Patterns of Stress and Suitability of Camera Surveys for White-tailed Deer

by

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Abstract

We collected fecal samples to examine stress levels in a fenced population of white-tailed deer (*Odocoileus virginianus*). The purpose of the study was to determine how stress levels fluctuated throughout the breeding season, if there was a difference between males and females, and if levels in a high density, fenced population differed from those in a free-ranging environment. Fecal glucocorticoid levels of males peaked during the rut, while those in females remained relatively stable throughout the breeding season. When we compared glucocorticoid levels of the fenced population with a free-range population, we found conflicting results across the two years of the study. Remote photography is increasing in its popularity as a tool for scientists and wildlife biologists. Camera surveys have been used to estimate population parameters among a variety of species. However, this survey technique involves placing bait in front of the camera in order to capture animals more frequently, which could introduce biases in parameter estimates. We monitored cameras placed at random, along game trails, and at feed stations to determine if sex/age structure could be accurately assessed in a population of white-tailed deer. Our results indicated that there was no single time period in which cameras placed at feed stations provided sex ratio and recruitment estimates similar to those acquired from randomly placed cameras. Trail-based camera surveys provided population estimates very similar to those from random sites, and may provide a feasible alternative to using baited camera stations.

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I. PATTERNS OF FECAL GLUCOCORTICOIDS IN FENCED AND FREE-RANGE WHITE-TAILED DEER

ABSTRACT

Analysis of voided feces has become a popular method of monitoring physiological parameters of many wildlife species. From November through February of 2006-2007 and 2007-2008, we collected fecal samples to examine glucocorticoid (specifically corticosterone) concentrations in a fenced population of white-tailed deer (*Odocoileus virginianus*). The purpose of the study was to determine how stress levels fluctuated throughout the breeding season, if there was a difference between males and females, and if levels of corticosterone in a high density, fenced population differed from those in a free-ranging environment. Fecal glucocorticoid levels of males peaked during the rut, while glucocorticoids in females remained relatively stable throughout the breeding season. When we compared glucocorticoid levels of the fenced population with a free-range population, we found conflicting results across the two years of the study. In 2007, corticosterone concentrations were greater in the free-range population, but in 2008 the fenced population exhibited greater levels of corticosterone. These findings may demonstrate the importance of using multiple years of data, as stress levels can be highly variable from one year to the next. We also observed a positive relationship between corticosterone and testosterone. Because the relationship between corticosterone and testosterone was weak during the post-rut, we hypothesize that the effect of testosterone on corticosterone is partially a result of testosterone-induced behavior, and not strictly a physiological link between two hormones.

INTRODUCTION

Recently, the major focus of white-tailed deer (*Odocoileus virginianus*) management on many properties has been to create quality hunting opportunities, in which hunters have a chance to harvest large-antlered males. However, due to management scenarios that often result in local herd characteristics that are less than desired, most locations around the country do not offer these opportunities. In many areas, landowners have taken proactive measures to generate desirable herd characteristics; one method, available to landowners with the financial means, is high-fencing. This method of enclosing a deer population within a deer-proof fence has increased in popularity because a landowner can create a scenario where the enclosed deer population is not influenced by surrounding areas (i.e. neighboring hunters, low quality deer). By enclosing an area behind a high-fence, the landowner controls population demographics and herd quality through carefully regulated harvest and nutrition regimes. Specifically, these strategies are implemented so that a high proportion of males can achieve their full antler potential.

To increase hunting opportunities, deer inside most high-fence enclosures are maintained at densities that exceed habitat carrying capacity; therefore, most landowners employ supplemental feeding programs to ensure that sufficient nutritional resources are available to support high population densities. To curb extreme overpopulation, landowners normally harvest high numbers of adult females, which often leads to skewed sex ratios favoring males. The general philosophy among landowners and many biologists regarding these high densities is that as long as the herd has adequate nutrition and appears to be in good physical condition, there are likely few negative consequences of the skewed densities and sex ratios, with the exception of increased buck mortality due to fighting. It is possible that deer maintained at high densities in high-fence enclosures could be experiencing elevated levels of social stress, which can have adverse effects on an individual as well as an entire population. Social stress can be caused by high population density (Blanc and Thériez 1998), unstable social structure (Sapolsky 1992, Foley et al. 2001), or elevated rates of aggressive encounters (Creel 2001). Male white-tailed deer have to compete for mates during the breeding season, and intense fighting can occur when two males of relatively equal size are competing for breeding opportunities. In high density populations, such as those within a high-fence enclosure, an abnormally high number of males increase the chances that aggressive encounters will occur. Since high-fenced areas are designed to produce numerous mature, large-antlered males, fights between equally matched males can be extremely intense, and even fatal (Marchinton and Hirth 1984). Additionally, the male dominated sex ratios that are common in these populations result in increased male competition for breeding rights, where more than one male, possibly three or four, may compete for the same female. These high density populations and skewed sex ratios can induce heavy competition for breeding rights, lead to more frequent aggressive encounters, and ultimately cause high levels of stress within the population.

Stress is often overlooked as a significant cost to wildlife, even though it can cause substantial changes in the physiological profile of an individual. When an organism perceives a threat, the anterior pituitary gland secretes adrenocorticotrophic hormone (ACTH), which causes the adrenal cortex to secrete glucocorticoids (Asterita 1985, Sapolsky 2002). Glucocorticoids, primarily cortisol and corticosterone, affect carbohydrate, protein, and fat metabolism. Specifically, glucocorticoids increase the rate of gluconeogenesis in the liver, decrease protein synthesis, increase protein catabolism, and mobilize fatty acids from adipose tissues (Asterita 1985). These processes make energy stores available to body tissues by increasing circulating levels of glucose, amino acids, and fatty acids (Asterita 1985, Sapolsky 2002). The stress response, and resulting release of glucocorticoids, enables an animal to cope with a stressful situation by mobilizing energy necessary for the response and minimizing energy expenditure in other tissues that are not needed for immediate survival. Chronic stress causes prolonged glucocorticoid activity which can have serious impacts on individuals. Prolonged stress continually diverts energy away from processes that are not required for immediate survival, such as growth, reproduction, and immune system responses (Munck et al. 1984, Sapolsky 2002). Although our understanding of the effects of stress on wildlife is still in its infancy, research to date suggests that there can be substantial physiological and/or long-term effects. Red deer (*Cervus elaphus*) maintained in high density, potentially stressful environments have been shown to have lower growth rates than those kept in low density, less stressful environments (Blanc and Thériez 1998). Ozoga and Verme (1982a) noted that as the population density of a supplementally-fed white-tailed deer herd increased, the productivity of yearling does decreased. They hypothesized that harassment by numerous males during the breeding season caused an energy deficiency in yearling does that led to lowered productivity. Stressful situations, such as fighting in mice (*Mus musculus*) and rats (*Rattus norvegicus*), have also been shown to impair immune system health (Stefanski and Engler 1998, 1999; Stefanski 2000, 2001; Stefanski et al. 2001). Although the stress response is an important survival mechanism that has evolved to improve an individual's ability to cope with stressful events, prolonged (chronic) stress responses can potentially have detrimental consequences.

Landowners often maintain high density deer herds within high-fence enclosures in order to increase production of trophy-sized deer. However, previous studies with other species have indicated that social stress increases with increasing density, leading to reduced growth rates (Blanc and Thériez 1998), decreased productivity (Ozoga and Verme 1982b), and increased susceptibility to disease (Stefanski and Engler 1998, 1999; Stefanski 2000, 2001; Stefanski et al. 2001). Consequently, maintaining high-fence populations at high densities may inadvertently contribute to reduced antler development, productivity, and immune system health – all factors that are contrary to the management goals of the landowner.

Previous methods of measuring physiologic stress have been limited to analysis of blood parameters (Franzmann et al. 1975, Denicola and Swihart 1997, Harlow et al. 1990). However, these collection methods are often of limited use with wildlife due to their invasive nature, and may not provide accurate stress assessment because of capture and handling-induced stressors that stimulate the pulsatile secretion pattern of glucocorticoids in blood (Hamilton and Weeks 1985, Harper and Austad 2000, Millspaugh et al. 2001). During the past two decades, a non-invasive technique has been developed and tested to monitor stress levels in free-ranging wildlife populations (Miller et al. 1991, Creel et al. 1997, Wasser et al. 1997, Wasser et al. 2000). This technique involves measuring stress hormones in voided feces, which are relatively easy to collect and can be obtained without disturbing the study animals. Glucocorticoids, hormones released during times of stress, are excreted in feces and urine in concentrations relative to concentrations that are circulating in the blood. Furthermore, fecal concentrations of glucocorticoids provide an average measure of glucocorticoid secretion during the previous 12-24 hours (Millspaugh et al. 2002), ensuring that the stress response being measured is chronic rather than acute. Previous studies with ungulates (Wasser et al. 2000, Dehnhard et al. 2001, Millspaugh et al. 2002, Huber et al. 2003), birds (Wasser et al. 2000, Washburn et al. 2003), primates (Heistermann et al. 2006), and numerous other species have confirmed the reliability of estimating stress levels using fecal glucocorticoids.

