

Chronobiological Patterns of White-Tailed Deer in Suburban Maryland: Implications for Deer Population Management, Human-Deer Conflict, and Zoonotic Disease Mitigation

Patrick Roden-Reynolds

University of Maryland at College Park

Cody Kent

University of Maryland at College Park

Andrew Li

USDA-ARS Beltsville Agricultural Research Center

Jennifer Murrow Mullinax (wildlife@umd.edu)

University of Maryland at College Park https://orcid.org/0000-0003-4695-059X

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Abstract

Understanding the ecology of the often dense white-tailed deer populations in urban and suburban landscapes is important for mitigating a variety of conflicts that arise with dense human populations, especially issues surrounding zoonotic disease mitigation and impacts to existing understory vegetation. We collared white-tailed deer in highly suburban areas of Howard County, Maryland. High-resolution GPS data enabled us to create autocorrelated kernel density home ranges and model deer speed, rates of activity, and proximity to residential buildings over time. Home ranges encompassed approximately 35% residential land and an average of 71 and 129 residential properties were found within female and male core ranges, respectively. Sex, time of day, and day of year all influenced deer speed, activity, and proximity to residences. Deer moved into residential areas nightly, especially in winter, and exhibited bouts of increased speed and activity shortly after sunrise and sunset, though with distinctive seasonal changes. We discuss how variation in home ranges and movements may influence population management success and explore year-round periods of increased risk of deer transporting ticks to residential areas. These findings focus our broad understanding of deer movements in suburban landscapes to improve deer population management, limit human-wildlife conflict, and manage against the spread of ticks and tick-borne disease in suburban areas.

Introduction

White-tailed deer (*Odocoileus virginianus*, hereafter "deer") are an adaptive species inhabiting rural (Walter et al. 2009), exurban (Storm et al. 2007; Rhoads et al. 2010), suburban, and urban areas (Kilpatrick et al. 2011; Urbanek and Nielsen 2013; Potapov et al. 2014), and are particularly abundant in the eastern United States, especially within suburban landscapes (Dechen Quinn et al. 2013; Walter et al. 2018). Such suburban areas are typically characterized by a network of residential neighborhoods, schools, businesses, and patches of open space or undeveloped land, which provide ample quality, safe habitat for deer (Potapov et al. 2014). Moreover, fragmented patches of open space, ornamental plantings, and supplemental feeding from suburban residents provide year-round food sources (Grund et al. 2002; Williams and Ward 2006) allowing for increased deer populations.

High deer densities have led to conflicts in urban and suburban areas, including increased risk of deervehicle collisions (Hussain et al. 2007; DeNicola and Williams 2008), over-browsing of natural and ornamental vegetation (Rooney and Waller 2003), as well as increasing concerns over tick-borne zoonotic diseases (Frank et al. 1998; Walter et al. 2011; Stafford et al. 2017). Of particular importance in suburban areas in the eastern U.S. are the black-legged tick (*Ixodes scapularis*), lone-star tick (*Amblyomma americanum*), and to a lesser degree American dog tick (*Dermacentor variabilis*) (White and Gaff 2018; Milholland et al. 2021). All three species can transmit a suite of pathogens such as *Rickettsia* spp. (Rocky Mountain spotted fever), *Ehrlichia* spp. (human ehrlichiosis), or *Borrelia* spp. (Lyme disease). White-tailed deer have been shown to host all parasitic tick stages, are a keystone host for several tick species, and play an important role in generally maintaining and supporting tick populations (Kilpatrick et al. 2014; Huang et al. 2019). .(Fritzen et al. 2011). As the majority of tick bite reports originate from suburban

homeowners' backyards (Stafford et al. 2017), movement of deer into residential zones is likely an important driver of tick-borne diseases in humans. As such, deer ecology and management continue to be an important component in the vector-borne zoonotic disease framework in suburban landscapes.

Most studies of suburban deer ecology have focused on general home range and habitat use analyses to make inferences about movement and activity. Suburban deer exhibit high site fidelity, and home ranges are typically smaller than rural deer but vary between seasons, time of day, and individuals (Etter et al. 2002; Grund et al. 2002; Porter et al. 2004; Kilpatrick et al. 2011). Deer find cover in undeveloped patches (Potapov et al. 2014), and movement, peaking at dawn and dusk (Rhoads et al. 2010), is enabled via private properties (residences or businesses), road rights-of-way, and riparian areas (Kilpatrick and Spohr 2000a, b; Grund et al. 2002). Yet, there is limited consensus on specific deer movements in suburban neighborhoods, with results ranging from slight avoidance to moderate preference for residential properties as foraging areas (Kilpatrick and Spohr 2000a, b; Grund et al. 2002; Storm et al. 2007; Kilpatrick et al. 2011; Potapov et al. 2014). However, all studies found some level of use of residential areas, with an increase in use during winter. Additionally, much of the existing research focused on hunting seasons and not on spring and summer studies that would have important implications for tick ecology. Given the specific needs of white-tailed deer managers in highly populated areas grappling with overabundant deer (Urbanek et al. 2011; Stafford and Williams 2017), information regarding fine scale diel and annual behaviors and movements in deer within suburban areas is needed.

