

Factors affecting space use overlap by white-tailed deer in an urban landscape

W. David Walter^{a*}, Jeff Beringer^b, Lonnie P. Hansen^b, Justin W. Fischer^a,
Joshua J. Millsbaugh^c and Kurt C. Vercauteren^a

^aUnited States Department of Agriculture, Animal and Plant Health Inspection Services, National Wildlife Research Center, Fort Collins, CO, USA; ^bMissouri Department of Conservation, Wildlife Research Center, Columbia, MO, USA; ^cDepartment of Fisheries and Wildlife Sciences, University of Missouri, Columbia, MO, USA

(Received 8 December 2009; final version received 13 September 2010)

Variation in the size and overlap of space use by white-tailed deer (*Odocoileus virginianus*) has broad implications for managing deer–human conflicts and disease spread and transmission in urban landscapes. Understanding which factors affect overlap of home range by various segments (i.e., age, sex) of an urban deer population has implications to direct contact between deer on disease epidemiology. We assessed size of home range and overlap of space use using the volume of intersection index (VI) for deer in an urban landscape by sex, age, season, and time of day. We found mean space use was larger for males than for females, for males <3 years old than for males ≥3 years old, and during nocturnal hours compared with diurnal hours. We also identified larger space use by both sexes during the nongrowing than the growing season. Overlap of space use for female and male deer in our urban landscape differed considerably depending on demographic (i.e., age) and environmental variables (i.e., time, season). For example, highest mean VIs occurred between 6-year-old females (mean = 0.51 ± 0.10) and 5- and 6-year-old males (mean = 0.49 ± 0.14); no mean VI was greater than 0.31 between females and males for any age combination. Variation in overlap of space use for urban deer provides new information for managing deer–human conflicts and direct transmission of disease between various segments of a deer population in an urban landscape.

Keywords: fixed kernel; home range; nocturnal; *Odocoileus virginianus*; season; space use; volume of intersection; white-tailed deer

1. Introduction

Understanding the spatial ecology of white-tailed deer (*Odocoileus virginianus*) in urban and residential landscapes is necessary due to growing deer–human conflicts and disease spread and prevalence in nonrural landscapes (Grund *et al.* 2002). Previous research on deer–human conflicts in developed landscapes focused on survival, behavior, and movements to assist in managing these often overabundant populations (Kilpatrick and Spohr 2000, Etter *et al.* 2002, Grund *et al.*, 2002). The female segment of deer populations is most often the focus of ecological research because the matrilineal relationship results in minimal to no dispersal of female offspring thus leading to local population densities (Aycrigg and Porter 1997, Nelson and Mech 1999, Grund *et al.* 2002). Although 40–60% of males

*Corresponding author. Email: wdwalter@aphis.usda.gov

disperse from the population (Nelson 1993, Etter *et al.* 2002), low mortality from lack of hunting in residential landscapes suggests that males are an important component of deer population demographics in these landscapes (Etter *et al.* 2002, Hansen and Beringer 2003, Storm *et al.* 2007).

Understanding the amount of overlap between various segments of a deer population could aid in predicting habitats or conditions most conducive to disease spread and persistence. Farnsworth *et al.* (2005) suggested disease prevalence was twice as high in developed than in undeveloped areas for mule deer (*Odocoileus hemionus*) but disease prevalence has not been investigated in a developed urban landscape. Previous research suggested that chronic wasting disease (CWD) in *Odocoileus* spp. was more prevalent in developed versus undeveloped areas (Farnsworth *et al.* 2005), within versus among female social groups (Schauber *et al.* 2007), males versus females (Miller and Conner 2005), and older age classes in males (Miller and Conner 2005). These findings need to be further explored for resource managers to understand spatial epidemiology of CWD or other infectious diseases in free-ranging ungulates near areas with high human densities.

Research on the spatial ecology of wildlife has evolved considerably with the integration of space use methods and geographic information systems (Pereira and Itami 1991, Bissonette *et al.* 1994, Gerrard *et al.* 1997). For example, the volume of intersection index (VI) can be calculated within ARC/INFO and has been used to measure joint space use for various species because VI is based on measuring overlap of utilization distributions (UDs) between two animals (Seidel 1992, Millsbaugh *et al.* 2004). Matrilineal deer herds and male bachelor groups can potentially be identified by VI because VI values range from 0 to 1, with 1 indicating complete overlap (Millsbaugh *et al.* 2004). Schauber *et al.* (2007) documented that direct contact rates increased with increasing VI suggesting that VI can be used to model potential for disease transmission between segments (e.g., intra-sexual) of free-ranging deer populations.

Detailed data analysis of deer space use and overlap among various segments (i.e., sex, age) of a population would provide resource managers with valuable data in managing wildlife disease and management issues in urban landscapes that differ considerably from rural landscapes. Furthermore, an adequate sample size of males by various age classes has not been available for understanding deer space use in urban landscapes (Henderson *et al.* 2000, Kilpatrick and Spohr 2000, Gaughan and DeStefano 2005). Our objectives were to assess spatiotemporal differences in overlap of space use for male and female deer from an urban population by age, time, and season. We had several predictions that included the following: (1) overlap of overall space use would be greater for males than for females because greater disease prevalence for males is indicative of greater space use and contact with conspecifics (*overall*; O'Brien *et al.* 2002, Farnsworth *et al.* 2005); (2) overlap of space use for older aged males would be higher with all other age classes, regardless of sex, because of breeding and social behaviors of prime-aged males (*age*; O'Brien *et al.* 2002, Miller and Conner 2005); (3) greater space use overlap would occur for males and females during nocturnal space use than diurnal space use, regardless of season, because foraging sites in the urban landscape would be exclusively used during nocturnal foraging episodes (*time*); (4) overlap of space use for both sexes would be similar for day and night during seasons of high availability of natural forage due to the preponderance of forage available during the growing season (*growing*); and (5) overlap of space use for both sexes would be greater at night than during day during

seasons of low natural forage availability and would indicate greater chance of contact between conspecifics during this season (*nongrowing*).

