# Extra-Home Range and Excursive Movements by White-Tailed Deer

by

Todd C. Jacobsen

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Approved by

Stephen S. Ditchkoff, Chair, Ireland Professor of Wildlife Sciences, Auburn University
Robert A. Gitzen, Assistant Professor of Wildlife Sciences, Auburn University
Stephen Demarais, Dale H. Arner Professor of Wildlife Ecology and Management, Mississippi State University

# Abstract

Little information is available concerning excursive movements by white-tailed deer. Past studies addressing these movements have approached excursion detection in a manner that we believe is severely limited and that precludes important insight concerning these unusual behaviors. We address this issue by presenting an alternative, novel method for detecting extra-home range movements by deer and other taxa. We also address a collection of issues surrounding the terminology and definition criteria applied to these movements by past studies.

Furthermore, we apply our novel detection method to GPS relocation data acquired from white-tailed deer in Alabama over 2014 – 2016. Our results indicate that extra-home range movements by deer occur throughout the year, but dramatically increase in frequency surrounding peak conception. By applying an extensive suite of spatial metrics to these movements, we also document additional trends which provide support for hypotheses concerning how and why excursive-type behaviors occur.

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## ABSTRACT

Instances of infrequent, long-distance movements by individual animals outside of typical home range areas—often referred to as “excursions”—have been sporadically documented by radio-tracking studies for several decades but are now being detected with greater frequency and detail with the widespread use of GPS-collar tracking technology. Most of these studies of excursive-type movements have employed the traditional approach of examining spatial relocation datasets to detect long-distance movements outside of seasonal home ranges. Our objective was to highlight several limitations of this current detection method, as well as to propose an alternative, novel method for detecting extra-home range movements such as excursive-type behaviors. To address this, we employed both the traditional method and our novel method to identify extra-home range movements in a dataset comprised of GPS relocations of 33 white-tailed deer (*Odocoileus virginianus*) in Alabama. Furthermore, we confronted additional issues associated with excursion definitions used in previous studies; nearly all studies that have examined excursions by white-tailed deer have employed a variety of distance and/or duration criteria with arbitrarily-defined values. We applied several recently used distance and/or duration definition criteria to this same dataset in order to evaluate potential methods-induced sources of variation in excursion summary statistics. Our novel extra-home range movement detection method documented 1.5 times as many extra-home range movements as did the traditional approach ($n$ = 320 and $n$ = 215, respectively) and identified 120 unique movements that were not detected by the traditional method, including some movements that extended nearly 5 km outside of home range boundaries. Applying a variety of previously used definition criteria to our dataset yielded between 15.6% and 100.0% of the extra-home range movements examined in our study. We conclude that past studies that have examined excursive-type behaviors in white-tailed deer have been limited by the use of an inadequate detection method, and that the variability and arbitrariness of terminology and definition criteria may preclude useful comparisons between studies. We believe that our novel approach to extra-home range movement detection and our proposed guidelines for future excursion studies will allow researchers to better investigate and understand these behaviors.

**KEY WORDS** excursion, exploratory, foray, home range, *Odocoileus virginianus*, sallies, Shifting-Window, trip, white-tailed deer.

A thorough understanding of animal space use and movement across a landscape is necessary to effectively implement fundamental principles of conservation biology and wildlife management. Spatial movement metrics such as home range size and fidelity, daily activity rates, step-length, and path tortuosity can be used to draw inferences concerning resource selection and habitat use (Forester et al. 2009), predator-prey interactions (Sand et al. 2005, Hansen et al. 2013), bio-climatic relationships (Inman et al. 2012), or the effects of anthropogenic factors on wildlife populations (Tucker et al. 2008). In turn, these inferences can provide a basis for biologically-driven management efforts such as preservation of key travel or migration corridors (Squires et al. 2013), protection for threatened species (Young et al. 2011, Johnson et al. 2013), or adjustments to hunting regulations and seasons (Proffitt et al. 2010, Cleveland et al. 2012). The methodology with which researchers analyze and quantify these animal space-use and movement metrics is constantly evolving to allow for better detection and more accurate and precise measurement of important behaviors. It can also lead to the reevaluation of how these behaviors are viewed as a whole (Cagnacci et al. 2010). For example, the emergence of fine-scale tracking technology has changed both the spatial and temporal scales at which animal relocations can be measured (Cagnacci et al. 2010, Hebblewhite and Haydon 2010), while increased statistical software capabilities have allowed for manipulation and analysis of spatial data which was either not possible or was cumbersome and imprecise (Pfeiffer and Hugh-Jones 2002, Liebhold and Gurevitch 2002, Nathan et al. 2008). This evolution and advancement in methodology can also be seen in emergence of home range estimators that incorporate time or other animal movement parameters into their models (e.g., Brownian and dynamic Brownian bridge movement models or movement kernel density estimators; Horne et al. 2007, Benhamou and Cornélis 2010, Kranstauber et al. 2012, Walter et al. 2015).

Recently, as GPS-tracking technology began allowing for fine-temporal monitoring of animal movements, attention in animal space-use and movement analyses has been drawn to irregular, long-distance movement behaviors outside of home range areas. Only a handful of studies have investigated extra-home range movements—regularly referred to as "excursions"—by ungulates (e.g., Kolodzinski et al. 2010, Karns et al. 2011, Olson et al. 2015), and the understanding behind these excursive movements is currently limited. Most recent studies investigating excursions have employed similar methods to detect these movements: they attempt to identify long-distance movements that fall outside of temporally fixed seasonal, or even annual, home ranges. However, this method of extra-home range movement detection appears to have substantial limitations both in theory and application. Like many previous spatial analysis methodologies, the limitations of this approach necessitate its reevaluation in order to effectively document excursive-type movements by animals.

The primary limitation behind the traditional method of detecting extra-home range movements is the circular logic found in the construction and use of a temporally fixed home range to then detect extra-home range movements occurring within that same temporal period. While the intention behind using such a seasonal or annual period is founded in a desire to establish a typical area of use for an individual from which deviations in movement patterns might occur (i.e., excursions), this methodology fails to account for the possibility of changes in space use following an excursive movement which could then subsequently influence the overall home range area used to detect excursions in the first place. Therefore, we believe the traditional approach for detecting excursions could potentially result in important biological trends being overlooked. To address this issue and other issues associated with the traditional method, we present an alternative, novel approach for detecting extra-home range movements that may shed additional light on the motivations and factors influencing excursive-type behaviors. Our alternative approach utilizes a shifting-window process to only utilize movements leading up to an extra-home range movement to define a typical area of space use, rather than using the movements before and after the movement to construct the home range area as is the case with the traditional method. This circumvents the assumption of "no changes in space use following an excursion", while also allowing for assessment of whether or not excursive movements do in fact lead to shifts in space use.

Despite the recent influx of excursion-related studies, a clear definition for these behaviors has yet to be established and a general scientific consensus has not been reached as to what constitutes an "excursive" versus an "extra-home range" movement behavior, at least within taxa (e.g., Kilgo et al. 1996, Kolodzinski et al. 2010, and Olson et al. 2015 with white-tailed deer, *Odocoileus virginianus*; Lovari et al. 2008 and Debeffe et al. 2014 with roe deer, *Capreolus capreolus*; Stopher et al. 2011 with red deer, *Cervus elaphus*). This presents an additional set of complications associated with previous excursion-based studies. As a result, we also set out to highlight the variability in excursion definition criteria used in previous studies that have attempted to document extra-home range, excursive-type movements. We applied a suite of literature-derived "excursion" definition criteria to a dataset from GPS-collared white-tailed deer to demonstrate how this spectrum of definition criteria may produce substantially different results and may lead to highly variable interpretations of excursive-type behaviors.

## METHODS

### Study Area

Movement data for white-tailed deer were collected from 4 study sites across the state of Alabama. Two of the sites—Barbour Wildlife Management Area (31°59.73 N, 85°27.57 W) and Oakmulgee Wildlife Management Area (32°57.39 N, 87°27.60 W)—were state-designated public hunting wildlife management areas (WMAs). The Barbour WMA in southeastern Alabama encompassed approximately 114 km$^2$ of public access land. This WMA contained a mixture of habitat types including longleaf pine (*Pinus palustris*) in various stages of regeneration, loblolly pine (*Pinus taeda*), mixed hardwood upland areas, as well as mixed hardwood bottoms. The Oakmulgee WMA in west-central Alabama was near the southern reaches of the Appalachian foothills and encompassed approximately 180 km$^2$ of land. Dominant vegetation included mature longleaf pine stands and widespread mature hardwood forests on upper ridges and slopes of the management area, as well as mature hardwood bottomlands.

The third study site was a private commercial timber production area in Pickens County (33°12.45 N, 87°52.01 W) and comprised 16 leasable hunting tracts collectively managed by timber company biologists. This site encompassed approximately 49 km$^2$ of loblolly pine in various stages of regeneration, as well as several post-harvest clearings. The fourth study site was located in Marengo County (32°14.08 N, 87°51.11 W) and encompassed approximately 31 km$^2$ of land. This site was made up of three adjoining private landholdings, as well as adjacent private commercial timber production areas and hunting leases held by these private landowners. This site was characterized by various stages of loblolly pine regeneration and mixed-age hardwood stands.

### Capture and Handling

During the summer of 2014, 30 deer (≥1 year old, either sex) were captured across the four study sites, and an additional 8 deer were captured during the summer of 2015. Deer were captured with the use of tranquilizer dart rifles (Pneu-Dart, Inc., Williamsport, Pennsylvania, USA) equipped with 2.5x50 Yukon Titanium Varmint Hunter night vision riflescopes (Yukon Advanced Optics Worldwide, Inc., Vilnius, Lithuania) from elevated tree stands and shooting houses, or from roadside vehicles. Deer were immobilized and sedated via intramuscular injection by a 2cc Type-U radio-transmitter dart (Pneu-Dart, Inc., Williamsport, Pennsylvania, USA) containing a Telazol-Xylazine hydrochloride mixture (125mg/ml Telazol administered at 4.0 mg/kg; Fort Dodge Animal Health, Fort Dodge, Iowa, USA; 100mg/ml xylazine hydrochloride administered at 2.0 mg/kg; Lloyd Laboratories, Shenandoah, Iowa, USA). Immediately after darting and telemetry location of sedated deer, deer were blindfolded to minimize stress, the tranquilizer dart surgically removed, and a blood coagulant applied to the dart site.

All deer were fitted with a G2110D programmed-release global positioning system (GPS) collar (Advanced Telemetry Systems, Inc., Insanti, Minnesota, USA) and equipped with 2 (1 per ear) plastic ear tags (Y-Tex Corporation, Cody, Wyoming, USA). The GPS collars were colored fluorescent orange and the ear tags colored bright yellow to aid hunters in the identification of GPS-collared deer. Hunters on all study areas were asked not to harvest GPS-collared deer. Once collaring and measurements were complete, deer were reverse-immobilized via intramuscular injection of the antagonist Tolazine (100mg/ml tolazoline hydrochloride administered at 2.0 mg/kg, Lloyd Laboratories). After administration of the Tolazine reversal, all deer were monitored until completely ambulatory and indicating full awareness of their surroundings. Animal handling procedures were approved by the Auburn University Institutional Animal Care and Use Committee (PRN# 2013-2323).

### Data Collection and Manipulation

GPS collars began collecting data from the time of capture and collar deployment until the programmed automatic release date during March – April 2016. GPS collars were programmed to obtain fixes every 3.5 hours from April 1 – September 30 and every 1 hour from October 1 – March 31. Fix rates were assigned in this way to maximize collar battery life over two successive breeding periods for each deer while still maintaining fine-scale data throughout the year, with more frequent fixes recorded during the period that encompassed pre-breeding, breeding, and post-breeding activities. Field tests to determine mean collar location error of G2110D GPS collars in a similar Southeastern ecosystem were conducted and described by Sullivan et al. (2016). Mean collar location error was 12.9 m (SD = 9.8 m) in that study. Given these results, we employed a slightly more-conservative 15-m collar location error rate throughout our study. Data were censored for accuracy by removing 2-dimensional fixes with HDOP (horizontal dilution of precision) >5 and 3-dimensional fixes with PDOP (position dilution of precision) >10 or HDOP >6 (D’Eon and Delparte 2005, Lewis et al. 2007).

Additionally, all data obtained within 7 days post-capture were censored from the study to avoid any potential effects of capture on deer movement.

## Extra-Home Range Movement Detection

Extra-home range movements were identified and analyzed from GPS relocations for each deer. Two different approaches were compared for this analysis. For this comparison, all movements occurring outside of a home range and meeting our detection criteria (described in the following section), whether excursive in nature or not, are referred to as "extra-home range movements."

*Seasonal method*.— The first approach in our analysis implemented the temporally fixed home range method that has been traditionally used for detecting excursive-type movements (Nelson and Mech 1981, Kolodzinski et al. 2010, Karns et al. 2011, Olson et al. 2015, Simoneaux 2015); hereafter, referred to as the Seasonal method. We used this term for simplicity, though we recognize that multi-season and annual periods have also been employed in past analyses (Hölzenbein and Schwede 1989, Sawyer et al. 1989). For detection of these movements using the Seasonal method, location data were separated into three seasons based on general vegetative and climatic changes that occur throughout the year in south-central Alabama: spring (1 March – 30 June; 121 days), summer (1 July – 31 October; 122 days), and fall/winter (1 November – 28 February; 119 days). For each deer, seasonal home ranges were constructed beginning 7 days post-capture if a minimum of 60 days still remained in the season of capture. If less than 60 days remained before the end of the season that capture occurred, our analysis began at the onset of the next season. In instances where >60 days of data were available in a given season but the data did not span the entirety of the season, a partial seasonal range was constructed. All home ranges constructed for our study were created using Brownian bridge movement models (BBMM, Horne et al. 2007) in R 3.1.1 (www.r-project.org). These home ranges were modelled at the 95% isopleth level and a grid cell size of 100 m was used to map the utilization distribution.

Extra-home range movements were defined as isolated strings of 1 or more GPS locations extending ≥0.5 km outside of the 95% seasonal home range contour. A conservative distance of 0.5 km was employed to capture all possible instances of excursive-type movement behaviors; however, we recognize that some movements exceeding this threshold may have been instances of subtle range expansions and random peripheral movements rather than instances of excursive behavior. The selection of a minimum distance threshold of this magnitude prevented the unnecessary examination of individual data points falling just outside the 95% home range contour while at the same time facilitating the capture of long-distance movements on a scale typical for white-tailed deer (e.g., Kolodzinski et al. 2010, Sullivan et al. 2016). Movements meeting these criteria were identified using R and later individually inspected for verification in ArcMap 10.2 (Environmental Systems Research Institute, Inc., Redlands, California, USA). Maximum distance for an extra-home range movement was determined as the shortest Euclidian distance from the edge of a 95% home range contour to the furthest point along that extra-home range movement. Extra-home range movement duration was counted as the elapsed time between the last fix inside the 95% home range contour prior to the start of the extra-home range movement until the first point returning inside the home range contour at the end of the movement. No minimum duration was established for extra-home range movements; however, during our high fix-interval sampling period (1 fix/hour), the minimum extra-home range movement duration possible was 2 hours, and minimum duration possible during our low fix-interval sampling period (1 fix/3.5 hours) was 7 hours.

