricultural fields and forested habitats in all 3 years to pellet transect data collected from late February to mid-March in 2019, 2020, and 2021 along 200-m transects placed randomly and oriented using ArcMap 10.7 (ESRI, Redlands, CA, USA). I did not estimate deer density in prairie due to insufficient effort in this habitat type (Table 2.2), as prairie made up only 2.6, 2.0, and 3.8% of the total area sampled in 2019, 2020, and 2021, respectively. Similarly, I did not estimate density in agricultural fields using the leaf-off method, as agricultural fields do not have $>50\%$ canopy coverage (Eberhardt and Van Etten 1956). I specifically sampled transects in 16 10.36-km² areas that I randomly selected from the Indiana Department of Natural Resources' deer reporting grid using ArcMap 10.7. Similar to the pellet-group monitoring, all 10.36-km² areas were located within deer management unit 3, in west-central Indiana, USA (Figure 2.1). During each of the 3 years of sampling, I surveyed a subset of the 16 areas. However, I included 2 of the areas in each year of my sampling (Figure 2.1). Transects were unevenly distributed across the 10.36-km² areas because of access constraints on private property. Field work was conducted each year by the same surveyors that examined the photos of pellet groups for that respective year. Each unique transect was surveyed by a single surveyor. To ensure perfect detection at distance 0, a single surveyor sampled each transect twice. During the first pass, the surveyor concentrated all attention directly on the transect line. During the second pass, the surveyor looked for pellet groups up to 2 m away from the transect line. Upon detecting a pellet group, the perpendicular distance from the transect line to the centroid of the pellet group was measured and the pellet group was removed so that no pellet group was accidentally counted again during the second pass.

Table 2.2. The number of 200-m transects sampled (Transects) and white-tailed deer pellet groups detected in each habitat type. Values are shown for all years when pellet transect sampling was conducted in deer management unit 3 of Indiana, USA.

Habitat	Year	Transects	Pellet groups
Agricultural fields	2019	61	66
Forest	2019	33	314
Prairie	2019	6	26
Agricultural fields	2020	65	35
Forest	2020	31	332
Prairie	2020	3	20
Agricultural fields	2021	47	86
Forest	2021	42	259
Prairie	2021	10	42

Agricultural fields comprised 83.94% of the area in my study sites. White-tailed deer spend less time in agricultural fields compared to areas of natural cover (Beier and McCullough 1990, Nixon et al. 1991). Thus, if defecation rate of deer is independent of local cover type, average density of pellet groups and corresponding encounter rate variance is likely lower in agricultural fields than in natural cover types. Because of this, I stratified transect placement into natural cover and agricultural fields to account for disparities in pellet group density. Specifically, I concentrated my sampling effort in natural cover disproportionate to its availability across my study area (Appendix A: Effort Stratification). I defined natural cover as forest, shrubland, grassland, pasture or hay field, and wetlands.

I fit year-specific detection functions for forested habitat using the Distance R package (Miller 2020). Specifically, I fit half-normal key functions with Hermite polynomial, simple polynomial, cosine, and no adjustments, and hazard-rate key functions with simple polynomial and no adjustments to estimate a detection function. In addition, I considered detection functions using the half-normal and hazard-rate key functions with observer as a factor covariate, as detection may differ between observers (Buckland et al. 2004). I selected the most parsimonious models using an information theoretic framework via AIC (Burnham and Anderson 2002). To

determine whether to use a pooled detection function across all 3 years in forest or year-specific detection functions in forest, I compared the sum of AICs from the best year-specific detection functions for each year to the AIC of the best detection function fit to the data from all 3 years (Buckland et al. 2015). I did not detect enough pellet groups in 2020 to fit year-specific detection functions in agricultural fields. Therefore, in addition to the aforementioned detection functions, I considered hazard-rate and half-normal detection functions in agricultural fields that used year or observer as a factor covariate (Buckland et al. 2004). I estimated year-specific density in agricultural fields using a pooled detection function for agriculture across all years and a stratified encounter rate. After preliminary examination of the perpendicular distances, I truncated distances >190 , >170 , and >140 cm in forest during 2019, 2020, and 2021, respectively, and distances >140 cm in agricultural fields. I assessed the fit of all detection functions using a Cramer-von Mises Goodness-of-Fit test (Buckland et al. 2004). I estimated the total density across both forest and agricultural fields in the areas I sampled each year using a weighted geographic stratification by

$$\hat{D}_y = \sum_{i=1}^2 \left(\frac{A_{iy}}{A_y} \right) \hat{D}_{iy} \quad (3)$$

where $\hat{D}_y$ is the density estimate across all strata in year y , A_{iy} is the total area of stratum i in year y , A_y is the total area of both strata in year y , $\hat{D}_{iy}$ is the stratum-specific density estimate in year y , and $var(\hat{D}_y) = \sum_{i=1}^2 \left(\frac{A_{iy}}{A_y} \right)^2 var(\hat{D}_{iy})$. During density estimation, I used a constant daily defecation rate of 26.8 pellet groups/deer/day (i.e., there was no uncertainty associated with daily defecation rate). The chosen rate was a mean from previous studies that obtained defecation rates from white-tailed deer during winter (Rogers 1987, Sawyer et al. 1990). Because I used a constant defecation rate, intermethod differences in density for a given habitat and year were attributable solely to differences in $\hat{t}$.

To compare density estimates (within each habitat and year) from each of the 3 methods for estimating $\hat{t}$, I used a paired bootstrap analysis. Specifically, I estimated $\hat{t}$ for each habitat and year using the single-observer and interobserver method by bootstrapping the pellet observations from photos 999 times, from which I estimated 999 paired $\hat{t}$ estimates for both methods. I then acquired 999 individual samples of pellet-transect data by using nonparametric bootstrapping to sample transects with replacement. For each of the 999 bootstrapped samples of pellet-transect data, I fit all of the detection functions stated above and used an automated model selection process

with AIC to account for model uncertainty (Buckland et al. 2001). Each pair of interobserver and single-observer $\hat{t}$ estimates, along with the constant leaf-off substitute for t , were applied as multipliers to a single bootstrapped pellet-transect sample. I inferred differences between densities in the same year and habitat using 2 different indices. The first was an index of consistency between the paired bootstrap densities given by the fraction of instances across the 999 bootstraps in which the difference in density was the same sign as the observed difference between $\hat{D}_{t_1}$ and $\hat{D}_{t_2}$. The second was an index of the magnitude of the difference between the sampling distributions for densities from each method, expressed as the overlap index, $\hat{\eta}$, i.e., the area of overlap of the 2 distributions of bootstrapped densities (Pastore and Calcagni 2019). I performed all statistical analyses in the programming language R (R Core Team 2021).

2.4 Results

2.4.1 Estimation of Persistence Times

After examination of all the pellet-group photos, the mean concordance between observers was 93.48% (SE = 1.35) and mean Somers' D was 0.87 (SE = 0.03). Point estimates of persistence time for the single-observer and interobserver methods were similar in all instances, although variance of the latter was greater due to interobserver discrepancies. I documented 98% leaf off on 29 November 2018, 15 December 2019, and 18 November 2020, which resulted in 118, 72, and 120 days between 98% leaf off and field sampling in 2019, 2020, and 2021, respectively (Table 2.3). The persistence time in forests using the leaf-off method was always greater than the estimated persistence time using either the interobserver or single-observer methods. The model containing age, mean daily precipitation, mean daily temperature, number of pellets upon deployment, habitat type, and year as additive predictors and an interactive effect between habitat type and year was the best model for the single-observer method ($AIC_c = 600.4$, weight = 0.996, conditional $R^2 = 0.665$, Table 2.1). Using Type 2 Wald χ^2 tests to identify strong predictors of pellet-group persistence within the best single-observer model, I found support for the importance of pellet group age ($\chi^2 = 127.33$, df = 1, $P \leq 0.001$, Figure 2.2E), mean daily precipitation ($\chi^2 = 9.59$, df = 1, $P = 0.002$, Figure 2.2B), mean daily temperature ($\chi^2 = 9.23$, df = 1, $P = 0.002$, Figure 2.2C), number of pellets upon deployment ($\chi^2 = 9.48$, df = 1, $P = 0.002$, Figure 2.2D), habitat type ($\chi^2 = 20.66$, df = 2, $P \leq 0.001$), and year ($\chi^2 = 10.41$, df = 2, $P = 0.005$). Additionally, I found

support for an interaction between habitat type and year ($\chi^2 = 16.22$, $df = 4$, $P = 0.003$, Figure 2.2A). Specifically, the probability of pellet groups persisting was negatively associated with age ($\beta = -0.06$, $SE = 0.01$), mean daily precipitation ($\beta = -4.04$, $SE = 1.31$), and mean daily temperature ($\beta = -0.20$, $SE = 0.07$), and was positively associated with the number of pellets upon deployment ($\beta = 0.02$, $SE = 0.01$). The habitat type $\times$ year interaction revealed that the probability of persistence was highest in 2018–2019 and lowest in 2020–2021 for forests and agricultural fields; however, the probability of persistence was similar in 2018–2019 and 2020–2021 and lowest in 2019–2020 in prairies (Figure 2.2A).

Table 2.3. Estimates of the mean number of days pellet groups from white-tailed deer persisted before degrading beyond recognition ($\hat{t}$; <6 individual pellets), based on photographs of pellet groups taken every 2 weeks, and corresponding white-tailed deer density estimates ($\hat{D}$; deer/km²) derived from pellet-transect sampling. Both monitoring of pellet groups and transect sampling occurred in deer management unit 3 within west-central Indiana, USA. Estimates of $\hat{t}$ and $\hat{D}$ are shown for agricultural fields (Ag) and forests during 2019, 2020, and 2021. Cumulative estimates of $\hat{D}$ across all 3 habitat types (Total) were computed from a weighted geographic stratification (Buckland et al. 2001). Estimates of $\hat{t}$ and $\hat{D}$ are specifically shown for 3 different methods for estimating $\hat{t}$: (1) a method that accounts for interobserver discrepancies on whether a pellet group is intact or decayed (Interobserver), (2) the number of days since 98% leaf off and field sampling (Urbanek et al. 2012; Leaf off), and (3) model-based estimation of mean persistence time from a single observer (Laing et al. 2003; Single observer).

Method	Habitat	Year	$\hat{D}$	SE($\hat{D}$)	CV($\hat{D}$)	$\hat{t}$	SE($\hat{t}$)	CV($\hat{t}$)
Interobserver	Ag	2019	0.84	0.37	0.43	131.67	24.80	0.19
Single observer	Ag	2019	0.86	0.35	0.41	128.49	4.92	0.04
Interobserver	Ag	2020	0.75	0.66	0.87	69.07	15.10	0.22
Single observer	Ag	2020	0.88	0.69	0.79	59.20	4.05	0.07
Interobserver	Ag	2021	5.48	2.46	0.45	71.89	8.03	0.11
Single observer	Ag	2021	5.85	2.55	0.44	67.31	2.01	0.03
Interobserver	Forest	2019	7.66	2.27	0.30	88.36	22.56	0.26
Leaf off	Forest	2019	5.73	0.86	0.15	118.00	0.00	0.00
Single observer	Forest	2019	8.16	1.25	0.15	82.95	2.03	0.02
Interobserver	Forest	2020	17.81	6.70	0.38	64.39	14.73	0.23
Leaf off	Forest	2020	15.93	4.76	0.30	72.00	0.00	0.00
Single observer	Forest	2020	20.07	6.07	0.30	57.15	2.62	0.05
Interobserver	Forest	2021	14.79	3.63	0.25	45.55	8.05	0.18
Leaf off	Forest	2021	5.61	0.95	0.17	120.00	0.00	0.00
Single observer	Forest	2021	15.26	2.70	0.18	44.14	2.20	0.05
Interobserver	Total	2019	1.50	0.41	0.27	NA	NA	NA
Single observer	Total	2019	1.57	0.35	0.23	NA	NA	NA
Interobserver	Total	2020	2.00	0.80	0.40	NA	NA	NA
Single observer	Total	2020	2.28	0.80	0.35	NA	NA	NA
Interobserver	Total	2021	7.61	2.32	0.30	NA	NA	NA
Single observer	Total	2021	8.01	2.32	0.29	NA	NA	NA

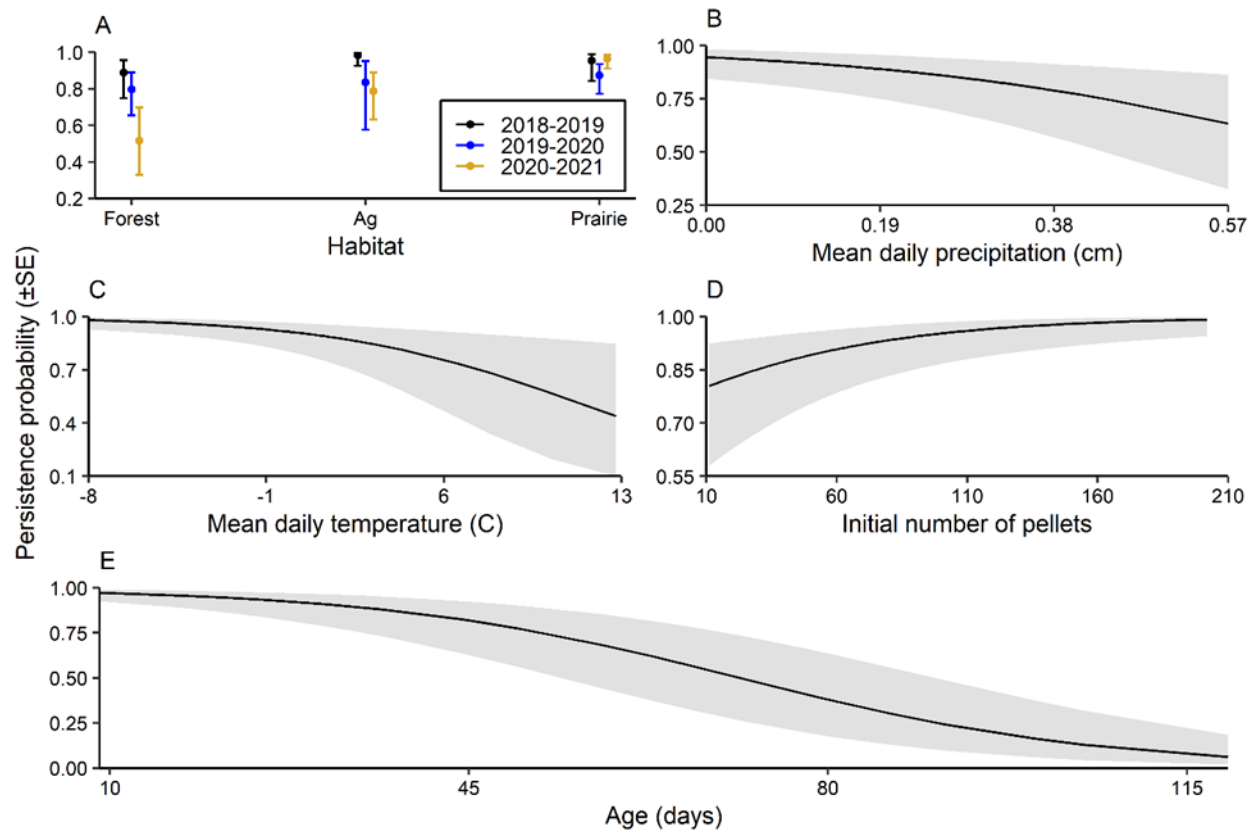


Figure 2.2. Effects plots showing the relationships between persistence probability of pellet groups from white-tailed deer and predictors including habitat type and year (A), the mean daily precipitation (B) and temperature (C) between the estimated date of defecation and each monitoring occasion, the initial number of pellets in each pellet group (D), and the age of the pellet group (E). I obtained these relationships from the best random-intercept logistic regression model using the single-observer method. Vertical bars and gray bands represent $\pm$ SE. Data was collected in deer management unit 3 in Indiana, USA, during 2019, 2020, and 2021.

2.4.2 Case Study

In total, I surveyed 279 transects and detected 1,092 pellet groups in forest and agricultural fields (Table 2.2). On average across all years of sampling, within each 10.36-km² area I sampled 5.30 (SE = 0.65) and 8.65 (SE = 0.93) transects in forest and agricultural fields, respectively. Akaike Information Criterion suggested preference for the use of year-specific detection functions over a pooled detection function in forest ($\Delta\text{AIC} = 32.71$). The AIC-best detection function for forest in 2019 was the half-normal key function with no adjustments (AIC = 3,101.67, $\Delta\text{AIC} = 1.60$, Cramer-von Mises goodness-of-fit statistic = 0.062, $P = 0.800$; Figure 2.3A). The AIC-best detection function for forest in 2020 and 2021 both included observer as a covariate, and were the hazard-rate key function (AIC = 3,195.85, $\Delta\text{AIC} = 0.05$; Cramer-von Mises goodness-of-fit statistic = 0.072, $P = 0.742$; Figure 2.3B) and the half-normal key function (AIC = 2,310.63, $\Delta\text{AIC} = 4.37$; Cramer-von Mises goodness-of-fit statistic = 0.061, $P = 0.809$; Figure 2.3C), respectively. For agriculture fields across all 3 years of sampling, the half-normal key function with year as a covariate emerged as the best detection function (AIC = 1,716.18, $\Delta\text{AIC} = 2.85$; Cramer-von Mises goodness-of-fit statistic = 0.031, $P = 0.973$; Figure 2.3D).

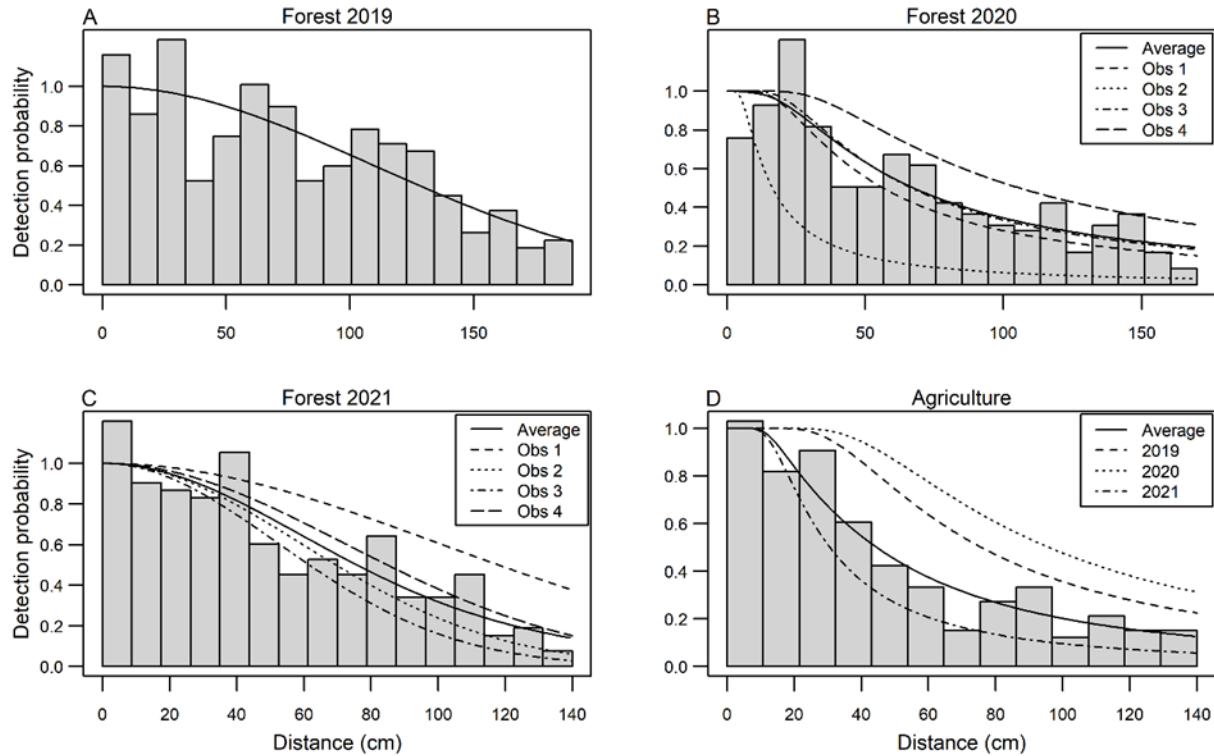


Figure 2.3. The AIC-best detection functions fit to distance-sampling data from pellet groups of white-tailed deer collected on line transects from late February to mid-March in 2019, 2020, and 2021 within forests and agricultural fields in deer management unit 3 of Indiana, USA. For forest in 2019, 2020, and 2021 the half-normal key function with no adjustments ($AIC = 3,101.67$, $\Delta AIC = 1.60$; Cramer-von Mises goodness-of-fit statistic = 0.062, $P = 0.800$; A), the hazard-rate key function with observer as a covariate ($AIC = 3,195.85$, $\Delta AIC = 0.05$; Cramer-von Mises goodness-of-fit statistic = 0.072, $P = 0.742$; B), and the half-normal key function with observer as a covariate ($AIC = 2,310.63$, $\Delta AIC = 4.37$; Cramer-von Mises goodness-of-fit statistic = 0.061, $P = 0.809$; C), respectively, were the AIC-best detection functions. For agricultural fields across all 3 years of sampling, the half-normal key function with year as a covariate was the AIC-best detection function ($AIC = 1,716.18$, $\Delta AIC = 2.85$; Cramer-von Mises goodness-of-fit statistic = 0.031, $P = 0.973$; D).

Density estimates from the leaf-off method were less than the density estimates from the interobserver or single-observer methods in all scenarios (Table 2.3). On average within years, forest density estimates from the leaf-off method were 32.6% (SE = 15.3) and 37.8% (SE = 13.0) less than the density estimates from the interobserver and single-observer method, respectively, and within years and habitat types, density estimates from the single-observer method were 8.0% (SE = 1.7) larger than the density estimates from the interobserver method. On average within years, the CVs of forest density estimates from the leaf-off method were 33.4% (SE = 8.3) and 2.1% (SE = 0.9) less than the CV of density estimates from the interobserver and single-observer method, respectively. Within years and habitat types, the CVs of density estimates from the single-observer method were 16.6% (SE = 4.8) less than the CVs of density estimates from the interobserver method (Table 2.3).

I did not find statistically significant differences between density estimates from the interobserver and single-observer method within a habitat type and year. However, I identified differences between density estimates from the single-observer and leaf-off methods within forests in 2021 (observed difference = 9.65, consistency = 1, $\hat{\eta}$ = 0.023; Figure A2, Table A1). Similarly, I revealed differences between density estimates from interobserver and leaf-off methods within forests in 2021 (observed difference = 9.17, consistency = 1, $\hat{\eta}$ = 0.044). I found evidence of marginal differences between the density estimates from the single-observer and leaf-off methods within forests in 2019 (observed difference = 2.42, consistency = 0.988, $\hat{\eta}$ = 0.267), and between the density estimates from the interobserver and leaf-off methods within forests in 2019 (observed difference = 1.92, consistency = 0.949, $\hat{\eta}$ = 0.325; Figure A2, Table A1). Five of the 6 smallest values of $\hat{\eta}$ corresponded to pairwise comparisons involving the leaf-off method.

2.5 Discussion

Ignoring variation from interobserver discrepancies in scoring the status of pellet groups has the potential to bias density estimates from multi-surveyor studies and confound management decisions reliant upon them. Specifically, if a multiobserver study seeking to estimate animal density via pellet sampling uses a single surveyor, the estimate of persistence may be dissimilar to that of all the individuals who sampled for pellet groups. For example, if the single individual used to estimate persistence exhibits a proclivity to classify pellet groups nearly decayed as intact, whereas the other surveyors classify similar pellet groups as decayed, the estimate of pellet group

persistence will be positively biased and the subsequent animal density estimate will be negatively biased. I present a straightforward interobserver method to account for observer variation in the status of pellet groups. Not surprisingly, the CV of density estimates using the interobserver method was larger than the CV of density estimates from the single-observer method. Inflation of the CV due to variation among observers is pertinent because managers strive for density estimates with good precision and thus smaller CVs that indicate acceptable levels of relative precision. My method requires independent scoring of a common set of pellet groups by multiple observers. An alternative solution is to estimate density as a weighted average of multiple single-observer estimates. One could specify nuisance survey strata (referred to as nuisance because they are not of biological interest) for each field surveyor i in each habitat h , to obtain an effort-weighted density estimate for each habitat across all observers using established methods (Buckland et al. 2001). In such an instance,

$$\hat{D}_h = \sum_{i=1} \left(\frac{L_{ih}}{L_h} \right) \hat{D}_{ih} \quad (4)$$

where $\hat{D}_h$ is the habitat specific density estimate across all surveyors, L_{ih} is the length of transect walked by surveyor i in habitat h , L_h is the total transect length walked by all surveyors in habitat h , and $\hat{D}_{ih}$ is the estimated density from surveyor i in habitat h . The stratum method has the advantage of relying on independent estimates of pellet persistence for each surveyor using the single-observer method, which might reduce variation in pellet persistence and subsequent density estimates in comparison to the interobserver method and may be more appropriate for spatially explicit modelling of density (Hedley and Buckland 2004, Sillett et al. 2012). However, this method could potentially decrease the sample size of pellet-group observations used to estimate each observer's persistence rate in a multi-season study where employment of surveyors is constrained to a single season. In such a case, smaller sample size may lead to increased variance in the estimated persistence rate of pellet groups and subsequent density estimates. Unfortunately, sample size of monitored pellet groups for each habitat in each year was insufficient to permit application of this stratum method to my study. Another approach to account for interobserver variation on the status of pellet groups is to model the status of each pellet group on each monitoring occasion within an occupancy-modelling framework in which the conventional use of temporally replicated sampling occasions is replaced with samples replicated across observers in a manner analogous to spatial replicates (MacKenzie et al. 2006).

I recommend that researchers and managers contemplating the leaf-off method consider adopting preferential measures of pellet persistence. The leaf-off method's 2 strong assumptions are as follows: 1) on the date of 98% leaf off all previously deposited pellet groups are visually obscured and 2) all subsequently deposited pellet groups persist until field sampling. Regarding the first assumption, timing of leaf fall is dependent on many factors including species, weather, and nutrients (Niinemets and Tamm 2005, Richardson et al. 2006). Because these predictors are often heterogeneously distributed in space, the leaf-fall period can span many weeks (Xie et al. 2018). Leaves falling from the canopy will thus cover pellet groups gradually and in a spatially heterogeneous fashion, especially in mixed-species stands where timing of leaf fall varies among species. For instance, a pellet group deposited on the forest floor when the canopy has already shed 85% of its leaves is far less likely covered by the remaining unshed leaves than a pellet group deposited when only 15% of leaves have been shed. Additionally, falling leaves may not cover all pellet groups deposited before leaf fall, and wind may partially or completely reveal previously covered pellet groups or cover pellet groups deposited after leaf off (Eberhardt and Van Etten 1956). In these cases, attempts to distinguish between pellet groups deposited before and after leaf fall are challenging; like others (Eberhardt and Van Etten 1956), I question the reliability of classifying pellet groups as pre- or post-leaf fall by solely visual and olfactory cues. Regarding the second assumption, winter severity and precipitation strongly influence the persistence of pellet groups. Similar to Barnes et al. (1997), I documented that persistence of pellet groups declined with warmer temperatures and precipitation. Therefore, in temperate latitudes warmer winters with many precipitation events will heighten the severity of violating the assumption that all pellet groups deposited after 98% leaf off will persist until field sampling. In most habitat types within each year of my study, mean estimated persistence time of pellet groups using the interobserver or single-observer methods was less than the number of days between leaf off and field sampling, indicating that decay of pellet groups was apparent after the date of 98% leaf off. Although actual density is rarely known in field settings, using the leaf-off method in areas with temperate winters and precipitation events will likely result in positive bias of pellet-persistence estimates, and negative bias of subsequent density estimates. During all years, variation in persistence was evident using either the interobserver or single-observer method; thus, assuming a constant t (as in the leaf-off method) is inappropriate and will underestimate the variance of corresponding density estimates.

The equivalent of the leaf-off method for prairie habitats requires the estimation of 98% herbaceous senescence, and the number of days between this date and field sampling is substituted for $\hat{t}$ (Eberhardt and Van Etten 1956). Thus, the same assumptions of the leaf-off method apply: all pellet groups deposited before 98% herbaceous senescence would be covered by herbaceous debris, all pellet groups deposited after 98% herbaceous senescence persist until field sampling, and there is no variation associated with $\hat{t}$. Like tree species, herbaceous prairie species senesce in a heterogeneous fashion (Wang et al. 2013). Therefore, the assumption that all pellet groups are covered on a single day seems tenuous. Similar to pellet groups in forests and agricultural fields, I found variation in the persistence of pellet groups in prairies, signifying that $\widehat{var}(\hat{t}) \neq 0$ in prairies. For these reasons, I suggest adoption of other measures of pellet persistence.

My attention focused on issues related to estimation of pellet group persistence, but estimation of the deposition rate of pellet groups ($\hat{s}$ in equation 1) presents similar challenges. Like others, in my case study I relied on published estimates of daily defecation rate for white-tailed deer, which I treated as a constant. Similar to $\hat{t}$, defecation rates likely vary temporally due to environmental conditions and have the potential to alter density estimates derived from pellet sampling methods (Fuller 1991). For this reason, in my case study I stress interpretation of relative differences in densities due to the 3 methods of estimating $\hat{t}$ rather than the actual densities themselves. Ideally, monitoring that seeks estimates of deer density would benefit from efficient methods for estimation of defecation rates at or near the spatiotemporal extent of the study, a topic that merits future consideration.

2.6 Management Implications

Managers seeking to estimate densities of species using dung sampling need to carefully consider the ecology of future study areas and the method used to estimate dung persistence time. Temperate climates with annual fluctuation in temperature and precipitation, coupled with mixed-species forests experiencing autumn leaf abscission over the course of several weeks (or multiple months), present situations that are likely to violate the assumptions underlying the leaf-off method. Additionally, managers employing several individuals for largescale monitoring should emphasize the criteria for classifying pellet groups as decayed or intact during training for fieldwork and should explicitly account for interobserver variation using either the method outlined herein or

suitable alternatives. I encourage future work on methods of incorporating interobserver variation in status of cue counts into estimates of persistence and density.

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CHAPTER 3. IMPERFECT DETECTION AND WILDLIFE DENSITY ESTIMATION USING AERIAL SURVEYS WITH INFRARED AND VISIBLE SENSORS

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3.1 Abstract

Aerial vehicles equipped with infrared thermal sensors facilitate quick density estimates of wildlife, but detection error can arise from the thermal sensor and viewer of the infrared video. I reviewed published research to determine how commonly these sources of error have been assessed in studies using infrared video from aerial platforms to sample wildlife. The number of annual articles pertaining to aerial sampling using infrared thermography has increased drastically since 2018, but past studies inconsistently assessed sources of imperfect detection. I illustrate the importance of accounting for some of these types of error in a case study on white-tailed deer (*Odocoileus virginianus*) in Indiana, USA, using a simple double-observer approach. In my case study, I found evidence of false negatives associated with the viewer of infrared video. Additionally, I found that concordance between the detections of two viewers increased when using a red-green-blue camera paired with the infrared thermal sensor, when altitude decreased, and when more stringent criteria were used to classify thermal signatures as deer. I encourage future managers and ecologists recording infrared video from aerial platforms to use double-observer methods to account for viewer-induced false negatives when video is manually viewed by humans. I also recommend combining infrared video with red-green-blue video to reduce false positives, applying stringent verification standards to detections in infrared and red-green-blue video, and collecting data at lower altitudes over snow when needed.

3.2 Introduction

Aerial platforms are commonly used for surveying in wildlife research and management (Pollock and Kendall 1987, Hone 2008). Sampling animals from an aerial platform facilitates quick population estimates (McMahon et al. 2021). Traditionally, aerial sampling has been

performed by human observers who ride in a plane or helicopter and detect animals out the sides of the aircraft (Pollock and Kendall 1987). Collecting data and estimating density under various distance-sampling, mark-recapture, or a combination of these two frameworks has thus been common (Barker 2008, Fewster and Pople 2008).

Infrared (IR) thermography, in which thermal cameras capture images from infrared radiation emitted from objects, has been adopted by wildlife researchers to estimate population abundance (Havens and Sharp 2015). In the context of aerial sampling, thermal sensors have been oriented two different ways when used to detect animals: (1) forward-looking infrared (FLIR) thermal sensors, which look forward from the aerial vehicle at oblique angles (Storm et al. 2011, Sudholz et al. 2021); and (2) vertical-looking infrared (VLIR) thermal sensors, which look directly beneath the aircraft (i.e., nadir orientation; Kissell and Nimmo 2011).

Using IR thermal sensors to sample wildlife may introduce error from at least two sources. Firstly, the thermal sensor may yield false negative errors by failing to detect animals. Similar to Brack et al. (2018), I refer to these as availability errors. Poor or no thermal contrast (e.g., thick vegetation, lack of cloud cover (resulting in poor thermal contrast), or overhangs) induce availability errors (Havens and Sharp 2015). Therefore, study designs often consider weather and altitude to minimize the potential of availability errors. The use of VLIR instead of FLIR also can help to alleviate availability errors caused by vegetative obstruction because the distance and angle, and thereby the amount of vegetative or topographical obstruction, between the thermal sensor and animal is lesser (Kissell and Nimmo 2011). In general, strategies to account for availability errors seem logistically challenging (discussed more below).

Other sources of error can arise while viewing the IR video if viewers incorrectly classify IR signatures (Stander et al. 2021). Specifically, false positives and negatives can be caused by the viewer or automated classification algorithm. Similar to Brack et al. (2018), I refer to false positives and negatives from the viewer as misidentification errors and perception errors, respectively. Because of the potential for misidentification errors, some researchers have simultaneously captured high-resolution red-green-blue (RGB) digital imagery with IR video, which is then used to confirm heat signatures as the target species (Franke et al. 2012, Schoenecker et al. 2018). An additional type of false positive can occur from double counting. Double counting can arise from overlapping transects, successive images containing the same individual, or animal movement in between neighboring transects (Brack et al. 2018; discussed more below).

I conducted a literature review to determine how frequently the aforementioned types of errors have been addressed in wildlife research using thermal sensors from aerial platforms. I then illustrated the potential importance of viewer errors in a case study where I simultaneously captured VLIR and RGB video across three different regions of Indiana, USA. To evaluate the magnitude and impact of perception errors in IR sampling, I estimated the density of white-tailed deer (*Odocoileus virginianus*) using the detections of two viewers and a single viewer. To assess the effects of study design on the concordance of IR detections, I computed density using video collected at multiple altitudes and differing ground conditions. Lastly, to better understand the importance of confirming IR signatures with RGB video, I estimated densities using: (1) only IR video; and (2) IR and RGB video.

3.3 Methods

3.3.1 Literature Review

I reviewed published studies that used thermal sensors to study wildlife from aerial vehicles by conducting the following keyword search on Web of Science™ on 1 January 2022: “(thermal OR infrared) AND wildlife AND (aerial OR plane OR airplane OR helicopter OR unmanned OR drone)”. For each article I recorded: (1) year of publication; (2) whether the study pertained to behavior, presence/absence, simple counts, or density/abundance estimation; (3) if imperfect detection was addressed in any way, and if so, whether uniform detection across the field-of-view of the camera, availability errors, perception errors, misidentification errors, or double-counting errors were addressed; (4) if photos, video, or active searching was used to collect data; (5) thermal sensor orientation (forward-looking or vertical-looking); (6) if IR, RGB, or IR and RGB video was recorded; (7) if the aerial vehicle was crewed or uncrewed; and (8) if automated software, human viewers, or automated software and human viewers were used to review video and detect the target species. I did not include articles that used data from only simulation, did not pertain to wildlife, did not use an aerial vehicle, were not fully available for review (e.g., only abstracts available), or previous review articles without a case study.

