Fine-scale Movements of Adult Male White-tailed Deer in Northeastern Louisiana during the Hunting Season

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Abstract: Understanding movement patterns of adult male white-tailed deer (*Odocoileus virginianus*) is important to explaining population dynamics, predation interactions, gene flow, and disease spread. Relatively few studies have investigated movement ecology of mature male deer, although recent trends in hunter-harvest selectivity have led to an increased representation of this cohort in many herds. Multiple co-occurring variables influence spatiotemporal variation in deer movements, but individuals should move at an optimum rate to maximize individual health and fitness while minimizing high-risk encounters. We used GPS telemetry data from 24 adult male deer (≥2.5 years old) in northeastern Louisiana to determine fine-scale movement patterns during the 2013–2014 and 2014–2015 hunting seasons. We calculated half-hour step lengths and performed generalized linear mixed models to examine the effects of habitat, age, breeding chronology, photoperiod, and refugia from hunting on step length. We used information-theoretic approaches to identify the most plausible model. On average, deer moved more in agriculture and mature hardwood areas. Also, older individuals moved less. Movements were greatest during the rut, especially at crepuscular and night hours. Our most plausible model suggested mature males tended to be more crepuscular in refuge areas where they were infrequently hunted compared to adjacent lands which were open to hunters the entirety of the season. Despite the amount of covariates we examined, our models explained a relatively small amount of movement variance. Future research should examine the degree of within-population heterogeneity in spatial behaviors and its resulting effects on individuals.

Key words: GPS, hunting pressure, Louisiana, movement, *Odocoileus virginianus*, refuge, white-tailed deer

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Understanding animal movements is necessary for explaining population dynamics, competition and predation interactions, gene flow, and disease and parasite spread. Under the optimality theory, animals should select behaviors which maximize individual fitness by balancing movements to seek needed resources (e.g., food acquisition, mate finding) with movements to avoid high-risk encounters such as predation (Reiss 1987). Hunted animals encounter a perplexing situation as ephemeral predators (i.e., hunters) shift the predation risk landscape both daily and seasonally. For many species, this process becomes more dynamic as hunting season occurs during the peak of their breeding cycle. In hunted polygamous species, males must balance the risk of natural and hunter-induced predation with increasing movements to seek mates (Gude et al. 2006). In response, animals can shift the focus of their movements to less risky areas (Burcham et al. 1999, Proffitt et al. 2009), times (Creel et al. 2008), mate-search strategies (Foley et al. 2015), or a combination which may differ among individuals (Bolnick et al. 2003).

The movement ecology of female and immature male white-tailed deer (*Odocoileus virginianus*; hereafter deer) has been extensively characterized at varying spatial scales (Tester et al. 1964, Beier and McCullough 1990, Kilpatrick et al. 2001, Brinkman et al. 2005, McCoy et al. 2005). However, recent trends in hunter-harvest selectivity have led to an increased representation of adult males in many populations (Adams and Hamilton 2011, Adams and Ross 2014). Historic over-exploitation in many deer herds has made studying this demographic difficult. Consequently, it has been difficult for researchers to study variables affecting movement of adult male white-tailed deer during the breeding season, despite this time aligning with hunting season. During the breeding season adult males exhibit increased movements to maximize encounters with females in estrus (Kammermeyer and Marchinton 1977, Tomberlin 2007, Webb et al. 2009, 2010, Foley et al. 2015). This change in movements may differ among age classes of deer and also may be influenced by environmental characteristics (Webb et al. 2007, Hellickson et al. 2008, Stewart et al. 2011, Quinn et al. 2013, Foley et al. 2015). For example, adult male deer may shift their movements toward increased nocturnal activity in areas of intense anthropogenic activity (Williams et al. 2011, Little et al. 2014) and avoid risky areas if refuge areas are available (Zagata and Haugen 1973, Kammermeyer and Marchinton 1976, Nixon et al. 1991, Sargent and Labisky 1995, Little et al. 2014). Home range size and movement rates typically decrease in refuge areas compared to hunted areas (Root et al. 1988, Sargent and Labisky 1995), although this trend has not been consistent across all studies, perhaps due to availability of cover (Karns et al. 2012). Together, these anthropogenic activities, such as hunting, and environmental variables consort to influence activity patterns across temporal and spatial scales. These activities in turn affect individual deer observability, disease transmission, harvest susceptibility, and deer-vehicle collisions (Vercauteren and Hygnstrom 1998, Schauber et al. 2007, Little et al. 2014).

Our objective was to evaluate environmental and anthropogenic factors influencing the movements of adult male deer. We examined the influence of age, circadian period, macrohabitat, hunting pressure, and reproductive phase and their interactions on deer movements across an entire hunting season. We hypothesized that movement of adult male deer would increase when they became reproductively active, but in areas with consistent hunting pressure they would decrease crepuscular and daytime movements with the onset of hunting. In a refuge area where hunter access was limited, we hypothesized that adult male circadian activity would not change throughout the season.

