Using Fractal Analyses to Characterize Movement Paths of White-Tailed Deer and Response to Spatial Scale

Authors: Webb, Stephen L., Riffell, Samuel K., Gee, Kenneth L., and Demarais, Stephen

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://bioone.org/journals/Journal-of-Mammalogy on 23 Sep 2020
Terms of Use: https://bioone.org/terms-of-use

USING FRACTAL ANALYSES TO CHARACTERIZE MOVEMENT PATHS OF WHITE-TAILED DEER AND RESPONSE TO SPATIAL SCALE

Stephen L. Webb,* Samuel K. Riffell, Kenneth L. Gee, and Stephen Demarais

Mississippi State University, Department of Wildlife and Fisheries, Box 9690, Mississippi State, MS 39762, USA (SLW, SKR, SD)
Samuel Roberts Noble Foundation, 2510 Sam Noble Parkway, Ardmore, OK 73401, USA (KLG)

It is often difficult to test hypotheses about how and why animal movement responds to environmental conditions, and at what spatial scales movement decisions are made, all of which are critical for sound management. We used fractal dimension (D) as a measure of tortuosity because it described animal movement patterns and was useful for testing hypotheses about effects of sex, home-range size, monthly rainfall, and reproductive phase on movement paths and for detecting changes in movement patterns of animals across a range of movement distances. We captured and fitted 33 (18 females and 15 males) white-tailed deer (*Odocoileus virginianus*) with global positioning system collars. We found that females moved more tortuously ($D = 1.75 \pm 0.035$ *SE*) than males ($D = 1.549 \pm 0.025$). These differences in movement were related to home-range size of females but not of males. Rainfall predicted D for females; thus, females may have been able to forage more intensively in a smaller area due to increased forage availability. Fractal D of females was greatest during the parturition period (1.468 ± 0.02), likely due to restricted movements in smaller areas or increased foraging. Home-range size of males was similar in spring and rut, but D was lower during rut, indicating that deer changed movement patterns within previously established home ranges. Movement patterns were similar at path lengths related to foraging patches and home ranges, whereas movement patterns changed as path length approximated the size of habitat patches.

Key words: conception, fractal dimension, global positioning system collars, home range, movements, *Odocoileus virginianus*, parturition, spatial scale, tortuosity, white-tailed deer

Movement of white-tailed deer (*Odocoileus virginianus*) is influenced by many ecological, environmental, and behavioral variables such as hunger, reproduction, physiological condition, habitat, and predators (Ferguson et al. 1996; Phillips et al. 2004; Wiens et al. 1995). Home-range size, which is directly influenced by movements, is related to sex (Miller et al. 2003); reproductive status (Bertrand et al. 1996); season (Nicholson et al. 1997); availability of forage (Relyea et al. 2000), which is partially determined by rainfall; and landscape heterogeneity (Kie et al. 2002). Therefore, measuring the spatial scale of deer movements may lead to greater understanding of how home-range size is determined and whether different movement patterns can be maintained within a home range.

Many studies of white-tailed deer have examined both large-scale movements (e.g., dispersal and migration) and movement within home ranges and among habitat types. These different types of movement occur at different hierarchical spatial scales. Small-scale movements, such as space-use patterns within a home range, may be influenced by physical habitat features, resource availability, or the distribution of conspecifics (Crist et al. 1992; McIntyre and Wiens 1999). Large-scale movements, such as dispersal, may be influenced by landscape structure or behavior as it relates to gene flow or population dynamics (Long et al. 2005). Many studies that have analyzed animal movement at multiple scales have done so at arbitrarily defined scales and thus suffer from many limitations (Johnson et al. 2002). How an animal perceives and responds to its environment (With 1994) needs to be identified to avoid falsely identifying a response by an animal to a scale-specific process (Johnson et al. 2002).

Quantitatively describing animal movement behavior is difficult (Doerr and Doerr 2004; McCulloch and Cain 1989). One method to quantify animal movement paths employs fractals (Mandelbrot 1983). Fractal dimension (D) gives a

* Correspondent: stephenwebb@hotmail.com

measure of tortuosity (Milne 1997) and provides a good measure to describe animal movement patterns and the relative importance of environmental (e.g., rainfall, which affects forage quality and quantity) and behavioral (e.g., sex and reproductive phase) factors influencing movement (Nams and Bourgeois 2004). When a movement path was straight (i.e., less tortuous or lower D), the animal was likely crossing the area and not choosing it for purposes other than travel. Straighter movement paths may be advantageous to animals searching for dispersed resources (Wiens et al. 1995) such as mates during rut in deer or forage during seasons of low forage availability. However, more-tortuous paths (i.e., higher D) indicated the area was receiving increased use (Nams and Bourgeois 2004) or that an animal was wandering and spending more time in an area (Etzenhouser et al. 1998). Therefore, tortuosity may be a useful measure of the importance of particular resources or scales that the animal perceives and for testing ecological and biological hypotheses otherwise difficult to study without a quantitative measure of animal movement.

Our 1st objective was to use fractal analyses to determine how environmental factors, such as monthly rainfall, and behavioral factors, such as sex and reproductive phase, affected deer movement paths. Our 2nd objective was to determine how tortuosity of the movement path influenced home-range size. Last, we wanted to identify how deer responded to landscape structure, as measured by path length. We reconstructed movement paths at fine temporal scales (15 min) using global positioning system collar relocations. With these highly accurate and frequent data we hoped to identify how deer responded to their environment and at what spatial scales. We developed 4 hypotheses: male deer will use the landscape at different spatial scales than female deer, because of physiology and energy requirements; home-range size will vary with tortuosity, because home-range size is directly influenced by movements; movement paths will vary with monthly rainfall, because increased rainfall typically results in increased forage availability; and movement paths will vary with reproductive state (i.e., rut or parturition), because males increase their searching for mates during rut and females are restricted to smaller areas around the time of parturition. Corresponding predictions included: male deer will use larger areas and movement paths will exhibit decreased tortuosity (i.e., lower D) compared to female deer; home-range size will increase with decreasing tortuosity; movement paths of deer will be more tortuous (i.e., higher D) as monthly rainfall increases; and movement paths will show decreased tortuosity (i.e., lower D) for males during rut and increased tortuosity (i.e., higher D) for females around the time of parturition.