White-tailed deer maintained at high densities in high-fence enclosures may be particularly susceptible to social stress. Because of their inability to avoid aggressive encounters, there is potential for a greater number of agonistic interactions and, in turn, elevated levels of stress. However, there have been no studies to date on stress in white-tailed deer exposed to these conditions. The understanding of this concept would greatly improve white-tailed deer management efforts, as well as provide significant insight into white-tailed deer physiology and behavior. The aim of this study was to develop an understanding of the relationship between social stress and population characteristics in white-tailed deer. The specific objectives were to: (1) determine whether levels of fecal glucocorticoids differed between fenced and non-fenced populations of white-tailed deer, (2) examine seasonal variation in levels of fecal glucocorticoids, and (3) determine whether levels of fecal glucocorticoids differed between males and females. We hypothesize that levels of fecal glucocorticoids will be greater in a fenced population, that levels will be greater during the peak of the breeding season for both males and females, and that males will exhibit greater levels of corticosterone than females.

METHODS

Description of Study Area

The property of Three Notch Wildlife Research Foundation (hereafter Three Notch) was located in east-central Alabama, approximately 10 km east of Union Springs in Bullock County. The study area encompassed 258.2 ha, and has been enclosed by 3-m deer-proof fencing since 1997. Food plots and supplemental feeding provided the deer herd with a high quality diet throughout the year. A high protein commercial deer feed (20% protein; Purina Antlermax, St. Louis, Missouri) was provided ad libitum. Approximately 20% of the available habitat (48 ha) was farmed to provide deer with an array of food sources. Warm-season food plots generally consisted of iron and clay peas (*Vigna sinensis*), corn (*Zea mays*), and various clovers (*Trifolium spp*.), while cool-season plots were usually made up of winter rye (*Secale cereale*) and white clover (*Trifolium repens*).

Forest cover on the site varied from open, mature stands of loblolly pine (*Pinus taeda*) in upland areas, to dense overstories of oaks (*Quercus spp*.) in creek drainages. Ridges were primarily dominated by loblolly pine or food plots, and lowland areas were planted in clover. Prescribed fire was used each year in upland areas to facilitate searches for shed antlers as well as to provide natural browse for deer. Water sources on the site included the headwaters of the Pea River and a large centrally-located pond (~ 20 ha) that provided the deer herd with an abundant year-round water source.

Hunting on the property was non-commercial, and generally limited only to the landowner and family members. Archery was the primary method of harvest, with approximately 50 deer harvested per year (approximately 30-40% bucks). Harvest was limited to mature bucks (5 years or older) and does of any age class. Due to limited hunting success (archery equipment only), the selective harvest of the landowner, and an abundance of food sources, the enclosure was overpopulated with a sex ratio favoring males. A mark-recapture camera survey conducted in the fall of 2007 (Jacobson et al. 1997) had estimated density at a minimum of 1 deer per 1.7 ha, which is more than 3 times the density normally found in this region, and a sex ratio of 2:1 (male:female).

Sampling Protocol

On Three Notch, fresh fecal samples were collected throughout the year. We defined fresh samples as those that were still soft, moist, and coated with mucous. In the absence of rainfall, glucocorticoid concentrations remain stable in feces for at least 7 days (Washburn and Millspaugh 2002), so all fecal samples should have provided reliable estimates of fecal glucocorticoid concentrations.

We collected fecal samples about three times per week during each of the 4 months surrounding the breeding season (Nov. 1, 2006 – March 22, 2007 and Nov. 1, 2007 – Feb. 28, 2008). Each day we randomly selected at least two starting points for our search effort, which allowed us to assume that each animal in the enclosure had an equal opportunity of being sampled throughout the study period. Once a location was selected, we searched for fresh fecal samples throughout the interconnecting network of game trails and bedding areas in the vicinity of our starting location. In southeastern Alabama, breeding activity usually ranges from November through February, with peak breeding activity occurring in late January (Causey 1990). By collecting samples before and after the time of peak breeding activity, we were able to examine how stress levels fluctuate before, during, and following the breeding season.

We also collected fecal samples from white-tailed deer that were not enclosed by a high fence. These samples were collected from hunter-harvested deer at deer processors in the vicinity of Auburn, Alabama throughout the hunting season (11 Jan. 2007 – 24 Jan. 2007 and 17 Nov. 2007 – 30 Jan. 2008). We obtained fecal samples by extracting feces from the last 15 cm of the colon. These data were assumed to reflect characteristics typical of deer found in east-central Alabama and were used to compare against those collected from our study area.

Glucocorticoid Analysis

Upon collection, fecal samples were homogenized (mixed), transported to the lab and frozen at -80ºC until processed. Approximately 10 g of each frozen sample was thawed and placed in a lyophilizer for 24 hrs. Once freeze-dried, they were ground, sifted through a stainless steel mesh (No. 25 standard US units), and thoroughly mixed (Wasser et al. 1994, 1996; Millspaugh et al. 2001, 2002). Glucocorticoids were extracted using a modification of Schwarzenberger et al. (1991). Dried feces (0.2 g) were placed in a test tube with 2.0 ml of 90% methanol and vortexed for 30 min. Samples were then centrifuged at 2,200 rpm for 20 min and the supernatant saved and stored at -80ºC until assayed. Glucocorticoids were measured using MP Biomedicals ^{125}I-corticosterone radioimmunoassay (RIA) kits (MP #07-120103, MP Biomedicals, Orangeburg, NY) that have been previously validated to accurately measure fecal glucocorticoid concentrations in white-tailed deer (Millspaugh et al. 2002). The protocol for the ^{125}I-corticosterone RIA was followed, except the volume of all reagents was halved. Fecal extracts were diluted 1:20 in assay buffer, and concentrations were expressed on a dry-weight basis (ng/g). The antiserum had the following cross-reactivities (provided by the company):

100% corticosterone, 0.34% desoxycorticosterone, 0.1% testosterone, 0.05% cortisol, 0.03% aldosterone, 0.02% progesterone, 0.01% androstenedione, and 0.01% 5α-dihydrotestosterone.

Testosterone Analysis

To determine the sex of fecal samples collected in the field, we also measured testosterone using a commercially available testosterone enzyme immunoassay (EIA) kit (DSL-10-4000, Diagnostic Systems Laboratories, Webster, Texas). Testosterone was extracted from feces following the same protocol as used for glucocorticoids. The particular kit that we used did not supply diluent, as the protocol for the assay does not call for any dilutions. Therefore, in order to dilute our samples we used the wash solution provided in the kit (buffered saline with a nonionic detergent, mixed with deionized water). To verify the use of the wash solution as a diluent, we diluted a selection of samples with both the wash solution and the 0 ng/g testosterone standard. There were no differences in our results, so we assumed that the wash solution was a suitable diluent for use in our EIA. Fecal extracts were diluted 1:32 in saline buffer prior to assay, and concentrations were expressed as ng/g (dry weight). The antiserum had the following cross-reactivities (provided by the company): 100% testosterone, 6.6% 5α-dihydrotestosterone, 2.2% 5-androstane-3β, 17β-diol, 1.8% 11-oxotestosterone, 0.9% androstenedione, 0.6% 5β-dihydrotestosterone, 0.5% 5β-androstane-3β, 17β-diol, 0.4% estradiol-17β, and 0.2% 5α-androstane-3α-ol-17-one. We conducted parallelism tests with serially diluted fecal extracts (1:2 – 1:64) and the standard curve (0.1 – 25 ng/mL) to validate this assay for use in white-tailed deer. To assess physiological relevance of the fecal testosterone measurements, we assayed fecal extracts of harvested animals (known sex), and calculated a range of testosterone concentrations for males and females. Male testosterone concentrations varied widely, but all were greater than females. To assign a sex to each field-collected sample (unknown origin), we calculated a 99% confidence interval for female concentrations, and deemed anything greater to be male.

Statistical Analysis

To satisfy the requirements of normality, all fecal data (corticosterone and testosterone) were transformed using the natural log (Fichtel et al. 2007). Data were analyzed using a factorial ANOVA (PROC GLM, SAS Institute 9.1, Cary, NC, USA) with period, sex, and year as main effects, and year*sex, year*period, period*sex, and year*period*sex as the interaction effects. We separated the breeding season into three periods: pre-rut (Nov.1 – Dec. 31), rut (Jan. 1 – Feb. 8), and post-rut (Feb. 9 – Mar. 22) to allow for comparison among periods prior to, during, and following the breeding season. Several females at Three Notch were harvested during the summers of 2007 (n = 13) and 2008 (n = 12) to aid in population control and to provide information on the timing of the breeding season via fetal aging. According to these data, peak of the breeding season occurred between the last week of January and the first week of February during both years of the study.

A separate ANOVA was used to compare males during the rut in the study population to the free-range population, with group (fenced, free-range) and year as main effects. Multiple comparisons were made of least-squares means with a Tukey-Kramer adjustment. The relationship between corticosterone and testosterone was examined with a correlation (PROC CORR, SAS Institute 9.1), using Pearson's correlation coefficient. In order to further explore this relationship, we created three equal sized groups based on testosterone concentration (Low = 80 – 179 ng/g, Medium = 180 – 512 ng/g, High = 519 – 10,965 ng/g), and examined mean corticosterone concentrations for each group during each phase of the breeding season. We performed a two-factor ANOVA, with period and testosterone group as the main effects. The level of significance was set at 0.05 for all statistical tests, which were performed using SAS 9.1 (SAS Institute, Cary, NC, USA).

