SPATIAL ECOLOGY OF MALE WHITE-TAILED DEER IN THE CROSSTIMBERS AND PRAIRIES ECOREGION

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THESIS ABSTRACT

SPATIAL ECOLOGY OF MALE WHITE-TAILED DEER IN THE CROSSTIMBERS AND PRAIRIES ECOREGION

Robert W. Holtfreter
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We examined daily movement paths of radio-collared male white-tailed deer (*Odocoileus virginianus*) during the breeding season (Oct. 1st- Dec. 15th), from 1995-1997, at the McAlester Army Ammunition Plant (McAAP) in southeastern Oklahoma. Results indicate that male white-tailed deer become increasingly active throughout the breeding season, with progressively dispersed daily movement patterns. Juvenile males were highly active prior to the peak of the breeding season when adult and mature male breeding effort was limited. We suggest this behavior may increase juvenile male reproductive fitness by increasing their likelihood of breeding does coming into estrous prior to the peak of the breeding season when competition with older males may be limited. Results additionally suggest that older males suppress the breeding efforts of juveniles when breeding competition peaks.

We additionally investigated spatial fidelity of radio-collared juvenile (1.5-2.5 years old), adult (3.5-4.5 years old), and mature ($\geq$5.5 years old) male white-tailed deer (*n*

= 52) to successive annual (1 Oct - 30 Dec) home range and core-use areas from 1995-1997. We examined annual home range overlap and center of activity shifts as separate measures of spatial fidelity. Center of activity shifts were considered significant where in excess of threshold values derived from the dispersion of deer location distributions. In addition to little ($\leq 50\%$) overlap between annual core area boundaries, male deer shifted centers of activity by ≥ 742 m at the core-use scale, independent of age class. Results suggest that internal home range dynamics in space use, among male deer of all ages, are more influential in landscape usage over time than estimates of overlap at the home range scale.

We also describe relationships between a suite of landscape metrics, measured within varying radii (250, 500, 1000, 2000 and 3000 m) of home range centers, and home range sizes of male white-tailed deer ($n = 72$). We additionally tested the hypothesis that a combination of landscape metrics, representing spatial heterogeneity, can explain variation in home range size among male white-tailed deer. Deer exhibited mean home ranges of 643 ha and mean core areas of 112 ha. Results suggest that where habitat patches are small, highly diverse, and evenly distributed, male white-tailed deer have small home ranges. Results also indicate that home ranges are small where edge density is high. Our best model of spatial heterogeneity explained 28% of the variability in home ranges size at the 1000 meter scale, indicating that male deer perceive their environment at a spatial scale intermediate between mean home range and core-use areas. These results highlight the importance of considering core areas when space by white-tailed deer is of interest.

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Style manual of journals used: Behaviour, Journal of Wildlife Management, Landscape Ecology

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CHAPTER I

I. MOVEMENT PATTERNS OF MALE WHITE-TAILED DEER SUGGEST THAT JUVENILE USE ALTERNATIVE BREEDING STRATEGIES

ABSTRACT

During breeding periods, access to mates is likely the primary factor that influences movement patterns of sexually mature males. Metrics used to describe movement patterns have been related to known habitat quality, with an emphasis on optimal foraging. When access to mates is the limiting resource for sexually mature males, we predicted movement patterns of males will be efficient in respect to social status and degree of mate access. We examined daily movement paths of radio-collared male white-tailed deer (*Odocoileus virginianus*) during the breeding season (Oct. 1st- Dec. 15th), from 1995-1997, at the McAlester Army Ammunition Plant (McAAP) in southeastern Oklahoma to determine if the degree of mate access attributed to juvenile, adult, and mature males would reflect metrics related to path complexity and activity rates. Results indicate that male white-tailed deer become increasingly active throughout the breeding season, with progressively dispersed daily movement patterns. Juvenile males were highly active prior to the peak of the breeding season when adult and mature male breeding effort was limited. We found this behavior may increase juvenile male reproductive fitness by increasing their likelihood of breeding does coming into estrous

prior to the peak of the breeding season when competition with older males may belimited. Following the peak of the breeding season, juvenile male breeding effort declined, while their movement patterns became more linear. During this period, oldermales became more active and maintained similar levels of path complexity exhibited earlier during the breeding season. This behavior supports the hypothesis that older males suppress the breeding efforts of juveniles when breeding competition peaks.

Introduction

Typical breeding behavior among polygnous species involves intense male display and physical competition to gain access to mates. As a result, a limited number of dominant males are able to monopolize large numbers of females (Dewsbury 1982), resulting in a disproportionate amount of mating success attributed to dominant individuals (Trivers 1972). Because dominance is generally correlated with body size, and body size with age, older males are more competitive than younger (e.g. subordinate) males (Clutton-Brock 1982, Gossow 1971, Mitchell et al. 1977). Where males are free to invest in mating efforts in the absence of the burdensome cost of parental care (Emlen and Oring 1977), breeding behaviors that increase mate access while limiting competition with dominant males may be used by subordinate males (Howard 1978). Such behaviors are considered alternative mating strategies, and may be observed among subordinate males should only a slight increase in reproductive success result (Sandell 1986).

During breeding periods, mature (e.g., dominant) males exhibit movement patterns indicative of the spatial distribution of females and the competitive advantage they hold over lesser males (e.g. bighorn sheep, *Ovis canadensis*, Hogg 1984). Differences in home range or territory establishment among males with varying fitness have also been documented in numerous species (e.g. stoats, *Mustela erminea*, Erlinge and Sandell 1986, Sandell 1986; cheetahs, *Acinonyx jubatus,* Caro 1998; red-backed voles, *Clethrionomys rufocanus bedfordiae*, Kawata 1988; fishers, *Martes pennanti*, Arthur et al. 1989, Arthur and Krohn 1991; black bears, *Ursus americanus*, Garshelis and Pelton 1981, Powell et al. 1997), with subordinate males using larger areas peripheral to dominant males, increasing the likelihood of encountering mates while limiting interaction with dominant males. However, the presence of alternative mating strategies at finer temporal scales (i.e. 24-hour periods) has been examined in the movement patterns of few, if any, mammalian species.

Metrics describing fine-scale movement patterns have been used to examine animal movement in relation to resource availability, where resource availability is normally associated with habitat quality. Studies have linked fine-scale movement behavior to habitat quality, habitat complexity, and energy expenditure. Measures of path complexity and movement rates are expected to reflect habitat quality (Odendaal et al. 1989, Crist et al. 1992, Miyatake et al. 1995, Stapp and Van Horne 1997, Etzenhouser et al. 1998). For example, where resources are heterogeneous, low in quality, or clumped in distribution, many species maximize foraging efficiency by moving at a faster rate and in a more linear fashion (Weins et al. 1995, Whittington et al. 2004). Conversely, where resources are high in quality, homogeneous, or evenly distributed, many species exhibit increased path tortuosity and decreased rates of movement (Odendaal et al. 1989, Crist et al. 1992, Miyatake et al. 1995, Stapp and Van Horne 1997, Etzenhouser et al. 1998).

In mammalian species, access to mates is likely the primary factor that influences movement patterns of sexually mature males during the breeding season (Powell et al. 1997). Accordingly, during breeding periods, male resource availability could also be defined in terms of availability of potential mates. In this study, we examined movement patterns of adult, male white-tailed deer (*Odocoileus virginianus*) over 24-hour periods during the breeding season to determine if the movement patterns of juvenile, adult, and mature males would reflect the competitive advantage social dominance conveys in the access of mates. Given the clumped distribution of female white-tailed deer in matrilineal groups (Porter et al. 1991), we predicted mature males would exhibit concentrated, tortuous paths during the breeding season, similar to animal movement paths observed in high quality habitats. Conversely, we predicted juvenile males would exhibit dispersed, linear paths, similar to animal movement paths observed within low quality habitat. Additionally, it has been hypothesized that, when present, dominant males suppress the breeding efforts of juvenile males (Marchinton et al.1990). Based on this hypothesis, we predicted that measures of juvenile male activity would decrease during the later periods of breeding season when male competition escalates. However, prior to the onset of the rut, when competition among males is still limited, we predicted juvenile males would exhibit more tortuous paths and increased measures of activity in effort to breed does coming into estrous early in the breeding season.

Methods

Study area

We collected data at the McAlester Army Ammunition Plant (McAAP) in southeastern Oklahoma, an 18,212 ha area that was operated under a quality deer management program since 1989 (Ditchkoff et al. 1996). McAAP was an ammunition storage and manufacturing plant, operated by the United States Department of Defense, where public access was limited. However, hunting was permitted during 6, 3-day traditional archery hunts in October and November of each year. Forest cover at McAAP consisted of post oak (*Quercus stellata*) and blackjack oak (*Quercus marilandica*) uplands, interspersed with riparian drainages of water oak (*Quercus nigra*). In the uplands, post oak and blackjack oak form plant associations with poison ivy (*Toxicodendrus radicans*), buckbrush, and greenbriar (*Smilax bona-nox*) with winged elm (*Ulmus alata*) associated with the upper reaches of upland drainages. In riparian areas, spotted oak (*Quercus shumardii*) and water oak combine with broadleaf uniola (*Chasmanthium latifolium*), and greenbriar. A more detailed description of the study area was presented by Ditchkoff et al. (1996).

Field methods

We captured eighty-one adult (≥1.5 years of age) male white-tailed deer using drop-nets between December 1994 and January 1997 on food plots baited with persimmons and whole corn. We did not sedate deer after capture or during handling. We aged captured deer by tooth wear and eruption (Severinghaus 1949) and fitted each with a radiocollar equipped with a 4-hour mortality sensor (Advanced Telemetry Systems; Isanti, Minnesota) as well as numbered ear tags.

During the breeding season, (Sep 30- Dec 10), from 1995-1997, we located fifty-two deer throughout 271, 24-hour periods. We collected 8 locations per deer, per 24-hour period throughout the breeding season. Locations were taken at approximate 3-hour intervals, with an average elapsed time between first and last locations of 20.5 ± 1.3

hours. We used a 3-element Yagi antenna and portable receiver to obtain ground-based telemetry readings from 285 permanent telemetry stations, which we then triangulated to obtain deer locations. We obtained Universal Transverse Mercator (UTM) coordinates for each telemetry station using differentially corrected global positioning system data (Geoexplorer, Trimble Navigation, Sunnydale, California). We plotted bearings in the field, resulting in a standard deviation of 2.49 degrees, and estimated UTM coordinates for each deer location using a modified White and Garrott (1990) program written using SAS (Statistical Analysis System, SAS Institute, Inc., Cary, North Carolina).

We considered deer one year older on the 1st of October of each year. We chose October 1st as the start of the breeding season, which also coincides with the point at which juvenile bucks (≤2.5 years-old), first exhibit adult (≥3.5 years-old) behavior. We divided adult males into 3 age-classes: juvenile (1.5-2.5 years-old); adult (3.5-4.5 years-old); and mature (≥5.5 years-old) according to Ditchkoff et al. (2001). We delineated age-classes in this fashion to represent the observed characteristics of male white-tailed deer at McAAP, and in regard to current biological information concerning the maturation process of juvenile male deer. The distinction between adult and mature males was made to account for complete skeletal maturity and peak antler growth at 4.5 years of age, as well as, distinct differences in body characteristics associated with dominance in mature male white-tailed deer (Verme and Ullrey 1984). We partitioned the breeding season into three 24-day periods corresponding to the pre-rut, Oct 1-Oct 23; rut, Oct 24-Nov 16; and post-rut, Nov 17-Dec 10.

Statistical analysis

As a measure of the dispersion of 24-hour movement paths, we calculated distance between temporal extremes (m) (DBE), or the straight-line distance from the first location to the last location within a 24-hour movement path. Mean squared distance (m) (MSD) of all locations from their respective daily center of activity was calculated as an additional measure of dispersion using ArcView 3.2 Animal Movement Extension software (Hooge and Eichenlaub 1997). We calculated movement rate (m/hour) as (L/E), where (E) was the elapsed time between the first and last locations and (L) was the sum of all movements made within each 24-hour period or total path length.

Two metrics were used to describe the complexity of 24-hour movement paths. Eccentricity (ECC; range 1 - ∞, values increase with linearity) was calculated as the ratio of the primary and secondary axes of the ellipse area encompassing daily locations for deer using ArcView 3.2 Animal Movement Extension software (Hooge and Eichenlaub 1997). Secondly, path tortuosity (range 1- ∞, value increases with patch complexity) was calculated by hand as the ratio (L/DBE), where L was total path length and DBE was the distance between extreme temporal locations (Turchin 1998). We performed statistical analyses using Statistical Analysis System software, analysis of variance (PROC GLM; SAS 1993) to test movement variables for differences by age-class, period, and age-class period interaction ($\alpha = 0.05$).

Results

Distance between extremes

During the breeding season, there was some evidence that mean (DBE) was greater (more dispersed) (ANOVA, $F_{2,\,190} = 1.34$, $P \geq 0.104$) for juvenile males than for mature males (Table 1), although not strongly supported by the data. Mean DBE did not increase (ANOVA, $F_{2,\,190} = 3.95$, $P = 0.551$) from the pre-rut period to the rut period, but did increase by 21% (ANOVA, $F_{2,\,190} = 3.95$, $P = 0.016$) from the rut period to the post-rut period (Table 2). Juvenile males followed a similar trend, with mean DBE increasing - 68% (ANOVA, $F_{4,\,190} = 0.83$, $P = 0.014$) from the rut to the post-rut (Fig. 1). There was no difference in mean DBE for adult (ANOVA, $F_{4,\,190} = 0.83$, $P \geq 0.447$), or mature males (ANOVA, $F_{4,\,190} = 0.83$, $P \geq 0.163$) between the three periods of the breeding season. The age-classes did not differ in mean DBE during either the pre-rut or rut periods (ANOVA, $F_{4,\,190} = 0.83$, $P \geq 0.179$), but juvenile males tended to exhibit greater mean DBE than adult (ANOVA, $F_{4,\,190} = 0.83$, $P = 0.094$) and mature males (ANOVA, $F_{4,\,190} = 0.83$, $P = 0.069$) during the post-rut period.

