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Estimating White-tailed Deer Abundance at Gettysburg National Military Park and Eisenhower National Historic Site

Natural Resource Technical Report NPS/NER/NRTR—2012/626

ON THE COVER
Top photo: Adult female white-tailed deer collared with a Global Positioning System device, photo taken by Benjamin Rebert.
Bottom photo: David Stainbrook with a sedated juvenile female white-tailed deer, photo taken by Amanda Sommerer.

Estimating White-tailed Deer Abundance at Gettysburg National Military Park and Eisenhower National Historic Site

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Contents

Page

Contents (continued)

Figures

Figures (continued)

Tables

Tables (continued)

Page

Tables (continued)

Page

Appendixes

Page

Executive Summary

The mission at Gettysburg National Military Park and Eisenhower National Historic Site (GNMP-ENHS) is to preserve the historic character of the parks to enable current and future generations to understand and interpret the events that took place at each park. Management objectives include maintaining the landscape as it existed during the historic 1863 Civil War battle (e.g., dense understory in woodlots) in GNMP and as it existed during Eisenhower's occupancy (e.g., patchwork of cropfields) in ENHS. Browsing by white-tailed deer (*Odocoileus virginianus*) diminished regeneration of native trees in woodlots and prevented crops from reaching maturity. Thus, to increase regeneration in woodlots and reduce crop damage, the National Park Service (NPS) began culling deer in 1995 to reach a density goal of 10 deer/km^2 of forest. However, park managers were interested in an accurate population estimate to determine if their management goal has been met and possible methods to monitor future abundance.

Deer density estimates, among all surveys and survey methods, ranged from 43−71 deer/km^2 of forest. In April 2010, for dusk mark-resight surveys we estimated density ($\hat{D}$) to be 43 deer/km^2 of forest ($\hat{N}$=368, 95% CI=322–421), for spotlight mark-resight surveys $\hat{D}$=48 deer/km^2 of forest ($\hat{N}$=403, 95% CI=297–546) and for distance sampling surveys $\hat{D}$=45 deer/km^2 of forest ($\hat{N}$=381, 95% CI=238–607). In November 2010, we estimated $\hat{D}$=50 deer/km^2 of forest ($\hat{N}$=425, 95% CI=196–921) for dusk mark-resight surveys, $\hat{D}$=71 deer/km^2 of forest ($\hat{N}$=598, 95% CI=420–852) for spotlight mark-resight surveys, and $\hat{D}$=43 deer/km^2 of forest ($\hat{N}$=366, 95% CI=255–525) for distance sampling surveys.

Our estimates indicated density is approximately four times greater than the park's goal of 10 deer/km^2 of forested land specified in the GNMP-ENHS deer management plan. However, NPS staff have observed increased tree regeneration and reduced crop damage on NPS-owned property since culling was initiated. Additionally, we observed more deer on private lands in the study area and fewer deer on NPS-owned property. Consequently, the NPS may want to consider re-evaluating deer density goals if landscape objectives are being met.

We investigated the feasibility and assumptions of multiple abundance estimators. We examined whether harvest data from culling operations could be used to estimate abundance within the GNMP-ENHS study area, which included lands adjacent to GNMP-ENHS, using a catch-per-unit-effort (CPUE) estimator. We investigated a change-in-ratio (CIR) estimator based on data collected during culling operations. Also, we captured and fitted adult and juvenile male and female deer with Global Positioning System (GPS) collars and performed surveys at dusk and at night from April 2009–November 2010 to estimate abundance using mark-resight methods. Also, we used these data to estimate an updated detection probability that could be used to adjust counts obtained during future dusk surveys.

Additionally, we conducted distance sampling surveys from roads at night to obtain population estimates and to test assumptions when roads are used as transects with distance sampling. A critical requirement of distance sampling is that transects are placed randomly on the landscape to obtain a representative sampling of the study area and to meet the assumption that the distribution of deer is uniform with respect to perpendicular distances to transects. Roads have been used as transects for distance sampling and provide logistical advantages, but roads may be correlated with habitat characteristics and the distribution of the animals. Distance sampling can be a useful estimator for monitoring abundance; however, if roads are used as

transects, the magnitude and direction of the bias are unknown unless information on the distribution of deer is available. We used GPS locations from GPS-collared deer to model the distribution of deer relative to roads using a resource selection function (RSF) and demonstrated how the RSF can be used to account for non-random placement of transects to obtain more accurate estimates of abundance. Finally, we provided the advantages and disadvantages of all tested methods for estimating future abundance or future trends in abundance.

The CPUE estimator could only provide an estimate of antlerless deer (males fawns and female deer) using the area available to culling operations at night. The CPUE estimator did not permit inferences about abundance on the complete study area because of the limited area where culling occurred and because no information could be obtained for antlered deer (adult males). We were unable to use the CIR estimator to obtain estimates of abundance using culling data because surveys to estimate the proportion of antlered and antlerless deer were not conducted prior to and immediately following culling operations. Additionally, an important assumption for both methods is that all harvested deer are known; however, information about deer harvested by hunters on private lands within the study area was not available.

We found that the average detection probability ($\hat{p}$) during the April 2010 dusk count was 0.25, compared to 0.54 from research conducted over 20 years prior. Previous research used only marked female deer, and a number of factors that influence detectability of deer likely changed over time.

During the hours when we conducted spotlight distance sampling surveys, the distribution of deer was not uniform with respect to the location of roads in both forested and non-forested areas. Deer avoided areas close to roads, were more likely to be found near the park boundary, and selected forested areas and open areas near forest edges. The estimator of detection probability from distance sampling was positively biased when deer avoided roads; thus, estimates of density in the sampled area were negatively biased. The roads we used as survey transects likely provide a representative sampling of the study area, because we failed to detect a statistically significant difference in proportion of forest habitat surveyed compared to a GIS map of the complete study area.

Population estimates based on harvest data, such as the CIR and CPUE estimators, can be cost-effective because they rely primarily on data already being collected during culling operations. However, collecting data for the CIR estimator was not feasible because of the timing of culling operations and not all deer harvested on surrounding private lands can be enumerated; hence, we were not able to estimate abundance using the CIR estimator. We were able to estimate abundance based on a CPUE estimator, but because culling is limited to only a portion of GMNP-ENHS, the estimates were not representative of the study area. We do not believe either estimator can provide accurate population estimates for GMNP-ENHS, given the safety constraints on where culling can occur. Estimators that require marked deer are expensive, but likely will be required if periodic verification of the accuracy of population estimates based on a sighting index is conducted. In the future, NPS staff could perform dusk surveys in early April and adjust counts by the 0.25 detection probability that we estimated during this research. However, conditions may change, leading to a different detection probability and biased estimates of abundance during future surveys. For instance, differences in observers, weather, habitat, etc., during surveys from year to year may provide misleading trend information. Using the distance sampling estimator as an index of abundance may provide better trend information over time because detection probability can be modeled for each observer for each survey, if bias related to avoidance of roads by deer remains constant.

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List of Acronyms

CIR	Change-in-ratio
CPUE	Catch-per-unit-effort
GNMP-ENHS	Gettysburg National Military Park and Eisenhower National Historic Site
GPS	Global Positioning System
GIS	Geographical Information System
L-P	Lincoln-Petersen
NPS	National Park Service
PA	Pennsylvania
RSF	Resource Selection Function

Introduction

The abundance of white-tailed deer (*Odocoileus virginianus*) in national parks has been a controversial issue for decades (Leopold 1963, Warren 1991). In the 1980s, resource managers at Gettysburg National Military Park and Eisenhower National Historic Site (GNMP-ENHS), Pennsylvania, were concerned that deer were adversely affecting park resources and leading to increased deer-vehicle collisions in and around the park (Frost et al. 1997). Tzilkowski and Storm (1993) estimated deer abundance on the study area to be 1,018 deer in 1992; a density of 136 deer/km^2 of forested land, which was >10 times the density recommended by the Pennsylvania Game Commission for Adams County at that time. Research at GNMP-ENHS concluded that deer reduced crop yields (Frost et al. 1997, Vecellio et al. 1994) and prevented forest regeneration (Storm et al. 1989).

The mission at GNMP-ENHS is to preserve the historic character of the parks to enable current visitors and future generations to interpret the significant historical events that took place at each park (USDOI 1995). Management objectives for GNMP include maintaining the landscape as it existed prior to and during the historic 1863 Civil War battle, which included a dense understory of native vegetation in woodlots (USDOI 1995, Frost et al. 1997, Newinski et al. 2006). Management objectives for ENHS include preserving the agricultural setting so the former president's agrarian use of the farm and management strategies are properly understood by visitors, which included growing crops of corn, milo, soybeans, small grains, and hay (US DOI 1995). Browsing by white-tailed deer diminished regeneration of native trees in woodlots and prevented crops from reaching maturity. The preferred management action identified in the Environmental Impact Statement was a combination of culling deer in the park and increased hunting efforts on private lands surrounding the park to reach a density of 10 deer/km^2 of forested land (USDOI 1995), diminish deer browsing, and allow regeneration in woodlots (Frost et al. 1997).

An important component of the White-tailed Deer Management Plan (USDOI 1995) for GNMP-ENHS is a reliable estimate of the number of deer in the park. Estimates of abundance are the basis for population models to predict the response of populations to specific management actions and are important for making decisions regarding how many deer to kill to meet management objectives (Storm et al. 1992, Frost et al. 1997). Estimates of deer density are important in national parks (especially in the National Capital Region Network) that have implemented or are considering deer population reduction, as evidenced by the number of parks that have implemented deer monitoring programs (Bates 2006).

Buckland et al. (2000) classified the three major areas of wildlife population estimation as mark-recapture (including mark-resight and mark-recovery), harvest models (including catch-effort and removal methods), and distance sampling. All of these can be used to estimate abundance of deer, but each has a different set of assumptions and requirements, which may be difficult to meet to obtain unbiased and precise population estimates.

The objective of the research performed at GNMP-ENHS was to employ and evaluate various population estimation techniques to calculate an updated estimate of abundance. Park managers can use abundance estimates to update management strategies to reach their long-term density goal of 10 deer/km^2 (25 deer/mi^2) of forested land (Frost et al. 1997). We used mark-resight, change-in-ratio (CIR), catch-per-unit-effort (CPUE), and distance sampling methods to estimate abundance of deer in the study area that included GNMP-ENHS (Table 1).

Also, we monitored movements from a marked population of deer to test assumptions behind these estimators. We investigated individual heterogeneity and temporal variation in sighting probabilities of deer during mark-resight surveys and evaluated the efficacy of applying mark-resight sighting probabilities to future surveys. Further, we evaluated the precision, accuracy, and logistical feasibility of CPUE and CIR methods, which rely on data collected during deer population reduction efforts. Finally, we tested whether using roads as transects with distance sampling provided unbiased estimates of deer abundance and evaluated correction methods.

Table 1. Summary of the methods used to survey white-tailed deer and the estimators used to estimate abundance along with a brief description of the methods applied, 2009–2010, Gettysburg, Pennsylvania.

Survey method	Estimator	Description
Dusk mark-resight surveys	Lincoln-Petersen Joint-hypergeometric	Repeated surveys conducted before twilight ends where the number of marked and unmarked deer are recorded
Spotlight surveys	Lincoln-Petersen Bowden's Joint hypergeometric	Repeated surveys conducted before twilight ends where the number of marked and unmarked deer are recorded
Culling and surveys	Change-in-ratio	Surveys to count deer are conducted prior to and immediately after deer are culled
Culling effort and kill	Catch per unit effort	The number of deer culled per unit of culling effort
Spotlight surveys and distance from transect	Distance sampling	Surveys are conducted at night when deer are most active and the distance from the deer to the survey transect is used to estimate probability of detection

Mark-resight

The mark-resight method, based on the Lincoln-Petersen estimator (Seber 1982) where resightings are used in place of recaptures, has been widely used to estimate abundance of ungulates (Rice and Harder 1977, Bartmann et al. 1987, McCullough and Hirth 1988, Storm et al. 1989, Neal et al. 1993, Focardi et al. 2002). Standard assumptions include: (1) geographically and demographically closed population; (2) marks are not lost; (3) marked individuals are correctly identified; (4) marked population has the same probability of sighting as unmarked population; (5) homogeneous sighting probabilities for all animals within a sampling occasion; and (6) individuals are not counted more than once within a sampling occasion (Neal et al. 1993, White and Shenk 2001). Neal et al. (1993) and McCullough and Hirth (1988) found the estimator was particularly sensitive to violations of assumption 5, when sighting probabilities vary among individuals (e.g., individual heterogeneity), resulting in bias. Bowden's estimator relaxes this assumption, which is often difficult to meet, but marked animals must be individually identifiable (Bowden and Kufeld 1995). The mark-resight method typically is used to assess population density on small areas because it is expensive and time consuming to capture a sufficient sample of marked deer in the population to obtain accurate estimates of abundance across large areas (Bartmann et al. 1987, Neal et al. 1993, Focardi et al. 2002, McClintock et al. 2006).

It is well known that road-based and aerial surveys underestimate population size of ungulates when the proportion of missed observations, or visibility bias, is not accounted for in the survey design and estimation (Caughley 1974, 1977). Steinhorst and Samuel (1989) developed a sightability model to adjust for visibility bias using marked animals to estimate sighting probabilities for each animal group during surveys, which could be applied to future surveys to estimate abundance (Samuel et al. 1987, Cogan and Diefenbach 1998). Mark-resight data of marked animals also is used to estimate sighting probabilities, but at the population level, and applied to future surveys to estimate abundance (Seber 1982). Applying sighting probabilities to future surveys is a less expensive alternative than maintaining a sample of marked deer in the population. However, if the assumptions of equal detectability (e.g., all individuals have the same probability of detection during a survey) or constant detectability over time (e.g., sighting probabilities do not change over time) fail, the estimator will be biased (Otis et al. 1978, Seber 1982, Pollock and Kendall 1987, Neal et al. 1993, Anderson 2001). Sighting probabilities can be influenced by variability among individuals (e.g., behavioral or physical differences such as group size, age, and sex; Downing et al. 1977, Samuel et al. 1992) and variability related to sampling and temporal changes (e.g., differences in observers, season, vegetation cover, and weather; Samuel et al. 1987, Cogan and Diefenbach 1998, Anderson 2001, McClintock et al. 2006).

Previous research conducted at GNMP-ENHS estimated sighting probability, termed the average detection probability, $\hat{\bar{p}}$, as the average proportion of 30–54 marked female deer resighted during April ($\hat{\bar{p}}$=0.54) and November ($\hat{\bar{p}}$=0.43) mark-resight surveys performed at dusk from 1987–1991 (Storm et al. 1992). Since 1993, the park has used $\hat{\bar{p}}$=0.54 from the Storm et al. (1992) study to adjust annual April dusk counts of unmarked deer to estimate abundance.

However, the mark-resight method used at GNMP-ENHS was the Lincoln-Petersen estimator, which assumes no heterogeneity in re-sighting probabilities (Seber 1982). Nevertheless, the estimator will be unbiased if the marked sample is representative of the population, such that the ratio of marked deer observed to marked deer available is the same as the ratio of unmarked deer seen to the total number of unmarked deer on the study area (Otis et al. 1978, Seber 1982, White et al. 1982). Because Storm et al. (1992) used only marked female deer to calculate $\hat{\bar{p}}$ for all deer during mark-resight surveys, and male deer tend to exhibit lower sighting probabilities than females (McCullough 1982, Sage et al. 1983, McCullough and Hirth 1988), we believe the estimate of $\hat{\bar{p}}$ may not be representative, leading to negatively biased estimates of abundance. This estimator only provides unbiased estimates if the assumption that male and female deer have the same probability of detection during surveys is true, which has not been investigated at GNMP-ENHS.

Furthermore, for the sighting probability to yield unbiased estimates of abundance in future surveys, the assumption that sighting probability has not changed over time must be met. This may not be valid at GNMP-ENHS, because the detection probability of deer may have changed in response to a number of factors, including the reduction of deer abundance and habitat changes over the past 20 years.

Resource managers at GNMP-ENHS began culling antlerless deer in 1995 and continued culling every fall and winter from roads and fields on National Park Service (NPS) owned property. Given the relatively small home ranges of antlerless deer (male fawns and female deer), removals likely caused a reduced density of antlerless deer near park roads and fields. Additionally, the culling operations may have caused surviving antlerless and antlered deer to avoid the areas near park roads, such that fewer deer would be seen from those roads during April dusk counts. Further, culling operations led to reduced browsing by deer on park woodlands, which led to increased seedling tree density (Niewinski et al. 2006), which would decrease visibility in woodlots. Therefore, we hypothesized that culling operations resulted in a decrease in $\hat{p}$ over time.

Additionally, several woodlots had trees removed to restore the park to its visual condition during the Civil War. Management included thinning or canopy opening of historic woodlots to stimulate tree regeneration (Niewinski et al. 2006) and removing entire sections of woodlots that were historically fields. We hypothesized that the increase in understory would reduce visibility and result in a decrease in $\hat{p}$, but removal of entire sections of woodlots would result in an increase in $\hat{p}$, such that the overall change in $\hat{p}$ solely based on the effects of woodlot management would be difficult to predict.

Overall, we hypothesized that dusk mark-resight surveys would yield decreased average detection probability values from those found in Storm et al. (1992) because the marked population included all age and sex classes and because past management of the deer herd and habitat resulted in a denser understory of vegetation. The first research objective was to estimate a new average detection probability by monitoring the proportion of marked male and female deer seen during dusk mark-resight surveys at GNMP-ENHS, for managers to estimate abundance during future surveys. Next, we investigated individual heterogeneity and temporal variation in sighting probabilities of deer. Finally, we estimated abundance during dusk surveys using the bias adjusted Lincoln-Petersen (L-P) estimator and during spotlight surveys using Bowden's estimator.

Harvest Models

Harvest model methods do not require marked animals and could be far less expensive than the mark-resight method when used to estimate population size, but have limited applicability because removals (e.g., harvests or captures) are necessary to meet assumptions. At GNMP-ENHS, managers primarily cull antlerless deer annually and collect harvest data required for harvest models.

Abundance can be estimated using CIR methods based on the change in the proportion of each class of animal after a differential harvest (e.g., cull only antlerless deer) and the total number harvested (Buckland et al. 2000). Assumptions include a geographically and demographically closed population, observed proportions of each class are unbiased and representative of the population (e.g., equal probability of harvest), and the total number of each class removed is known (Seber 1982, Conner et al. 1986). However, assumptions may be difficult to meet (e.g., not all harvested animals are retrieved) and a large proportion of the population must be harvested to observe a noticeable change in the proportion of each class and obtain reliable estimates (Conner et al. 1986, Buckland et al. 2000).

The CPUE is another commonly used method, which assumes catch per unit effort (e.g., animals killed per hour of culling) is proportional to population abundance and that the population is closed (Seber 1982, Buckland et al. 2000). However, assumptions may be difficult to meet (Quinn and Deriso 1999), and removal of a large proportion of the population is often required to obtain reliable estimates (Lewis and Farrar 1968, Lancia et al. 1996).

Distance Sampling

Distance sampling using line transects is a generalization of the strip transect sampling method and relaxes the assumption that all objects within sample strips are detected (Buckland et al. 2001). Distance sampling allows a proportion of objects to be missed away from the line or transect, thus allowing a wider strip to be sampled and increasing sample size and efficiency (Buckland et al. 2001). Distance sampling often provides a practical, cost-effective method of estimating density for a broad range of applications, from walking transects to detect inanimate objects or plants in a terrestrial setting to traversing transects in a ship to detect moving objects such as whales in a marine setting (Thomas et al. 2010).

The appeal of the distance sampling estimator over mark-recapture methods is that the method does not require marked animals and could be far less expensive when used to estimate population size (Focardi et al. 2002). Also, it is more applicable to a wider range of species than harvest models because removals are not required. However, it may be difficult to meet all assumptions to obtain accurate population estimates. A critical requirement or assumption with line-transect distance sampling is that randomly placed transects are used (Buckland et al. 2001, Thomas et al. 2010). A systematic placement of parallel transects located at a random starting point generally meets this design requirement, because these transects are randomly located and they sample across the area of interest (Buckland et al. 2001).

However, assumptions may be difficult to meet to obtain unbiased population estimates of highly mobile animals such as deer (Buckland et al. 2001, Koenen et al. 2002, Fewster et al. 2008). Assumptions include: (1) surveys are conducted from randomly placed transects; (2) all objects on or near a point or transect are detected with certainty; (3) objects are detected at their initial location and any movement prior to detection is independent of observers; and (4) measurements are accurate (Buckland et al. 2001). Assumptions can be met easily when applying distance sampling methods to count dung (Buckland et al. 2001, Marques et al. 2001). However, accuracy of density estimates rely on estimates of both defecation rates and dung decay rates, which often are estimated using penned deer, and can vary spatially, seasonally, and by differences in feeding behavior related to sex and age (Van Etten and Bennet 1965, Mitchell et al. 1985).

Randomly placed transects are critical to meet assumptions that: (1) regardless of the distribution of objects on the landscape, the distribution of objects is uniform with respect to perpendicular distances to transects (e.g., the uniformity requirement or assumption; Fewster et al. 2008, Marques et al. 2010); and (2) data collected are a representative sample of the population (e.g., the density of deer in the sample is representative of the larger area of interest; Buckland et al. 2001). The first assumption is critical for modeling an unbiased estimate of detection probability as the decrease in the number of observations as distance from the transect increases; the second assumption is critical for extrapolating estimates from the sampled area to the larger area of interest (Buckland et al. 2001).

Further, deer density is often correlated with habitat types (e.g., forest cover vs. open areas), which can also influence the proportion of objects detected. Therefore, if transects are randomly placed, then the proportion of each habitat type in the sampled area should represent the proportion of each habitat type in the larger area of interest. The preferred sampling method to use when multiple habitats exist is to stratify transects by habitat (e.g., randomly place transects in fields and then randomly place additional transects in forests) in proportion to their occurrence in the whole study area (Buckland et al. 2001).

Common methods of ground navigation of random transects or points include walking, horseback, and all-terrain vehicles; but these methods may result in deer moving in response to observers before detection, which results in negatively biased estimates of density (e.g., see Koenen et al. 2002). Aerial surveys can avoid the problem of deer movement in response to the observer, but are expensive, animals may move in response to a low-flying plane or helicopter, and it is difficult to ensure that all deer on the transect are detected, especially in forested landscapes (Naugle et al. 1996, Haroldson et al. 2003, Thomas et al. 2010). Surveying from roads using distance sampling is a convenient and commonly used method (e.g., Gill et al. 1997, Heydon et al. 2000, Koganezawa and Li 2002**,** Ruette et al. 2003, Ward et al. 2004, Bates 2006), which can reduce movement in response to observers. However, roads are not random; thus, sampling from them violates the critical assumption of randomly placed transects and can result in biased estimates of density, which are unrepresentative of the population (Anderson 2001, Buckland et al. 2001). If unrepresentative, surveys conducted from roads may only provide an estimate of density of the population near roads, which may have limited value for making management decisions (Buckland et al. 2001). Furthermore, if the distribution of deer was correlated with the location of roads, perhaps because the location of roads was correlated to habitat types important to deer, then the estimator for detection probability may be biased, leading to a biased estimator of density. The direction of the bias would depend on whether deer were avoiding or selecting areas near roads, and the magnitude of the bias would depend on the amount of non-uniformity of the distribution of deer relative to transects. Few studies have tested both the uniformity requirement and representativeness of a sample from roads (see Koenen et al. 2002, McShea et al. 2011), or appropriately corrected for all bias.

If the distribution of deer relative to perpendicular distance to transect is not uniform, then detection probability will be biased. To demonstrate potential bias in detection probability, we created five hypothetical examples of the distribution of deer relative to the distribution of transects (dashed line) and compared these distributions to assumed distributions from distance sampling observation data (dotted line at y-intercept of solid line of detection function; Figures. 1–5). When there are fewer observations of objects near transects, the detection function y-intercept is typically an average of data from the first few bins. Because the true distribution of deer and the assumed distribution from observation data can have different y-intercepts, a simplified way to visualize the direction of the bias in the detection probability from a distance sampling survey under each scenario is to subtract the area under the dotted line from the area under the dashed line. A positive value indicates that detection probability would be positively biased from observation data, resulting in a negatively biased estimator of abundance.

The first scenario (Figure 1) is the assumed distribution with random transects, where deer are distributed uniformly relative to perpendicular distance from transects. The actual distribution of deer (dashed line) is equal to the assumed distribution (dotted line), such that no bias is expected in detection probability (Figure 1). The second scenario (Figure 2) is where deer avoid areas near transects, then are distributed uniformly relative to perpendicular distance from transects after some distance *x*. The detection probability is actually 1.0 near transects, but there are less deer there to see (Figure 2). Thus, detection probability would be positively biased because the assumed proportion of missed observations beyond distance *x* is less than actual (Figure 2). The third scenario (Figure 3) is where deer are distributed non-uniformly relative to perpendicular distance from transects, such that avoidance of areas near transects increases with distance from the transect. From the observation data, it would appear that detection probability is very high, such that few deer were missed (Figure 3). However, because there are more deer at greater

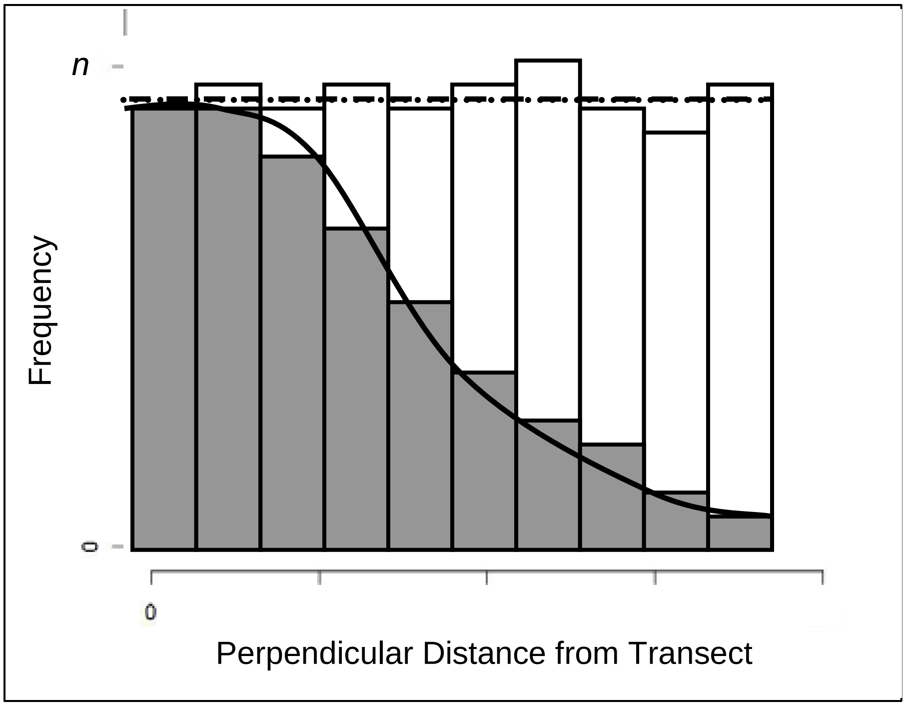

Figure 1. Hypothetical example where deer are distributed uniformly relative to perpendicular distance from transects. The solid portions of bins indicate observed deer from distance sampling survey and the open portion of bins indicate missed deer. The solid line is the fitted detection function, the dashed line is the true distribution of deer relative to the distribution of transects, and the dotted line is the assumed distribution of deer based on observations. This is the assumed distribution with random transects (i.e., dashed and dotted lines match), such that no bias is expected.

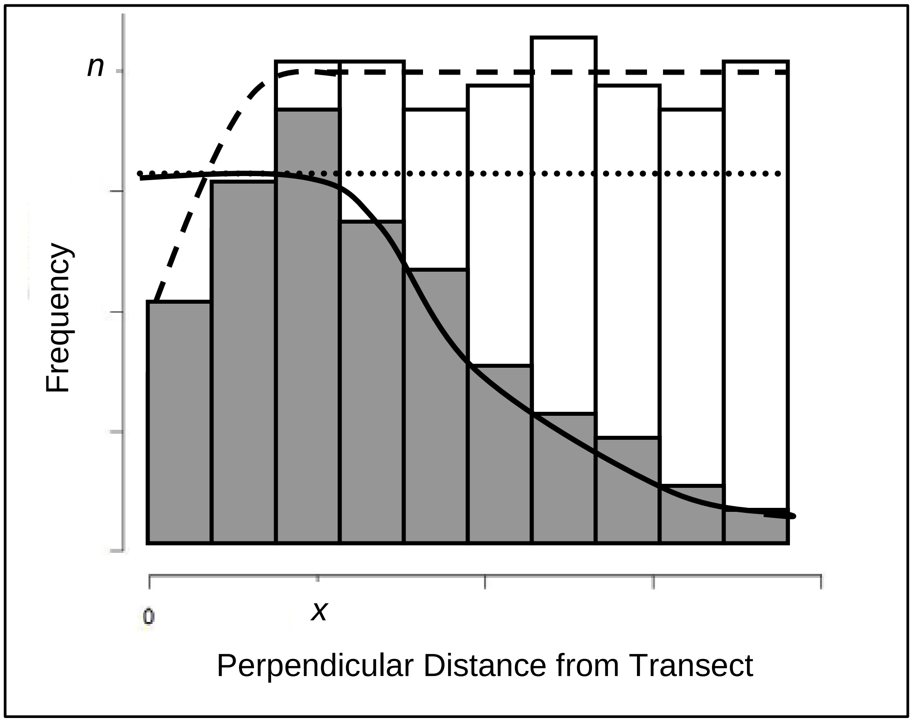

Figure 2. Hypothetical example where deer are avoiding areas near transects, but then distributed uniformly relative to perpendicular distance from transects after some distance *x*. The solid portions of bins indicate observed deer from distance sampling survey and the open portion of bins indicate missed deer. The solid line is the fitted detection function, the dashed line is the true distribution of deer relative to the distribution of transects, and the dotted line is the assumed distribution of deer based on observations. The detection probability would be positively biased with this distribution.

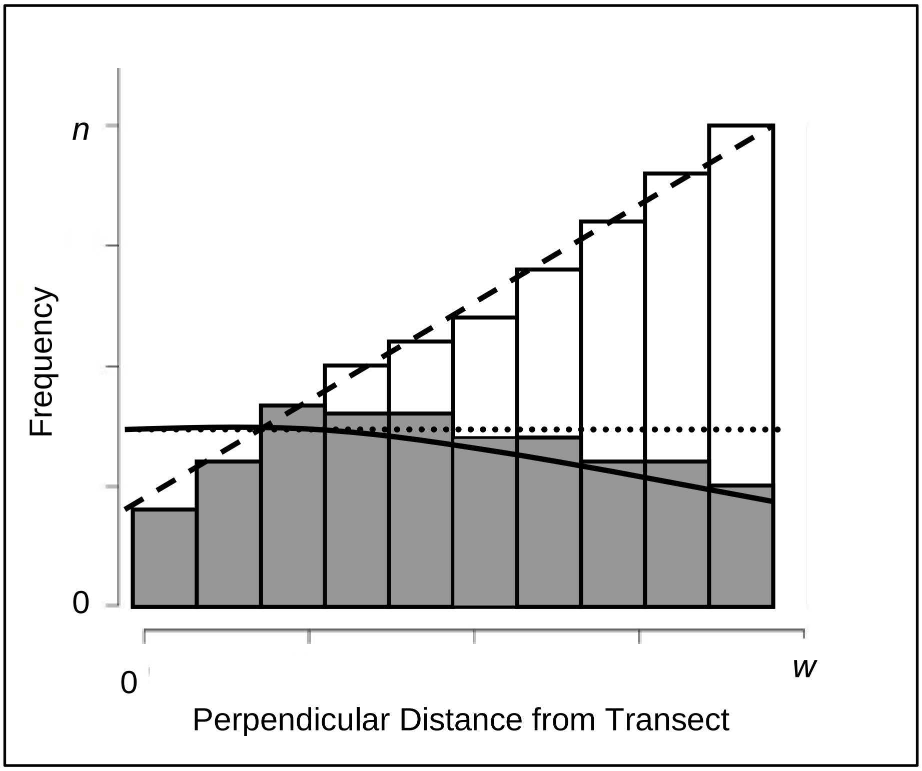

Figure 3 Hypothetical example where deer are distributed non-uniformly relative to perpendicular distance from transects, such that they are avoiding areas near transects. The solid portions of bins indicate observed deer from distance sampling survey and the open portion of bins indicate missed deer. The solid line is the fitted detection function, the dashed line is the true distribution of deer relative to the distribution of transects, and the dotted line is the assumed distribution of deer based on observations. The detection probability would be positively biased with this distribution.

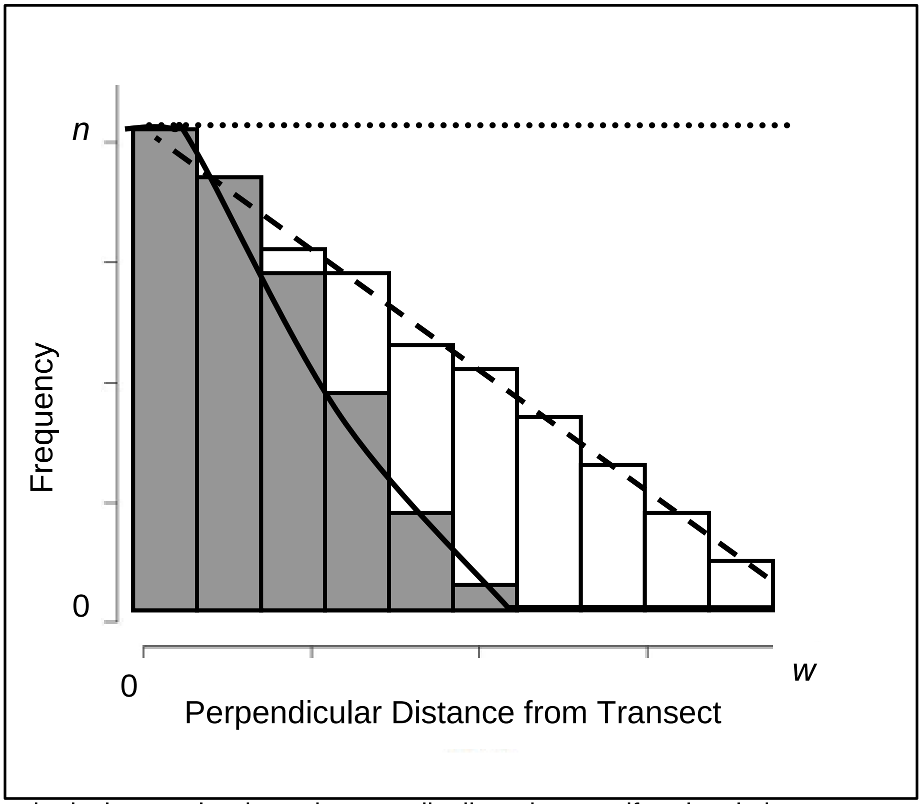

Figure 4. Hypothetical example where deer are distributed non-uniformly relative to perpendicular distance from transects, such that they are selecting for areas near transects. The solid portions of bins indicate observed deer from distance sampling survey and the open portion of bins indicate missed deer. The solid line is the fitted detection function, the dashed line is the true distribution of deer relative to the distribution of transects, and the dotted line is the assumed distribution of deer based on observations. The detection probability would be negatively biased with this distribution.

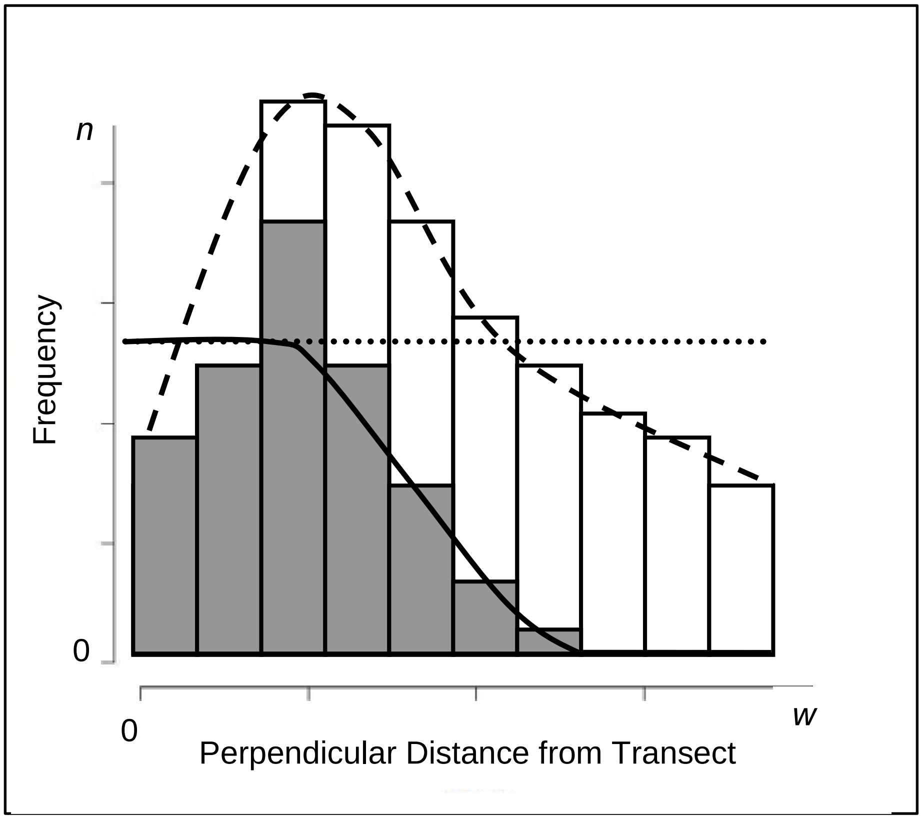

Figure 5. Hypothetical example where deer are distributed non-uniformly relative to perpendicular distance from transects, where they are avoiding areas near transects and far from transects. The solid portions of bins indicate observed deer from distance sampling survey and the open portion of bins indicate missed deer. The solid line is the fitted detection function, the dashed line is the true distribution of deer relative to the distribution of transects, and the dotted line is the assumed distribution of deer based on observations. The detection probability would be positively biased with this distribution.

distances to see, and therefore miss, the detection probability would be positively biased (Figure 3). The fourth scenario (Figure 4) is the opposite of the third, where deer are distributed non-uniformly relative to perpendicular distance from transects, such that deer are attracted to transects and attraction decreases with distance from the transect. The detection function drops off quickly, and the assumed proportion of deer that are missed is greater than actual because there are less deer to see at further distances; therefore, detection probability would be negatively biased (Figure 4). The last scenario (Figure 5) is where deer are distributed non-uniformly relative to perpendicular distance from transects, such that deer avoid areas near transects and areas far away from transects. This is similar to the second scenario, except the number of deer decreases at further distances (Figure 5). The assumed proportion of deer missed at further distances is greater than actual, but the assumed proportion of deer missed at intermediate distances is less than actual, such that overall, detection probability would be positively biased (Figure 5).

These hypothetical examples demonstrate that without knowledge of the true distribution or density gradient of the object of interest with respect to the distribution of transects, inspection of the detection histogram provides no insight into the true detection function, unless assumed uniform because random transects were used. For example, the detection histogram from the fourth scenario (solid bins in Figure 4) shows no avoidance of areas near the transect. Without knowledge that the object of interest is more prevalent near transects, abundance would be overestimated.