*Shifting-Window method*.— Similar to the Seasonal method for detecting extra-home range movements, all home ranges were constructed in R using a BBMM (95% contour, 100-m grid cell size) for the “Shifting-Window” method, and extra-home range movements were again defined as isolated strings of 1 or more GPS locations extending ≥0.5 km outside of the 95% home range contour. However, rather than using seasonal home range periods as the basis for our home range models, this method utilized a “shifting” home range period. The purpose of the Shifting-Window method was to allow for extra-home range movement detection on each day of GPS collar data compared against the home range utilized on the previous 60 days. In this manner, the home range used to detect extra-home range movements is only comprised of spatial data collected prior to the extra-home range movement that was being examined, rather than with spatial data occurring both before *and* after an extra-home range movement (such as in the Seasonal method). For each deer, beginning 7 days post-capture, a 60-day pre-movement event home range (PreHR) was constructed. A PreHR period of 60 days was selected because it was short enough to adequately capture most external resource availability shifts or internal biological changes that may have influenced home range establishment and resource use, but also long enough to establish a representative area of typical use for a deer at a local level. Immediately following this 60-day PreHR period, a 2-day window was established in which we determined if any extra-home range movements occurred (using the excursion criteria previously described). A 2-day window was implemented because it was usually short enough to prevent more than one extra-home range movement from being captured, as well as short enough to prevent the detection of any non-excursion-type changes in space use by deer. We also utilized this window length because it was long enough to capture most typical excursive-type movements (Kolodzinski et al. 2010) and minimized unnecessary data manipulation. If, however, an extra-home range movement was detected that extended beyond the 2-day window, that window was extended until the deer returned back to its home range from the movement, or in the case of a dispersal event, until the individual began exhibiting the first indication of fidelity to a new area. In the latter case, a simple cursory review of the movement in the days following the initial extra-home range movement was used to confirm this area fidelity.

This Shifting-Window method was repeated for each day of GPS collar data for each deer. For example, a 60-day PreHR starting on 25 March would extend 59 days through 23 May. The 2-day extra-home range movement detection window would then be initiated on 24 May and extend through 25 May. If an extra-home range movement was detected during this window and the deer had not returned back to its home range by 25 May, the window would be extended until the deer returned. This entire process would then be repeated with a 1-day shift in PreHR period and extra-home range movement detection window for each day of deer data, so that the next 60 day PreHR would start on 26 March and span through 24 May. The subsequent 2-day detection window would then span from 26 May through 27 May. This process would then again repeat throughout the remaining days of data until the last day of the 2-day detection window landed on the last day of available collar data.

### Excursion Definition Criteria

We examined previous publications and theses/dissertations in which excursive behaviors by white-tailed deer were documented and then selected those studies that used fixed minimum distance and/or duration values to define excursive-type behaviors outside of 95% home range contours. Studies could either contain an excursion definition using a distance criterion only, a duration criterion only, use both distance “AND” duration criteria together, or use an inclusive distance “OR” duration criterion option. The criteria from these studies were each separately applied to the sample dataset of extra-home range movements previously generated by our Shifting-Window method to compare the number of extra-home range movements detected with each definition. The criteria from these studies were selected due to the simplicity with which they could be applied to our sample dataset. For the studies which employed the “OR” conjunction in their criteria and where the latter half of the argument was not a fixed distance or duration (i.e., minimum distance OR if ≥50% of daily points were outside of the seasonal home range), then the latter half of the criteria was not applied to the analysis for computational simplicity. Lastly, we applied an example distance-duration criteria (≥1.0 km, ≥12 h outside the 95% contour) to the dataset generated by our Shifting-Window analysis to demonstrate the effects of using either the “AND” or “OR” conjunctions as part of the excursion definition criteria.

## RESULTS

Data were obtained for 35 of the 38 deer collared during the course of our study. The 3 collars for which no data were obtained failed to release from the deer at their programmed drop-off date. After censoring data to 7-days post-capture, 33 collars had collected data for at least 60 days, with a mean collar duration of 379.6 days (SD = 174.1 days) and a max duration of 577 days.

### Extra-Home Range Movement Detection

The Seasonal excursion detection method found that 30 of 33 deer exhibited a total of 215 extra-home range movements extending ≥0.5 km outside of the 95% seasonal home range contours (Table 1.1). The Shifting-Window method found that 32 of 33 deer exhibited a total of 320 extra-home range movements extending ≥0.5 km outside of the 95% home range contours.

Neither method detected any excursions for one female. Extra-home range movements that were not available for comparison by one method or the other due to logistical limits of each method were excluded from further analysis (*n* = 17 extra-home range movements detected by the Seasonal method that occurred during the first 60-day PreHR of the Shifting-Window method, and *n* = 18 extra-home range movements detected by the Shifting-Window method that occurred when less than 60 days of data were available in a given season). One hundred eighty-two of the remaining extra-home range movements available for direct comparison were detected by both methods. When detected by the Shifting-Window method, these shared movements were 5.6% longer on average than when these same movements were detected by the Seasonal method. The maximum distance of an extra-home range movement that was detected by the Shifting-Window method but missed by the Seasonal method was 4.9 km outside a home range contour; in contrast, the maximum distance of a movement detected by the Seasonal method but missed by the Shifting-Window method was 1.2 km.

### Excursion Definition Criteria

We found 7 previous studies that implemented fixed minimum distance and/or duration criteria for detecting excursive-type movements. The criteria from these studies were applied to the 320 extra-home range movements identified by our Shifting-Window analysis (Table 1.2). The criteria used by Sullivan et al. (2016) matched the criteria used to generate our sample dataset and identified 100% of the extra-home range movements. Aside from this study, the criteria used by other studies identified between 15.6% and 77.5% of the extra-home range movements from our sample dataset, with a mean detection rate of 45.6%.

When our standardized example criteria (≥1.0 km, ≥12 h) were applied to the sample dataset (Figure 1.1), the “distance OR duration” qualifier criteria identified 85.3% of the extra-home range movements (sectors I, II, and III). The “duration only” qualifier criterion identified only 45.0% of the extra-home range movements (sectors II and III), followed by the “distance only” qualifier criterion at 40.3% (sectors I and II). When the “distance AND duration” criteria were applied, only 24.1% of extra-home range movements were identified (sector II). Using either the “duration only” or the “distance and duration” criteria on our sample dataset omitted 18 movements and 4 movements extending 2.0 km and 4.0 km beyond the home range, respectively, with a maximum movement distance of 8.0 km missed. Likewise, 19 extra-home range movements lasting >24 h were omitted when using either the “distance only” or the “distance and duration” criteria, including movements lasting 56, 68, and 123 h.

## DISCUSSION

### Extra-Home Range Movement Detection

The traditional method for detecting extra-home range, excursive-type movements by white-tailed deer and other ungulates involves constructing a temporally-fixed, seasonal (or even annual) home range for an individual and then examining GPS locations recorded during that seasonal period for any long-distance movements outside of the seasonal home range (e.g., Nelson and Mech 1981, Schauber et al. 2007, Lovari et al. 2008, Bocci et al. 2013, Magle et al. 2015). Failure of the Seasonal approach to detect a substantial proportion of extra-home range movements identified by the Shifting-Window method was likely due to the fundamentally flawed nature of using these temporally fixed time periods for home range construction and excursion detection. The Seasonal approach fails to account for the possibility of changes in space use during a season which may have been influenced by extra-home range movements occurring earlier in the season, or the possibility of the extra-home range movements themselves influencing the utilization distribution of the home range. Therefore, subsequent movements occurring after an extra-home range movement—especially those when an individual chooses to further exploit the area initially explored by the movement—are often partially or completely masked during traditional analyses. We suggest that this has been one of the primary obstacles to understanding excursive behaviors by ungulates such as white-tailed deer. Recent studies have rejected commonly held theories regarding excursive-type behaviors and have been unable to offer any alternative hypotheses for why they occur (Kilgo et al. 1996, Olson et al. 2015, Simoneaux et al. 2015). This will likely remain an issue as long as extra-home range movements and the successive space use following an extra-home range movement are used to construct the home ranges that are themselves used for detecting the extra-home range movements in the first place.

The amount of time (and thus, amount of movement data) between the start of a season and a detected extra-home range movement can be highly variable when the Seasonal method is implemented. One of the primary reasons a seasonal home range has been used in past studies for detecting excursions is because it theoretically provides an adequate representation of an individual's normal space use over an extended period when the individual's behavior is less likely to change (Harris et al. 1990, Powell 2000). Using an extended period of time may help prevent detection of excursive-type movements that would be considered novel over a short time span but may actually be a part of a regular activity pattern when viewed on a broader temporal scale. However, the Seasonal method again often fails in this regard because it does not always adequately document space use prior to an extra-home range movement. If an extra-home range movement occurs near the end of a season, then an adequate representation of "normal" space use can be established, and the confidence that the movement is an aberrant behavior and excursive in nature (making it of research interest) is reasonably high. However, it is also possible for extra-home range movements to occur during the early part of a given season. In these instances, seasonal home ranges would be primarily comprised of movement data occurring after the movement event, rather than before the movement event. This defeats the purpose of using an established pattern of movement to detect deviations from this pattern (such as excursive-type movements). Therefore, we argue that if the Seasonal method is employed, any extra-home range movements occurring during the first 60 days of each given season do not represent biologically valid forays outside of typical areas of space use. In our comparison of detection methods, 17 extra-home range movements detected by the Seasonal method were omitted from analysis because they occurred during the first 60-day PreHR period of the Shifting-Window method, and thus were not available for detection by the Shifting-Window method. However, given our argument for establishing a period of typical space use prior to each instance of extra-home range movement detection (rather than only in some instances in which extra-home range movements occur later on in a season), this becomes an advantage, rather than a disadvantage, of employing the Shifting-Window method. Furthermore, the Seasonal method frequently fails to provide an adequate representation of space use over the course of a season due to data collection limitations. In our analysis, 29.3% of extra-home range movements detected by the Seasonal method were detected under a partially constructed season, meaning that there was not enough data available to construct a home range for the entire length of the season in which the movement was detected. This occurred regularly at the beginning and end of data collection for each deer.

We recognize that the length of the 60-day PreHR period utilized by our Shifting-Window method may not necessarily be the most appropriate duration for establishing a home range and detecting deviations from “normal” space use in every instance. However, this same Shifting-Window approach can be implemented with a PreHR period of both shorter or longer duration (such as a PreHR period of 30, 45, 90, 120, or 365 days). For example, when attempting to detect extra-home range movements by highly mobile species or by those species with large home ranges such as wolverines (*Gulo gulo*, Whitman et al. 1986), African wild dogs (*Lycaon pictus*, Creel and Creel 2002), or griffon vultures (*Gyps fulvus*, Monsarrat et al. 2013), a much longer temporal period may be desired in order to accurately establish a typical area of space use. In contrast, where species have clearly defined home range boundaries, such as in red squirrels (*Tamiasciurus hudsonicus*, Gurnell 1984) or some coyote populations (*Canis latrans*, Shivik and Gese 2000), a shorter-duration period may be adequate for defining the boundaries of an individual’s “typical” space use provided that relocation sample size is adequate (Seaman et al. 1999). However, it should be noted that if extremely long PreHR periods are desired (such as when $n$ = 120, 240, or 365 days), no extra-home range movements are available for detection until $n + 1$ days after the start of data collection.

Other adjustments to our Shifting-Window method can, and should, be made, especially involving instances of migration events or dispersal activity. When instances of juvenile dispersal were observed in our study, we postponed our Shifting-Window search until 60 days after the dispersal event. This was done to allow individuals to determine and establish new patterns of space use on a landscape prior to detecting abnormal, extra-home range movements outside of this area. Though migratory events by deer do not occur in the region where our study was conducted, postponing the start of the extra-home range movement detection process until after $n$-days post-completion of the migration event (where $n$ is the number of days used to establish the PreHR period elsewhere in the analysis) is also recommended.

## Excursion Definition Criteria

In discussing the concept of territoriality in vertebrates, Maher and Lott (1995:1581), stated that, “The potential for instructive comparisons is high, but the comparative approach requires common terminology. Vague or implicit definitions of spacing systems undermine the rigour of comparisons…Workers pursuing research in this area can enhance their contribution by using clear conceptual and operational definitions of territoriality, making them explicit at the outset.” Similarly, Progulske and Baskett (1958:189) remarked that “Comparisons [of white-tailed deer movements] are difficult because of the differing techniques of investigation and expressions of results.” We found these arguments to also be true concerning the criteria and terminology used to describe and define excursive-type movements by white-tailed deer. We suggest that these conflicting and confusing differences, while still providing some insight into animal behavior, can hinder study design replication and can preclude “instructive comparisons” between studies. In order to address this, we present four guidelines for future studies investigating extra-home range movements and excursive-type behaviors by all species. We argue that future studies of this nature should 1) use clear, unifying terminology, 2) clearly present the definition criteria used for detecting these movements as well as the justification behind using those criteria 3) apply definition criteria suited to the species or taxonomic group of interest, and 4) also tailor definition criteria and terminology depending on the biological question being asked.

*1) Terminology*.— Among white-tailed deer literature that document some degree of extra-home range movement behaviors, at least 5 different terms have been used to describe these movements. The term “excursion” has been the most widely-used term characterizing extra-home range movements, though the terms “trip”, “foray”, “sallies”, and “exploratory movement” have also been used to document instances of irregular, infrequent, long-distance movement behaviors. However, the majority of studies use these 5 respective terms exclusively, meaning that a keyword search of the literature on an internet search engine or academic database and including only one of the terms would return a substantially limited set of results. While the first four terms listed here are close synonyms, the fifth term—"exploratory movement"—implies a motivation for the behavior, and that movements venturing outside a normal area are investigative, wandering, or searching in nature. This excludes the possibility that extra-home range movements may be directed toward a known end goal, regardless of whether or not this goal has been visited before in the past. While some extra-home range movements may indeed be exploratory in nature, no evidence has been presented to support this as an exclusive motivation (Karns et al. 2011, Olson et al. 2015, Simoneaux et al. 2015). In order to reach a more clear understanding of the behaviors and motivations that are manifested in these movements, we propose an operational definition of the term "excursion" to mean "any non-random, non-permanent, purposeful movement outside of a typical area of use", and suggest that all studies examining non-migratory, extra-home range movements utilize the term "excursions" when referring to these long-distance movements outside of home ranges. However, the use of this term within a study should not necessarily be exclusive, as synonyms of "excursions" may be useful as supplemental terms. It should also be noted that use of the term "excursion" does not necessarily imply that all of these movements should be viewed in the same context or held to the same criteria (see guidelines 2, 3, and 4 below).

*2) Criteria and justification.—* No two white-tailed deer studies examined here employed the same criteria for defining and distinguishing excursive-type behaviors from all other extra-home range movements. This means that previous instances of study design replication and reproduction (“the cornerstone of science”, Simons 2014) are likely non-existent on the topic of excursive-type behaviors, and that future reproducibility will be subject to selecting from a large pool of likely inadequate methodologies. When criteria from those studies implementing fixed minimum distance and/or duration values outside of 95% home range contours were applied to our data, the spectrum of excursion definition criteria from the literature led to dramatically variable detection rates of extra-home range movement. From 0% to almost 85% of the extra-home range movements in our sample dataset were missed by these criteria; however, all but one of these studies used the same term—“excursion”—to describe the movements being measured. Further variations in detection criteria have been reported in additional studies focused on excursions by white-tailed deer. Some of these (e.g., Hood and Inglis 1974, Inglis et al. 1979, Kilgo et al. 1996) calculated excursion distances from home range or activity centers, rather than contours, and Basinger (2013) measured excursion distances from 90%, rather than 95%, home range contours. Additionally, when our single example criteria were applied to our sample dataset, a wide range of extra-home range movement detection rates were obtained (24 – 85%) just by interchanging the “AND/OR” conjunctions between terms. Depending on the criteria used, several extremely long distance or long duration movements would have been excluded (e.g., 19 movements lasted less than the 12 h criteria but extended over 2.0 km, and 19 other movements extended less than the 1.0 km criteria but lasted longer than 24 h in duration). It could be strongly argued that these particular movements were clearly not artifacts of random home range periphery behavior (a valid reason for dismissing certain extra-home range movements), but instead were unmistakable excursions outside of a typical area of use. These types of omissions of excursion data not only risk missing important biological movements, but also lead to results that are not comparable between studies due to large differences in excursion frequencies. These examples highlight the need for caution when comparing what appear to be similar assessments of excursive-type behaviors, as well as the need for complete reporting of all criteria used to define excursive-type behaviors.