MATERIALS AND METHODS

Study area.—This study was conducted on the 1,214-ha Samuel Roberts Noble Foundation Wildlife Unit located in southern Oklahoma (Coal, Hughes, and Pontotoc counties),

8.0 km south of Allen, Oklahoma, in the Cross Timbers and Prairies ecoregion (Gee et al. 1994). A 2.5-m-tall high-tensile electric fence containing 15 smooth wire strands with alternating positive and negative wires was erected around 1,184 ha of the study area in 1992 (Webb et al. 2009) to facilitate white-tailed deer management programs and discourage human trespass. The Samuel Roberts Noble Foundation Wildlife Unit was approximately 60% wooded with a high degree of interspersion (Gee et al. 1994). Mean annual precipitation during years when collars were deployed (1999–2005) was 96.4 cm (range 64.8–117.6 cm; Ada, Oklahoma—National Climatic Data Center 1999–2005). Mean January temperature was 4.8°C and mean July temperature was 27.7°C during the study (Ada, Oklahoma—National Climatic Data Center 1999–2005).

Capture and handling.—We captured deer using a drop-net (Gee et al. 1999; Ramsey 1968) baited with corn during winter. We sedated deer using xylazine (3–6 mg/kg; Phoenix Scientific, St. Joseph, Missouri) or a Telazol–xylazine mixture (Telazol [Fort Dodge Animal Health, Fort Dodge, Iowa] at 4.4 mg/kg plus xylazine at 2.2 mg/kg) and used yohimbine (Abbott Laboratories, North Chicago, Illinois) at 0.125 mg/kg or tolazine (Lloyd Laboratories, Shenandoah, Iowa) at 0.4 mg/kg as an antagonist to the xylazine. Total sample size consisted of 33 deer (18 females and 15 males) captured in 1998–2004 and fitted with a G2000 remote-release global positioning system collar (Advanced Telemetry Systems, Isanti, Minnesota) and plastic livestock ear tags. Capture, handling, and marking procedures followed guidelines approved by the American Society of Mammalogists (Gannon et al. 2007).

Data collection.—Global positioning system collars were programmed to collect data during various times of the year. Seventeen collars collected data during spring (9 females and 8 males), 9 during summer (8 females and 1 male), and 7 during winter (1 female and 6 males). A very-high-frequency transmitter incorporated into the global positioning system collars provided data on animal activity, ambient temperature, and mortality. A global positioning system fix was attempted every 15 min for approximately 60–75 days. We remotely triggered release of the collar after approximately 4 months and downloaded location estimates.

We harvested 37 adults (≥1.5 years of age) and 4 fawns (≤1 year of age) during late winter (January–February) and early spring (May) of 1986 ($n = 24$) and 1987 ($n = 17$) to determine the peak and ranges of conception and parturition. All fawns were harvested in 1987. Age of females was estimated according to tooth replacement and wear techniques (Severinghaus 1949) and females were placed into 2 age groups: fawns (≤1 year of age) and adults (≥1.5 years of age). We counted, determined the sex of, and measured all fetuses using forehead–rump length to determine age in days (Hamilton et al. 1985) and back dating to determine conception date. To determine parturition date, we added 200 days to the conception date, based on data from Cheatum and Morton (1942), Golley (1957), Haugen (1959), Haugen and Davenport (1950), and Verme (1965).

Home-range estimation and movements.—We calculated 95% fixed-kernel (Worton 1989) home ranges in Home Range Tools for ArcGIS (Rodgers et al. 2005) as an index of the extent of space used by deer. We used unit variance standardization and the reference bandwidth smoothing parameter (h_{ref}) when calculating 95% volume probability polygons. We used all relocations of individual deer during all seasons to describe sex-specific trends in movement paths. We then reconstructed movement paths within season (spring: March–May; summer: June–August; and winter: November–February), including a rut and parturition season, for each sex. The 1st and last dates of conception for males and the 1st and last dates of parturition for females were used as the range of dates for estimating D by reproductive season. Rut and parturition seasons also were subdivided to look for changes in periods within each of the reproductive seasons. Preparturition was approximately 3 weeks before (14 May–7 June) peak parturition (8–22 June), and postparturition was approximately 3 weeks afterward (23 June–14 July). Rut was a 2-week period from 18 November to 1 December, whereas postrut was approximately 3 weeks afterward (2–23 December). Prerut data were not included because only 1 deer was tracked during this time. Monthly movement path estimates were based on calendar months and daily movement path estimates were based on a 24-h day beginning at midnight (i.e., 0000 h).

Fractal analyses.—Fractal variables were calculated in Fractal 5.0 (V. O. Nams, Nova Scotia Agricultural College, Truro, Nova Scotia, Canada). Typically, D ranges from 1.0 to 2.0 but can be >2.0. This situation arises when the line tracing the movement path completely crosses itself many times, creating an additional dimension from the layering of the lines (Mandelbrot 1984). This may occur if movement is constrained within a limited area (Bascompte and Vilà 1997). Similarly, we expected to find $D > 2.0$ with our data because the electric fence surrounding the property constrained 91% of deer movements when properly maintained (Webb et al. 2009). Deer in this region also have shown high levels of home-range (i.e., site) fidelity (Hellickson et al. 2008; Webb et al. 2007b).

