

Landscape effects on scales of movement by white-tailed deer in an agricultural–forest matrix

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Abstract Understanding how organisms respond to landscape heterogeneity is foundational to landscape ecology. We characterized seasonal scales of movement of white-tailed deer (*Odocoileus virginianus*) in an agricultural–forest matrix using first-passage time analysis (FPT) for 62 GPS-collared individuals. We investigated whether those scales were driven by demographic or landscape features. We found FPT for each individual across all seasons was typically dominated by a peak in variance of FPT/area at scales (radii) from 425 to 1,675 m. These peaks occurred at scales consistent with seasonal space use. We observed additional lower magnitude peaks at larger scales (3,000–6,000 m) and small scales (25–150 m). Peaks at larger scales were associated with seasonal migrations and dispersal events. Small scale peaks may represent resting or foraging behavior. Female movements were organized at smaller scales than males in the spring/summer season. Models relating landscape features to movement scales suggest that deer perceive and move within the landscape differently as the roles of dominant land-cover types shift seasonally. During winter, configuration (interspersal/juxtaposition) of land-cover types is more important to deer than during spring/summer and fall.

During spring/summer and fall, movement behavior may be dictated by reproductive and harvest activities.

Keywords First-passage time · GPS collars · Landscape structure · Scales of movement · Seasonality · White-tailed deer

Introduction

Animal movements are a fundamental process driving multiple aspects of ecology and behavior including population dynamics and genetic structure (Cushman et al. 2006), foraging (McKenzie et al. 2009; Valeix et al. 2010), community structure (Fortin et al. 2005), disease spread (Loehle 1995; Conner et al. 2008), and spatial dispersion (Turchin 1998). Over limited time periods, animal movement may be effectively characterized by simple movement models, such as correlated random walks (Turchin 1998). However, movement across longer time periods represents a complex response to multiple biotic and abiotic factors including risk, social dynamics, internal state, and habitat quality and availability (Gautestad and Mysterud 2005; Nathan et al. 2008). When the availability and influence of those factors varies across time and space, we expect organisms to alter their movements to maximize fitness. In general, animals are expected to spend more time and move differently in areas

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where resources are more abundant. Bell (1991) describes multiple manners in which animals may alter movement patterns in response to resources including looping, zigzags, slowing down, changing arrival-departure direction, and orienting movements with patch edges. Because of these behavioral responses to the landscape, simple models of movement may not adequately represent animal movement across larger temporal and spatial scales. Identifying the factors associated with changes of movement behavior and the scales at which those movements occur may improve our ability to model movements across greater extents (Morales et al. 2004).

Habitat resources may be organized hierarchically at multiple scales. While this hierarchy may be conceptually understood (Senft et al. 1987), it is difficult to delineate explicitly due to perceptual differences between the observer and study organism. Wiens (1976) stressed the need to abandon our conceptions of environmental scale and focus on the perceptions of organisms. As a result of selective pressures, organisms should possess abilities to detect and respond to those scales by altering movements (Fauchald 1999; Fauchald and Tveraa 2006). Thus, movement paths should serve as a record of how an organism responded to spatial pattern (McIntyre and Wiens 1999).

In central New York State, landscape heterogeneity arises from historical agriculture and reforestation and is dominated by forest (44%) and agriculture (34%). If white-tailed deer in this region are responding to those specific drivers of landscape heterogeneity (forest and agriculture) then the relative ease by which they may be monitored makes them a model species for understanding the relationship between movement patterns and landscape characteristics. Dechen Quinn (2010) found that white-tailed deer in this region select for deciduous forest and agriculture through most of the year, but coniferous forest in the winter. The author found space-use to be influenced by both forage and cover resources, reporting that annual space use was predicated on compositional requirements of those resources and the arrangement of those resources at a local scale. These findings suggest that deer are responding to both compositional and configuration aspects of the landscape. Response by deer to spatially explicit components of the landscape is complicated by the fact that they exhibit multiple sex- and age-specific behaviors. These behaviors, such as parental

care, rut, dispersal, or seasonal migration, result in differing energetic requirements across seasons and may augment or reduce the impact of landscape characteristics on movement.

We can characterize the spatial scales at which individual deer are responding to the landscape using first-passage time (FPT) analysis of their movement paths (Fauchald and Tveraa 2003; Frair et al. 2005; Pinaud 2008). FPT analysis is designed explicitly to measure the variation in time spent within a window (circle) of a set size that is moved along an animal's path. This analysis is repeated with a range of circle sizes, and peaks in variation of passage time versus circle radius identify the scales at which the animal's movements are clustered. These scales may be indicative of the size of the landscape patches as perceived by the animal (Frair et al. 2005; Pinaud 2008). For this study, we used FPT to answer two questions. Do white-tailed deer occupying an agriculture–forest matrix exhibit distinct scales of movement? If deer exhibit variation in scales of movement, then are those scales related to local landscape characteristics?

We hypothesized that scales of movement by deer would both be evident and correspond to well studied deer space-use behaviors including localized foraging, home ranges, dispersal, and seasonal migration. We expected scales of movement by deer to vary across seasons in response to spatial characteristics of the landscape. Specifically, we predicted that deer movements would be organized at larger scales where aspects of landscape composition and configuration necessitated greater travel distances to acquire requisite resources.