3.3.2 Case Study

3.3.2.1 Study Sites

I sampled deer populations in Indiana's Deer Regional Management Units 3, 4, and 9 (Swihart et al. 2020, Delisle et al. 2022). I surveyed two different 6.4 x 6.4-km areas within each Regional Management Unit (hereafter, RMU), resulting in six total areas flown (Figure 3.1). I randomly selected these areas from the deer reporting grid used by the Indiana Department of Natural Resources to collect spatially explicit harvest data. Regional Management Unit 3 is an intensively farmed region with 79% row-crop agriculture, 10% forest, 3% grassland, and 1% wetland. Unlike RMU 3, RMU 4 is mainly forested with 19% row-crop agriculture, 56% forest, 16% grassland, and <1% wetland. Lastly, RMU 9 is 56% row-crop agriculture, 8% forest, 11% grassland, and 13% wetland. All three RMUs follow a four-season temperate weather pattern.

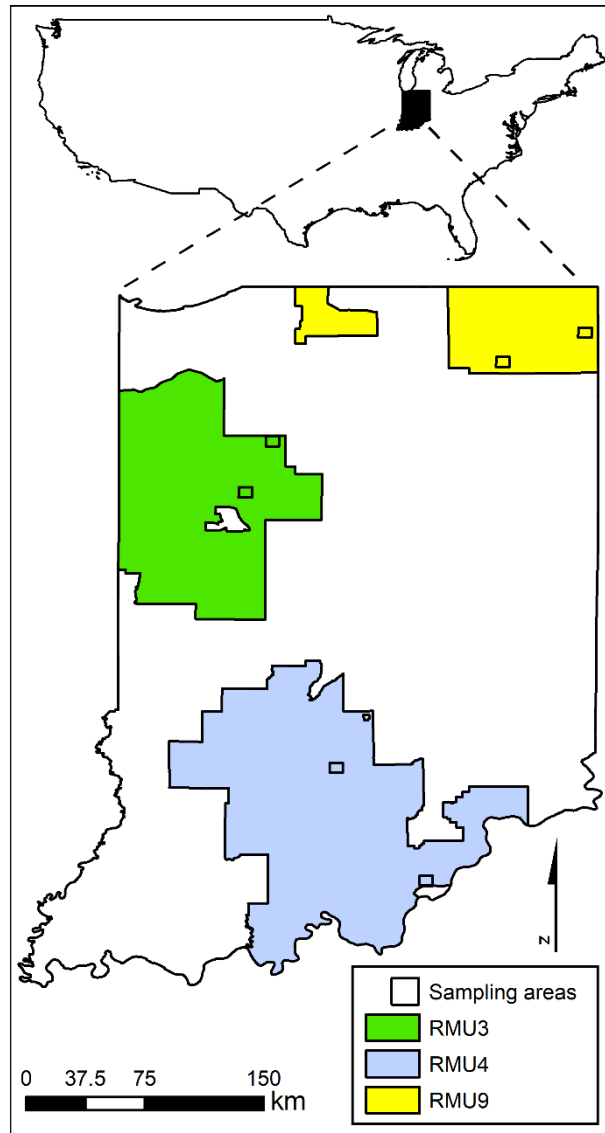


Figure 3.1. Sampling areas within the Deer Regional Management Units (RMU) of Indiana, USA, that I surveyed. White-tailed deer (*Odocoileus virginianus*) were detected using thermal and color sensors in a crewed aerial platform during daylight hours from 8 February – 10 March 2021.

3.3.2.2 Data Collection

In each sampling area, I flew 16 systematically placed 6.4-km transects. Adjacent transects were separated by 400 m and aligned north to south. I flew transects in a Sky Arrow Light Sport Aircraft (Magnaghi Aeronautica S.p.A.) at speeds of ~105 kph. I flew at an altitude of 450 m in RMU 3 when there was snow cover, an altitude of 450 m in RMU 4 when there was no snow cover, and an altitude of 300 m when there was snow cover in RMU 9. Flights occurred during daytime hours (30 minutes after sunrise to 30 minutes before sunset) from 8 February – 10 March 2021 when deciduous trees had already shed leaves. I surveyed during daytime so RGB video could be captured simultaneously. Regardless of ground condition or altitude, I only collected aerial data on overcast days while flying under cloud cover, which heightened the thermal contrast between background temperatures and body temperatures of deer.

During flights, I recorded VLIR and RGB video using an IR-TCM HD 1024 stationary thermal sensor equipped with a 60 mm lens (Jenoptik, Jena, Germany), and a Nikon D810 DSLR camera equipped with a Nikon AF DC-NIKKOR 135mm f/2D lens (Nikon Inc., Melville, NY). Cameras were affixed to opposite sides of the aircraft and focused on the ground directly beneath the aircraft. I simultaneously recorded IR and RGB video while georeferencing and digitally storing the video using a GeoDVR Mini (Remote GeoSystems, Inc.) equipped with a Garmin global positioning system (Garmin Ltd.).

I viewed IR and RGB video using the LineVision – Ultimate software (Remote GeoSystems, Inc.). While viewing video, two independent viewers that were highly trained and experienced in viewing IR video (3 sampling seasons of experience) recorded 4 different qualitative classes of detections (Figure 3.2): (1) detections from IR video for which the heat signature had any potential to be a deer but the viewer was not confident that the heat signature was a deer (lenient IR detections); (2) detections from IR video in which the viewer was confident that the heat signature was from a deer (stringent IR detections); (3) RGB confirmations of lenient or stringent IR heat signatures in which the object in the RGB video had any potential to be a deer but the viewer was not confident the object was a deer (lenient RGB confirmations); and (4) RGB confirmations of lenient or stringent IR heat signatures in which the viewer was confident that the object in the RGB video was a deer (stringent RGB confirmations). When assigning IR heat signatures or RGB objects, stringent detections were those with a shape that was clearly defined and unambiguous so that I believed no other object than a deer could be producing such an IR heat

signature or RGB object. No other species of similar shape and color to that of white-tailed deer were present in my field site. To avoid bias, the two viewers scored videos independently (i.e., did not aid each other when classifying images) and only defined an RGB confirmation as either 3 or 4 after first defining an IR detection as 1 or 2 (Figure 3.2). For all detections, I recorded whether or not the detection was within concealed (forest, wetland) or open (grassland, agricultural field) habitat. I used the LineVision – Ultimate software to measure the perpendicular distance from the middle of the thermal sensor’s field-of-view to the IR heat signature. Lastly, I recorded how many other lenient or stringent IR detections were within the immediate vicinity of the IR detection (henceforth referred to as group size). I considered IR detections to be in the immediate vicinity of each other if the detections could appear in the field-of-view of the thermal sensor at the same time.

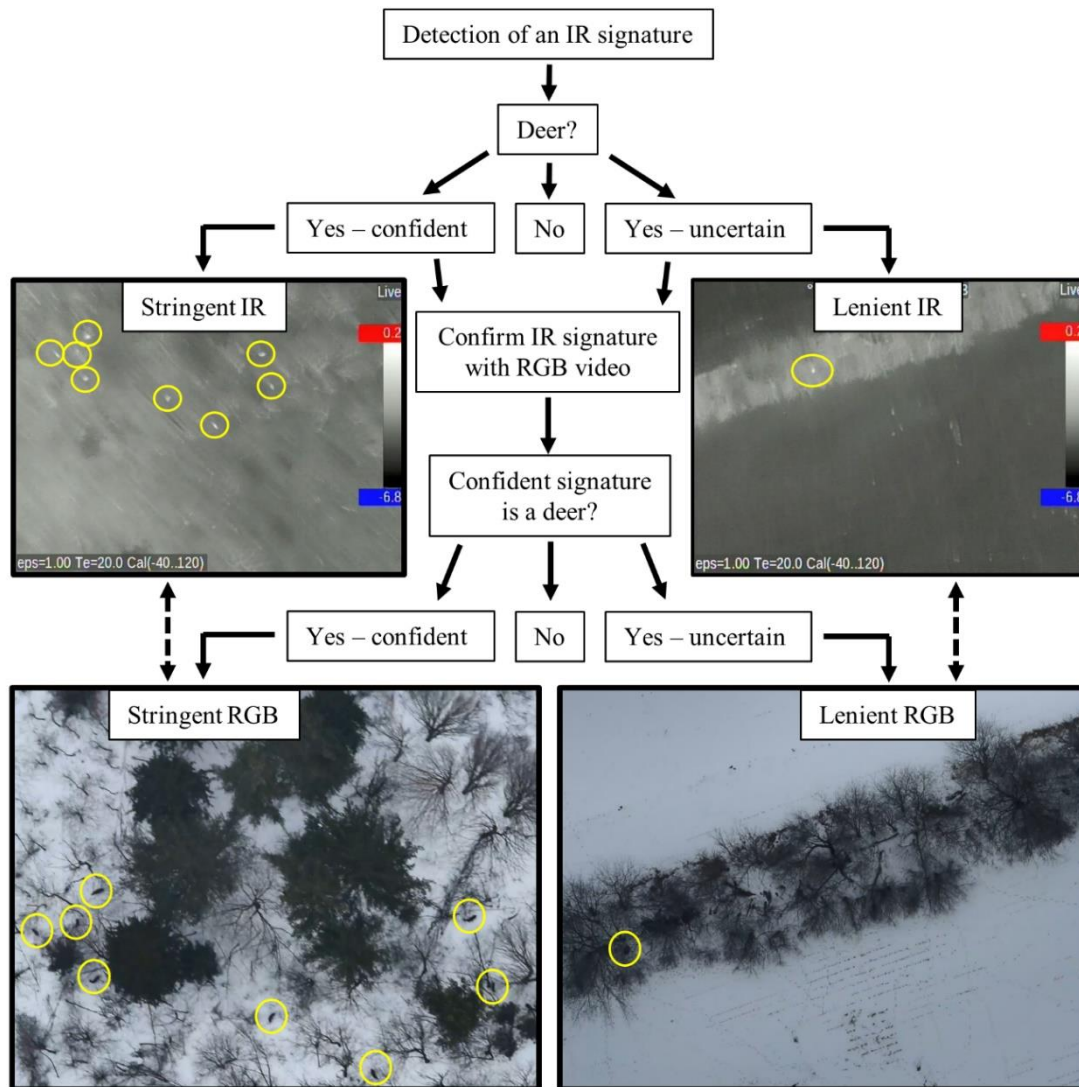


Figure 3.2. Workflow for classifying infrared (IR) heat signatures and corresponding objects in red-green-blue (RGB) as either white-tailed deer (*Odocoileus virginianus*), not deer, or unsure. Video was captured in a crewed aircraft in Indiana, USA, from 8 February – 10 March 2021. All potential IR heat signatures are classified as either lenient IR detections (defined as detections from IR video for which the heat signature had any potential to be a deer but the viewer was not confident the heat signature was a deer) or stringent IR detections (defined as detections from IR video in which the viewer was confident that the heat signature was from a deer). All RGB confirmations were classified as either lenient RGB confirmations (defined as RGB confirmations of lenient IR heat signatures in which the object in the RGB video had any potential to be a deer but the viewer was not confident the object was a deer) or stringent RGB confirmations (defined as RGB confirmations of lenient IR heat signatures in which the viewer was confident that the object in the RGB video was a deer). When assigning IR heat signatures or RGB objects, stringent detections were those with a shape that was clearly defined and unambiguous so that I believed no other object than a deer could be producing such an IR heat signature or RGB object. No other species of similar shape and color to that of white-tailed deer were present in my field site.

I compiled four detection histories using these four detection classes: (1) detection history using lenient and stringent IR detections; (2) detection history using only stringent IR detections; (3) detection history using lenient or stringent RGB confirmations of lenient or stringent IR detections; and (4) detection history using stringent RGB confirmations of lenient or stringent IR detections. I did not assess a scenario in which RGB was used to only confirm stringent IR detections because if RGB is available, I would expect users to check all potential IR heat signatures.

3.3.2.3 Single Viewer

I estimated density from the four different types of detection histories using the observations of a single viewer (ZJD) in each of the altitudes and ground conditions I sampled. I first considered the possibility that detection probability decreased with increasing distance from the middle of the thermal sensor's field-of-view. However, I found evidence that detection probability across the field-of-view was uniform according to Akaike's Information Criterion (AIC) and visual plots of several candidate detection functions (Appendix B: Distance Sampling Analysis for more details). Therefore, I used plot sampling techniques to estimate density (Buckland et al. 2015) with the following formula:

$$\hat{D} = \frac{n}{A} \quad (1)$$

Where n = the total number detections, and A = the total area sampled = $Lw2$, where L = the total length of transect sampled, and w = the transect half width. Because the variation from plot sampling techniques comes from the encounter rate (i.e., there is no variation from a detection function), I used an approach modified from the "R2" method in Fewster et al. (2009) to estimate the standard error as

$$SE(\hat{D}) = \sqrt{\frac{K}{A^2(K-1)} \sum_{k=1}^K a_k^2 \left(\frac{n_k}{a_k} - \frac{n}{A} \right)^2} \quad (2)$$

where K = the total number of transects, a_k = the total area sampled on transect k , and n_k = the total number of detections on transect k .

3.3.2.4 Double Viewer

To ensure that the detection and error rates of the double- and single-viewer methods were directly comparable, I used the detections from the single viewer as one of the double viewers. I calculated the concordance between the two viewers (ZJD and PGM) for all 4 detection histories at each altitude and ground condition. To assess the need for RGB video, I determined the percentage of stringent and lenient IR detections that were confirmed by RGB video to be deer, an object other than deer, or unresolved. I evaluated the value of multiple viewers by calculating the probability of a single viewer detecting a deer conditional upon the other viewer, and the probability of either viewer detecting the deer using the “mrds” package (Laake et al. 2022) in R (R Core Team 2022). Specifically, I fit logistic conditional detection models with a logit link in the form of eq. 6.32 in Laake and Borchers (2004). I used an independent observer configuration and assumed full independence (Burt et al. 2014). I fit a mark-recapture model for each possible additive combination of the following covariates: distance from the transect line, group size, and observer (viewer 1 or viewer 2). I used AIC to decide between competing mark-recapture models. I repeated this model fitting process for each of the four different types of detection histories in each of the altitudes and ground conditions I sampled. I did not test the effect of habitat type (open vs concealed) on detection probability because I detected too few deer in open habitat. Additionally, I purposefully sampled when there was no leaf cover in the canopy to avoid reduced probability of infrared detection in wooded areas.

After selecting the best mark-recapture model, I estimated density in the sampled area using a Horvitz-Thompson-like estimator (Borchers et al. 1998) in the “mrds” R package. Variation from the mark-recapture model was estimated using the delta method (Borchers et al. 1998), and variation from the random sample selection was estimated using the encounter-rate estimator in Innes et al. (2002) in the form of the “R2” method in Fewster et al. (2009).

3.4 Results

3.4.1 Literature Review

My search revealed 62 articles on the use of IR thermography in aerial sampling of wildlife since 1991. The number of articles increased sharply from 2018 to 2021 (Figure B2). Uncrewed aerial vehicles have shown a particularly pronounced increase in usage, which is consistent with

past reviews focused on uncrewed aerial vehicles (Linchant et al. 2015). Although the usage of dual platforms containing IR and RGB cameras has increased since 1991, only 9 of 23 articles estimating density or abundance used a dual platform; two of these articles did not use RGB to confirm IR heat signatures, but instead assessed whether or not RGB could solely be used to estimate density. Two articles did not specify if they used FLIR or VLIR. Of the 62 articles I reviewed, 19 did not address any type of error, 16 addressed one type of error, 18 addressed two types of error, 8 addressed three types of error, 1 addressed four types of error, and no articles addressed all 5 types of error. Twenty-four articles used photos, 32 articles used video, and 16 articles used active searching methods to locate IR heat signatures.

Imperfect detection across the field-of-view of the thermal sensor was assessed by 7 articles; availability errors were addressed by 19 articles; perception errors were addressed by 9 articles; misidentification errors were addressed by 34 articles; and double-counting errors were addressed by 11 articles. Perfect detection across the field-of-view of the thermal sensor was found in 4 of 7 (57%) of the articles that tested for uniform detection probability. Sixteen of the 23 articles (70%) estimating density assessed imperfect detection to some degree. Of these, 7 assessed uniform detection probability across the camera's field-of-view, 5 addressed availability errors, 2 addressed perception errors, 9 addressed misidentification errors, and 6 addressed double-counting errors (Table 3.1).

Table 3.1. Contingency table reporting the total number of articles that: used forward-looking or vertical-looking infrared thermography; did not assess imperfect detection; assessed imperfect detection in terms of uniform detection probability across the field-of-view of the thermal sensor (Uniform), availability errors (AE), perception errors (PE), misidentification errors (ME), or double-counting errors (Double); used infrared (IR), red-green-blue (RGB), or IR and RGB cameras; used crewed or uncrewed aircraft; and used automated viewing software (AI), manual human viewing (human), or both AI and human. Categories are mutually exclusive (e.g., an article using IR and RGB cameras would not satisfy the individual IR and RGB categories). Articles were obtained through a Web of Science™ search conducted on 1 January 2022 for the following: “(thermal OR infrared) AND wildlife AND (aerial OR plane OR airplane OR helicopter OR unmanned OR drone)”.

Platform orientation:			Forward looking						Vertical looking						Subtotal
Aircraft	Sensor	Review	Assess detection?						Assess detection						
			No	Uniform	AE	PE	ME	Double	No	Uniform	AE	PE	ME	Double	
Crewed	IR	AI	0	0	0	0	0	0	0	0	0	0	0	0	0
		Human	6	0	3	0	1	2	2	2	1	0	1	2	15
		Both	0	0	0	0	0	0	0	1	0	1	1	0	1
	RGB	AI	0	0	0	0	0	0	0	0	0	0	0	0	0
		Human	0	0	0	0	0	0	0	0	0	0	0	0	0
		Both	0	0	0	0	0	0	0	0	0	0	0	0	0
	IR + RGB	AI	0	0	0	0	0	0	0	0	0	0	0	0	0
		Human	0	0	0	0	1	1	1	2	2	0	6	1	8
		Both	1	0	0	0	0	0	0	1	0	2	2	0	3
Uncrewed	IR	AI	0	0	0	0	0	0	0	0	0	0	0	0	0
		Human	3	0	1	0	5	0	3	1	0	0	1	2	14
		Both	0	0	0	0	0	0	1	0	2	2	3	2	4
	RGB	AI	0	0	0	0	0	0	0	0	0	0	0	0	0
		Human	0	0	0	0	0	0	0	0	0	0	0	0	0
		Both	0	0	0	0	0	0	0	0	1	0	0	0	1
	IR + RGB	AI	0	0	0	0	1	0	0	0	0	0	0	0	1
		Human	1	0	2	1	2	0	0	0	5	1	8	0	11
		Both	0	0	0	0	0	0	0	0	1	2	2	0	2
Subtotal			11	0	6	1	10	3	7	7	12	8	24	7	60

3.4.2 Case Study

Across the four classes of detection histories, concordance between the two viewers increased when altitude was lower and when snow covered the ground (Table 3.2). I were unable to confirm IR signatures using RGB video in the areas that did not have snow cover on the ground, and therefore I do not present any statistics for the lenient IR with lenient or stringent RGB confirmation histories for this sampling scenario. At altitudes of 300 m, 77.2% (SE = 4.5), 6.5% (SE = 3.6), and 16.4% (SE = 0.9) of stringent IR detections were confirmed to be deer, not deer, or unresolved, respectively, and 19.7% (SE = 6.6), 60.6% (SE = 13.3), and 19.7% (SE = 6.6) of lenient IR detections were confirmed to be deer, not deer, or unresolved, respectively. At altitudes of 450 m, 81.8% (SE = 0.9), 10.2% (SE = 4.3), and 8.1% (SE = 5.2) of stringent IR detections were confirmed to be deer, not deer, or unresolved, respectively, and 21.1% (SE = 21.1), 54.0% (SE = 4.0), and 25.0% (SE = 25.0) of lenient IR detections were confirmed to be deer, not deer, or unresolved, respectively.

Table 3.2. Concordance between two viewers' detections of white-tailed deer (*Odocoileus virginianus*) from aerially captured infrared (IR) and red-green-blue (RGB) video collected in Indiana, USA, from 8 February – 10 March 2021. Both videos were simultaneously captured on an aircraft flown at two different altitudes and over two different ground conditions. Viewers detected deer under four different scenarios: (A) detections from only IR video for which the heat signature had any potential to be a deer; (B) detections from only IR video in which the viewer was confident that the heat signature was from a deer; (C) RGB confirmations of any IR heat signatures in which the object in the RGB video had any potential to be a deer; and (D) RGB confirmations of any IR heat signatures where viewers were confident that the object in the RGB video was a deer. Concordance is not reported for C or D at 450 m altitude over bare ground because I were unable to utilize RGB video in these conditions. When assigning IR heat signatures or RGB objects, stringent detections were those with a shape that was clearly defined and unambiguous so that I believed no other object than a deer could be producing such an IR heat signature or RGB object. No other species of similar shape and color to that of white-tailed deer were present in my field site.

Ground	Altitude	A	B	C	D
Snow	300	70.81	72.98	81.68	86.02
Snow	450	56.10	56.10	61.79	55.28
Bare	450	31.30	43.48	NA	NA

Across all ground conditions, altitudes, and detection histories, the probabilities of either of two viewers detecting a heat signature were on average 3.9% (SE = 1.6) larger than the probabilities of viewer 1 detecting a heat signature (Table 3.3). At 300 m altitude, the probability of detection remained fairly consistent across the different detection histories. However, at 450 m altitude, probability of detection differed between the detection histories, with increasing certainty thresholds of objects in the IR and RGB video associated with lower detection probability (Table 3.3).

The densities and AIC-best mark-recapture models for each of the 4 detection histories at each altitude and ground condition are presented in Table 3.3 and Table 3.4, respectively. Observer was the only covariate in each of the AIC-best mark-recapture models. The densities across all ground conditions, altitudes, and classes of detection histories from the mark-recapture estimator were on average 9.2% (SE = 2.8) larger than the density estimates that used the detections from a single viewer (Table 3.3). Unlike detection probability, the densities across different detection histories at 450 m altitude were fairly consistent, but the densities at 300 m altitude differed among classes of detection histories. Increasing certainty thresholds of objects in the IR and RGB video captured at 300 m resulted in lower density estimates.

Table 3.3. Density estimates ($\hat{D}$) and detection probabilities ($\text{Pr}(\text{det})$) of white-tailed deer (*Odocoileus virginianus*) from aerially captured infrared (IR) and red-green-blue (RGB) video collected in Indiana, USA, from 8 February – 10 March 2021. Corresponding standard errors ($\text{SE}(\hat{D})$) and coefficients of variation ($\text{CV}(\hat{D})$) are reported for density estimates, and standard errors ($\text{SE}(\text{Pr}[\text{Det}])$) are reported for $\text{Pr}(\text{Det})$. Video was captured at differing altitudes (300 m and 450 m) and ground conditions (bare ground and snow cover). Densities were estimated from two viewers using mark-recapture (MR) methods, or a single viewer using plot sampling (PS) methods. For PS, $\text{Pr}(\text{det})$ = the probability of viewer 1 detecting a deer, and for MR, $\text{Pr}(\text{det})$ = the probability of either viewer detecting a deer. Densities were estimated using four different types of detection histories: (1) detections from only IR video for which the heat signature had any potential to be a deer (Lenient IR); (2) detections from only IR video in which the viewer was confident that the heat signature was from a deer (Stringent IR); (3) RGB confirmations of any IR heat signatures in which the object in the RGB video had any potential to be a deer (Lenient RGB); and (4) RGB confirmations of any IR heat signatures where viewers were confident that the object in the RGB video was a deer (Stringent RGB). When assigning IR heat signatures or RGB objects, stringent detections were those with a shape that was clearly defined and unambiguous so that I believed no other object than a deer could be producing such an IR heat signature or RGB object. No other species of similar shape and color to that of white-tailed deer were present in my field site.

Table 3.3 continued

Ground	Altitude	Method	Detection history	$\hat{D}$	$SE(\hat{D})$	$CV(\hat{D})$	Pr(Det)	$SE(Pr[Det])$
Snow	300	MR	Lenient IR	19.89	2.91	0.15	0.98	<0.01
			Stringent IR	18.02	2.76	0.15	0.99	<0.01
			Lenient RGB	16.68	3.02	0.18	0.99	<0.01
			Stringent RGB	13.40	2.96	0.22	0.99	<0.01
		PS	Lenient IR	18.79	2.92	0.16	0.98	0.01
			Stringent IR	17.32	2.72	0.16	0.98	0.01
			Lenient RGB	16.15	2.98	0.18	0.98	0.01
			Stringent RGB	12.93	2.89	0.22	0.98	0.01
	450	MR	Lenient IR	5.43	1.84	0.34	1.00	<0.01
			Stringent IR	5.27	1.67	0.32	0.95	0.02
			Lenient RGB	5.60	1.89	0.34	0.94	0.02
			Stringent RGB	5.67	1.93	0.34	0.91	0.03
		PS	Lenient IR	5.43	1.84	0.34	1.00	<0.01
			Stringent IR	4.64	1.41	0.30	0.88	0.04
			Lenient RGB	4.69	1.46	0.31	0.84	0.04
			Stringent RGB	4.59	1.44	0.31	0.81	0.05
Bare	450	MR	Lenient IR	5.57	1.18	0.21	0.88	0.05
			Stringent IR	3.97	0.90	0.23	1.00	<0.01
		PS	Lenient IR	4.70	0.98	0.21	0.84	0.07
			Stringent IR	3.97	0.90	0.23	1.00	<0.01

Table 3.4. The AIC-best mark-recapture models fit to detection histories of white-tailed deer (*Odocoileus virginianus*). Detections were extracted from aerially captured infrared (IR) and red-green-blue (RGB) video collected in Indiana, USA, from 8 February – 10 March 2021. Video was captured at differing altitudes (300 m and 450 m) and ground conditions (bare ground and snow cover). Mark-recapture models were fit using four different types of detection histories: (1) detections from only IR video for which the heat signature had any potential to be a deer (Lenient IR); (2) detections from only IR video in which the viewer was confident that the heat signature was from a deer (Stringent IR); (3) RGB confirmations of any IR heat signatures in which the object in the RGB video had any potential to be a deer (Lenient RGB); and (4) RGB confirmations of any IR heat signatures where viewers were confident that the object in the RGB video was a deer (Stringent RGB). When assigning IR heat signatures or RGB objects, stringent detections were those with a shape that was clearly defined and unambiguous so that I believed no other object than a deer could be producing such an IR heat signature or RGB object. No other species of similar shape and color to that of white-tailed deer were present in my field site. Distance = the perpendicular distance in between the transect line and the deer. Observer = the observer that detected the deer. Group size = the number of deer in the same group as the detected deer.

Ground	Altitude	Detection history	Covariates	AIC	ΔAIC^a
Snow	300	Lenient IR	Distance + Observer	-1644.62	1.88
		Stringent IR	Distance + Observer	-1500.63	1.88
		Lenient RGB	Distance + Group size + Observer	-1269.93	0.49
		Stringent RGB	Distance + Group size + Observer	-1024.25	2.22
	450	Lenient IR	Observer	-549.94	1.59
		Stringent IR	Observer	-458.13	1.06
		Lenient RGB	Observer	-440.42	1.94
		Stringent RGB	Observer	-426.68	0.70
Bare	450	Lenient IR	Group size + Observer	-504.14	12.75
		Stringent IR	Group size + Observer	-446.28	8.17

^a Difference between the best model and next best model.

3.5 Discussion

I found that RGB video confirmation, lower altitudes, snow cover, and increasing levels of object scrutiny substantially increased concordance between my two viewers. Consequently, I strongly encourage future researchers to apply stringent verification standards and RGB confirmation to data collected from low-altitude flights over snow when surveying in similar study areas and for comparable species. Classifying IR heat signatures as deer is a viewer-dependent task, and thus contains a degree of subjectivity. Indeed, concordance between my two viewers dropped to as low as 30% in areas that did not have snow cover, regardless of detection history, even though both viewers had undergone extensive training to examine IR video that I captured from aerial platforms. Other studies have reported lack of concordance between the classifications of multiple viewers of both aerial video (Beaver et al. 2020, Preston et al. 2021) and other types of population data (Delisle et al. 2022). In instances when high certainty cannot be obtained due to the natural history of the target species (e.g., arboreal species inhabiting dense canopies or little color contrast between the animal and background; Corcoran et al. 2019), ground truthing may be required.

Similar to others, my literature review revealed that uncrewed aerial vehicles are increasingly popular in wildlife monitoring (Linchant et al. 2015). One major advantage of these vehicles is the capability of flying at much lower altitudes compared to crewed aircraft, which helps to increase video quality and thus reduce misidentification and perception errors (Linchant et al. 2015). If battery life is of no concern, some researchers have even reduced altitude upon detection of a potential heat signature in non-forested habitats, and honed in for more certain confirmation (Smith et al. 2020). Furthermore, crewed aerial vehicle accidents account for 66% of wildlife biologist deaths while on the job (Sasse 2003). Uncrewed aerial vehicles are a much safer alternative. Lastly, uncrewed aerial vehicles have an appealing ease of use, which facilitates quick data collection (McMahon et al. 2021). That being said, large-scale management may still struggle to efficiently sample with uncrewed aerial vehicles due to line-of-sight restrictions and short battery life (Linchant et al. 2015). Practical application over large extents likely will require improved battery life and more lenient regulations pertaining to line-of-sight operation.

I tested the effects of ground condition (snow vs bare) and altitude on the ability to use RGB video to confirm heat signatures. Because I did not sample the same areas repeatedly at different altitudes and ground conditions, I were unable to infer how detection probability changes

as a function of altitude and ground condition. Flight speed is an additional variable of interest to wildlife managers using aerial methods. Although I attempted to fly surveys at a constant speed to ensure repeatability, the ability to effectively sample at faster flight speeds would be more cost and time efficient, and may also facilitate sampling larger areas. Therefore, I encourage future researchers to examine the effects of altitude and ground condition on detection probability, and the effects of flight speed on the efficacy of RGB confirmation, concordance between independent observers, and detection probability.

Simultaneously capturing IR and RGB video increases logistical difficulties and monetary costs associated with aerial sampling. Logistically, synchronizing the two video streams to ensure viewers can examine the same image in IR and RGB could prove difficult to non-experts (Bushaw et al. 2020). I used the GeoDVR Mini to simultaneously capture, georeference, and store IR and RGB video streams, which required little technical expertise. Additionally, the GeoDVR Mini named and stored video files for simultaneous examination of images in IR and RGB bands within the LineVision – Ultimate software. I thus avoided the step of manually lining up two separate videos streams, which can be challenging for large video files. Monetarily, the purchase of an additional RGB camera increased the cost of sampling. However, the added cost of the RGB camera (\$4,089 USD) was small compared to the IR thermal sensor (\$33,488 USD). The additional cost was essential, as RGB confirmation substantially improved my object classifications. Other researchers surveying for species inhabiting more open habitat may only need RGB video if the target individuals are large enough or colored to be easily distinguishable from the background terrain (e.g., Edwards et al. 2021). If surveys include multiple species producing indistinguishable heat signatures (e.g., Gentle et al. 2018), RGB video may facilitate species classification (Lee et al. 2019).

False positive and negative errors can affect bias and precision of occupancy and density estimates (Otis et al. 1978, Royle and Link 2006, Miller et al. 2011, Strickfaden et al. 2020). In the context of aerial sampling with thermal sensors, availability errors can arise from the thermal sensor when the thermal sensor fails to capture the IR heat signature of an animal within the field-of-view (Bushaw et al. 2020). Perception errors arise when the viewer, or automated viewing software, fails to detect an IR heat signature that is present in the video stream (Preston et al. 2021). Strategies to specifically account for perception errors are few and vary in terms of their validity. Manual viewing has been used to count perception errors from automated software (e.g.,

Lethbridge et al. 2019, Conn et al. 2021), but this relies on the dubious assumption that human viewers do not commit perception errors – an assumption my work does not support. When counting walrus using IR thermography, Burn et al. (2009) modelled detection probability as a function of group size to help alleviate perception errors. Conducting auxiliary ground truthing by walking the flown transects and recording the coordinates of confirmed individuals can quantify perception errors (Corcoran et al. 2019). This strategy may be more effective for sedentary species, as mobile species will likely flush or move before being sampled by walkers. Double-observer methods are well known in ecological studies (Nichols et al. 2000), and enable the modelling of heterogeneity in detection probability across predictors (Laake and Borchers 2004). Moreover, open access software for fitting such models is readily available for ecologists and managers (Laake et al. 2022). Even so, to my knowledge, I am the first to utilize this framework to estimate and correct for perception errors in IR sampling. I encourage future users of IR thermal sensors to employ double-viewer methods when estimating population density from video captured with aerial platforms that is manually viewed.

Unlike perception errors, accounting for availability errors is much more logistically challenging. Such error could be induced by dense overhead cover or poor thermal contrast (Havens and Sharp 2015). Several past studies have quantified availability errors by simultaneously conducting additional studies to determine how many individuals are available for IR sampling. These have consisted of ground surveys (Kays et al. 2019, Brunton et al. 2020, Witt et al. 2020, McKellar et al. 2021) and telemetric studies (Latham et al. 2021). Both of these strategies are problematic for study species that are highly mobile. Kissell and Tappe (2004) used human surrogates to quantify availability errors; a potentially useful strategy that nonetheless assumes: (1) IR heat signatures of the surrogates are identical to the IR heat signatures from the study animal; (2) habitat in which the surrogates are placed is representative of the actual area to be sampled; and (3) conditions that affect IR heat signatures in the surrogate study replicate those in the actual study. Distance sampling is an alternative method to address availability errors by accounting for decreased detection probability associated with increasing distance from the aerial transect line (Gentle et al. 2018, Schoenecker et al. 2018). Among other things, distance sampling assumes all objects directly on the line are detected with certainty (Buckland et al. 2001). Mark-recapture distance sampling can adjust density estimates when objects are not detected with certainty on the transect line (Burt et al. 2014). However, assessing availability errors with mark-

recapture methods is challenging for aerial sampling because: (1) repeat flights typically occur immediately following initial flights and thus experience the same thermal conditions which in turn causes the thermal sensor to detect the same individuals; and (2) when surveying for mobile species, animal movement in between repeat flights may confound how many individuals are within the field-of-view of the thermal sensor. For these same reasons, double-observer methods to correct for perception errors are problematic when using automated viewing algorithms to detect heat signatures. I encourage future work on procedures to estimate availability errors, especially with more mobile study species.