To investigate whether using roads as transects violated critical assumptions, we collected GPS locations from marked deer on the study area during distance sampling surveys. We modeled these GPS locations with respect to the roads we used as transects to test whether the distribution of deer relative to the distribution of transects was uniform. Additionally, we used these GPS locations with landscape covariates to model relative habitat use of deer on the study area, which we used to test whether the roads we chose as transects provided a representative sample of the study area. Then, we developed methods to adjust for potential bias in detection probability when deer were distributed non-uniformly relative to transects and used the model of relative habitat use to adjust for a possible non-representative sample. The final objective was to compare bias adjusted estimates of abundance for the study area to estimates of abundance when violations of assumptions were ignored.

Study Area

The study area (Figures 6 and 7) encompassed 2,913 ha (7,197 acres, 29.14 km^2, 11.25 mi^2) of land, which included 1,790 ha of NPS owned land (61% of the study area) and 1,122 ha of private land surrounding Gettysburg, Pennsylvania. The study area was divided into 11 compartments (mean size of 264 ha each) to ease dusk deer counting surveys (Storm et al. 1992). We used the same study area and compartment boundaries from Storm et al. (1992) for this analysis because the park manages its deer population based on this area. However, the study area size differs slightly from Storm et al. (1992) because they used a dot grid over aerial photographs to calculate areas, whereas we used a GIS (ArcView 9.3, Environmental Systems Research Institute. Redlands, California, USA).

We used all available roads within each compartment for dusk mark-resight surveys. However, we selected survey transects for spotlight mark-resight and distance sampling from existing roads within the study area (Figure 7). We identified 26 survey routes or transects of similar length (range = 0.43–3.46 km, mean length = 1.83 km) rather than a few long routes to better estimate the variance related to encounter rate (Buckland et al. 2001). We chose as many roads as possible in the study area for more complete coverage, but selected roads with less vehicular traffic, such as NPS roads (e.g., closed to public travel after hours) rather than highways, for safety reasons. Transects included only segments of roads where spotlights could be used (e.g., sections near buildings, livestock, etc. were excluded).

According to Storm et al. (1989), approximately 48% (1,389 ha) of the study area was agricultural land; 26% (749 ha) was forested; 12% (355 ha) was forbs/shrubland; 8% (216 ha) was commercial, which also included a golf course and cemeteries; 5% (141 ha) was residential; and 1% (12 ha) consisted of lakes, ponds, and streams. As of 2009, approximately 50% was agricultural/grassland, 27% was forested/woodland, 17% was built-up (commercial, residential, and transportation), 3% was recently cleared land, 2% was shrubland, and 1% consisted of lakes, ponds, and streams (GNMP-ENHS, unpublished data). For this study, however, we combined forested/woodland and shrubland as forested because both are important as deer hiding cover, which accounted for 29% (848 ha) of the study area, of which 17% (502 ha) was owned by the NPS (Appendix A). The primary differences in vegetation between 1989 and 2009 included forbs/shrubland that aged into forest, recently cleared shrublands and forests, and an increase in built-up land.

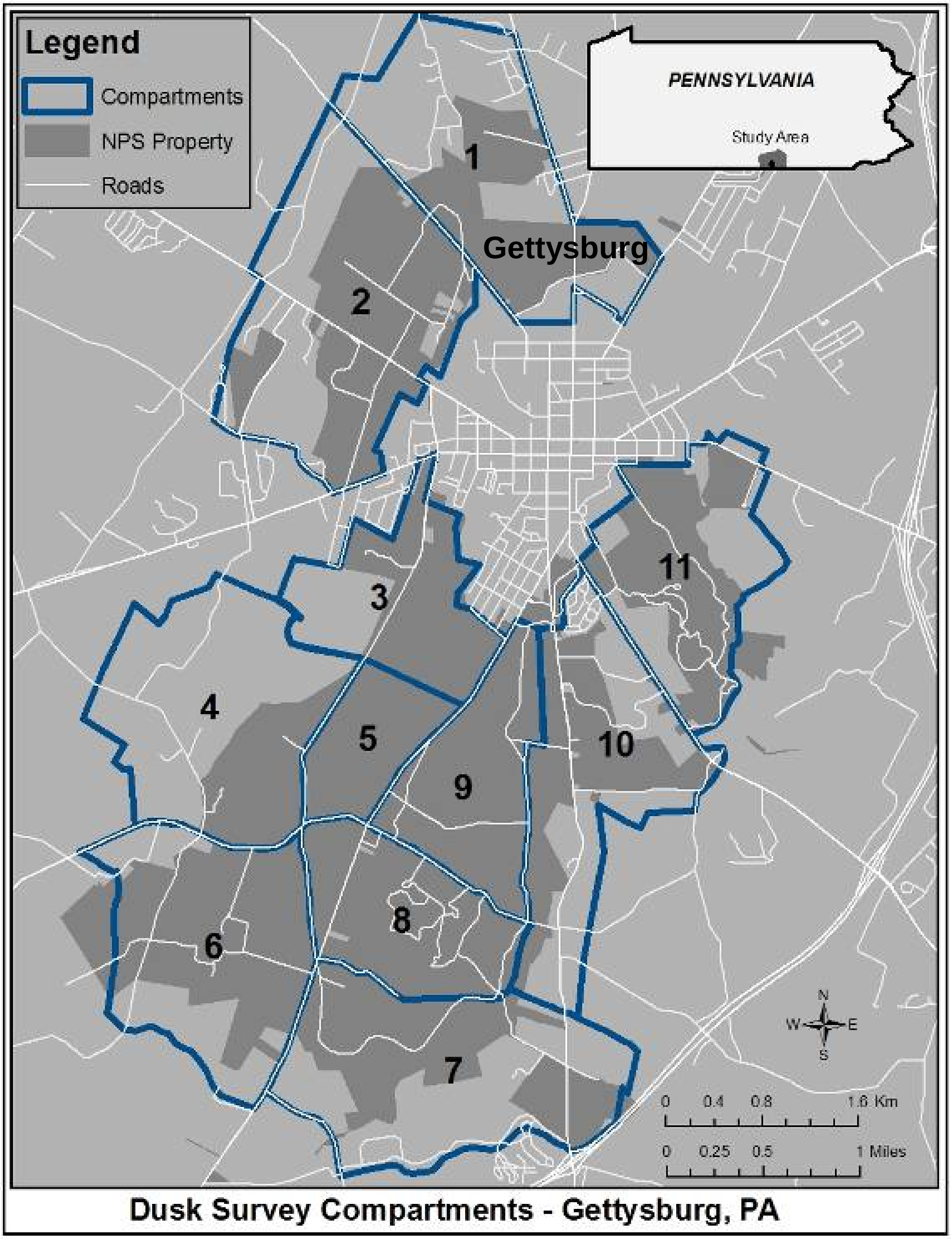

Figure 6. The 11 compartments in which white-tailed deer were counted during dusk mark-resight surveys from April 2009 to November 2010 in the 2,913 ha study area in Adams County, Pennsylvania. The areas in dark gray are National Park Service (NPS) owned property and areas in light gray are privately owned property.

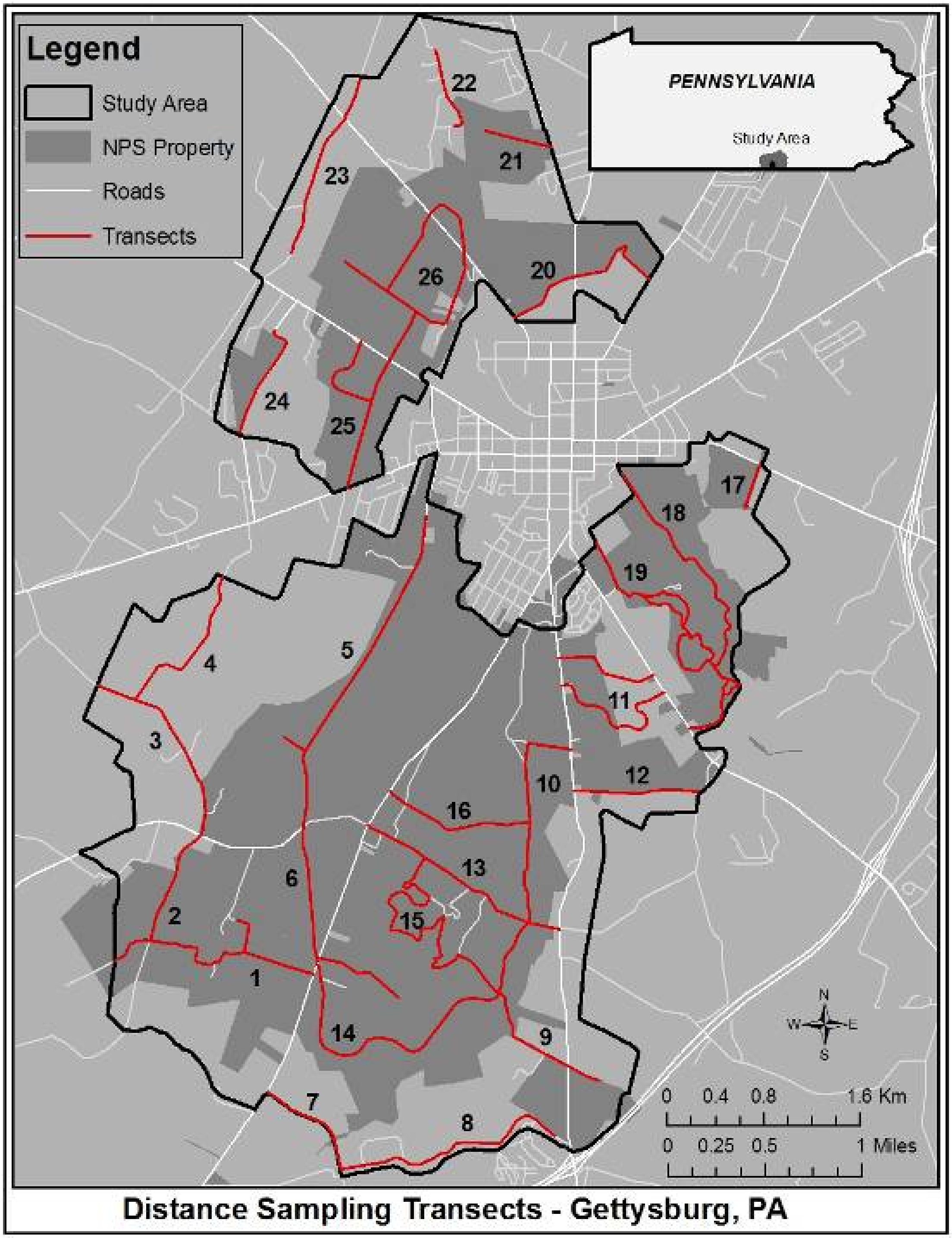

Figure 7. The 26 transects used during distance sampling and spotlight mark-resight surveys for white-tailed deer, performed in the 2,913 ha study area surrounding Gettysburg, Pennsylvania from April 2009 to November 2010. Roads not used as transects are shown in white. The areas in dark gray are National Park Service (NPS) owned property and areas in light gray are privately owned property.

Methods

Deer Capture

We captured deer throughout the study area during January–April of 2009 and January–April of 2010 using rocket nets (Beringer et al. 1996, Haulton et al. 2001) and modified Clover traps (Clover 1956, Beringer et al. 1996, Haulton et al. 2001) over bait (shelled corn and apples). We sedated deer captured with rocket nets via an intramuscular injection of xylazine hydrochloride (100 mg/mL) at approximately 1 mg/1.8 kg body mass (Rosenberry et al. 1999). Prior to release (10–30 min), we administered tolazoline hydrochloride (100 mg/mL) intramuscularly to reverse the effects of the xylazine hydrochloride at approximately 1 mg/0.2 kg body mass (Rosenberry et al. 1999). We manually restrained and blindfolded deer captured in Clover traps and did not sedate them if they could be handled safely. We released non-sedated deer within five minutes. The capture and handling of deer followed protocols approved by The Pennsylvania State University Institutional Animal Care and Use Committee (IACUC # 29677).

Deer <1 year of age at time of capture were considered juveniles, and all deer >1 year of age were considered adults. We based age-class determination on body size and eruption of adult lower incisors and additionally, for adult males, evidence of antler growth in the previous year. We fitted all captured deer with ear tags (Original Tags™, Temple Tag Co., Temple, TX, USA) imprinted with a unique ID number and toll-free telephone number. Additionally, we fitted all captured deer with Global Positioning System (GPS) collars (PRO Light-3, VECTRONIC Aerospace GmbH, Berlin, Germany), which were imprinted with a toll-free telephone number for reporting, "Penn State University," and "REWARD."

We attached a narrow strip of red reflective tape to the front of the GPS-collar battery pack to aid in detection of GPS-collared deer. The reflective strip was positioned such that it could only be seen when deer were looking at a spotlight, yet it did not increase the probability of detection and it enabled us to easily determine whether a deer was GPS-collared or not after detection. We used three different size diameters of collars (38, 46, and 56 cm) weighing 838, 863, and 891 g, respectively, with the harnesses capable of additional adjustment of size to best fit each deer. On mature adult males, we used the largest collars with a 4 cm layer of degradable foam to allow for growth and swelling of the neck during the rut. On juvenile males, we used the medium-sized collars with an 8 cm layer of degradable foam to keep the collar from being cast, yet allowing for growth and swelling of the neck during the rut. On all female deer, we used the smallest collars. We set the GPS schedule to take a GPS fix every five minutes (approximately 48 locations per deer per night) during the time that we conducted surveys; collars transmitted GPS locations daily to a computer via a cellular-phone network.

Dusk Mark-resight Surveys

In April 2009, we performed surveys using the protocols currently used by GNMP-ENHS for its April dusk deer counts, which, due to staff limitations, was adjusted from the method of Storm et al. (1992) so that only 2–3 people were required to perform a survey. We used only one survey crew consisting of a driver and 1–2 observers using binoculars and seated in a pick-up truck to count deer. Observers surveyed two to four of the 11 compartments of the study area (Figure 6) each evening until all 11 compartments were surveyed. Thus, a single survey was accomplished in three or four days. We repeated surveys until the entire study area was surveyed three times.

We performed mark-resight surveys in the study area during November 2009, April 2010, and November 2010 at dusk (60 minutes prior to sunset until about 30 minutes after sunset), which were the same months when Storm et al. (1992) performed surveys. We used the protocol established by Storm et al. (1989, 1992), which required each of the 11 compartments to be surveyed simultaneously by one or more people, who continuously traveled on all survey roads in the assigned compartment. Observers used binoculars to classify deer as marked or unmarked, juvenile or adult, antlered or antlerless, and noted the habitat (woods or field) in which they observed the deer (Storm et al. 1989, 1992). With this method, observers surveyed the entire study area (Figure 6) in one evening, meeting the assumptions of most mark-resight estimators regarding deer movements (i.e., a given deer could not be counted in multiple compartments during a single survey). The survey period included three surveys conducted during three consecutive days with suitable weather conditions (wind <32 km/hr, no rain or only drizzle, visibility >1.6 km) to increase precision of abundance estimates.

We used the Lincoln-Petersen (L-P) estimator to estimate abundance (*N*) for each evening of each dusk count survey where

$$\hat{N} = \frac{(n_1 + 1)(n_2 + 1)}{(m_2 + 1)} - 1,$$

n_1 was the number of marked deer available (in the study area) each evening, n_2 was the total number of deer that were identified as marked or unmarked, and m_2 was the number of marked or GPS-collared deer seen (Seber 1982). We determined the number of GPS-collared deer in the study area (n_1) each evening for each survey by monitoring GPS locations. We calculated variance as

$$\hat{\mathrm{var}}(\hat{N}) = \frac{(n_1 + 1)(n_2 + 1)(n_1 - m_2)(n_2 - m_2)}{(m_2 + 1)^2 (m_2 + 2)},$$

standard error as $\hat{\mathrm{SE}}(\hat{N}) = \sqrt{\hat{\mathrm{var}}(\hat{N})}$**,** and the coefficient of variation (CV) as $\hat{\mathrm{CV}} = \sqrt{\hat{\mathrm{var}}(\hat{N})} / \hat{N} \times 100$ (Seber 1982). According to Chao (1989), we calculated log-normal 95% lower ($m + (\hat{N} - m)/C,$) and upper ($m + (\hat{N} - m) \times C$) confidence intervals, where $m = n_1 + n_2 - m_2$ and

$$C = \exp\left\{ z_{\alpha/2}\sqrt{\ln\left(1+\frac{\widehat{\mathrm{var}}(\hat{N})}{(\hat{N} - m)^2}\right)}\right\}.$$

The L-P estimator assumes a closed population; thus, to meet this assumption, it is critical to survey the entire study area in one evening. Therefore, the current survey method used by park managers violated this assumption because it took multiple days to survey the entire study area, which could result in immigration or emigration and multiple observations of the same individual. Additionally, by only making one trip through each compartment, we expected that the sighting probability, and hence the number of deer seen, would be lower than when each compartment was surveyed continuously each evening.

Using the survey methods outlined by Storm et al. (1992), each survey period provided three independent estimates of *N*. We calculated an arithmetic average of the L-P estimates for the three evenings, the standard error as the standard deviation of the three estimates, and log-normal 95% lower and upper confidence intervals, respectively, of $\hat{N}/C$, $N \times C$, according to Chao (1989), where

$$C = \exp\left\{ 1.96\sqrt{\ln\left(1+\frac{\widehat{\mathrm{var}}(\hat{N})}{(\hat{N})^2}\right)}\right\}.$$

In addition, we used the joint hypergeometric maximum likelihood estimator (JHE) in program NOREMARK (Bartmann et al. 1987, White and Garrott 1990, Neal 1990, Neal et al. 1993, White 1996) to combine data from the three surveys for each survey period into a single population estimate. The JHE is similar to the L-P estimator but uses data from multiple surveys to estimate *N* by maximizing the likelihood

$$\mathcal{L}(N \mid M_i, n_i, m_i) = \prod_{i=1}^{k} \frac{\binom{M_i}{m_i}\binom{N - M_i}{n_i - m_i}}{\binom{N}{n_i}},$$

where M_i is the number of marked deer available each evening, n_i is the number of identified deer seen (marked plus unmarked) each evening, and mi is the number of marked deer seen each evening. We used profile likelihood confidence intervals.

We calculated a new average detection probability for all deer for each dusk mark-resight survey as $\hat{\hat{p}}_j = \sum m_{2ij} / \sum n_{1ij}$, where m_{2ij} equals the number of marked deer seen during the i^{th} day of the j^{th} survey and n_{1ij} equals the number of marked deer available during the i^{th} day of the j^{th} survey.

Spotlight Mark-resight Surveys

We conducted additional mark-resight surveys by spotlight after dusk in the study area prior to culling efforts (August 2009 and 2010), during culling efforts (November 2009 and 2010), after the culling operation (January 2010), and following the deer capture season (April 2009 and 2010). We surveyed in April and November because these are the same months that Storm et al. (1992) performed surveys and to allow comparison with dusk count estimates. We chose to perform additional surveys in August and January to investigate the robustness of abundance estimates with respect to changes in visibility on the landscape. In August, visibility is poor because of dense foliage in forests and corn and tall grasses in fields. In January, visibility is better in both forests and fields because there are no leaves on trees and all row crops have been harvested. We made minor adjustments to the day of the month for surveys during the 2010 season to avoid dates with high visitor traffic in and around the park.

We started spotlight surveys 30 minutes after sunset and continued for approximately 3–5 hours each night. It took approximately 2–3 nights to survey the study area once. During the survey period we surveyed the study area three times to improve precision of abundance estimates. We performed surveys using a driver and two observers standing in the bed of a pick-up truck, using handheld spotlights (240 SL BLITZ, TUFFLIGHTS.COM), in which each observer was responsible for illuminating the area on their side of the road to detect deer.

We included additional roads and viewpoints to fields within the study area, but not viewable from transects to improve coverage of the study area. We traversed transects at 10–25 km/hr and varied initial starting points and routes to minimize temporal influences in deer detection that may have existed because of deer activity patterns. We divided transects into three groups for surveying each night based on geographic location (e.g., North, Southwest, and Southeast). We did not survey on a particular night if adverse environmental conditions existed (wind ≥32 km/hr, rain, visibility ≤1.6 km).

Once an observer spotted a deer or group of deer, the driver stopped, the observer shined a spotlight on the deer or group of deer and looked for the presence of GPS collars with assistance from the other observer using binoculars. The observer also aged each deer as a fawn or adult and noted whether it was antlered or antlerless. If it was not possible to determine if a deer was GPS-collared, it was recorded as unidentified. We used a GIS to identify all observed unidentified deer as marked or unmarked and to individually identify all marked deer seen by comparing GPS locations taken during the time of the observation to the location of the observation.

The assumption of a closed population for the L-P estimator could not be met during each spotlight survey because it took 2–3 days to completely cover the study area. Therefore, we used Bowden's estimator to estimate abundance ($\hat{N}$) for each spotlight survey period (Bowden and Kufeld 1995). The assumptions for Bowden's estimator are less restrictive than the assumptions for the L-P estimator and other mark-resight estimators (e.g., Bowden's estimator does not require the assumptions of homogeneous detection probabilities and independent sighting trials; Diefenbach 2009). Additionally, one does not have to survey the entire study area and the probability of sighting a deer can vary among individual deer over time (Bowden and Kufeld 1995, Diefenbach 2009). Bowden's estimator also assumes a geographically and demographically closed population, although temporary emigration is allowed (Bowden and Kufeld 1995). Other assumptions include individually identifiable marks (i.e., GPS-collars), marks are placed on a random sample of individuals, marks are not lost during the sighting attempts, and marked and unmarked deer are equally likely to be observed (Bowden and Kufeld 1995). Bowden's estimator estimates the number of deer that have used the study area at any point during the entire study (e.g., fate of marked individuals is typically unknown), whereas the L-P estimator estimates abundance of deer in the study area each evening (Bowden and Kufeld 1995). However, we estimated the number of deer that used the study area at any point during each survey period (e.g., 1 week) by monitoring GPS locations of the marked population.

For each mark-resight survey using Bowden's estimator, we let y_i be the number of sightings of marked deer *i*, $\bar{y} = \sum_{i=1}^{n} (y_i / n)$ be the mean number of times the *n* marked and available deer were sighted, $s_y^2 = \sum_{i=1}^{n} \left[(y_i - \bar{y})^2 / (n-1)\right]$ be the sample variance of the mean sightings per marked deer, and Y be the total number of sightings of marked and unmarked deer (Bowden and Kufeld 1995). We determined the number of available marked deer (*n*) by monitoring GPS locations of all GPS-collared deer. If a marked deer was in the study area during the time that we performed a survey, then we considered it available for that survey.

The intuitive estimator of abundance, $\tilde{N} = Y/\bar{y}$, tends to be positively biased with small sample sizes; therefore, we used an approximately unbiased estimator for *N*, developed by Bowden and Kufeld (1995), where

$$\hat{N} = \left(\tilde{N} + \frac{s_y^2}{\bar{y}^2}\right) \Big/ \left(1 + \frac{s_y^2}{n\bar{y}^2}\right),$$

with estimated variance

$$\widehat{\text{var}}(\hat{N}) = \hat{N}^2 \left\{ \left(\frac{1}{n} - \frac{1}{\hat{N}}\right) \left(\frac{s_y^2}{\bar{y}^2}\right) \Big/ \left(1 + \frac{s_y^2}{n\bar{y}^2}\right)^2 \right\},$$

coefficient of variation (CV), $\widehat{CV} = \sqrt{\widehat{Var}(\hat{N})}/\hat{N} \cdot 100\%$, and logarithm transformed lower $(\hat{N}/C)$ and upper $(\hat{N} \cdot C)$ 95% confidence intervals where

$$C = \exp\left(t_{1-\alpha/2,n-1}\sqrt{\left[\frac{1}{n} - \frac{1}{\hat{N}}\right]\frac{s_y^2}{\bar{y}^2}}\right)$$

Change-in-ratio Estimator

The CIR technique (Paulik and Robson 1969, Seber 1982, Conner et al. 1986) requires two distinguishable classes of animals (e.g., antlerless and antlered). If the proportion of antlerless and antlered deer in the population changes before and after culling operations (e.g., only antlerless deer are culled) and all antlerless deer removed during the culling period are known, we can estimate total population size before removals as

$$\hat{N}_1 = \frac{R_x - (R \times P_2)}{P_1 - P_2},$$

where R_x is the number of antlerless deer removed (known), $R = R_x - R_y$ = total number of antlerless and antlered deer removed (known), $P_1 = X_1 / N_1$ = the proportion of antlerless deer before culling, and $P_2 = X_2 / N_2$ = the proportion of antlerless deer after culling operations (Conner et al. 1986). Additionally, P_1 and P_2 would need to be estimated using some independent sampling scheme (e.g., spotlight surveys before and after culling operations). Assumptions of the CIR method used in this analysis include: (1) a closed population, except for removals; (2) observed proportions of antlerless and antlered deer in the sample are unbiased estimates of the true proportions in the study area; (3) all deer removed from the study area are known; and (4) the proportion of antlerless deer in the harvest is different from that in the pre-culling population. However, to meet the second assumption for $\hat{P}_1$ and $\hat{P}_2$, sighting probabilities must remain constant throughout the period of culling. We could calculate variance of estimates as

$$\hat{\text{var}}(\hat{N}_1) = \frac{\hat{N}_1^{\,2}\,\text{var}(\hat{P}_1) + \hat{N}_2^{\,2}\,\text{var}(\hat{P}_2)}{(\hat{P}_1 - \hat{P}_2)^2},$$

and

$$\hat{\text{var}}(\hat{X}_1) = \frac{\hat{N}_1^{\,2}\hat{P}_2^{\,2}\,\text{var}(\hat{P}_1) + \hat{N}_2^{\,2}\hat{P}_2^{\,2}\,\text{var}(\hat{P}_2)}{(\hat{P}_1 - \hat{P}_2)^2}.$$

When sampling was with replacement, we could calculate variance of detection probability as

$$\hat{\text{var}}(\hat{P}_i) = \frac{\hat{P}_i(1 - \hat{P}_i)}{n_i},$$

where n_i is the sample size and $\hat{P}_i = x_i / n_i$

Catch-per-unit-effort Estimator

We used a conditional likelihood approach to estimate *N* using catch-effort data (Gould and Pollock 1997) for female white-tailed deer harvested during culling operations at GNMP-ENHS. Culling efforts at GNMP-ENHS target antlerless deer, which include females and fawn males. Additionally, later in the season some adult males (>1.5 years old) are culled because their antlers were cast. Therefore, to accurately model catch-effort, we used only data for culled female and fawn male deer in the analysis to estimate abundance of antlerless deer in the population. We defined effort as the total number of hours a gunman spent per week during culling operations.

We estimated *N* using program MARK (White and Burnham 1999). We used closed capture models with the Huggins parameterization because with this approach *N* is conditioned out of the likelihood and allowed us to model capture probabilities as a function of culling effort. We modeled capture probabilities similar to a removal model, in which the probability of recapture is zero because culled deer were removed from the population. We modeled capture probabilities (p) as a linear function of culling effort with the logit link, i.e., $\text{logit}(p) = \beta_0 + \beta_1 \times$(hours of culling effort). Input and output from the analyses run in program MARK is provided in Appendix B.

Distance Sampling Surveys

We conducted distance sampling surveys, at the same time we conducted mark-resight spotlight surveys, at GNMP-ENHS prior to culling efforts (August 2009 and 2010), in the middle of culling efforts (November 2009 and 2010), after the culling operation (January 2010), and following the capture season (April 2009 and 2010). We started surveys no earlier than 30 minutes after sunset, and surveys lasted approximately 3–5 hours. Two observers illuminated their respective sides of the transect with handheld spotlights while standing in the bed of a pick-up truck. When deer were detected, we recorded group size, distance and direction to the group, x–y coordinates of the observer, and whether the deer was located in a field or the forest (Appendix C). We defined groups based on behavioral cues and proximity to one another. Each deer in a group was no more than one-half the distance from the closest deer in its group than to the next closest deer of a neighboring group. We obtained distance and direction using a handheld PC/GPS unit (HP–iPAQ rx5900, Hewlett-Packard Company, Palo Alto, CA, USA), running Cybertracker data collection software (http://www.cybertracker.co.za), linked to a laser rangefinder (LTI-TruPulse 360, Laser Technology, Inc., Centennial, CO, USA) via Bluetooth. We calculated perpendicular distances as the shortest distance between the transect and the location of each observation, using a GIS.

We traversed transects at 10–25 km/hr and varied initial starting points to minimize temporal influences in deer detection that may have existed because of deer activity patterns. We divided transects into three groups and surveyed each night based on geographic location (e.g., North, Southwest, and Southeast), such that it took approximately 2–3 nights to survey all transects once and approximately 6–9 nights to survey all transects three times. We did not survey on a particular night if adverse environmental conditions existed (wind $\geq$32 km/hr, rain, visibility $\leq$1.6 km).

We used program DISTANCE (Thomas et al. 2010) to estimate density of deer groups and employed a size-bias regression method to model group size as a function of distance from the transect. If this regression was not significant ($\alpha = 0.05$), we used mean group size. Because the detection function is likely different for open areas than for wooded areas, we used the habitat type for each observation (field or forest) as a covariate, using multiple covariate distance sampling (MCDS). To account for differences in observer detection rates (see Diefenbach et al. 2003), we tested additional models including both habitat type and observer as covariates. We used both half-normal and hazard-rate key functions to model the detection function. We constrained models to use no adjustment terms to ensure the detection function was monotonically non-increasing (Marques et al. 2007). We used right truncation distances of 250 meters and 80 meters, because few observations occurred beyond these distances in fields and forests, respectively. We used Goodness of Fit tests and Akaike's Information Criterion (AIC; Burnham and Anderson 1998) as aids in model selection for the detection function curve.

Resource Selection Model

We collected GPS locations of deer during the time we performed distance sampling surveys to model habitat use by creating a Resource Selection Function (RSF; Manly et al. 2002) for each survey using a zero-inflated negative binomial model (ZINB; count model was negative binomial with a log link and zero-inflated model was binomial with a logit link) for each deer. In a GIS, we randomly placed 3,000 sampling units (100 m diameter circles) across the study area. The response variable or measure of use (y) was the number of GPS locations in each sampling unit, and we used habitat covariates (X_k) as predictor variables in models to estimate each parameter (β_k), such that the $RSF = e^y$, *where* $y = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_3 + \ldots \beta_k X_k$ (Millspaugh et al. 2006, Sawyer et al. 2006). We measured habitat covariates as the percentage of forested land within each sampling unit and distance (m from center of each sampling unit) to the nearest road, forest-field edge, and NPS property boundary. To reduce edge effects, we allowed center points of circles to extend to the study area boundary, and quantified covariates outside of the study area. We fitted ZINB models with the pscl library in program R (Bates et al. 2008 and R Developmental Core Team, 2009; Appendix D). We used the zero-inflated negative binomial model because count data are oftentimes overdispersed (negative binomial model) and ≥95% of sampling units contained no locations for each deer (zero-inflated model). In addition, we used offset terms equal to the natural logarithm of the total number of GPS locations per deer to scale the RSF equally among deer. To aid in model convergence we normalized each covariate $\left[(X_k - \bar{X}_k)/SD(X_k)\right]$.

We developed eight models selected *a priori* that always included an intercept and various combinations of habitat covariates that we believed were important for selection or avoidance of deer in the study area (Table 2). We predicted a positive relationship between deer selection and increasing distance from the nearest road, such that deer would avoid areas near roads. We also modeled a quadratic relationship to allow for nonlinearity, where we predicted deer would avoid areas very close to roads the most, but avoidance would become less critical as distance from the road increased. Because forested areas are relatively sparse in the study area (<30% is forested) and open areas tended to be large, we predicted a positive relationship between deer selection and percent forest. We also modeled a quadratic relationship to allow for nonlinearity and incorporate a possible threshold level of fragmentation. However, we believed there would be seasonal variation (e.g., row crops such as corn in the summer and early fall may decrease selection of heavily forested areas). We predicted a negative relationship between deer selection and distance to forest-field edges, such that during surveys, deer would select for open areas near forest edges. In addition, we modeled a quadratic relationship to allow for nonlinearity. Finally, we predicted a negative relationship between deer selection and distance to NPS boundary, such that deer would select for areas close to the park boundary and near private property rather than in the interior. The NPS shoots deer primarily in the central regions of the park, and there are

Table 2. Zero-inflated negative binomial models selected *a priori* for analyzing resource selection for each white-tailed deer collared with a global positioning system device during each distance sampling survey, Gettysburg, Pennsylvania, 2009–2010.

Model	***k***[a]	**Covariates**[b]
1	5	I + PF + FFE
2	7	I + PF + PF^2 + FFE + FFE^2
3	7	I + PF + FFE + NPS + RD
4	8	I + PF + FFE + FFE^2 + NPS + RD
5	9	I + PF + PF^2 + FFE + FFE^2 + NPS + RD
6	11	I + PF + PF^2 + FFE + FFE^2 + NPS + NPS^2 + RD + RD^2
7	9	I + PF + FFE + FFE^2 + NPS + RD + PF×RD
8	10	I + PF + FFE + FFE^2 + NPS + RD + PF×FFE + PF×FFE^2

[a] k = no. of model parameters.
[b] I = Intercept, PF = Percent Forest, FFE = distance to nearest forest-field edge, NPS = distance to nearest National Park Service owned land boundary, RD = distance to nearest road, and a multiplication sign indicates interaction terms.

more anthropogenic disturbances because of park visitors. Furthermore, we included an interaction of distance to the nearest road and percent forest in model 7 (Table 2) because open areas and fields tend to be near roads (e.g., roads provide access to fields). Also, we included an interaction between percent forest and distance to the nearest forest-field edge in model 8 (Table 2) to examine whether deer were selecting for forest-field edges near heavily forested areas or in more open and fragmented areas.

We used an information-theoretic approach (Burnham and Anderson 2002) to compare models identified *a priori* (Table 2). We calculated an AIC value for each model for each deer, and then selected the model with the lowest sum of AIC values across deer as the best model. Using the best model, we calculated parameter estimates and weighted each i^{th} parameter estimate for each j^{th} deer ($\hat{\beta}_{ij}$) by the inverse of its estimate of standard error so the weighted average for each i^{th} parameter for all deer is then

$$\bar{\hat{\beta}}_i = \frac{\sum_j \left(\hat{\beta}_{ij} \times \frac{1}{SE\left(\hat{\beta}_{ij}\right)} \right)}{\sum_j \frac{1}{SE\left(\hat{\beta}_{ij}\right)}}$$

We calculated a weighted population variance estimate for each i^{th} parameter of deer j as,

$$S_i^{\,2} = \frac{V_{1i}}{V_{1i}^{\,2} - V_{2i}} \sum_{j=1}^{n} \sum_{i=1}^{n'} w_{ij} (x_{ij} - \bar{x}_i)^2,$$

where $w_{ij} = 1/\hat{\sigma}_{ij}^{\,2}$, $V_{1j} = \sum_{j=1}^{n} \sum_{i=1}^{n'} w_{ij}$, $V_{2i} = \sum_{j=1}^{n} \sum_{i=1}^{n'} w_{ij}^2$, n was the total number of deer, n' was the total number of parameters, and $\hat{\sigma}_{ij}^{\,2}$ was the variance for the i^{th} parameter for the j^{th} deer.

Resource Selection Map

After we obtained weighted parameter estimates from the selected ZINB model using random sampling units, we used a GIS to place a 5×5 m grid of cells systematically across the study area. Next, we quantified the same distance covariates used in the ZINB to the center of each grid cell and used a 100 m diameter circle around each grid cell center point to quantify percent forest. Then, we calculated an RSF value for each grid cell as $RSF = e^{y}$, where $y = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_3 + \ldots \beta_k X_k$, using weighted parameter estimates from the selected ZINB model and covariate values for each grid cell. Greater RSF values represented greater use by deer.

Are Deer Uniformly Distributed with Respect to Roads?

To examine whether the distribution of deer relative to the distribution of transects was uniform, we modeled the distribution of GPS locations from GPS-collared deer with respect to the perpendicular distance to each transect for locations in open areas and locations in forests using program DISTANCE. For each transect, we measured the shortest distance to every GPS location using a GIS. Then, using program DISTANCE, we right-truncated data at 80 m and 250 m and fitted uniform detection functions with no adjustment terms. Also, to the same data we fitted a combination of key functions (uniform, half-normal, hazard-rate) and series expansions (cosine, simple polynomial, and hermite polynomial), and used automated selection (via AIC) of up to three adjustment terms and no constraint the detection function be monotonically non-increasing. If the uniform curve with no adjustment terms had the lowest AIC, then we concluded that the distribution of deer was uniform (not correlated) with respect to the distribution of transects.

Do Roads Provide a Representative Sample of the Study Area?

In a GIS, we calculated the percentage of forested land near transects and compared that to the percentage of forested land within the entire study area. If transects were representative of the study area, the proportion of forested land within the sampled area would be similar to the proportion of forested land in the study area.

Furthermore, we used information from the RSF map to investigate whether resource selection near transects was representative of resource selection across the study area. We used the RSF to estimate the proportion of the study area population near transects during each survey, $\hat{p}_{RSF}$,

$$\hat{p}_{RSF} = \frac{\sum RSF(survey\ zone)}{\sum RSF(study\ area)}.$$

We calculated $\hat{p}_{RSF}$ for two different truncation distances (80 m and 250 m), hereafter termed survey zones (Appendix E). If transects were representative of the study area, we would expect $\hat{p}_{RSF}$ to equal the proportion of the study area surveyed using either 80 m or 250 m transects. We calculated standard errors and 95% confidence intervals for $\hat{p}_{RSF}$ using parametric bootstrapping, incorporating the standard errors for each parameter in the RSF model. If the 95% confidence interval for $\hat{p}_{RSF}$ overlapped the proportion of the study area surveyed, then we failed to reject the null hypothesis that transects were representative.

Distance Sampling Estimator – Adjusting for Nonrandom sampling

If deer are not distributed uniformly with respect to distance sampling transects (i.e., roads), then two types of error could be introduced into the distance sampling population (or density) estimate. First, the detection function may be incorrectly modeled (see Figures 1–5) and second, transects are not representative of the study area. We incorporated information from the RSF to account for nonrandom sampling and potentially developed an estimator with less bias.

If detection is different in open areas versus forested areas, MCDS can accurately account for these differences if the transect is representative of the study area (i.e., the percentage of forest within the survey zone is the same as the complete study area). To attempt to circumvent the potential problem that transects were not representative of the study area, we estimated abundance in the survey zone divided by $\hat{p}_{RSF}$

$$\hat{N} = \frac{\hat{N}_{(survey\ zone)}}{\hat{p}_{RSF}}$$

where

$$\hat{N}_{(survey\ zone)} = \hat{D} \times Area_{(survey\ zone)} = \frac{n \times E(S)}{2wL\hat{P}_a} \times Area_{(survey\ zone)} = \frac{n \times E(S)}{\hat{P}_a},$$

and the area of each survey zone ($Area_{(survey\ zone)}$) = 2*wL*, such that *w* is the width or right-truncation distance and *L* is the total length of transects. Thus, area cancels out of the equation, yielding abundance within the surveyed area as the number of groups detected (*n*) within *w* multiplied by the mean cluster size $E(S)$ and divided by the probability of detection ($\hat{P}_a$).

