

**Factors Influencing Reproductive Success and Camera Survey Efficiency of
White-tailed Deer**

by

Peter Kendrick Acker

A thesis submitted to the Graduate Faculty of
Auburn University
in partial fulfillment of the
requirements for the Degree of
Master of Science

Auburn, Alabama
August 3, 2013

Keywords: breeding success, camera survey, reproductive success, white-tailed deer

Copyright 2013 by Peter Kendrick Acker

Approved by

Stephen S. Ditchkoff, Chair, Ireland Professor of Wildlife Sciences
Todd D. Steury, Associate Professor of Wildlife Sciences
Mark D. Smith, Associate Professor of Wildlife Sciences

Abstract

This study was two-fold, and was conducted on a 174-ha fenced enclosure. First, we examined reproductive success of male white-tailed deer (*Odocoileus virginianus*), where recent research has begun to shed light on the fact that younger, smaller, subdominant males regularly participate in breeding. Through genetic herd reconstruction, we examined factors that influenced reproductive success. Between August 2008 and September 2012, we captured a total of 138 individual deer and used microsatellite analysis to assign paternities. We assigned 78 paternities at the 95% confidence level and an additional 26 at 80% confidence with program CERVUS. Using a Poisson regression model, we found that age, antler size, and body size were all associated positively with number of fawns sired. Certain body and antler measurements proved to be better predictors of breeding success than others. We also found that the impact of age on male breeding success was influenced by male age structure, where the relative importance of an increase in sire age decreased as male age structure increased.

Secondly, we examined methods for increasing efficiency of camera surveys for white-tailed deer. During September and October 2010 we completed 2, 7-day camera surveys after a 5-day pre-bait period to compare the efficacy of a camera set on a 10-minute-delay placed beside one with a 5-minute-delay. Then during September 2011, we surveyed for 15 days to examine the necessity of prebaiting. We suggest that increases in the delay period of an infrared-triggered camera can reduce the number of images, and

thus processing labor, without negatively impacting the number of different individuals detected; however, elimination of a pre-baiting period may negatively influence the efficacy of camera surveys.

Acknowledgments

I am grateful to Dr. Steve Ditchkoff for allowing me the opportunity to take on this project, and for being available to answer questions, evaluate ideas, and provide input and support. I am also thankful to Dr. Todd Steury for his assistance, especially in the realm of statistics, and to Dr. Mark Smith for his editing input as well. I appreciate the sources of funding for this project: the Center for Forest Sustainability at Auburn University, Code Blue Scents/EBSCO Industries, and SouthFresh Feeds, as well as a large group of individuals who provided private support during the study.

The contributions of Chad Newbolt cannot be overstated – both in the field and in the office. Thanks also to Tim Neuman and Stephanie Irvin, and to the dozens of undergraduate volunteers who willingly helped with darting efforts.

Lastly, my family has been a source of incredible support and love throughout this process. My wife, Sally, puts up with night and weekend field work on a regular basis and is always encouraging. The positive influence of my wonderful parents has made this all possible. I am thankful to you all.

Table of Contents

Abstract.....	ii
Acknowledgments.....	iv
List of Figures.....	vii
List of Tables.....	viii
Chapter I: Age, Antler and Body Size Influence Breeding Success of Adult, Male White-tailed Deer.....	1
Abstract.....	1
Introduction.....	2
Study Area.....	5
Methods.....	6
Capture.....	6
Handling.....	7
Fawn Capture and Handling.....	8
Statistics and Genetic Analysis.....	9
Results.....	11
Discussion.....	13
Literature Cited.....	20
Chapter II: Seeking Improved Efficiency of Camera Survey Techniques for White-tailed Deer.....	35
Abstract.....	35
Introduction.....	36

Study Area	38
Methods.....	39
Trigger Delay	39
Prebaiting	40
Results.....	42
Trigger Delay	42
Prebaiting	42
Discussion.....	44
Trigger Delay	44
Prebaiting	47
Literature Cited	49

List of Figures

Figure 2.1. Cumulative number of unique individuals identified per infrared-triggered trail camera for 5- and 10-minute trigger delays by survey day inside a 174-ha fenced enclosure in Camp Hill, AL during September 20 - 26, 2010	54
Figure 2.2. Cumulative number of unique individuals identified per infrared-triggered trail camera for 5- and 10-minute trigger delays by survey day inside a 174-ha fenced enclosure in Camp Hill, AL during October 4 - 10, 2010.....	55

List of Tables

Table 1.1. Percentage of fawns sired by sire age class inside a 174-ha fenced enclosure in Camp Hill, AL from 2008 - 2012	28
Table 1.2. Number of males by age class in 174-ha a fenced enclosure in Camp Hill, AL from 2008 - 2012	29
Table 1.3. Loadings for Principle Components Analysis on relationship between sire age, body length, and gross Boone and Crockett (B&C) score in white-tailed deer in a 174-ha fenced enclosure in Camp Hill, AL from 2008 - 2012	30
Table 1.4. Factors influencing number of fawns sired by male white-tailed deer in a 174-ha fenced enclosure in Camp Hill, AL from 2008 - 2012	31
Table 1.5. Factors influencing number of fawns sired by male white-tailed deer after accounting for the mean age of the male population in a given year, in a 174-ha fenced enclosure in Camp Hill, AL from 2008 - 2012	32
Table 1.6. AIC values for various models tested, along with the change in AIC from the best model	33
Table 2.1. Results of 2, 7-day trail camera surveys between 20 September - 10 October 2010, including number of deer captured and identified with both 5- and 10-minute trigger delays inside a 174-ha fenced enclosure in Camp Hill, AL	53

**Chapter I: Age, Antler and Body Size Influence Breeding Success of Adult, Male
White-tailed Deer**

ABSTRACT

White-tailed deer (*Odocoileus virginianus*) herds have a social order of male dominance theorized to be associated with reproductive success, and tradition holds that more dominant males are more successful breeders. However, recent research has begun to shed light on the fact that younger, smaller, subdominant males also participate in breeding to a greater degree than was originally believed. Through genetic herd reconstruction, we examined factors that influenced reproduction in a white-tailed deer herd enclosed in a 174-hectare high fence research facility. Between August 2008 and September 2012, we captured 138 individual deer and used microsatellite analysis to assign paternities. We assigned 78 paternities at the 95% confidence level and an additional 26 at 80% confidence with program CERVUS. Using a Poisson regression model, we found antler size, antler characteristics, and body size characteristics that were all associated positively with male breeding success; however, certain body and antler measurements proved to be better predictors of breeding success than other factors tested. The impact of age on male breeding success interacted with male age structure, where the relative importance of an increase in sire age decreased as male age structure increased. We examined and found no relationships between breeding success and relative antler symmetry. These data indicate that a multitude of variables influence male breeding

success in white-tailed deer, and broaden our comprehension of the species' reproductive ecology.

INTRODUCTION

In polygynous mammals, theories of sexual selection suggest that females who invest considerable resources in reproduction (e.g., gestation and lactation) will reap fitness benefits by being selective during mate selection (Andersson 1994). In contrast, males have little investment in reproduction (sperm production requires very little resources) once a mating opportunity has been acquired and should work to maximize the number of reproductive opportunities regardless of the quality of their potential mates (Darwin 1871). Because of these cost differentials, males invest resources in a manner that will make them successful competitors for mates. This concept is true for polygynous species, where tradition holds that males with greater body mass and more elaborate and symmetrical secondary sexual characteristics, along with greater age, accrue greater reproductive success (Andersson 1994). Male adult body mass has repeatedly been associated positively with reproductive success in numerous species (Northern elephant seal, *Mirounga angustirostris*: Haley 1994; Fallow deer, *Dama dama*: McElligott et al. 2001; Soay sheep, *Ovis aries*: Preston et al. 2003), as has amount of ornamentation (*Ovis* spp.: Geist 1971; Soay sheep, Preston et al. 2003; black-capped chickadee, *Poecile atricapillus*: Doucet et al. 2004), sire age (song sparrow, *Melospiza melodia*: Nol and Smith 1987; African elephants, *Loxodonta africana*, Poole 1989; brown bear, *Ursus arctos*: Zedrosser et al. 2007), and symmetry of secondary sexual characteristics (swallow, *Hirundo rustica*: Møller 1992;).

Within the Cervidae, seminal research on red deer (*Cervus elaphus*) has similarly shown that the most reproductively successful males are those that are older (until senescence) and have greater body and antler mass (Clutton-Brock et al. 1982). Much of this is attributed to effects of age and body and antler mass on fighting ability, the successful outcomes of which are thought to then confer greater reproductive success (Clutton-Brock et al. 1979). Of note however is that the red deer breeding strategy is one of harem defense, where a dominant male will tend, mate with, and defend a group of females, which can allow dominant stags a very high proportion of breeding opportunities. In one study, researchers saw sub-adult stags breed very little and only around half of the stags over four years of age breed successfully (Gibson and Guinness 1980).

These positive relationships between age, body mass, and antler size are also what one would expect to find in white-tailed deer (*Odocoileus virginianus*), where white-tailed deer utilize a mate-guarding, or tending bond, mating system in which a male will remain with an estrous female for a period of time, similar to the domestic cat (*Felis catus*; Say et al. 2001), chimpanzee (*Pan troglodytes*; Watts 1998), and kudu (*Tragelaphus strepsiceros*; Owen-Smith 1984). In one study of a simulated wild environment, Sorin (2004) found that male age was associated positively with both the number of females with which a male produced offspring and the number of offspring produced. DeYoung et al. (2009) showed that wild males ≥ 3.5 years sired 70, 67, and 32% of offspring on study sites where those same males comprised 57, 30, and 19% of the populations, respectively. In a captive setting, data from DeYoung et al. (2006) seem

to indicate that body mass also plays a role in reproductive success in captive white-tailed deer.

Although red deer and white-tailed deer are both members of Cervidae, paternity studies in white-tailed deer (Sorin 2004; DeYoung et al. 2006; DeYoung et al. 2009) reveal sizeable disparity in the ability to which a dominant male is able to monopolize breeding opportunities versus red deer (Gibson and Guinness 1980; Clutton-Brock et al. 1982, 1988). In red deer, subadult males rarely produce offspring, and nearly half of all mature males >4 years did not reproduce (Gibson and Guinness 1980). In white-tailed deer, however, this was not the case in recent studies that found no substantiation for a small number of older males controlling breeding (DeYoung et al. 2009), even in captive populations (DeYoung et al. 2006). Harem-defense is not thought to be an optimal strategy in the dense cover that white-tailed deer prefer (Demarais et al. 2000), so in white-tailed deer a male will single out one estrous female and tend to her individually for an extended period of time, potentially allowing less dominant males breeding opportunities if other estrous females are present in the area. Most females in temperate populations coming into estrous within 2-4 weeks of one another (Marchinton and Hirth 1984) should exacerbate this situation: synchronization of estrous cycles reduces both male-male sexual competition and the number of potential sires per female (Emlen and Oring 1977). If this is the case, one would expect to see more sub-dominant (younger, and/or smaller body mass, and/or smaller antlered) white-tailed males obtain breeding opportunities than is the case for red deer, especially during the peak of the breeding season. Evolutionarily, this broader male breeding population should confer greater genetic diversity, an advantage in a changing landscape.