RESULTS

Fecal Glucocorticoids

We collected and assayed 537 fecal samples (438 male, 99 female) from the high-fenced population. Male glucocorticoid concentrations ranged from 9.42 ng/g to 362.82 ng/g ($\bar{x}$ = 33.02 ± 1.25), and females ranged from 8.43 ng/g to 47.95 ng/g ($\bar{x}$ = 18.38 ± 0.63). We found a significant period*sex interaction (Factorial ANOVA: $F_{2,525} = 7.46$, $P < 0.001$), where fecal glucocorticoid levels of males were greater during the rut than the pre-rut ($P < 0.001$; Fig. 1), and post-rut ($P < 0.001$), while female glucocorticoid levels remained relatively stable throughout the breeding season. Male corticosterone concentrations were greater than females during the pre-rut ($P < 0.001$) and rut ($P < 0.001$).

Limited data collection allowed us to only compare males of the fenced population and the free-range population during the rut. There was a clear year effect in our data (two-factor ANOVA: $F_{1, 228} = 39.82$, $P < 0.001$). The free-range sample had a 75% greater mean corticosterone concentration than the fenced population in 2007 ($P < 0.001$; Fig. 2A). However, in 2008 the fenced population had an almost 84% greater mean concentration of corticosterone than the free-range ($P < 0.001$).

Testosterone

Mean testosterone concentrations for females and males were 36.03 ± 1.52 ng/g and 825.86 ± 67.27 ng/g, respectively. Testosterone concentrations varied widely for males [range (excluding fawns): 80 ng/g – 10,965 ng/g], but were fairly consistent for females (range: 9.28 ng/g – 69.05 ng/g). Male testosterone peaked during the rut (Factorial ANOVA: $F_{2,523} = 12.59$, $P < 0.001$; Fig. 3), more than doubling in concentration from pre-rut levels, then returned to pre-rut levels during the post-rut.

Comparing fecal testosterone concentrations in the fenced and free-range populations, we found a year*group interaction (two-factor ANOVA: $F_{1,223} = 12.26$, $P < 0.001$). There was no difference in testosterone concentration between the two groups during the first year ($P = 0.998$; Fig. 2B), but the fenced population had a greater mean concentration than the free-range population in the second year ($P < 0.001$). Examining the two groups individually, the fenced population exhibited a greater mean concentration in the second year than the first ($P = 0.004$), and the free-range population showed a decrease in the second year, though not statistically significant ($P = 0.07$).

We found a significant correlation between male corticosterone concentrations and corresponding testosterone levels ($n = 466$, $r = 0.596$, $P < 0.001$; Fig. 4). To clarify this relationship, we created three equal sized groups based on testosterone concentration, and examined corticosterone concentrations for each group during each phase of the breeding season. We found a significant period*group interaction (two-factor ANOVA: $F_{4,429} = 7.62$, $P < 0.001$; Fig. 5), where, during the pre-rut and rut, the high testosterone group had a greater corticosterone concentration than both the low and medium groups ($P < 0.001$ and $P < 0.02$, respectively). The medium group was also greater than the low group during the pre-rut ($P = 0.031$), but there was no difference ($P = 0.304$) between the low and medium groups during the rut. Interestingly, we observed no difference ($P > 0.993$) in corticosterone concentration among the three groups during the post-rut period.

DISCUSSION

Fenced vs. Free-Range

The major focus of this study was to determine if a population of white-tailed deer at high density with ample nutrition was subject to abnormally elevated levels of stress. However, there was an odd year effect in our data when we compared the fenced population to those harvested under free-range conditions, which makes it difficult to draw firm conclusions. While we only used data from the rut for this particular analysis, there was a high degree of variability in mean corticosterone concentrations between years in both the free-range and high-fenced populations. Our original hypothesis that the high density, fenced population would undergo a more pronounced stress response during the rut than the free-range population was rejected during the first year, but the data from the second year supported our original hypothesis. First and foremost, these findings may demonstrate the importance of using multiple years of data, as stress levels can be highly variable from one year to the next.

The variability that we observed can best be explained by nutritional differences between populations from year to year. In the first year, when stress levels in free-range deer were greater, the quality of nutrition would have been much greater in the fenced population due to the extensive food plots and supplemental feeding program. In contrast, there was above average hard mast production during the second year, which may have ‘leveled the nutritional playing field’ between the fenced and free-range populations. With the high mast availability, deer at Three Notch consumed little supplemental feed in early fall, and the landowner elected to suspend the supplemental feeding program until February. The measured increase in stress levels during the second year may be reflective of the fact that bucks at Three Notch rely heavily on supplemental feed during the rut to meet their nutritional demands. The disparity in fecal glucocorticoid measurements from year to year, and between groups is likely due to this change in available nutrition.

During the rut when males are continually searching for receptive females, nutrition is not a priority. It has been well documented that male ungulates reduce feeding effort during the breeding season, which is most often attributed to the conflicting time constraints of finding food and/or participating in rutting activities (e.g. fighting, dominance displays, chasing; Espmark 1964, Coblentz 1976, Lincoln and Short 1980, Geist 1982). In year one, males in our fenced population were surrounded by high quality forages (e.g., food plots and supplemental feed) at concentrations greater than what is normally available for most free-ranging deer, and, thus could have obtained adequate nutrition without sacrificing time that could be spent searching for potential mates.

In 2008, without supplemental feeding during the rutting period, males at Three Notch experienced greater levels of stress than the previous year. Though not statistically significant (t-test: $t_{20} = 1.18$, $P = 0.126$), harvest data suggested that male body weights were greater in 2007 (n = 14, $\bar{x} = 86.28$ kg) when supplemental feeding was available, than in 2008 (n = 8, $\bar{x} = 81.65$ kg). Declining nutritional intake has been associated with elevated stress in a number of mammalian species (Saltz and White 1991, DelGiudice et al. 1992, Tsuma et al. 1996). Saltz and White (1991) found that urinary cortisol:creatinine ratios increased with increasing density and decreasing nutrition, but in most cases an increase in available food by supplemental feeding reduced cortisol levels. Glucocorticoids increase the rate of gluconeogenesis in the liver, decrease protein synthesis, increase protein catabolism, and mobilize fatty acids from adipose tissues. These processes are designed to ensure adequate fuels for the body in the absence of adequate nutrition, and an increase in stress levels can be attributed to this metabolic compensation during periods of undernourishment (Foster and McGarry 1988). Additionally, a study in Michigan's Upper Peninsula of a supplementally-fed population of white-tailed deer, did not provide any evidence of a density-dependent increase in glucocorticoid secretion. The population was allowed to grow from 23 to 159 animals, but because of a year-round supply of high quality supplemental feed, the authors did not find that stress levels increased with increasing population density (Seal et al. 1983). Our results indicate that a high density, fenced population of white-tailed deer may need to have access to high quality supplemental feed specifically during the rut, to alleviate the stresses of breeding and lack of winter forage.

Seasonal Variation

Our data revealed that there was a period effect, where the intensity of rutting activity apparently drives corticosterone levels in male white-tailed deer. Pre-rut levels were elevated in males, which we attribute to rising testosterone levels and subsequent increases in male-male aggressive interactions, sparring matches, and dominance displays that serve to firmly establish social status. Corticosterone levels of males in the fenced population increased by an average 66% during the rutting period, when sparring matches would have increased in intensity and frequency, and males would have been continually chasing females to secure breeding opportunities (Marchinton and Hirth 1984). There have been conflicting reports regarding seasonal rhythms in glucocorticoid secretion in white-tailed deer. Bubenik et al. (1975) found no evidence of seasonal variation in cortisol secretion, but others have found greater glucocorticoid secretion during the rutting season (Bubenik et al. 1983, Bubenik and Leatherland 1984). These conflicting reports could be a result of the inconsistencies in measures of stress hormones that are associated with blood collection (Harper and Austad 2000, Millspaugh et al. 2001). Non-invasive measures, such as the one used in this study, most likely provide a more accurate examination of how glucocorticoid secretion fluctuates over time (each data point represents average glucocorticoid secretion over a 1-2 day period). However, other studies have found that glucocorticoid secretion did not coincide with the breeding season. Millspaugh et al. (2001) found the greatest stress levels in one elk (*Cervus elaphus*) population were during the summer months when they were subject to increased human disturbance. Studies on other mammalian species have shown an increase in stress as a direct result of agonistic interactions (Sapolsky 1992, Muller and Wrangham 2004, Bergman et al. 2005). Fichtel et al. (2007) found increased stress levels in Verreaux's sifakas (*Propithecus verreauxi*) during the breeding season. They surmised that since the breeding season coincided with the rainy season where food is most abundant, the increase in stress was a result of aggressive encounters between individuals. In our study, it is not clear whether increase in corticosterone levels during the rut was driven by nutritional deficiencies (e.g., nutritional stress), or if it was mainly a result of increased rates of agonistic encounters (e.g., social stress). More than likely, both nutrition and social dynamics influenced stress levels in our study populations.

