Survival of Adult White-tailed Deer and Movement Relative to Temporal Patterns of Predation Risk

by

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Abstract

Estimates of survival and cause-specific mortality are important tools for guiding management decisions of game species. Concerning the management of white-tailed deer (*Odocoileus virginianus*), region-specific information is needed as survival is highly variable across the species' wide geographic distribution. Hunter attitudes and selective preferences can also vary considerably between public and private lands, creating the potential for vastly different deer population demographics within a region. We monitored the survival of adult white-tailed deer on public and private lands in Alabama to address a lack of available information within the southeastern United States. Survival did not vary between land-ownership types, despite more restrictive harvest regulations on public land. Our results likely reflect the growing involvement by private-land hunters in Quality Deer Management programs, where self-implemented harvest restrictions may be in excess of state regulations.

Additionally, little is known regarding the capability of large ungulates to discern temporal patterns of predation risk, which is foundational to our understanding of predator-prey interactions. We placed global positioning system (GPS) collars on adult white-tailed deer to monitor their behavioral response to temporal patterns of recreational hunting. Deer responded in a manner reflecting the presence of hunters on the landscape, demonstrating the capability of large ungulates to accurately detect environmental threats, and employ avoidance strategies to reduce the likelihood of predatory encounters.

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Table of Contents

List of Tables

List of Figures

List of Abbreviations

ADCNR	Alabama Department of Conservation and Natural Resources
AIC	Akaike's Information Criterion
ATS	Advanced Telemetry Systems
DOW	Day of the week
DVC	Deer-vehicle collision
GPS	Global Positioning System
HDOP	Horizontal dilution of precision
LO	Land-ownership type
LRT	Likelihood ratio test
PDOP	Position dilution of precision
QDM	Quality Deer Management
VHF	Very high frequency
WMA	Wildlife Management Area

Chapter 1: Adult white-tailed deer (*Odocoileus virginianus*) survival and cause-specific mortality on public and private lands.

Abstract

The importance of science-based decision-making within natural resource management has become widely recognized over recent decades. With regards to the management of white-tailed deer (*Odocoileus virginianus*), region-specific estimates of survival and cause-specific mortality serve as valuable tools for guiding harvest recommendations that will promote healthy and sustainable populations. While hunter harvest has a significant impact on adult deer survival across much of the species range, attitudes and selective preferences may vary between public- and private-land hunters, creating the potential for vast differences in deer population dynamics between land-ownership types. While this possibility has not yet been thoroughly explored, such differences may present a challenge to state agencies whose management strategies are based on information from a single land-ownership type. From 2014-2016, we radio-marked and monitored the survival of adult white-tailed deer on public and private land in Alabama, USA. We assessed the relative importance of covariates including sex, age, and land-ownership type (i.e., public vs. private land) on adult white-tailed deer survival and hunting-related mortality using an information-theoretic approach. Hunter harvest accounted for 77% of all observed mortalities. However, harvest-related mortality did not vary between public and private study areas, likely as a result of Quality Deer Management practices on private land that emulated the effects of more restrictive harvest regulations on public land. Our findings suggest that adult white-tailed deer survival rates may be broadly applicable where harvest restrictions on public

land are in excess of those on private property. However, where restrictions apply evenly across land-ownership types, differences in harvest rates and overall survival may exist.

Introduction

Among long-lived wildlife species, such as white-tailed deer (*Odocoileus virginianus*), adult survival has a significant influence on population dynamics (Brodie et al. 2013). In fact, fluctuations in adult female survival may have a greater impact on population growth than do comparable changes in other vital rates (Chitwood et al. 2015). Age-specific survival rates are another important component of white-tailed deer population dynamics, as they directly influence the age structure of the herd. Male age structure, in particular, is a key demographic parameter within white-tailed deer populations impacting numerous biological processes such as the timing and duration of breeding season (Jacobson 1992, Miller et al. 1995), which can ultimately influence fawn survival and recruitment (DeYoung and Miller 2011).

State wildlife agencies manage for white-tailed deer populations that are of a size and age structure that is biologically and socially acceptable (Demarais et al. 2000). Thus, estimates of sex- and age-specific survival are utilized by wildlife professionals to inform management decisions. However, white-tailed deer survival can vary considerably across the species range due to factors such as habitat composition, disease outbreaks, and winter severity, as well as pressure from recreational hunters and other predator communities (DeYoung 2011). Therefore, region-specific survival estimates are most meaningful for application in local management efforts. While a number of studies across the southeastern United States have examined survival rates of adult male deer (DeYoung 1989, Heffelfinger et al. 1990, Bowman et al. 2007, Thayer et al. 2009), survival estimates of adult females are lacking in comparison (Robinson et al. 2014, Kilgo et al. 2016). Among studies that have examined female survival, 2 were conducted in the absence of recreational hunting (Kie and White 1985, Land et al. 1993) and another in the near absence of recreational hunting (Chitwood et al. 2015), potentially limiting their utility within landscapes where hunter harvest is a primary component of adult mortality. Additionally, there is a paucity of information comparing adult survival rates between public and private lands within a geographic region. Differences in attitudes (Stedman et al. 2008) and selective preferences (Wiskirchen et al. 2016) between public- and private-land hunters create the potential for survival rates to vary markedly between land-ownership types. Thus, a lack of information comparing the two may represent a potential shortcoming of current management practices that are based on a single set of survival estimates, yet assumed to apply across all properties within a management region.

Our goal was to conduct a comprehensive evaluation of adult white-tailed deer survival within Alabama, USA, to inform future management decisions across the Southeast that are dependent upon accurate information from various land management types. Our specific objectives were to 1) determine sex- and age-specific survival rates of adult deer across monitored populations, 2) assess the relative contribution of various cause-specific mortality agents toward annual survival, and 3) compare survival between public and privately-owned properties. In doing so, we address some of the limitations to our current knowledge of white-tailed deer survival within the southeastern United States.

Methods

Study Areas

Our study was conducted at 4 locations within Alabama, USA (Figure 1.1), including 2 public-use Wildlife Management Areas (WMAs) managed by the Alabama Department of Conservation and Natural Resources (ADCNR), as well as 2 private tracts of land. Alabama was separated into 2 hunting zones (i.e., A and B) by the ADCNR for the purpose of designating deer season dates that would correspond to the timing of breeding in each region. Zone A was comprised of northern, central, and portions of southeastern Alabama, where deer breeding occurred earliest and where hunting extended from 15 Oct-31 Jan annually. Zone B was comprised of the remainder of southern Alabama, where breeding occurred later and, consequently, deer hunting extending from 25 Oct-10 Feb annually. One public WMA and one privately-owned study area was located in each hunting zone. At each study area, one antlerless and one antlered deer could be legally harvested per hunter per day, with a maximum of 3 antlered deer harvests allowed per hunter throughout the season. On privately-owned study areas, 1 of the 3 antlered deer was required to possess ≥4 antler points (≥2.54 cm) on at least one side to be legally harvested. Additional restrictions for harvested, antlered deer applied on public-use study areas, with each WMA having unique requirements.

Barbour WMA (hereafter "Barbour") was composed of 11,418 ha of public-use land within Bullock and Barbour Counties, AL (Zone B; 31°59.73 N, 85°27.57 W). As opposed to private-land study areas where an antler point restriction applied to only 1 of 3 harvested males, each antlered deer harvested at Barbour was required to possess ≥3 antler points (≥2.54 cm) on at least one side. Barbour consisted of gently rolling terrain, characteristic of northern portions of Alabama's lower coastal plain (Gray et al. 2002), and the habitat was predominantly mixed pine-hardwood stands consisting of loblolly (*Pinus taeda*) and short-leaf pine (*P. echinata*), oaks (*Quercus* spp.), maples (*Acer* spp.), sweetgum (*Liquidambar styraciflua*), sycamore (*Platanus occidentalis*), and yellow poplar (*Liriodendron tulipifera*). Within bottomlands and along drainages and riparian corridors, hardwoods were dominant with interspersed pine. Alternately, uplands were predominantly pine interspersed with hardwoods, and portions of upland areas were in the early stages of longleaf pine (*Pinus palustris*) restoration. Approximately 200 wildlife openings (0.5-8.0 ha) were scattered across Barbour and planted with a cool season mixture of chicory (*Cichorium intybus*), clovers (*Trifolium* spp.), grains (oats, *Avena fatua*; wheat, *Triticum aestivum*), rape (*Brassica napus*), and winter peas (*Pisum sativum*). Warm season plantings included browntop millet (*Urochloa ramosa*), chufa (*Cyperus esculentus*), corn (*Zea mays*), cowpeas (*Vigna unguiculata*), sunflower (*Helianthus* sp.), and sun hemp (*Crotalaria juncea*). Portions of Barbour received prescribed fire on a 3- to 5-year return interval. Although Barbour was primarily managed for wildlife, infrequent timber harvests (i.e. thinnings or clear cuts) were conducted within small (i.e., ≤50 ha) portions of the area. A network of maintained gravel and dirt roads extended throughout Barbour with 2 paved roads (Barbour Co Rds. 47 and 49) passing through the area.

Oakmulgee WMA (hereafter “Oakmulgee”) was composed of 18,009 ha of public-use land spanning Bibb, Hale, Perry, and Tuscaloosa Counties, AL (Zone A; 32°57.39 N, 87°27.60 W). During the 2014/15 deer hunting season, harvest restrictions on Oakmulgee were the same as on private land. Prior to the 2015/16 deer hunting season, however, Oakmulgee was split into 2 management zones of approximately equal size. An additional antler point restriction was implemented on one of these zones, requiring each antlered deer to possess ≥3 points (≥2.54 cm) on at least one side to be legally harvested. Oakmulgee was situated in the southern foothills of the Appalachians, with terrain that was more rugged than that of Barbour consisting of rolling hills with steep to moderate slopes. Other differences included a more widespread application of prescribed fire on Oakmulgee compared to Barbour, as well as the presence of mature longleaf pine stands that dominated the upland ridges. Additionally, timber harvests were conducted with greater regularity and over larger (≤150 ha) areas. Approximately 100 wildlife openings (0.5 -

4.0 ha) were scattered across Oakmulgee and planted with a cool season mixture of clovers and grains (oats; rye, *Secale cereale*; wheat), and warm season varieties such as chufa, corn, proso millet (*Panicum miliaceum*), sorghum (*Sorghum bicolor*), and sunflower. Oakmulgee contained a lower density of gravel and dirt roads than Barbour and was intersected by 3 paved roads (Hale Co Rds. 49 and 50 and Hwy 25).

Our third study area (hereafter "Marengo") was located in Marengo County, AL (Zone B; 32°14.08 N, 87°51.11 W) and composed of 3,116 ha of privately-owned land. Approximately half of the area was owned as separate parcels by private individuals, and the remainder was owned by The Westervelt Company and leased to private individuals for hunting. The terrain and habitat composition within Marengo were comparable to those of Barbour due to similar positioning within the northern portion of Alabama's lower coastal plain (Gray et al. 2002), with the exception that longleaf pine was absent from Marengo and prescribed fire was rarely applied. The majority of the area under ownership of The Westervelt Company was managed for timber production and existed in various regenerative stages of planted loblolly and shortleaf pine. Food plots were common and were planted in cool-season blends of wheat and clover or winter peas, and soybeans (*Glycine max*) in the warm season. Marengo contained a lower density of gravel and dirt roads than within either Barbour or Oakmulgee, and no paved roads intersected Marengo.

Our final study area (hereafter "Pickens") was located in Pickens County, AL (Zone A; 33°12.45 N, 87°52.01 W) and was composed of 4,899 ha of land, privately owned by The Westervelt Company and leased in approximately 400-ha tracts to hunting clubs. The terrain within Pickens resembled that of Oakmulgee, characterized by rolling hills with steep to moderate slopes. The habitat of Pickens was predominantly loblolly and shortleaf pine that was managed for timber production and existed in various regenerative stages. Hardwoods were restricted to drainages and streamside management zones. Like Marengo, food plots were common within Pickens and normally planted in clovers or winter peas in the cool season and left dormant in the warm season. Road density within Pickens was also similar to Marengo, with no paved roads intersecting the area.

Capture and Monitoring

From Oct 2013 – Mar 2014, and during subsequent summers (May – Sept) of 2014 and 2015, adult (≥1 year old) male and female white-tailed deer were immobilized using tranquilizer dart guns and radio-transmitter darts (Pneu-Dart, Inc., Williamsport, Pennsylvania). Darts contained a 2-ml mixture of Telazol (Fort Dodge Animal Health, Fort Dodge, Iowa; 100 mg/ml at a rate of 4.0 mg/kg) and xylazine-hydrochloride (Lloyd Laboratories, Shenandoah, Iowa; 100 mg/ml at a rate of 2.0 mg/kg) administered as an intramuscular injection upon impact. To reduce the likelihood of capture-related stress, a minimum of 10 minutes was allowed to elapse before leaving the darting location to ensure full sedation of darted deer prior to approach by researchers. A hand-held, 3-element Yagi antenna and receiver (Mod R410; Advanced Telemetry Systems, Isanti, Minnesota) were used to detect dart transmitters and locate sedated deer. Upon capture, deer were blindfolded to further minimize handling stress. Darts were removed and a coagulant immediately applied to the wound to prevent blood loss.

Each captured deer was fitted around the neck with a very high frequency (VHF) radio-collar equipped with an 8-hour mortality sensor (Mod M2510B; Advanced Telemetry Systems), and a small metal ear tag (Style #681, Hasco Tag Company, Dayton, Kentucky) with a unique ID number was attached to one ear. Collars fitted to females ≤2.5 years of age and all males were lined with a pliable foam material to allow for neck growth and swelling (Thomas et al. 1965).

Age of each captured deer was estimated using a combination of tooth replacement and wear (Severinghaus 1949) and live body characteristics (Demarais et al. 1999) to maximize aging accuracy (Bowman et al. 2007). After handling was complete, a 3-ml intramuscular injection of tolazoline (Lloyd Laboratories; 100 mg/ml at a rate of 2.0 mg/kg) was administered as an antagonist to the xylazine-hydrochloride sedative, and deer remained under observation until they moved from the capture location under their own power. Capture and handling methods were approved by the Auburn University Institutional Animal Care and Use Committee (PRN 2013-2323), and followed the guidelines of the American Society of Mammalogists (Sikes and Gannon 2011). Captures were approximately balanced with respect to study area, and efforts were made to reach an equal distribution of collars across sexes and age classes at each location.

Telemetry studies involving radio-collared white-tailed deer have been shown to yield unbiased survival estimates (Buderman et al. 2014); however, steps were taken to inform the public about the ongoing study to further improve our estimates of survival. On privately-owned study areas (i.e., Marengo and Pickens), hunters were spoken with directly by a researcher or landowner about the possibility of observing radio-collared deer. The purpose of the collars was explained and hunters were asked to treat radio-collared deer as they would an un-collared deer and encouraged not to allow the presence of a collar to influence harvest decisions. On public study areas (i.e., Barbour and Oakmulgee), hunters were spoken with opportunistically by researchers and wildlife agency personnel. In addition, signs containing information about radio-collared animals and requests to treat collared deer as un-collared individuals were conspicuously displayed at entrances to, and major intersections within, WMAs as well as at WMA check stations and local deer processing operations. Articles describing the study were written and published on the ADCNR website, in a fall issue of the ADCNR monthly magazine, and various other regional news and social media outlets. Additionally, a discussion thread describing existing deer research was created on a popular hunter forum within Alabama and periodically updated by researchers. All radio-collars and ear tags displayed a phone number for hunters to contact in the case of a harvested, marked individual.