Mean squared distance

The data did not strongly support an age-class effect (ANOVA, $F_{2,\,190} = 1.70$, $P \geq 0.104$) in average MSD during the breeding season; although there was some evidence mean MSD was greater for juvenile males than for mature males (Table 1). Conversely, mean MSD increased 86% (ANOVA, $F_{2,\,190} = 4.66$, $P = 0.002$) from the pre-rut period to the post-rut period. Juvenile males did not differ in mean MSD throughout the three periods of the breeding season (ANOVA, $F_{4, 190} = 0.53$, $P \geq 0.632$), however, adult males exhibited a 30% increase (ANOVA, $F_{4, 190} = 0.53$, $P = 0.048$) from the rut to the post-rut period and mature males increased 29% (ANOVA, $F_{4, 190} = 0.53$, $P = 0.013$) from the pre-rut to the post-rut period (Fig. 2). The age-classes did not differ in mean MSD during the rut or post-rut periods (ANOVA, $\mathrm{F}_{4, 190} = 0.53$, $\mathrm{P} \geq 0.190$), however, juvenile males generally exhibited greater (ANOVA, $F_{4, 190} = 0.53$, $P \geq 0.056$) mean MSD than mature males during the pre-rut period.

Movement rate

Average movement rate did not differ (ANOVA, $F_{2, 190} = 0.23$, $P = 0.543$) throughout the breeding season by age-class (Table 1), however, mean movement rate increased 30% (ANOVA, $F_{2, 190} = 4.05$, $P = 0.011$) from the pre-rut to the rut, and remained elevated (ANOVA, $F_{2, 190} = 4.34$, $P = 0.623$) during the post-rut (Table 2). Mean movement rate of adult and mature males increased 24% (ANOVA, $F_{4, 190} = 1.54$, $P = 0.024$) and 27% ($F_{4, 190} = 1.54$, $P = 0.032$), respectively, from the pre-rut to the rut, remaining elevated (ANOVA, $F_{4, 190} = 1.54$, $P \geq 0.198$) during the post-rut (Fig. 3). In contrast, mean movement rate of juvenile animals did not change (ANOVA, $F_{4, 190} = 1.54$, $P = 0.621$) from the pre-rut to the rut or from the rut to the post-rut (ANOVA, $F_{4, 190} = 1.54$, $P = 0.247$). During the pre-rut period, mean movement rate of juvenile males tended to be greater (ANOVA, $F_{4, 190} = 1.54$, $P = 0.075$) than adult males and was 23% greater

(ANOVA, $F_{4,\,190} = 1.54$, $P = 0.050$) than mature males. Movement rates did not differ (ANOVA, $F_{4,\,190} = 1.54$, $P \geq 0.393$) between the age-classes during the rut, however, evidence suggested adult and mature males moved at a greater mean rate (ANOVA, $F_{4,\,190} = 1.54$, $P \geq 0.165$) than juvenile males during the post-rut period, although this factor was not strongly supported by the data.

Eccentricity (ellipse shape)

During the breeding season, mature males exhibited movement path ellipses which were, on average, 3.8% more circular (ANOVA, $F_{2,\,190} = 2.78$, $P = 0.030$) than those exhibited by adult males, and 5.1% more circular (ANOVA, $F_{2,\,190} = 2.78$, $P = 0.055$) than those of juvenile males, although the latter tendency was not strongly supported by the data (Table 1). Conversely, mean eccentricity did not differ by period (ANOVA, $F_{2,\,190} = 1.12$, $P \geq 0.137$, Table 2). The age-classes did not differ in mean eccentricity during the pre-rut period (ANOVA, $F_{4,\,190} = 0.39$, $P \geq 0.\ 158$), or during the rut (ANOVA, $F_{4,\,190} = 0.39$, $P \geq 0.\ 282$), however, there was some indication that mean eccentricity was greater (more linear) for juvenile and adult males (ANOVA, $F_{4,\,190} = 0.39$, $P \geq 0.088$) than for mature males during the post-rut period (Fig. 4).

Path tortuosity

Mean path tortuosity was greater for adult males than for mature (ANOVA, $F_{2,\,190} = 5.45$,

$P \geq 0.004$) and juvenile males (ANOVA, $F_{2, 190} = 5.45$, $P \geq 0.009$, Table 1) throughout the breeding season. Mean tortuosity of movement paths remained constant (ANOVA, $F_{2, 190} = 1.66$, $P = 0.669$) from the pre-rut to the rut, but tended to become more linear (ANOVA, $F_{2, 190} = 1.66$, $P = 0.123$) during the post-rut, although not strongly supported by the data (Table 2). Mean path tortuosity became 64% (ANOVA, $F_{4, 190} = 3.75$, $P = 0.003$) more linear from the pre-rut to the post-rut for juvenile males (Fig. 5). Adult males exhibited a 9% (ANOVA, $F_{4, 190} = 3.75$, $P = 0.011$) increase in mean path tortuosity from the pre-rut to the rut, and evidence suggested mean tortuosity continued to increase (ANOVA, $F_{4, 190} = 3.75$, $P = 0.092$) during the post-rut period. Mean path tortuosity of mature males stayed constant (ANOVA, $F_{4, 190} = 3.75$, $P \geq 0.707$) among the time periods comprising the breeding season. During the pre-rut period mean tortuosity was greater (ANOVA, $F_{4, 190} = 3.75$, $P \geq 0.044$) for juvenile males than for mature males, and also tended to be greater (ANOVA, $F_{4, 190} = 3.75$, $P \geq 0.144$) for juvenile males than adult males, but the difference was not strongly supported by the data. Adult males showed greater tortuosity during the rut period than both juvenile (ANOVA, $F_{4, 190} = 3.75$, $P \geq 0.004$) and mature (ANOVA, $F_{4, 190} = 3.75$, $P \geq 0.004$) males. During the post-rut, adult and mature males did not differ (ANOVA, $F_{4, 190} = 3.75$, $P = 0.230$) in mean path tortuosity, however, juvenile males exhibited 25% (ANOVA, $F_{4, 190} = 2.71$, $P \leq 0.008$) lower mean path tortuosity than adult males.

Discussion

It is apparent that prior to and during the rut, movement paths of all male white-tailed deer are relatively tortuous, declining only during the post-rut. During the pre-rut period, the high path tortuosity exhibited by all male deer is likely driven by food resources more so than the availability of mates, as movement rates are much slower during this period, consistent with optimal foraging theory (Emlen 1966). However, during the rut, when male deer reduce foraging effort and mate availability has peaked, high path tortuosity exhibited by male deer is likely a response to increased mate access, and consistent with our prediction, movement rates increase significantly. Likewise, during the post-rut period, male deer continue to reduce foraging activity and movement rates remain elevated. However, mate competition likely increases as available mates decline and testosterone levels remain elevated (Ditchkoff et al. 2001). Consistent with our prediction, it is at this point that movement paths of all male deer become more linear.

Contrary to our original prediction that path complexity would increase with age during periods of increased mate access; older males (e.g. dominant) tended to maintain moderate levels of path tortuosity throughout the breeding season. Moderate levels of path tortuosity may reflect the non-territorial nature of male white-tailed deer. Hogg (1984) found that dominant male big horn sheep focused their breeding efforts within traditional geographic centers of tending, which estrous ewes returned to each year. Tending rams defended estrous ewes from lesser males during the approximate 2-3 days they remained in estrous. Conversely, white-tailed deer are not known to use traditional breeding grounds and does typically remain in estrous for only 24-hours (Marchinton and

Hirth 1984). While male big horn sheep are know to aggressively hinder movements of ewes in estrous (Hogg 1984), tending male white-tailed deer typically feed and bed with does in estrous until copulation has occurred, after which time they will defend the doe, wherever she may go, for several hours. It is important to note that male white-tailed deer defend only the doe, not a specific geographic area or territory (Marchinton and Hirth 1984). The movement patterns of dominant male white-tailed deer reflect these behavioral characteristics with moderate levels of path tortuosity representing tending behavior disconnected from any central geographic location.

While adult and mature males maintain moderate levels of path tortuosity throughout the breeding periods, juvenile males do exhibit a significant decrease in path tortuosity during the post-rut. In contrast to both juvenile male red deer and big horn sheep, juvenile male white-tailed deer do not have the luxury of employing aggressive alternative breeding strategies during the breeding season. The harem-holding nature of dominant male red deer allows for juvenile male coursing behavior, in which juvenile males attempt to scatter harems or run off hinds (Clutton-Brock 1982). Likewise, lesser male big horn sheep incur less risk of injury when coursing dominant males due to the relative benign nature of percussion weapons (Hogg 1984). White-tailed deer do not hold harems, and risk of serious injury is more likely during competition with perforating antlers, than with blunt horns. We interpret the movement patterns of juvenile male white-tailed deer during the post-rut to be reflective of this, as spatially, their linear movements may serve to limit hostile interactions with dominant males while continuing to search for possible mating opportunities.

The high degree of effort expended by juvenile males during the pre-rut could be interpreted as a function of both inexperience and the necessary energy expenditure needed to establish their placement in the dominance hierarchy (Hirth 1977). However, given the inactivity of dominant males during the pre-rut period, it may be possible that juvenile males attempt to court and tend does prior to the onset of the rut. Yearling bison bulls (Komers et al. 1994*b*), yearling male reindeer (Mysterud et al. 2003), and sub-adult male bighorn sheep (Singer and Zeigenfuss 2002) have been found to exhibit an increase in reproductive effort when prime-aged males were scarce or absent. Although adult and mature male white-tailed deer were present during the pre-rut period, their general inactivity may create conditions similar to populations where demographics are skewed toward juvenile males (Mysterud et al. 2004).

The inactivity of older males during the pre-rut period may be explained by experience gained during previous breeding seasons. Lincoln et al. (1972) indicated prior breeding experience may influence the timing of rutting behavior in adult male ungulates, limiting breeding effort until shortly before the peak of the rut. Additionally, Clutton-Brock (1982), found that the duration of breeding effort for some adult red deer stags was shorter than the duration of peak hind conception, resulting in a proportion of held hinds conceiving either before or after their period of holding. In the Cross Timbers and Prairies Ecoregion where these data were collected, the peak of conception falls on approximately the 20th of November, yet does may conceive as early as October 13th (TPWD 2007). Actively searching juvenile males may increase their reproductive potential by tending to the small portion of does that come into estrous before the peak in breeding effort among dominant males. Spatially, the movement patterns of juvenile males during the pre-rut period would not constitute an alternative breeding strategy, being similar to those of dominant males during the rut. However, should the evolution of early rutting behavior among juvenile males serve to increase their reproductive success even slightly, the temporal partitioning of their breeding effort may constitute an alternative breeding strategy.

The understanding of movement patterns associated with typical breeding behavior in older (e.g. dominant) males and alternative breeding strategies among lesser males would undoubtedly be aided by confirming the presence of females in relation to males. Moreover, paternity testing could be used to determine the degree to which alternative breeding strategies convey a selective advantage. While our data from the post-rut period was consistent with the hypothesis that dominant males suppress the breeding effort of juvenile males (Marchinton et al. 1990), examination of juvenile male survival following the breeding season would aide in supporting the degree to which juvenile breeding suppression by dominant males occurs.

References

Arthur, S.M., Krohn, W.B. & Gilbert, J.R. (1989). Home range characteristics of adult fishers.-J. Wildl. Manage. 53: 674-679.

Arthur, S.M., & Krohn, W.B. (1991). Activity patterns, movements, and reproductive ecology of fishers in southcentral Maine.-J. Mammal. 72: 379-385.

Caro, T., editor. (1998). Behavioral ecology and conservation biology. Oxford: Oxford University Press.

Clutton-Brock, T.H., Guinness, F.E. & Albon S.D. (1982). Red deer: behavior and ecology of two sexes. Chicago: The University of Chicago Press.

Crist, T.O., Guertin, D.S., Wiens, J.A. & Milne, B.T. (1992). Animal movement in heterogeneous landscapes: an experiment with Eleodes beetles in shortgrass prairie.-Funct. Ecol. 6: 536-544.

Dewsbury, D.A. (1982). Ejaculate cost and male choice.-Am. Nat. 119: 601-610.

Ditchkoff, S.S., Welch, Jr., E.R., Lochmiller, R.L., Masters, R.E., Starry, W.R. & Dinkines, W.C. (1996). Wounding rates of white-tailed deer with traditional archery equipment.- Proc. Annu. Conf. Southeast. Assoc. Fish and Wildl. Agencies. 52: 244-248.

Ditchkoff, S.S., Spicer, L.J., Masters, R.E., & Lochmiller, R.L. (2001). Concentrations of insulin-like growth factor-I in adult male white-tailed deer (Odocoileus virginianus): Associations with serum testosterone, morphometric measurements, and age during and after the breeding season.-Comp. Biochem. Physiol. 129: 887-895.

Emlen, J.M. (1966). The role of time and energy in food preference.-Am. Nat. 100: 611-617.

Emlen, S.T., & Oring, L.W. (1977). Ecology, sexual selection, and the evolution of mating systems.-Science. 197: 215-223.

Erlinge, S., & Sandell, M. (1986). Seasonal changes in the social organization of male stoats, Mustela ermniea in Sweden.-Oikos. 47: 57-62.

Etzenhouser, M.T., Owens, M.K., Spalinger, D. E., & Murden, S. B. (1998). Foraging behavior of browsing ruminants in a heterogeneous landscape.-Landcape Ecol. 13: 55-64.

Garshelis, D.L., & Pelton, M.R. (1981). Movements of black bears in the Great Smoky Mountains National Park.-J. Wildl. Manage. 45: 912-925.

Gossow, H. (1971). Sociological and rank: order aspects with an alpine red deer population.-Allg. Forst Jagdtg. 142: 169-173.

Hirth, D.H. (1977). Social behavior of white-tailed deer in relation to habitat.-Wildlife Monogr. 53.