To incorporate the relative proportions of forests and fields in the sampled area into the estimate of detection probability, we estimated average detection probabilities for fields ($\overline{p}_{Field}$) and forests ($\overline{p}_{Forest}$) separately and applied those across the area of each survey zone based on the proportion of each habitat. We calculated $\overline{p}_{Field}$ and $\overline{p}_{Forest}$ by first modeling detection functions for fields and forests separately using conventional distance sampling methods (CDS) for detections in each survey zone (80 m and 250 m) for each survey month. Because of the small sample size of detections of deer in forests, we pooled observations across years by survey month. Models included different combinations of key functions (uniform, half-normal, and hazard-rate) and series expansions for up to three adjustment terms (cosine, simple polynomial, and hermite polynomial) chosen with sequential automated selection based on AIC. We constrained models to be strictly monotonically non-increasing. We used goodness of fit tests and AIC (Burnham and Anderson 1998) as aids in model selection for the best fit of the detection function curves for fields and forest.

Next, we created a 5 m × 5 m grid over each survey zone and calculated a detection probability value, $\hat{p}_i$, for each i^{th} grid cell based on its distance from the nearest transect and whether it was predominated by a field or forest (i.e., y value from the detection curve for fields or forests [Appendix F]), such that

$$\overline{p}_{Field} = \frac{\sum \hat{p}_{i(Field)}}{n_{(\#grid\ cells\ in\ Fields)}}$$

and

$$\overline{p}_{Forest} = \frac{\sum \hat{p}_{i(Forest)}}{n_{(\#grid\ cells\ in\ Forests)}}.$$

We calculated standard errors and 95% confidence intervals for $\overline{p}_{Field}$ and $\overline{p}_{Forest}$ using parametric bootstrapping based on 1,000 samples.

We calculated abundance in each survey zone as,

$$\hat{N}_{(survey\ zone)} = \frac{\overline{n}_{Field}}{\overline{p}_{Field}} \times E(S)_{Field} + \frac{\overline{n}_{Forest}}{\overline{p}_{Forest}} \times E(S)_{Forest},$$

where $\overline{n}_{Field}$ was the number of observed groups of deer in fields divided by the number of surveys, $\overline{p}_{Field}$ was the average detection probability in fields, $E(S)_{Field}$ was the mean group size in fields, $\overline{n}_{Forest}$ was the number of observed groups of deer in forests divided by the number of surveys, $\overline{p}_{Forest}$ was the average detection probability in forests, and $E(S)_{Forest}$ was the mean group size in forests. We calculated each variable separately for each survey zone. In addition, we calculated standard errors and 95% confidence intervals for $E(S)_{Field}$ and $E(S)_{Forest}$ using non-parametric bootstrapping, where we sampled with replacement from the observed group sizes, such that we created 1,000 estimates of mean cluster size for fields and forests for each survey.

We calculated standard errors and 95% confidence intervals for $\hat{N}$ by using the 1,000 bootstrapped estimates of $\overline{p}_{Field}$, $\overline{p}_{Forest}$, $E(S)_{Field}$, $E(S)_{Forest}$, and $\hat{p}_{RSF}$ in the equation

$$\hat{N} = \frac{\frac{\overline{n}_{Field}}{\overline{p}_{Field}} \times E(S)_{Field} + \frac{\overline{n}_{Forest}}{\overline{p}_{Forest}} \times E(S)_{Forest}}{\hat{p}_{RSF}}.$$

Results

Capture and Sample Sizes

During January–April 2009, we captured and GPS-collared 38 deer of all age and sex classes in the study area, of which 16 to 28 were available (present in the study area) during the dusk surveys (Table 3) and 18 to 31 were available during distance sampling and mark-resight spotlight surveys (Table 4) prior to the second capture season. The total number available per survey decreased over time because of mortality, cast collars, dispersal, and temporary emigration from the study area, all of which were more prevalent in males (Table 3 and Table 4). At the start of the January 2010 trapping season, 18 GPS-collared deer from the 2009 trapping season were present on the study area, which we treated as adults during 2010. From January 2010 to April 2010, we captured 20 additional deer. After this second capture season, 14 to 23 GPS-collared deer were available during dusk surveys (Table 3) and 20 to 30 were available during spotlight surveys (Table 4).

Table 3. Number of marked white-tailed deer, by age and sex class, present in the study area during each complete round of dusk mark-resight surveys, Gettysburg, Pennsylvania, 2009–2010.

		Juveniles		Adults		Total No.
Survey period	Survey	Male	Female	Male	Female	of marked deer
Apr 9–16, 2009	1	6	3	5	11	25
	2	6	3	8	11	28
	3	6	3	6	11	26
Nov 20–25, 2009	1	0	3	3	9	15
	2	1	3	4	9	17
	3	0	3	3	10	16
Apr 1–4, 2010	1	3	1	6	13	23
	2	3	1	5	14	23
	3	3	2	6	12	23
Nov 15–19, 2010	1	0	1	3	12	16
	2	0	1	5	11	17
	3	0	1	2	11	14

Table 4. Number of marked white-tailed deer, by age and sex class, on the study area during at least some portion of each spotlight mark-resight survey, Gettysburg, Pennsylvania, 2009–2010.

	Juveniles		**Adults**		**Total No.**
Survey period	**Male**	**Female**	**Male**	**Female**	**marked deer**
Apr. 9–16, 2009	7	3	9	12	31
Aug. 3–9, 2009	7	3	8	12	30
Nov. 20–25, 2009	1	3	4	10	18
Jan. 5–8, 2010	1	2	5	11	19
Apr. 1–4, 2010	4	2	9	15	30
Aug. 25–30, 2010	3	1	8	12	24
Nov. 15–19, 2010	0	2	6	12	20

Dusk Mark-Resight Surveys

During the April 2009 survey period, we used the current survey method used by park managers, where it takes observers multiple days to survey the study area completely. Thus, assumptions of the method developed by Storm et al. (1989) were violated and few marked and unmarked deer were observed relative to the number available (Table 5). No marked deer were observed during the last two surveys; therefore, we could only estimate abundance for the first survey and could not estimate abundance using the JHE or calculate an arithmetic average of L-P estimates (Table 5, Figure 8).

During the November 2009 survey period, no marked deer were observed on the third survey (Table 5). However, using data from the first two surveys, we calculated a JHE abundance estimate of $\widehat{N}$ = 574 (95% CI = 275 – 1,748) and an arithmetic average of L-P estimates of $\widehat{N}$ = 410 (95% CI = 259 – 650, CV = 24), and $\hat{\bar{p}}$ = 0.13 (Table 5, Figure 8). During the April 2010 survey period, marked deer were seen during all three surveys, which allowed us to calculate a JHE abundance estimate of $\widehat{N}$ = 414 (95% CI = 292 – 649), an arithmetic average of the L-P abundance estimates of $\widehat{N}$ = 368 (95% CI = 322 – 421, CV=7), and $\hat{\bar{p}}$ = 0.25 (Table 5, Figure 8). During the November 2010 survey period, we observed marked deer during all three surveys, which allowed us to calculate a JHE abundance estimate of $\widehat{N}$ = 465 (95% CI = 300 – 835), an arithmetic average of the L-P abundance estimates of $\widehat{N}$ = 425 (95% CI = 196 – 921, CV = 41), and $\hat{\bar{p}}$ = 0.23 (Table 5, Figure 8).

Table 5. Abundance ($\widehat{N}$) and density ($\widehat{D}$) estimates of white-tailed deer for the study area using the Lincoln-Petersen estimator and detection probabilities ($\hat{p}$) for each survey of dusk mark-resight surveys, Gettysburg, Pennsylvania, 2009–2010.

Survey period	Survey	Day of Month	n_1 [b]	n_2 [c]	m_2 [d]	$\widehat{D}$	$\widehat{N}$	SE	CV	95% CI	$\hat{p}$
Apr 2009[a]	1	7–9	25	48	2		421	193.5	46	198–1,034	0.08
	2	10–13	28	51	0						
	3	14–16	26	55	0						
Nov 2009	1	20	15	89	2		479	212.7	44	237–1,158	0.13
	2	21	17	56	2		341	151.9	45	168–826	0.12
	3	22	16	84	0						
Apr 2010	1	1	23	84	5		339	107.3	32	204–654	0.22
	2	2	23	94	5		379	120.4	32	227–732	0.22
	3	3	23	128	7		386	102.0	26	254–679	0.30
Nov 2010	1	15	16	92	5		263	77.5	29	168–496	0.31
	2	17	17	111	4		402	136.7	34	236–816	0.24
	3	18	14	121	2		609	269.4	44	302–1,471	0.14

[a]The April 2009 survey was performed such that each survey took 3–4 days to completely survey the study area.
[b]n1 = Number of marked deer available.
[c]n2 = Total number of deer observed (marked and unmarked).
[d]m2 = Number of marked deer observed during survey.

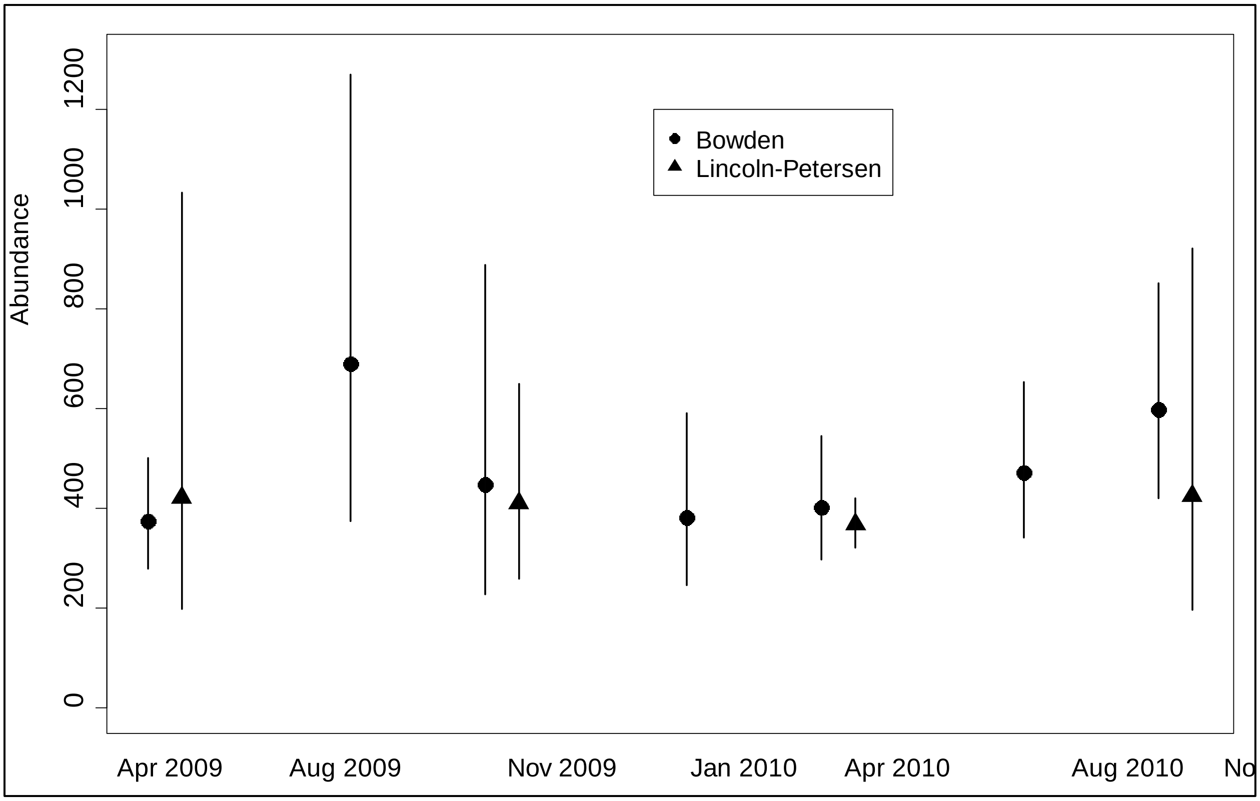

Figure 8. Abundance estimates ($\widehat{N}$) of white-tailed deer and associated 95% confidence interval bars from mark-resight surveys using the Bowden estimator for spotlight surveys and an arithmetic average of the Lincoln-Petersen estimates for dusk surveys from April 2009 to November 2010, Gettysburg, Pennsylvania.

Spotlight Mark-resight Surveys

Estimates of abundance using Bowden's estimator ranged from 375 (95% CI=279–502) to 691 (95% CI=375–1,271; Table 6 and Figure 8). April 2009 and 2010 survey periods, which occurred after each trapping season, had the largest *n* and yielded the most precise estimates across years with an average CV of 15% (Table 6). August and November 2009 survey periods, which coincided with high visitor use of the park (i.e., Labor Day in August and Remembrance Day in November), yielded the worst precision. Ignoring those two surveys, detection probability tended to be highest in August and April and slightly lower in November and January (Table 6).

Table 6. Abundance ($\hat{N}$) and density ($\hat{D}$) estimates of white-tailed deer and measures of precision using Bowden's estimator for each spotlight mark-resight survey period, Gettysburg, Pennsylvania, 2009–2010.

Survey period	n [a]	Y [b]	$\bar{y}$ [c]	($\hat{D}$)	$\hat{N}$	SE	CV	95% CI
Apr 9–16, 2009	31	444	1.16		375	52.6	14	279–502
Aug 3–9, 2009	30	375	0.50		691	185.6	27	375–1,271
Nov 20–25, 2009	18	329	0.67		449	128.0	29	227–889
Jan 5–8, 2010	19	356	0.89		382	74.1	19	247–592
Apr 1–4, 2010	30	439	1.07		403	58.7	15	297–546
Aug 25–30, 2010	24	604	1.25		472	72.3	15	341–653
Nov 15–19, 2010	20	492	0.80		598	98.2	16	420–852

[a] n = total no. of individual marked deer that used the study area during the survey period.
[b] Y = total no. of identified deer seen during the survey period.
[c] $\bar{y}$ = mean no. of times an available marked deer was seen during the survey period.

Heterogeneity in Detection Rates

The few marked deer observed during mark-resight dusk surveys precluded investigation of heterogeneity in detection rates for each dusk survey with respect to sex and age. We observed a sufficient number of marked deer during mark-resight spotlight surveys to investigate heterogeneity in detection rates. We found comparable rates of detection in adult males and adult females during April survey periods, higher rates in adult males than adult females during August survey periods and the January survey period, and lower rates in adult males than adult females during November survey periods (Table 7). Detectability was low for both adult females and juvenile females during the August 2009 survey period and for adult males during the November 2009 survey period (Table 7).

Change-in-Ratio (CIR) Estimator

We could not use the CIR method using previously collected culling data because independent surveys were not conducted to estimate P_1 and P_2 before and after culling operations. Furthermore, we could not meet the assumption that all harvest was reported because information regarding deer harvested by hunters on private lands within the study area was not available to the NPS.

Catch-per-unit-effort (CPUE) Estimator

Estimates of abundance using the CPUE estimator were restricted to antlerless deer using areas available for culling on the study area. Abundance estimates ranged from 81 (95% CI=72–122) to 469 (95% CI=403–589; Table 8). Complete input and output from the analyses is provided in Appendix B.

Table 7. Mean number of times an available marked white-tailed deer was seen ($\bar{y}$) during the survey period and mean per survey ($\bar{\bar{y}}$), by age (A=Adult, J=Juvenile) and sex (M=Male, F=Female), for each mark-resight spotlight survey using Bowden's estimator, Gettysburg, Pennsylvania, 2009–2010. Estimates were not calculated when < 3 marked deer were available for a given sex-age class.

	$\bar{y}$				$\bar{\bar{y}}$			
Survey period	**AM**	**AF**	**JM**	**JF**	**AM**	**AF**	**JM**	**JF**
Apr 9–16, 2009	1.11	1.18	1.00	1.40	0.37	0.39	0.33	0.47
Aug 3–9, 2009	0.75	0.18	1.00	0.20	0.25	0.06	0.33	0.07
Nov 20–25, 2009	0.00	0.80		1.33	0.00	0.29		0.48
Jan 5–8, 2010	1.20	0.82			0.48	0.32		
Apr 1–4, 2010	1.00	0.93	1.75		0.33	0.31	0.58	
Aug 25–30, 2010	1.50	1.08	1.33		0.50	0.36	0.44	
Nov 15–19, 2010	0.67	0.92			0.22	0.31		

Table 8. Abundance estimates ($\hat{N}$) of antlerless white-tailed deer and measures of precision using the catch-per-unit-effort estimator with culling data of antlerless deer, Gettysburg, Pennsylvania, 1996–2011.

Culling period	$\hat{N}$	SE	**95% CI**
Oct 1996–Mar 1997	469	45.7	403–589
Oct 1997–Feb 1998[a]			
Feb 1999–Mar 1999[b]			
Nov 1999–Mar 2000	147	15.1	130–195
Oct 2000–Feb 2001	461	144.7	296–924
Oct 2001–Feb 2002	236	78.2	154–503
Oct 2002–Mar 2003	171	9.7	158–199
Oct 2003–Mar 2004	361	191.9	197–1120
Oct 2004–Mar 2005	129	7.5	121–153
Oct 2005–Feb 2006	158	26.4	127–241
Oct 2006–Mar 2007	82	1.4	81–89
Oct 2007–Jan 2008 [b]			
Oct 2008–Dec 2008	81	10.6	72–122
Oct 2009–Dec 2009[c]			
Oct 2010–Feb 2011	170	65.2	108–410

[a]Culling was not performed in 1998.
[b]Sample size (number of weeks and number of deer culled) was too small for reliable estimates.
[c]No effort data available for analysis.

Distance Sampling Surveys

Models including both observer and habitat as covariates performed worse (based on AIC) than models including only habitat as a covariate for all survey periods for both 250- and 80-m truncation distances. The best models for a right-truncation distance of 250 m included a half-normal detection function for all surveys except for the August 2009 survey, where hazard-rate detection function provided a better fit (Table 9). Estimates of abundance ranged from 253 (95% CI=167–385) to 444 (95% CI=304–650; Table 9). The best models for a right-truncation distance of 80 m included a half-normal detection function for the April 2009 and 2010, January 2010, and November 2010 surveys and a hazard-rate detection function for the August 2009 and 2010 and the November 2009 surveys (Table10). Estimates of abundance from best models ranged from 218 (95% CI=142–336) to 381 (95% CI=238–607; Table 10). Model convergence issues occurred using the 80-m truncation distance, likely because of fewer observations of deer. Number of deer observed, number of deer groups observed, and mean group size are provided in Appendixes G and H.

Resource Selection Model

The number of GPS-collared deer used in the RSF ZINB model analysis ranged from 17 to 29 per survey, the total number of GPS locations taken per survey from those deer ranged from 4,542 to 15,472, and sample sizes were similar among deer (Table 11). Model 6, which included a quadratic term for the covariates percent forest, and distance to nearest road, forest-field edge, and NPS owned land boundary, was the parsimonious model for predicting resource selection for all deer during all seven surveys (Table 12). Deer selected forested areas during all surveys, with the exception of the August surveys, which was the only survey period when standing corn was present (Appendix I). For all distance sampling surveys, deer selected forest-field edges, avoided areas close to roads but selected areas at intermediate distances from roads

Table 9. Estimates of deer/km^2 ($\hat{D}$), deer/km^2 of forest ($\hat{D}_f$), and abundance ($\hat{N}$) of white-tailed deer in the study area with measures of precision from each distance sampling survey, using habitat type (field or forest) of each observation as a covariate and right truncating observations beyond 250 m, Gettysburg, Pennsylvania, 2009–2010.

Survey period	Detection function[a]	*k*[b]	*n*[c]	$\hat{D}$	$\hat{D}_f$	*E(S)*[d]	$\hat{P}$[e]	$\hat{N}$	95% CI	CV
Apr 2009	hn	2	106	11.1		3.41	0.49	324	232–453	0.17
Aug 2009	hz	3	143	8.7		2.00†	0.50	253	167–385	0.21
Nov 2009	hn	2	143	10.6		1.71†	0.38	310	204–472	0.21
Jan 2010	hn	2	99	9.6		3.35	0.60	280	189–414	0.20
Apr 2010	hn	2	90	15.3		3.52	0.38	444	304–650	0.19
Aug 2010	hn	2	167	10.7		2.33†	0.55	312	217–448	0.18
Nov 2010	hn	2	184	13.1		1.90†	0.40	382	275–531	0.17

[a] hn = half-normal and hz = hazard-rate.
[b] k = Number of parameters in detection function.
[c] n = no. of observed groups of deer.
[d] E(S) = expected group size of deer (mean group size or †size-biased regressed group size).
[e] $\hat{P}$ = detection probability within 250 m of transects.

Table 10. Estimates of density ($\hat{D}$) and abundance ($\hat{N}$) of white-tailed deer in the study area with measures of precision from each distance sampling survey, using habitat type (field or forest) of each observation as a covariate and right truncating observations beyond 80 m, Gettysburg, Pennsylvania, 2009–2010.

Survey	Detection function[a]	K[c]	N[d]	$\hat{D}$ (deer/km^2)	$E(S)$[e]	$\hat{P}$[f]	$\hat{N}$	95% CI	CV
Apr 2009	Hn[b]	2	59	9.2	3.32	1.00	268	170–423	0.23
Aug 2009	Hz[b]	3	83	9.9	2.28	0.90	289	200–418	0.19
Nov 2009	Hz	3	98	10.9	2.08	0.95	318	215–469	0.19
Jan 2010	Hn[b]	2	44	7.5	3.00	0.96	218	142–336	0.22
Apr 2010	Hn[b]	2	56	13.1	3.34	0.81	381	238–607	0.24
Aug 2010	hz	3	94	12.2	2.65	0.97	354	256–491	0.16
Nov 2010	hn[*]	2	123	12.6	2.03	0.94	366	255–525	0.18

[a] hn = half-normal and hz = hazard-rate.
[b] Numerical convergence problems estimating parameters of detection function.
[c] k = Number of model parameters in detection function.
[d] n = Number of observed groups of deer.
[e] E(S) = expected group size of deer (mean group size or †size-biased regressed group size).
[f] $\hat{P}$ = detection probability within 80 m of transects.

Table 11. Number of white-tailed deer collared with global positioning system (GPS) devices and the number of GPS locations used to estimate resource selection for each distance sampling survey, Gettysburg, Pennsylvania, 2009–2010.

Survey period	No. deer	No. locations	Mean no. locations per deer	Minimum no. locations per deer	Maximum no. locations per deer
Apr 9–16, 2009	29	15,472	534	395	556
Aug 3–9, 2009	23	7,316	318	202	336
Nov 20–25, 2009	17	5,586	329	60	359
Jan 5–8, 2010	17	3,688	217	200	232
Apr 1–4, 2010	26	7,263	279	55	300
Aug 25–30, 2010	22	3,923	178	171	180
Nov 15–19, 2010	17	4,542	267	244	274

Table 12. Model selection results for eight models of resource selection by white-tailed deer, Gettysburg, Pennsylvania, 2009–2010. The delta-Akaike's Information Criterion (ΔAIC) values were summed across all white-tailed deer collared with global positioning system devices for each model and survey period.

	Resource Selection Model[a]							
Survey period	1	2	3	4	5	6	7	8
Apr 9–16, 2009	745.54	628.88	330.00	273.53	249.76	0	205.37	181.36
Aug 3–9, 2009	991.07	918.72	414.76	349.60	317.45	0	391.06	267.95
Nov 20–25, 2009	715.36	630.24	400.29	348.67	286.34	0	350.11	227.07
Jan 5–8, 2010	479.12	440.87	163.59	170.51	145.90	0	113.57	35.14
Apr 1–4, 2010	1,265.72	1,131.60	460.76	355.15	321.28	0	303.30	268.24
Aug 25–30, 2010	1,078.18	949.27	361.62	292.93	305.47	0	273.95	199.18
Nov 15–19, 2010	847.12	679.03	267.63	148.93	145.62	0	152.69	113.48

[a] See Table 2 for description of each model.

(approximately 100–150 m), and avoided areas in the park interior and near the park boundary (Appendix I). For ease of interpretation, we plotted RSF estimates (Appendix J) and developed fine-scale maps of relative use on the study area based on RSF parameter estimates for each survey (Figure 9, Appendix K).

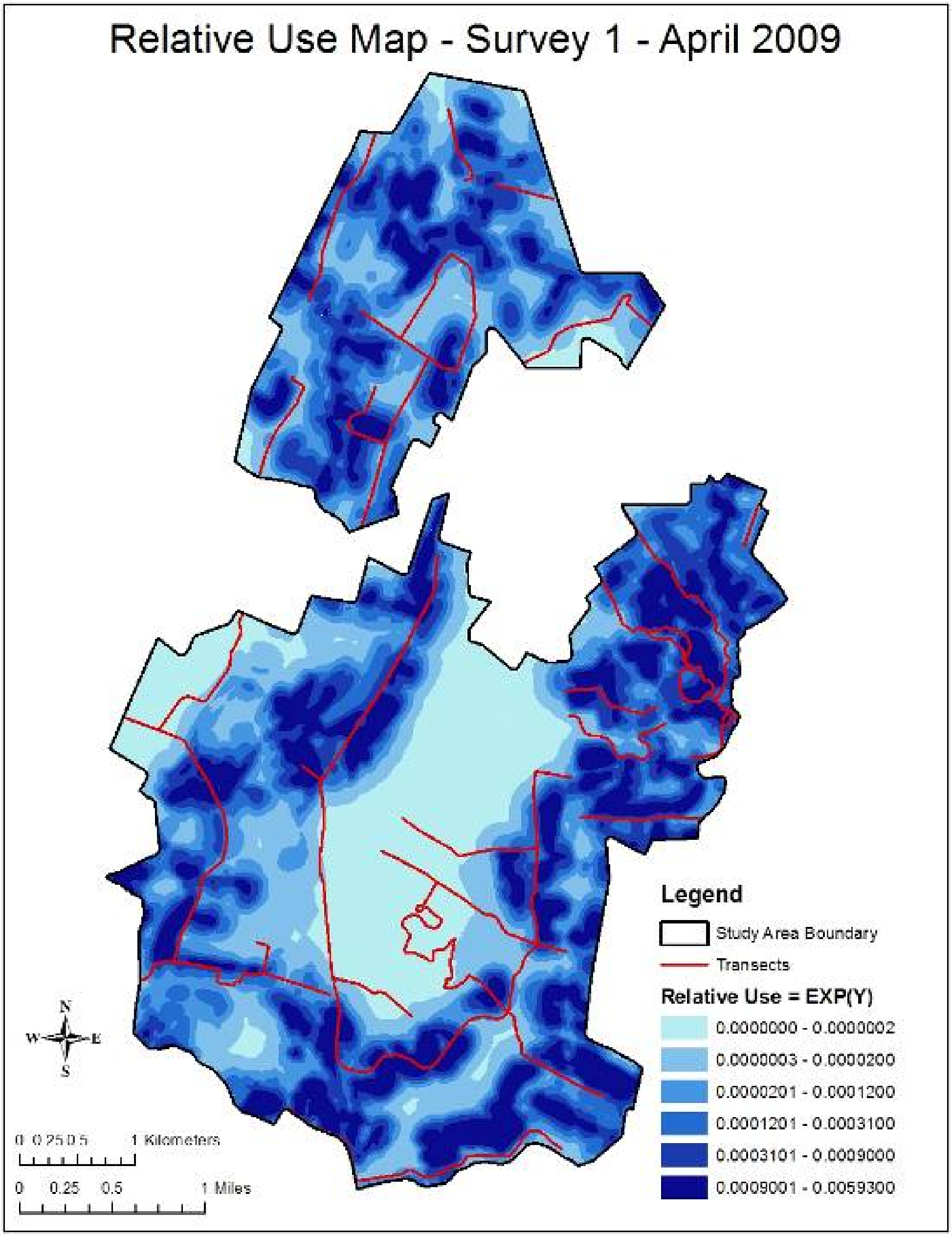

Figure 9. Map of relative use of white-tailed deer (5×5-m grid) in the study area during the April 2009 distance sampling survey period, Gettysburg, Pennsylvania. See Appendix K for maps from additional surveys.

Are Deer are Uniformly Distributed with Respect to Roads?

The number of GPS-collared deer used in the analysis ranged from 16–22 for open areas within 80 m of transects, 17–29 for open areas within 250 m of transects, 14–27 for forested areas within 80 m of transects, and 16–31 for forested areas within 250 m of transects (Table 13). For both open and forested areas, fewer deer used areas within 80 m than within 250 m of transects (Table 13). Further, the uniform detection function with no adjustment terms performed worse (based on AIC) than models including adjustment terms in modeling the distribution of GPS locations for both locations in open areas and forested areas relative to transects during all surveys for both 80- (Table 14) and 250-m (Table 15) right-truncation distances (Figure 10, Appendix L).

Table 13. The number of GPS-collared deer (*n*) and number of GPS locations used to model the distribution of global positioning system (GPS) locations of GPS-collared white-tailed deer relative to perpendicular distance to each transect during each distance sampling survey, Gettysburg, Pennsylvania, 2009–2010. Locations were categorized between forested and open areas and between 80-m and 250-m of transects.

	Open area				Forested area			
	80 m		250 m		80 m		250 m	
Survey period	n_1	No. locations	*n*	No. locations	*n*	No. locations	*n*	No. locations
Apr 9–16, 2009	22	625	29	3,445	27	3,762	31	9,104
Aug 3–9, 2009	20	1,380	25	4,991	22	1,168	25	2,736
Nov 20–25, 2009	16	432	19	2,393	15	632	17	2,406
Jan 5–8, 2010	16	384	18	1,548	14	727	18	1,571
Apr 1–4, 2010	26	756	28	3,413	23	1,027	28	3,171
Aug 25–30, 2010	19	1,491	25	7,691	20	671	24	3,486
Nov 15–19, 2010	16	560	17	1,496	14	987	16	2,120

Table 14. Model selection results from modeling a uniform key detection function and the best key detection function with up to three adjustment parameters. The detection functions modeled distances from each global positioning system (GPS) location to each transect during each distance sampling survey period, Gettysburg, Pennsylvania, 2009–2010. The GPS locations were collected in open and forested habitats from GPS-collared white-tailed deer and right-truncated beyond 80 m from transects.

	Open Habitat				Forested Habitat			
Survey	Model[a]	*k*[b]	AIC[c]	ΔAIC[d]	Model[e]	*k*[b]	AIC[c]	ΔAIC[d]
Apr 2009	Best	3	5,363	0	Best	2	32,390	0
	Uniform	0	5,478	114	Uniform	0	32,970	580
Aug 2009	Best	3	11,857	0	Best	3	10,015	0
	Uniform	0	12,094	238	Uniform	0	10,236	222
Nov 2009	Best	2	3,700	0	Best	3	5,361	0
	Uniform	0	3,786	86	Uniform	0	5,539	178
Jan 2010	Best	3	3,321	0	Best	2	6,342	0
	Uniform	0	3,365	45	Uniform	0	6,372	30
Apr 2010	Best	3	6,313	0	Best	3	8,929	0
	Uniform	0	6,626	312	Uniform	0	9,001	72
Aug 2010	Best	3	12,496	0	Best	3	5,641	0
	Uniform	0	13,067	571	Uniform	0	5,881	240
Nov 2010	Best	2	4,898	0	Best	3	8,545	0
	Uniform	0	4,908	9	Uniform	0	8,650	105

[a] The best model was a uniform distribution with cosine adjustment terms, but January 2010 was a half-normal key detection function with cosine adjustment terms and November 2010 was a uniform key detection function with hermit polynomial adjustment terms.
[b] k = no. of model parameters.
[c] Akaike's Information Criterion (AIC).
[d] Difference in AIC between each model and the model with the smallest AIC value.
[e] The best model was a uniform distribution with cosine adjustment terms, except April 2009 was a half-normal key detection function and cosine adjustment terms.

Table 15. Model selection results from modeling a uniform detection function and the best detection function with up to three adjustment parameters. The detection functions modeled distances from each global positioning system (GPS) location to each transect during each distance sampling survey period, Gettysburg, Pennsylvania, 2009–2010. The GPS locations were collected in open and forested habitats from GPS-collared white-tailed deer and right-truncated beyond 250 m from transects.

	Open Habitat				Forested Habitat			
Survey	**Model**[a]	***k***[b]	**AIC**[c]	**ΔAIC**[d]	**Model**[a]	***k***[b]	**AIC**[c]	**ΔAIC**[d]
Apr 2009	Best	3	37,635	0	Best	2	99,252	0
	Uniform	0	38,043	408	Uniform	0	100,535	1,283
Aug 2009	Best	3	54,638	0	Best	3	29,982	0
	Uniform	0	55,115	477	Uniform	0	30,213	231
Nov 2009	Best	2	26,087	0	Best	3	26,439	0
	Uniform	0	26,426	339	Uniform	0	26,569	130
Jan 2010	Best	2	17,071	0	Best	3	17,235	0
	Uniform	0	17,094	23	Uniform	0	17,348	114
Apr 2010	Best	3	37,068	0	Best	3	34,446	0
	Uniform	0	37,689	622	Uniform	0	35,017	571
Aug 2010	Best	3	83,872	0	Best	3	37,999	0
	Uniform	0	84,931	1,059	Uniform	0	38,496	497
Nov 2010	Best	3	16,102	0	Best	2	23,229	0
	Uniform	0	16,222	120	Uniform	0	23,411	182

[a] The best model was a uniform distribution with cosine adjustment terms, except August 2009 was a half-normal key detection function with cosine adjustment terms and November 2010 was a uniform key detection function with hermit polynomial adjustment terms.
[b] k = no. of model parameters.
[c] Akaike's Information Criterion (AIC).
[d] Difference in AIC between each model and the model with the smallest AIC value.
[e] The best model was a uniform distribution with cosine adjustment terms, except August 2009 and January 2010 were half-normal key detection functions with cosine adjustment terms and November 2010 was a uniform key detection function with hermit polynomial adjustment terms.

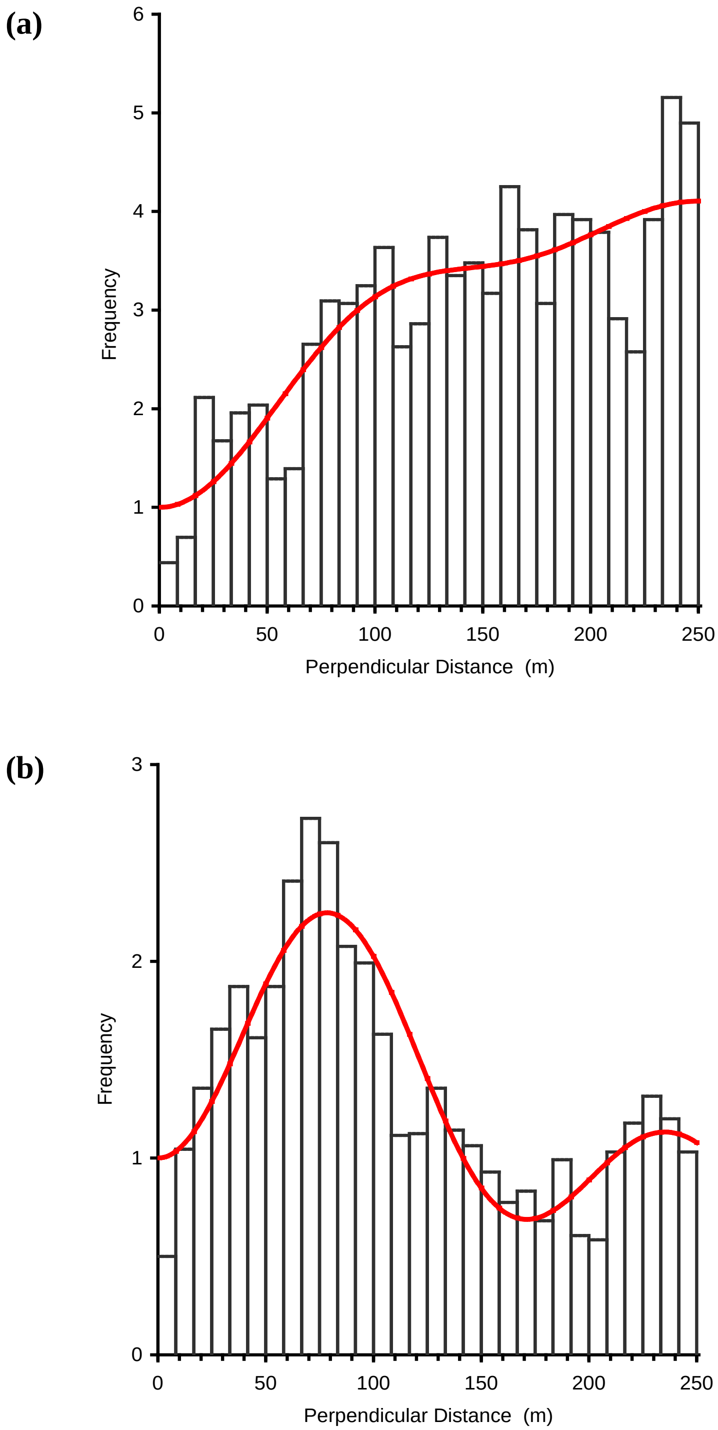

Figure 10. Binned data for the distribution of global positioning system (GPS) locations from GPS-collared white-tailed deer in (a) open areas and (b) forested areas relative to perpendicular distance from transects, with associated best-fit line, during the first distance sampling survey period, April 9–16, 2009, performed in the study area at Gettysburg, Pennsylvania. See Appendix L for figures during additional survey periods.

Do Roads Provide a Representative Sample of the Study Area?

We sampled slightly more forested areas from the roads we chose as transects relative to the proportion of forested areas in the study area; 4% more forested areas within 250 m of transects and 6% more forested areas within 80 m of transects (Table 16).

Resource use within 250 m of transects ranged from 1% (0.585 [95% CI = 0.099 – 0.626]) to 16% (0.672 [95% CI = 0.472 – 0.739]) greater than the expected value of 0.58 (the proportion of the total study area surveyed), such that the average $\hat{p}_{RSF}$ = 0.647 (SD = 0.029) and the range of percent difference was 1–16% (Table 17). Because bootstrapped 95% confidence intervals of $\hat{p}_{RSF}$ were wide, we failed to reject the null hypothesis that transects were representative for all surveys except the August 2009 survey (Table 17).

Resource use within 80 m of transects showed much variation across years and seasons, ranging from -28% to 27% more than expected (0.224 = the proportion of the total study area surveyed), such that $\hat{p}_{RSF}$ ranged from 0.1613 (95% CI = 0.014 – 0.291) to 0.2841 (95% CI = 0.113 – 0.355; Table 18). However, the average $\hat{p}_{RSF}$ across seasons and years was 0.220 (SD= 0.037), such that the average percent difference was only -2% (SD=0.16; Table 18). Bootstrapped 95% confidence intervals of $\hat{p}_{RSF}$ contained the value of 0.224 for every survey. Therefore, we failed to reject the null hypothesis that transects were representative for all surveys (Table 18).

Table 16. Land area and forested area (in km^2) quantified in 2008 for the study area and 250 m and 80 m from distance sampling survey transects, the proportion of the study area that each survey zone encompassed, and the percent forested land in the study area and in each survey zone, Gettysburg, Pennsylvania.

Zone	Area (km^2)	Prop. of Study Area	Forested Area (km^2)	% Forested
Study Area	29.13	1.000	8.48	29
250m Zone	16.89	0.580	5.61	33
80m Zone	6.53	0.224	2.28	35

Table 17. Estimates of the proportion of the study area population of white-tailed deer ($\hat{p}_{RSF}$) within the 250 m survey zone during each distance sampling survey, Gettysburg, Pennsylvania, 2009–2010.