Captured deer were monitored for mortality events on a weekly basis over a continuous, 2-year period beginning on 15 Feb 2014 and ending on 14 Feb 2016. Upon detection of a mortality event, an immediate search was conducted to recover the remains and attempt to determine the cause. Cause of death was assessed by performing a field necropsy on the remains (Roffe et al. 1994), as well as examining any persisting evidence within the surrounding area (e.g., tracks, scat, drag lines). Mortalities were initially classified as legal harvest, illegal harvest, unknown harvest, natural, unknown natural, and unknown (Bowman et al. 2007). Deer taken by legal means were classified as legal harvest, whereas deer believed to be poached (e.g., cut collars found near roads or within posted “no hunt” areas) were classified as illegal harvest. Cut collars found away from roads and within areas and dates of legal hunting were classified as unknown harvest as the legality of the harvest was uncertain. Mortalities due to identifiable, natural causes were classified as natural mortalities. Mortalities not caused by humans, but for which the exact cause could not be determined, were classified as unknown natural. Mortalities for which the cause was entirely uncertain were classified as unknown mortalities.

Data Analysis

We calculated annual and seasonal survival rates in Program MARK (White and Burnham 1999) using a known fates model with a staggered entry approach (Pollock et al. 1989). When estimating annual survival, the year began on 15 Feb and ended on 14 Feb the following year. Seasonal survival estimates were based on 3 biologically relevant time periods throughout the year: post-breeding (15 Feb – 15 Jun), parturition (16 Jun – Oct 14), and breeding season (15 Oct – 14 Feb). The breeding season encompassed peak breeding activity as well as the entirety of the deer hunting season across all study areas (15 Oct – 10 Feb). Timing of peak breeding was determined by utilizing the most recent 10 years of a historic conception dataset collected by ADCNR biologists, containing information from each study area. Individuals were classified as either <3.5 years old or ≥3.5 years old for assessment of age-specific survival. These groupings were used as males younger than 3.5 years typically lack substantial antler development relative to older individuals (Ditchkoff et al. 2000), and may therefore be selected differently by hunters compared to older males. This is a potentially relevant distinction to make, given the presence of antler point restrictions within Alabama during our study period that rendered a portion of young males unavailable for harvest (Strickland et al. 2001, Hansen and Beringer 2003). Additionally, 1.5- and 2.5-year-old males and females may exhibit a high rate of dispersal, with a lower likelihood of dispersal events among older deer (Hawkins et al. 1971, Nixon et al. 1991). As dispersal involves leaving the natal home range and entering relatively unfamiliar areas, dispersal events are risky and may contribute to disparities in survival between young and old individuals (Roseberry and Klimstra 1974, Nixon et al. 1991, Hölzenbein and Marchinton 1992).

Due to a limited number of observed mortalities within some cause-specific categories, we combined all harvest-related (i.e., legal harvest, illegal harvest, and unknown harvest) and natural (i.e., natural and unknown natural) deaths into single categories for estimating cause-specific mortality rates (Bowman et al. 2007) in Program MARK. Mortality due to harvest, for example, was then calculated using a 2-step process. First, all non-hunting moralities were censored to derive an estimate of survival ($\hat{S}$) influenced only by harvest. Second, a harvest-related mortality rate was calculated as $1 - \hat{S}$ (Thayer et al. 2009). Confidence intervals around estimates of cause-specific mortality were calculated in a similar manner, using $1-[UCL\ of\ \hat{S}]$ for the lower confidence limit and $1-[LCL\ of\ \hat{S}]$ for the upper confidence limit. Individuals were left-censored from estimates of survival and cause-specific mortality until the first full season following capture, and were right-censored if an animal disappeared from the study and was never relocated (Keller et al. 2013). Individuals were not included in survival calculations for the season in which they were captured to avoid biasing estimates of survival upward (Pac and White 2007).

We developed 2 model sets in Program MARK to assess the relative importance of several covariates in explaining overall survival and the probability of hunter harvest among adult white-tailed deer. The first set of models was built using a censored dataset (i.e., all non-hunting mortalities removed) to explicitly examine the effect of sex, age class (i.e., <3.5 years old and ≥3.5 years old), year, and land-ownership type (i.e., public vs. private) on the probability of hunter harvest. In addition to reduced main-effect models for covariates, models with an interaction term between each covariate and land-ownership type were included. Lastly, a continuous model providing a single survival estimate was included in the first model set (Table 1.1). The second set of models was built using the entire survival dataset (i.e., no cause-specific mortalities censored) in which overall survival was modeled as a function of sex, age class, season (i.e., post-breeding, parturition, and breeding), year, and land-ownership type. We fitted reduced main-effect models, as well as models that included an interaction term between each main effect and land-ownership type to explicitly examine differences in overall survival between public and private land. We also included a constant model, providing a single survival estimate for the entire study, as well as interaction models containing combinations of sex, age, season, year, and land-ownership type (Table 1.2). All models were run using a logit link function and evaluated based on Akaike's Information Criterion adjusted for small sample size (AIC_c; Burnham and Anderson 2002).

Results

Over the course of the study, 82 adult white-tailed deer were captured and radio-marked. Three individuals died prior to their first full season following capture. Thus, survival estimates are based on the remaining 79 individuals (33 M, 46 F). Mean age at the point of entry into the study was 3.2 years (range = 1.0 to 6.5 years) and mean age at death was 4.0 years (range = 2.5 to 6.5 years). Thirty mortalities were documented throughout the study, 77% (23/30) of which were due to hunting-related causes. Among hunting-related mortalities, 17 (74%) were legal harvests, 5 (22%) were illegal harvests, and 1 (4%) was inconclusive as to the legality of the harvest. Natural mortality was relatively low, accounting for 17% (5/30) of the observed mortalities. These included post-breeding exhaustion (n = 1), hemorrhagic disease (n = 1), and natural mortalities of unknown causes (n = 3). Lastly, 6% (2/30) of the observed mortalities could not be confidently categorized as either natural or hunting-related (Table 1.3).

The seasonal model received the greatest support among those considered in the first model set, which excluded non-harvest mortality, indicating that variation in the data was best explained by differences in harvest rates between post-breeding, parturition, and breeding seasons. On both public and private land, hunting-related mortality occurred almost exclusively within the breeding season, with only a single, illegal harvest documented during the post-breeding season and no hunting-related mortalities observed during the parturition season (Table 1.3). Each model containing an interaction term between a main biological effect and land-ownership type (e.g., Season x LO), was ranked below the corresponding main-effect model (e.g., Season), indicating a lack of support for variation in hunter harvest between public and private land for any of the modeled covariates (Table 1.1).

The top-ranked model among those considered within the second model set, representing overall survival (i.e., no cause-specific mortalities censored), included the interacting effects of sex, age class, and season. Survival was lowest during the breeding season, ranging from 0.542-0.891 (0.346-0.950; 95% C.I.) across sexes and age classes, primarily as a result of the coincident timing with hunting which accounted for the majority of observed mortalities within each group. Survival during post-breeding and parturition seasons was 3.18 (0.36-27.88; 95% C.I.) and 3.67 (0.42-32.02; 95% C.I.) times as likely as during the breeding season, respectively, ranging from 0.800-1.000 (0.459-1.000; 95% C.I.). Across seasons, female survival was 6.91 (2.15-22.21; 95% C.I.) times as likely as that of males, and survival of immature (<3.5 years old) deer was 2.97 (0.71-12.34; 95% C.I.) times as likely as that of mature (≥3.5 years old) deer (Table 1.4). Each model containing an interaction term between a main biological effect and land-ownership type was, again, ranked lower than the model containing only the corresponding main effect, indicating that there was no meaningful variation in overall survival between public and private land for any of the modeled covariates (Table 1.2). Only minor discrepancies in survival existed for corresponding seasons between public and private land, and study-wide survival on private land was only 1.36 (0.32-5.69; 95% C.I.) times as likely as on public land (Table 1.5).

Discussion

Adult white-tailed deer survival rates within Alabama varied by sex and age class, with males experiencing lower survival than females, and mature (≥3.5 years old) deer experiencing lower survival than immature (<3.5 years old) deer. These differences can be largely attributed to hunter selectivity, as harvest was the primary source of mortality indiscriminant of sex or age class. Across ecoregions and white-tailed deer subspecies, male survival is typically less than that of females (Hawkins et al. 1970, Gavin et al. 1984, Dusek et al. 1989, and Nixon et al. 1991, Lopez et al. 2003, Harveson et al. 2007). Lower male survival is linked to greater mobility of males compared to females, which increases exposure to various dangers including the risk of hunter harvest (Hölzenbein and Marchinton 1992, Little et al. 2014). Among hunted populations of white-tailed deer in the southern United States, previous reports of adult male survival have been variable, with annual rates ranging from 50-84% (DeYoung 1989, Ditchkoff et al. 2001, Bowman et al. 2007, Thayer et al. 2009, Webb et al. 2010). Our estimate of annual survival for immature males was similar, falling within the previously reported range. However, the mature segment of the male age distribution experienced much lower annual survival at 32% (15-52%; 95% C.I.). Low estimates of annual survival could be the result of a small sample size within the particular age category. However, we feel that the observed survival rate of mature males was reflective of intense hunter selection among this herd demographic on both public and private land.

Previously reported estimates of adult female survival have been greater and less variable than those of adult males, with annual estimates ranging from 77-87% (Land et al. 1993, Storm et al. 2007, Webb et al. 2010, Chitwood et al. 2015, Kilgo et al. 2016) within southern populations. Again, our estimates were similar, despite previous reports being based on un-hunted (Land et al. 1993), nearly un-hunted (Chitwood et al. 2015), and enclosed (Webb et al. 2010) deer populations. Consistent adult female survival despite variation in selective pressures across studies may serve as supporting evidence for the compensatory mortality hypothesis (Connell 1978), which suggests that harvest-related mortality in heavily hunted game populations may be offset by a lower occurrence of non-hunting mortality (e.g., predation) that may influence survival more heavily in populations that lack substantial hunting pressure (Cooley et al. 2009). While the effect of hunting on deer survival was greater within our study than natural sources of mortality, natural mortality can be a primary component of female survival in Southeastern deer populations where hunting is absent or uncommon (Land et al. 1993, Chitwood et al. 2015). Furthermore, consistent adult female survival across studies through possible compensatory mechanisms suggests that estimates may be robust across Southeastern white-tailed deer populations. This possibility presents an advantage to wildlife managers within the region, as uniform rates of adult female survival reduce the need for local estimates for application in deer management decisions.

Our findings also corroborate previous studies examining survival of white-tailed deer in southern populations where mortality rates have varied by age class (Kie and White 1985, Heffelfinger et al. 1990, Hansen and Beringer 2003, Bowman et al. 2007, Webb et al. 2007). In many instances, survival of young deer has been shown to be greatest and tends to decrease with age. This pattern has been observed for male (Heffelfinger et al. 1990, Hansen and Beringer 2003, Bowman et al. 2007, Webb et al. 2007) and female white-tailed deer (Kie and White 1985). Although we did not examine individual age classes (i.e., 1.5, 2.5, 3.5, etc.) for a linear trend, we found that survival of immature deer was greater than that of mature deer among both males and females. Greater survival of immature male and female deer may be explained by lower harvest pressure compared to older individuals as a result of antler restrictions or Quality Deer Management (QDM) practices (Hansen and Beringer 2003, Bowman et al. 2007), or by increased susceptibility to natural mortality with age (Nixon et al. 1991, Land et al. 1993, Ditchkoff et al. 2001). Natural mortality was low within our study across both age classes, and we did not document any natural mortalities among male or female deer <3.5 years of age. Although a larger sample would likely have revealed that natural mortality is present within both age classes, our lack of natural mortality among male and female deer <3.5 years of age reflects the low rate of natural mortality among adults within our monitored populations, with natural mortality having the least effect on young adult deer.

Despite evidence that deer-vehicle collisions (DVCs) are common within Alabama and likely account for thousands of deer mortalities across the state annually (Adams et al. 2009), we did not confirm any DVC-related mortalities during our study. The potential for DVCs is greatest within urban and suburban landscapes where high deer and road densities occur simultaneously (Ng et al. 2008). The density of paved roads within each of our study areas was low which could explain the lack of confirmed collision-related mortalities among monitored deer, as the likelihood of DVCs was relatively low. However, the absence of confirmed DVCs does not preclude the possibility that a DVC-related mortality occurred and was mistaken for an illegal harvest, as both events could result in cut collars discarded at the roadside. For this reason, we recommend that managers interpret our estimate of 17% overall mortality due to illegal harvest with caution, as this number could be biased upward. However, in most instances when a mortality was classified as an illegal harvest, there was additional supporting evidence to suggest a deer had been take illegally rather than hit by a vehicle and removed from the study area.

The lack of variation in overall survival or hunting-related mortality of adult white-tailed deer between public and private study areas was a surprising outcome given previous research demonstrating that vast differences in hunter attitudes and selective preferences between land-ownership types are possible. Stedman et al. (2008) found that public-land hunters in Pennsylvania were less likely to consider deer hunting to be “very important” compared to private-land hunters who expressed a greater degree of commitment. Thus, private-land hunters displayed a greater amount of effort, spending more days afield compared to public-land hunters. Additionally, private-land hunters were more likely to hold beliefs that resembled those of land managers and act accordingly. Differences in hunter philosophies were reflected in hunter selection as private-land hunters were more likely to harvest antlerless deer and less likely to hunt with the goal of harvesting an antlered deer only. As a result, 64% of private-land hunters in Pennsylvania harvested a deer compared to only 41% of public-land hunters. Conversely, Wiskirchen et al. (2016) monitored the survival of visibly-marked deer in Alabama following a request that marked animals not be harvested. Visibly-marked deer experienced a 113% greater harvest rate on public compared to private land, possibly reflecting the strong value certain hunters place on the opportunity to take at least one deer (Siemer et al. 2015). Similar harvest rates across our study areas could be a reflection of the hunter values seen in previous studies, where a high level of commitment and high success rate of private-land hunters was met by the strong desire of public-land hunters in Alabama to harvest at least one legal deer.

Similarities in sex-specific survival and hunting-related mortality rates between land-ownership types in our study was a particular surprise given the more restrictive harvest regulations that applied on public lands with respect to the male segment of the population. At Barbour, every harvested male was required to possess ≥3 points on at least one main antler beam. At Oakmulgee, the same restriction applied to half of the area during the second year of our study. Conversely, antler point restrictions applied only to 1 of the season limit of 3 harvested males on private properties during our study. Similarities in survival and harvest rates of white-tailed deer, despite dissimilar harvest regulations, could reflect opposing hunter philosophies and management strategies between land-ownership types. In Arkansas, 60% of hunting clubs on private land followed self-implemented harvest restrictions in excess of state-mandated regulations (Collier and Krementz 2006). These differences were largely attributed to the widespread involvement by private-land hunters in QDM programs. Quality deer management has become increasingly popular on private lands across the range of white-tailed deer (Hamilton et al. 1995), and this could explain why variation in harvest-related mortality between land-ownership types was not supported by our model-selection approach. More restrictive harvest regulations on public land may have been balanced with additional, self-implemented harvest restrictions on private land, resulting in similar overall harvest trends. This hypothesis may be further supported by a comparison between harvest trends observed in this study and those of properties that are known to be managed under the principles of QDM. Bowman et al. (2007) monitored the effects of QDM on survival of male white-tailed deer within Mississippi and noted that young age classes (<3.5 years old) of males had greater annual survival than older males, attributable largely to differences in hunter selection. Conversely, in areas where QDM is not practiced and antler restrictions are not implemented, young deer may experience greater mortality than older individuals (Maguire and Severinghaus 1954, Roseberry and Klimstra 1974, McCullough 1979, Nelson and Mech 1986), as young deer are more susceptible to unbiased harvest than older deer due to naivety toward the threat imposed by hunters (Dasmann and Taber 1956, Van Etten et al. 1965). Our results resemble the harvest trends of a QDM strategy, with greater survival and lower harvest-related mortality of young males compared to older age classes. This suggests that antler point restrictions on public land may have been successful in protecting young males, and that private-land hunters may have electively restricted their harvest of young males, resulting in similar harvest trends. Based on these findings, we might expect consistent harvest trends in other regions having more restrictive regulations on public lands compared to privately-owned property, due to the growing popularity of QDM (Hamilton et al. 1995). However, where similar harvest regulations apply to public and private lands, meaningful differences in harvest rates may exist.