Our objective was to evaluate deer habitat use and movement throughout a highly residential landscape across the annual cycle using high resolution telemetry data. We characterized suburban land use within home ranges, quantified speed and activity, and evaluated the potential for human conflicts based on the proximity or Euclidean distance to inidivual residential properties. This quantitative, fine-scale information on deer usage of suburban yards and neighborhoods will inform any manager tasked with deer population or zoonotic disease management.

Methods

Study Area

Deer were captured in five county parks in Howard County, Maryland (Online Resource 1, Table S1) approximately 29 km south of Baltimore, MD and 43 km north of Washington D.C. All parks had some level of recreational use, including sports fields, playgrounds, hiking, and dog walkers. Select county parks were managed via sharpshooting with licensed marksmen or had managed hunting with all culling efforts occurring less than 5 days per park each year. Howard County has a human population of approximately 325,690 people and is 650 km² with a density of 501 people/km² (United States Census Bureau 2019). All five study sites were within the metropolitan boundary of Howard County, which is characterized by greater urban development (Fig. 1). Within the metropolitan zone, human population density increased to 964 persons/km², versus the more rural western portion of the county with 124 persons/km² (Kraft 2008). On average, annual rainfall was 1.09 m and annual snowfall was 0.58 m

(Kraft 2008). In winter, the average temperature was 0.78°C and the average daily minimum temperature was – 4.9°C. In summer, the average temperature was 22.9°C and the average daily maximum temperature was 29.6°C (Kraft 2008). Forest cover within the county trapping sites was predominantly oak (*Quercus* spp.), hickory (*Carya* spp.), and Tulip poplar (*Liriodendron tulipifera*) in the overstory. The understory was often dominated with invasives such as Autumn olive (*Elaeagnus umbellate*), Amur honeysuckle (*Lonicera maackii*), and multiflora rose (*Rosa multiflora*). However native species such as *Rubus* spp., maple (*Acer* spp.), eastern red cedar (*Juniperus virginiana*), and black cherry (*Prunus serotina*) were common (Kraft 2008).

Trapping Methods

Deer were captured between January and April in 2017 and 2018 using drop nets (15.2 m x 15.2 m) and box traps (0.9 m width x 1.22 m height x 1.83 m length; Wildlife Capture Services, Flagstaff, AZ) baited with whole kernel corn and apples. Four box traps were placed in areas of high deer activity but also hidden from human view to reduce interference. Box traps were set in the evening and checked once a day at dawn. Exact drop net placement within each site was selected to reduce interference with human recreational activity while maintaining ease of vehicle access (Roden-Reynolds et al. 2020). When an animal was identified under a drop net, the field crew activated or dropped the net, physically restrained the animals, and anaesthetized animals by hand syringe in the gluteal muscle mass using BAM™ (Wildlife Pharmaceuticals, Windsor, CO). The fixed-dose BAM™ formulation contained 27.3 mg of Butorphanol, 9.1 mg of Azaperone, and 10.9 mg of Medetomidine per 1 ml of solution. BAM™ was administered based on visually estimated weight according to label directions. After injection, face blinds were applied, and deer were moved to a ground tarp for processing. During the processing period, we sexed each individual and estimated age by examining tooth wear and replacement (Severinghaus 1949). Lotek GlobalStar L collars (satellite GPS collars with VHF beacon) were deployed on individuals deemed greater than 1 year of age with sufficient neck circumference of \geq 30.0 cm. Often collars were retrofitted with foam and tape to reduce the collar shifting on the neck and subsequent irritation (Collins et al. 2014). After a minimum 20-min processing period, BAM™ was reversed with intramuscular administration of Atipamezole (25 mg/ml) and Naltrexone (50 mg/ml) (Wildlife Pharmaceuticals, Windsor, CO) in amounts based on initial injection volume of BAM™. Based on manufacturer recommendations, a reversal of 0.5 ml (25 mg) of Naltrexone was recommended for all set doses of BAM™, and for every 0.5 ml of BAM™ administered, at least 1.0 ml (25 mg) of atipamezole was administered. Deer were immediately released after recovery and monitored until they exited the area. Collared deer were monitored via VHF for the first three days after deployment and then biweekly to assess collar functioning and deer activity.

GPS collars remained on for a pre-programmed duration (~ 116 or 62 weeks, depending on deployment date) and recorded a GPS location and timestamp onboard every hour. GPS collars also attempted to remotely uploaded locations to a cloud service every third hour. Collars were also equipped with dual-axis accelerometers that recorded motion in the x- and y-axes detecting forward and backward motion and sideways or rotary motion. Activity was recorded simultaneously on each axis (Activity X and Activity Y)

as the difference in acceleration (rate of change in velocity) between two consecutive measurements and recorded across a relative scale of 0 and 255, which was then averaged across a 5-minute period overlapping that of the GPS location timestamps. The activity data was not a direct measurement of acceleration or movement but an index of change in motion, where high activity values indicated more change in motion and low activity resulted in less change in motion between simultaneous recordings.