Hogg, J.T. (1984). Mating in bighorn sheep: multiple creative male strategies.-Science. 225: 526-529.

Howard, R.D. (1978). The evolution of mating strategies in bullfrogs, Rana catesbeiana.-Evolution. 32: 850-871.

Kawata, M. (1988). Mating success, spatial organization, and male characteristics in experimental field populations of the red-backed vole Clelhrionomys rufocanis bedfordiae.-J. Anim. Ecol. 57: 217-235.

Komers, P.E., Messier, F. & Gates, C.C. (1994b). Plasticity of reproductive behaviour in wood bison bulls: when subadults are given a chance.-Ethol. Ecol. Evol. 6: 313-330.

Lincoln, G.A., Guinness, F.E. & Short, R.V. (1970). The way in which testosterone controls the social and sexual behaviour of the red deer stag (Cervus elaphus).-Horm. Behav. 3: 375-396.

Marchinton, R.L., & Hirth, D.H. (1984). Behavior. In: White-tailed deer: ecology and management (Ed. by L. K. Halls), pp. 129-168. Harrisburg: Stackpole Books.

Marchinton, R.L., Miller, K.V., Hamilton, R.J., & Guynn, D.C. (1990). Quality deer management: biological and social impacts on the herd. In: Proceedings of the Tall Timbers Game Bird Seminar (Ed. by C. Kyser, D.C. Sisson, & J.L. Landers), pp 7-15. Tallahassee: Tall Timbers Research Station.

Mitchell, B., Staines, B.W. & Welch, V. (1997). Ecology of red deer: a research review relevant to their management. Cambridge: Institute of Terrestrial Ecology.

Miyatake, T., Kawasaki, K., Kohoma, T., Moriya, S. & Shimoji, Y. (1995). Dispersal of male sweet potato weevils (Coeoptera: Curculionidae) in fields with or without sweet potato plants.-Environ. Entomol. 24: 1167-1174.

Mysterud, A., Holand, O., Roed, K.H., Gjostein, H., Kumpula, J.M. & Nieminen, M. (2003). Effects of age, density and sex ratio on reproductive effort in male reindeer (Rangifer tarandus).-J. Zool. 261: 341-344.

Mysterud, A., Langvatn, R. & Stenseth, N.C. (2004). Patterns of reproductive effort in male ungulates.-J. Zool. 264: 209-215.

Singer, F.J. & Zeigenfuss, L.C. (2002). Influence of trophy hunting and horn size on mating behavior and survivorship of mountain sheep.-J. Mammal. 83: 682-698.

Stapp, P., & Van Horne, B. (1997). Response of deer mice (Peromyscus maniculatus) to shrubs in shortgrass prairie: linking small-scale movements and the spatial distribution of individuals.-Funct. Ecol. 11: 644–651.

Odendaal, F.J., Turchin, P. & Stermitz, F.R. (1989). Infuence of host-plant density and male harassment on the distribution of female Euphydryas anicia (Nymphalidae).-Oecologia. 78: 283–288.

Porter, W.F., Mathews, N.E., Underwood, H.B., Sage, R.W. & Behrend, D.F. (1991). Social organization in deer: implications for localized management.-Environ. Manage. 15: 809-814.

Powell, R.A., Zimmerman, J.W. & Seaman D.E. (1997). Ecology and behaviour of North American black bears. London: Chapman & Hall.

Sandell, M. (1986). Movement patterns of male stoats Mustela erminea during the mating season: differences in relation to social status.-Oikos. 47: 63-70.

SAS Institute. (1993). SAS/STAT software. SAS Institute, INC, Cary, North Carolina.

Severinghaus, C.W. (1949). Tooth development and wear as criteria for age in white-tailed deer.-J. Wildl. Manage. 13: 195-216.

Texas Parks and Wildlife. (2007). The rut in white-tailed deer. Available: http://www.tpwd.state.tx.us/huntwild/hunt/planning/rut_whitetailed_deer/#E11E6 Accessed: 16 August 2007.

Trivers, R. (1972). Parental investment and sexual selection. In: Sexual Selection and The Descent of Man, (Ed. by B. Campbell), pp. 136-179. Chicago: Aldine.

Turchin, P. (1998). Quantitative analysis of movement: measuring and modeling population redistribution of animals and plants. Sunderland: Sinauer Associates.

Verme, L.J. & Ullrey D.E. (1984). Physiology and nutrition. In: White-tailed deer ecology and management, (Ed. by L. K. Halls), pp. 91-118. Harrisburg: Stackpole Books.

Wiens, J.A., Crist, T.O., With, K.A. & Milne, B.T. (1995). Fractal patterns of insect movement in microlandscape mosaics.-Ecology. 76: 663–666.

Whittington, J.C., St. Clair, C. & Mercer, G. (2004). Path tortuosity and permeability of roads and trails to wolf movement.-Ecology and Society. 9, 4: http://www.ecology andsociety.org/vol9/iss1/art.

Table 1. Measures of daily path dispersion (DBE[a], MSD[b]), path complexity (ECC[c], tortuosity[d]), and movement rate[e] of juvenile (1.5 - 2.5 years of age), adult (3.5 - 4.5 years of age) and mature (≥ 5.5 years of age) male white-tailed during the breeding season (Oct 1 - Dec 15) in Southeastern Oklahoma

Age class	***n***	**Variable**	**Mean**	**SE**	**Min**	**Max**
		DBE (m)	850.85	78.72	34.26	3,257.95
		MSD (m)	424,059.86	43,496.27	40,240.55	1,870,093.70
		Rate (m/hr)	184.18	8.45	77.75	385.73
		Eccentricity	1.66	0.44	1.12	3.22
juvenile	94	Tortuosity	8.16	1.7	1.05	102.05
		DBE (m)	798.28	50.92	21.33	2,729.92
		MSD (m)	381,036.00	32,008.17	37,215.97	1,970,238.03
		Rate (m/hr)	172.86	6.37	53.25	450.96
		Eccentricity	1.64	0.41	1.07	3.17
adult	117	Tortuosity	9.03	1.55	1.18	174.15

Table 1. Continued.

Age class	*n*	Variable	Mean	SE	Min	Max
		DBE (m)	692.14	51.26	106.3	2,537.61
		MSD (m)	326,069.72	32,224.89	32,436.24	1,828,431.27
		Rate (m/hr)	168.42	7.93	42.31	437.56
		Eccentricity	1.58	0.45	1.04	3.28
mature	60	Tortuosity	7.24	0.62	1.46	27.02

[a] DBE is the distance between extreme temporal locations during a 24-hour period.

[b] MSD is the mean squared distanced from daily centers of activity to all locations.

[c] Eccentricity is the ratio of the primary and secondary axes of ellipse areas encompassing 24-hour movement paths. [d] Tortuosity is the ratio of total 24-hour path length to the distance between extreme temporal locations. [e] Rate is equal to total 24-hour path length divided by the elapsed time between first and last locations.

Table 2. Measures of daily path dispersion (DBE[a], MSD[b]), path complexity (ECC[c], tortuosity[d]), and movement rate[e] of juvenile (1.5 - 2.5 years old), adult (3.5 - 4.5 years old) and mature (≥ 5.5 years old) male white-tailed during the pre-rut, Oct 1-Oct 23; rut, Oct 24-Nov 16; and post-rut, Nov 17-Dec 10 periods of the breeding season in Southeastern Oklahoma

Period	***n***	**Variable**	**Mean**	**SE**	**Min**	**Max**
		DBE (m)	645.13	44.34	21.33	2,341.15
		MSD (m)	260,265.35	24,521.32	32,436.24	1,475,750.00
		Rate (m/hr)	146.19	5.58	42.31	313
		Eccentricity	1.63	0.43	1.06	3.28
pre-rut	94	Tortuosity	9.23	2.1	1.18	174.15
		DBE (m)	789.53	52.62	74.16	2,730.00
		MSD (m)	406,656.73	32,209.00	40,240.60	1,970,238.03
		Rate (m/hr)	184.57	6.52	63.95	451
		Eccentricity	1.6	0.36	1.04	2.87
rut	117	Tortuosity	8.57	0.82	1.62	48.51

Table 2. Continued.

Period	*n*	Variable	Mean	SE	Min	Max
		DBE (m)	955.68	82.43	108.63	3,258.00
		MSD (m)	485,040.00	50,403.26	38,827.00	1,828,431.27
		Rate (m/hr)	197.06	10.37	82.57	437.56
		Eccentricity	1.66	0.53	1.07	3.22
post-rut	60	Tortuosity	6.11	0.61	1.05	27.02

[a] DBE is the distance between extreme temporal locations during a 24-hour period.

[b] MSD is the mean squared distanced from daily centers of activity to all locations.

[c] Eccentricity is the ratio of the primary and secondary axes of ellipse areas encompassing 24-hour movement paths. [d] Tortuosity is the ratio of total 24-hour path length to the distance between extreme temporal locations. [e] Rate is equal to total 24-hour path length divided by the elapsed time between first and last locations.

Figure 1. Mean distance (m) between 24-hour movement path extreme temporal locations (DBE) for juvenile (1.5-2.5 years of age), adult (3.5-4.5 years of age) and mature (≥ 5.5 years of age) male white-tailed during the pre-rut, Oct 1-Oct 23; rut, Oct 24-Nov 16; and post-rut, Nov 17-Dec 10 periods of the breeding season in Southeastern Oklahoma.

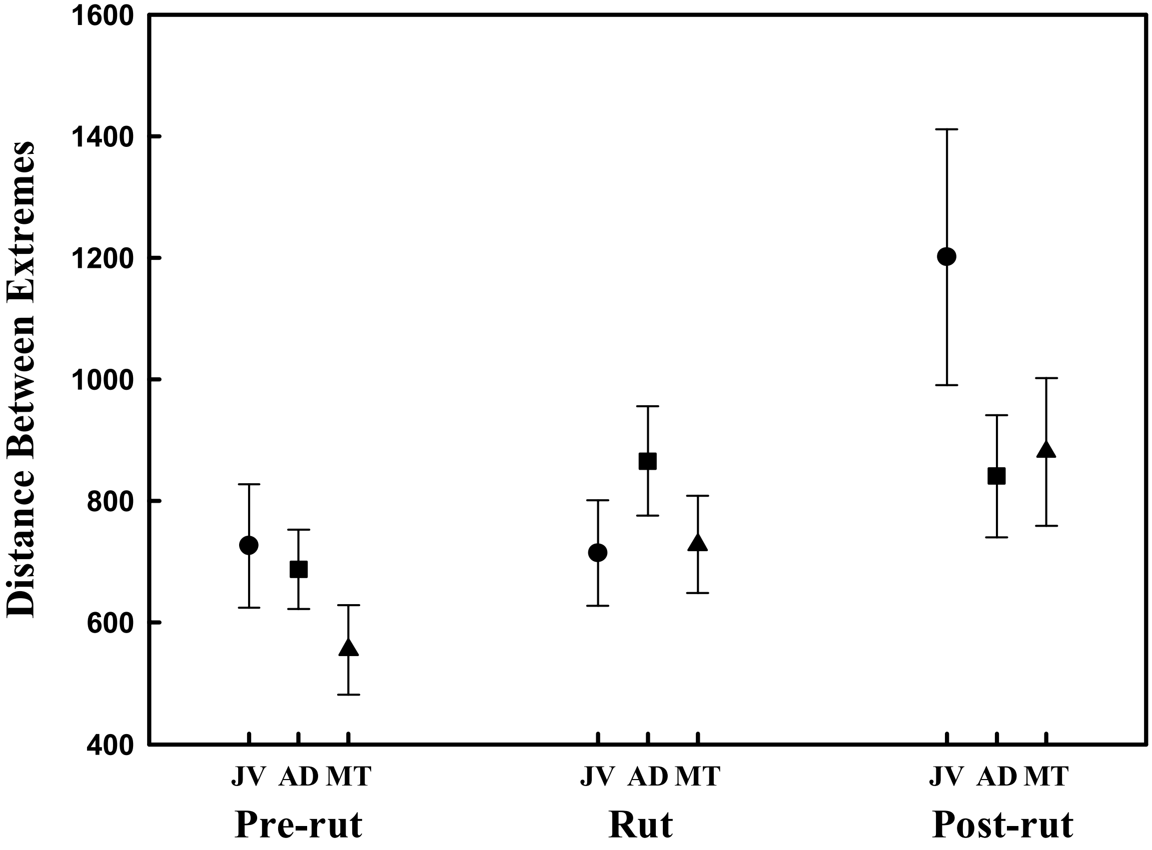
Distance Between Extremes
1600
1400
1200
1000
800
600
400
JV AD MT
Pre-rut
JV AD MT
Rut
JV AD MT
Post-rut

Figure 2. Average mean squared distance (MSD) from 24-hour movement path centers of activity to daily locations for juvenile (1.5-2.5 years of age), adult (3.5-4.5 years of age) and mature (≥ 5.5 years of age) male white-tailed during the pre-rut, Oct 1-Oct 23; rut, Oct 24-Nov 16; and post-rut, Nov 17-Dec 10 periods of the breeding season in Southeastern Oklahoma.