Considering the paucity of information regarding some of the factors that influence breeding success in adult, male white-tailed deer, we set out to improve our understanding of this subject. We conducted our study in a 174-ha captive research facility that simulated free-ranging behavior, and allowed us to obtain detailed information on nearly 90% of individuals in the population. Our specific objectives were to examine: (1) factors that influence reproductive success of male white-tailed deer, including age, body size, and antler characteristics; and (2) the extent to which these characteristics allow individual, dominant deer to monopolize breeding opportunities. We define reproductive success as the number of fawns sired.

STUDY AREA

This study took place at the Auburn University Deer Lab in Camp Hill, AL, USA; a 174-ha deer enclosure bounded by 2.6-m, deer-proof fencing. The vegetation was approximately 40% open hay fields, with the balance in oak (*Quercus* spp.)-hickory (*Carya* spp.) hardwoods and planted loblolly pine (*Pinus taeda*) stands of varying age. Elevation ranged from approximately 190 to 225 m above sea level. This facility was constructed in 2007 and enclosed local, wild deer, the descendants of which form the current study population.

Three protein-pellet feeders supplemented the deer's diet year-round with free choice "Deer Feed", an extruded 18% protein product (SouthFresh Feeds, Demopolis, AL) that was available ad libitum. Three timed, corn feeders were also in operation on the site when researchers were actively darting deer for capture as part of this and other research (approx. September – June). Two, 0.8-ha food plots were planted within the

facility, in addition to a 0.8-ha food-plot/capture facility, gated and high-fenced with a deer working area attached. Annual 14-day camera surveys each February provided population estimates between 68-108 individuals inside the facility over the survey period (261.98 – 416.08 deer/sq mi, respectively), with 86.76% of all deer tagged as of February 2012. Buck:doe ratios ranged from 1:2 in 2007, to 1.5:1 in 2012. During the summer, daily low- and high-temperature means were 21° C and 32° C respectively.

METHODS

Capture

Each year, our goal was to capture every individual within the facility, in order to keep records on antler and body size updated. We used 2 methods for this; we used a 0.8-ha fenced capture facility within the Deer Lab which served to attract deer through open gates, at which time we manually closed them inside, coaxed them to funnel into a walled hallway, and then individually separated them into covered working boxes. Once segregated, we then sedated the deer. We also captured deer using dart rifles powered by .22 blanks and equipped with night vision scopes, firing 2.0 CC darts each equipped with a VHF transmitter (Pneu-Dart Inc, Williamsport, PA). Darting took place in the evening from tree stands situated over sites baited with whole corn or protein pellets, the two most effective baits for white-tailed deer, according to Koerth and Kroll (2000). We sedated all deer for data collection with a combination of Telazol (125 mg/mL) and Xylazine (100 mg/mL), which we later reversed with an intramuscular injection of Tolazine (100 mg/mL). Our strategy was to dart males in the fall and winter once antlers hardened and we could obtain accurate and consistent antler measurements. Following the breeding

season, between 10 February - 10 July 2010, 2011, and 2012, we captured pregnant females of at least 1.5 years of age and inserted Vaginal Implant Transmitters (M3930, Advanced Telemetry Systems, Isanti, MN) to allow us to capture newborn fawns. We waited until fawns were at least 6 months of age before attempting to capture them if they were not captured as neonates. These methods were part of Institutional Animal Care and Use Committee at Auburn University's approved protocols (2008-1241, 1010-1785), and followed the American Society of Mammalogists' guidelines (Sikes et al. 2011).

Handling

Once sedated, we measured all deer with a flexible vinyl measuring tape for gross non-typical Boone and Crockett (B&C) antler score (where applicable; Boone and Crockett Club 1997), skull length, total body length, tail length, right hind-foot length and chest circumference. The B&C scoring system measures the length of each tine and main beam and 4 mass measurements for each antler, and inside spread. We utilized gross score only, and did not incorporate deductions for asymmetry as is common in calculating a net B&C score. Skull measurements were from the tip of the nose to the posterior end of the sagittal crest; body length from the tip of the nose to the base of the tail dorsally hugging the skull and spine; tail length from the base of the tail dorsally to the end of the tail bone; and hind foot length from the tip of the hoof to the posterior end of the tuber calcis, as in Ditchkoff et al. (2001a). We measured chest circumference immediately posterior to the front legs. All body measurements were recorded to the nearest 0.1 cm. Fluctuating asymmetry of antlers was calculated as the difference in gross score between right and left antlers divided by the larger antler, as in Ditchkoff et al. (2001b). We evaluated tooth wear and replacement to estimate age of captured deer

(Severinghaus 1949); however, many deer in our population were captured as fawns and thus were of known age. All potentially bilateral measurements (basal circumference, beam length, hind foot length) were conducted on the animal's right side. In addition, we collected a tissue sample with an ear notch to later test for parentage. We assigned each deer a unique number according to single digit birth year followed by the ordinal number of deer captured from that birth year (e.g., deer 819 was born in 2008, and was the 19th deer caught from that birth year). After shaving appropriate areas in the hide with hair clippers and then a razor and shaving cream, we freeze branded the number onto the deer; birth year on the front quarter and ordinal number on the rear quarter. We also wrote the number on plastic cattle ear tags, and placed one in each ear along with an individual electronic ID in the right ear.

We inserted vaginal implant transmitters (VITs) approximately 20 cm into the vaginal canal of pregnant females with silicone wings pressed against the cervix. We monitored VITs at least once per week for functionality until 10 July. At that point we increased monitoring efforts in advance of predicted fawn drop, when we checked transmitters three or more times daily in anticipation of fawning, until the does expelled all VITs (Saalfeld and Ditchkoff 2007; Jackson and Ditchkoff 2013).

Fawn Capture and Handling

Upon expulsion, we located VITs and searched for fawns between 2 and 8 hours after birth. Using the transmitter's event timer code, we calculated time of birth to within 30 minutes. Upon following the VHF signal to the general location of the transmitter, we located the doe and searched in her previous vicinity to find any fawns that had been moved from the birth site. Failing that, we proceeded to the transmitter and began

searching in concentric, widening circles until spotting the fawn. A thermal imaging camera (Raytheon Palm IR 250D, Waltham, MA) was used in locating the fawn. Once captured, we weighed and sexed the fawn, and collected a tissue sample from an ear notch. We placed small plastic eartags in each ear for identification, and attempted to handle fawns as briefly and efficiently as possible to minimize trauma. According to Carstensen Powell et al. (2005), handling should have little to no effect on fawn survival, including marking-induced abandonment.

Statistics and Genetic Analysis

DNA Solutions, Inc. (Oklahoma City, Oklahoma) carried out the genetic work using microsatellite analysis of 12 loci (Cervid1, BM6506, N, INRA011, BM6438, O, BL25, K, Q, D, OarFCB193, and P) found in Anderson et al. (2002) and 2 loci (L and S) from Meredith et al. (2005). Ear notch tissue samples were lysed (Qiagen cell lysis solution, 1 μ M DTT, and 41 μ g/ml Proteinase K) overnight at 57 °C. DNA was extracted following Qiagen QIAextractor protocols (Qiagen Inc., Valencia, California). With the Qiagility liquid handling robot, 1 μ l of the purified DNA (~40ng) was amplified in a 10 μ l reaction containing 1x Qiagen multiplex PCR master mix (hot start taq polymerase, MgCl₂, and PCR buffer) and 1x primer master mix 1 or 2. Primer master mix 1 contained forward and reverse primers for loci Cervid 1, INRA011, BM6506, L, N, Q, and S. Primer master mix 2 contained forward and reverse primers for loci OARFCB193, BM6438, BL25, O, P, K, and D. An ABI 9700 thermalcycler then generated allele fragments for identification with the profile as follows: one cycle of 95° for 12 min followed by 35 cycles of 95° for 0.5 min, 54° for 1.5 min, and 72° for 1 min, and finally a cycle of 60° for 30 min. Formamide was used to prepare PCR amplified products, which

were then electrophoresed using an AB 3130XL (Applied Biosystems, Foster City, California). Genemapper 4.0 (Applied Biosystems) was used to collect and analyze the data. Visual inspection of electropherogram traces confirmed all allele calls.

We used Cervus 3.0 (Kalinowski et al. 2007) to assign paternity through the use of likelihood ratios to the 80% level as in DeYoung et al. (2009). We then compared Akaike's Information Criterion (AIC) of poisson regression values from statistical program R (R Development Core Team 2010) to compare relationships between male reproductive success with number of fawns sired as the response variable as a function of our morphometric measurements and age. Because we had variation in the number of data points per individual, we used the effect of individual sire as a random effect in all models. Antler measurements were included if they were collected on the hardened, fully-developed antlers the deer carried during the breeding season, and skeletal measurements were included if they were collected within +/- 4 months of the breeding season. Owing to the changing age structure of the population, especially in the first several years since establishment of the facility, we also analyzed relationships relative to mean age of the male population of the given year. We realized that many of our tested characteristics would be collinear because body mass and antler size are commonly correlated with age. To test for this, we ran a simple regression in R and analyzed the variance inflation factors (VIF) between sire age and 8 morphometric variables (gross B&C score, inside spread, beam length, basal circumference, chest girth, hind foot length, skull length, and body length). To further tease apart effects of collinearity, we chose sire age, gross B&C score, and body length on which to run a standardized Principal

Components Analysis (PCA), then analyzed scores to examine any correlation with reproductive success.

RESULTS

From all individuals captured and genetically sampled from 2008 - 2012 ($n = 138$), we were able to assign 104 paternities (75.4%) to known male sires with at least 80% confidence. Overall, we had 28.5% (SE = 0.071; Table 1.1) of fawns sired by males ≤ 1.5 yrs and 42.5% (SE = 0.083) by males ≤ 2.5 yrs. Mean age of the male population increased each year from 1.3 years of age (SE = 0.269) in 2008 to 2.9 years of age (SE = 0.139) in 2012 (Table 1.2). We inserted 17, 10, and 12 VITs into pregnant does during 2010, 2011, and 2012, respectively. We captured 15, 5, and 10 neonatal fawns during those years, respectively. Preliminary data from VHF collars ($n = 11$) indicated a low (9.1%) incidence of predation, while 2 fawns died from abandonment (18.2%).