Methods

Study area

The study area encompassed 8,300 km² in Onondaga, Cortland, Madison and Oneida Counties of central New York State. Land cover was a mix of forest (44%) and agriculture (34%) with small communities (9% developed). Forests were dominated by hardwoods, notably maple (*Acer* spp.) and American beech (*Fagus grandifolia*). Conifer plantations originating in the 1930s were composed of pine (*Pinus* spp.) and spruce (*Picea* spp.). Agricultural crops were mostly related to dairy and included corn, winter wheat, oats, alfalfa,

and soybeans. Elevations range from 93 to 652 m and the region lies to the south and east of Lake Ontario. Average total annual precipitation is 101 cm/year. Winters are variable with heavy snow events and frequent thaws. Snowfall in the region averages 251 cm/year and ranged from 241 to 336 cm/year during this study (National Climatic Data Center). Road density in the region was 1.85 km/km²; 98.5% of the landscape was <1.6 km from a road (New York State Office of Cyber Security and Critical Infrastructure Coordination 2009).

Movement data

Global positioning system (GPS) collars (model GPS2000, Advanced Telemetry Systems, Inc.) collected location data from 62 white-tailed deer (23 males and 39 females) between February 2006 and April 2008. Deer were captured during January–April 2006 and 2007 (Dechen Quinn 2010). Collars were programmed to take a GPS location every 5 h and GPS locations were stored on board the collars. The collars were remotely detached from study animals and retrieved after approximately 1 year ($\bar{x} = 271$ days, range = 30–600 days). Mean success rate for acquiring a positional fix was 0.86 (SD = 0.09). We determined positional error associated with GPS

locations to be <10 m in most cases ($\bar{x} = 5.3$ m, SD = 5.3 m). The radii at which peaks in FPT analyses occurred was insensitive to simulated positional error of this magnitude (Williams 2010). We subset animal movement paths by season, including deer monitored over the entire period only: winter (January 1–April 30, $n = 50$), spring/summer (May 1–September 30, $n = 47$), fall (October 1–December 31, $n = 30$), and annual (paths >12 months long, $n = 24$). All analyses and statistical tests were done in the R v2.9.2 statistical programming language (R Development Core Team 2009).

First-passage time analyses

We conducted FPT analyses in the *adehabitat* package of R (Calenge 2006). For each GPS location along an individual movement path, we calculated the time spent moving along the path within a circle of a given radius. Where the circle intersected the path between GPS locations, we calculated time spent along the resulting path segment by assuming constant rates of travel along the corresponding step (Fig. 1). Missed fixes created some breaks along the movement path and we did not calculate passage times for affected locations. We evaluated the passage time along each path using circles with radii ranging from 25 to

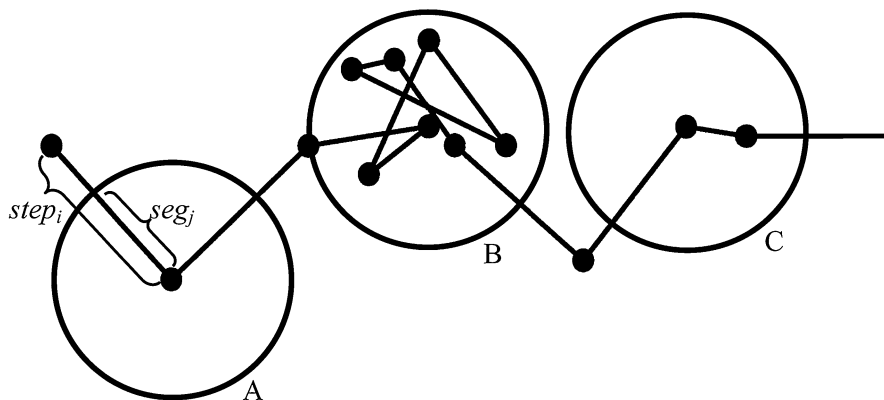


Fig. 1 Example of passage-time calculation for a hypothetical movement path. Passage time is calculated at each GPS location (filled circles) along an individual movement path (solid line) as the time spent moving along the path within a circle of given radius. Where the circle intersected the path between GPS locations (e.g., circle A), we calculated time spent along the resulting path segment (seg_j) by assuming constant rates of travel along the corresponding step ($step_i$). Assuming a constant

fix schedule for this path, a relatively great amount of time was spent in circle B compared to circles A and C. The variation in passage time across all circles of a given size along a movement path represents the degree to which aggregation of movements occurs differs along the path. FPT identifies the circle size(s) where variation in passage time per unit area is maximized

10,000 m at 25 m intervals. The variation in passage time across all circles of a given size along a movement path represents the degree to which aggregation of movements differs along the path. Mean passage time and the corresponding variation around that mean are expected to increase as a function of increasing circle size. Thus, we divided the variance in passage time by the area of the evaluation scale (circle size). We identified peaks in the variance of passage time per unit area ($\text{varFPT}/\text{area}$) for individual deer in each season (Frair et al. 2005).

Landscape and demographic effects

We evaluated differences between the dominant scales of movement both by season and by sex–age class of male and female adults (≥ 18 months) and yearlings (< 18 months), across all seasons using Wilcoxon rank sum tests. We included landscape composition and configuration metrics in the set of variables potentially associated with scales of movement by deer. We conducted landscape analyses using the 2001 National Land Cover Database for New York State (Homer et al. 2004). We reclassified the landscape categories to Anderson Level I with one exception (Anderson et al. 1976). A portion of the study area near Rome, NY, had large patches classified as woody wetland used by deer in a manner similar to other forest cover. Rather than classifying that habitat as the Anderson wetland category, we included woody wetland in the Anderson Level I forest class.