False positives from double counting the same individuals present an additional source of error that can positively bias estimates. Generally, double counting occurs from recording the same individual twice on overlapping images or videos, and recording the same moving individual twice on neighboring transects (Brack et al. 2018). Fortunately, strategies to account for or avoid double counting exist. Lu et al. (2022) developed a hierarchical framework that utilized entity resolution to identify the same individuals in overlapping images and thus avoid double counting when IR images are analyzed instead of video (e.g., Chrétien et al. 2015). Double counting the same individuals on neighboring transects is not problematic when animal movement is random and spatial sampling effort is accounted for (Buckland et al. 2001). Reactive movement is problematic if individuals consistently run off the transect before the aircraft samples (due to noise) or if the aircraft continually pushes individuals and, thus, repeatedly samples the same individuals (Buckland et al. 2001). I did not document any reactive movement of deer towards my aircraft at any altitude during test flights and collection of data. While I recommend surveying at low altitudes, I also encourage future users of aerial platforms to be aware of reactive movement induced by the aerial platform (Mulero-Pázmány et al. 2017). Such reactive movement can bias density estimates if not accounted for (Buckland et al. 2005; Glennie et al. 2015, 2021). Perhaps the easiest way to avoid double counting on neighboring transects is to space transects far enough apart to completely avoid this error (e.g., Dunn et al. 2002). Regardless, I encourage future researchers to conduct test flights to evaluate reactive movement induced by the aerial vehicle.

In wildlife modelling, accounting for false positives has received considerably less attention than false negatives (Kéry and Royle 2016, 2020; Strickfaden et al. 2020). Small amounts of false positives can substantially bias estimates (Miller et al. 2011). Because of this, modelling false positive rates has increased in areas such as genetics (Augustine et al. 2020), acoustic

monitoring (Chambert et al. 2018), and citizen science (Clare et al. 2019). Many of the strategies to count misidentification errors in IR aerial sampling mimic those used for counting perception errors. Several studies have counted misidentification errors associated with automated viewing software by manually examining the IR video (e.g., Lhoest et al. 2015, Chrétien et al. 2016, Lethbridge et al. 2019), but this strategy assumes that the manual examiner does not commit misidentification errors. Simultaneous ground surveys have been conducted to assess misidentification errors (Corcoran et al. 2019, Bushaw et al. 2020, Stander et al. 2021). Such ground surveys appear more promising if the target species is sedentary and can thus reasonably be assumed to not move in between flights and ground truthing. Geographic coordinates of all other objects or animals can then be compared to those of the target individuals, and used to count misidentification errors (Corcoran et al. 2019). Other researchers have reduced the altitude of an uncrewed aircraft (Bushaw et al. 2019, Smith et al. 2020), or circled a crewed aircraft (Gillette et al. 2015), to confirm IR heat signatures as the target species. Circling or altitude-reduction strategies may not be feasible for largescale spatial sampling of common species, as time expenditures would drastically increase. My results suggest that the use of RGB video to confirm IR heat signatures as belonging to the target species is a promising method for reducing misidentification errors when possible. Unfortunately, my review found that supplemental RGB video has inconsistently been implemented by those relying on IR thermal sensors to sample wildlife, especially in crewed vehicles. I found strong evidence for the need to use RGB video to confirm that IR heat signatures are deer – 19.3% (SE = 4.1) of lenient IR detections that would otherwise have been ignored were confirmed as deer, and 18.3% (SE = 2.8) of stringent IR detections that would otherwise have been counted were instead confirmed as not deer or unsure. Similar to previous research, I found the efficacy of RGB confirmation to be higher at lower altitudes (Millette et al. 2011). Additionally, I found snow to be essential when using RGB video to confirm IR heat signatures, as white-tailed deer blend in well with bare or leaf-covered ground in forested habitat. Thus, my ability to distinguish deer from debris or ground features was poor, at least at 450 m altitude. Therefore, to minimize misidentification errors, I recommend using RGB video to confirm IR heat signatures and sampling during snow cover from flights at lower altitudes. Reliance on snow and low altitude for RGB confirmations may be less important for those sampling in open habitats, when the target species has natural color contrast with the background terrain, and for endotherms with larger body masses than white-tailed deer. In instances when snow

cover is unavailable, uncrewed aircraft may be a suitable alternative to crewed aircraft, as these platforms can be flown at much lower altitudes than crewed aircraft and thus may not need to rely on snow or a double-sensor platform. Nonetheless, I encourage future work to quantify and account for misidentification errors in aerial sampling.

3.6 References

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CHAPTER 4. USING COST-EFFECTIVENESS ANALYSIS TO COMPARE DENSITY-ESTIMATION METHODS FOR LARGE-SCALE WILDLIFE MANAGEMENT

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4.1 Abstract

Density estimates for animal populations often inform conservation and management decisions. Many methods to estimate animal density exist, but deciding between competing alternatives traditionally has depended upon assessing multiple factors (e.g., precision, total cost, area sampled) independently and often in an ad hoc manner. Cost-effectiveness analysis is a simple tool that economists use to decide objectively between competing alternatives. I extend cost-effectiveness analysis to simultaneously integrate precision and per-area cost of sampling when selecting between competing techniques used to estimate animal density both after a single application of a method and across several applications of capital equipment. My extension allows for weighting of factors that may vary with the objectives and constraints of decision makers. I apply my extension of cost-effectiveness analysis to a case study in which population density of white-tailed deer (*Odocoileus virginianus*) was estimated in three large management units in Indiana, USA, using three competing distance-sampling methods: fecal-pellet, camera-trap, and aerial sampling. The unweighted cost effectiveness of aerial sampling with color and infrared sensors was usually superior after a single application of each method, and was always superior across several applications in vastly differing landscapes. Pellet sampling was the most cost effective after a single application of each method in an agriculturally dominated management unit. Although camera sampling has increased in popularity, the cost effectiveness of camera sampling was poorer than the other two methods, even when allowing for potential future innovations to streamline data processing. Cost-effectiveness analysis can be useful when selecting among competing methods for monitoring animal populations of conservation and management importance. The same principles used in my cost-effectiveness analysis can be used to decide between competing alternatives related to any ecological monitoring in addition to density estimation.

4.2 Introduction

Wildlife management benefits from estimates of animal density that are precise, cost-effective, and representative of the actual population (Williams et al. 2002). Such density estimates can inform conservation and management decisions that regulate harvest (Devers et al. 2021, Tombre et al. 2021), diminish animal-induced habitat degradation (Spake et al. 2020), minimize wildlife-human conflict (Conover 2001, Hussain et al. 2007), update the protection status of rare species and critical habitat (Meylan and Donnelly 1999, Hawkins and Racey 2005), and mitigate demographic responses to habitat or climate change (Péron et al. 2012, Lewis et al. 2015). Agencies often must implement conservation and management decisions across large functional jurisdictional units that span hundreds to thousands of km² (Sinclair 1991, Thiemann et al. 2008, Wallace et al. 2010) and thus require methods of density estimation that are applicable to large spatial extents.

When managers consider potential methods for estimating animal density, the utility of those methods often depends upon multiple factors including monetary costs and performance of the density estimator (Lyra-Jorge et al. 2008, De Bondi et al. 2010, Laguardia et al. 2021). Monetary costs include capital costs (Glover-Kapfer et al. 2019), recurring expenditures from sampling operations (De Bondi et al. 2010), and labor required for data processing (Delisle et al. 2021, Palencia et al. 2021). The performance of a density-estimation method can be assessed by the total area over which density is inferred (Laguardia et al. 2021) and the relative precision of the resulting density estimate (Campbell et al. 2004). Although desired, bias is extremely difficult to assess on density estimates of wildlife populations. Generally, these factors pertain to cost effectiveness. In economic analyses, cost effectiveness is routinely presented as the ratio of the cost of an alternative in dollars and some measure of performance of that alternative (Boardman et al. 2011).

Numerous studies have compared methods for estimating animal density (e.g., Parmenter et al. 2003, Urbanek et al. 2012, Anile et al. 2014, Keiter et al. 2017) but focused primarily on separately comparing the precision and total cost associated with different methods. Other published comparisons of methods for estimating animal density have mistakenly referred to the total cost or total effort of a method as a measure of cost effectiveness. Therefore, as an aid to resource managers, I extend simple methods of cost effectiveness analysis borrowed from economics to decide between competing techniques used to estimate animal density. I then apply

cost-effectiveness analysis to evaluate three different field techniques to estimate the density of white-tailed deer (*Odocoileus virginianus*) across three large management units in Indiana, USA. Specifically, I assess the cost effectiveness of fecal-pellet, camera-trapping, and aerial methods using distance-sampling estimators. I also evaluate if and how cost effectiveness differed for each method as a function of landscape composition.

4.3 Methods

4.3.1 Cost-Effectiveness Analysis

Cost effectiveness, CE , is the ratio of the cost, C , of an alternative and some measure of performance (i.e., effectiveness), E , of that alternative (Boardman et al. 2011), expressed as $CE = C/E$. Because wildlife managers often desire density estimates across large areas over which management is implemented, cost per unit land area, C/a , is a relevant measure of costs. Similarly, wildlife managers strive for density estimates that are relatively precise to facilitate detection of changes in density across repeatedly sampled areas and yield more confidence in single estimates. Given this, a relative measure of precision, e.g., the inverse of the coefficient of variation (CV), is often the only measure of effectiveness of interest regarding a method to estimate animal density (Skalski et al. 2005). Therefore, a cost-effectiveness ratio (sensu Boardman et al. 2011, p. 465) for this situation can be expressed as

$$CE = \frac{C/a}{1/CV} \quad (1)$$

which is simply the cost per unit land area standardized by relative precision. Cost, C , is the total cost of the alternative, including the capital cost of equipment and the recurring cost associated with collecting, processing, and analyzing the data. Consistent with past research, area, a , is the total area over which density is inferred (Laguardia et al. 2021). When deciding among competing methods for estimating density, the most cost-effective alternative is the method with smallest cost effectiveness. Feasibility constraints on C (e.g., maximum allowance for personnel hiring or vehicle purchasing) or minimum required precision (i.e., maximum allowance for CV) can be set *a priori* to remove alternatives that do not meet the minimum standards of an agency (discussed more below).

Management often benefits from knowledge of spatiotemporal changes in density or abundance, rather than a single density estimate in time and space (Schaub and Kéry 2021). Consequently, many agencies estimate density on a recurring seasonal or yearly basis, and thus invest in what is hoped to be long-lived equipment. I therefore calculate C as an annuity, or an “annualized” total cost. Formally, I assume that: (1) capital equipment (e.g., camera traps, aerial sampling equipment) is purchased at cost CC and will last N applications, (2) there are recurring costs for each application of the method (e.g., labor to collect, process, and analyze the data), and (3) the same measure of precision $1/CV$ is returned and area a sampled for each application of the method. In this case, the resulting annualized cost is

$$C = CC/A(r, N) + FOC + DPC \quad (2)$$

where FOC = field-operating cost per application, DPC = data-processing cost per application, $A(r, N) = [(1 + r)^N - 1]/[r(1 + r)^N]$ = the annuity factor (Campbell and Brown 2016), and r = a discount rate. I specify r at 0.03, which is approximately equal to the real social rate of time preference in the US and is consistent with federal guidance on the choice of discount rate for economic analysis (Office of Management and Budget 2003). Effectively, $A(r, N)$ takes a large up-front capital expenditure and “annualizes” the capital expenditure, i.e., converts the capital expenditure into an annual expenditure such that, if you were to take the present value of all expenditures over the N applications of the capital’s life at a discount rate of r , then it would equal CC .

I recognize that the relative importance of factors contributing to a method’s cost effectiveness could vary due to the management objective as well as political, financial, or bureaucratic constraints acting on a management agency. To explicitly allow for variation in relative importance, I modified Eq. 1 to allow for user-specified weights, denoted by w , for cost-effectiveness input parameters such that

$$CE_{anw} = \frac{\left(\frac{CC}{A(r, N)} * w_{CC} + FOC * w_{FOC} + DPC * w_{DPC} \right) / (a * w_a)}{(1/CV)w_{CV}} \quad (3)$$

where $w_p, p \in \{CC, FOC, DPC, a, CV\}$ = manager-specified weights for each parameter. To determine weights, an importance score, i_p , ranging from 0 (no importance) to 100 (critically important), can be given to each parameter in Eq. 3. Then a compositional weight for parameter p is given by $w_p = \frac{pi_p}{\sum_{p=1}^P i_p}$. When $w = 1$ for all P parameters, Eq. 3 simplifies to Eq. 1.

4.3.2 Case Study

4.3.2.1 Study Area

I conducted sampling during the late winter of 2020-21 in deer Regional Management Units (RMU) 3, 4, and 9 in Indiana, USA (Figure 4.1; Swihart et al. 2020). Weather regimes in each RMU followed a four-season temperate pattern. RMU 3 (10,233 km²) was predominantly row-crop agriculture (8,113 km²), with intermittent patches of forest and grasslands (1,446 km²), and is located within the Central and Eastern Corn Belt Plains ecoregions (U.S. Environmental Protection Agency 1997). Soils were predominantly silty loams. Within patches of forest, common tree species included black cherry (*Prunus serotina*), black oak (*Quercus velutina*), black walnut (*Juglans nigra*), pin oak (*Q. palustris*), sassafras (*Sassafras albidum*), and white oak (*Q. alba*), and common herbaceous species included black snakeroot (*Sanicula marilandica*), enchanter's nightshade (*Circaea lutetiana*), garlic mustard (*Alliaria petiolata*), sweet cicely (*Osmorhiza claytonii*), and Virginia knotweed (*Polygonum virginianum*). Private property comprised 98.4% of the total area in RMU 3.

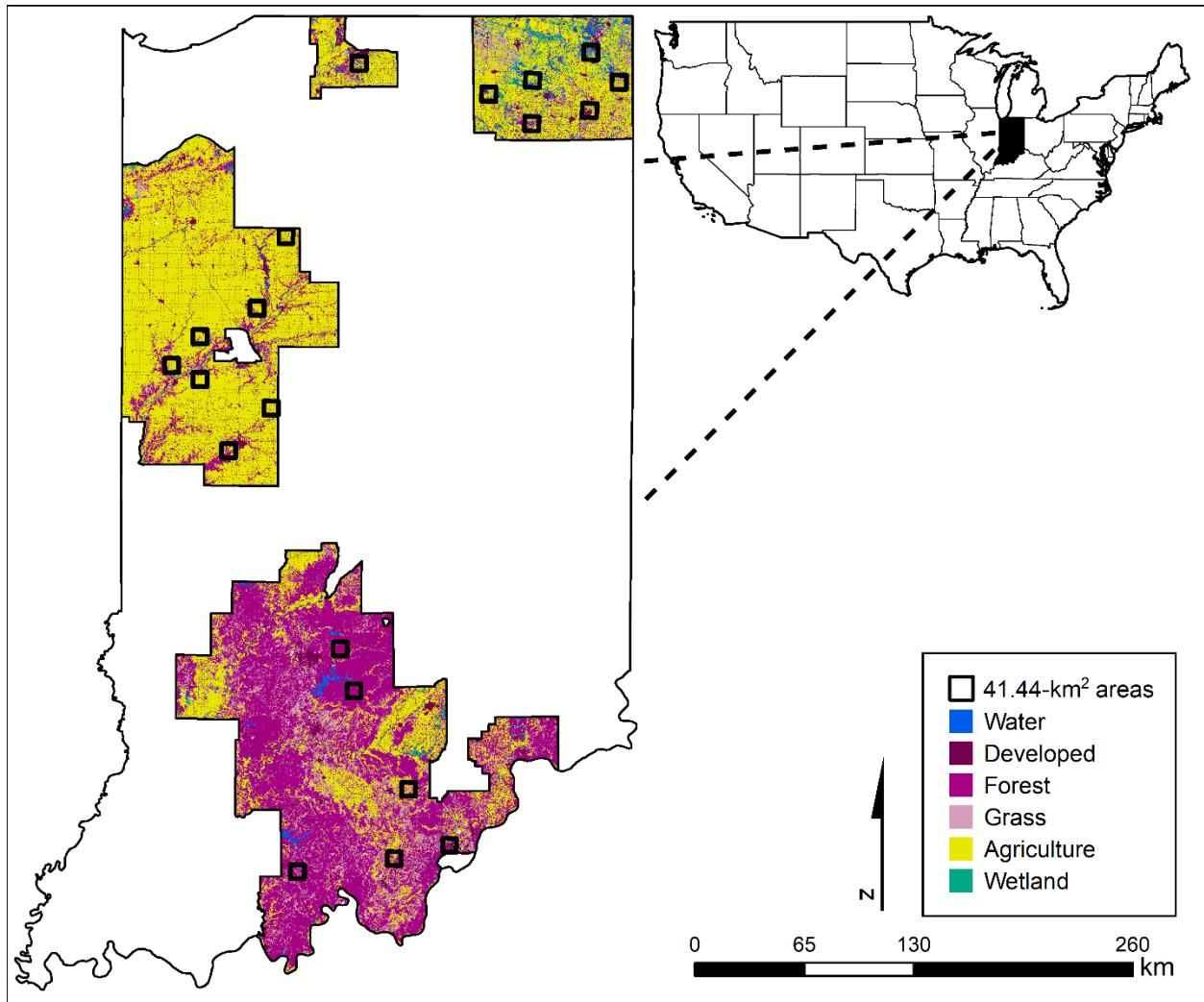


Figure 4.1. Land cover types within deer Regional Management Units 3 (west central), 4 (southern), and 9 (northeastern) in Indiana, USA. The 41.44-km² areas I conducted fecal-pellet, camera-trap, and aerial sampling for white-tailed deer in Spring 2021 are shown within Regional Management Units.

Unlike RMU 3, RMU 4 (16,187 km²) was predominantly forested (9,208 km²), contained far less agricultural land (3,141 km²), and was located within the Interior Plateau Interior River Valleys and Hills, and Eastern Corn Belt Plains ecoregions (U.S. Environmental Protection Agency 1997). Soil types in the western two-thirds of RMU 4 were bedrock soils with sandstone, limestone, and siltstone, whereas soils in the eastern third were primarily silty loams. Forests were primarily mesic hardwoods that contained American beech (*Fagus grandifolia*), black oak, sugar maple (*Acer saccharum*), tulip poplar (*Liriodendron tulipifera*), and white oak. Dominant herbaceous species included common blue violet (*Viola sororia*), enchanter's nightshade, honewort (*Cryptotaenia canadensis*), jack-in-the-pulpit (*Arisaema triphyllum*), and wild licorice (*Galium circaezans*). Private property comprised 88.1% of the total area in RMU 4.

Lastly, RMU 9 (4,716 km²) was a mixture of forests (400 km²), wetlands (607 km²), and row-crop agriculture (2663 km²), and was located within the Southern Michigan/Northern Indiana Drift Plains and Eastern Corn Belt Plains ecoregions (U.S. Environmental Protection Agency 1997). Soil types included silty and sandy loams, neutral clays, and muck soils. Forest patches ranged from mesic to hydric hardwoods that contained American basswood (*Tilia Americana*), black cherry, red maple (*A. rubrum*), sugar maple, and silver maple (*A. saccharinum*). Dominant herbaceous species included black snakeroot, common blue violet, enchanter's nightshade, garlic mustard, and Virginia knotweed. Private property comprised 97.4% of the total area in RMU 9.

Within each RMU, I focused aerial sampling within 41.44-km² areas that I randomly selected from Indiana's deer harvest reporting grid. This reporting grid spans the entirety of each RMU, and spatially separates each RMU into 6.44 × 6.44-km areas from which the Indiana Department of Natural Resources records deer harvests. For fecal-pellet and camera-trap sampling, I sampled 10.36-km² square sub-areas (henceforth referred to as sub-areas) placed within the larger 41.44-km² areas in which I conducted aerial sampling. I placed sub-areas to ensure that habitat composition was reflective of the greater 41.44-km² area and that property access across the sub-area was as homogeneously distributed as possible. In total, I sampled 7, 6, and 7 different areas within RMUs 3, 4, and 9, respectively. The number of areas I sampled in each RMU was dependent on a larger project with aims of estimating deer density across each RMU by sampling several additional years and areas.

4.3.2.2 Modelling Methods

I estimated density using conventional distance sampling (Buckland et al. 2001) for each of the three methods I evaluated. For robust estimation of density, five assumptions of distance sampling must be met. These include: (1) objects on the line or point are detected with certainty (2) objects are detected at their initial location, (3) distances from the transect or point are measured exactly, (4) objects are distributed independently of transects or points, and (5) detections are independent events (Buckland et al. 2001). I present relevant considerations for meeting each of these assumptions in the methods sections below. For each method, I estimated density in both open (defined as agricultural fields, pasture, and herbaceous grasslands) and concealed (defined as wetlands and forest) habitats in each RMU. Total density for each method across both open and concealed habitats in each RMU was estimated using a weighted geographic stratification as $\hat{D}_y = \sum_{i=1}^2 \left(\frac{A_{iy}}{A_y} \right) \hat{D}_{iy}$ where $\hat{D}_y$ is the density estimate across both habitats in RMU y , A_{iy} is the total area of habitat i in RMU y , A_y is the total area of both habitats in RMU y , $\hat{D}_{iy}$ is the habitat-specific density estimate in RMU y , and $var(\hat{D}_y) = \sum_{i=1}^2 \left(\frac{A_{iy}}{A_y} \right)^2 var(\hat{D}_{iy})$.

4.3.2.3 Fecal-Pellet Sampling

Sampling of fecal pellets is a common method used to estimate the densities of many wildlife species (Wood 1988, Barnes 2001, Marques et al. 2001, Todd et al. 2008). To sample for fecal-pellet groups of white-tailed deer, I surveyed 200-m line transects from 1-24 March 2021 across the three RMUs. The assumption that fecal-pellet groups were detected at their initial location was easily met as fecal-pellet groups are stationary. Transect location and orientation was determined randomly using ArcMap 10.7, subject to the dual constraints of property access and separation from the nearest neighboring transect by ≥ 200 m. Random placement ensured that I met the assumption that fecal-pellet groups were distributed independently of the transect. I sampled concealed habitat disproportionate to its availability because white-tailed deer spend less time in agricultural fields compared to areas of natural cover (Beier and McCullough 1990, Nixon et al. 1991). Pellet transects in adjoining states were used to guide decisions on transect spacing and number (Urbanek et al. 2012, Anderson et al. 2013). Details of my stratified sampling are provided in Delisle et al. (2022b).

During field sampling, each transect was surveyed by one of multiple surveyors who conducted fecal-pellet sampling. A single surveyor walked each transect twice to help meet the assumption that objects on the line are detected with certainty. During the first pass, the surveyor focused all attention directly on the transect line to ensure perfect detection at distance 0. During the second pass, the surveyor focused attention around the line. Upon detection of a fecal-pellet group, each surveyor recorded the perpendicular distance from the transect line to the center of the fecal-pellet group which met the assumption that distances were measured accurately. If a fecal-pellet group was detected on the first pass, the group was removed so that no fecal-pellet group was accidentally counted twice on the second pass; thus, the assumption that detections are independent events was met.

To estimate deer density in concealed and open habitats using fecal-pellet sampling, I used the formula from Marques et al. (2001):

$$\hat{D} = \frac{\left(\frac{n}{L}\right) * \hat{f}(0) * 0.5}{\hat{t} * \hat{s}} \quad (4)$$

In Eq. 4, $\hat{D}$ = the density estimate of the animal population, n = the number of dung piles detected, L = transect length, $\hat{f}(0)$ = the estimated probability density function of perpendicular distances measured from the transect line to detected dung piles evaluated at distance 0, $\hat{s}$ = the estimated defecation rate of the animal, and $\hat{t}$ = the estimated persistence time for dung piles deposited during the study period. To estimate $\hat{t}$ in each RMU, I used the inter-observer method from Delisle et al. (2022b). Specifically, I used a weighted habitat-specific $\hat{t}$ for each RMU, with weights based on the sampling effort in each habitat type in each sub-area (for a more in-depth overview on my estimation of $\hat{t}$ see Appendix C: Estimation of Persistence). I used the same $\hat{s}$ of 26.8 fecal-pellet groups/deer/day for density estimates in each RMU (Delisle et al. 2022b). I included variation from $\hat{t}$ but not $\hat{s}$ in the final density estimates from pellet sampling because I did not experimentally estimate $\hat{s}$. Instead, I used $\hat{s}$ from previous research in similar study areas (Delisle et al. 2022b).

To model the detection process, I fit half-normal key functions with either Hermite polynomial, simple polynomial, cosine, or no adjustment terms, and hazard-rate key functions with either simple polynomial or no adjustment terms. Additionally, I fit hazard-rate and half-normal key functions with the following combinations of covariates: (1) observer, (2) sub-area, (3) local microhabitat each transect was located within (cornfield, soybean field, deciduous, mixed, or

evergreen forest, woody wetland, herbaceous grassland, and pasture/hay), (4) observer and sub-area, (5) observer and microhabitat, (6) sub-area and microhabitat type, and (7) observer, sub-area, and microhabitat type. I used AIC for model selection (Buckland et al. 2001). To evaluate if I should fit a pooled detection function and stratified encounter rate over concealed and open habitat types or separate stratified detection functions, I fit unique detection functions for concealed and open habitat and a pooled detection function across both habitats and all RMUs. I then compared the sum of the AICs from the best stratified detection functions with the AIC from the pooled detection function to choose between a pooled and stratified detection function (Buckland et al. 2015). I repeated this process to evaluate if I should fit a single pooled or several stratified detection functions across grassland and agriculture (within open habitat) and across the RMUs (i.e., grassland-, agriculture-, and RMU-specific detection functions). I fit all detection functions using the “Distance” package in R (Miller 2021).

4.3.2.4 Camera-Trap Sampling

Camera-trap sampling is an increasingly popular method used to estimate animal density (Delisle et al. 2021). I deployed Browning Strike Force HD motion-triggered camera traps from 2 February – 15 March 2021. I strived to deploy 20 camera traps per sub-area, which Buckland et al. (2001) recommended as the minimum number of sampling locations to estimate the encounter rate variance. However, access to private property limited the number of cameras in some sub areas. I randomly selected camera trap locations using ArcMap 10.7 subject to the same access and proximity constraints as fecal-pellet transects, which met the assumption that deer were distributed independently of camera locations. In wooded areas, I affixed camera traps to trees at a height of 1 m and in areas without trees, I affixed camera traps to t-posts at 1 m height. Affixing cameras at a height of 1 m assured that I would meet the assumption of detecting deer at distance 0 with certainty, as deer could not pass beneath the camera. I oriented all camera traps to face north to avoid sun glare at dawn and dusk. In rare instances, locations of camera traps were slightly altered from random (<20 m) to ensure a suitable location. When triggered, camera traps captured a burst of 3 photos usually separated by 0.3 sec. I set minimum time delays between triggers to 1 or 5 sec. Quickly triggering upon detection helped ensure that deer were detected at their initial location.

To estimate deer density in each RMU and habitat type (concealed and open) using camera traps, I relied on the distance-sampling method of Howe et al. (2017):

$$\hat{D} = \frac{2t \sum_{k=1}^K n_k}{\theta w^2 \sum_{k=1}^K T_k \hat{P}_k} * \frac{1}{\hat{A}} \quad (5)$$

In Eq. 5, $\hat{D}$ = estimated density, k = the camera trap sampled, n_k = the total detections at camera trap k , t = the time interval between consecutive detections (sec), θ = the angle of view (radians) of the camera trap, w = the truncation distance (m), T_k = the total time sampled (sec), $\hat{P}_k$ = the probability of detection in the camera-trap sampling area at a given t demarcated by θ and w , and $\hat{A}$ = the estimated fraction of a camera-trap day spent active and thus available for camera-trap sampling. For my application, I most often measured the distance to a deer in the first photo contained within a burst, and therefore I used $t = 1.6$ or 5.6 sec for most cameras. To estimate $\hat{A}$ of white-tailed deer in each RMU, I first used the average anchoring method from Vazquez et al. (2019) to double-anchor deer detection times by the average sunset and sunrise times across the spatiotemporal extent of my sampling in each RMU. I then estimated $\hat{A}$ by fitting circular kernel distributions to the double-anchored detection times using the methods of Rowcliffe et al. (2014), and estimated the standard error (SE) of $\hat{A}$ with nonparametric bootstrapping (Rowcliffe et al. 2014) using the “activity” package in R (Rowcliffe 2021). Similar to conventional multipliers, the resulting SE for $\hat{A}$ was propagated into the design-based SE of $\hat{D}$ using the delta method (Buckland et al. 2001).

I estimated distances from the camera trap to deer in photos by using reference videos of deployers holding signs that indicated their distance from the camera trap at the edges and center of the camera trap’s field-of-view (Howe et al. 2017). This helped to meet the assumption that distances were measured accurately. To estimate a detection function, I fit half-normal key functions with either 2 Hermite polynomial adjustments or no adjustments, uniform key functions with either one or two cosine adjustment, and hazard-rate key functions with either no, one or two cosine adjustments. Additionally, I fit half-normal and hazard-rate key functions with several different combinations of factor covariates including: (1) whether the camera trap’s flash fired upon detection (night vs day), (2) local microhabitat surrounding the camera trap (same microhabitats as in fecal-pellet sampling), (3) RMU, (4) RMU and camera-trap flash, (5) camera-trap flash and microhabitat, (6) RMU and microhabitat, and (7) camera-trap flash, microhabitat, and RMU. I estimated the SE of $\hat{D}$ using nonparametric bootstrapping to sample camera traps with replacement. Similar to fecal-pellet sampling, I fit all detection functions using the “Distance” package in R (Miller 2021).

I measured distances to the same deer in consecutive photo bursts, as is standard with camera-trap distance sampling. Because recording distances to the same individual introduces overdispersion and violates the assumption of independent detections, I used the two-step procedure proposed by Howe et al. (2019) for model selection. Specifically, I used QAIC to select the best model within the same key function. I used the average number of detections per individual per camera visit as a measure of the overdispersion factor, $\hat{c}$. After selecting the best model within key functions, I selected the best overall model by dividing the χ^2 goodness-of-fit (GOF) statistic by the degrees of freedom of the model. I chose the key function with the lowest quotient as the best model. To determine whether to fit a pooled detection function across both open and concealed habitat types, or to fit unique detection functions for open and concealed habitat types, I compared the sum of the QAIC from the best models (according to the two-step process) fit separately and the QAIC of the best pooled detection function.

4.3.2.5 Aerial Sampling

Aerial sampling has been used to estimate population abundance of many wildlife species (e.g., Haufler et al. 1993, Jachmann 2002, Winiarski et al. 2017, Stapleton et al. 2016). In the context of distance sampling, counts obtained from visual surveys on aerial platforms assume perfect detection along either the transect line or the distance at which left truncation is specified (Laake et al. 2008). I used a vertical-looking infrared (VLIR) platform coupled with high-resolution color video in an attempt to meet this assumption more readily than when sampling with observers counting from the sides of fixed-wing aircraft (e.g., Caughley and Grice 1982, Fleming and Tracey 2008) or when using forward-looking infrared (FLIR) cameras that increase distance and vegetative obstruction between the thermographer and animals (Bernatas and Nelson 2004, Storm et al. 2011, Smith et al. 2020). Vertical-looking infrared permits detection of deer directly beneath the aerial platform (Kissell and Nimmo 2011). Combining VLIR with high-resolution color video was adopted to further augment VLIR capabilities (Franke et al. 2012, Chrétien et al. 2016).

I conducted aerial sampling during daylight hours from 8 February – 10 March 2021. During my flights, I flew 16 x ~6.44-km transects that were aligned north to south in each 41.44-km² area. Based on prior work with deer, each transect was separated by 400 m (Kissell and Nimmo 2011). Transects were systematically aligned but randomly placed, ensuring that deer were

distributed randomly in relation to the transects. I flew at an altitude of ~450 m and speed of ~65 mph in a Sky Arrow Light Sport Aircraft to minimize the chance of deer movement in response to the aircraft. Altitude was restricted to 300 m in some 41.44-km² areas due to low cloud cover. The width of the field-of-view of the camera was 126.5 m and 84.3 m for flights conducted at 450 m and 300 m above ground altitude, respectively, and thus there was never overlap between neighboring transects. I found that flights at these altitudes did not induce reactive movement in deer beneath the plane. However, there still was the possibility of nonreactive movement, and therefore potential, albeit small, for double counting due to fast random movement from one transect to another neighboring transect during flights. Due to the speed of my flights, I believe the probability of double counting individuals was extremely small. Moreover, random double counting at two different transects does not pose a serious problem, as random movement in the opposite direction was just as probable (Buckland et al. 2001). Finally, estimators of the encounter-rate variance are robust to violation of the assumption that detections are independent (Buckland et al. 2015), which could arise from double counting.

I recorded VLIR video of the ground beneath the plane with an IR-TCM HD 1024 stationary thermography camera combined with a telephoto 60mm lens (Jenoptik, Jena, Germany). Simultaneously, I recorded vertical-looking red-green-blue (RGB) video of the same areas using a Nikon D810 DSLR camera combined with the Nikon AF DC-NIKKOR 135mm f/2D lens (Nikon Inc., Melville, NY). Cameras were affixed to either side of the aircraft and pointed directly at the ground during flight. VLIR and RGB footage were synchronously recorded, georeferenced, and stored digitally using a GeoDVR Mini (Remote GeoSystems, Inc.) and Garmin GPS (Garmin Ltd.).

After I conducted my flights, I viewed the VLIR and RGB video in the lab using the LineVision – Ultimate software (Remote GeoSystems, Inc.). Upon detecting a heat signature in the VLIR video that I suspected to be a deer, RGB video was used for confirmation. In addition, I measured the perpendicular distance from each deer to the centerline of the video, and recorded whether the deer was located in concealed or open habitat. The LineVision software is equipped with a feature that allows measuring of distance, which ensured that I measured distances accurately. Similar to other past research using VLIR (Kissell and Nimmo 2011), after preliminary examination of the aerial sampling distance data, I found uniform detection across all distances from the transect line to the field-of-view edge of the camera (Appendix C: Aerial Detection Probability, Delisle et al. 2022a). However, I did document false negatives caused by viewers

missing infrared signatures (i.e., perception errors; Brack et al. 2018). Therefore, I estimated the probability of a single viewer detecting an infrared signature, and the standard error of that probability, using the mark-recapture methods described in Delisle et al. (2022a) on a subset of my aerial data from each altitude.

I estimated deer density in each RMU and habitat (open and concealed) by using the equation from Buckland et al. (2015) with the probability of detecting an infrared heat signature as a multiplier:

$$\hat{D} = \frac{n}{b} * \frac{1}{pr(det)} \quad (6)$$

Where n = the number of deer detected, b = the total area sampled, and $pr(det)$ = the probability of detecting an infrared heat signature. I calculated b with the field-of-view of the infrared sensor and the above-ground altitude maintained by the pilot. I used the field-of-view of the infrared sensor instead of the color sensor because I identified candidate heat signatures in the infrared video before consulting color video. I estimated the standard error (SE) of $\hat{D}$ using an approach modified from the “R2” method in Fewster et al. (2009), where

$$SE(\hat{D}) = \sqrt{\frac{K}{A^2(K-1)} \sum_{k=1}^K a_k^2 \left(\frac{n_k}{b_k} - \frac{n}{A} \right)^2} \quad (7)$$

And K = the number of transects, A = the total area sampled, n = the total number of detections, b_k = the total area sampled on transect k , and n_k = the total number of detections on transect k . I then propagated the error from the probability of detecting an infrared heat signature into $SE(\hat{D})$ using the delta method.