Home Range Analysis

All analyses were conducted in R Version 4.0.2 (R Core Team 2020). We calculated 95% home range and 50% core range contours with autocorrelated kernel density estimators (AKDE) using ctmmweb (Fleming et al. 2015; Calabrese et al. 2016; Dong et al. 2018) and calibrated with a 10m error, the average locational error for our field-tested collar units. This method accounted for autocorrelation from our large, high-resolution (e.g. hourly) location datasets, generating a larger, yet more accurate estimation of home ranges than traditional kernel methods when data is autocorrelated (Fleming et al. 2014, 2015). We created annual home ranges for each individual that had at least 10 months of data available from the deployment date (Kilpatrick et al. 2011). Separate home ranges for summer (June 21st -September 22nd) and winter (December 21st -March 20th) were also created if the dataset from each deer fully overlapped those dates. White-tailed deer were typically resident species but did exhibit some individual shifting of their home ranges in this region, which would have resulted in poor home range estimation (Rhoads et al. 2010; Calabrese et al. 2016). As such, the autocorrelation structure of each dataset was visualized using variograms, and we removed any home ranges from further analysis when the variograms did not reach an asymptote (Fleming et al. 2014; Calabrese et al. 2016). When individual collars were not recovered, we utilized the remotely uploaded datasets. The remote datasets often contained missing data leading to variable gaps in sampling frequency, therefore, we analyzed those datasets with optimal weighting enabled. Optimal weighting applied weights to locations based on temporal sampling bias to correct for oversampled times (Fleming et al. 2018).

Ownership and proportion of residential land was quantified within the 95% and 50% home range contours using ArcGIS and Howard County GIS Land Use layer (Howard County GIS 2015). Groupings from the land use layer were reclassified (Online Resource 1, Table S2). We tabulated the number of residential properties within the 50% core range contours in ArcGIS using property boundaries data layers (Howard County GIS 2015). Residences were grouped into single residence properties (e.g. detached houses, townhouses) and multiple residence properties (e.g. apartments, condos). Properties having multiple individual residences, such as apartment buildings, were counted as one residential building because they shared a single property, with a continuous property boundary. Proportion of land use cover and residential building density were calculated around each trap site to document differences among specific parks within our study area. We calculated the average cumulative distance moved by deer each day and used that distance as a buffer radius around drop-net trap sites at each park to demarcate individual study areas for comparison. Finding the data to be non-normal, we used Wilcoxon rank sum test to compare home range size, housing density within ranges, land use within ranges, with data grouped and averaged by season, sex, or both depending on the analysis.

Movement characteristics

The first 14 days of each deer's GPS dataset was removed from speed, activity, and distance to building analyses to reduce any potential bias caused from capture and collaring (Dechen Quinn et al. 2012). We restricted speed, activity, distance to residential buildings analyses to data only with consistent hourly fix rate. Only datasets with consistent GPS locations recorded at 1 hour ± 3 minutes were included in the speed, activity, and distance to residential building analysis to decrease fix rate bias (Pépin et al. 2004; Rowcliffe et al. 2012; Massé and Côté 2013). We measured the Euclidean distance and time between each successive points to determine the minimum hourly recorded deer speed (meters/hour). To assess activity, as both Activity X and Activity Y axes were highly correlated, they were summed to a single activity score (Edmunds et al. 2018). The activity data was heavily zero-inflated and was transformed into a Bernoulli variable, where an activity score greater than one was coded as 1 and score less than one coded as 0. We measured the Euclidean distance from GPS locations of deer to the nearest residential building using land use and building data layers (Howard County GIS 2015).

We analyzed sex-specific ultradian and infradian patterns in speed, activity, and distance to residential buildings with general additive models (GAM) using package mgcv and the function bam(). All models contained smooth tensor-product interactions between hour of day, day of year, and sex, all lower-order interactions, and an independent identically distributed random effect of individual deer. All smooth terms used cyclic penalized cubic regression splines and smooth parameter selection was done using fast restricted maximum likelihood (fREML). Within this framework, model selection is performed automatically for the smoothing parameter to prevent overfitting the data and producing a model that is too "wiggly" (Wood 2004). Speed was modeled with a gamma distribution and a log link, and a small number (< 1%) of observations that were exactly 0 were excluded from analysis. Activity was modeled with a binomial distribution and logit link. We also attempted to model the raw activity scores with a zeroinflated Poisson model, which found similar results but failed to meet model assumptions so was not included. When modeling distance to the nearest residential building, we encountered strong residual temporal autocorrelation. Due to constraints with bam() when including temporal autocorrelation, distance to building was normalized with a square root-transformation and an autoregressive AR(1) autocorrelation structure was included. Significance of all three models was assessed with an analysis of variance (ANOVA).

