INFLUENCE OF FORAGE QUALITY ON HOME RANGE SIZE OF WHITE-TAILED DEER

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Abstract: We examined the relationship between the nutritional quality of forages and home range sizes of 10 adult female white-tailed deer (*Odocoileus virginianus*) in pine (*Pinus* spp.) flatwoods habitat of northern Florida from September 1990 — August 1991. We collected samples of 3 browse species, common gallberry (*Ilex glabra*), lowbush blueberry (*Vaccinium myrsinites*), and greenbriar (*Smilax laurifolia*), monthly from the core areas of the annual home ranges of the deer for the determination of crude protein (CP) and phosphorus (P) content and *in vitro* organic matter digestibility. Monthly home ranges sizes were correlated positively with monthly CP when CP levels were below modeled threshold levels: September–December (maintenance) — 6%; January–April (gestation) — 8%; and May–August (lactation) — 12%. Conversely, for months when CP levels were above these threshold levels, monthly home range size was correlated negatively with respective monthly P levels. We conclude that home range size may be partially influenced by the relative nutritional quality of forages.

Key words: flatwoods, Florida, home range, nutrition, *Odocoileus virginianus*, white-tailed deer.

J. Wildl. Res. 2(1): 25–29, 1997

INTRODUCTION

Many biotic and abiotic factors have been advanced as influence on mammalian home range size (McNab 1963, Harestad and Bunnell 1979). However, few studies have documented empirically the relationships between home range size and specific environmental influences (but see Litvaitis et al. 1986, Bowers et al. 1990). Harestad and Bunnell (1979) suggested that seasonal fluctuations in food quality affect home range size. Herein, we report an attempt to verify this relationship for white-tailed deer (*Odocoileus virginianus*) in northern Florida. Deer in Florida differ from their more temperate counterparts in reproductive phenology (Richter and Labisky 1985), seasonal movements (Labisky et al. 1991, Fritzen 1992, Kilgo 1992), and population density and productivity (Harlow and Jones 1965, Richter and Labisky 1985). Deer populations in pine flatwoods (*Pinus* spp.) of northern Florida apparently are not limited by either forage quantity (Harlow 1959) or forage energy (Smith and Hunter 1978). However, the poor nutrient content of forages in flatwoods may stress deer during some seasons (Smith and Hunter 1978, Tanner and Terry 1982, Kilgo and Labisky 1995). Therefore, foraging efforts by deer in flatwoods should be directed at optimizing a nutrient mix (Nudds 1980).

Deer may adjust their foraging strategy in response to fluctuations in forage quality either by modifying use of space within the home range or by altering the size of home range. The purpose of this study was to determine the effects of fluctuations in forage quality on the sizes of home ranges of adult female white-tailed deer throughout an annual cycle. We hypothesized that home range sizes of adult does would increase as nutritional quality of forage in the core areas of home ranges decreased from peak levels (Robbins 1983). This increase in home range size was expected to continue until a low threshold level of crude protein was reached, below which intake would be reduced (Van Soest 1982) because nutrient requirements could not be met (Robbins 1983). With reduced intake, home range size (viewed as an expression of foraging effort) also was expected to be reduced (Robbins 1983). Conversely, deer movements were expected to increase with the resumption of plant growth in spring. Thus, when nutrient levels were above the hypothesized crude protein threshold, correlation between home range size and nutrient level was expected to be negative; when nutrient levels were below threshold, correlation was expected to be positive.

Funding was provided by the Florida Game and Fresh Water Fish Commission, the United States Forest Service, and the University of Florida. D.E. Fritzen assisted in many phases of the research. L.E. Sollenberger and R. Fethiere conducted forage quality analysis. A. Ghosh and K.M. Portier provided advice on statistical analyses. B.R. Chapman, C.N. Huegel, S.R. Humphrey, K.V. Miller, G.W. Tanner, and R.J. Warren reviewed earlier drafts of the manuscript. J.W. Ault, C.T. Lee, and S.K. Stafford provided assistance in capturing deer and in expediting field logistics. This research was approved by the University of Florida Institutional Animal Care and Use Committee (Project No. 7239). This paper is a contribution (Journal Series R–02904) of the Florida Agric. Exp. Station, Gainesville.