4.3.2.6 Comparing Methods and Cost-Effectiveness Analysis

I compared the performance of fecal-pellet, camera-trap, and aerial sampling along multiple dimensions associated with a single application of each field method in each RMU. These dimensions included the CV of the density estimate, the spatial extent of sampling, the initial cost required to attain an estimate, and the recurring costs for continued use. I compared the relative precision of each density estimate using the coefficient of variation (CV). For spatial extent I compared the total area, a , surveyed by each method. Consistent with Laguardia et al. (2021), I defined a as the area of the sub-areas within each RMU for fecal-pellet and camera-trap sampling,

and the area of the 41.44-km² areas in each RMU for aerial sampling. I assessed three measures of sampling costs: (1) capital, (2) field-operations, and (3) data-processing costs. The capital cost was defined as the annualized upfront expense for equipment. I did not consider the capital cost of field vehicles used for fecal-pellet and camera-trap sampling. In cases where I used the same field equipment for estimating density in each RMU for a particular method, the annualized upfront capital cost was divided between the three RMUs to calculate the cost per-use via the following formula:

$$CC_i = \frac{CC_I/A(r, N)}{U_I} * U_i \quad (8)$$

where CC_i = the repeated capital cost for the i th RMU, CC_I = the total cost of the repeatedly used capital across all I RMUs, U_I = the total usage (e.g., number of transects or points sampled with capital) of the repeatedly used capital across all I RMUs per application, and U_i = the usage of the repeatedly used capital for the i th RMU. In cases where select field operations were performed to conduct field work on all RMUs (e.g., installing sensors on the aircraft), this cost was divided between RMUs by removing the annuity factor and replacing capital cost with the cost of the select field operations in Eq. 8. I decided to split shared costs between RMUs because the Indiana Department of Natural Resources requires future density estimates across no fewer than 3 RMUs per sampling year, and I suspect that other states may also require estimates in multiple sites. The field-operations cost was defined as the recurring cost associated with each field application of the method to estimate density. Lastly, I defined the data-processing cost as the cost to process the data in the lab, which included the hourly cost of entering data, viewing and scoring aerial footage, classifying species within camera-trap photos, measuring distances to deer within camera-trap photos, and analysis.

I calculated the cost effectiveness of each method using Eqs. 1 and 2. I calculated annualized capital costs assuming $N = 1, 2, \dots, 15$ applications to assess the sensitivity of my cost-effectiveness ratios to the lifespans of capital equipment. Lastly, I repeated these analyses while allowing for user-specified weights using Eq. 3. I specified weights using the importance scores given by the Indiana state deer biologist (JNC). Specifically, I used the following importance scores: $i_{cv} = 100$, $i_{CC} = 10$, $i_{FOC} = 40$, $i_{DPC} = 20$, and $i_a = 100$, which corresponded to weights of: $w_{cv} = 1.852$, $w_{CC} = 0.185$, $w_{FOC} = 0.741$, $w_{DPC} = 0.370$, and $w_a = 1.852$. I performed all analyses using the R programming language (R version 4.1.2; R Core Team 2021).

4.4 Results

4.4.1 Fecal-Pellet Sampling

In total, I surveyed 263 transects covering 52.6 km and detected 1,262 fecal-pellet groups across all three RMUs. A stratified detection function across open and concealed habitats was most parsimonious when I fit candidate detection functions to cumulative data collected across all RMUs ($\Delta\text{AIC} = 872.1$). Following this, a pooled detection function and stratified encounter rate were most parsimonious across the RMUs for both open ($\Delta\text{AIC} = 45.8$) and concealed ($\Delta\text{AIC} = 476.6$) habitats. Lastly, a pooled detection function and stratified encounter rate were most parsimonious across grassland and agriculture within open habitats ($\Delta\text{AIC} = 43.9$). Thus, I used unique detection functions for open and concealed habitat, and a stratified encounter rate to estimate RMU-specific densities for each habitat type. I truncated all detections >110 cm and >150 cm from the transect line in open and concealed habitat, respectively, to remove a right tail of distances with low associated detection probabilities (Buckland et al. 2001). Truncation removed a total of 100 detections. Following truncation, the hazard-rate detection function with no adjustments or covariates ($\Delta\text{AIC} = 1.02$, Cramer-von Mises GOF $P = 0.89$) and the half-normal detection function with observer and sub-area as covariates ($\Delta\text{AIC} = 2.5$, Cramer-von Mises GOF $P = 0.21$) were the AIC-best models in open and concealed habitat types, respectively. Because a pooled detection function and stratified encounter rate were most parsimonious, I estimated $\hat{D}$ and $SE(\hat{D})$ in open habitat (across grassland and agriculture) using the methods in Buckland et al. (2001) section 3.7.1. In RMU 3, 4, and 9, I estimated $\hat{t}$ at 45.2 (SE = 3.1), 31.9 (SE = 5.4), and 51.9 (SE = 3.1) days in concealment; 71.5 (SE = 3.1), 53.7 (SE = 10.4), and 78.3 (SE = 3.5) days in agricultural fields; and 106.5 (SE = 3.9), 77.3 (SE = 8.4), and 111.6 (SE = 5.9) days in prairies, respectively.

The average density from fecal-pellet sampling across RMUs in open, concealed, and across both habitats was 6.48 (SE = 2.33), 15.20 (SE = 0.23), and 9.59 (SE = 1.89) deer/km², respectively. The average CV of density in open, concealed, and across both habitats was 0.50 (SE = 0.08), 0.20 (SE = 0.03), and 0.28 (SE = 0.02), respectively. Within each RMU, the densities in concealed habitat were always larger than those in open habitat (Table 4.1). Similarly, within each RMU, the CVs of densities in concealed habitat were always smaller than those in open habitat (Table 4.1). The average capital, data-processing, and field-operations costs across RMUs was

\$427 (SE = 50), \$116 (SE = 9) and \$4,045 (SE = 396; Table 4.2), respectively. The total area for fecal-pellet sampling was 72.5 km² for both RMU 3 and 9, and 62.2 km² for RMU 4. The average cost effectiveness and weighted cost effectiveness across RMUs for fecal-pellet sampling was 18.27 (SE = 1.26) and 12.40 (SE = 0.87), respectively.

Table 4.1. Density estimates of white-tailed deer from fecal-pellet data collected from 1–24 March 2021 in three different regional management units (RMU) of Indiana, USA. Densities and corresponding measures of precision were estimated using conventional distance sampling, and are shown for concealed, open, and across both concealed and open (Total) habitat types. The number of 200 m-transects surveyed (k) and number of detections after truncation (n) are presented for each RMU and habitat type.

Habitat	RMU	k	n	$\hat{D}$	$SE(\hat{D})$	$CV(\hat{D})$
Concealed	3	42	246	14.919	2.694	0.181
Concealed	4	88	395	15.011	3.763	0.251
Concealed	9	46	298	15.661	2.506	0.16
Open	3	57	122	4.737	1.932	0.408
Open	4	9	9	3.607	2.393	0.663
Open	9	21	92	11.097	4.893	0.441
Total	3	99	368	5.922	1.736	0.293
Total	4	97	404	10.673	2.503	0.235
Total	9	67	390	12.189	3.771	0.309

Table 4.2. The capital (USD; CC), field operation (USD; FOC), and data processing cost (USD; DPC), area over which density was inferred (km²), coefficient of variation (CV), cost effectiveness (CE), and weighted cost effectiveness (CE_w) associated with density estimates from fecal-pellet (PS), camera-trap (CS), and aerial (AS) sampling in regional management units (RMU) 3, 4, and 9 within Indiana, USA. Weights were assigned by the Indiana state deer biologist. Capital costs were annualized across a single application. I underline the best index within each RMU.

Method	RMU	CC	FOC	DPC	Area	CV	CE	CE _w
PS	3	<u>482</u>	<u>4107</u>	<u>110</u>	72	0.29	<u>18.98</u>	12.82
PS	4	<u>472</u>	4699	<u>104</u>	62	0.24	19.94	13.64
PS	9	<u>326</u>	<u>3330</u>	<u>134</u>	72	0.31	15.79	10.72
CS	3	19714	7986	3126	72	<u>0.15</u>	65.61	22.82
CS	4	15967	6156	2412	62	0.18	69.03	23.66
CS	9	19475	7330	5181	72	0.12	52.71	18.05
AS	3	28606	4260	729	<u>290</u>	0.17	19.34	<u>5.02</u>
AS	4	24520	<u>3819</u>	695	<u>249</u>	<u>0.13</u>	<u>15.18</u>	<u>3.99</u>
AS	9	28606	4362	723	<u>290</u>	<u>0.11</u>	<u>12.19</u>	<u>3.18</u>

4.4.2 Camera-Trap Sampling

I deployed 428 camera traps and captured a total of 1,015,178 photos. I removed 21 camera traps from my analysis due to poor placement (e.g., pointed downward or upward) resulting in 407 camera traps used to estimate density (Table 4.3). I restricted attention to data collected during a 2-week period from 25 February – 10 March 2021 in order to streamline data analysis. Within this 2-week period, I captured 294,335 photos (2.22 terabyte of data), 81,740 of which contained deer. I measured a total of 30,732 and 9,505 distances in concealed and open habitat, respectively. During preliminary investigation of the data, I observed a spike in detections near camera traps in open habitat. Because of this, I did not consider the hazard-rate key function during model selection in open habitat, because this model can fit unnaturally large spikes at close distances resulting in an unnaturally abrupt decline in detectability as distance increases. This may underestimate $\hat{P}_k$ in Eq. 7 and thus overestimate the corresponding density estimate (Buckland et al. 2001). After removing the hazard rate model from consideration in open habitat, I found a stratified detection function across open and concealed habitat to be most parsimonious ($\Delta\text{QAIC} = 1,298.2$). I found the uniform key function with 1 cosine adjustment ($\Delta\chi^2/\text{df} = 332.2$) and the

uniform key function with 2 cosine adjustment terms ($\Delta\chi^2/df = 190.7$) to be the best detection functions in open and concealed habitats, respectively. In RMU 3, 4, and 9, I estimated $\hat{A}$ at 0.38 (SE = 0.02), 0.43 (SE = 0.03), and 0.42 (SE = 0.01), respectively.

Table 4.3. Density estimates of white-tailed deer from camera-trap sampling data collected from 25 February – 10 March 2021 in three different regional management units (RMU) of Indiana, USA. Densities and corresponding measures of precision were estimated using conventional distance sampling, and are shown for concealed, open, and across both concealed and open (Total) habitat types. The number of cameras deployed (k) and the number of detections after truncation (n) are presented for each RMU and habitat type.

Habitat	RMU	k	n	$\hat{D}$	$SE(\hat{D})$	$CV(\hat{D})$
Concealed	3	85	6,549	11.791	1.893	0.161
Concealed	4	91	4,642	6.600	1.223	0.185
Concealed	9	108	19,541	24.055	3.513	0.146
Open	3	60	2,459	3.806	0.789	0.207
Open	4	23	2,040	7.029	2.388	0.340
Open	9	40	5,006	10.642	1.875	0.176
Total	3	145	9,008	4.736	0.731	0.154
Total	4	114	6,682	6.763	1.183	0.175
Total	9	148	24,547	13.851	1.655	0.120

The average density from camera-trap sampling across RMUs in open, concealed, and across both habitats was 7.16 (SE = 1.97), 14.15 (SE = 5.17), and 8.45 (SE = 2.76) deer/km², respectively. The average CV of density in open, concealed, and across both habitats was 0.24 (SE = 0.05), 0.16 (SE = 0.01), and 0.15 (SE = 0.02), respectively. Density estimates in concealed habitat were larger than those in open habitat in RMU 3 and 9, but the reverse was true for RMU 4 (Table 4.3). The CVs of densities in concealed habitat were always smaller than those in open habitat (Table 4.3). Similar to fecal-pellet sampling, total density was largest for RMU 9 and smallest for RMU 3. The average capital, data-processing, and field-operations costs across RMUs was \$18,385 (SE = 1,211), \$3,573 (SE = 830), and \$7,157 (SE = 535; Table 4.2), respectively. The total area for camera-trap sampling was 72.5 km² each for RMUs 3 and 9, and 62.2 km² for RMU 4.

The average cost effectiveness and weighted cost effectiveness across RMUs for camera-trap sampling was 62.45 (SE = 4.97) and 21.51 (SE = 1.75), respectively.

4.4.3 Aerial Sampling

I recorded video on 111, 96, and 112 transects in RMUs 3, 4, and 9, respectively. On a single transect in RMU 3, my video recording system failed to record, which resulted in 111 transect videos instead of 112. I recorded 6.90, 5.49, and 6.67 hours of video in RMUs 3, 4, and 9, respectively (240 gigabyte of data).

The probability of detecting an infrared heat signature classified as a deer was 0.81 (SE = 0.05), 0.99 (SE < 0.01), and 0.93 (SE = 0.02) in RMUs 3, 4 and 9, respectively (Delisle et al. 2022a). The average density from aerial sampling across RMUs in open, concealed, and across both habitats was 1.31 (SE = 0.49), 21.64 (SE = 7.95), and 6.11 (SE = 2.06) deer/km², respectively. The average CV of density in open, concealed, and across both habitats was 0.36 (SE = 0.01), 0.14 (SE = 0.02), and 0.13 (SE = 0.02), respectively. Within each RMU, the densities in concealed habitat were always larger than those in open habitat (Table 4.4). Similarly, within each RMU, the CVs of densities in concealed habitat were always smaller than those in open habitat (Table 4.4). The average capital, data-processing, and field-operations costs across RMUs was \$27,244 (SE = 1,362), \$716 (SE = 10) and \$4,147 (SE = 167; Table 4.2), respectively. The total area for aerial sampling was 290.1 km² each for RMUs 3 and 9, and 248.6 km² for RMU 4. The average cost effectiveness and weighted cost effectiveness across RMUs for aerial sampling was 15.83 (SE = 2.11) and 4.11 (SE = 0.54), respectively.

Table 4.4. Density estimates of white-tailed deer from aerial-sampling data collected from 8 February to 10 March 2021 in three different regional management units (RMU) of Indiana, USA. Densities and corresponding measures of precision were estimated using plot sampling methods, and are shown for concealed, open, and across both concealed and open (Total) habitat types. The area captured by the field-of-view of the vertical-looking infrared thermographer (a_t), as well as the number of detections after truncation (n) are presented for each RMU and habitat type.

Habitat	RMU	a_t	n	$\hat{D}$	$SE(\hat{D})$	$CV(\hat{D})$
Concealed	3	13.8	250	22.349	4.074	0.182
Concealed	4	50.34	379	7.528	1.036	0.138
Concealed	9	20.54	671	35.038	3.662	0.105
Open	3	76.35	42	0.679	0.247	0.363
Open	4	22.55	22	0.976	0.362	0.371
Open	9	39.29	83	2.266	0.773	0.341
Total	3	90.15	292	3.202	0.534	0.167
Total	4	72.89	401	5.035	0.657	0.13
Total	9	59.83	754	10.105	1.063	0.105

4.4.4 Comparing Methods and Cost-Effectiveness Analysis

Total density estimates from aerial sampling were consistently smaller than density estimates from the other methods. All three methods suggested that total densities of deer were largest in RMU 9 and smallest in RMU 3. Aerial and camera-trap sampling always had the lowest CVs. The lowest capital, field-operating, and data-processing costs were associated with fecal-pellet sampling, except field-operating costs for aerial sampling in RMU 4 (Table 4.2). Specific sources of capital, field-operating, and data-processing costs are presented in Table 4.5.

Table 4.5. A breakdown of cost (USD) sources comprising capital (CC), field-operating (FOC), and data-processing (DPC) cost for aerial, camera-trap, and fecal-pellet sampling methods used to estimate white-tailed deer (*Odocoileus virginianus*) density in Indiana, USA. Deer densities were estimated in Deer Regional Management Units (RMU) 3, 4, and 9. Costs per unit, hour of operation, or mile (Cost/UHM) and the number of units, hours of operation, or miles (# of UHM) for each source of cost are presented.

Method	Type	Source	Cost/UHM	# of UHM	RMU 3	RMU 4	RMU 9
Pellet	CC	Field equipment	272.13	Variable ^a	468	458	317
		Field labor	17.76	534	3229	3894	2362
	FOC	Travel (gas)	0.58	892	161	189	168
		Study design labor	26.39	18	166	143	166
		Land permission	1575.00	NA	551	473	551
		Analysis labor	24.38	14	110	104	134
Camera	CC	Camera equipment ^b	119.02	428	18210	14758	17972
		Field equipment ^c	272.13	4	388	305	396
		Equipment shipping	1520.00	1	542	438	540
	FOC	Field labor ^d	18.35	784	5515	4007	4866
		Travel (gas)	0.58	1784	321	379	335
		Study design labor	26.39	7	65	55	65
		Batteries	1.67	2568	1533	1242	1513
		Land permission	1575.00	NA	551	473	551
	DPC	Downloading labor	24.38	40	349	283	344
		Classification labor ^e	14.40	169	870	557	1008
		Distance labor	13.79	424	1420	1086	3342
		Analysis labor	24.38	60	488	488	488
Aerial	CC	IR sensor	33488.00	1	11721	10046	11721
		Color sensor	4088.90	1	1431	1227	1431
		Pod engineering	95.00	209	6949	5957	6949
		GeoDVR ^f	18510.00	1	6479	5553	6479
		Equipment shipping	3410.25	1	1194	1023	1194
	FOC	Plane usage	237.00	37	2989	2714	3081
		Operational labor	24.38	37	307	279	317

Table 4.5 continued

	Study design labor	26.39	9	83	71	83
	Sensor installation	95.00	18	599	513	599
	Sensor removal	95.00	9	283	242	283
<u>DPC</u>	Viewing labor	24.38	28	241	207	236
	Analysis labor	24.38	60	488	488	488

^a Field equipment for pellet sampling included 8 tape measures and 4 GPS units.

^b Camera equipment includes the cost of cameras, security boxes, python cables, and SD cards.

^c Field equipment includes the cost of compasses, tape measures, and GPS units.

^d Field labor cost/hr is a weighted average (weighted based on hours of labor) between coordinator (\$25.58 USD/hr), technician (\$13.32 USD/hr), and graduate student (\$24.38 USD/hr) labor.

^e Classification labor is a weighted average (weighted based on hours of labor) between technician (\$13.32 USD/hr) and graduate student (\$24.38 USD/hr) labor.

^f GeoDVR includes the price of the GeoDVR as well as upgrades and accessories that I required.

After a single application (i.e., capital costs annualized across a single application), aerial sampling was the most cost effective in RMUs 4 and 9, while fecal-pellet sampling was the most cost effective in RMU 3 (Table 4.2). However, when differential weights were used with input parameters, aerial sampling was always the most cost-effective method after a single application of each method. When annualizing the capital costs of each method across 1, 2...,15 applications, the cost effectiveness of aerial sampling improved with increasing number of applications at a more rapid rate than that of fecal-pellet sampling. Although cost effectiveness of camera-trap sampling was most sensitive to the number of applications, camera-trap sampling still never surpassed either fecal-pellet or aerial sampling, regardless of whether differential weights were used or how many applications capital cost was annualized across (Figure 4.2).

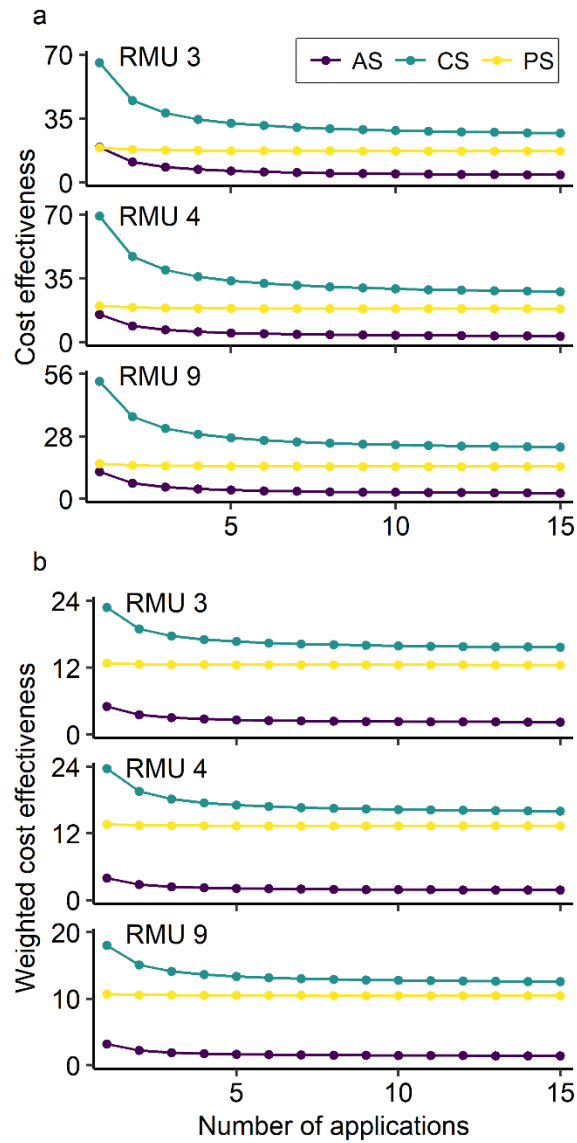


Figure 4.2. The cost-effectiveness (a) and weighted cost-effectiveness (b) of aerial (AS), camera-trap (CS), and fecal-pellet sampling (PS) when estimating the density of white-tailed deer (*Odocoileus virginianus*) in Regional Management Units (RMU) 3, 4, and 9 within Indiana, USA. Capital cost was annualized across 1, 2...,15-application lifespans.

4.5 Discussion

Cost-effectiveness analysis is a simple and powerful tool to decide between competing methods to estimate animal density. Past evaluations of methods used for estimating animal densities usually compared the cost and various factors related to the performance of methods separately (e.g., Anderson et al. 2013, Hedges et al. 2013, Zero et al. 2013). Unfortunately, such comparisons can lead to conflicting results that can confound decision makers (e.g., one method is more precise, but another requires less money). Therefore, I developed a cost-effectiveness model that integrates cost, performance, and scale into a single, comparable, and easily interpretable value (e.g., cost per unit land area standardized by relative precision) for methods estimating density.

Wildlife management agencies are limited by funding (Leopold et al. 2018), and thus decisions about the cost effectiveness of a management technique should affect the selection and quantity of management activities in which managers engage (Anderson and Loomis 2006). However, whether a method can actually be implemented (i.e., feasibility; Hopfensperger et al. 2007, Bowen et al. 2009) may depend on factors other than those included in cost-effectiveness analysis. Laguardia et al. (2021) introduced a metric they termed an integrated feasibility index which incorporated similar parameters as my model (cost, scale, and precision), but their index does not assess feasibility *sensu stricto*. Indeed, simple rearrangement reveals that their index is a modified cost-effectiveness ratio of the form given in Eq. 1. More appropriately, factors that determine feasibility are a result of constraints placed on an agency by internal or external forces. Internal constraints may be related to operational priorities, which limit the amount of money that can be spent on a project or the number of personnel assigned to the task. External constraints are often beyond the control of natural resource agencies, and may include bureaucratic restrictions such as limits on the maximum number of personnel allowed for hiring, or the maximum number of vehicles allowed for purchasing, regardless of whether the agency can afford more personnel or vehicles. External constraints may limit feasibility even when internal constraints are absent. Therefore, agencies must identify the factors affecting the feasibility of a method before consideration, and adjust how methods are applied to ensure feasibility prior to assessing cost effectiveness.

Due to limited funding, wildlife agencies may be more inclined to spend funds on methods that have the potential to collect additional biological information in conjunction with the target

data. When using my study-design methods, camera-trap sampling can also be used to estimate the density or occurrence of many other species captured in images, and can answer other questions related to behavior, health, and demographics (Delisle et al. 2021). Aerial sampling using infrared thermographers can estimate the density of other medium to large endotherms (Chrétien et al. 2015). When conducting field work for fecal-pellet sampling, fecal pellets may be simultaneously collected for genetic analyses (Kaunisto et al. 2016), or other animal sign recorded (Wood 1988). Similar to feasibility constraints, the value put on the potential to collect additional information depends on management objectives and funding; therefore, I did not explicitly consider the potential to collect additional information. If agencies do consider the additive utility of competing methods, then the added utility should be discounted appropriately according to its value relative to the importance of the primary purpose of the survey.

I used aerial, fecal-pellet, and camera-trap sampling to estimate the density of a common ungulate in three large regions. Based on weighted and non-weighted cost-effectiveness analysis, aerial sampling was the most cost-effective when annualizing the capital cost of each method across multiple applications. Aside from annualizing capital costs across only a single application, the superior cost effectiveness of aerial sampling was apparent in all three RMUs, which suggests consistency even for landscapes with vastly different habitat compositions and varying densities. These findings are dependent on my method which splits the shared costs across RMUs (Eq. 8). I decided to split shared costs between RMUs because future management objectives of the Indiana Department of Natural Resources seek to estimate deer density (1) in the remaining RMUs within the state, (2) across no fewer than 3 RMUs per sampling year, and (3) repetitively across many future sampling years. The RMUs included in the current study span the range of landscape conditions in the state, and thus I believe the better long-term cost effectiveness of aerial sampling will hold true in the remaining RMUs. More generally, I suspect that the superior long-term cost effectiveness of aerial sampling will translate to density estimation of other common endothermic species that can be detected using infrared thermographers in similarly sized or larger areas outside of Indiana.

There is no greater concern than human safety when conducting wildlife research. Although I found aerial sampling to be the most cost-effective method, safety concerns can be problematic for aerial sampling, as aircraft accidents are responsible for 66% of on-the-job deaths of wildlife biologist (Sasse 2003). Of course, other methods reliant on terrestrially based human

labor may also be dangerous in certain situations. Safety is a factor influencing whether a method is feasible, not cost effective. For instance, many project coordinators would deem transect sampling for mountain goat (*Oreamnos americanus*) on cliffs to be unacceptably dangerous and thus not feasible. Therefore, safety concerns, similar to all feasibility constraints, should be identified before conducting field sampling.

A substantial portion of my field operating costs for camera-trap and fecal-pellet sampling were associated with acquiring permission to sample on private property. Aerial sampling forgoes this requirement, as airspace is not privately owned. I predict narrower differences between the cost-effectiveness ratios of aerial sampling and fecal-pellet and camera-trap sampling for studies similar to mine but conducted in areas dominated by public lands. In comparison to the other methods I considered, camera-trap sampling had higher field-operation and data-processing costs (i.e., recurring costs). Specifically, data processing costs for camera-trap sampling per RMU were 30.1 (SE = 4.5) and 5.0 (SE = 1.1) times greater than those from fecal-pellet and aerial sampling, respectively. Such discrepancies might discourage future researchers from using camera traps to estimate trends in density across large spatiotemporal expanses, but this finding reflects the current technology available for accurately processing data. Models for automated species tagging (Willi et al. 2019, Norouzzadeh et al. 2021) and distance estimation (Haucke et al. 2021, Zuleger et al. 2022) appear promising and, if easy-to-use forms are readily available in the future, could substantially decrease the cost of processing data from camera-traps. To predict future cost effectiveness, I simulated a reduction in the data-processing cost of camera-trap sampling to \$200; however, the weighted and unweighted cost-effectiveness ratios showed the same preference rankings across methods. Therefore, despite the increased usage of camera traps (Delisle et al. 2021), my study suggests the cost effectiveness of camera-trap sampling for estimating density across larger heterogeneous landscapes is poor in comparison to alternative methods.

Within each RMU, densities from aerial sampling in open and concealed habitats were considerably lower and higher (except in RMU 4), respectively, than the other two methods. These patterns likely resulted because I conducted aerial sampling diurnally when deer were less likely to use open habitats (Larson et al. 1978). My density estimates from camera traps and pellet counts both incorporated nighttime hours when deer are far more likely to use open habitat types (Larson et al. 1978). Specifically, density estimates from pellet sampling represent an average density across the time it takes pellet groups to decay (Marques et al. 2001), and densities from camera

sampling are an average density across the snapshot moments during the time cameras are sampling. Therefore, interpretation of differences between density estimates from the three methods should focus on the total density across both open and concealed habitat types.

Density estimates from aerial and camera-trap sampling had lower CVs than the estimates from pellet sampling. Uncertainty from many different sources can impact the variation of density estimates (Williams et al. 2002). These sources of variation include detectability as a function of distance (Buckland et al. 2001), observer (Buckland and Garthwaite 1991), or a combination of these and other covariates (Burt et al. 2014); multipliers such as activity or availability levels (Howe et al. 2017), group size (Hamilton et al. 2017), and persistence or production of cues (Marques et al. 2001, Buckland et al. 2008); classification discrepancies among observers (Delisle et al. 2022b); and the encounter rate between transects or points (Fewster et al. 2009). My estimates from aerial sampling only had variation from the encounter rate and detectability differences between viewers of infrared video. Similarly, the estimates from camera trapping and pellet sampling had variation from the encounter rate, detection function, and multipliers (activity level and dung persistence rate), but spatial replicates were more plentiful for camera trapping. These additional sources of variation and fewer spatial replicates likely contributed to the higher CVs of density estimates from pellet sampling.

Although I used three common field-sampling methods under, perhaps, the most common statistical estimator used for estimating wildlife density (distance sampling), other sampling methods and estimators exist. Field-sampling methods related to density estimation that I did not consider include, but are not limited to, drones (Chrétien et al. 2016) and spotlighting (McCullough 1982). Similarly, other statistical estimators of density include, but are not limited to, capture-recapture methods (Royle et al. 2013), N-mixture models (Royle 2004), and random encounter or random encounter staying time models (Rowcliffe et al. 2008, Nakashima et al. 2018). I chose to implement fecal-pellet, camera-trapping, and aerial sampling methods under a distance-sampling framework because these strategies could be reasonably applied while meeting study-design and sampling assumptions. Even subtle changes to field sampling and statistical methods could alter costs or precision. For instance, guidelines with case studies are needed on how best to account for factors such as reactive behavior toward cameras. I encourage future comparisons of the cost effectiveness of other field sampling and statistical methods, and how cost effectiveness is

influenced by finer examination of other field-sampling and statistical decisions within common density estimators.

I extended cost-effectiveness analysis to specifically decide between density-estimation methods, and I believe that the same principles can be used to decide between competing alternatives related to many types of ecological monitoring. For example, several methods exist that aim to reduce human-wildlife conflict (Tarlow and Blumstein 2007) or measure the impacts of herbivores on plant communities (Kirschbaum and Anacker 2005, Royo et al. 2016). Simple alterations to my cost-effectiveness analysis can aid these decisions. Similarly, methods that integrate multiple data types to produce a single estimate (i.e., fusion models) are becoming more popular due to increased precision (Zipkin et al. 2021). My approach to cost-effectiveness analysis offers a formal framework to determine whether the improved precision is worth the extra cost and effort to collect multiple data types.

4.6 Management Implications

When considering the cost effectiveness of field methods, the relative importance of cost, precision, and area sampled depends on context, and each agency will have its own set of parameters with which to contend (Leopold et al. 2018). Unfortunately, most cost-effectiveness analyses do not take this into consideration. If context is not fully considered, then cost-effectiveness analysis can lead to error in judgement. When I used equal weights of importance for input parameters, the cost-effectiveness ratios of aerial and fecal-pellet sampling were very similar after a single application of each method. However, because the deer manager in Indiana allocated low importance to cost-related parameters and placed much greater value on the precision of the density estimate, aerial sampling was clearly identified as the most cost-effective approach. In general, wildlife managers should use my weighted cost-effectiveness ratio (Eq. 3), because it permits users to specify importance of each parameter and thus flexibly accommodates the unique context faced by each agency. Context-independent comparisons of methods across agencies or jurisdictions should use cost-effectiveness ratios computed using Eq. 1 and 2.

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CHAPTER 5. MODELLING DENSITY SURFACES OF DEMOGRAPHIC CLASSES USING CAMERA-TRAP DISTANCE SAMPLING

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5.1 Abstract

Spatially explicit densities of wildlife are important for understanding environmental drivers of populations, and density surfaces of demographic classes allow exploration of links between demographic ratios and environmental conditions. Although spatially explicit densities and class densities are valuable, conventional design-based estimators remain prevalent when using camera-trapping methods for unmarked populations. I developed a density surface model that utilized camera-trap distance sampling data within a hierarchical generalized additive modelling framework. I estimated density surfaces of demographic classes of a common ungulate, white-tailed deer (*Odocoileus virginianus*), across three large management regions in Indiana, USA. I then extended simple statistical theory to test for differences in two ratios of density. Deer density was influenced by landscape fragmentation, wetlands, and anthropogenic development. I documented class-specific responses of density to availability of concealment cover, and found strong evidence that increased recruitment of young was tied to increased resource availability from anthropogenic agricultural land use. The coefficients of variation of the total density estimates within the three regions I surveyed were 0.10, 0.10, and 0.06. My strategy extends camera-trap distance sampling, and enables managers to use camera traps to better understand spatial predictors of density. My density estimates were more precise than previous estimates from camera-trap distance sampling. Population managers can use my methods to detect finer spatiotemporal changes in density or ratios of demographic-class densities. Such changes in density can be linked to land use, or to management regimes on habitat and harvest limits of game species.

5.2 Introduction

Ecologists and wildlife managers require estimates of population density for more comprehensive ecological knowledge and effective application of management (Williams et al. 2002). For many species, density estimates specific to age, sex, or other demographic classes can provide additional information to ecologists and managers. For instance, class-specific densities may aid management of game species when classes are unequally harvested to achieve population goals (Keehner et al. 2015), or of species for which recruitment is associated with food availability (Costello et al. 2003).

Camera traps are commonly used to estimate wildlife density (Delisle et al. 2021). When monitoring demographic classes, camera traps are especially advantageous because they allow viewers of images to carefully consider class membership of individuals. Other methods requiring the physical presence of surveyors in the field may not facilitate such careful determination of class membership. Thus, inaccuracies may arise when surveyors must determine class membership in challenging field conditions. Difficulties may be especially great when class membership must be assigned quickly before sampled individuals are out of sight, as often happens when sampling extremely mobile species, species that flee in response to surveyors, or when surveyors are aboard a moving platform.

Several methods exist for estimating density of unmarked populations using camera traps (Gilbert et al. 2021). Although each method has unique advantages, camera-trap distance sampling remains appealing because it rests upon a well-established and intuitive statistical foundation (Buckland et al. 2001, Howe et al. 2017). However, one limitation of conventional distance sampling is that a single design-based density, estimated from an average count across sampled locations, is inferred across entire study areas (Buckland et al. 2001). This approach can obscure local fluctuations in density along environmental gradients (e.g., topography, food proximity). Accordingly, ecologists are frequently interested in relationships between density and local covariates.

Density surface modelling uses distance sampling data to estimate spatially explicit density in two steps (Miller et al. 2013). Firstly, detectability is modelled with a detection function fit to distance-sampling data, which accounts for decreased detection probability associated with increasing distance from the surveyor. Secondly, counts on sampling locations are modelled as a function of spatially explicit predictors. Generalized additive modelling is often used within the

second step, which facilitates nonlinear relationships that are common in ecology (Wood 2017). The fitted model is then used to predict density in unsampled areas, which yields more accurate density estimates across study areas, especially for species whose density relates to spatial fluctuations of habitat characteristics (Miller et al. 2013).

Within the second step of density surface modelling, hierarchical generalized additive models are uniquely appealing for researchers interested in demographic classes. Specifically, they can simultaneously model multiple biologically determined subsets of data while maintaining global relationships exhibited by the entire data set (Pedersen et al. 2019). Such fitted relationships, termed factor-smooth interactions, can enable unique spatial modelling of class-specific densities in a single model. Class specificity is especially useful when class density exhibits unique relationships with spatially explicit predictors. Considering class-specific relationships may yield more accurate estimates of overall density and between-class ratios of density, more robust understanding of ecological relationships, and better fit of models.