Results

GPS Data

We collected data from 51 deer (33 female, 18 male), with an average estimated age of 2.7 ± 0.9 (range: 1–5). Across our study areas, this included 13 deer collared at Cedar Lane Park, 10 at Blandair Regional Park, 9 at Middle Patuxent Environmental Area, 9 at Rockburn Branch Park, and 10 at Wincopin Trails System. We recovered 27 full store-on-board datasets with hourly fix rate after collars remotely dropped off or mortality events. Malfunctions and drained batteries prevented recovery of 24 collars, limiting data

from those collars to a subset with a variable fix rate remotely transmitted via satellite to an online database. Datasets with consistent hourly fix rate for speed, activity, distance to residential buildings analyses included 15 females and 12 males. Roadkill was the greatest source of documented mortality (n = 8), followed by hunter harvest (n = 5) and unknown mortality sources (n = 2).

Home Range

Annual and winter home ranges did not differ among parks, but summer ranges were different (home range: $X^2 = 13.27$, df = 4, p-value = 0.01; core ranges: $X^2 = 13.68$, df = 4, p-value = 0.008), with deer at Cedar Lane producing larger summer home ranges than Rockburn and Blandair parks. Due to lack of data from some parks, park datasets were combined and analyzed as one unit. Average home range size was variable across sexes and seasons (Table 1). Summer home and core ranges were significantly smaller than winter ranges for both sexes (Table 2). Male annual 95% and 50% ranges were not significantly different than female ranges (Table 2).

Table 1
Autocorrelated kernel density home range estimates (hectares), standard deviation, and range of 95% and 50% contour sizes for female and male white-tailed deer in Howard County, Maryland, USA, 2017–2019.

	N	95% Contour		50	ur		
		Mean	SD	Range	Mean	SD	Range
Female Annual	10	106.0	96.2	21.7-315.0	20.0	17.2	3.7-53.3
Female Summer	21	43.4	39.2	7.1-173.0	9.97	10.6	1.4-47.2
Female Winter	8	89.1	53.0	27.4-154.0	18.1	9.98	5.7-27.9
Male Annual	4	317.0	184.0	60.7-473.0	43.0	31.1	8.1-83.7
Male Summer	11	137.0	111.0	18.7-338.0	27.6	25.9	1.95-67.7
Male Winter	6	347.0	226.0	75.6-717.0	68.5	35.3	12.4-106.0

Table 2
Wilcoxon Rank Sum test of annual home range sizes, seasonal home range sizes, seasonal proportion of residential properties, and seasonal housing density by home range contours and sex of white-tailed deer in Howard County, Maryland, USA, 2017–2019.

Wilcoxon Rank Sum Test	Sex	Contour Level	W	p-value
Annual range size – male versus female	Both	95	7	0.076
		50	8	0.110
Summer/winter size	Female	95	85	0.013
		50	81	0.009
Summer/winter size	Male	95	19	0.033
		50	16	0.017
Summer/winter proportion of residential	Female	95	63	0.324
		50	74	0.640
Summer/winter proportion of residential	Male	95	22	0.300
		50	15	0.080
Summer/winter housing density	Female	50	65	0.366
Summer/winter housing density	Male	50	21	0.246

Parks and residential land were the dominant land use classes within home ranges across all years and seasons (Fig. 2). Other minor land use classes included institutional land (e.g. school grounds, cemeteries) and undeveloped land. A higher proportion of park land was found within core ranges whereas more residential land was within the home ranges for both seasons. More residential land was used during winter months; however, this interaction was not statistically significant (Table 2). The average cumulative distance moved by deer each day was 2,145 m and was used as a buffer radius to demarcate individual trap site study areas for comparison. Specific park study area land use compositions are available in Online Resource 1, Table S3.

Average housing density (residential buildings/ha) within deer annual core ranges for females and males was 3.36 ± 2.62 and 2.16 ± 1.88 respectively, but not significantly different (W = 305, p-value = 0.10, Table 3). We found higher average housing densities within winter core ranges than summer core ranges but was not significantly different for either sex (Table 2). Specific park study area housing density is available in Online Resource 1, Table S4.

Table 3

Mean, standard deviation, and range of number of residential properties and housing density (residential buildings/ha) within 50% core range contours for female and male white-tailed deer in Howard County, Maryland 2017–2019.

Sex	Season	Mean	SD	Range	Density	SD	Range	N
Female	Annual	71.3	85.3	3-244	3.36	2.62	0.59-7.27	10
	Summer	35.3	74.8	0-350	2.67	2.27	0.00-7.42	21
	Winter	63.0	61.1	6-194	3.38	2.41	1.04-7.58	8
Male	Annual	128.0	159.0	5-350	2.16	1.88	0.50-4.18	4
	Summer	89.2	123.0	0-303	1.64	1.95	0.00-4.54	11
	Winter	212	213.0	15-570	2.67	1.82	0.28-5.38	6

Movement Characteristics

The three-way interaction between hour of day, day of year, and sex was a significant predictor of speed, activity, and distance to residential buildings and all lower-order effects were retained (Table 4), though the proportion of variance explained was generally low for all three models ($R^2 = 0.08, 0.08, and 0.30$ respectively). Both females and males greatly increase speed during periods immediately following sunrise and sunset, but the magnitude of speed differed among parts of the year with greatest speeds occurring in non-summer months (Fig. 3a). Speed increased in winter compared to summer for both sexes, but females did exhibit greater speeds in the summer and males showing much greater speeds during rut, especially during nighttime hours (Online Resource 1, Fig. S1).