Our study provides a comprehensive assessment of sex- and age-specific survival, as well as cause-specific mortality, of adult white-tailed deer across Alabama. While certain aspects of our findings agree with previously conducted studies across the southeastern United States, we note a dramatic impact that hunter harvest may have within the region, particularly with regards to the mature male segment of the population. Hunter selection of mature males is likely driven by a combination of state-mandated harvest restrictions that protect young males, as well as a growing involvement in QDM practices. Although we did not find meaningful differences in overall survival or harvest-related mortality between land-ownership types in Alabama, our study provides a basis for similar comparisons to be made within other regions where hunter philosophies or harvest selection criteria may have a non-uniform impact on herd demographics.

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Table 1.1 – Summary of model set explaining the probability of harvest-related mortality among 79 adult (≥1.0-year-old) white-tailed deer during 2014-2016 in Alabama, USA.

Model	K[1]	AIC_c[2]	Delta AIC_c	Weight	Likelihood
Season	3	126.4	0.0	0.92	1.00
Season x LO[3]	6	131.4	5.0	0.08	0.08
Year	2	153.2	26.8	0.00	0.00
Constant[4]	1	156.0	29.5	0.00	0.00
Sex	2	156.5	30.1	0.00	0.00
Year x LO	4	156.8	30.4	0.00	0.00
Age	2	157.7	31.2	0.00	0.00
LO	2	157.9	31.5	0.00	0.00
Sex x LO	4	160.3	33.9	0.00	0.00
Age x LO	4	160.7	34.3	0.00	0.00

[1] Number of estimated model parameters.

[2] Akaike's Information Criterion with small-sample bias adjustment (Burnham and Anderson 2002).

[3] Model variable LO = land ownership (i.e., public or private land).

[4] Constant model; 1 estimate for the entire study.

Table 1.2 – Summary of model set explaining overall survival among 79 adult (≥1.0-year-old) white-tailed deer during 2014-2016 in Alabama, USA.

Model	K[1]	AIC_c[2]	Delta AIC_c	Weight	Likelihood
Sex x Age x Season	12	167.1	0.0	0.41	1.00
Sex x Season	6	168.3	1.2	0.23	0.56
Age x Season	6	168.7	1.6	0.19	0.45
Season	3	169.1	1.9	0.16	0.38
Season x LO[3]	6	175.1	7.9	0.01	0.02
Sex x Age	4	176.6	9.4	0.00	0.01
LO x Year x Season	12	182.2	15.1	0.00	0.00
Sex	2	185.0	17.8	0.00	0.00
Sex x Year	4	185.1	18.0	0.00	0.00
Age x Year	4	185.6	18.4	0.00	0.00
Year	2	187.3	20.2	0.00	0.00
Age	2	187.4	20.2	0.00	0.00
Constant[4]	1	187.7	20.6	0.00	0.00
Sex x LO	4	188.6	21.5	0.00	0.00
LO	2	189.8	22.6	0.00	0.00
Age x LO	4	190.2	23.1	0.00	0.00
Year x LO	4	191.3	24.2	0.00	0.00

[1] Number of estimated model parameters.

[2] Akaike's Information Criterion with small-sample bias adjustment (Burnham and Anderson 2002).

[3] Model variable LO = land ownership (i.e., public or private land).

[4] Constant model; 1 estimate for the entire study.

Table 1.3 – Number of cause-specific mortalities observed among 79 adult (≥1.0-year-old) white-tailed deer from 2014-2016 on public and private land, by season and sex, in Alabama, USA.

		Cause of Death			
Land Ownership	Season[1]	Harvest[2]	Natural[3]	Unknown	Total
Public	Post-breeding	0	1 (1 M, 0 F)	0	1 (1 M, 0 F)
	Parturition	0	1 (1 M, 0 F)	0	1 (1 M, 0 F)
	Breeding	12 (5 M, 7 F)	0	1 (1 M, 0 F)	13 (6 M, 7 F)
Private	Post-breeding	1 (0 M, 1 F)	0	0	1 (0 M, 1 F)
	Parturition	0	2 (1 M, 1 F)	0	2 (1 M, 1 F)
	Breeding	10 (7 M, 3 F)	1 (1 M, 0 F)	1 (1 M, 0 F)	12 (9 M, 3 F)
	Total	23 (12 M, 11 F)	5 (4 M, 1 F)	2 (2 M, 0 F)	30 (18 M, 12 F)

[1] Post-breeding = 15 Feb-15 Jun, Parturition = 16 Jun-14 Oct, and Breeding = 15 Oct-14 Feb.

[2] Harvest = legal harvest, illegal harvest, and unknown harvest.

[3] Natural = natural and unknown natural.

Table 1.4 – Survival and cause-specific mortality rates of adult (≥1.0 year old) white-tailed deer, by sex and age, from 2014-2016 in Alabama, USA.

						Cause-specific mortality					
				Survival		Harvest[1]		Natural[2]		Unknown	
Sex	Age	Interval[3]	*n*	Rate	95% C.I.	Rate	95% C.I.	Rate	95% C.I.	Rate	95% C.I.
M	<3.5	Post-breeding	16	1.000	1.000-1.000	0.000	0.000-0.000	0.000	0.000-0.000	0.000	0.000-0.000
		Parturition	28	1.000	1.000-1.000	0.000	0.000-0.000	0.000	0.000-0.000	0.000	0.000-0.000
		Breeding	19	0.789	0.554-0.919	0.211	0.081-0.446	0.000	0.000-0.000	0.000	0.000-0.000
		Annual	26	0.821	0.598-0.930	0.179	0.070-0.402	0.000	0.000-0.000	0.000	0.000-0.000
	≥3.5	Post-breeding	10	0.900	0.533-0.986	0.000	0.000-0.000	0.100	0.014-0.467	0.000	0.000-0.000
		Parturition	10	0.800	0.459-0.950	0.000	0.000-0.000	0.200	0.050-0.541	0.000	0.000-0.000
		Breeding	25	0.542	0.346-0.725	0.381	0.203-0.598	0.071	0.010-0.370	0.133	0.034-0.405
		Annual	22	0.317	0.150-0.515	0.508	0.292-0.747	0.313	0.129-0.618	0.176	0.046-0.522

F	<3.5	Post-breeding	10	1.000	1.000-1.000	0.000	0.000-0.000	0.000	0.000-0.000	0.000	0.000-0.000
		Parturition	14	1.000	1.000-1.000	0.000	0.000-0.000	0.000	0.000-0.000	0.000	0.000-0.000
		Breeding	15	0.733	0.467-0.896	0.267	0.104-0.533	0.000	0.000-0.000	0.000	0.000-0.000
		Annual	16	0.723	0.433-0.887	0.277	0.077-0.567	0.000	0.000-0.000	0.000	0.000-0.000
	≥3.5	Post-breeding	27	0.963	0.779-0.995	0.037	0.005-0.221	0.000	0.000-0.000	0.000	0.000-0.000
		Parturition	31	0.968	0.804-0.995	0.000	0.000-0.000	0.032	0.005-0.196	0.000	0.000-0.000
		Breeding	55	0.891	0.778-0.950	0.109	0.050-0.222	0.000	0.000-0.000	0.000	0.000-0.000
		Annual	37	0.802	0.647-0.896	0.176	0.088-0.331	0.028	0.004-0.180	0.000	0.000-0.000

[1] Harvest = legal harvest, illegal harvest, and unknown harvest.

[2] Natural = natural and unknown natural.

[3] Post-breeding = 15 Feb-15 Jun, Parturition = 16 Jun-14 Oct, Breeding = 15 Oct-14 Feb, and Annual = 15 Feb-14 Feb.

Table 1.5 – Seasonal survival rates by year of adult (≥1.0-year-old) white-tailed deer on public and private land in Alabama, USA, during 2014-2016.

Land Ownership	Year	Season[1]	*n*	Survival	
				Rate	95% C.I.
Public	2014/15	Post-breeding	6	1.000	1.000-1.000
		Parturition	12	1.000	1.000-1.000
		Breeding	31	0.742	0.563-0.865
	2015/16	Post-breeding	23	0.957	0.748-0.994
		Parturition	27	0.963	0.779-0.995
		Breeding	28	0.821	0.636-0.924
Private	2014/15	Post-breeding	17	1.000	1.000-1.000
		Parturition	21	0.952	0.729-0.993
		Breeding	25	0.680	0.478-0.831
	2015/16	Post-breeding	17	0.941	0.680-0.992
		Parturition	23	0.957	0.748-0.994
		Breeding	29	0.862	0.685-0.947

[1] Post-breeding = 15 Feb-15 Jun, Parturition = 16 Jun-14 Oct, and Breeding = 15 Oct-14 Feb.

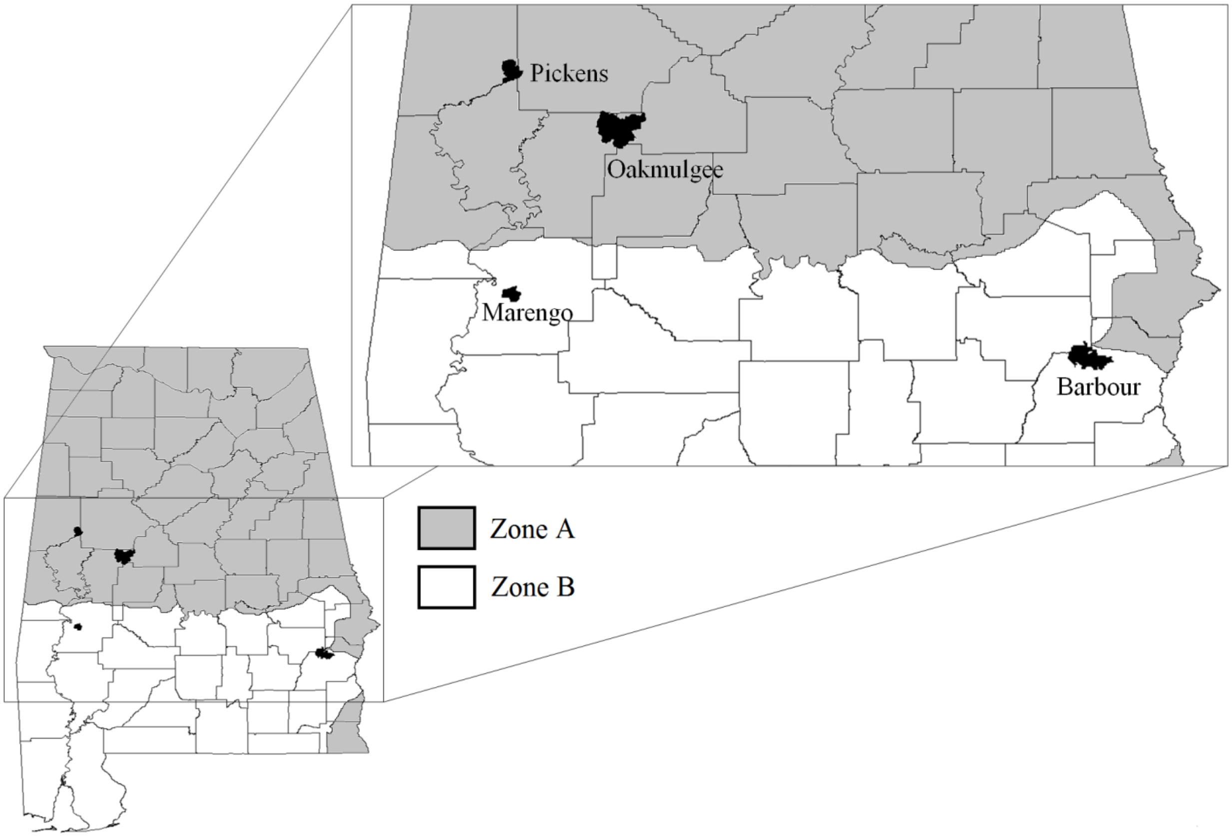

Figure 1.1 – A map of Alabama, USA, indicating county delineations and relative location of each study area within deer hunting Zones A and B from 2014-2016.

Chapter 2: Antipredator behavior of a large ungulate reflects temporal patterns of predation risk.

Abstract

A wide variety of antipredator strategies are employed across prey taxa. However, little is known regarding the influence of temporal variation in predation risk on prey animal behavior, despite the fundamental nature of this relationship to our understanding of predator-prey dynamics. To address this paucity of information, we equipped adult male and female white-tailed deer (*Odocoileus virginianus*) with global positioning system (GPS) collars from 2014-2016 to examine the behavioral response to daily and weekly temporal patterns of risk imposed by recreational hunters. During weekends (Fri – Sun), which were periods of elevated predation risk, deer decreased their movement rate by 18%, net displacement by 31%, and probability of activity by 25% during daylight hours, reflecting the presence of hunters on the landscape. However, similar fluctuations in behavior were not detected at night. Antipredator behavior was non-uniform throughout monitored deer populations, however, with variation between sexes and age classes reflecting the survival- and fitness-related trade-offs that impact prey decisions at the individual level. These findings demonstrate the perceptive capabilities of large ungulates that enable them to detect temporal variation in risk and respond in a manner that reduces the likelihood of predatory encounters, while still meeting other maintenance and reproductive requirements.

Introduction

Many animals must contend with the threat of injury or death imposed by predators. Thus, prey are forced to balance their time between a state of vigilance or other form of predator-avoidance and a state of resource acquisition (i.e., foraging, locating receptive mates, defending territories, etc.) to maximize survival and lifetime fitness (Lima and Dill 1990, Sih et al. 2000). Too little of either state could result in suppressed fitness, bodily injury, or even death (Welton et al. 2003, Ferrari et al. 2009). Thus, prey that can detect and quickly respond to predators should be at a selective advantage to those that cannot (Mirza et al. 2006). Due to the adaptability of predator-detection and avoidance mechanisms, examples of such behaviors from nature are replete within the scientific literature (Kats and Dill 1998, Sih and McCarthy 2002, Brown et al. 2006).

Kats and Dill (1998) chronicled antipredator techniques used by more than 150 prey species in response to predator-associated odors within their environment. Among such examples, anemones (*Stomphia coccinea*) were observed avoiding encounters with a predatory starfish (*Crossaster papposus*) by detaching from the ocean substrate and “swimming” from the invaded area (Yentsch and Pierce 1955). Snails avoid predators by using their foot to propel themselves from high-risk areas (Snyder and Snyder 1971), by burying themselves in the substrate (Phillips 1977), or by crawling out of the water onto emergent vegetation (Feder 1963, Szal 1971, Alexander and Covich 1991). Among more complex prey species, we see the development of more complex predator-avoidance mechanisms. Eublepharid gecko lizards (*Coleonyx brevis*) orient their autotomous tail upward toward approaching predators, presumably to confuse the assailant or misdirect attacks away from the body, and are frequently able to escape by leaving their tail behind (Dial and Fitzpatrick 1981). Another antipredator tactic, alarm calling among tamarin primates (*Saguinus labiatus*) is used to communicate predation threats to conspecifics with different types of vocalizations used to indicate the level of threat posed by the particular antagonist (Caine and Weldon 1989).