Methods

Study Area

We conducted research on the Tensas River National Wildlife Refuge (TRNWR) and adjacent private lands located in northeastern Louisiana in the upper Tensas River Basin. The 30,750-ha refuge was established in 1980 and was once predominately agriculture after being extensively logged. Since acquisition by the U.S. Fish and Wildlife Service, forests on the refuge have grown into mature bottomland hardwood and swamps, and former agricultural fields have been replanted in native hardwoods. The refuge was bordered almost entirely by agriculture on all sides, making it an island of habitat for many species including deer and the federally threatened Louisiana black bear (*Ursus americanus luteolus*).

The Tensas River and surrounding areas were once the location of the main channel of the Mississippi River and remain in the western Mississippi River floodplain. Topography on the refuge was typical of a Mississippi River floodplain with ridge/swale, oxbow lakes, and backwater swamps present. Overstory vegetation consisted of water oak (*Quercus nigra*), willow oak (*Q. phellos*), hickory (*Carya* spp.), sweetgum (*Liquidambar styraciflua*), elm (*Ulmus* spp.), ash (*Fraxinus* spp.), and sugarberry (*Celtis laevigata*) with interspersed baldcypress (*Taxodium distichum*)—tupelo (*Nyssa aquatica*) swamps. The understory consisted of dwarf palmetto (*Sabal minor*), poison ivy (*Toxicodendron radicans*), blackberry (*Rubus* spp.), trumpet creeper (*Campsis radicans*), and greenbrier (*Smilax* spp.). Early to mid-successional hardwood plantings established for carbon credits were distributed throughout the refuge. These hardwood plantings were initiated between 1985 and 2009 and comprised about 6,110 ha (20%) of the refuge. During the study, agricultural crops grown on the refuge and surrounding private lands included corn (*Zea mays*), cotton (*Gossypium hirsutum*), soybeans (*Glycine max*), and rice (*Oryza* spp.).

Hunting pressure differed on the study area depending on whether deer were using public or private lands and whether deer on public lands were in areas open to hunting or in areas generally closed to hunting. Although most of the study area was the TRNWR, deer we captured spent time on both public and private lands. Deer hunting season on private land began with archery hunting on 1 October and lasted until 31 January (123 days) with 20 days of primitive weapon hunting and 65 days of modern firearms hunting. Although the general hunting season on TRNWR began on 1 October (small game hunting), deer hunting began on 2 November and consisted of 83 days of archery in 2013–14, or began on 1 November and consisted of 84 days of archery during 2014–2015. Deer hunting season on TRNWR also included 7 days of modern firearms hunting (2 days of youth only, 1 day antlerless only, 4 days of lottery hunts) and 2 days of primitive weapons hunting. The Greenlea Unit of the TRNWR was a 1,066-ha area closed to hunting with the exception of 3 days of staff-guided lottery deer hunts using modern firearms on 27 December 2013, 3 and 11 January 2014, 23 and 30 December 2014, and 10 January 2015. Approximately 20 hunters were guided on each of these hunts.

Data Collection

We captured adult (≥2.5 yrs) male deer during January–March 2013 and 2014 using a combination of drop nets, rocket nets and free-range darting with 3-mL Pneu-Dart transmitter darts (Pneu-Dart Inc., Williamsport, Pennsylvania, and Daninject, Børkop, Denmark). We anesthetized deer using a combination of ketamine (1.5 mg/kg) and xylazine (2.5 mg/kg) when caught under a net or Telazol (5 mg/kg) and xylazine (2.5 mg/kg) when darting. We estimated age by tooth wear and replacement (Severinghaus 1949). We fitted deer with either Lotek 7000mu GPS collars (Lotek Engineering, Ontario, Canada) or Followit Tellus GPS collars (Followit AB, Lindesberg, Sweden). Both types of collars allowed for remote data download via Ultra High Frequency (UHF) signal. Following instrumentation, anesthesia was reversed using 3 mL of Tolazoline, half intravenously and half intramuscularly, and researchers remained with animals until ambulatory. Capture and handling protocol was approved by the University of Georgia Institutional Animal Care and Use Committee, permit #A2012 06-006-Y3-A2.

We programmed collars to collect 30-minute locations during the Louisiana state-wide hunting season (1 October–31 January). If a deer was captured in 2013 and survived to 2015, then collars collected locations during both the 2013–2014 and 2014–2015 hunting seasons. We monitored VHF signals once/week to determine activity mode of the collar (active, mortality, low battery). We remotely downloaded data from collars at the end of each hunting season and imported them to ArcGIS 10.2 (Environmental Systems Research Institute, Inc., Redlands, California). We censored data to eliminate non-fix and impossible locations.

Deer Movement.—We calculated step lengths (the linear distance between consecutive points) for each 30-minute interval using the command "movement pathmetrics" in Geospatial Modeling Environment (GME), version 0.7.3.0 (Beyer 2012). Hereafter, we refer to step length as movement. In a mortality event, we calculated movement to the day before death. Two movements were possible each hour.