Although the advantages of camera-trap distance sampling, density surface modelling, and hierarchical generalized additive models are evident, to my knowledge, no study has combined these approaches to model the spatially explicit density of classes. I combine these tools to model the class density of a common North American game ungulate, white-tailed deer (*Odocoileus virginianus*), across three large regional areas over which management is implemented in Indiana, USA. I then use density estimates of classes to compare recruitment rates and adult sex ratios in these three areas. First, because recruitment of white-tailed deer is directly linked to food availability (McCullough 1979) and deer readily forage on agricultural crops (Rouleau et al. 2002), I hypothesized that recruitment rates of deer would be higher in areas with more agricultural land use. Specifically, I predicted larger ratios of young deer:adult female deer (fawns and does, respectively) densities in areas where the fraction of land being used for agriculture is larger. Second, annual deer harvest reports from the years and areas I sampled (Caudell and Vaught 2019, 2020; Boggess and Vaught 2021) showed that ratios of harvested adult male (buck) deer:harvested does were similar in two of the areas I sampled, but higher in the third area I sampled that had the highest relative amount of land devoted to agriculture. Therefore, I predicted that the ratios of buck:doe densities would be lowest in the most highly agricultural region.

5.3 Materials and Methods

5.3.1 Study Area

I sampled in Deer Regional Management Units (RMUs) 3, 4, and 9 in Indiana, USA (Swihart et al. 2020) during the winters of 2019, 2020, and 2021 (Figure 5.1). RMU 3 is predominantly agriculture (79%), but also contains patches of forest (10%), grassland (3%), and wetland (1%). RMU 4 contains more forest (56%), a mixture of agriculture (19%) and grassland (16%), and sparse patches of wetland (<1%). Lastly, RMU 9 is intermediate in agriculture between the other RMUs (56%), and has nearly even amounts of wetland (13%), grassland (11%), and forest (8%). Approximately 95% of these RMUs is privately owned.

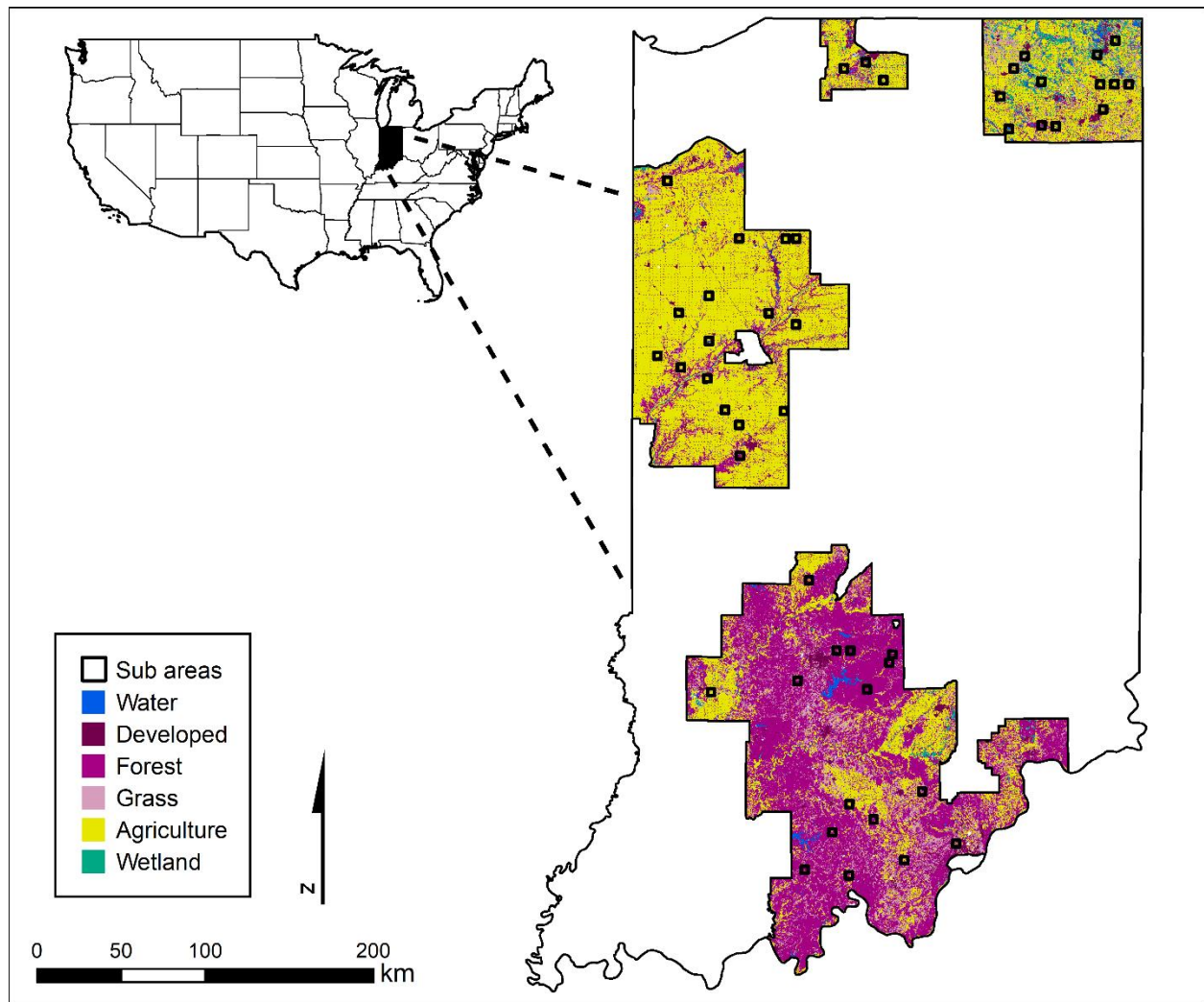


Figure 5.1. Landcover types within Regional Management Units 3 (west-central), 4 (southern), and 9 (northeastern) in Indiana, USA. I deployed cameras within 10.36-km² sub areas.

Within RMUs, I sampled in randomly chosen 41.44-km² cells from the deer-harvest reporting grid that the Indiana Department of Natural Resources uses to collect spatially explicit harvest data. I did not preferentially sample 41.44-km² cells that I believed would have more or less deer. Specifically, I sampled inside 10.36-km² areas (sub areas) that I placed inside the larger cell. I attempted to place sub areas within larger cells to ensure property permission was homogeneously distributed, and habitat composition within sub areas was representative of the larger cell. During each year, I sampled 20 sub areas across all three RMUs. Thus, in two years I sampled seven sub areas in each RMU, and in one year I sampled six sub areas. I repeatedly sampled two sub areas in each RMU during each year to assess interannual variation uncoupled from spatial variation, resulting in sampling of 48 unique sub areas.

5.3.2 Data Collection and Analysis

I randomly deployed Browning Strike Force HD or BTC-5HDE motion-triggered camera traps in forest, grassland, wetland, and agricultural fields within sub areas in each RMU using ArcMap 10.7. In forests, I affixed cameras to trees at 1-m height and oriented cameras north to avoid sun glare at dawn and dusk. In non-forested areas, I affixed cameras to metal posts (that I hammered into the ground) at the same height and orientation. Cameras were deployed during February–April in 2019, 2020, and 2021. Because of the large number of photos, I collected data from images during 2-week sampling periods from 12–25 February 2019, 9–22 March 2020, and 25 February–10 March 2021. The 2-week sampling windows differed slightly each year due to logistical constraints during camera deployment. Before each sampling window, cameras were deployed for 7 days minimum to allow for deer habituation to cameras. In rare instances (5%), cameras did not sample the entire 2 weeks because of unpredictable circumstances in the field (e.g., human moving camera). When triggered, cameras captured a 3-photo burst with a 0.3-s delay between photos and a minimum 1-s delay before subsequent bursts. In some instances (~25%), settings were slightly altered accidentally or because BTC-5HDE cameras did not permit minimum delays <5 s. I recorded the spatiotemporal effort of each camera as in Howe et al. (2017). When cameras did not sample the entire 2-week window, or when photo delays were set incorrectly, I adjusted the spatiotemporal sampling effort accordingly. If I deployed cameras in sub areas that I sampled each year, I treated repeatedly sampled points as a single spatial replicate and combined the spatiotemporal sampling effort across all years.

I used camera-trap distance sampling to model the observation process (Howe et al. 2017). I recorded reference videos as in Howe et al. (2017), which I used to measure the distances between cameras and deer within each image from 1 to 15 m integer distances. I did not measure distances to bedded deer, or deer that became interested in the camera. Each deer was recorded as doe, buck, fawn, or unknown. I binned distances between cameras and deer at 0, 1, 2, 3, 4, 5, 6, 7, 8, 10, 12, and 15 m and estimated several detection functions with the “Distance” package in R (Miller 2022, R Core Team 2022). I did not consider distances >15 m. Candidate detection functions included half-normal key functions with 0, 1, and 2 Hermite polynomial adjustments; uniform key functions with 1 and 2 cosine adjustments; and hazard-rate key functions with 0, 1, and 2 cosine adjustments. I also considered half-normal and hazard-rate key functions with the following factor covariates: (1) night or day (determined by camera flash), (2) microhabitat surrounding the camera (cornfield, soybean field, deciduous, mixed, or evergreen forest, woody or herbaceous wetland, herbaceous grassland, and pasture/hay), (3) RMU, (4) RMU and night or day, (5) night or day and microhabitat, (6) RMU and microhabitat, and (7) night or day, microhabitat, and RMU. Because repeatedly measuring distances to the same deer in subsequent images introduces overdispersion into the detection function, I used the methods of Howe et al. (2019) to select a final detection function with Akaike’s Information Criterion adjusted for overdispersion (QAIC).

Vegetative obstruction in front of cameras may influence detection probability. Therefore, I tested a pooled detection function across open (agricultural fields and grasslands) and concealed (forests and wetlands) areas, and separate detection functions for open and concealed areas. To do this, I compared the QAIC of the best pooled model to the sum of the QAIC values of the best models fit separately. I chose the strategy that produced lowest QAIC value.

Density surface modelling assumes that all individuals are available for sampling. Because deer are not available for camera sampling when bedded, I estimated the activity level of deer to account for this. I recorded the times individual deer were first detected by cameras upon entering the field-of-view. Because deer are crepuscular (Beier and McCullough 1990), I double-anchored detection times with the average sunset and sunrise times during my sampling (Vazquez et al. 2019). I estimated the activity level of deer in each RMU by fitting circular kernel densities to double-anchored detection times, and standard errors of activity levels with nonparametric bootstrapping using the “activity” package in R (Rowcliffe et al. 2014, Rowcliffe, 2021).

After selecting detection functions and estimating deer activity levels, I fit density surface models using the “dsm” package in R (Miller et al. 2022) in the form:

$$\log(E[n_i]) = \beta_0 + \sum_m f_m(x_{im}) + \sum_{fac} \beta_{fac} + \log(\hat{v}_i) \quad (1)$$

where n_i = the count of deer at camera i , β_0 = the intercept, f_m = the smooth functions of spatially explicit predictors x_{im} , β_{fac} = any factor variables considered, and $\hat{v}_i$ = the product of detection probability and activity level of deer at camera i used as an offset. I modelled smooths with thin plate regression splines (Wood 2003). In preliminary analysis, overfitting was apparent (e.g., extremely wiggly relationships). To prevent overfitting, I specified the gamma parameter at 2 (Wood 2017 section 4.6.1). I found goodness-of-fit (via observed vs expected counts) of the quasi-Poisson distribution to outperform other count distributions (e.g., Poisson, negative binomial, Tweedie). Therefore, I used this distribution for all models.

I tested several spatially explicit predictors of density at each camera including metrics of distance and landscape composition or structure within buffers around cameras. For distance metrics, I tested the distance to wetland, which I calculated in R using the 2019 National Land Cover Database land cover raster (Dewitz and U.S. Geological Survey 2021). I used the “landscapemetrics” package (Hesselbarth et al. 2019) in R to test several landscape-composition or structure indices within buffers, including the contagion index, coefficient of variation of the core area of patches, and total area of concealment cover (defined as forest or wetland) and wetland (McGarigal and Marks 1995). I used the Indiana primary and secondary roads state-based shapefile (US Census Bureau, Department of Commerce) and R to calculate the total road length within buffers. Other metrics were tested and eliminated from consideration due to concurvity (a measure similar to collinearity for smooth models; Wood 2017) with these better predictors. I evaluated indices in buffers with radii of 250, 750, 1425, 4000, and 8000 m (Appendix D: Buffer Radii). I chose a final buffer size for each metric based on the strength of the relationship with deer counts. I did not use the same metrics with multiple buffer radii due to concurvity.

For each predictor, I used observed vs expected counts to choose between the following types of class-smooth interactions for each predictor: (1) single common smoother across all classes (i.e., global smoother; no factor-smooth interaction); (2) global smoother and class-specific smoothers with identical wiggleness; (3) global smoother and class-specific smoothers with differing wiggleness; (4) class-specific smoothers with identical wiggleness but no global smoother;

and (5) class-specific smoothers with differing wiggleness but no global smoother (Pedersen et al. 2019). Additionally, I considered habitat type (forest, wetland, grassland, and agricultural field) and an interaction between class and RMU as factor variables. Upon deciding which smooth type to fit for each predictor, I fit a global model containing all the best factor-smooth types for each predictor. I then used F-tests to identify and remove factor-smooths in the global model with weak ($P > 0.05$) relationships with deer counts.

To predict spatially explicit class density, I created a grid over each RMU. I specified the resolution of grid cells to be 30 x 30 m because: (1) this was comparable to the area each camera sampled; and (2) I did not expect deer density to change perceptibly over this area. Within each grid cell, I calculated each predictor of deer density that I parameterized in my final density surface model, and used the final fitted model to predict buck, doe, fawn, and unknown density. I did not predict density in developed, barren (rock, sand, or clay), or scrub/shrub habitats because I did not sample these habitats. Additionally, I used the “dsmextra” package in R (Bouchet et al. 2020) to calculate Euclidean and Mahalanobis distances (Mesgaran et al. 2014) and identify cells with covariates exhibiting univariate or combinatorial extrapolation outside the range of the covariates I sampled. I estimated densities that both considered and did not consider extrapolated cells (extrapolated and non-extrapolated densities, respectively).

I used a modified formula from Gerrodette and Forcada (2005) to prorate unknown-specific density in each cell to the known classes:

$$\hat{D}_i(pr) = \hat{D}_i + \hat{D}_u \left[\frac{w_i \hat{D}_i}{w_i \hat{D}_i + \sum_k w_k \hat{D}_k} \right] \quad (2)$$

where i refers to known class i (bucks, does, or fawns), u refers to the unknown class, k refers to all other classes $\neq i$, $\hat{D}_i(pr)$ = the prorated density of class i , $\hat{D}_i$ = the density of class i before proration, $\hat{D}_u$ = the density of the unknown class, and w_i = the fraction of class i that is at risk of being unidentifiable. For does and fawns, $w_i = 1$. However, because only a fraction of bucks had shed their antlers during my sampling, I specified w_i for bucks as the fraction of bucks detected that shed both antlers in the RMU the cell was within. I considered bucks with antlers to be wholly identifiable, as antlers are easily distinguishable in images. To estimate the final density of demographic classes in each RMU and habitat-specific densities, I averaged the predicted class density across the entire grid of each RMU and across habitats within each RMU, respectively. I

estimated total deer densities (all classes combined) by summing the predicted density of all classes in each cell, and averaging the sum across cells.

Because of the size of my prediction grids (~4 to ~16 million cells), I used posterior simulation in combination with Welford's online algorithm (Welford 1962, Knuth 2014) to estimate the variance and confidence intervals of all densities through the following process in Miller et al. (2022):

1. Sample from the posterior of the model's parameters (approximately multivariate normal distributed).
2. Use sampled parameters to generate class-specific predictions of density across the prediction grid.
3. Save necessary summary statistics needed to calculate the variance per Welford's algorithm.

I repeated the above algorithm 1000 times, and prorated the simulated unknown densities using equation 2. I estimated variances of all density estimates from the 1000 simulated densities (using Welford's algorithm) and propagated variance from the activity level via the delta method. I approximated 95% confidence intervals using the percentile method (Efron 1981).

For each RMU, I estimated fawn:doe ratios by $\frac{\hat{D}(f)}{\hat{D}(d)}$, where $\hat{D}(f)$ and $\hat{D}(d)$ = the density estimate of fawns and does, respectively. I estimated the variance of fawn:doe ratios using a first-order Taylor series expansion (Seltman 2012):

$$\begin{aligned} Var \left[\frac{\hat{D}(f)}{\hat{D}(d)} \right] = & \frac{E[\hat{D}(f)]^2}{E[\hat{D}(d)]^2} \left(\frac{Var[\hat{D}(f)]}{E[\hat{D}(f)]^2} + \frac{Var[\hat{D}(d)]}{E[\hat{D}(d)]^2} \right. \\ & \left. - 2 \frac{Cov[\hat{D}(f), \hat{D}(d)]}{E[\hat{D}(f)]E[\hat{D}(d)]} \right) \end{aligned} \quad (3)$$

where $Var \left[\frac{\hat{D}(f)}{\hat{D}(d)} \right]$ = the variance of the fawn:doe ratio, $E[\hat{D}(f)]$ and $E[\hat{D}(d)]$ = the expected density of fawns and does, respectively, and $Cov[\hat{D}(f), \hat{D}(d)]$ = the covariance of $\hat{D}(f)$ and $\hat{D}(d)$ estimated from the 1000 simulated densities. I repeated this process for buck:doe ratios. To infer differences in ratios between RMUs, I used a Z test:

$$Z = \frac{rat_1 - rat_2}{\sqrt{Var(rat_1 - rat_2)}} \quad (4)$$

where rat_1 and rat_2 = the two ratios being compared, and $Var(rat_1 - rat_2) = Var(rat_1) + Var(rat_2)$. I implemented a 1-tailed test in instances when my hypotheses on ratios of density between RMUs were directional.

5.4 Results

I deployed 1295 cameras but removed 73 cameras from analysis because of faulty placement. After accounting for repeatedly sampled points across years, I used data from 1018 independent locations and measured 83,824 distances (Table 5.1).

I observed a spike in detections at close distances in open areas. Therefore, I removed all hazard-rate models from consideration in open areas, because this model can fit unnatural spikes at close distances. In this instance, the hazard-rate key function can model unnaturally abrupt declines in detection probability, which underestimates detectability and overestimates density (Buckland et al. 2001).

A separate detection function for open and concealed areas was the QAIC-best strategy ($\Delta QAIC = 1492.4$). Subsequently, the uniform key function with 1 cosine adjustment term ($\Delta\chi^2/df = 329.2$) and the uniform key function with 2 cosine adjustment terms ($\Delta\chi^2/df = 550.7$) were the best detection functions in open and concealed areas, respectively (Figure 5.2). I estimated activity levels of 0.41 (SE = 0.01), 0.39 (SE = 0.02), and 0.44 (SE = 0.01) in RMUs 3, 4, and 9, respectively (Figure 5.3).

Table 5.1. Number of cameras deployed and distances measured to white-tailed deer in open (agriculture and grasslands) or concealed (forest and wetland) habitats within three different Regional Management Units (RMU) in Indiana, USA.

RMU	Habitat	Cameras	Distances
3	Open	146	3796
4	Open	58	3501
9	Open	117	7539
3	Concealed	181	15194
4	Concealed	249	14155
9	Concealed	267	39639

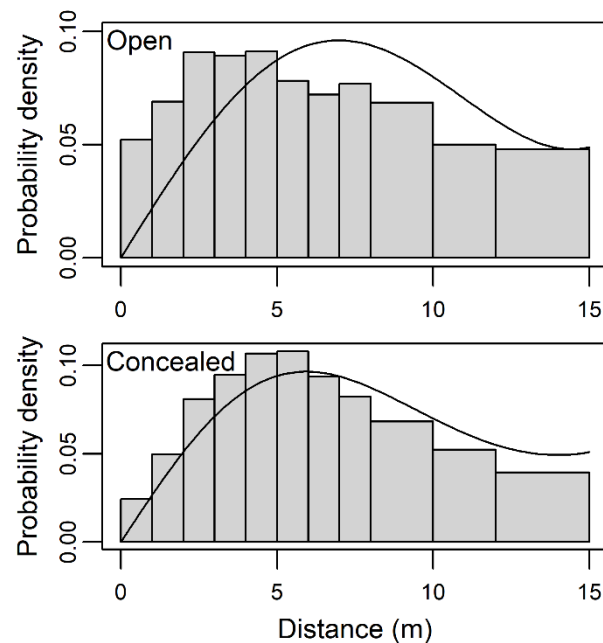


Figure 5.2. Probability density functions of distances (m) between white-tailed deer and camera traps in Indiana, USA. In open areas, the uniform key function with 1 cosine adjustment term is presented. In concealed areas, the uniform key function with 2 cosine adjustment terms is presented.

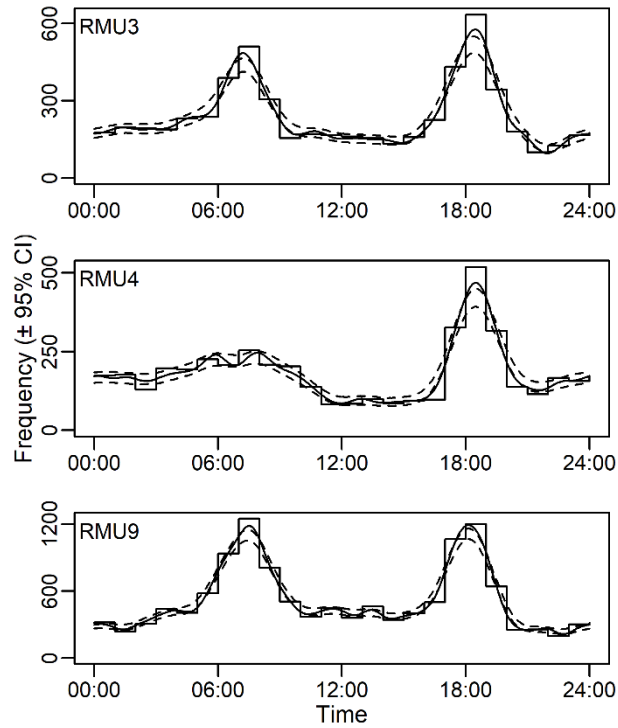


Figure 5.3. Activity probability distributions of white-tailed deer in Regional Management Units (RMU) 3, 4, and 9 in Indiana, USA. Solid lines represent the fit kernel density, and dotted lines represent 95% confidence intervals.

After fitting each type of factor-smooth interaction for each predictor, goodness-of-fit via observed vs expected counts suggested that a single global smooth was best for the contagion index <4000 m and the amount of wetland <8000 m; class-specific smoothers with the same wiggleness without a global smoother were best for the coefficient of variation of the core area of patches <4000 m; a global smoother and class-level smoothers with differing wiggleness were best for distance to wetland; and a global smoother with class-level smoothers of the same wiggleness was best for the amount of concealment cover <1425 m and amount of road length <8000 m. F-tests on a global model containing all the best factor-smooth interactions suggested that factor-smooth interactions were unnecessary for the amount of road <8000 m, distance to wetland, and the coefficient of variation of the core area of patches <4000 m. Therefore, I replaced these factor-smooth interactions with global smooths, but kept the factor-smooth interaction for the amount of concealment cover <1425 m within my final model (deviance explained = 46.2%).

I found strong evidence to include factor terms for habitat ($df = 3$, $F = 36.47$, $P < 0.001$), sex ($df = 3$, $F = 30.06$, $P < 0.001$), RMU ($df = 2$, $F = 2.38$, $P = 0.093$), and the interaction between

sex and RMU ($df = 6$, $F = 2.34$, $P = 0.037$). Similarly, I found strong evidence for the smooths of contagion index <4000 m ($edf = 13.17$, $F = 1.38$, $P < 0.001$; Figure 5.4A), coefficient of variation of the core area of patches <4000 m ($edf = 11.11$, $F = 0.81$, $P < 0.001$; Figure 5.4B), distance to wetland ($edf = 4.13$, $F = 0.21$, $P < 0.001$; Figure 5.4C), amount of wetland <8000 m ($edf = 12.18$, $F = 1.21$, $P < 0.001$; Figure 5.4D), global smooth for the amount of concealment cover <1425 m ($edf = 9.77$, $F = 4.80$, $P < 0.001$; Figure 5.4E), class-specific smooths for the amount of concealment cover <1425 m ($edf = 4.73$, $F = 0.05$, $P < 0.001$; Figure 5.4E), and length of road <8000 m ($edf = 7.05$, $F = 0.37$, $P < 0.001$; Figure 5.4F). Specific effects of factor terms, smoothed relationships, spatial density surfaces, and spatial coefficient of variation (CV) surfaces are presented in Figure D1, and Figures 5.4–5.6, respectively.

Extrapolated densities and ratios of extrapolated densities were much more variable and never exhibited statistical differences (Appendix D: Extrapolated Densities). Henceforth, I only present non-extrapolated densities. Within each RMU, density was highest in wetlands and lowest in agricultural fields (Table 5.2). The CV of total densities in RMU 3, 4, and 9 were 0.10, 0.10, and 0.06, respectively. The average class- and habitat-specific CV was 0.15 ($SE = 0.02$) and 0.14 ($SE = 0.03$), respectively. Buck:doe ratios between RMUs and fawn:doe ratios in RMU 3 and 9 (observed difference = 0.11, $Z = 1.26$, $P = 0.104$) did not exhibit strong differences (Table 5.3). However, the fawn:doe ratio in RMU 3 was significantly larger than RMU 4 (observed difference = 0.19, $Z = 2.21$, $P = 0.013$) and RMU 9 was significantly larger than RMU 4 (observed difference = 0.08, $Z = -1.66$, $P = 0.048$).

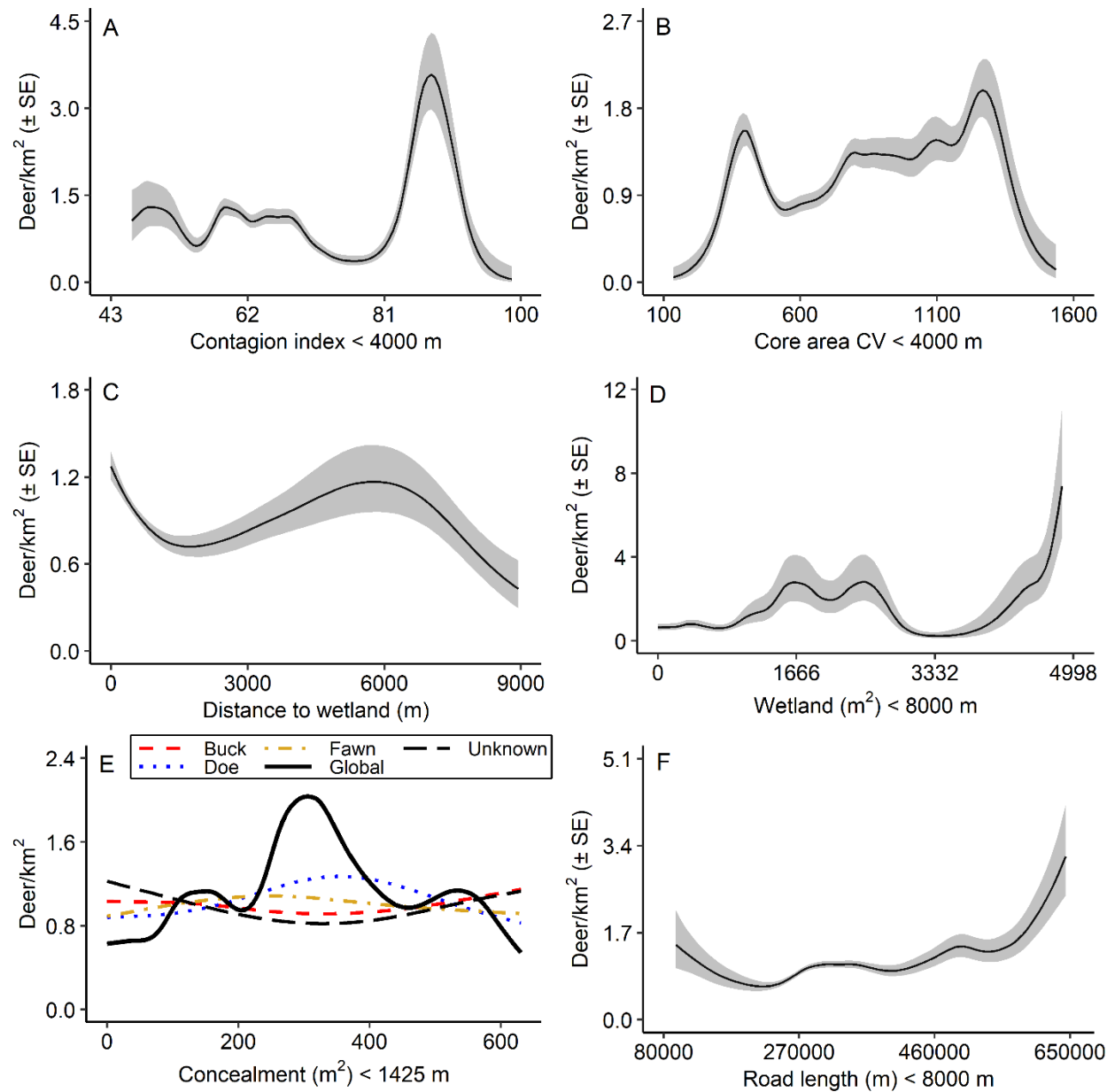


Figure 5.4. Partial effects plot of my final density surface model fit to camera-trap distance sampling data from white-tailed deer within Indiana, USA. Predictors include the contagion index of habitat <4000 m of the camera (A), coefficient of variation of the core area of patches <4000 m of the camera (B), distance (m) from the camera to the nearest wetland (C), amount (m²) of wetland <8000 m of the camera (D), amount (m²) of concealment cover <1425 m of the camera (E), and length (m) of road <8000 m of the camera (F). For the amount of concealment cover <1425 m of the camera, I used a factor-smooth interaction that implemented a global smoother and class-level smoothers with the same wigginess.

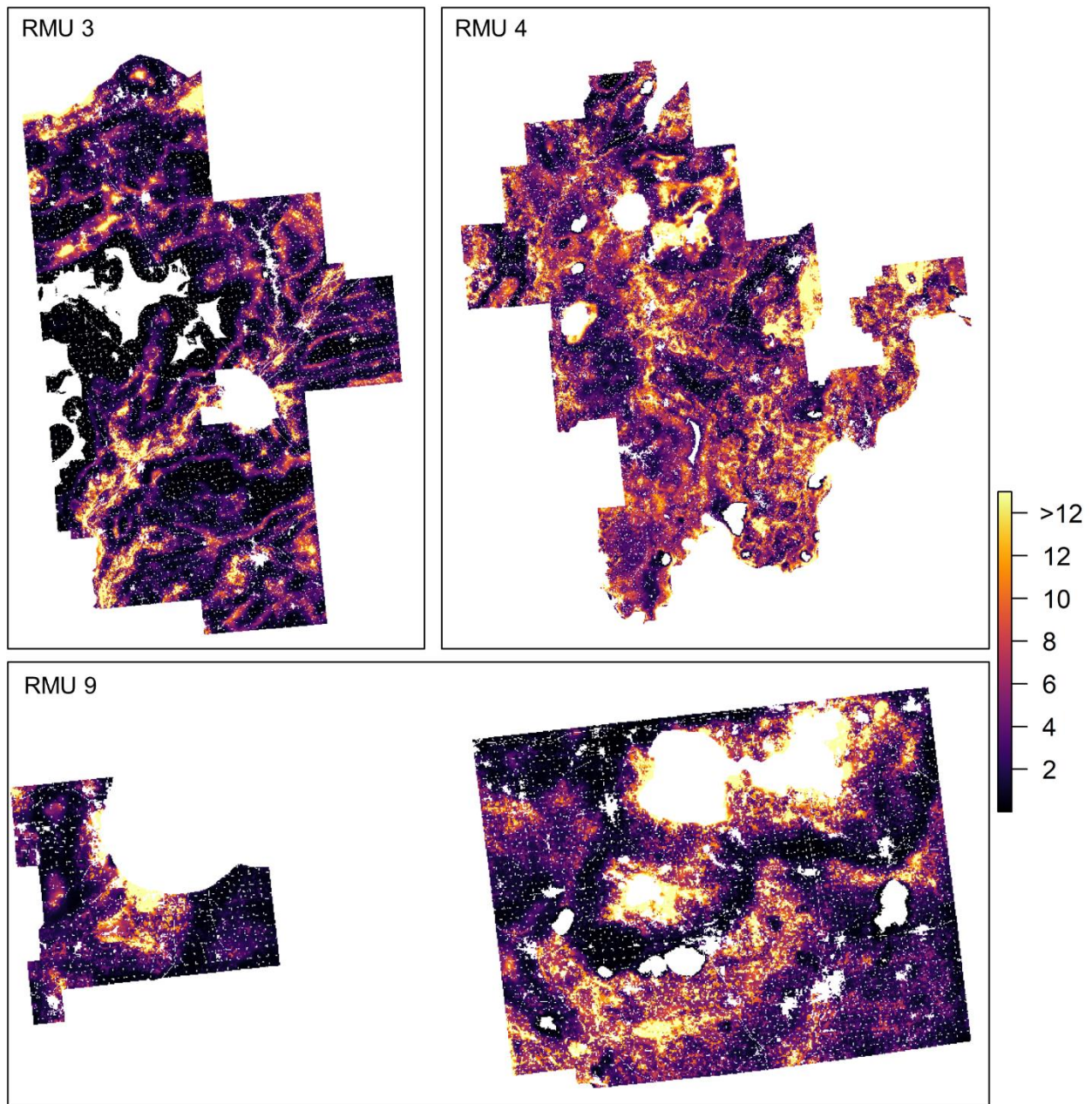


Figure 5.5. Predicted densities (deer/km²) of white-tailed deer across Regional Management Units (RMU) 3, 4, and 9 of Indiana, USA, from a density surface model fit to camera-trap distance sampling data. Cells exhibiting univariate or combinatorial extrapolation are not depicted.

