Spatiotemporal Breeding Strategies within a High Density, Male-skewed White-tailed Deer Population

by

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Abstract

Animal movement is an integral part of most ecological, behavioral, or evolutionary processes observed in nature, and it has wide implications to numerous broad issues ranging from dispersal and migration to habitat fragmentation and probabilistic models of biological invasions. One facet of movement ecology revolves around optimal foraging and search theory – how do animals move through their environment and utilize the resources necessary for their survival. To quantify an animal's search behavior, I developed a search intensity metric (SIM) that incorporated daily movement trajectories into a grid overlay of the study site (distance traveled/area encountered). Using the data's variability between individuals to inform selection of an appropriate grid dimension, the SIM maximizes differences between individuals/groups but within populations. After providing 3 study cases to illustrate the SIM's effectiveness and addressing how it differs from other metrics (e.g., fractal dimensions or tortuosity), I used it – in combination with other basic spatial metrics – to identify spatiotemporal breeding strategies employed by different age-class male white-tailed deer (*N* = 34) at Three Notch Wildlife Research Foundation in Bullock County, Alabama (2009–2011). With a male-skewed sex ratio and high density population, mature males concentrated their effort both temporally and spatially within the peak breeding period (and immediately thereafter during the post-breed season); conversely, juvenile and adult males exhibited roaming spatial behaviors likely due to displacement by more dominant rivals. Temporally, juvenile males focused reproductive effort

before the other age classes in the population and possibly adopted “sneaker” strategies later in the breeding season.

With a large sample of antlers (*N* = 487) from the same population, I examined factors affecting antler breakage and identified total number of points (positive relationship) and beam circumference (negative relationship) to be important predictors of antler breakage probability. Increased spongiosa within antlers (with greater mass) provided greater protection against breakage, whereas smaller-diameter antlers with many antler points experienced greatest breakage rates. In white-tailed deer males with significant bilateral asymmetry in antler structure, I examined 71 skulls (collected from across Alabama) from harvested white-tailed deer to assess probable cause for spike-on-one-side (SOOS) antler development. With increasing age of specimens, my likelihood of assigning probable cause (i.e., an injury to the skull and/or pedicle) increased (peaking at 76% in $\geq$3 year old males). Understanding how injuries to the antlerogenic periosteum allowed me to make age-specific recommendations for culling different age-class SOOS males.

Finally, we investigated various aspects of maternal life history including senescence, fetal sex ratio allocation, and timing of conception by examining 1,355 reproductive tracts of female white-tailed deer in Alabama (1995–2011). Of several variables (maternal age/mass and litter size) evaluated, only days from average conception date was significant in predicting fetal sex ratio with daughters becoming more likely the further conceived from the peak breeding window. Maternal age and mass (as well as maternal age*mass interaction) influenced when a female was bred (conception timing) relative to the other females in the population (e.g., within younger age classes, larger females were more likely to conceive closer to the peak of conception

than smaller females). Also, I found support for reproductive senescence which was previously undetected in white-tailed deer.

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A Novel Approach to Quantify Varying Search Strategies within Animal Populations

Abstract

To more explicitly measure movement path traits that an animal uses to explore its environment, I developed the search intensity metric (SIM). Using biologically meaningful units (meters/hectare), the SIM delineates linear versus tortuous paths of organisms. Unlike metrics possessing unit-less values (e.g., fractal dimension 1–2) or methodologies which don't accurately reflect search intensity (e.g., tortuosity), SIM uses the data's natural variation to identify spatial search behavior differences between individuals and/or subsamples. Specifically, movement path trajectories (daily or otherwise) are overlaid with a square grid to calculate SIM values (path length/area encountered). Selected grid size is determined by that dimension which maximizes the within-sample variation. I present 3 case studies to detail this methodology, discuss data patterns, identify sample size dependent issues, and relate the metric to biology and ecology by examining a population in the context of SIM analysis and testable hypotheses.

Introduction

The study of animal movement (formally the field of movement ecology) has yielded tremendous insights into issues ranging from the mechanistic processes of migration and dispersal, to constructing probabilistic models of re-colonization by rare species, or mapping risk of biological pest invasions (Nathan 2008). Development of new analysis procedures has evolved concomitantly with the capabilities of Global Positioning System (GPS) technology to collect spatial/location datasets with greater precision (temporally and spatially) than ever before. Methodologies used to analyze those data have developed from simple measurements, such as step length and velocity, to computationally complex movement path analyses such as fractal dimensions, sinuosity, and random walk models (Wilkinson 1952, Mandelbrot 1983, Williams 1992, Turchin 1998). Several relatively simple metrics are available that may be interpreted as providing a measure of search intensity. For example, diel home range size provides an approximate measure of how much area is encountered within a 24-hour period (Mohr 1947, Kilgo et al. 1998), but provides no gauge of whether the animal spent considerable time within specific habitat patches or if travel was linear within the home range. Conversely, total movement distance indicates how many steps an organism has taken or how active that individual has been, but provides no information regarding the tortuosity (crookedness) of the movement. Net displacement (distance between the start and end point of a movement path) captures animal movement in interpretable units but yields no insight into path complexity or even total distance traveled (Wiens et al. 1995).

On the premise that certain movement path characteristics are better suited for locating resources of varying distributions (optimal foraging and search theory; Crist et al. 1992), metrics such as tortuosity, fractal dimensions, sinuosity, and eccentricity, have been used to differentiate between divergent foraging and searching strategies, but these do not always accurately reflect search intensity. For instance, the straightness index (animal’s actual movement path divided by a straight line connecting the start and end point) of 2 individuals may indicate differences in path complexity, but the values themselves do not address how far one organism moves (i.e., how much ground is searched) versus another and the values (0 to 1) are unit-less, leading to difficulty in interpretation (Batschelet 1981, Benhamou 2004). Although the sinuosity index is related to unit length (e.g., cm for movement patterns of some insects) and can be re-scaled to compare patterns between scale-variant taxa, the locations used to construct movement paths must be at regular temporal intervals and the metric is computationally complicated (Benhamou

2004). Additionally, discussions of tortuosity are often confusing because of the wide assortment of different metrics used within the movement ecology literature (Batschelet 1981, Fortin 2003, Benhamou 2004, Whittington et al. 2004, Laube et al. 2007, Holtfreter 2008). Likewise, a movement path with fractal dimension value of *X* indicates something of the relative spatial complexity of an animal's trajectory, but possesses little to no interpretable biological meaning in and of itself (Wiens et al. 1995, Turchin 1996, Etzenhouser et al. 1998). If testing for age- or sex-specific differences of individuals' spatial behavior is a goal, it is somewhat disconcerting that 2 spatially dissimilar movement paths (and more importantly biologically dissimilar) can oftentimes yield nearly identical fractal values (Wiens et al. 1995, Etzenhouser et al. 1998, Webb et al. 2009). Though not widely utilized, the assessment corridor (AC) technique (Doerr and Doerr 2005) is another method that attempts to describe how an organism searches its environment. The AC method uses chronologically connected animal locations to approximate a movement path and then uses the animal's assumed "perceptual range" to create a buffer around the movement path to depict how much area the animal searched. Although the authors state that this method is useful for comparing search behavior among individuals within a population, the "perceptual range" of an animal is largely unknown and could vary based on environmental conditions, wind speed and direction (olfactory cues), distance to nearest visual obstruction, habitat, and even the experience of the individual.

In addition to computed metrics, movement modeling provides another means and perspective for examining search behaviors. Whereas movement models (e.g., Levy walks, Brownian motion, correlated random walks; Viswanathan et al. 1999) optimize search behavior for target resources at different levels of resource abundance, individuals within populations may not fall into discrete categories as defined by these explicit models. In addition, movement models only apply to scenarios where the organism has no *a priori* information about the location of the resource of interest (Bartumeus et al. 2005). Though truly naïve searches do occur, nearly all animals utilize some level of spatial memory to secure resources (Benhamou 1994). These models describe movement as stochastic processes and generally provide useful insights into long term movement trajectories over large spatial and temporal scales (Bartumeus et al. 2005). Though movement models are useful when exploring population-level spatial patterns, comparisons of short-interval, small-scale movement behaviors between individual animals are inherently difficult to simulate.

Benhamou (2004) suggested that estimators of animal movement should 1) be unbiased and prevent any over- or under-estimation of the mean, and 2) possess properties that decrease the metric's variation with increasing number of locations per movement path. My search intensity metric (SIM) fulfills these requirements and provides researchers with biologically meaningful units that reflect the biology/ecology of the organism. Whereas the array of metrics available to ecologists today is vast and diverse, the SIM quantifies search intensity using relatively simple calculations while complementing existing analyses. Coupling the path length of an organism's daily (or other temporally defined) movement path with a grid system to calculate area encountered, the metric provides a measure of search intensity in meters traveled per unit area encountered. Similar to the first-passage time (FPT) metric (Fauchald and Tveraa 2003) which quantifies search effort using the amount of time spent within a given area, the SIM measures search intensity in terms of how much movement occurs within a given area (Pinaud 2008). More specifically, because the SIM uses location data from individuals within the population to determine spatial scale of analyses (based on the variation of individual movement paths within the population), the method is a unique tool for comparing site-specific spatial behavior of individuals. First, I will discuss the SIM from a statistical perspective and then present 3 case studies to illustrate the potential applicability of the technique.

Methods

The SIM is based on 2 primary components of animal movement – sum of total step lengths and amount of area encountered for a predefined time interval; consequently, SIM values represent a ratio of path length to area encountered (e.g., meters per hectare). For most spatial statistics using step lengths, the between-step time interval determines how close recorded step length distances are to actual step lengths. Because the SIM is chiefly designed to compare individuals within a population, temporal interval for each step length is not critical as long as individuals within the population are monitored using the same protocol; however, shorter time intervals between locations increase how closely movement paths represent reality (Laundre et al. 1987, Estevez and Christman 2006). Because successfully acquiring every fix attempt is not a realistic expectation, only daily paths with $\geq$75% successful locations and with a minimum resolution of 1 location per hour (24 daily fixes) should be used in SIM analysis. In the 3 case studies I present, step lengths will be summed over 24-hour periods with fixes taken every 20, 12, and 30 minutes, respectively. For analysis of organisms that don’t exhibit circadian rhythms [e.g., reindeer (*Rangifer tarandus*); Oort et al. 2005], or when examining more general patterns on a temporal scale >24 hours, researchers should eliminate movement paths with <75% fixes for the pertinent time interval.

The SIM determines the amount of area encountered by utilizing a grid cell matrix generated using the tool ‘genvecgrid‘ within Geospatial Modelling Environment (GME; Beyer 2012) or other appropriate GIS software package. It is important to generate grids to cover the entire spatial extent of the dataset. Specifically, after counting all grid cells encountered by a movement path, the SIM determines the total area encountered by multiplying the area of a single grid cell by the total number of grid cells encountered. For a single movement path during a defined time interval, grid cells encountered are counted (with or without replacement depending on traits of the sought after resource) by intersecting movement path with the underlying grid (ESRI 2011). Determining grid cell size is the most time consuming task associated with the SIM, but the dimensions of the grid are based on the study population's data in a way that maximizes differences between individual search behaviors and patterns. Using the daily movement paths of the entire dataset, users must run the SIM on a spectrum of grid cell sizes from small to large and select the optimal dimension that best magnifies differences between individual's search patterns and behaviors.

Coefficient of variation (CV) is the key component in selecting optimal grid size. It is calculated by dividing the standard deviation of all SIM values for a study population for a particular grid cell size by the mean SIM value for that same grid cell size. The process of selecting minimum and maximum grid cell sizes is based on some general rules. First, the dimensions of the grid cell size should not exceed the length of the shortest daily movement path within the sample. Second, to standardize the optimal grid cell size, divide the average daily movement path length by 24 to get L (average hourly movement rate) for a starting point from which grid cell sizes, $0.25L$-$1.75L$, can be tested in $0.25L$ increments. To select the optimal grid cell size, plot $0.25L$-$1.75L$ on the x-axis and CV on the y-axis to visualize the data distribution (Figure 1). A modified "bell" curve should be evident. On the lower spectrum, the "bell" curve is evident; however, the right tail begins increasing as grid cell size increases past the $1.75L$ (700 meters) threshold. The optimal grid size should be selected from the peak of Curve A which is driven by the "biology" of movement path trajectories. Curve B should be ignored and is both a mathematical artifact of larger grid cell sizes that artificially inflate CV based on how similar movement trajectories fall on the grid extent (i.e., movement falls on vertex of 4 grid cells or completely within a single grid cell), and a reflection of variation in daily path length as grid cell size reaches a maximum extent that encompasses the entire study area. Theoretically, if low variation exists between daily path lengths, the extreme right tail of Curve B may precipitously drop because CV solely reflects path length variation when a single grid cell size covers the extent of the study area. Occasionally, the range of $0.25L$-$1.75L$ will include the peak of curve A (optimal grid cell size) and greater CV values as curve B begins to increase. Additionally, the peak of curve A where the CV is maximized may be rather broad (though not necessarily so) indicating that the process of selecting optimal grid cell size is rather robust. If grid cell size is too small, nearly all movements would enter previously un-encountered ground (phenomenon known as depletion; Halley et al. 2004) and the only intense searching would occur where a daily movement path intersected with itself. Conversely, computing the SIM with grid cells that are too large would result in movements rarely leaving a grid cell and movements appearing to be an intense searching of the same ground continuously. In both cases, non-optimal grid cell sizes would homogenize the apparent SIM between individuals. Biologically, large SIM values are indicative of intensive searching. Smaller SIM values reflect more dispersed, less intensive search patterns.

Results and Discussion

Study Case #1

For this initial example, I document the process of calculating SIM and identify challenges that users may face with the inherent statistical properties of the technique and potential obstacles related to the study species' biology and ecology. At the Temple Ranch in

Duval County, Texas (NW of San Diego, Texas), colleagues from Texas A&M University deployed GPS collars on 3 mature male wild turkeys (*Meleagris gallopavo intermedia*) from April 1 – May 10 during 2009 which collected locations every 20 minutes from 0600-2000 and every 180 minutes from 2000-0600 when turkeys were roosted. Due to roosting behavior (usually occurring in the same tree or cluster of trees each night; Holdstock et al. 2006), wild turkeys in south Texas are essentially central place foragers, thereby increasing the overlap within daily movement path trajectories as individuals start and end each day at the same location. Collars recorded an average of 43 fixes per daily movement path (out of a potential 46 daily fixes). I omitted daily movement paths with fewer than 35 locations from the SIM analysis based on the minimum resolution threshold. Fix acquisition success was high (93%), and the 3 mature male wild turkeys contributed 40 daily movement paths each (out of 40 available days) with a mean daily path lengths of 5821, 5708, and 5021 meters, respectively.

For a starting point to find optimal grid cell size, I divided 5517 meters (average daily movement path length for all turkeys) by 24 to calculate L = 230 meters and examined the CV for each grid cell size of 57.5, 115, 172.5, 230, 287.5, 345, and 402.5 meters (0.25L-1.75L in 0.25L increments) for the 120 total daily movement paths. I selected 345 meters as the optimal grid cell size (Figure 2; corresponds to an area of 11.9 hectares) and used the corresponding SIM values for the analysis. Other than a few isolated peaks of restricted, intense searching, all 3 adult male turkeys exhibited similar SIM patterns (Figure 3). Based on comparison of the GPS-recorded daily movement paths of turkeys ‘01’ and ‘02’ (Figure 4), these 2 birds inhabited the same flock during the first 5 days of the sampling period and mirrored one another’s movement path. Closely examining the daily SIM values for these 2 individuals reveals some variation but was likely a function of differences between which specific grid cells intersected each individual movement trajectory as well as possible GPS error. For species that belong to aggregations (e.g., herd of animals or flock of birds), the process of selecting the random sub-sample for initial grid cell size selection could be affected by pseudoreplication through having multiple animals' movement paths from the same flock or herd being used. Within the study period, individuals exhibited intensive searching as well as more dispersed daily movement patterns (Figure 5).

For comparing individuals within the same population, Figure 6 demonstrates that as grid cell size fluctuates, sex-, age-, or individual-specific comparisons will likely remain consistent even at non-optimal grid cell sizes. As grid cell size decreases, the area encountered for a given movement trajectory decreases and SIM increases. Conversely, as grid cell size increases, the area of the grid cells encountered for the same movement path length increases and SIM decreases. The SIM values are virtually identical between individual birds and attests to the fact that these 3 adult male wild turkeys searched their environment in a very similar manner, to be expected considering all 3 individuals were the same sex and age. I caution that the optimal grid cell size not be interpreted as a scale at which the organism perceives its environment or "perceptive resolution" (With 1994); the optimal grid cell size is simply the grid dimension which maximizes the CV among all daily movement paths for all individuals in the dataset and allows researchers to delineate movement paths that exhibit different search intensities.

Study Case #2

Near the city of Terre Haute in Vigo County, Indiana, sharp-shinned hawks (*Accipiter striatus*) were captured according to protocol described in Roth and Lima (2007). Similar to the wild turkeys above, sharp-shinned hawks are central place foragers while maintaining a single nest site (Coleman et al. 2002). Hawks were followed with traditional radio telemetry equipment and, on average, 52 locations were recorded daily. Randomly selecting 7 individuals, I used 124 individual daily paths (average of 18 days per hawk) from November 2001 – March 2002 and November 2002 – March 2003. Locations were recorded approximately 5 times per hour from 0730 – 1800 (excluded night when hawks were roosted). On average, the 7 sharp-shinned hawks traveled 11,785 meters daily; therefore, I started the search with L = 500 meters and tested grid dimensions (125, 250, 375, 500, 625, 750, and 875 meters) to determine optimal grid cell size. Five hundred meters (25 hectares; Point A) was the optimal grid cell size; however, 875 meters (Point B) had a greater CV and was within the grid cell search spectrum (Figure 7). To address this issue, I calculated the CV for additional grid dimensions of 1000, 1250, and 1500 meters. With the 3 extra data points in place, one can more clearly see the separation of Curve A (driven by the biology expressed through the data) and Curve B (mathematical artifact of increasing grid cell sizes and how daily paths fall onto that grid). To illustrate how SIM values derived from larger grid cell sizes can be biased due to mathematical artifact, I examined 2 movement paths intersected with the 875 meter grid size. It is clear that the grid cells are becoming too large to reliably convey biological differences in movement paths, as paths of similar lengths (6176 and 6965 meters) and structure intersect 2 (solid black line) versus 6 grid cells (dashed gray line), respectively (Figure 8). The differences are only a function of where the grids fall out on the landscape (and subsequently where the paths cross them), rather than actual behavioral differences between the two movement trajectories. By contrast, if the same 2 movement trajectories are plotted against the optimal 500 meter grid (Figure 9), number of grids encountered is much more consistent. When outliers are removed from the dataset, Point B falls into line with the rest of Curve B, and Point A is obviously the optimal grid cell size as the modified “bell” curve is more accentuated and noticeable than before (Figure 10). In the case of larger samples, anomaly peaks shouldn’t occur, but in Study Case #2 with only 124 daily movement paths, 3 trajectories had a measurable impact on CV causing multiple "optimal" peaks in the data distribution. When multiple peaks exist and there is uncertainty as to which one is the optimal grid cell size, it is wise to examine the trajectories within the ESRI mapping environment to determine which peak is due to grid cell placement and which is a function of biology. I suggest the lower grid cell size should be used.

Study Case #3

From 2009–2011 researchers deployed GPS collars on 37 male white-tailed deer (*Odocoileus virginianus*) near Dorchester, South Carolina. The collars were programmed to acquire fixes every 30 minutes (48 locations/day) from August 23 – November 22 of each year to encompass the entire breeding season. After removing days with <75% fix success ($n = 350$), 2600 daily movement paths were analyzed using the SIM. Mean daily path length was 4849 meters, resulting in $L = 200$; therefore, grid cells ranging in size from 50–350 meters were tested in 50 meter increments. The coefficient of variation was maximized using 150 meter (2.25 ha) grid cells (Figure 11). In contrast to the central foraging ecology of the previous 2 species/study cases, white-tailed deer exhibit patch foraging and the SIM metric detected differences in individual search intensity. Theoretically, search pattern differences in patch foragers should be more obvious because central place foragers possess inherent tortuous tendencies de facto of their daily return to a central den, nest, or roost site.

In order to determine the robustness of the SIM to varying grid cell sizes, I compared mean SIM values among three age classes: yearlings (1.5 yr), subadults (2.5 yr), and adults (3.5 yr and older) during the peak of the breeding season. SIM differed among age classes at the optimal grid cell size (150 meters). Mean SIM values for yearlings, subadults, and adults were 101.79 (95% CI = 98.13 – 105.45), 88.41 (95% CI = 85.83 – 90.99), and 95.26 (95% CI = 92.67

– 97.84), respectively. I plotted mean SIM values for each age class over the entire range of grid cell sizes tested (Figure 12); even at grid cell sizes 100–300 meters, search intensity differed among age classes (*100m*: $F_{2,840} = 15.39$, $P < 0.001$, TukeyHSD < 0.008; *150m*: $F_{2,840} = 17.4$, $P < 0.001$, TukeyHSD < 0.006; *200m*: $F_{2,840} = 14.25$, $P < 0.001$, TukeyHSD < 0.013; *250m*: $F_{2,840} = 15.63$, $P < 0.001$, TukeyHSD < 0.059; *300m*: $F_{2,840} = 15.77$, $P < 0.001$, TukeyHSD < 0.016). The SIM metric is fairly robust to grid cell size selection, as the use of any dimension 100–300 meters would lead the investigator to reach the same conclusions.

Conclusion

As a novel technique in the hands of movement ecologists, the SIM provides researchers a tool to compare search behavior patterns between groups of individuals within a population. Allowing the spatial characteristics of the dataset to influence the selection of key parameters ensures that biological/ecological differences are magnified and not muddled, as can be the case with some previously discussed metrics. The process of selecting optimal grid size is quite robust, and the metric's values possess units that are real and definable possessing meaningful biological information. The SIM is equally applicable to species of differing space use patterns (e.g., central foraging versus patch foraging), and units (e.g., m/ha versus cm/m^3) can be adjusted to study organisms operating at any scale (e.g., insects versus megafauna). However, the metric is not without drawbacks. The multi-step process of deriving optimal grid cell size (not to mention the subtle ambiguities between biologically- and mathematically-driven peaks in CV) and computing SIM values is somewhat complicated and time consuming. Also, outliers (due to grid placement or abnormal organismal behavior) within smaller sample sizes of individual movement paths can have substantial impacts on observed differences in search behavior. Even with these documented difficulties, I anticipate that the strategic use of the SIM will supplement existing statistical tools and techniques within the movement ecology field.

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Figure 1. Coefficient of variation (CV) versus grid cell size for hypothetical study population with $L = 400$. Data plotted to the left of the dashed line is the optimal grid cell search $0.25L$ – $1.75L$. Data to the right of the dashed line illustrates how CV responds to increasing grid cell sizes. Curve A is driven by the spatial behavior of the organism, while Curve B is a mathematical artifact of how movement trajectories are intersected by increasing grid cell sizes.