Landscape variables were calculated at multiple extents using Fragstats (McGarigal et al. 2002). These extents were based on buffers of increasing distance (500, 1,000, 2,000, and 5,000 m) from the centroid of the seasonal home ranges of each deer (95% polygon fixed kernel density estimator). Centroids of home range polygons were identified using ArcGIS 9.2 (ESRI 1999–2006). Where home ranges consisted of disjunct polygons, we forced the centroids to occur within a polygon. We evaluated correlations between prospective predictor variables to avoid multicollinearity within candidate models. For example, percentage of forest and agriculture were highly correlated ($r = -0.57$ across all scales, $r = -0.73$ within the 500 m buffer) and thus only percentage of forest was included in candidate models. Thus, we reduced the potential explanatory variables to three landscape

metrics: percent forest (FOR), percent rangeland (RANGE), and interspersion/juxtaposition index (IJI). Rangeland is an Anderson Level I classification category which includes land-cover categories identified as shrub/scrub and grassland by the NLCD (Anderson et al. 1976; Homer et al. 2004). Inspection of the Anderson reclassified NLCD data within this study area suggests that edge habitat between forest and agriculture is frequently identified as rangeland (11% of landscape). IJI measures the intermixing of patch types within a landscape from low values when patches are less aggregated and adjacent to few other patch types to high values when patches are disaggregated and highly interspersed. We summarized landscape metrics across landscape extents and evaluated differences in variation using Levene's test.

We developed a set of 17 candidate linear models to evaluate hypotheses about associations between scales of movement by deer (FPT peak radius) and landscape characteristics at multiple scales (Table 1). We evaluated a study-area effect on scales of movement by deer using a two-level variable distinguishing individuals within the Oneida and Cortland sites of the study area. To evaluate the importance of this site effect, it was included in 1 set of the 17 candidate models, but not in a second set. This addition resulted in 34 potential models. The set of candidate models included a global model with every landscape metric, demographic category, and study-area. Because data sets differed for each season we evaluated the candidate model set separately for annual, spring/summer, fall, and winter movements. We evaluated model residuals for evidence of spatial autocorrelation using correlograms (*ncf* package in R) and semivariograms (*gstat* package) (Fortin and Dale 2005). We conducted model selection using Akaike's Information Criterion (AIC) to determine which demographic and landscape characteristics were most likely associated with movement scales of deer across multiple landscape extents. Best models were evaluated based upon ΔAICc , where models within 2 units of the top performing model were considered competing models. When there were competing models, we used model averaging. We evaluated the predictive power of the top performing model within each season using leave-one-out cross validation and a Chi-square goodness-of-fit test to evaluate correspondence of observed and predicted scales of movement binned by quantiles.

Table 1 Candidate models for relating the dominant scales at which white-tailed deer movements are organized (as identified by first-passage time analyses) to demographic and landscape characteristics

Model hypothesis	Model components
Global model	FPTscales \sim factor(SEX) + factor(AGE) + FOR + RANGE + IJI
Demographics and composition	FPTscales \sim factor(SEX) + factor(AGE) + FOR + RANGE
Demographics and configuration	FPTscales \sim factor(SEX) + factor(AGE) + IJI
Composition and configuration	FPTscales \sim FOR + RANGE + IJI
Age, composition, and configuration	FPTscales \sim factor(AGE) + FOR + RANGE + IJI
Age and composition	FPTscales \sim factor(AGE) + FOR + RANGE
Age and configuration	FPTscales \sim factor(AGE) + IJI
Sex, composition, and configuration	FPTscales \sim factor(SEX) + FOR + RANGE + IJI
Sex and composition	FPTscales \sim factor(SEX) + FOR + RANGE
Sex and configuration	FPTscales \sim factor(SEX) + IJI
Sex	FPTscales \sim factor(SEX)
Age	FPTscales \sim factor(AGE)
Composition	FPTscales \sim FOR + RANGE
Configuration	FPTscales \sim IJI
Forest	FPTscales \sim FOR
Rangeland	FPTscales \sim RANGE
Null	FPTscales \sim NULL

Results

First-passage time analyses

We observed consistent patterns for scales of movement as detected by FPT analyses among white-tailed deer in central New York. The highest peak in variance of FPT/area for each individual across annual paths corresponded at radii ranging from 575 to 1,675 m ($\bar{x} = 1,049$ m and $SD = 311$ m) (examples: Fig. 2). In addition to high peaks in varFPT/area, we observed additional lower magnitude peaks at larger scales (3,000–6,000 m) for 32% ($n = 20$) of individual deer (Fig. 2). For those individuals, the additional peaks most frequently related to winter path segments (70%, $n = 14$). Peaks at larger scales were also observed for annual (29%, $n = 7$), spring/summer (10%, $n = 5$), and/or fall (11%, $n = 4$) seasonal path segments. These peaks occurred only among individuals that exhibited disjunct seasonal space use, which may have equated to seasonal migration or dispersal. Twelve individuals (19%) exhibited high values of varFPT/area at the smallest scales evaluated that declined with increasing scale (25–150 m). No peaks in varFPT/area were observed for 8% ($n = 5$) of individuals.

