Behavioral Phenomena and Population Estimation of White-Tailed Deer Based on Camera Trap Data

By Meghan Hills

Completed on 30 July 2016

In partial fulfillment of the requirements for graduation with the Dean's Scholars Honors Degree in Biology.

Dr. Lawrence Gilbert
Supervising Professor

1 August 2016
Date

Dr. Ruth Buskirk
Honors Advisor in Biology

7 August 2016
Date

Table of Contents

Abstract 3
Introduction 4
Materials and Methods 5
- Figure 1 5
- Figure 2 7
- Figure 3 8
- Table 1 8
- Figure 4 9

Results 14
- Table 2 14
- Figure 6 14
- Figure 7 15
- Figure 8 15
- Table 3 16
- Figure 9 16
- Figure 10 17
- Figure 11 18
- Figure 12 18
- Table 4 19
- Figure 13 19
- Figure 14 20
- Table 5 20
- Figure 15 21
- Figure 16 21
- Figure 17 22
- Table 6 22

Discussion 22
- Figure 16 25
- Figure 17 26

Acknowledgements 27
References 28

Abstract

When shaping management actions and conservation programs, it is essential to understand the population dynamics of a species. One species that sees extensive management and research effort is the white-tailed deer (*Odocoileus virginianus*), as it is both ecologically and recreationally important in many places. Although there are a multitude of ways to study and estimate the population dynamics of white-tailed deer, one method in particular comes with significant advantages: camera trapping.

For this study, nine camera traps were set up at deer scrapes across a private ranch in south Texas. After collecting images during the fall/winter rut of 2015, the cameras' photos were amassed, and photographed bucks were identified based on unique antler formations. The photo data were then analyzed for a variety of purposes: (a) to determine whether bucks visit scrapes non-randomly; (b) to examine patterns in the ranges of dominant individuals; (c) to assess whether diversity indexes identify fundamental differences in the collections of bucks visiting scrapes. Finally, a novel population estimation technique was applied by adapting and applying the program EstimateS.

There were a total of 129 bucks identified over the study region. I determined that bucks did indeed visit camera sites non-randomly and that they visited certain scrapes preferentially. This might have to do with the resources available in specific areas. Additionally, I observed that particular dominant individuals have home ranges that overlap, while others are much more solitary. This suggests that the sites themselves are differentially defensible, and that whether a location is dominated has to do with both the resources it offers and its ability to be monopolized. Results of the population estimation technique suggested that there were a number of bucks that remained undetected by the cameras. Future research could work to ascertain the accuracy of the population estimations made by EstimateS.

Introduction

Knowledge of a population's dynamics (e.g., size, density, distribution) is critical for management actions and conservation programs (Koerth *et al.* 1997). Estimates of population size before and after management action are central to judging the success of the action (Curtis *et al.* 2009).

In this study, the population of interest is one of white-tailed deer (*Odocoileus virginianus*) in south Texas. Deer are important both ecologically and recreationally, so it's no surprise they are the target of many management and research efforts (Côté 2011; Hansen 2011; Jacobson *et al.* 2011; Donohue *et al.* 2013).Common population estimation techniques for white-tailed deer include: drive, spotlight, strip, aerial, thermal- and infrared-scanning counts; mark-recapture estimators; population reconstruction; and guesses (Jacobson *et al.* 1997). There are significant downsides to each of these methods. Counts and mark-recapture techniques can be expensive, labor-intensive, and limited to certain habitats (i.e., those with high visibility and minimal forest cover; Jacobson *et al.* 1997); helicopter surveys, which are common in Texas, can be impractical for small landholdings and leases due to expense and limitations in scheduling (Koerth *et al.* 1997); population reconstructions depend on past mortality data and fail to provide a current population estimates (Jacobson *et al.* 1997); and guesses can be limited in accuracy and confidence.

Another technique for population estimation is camera trapping, in which fixed, motion-triggered cameras are used to "trap" images of passing animals (Rowcliffe *et al.* 2008). There are numerous advantages to camera trapping, including low equipment and labor costs; minimal disturbances to the environment; usefulness for gaining information on cryptic species and in places where other field methods are difficult or unreasonable; the ability to collect data during both day and night; and the allowance of ample time for researchers to identify captured (i.e., photographed) individuals (Rowcliffe *et al.* 2008; Curtis *et al.* 2009).

Capture-recapture models can be used to estimate population abundance (Rowcliffe *et al.* 2008). These models have been used to estimate populations of fish, birds, and small mammals, none of which can be counted easily via traditional distance sampling techniques (e.g., point and line transects; Karanth 1995). With camera trapping, individuals of a species can be "recaptured" or "retrapped" in photographs (Curtis *et al.* 2009). This of course requires that the species' individuals be recognizable in at least one trait (Rowcliffe *et al.* 2008), which limits the number of species for which camera trap capture-recapture methods can be used. Understandably, camera trap studies have become commonplace for striped and spotted felids (Rowcliffe *et al.* 2008). Deer are also candidates for camera trap studies, as antler, pelage, and body characteristics can give adult male deer unique, recognizable profiles (Jacobson *et al.* 1997).

Probability-based capture-recapture estimators can model factors such as capture probabilities, which can be heterogeneous among individuals in a population due to social structure (Karanth 1995) and home range. For instance, repeated sightings of an individual by one camera are more likely to occur if that camera is located in the core area of the buck's home range than if it's located on the periphery (Jacobson *et al.* 1997). At the very least, camera traps can provide a minimum estimate of the adult bucks present in a population (Jacobson *et al.* 1997). They can also go so far as to allow estimation of an entire deer population's abundance, distribution, and movement patterns.

In this study, I use nine camera traps to study a south Texas population of white-tailed deer. There are two sections to the analysis. In the first section, I assess the null hypothesis that all male deer over the study area are homogeneous in their movements. If this is the case, all bucks should be photographed randomly at all camera sites. In examining this, I look at various statistics of the dataset, some of which involve Shannon diversity indexes of the camera sites, and some of which involve focusing only on the dominant bucks of the deer population. In the second section of the analysis, I test the use of novel statistical methods to estimate the size of the unknown population. To do this, I use a computer program called EstimateS and adapt it to function as an estimator of population size. Generally, I apply various analytical techniques to evaluate the use of camera traps in considering and understanding a population of white-tailed deer.

Materials and Methods

A Note About the Dataset

The dataset used in this work was collected and made available by Dr. Lawrence Gilbert. He was responsible for setting up the camera traps, as well as amassing and processing the images they captured. Additionally, Dr. Gilbert was the chief agent in identifying individual bucks.

For my part, I assisted in fine-tuning buck IDs, entering the data into Microsoft Excel, and checking the dataset for discrepancies, inconsistencies, and mistakes.

Knowledge of the study site and data collection process comes from personal communication with Dr. Gilbert.

Site Description

The camera survey was conducted in south Texas, on a private ranch that overlaps Maverick and Dimmit Counties, both of which are located in the western Rio Grande Plains. Although the ranch is about 25,000 acres total, for the purposes of this research we focused on a 5,200-acre region on the northeast side of the full ranch (see Fig. 1). This section of the ranch is surrounded by high fences, with the exception of an unfenced portion about 0.75 miles in length, located on the region's southwest side. Unless otherwise specified, all further mentions of the study site are in reference to this particular 5,200-acre region of interest.

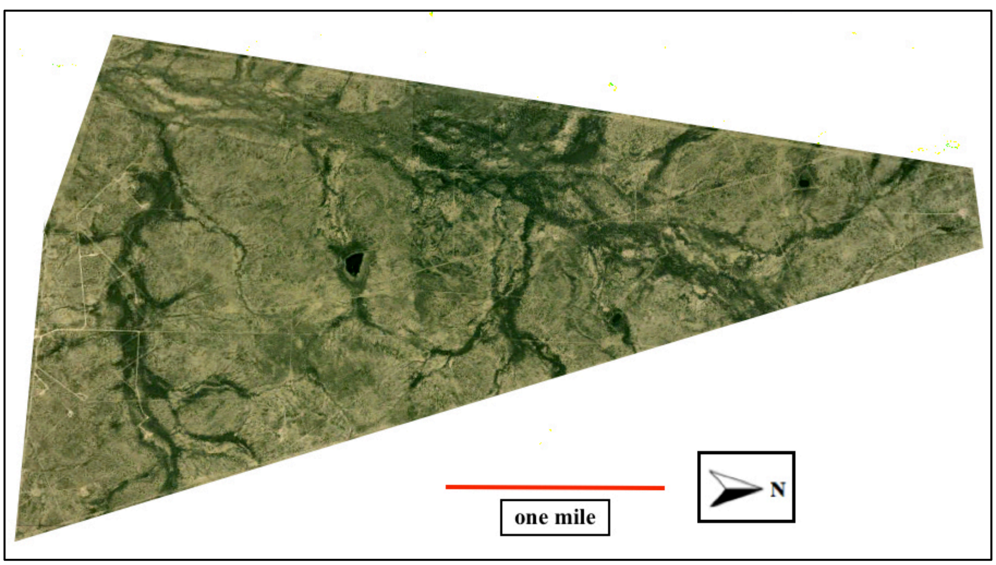

Figure 1: A map of the 5,200-acre study area in south Texas.

Via its unfenced side, deer could move between the 5,200-acre study area and the surrounding ranch. Movement into and out of the full ranch, however, was not possible. Since movement to and from the study site was so restricted, and since only one camera trap (on the study site's extreme southwest side and near the fence gap; site 7) documented any such exchange with the larger ranch, we can for our purposes assume that the deer population was largely contained in the study site (Lawrence Gilbert, personal communication).

The terrain of the study area consisted of flat land and low rolling hills (Donohue *et al.* 2013). Annual rainfall is less than 25 inches, though it is highly variable; year-round temperatures yield hot summers and mild winters in this semi-arid environment (Donohue *et al.* 2013). The 5,200-acre site was dominated by native brush species such as mesquite, acacia, desert hack berry, and various cacti. Drainage zones boasted thick vegetation, characterized by Texas persimmon, sugar hack berry, and the occasional cedar elm above dense thickets of white brush. Portions of these flat drainage zones were cleared for fall and winter food plots (mainly oats), and both protein and corn feeders were paired with each food plot to supplement the diet of the deer.

Although the ranch is privately owned, there is nevertheless a staff of biologists who monitor and manage its ecosystems and wildlife—especially the antlered deer—very closely. One way they do this is by culling both sexes of deer to keep population densities at or below about twenty acres per individual. This serves to maintain the balance of natural resources and the sustainability of native browse plants, both of which are crucial efforts since the health of the deer depends on both population density and habitat quality. Though the staff culls both sexes of deer, they do cull bucks differentially, depending on antler traits. People occasionally hunt for deer on the ranch, and killing a buck with large, impressive antlers is seen as preferable to killing one with smaller antlers. For this reason, the biologists want to "select for" bucks with larger antlers. To accomplish this, the bucks' antlers are compared within age classes, and individuals with less desirable antlers are culled. For first year bucks, multiple points on antlers are favorable to spikes and forks, so bucks with the latter are culled; for three year old bucks, individuals with eight points or less and lacking symmetrical antlers are culled. By implementing this process, the staff imposes selection based on antlers. Though it may shift the population's average for antler quality only slightly, the number and caliber of "trophy" bucks does indeed increase over years of such population management.

Another way the deer population is managed is by being fed protein. This serves primarily to allow a higher number of bucks to survive to the age at which full antler development can be seen (ages six to nine; Hewitt *et al.* 2014).

Yet another tactic the staff uses to help the deer population is removing as many coyotes from the ranch as possible. Coyotes are a primary mortality factor for fawns (Lawrence Gilbert, personal communication), so by limiting this threat to the deer, the staff allows more male fawns to survive to antler-growing age. That eliminated coyote-caused mortality is then replaced by the differential culling based on antlers that the staff carries out.