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STUDY AREA

The study was conducted in the 63,631-ha Osceola National Forest (ONF), located in Baker and Columbia counties of northern Florida. Mean annual temperature and rainfall were 21.0°C and 146.8 cm, respectively (National Oceanic and Atmospheric Administration 1991). The vegetation consisted of pine flatwoods (65%), dominated by longleaf (*Pinus palustris*) and slash pine (*P. elliottii* var. *elliottii*), and interspersed swamps (35%). Saw-palmetto (*Serenoa repens*) and common gallberry (*Ilex glabra*) dominated the flatwoods understory (Avers and Bracy 1979). Pinelands were prescribed-burned (Mannan et al. 1994) at intervals of 3–5 years. The swamps were of two types: mixed bay (15%) and cypress (*Taxodium* spp.) — black gum (*Nyssa sylvatica* var. *sylvatica* and *N.s.* var. *biflora*; 20%). Dominant tree species in mixed bay swamps included sweet bay (*Magnolia virginiana*), red maple (*Acer rubrum*), slash pine, and tupelo gum (*N. aquatica*); dominant understory species included fetterbush (*Lyonia lucida*) and swamp bay (*Persea palustris*). Cypress, black gum, and sweet bay dominated cypress-black gum swamps, with the understory comprised mainly of fetterbrush.

The estimated density of deer was 1/25±10 ha (Labisky et al. 1991). Harvest regulations during the 1990-91 season permitted the taking of either sex during archery season (21 Sep.–6 Oct.), but only males with ≥2.5 cm antlers during muzzleloader (18 Oct.–25 Oct.) and general gun (10 Nov.–5 Jan.) seasons.

METHODS

We captured deer during winters of 1988–1990 using corral traps (Stafford et al. 1966) and rocket nets (Hawkins et al. 1968), and fitted them with radio-collars. We determined radio-locations by triangulation from 3 locations by 1 observer using a handheld, directional "H" antenna. All azimuths were taken within a 30-min period. Locations were plotted as the center of the error triangle formed by the intersection of the 3 directional bearings. We determined the error of directional bearings as described by Fritzen et al. (1995). Single-blind experiments involving triangulation of transmitters placed at locations 375 m distant from the receiver (mean actual distance from receiver to transmitter, derived from 50 randomly selected animal-locations, was 377 m) were performed by both individuals collecting telemetry data with both radio-receivers at three different sites on the study area. Mean error of directional bearings (n=113) was 2.1±1.8 degrees. This location error yielded an actual distance error of approximately 30 m (error triangle size =272 m^2).

Each radio-instrumented deer was located 8X/mo (2X/wk) with two locations in each of four major diel periods: morning (sunrise ±2 hours), day, evening (sunset ±2 hours), and night. This monitoring schedule was designed to minimize bias that may be associated with unstratified temporal monitoring (e.g., autocorrelation). Greater than 95% of successive locations were separated by ≥24 hrs. However, we were forced to accept a separation interval of 12–24 hrs for a few locations due to logistical constraints. Monthly home ranges were calculated by

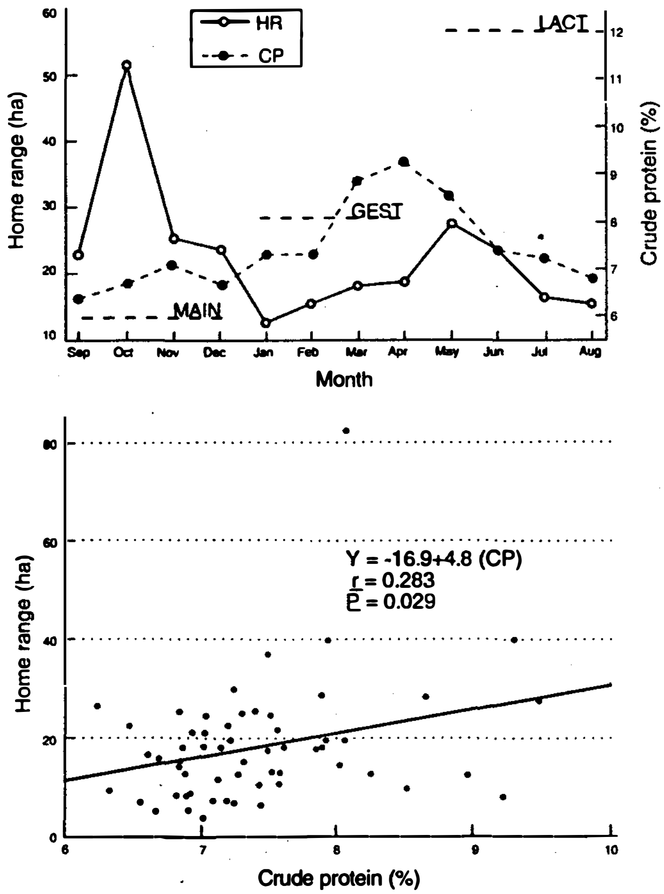

Fig. 1. Top: Comparison of mean monthly home range size (HR) of 10 adult female white-tailed deer and mean monthly crude protein (CP) levels in three principal forage species from the Osceola National Forest, Florida, September 1990 — August 1991, with Model 5 threshold levels (MAIN = maintenance, GEST = gestation, and LACT = lactation). Bottom: Linear relationship between monthly home range sizes of individual deer and their respective CP levels for months in which CP was below the Model 5 threshold.