To obtain an overall estimate of D for entire movement paths, seasonal paths, monthly paths, and daily paths, we used the FractalMean estimator (Nams 2006). Data for all individuals within each sex were combined during the parturition and rut periods to determine mean seasonal D. The purpose of estimating overall D was to compare tortuosity of movement paths that were measured over the same range of movement distances (i.e., path lengths—Nams and Bourgeois 2004) for all individuals. FractalMean is based on the traditional dividers method (Mandelbrot 1967), but samples the path twice (i.e., once each forward and backward) and corrects for truncation of gross distance by estimating straight-line distance between the end of the last step and the end of the path (Nams 2006). To ensure that D was a useful measure of tortuosity, it was measured over the same path lengths (Doerr and Doerr 2004) for all deer, regardless of sex, from one-twentieth of the diameter of the smallest home range to 5

times the diameter of the largest home range, assuming a circular home range. Although some researchers caution against using fractal analyses because D is not necessarily scale invariant (Turchin 1996), scale invariance itself can provide important information about how animals respond to their environment (Doerr and Doerr 2004). Thus, we compared relative D between sexes, seasons, or reproductive periods to identify patterns of scale variance and invariance across a range of path lengths.

We used the VFractal estimator (Nams 1996) and associated confidence intervals (*CI*s) to look for changes in D with changes in movement path length for each sex by combining all individuals within each sex. When results were combined, VFractal treated each movement path (i.e., 1 path/deer) as 1 replicate (Nams 1996). Thus, all error estimates were based on measures of among-path variation, which allowed for extrapolation to each sex. We also weighted each movement path by N (i.e., number of sampling intervals at each movement path length).

Plotting D versus movement path length can be useful for detecting major differences in tortuosity with changes in movement distance. Thus, we plotted D, variances of tortuosity of successive path segments, and correlations of tortuosity of successive path segments to detect changes in movement patterns and to determine how animals responded to habitat patches using movement path length (Doerr and Doerr 2004; Nams 2005). Variances of tortuosity of successive path segments should be high at and below patch size and drop when path lengths were larger than patch size (Nams 2005). Correlations of tortuosity of successive path segments should be positive when path lengths were below patch size, negative at patch size, and 0 when path lengths were larger than patch size (Nams 2005). These plots were used to assess changes in movement patterns across a range of movement path lengths (Wiens 1989) for each sex.

Analyses.—Linear regression models were used to determine if D (response variable) was related to monthly rainfall (explanatory variable) and if D (explanatory variable) influenced extent of space used by deer (i.e., home-range size; response variable). We also ran a regression to predict extent of space use (i.e., home-range size; response variable) using path length (explanatory variable) where D 1st reached a maximum value. A 2-sample *t*-test was used to assess differences in D between sexes and differences in home-range size of deer between reproductive seasons and nonreproductive seasons. Because length of the reproductive season was shorter than that of nonreproductive seasons, we randomly chose the same number of consecutive weeks during the nonreproductive season when calculating home-range size to reduce the influence of varying temporal scales. A Satterthwaite approximation was used when variances were not equal (Zar 1999). We tested for differences in D estimates by period (i.e., pre-, peak, and postparturition for females and rut and postrut for males) using a repeated-measures design (PROC MIXED—SAS Institute Inc. 2003) with period as a repeated measure and deer as subject, which specifies the unit

within which observations are correlated (Littell et al. 2006). We selected our covariance structure using restricted maximum likelihood and Akaike's information criterion corrected for sample size (AIC$_c$—Burnham and Anderson 2002). Based on model results, we used a compound symmetry covariance structure for our models. We made multiple comparisons using Tukey's mean separation test when a significant F-test occurred. For all repeated-measures analyses, we used the Kenward–Roger adjustment to account for unbalanced data, multiple random effects, and any model with correlated errors (Kenward and Roger 1997; Littell et al. 2006). To assess predictive power of models, we used the coefficient of determination (r^2). We conducted all analyses using SAS 9.1 (SAS Institute Inc. 2003). We used an a priori $\alpha = 0.05$ for statistical tests. All means are reported $\pm$ SE.

RESULTS

Collar performance.—We collected data on 33 deer (18 females and 15 males) for a total of 135,627 locations. On average, collars collected $4,110 \pm 344$ locations for an average of 57 ± 3 days. All 8 females tracked during summer provided data during parturition, whereas 4 of 6 males tracked during winter provided data during rut. Overall, successful locations were obtained for $72\% \pm 4\%$ of the attempted fixes.

Breeding dates.—Only 1 of 4 fawns was pregnant, whereas 95% (35 of 37) of adult females were pregnant with 1–3 fetuses. Mean conception date of adult females was 30 November $\pm$ 1.5 days (range: 4 November–24 December) with most conceptions occurring over a 2-week period beginning 18 November. Peak parturition was estimated to be 15 June $\pm$ 1.5 days (range: 23 May–12 July) with most parturitions occurring over a 2-week period beginning 8 June.

Sex differences in movement paths.—Females moved more tortuously than males ($t = 4.51$, $d.f. = 31$, $P < 0.001$). Estimates of D were higher for females (1.75 ± 0.035) than males (1.549 ± 0.025). Female D values during spring and summer were 1.724 ± 0.047 ($n = 9$) and 1.805 ± 0.049 ($n = 8$), respectively. Estimates of D for males were 1.588 ± 0.037 ($n = 8$) and 1.502 ± 0.031 ($n = 6$) during spring and winter, respectively. Only 1 female and 1 male were tracked during winter and summer, respectively. Fractal D was 1.54 for the 1 female tracked during winter and 1.514 for the 1 male during summer.