These facts about deer management are noteworthy because they: (a) may affect the behavior of the deer; (b) yield the ranch a non-pristine environment; and (c) led to bucks being removed from the population during our sampling time frame. These aspects of our study site are important to keep in mind as we draw conclusions from the data.

Using the Cameras

Although camera traps for deer are commonly placed at feeders (Jacobson *et al.* 1997; Koerth *et al.* 1997; Donohue *et al.* 2013), we decided instead to position our cameras at scrapes, which are made by male deer as a form of marking behavior (Kile & Marchinton 1977). Scrapes consist of a pawed depression in the soil underneath a one- to two-meter high overhanging tree limb (Marchinton & Hirth 1984), and they're typically located in conspicuous areas, such as game trails, roads, and small clearings in vegetation (Kile & Marchinton 1977). The scrape-making buck can "mark" the overhanging limb by nuzzling, licking, and pulling on it with his mouth (Kile & Marchinton 1977), and he often urinates on the pawed ground (Miller *et al.* 1987). The behavior of scrape-making depends on a buck's physical and behavioral maturity, not just his degree of dominance, and it serves to advertise his presence and establish his dominance in the area (Miller *et al.* 1987). The creator of the scrape will not physically defend it against an intruding buck if the latter exhibits subordinate postures (Kile & Marchinton 1977).

Scrapes are ideal locations for camera traps for multiple reasons. For one, unlike food sites and bait stations, scrapes do not attract other (i.e., non-deer) animals (Koerth *et al.* 1997), thereby lessening the number of unwanted photos taken by the cameras. This makes for more efficient processing of the collected images. Another consideration is that food sites may be differentially accessible to certain deer in the area; subordinates, for example, may be excluded some or all of the time due to the particular social pressures inherent when resources are at stake (Donohue *et al.* 2013).

To locate scrapes, Dr. Gilbert walked around the areas surrounding nine food plots, as scrapes can be found along major trails and road edges in food plots' vicinities. He positioned cameras to face spots where tracks and ground disturbances indicated frequent buck activity and suggested the existence of a scrape.

We assigned a simple number to each of the nine food plot sites for easy reference. If there were several cameras in the area around a single food plot, we lumped their images and assigned them the same site number. See Figure 2 for the sites' locations across a map. Note that, because the cameras were set up and the photos looked through in random order, the sites were given numbers in a random order as well. For this reason, we happened to skip the number 6 as a site number, and we also happened to assign a site number 32. These two small quirks made no difference to data analysis.

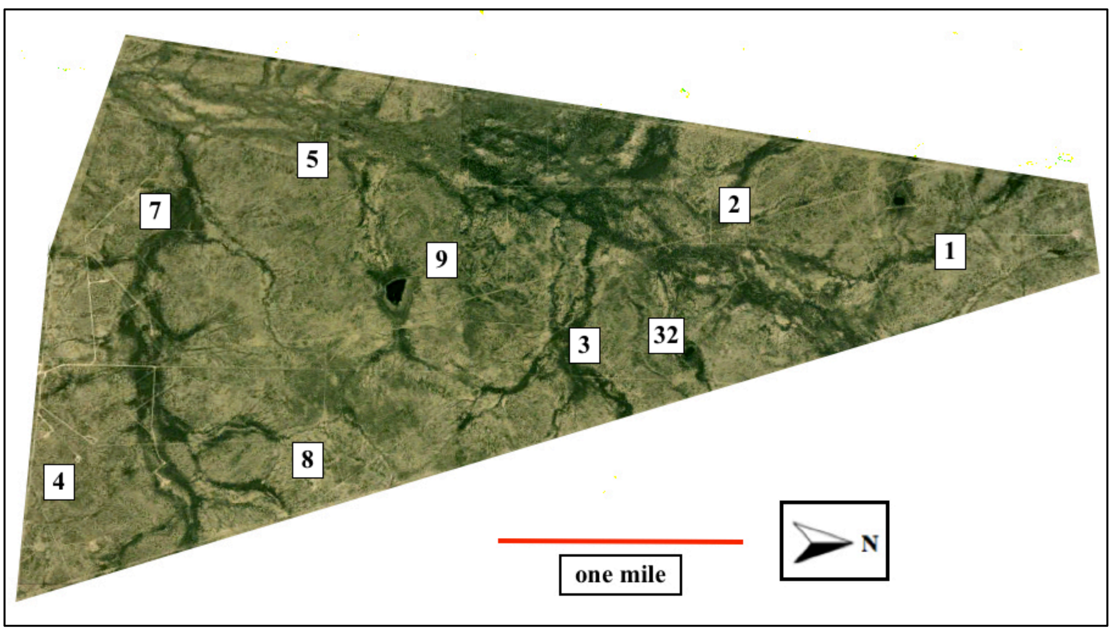

Figure 2: A map of nine camera sites across the 5,200-acre study area in south Texas.

We used Cuddeback® Attack® (Cuddeback, De Pere, USA) cameras to capture photographs. These had a 0.25-second trigger speed. Each camera had a two to eight gigabyte (GB) secure digital (SD) memory card.

Cameras' memory cards were collected after a period of a few months, and the images they'd captured were downloaded to a computer. The time period over which all cameras were operational was between 18 October 2015 and 30 April 2016. Specific start and end dates were variable between cameras; see Figure 3 for a schematic of all cameras' dates and durations of operation. Photos were taken continuously by each camera within its operational time frame.

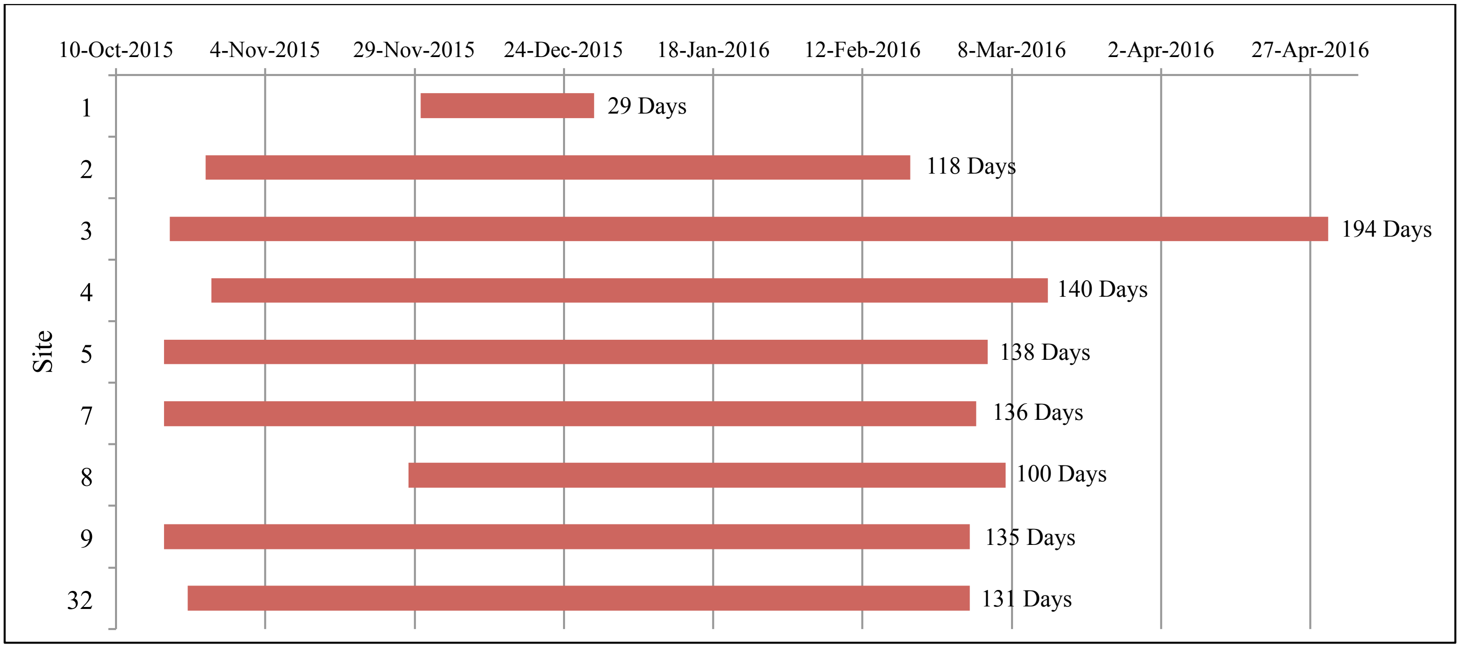

Figure 3: The dates and duration for which each camera was in operation.

Identification of Individuals

A total of roughly 12,600 photos were collected by all of the cameras over each of their sampling time frames. Once these photos had been retrieved, we filtered them to collect only those of antlered bucks; this left us with 1,846 photos. See Table 1 for the numbers of buck photos collected at each camera site.

Table 1: The number of buck photos collected at each camera site.

Site	Total Number of Buck Photos
1	65
2	213
3	186
4	164
5	318
7	290
8	321
9	226
32	63
Total	1846

For each of these photos, Dr. Gilbert used Adobe® Photoshop® CS6 to crop and enhance the image using the "Auto Tone" or "Auto Color" options. Some images needed additional adjustment in their color levels, brightness, and contrast. Because of these enhancements, the buck photos were easier to work with and analyze in subsequent steps.

After all of the photos had been treated in Photoshop, they were uploaded online to Picasa Web Albums™, and they were placed in folders designated by the site at which they were taken. Within these folders, images were sorted roughly by size of antlers: photos of bucks with larger antlers were located near the beginning of the folder, and photos of bucks with smaller antlers were located near the end.

Once the photos were sorted in their folders, we looked at each photo and identified the buck in it based on his unique antler formation. Like Jacobson *et al.* (1997), we utilized antler configuration details, such as number of points, length of points, angles of branches and tines, and relative locations of projections along the main beam. Occasionally, we used other body characteristics, such as facial markings and body shape.

During the first stage of the identification process, the bucks were given decimal numbers. The number before the decimal indicated the camera site, and the numbers after the decimal represented the particular individual. For example, in the site 1 folder, the first buck was labeled 1.01, the second buck 1.02, and the fifth buck 1.05; in the site 4 folder, the first buck was labeled 4.01, the second buck 4.02, and the fifth buck 4.05. Because the folders were organized roughly by antler size, the order in which bucks were given their numbers was also based roughly on antler size. Therefore, the buck with the largest antlers at a site would have one of the first numbers (like .01 or .02), and a buck with smaller antlers would have a later number (like .24 or .39).

Photographs in which the buck identification was unclear were excluded from analysis. See Figure 4 for a graph depicting photos from each site that were both used and unused in analysis. Unless otherwise specified, all further mentions of sites' and bucks' photo counts are in reference to only those photos actually used in analysis.