the minimum convex polygon (MCP) method (Mohr 1947), using Home Range computer software (Ackerman et al. 1989). The MCP was selected over the harmonic mean method (Dixon and Chapman 1980) because, due to the small sample sizes, minor adjustments in scale and grid density yielded radical changes in the size and shape of the harmonic mean estimates. Also, a relative index of the minimum area used by deer was deemed more important for the purposes of this study than a precise measure of home range size in a particular month. Annual home range-core areas of the study animals were determined by harmonic mean analysis of radio-locations obtained during the 12 months prior to the study via the same monitoring schedule (Labisky et al. 1991). The mean proportion of harmonic mean home range size included in core areas was 38% and the mean percentage of total harmonic utilization volume (Ackerman et al. 1989) was 65%.

Three plant species were selected for evaluation of forage quality during the annual cycle: common gallberry, lowbush blueberry (*Vaccinium myrsinites*), and greenbriar (*Smilax laurifolia*); these species were among the most important deer foods during fall in northern Florida flatwoods, and they comprised 36% of diet volume (22.1%, 9.5%, and 4.3%, respectively) of deer at ONF during winter (Harlow 1961, Harlow and Jones 1965). These species also were the most common of the 5 top-ranked browses (Harlow 1961, Harlow and Jones 1965) within home ranges of monitored deer. Though some nutritious items appear in the diet on a seasonal basis (e.g., palmetto mast, mushrooms, forbs), a relative index of range quality during the annual cycle (i.e., forages available and utilized year-round) was necessary to test our hypothesis.

One sample of each species was collected from ≥10 plants

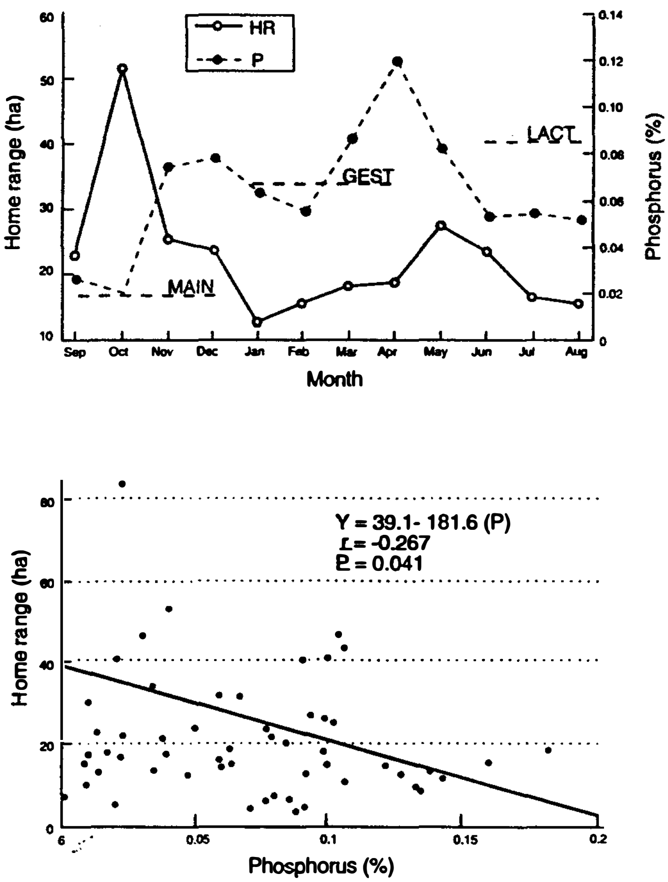

Fig. 2. Top: Comparison of mean monthly home range size (HR) of 10 adult female white-tailed deer and mean monthly phosphorus (P) levels in three principal forage species from the Osceola National Forest, Florida, September 1990—August 1991, with Model 5 threshold levels for CP (MAIN = maintenance, GEST = gestation, and LACT = lactation). Placement of threshold lines is not exact; lines were positioned relative to each monthly P point based on whether the respective month's CP was above or below threshold. Bottom: Linear relationship between monthly home range sizes of individual deer and their respective P levels for months in which CP was below the Model 5 threshold.

Table 1. Hypothetical crude protein (%) threshold models used to evaluate correlation between home range size and forage quality parameters. Threshold levels were used to categorize months as above- or below-threshold for correlation analysis.