Furthermore, when a set of criteria for determining excursive-type movements is selected, a detailed biological justification explaining the selection of those criteria should be included in the methodology. In instances where fixed distances and durations are applied as definition criteria to distinguish between extra-home range movements and excursive movements, these values (e.g., 1.0 km, 1.6 km, 6 h, 12 h, 24 h) are often logical cutoff values, but are still arbitrary in nature. Additionally, the use of individual-based movement metrics (e.g., >2x the standard deviation of center-to-fix distance, Inglis et al. 1979) are arbitrary themselves and usually do not adequately measure all instances of biologically (or statistically) founded spatial outliers. Most, if not all, previous studies fail to provide justification for their methodology selection, likely because there is no clear biological support for these values, especially in choosing one fixed value over another. While it might be argued that the fixed value of 0.5 km used in this analysis of detection methodology is in itself arbitrary, we reiterate that this value was selected as a conservative threshold among excursion studies in order to prevent any possible excursive-type movements from being missed. Furthermore, this value was not used for the purposes of distinguishing between excursive-type movements and other extra-home range movements. We argue that future analyses examining excursive-type movements should clearly document all components of the analysis for the purposes of critique, as well as for reproducibility and comparison between studies (Dungan et al. 2002). Further, it is critical that considerable attention and documentation be given to the reasons why a particular criterion was selected and utilized. We also suggest the need for a general consensus on non-arbitrary "excursion" definition criteria, at least when these movements are viewed in a similar context (see guidelines 3 and 4 below). Arriving at this consensus may require exploring and/or improving alternative means of identifying spatially segregated and abnormal movements such as cluster analyses and spatial outlier detection methods (e.g., Ester et al. 1996, Ng and Han 2002, Achtert et al. 2011).

*3) Species/taxa of interest*.— Though our analysis focused exclusively on extra-home range, excursive-type behaviors found in published studies on white-tailed deer, movements of a similar nature have been documented and explored in the context of ungulate species such as roe deer (Richard et al. 2008, Lovari et al. 2008, Bocci et al. 2013, and Debeffe et al. 2014) and red deer (*Cervus elaphus*, Catt and Staines 1987, Wahlstrom and Liberg 1995, Sunde et al. 2009, Mysterud et al. 2011, and Stopher et al. 2011), as well as in other mammals (*Vulpes vulpes*, Tsukada 1997), avian species (*Buteo buteo*, Hodder et al. 1998), herpetofauna (*Sceloporus olivaceus*, Kerster 1964), and ichthyofauna (*Esox lucius*, Knight et al. 2008). It is highly possible that many of these species exhibit long-distance, excursive-type movements for biologically similar reasons, particularly concerning pre-dispersal movements by juveniles or in terms of resource (mate, mineral, or food) acquisition. However, a single, particular criterion may not be appropriate across all taxa. The term "long-distance movement" should depend somewhat on the scale of the home range and the normal scale of movement for the species in question. Similarly, in many instances, it may not be appropriate to compare all behaviors characterized as "excursions" even within taxa using the same criteria. White-tailed deer, roe deer, and red deer all employ different space-use tactics (e.g., territoriality) and breeding systems (e.g., harems), at least during certain times of the year (Hirth 1977, Clutton-Brock et al. 1982, Kjellander et al. 2004). Though each species has been shown to exhibit extra-home range movements, it is possible that different factors drive these behaviors in each species. Currently, excursion studies concerning roe deer and red deer (Lovari et al. 2008, Richard et al. 2008, Stopher et al. 2011, Bocci et al. 2013, Debeffe et al. 2014) have limited their analyses to breeding seasons only and thus a thorough review of the potential factors driving excursions has not been conducted. Furthermore, space use within and around the home range of a territorial species versus a non-territorial species is likely to be inherently different. Short-distance movements outside of the defined home range of a territorial species could be more biologically meaningful than short- or even long-distance movements outside the 95% home range contour of a species that does not exhibit territorial behavior. Therefore, even if individuals of each species were exhibiting excursive-type behaviors for the same reason (such as for inbreeding avoidance during breeding season), utilizing the same fixed-distance criteria to define these behaviors would be inappropriate and likely ineffective.

*4) Question of interest*— At the heart of the confusion among excursion studies is the following question: are researchers attempting to use a particular behavior to characterize the movement, or are they using the movement to characterize the behavior? In other words, are researchers trying to define “excursions” and “forays” based on the motivations behind the behaviors (e.g., breeding-related extra-home range movements), or based on what the movements themselves look like across a landscape (e.g., straight-line return movements extending beyond distance $X$ and duration $Y$)? This may appear like a trivial case of semantics; however, we argue that both approaches have regularly been employed and have further complicated the topic of excursions. Researchers investigating extra-home range movements during the breeding season may desire to understand how highly tortuous movements by males just outside the periphery of home ranges relate to female receptivity and conception. In contrast, researchers investigating the spread of chronic wasting disease from localized hot zones to outlying counties may only be interested in the occurrence and frequency of extremely long-distance, extra-home range movements by deer. Still others may be solely interested in determining the motivations behind why animals leave their home ranges on these movements in the first place. We suggest that if extra-home range movements are to be documented and discussed, researchers should clearly state why these movements are of interest and in what context these movements are to be viewed. This should aid in providing justification for the criteria used to describe and identify excursive-type behaviors, as well as justifying why the selected approach is appropriate for the taxa and question of interest.

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Table 1.1. Extra-home range movements detected by Seasonal and Shifting-Window methods [*n* and %] for white-tailed deer in Alabama, 2014 – 2016.

| | EHRM[a] detection method | | | |
|---|---|---|---|---|
| | Seasonal | | Shifting-Window | |
| Comparison | *n* | % | *n* | % |
| Total EHRMs detected | 215 | | 320 | |
| EHRMs 0.5 – 1.0 km | 109 | 50.7 | 191 | 59.7 |
| EHRMs ≥1.0 km | 106 | 49.3 | 129 | 40.3 |
| EHRMs available for direct comparison[b] | 198 | | 302 | |
| Unique EHRMs[c] | 16 | 8.1 | 120 | 39.7 |
| EHRMs 0.5 – 1.0 km | 14 | 87.5 | 105 | 87.5 |
| EHRMs ≥1.0 km | 2 | 12.5 | 15 | 12.5 |

[a] Extra-home range movement/s (EHRM/s)

[b] Some excursions were not available for comparison by the opposing method due to excursions occurring during the first 60 days (Shifting Window method) or if there were less than 60 days of data available in a given season (Seasonal method).

[c] EHRMs detected by the given method but not detected by the opposing method.

Table 1.2. Extra-home range movements [*n* and %] detected when various criteria from white-tailed deer studies were applied to our sample dataset from 33 deer in Alabama, 2014-2016.

| Criteria | Study reference | Criteria | EHRMs detected[a,b] | % |
|---|---|---|---|---|
| Distance only | Sample dataset | ≥0.5 km | 320 | NA |
| | Nelson and Mech 1981 | >1.6 km | 79 | 24.7 |
| | Kolodzinski et al. 2010[c] | >0.75 km | 185 | 57.8 |
| | Lutz et al. 2016 | >1.5 km | 83 | 25.9 |
| | Sullivan 2016[c] | ≥0.5 km | 320 | 100.0 |
| Duration only | N/A[d] | N/A | N/A | N/A |
| Distance AND duration | Karns et al. 2011 | >0.5 km, ≥6 h | 248 | 77.5 |
| | Olson et al. 2015 | ≥1.6 km, ≥12 h | 56 | 17.5 |
| | Simoneaux 2015 | ≥1.6 km, >13 h | 50 | 15.6 |
| Distance OR duration | N/A | N/A | N/A | N/A |

[a] Extra-home range movements (EHRMs)

[b] Number of EHRMs detected from the sample Shifting Window dataset

[c] Indicates additional "OR" criteria (i.e., if ≥50% of daily points are outside of the seasonal home range) which were not considered here

[d] Indicates that there were no studies documented with these criteria

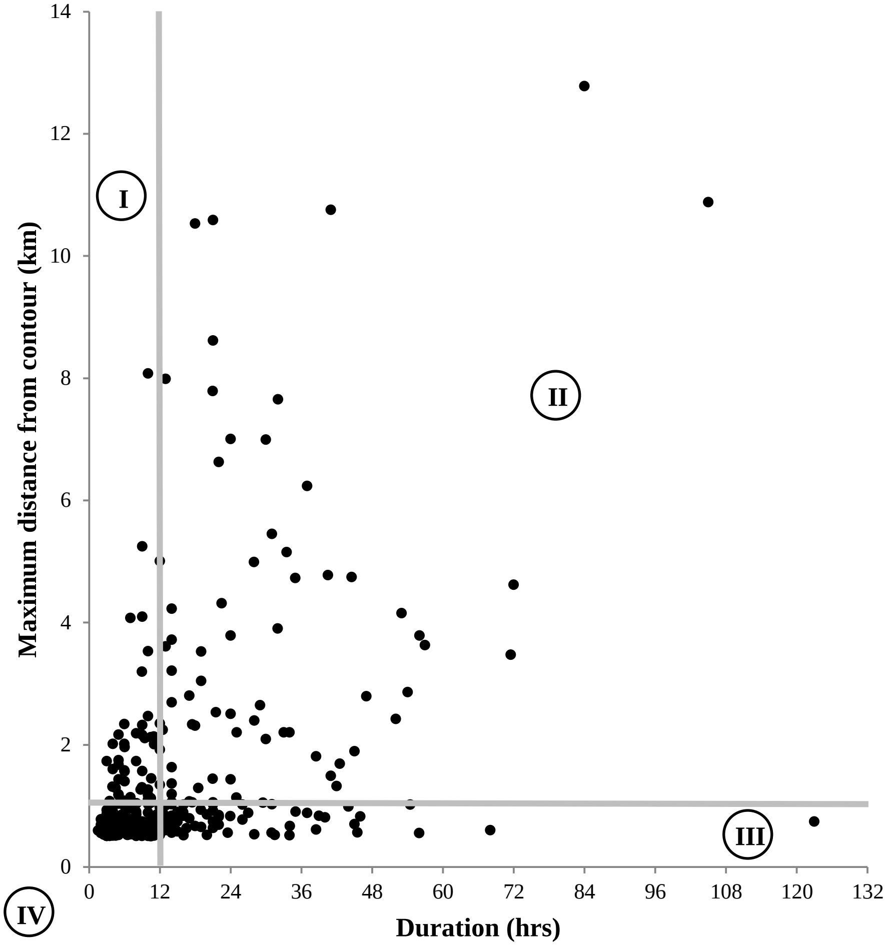

Figure 1.1. Sample dataset of 320 extra-home range movements by white-tailed deer in Alabama, 2014 – 2016, identified by the Shifting-Window method. Data were generated using a cutoff value of ≥0.5 km outside of 95% home range contours. Sectors of this graph, delineated by vertical and horizontal lines and denoted by the numerals I-IV, indicate portions of this dataset which may or may not be included in an example study where definition criteria for excursive-type behaviors include a distance value of ≥1.0 km AND/OR a duration value of ≥12 h.

## Chapter 2: Extra-home range movements and excursive behaviors by white-tailed deer

### ABSTRACT

Little is known about excursive movements outside of home range areas by white-tailed deer (*Odocoileus virginianus*). Detailed information concerning the motivation behind excursive movements, and the attributes of these long-distance movement paths themselves, may provide insight for population, habitat, and disease management at multiple spatial scales. We examined extra-home range and excursive-type movements in white-tailed deer by equipping 38 individuals of both sexes and multiple age classes with GPS collars across central Alabama. Using a novel method to detect extra-home range movements (EHRMs) by deer, EHRMs were identified in all months except June with a peak in EHRM rate for males occurring in the 30 days prior to mean female conception date. Males were 2.4-25.4 times as likely to undertake an EHRM during this period than during any other period. Females also tended to exhibit more EHRMs during this period. In all months where EHRMs were detected for both sexes, males exhibited greater EHRM rates than did females. Juvenile deer exhibited greater EHRM rates than deer ≥2 years old, and juvenile males undertook EHRMs at over twice the rate of juvenile females. All juvenile males and one adult male exhibited multiple repeat EHRMs to areas prior to dispersing to those areas. Most (95.4%) 30-day post-EHRM home ranges included some or all of the area explored by the EHRM. We hypothesize that most long-distance EHRMs are purposeful movements to investigate the availability of, or to acquire, specific resources that are not readily available within an individual’s home range and that the excursive behavior is the mechanism by which various, non-exclusive needs can be met. These needs may include food, mineral, or mate resources, or, for juveniles, potential dispersal sites that meet some or all of these collective needs. It may also include the desire to locate areas with less perceived predation risk or environmental stress. EHRM movement rates fell between daily movement rates of inter-home range movements and those of migratory movements reported in other studies. EHRM paths leaving the home range were more tortuous than subsequent return movements, and over 65% of all EHRMs exhibited periods of localized inactivity along the path. Periods of inactivity were located at the inflection point for 23% of EHRMs with identifiable inflection points. We failed to document any noticeable directional trends among EHRMs at individual sites or when viewed collectively. However, we detected a strong trend of deer utilizing their original outward EHRM paths to return back to their home ranges, and also observed a dramatic peak in EHRM initiation occurring during the 2 hours immediately surrounding sunrise (2.4-13.0 times as likely than any other 2-h period). Our results offer support for various hypotheses concerning the motivations behind infrequent, long-distance movement behaviors as well as document the spatial and temporal characteristics of these movement paths.

**KEYWORDS** breeding, dispersal, excursion, exploratory movement, foray, home range, *Odocoileus virginianus*, sallies, white-tailed deer

Substantial investments have been made by the scientific community to understand the factors and mechanisms associated with the concept of an animal’s “home range”, formally described by Burt (1943). This “home range” is most often approached from the context of a 95% contour or isopleth (e.g., Harris et al. 1990, Worton 1995, Powell 2000, Kie et al. 2010), and is usually derived from VHF or GPS-collar relocation data. Home range sizes and core area:home range ratios are widely employed to examine the relationship between space use and individual and population level characteristics such as body size (McNab 1963, Lindstedt et al. 1986), sex (Cederlund and Sand 1994, Mysterud et al. 2001), population density (Trewhella et al.

1988, Kilpatrick et al. 2001), or space-use strategy (Mitani and Rodman 1979, Grant et al. 1992). Furthermore, relocation data have been used to delineate home ranges for examining external factors such as resource availability and utilization (Cranford 1977, Wolff 1985), landscape heterogeneity (Kie et al. 2002, Anderson et al. 2005, Saïd and Servanty 2005), or vegetative cover (Tufto et al. 1996, Koehler and Pierce 2003).