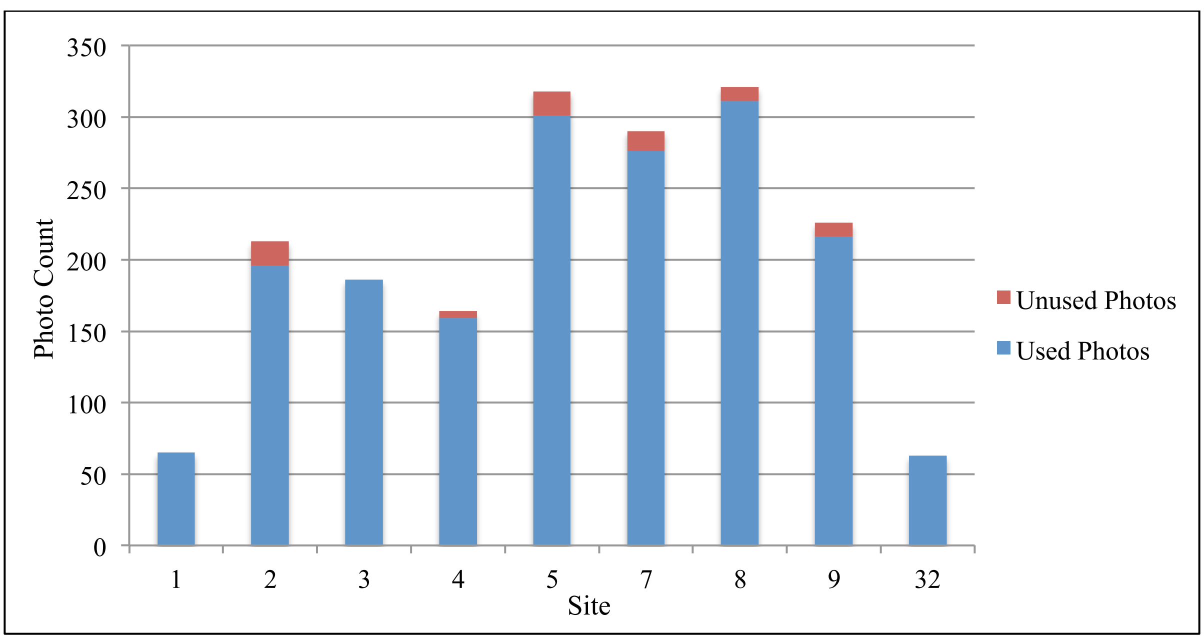

Figure 4: The numbers of used and unused photos from each camera site.

Picasa Web Albums™ is a registered trademark of Google. It was closed on 1 May 2016 (Picasa 2016).

Following the identification of each site's bucks, we looked through all the sites' photos to find bucks that appeared in multiple places. Once a buck was identified as one who appeared in multiple places, he was given a simple master number (e.g., 1, 2, …, *n*). For example, if buck 1.04 (at site 1) was the same individual as buck 3.02 (at site 3), we would assign it the lowest available master number and note that those decimal numbers equated to the same individual. If a buck was identified as only appearing at one site, he, too, was given the lowest available master number. In general, master numbers were assigned roughly on the basis of antler size.

As we identified individuals in repeat photographs and assigned master numbers, there were some instances in which we made judgments that were later changed. In some of these cases, we amended the initial decision that there were two bucks and concluded that it was actually one buck. In such a scenario, the buck was given the lower of the two master numbers. The higher of the two numbers could then be assigned to a new buck, or it could remain a gap in the bucks' master number list.

We ultimately assigned 129 master numbers. Therefore, we identified 129 individual male deer in the 5,200-acre region.

Dominant Bucks

The first portion of the analysis involved observing the photographs and movement patterns of dominant bucks specifically. Because Dr. Gilbert has extensive experience with white-tailed deer, he determined which of the 129 captured individuals were dominant. It is known that dominance depends on weight, antler size, experience, and testosterone levels (Miller *et al.* 1987), so these were factors that Dr. Gilbert took into account when determining which bucks could be considered dominant.

Diversity Indexes

To look for patterns in the various camera sites and their collections of bucks, one metric I used was the Shannon diversity index (H). This index is traditionally a measurement of species diversity, and it takes into account both the number of species in an area ("richness"; S) and the evenness (E) with which those species occur (Lloyd & Ghelardi 1964). The maximum possible value for an area is reached if all species there are present in equal proportions (Lloyd & Ghelardi 1964). The equation for calculating H is:

$$H = -\sum_{i=1}^{S} p_i \ln p_i$$

where S is the total number of species present in the area, and p_i is the proportion of the ith species in the area (Whittaker 1972).

Instead of using H in its traditional sense, I adapted it to apply to this study: it was not calculated for the purpose of comparing diversity of *species*, but instead for comparing diversity of *individuals* at camera sites. To do this, H was calculated for each of the nine camera sites, and the values represented the number of individual bucks that were photographed by a camera (the "richness," S, at that camera), as well as the evenness with which they were sighted there. Therefore, p_i in the equation became the proportion of all buck photos at a site containing the ith buck. Because the Shannon index is relatively independent of sample size (Whittaker 1972), it was a useful metric to compare camera sites' collections of visiting bucks.

Since H takes both S and E into account in its calculation, it was of interest to examine whether richness or evenness played a larger role in determining camera sites' values of H. To accomplish this, Shannon's evenness (*E*) of each camera site was calculated using the following formula:

$$E = {}^{H}\!/_{\ln S}$$

where *H* is the Shannon diversity index for the camera site, and *S* is the number of visiting bucks at that site.

Background for EstimateS

For the first part of our data analysis, we used a program called EstimateS (Colwell 1994–2016). According to the user's guide, EstimateS is "a free software application…designed to help you assess and compare the diversity and composition of species assemblages based on sampling data" (Colwell 2013). For our purposes, we wanted to use the program not to estimate a number of species, but to estimate a number of individuals. This required an understanding of the spirit of the software, so to speak; a grasp on the assumptions on which it is based, as well as the implications of its output.

Typical input for EstimateS is data—usually in the form of species counts (species richness)—from a survey of an area's biodiversity. Given such data, EstimateS can run a number of statistical analyses and generate a variety of biodiversity estimators and indices. This output serves to predict the answer to a common research question: how would the data be different if the dataset were larger? Or, more specifically: how many species would have been counted if the survey had been more extensive? The statistics of EstimateS address these queries by estimating characteristics of the local assemblage from which the data was taken. The local assemblage is the complete collection of biodiversity within which the survey was conducted. Although the survey may have undertaken to count the number of species (generally only those of a particular taxonomic similarity [Gotelli & Colwell 2011]) in the assemblage, in virtually all cases some species remain unobserved and undetected by the survey.

One way to represent a species count is with a species accumulation curve, or a graph in which the cumulative number of species observed is plotted against some measure of survey effort. As can be seen in the example species accumulation curve in Figure 5, these curves always increase monotonically and have a slope that decelerates (Gotelli & Colwell 2011). The slope is initially high because the most common species in an area are observed quickly and easily; it gradually decreases, however, as rarer species are only encountered after more survey time and effort.

The measure of survey effort on the *x*-axis of a species accumulation curve can be quantified in one of two ways: (a) the number of samples taken in the survey, or (b) the number of individuals in the survey. Choosing which of these two alternatives to use when drawing a species accumulation curve depends entirely on the method by which the data was collected. If there were multiple samples taken in the survey, the data is "sample-based"; if only one sample was taken, the data is "individual-based." With sample-based data, the numerous samples—each with some number of individuals—are pooled, and the species accumulation curve is built by examining each sample in turn. Contrast that with individual-based data, with which the species accumulation curve is built by looking at each individual in turn. A curve constructed from sample-based data would have an *x*-axis of "number of samples" (upper axis of Fig. 5); a curve constructed from individual-based data would have an *x*-axis of "number of individuals" (lower axis of Fig. 5).

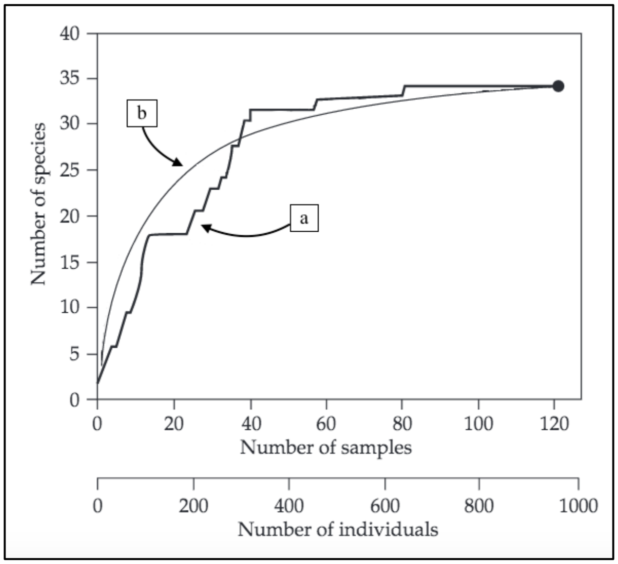

Figure 5: Example species accumulation curves. (a) The rough shape characteristic of a curve generated once from a dataset. (b) The smooth shape formed after averaging multiple iterations of a dataset's accumulation curves. Adapted from Gotelli & Colwell (2011).

After a species accumulation curve is generated from a dataset, it will be rough and uneven (see Fig. 5a). This is due to random sampling effects, along with spatial and temporal patchiness of species in the order of the data (Colwell *et al.* 2004). To create a smooth curve, the data—whether it be sample-based or individual-based—can be repeatedly pooled and randomized, and a new species accumulation curve drawn every time. Finally, the various differently-shaped curves can be averaged together, thus creating a smooth curve that gives the expected number of species in a given number of samples or individuals (see Fig. 5b; Gotelli & Colwell 2011).

A species accumulation curve drawn from a dataset will culminate at the *y*-value of *S*, the number of species observed in the survey. But in order to answer the research questions posed three paragraphs ago, the curve must be extended beyond the limit of the dataset. This can be done in a process called extrapolation, and EstimateS has the capability of performing such an analysis. Extrapolations allow a researcher to infer how many additional species would have been counted if his dataset had been larger; or, put another way, it gives the researcher an estimate as to how many species eluded detection in his survey. As the extrapolated species accumulation curve approaches a horizontal asymptote, the value of that asymptote is interpreted to be the assemblage's "true" species richness (Colwell *et al.* 2004). Although the procedure of extrapolation can be invaluable to a researcher, it does have a caveat worth noting: the species accumulation curve should not be extended beyond three times its original size (Colwell *et al.* 2004). With this in mind, EstimateS gives the option of extrapolating data by a factor of either two or three (Colwell 2013).

When working with either sample-based or individual-based data, there are some underlying assumptions to be considered. With individual-based data, an assumption is that there is random mixing of individuals in the survey area (Colwell *et al.* 2004). With sample-based data, because the samples are pooled to create the species accumulation curve, they need to be replicates of one another (Colwell 2013). In statistical terms, this means that the samples must be randomly generated from a single assemblage, and that the order and organization of them in space and time is not important (Colwell *et al.* 2004). Another implication of this assumption is that a given species has an equal probability of being recorded in any sample (Colwell *et al.* 2004). Also to do with sample-based data is the assumption that a species' presences and absences in various samples are independent of one another; the species' being seen in one sample is unrelated to whether it was seen in another sample (Colwell *et al.* 2004). Finally, a critical assumption for statistical inference with either type of data is that the assemblage is closed, with a constant total number of species and a stable abundance distribution (Gotelli & Colwell 2011). If this assumption is not met and the assemblage fluctuates in size and composition over time, statistical analyses such as the ones described above will likely be invalid; this is because the survey would serve only as a snapshot of a continually-shifting assemblage, and it may therefore fail to represent the community's true structure (Magurran 2007).

Adapting EstimateS

Although EstimateS is designed to estimate the number of species in a local assemblage, we aimed to use it for a different objective: estimating the number of individual bucks across the 5,200 acres of our study area. To accomplish this, the jargon of EstimateS—and of techniques for estimating species richness in general—had to be adapted to fit our purposes. The first translation was the most obvious: when EstimateS called for data or reported results on different *species*, we interpreted it to mean different *individuals*. When *samples* of the data were relevant, we understood them to be our various *camera sites*. The reference to a *local assemblage* was taken to mean the *full collection of bucks visiting a given camera site*. In this way, we were able to interpret the language of EstimateS as one of estimating population abundance. From this point on, these pairs of synonyms will be used interchangeably when talking about the data and results of EstimateS.

Process in EstimateS

Before the data could be loaded into EstimateS, it needed to be in the correct format for the program. EstimateS has the ability to work with four different "filetypes," or organization schemes for a dataset. Two of them apply to sample-based data, and two apply to individual-based data. For this study, we did two different analyses using two of the four filetypes: filetype 1, which is applicable to sample-based abundance data in the form of one set of replicated samples; and filetype 4, which is applicable to individual-based abundance data in the form of a batch of samples (Colwell 2013).