We hypothesized that increased harassment by males during the rut would have caused elevated stress in the female segment of the population as well. Surprisingly, female corticosterone levels remained relatively stable throughout the breeding season. Apparently, harassment by males did not elicit an elevated stress response in females. We propose that it would be advantageous for a female to avoid an increase in glucocorticoid secretion, especially during the breeding season. Elevated levels of glucocorticoids are known to suppress reproductive function in several ways (Wingfield and Sapolsky 2003), one of which is ovarian response to luteinizing hormone (LH) secretion. LH is required to initiate estrus, and increases dramatically at the beginning of estrus (Plotka et al. 1980). Since LH is required for estrus, and glucocorticoids inhibit this reproductive hormone, it would be evolutionarily beneficial for a female deer to avoid undergoing a stress response during the breeding season. This could be one possible explanation for why we did not observe any changes in female glucocorticoid secretion over the course of the breeding season. If a significant stress response is noted in females during the breeding season, it would be a strong indication that social dynamics in the population may be having a negative impact on reproduction. Even though we did not observe a spike in female corticosterone, there can be other negative effects on females as a result of extremely high densities. In another study of white-tailed deer at high density, Ozoga and Verme (1982a) observed reduced productivity in yearling does in what they hypothesized to be a result of constant harassment by bucks during the rut which resulted in an energy deficiency. They also reported increased fawn mortality at high density, which was attributed to overcrowding and limited fawn-rearing space.

Corticosterone and Testosterone

Male testosterone peaked during the rut, which followed a periodic pattern similar to corticosterone. This seasonal fluctuation was expected, and has been reported elsewhere in reindeer (*Rangifer tarandus*; Leader-Williams 1988), axis deer (*Axis axis*; Bubenik et al. 1991), Père David's deer (*Elaphurus davidianus*; Li et al. 2001), and white-tailed deer (Mirarchi et al. 1978, Bubenik et al. 1983, Ditchkoff et al. 2001). However, fluctuations of mean testosterone levels between years in each population were surprising. We cannot find any previous documentation where mean testosterone levels changed substantially over multiple years in white-tailed deer or other deer species, and, if so, there is no indication that testosterone was significantly different from one year to the next. We do not have a solid explanation as to why levels of testosterone differed in the two years of the study, but we are relatively certain that laboratory errors were not responsible, since, in year two, the average testosterone concentration in the fenced group increased while the free-range group decreased. We would suspect that if laboratory error was responsible for the differences, our results in year two would have differed from year one in the same direction for both groups.

Nonetheless, the change in testosterone from year one to year two is an interesting pattern, especially in regards to how it mirrors the accompanying changes in corticosterone. When males of the fenced population had greater testosterone than the free-range population, they also exhibited greater corticosterone levels. It appears that testosterone may play a major role in glucocorticoid secretion during the breeding season.

During the pre-rut and rut periods, each testosterone group (low, medium, high) corresponded to progressively greater corticosterone concentrations. However, this relationship was not evident in the post-rut period. The time of actual conception occurs within a two-week period in this high-fenced population (McCoy, unpublished data) because the abundance of males assures that most, if not all, females are bred when they first come in estrous. Given this information, the sharp decline in testosterone and corticosterone following the breeding season is likely due to the almost instantaneous cessation of breeding activity. Males with high testosterone in the post-rut did not exhibit the same elevated levels of corticosterone as in the pre-rut and rut. This may be evidence that the effect of testosterone on corticosterone is partially a result of testosterone-induced behavior, and not strictly a physiological link between two hormones.

MANAGEMENT IMPLICATIONS

Analysis of voided feces has become a popular method of monitoring physiological parameters of many wildlife species. In our study, we found that stress levels can be highly variable from one year to the next, and as a result should be monitored over a significant period of time to observe any trends or draw any firm conclusions regarding physiological health. The spike in corticosterone concentrations of male white-tailed deer during the rut was consistent from year to year, and is a natural phenomenon that will happen as a result of breeding competition. Likely, the overall health of individuals is not compromised as a result of this stressful time period. As stated before, acute stress responses are designed to benefit an organism during times of stress. However, in populations where the breeding season is extended due to an unbalanced sex ratio or age structure, the period of time during which males would experience elevated levels of stress would increase, thus possibly compromising the health of the individual. The best thing we can do as wildlife managers is to provide as much nutrition as possible during this stressful period, as well as maintain a population with a properly balanced sex ratio in order to minimize the length of the breeding season.

Monitoring stress levels of females may be a more useful tool in managing white-tailed deer populations. In our study, female stress levels remained constant throughout the breeding season, concurrent with the notion that females may resist excessive glucocorticoid secretion since it could suppress reproductive capabilities. If female stress levels were to dramatically increase during the breeding season, there could be a possibility of reduced reproductive success, thus hinting that social dynamics were impacting the health of the population.

We conducted all of our research during the breeding season, from November to mid-February. We believe it would be interesting and beneficial to investigate stress levels throughout the year to determine any other potentially stressful times, such as antler regeneration and fawning. Ozoga and Verme (1982a) reported high fawn mortality in a study on a high density population, which they attributed to limited fawn rearing space. An examination of the associations between concentrations of fecal stress hormones and the periods of parturition and lactation would help provide a more complete picture of the role that stress plays in white-tailed deer populations.

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Figure 1.1. Mean corticosterone concentrations for a fenced population of white-tailed deer during the pre-rut (Nov. 1 – Dec. 31), rut (Jan. 1 – Feb. 8), and post-rut (Feb. 9 – Mar. 22) periods of the breeding season at Three Notch in east-central Alabama.

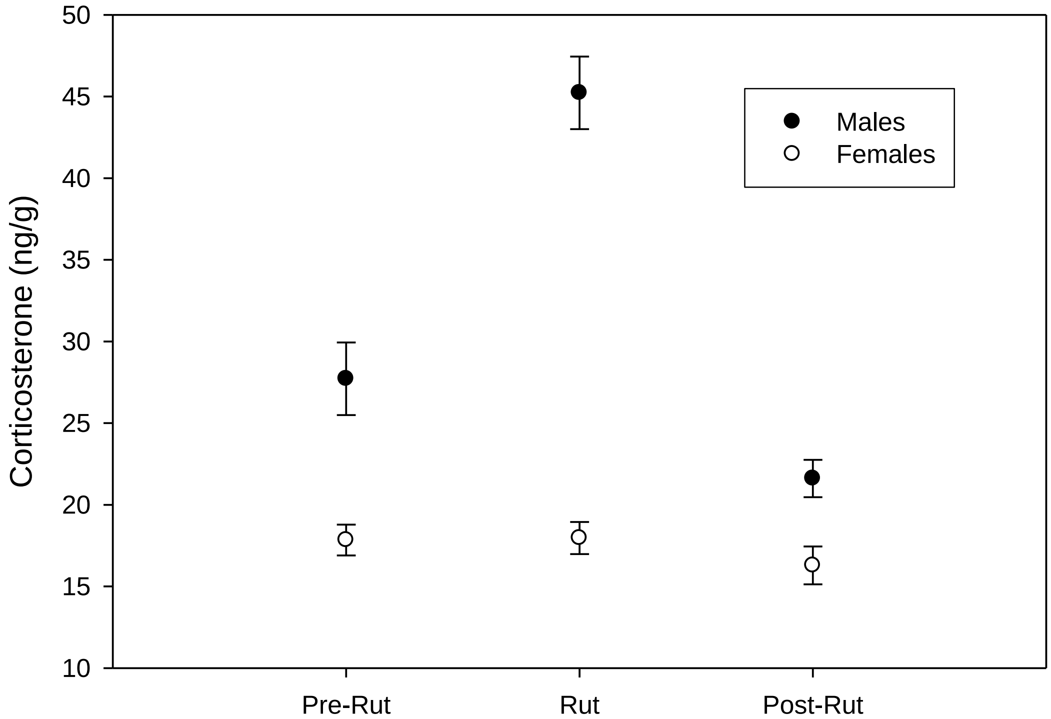

Corticosterone (ng/g)
50
45
40
35
30
25
20
15
10
Pre-Rut
Rut
Post-Rut
Males
Females

Figure 1.2. Mean corticosterone (A) and testosterone (B) concentrations for fenced and free-range white-tailed deer populations during the rut (Jan. 1 – Feb. 8) in 2007 and 2008 in east-central Alabama.