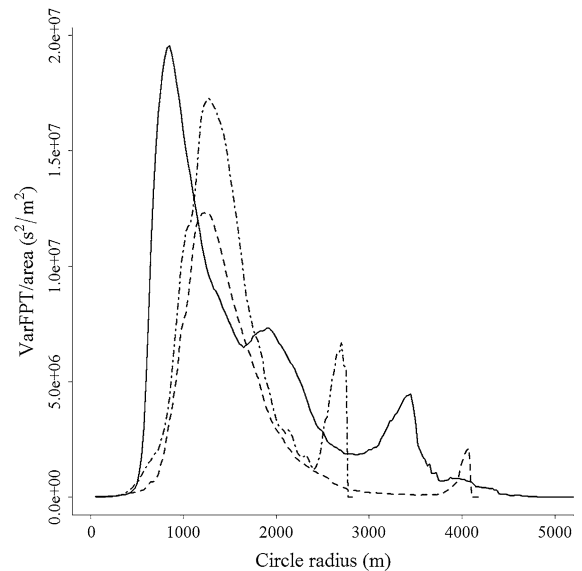


Fig. 2 Plots of area adjusted variance in first-passage time (varFPT/area, s^2/m^2) as a function of the scale used to determine passage time along the observed movement path (radius of circle, m) for three white-tailed deer in central New York. Peaks in varFPT/area indicate the landscape scale(s) to which individuals are responding by altering time spent along their movement path

Scales of movement varied seasonally (Fig. 3), with some intra-seasonal differences among sex and age classes (Figs. 4, 5). Movement scales in spring/summer (median = 775 m) were smaller than those in winter (median = 962.5 m, $W = 1584.5$, $P = 0.002$) and along annual paths (median = 975 m, $W = 793.5$, $P = 0.003$), but not fall (median = 800 m, $W = 781.5$, $P = 0.213$). The dominant scale of movement for fall was less than those detected along annual paths ($W = 482.5$, $P = 0.018$) and winter ($W = 958.5$, $P = 0.019$). Median dominant scale of movement for females (650 m) was 400 m less than that of males within spring/summer ($W = 370.5$, $P = 0.001$), but not other seasons (Fig. 4). We observed no differences in scales of movement due to age (Fig. 5).

Landscape and demographic effects

Composition landscape characteristics were scale dependent. Percent forest (FOR) was greatest and most variable within 500 m buffers of home range centroids ($\bar{x} = 59\%$, $SD = 21.8$, range = 3–100%) and lowest and least variable within 5,000 m buffers of those same point locations ($\bar{x} = 44\%$, $SD = 9.8$, range = 30–62%). Percent rangeland (RANGE) was also greatest and most variable within the 500 m buffers ($\bar{x} = 13\%$, $SD = 7.23$, range = 1–53%) and

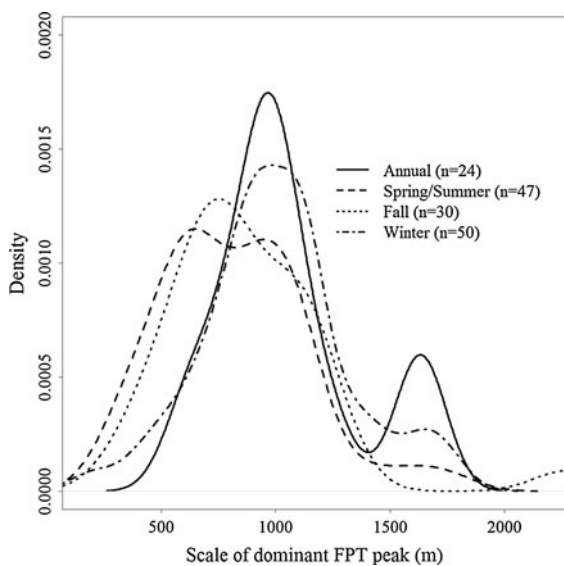


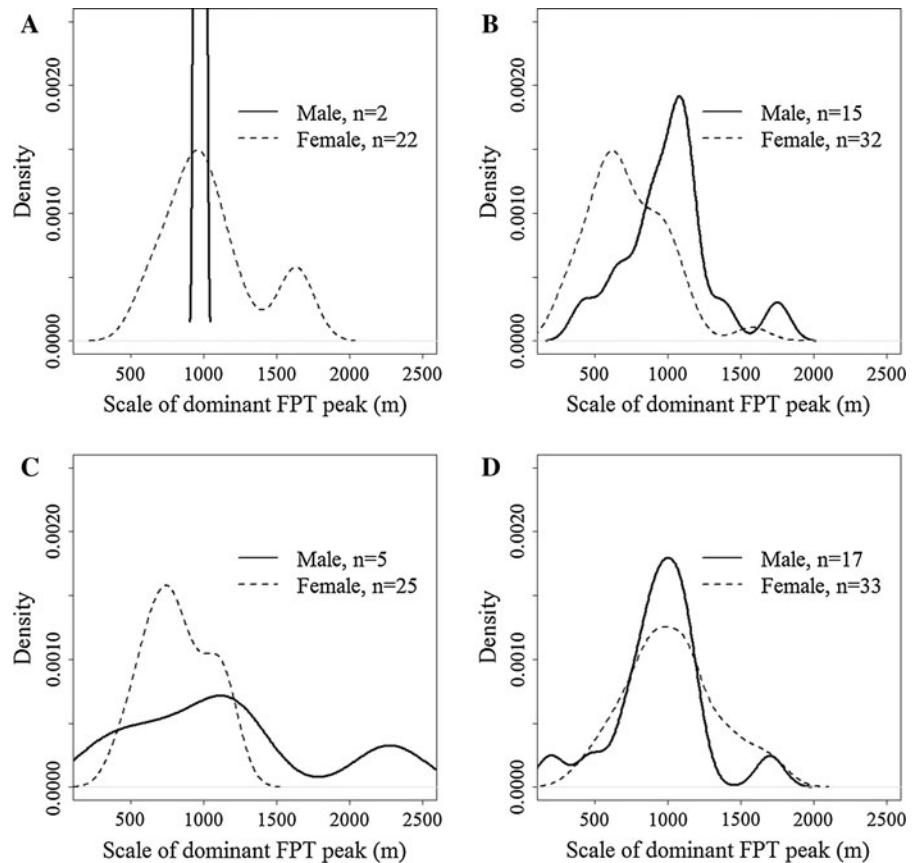
Fig. 3 Density plots of the dominant seasonal scales at which individual white-tailed deer movement paths are organized in central New York