Explanatory variables.—We used National Oceanic and Atmospheric Administration sunrise and sunset tables to divide days into 3 periods based on the amount of light available (Endler 1993). The crepuscular period was the 6-hour period which included dawn (the hour bisected by sunrise and the hours immediately before and after sunrise) and dusk (the hour bisected by sunset and the hours immediately before and after sunset). The day period was the hours between dawn and dusk, and night period was the hours between dusk and dawn.

To examine if macrohabitat features influenced the movement of deer, we created broadly defined landcover types for the study area. Because our study area was largely agriculture and hardwoods, we confined our macrohabitat categories to agriculture (e.g., milo, corn, cotton, soybeans, rice), regenerating hardwood (planted hardwoods), or mature hardwood. We assigned each deer location as being present in agriculture, regenerating hardwood, or mature hardwood.

To examine the effect of reproductive phase on deer movement, we categorized each movement based on the reproductive phase in which it occurred. We used conception data from a concurrent study in the Tensas River National Wildlife Refuge using vaginal implant transmitters in pregnant females to delineate parturition dates of fawns. Parturition event dates were backdated 200 days to estimate conception events. Based on these data, we assigned a reproductive phase to each day of our study. The mode day of conception was 20 December and mode date of parturition was 8 July (Figure 1). From these data, we divided the entire period of intensive monitoring, which was centered on the hunting season, into four phases based on breeding phenology: non-breeding (1 October–25 November),

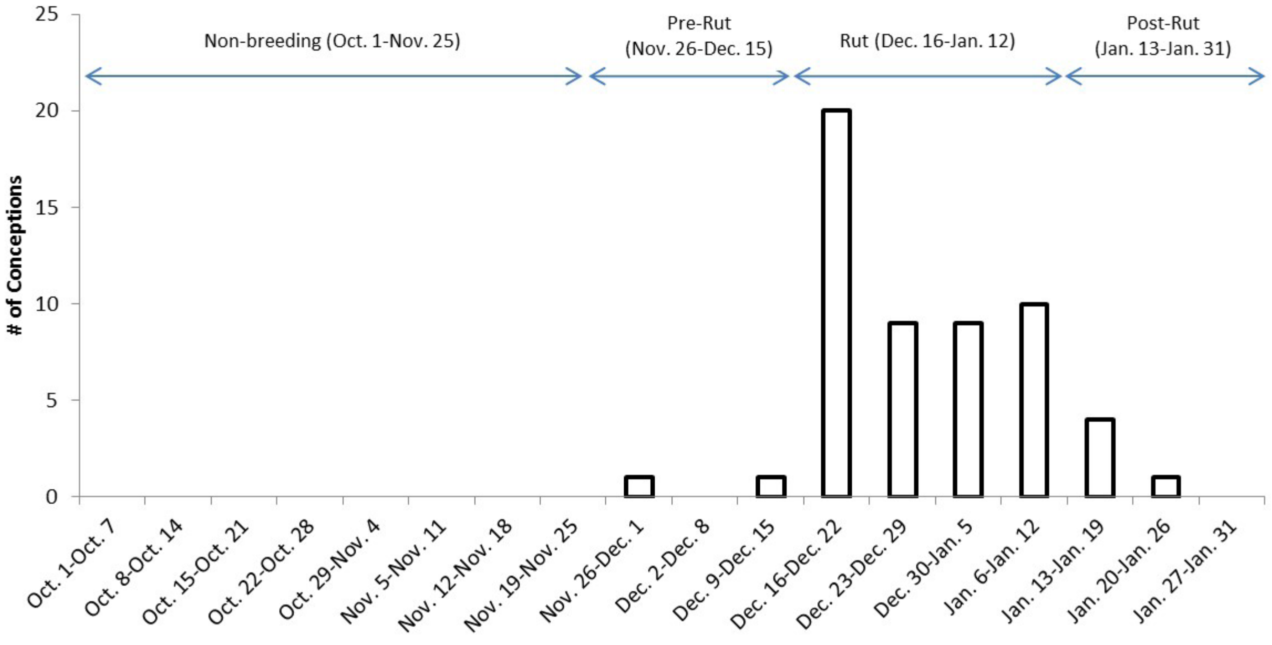

Figure 1. Number of conceptions per week from 1 October to 31 January of 2013–14 and 2014–15. Conception data was based on a concurrent study in the Tensas River National Wildlife Refuge using vaginal implant transmitters in pregnant females to delineate parturition dates of fawns. Parturition event dates were backdated 200 days to estimate conception events. Based on these data, we assigned a reproductive phase to each day of our study. We used this to calculate the effect of reproductive phase on the movements of 24 adult white-tailed deer in northeastern Louisiana during the 2013–14 and 2014–15 hunting seasons.