Table 4

Anova output values of speed, activity, and distance to residential building GAM models for white-tailed deer in Howard County, Maryland 2017–2019. Test statistic is F for the speed and distance to residential building models and

 χ^2 for the activity model.

Model	Model Terms	activity mo	F	Р
Speed				
	Sex	1	1.972	0.16
	Day	15.77	13.237	< 0.001
	Hour	19.86	150.39	< 0.001
	Day*Sex	23.66	56.51	< 0.001
	Hour*Sex	12.9	11.96	< 0.001
	Day*Hour	224.03	1.54	< 0.001
	Day*Hour*Sex	89.82	0.31	< 0.001
	Deer ID	24.36	78.95	< 0.001
Activity				
	Sex	1	3.95	0.05
	Day	20.05	6640	< 0.001
	Hour	20.85	3471.9	< 0.001
	Day*Sex	10.99	1156.8	< 0.001
	Hour*Sex	14.93	253.2	< 0.001
	Day*Hour	310.52	4227	< 0.001
	Day*Hour*Sex	91.29	476.1	< 0.001
	Deer ID	23.44	943.6	< 0.001
Distance	e to residential bui	lding		
	Sex	1	0.46	0.49
	Day	11.84	169.75	< 0.001
	Hour	17.53	32.5	< 0.001
	Day*Sex	17.99	21.44	< 0.001
	Hour*Sex	11.59	2.83	< 0.001
	Tiodi ock			

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Model	Model Terms	DF	F	Р	
	Day*Hour*Sex	75.53	0.08	< 0.001	
	Deer ID	24.86	303.418	< 0.001	

Activity peaked during crepuscular periods but rebounded throughout the day particularly during the summer, with diurnal activity decreasing during winter (Table 4, Fig. 3b). Distinct resting periods of decreased activity were identifiable throughout the day shortly after crepuscular peaks in speed and activity. Differences in female and male activity were strongest from June to November when female diurnal activity increased and males exhibited more bouts of rest (Online Resource 1, Fig. S2).

Both males and females moved towards residential buildings during nighttime hours and further away during the day (Table 4). Regardless of time of year, deer begin to steadily move towards residential areas around 17:00, with proximity to buildings peaking around 4:00, and having fully returned to maximum distance from buildings by 8:00. Additionally, both sexes increased their distance from residential buildings during the fall (Fig. 3c), with males additionally avoiding residential areas from November to December (Online Resource 1, Fig. S3).

Discussion

Our results demonstrate a pattern of deer avoiding residential areas during the day, with core ranges primarily encompassing park lands. Deer movement expands outwards into residential areas primarily at night, with large periods of movement focused around crepuscular hours. These nightly movements become more intense during the winter months, with expanded home ranges that include more residential areas and a complementary shift toward residential building structures. Additionally, we note several sexspecific trends related to life-history patterns and tie these findings to deer management, both generally and specifically for tick-borne diseases.

Deer Ecology

Similar to past work, we see a high variability in home range size across individuals (Kilpatrick et al. 2011), possibly arising from factors such as age, sex, social status, or population density. Each of these factors can influence individual space use on the landscape during biologically-relevant seasons such as mating or parturition, making them more likely to defend resources or seek new habitat patches, which would influence home range size. Furthermore, the reduced urban and suburban summer home ranges we observed may be related to the increase in forage availability in natural spaces, enabling deer to travel less to obtain necessary resources (Walter et al. 2011; Massé and Côté 2013). Our home and core range sizes were larger than past studies involving urban and suburban deer (Kilpatrick and Spohr 2000a, b; Etter et al. 2002; Grund et al. 2002; Kilpatrick et al. 2011), possibly due to the use of fixed or adaptive kernel methods in past work, but they were still smaller than other studies in rural or exurban areas (Storm et al. 2007; Walter et al. 2009). The newer Autocorrelated Kernel Density Estimators are sensitive to any

significant shifting of space use which can cause disjoint or bimodal home ranges and overestimate space use, though our removal of nearly 20% of home ranges that did not asymptote avoided overestimating home range size. However, bimodal home ranges can arise from deer exploiting disjoint patches in highly fragmented suburban landscapes resulting in multiple home range centers, and they have been reported before in Maryland, with distances as great as 6km between home range centers (Eyler 2001; Rhoads et al. 2010).

Home ranges of white-tailed deer predominantly contained park land; but residential land comprised a substantial portion of each home range level which increased during winter months (Fig. 2), alongside the general increase in home range size, however this interaction was not significant. Past studies have highlighted the increased use of residential areas during winter months (Kilpatrick and Spohr 2000a; Grund et al. 2002; Storm et al. 2007), as deer may be exploiting ornamental plants, bird feeders, food scraps, and gardens for palatable forage during winter months (Williams and Ward 2006). Year-round supplemental feeding and baiting, which was documented throughout our study area may have also impacted deer movements as well. Importantly, while management has largely been focused on public properties, a major portion of deer space use is on private lands (e.g. homeowner properties, school grounds, religious facilities). Focus in management is shifting to include or involve private residences (Peterson et al. 2003), and accounting for this private land use could greatly increase population management effectiveness.