However, aside from migration movements between seasonal home ranges and general relocation metrics such as overall movement rate or path tortuosity (Rettie and Messier 2001, Webb et al. 2011), very little attention has been paid to use of space by organisms outside their mathematically derived home-ranges. For the most part, these extra-home range movements are typically viewed as "noise" or as behavioral outliers in spatial datasets and are frequently overlooked (Catt and Staines 1987, Jones 1989, Geffen et al. 1992, Mosnier et al. 2003). While it may be biologically and mathematically reasonable to exclude these relocations from the definition of an organism's home range, vital insight into the behavioral ecology of a species may be missed when these extra-home range movements represent biologically meaningful behaviors but are ignored in the larger spatial dataset.

Additionally, the perception of the composition of extra-home range movements has changed as spatial ecology and movement studies rapidly shifted towards GPS-tracking technology at the start of the new century. Finer temporal-scale observations of daily movement patterns provided by GPS-collared individuals now allow for almost complete, continuous documentation of 2- and 3-dimensional movements across a landscape for an ever-increasing number of species (Bowman et al. 2000, Lewis et al. 2007). This in turn has allowed for increased detection of irregular, infrequent movements such as excursive-type behaviors outside of an animal's home range. A handful of studies have been published in the last decade that have begun to analyze excursive behaviors in ungulate species, particularly among white-tailed deer (*Odocoileus virginianus*; Kolodzinski et al. 2010, Karns et al. 2011, Olson et al. 2015) and roe deer (*Capreolus capreolus*; Lovari et al. 2008, Debeffe et al. 2014). Despite these studies, little is known about movements outside of home range areas, particularly concerning the motivation and factors driving their occurrence; however, this may partially be a function of the nature and extent of previous studies on the subject. Nearly all previous studies have limited their analysis of extra-home range movements to a single season and/or sex, and usually within a single year. Furthermore, in instances where more than just a brief mention was given of their occurrence, statistical analyses of excursions have primarily been limited to the distance, duration, and frequency of these movements (e.g., Kolodzinski et al. 2010, Simoneaux 2015).

Current research on movement theory has shaped and refined the principles explaining movement actions and events into three fundamental mechanisms: an “internal state”, a “motion capacity”, and a “navigation capacity” (Nathan et al. 2008). Each of these components can be, and have been, examined discretely, yet understanding the interactions among these components collectively is critical to understanding animal movement and behavior, particularly when the organism of interest and its associated environment are also subject to intense population and landscape management. Approaching extra-home range and excursive-type behaviors from these three perspectives can yield insights concerning animal resource availability and habitat quality, the physiological needs of an animal, as well as the potential for disease transmission and gene flow across a landscape. Furthermore, for intensively managed species such as white-tailed deer, a thorough investigation of these behaviors could have important implications for management and harvest guidelines, especially since deer are typically managed at the scale of individual properties or tracts of land (Hamilton et al. 1995, Webb et al. 2007).

Previous hypotheses concerning why deer undertake excursions are varied, sometimes conflicting, and often posited with the disclaimer that little or no supportive evidence has been found to support the particular theory. Such theories include both male and female breeding related movements, food-driven movements, mineral lick visitations, trips back to natal ranges, hunting pressure, and female aggression during pre-parturition (e.g., Kilgo et al. 1996, Karns et al. 2011, Olson et al. 2015). Our objectives were to investigate extra-home range movements by deer in light of these hypotheses. Furthermore, we expanded upon the typical movement and spatial descriptors of these behaviors—namely, excursion distance, duration, and directionality. By applying the three components of movement theory, we provide evidence for not only why but also how, when, where, and with what capacity deer traverse the landscape when undertaking these unusual extra-home range movements.

## METHODS

### Study Area

Data from this study were obtained from four sites across central Alabama (Figure 2.1). Two study sites—Barbour Wildlife Management Area (31°59.73 N, 85°27.57 W; hereafter, referred to as Barbour) and Oakmulgee Wildlife Management Area (32°57.39 N, 87°27.60 W; hereafter referred to as Oakmulgee)—were state-designated wildlife management areas (WMAs). Barbour was in southeastern Alabama, encompassed approximately 114 km$^2$ of land in Barbour and Bullock Counties, and was available for public access and hunting during most of the year. This WMA contained a mixture of habitat types including longleaf pine (*Pinus palustris*) in various stages of regeneration, loblolly pine (*Pinus taeda*), mixed hardwood upland areas, as well as mixed hardwood bottoms. In addition, the WMA maintained approximately 200 cool- and warm-season food plots totaling 90 ha. Oakmulgee was in west-central Alabama near the southern reaches of the Appalachian foothills, encompassed approximately 180 km$^2$ of land in Hale, Bibb, Perry, and Tuscaloosa Counties, and was also available for public access and hunting during most of the year. Dominant vegetation at this site included mature longleaf pine stands and widespread mature hardwood forests on upper ridges and slopes of the management area, as well as mature hardwood bottomlands. This WMA contained approximately 100 food plots, ranging in size from 0.2 – 1.6 ha and totaling approximately 60 ha.

The third study site, located in Pickens County (33°12.45 N, 87°52.01 W; hereafter, referred to as Pickens), was owned by a private commercial timber production company and comprised 16 leasable hunting tracts collectively managed by timber company biologists. This site encompassed approximately 49 km$^2$ of loblolly pine in various stages of regeneration and thinning, as well as several post-harvest clearings and hardwood-lined streamside management zones. Hunting lease holders planted and managed food plots on individual leased tracts, with approximately 2 – 5 plots occurring per 100 ha (most plots <0.5 ha in size). The fourth study site was located in Marengo County (32°14.08 N, 87°51.11 W; hereafter, referred to as Marengo) and encompassed approximately 31 km$^2$ of privately-held land. This site was made up of three adjoining private landholdings as well as the private timber company hunting leases adjacent to these properties. This site was characterized by various stages of loblolly pine regeneration, mixed-age hardwood stands, and several food plots, with a mean of 1.3 plots per 100 ha and ranging from approximately 0.25 – 1.75 ha in size. Both Barbour and Marengo were located in the Lower Coastal Plain geologic region of the state, while Oakmulgee and Pickens were located within the Upper Coastal Plain. All sites were characterized by some degree of rolling hills, and mean elevations ranged from approximately 90 – 120 meters above sea level. During 2014 –

2015, the hunting season for Oakmulgee and Pickens spanned from 15 October – 31 January, and from 25 October – 10 February for Barbour and Marengo. Specific dates of weapon restrictions and harvest regulations varied within these periods, particularly on the two WMA sites.

### Capture and Handling

During May – September of 2014, 30 deer (≥1 year old, males and females) were captured across the four study sites, with an additional 8 deer captured during May – July of 2015. Deer were captured with the use of Pneu-dart Model 193 cartridge-fired dart guns (Pneu-Dart, Inc., Williamsport, Pennsylvania, USA) that were equipped with 2.5x50 Yukon Titanium Varmint Hunter night vision riflescopes (Yukon Advanced Optics Worldwide, Inc., Vilnius, Lithuania). Darting of deer occurred from elevated tree stands and shooting houses or from roadside vehicles. Deer were immobilized and sedated via intramuscular injection by a 2cc Type-U radio-transmitter dart (Pneu-Dart, Inc., Williamsport, Pennsylvania, USA) containing a Telazol-Xylazine hydrochloride mixture (125mg/ml Telazol administered at 4.0 mg/kg; Fort Dodge Animal Health, Fort Dodge, Iowa, USA; 100mg/ml xylazine hydrochloride administered at 2.0 mg/kg; Lloyd Laboratories, Shenandoah, Iowa, USA). Immediately after darting and telemetry location of sedated individuals, deer were blindfolded to minimize stress, the tranquilizer dart removed, and a blood coagulant applied to the dart site.

All deer were fitted with a G2110D programmed-release global positioning system (GPS) collar (Advanced Telemetry Systems, Inc., Insanti, Minnesota, USA) and equipped with 2 (1/ear) large plastic cattle ear tags (Y-Tex Corporation, Cody, Wyoming, USA). The GPS collars were colored fluorescent orange and ear tags colored bright yellow to aid hunters in the identification of GPS-collared deer; hunters on all study areas were asked not to harvest GPS-collared deer.

Deer were field-aged using tooth replacement and wear (Severinghaus 1949), and age estimates were supported with other physiological characteristics assessed in the field. Trail camera photographs of collared deer at darting sites were also used post-hoc to verify these age estimates. All deer exhibiting tooth wear equal to or greater than that characteristic of a 5-year-old deer were grouped into one age class. For analysis purposes, deer were considered to progress into subsequent age classes on 1 June of each year. After data collection was complete, deer were reverse-immobilized via intramuscular injection of the antagonist Tolazine (100mg/ml tolazoline hydrochloride administered at 2.0 mg/kg, Lloyd Laboratories). Upon administration of the Tolazine reversal, all deer were monitored until completely ambulatory and indicating full awareness of their surroundings. Animal handling procedures were approved by the Auburn University Institutional Animal Care and Use Committee (PRN# 2013-2323).

### Data Collection and Manipulation

GPS collars collected data from the time of capture and collar deployment until the programmed automatic-release date during late March – early April 2016. Collars were programmed to attempt relocation fixes every 3.5 hours from 1 April – 30 September and once per hour from 1 October – 31 March. Fix rates were assigned in this way to maximize collar battery life over two successive breeding periods for each deer while still maintaining fine-scale data throughout the year, with more frequent fixes recorded during the period that encompassed breeding activities. Field tests to determine mean collar location error of G2110D collars (12.9 m; SD=9.8 m) in a similar environment in the southeastern US were conducted and described by Sullivan et al. (2016). Given this, we employed a slightly more-conservative 15-m collar location error rate for our analyses. After offloading GPS data from the collars, the data were censored for accuracy by removing 2-dimensional fixes with HDOP (horizontal dilution of precision) >5 and

3-dimensional fixes with PDOP (position dilution of precision) >10 or HDOP >6 (D'Eon and Delparte 2005, Lewis et al. 2007). All data obtained within 7 days post-capture were also censored from our analyses to avoid any potential effects of capture on deer movement and behavior.

## Extra-Home Range Movement Detection

*Criteria and terminology.*— In our analysis, as in the majority of previous analyses examining excursive-type movements, 95% home range contours were used to delineate the boundaries of an individual's home range. Most previous studies have employed arbitrary minimum distance and/or duration criteria to distinguish between excursive movements and those that are random peripheral movements occurring as part of an individual's daily activities yet still fall outside of the home range contour (e.g., Kolodzinski et al. 2010, Karns et al. 2011, Magle et al. 2015, Olson et al. 2015, Simoneaux et al. 2015). To reduce the potential of missing movements outside of the home range that are biologically meaningful examples of excursions, while at the same time minimizing the amount of non-meaningful periphery movements detected, we employed a conservative distance threshold of ≥0.5 km with no minimum duration cutoff for movements to be considered in our analysis. However, since no method currently exists to accurately distinguish between excursive-type movements and other random periphery movements, all movements detected by our analysis that were located outside the 95% home range contour and that met our minimum distance criteria are hereafter referred to as extra-home range movements (EHRMs). We determined the maximum distance of an EHRM as the shortest Euclidian distance from the edge of a 95% home range contour to the furthest point along that EHRM. While no minimum duration was established for these movements, characteristics of the dataset dictated that during our more intensive fix interval sampling period (1 fix/hour), the minimum EHRM duration possible was 2 hours, and minimum duration possible during our less intensive fix interval sampling period (1 fix/3.5 hours) was 7 hours.

*Home range construction.—* Home ranges and associated 95% contours were constructed in R 3.1.1 (www.r-project.org) using Brownian bridge movement models (BBMM, Horne et al. 2007). A grid cell size of 100 m was used to model the utilization distribution for each home range. However, rather than constructing a home range spanning the length of a given season and searching for extra-home range movements outside of this seasonal home range, which has been the method traditionally used for excursion detection (e.g., Kolodzinski et al. 2010, Karns et al. 2011, Basinger et al. 2013, Magle et al. 2015, Olson et al. 2015), we employed a novel analysis for EHRM detection. This detection method, referred to as the "Shifting-Window" method, was generated because of the inability of the traditional approach to account for changes in space use following and related to an EHRM. For example, an individual could undertake an EHRM and subsequently adjust its space use within the same season to utilize the area explored by the EHRM. However, because the traditional method uses all movements occurring within a season to construct a home range—including those movements occurring both before and after an EHRM—most instances of EHRM-related changes in space use would become masked by the overall seasonal home range. The Shifting-Window method accounted for this by only using movements occurring before an EHRM to define the home range area.

To perform our Shifting-Window analysis, we first established a typical area of use for each individual by constructing an initial 60-day home range area, denoted as the "PreHR". The PreHR started at the beginning of a deer's dataset at day $n$ and spanned until day $n$ + 59. Immediately following the end of this PreHR period, we then examined all movements occurring over the subsequent 2-day window (days $n$ + 60 and $n$ + 61) to see if any movements occurred which extended ≥0.5 km outside the 60-day PreHR. A 2-day window was used because we assumed it was long enough to adequately capture most multi-day excursions, but usually short enough to prevent more than one EHRM from being captured and to avoid capturing any major changes in space use not related to EHRMs. If any EHRMs occurred during the 2-day window but continued beyond the second day, the window was simply extended until the deer returned back to its home range. We repeated this process by shifting the PreHR and 2-day window by one day, so that the next PreHR began on day $n + 1$ and lasted until day $n + 60$, with the 2-day window now spanning days $n + 61$ and $n + 62$. The PreHR and 2-day window were shifted in this manner throughout each day of GPS relocation data for each deer. Using this method, EHRMs were only required to extend outside of the area used over the previous 60 days, rather than outside of an entire seasonal home range that was comprised of movements occurring both before and after each EHRM. Movements outside each PreHR period that met our minimum distance criteria and occurred during each 2-day shifting EHRM detection window were identified using R and later individually inspected for verification in ArcMap 10.2 (Environmental Systems Research Institute, Inc., Redlands CA, USA).

### Spatial Metrics

*Rate of occurrence*.— We calculated EHRM frequency relative to sex and age of individual deer by using generalized linear models (GLMs) for analysis of deer in the 1-year-old age class (for which each individual deer only had one year of data), and generalized linear mixed models (GLMMs) for deer in adult age classes (≥2 years old) with a random effect of deer to control for pseudoreplication of individuals when measured over multiple years. Frequency of EHRMs was modeled using a binomial error distribution and logit link applied to the count of days with and without EHRMs by yearly age class (odds of going on an EHRM versus not going on an EHRM).

*Timing of occurrence.*— Conception data were obtained for each study site by back-calculating deer fetal age data (Hamilton et al. 1985) provided by the Alabama Department of Conservation and Natural Resources (C. Cook, unpublished data). Mean date of female conception was calculated for each site individually due to the high variability of breeding dates throughout the state. All samples were obtained at each study site directly or on properties located within a radius of approximately 20 km from the center of each study site. Mean conception dates for Barbour, Oakmulgee, Pickens, and Marengo were 24 January, 31 December, 9 January, and 24 January, respectively. To determine the relationship between EHRM frequency and time of year, EHRM data were censored to only include those movements that lasted ≥7 h due to the variable collar fix intervals used during different times of the year. In this manner, all EHRMs had an equal chance of detection at any given time of the year. EHRM data for each study site were transformed to number of days to/from mean conception date for that given site. We modeled EHRM occurrence rate between sexes by applying GLMs using a binomial error distribution and logit link to the count of days with and without EHRMs for all deer, by sex, for 30-day periods (odds of going on an EHRM versus not going on an EHRM).