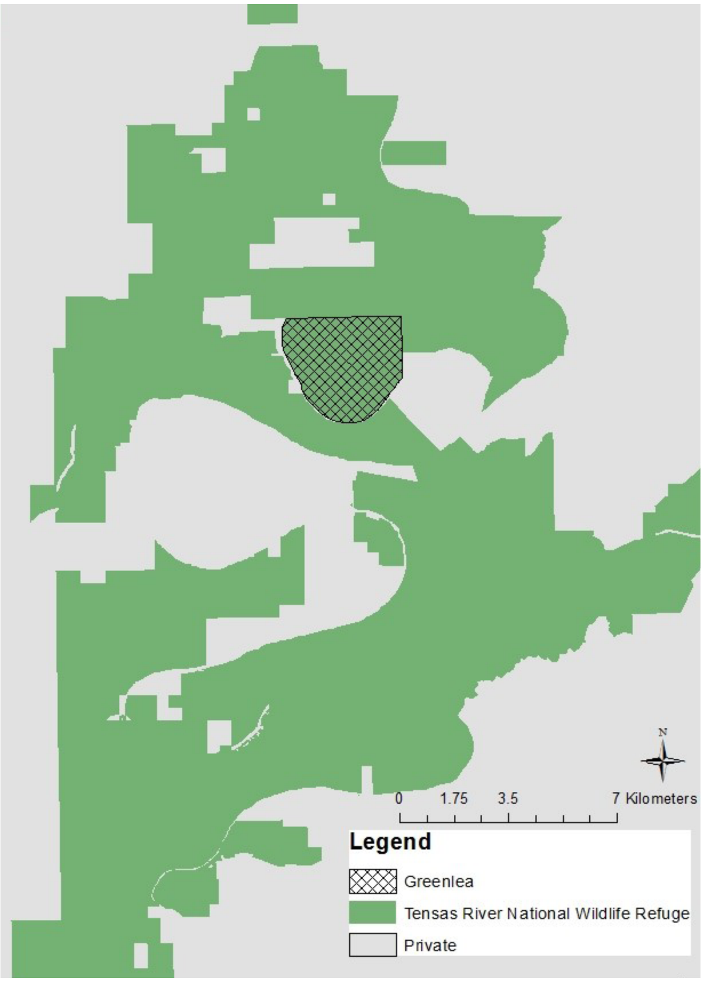

Figure 2. Map of the study area including the Tensas River National Wildlife Refuge (open-access hunting), Greenlea Unit (refuge), and adjacent private lands in northeastern Louisiana. Locations (30-min) were obtained for 24 adult male white-tailed deer that inhabited the area throughout the 2013–14 and 2014–15 hunting season.

pre-rut (26 November–15 December), rut (16 December–12 January), and post-rut (13 January–31 January).

To examine the effect of age on deer movement, we assigned deer as 3.5, 4.5, or 5.5 and older based on estimated age at time of capture. We conducted a preliminary analysis by determining the mean movement of each deer per age and determining a mean and standard error of movement for each age in our sample to determine if these ages could be combined into age classes. Because our preliminary analysis suggested 3.5- and 4.5-yr-old deer had similar average step lengths for our study, we combined ages into two classes: young mature (3.5 and 4.5 yrs old) or old mature (≥5.5 yrs old; see results). If a deer was collared for two years, his age was updated for the second hunting season.

To examine the effect of hunting on deer movements, we categorized locations based on hunting pressure. All visitors to TRNWR were required to check-in via self-clearing permits and visitor numbers for each week of our study were provided by TRNWR staff. While the specific activity for each visitor was not recorded, we assume most of this use was by hunters. Because the summary data provided to us did not align with our predefined weeks, we calculated a three-week moving window average of visitor use as a surrogate for hunting pressure per week. These data demonstrated that most land in the TRNWR received relatively consistent hunting pressure. While we were unable to directly measure hunting pressure on private lands, the primary use of those properties was deer hunting. Private lands and areas of TRNWR open to hunting differed from the Greenlea Unit, which was only hunted for three days annually and otherwise acted as a centrally located refuge in our study area (Figure 2). Therefore, we assigned each deer location as occurring in open access (i.e., outside of Greenlea) or refuge (i.e., inside of Greenlea).

Data Analysis

We first conducted exploratory analyses to determine how period, macrohabitat, reproductive phase, age, and hunting pressure may influence movement. We categorized each movement based on these aforementioned variables, then calculated a mean movement (i.e., step length) for each individual deer based on each explanatory variable. This provided a sample mean and standard error for movements before we began our modeling exercise. We conducted statistical analyses using R version 3.0.2 (R Core Team 2013).

We conducted generalized linear mixed modeling (GLMM) analyses using the lme4 package (Bates et al. 2011) and LMER Convenience Functions (Tremblay 2011) to investigate various predictors on deer movement. The GLMMs allowed incorporation of a flexible covariance structure into the modeling framework, resulting in better estimates of variability than standard generalized linear models (Clayton and Kaldor 1987, Breslow and Clayton 1993). We assumed observations of step length between 30-minute locations to be normally distributed. We included age class, period, reproductive phase, refugia, and macrohabitat as predictor variables in our analysis. To examine for potential multicollinearity, we calculated Pearson correlations (r) for all pairs of predictor variables. We found no variables to be significantly correlated (cutoff of $r = \pm 0.70$; Dormann et al. 2013) and, therefore, we included any combination of variables in the same model. To account for multiple observations for each deer and variation within years, we treated each deer and year of the study as a normally distributed random effect with a mean of zero and an estimated variance in each model.