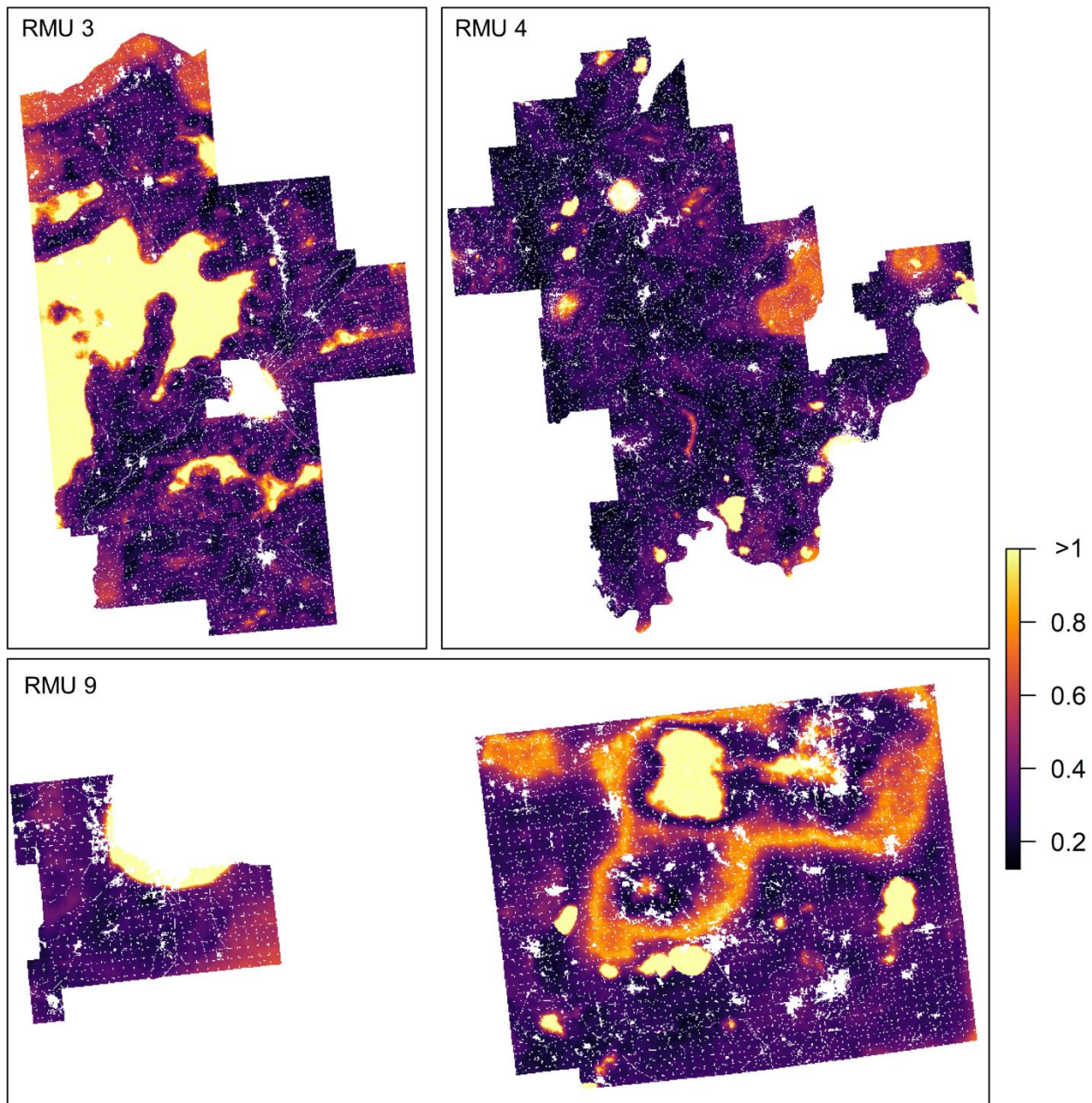


Figure 5.6. Coefficient of variation of predicted densities of white-tailed deer across Regional Management Units (RMU) 3, 4, and 9 of Indiana, USA, from a density surface model fit to camera-trap distance sampling data.

Table 5.2. Density estimates (deer/km²) of white-tailed deer in Regional Management Units (RMU) 3, 4, and 9 in Indiana, USA. Densities were estimated with a density surface model fitted to camera-trap distance sampling data. Habitat- and class-specific densities were estimated only across areas that were within the univariate or combinatorial range of environmental covariates I sampled. UCI = upper 95% confidence interval. LCI = lower 95% confidence interval.

Type	RMU	Habitat/Class	$\hat{D}$	SE($\hat{D}$)	CV($\hat{D}$)	UCI($\hat{D}$)	LCI($\hat{D}$)
Habitat	3	Agriculture	2.33	0.24	0.10	2.06	2.94
		Grassland	5.40	0.76	0.14	4.64	7.52
		Wetland	17.81	4.52	0.25	13.68	31.39
		Forest	9.99	1.13	0.11	8.92	13.28
	4	Agriculture	3.70	0.61	0.17	3.21	5.35
		Grassland	5.81	0.72	0.12	4.92	7.69
		Wetland	22.66	9.14	0.40	15.93	47.42
		Forest	7.29	0.65	0.09	6.71	8.99
	9	Agriculture	2.79	0.20	0.07	2.56	3.31
		Grassland	5.00	0.50	0.10	4.44	6.41
		Wetland	10.24	0.93	0.09	9.26	12.87
		Forest	9.26	0.46	0.05	8.78	10.50
Class	3	Doe	2.07	0.31	0.15	1.73	2.93
		Buck	0.74	0.13	0.18	0.58	1.09
		Fawn	0.68	0.13	0.19	0.52	0.99
	4	Doe	4.24	0.56	0.13	3.69	5.69
		Buck	1.57	0.26	0.17	1.24	2.19
		Fawn	0.57	0.14	0.25	0.39	0.96
	9	Doe	2.96	0.26	0.09	2.68	3.69
		Buck	1.09	0.12	0.11	0.93	1.43
		Fawn	0.65	0.08	0.13	0.54	0.87
Total	3	Total	3.50	0.36	0.10	3.15	4.55
	4	Total	6.38	0.64	0.10	5.82	8.11
	9	Total	4.70	0.29	0.06	4.44	5.55

Table 5.3. Ratios of densities of different classes of white-tailed deer in Regional Management Units (RMU) 3, 4, and 9 of Indiana, USA. Ratios were computed with densities that only considered areas that were within the univariate or combinatorial range of environmental covariates I sampled.

Classes	RMU	Ratio	Var(Ratio)
Buck:Doe	3	0.358	0.007
	4	0.370	0.006
	9	0.370	0.003
Fawn:Doe	3	0.328	0.006
	4	0.135	0.001
	9	0.220	0.001

5.5 Discussion

I present a novel strategy to estimate and test for differences between density surfaces of classes within a population. I first implemented a density surface model with camera-trap distance sampling data, which linked variation in local density to environmental predictors across large spatial expanses with widely differing landscape characteristics. Secondly, the framework of hierarchical generalized additive modelling allowed fitting and assessment of various factor-smooth interactions, thereby illuminating differential class-specific responses to external factors within a single statistical model. Thirdly, I extended foundational statistical theory to tractably test for differences in ratios of density, which further elucidated differences in ratios of classes related to landscape characteristics.

I found metrics associated with landscape fragmentation, anthropogenic development, and concealment cover to predict local density. These predictors can be tied to naturally or anthropogenically sourced increases in food availability. Density was largest in areas with moderately high contagion values, which indicates moderately low amounts of landscape fragmentation. Similarly, density responded positively to increased road lengths, which further fragment landscapes (Schonewald-Cox and Buechner 1992) and increase edges that contain greater concentrations of plants that deer forage (Ford et al. 1993). Lastly, density was highest when intermediate amounts of concealment cover were present. Because agriculture dominates areas without concealment cover in the RMUs, the amount of agriculture within buffers is negatively related to concealment cover (Pearson's product-moment correlation = -0.93, $P < 0.001$).

Since deer readily consume calorie-dense crops (Rouleau et al. 2002), intermediate levels of agriculture and concealment cover may optimize food availability from crops and natural forage. Cumulatively, optimal values of these three metrics heighten available food on the landscape which, in turn, support denser populations.

Camera traps are an effective tool for identifying classes within a population. Hierarchical density surface models provide an established method to model class data and examine class-specific relationships between density and environmental predictors with open-source software. When implementing this strategy, I found larger doe and fawn densities to be related to intermediate amounts of concealment, while larger buck densities were linked to areas with small or large amounts of concealment. Class-specific differences in habitat selection of deer has been documented by past research. Specifically, bucks may select areas with lower quality foraging opportunities compared to does and fawns (McCullough 1979). My class-specific density surfaces support this relationship. Because lack of concealment is predominantly associated with agriculture, large amounts of concealment may not provide as much calorie-dense waste grain as areas with intermediate amounts of concealment. Conversely, areas with scarce amounts of concealment may have insufficient natural browse for foraging during daylight.

I extended existing statistical theory to provide a tractable method to compare ratios of density. Using this method, I found statistically higher recruitment rates in areas with more agricultural use, which supported my hypothesis. Although agriculture is one of the greatest causes for biodiversity loss (MEA 2005), many adaptable species, such as deer, are able to consume crops for nutritional gains (Putman and Moore 1998). In these species, supplemental caloric intake from agriculture may support unnaturally high recruitment rates for dense populations, even when natural food resources are limited. Indeed, deer densities in forests were positively related to recruitment ratios in my study, which contradicts density-dependent theories on recruitment (Keyser et al. 2005).

Despite larger buck:doe harvest ratios in RMU 3, I did not document smaller buck:doe ratios in this region. However, yearling bucks often disperse larger distances from natal areas than does (DeYoung 2011), and dispersal distances of bucks are negatively related to forest-cover availability (Long et al. 2005), which is limited in RMU 3. Therefore, larger-magnitude dispersal of young bucks coupled with greater recruitment in RMU 3 may have increased the buck:doe ratio in RMU 3 to values similar to those in the other RMUs.

Extrapolation beyond the range of covariates sampled in the field can lead to dubious inference in ecological studies, as it assumes that the form of the fitted model remains appropriate (Jones et al. 2022). I exemplified this by using Euclidean and Mahalanobis distances to identify cells in my prediction grids that exhibited univariate or combinatorial extrapolation (Mesgaran et al. 2014), and computed densities that included and did not include these cells. Although extrapolation did not appear to affect the point estimates of density in two of the RMUs, the variances of extrapolated densities were considerably higher, and larger spatially explicit CVs usually corresponded to extrapolation (Table D1). Conversely, point estimates of density were affected in RMU 9 by including extrapolated cells. Therefore, I encourage readers to interpret extrapolated and non-extrapolated densities accordingly; although the total non-extrapolated density in RMU 9 was smaller than RMU 4, cells exhibiting extrapolation in RMU 9 could alter this conclusion to an unknown degree. More thorough sampling across the range of environmental predictors of density that I used in my density surface model would be needed to minimize such sampling-based discrepancies and should be a design consideration for future studies that intend to use the methods I describe.

Wildlife research and management benefits from precise density estimates (Williams et al. 2002). The CV typically is used to assess relative precision of estimates (Skalski et al. 2005). In conventional camera-trap distance sampling, the encounter-rate variance is predominantly responsible for variance of density estimates (Howe et al. 2017). Large encounter-rate variances can cause larger CVs of densities from this estimator (>0.25 or even >0.40 ; Bessone et al. 2020; Cappelle et al. 2021). Density surface modelling avoids design-based estimation of the encounter-rate variance by modelling encounter rates at cameras as a function of environmental predictors. This difference in modelling approaches may be partially responsible for the lower CVs of my density estimates. Therefore, I believe future managers using camera traps to sample wildlife will benefit from using spatially explicit methods such as mine, as this will facilitate detection of meaningful changes in density and provide confidence in single estimates.

5.6 References

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CHAPTER 6. FEAR AND CONCEALMENT PREDICT GROUP SIZE OF A COMMON UNGULATE

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6.1 Abstract

Many species exhibit group formation in nearly all ecosystems. Hypotheses on the drivers of group size include perceived predation risk, food resources, and concealment from danger. However, several previous studies have limited inference due to testing group-formation hypotheses individually. I used camera traps, detectability estimates from distance sampling, and hierarchical Bayesian modelling to index group size and test multiple group-formation hypotheses in white-tailed deer (*Odocoileus virginianus*), within Indiana, USA. I found a strong relationship between my index of group size and the following: (1) three-way interaction of spatiotemporal fluxes in natural predation risk and anthropogenic development; and (2) two-way interaction between the habitat type in which a camera was placed (open area or concealment) and the amount of concealment within the larger landscape. Specifically, I documented the largest groups in areas near anthropogenic development, in areas with high predator use intensity, and during times of day when predators were active. Additionally, groups were larger in locations with concealment when the area of concealment within the surrounding landscape was small, and larger in open areas when the amount of concealment within the surrounding landscape was large. My methods can aid future behavioral and ecological studies, as I present a clear and easily replicable strategy that infers group membership from spatiotemporal proximity, corrects for differences in detectability, and enables sampling across large spatial and long temporal scales. I identified that fear of natural predators and anthropogenic disturbance interactively explained variation in group size.

6.2 Introduction

Numerous ecological hypotheses offer explanations for why animals choose, or are constrained, to group together with conspecifics (Krause et al. 2002, Ward and Webster 2016). Many of these hypotheses are tied to structural attributes of the environment or population by which group formation is driven, including: perceived or actual risk of predation (Hill and Lee

1998); anthropogenic disturbance (Averbeck et al. 2012); food availability or food quality (Beauchamp 2007); and availability of concealment (Webb et al. 1996). A common assumption across all group-formation hypotheses is that group size is adaptive and thus increases fitness by virtue of improved individual survival or breeding success (Turner and Pitcher 1986). I consider these hypotheses in detail below, and then assess their support in explaining variation in group size of white-tailed deer (*Odocoileus virginianus*; henceforth deer) – a common ungulate in the Midwestern USA (henceforth Midwest) that often forms loose groups. The fluid nature of deer aggregations allows individuals to leave or join groups at will (Lagory 1986), making deer an ideal model species to test group-formation hypotheses along various environmental gradients over which deer group size may fluctuate.

Predation risk has been linked to group formation via several different hypotheses, each of which predicts that group size increases with predation risk (Bertram 1978, Roberts 1996, Caro 2005). A corollary of these predation-risk hypotheses is that larger groups should be able to feed in riskier areas, which may increase the amount of available food within the landscape (Fortin et al. 2009). Within the Midwest, natural predators of deer are predominantly restricted to coyotes (*Canis latrans*; Kilgo et al. 2012). Although coyotes prey principally on small vertebrates (Randa et al. 2009) and may not influence deer abundance across regional scales (Bragina et al. 2019), several studies have documented their behavioral effects on deer (Lingle and Pellis 2002, Cherry et al. 2015, Higdon et al. 2019). Moreover, predators could be affecting group size at multiple spatial and temporal scales. For instance, intense local use of an area by predators may promote increased group size at local spatial scales, whereas temporal shifts in regional predator activity may promote increased group size during active periods. Given the extent of behavioral responses to predators, fluctuations in deer group size across spatiotemporal gradients of predation risk may exist.

Anthropogenic disturbance constitutes a unique combination of actual and perceived risk (Averbeck et al. 2012) that could influence group size. Actual risk occurs during seasons when and where game species are hunted (Benhaiem et al. 2008) or animal-vehicle collisions occur (Sullivan 2011). Additionally, species may respond to perceived risk from other anthropogenic activity during times or in areas that are not hunted (McBlain et al. 2020). For instance, Ritzel and Gallo (2020) found that increased vigilance was a common mammalian response to urbanization. Deer in the Midwest experience a variety of anthropogenic disturbances, including development

and recreational activity (Brown et al. 2000). Furthermore, responses in ungulate behavior have been documented along urban gradients (Bonnot et al. 2013). Maurer et al. (2022) specifically documented larger groups of Key deer (*Odocoileus virginianus clavium*) in elevated areas near urban development. Therefore, larger deer groups may be expected to occur near areas experiencing more anthropogenic disturbance.

Food resources constitute another potential determinant of group size. If food is limited, individuals may reduce intraspecific competition for food by feeding in different areas than other individuals, resulting in smaller groups (Jarman 1974). Conversely, individuals may be able to feed while maintaining contact with group members in areas with plentiful food (Jarman 1974). In addition to food availability, food quality may influence group size. The forage-maturation hypothesis predicts that herbivores benefit from foraging in groups, as group feeding better maintains vegetation at younger, more nutritious, life stages (Esmaeili et al. 2021). Deer in the Midwest may exhibit such a response, as landscape fragmentation fluctuates between varying degrees of anthropogenic land use. Such landscape fragmentation results in more forest edges with larger amounts of woody food (Ford et al. 1993) that support higher levels of foraging by deer (Williamson and Hirth 1985). Forest edges are especially pertinent in the winter when deer heavily rely on woody vegetation because herbaceous plants and crop residues are limited (Hewitt 2011).

Concealment, what I define as vegetative cover (e.g., forest or wetland) required when inactive or to hide from predators, is an essential resource for many species (Signorell et al. 2010) and may affect group size at different spatial scales. At a larger landscape scale, sparse amounts of concealment may produce larger groups because of spatial confinement (Atwood 2006). Confinement-induced group size could be especially important for crepuscular or nocturnal species that require cover during daytime rest but otherwise feed in surrounding open areas. Such is often the case for species in agriculturally dominated landscapes when crops are consumed at night (Delahay et al. 2006). At finer spatial scales, the immediate presence of concealment may influence group size because risk may increase in open areas (Lagory 1986). Deer in the Midwest are an ideal model species to test these concealment hypotheses because agriculture dominates the landscape, producing a gradient of concealment at both local and landscape spatial scales.

Numerous past studies have tested these hypotheses individually (Kasozi and Montgomery 2020). However, in addition to acting independently, multiple, possibly interacting mechanisms could drive group size. For instance, in areas lacking predators, herbivores may not form large

groups when foraging in open areas outside of concealment. But in areas with abundant stalking or pursuing predators, herbivores may form larger groups in open areas. Considering such interactions may lead to more robust explanations of group formation and improvements in models that predict group size.

I use camera traps to index deer group size across three heterogeneous regions of Indiana, USA. I assessed the effects of: (1) spatiotemporal fluctuations in predation risk from natural predators; (2) anthropogenic disturbance; (3) natural food; and (4) concealment. Specifically, for (1) above, I hypothesized an interactive effect of coyote use intensity (i.e., how much coyotes use a local area) and regional coyote activity levels. I predicted larger groups during times of day when coyotes were active in areas where coyote use intensity was high. However, I predicted no changes in group size where coyote use intensity was low because low use intensity suggests minimal predation risk irrespective of coyote activity levels. For (2) I hypothesized that greater anthropogenic disturbance would cause larger groups due to increased perceived risk. Accordingly, I predicted larger groups as distance to anthropogenic development decreased. For (3) I hypothesized that deer group size would respond to availability and quality of natural winter food. Because forest edges are associated with increased winter food availability that is consumed by deer, I predicted a positive relationship between group size and forest edge density. Similarly, because deer selectively consume woody food (Brown and Doucet 1991), I also predicted larger groups in areas with higher availability of preferred woody twigs. Lastly, for (4) I hypothesized that deer will be forced to congregate within concealment to greater degrees when concealment in the surrounding landscape is limited. Thus, I predicted larger groups in areas with less concealment in the surrounding landscape. Similarly, because of the increased perceived risk associated with open areas, I hypothesized deer would respond with larger groups in open areas locally lacking concealment. In addition to models based on a single hypothesis, I also consider models incorporating combinations of these hypotheses (more below). Additional details on hypotheses and predictions are provided in Table 6.1.

Table 6.1. Model comparisons and estimates of baseline predictors of deer group size based on a priori hypotheses. Aside from natural risk which contained two additive predictors and a single two-way interaction, only a single predictor was fitted in models. LCI and UCI = lower and upper 95% credible interval, respectively; Δ LOO = difference between the approximate leave-one-out cross validation of the best model and competing model; SE = standard error of component-wise differences of the LOO value from the best model; CAL = coyote activity level; CUI = coyote use intensity; OA = open areas (baseline = concealment); PNTD = preferred and neutral twig density; DRB = distance to road or building; FED = forest edge density <750 m; CA = concealment area <8 km.

Hypothesis	Predictor	Prediction	Estimate	LCI	UCI	Δ LOO	SE
Natural risk	CAL	+	-0.164	-0.198	-0.131	0.0	0.0
	CUI	+	0.038	-0.001	0.081		
	CUI * CAL	+	0.031	0.006	0.056		
Concealment risk	OA	+	-0.245	-0.350	-0.139	-134.2	12.0
Food	PNTD	+	-0.001	-0.069	0.065	-193.3	11.6
Anthropogenic risk	DRB	-	0.061	0.012	0.111	-196.0	11.6
Food	FED	+	0.064	0.008	0.124	-197.9	11.8
Confinement	CA	-	-0.130	-0.252	0.002	-205.1	11.7

6.3 Methods

6.3.1 Study Areas

I sampled in deer Regional Management Units 3, 4, and 9 in Indiana, USA. Regional Management Units were delineated by known mortality rates of deer within Indiana counties so that counties with nearer spatial proximity and similar deer mortality rates were clustered into a single unit. Thus, mortality rates of deer are more similar within Regional Management Units than between Regional Management Units (Swihart et al. 2020). The Indiana Department of Natural Resources uses these Regional Management Units when setting harvest limits on deer for human hunters.

Regional Management Unit 3 spans west-central Indiana and is predominantly row-crop agriculture (79%) with fragmented concealment (defined as forest or wetland; 11%) and minimal development (6%). Regional Management Unit 4 covers southcentral Indiana and contains much more concealment (56%), a mixture of row-crop agriculture (19%) and grassland (16%), and similar amounts of development (6%). Lastly, Regional Management Unit 9 is in northeast Indiana, and is mostly row-crop agriculture (56%) with a mixture of wetland (13%), grassland (11%), forest (8%), and development (9%).

6.3.2 Data Collection

Sampling of Regional Management Units was completed inside randomly chosen 41.44-km² cells from the deer harvest reporting grid used by the Indiana Department of Natural Resources to collect spatially explicit harvest data of deer. I specifically deployed cameras inside 10.36-km² sampling areas (henceforth sampling areas) nested within larger 41.44-km² cells (Figure 6.1). I placed 10.36-km² sampling areas within randomly selected 41.44-km² cells to ensure that (i) habitat composition was representative of the larger 41.44-km² cell, and (ii) access to private property across the sampling areas was as homogeneously distributed as possible (~95% of Indiana is privately owned).

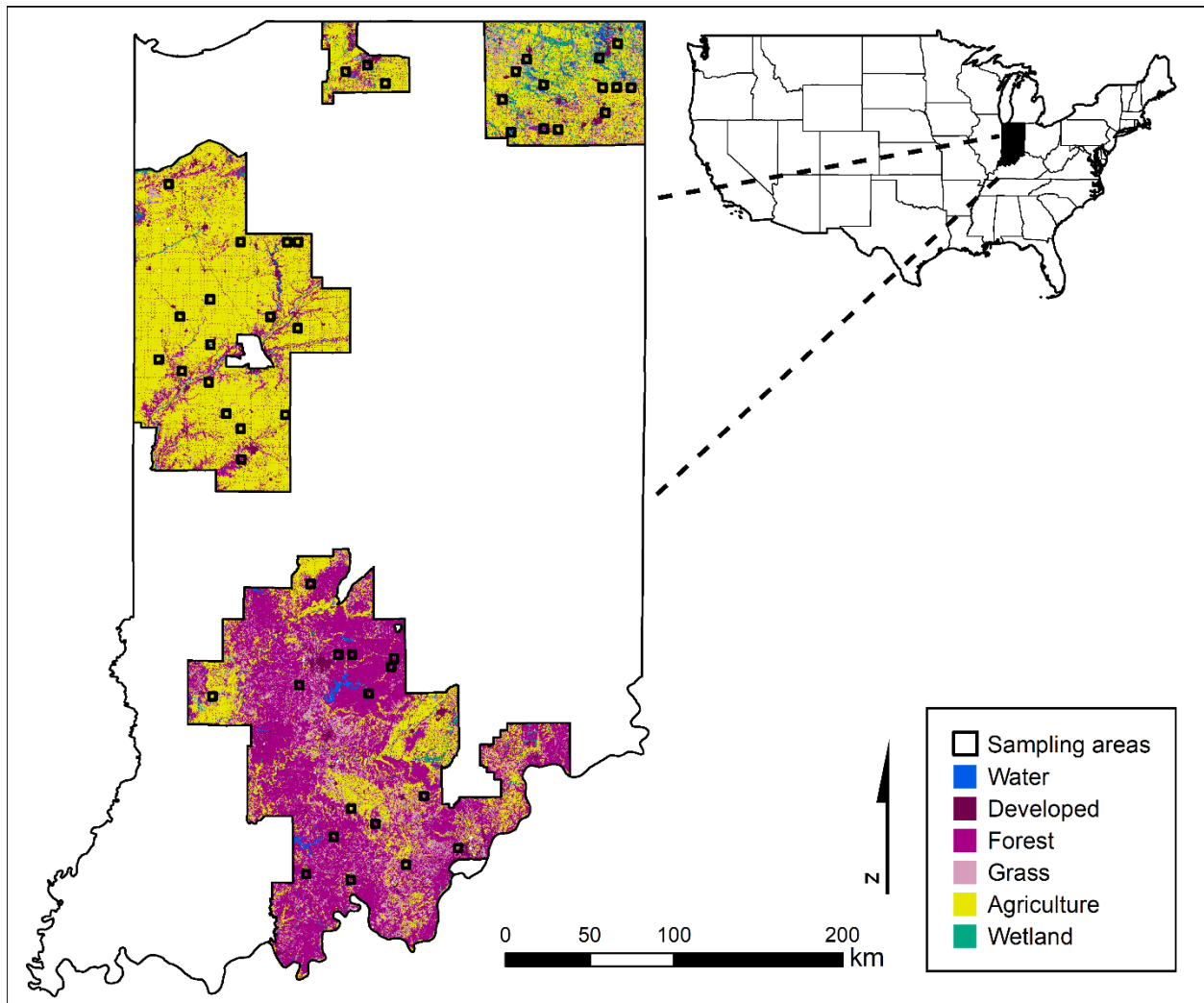


Figure 6.1. Landcover types in each Deer Regional Management Units (RMU) of Indiana, USA, within which I sampled white-tailed deer. I sampled within 16 different 10.36-km² sampling areas in each RMU during 2019, 2020, and 2021.

I deployed and collected data with Browning Strike Force HD motion-triggered camera traps within a 2-week sampling window from 12–25 February 2019, 9–22 March 2020, and 25 February–10 March 2021. Sampling windows differed due to logistical issues. Cameras were positioned randomly using ArcMap 10.7, contingent upon being >200 m from the nearest-neighboring camera. I affixed cameras to trees at 1-m height, and oriented cameras north to avoid glare at sunrise and sunset. If no trees were present, I affixed cameras to metal posts hammered into the ground at the same height and orientation. Locations were minimally adjusted (<20 m) in rare instances to ensure sampling suitability (e.g., extremely steep topography, flooding, fallen tree). When triggered, cameras captured three photos separated by 0.3 seconds, with photo bursts separated by ≥ 1 sec.

I recorded the time of initial detection when individual deer entered the field-of-view of the camera. I then calculated the elapsed time between consecutive deer entering the camera's field-of-view. I examined empirical cumulative distribution functions of the times between initial detections of consecutive deer in each region in open areas and concealment. After removing differences >50 min, I found that, regardless of concealment or region, empirical cumulative distribution functions started a long flat tail at 10 min. I thus decided that elapsed times >10 min would constitute a new group (Appendix E: Group Membership). After defining groups, I indexed group size by summing the total number of putative individuals detected >10 min of the previously detected deer. I used these counts as indexes because: (1) deer were unmarked and thus double counting was possible; and (2) some group members may not pass in front of, or be detected by, the camera trap.

6.3.3 Baseline Predictors of Group Size

6.3.2.1 Natural Predation

I indexed coyote use intensity (*UI*) for each camera by $UI = \frac{\sum_{i=1}^I d_i}{T}$ where d_i = the number of coyotes present in photo i summed across all I photos, and T = the total time the camera was sampling (sec). I estimated the regional activity level of coyotes when each deer group was detected by double anchoring the initial detection times of coyotes with the average sunset and sunrise times across the spatiotemporal extent of my sampling (Vazquez et al. 2019). I fit a circular

kernel density to these double-anchored times (Rowcliffe et al. 2014) with the “activity” package in R (Rowcliffe 2021, R Core Team 2022), which was used to determine the activity level of coyotes when I detected deer groups. I estimated coyote activity across all cameras because of data paucities on most cameras.

6.3.2.2 Anthropogenic Disturbance

I calculated the distance (m) to nearest road or building (i.e., whichever was nearest) as an index of anthropogenic disturbance using the 2015 Indiana primary and secondary roads shapefile (US Census Bureau, Department of Commerce) and US building footprints shapefile from Microsoft (<https://github.com/Microsoft/USBuildingFootprints>) in R.

6.3.2.3 Natural Food Availability

I assessed the effects of natural food availability and quality on group size with the density of forest edges in the immediate area surrounding the camera, and density of twigs that were preferentially and neutrally consumed. I used a buffer with a radius of 750 m to define the immediate surrounding area because 750 m approximates the radius of a circular doe home range after the hunting season in agricultural areas (Nixon et al. 1991, Vercauteren and Hygnstrom 1998). The density of forest edge was calculated in R with the National Land Cover Database 2019 land cover raster file (Dewitz 2021).

To estimate total density of woody twigs that were preferentially and neutrally consumed within forest patches, I sampled five 1-m² quadrats placed every 10 m along 50-m transects. Transect were randomly placed and oriented using ArcMap 10.7. The number of transects sampled per forest patch was determined by $A_i/2NT_i < NT_i$, where NT_i = the number of transects in forest patch i , and A_i = the area (ha) of forest patch i . I counted all living woody twigs in 3-dimensional space 20-180 cm above the quadrat (Frerker et al. 2013), and estimated twig density (D_i) by $D_i = t_i/n_i$, where t_i = the total number of twigs counted in forest patch i , and n_i = the total number of quadrats surveyed within forest patch i . I used a Pearson’s chi-square test for count data (Ebbert 2019) to classify twig species as significantly (consumed at a higher rate than expected; $\alpha \leq 0.05$) or neutrally (consumed at a similar rate than expected; $\alpha > 0.05$) preferred for consumption. I used this preference ranking to index nutritional quality, as deer prefer higher quality vegetation (Bee

et al. 2009). I assigned cameras placed in forest patches the food indices associated with the patch the camera was deployed in. For cameras not deployed in forest patches, I assigned the average indices from the 10.36-km² sampling area in which the camera was deployed.

6.3.2.4 Availability and Presence of Concealment

I calculated the area of forest and wetland <8 km from the camera using the National Land Cover Database 2019 land cover raster in R as a measure of availability of concealment in the surrounding landscape. I chose a buffer of 8 km to define the surrounding landscape because this approximates the average dispersal distance of young bucks (DeYoung 2011). Secondly, concealment at the position of cameras was classified at deployment as present (forest or wetland) or absent (grassland or agriculture). Other predictors of group size were tested but deemed less informative or to have multicollinearity issues with better predictors; they are presented in Appendix E.

6.3.4 Data Analysis

I modeled my index of group size in a Bayesian hierarchical model with a negative binomial response using the “brms” package (Bürkner 2017) in R, which utilizes Hamiltonian Monte Carlo and NUTS samplers (Hoffman and Gelman 2014) implemented in Stan (Stan Development Team 2022). To account for spatial autocorrelation and repeated observations on the same camera, I included random intercepts for camera identity nested within the 10.36-km² sampling area nested within the Regional Management Unit. I left-truncated the negative binomial distribution at 1 because a group size of 0 is impossible (Bürkner 2017).

Detectability of deer may change depending on vegetative obstruction in front of the camera trap. Therefore, I used distance-sampling detection functions (Howe et al. 2017) fit to distances collected from deer in the same photographs captured for this project (unpublished manuscript, Z.J. Delisle, D.L. Miller, R.K. Swihart). In so doing, I found that unique detection functions fit to open areas and concealment were most appropriate.

To correct my index of group size for differing detection probabilities within open areas and concealment, I used corresponding detection probabilities of deer in both areas (open areas = 0.40; concealment = 0.33) as offsets in my model. I did not propagate uncertainty associated with

the detection functions into my regression coefficients because uncertainty in detection probability was minimal (coefficient of variation: open areas = 0.007, concealment = 0.007).

I standardized (i.e., subtracted the mean and divided by the standard deviation) all continuous predictors. I first fit baseline models with either single predictors or the interaction between coyote activity level and use intensity, to test the predictive ability of each covariate (Table 6.1). I ran 3 Markov chains for a total of 4000 iterations per chain. The first 1500 iterations per chain were discarded. I set my initial values to 0. Gaussian priors were applied for all regression coefficients (mean = 0, standard deviation = 0.05) and nested random effects (mean = 0, standard deviation = 4).

6.3.5 Complex Models

After fitting my index of group size in the baseline models, I proceeded to construct three more complex hypotheses by fitting interactive combinations of strong and marginal predictors from the baseline models (Table 6.2). A strong relationship was defined as one in which the 95% credible interval did not overlap 0, whereas a marginal relationship was defined as when only a single 95% CI overlapped 0 by <0.01 .

Table 6.2. Model comparisons and estimates of interactive predictors of deer group size based on complex a priori hypotheses derived from strong or marginal baseline predictors of group size. LCI and UCI = lower and upper 95% credible interval, respectively; Δ LOO = difference between the approximate leave-one-out cross validation of the best model and competing model; SE = standard error of component-wise differences of the LOO value from the best model; CAL = coyote activity level; CUI = coyote use intensity; DRB = distance to road or building; OA = open areas (baseline = concealment); CA = concealment area <8 km.

Hypothesis	Predictor	Estimate	LCI	UCI	Δ LOO	SE
Anthropogenic risk * natural risk	CAL	-0.156	-0.190	-0.122	0.0	0.0
	CUI	0.046	-0.016	0.111		
	DRB	0.023	-0.025	0.071		
	CUI * CAL	0.078	0.029	0.128		
	CAL * DRB	-0.039	-0.073	-0.004		
	CUI * DRB	-0.009	-0.061	0.043		
	CUI * CAL * DRB	-0.041	-0.080	-0.003		
Confinement * concealment risk	OA	-0.219	-0.327	-0.106	-149.9	13.0
	CA	-0.173	-0.297	-0.045		
	OA * CA	0.154	0.031	0.279		
Anthropogenic risk * concealment risk	OA	-0.245	-0.358	-0.136	-151.6	12.5
	DRB	0.055	0.001	0.108		
	OA * DRB	-0.050	-0.169	0.073		

Firstly, I hypothesized that group sizes would differ in open areas and concealment when under differing amounts of anthropogenic risk. I predicted that groups would be larger in open areas when distance to road or building was small because of more direct exposure to anthropogenic activity in open areas. Secondly, I hypothesized that open areas and concealment would yield differing group sizes in areas with varying amounts of concealment within the landscape surrounding each camera. I predicted larger groups in concealment than in open areas when small amounts of concealment are present in the surrounding landscape, because deer will be confined to small forest patches when needing concealment (e.g., when bedding or not feeding on agriculture). I predicted larger groups in open areas when there are large amounts of concealment in the surrounding landscape because deer will congregate in limited open areas to consume waste grain. Lastly, I hypothesized that group size would interactively respond to risk associated with distance to the nearest building or road, coyote use intensity, and coyote activity level. Specifically, I predicted the most positive relationship between group size and coyote activity level to be when use intensity was high and distance to road was small (Table 6.2).

6.3.6 Final Models

I acknowledge that more complex combinations of factors than hypothesized above could affect group size. Accordingly, after evaluating the strength of baseline and complex models above, I fit all additive combinations of strong or marginal complex interactions and strong or marginal baseline predictors that were not part of strong or marginal complex interactions. I used approximate leave-one-out cross validation (LOO) for model selection and only report models within 2SE of component-wise differences of the LOO value from the best model (Vehtari et al. 2017). I first compared LOO values of baseline models only. Secondly, I evaluated LOO values of the models containing complex interactions. Lastly, I compared the LOO values from additive combinations of strong or marginal predictors along with baseline and complex interactive models (i.e., all models).