Ungulates also exhibit a variety of evasive behaviors in response to predation risk from non-human predators (Swihart et al. 1991, Altendorf et al. 2001, Latombe et al. 2014) as well as recreational hunters (Conner et al. 2001, Jarnemo and Wikenros 2014, Little et al. 2016, Marantz et al. 2016). Within many ungulate populations, hunting has become the leading source of adult mortality (Breitenmoser 1998, Ericsson 1999, Ditchkoff et al. 2001, Milner et al. 2006, Webb et al. 2011). Despite a relatively short evolutionary history together as predator and prey, within human-dominated landscapes, ungulates may respond even more strongly to the presence of humans than to the presence of historic predators (Proffitt et al. 2009, Ciuti et al. 2012). Ungulates such as elk (*Cervus elaphus*), mule deer (*Odocoileus hemionus*) and white-tailed deer (*O. virginianus*) may respond to human hunters through changes in space use by seeking refugia (Zagata and Haugen 1973, Kammermeyer and Marchinton 1976, Pilcher and Wampler 1981, Swenson 1982, Millspaugh et al. 2000), displaying excursive movements (Marchinton 1968, Ellisor 1969, Sparrowe and Springer 1970, Hood and Inglis 1974, Eckstein et al. 1979, Karns et al. 2011), and avoiding recently-hunted locations (Sullivan 2016). Ungulates may also respond to hunters by either increasing (Marshall and Whittington 1968, Root et al. 1988, Labisky et al. 1995, Naugle et al. 1997, Kilpatrick and Lima 1999) or decreasing movement (Vogel 1989, Storm et al. 1995, VerCauteren and Hygnstrom 1998, Little et al. 2016) depending largely upon the level of hunting activity and availability of escape cover within hunted areas (DeYoung and Miller 2011).

While many hundreds of examples now demonstrate that prey, including large ungulates, are capable of detecting predators and eliciting avoidance behaviors, much less is known about the effect of spatiotemporal variation in predation risk on prey species behavior (Ferrari et al. 2009, Cleveland et al. 2012). As predator and prey move across the landscape, their proximity to one another, and the density of predators around prey animals, can rapidly change (Lima and Bednekoff 1999). Therefore, vigilance and antipredator behaviors should fluctuate in a corresponding temporal pattern as prey strive to reduce the survival and fitness-related costs associated with under- or overreacting to the level of predation risk at a given moment. Lima and Bednekoff (1999) first proposed this idea within their "risk allocation hypothesis," which offers several predictions for how prey should respond to predators within different risk-level scenarios. Despite its intuitive nature, many subsequent laboratory and field tests of the risk allocation hypothesis have provided conflicting support or opposing evidence (Ferrari et al. 2009).

Understanding how temporal variation in predation risk influences antipredator behavior is fundamental to our knowledge of predator-prey interactions and the evolution of prey life-history strategies. Furthermore, how a temporally variable landscape of fear affects game species is of particular interest, having implications for the success of millions of recreational hunters (USFWS 2014), as well as our ability to manage game populations across North America (Riley et al. 2003). Further examination of ungulate response to hunting, with particular attention to specific temporal patterns of predation risk, is an important step toward improving our understanding of predator-prey ecology and could shed light on the ability of the world's keystone herbivores to perceive and react to environmental threats.

The goal of this study was to determine how white-tailed deer respond to temporal patterns of risk imposed by recreational hunters. Our specific objectives were to 1) identify temporal patterns of hunting activity within selected deer populations, 2) examine changes in space use and activity of deer in relation to temporal patterns of risk, and 3) determine the effect of sex and age of deer on antipredator response. We address these objectives prior to the breeding season, as breeding activity has been cited as a confounding factor among previous investigations of deer response to recreational hunting (Sargent and Labisky 1995, Tomberlin 2007, Karns et al. 2012).

Methods

Study Areas

Our study took place at 4 locations within Alabama, USA (Figure 2.1). The first was Barbour Wildlife Management Area (hereafter referred to as “Barbour”). Barbour was composed of 11,418 ha of public-use land, managed by the Alabama Department of Conservation and Natural Resources (ADCNR) and located within Bullock and Barbour Counties, AL (31°59.73 N, 85°27.57 W). Archery (i.e., bow and crossbow) hunting for white-tailed deer extended from 25 Oct-10 Feb annually, with firearm portions (i.e., youth, primitive weapons, rifle) restricted between the dates of 14 Nov-10 Feb during the 2014/15 season and 13 Nov-10 Feb during the 2015/16 season. Barbour was split into 2 zones of approximately equal size with some portions of the firearm season limited to a single zone; however, archery hunting remained open across the entire area in such cases. Other times, all of Barbour was open to both archery and firearm hunting. Barbour consisted of gently rolling terrain, characteristic of northern portions of Alabama’s lower coastal plain (Gray et al. 2002), and the habitat was predominantly mixed pine-hardwood stands consisting of loblolly (*Pinus taeda*) and short-leaf pine (*P. echinata*), oaks (*Quercus* spp.), maples (*Acer* spp.), sweetgum (*Liquidambar styraciflua*), sycamore (*Platanus occidentalis*), and yellow poplar (*Liriodendron tulipifera*). Within bottomlands or along drainages and riparian corridors, hardwoods were dominant with interspersed pine. Alternately, uplands were predominantly pine interspersed with hardwoods, and portions of upland areas were in the early stages of longleaf pine (*Pinus palustris*) restoration. Approximately 200 wildlife openings (0.5-8.0 ha) were scattered across Barbour and planted with a cool season mixture of chicory (*Cichorium intybus*), clovers (*Trifolium* spp.), grains (oats, *Avena fatua*; wheat, *Triticum aestivum*), rape (*Brassica napus*), and winter peas (*Pisum sativum*). Additionally, warm season plantings included browntop millet (*Urochloa ramosa*), chufa (*Cyperus esculentus*), corn (*Zea mays*), cowpeas (*Vigna unguiculata*), sunflower (*Helianthus* sp.), and sun hemp (*Crotalaria juncea*). Portions of Barbour received prescribed fire on a 3- to 5-year return interval and although primarily managed for wildlife, infrequent timber harvests (i.e. thinnings or clear cuts) were conducted within small (i.e., ≤50 ha) portions of the area. A network of maintained gravel and dirt roads extended throughout Barbour with 2 paved roads (Barbour Co Rds. 47 and 49) passing through portions of the area.

Oakmulgee Wildlife Management Area (hereafter referred to as "Oakmulgee") was an 18,009-ha, public-use area spanning Bibb, Hale, Perry, and Tuscaloosa Counties, AL (32°57.39 N, 87°27.60 W). Oakmulgee was part of the Taledega National Forest and jointly managed by the ADCNR and the U.S. Forest Service. Archery hunting for white-tailed deer extended from 15 Oct-31 Jan annually with the firearm portions restricted between the dates of 14 Nov-31 Jan during the 2014/15 season and 13 Nov-31 Jan during the 2015/16 season. Like Barbour, Oakmulgee was split into 2 zones of approximately equal size. However, during both archery and firearms portions of the season, hunters were allowed access to either zone. Oakmulgee was situated in the southern foothills of the Appalachians, with terrain that was more rugged than that of Barbour consisting of rolling hills with steep to moderate slopes. Other differences included a more widespread application of prescribed fire on Oakmulgee compared to Barbour, as well as the presence of mature longleaf pine stands that dominated the upland ridges. Additionally, timber harvests were conducted with greater regularity and over larger (≤150 ha) areas.

Approximately 100 wildlife openings (0.5 - 4.0 ha) were scattered across Oakmulgee and planted with a cool season mixture of clovers and grains (oats; rye, *Secale cereale*; wheat) and warm season varieties such as chufa, corn, proso millet (*Panicum miliaceum*), sorghum (*Sorghum bicolor*), and sunflower. Oakmulgee had a lower density of gravel and dirt roads than Barbour and was intersected by 3 paved roads (Hale Co Rds. 49 and 50 and Hwy 25).

Our third study area (hereafter referred to as “Marengo”) was located in Marengo County, AL (32°14.08 N, 87°51.11 W) and was composed of 3,116 ha of privately-owned land, approximately half of which was owned as separate parcels by private individuals, and the remainder owned by The Westervelt Company and leased to private individuals for hunting. Deer hunting season dates at Marengo were the same as those of Barbour. The terrain and habitat composition within Marengo were also comparable to those of Barbour due to similar positioning within the northern portion of Alabama’s lower coastal plain (Gray et al. 2002), with the exception that longleaf pine was absent and prescribed fire was rarely applied. The majority of the Marengo ownership of The Westervelt Company was managed for timber production and existed in various regenerative stages of planted loblolly and shortleaf pine. Food plots were common, particularly on portions of Marengo owned by private individuals, and were typically planted in cool-season blends of wheat and clover or winter peas, and soybeans (*Glycine max*) in the warm season. There was a lower density of gravel and dirt roads than within either Barbour or Oakmulgee, and no paved roads intersected Marengo.

Our final study area (hereafter referred to as “Pickens”) was located in Pickens County, AL (33°12.45 N, 87°52.01 W) and was composed of 4,899 ha of land, privately owned by The Westervelt Company and leased in approximately 400-ha tracts to hunting clubs. Deer season dates at Pickens were the same as those of Oakmulgee. The terrain within Pickens also resembled that of Oakmulgee, characterized by rolling hills with steep to moderate slopes, and the habitat was predominantly loblolly and shortleaf pine managed for timber production and existing in various regenerative stages. Hardwoods were restricted to drainages and streamside management zones. Like Marengo, food plots were common within Pickens and normally planted in clovers or winter peas in the cool season and left dormant in the warm season. Road density within Pickens was also similar to Marengo, with no paved roads intersecting the area.

Capture and Handling

During summers (May - Aug) of 2014 and 2015, adult (≥1 year old) male and female white-tailed deer were immobilized using tranquilizer dart guns and radio-transmitter darts (Pneu-Dart, Inc., Williamsport, Pennsylvania). Darts contained a 2-ml mixture of Telazol (Fort Dodge Animal Health, Fort Dodge, Iowa; 100 mg/ml at a rate of 4.0 mg/kg) and xylazine-hydrochloride (Lloyd Laboratories, Shenandoah, Iowa; 100 mg/ml at a rate of 2.0 mg/kg) administered as an intramuscular injection upon impact. To reduce the likelihood of capture-related stress, a minimum of 10 minutes was allowed to elapse before leaving the darting location to ensure full sedation of darted deer prior to approach by researchers. A hand-held, 3-element Yagi antenna and receiver (Mod R410; Advanced Telemetry Systems [ATS], Isanti, Minnesota) were used to detect dart transmitters and locate sedated deer. Upon capture, deer were blindfolded to further minimize handling stress. Darts were removed and a coagulant immediately applied to the wound to prevent blood loss.

Captured deer were fitted around the neck with a GPS collar equipped with a 4-hour mortality sensor (Mod G2110D; ATS) and in each ear with a 2-piece, yellow ear tag (Y-Tex Corporation, Cody, Wyoming) displaying a unique ID and contact phone number. Collars were lined with a pliable foam material to allow for neck growth and breeding-season swelling

(Thomas et al. 1965), and to keep collars in the upright position to improve data collection and accuracy (D'Eon and Delaparte 2005). Age of each captured deer was estimated using a combination of tooth replacement and wear (Severinghaus 1949) and live body characteristics (Demarais et al. 1999) to maximize aging accuracy (Bowman et al. 2007). After handling was complete, a 3-ml intramuscular injection of tolazoline (Lloyd Laboratories, Shenandoah, Iowa; 100 mg/ml at a rate of 2.0 mg/kg) was administered as an antagonist to the xylazine-hydrochloride sedative. Deer remained under observation until they moved from the capture location under their own power. Capture and handling methods were approved by the Auburn University Institutional Animal Care and Use Committee (PRN 2013-2323), and followed the guidelines of the American Society of Mammalogists (Sikes and Gannon 2011).

Capture efforts took place across all 4 study areas each summer, and within both management zones of public-use study areas (i.e., Barbour and Oakmulgee). Initially, deer were sampled randomly, without regard for sex or age class, from each population. Toward the end of the capture effort, however, sampling focused on ensuring sufficient representation of each sex and age class across all areas. GPS collars were fluorescent orange in color and, paired with yellow ear tags, were intended to be highly visible to hunters who were asked not to harvest GPS-collared deer in order to avoid sample-size reduction (Wiskirchen et al. 2016). Collared deer were monitored biweekly for mortality events and upon detection of mortality, researchers attempted to determine the cause by examining the remains as well as any persisting evidence within the immediate area (e.g., tracks, scat, drag lines). Mortalities were then classified as harvest-related, natural, or unknown.

Data Collection and Censoring

GPS collars were programmed to take 1 locational fix every hour through the entirety of each deer hunting season. All collars, whether deployed in 2014 or 2015, were scheduled to automatically release from deer on 31 Mar 2016. Upon release or detection of mortality, whichever occurred first, collars were retrieved from the field and data were offloaded using ATS WinCollar software. The mean locational error of the data was reduced by removing all three-dimensional fixes with position dilution of precision (PDOP) values >10 or horizontal dilution of precision (HDOP) values >6, as well as all 2-dimensional fixes with HDOP values >5 (Moen et al. 1997, Dussault et al. 2001, D'Eon and Delparte 2005). In addition, all fixes <7 days post-capture were removed to reduce the possibility of biased movements due to capture-related stress (Karns et al. 2012) and fixes <7 days pre-mortem were removed in the case of natural or unknown morality. Time of death for natural or unknown mortalities was determined by examining the data in ArcMap 10.0 (ArcMap version 10.0, ESRI Inc., Redlands, California 2013) and was assumed to be the time at which successive locations ceased to move across the landscape.

Temporal Patterns of Risk and Exposure Period

Two temporal patterns of risk were identified, resulting from temporal variability in recreational hunting activity across study areas. The first was a daily temporal pattern, common within hunted populations of white-tailed deer (Proffitt et al. 2009, Ciuti et al. 2012), where predation risk alternated between present and absent during diurnal and nocturnal hours, respectively. Deer hunting was permissible starting 30 minutes before sunrise and ending 30 minutes after sunset. Thus, these bounds were used to designate the DIURNAL and NOCTURNAL temporal periods. Area-specific sunrise and sunset data were obtained from the U.S. Naval Observatory website for the municipality nearest each study area.

Antipredator behavior among game and non-game species has been known to fluctuate with weekly patterns of hunting (Evans and Day 2002) and non-hunting, human activity (Bautista et al. 2004). Therefore, a second, weekly temporal pattern of risk was identified by examining known hunting effort within each study area by day of the week (i.e., Sunday, Monday, Tuesday, etc.). Estimates of area-specific hunting pressure, which are a commonly used proxy for predation risk (Murphy 1962, Diefenbach et al. 2005, Rhoads et al. 2013, Little et al. 2014), were obtained in 1 of 2 ways. On privately-owned study areas (i.e., Marengo and Pickens), hunters were asked to submit records from individual outings documenting the date and number of hours spent afield. From these records, daily predation risk on private study areas was represented as hours/ha. On public-use areas (i.e., Barbour and Oakmulgee), hunters collected a permit from the Wildlife Management Area office for each day of gun hunting, with daily permit totals representing the number of hunters on each area. Thus, daily predation risk on public-use areas was represented as hunters/km^2. We chose to represent daily hunting pressure in terms of hours/ha and hunters/km^2 due to the availability of information from each of our study areas and for ease of comparison to previously reported levels of hunting pressure.