Because deer are crepuscular (Kammermeyer and Marchinton 1977) but reproductive phase may affect deer movement, our first model examined if the effects of period and reproductive phase and their subsequent interaction best explained deer movement. To avoid encounters with hunters, deer may shift to more nocturnal movements (Karns et al. 2012, Little et al. 2014), so our second model examined if the effects of refugia and period, and their subsequent interaction, best explained deer movement. Our third model examined the interaction between period and reproductive phase, with the additive effect of refugia. Similarly, our fourth model examined if reproductive phase had an additive effect with the interaction of refugia and period.

Because differing age classes of males may use different breeding strategies (Brown 1974, Webb et al. 2007, Hellickson et al. 2008, Foley et al. 2015), our fifth model examined if the additive effect of age class and reproductive phase best predicted deer movement. Lastly, because habitat may be one of the most influential variables on deer movement (Beier and McCullough 1990, Vercauteren and Hygnstrom 1998, Lesage et al. 2000, Brinkman et al. 2005, Long et al. 2005, Quinn et al. 2013) and likely has an additive effect with reproductive phase and period, we examined if the combination of macrohabitat, reproductive phase, and period best predicted deer movement. Because we believed *a priori* that all of these variables influenced deer movement, we estimated effect sizes based on the additive effects of each of our fixed-effect variables in a global model (Table 1).

While some debate remains about the appropriateness of information criteria approaches with GLMMs (Vaida and Blanchard 2005), we used Akaike's information criterion (Akaike 1973) with small sample adjustment (AICc; Hurvich and Tsai 1989) to determine which model best explained variation in movement. We compared our seven predictive models with a global model consisting of all explanatory variables using deer and year as random effects, and we compared a null model consisting of an intercept estimate using deer and year as random effects. We considered the model with the smallest AICc value to be the most plausible, and models within a ΔAIC of less than 2 to be equally plausible. We calculated Akaike weights (w_i) to assess the empirical support for each model and select the most appropriate candidate model. To examine the power of each model to predict movement, we also calculated marginal R^2 (variability explained by only fixed-effects) and conditional R^2 (variability explained by both fixed and random effects) in program R, package MuMIn (Nakagawa and Schielzeth 2013, Johnson 2014). After selecting the most plausible mixed-effect model based on AICc, we used the predict function (R Core Team 2013) to calculate expected movement values and 95% confidence intervals based on the fixed effect variables.

Results

We captured 14 adult male deer in 2013, of which 14 survived to the 2013–2014 hunting season and 8 survived to the 2014–2015 hunting season. We captured an additional 16 adult males in 2014, of which 13 survived to the 2014–2015 hunting season. We lost data from 3 deer because of collar malfunction, leaving us with 24 data-sets. Ten deer were harvested during the hunting season, resulting in 14–24 data-sets per week.

Movement tended to be larger during crepuscular hours (mean ± SE; 105 ± 5 m per 30 min) and night (95 ± 5 m per 30 min) compared to during the day (38 ± 3 m per 30 min; Figure 3). Deer on average moved similarly in agriculture (92 ± 8 m) and mature hardwoods (92 ± 6 m per 30 min) but less in regenerating hardwood (69 ± 5 m per 30 min; Figure 3). Movements tended to be greatest during the rut (120 ± 9 m per 30 min) followed by pre-rut (89 ± 5 m per 30 min), post-rut (90 ± 10 m per 30 min), and the non-breeding phase (63 ± 3 m per 30 min; Figure 3). Young mature males (82 ± 5 m per 30 min) on average moved more than older mature males (69 ± 6 m per 30 min; Figure 3). Lastly, deer tended

Table 1. Generalized linear mixed models used to evaluate relative importance of age class, period, macrohabitat, hunting pressure, and reproductive phase on the movement of adult male white-tailed deer during the 2013–14 and 2014–15 hunting seasons in northeastern Louisiana.

No.	Model name	Hypothesis	Models
1	Global	All main effects at deer level will change response parameter.	y = Age Class + Refugia + Period + Macrohabitat + Reproductive Phase + *Rj*[a]
2	Diel movements and breeding	Response is dependent on the interaction effect of breeding chronology and time of day.	y = Reproductive Phase ∗ Period + *Rj*
3	Predation avoidance	Response is dependent on the interaction of refugia and diel movements.	y = Refugia ∗ Period + *Rj*
4	Diel movements and breeding with pressure	Response is dependent on the interaction of reproductive phase and diel movements, with an additive effect of refugia.	y = Reproductive Phase ∗ Period + Refugia + *Rj*
5	Predation avoidance with breeding	Response is dependent on the interaction of refugia and diel movements with an additive effect from breeding chronology.	y = Refugia ∗ Period + Reproductive Phase + *Rj*
6	Age-related breeding strategies	Response is dependent on the additive effect of age class and breeding chronology.	y = Age Class + Reproductive Phase + *Rj*
7	Habitat and exploratory analysis	Response is dependent on the additive effects of habitat, breeding chronology, and time of day.	y = Macrohabitat + Reproductive Phase + Period + *Rj*
8	Random effects	Response is dependent on random variables deer and year.	y = *Rj*