Survey	$\hat{p}_{RSF}$	SE($\hat{p}_{RSF}$)	95% CI	% Difference[a]
Apr 9–16, 2009	0.672	0.068	0.472–0.739	16
Aug 3–9, 2009	0.667	0.026	0.603–0.701	15
Nov 20–25, 2009	0.652	0.107	0.247–0.727	12
Jan 5–8, 2010	0.647	0.053	0.494–0.684	12
Apr 1–4, 2010	0.645	0.121	0.204–0.719	11
Aug 25–30, 2010	0.585	0.133	0.099–0.626	1
Nov 15–19, 2010	0.663	0.053	0.494–0.684	14

[a] Difference between $\hat{p}_{RSF}$ and p = 0.580, the proportion of the total study area that the 250 m survey zone encompassed, such that a positive value denoted selection by deer for areas less than 250 m from transects.

Table 18. Estimates of the proportion of the study area population of white-tailed deer ($\hat{p}_{RSF}$) within the 80 m survey zone during each distance sampling survey, Gettysburg, Pennsylvania, 2009–2010.

Survey	$\hat{p}_{RSF}$	**SE(** $\hat{p}_{RSF}$ **)**	**95% CI**	**% Difference[a]**
Apr 9–16, 2009	0.223	0.072	0.097–0.367	0
Aug 3–9, 2009	0.226	0.068	0.108–0.364	1
Nov 20–25, 2009	0.216	0.096	0.050–0.403	-4
Jan 5–8, 2010	0.232	0.065	0.113–0.355	4
Apr 1–4, 2010	0.200	0.081	0.043–0.353	-11
Aug 25–30, 2010	0.161	0.076	0.014–0.291	-28
Nov 15–19, 2010	0.284	0.065	0.113–0.355	27

[a] Difference between $\hat{p}_{RSF}$ and p = 0.224 the proportion of the total study area that the 80 m survey zone encompassed, such that a positive value denoted selection by deer for areas less than 80 m from transects.

Distance Sampling Estimator: Adjusting for Nonrandom Sampling

Estimated detection probabilities using CDS for areas within 250 m of transects ranged from 0.56 to 0.80 for open areas and 0.24 to 0.35 for forested areas (Table 19). Our correction to the detection probability for the proportion of open areas versus forested areas within 250 m of transects increased estimates of detection probability in fields and forests by an average of 5% and 8%, respectively (Table 19).

Estimated detection probabilities using CDS equaled 1.0 for open areas and ranged from 0.60 to 1.0 for forested areas within 80 m of transects (Table 20). Our correction to the detection probability for the proportion of open areas versus forested areas within 80 m of transects had little effect on estimated detection probability because it only increased detection probability in forests by an average of 1% (Table 20).

Table 19. Detection probabilities of white-tailed deer for fields and forests in the 250 m survey zone for each distance sampling survey month (pooled across years), Gettysburg, Pennsylvania, 2009–2010.

	CDS[a]				**Corrected[b]**			
Survey month	p_{Field}	$SE(p_{Field})$	p_{Forest}	$SE(p_{Forest})$	$\overline{p}_{Field}$	$SE(\overline{p}_{Field})$	$\overline{p}_{Forest}$	$SE(\overline{p}_{Forest})$
April	0.69	0.06	0.34	0.02	0.73	0.05	0.42	0.02
August	0.59	0.03	0.24	0.04	0.66	0.04	0.31	0.05
November	0.56	0.04	0.30	0.02	0.63	0.04	0.38	0.02
January	0.80	0.09	0.35	0.05	0.83	0.08	0.44	0.05

[a] Detection probabilities for field and forest and associated standard errors were calculated separately using conventional distance sampling (CDS) methods in program DISTANCE.
[b] Corrected average detection probabilities for field and forest were calculated by applying the detection function across the 5 m grid over the landscape based on whether each grid cell was forested or open and its distance to the nearest transect. Standard errors for corrected detection probabilities were calculated using non-parametric bootstrapping.

Table 20. Detection probabilities of white-tailed deer for fields and forests in the 80 m survey zone for each distance sampling survey month (pooled across years), Gettysburg, Pennsylvania, 2009–2010.

Survey month	CDS[a]				Corrected[b]			
	p_{Field}	$SE(p_{Field})$	p_{Forest}	$SE(p_{Forest})$	$\overline{p}_{Field}$	$SE(\overline{p}_{Field})$	$\overline{p}_{Forest}$	$SE(\overline{p}_{Forest})$
April	1.00	0.00	0.82	0.10	1.00	0.00	0.82	0.08
August	1.00	0.00	0.60	0.09	1.00	0.00	0.61	0.08
November	1.00	0.00	0.89	0.06	1.00	0.00	0.90	0.17
January	1.00	0.00	1.00	0.00	1.00	0.00	1.00	0.00

[a] Detection probabilities for field and forest and associated standard errors were calculated separately using conventional distance sampling (CDS) methods in program DISTANCE.
[b] Corrected average detection probabilities for field and forest were calculated by applying the detection function across the 5 m grid over the landscape based on whether each grid cell was forested or open and its distance to the nearest transect. Standard errors for corrected detection probabilities were calculated using non-parametric bootstrapping.

For the 250 m survey zone, estimates of abundance adjusted by the distribution of deer based on the RSF ranged from 255 (95% CI = 207 – 477) to 461 (95% CI = 389 – 1,332; Table 21) and differed from MCDS estimates (not corrected) between -74% and 32%, with an average percent difference of -5% (SD=0.33; Table 22). Precision for the corrected estimates was greater than that of MCDS estimates for all surveys except the August 2010 survey (Figure 11).

For the 80 m survey zone, estimates of abundance adjusted by the distribution of deer based on the RSF ranged from 222 (95% CI = 137 – 420) to 547 (95% CI = 294 – 2,943; Table 23). Corrected estimates differed from MCDS estimates between -19% and 35%, with an average percent difference of 5% (SD=0.19; Table 22, Figure 12). However, precision for corrected estimates was worse than that of MCDS estimates for every survey (Figure 12).

Table 21. Estimates of abundance of white-tailed deer for the study area ($\hat{N}_{Corrected}$) adjusted using information on the distribution of deer based on a resource selection function with associated measures of precision and parameters for the 250-m distance sampling survey zone, Gettysburg, Pennsylvania, 2009–2010.

Survey	$\bar{p}_{Field}$ [a]	$\bar{p}_{Forest}$ [a]	$E(S)_{Field}$ [b]	$E(S)_{Forest}$ [b]	$\bar{n}_{Field}$ [c]	$\bar{n}_{Forest}$ [c]	$\hat{N}_{Survey\ Zone}$ [d]	$\hat{p}_{RSF}$ [e]	$\hat{N}_{Corrected}$	$SE(\hat{N}_{Corrected})$	**95% CI**
Apr 2009	0.73	0.42	3.73	2.90	21	14	205	0.6723	305	68.95	253–404
Aug 2009	0.66	0.31	2.47	1.92	44	4	189	0.6670	283	31.01	239–346
Nov 2009	0.63	0.38	2.20	2.10	40	11	203	0.6516	311	1,389.57	255–496
Jan 2010	0.83	0.44	3.46	2.95	31	8	186	0.6472	287	81.63	229–395
Apr 2010	0.73	0.42	3.89	2.50	22	8	165	0.6446	255	831.16	207–477
Aug 2010	0.66	0.31	3.12	1.85	51	4	270	0.5849	461	3,915.83	389–1,332
Nov 2010	0.63	0.38	2.27	1.81	42	19	244	0.6632	367	82.22	323–465

[a] $\bar{p}$ = the average detection probability in fields and forests.

[b] $E(S)$ = mean cluster size in fields and forests.

[c] $\bar{n}$ = average number of observed clusters in fields and forests per complete round.

[d] $\hat{N}_{Survey\ Zone}$ = the estimate of abundance within the 250 m survey zone.

[e] $\hat{p}_{RSF}$ = the proportion of the study area population within the 250 m survey zone.

Table 22. Percent difference between abundance estimates of white-tailed deer using multiple covariate distance sampling and bias-adjusted estimates of abundance using the correction factor for each distance sampling survey Gettysburg, Pennsylvania, 2009–2010.

Survey	250-m Zone[a]	80-m Zone[a]
Apr 2009	-6%	18%
Aug 2009	11%	3%
Nov 2009	0%	10%
Jan 2010	3%	2%
Apr 2010	-74%	-15%
Aug 2010	32%	35%
Nov 2010	-4%	-19%

[a] A positive value denotes the correction factor increased the estimate of abundance from the distance sampling estimator when roads were used as transects.

Table 23. Estimates of abundance of white-tailed deer for the study area ($\hat{N}_{Corrected}$; corrected for bias from non-random placement of transects and for a non-uniform distribution of deer relative to transects) with associated measures of precision and parameters for the 80 m distance sampling survey zone, Gettysburg, Pennsylvania, 2009–2010.

Survey	$\overline{p}_{Field}$ [a]	$\overline{p}_{Forest}$ [a]	$E(S)_{Field}$ [b]	$E(S)_{Forest}$ [b]	$\overline{n}_{Field}$ [c]	$\overline{n}_{Forest}$ [c]	$\hat{N}_{Survey\ Zone}$ [d]	$\hat{p}_{RSF}$ [e]	$\hat{N}_{Corrected}$	$SE(\hat{N}_{Corrected})$	95% CI
Apr 2009	1.00	0.82	3.71	3.06	8	12	73	0.2233	327	186.33	193–730
Aug 2009	1.00	0.61	2.35	1.82	24	4	67	0.2260	298	115.58	185–566
Nov 2009	1.00	0.90	2.07	2.10	24	11	76	0.2157	353	4,470.72	188–1,232
Jan 2010	1.00	1.00	2.93	3.20	11	6	52	0.2320	222	102.76	137–420
Apr 2010	1.00	0.82	3.97	2.50	11	8	67	0.2004	333	1,981.78	178–1040
Aug 2010	1.00	0.61	2.78	1.85	27	4	88	0.1613	547	16,080.75	294–2,943
Nov 2010	1.00	0.90	2.22	1.80	23	18	87	0.2841	307	220.81	242–797

[a] $\overline{p}$ = the average detection probability in fields and forests.

[b] $E(S)$ = mean cluster size in fields and forests.

[c] $\overline{n}$ = average number of observed clusters in fields and forests per complete round.

[d] $\hat{N}_{Survey\ Zone}$ = the estimate of abundance within the 80 m survey zone.

[e] $\hat{p}_{RSF}$ = the proportion of the study area population within the 80 m survey zone.

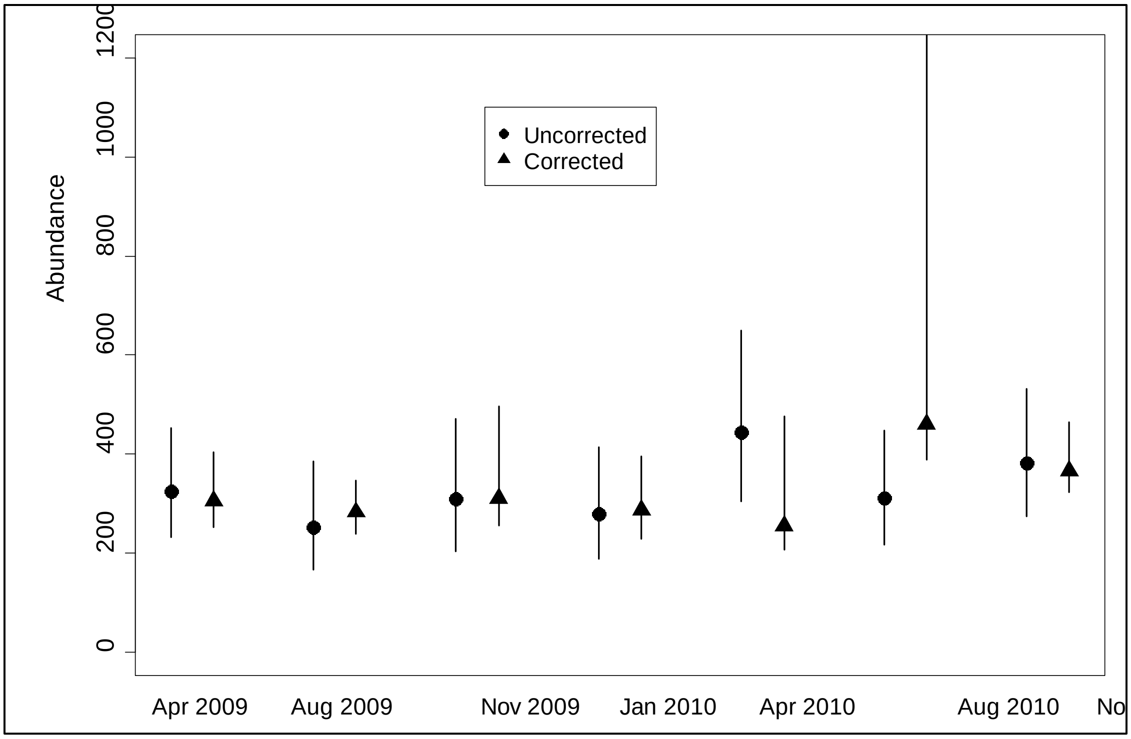

Figure 11. Abundance estimates ($\widehat{N}$) of white-tailed deer in the study area and associated 95% confidence interval bars using multiple covariate distance sampling (MCDS: ignoring any violations of assumptions) and bias-adjusted estimates of abundance using the correction factor for each distance sampling survey using the 250 m survey zone, Gettysburg, Pennsylvania, 2009–2010. The upper value of the 95% confidence interval for the August 2010 survey (1,332) extends beyond the y-axis limit shown.

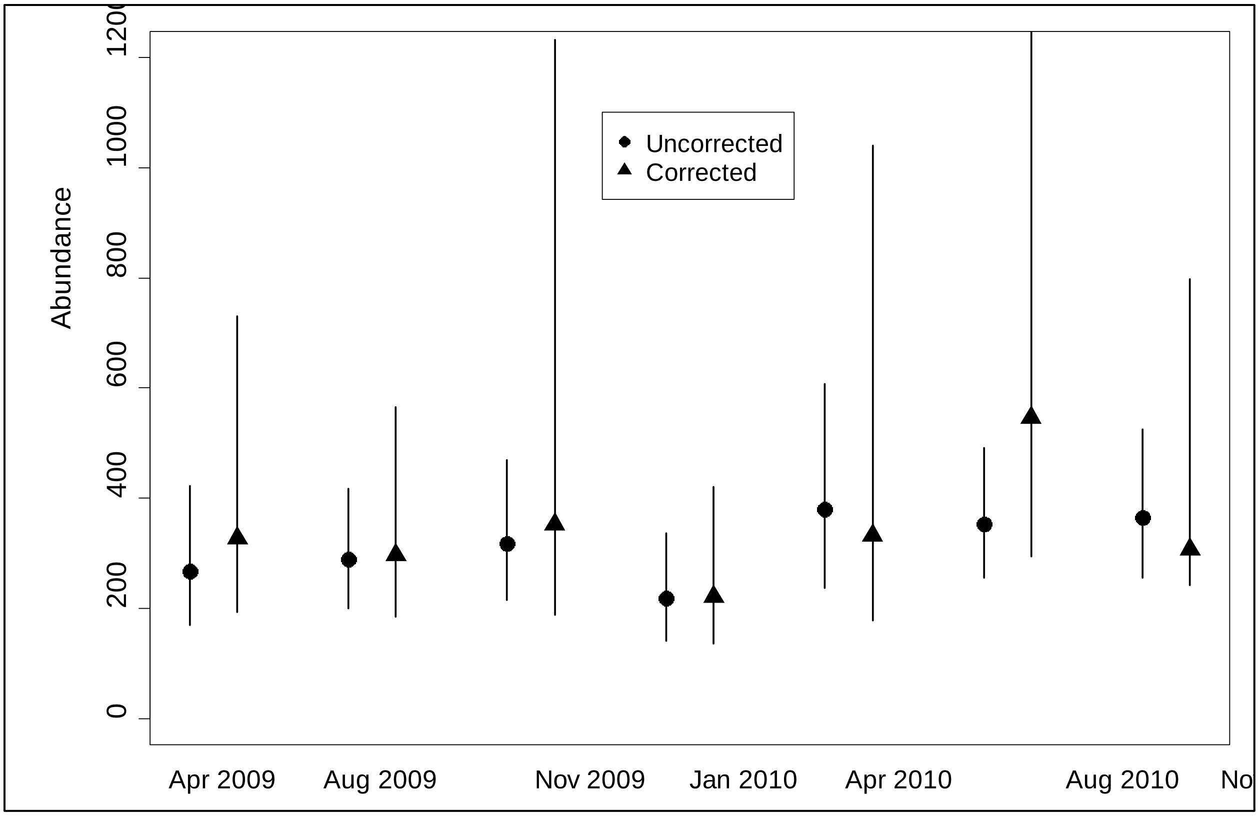

Figure 12. Abundance estimates ($\widehat{N}$) of white-tailed deer in the study area and associated 95% confidence interval bars using multiple covariate distance sampling (MCDS: ignoring any violations of assumptions) and bias-adjusted estimates of abundance using the correction factor for each distance sampling survey using the 80 m survey zone, Gettysburg, Pennsylvania, 2009–2010. The upper value of the 95% confidence interval for the August 2010 survey (2,943) extends beyond the y-axis limit shown.

Discussion

Mark-resight

We estimated the average detection probabilities of both marked male and female deer during April and November dusk counts (Table 5), which were lower than the Storm et al. (1992) study for all four surveys. Additionally, we estimated abundance during dusk counts using the L-P estimator and during spotlight surveys using Bowden's estimator. However, an important assumption for accuracy in average detection probability and L-P estimates is that rates of detection are constant across individuals within a given survey (Seber 1982). We found that detection rates varied by age and sex for each survey, with the exception of the April surveys, where adult males and adult females were detected at similar rates (Table 7). Therefore, if the marked sample was truly representative of the unmarked population, bias related to violating the assumption of homogenous detection probability would be minimized during surveys conducted in early April.

Several studies suggested that sightability of adult males is generally lower than sightability of females throughout the year, but increases during the summer months (Downing et al. 1977, McCullough et al. 1982, Sage et al. 1983). Our results are consistent with these studies for the August survey, but we only observed lower rates of detection for adult males than for adult females during the November survey (Table 7). However, results of detection probability for the study area at GNMP-ENHS may not be representative of typical land in other areas of Pennsylvania. The NPS culls only antlerless deer on NPS-owned property in the study area, and the NPS-owned property is closed to hunting. Additionally, not all privately owned property in the study area is open to hunting. Therefore, adult males may exhibit greater rates of detection relative to females in the study area because highly detectable antlerless deer are more likely to be culled and removed from population, but adult males are not, unless they are harvested off the park during the hunting season. The Storm et al. (1992) study occurred prior to culling, so although we concluded rates of detection between adult males and adult females were similar in April, rates of detection between males and females may not have been similar during that study, when detection probability was based only on marked female deer.

Although we observed heterogeneous detection probabilities, estimates of average detection probability would be representative of the population if the marked sample represented all age and sex classes of the population (Otis et al. 1978, Seber 1982, White et al. 1982). Additionally, abundance estimates from the L-P and Bowden's estimators were similar (Figure 8), suggesting that individual heterogeneity had minimal effect on accuracy of abundance estimates within a given survey period because the L-P estimator assumes homogeneous detection probabilities and Bowden's estimator does not. However, variance associated with L-P estimates may not be accurate. Additionally, caution should be used when comparing L-P and Bowden's estimates of abundance (Figure 8). The L-P estimator estimates the number of deer in the study area during a given survey evening, whereas Bowden's estimator estimates the number of deer that used the study area during an entire survey period (three surveys over 4–7 days) and is greater when temporary emigration occurs (Bowden and Kufeld 1995).

Additionally, for the average detection probability to yield unbiased estimates of abundance in future surveys, the assumption that detection probability will not change over time must be met. Therefore, park managers can use the estimate of average detection probability we estimated from the April 2010 survey of 0.25 as their updated sighting probability for future April dusk surveys, but they would have to assume that detection probability stays constant over time. Even if the same observers conduct future surveys, factors related to the environment (e.g., habitat conditions) and deer behavior may change over time (Anderson 2001). Therefore, using the sighting probability that we calculated may provide future density estimates that are inaccurate, such that detection probability may need to be updated again. For instance, park managers may observe an increasing trend in abundance over time using a constant sighting probability when abundance is actually stable because the true detection probability increased.

The April 2010 survey provided the greatest precision for both the L-P and Bowden's estimators (CV = 7% and 15% respectively; Figure 8). Visibility was excellent during the April and January surveys because there was no foliage on deciduous trees and shrubs, nor any crops or high vegetation in fields. However, vegetation decreased visibility for August surveys and standing corn decreased visibility for August and November surveys, leading to less robust estimates. Additionally, the deer population is at its peak in the summer because of fawn recruitment and subsequently decreases because of mortality (e.g., NPS culling begins before the November survey; Figure 8).

However, because the true population size is unknown, we could not evaluate accuracy. Park managers can use the estimates of abundance we obtained to update management strategies to reach their long-term density goal of 10 deer/km^2 (25 deer/mi^2) of forested land or 85 deer on the study area (Frost et al. 1997). We estimated density as 43 deer/km^2 (112 deer/mi^2) of forested land using the arithmetic average of L-P abundance estimates from the April 2010 dusk survey (Table 5). This is a reduction of 68% from the estimated density of 136 deer/km^2 of forested land in 1992 (Tzilkowski and Storm 1993), but four times greater than the park's goal of 10 deer/km^2 of forested land.

Change-in-ratio Estimator

We were unable to use the CIR estimator to obtain estimates of abundance using culling data because surveys to estimate the proportion of antlered and antlerless deer were not conducted prior to and immediately following culling operations. Spotlight surveys performed during August 2009 and 2010 could have been used along with surveys from November 2009 and 2010, however, the sample size of culled deer and weeks of culling effort were too small prior to November surveys to provide reliable estimates. The January survey could not be used because adult males may cast antlers prior to the January survey. Additionally, an important assumption is that all harvested deer are known, but information about deer harvested by hunters on private lands within the study area is not available.

Catch-per-unit-effort Estimator

The CPUE estimator provided a convenient abundance estimator using data already collected during annual culling efforts. However, the NPS can only safely shoot deer on a small percentage of the study area. Therefore, abundance estimates provided an estimate of deer using the area available to culling operations at night and did not allow inferences about abundance on the complete study area. For instance, the population of deer could be increasing in areas where culling cannot be performed, but the CPUE estimator would not be able to detect such a change. Additionally, because the NPS avoids culling antlered deer, we could only use data to provide an estimate of antlerless deer on the area available to culling. Also, because the number of antlerless deer harvested by hunters on nearby private lands is unknown, estimates may be biased even for the area where culling occurs.

Distance Sampling: Testing Assumptions

Our results documented bias in abundance estimates related to using existing, non-randomly placed roads as transects for distance sampling. We used GPS locations from GPS-collared adult and juvenile male and female deer in the study area to test two assumptions that are critical to meet for unbiased estimates, and are typically met using randomly placed transects. The first is that the distribution of deer is uniform with respect to perpendicular distance from transects, which allows the estimator for detection probability to be unbiased (Buckland et al. 2001). The second is that the sample from transects is representative of the entire study area, which allows the estimate of density in the sample to be extrapolated to abundance in the larger area of interest (Buckland et al. 2001). Previous studies that investigated roads as transects failed to investigate both critical assumptions; and conclusions tended to be speculative, based only on observation data, or relied on VHF telemetry locations, where the error associated with locations prevented fine scale measurement of avoidance of roads (e.g., Heydon et al. 2000, Ruette et al. 2003, Ward et al. 2004, Butler et al. 2005, Venturato et al. 2010, Erxleben et al. 2011).

We found that the distribution of GPS-collared deer was not uniform with respect to the roads we used as transects in both forested and non-forested areas (Table 14, Table 15), which violated the first assumption. For instance, GPS-collared deer tended to avoid areas within approximately 50 m of transects and the avoidance distance was larger in open areas than in forested areas (see Figure 10, Appendix L). Additionally, during mark-resight surveys we observed that deer avoided roads. Several studies using roads as transects with distance sampling also observed fewer detections near transects than expected for deer (*Odocoileus hemionus*; e.g., Rost and Bailey 1979, Kie and Boroski 1995; *Cervus nippon*; e.g., Koganezawa and Li 2002, *Capreolus capreolus*; e.g., Ward et al. 2004), moose (*Alces alces*; e.g., Yost and Wright 2001), and foxes (*Vulpes vulpes*; e.g., Heydon et al. 2000, Ruette et al. 2003), but were unable to definitively test why. Fewer detections near the road could be caused by a number of reasons, including avoidance of the areas near roads (e.g., because of disturbance or correlation of habitat with roads; Fewser et al. 2008), movement away from roads in response to observers, or missed observations near roads (Buckland et al. 2001). Considering we also observed fewer GPS locations near transects during surveys (Figure 10), we believe the likely cause was avoidance of roads. We do not rule out movement of deer in response to the vehicle or the spotlight before detection. However, upon inspection of intensive GPS data, we rarely observed flight responses of GPS-collared individuals with respect to observers before detection, and observers were trained to always look ahead to ensure all observations on the transect were detected and that observations were recorded at their initial location. Thus, because deer avoided areas close to roads, using the distance sampling estimator with roads as transects would lead to positively biased estimates of detection probability (e.g., similar to Figure 5), which would lead to negatively biased estimates of density.

However, we found that the roads we chose as transects provided a representative sample of forested areas on the study area. Additionally, we failed to reject the null hypothesis that habitat use (or the proportion of deer present) was in proportion to availability for both the 80 m and 250 m survey zones during all surveys, except the August 2009 survey. However, the statistical power to reject the null hypothesis was poor because 95% confidence intervals were wide (Table 17, Table 18), likely because of the RSF calculation and bootstrapping process; thus, the null hypothesis test may not have been a meaningful test. From GPS data, we observed a non-linear trend in the number of locations in relation to roads, so there is likely a similar trend in deer density in relation to roads. Therefore, finding that the sample within 80 m from roads was representative of deer density in the study area could be because mean density within that interval was representative. For instance, the interval from 0–40 m may under-represent density, whereas the interval from 40–80 m may over-represent density, such that the average is representative. However, the decrease in precision associated with smaller transect widths precluded testing the representativeness of smaller intervals.

In conclusion, the distribution of deer with respect to the roads used as transects was not uniform, such that estimates of density from the sample were negatively biased. Therefore, regardless of whether the sample from roads was representative of the larger study area, extrapolating density from the sample to the study area would provide negatively biased estimates of density for the study area, unless estimates of density in the sample can be corrected.

Distance Sampling: Correction Methods

Several studies attempted to correct estimates of density when few detections were observed near transects by employing left-truncation methods or a wide first interval (e.g., Heydon et al. 2000, Koganezawa and Li 2002, Ruette et al. 2003, Ward et al. 2004). There are two types of left-truncation; rescaling (displace the transect line to some distance x and censor truncated observations; Buckland et al. 2001) or full-left truncation (where the detection function is extrapolated back to distance 0 from some distance x; Alldredge and Gates 1985). If the distribution of animals with respect to perpendicular distance to transects is uniform, then in certain circumstances, both left-truncation methods can provide more representative estimates (e.g., when observations on the transect are missed directly under an airplane; Buckland et al. 2001). In the case of roads as transects, if animals are avoiding the areas close to the road, but then the distribution relative to transects becomes uniform after some distance x (e.g., similar to Figure 2), then the rescaling method can provide more representative estimates (Buckland et al. 2001). However, detection probability at distance x must be 1.0 and the density of deer in the area less than distance x from roads needs to be incorporated into the estimate of overall abundance (Buckland et al. 2001). Additionally, the assumption that the sample from roads is representative of the population would need to be tested and a correction applied if the sample is found to be unrepresentative. Full-left truncation and increasing the width of the first interval would not be appropriate to use because there are fewer animals in the area less than distance x, which would result in an over-estimate of density near transects (Buckland et al. 2001). Neither method of left-truncation would be appropriate to use given the distributions we observed (Appendix L), because the distributions did not typically become uniform after road avoidance. Fitting a hazard-rate function to data can be useful to assign a detection probability of 1.0 to distances close to the transect. However, because the true distribution is non-uniform, detection probability would remain positively biased, such that when the detection function does begin to decline, actual detection probability may be much lower than estimated (see Figure 5). These problems highlight the necessity for new methods to correct estimates when animals are distributed non-uniformly relative to transects.

We developed a correction factor to yield more representative estimates of abundance for the study area. First, we reduced potential for bias in the detection probability by using a narrow transect width (80 m) where detection probability was near 1.0 (Table 20). However, because deer avoided areas near roads (Appendix L), the estimate of density in the 80 m survey zone was likely unrepresentative of the study area. Therefore, we adjusted the estimate in the 80 m survey zone by the proportion of the study area population present in the 80 m survey zone, based on the RSF (Table 18, Table 22). However, we believe the estimated detection probabilities from CDS in forested areas were higher than actual (e.g., we doubt that we detected every deer in forests within 80 m of transects during the January 2010 survey; Table 20), such that corrected estimates of abundance were negatively biased. Using an even narrower distance would be more appropriate to reduce bias in detection probability; however, the narrower the width, the less precision for two reasons. First, the number of observations decreases, which increases the variance associated with the distance sampling estimator. Second, because $\hat{p}_{RSF}$ becomes smaller as w decreases, the bootstrapped estimates of $\hat{p}_{RSF}$ lead to less robust estimates of abundance because $\hat{p}_{RSF}$ is used in the denominator.

The method we used to correct for bias in the detection probability was not appropriate for the 250 m survey zone. Therefore, the estimator of detection probability was likely positively biased for both the MCDS and RSF corrected estimators, resulting in negatively biased estimates of abundance. Additionally, the correction to the detection probability for the proportion of forested and open areas inflated the detection probability even more. We believe this was because sections of forest obstructed observer detection in many secluded open areas within 250 m. However, grid cells for these secluded areas were assigned a detection probability based on the distance from transect, when in reality detection probability should have been 0. Given the proportion of forested areas within the sampled area was representative of the study area, using the original CDS detection probabilities would have been more appropriate. Nevertheless, our goal was to demonstrate a method to correct for a non-representative sample of habitat.

Original estimates of abundance using MCDS varied little from corrected estimates of abundance for both the 250 m and 80 m survey zones (Figure 11, Figure 12). We believe this was because the correction for detection probability was not sufficient, such that both MCDS and corrected estimates of abundance were negatively biased. Further, because we observed avoidance of areas near roads, we expected the RSF correction factor to increase estimates of abundance; however, this was complicated by increased use of intermediate distances from roads (Table 22, Appendix L). Additionally, because we minimized bias in the detection probability for the 80 m survey zone, we expected the difference between MCDS and corrected estimates of abundance for the 80 m survey zone to be greater than for the 250 m survey zone; however, this was rarely the case (Table 22). We believe the RSF correction did little because transects happened to be near areas of intermediate and high use (Figure 9 , Appendix K) and provided a representative sample of habitat used by deer (Table 16). If the roads used as transects happened to be in areas of low resource use or if forested areas along transects were underrepresented, the correction factor would have had a greater effect on $\hat{N}$.

We modeled relative use on the study area using the RSF with GPS locations and landscape covariates important for selection or avoidance by deer. For results to be accurate, the assumption that the marked population was representative of the unmarked population, with respect to habitat use, must be met. The proportion of each age and sex class marked should be representative of the population and the marked population should be distributed on landscape representative to the density of deer on the landscape. We captured all age and sex classes of deer throughout the study area and relative to local densities. Although we did not know the true sex ratio or age structure, we believe the marked population was representative of the unmarked population; thus, we believe we satisfied these assumptions. However, the issue of the NPS culling deer on the park may have resulted in inaccuracy in the RSF model. For instance, we observed fewer deer on NPS owned property compared to private lands, likely because of the culling operations on NPS owned property. It was difficult with the RSF to model differences in density of deer related to hunting on private land and culling in the park , but we used distance to the nearest NPS boundary as an indicator variable, with the assumption that the majority of the culling occurs in the central regions of the park (e.g., further distances). For example, we observed few deer on portions of NPS owned property with suitable habitat for deer, where the RSF predicted use would be high. We cannot estimate any potential bias, but if bias related to the RSF predicted greater use in the park than expected, a negative bias in the corrected density estimator would have been introduced.

We used GPS locations during the time we conducted distance sampling surveys (typical accuracy <20 m and fix rate >90%) to examine the distribution of deer relative to transects. However, using ground-based VHF telemetry data to test assumptions may not provide the accuracy or number of intensive locations required to accurately model the distribution of animals relative to transects during the time that surveys are conducted (e.g., Butler et al. 2005, Venturato et al. 2010, Erxleben et al. 2011). For instance, the lack of accuracy with VHF telemetry locations may prevent detection of avoidance of areas close to roads (e.g., <50 m). Furthermore, it is paramount that locations are collected during the time that surveys are conducted, especially when temporal and seasonal variation in habitat use exists. For instance, modeling the distribution of VHF locations taken during the day over a period of five months may not be appropriate for making inferences to the distribution of animals during surveys conducted in a one-week period or at night. Hounsome et al. (2005) properly addressed these issues with VHF locations, which they used to predict the proportion of badgers (*Meles meles*) using open areas during distance sampling surveys, but they experienced issues related to a low sample size of locations during surveys.

In addition, measuring the distance from each animal's location to the nearest road may not represent the distribution of that animal relative to the distribution of roads or the roads used as transects. For instance, in areas with a high density of roads, there may be more areas close to roads and few areas more than 200 m from a road. Conversely, in areas of low road density, there may be more areas further from roads than near roads. Therefore, it is vital to measure the distance from each location to each transect used, not just to the nearest transect. Venturato et al. (2010) used distances from VHF locations to the nearest road, but compared these to random locations, such that a reasonable comparison could be made; however, the analysis lacked statistical power to detect a difference.

In conclusion, our correction method could have provided more representative estimates of abundance for the study area than MCDS estimates (i.e., ignoring violations of assumptions) when roads were used as transects to sample deer with distance sampling. However, the method did not account for all of the bias and resulted in decreased precision because of the narrow width (e.g., 80 m) required to minimize bias in detection probability.

Conclusions

Our results suggest the assumption of homogeneity in detection rates for the L-P estimator was violated. If the sample of marked individuals was truly representative of the unmarked population (i.e., adult and juvenile male and female marked deer in proportion to the true sex and age ratio of deer on the study area) then the L-P estimator would provide accurate estimates. However, the variance may not be representative, especially if individuals exhibited heterogeneity in detection rates. Bowden's estimator does not require the assumption of homogeneous detection probability, however, and provided similar population estimates. Although mark-resight methods can provide accurate and precise estimates of abundance, data collection is logistically difficult to implement and expensive. Capturing deer is time consuming and costly and must be conducted on an annual or biennial basis to retain a sufficient sample size of marked deer in the population. Additionally, to use detection probability from mark-resight surveys to estimate abundance in future surveys (e.g., as a sighting index), the assumption that detection probability does not change over time must be met, which is highly unlikely because many factors related to detection rates can change over time (Anderson 2001). Therefore, the updated sighting index we calculated may not provide an unbiased estimator of abundance for future surveys.

Population estimates based on harvest data, such as the change-in-ratio and CPUE estimators are potentially cost-effective because they rely primarily on data already being collected during culling operations. However, collecting data for the change-in-ratio estimator does not appear to be feasible. We were able to estimate abundance based on a CPUE estimator but because culling is limited to only a small portion of GMNP-ENHS, the estimates were not representative of the study area. We do not believe either estimator is feasible for GMNP-ENHS.

There is no perfect solution for meeting all assumptions of distance sampling when surveying for highly mobile animals such as deer. Even if random transects are used, it is difficult to detect all animals on the transect from aerial surveys (Fewster et al. 2008), and walking transects often results in avoidance of the observer (e.g., Koenen et al. 2002). Additionally, as discussed in Buckland et al. (2001) and Fewster et al. (2008), the use of non-random roads or tracks as transects for distance sampling can result in considerable bias because the location of roads or the disturbance from roads may affect distribution of animals. We found the distribution of deer was related to the distribution of the roads we surveyed (Figure 10, Appendix J). Deer avoided areas near transects and often selected for intermediate distances. Therefore, we believe detection probabilities were positively biased, leading to negatively biased estimates of abundance.

We compared distance sampling estimates of abundance to mark-resight estimates of abundance (Figure 13) and found that distance sampling estimates were always lower. This is consistent with our prediction that distance sampling from roads provided positively biased detection probabilities. We attempted to correct for bias when roads were used as transects for distance sampling by restricting analysis to a narrow width and then adjusting estimates by the RSF (Figure 12). However, this method may not have corrected for all of the bias (e.g., point estimates were also negatively biased compared to mark-resight; Figure 13) and reduced precision. Our results regarding bias in detection probability can be generalized to distance sampling using roads as transects for any animal not distributed independently of roads, especially highly mobile animals, and where roads do not provide a representative sample of the larger area of interest.

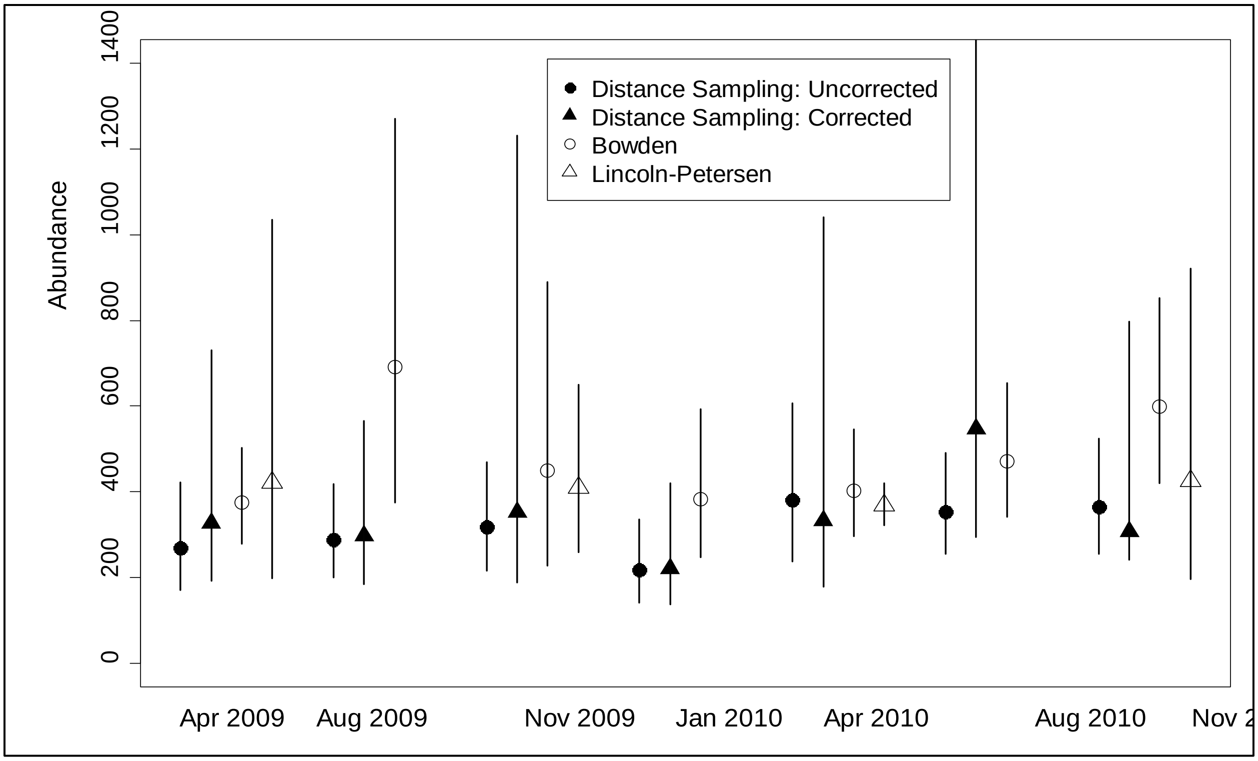

Figure 13. Abundance estimates ($\hat{N}$) of white-tailed deer in the study area and associated 95% confidence interval (CI) bars using distance sampling methods (filled symbols) with an 80 m survey zone and Bowden's estimator and Lincoln-Petersen mark-resight methods (unfilled symbols) for each survey period, Gettysburg, Pennsylvania, 2009–2010. The upper value of the 95% CI for the August 2010 survey (2,943) extends beyond the y-axis limit shown.