lowest and least variable within 5,000 m buffers ($\bar{x} = 11\%$, $SD = 2.66$, range = 5–16%). Percent agriculture was lowest and most variable within the 500 m buffers ($\bar{x} = 26\%$, $SD = 20.5$, range = 0.2–85%) and increased with increasing extent ($\bar{x}_{5000m} = 31\%$, $SD_{5000m} = 8.6$, range_{5000m} = 16–48%). Interspersion/juxtaposition (IJI) exhibited no scale-dependant changes in the mean (range _{\bar{x}} = 63.5–71%), but showed decreasing variation with increasing scale ($SD_{500m} = 18.7\%$, range_{500m} = 10–99%, $SD_{5000m} = 4.5\%$, range_{5000m} = 55–73%, $F_{1,140} = 49.01$, $P < 0.001$). Models associating landscape characteristics based upon a 500 m buffer of the seasonal home-range centroid with scales of movement by individual deer had AIC_c scores lower than models using landscape metrics based on greater landscape extents. This performance was consistent for all seasons and annual paths.

There were multiple competing hypotheses explaining scales of movement by deer along annual paths, spring/summer paths, and winter paths (Table 2). Model averaging indicated predicted annual movements in Oneida were organized at scales 342 m greater than in Cortland. Annual scales of movement increased with increasing IJI. Sex was the predominant variable associated with movement scales of deer in the spring/summer season (included in the top 12 models which accounted for 92% of the weight of evidence for the model set). In spring/summer, model averaging predicted that male movements are organized at scales 276 m greater than females. We found no evidence of consistently important variables for describing scales of movement by deer in the fall. Competing models for the fall season included the NULL model which had 15% of the weight of evidence for the model set. We found that models predicting scales of movement for these three seasons performed poorly (Table 3; Fig. 6A–C).

During winter, deer movement scales were best explained by the global model (Table 2). We found the top four models accounted for 99.8% of the weight of evidence for the model set and all included IJI and AREA as important explanatory variables. Scales of movement by deer in winter increased with increasing interspersion of land-cover patches ($\beta_{IJI} = 11.1$ m/%IJI, $SE = 2.8$). Predicted winter deer movements were organized at scales 444 m ($SE = 82$ m) greater in Oneida than those in Cortland. As the percentages of forest and rangeland surrounding the centroid of

Fig. 4 Density plots of the dominant scales at which male and female white-tailed deer movement paths are organized in central New York for annual (A), spring/summer (B), fall (C), and winter (D) path segments



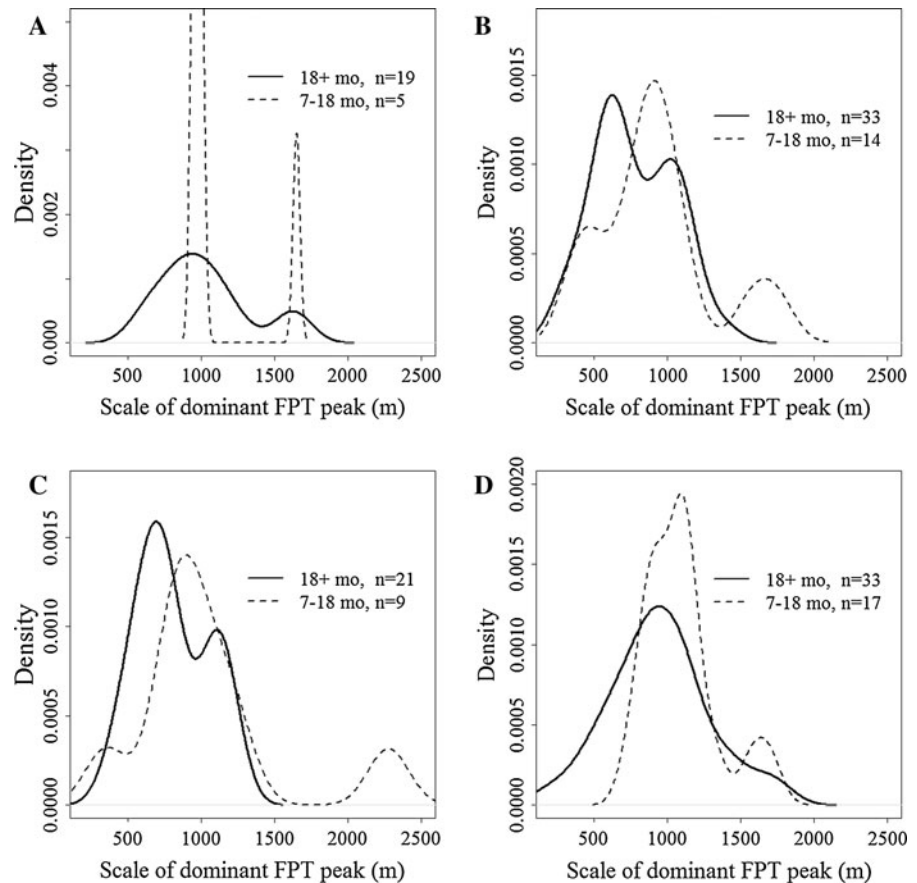
winter home ranges increased, deer exhibited smaller scales of movement. Observed and predicted scales were significantly correlated ($r_s = 0.625$, $P < 0.001$) and regression analyses revealed a larger slope ($\beta = 0.47$, $SE = 0.09$) than during other seasons (Table 3; Fig. 6D). Goodness-of-fit tests found no significant difference in counts of binned observed and predicted movement scales (Table 3).