a. *Rj* = Random variables of individual and year of study

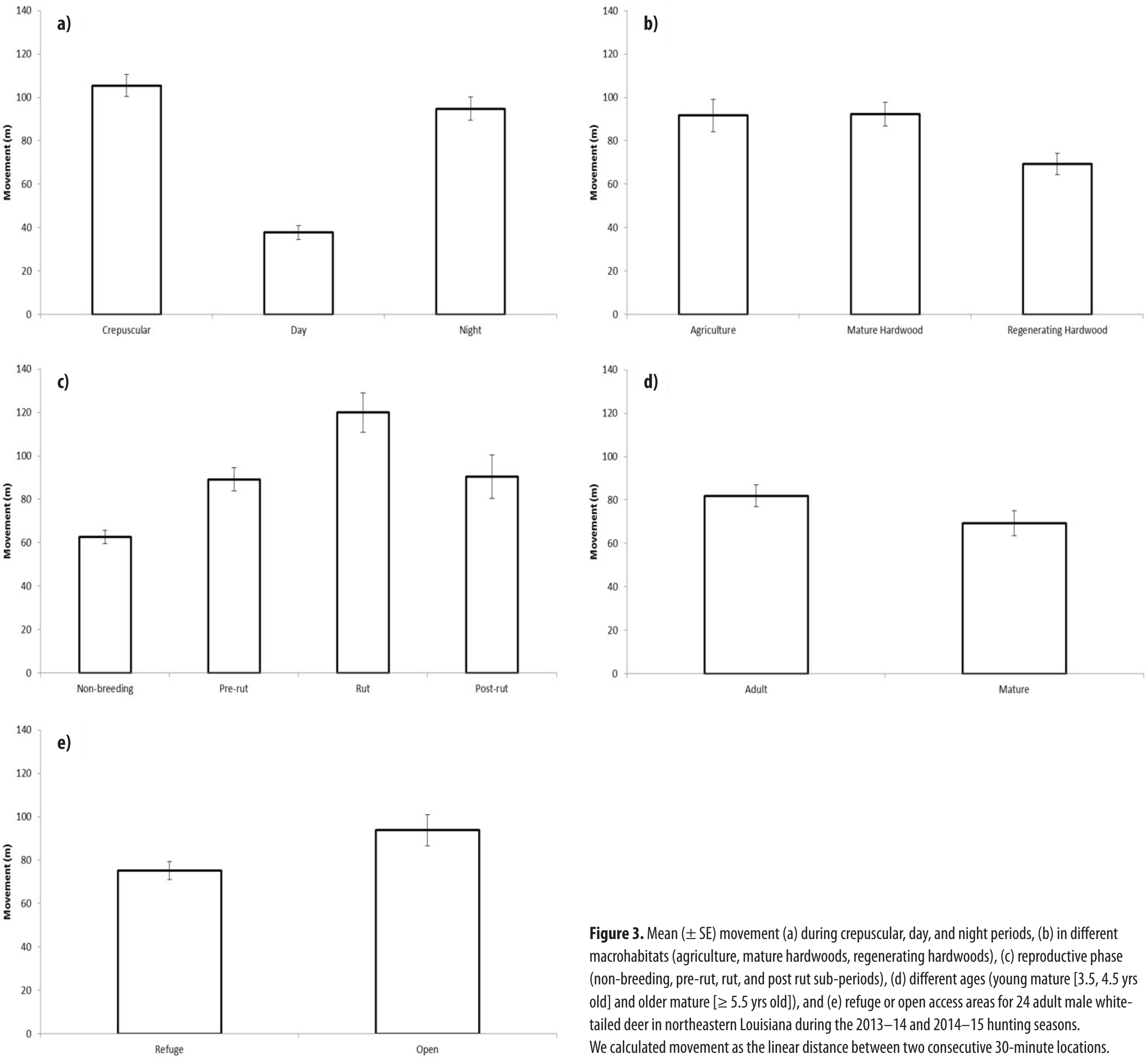

Figure 3. Mean (± SE) movement (a) during crepuscular, day, and night periods, (b) in different macrohabitats (agriculture, mature hardwoods, regenerating hardwoods), (c) reproductive phase (non-breeding, pre-rut, rut, and post rut sub-periods), (d) different ages (young mature [3.5, 4.5 yrs old] and older mature [≥ 5.5 yrs old]), and (e) refuge or open access areas for 24 adult male white-tailed deer in northeastern Louisiana during the 2013–14 and 2014–15 hunting seasons. We calculated movement as the linear distance between two consecutive 30-minute locations.

to move more in areas with open hunting (94 ± 7 m per 30 min) than on the refuge area (75 ± 4 m per 30 min; Figure 3).