An inaccurate estimator with good precision may be more useful for management and monitoring trends than an accurate estimator with poor precision. Additionally, the logistical advantages of using roads as transects may outweigh disadvantages (Heydon et al. 2000). Nevertheless, any study using roads or tracks as transects with distance sampling should carefully consider the effects on bias. For instance, if roads are used as transects and animals avoid roads, abundance estimates should be treated as indices of abundance rather than point estimates. Anderson (2001) highlights some of the problems with using indices of abundance. However, using distance sampling estimates as indices of abundance can reduce some sampling variability because the method can incorporate differences in observer detection rates (see Diefenbach et al. 2003) and model detection probability with additional covariates, such as habitat types (Marques et al. 2007).

If using roads as transects is the only feasible option, the following methods may decrease potential bias. As proposed by Buckland et al. (2001), selecting a large number of short sections and stratifying transects by habitat such that the proportion of total lengths in each habitat are equal to the proportion of their availability in the larger study area can reduce bias. Additionally, using roads or tracks with very low or no traffic volume may reduce bias. Rost and Bailey (1979) observed an increase in avoidance of areas near roads by deer depending on the level of traffic volume. Further, Gill et al. (1997) used a thermal imager along unimproved forest tracks, which were closed to public traffic, to survey deer using distance sampling methods. They did not evaluate the distribution of deer relative to those tracks, but did not observe fewer deer near tracks, nor did they conclude that deer were moving in response to their vehicle. Therefore, use of thermal imagers could reduce movement of animals in response to observers, ensure that all animals on or near the transect are detected, increase the number of observations, and reduce disturbance to the public. However, thermal imagers are costly, and without investigating the true distribution of animals relative to transects, the magnitude and direction of the bias remain unknown.

We estimated of abundance of deer on the study area containing GNMP-ENHS using both mark-resight and distance sampling estimators (Appendix M), which negatively biased or not, were all above the deer density goal of 10 deer/km^2 (25 deer/mi^2) of forested land. We believe several logistical constraints preventing park managers from reaching this goal. The NPS owns 61% of the land within the study area, but NPS owned forested land comprises only 17% of the study area. Park managers can only cull deer on park owned property and from roads where areas on both sides are owned by the park. Because of public roads and buildings in and around the park, managers can safely shoot deer only on a small proportion of the park, which tends to be areas in the park interior. The small area that managers can safely cull deer may be the reason it has proven difficult to reduce deer density on the entire study area to 10 deer/km^2 of forested land.

Furthermore, although we found that deer density in the study area was above the long-term goal, park managers have observed increased regeneration of hardwood seedling trees on park woodlands (Niewinski et al. 2006; Randy Krichten, GNMP-ENHS vegetation manager, personal communication). Additionally, we observed few deer in the interior of the park during surveys. Most of the deer tended to be on private lands and on the edge of the park near private lands (i.e., areas where park managers cannot shoot deer). Given that an important objective at GNMP-ENHS is to preserve the historic character of the landscape, the requirement for a precise and often expensive measure of deer abundance for meeting deer culling goals may be unnecessary. Regardless of whether or not the deer density goal of 10 deer/km^2 of forested land in the study area is reached, the objective of preserving the historic character of the landscape still may be attained. The NPS may want to consider re-evaluating deer density goals for GNMP-ENHS if data to assess current vegetation conditions become available (e.g., measures of regeneration, species diversity, and deer browsing).

Management Implications

Our results indicated the deer population was above the goal of 10 deer/km^2 of forested land as defined in the parks' deer management plan (U.S. Department of the Interior 1995, Frost et al. 1997). However, evidence suggests that forest regeneration and crop production are no longer adversely affected by deer browsing and grazing (Niewinski et al. 2006). Consequently, data on vegetation conditions may be useful when assessing whether deer density goals should be updated rather than relying solely on deer density estimates. Estimators that require marked deer are expensive and periodic verification of the accuracy of population estimates based on a sighting index may be required.

The NPS can continue to perform dusk surveys in early April and adjust counts by the 0.25 detection probability that we estimated during this research. However, conditions may change, leading to a different detection probability and biased estimates of abundance during future surveys. For instance, differences in observers, weather, habitat, etc. during surveys from year to year may provide misleading trend information. Using the distance sampling estimator as an index of abundance may provide more accurate trend information over time because detection probability can be modeled for each observer for each survey. We provide a summary of the advantages and disadvantages of the various methods examined in this study in Appendix N.

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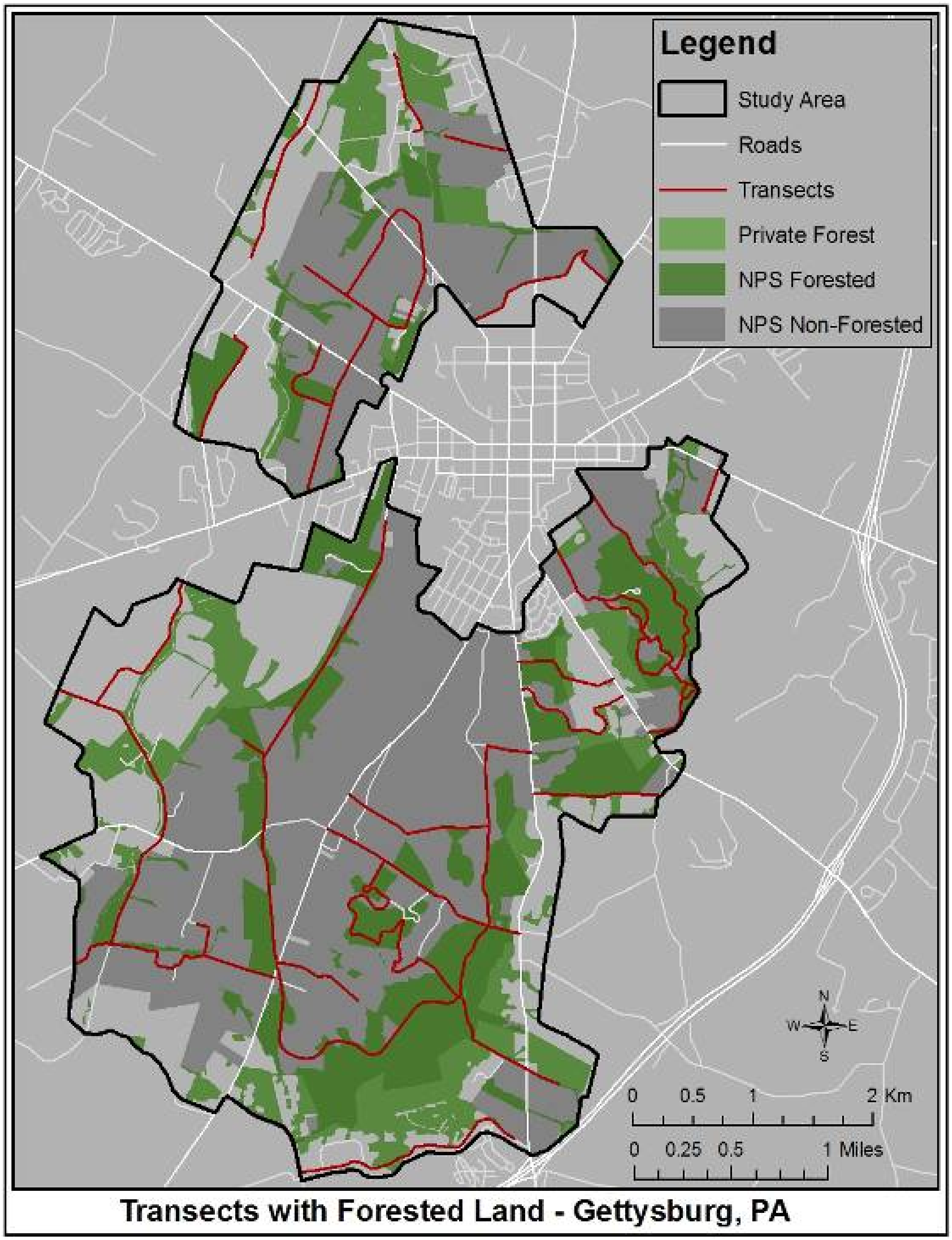
Appendix A. Map of forested land in the study area.



Appendix B. Input and output for analysis of Catch-Per-Unit-Effort data.

Below is output from program MARK for each season of culling.

Input File: 2010-2011

```
/* Gettysburg White-tailed deer CPUE, 2010-2011 culling season, number of antlerless deer harvested per week*/
                  1000000000000 10;
                  0100000000000  7;
                  0010000000000 14;
                  0001000000000  7;
                  0000100000000  7;
                  0000010000000  3;
                  0000001000000 11;
                  0000000100000  4;
                  0000000010000  7;
                  0000000001000 10;
                  0000000000100  1;
                  0000000000010  4;
                  0000000000001  2;


  Program  MARK  - Survival Rate Estimation with Capture-Recapture Data
  Compaq(Win32) Vers. 6.0 Dec 2009     15-Nov-2011 18:36:57
 - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - -

 INPUT --- proc title CPUE_2010_2011;
   Time in seconds for last procedure was 0.00
 INPUT --- proc chmatrix occasions=13 groups=1 etype=Huggins
 INPUT --- mixtures=2 NoHist hist=300;
 INPUT ---    glabel(1)=Group 1;
 INPUT ---    time interval 1 1 1 1 1 1 1 1 1 1 1 1 1;
    Number of unique encounter histories read was 13.
    Number of individual covariates read was 0.
    Time interval lengths are all equal to 1.
    Data type is Huggins Closed Captures.
    Time in seconds for last procedure was 0.00
 INPUT --- proc estimate link=Logit varest=2ndPart ;
 INPUT --- model={Logit_2010_2011};
 INPUT ---    fixed=1;
 INPUT ---              parm(14)=0;
 INPUT ---    group=1 p rows=1 cols=13 Square Time=1;
 INPUT ---    group=1 c rows=1 cols=12 Square Constant=14;

 INPUT ---    design matrix constraints=14 covariates=3;
 INPUT ---          1 0 12; (right column = hours of culling effort per week)
 INPUT ---          1 0 6;
 INPUT ---          1 0 12;
 INPUT ---          1 0 12;
 INPUT ---          1 0 6;
 INPUT ---          1 0 6;
 INPUT ---          1 0 12;
 INPUT ---          1 0 6;
 INPUT ---          1 0 12;
 INPUT ---          1 0 12;
 INPUT ---          1 0 6;
 INPUT ---          1 0 6;
 INPUT ---          1 0 6;
 INPUT ---          0 1 0;

 Link Function Used is LOGIT
```

Variance Estimation Procedure Used is 2ndPart
M(t+1):
87
-2logL(saturated) = -191.57235
Effective Sample Size = 1131

Number of function evaluations was 17 for 2 parameters.
Time for numerical optimization was 0.01 seconds.
-2logL {Logit_2010_2011} = 426.37954
Penalty {Logit_2010_2011} = 0.0000000
Gradient {Logit_2010_2011}:
0.3350280E-05 0.4414354E-05
S Vector {Logit_2010_2011}:
10.43585 1.337301
Time to compute number of parameters was 0.01 seconds.
Threshold = 0.6000000E-07 Condition index = 0.1281449
Conditioned S Vector {Logit_2010_2011}:
1.000000 0.1281449
Number of Estimated Parameters {Logit_2010_2011} = 2
DEVIANCE {Logit_2010_2011} = 617.95189
DEVIANCE Degrees of Freedom {Logit_2010_2011} = 11
c-hat {Logit_2010_2011} = 56.177445
AIC {Logit_2010_2011} = 430.37954
AICc {Logit_2010_2011} = 430.39018
BIC {Logit_2010_2011} = 440.44126
Pearson Chisquare {Logit_2010_2011} = 8.0521938

LOGIT Link Function Parameters of {Logit_2010_2011}

Parameter	Beta	Standard Error	95% Confidence Interval Lower	Upper
1:	-4.0900297	0.7785328	-5.6159540	-2.5641053
2:	0.0000000	0.0000000	0.0000000	0.0000000
3:	0.1312825	0.0406104	0.0516862	0.2108788

Real Function Parameters of {Logit_2010_2011}

Parameter		Estimate	Standard Error	95% Confidence Interval Lower	Upper
1:p		0.0748382	0.0382920	0.0266326	0.1929967
2:p		0.0354912	0.0215583	0.0105952	0.1122490
3:p		0.0748382	0.0382920	0.0266326	0.1929967
4:p		0.0748382	0.0382920	0.0266326	0.1929967
5:p		0.0354912	0.0215583	0.0105952	0.1122490
6:p		0.0354912	0.0215583	0.0105952	0.1122490
7:p		0.0748382	0.0382920	0.0266326	0.1929967
8:p		0.0354912	0.0215583	0.0105952	0.1122490
9:p		0.0748382	0.0382920	0.0266326	0.1929967
10:p		0.0748382	0.0382920	0.0266326	0.1929967
11:p		0.0354912	0.0215583	0.0105952	0.1122490
12:p		0.0354912	0.0215583	0.0105952	0.1122490
13:p		0.0354912	0.0215583	0.0105952	0.1122490
14:c	Fixed	0.0000000	0.0000000	0.0000000	0.0000000

Estimates of Derived Parameters
Population Estimates of {Logit_2010_2011}

Group	N-hat	Standard Error	95% Confidence Interval Lower	Upper
1	**169.56119**	**65.185437**	**108.09954**	**410.05681**

```
  Time in seconds for last procedure was 0.05

INPUT --- proc stop;
  Time in minutes for this job was 0.00

     E X E C U T I O N   S U C C E S S F U L
```

Input File: 2009-2010

/ Gettysburg White-tailed deer CPUE, 2009-2010 culling season, number of antlerless deer harvested per week*/*

```
100000  15;
010000   8;
001000   1;
000100  16;
000010   4;
000001  17;
```

(No culling effort data were reported to run analysis)

Input File: 2008-2009

```
/* Gettysburg White-tailed deer CPUE, 2008-2009 culling season, number of antlerless deer harvested per week*/
                    100000000 23;
                    010000000 13;
                    001000000  8;
                    000100000  5;
                    000010000  5;
                    000001000  8;
                    000000100  3;
                    000000010  0;
                    000000001  4;

  Program  MARK  - Survival Rate Estimation with Capture-Recapture Data
  Compaq(Win32) Vers. 6.0 Dec 2009     15-Nov-2011 18:40:04
 - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - -
  INPUT --- proc title CPUE_2008_2009;
    Time in seconds for last procedure was 0.00
 INPUT --- proc chmatrix occasions=9 groups=1 etype=Huggins mixtures=2
 INPUT --- NoHist hist=300;
 INPUT ---    glabel(1)=Group 1;
 INPUT ---    time interval 1 1 1 1 1 1 1 1 1;
    Number of unique encounter histories read was 9.
    Number of individual covariates read was 0.
    Time interval lengths are all equal to 1.
    Data type is Huggins Closed Captures.
    Time in seconds for last procedure was 0.00

 INPUT --- proc estimate link=Logit varest=2ndPart ;
 INPUT --- model={Logit_2008_2009};
 INPUT ---    fixed=1;
 INPUT ---             parm(10)=0;
 INPUT ---    group=1 p rows=1 cols=9 Square Time=1;
 INPUT ---    group=1 c rows=1 cols=8 Square Constant=10;

 INPUT ---    design matrix constraints=10 covariates=3;
 INPUT ---          1 0 24; (right column = hours of culling effort per week)
 INPUT ---          1 0 16;
 INPUT ---          1 0 8;
 INPUT ---          1 0 6;
 INPUT ---          1 0 8;
 INPUT ---          1 0 8;
 INPUT ---          1 0 8;
 INPUT ---          1 0 8;
 INPUT ---          1 0 8;
 INPUT ---          0 1 0;

 Link Function Used is LOGIT
 Variance Estimation Procedure Used is 2ndPart
 M(t+1):
     69
 -2logL(saturated) = -195.40873
 Effective Sample Size = 621

 Number of function evaluations was 13 for 2 parameters.
 Time for numerical optimization was 0.01 seconds.
 -2logL {Logit_2008_2009} = 266.43044
 Penalty {Logit_2008_2009} = 0.0000000
 Gradient {Logit_2008_2009}:
  0.000000     0.2889043E-05
 S Vector {Logit_2008_2009}:
  25.48019      1.299595
 Time to compute number of parameters was 0.01 seconds.
  Threshold =  0.6000000E-07     Condition index =  0.5100412E-01
```

Conditioned S Vector {Logit_2008_2009}:
1.000000 0.5100412E-01
Number of Estimated Parameters {Logit_2008_2009} = 2
DEVIANCE {Logit_2008_2009} = 461.83917
DEVIANCE Degrees of Freedom {Logit_2008_2009} = 6
c-hat {Logit_2008_2009} = 76.973195
AIC {Logit_2008_2009} = 270.43044
AICc {Logit_2008_2009} = 270.44985
BIC {Logit_2008_2009} = 279.29310
Pearson Chisquare {Logit_2008_2009} = 7.0666374

LOGIT Link Function Parameters of {Logit_2008_2009}

Parameter	Beta	Standard Error	95% Confidence Interval Lower	Upper
1:	-1.8859677	0.6560955	-3.1719148	-0.6000205
2:	0.0000000	0.0000000	0.0000000	0.0000000
3:	0.0403147	0.0256260	-0.0099124	0.0905417

Real Function Parameters of {Logit_2008_2009}

Parameter	Estimate	Standard Error	95% Confidence Interval Lower	Upper
1:p	0.2852809	0.0578003	0.1863299	0.4102832
2:p	0.2242736	0.0584836	0.1301301	0.3584594
3:p	0.1731521	0.0686180	0.0756601	0.3488560
4:p	0.1619107	0.0707719	0.0649905	0.3493622
5:p	0.1731521	0.0686180	0.0756601	0.3488560
6:p	0.1731521	0.0686180	0.0756601	0.3488560
7:p	0.1731521	0.0686180	0.0756601	0.3488560
8:p	0.1731521	0.0686180	0.0756601	0.3488560
9:p	0.1731521	0.0686180	0.0756601	0.3488560
10:c Fixed	0.0000000	0.0000000	0.0000000	0.0000000

Estimates of Derived Parameters
Population Estimates of {Logit_2008_2009}

Group	N-hat	Standard Error	95% Confidence Interval Lower	Upper
1	**81.032219**	**10.592074**	**71.726275**	**122.**10334

Time in seconds for last procedure was 0.03

INPUT --- proc stop;

Time in minutes for this job was 0.00

E X E C U T I O N S U C C E S S F U L

Input File: 2007-2008

```
/* Gettysburg White-tailed deer CPUE, 2007-2008 culling season, number of antlerless deer harvested per week*/
                        10000  26;
                        01000  32;
                        00100  15;
                        00010   7;
                        00001   0;

  Program  MARK  - Survival Rate Estimation with Capture-Recapture Data
  Compaq(Win32) Vers. 6.0 Dec 2009     15-Nov-2011 18:42:23
- - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - -
  INPUT --- proc title CPUE_2007_2008;
    Time in seconds for last procedure was 0.00
 INPUT --- proc chmatrix occasions=5 groups=1 etype=Huggins mixtures=2
 INPUT --- NoHist hist=300;
 INPUT ---    glabel(1)=Group 1;
 INPUT ---    time interval 1 1 1 1 1;
    Number of unique encounter histories read was 5.
    Number of individual covariates read was 0.
    Time interval lengths are all equal to 1.
    Data type is Huggins Closed Captures.
    Time in seconds for last procedure was 0.00

 INPUT --- proc estimate link=Logit varest=2ndPart ;
 INPUT --- model={Logit_2007_2008};
 INPUT ---    fixed=1;
 INPUT ---             parm(6)=0;
 INPUT ---    group=1 p rows=1 cols=5 Square Time=1;
 INPUT ---    group=1 c rows=1 cols=4 Square Constant=6;

 INPUT ---    design matrix constraints=6 covariates=3;
 INPUT ---          1 0 32; (right column = hours of culling effort per week)
 INPUT ---          1 0 32;
 INPUT ---          1 0 24;
 INPUT ---          1 0 16;
 INPUT ---          1 0 7;
 INPUT ---          0 1 0;


Link Function Used is LOGIT

Variance Estimation Procedure Used is 2ndPart
M(t+1):
    80

-2logL(saturated) = -345.93435
Effective Sample Size = 400

Number of function evaluations was 20 for 2 parameters.
Time for numerical optimization was 0.01 seconds.
-2logL {Logit_2007_2008} = 207.01529
Penalty {Logit_2007_2008} = 0.0000000
Gradient {Logit_2007_2008}:
 0.1313286E-03-0.4365267E-02
S Vector {Logit_2007_2008}:
  2.608982     0.3415712E-03
Time to compute number of parameters was 0.01 seconds.
  Threshold =  0.6000000E-07     Condition index =  0.1309213E-03
Conditioned S Vector {Logit_2007_2008}:
  1.000000     0.1309213E-03
Number of Estimated Parameters {Logit_2007_2008} = 2
DEVIANCE {Logit_2007_2008} = 552.94965
DEVIANCE Degrees of Freedom {Logit_2007_2008} = 2
```

c-hat {Logit_2007_2008} = 276.47482
AIC {Logit_2007_2008} = 211.01529
AICc {Logit_2007_2008} = 211.04552
BIC {Logit_2007_2008} = 218.99822
Pearson Chisquare {Logit_2007_2008} = 3.7379911

LOGIT Link Function Parameters of {Logit_2007_2008}

Parameter	Beta	Standard Error	95% Confidence Interval Lower	Upper
1:	-14.525429	54.107735	-120.57659	91.525733
2:	0.0000000	0.0000000	0.0000000	0.0000000
3:	0.1099689	0.0193473	0.0720482	0.1478895

Real Function Parameters of {Logit_2007_2008}

Parameter		Estimate	Standard Error	95% Confidence Interval Lower	Upper
1:p		0.1659445E-004	0.8978823E-003	0.1452352E-050	1.0000000
2:p		0.1659445E-004	0.8978823E-003	0.1452352E-050	1.0000000
3:p		0.6884876E-005	0.3725207E-003	0.6035067E-051	1.0000000
4:p		0.2856452E-005	0.1545540E-003	0.2505622E-051	1.0000000
5:p		0.1061690E-005	0.5744509E-004	0.9310597E-052	1.0000000
6:c	Fixed	0.0000000	0.0000000	0.0000000	0.0000000

Estimates of Derived Parameters
Population Estimates of {Logit_2007_2008}

Group	N-hat	Standard Error	95% Confidence Interval Lower	Upper
1	**1818543.1**	**98396266.**	**7237.3780**	**0.4620140E+009**

Time in seconds for last procedure was 0.02

INPUT --- proc stop;

Time in minutes for this job was 0.00

E X E C U T I O N   S U C C E S S F U L

Input File: 2006-2007

```
/* Gettysburg White-tailed deer CPUE, 2006-2007 culling season, number of antlerless deer harvested per week*/
                   100000  32;
                   010000  24;
                   001000  11;
                   000100  11;
                   000010   1;
                   000001   2;


  Program  MARK  - Survival Rate Estimation with Capture-Recapture Data
  Compaq(Win32) Vers. 6.0 Dec 2009     15-Nov-2011 18:44:35
 - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - -
  INPUT --- proc title CPUE_2006_2007;
    Time in seconds for last procedure was 0.00
 INPUT --- proc chmatrix occasions=6 groups=1 etype=Huggins mixtures=2
 INPUT --- NoHist hist=300;
 INPUT ---    glabel(1)=Group 1;
 INPUT ---    time interval 1 1 1 1 1 1;
    Number of unique encounter histories read was 6.
    Number of individual covariates read was 0.
    Time interval lengths are all equal to 1.
    Data type is Huggins Closed Captures.
    Time in seconds for last procedure was 0.00

 INPUT --- proc estimate link=Logit varest=2ndPart ;
 INPUT --- model={Logit_2006_2007};
 INPUT ---    fixed=1;
 INPUT ---             parm(7)=0;
 INPUT ---    group=1 p rows=1 cols=6 Square Time=1;
 INPUT ---    group=1 c rows=1 cols=5 Square Constant=7;

 INPUT ---    design matrix constraints=7 covariates=3;
 INPUT ---          1 0 34; (right column = hours of culling effort per week)
 INPUT ---          1 0 34;
 INPUT ---          1 0 24;
 INPUT ---          1 0 14;
 INPUT ---          1 0 8;
 INPUT ---          1 0 4;
 INPUT ---          0 1 0;

 Link Function Used is LOGIT
 Variance Estimation Procedure Used is 2ndPart
 M(t+1):
    81
 -2logL(saturated) = -326.86805
 Effective Sample Size = 486

 Number of function evaluations was 8 for 2 parameters.
 Time for numerical optimization was 0.01 seconds.
 -2logL {Logit_2006_2007} = 234.70545
 Penalty {Logit_2006_2007} = 0.0000000
 Gradient {Logit_2006_2007}:
  0.1568957E-05 0.2668945E-05
 S Vector {Logit_2006_2007}:
   69.60926     0.5062953
 Time to compute number of parameters was 0.01 seconds.
   Threshold =  0.6000000E-07     Condition index =  0.7273390E-02
 Conditioned S Vector {Logit_2006_2007}:
   1.000000     0.7273390E-02
 Number of Estimated Parameters {Logit_2006_2007} = 2
 DEVIANCE {Logit_2006_2007} = 561.57350
 DEVIANCE Degrees of Freedom {Logit_2006_2007} = 4
```

c-hat {Logit_2006_2007} = 140.39337
AIC {Logit_2006_2007} = 238.70545
AICc {Logit_2006_2007} = 238.73029
BIC {Logit_2006_2007} = 247.07787
Pearson Chisquare {Logit_2006_2007} = 4.8622561

LOGIT Link Function Parameters of {Logit_2006_2007}

Parameter	Beta	Standard Error	95% Confidence Interval Lower	Upper
1:	0.8115043	0.9814063	-1.1120522	2.7350607
2:	0.0000000	0.0000000	0.0000000	0.0000000
3:	-0.0332297	0.0297966	-0.0916310	0.0251716

Real Function Parameters of {Logit_2006_2007}

Parameter		Estimate	Standard Error	95% Confidence Interval Lower	Upper
1:p		0.4210889	0.0420464	0.3415556	0.5049397
2:p		0.4210889	0.0420464	0.3415556	0.5049397
3:p		0.5034979	0.0754951	0.3594117	0.6470054
4:p		0.5857173	0.1394396	0.3143156	0.8134518
5:p		0.6331297	0.1736432	0.2850449	0.8819374
6:p		0.6634229	0.1929651	0.2659624	0.9146965
7:c	Fixed	0.0000000	0.0000000	0.0000000	0.0000000

Estimates of Derived Parameters
Population Estimates of {Logit_2006_2007}

Group	N-hat	Standard Error	95% Confidence Interval Lower	Upper
1	**81.695403**	**1.3614069**	**81.059406**	**89.140328**

Time in seconds for last procedure was 0.03

INPUT --- proc stop;

Time in minutes for this job was 0.00

E X E C U T I O N   S U C C E S S F U L

Input File: 2005-2006

```
/* Gettysburg White-tailed deer CPUE, 2005-2006 culling season, number of antlerless deer harvested per week*/
                 1000000  32;
                 0100000  11;
                 0010000  18;
                 0001000  24;
                 0000100   2;
                 0000010  11;
                 0000001  11;


  Program  MARK  - Survival Rate Estimation with Capture-Recapture Data
  Compaq(Win32) Vers. 6.0 Dec 2009     15-Nov-2011 18:46:23
 - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - -
  INPUT --- proc title CPUE_2005_2006;
    Time in seconds for last procedure was 0.00
 INPUT --- proc chmatrix occasions=7 groups=1 etype=Huggins mixtures=2
 INPUT --- NoHist hist=300;
 INPUT ---    glabel(1)=Group 1;
 INPUT ---    time interval 1 1 1 1 1 1 1;
    Number of unique encounter histories read was 7.
    Number of individual covariates read was 0.
    Time interval lengths are all equal to 1.
    Data type is Huggins Closed Captures.
    Time in seconds for last procedure was 0.00
 INPUT --- proc estimate link=Logit varest=2ndPart ;
 INPUT --- model={Logit_2005_2006};
 INPUT ---    fixed=1;
 INPUT ---            parm(8)=0;
 INPUT ---    group=1 p rows=1 cols=7 Square Time=1;
 INPUT ---    group=1 c rows=1 cols=6 Square Constant=8;

 INPUT ---    design matrix constraints=8 covariates=3;
 INPUT ---         1 0 24; (right column = hours of culling effort per week)
 INPUT ---         1 0 16;
 INPUT ---         1 0 32;
 INPUT ---         1 0 24;
 INPUT ---         1 0 8;
 INPUT ---         1 0 24;
 INPUT ---         1 0 24;
 INPUT ---         0 1 0;

 Link Function Used is LOGIT
 Variance Estimation Procedure Used is 2ndPart
 M(t+1):
    109
 -2logL(saturated) = -427.97150
 Effective Sample Size = 763

 Number of function evaluations was 13 for 2 parameters.
 Time for numerical optimization was 0.01 seconds.
 -2logL {Logit_2005_2006} = 397.57053
 Penalty {Logit_2005_2006} = 0.0000000
 Gradient {Logit_2005_2006}:
 -0.1409835E-05 0.1991025E-05
 S Vector {Logit_2005_2006}:
   15.86580      1.915100
 Time to compute number of parameters was 0.01 seconds.
   Threshold =  0.6000000E-07     Condition index =  0.1207061
 Conditioned S Vector {Logit_2005_2006}:
   1.000000     0.1207061
 Number of Estimated Parameters {Logit_2005_2006} = 2
 DEVIANCE {Logit_2005_2006} = 825.54203
```

DEVIANCE Degrees of Freedom {Logit_2005_2006} = 5
c-hat {Logit_2005_2006} = 165.10841
AIC {Logit_2005_2006} = 401.57053
AICc {Logit_2005_2006} = 401.58632
BIC {Logit_2005_2006} = 410.84505
Pearson Chisquare {Logit_2005_2006} = 14.127068

LOGIT Link Function Parameters of {Logit_2005_2006}

Parameter	Beta	Standard Error	95% Confidence Interval Lower	Upper
1:	-3.0319205	0.5289222	-4.0686080	-1.9952330
2:	0.0000000	0.0000000	0.0000000	0.0000000
3:	0.0579682	0.0172707	0.0241176	0.0918188

Real Function Parameters of {Logit_2005_2006}

Parameter		Estimate	Standard Error	95% Confidence Interval Lower	Upper
1:p		0.1623721	0.0446453	0.0924512	0.2694724
2:p		0.1086671	0.0345051	0.0571804	0.1968349
3:p		0.2356032	0.0641237	0.1329864	0.3824721
4:p		0.1623721	0.0446453	0.0924512	0.2694724
5:p		0.0712149	0.0283911	0.0320006	0.1509881
6:p		0.1623721	0.0446453	0.0924512	0.2694724
7:p		0.1623721	0.0446453	0.0924512	0.2694724
8:c	Fixed	0.0000000	0.0000000	0.0000000	0.0000000

Estimates of Derived Parameters
Population Estimates of {Logit_2005_2006}

Group	N-hat	Standard Error	95% Confidence Interval Lower	Upper
1	**158.31858**	**26.433710**	**127.41862**	**241.05781**

Time in seconds for last procedure was 0.03

INPUT --- proc stop;

Time in minutes for this job was 0.00

E X E C U T I O N   S U C C E S S F U L

Input File: 2004-2005

```
/* Gettysburg White-tailed deer CPUE, 2004-2005 culling season, number of antlerless deer harvested per week*/
                    100000000000 18;
                    010000000000 23;
                    001000000000 15;
                    000100000000 20;
                    000010000000  5;
                    000001000000 14;
                    000000100000  8;
                    000000010000  2;
                    000000001000  3;
                    000000000100  0;
                    000000000010  4;
                    000000000001  4;


  Program  MARK  - Survival Rate Estimation with Capture-Recapture Data
  Compaq(Win32) Vers. 6.0 Dec 2009     15-Nov-2011 18:48:13
- - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - -
  INPUT --- proc title CPUE_2004_2005;
    Time in seconds for last procedure was 0.00
 INPUT --- proc chmatrix occasions=12 groups=1 etype=Huggins
 INPUT --- mixtures=2 NoHist hist=300;
 INPUT ---    glabel(1)=Group 1;
 INPUT ---    time interval 1 1 1 1 1 1 1 1 1 1 1;
     Number of unique encounter histories read was 12.
     Number of individual covariates read was 0.
     Time interval lengths are all equal to 1.
     Data type is Huggins Closed Captures.
     Time in seconds for last procedure was 0.02

 INPUT --- proc estimate link=Logit varest=2ndPart ;
 INPUT --- model={Logit_2004_2005};
 INPUT ---    fixed=1;
 INPUT ---            parm(13)=0;
 INPUT ---    group=1 p rows=1 cols=12 Square Time=1;
 INPUT ---    group=1 c rows=1 cols=11 Square Constant=13;

 INPUT ---    design matrix constraints=13 covariates=3;
 INPUT ---         1 0 16; (right column = hours of culling effort per week)
 INPUT ---         1 0 16;
 INPUT ---         1 0 25;
 INPUT ---         1 0 16;
 INPUT ---         1 0 8;
 INPUT ---         1 0 15;
 INPUT ---         1 0 16;
 INPUT ---         1 0 16;
 INPUT ---         1 0 8;
 INPUT ---         1 0 8;
 INPUT ---         1 0 17;
 INPUT ---         1 0 7;
 INPUT ---         0 1 0;

 Link Function Used is LOGIT

 Variance Estimation Procedure Used is 2ndPart
 M(t+1):
    116
 -2logL(saturated) = -378.75384
 Effective Sample Size = 1392

 Number of function evaluations was 12 for 2 parameters.
 Time for numerical optimization was 0.01 seconds.
```

-2logL {Logit_2004_2005} = 522.05532
Penalty {Logit_2004_2005} = 0.0000000
Gradient {Logit_2004_2005}:
-0.7746220E-05 0.000000
S Vector {Logit_2004_2005}:
51.36307   1.720590
Time to compute number of parameters was 0.01 seconds.
Threshold = 0.6000000E-07   Condition index = 0.3349857E-01
Conditioned S Vector {Logit_2004_2005}:
1.000000   0.3349857E-01
Number of Estimated Parameters {Logit_2004_2005} = 2
DEVIANCE {Logit_2004_2005} = 900.80916
DEVIANCE Degrees of Freedom {Logit_2004_2005} = 9
c-hat {Logit_2004_2005} = 100.08991
AIC {Logit_2004_2005} = 526.05532
AICc {Logit_2004_2005} = 526.06396
BIC {Logit_2004_2005} = 536.53231
Pearson Chisquare {Logit_2004_2005} = 20.486403

LOGIT Link Function Parameters of {Logit_2004_2005}

			95% Confidence Interval	
Parameter	*Beta*	*Standard Error*	*Lower*	*Upper*
1:	*-1.9352846*	*0.4929352*	*-2.9014375*	*-0.9691316*
2:	*0.0000000*	*0.0000000*	*0.0000000*	*0.0000000*
3:	*0.0258790*	*0.0239226*	*-0.0210092*	*0.0727672*

Real Function Parameters of {Logit_2004_2005}

				95% Confidence Interval	
Parameter		*Estimate*	*Standard Error*	*Lower*	*Upper*
1:p		*0.1792818*	*0.0285161*	*0.1299869*	*0.2420694*
2:p		*0.1792818*	*0.0285161*	*0.1299869*	*0.2420694*
3:p		*0.2161390*	*0.0381757*	*0.1505937*	*0.3001323*
4:p		*0.1792818*	*0.0285161*	*0.1299869*	*0.2420694*
5:p		*0.1508112*	*0.0412300*	*0.0863328*	*0.2502557*
6:p		*0.1755055*	*0.0295897*	*0.1247835*	*0.2411640*
7:p		*0.1792818*	*0.0285161*	*0.1299869*	*0.2420694*
8:p		*0.1792818*	*0.0285161*	*0.1299869*	*0.2420694*
9:p		*0.1508112*	*0.0412300*	*0.0863328*	*0.2502557*
10:p		*0.1508112*	*0.0412300*	*0.0863328*	*0.2502557*
11:p		*0.1831213*	*0.0277643*	*0.1348047*	*0.2438741*
12:p		*0.1475268*	*0.0430280*	*0.0813071*	*0.2528358*
13:c	*Fixed*	*0.0000000*	*0.0000000*	*0.0000000*	*0.0000000*

Estimates of Derived Parameters
Population Estimates of {Logit_2004_2005}

			95% Confidence Interval	
Group	*N-hat*	*Standard Error*	*Lower*	*Upper*
1	*129**.26574***	***7.4912804***	***120.73037***	***153.20215***

Time in seconds for last procedure was 0.05

INPUT --- proc stop;

Time in minutes for this job was 0.00

E X E C U T I O N   S U C C E S S F U L

Input File: 2003-2004

```
/* Gettysburg White-tailed deer CPUE, 2003-2004 culling season, number of antlerless deer harvested per week*/
                    100000000000 45;
                    010000000000 28;
                    001000000000 11;
                    000100000000  9;
                    000010000000  4;
                    000001000000  4;
                    000000100000  4;
                    000000010000  9;
                    000000001000  3;
                    000000000100  7;
                    000000000010 15;
                    000000000001 13;


  Program  MARK  - Survival Rate Estimation with Capture-Recapture Data
  Compaq(Win32) Vers. 6.0 Dec 2009     15-Nov-2011 18:58:32
 - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - -
  INPUT --- proc title CPUE_2003_2004;
    Time in seconds for last procedure was 0.00
 INPUT --- proc chmatrix occasions=12 groups=1 etype=Huggins
 INPUT --- mixtures=2 NoHist hist=300;
 INPUT ---    glabel(1)=Group 1;
 INPUT ---    time interval 1 1 1 1 1 1 1 1 1 1 1;
     Number of unique encounter histories read was 12.
     Number of individual covariates read was 0.
     Time interval lengths are all equal to 1.
     Data type is Huggins Closed Captures.
     Time in seconds for last procedure was 0.02
 INPUT --- proc estimate link=Logit varest=2ndPart ;
 INPUT --- model={Logit_2003_2004};
 INPUT ---    fixed=1;
 INPUT ---             parm(13)=0;
 INPUT ---    group=1 p rows=1 cols=12 Square Time=1;
 INPUT ---    group=1 c rows=1 cols=11 Square Constant=13;

 INPUT ---    design matrix constraints=13 covariates=3;
 INPUT ---         1 0 35; (right column = hours of culling effort per week)
 INPUT ---         1 0 32;
 INPUT ---         1 0 8;
 INPUT ---         1 0 16;
 INPUT ---         1 0 7;
 INPUT ---         1 0 7;
 INPUT ---         1 0 8;
 INPUT ---         1 0 27;
 INPUT ---         1 0 8;
 INPUT ---         1 0 16;
 INPUT ---         1 0 17;
 INPUT ---         1 0 16;
 INPUT ---         0 1 0;

Link Function Used is LOGIT

 Variance Estimation Procedure Used is 2ndPart
 M(t+1):
    152
 -2logL(saturated) = -578.95538
 Effective Sample Size = 1824

 Number of function evaluations was 15 for 2 parameters.
 Time for numerical optimization was 0.01 seconds.
 -2logL {Logit_2003_2004} = 670.01713
```