2. Study area

The study area was a 67-km² suburban area located in St. Louis County, Missouri, that included a mix of affluent housing developments and green space surrounded by urban development. Green space included residential neighborhoods and undeveloped business properties with the largest undeveloped property being the 230-ha Edgar M. Queeny County Park. Major land cover types were residential (44%), wooded (27%), and open (17%) with developed commercial properties, open water, and construction sites comprising the remaining 12% of the study area (Beringer *et al.* 2002). Interstate highways 64 and 270 were the major roadways in the area with numerous local and state roads throughout residential and commercial properties (Figure 1). Deer densities in 1997 were 31 deer/km² with recruitment (young per adult female) decreasing from 1.37 to 0.86 from 1997 to 1999 (W.D. Walter, unpublished data). Mean survival rates for radiocollared deer were 0.86 and 0.55 for females and males, respectively, with a majority of mortality (33%) from vehicle-kill. No hunting occurred at the site but 9% of radiocollared males that dispersed were harvested off-site (Hansen and Beringer 2003).

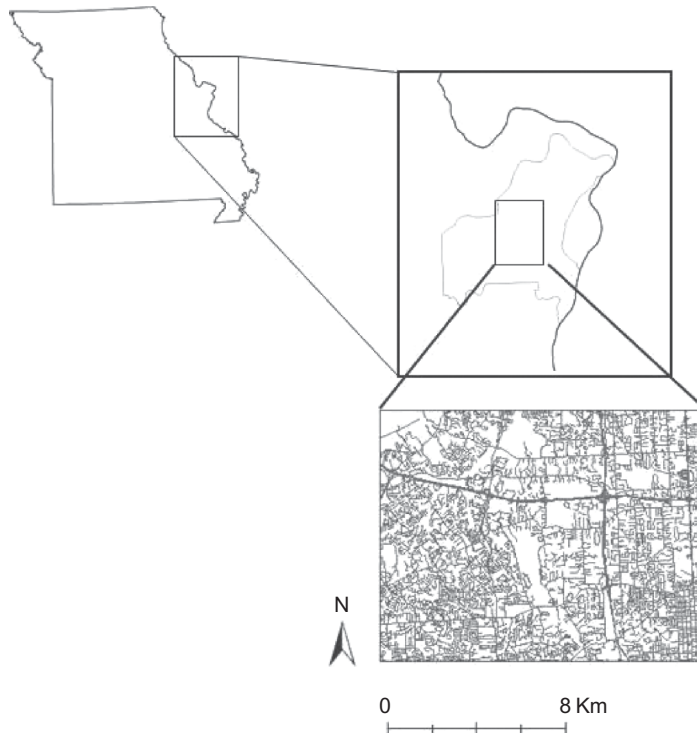


Figure 1. Study area in eastern Missouri about 11 km west of the city of St. Louis in St. Louis County, Missouri.

3. Methods

3.1. Data collection

3.1.1. Animal capture

We captured white-tailed deer with rocket nets and netted-cage traps from December 1996 to June 2000. We manually restrained or sedated deer with a 2.4:1 mixture of ketamine and xylazine and aged deer as fawn (<1 year) or adult (≥ 1 year) based on body size and, for males, antler development. All deer received numbered metal ear tags and most received motion-sensitive VHF radio transmitters with a 4-hour mortality switch (Advanced Telemetry Systems, Inc., Isanti, MN, USA; Lotek Engineering, Newmarket, ON, Canada; Telonics, Inc., Mesa, AZ, USA). Deer were captured and handled in accordance with methods approved by the urban deer working group of the Missouri Department of Conservation.

3.1.2. Radiotelemetry protocol

We located deer 2–3 times per week with a 4-element Yagi antenna (Advanced Telemetry Systems, Inc.) mounted on a vehicle attached to a scanning device and using an electronic compass (Cox *et al.* 2002). The average number of days that deer were monitored for inclusion in analysis of home range and overlap of space use was 696 days (range: 114–1288). We located deer by ground-based telemetry or by direct observation during three distinct time periods over a 24-hour period (9 am–5 pm, 5 pm–1 am, 1 am–9 am). We sampled during a predefined time frame (i.e., 8-hour time intervals) and collected locations representative of an animal's movements during this time frame (i.e., nocturnal and diurnal locations) to identify locations that were representative of an animal's movements (Beyer and Haufler 1994). One day a week, 6 adult deer (3 females, 3 males) were located about every 1.5 hours during a 24-hour period to obtain detailed information on deer movements in this urban environment. We used aircraft with mounted antennae to search for deer we were unable to locate through ground telemetry or to locate deer that left the area of initial capture. We estimated locations and associated error polygons for radiocollared deer with program Geotelm using the maximum likelihood estimator ($SD = 6.4$).

Before estimating size of home range, we determined the minimum number of locations needed to reach an asymptote using an area-observation for 10 deer of each sex with ≥ 100 locations (Odum and Kuenzler 1955, Gese *et al.*, 1990). We only used deer with ≥ 100 locations in a bootstrap procedure because 100 locations would be an adequate number to assess size of home range (Seaman *et al.* 1999). We conducted a bootstrap procedure in the Animal Movement Extension of ArcView 3.2 (ArcView; Environmental Systems Research Institute, Redlands, CA, USA; Hooze and Eichenlaub 2000) with 10 iterations that had starting sample sizes of 30 in increments of 20 until the number of locations for each deer was reached (Anderson *et al.* 2005). The mean minimum number of locations needed to estimate fixed-kernel home-range size for female and male deer was 62 and 52, respectively. We only included deer that had more than the mean minimum number of locations to estimate fixed-kernel home-range size.