Evidence from the global GLMM and model ranking suggested that reproductive phase and period best predicted movements. The interaction between these two variables and the additive effect of hunting pressure was the most plausible model and accounted for 52% of the model weight (Tables 2 and 3). However, the model incorporating only reproductive phase and period had a ΔAIC of 0.13 and accounted for 48% of the model weight, suggesting that hunting pressure may have had a minimal predictive ability on movement. Both of these models had a marginal R^2 of 0.069 and a conditional R^2 of 0.092 (Table 2), suggesting that the models poorly explained the observed variation in movement. Using the most plausible model, our predicted movements were, on average, greater when deer were in areas of open hunting. However, when examining across reproductive phase and photoperiod, movements during the crepuscular period and rut phase were similar on the Greenlea refuge (mean ± 95% CI; 142 ± 15 m per 30 min) and on open access hunting lands (133 ± 15 m per 30 min), and as expected were greatest during the rut (Figure 4).

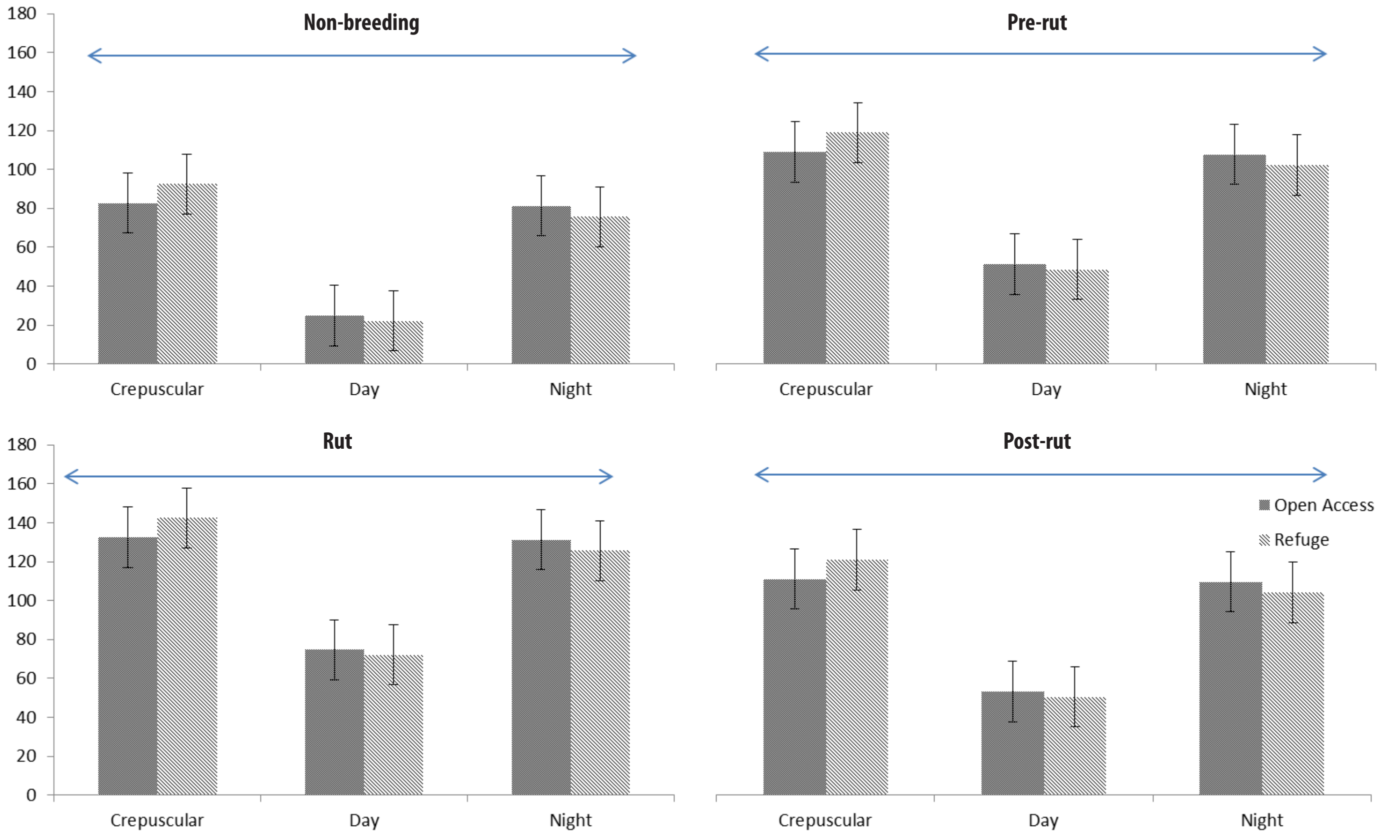

Figure 4. Predictions from the model with the lowest AICc score depicting adult male deer movement during crepuscular, day, and night periods in open access and refuge areas in northeastern Louisiana during the non-breeding, pre-rut, rut, and post-rut reproductive phases in 2013–14 and 2014–15. Error bars represent the 95% confidence interval.

Table 2. Akaike information criterion with small sample bias adjustment (AICc), number of parameters (K), ΔAICc, Akaike weights (*w*) for candidate models (*i*) relating to variables influencing step length of adult male white-tailed deer in northeastern Louisiana during the 2013–14 and 2014–15 hunting seasons.