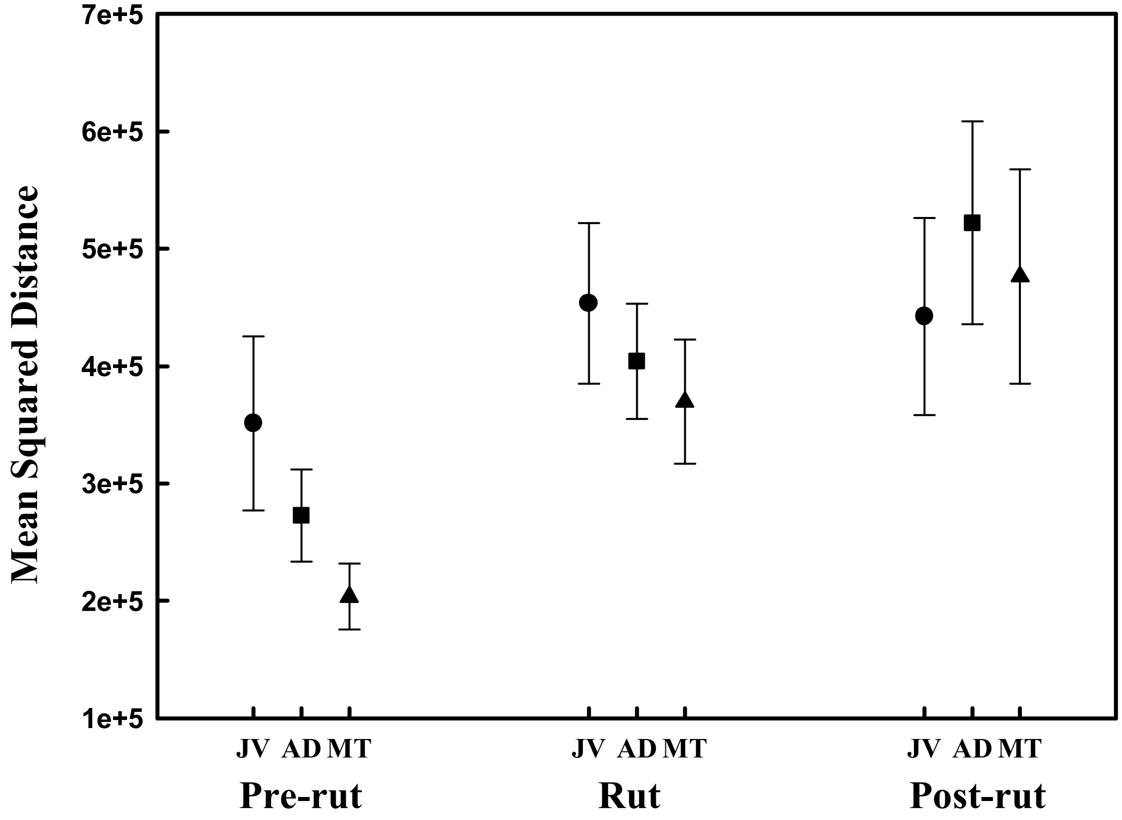
Mean Squared Distance
7e+5
6e+5
5e+5
4e+5
3e+5
2e+5
1e+5
JV
AD
MT
Pre-rut
JV
AD
MT
Rut
JV
AD
MT
Post-rut

Figure 3. Mean movement rate (m/hr), or total 24-hour path length divided by the elapsed time between first and last locations, for juvenile (1.5-2.5 years of age), adult (3.5-4.5 years of age) and mature (≥ 5.5 years of age) male white-tailed during the pre-rut, Oct 1-Oct 23; rut, Oct 24-Nov 16; and post-rut, Nov 17-Dec 10 periods of the breeding season in Southeastern Oklahoma.

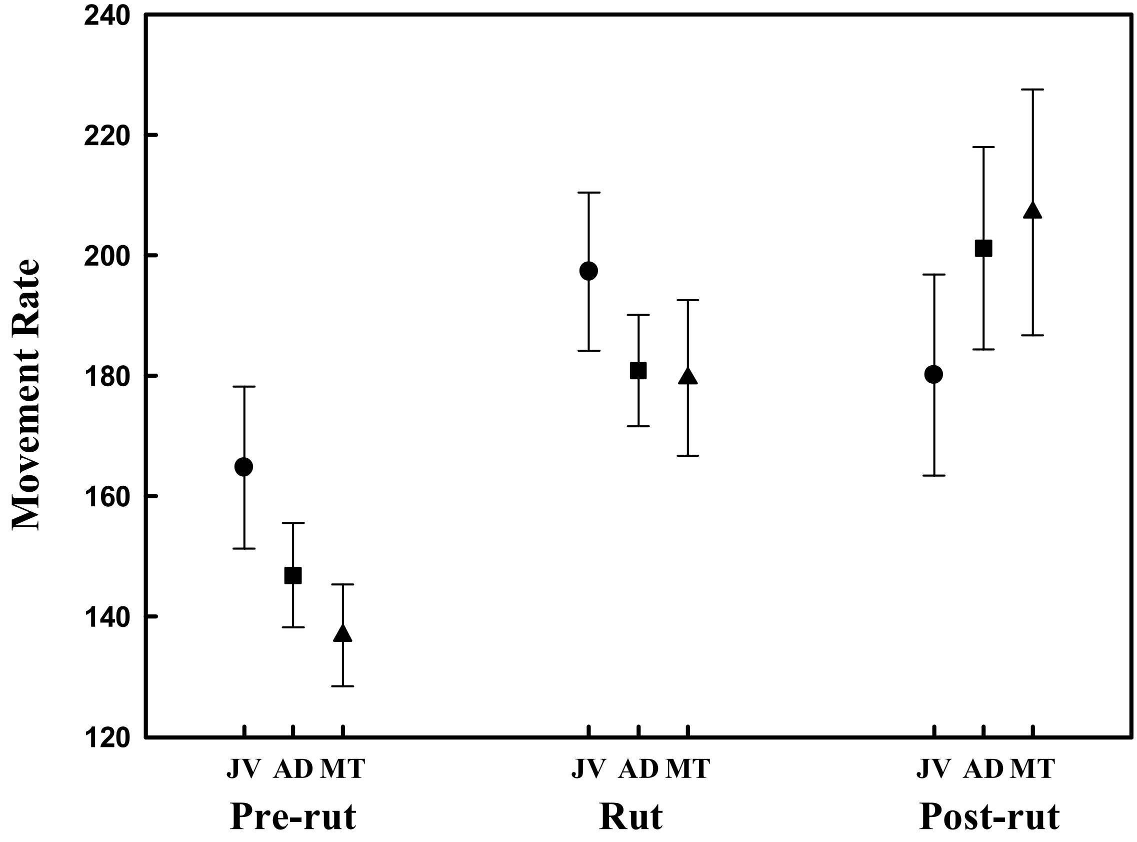
240
220
200
180
160
140
120
Movement Rate
JV AD MT
Pre-rut
JV AD MT
Rut
JV AD MT
Post-rut

Figure 4. Mean 24-hour movement path ellipse eccentricity, defined as the ratio of the primary and secondary axes of ellipse areas encompassing 24-hour movement paths, for juvenile (1.5-2.5 years of age), adult (3.5-4.5 years of age) and mature (≥ 5.5 years of age) male white-tailed during the pre-rut, Oct 1-Oct 23; rut, Oct 24-Nov 16; and post-rut, Nov 17-Dec 10 periods of the breeding season in Southeastern Oklahoma.

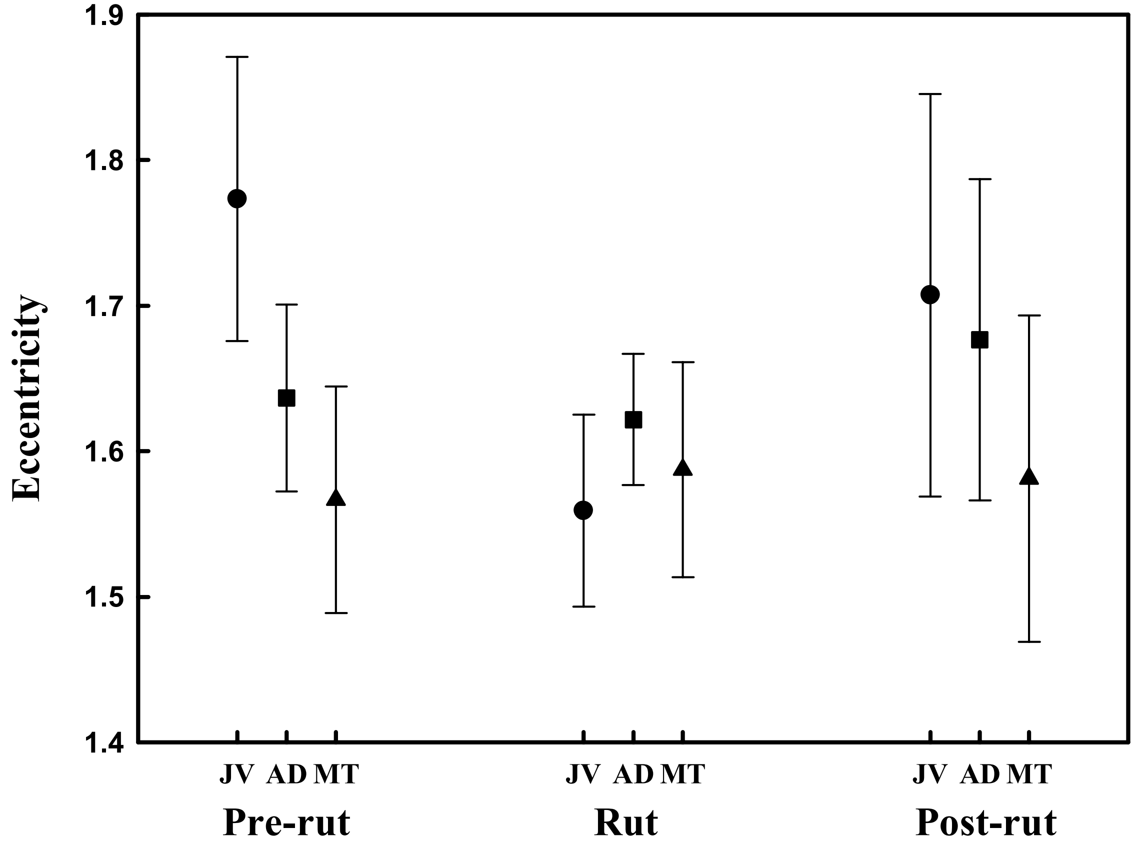
1.9
1.8
1.7
1.6
1.5
1.4
Eccentricity
JV
AD
MT
JV
AD
MT
JV
AD
MT
Pre-rut
Rut
Post-rut

Figure 5. Mean 24-hour path tortuosity, defined as the ratio of total path length to the distance between extreme temporal locations, for juvenile (1.5-2.5 years of age), adult (3.5-4.5 years of age) and mature (≥ 5.5 years of age) male white-tailed during the pre-rut, Oct 1-Oct 23; rut, Oct 24-Nov 16; and post-rut, Nov 17-Dec 10 periods of the breeding season in Southeastern Oklahoma.

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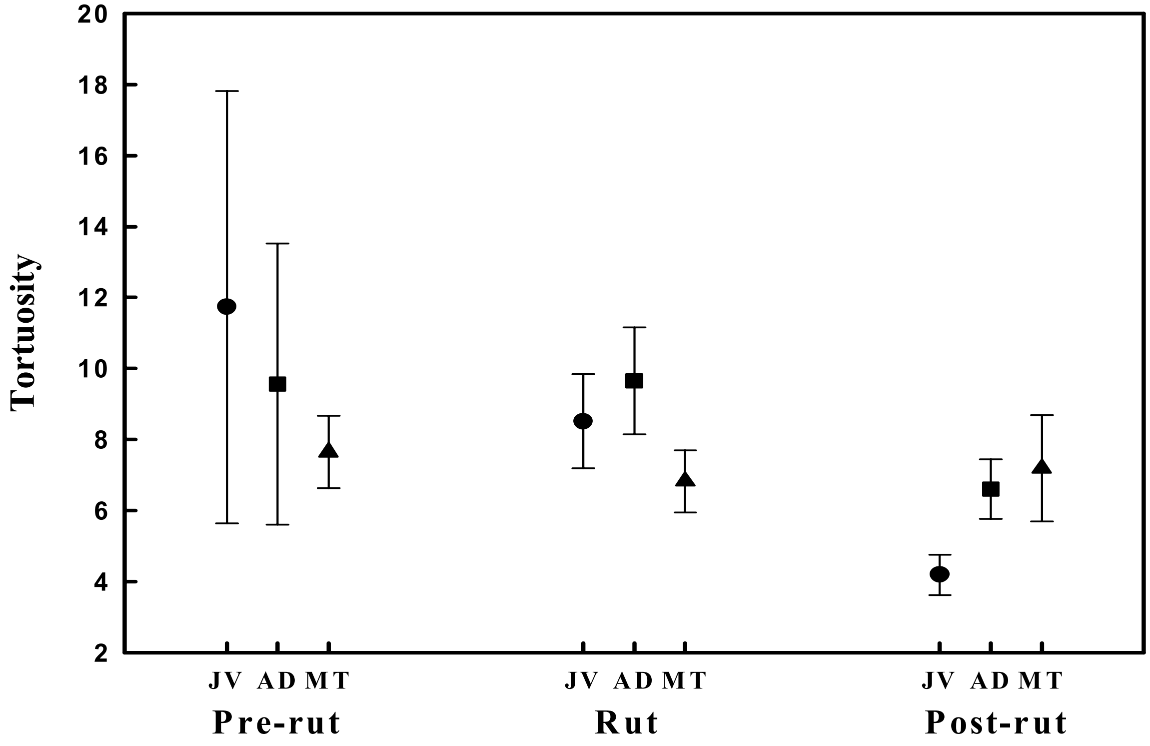

Tortuosity
20
18
16
14
12
10
8
6
4
2
JV AD MT
Pre-rut
JV AD MT
Rut
JV AD MT
Post-rut

II. SPATIAL FIDELITY IN ADULT MALE WHITE-TAILED DEER

ABSTRACT

A thorough review of the scientific literature suggests that our understanding of the spatial ecology of adult male deer is somewhat limited. More specifically, while data exist on female deer and yearling males, little if any data are available that describe the spatial ecology of mature males. Specifically, data concerning home range fidelity among sexually mature males would improve population models and has implications for deer managers in relation to property size and achieving goals set by Quality Deer Management. We investigated spatial fidelity of radio-collared juvenile (1.5-2.5 years old), adult (3.5-4.5 years old), and mature (≥5.5 years old) male white-tailed deer (*n* = 52) to successive annual (1 Oct - 30 Dec) home range and core-use areas from 1995-1997, at McAlester Army Ammunition Plant in Oklahoma. We examined annual home range overlap and center of activity shifts as separate measures of spatial fidelity. Center of activity shifts were considered significant where in excess of threshold values derived from the dispersion of deer location distributions. In addition to little (≤ 50%) overlap between annual core area boundaries, male deer shifted centers of activity by ≥ 742 m at the core-use scale, independent of age class. Results suggest that internal home range dynamics in space use, among male deer of all ages, are more influential in landscape usage over time than estimates of overlap at the home range scale.