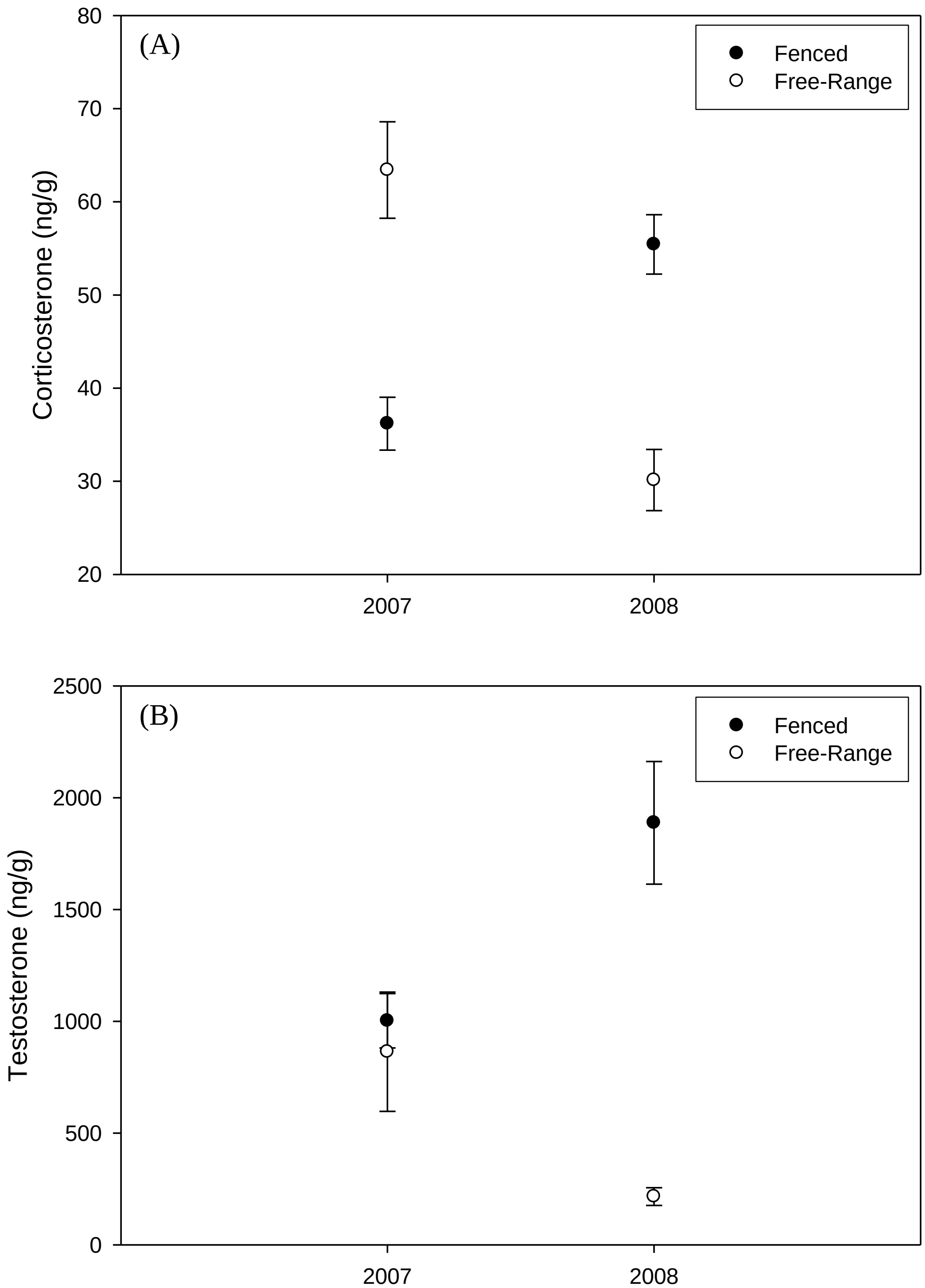

(A)
Fenced
Free-Range
Corticosterone (ng/g)
80
70
60
50
40
30
20
2007
2008
(B)
Fenced
Free-Range
Testosterone (ng/g)
2500
2000
1500
1000
500
0
2007
2008

Figure 1.3. Mean testosterone concentrations for a fenced population of white-tailed deer during the pre-rut (Nov. 1 – Dec. 31), rut (Jan. 1 – Feb. 8), and post-rut (Feb. 9 – Mar. 22) periods of the breeding season.

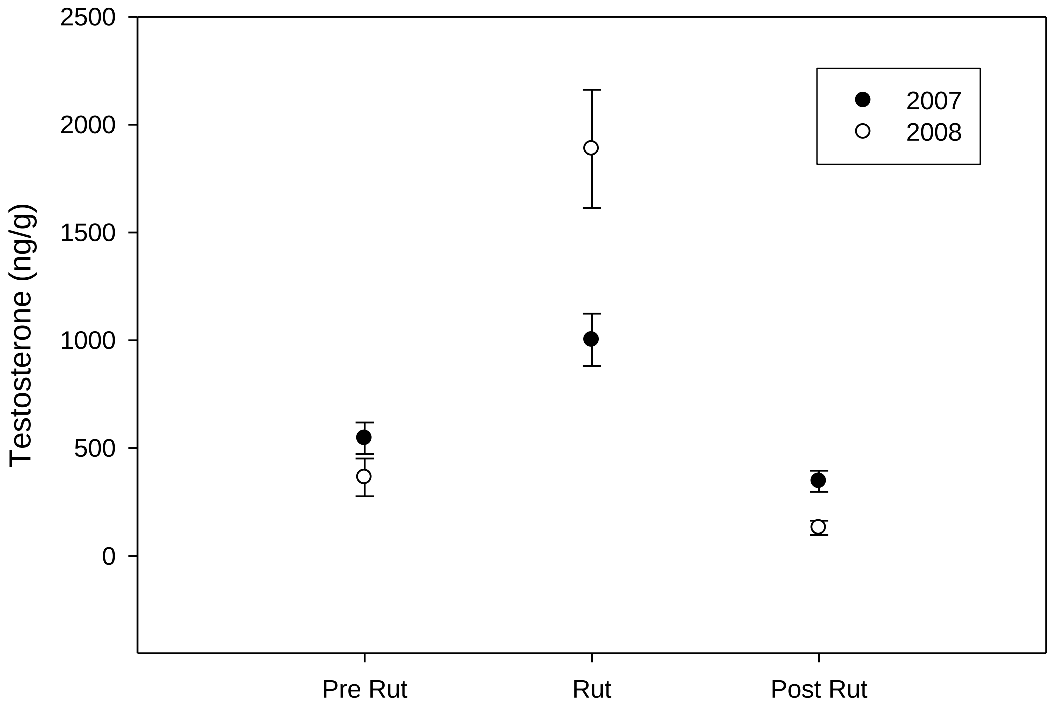

Testosterone (ng/g)
2500
2000
1500
1000
500
0
2007
2008
Pre Rut
Rut
Post Rut

Figure 1.4. Correlation showing the relationship between testosterone and corticosterone of male white-tailed deer in east-central Alabama.

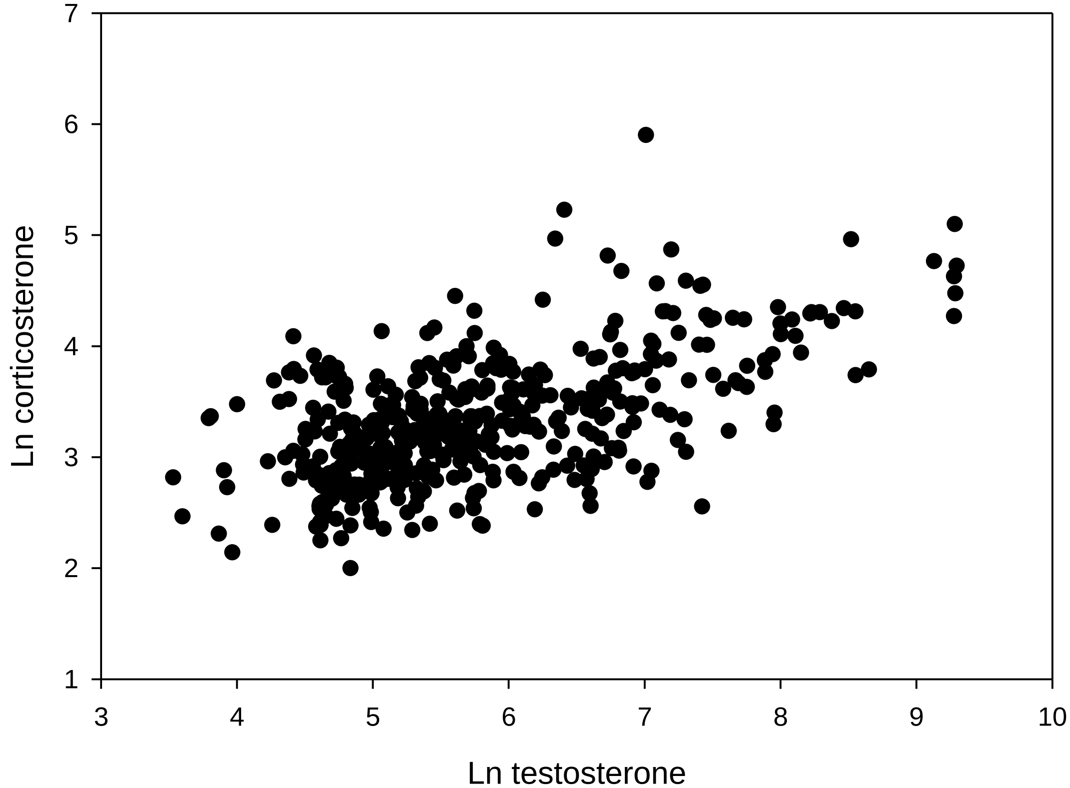
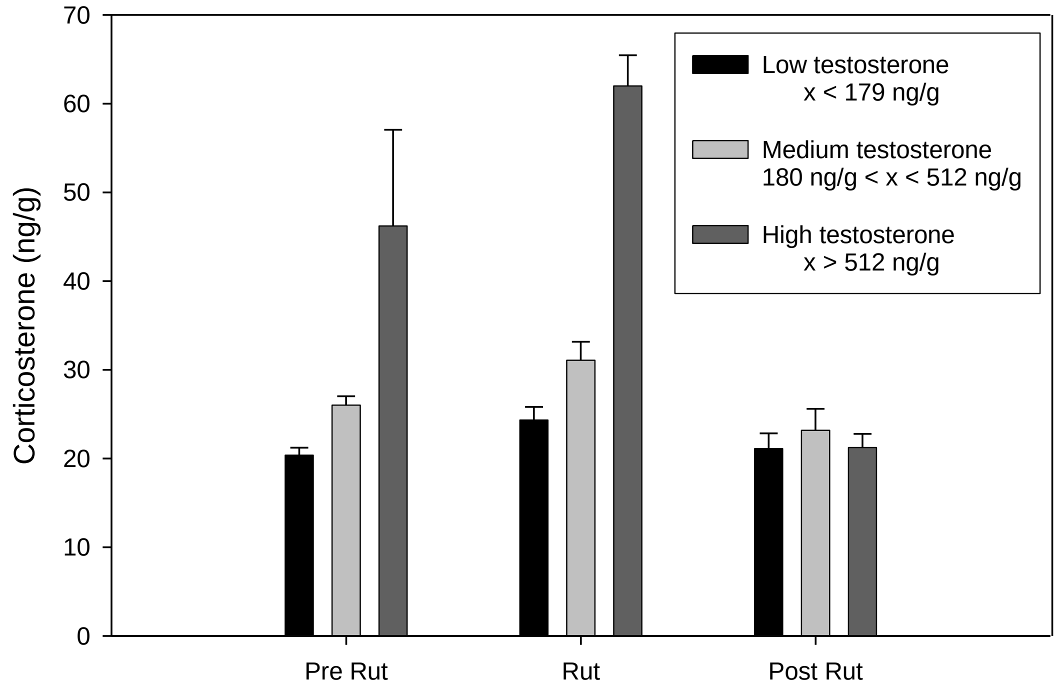