*Distance, duration, and movement rate.*— Maximum distance of EHRMs was calculated as the nearest distance from the edge of a 95% home range contour to the furthest point along an EHRM path. Duration was defined as the time elapsed between the last GPS relocation point inside the home range before the EHRM and the first relocation point back inside the home range. Total path length was calculated as the sum of the distances between steps from the first to the last relocation points of the EHRM. Rate of travel was calculated as the total path length divided by total duration. Maximum distance:total path length ratio was also calculated to provide an approximate measure of path tortuosity over the course of the excursion, where greater values suggest less tortuous and more direct EHRM paths. One-way dispersal events were excluded from this metric, and the maximum value possible for this ratio was 0.5 (a 1:2 maximum distance:total path length ratio). Data were analyzed seasonally (spring—1 March to 30 June, 121 days; summer—1 July to 31 October, 122 days; fall/winter—1 November to 28 February, 119 days) based on general changes in vegetative characteristics and weather patterns in Alabama. Linear mixed effects models were used for these spatial metrics, with age, sex, and season as main effects and with individual deer and study site treated as random effects. As these analyses were exploratory in nature, a more liberal alpha value of $P \leq 0.10$ was used to determine significant differences between groups (Harrell 2001), and interaction terms that did not improve the model were removed.

*Outward and return movements*.— An additional set of analyses were run on only those EHRMs with visually discernable points of inflection along the EHRM. The inflection point of an EHRM was defined as the last point along the EHRM where outward movement away from the home range ceased, and where this outward movement was predominantly followed by relocations progressing back towards the home range. EHRMs with clear inflection points were divided into their two components where movements before the inflection point defined the outward path and those after defined the return path. These outward and return paths were analyzed separately. Path length and duration of the outward and return paths of each EHRM were calculated. While overall path tortuosity for all EHRMs was calculated, the tortuosity of individual outward paths was also calculated using a sinuosity index (Benhamou 2004), where the Euclidian distance from the first point of the EHRM to the inflection point was divided by the total path length between the first point and the inflection point. The same procedure was performed with the inflection point and last point of the EHRM to determine tortuosity of return paths. A straight line from the EHRM starting or ending point to the inflection point would yield a straightness index value of 1.0. However, it should be noted that this straightness index may be biased towards EHRMs exhibiting more linear-type out-and-back behavior, as it was not possible to determine points of inflection for some EHRMs with extremely high variability in movement patterns and space use. Additionally, this straightness index may have been inflated for EHRMs that occurred during our less intensive fix rate period (Benhamou 2004). Comparisons between outward and return paths were made using paired *t*-tests. Linear mixed effects models were used to test relationships between outward path metrics and factors of age, sex, and season, with deer and study site treated as random effects. Again, a more liberal alpha value of $P \leq 0.10$ was used to determine significant differences between groups (Harrell 2001). Interaction terms that did not improve the model were removed.

*Bearing*.— For EHRMs with discernable inflection points, bearing was calculated as the compass direction from the first point of the EHRM to the inflection point. Bearing mean and mean resultant vector length Rho (ρ) were calculated for each study site. This metric provides a measure of directional strength for a dataset, where ρ equals 0.0 for two directional vectors 180° apart, and ρ equals 1.0 for two vectors with the same directional bearing.

*Path similarity*.— To determine the degree to which a deer followed its original outward path when returning back from an EHRM, a path similarity metric was calculated. This metric was only calculated for those EHRMs with clear inflection points. We constructed a 200-m radius buffer around each path segment of those EHRMs with identifiable inflection points, and divided the amount of path overlap between the outward and return path buffers by the area of the outward path buffer. A path overlap of 100% would indicate that a deer followed the original outward path completely when returning from the EHRM, and a path overlap value approaching 0% would indicate that little to none of the outward path was followed on the return trip back to the home range. The path similarity metric was calculated in this manner to determine the degree to which each deer adhered to the outward path on the return trip, regardless of any additional area explored on the return trip.

*Inactivity*.— To examine the occurrence and frequency of periods of inactivity along EHRMs, we only included those EHRMs that occurred during our greater-intensity data collection period (1-h fixes, October through March). For this analysis, we were not solely concerned with strict "inactivity" such as bedding behavior, but rather, we were also interested in capturing instances of "localized inactivity" such as feeding, mineral lick use, or mate tending behavior over a relatively small spatial extent. A minimum step length of 5 GPS-collar error standard deviations was recommended by Jerde and Visscher (2005) for determining if an individual was truly active or not. To attempt to capture localized inactivity, we extended this threshold to 100 m (approximately 10 collar error standard deviations) between successive relocations. Inactivity was calculated as total time spent inactive as well as the percent of total EHRM duration during which a deer was inactive.

*Start time*.— The first fix of each EHRM was used to define EHRM start time. Start times were transformed in relation to sunrise for each given day that an EHRM occurred. Sunrise times were obtained for each of the four study sites across Alabama from the US Naval Observatory Astronomical Applications Department (http://aa.usno.navy.mil/data/docs/RS_OneYear.php). We modeled the conditional probability of EHRM start time using a GLM with a binomial error distribution and logit link for the count of EHRMs occurring during each 2-h period (odds of going on an EHRM versus not going on an EHRM).

*Pre-post home range overlap*.— To quantify the amount of new home range area used subsequent to the completion of an EHRM, we constructed a home range using the data from the 30 days following an EHRM and referred to this as the "PostHR". We selected a period of 30 days because we believed it would allow ample time for a deer to incorporate an area explored by an EHRM into its regular pattern of activity via return trips if a deer chose to return to that area, while minimizing the probability of general or non-EHRM based seasonal expansion into other areas. The area of new usage following each EHRM was calculated as the ratio between the area of the PostHR that did not overlap with the PreHR, and the total PostHR area. Area ratios were only calculated for each EHRM that had ≥30 days of data available following the EHRM movement. Area ratios were classified into 3 possible scenarios, with 4 sub-categories possible within Scenario 3 (Scenarios 3A-3D). In Scenario 1, no relocation points that occurred along the EHRM were within the 30-day PostHR. In this scenario, we could be certain that the home range used over the 30-days following the EHRM was not influenced by a resource of interest located along the path of the EHRM. In Scenario 2, the PreHR and PostHR did not overlap, but the PostHR contained at least 1 point visited during the EHRM (such as after a dispersal event). In this scenario, we could be reasonably certain that the PostHR was directly influenced by knowledge or experience gained while a deer was on the EHRM. It should be noted that instances of dispersal to an area, where the disjunct, post-dispersal area was previously included as part of the PreHR due to repeated visits prior to dispersal, were excluded from this analysis. In Scenario 3, the PostHR contained at least some points visited by the EHRM and exhibited some degree of overlap with the Pre EHRM home range area. Scenario 3 was divided into 4 sub-categories (Scenarios 3A-3D) based on the percentage of new, non-overlapping home range area explored subsequent to the EHRM (i.e., >0 – 25%, 25 – 50%, 50 – 75%, 75 – 99.9% new home range area, respectively).

## RESULTS

### Extra-Home Range Movement Detection

Data were obtained for 35 of the 38 deer collared during the course of our study. The 3 collars for which no data were obtained failed to release from the deer upon reaching their programmed drop-off date. After censoring data to 7-days post-capture, 33 deer collars had collected data for at least 60 days, with a mean collar duration of 379.6 days (SD = 174.1 days) and a max duration of 577 days. We detected a total of 320 EHRMs for 32 of 33 deer. A female of 5-years-of-age or greater that was collared for 147 days did not exhibit any EHRM behaviors in the 87 days after establishment of her first PreHR (20 July – 15 October 2015).

### Spatial Metrics

*Rate of occurrence.*— Male deer were 1.5 (1.0 – 2.3, 95% CL; $P = 0.061$) times as likely to undertake EHRMs as female deer. When examined by age, yearling males were 2.1 (1.1 – 3.9, 95% CL; $P = 0.016$) times as likely to go on movements outside of their home ranges as yearling females, whereas adult males $\geq 2$ years old were 1.5 (1.0 – 2.2, 95% CL; $P = 0.034$) times as likely to leave their home ranges on EHRMs as adult females The greatest EHRM rate documented for an individual yearling male was 26 EHRMs over 387 days (0.067 per day), with a maximum rate of 27 EHRMs over 455 days (0.059 per day) documented for an adult male. The maximum EHRM rate for a yearling female was 6 EHRMs over 167 days (0.036 per day) and 3 EHRMs over 94 days (0.032 per day) for an adult female. In examining EHRM rate by yearly age class, deer were 1.3 (1.1 – 1.5, 95% CL; $P = 0.003$) times as likely to go on an EHRM for each 1-year decrease in age.

*Timing of occurrence.*— The timing of EHRMs was calculated for the 227 EHRMs that lasted ≥7 h. Extra-home range movements of this duration were documented to occur in every month of the year except June. Male deer were 2.4 – 25.4 ($0.001 \leq P \leq 0.004$) times as likely to go on EHRMs during the 30 days preceding mean conception than during any other 30-day period throughout the year (Figure 2.2). Female deer were 1.3-10.6 ($0.010 \leq P \leq 0.457$) times as likely to go on EHRMs during this period than during any other period. Additionally, males were 3.04 (1.80 – 5.12, 95% CL; $P < 0.001$) times as likely as females to undertake EHRMs during the 30 days prior to mean conception.

*Distance, duration, and movement rate.*— Mean maximum distance travelled outside the home range for deer was 1,576 m (SE = 105 m). On average, female EHRMs extended 805 m (± 485 m, ± 95% CI; $P = 0.003$) farther than male EHRMs. However, males went on 1.6 times as many ($P < 0.001$) EHRMs that extended between 0.5 and 1.0 km from their home range as did females (Figure 2.3). In summer, EHRMs were 819 m (± 717 m, ± 95% CI; $P = 0.026$) farther than in spring and 502 m (± 527 m, ± 95% CI; $P = 0.063$) farther than in the fall/winter season. Spring and fall/winter distances did not differ ($P = 0.300$). Yearling deer travelled 855 m (± 574 m, ± 95% CI; $P = 0.004$) farther than deer ≥2 years old. Adult deer did not differ in EHRM distance among ages ($0.388 \leq P \leq 0.863$). No interactions between EHRM distance and age, sex, or season were detected in our models. The maximum distance documented for an EHRM outside of a 95% home range contour was 12,776 m. This movement was performed by a 1-year-old male at the end of October, lasted a total of 84 h before the deer returned to its home range, and was characterized by nearly continuous movement.

Mean EHRM duration was 15.8 h (SE = 0.88 h). Of the EHRMs extending over 1.0 km outside of home range contours, 58.9% and 30.2% lasted ≥12 h and ≥24 h, respectively (Figure 2.4). We did not find any effect of sex on EHRM duration (*P* = 0.459), nor did we find an effect of season (*P* ≥ 0.565 for all seasonal contrasts). No interactions between EHRM duration and age, sex, or season were detected in our models. Maximum duration detected for an EHRM was 123 h; this movement was exhibited by a 4-year-old male in mid-November. However, aside from two unusual exceptions (when this 4-year-old male left its home range on the 123-h EHRM and spent multiple days going back and forth between a food plot and a likely bedding area, and also when a yearling deer dispersed, stopped along its journey for 4 days, and then moved to new area to establish a new home range), the greatest EHRM duration detected was 84 h, which was also the farthest EHRM documented.

Using a maximum distance:total path length ratio to calculate overall EHRM straightness, we found that EHRMs by males were 15.0% (± 4.7%, ± 95% CI; *P* < 0.001) less straight than those by females. EHRMs during fall/winter were 5.2% (± 5.4%, ± 95% CI; *P* = 0.062) less straight than EHRMs during spring. Fall/winter EHRMs were 4.9% (± 4.8%, ± 95% CI; *P* = 0.046) less straight than those in summer, but we did not detect a difference between spring and summer (0.3% ± 6.6%, ±95% CI; *P* = 0.927). EHRMs by deer 5 years old and older were 12.1% (± 10.4%, ± 95% CI; *P* = 0.024) straighter than EHRMs by all other age classes, but we found no other differences between age classes. No interactions between EHRM maximum distance:total path length ratio and age, sex, or season were detected in our models. Mean movement rate throughout each EHRM was 414 m/h, with a maximum movement rate of 1,266 m/h.

*Outward and return movements.*— Discernable points of inflection were documented for 271 of 320 EHRMs. Three additional EHRMs were instances of dispersal, where deer did not return to their original home range after the EHRM. The rate of male EHRMs with unidentifiable points of inflection (21.4% of male EHRMs) was 6.6 times greater than that of female EHRMs (3.2% of female EHRMs; SE = 0.040; $P < 0.001$). On average, the outward EHRM path length was 347 m (± 170 m, ± 95% CI; $P < 0.001$) greater than the return path length. Additionally, outward movements were 1.1 h (± 1.3 h, ± 95% CI; $P = 0.046$) greater in duration and 6.1% (± 2.4%, ± 95% CI; $P < 0.001$) more tortuous than return paths. Male outward EHRM paths were 11.8% (± 5.2%, ± 95% CI; $P < 0.001$) more tortuous than those of females. In fall/winter, outward paths were 6.9% (± 6.3%, ± 95% CI; $P = 0.039$) more tortuous than in spring, but there were no differences between fall/winter and summer or between spring and summer and ($P > 0.303$). No interactions between outward movement paths and age, sex, or season were detected in our models.

*Bearing.*— Directional bearing was calculated for the 271 EHRMs with identifiable inflection points. When all EHRMs were considered together, there was no clear directional trend in movements ($\rho = 0.14$; Figure 2.5), nor were there any site specific trends in EHRM directional bearing ($0.27 \leq \rho \leq 0.62$ for each study site).

*Path similarity.*— Path similarity was calculated for the 271 EHRMs with identifiable inflection points. We documented that 65.7% EHRMs exhibited ≥50% path overlap with their original outward paths while on their return trips, and 34.3% followed ≥70% of their outward paths on their return trips (Figure 2.6).

*Inactivity*.— Measurements of inactivity were calculated for the 285 EHRMs that were detected during our 1-h fix interval period (Figure 2.7). We documented at least 1 period of inactivity in 65.6% of these movements. However, when only examining those EHRMs with 1-h fixes and that lasted ≥6 h ($n = 213$), 82.2% (61.4% of all EHRMs with 1-h fixes) exhibited instances of ≥1 h of localized inactivity. Furthermore, of those EHRMs that lasted ≥6 h, 59.6% (44.6% of all EHRMs with 1-h fixes) exhibited instances of localized inactivity that extended for ≥3 h. Lastly, of those EHRMs that were collected during our 1-h fix interval and had clear inflection points ($n = 237$), 22.8% of these exhibited instances of inactivity at the inflection point, or terminus, of their respective EHRM.

*Start time*.— Extra-home range movements occurring within 1 h ± of sunrise (31.6% of all EHRMs) were  2.4 (1.6 – 3.5, 95% CL, compared to 1-3 hours after sunrise) to 13.0 (6.7 – 25.0, 95% CL, compared to 7 – 9 hours after sunrise) times more likely to occur than during any other period ($P < 0.001$ for all period contrasts; Figure 2.8).