3.1.3. Overall space use

We calculated 95% UD home ranges for each deer using all locations collected for the duration of this study. We used the fixed-kernel method to estimate home range (hereafter referred to as space use; Worton 1989, Seaman and Powell 1996) because it considered

density of locations and was considered most accurate at determining outer boundary areas (i.e., 95% isopleths) compared with adaptive kernel (Seaman *et al.* 1999). We selected 95% over 100% estimates of home range because of the uncertainty in estimating the periphery of the range for UD's (Seaman *et al.* 1999). Furthermore, previous research has suggested that social group relationships based on genetic analysis of deer are more responsible for disease persistence in an area than random movements away from core areas of home range (Gear *et al.* 2010). Space use and the amount of smoothing were determined by the least squares cross-validation (h_{LSCV}) method with the default parameter in the Home Range Extension of ArcView (Worton 1989, 1995, Rodgers and Carr 1998).

We calculated 95% UD grids for each deer's overall space use in the Home Range Extension of ArcView (Rodgers and Carr 1998). The UD grids between pairs of deer were then compared to determine UD overlap in ArcMacro Language using an iterative code for VI. The code enabled all-possible pair-wise comparisons for all deer that were included in the associated text file. We considered all $VI < 0.1$ to be insignificant overlap and removed these comparisons from analysis. To assess our predictions, we compared VI for all possible male and female combinations with $VI > 0.1$.

3.1.4. Age-specific space use

Most deer were captured within their first year of birth and we entered each deer into the next age category on 1 June of each year to calculate age-specific space use. We included young-of-the-year (<1 year-of-age) with yearlings (1 year-of-age) due to low sample size of the young-of-the-year age class and the low incidence of CWD in young-of-the-year and yearlings (Joly *et al.* 2006). We determined size of home range for each deer at each age to compare VIs of deer between different ages. Our deer ages were 1.5, 2.5, 3.5, 4.5, 5.5, and 6.5 with no deer or too small a sample size for deer >6.5 years of age.

3.1.5. Time space use

We determined space use separately for each deer for diurnal and nocturnal time periods using pooled annual locations collected for a particular animal during the course of this study. Diurnal and nocturnal locations for deer were determined for each month based on mean monthly sunrise and sunset times; mean monthly times were used to account for daylight savings time in our assessment of nocturnal start times (National Oceanic and Atmospheric Administration 2003). Monthly diurnal periods were determined from mean sunrise time minus 60 min to mean sunset time plus 60 min to include deer activity that occurred in daylight hours. Monthly nocturnal periods were determined from mean sunset time plus 60 min to mean sunset time minus 60 min to include deer activity patterns (Beyer and Haufler 1994).

3.1.6. Seasonal space use

We determined space use separately for each deer for two seasons based on corn-growing seasons in the Midwest obtained from the USDA National Agricultural Statistics Service (United States Department of Agriculture 2002). We considered the mean corn-growing season across several Midwest states to represent actual phenological stages better than arbitrary monthly definition of seasons. Mean Julian days from 2000 to 2006 were averaged across several states in the Midwest to determine season dates (Walter *et al.* 2009). The two seasons based on corn crop growing seasons were defined as (1) *growing* – mean date that $\geq 75\%$ of corn crops emerged to mean date that $\geq 75\%$ of corn crops were harvested

(1 June–30 October) and (2) *nongrowing* – mean date that $\geq 75\%$ of corn crops were harvested to mean date that $\geq 75\%$ of corn crops emerged (1 November–31 May).

3.2. Statistical analysis

3.2.1. Overall space use

Differences in overall size of home range by sex were evaluated with a one-way analysis of variance with significance indicated by $P \leq 0.05$. All home ranges were tested for normality, log transformed, and compared using a one-way analysis of variance with Tukey's multiple comparison to test the difference between sexes of different ages and during different seasons. Overall home range was compared with hypothesis-testing statistics (i.e., one-way analysis of variance) for comparisons with previous research.

3.2.2. Model selection

We modeled overlap of space use using VIs and based model selection on Akaike's information criteria (AIC) to select the most parsimonious model with second-order adjustment (AIC_c) to correct for small-sample bias (Burnham and Anderson 2002). We included a category-sex variable because previous research on white-tailed deer suggested that interactions of deer vary depending on sex, breeding behavior, and season (Marchinton and Hirth 1984, McShea and Schwede 1993, Gaughan and DeStefano 2005). We included the category-sex variable to represent spatial overlap of category-sex combinations instead of an interaction term to prevent over-parameterization of the model (Burnham and Anderson 2002). For example, comparison of VIs between a category (e.g., night home range) of two female deer is equal to comparison of VIs between two female deer at night so interaction terms would result in two similar parameters in each model. For each study objective, we evaluated an intercept-only model, two main effects models, an additive model, and a category-sex model, with models considered a candidate if they had a $\Delta AIC < 2.0$ (Table 2; Burnham and Anderson 2002). We assessed the degree that 95% confidence intervals of parameter estimates overlapped 0 to support AIC_c as evidence of important effects. All VIs were log transformed prior to entering into the model and statistical analyses were performed using the Statistical Analysis Software (SAS Institute 2003).