6.4 Results

I deployed cameras at 1,018 unique locations and detected deer entering the field-of-view of my camera traps 24,352 times at 831 locations resulting in a total of 8,794 indexed deer groups

(Table 6.3). I did not detect any deer at 187 cameras. The average index of group size was 2.76 deer (SE = 0.03) before correcting for detectability (Appendix E). When only considering baseline models, I found the model containing the interaction between coyote activity level and coyote use intensity to be the only competing LOO-best model (ΔLOO over next best model = -134.2, SE = 12.0; Table 6.1). Subsequently, when only considering the three complex models containing two- or three-way interactions, I found the model containing the three-way interaction between distance to nearest building or road, coyote use intensity, and coyote activity level to be the only competing LOO-best model (ΔLOO over next best model = -149.9, SE = 13.0; Table 6.2).

Table 6.3. Total number of cameras deployed, unique detections of white-tailed deer, and indexed groups of deer in Deer Regional Management Units (RMU) 3, 4, and 9 of Indiana, USA, within concealment (forest and wetland) or open areas (grassland and agricultural field) during 2019, 2020, and 2021.

RMU	Cover	Cameras	Detections	Groups
3	Concealment	181	4561	1680
3	Open areas	146	1159	485
4	Concealment	249	4801	2077
4	Open areas	58	1236	482
9	Concealment	267	10029	3268
9	Open areas	117	2566	802

When further considering all baseline models in Table 6.1, complex models in Table 6.2, and final models containing additive combinations of strong or marginal complex interactions or baseline predictors, I found that the LOO-best model contained: (1) the two-way interaction between the amount of concealment within the larger surrounding area and occurrence of local concealment; and (2) the three-way interaction between distance to nearest building or road, coyote use intensity, and coyote activity level (Table 6.4). The only other possible best model (i.e., $<2\text{SE}$ of the best model) was the model containing the two interactions in the LOO-best model, along with forest edge density in the immediate area of the camera (ΔLOO = -1.9, SE = 1.4). However, the additive predictor, forest edge density, in the second-best model had neither strong nor marginal support (estimate = 0.044, 95% credible intervals = -0.013 to 0.101). Plots of posterior distributions, posterior predictive checks, and trace plots are provided in Appendix E.

Table 6.4. Estimates of all predictors contained within the final LOO-best model for regressing group size of white-tailed deer. LCI and UCI = lower and upper 95% credible interval, respectively; CA = concealment area <8 km; OA = open areas (baseline = concealment); CAL = coyote activity level; CUI = coyote use intensity; DRB = distance to road or building.

Hypothesis	Predictor	Estimate	LCI	UCI
Confinement * concealment risk + anthropogenic risk * natural risk	CA	-0.173	-0.293	-0.048
	OA	-0.135	-0.243	-0.025
	CAL	-0.147	-0.181	-0.112
	CUI	0.053	-0.010	0.116
	DRB	0.018	-0.031	0.067
	CA * OA	0.176	0.055	0.298
	CAL * CUI	0.083	0.034	0.132
	CAL * DRB	-0.041	-0.076	-0.007
	CUI * DRB	-0.014	-0.066	0.037
	CAL * CUI * DRB	-0.044	-0.083	-0.006

Based on the final LOO-best model, the index of group size was larger in open areas when the amount of concealment in the surrounding landscape was largest, and larger in concealment when the amount of concealment in the surrounding landscape was smallest (Figure 6.2). At large distances to the nearest road or building, group size decreased as coyote activity level increased, regardless of coyote use intensity (Figure 6.3). However, when distance to the nearest road or building was small, group size was the most positively related to coyote activity level when coyote use intensity was high.

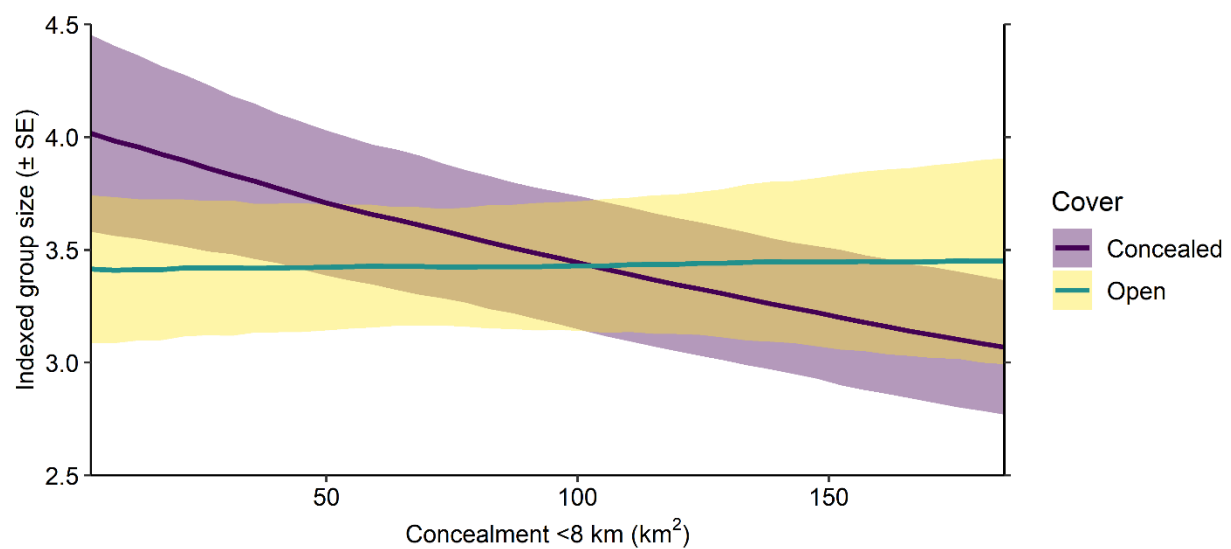


Figure 6.2. Conditional effects plot of the relationship between an index of white-tailed deer group size ($\pm$ SE) and a two-way interaction between the cover type in which the camera was placed (open area or concealment) and the amount of concealment (km²) within 8 km of the camera in Indiana, USA.

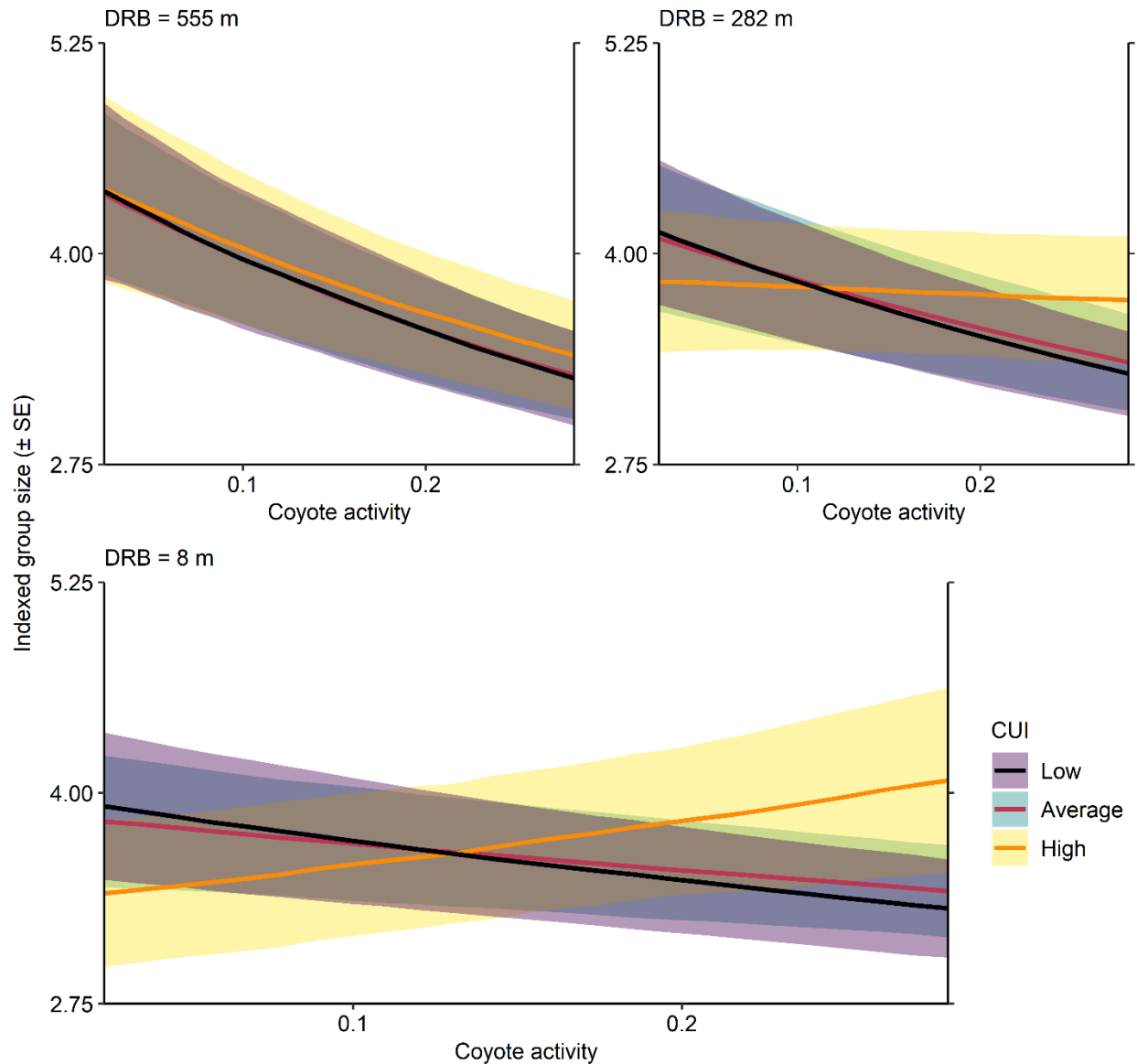


Figure 6.3. Conditional effects plot of the relationship between my index of white-tailed deer group size ($\pm$ SE) and the three-way interaction between coyote use intensity (CUI; total detections/total time the camera sampled), coyote activity level, and distance to the nearest road or building (DRB; m) in Indiana, USA. I depict three plots with different distances to the nearest road or building: DRB = 555 m (1.5 standard deviations more than average distance); DRB = 282 m (average distance); and DRB = 8 m (1.5 standard deviations less than average distance). Within each plot, three levels of CUI are presented: (Low) CUI = 0 (minimum observed CUI); (Average) CUI = 26,104; and (High) CUI = 159,555 (1.5 standard deviations more than average CUI).

6.5 Discussion

My results highlight a two-pronged landscape of fear (Brown et al. 1999) in which anthropogenic development and spatiotemporal use intensity of natural predators interactively influenced group size. Deer were annually harvested by humans in the months immediately preceding each of my field seasons, likely enhancing fear responses to anthropogenic sources. In addition, coyotes, which emerged as the dominant carnivore in Indiana only after extirpation of larger carnivores (Lyon 1934), are well adapted for urbanization and can persist in urban areas near roads and buildings (Jones et al. 2016; Appendix E). Interactively, anthropogenic development and spatiotemporal pulses of coyote use intensity likely heightened fear of multiple mortality sources to which deer responded by forming larger groups.

Findings from my study suggest that landscape availability of concealment and open areas, not fear associated with open areas per se, better explains concealment-related predictors of group size in my study. I found groups to be larger in concealment and smaller in open areas, which contradicts past research and my baseline predictions (Lagory 1986). Instead, my analysis revealed a more complex interaction between local occurrence of concealment and the amount of concealment within the surrounding landscape. Specifically, groups were largest at camera stations in concealment when landscape-level concealment was limited, and largest at cameras in open areas when landscape-level concealment was plentiful.

In my study area, perceived mortality risks and context-dependent availability of concealment appear to have outweighed foraging considerations as predictors of group size in deer. I found minimal support for group size responding to woody food availability or quality. The latter result could be due to the lower relative nutritional quality of natural woody foods (Hewitt 2011). Regarding availability, winter food resources in my study area may not be limited; forest edges and associated woody browse were prevalent. Decorative ornamental plants surrounding human residences were common and often contain highly palatable plants (Swihart et al. 1995). Waste grain left behind in agricultural fields after harvest also represents a plentiful wildlife food source (Warner et al. 1989). These results are contingent upon the following: (1) my study population was hunted just months before my sampling; and (2) timing of my sampling during winter resulted in no available natural herbaceous food.

Camera traps are excellent tools to index group size. In a recent review, 91% of articles studying group size defined groups based on direct observations of humans (Kasozi and

Montgomery 2020). Direct human observations may suffer from small sample sizes or few spatial replicates due to logistical constraints, and bias from extreme differences in detectability in concealment vs open areas due to camouflage of the target species and direct lines-of-sight. Conversely, camera traps enable indexing of group sizes across large spatiotemporal expanses to test complex hypotheses that otherwise would be logistically challenging or impossible to test with human observers. Additionally, collection of data across time facilitates various spatiotemporal metrics related to other species that may influence group formation of the target species. Past researchers indexed group size with camera traps but used the total number of individuals within a single photo as the index (Lashley et al. 2014, Cherry et al. 2015, Maurer et al. 2022). I extended these studies and developed a clear and easily replicable method that uses detection times to infer group membership based on temporal proximity of subsequently detected individuals. Although there are many ways in which scientists have defined group membership (Kasozi and Montgomery 2020), in the context of camera traps, my method facilitates a broader definition of group membership, which may be useful for species whose spatial proximity often exceeds the limits of the field-of-view of camera traps.

I used deer as my model species to test several hypotheses related to group formation, but my methods can be used in other systems and species. However, my methods can also be used to test other group formation hypotheses. During prolonged cold weather, increasing group size and huddling together can reduce the cost of thermogenesis (Gilbert et al. 2010). Many camera traps are equipped with temperature gauges; thus, spatiotemporally explicit thermal data can be collected concurrently with group size indices to test group-formation hypotheses related to thermoregulation in colder climates. Additionally, groups can arise due to kinship or mating (Giraldeau and Caraco 1993). Camera traps deployed at mating or nest sites may be useful to test group-formation hypotheses related to these factors and could likewise benefit from application of the methods described in this paper.

I have shown that many variables representing multiple hypotheses may drive the group size of deer under specific conditions. Such complex responses not only increase my understanding of this behavioral phenomenon, but may call for considerations in other professions and ecological fields. Examinations of trait-mediated trophic cascades induced by ungulate responses to predation risk have been predominantly restricted to spatial avoidance of predators and decreases in feeding caused by increases in time spent vigilant (Chitwood et al. 2022). Further examining how

responses in the group size of ungulates affects plant communities, and potentially other vertebrate or invertebrate species, might illuminate other top-down relationships that better explain the full ecological ramifications of grouping. Similarly, deer-vehicle collisions represent a major economic cost and sometimes fatal hazard for humans (Conover 1997). If group size of deer correlates with rates of deer-vehicle collisions, then city planners may consider balancing the relationship between development, risk of natural predation, and fragmentation of concealment when planning new urban or suburban developments to reduce deer-vehicle collisions.

6.6 References

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CHAPTER 7. SYNTHESIS

Throughout my dissertation, I develop strategies to advance common distance- or plot-sampling approaches used to model the densities of animal populations and choose between several density estimators; and furthered the understanding of the population and group-size ecology of white-tailed deer. In Chapter 2, when estimating density with pellet sampling, I found strong differences between estimates using the leaf-off method and other modelling approaches, and documented that interobserver discrepancies when scoring pellet groups added considerable variation to density estimates. In Chapter 3, I illustrated the importance of accounting for several types of error when estimating density via aerial sampling by recording infrared and color video beneath an aircraft, and using a simple double-observer approach, I found evidence of false negatives associated with the viewer of infrared video. In Chapter 4, I extended cost-effectiveness analysis to simultaneously integrate precision and per-area cost of sampling when selecting between density estimators. My extension facilitated weighting of factors that may vary with the objectives and constraints of managers, and annualization of capital costs across several applications of use. Using my new tool, I found that cost effectiveness of aerial sampling with color and infrared sensors is the most cost-effective method for monitoring deer populations in Indiana.

In Chapter 5, I developed a density surface model that utilized camera-trap distance sampling data within a hierarchical generalized additive model to estimate density surfaces of demographic classes of deer, and found landscape fragmentation, wetlands, and anthropogenic development to be strong predictors of deer density. I then extended simple statistical theory to test for differences in two ratios of density, documented class-specific responses of density to availability of concealment cover, and found strong evidence that increased recruitment of young was tied to increased resource availability from anthropogenic agricultural land use. Lastly, in Chapter 6, I used camera traps, detectability estimates from distance sampling, and hierarchical Bayesian modelling to index group size and test multiple group-formation hypotheses in deer. I documented the largest groups in areas near anthropogenic development, in areas with high predator use intensity, and during times of day when predators were active. I found larger groups in concealment when the availability of concealment within the surrounding landscape was small,

and larger groups in open areas when the availability of concealment within the surrounding landscape was large.

7.1 Future research

There are many opportunities for future researchers to build off my work and answer future questions that advance our understanding of density estimation and group-size ecology. For pellet sampling, I focused Chapter 2 on estimation of pellet-group persistence. Defecation rate is equally important when estimating density from pellet counts. However, we need to improve our ability to estimate defecation rates to better the accuracy of pellet-based density estimators, as many past researchers simply implied defecation rates retrieved from the literature (including myself). One potentially suitable method might be the use of camera traps. Monitoring, with certainty, an area with camera traps would facilitate calculation of the amount of time deer spent in the monitored area. Pellet groups could then be counted inside the monitored area, and a defecation rate for that area would be easily obtainable. Furthermore, researchers could monitor multiple areas and thus estimate measures of variance for the defecation rate. Another approach would be to attach cameras to the rumps of deer and simply count the number of defecations. Variance of the defecation rate could then be estimated across individuals.

Past researchers have consistently improved aerial sampling since its adoption, both technologically and statistically, but further improvements can still be made. Feasible procedures to estimate availability errors, especially with more mobile study species, are lacking. Similarly, future research can examine the effects of altitude and ground condition on detection probability by repeatedly sampling the same flight path. Management would also benefit from an examination testing the effects of flight speed on the efficacy of red-green-blue confirmation, concordance between independent observers, and detection probability. Ramifications of flight speed are specifically useful because faster planes would enable more time- and cost-efficient sampling.

In several of my chapters, I found substantial evidence that deer became attracted to camera traps; specifically, camera traps placed in non-forested areas. Because of this, when estimating density in non-forested areas, I utilized practical methods that I suspect would reduce bias caused by attraction towards camera traps. However, future research would benefit from testing these, and potentially other, methods that aim to reduce bias in density estimates caused by reactive behavior

towards camera traps. Therefore, future research should conduct simulations where true density is known, and test methods for reducing bias.

My results revealed evidence for complex and interactive relationships between group size of deer and environmental predictors across large landscapes. Future research may build off these findings and examine how changes in group sizes effect other species. For instance, larger group sizes may impact vegetative communities that deer consume. Such examinations would yield a more complete understanding of trait-mediated trophic cascades caused by grouping.

7.2 Management considerations

Going forward, I encourage the Indiana Department of Natural Resources to think carefully about the goals of deer monitoring in Indiana. Specifically, I stress the consideration of feasibility (i.e., whether a task is possible), which is discussed in Chapter 4. For instance, if the Indiana Department of Natural Resources desires buck:doe or fawn:doe ratios of density, the only feasible method (of those that I considered) to estimate these density ratios is camera sampling, which is the least cost-effective of the methods I compared in Chapter 4. Similarly, if habitat-specific estimates are desired by the Indiana Department of Natural Resources, then aerial sampling is not strictly feasible. Habitat-specific density estimates will be dependent on the time-of-day when flights are conducted, as deer are more likely to occupy open areas at crepuscular or nocturnal hours. Considerations such as these should be evaluated while also contemplating information that may aid deer management in the future (e.g., fawn:doe ratios may not be helpful now, but will these ratios be needed five years from now?).

Irrespective of the chosen monitoring method for deer management in Indiana, I encourage collection of population data that is both environmentally and spatially representative of the larger regional area over which density is being inferred. In Chapter 5, I showed that deer density can be spatially predicted by several different environmental covariates. The study design of future monitoring should consider sampling the full range of each environmental predictor of deer density contained within the larger region over which inference of density is desired. However, because deer density is a random variable, spatial changes in density that cannot be explained by previous environmental predictors are likely to occur. Therefore, data should also be spatially representative of the larger region over which inference of density is desired.

APPENDIX A. DENSITY FROM PELLET GROUPS: COMPARING METHODS FOR ESTIMATING DUNG PERSISTENCE TIME

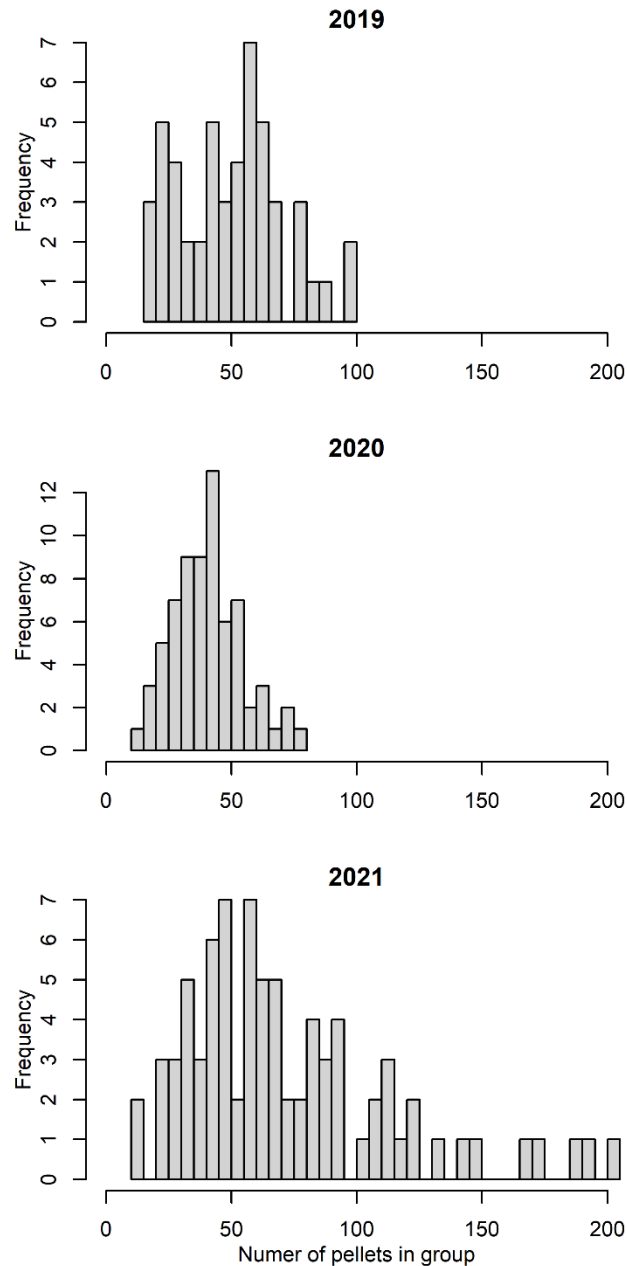


Figure A1. Distributions of the number of pellets in each pellet group monitored to estimate persistence rate. Unique distributions are presented for each year of monitoring. The 2020 distribution is shown after I randomly subsampled pellet groups using weighted probabilities derived from the other 2 monitoring seasons.

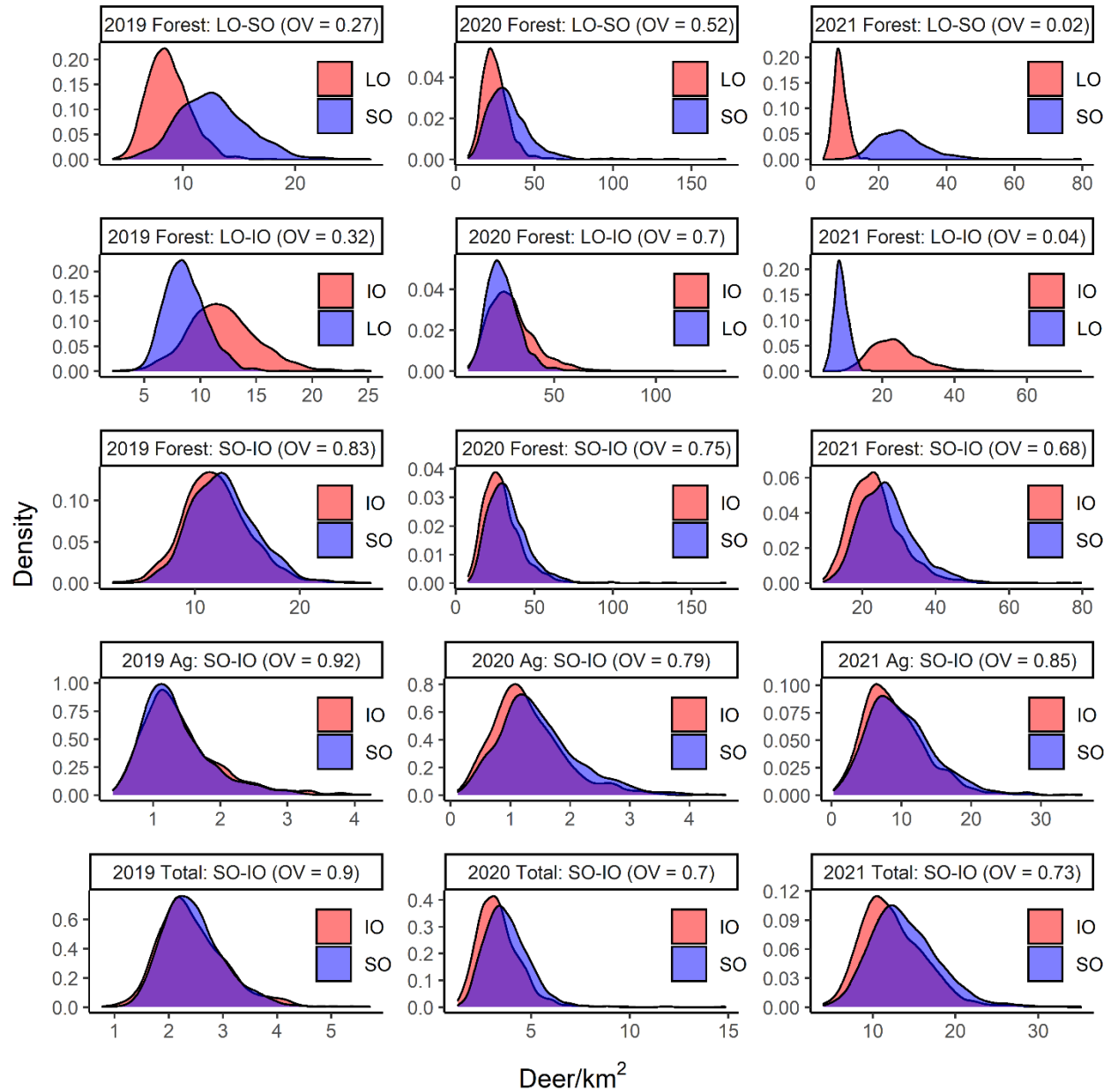


Figure A2. Distributions of bootstrapped density estimates of white-tailed deer (deer/km²) using the leaf-off (LO), single-observer (SO), and inter-observer (IO) methods for estimating the persistence of pellet groups. Comparisons and corresponding overlap (OV) are designated in the title of each panel (Pastore and Calcagni 2019).

Table A1. Comparisons of density estimates (white tailed deer/km²) using the leaf-off (LO), single-observer (SO), and Inter-observer (IO) methods for estimating persistence of pellet groups. Comparisons are within respective habitats and years of sampling in deer management unit 3 of west-central Indiana, USA.

Comparison ^a	Habitat	Year	Observed			Overlap index, $\hat{\eta}^e$
			difference ^b	Bias ^c	Consistency ^d	
LO - SO	Forest	2019	-2.423	-1.591	0.988	0.267
LO - SO	Forest	2020	-4.141	-4.184	0.934	0.521
LO - SO	Forest	2021	-9.646	-8.536	1.000	0.023
LO - IO	Forest	2019	-1.924	-1.404	0.949	0.325
LO - IO	Forest	2020	-1.882	-2.570	0.747	0.697
LO - IO	Forest	2021	-9.173	-5.828	1.000	0.044
SO - IO	Forest	2019	0.499	0.187	0.697	0.830
SO - IO	Forest	2020	2.259	1.614	0.848	0.750
SO - IO	Forest	2021	0.473	2.708	0.859	0.679
SO - IO	Ag	2019	0.021	-0.076	0.455	0.917
SO - IO	Ag	2020	0.125	0.049	0.905	0.793
SO - IO	Ag	2021	0.373	0.582	0.946	0.850
SO - IO	Total	2019	0.067	-0.050	0.560	0.901
SO - IO	Total	2020	0.281	0.163	0.898	0.705
SO - IO	Total	2021	0.396	1.070	0.942	0.730

^aPairs of methods being compared, shown in the formula used to calculate Observed difference and bias.

^bThe observed difference between the point estimates of density from the two methods being compared.

^cThe bias of the observed difference between the density estimates from two methods calculated by $\hat{\theta}_B - \hat{\theta}$, where $\hat{\theta}_B$ = mean bootstrapped difference between the two paired densities and $\hat{\theta}$ = the observed difference between the point estimates of density from the two methods being compared.

^dThe fraction of instances across 999 paired bootstrapped estimates where $\hat{D}_{t_1} > \hat{D}_{t_2}$ and $\hat{D}_{t_1}$ is also the larger density according to the observed differences between $\hat{D}_{t_1}$ and $\hat{D}_{t_2}$.

^eThe overlap between distributions of the 999 bootstrapped densities from the two methods being compared (Pastore and Calcagni 2019).

Effort Stratification

Agricultural fields comprised much of the area in my study sites. White-tailed deer spend less time in agricultural fields compared to areas of natural cover (Beier and McCullough 1990, Nixon et al. 1991). Thus, if defecation rate of deer is independent of local cover type, average deer pellet group density and corresponding encounter rate variance is likely lower in agricultural fields than in natural cover types. Because of this, I stratified transects into two groups, natural cover and agricultural fields, to account for likely disparities in pellet group density. Specifically, I used studies in neighboring states to derive estimates of selection ratios (Manly et al. 2007) for natural cover (2) and agricultural fields ($\frac{1}{4}$; Beier and McCullough 1990, Nixon et al. 1991). I combined these estimates of relative use with predicted pellet-group density derived from data in neighboring states (Urbanek et al. 2012, Anderson et al. 2013). I approximated deer densities in my study areas using deer mortality data collected from 2012-2017 (Swihart et al. 2020) and assumed a 25% annual mortality rate by March. For stratification, I used the proportion of each cover type for the county within which each study area was located to bracket the optimal transect ratio by taking the average of equations 7.26 ($LvL = Av\sqrt{Dv} \sum Av\sqrt{Dv}$) and 7.37 ($\pi j = AjDj \sum AvDv$) in Buckland et al. (2001) at a desired CV of 0.15.

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APPENDIX B. IMPERFECT DETECTION AND WILDLIFE DENSITY ESTIMATION USING AERIAL SURVEYS WITH INFRARED AND VISIBLE SENSORS

Distance Sampling Analysis

Methods

I right truncated distances >53 m and >38 m at 450 m and 300 m altitude, respectively (Buckland et al. 2001), for the following reasons. I observed that distances >53 m and >38 m recorded at 450 m and 300 m altitude, respectively, experienced variable coverage due to turbulence and cross winds. Specifically, when the plane shook during turbulence the thermographer also shook. This caused the thermographer to capture potential infrared detections beyond these distance thresholds, albeit for only a very brief period (< 0.1 sec). In addition to turbulence, small aircraft such as the one I used will not align parallel to the transect line when consistent winds are not parallel to the transect line. Such situations with wind caused the thermographer's field-of-view to not squarely align with the transect. This further limited the time that infrared heat signatures associated with large distances remained in the thermographer's field-of-view. Because of these reasons, viewers of the infrared video experienced difficulties attempting to consistently detect infrared heat signatures associated with these greater distances.

After right truncating distances, I estimated detection functions, which included the half-normal key function with no adjustments and with 1 and 2 cosine, simple polynomial, and Hermite polynomial adjustments; the hazard-rate key function with no adjustments and with 1 and 2 simple polynomial adjustments; and the uniform key function with no adjustments and with 1 and 2 cosine adjustments (Buckland et al. 2001). I fit these candidate detection functions separately to the data collected at each altitude, by each observer, and two different combinations of detection history types that included: (1) lenient and stringent infrared detections, and (2) stringent infrared detections. I used Program Distance (Version 7.2) to estimate detection functions (Thomas et al. 2010).

Results

See Table B1 and Figure B1 for results. Visual plots and AIC both suggested that the uniform key function with no adjustments terms was the most appropriate detection function for all scenarios.

Table B1. AIC-based model selection results for fit detection functions. The top four AIC-best detections functions are shown for each altitude (m) , observer, and type of infrared detections used (lenient = Len, stringent = Strin).

Altitude (m)	Observer	Type ^a	Key function	Adjustment	Terms ^b	ΔAIC^c
450	1	Len + Strin	Uniform	NA	NA	0
			Uniform	Cosine	1	2
			Half normal	NA	NA	2
			Hazard rate	NA	NA	3.61
		Strin	Uniform	NA	NA	0
			Half normal	NA	NA	1.80
			Uniform	Cosine	1	1.81
			Half normal	Cosine	1	3.46
	2	Len + Strin	Uniform	NA	NA	0
			Uniform	Cosine	1	2
			Half normal	NA	NA	2
			Hazard rate	NA	NA	3.93
		Strin	Uniform	NA	NA	0
			Hazard rate	NA	NA	1.52
			Half normal	NA	NA	1.70
			Uniform	Cosine	1	1.95
300	1	Len + Strin	Uniform	NA	NA	0
			Uniform	Cosine	1	2
			Half normal	NA	NA	2.01
			Hazard rate	NA	NA	3.98
		Strin	Uniform	NA	NA	0
			Uniform	Cosine	1	2
			Half normal	NA	NA	2.01
			Hazard rate	NA	NA	3.85
	2	Len + Strin	Uniform	NA	NA	0
			Uniform	Cosine	1	2
			Half normal	NA	NA	2
			Hazard rate	NA	NA	2.75
		Strin	Uniform	NA	NA	0
			Hazard rate	NA	NA	1.45
			Uniform	Cosine	1	2
			Half normal	NA	NA	2

^a Type of infrared detections used to estimate the detection function.

^b Number of adjustment terms used.

^c Difference between the AIC of the best model and the model under consideration.

Table B2. The number of articles using infrared thermal sensors from aerial platforms that addressed different error types. Error types considered were detection probability across the field-of-view of the sensor (Uniform), availability errors (AE), perception errors (PE), misclassification errors (ME), and double counting errors (Double).