Discussion

Our findings support three principal observations about the movement behavior of white-tailed deer in a forest–agriculture environment. First, the movement paths of deer are organized with a clear dominant peak at a scale of 425 to 1,675 m. Second, this dominant peak corresponds well with the scale of home range of deer in this environment (Dechen Quinn 2010). Third, habitat characteristics of the landscape successfully predict movement behavior, but only in winter.

We predicted that deer occupying an agriculture–forest matrix would exhibit distinct scales of movement and were able to detect those scales using FPT analyses. We observed multiple peaks in varFPT/area for most deer. Peak varFPT/area for each individual across all seasons occurred at scales from 425 to 1,675 m, with additional peaks at larger scales (3,000–6,000 m), and small scales (25–150 m) (Fig. 2). We suggest that these three peaks reflect distinct behavior patterns in the movements of deer. The dominant peaks in varFPT/area at scales from 425 to 1,675 m, which were identified for most individuals, appeared to be associated with seasonal space use. Radii in the range of these peaks represent a range in circular area of 0.57–8.81 km². Annual home-range sizes as determined by the 95% kernel distributions of the same GPS data ranged from 0.24 to 7.88 km² (Dechen Quinn 2010). The scale at which the peak occurred was correlated with home-range size for individuals monitored for >12 months ($r = 0.47$, $P < 0.001$), in spring/summer ($r = 0.43$, $P = 0.002$), fall ($r = 0.45$, $P = 0.005$), and winter ($r = 0.38$, $P = 0.002$).

Fig. 5 Density plots of the dominant scales at which yearling and adult white-tailed deer movement paths are organized in central New York for annual (A), spring/summer (B), fall (C), and winter (D) path segments



Home-range size, regardless of the method of delineation, is an estimate of total space use over the period of observation, whereas FPT analyses may identify smaller-scale movements along the path within that home range. For example, if an individual seasonally uses only portions of the area within a delineated home range, then one would expect the dominant peak in varFPT/area to occur at a scale smaller than that of the home range. Conversely, if that individual moved among those areas throughout the year, one would expect a peak to occur at a scale more closely corresponding to that identified by the home range. The close correspondence between the dominant peak of FPT and home-range suggests that deer in the forest–agriculture matrix do not show localized use of smaller portions of their home range but, within a 5-h time interval, are using much of their home range.

We observed additional peaks at large scales (3,000–6,000 m) for 20 individuals. These peaks correspond to seasonal movements and possibly

dispersals. Although we observed seasonal migrations from summer/fall range to winter areas for 24 individuals, only 14 exhibited peaks in varFPT/area at larger scales in winter. Some of those individuals utilized distinct space seasonally, but within distances only slightly larger than the scale of their dominant peak location. These movements resulted in overlapping peaks in FPT. In such cases, movement behaviors occurring within home range and migration were difficult to resolve using FPT analyses. Many of the individuals that exhibited larger scale peaks in winter displayed no such peaks in FPT analyses of their annual path. Fauchald and Tveraa (2006) suggest that small-scale movement behaviors may be overwhelmed by the large variation of more dominant signals and propose analyzing smaller path segments to identify movements organized at those smaller scales. It follows that scales of movement at larger landscape extents may also be overwhelmed by variation in movement at smaller extents and not be detected when the path is very long.

Table 2 Model comparisons (top 5 per season) relating demographic and landscape characteristics to scales of movement by white-tailed deer in central NY

Season	Model	K	AICc	ΔAICc	Prob(HI>Data)
Entire year	FPTscales ~ IJI + AREA	4	330.97	0.00	0.35
	FPTscales ~ factor(SEX) + IJI + AREA	5	332.27	1.29	0.18
	FPTscales ~ RANGE + AREA	4	332.94	1.96	0.13
	FPTscales ~ factor(AGE) + IJI + AREA	5	333.31	2.34	0.11
	FPTscales ~ FOR + RANGE + AREA	5	335.01	4.04	0.05
Spring/ Summer	FPTscales ~ factor(SEX)	3	669.93	0.00	0.35
	FPTscales ~ factor(SEX) + AREA	4	671.61	1.68	0.15
	FPTscales ~ factor(SEX) + IJI	4	672.12	2.20	0.12
	FPTscales ~ factor(SEX) + FOR + RANGE	5	672.92	3.00	0.08
	FPTscales ~ factor(SEX) + IJI + AREA	5	673.39	3.46	0.06
Fall	FPTscales ~ FOR	3	405.28	0.00	0.16
	FPTscales ~ NULL	2	405.37	0.08	0.15
	FPTscales ~ IJI	3	406.95	1.67	0.07
	FPTscales ~ FOR + AREA	4	407.10	1.82	0.07
	FPTscales ~ factor(AGE)	3	407.26	1.97	0.06
Winter	FPTscales ~ factor(SEX) + factor(AGE) + FOR + RANGE + IJI + AREA	8	623.73	0.00	0.66
	FPTscales ~ factor(SEX) + IJI + AREA	5	626.47	2.73	0.17
	FPTscales ~ factor(AGE) + FOR + RANGE + IJI + AREA	7	627.58	3.85	0.10
	FPTscales ~ factor(AGE) + IJI + AREA	5	628.19	4.46	0.07
	FPTscales ~ IJI	3	638.68	14.95	0.0004