Plots of D versus path length revealed that tortuosity of movement paths increased with increasing movement distance, except at the largest path lengths for females (≥ 416 m) and males (≥ 693 m; Figs. 1a and 2a). Both females and males showed scale variant and invariant movement patterns over a range of path lengths. Plots of D versus path length resembled a logistic curve for both sexes, but with more abrupt changes between path lengths for males. Females showed 1 change in movement patterns at path lengths of approximately 416 m (Fig. 1a). Plots of variance (Fig. 1b) and correlation (Fig. 1c) did not reveal obvious changes in movement patterns for females. Movement patterns of males were similar over a
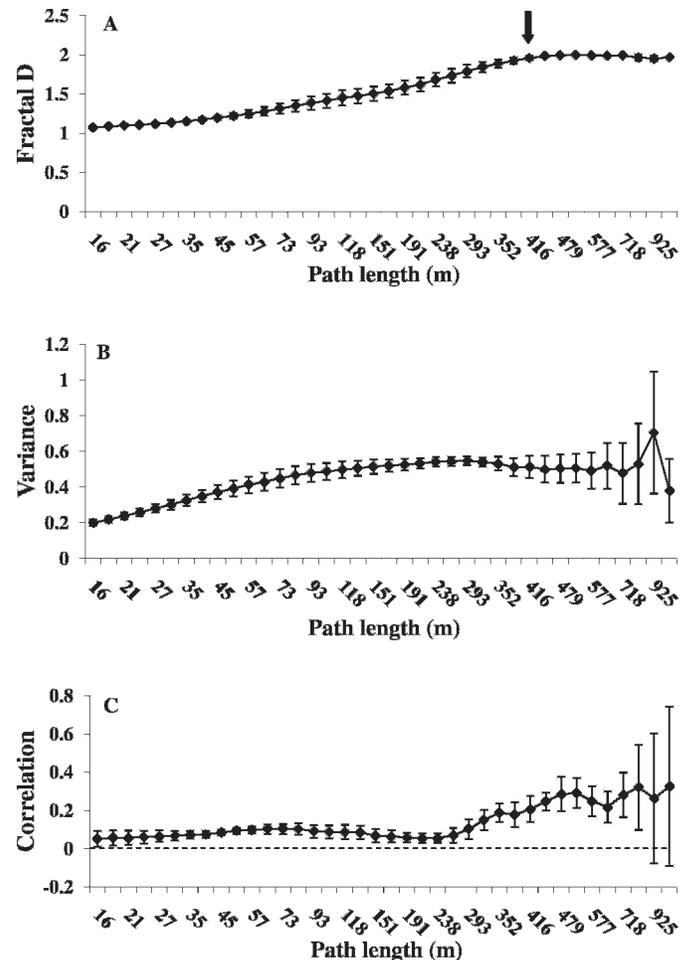

FIG. 1.—a) Mean fractal D), b) variance of tortuosity of adjacent path segments, and c) correlation of tortuosity of adjacent path segments with corresponding 95% confidence intervals for female white-tailed deer (*Odocoileus virginianus*; $n = 18$) at varying path lengths. Path length is measured as the straight-line length of the movement path used in each set of calculations. a) Arrow represents point of inflection on plot of mean D and c) dashed line represents correlation = 0.

wider range of path lengths (17–333 m and ≥ 693 m) than those of females (16–100 m and >400 m) and showed 2 changes in movement patterns. The 1st change occurred near path lengths of 333 m (point of inflection [Fig. 2a] and drop in correlation [Fig. 2c]), and the 2nd was near path lengths of 693 m (point of inflection [Fig. 2a] and peak in variance [Fig. 2b]). There was a clear drop in correlations at path lengths of 333 m and a peak in variance at 693 m for males, which may indicate that perceived patch size was within this range. Because there was no clear drop in correlation or peak in variance it was difficult to determine perceived patch size for females.

Home-range size.—Estimated home-range size was 83 ± 14 ha and 315 ± 30 ha for females and males, respectively, averaged across seasons. Fractal D was negatively related to home-range size of females ($r^2 = 0.256$, $P = 0.032$; home-range size $= 441.6 - 204.8 \times D$), indicating that as movements became more tortuous or intensive, home-range
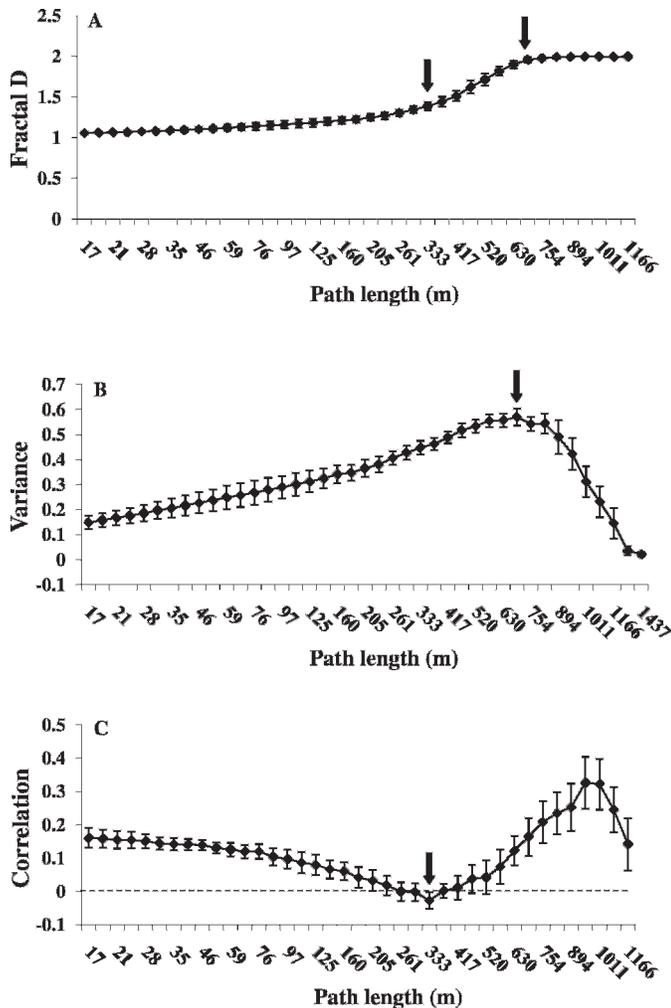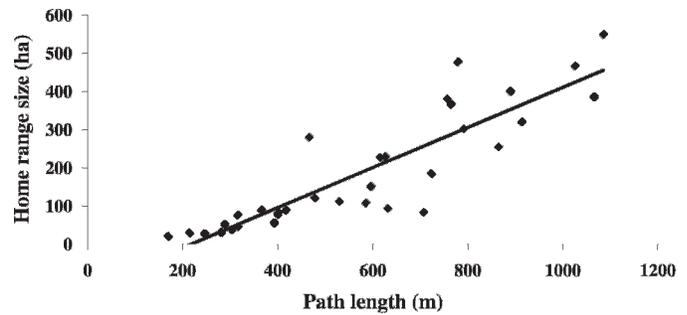
FIG. 3.—Relationship between path length (m), when *D* 1st reached a maximum value, and home-range size (ha) in white-tailed deer (*Odocoileus virginianus*). Path length is equivalent to the straight-line length of the divider used to measure the movement path.