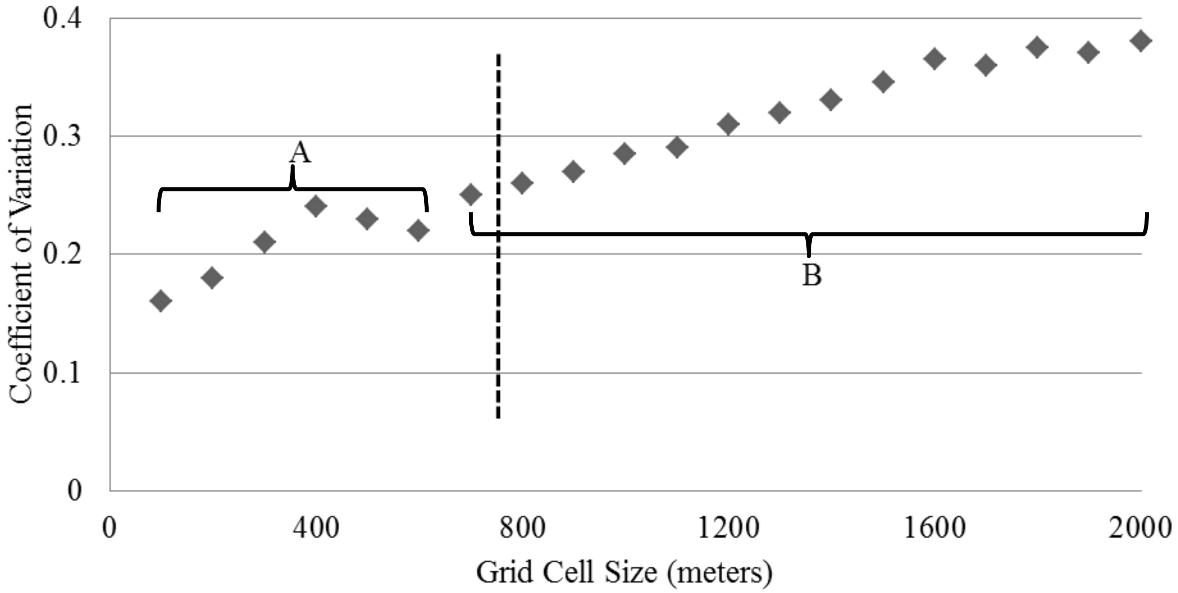


Figure 2. Coefficient of variation (ratio of standard deviation to mean) for different grid cell sizes tested for wild turkey GPS data, Temple Ranch, Texas, 2009.

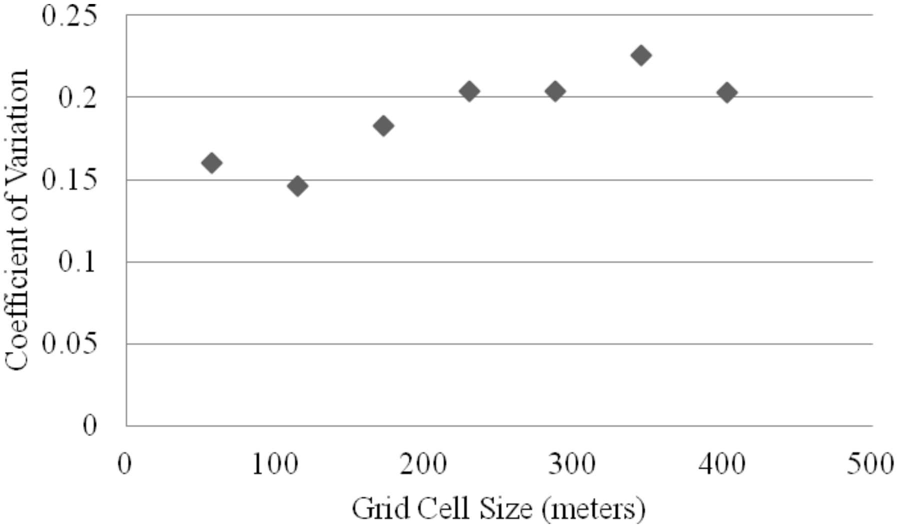


Figure 3. Daily search intensity metric (SIM) values for 3 adult male wild turkeys, Temple Ranch, Texas, 2009.

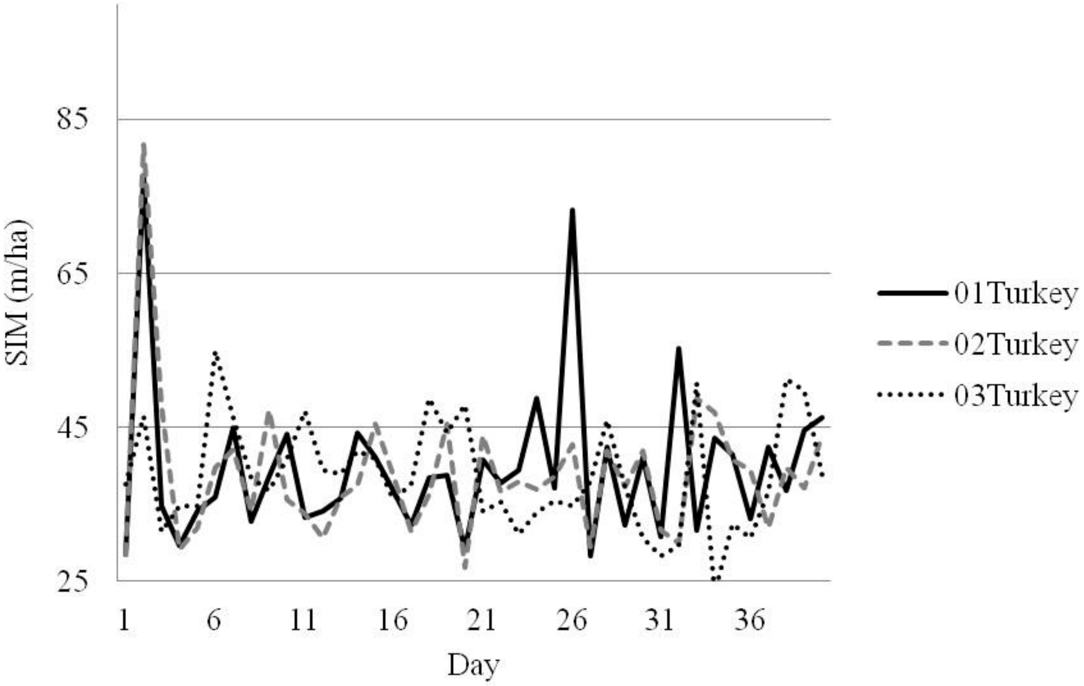


Figure 4. Daily movement paths for April 1-5 for individual adult male wild turkey 01 (solid line) and 02 (dashed line), Temple Ranch, Texas, 2009. Grid dimensions are 345 meters by 345 meters per cell.

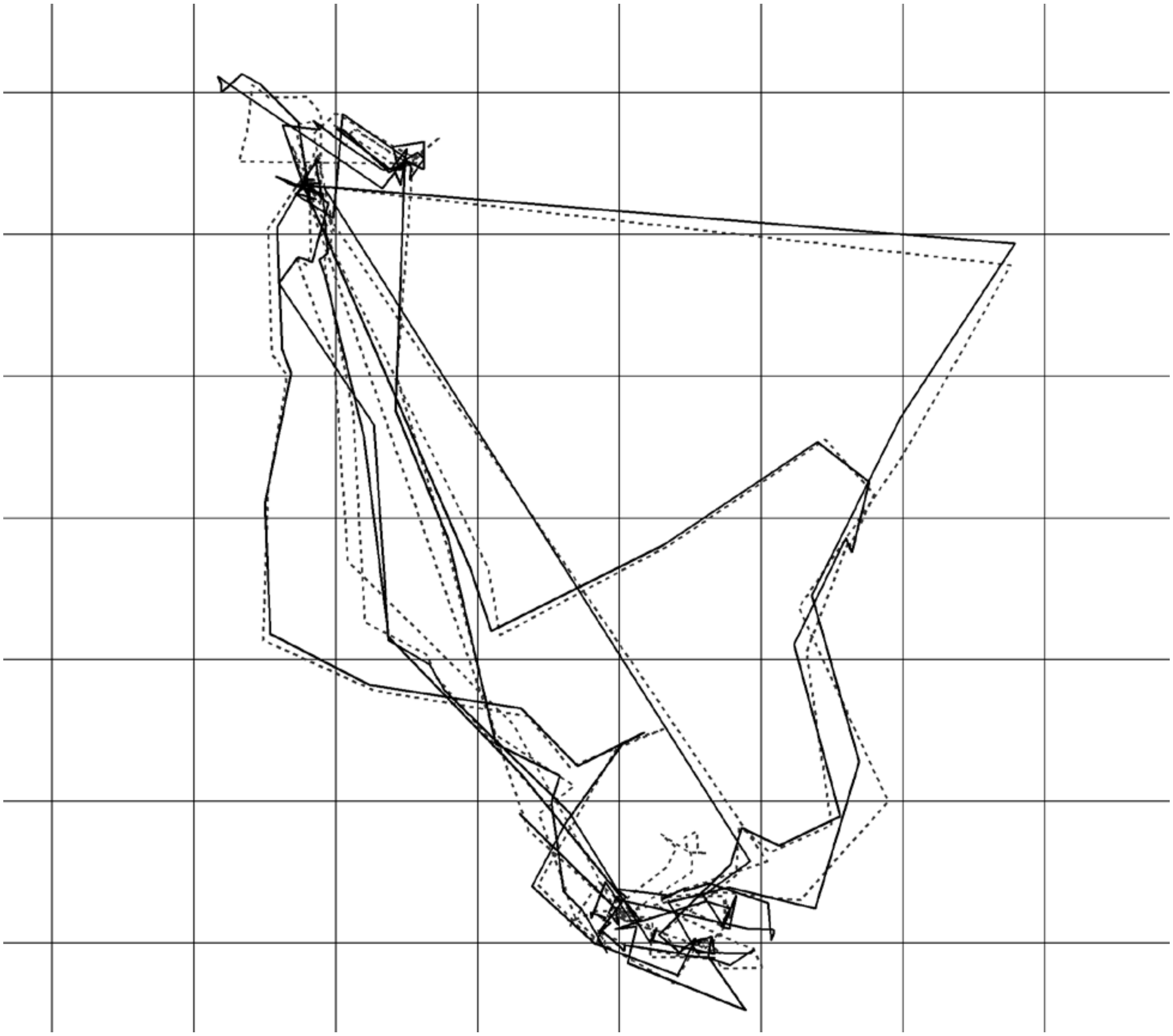


Figure 5. Daily movement paths with maximum (dashed line; 81.689 meters/hectare; Turkey 02 on April 2) and minimum (solid line; 23.391 meters/hectare; Turkey 03 on May 3) search intensity metric (SIM) value, Temple Ranch, Texas, 2009. Grid dimensions are 345 meters by 345 meters per cell.

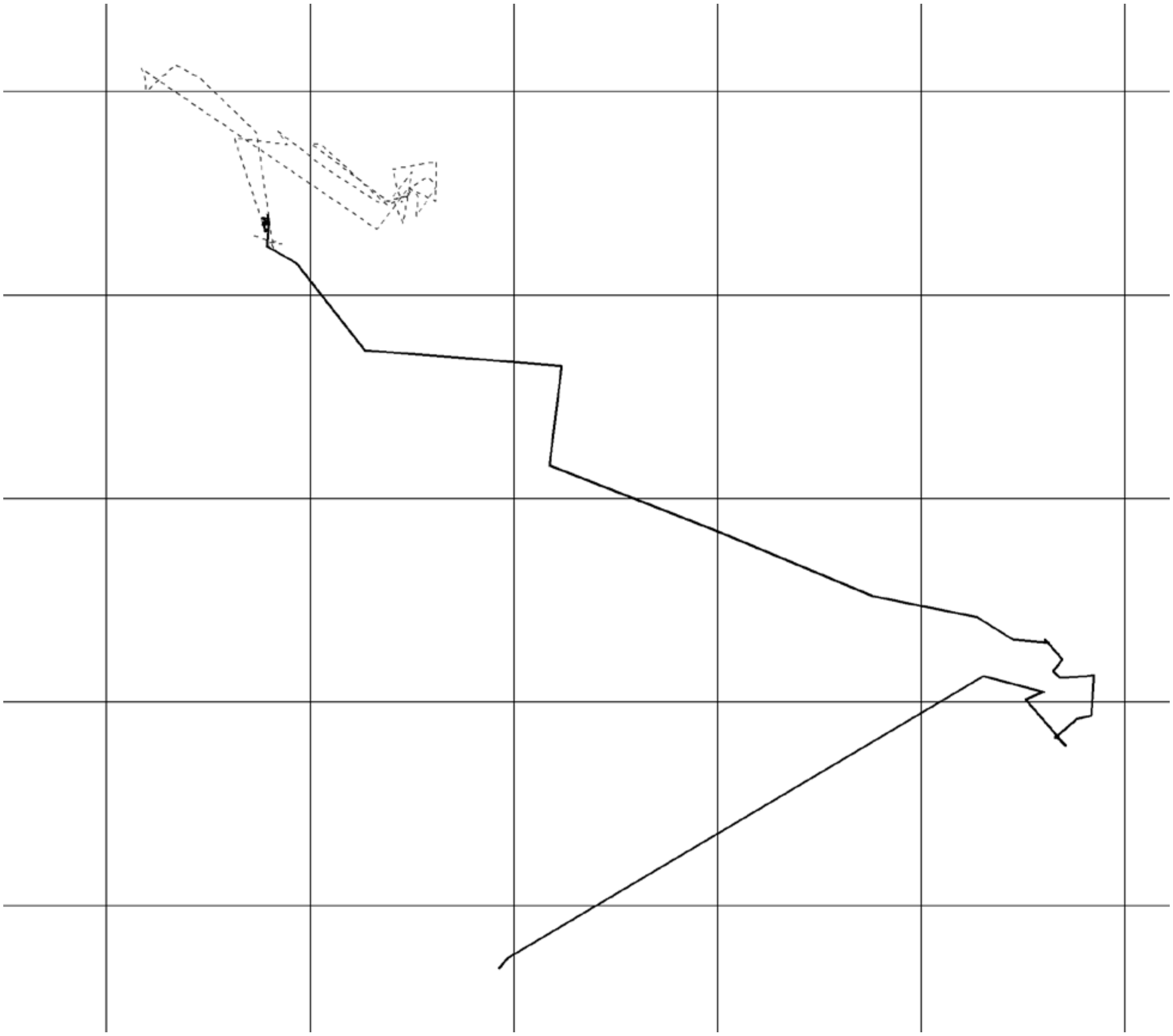


Figure 6. Comparison of mean SIM values for each individual adult male wild turkey for grid cell sizes tested in optimization search, Temple Ranch, Texas, 2009.

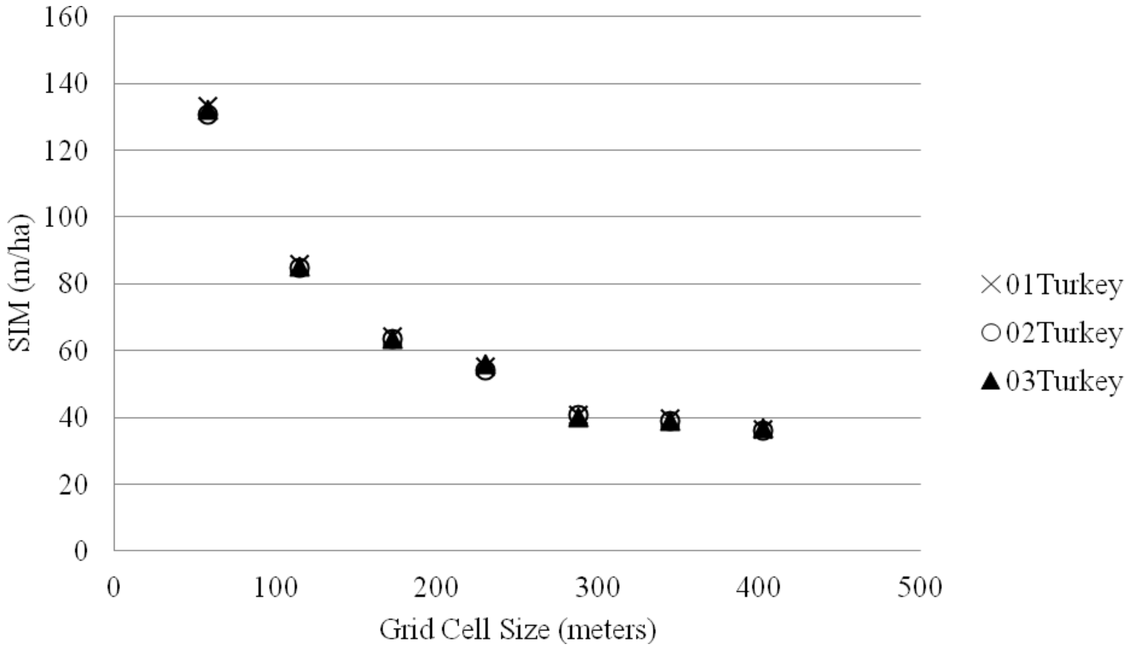


Figure 7. Coefficient of variation (ratio of standard deviation to mean) for different grid cell sizes tested for sharp-shinned hawks with outliers included, Indiana, 2001–2003. Additionally, CV values for grid cell sizes 1000, 1250, and 1500 meters are included to illustrate more of Curve B (see Figure 1).

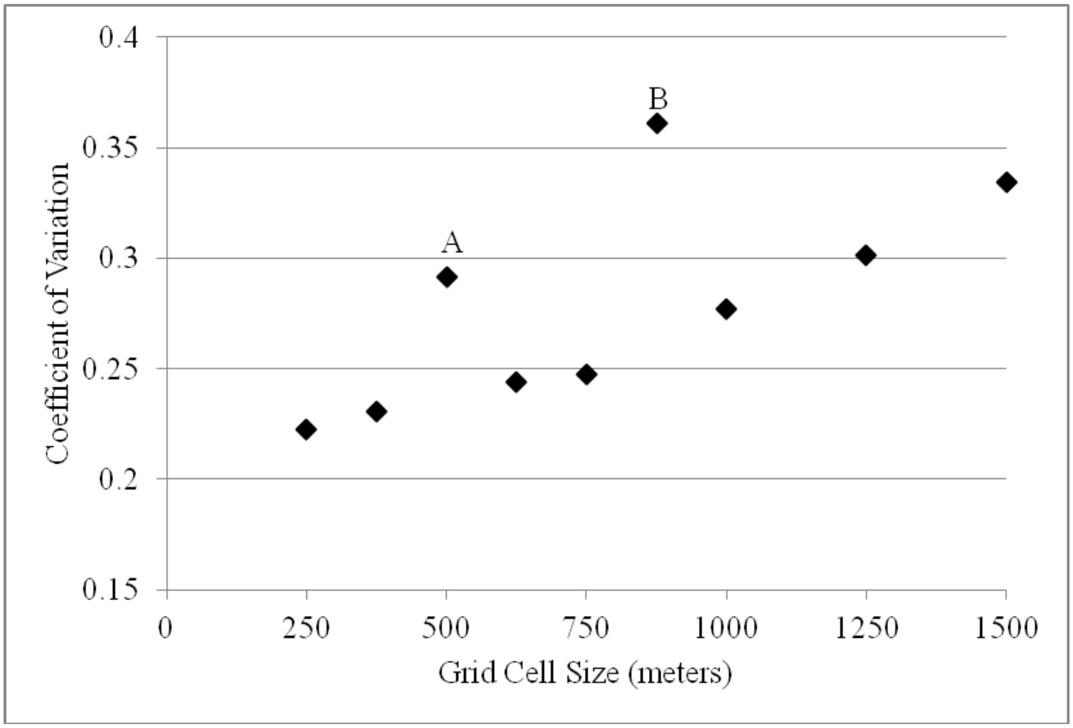


Figure 8. Daily path trajectory for 30 December 2001 (dashed gray line) and 11 January 2003 (solid black line) of sharp-shinned hawks with 875 meter grids, Indiana, 2001–2003.

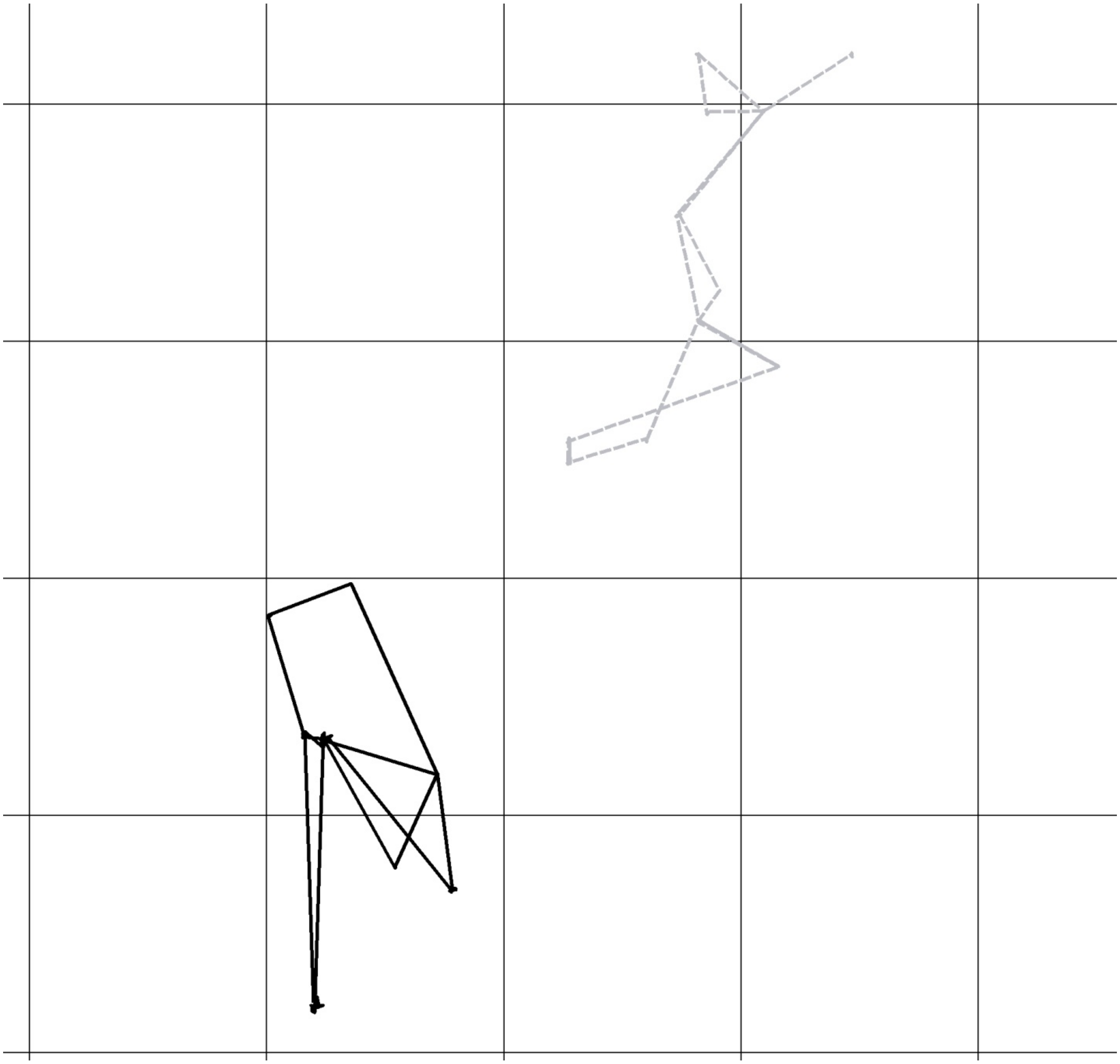


Figure 9. Daily path trajectory for 30 December 2001 (dashed gray line) and 11 January 2003 (solid black line) of sharp-shinned hawks with 500 meter grids, Indiana, 2001–2003.