7
6
5
4
3
2
1
3
4
5
6
7
8
9
10
Ln corticosterone
Ln testosterone

Figure 1.5. Mean corticosterone concentrations of a fenced population of male white-tailed deer during the pre-rut (Nov. 1 – Dec. 31), rut (Jan. 1 – Feb. 8), and post-rut (Feb. 9 – Mar. 22) periods of the breeding season with low (< 179 ng/g), medium (between 180 ng/g and 512 ng/g), and high (> 512 ng/g) testosterone levels.


70
60
50
40
30
20
10
0
Corticosterone (ng/g)
Pre Rut
Rut
Post Rut
Low testosterone
x < 179 ng/g
Medium testosterone
180 ng/g < x < 512 ng/g
High testosterone
x > 512 ng/g

II. BIAS ASSOCIATED WITH BAITED CAMERA SITES FOR ASSESSING POPULATION CHARACTERISTICS OF WHITE-TAILED DEER

ABSTRACT

Because of its ease of use and cost efficiency, remote photography seems to be increasing in popularity as a tool for scientists and wildlife biologists. Camera surveys have been used to estimate population parameters among a variety of species, including white-tailed deer. However, this survey technique often involves placing bait in front of the camera in order to capture animals more frequently, which could introduce biases in parameter estimates. From September 2008 to March 2009, we monitored cameras placed at random, along game trails, and at feed stations to determine if sex/age structure could be accurately assessed in a population of white-tailed deer. Since cameras placed at random should provide the least biased estimates of population structure, we compared estimates from feed stations and trail-based cameras to those from random sites to determine if they accurately assess population structure. Our results indicated that there was no single time period in which cameras placed at feed stations provided sex ratio and recruitment estimates similar to those acquired from randomly placed cameras. Trail-based camera surveys provided population estimates very similar to those from random sites, and may provide a feasible alternative to using baited camera stations.

INTRODUCTION

The use of remote photography in wildlife science has become increasingly popular in recent years, especially since the development of infrared-triggered camera systems. Cameras have proved useful in answering a variety of wildlife related questions including studies of nest predation (Hunt and Ogden 1991), feeding ecology (Hanula and Franzreb 1995), activity patterns (van Shaik and Griffiths 1996), and species presence (Foster and Humphrey 1995). Camera systems are less invasive and more cost efficient than most observation methods (Cutler and Swann 1999). In addition, cameras are less labor intensive (Seydack 1984), provide permanent documentation of captured animals (Bull et al. 1992), and provide the opportunity to gather data during otherwise difficult times (e.g., inclement weather, at night).

Remote photography has also been used to estimate population parameters among a variety of species (Jaeger et al. 1991, Mace et al. 1994, Trolle and Kery 2003, Karanth et al. 2004), including white-tailed deer (*Odocoileus virginianus*; Jacobson et al. 1997). Because of the importance of the white-tailed deer as a game species, reliable estimates of population parameters are critical to making management and harvest decisions. Numerous methodologies have been employed to estimate population parameters of white-tailed deer populations, but most have drawbacks. Aerial surveys, by way of helicopter counts, are costly and aren't practical in most regions of the white-tailed deer range (Koerth et al. 1997). Line transects involving pellet group and track counts (Mooty and Karns 1984) are labor intensive and do not provide information regarding age structure or sex ratios. Historically, spotlight surveys may be the most commonly used method of estimating population parameters, but they have low, and highly variable detection probabilities (Collier et al. 2007). Thermal imaging equipment has also been used to detect animals, but equipment costs are extremely high (Collier et al. 2007).

Remote photography, because of its ease of use and cost efficiency, seems to be increasing in popularity as a tool for scientists and wildlife biologists, and is even a popular technique for managing deer populations among landowners outside the scientific community. Jacobson et al. (1997) developed a technique to estimate population density of deer in Mississippi using infrared-triggered cameras. The authors identified individual males based on antler configurations and used ratios of all animals photographed to determine population size and sex ratios. However, this census technique involves placing bait (usually shelled corn) in front of the camera in order to capture animals more frequently (Jacobson et al. 1997, Koerth et al. 1997). Jacobson et al. (1997) cautioned that individuals may not use bait equally, and, as a result, the possibility exists for biased estimates. Unequal detectability (Larrucea et al. 2007) among sexes and/or age classes would bias parameter estimates, and could ultimately lead to misinformed management decisions.

We had a unique opportunity in a fenced, high-density population to monitor random camera sites, which should provide the least biased estimate of population structure. Our main objective in this study was to compare proportions of animals captured at feed stations and along game trails to those captured at random sites in order to determine if animals captured at baited sites and along trails differed from those captured at random locations. Since important management decisions are based on sex ratios and recruitment rates gleaned from photographic data, verifying that these parameters are accurately assessed in the presence of bait is critical. We also examined seasonal fluctuations in feeder use, with a specific emphasis on determining the best time of year to conduct a camera survey that yields the least biased population parameters.

METHODS

Description of Study Area

The property of the Three Notch Wildlife Research Foundation (hereafter Three Notch) was located in east-central Alabama, approximately 10 km east of Union Springs in Bullock County. The study area encompassed 258.2 ha, and has been enclosed by 3-m deer-proof fencing since 1997. Food plots and supplemental feeding provided the deer herd with a high quality diet throughout the year. A high protein commercial deer feed (20% protein; Purina Antlermax, St. Louis, Missouri) was provided ad libitum in 12 permanent feed troughs uniformly distributed across the property. Approximately 20% of the available habitat (48 ha) was farmed to provide deer with an array of food sources. Warm-season food plots generally consisted of iron and clay peas (*Vigna sinensis*), corn (*Zea mays*), and various clovers (*Trifolium spp*.), while cool-season plots were usually made up of winter rye (*Secale cereale*) and white clover (*Trifolium repens*).

Forest cover on the site varied from open, mature stands of loblolly pine (*Pinus taeda*) in upland areas, to dense overstories of oaks (*Quercus spp*.) in creek drainages. Ridges were primarily dominated by loblolly pine or food plots, and lowland areas were planted in clover. Prescribed fire was used each year in upland areas to facilitate searches for shed antlers as well as to provide natural browse for deer. Water sources on the site included the headwaters of the Pea River and a large centrally-located pond (~ 20 ha) that provided the deer herd with an abundant year-round water source.

Hunting on the property was non-commercial, and generally limited only to the landowner and family members. Archery was the primary method of harvest, with approximately 40 deer harvested per year (approximately 30-40% bucks). Harvest was limited to mature bucks (5 years or older) and does of any age class. Due to limited hunting success (archery equipment only), the selective nature of the landowner, and an abundance of food sources, population control within the enclosure was a challenge. Also, since only mature males were harvested, there was a relatively low harvest of young bucks. These factors had combined to create a high density population with a skewed sex ratio favoring males. A pre-study camera survey using the methodology of Jacobson et al. (1997) had estimated density at a minimum of 1 deer per 1.7 ha, which is more than 3 times the density normally found in this region. Analysis of this camera survey data also indicated that the adult sex ratio favored males, at approximately a 2:1 (male:female) ratio.