Combination	Number of articles
Uniform + AE	0
Uniform + PE	2
Uniform + ME	5
Uniform + Double	2
AE + PE	4
AE + ME	15
AE + Double	4
PE + ME	9
PE + Double	1
ME + Double	6
Uniform + AE + PE	0
Uniform + AE + ME	0
Uniform + AE + Double	0
Uniform + PE + ME	2
Uniform + PE + Double	0
Uniform + ME + Double	1
AE + PE + ME	4
AE + PE + Double	1
AE + ME + Double	3
PE + ME + Double	1
Uniform + AE + PE + ME	0
Uniform + AE + PE + Double	0
Uniform + AE + ME + Double	0
Uniform + PE + ME + Double	0
AE + PE + ME + Double	1
Uniform + AE + PE + ME + Double	0

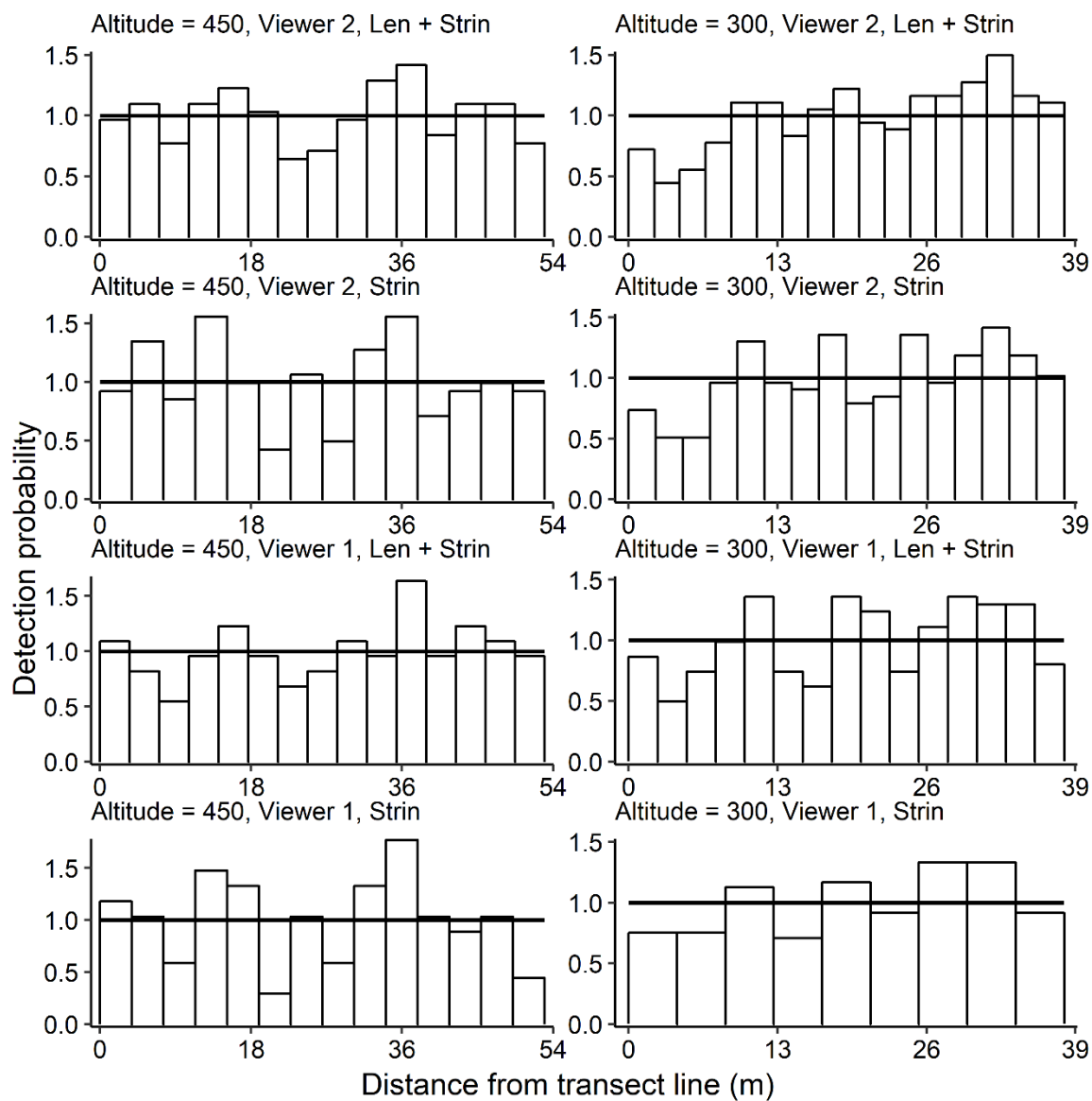


Figure B1. Plots of the AIC-best detection function for each altitude (m), observer, and type of infrared detections used (lenient = Len, stringent = Strin).

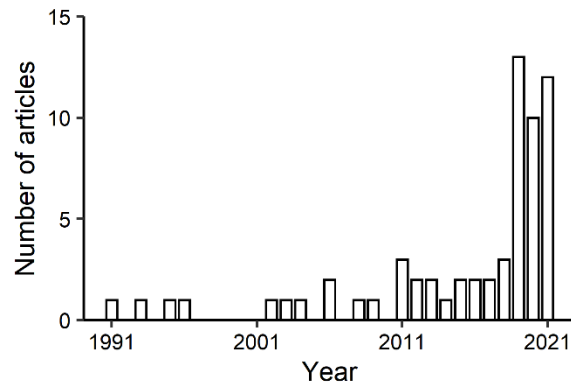


Figure B2. The number of articles published annually using aerial sampling techniques combined with infrared thermography to monitor wildlife.

References

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APPENDIX C. USING COST-EFFECTIVENESS ANALYSIS TO COMPARE DENSITY-ESTIMATION METHODS FOR LARGE-SCALE WILDLIFE MANAGEMENT

Estimation of Persistence

To estimate the persistence time of pellet groups, I used the 2021 decay data and the fitted models from Delisle et al. (2022b). Following the inter-observer method in Delisle et al. (2022b), I predicted the probability of persistence $\hat{y}_i$ for each observation i of my monitored pellet groups. The decay data from Delisle et al. (2022b) were collected in RMU 3. To account for regional variation in pellet decay due to weather, I substituted weather data from each test landscape within which I conducted pellet sampling. I obtained a final estimate of persistence for each Regional Management Unit x habitat (forest, grassland, and agricultural field) combination using methods described in Delisle et al. (2022b). To estimate persistence rates in each habitat type across an RMU, I used an effort-weighted average of the persistence rates for a given habitat type in each test landscape, i.e., $\hat{t}_h = \sum_{l=1}^L \left(\frac{k_{lh}}{k_h} \right) \hat{t}_{lh}$, where $\hat{t}_h$ is the estimated persistence rate in habitat h across the entire RMU, k_{lh} is the total number of transects sampled in habitat h in test landscape l , k_h is the total number of transects sampled in habitat h across the entire RMU, $\hat{t}_{lh}$ is the estimated persistence rate in habitat h in test landscape l , L is the total number of test landscapes, and $var(\hat{t}_h) = \sum_{l=1}^L \left(\frac{k_{lh}}{k_h} \right)^2 var(\hat{t}_{lh})$.

Aerial Detection Probability

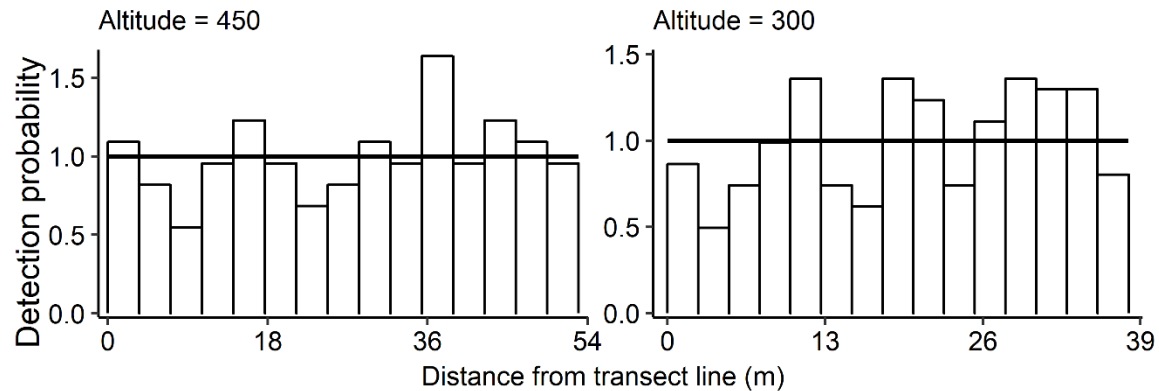


Figure C1. Detection probability of white-tailed deer in Indiana, USA, across the field-of-view of an infrared sensor. Infrared video was captured at 450 m and 300 m above-ground attitude in a crewed aircraft (Delisle et al. 2022a).

References

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APPENDIX D. MODELLING DENSITY SURFACES OF DEMOGRAPHIC CLASSES USING CAMERA-TRAP DISTANCE SAMPLING

Buffer Radii

Buffers with radii of 250 and 750 m were chosen for local habitat composition and configuration metrics, as both of these lengths are well within the average home range sizes of deer in the Midwest (Nixon et al. 1991, Vercauteren and Hygnstrom 1998). I chose a buffer radius of 1425 m because this approximates the diameter of a circular doe home range during the same time of year as my sampling and in similar areas with heavy agricultural use (Nixon et al. 1991, Vercauteren and Hygnstrom 1998). Lastly, I tested buffers with radii of 4000 and 8000 m because these approximate the minimum and average dispersal distances of young male deer (Hewitt 2011).

Factor Terms

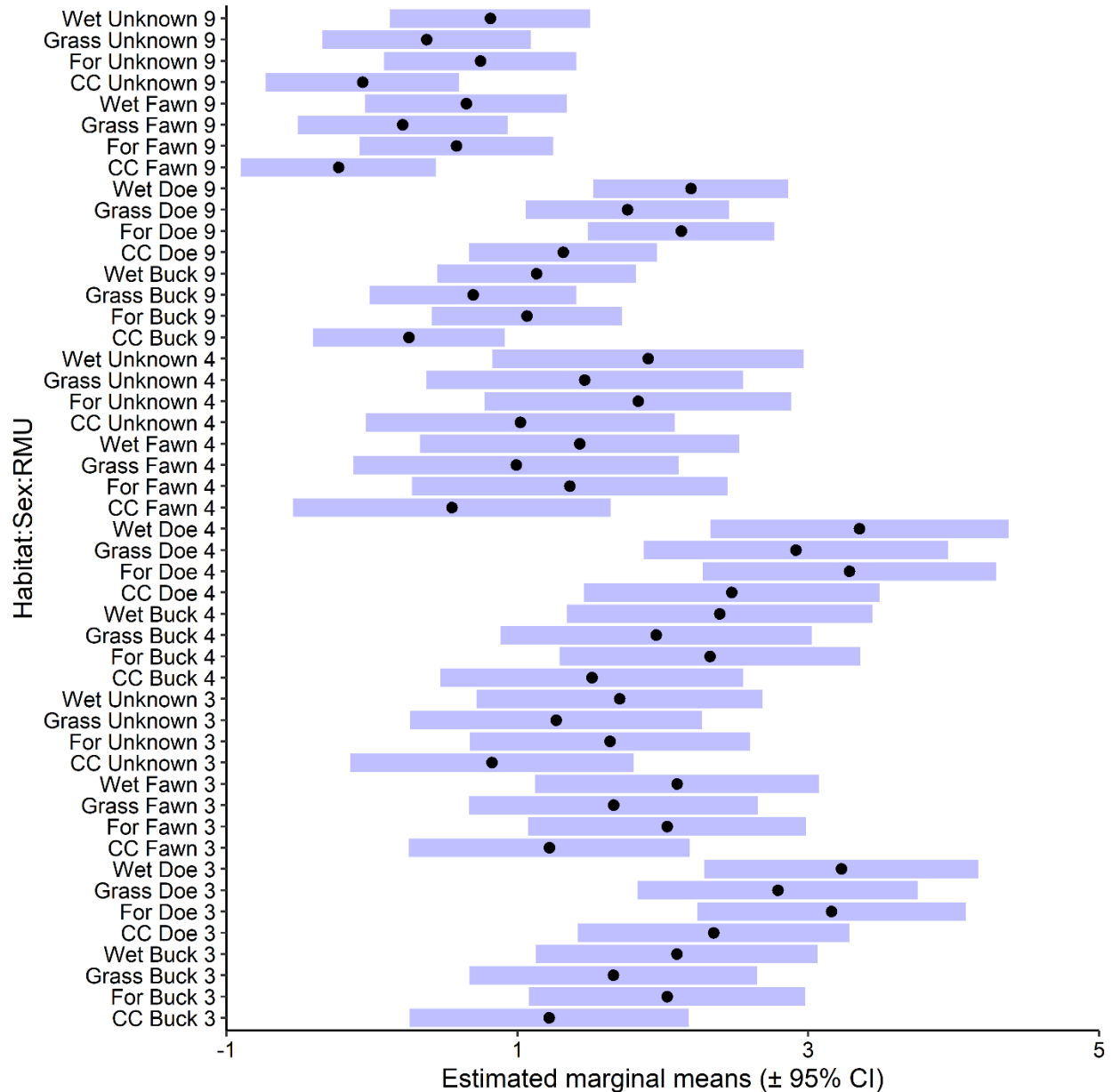


Figure D1. Estimated marginal means (i.e., least squares means) of combinations of factor terms from a density surface model estimating density of white-tailed deer (*Odocoileus virginianus*) within Regional Management Units (RMU) 3, 4, and 9 in Indiana, USA. The model was fit to camera-trap distance sampling data collected during the winter of 2019, 2020, and 2021. Factor terms include habitat (Wet = wetland, Grass = grassland, For = forest, CC = cultivated crops), sex (buck, doe, fawn, and unknown), and RMU. Marginal means were estimated with the ‘emmeans’ package in R (Lenth et al. 2022).

Extrapolated Densities

Within RMUs 3 and 4, densities estimated across all areas, including areas that exhibited univariate or combinatorial extrapolation past the sampled range of environmental covariates (henceforth referred to as extrapolated densities), were similar to the densities estimated only in areas that were within the range of environmental covariates I sampled (henceforth referred to as non-extrapolated densities; Table D1). However, extrapolated densities estimated were, on average, 2.7 (SE = 0.1) times larger than non-extrapolated densities in RMU 9. On average, the CVs of extrapolated densities were 107.8 (SE = 45.8) times larger than those of non-extrapolated densities across all RMUs, habitat types, and classes. Fawn:doe ratios never exhibited differences when estimated with extrapolated densities (Table D2).

Table D1. Habitat-specific, class-specific, and total density estimates (deer/km²) of white-tailed deer (*Odocoileus virginianus*) in Regional Management Units (RMU) 3, 4, and 9 of Indiana, USA. Densities were estimated with a density surface model fitted to camera-trap distance sampling data collected in the winter of 2019, 2020, and 2021. Habitat-specific densities are presented for agricultural fields (Ag), grasslands and pastures (Grass), wetlands (Wet), and forests (For). Densities were estimated across all areas, including areas that exhibited combinatorial or univariate extrapolation past the range of environmental covariates that I sampled. UCI = upper 95% confidence interval. LCI = lower 95% confidence interval.

Type	RMU	Class	$\hat{D}$	$SE(\hat{D})$	$CV(\hat{D})$	$UCI(\hat{D})$	$LCI(\hat{D})$
Habitat	3	Ag	2.17	0.23	0.10	1.93	2.78
		Grass	5.69	1.04	0.18	4.90	8.88
		Wet	18.32	4.77	0.26	14.40	32.98
		For	10.42	1.63	0.16	9.37	15.34
	4	Ag	3.76	5.25	1.39	3.31	5.82
		Grass	6.38	8.64	1.35	5.55	20.32
		Wet	23.53	66.84	2.84	17.63	64.89
		For	7.85	54.71	6.97	7.32	19.40
	9	Ag	6.42	26.59	4.14	4.96	69.62
		Grass	10.17	104.35	10.26	8.79	230.88
		Wet	34.06	164.95	4.84	23.84	472.77
		For	29.30	1552.14	52.97	20.62	2755.89
Class	3	Doe	1.99	0.35	0.17	1.67	2.96
		Buck	0.71	0.14	0.20	0.56	1.10
		Fawn	0.65	0.14	0.21	0.50	1.03
	4	Doe	4.56	29.79	6.54	3.92	11.36
		Buck	1.69	20.68	12.24	1.36	4.15
		Fawn	0.62	2.04	3.29	0.43	1.76
	9	Doe	8.35	146.71	17.56	4.45	247.38
		Buck	2.91	58.38	20.09	1.45	94.13
		Fawn	1.75	89.71	51.26	0.87	66.79
Total	3	Total	3.35	0.40	0.12	3.04	4.52
	4	Total	6.87	36.27	5.28	6.37	17.09
	9	Total	13.01	191.77	14.74	10.42	398.85

Table D2. Ratios of densities of different demographic classes of white-tailed deer (*Odocoileus virginianus*) in Regional Management Units (RMU) 3, 4, and 9 of Indiana, USA. Densities to compute ratios were estimated with a density surface model fitted to camera-trap distance sampling data collected in the winter of 2019, 2020, and 2021. Ratios were computed with densities that I estimated across all areas, including areas that exhibited combinatorial or univariate extrapolation past the range of environmental covariates that I sampled.

Classes	RMU	Ratio	Var(Ratio)
Buck:Doe	3	0.357	0.009
	4	0.371	26.539
	9	0.348	83.000
Fawn:Doe	3	0.328	0.008
	4	0.136	0.985
	9	0.209	124.529

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APPENDIX E. FEAR AND CONCEALMENT PREDICT GROUP SIZE OF A COMMON UNGULATE

Group Membership

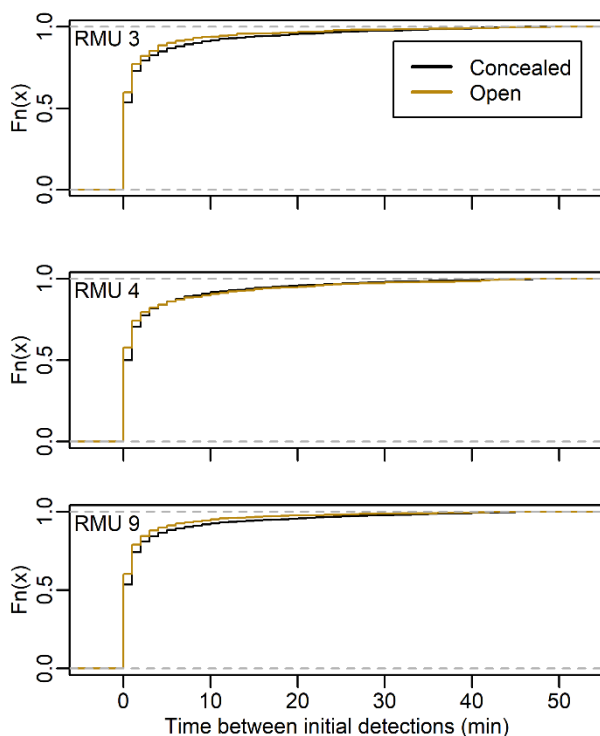


Figure E1. Empirical cumulative distribution functions of the times in between initial detections of deer in each Regional Management Unit (RMU). Unique empirical cumulative distribution functions are shown for open (agricultural field and grassland) and concealed (forest and wetland) habitat types in Indiana, USA.

Other Predictors

Anthropogenic Disturbance

I also tested length of roads, number of buildings, average impervious surface in the immediate area, and human and domestic dog use intensity. For length of roads, number of buildings, and mean impervious surface metrics (% of developed surface over 30x30 m cells), I used a buffer with a radius of 750 m to define the immediate surrounding area, because 750 m approximates the radius of a circular home range for does after the hunting season in agricultural areas (Nixon et al. 1991, Vercauteren and Hygnstrom 1998). I used the 2015 Indiana primary and

secondary roads shapefile (US Census Bureau, Department of Commerce) and US building footprints shapefile from Microsoft (<https://github.com/Microsoft/USBuildingFootprints>) to calculate the length of roads and number of buildings within buffers in R (R Core Team 2022). The mean impervious surface index was calculated in R using the 2019 National Land Cover Database impervious surface raster (Dewitz and U.S. Geological Survey 2021). I calculated the index of human and dog use intensity identically to the coyote use intensity index in the main text by substituting for coyotes the number of dogs or humans in each image.

I did not consider the average impervious surface <750 m in more complex models due to multicollinearity issues with the amount of concealment <8000 m, which was a stronger predictor.

Natural Food Availability

I additionally assessed the density of all twigs; density of twigs that were avoided by deer; fraction of the total twig density that was preferred or neutral; and fraction of the total twig density that was avoided.

References

- Dewitz, J., and U.S. Geological Survey. 2021. National Land Cover Database (NLCD) 2019 Products (ver. 2.0, June 2021): U.S. Geological Survey data release, <https://doi.org/10.5066/P9KZCM54>
- Nixon, C.M., L.P. Hansen, P.A. Brewer, and J.E. Chelsvig. 1991. Ecology of White-Tailed Deer in an Intensively Farmed Region of Illinois. *Wildlife Monographs* 118:1–77.
- R Core Team. 2022. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Vercauteren, K.C., and S.E. Hygnstrom. 1998. Effects of Agricultural Activities and Hunting on Home Ranges of Female White-Tailed Deer. *The Journal of Wildlife Management* 62:280–285.

Average Group Sizes

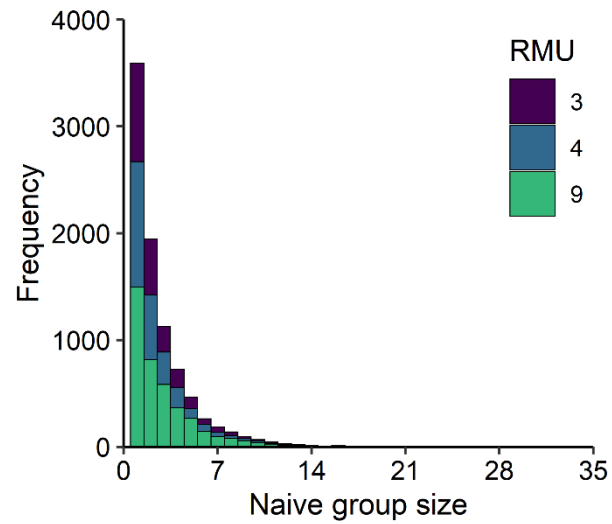


Figure E2. Histogram showing the frequency of group sizes of white-tailed deer in each Regional Management Unit (RMU) sampled in Indiana, USA. Presented group sizes are not corrected for detectability (i.e., naïve).

Baseline Predictors

Table E1. Estimates and confidence intervals for Bayesian regression models explaining the group size of white-tailed deer in Indiana, USA, as a function of various predictors. Only a single predictor was used in each model, aside from the natural predation model where coyote use intensity and coyote activity level were both specified in an interactive model. Data were collected by camera traps in 2019, 2020, and 2021.

Predictor	Estimate	LCI	UCI
concealment presence	-0.245	-0.350	-0.139
proportion of group that is fawn	7.749	4.728	12.798
forest edge density <750 m	0.064	0.008	0.124
distance to concealment	-0.084	-0.124	-0.045
interaction: coyote use intensity and activity level	0.031	0.006	0.056
distance to nearest road or building	0.061	0.012	0.111
impervious surface average <750 m	-0.044	-0.091	0.005
concealment area <8000 m	-0.130	-0.252	0.002
human and dog use intensity	0.027	-0.017	0.072
proportion of twig density that is avoided twigs	0.009	-0.049	0.067
density of preferred and neutral twigs	-0.001	-0.069	0.065
proportion of twig density that is preferred and neutral twigs	-0.009	-0.072	0.053
density of avoided twigs	-0.010	-0.070	0.051
total twig density	-0.014	-0.081	0.053
buildings <750 m	-0.023	-0.066	0.020
road length <750 m	-0.031	-0.080	0.019

Trace Plots and Posterior Predictive Checks

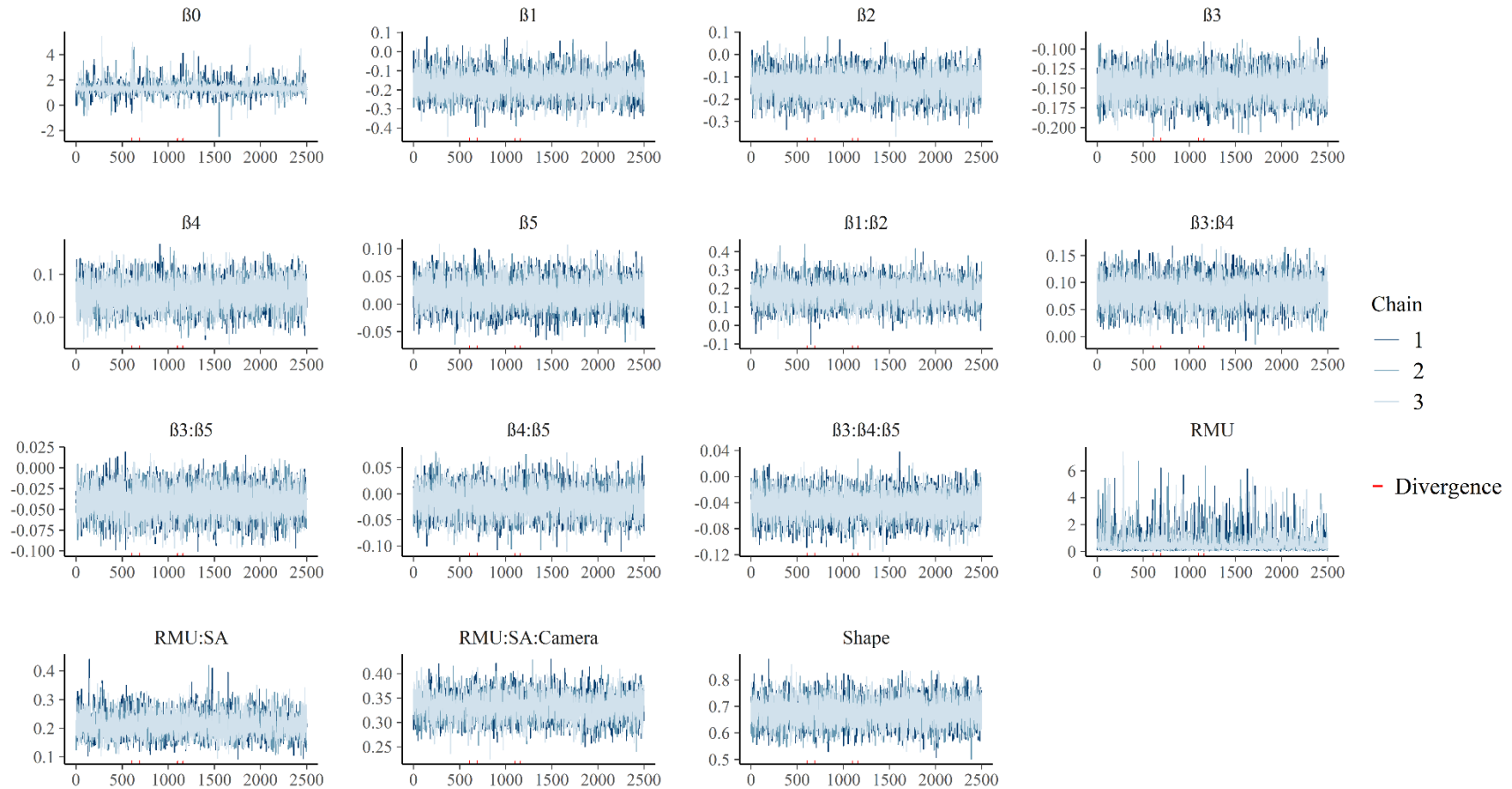


Figure E3. Trace plots of parameters from the best Bayesian model fitting an index of group size of white-tailed deer to various interactive and additive predictors. β_0 = intercept. β_1 = amount of concealment < 8000 m. β_2 = concealment presence. β_3 = coyote activity level. β_4 = coyote use intensity. β_5 = distance to nearest building or road. RMU = Regional Management Unit. SA = sampling area. Camera = the location ID of the camera. Fixed effects in the model included the following: (1) two-way interaction between the amount of concealment within the larger surrounding area and occurrence of local concealment; and (2) three-way interaction between distance to nearest building or road, coyote use intensity, and coyote activity level.

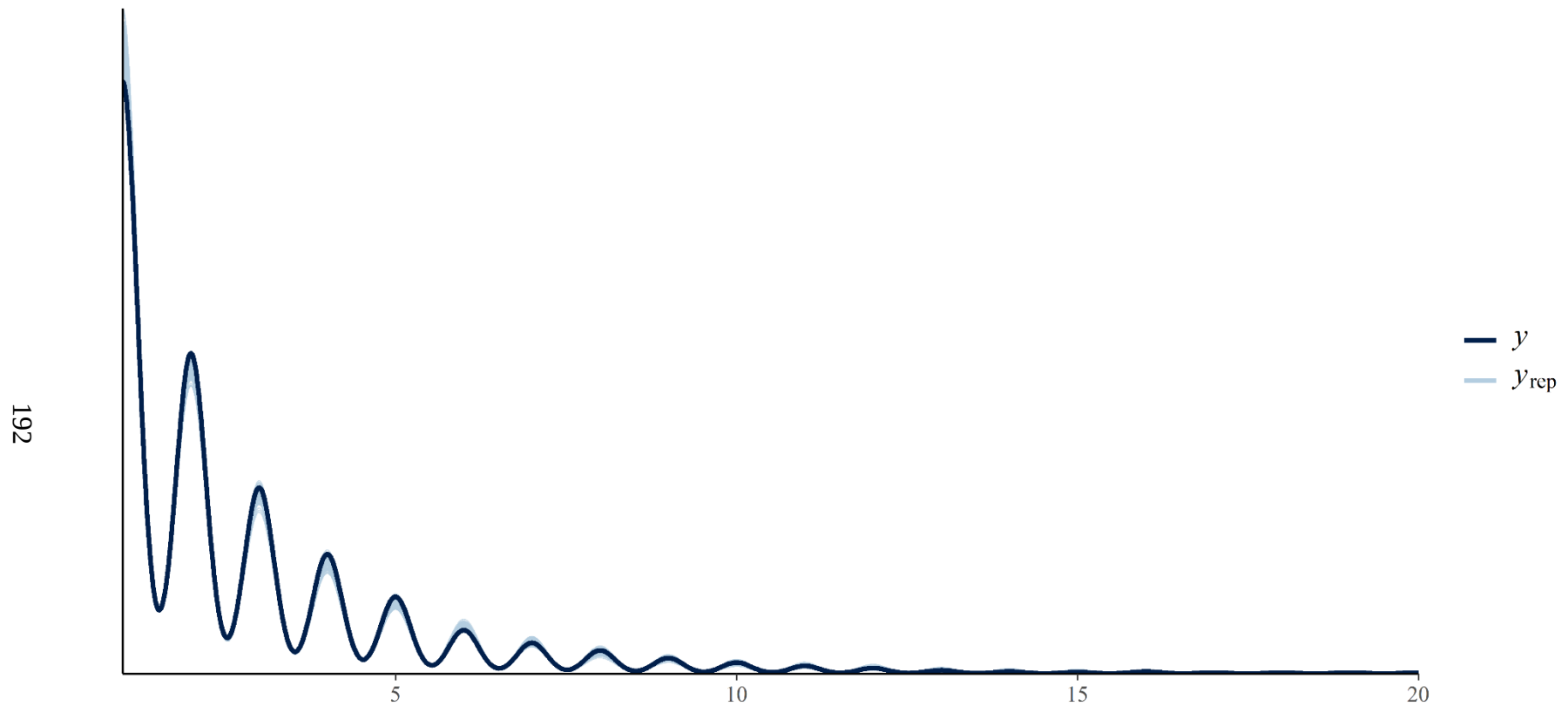


Figure E4. Observations plotted over draws from the posterior predictive distribution of a Bayesian model regressing an index of group size as a function of the following fixed effects: (1) two-way interaction between the amount of concealment within the larger surrounding area and occurrence of local concealment; and (2) three-way interaction between distance to nearest building or road, coyote use intensity, and coyote activity level.

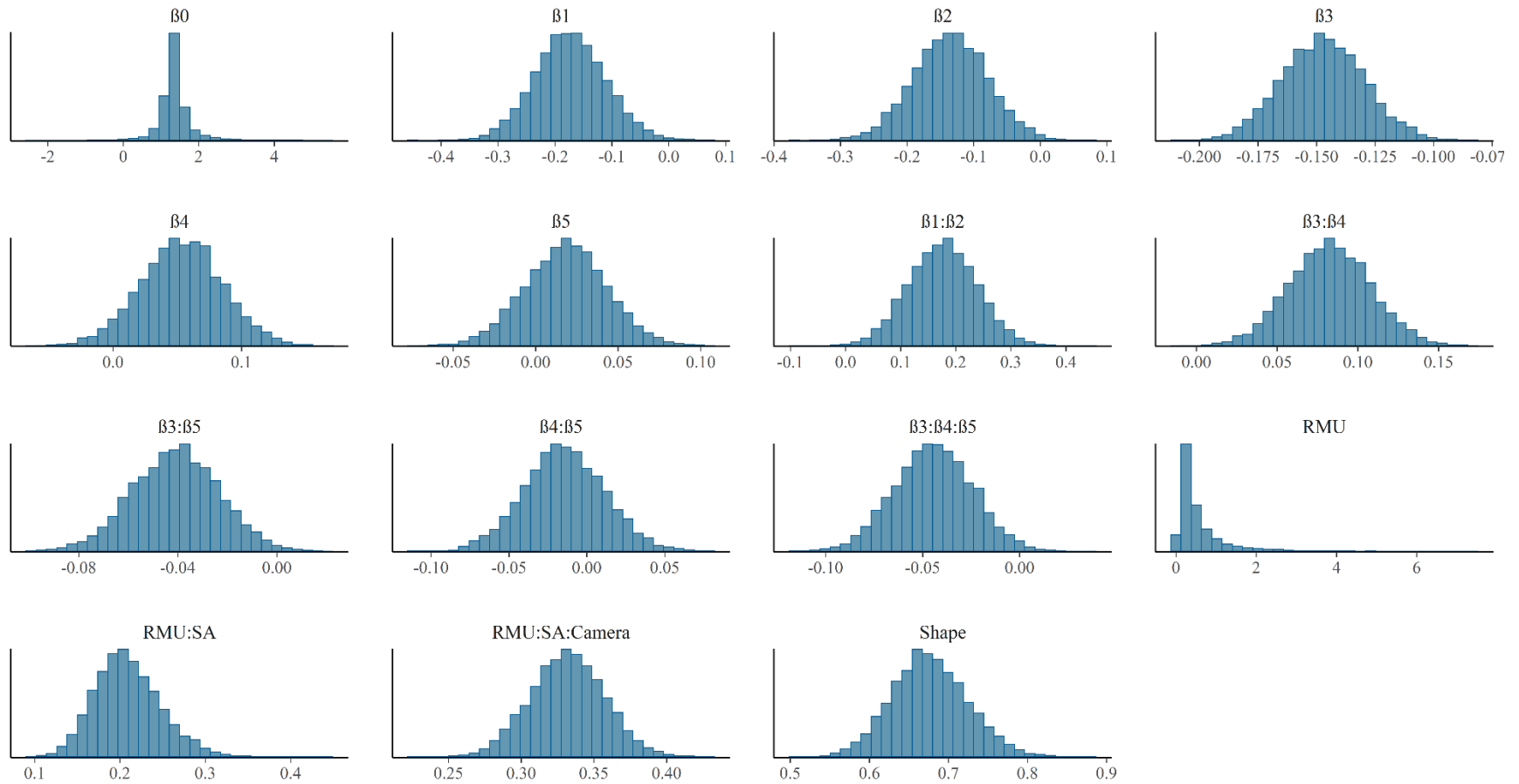


Figure E5. Posterior distributions of a Bayesian model regressing an index of group size as a function of the following fixed effects: (1) two-way interaction between the amount of concealment within the larger surrounding area and occurrence of local concealment; and (2) three-way interaction between distance to nearest building or road, coyote use intensity, and coyote activity level.

Coyote and Deer Interaction Captures by Camera Trap