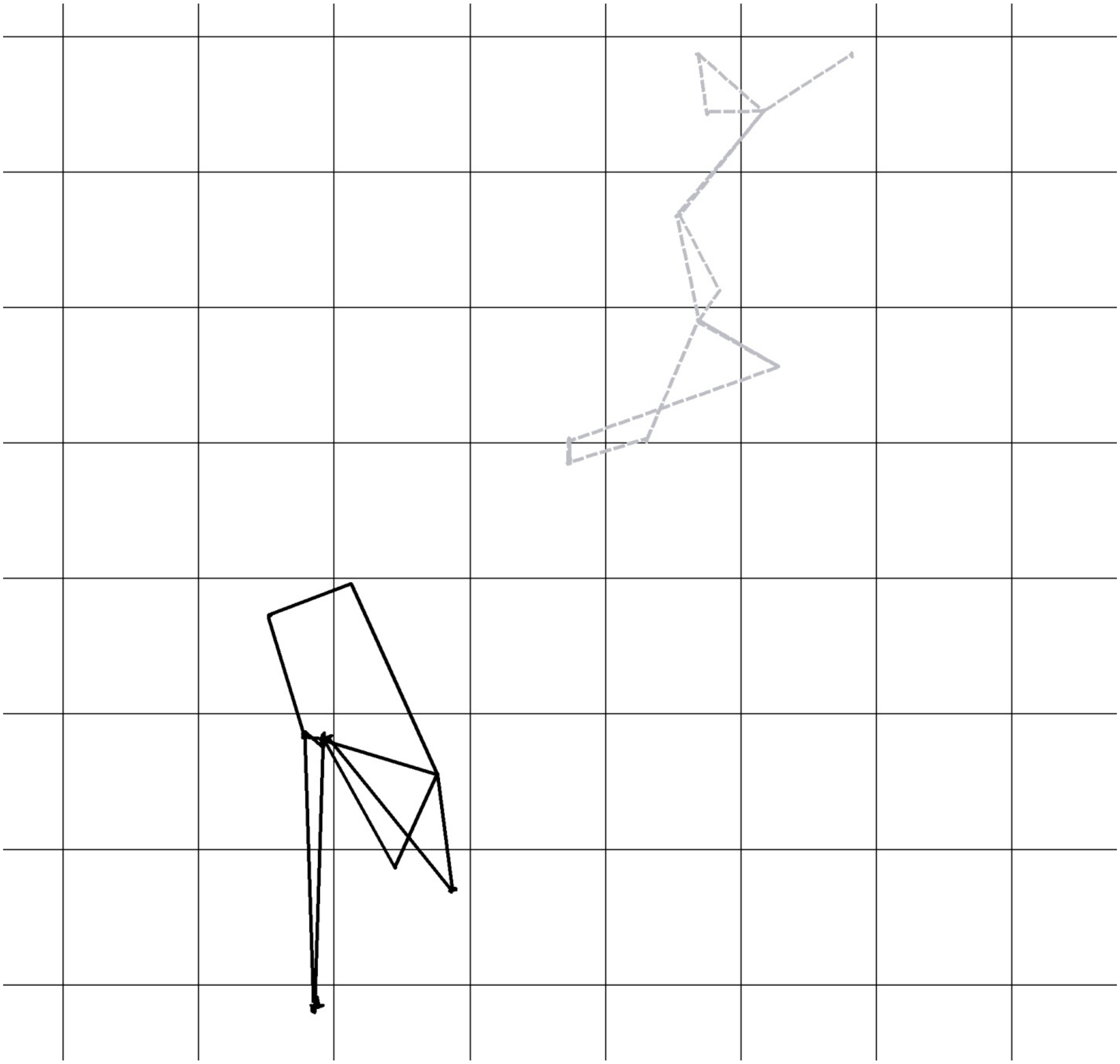


Figure 10. Coefficient of variation (ratio of standard deviation to mean) for different grid cell sizes tested for sharp-shinned hawks without outliers, Indiana, 2001–2003.

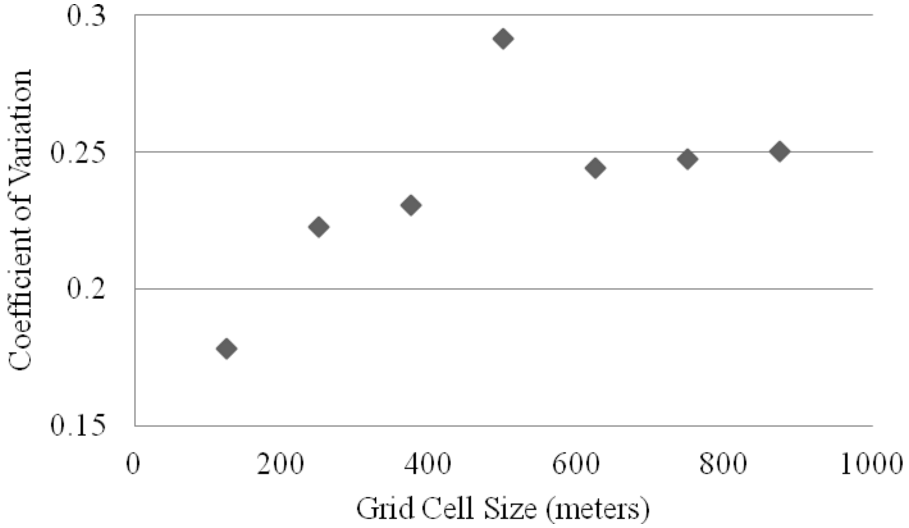


Figure 11. Coefficient of variation (ratio of standard deviation to mean) for different grid cell sizes tested for white-tailed deer in South Carolina, 2009–2011.

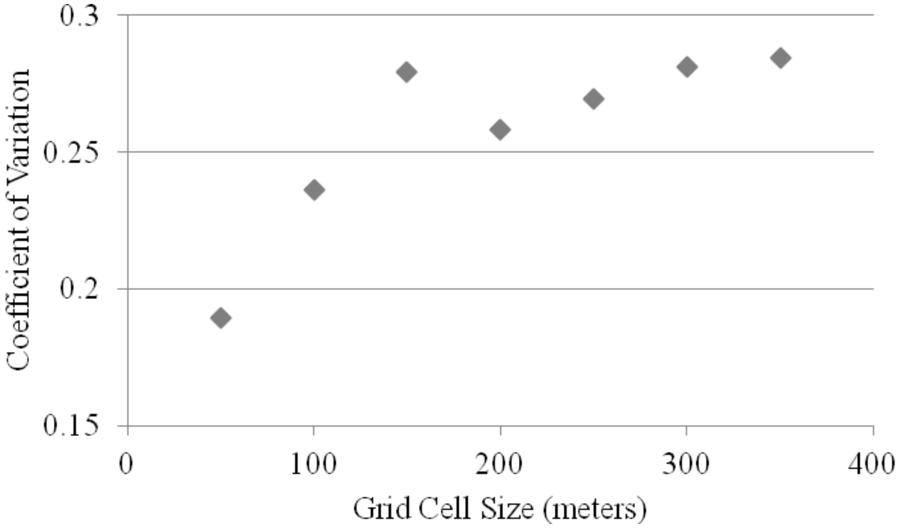
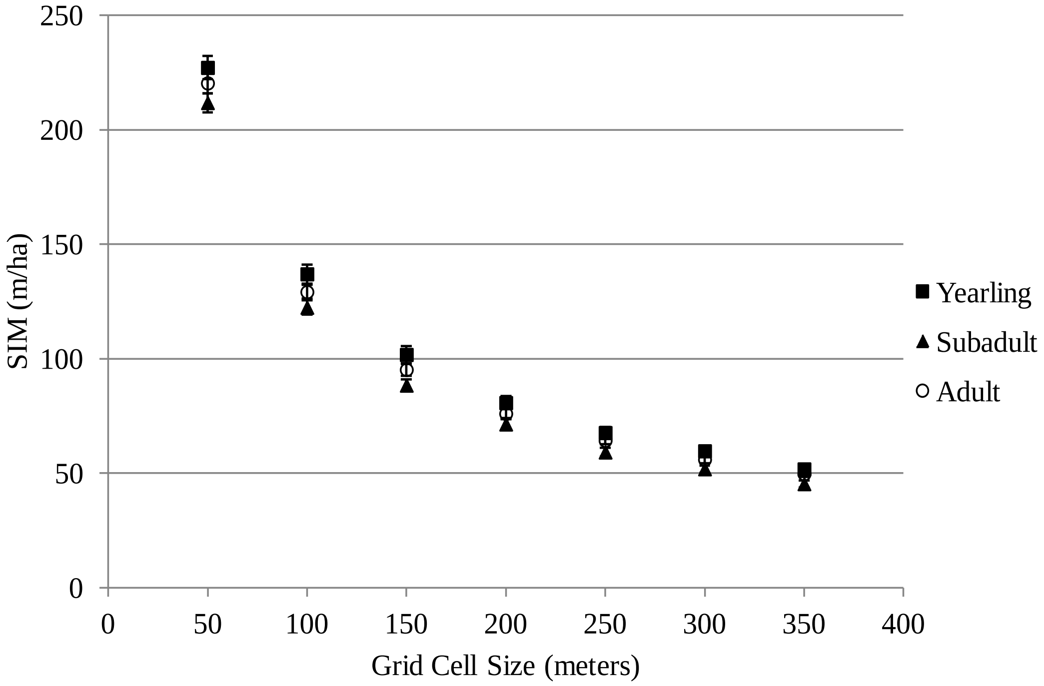


Figure 12. SIM values for yearling, subadult, and adult male white-tailed deer (South Carolina, 2009–2011) during the peak of breeding at varying grid cell sizes. Age class distribution (yearling>adult>subadult) follows the same pattern no matter the grid cell size used.



Spatiotemporal Breeding Strategies within a High Density, Male-skewed Population of White-tailed Deer

Abstract

Within male dominance polygyny mating systems, maximization of breeding success is restricted by somatic growth requirements in younger males, and limited by dominance hierarchies and reproductive effort expenditure in older males. I documented different movement patterns that are likely correlated with breeding strategies of white-tailed deer in a captive population where a male-biased sex ratio (2:1) and high deer density (1 deer/1.7 ha) intensified breeding season competition. To evaluate spatial and temporal breeding strategies employed by each age class [juvenile (1.5 years old), adult (2.5–3.5 years old), and mature (≥4.5 years old)], I GPS-radiocollared 34 male deer from 2009–2011 to evaluate space use patterns and search behaviors during a REFERENCE, PRE-BREED, BREED, and POST-BREED period. Mature males occupied smaller ranges during the REFERENCE and PRE-BREED periods, but juvenile home range size was smallest during the POST-BREED period. Adult and mature male home range and core area size did not decrease between the BREED and POST-BREED period. Juvenile and adult males searched more intensely during the BREED period and less so during the POST-BREED; however, mature males maintained similar search intensities throughout the entire study and exceeded juvenile and adult male levels during the REFERENCE and PRE-BREED period but was similar during the BREED and POST-BREED periods. Mature males adopted a staying strategy which likely enabled them to stay within a known dominance hierarchy and secure copulations by outcompeting rivals. Juveniles and adults assumed more subordinate roles evidenced by larger home ranges and more dispersed movement as searching

for a receptive, unoccupied estrous female was difficult within the study population – a strategy commonly referred to as roaming. In addition, whether due to inexperience or depleted energy reserves relative to somatic growth requirements, juvenile males' reproductive effort was temporally concentrated earlier than adult and mature males. Home range and movement rate reductions during the POST-BREED period by juvenile males suggested a strategy switch to female group association (e.g., "sneaker"). For ungulates within a male dominance polygyny, my study demonstrates multiple age-specific alternative breeding strategies with both spatial and temporal components.

Introduction

Ungulates' spatial dynamics are influenced by habitat, climate, forage availability, mate distribution, intrasexual competition, and other variables (Powell 2000). Though forage distribution is likely the main determinant of space use during the non-breeding season (Vercauteren and Hygnstrom 1998), male spatial dynamics are directly governed by the distribution of females (Emlen and Oring 1977, Ims 1987, Holand et al. 2003) during the breeding season. Female group dynamics, operational sex ratio, population density, and resource distribution influence the mating systems of ungulates and favor specific optimal strategies of cohorts and life-cycle stages (Emlen and Oring 1977). Among ungulates, polygyny is the dominant mating system (Fraser 1968, Jarman 1983) and may be expressed through space defense [e.g., fallow deer lekking (*Dama dama*); Clutton-Brock et al. 1988], resource defense [e.g., Indian blackbuck territoriality (*Antilope cervicapra*); Prasad 1989], female defense [e.g., red deer harems (*Cervus elaphus*); Clutton-Brock et al. 1982], or male dominance polygyny [e.g., scramble competition in white-tailed deer (*Odocoileus virginianus*); Ozoga and Verme 1985].

Male white-tailed deer acquire breeding rights by outcompeting rivals for access to estrous females – male dominance polygyny (Halls 1984). Rising testosterone levels accelerate male white-tailed deer space use patterns and movement rates (Guyse 1978, Hosey 1980, Tomberlin 2007), and increased breeding season activity reflects searching behavior for receptive females and establishment of tending bonds (Brown 1971, Richardson and Petersen 1974, Karns et al. 2011). Though monopolization of breeding rights does not occur in white-tailed deer, dominance is associated positively with body size (Lincoln et al. 1972, Bubenik and Schams 1986, Mysterud et al. 2004), and older males usually have greater reproductive success while younger cohorts sire proportionally fewer offspring. This disparity is accentuated particularly when population age structures are skewed toward mature, more experienced conspecifics (Dewsbury 1982, Ditchkoff et al. 2001, Mysterud et al. 2004, Sorin 2004, DeYoung et al. 2006).

As reproductive success differs among age classes of males, optimal mating strategies employed between subordinate and dominant individuals also vary. Due to their social immaturity but adequate sexual capability, juvenile (~18 months old) male white-tailed deer may employ alternative breeding strategies to “make the best of a bad job” and opportunistically secure copulations (Ozoga and Verme 1985, Whitehead 1990, Koprowski 1993, Komers et al. 1997, Acker 2013). Adopting a close affiliation with a group of females is a viable alternative breeding strategy (Roed et al. 2002). Because females move less and occupy smaller home ranges than their male counterparts, this sedentary strategy minimizes the cost of excessive traveling while maintaining a constant possibility that if a female enters estrus without a mature male present, successful reproduction may occur (Sandell 1986, Roed et al. 2002). Alternatively, juveniles may be forced to adopt vagrant or transient movement patterns (possibly initiated at natal dispersal) through harassment and displacement by older, more aggressive conspecifics

(Erlinge and Sandell 1986, Sandell 1986). As transient individuals possess the lowest social standing within any population, stationary juveniles at least maintain social status within a female subgroup while minimizing energy expenditure (Sandell 1986). Physiologically, prime-aged males can sustain high reproductive effort longer and more efficiently than immature males (Emlen and Oring 1977, Clutton-Brock 1984, Mysterud et al. 2004). Energy reserves become a greater proportion of body mass and locomotive efficiency improves as body size increases (Lindstedt and Boyce 1985, Murray 1991). In addition to spatial differences between subordinate and dominant breeding strategies, greater somatic growth requirements, more restrictive physiological thresholds, and inadequate experience likely influence both the temporal duration and distribution of reproductive effort by young male cohorts (Kojola 1991, Komers et al. 1994a, Komers et al. 1994b, Clutton-Brock et al. 1997, Holtfreter 2008, Mason et al. 2012).

As males mature, they invest disproportionately more resources towards reproduction due to lower residual reproductive value (Komers et al. 1994b, Ericsson et al. 2001, Mysterud et al. 2004). Among dominant males, female distribution, population density, and operational sex ratio determine which spatial breeding strategies are likely to maximize encounter rates with estrous females. When rivals are numerous and female density is high, dominant males are predicted to concentrate movements within a smaller area to maintain a stable dominance hierarchy and to copulate with each nearby receptive female through competitive exclusion (Whitehead 1990). In low density populations with fewer competitors and more dispersed female distribution, mature males may adopt a roaming strategy characterized by more linear movements to increase the likelihood of encountering receptive females (Erlinge and Sandell 1986, Sandell 1986, Benhamou 2004). In many hunted populations, adult males may sire a relatively greater proportion of the population's offspring as mature adults are usually uncommon or even rare

(Ditchkoff et al. 2001). Even when mature males are abundant, some large-bodied younger adults may dominate small-bodied mature or senescent males. Regardless, predicting adult male spatial behavior is more uncertain and the strategies adopted may vary widely due to reasons cited above.

Incorporating optimal foraging and search theory, Holtfreter (2008) used tortuosity to examine age-specific differences in male white-tailed deer breeding season movement. Tortuosity did not change before or during the breeding period, but path complexity decreased (especially for juvenile males) following peak breeding activity. Generally, more complex path structure and slower movement rates indicate abundant, widely-distributed resources whereas more linear paths signify scarce or clumped distribution of resources (Wiens et al. 1995, Nams and Bourgeois 2004). Linear search patterns after the peak of breeding season likely increased the probability of locating one of the few remaining receptive females (Holtfreter 2008). Though Webb et al. (2009) did not examine specific age classes of white-tailed deer, movement increased and became more linear during the breeding season while home range size remained similar. This could only occur if males covered a greater proportion of their home range on a daily basis, presumably to increase encounter rates with receptive females (Wiens et al. 1995). Foley (2011) reported similar findings, but noted that juveniles did not move as much as mature conspecifics. Also, diel home range size peaked for middle-aged and mature males during the breeding season but was delayed for juveniles until after the peak of breeding. In that population, juveniles employed an alternative spatial and temporal breeding strategy while middle-aged and mature males engaged in similar strategies (Foley 2011). These 3 studies each used different methods of quantifying search behavior (Holtfreter 2008 – tortuosity and eccentricity; Webb et al. 2009 – fractal dimensions; Foley 2011 – assessment corridor).

The goal of my research was to investigate age-specific breeding strategies of male white-tailed deer by incorporating both spatial and temporal aspects of behavior. My primary null expectation was that space use characteristics did not differ between age classes within each phase of the breeding season. Alternatively, space use characteristics might vary temporally and according to age class. My study site, characterized by a high density captive deer population, had been manipulated to have a male-biased sex ratio with abundant prime-aged males (McCoy and Ditchkoff 2012). Due to a male-skewed operational sex ratio, population demographics fostered intense intrasexual competition (Emlen and Oring 1977, Festa-Bianchet et al. 1998, Roed et al. 2002, Mysterud et al. 2004), and provided a unique opportunity to examine male breeding strategies in a system where mature males likely acquired the majority of siring opportunities with high potential for alternative breeding strategies by subordinate individuals (Sandell 1986, Clutton-Brock et al. 1988, Sandell and Liberg 1992, Mysterud et al. 2003).

For mature males ($\geq$4.5 years old), I expected that low mate availability and high rival density would lead to a highly dynamic system where dominant males would adopt a roving/roaming strategy characterized by greatest movement rates and space use among age classes. I also expected that linear searching to maximize receptive female encounter rates would be moderated by periodic, highly concentrated movement paths of tending/chasing females. Alternatively, staying strategies could have prevailed if high competitor density concentrated movements within a smaller area where individuals attempted to out-compete and/or suppress familiar rivals within a stable dominance hierarchy. Conversely, I expected the scarcity of females and high density of phenotypically-superior males to cause transient/vagrant patterns for younger, subordinate males characterized by linear movements and unstable space use patterns due to displacement. If dominant males were tolerant of juvenile male affiliation with matrilineal groups, juvenile male white-tailed deer likely adopted a female group association strategy that mimicked female space use patterns (e.g., small home range and core areas, lower movement rates, and search patterns driven by foraging rather than mate acquisition). Temporally, I surmised that juvenile males would shift reproductive effort to the post-breeding season after the majority of females had been bred and intraspecific competition had declined. It was difficult to predict spatial behaviors for middle-aged males because some individuals likely mirrored juvenile males, while more superior individuals likely engaged in the breeding season as a dominant competitor.

Study Site

My study site was the Three Notch Wildlife Research Foundation (hereafter Three Notch), approximately 10 km east of Union Springs, AL, in Bullock County. The study area encompassed 258.2 ha and had been enclosed by 3-meter deer-proof fencing since 1997. Approximately 20% of the site (48 ha) was farmed to provide deer with an array of food sources. Warm-season food plots generally consisted of iron and clay peas (*Vigna sinensis*), corn (*Zea mays*), and various clovers (*Trifolium* spp.), while cool-season plots were comprised of winter rye (*Secale cereale*) and white clover (*Trifolium repens*). Forest cover (192 ha) on the site was dominated by managed loblolly pine (*Pinus taeda*) stands of various ages, though forest types ranged from open, mature stands of loblolly pine with wiregrass-dominated (*Aristida* spp.) understory in upland areas to dense overstories of oaks (*Quercus* spp.) in creek drainages. With ridges primarily dominated by loblolly pine or food plots, lowland areas held plantings of clover. Annual prescribed fires were conducted in upland areas to provide natural browse for deer. Water sources on the site included the headwaters of the Pea River and a large centrally-located pond (~ 15 ha) that provided abundant year-round water (McCoy et al. 2011). Permanent feeding stations (*n* = 12) were uniformly distributed across the property providing high protein pelletized feed (20% protein; Purina Antlermax, St. Louis, Missouri) available ad libitum.

Hunting on the property was non-commercial and generally limited only to the landowner and family members. Using archery equipment as the primary method of harvest, approximately 40 deer were harvested per year (approximately 30-40% males). Harvest was limited to mature males (5 years or older) and females of any age. Due to limited hunting success (archery equipment only), the selective harvest of the landowner, and an abundance of food sources, the sex ratio favored males. Density was at least a deer per 1.7 ha with a 2:1 (male:female) sex ratio (McCoy et al. 2011). Due to the strict harvest guidelines protecting younger age class males, adult and mature ($\geq$2.5 years old) males outnumbered juvenile (1.5 years old) males nearly 6 to 1 (McCoy et al. 2011).

Methods

Capture Protocol

During September and October of 2009-2011, I deployed GPS collars (Model G2110D; Advanced Telemetry Systems, Isanti, Minnesota) on male white-tailed deer. In order to identify individuals within the age classes of juvenile (1.5 years old), adult (2.5−3.5 years old), and mature ($\geq$4.5 years old), I estimated deer age in the field by using antler and body characteristics (Richards and Brothers 2003). I used a Pneu-dart Model 193 dart projector (Pneu-dart, Inc., Williamsport, Pennsylvania) and 2-ml radio transmitter darts (Pneu-dart, Inc., Williamsport, Pennsylvania) to administer anesthetic drug concentrations of 125 mg/ml Telazol and 100 mg/ml Xylazine (Kreeger et al. 2002). I used telemetry equipment (Communications Specialists, Inc., Orange, California) to locate the dart transmitter and recover the deer. If the deer exhibited signs of inadequate sedation, I administered an additional 0.5-ml Telazol/Xylazine booster intramuscularly by syringe. Once immobilized, I applied eye ointment (Paralube, Pharmaderm, Melville, New York) to prevent corneal drying and blindfolded the deer to minimize stress. I positioned deer sternally or on right side for processing and monitored vital signs (open airway, pulse, respiration, and temperature) every 15 minutes throughout the entire process. Using a scalpel, I surgically removed darts by making a small incision over each retention barb. I attached a GPS collar (400 grams) leaving an 8 cm space from the deer's neck to accommodate for neck swelling during the breeding season. To assist in field identification, each deer received a colored and numbered cattle ear tag (National Band and Tag, Co., Newport, Kentucky). I shaved hair from each hindquarter and used liquid nitrogen to freeze brand each hindquarter with the same identification number. Brands and dart excision were washed in rubbing alcohol to help cleanse the wound. At 70 minutes post-injection, I reversed Xylazine/Telazol-anesthetized deer with 3.0 ml Tolazoline (100 mg/ml) administered intramuscularly (Tomberlin 2007). I monitored each deer until it left the processing site. The research protocol was reviewed and approved by the Institutional Animal Care and Use Committee at Auburn University **(**PRN# 2009-1493**)**.

GPS Collar Programming

I programmed GPS collars to collect locations once every 8 hours before the primary study period (deployment –November 30) and then once every 15 minutes during December 1 – February 23. Unlike most of the white-tailed deer's range, the peak of breeding activity in southeastern Alabama occurs in mid-late January (Causey 1990). GPS collars recorded geographic coordinates, date, time, environmental temperature, location status, satellites referenced, position dilution of precision (PDOP), horizontal dilution of precision (HDOP), and elevation with each location. Collars were equipped with a mortality sensor that emitted a double-pulse VHF signal after 8 hours of inactivity. I set time-delay drop-off mechanisms to release immediately after the primary data collection period. To ensure collars were properly functioning and check on the status of the study animals, I monitored deer weekly using radio telemetry equipment. If the mortality sensor was activated (indicating a deceased study animal or slipped collar), I retrieved the collar using radio telemetry.