= 8.5, *P* = 0.01) than during spring (122 ± 25 ha, *n* = 9). We found no difference in mean home-range size of males (*t* = −0.87, *d.f.* = 10, *P* = 0.406) between rut (330 ± 40 ha, *n* = 4) and spring (401 ± 53 ha, *n* = 8). Fractal *D* was 1.866 for females during parturition (i.e., during pre-, peak, and postparturiton) and 1.537 for males during rut (i.e., during rut and postrut). Fractal *D* differed (*F* = 8.65, *d.f.* = 2, 305, *P* < 0.001) among parturition periods for females (Fig. 4a). Fractal *D* during peak parturition (1.468 ± 0.02) was significantly greater than during preparturition (1.415 ± 0.021) and postparturition (1.384 ± 0.011) for females. However, there was no difference in *D* between pre- and postparturition. Fractal *D* for males did not differ (*F* = 0.25, *d.f.* = 1, 115, *P* = 0.621) between rut (1.257 ± 0.009) and postrut (1.268 ± 0.008; Fig. 4b).

DISCUSSION

White-tailed deer exhibited both scale-variant and -invariant movement patterns. Movement patterns were similar when movements were within foraging patches or home ranges, whereas movement patterns changed as deer moved among habitat patches of different sizes. The path lengths at which *D* was ∼2 were within the range of the radius of a deer's home range (i.e., assuming a circular home range), thus the path length at which *D* 1st reached 2 was a useful predictor of home-range size. This offers support that movements at the largest path lengths examined were movements across home ranges.

Our prediction that tortuosity would influence home-range size of deer was partially correct. Because deer occupy well-defined home ranges (Hellickson et al. 2008; Webb et al. 2007b), their movements were much more tortuous when viewed at these path lengths. Movements within home ranges may reflect different behaviors such as movements within foraging patches, movements among habitat patches, and movements across the home range. Therefore, movements at the largest path lengths, reflecting movements across home ranges, had the largest *CI*s for tortuosity, suggesting that movements of individuals are highly variable when measured at large path lengths. This may explain why we were only able to predict home-range size from *D* for females. Because males
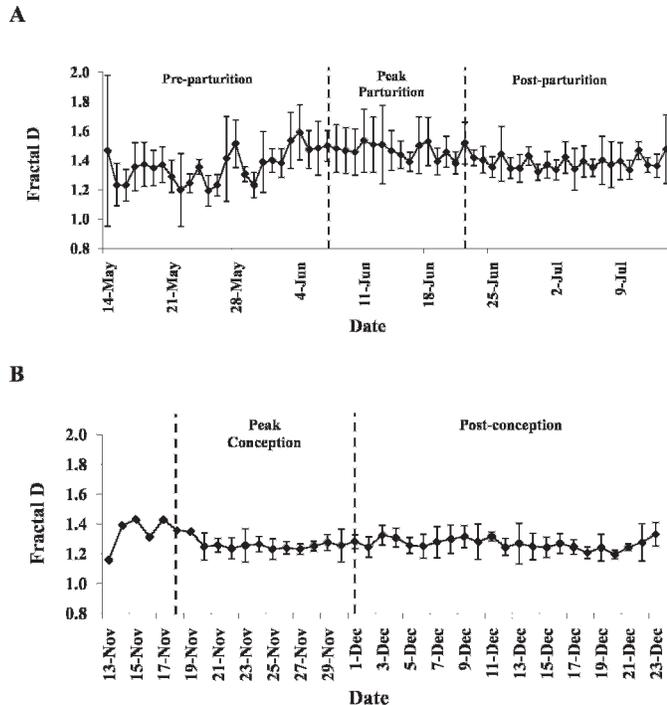
FIG. 2.—a) Mean fractal *D*, b) variance of tortuosity of adjacent path segments, and c) correlation of tortuosity of adjacent path segments with corresponding 95% confidence intervals for male white-tailed deer (*Odocoileus virginianus*; *n* = 15) at varying path lengths. Path length is measured as the straight-line length of the movement path used in each set of calculations. Arrows represent points of inflection on plots of a) mean *D*, b) variance, and c) correlation and c) dashed line represents correlation = 0.

size decreased. There was no relationship (*P* = 0.432) between home-range size and *D* for males. A significant positive linear relationship (*r²* = 0.781, *P* < 0.001) between path length when maximum *D* was 1st reached and home-range size was detected after pooling data for both sexes (Fig. 3). Home-range size was predicted by the model: home-range size = −114.5 + 0.526 × path length (Fig. 3).

Monthly rainfall.—We found a significant positive linear relationship between monthly rainfall and *D* for females (*D* = 1.454 + 0.013 × rainfall; *r²* = 0.174, *P* = 0.002). As rainfall increased, so did tortuosity of monthly movement paths. There was also a positive (*D* = 1.445 + 0.12 × rainfall), but nonsignificant, linear relationship between monthly rainfall and *D* for males (*r²* = 0.086, *P* = 0.059).