All models reflect landscape metrics calculated based on an extent defined by a 500 m radius from the centroids of individual space use

Table 3 Characteristics (rank correlation, regression, and goodness-of-fit) of the accuracy for leave-one-out cross validation of selected models predicting scales of movement among deer in central New York

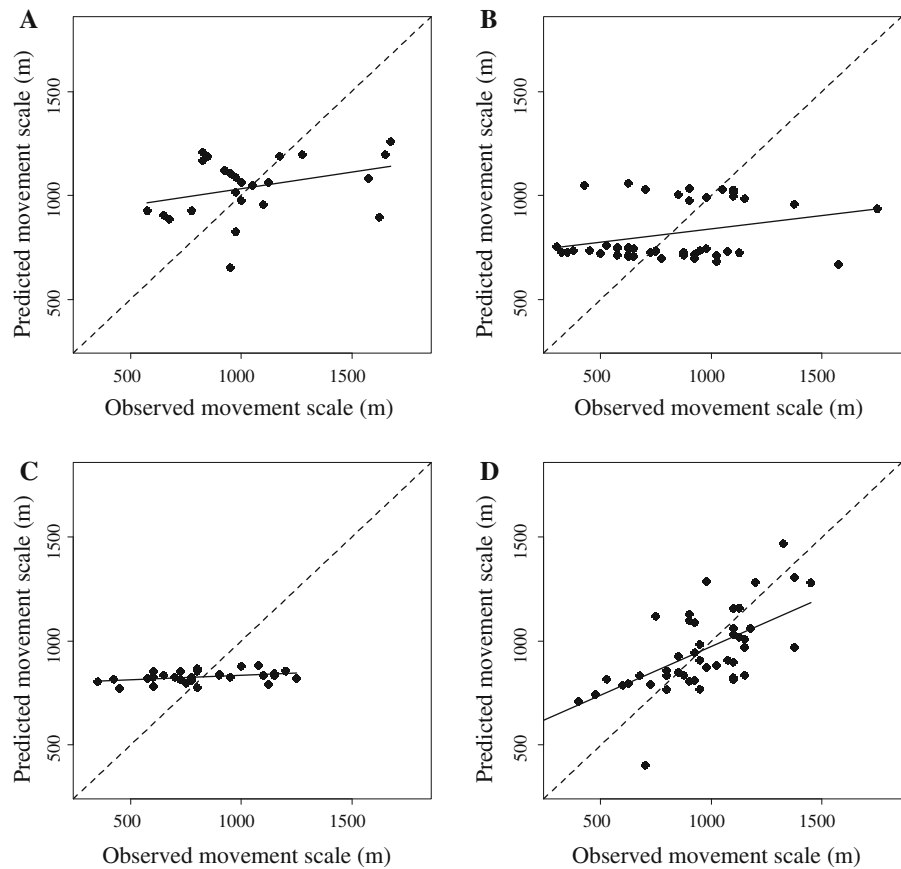
Season	Model	Rank correlation		Expected vs. observed regression			χ^2 (df = 4)
		r_s	P	b_0 (SE)	b_1 (SE)	R^2	P
Entire year	FPTscales ~ Model averaging	0.340	0.104	871 (103)	0.16 (0.09)	0.12	<0.001
Spring/summer	FPTscales ~ Model averaging	0.297	0.042	711 (53.5)	0.13 (0.06)	0.09	<0.001
Fall	FPTscales ~ Model averaging	0.392	0.035	791 (17.4)	0.04 (0.02)	0.15	<0.001
Winter	FPTscales ~ SEX + AGE + FOR + RANGE + IJI + AREA	0.625	<0.001	506 (85.9)	0.47 (0.09)	0.58	0.618

We observed few larger scale peaks in varFPT/area during the spring/summer ($n = 5$) and fall ($n = 4$) seasonal segments that may reflect dispersal. Larger scale peaks in the spring/summer were the result of individuals dispersing in May and June (2 male fawns, 2 female fawns). Dispersal of young males during this time is common as they are displaced from their natal range by mothers approaching parturition (Hölzenbein and Marchinton 1992; Woodson et al. 1980). However, female dispersal is less common, and may be

voluntary or orphan behavior (Nelson and Mech 1992). One male yearling exhibited a larger scale peak at 3,000 m within the spring/summer season which was not clearly dispersal behavior, but appeared to result from multiple extra home-range movements.

Larger scale peaks in the fall appear to be atypical and more difficult to explain. Three females which exhibited these peaks made frequent movements out from centrally used locations in November and December. One of those was a female fawn which

Fig. 6 Regression of predicted versus observed detected scale of movement of deer in central New York for leave-one-out cross validation of the best performing models for each season: (A) annual, (B) spring/summer, (C) fall, and (D) winter



had dispersed to a new area. Such movements could be in response to interactions with established female social groups that inhibit establishment of more typically observed space use. Similarly a yearling male that dispersed a long distance in the spring, occupied a relatively small landscape extent through the summer, and dispersed again in the fall may have been displaced by adult males who begin establishing aggressive hierarchies at the onset of the rut.

Small scale peaks (<100 m) were inconsistent across individuals ($n = 12$ of 62), occurring at scales potentially associated with foraging or resting behavior. However, the 5-h schedule for position acquisition may be too infrequent to identify variation in time spent along a path at scales <100 m because the mean displacement of deer per 10 h period is 550 m (Williams 2010). Similar peaks in varFPT/area were observed for individual elk in Alberta (Frair et al. 2005). They interpreted these peaks as identifying the scale at which resting behaviors were occurring, with a caution to the potential impact of error on interpretation of the analyses at small scales.