4. Results

Mean size of overall home range was greater for males (mean = $3.58 \text{ km}^2 \pm 0.32$ (SE)) than for females (mean = $0.95 \text{ km}^2 \pm 0.07$; $F_{1157} = 115.38$, $P < 0.001$). Size of home range for females increased for the older age classes but decreased for males in the older age classes (Table 1). Variability in the mean size of home range for females was relatively similar across age category (range: $0.66\text{--}1.13 \text{ km}^2$) but size of home range was the largest for 1.5-year-old males (mean = $4.41 \text{ km}^2 \pm 0.63$) and the smallest for 5.5-year-old males (mean = $2.21 \text{ km}^2 \pm 1.73$; Table 1). During the growing season, size of home range for female deer at night (mean = $0.99 \text{ km}^2 \pm 0.45$) was double than during the day (mean = $0.45 \text{ km}^2 \pm 0.14$), but male home ranges were similar between day and night (Table 1). During the nongrowing season, size of home range for female deer at night (mean = $5.24 \text{ km}^2 \pm 0.70$) was about 6 times larger than during the day (mean = $0.88 \text{ km}^2 \pm 0.17$) but no differences occurred for home ranges of males between day and night (Table 1).

Table 1. Mean \pm SE for 95% fixed-kernel estimates of size of home range (km²) for combined (overall), seasonal (growing, nongrowing), time (day, night), age class¹, and age category² of white-tailed deer in St. Louis County, Missouri from 1996 to 2000. Estimates of home range with similar letters do not differ at $P < 0.05$.

Site	Female	n^3	Male	n
Overall				
Day	1.73 \pm 0.68 ^a	58	3.71 \pm 0.68 ^{cd}	24
Night	1.01 \pm 0.10 ^a	47	4.80 \pm 0.56 ^{ce}	23
Growing				
Day	0.45 \pm 0.14 ^b	19	2.39 \pm 0.58 ^f	22
Night	0.99 \pm 0.45 ^{ab}	11	2.09 \pm 0.25 ^{df}	14
Nongrowing				
Day	0.88 \pm 0.17 ^a	40	4.15 \pm 0.91 ^{ce}	16
Night	5.24 \pm 0.70 ^{ce}	13	5.39 \pm 0.66 ^e	14
Age class				
Yearling	1.09 \pm 0.16	39	5.04 \pm 0.80	29
Adult	3.48 \pm 1.47	76	3.07 \pm 0.33	32
Prime	3.23 \pm 2.26	34	2.22 \pm 0.49	10
Age category				
1.5	1.13 \pm 0.21	18	4.41 \pm 0.63	19
2.5	0.85 \pm 0.09	22	2.64 \pm 0.42	10
3.5	0.98 \pm 0.13	42	3.92 \pm 0.59	14
4.5	0.66 \pm 0.26	11	2.53 \pm 0.57	8
5.5	0.96 \pm 0.14	12	2.21 \pm 1.73	2

¹Age class refers to yearlings (<2 years of age), adults (2–3 years of age), and prime (>3 years of age).

²Age category refers to the actual age of the deer during the year radiolocations were collected (e.g., 1.5, 2.5, and 3.5).

³ n refers to the number of deer used to determine mean size of home range for each category.

Sex was the best supported variable for VIs of deer by age (Table 2). Highest mean VIs occurred for 6-year-old females (mean = 0.51 \pm 0.10) and 5- and 6-year-old males (mean = 0.49 \pm 0.14); no mean VI was greater than 0.31 between females and males for any age combination. Sex ($w_i = 0.605$) was also the best supported variable for VIs of deer in time comparison, with sex plus time ($w_i = 0.346$) also highly supported (Table 2). Highest overlap occurred between day and night VIs of females (Table 3). Highest mean VIs occurred at night between females (mean = 0.29 \pm 0.02) and day and night between males (mean = 0.31 \pm 0.01); no mean VI was greater than 0.16 for any time combination between females and males.

Sex was the best supported variable for VIs of deer during the growing season ($w_i = 0.801$). During the growing season, highest mean VIs occurred between night and day for females (mean = 0.34 \pm 0.03) and for males (mean = 0.30 \pm 0.02). No mean VI was greater than 0.14 between females and males for any time combination during the growing season. Sex ($w_i = 0.529$) was the best supported variable for VIs of deer during the nongrowing season with time – sex ($w_i = 0.256$) and time plus sex ($w_i = 0.215$) as competing models (Table 2). During the nongrowing season, highest mean VIs occurred at night for females (mean = 0.42 \pm 0.06) and day and night for males (mean = 0.34 \pm 0.02; Table 3). No mean VI was greater than 0.13 for any time combination between females and males during the nongrowing season.

Table 2. Results of model selection for log of the volume of intersection scores for overlapping 95% fixed-kernel home ranges by age, time (i.e., day, night), and season (i.e., growing, nongrowing) for white-tailed deer in Missouri, 1997–2000. Model rankings based on number of parameters (K), Akaike's information criteria adjusted for small-sample size (AIC_c), AIC differences (ΔAIC_c), and Akaike weights (w_i).

Model	K	AIC_c	ΔAIC_c	w_i
Age¹				
Sex	3	1156	0	0.8373
Age + sex	23	1159	3	0.1627
Sex–age	84	1217	61	<0.001
Intercept	1	1271	115	<0.001
Age	21	1276	120	<0.001
Time²				
Sex	3	919	0	0.6046
Time + sex	5	920	1	0.3458
Time + sex + time–sex	10	924	5	0.0496
Time	3	1123	204	<0.001
Intercept	1	1126	207	<0.001
Growing³				
Sex	3	247	0	0.8008
Time + sex	5	250	3	0.1895
Time–sex	10	255	9	0.0096
Intercept	1	370	123	<0.001
Time	3	372	125	<0.001
Nongrowing⁴				
Sex	3	445	0	0.5291
Time–sex	5	446	1	0.2559
Time + sex	11	447	2	0.2149
Time	3	606	161	<0.001
Intercept	1	611	166	<0.001

¹Overlap in home ranges between combinations of sex and deer aged 1.5, 2.5, 3.5, 4.5, 5.5, and 6.5.

²Overlap in home ranges between combinations of sex and time (i.e., day, night).

³Overlap in home ranges between combinations of sex and time (i.e., day, night) during the growing season (1 June–30 October).