INTRODUCTION

White-tailed deer (*Odocoileus virginianus*) have been extensively studied because of their importance as a game animal in North America. This research has led to an unprecedented understanding of the ecology and biology of the species, and allows for development of detailed population management plans that can be implemented with a high probability of success. In most cases, the basis for these management plans is to improve or enhance the quality of the male segment of the population, and to meet the hunting objectives of stakeholders; however, a thorough review of the scientific literature suggests that our understanding of the spatial ecology of adult male deer is somewhat limited. More specifically, while data exist on female deer and yearling males, little if any data are available that describe the spatial ecology of mature males.

Female white-tailed deer have been reported to exhibit a high degree of home range fidelity (Porter et al. 1991), defined as the continual reoccurrence of an animal within a home range throughout defined time periods (White and Garrott 1990). Porter et al. (1991) used the analogy of overlapping rose petals to describe the spatial arrangement of home ranges within matriarchal social groups of does, and further advanced the hypothesis of gradual population expansion via this type of spiral home range arrangement. Dispersal of yearling males from natal home ranges has similarly been well documented (Nelson and Mech 1984); however, little is known about the spatial fidelity of adult males following dispersal. Data concerning home range fidelity among sexually mature males would improve population models; however, such data also has implications for deer managers. Where adult males exhibit strong home range fidelity following dispersal, mangers would be certain characteristics of harvested bucks (i.e. antler growth) could be contributed, at least in part, to local management practices and not the practices of neighboring properties. Such data would also provide managers with an indication of the likelihood of observed deer remaining on managed properties throughout adulthood, which is an important tenet of Quality Deer Management (Marchinton et al. 1990).

While few studies have examined home range fidelity in adult male white-tailed deer, extensive overlap between annual home range boundaries for adult bucks has been reported (Tierson et al. 1985; Lesage et al. 2000; Webb et al. 2007), suggesting that adult bucks exhibit strong site fidelity. Shifts in animal locations may occur on an annual basis, however, without impacting spatial overlap between corresponding home range boundaries (Plowman et al. 2006). Accordingly, the examination of annual center of activity shifts in addition to home range overlap will provide a finer scale analysis of home range fidelity for comparison.

The area within an animal's home range is generally not used proportionally (Burt 1943). Accordingly, areas of concentrated use have been defined as core-use areas and the assumption is made that these areas contain more dependable resources than little used peripheral areas within the home range (Leuthold 1977). Where core area resources become depleted, deer likely shifts patterns of concentrated use; however, while minor home range shifts have reported among female deer in response to resource availability (Byford 1970a), little is known about the annual dynamics of core-use areas within the home ranges of adult males.

Until recently, male-biased harvests resulted in populations with very few mature (≥4.5 years of age) males (Miller and Marchinton 1995). Subsequently, few studies have examined variation in spatial fidelity with age. Home range fidelity likely improves recognition of competitors among males of all ages, thereby facilitating the establishment of clear dominant-subordinate roles and limiting costly agonistic interactions among unknown males (Logan and Sweanor 2001). Alternatively, juvenile males may not form stable home ranges until 3 years or 4 years of age (Nelson and Mech 1984) which may be in response to agonistic interactions with dominant males (Shields 1987). The goal of this study was to investigate annual home range and core area fidelity for juvenile (≤ 2.5 years of age), adult (3.5-4.5 years of age), and mature (≥ 5.5 years of age) male white-tailed deer in a population where greater than 50% of males were ≥3.5 years of age (Ditchkoff et al. 2000). Our objective was to investigate the dynamics of deer space use by examining home range and core area overlap as well as center of activity shifts between annual home ranges and core use areas. We additionally present results for comparison of home range and core area size between years and by age class as a framework for discussion of the spatial fidelity of male deer.

STUDY AREA

We collected data from the McAlester Army Ammunition Plant (McAAP) in southeastern Oklahoma, an 18,212 ha area that was operated under a quality deer management program since 1989 (Ditchkoff et al. 1996). McAAP was an ammunition storage and manufacturing plant, operated by the United States Department of Defense, where public access was limited (Ditchkoff et al. 1996). Deer density at McAAP was estimated at 1 deer/ 6.67 ha, with an approximate sex ratio of 1 buck/1.5 does. Forest cover at McAAP consisted of post oak (*Quercus stellata*) and blackjack oak (*Quercus marilandica*) uplands, interspersed with riparian drainages of water oak (*Quercus nigra*; Table 1). In the uplands, post oak and blackjack oak formed plant associations with poison ivy (*Toxicodendrus radicans*), buckbrush (*Ceanothus cuneatus*), and greenbriar (*Smilax bona-nox*). In riparian areas, spotted red oak (*Quercus shumardii*) and water oak combined with broadleaf uniola (*Chasmanthium latifolium*), and greenbriar.

METHODS

Capture and Handling

We captured fifty-two sexually mature (≥1.5 years of age) male white-tailed deer using drop-nets between December 1994 and January 1997 on food plots baited with persimmons and whole corn. We did not sedate deer after capture or during handling. We aged captured deer by tooth wear and eruption (Severinghaus 1949); however, visual inspection of body size and antler characteristics aided the process. We fitted captured deer with numbered ear tags and a radiocollar equipped with a 4-hour mortality sensor (Advanced Telemetry Systems; Isanti, Minnesota). This research was approved by the Oklahoma State University Institutional Animal Care and Use Committee as protocol number 461.

Data Collection and Radiotelemetry

From October-January of each year we located deer 3-4 times each week and once weekly from January-September. To reduce sampling bias, we took locations at random throughout each 24 hour period (Beyer and Haufler 1994) from permanent telemetry stations. We used a 3-element Yagi antenna and portable receiver to obtain ground-based telemetry readings, which we triangulated to obtain deer locations. We obtained Universal Transverse Mercator (UTM) coordinates for each telemetry station using differentially-corrected global positioning system data (Geoexplorer, Trimble Navigation, Sunnydale, California). We plotted bearings with a standard deviation of 2.49 degrees. We estimated UTM coordinates for each deer location using a modified White and Garrott (1990) program written using SAS (SAS Institute 1989).

Home-Range Estimation

We quantified 95% home ranges and 50% core-use areas using the fixed kernel home range estimator with least squares cross validation smoothing (Seaman et al. 1999) using the Animal Movement Extension (Hooge and Eichenlaub 1997) in ArcView 3.2 software. We used the reference bandwidth (h_{ref}) when calculating the 95% and 50% probability contours and grid extent was auto-calculated. The reference bandwidth is an estimate of the ideal bandwidth, assuming a bivariate normal distribution of locations (Silverman 1986). We calculated home ranges for individual deer with an average of 33 locations; however, the minimum number of locations used was 23. Similar to Webb et al. (2007), annual home ranges were calculated from 1 October to 30 September for both years of the study. We divided adult males into 3 age classes for comparison: juvenile (≤ 2.5 years-old); adult (3.5 - 4.5 years-old), and mature (≥5.5 years of age) after Ditchkoff et al. (2001). Differences in home range and core area size between the age classes of male deer were compared using analysis of variance in SAS (SAS Institute 1989).

Home Range Overlap

We calculated percent home range overlap as:

$$100 * \left[\frac{OV}{A_1} \right]$$

where OV was equal to the area (ha) of overlap between sequential home range and A_1 was equal to area (ha) of the first years home range (Lesage et al. 2000, Cambell et al. 2004). We estimated percent core area overlap in the same manner. Differences in home range and core area overlap between the age classes of male deer were compared using analysis of variance in SAS (SAS Institute 1989).

Center of Activity Shifts

We transferred annual home range and core area polygons and point coverages to ArcGIS 9.2 and deleted all points outside of their respective polygons. We used the resulting point coverages to test the null hypothesis that deer locations for home range and core use areas did not differ in center of activity between years. Activity centers were defined as the bivariate median (Berry et al. 1984) for locations within each deer's annual home range. To examine center of activity shifts, we calculated the distance (m) between bivariate median centers of consecutive home range or core area distributions. Mean center of activity shifts were considered significant where they exceeded a threshold value. The threshold value was calculated by multiplying the mean dispersion (mean distance between center of activity and each location) for locations from year 1 by 0.5 (Plowman et al. 2006). We compared dispersion estimates for consecutive home range areas for each deer using a paired t-test in SAS (SAS Institute 1989). Differences in home range dispersion between the age classes of male deer were compared using analysis of variance in SAS (SAS Institute 1989). We estimated annual differences in core area center of activity shifts in the same manner.

RESULTS

Home Range and Core Area Size - Mean ± SE hectares

Male white-tailed exhibited few differences in home range or core area size by year or age class; however, mean core-use area tended to increase ($T_{17} = 1.97$; $P = 0.065$; Table 1) from year 1 (75 ± 13) to year 2 (104 ± 15) for juvenile males. Mature males also tended to exhibit larger (129 ± 36; $F_{2,\,46} = 1.55$; $P = 0.107$) mean core areas during the first year of the study than did juvenile males. The age classes did not differ in home range size ($F_{2,\,46} = 0.77$; $P \geq 0.285$) or core-use area ($F_{2,\,46} = 0.11$; $P \geq 0.680$) during the second year of the study.

Home Range and Core Area Overlap

Male deer exhibited a high degree of overlap between sequential home range boundaries, ranging from a mean of 58% for mature males to 68% for adult males; however, core area overlap was substantially less, ranging from 36% for mature males to 50% for juveniles (Table 2). Mean home range overlap ($F_{2, 46} = 1.04$; $P \geq 0.156$) and mean core area overlap ($F_{2, 46} = 0.72$; $P \geq 0.238$) did not differ by age class (Table 2).

Center of Activity Shifts: Home Range - (Mean ± SE meters)

At the home range scale, mean (630 ± 138) center of activity shifts tended to exceed mean (394 ± 30) threshold value for juvenile ($T_{17} = 1.82$; $P = 0.086$; Table 3) males. Adult males followed suite with mean (793 ± 131) center of activity shifts tending to exceed mean threshold value (460 ± 46; $T_{19} = 2.01$; $P = 0.058$); however, mean (892 ± 198) center of activity shifts did not differ ($T_8 = 0.47$; $P = 0.650$) from mean (499 ± 67) threshold values for mature males. Additionally, mean center of activity shifts did not strongly differ ($F_{2, 46} = 1.04$; $P \geq 0.156$) by age class.

Center of Activity Shifts: Core Use - (Mean ± SE meters)

At the core-use scale, mean (810 ± 199) center of activity shifts surpassed mean (272 ± 65) threshold values for juvenile ($T_{17} = 2.63$; $P = 0.002$; Table 4) males. Adult males were similar with mean (1,045 ± 235) center of activity shifts exceeding mean threshold value (309 ± 46; $T_{19} = 3.52$; $P = 0.018$) males. Mean (742 ± 299) center of activity shifts also tended to exceed ($T_8 = 1.77$; $P = 0.116$) mean (299 ± 71) threshold vales for mature males, but the difference was not strongly supported by the data. Mean center of activity shifts; however, did not differ ($F_{2, 46} = 1.04$; $P \geq 0.156$) by age class.

DISCUSSION

We examined spatial fidelity among three age classes of sexually mature male white-tailed deer via annual home range overlap and center of activity shifts. Regardless of age class, male deer maintained home ranges consistent in size (Table 1) and with considerable overlap between years (Table 2). Previous studies similarly reported a high percentage of overlap between annual home range boundaries for individual adult males (Tierson et al. 1985; Lesage et al. 2000; Webb et al. 2007), suggesting that bucks do not shift their home range areas among years. The extent of landscape use throughout the lifetime of adult males has been defined by such overlap (Webb et al. 2007), having implications for deer management; however, we detected shifts in deer locations on an annual basis that were not reflected by spatial overlap between corresponding home range boundaries. Independent of age class, male deer exhibited far smaller core areas and far less overlap between annual core area boundaries, which was reflected in the magnitude and significance of center of activity shifts. Resources are thought to be more dependable within core areas (Leuthold 1977); however, if resources are concentrated and foraging activities result in depletion of those food sources, deer may shift space use to include areas with a greater abundance of forage. Given the small size of core-use areas exhibited by males in this study and the likelihood that deer spend most of their time within core areas (Burt 1943; Ewer 1968), major shifts in central tendency at the core-use scale likely influenced the spatial dynamics of individual home ranges.

Results suggest that following natal dispersal, male deer form small core-use areas that vary in location dependent on the temporal fluctuation in availability of resources. Additionally, lack of spatial fidelity at the core-use scale likely influences shifts in the little used peripheral areas within deer home ranges; however, where home ranges are much larger than core-areas, the magnitude of shifts in central tendency at the core-use scale may not be great enough to alter home range overlap. Furthermore, our results do not support the prediction that home range formation extends into adulthood for juvenile males. The age classes varied little in home range size and core area as well as annual overlap at both scales. Mature males did not exhibit significant shifts in central tendency between the years that they were monitored; however, this is likely a result of a low sample size as only nine mature males were present during both years of the study.

Studies involving the manipulation of habitat within deer core areas may shed additional light on influential factors contributing to the annual shifts in central tendency seen here. Additionally, models which incorporate the internal dynamics in space use exhibited by male deer over time may be beneficial in determining the effective extent of landscape use over the lifetime of adult bucks.

MANAGEMENT IMPLICATIONS

Managers should be skeptical of models which predict the size of properties needed to retain adult males throughout their lifetime based solely on temporal overlap at the home range scale. While these models may provide an indication of susceptibility of adult males to harvest on neighboring properties, dynamics of space use at the core-use scale are likely more influential in the retention of male deer over time. Within areas heavily used by male deer, attention should be paid to the concentration and quality of deer forage as better predictors of deer retention.