Equipment

We used eight commercially available PixController DigitalEye 7.2 MP trail cameras (PixController Inc., Export, PA). These units consisted of a 7.2 megapixel Sony camera attached to a passive infrared (PIR) motion sensor, all encased within a weather-resistant shell. A number of different settings could be used, but we chose to use the integrated Trail Mode, for cameras set randomly and along well-used trails. This feature keeps the digital camera powered up for 30 seconds after taking a photo so that all animals passing by at a given time have a chance to be photographed. Each additional time the PIR sensor is triggered, the 30 second window is extended. Previous research has shown that deer feed at trough feeders for a mean of 2.6 (Zaiglin and DeYoung 1989) to 10 minutes (Kozicky 1997), so we used time interval of 5 minutes for cameras placed at feed stations, to reduce the number of replicate pictures of the same individuals (Koerth and Kroll 2000).

Study Design

We monitored cameras placed at random, along heavily used game trails, and at feed stations from September 11, 2008 – March 5, 2009. Each sampling period consisted of one week, for a total of 19 sampling periods. During each sampling period we randomly generated 3 GPS locations for the random and 3 locations for the trail treatments, and randomly selected two of the 12 feed stations to place our cameras. In order to standardize our random sites, we oriented all random cameras facing north, so as to minimize observer bias in placement as well as to avoid glare from the rising or setting sun. When placing cameras on trails, we navigated to the randomly generated GPS location and then searched for the closest, heavily-used game trail. At feed stations, which were generally located in open fields, we attached cameras to a T-post driven into the ground approximately 3 m away from the feed trough. Cameras at these feed stations were oriented at a ~45 degree angle to the feed trough, so as to attain maximum coverage of the feeding area.

Data Analysis

We recorded the number of fawns, does, and bucks in each photograph. Bucks were categorized into three age classes based on antler and body characteristics: yearling (1.5 years), adult (2.5-3.5 years), and mature (≥ 3.5 years). In our analysis, we only included photographs where the age and sex of the deer could be positively identified. To further improve our ability to correctly identify animals, we only used photographs of deer that were within ~10 m of the camera. At random and trail sites where the cameras were set to take photographs without delay, some deer were photographed multiple times on the same occasion. In these instances, we only counted individuals once. We used four seasons to determine any seasonal effects: fall (Sept. 11 – Oct. 31), pre-rut (Nov. 1 – Dec. 26), rut (Jan. 6 – Feb. 7), and post-rut (Feb. 8 – Mar. 5).

We modeled the data using R (R Development Core Team 2009). Specifically, we used the function ‘lmer’ within the package ‘lme4’ (Bates and Maechler 2009) to run a mixed-effects Poisson regression. We used the number of fawns, does, yearling or adult bucks in each picture as our dependent variable, and the total number of deer in each photograph as an offset. The model consisted of all main effects of season, treatment (random, trail, or feeder placement), and animal class, all associated interactions, and camera site as a random effect. Upon initial examination, no differences were detected between ‘adult’ and ‘mature’ bucks, so on the basis of parsimony, we combined these into one variable and re-ran the model. We ran a negative binomial (quasipoisson) to test for overdispersion, and determined that the mixed-effects Poisson model was adequate. We used ‘doe’ as the reference class, random as the reference treatment, and fall as the reference season. When making comparisons, we calculated 95% confidence intervals of the effect sizes of each parameter to determine if they differed from zero.

RESULTS

We counted a total of 5,311 deer in 3,972 distinct photographs. Not surprisingly, we photographed more deer at feed stations (n = 4,003; 75.37%) than at random (n = 461; 8.68%) or trail (n = 847; 15.95%) sites. At feed stations, specifically, we photographed more deer during the fall (n = 2,729; 68.17%) than during the pre-rut (n = 467; 11.67%), rut (n = 360; 8.99%), or post-rut (n = 447; 11.17%) periods. Combining all photographs taken at random locations throughout the study revealed a population structure of 14% fawns, 23% does, 12% yearling bucks, and 51% adult bucks. Cameras placed on game trails yielded similar estimates of population structure: 14% fawns, 29% does, 15% yearling bucks, and 42% adult bucks.

Doe use of feeders was similar to random sites during all seasons, but there appeared to be differences in the use of feeders compared to random sites among fawns, yearling bucks, and adult bucks (Table 1, Fig. 1). During the fall, the proportion of fawns captured at random was 3.10 times greater than those captured at feed stations (95% CL = 1.63 - 5.75), and yearling buck proportions were 1.86 times greater at feeders than at random sites (95% CL = 1.05 - 3.29). During the pre-rut, the proportions of yearling and adult bucks photographed at random were 1.77 (95% CL = 1.03 - 3.04) and 1.53 (95% CL = 1.06 - 2.20) times greater than those at feed stations, respectively. Likewise, during the rut, the proportions of yearling and adult bucks photographed at random were 2.41 (95% CL = 1.23 - 4.71) and 4.85 (95% CL = 3.35 - 7.03) times greater than those at feed stations, respectively. The proportions of fawns captured with cameras at feed stations were 1.67 (95% CL = 1.14 - 2.44), 5.47 (95% CL = 3.19 - 4.39), and 2.61 (95% CL = 1.28 - 5.31) times greater than those captured at random sites during the pre-rut, rut, and post-rut periods, respectively. Trail-based cameras provided estimates similar to those from random cameras in all but two cases. The proportions of adult bucks photo-captured at random sites during the fall and post rut were 1.37 (95% CL = 1.02 - 1.86) and 1.51 (95% CL = 1.04 - 2.18) times greater than those from trail-based cameras, respectively.

The proportion of adult bucks caught at random during the pre-rut was, at the least, 1.87 (95% CL = 1.28 - 2.74) times less than any of the other periods: as a result, we observed greater proportions of does and fawns at random and trail sites during this time.

DISCUSSION

Infrared-triggered cameras have become a popular and useful tool for indexing wildlife populations, especially white-tailed deer. However, the use of bait to attract animals to a camera site may bias population estimates since whether all animals use bait equally is unknown (Cutler and Swann 1999, Roberts et al. 2006). We found that feed stations did not provide assessments of population structure similar to those generated using random cameras during any single time period. Koerth and Kroll (2000), in a similar study, hypothesized that baited camera sites did not provide accurate estimates of sex and age structure during any single time period, although they did not have a baseline estimate of population structure to compare. If feed stations are to be used for examining populations characteristics, both the fall (pre-season) and post-rut periods provided estimates of adult population structure similar to those generated by random cameras, but did not provide accurate data for fawns. In populations that breed in November, a fall camera survey may provide more accurate data on fawn abundance than was detected in this study, making it the best time to conduct a camera survey when using baited sites. In populations where a majority of breeding occurs in January, multiple-season camera surveys would be necessary to accurately estimate all population parameters. Because post-rut surveys provide population estimates after the hunting season, they are not suitable for use in preparing harvest recommendations. However, feed stations may be useful in constructing pre-season harvest prescriptions, as they provided an estimate of adult population structure similar to randomly placed cameras during the fall period.

The lack of feeder use by bucks and heavy use by fawns during the pre-rut and rut periods suggests that interpretation of population structure during these periods may be biased. Not surprisingly, adult bucks were underrepresented at feed stations during the rut, as male ungulates reduce feeding effort during the breeding season due to the conflicting time constraints of finding food and/or participating in rutting activities (e.g. fighting, dominance displays, chasing; Espmark 1964, Coblentz 1976, Lincoln and Short 1980, Geist 1982). Along the same lines, fawns do not actively participate in rutting activities, and may be more inclined to visit feed stations in the absence of older individuals that are involved in breeding.

Estimating sex ratio is an integral part of deer management as well as a key aspect of estimating population density (Jacobson et al. 1997). Sex ratio estimates may be inaccurate when generated from camera surveys at feed stations during any time period other than the fall. For example, in our study the predicted sex ratio using random sites during the fall survey was 2.64 (bucks:doe). Using photographs from feed stations during this same period yielded a sex ratio estimate of 2.45, very similar to the random estimate. However, our data from feed stations yielded sex ratios that were not consistent with those generated from photographs collected at random sites throughout the remainder of the study. Sex ratio estimates at feed stations during the pre-rut, rut, and post-rut periods were 0.84, 0.83, and 3.73, respectively, while estimates generated with data from random sites during the same periods were 1.42, 4.89, and 5.10, respectively.

We hypothesize that the extreme sex ratio estimates garnered from the random sites during the rut and post-rut were due to the extreme harvest pressure on females, thus the proportion of does in the population dropped significantly by the end of the study. At Three Notch, according to previous population estimates, there were approximately 35 - 40 does in the population before hunting season (~25% of the population), so the harvest of does during the course of the study would have reduced the proportion by a significant amount. In this case, specifically, 13 does were harvested during the fall and pre-rut periods, which would have dropped the proportion of does in the population from 25% to 14-18%, which is very close to the estimates acquired from our random cameras during the rut and post-rut periods.