Data Management and Censoring

I omitted 3-dimensional (3D) locations with PDOP > 10 or HDOP > 6 and 2-dimensional (2D) locations with PDOP > 5 or HDOP > 3 from analyses (Adams 2003, D'Eon and Delparte 2005). I also deleted locations with impossible elevations outside the range of 100 meters to 215 meters (D'Eon et al. 2002). For deer that were captured or died during December 1 – February 23, I omitted locations within 7 days of those events to reduce possible bias (Karns et al. 2012). After data censoring, I imported GPS locations into ArcMap 9.3 (Environmental Systems Research Institute, Inc., Redlands, California, USA) for data analysis using North American Datum (NAD) 1983 UTM Zone 16 North (meters) projection.

Study Periods

I segmented the primary data collection period (December 1 – February 23) into 4 periods: REFERENCE period (December 1 – December 21), PRE-BREED period (December 22 – January 13), BREED period (January 14 – February 3), and POST-BREED period (February 4 – February 23). Based on fetal survey data (Hamilton et al. 1985), the peak conception date was January 22 for 2009 with a range from January 17 – February 2, January 25 for 2010 with a range from January 21 – January 31, and January 27 for 2011 with a range from 20 January – 2 February. To calculate daily metrics (movement and search intensity metric), I defined each 24-hour period using noon as the beginning and noon of the next day as the end.

Home Range, Core Area, and Intensity of Use

I estimated home ranges (90% isopleth) and core areas (50% isopleth) in hectares for each deer for each study period using the adaptive local convex-hull (LoCoH) method (NNCH script from adehabitat package in R; Getz et al. 2007). Because study animals were bounded on all sides by the deer-proof fencing and a centrally-located lake bordered at least one side of nearly every deer's home range, LoCoH was suited to identify those impassable spatial boundaries within each deer's home range (Figure 1; Getz and Wilmers 2004, Getz et al. 2007). I used the "minimum spurious hole covering" (MSHC) rule to select the smallest value of *a* that produced a coverage with the same topology as the given data set (Getz et al. 2007). I used the maximum distance between any 2 points in the dataset as an initial value for *a* (*a* = 1898 meters), then tested other values to choose *a* (mean = 1936 meters; average difference between maximum distance *a* and selected value = 501 meters) which minimized the number of spurious holes in the home range coverage but mimicked true home range boundaries (e.g., lakeshore and high fence) most closely. I calculated intensity of use by using the ratio of core area (50%) to home range (90%) (Lent and Fike 2003). Values closer to 1 reflected a concentration of activities inside a larger portion of the total home range, and values approaching 0 indicated an animal concentrating its time within its core area.

Daily Movement

I calculated Euclidean distances (meters) between locations using Hawth's Analysis Tools (Beyer 2004, Nams 2006). Gaps in the dataset (because of missed or deleted GPS locations) were ignored because I examined movement path length for each day within my study period. Obviously, a 24-hour period of consecutive successful locations would provide the best possible estimate of true distance traveled. Because a greater number of missed locations within a day would lead to greater underestimation of true distance traveled, I recorded how many missed or deleted GPS locations existed within every 24-hour period. To ensure that movement within each day was comparable, at least 75% (72 out of 96 possible locations) of locations had to be successfully acquired. I removed days that did not meet those thresholds from data analysis.

Search Intensity Metric

I calculated daily search intensity metric (SIM) values for each individual for each day meeting the 75% criteria mentioned above (Karns et al. in prep). After using the $0.25L$–$1.75L$ method (where L was the average hourly movement path length) to select the optimal grid cell size (Figure 2; Karns et al. in prep), I generated a grid covering the entire extent of the study site (Beyer 2012). Each grid cell measured 180 meters by 180 meters and encompassed 3.24 hectares, and the same grid was applied to all individuals within the study. I calculated SIM as the ratio of total daily path length (meters) to number of grid cells intersected (hectares; Karns et al. in prep). High values (e.g., SIM > 150) reflected highly tortuous search paths and lower values (e.g., SIM < 75) indicated linear paths with less intensive search intensity. Data were summarized within age class and study period.

Analysis

Using linear mixed-effect models (package nlme; Pinheiro et al. 2013) in Program R 2.15.3, I tested for differences in home range (90%) and core area (50%) size, intensity of use, movement, and SIM between age classes (juvenile, adult, and mature males) and study periods (REFERENCE, PRE-BREED, BREED, and POST-BREED). Starting with the global model (fixed effects of age and period and age*period interaction) for each metric, I determined best model by a combination of using backwards stepwise regression and comparing Akaike information criterion (AIC) values. To examine differences between main and interaction effects, I employed function ‘relevel’. I included random effect of individual in all analyses. Significance level (α) was set to 0.05.

Results

Capture Success and Collar Deployment

From 2009–2011, I deployed 15, 14, and 11 collars, respectively, on male white-tailed deer. The number of deployments decreased throughout the study because 1 GPS collar became inoperable in 2009 and another 3 were unrecoverable during the second year of the study. Within years 2009–2011, I retrieved useable data from 13, 11, and 10 collars, respectively, for a total sample size of 34. Within juvenile (*n* = 10), adult (*n* = 13), and mature (*n* = 11) age classes, I pooled individuals across years. Juvenile, adult, and mature age classes had 7, 9, and 10 complete datasets, respectively. Reasons for incomplete datasets included malfunctioned collar due to weakened battery (*n* = 1), mechanical collar failure (*n* = 2), mortality due to injuries sustained during the breeding season (*n* = 2), and epizootic hemorrhagic disease (EHD) mortality (*n* = 3).

Data Management and Censoring

Of 248,352 possible locations, I omitted 9.55% (*n* = 23,709) of locations due to incomplete data or failure to meet HDOP, PDOP, and/or elevation data quality thresholds. Pertaining to the movement and SIM metrics, 92.04% of the days met the ≥72 location requirement; however, one collar during 2011 had location acquisition rates that were atypically low and failed to record a single 24-hour period meeting the ≥72 location requirement. Removing that individual from those analyses, over 95% of the days (2383 of 2505) met the minimum number of locations requirement resulting in an average of 90 (out of a possible 96) locations per day.

Home Range, Core Area, and Intensity of Use

For home range (90% isopleth), the global model was best with age ($P < 0.01$), period ($P < 0.01$), and the interaction ($P < 0.01$; Figure 3). Adult home range size (90% isopleth) differed between each study period. For juveniles, the POST-BREED (35.30 ha) period was similar to REFERENCE (30.33 ha; $P = 0.44$) and PRE-BREED (47.12 ha; $P = 0.07$) periods, but differed in all other comparisons. For mature male white-tailed deer, home range differed between REFERENCE (13.42 ha) and BREED (50.03 ha; $P < 0.01$) periods, REFERENCE and POST-BREED (45.47 ha; $P < 0.01$) periods, PRE-BREED (20.92 ha) and BREED ($P < 0.01$) periods, and PRE-BREED and POST-BREED ($P < 0.01$) periods. Within the first 3 study periods, mature males occupied smaller home ranges than adults and juveniles [marginal difference between mature (50.03 ha) and juveniles (64.50 ha) during BREED period ($P = 0.05$)] except during the POST-BREED period. Home ranges of adult and juvenile male white-tailed deer were similar except during the POST-BREED period when adult home ranges (53.52 ha) remained large but juveniles declined (35.30 ha; $P = 0.02$)

Similar to the 90% isopleth home range, age ($P = 0.02$), period ($P < 0.01$), and the interaction ($P = 0.05$) influenced core area size (50% isopleth; Figure 4). Within age classes, adult and mature male white-tailed deer were alike in that BREED and POST-BREED core areas were greater than REFERENCE and PRE-BREED periods, but REFERENCE and PRE-BREED periods and BREED and POST-BREED periods did not differ from one another. Juvenile core area size increased from the REFERENCE to PRE-BREED period, increased from the PRE-BREED to BREED period, and decreased to REFERENCE period levels thereafter. During the REFERENCE period, core area size (50% isopleth) was similar between age classes. Mature males occupied smaller core areas than juveniles and adults during the PRE-BREED period, and remained smaller than adult core area size in the BREED period (similar to juveniles during BREED period). In the POST-BREED period, juveniles had a smaller core area than adult but remained similar to mature males. For intensity of use, study period was the only important predictor ($P < 0.01$). During the BREED and POST-BREED periods, the core areas of male white-tailed deer were less concentrated than during the REFERENCE and PRE-BREED periods (Figure 5).

Daily Movement

The global model was best for daily movement; age ($P < 0.01$), period ($P < 0.01$), and age*period interaction ($P < 0.01$; Figure 6). Adult and mature male white-tailed deer increased their daily movement from the REFERENCE period through the BREED period and then decreased movement (28% and 7% decrease for adult and mature males, respectively) during the POST-BREED period. For juveniles, the pattern was similar except that POST-BREED movement decreased nearly to REFERENCE period levels. During the REFERENCE and PRE-BREED periods, juvenile and adult males traveled more than mature individuals, but did not differ from one another. During the BREED period, adults traveled approximately 35% more than juvenile and mature male white-tailed deer. Adult and mature males moved greater distances during the POST-BREED period than juveniles.

Search Intensity Metric

The global model was best with period ($P < 0.01$) and interaction age*period ($P < 0.01$) significant (Figure 7). Interestingly, age was not as important ($P = 0.20$). Though juveniles did not change between the REFERENCE and PRE-BREED period, they searched more intensely during the BREED period and then slightly less during the POST-BREED period. Adult male white-tailed deer followed the same pattern, while mature males did not alter search intensity throughout the study period. Mature males had greater search intensity than juveniles (REFERENCE period) and adults (REFERENCE and PRE-BREED periods) early in the overall study period. During the BREED and POST-BREED periods, search intensity did not differ between age classes of male white-tailed deer.

Discussion

The validity of my study stems from several explicit assumptions related to male white-tailed deer movements, female white-tailed deer distribution, and intrasexual competition during the breeding season. Much of the scientific literature addressing alternative mating strategies and optimal foraging are derived from free-ranging animal populations; therefore, I am assuming generalization to the confined study population. Also, I assumed all male white-tailed deer exhibited similar utilization rates of permanent supplemental feed stations, and human-caused flight disturbances occurred randomly with respect to age classes and study periods. During the breeding season, each individual male's movements were chiefly motivated by the goal of gaining copulations with receptive female white-tailed deer. As well, I assumed even female white-tailed deer distribution across the study site providing all males with adequate availability to females. Lastly, due to the male-skewed operational sex ratio and high population density, receptive female white-tailed deer would rarely be unoccupied – meaning the vast majority of receptive females would represent an "unusable" resource for all juvenile males and subordinate adult males.

My findings provide evidence of age-specific spatial and temporal breeding strategies in a male-skewed, high density population of white-tailed deer. Restricted space use and movement rates through the BREED period indicated that mature males likely adopted a staying strategy, perhaps opting to remain within stable social structure and secure copulations by outcompeting known rivals (Sandell 1986). Given the demographic traits of the population, I expected that dominant individuals would have larger home ranges than subordinate conspecifics (Stamps and Krishnan 1998, Estevez and Christman 2006), but this was not the case. Interestingly, search intensity for mature males stayed similar throughout the study period, suggesting that intensity of searching for females did not differ from that of foraging behavior prior to the breeding season, consistent with findings by Holtfreter (2008). Because mature male space use (i.e., home range and core area size) increased during the BREED and POST-BREED periods, it appears that the spatial scale of these search patterns also expanded during those periods. Relative to other age classes, mature males had reduced home range and core area size. One possible explanation is that mature males inhabited higher quality habitat than younger conspecifics (i.e., suggestive of an ideal despotic distribution; Messier et al. 1990, Calsbeek and Sinervo 2002). Coupled with lower movement levels, older-aged males seemed to conserve energy prior to the breeding season, and this may indicate that experience enabled them to focus reproductive effort most intensively during and immediately following the peak of conception (Forslund and Part 1995, Mason et al. 2012).

Though the results were more mixed for juveniles, I believe that adolescent males adopted a searching tactic reminiscent of mature individuals (anecdotally supported by observations). In contrast to mature males, effort was focused earlier in the breeding season and declined significantly in the POST-BREED period. Outside of a few rare instances, juvenile male reproductive effort likely secured few copulations because the vast majority of females were not yet receptive during the PRE-BREED period (0 conception dates during PRE-BREED period out of 25 reproductive tracts sampled). Holtfreter (2008) reported a similar post-breeding season decrease in juvenile male white-tailed deer reproductive effort. Within female defense systems of other Cervid species, juvenile males exhibit an opposite pattern and effort usually increases after the peak of breeding possibly because energy costs to dominant individuals for assembling and guarding a harem is not sustainable for longer periods of time (Gibson and Guinness 1980, Komers et al. 1994b, Clutton-Brock et al. 1997). Also, delaying reproductive effort until later in the breeding season allows younger males additional time for somatic growth investment (Schultz et al. 1991). High intrasexual competitor density, inferior status within dominance hierarchies, and scarcity of receptive females likely prevented nearly all potential mating opportunities for juveniles during the BREED period. During the POST-BREED period (only age class where POST-BREED movement rate was less than PRE-BREED period), it is possible that juveniles' reduction in home range, core area, and movement rate indicated a switch to a more sedentary female group association (Sandell 1986, Roed et al. 2002) and sneaker strategy (LeBoeuf 1974, Hogg 1984, Yoccoz et al. 2002). Though breeding opportunities were not likely during the POST-BREED period, successful matings could have occurred under these circumstances, particularly if a female fawn associated with the same matrilineal herd reached her minimum mass threshold (DelGiudice et al. 2007) and entered estrus later in the season.

Interestingly, adult male white-tailed deer mirrored juvenile male behavior in many ways. Due to the preponderance of mature males in the population, adult males may have been forced to adopt more subordinate roles in the breeding population than would normally occur in most populations (Miller and Marchinton 1995, Ditchkoff et al. 2001). In fact, the only real difference between adult and juvenile males was the ability of adult males to sustain elevated reproductive effort through the POST-BREED period, possibly due to fewer somatic energy constraints due to reduced growth requirements (Solberg et al. 2008) and greater experience than more naïve adolescent males. Exhibiting evidence of adopting a roaming strategy (Sandell and Liberg 1992, Forchhammer and Boomsma 1998), adult males traveled approximately 3 km more daily than mature males during the BREED period. Due to displacement by dominant individuals, adult males probably had to travel more than mature males to attempt to find unoccupied receptive females; however, adult males likely garnered occasional copulations as phenotypically-large adults could potentially outcompete some low-ranking mature males (Townsend and Bailey 1981). Because adult males had the greatest movement rates, encounter rates with receptive females should actually have been greatest for adult males (Viswanathan et al. 1999).

With regards to basic spatial ecology of white-tailed deer, my results support studies suggesting that high density (Henderson et al. 2000, Kjellander et al. 2004) and high habitat diversity and quality (Kie et al. 2002) translates to reductions in home range and core area size. Also, supplemental feeding often reduces home range size in vertebrates (Boutin 1990). In comparison to 5 adult male space use studies conducted in the Southeastern United States (unpublished data, McCoy 2013; Vanderhoof and Jacobson 1993, Labisky et al. 1999, Holtfreter 2008, Thayer 2009), average home range size for Three Notch male white-tailed deer was nearly 500% smaller than free-ranging counterparts [24–94 ha (minimum – maximum; $\bar{X}$ = 58 ha) versus 79–691 ha (minimum–maximum; $\bar{X}$ = 340 ha)]. In an enclosure that encompasses barely enough room to contain the average home range of free-ranging male white-tailed deer, it is remarkable that the captive population formed such small home ranges (on average, each male only utilized 23% of the available site), further supporting the effects of high population densities, exceptional habitat quality, and supplemental feeding on home range size. My results conflict with patterns observed by previous studies (McBride and Foenander 1962, Stamps and Krishnan 1998) that dominant individuals maintain larger, more exclusive home ranges and low-ranking males are restricted to much smaller ranges.

No differences in SIM between male age classes during the breeding season may be partially due to the confounding effect of the fence as it forced deer to periodically change direction, resulting in a decrease of potential differences for the SIM metric. Prior studies have noted that movement barriers can have 2 effects on an animal’s movement trajectory: 1) a “rebounding” effect (Haddad 1999, Estevez and Christman 2006) or 2) a “trapping” effect where the animal continues to follow the barrier once encountered (Erlandsson et al. 1999). Depending on what pattern occurred most frequently at my study site, SIM values could be grossly inflated in a particular age class if “trapping” (or fence walking) occurred more often in one age class than another; however, concerns would be alleviated if all age classes responded similarly. To test for this effect, I calculated the proportion of time each male spent within 10 meters of the fence and compared between age classes for each of the 4 study periods. There was no significant effect of age, though the proportion of time spent within 10 meters of the fence enclosure did increase during the BREED period (63% increase related to other 3 study periods). This result was not surprising as overall movement rates also peaked during this period. To test if increased fence “encounters” during the BREED period could have caused the increase in SIM values during that period, I removed all days throughout the dataset when individual deer paced the fence (e.g., “trapped” behavior) for 4 or more consecutive hours. All relationships and effects remained unchanged, suggesting the enclosure did not have a significant bearing on patterns reported above.

The semi-controlled conditions of the enclosed study site allowed harvest and management to exaggerate the density and sex ratio of the population to intensify breeding competition and force age-specific adoption of alternate breeding strategies. The temporal component to juvenile mating effort was opposite between a male dominance polygyny and female defense mating system, and risk-averse tendencies induced a change in spatial tactics in young males between different stages of the breeding season. In mature males, a staying strategy was optimal even though female density was relatively low. Presumably, mature male density may have exceeded a threshold where the increased rate/risk of antagonistic rival interactions became disadvantageous for roaming strategies by dominant males. High mature male density caused younger adult males to adopt subordinate roles, mirroring juvenile behavior in many ways. Other ongoing studies will reveal more about optimal and alternate strategy selection under different population demographics and environments. In future research, fitness (measured through reproductive success) should be compared to the spatial and temporal allocation of reproductive effort by different age class male white-tailed deer.

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Figure 1. The LoCoH home range estimator’s performance when animal’s range is bounded by impassable boundaries [e.g., 3-meter deer-proof fencing (black polyline)]; breed period home range (90% isopleth; gray polygons) and core area (50% isopleth; cross-hatched polygons) of 3.5 year-old adult male white-tailed deer at Three Notch Wildlife Research Foundation, Bullock County, Alabama, 2011.

Figure 2. Grid cell testing dimensions (meters) and coefficient of variance (standard deviation/mean) to identify optimal grid cell dimension for search intensity metric analysis of male white-tailed deer, Three Notch Wildlife Research Foundation, Bullock County, Alabama, 2009–2011.

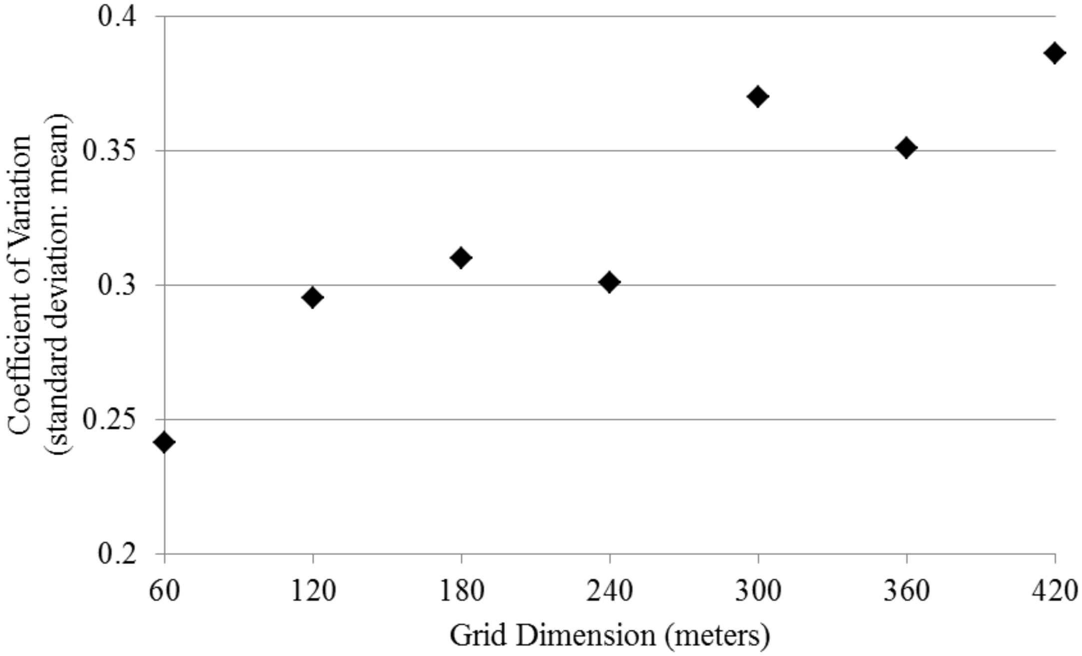


Figure 3. Mean home range (hectares; 90% isopleth) within each study period generated by LoCoH method for different age class male white-tailed deer at Three Notch Wildlife Research Foundation, Bullock County, Alabama, 2009–2011. Error bars represent 95% confidence intervals.

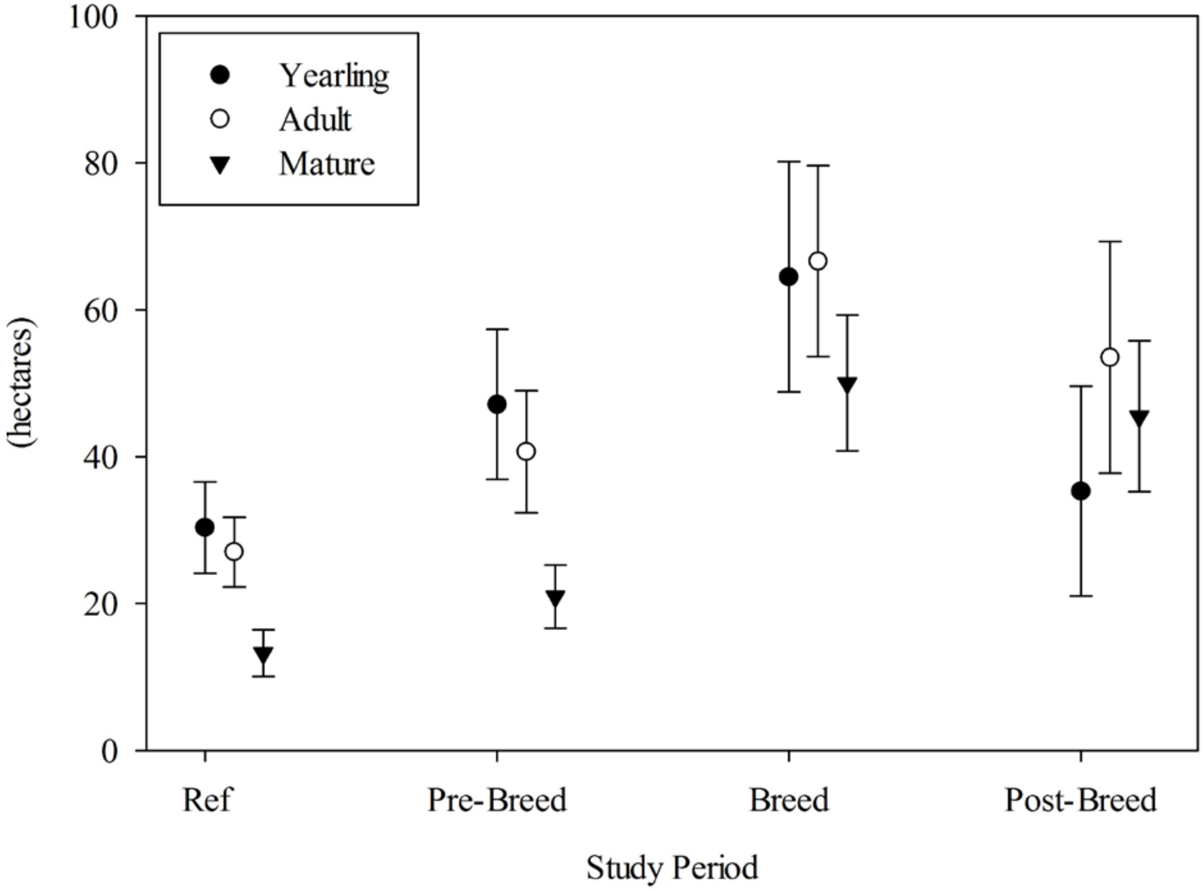


Figure 4. Mean core area (hectares; 50% isopleth) within each study period generated by LoCoH method for different age class male white-tailed deer at Three Notch Wildlife Research Foundation, Bullock County, Alabama, 2009–2011. Error bars represent 95% confidence intervals.