Consistent with Rhoads et al. (2010), we documented that speed is increased directly after sunrise and sunset throughout the year, and that the dawn peak is more evident during non-winter months (Fig. 3a). Female speeds in this study were lowest at the end of May through the beginning of June, corresponding to abundant food sources and peak fawning season in this region (McGinnes and Downing 1977; Dion et al. 2020). Overall female speeds gradually increased starting in mid-June, especially during the day, until peaking in late September and early October then subsiding. The spike in speed for males corresponding to mating behavior is easily distinguishable during the first few weeks in November as they search for mates (Rhoads et al. 2010; Massé and Côté 2013).

Consistent with speed, activity peaks closely follow sunrise and sunset. Clear resting and likely bedding periods (low speed, low activity) directly followed the crepuscular peaks, perhaps attributed to ruminating behavior after foraging events (Massé and Côté 2013). However, following these periods, and in contrast to low levels of speed outside of crepuscular hours, we documented an increase in activity levels, potentially related to foraging. Moreover, this pattern is more exaggerated during the long summer days, particularly for females. An interesting contrast is the decrease in daytime winter activity yet increased overall winter movements compared to summer. Much of these trends can likely be attributed to changing distribution of forage and cover, but contrary to what Massé and Côté (2013) documented, we see inverse relationships between summer and winter movement and activity. Winter likely required more movement from place to place to find forage, but less activity and more bedding occurred due to reduced resources, lower quality resources, and conservation of energy behavior (Massé and Côté 2013).

Most notably, we documented deer moving into residential areas, shown by a decrease in distance to residential buildings, during nighttime hours, especially during winter. This is broadly in agreement with the trends in housing density and home range size through various seasons, illustrating that home range expansions during the winter season are driven by nocturnal movements into residential areas. Deer distances to residential buildings did not track with changes in the timing of sunrise and sunset as for speed and activity, perhaps because deer were responding to a decrease in human activity. Human activity levels are likely determined by school or work schedules and less dependent on photoperiod. Similarly, we could expect deer distance to buildings to increase before sunrise due to the tendency of using residential areas when it is dark, but during mid-summer, deer did not begin to leave residential areas until after sunrise, which may be attributed to humans maintaining similar timing of activity even if the sun rises early in the mornings or more available cover which may have reduced pressure to vacate. Though this timing did not change, deer did maintain greater distance from residential buildings from April to June likely because natural forage is abundant during these times allowing them to better avoid human conflict. As male movements increased searching for mates during breeding season, we might have expected males to be closer to residences as ranges expanded and naturally included more residential areas. Additionally, the breeding season is known to cause increases in bold or aggressive behavior in males (Ozoga and Verme 1985) which could increase movement near residential areas due to reduced fear. Deer winter movements into residential areas have been associated with available food resources, yet male cervids are known to starve or incur poor body condition during breeding seasons (Mysterud et al. 2008). Interestingly, we still documented a strong avoidance of residential areas during that time.

It should be noted that all three models of movement characteristics, especially speed and activity models, explained only a small amount of the overall variance. This is unsurprising, given that these behaviors are likely driven by very specific events (e.g., interactions with homeowners, park users, or pets). Nevertheless, while these analyses illustrated the need for more work on specific behavioral responses to specific events, we were able to document clear, if broad, trends in these patterns which help illustrate how deer utilize and move through urban landscapes.

Management

Many government agencies use visual or camera surveys to collect data on deer populations. Our paper shows deer space use changes depending on time of day and time of year and surveys are only as good as the survey locations. Any such, survey should sample both residential and park areas at the same time when feasible. Many such population trend data and population estimators are often conducted at night due to increased visibility of deer. The data presented here shows nighttime estimates in residential areas may overestimate abundance. Any sampling design for deer population estimates should account for variable daily cycles in space use in suburban and urban areas.

Hunting or culling can be a successful management tool but requires deer to be accessible. This study has documented several nuanced movements and behaviors that can impact urban and suburban deer management and will be important information for managers planning culling or sharpshooting efforts.

Hunting has often been perceived as best during crepuscular periods because generally deer are moving more during these periods; however, any increase in diurnal speed or activity during hunting seasons can increase chance encounters with hunters. Although this study supports those crepuscular peaks in speeds, we documented that hour by hour deer do not generally rest throughout the main parts of the day. We see a strong midday peak in activity especially during non-summer months, with midday speeds also increasing during mating periods and late winter for males. Additionally, the 'October lull' has been described by hunters as a period of low movement rates and activity in white-tailed deer, but previous research has generally not supported this (Tomberlin 2007; Simoneaux et al. 2016). We documented evidence for both a lull in daytime speed for males during October as well as an overall increase in speed and activity from previous months that is only manifested during crepuscular and nocturnal periods in these suburban areas. As increased deer movement during daylight increases hunter opportunity for harvest, managers may look to avoid planning hunts earlier than mid-October during the periods of lower movement in this region.