Of the 104 paternities we were able to assign, 54 had associated antler and body measurements because the males were captured during the year they sired an offspring, and we were able to collect morphometric data for that year. No factors were reliable predictors of breeding success ($P > 0.05$) in the global model (fawns sired as a function of age and our 8 morphometric variables), presumably due to high collinearity among variables that resulted in inflated variances. Variance inflation factors ranged from 1.84 - 24.65 ($\bar{x} = 9.64$). The results of our PCA indicated in the first component (PC1; Table 1.3) that larger-bodied, older, larger-antlered deer sired a greater number of offspring than younger, smaller males ($\beta = -0.182$; $P = 0.013$). After accounting for a given age,

body length, and antler score, individuals with a greater ratio of age:body length reproduced more (PC2; $\beta = 0.453$; $P = 0.014$).

Poisson regression indicated positive relationships ($P < 0.05$) between fawns sired and the following characteristics when modeled individually: B&C score, inside spread, chest girth, hind foot length, skull length, basal circumference, and body length (Table 1.4). Tests on fluctuating asymmetry suggested that relative score difference was not associated with breeding success ($P = 0.730$). Beam length had a marginal, positive relationship with breeding success ($P = 0.051$), but age was not associated with breeding success when modeled individually ($P = 0.758$). Owing to collinearity among many of our tested factors, we chose to use mean age in a given year as the one covariate to include in other models that would account for the male age structure maturing over time. When we examined the same age, antler, and body characteristics with respect to the mean male age in a given year, we found that all variables except fluctuating asymmetry were associated positively with number of fawns sired ($P < 0.001$; Table 1.5). We also saw a significant interaction between sire age and the mean male age of the population that year ($P = 0.005$).

Of all of the single measurable variables tested alone, antler measurements (e.g., gross B&C score, beam length, basal circumference, and inside spread) seemed to be the best predictors of breeding success, as evidenced by the lowest AIC values for their corresponding models (77.10, 78.29, 78.36, and 79.00 respectively; Table 1.6). The lowest AIC value for single variables with respect to the mean age of the male population's in a given year suggests that B&C score may be the best predictor tested of this category (62.18). Including mean age also improved AIC values of mixed models

and we found that our overall best predictor of breeding success incorporated age, gross B&C score, and mean age (AIC = 61.25). Models of body length, B&C score, sire age, and mean age (AIC = 62.93); and body length, B&C score, and mean age (AIC = 63.58) were also among the best tested.

DISCUSSION

Sire age was not a reliable predictor of breeding success as a lone variable in the model and we attribute this to the changing age structure of the population. Owing to an immature age structure at the outset of this study and the high survival rate in the population, mean age of males increased during each year. In 2008, 1.5-year-old males accounted for a very high percentage (44.0%) of fawns sired. This was to be expected, considering there were only 2 males ≥ 3.5 years of age. However, 1.5-year-old males only accounted for <13% of fawns sired in each of the following years. As expected, when we accounted for mean age of males in any given year, age became a significant positive predictor of number of fawns sired, and we saw an interaction between sire age and mean age. As demonstrated elsewhere, when mature males are present in a population they tend to sire more offspring than younger males (DeYoung et al. 2002; Sorin 2004; DeYoung et al. 2006; DeYoung et al. 2009). This falls into line with red deer research (Clutton-Brock et al. 1979; Gibson and Guinness 1980) and other species (Zedrosser et al. 2007).

Antler size, in terms of basal circumference, main beam length, inside spread, and gross B&C score, was associated positively with number of fawns sired. Antlers have been predicted to be an honest indicator of genetic quality in white-tailed deer (Ditchkoff

et al. 2001a) and previous research regarding amount of ornamentation has demonstrated that older, larger, more ornamented red deer are more dominant and responsible for most of the breeding (Clutton-Brock et al. 1982; Kruuk et al. 2002). Amount of ornamentation has also been demonstrated to have a positive effect on reproductive success in Soay sheep (Preston et al. 2003). Our best single predictors of breeding success were also antler-related: gross B&C score, an accepted method of quantifying antler mass (Ditchkoff et al. 2001b), was the best single predictor of fawns sired. This further supports previous research suggesting that antler mass in red deer was positively related to reproductive success (Clutton-Brock et al. 1982) and an indicator of sperm production and quality (Malo et al. 2005).

Multiple individual measurements of body size were positive predictors of breeding success: skull length, body length, chest girth, and hind foot length. Body size has been shown to positively influence reproductive success via intrasexual competition by allowing greater access to females, or resources, or both (Andersson 1994). A positive effect of body size on reproductive success was expected and is similar to traditional theory and what prior studies have seen in other vertebrate species, such as sockeye salmon (*Oncorhynchus nerka*; Quinn and Foote 1994), adders (*Vipera berus*; Madsen et al. 1993), and savanna baboons (*Papio cynocephalus*; Berkovitch 1989). This has been similarly demonstrated in other cervids (red deer, Clutton-Brock et al. 1982) and specifically white-tailed deer, where in captivity, DeYoung et al. (2006) reported that the heaviest male in each pen was dominant for at least some of the breeding season.

Fluctuating asymmetry of antlers is a physical characteristic that has the potential to be associated with breeding success in male white-tailed deer. The importance of

fluctuating asymmetry is based on upon the assumption that both sides of an individual are genetically identical and equally affected by external influences, therefore both sides should develop similarly (Baker and Hoelzel 2013). Asymmetrical development may be a response to inability to cope with stressors, presumably due to lack of genetic quality or variability (Vøllestad et al. 1999). For this reason, the amount of asymmetry among secondary sexual characteristics has been often theorized to be inversely related to genetic quality (Zachos et al. 2007) and previous research on various taxa has indicated that asymmetry of secondary sexual characteristics is related negatively to reproductive success (Møller 1992). Ditchkoff et al. (2001b) found that white-tailed deer antlers follow the patterns predicted of a trait that honestly reflects genetic quality. However, we did not find evidence that fluctuating asymmetry of antlers was associated with breeding success in our population. Granted, our approach to quantifying fluctuating asymmetry was based only on antler measurements with no reference given to three-dimensional asymmetry (Ditchkoff and deFreese 2010). Moreover, our comparisons do not fully account for all aspects of antler symmetry; antlers could be highly asymmetrical, while still sharing very similar measurements in our data set.

Male fawns sired considerably more fawns than expected, which is a relatively novel finding that has not been shown in prior research with wild white-tailed deer. However, it should not be surprising considering male fawns can be sexually mature; though lacking a presence of mature males, Schultz and Johnson (1992) documented that 12.5% of captive male fawns sired offspring with female fawns. Townsend and Bailey (1981) found that some male fawns begin to rise in social rank over adult and yearling does by the time of their first rut. We saw a lack of noticeable patterns with regard to

which particular male fawns sired offspring. Fawns were successful breeders during each year of the study, with only one incident of a male fawn successfully siring more than one offspring. Links to body size were unclear as well because of the 55 males who were fawns during the study, we only were able to collect body measurements on 9 (16.4%). At times, genetic programs such as CERVUS may have difficulty segregating siblings and parents at the 80% confidence level due to genetic similarity. In addition, the unreliability of aging older deer by tooth wear and replacement can make aging potentially less accurate (Gee et al. 2002). To check these possible disparities, we examined only sires attributed to the 95% confidence level and found that within that subset 8.97% of sires were ascribed to buck fawns ($n = 7$, $SE = 0.041$). In addition, we had 5 instances of a buck fawn siring fawns with 95% confidence, with both sire and fawn captured before 1 year or age. It would be beneficial to examine which females are copulating with these male fawns, but that was beyond the scope of this study.

Although our data indicated that age, body size, and antler size were positive predictors of breeding success, a significant proportion of fawns were sired by subdominant males that were younger than 3.5 years. Research utilizing molecular markers to assign paternity has previously indicated that reproductive success in male vertebrates is less skewed toward dominant males than sexual selection theory or observational data would suggest (Westneat 2000). Researchers have begun to question assumptions on the degree of breeding monopolization in white-tailed deer as it seems that even the presence of mature males does not completely exclude reproductive success of immature males (Sorin 2004, DeYoung et al. 2006, DeYoung et al. 2009). Ott et al. (2003) reported that yearling bucks sired fawns in each of 2 large (200 ha) enclosures that

also contained a high density of mature males. Sorin (2004) observed that even in a population with 14 males \geq 3.5-years, 3 of 16 yearling males successfully reproduced. Additionally, DeYoung et al. (2009) observed yearling males sire 14%, 11%, and 32% of fawns in studies at 3 separate locations. Even in a captive setting where extremely high density (approaching 20 deer/ha) should presumably result in a harem-defense type breeding system, DeYoung et al. (2006) found that dominant males sired as low as 64% of the offspring in a pen.

A tending-bond mating strategy combined with evidence of highly synchronous estrous cycles should result in subdominant males obtaining breeding opportunities. Say et al. (2001) gave a parallel example in domestic cats, which face a similar breeding quandary. As induced ovulators, a dominant male cat is faced with a choice when 'tending' a receptive female: he can stimulate her to ovulate, then breed and guard her for maximum probability of reproductive success or he can leave her following copulation to find another receptive female. This creates a dilemma for dominant males when estrous cycles are synchronized, as in deer, and Say et al. (2001) found that dominant male cats were similarly unable to monopolize breeding opportunities under those circumstances. The breeding system in domestic cats may be similar to that of white-tailed deer, since deer are known to exhibit a reproductive process of individual tending and synchronous estrous cycles (Marchinton and Hirth 1984). Because dominant bucks are unable to defend multiple females at one time, younger, less physically-developed males should have breeding opportunities available to them. This would be especially true during the peak of the breeding season when multiple females enter estrous during the same period. In contrast, red deer stags, which have a harem breeding system, are better able to

monopolize breeding opportunities (Gibson and Guinness 1980) because they can guard recently bred females from other males while simultaneously tending other receptive females.

The types of breeding opportunities that are available to subdominant males require more research. Aforementioned research has suggested that breeding pairs are generally close in age (Sorin 2004). This could be due to female choice, where older, higher-ranking females select older, dominant males for breeding (Poole 1989). It could also be a result of male choice - a much less-common suggestion in highly polygynous, sexually dimorphic species; however, a strong hypothetical possibility when a tending-bond mating system is combined with synchronized estrous. A dominant male encountering two estrous females at the same time would be forced to choose only the more desirable female to tend and breed to best increase his fitness (Clutton-Brock 2007). In this circumstance, the male is faced with a greater cost of conception than is commonly found in polygynous mammals (since the time taken to tend her during the rut is very valuable) and he should choose the more fit female, likely also of prime age. This would provide opportunities for younger males to obtain breeding opportunities.