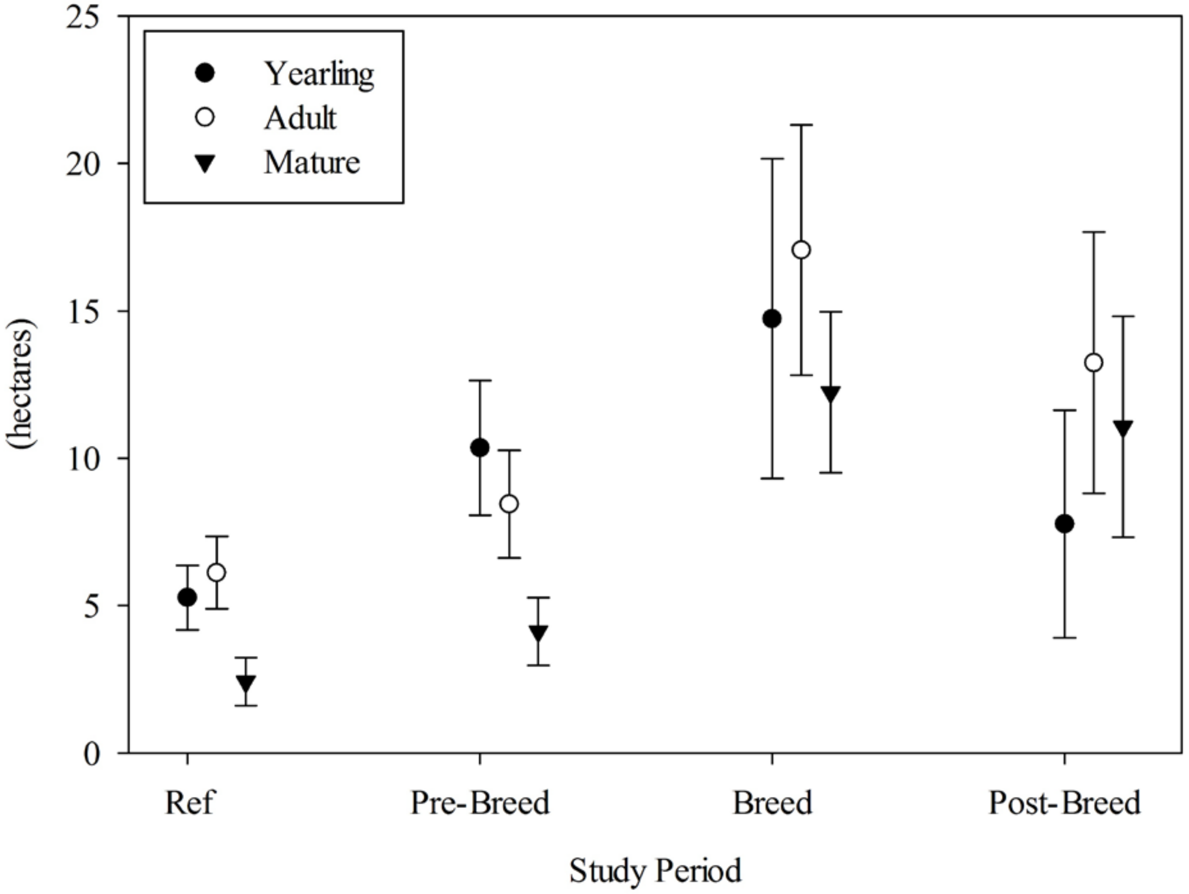


Figure 5. Mean intensity of use (ratio of area within 50% isopleth: 90% isopleth) within each study period for male white-tailed deer at Three Notch Wildlife Research Foundation, Bullock County, Alabama, 2009–2011. Error bars represent 95% confidence intervals.

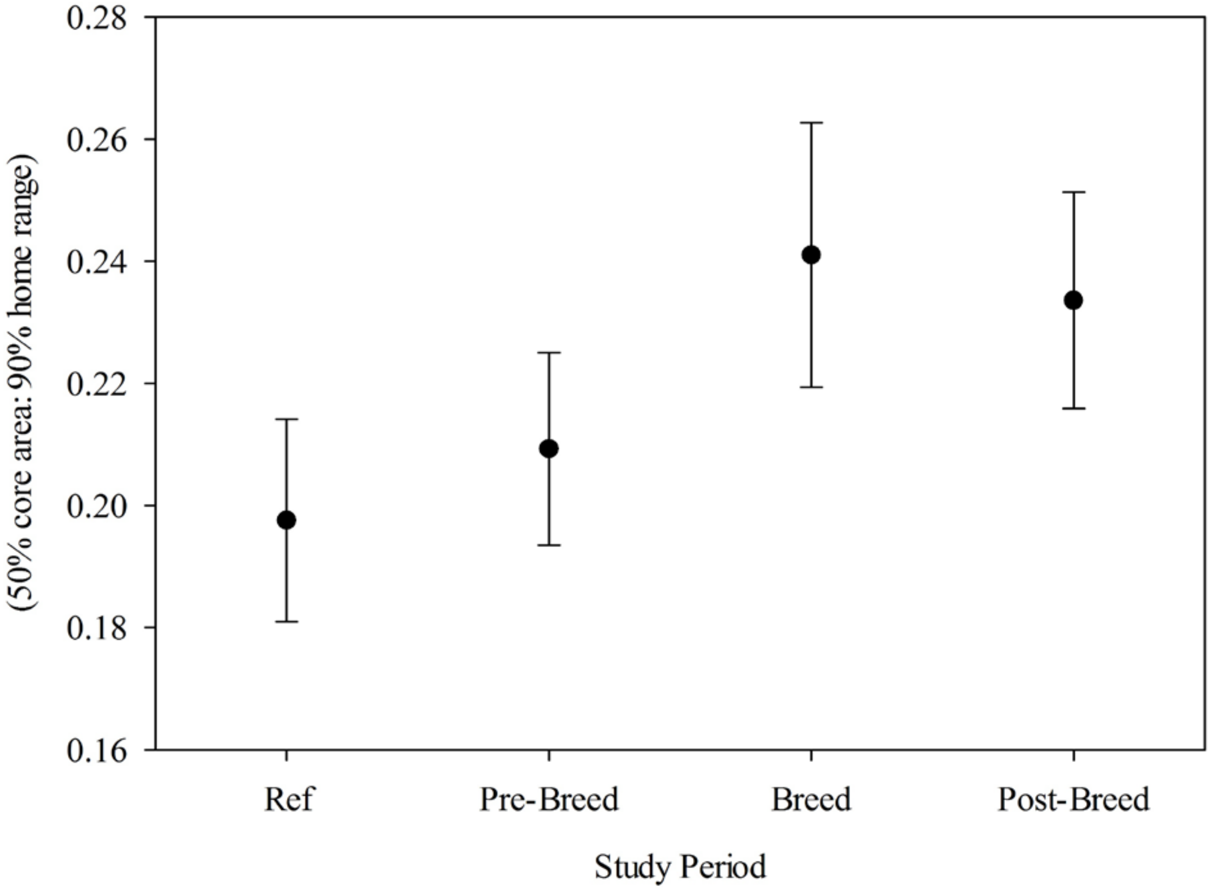


Figure 6. Mean daily movement (meters) within each study period for different age class male white-tailed deer at Three Notch Wildlife Research Foundation, Bullock County, Alabama, 2009–2011. Error bars represent 95% confidence intervals.

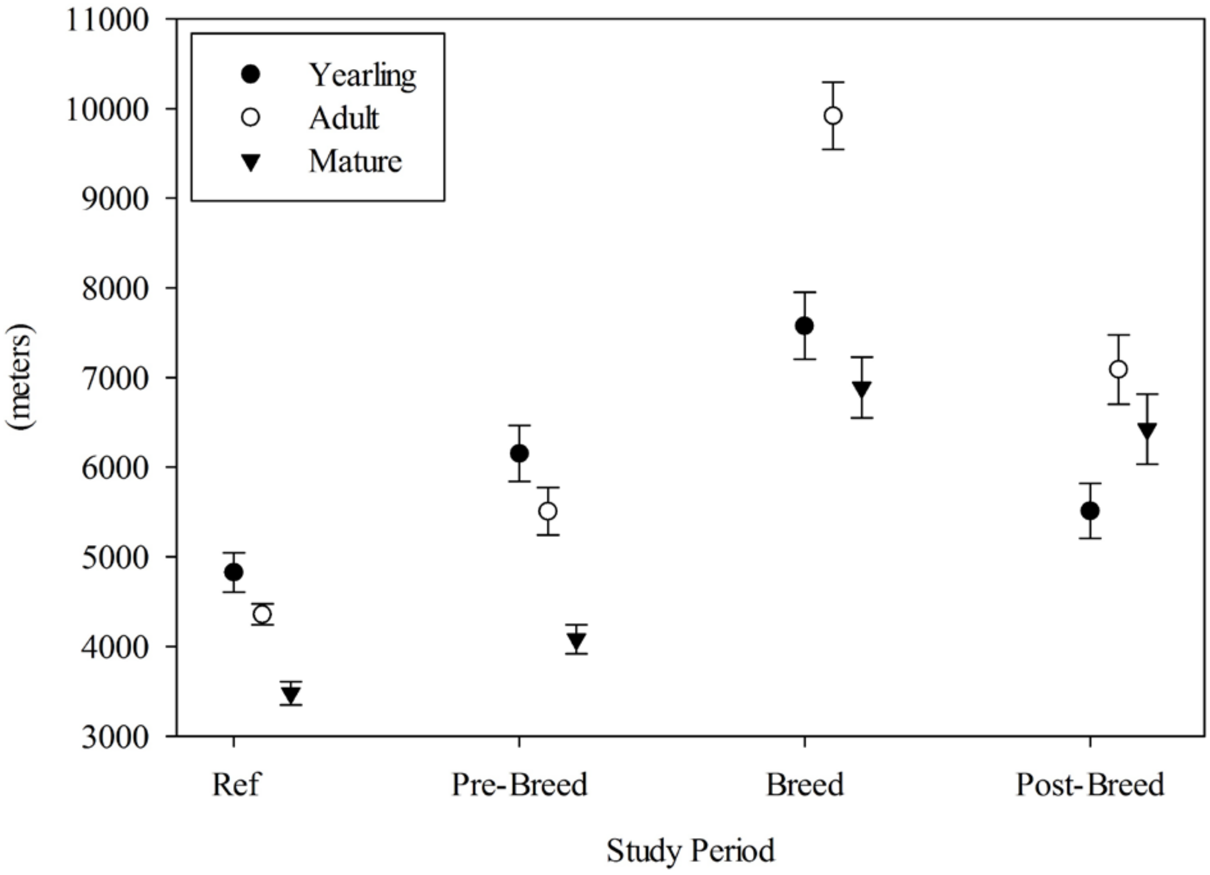
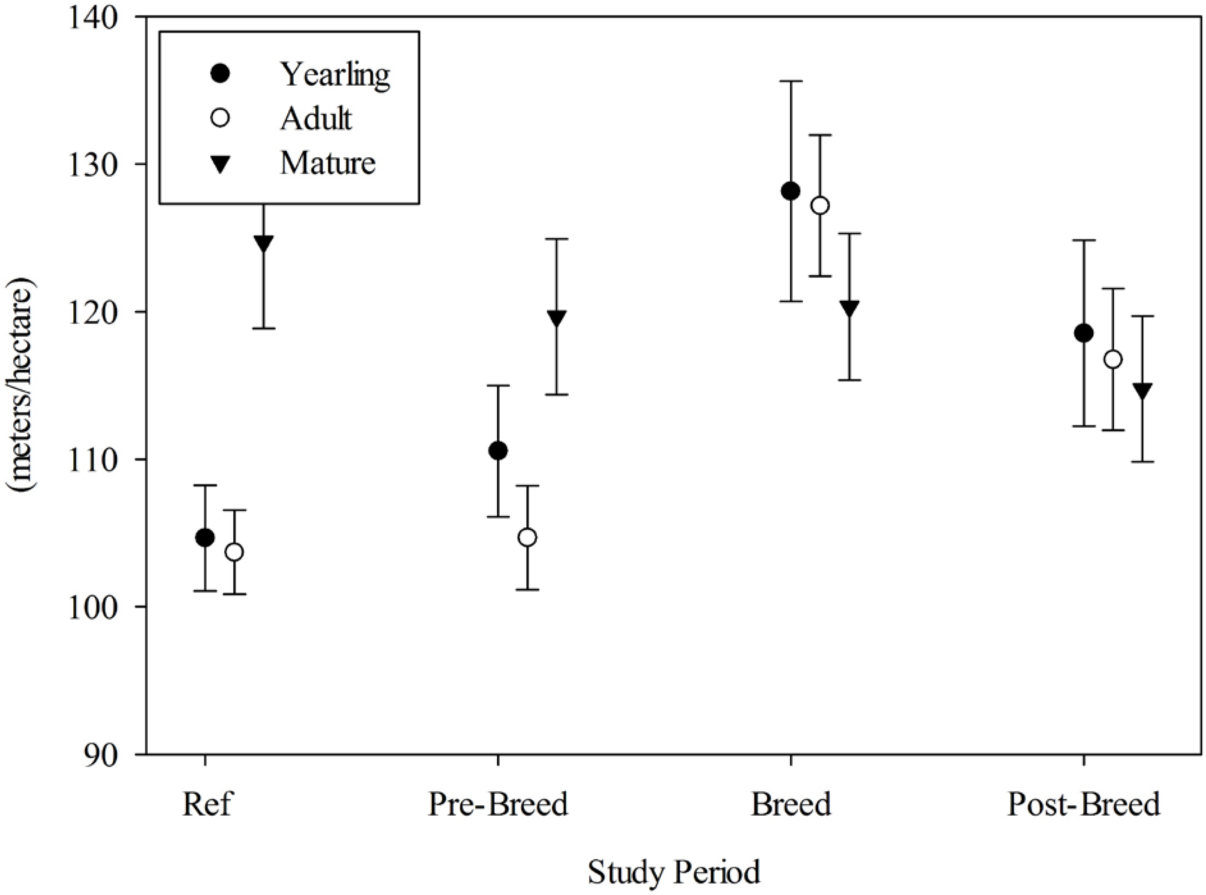


Figure 7. Mean search intensity metric (SIM) values (meters/hectare) within each study period for different age class male white-tailed deer at Three Notch Wildlife Research Foundation, Bullock County, Alabama, 2009–2011. Error bars represent 95% confidence intervals.



Antler Breakage Patterns in White-tailed Deer

Abstract

Antlers contribute greatly to the life history and ecology of most species in the deer family (Cervidae). Diet composition and quality, precipitation, age, antler size, dominance rank, and demographic parameters (e.g., adult sex ratio, density) of the population may explain variation in antler breakage rates between individuals and subpopulations. Our objectives were to examine the effects of some of these variables on probability of antler breakage and provide a general description of antler breakage patterns in white-tailed deer (*Odocoileus virginianus*). From 2001–2010, we collected 487 shed antlers from captive white-tailed deer managed at relatively high densities with a sex ratio skewed towards males. Overall antler breakage rate was 30% with approximately 51% of antlered males possessing $\geq$1 broken antler (at least one antler point or the main beam broken). Beam circumference ($\beta = -0.016$) and total number of antler points ($\beta = 0.169$) had the greatest effect on probability of antler breakage. The main beam and G2 antler point were least susceptible to breakage. No effect of seasonal precipitation was documented, but supplemental feed was available ad libitum possibly alleviating nutritional stress due to drought and reducing the effect of precipitation levels on antler breakage. The study provides a general description of antler breakage in a white-tailed deer herd and reaffirms that antler breakage is likely a byproduct of many interwoven individual antler, herd demographic, and environmental variables. From statewide agencies to individual properties, managers should consider how antler breakage patterns may affect harvest regulations based on antler characteristics and how management schemes designed to maximize trophy antler potential may be impacted.

Introduction

The ecology and behavior of white-tailed deer (*Odocoileus virginianus*) and most other cervids are inextricably linked to the family's most notable secondary sexual characteristic – antlers (Geist 1966). In a polygynous mating system, males must aggressively contend for females during the breeding season, and antler and body size are usually correlated with dominance (Geist 1966, Clutton-Brock 1987). Because antlers are used for intrasexual combat, the largest antlered individuals are often most successful in competition and may sire more offspring (Kruuk et al. 2002). Cervid antlers follow an annual cycle of growth, mineralization, and shedding with subsequent sets of antlers progressing in both mass and dimension. Mature males usually have larger antlers than younger animals, though antler size may decrease in post-mature, senescent individuals (Anderson and Medin 1969, Scribner et al. 1989, Stewart et al. 2000, Vanpe et al. 2007). Antler symmetry may convey individual genetic quality (Moller and Pomiankowski 1993, Ditchkoff et al. 2001); however, pedicle, antler, and body injuries may adversely affect antler development (Marburger et al. 1972, Hicks and Rachlow 2006). Antler breakage or malformation, whether it occurs in the growth (velvet) or mineralized (after velvet shedding) stages, could reduce a male's ability to compete and breed successfully (Espmark 1964, Lincoln 1972).

Though researchers have studied antlers in terms of their morphometry (McCullough 1982), composition (Miller et al. 1985, McDonald et al. 2005), density (Miller et al. 1985), break strength (McDonald et al. 2005, Landete-Castillejos et al. 2010), and growth processes (French et al. 1956, Scribner et al. 1989), no studies have examined patterns or rates of breakage in white-tailed deer antlers – an aspect of antler biology that potentially affects white-tailed deer management/harvest regulations and the evolutionary role of mate selection through quality advertisement (fluctuating asymmetry; Ditchkoff et al. 2001). McDonald et al. (2005) found that increased rainfall may affect the mineral composition of shed antlers and increase the force required to break antlers. Cowan and Long (1962) noted that antlers attain normal development when adequate rainfall produces plentiful summer forage. It is believed the ratio of spongy bone (spongiosa) to hard sheath greatly influences the propensity of antlers to break (Chapman 1980). Increasing the percentage of spongiosa enhances an antler's capacity to withstand the impact forces experienced during fights between male competitors (Chapman 1980). Miller et al. (1985) noted that the proportion of spongiosa increased in antlers with greater mass, and it was hypothesized that younger deer with smaller antlers should experience higher rates of antler breakage from a purely physical standpoint (a pattern followed by red deer [*Cervus elaphus*]; Lincoln 1972). The most mineralized portions of an antler (i.e., tines closest to the antler base and distal portion of individual tines) are the densest with the least spongiosa, and antlers were least dense in the portion of the main beam between the second and third tines (Miller et al. 1985).

McDonald et al. (2005) suggested that factors unrelated to the physical composition of antlers may better explain antler breakage rates within and between populations; reasons such as adult sex ratio, population density, nutritional deficiencies, and individual dominance and aggression levels were cited. Age-related differences in aggression and dominance may have an impact on the frequency of fighting among younger, smaller-antlered males versus older, larger-antlered males (Johnson et al. 2007*a*). Similarly, a population with an even sex ratio or high density of males may experience greater intensity of intrasexual competition and relatively greater antler breakage rates compared to a deer population with a sex ratio skewed towards females (McDonald et al. 2005). This dynamic may be exacerbated within enclosed deer populations where agonistic interactions may increase due to high mature male densities. Johnson et al. (2005, 2007a) described a population of tule elk (*Cervus elaphus nannodes*) that exhibited an antler breakage rate of 82% possibly due to nutritional deficiencies (Johnson et al. 2007*b*) - much greater than the proposed 5% average for members of the Cervidae family (Henshaw 1971).

Our objectives were to document the morphological patterns of antler breakage and correlate breakage to: 1) characteristics such as antler circumference and number of typical and total antler points and 2) precipitation. We hypothesized that antlers with greater basal circumference (i.e., higher spongy bone: compact bone ratio) would have greater resistance to breakage. However, we surmised that an equally plausible hypothesis was that despite possessing some antler traits resistant to breakage, large-antlered males would suffer greater breakage rates because of increased fighting bouts and having more points available to break. Also, we hypothesized that drier years would cause antler mass to be below average with less spongiosa and increase likelihood of antler breakage.

Study Site

Three Notch Wildlife Research Foundation (hereafter Three Notch) is a privately-owned property located 10 km east of Union Springs, Alabama. The study area encompasses 258.2 ha and has been enclosed by 3-m deer-proof fencing since 1997. Approximately 20% of the available habitat (48 ha) is farmed to provide deer with an array of both cool-season and warm-season forages. The remainder of the habitat is a matrix of loblolly pine (*Pinus taeda*) stands and mature hardwood forest. Prescribed fire is used each year in upland areas to facilitate searches for shed antlers as well as to provide natural browse for deer. Also, supplemental protein pellets

(20% protein) are available ad libitum throughout the year at permanent feeding stations distributed throughout the property (1 feeder/22 ha).

Shed antler collections began 4 years after the high-fence was erected in 1997. The initial population structure was skewed towards females, and yearling males comprised the majority of the male segment of the population. By 2001, the sex ratio became even (1 female:1 male) through aggressive antlerless deer harvest, and the number of individual males in mature age classes increased because bucks were protected from harvest for the initial 3 years following fence closure. Due to limited hunting success (archery equipment only), the selective harvest of the landowner, and an abundance of food sources, the enclosure became densely populated with a sex ratio favoring males. A mark-recapture camera survey (Jacobson et al. 1997) conducted in the fall of 2007 produced a density estimate with a minimum of 1 deer per 1.7 ha, which is more than 3 times the density normally found in this region, and an adult sex ratio of 2:1 (male:female; McCoy et al. 2011).

Methods

From April 2001 – June 2010, we collected shed antlers during both organized and opportunistic searches at Three Notch. We omitted antlers damaged by considerable rodent gnawing, decomposition, or accidental contact with farming equipment. By examining the weathering, color, and position of antlers in the forest duff layer, we included only antlers recovered within 6 months of shedding to ensure that all samples were correctly classified by year. With no way of knowing whether seemingly similar-looking right and left side antlers came from the same individual, we analyzed only left antlers to avoid pseudoreplication.

For each antler, we recorded calendar year of growth (different from year of collection), beam circumference (nearest mm), number of typical points, total number of points (included both typical and non-typical points), and whether the main beam and each point was intact or broken. All measuring was done by the same investigator to ensure consistency, and measurements were made using a 6.35 mm-wide metal measuring tape with mm markings. Beam circumference was measured at the narrowest point of the main beam between the antler base and the first typical antler point (same as H1 measurement of the Boone and Crockett measuring protocol; Ditchkoff et al. 2001). Typical antler points were those that originate upwards from the main beam and were numbered in sequence from the antler base to the end of the main beam, such that the G1 tine was the nearest antler point to the base. We considered a projection to be a point only if it measured at least 2.54 cm (1") in length and its length exceeded its width. Non-typical points were all other antler points (e.g., points originating from an already existing antler point, points originating from the main beam but pointing in a downwards or otherwise abnormal direction). "Broken" antlers had at least one antler point or the main beam broken in a transverse manner (Jin and Shipman 2010), and "intact" antlers did not possess any breaks. Beveled antler tips (i.e., chipped or slight wear caused by polishing), cracks, and other antler imperfections were not included as antler breakage because they did not affect the overall appearance or apparent function of the antler (Jin and Shipman 2010).

We obtained precipitation data from the nearest National Oceanic and Atmospheric Administration weather station in Troy, Alabama (42 km southeast; National Climatic Data Center 2010). Though we recovered shed antlers during the subsequent calendar year in which they were grown, we matched precipitation data to the year in which antlers were grown but not shed. We used logistic regression to explore the effects of annual and growing season (April – September) precipitation on the probability of antler breakage. Also, we used logistic regression (binomial response value of 1 = broken antler and value of 0 = intact antler) and evaluated a set of models relating the effects of total antler points, typical antler points, and beam circumference to probability of antler breakage and ranked models using AIC (Akaike's information criteria; Burnham and Anderson 2002).