LITERATURE CITED

Aycrigg, J. L., and W. F. Porter. 1997. Sociospatial dynamics of white-tailed deer in the central Adiiondack Mountains, New York. Journal of Mammalogy 78:468-482.

Berry, K. J., P. W. Mielke, and K. L. Kvamme. 1984. Efficient permutation procedures for analysis of artifact distributions. Pages. 54–74. in H. Hietala editor. Intrasite spatial analysis in archaeology. Cambridge University Press, Cambridge, Massachusetts, USA.

Beyer, D. E., Jr., and J. B. Haufler. 1994. Diurnal versus 24-hour sampling of habitat use. Journal of Wildlife Management 58:178-180.

Bideau, E., J. F. Gerard, J. P. Vincent, and M. L. Maublanc. 1993. Effects of age and sex on space occupation by European Roe Deer. Journal of Mammalogy 74:745-751.

Burt, W. H. 1943. Territoriality and home range concepts as applied to mammals. Journal of Mammalogy 24:346–352.

Cambell, T. A., B. R. Laseter, W. M. Ford, and K. V. Miller. 2004. Feasibility of localized management to control white-tailed deer in forest regeneration areas. Wildlife Society Bulletin 32:1124-1131.

Cederlund, G. N., and H. Okarma. 1988. Home range and habitat use of adult female moose. Journal of Wildlife Management 52:336-343.

Ditchkoff, S. S., E. R. Welch, Jr., R. L. Lochmiller, R. E. Masters, W. E. Starry, and W. C. Dinkines. 1996. Wounding rates of white-tailed deer with traditional archery equipment. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 52:244-248.

Ewer, R. F. 1968. Ethology of mammals. Logos Press, London, England.

Grund, M. D., J. B. McAninch, and E. P. Wiggers. 2002. Seasonal movements and habitat use of female white-tailed deer associated with an urban park. Journal of Wildlife Management 66:123-130.

Hooge, P. N., and B. Eichenlaub. 1997. Animal movement extension to Arc-view. Version 1.1. Alaska Biological Center, U.S. Geological Survey, Anchorage, USA.

Inglis, J. M., R. E. Hood, B. A. Brown, and C. A. DeYoung. 1979. Home range of white-tailed deer in Texas coastal prairie brushland. Journal of Mammalogy 60:377-389.

Leach, R. H., and W. D. Edge. 1994. Summer home range and habitat selection by white-tailed deer in the Swan Valley, Montana. Northwest Science 68:31-36.

Lesage, L., M. Creˆte, J. Huot, A. Dumont, and J. P. Ouellet. 2000. Seasonal home range size and philopatry in two northern white-tailed deer populations. Canadian Journal of Zoology 78:1930–1940.

Leuthold, W. 1977. African Ungulates: a comparative review of their ethology and behavioral ecology. Springer-Verlag Berlin Heidelberg, Germany.

Loft, E. R., J. G. Kie, and J. W. Menke. 1993. Grazing in the Sierra Nevada: home range and space use patterns of mule deer as influenced by cattle. California Fish and Game 79:145-166.

Logan, K. A., and L. L. Sweanor. 2001. Desert puma: evolutionary ecology and conservation of an enduring carnivore. Island Press, Washington D.C., USA.

Marchinton, R. L., and D. H. Hirth. 1984. Behavior. Pages 129–168 in L. K. Halls, editor. White-tailed deer ecology and management. Stackpole Books, Harrisburg, Pennsylvania, USA.

Marchinton, R.L., K.V. Miller, R.J. Hamilton, and D.C. Guynn. 1990. Quality deer management: biological and social impacts on the herd. Pages 7-15 in C. Kyser, D. C. Sisson, and J. L. Landers, editors. Proceedings of the Tall Timbers Game Bird Seminar. Tallahassee, Florida, USA.

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

Miller, K. V., and R. L. Marchinton. 1995. Quality white-tails: the how and why of quality deer management. Stackpole, Mechanicsburg, Pennsylvania, USA.

Nelson, M. E., and L. D. Mech. 1984. Home-range formation and dispersal of deer in northeastern Minnesota. Journal of Mammalogy 65:567-575.

Nelson, M. E. 1993. Natal dispersal and gene flow in white-tailed deer in northeastern Minnesota. Journal of Mammalogy 74:316-322.

Porter, W. F., N. E. Mathews, H. B. Underwood, R. W. Sage, and D. F. Behrend. 1991. Social organization in deer: implications for localized management. Environmental Management 15:809-814.

Plowman, B. W., L. M. Conner, M. J. Chamberlain, B. D. Leopold, and L. W. Burger. 2006. Annual dynamics of bobcat (*Lynx rufus*) home range and core use areas in Mississippi. American Midland Naturalist 156:386-393.

SAS Institute. 1989. SAS/STAT user's guide. Version 6. Fourth edition. SAS Institute, INC, Cary, North Carolina, USA.

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

Seaman, D. E., J. J. Millspaugh, B. J. Kernohan, G. C.Brundige, K. J. Raedeke, and R. A. Gitzen. 1999. Effects of sample size on kernel home range estimators. Journal of Wildlife Management 63:739–747.

Shields, W. M. 1987. Dispersal and mating systems: investigating their causal connections. Pages 3-24 in B. D. Chepko-Sade and Z. T. Halpin, editors. Mammalian dispersal patterns: the effects of social structure on population genetics. University of Chicago Press, Chicago, Illinois, USA.

Tierson, W. C., G. F. Mattfeld., R. W. Sage, Jr., and D. F. Behrend. 1985. Seasonal movements and home ranges of white-tailed deer in the Adirondacks. Journal of Wildlife Management 49:760-769.

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

White, G. C., and R. A. Garrott. 1990. Analysis of wildlife radio-tracking data. Academic Press, San Diego, USA.

Table 1. Mean[a] home range size (ha) (95% fixed kernel estimation) and core area (50%) (ha) for juvenile (1.5-2.5 years of age), adult (3.5-4.5 years of age), and mature ($\geq$ 5.5 years of age) male white-tailed deer in Southeastern Oklahoma, USA.

		Home range area (ha)					**Core-use area (ha)**				
		Year 1		**Year 2**			**Year 1**		**Year 2**		
Age class	***n***	$\bar{x}$	**SE**	$\bar{x}$	**SE**	***P*[b]**	$\bar{x}$	**SE**	$\bar{x}$	**SE**	***P***
juvenile	18	506[a]	72	588[a]	73	0.197	75[a]	13	104[a]	15	0.065
adult	20	645[a]	100	713[a]	106	0.428	108[a]	19	113[a]	21	0.686
mature	9	764[a]	202	542[a]	109	0.131	129[a]	36	100[a]	21	0.394

Table 1. Continued.

[a] Means (ha) and standard errors (ha) are given for years 1 and 2 of the study. [b] *P*-values are based on paired t-tests for differences between years of the study within each age class ($\alpha > 0.05$). Means with differing letters indicate difference between age classes within study years ($\alpha > 0.05$).

Table 2. Percent overlap [a] for consecutive annual home ranges[b] and core areas (95%, 50% fixed kernel estimation), for juvenile (1.5-2.5 years of age), adult (3.5-4.5 years of age), and mature ($\geq$ 5.5 years of age) male white-tailed deer in Southeastern Oklahoma, USA.

		Home range overlap (%)				**Core-use area overlap (%)**			
Age-class	***n***	$\bar{x}$	**SE**	**Min**	**Max**	$\bar{x}$	**SE**	**Min**	**Max**
Juvenile	18	65.0[a]	3.4	39.2	90.0	50.0[a]	8.0	0.0	100.0
Adult	20	68.0[a]	4.2	36.1	100.0	45.1[a]	6.2	0.0	92.4
Mature	9	58.0[a]	6.0	14.0	69.0	36.0[a]	5.5	13.7	68.9

Table 2. Continued.

[a] Home range overlap was calculated as $100*[OV/A_1]$, where *OV* was the area (ha) of overlap between consecutive home ranges.

[b] Annual home ranges and core areas were estimated for 1 October to 30 September. Means with separate letters were significantly different ($P > 0.05$).

Table 3. Threshold values[a] of locations and distance (m[b]) between consecutive centers of activity[c] for annual home ranges[d]. Means are given for juvenile (≤ 2.5 years of age) and adult (3.5-4.5 years of age), and mature (≥ 5.5 years of age) male white-tailed deer in Southeastern Oklahoma, USA.

		Threshold value (m)				**Center of activity shifts (m)**				
Age class	***n***	$\bar{x}$	**SE**	**Min**	**Max**	$\bar{x}$	**SE**	**Min**	**Max**	***P***
Juvenile	18	394	30	212	707	630[a]	138	18	2,082	0.086
Adult	20	460	46	201	994	793[a]	194	131	3,995	0.058
Mature	9	499	67	274	913	892[a]	198	112	2,029	0.650

Table 3. Continued.

[a] Threshold values were calculated as the mean distance between locations within 95% home range polygons and the bivariate median of those locations multiplied by 0.5. [b] Means, standard errors, and minimum and maximum values are given in meters. [c] Home range centers were calculated as the bivariate median for locations within 95% home range polygons. [d] Annual home range areas were estimated for 1 October to 30 September. Means with separate letters were significantly different ($P > 0.05$). P-values are given for paired t-test comparison of threshold values and center of activity shifts.

Table 4. Threshold values[a] of locations and distance (m[b]) between consecutive centers of activity[c] for annual core-use areas[d]. Means are given for juvenile (≤ 2.5 years of age), adult (3.5-4.5 years of age), and mature (≥ 5.5 years of age) male white-tailed deer in Southeastern Oklahoma, USA.

		Threshold value (m)				**Center of activity shifts (m)**				
Age-class	***n***	$\bar{x}$	**SE**	**Min**	**Max**	$\bar{x}$	**SE**	**Min**	**Max**	***p***
Juvenile	18	272	65	13	939	810[a]	199	47	2,616	0.018
Adult	20	309	46	74	931	1,045[a]	235	182	4,219	0.002
Mature	9	299	71	88	717	742[a]	227	118	2,360	0.116

Table 4. Continued.

[a] Threshold values were calculated as the mean distance between locations within 50% core area polygons and the bivariate median of those locations multiplied by 0.5. [b] Means, standard errors, and minimum and maximum values are given in meters. [c] Core area centers were calculated as the bivariate median for locations within 50% core area polygons. [d] Annual core-use areas were estimated for 1 October to 30 September. Means with separate letters were significantly different ($P < 0.05$). P-values are given for paired t-tests for the comparison of threshold values and center of activity shifts.

III. SPATIAL HETEROGENEITY AT VARYING SCALES: EFFECTS ON HOME RANGE SIZE IN MALE WHITE-TAILED DEER

ABSTRACT

The spatial arrangement of landscape features and their relation to home range size among white-tailed deer has yet to be examined. Spatial heterogeneity is thought to have vital effects on many ecosystem processes and can be observed at multiple spatial extents or scales. We describe relationships between a suite of landscape metrics, measured within varying radii (250, 500, 1000, 2000 and 3000 m) of home range centers, and home range sizes of male white-tailed deer (*n* = 72) in southeastern Oklahoma. We additionally tested the hypothesis that a combination of landscape metrics, representing spatial heterogeneity, can explain variation in home range size among male white-tailed deer. Deer exhibited mean home ranges of 643 ha and mean core areas of 112 ha. Results suggest that where habitat patches are small, highly diverse, and evenly distributed, male white-tailed deer have small home ranges. Results also indicate that home ranges are small where edge density is high. Our best model of spatial heterogeneity explained 28% of the variability in home ranges size at the 1000 meter scale, indicating that male deer perceive their environment at a spatial scale intermediate between mean home range and core-use areas. These results highlight the importance of considering core areas when space by white-tailed deer is of interest.

Introduction

Among many species, variation in home range size has been related to numerous factors including trophic level (Harestad and Bunnell 1979), reproductive status (Bertrand et al. 1996), body size (Swihart et al. 1988), season (Nicholson et al. 1997), subspecies (Anderson and Wallmo 1984), and intra- (Riley and Dood 1984) and inter-specific competition (Loft et al. 1993). Home range size in white-tailed deer (*Odocoileus virginianus*) has been related to factors including population density (Lesage et al. 2000), climate (Marchinton and Hirth 1984), forage and water availability (Severinhaus and Cheatum 1956; Byford 1970*a* ; Verme 1973; Vercauteran and Hygnstrom 1998), age (Hirth 1977; Nelson and Mech 1984; Leach and Edge 1994; Aycrigg and Porter 1997; Lesage 2000; Webb et al. 2007) and sex (Olson 1938, Michael 1965; Marchinton and Hirth 1984). Despite numerous investigations of home range size among white-tailed deer, mechanisms behind such varied uses of habitats across landscapes are poorly understood (Nicholson et al. 1997). Spatial heterogeneity, defined as complexity and variability in the structural properties of ecological systems (Li and Reynolds 1994), has recently been shown to influence home range size in mule deer (*Odocoileus hemionus*; Kie at al. 2002) and axis deer (*Axis axis*; Moe and Wegge 1994). Spatial heterogeneity is thought to have vital effects on many ecosystem processes (Turner and Gardner 1991), which include predator–prey relationships (Pierce et al. 2000), population genetics (Good et al. 1997), epidemiology (Lloyd and May 1996), host–parasite relationships (Ives 1995), interspecific competition (Pacala and Roughgarden 1982) and population dynamics (Henein et al. 1998). However, the spatial arrangement of landscape features and their relation to home range size among white-tailed deer has yet to be examined.

Spatial heterogeneity can be observed at multiple spatial extents or scales (Kie et al. 2002), however, many ecological phenomena can be scale dependent (Saab 1999). In order to determine how the size and configuration of habitat patches affects the distribution of animals, we must develop an understanding of how animals perceive and respond to variation in scale within their environments (Buechner 1989; Turner et al. 1989; Wiens 1989; Wiens and Milne 1989; Kie et al. 2002). Additionally, failing to select the correct scale for analysis of spatial data can lead to misinterpretations of biological data (Wiens 1989, Powell 1994, Bowyer et al. 1996). Consequently, the spatial extent at which spatial heterogeneity is defined and measured must be carefully considered (Kie et al. 2002).