Candidate model	Model no.	K	AICc	ΔAICc	wi	Conditional R^2	Marginal R^2
Diel movements and breeding with pressure	4	16	1926219	0	0.52	0.092	0.069
Diel movements and breeding	2	15	1926219	0.13	0.48	0.092	0.069
Predation avoidance with breeding	5	12	1926435	215.8	0	0.091	0.068
Global	1	13	1926444	224.85	0	0.093	0.069
Habitat and exploratory Analysis	7	11	1926452	232.74	0	0.091	0.068
Predation Avoidance	3	9	1929821	3601.64	0	0.068	0.046
Age-related breeding strategies	6	8	1933738	7518.67	0	0.047	0.025
Random effects	8	4	1937289	11069.24	0	0.022	0.000

Table 3. Parameter estimates for the top ranked model estimating the steplength of 24 adult male white-tailed deer based on the interaction of reproductive phase and diel movements, with an additive effect of refugia from hunters. Model ranking was performed using Akaike's information criterion for small sample size (AICc). Interactions effects are demarcated by colons between two covariates. Standard errors (SE), and *t*-values are also presented.

Covariate	Estimate	Coefficient (SE)	*t*-value
(Intercept)	90.92	7.93	11.47
Post-rut	19.08	2.23	8.58
Pre-rut	30.67	1.83	16.79
Rut	43.09	1.76	24.46
Daytime photoperiod	–62.14	1.19	–52.27
Nighttime photoperiod	–18.03	1.14	–15.80
Refuge	–0.40	1.09	–0.36
Post-rut:Daytime photoperiod	1.10	2.99	0.37
Pre-rut:Daytime photoperiod	–17.98	2.41	–7.47
Rut: Daytime photoperiod	–5.61	2.36	–2.37
Post-rut:Nighttime photoperiod	21.12	2.75	7.67
Pre-rut:Nighttime photoperiod	4.29	2.30	1.86
Rut: Nighttime photoperiod	19.63	2.19	8.97
Deer	315.48[a]	N/A	N/A
Year	97.03[a]	N/A	N/A

a. Deer and Year were considered a random effect in the model; thus, they are variance estimates

Discussion

We found the spatiotemporal variation in deer movements are driven by circadian periods and phase of the reproductive season. Deer movement was greatest during crepuscular and nocturnal periods, with movements peaking during the rut phase of the reproductive season. Our exploratory analyses suggested that deer moved less in regenerating hardwoods, where thicker understory vegetation is well suited for bedding cover. Likewise, older deer tended to move less than younger adults. Male deer tended to move more in areas of open-access hunting, but our most plausible model predicted movements on Greenlea to be more crepuscular on average than those on open-access hunting lands.

Although our results confirmed our predictions of effects of period and reproductive phase on movement, we were surprised with the little support our macrohabitat and individual age variables garnered. It has been well established in the literature that age influences experience which in turn affects behavior (Nixon et al. 1991, Long et al. 2005, Williams et al. 2011). However, the lack of a consistent pattern suggests that age alone does not predict behavioral states, and that experience may lead to individual specialization in which manifested behaviors are more predicted based on past failures and successes than by age-related experience (Bolnick et al. 2003, Foley et al. 2015). Alternatively, our observed similarities in movement between age classes could be an artifact of our sample of deer being similarly aged. Had our study encompassed immature deer as well as older, senescent deer, the impact of age may have been more notable. The importance of habitat in behavioral processes is unquestionable, but the scale of our macrohabitat variables may have been uninformative based on the fine-scale spatial resolution of our data set.

Under the optimization theory, deer are predicted to increase movement rates in areas of high predation risk as they look for safer areas (Reiss 1987). Supporting this theory, and similar to other findings (Cleveland et al. 2012, Little et al. 2014), we noted that deer tended to move more on average in open-access hunting lands compared to the Greenlea Unit. However, these movements were largely during the night and day periods, suggesting deer in open access lands may have moved less and spent time in safe patches during crepuscular periods. In many taxa, increased movement rates result in lower survival and fitness (Biro et al. 2003), but for hunted species such as deer, focusing these increased movements during nocturnal periods may offset harvest-susceptibility. Deer in Greenlea tended to be more crepuscular, further suggesting that open-access hunting made deer more nocturnal. However, these patterns were not pronounced suggesting that the degree of hunting pressure present on our study site may not have been enough to warrant a major shift in behavior, similar to the findings of Karns et al. (2012).

Our regression analyses indicated our models explained a relatively small amount of movement variance, even when individual deer and years were included as random variables. We offer that it is difficult to capture the diverse amount of environmental variables experienced by an animal when measuring fine-scale movements. For example, weather patterns, local deer density, and sex ratios may influence deer movements in conjunction (Beier and McCullough 1990, Sargent and Labisky 1995, Labisky and Fritzen 1998, D'Angelo et al. 2004, Webb et al. 2010, Williams et al. 2011), yet we could not quantify these parameters at an informative scale for our data set. It is also possible that measurable variables are having less influence on deer movement than previously suspected. For example, variations in behavior may be reflective of individual specialization, making predictions to the general population difficult and tenuous (Bolnick et al. 2003, Vander Zanden et al. 2010). Future research should examine the degree of within-population heterogeneity in spatial behaviors and its resulting effects on individuals.

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