Recruitment estimates (fawns per doe) are also very important for deer managers, and provide critical information regarding reproductive health of the herd. During the fall, fawns were captured in photographs infrequently at all three camera treatments. This is most likely due to the fact that fawns in our study area are born during late summer (Causey 1990) and were not yet very mobile. As a result, in most parts of Alabama and other areas where breeding occurs in January, pre-season camera surveys are likely to underestimate recruitment because fawns are not active during this time period. In regions where breeding occurs in November, fall camera estimates of recruitment may be more accurate, making a pre-season survey the best time to estimate population parameters when using bait sites. In contrast, we found that estimates of recruitment would be grossly overestimated at feed stations during the remainder of the study period. Our estimates of recruitment using random sites were very similar throughout the season: 0.72, 0.74, and 0.80 for the pre-rut, rut, and post-rut periods, respectively. However, during those same periods we estimated recruitment at 1.13, 2.84, and 2.05, respectively, at feed stations. From our study feed stations apparently are not suitable locations for accurately estimating recruitment.

Our results suggest that trails provide population estimates that are very similar to randomly placed cameras during most seasons, and thus, may provide an alternative and less biased means for conducting camera surveys. Because we recorded almost twice as many photographs at trail sites than random sites, trail-based camera surveys could also be more efficient and provide larger sample sizes than randomly placed cameras. These results can be extended to studies that are designed to collect biological samples for white-tailed deer (e.g., hair, urine, feces). Sampling studies are often hampered by the fact that they cannot generate a large sample size with random sampling (line transects, etc.). Since trails seem to offer an unbiased estimation of population structure, researchers may be able to collect unbiased samples more efficiently by concentrating their sample collection in areas of significant animal use, such as game trails (Ditchkoff and Servello 2002, Beier et al. 2005, McCoy unpub. data).

The accuracy of random and trail-based camera sites hinges on an assumption that movement rates are the same for all classes of animals during each time period. For example, fawns are not very active for the first few weeks after birth (Jackson et al. 1972, Schwede et al. 1994), so they are likely underrepresented in fall surveys. Additionally, our data suggest that adult bucks may have suppressed activity levels during the pre-rut (underrepresented at all camera sites during this time), possibly in anticipation of the excessive energy demands associated with the rut. Holtfreter (2008) reported that movement rates of mature bucks increased 27% from the pre-rut to the rut, and remained elevated during the post-rut. Several other studies have documented increased movement rates of male white-tailed deer from pre-rut to rut (Kammermeyer and Marchinton 1976, Beier and McCullough 1990, Tomberlin 2007).

Another important factor to consider, when using baited camera sites, is individual variation in behavior and preference. Our study is based on overall proportions of animals captured at each treatment, but we were not able to take into consideration possible variability in individual behavior and tendencies. Campbell et al. (2006) found that radio-collared does in West Virginia displayed high variability in response to bait sites, where some deer did not use bait sites at all and others used as many as 4 different sites within a two week period. If baited sites are to be used, one may need to consider this variability among individuals, but variability in individual behavior may be similar across all sex and age classes, thus not compromising sex ratio and recruitment estimates.

MANAGEMENT IMPLICATIONS

We were able to photograph 461 deer at random locations throughout a 6 month long survey conducted in a high-fence enclosure. Aside from possible variability in seasonal movement patterns, randomly placed cameras should provide the most accurate description of population structure due to their random nature. However, in other free-ranging populations fewer deer would likely be photographed at random locations because of much lower population densities. Additionally, surveys on trails may have lower sample sizes than were found in this study. Sampling schemes designed to assess population structure using random or trail-based cameras need to account for the manner in which population density may influence sample size. The number of cameras used, or the amount of time that cameras are deployed may need to be increased. The use of bait or other attractants to increase activity around cameras, as has been done historically, does not provide population estimates similar to those generated by random or trail-based cameras except for certain periods during the year. We note that the periods during which bait sites may allow for accurate population estimates will vary regionally, or even statewide, as the timing of the breeding season and its effects on deer activity patterns varies.

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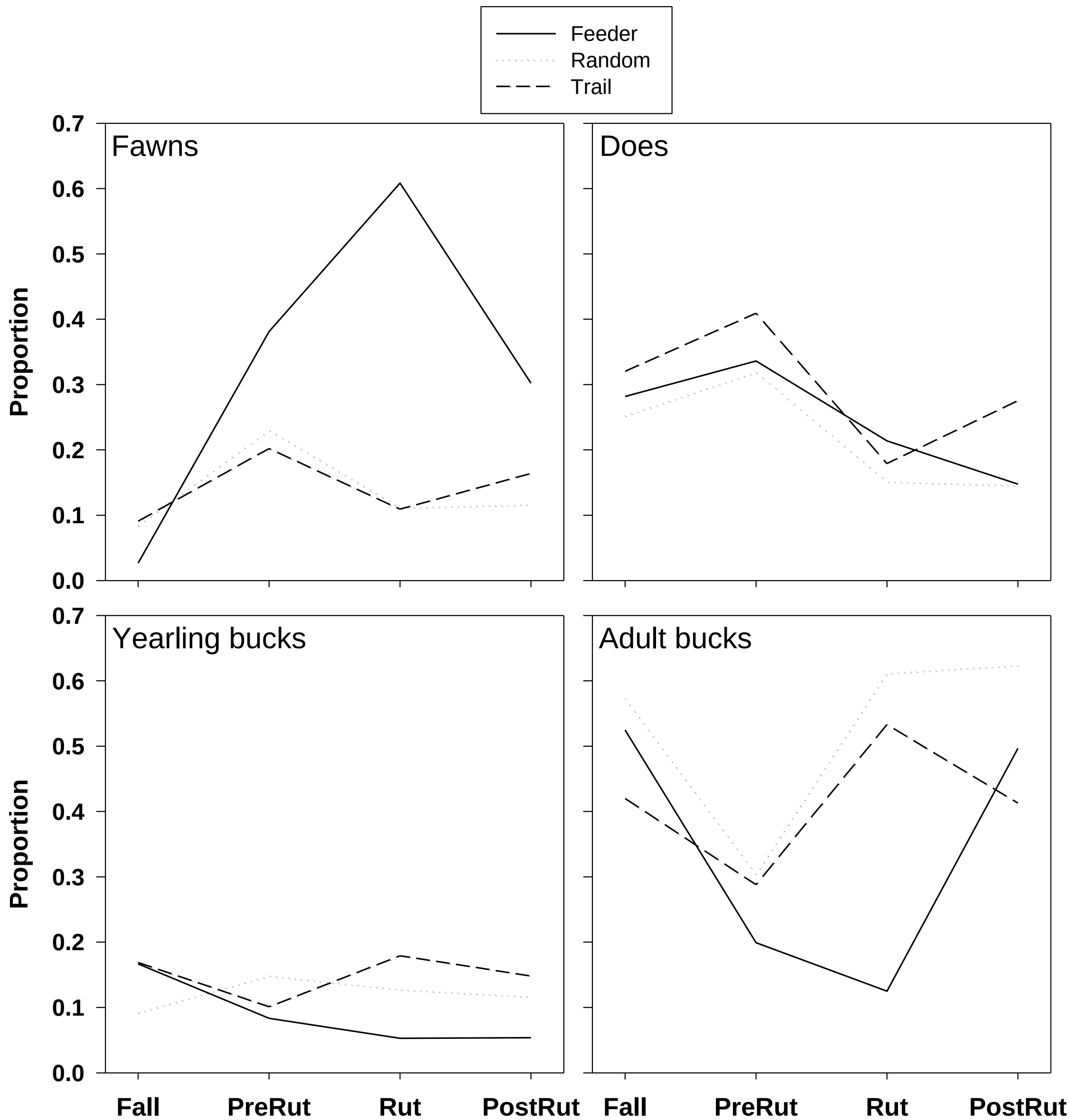
Table 2.1. Proportions of fawns, does, yearling bucks, and adult bucks captured with infrared-triggered cameras during the fall (11 Sept. – 31 Oct.), pre-rut (1 Nov. – 26 Dec.), rut (6 Jan. – 7 Feb.), and post-rut (8 Feb. – 5 Mar.) at Three Notch in east-central Alabama.

	Fawns			Does			Yearling bucks			Adult bucks		
Season	Feeder	Random	Trail	Feeder	Random	Trail	Feeder	Random	Trail	Feeder	Random	Trail
Fall												
Count	73	11	21	769	33	74	455	12	39	1432	75	97
Proportion	0.03	0.08	0.09	0.28	0.25	0.32	0.17	0.09	0.17	0.52	0.57	0.42
Pre-rut												
Count	178	31	40	157	43	81	39	20	20	93	41	57
Proportion	0.38	0.23	0.20	0.34	0.32	0.41	0.08	0.15	0.10	0.20	0.30	0.29
Rut												
Count	219	14	25	77	19	41	19	16	41	45	77	122
Proportion	0.61	0.11	0.11	0.21	0.15	0.18	0.05	0.13	0.18	0.13	0.61	0.53
Post-rut												
Count	135	8	31	66	10	52	24	8	28	222	43	78
Proportion	0.30	0.12	0.16	0.15	0.14	0.28	0.05	0.12	0.15	0.50	0.62	0.41

Figure 2.1. Proportions of fawns, does, yearling bucks, and adult bucks captured at feed stations, random, and trail sites during the fall (11 Sept. – 31 Oct.), pre-rut (1 Nov. – 26 Dec.), rut (6 Jan. – 7 Feb.), and post-rut (8 Feb. – 5 Mar.) at Three Notch in east-central Alabama.


Feeder
Random
Trail
Fawns
Does
Yearling bucks
Adult bucks
Proportion
Proportion
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
Fall
PreRut
Rut
PostRut