⁴Overlap in home ranges between combinations of sex and time (i.e., day, night) during the nongrowing season (1 November–31 May).

5. Discussion

Space use for female and male deer in our urban landscape differed considerably depending on demographic (i.e., age) and environmental variables (i.e., time, season). No studies on urban white-tailed deer have adequate sample sizes of both sexes to assess age- and season-specific size of home range. We documented that size of home range was greater for younger deer of both sexes and size of home range decreased or leveled off in the older age classes for both sexes after 3.5 years of age. As female and male deer mature, establishing a territory or dominance leads to reduced size of home range in our urban deer population that is similar to rural populations of deer (Marchinton and Hirth 1984, Ozoga and Verme 1986). Additionally, we found that size of home range was greater for both sexes during the nongrowing season than the growing season in the urban landscape. This is similar to previous research on rural deer throughout the Midwest (Walter *et al.* 2009), likely from

Table 3. Parameter estimates and 95% confidence intervals for the best models (i.e., differences in $AIC_c \leq 2.0$; Burnham and Anderson 2002) relating log of the volume of intersection scores of overlapping 95% fixed-kernel home range by age, time (i.e., day, night), and season (i.e., growing, nongrowing) for white-tailed deer in Missouri, 1997–2000.

Model	Estimate	95% CI
Age ¹		
Sex		
Female–female	–0.048	–0.121 to 0.025
Female–male	–0.394	–0.472 to –0.316
Male–male	0.00	0.00 to 0.00
Time ²		
Sex		
Female–female	–0.055	–0.127 to 0.017
Female–male	–0.536	–0.613 to –0.460
Male–male	0.00	0.00 to 0.00
Sex + time		
Female–female	–0.054	–0.126 to 0.017
Female–male	–0.532	–0.608 to –0.455
Male–male	0.00	0.00 to 0.00
Day–day	–0.028	–0.113 to 0.057
Day–night	0.033	–0.042 to 0.107
Night–night	0.00	0.00 to 0.00
Growing ³		
Sex		
Female–female	0.090	–0.037 to 0.218
Female–male	–0.642	–0.753 to –0.530
Male–male	0.00	0.00 to 0.00
Nongrowing model ⁴		
Sex		
Female–female	–0.028	–0.135 to 0.079
Female–male	–0.719	–0.831 to –0.608
Male–male	0.00	0.00 to 0.00
Sex–time		
Female–female–day–day	–0.073	–0.275 to 0.130
Female–female–day–night	0.046	–0.151 to 0.243
Female–female–night–night	0.342	0.046 to 0.637
Female–male–day–day	–0.625	–0.829 to –0.421
Female–male–day–night	–0.685	–0.904 to –0.466
Female–male–night–day	–0.745	–1.00 to –0.489
Female–male–night–night	–0.727	–1.068 to 0.386
Male–male–day–day	0.025	–0.176 to 0.226
Male–male–night–day	0.150	–0.085 to 0.384
Male–male–night–night	0.00	0.00 to 0.00
Sex + time		
Female–female	–0.013	–0.122 to 0.096
Female–male	–0.699	–0.814 to –0.586
Male–male	0.00	0.00 to 0.00
Day–day	–0.096	–0.247 to 0.054
Day–night	–0.035	–0.178 to 0.109
Night–night	0.00	0.00 to 0.00

¹Overlap in home ranges between combinations of sex and deer aged 1.5, 2.5, 3.5, 4.5, 5.5, and 6.5.

²Overlap in home ranges between combinations of sex and time (i.e., day, night).

³Overlap in home ranges between combinations of sex and time (i.e., day, night) during the growing season (1 June–30 October).

⁴Overlap in home ranges between combinations of sex and time (i.e., day, night) during the nongrowing season (1 November–31 May).

the lack of natural forage availability during the late-autumn and winter periods represented by the nongrowing season and associated searching of forage by both sexes of deer.

Size of home range at night was greater for females during nongrowing season compared with day, which was likely from less activity and disturbance by humans during nocturnal hours (Montgomery 1963, Hayes and Krausman 1993). Studies have documented increases in size of home range at night for rural deer populations but no research has investigated nocturnal size of home range for urban deer populations (Montgomery 1963, Vogel 1989). Deer in suburban communities consumed ornamental plants, grass lawns, and bird seed during nocturnal feeding bouts that are characteristic of urban landscapes (Kilpatrick and Spohr 2000, Grund *et al.* 2002). Size of home ranges was smaller during the day than at night because we hypothesize that deer are relegated to the forested patches for security cover but leave under the security of night to forage in more presumed risky habitats (i.e., lawns, ornamental plants).

Unlike rural deer populations, size of home range for both sexes of deer was larger during the nongrowing season than the growing season (Tierson *et al.* 1985, Van Deelen *et al.* 1998, Lesage *et al.* 2000). Our nongrowing season corresponded to autumn–winter seasons in previous research that typically encompass months with limited natural forage availability. Larger size of home range during nongrowing seasons in our urban deer population was likely a reflection of the different foraging strategies exhibited by urban versus rural deer (Gaughan and DeStefano 2005). Rural deer typically find wintering yards or more ideal habitat for thermal cover and foraging habitat to minimize movements during forage-limited seasons while naturally reducing intake rates (Silver *et al.* 1969, Worden and Pekins 1995). However, urban deer find suitable thermal cover and foraging habitat in close proximity in the urban landscape by foraging on ornamental plants, residential/commercial lawns, and supplemental feed (e.g., bird feeders). Therefore, urban deer populations travel greater distances during the nongrowing season to find suitable resources compared with the growing season when the juxtaposition of suitable habitats leads to smaller deer movements compared with their rural counterparts (Gaughan and DeStefano 2005).