*Pre-post home range overlap*.— The degree of overlap by post-EHRM home ranges on pre-EHRM home ranges was calculated for 282 EHRMs that had ≥30 days of data following the EHRM movement. PostHRs were greater in size than PreHRs in 67.4% of cases, and were 2.1 times larger than PreHRs on average. Only 4.3% of overlap areas fell under Scenario 1 (no EHRM points in the 30-day PostHR), and 0.4% of overlap areas (1 set of home range areas) fell under Scenario 2 (PostHR containing some EHRM points but no overlap between the PreHR and PostHR). Of the remaining overlap areas, 36.5%, 23.0%, 22.3%, and 13.5% fell under scenarios 3A through 3D (>0 – 25%, 25 – 50%, 50 – 75%, 75 – 99.9% new PostHR area), respectively.

## DISCUSSION

### The Internal State: Why Move?

Previous excursion-based studies conducted during and around the breeding season suggest that excursive behaviors by white-tailed deer are likely driven by mate acquisition and/or mate selection (e.g., Labisky and Fritzen 1998, Kolodzinski et al. 2010, Karns et al. 2011, Basinger 2013, Sullivan 2016). However, those that were conducted during the spring (e.g., Olson et al. 2015) or over multiple seasons (e.g., Kilgo et al. 1996, Simoneaux 2015) posit a range of hypotheses for excursive behaviors which include juvenile pre-dispersal explorations, trips by adults back to natal ranges, explorations for food, water, mineral sites, or refugia, or female aggression surrounding parturition (e.g., Hölzenbein and Marchinton 1992, Kilgo et al. 1996, Karns et al. 2011, Olson et al. 2015, Lutz et al. 2016), though many of these hypotheses have been rejected at some point or another. Based on the year-round documentation of EHRMs in our study by both males and females, in combination with a dramatic peak in EHRM frequency by males over the 30 days prior to peak conception, we suggest that extra-home range and excursive-type behaviors can be encompassed and summarized by a single, over-arching factor: these behaviors are purposeful movements to investigate or acquire resources that are not readily available within an individual's home range. However, this does not mean that each excursion is driven by a motivation to acquire the same resource. Rather, we suggest that the excursion is the mechanism by which a variety of different, non-exclusive needs can be met, and that the movement behaviors employed to meet these needs are often manifested similarly across individuals.

*Excursions as movements for physiological maintenance.*— We documented via our Pre-PostHR overlap analysis that 95.4% of post-EHRM home ranges included some or all of the area explored by the EHRM in the 30 days following the initial movement outside the home range. Additionally, 22.3% of PostHRs that included the area explored by the EHRM had ≤50% overlap with the PreHR, indicating a dramatic shift in space use during the 30 days following an EHRM. While we recognize that these shifts in space-use immediately following an EHRM may be due to reasons such as increased area usage while attempting to locate available mates, we also documented instances of post-EHRM shifts in space use to areas explored by EHRMs occurring throughout the year. This suggests than individuals undertaking EHRMs may be discovering resources of interest along these trips and subsequently shifting their daily movements to incorporate the explored areas into their home ranges. However, the hypothesis that food, water, and or mineral needs may be motivating excursive behaviors —factors related to the internal maintenance of individual organisms—has been regularly rejected, primarily because these resources were readily available within home ranges or were uniformly distributed across the study sites occupied by monitored individuals (Kilgo et al. 1996, Olson et al. 2015). Additionally, this hypothesis was rejected by Karns et al. (2011) due to a lack of observations of repeated excursions to an area. They argued that the cost and risk associated with these long-distance movements was likely not worth the benefit to internal maintenance gained by one or two visits to a food or mineral-related source. On the contrary, we believe that in many cases, the frequency with which individuals return to original excursion destinations is much greater than previously reported, primarily because traditional methods of excursion detection preclude the possibility of detecting shifts in space use following an EHRM.

We observed several specific examples of home range shifts encompassing areas explored by EHRMs in our study. In one instance, an adult male left his pine-dominated home range on an EHRM in mid-November, stopped along two small hardwood areas during the EHRM, and subsequently shifted his home range to incorporate those two areas into not only his home range but also into his core area of use over the next 30 days. In another instance, an adult male ventured from his home range in early November, and while on this EHRM, spent 5 days going back and forth between a regenerating clearcut bedding area and a food plot planted in a mixture of cool season forage. This deer also subsequently adjusted his movement activity over the next 30 days to incorporate this food plot into his home range area. We hypothesize that both deer shifted their space use to incorporate a food source in each case (hard mast and cool-season food plot, respectively). Had the movements of these two deer—and those of several other deer in our study—been analyzed from a traditional perspective using a seasonal home range, all or most of these EHRMs and subsequent shifts in space use into the areas explored would have been undetected. Therefore, it is likely that previous excursion-based studies have failed to document most instances of excursions that are followed by post-excursive shifts in space use, and have only primarily been detecting "unproductive" excursive movements or excursive movements where the needs of a deer were met along trip.

Exploratory movements outside of a known home range are risky and costly behaviors, both in terms of safety and energy utilization (Yoder et al. 2004, Karns et al. 2011, Sih and Del Giudice 2012, Fagan et al. 2013). Our distance and duration values are similar to those reported by other studies that confirm the relative brevity of excursive movements by white-tailed deer. Olson et al. (2015) reported a maximum excursion distance and duration of 8.0 km and 40 hours, respectively, and Simoneaux (2015) reported a maximum excursion distance of 4.9 km and a maximum duration of 52 hours. This suggests either that deer adequately located a resource of interest within a relatively short period, or that it is not profitable for an individual to be absent from known resources within a home range much past this time frame. We theorize that deer recognize the point at which the incurred cost appears to outweigh any remaining potential benefit of the long-distance movement (Parker and Stuart 1976) and return to their home range within a matter of days. It appears that extended trips by deer outside their home ranges for ≥4 days are extremely unlikely, and that a maximum duration threshold exists at which either the needs of the individual are typically met or the risks of traveling farther outweigh the possible benefits.

*Excursions as movements for breeding-related resources: males*.— The dramatic peak in EHRM frequency by males that we observed in the 30 days prior to mean conception date, followed by the abrupt decrease in male EHRM activity over the 30 and 60 days following this period, suggests a strong relationship between male EHRMs and breeding-related activities during late winter in our study. Furthermore, the increased levels of overall path tortuosity and the elevated rate of EHRMs without discernable inflection points observed for males, as well as the increased tortuosity in the fall/winter for all deer compared to spring and summer seasons, also suggest that a different motivation may be driving EHRMs during this time of year. It is well established that home ranges of male white-tailed deer tend to increase in size during the breeding period (e.g., Downing et al. 1969, Hosey 1980, Nelson and Mech 1981, Beier and McCullough 1990). Changes in path complexity and increases in movement rates and activity beginning at the onset of rut have also been noted for males (Kammermeyer and Marchinton 1976, Holtfreter 2008, Webb et al. 2009, 2010). These behavioral shifts by males reflected by changes in movement patterns are suggested to be an effort to actively locate and gain access to available mates (Holtfreter 2008, Long et al. 2013). Similarly, EHRMs and excursions may provide a mechanism for males to locate mates when there are no receptive females within a male’s home range area. Karns et al. (2011) noted that the timing of peak excursive activity by male deer in their study coincided with pre-breeding and breeding periods, and that the few additional excursions documented during post-breeding periods were possibly due to a second rut, where females not bred during peak rut periods became receptive again. Basinger (2013) also found that a majority of excursions observed during the breeding season occurred during peak rut. We believe that the significant increase in EHRM frequency by males observed in our study was primarily motivated by the search for receptive females. Additionally, we believe that the sharp decrease we observed in male EHRM frequency following peak conception was likely due to both a lack of un-bred females by that point, and/or an effort by males to recover from the extremely high physiological cost associated with rutting behaviors (Bobek et al. 1990, Ditchkoff et al. 2001).

A second notable peak in EHRM frequency by males was documented for the period spanning 60 – 90 days after mean conception date, and was subsequently followed by another drastic decline in EHRM frequency that continued for the following 90 days. This peak in male EHRM frequency was second only to the peak observed immediately prior to mean conception date. It is unclear why a change in behavior was observed during this period, but it could coincide with a period of late-onset estrus in female fawns (Verme and Ozoga 1987).

*Excursions as movements for breeding-related resources: females*.— We did not detect a substantial increase in EHRM frequency by females surrounding the breeding period as we did with males; however, the period occurring during the 30 days prior to conception was still characterized by the greatest frequency of observed EHRMs for females. Although conception during estrus obviously occurs for many deer at the end of this period, a "silent" first estrus may also occur for some individuals earlier in this same period (Plotka et al. 1977). Additionally, this peak in EHRM frequency was followed by a continual decrease in EHRMs until 90 days following peak conception, mirroring the post-conception decline in EHRMs exhibited by males. As with the males in our study, the observation of EHRMs by females throughout the year suggests that some, but not all, EHRMs occurring during the breeding season are motivated by breeding related factors (Sullivan 2016).

Several studies have suggested that a “sit-and-wait” strategy is the most advantageous breeding strategy for female deer when males are readily available (Hölzenbein and Schwede 1989, Labisky and Fritzen 1998). However, if males are sparse, females may engage in an “active search” strategy as they near estrus by increasing their home range size and movement rates (Labisky and Fritzen 1998, D’Angelo et al. 2004). Kolodzinski et al. (2010) and Sullivan (2016) also both documented peak excursion rates by females occurring around conception, though both studies occurred on areas with ample male density. In contrast, they suggested that excursions occurring around conception were attempts to exhibit some degree of mate choice and mate selectivity. This could explain the elevated EHRM rates detected for females in our study, given our relatively similar population parameters. However, studies on roe deer (Lovari et al. 2008, Debeffe et al. 2014) and red deer (Stopher et al. 2011) have failed to document that excursions by females result in the selection of specific, genetically fit, or unrelated males. For both males and females in our study, it is impossible to determine if some EHRMs were influenced by hunting activities, as hunting seasons overlapped substantially with the breeding season; however, hunting pressure was not found to noticeably influence excursion rates in other studies (Sawyer et al. 1989, Kolodzinski et al. 2010, Karns et al. 2011, Basinger 2013).

*Excursions as mechanisms for juvenile dispersal*.— Our results indicated that juvenile males were 2.1 times as likely to undertake EHRMs as juvenile females. This difference in EHRM rate was not driven strictly by the 3 juvenile male dispersal events detected by our analysis. Prior to these dispersals, as well as prior to the dispersal observed for 1 adult male, we observed several EHRMs occurring either along the route or to the actual area of final dispersal. An additional juvenile male dispersal was observed by visual inspection of our data but was not detected during our Shifting-Window analysis due to these repeated return trips to the final dispersal site.

Each dispersing individual exhibited between 1 – 13 return trips (mean = 4.8) along or to the final area of dispersal prior to the final dispersal event. We theorize that these EHRMs are examples of excursive, exploratory "test trips" to a novel area in order to reduce the potential costs and risks of dispersing to a completely unfamiliar and novel territory in which the individual has no knowledge of the resources available or degree of intraspecific competition. This is further supported by our consistent documentation of EHRMs to multiple different areas in-between trips, possibly to future dispersal sites. Exploratory movements by juveniles, many of which did not result in dispersal, were also observed by Skuldt et al. (2008) and Lutz et al. (2016). Lutz et al. (2016) suggested that these movements may have been failed dispersal attempts or that they satisfied physiological or physiological cues to disperse but did not actually result in the establishment of new home range areas. Dispersal by juvenile white-tailed deer has been well documented (Kammermeyer and Marchinton 1976, Nixon et al. 1991, Nelson 1993, Rosenberry et al. 1999, Long et al. 2008), with the predominant theory of dispersal suggesting that long-distance movements away from natal ranges serve to simultaneously reduce the chance of inbreeding while at the same time alleviate the effects of intersexual competition, particularly among male individuals of a species. The exhibition of dispersal activities by all juvenile males in our study, coupled with the observation of widespread, pre-dispersal EHRMs to areas of final dispersal movements by these individuals, provides further evidence that excursions represent exploratory movements for resources (e.g., potential unrelated mates or quality food resources) not readily available within an individual's home range. This may include resources that are unavailable due to intraspecific competition pressure from more mature individuals as well.

One of the most intriguing findings during this study, and the one that warrants the most additional research, concerns a set of tandem EHRMs by 3 deer that appeared to comprise a family group at Oakmulgee. Over the fall-spring of 2014-15, we documented 5 tandem EHRMs by a 3-year-old female and a 1-year-old female which had nearly completely overlapping home ranges. All of the tandem EHRMs extended to the northwest of their home range areas and followed the same EHRM path, with the longest tandem EHRM extending approximately 8 km outside their home ranges. In the summer of 2015, a yearling male was also captured and collared in the vicinity of the two females, with his home range almost completely overlapping those of the two females. In October 2015, the now-2-year-old female and the yearling male embarked on an EHRM together along the same route that the two females had used for their previous EHRMs, except that this tandem movement extended approximately 10.5 km outside their home ranges. This was also the first EHRM documented for the male since he was collared. Only 6 days after this tandem movement, the yearling male took a solo EHRM along the same path as the previous tandem EHRM, but approximately 2.5 km down this path, he branched off and explored a new area to the north of the frequented route. The younger female and yearling male repeated their tandem EHRM behavior along their traditional route once more together, but on 30 November, the yearling male dispersed by himself along the previous EHRM route and established his new home range in the area explored previously in October.

Though genetic tests of hair samples extracted from the GPS collars post-collar-release were inconclusive, we strongly believe that these three deer represent a multi-generational family group. Given the close association between these three deer and their EHRMs, we hypothesize that the observed examples of tandem excursive behavior may represent a maternally-taught or learned behavior, and one that may extend over multiple generations. Wiles and Weeks et al. (1986) suggested that white-tailed deer dams teach their fawns to visit particular mineral licks, and that deer may return to distant lick sites out of tradition. Though the exact motivation behind the excursions observed for the 3 deer is unknown, these tandem excursions may represent a similar scenario. Like mineral sites, it is also possible that the route, or the behavior of "excursing" itself, may be what is passed on and taught to offspring. In conjunction with this newly observed tandem-excursion behavior, we also suggest that exploratory, pre-dispersal "test trips" may originally stem from this maternally-taught behavior and may ultimately be a mechanism of juvenile dispersal. This is supported by evidence documented by Hölzenbein and Marchinton (1992), who observed that orphaned juvenile males exhibited greater fidelity to natal ranges than did non-orphaned juvenile males. However, as we were only able to document instances of tandem excursions between three individuals at one site, we strongly recommend that further studies attempt to collar multiple individuals of both sexes from family groups and examine genetic relatedness between these individuals in order to test the theory of learned excursive behaviors, as well as the theory that learned excursive behaviors may be a mechanism for juvenile dispersal.

### The Motion Capacity: How to Move?

The characteristics by which an individual moves across the landscape are reflective of both external and internal factors (Folse et al. 1989, Benhamou 1994, Bartumeus et al. 2005, Nathan et al. 2008). Though movement rate was calculated over all EHRM relocation fixes, including periods of inactivity which may have decreased overall EHRM movement rate, the mean movement rate detected for EHRMs during our study was under 0.5 km/h, with a maximum of just over 1.2 km/h. In contrast, while monitoring migratory movements by white-tailed deer, Nelson et al. (2004) determined mean rate of travel during moving periods at 1.2 km/h. A mean rate of diel travel of 0.15 km/h was documented for deer throughout non-migratory rut periods by Labisky and Fritzen (1998), and even during periods of extensive hunting with dogs, mean rate of travel documented by D'Angelo et al. (2003) did not exceed 0.23 km/h. Therefore, the movement rates documented for EHRMs in our study were less than those documented during a migration event, but were greater than the mean daily movement rates documented in other studies. This suggests that EHRMs likely reflect a unique type of movement behavior.