To determine if certain antler points were more or less likely to break, we used logistic regression (binomial response value of 1 = broken antler tine and value of 0 = intact antler tine). We included antler tine (i.e., G1…G4) as a categorical variable and individual shed antler as a random effect. By examining the interaction term between number of typical antler points and individual antler tine, we could differentiate whether or not a G3 antler point was more likely to break when it was the leading tine on an antler with 4 typical points versus when it was protected by a G4 antler point on a shed antler with 5 typical antler points. Spikes and 6 point antlers were omitted from analysis due to low sample size ($n = 6$ and $n = 6$, respectively). Also, we used linear regression to examine the relationship between time (years 2000-2009) and variables beam circumference, total points, and typical points. We used Program R (R version 2.10.1, 2009) for statistical analyses, and α was considered significant at <0.05.

Results

We collected 487 shed antlers from 2001-2010 of which 147 (30%) exhibited antler breakage (Figure 1). The number of typical and total antler points remained similar between years. For the entire study period, mean number of typical and total antler points were 3.93 and 4.16, respectively. In 2000-2001, average beam circumference was 94.4 $\pm$ 1.4 mm ($\bar{x} \pm$ SE) and increased to 102.0 $\pm$ 1.7 mm during 2002-2009 ($F_{1, 485} = 20.11$, $P < 0.001$). Overall, beam circumference ranged from 45-174 mm, and the maximum number of typical and total points was 6 and 9, respectively.

The best model examining probability of antler breakage included beam circumference (model averaged $\beta = -0.016$) and total number of antler points (model averaged $\beta = 0.169$) – variables with negative and positive effects, respectively (Table 1). Typical number of antler points was a redundant subset of total number of antler points. Total number of antler points had a greater effect than typical antler points in the global model (all three antler variables included) and a greater relative importance weight (total number of antler points was 1.23 times as likely to be included in best model as typical number of antler points). The model containing only beam circumference and total number of antler points was best ($\mathrm{AIC_c} = 593.9$), though 2 additional models had $\mathrm{AIC_c}$ values within 2 $\Delta\mathrm{AIC_c}$ (Table 1). In the 3 top models ranked by $\mathrm{AIC_c}$ values, beam circumference was included in every model (relative importance weight = 0.91).

Neither annual precipitation ($\beta = -0.008$, $Z = -0.713$, $P = 0.476$) nor growing season precipitation ($\beta = -0.007$, $Z = -0.677$, $P = 0.498$) had an effect on annual probability of antler breakage.

Our analysis of antler breakage patterns indicated that G2 antler points were less likely to break than all other antler points. Probability of main beam breakage (0.043) was less than that experienced by all individual antler points except the G2 (0.060; $X^2_1 = 33.851$, $P < 0.001$; Figure 2). In analysis of whether or not specific antler tines were more prone to breakage dependent on number of typical points on the antler, the interaction effect was not significant. Though strictly typical antlers did not experience greater breakage than antlers possessing non-typical points ($X^2_1 = 0.068$, $P = 0.795$), typical points (0.110) were more prone to breakage than non-typical points (0.049; $X^2_1 = 6.999$, $P = 0.008$).

Discussion

Based on our overall reported antler breakage rate (30%), the estimated percentage of individual males with at least one broken antler would be 51% and is likely greater than for the majority of free-ranging populations. The white-tailed deer population we examined experienced considerable antler damage in relation to previous hypotheses made for family Cervidae (Henshaw 1971), though not as extreme as the aforementioned tule elk study (82%; Johnson et al. 2005). Our observations were comparable to antler breakage in another enclosed deer population (Ozoga and Verme 1982). The high density and male-skewed sex ratio of the study population probably increased the frequency of sparring and fighting matches between conspecifics. We expect that female-biased populations with fewer older males would have lower occurrence of antler breakage. Though the proportion of males suffering breakage may fluctuate significantly between populations due to different herd demographics, nutritional deficiencies, or behavioral differences, morphological breakage patterns (e.g., which points are most/least likely to break) should remain relatively constant.

We found that beam circumference and total number of antler points were the best predictors of antler breakage. Deer possessing antlers with greater numbers of antler points and smaller-diameter antlers experienced greater rates of breakage. Because basal circumference is positively correlated with age (Roseberry and Klimstra 1975), it may be that younger deer with above average number of total antler points are most prone to breakage. Older individuals with increased spongiosa due to larger-diameter antlers were able to better absorb forces experienced during breeding season behaviors. All antler points (except G2 point) break at similar frequencies, so antlers with 4 or 5 total antler points are at greater risk of antler breakage than antlers possessing 2 or 3 points simply because there are more opportunities for breakage to occur. Number of typical antler points (relative importance weight = 0.46) is also a good predictor of antler breakage though it is redundant to total number of antler points (relative importance weight = 0.57). Seemingly similar traits, the model averaged parameter coefficient for total number of points (0.169) was greater than that of typical number of antler points (0.088). Older males are more likely to have non-typical points (Ditchkoff et al. 2000); therefore, total number of antler points may have greater explanatory power because older males may be more likely to engage in fighting. Another possible explanation is that prominent non-typical points may induce abnormal torque or strain on antlers causing increased breakage rates.

In our study, precipitation levels did not have an effect on annual antler breakage rates, though, the effect of rainfall may have been masked because deer had year-round access to supplemental protein pellets. Even during growing seasons of low rainfall, precipitation levels are normally sufficient to produce adequate quantity of deer forage to maintain healthy antler growth in the Southeast (Shea et al. 1992; Bonner and Fulbright 1999). Conversely, white-tailed deer and other cervid species living in semi-arid climates may experience suppressed antler development (e.g., smaller-diameter antlers) during extended drought periods which may lead to greater antler fragility and increased rates of breakage because of decreased forage availability (Marburger and Thomas 1965, McDonald et al. 2005).

It would seem that the G1 antler point is the most protected of all antler tines; though functionally, the G1 antler point is designed to stop an opponent’s antlers from delivering a direct blow to the deer’s skull (Goss 1990). Therefore, it is surprising that the G1 antler point was as likely to fracture as a G3 or G4 antler point receiving the majority of direct blows during intrasexual conflicts and is not more resilient to breakage given its important role. Though it probably does receive less direct contact than other antler tines, the G1 antler tine is the most mineralized of all antler tines (Miller et al. 1985), and the shortage of spongiosa may be partially responsible for our finding that it is as likely to fracture as other tines. An antler's G2 point was least susceptible to breakage. The G2 antler point is usually the longest tine on a given antler and serves as the primary weapon when the deer's head is lowered towards a competitor (Allen 1901). Logically, the standard 4 or 5 point antler configuration of an adult white-tailed deer provides at least one leading antler point (G3 and/or G4 antler point) which may deflect away the impacts of fighting and protect the integrity of the G2 antler point at the expense of the G3 and/or G4 point being broken. Interestingly, our analysis revealed that G4 points did not reduce the corresponding G3 antler point's likelihood of antler breakage in 5 point antler configurations.

Main beams experienced less breakage than antler points. In addition to preserving the basic functionality of the antler, the main beam and G2 antler point are the most visually prominent features of a lateral antler profile - a critical component for how males assess the quality of their competitors (Ditchkoff et al. 2001). White-tailed deer antlers develop several months before the onset of the breeding season, and asymmetry due to antler breakage could indicate a male's poor competitive ability to rival males and potential mates alike. Though the theory of fluctuating asymmetry is primarily driven by how evenly both sides of a bilateral ornament is developed by an individual, antler breakage may be another mechanism of how quality is conveyed between competitors. Intense white-tailed deer management schemes leading to unnaturally high breakage rates could potentially shift gene flow away from males possessing antlers that are susceptible to breaking if female mate selection is at least partially predicated on male quality advertisement through antlers (Ditchkoff et al. 2001).

The shed antlers collected during the first 2 years of the study had smaller dimensions than those collected later. Because the high fence was erected in 1997, the number of mature males (≥5.5 years old) possessing antlers that reached their full potential did not stabilize until at least 2001. Interestingly, antler breakage peaked at 43% in 2002. Though purely speculative, perhaps fighting may have increased in frequency due to the growing population density of mature males and the relative scarcity of breeding females as compared to previous years. Ozoga and Verme (1982) documented a similar pattern where antler breakage increased from virtually nothing to a rate of 34% as the density of adult males increased in a captive white-tailed deer herd. Their findings lend additional evidence that herd demographics play an important role in antler breakage.

Breakage is likely a byproduct of the antler's characteristics, the individual's behavior and social status, demographics at the subpopulation level, and possibly external environmental variables. The general patterns of antler breakage that we reported for a high density, male-dominated population further describe the intricacies of Cervidae weaponry and provide a different perspective for the oft observed (Henshaw 1971), yet seldom studied phenomenon of antler breakage in white-tailed deer. Our results suggest that food supplementation may alleviate antler breakage in years of drought when antler circumference may otherwise decrease because of limited resources and reduced antler growth. White-tailed deer managers (especially where trophy antler quality is a primary objective) should be aware that as management intensity increases, increased probability of antler breakage may be a concurrent consequence – an important detriment to the goal of maximizing trophy antler potential. Lastly, state agencies that place antler point harvest restrictions (e.g., Pennsylvania; Norton et al. 2012) on male white-tailed deer should understand how antler breakage patterns can potentially reduce the number of eligibly harvested males in a population, thereby affecting harvest goals.

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Table 1. Factors influencing the probability of white-tailed deer antler breakage, Three Notch, Alabama, 2000–2009.

Model	No. parameters	ΔAIC_c[a]	AIC_w[b]
S (beam circumference + total antler points)	3	0.00	0.374
S (beam circumference + typical antler points)	3	0.652	0.270
S (global model - all 3 parameters)	4	1.667	0.163
S (beam circumference)	2	2.507	0.107
S (constant)[c]	1	4.598	0.038
S (total antler points)	2	5.559	0.023
S (typical antler points)	2	6.390	0.015
S (total antler points + typical antler points)	3	7.314	0.010

[a] Difference between model's Akaike's Information Criterion corrected for small sample size and the lowest AIC_c value.

[b] AIC_c relative weight attributed to model.

[c] Model of no effects on probability of antler breakage.

Figure 1. Annual antler breakage rates calculated from white-tailed deer shed antlers, Three Notch, Alabama, 2000–2009 (error bars represent SE).

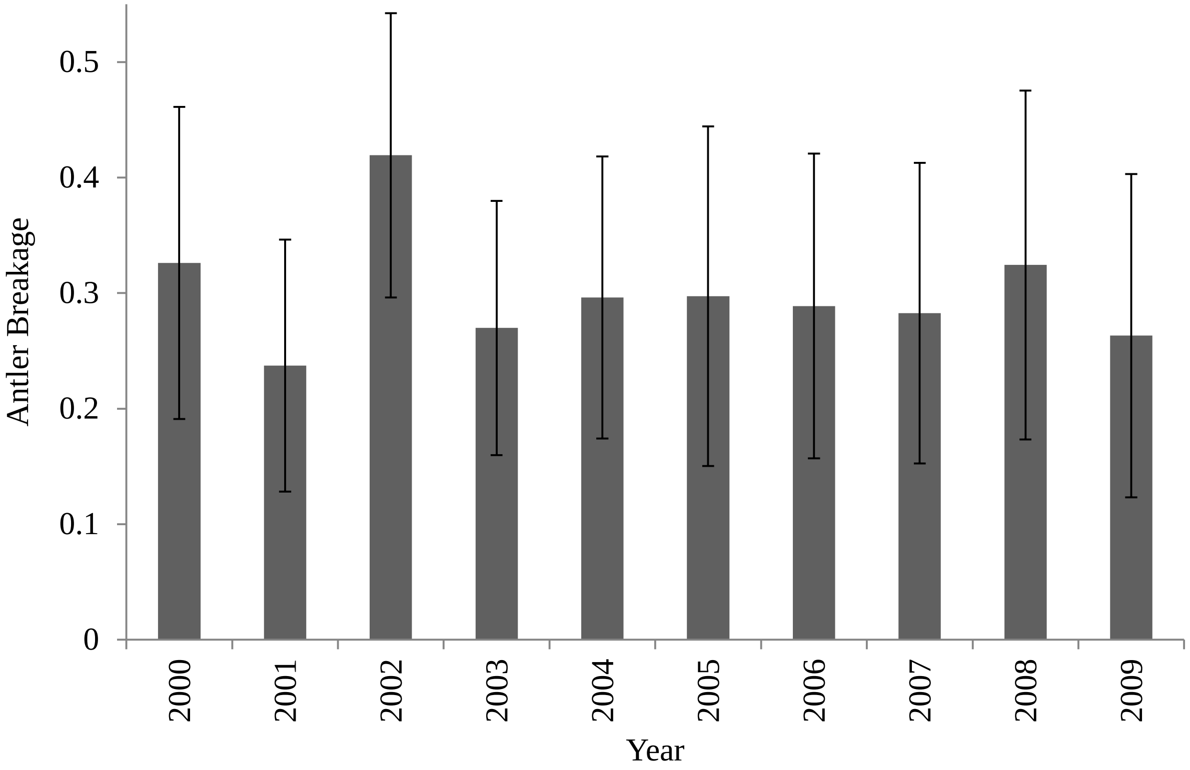
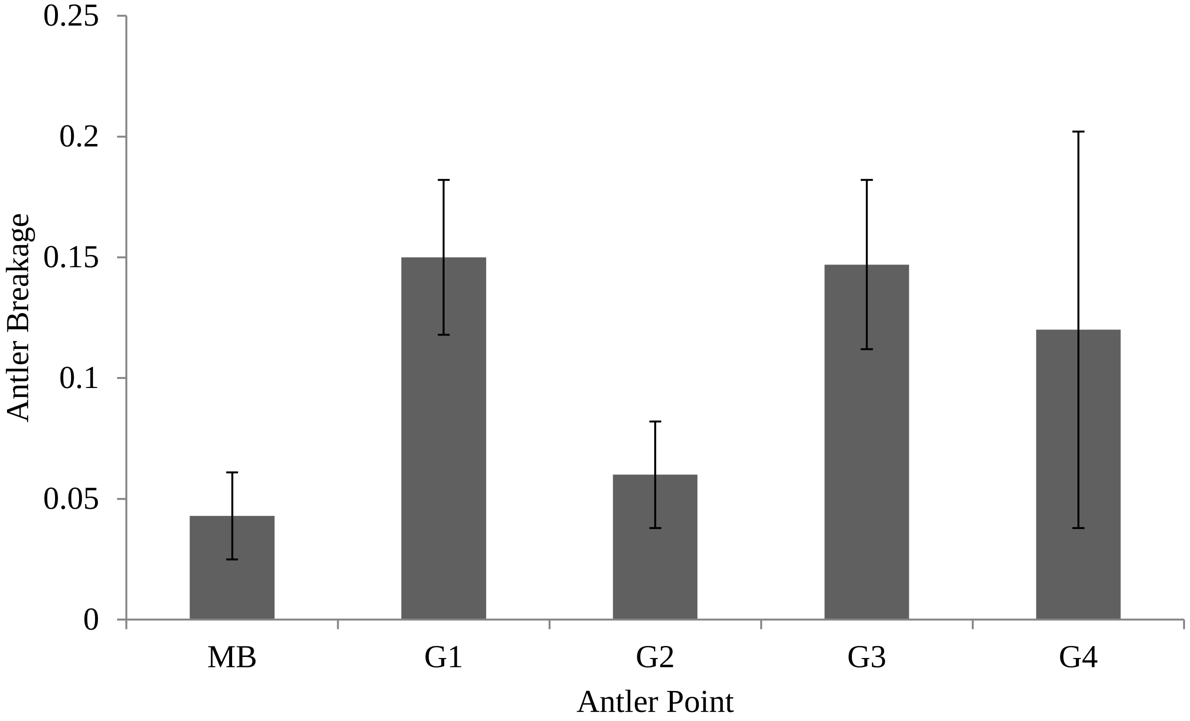


Figure 2. Antler breakage rates for main beam and individual antler points of white-tailed deer shed antlers, Three Notch, Alabama, 2000–2009 (error bars represent SE).



Trauma-induced Malformed Antler Development in Male White-tailed Deer

Abstract

Though normal antlers are branched and bilaterally symmetrical, male white-tailed deer (*Odocoileus virginianus*) sometimes develop malformed antlers. As management for antler quality has grown more popular in recent years, there has been concern that spike-on-one-side (SOOS) antler configuration has a genetic cause. We hypothesized that the majority of SOOS antlers are the artifact of injuries to the antlerogenic periosteum region. We collected 71 SOOS specimens over 2 hunting seasons (2010–2011 and 2011–2012) in Alabama, USA, and identified probable cause for malformed antler development. We confidently assigned cause to 62% of specimens, and frequency of skull and/or pedicle trauma increased with age classes (yearling, 2.5-yr-old, and ≥3.5-yr-old M). It was difficult to determine the reason that yearling males developed SOOS antler traits (30%), but ease of prescription increased with male age (76% for ≥3.5-yr-old M). Based on the physiology of skull and/or pedicle versus skeletal injuries, we recommended different culling strategies for yearling versus adult male white-tailed deer according to management objectives.

Introduction

Antlers of family Cervidae are one of the most intensely studied secondary sexual characteristics in the animal kingdom. Normal antler configuration of ungulate species is bilaterally symmetrical with small side-to-side inconsistencies that have led to many debates regarding the role of fluctuating asymmetry and male quality advertisement and mate choice in recent years (Møller 1990, Ditchkoff et al. 2001, Bartoš et al. 2007). However, more severe antler aberrations may result from endocrine system imbalances (Bubenik et al. 2001), gonadal trauma (Penrose 1924), nutritional deficiencies (Gogan et al. 1988, Johnson et al. 2007), skeletal injuries (Marburger et al. 1972, Davis 1983), and/or pedicle damage (Rachlow et al. 2003).

White-tailed deer (*Odocoileus virginianus*) typically develop matching antlers with 3 or 4 antler points originating from the dorsal side of a curved main beam. To establish terminology, our research focuses on an abnormal antler configuration that we refer to as spike-on-one-side (explicitly defined in ‘Materials and Methods’ below). The notion that spike-on-one-side antlers in white-tailed deer are the product of inferior genotypes has been embraced by many within the public, and belief that those defective individuals should be culled with the objective of improving the residual genetic quality of the population is common. Genotype has an influence on antler development but only so much as dictating species-specific antler configurations and determining an individual’s relative size within populations (Scribner et al. 1989, Suttie 1990, Hicks and Rachlow 2006), and antler abnormalities are usually a product of the environment (Penrose 1924, Marburger et al. 1972, Davis 1983, Rachlow et al. 2003).

With a central objective of understanding why spike-on-one-side antlers occur in white-tailed deer, we made 2 preliminary observations during the past decade that led us to hypothesize that the primary cause of spike-on-one-side antlers in white-tailed deer was physical trauma to the skull and/or pedicle: 1) many skulls from spike-on-one-side white-tailed deer had damage to the pedicle or immediately surrounding region; and 2) on the occasion that a male white-tailed deer cast an antler irregularly (casting occurs earlier than normal and possesses a chunk of pedicle or skull attached to the antler base), the damaged pedicle usually grew an abnormal antler the following year. Because white-tailed deer are the most popular big game animal in North America and management becomes more intensive with each passing year, this study’s results will be of particular interest to not only wildlife managers across the nation, but to the general public as well.

Materials and Methods

From October to January 2010–2011 and 2011–2012, we collected antlers from hunter-harvested white-tailed deer with spike-on-one-side antler configurations that were harvested on public hunting wildlife management areas and privately owned or leased recreational properties in Alabama, USA. We defined spike-on-one-side antlers as having ≥50% side-to-side difference in gross typical Boone and Crockett score (Ditchkoff et al. 2001) or a typical antler-point differential of ≥2 points (Fig. 1). Typical antler points are those that originate upward from the main beam and measure ≥2.54 cm in length (Wright and Nesbitt 2003). Though a complete necropsy of each deer would have been ideal (as has been done in one previous study; Marburger et al. 1972), logistical and budgetary constraints dictated that an intact skull or skull cap (≥2.54 cm of bone in all directions from both pedicles) suffice. Participants recorded year and county of harvest, categorized ownership of the property where the specimen was harvested, and noted any apparent injuries or abnormalities of the deer (e.g., broken leg or old gunshot wound). After removing all soft tissue from each sample using bicarbonate of soda (sal soda; Church and Dwight Co., Inc.; Ewing, NJ) and boiling water, we estimated deer age (tooth replacement and wear; Severinghaus 1949), recorded number of typical antler points per side, and categorized any damage and/or abnormalities as skull and/or pedicle trauma (e.g., signs of callus tissue around pedicle or intercranial sutures or fractured pedicle; Fig. 2), deformed pedicles (e.g., no apparent injuries but one pedicle obviously smaller in diameter than another or existing away from normal location), or other anomalies (e.g., intracranial and/or subcutaneous abscesses, supernumerary pedicles). Breakage during hard antler (e.g., transverse fracture of the antler main beam) and damage sustained during velvet development (described in Jin and Shipman 2010) were readily identifiable and noted accordingly. All samples were returned to study participants post-examination.

Results

We obtained 29 samples in 2010–2011 and 42 samples in 2011–2012 for a total of 71 spike-on-one-side antler samples. The vast majority came from private lands (N = 64), with the remainder coming from Cahaba River Wildlife Management Area (N = 4), Barbour County Wildlife Management Area (N = 2), and Lowndes County Wildlife Management Area (N = 1). Eighteen Alabama counties were represented, with Tuscaloosa and Bullock counties contributing the greatest number of samples (with 11 each). Counting only typical points, right antlers possessed a mean of 2.51 points and left antlers carried 2.45 points; we detected no directional asymmetry (t_{70} = 0.22; P = 0.83). In total, we assigned probable cause of spike-on-one-side antler formation for 3 of 10 (30%) yearling, 9 of 20 (45%) 2.5-year-old, and 31 of 41 (76%) ≥3.5-year-old males.

For the yearling males, we detected no instances of skull and/or pedicle trauma, deformation of pedicles, or other anomalies. We could not ascribe probable cause for 7 of the 1.5-year-old spike-on-one-side samples, and the remaining 3 were simply due to hard antler breakage.

For 2.5-year-old males, we documented a single case each of breakage during hard antler and velvet development. Two males sustained intracranial abscesses in which the sutures connecting the parietal and frontal bones had been eroded (Karns et al. 2009). In one case, the cranial sutures had been replaced by a layer of callus tissue; this suggested that either the previous year’s pedicle had cast irregularly and subsequently healed, or that the animal had sustained injury from an intrasexual competitor or its external environment. Another male had a subcutaneous abscess posterior to the right pedicle, yet the skeletal integrity of the skull and/or pedicle had not been damaged (as in the case of a true intracranial abscessation). If the abscess was present during early antler development, it certainly could have impeded normal antler growth on that side. Two males had noticeable differences in pedicle diameter—the pedicle from which the spike-on-one-side antler developed was smaller than the normal pedicle in one case, but the pattern was reversed in the other specimen. The last 2 2.5-year-old males that we were able to assign probable cause for spike-on-one-side antler formation had both skull and/or pedicle damage and malformed pedicles.

We detected spike-on-one-side inducing injuries or abnormalities in 31 of the 41 ≥3.5-year-old males. In 14 cases, portions of the cranial sutures and/or skull (frontal and/or parietal bones) sustained damage and pedicles were malformed or misshapen. Three of these specimens showed symptomatology of intracranial abscessation. Seven additional males sustained damage restricted to the skull and not affecting pedicle structure. Another 5 samples possessed malformed pedicles but suffered no apparent injuries to the actual cranium. Lastly, we documented several ≥3.5-year-old males with anomalies not fitting into one of the aforementioned categories—1 sample with pedicle located on the lateral side of the cranium, 1 specimen missing portions of the nasal and frontal bones due to prior trauma, 2 cases of accessory pedicles (Bubenik and Hundertmark 2002), and 1 case of ‘double-head’ antler formation (Kierdorf et al. 2004).