Penalty {Logit_2003_2004} = 0.0000000
Gradient {Logit_2003_2004}:
0.6436566E-05 0.1412873E-04
S Vector {Logit_2003_2004}:
20.30279 1.206740
Time to compute number of parameters was 0.01 seconds.
Threshold = 0.6000000E-07 Condition index = 0.5943713E-01
Conditioned S Vector {Logit_2003_2004}:
1.000000 0.5943713E-01
Number of Estimated Parameters {Logit_2003_2004} = 2
DEVIANCE {Logit_2003_2004} = 1248.9725
DEVIANCE Degrees of Freedom {Logit_2003_2004} = 10
c-hat {Logit_2003_2004} = 124.89725
AIC {Logit_2003_2004} = 674.01713
AICc {Logit_2003_2004} = 674.02372
BIC {Logit_2003_2004} = 685.03470
Pearson Chisquare {Logit_2003_2004} = 19.477288

LOGIT Link Function Parameters of {Logit_2003_2004}

Parameter	*Beta*	*Standard Error*	*95% Confidence Interval Lower*	*Upper*
1:	*-4.2987958*	*0.8727597*	*-6.0094047*	*-2.5881868*
2:	*0.0000000*	*0.0000000*	*0.0000000*	*0.0000000*
3:	*0.0633886*	*0.0097405*	*0.0442973*	*0.0824799*

Real Function Parameters of {Logit_2003_2004}

Parameter		*Estimate*	*Standard Error*	*95% Confidence Interval Lower*	*Upper*
1:p		*0.1110366*	*0.0655545*	*0.0328663*	*0.3146428*
2:p		*0.0936075*	*0.0575099*	*0.0266257*	*0.2805309*
3:p		*0.0220599*	*0.0176311*	*0.0045253*	*0.1006664*
4:p		*0.0361040*	*0.0266466*	*0.0082821*	*0.1438324*
5:p		*0.0207330*	*0.0167299*	*0.0041930*	*0.0962134*
6:p		*0.0207330*	*0.0167299*	*0.0041930*	*0.0962134*
7:p		*0.0220599*	*0.0176311*	*0.0045253*	*0.1006664*
8:p		*0.0699600*	*0.0457251*	*0.0186204*	*0.2297178*
9:p		*0.0220599*	*0.0176311*	*0.0045253*	*0.1006664*
10:p		*0.0361040*	*0.0266466*	*0.0082821*	*0.1438324*
11:p		*0.0383760*	*0.0280304*	*0.0089250*	*0.1502751*
12:p		*0.0361040*	*0.0266466*	*0.0082821*	*0.1438324*
13:c	*Fixed*	*0.0000000*	*0.0000000*	*0.0000000*	*0.0000000*

Estimates of Derived Parameters
Population Estimates of {Logit_2003_2004}

Group	*N-hat*	*Standard Error*	*95% Confidence Interval Lower*	*Upper*
1	***360.88283***	***191.85902***	***197.09530***	***1119.5518***

Time in seconds for last procedure was 0.03

INPUT --- proc stop;

Time in minutes for this job was 0.00

E X E C U T I O N   S U C C E S S F U L

Input File: 2002-2003

```
/* Gettysburg White-tailed deer CPUE, 2002-2003 culling season, number of antlerless deer harvested per week*/
                    1000000  45;
                    0100000  29;
                    0010000  21;
                    0001000  25;
                    0000100  14;
                    0000010   1;
                    0000001  13;


  Program  MARK  - Survival Rate Estimation with Capture-Recapture Data
  Compaq(Win32) Vers. 6.0 Dec 2009     15-Nov-2011 20:04:59
 - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - -
  INPUT --- proc title CPUE_2002_2003;
    Time in seconds for last procedure was 0.00
 INPUT --- proc chmatrix occasions=7 groups=1 etype=Huggins mixtures=2
 INPUT --- NoHist hist=300;
 INPUT ---    glabel(1)=Group 1;
 INPUT ---    time interval 1 1 1 1 1 1 1;
    Number of unique encounter histories read was 7.
    Number of individual covariates read was 0.
    Time interval lengths are all equal to 1.
    Data type is Huggins Closed Captures.
    Time in seconds for last procedure was 0.02
 INPUT --- proc estimate link=Logit varest=2ndPart ;
 INPUT --- model={Logit_2002_2003};
 INPUT ---    fixed=1;
 INPUT ---             parm(8)=0;
 INPUT ---    group=1 p rows=1 cols=7 Square Time=1;
 INPUT ---    group=1 c rows=1 cols=6 Square Constant=8;

 INPUT ---    design matrix constraints=8 covariates=3;
 INPUT ---          1 0 28; (right column = hours of culling effort per week)
 INPUT ---          1 0 22;
 INPUT ---          1 0 13;
 INPUT ---          1 0 29;
 INPUT ---          1 0 29;
 INPUT ---          1 0 16;
 INPUT ---          1 0 28;
 INPUT ---          0 1 0;

 Link Function Used is LOGIT

 Variance Estimation Procedure Used is 2ndPart
 M(t+1):
    148
 -2logL(saturated) = -678.13502
 Effective Sample Size = 1036

 Number of function evaluations was 12 for 2 parameters.
 Time for numerical optimization was 0.01 seconds.
 -2logL {Logit_2002_2003} = 524.43738
 Penalty {Logit_2002_2003} = 0.0000000
 Gradient {Logit_2002_2003}:
  0.3550283E-05 0.4885890E-05
 S Vector {Logit_2002_2003}:
   52.62045      2.292650
 Time to compute number of parameters was 0.01 seconds.
   Threshold =  0.6000000E-07     Condition index =  0.4356957E-01
 Conditioned S Vector {Logit_2002_2003}:
   1.000000     0.4356957E-01
 Number of Estimated Parameters {Logit_2002_2003} = 2
```

DEVIANCE {Logit_2002_2003} = 1202.5724
DEVIANCE Degrees of Freedom {Logit_2002_2003} = 5
c-hat {Logit_2002_2003} = 240.51448
AIC {Logit_2002_2003} = 528.43738
AICc {Logit_2002_2003} = 528.44899
BIC {Logit_2002_2003} = 538.32362
Pearson Chisquare {Logit_2002_2003} = 9.7772200

LOGIT Link Function Parameters of {Logit_2002_2003}

Parameter	Beta	Standard Error	95% Confidence Interval Lower	Upper
1:	-2.2021912	0.4514669	-3.0870664	-1.3173161
2:	0.0000000	0.0000000	0.0000000	0.0000000
3:	0.0457531	0.0172881	0.0118683	0.0796379

Real Function Parameters of {Logit_2002_2003}

Parameter		Estimate	Standard Error	95% Confidence Interval Lower	Upper
1:p		0.2847329	0.0396905	0.2136469	0.3683905
2:p		0.2322547	0.0329111	0.1740230	0.3028281
3:p		0.1669498	0.0364114	0.1071162	0.2508170
4:p		0.2941420	0.0418992	0.2191051	0.3822960
5:p		0.2941420	0.0418992	0.2191051	0.3822960
6:p		0.1869211	0.0345472	0.1283449	0.2641303
7:p		0.2847329	0.0396905	0.2136469	0.3683905
8:c	Fixed	0.0000000	0.0000000	0.0000000	0.0000000

Estimates of Derived Parameters
Population Estimates of {Logit_2002_2003}

Group	N-hat	Standard Error	95% Confidence Interval Lower	Upper
1	**170.61577**	**9.7336110**	**158.08105**	**198.73611**

Time in seconds for last procedure was 0.02

INPUT --- proc stop;

Time in minutes for this job was 0.00

E X E C U T I O N   S U C C E S S F U L

Input File: 2001-2002

```
/* Gettysburg White-tailed deer CPUE, 2001-2002 culling season, number of antlerless deer harvested per week*/
                1000000000000000  5;
                0100000000000000 12;
                0010000000000000 20;
                0001000000000000 22;
                0000100000000000 10;
                0000010000000000 15;
                0000001000000000 13;
                0000000100000000  9;
                0000000010000000 13;
                0000000001000000 11;
                0000000000100000  9;
                0000000000010000 15;
                0000000000001000  2;
                0000000000000100  5;
                0000000000000010 10;
                0000000000000001  1;


  Program  MARK  - Survival Rate Estimation with Capture-Recapture Data
  Compaq(Win32) Vers. 6.0 Dec 2009     15-Nov-2011 20:10:00
 - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - -
  INPUT --- proc title CPUE_2001_2002;
   Time in seconds for last procedure was 0.00
 INPUT --- proc chmatrix occasions=16 groups=1 etype=Huggins
 INPUT --- mixtures=2 NoHist hist=300;
 INPUT ---    glabel(1)=Group 1;
 INPUT ---    time interval 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1;
    Number of unique encounter histories read was 16.
    Number of individual covariates read was 0.
    Time interval lengths are all equal to 1.
    Data type is Huggins Closed Captures.
    Time in seconds for last procedure was 0.02
 INPUT --- proc estimate link=Logit varest=2ndPart ;
 INPUT --- model={Logit_2001_2002};
 INPUT ---    fixed=1;
 INPUT ---           parm(17)=0;
 INPUT ---    group=1 p rows=1 cols=16 Square Time=1;
 INPUT ---    group=1 c rows=1 cols=15 Square Constant=17;

 INPUT ---    design matrix constraints=17 covariates=3;
 INPUT ---         1 0 9; (right column = hours of culling effort per week)
 INPUT ---         1 0 9;
 INPUT ---         1 0 15;
 INPUT ---         1 0 15;
 INPUT ---         1 0 9;
 INPUT ---         1 0 9;
 INPUT ---         1 0 14;
 INPUT ---         1 0 10;
 INPUT ---         1 0 15;
 INPUT ---         1 0 16;
 INPUT ---         1 0 15;
 INPUT ---         1 0 10;
 INPUT ---         1 0 5;
 INPUT ---         1 0 14;
 INPUT ---         1 0 9;
 INPUT ---         1 0 5;
 INPUT ---         0 1 0;


 Link Function Used is LOGIT
```

Variance Estimation Procedure Used is 2ndPart
M(t+1):
118
-2logL(saturated) = -276.85631
Effective Sample Size = 1888

Number of function evaluations was 16 for 2 parameters.
Time for numerical optimization was 0.01 seconds.
-2logL {Logit_2001_2002} = 642.24177
Penalty {Logit_2001_2002} = 0.0000000
Gradient {Logit_2001_2002}:
0.000000   -0.1084242E-04
S Vector {Logit_2001_2002}:
10.10750   2.033348
Time to compute number of parameters was 0.01 seconds.
Threshold = 0.6000000E-07   Condition index = 0.2011723
Conditioned S Vector {Logit_2001_2002}:
1.000000   0.2011723
Number of Estimated Parameters {Logit_2001_2002} = 2
DEVIANCE {Logit_2001_2002} = 919.09808
DEVIANCE Degrees of Freedom {Logit_2001_2002} = 14
c-hat {Logit_2001_2002} = 65.649863
AIC {Logit_2001_2002} = 646.24177
AICc {Logit_2001_2002} = 646.24813
BIC {Logit_2001_2002} = 657.32831
Pearson Chisquare {Logit_2001_2002} = 22.978412

LOGIT Link Function Parameters of {Logit_2001_2002}

Parameter	*Beta*	*Standard Error*	*95% Confidence Interval Lower*	*Upper*
1:	*-3.9118195*	*0.6146556*	*-5.1165444*	*-2.7070945*
2:	*0.0000000*	*0.0000000*	*0.0000000*	*0.0000000*
3:	*0.0685671*	*0.0288405*	*0.0120397*	*0.1250946*

Real Function Parameters of {Logit_2001_2002}

Parameter		*Estimate*	*Standard Error*	*95% Confidence Interval Lower*	*Upper*
1:p		*0.0357529*	*0.0170498*	*0.0138701*	*0.0890430*
2:p		*0.0357529*	*0.0170498*	*0.0138701*	*0.0890430*
3:p		*0.0529847*	*0.0240978*	*0.0213608*	*0.1254264*
4:p		*0.0529847*	*0.0240978*	*0.0213608*	*0.1254264*
5:p		*0.0357529*	*0.0170498*	*0.0138701*	*0.0890430*
6:p		*0.0357529*	*0.0170498*	*0.0138701*	*0.0890430*
7:p		*0.0496478*	*0.0225694*	*0.0200470*	*0.1177061*
8:p		*0.0381935*	*0.0179252*	*0.0150301*	*0.0936600*
9:p		*0.0529847*	*0.0240978*	*0.0213608*	*0.1254264*
10:p		*0.0565326*	*0.0258086*	*0.0226840*	*0.1339659*
11:p		*0.0529847*	*0.0240978*	*0.0213608*	*0.1254264*
12:p		*0.0381935*	*0.0179252*	*0.0150301*	*0.0936600*
13:p		*0.0274119*	*0.0142866*	*0.0097635*	*0.0745595*
14:p		*0.0496478*	*0.0225694*	*0.0200470*	*0.1177061*
15:p		*0.0357529*	*0.0170498*	*0.0138701*	*0.0890430*
16:p		*0.0274119*	*0.0142866*	*0.0097635*	*0.0745595*
17:c	*Fixed*	*0.0000000*	*0.0000000*	*0.0000000*	*0.0000000*

Estimates of Derived Parameters
Population Estimates of {Logit_2001_2002}

Group	*N-hat*	*Standard Error*	*95% Confidence Interval Lower*	*Upper*

```
---------  --------------  --------------  --------------  --------------
    1   235.96146       78.222706       154.12928       503.14207

   Time in seconds for last procedure was 0.03

 INPUT --- proc stop;

   Time in minutes for this job was 0.00

      E X E C U T I O N   S U C C E S S F U L
```

Input File: 2000-2001

```
/* Gettysburg White-tailed deer CPUE, 2000-2001 culling season, number of antlerless deer harvested per week*/
                    10000000000000000  9;
                    01000000000000000 18;
                    00100000000000000 18;
                    00010000000000000 19;
                    00001000000000000 13;
                    00000100000000000 10;
                    00000010000000000 18;
                    00000001000000000 16;
                    00000000100000000 12;
                    00000000010000000  8;
                    00000000001000000  9;
                    00000000000100000 16;
                    00000000000010000 11;
                    00000000000001000  5;
                    00000000000000100 12;
                    00000000000000010 10;
                    00000000000000001  1;


  Program  MARK  - Survival Rate Estimation with Capture-Recapture Data
  Compaq(Win32) Vers. 6.0 Dec 2009     15-Nov-2011 20:11:50
 - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - -
  INPUT --- proc title CPUE_2000_2001;
    Time in seconds for last procedure was 0.02
 INPUT --- proc chmatrix occasions=17 groups=1 etype=Huggins
 INPUT --- mixtures=2 NoHist hist=300;
 INPUT ---    glabel(1)=Group 1;
 INPUT ---    time interval 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1;
    Number of unique encounter histories read was 17.
    Number of individual covariates read was 0.
    Time interval lengths are all equal to 1.
    Data type is Huggins Closed Captures.
    Time in seconds for last procedure was 0.00
 INPUT --- proc estimate link=Logit varest=2ndPart ;
 INPUT --- model={Logit_2000_2001};
 INPUT ---    fixed=1;
 INPUT ---             parm(18)=0;
 INPUT ---    group=1 p rows=1 cols=17 Square Time=1;
 INPUT ---    group=1 c rows=1 cols=16 Square Constant=18;

 INPUT ---    design matrix constraints=18 covariates=3;
 INPUT ---          1 0 9; (right column = hours of culling effort per week)
 INPUT ---          1 0 13;
 INPUT ---          1 0 14;
 INPUT ---          1 0 19;
 INPUT ---          1 0 14;
 INPUT ---          1 0 14;
 INPUT ---          1 0 14;
 INPUT ---          1 0 14;
 INPUT ---          1 0 13;
 INPUT ---          1 0 9;
 INPUT ---          1 0 10;
 INPUT ---          1 0 10;
 INPUT ---          1 0 10;
 INPUT ---          1 0 3;
 INPUT ---          1 0 13;
 INPUT ---          1 0 20;
 INPUT ---          1 0 1.0;
 INPUT ---          0 1 0;
```

Link Function Used is LOGIT

Variance Estimation Procedure Used is 2ndPart
M(t+1):
205
-2logL(saturated) = -657.94304
Effective Sample Size = 3485
Number of function evaluations was 16 for 2 parameters.
Time for numerical optimization was 0.01 seconds.
-2logL {Logit_2000_2001} = 1137.9305
Penalty {Logit_2000_2001} = 0.0000000
Gradient {Logit_2000_2001}:
0.4448718E-05 0.2033324E-04
S Vector {Logit_2000_2001}:
14.22245 3.036982
Time to compute number of parameters was 0.01 seconds.
Threshold = 0.6000000E-07 Condition index = 0.2135344
Conditioned S Vector {Logit_2000_2001}:
1.000000 0.2135344
Number of Estimated Parameters {Logit_2000_2001} = 2
DEVIANCE {Logit_2000_2001} = 1795.8736
DEVIANCE Degrees of Freedom {Logit_2000_2001} = 15
c-hat {Logit_2000_2001} = 119.72490
AIC {Logit_2000_2001} = 1141.9305
AICc {Logit_2000_2001} = 1141.9340
BIC {Logit_2000_2001} = 1154.2430
Pearson Chisquare {Logit_2000_2001} = 15.744059

LOGIT Link Function Parameters of {Logit_2000_2001}

Parameter	*Beta*	*Standard Error*	*95% Confidence Interval Lower*	*Upper*
1:	*-4.1109928*	*0.5204179*	*-5.1310119*	*-3.0909737*
2:	*0.0000000*	*0.0000000*	*0.0000000*	*0.0000000*
3:	*0.0618236*	*0.0179409*	*0.0266594*	*0.0969878*

Real Function Parameters of {Logit_2000_2001}

Parameter		*Estimate*	*Standard Error*	*95% Confidence Interval Lower*	*Upper*
1:p		*0.0277985*	*0.0120706*	*0.0117745*	*0.0642130*
2:p		*0.0353221*	*0.0146363*	*0.0155322*	*0.0783205*
3:p		*0.0374903*	*0.0154099*	*0.0165859*	*0.0825308*
4:p		*0.0503859*	*0.0203760*	*0.0225101*	*0.1089351*
5:p		*0.0374903*	*0.0154099*	*0.0165859*	*0.0825308*
6:p		*0.0374903*	*0.0154099*	*0.0165859*	*0.0825308*
7:p		*0.0374903*	*0.0154099*	*0.0165859*	*0.0825308*
8:p		*0.0374903*	*0.0154099*	*0.0165859*	*0.0825308*
9:p		*0.0353221*	*0.0146363*	*0.0155322*	*0.0783205*
10:p		*0.0277985*	*0.0120706*	*0.0117745*	*0.0642130*
11:p		*0.0295190*	*0.0126430*	*0.0126451*	*0.0673735*
12:p		*0.0295190*	*0.0126430*	*0.0126451*	*0.0673735*
13:p		*0.0295190*	*0.0126430*	*0.0126451*	*0.0673735*
14:p		*0.0193500*	*0.0093204*	*0.0074784*	*0.0491344*
15:p		*0.0353221*	*0.0146363*	*0.0155322*	*0.0783205*
16:p		*0.0534276*	*0.0216392*	*0.0238190*	*0.1154875*
17:p		*0.0171380*	*0.0085944*	*0.0063735*	*0.0452553*
18:c	*Fixed*	*0.0000000*	*0.0000000*	*0.0000000*	*0.0000000*

Estimates of Derived Parameters
Population Estimates of {Logit_2000_2001}

			95% Confidence Interval	
Group	*N-hat*	*Standard Error*	*Lower*	*Upper*
1	***460.75461***	***144.72302***	***296.03011***	***923.55809***

Time in seconds for last procedure was 0.03

INPUT --- proc stop;

Time in minutes for this job was 0.00

E X E C U T I O N   S U C C E S S F U L

Input File: 1999-2000

```
/* Gettysburg White-tailed deer CPUE, 1999-2000 culling season, number of antlerless deer harvested per week*/
                    10000000000000 10;
                    01000000000000  6;
                    00100000000000  5;
                    00010000000000 30;
                    00001000000000  7;
                    00000100000000  6;
                    00000010000000  8;
                    00000001000000  9;
                    00000000100000  2;
                    00000000010000  6;
                    00000000001000 10;
                    00000000000100 10;
                    00000000000010  8;
                    00000000000001  3;


  Program  MARK  - Survival Rate Estimation with Capture-Recapture Data
  Compaq(Win32) Vers. 6.0 Dec 2009     15-Nov-2011 20:13:43
 - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - -
  INPUT --- proc title CPUE_1999_2000;
    Time in seconds for last procedure was 0.00
 INPUT --- proc chmatrix occasions=14 groups=1 etype=Huggins
 INPUT --- mixtures=2 NoHist hist=300;
 INPUT ---    glabel(1)=Group 1;
 INPUT ---    time interval 1 1 1 1 1 1 1 1 1 1 1 1 1;
     Number of unique encounter histories read was 14.
     Number of individual covariates read was 0.
     Time interval lengths are all equal to 1.
     Data type is Huggins Closed Captures.
     Time in seconds for last procedure was 0.00
 INPUT --- proc estimate link=Logit varest=2ndPart ;
 INPUT --- model={Logit_1999_2000};
 INPUT ---    fixed=1;
 INPUT ---             parm(15)=0;
 INPUT ---    group=1 p rows=1 cols=14 Square Time=1;
 INPUT ---    group=1 c rows=1 cols=13 Square Constant=15;

 INPUT ---    design matrix constraints=15 covariates=3;
 INPUT ---          1 0 9; (right column = hours of culling effort per week)
 INPUT ---          1 0 4;
 INPUT ---          1 0 5;
 INPUT ---          1 0 12;
 INPUT ---          1 0 5;
 INPUT ---          1 0 6;
 INPUT ---          1 0 8;
 INPUT ---          1 0 8;
 INPUT ---          1 0 8;
 INPUT ---          1 0 8;
 INPUT ---          1 0 17;
 INPUT ---          1 0 8;
 INPUT ---          1 0 13;
 INPUT ---          1 0 13;
 INPUT ---          0 1 0;

 Link Function Used is LOGIT

 Variance Estimation Procedure Used is 2ndPart
 M(t+1):
    120
 -2logL(saturated) = -332.15060
 Effective Sample Size = 1680
```

Number of function evaluations was 15 for 2 parameters.
Time for numerical optimization was 0.01 seconds.
-2logL {Logit_1999_2000} = 609.32125
Penalty {Logit_1999_2000} = 0.0000000
Gradient {Logit_1999_2000}:
0.5141472E-05 0.000000
S Vector {Logit_1999_2000}:
25.93310 3.014233
Time to compute number of parameters was 0.01 seconds.
Threshold = 0.6000000E-07 Condition index = 0.1162311
Conditioned S Vector {Logit_1999_2000}:
1.000000 0.1162311
Number of Estimated Parameters {Logit_1999_2000} = 2
DEVIANCE {Logit_1999_2000} = 941.47186
DEVIANCE Degrees of Freedom {Logit_1999_2000} = 12
c-hat {Logit_1999_2000} = 78.455988
AIC {Logit_1999_2000} = 613.32125
AICc {Logit_1999_2000} = 613.32841
BIC {Logit_1999_2000} = 624.17435
Pearson Chisquare {Logit_1999_2000} = 28.022163

LOGIT Link Function Parameters of {Logit_1999_2000}

			95% Confidence Interval	
Parameter	*Beta*	*Standard Error*	*Lower*	*Upper*
1:	*-3.4223455*	*0.2684167*	*-3.9484423*	*-2.8962487*
2:	*0.0000000*	*0.0000000*	*0.0000000*	*0.0000000*
3:	*0.1410885*	*0.0321261*	*0.0781214*	*0.2040556*

Real Function Parameters of {Logit_1999_2000}

				95% Confidence Interval	
Parameter		*Estimate*	*Standard Error*	*Lower*	*Upper*
1:p		*0.1040932*	*0.0222461*	*0.0678562*	*0.1564342*
2:p		*0.0542697*	*0.0108482*	*0.0365349*	*0.0798993*
3:p		*0.0619833*	*0.0120554*	*0.0421562*	*0.0902567*
4:p		*0.1506792*	*0.0381809*	*0.0899666*	*0.2414905*
5:p		*0.0619833*	*0.0120554*	*0.0421562*	*0.0902567*
6:p		*0.0707113*	*0.0136853*	*0.0481534*	*0.1026964*
7:p		*0.0916513*	*0.0186768*	*0.0610340*	*0.1354125*
8:p		*0.0916513*	*0.0186768*	*0.0610340*	*0.1354125*
9:p		*0.0916513*	*0.0186768*	*0.0610340*	*0.1354125*
10:p		*0.0916513*	*0.0186768*	*0.0610340*	*0.1354125*
11:p		*0.2642798*	*0.0833597*	*0.1342208*	*0.4542435*
12:p		*0.0916513*	*0.0186768*	*0.0610340*	*0.1354125*
13:p		*0.1696379*	*0.0453916*	*0.0979870*	*0.2775600*
14:p		*0.1696379*	*0.0453916*	*0.0979870*	*0.2775600*
15:c	*Fixed*	*0.0000000*	*0.0000000*	*0.0000000*	*0.0000000*

Estimates of Derived Parameters
Population Estimates of {Logit_1999_2000}

			95% Confidence Interval	
Group	*N-hat*	*Standard Error*	*Lower*	*Upper*
1	***147.16341***	***15.100165***	***129.82350***	***195.11077***

Time in seconds for last procedure was 0.06

INPUT --- proc stop;

Time in minutes for this job was 0.00

E X E C U T I O N   S U C C E S S F U L

Input File: 1998-1999

```
/* Gettysburg White-tailed deer CPUE, 1998-1999 culling season, number of antlerless deer harvested per week*/
                        1000  12;
                        0100  23;
                        0010  23;
                        0001  15;


  Program  MARK  - Survival Rate Estimation with Capture-Recapture Data
  Compaq(Win32) Vers. 6.0 Dec 2009     15-Nov-2011 20:15:41
- - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - -
  INPUT --- proc title CPUE_1998_1999;
    Time in seconds for last procedure was 0.00
 INPUT --- proc chmatrix occasions=4 groups=1 etype=Huggins mixtures=2
 INPUT --- NoHist hist=300;
 INPUT ---    glabel(1)=Group 1;
 INPUT ---    time interval 1 1 1 1;
    Number of unique encounter histories read was 4.
    Number of individual covariates read was 0.
    Time interval lengths are all equal to 1.
    Data type is Huggins Closed Captures.
    Time in seconds for last procedure was 0.00
 INPUT --- proc estimate link=Logit varest=2ndPart ;
 INPUT --- model={Logit_1998_1999};
 INPUT ---    fixed=1;
 INPUT ---              parm(5)=0;
 INPUT ---    group=1 p rows=1 cols=4 Square Time=1;
 INPUT ---    group=1 c rows=1 cols=3 Square Constant=5;

 INPUT ---    design matrix constraints=5 covariates=3;
 INPUT ---         1 0 13; (right column = hours of culling effort per week)
 INPUT ---         1 0 27;
 INPUT ---         1 0 18;
 INPUT ---         1 0 17;
 INPUT ---         0 1 0;

 Link Function Used is LOGIT

 Variance Estimation Procedure Used is 2ndPart
 M(t+1):
     73
 -2logL(saturated) = -289.47535
 Effective Sample Size = 292

 Number of function evaluations was 20 for 2 parameters.
 Time for numerical optimization was 0.01 seconds.
 -2logL {Logit_1998_1999} = 199.40117
 Penalty {Logit_1998_1999} = 0.0000000
 Gradient {Logit_1998_1999}:
 -0.4302933E-03-0.1421832E-01
 S Vector {Logit_1998_1999}:
   2.922992     0.2777771E-03
 Time to compute number of parameters was 0.01 seconds.
   Threshold =  0.6000000E-07     Condition index =  0.9503177E-04
 Conditioned S Vector {Logit_1998_1999}:
   1.000000     0.9503177E-04
 Number of Estimated Parameters {Logit_1998_1999} = 2
 DEVIANCE {Logit_1998_1999} = 488.87653
 DEVIANCE Degrees of Freedom {Logit_1998_1999} = 2
 c-hat {Logit_1998_1999} = 244.43826
 AIC {Logit_1998_1999} = 203.40117
 AICc {Logit_1998_1999} = 203.44269
 BIC {Logit_1998_1999} = 210.75468
```

Pearson Chisquare {Logit_1998_1999} = 2.4746226

LOGIT Link Function Parameters of {Logit_1998_1999}

Parameter	Beta	Standard Error	95% Confidence Interval Lower	Upper
1:	-12.137729	60.000070	-129.73787	105.46241
2:	0.0000000	0.0000000	0.0000000	0.0000000
3:	0.0380050	0.0216643	-0.0044571	0.0804671

Real Function Parameters of {Logit_1998_1999}

Parameter		Estimate	Standard Error	95% Confidence Interval Lower	Upper
1:p		0.8774396E-005	0.5264400E-003	0.7448092E-056	1.0000000
2:p		0.1493791E-004	0.8962144E-003	0.1270355E-055	1.0000000
3:p		0.1061068E-004	0.6366056E-003	0.9015901E-056	1.0000000
4:p		0.1021499E-004	0.6128667E-003	0.8678200E-056	1.0000000
5:c	Fixed	0.0000000	0.0000000	0.0000000	0.0000000

Estimates of Derived Parameters
Population Estimates of {Logit_1998_1999}

Group	N-hat	Standard Error	95% Confidence Interval Lower	Upper
1	**1639077.5**	**98338311.**	**6080.7433**	**0.4471457E+009**

Time in seconds for last procedure was 0.02

INPUT --- proc stop;

Time in minutes for this job was 0.00

E X E C U T I O N   S U C C E S S F U L

Input File: 1996-1997

```
/* Gettysburg White-tailed deer CPUE, 1996-1997 culling season, number of antlerless deer harvested per week*/
                    10000000000000000000000 32;
                    01000000000000000000000 18;
                    00100000000000000000000 11;
                    00010000000000000000000 14;
                    00001000000000000000000 29;
                    00000100000000000000000 21;
                    00000010000000000000000 26;
                    00000001000000000000000 22;
                    00000000100000000000000 31;
                    00000000010000000000000 10;
                    00000000001000000000000 17;
                    00000000000100000000000 13;
                    00000000000010000000000  4;
                    00000000000001000000000 25;
                    00000000000000100000000  4;
                    00000000000000010000000 11;
                    00000000000000001000000 10;
                    00000000000000000100000  8;
                    00000000000000000010000  4;
                    00000000000000000001000  1;
                    00000000000000000000100  2;
                    00000000000000000000010  6;
                    00000000000000000000001  6;


  Program  MARK  - Survival Rate Estimation with Capture-Recapture Data
  Compaq(Win32) Vers. 6.0 Dec 2009     15-Nov-2011 20:17:39
 - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - -
  INPUT --- proc title CPUE_1996_1997;
    Time in seconds for last procedure was 0.00
 INPUT --- proc chmatrix occasions=23 groups=1 etype=Huggins
 INPUT --- mixtures=2 NoHist hist=300;
 INPUT ---    glabel(1)=Group 1;
 INPUT ---    time interval 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1;
    Number of unique encounter histories read was 23.
    Number of individual covariates read was 0.
    Time interval lengths are all equal to 1.
    Data type is Huggins Closed Captures.
    Time in seconds for last procedure was 0.03
 INPUT --- proc estimate link=Logit varest=2ndPart ;
 INPUT --- model={Logit_1996_1997};
 INPUT ---    fixed=1;
 INPUT ---              parm(24)=0;
 INPUT ---    group=1 p rows=1 cols=23 Square Time=1;
 INPUT ---    group=1 c rows=1 cols=22 Square Constant=24;

 INPUT ---    design matrix constraints=24 covariates=3;
 INPUT ---         1 0 18; (right column = hours of culling effort per week)
 INPUT ---         1 0 11;
 INPUT ---         1 0 11.5;
 INPUT ---         1 0 14;
 INPUT ---         1 0 21.5;
 INPUT ---         1 0 14.5;
 INPUT ---         1 0 19.5;
 INPUT ---         1 0 16;
 INPUT ---         1 0 25;
 INPUT ---         1 0 17.5;
 INPUT ---         1 0 24;
 INPUT ---         1 0 8.5;
 INPUT ---         1 0 9.5;
 INPUT ---         1 0 19.5;
```

INPUT --- 1 0 4.5;
INPUT --- 1 0 8;
INPUT --- 1 0 20;
INPUT --- 1 0 9;
INPUT --- 1 0 5.5;
INPUT --- 1 0 7.5;
INPUT --- 1 0 10;
INPUT --- 1 0 10;
INPUT --- 1 0 10;
INPUT --- 0 1 0;

Link Function Used is LOGIT

Variance Estimation Procedure Used is 2ndPart
M(t+1):
325
-2logL(saturated) = -1232.7730
Effective Sample Size = 7475

Number of function evaluations was 17 for 2 parameters.
Time for numerical optimization was 0.01 seconds.
-2logL {Logit_1996_1997} = 1920.2695
Penalty {Logit_1996_1997} = 0.0000000
Gradient {Logit_1996_1997}:
0.4541535E-05 0.1630901E-04
S Vector {Logit_1996_1997}:
61.70067 7.255819
Time to compute number of parameters was 0.01 seconds.
Threshold = 0.6000000E-07 Condition index = 0.1175971
Conditioned S Vector {Logit_1996_1997}:
1.000000 0.1175971
Number of Estimated Parameters {Logit_1996_1997} = 2
DEVIANCE {Logit_1996_1997} = 3153.0425
DEVIANCE Degrees of Freedom {Logit_1996_1997} = 21
c-hat {Logit_1996_1997} = 150.14488
AIC {Logit_1996_1997} = 1924.2695
AICc {Logit_1996_1997} = 1924.2711
BIC {Logit_1996_1997} = 1938.1082
Pearson Chisquare {Logit_1996_1997} = 35.104792

LOGIT Link Function Parameters of {Logit_1996_1997}

			95% Confidence Interval	
Parameter	*Beta*	*Standard Error*	*Lower*	*Upper*
1:	*-4.0065385*	*0.2848202*	*-4.5647861*	*-3.4482908*
2:	*0.0000000*	*0.0000000*	*0.0000000*	*0.0000000*
3:	*0.0715328*	*0.0108004*	*0.0503640*	*0.0927015*

Real Function Parameters of {Logit_1996_1997}

			95% Confidence Interval	
Parameter	*Estimate*	*Standard Error*	*Lower*	*Upper*
1:p	*0.0618645*	*0.0103096*	*0.0444841*	*0.0854283*
2:p	*0.0384319*	*0.0075599*	*0.0260679*	*0.0563211*
3:p	*0.0397757*	*0.0077086*	*0.0271330*	*0.0579583*
4:p	*0.0471969*	*0.0085368*	*0.0330170*	*0.0670446*
5:p	*0.0780901*	*0.0126130*	*0.0566805*	*0.1066723*
6:p	*0.0488316*	*0.0087233*	*0.0343094*	*0.0690612*
7:p	*0.0683925*	*0.0111886*	*0.0494616*	*0.0938535*
8:p	*0.0540636*	*0.0093365*	*0.0384259*	*0.0755652*
9:p	*0.0981263*	*0.0160013*	*0.0709223*	*0.1342573*
10:p	*0.0598209*	*0.0100470*	*0.0429079*	*0.0828238*

11:p		*0.0919753*	*0.0149001*	*0.0666432*	*0.1256404*
12:p		*0.0323421*	*0.0068778*	*0.0212640*	*0.0489033*
13:p		*0.0346572*	*0.0071398*	*0.0230841*	*0.0517252*
14:p		*0.0683925*	*0.0111886*	*0.0494616*	*0.0938535*
15:p		*0.0244913*	*0.0059318*	*0.0151980*	*0.0392408*
16:p		*0.0312413*	*0.0067513*	*0.0204023*	*0.0475590*
17:p		*0.0707068*	*0.0115154*	*0.0512039*	*0.0968796*
18:p		*0.0334803*	*0.0070072*	*0.0221577*	*0.0502914*
19:p		*0.0262597*	*0.0061558*	*0.0165454*	*0.0414374*
20:p		*0.0301767*	*0.0066276*	*0.0195718*	*0.0462569*
21:p		*0.0358740*	*0.0072759*	*0.0240442*	*0.0532067*
22:p		*0.0358740*	*0.0072759*	*0.0240442*	*0.0532067*
23:p		*0.0358740*	*0.0072759*	*0.0240442*	*0.0532067*
24:c	*Fixed*	*0.0000000*	*0.0000000*	*0.0000000*	*0.0000000*

Estimates of Derived Parameters
Population Estimates of {Logit_1996_1997}

			95% Confidence Interval	
Group	*N-hat*	*Standard Error*	*Lower*	*Upper*
1	***468.95714***	***45.740031***	***403.38794***	***589.37306***

Time in seconds for last procedure was 0.09

INPUT --- proc stop;

Time in minutes for this job was 0.00

E X E C U T I O N   S U C C E S S F U L

Appendix C. Datasheet used to record data during distance sampling surveys.

(a) Distance sampling and spotlight mark-resight datasheet used during research conducted at Gettysburg National Military Park and Eisenhower National Historic Site, where it was important to individually identify marked deer using Bowden’s estimator.

Distance Sampling Data Sheet

Date ______________
Start Time ____________
Sunset Time ____________
End Time ____________

Driver _____________
Driver’s Side Observer __________
Passenger’s Side Observer _________

Transects Surveyed (in order)
____

Temp (Far.) ________
Cloud Cover (%) 0 25 50 75 100
Wind __________ mph
Precip None Sprinkle Drizzle Sleet Snow
Ground Dry Damp Wet Snow
Visibility 0 1 2 3 or **Miles** ______

	Unmarked				Unidentified (mark sex too)	Marked				Transect	Woods /Field	Time Seen	Observer (initials)	Range (meters)	Azimuth (degrees)	GPS Location	
	Fawn	Antler-less	Antlered	Sex Unknown		Fawn	Antler-less	Antlered	Sex Unknown							Latitude	Longitude
1																	
2																	
3																	
4																	
5																	
6																	
7																	
8																	
9																	
10																	
11																	
12																	
13																	
14																	
15																	
16																	
17																	
18																	
19																	
20																	
21																	
22																	
23																	
24																	
25																	
26																	
27																	
28																	
29																	
30																	

(b) Example distance sampling datasheet for future surveys conducted at Gettysburg National Military Park, where estimates could be used as indices of abundance to monitor trends along with vegetation information.