Although knowledge of daily hunting pressure across study areas was likely imperfect as a result of unreported records of hunting activity, we had no reason to believe that missing records were more likely from one day than from any other day of the week. Thus, we assumed that our data for hunting pressure represented the relative risk throughout the week. From individual daily estimates, mean (± 1 SE) predation risk was calculated for each day of the week. In this way, we identified a weekly temporal pattern of predation risk where hunting activity was greater on weekends (i.e., Fridays, Saturdays, and Sundays) than throughout the rest of the week, with additional variation in hunting pressure within weekend and weekday periods. Based on the observed weekly patterns of predation risk, 2 additional temporal periods were designated, 1 representing course differences in risk between weekends and weekdays (DAY_TYPE) and the other accounting for fine-scale temporal variation in risk by individual day of the week (DOW).

Within hunted populations of white-tailed deer, breeding and hunting seasons typically coincide (Tomberlin 2007). As a result, previous studies examining deer response to hunting have cited breeding activity as a potentially confounding factor, limiting the ability of researchers to distinguish breeding-related movements from hunter-avoidance behaviors (Sargent and Labisky 1995, Karns et al. 2012). To limit the potentially confounding effect of breeding activity in our study, we selected a risk-exposure period for each site that occurred within the hunting season, yet excluded the majority of the breeding season. This was possible given the lengthy, 108-day deer-hunting season within Alabama, much of which occurred prior to the onset of breeding. To determine area-specific breeding seasons, we used the most recent 10 years of a historic conception dataset collected by ADCNR biologists, containing information from each of our study areas. We then selected a period for each study area that occurred after the opening day of youth season (14 Nov in 2014 and 13 Nov in 2015), when hunting activity was expected to become a consistent source of predation risk, but that contained <5% of annual conceptions. Due to temporal variability in peak breeding between study areas, the risk-exposure period varied from 23 to 58 days ($\bar{x} = 42.75$) depending on year and study area.

Movement Parameters

White-tailed deer response to identified temporal patterns of risk was evaluated using 4 movement parameters assumed to be indicators of antipredator behavior: movement rate, net displacement, percent (%) diurnal movement, and probability of activity. These parameters were selected because each was predicted to fluctuate with changes in hunting pressure and because together, they represented a diverse array of animal behaviors, providing information on both spatial and temporal response to temporal patterns of risk.

Movement rate is a commonly-employed metric among studies of animal space use (Holzenbein and Schwede 1989, D’Angelo et al. 2004, Webb et al. 2010, Little et al. 2016). Given that movement rate is closely linked to the likelihood of predation among some prey species (Martel and Dill 1995, Yoder et al. 2004) and vulnerability to harvest among white-tailed deer (Roseberry and Klimstra 1974, Little et al. 2014), we expected movement rate to fluctuate in response to hunting pressure as failure to show such a response would be maladaptive. Movement rate was calculated as the Euclidean distance, or step length, between successive hourly fixes (m/hr). In the case of a failed fix attempt resulting in a movement window exceeding 1 hour, no movement rate was calculated to avoid differential bias associated with estimating total movement over variable-length periods (Little 2011). Therefore, all estimates of movement rate were based on the step length during 1-hour periods and rates were classified as “diurnal” or “nocturnal” based on the daily temporal period in which they occurred. Residuals of fitted values were found to have a right-skewed distribution, therefore, movement rates were natural log-transformed, after adding 1.0 m/hr to each value (Warton and Hui 2011), to meet the assumptions of parametric tests.

Net displacement is another commonly-employed spatial metric (Kareiva and Shigesada 1983, Crist et al. 1992, Wu et al. 2000, Gutenkunst et al. 2007) and can be used to evaluate the amount of space use over a period of interest (Christ et al. 1992), where large net displacement values correspond to extensive spatial exploration and small net displacement values representing stationary behavior or localized movement. Net displacement was calculated as the Euclidean distance (m) from a pre-defined starting point to each subsequent point along the movement path throughout the period of interest. Net displacement was calculated for each successful fix and classified as “diurnal” or “nocturnal” based on the daily temporal period in which it occurred. Net displacement values for locations that fell within the DIURNAL period were calculated in relation to the first diurnal location of each day as the starting point, while nocturnal net displacement values were calculated in relation to the first nocturnal location of each day as the starting point (i.e., the first location following the diurnal period). Net displacement values were natural log-transformed, after adding 1.0 m to each value, to correct for a right-skewed distribution of residuals across fitted values (Warton and Hui 2011).

White-tailed deer may become “more nocturnal” in response to hunting by increasing their nocturnal activity, while displaying no increase in activity during diurnal hours when hunters are present (Kilgo et al. 1998). Percent diurnal movement was used to indicate how “nocturnal” deer became in response to risk exposure imposed by hunters during diurnal hours. Percent diurnal movement was calculated as L_D/L_T, where L_D was total diurnal step length and L_T was the total daily step length. Diurnal and daily step lengths were the sum of hourly movements over the course of the diurnal and diel periods, respectively. Increasing values of % diurnal movement indicate that deer were allocating more of their daily movement to diurnal hours, whereas decreasing values indicated a proportionate decrease in diurnal movement, suggesting animals had become “more nocturnal.” Days were excluded from calculations of % diurnal movement that contained ≤3 diurnal or nocturnal fixes to avoid biased estimates resulting from entirely missed or severely underrepresented diurnal or nocturnal periods.

Probability of activity expressed the likelihood that deer were moving during a specified period of interest. Activity and non-activity states were determined for each DIURNAL and NOCTURNAL hourly period based on the Euclidean distance between successive fixes and treated as a binary variable with "active" assigned to step lengths ≥49.05 meters and "inactive" assigned to step lengths below that threshold. This activity threshold was selected based on Jerde and Visscher (2005) who recommended using a value ≥5 standard deviations of the mean locational error to be sure animal movement has occurred when utilizing GPS location data. Sullivan et al. (2016) field tested the locational accuracy of the same model collar used in the present study, within similar habitat types, and found a mean locational error of 12.95 m (SD = 9.81 m) used to derive our activity threshold. Similar to calculations of movement rate, only consecutive, 1-hour periods were considered when assigning activity states to avoid differential bias associated with quantifying total movement over variable-length periods (Little 2011).

For our analysis in which both diurnal and nocturnal periods were of interest, a "day" extended from the start of the DIURNAL period (i.e., 30 minutes prior to sunrise) until the start of the DIURNAL period the following day. This definition was used as we felt it to be more representative of how prey animals likely perceive diel patterns compared to how humans typically define a day (i.e., nocturnal periods separated by the diurnal period), and to allow for examination of movement behavior during NOCTURNAL periods in relation to the level of risk exposure from the previous DIURNAL period. As an example, Friday, 18 Dec 2015, began 30 minutes prior to sunrise (6:18 A.M., CST) and extended until 30 minutes before the next sunrise (also 6:18 A.M., CST), at which point Saturday, 19 Dec 2015, began.

Data Analysis

Each of the 4 movement parameters were modeled as separate response variables within either a linear mixed-effects model (i.e., movement rate, net displacement, % diurnal movement) or a generalized linear mixed-effects model (i.e., probability of activity) with a binomial distribution in R (v3.1.1; R Core Development Team 2015). To explore the effects of the

DIURNAL and NOCTURNAL temporal periods on antipredator behavior, data from 3 of the movement parameters (i.e., movement rate, net displacement, probability of activity) were subdivided into 2 groups based on the diel period to which they corresponded. Percent diurnal movement was not subdivided because it incorporated both diurnal and nocturnal movement.

Both DIURNAL and NOCTURNAL datasets for each movement parameter, when applicable, were modeled with 2 sets of explanatory variables to examine the effect of weekly temporal patterns of risk (i.e., DAY_TYPE and DOW) on deer antipredator behavior. Differences between weekend and weekday behavior were explored via DAY_TYPE models, which included DAY_TYPE (i.e., weekend or weekday) as a main effect, as well as main effects of SEX, AGE, and YEAR. Deer age was modeled as a 2-factor, categorical variable with animals separated into 2 general groups: <3.5 years old and ≥3.5 years old. Excursive movements and dispersal events are most common among <3.5-year-old white-tailed deer, with older individuals often having more well-established home ranges (Marchinton and Hirth 1984, Long et al. 2005). Additionally, age classes of deer may perceive or react to the threat of human hunters differently due to variation in previous experience with hunters (Kilpatrick and Lima 1999) as well as differences in hunter selection between old and young individuals (Coe et al. 1980). Hereafter, deer <3.5 years old and ≥3.5 years old will be referred to as "immature" and "mature" respectively. Additionally, DAY_TYPE models included SEX*DAY_TYPE, AGE*DAY_TYPE, SEX*AGE, and SEX*AGE*DAY_TYPE interactions to examine the effect of sex and/or age class on deer response to the weekly temporal pattern of risk. Alternately, differences in daily behavior were explored via DOW models, which contained all of the same main effects previously mentioned, however DOW (i.e., Sunday, Monday, Tuesday, etc.) was substituted for each occurrence of DAY_TYPE to allow for examination of antipredator behavior in relation to a greater degree of temporal variation.

Each model also included STUDY_AREA and DEER as nested random effects, reflecting the spatially nested study design and accounting for unmeasured variation between geographic locations and individuals. Additionally, JULIAN_DATE was modeled as a nested random effect in all models, except those with % diurnal movement as the response variable, to account for greater correlation among movements within, than between, days. Percent diurnal movement was not modeled with JULIAN_DATE as a random effect since there was only a single parameter estimate per day. The complete random effects statements therefore, for % diurnal movement and all other models respectively, were DEER nested within STUDY_AREA, and JULIAN_DATE nested within DEER nested within STUDY_AREA.

To improve model parsimony and interpretability, a limited step-down approach was used to assess whether 2- and 3-way interactions could be omitted (Harrell 2001). With this approach, each full model was first compared to a reduced model by excluding the 3-way interaction term. A likelihood ratio test (LRT) was then used to compare full and reduced models, and the interaction in question was dropped if the LRT resulted in a p-value >0.10 (Harrell 2001). A liberal p-value was used to determine if interactions should be retained or removed, per the recommendation of Harrell (2001), to achieve an appropriate balance between parsimony and model accuracy. If the 3-way interaction was removed, the reduction process continued with each 2-way interaction being considered separately as a candidate for removal. Two-way interactions were removed in the order of greatest improvement (i.e., highest p-value) to the previous model based on results from each LRT. The reduction process was complete when no more interactions could be removed, as main effects were not candidates for removal, and inferences were based on final models.

Results

We deployed GPS collars on 38 adult white-tailed deer across study areas, 6 of which were not included in the analysis due to collar program malfunctions (*n* = 2), an unknown mortality (*n* = 1) prior to the start of the risk-exposure period, and failure by collars to detach from fitted deer on the scheduled drop-off date (*n* = 3). Of the remaining 32 animals (16 M, 16 F), 20 contributed movement information from both the 2014/15 and 2015/16 deer hunting seasons. Movement rate and probability of activity were analyzed from 39,895 locations, net displacement from 38,673 locations, and % diurnal movement from 42,300 locations within the risk-exposure period.

Hunting Effort

Hunting pressure on public-use areas averaged 0.58 (SE = 0.10) hunters/km^2/day on weekends and declined by 67% to an average of 0.19 (SE = 0.04) hunters/km^2/day on weekdays. On privately-owned areas, hunting pressure averaged 0.009 (SE = 0.001) hours/ha/day on weekends and declined by 83% to an average of 0.002 (SE < 0.000) hours/ha/day on weekdays (Figure 2.2). On both public and private land, hunting pressure was greatest on Saturdays, averaging 0.72 (SE = 0.19) hunters/km^2/day and 0.013 (SE = 0.002) hours/ha/day respectively.

DIURNAL Temporal Period

Within final DAY_TYPE, DIURNAL-period models, and the final DAY_TYPE % diurnal movement model which incorporated both diurnal and nocturnal movement, no interactions between DAY_TYPE and other main effects were retained. Likewise, the main effect of DAY_TYPE did not explain deer behavior within any of the final models (*P* > 0.404), suggesting similar behavior between weekends and weekdays, regardless of sex or age class of deer. Similarly, no interactions between DOW and other main effects were retained within final DOW models, with the exception of a potentially meaningful (*P* = 0.069) AGE*DOW interaction for probability of activity, indicating that the likelihood of activity throughout the week varied between mature and immature deer. Furthermore, the main effect of DOW helped explain variation in movement rate ($P < 0.001$) and net displacement ($P = 0.003$), and was a potentially meaningful parameter explaining variation in % diurnal movement ($P = 0.069$), suggesting that each type of behavior varied by day of the week. However, the absence of additional interactions containing DOW suggests that, with the exception of probability of activity, weekly fluctuations in movement were similar between males and females and between age classes of deer.

All final DAY_TYPE and DOW, DIURNAL-period and % diurnal movement models retained a SEX*AGE interaction, suggesting that differences in behavior between mature and immature deer varied by sex. Lastly, final DIURNAL models indicated greater movement rate, net displacement, and probability of activity during the first hunting season (i.e., 2014/15) compared to the second (i.e., 2015/16, $P < 0.001$). Final DAY_TYPE and DOW, DIURNAL models were identical with the exception of how well each respective weekly temporal period explained deer behavior. Thus, interactions and main effects were evaluated with respect to DOW models only.

We observed no change in diurnal movement rate from Thursday to Friday ($P = 0.334$) or Friday to Saturday ($P = 0.863$). However, from Saturday to Sunday, Saturday to Monday, and Saturday to Tuesday, there were 19% (8-30%, 95% C.I.; $P < 0.001$), 13% (3-24%, 95% C.I.; $P = 0.012$), and 12% (2-23%, 95% C.I.; $P = 0.016$) decreases in movement rate, respectively. By Wednesday ($P < 0.001$) and Thursday ($P = 0.017$), movement rate had increased and was again greater than movement rate on Sunday. Additionally, we observed a potentially meaningful SEX*AGE interaction (*P* = 0.051, interactions were retained at *P* < 0.10 to avoid oversimplifying final models) such that mature males moved 14% (-1-31%, 95% C.I.) less than immature males, however mature female movement rate was only 9% (-7-27%, 95% C.I.) less than that of immature females.

Similar to movement rate, we observed no change in net displacement from Thursday to Friday (*P* = 0.179) or from Friday to Saturday (*P* = 0.761). However, from Saturday to Sunday and from Saturday to Monday, there were 28% (9-49%, 95% C.I.; *P* = 0.002) and 23% (5-44%, 95% C.I.; *P* = 0.009) decreases in net displacement, respectively. By Wednesday (*P* = 0.006), net displacement had increased and was again greater than on Sunday. Additionally, there was a significant SEX*AGE interaction (*P* = 0.004) such that net displacement of mature males was 31% (3-67%, 95% C.I.) less than that of immature males. Conversely, net displacement did not differ between mature and immature females (*P* = 0.769).