Discussion

Pedicle damage or trauma to the frontal and/or parietal bones was the leading cause (*N* = 34) of spike-on-one-side antlers in our study. From a strict physiological perspective, pedicles develop as permanent protuberances of the frontal bones and the antler development region is inclusively termed the antlerogenic periosteum (Goss 1995, Kierdorf and Kierdorf 2001*a*, Li et al. 2009), though the exact boundary of the antlerogenic periosteum is not clear. Pedicle damage can take many forms—irregular antler casting due to insufficient osteoclast resorption (Rachlow et al. 2003, Price et al. 2005); incomplete development of the pedicle (Kierdorf and Kierdorf 2001*b*); damage especially to the lateral portion of the pedicle where the blood vessel supply is located (Goss 1961, Jaczewski 1990); damage to the nerve endings of the pedicle (Wislocki and Singer 1946, Bubenik and Pavlansky 1965, Suttie 1990, Li et al. 1993)—but the result is generally the same for all these forms, suppressed antler development. We did not attempt to differentiate between these injuries, but rather, we lumped all pedicle damage into a single category. Anecdotally, there is evidence that cast antlers with a residual portion of pedicle and/or skull material have a high probability of developing spike-on-one-side antler characteristics in the subsequent year (Rachlow et al. 2003), and that males already possessing spike-on-one-side antler traits commonly cast antlers with fractured pedicles. We termed antler bases with portions of the skull and/or pedicle still attached—'dirty sheds.'

Our study could not identify probable cause for 27 specimens, but that number would likely decrease if we had been able to conduct rigorous necropsies and examine more than just the skull of each specimen. Of 32 Texas (USA) white-tailed deer harvested with abnormal antlers, Marburger et al. (1972) documented 22 instances (69%) of old gunshot wounds or healed leg fractures. In mule deer (*O. hemionus*), Robinette and Jones (1959) associated abnormal antler growth in males with foreleg, hindleg, rib, and/or mandible injuries. With more rigorous protocol in our study, one can surmise that at least several, if not many, of the 27 deer without obvious skull and/or pedicle injury experienced past injury to other regions of their bodies.

Considering the results of our study with the Marburger et al. (1972) paper, it does not appear likely that genotype plays a major role in spike-on-one-side antler development in white-tailed deer. Spike-on-one-side antlers in elk (*Cervus elaphus*) are overwhelmingly due to damaged or abnormal pedicles (Rachlow et al. 2003) and underlying genetic causes were not identified (Hicks and Rachlow 2006), lending further support to our assertions. Those studies being noted, we do acknowledge the possibility that skull and/or pedicle injuries may be genetically linked to the individual's underlying physiology (e.g., bone density, antler or bone mineralization); however, our approach did not examine this aspect because we felt it had been adequately addressed in the cervid research cited above. Also, another non-genetic potential cause of spike-on-one-side antlers—gonadal trauma—was not considered in our study (Penrose 1924).

Within age classes, it was particularly difficult to ascertain the reason that yearling males developed spike-on-one-side antler formations. Other than the 3 instances of hard antler breakage, we did not ascribe probable cause to any other 1.5-year-old specimens. Though a portion of 6-month-old males do grow small, immature antlers (usually ≤2.54 cm long; Waldo and Wislocki 1951), they are not prone to engage in breeding season activities such as intrasexual combat, thereby lessening the chance of incurring skull and/or pedicle injury that would lead to spike-on-one-side antlers in the following year. Rather, we surmise that some spike-on-one-side antlers in yearling males may have been due to skeletal injuries. Prior research suggests that antler abnormalities due to skeletal trauma (Marburger et al. 1972) have a good chance of returning to normalcy during subsequent years, or at least lessening the severity of the abnormality; though spike-on-one-side antlers may be more permanent if the skeletal injury is a limb amputation (Davis 1983). Conversely, abnormal antlers due to cranial injury (skull or pedicle) often re-aggravate because clean separation during antler casting is unlikely. This causes additional damage and leads to a greater chance of permanency (Kierdorf et al. 2004); in fact, spike-on-one-side antlers stemming from skull and/or pedicle trauma sometimes get progressively worse in successive seasons of antler development due to repeated injuries (Kierdorf et al. 2004). Based on our findings that most yearling abnormalities likely arise from non-cranial injuries, we recommend that yearling white-tailed deer not be culled for management purposes because immature male white-tailed deer are likely to develop normal antlers in the future.

For the majority of older-age-class males, obvious skull and/or pedicle injuries made it much simpler to ascertain cause of spike-on-one-side antlers, and we determined probable cause for 45% of 2.5-year-old males and over 75% of ≥3.5-year-old males. Logically, the more antler-growth cycles a white-tailed deer undergoes the greater the probability of sustaining significant damage to the skull or pedicle. In adult white-tailed deer, skull and/or pedicle damage is likely to be sustained through breeding activities such as fighting with conspecifics and rubbing trees (Bubenik et al. 2001). When the antlerogenic periosteum is damaged, the pedicle may lose some of its structural integrity and strength, and during the healing process becomes fused with portions of the surrounding cranial region; this virtually ensures additional damage when antler casting occurs again (mechanism of re-aggravation; Kierdorf et al. 2004). Because far more antler abnormalities in older-age-class males are due to skull and/or pedicle trauma and these types of injures tend to re-aggravate (Kierdorf et al. 2004), spike-on-one-side antlers are more likely permanent and repeated in subsequent years (Figs. 3 and 4), indicating that culling individuals may be a more reasonable management practice in environments where trophy antler quality is a primary objective (Goicea and Dănilă 2009). In addition, brain abscess symptoms sometimes correspond to spike-on-one-side antlers ($N = 5$), and afflicted individuals are already predisposed to mortality by natural causes (Karns et al. 2009). However, in situations where herd numbers are well below carrying capacity and the male age structure of the population is underdeveloped, preserving mature males regardless of antler configuration may benefit herd health through stabilization of the breeding season (Miller and Marchinton 1995).

Though infrequent in our results, other injuries and their effects on antler development bear mentioning. Across age classes, we documented 4 cases of hard antler breakage (Karns and Ditchkoff in press) and a single instance of damage incurred to a developing antler main beam in a 2.5-year-old male. Antler development emanates primarily from the apical portion of each antler branch, and injury to that portion of the velvet antler virtually terminates further growth (Goss 1961, Suttie and Fennessy 1985). Surprisingly, injuries sustained during velvet antler development are often 'remembered' in subsequent sets of antlers—a phenomenon coined trophic memory by Bubenik and Pavlansky (1965)—though the abnormality is usually progressively forgotten as years pass (Bubenik 1990). Also, we observed a rare occurrence of double-head antlers in a ≥3.5-year-old male where old antlers failed to cast (presumably because of insufficient osteoclastic resorption; Kierdorf et al. 1994) and new antlers developed abnormally from the grossly enlarged, lateral outside portions of both pedicles (Kierdorf et al. 2004). We examined 2 separate cases of accessory pedicles both occurring in ≥3.5-year-old males (Jaczewski 1990, Bubenik and Hundertmark 2002). In each occasion, the accessory pedicle was located anterior to the normal pedicle on only one side of the cranium, and on that side the normal antler was significantly shorter in length than the opposite side. One accessory antler measured 4 cm in length while the other measured nearly 12 cm in length and possessed 3 total antler points. Moderate callus of the antlerogenic periosteum surrounding the base of the supernumerary pedicles indicated that prior damage to the skull and/or pedicle had instigated their eruption (Jaczewski 1990, Bubenik and Hundertmark 2002). The final noteworthy exception was a mature spike-on-one-side male with such severe damage to the cranium that portions of the nasal and frontal bones were completely missing, yet the antlerogenic periosteum appeared intact. The animal was in good health when harvested, but the injuries surely impacted its ability to grow normal antlers (Robinette and Jones 1959).

Management Implications

Managers should note that malformations usually negatively affect only one side of the animal's antlers, leaving the normal half for one's assessment of its true genotypic antler make-up. The value of a management system placed on trophy-antler quality at maturity and the population's relationship to carrying capacity should dictate culling decisions for yearling and adult spike-on-one-side males.

Acknowledgments

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Figure 1. These 4 skulls accurately demonstrate the definition of spike-on-one-side antlers in white-tailed deer, as defined in the Materials and Methods.

Figure 2. Characteristic damage sustained by spike-on-one-side male white-tailed deer antlers posterior to the base of the right pedicle and surrounding cranial region.

Figure 3. Though this particular white-tailed deer was not included in the formal analysis of the study (deer still alive as of manuscript submission), photographs of Deer no. 817 at Auburn University's Deer Lab (AL, USA) illustrates the progression of spike-on-one-side antlers from 1.5 to 3.5 years old. See Figure 4 for close-up photograph of Deer no. 817's damaged pedicle at age 1.5 years.

Figure 4. At age 1.5 years, white-tailed Deer no. 817 at Auburn University's Deer Lab sustained pedicle damage when the antler was broken off 2 months prior to normal antler casting, Auburn, Alabama.

Maternal Life History of White-tailed Deer: Factors Affecting Foetal Sex Allocation, Conception Timing, and Senescence

Abstract

Maternal life history is complex and likely affected by a variety of factors. We examine how maternal condition and environmental factors affect aspects of maternal life history in white-tailed deer (*Odocoileus virginianus*). We used reproductive tract data collected from 1995 to 2011 to evaluate the effects of maternal age, mass, and other factors on foetal sex ratio allocation, conception timing, and reproductive senescence. Female body condition did not significantly affect foetal sex ratio allocation, but conception timing was significantly associated as females conceiving further from the peak window of breeding were more likely to produce daughters. This result differs from previous studies that have supported the Trivers-Willard or Local Resource Competition hypotheses. Conception timing was related to female age, mass, and an interaction between these variables. We found evidence for reproductive senescence in female white-tailed deer, a phenomenon associated with variables female age, age^2, and mass.

Introduction

Maternal life history can be viewed as a series of complex choices involving tradeoffs among known costs, unknown risks, and guaranteed benefits, with the goal being to maximize fitness. Based on one’s attributes and environmental conditions, different strategies may be used to achieve this goal. Theoretically, each breeding episode constitutes another choice, and physiological condition influences whether or not a female may be capable of producing and, in some species, supporting offspring. Tradeoffs may be intra-individual or inter-generational; tradeoffs may affect not only the maternal individual but also the offspring produced (Stearns

1989). Females may achieve greater fitness by successfully producing more males than females, as dominant males usually provide the greatest fitness return to mothers, but only if those males are likely to be successful breeders (Trivers and Willard 1973, Clutton-Brock et al. 1981). However, there is a cost to producing males, as males often require more resources to produce (Clutton-Brock et al. 1981). Therefore, condition is thought to affect not only whether offspring are produced, but how many and which sex. Condition may also affect when offspring are produced, as individuals in better condition often breed earlier than those in poor condition (Clutton-Brock et al. 1981). Each female should follow the tactic which best suits her current condition and the resources available at each breeding opportunity that maximizes her fitness. Foetal sex allocation, optimal timing of litter conception, and declines in fecundity associated with senescence are important aspects of maternal life history strategy and have evolutionarily significant effects at the population level.

The number of males and females in a litter of offspring should be influenced by attributes of the mother or the environment. For example, Trivers and Willard (1973) proposed that females in good condition should have male-biased litters because investment in more expensive males would result in a greater increase of her indirect fitness through future reproductive success of a dominant son. On the other hand, poor condition females should reproductively invest in more daughters because their reproductive success is less dependent on maternal condition than a son that would have to compete with physically advantaged males for breeding opportunities. Data from numerous Cervid species have shown support for the Trivers-Willard hypothesis [red deer (*Cervus elaphus*) - Clutton-Brock et al. 1984; elk (*Cervus canadensis*) – Kohlmann 1999; mule deer (*Odocoileus hemionus*) – Kucera 1991; white-tailed deer (*Odocoileus virginianus*) – Burke and Birch 1995; reindeer (*Rangifer tarandus*) – Kojola and Eloranta 1989]. However, patterns of foetal sex ratio allocation are by no means fixed. A major opposing hypothesis (Local Resource Competition; Clark 1978) posits that the gender composition of litters are more strongly influenced by abundance of local resources with mothers in good condition investing more heavily in daughters, females in poor condition giving birth to more males (Caley and Nudds 1987). This directly opposes predictions of the Trivers-Willard hypothesis, but the Local Resource Competition hypothesis reasons that because males are the dispersing sex, a mother residing in areas of low resource abundance gains more by producing the gender (males in many species; white-tailed deer – Rosenberry et al. 1999) that is more likely to disperse from its natal range (Clark 1978, Hewison and Gaillard 1996).

To complicate our understanding of the effects of maternal condition and local resource abundance on foetal sex ratio allocation, timing of conception within the breeding season also is correlated with maternal condition and local resource abundance, but is itself a life history strategy. Depending upon when conception occurs within a breeding season, timing of parturition may greatly influence either resources available to neonates both through direct forage intake, or indirectly through maternal condition and lactation quality (Rutberg 1987) or risk of predation (Estes 1976). Consequently, older females in better condition usually conceive in the early and peak stages of the breeding season with young adults and juveniles producing the bulk of late-born litters, balancing reproductive investment with maternal somatic growth and maintenance costs (Adams and Dale 1998, Holand et al. 2006, Kohlmann 1999, Ditchkoff et al. 2009). With respect to foetal sex ratio allocation, early and peak conception mothers are more likely to invest more heavily in sons that may have a physiologically competitive advantage along with a reduced chance of juvenile mortality due to predator swamping (obviously, more synchronous parturition/conception maximizes this latter effect; Estes 1976). Conversely, juvenile mothers conceiving later in the breeding season would likely maximize their indirect fitness with daughters that are much more likely to successfully reproduce, and direct fitness by producing the offspring that require the lest investment (Ditchkoff et al. 2009). So, it is not known if foetal sex ratio allocation is directly due to mother's condition and local resource abundance, or primarily due to timing of conception, which itself is correlated with mother's condition and local resource abundance.

If population survival rates allow females to progress through prime-aged adulthood and enter senescence, the dynamics of foetal sex ratio allocation and reproductive investment change. Simply stated, senescence is a decline in reproductive, vital, or survival rates with increasing age of an organism (Berube et al. 1999, Ericsson et al. 2001, Gaillard et al. 1994). Fuller et al. (1989) reported senescent white-tailed deer females had similar mass to sub-adult females, indicating a post-prime decrease in body mass likely resulting in reduced litter size but not necessarily a bias towards female or male offspring (Weladji et al. 2002). Little to no other data exist that examine foetal sex ratio in relation to senescent reproduction by females. Reproductive senescence can take other forms including, decreased ova production leading to decreased litter size, decreased litter size due to increased resorption rates, and decreased litter survival due to reduced parental investment (Hewison and Gaillard 2001). While distinguishing between the two causes of decreased litter size may be difficult, especially on studies of wild populations, a reduction in litter size due to either cause would demonstrate reproductive senescence within the species.

Using a large sample of white-tailed deer, the main objective of my study was to examine how foetal sex ratio varies as a function of age and condition of mother, litter size, timing of conception, and regional variation (putatively due to variation in resource abundance). To test the Trivers-Willard and the Local Resource Competition hypotheses, we predicted condition of the mother would be the most significant variables affecting foetal sex ratio. We hypothesized that due to the complex nature of maternal life history, foetal sex ratio may also be affected by other variables such as age, litter size, timing of conception, and regional variation. Also, we explored the relationship between date of conception and maternal mass (condition) and age, and examined if litter size varied as a function of maternal age, condition, and timing of conception. We expected that older does would conceive before younger individuals and heavier individuals would conceive before lighter ones. We also expected that litter size would primarily be a function of maternal age and condition, with age having a curvilinear effect; both young and old individuals would produce smaller litters than average age individuals. This research is valuable because we thoroughly evaluate the relationship between aspects of maternal life history and the possible variables affecting them using a long-term, state-wide dataset collected on deer reproduction in Alabama. These data provide a unique opportunity for testing the above expectations, because data were collected randomly (not hunter harvest) from wild populations over a large temporal and spatial scale. The large temporal and spatial scale helped mitigate issues of variation in local resource abundance, while the large dataset allowed us to discern which physical variables were most important to maternal life history.

Materials and methods

We obtained our data on reproductive tracts of female white-tailed deer (N = 1355) from the Alabama Division of Wildlife and Freshwater Fisheries. During the spring-summer seasons of 1995–2011, females were collected by sharpshooting with firearms as part of the agency's annual white-tailed reproductive surveys. Collections took place from January to July on numerous sites across the state of Alabama (southeastern United States) ranging from public wildlife management areas to large-acreage private landholdings. Annual samples ranged from 9 to 212 (mean = 79.7), and surveys occurred for 2.25 years on average per site (range 1 to 12). White-tailed deer foetuses were backdated to conception date according to the protocol outlined in Hamilton, Tobin & Moore (1985). If more than one foetus was present, the average foetal age was used to estimate conception date. Other data collected included site, county (38 represented), Alabama deer management district (as established by the Alabama Department of Conservation and Natural Resources), date of collection, age and uneviscerated mass of mother, and number and sex of foetuses. District 1 encompassed northwestern Alabama, District 2 covered northeastern Alabama, District 3 included the west-central region, District 4 encompassed the southeastern quadrant of the state, and District 5 included the southwestern coastal plain (Fig. 1). Females were aged by tooth wear and replacement (Severinghaus 1949); due to small sample size and increased difficulty aging older deer, females aged as 8.5 or older were combined into one age category. The full data set was used in analysis of female reproductive output, while a reduced data set of only pregnant individuals was used to examine conception date and foetal sex ratio ($N = 1129$).

Using Program R (R version 2.10.1, 2009), we analyzed the potential effects of female age and mass, number of total foetuses, and conception timing on foetal sex ratio using generalized linear models with a binomial distribution in y-values. We used two variables to look at conception timing – ‘early versus late’ and ‘days to mean’ – and never included both variables in the same model. We calculated ‘early versus late’ and ‘days to mean’ for each doe based on the average conception date for each site per year (site-year). To do this we calculated the mean conception date for each year of collection for a given site. The ‘early versus late’ variable was the actual difference between the conception date and the mean conception date while the ‘days to mean’ variable was the absolute value of this difference; such that for a site with mean conception date of January 15, a foetus conceived on January 22 would receive a value of 7 for both variables and a foetus conceived on January 10 would have a value of -5 for ‘early versus late’ and 5 for ‘days to mean’. We only analyzed site-years that had at least 5 females collected. In addition, we tested for effects of female age, mass, and interaction between these two variables on ‘early versus late’ using a linear model and ‘days to mean’ using a generalized linear model (family = Poisson). We designated district as a categorical random variable in all models to serve as a surrogate for regional differences in resource abundance. Also, we analyzed data for the reproductive performance of females. We used a generalized linear model with a Poisson distribution for the response to analyze the full data set for female production (number of foetuses produced) as a function of female age, age^2 and mass.

Results

Foetal sex ratio was fairly uniform across districts with only District 1 being significantly different from Districts 2, 3, and 4 (Fig. 2). Running the global model for the dependent variable foetal sex ratio with the ‘early versus late’ variable to account for time of conception indicated no significant relationship with independent variables for female age, mass, number of foetuses, and ‘early versus late’. The global model with the ‘days to mean’ variable accounting for conception timing indicated only one significant independent variable: ‘days to mean’ (P = 0.047, β = -0.013, SE = 0.007) – meaning that as the number of days to mean conception date increased, daughters were more likely. Female age, mass, and number of foetuses were not significant (Fig. 3). Higher variation in patterns of more divergent conception dates was likely attributable to low sample sizes. A change in the conception date by one complete oestrous cycle (28 days; Plotka et al. 1977) resulted in a doe being 1.445 times (confidence interval: 1.200–1.738) as likely to produce a daughter.

We found no significant relationship between the conception timing response variable ‘early versus late’ and either female age, mass, or the interaction between these variables. However, female age (P = <0.001, β = -0.291, SE = 0.044), mass (P = <0.001, β = -0.031, SE = 0.003), and the interaction between these variables (P = <0.001, β = 0.007, SE = 0.001) were significantly associated with the conception timing response variable ‘days to mean’. Results indicated that heavier does less than 4.5 years old were more likely to conceive closer to the average conception date than lighter does of the same age, while heavier does older than 4.5 years were more likely to conceive further from the average conception date than lighter does of the same age (Fig. 4).

Pregnancy rates for fawns (6 months old), yearlings (1.5 years old), and adult ($\geq$ 2.5 years old) females were 30%, 91%, and 96%, respectively. The percentage of barren females for older ($\geq$ 7.5 years old) individuals increased slightly to 10.4% (N = 29) as compared to 3.4% of 2.5-6.5 year old females (N = 1116; P = 0.139). All litters from pregnant fawns contained one embryo. Pregnant yearling and adult females produced 1.3 and 1.8 embryos/litter, respectively (Fig. 5). Litters of triplets and quadruplets were produced by 4.6% and 0.2% of pregnant adult female white-tailed deer, respectively, but we did not document triplets or quadruplets in individuals over 6.5 years of age. We found female production was significantly correlated with all considered independent variables – female age (P = <0.001, β = 0.249, SE = 0.066), age^2 (P = <0.010, β = -0.026, SE = 0.008), and mass (P = <0.001, β = 0.021, SE = 0.003; Fig. 6) – such that fawn production peaked between ages four and five and declined thereafter with more foetuses produced by heavier females than lighter females of the same age.

Discussion

Foetal Sex Ratio

In global models examining the effect of doe age, doe mass, number of foetuses produced and conception timing (‘early versus late’ and ‘days to mean’ as described in Methods) on foetal sex ratio, only ‘days to mean’ was a significant variable. The results indicate that the condition of the doe was not a factor in determining foetal sex ratio in this study, and that conception timing was a more important factor than maternal condition. Specifically, the difference between the time of conception and the average conception for a site-year was a better predictor than early vs. late seasons. The lack of significant relationship between doe mass and foetal sex ratio differs with studies that support the Trivers-Willard hypothesis (Kucera 1991, Burke and Birch 1995, Kohlmann 1999, Sheldon and West 2004) and the Local Resource Competition hypothesis (Verme 1969, Clark 1978, Skogland 1986, Caley and Nudds 1987, Hiraiwa-Hasegawa 1993). Although both hypotheses make predictions about doe condition, rather than mass, we believe that by accounting for age and district of collection (surrogate for resource abundance) in the model, mass becomes an adequate measure of doe condition. Doe age as a singular variable has also been shown to have a significant effect on foetal sex ratio (Nixon 1971, Ozoga and Verme 1982, Verme 1983, Richter and Labisky 1985, Sade 2004), however we were unable to detect any effect of age on foetal sex ratio, which is supported by other studies (Kohlmann 1999, Monard et al. 1997, Weladji et al. 2002, Saalfeld et al. 2007).

Changes in sex ratio based on timing of conception have been shown in many studies; however, how this timing was measured has varied. Verme and Ozoga (1981) found that more females were conceived within the first 36 hours of oestrous in comparison to later bred white-tailed does. Conversely, many studies of ungulates have found that females conceiving early in the reproductive season are more likely to produce males or expensive litters in comparison to litters conceived later in the season (Kohlmann 1999, Saether et al. 2004, Hemmer 2006, Holand et al. 2006, Ditchkoff et al. 2009, Veeroja et al. 2010). We chose to use two variables to look at conception time in different ways, as the actual difference in conception timing, ‘early versus late’, and the spread of the conception timing, ‘days to mean’. Both variables use the difference of the site-year average conception date and the individual’s conception date. These variables differ from previous studies because they consider changes in sex ratio by season on a much smaller scale than previous population studies which are state or region wide and may cover many years. Using variables that account for the mean date of conception is especially important in Alabama where populations are descendants of numerous reintroduction efforts of the early to middle 1900s. These original deer were derived from various and diverse stocking populations resulting in equally variable breeding seasons throughout the fall and winter across the state (Leuth 1967). Population wide studies have shown that more males tend to be conceived earlier in the breeding season (Kohlmann 1999, Hemmer 2006, Ditchkoff et al. 2009, Veeroja et al. 2010); however, our analyses suggest males are conceived closer to the average conception date for a site-year. Consequently, males are likely to be born during the peak of fawning, which may be an advantageous strategy by helping to prevent predation of male fawns due to swamping. Swamping to help prevent predation of fawns is more likely to be advantageous at the local population level, rather than at the regional population level, especially when regional population level conception dates range greatly. Swamping has been shown to successfully decrease chances of mortality due to predation, as young born during non-peak times are more likely to die due to predation (Estes 1976, Guinness et al. 1978, Gregg et al. 2001).