We used Microsoft Excel to arrange our data into two spreadsheets—one for each of the two filetypes we would be analyzing. For filetype 1, all of the data was combined into one dataset and treated as sample-based data. Each column was a sample (i.e., data from a certain camera site), and each row was an individual buck. For filetype 4, each camera site was its own dataset, and they all just happened to be inputted into EstimateS in a single batch. For detailed information on formatting data for the four filetypes, see the EstimateS user's guide (Colwell 2013).

Once the two spreadsheets were compiled and organized as filetypes 1 and 4, each was converted into a tab-delimited plain text file, as this is the type of file that EstimateS accepts. The data was then loaded into the program. Before running any analyses, there were some settings to be checked and chosen. Under the "Diversity" menu, "Diversity Settings" was selected, and its screen appeared. The number of randomizations to be run when creating the data's species accumulation curve is set to 100 by default, and we left this unchanged. The one important change made in "Diversity Settings" was the selection of the option to "extrapolate rarefaction curves," and this was specified to be done by a factor of three. By instructing EstimateS to do this, we were allowing it to extend our data's accumulation curve by three times its original size, thus giving us an estimate as to the expected number of bucks in the assemblage.

Results

As Figure 3 shows, each camera trap was in operation for a different duration, ranging from 29 to 194 days, and each captured between 63 and 311 photos of bucks in the process. Table 2 gives each camera's days of operation, number of buck photos, and first and last photo dates.

Table 2: Each camera's days of operation, number of photos of bucks, and first and last photo dates.

Site	Days of Operation	Number of Buck Photos	Earliest Photo	Latest Photo
1	29	65	30 Nov. 2015	29 Dec. 2015
2	118	196	25 Oct. 2015	20 Feb. 2016
3	194	186	19 Oct. 2015	30 Apr. 2016
4	140	159	26 Oct. 2015	14 Mar. 2016
5	138	301	18 Oct. 2015	4 Mar. 2016
7	136	276	18 Oct. 2015	2 Mar. 2016
8	100	311	28 Nov. 2015	7 Mar. 2016
9	135	216	18 Oct. 2015	1 Mar. 2016
32	131	63	22 Oct. 2015	1 Mar. 2016

To get a sense of how the variable operating time frames impacted the amount of data collected by each camera, I plotted each site's number of buck photos against its duration of operation. This is show in Figure 6 below.

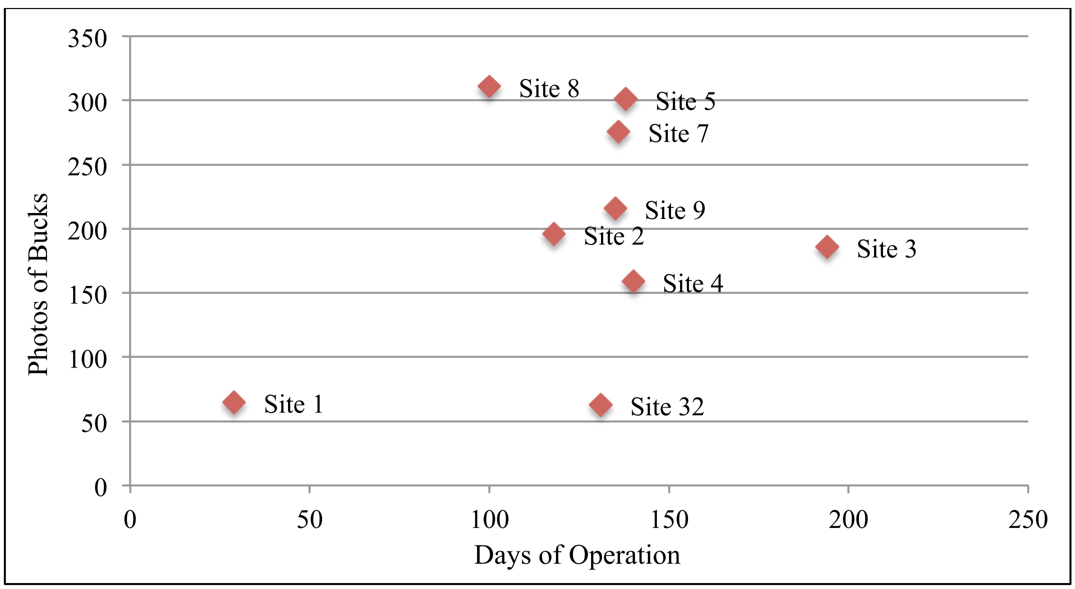

Figure 6: Each site's number of buck photos versus its number of days of operation.

From personal communication with Dr. Gilbert, the determination was made as to which of the study area's bucks could be considered dominant individuals. We are confident in the belief that the dominant bucks captured were those with master numbers 1–8 and 15.

Figure 7 gives each buck's total photo count across all sites. Dominant individuals' bars are denoted by red coloration.

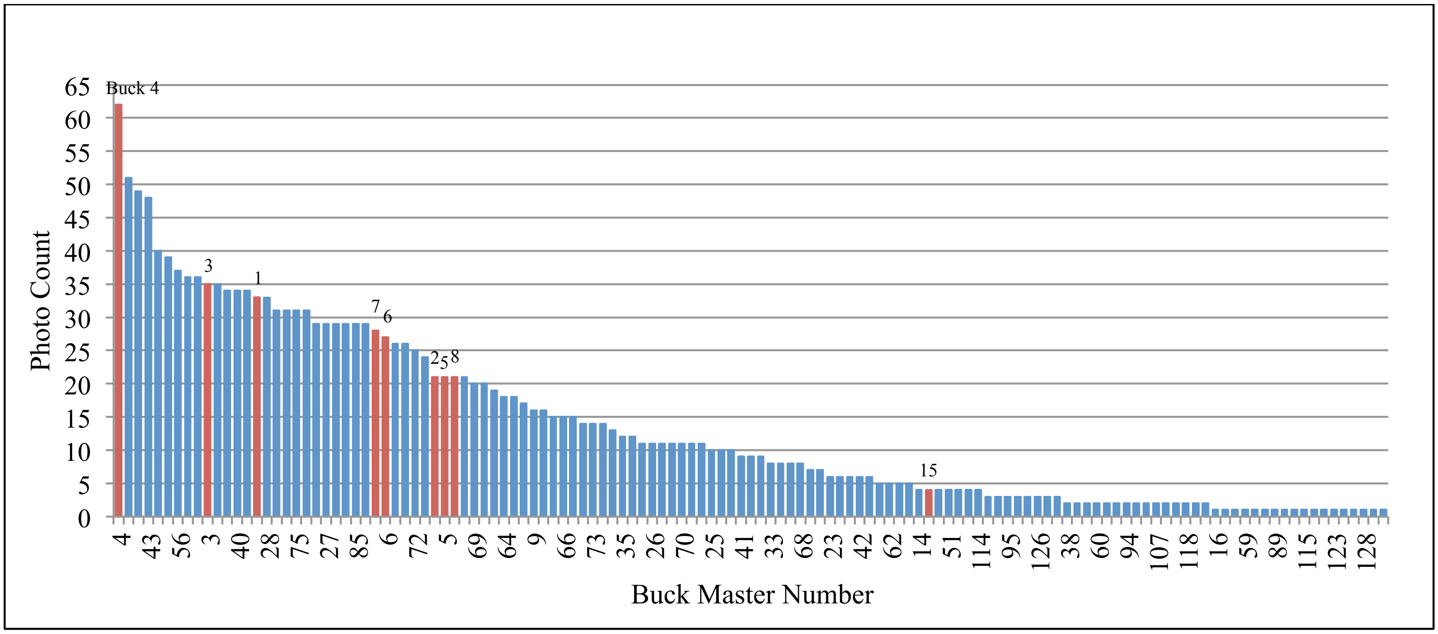

Figure 7: Photo counts of all identified bucks. Red bars indicate dominant individuals (master numbers 1–8 and 15).

Each site was visited by a unique combination of bucks. At any given camera site, most bucks were photographed only a few times, while a limited number of bucks were photographed many times. Figure 8 shows this by displaying all sites' rank abundance curves. These curves rank the photo counts of every buck seen at a given site, providing an idea of the frequency with which various individuals were photographed there.

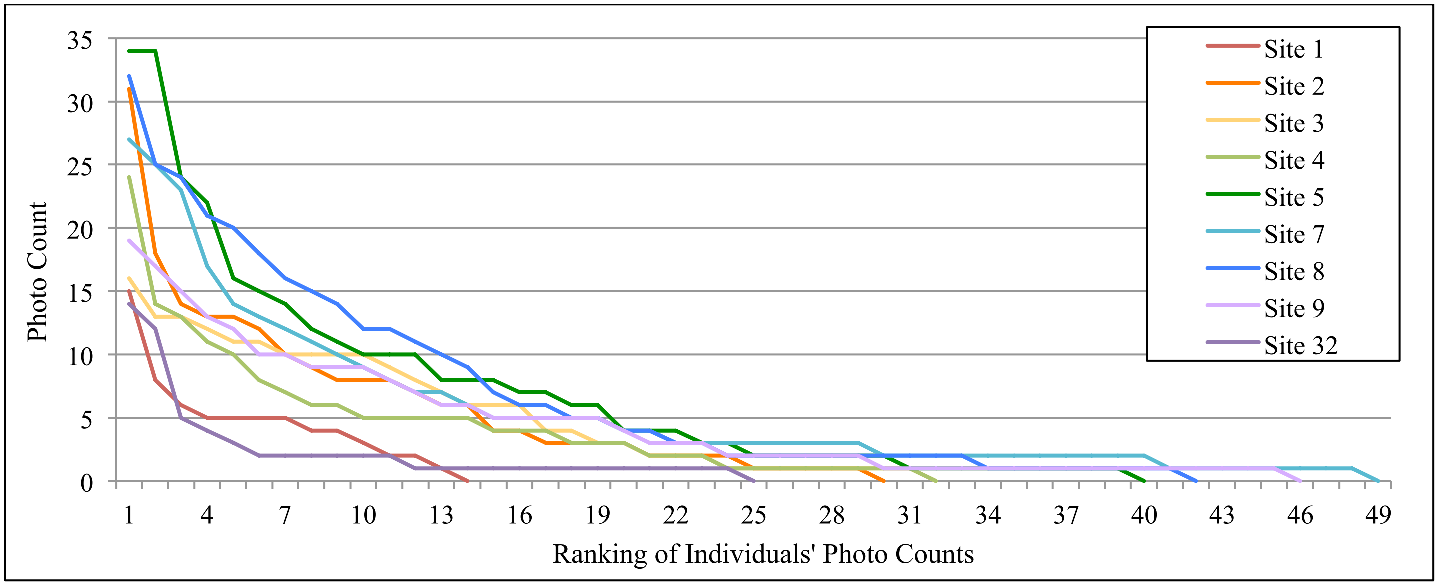

Figure 8: All sites' rank abundance curves. These show the rankings of the photo counts of a camera site's visiting bucks.

Table 3 breaks down each site's collection of visiting bucks into the numbers of those photographed fewer than a dozen times and those photographed at least a dozen times.

Table 3: The number of individual bucks who were photographed at each site, as well as the breakdown of the number and proportion of them who visited fewer than and at least 12 times.

Site	Total Individuals Captured	Individuals with <12 Captures		Individuals with ≥12 Captures	
		Number	Proportion	Number	Proportion
1	13	12	0.923	1	0.077
2	29	23	0.793	6	0.207
3	31	27	0.871	4	0.129
4	31	28	0.903	3	0.097
5	39	31	0.795	8	0.205
7	48	41	0.854	7	0.146
8	41	30	0.732	11	0.268
9	45	40	0.889	5	0.111
32	24	23	0.958	2	0.083

One aim of this research was to observe whether dominant bucks had "preferred" sites that differed from other dominants' preferred sites. To address this, Figure 9 was constructed to display dominant bucks' sightings at each camera site. The *x*-axis is ordered with respect to sites' maximum photo counts (with highest on the left).