Distance Sampling Data Sheet

Date ________________
Start Time __________
Sunset Time __________
End Time __________

Driver ____________
Driver's Side Observer __________
Passenger's Side Observer __________

Transects Surveyed (in order)

____

Temp (Far.) _______
Cloud Cover (%) 0 25 50 75 100
Wind __________ mph
Precip None Sprinkle Drizzle Sleet Snow
Ground Dry Damp Wet Snow
Visibility 0 1 2 3 or **Miles** _____
Comments: ________________________________
____
____

	Number of Each Sex in Group				Transect	Woods /Field	Time Seen	Observer (initials)	Perpendicular Distance (meters)
	Fawn	Antlerless	Antlered	Unknown					
1									
2									
3									
4									
5									
6									
7									
8									
9									
10									
11									
12									
13									
14									
15									
16									
17									
18									
19									
20									
21									
22									
23									
24									
25									
26									
27									
28									
29									
30									
31									
32									
33									
34									
35									

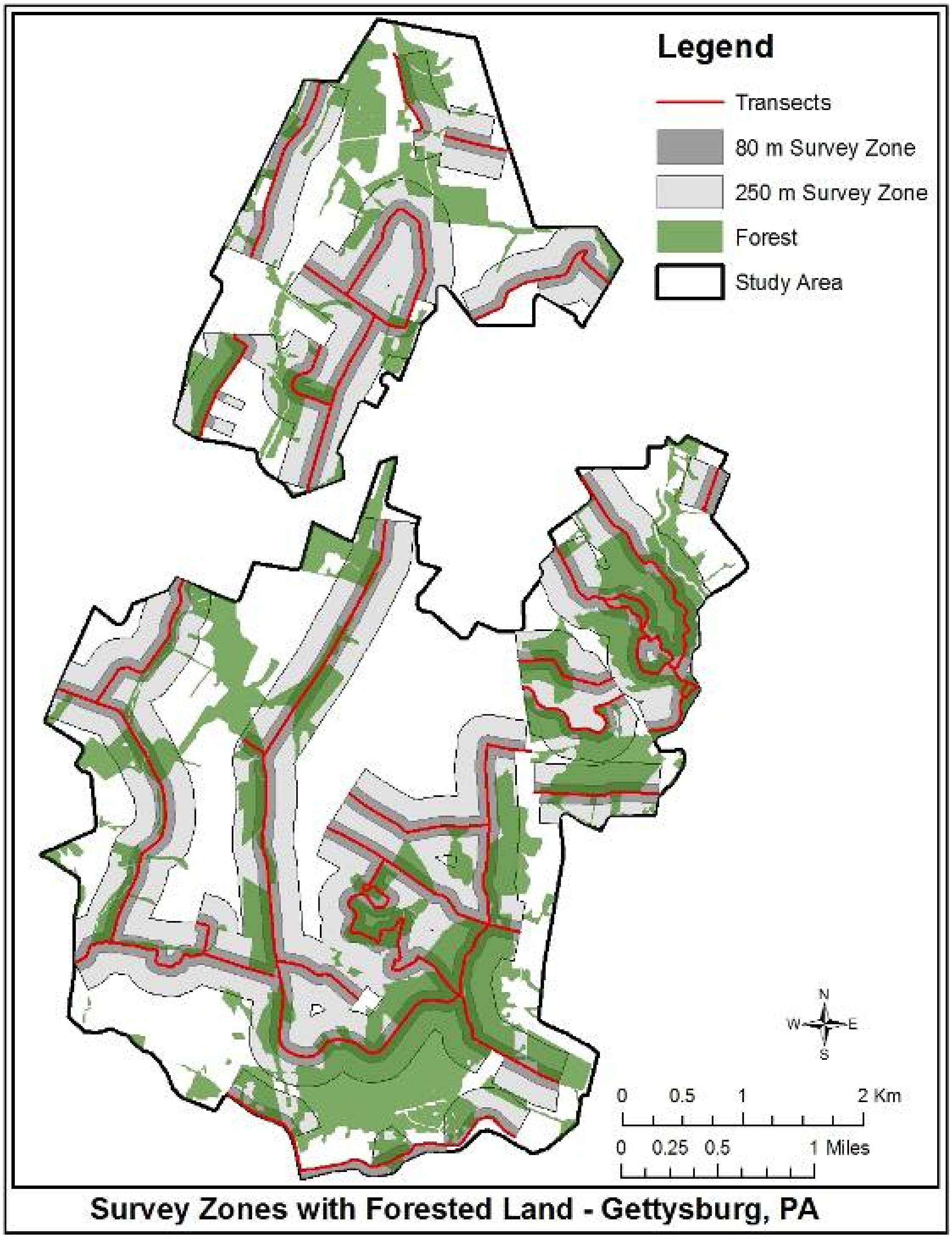
Notes:

Appendix D. Example R code for zero-inflated negative binomial modeling of the resource selection function.

Below is R code for model 1 for one deer, using GPS locations for that one deer during the April 2010 distance sampling survey

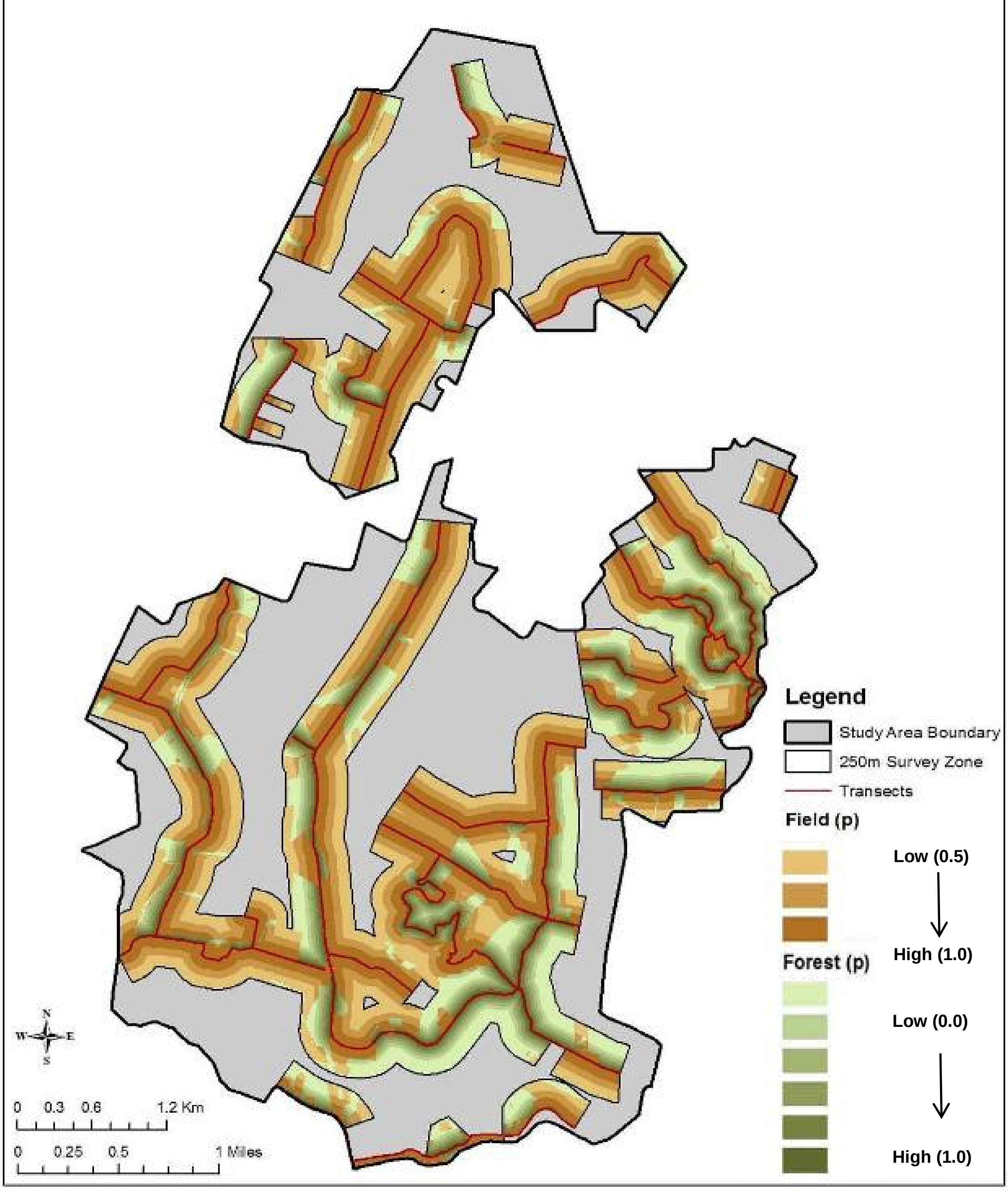
```
>df3<-read.table("April_10_Input_File.txt", na.strings="NA",header=T)

# Center each covariate so that 0 is now the grand mean
>df3$dist_road.c<-(df3$Dist_Road.m-mean(df3$Dist_Road.m))
>df3$dist_NPS_edge.c<-(df3$Dist_NPS_Edge.m-mean(df3$Dist_NPS_Edge.m))
>df3$dist_forest_field_edge.c<-(df3$Dist_Forest_Field_Edge.m-mean(df3$Dist_Forest_Field_Edge.m))

# Normalize each covariate by dividing by its standard deviation
>df3$norm_dist_road.c<-(df3$dist_road.c/sd(df3$dist_road.c))
>df3$norm_dist_NPS_edge.c<-(df3$dist_NPS_edge.c/sd(df3$dist_NPS_edge.c))
>df3$norm_dist_forest_field_edge.c<-(df3$dist_forest_field_edge.c/sd(df3$dist_forest_field_edge.c))

# Divide covariate Percent Forest by 100 (constrain from 0-1)
>df3$Per_Forest<-(df3$Per_Forest/100)

# Subset data for each deer (shown here for deer with low tag number 7)
>df.LT7<-subset(df3, df3$LT=="7")

# Create the offset term for each deer (shown here for deer with LT 7)
>offset.LT7<-rep(log(sum(df.LT7$GPS_Locs_April_10)), times=3000)

# Model 1 - Percent Forest + Distance to Forest-field edge
>library(pscl)

>m1.7<-zeroinfl(GPS_Locs_April_10~1+Percent_Forest+
norm_dist_forest_field_edge.c|1,subset(df3,df3$LT=="7"),dist="negbin", offset=offset.LT7)

>summary(m1.7)
Pearson residuals:
    Min      1Q  Median      3Q     Max
-0.1277 -0.1254 -0.1198 -0.1170 38.7838

Count model coefficients (negbin with log link):
                              Estimate Std. Error z value Pr(>|z|)
(Intercept)                    -5.9978     0.3443 -17.418  < 2e-16 ***
Per_Forest                      1.8523     0.3813   4.858 1.19e-06 ***
norm_dist_forest_field_edge.c  -0.3688     0.2226  -1.657   0.0975 .
Log(theta)                     -0.2663     0.3874  -0.687   0.4919

Zero-inflation model coefficients (binomial with logit link):
            Estimate Std. Error z value Pr(>|z|)
(Intercept)   3.2383     0.1896   17.07   <2e-16 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Theta = 0.7662
Number of iterations in BFGS optimization: 60
Log-likelihood: -628.9 on 5 Df
```

Appendix E. Map of survey transects in the study area and area encompassed 80 and 250 m from the transect.



Appendix F. Map of the probability of detecting groups of deer during distance sampling surveys.

Shown for January 2010 survey, where p = detection probability for fields and forests.



Appendix G. Number of deer and number of groups of deer observed during distance sampling surveys.

(a) Summary of observations in the 250 m survey zone for each survey, Gettysburg, Pennsylvania, 2009–2010. From left to right: The actual number of deer seen in fields and forests, the number of groups seen in fields (n_{Field}) and forests (n_{Forest}), the number of complete rounds of all transects, the average number of groups seen in fields per round ($\bar{n}_{Field}$), and the average number of groups seen in forests per round ($\bar{n}_{Forest}$).

Survey	**Deer(Field)**	**Deer(Forest)**	n_{Field}	n_{Forest}	**# Rounds**	$\bar{n}_{Field}$	$\bar{n}_{Forest}$
Apr 2009	239	122	64	42	3	21	14
Aug 2009	323	23	131	12	3	44	4
Nov 2009	246	65	112	31	2.8	40	11
Jan 2010	270	62	78	21	2.5	31	8
Apr 2010	257	60	66	24	3	22	8
Aug 2010	480	24	154	13	3	51	4
Nov 2010	288	103	127	57	3	42	19

(b) Summary of observations in the 80 m survey zone for each survey, Gettysburg, Pennsylvania, 2009–2010. From left to right: The actual number of deer seen in fields and forests, the number of groups seen in fields (n_{Field}) and forests (n_{Forest}), the number of complete rounds of all transects, the average number of groups seen in fields per round ($\bar{n}_{Field}$), and the average number of groups seen in forests per round ($\bar{n}_{Forest}$).

Survey	**Deer(Field)**	**Deer(Forest)**	n_{Field}	n_{Forest}	**# Rounds**	$\bar{n}_{Field}$	$\bar{n}_{Forest}$
Apr 2009	89	107	24	35	3	8	12
Aug 2009	169	20	72	11	3	24	4
Nov 2009	139	65	67	31	2.8	24	11
Jan 2010	82	48	28	15	2.5	11	6
Apr 2010	127	60	32	24	3	11	8
Aug 2010	225	24	81	13	3	27	4
Nov 2010	153	97	69	54	3	23	18

Appendix H. Mean group size of deer during distance sampling surveys.

(a) Summary of mean cluster sizes for fields and forests in the 250 m survey zone for each survey, Gettysburg, Pennsylvania, 2009–2010. Standard errors were calculated using non-parametric bootstrapping.

Survey	$E(S)_{Field}$	$SE[E(S)_{Field}]$	$E(S)_{Forest}$	$SE[E(S)_{Forest}]$
Apr 2009	3.7	0.35	2.9	0.22
Aug 2009	2.5	0.15	1.9	0.30
Nov 2009	2.2	0.14	2.1	0.16
Jan 2010	3.5	0.29	3.0	0.33
Apr 2010	3.9	0.39	2.5	0.39
Aug 2010	3.1	0.17	1.9	0.28
Nov 2010	2.3	0.11	1.8	0.14

(b) Summary of mean cluster sizes for fields and forests in the 80 m survey zone for each survey, Gettysburg, Pennsylvania, 2009–2010. Standard errors were calculated using non-parametric bootstrapping.

Survey	$E(S)_{Field}$	$SE[E(S)_{Field}]$	$E(S)_{Forest}$	$SE[E(S)_{Forest}]$
Apr 2009	3.7	0.66	3.1	0.25
Aug 2009	2.4	0.20	1.8	0.31
Nov 2009	2.1	0.16	2.1	0.16
Jan 2010	2.9	0.38	3.2	0.39
Apr 2010	4.0	0.67	2.5	0.37
Aug 2010	2.8	0.21	1.9	0.28
Nov 2010	2.2	0.15	1.8	0.14

Appendix I. Parameter estimates and standard errors for covariates included in the resource selection function for each survey, April 2009–November 2010.

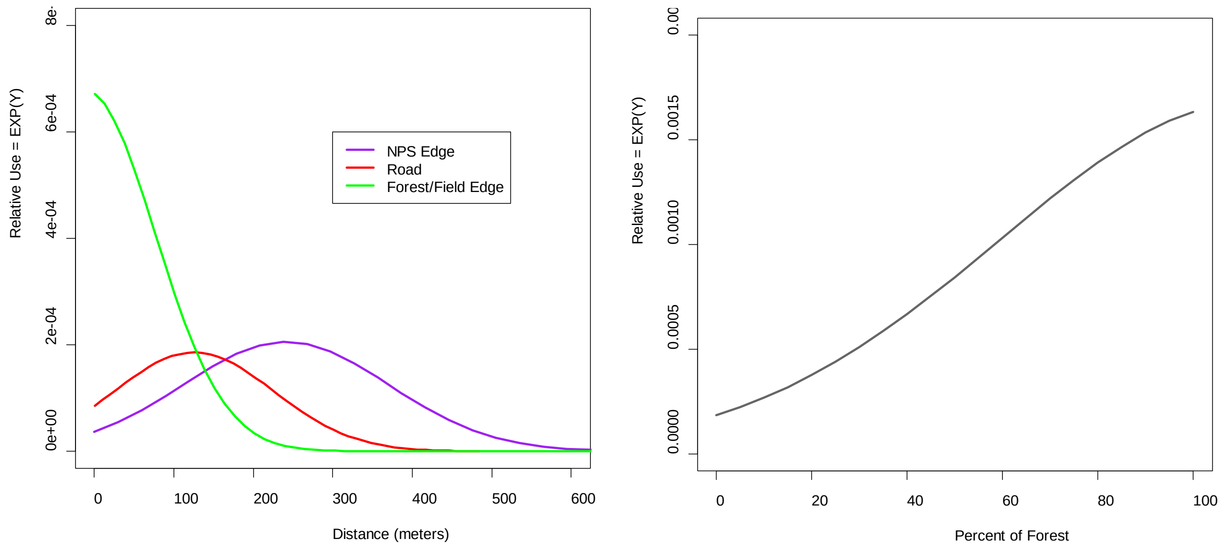
Weighted and standardized parameter estimates and associated standard errors from the zero-inflated negative binomial model 6 for all distance sampling surveys, Gettysburg, Pennsylvania, 2009–2010. Also, n is the number of collared deer used in each analysis.

	April 2009 (*n*=29)		**August 2009 (*n*=23)**		**November 2009 (*n*=17)**		**January 2010 (*n*=17)**		**April 2010 (*n*=26)**		**August 2010 (*n*=22)**		**November 2010 (*n*=17)**	
Cov[a]	b_i	**SE**	b_i	**SE**	b_i	**SE**	b_i	**SE**	b_i	**SE**	b_i	**SE**	b_i	**SE**
I	-8.592	0.676	-7.026	0.573	-7.150	1.539	-7.444	0.712	-8.993	1.276	-6.530	0.861	-7.500	1.369
PF	3.886	0.331	-0.262	0.361	2.925	0.494	0.357	0.316	1.997	0.283	1.012	0.235	2.469	0.486
PF^2	-1.711	0.276	0.235	0.306	-2.067	0.505	0.047	0.302	-0.535	0.291	-1.867	0.276	-1.666	0.484
FFE	-2.339	0.209	-1.240	0.420	-1.889	0.287	-1.321	0.591	-0.898	0.436	-0.357	0.541	-0.531	0.595
FFE^2	-1.057	0.213	-1.163	0.222	-1.239	0.365	-0.736	0.309	-0.468	0.337	-0.447	0.382	-0.313	0.551
RD	0.037	0.449	-0.240	0.582	0.004	0.696	-0.231	0.527	0.179	0.542	0.358	0.696	-0.640	0.549
RD^2	-0.463	0.261	-0.922	0.289	-0.524	0.332	-0.472	0.377	-0.334	0.377	-0.359	0.370	-0.587	0.417
NPS	-1.044	0.375	-1.121	0.585	-1.224	0.560	-2.648	0.536	-1.398	0.649	-1.814	0.523	-2.319	0.418
NPS^2	-2.630	0.184	-3.363	0.372	-1.747	0.421	-2.260	0.438	-2.512	0.258	-2.918	0.280	-1.427	0.310

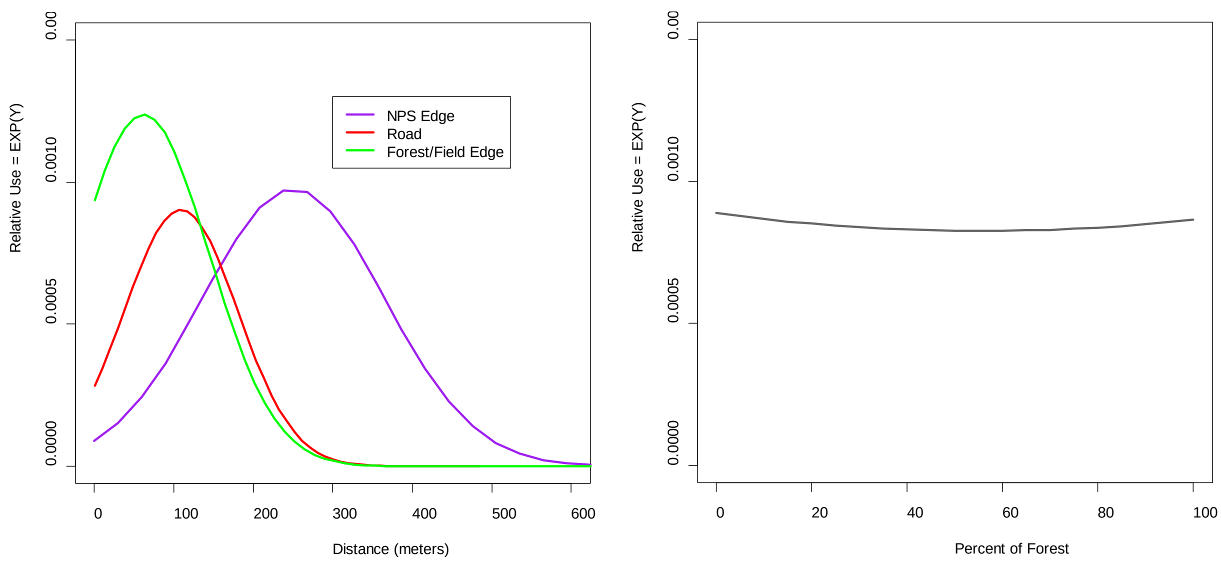
[a] Covariates: I = Intercept, PF = Percent Forest, FFE = distance to nearest forest-field edge, RD = distance to nearest road, and NPS = distance to nearest National Park Service owned land boundary.

Appendix J. Relative resource use graphed with respect to covariates used in the resource selection function.

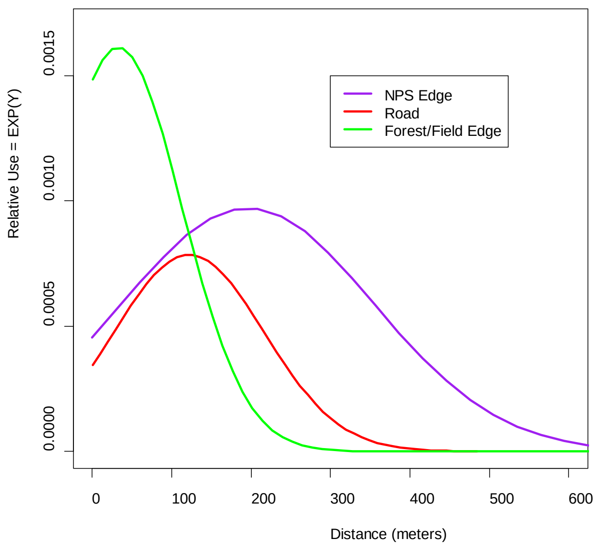
(a) Plotted parameter values from Appendix I, April 2009.

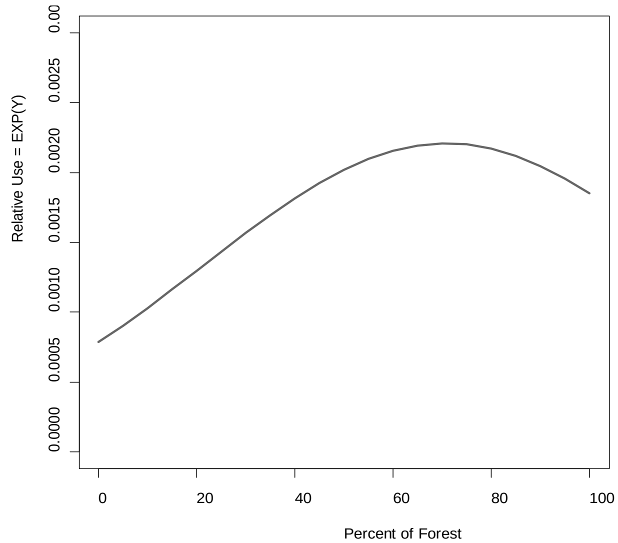


(b) Plotted parameter values from Appendix I, August 2009.

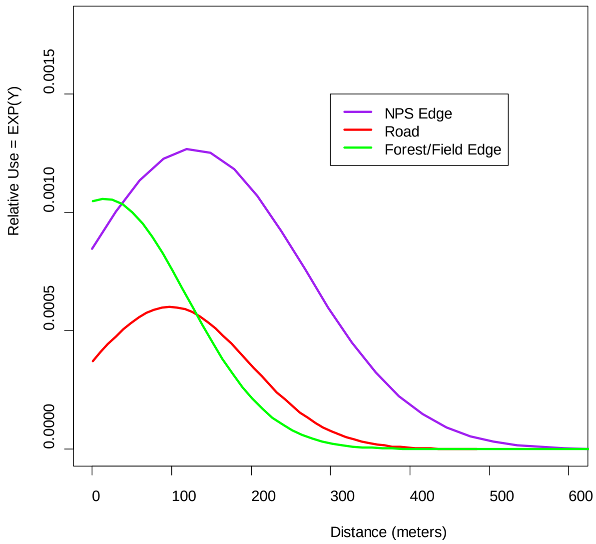


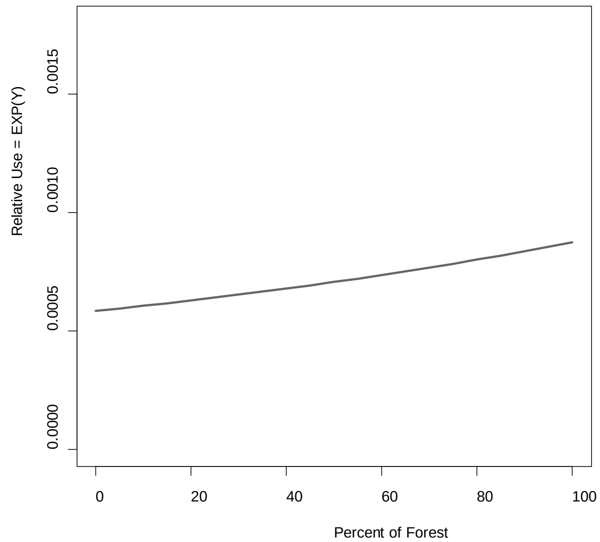
(c) Plotted parameter values from Appendix I, November 2009



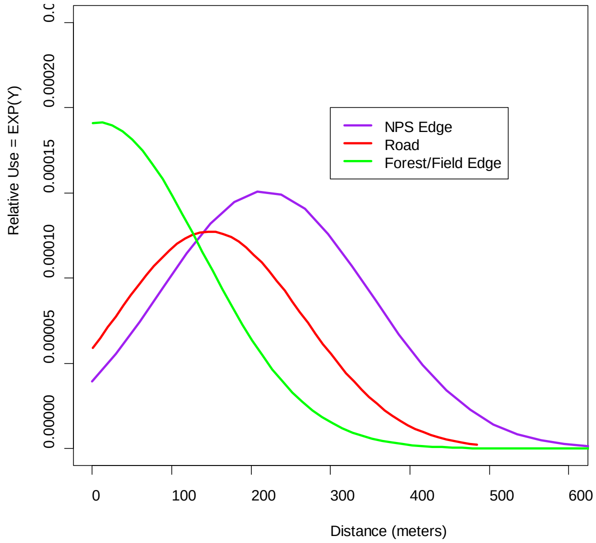


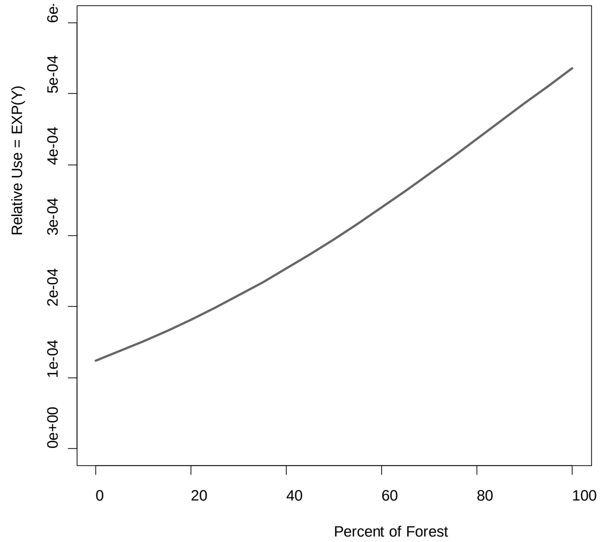
(d) Plotted parameter values from Appendix I, January 2010.



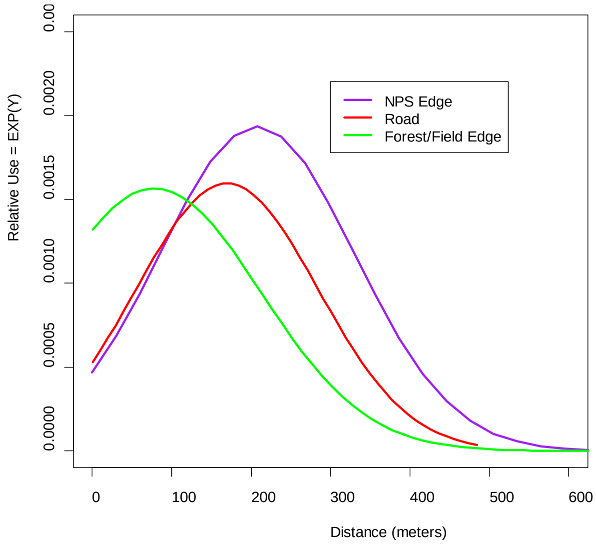


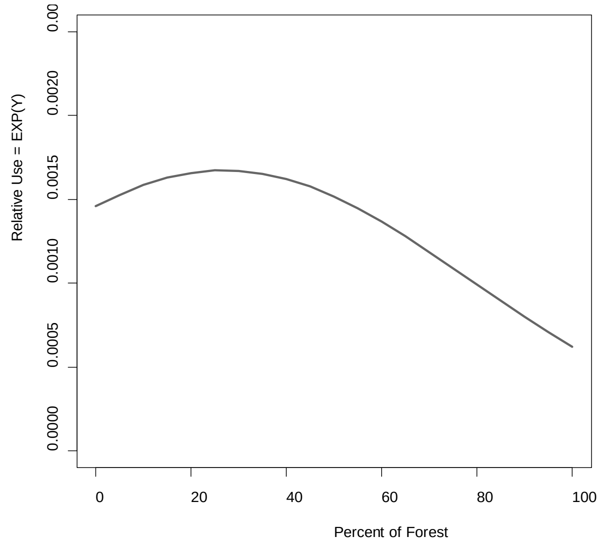
(e) Plotted parameter values from Appendix I, April 2010



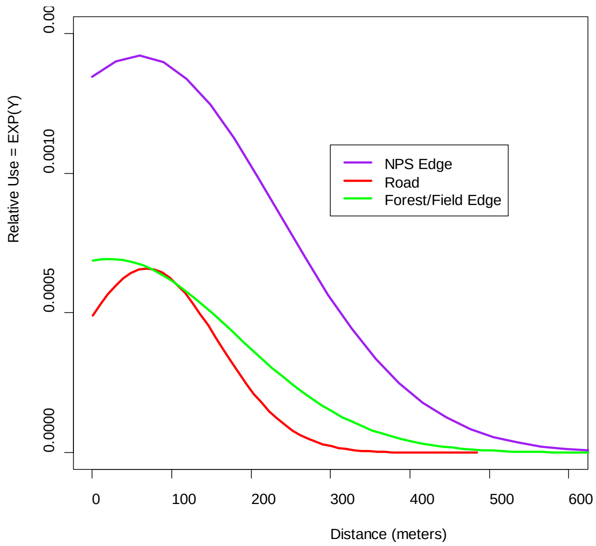


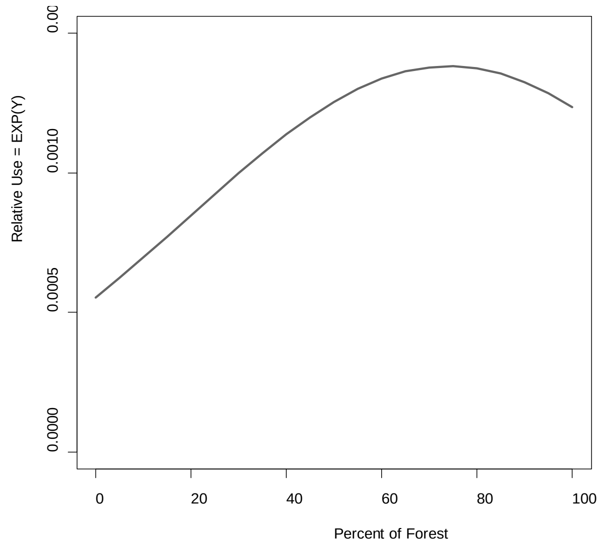
(f) Plotted parameter values from Appendix I, August 2010





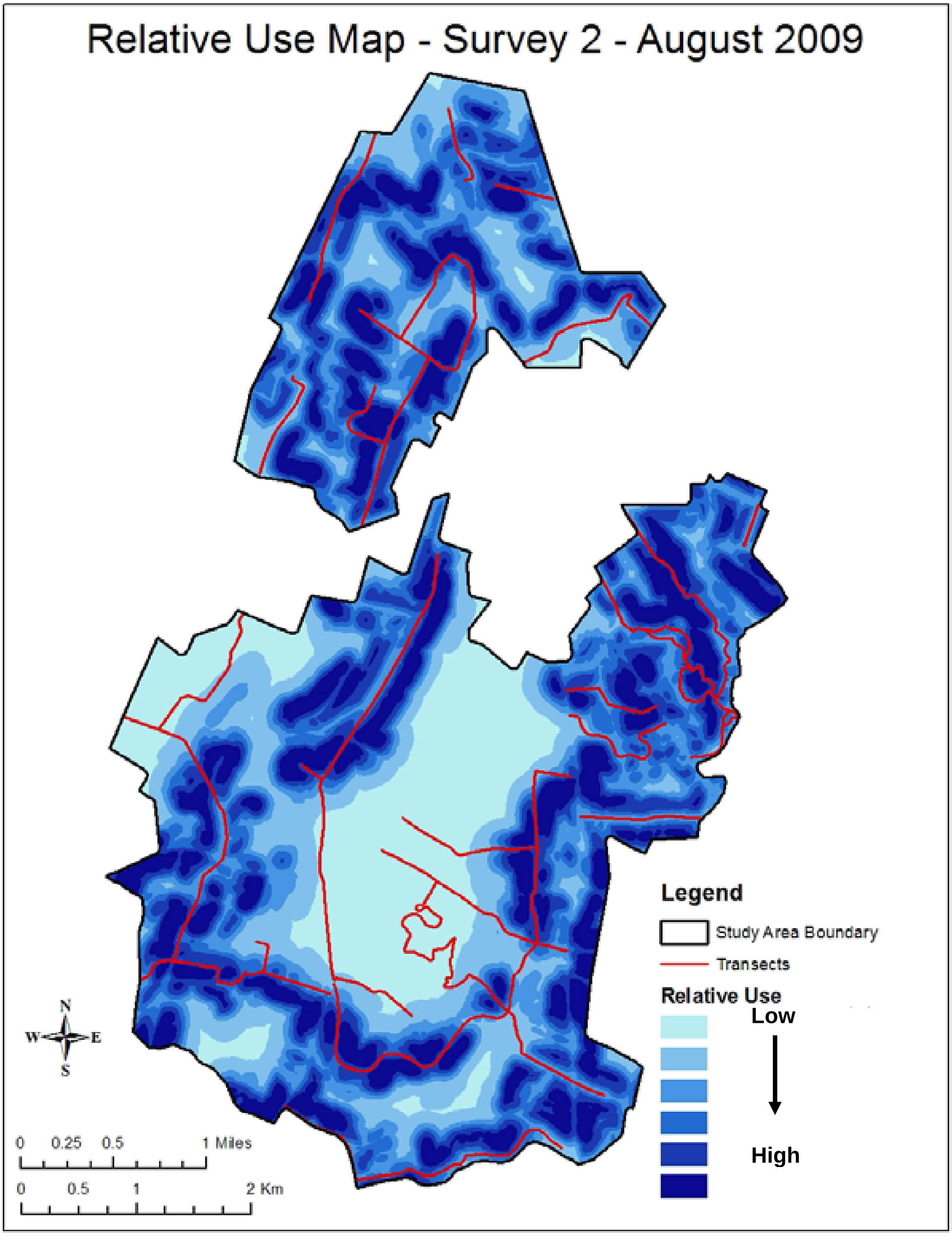
(g) Plotted parameter values from Appendix I, November 2010



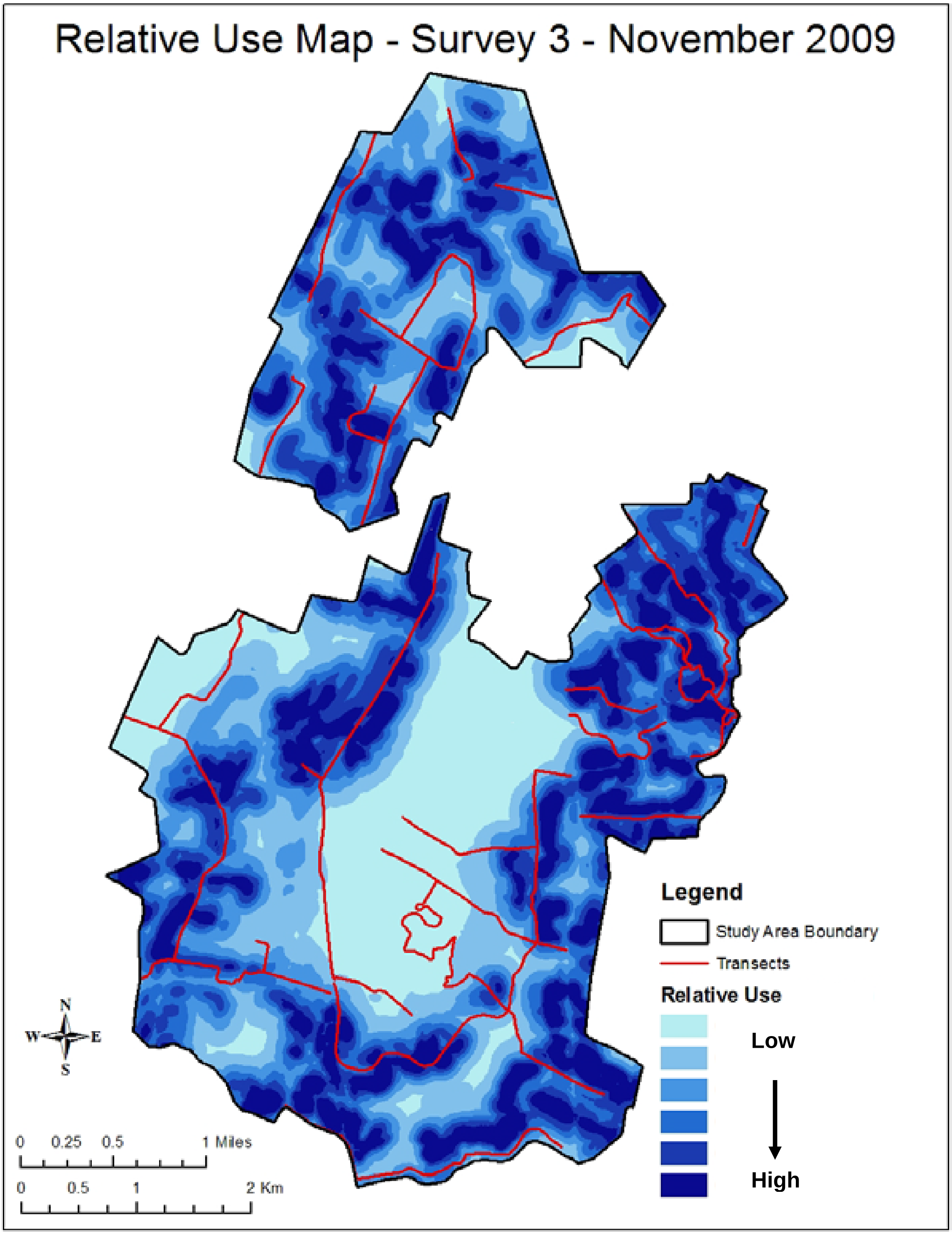


Appendix K. Maps of resource selection by deer during line transect surveys conducted August 2009 through November 2010.