Safe locations for hunting or sharpshooting in suburban areas are highly limited, especially the required distance from occupied residences (Maryland > 91m). As 66% of our locations were closer than 91m to residential buildings, frequently reassessing hunting safety zones when feasible and encouraging hunting methods that utilize archery equipment would likely increase management efficiency. Lastly, sharpshooting operations often occur at night on park properties as a more discrete and efficient method to reduce deer populations in sensitive or highly populated areas. However, our study shows that deer often move out of park areas and into residential yards at night. Furthermore, this movement of deer into residential yards is often intensified during typical hunting months, even in areas that are not routinely harvested. Managers might consider moving any culling operations, with appropriate sharpshooting tactics and permissions, closer to residential areas in fall and winter or operate male culling efforts during summer periods away from residences.

Zoonotic Disease

Vector-borne zoonotic diseases such as Lyme disease are increasingly a major public-health problem. Our results illustrate that each individual deer has the potential to interact with hundreds of residential properties, emphasizing their potential for transporting ticks and other parasites. In our study, average male core ranges contained more residential properties than females (Table 3), that is just a byproduct of males having larger home ranges. In fact, female deer core ranges contained greater average housing densities and were consistently in closer proximity to residential buildings. Regardless of sex, we found a much greater number of individual residential properties within deer core ranges compared to past research (Kilpatrick and Spohr 2000a, b; Storm et al. 2007; Kilpatrick et al. 2011).

When considering the multi-stage life cycle of ticks in Maryland, tick activity has several distinct components relevant to deer activity and movement, especially as they relate to distance to residential buildings and spreading of ticks to homeowner's backyards. There are two major peaks in adult tick activity among the three disease-carrying tick species in Maryland. In spring, Lone star and American dog ticks are extremely active, while the adult black-legged tick becomes very active in October and November

(Orr et al. 2013). This spring and fall activity coincide with times of major deer movements, potentially leading to increased tick dispersal. Winter months pose the greatest risk for deer transporting ticks to residential areas, with female deer posing the greatest risk of increasing ticks near homes. Increased use of residential areas during winter months combined with prolonged tick activity and lessened tick mortality due to climate change may increase or intensify chances of people becoming exposed to tick bites and tick-borne disease in their own backyards (Ogden and Lindsay 2016; Dumic and Severnini 2018). Further, while deer use of residential areas during summer is less intense than winter, the majority of deer still place approximately 35% of their home ranges in residential spaces. Summer is a very high tick activity time concurrent with increased human outdoor activity, and likely leads to increased risk of encountering ticks. Because of these high-risk periods during summer and winter combined with peak adult tick activity seasons occurring in fall and spring we recommend considering tick management year-round.

Conclusion

White-tailed deer are well established in many suburban environments, and the issues surrounding human-deer conflict, such as over-browsing and contributing to the maintenance of tick populations carrying Lyme disease in the environment, continue to grow. Understanding the unique deer behaviors in suburban areas, such as the movement differences between sex, time of day, and day of year, highlight the importance of continuing research on urban and suburban deer ecology. Deer core ranges in our study encompassed a great number of residential properties, that increased during winter. Residential areas are exploited by deer at night when humans are less active until retreating to cover throughout the day. Variable patterns in midday speed and activity provide insight into foraging behaviors as well as implications for population management. We provide information on home range, speed, activity, and distance to residential buildings that can be used to inform ongoing management and future research, especially as it pertains to risks associated with spaces used by both deer and humans.

Declarations

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Conflicts of interest/Competing interests

The authors have declared that no competing interests exist.

Availability of data and material

Not Applicable

Code availability

Not Applicable

Authors' contributions

Andrew Li and Jennifer Mullinax conceptualized the study. Patrick Roden-Reynolds, Cody Kent, and Jennifer Mullinax designed the statistical analysis. Patrick Roden-Reynolds and Cody Kent wrote the code for the analysis. Patrick Roden-Reynolds and Jennifer Mullinax wrote the manuscript. All authors participated in editing of the final version of the manuscript.

Ethics approval

The deer trapping protocol was approved by the Animal Care and Use Committee (IACUC approval #16-024) of the United States Department of Agriculture Beltsville Agricultural Research Center.