It is possible that the small scale peaks we observed in some study animals were an artifact of our analytical methods. In following the methodology of Frair et al. (2005) by dividing the variation in passage time by area, we made assumptions about the rate at which the variance of passage time increases per unit area. These assumptions have important consequences for the shape of resulting varFPT/area plots, particularly at small scales. For example, if the rate at which variation in passage time increases across a range of landscape extents is less than a power of 2, then plots of varFPT/area versus the radius of the landscape extent will display similar patterns to those identified as small-scale movements above.

Landscape characteristics

We found percentage forest and agriculture to be highly correlated within 500 m buffered centroids of deer home ranges ($r = -0.73$). The correlation between these two variables remained high ($r > -0.5$) out to 2,000 m buffer landscape extents, but

declined dramatically beyond that distance ($r = -0.28$ for the 5,000 m buffer). It is possible that this relationship is simply an artifact of spatial scale and classification resolution or land-use patterns. However, this high correlation at spatial scales similar to those being used by deer may reflect selection of this particular combination of cover types by deer (Dechen Quinn 2010). Deer are well-documented users of edge habitat and multiple cover types, particularly in forest and agricultural environments (Alverson et al. 1988), and we would expect high-use areas (home range) to be dominated by these land-cover categories. Dechen Quinn (2010) found deer home ranges in central New York to consist primarily of forest, agriculture, and rangeland at a ratio of 2:1:1. These cover types make intuitive sense as an explanation for habitat use by deer because primary energetic requirements may be dictated by food and cover needs. While deer may be using additional habitat categories, those types are used too seldom to be included in kernel designations of home ranges or are not sufficiently expansive to result in land-cover pixels being classified as such. The result is that areas of the landscape used by deer appear to have low diversity when measured at these geographic scales.

Demographic and landscape influences within season

We predicted that scales of movement by deer would vary by season in response to landscape characteristics. More specifically, we predicted that those movement scales would be associated with both composition and configuration aspects of the landscape. Our results support this hypothesis for winter but not for other seasons of the year.

Winter is the only season where our model was successful at predicting scales of movement by deer. During winter, increased amounts of rangeland within the buffered home range centroid were related to decreased scales of movement. Grass and shrub habitat between forest and agriculture is frequently identified as rangeland in our study area and may provide important food resources during winter. If so, increased amounts of food resources in an area may reduce the need for deer to move greater distances to forage.

We predicted that increasing interspersion of resources would reduce the distance of travel to gain a particular resource and thus, result in smaller scales of movement by deer. Scales of movement were positively related to interspersion of land-cover types (JI) during winter. Forest is an important cover resource in winter (Hurst and Porter 2008) but available woody browse is of poor nutritional quality (Worden and Pekins 1995). Agricultural land provides little cover during this season, but may provide important food resources in the form of waste grain (Weckerly and Nelson 1990). Forbs and shrubs along edges constituted rangeland and serve as an important food resource during winter (Weckerly and Nelson 1990). Thus, our models appear to be capturing this energetic need to move among forest, agriculture and rangeland cover types to satisfy basic life requisites during winter.

During spring/summer and fall, movement paths were organized at smaller scales than in winter or across annual paths. The dominant land-cover types (forest, rangeland and agriculture) serve as both food and cover resources during the growing season, reducing the need for individuals to move among the cover types to satisfy life requisites. The poor performance of models relating the dominant scale of movement to the landscape variables suggests that deer are moving in response to some other need. Sex was an important factor in models explaining scales of movement during spring/summer with females moving at smaller scales than males. These smaller movements may reflect adult females isolating themselves and reducing movement in mid- to late-May for parturition and early nursing of fawns (Ozoga et al. 1982; Bertrand et al. 1996). Later summer movements may reflect energetics of fawn rearing because lactating females are likely utilizing habitat that maximizes energy gained per movement cost.

We expected that scales of movement by male deer would be greater than females during the fall but were limited by small sample sizes in the fall and lacked the power to detect such a difference. The fact that models of fall movements performed poorly is potentially due to the overriding influence of other activities including, dispersal, rut, and hunter harvest (Long et al. 2008) or increased human harvest activities (Kilgo et al. 1998; Kilpatrick and Lima 1999). Several collared deer dispersed during the fall. Dispersal events not only resulted in additional large scale peaks in varFPT/area, but were also followed by movements

which were organized at extents larger than typical home ranges.

It is important to note the limitations of our data. The technology associated with GPS collars is evolving rapidly and at the time we deployed our collars, recording locations at 5-h intervals for 12 months optimized battery life. However, because GPS locations were collected at 5 h intervals we could not identify behaviors occurring at time scales <10 h. Given mean displacement over 10 h time spans was 550 m, and given the accuracy of classifying habitat via NLCD, we could not identify habitat characteristics or behavioral patterns at finer resolution. These limitations do not alter our findings regarding scales of movements as measured by FPT, nor do they affect our observations about the importance of landscape features in winter as compared to spring/summer and fall. However, our observations, in light of these limitations offer intriguing possibilities for a better understanding of the role of habitat in future studies where time intervals between locations are shorter.

It seems clear that deer movements as evaluated by FPT analyses are organized at distinct scales. These scales correspond to well documented behaviors of deer and our analyses affirm that home-range size, migration, and dispersal distances appear to be appropriate evaluations of the scales at which deer are responding to the landscape. Our finding that landscape characteristics are only associated with scales of deer movements in the winter is important. This finding suggests that deer are responding to the landscape differently through the year and that efforts to model deer movement should consider incorporating seasonal differences in how this species perceives an agricultural–forest landscape.

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