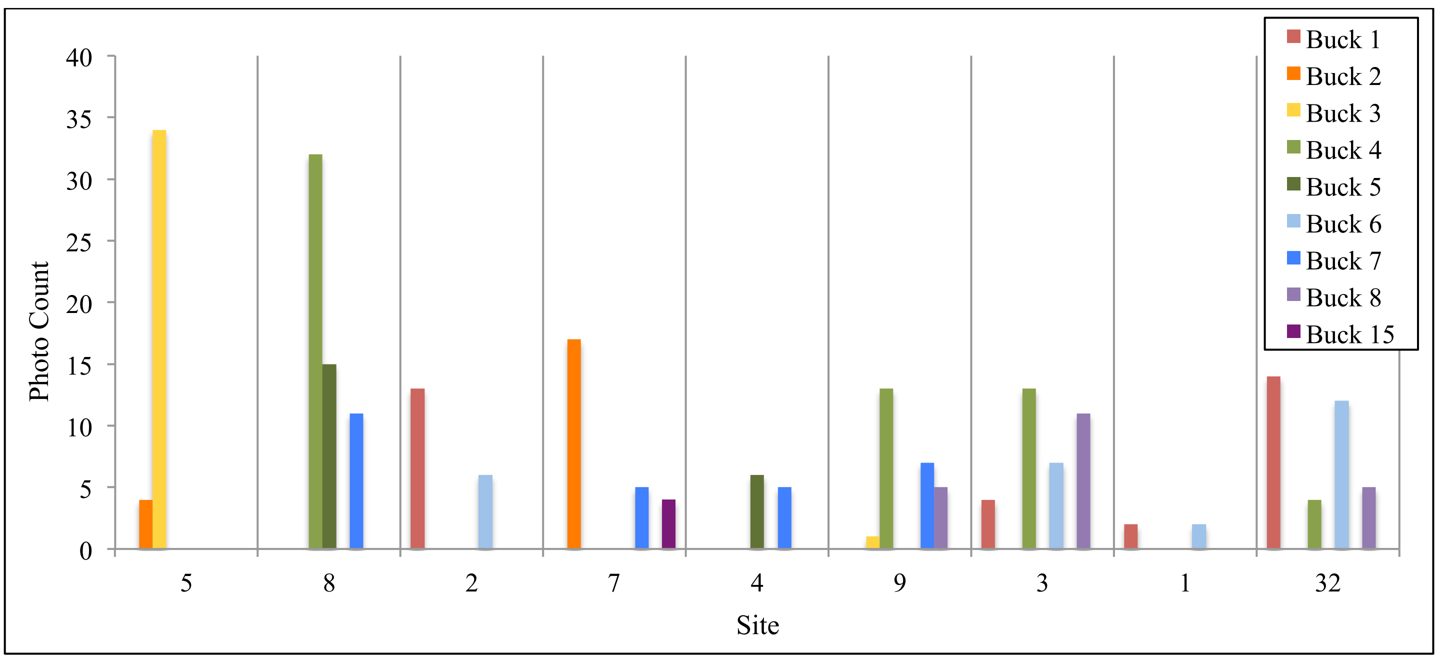

Figure 9: Photo counts of dominant bucks 1–8 and 15 at each site.

Another method of understanding dominant bucks' activity patterns involved taking a new look at each site's rank abundance curve (see Fig. 8). This time, the photo counts of dominant bucks were highlighted. Figure 10 shows the result of this; dominant bucks' photo counts are marked with red circles.

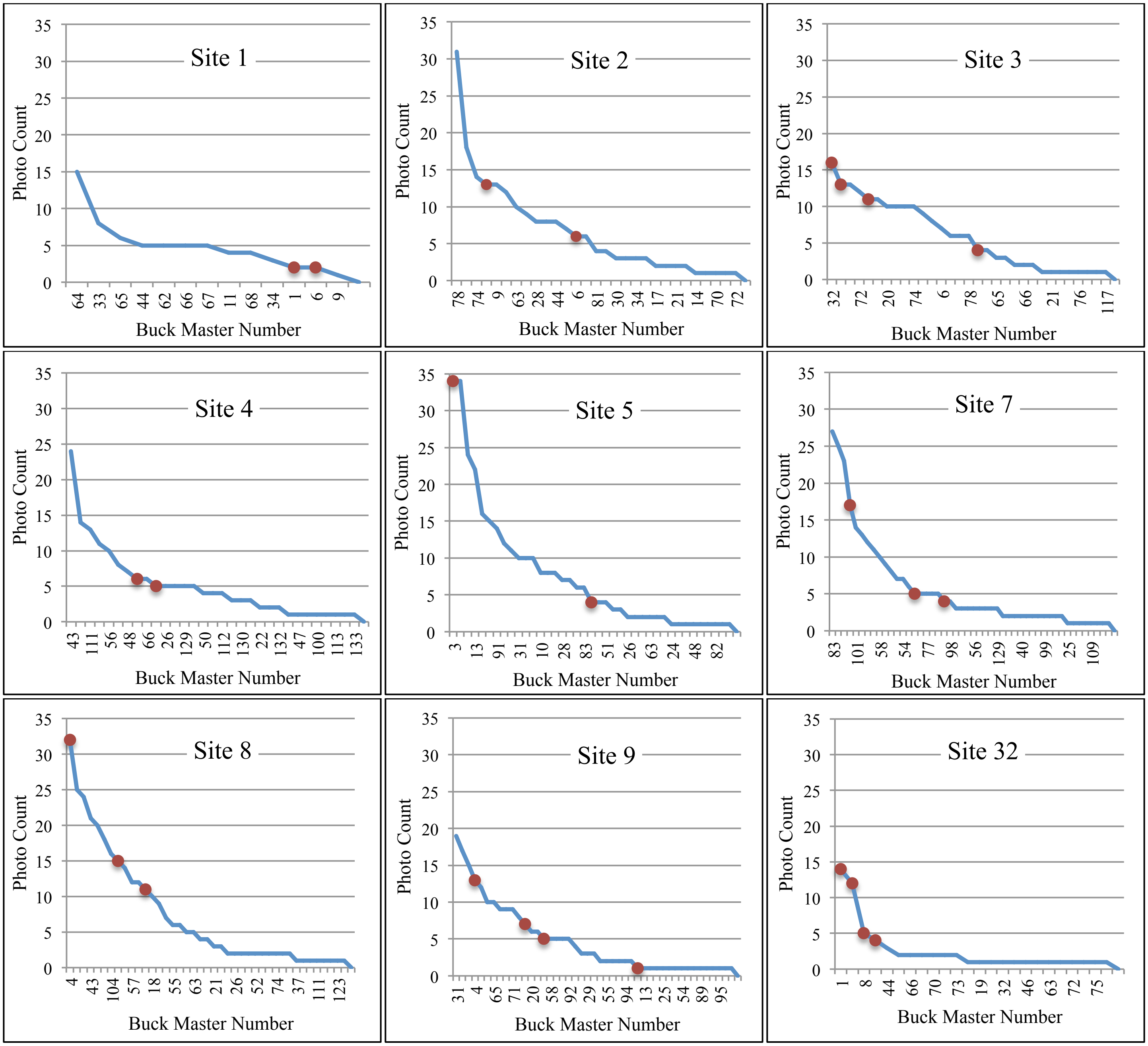

Figure 10: Each site's rank abundance curve. Red circles denote photo counts of dominant bucks (master numbers 1–8 and 15).

Next, it was of interest to compare sightings of only the dominant bucks. Figure 11 shows which and with what frequency dominant bucks visited each site.

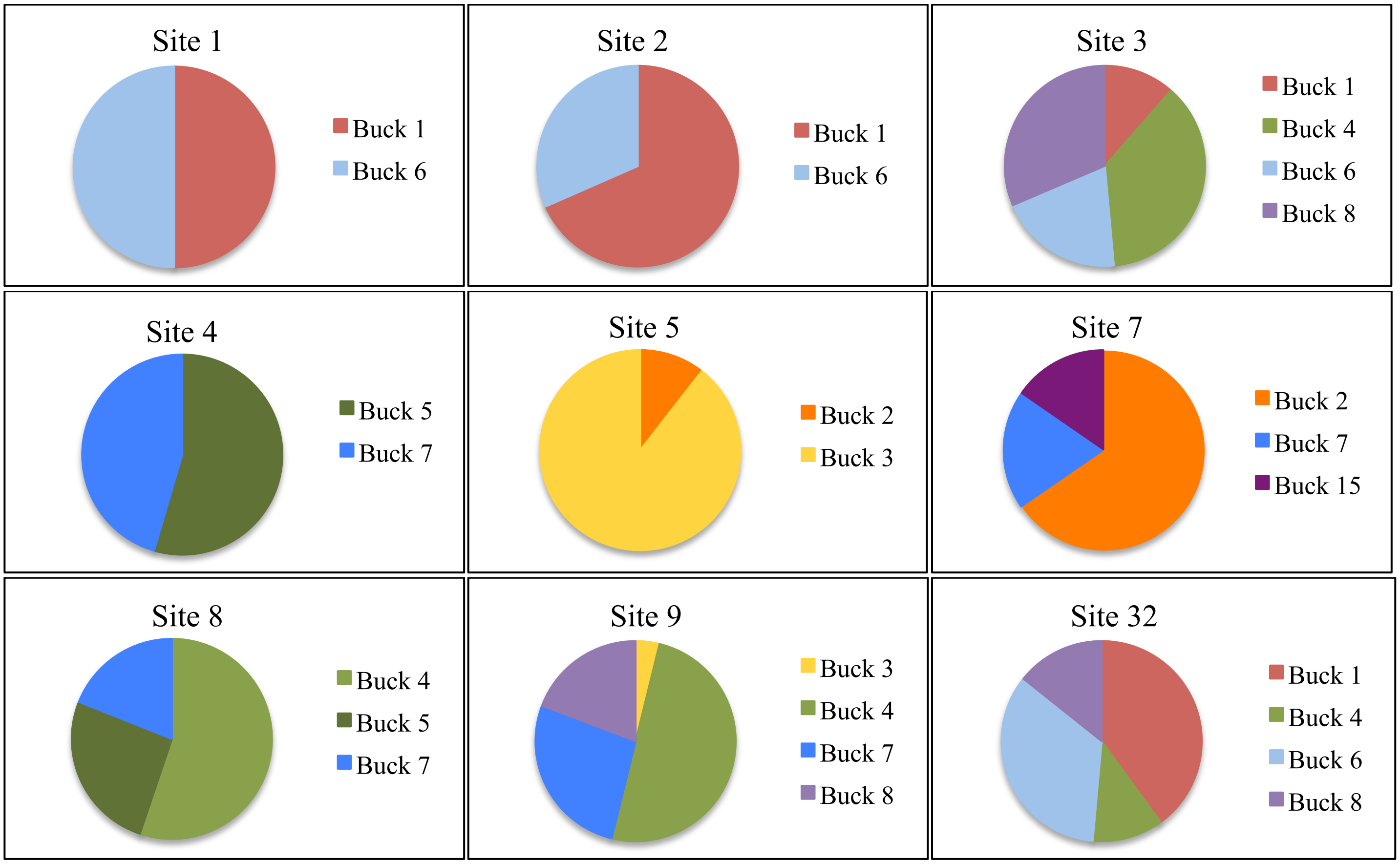

Figure 11: Comparison of which and with what frequency dominant bucks visited each site.

Overlaying the charts from Figure 11 onto a map of their respective camera sites in the study area results in a general visualization of each dominant buck's range. This is shown in Figure 12 below.