Reproductive phase.—Mean home-range size of females (38 ± 4 ha, *n* = 8) during parturition was smaller (*t* = −3.3, *d.f.*

A

B

Fig. 4.—Mean daily fractal *D* for a) female and b) male white-tailed deer (*Odocoileus virginianus*) during parturition and rut periods, respectively.

typically have larger home ranges than females (Marchinton and Hirth 1984; Miller et al. 2003), they are able to move longer distances with decreased tortuosity while still remaining within their home ranges. Individual differences in movements within home ranges may be due to the spatial distribution of resources, quality of habitat within the home range, and physiological state of the individual. Foraging behavior of white-tailed deer and Spanish goats (*Capra hircus*), as measured by *D*, was dependent upon the spatial distribution of both food and nonfood items (Etzenhouser et al. 1998). Therefore, a description of vegetation communities and estimates of available forage within home ranges may provide additional insight into thoroughness of food-searching behavior within home ranges.

Previous research has found that females reduced home-range size, mobility, and social interactions during parturition (Bertrand et al. 1996; D'Angelo et al. 2004; Ozoga et al. 1982). We also found that home-range size of females was significantly smaller during parturition periods than during spring. As we predicted, estimates of *D* for females were higher during peak parturition than during pre- and postparturition. More-tortuous movement paths during peak parturition may have been due to females being confined to a smaller home-range area due to limited mobility of newborn fawns or to increased foraging to meet increased nutritional demands. Similarly, female Iberian wolves (*Canis lupus signatus*) increased tortuosity (i.e., higher *D*) when cubs were present because females were confined to a smaller area near den sites (Bascompte and Vilà 1997). More-tortuous paths (i.e., higher *D*) indicate that an area receives increased use (Nams and

Bourgeois 2004). Therefore, fractal analyses offer an index to intensity of use of an area, whereas other movement metrics (e.g., home-range size and distance travelled) are only able to provide an index to the extent of space used.

Fractal *D* for males was lower during rut (1.257) relative to *D* for males during spring (1.588) and winter (1.502). Therefore, male deer appear to change their movement patterns in response to breeding. Although males may increase home-range size during rut (Marchinton and Hirth 1984), we did not observe any differences in home-range size between the rut and spring periods. This indicates that deer did not move outside of previously established home ranges in search of receptive females but did change their movement patterns within their home range. More linear movements (i.e., lower *D*) within home ranges exhibited by males during rut may increase encounters with females when individuals are randomly dispersed (Wiens et al. 1995). Benefits of increased search behavior during rut may include increased reproductive success and fitness, and outweigh costs of distance travelled and energy expended. Increased search behavior within familiar areas used by deer (i.e., home range) may reduce postrut mortality. One study conducted in Texas found that male white-tailed deer had high annual survival rates (Webb et al. 2007a) and small home-range sizes (Webb et al. 2007b). Movements confined within home ranges may reduce mortality, stress, and energy expenditure.

We predicted that movement paths of deer would be more tortuous as rainfall increased due to the increased abundance of forage. We found as rainfall increased, monthly movement paths became more tortuous, although not significantly for males. Increased rainfall should have a positive effect on growth of plants. The increase in the amount of available forage may have allowed deer to forage more intensively within a smaller area resulting in more-tortuous movement paths. When rainfall is limited, deer will likely spend less time in an area and more time searching for available forage, which would lead to straighter movement paths and increased home-range size. Home-range size may increase as forage is depleted due to browsing (Harestad and Bunnell 1979; McNab 1963) or decreased rainfall. Therefore, large home-range sizes will likely result from decreased tortuosity of movement paths, when forage is limited.

Differences in sex-specific movements may be related to annual reproductive cycles, energy demands, and forage availability (Teer 1996). Following our initial prediction, male deer exhibited less-tortuous movement paths compared to females, and both sexes displayed different responses to their environment at varying movement distances as measured by path length. These differences in movements were likely due to 1 or several causes and may be partially explained by home-range size, reproductive phase, and monthly rainfall (see above). It appears as though males and females perceive the structure of the landscape at different path lengths as indicated from plots of *D* and variances and correlations of tortuosity of successive path segments. Males showed a clear drop in correlations, indicating that movement paths shorter than

333 m may be within foraging patches (see Fig. 2c). Movements changed at scales from 333 to 692 m, which may be the range in size of habitat patches on the study area perceived by males. As mentioned previously, movement paths longer than 692 m were likely movements across the home range of the deer. However, females may perceive patch size at smaller path lengths (<416 m). Because we did not observe any drops in correlation below 0 for females, foraging activities may be completely contained within patches. Similar to males, movement patterns of females were similar within home ranges (path lengths > 416 m).

Identifying how animals respond to their environment should be a central theme in studies of habitat selection because animals select habitats in a hierarchical fashion (Johnson 1980). Studies of animal movements should focus on identifying the spatial scales, measured as movement path length, at which animals perceive environmental conditions rather than scales perceived by humans (Ferguson et al. 1996), which is typical of most habitat studies. Thus, researchers must ensure that habitats are classified at the spatial scale at which animals perceive them (Nams and Bourgeois 2004) or at the scale at which particular behaviors occur (Johnson et al. 2002). A behavior may occur over a narrow range of movement distances, thus researchers should avoid inappropriately extrapolating data over other movement distances when multiple movement patterns have been identified. Fractal *D* proved useful in identifying unique movement patterns at varying path lengths for habitat studies, which should lead to more-accurate assessments of habitat use.