Of course factors other than those measured, such as behavior, also play a substantial role in determining breeding success. As an example, in the birth year 2009, the 2.5-yr-old cohort ($n = 3$ males) sired 6 fawns; one buck was responsible for 5 of these fawns. That male later became the largest-antlered deer in the enclosure during the year he was 5.5 years of age and his early breeding success could have been a function of increased dominance due to some other factor than what we measured. Other options such as the “sneaker” alternative mating strategy of kleptogamy may also be playing a

role (Clutton-Brock 1979). This strategy is one in which a non-dominant, typically less ornate male gains copulations without contests, territories, or aggressive behavior (Sinervo and Lively 1996). An interesting potential parallel to our case is that of the side-blotched lizard (*Uta stansburiana*), where researchers categorized males into three levels of aggressiveness/dominance and demonstrated that less aggressive males with smaller territories were the dominant reproducers in certain years; whereas the sneaker strategy of non-aggressive males, which held no territory and resembled females, was the most effective strategy in other years (Sinervo and Lively 1996).

There are several other factors that could also indirectly influence breeding success through modifications in behavior, condition, or attractiveness to mates. Testosterone levels are most likely a factor at work and may cause more aggressive behavior in deer (West and Nordan 1976, Miller et al. 1987). Greater testosterone levels have been shown in tree lizards (*Urosaurus ornatus*) to be associated positively with an individual's ability to acquire and hold a territory (Hews et al. 1994) and have been linked to dominance in white-tailed deer (Miller et al. 1987) and increased aggressive behavior in many vertebrates (Moore and Lindzey 1992, Hews et al. 1994). Because testosterone levels vary within an age class in white-tailed deer (Ditchkoff et al. 2001c), it is plausible for high quality younger males with elevated testosterone levels to exhibit dominance over older males and acquire breeding opportunities. Degree of parasitism also has the potential to influence breeding success and parasite load has been related to genetic quality as well as antler characteristics (Ditchkoff et al. 2001a). This relationship is especially difficult to understand since low parasite load may be positively related to

genetic quality (Ditchkoff et al. 2001a) but is also inversely related to antler development (Lochmiller 1996) and androgenic hormones such as testosterone (Folstad et al. 1999).

Our data indicate that a multitude of interrelated factors may influence reproductive success in white-tailed deer. Age, antler, and body characteristics did play a positive role in the number of offspring sired by males yet subdominants were also reproducing more than is common in other well-studied Cervid species (Gibson and Guinness 1980). Although we conducted our research in a semi-captive facility, we acknowledge that we were not able to collect every offspring sired. This is a consequence of studying animals in their natural environment; however, the study site was a highly monitored area where we had the ability to find, genetically sample, and incorporate deceased individuals into our database in order to minimize any potential bias. Further research is necessary to continue to elucidate the intricate host of factors involved in this system. Due to this complexity, any future research will likely also need to take place in a research setting where it is possible to have intimate knowledge of every animal in the population.

LITERATURE CITED

Anderson, J. D., R. L. Honeycutt, R. A. Gonzales, K. L. Gee, L. C. Skow, R. L.

Gallagher, D. A. Honeycutt, and R. W. DeYoung. 2002. Development of microsatellite DNA markers for automated genetic characterization of white-tailed deer populations. *Journal of Wildlife Management* 66:67-74.

Andersson, M. 1994. *Sexual selection*. Princeton University Press, New Jersey, USA.

- Baker, K. H., and A. R. Hoelzel. 2013. Fluctuating asymmetry in populations of British roe deer following historical bottlenecks and founder events. *Mammalian Biology*:in press.
- Bercovitch, F. B. 1989. Body size, sperm competition, and determinants of reproductive success in male savanna baboons. *Evolution* 43:1507-1521.
- Boone and Crockett Club. 1997. Measuring and scoring North American big game trophies. Second edition. Boone and Crockett Club, Missoula, Montana, USA.
- Carstensen Powell, M., G. D. DelGiudice, and B. A. Sampson. 2005. Low risk of marking-induced abandonment in free-ranging white-tailed deer neonates. *Wildlife Society Bulletin* 33:643-655.
- Clutton-Brock, T. H. 2007. Sexual selection in males and females. *Science* 318:1882-1885.
- Clutton-Brock, T. H., S. D. Albon, and F. E. Guinness. 1988. Reproductive success: studies of individual variation in contrasting breeding systems. University of Chicago Press, Illinois, USA.
- Clutton-Brock, T. H., F. E. Guinness, and S. D. Albon. 1982. Red deer: behavior and ecology of two sexes. University of Chicago Press, Illinois, USA.
- Clutton-Brock, T. H., S. D. Albon, R. M. Gibson, and F. E. Guinness. 1979. The logical stag: adaptive aspects of fighting in red deer. *Animal Behavior* 27:211-225.
- Darwin, C. R. 1871. The descent of man, and selection in relation to sex. John Murray, London.

- Demarais, S., K. V. Miller, and H. A. Jacobson. 2000. White-tailed deer. Pages 601-628 *in* S. Demarais and P. R. Krausman, eds. Ecology and management of large mammals in North America. Prentice Hall, Upper Saddle River, New Jersey, USA.
- DeYoung, R. W., S. Demarais, K. L. Gee, R. L. Honeycutt, M. W. Hellickson, and R. A. Gonzales. 2009. Molecular evaluation of the white-tailed deer mating system. *Journal of Mammalogy* 90:946-953.
- DeYoung, R. W., S. Demarais, R. L. Honeycutt, K. L. Gee, and R. A. Gonzales. 2006. Social dominance and male breeding success in captive white-tailed deer. *Wildlife Society Bulletin* 34:131-136.
- Ditchkoff, S. S., and R. L. deFreese. 2010. Assessing fluctuating asymmetry of white-tailed deer antlers in a three-dimensional context. *Journal of Mammalogy* 91:27-37.
- Ditchkoff, S. S., R. L. Lochmiller, R. E. Masters, S. R. Hooper, and R. A. Van Den Bussche. 2001a. Major-histocompatibility-complex-associated variation in secondary sexual traits of white-tailed deer: evidence for “good genes” advertisement. *Evolution* 55:616-625
- Ditchkoff, S. S., R. L. Lochmiller, R. E. Masters, W. R. Starry, and D. M. Leslie, Jr. 2001b. Does fluctuating asymmetry of antlers in white-tailed deer follow patterns predicted for sexually selected traits? *Proceedings of the Royal Society of London, Series B: Biological Sciences* 268:891-898.
- Ditchkoff, S.S., L. J. Spicer, R. E. Masters, and R. L. Lochmiller. 2001c. Concentrations of insulin-like growth factor-I in adult male white-tailed deer: associations with serum testosterone, morphometrics, and age during and after the breeding season. *Comparative Biochemistry and Physiology Part A* 129:887-895.

- Doucet, S. M., D. J. Mennill, R. Montgomerie, P. T. Boag, and L. M. Ratcliffe. 2004. Achromatic plumage reflectance predicts reproductive success in male black-capped chickadees. *Behavioral Ecology* 16:218-222.
- Emlen, S. T. and L. W. Oring. 1977. Ecology, sexual selection and evolution of mating systems. *Science* 197:215-223.
- Folstad, I., A. C. Nilssen, O. Halvorsen, and J. Andersen. 1989. Why do male reindeer have higher abundances of second and third instar larvae of *Hypoderma tarandi* than females? *Oikos* 55:87-92.
- Gee, K. L., J. H. Holman, M. K. Causey, A. N. Rossi, J. B. Armstrong. 2002. Aging white-tailed deer by tooth replacement and wear: a critical evaluation of a time-honored technique. *Wildlife Society Bulletin* 30:387-393.
- Geist, V. 1971. Mountain sheep: a study in behavior and evolution. University of Chicago Press, Illinois, USA.
- Gibson, R. M., and F. E. Guinness. 1980. Differential reproduction among red deer stags on Rhum. *Journal of Animal Ecology* 49:199-208.
- Haley, M. P. 1994. Resource-holding power asymmetries, the prior residence effect, and reproductive payoffs in male northern elephant seal fights. *Behavioral Ecology and Sociobiology* 34:427-434.
- Harvey, I. F., and K. J. Walsh. 1993. Fluctuating asymmetry and lifetime mating success are correlated in males of the damselfly. *Ecological Entomology* 18:198-202.
- Hews, D. K., R. Knapp, and M. C. Moore. 1994. Early exposure to androgens affects adult expression of alternative male types in tree lizards. *Hormones and Behavior* 28:96-115.

- Jackson, A. M., and S. S. Ditchkoff. 2013. Survival estimates of white-tailed deer fawns at Fort Rucker, Alabama. *American Midland Naturalist* 169:in press.
- Kalinowski, S. T., M. L. Taper, and T. C. Marshall. 2007. Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. *Molecular Ecology* 16:1099-1106.
- Koerth, B. H., and J. C. Kroll. 2000. Bait type and timing for deer counts using cameras triggered by infrared monitors. *Wildlife Society Bulletin* 28:630-635.
- Kruuk, L. E. B., J. Slate, J. M. Pemberton, S. Brotherstone, F. Guinness, and T. H. Clutton-Brock. 2002. Antler size in red deer: heritability and selection but no evolution. *Evolution* 56:1683-1695.
- Lochmiller, R. L. 1996. Immunocompetence and animal population regulation. *Oikos* 76:594-602.
- Madsen, T., R. Shine, J. Loman, and T. Håkansson. 1993. Determinants of mating success in male adders. *Animal Behaviour* 45:491-499.
- Malo, A. F., E. R. Roldan, J. Garde, A. J. Soler, and M. Gomendio. 2005. Antlers honestly advertise sperm production and quality. *Proceedings of the Royal Society of London, Series B: Biological Sciences* 272:149-157.
- Marchinton, R. L., and D. H. Hirth. 1984. *White-tailed deer: ecology and management*. Stackpole, Harrisburg, Pennsylvania, USA.
- McElligott, A. G., M. P. Gammell, H. C. Harty, D. R. Paini, D. T. Murphy, J. T. Walsh, and T. J. Hayden. 2001. Sexual size dimorphism in fallow deer: do larger, heavier males gain greater mating success? *Behavioral Ecology and Sociobiology* 49:266-272.