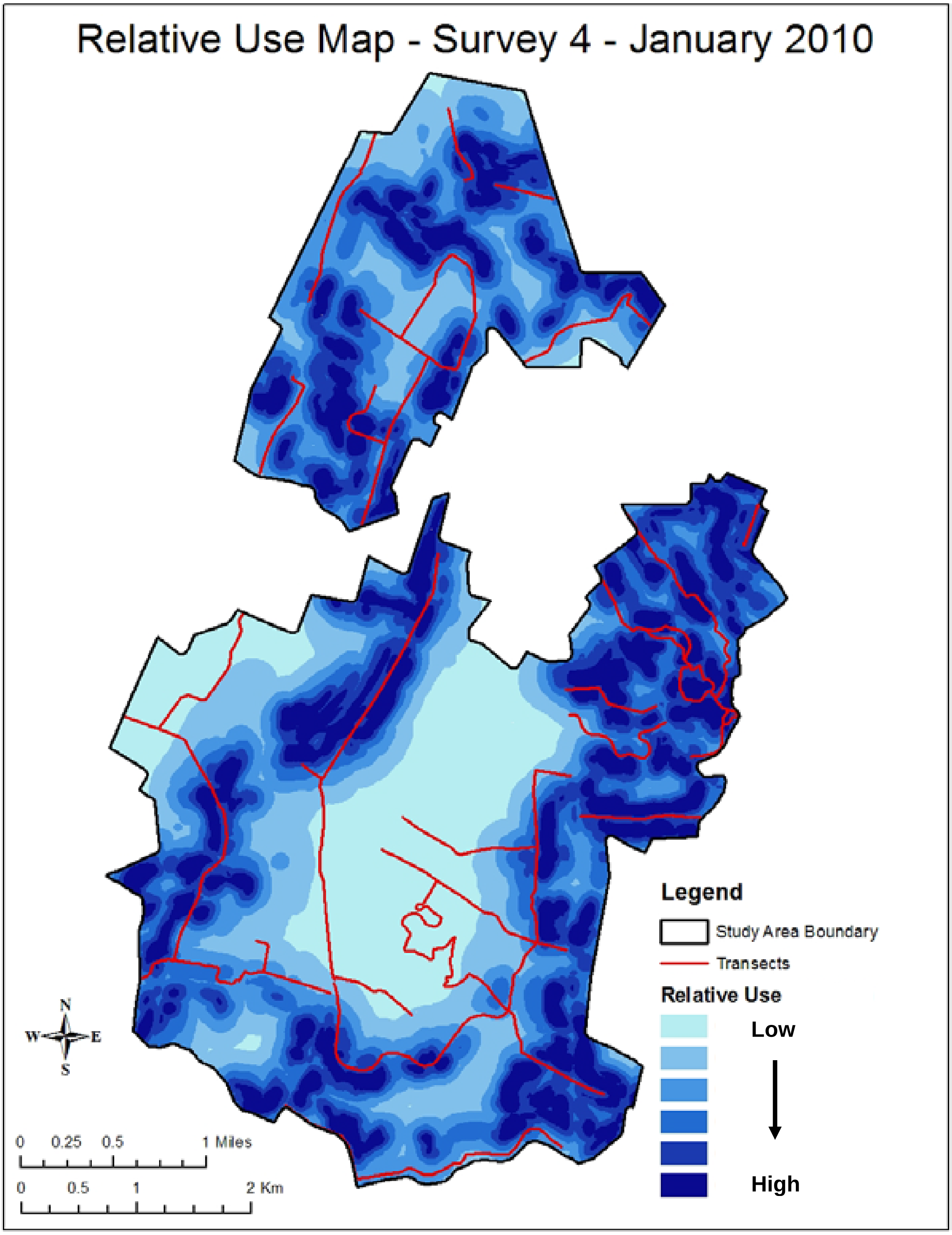
(a)



(b)

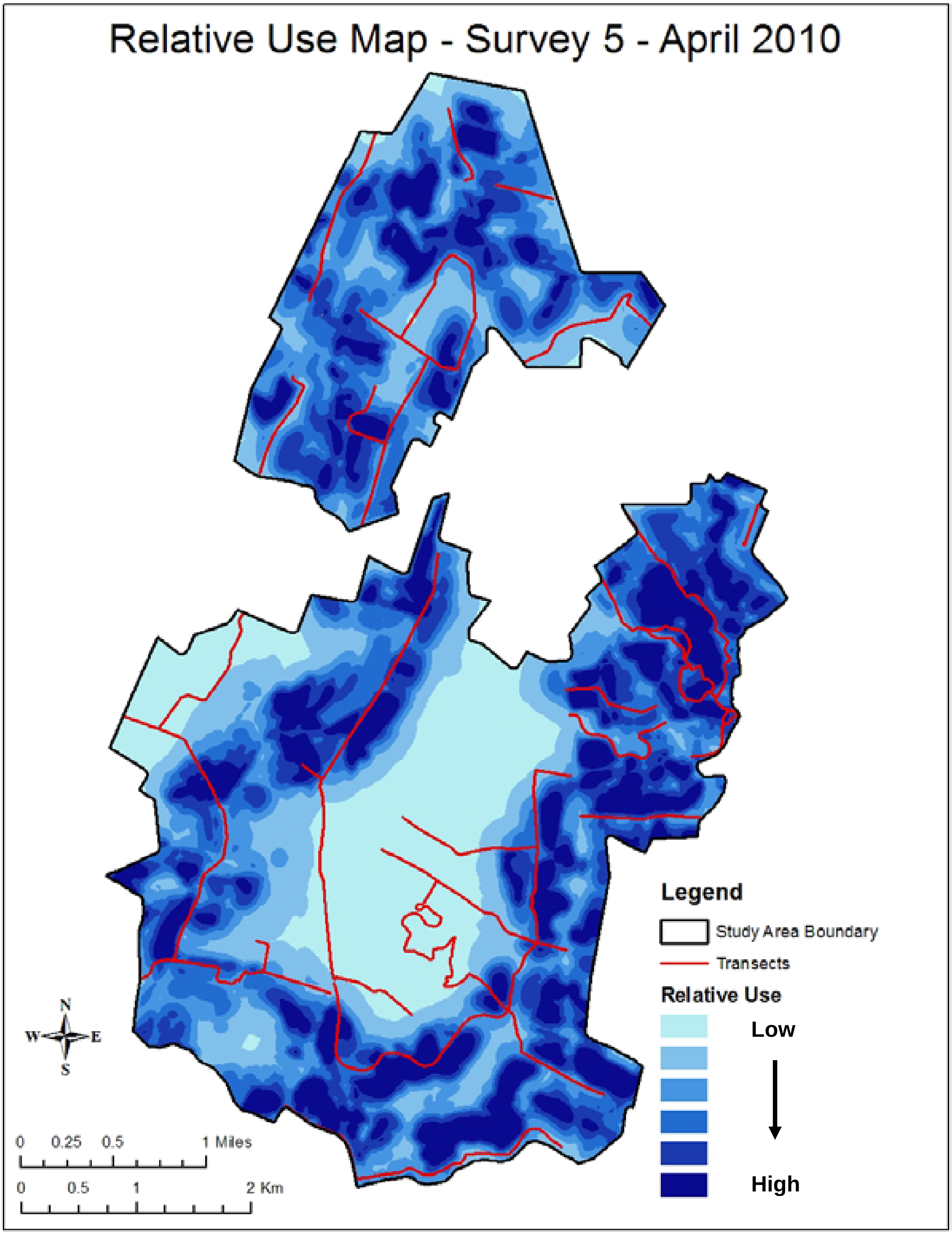

Relative Use Map - Survey 3 - November 2009
Legend
Study Area Boundary
Transects
Relative Use
Low
High
N
W
E
S
0 0.25 0.5 1 Miles
0 0.5 1 2 Km

(c)

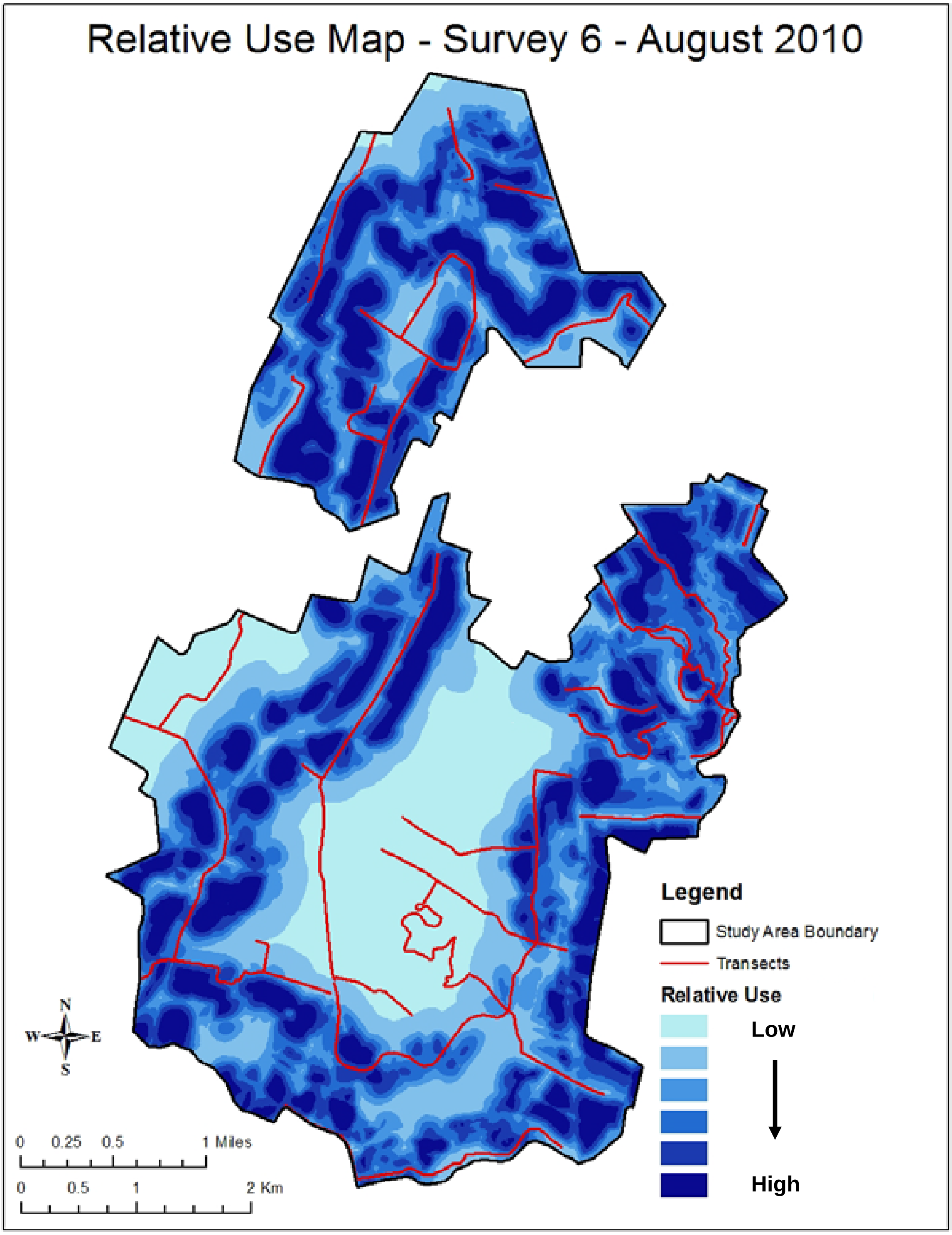


Relative Use Map - Survey 4 - January 2010
Legend
Study Area Boundary
Transects
Relative Use
Low
High
N
W
E
S
0 0.25 0.5 1 Miles
0 0.5 1 2 Km

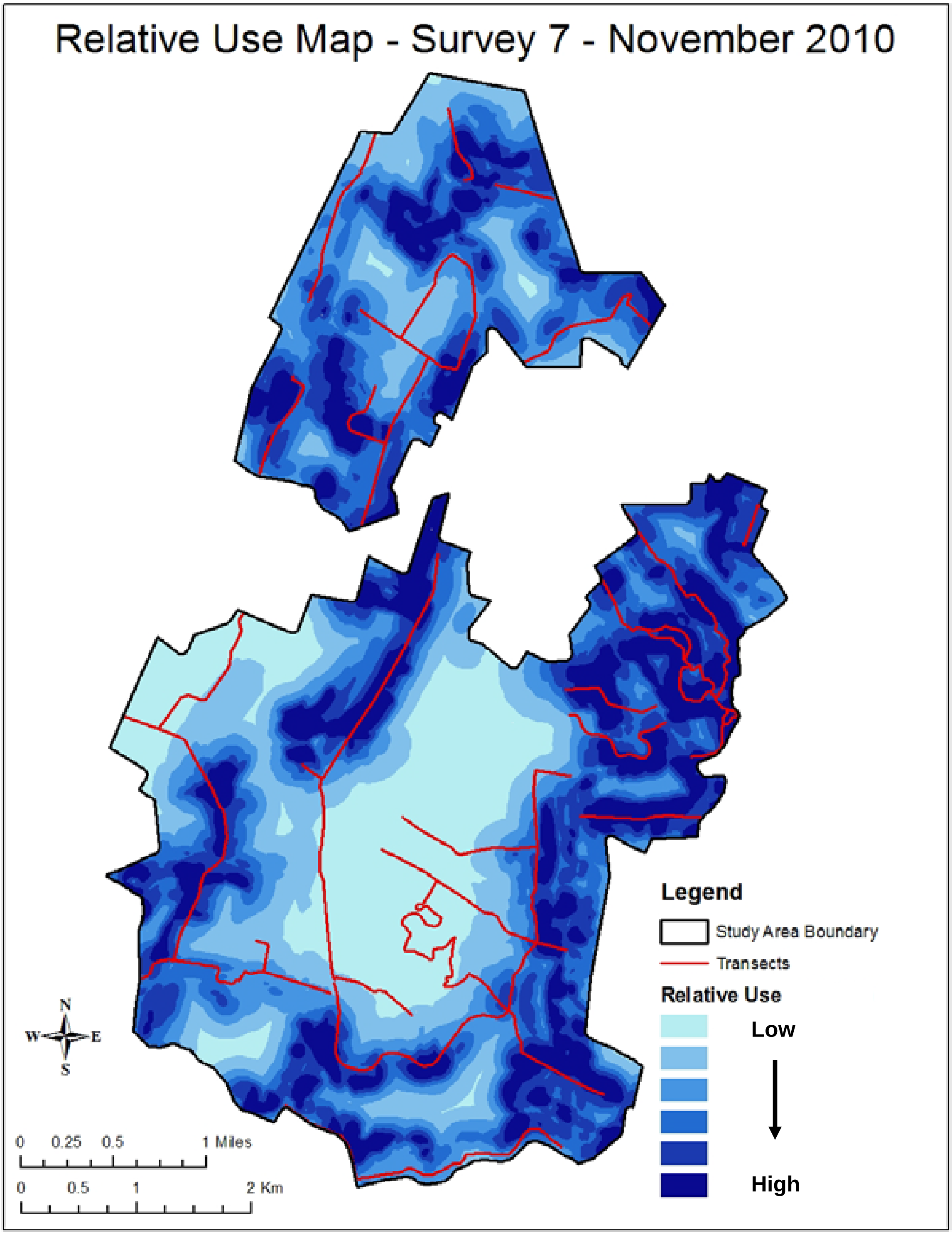
(d)


Relative Use Map - Survey 5 - April 2010
Legend
Study Area Boundary
Transects
Relative Use
Low
High
N
W
E
S
0 0.25 0.5 1 Miles
0 0.5 1 2 Km

(e)

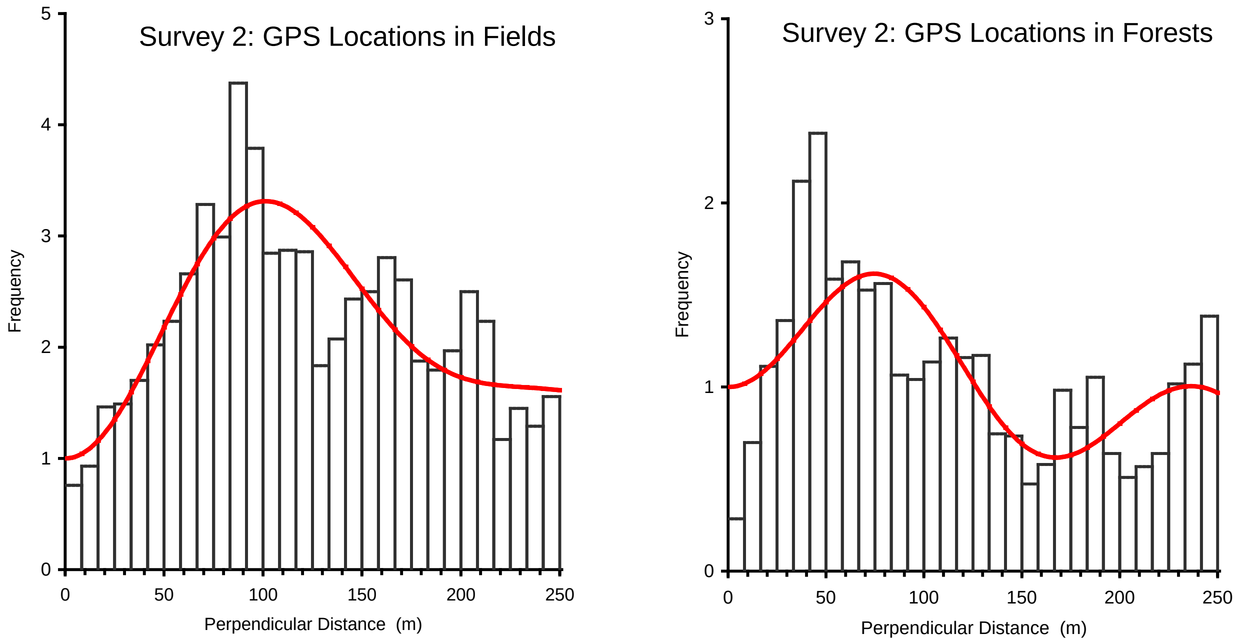

Relative Use Map - Survey 6 - August 2010
Legend
Study Area Boundary
Transects
Relative Use
Low
High
N
W
E
S
0 0.25 0.5 1 Miles
0 0.5 1 2 Km

(f)

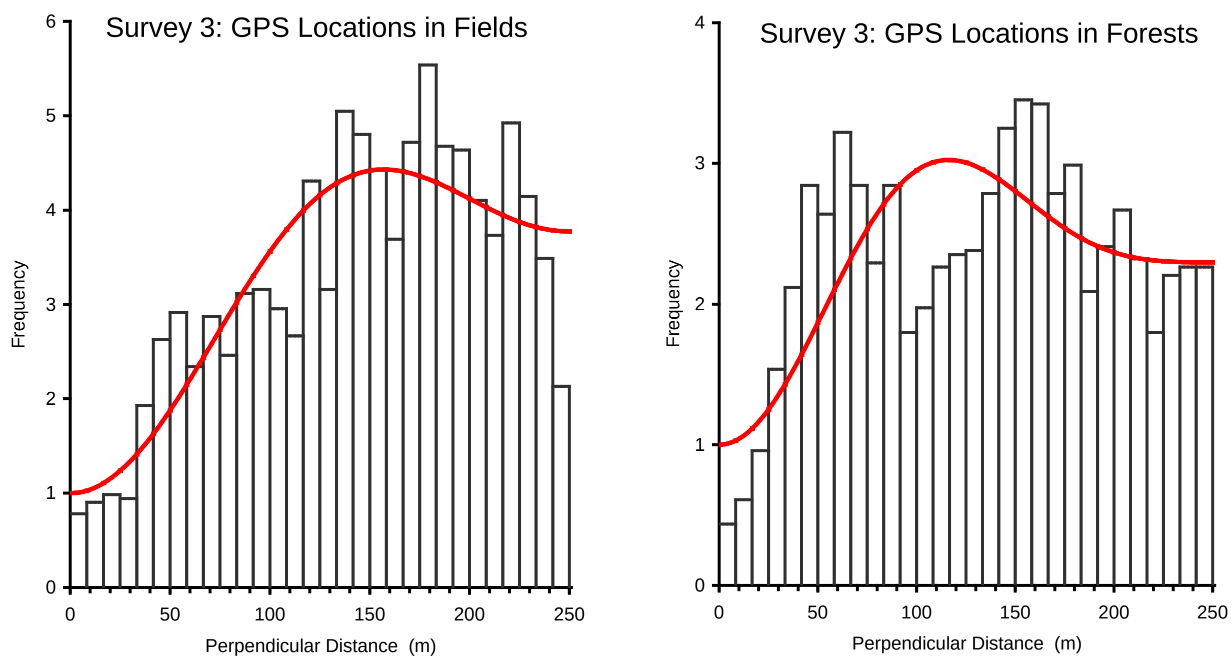

Relative Use Map - Survey 7 - November 2010
Legend
Study Area Boundary
Transects
Relative Use
Low
High
N
W
E
S
0 0.25 0.5 1 Miles
0 0.5 1 2 Km

Appendix L. Frequency histograms of number of deer observed as a function of perpendicular distance from the transect.

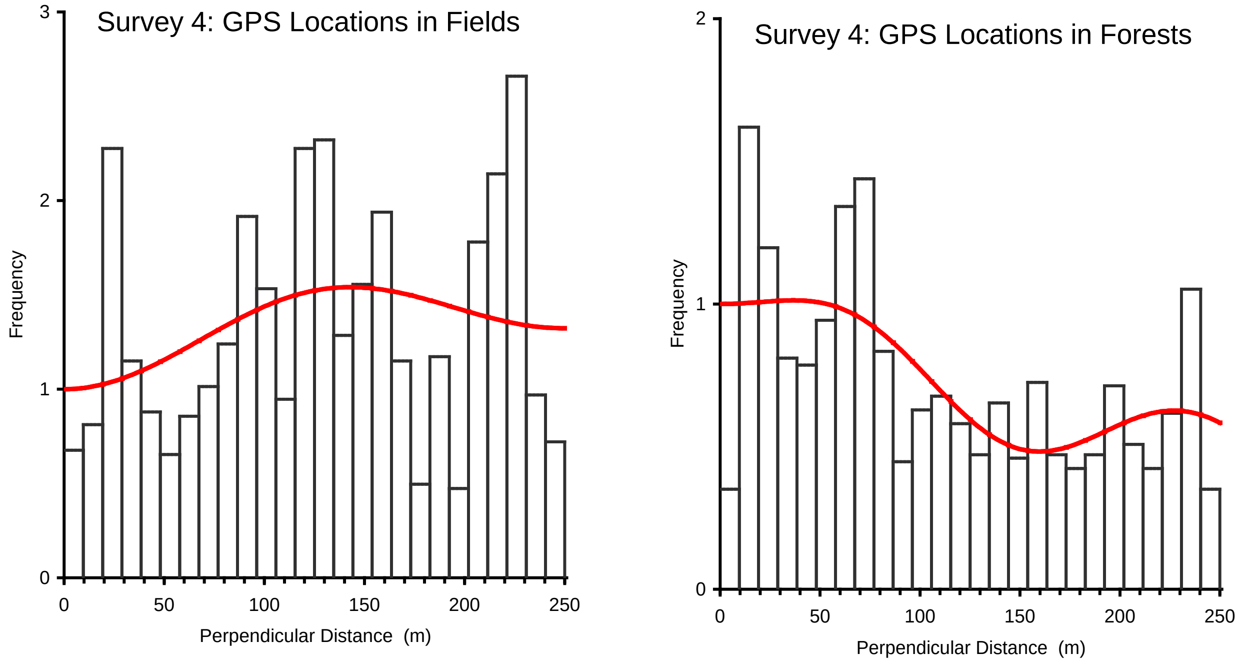
(a) Distribution of global positioning system (GPS) locations in open areas and forested areas relative to perpendicular distance from transects during the second distance sampling survey, August 3–9, 2009.



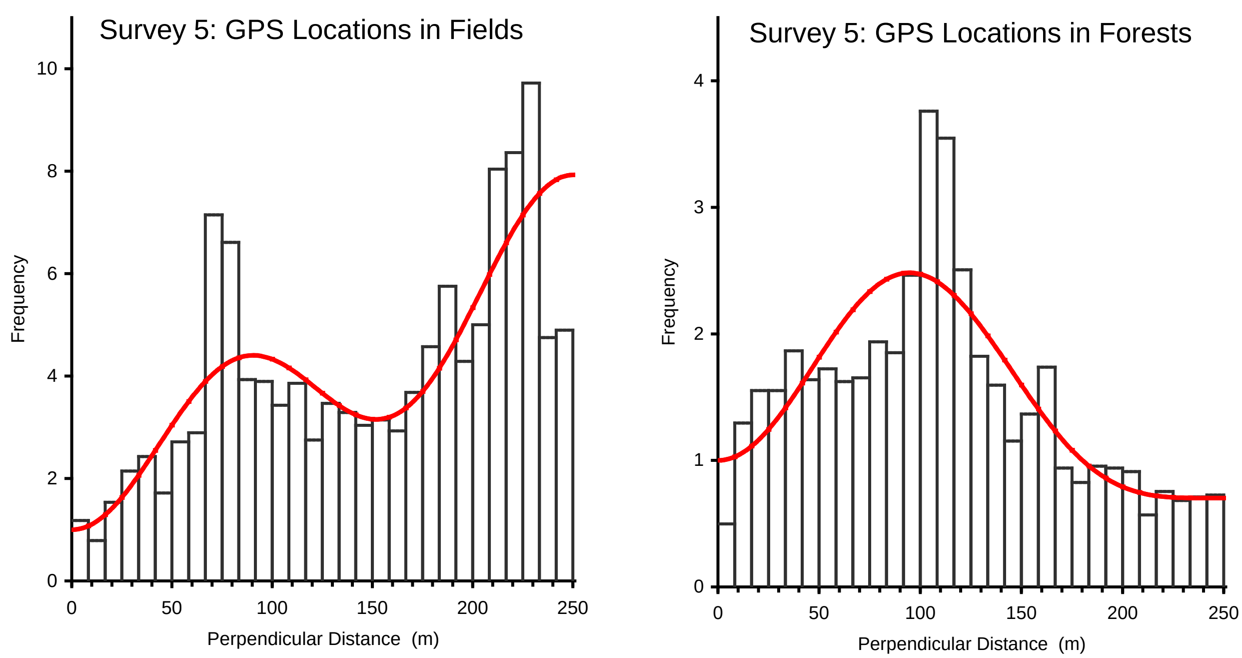
(b) Distribution of GPS locations in open areas and forested areas relative to perpendicular distance from transects during the third distance sampling survey, November 20–25, 2009.



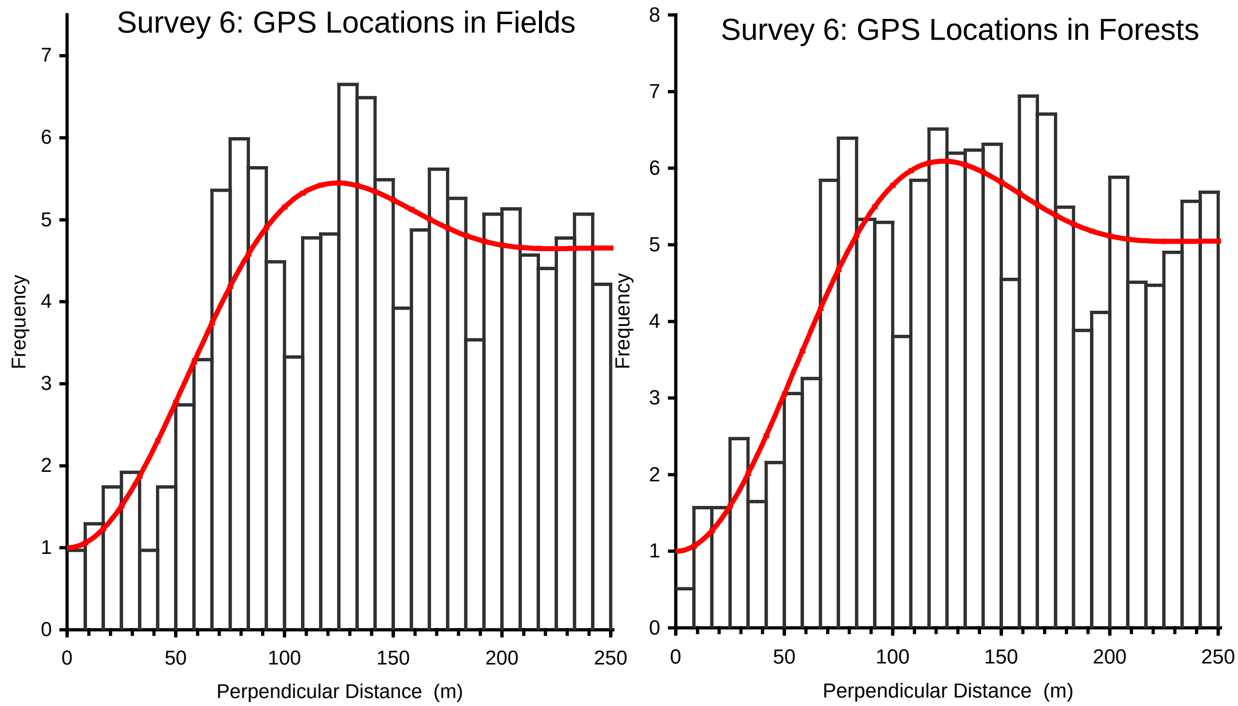
(c) Distribution of GPS locations in open areas and forested areas relative to perpendicular distance from transects during the fourth distance sampling survey, January 5–8, 2010.



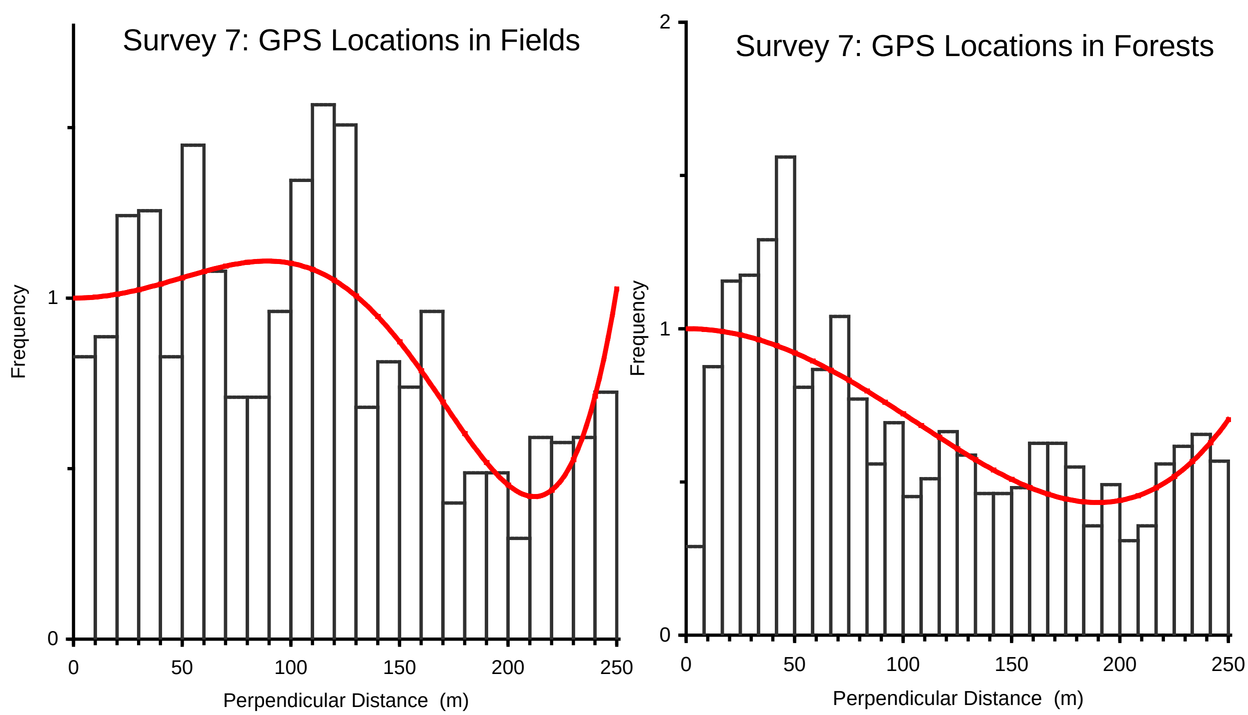
(d) Distribution of GPS locations in open areas and forested areas relative to perpendicular distance from transects during the fifth distance sampling survey, April 1–4, 2010.



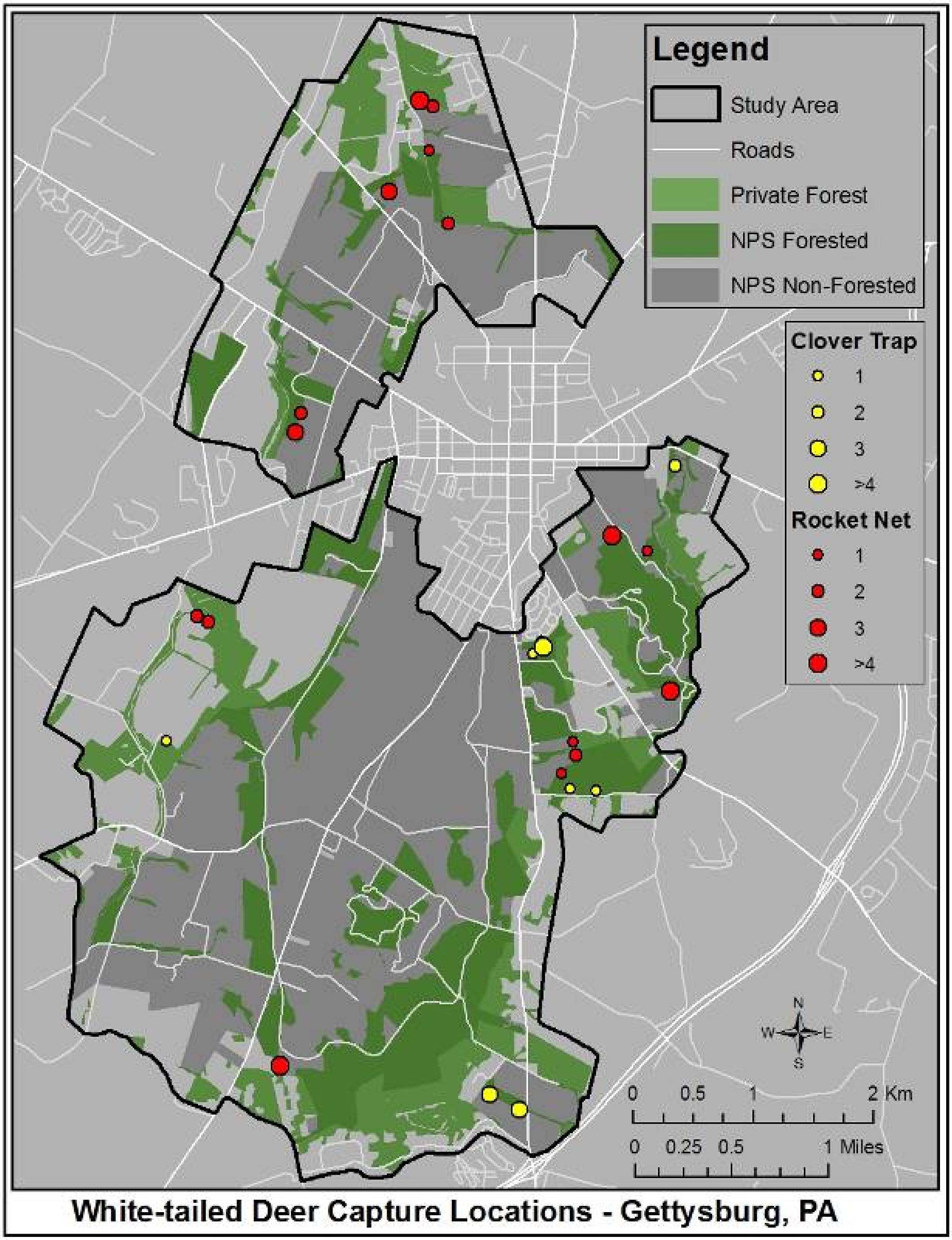
(e) Distribution of GPS locations in open areas and forested areas relative to perpendicular distance from transects during the sixth distance sampling survey, August 25–30, 2010.



(f) Distribution of GPS locations in open areas and forested areas relative to perpendicular distance from transects during the seventh distance sampling survey, November 15–19, 2010.



Appendix M. Locations where deer were captured in Gettysburg National Military Park and Eisenhower National Historic Site.



Appendix N. Summary of advantages and disadvantages of potential survey methods at Gettysburg National Military Park and Eisenhower National Historic Site.

Spotlight or Dusk mark-resight surveys using estimated detection probability (0.25 from April 2010)

Effort: At least 11 observers, each in their own vehicle are required for approximately 2–three hours each evening for three evenings.

Pros: Short survey period (3 evenings), volunteers can be used to minimize costs, and surveys are conducted prior to dark, which minimizes public disturbance.

Cons: Detection probability of all deer is assumed to be homogeneous, which is typically violated. Additionally, detection probability must stay constant over time, which is difficult to meet because of changes in observers, habitat, weather, deer behavior, etc. Therefore, using this method for point estimates or as an index of abundance may provide inaccurate and misleading trend data.

Change-in-ratio Estimator

Effort: The number of observers and time required depends on the sampling scheme used to estimate detection probability.

Pros: Harvest data are collected during culling operations (no extra effort).

Cons: Assumption of a closed population is likely violated during the period of culling, difficult to obtain unbiased estimates of detection probability for antlerless and antlered deer, and a large proportion of the antlerless population must be harvested to detect a noticeable change in detection probability for reliable estimates. The assumption that all removals are known is likely violated because deer harvested by hunters on private lands on the study area are not reported to park managers and not all mortally wounded deer are retrieved.

Catch-per-unit-effort Estimator

Effort: All required data are collected during annual culling operations.

Pros: No extra costs because all necessary information is collected during culling operations.

Cons: Assumption of a closed population is likely violated during the period of culling and not all harvested deer are reported by hunters or successfully retrieved to meet the assumption that all harvests are known (restricting the analysis and the majority of culling to before firearms season will minimize bias). Additionally, antlerless deer are targeted, however, adult males show up in the harvest later in the season after they have cast their antlers, which causes an artificial increase in catch-per-unit-effort. Thus, data analysis must be restricted to females and fawn males only. The primary problem with this technique is that the scope of inference regarding abundance is restricted to areas where culling can be performed (and that area should stay constant throughout the culling period). Therefore, the estimator yields no insight into abundance on areas not available to culling and will provide inaccurate abundance estimates when used to evaluate abundance for the entire study area.

Distance Sampling Estimator

Effort: At least three people (driver and two observers) in one vehicle for approximately five hours each night for 6–10 nights.

Pros: Works well as an index of abundance because detection probabilities can be modeled for each observer and habitat type.

Cons: Several assumptions are violated when roads are used as transects, which we found led to negatively biased abundance estimates. However, if the bias is consistent from year to year then this technique can be used as an index of abundance.

The Department of the Interior protects and manages the nation's natural resources and cultural heritage; provides scientific and other information about those resources; and honors its special responsibilities to American Indians, Alaska Natives, and affiliated Island Communities.

NPS 305116996; 446/116996, September 2012

National Park Service
U.S. Department of the Interior

Northeast Region
Natural Resource Stewardship and Science
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