Overlap of space use as determined by VIs in our urban deer population was correlated with sex, time, and season more so than age of deer. Researchers have suggested that the prevalence of CWD increased with age of male mule deer (*O. hemionus*) in Colorado and white-tailed deer in Wisconsin (Miller and Conner 2005, Grear *et al.* 2006). Unlike male deer in rural landscapes, male white-tailed deer in our developed landscape had a decrease in size of home range with age, and age did not influence our overlap of space use for models (i.e., $\Delta AIC_c < 2.0$) between male deer. Older male deer (i.e., ≥ 3 years old) had smaller space use than younger deer (i.e., < 3 years old), but younger deer are less likely to be infected with CWD because female to fawn transmission of CWD is likely low and has only recently been documented to occur in white-tailed deer at very low prevalence ($< 0.5\%$ over 2 years; Grear *et al.* 2006). Behavior of older males to congregate in bachelor groups during winter months and breeding behavior were suspected to play a prominent role in direct transmission of CWD (Farnsworth *et al.* 2005, Grear *et al.* 2006). However, smaller space use for our males suggested that, for older white-tailed deer, indirect transmission may be more likely by contamination of soil or other environmental sources with the infectious prion protein for CWD as recently proposed (Miller and Conner 2005, Schuler 2006). Our results could assist in setting up similar study designs to assess age-specific size of home range to contribute to understanding whether the initial infected individual was infected by direct or indirect transmission.

We documented an increase in space use by both sexes during nocturnal hours indicating deer that shed CWD infectious material may contaminate the residential or open habitats that deer typically do not occupy during the day (Figure 2). We found greater overlap of space use between males and females for our time comparison (i.e., day, night) that could have broad

implications for disease transmission and deer–human conflicts. Baiting of deer has been implicated in concentrating deer populations in a single area (Kilpatrick and Stober 2002, Miller *et al.* 2003). Similar to bait sites or winter deer yards, forested diurnal or nocturnal feeding habitats can congregate males and females and their social groups into a single area at high densities or into developed areas they usually do not occupy (Vogel 1989, Nixon *et al.* 1991, DeNicola *et al.* 2008), thereby increasing deer–human conflicts in these areas or allowing CWD-infected deer to contribute to direct and indirect transmission as proposed for mule deer in developed areas (Farnsworth *et al.* 2005).

Considerable overlap of space use by both sexes during day and night suggested that day-bedding habitats or nocturnal feeding habitats may contribute to disease transmission in urban landscapes to a greater extent than for deer in rural landscapes. Rural deer populations at lower densities exhibit greater philopatry, decrease space use, and have minimal overlap with conspecific matrilineal groups but this overlap may increase during winter months (Mathews and Porter 1993, Lesage *et al.* 2000, Grund *et al.* 2002). Aggregations of deer in preferred bedding or feeding habitats may contribute to high densities of deer during the nongrowing season similar to mule deer in residential landscapes of Colorado (Farnsworth *et al.* 2005, Miller and Conner 2005). Direct transmission among females within the same matrilineal group has been considered a likely source of CWD transmission in both mule and white-tailed deer (Miller and Conner 2005, Grear *et al.* 2006, Schaubert *et al.* 2007). Female deer in our urban landscape increased their space use during the nongrowing season likely leading to greater chance of direct contact with males and females that are not in their matrilineal group. Schaubert *et al.* (2007) suggested that overlap in space can be indicative of

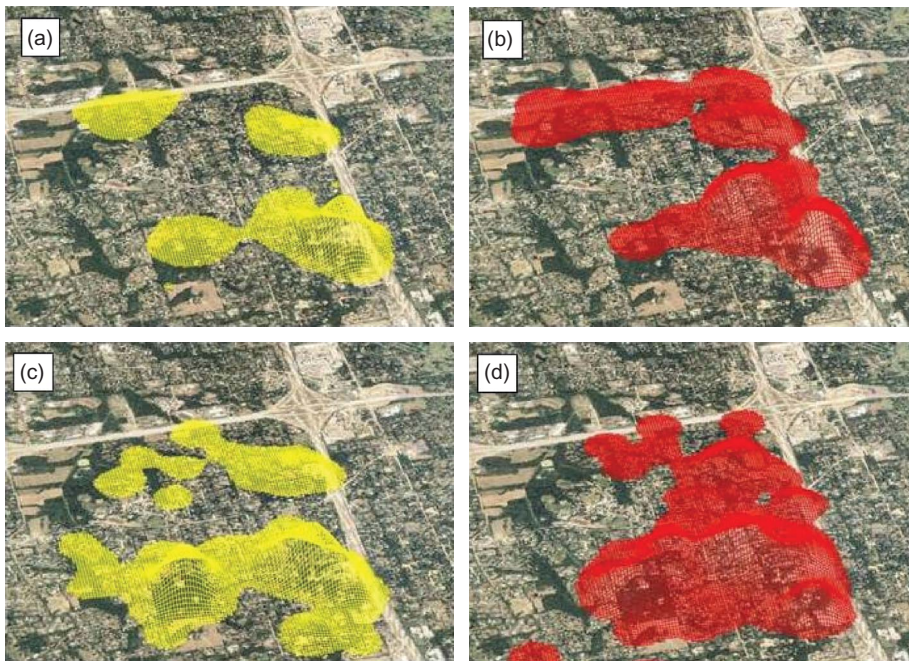


Figure 2. Utilization distributions of a representative male white-tailed deer on an aerial photograph documenting differences in space use for the growing season during the (a) day and (b) night and during the nongrowing season during the (c) day and (d) night in an urban landscape in eastern Missouri.

direct disease transmission of females between-groups but not within-groups due to expected joint space use of females in matrilineal groups. Our data suggested that direct transmission of disease between females in different matrilineal groups could be more prominent in urban landscapes, similar to findings for mule deer (Farnsworth *et al.* 2005). With the limited forest cover and foraging habitat, direct contact between unrelated female groups could occur exacerbating the spread of disease upon introduction to the urban landscape.