- Meredith, E. P., J. A. Rodzen., K. F. Levine, and J. D. Banks. 2005. Characterization of an additional 14 microsatellite loci in California elk for use in forensic and population applications. *Conservation Genetics* 6:151-153.
- Miller, K. V., R. L. Marchinton, K. J. Forand, and K. L. Johansen. 1987. Dominance, testosterone levels, and scraping activity in a captive herd of white-tailed deer. *Journal of Mammalogy* 68:812-817.
- Møller, A. P. 1992. Female swallow preference for symmetrical male sexual ornaments. *Nature* 357:238-240.
- Moore, M. C., and J. Lindzey. 1992. The physiological basis of sexual behavior in male reptiles. Pages 70-113 *in* C. Gans and D. Crews, editors. *Biology of the Reptilia*. University of Chicago Press, Illinois, USA.
- Nol, E., and J. N. M. Smith. 1987. Effects of age and breeding experience on seasonal reproductive success in the song sparrow. *Journal of Animal Ecology* 56:301-313.
- Ott, J. R., D. Frels, W. Armstrong, J. Carroll, R. DeYoung, M. Mitchell, D. Honeycutt, L. Skow, J. Baccus, R. Honeycutt, and R. Gonzales. 2003. Comparative mating success of male white-tailed deer in relation to age and antler quality. *Proceedings of the Annual Southeast Deer Study Group* 26:21.
- Owen-Smith, N. 1984. Spatial and temporal components of the mating systems of kudu bulls and red deer stags. *Animal Behaviour* 32:321-332.
- Poole, J. H. 1989. Mate-guarding, reproductive success and female choice in African elephants. *Animal Behavior* 37:842-849.
- Preston, B. T., I. R. Stevenson, J. M. Pemberton, D. W. Coltman, and K. Wilson. 2003. Overt and covert competition in a promiscuous mammal: the importance of weaponry

- and testes size to male reproductive success. *Proceedings of the Royal Society of London, Series B: Biological Sciences* 270:633-640.
- Quinn, T. P., and C. J. Foote. 1994. The effects of body size and sexual dimorphism on the reproductive behavior of sockeye salmon. *Animal Behaviour* 48:751-761.
- R Development Core Team. 2010. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Saalfeld, S. T., and S. S. Ditchkoff. 2007. Survival of neonatal white-tailed deer in an exurban population. *Journal of Wildlife Management* 71:940-944.
- Say, L., D. Pontier, and E. Natoli. 2001. Influence of oestrus synchronization on male reproductive success in the domestic cat. *Proceedings of the Royal Society of London, Series B: Biological Sciences* 268:1049-1053.
- Schultz, S. R., and M. K. Johnson. 1992. Breeding by male white-tailed deer fawns. *Journal of Mammalogy* 73:148-150.
- Severinghaus, C. W. 1949. Tooth development and wear as critical of age in white-tailed deer. *Journal of Wildlife Management* 13:195-216.
- Sikes, R. S., W. L. Gannon, and The Animal Care and Use Committee of the American Society of Mammalogists. 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *Journal of Mammalogy* 92:235-253.
- Sinervo, B., and C. M. Lively. 1996. The rock-paper-scissors game and the evolution of alternative male strategies. *Nature* 380:240-243.
- Sorin, A. B. 2004. Paternity assignment for white-tailed deer: mating across age classes and multiple paternity. *Journal of Mammalogy* 85:356-362.

- Townsend, T. W., and E. D. Bailey. 1981. Effects of age, sex, and weight on social rank in penned white-tailed deer. *American Midland Naturalist* 106:92-101.
- Vøllestad, L. A., K. Hindar, and A. P. Møller. 1999. A meta-analysis of fluctuating asymmetry in relation to heterozygosity. *Heredity* 83:206-218.
- Watts, D. P. 1998. Coalitionary mate guarding by male chimpanzees at Ngogo, Kibale National Park, Uganda. *Behavioral Ecology and Sociobiology* 44:43-55.
- West, N. O. and H. C. Nordan. 1976. Hormonal regulation of reproduction and the antler cycle in the male Columbian black-tailed deer. *Canadian Journal of Zoology* 54:1617:1636.
- Westneat, D. F. 2000. Toward a balanced view of the sexes: a retrospective and prospective view of genetics and mating patterns. Pages 253-306 *in* M. Appolonio, M. Festa-Bianchet, and D. Mainardi, editors. *Vertebrate mating system*. World Scientific Publishing, Singapore.
- Zachos, F. E., G. B. Hartl, and F. Suchentrunk. 2007. Fluctuating asymmetry and genetic variability in the roe deer: a test of the developmental stability hypothesis in mammals using neutral molecular markers. *Heredity* 98:392-400.
- Zedrosser, A., E. Bellemain, P. Taberlet, and J. E. Swenson. 2007. Genetic estimates of annual reproductive success in male brown bears: the effects of body size, age, internal relatedness and population density. *Journal of Animal Ecology* 76:368-375.

Table 1.1. Percentage of fawns sired by sire age class inside a 174-ha fenced enclosure in Camp Hill, AL from 2008 - 2012.

Year	Number of males	Paternities	Sire age (years)				
			0.5	1.5	2.5	3.5	4.5+
2008	23	25	8.0	44.0	20.0	28.0	-
2009	35	25	8.0	8.0	24.0	16.0	44.0
2010	38	28	14.3	7.1	3.6	32.1	42.9
2011	43	18	11.1	5.6	27.8	5.5	50.0
2012 ^a	45	8	25.0	12.5	0.0	0.0	62.5
Total	104	104	11.5	16.4	16.4	20.1	35.6

^a 2012 data set is incomplete because the study was completed prior to being able to capture sired fawns in subsequent years.

Table 1.2. Number of males by age class in 174-ha a fenced enclosure in Camp Hill, AL from 2008 - 2012.

Year	Age class (years)							Mean male age
	0.5	1.5	2.5	3.5	4.5	5.5	6.5	
2008	11	8	3	2	0	0	0	1.33
2009	13	10	7	3	2	0	0	1.67
2010	8	12	9	6	3	1	0	2.17
2011	6	8	12	8	6	2	1	2.71
2012	9	8	6	9	7	5	1	2.86

Table 1.3. Loadings for Principle Components Analysis on relationship between sire age, body length, and gross Boone and Crockett (B&C) score in white-tailed deer in a 174-ha fenced enclosure in Camp Hill, AL from 2008 - 2012.

	Age	Body length	B&C score	P^a
Component 1	-0.585	-0.543	-0.602	0.013
Component 2	0.505	-0.825	0.254	0.014
Component 3	0.635	0.156	-0.757	0.968

^a P is the value for the test of the relationship between components and number of offspring sired.

Table 1.4. Factors influencing number of fawns sired by male white-tailed deer in a 174-ha fenced enclosure in Camp Hill, AL from 2008 - 2012.

Variable	Coefficient estimate	SE	<i>P</i>
Hind foot length	0.386	0.132	0.003
Body length	0.059	0.021	0.005
Skull length	0.284	0.103	0.006
Chest girth	0.062	0.026	0.015
Gross B&C score	0.016	0.007	0.024
Basal circumference	0.453	0.228	0.047
Beam length	0.084	0.043	0.051
Inside spread	0.106	0.061	0.080
Fluctuating asymmetry	-0.008	0.023	0.730
Sire age	0.025	0.082	0.758

Table 1.5. Factors influencing number of fawns sired by male white-tailed deer after accounting for the mean age of the male population in a given year, in a 174-ha fenced enclosure in Camp Hill, AL from 2008 - 2012.

Variable	Coefficient estimate	SE	<i>P</i>
Basal circumference	0.775	0.203	≤0.001
Age	0.467	0.117	≤0.001
Beam length	0.143	0.041	≤0.001
Chest girth	0.084	0.022	≤0.001
Skull length	0.308	0.096	≤0.001
Inside spread	0.184	0.059	0.002
Body length	0.057	0.018	0.002
Hind foot length	0.346	0.114	0.002
Gross B&C score	0.012	0.004	0.006

Table 1.6. AIC values for various models tested, along with the change in AIC from the best model.

Candidate models	<i>K</i>	AIC	Δ AIC	<i>w</i>
Mean male age + sire age + B&C score	3	61.25	0.00	0.420
Mean male age + B&C score	2	62.18	0.93	0.264
Mean male age + sire age + B&C score + body length	4	62.93	1.38	0.182
Mean male age + B&C score + body length	3	63.58	2.33	0.131
Mean male age + sire age + body length	3	69.97	8.72	0.002
Mean male age + global ^a	10	72.26	11.01	<0.001
B&C score + body length	2	75.11	13.86	<0.001
Mean male age + body length	2	76.55	15.30	<0.001
Sire age + B&C score + body length	3	77.03	15.78	<0.001
B&C score	1	77.10	15.85	<0.001
Main beam length	1	78.29	17.04	<0.001
Basal circumference	1	78.36	17.11	<0.001
Sire age + B&C score	2	78.85	17.60	<0.001
Inside spread	1	79.00	17.75	<0.001
Hind foot length	1	80.31	19.06	<0.001
Body length	1	80.89	19.64	<0.001
Global ^a	9	81.04	19.79	<0.001
Skull length	1	81.30	20.05	<0.001
Chest girth	1	83.88	22.63	<0.001

Table 1.6, continued. AIC values for various models tested, along with the change in AIC from the best model.

Candidate models	<i>K</i>	AIC	Δ AIC	<i>w</i>
Mean male age + sire age	2	205.50	144.25	<0.001
Sire age	1	221.60	160.35	<0.001

^a Global model variables: sire age, B&C score, inside spread, main beam length, basal circumference, chest girth, hind foot length, skull length, body length.

Chapter II: Seeking Improved Efficiency of Camera Survey Techniques for White-tailed Deer

ABSTRACT

Digital technology now provides increased battery life and storage capacity in today's infrared-triggered trail cameras (hereafter: cameras) versus what was previously available, resulting in a dramatic rise in man-hours required to review countless photographs. We examined techniques to reduce processing time when using trail cameras to survey and estimate population parameters of white-tailed deer (*Odocoileus virginianus*). The study took place at the Auburn University Deer Lab, in Camp Hill, AL; a 174-ha enclosure containing approximately 90 adult deer, the majority of which were tagged and individually identifiable. We used one site per 43.5 ha, and corn as bait, for all surveys. During September and October 2010 we completed 2, 7-day camera surveys after a 5-day pre-bait period to compare the efficacy of a camera set on a 10-minute-delay placed beside one with a 5-minute-delay. At 7 of 8 sites over the 2 surveys, the 10-min delay captured as many or more individuals than the 5-min camera, yet took only 52% the number of pictures. During September 2011, we surveyed for 15 days to examine the necessity of prebaiting. The number of individual deer detected was positively influenced by the addition of a 3- to 5-day pre-bait period. We found no significant change in sex ratio over time. We suggest that increases in the delay of an camera can reduce the number of images without negatively impacting the number of different individuals

detected, but elimination of a pre-baiting period may negatively influence the efficacy of camera surveys.