Consent to participate

Not Applicable

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Figures

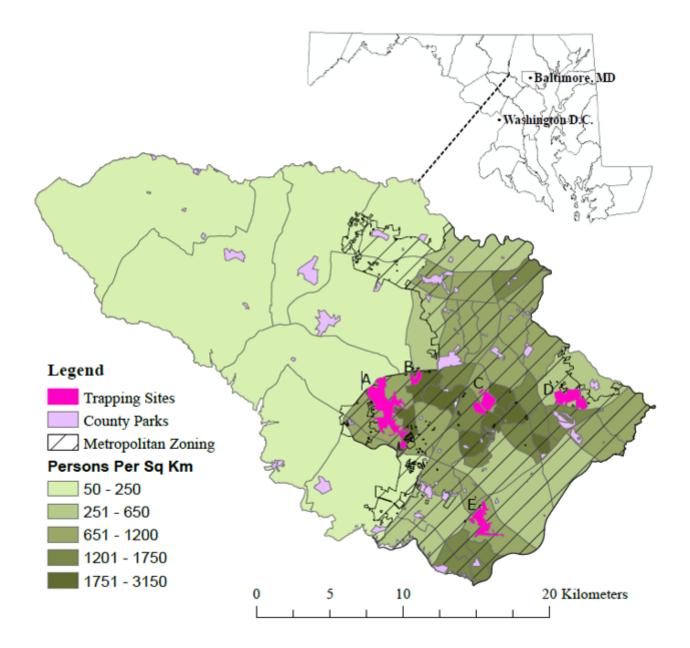


Figure 1

Map of Howard County, Maryland population density by census tract in persons per square kilometer (2017) and metropolitan zone containing the five county parks selected for deer trapping from 2017-2019. Other county parks are depicted as purple polygons. Individual trapping sites are labeled as A: Middle Patuxent Environmental Area, B: Cedar Lane Park, C: Blandair Regional Park, D: Rockburn Branch Park, and E: Wincopin Trails System/Savage Park. Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

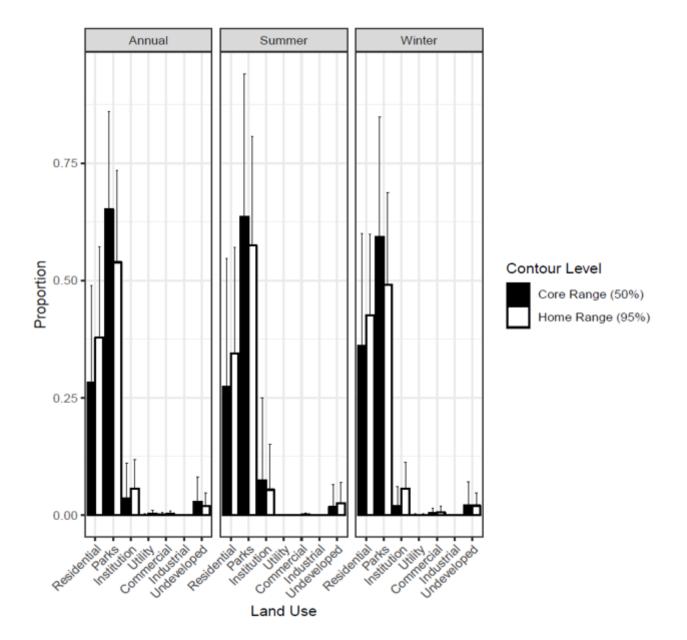


Figure 2

Proportion of land use cover and standard deviation error bars within white-tailed deer home range 95% and core range 50% contours for combined sexes across seasons in Howard County, Maryland 2017-2019. Land use cover classes are reclassified from Howard County GIS (2015) and defined in Online Resource 1, Table S2.

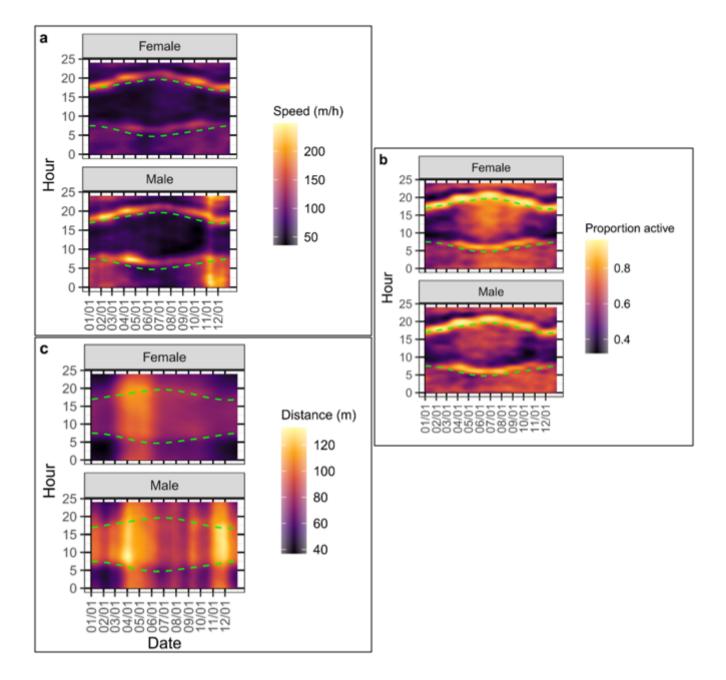


Figure 3

Model predictions for speed, activity, and distance to residential buildings by hour of day and day of year for female and male white-tailed deer in Howard County, Maryland 2017-2019, ignoring the random effect of individual. Curved, dashed lines denote sunrise and sunset. a) Depicts speed (meters/hour), b) depicts proportion of active deer, c) depicts distance to residential buildings. The smoothness parameter was selected automatically during model fitting, and the three-way interaction between time, date, and sex was significant for all models.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

• OnlineResource1.pdf