6. Conclusions

We identified detailed overlap of space use for a population of white-tailed deer at high densities (31 deer/km²) in an urban eastern Missouri landscape. Similar to results on mule deer wintering in developed landscapes, we found that considerable overlap of space use by male and female white-tailed deer occurs during nocturnal hours and the nongrowing season in our urban landscape. Efforts to reduce overall CWD prevalence through deer removal or environmental decontamination in urban landscapes should focus primarily on preferred thermal cover and foraging habitats that can result in congregations of deer during periods of inactivity. Additional measures to reduce population levels of deer or to create additional habitats for inactive deer could delay the spread of direct disease transmission in urban deer populations. If severe population reduction is not feasible to control disease spread, habitat management that causes deer to exhibit philopatry to space use with minimal overlap among adjacent matrilineal groups could minimize direct transmission by deer.

Acknowledgements

Funding for this research was provided by private citizens from the City of Town and Country, Missouri, the Missouri Department of Conservation, Federal Aid in Wildlife Restoration Project W-13-R-48, and the National Wildlife Research Center of the United States Department of Agriculture, Animal and Plant Health Inspection Service, and Wildlife Services.

References

- Anderson, D.P., *et al.*, 2005. Factors influencing female home range sizes in elk (*Cervus elaphus*) in North American landscapes. *Landscape Ecology*, 20, 257–271.
- Ayrigg, J.L. and Porter, W.F., 1997. Sociospatial dynamics of white-tailed deer in the central Adirondack Mountains, New York. *Journal of Mammalogy*, 78, 468–482.
- Beringer, J., *et al.*, 2002. Efficacy of translocation to control urban deer in Missouri: costs, efficiency, and outcome. *Wildlife Society Bulletin*, 30, 767–774.
- Beyer, D.E. Jr. and Haufler, J.B., 1994. Diurnal versus 24-hour sampling of habitat use. *Journal of Wildlife Management*, 58, 178–180.
- Bissonette, J.A., Sherburne, S.S., and Ramsey, R.D., 1994. Analysing telemetry data with a GIS-based vector structure. *International Journal of Geographical Information Systems*, 8, 533–543.
- Burnham, K.P. and Anderson, D.R., 2002. *Model selection and multimodel inference: a practical information-theoretic approach*. New York: Springer-Verlag.
- Cox, R.R. Jr., *et al.*, 2002. Using an electronic compass to determine telemetry azimuths. *Wildlife Society Bulletin*, 30, 1039–1043.
- DeNicola, A.J., Etter, D.R., and Almendinger, T., 2008. Demographics of non-hunted white-tailed deer populations in suburban areas. *Human-Wildlife Conflicts*, 2, 102–109.
- Etter, D.R., *et al.*, 2002. Survival and movements of white-tailed deer in suburban Chicago, Illinois. *Journal of Wildlife Management*, 66, 500–510.
- Farnsworth, M.L., *et al.*, 2005. Human land use influences chronic wasting disease prevalence in mule deer. *Ecological Applications*, 15, 119–126.

- Gaughan, C.R. and DeStefano, S., 2005. Movement patterns of rural and suburban white-tailed deer in Massachusetts. *Urban Ecosystems*, 8, 191–202.
- Gerrard, R.A., et al., 1997. Selecting conservation reserves using species-covering models: adapting the ARC/INFO GIS. *Transactions in GIS*, 2, 45–60.
- Gese, E.M., Andersen, D.E., and Rongstad, O.J., 1990. Determining home-range size of resident coyotes from point and sequential locations. *Journal of Wildlife Management*, 54, 501–506.
- Grear, D.A., et al., 2006. Demographic patterns and harvest vulnerability of chronic wasting disease infected white-tailed deer in Wisconsin. *Journal of Wildlife Management*, 70, 546–553.
- Grear, D.A., et al., 2010. Influence of genetic relatedness and spatial proximity on chronic wasting disease infection among female white-tailed deer. *Journal of Applied Ecology*, 47, 532–540.
- Grund, M.D., McAninch, J.B., and Wiggers, E.P., 2002. Seasonal movements and habitat use of female white-tailed deer associated with an urban park. *Journal of Wildlife Management*, 66, 123–130.
- Hansen, L.P. and Beringer, J. 2003. Survival of rural and urban white-tailed deer in Missouri. *Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies*, 57, 326–336.
- Hayes, C.L. and Krausman, P.R., 1993. Nocturnal activity of female desert mule deer. *Journal of Wildlife Management*, 57, 897–904.
- Henderson, D.W., et al., 2000. Responses of urban deer to a 50% reduction in local herd density. *Wildlife Society Bulletin*, 28, 902–910.
- Hooge, P.N. and Eichenlaub, B., 2000. Animal movement extension in ArcView, Version 2.0. Alaska Biological Science Center, US Geological Survey, Anchorage, AK, USA.
- Joly, D.O., et al., 2006. Spatial epidemiology of chronic wasting disease in Wisconsin white-tailed deer. *Journal of Wildlife Diseases*, 42, 578–588.
- Kilpatrick, H.J. and Spohr, S.M., 2000. Spatial and temporal use of a suburban landscape by female white-tailed deer. *Wildlife Society Bulletin*, 28, 1023–1029.
- Kilpatrick, H.J. and Stober, W.A., 2002. Effects of temporary bait sites on movements of suburban white-tailed deer. *Wildlife Society Bulletin*, 30, 760–766.
- Lesage, L., et al., 2000. Seasonal home range size and philopatry in two northern white-tailed deer populations. *Canadian Journal of Zoology*, 78, 1930–1940.
- Marchinton, R.L. and Hirth, D.H., 1984. Behavior. In: L.K. Halls, ed.. *White-tailed deer: ecology and management*. Harrisburg, PA: Stackpole Books, 129–168.
- Mathews, N.E. and Porter, W.F., 1993. Effect of social structure on genetic structure of free-ranging white-tailed deer in the Adirondack Mountains. *Journal of Mammalogy*, 74, 33–43.
- McShea, W.J. and Schwede, G., 1993. Variable acorn crops: responses of white-tailed deer and other mast consumers. *Journal of Mammalogy*, 74, 999–1006.
- Miller, M.W. and Conner, M.M., 2005. Epidemiology of chronic wasting disease in free-ranging mule deer: spatial, temporal, and demographic influences on observed prevalence patterns. *Journal of Wildlife Diseases*, 41, 275–290.
- Miller, R., et al., 2003. Evaluation of the influence of supplemental feeding of white-tailed deer (*Odocoileus virginianus*) on the prevalence of bovine tuberculosis in the Michigan wild deer population. *Journal of Wildlife Diseases*, 39, 84–95.
- Millspaugh, J.J., et al., 2004. Comparability of three analytical techniques to assess joint space use. *Wildlife Society Bulletin*, 32, 148–157.
- Montgomery, G.G., 1963. Nocturnal movements and activity rhythms of white-tailed deer. *Journal of Wildlife Management*, 27, 422–427.
- National Oceanic and Atmospheric Administration. 2003. Washington, D.C., USA. Available from: <http://www.noaa.gov/> [Accessed 10 March 2005].
- Nelson, M.E., 1993. Natal dispersal and gene flow in white-tailed deer in northeastern Minnesota. *Journal of Mammalogy*, 74, 316–322.
- Nelson, M.E. and Mech, L.D., 1999. Twenty-year home-range dynamics of a white-tailed deer matriline. *Canadian Journal of Zoology*, 77, 1128–1135.
- Nixon, C.M., et al., 1991. Ecology of white-tailed deer in an intensively farmed region of Illinois. *Wildlife Monographs*, 118, 1–77.
- O'Brien, D.J., et al., 2002. Epidemiology of *Mycobacterium bovis* in free-ranging white-tailed deer, Michigan, USA, 1995–2000. *Preventive Veterinary Medicine*, 54, 47–63.
- Odum, E.P. and Kuenzler, E.J., 1955. Measurement of territory and home range size in birds. *Auk*, 72, 128–137.