In California, Kie et al. (2002) described relationships between numerous landscape metrics measured at four increasing spatial scales and the size of home ranges of female mule deer and black-tailed deer (*Odocoileus hemionus*), while additionally testing the hypothesis that a combination of landscape metrics representing spatial heterogeneity could explain much of the variability in home range size among deer. They found small home range size among female mule deer to be closely associated with fine-grained habitats (defined as those with an abundance of edge, irregularly-shaped habitat patches, and a high fractal dimension), which was similar to findings among axis deer (Moe and Wegge 1994). White-tailed deer typically exhibit smaller home ranges than mule deer, particularly in the southeastern United States (Marchinton and Hirth

1984). This may be in relation to a greater abundance of fine-grained habitats in the Southeast; however, variability in home range size among white-tailed deer based on these components has not been examined.

Kie at al. (2002) also found home ranges to be large where edge density was minimal and where similar habitat patches were poorly dispersed and interspersed. As a result of common usage, more so than scientific scrutiny, white-tailed deer are broadly considered to be an "edge species" (Guthery and Bingham 1992; Tufto et al. 1996), and while Beier and McCullough (1990) suggested that small home range size in their study may have been a result of high interspersion of habitat types, no studies have specifically examined the relationship between these components and home range size in white-tailed deer.

Kie et al. (2002) additionally showed that a suite of landscape metrics, measured within a 2000 meter radius (1257 ha) of home range centers, explained 57% of the variability in home range size among female mule deer, indicating that characterization of landscape structure is more complex than simple interpretations of individual metrics. Their results also suggest that deer perceive the environment at scales greater than what they choose as a home range, as 94% of deer within their study inhabited home ranges well within this 2000 meter radius.

We follow the methodology of Kie et al. (2002) in describing relationships between a suite of landscape metrics, measured at increasing spatial scales, and home range size in male white-tailed deer at a study site in southeastern Oklahoma. Kie et al. (2002) hypothesized that deer may perceive their environment at a scale greater than

2000 meters from the center of their home range; however, they were unable to test this hypothesis due to the limited size of their study areas. We test this hypothesis by broadening our analysis to a 3000 meter scale, predicating that male deer, as the dispersing sex (Nixon et al. 1991), would perceive spatial heterogeneity at a scale greater than females. We additionally predicted that home range size would be smaller where landscapes were composed of fine-grained habitats, and where edge density and interspersion of habitat patches was high.

Study area

We collected data from the McAlester Army Ammunition Plant (McAAP) in southeastern Oklahoma, an 18,212 ha area that was operated under a quality deer management program since 1989 (Ditchkoff et al. 1996). McAAP was an ammunition storage and manufacturing plant, operated by the United States Department of Defense, where public access was limited (Ditchkoff et al. 1996). Deer density at McAAP was estimated at 1 deer/ 6.67 ha, with an approximate sex ratio of 1 buck/1.5 does. Forest cover at McAAP consisted of post oak (*Quercus stellata*) and blackjack oak (*Quercus marilandica*) uplands, interspersed with riparian drainages of water oak (*Quercus nigra*; Table 1). In the uplands, post oak and blackjack oak formed plant associations with poison ivy (*Toxicodendrus radicans*), buckbrush (*Ceanothus cuneatus*), and greenbriar (*Smilax bona-nox*). In riparian areas, spotted red oak (*Quercus shumardii*) and water oak combined with broadleaf uniola (*Chasmanthium latifolium*), and greenbriar.

Methods

Capture and handling

Fifty-two male (≥1.5 years of age) white-tailed deer were captured using drop-nets between December 1994 and January 1997 on food plots baited with persimmons and whole corn. Deer were not sedated after capture or during handling. Captured deer were aged by tooth wear and eruption (Severinghaus 1949) and fitted with numbered ear tags and a radiocollar equipped with a 4-hour mortality sensor (Advanced Telemetry Systems; Isanti, Minnesota, USA)

Data collection and radiotelemetry

From October-January of each year deer were located 3-4 times each week and once weekly from January-September. To reduce sampling bias, locations were taken at random throughout each 24 hour period (Beyer and Haufler 1994). A 3-element Yagi antenna and portable receiver were used to obtain ground-based telemetry readings from 285 permanent telemetry stations. Universal Transverse Mercator (UTM) coordinates were obtained for each telemetry station using differentially corrected global positioning system data (Geoexplorer; Trimble Navigation, Sunnydale, California). UTM coordinates for each deer location were estimated using a modified White and Garrott

(1990) program written using SAS with a standard deviation of 2.49 degrees.

Home-range analysis

We quantified 95% home ranges and 50% core areas by fixed kernel analysis with least squares cross validation smoothing (Seaman et al. 1999) for deer with ≥20 locations using the Animal Movement Extension (Hooge and Eichenlaub 1997) in ArcView 3.2 (ArcView 3.2; Redlands, California).

Landscape classification

A thirty meter resolution landsat image, multi-resolution merged into a habitat coverage of the state of Oklahoma, (USGS Biological Resources Division Gap Analysis Program; Scott et al. 1996) was clipped to the extent of the study area (ArcGIS 9.2; Redlands, California), and reclassified based on percent canopy closure (Table 2), defined by National Vegetation Classification System (NVCS) guidelines.

Landscape analysis

We delineated radii at 5 increasing scales (250, 500, 1000, 2000, and 3000 m) from the center (estimated as the mean *X* and *Y* coordinates) of deer home ranges. The corresponding areas within each scale were 20, 79, 314, 1256, and 2826 ha, respectively. At each scale, we used the raster version of FRAGSTATS (McGarigal and Marks 1995), provided in the Patch Analyst extension (Rempel and Carr 2008) for ArcGIS 9.2, to quantify 35 landscape metrics in relation to six categories related to spatial heterogeneity; (1) core area, (2) patch shape, (3) contagion/interspersion, (4) isolation/proximity, (5) area/density/edge, and (6) diversity (McGarigal and Marks 1995). The eventual goal of defining spatial heterogeneity across landscapes is to establish relationships between these measure of landscape structure and accompanying ecological processes, such as home range size (Li and Reynolds 1994).

Statistical analysis

Following the methodology of Kie et al. (2002), we selected metrics to represent the six components of spatial heterogeneity described by McGarigal and Marks (1995) as individual variables in a multiple regression model with the natural log of home range size for each male deer as the dependent variable. Prior to selecting individual variables from each category, we eliminated 16 metrics from consideration as many landscape metrics offered in FRAGSTATS are simple analogues of each other, or provide absolute or relative measures of the same component (McGarigal and Marks 1995). From the remaining 19 metrics, individual variables were chosen based on the strength of simple Pearson correlation coefficients (*r*) among landscape metrics and the natural log of (n = 72) male white-tailed deer home range sizes, using a step-down Bonferroni adjustment for experiment-wide error rate (Huang and Hsu 2007). We used the natural log of home ranges as we found many landscape metrics to be nonlinearly related to home range size (Kie et al. 2002).

In multiple regression models tested at each spatial scale, patch diversity was represented by a modified Simpson's evenness index (MSIEI); patch proximity by mean nearest neighbor (MNN); patch area by mean patch size (MPS); patch edge by edge density (ED); and patch shape by mean patch fractal dimension (MPFD). We were unable to include a metric related to core area within our models as we found core area metrics to be closely associated with edge density. We used multiple coefficients of variation (R^2) and Akaike's Information Criterion (AIC) to examine model fit and overall explanatory power (Burnham and Anderson 1998), and additionally examined variation-inflation factors to prevent multicollinearity from biasing our multiple regressions (SAS Institute 2003). To test model validity, we created a null model at the 1000-m scale by randomly assigning home range sizes to our suite of landscape metrics. We then reanalyzed our data.

Results

Home range size averaged 643 ± 59 ha for male deer within the study, while core areas average 112 ± 13 ha. Increasingly throughout the three smaller spatial scales, where habitat diversity (MSIEI, modified Simpson's evenness index: range 0- ∞, value increases as the number of different patch types increase and the area among patch types becomes more equal) and abundance of edge (ED: m/100 ha) was high, the natural log of home range size (hereafter simply home range size) was small (Table 3). Conversely, where mean patch size (MPS: ha) was large, home ranges were also large. These relationships, however, began to decline at the 2000 meter scale and tended to not be significant at the

3000 meter scale. Metrics related to patch shape (MSI, mean shape index; MPFD, mean patch fractal dimension), interspersion (IJI), and proximity (MNN, mean nearest neighbor: m) were not strongly correlated with home range size at any of the spatial scales.

Models of habitat heterogeneity at each scale varied in their ability to explain variation in home range size; however, overall model fit and explanatory power did not increase or decrease linearly throughout the five spatial scales (Table 4). Models increased in explanatory power from the 250 meter scale (AIC = -65.74; $R^2 = 0.14$; $P = 0.062$) to peak at the 1000 meter scale (AIC = -78.55; $R^2 = 0.28$; $P < 0.001$), and declined thereafter at the two largest scales. The null model created by randomly assigning home range sizes to the suite of landscape metrics at the 1000 meter scale was not significant ($P = 0.498$; $R^2 = 0.06$; AIC = -59.16).

Discussion

Fine-grained habitats, defined as those with small irregularly-shaped patches, and a high fractal dimension, have been shown to be correlated with small home range size in mule deer (Kie et al. 2002) and axis deer (*Axis axis*; Moe and Wegge 1994). We predicted home range size in male white-tailed would be similarly related to fine-grained habitats. Our results suggest this to partially be true, as at most spatial scales home range size was large where mean patch size (MPS) was large; however, the shape of patches (MSI) and their fractal dimension (MPFD) was not strongly correlated with home range size at any spatial scale. In addition, contrary to our prediction, home range size was not strongly correlated with interspersion (IJI) of habitat types, although home range size was small where habitat patches were diverse and evenly distributed (MSIEI), with the key difference between the metrics being the number of diverse habitats present within the landscape. We interpret these results to indicate that where diversity of habitat patches is low, despite high interspersion, or where patches are large, deer must travel further to meet their life requisites, similar to where habitat patches are clumped in distribution or poorly interspersed. Conversely, where habitat patches are small, highly diverse, and evenly distributed, deer do not have to move far when disturbed or when resources become depleted. Accordingly, where densities of white-tailed deer exceed desirable levels (e.g., interfering with forest regeneration plans or contributing to vehicle collisions), densities may be lowered by providing large blocks of homogeneous habitat.

From the time when Leopold (1951) first illustrated the concept of edge, it has become a central tenet of wildlife ecology, more so out of common usage rather than scientific scrutiny (Guthery and Bingham 1992). This statement particularly holds true in the case of white-tailed deer (Tufto et al. 1996). Our results indicate that deer exhibit smaller home ranges where edge density is high; however, we suggest that this may not always be the case for populations of white-tailed deer, as a high amount of edge does not necessarily equate to habitat quality, especially where some habitats are of little importance to deer (i.e old forest). The usefulness of habitats for deer should be taken into account before the assumption is made that landscapes with high amounts of edge will benefit managed populations.

Kie et al. (2002) hypothesized that female mule deer may perceive spatial heterogeneity at scales broader than 2000 meters from the center of their home ranges, based on an increasing trend in the ability of their models of spatial heterogeneity to explain variation in home range size with spatial scale. Our results, however, are not consistent with this hypothesis, as our best model explained a maximum of 28% of the variability in home range sizes of males at the 1000 meter scale. The 1000 meter scale represents an area of 314 ha, while the mean home range size for deer within the study was 643 ha with mean core area being 122 ha. This suggests that male white-tailed deer may perceive potential habitats at scales intermediate between what they eventually choose as a home range and what they choose as a core area. It is generally accepted that the area within an animal's home range is not used equally (Bert 1943), with the assumption that core-use areas contain more dependable resources than less frequently used peripheral areas within the home range (Leuthold 1977). Likewise, Holtfreter et al. (2008) found that shifts in central tendency at the core-use scale, among male white-tailed deer, influenced the spatial dynamics of individual home ranges, more so than shifts at the home range scale. Our results suggest that deer may choose core areas based on their perception of spatial heterogeneity at finer scales than home range size dictates, indicating that analysis of 95% home range areas may not represent the ecology of the species.

If deer are unable to perceive spatial heterogeneity at scales equivalent to home range areas, the analysis of habitat selection within the home range may be biased by overestimating the spatial extent at which deer perceive their environment and thus the availability of habitat to deer. Rather, deer may be establishing home ranges in a fashion that allows them the flexibility to shift their core use areas as resources or needs change over time. If this is the case, it would suggest that an improved understanding of how deer perceive the environment would require incorporating core use data into analyses. We suggest that when space use by white-tailed deer is of interest in management objectives or research studies, either the primary scale for consideration should be core areas or analyses should incorporate both home range and core area data.

Additional research is needed to determine if land-management practices that influence landscape characteristics have an effect on home range size in white-tailed deer. Further analysis is needed to clarify the relationship between deer home range size and spatial heterogeneity at varying spatial scales. Specifically, landscape pattern analysis may be useful in identifying inherent relationships between spatial heterogeneity at various scales. The use of resource selection functions to quantify habitat selection at increasing spatial scales may also provide additional insight into variation in the size of deer home ranges.