Due to a lack of available data we were unable to test for the effects of paternal or maternal status, or differential allocation on foetal sex ratio. Roed et al. (2007) supported the differential allocation hypothesis (mothers mating with attractive males may increase fitness by producing more sons, because male offspring may inherit traits conducive to siring success) by showing that female reindeer mating with attractive males produced more sons, and mating was delayed when only young males were present. If white-tailed deer behave similarly to reindeer, a plausible explanation for increased male sex ratio at the peak of conception may be due to females preferentially mating with attractive males and producing more sons in comparison to when mating with younger males; this would support the differential allocation hypothesis. An alternative hypothesis would be that males during peak rut (which is likely to coincide with peak conception) have high testosterone levels, and testosterone levels have been known to affect sex ratio (James 1996).

Date of conception

Due to the significant interaction term (female age*mass), our results indicate that for younger white-tailed deer, smaller females conceive further from the average conception date than heavier females, and older heavier females conceive further from the average conception date than maternal females of similar age but smaller size. Because ‘early versus late’ was not significant (but ‘days to mean’ was), there was no discernible temporal bias for time of conception being before or after mean conception date for older or younger females of different mass classes. Our results and interpretation failed to corroborate the findings of previous studies – adult females breed first, followed by yearlings, and finally fawns (Roseberry and Klimstra 1970, Johns et al. 1977, Verme 1989), but indicated that age as well as mass played a significant role in determining timing of conception. Cothran at al. (1987) failed to detect a difference in conception date based on maternal age, but instead, maternal condition (fat levels) was associated positively with early breeding. Though we did not collect data on previous year's reproductive output by females (e.g., counting corpora lutea; Cheatum 1949, Mansell 1971), other studies have shown that females not successful in gestating during the previous year enter the following season in top condition and conceived earlier than other females (Verme 1962, Mansell 1974). Langvatn et al. (1994; red deer) lends additional evidence that female condition is important in determining conception date. They found that under high population densities, average body condition declined, and ovulation was delayed by even prime-aged females.

In our study region, there still seems to be a competitive advantage associated with breeding near the peak of conception even with temperate seasonal extremes (Bunnell 1980). One might expect this phenomenon to be most pronounced in regions of harsh climates and shortened growing seasons, though we do not know of any studies that have examined varying degrees of conception synchrony within ungulate populations. Conceiving during the peak of breeding not only has important consequences regarding maternal condition and availability of high quality forage during parturition, lactation, and weaning, but breeding season synchrony also influences the effectiveness of predator swamping (Estes 1976, Bunnell 1980).

Senescence

Our model for female production showed evidence of senescence in white-tailed deer. The bell-shaped relationship (Fig. 6) between number of embryos and age indicated that reproductive output peaked at 4.5–5.5 years of age and declined as individuals aged. Prior studies failed to show senescence among female white-tailed deer, but acquiring adequate sample sizes of older individuals was problematic in some studies (Roseberry and Klimstra 1970, Nelson and Mech 1990, Nussey et al. 2008). DelGiudice et al. (2007) found no decline in fertility of older females in Minnesota, and older age classes maintained near 100% pregnancy rates. In other species of Order Artiodactyla, reproductive senescence has been demonstrated in Columbian black-tailed deer (*Odocoileus hemionus columbianus*; Thomas 1983), roe deer (*Capreolus capreolus*; Hewison and Gaillard 2001), reindeer (Weladji et al. 2002, Weladji et al. 2010), bighorn sheep (*Ovis canadensis*; Berube et al. 1999), moose (*Alces alces*; Ericsson et al. 2001), and red deer (Nussey et al. 2006, Carranza et al. 2004, Langvatn et al. 2004). The optimal way to examine senescence is to follow individuals throughout their lifetime employing a longitudinal approach (Nussey et al. 2008). In free-ranging white-tailed deer, no research using this study design has been published. Our research, like most other studies, follows a transversal study design (based on a cross-section of a life table) in which each female was only sampled once at the time of death (Gaillard et al. 1994).

Conclusion

For our study, the only factor affecting foetal sex ratio allocation was how closely females conceived relative to the peak of breeding. With no difference in effect of early versus late conception timing on foetal sex ratio, it is apparent that the window of peak conception is optimal because of pressing factors present both before and after that period. Also, timing of conception was affected by maternal age and mass and suggested that large-bodied, mature females (possibly in superior condition because the prior year's litter/offspring was stillborn or depredated) bred on the fringes of the peak conception period, while younger females in prime condition conceived closer to the peak of breeding. As expected, post-mature female white-tailed deer in poorer condition exhibited a decline in reproductive output. All evidence supports the assertion that white-tailed deer reproduction, and ultimately fitness, is sensitive to a complex array of physiological and biological factors.

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Figure 1. Map of Alabama Department of Conservation and Natural Resources management regions.

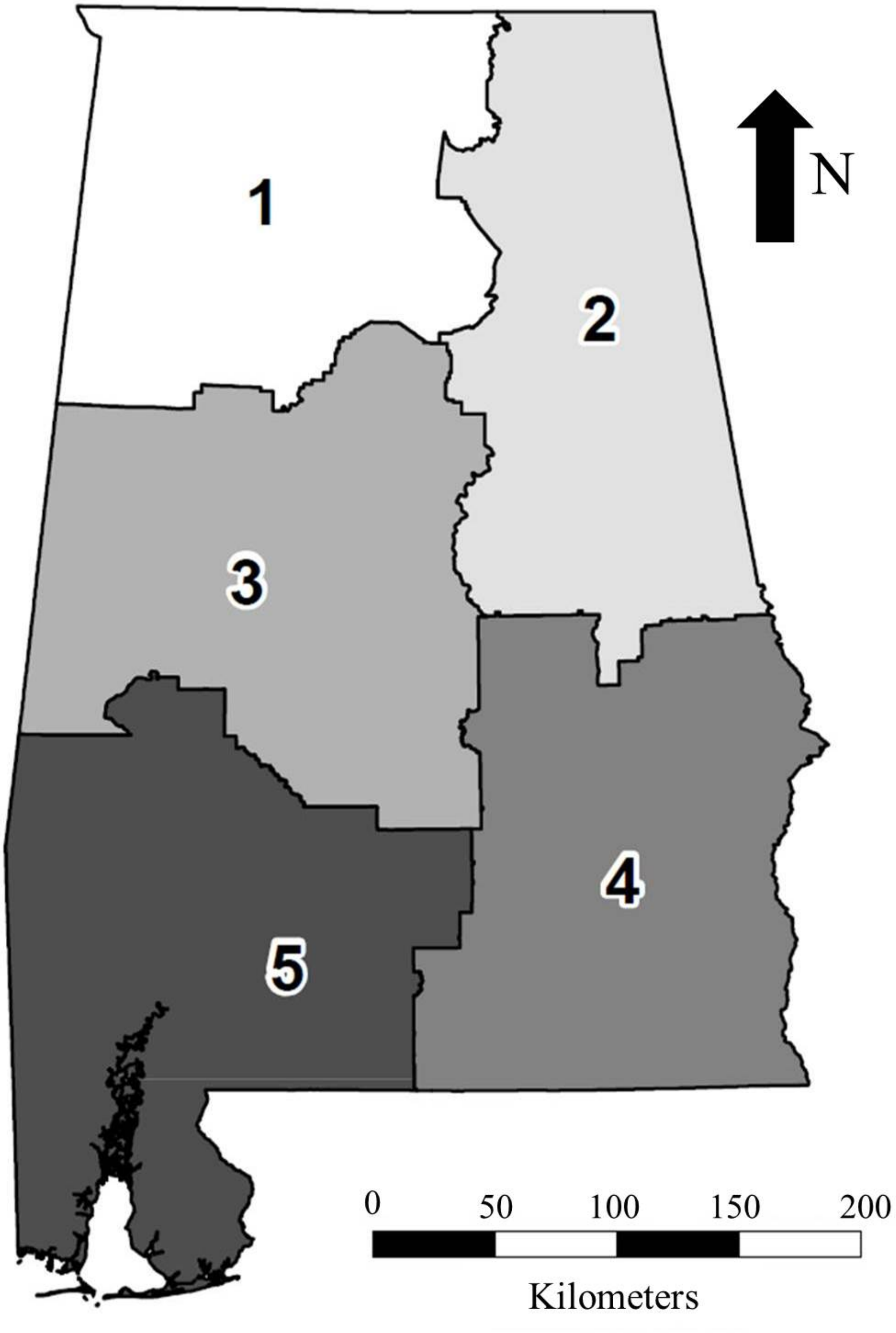

Figure 2. Foetal sex ratio by deer management district in Alabama averaged across all years (1995–2011). The data set used in this analysis included only pregnant does (N = 1129). Labels A and B indicate which districts are significantly different ($P < 0.05$) from each other.

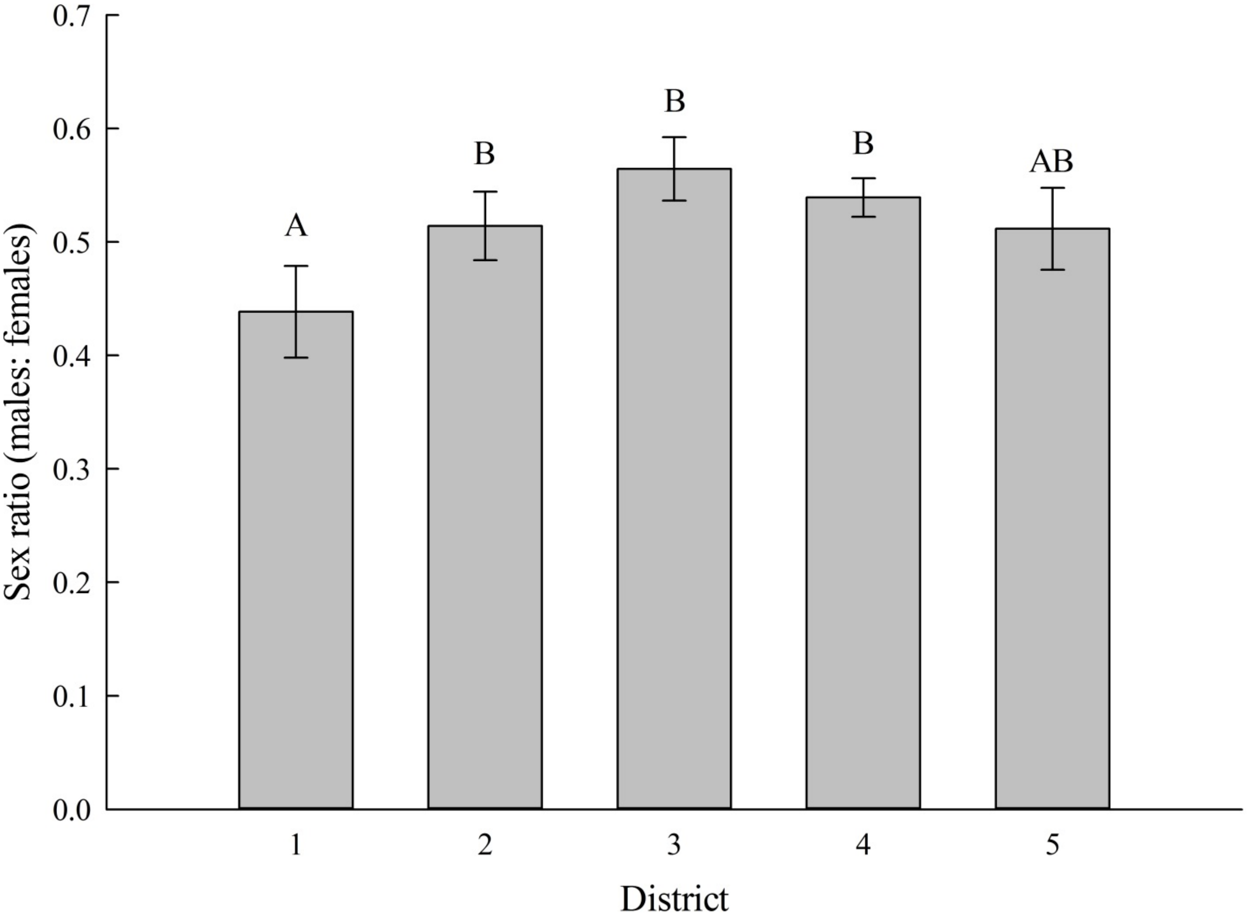

Figure 3. The predicted model effects of days from average conception on foetal sex ratio plotted with the actual foetal sex data from all pregnant does (*N* = 1129) collected in Alabama, 1995–2011, grouped into 5 day intervals.

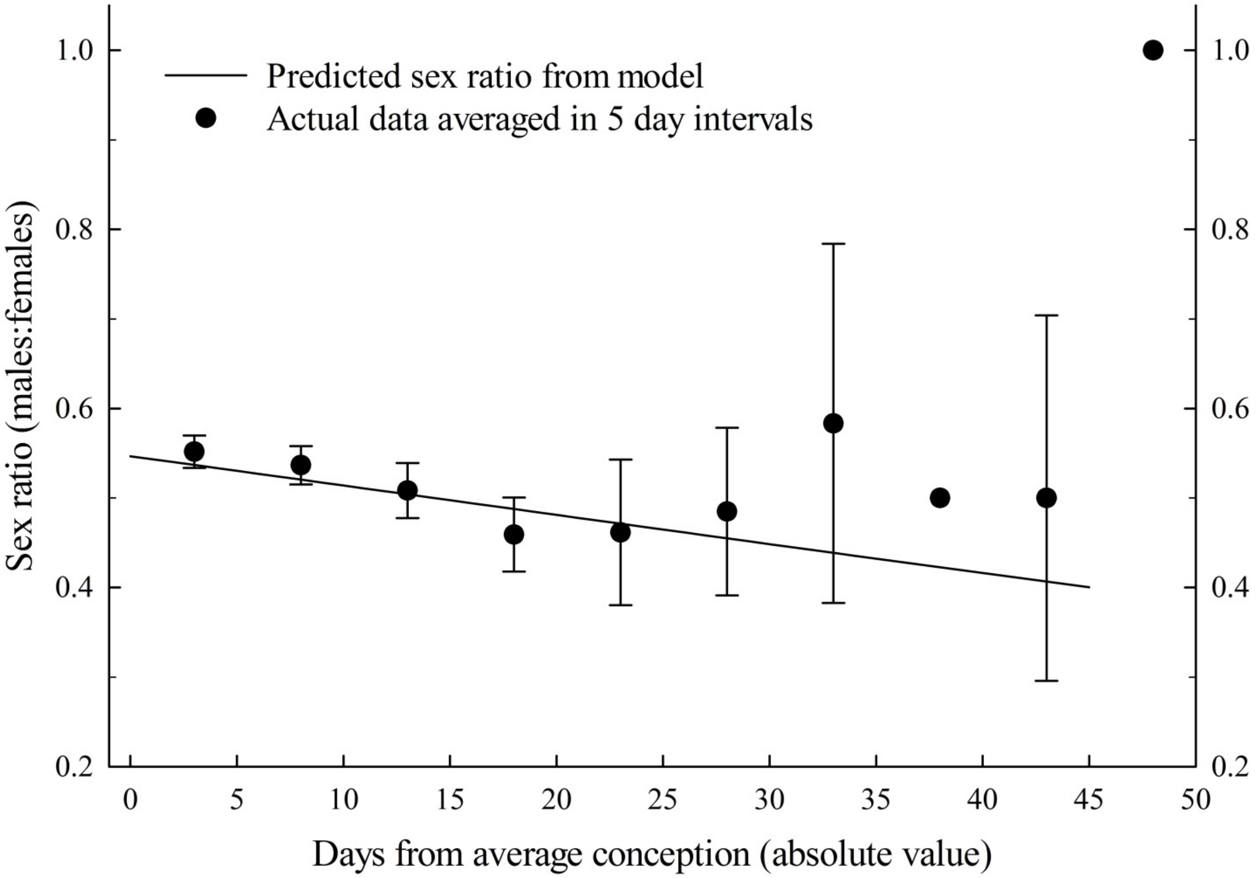

Figure 4. The global model for the effects of doe age, doe mass, and an interaction between doe age and doe mass on days from average conception for all pregnant does ($N = 1129$) collected in Alabama, 1995–2011.

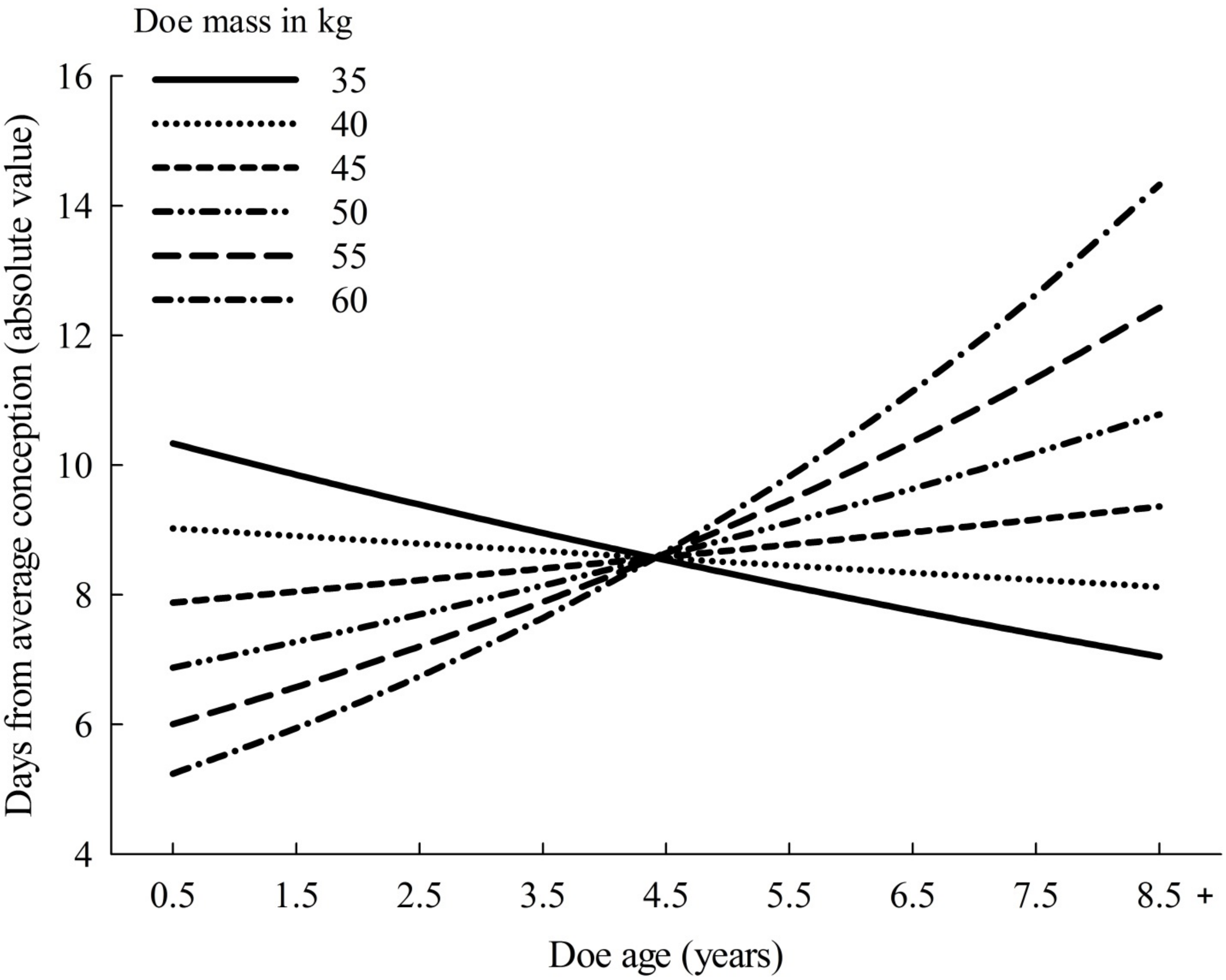

Figure 5. The percent of each litter size by doe age for all does (N = 1355) collected in Alabama, 1995–2011.

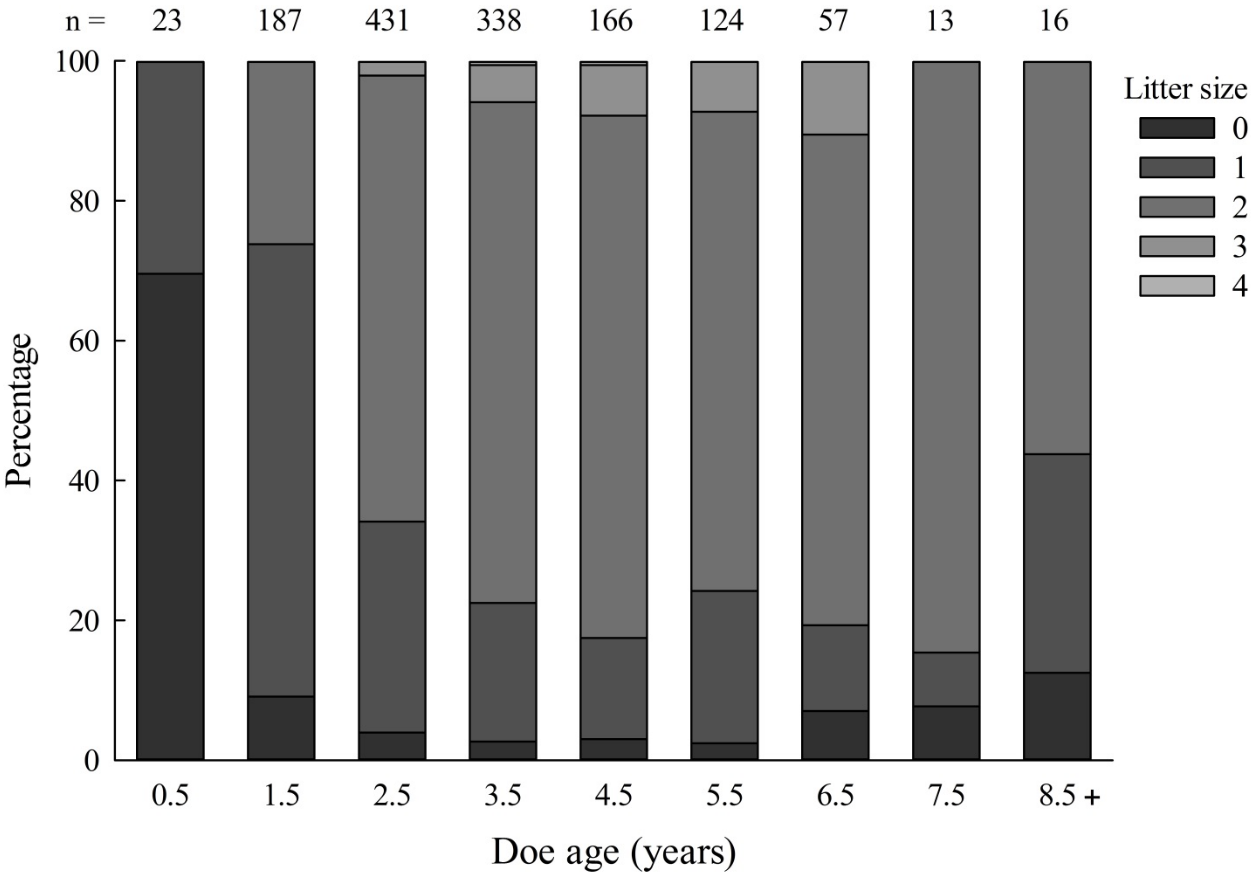

Figure 6. Effects of age, mass, and age^2 on the number of foetuses produced by all does (N = 1355) collected in Alabama, 1995–2011.