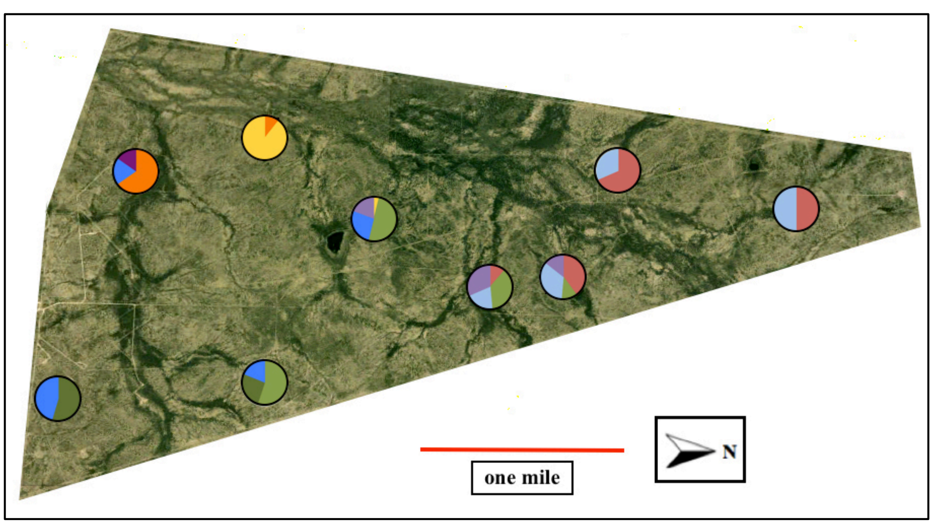

Figure 12: Dominant bucks' sightings at each camera site overlaid on a map of the study area.

Diversity Indexes

For each site as well as the overall study area, I calculated both the Shannon diversity index (*H*) and the evenness (*E*). The results, as well as the number of individuals seen at each site (i.e., that site's "richness"; *S*) are shown in Table 4 below.

Table 4: Each site's number of visiting bucks (*S*), evenness value (*E*), and Shannon diversity index (*H*).

Site	*S*	*E*	*H*
1	13	0.924	2.37
2	29	0.885	2.98
3	31	0.911	3.13
4	31	0.894	3.07
5	39	0.868	3.18
7	47	0.888	3.42
8	41	0.870	3.23
9	45	0.891	3.39
32	24	0.843	2.68
Overall	129	0.906	4.403

Each value for *H* is plotted against the respective value for *E* in Figure 13.

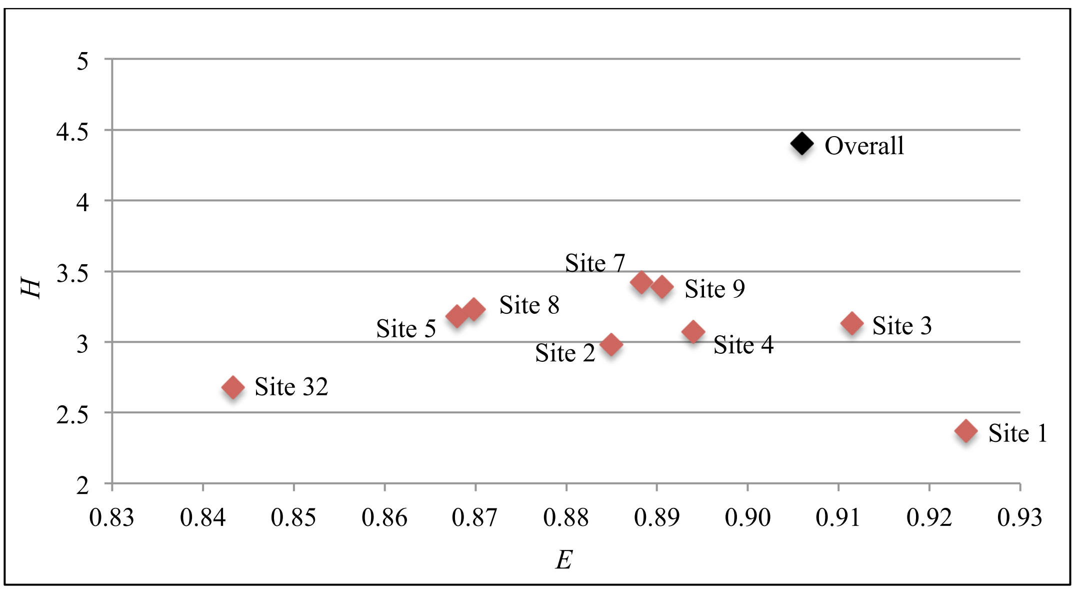

Figure 13: Sites' Shannon diversity indexes (*H*) plotted against their evenness values (*E*).

In Figure 14 below, each site's value for H is plotted against the number of individuals seen at that site (S).

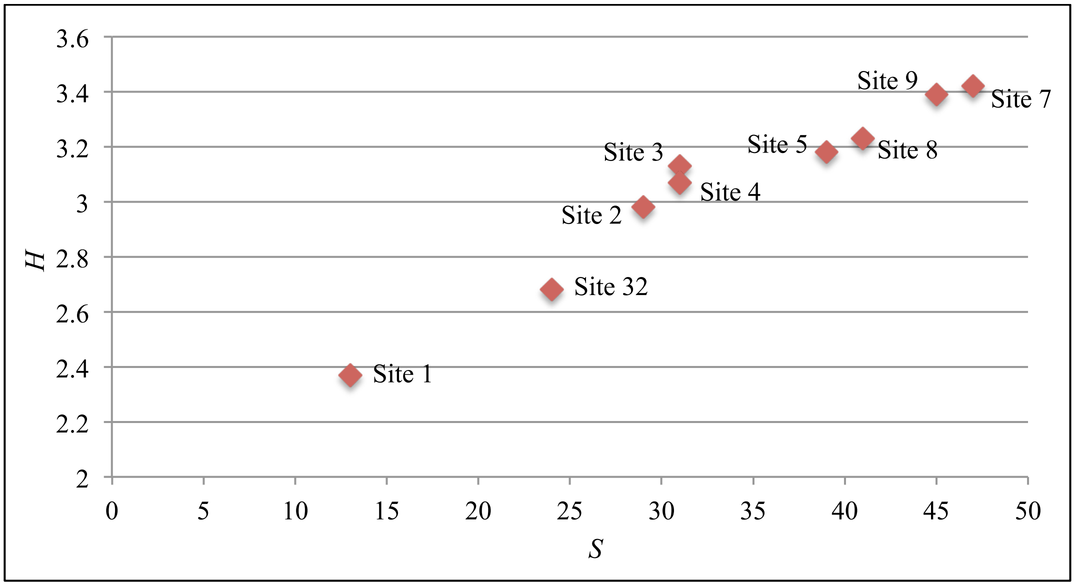

Figure 14: Sites' Shannon diversity indexes (H) plotted against their number of visiting bucks (S).

Evenness was also calculated for each site with attention paid only to dominant bucks' sightings (E_{dom}). Table 5 gives these values, as well as the number of dominant bucks seen at each site (S_{dom}).

Table 5: Each site's number of visiting dominant bucks (S_{dom}) and evenness value for dominant bucks (E_{dom}).

Site	S_{dom}	E_{dom}
1	2	1
2	2	0.9
3	4	0.938
4	2	0.994
5	2	0.485
7	3	0.804
8	3	0.904
9	4	0.824
32	4	0.908

The values for S_{dom} and E_{dom} from Table 5 are plotted against one another in Figure 15 below.

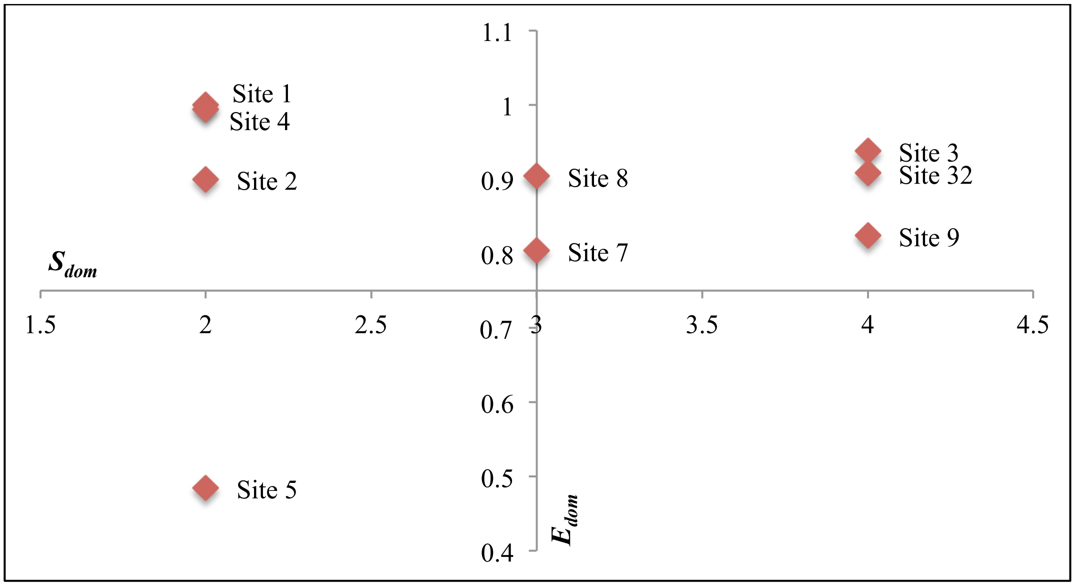

Figure 15: Sites' evenness values of visiting dominant bucks (E_{dom}) plotted against their numbers of visiting dominant bucks (S_{dom}).

EstimateS

The EstimateS filetype 1 analysis, in which the data were treated as though they were sample-based, applied to the entire study area's assemblage of bucks. Figure 16 is a graph of the extrapolation that predicted the total number of bucks we could expect to capture over the 5,200-acre study region. The 129 bucks that were identified are marked with a red vertical line; this shows the end of the collected data and the beginning of the EstimateS extrapolation. The extrapolation predicts what we could expect with triple the number of "samples" (i.e., camera sites). The results suggest that we would expect to photograph 164.93 different bucks if we had 27 camera sites across the study area. The dashed lines represent the 95% confidence interval of the extrapolation.

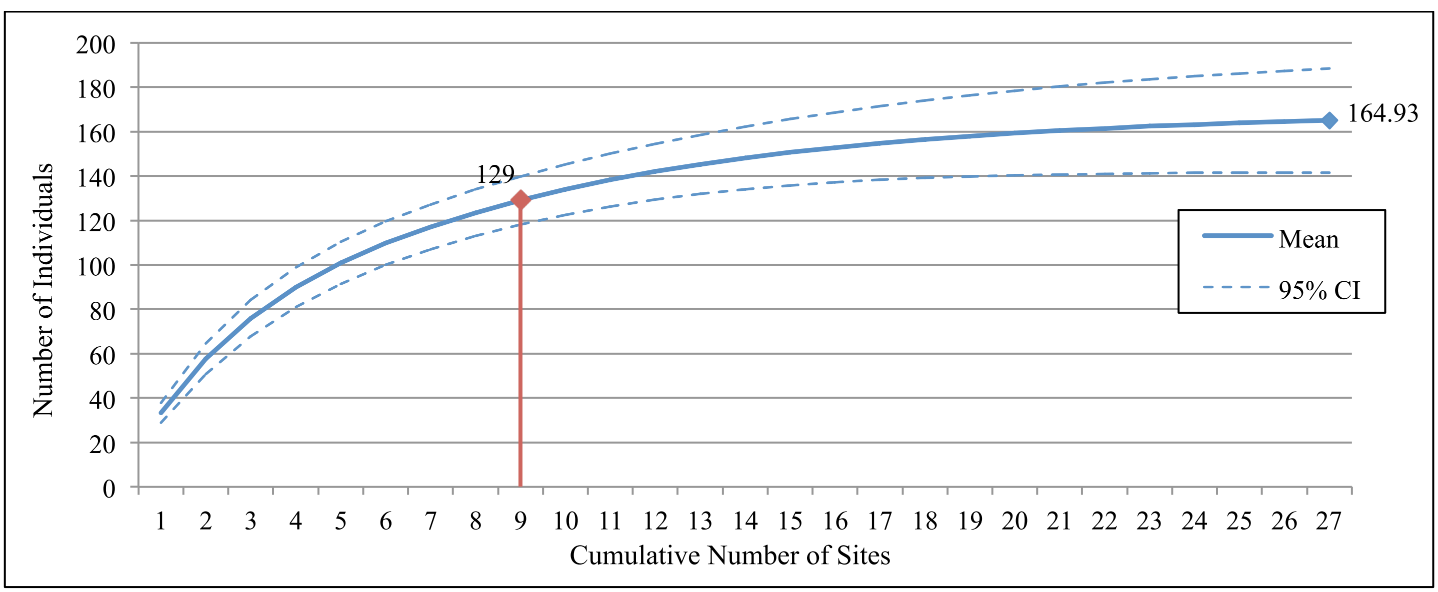

Figure 16: The filetype 1 triple extrapolation in EstimateS, predicting the number of bucks expected over the entire region's assemblage of deer. The red vertical line marks the end of the collected data (at the 129 bucks we identified) and the beginning of the extrapolation. It suggests we could expect to see 164.93 bucks over the study area. The dashed line demarks the 95% confidence interval along the extrapolation.