No previous studies on deer have examined EHRMs or excursions in terms of the individual outward and return path segments. We found that outward EHRM paths were slightly longer in duration, had a longer overall path length, and were more tortuous than return EHRM paths, indicating that return trips were probably more direct than their original outward movements. These findings support our previously discussed theories for EHRM motivation. Regardless of whether EHRMs represent movements to locate food, mineral, mate, or future dispersal site resources, movements that are exploratory and searching in nature are likely to exhibit more tortuous paths than the return movements back to an individual's known home range area (Benhamou 2004, 2006; Fagan et al. 2013). These data are similar to those reported for Magellanic penguins (*Spheniscus magellanicus*; Sala et al. 2012), that exhibited more direct paths when returning to colonies from foraging expeditions compared to paths during outbound trips and foraging movements.

Most EHRMs examined in our analysis—65.6% of all EHRMs and 82.2% of EHRMs lasting ≥6 h—exhibited periods of localized inactivity. Though Karns et al. (2011) did not document how they defined "periods of little to no movement" in their study, their reported value of 59% for excursions lasting ≥6 h and exhibiting little to no movement over a period of ≥3 h was nearly identical to the number of EHRMs documented in our analysis (60%) under the same criteria. The widespread occurrence of inactivity along EHRMs, particularly at the inflection point/terminus of these movements, suggests that deer may travel fairly continuously throughout EHRMs unless a resource of interest is discovered; at this point, deer may restrict their movements over a localized area to exploit or further investigate the resource prior to returning back to their home range. Kolodzinski et al. (2010) also noted periods of inactivity lasting a few hours before females on breeding season excursions returned back to their home ranges, and Hölzenbein and Schwede (1989) observed that a female on an excursion was tended by a male and remained with him in the same area until returning back to her home range. Other instances of inactivity in our study which occurred along the EHRM path, but not at the terminus, may also be examples of resource exploitation while travelling on an EHRM before reaching its inflection point.

## The Navigation Capacity: When and Where to Move?

We did not detect any overarching directional trends in EHRMs across deer at individual study sites, or when EHRMs from all study sites were combined. Most EHRMs that appeared to show some degree of directionality trend were repeat EHRMs along the same path or to the same final destination by the same individual deer, or were tandem EHRMs by multiple individuals along the same path. However, we observed that some EHRMs were likely influenced by localized geographic features such as rivers (e.g., the Sipsey River at Pickens) or roads within a given site –geographic features that have also been documented to influence juvenile dispersal movements (Long et al. 2010).

In contrast to our results, Kilgo et al. (1996) documented significant, non-uniform dispersal and excursion movements by deer (*n* = 10 dispersals and *n* = 13 excursions across 12 deer), but did not observe any topographical or vegetative features at their northern Florida study site that explained this directionality. Olson et al. (2015) also documented strong directional trends of excursions (*n* = 26 across 9 deer) in north-central Pennsylvania, but posited that these movements were not influenced by regional topography. We suggest that these previous studies documenting directional trends but failing to identify causal relationships may have been influenced by low excursion sample sizes, repeated excursions by individuals to the same area or along the same path, or topographical or other geographical features that were undetected. This is supported by the findings by Long et al. (2010), which documented that the directionality of juvenile dispersal from a site in eastern Pennsylvania paralleled the contour of long ridges in the area, but that dispersal was uniform in directionality at a study site where topography was irregular and less extreme.

We observed a strong pattern of deer closely following some or all of their original outward paths when returning from EHRMs. White-tailed deer have several exocrine glands that are often used in conjunction with marking behaviors and the creation of scent trails, particularly during the breeding season (Moore and Marchinton 1974, Sawyer et al. 1989, Ditchkoff 2011). Additionally, Rogers (1988) suggested that homing behaviors exhibited by various translocated carnivores and herbivores (including deer) may be influenced by olfactory cues, rather than by true internal navigation, yet this has not been applied to comparatively small-scale movement behaviors such as EHRMs. Once deer on EHRMs locate a resource of interest or have abandoned the search and begin orienting back toward the home range, they likely employ these olfactory, visual, and/or spatial memory cues (Folse et al. 1989, Brooks and Harris 2008, Gautestad 2011, Fagan et al. 2013) deposited or noted on the outward trip to efficiently navigate back towards their home range along the same EHRM path.

Lastly, we noticed a clear initiation of EHRMs immediately surrounding sunrise in our study. This is the first instance to document the temporal onset of EHRMs and excursive-type behaviors based on a particular environmental cue. Increased activity by deer around dawn has been well established (Montgomery 1963, Ozoga and Gysel 1972, Zagata and Haugen 1974, Kammermeyer and Marchinton 1977, Beier and McCullough 1990); however, several of these studies suggest that deer return to bedding areas shortly after sunrise and are inactive until dusk. Peaks in movement activity by ungulate species around crepuscular periods are believed to be an antipredator response (Loe et al. 2007, Long et al. 2013, Bonnot et al. 2016). While threats to adult deer from natural predators are relatively low in Alabama, anthropogenic threats in the form of hunting pressure during daytime hours should result in increased antipredator responses during daylight hours (Lima and Bednekoff 1999, Sönnichsen et al. 2013) However, the subsequent decrease in activity following sunrise was not observed in the context of EHRMs in our study, particularly as most EHRMs extended for several hours and nearly all were characterized by fairly continuous movements throughout. Given our theory that EHRMs by white-tailed deer are driven by the need to acquire resources not readily available within the home range area, it is possible that deer may be more willing to incur risk to meet these needs (Bachman 1993) than when engaged in normal daily activities.

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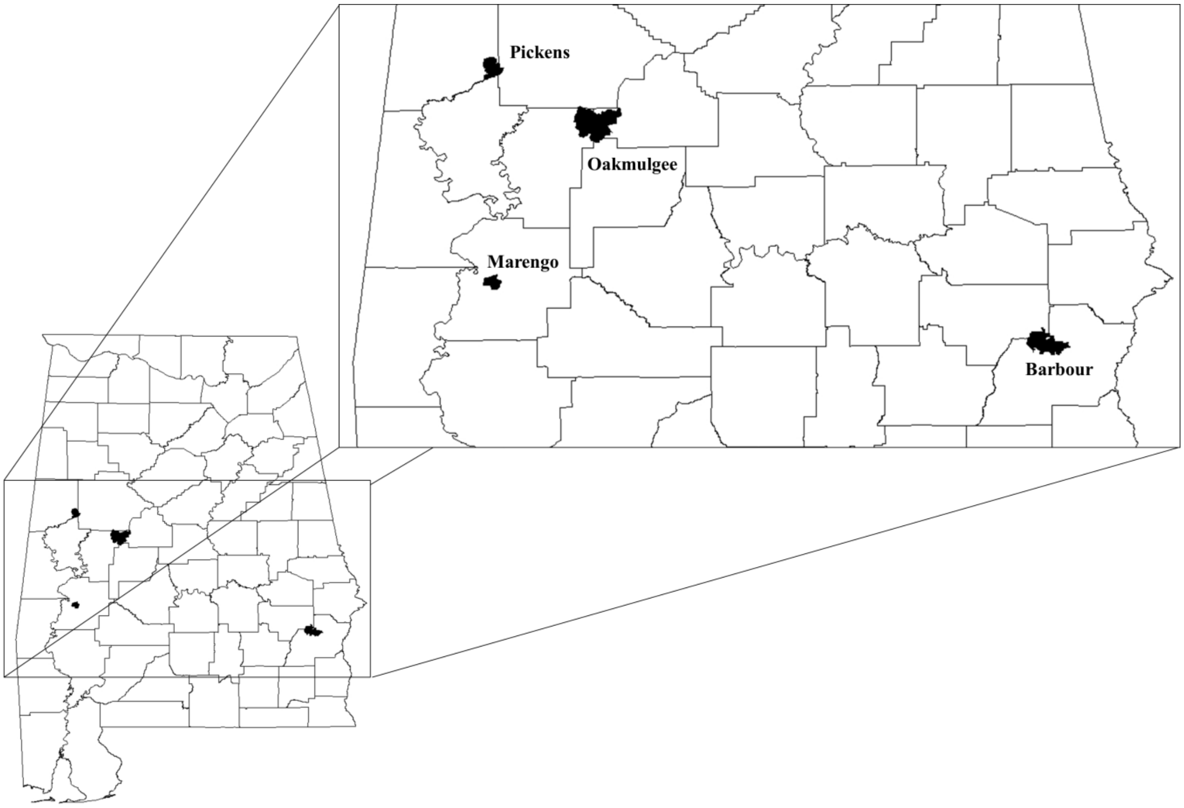

Figure 2.1. The four study sites in central Alabama on which white-tailed deer where captured, GPS-collared, and monitored from 2014 – 2016. Deer were collared on the Barbour and Oakmulgee WMAs, as well as on two private land conglomerates in Marengo and Pickens counties.

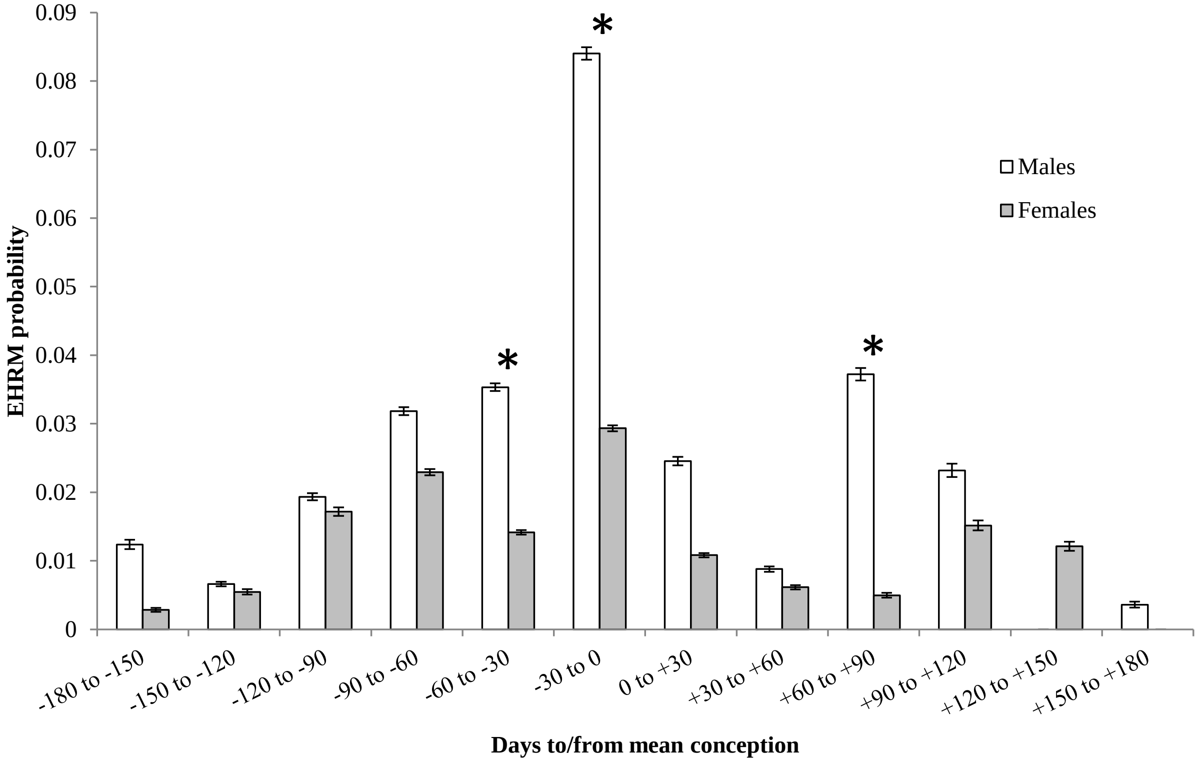

Figure 2.2. Probabilities of EHRMs occurring throughout the year in relation to mean date of conception for both male and female white-tailed deer in Alabama, 2014 – 2016. Asterisks indicate that the probabilities of an EHRM were significantly different for males and females in the given period. Error bars represent 95% confidence limits for the true probability based on a normal approximation.

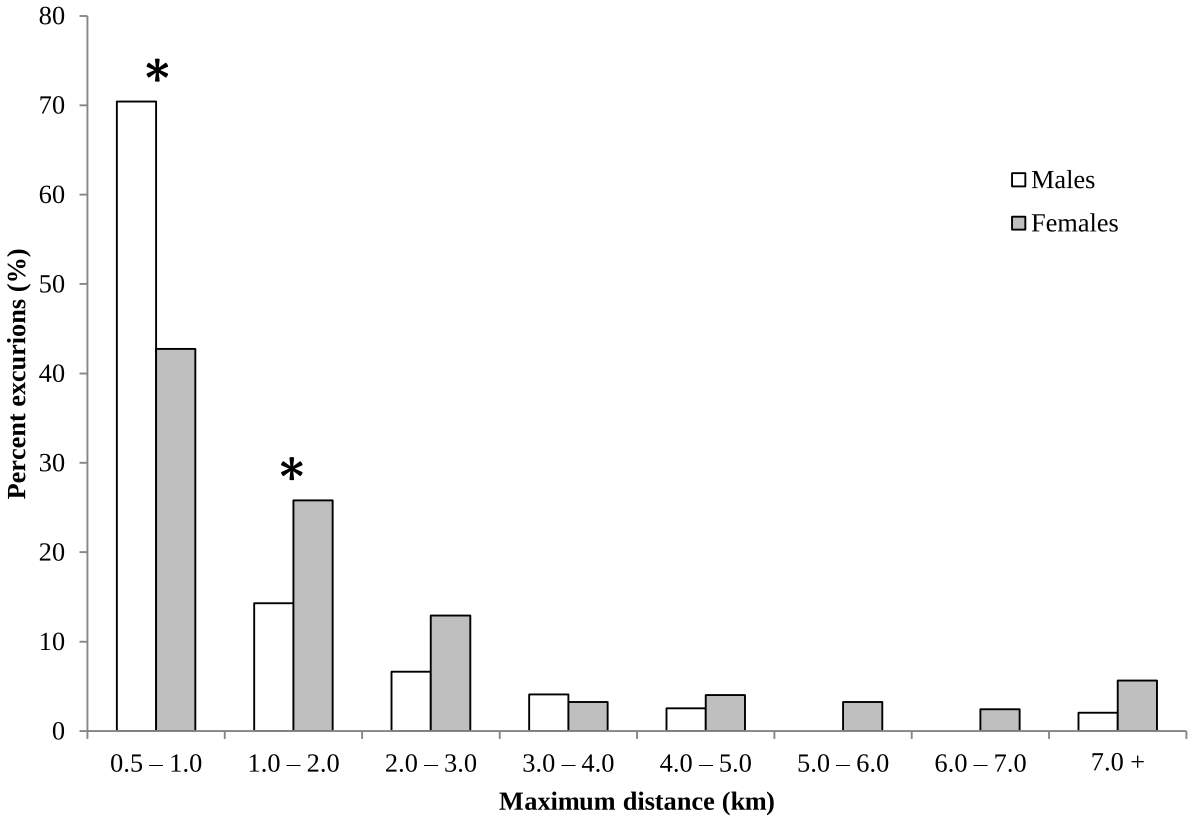

Figure 2.3. Maximum EHRM distance travelled outside of 95% home range contours for male and female white-tailed deer in Alabama, 2014 – 2016. Asterisks indicate significant differences between sexes at the given distance range.