INTRODUCTION

Infrared-triggered trail cameras (hereafter: cameras) are a prevalent (Cutler and Swann 1999) and user-friendly (Kucera and Barrett 1993) tool for conducting wildlife population surveys and can obtain data that would otherwise be much more arduous to gather (Swann et al. 2004, Larrucea et al. 2007). Cameras are less invasive than many other techniques, even in working with rare or taciturn species such as the red-cockaded woodpecker (*Picoides borealis*, Franzreb and Hanula 1995) and tiger (*Panthera tigris*, Karanth and Nichols 1998). Cameras can be left in the field for several days to weeks to gather round-the-clock observational data without the need for an observer. Specifically for white-tailed deer (*Odocoileus virginianus*), cameras have become the tool of choice when conducting population surveys (McKinley et al. 2006). Many researchers have used camera surveys to generate population data comparable to parameters from Lincoln-Peterson indices (Jacobson et al. 1997, Curtis et al. 2009), helicopter counts (Koerth and Kroll 2000), and known populations (McKinley et al. 2006, Curtis et al. 2009).

Whereas researchers and managers have a variety of other techniques they can use to survey white-tailed deer populations, most of these have certain limitations or disadvantages. Direct population assessments such as drive, strip, and road-based surveys, mark-recapture procedures, and population indices are frequently limited to open habitat types and/or require a large labor force (Lancia et al. 1994). Road-based spotlight surveys have been shown to result in highly variable detection probabilities and questionable population size estimates (Collier et al. 2007, Collier et al. 2013.).

McCullough (1979) found that drive counts can under- or over-estimate population size by as much as 20-30% as compared to a reconstructed population. Population reconstruction, the practice of estimating previous population data based on collecting and aging all dead individuals, requires intensive search efforts and accurate aging procedures; moreover, it typically does not produce a complete data set for a given year until each individual from that year is dead and researchers have found the remains (McCullough 1979, Lancia et al. 1994). Change-in-ratio techniques, the comparison of harvested buck:doe ratios with ratios before and after a hunting season, requires 2 accurate population surveys to gather the pre- and postharvest data and accurate harvest information (Downing 1980). In contrast to other techniques, cameras are an economical alternative – not simply in financial output, but in amount of required labor and the complexities of necessary equipment (Roberts et al. 2006).

Although cameras have become very popular for deer surveys, modern advances in camera affordability, ease of use, battery life, and storage capacity have introduced a new problem: managers may now have to deal with having more images to process than can be examined in a timely manner. No studies have compared the effectiveness of various trigger-delay times as related to a white-tailed deer survey. Many deer survey studies use a 4- to 5-minute delay (Jacobson et al. 1997, Koerth and Kroll 2000, Curtis et al. 2009), but this may not be optimal; were a longer delay able to detect as many deer it would also presumably provide fewer images for review and thus be much more efficient from a labor perspective. In addition, deer survey methods commonly include a 5- to 8-day prebaiting period (McKinley et al. 2006, Curtis et al. 2009); however, little research exists behind this practice. If managers are already visiting camera sites to prebait, it may

be more efficient to place cameras over this initial bait. With wild pigs (*Sus scrofa*), Williams (2009) reported the average time to first visit at a corn-baited station as 74.6 hours, thus justifying a prebaiting period of several days. However, no research has been conducted on optimal length of prebaiting periods for deer camera surveys.

Our goal for this project was to explore options for improving efficiency (man hours, cost, etc.) of baited camera surveys for white-tailed deer. Specifically, the objectives were to (1) compare detections and total pictures taken by 5- and 10-minute trigger-delay settings over 2, 7-day camera surveys, and (2) examine data from a 15-day survey, comparing sex ratios, number of captures, and number of identifications to determine the efficacy of prebaiting for 0, 3, or 5 days.

STUDY AREA

This study took place at the Auburn University Deer Lab in Camp Hill, AL, USA; a 174-ha deer enclosure bounded by 2.6-m deer-proof fencing. Three protein-pellet feeders supplemented the deer's diet year-round with ad libitum "Deer Feed", an extruded 18% protein product (SouthFresh Feeds, Demopolis, AL). Three timed corn feeders were also in operation on the site when researchers were actively darting deer as part of other research. The vegetation was approximately 40% open hay fields, with the balance in oak (*Quercus* spp.)-hickory (*Carya* spp.) hardwoods and planted loblolly pine (*Pinus taeda*) stands of varying age. Elevation ranged from approximately 190 to 225 m above sea level.

Two, 0.8-ha food plots were planted within the enclosure in addition to a 0.8-ha food-plot/capture facility, gated and high-fenced with a deer working area attached. As of

July 2010, the deer herd inside the Camp Hill enclosure consisted of an estimated 67-87 adult (>1-yr-old) deer of which we had ear-tagged, freeze-branded, and collected data on at least 58 individuals that were in the population. The herd consisted of 55 (during fall 2010) - 58 (fall 2011) % males (C. H. Newbolt, unpublished data). During the summer, daily low- and high-temperature means were 21° C and 32° C, respectively.

METHODS

Trigger Delay

We conducted two surveys in the early fall (September and October, 2010), approximately 2.5 months prior to the onset of major rutting activity, when most land managers would be conducting camera surveys. In addition, one study compared coefficients of variation (CV) for age and sex ratios by month and found the best age ratio results during September and sex ratio results during October (Koerth and Kroll 2000).

To test for a more efficient delay setting, beginning 15 September 2010 we established 4 pre-baited sites systematically distributed throughout the property for a coverage of 43.5 ha/camera site, slightly greater than Koerth et al. (32.5 ha; 1997) and Curtis et al. (33-38 ha; 2009), similar to some of McKinley et al. (41-81 ha; 2006), but less than Jacobson et al. (65-259 ha; 1997). Once we determined a general location, we selected specific sites beneath forest canopy and removed any understory vegetation that would adversely obstruct the camera's view from within a 5- by 10m area. Using 22 kg of whole corn replenished every third day, we pre-baited for 5 days, then set up and monitored cameras for 7 days. After a 2-day rest period, we set up 4 new sites and again

pre-baited for 5 days before monitoring for 7 days. At each site we set 2 infrared-triggered PixController trail cameras (DigitalEye 7.2, PixController Inc., Export, PA); 1 on a 5-min, minimum delay between trigger activations and the other on a 10-min, minimum delay. We standardized all other camera settings (sensitivity, flash brightness, ISO speed) and selected cameras at random from our collection (n = 15). After the first 7-day monitoring period we re-randomized the camera selection and mounted different cameras on each mounting board, but retained the same system of 2 side-by-side cameras per site.

At each site, for each survey, we placed the cameras side-by-side on steel mounting boards hung on 2" galvanized pipe driven into the ground, such that lens height for each was 1.5 m above ground level. We mounted each camera in a random position (left or right) 4 m from the bait and facing at a downward angle of 15°, similar to Holtfreter et al. (2008). We exchanged memory cards and replaced batteries as necessary to avoid any lapse in data collection.

For consistency in all camera surveys, one person reviewed all pictures from all surveys and compiled all data. Deer were only counted if ear tag numbers were legible; even though many antlered bucks were identifiable by antler configurations. Only pictures with identifiable deer were used. Pictures were then subdivided and tabularized as 'captures' - each identifiable deer in a picture became one capture.

Prebaiting

In 2011, again beginning 15 September, we utilized the same 4 site locations as the second survey of 2010, with the same camera placement and bait setup. We used 1 camera per site, set on a 10-min delay to determine if camera surveys capture as much or

more information with less effort by placing cameras on bait immediately without the typical prebaiting period. For this survey, we baited the sites, activated cameras over the bait immediately, and kept the sites baited every third day for 15 days. Because both the number of unique deer identified and the number of deer captures are vital information for camera survey methods, we compared deer identified and total captures for days 1-10, days 4-13, and days 6-15, as if we had run a 10-day survey after 0, 3, or 5 days of prebaiting, respectively. We examined the change in sex ratios of deer identifications and captures in 1-, 3-, 5-, and 10-day periods over time using linear regression. In addition, we regressed the number of total identifications and captures to examine trends over time. Using the nonlinear least squares function in statistical program R (R version 2.11.1, www.r-project.org, accessed 18 July 2012), we fitted the line $y = Ax/(B+x)$ to these data (captures, identifications, sex ratio captures, sex ratio identifications), where A was the asymptote and B was the value of x at one-half of A. A day was defined as the 24-hour period from noon until noon, since deer activity was at a minimum near mid-day.

Because of the great numbers of uniquely identifiable deer inside Deer Lab (we knew the age and sex of most deer photographed), we were able to analyze detectability of individual deer and compare detections as a function of age and sex. We only used deer we detected in the 2010 surveys and used a generalized linear model in R to compare detections as a function of old (≥ 3.5 -yrs-old) versus young (< 3.5 -yrs-old) deer and males versus females. Detectabilities were all calculated per 24-hr period, and then compared with each other using a Generalized Linear Model, resulting in odds ratios. This allowed us to work with detection probabilities with a limited number of days,

without transformations. Also, since probabilities are limited to between 0 and 1, odds ratios are easier to comprehend in comparison to one another.

RESULTS

Trigger Delay

In the two surveys, the 5-minute cameras averaged 191.50 (SE = 33.66) and 347.50 (SE = 48.94) images containing identifiable deer, respectively, whereas the 10-minute cameras averaged 106.25 (SE = 19.73) and 179.75 (SE = 10.01) images, respectively. The 5-min cameras cumulatively identified an average of 9 (SE = 2.48) and 19 (SE = 2.21) unique deer/camera/survey, compared to 9.25 (SE = 2.39) and 18.75 (SE = 1.85) unique deer/camera/survey for the 10-min cameras (Table 2.1). The 10-min cameras identified as many or more deer than the 5-min at 7 of the 8 total sites surveyed in 2010, and the same number of deer nearly every day of both the first (Figure 2.1) and the second survey (Figure 2.2). Detectability did not differ by age during the first 2010 survey. However, in the second 2010 survey we found that deer <3.5-yr-old were 1.97 times as likely to be detected as deer ≥ 3.5 (+/- 1.818, 95% CI; $P = 0.024$). Does were 1.77 and 2.36 times as likely to be detected as bucks (+/- 1.648, 95% CI; $P = 0.024$ and +/- 1.825, 95% CI; $P = 0.005$, respectively) during the first and second 2010 surveys, respectively.