Mean values <0.50 for % diurnal movement indicated that deer were typically more active at night than during the day (Figure 2.3). We observed no change in how “nocturnal” deer were from Thursday to Friday (*P* = 0.793) or from Friday to Saturday (*P* = 0.948). However by Sunday, deer had allocated 3% (1-6%, 95% C.I.) more of their daily movement to nocturnal hours compared to Saturday (*P* = 0.013). By Wednesday, diurnal movement had again increased and made up 4% (1-7%, 95% C.I.) more of the total daily movement than it had on Sunday (*P* = 0.003). Additionally, we found a significant SEX*AGE interaction (*P* < 0.001), indicating that mature males allocated 10% (7-14%, 95% C.I.) less of their daily movement to diurnal hours compared to immature males. However among females, there was no difference in % diurnal movement between age classes (*P* = 0.789).

The final DOW model for probability of activity contained a potentially meaningful (*P* = 0.068) AGE*DOW interaction where the likelihood of activity was found to vary throughout the week among both mature (*P* = 0.035) and immature deer (*P* = 0.002), but in a different temporal pattern (Figure 2.4). Among both mature and immature deer, there was no change in the probability of activity from Thursday to Friday (*P* > 0.158). However, over the course of the weekend from Friday to Sunday, there was a gradual and consistent decline in the probability of activity among mature deer, resulting in activity being 25% (7-46%; 95% C.I.) less likely on Sunday compared to Friday (*P* = 0.006). Conversely, activity was a 16% (-6-44%; 95% C.I.) more likely on Saturday compared to Friday among immature deer (*P* = 0.182) followed by a dramatic, 45% (16-82%; 95% C.I.) decrease in the probability of activity by Sunday (*P* < 0.001). By Wednesday, mature deer were again more likely to be active than they had been on Sunday (*P* = 0.002), however probability of activity among immature deer did not surpass that of Sunday until Thursday (*P* = 0.002). The final DOW model for the probability of activity also contained a significant SEX*AGE interaction (*P* = 0.033) such that mature females were 48% (9-101%; 95% C.I.) more likely to be active than mature males, however the probability of activity did not differ between immature males and females (*P* = 0.591).

NOCTURNAL Temporal Period

As with DIURNAL models, the final DAY_TYPE, NOCTURNAL-period models retained no interactions between DAY_TYPE and other main effects with only 1 exception. The final NOCTURNAL model for movement rate retained a potentially meaningful (*P* = 0.095) SEX*AGE*DAY_TYPE interaction indicating that there may have been a difference in movement rate at night between weekends and weekdays, however such a difference likely varied by sex and age class of deer. Furthermore, the main effect of DAY_TYPE did not explain deer behavior within NOCTURNAL models for net displacement or probability of activity ($P >$ 0.168). Likewise, final DOW models for the NOCTURNAL period retained no interactions between DOW and other main effects, and the main effect of DOW was also not an explanatory variable for any of the movement parameters ($P >$ 0.122, Figure 2.5). The near absence of interactions containing DAY_TYPE or DOW indicates that, in general, weekly patterns of nocturnal behavior did not show appreciable variation by sex or age class of deer. Furthermore, the lack of support for both DAY_TYPE and DOW as main effects indicates consistent behavior between weekends and weekdays, and across days of the week, during the NOCTURNAL period.

Final DAY_TYPE and DOW models for movement rate and probability of activity did, however, each contain a significant SEX*AGE interaction ($P <$ 0.004), indicating that nighttime movement rates and the likelihood of activity were different between mature and immature deer, but the magnitude of difference was dependent on sex. Namely, mature males were 51% (24-84%; 95% C.I.) more likely to be active during nocturnal hours than immature males, and movement rate was 39% (21-59%; 95% C.I.) greater among mature males than immature males. Conversely, there was no difference in movement rate ($P =$ 0.271) or probability of activity ($P =$ 0.309) between female age classes. Lastly, YEAR was not a significant parameter in any of the final NOCTURNAL models ($P >$ 0.167), indicating consistent nocturnal movement, space use, and activity between years.

Discussion

Differences in patterns of behavior throughout the week between diurnal and nocturnal periods suggest that white-tailed deer are able to distinguish between the presence and absence of hunters on the landscape, and adjust their antipredator behavior accordingly. This finding serves as supporting evidence for the risk allocation hypothesis (Lima and Bednekoff 1999) which predicts that predator-avoidance behaviors will fluctuate in a manner that corresponds to the temporal pattern of risk. Furthermore, our results demonstrate that even low levels of hunting pressure may, at times, be enough to elicit an antipredator response within ungulate populations. Previous studies examining ungulate response to hunting have encompassed a wide array of pressure intensities (Karns et al. 2012), ranging from 4 hunters/km^2 (Diefenbach et al. 2005) to 77 hunters/km^2 (Murphy 1962), and from 0.05 hours/ha (Little et al. 2016) to 1.31 hours/ha (Root et al. 1988). In comparison, our estimates were much less, even than previously-reported levels of hunting below which no behavioral response has been detected (0.45 hours/ha/day, Root et al. 1988; 0.05 hours/ha/day, Little 2011). However, previous studies have usually been conducted during the breeding season, as periods of hunting and breeding typically coincide within ungulate populations (Tomberlin 2007). Conversely, our study took place prior to breeding, which not only limited a nearly ubiquitous confounding factor (Karns et al. 2012), but also allowed for examination of the effect of hunting during a time when deer may be more sensitive to predatory threats. Intense competition for mates between male conspecifics (Mysterud et al. 2004), and to a lesser degree among females (Sullivan 2016), during the rut may cause breeding activity to dominate behavior until an environmental stimulus surpasses the strong desire to breed (Neumann et al. 2009). Thus, there may be a greater disturbance threshold needed to elicit a behavioral response during the breeding season than at other times of the year.

Based on our findings compared to previous studies, it seems that outside of the breeding season white-tailed deer may be more willing to employ behavioral trade-offs to avoid predators, even when the risk of predation is relatively low. This possibility has implications for the physical condition of deer preparing to enter the rigors of the winter and breeding season.

Autumn is an important time for building fat stores as food intake may decline 20-50% during winter when hormonal changes cause a decrease in appetite and a shift in focus toward acquiring mates (Ozoga and Verme 1970, Thompson et al. 1973, Holter et al. 1977, Wheaton and Brown 1983). Therefore, disturbances that precede the breeding season and result in decreased movement or activity may cause deer to enter the breeding season in suboptimal body condition, which could ultimately impact winter survival (Mautz 1978) and reproductive potential (Verme 1969, Abler et al. 1976).

We further attribute our ability to detect behavioral changes within relatively low-risk environments to having accounted for fine-scale temporal variation in risk throughout the week. Our DIURNAL, DAY_TYPE models suggested no change in behavior between weekends and weekdays, despite a substantial difference in hunting activity. Yet, when a greater degree of temporal variation was incorporated (i.e., DOW), more accurately reflecting temporal variation in hunting pressure by day of the week, a population-level response became evident. We did not, however, observe an immediate response to increased hunting pressure on weekends as would be predicted by the risk allocation hypothesis (Lima and Bednekoff 1999). Rather, we observed a "delayed" response to weekend hunting where a population-level change in deer behavior was not evident until Sunday. Likewise, despite a decrease in hunting pressure on Mondays and Tuesdays compared to that on weekends, indicators of deer behavior did not typically return to pre-weekend levels until Wednesday. The "delayed" population-level response could suggest that individual white-tailed deer did not immediately respond to temporal changes in predation risk. This possibility seems unlikely, however, as detection of, or direct encounters with, predators should elicit a rapid antipredator response (Lima and Bednekoff 1999).

For a more plausible explanation, we must consider the possibility that deer did immediately respond to increased hunting pressure at the onset of the weekend, but not in ways that were detectable by our selected behavioral metrics. Karns et al. (2012) found no population-level response to hunting pressure among adult, male white-tailed deer in Maryland. However, researchers detected a number of temporary and short-distance flight responses that were the result of direct encounters with hunters, and they attributed their ability to detect these fine-scale movements to high-resolution GPS data collected at 20-minute intervals. Likewise, Neumann et al. (2009) found no behavioral response by moose (*Alces alces*) to hunting pressure using a GPS fix rate of 30 - 60 minutes. However, the researchers postulated that behavioral changes may have been detectable on an individual basis rather than at the population level. Our 1-hour, GPS fix intervals used in comparing 12- or 24-hour movement averages may have precluded our ability to detect fine-scale or individually-based behavioral changes at the beginning of the weekend. Furthermore, our behavioral metrics did not allow detection of the full array of possible antipredator behaviors that have previously been observed among hunted ungulates. For example, deer have been shown to alter their habitat utilization in response to hunting pressure by avoiding open habitats and showing preference for areas that provide more cover (Sparrowe and Springer 1970, Eckstein et al. 1979, Kilpatrick et al. 2002, Stamnes 2014). When dense “escape cover” is available within a pre-existing home range, deer will normally utilize those habitats rather than leaving the area to seek refuge elsewhere (Kufeld et al. 1988, Kilgo et al. 1998). Habitats providing dense cover were readily available at all 4 of our study areas in the form of regenerating pine stands and other early successional vegetation. Therefore, deer may have made fine-scale or temporary shifts in space use in response to early-weekend hunters which were undetected by our metrics.

Despite detecting no initial response, all 4 of our metrics indicated a population-level change in behavior by Sunday, which may have been the result of accumulated encounters with hunters by the third day of the weekend. Laurila et al. (2004) observed a graded behavioral response by common frog (*Rana temporaria*) tadpoles to a predatory dragonfly (*Aeshna* sp.), where tadpole activity decreased with each additional predatory encounter throughout phases of development. Our results could also be indicative of a graded response where antipredator behaviors may have become more pronounced with each additional encounter with hunters until a population-level response was finally evident by the third day of exposure to weekend hunting. The risk allocation hypothesis predicts greatest antipredator response during short and infrequent periods of risk, with prolonged exposure to predators yielding an increasingly reduced response as the need to participate in other survival-related activities, such as foraging, increase over time (Lima and Bednekoff 1999). Based on this prediction, it may seem that our findings and the risk allocation hypothesis do not agree. However, it is important to note that exposure to hunters was not continuous over the course of the weekend, and nocturnal periods may have allowed deer to compensate for lost foraging opportunities during the day. Nocturnal movement was consistently greater than diurnal movement throughout our study, as indicated by % diurnal movement values <0.50, which may lend support to this hypothesis. Therefore, consecutive diurnal periods over the course of the weekend, during which encounters with hunters may have accumulated, could have been perceived as increasing risk over time, thus leading to a graded and increasing antipredator response.

Following the behavioral depression on Sundays that was consistent across all metrics of diurnal movement, daytime behaviors did not return to their pre-weekend state until Wednesdays or Thursdays, despite a decrease in hunting pressure on Mondays and Tuesdays. Other studies have observed a similar display of extended antipredator behavior following periods of risk, and have postulated that this may be the result of some uncertainty as to whether or not predators have vacated the field (Sih 1992, Little 2011). However, there was a noticeable difference in patterns of behavior between diurnal and nocturnal periods within our study suggesting that deer were able to accurately differentiate between the presence and absence of hunters. Alternately, the “delayed” return to pre-weekend behavior could support previous findings which suggest that prey species may have an ability to learn, and respond in a predictive manner, to temporal patterns of predation risk (Ferrari et al. 2008). For 9 days, Ferrari et al. (2008) exposed larval wood frog (*Rana sylvatica*) tadpoles to the odors of a predatory salamander (*Ambystoma tigrinum*) and injured conspecifics during the evening period (salamander present and feeding), with salamander-only odors in the morning (salamander present but not feeding—evening risk). Simultaneously, a second group of tadpoles was exposed to the opposite treatment (morning risk). When subsequently exposed to salamander-only odors in the evening, evening-risk tadpoles responded more strongly than the morning-risk group, presumably due to the learned pattern of risk during evening periods (Ferrari et al. 2008). White-tailed deer have been shown to avoid recently hunted stand locations resulting from a learned spatial pattern of risk (Sullivan 2016). Thus, it seems plausible that deer may possess a similar ability to learn the temporal pattern of risk and respond accordingly. Our results suggest that 3 days of exposure to the temporal pattern of risk throughout the weekend may have caused deer to associate diurnal periods with the risk of predation, resulting in heightened antipredator behavior despite a decrease in hunting activity on Mondays and Tuesdays. Previous studies have found that 3 days of exposure to predators has been sufficient to allow some prey species to make an adequate assessment of temporal pattern of risk (Sih and McCarthy 2002, Laurila et al. 2004, Foam et al.

2005, Brown et al. 2006, Ferrari et al. 2009). Little (2011) found that 3 days of exposure was insufficient to allow adult male white-tailed deer to accurately assess the temporal pattern of hunting pressure, however, the study was conducted during the breeding season when males may be less sensitive to environmental threats (Neumann et al. 2009).

Differences in parental investment between male and female ungulates may lead to dissimilar energy demands when caring for young (Edwards 1983, Ruckstuhl and Kokko 2002), as well as differential susceptibility to predation (Labisky and Fritzen 1998). Thus, we should expect antipredator responses to vary by sex as males and females balance the survival- and fitness-related costs within risky environments (Wolfe et al. 2000, White and Berger 2001, Neumann et al. 2009). We found that mature females were 48% more likely to be active than mature males during the day, which could be explained by additional fitness-related considerations of females compared to males. In Alabama, fawning typically occurs during late summer and early fall (Leuth 1955, Gray et al. 2002) with some fawns being born as late as October (Leuth 1967). Given that highly-nutritious natural forage is often limited at this time of year (Cook and Gray 2003), females in this region may need to maintain heightened levels of activity in order to produce milk of sufficient quality to ensure the survival of their young (Beier and McCullough 1990, Rhind et al. 2002). In Alabama, weaning may not occur until 6 months of age (Cook and Gray 2003), causing nutrient intake to remain a priority well into the hunting season. Thus, mature females may be less willing to reduce activity compared to mature males due to differences in the impact on long-term fitness (Clark 1994).

Increased experience with hunters over time could cause ungulates to become more wary with age (Kilpatrick and Lima 1999), thereby leading to differences in antipredator response between age classes or from one year to the next. Our findings corroborate these predictions given observed behavioral differences between mature and immature individuals over the course of the study, with differences often being dependent on sex and daily temporal period of risk (i.e., DIURNAL/NOCTURNAL). During the day when hunters were present, mature bucks displayed lower movement rates, occupied smaller areas, and utilized a smaller proportion of their total daily movement compared to immature males. At night, however, mature bucks displayed greater movement and were more likely to be active than immature males. Conversely, we observed much less, if any, behavioral differences between mature and immature females, whether during the day or night. As previously postulated, differences between age classes of males could be a result of differences in the familiarity with humans as a potential threat (Kilpatrick and Lima 1999) as much of what contributes to antipredator response is a result of the ability to learn and adapt over time (Brown and Chivers 2005). A lack of meaningful differences between mature and immature females, however, likely reflects the strong spatial association that is common between a dam and her fawn and yearling offspring (Hawkins and Klimstra 1970). As a result of these matriarchal groupings, we should expect mature and immature female behavior to display a greater degree of similarity than among age classes of males, as our findings confirm. Additionally, we observed a decline in diurnal movement rate, net displacement, and probability of activity from the first hunting season to the second. While a number of abiotic factors may have contributed to these differences, including average temperature (Webb et al. 2010), cloud cover (Progulske and Duerre 1964), and rainfall (Bello et al. 2004), we did not see a similar decline in nocturnal movement. Thus, deer age may have been a more likely contributing factor, as the average age in our sample had increased from 3.1 years of age during the 2014/15 season to 3.6 years of age during 2015/16.