References

Anderson AE, Wallmo OC (1984) Odocoileus hemionus. Mammalian Species 219:1–9

Aycrigg JL, Porter, WF (1997) Sociospatial dynamics of white-tailed deer in the central Adiiondack Mountains, New York. J Mammal 78: 468-482

Beier P, McCullough DR (1990) Factors influencing white-tailed deer activity patterns and habitat use. Wildlife Monogr 109:1–51

Bertrand MR, DeNicola AJ, Beissinger SR, Swihart RK (1996) Effects of parturition on home ranges and social affiliations of female white-tailed deer. J Wildl Manage 60:899–909

Beyer DE Jr, Haufler JB (1994) Diurnal versus 24-hour sampling of habitat use. J Wildl Manage 58:178-180

Buechner M (1989) Are small-scale landscape features important factors for field studies of small mammal dispersal sinks? Landscape Ecol 2:191–199

Byford JL (1970a) Movement responses of white-tailed deer to changing food supplies. Proc Annu Conf Southeast Assoc Fish and Wildl Agencies 23: 63-78

Burnham KP, Anderson DR (1998) Model selection and inference: a practical information-theoretical approach. Springer-Verlag, New York, New York

Burt WH (1943) Territoriality and home range concepts as applied to mammals. J Mammal 24:346–352

Ditchkoff SS, Welch ER Jr, Lochmiller RL, Lochmiller RE, Masters RE, Starry WE, Dinkines WC (1996) Wounding rates of white-tailed deer with traditional archery equipment. Proc Annu Conf Southeast Assoc Fish and Wildl Agencies 52: 244-248

Good SV, Williams DF, Ralls K, Fleischer RC (1997) Population structure of *Dipodomys ingens* (Heteromyidae): the role of spatial heterogeneity in maintaining genetic diversity. Evolution 51:1296–1310

Guthery FS, Bingham RL (1992) On Leopold's principle of edge. Wildl Soc Bull 20:340–344

Harestad AS, Bunnell FL (1979) Home range and body weight: a reevaluation. Ecology 60:389–402

Henein K, Wegner J, Merriam G (1998) Population effects of landscape model manipulation on two behaviourally different woodland small mammals. Oikos 81:168–186

Hirth DH (1977) Social behavior of white-tailed deer in relation to habitat. Wildlife Monogr 53

Holtfreter RW (2008) Spatial ecology of male white-tailed in the crosstimbers and prairies ecoregion. Thesis, Auburn University

Hooge PN, Eichenlaub B (1997) Animal movement extension to Arc-view. Version 1.1. Alaska Biological Center, U.S. Geological Survey, Anchorage, USA

Huang Y, Hsu JC (2007) Hochberg's step-up method: cutting corners off Holm's step-down method. Biometrics 94:965-975

Kie JG, Bowyer RT, Nicholson MC, Boroski BB, Loft ER (2001) Landscape heterogeneity at differing scales: effects on spatial distribution of mule deer. Ecology 83:530-544

Leach RH, Edge WD (1994) Summer home range and habitat selection by white-tailed deer in the Swan Valley, Montana. Northwest Sci 68:31-36

Leopold AS, Riney T, McCain R, Tevis L (1951) The Jawbone deer herd. California Department of Fish and Game, Game Bulletin 4:1–139

Lesage L, Crete M, Hout J, Dumont A, Ouellet J (2000) Seasonal home range size and philopatry in two northern white-tailed deer populations. Can J Zool 78: 1930-1940

Leuthold W (1977) African Ungulates: a comparative review of their ethology and behavioral ecology. Springer-Verlag Berlin Heidelberg, Germany

Li H, Reynolds JF (1994) A simulation experiment to quantify spatial heterogeneity in categorical maps. Ecology 75:2446–2455

Loft ER, Kie JG, Menke JW (1993) Grazing in the Sierra Nevada: home range and space use patterns of mule deer as influenced by cattle. California Fish and Game 79:145-166

Lloyd AL, May RM (1996) Spatial heterogeneity in epidemic models. J Theor Biol 179:1–11

Marchinton RL, Hirth DH (1984) Behavior. In: Halls LK (ed) White-tailed deer ecology and management. Stackpole Books, Harrisburg, Pennsylvania, pp 129–168

McGarigal K (2002) Landscape pattern metrics. In: El-Shaarawi AH, Piegorsch WW (eds) Encyclopedia of Environmentrics, vol 2. John Wiley & Sons, Sussex, pp 1135-1142

McGarigal K, Marks BJ (1995) FRAGSTATS: spatial pattern analysis program for quantifying landscape structure. USDA Forest Service GTR-PNW-GTR-351.NVCS

Michael ED (1965) Movements of white-tailed deer on the Welder Wildlife Refuge. J. Wildl. Manage. 29:44-52

Moe SR, Wegge P (1994) Spacing behaviour and habitat use of axis deer (*Axis axis*) in lowland Nepal. Can J Zool 72:1735–1744

Nicholson MC, Bowyer RT, Kie JG (1997) Habitat selection and survival of mule deer: tradeoffs associated with migration. J Mammal 78:483–504

Nixon CM, Hamsen LP, Brewer PA, Chelsvig JE (1991) Ecology of white-tailed deer in an intensively farmed region of Illinois. Wildlife Monogr 118

Olson HF 1(938) Deer tagging and population studies in Minesota. Trans. N. Amer. Wildl. Conf. 3:280-286

Pacala SW, Roughgarden J (1982) Spatial heterogeneity and interspecific competition. Theor Popul Biol 21:92–113

Pierce BM, Bleich VC, Bowyer RT (2000) Social organization of mountain lions: does a land-tenure system regulate population size? Ecology 81:1533–1543

Rempel RS, Carr AP (2008) Patch Analyst extension for ArcGIS 9.2: version 4. Available from http://flash.lakeheadu.ca/~rrempel/patch/index.html (accessed February 2007)

Riley SJ, Dood AR (1984) Summer movements, home range, habitat use, and behavior of mule deer fawns. J Wildl Manage 48:1302–1310

Saab V (1999) Importance of spatial scale to habitat use by breeding birds in riparian forests: a hierarchical analysis. Ecol Appl 9:135–151

SAS Institute (1993) SAS/STAT software: the genmod procedure, release 6.09. SAS Institute, INC, Cary, North Carolina

Scott JM, Tear TH, Davis FW (eds) (1996) Gap Analysis. A Landscape Approach to Biodiversity Planning. American Society for Photogrammetry and Remote Sensing, Bethesda, Maryland

Seaman DE, Millspaugh JJ, Kernohan BJ, Brundige GC, Raedeke KJ, Gitzen RA (1999) Effects of sample size on kernel home range estimators. J Wildl Manage 63:739–747

Severinghaus, CW (1949) Tooth development and wear as criteria for age in white-tailed deer. J Wildl Manage 13: 195-216

Severinghaus CW, Cheatum EL (1956) Life and times of the white-tailed deer. In: Taylor WP (ed) The deer of North America. Stackpole Books, Harrisburg, Pennsylvania, pp 57-186

Swihart RK, Slade NA, Bergstrom BJ (1988) Relating body size to the rate of home range use in mammals. Ecology 69:393–399

Tierson WC, Mattfeld GF, Sage RW Jr, Behrend DF (1985) Seasonal movements and home ranges of white-tailed deer in the Adirondacks. J Wildl Manage 49: 760-769

Tufto J, Andersen R, Linnell J (1996) Habitat use and ecological correlates of home range size in a small cervid: the roe deer. J Anim Ecol 65:715–724

Turner, MG (1989) Landscape ecology: the effect of pattern on process. Ann Rev Ecol Syst 20:171-197

Turner MG, O'Neill RV, Gardner RH, Milne BT (1989) Effects of changing spatial scale on the analysis of landscape pattern. Landscape Ecol 3:153–162

Turner MG, Gardner RH (1991) Quantitative methods in landscape ecology: the analysis and interpretation of landscape heterogeneity. Springer-Verlag, New York, New York

VerCauteren KC, Hygnstrom SE. (1998) Effects of agricultural activities and hunting on home ranges of female white-tailed deer. J Wildl Manage 62:280-2851

Verme LJ (1973) Movements of white-tailed deer in Upper Michigan. J. Wildl Manage 37: 545-552

Webb SL, Hewitt DG, Hellickson MW (2007) Scale of management for mature male white-tailed deer as influenced by home range and movements. J Wildl Manage 71:1507–1512

Wiens JA, Milne BT (1989) Scaling of 'landscapes' in landscape ecology, or, landscape ecology from a beetle's perspective. Landscape Ecol 3:87–96

White GC, Garrott RA (1990) Analysis of wildlife radio-tracking data. Academic Press, San Diego

Table 1. Reclassified habitat coverage for McAlester Army Ammunition Plant, Oklahoma (USGS GAP Analysis Program 2005) based on percent canopy closure according to National Vegetation Classification System (NVCS) guidelines.

Reclassification	**Original classifications**	**Species**
Forest	Shortleaf Pine - Oak Forest	*P. echinata, Quercus* spp.
	Oak - Pine Forests	*Quercus* spp., *P. echinata*
	Oak - Cedar Forests	*Quercus* spp., *J. virginiana*
	Eastern Crosstimbers	*Q. stellata*, *Q. marilandica*, *Carya texana, Q. velutina*
	Central Crosstimbers	*Q. stellata*, *Q. marilandica*, *Carya texana*
	East - Central Bottomland Forests	*Ulmus americana*, *Quercus shumardii*, *Celtis* spp.
Woodland	Eastern Red Cedar Woodland	*J. virginiana*
	Eastern Red Cedar - Oak Woodland	*J. virginiana*, *Quercus* spp.
	Oak Woodland	*Q. marilandica*, *Q. stellata*

Table 1. Continued.

Reclassification	Original classifications	Species
Savanna	Tallgrass Oak Savanna	*Andropogon gerardii*- *Sorghastrum nutans*- *Quercus* spp.
	Midgrass Oak Savanna	*Quercus* spp.- *Schizachyrium scoparium*
	Tallgrass Cedar Savanna	*Andropogon gerardii*- *Sorghastrum nutans*- *Juniperus virginana*
Prairie	Tallgrass Prairie	*Andropogon gerardii*, *Schizachyrium scoparium*, *Sorghastrum nutans*, *Panicum virgatum*
	Midgrass Prairie	*S. scoparium*, *B. curtipendula*
	Crop - Warm Season	n/a
	Introduced Pasture - Warm Season	n/a
Barren	Barren Ground	n/a
	Residential	n/a
	Industrial	n/a
Riparian	Riverine	n/a
	Lake/Reservoir	n/a
	Pond	n/a

Table 2. Area (ha) and overall percentage of habitat types reclassified by canopy coverage (NVCS) at McAlester Army Ammunition Plant, Oklahoma.

Habitat Type	**Percent canopy coverage**	**Area (ha)**	**Area (%)**
Forest	61 -100% (trees >5 m)	7,284	40
Woodland	26 - 60% (trees >5 m)	4,006	22
Savanna	>26% (0.5 - 5 m shrubs)	2,549	14
Prairie	<25% (trees or shrubs)	3,278	18
Barren	n/a	728	4
Riparian	n/a	364	2

Table 3. Pearson correlation coefficients (r) between selected landscape metrics measured at 5 increasing spatial scales from the center of male white-tailed deer (*Odocoileus virginianus*) home ranges and ln(home range size) (95% fixed-kernel analysis) in southeast Oklahoma.

			Spatial Scale				
Type	**Landscape Metric**	**Description (units)**	**250 m**	**500 m**	**1000 m**	**2000 m**	**3000 m**
Patch shape	MPFD	Mean patch fractal dimension	0.16	-0.17	0.01	-0.22	-0.16
	MSI	Mean shape index	-0.12	-.010	-0.00	-0.04	0.10
Proximity	MNN	Mean nearest neighbor (m)	0.01	0.23	0.22	0.23	-0.14
Edge	ED	Edge Density (m/ha)	-0.29	-0.34	-0.43*	-0.27	-0.01
Patch	MPS	Mean patch size (ha)	0.26	0.36	0.47*	0.30	0.07
Diversity	MSIEI	Modified Simpson's evenness index	-0.37*	-0.39*	-0.38*	-0.18	0.19
Interspersion	IJI	Interspersion/Juxtaposition index	-0.23	-0.12	-0.06	-0.09	0.27

* $P < 0.05$; following a step-down Bonferroni adjustment (Huang and Hsu 2007).

Table 4. Effects of scale on regression models of home range sizes ($n = 72$) in adult male white-tailed deer (*Odocoileus virginianus*) incorporating landscape metrics related to spatial heterogeneity, after McGarigal and Marks (1995) and Kie et al. (2002).

		^{a}MNN (m)		**^{b}MPFD**		**^{c}MSIEI**		**^{d}MPS (ha)**		**^{e}ED (m/100 ha)**	
Scale (m)	b_0	b_1	r^2	b_2	r^2	b_3	r^2	b_4	r^2	b_5	r^2
250	10.26	-0.0022^{ns}	0.00	-3.179^{ns}	0.02	-1.0207^{ns}	0.13	0.1088^{ns}	0.07	0.0010^{ns}	0.08
500	21.45	0.0029^{ns}	0.05	-15.060^{ns}	0.03	-0.4880^{ns}	0.15	0.4632^{ns}	0.13	0.0022^{ns}	0.12
1000	-19.62	-0.0057^{ns}	0.05	25.24^{ns}	0.00	-1.0700^{ns}	0.15	0.3439^{ns}	0.22	-0.0050^{ns}	0.19
2000	30.08	-0.0041^{ns}	0.05	-22.48^{ns}	0.05	0.1049^{ns}	0.03	-0.1021^{ns}	0.09	0.0286^{ns}	0.08
3000	21.17	-0.0474^{ns}	0.02	-17.13^{ns}	0.02	1.45^{ns}	0.04	1.57^{ns}	0.00	0.0069^{ns}	0.00

Table 4. Continued.

Scale (m)	***AIC***	**R^2**	***Overall P***
250	-65.74	0.14	0.062
500	-69.66	0.19	0.014
1000	-78.55	0.28	<0.001
2000	-63.15	0.11	0.151
3000	-65.51	0.14	0.067

Home ranges are from McAlester Army Ammunition Plant, Oklahoma. Regression coefficient (b_i) and coefficient of partial determination (r^2) are given for each landscape metric; Akaike's Information Criterion (*AIC*), coefficient of determination (R^2), and overall *P* value for the full model are given at each scale. * $P < 0.05$; "ns" indicates nonsignificance ($P \geq 0.05$).

[a] mean patch size [b] mean patch fractal dimension [c] modified Simpson's diversity index [d] mean nearest neighbor [e] edge density