- Ozoga, J.J. and Verme, L.J., 1986. Relation of maternal age to fawn-rearing success in white-tailed deer. *Journal of Wildlife Management*, 50, 480–486.
- Pereira, J.M.C. and Itami, R.M., 1991. GIS-based habitat modeling using logistic multiple regression: a study of the Mt. Graham red squirrel. *Photogrammetric Engineering & Remote Sensing*, 57, 1475–1486.
- Rodgers, A.R. and Carr, A.P., 1998. HRE: the home range extension for ArcView™: user's manual. Beta test version 0.9, July 1998. Ontario Ministry of Natural Resources, Centre for Northern Forest Ecosystem Research, Thunder Bay, ON, Canada.
- SAS Institute. 2003. The SAS system for Windows, Version 9.1. SAS Institute, Cary, NC.
- Schauber, E.M., Storm, D.J., and Nielsen, C.K., 2007. Effects of joint space use and group membership on contact rates among white-tailed deer. *Journal of Wildlife Management*, 71, 155–163.
- Schuler, K.L. 2006. *Monitoring for chronic wasting disease in mule deer and white-tailed deer at Wind Cave National Park: investigating an emerging epizootic*. Thesis (PhD). South Dakota State University, Brookings, S D, USA.
- Seaman, D.E. and Powell, R.A., 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. *Ecology*, 77, 2075–2085.
- Seaman, D.E., et al., 1999. Effects of sample size on kernel home range estimates. *Journal of Wildlife Management*, 63, 739–747.
- Seidel, K.D. 1992. *Statistical properties and applications of a new measure of joint space use for wildlife*. Thesis (MS). University of Washington, Seattle, WA.
- Silver, H., et al., 1969. Fasting metabolism of white-tailed deer. *Journal of Wildlife Management*, 33, 490–498.
- Storm, D.J., et al., 2007. Deer-human conflict and hunter access in an exurban landscape. *Human-Wildlife Conflicts*, 1, 53–59.
- Tierson, W.C., et al., 1985. Seasonal movements and home ranges of white-tailed deer in the Adirondacks. *Journal of Wildlife Management*, 49, 760–769.
- United States Department of Agriculture. National Agricultural Statistics Service. 2002. Available from: http://www.noss.usda.gov/Data_and_Statistics/Quick_Stats/index.asp [Accessed 18 May 2007].
- Van Deelen, T.R., et al., 1998. Migration and seasonal range dynamics of deer using adjacent deeryards in northern Michigan. *Journal of Wildlife Management*, 62, 205–213.
- Vogel, W.O., 1989. Response of deer to density and distribution of housing in Montana. *Wildlife Society Bulletin*, 17, 406–413.
- Walter, W.D., et al., 2009. Regional assessment on influence of landscape configuration and connectivity on range size of white-tailed deer. *Landscape Ecology*, 24, 1405–1420.
- Worden, K.A. and Pekins, P.J., 1995. Seasonal change in feed intake, body composition, and metabolic rate of white-tailed deer. *Canadian Journal of Zoology*, 73, 452–457.
- Worton, B.J., 1989. Kernel methods for estimating the utilization distribution in home-range studies. *Ecology*, 70, 164–168.
- Worton, B.J., 1995. Using Monte Carlo simulation to evaluate kernel-based home range estimators. *Journal of Wildlife Management*, 59, 794–800.