Fractal analyses provided a means of quantifying animal movements, detecting changes in movement patterns, and testing biological and ecological hypotheses. We found many uses, potential uses, and areas needing improvement for fractal analyses characterizing movement paths of deer. Fractal *D* was useful for describing sex-specific movement patterns and for conservatively identifying how deer responded to their environment over a range of movement distances. Thus, *D* will be useful at making comparisons between sexes and among ages, populations, and species (Ferguson et al. 1996). There appears to be some utility in using rainfall as a predictor of *D*, which may provide insight into forage availability or energy requirements of the animal. Specific research should address the relationship between forage availability and energy demands with measures of tortuosity. Movement and tortuosity influence home-range shape and size. However, tortuosity of movement paths also provides a useful predictor of home-range size, which indicates that tortuosity can be used as an index to intensity of space use. Fractal *D* represents an exponent in scaling relationships and is only a relative measure of tortuosity with no unit of measurement. Therefore, other metrics, such as distance moved or rate of travel should be incorporated into movement analyses for a complete description of animal movements. Last, and most importantly, resource use studies will provide more useful information if conducted at appropriate spatial scales relative to the behavior of the animal.

LITERATURE CITED

BASCOMPTE, J., AND C. VILÀ. 1997. Fractals and search paths in mammals. Landscape Ecology 12:213–221.

BERTRAND, M. R., A. J. DENICOLA, S. R. BEISSINGER, AND R. K. SWIHART. 1996. Effects of parturition on home ranges and social affiliations of female white-tailed deer. Journal of Wildlife Management 60:899–909.

BURNHAM, K. P., AND D. R. ANDERSON. 2002. Model selection and inference: a practical information-theoretic approach. 2nd ed. Springer-Verlag, New York.

CHEATUM, E. L., AND G. H. MORTON. 1942. Techniques used in determining the period of rut among white-tailed deer in New York State. Transactions of the North American Wildlife Conference 7:334–342.

CRIST, T. O., D. S. GUERTIN, J. A. WIENS, AND B. T. MILNE. 1992. Animal movement in heterogeneous landscapes: an experiment with *Eleodes* beetles in shortgrass prairie. Functional Ecology 6:536–544.

D'ANGELO, G. J., C. E. COMER, J. C. KILGO, C. D. DRENNAN, D. A. OSBORN, AND K. V. MILLER. 2004. Daily movements of female white-tailed deer relative to parturition and breeding. Proceedings of the Southeastern Association of Fish and Wildlife Agencies 58:292–301.

DOERR, V. A. J., AND E. D. DOERR. 2004. Fractal analysis can explain individual variation in dispersal search paths. Ecology 85:1428–1438.

ETZENHOUSER, M. J., M. K. OWENS, D. E. SPALINGER, AND S. B. MURDEN. 1998. Foraging behavior of browsing ruminants in a heterogeneous landscape. Landscape Ecology 13:55–64.

FERGUSON, S. H., W. J. RETTIE, AND F. MESSIER. 1996. Fractal measures of female caribou movements. Rangifer 10:139–147.

GANNON, W. L., R. S. SIKES, AND THE ANIMAL CARE AND USE COMMITTEE OF THE AMERICAN SOCIETY OF MAMMALOGISTS. 2007. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. Journal of Mammalogy 88:809–823.

GEE, K. L., J. H. HOLMAN, AND S. DEMARAIS. 1999. A man-power efficient drop-net system for capturing white-tailed deer. Proceeding Abstracts of the Annual Southeast Deer Study Group Meeting 22:31.

GEE, K. L., M. D. PORTER, S. DEMARAIS, F. C. BRYANT, AND G. V. VREEDE. 1994. White-tailed deer: their foods and management in the Cross Timbers. 2nd ed. Samuel Roberts Noble Foundation Publication NF-WF-94-01. Samuel Roberts Noble Foundation, Ardmore, Oklahoma.

GOLLEY, F. B. 1957. Gestation period, breeding and fawning behavior of Columbian black-tailed deer. Journal of Mammalogy 38:116–120.

HAMILTON, R. J., M. L. TOBIN, AND W. G. MOORE. 1985. Aging fetal white-tailed deer. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 39:389–395.

HARESTAD, A. S., AND F. L. BUNNELL. 1979. Home range and body weight—reevaluation. Ecology 60:389–402.

HAUGEN, A. O. 1959. Breeding records of captive white-tailed deer in Alabama. Journal of Mammalogy 40:108–113.

HAUGEN, A. O., AND L. A. DAVENPORT. 1950. Breeding records of whitetail deer in the Upper Peninsula of Michigan. Journal of Wildlife Management 14:290–295.

HELLICKSON, M. W., T. A. CAMPBELL, K. V. MILLER, R. L. MARCHINTON, AND C. A. DEYOUNG. 2008. Seasonal ranges and site fidelity of adult male white-tailed deer (Odocoileus virginianus) in southern Texas. Southwestern Naturalist 53:1–8.

JOHNSON, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71.

JOHNSON, C. J., K. L. PARKER, D. C. HEARD, AND M. P. GILLINGHAM. 2002. Movement parameters of ungulates and scale-specific responses to the environment. Journal of Animal Ecology 71:225–235.

KENWARD, M. G., AND J. H. ROGER. 1997. Small sample inference for fixed effects from restricted maximum likelihood. Biometrics 53:983–997.

KIE, J. G., R. T. BOWYER, M. C. NICHOLSON, B. B. BOROSKI, AND E. R. LOFT. 2002. Landscape heterogeneity at differing scales: effects on spatial distribution of mule deer. Ecology 83:530–544.

LITTELL, R. C., G. A. MILLIKEN, W. W. STROUP, R. D. WOLFINGER, AND O. SCHABENBERGER. 2006. SAS for mixed models. 2nd ed. SAS Institute, Inc., Cary, North Carolina.

LONG, E. S., D. R. DIEFENBACH, C. S. ROSENBERRY, B. D. WALLINGFORD, AND M. D. GRUND. 2005. Forest cover influences dispersal distance of white-tailed deer. Journal of Mammalogy 86:623–629.