Prebaiting

The mean time from placement of bait to first deer visit, over the 4 camera sites, was 11.26 hours (SE = 5.04 hr). During the first 10 days we identified 37 unique deer ($\bar{x} = 13.00$ unique identifications/camera, SE = 1.47) with a mean of 187.00 captures/camera

(SE = 11.50). Days 4-13 identified 46 unique deer ($\bar{x} = 14.75/\text{camera}$, SE = 1.55) with a mean of 199.50 captures/camera (SE = 15.18). Days 6-15 also identified 46 unique deer ($\bar{x} = 15.25/\text{camera}$, SE = 1.31) with a mean of 213.00 captures/camera (SE = 16.91). No statistical difference was present between mean unique identifications per camera based on prebaiting period. Mean captures per camera multiplied by number of cameras do not equal total deer captured, since certain deer were captured on multiple cameras.

Sex ratios of deer identified did not differ by any time period ($P = 0.31$). The sex ratios of deer captures, however, changed over time with the percentage of buck captures increasing by 1.5% per day ($P = 0.050$). Interestingly, buck percentages began with linear intercepts of 26.85% for identifications ($P < 0.001$) and 23.31% for captures ($P = 0.001$), yet asymptotic values of 42.36% (+/- 17.11%, 95% CI; $P < 0.001$) and 45.23% (+/- 11.45%, 95% CI; $P < 0.001$), respectively.

Number of total deer identifications increased by approximately 0.30 identifications/camera/day ($P < 0.001$), while we saw no relationship between number of captures over time ($P = 0.137$). For captures over time, we found an asymptotic value of 23.48 (+/- 5.16, 95% CI) captures/camera/day ($P < 0.001$). For unique identifications, we found that the asymptotic value was 9.59 (+/- 1.57, 95% CI; $P < 0.001$) identifications/camera, and the value of identifications reached half of their asymptotic value at 1.83 (+/- 1.36, 95% CI; $P = 0.011$) days.

DISCUSSION

Trigger Delay

As expected, the 10-min delay cameras took roughly half the number of pictures as the 5-min. Though many costs have been previously documented for bait, film development, and time spent preparing and maintaining camera sites, previous research is replete in identifying labor cost of reviewing thousands of images as noteworthy. The time taken to review the images in this study would not be relative to the average land manager, either, since we were gathering much more data during the review of images than would be common. Suffice it to say that taking half as many images would likely reduce the amount of time required to review images by 50%, and would reduce labor costs accordingly.

Of interest, however, is that the 10-min dataset positively identified as many or more unique deer than the 5-min at 7 of 8 sites. The cumulative numbers of deer identified per day were also very similar in both surveys. This may have been expected in areas of lower deer density where visits would not be as likely to overlap - thus, deer would not be as likely to arrive to the bait site while the camera was still in a 10-minute delay from a previous trigger. If the camera delay were of greater duration and deer density great enough, then individuals could theoretically arrive and depart while the camera was within the delay mode from taking an image of a different deer and not be identified. Our study area had a high deer density (~ 45 deer/km² at time of survey). Feeding bout length has been documented to average >10 minutes when bait is scattered on the ground (Kozicky 1997), suggesting that such missed identifications with a 10-min delay should be rare.

In one of our surveys, deer <3.5 years had greater odds of being detected than older deer. It is generally held that smaller individuals need to feed more often than larger (Peters 1983), so one might expect younger deer, being smaller, to be more likely to utilize bait stations. The body size hypothesis suggests that larger animals occupy greater home ranges and feed on lesser quality forage to meet greater metabolic requirements (Weckerly 1993). Larger gastrointestinal tracts in individuals of greater body mass allows for slower food passage, less frequent feeding bouts, and lower quality forages that tend to have greater fiber content (Alexander 1993). This could have detrimental implications on the assumption of equal detectability in surveys, a basic tenet of wildlife sampling (Krebs 1999), which has been demonstrated to be invalid in previous research with camera surveys (Larrucea et al. 2007) and with white-tailed deer specifically (McCoy et al. 2011).

We also found detectability differences due to sex. In light of previous research (Jacobson et al. 1997), males may be expected to have increased odds of detection over females. Males generally inhabit greater home ranges than females (Stewart et al. 2011); Jacobson et al. (1997) attributed an increased capture rate of bucks to these greater home ranges and their study's lower camera density (maximum of 1/65ha). Wild female deer 50% kernel core areas having been documented to be as small as 23-26 ha (Etter et al. 2002, Campbell et al. 2006); therefore a camera density similar to Jacobson et al. (1997) may miss capturing certain females whose core areas do not overlap camera stations as frequently as those whose core areas do overlap camera stations over the short time period of a camera survey. At our greater camera density (1/43.5 ha), we should theoretically have a camera site within more female core areas than Jacobson et al.

(1997), which may partially explain why our females had greater odds of detection than males.

Another reason for the difference in detectability due to sex is that the Jacobson et al. (1997) study took place in late winter, and ours in early fall. Does were lactating during our surveys (two-year range of parturition dates, $n = 19$: 27 July – 29 August, P. K. Acker, unpublished data), which is noted as the time of greatest energy expenditure for a female (Moen 1978). Lactation has been said to double a female's energy requirements, and in red deer (*Cervus elaphus*), lactating females were shown to graze 2 hours longer per day on more preferred foods than non-lactating females (Clutton-Brock et al. 1982). The nutritional demands of lactation require females to choose higher-quality diets (Barboza and Bowyer 2000) which should result in greater frequency of bait site visitation. The body size hypothesis could again be cited as a cause for increased odds of female detectability; however, it has not been shown to be responsible for intersexual resource partitioning in various *Odocoileus* species. Beier and McCullough (1990) could not attribute differences in white-tailed deer site fidelity and home range sizes to body size alone. Weckerly (1993), working with black-tailed deer (*O. hemionus columbianus*), similarly rejected the body size hypothesis as the cause of intersexual resource partitioning. In light of these studies, we do not think the body size hypothesis explains the greater odds of female detectability we noticed. In the end, regardless of the reasoning, the detectability differences by sex also violate the assumption of equal detectability (Krebs 1999).

Prebaiting

The number of deer identified at bait sites increased as the time since establishment of sites increased. Several days of elapsed time allowed deer activity to increase at the sites, shown by the greater number of total captures and unique deer captured per camera during the later survey periods. For all practical purposes, the 3-day prebait period was just as effective as the 5-day, as both identified the same number of deer (46). However, the 3-day prebait produced fewer images containing deer to have to sort (760 vs 814) along with fewer days to have to maintain baited camera sites. The 5-day prebait period did produce more total captures of deer (852 vs 798), but our criterion for identification (reading eartags) is probably more stringent than most managers who only pay attention to antler characteristics of males. Thus, the additional captures of deer that had already been identified may not be beneficial.

We compared sex ratios of identifications and captures each day as well as each 3-, 5-, and 10-day period, and found no relationships except at the daily level for sex ratio of deer captures. These sex ratios did change over time as the percentage of bucks captured increased by 1.5% per day over the 15 days. Buck percentage of identifications showed a similar trend (increase of 1.2% per day) but no significant relationship. Asymptotic values of near 50% for both captures and identifications approached the true value of our marked population inside the Deer Lab of 55-58% bucks, and the true ratio was well within our 95% confidence intervals. We suggest that over the duration of the survey, new bucks were identified and captured at a progressively greater rate as time passed, and approached but did not reach a point where they were represented on camera at the same proportion that they were present in the population. One explanation for this

could involve bucks' larger home ranges: with a larger home range, a buck would conceivably take longer to discover a new food source somewhere within that home range, provided that both sexes tend to move at similar rates and in similar manners. However, two studies over the same early fall time period in Maryland documented female white-tailed deer traveling an average of 3.36 km/day (Kolodzinski 2008), whereas bucks moved 6.40 km/day (Karns 2012).

With any camera survey, more new individuals should be identified each day for some length of time, until an asymptote is approached. We saw the rate of new individuals increase at an additional 0.30 identifications/camera/day. Identifications reached half of their theoretical asymptotic value in 1.83 days and reached 75% in 5.50 days. Likewise, a corresponding increase in number of captures would also be expected. We show this positive trend (increase of 0.45 captures per day); it simply was not significant ($P = 0.137$).

For managers hampered by too many pictures to review, the use of a longer trigger delay could compile as much survey information with a fraction of the number of photographs, thereby reducing costs associated with labor. Additionally, our data suggest that the standard, yet heretofore untested, prebait period of at least 3-5 days is necessary to allow buck:doe capture ratios to approach actual population parameters. However, our data were similar to that reported in previous studies (Larrucea et al. 2007, McCoy et al. 2011), where there was differential detection of different age and sex classes of deer at baited sites. These data once again call into question the suitability of traditional camera survey techniques for estimating population demographics of white-tailed deer.

LITERATURE CITED

- Alexander, R. M. 1993. The relative merits of foregut and hindgut fermentation. *Journal of Zoology* 231:391-401.
- Barboza, P. S., and R. T. Bowyer. 2000. Sexual segregation in dimorphic deer: a new gastrocentric hypothesis. *Journal of Mammalogy* 81:473-489.
- Beier, P., and D. R. McCullough. 1990. Factors influencing white-tailed deer activity patterns and habitat use. *Wildlife Monographs* 109:1-51.
- Campbell, T. A., C. A. Langdon, B. R. Laseter, W. M. Ford, J. W. Edwards, and K. V. Miller. 2006. Movements of female white-tailed deer to bait sites in West Virginia, USA. *Wildlife Research* 33:1-4.
- Clutton-Brock, T. H., G. R. Iason, S. D. Albon, and F. E. Guinness. 1982. Effects of lactation on feeding behaviour and habitat use in wild red deer hinds. *Journal of Zoology* 198:227-236.
- Collier, B. A., S. S. Ditchkoff, J. B. Raglin, and J. M. Smith. 2007. Detection probability and sources of variation in white-tailed deer spotlight surveys. *Journal of Wildlife Management* 71:277-281.
- Collier, B. A., S. S. Ditchkoff, C. R. Ruth, and J. B. Raglin. 2013. Spotlight surveys for white-tailed deer: Monitoring panacea or exercise in futility? *Journal of Wildlife Management* 77:165-171.
- Curtis, P. D., B. Bazartseren, P. M. Mattison, and J. R. Boulanger. 2009. Estimating deer abundance in suburban areas with infrared-triggered cameras. *Human-Wildlife Conflicts* 3:116-128.