Probability of activity was found to vary by day of the week, but the pattern of variation was different for mature and immature deer. Although variation in the weekly pattern of activity extended to both males and females, we believe differences between mature and immature individuals were largely driven by the male cohort. As the probability of activity among mature deer decreased steadily over the course of the weekend, immature deer displayed an initial increase in probability of activity, followed by a dramatic decrease in activity by Sunday. These differences in response to increased weekend hunting activity could, once again, reflect an increased ability by older individuals to perceive and quickly respond to hunters as a result of amassed experience over time (Kilpatrick and Lima 1999). Our results could also reflect differences in site fidelity between age classes (Hellickson et al. 2008), as older individuals having well-established home ranges (Marchinton and Hirth 1984, Long et al. 2005) may become more immediately sedentary in response to environmental threats, whereas young individuals may display initial flight behaviors in an effort to seek safety.

Our findings demonstrate the keen perceptive ability of large ungulates to detect and respond to predatory threats, and suggest that even extremely low levels of disturbance may, at times, be sufficient to elicit a behavioral trade-off within ungulate populations. However, the degree of antipredator response may vary within a prey population based on age and sex, likely due to differences in experience with predators, as well as additional fitness-related considerations. Thus, the concept of a disturbance-level threshold that must be exceeded to elicit a behavioral response within ungulate populations (Root et al. 1988, Karns et al. 2012) may be an oversimplification of reality, as predation risk influences prey in a non-uniform manner. Additionally, the presence of predators will likely have a different effect from one ungulate population to the next depending on herd-specific demographic parameters, such as sex ratio and age structure. The complexity of predator-prey relationships presents a challenge to researchers when the goal is to generalize the behavioral response to certain types or magnitudes of disturbance. At times, however, such generalizations may be desired to help understand the effect of predator communities among prey at the population-level. Our results demonstrate the importance of taking into account the temporal variation in risk, inherent within all predator-prey relationships, in order to accurately reflect population-level antipredator response. Thus, we recommend that future studies on the topic take a similar approach as failure to do so may result in underestimating the impact that predator-mediated disturbances have on prey survival and lifetime fitness.

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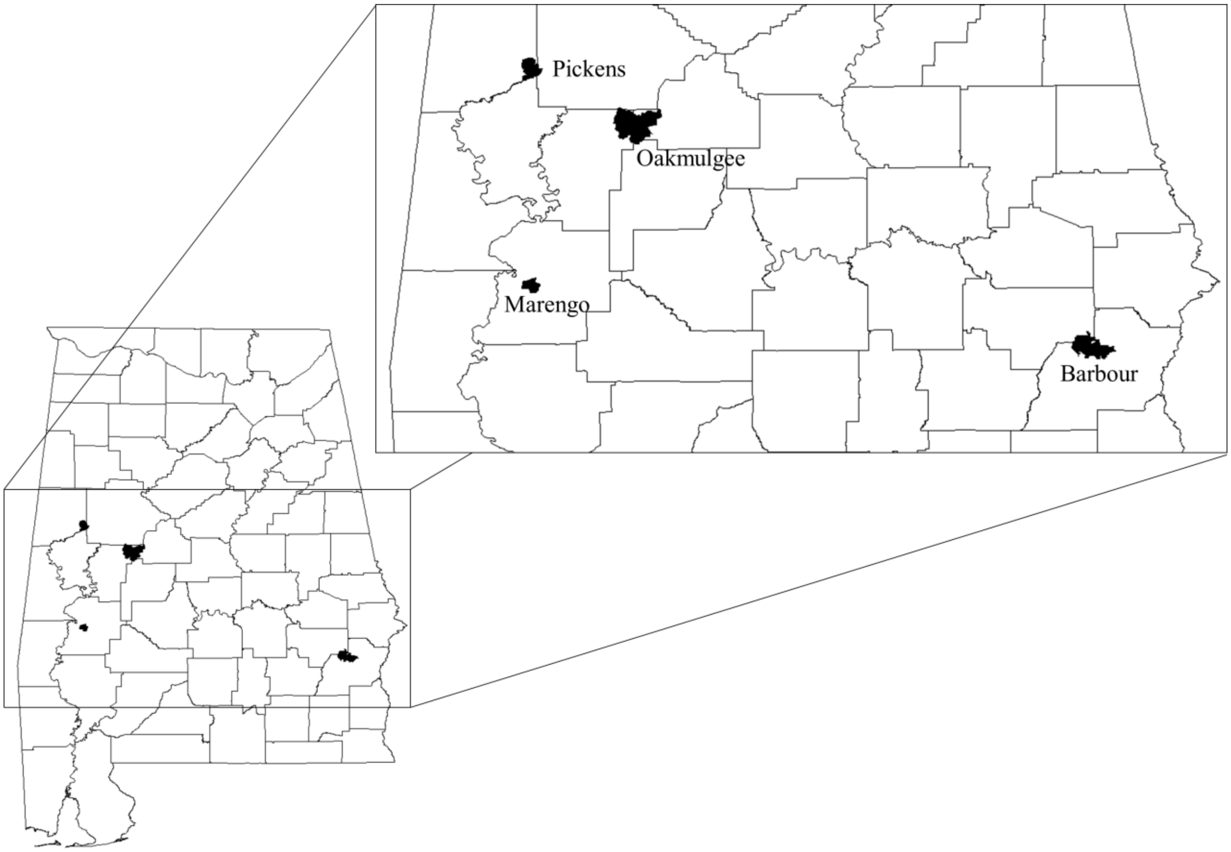

Figure 2.1 – A map of Alabama, USA, indicating county delineations and relative location of each study area from 2014-2016.

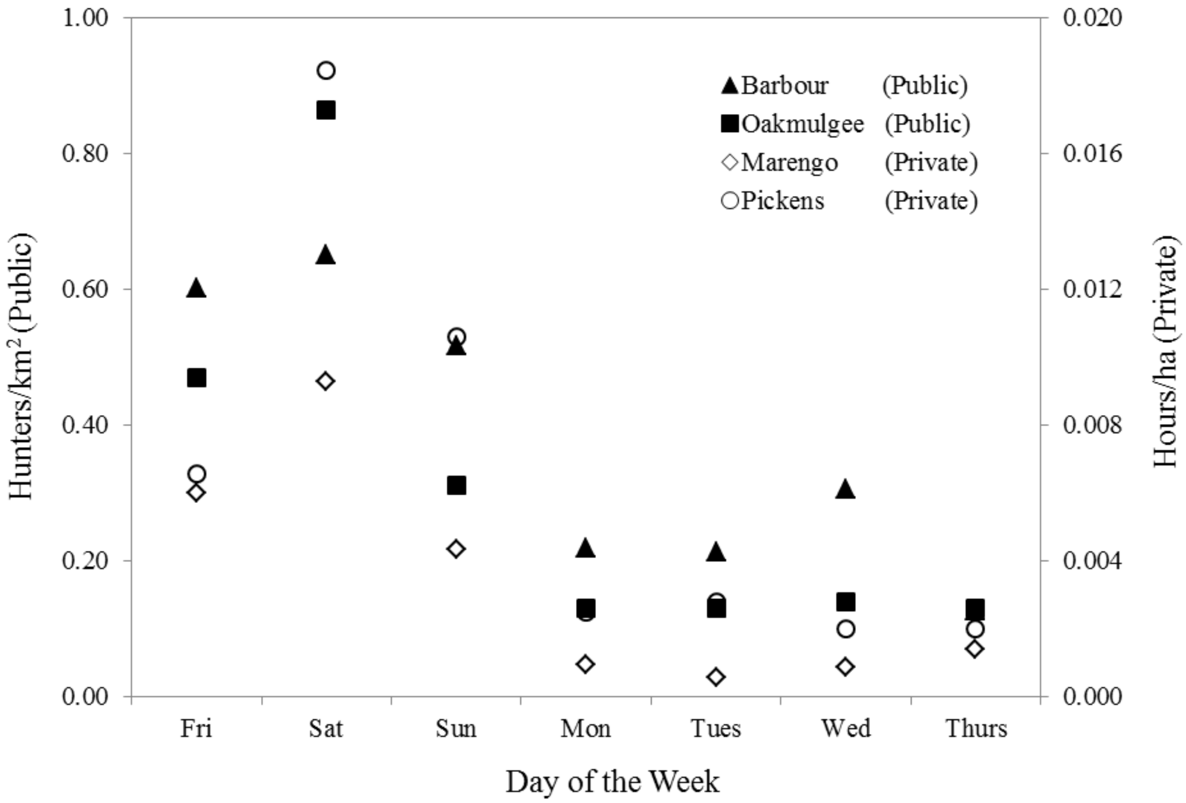

Figure 2.2 – Estimated mean hunting pressure for study areas in Alabama, USA, by day of the week throughout the period of risk exposure. Means are based on available records of hunting effort from both the 2014/15 and 2015/16 deer hunting seasons.

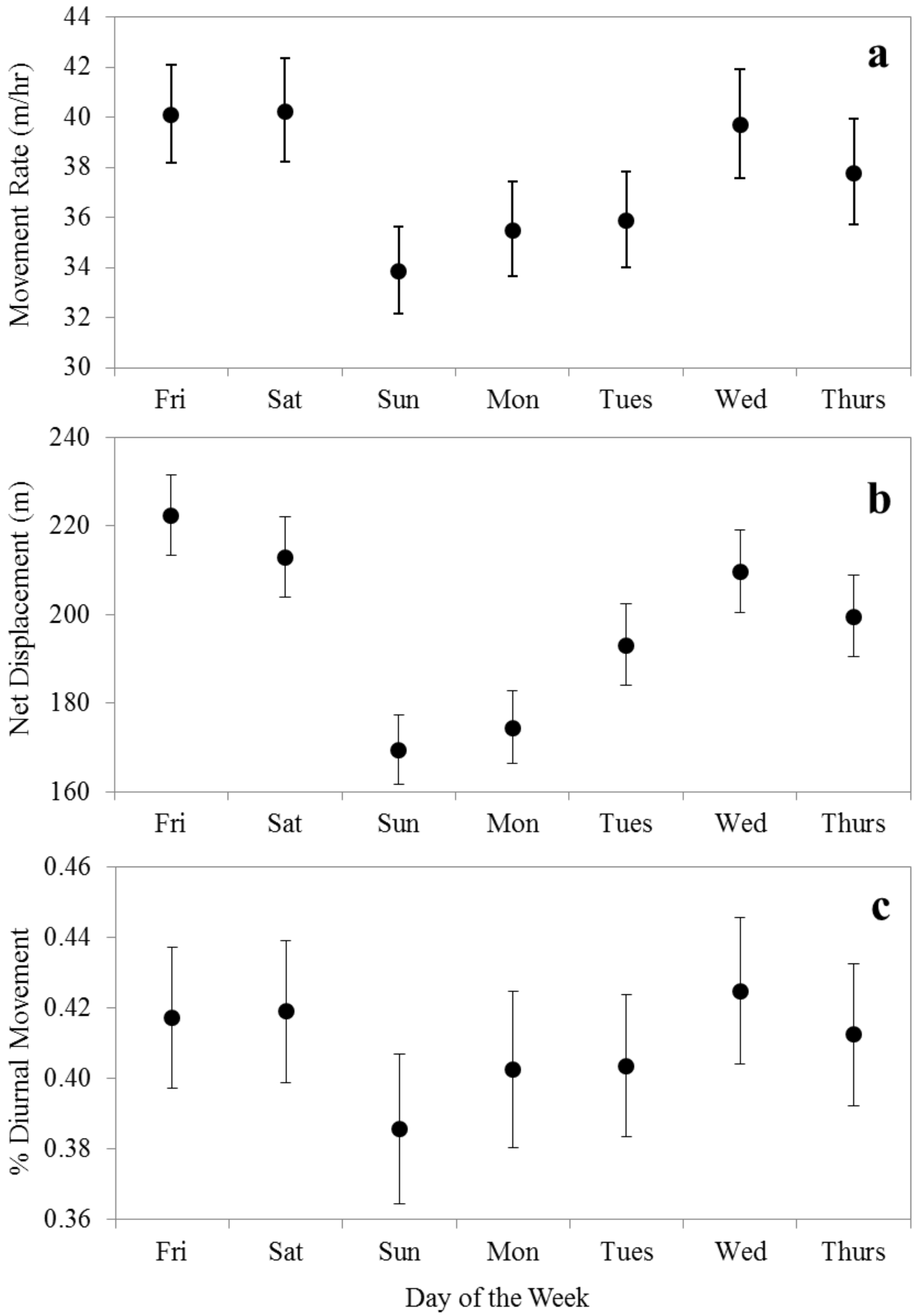

Figure 2.3 – Mean (± 95% C.I.) DIURNAL movement rate (a), net displacement (b), and % diurnal movement (c) of adult white-tailed deer by day of the week during 2014/15 and 2015/16 risk-exposure periods within Alabama, USA.

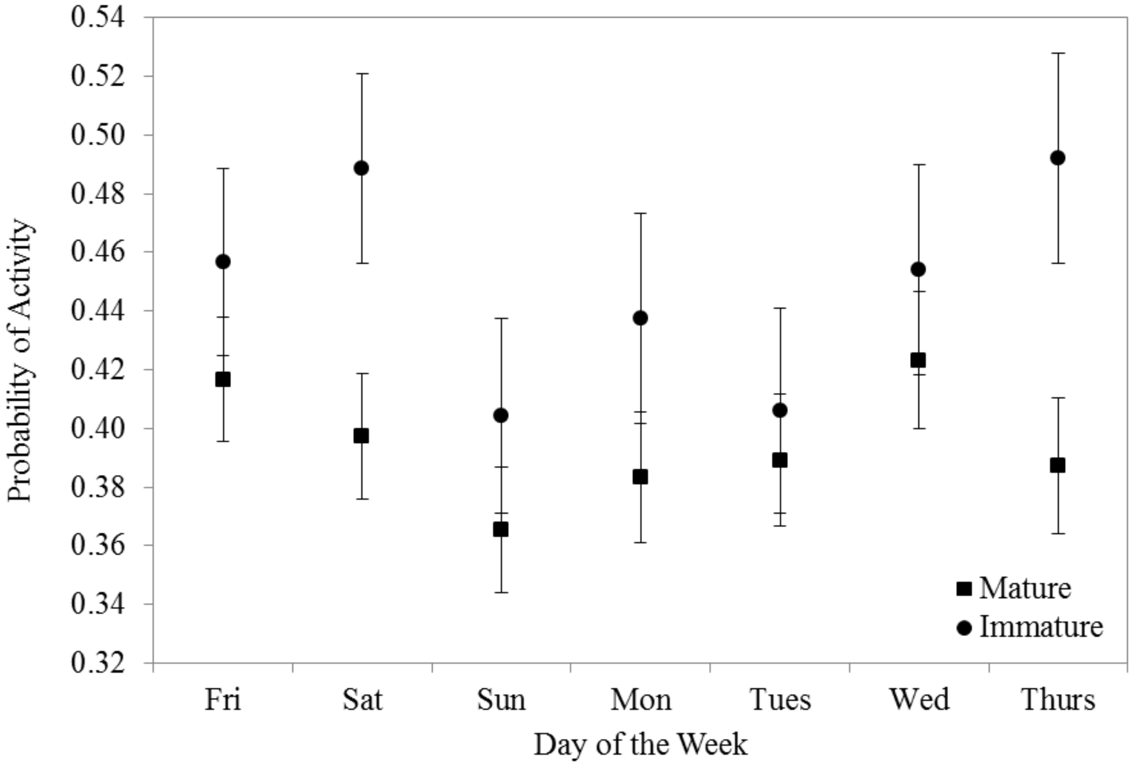

Figure 2.4 – Mean (± 95% C.I.) DIURNAL probability of activity for mature (≥3.5 years old) and immature (<3.5 years old) white-tailed deer by day of the week during 2014/15 and 2015/16 risk-exposure periods within Alabama, USA.