MANDELBROT, B. B. 1967. How long is the coast of Britain? Statistical self-similarity and fractional dimension. Science 156:636–638.

MANDELBROT, B. B. 1983. The fractal geometry of nature. W. H. Freeman and Company, San Francisco, California.

MANDELBROT, B. B. 1984. Fractals in physics: squig clusters, diffusions, fractal measures, and the unicity of fractal dimensionality. Journal of Statistical Physics 34:895–930.

MARCHINTON, R. L., AND D. H. HIRTH. 1984. Behavior. Pp. 129–168 in White-tailed deer ecology and management (L. K. Halls, ed.). Stackpole Books, Harrisburg, Pennsylvania.

MCCULLOCH, C. E., AND M. L. CAIN. 1989. Analyzing discrete movement data as a correlated random walk. Ecology 70:383–388.

MCINTYRE, N. E., AND J. A. WIENS. 1999. Interactions between landscape structure and animal behavior: the roles of heterogeneously distributed resources and food deprivation on movement patterns. Landscape Ecology 14:437–447.

MCNAB, B. K. 1963. Bioenergetics and the determination of home range size. American Naturalist 47:133–140.

MILLER, K. V., L. I. MULLER, AND S. DEMARAIS. 2003. White-tailed deer (Odocoileus virginianus). Pp. 906–930 in Wild mammals of North America: biology, management, and conservation (G. A. Feldhamer, B. C. Thompson, and J. A. Chapman, eds.). Johns Hopkins University Press, Baltimore, Maryland.

MILNE, B. T. 1997. Applications of fractal geometry in wildlife biology. Pp. 32–69 in Wildlife and landscape ecology: effects of pattern and scale (J. A. Bissonette, ed.). Springer-Verlag, New York.

NAMS, V. O. 1996. The VFractal: a new estimator for fractal dimension of animal movement paths. Landscape Ecology 11:289–297.

NAMS, V. O. 2005. Using animal movement paths to measure response to spatial scale. Oecologia 143:179–188.

NAMS, V. O. 2006. Improving accuracy and precision in estimating fractal dimension of animal movement paths. Acta Biotheoretica 54:1–11.

NAMS, V. O., AND M. BOURGEOIS. 2004. Fractal analysis measures habitat use at different spatial scales: an example with American marten. Canadian Journal of Zoology 82:1738–1747.

NATIONAL CLIMATIC DATA CENTER. 1999–2005. Climatological data annual summary: Oklahoma. Vols. 108–114. National Oceanic and Atmospheric Administration, United States Department of Commerce, Asheville, North Carolina.

NICHOLSON, M. C., R. T. BOWYER, AND J. G. KIE. 1997. Habitat selection and survival of mule deer: tradeoffs associated with migration. Journal of Mammalogy 78:483–504.

OZOGA, J. J., L. J. VERME, AND C. S. BIENZ. 1982. Parturition behavior and territoriality in white-tailed deer: impacts on neonatal mortality. Journal of Wildlife Management 46:1–11.

PHILLIPS, M. L., W. R. CLARK, S. M. NUSSER, M. A. SOVADA, AND R. J. GREENWOOD. 2004. Analysis of predator movement in prairie landscapes with contrasting grassland composition. Journal of Mammalogy 85:187–195.

RAMSEY, C. W. 1968. A drop-net deer trap. Journal of Wildlife Management 32:187–190.

RELYEA, R. A., R. K. LAWRENCE, AND S. DEMARAIS. 2000. Home range of desert mule deer: testing the body-size and habitat-productivity hypotheses. Journal of Wildlife Management 64:146–153.

RODGERS, A. R., A. P. CARR, L. SMITH, AND J. G. KIE. 2005. HRT: Home Range Tools for ArcGIS. Ontario Ministry of Natural Resources, Centre for Northern Forest Ecosystem Research, Thunder Bay, Ontario, Canada.

SAS INSTITUTE INC. 2003. SAS OnlineDoc, version 9. SAS Institute Inc., Cary, North Carolina.

SEVERINGHAUS, C. W. 1949. Tooth development and wear as criteria of age in white-tailed deer. Journal of Wildlife Management 13:195–216.

TEER, J. G. 1996. The white-tailed deer: natural history and management. Pp. 193–210 in Rangeland wildlife (P. R. Krausman, ed.). Society for Range Management, Denver, Colorado.

TURCHIN, P. 1996. Fractal analyses of animal movement: a critique. Ecology 77:2086–2090.

VERME, L. J. 1965. Reproduction studies on penned white-tailed deer. Journal of Wildlife Management 29:74–79.

WEBB, S. L., K. L. GEE, S. DEMARAIS, B. K. STRICKLAND, AND R. W. DEYOUNG. 2009. Efficacy of a 15-strand high-tensile electric fence to control white-tailed deer movements. Wildlife Biology in Practice 5:45–57.

WEBB, S. L., D. G. HEWITT, AND M. W. HELLICKSON. 2007a. Survival and cause-specific mortality of mature male white-tailed deer. Journal of Wildlife Management 71:555–558.

WEBB, S. L., D. G. HEWITT, AND M. W. HELLICKSON. 2007b. Scale of management for mature male white-tailed deer as influenced by home range and movements. Journal of Wildlife Management 71:1507–1512.

WIENS, J. A. 1989. Spatial scaling in ecology. Functional Ecology 3:385–397.

WIENS, J. A., T. O. CRIST, K. A. WITH, AND B. T. MILNE. 1995. Fractal patterns of insect movement in microlandscape mosaics. Ecology 76:663–666.

WITH, K. A. 1994. Using fractal analysis to assess how species perceive landscape structure. Landscape Ecology 9:25–36.

WORTON, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70:164–168.

ZAR, J. H. 1999. Biostatistical analysis. 4th ed. Prentice Hall, Inc., Upper Saddle River, New Jersey.