The filetype 4 analyses, in which the data were treated as though they were individual-based, are combined and displayed in Figure 17. These extrapolations were done to predict each camera site's assemblage, and the result for each site is labeled on its respective curve.

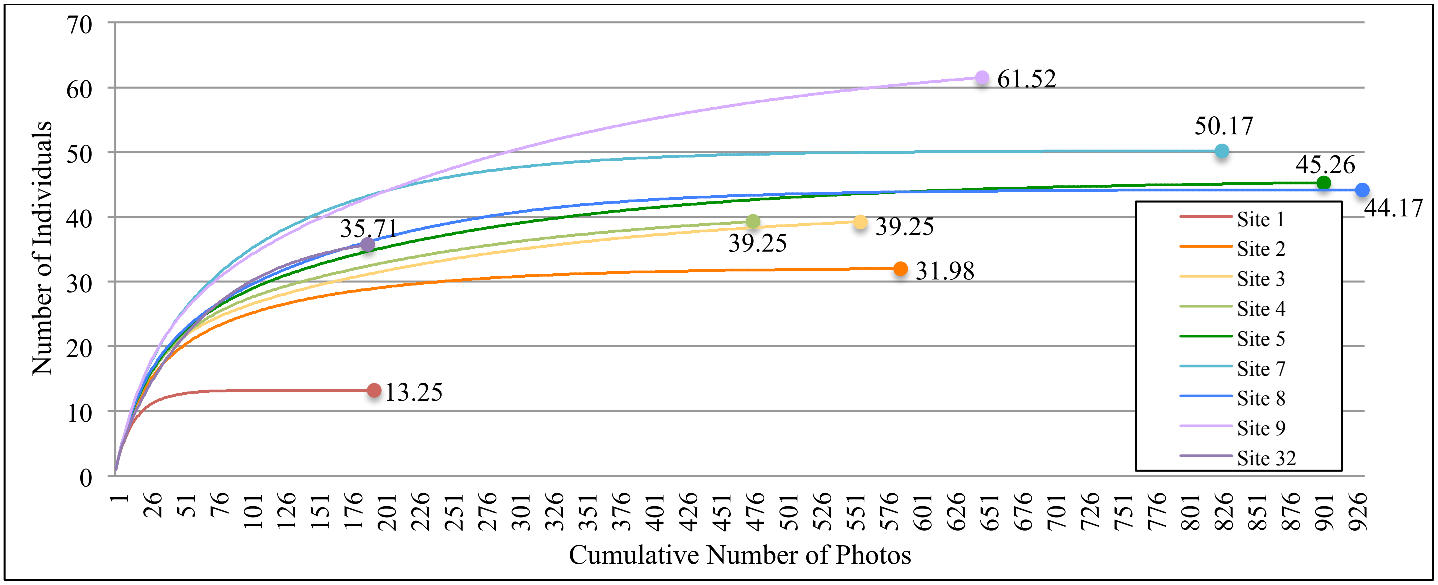

Figure 17: The filetype 4 triple extrapolations in EstimateS, predicting the number of bucks expected at each camera site. The final prediction for each site is labeled at the end of that site's curve.

Table 6 provides the Figure 10 results in written form. It gives the number of different bucks identified at each site, along with each site's predicted number of bucks after an EstimateS filetype 4 triple extrapolation.

Table 6: The number of different bucks observed at each camera site, along with the prediction from the EstimateS filetype 4 extrapolations of each site's expected number of bucks.

Site	Observed Number of Bucks	Predicted Number of Bucks
1	13	13.25
2	29	31.98
3	31	39.25
4	31	39.25
5	39	45.26
7	47	50.17
8	41	44.17
9	45	61.52
32	24	35.71

Discussion

Figure 6

As Table 2 and Figure 6 make clear, the camera at site 1 operated for a very short amount of time relative to the other sites' cameras. For this reason, it requires its own consideration for all of the analyses to follow, as both the volume and nature of the data that it collected were affected by its short window of operation.

Figure 6 suggests some relation between a camera's days of operation and the number of photos of bucks it captured. This relation, however, appears limited: sites 2, 4, 5, 7, 8, 9, and 32 all had operational time frames within 40 days (in length) of each other, but the number of bucks they photographed differed by nearly a factor of five (site 32 captured 63 photos of bucks; site 8 captured 311). This tells us that there is, in fact, a discrepancy in the number and combination of bucks who visited the various camera sites. If all sites had a homogenous set of bucks that visited locations at random, we would expect Figure 6 to show a linear relationship, as more photographing days would yield a larger collection of buck photos. As can be seen in the graph, however, the relation is not particularly linear.

Site 32 appears to have a limited number of visiting bucks. This is likely because it's dissimilar to the other sites in that it was an isolated scrape along a trail to a watering site, while the other cameras were located around food plots that attracted many deer. Additionally, the photo data for the other sites were actually lumped from multiple cameras around a single food plot, and this was not the case for site 32. In total, site 32 had a narrower area—and fewer resources—with which to attract visiting bucks.

Unlike site 32, site 8 seems to have an extensive collection of visitors. Also noteworthy, site 3 had the longest operational duration by a margin of nearly 30%, but it nevertheless had a middle-ranking number of visiting bucks. Interestingly, the manager of the ranch saw no large bucks at site 3 in the fall of 2015. This may have been because it was located in the core of buck 8's home range, and he was preventing other bucks from visiting. After that buck was killed in early January, dominant bucks 1, 4, and 6 all began showing up at site 3. This is strong evidence that certain dominant bucks are more monopolizing of sites and resources than other dominant bucks.

Additionally, all of this seems to hint at a disparity between the camera sites themselves, as the population of bucks go to the sites differentially.

Figure 7

As can be seen in Figure 7, the range of bucks' photo counts went from 62 to 1. There were quite a few bucks that did not get photographed many times (52 bucks were photographed five times or less; 69 bucks were photographed ten times or less).

The figure's red bars mark dominant bucks' photo counts; these ranged from 62—the maximum photo count of any buck—to 4. Buck 15 was the dominant individual with the fewest photographs. Aside from him, dominant bucks' average photo counts were higher than all bucks' photo counts: 28 for the former and 13.74 for the latter. Therefore, they were captured more frequently than the average individual, suggesting that they do visit scrapes more often than do their subordinates.

Figure 8

All camera sites had different combinations of visiting bucks. As Figure 8 and Table 3 point out, one commonality between all the sites is the fact that most visiting bucks were seen at a given site only a few times, while only a select few bucks were seen at that same location many times. This suggests that most bucks move around within their range enough to prevent them from visiting a single scrape more than a handful of times.

Dominant Bucks: Figures 9 – 12

Figure 9 gives us an understanding of where each dominant buck was most often spotted. Most striking is that buck 3 was photographed almost solely at site 5, while most other individuals are typically photographed at an array of sites. He was the most dominant buck in the whole area in terms of body size and antler allocation (Lawrence Gilbert, personal communication). Because he focused almost entirely on site 5, it's plausible that that location is the most desirable area to monopolize. It has both corn and protein feeders, along with a permanent water source nearby and a small, defendable food plot. Buck 3 evidently spent much time in combat with other bucks, as photos showed him with many inches of antlers broken off between early November and mid-December.

Some bucks seem to have strong preferences as to the sites that they visit; in these cases, they're more frequently photographed at one site than any other. Figure 9 doesn't appear to suggest that dominant bucks intensely avoid each other. On the contrary, it appears commonplace for a site to have two to four dominant bucks who drop by. However, temporal avoidance by dominant bucks is both possible and probable, though it was not explored in this study. This would provide an interesting premise for future research. Additionally, it is plausible that, for sufficiently large food plots (i.e., 200-300 meters wide), different dominant bucks control different segments of the plot. This is another consideration for future research.

A cursory glance at Figure 10 proves one basic yet crucial point: not all dominant bucks visit a given scrape with equal frequencies. Some were seen at a site many times, others not at all; dominants had a wide range of photo counts at many of the cameras. If a buck was seen with high frequency at a camera, it's probable that that site was located near the core of his home range. If a buck was seen with low frequency at a camera, the site was likely located on the fringe of his home range. And if a buck was never seen at a camera, his home range must not have extended to that site. These photo counts can therefore give an idea of the various home ranges of dominant individuals.

As mentioned previously, the temporal aspect of these data was not explored in this study; it would be interesting for future research to examine this. It seems possible that one dominant buck may create a scrape to communicate with and attract females, and then, when he is temporarily absent, other dominant bucks come by and poach desirable resources. If this is the case, the data would show one dominant buck being the primary resident at a site and, when he temporarily wanders elsewhere, other dominant bucks momentarily showing up there and leaving before the main buck comes back. All in all, it would show severe avoidance between certain dominant bucks.

Figures 11 and 12 delve further into the idea of dominant bucks having particular home ranges that coincide somewhat—but don't overlap entirely—with certain other dominant bucks' home ranges. It's clear than buck 1 (red) sticks to the north end of the region. He has considerable overlap with buck 6 (light blue), which seems to hint at the fact that these two dominants are particularly tolerant of one another. The ranges of bucks 4 (light green) and 8 (light purple) also overlap with those of bucks 1 and 6 in the center of the map, and that pair seems quite tolerant of each other as well. Buck 4's range also extends a bit toward the southwest, and in that area he encounters the ranges of bucks 5 (dark green) and 7 (dark blue), who seem tolerant of each other as well as him. Most solitary is buck 3 (yellow), who almost completely limits himself to the southwest site 5; only one other dominant—buck 2 (orange)—also shows up at site 5, and that is with little frequency compared to buck 3. Buck 2's range appears more centrally located to the southeast, at site 7. There he encounters the ranges of bucks 7 and 15 (dark purple). It is of note that buck 15's range is limited in both size (he is only seen at site 7) and frequency (his total photo count is only 4); this strongly suggests that the majority of his home range exists outside of the 5,200-acre region of interest, and that he traveled into the area via the fence gap.

The number of sites at which pairs of dominant bucks have overlapping ranges are counted in Figure 16 below.

Buck	1	2	3	4	5	6	7	8	15
1		0	0	2	0	4	0	2	0
2			1	0	0	0	1	0	1
3				1	0	0	1	1	0
4					1	2	2	3	0
5						0	2	0	0
6							0	2	0
7								1	1
8									0
15									

Figure 16: Counts of sites at which each pair of dominant bucks 1–8 and 15 co-occur.