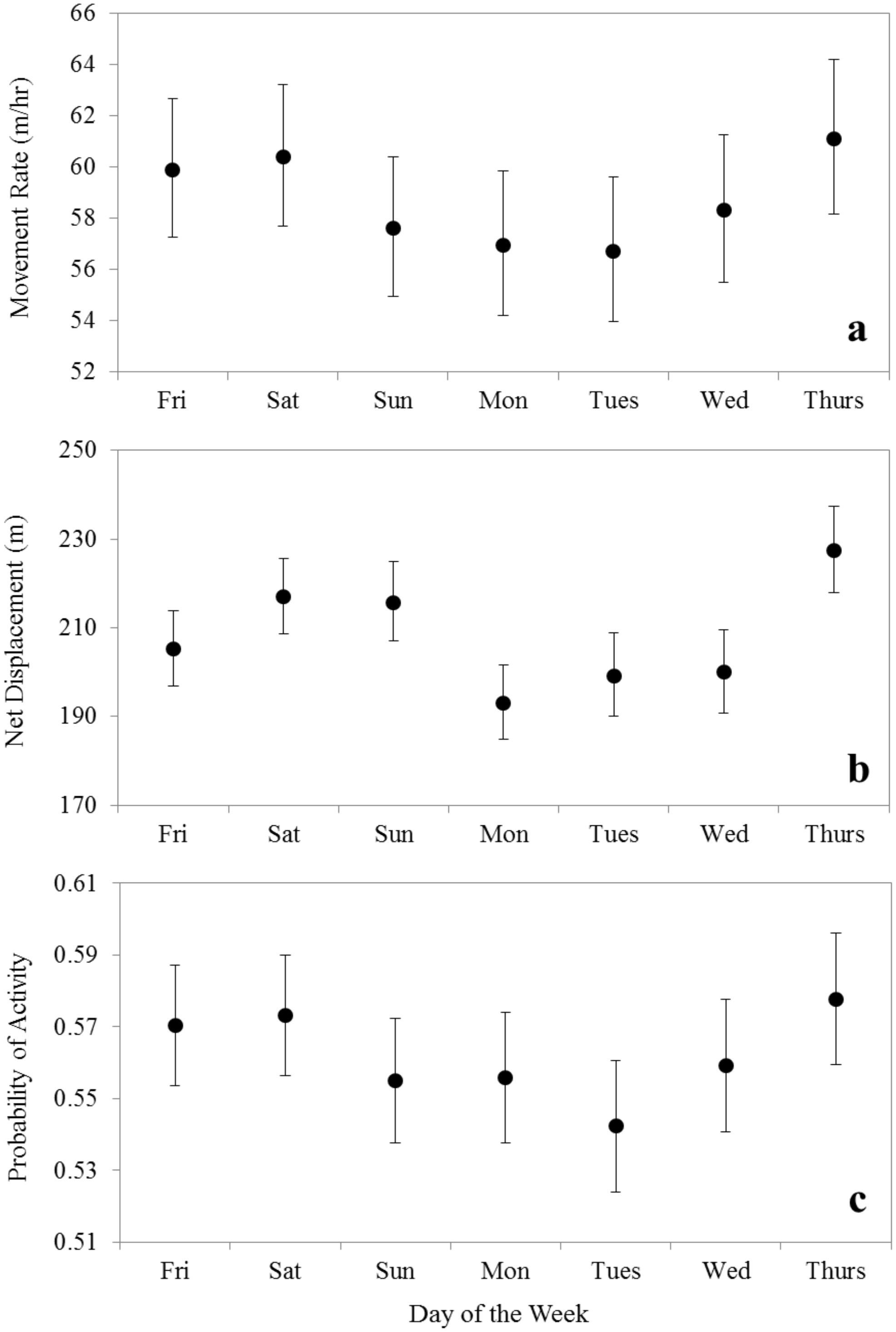

Figure 2.5 – Mean (± 95% C.I.) NOCTURNAL movement rate (a), net displacement (b), and probability of activity (c) of adult white-tailed deer by day of the week during 2014/15 and 2015/16 risk-exposure periods within Alabama, USA.

Appendix 1.1 – Capture history, demographic information, and fate of capture white-tailed deer from 2014-2016 in Alabama, USA.

Deer ID	Frequency	Location	Capture Date	Sex	Age at Capture	Entry Date	Age at Entry	Exit Date	Age at Exit	Radio Days	Fate
034	150.485	Marengo	19-Oct-13	M	3.5	15-Feb-14	3.5	14-Feb-16	5.5	729	Lived
035	150.334	Marengo	25-Oct-13	M	1.5	15-Feb-14	1.5	31-Jan-16	3.5	715	Legal harvest
036	150.174	Marengo	27-Oct-13	F	2.5	15-Feb-14	2.5	14-Feb-16	4.5	729	Lived
037	150.463	Marengo	27-Oct-13	F	4.5	15-Feb-14	4.5	14-Oct-15	6.0	606	Unknown natural
038	150.315	Marengo	2-Nov-13	F	2.5	15-Feb-14	2.5	14-Feb-16	4.5	729	Lived
051	150.453	Marengo	2-Nov-13	F	5.5	15-Feb-14	5.5	14-Feb-16	7.5	729	Lived
039	150.553	Marengo	3-Nov-13	F	3.5	15-Feb-14	3.5	15-Jan-15	4.5	334	Legal harvest
053	150.533	Marengo	3-Nov-13	M	4.5	15-Feb-14	4.5	15-Jan-16	6.5	699	Unknown mortality
040	150.473	Marengo	9-Nov-13	F	2.5	15-Feb-14	2.5	14-Feb-16	4.5	729	Lived
054	140.384	Marengo	9-Nov-13	M	3.5	15-Feb-14	3.5	30-Nov-14	4.5	288	Legal harvest
041	150.364	Barbour	7-Dec-13	F	5.5	15-Feb-14	5.5	14-Feb-16	7.5	729	Lived
056	150.093	Barbour	7-Dec-13	F	3.5	15-Feb-14	3.5	14-Feb-16	5.5	729	Lived

042	150.353	Pickens	11-Dec-13	M	3.5	15-Feb-14	3.5	15-Aug-14	4.0	181	EHD
043	150.394	Pickens	14-Dec-13	M	2.5	15-Feb-14	2.5	31-Dec-14	3.5	319	Legal harvest
057	150.504	Barbour	16-Dec-13	F	4.5	15-Feb-14	4.5	30-Nov-14	5.5	288	Legal harvest
045	150.443	Pickens	9-Jan-14	M	2.5	15-Feb-14	2.5	14-Feb-15	3.5	364	Post-rut exhaustion
047	150.514	Barbour	15-Jan-14	M	2.5	15-Feb-14	2.5	31-Jan-16	4.5	715	Legal harvest
061	150.523	Pickens	17-Jan-14	M	1.5	15-Feb-14	1.5	30-Nov-15	3.5	653	Censored
062	150.584	Pickens	21-Jan-14	F	2.5	15-Feb-14	2.5	14-Feb-16	4.5	729	Lived
063	150.345	Pickens	23-Jan-14	M	1.5	15-Feb-14	1.5	14-Feb-16	3.5	729	Lived
048	150. 493	Pickens	27-Jan-14	M	3.5	15-Feb-14	3.5	31-Dec-14	4.5	319	Legal harvest
049	150.575	Barbour	29-Jan-14	F	4.5	15-Feb-14	4.5	14-Feb-16	6.5	729	Lived
065	150.004	Barbour	29-Jan-14	M	2.5	15-Feb-14	2.5	31-Mar-15	3.5	409	Unknown natural
066	150.225	Oakmulgee	22-Feb-14	F	0.5	16-Jun-14	1.0	14-Feb-16	2.5	608	Lived
067	150.053	Barbour	25-Feb-14	F	4.5	16-Jun-14	5.0	14-Feb-16	6.5	608	Lived
069	150.594	Barbour	26-Feb-14	M	1.5	16-Jun-14	2.0	14-Feb-16	3.5	608	Legal harvest

068	150.305	Barbour	26-Feb-14	M	1.5	16-Jun-14	2.0	31-Jan-15	2.5	229	Legal harvest
139	150.404	Barbour	2-Mar-14	M	2.5	16-Jun-14	3.0	31-Aug-15	4.0	441	Unknown natural
31N	150.563	Marengo	20-May-14	M	2.0	16-Jun-14	2.0	14-Feb-16	3.5	608	Lived
32N	150.545	Marengo	20-May-14	F	5.0	16-Jun-14	5.0	30-Apr-15	5.5	318	Illegal harvest
33N	150.423	Marengo	21-May-14	M	2.0	16-Jun-14	2.0	15-Jan-15	2.5	213	Illegal harvest
52N	150.276	Marengo	22-May-14	M	2.0	16-Jun-14	2.0	14-Feb-16	3.5	608	Lived
137	150.144	Barbour	26-May-14	F	5.0	16-Jun-14	5.0	31-Dec-15	6.5	563	Legal harvest
072	150.434	Marengo	16-Jun-14	M	2.0	15-Oct-14	2.5	14-Feb-16	3.5	487	Lived
58N	150.324	Marengo	9-Jul-14	M	2.0	15-Oct-14	2.5	31-Jan-15	2.5	108	Legal harvest
140	150.284	Pickens	14-Aug-14	F	6.0	15-Oct-14	6.5	14-Feb-16	7.5	487	Lived
134	150.134	Oakmulgee	16-Aug-14	F	2.0	15-Oct-14	2.5	15-Jan-15	2.5	92	Illegal harvest
129	150.253	Oakmulgee	26-Aug-14	F	2.0	15-Oct-14	2.5	15-Jan-15	2.5	92	Illegal harvest
131	150.185	Pickens	26-Aug-14	F	1.0	15-Oct-14	1.5	15-Jan-16	2.5	457	Legal harvest
075	150.073	Oakmulgee	27-Aug-14	F	4.0	15-Oct-14	4.5	14-Feb-16	5.5	487	Lived

074	150.204	Oakmulgee	31-Aug-14	M	2.0	15-Oct-14	2.5	15-Dec-15	3.5	426	Legal harvest
133	150.195	Oakmulgee	1-Sep-14	F	2.0	15-Oct-14	2.5	14-Feb-16	3.5	487	Lived
126	150.123	Oakmulgee	4-Sep-14	F	2.0	15-Oct-14	2.5	15-Jan-15	2.5	92	Illegal harvest
141	150.013	Oakmulgee	4-Sep-14	F	3.0	15-Oct-14	3.5	14-Feb-16	4.5	487	Lived
144	150.064	Oakmulgee	4-Sep-14	F	5.0	15-Oct-14	5.5	14-Feb-16	6.5	487	Lived
127	150.112	Oakmulgee	5-Sep-14	M	1.0	15-Oct-14	1.5	14-Feb-16	2.5	487	Lived
149	150.033	Oakmulgee	5-Sep-14	F	1.0	15-Oct-14	1.5	14-Feb-16	2.5	487	Lived
128	150.264	Oakmulgee	7-Sep-14	F	3.0	15-Oct-14	3.5	14-Feb-16	4.5	487	Lived
135	150.154	Oakmulgee	7-Sep-14	M	2.0	15-Oct-14	2.5	15-Dec-14	2.5	61	Legal harvest
150	150.244	Oakmulgee	7-Sep-14	F	6.0	15-Oct-14	6.5	14-Feb-15	6.5	122	Unknown harvest
145	150.236	Oakmulgee	16-Sep-14	F	2.0	15-Oct-14	2.5	14-Feb-16	3.5	487	Lived
132	150.414	Pickens	16-Sep-14	F	3.0	15-Oct-14	3.5	15-Jan-15	3.5	92	Legal harvest
148	150.104	Barbour	21-Sep-14	F	5.0	15-Oct-14	5.5	14-Feb-16	6.5	487	Lived
138	150.373	Barbour	21-Sep-14	F	3.0	15-Oct-14	3.5	14-Feb-16	4.5	487	Lived

130	150.082	Barbour	21-Sep-14	F	1.0	15-Oct-14	1.5	14-Feb-16	2.5	487	Lived
147	150.165	Barbour	25-Sep-14	F	4.0	15-Oct-14	4.5	14-Feb-16	5.5	487	Lived
142	150.293	Barbour	27-Sep-14	F	3.0	15-Oct-14	3.5	15-Jan-15	3.5	92	Legal harvest
095	150.353	Pickens	13-May-15	M	3.0	16-Jun-15	3.0	15-Jan-16	3.5	213	Legal harvest
076	150.423	Barbour	21-May-15	M	3.0	16-Jun-15	3.0	14-Feb-16	3.5	243	Lived
086	150.244	Barbour	22-May-15	M	4.0	16-Jun-15	4.0	31-Dec-15	4.5	198	Unknown mortality
077	150.394	Barbour	25-May-15	M	2.0	16-Jun-15	2.0	14-Feb-16	2.5	243	Lived
091	150.004	Barbour	29-May-15	M	2.0	16-Jun-15	2.0	14-Feb-16	2.5	243	Lived
079	150.043	Pickens	1-Jun-15	F	5.0	16-Jun-15	5.0	14-Feb-16	5.5	243	Lived
150N	150.493	Pickens	3-Jun-15	F	5.0	16-Jun-15	5.0	14-Feb-16	5.5	243	Lived
081	150.253	Pickens	4-Jun-15	F	3.0	16-Jun-15	3.0	14-Feb-16	3.5	243	Lived
082	150.214	Pickens	8-Jun-15	F	1.0	16-Jun-15	1.0	14-Feb-16	1.5	243	Lived
078	150.025	Pickens	8-Jun-15	F	1.0	16-Jun-15	1.0	14-Feb-16	1.5	243	Lived
085	150.384	Pickens	9-Jun-15	M	1.0	16-Jun-15	1.0	14-Feb-16	1.5	243	Lived

084	150.304	Barbour	11-Jun-15	M	3.0	16-Jun-15	3.0	14-Feb-16	3.5	243	Lived
100	150.324	Pickens	29-Jun-15	M	3.0	15-Oct-15	3.5	14-Feb-16	3.5	122	Lived
090	150.504	Pickens	8-Jul-15	M	2.0	15-Oct-15	2.5	14-Feb-16	2.5	122	Lived
094	150.154	Pickens	9-Jul-15	F	4.0	15-Oct-15	4.5	14-Feb-16	4.5	122	Lived
089	150.293	Pickens	9-Jul-15	F	5.0	15-Oct-15	5.5	14-Feb-16	5.5	122	Lived
097	150.443	Pickens	13-Jul-15	M	2.0	15-Oct-15	2.5	14-Feb-16	2.5	122	Lived
080	150.553	Pickens	13-Jul-15	F	3.0	15-Oct-15	3.5	14-Feb-16	3.5	122	Lived
101	150.545	Pickens	14-Jul-15	F	4.0	15-Oct-15	4.5	14-Feb-16	4.5	122	Lived
088	150.414	Pickens	20-Jul-15	F	3.0	15-Oct-15	3.5	14-Feb-16	3.5	122	Lived
083	150.123	Oakmulgee	22-Jul-15	F	4.0	15-Oct-15	4.5	14-Feb-16	4.5	122	Lived
093	150.134	Oakmulgee	23-Jul-15	F	4.0	15-Oct-15	4.5	14-Feb-16	4.5	122	Lived