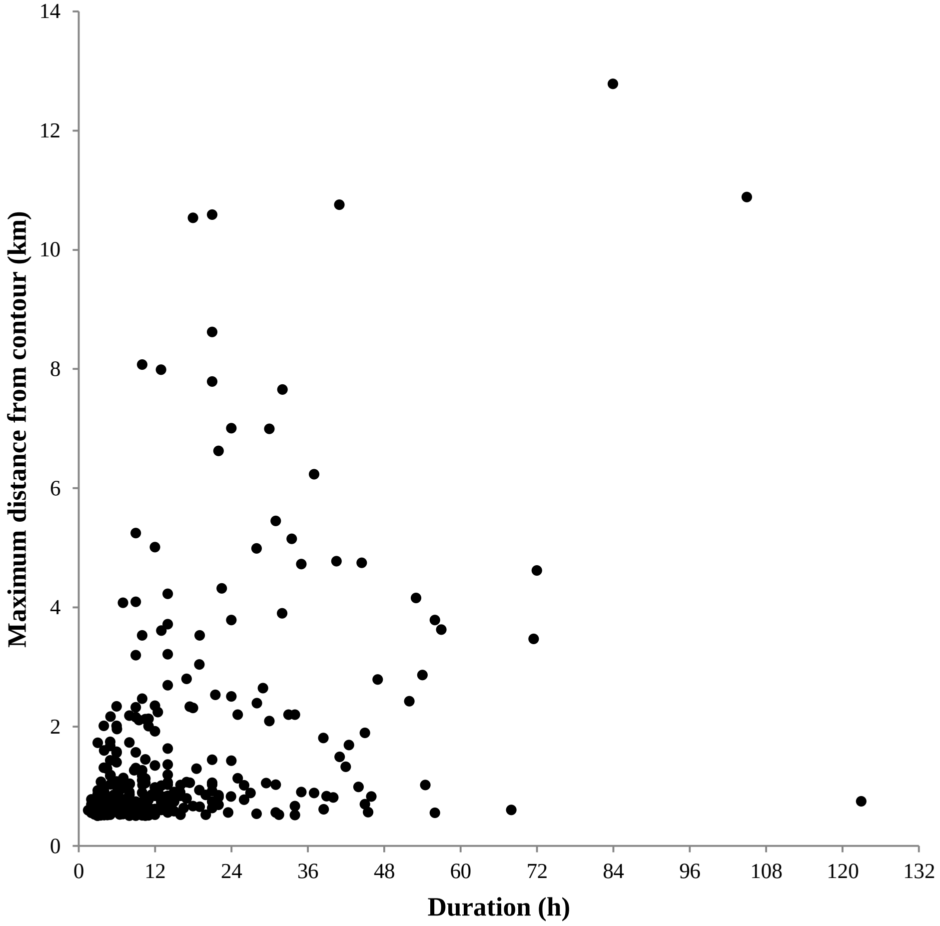

Figure 2.4. Maximum distance [km] and duration [h] of 320 extra-home range movements documented for white-tailed deer in Alabama, 2014 – 2016.

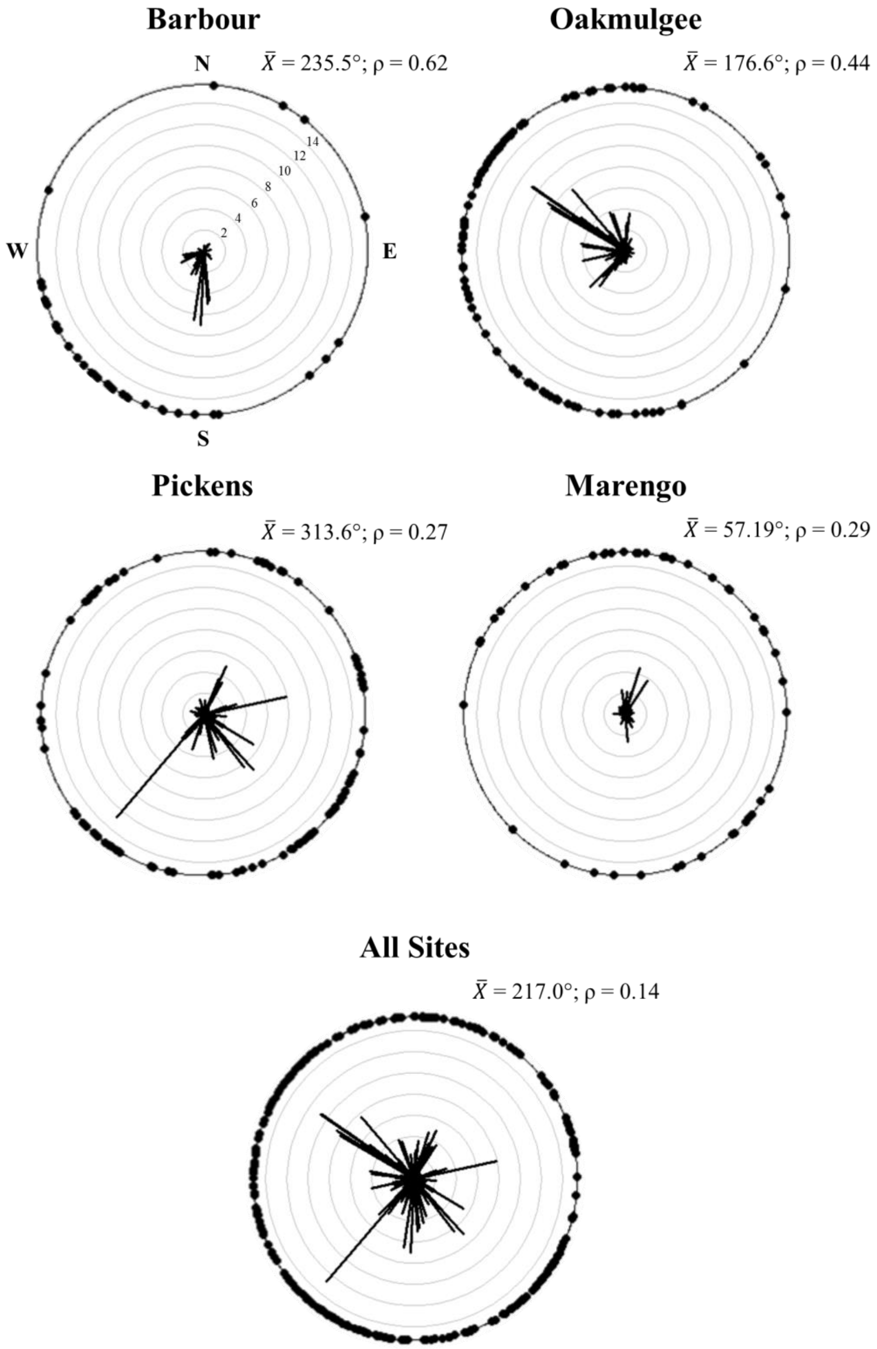

Figure 2.5. Bearing of EHRMs with identifiable inflection points at each study site for white-tailed deer in Alabama, 2014 – 2016. Bearing was determined as the vector extending from the first point of the EHRM to the inflection point. Rho (ρ) values indicate the strength of the combined directional vectors. Concentric circles represent EHRM maximum distance, in 2-km intervals, from 95% home range contours.

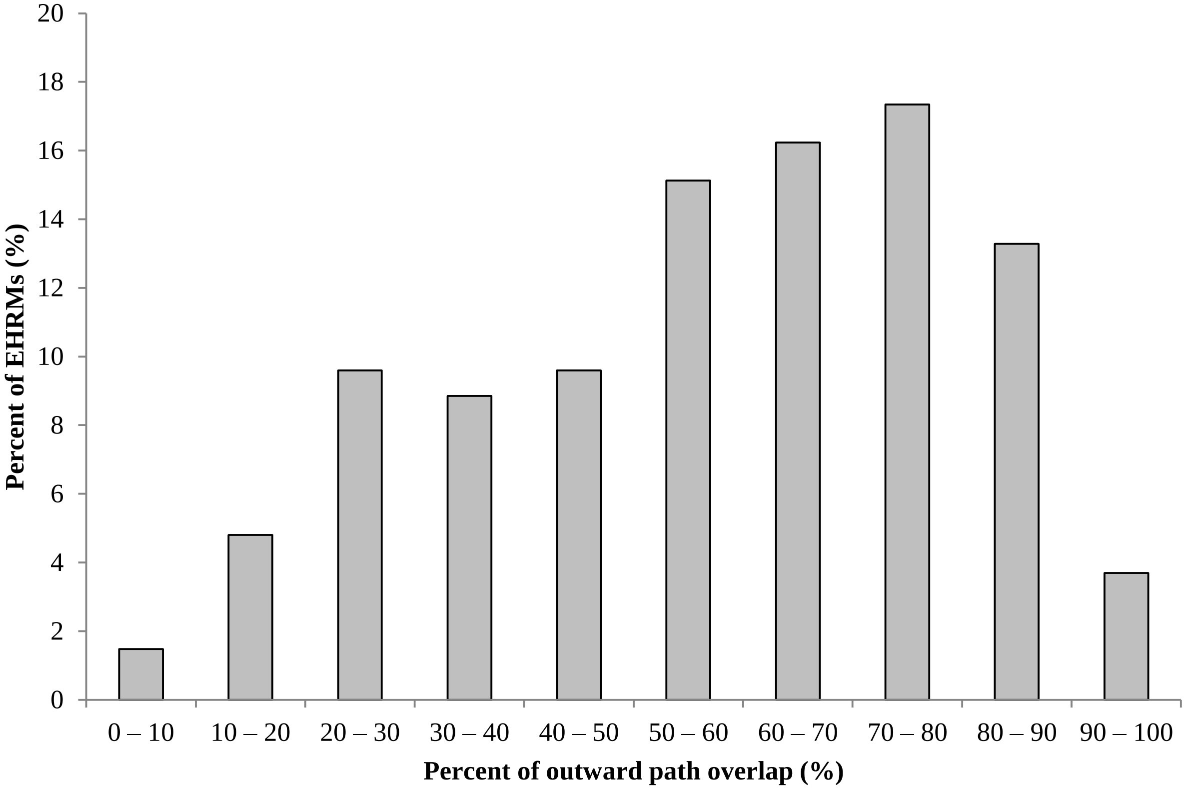

Figure 2.6. Degree of overlap of outward EHRM paths by their respective return EHRM trips for white-tailed deer in Alabama, 2014 – 2016.

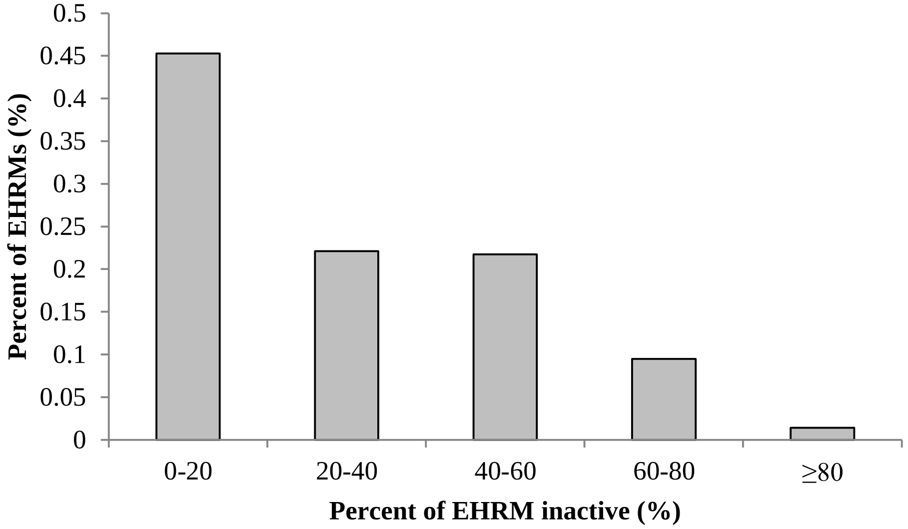

Figure 2.7. Percent of EHRMs with varying degrees of inactivity along each EHRM for white-tailed deer in Alabama, 2014 – 2016.

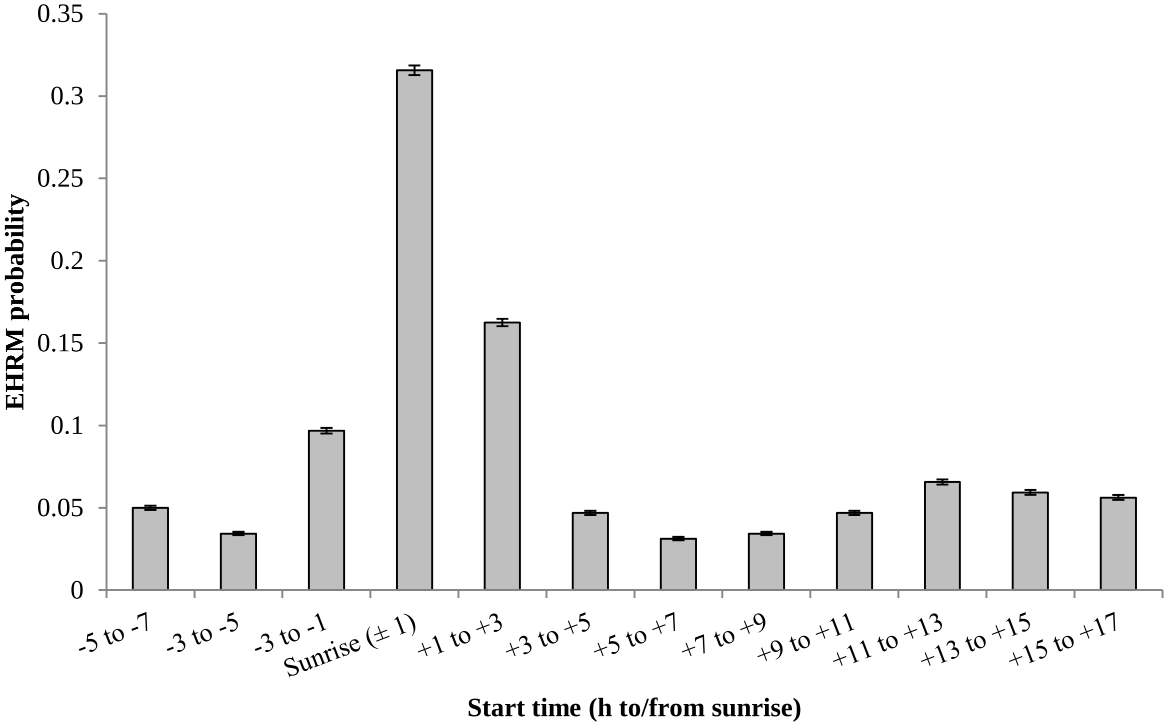

Figure 2.8. Probabilities of EHRM start time in relation to sunrise ("-" indicates prior to sunrise, "+" indicates after sunrise) for white-tailed deer in Alabama, 2014 – 2016. Error bars represent 95% confidence limits for the true probability based on a normal approximation.