As was mentioned earlier and Figure 16 points out, bucks 1 and 6 visit many of the same sites. In fact, all sites at which one was seen the other was also seen. This indicates a high level of tolerance—or temporal avoidance—between these two dominant bucks. Another pair with high tolerance (or temporal avoidance) towards one another seems to be bucks 4 and 8. In general, this all seems to suggest that a dominant buck has differential tolerances or avoidances towards other dominant bucks; some pairs of individuals have ranges that overlap significantly, while other pairs may never pass through the same location. It begs the question of whether these different tolerance or avoidance levels result *in* or are a result *of* home ranges being what they are. Does tolerance or avoidance between dominants stem from *needing* to be tolerant/avoidant because home ranges overlap, or do certain bucks' home ranges end up overlapping because that pair of bucks happened to be tolerant with or successfully avoidant of one another? This question would be an interesting point for future research to address.

Diversity Indexes: Figures 13 – 15

After calculating the Shannon diversity index (H) of each site, it was of interest to see whether evenness (E) or richness (S) played a larger role in determining sites' values of H. To investigate this, Figures 13 and 14 were constructed, each plotting either E or S (respectively) against H. As the figures show, S has a very strong correlation with H, and E much less so. This means that the number of bucks visiting a given site has much more to do with that site's Shannon diversity index than does the evenness with which those bucks visited the site. In fact, the correlation between S and H is so strong as to suggest that calculating H is practically pointless: a comparison based solely on sites' values of S results in almost exactly the same ranking as a comparison of sites' H values (with the exception of the two middle-ranking sites (3 and 4) being switched).

As mentioned in the discussion of Figure 6, site 1 cannot be analyzed with the rest of the cameras, since it was in operation for a much shorter time frame and therefore collected far less data. From Figure 14, and excluding site 1, it seems as though the sites that most bucks prefer can be determined: sites 5, 7, 8, and 9 are likely "hotspots" for bucks, while sites 2, 3, 4, and 32 are less so. This conclusion agrees with those from Figure 6, in which sites 5, 7, 8, and 9 appeared to be the most frequently visited spots for bucks.

Next, it was of interest to calculate sites' *S* and *E* values with respect to only dominant bucks; these new, tweaked variables were labeled S_{dom} and E_{dom}. Doing so would give further information to the understanding of how dominant individuals move over the study area and overlap in home ranges. The plot in Figure 15 can be generalized as having the structure shown in Figure 17 below.

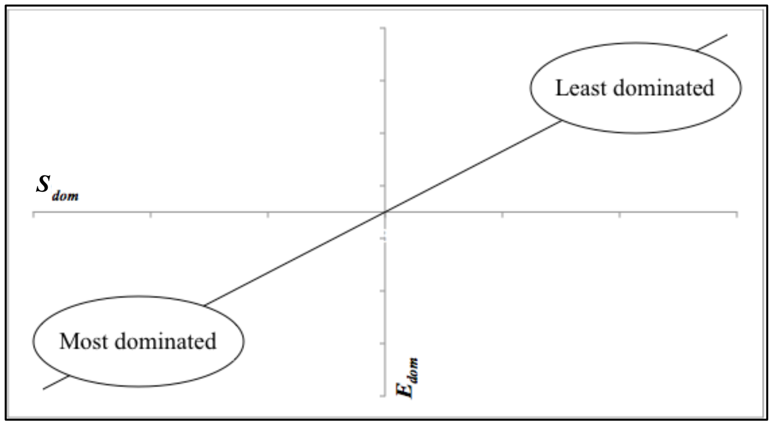

Figure 17: A generalized structure of Figure 15, in which sites' number of visiting dominant bucks are plotted against their evenness value for dominant bucks.

The location on the plot on which a site falls determines the degree of "dominance" occurring at that site, where dominance is defined as being greatest when very few individuals (i.e., one or two) have an uneven frequency of occurrence. In the most extreme case of dominance, a site would have a single individual being the only visitor and therefore completely monopolizing the resources that that site has to offer. In a less severe case, several individuals would visit a site more or less equally, and no single one would have a monopoly on the location.

With this general structure in mind, it's easy to draw some immediate conclusions from Figure 15. For one, site 5 is by far the most "dominated" of the camera sites; this idea is backed up by Figures 11 and 12, which demonstrated how site 5 is visited by only two dominant bucks, one of whom is much more frequent a visitor than the other. Figure 15 also puts sites 3, 9, and 32 into the "least dominated" region of Figure 17. These three sites all have four visiting dominant bucks, and none of those bucks contribute to more than 50% of all dominant visitations at any site. Therefore, those sites are much less monopolized than is site 5. Figure 15 appears to group the remaining five sites into two clusters: sites 1, 2, and 4; and sites 7 and 8. These five sites are somewhere in the middle of the "dominated" spectrum; they are monopolized neither a little nor a lot.

EstimateS: Figures 16 & 17

There was one assumption to be met for both the filetype 1 and filetype 4 analyses in EstimateS: the assumption of a closed community. We expect that this was sufficiently met. The only point of caution stems from the 0.75-mile unfenced length on the southwest border of the study area. It is possible that this opening served as a passage for bucks' dispersal into and out of the 5,200-acre region, which might have jeopardized the assumption of a closed community. That said, we believe that although there may have been a few individuals who came into the study area and a few who exited the study area during the months of data collection, those numbers likely cancel each other out. For this reason, we consider the closed community assumption to have been adequately met.

For the filetype 1 dataset, which was comprised of all sites' data, the observed total number of bucks was 129. After extrapolation, the predicted number of bucks across all sites was 164.93. However, because this particular analysis treated the data as sample-based, the validity of it must be called into question. There are a number of assumptions for sample-based data, and it is probable that these were largely violated. For one, the samples are assumed to be replicates of one another, and this was not the case with our data. Each "sample" (i.e., camera site) had its own unique assemblage of visiting bucks, so pooling the samples and treating them interchangeably is likely a flawed treatment of the data. Moreover, the samples are not taken randomly from the entire area's assemblage, and organization of the sites in space did affect the data collected at each. Consequently, bucks had unequal probabilities of being seen at each site (for instance, an individual being seen at one site had a higher probability of also being seen at a nearby site than a farther one). For these reasons, the filetype 1 analysis is probably largely unsound.

For the filetype 4 dataset, which treated each site as a separate sample, the predicted number of visiting bucks at each site varied considerably (see Table 3). This is further evidence that the assumptions for the filetype 1 analysis in EstimateS were violated—we would expect truly replicated samples to have approximately equal predictions for the number of visiting bucks at each site. Filetype 4 treated the data as though it were individual-based, and the relevant assumption was met: since each site was processed on its own, we can expect each site's local assemblage of bucks to be randomly mixed (i.e., every buck that visited a given site had an equal chance of walking in front of the camera and being photographed). As can be seen in Figure 10, some sites' extrapolation curves appear to reach an asymptote, while other sites' curves do not. These asymptotes represent the "true" number of bucks visiting each site.

The sites with extrapolation curves that fail to reach asymptotes may have needed more data (i.e., additional photos) to be extensive enough for robust statistical analyses. In fact, doing this kind of analysis—running an EstimateS extrapolation with filetype 4 data and checking for an asymptote—could be a method for future research; it would be a way to determine whether sufficient camera trap data has been collected in a study. In this study, it's likely that additional cameras around certain food plots (those that failed to reach accumulation asymptotes) would capture the necessary additional data for an asymptote to be reached. This is, of course, testable, and it's a possible direction for future research.

Acknowledgements

This work would not have been possible without the data from and help of Dr. Lawrence Gilbert. He was the chief identifier of bucks, and his initial data analysis and suggestions were instrumental in getting this project off the ground. I'd also like to acknowledge Dr. Lauren Ancel Meyers for her advice on methods and directions for data analysis, especially her salient suggestion to adapt and apply Shannon diversity indexes in this context. Finally, I'd like to thank Dr. Scott Hills for his invaluable work and input on numerous aspects of this study and report; he guided me more times than I can count.

References

Beals, M. (2000). Diversity Indices: Shannon's *H* and *E*. *Alternative Routes to Quantitative Literacy for the Life Sciences*. Available at: http://www.tiem.utk.edu/~gross/bioed/bealsmodules/shannondi.html. Last accessed 18 July 2016.

Colwell, R.K. (1994–2016). EstimateS 9. *EstimateS: Statistical Estimation of Species Richness and Shared Species from Samples*. Available at: http://purl.oclc.org/estimates.

Colwell, R.K. (2013). EstimateS 9.1.0 user's guide. *EstimateS: Statistical Estimation of Species Richness and Shared Species from Samples*. Available at: http://viceroy.eeb.uconn.edu/estimates/EstimateSPages/EstSUsersGuide/EstimateSUsersGuide.htm.

Colwell, R.K., Mao, C.X. & Chang, J. (2004). Interpolating, extrapolating, and comparing incidence-based species accumulation curves. *Ecology*, 85, 2717–2727.

Côté, S.D. (2011). Impacts on ecosystems. In: *Biology and Management of White-tailed Deer* (ed. Hewitt, D.G.). CRC Press, Boca Raton, Florida, pp. 379–398.

Curtis, P.D., Boldgiv, B., Mattison, P.M. & Boulanger, J.R. (2009). Estimating deer abundance in suburban areas with infrared-triggered cameras. *Human–Wildlife Interactions*, 3, 116–128.

Donohue, R.N., Hewitt, D.G., Fulbright, T.E., Deyoung, C.A., Litt, A.R. & Draeger, D.A. (2013). Aggressive behavior of white-tailed deer at concentrated food sites as affected by population density. *Journal of Wildlife Management*, 77, 1401–1408.

Gotelli, N.J. & Colwell, R.K. (2011). Estimating species richness. In: *Biological Diversity: Frontiers in Measurement and Assessment* (eds. Magurran, A.E. & McGill, B.J.). Oxford University Press, New York, pp. 39–54.

Hewitt, D.G., Hellickson, M.W., Lewis, J.S., Wester, D.B. & Bryant, F.C. (2014). Age-related patterns of antler development in free-ranging white-tailed deer. *Journal of Wildlife Management*, 78, 976–984.

Hansen, L. (2011). Extensive management. In: *Biology and Management of White-tailed Deer* (ed. Hewitt, D.G.). CRC Press, Boca Raton, Florida, pp. 409–451.

Jacobson, H.A., Kroll, J.C., Browning, R.W., Koerth, B.H. & Conway, M.H. (1997). Infrared-triggered cameras for censusing white-tailed deer. *Wildlife Society Bulletin*, 25, 547–556.

Karanth, K.U. (1995). Estimating tiger *Panthera tigris* populations from camera-trap data using capture-recapture models. *Biological Conservation*, 71, 333–338.

Kile, T.L & Marchinton, R.L. (1977). White-tailed deer rubs and scrapes: spatial, temporal and physical characteristics and social role. *American Midland Naturalist*, 97, 257–266.

Koerth, B.H., McKown, C.D. & Kroll, J.C. (1997). Infrared-triggered camera versus helicopter counts of white-tailed deer. *Wildlife Society Bulletin*, 25, 557–562.

Lloyd, M. & Ghelardi, R.J. (1964). A table for calculating the `equitability' component of species diversity. *Journal of Animal Ecology*, 33, 217–225.

Magurran, A.E. (2007). Species abundance distributions over time. *Ecology Letters*, 10, 347–354.

Marchinton, R.L. & Hirth D.H. (1984). Behavior. In: *White-tailed Deer: Ecology and Management* (ed. Halls, L.K.). Stackpole Books, Harrisburg, Pennsylvania, pp. 129–168.

Miller, K.V., Marchinton, R.L., Forand, K.J. & Johansen, K.L. (1987). Dominance, testosterone levels, and scraping activity in a captive herd of white-tailed deer. *Journal of Mammalogy*, 68, 812–817.

Picasa. (2016). *Wikipedia*. Available at: https://en.wikipedia.org/wiki/picasa. Last accessed 3 July 2016.

Rowcliffe, J.M., Field, J., Turvey, S.T. & Carbone, C. (2008). Estimating animal density using camera traps without the need for individual recognition. *Journal of Applied Ecology*, 45, 1228–1236.

Whittaker, R.H. (1972). Evolution and measurement of species diversity. *Taxon*, 21, 213–251.