- Cutler, T. L., and D. E. Swann. 1999. Using remote photography in wildlife ecology: a review. *Wildlife Society Bulletin* 27:571-581.
- Downing, R. L. 1980. Vital statistics of animal populations. Pages 247-267 in S. D. Schemnitz, editor. *Wildlife management techniques manual*. Fourth edition. The Wildlife Society, Washington, D.C., USA.
- Etter, D. R., K. M. Hollis, T. R. Van Deelen, D. R. Ludwig, J. E. Chelsvig, C. L. Anchor, and R. E. Warner. 2002. Survival and movements of white-tailed deer in suburban Chicago, Illinois. *Journal of Wildlife Management* 66:500-510.
- Franzreb, K. E., and J. L. Hanula. 1995. Evaluation of photographic devices to determine nestling diet of the endangered red-cockaded woodpecker. *Journal of Field Ornithology* 66:253-259.
- Holtfreter, R. W., B. L. Williams, S. S. Ditchkoff, and J. B. Grand. 2008. Feral pig detectability with game cameras. *Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies* 62:17-21.
- Jacobson, H. A., J. C. Kroll, R. W. Browning, B. H. Koerth, and M. H. Conway. 1997. Infrared-triggered cameras for censusing white-tailed deer. *Wildlife Society Bulletin* 25:547-556.
- Karanth, K. U., and J. D. Nichols. 1998. Estimation of tiger densities in India using photographic captures and recaptures. *Ecology* 79:2852-2861.
- Karns, G. R., R. A. Lancia, C. S. DePerno, and M. C. Connor. 2012. Impact of hunting pressure on adult male white-tailed deer. *Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies* 66:120-125.

- Koerth, B. H., and J. C. Kroll. 2000. Bait type and timing for deer counts using cameras triggered by infrared monitors. *Wildlife Society Bulletin* 28:630-635.
- Kolodzinski, J. J. 2008. Movements of white-tailed deer at Chesapeake Farms, Maryland and the Great Cypress Swamp, Delaware. Thesis, University of Georgia, Athens, Georgia, USA.
- Kozicky, E. L. 1997. A protein pellet feed-delivery system for white-tailed deer. Management Bulletin 1. Caesar Kleberg Wildlife Research Institute, Texas A&M University, Kingsville, Texas, USA.
- Krebs, C. J. 1999. *Ecological methodology*. Second edition. Addison-Welsey, Menlo Park, California, USA.
- Kucera, T. E., and R. H. Barrett. 1993. The Trailmaster camera system for detecting wildlife. *Wildlife Society Bulletin* 21:505-508.
- Lancia, R. A., J. D. Nichols, and K. H. Pollock. 1994. Estimating the number of animals in wildlife populations. Pages 215-253 in T. A. Bookout, editor. *Research and management techniques for wildlife and habitats*. Fifth edition. The Wildlife Society, Washington, D.C., USA.
- Larrucea, E. S., P. F. Brussard, M. M. Jaeger, and R. H. Barrett. 2007. Cameras, coyotes, and the assumption of equal detectability. *Journal of Wildlife Management* 71:1682-1689.
- McCoy, J. C., S. S. Ditchkoff, and T. D. Steury. 2011. Bias associated with baited camera sites for assessing population characteristics of deer. *Journal of Wildlife Management* 75:472-477.

- McCullough, D. R. 1979. The Georges Reserve deer herd: population ecology of a K-selected species. University of Michigan Press, Ann Arbor, Michigan, USA.
- McKinley, W. T., S. Demarais, K. L. Gee, and H. A. Jacobson. 2006. Accuracy of the camera technique for estimating white-tailed deer population characteristics. *Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies* 60:83-88.
- Moen, A. N. 1978. Seasonal changes in heart rates, activity, metabolism, and forage intake of white-tailed deer. *Journal of Wildlife Management* 42:715-738.
- Peters, R. H. 1983. The ecological implications of body size. Cambridge University Press, Cambridge, United Kingdom.
- R Development Core Team. 2010. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Roberts, C. W., B. L. Pierce, A. W. Braden, R. R. Lopez, N. J. Silvy, P. A. Frank, and D. Ransom, Jr. 2006. Comparison of camera and road survey estimates for white-tailed deer. *Journal of Wildlife Management* 70:263-267.
- Stewart, K. M., R. T. Bowyer, and P. J. Weisberg. 2011. Spatial use of landscapes. Pages 181-217 *in* D. G. Hewitt, editor. *Biology and management of white-tailed deer*. CRC Press, Boca Raton, Florida, USA.
- Swann, D. E., C. C. Hass, D. C. Dalton, and S. A. Wolf. 2004. Infrared-triggered cameras for detecting wildlife: an evaluation and review. *Wildlife Society Bulletin* 32:357-365.
- Weckerly, F. W. 1993. Intersexual resource partitioning in black-tailed deer: a test of the body size hypothesis. *Journal of Wildlife Management* 57:475-494.

Table 2.1. Results of 2, 7-day trail camera surveys between 20 September - 10 October 2010, including number of deer captured and identified with both 5- and 10-minute trigger delays inside a 174-ha fenced enclosure in Camp Hill, AL.

Survey	Delay	Deer captured			Deer identified		
		Total	\bar{x}	SE	Total	\bar{x}	SE
Survey 1							
	5-min	877	219.25	46.03	36	9.00	2.48
	10-min	468	117.00	23.48	37	9.25	2.39
Survey 2							
	5-min	1638	409.50	54.57	76	19.00	2.21
	10-min	829	207.25	14.33	75	18.75	1.85

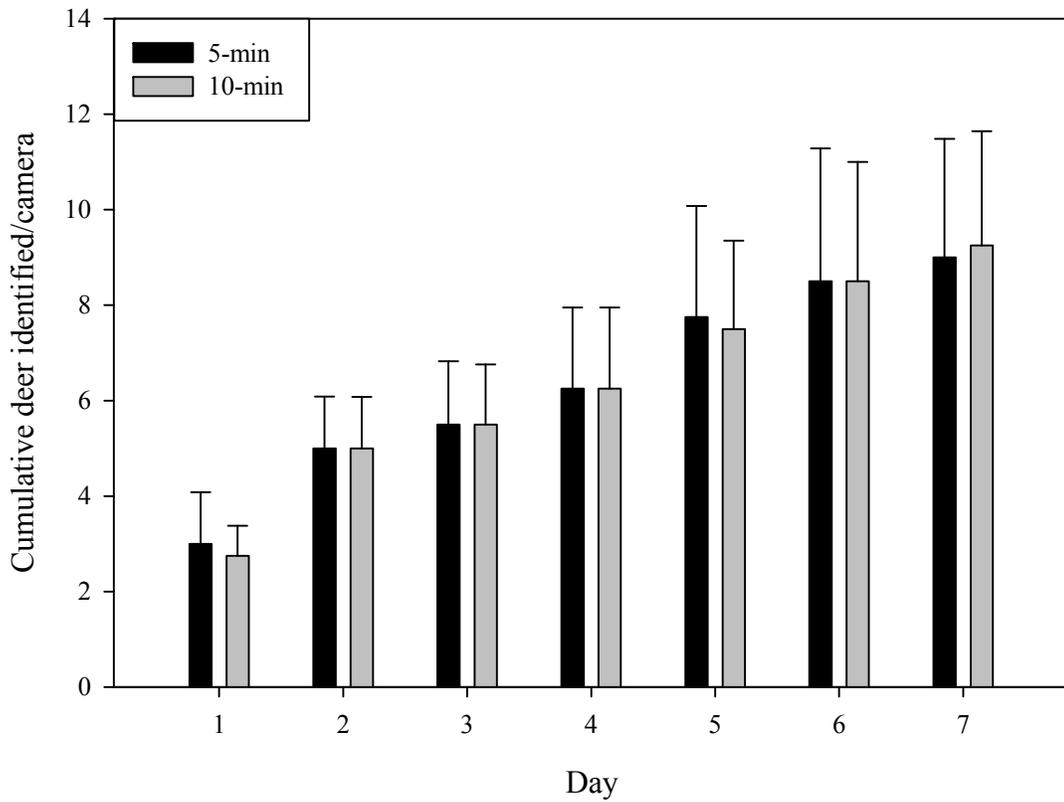


Figure 2.1. Cumulative number of unique individuals identified per infrared-triggered trail camera for 5- and 10-minute trigger delays by survey day inside a 174-ha fenced enclosure in Camp Hill, AL during September 20 - 26, 2010.

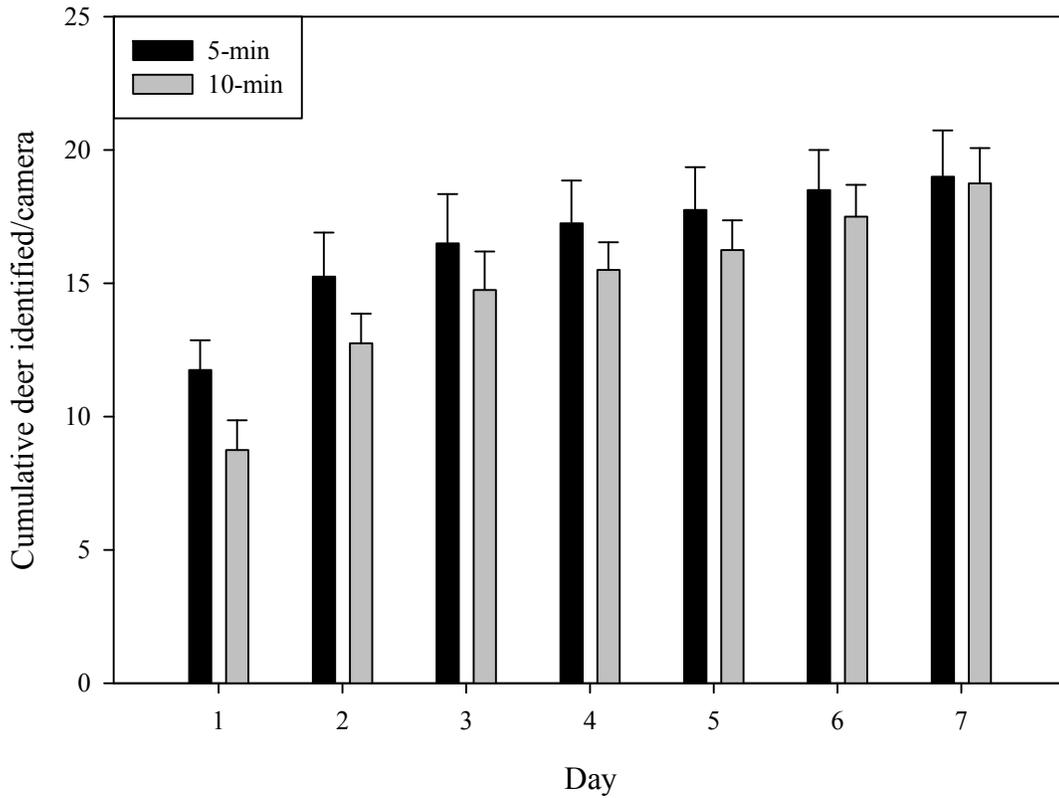


Figure 2.2. Cumulative number of unique individuals identified per infrared-triggered trail camera for 5- and 10-minute trigger delays by survey day inside a 174-ha fenced enclosure in Camp Hill, AL during October 4 - 10, 2010.