Model	Approach[b]	Period[a]		
		Maintenance	Gestation	Lactation
1	1	7.0	7.0	7.0
2	2	8.0	13.0	18.0
3	2	6.0	10.0	14.0
4	2	6.0	9.0	13.0
5	2	6.0	8.0	12.0

[a]Maintenance: September–December; gestation: January–April; lactation: May–August. [b]Approach 1 was based on the level at which intake is reduced in ruminants (Van Soest 1982). Approach 2 was based on nutritional requirements for the respective period (Verme and Ullrey 1984). See text for detailed discussion.

randomly selected from within the core area of the annual home range of each monitored doe at monthly intervals from September 1990 to August 1991. Samples consisted of leaves (15 g dry matter) of the current annual growth collected from ground level to 1.5 m. They were analyzed for nitrogen [N; crude protein (CP) = 6.25 × N] and phosphorus (P) content, and *in vitro* organic matter digestibility (IVOMD). Treatment and analysis of forage samples are described in Kilgo and Labisky (1995).

Monthly home range sizes were compared with a *k*-sample Kruskal-Wallis test because home range sizes were not distributed normally (p<0.001, PROC UNIVARIATE; SAS Institute 1989). Correlation analyses of home range size with each nutritional parameter were based on the hypothesized CP threshold, above which correlation was expected to be negative, and below which it was expected to be positive. Thus, it was necessary to determine whether CP during each month was above or below the threshold value. Because estimates of this threshold have not been reported, values were derived using 2 approaches. In Approach 1, the threshold was set at 7% CP, because intake by ruminants is depressed when dietary protein drops below this level (Van Soest 1982). In Approach 2, the threshold was set based on nutrient requirements of deer, which vary throughout the year. Thus, we partitioned the year into 3 periods (Verme and Ullrey 1984), based on parturition dates from Osceola (Richter and Labisky 1985, Labisky et al. 1991):(1) maintenance (Sep.–Dec.);(2) gestation (Jan.–Apr.); and (3) lactation (May–Aug.). Estimates of CP requirements in white-tailed deer are 6–10% for maintenance (French et al. 1956, McEwen et al. 1957) and 14–24% for growth (Ullrey et al. 1967, Smith et al. 1975). Verme and Ullrey (1984) suggested that requirements for lactation likely approximate those for growth, and requirements for gestation are intermediate to those for maintenance and lactation. Accordingly, threshold values for the 3 periods were assigned using the median value of the estimated ranges for maintenance, gestation (intermediate), and lactation (growth) as follows: (1) maintenance = 8%, gestation

= 13%, and lactation = 18%. The 3 periods, with their varying requirements, were designated only for the purpose of determining which months were above or below threshold; i.e., the periods were not tested statistically.

For each of the 2 hypothesized threshold approaches, Pearson correlation coefficients, which described the relationships between home range size and nutritional parameter, were calculated for data from (1) all months in which CP was above threshold, and from (2) all months in which CP was below threshold. However, observed CP for every month was below the Approach 2 levels. Consequently, threshold levels for each period were decreased incrementally, yielding 3 additional Approach 2 models; thus, 5 potential threshold models were tested (1 model for Approach 1 and 4 models for Approach 2; Table 1). The probability level of the correlation analysis determined the best model. No attempts were made to establish threshold levels for P and IVOMD. Monthly data for P and IVOMD were tested for correlation with home range size using the same designations of above-or below-threshold as were determined for CP; i.e.; data for IVOMD were tested as above threshold using those months in which CP was above threshold, and as below-threshold using those months in which CP was below threshold.

For any relationship determined to be significant, analysis of covariance (PROC GLM; SAS Institute 1989), with deer as blocks, forage quality parameter as the covariate, and an interaction term (forage quality parameter*deer) was used to test null hypothesis that the slopes of the individuals did not differ. Failure to reject this null hypothesis predicated pooling of individuals.

RESULTS

Individual animal were pooled for all analyses. Analysis of covariance revealed no differences among slopes of individuals for the relationship between home range size and P (p>0.05). The slope of one deer differed (more steeply ascending, p<0.001) from the others for the relationship between home range size and CP. However, inasmuch as this deer had only minor impact on the results (with: r=–0.27, p=0.04; without: r=–0.26, p=0.055), it was retained in the sample.

Home range sizes of 10 radio-instrumented adult females differed among months (Kruskal-Wallis Test, p=0.049). Home ranges were largest (51.7 ha) in October and smallest in January (12.8 ha). Generally, home ranges were largest in fall (maintenance period), intermediate in spring and early summer (parturition and early lactation period), and smallest in winter (gestation period) and late summer (late lactation period).

Monthly home range sizes were correlated positively with monthly CP when CP was below the threshold levels for Model 5 (r=0.28, p=0.02; Fig. 1). When CP was above Model 5 threshold levels, however, correlation was not significant (r= –0.11, p=0.41). The converse was true of the relationship between monthly home range size and monthly P levels; these variables were correlated negatively (r=–0.27, p=0.04) when CP was above Model 5 threshold levels, but not when CP was below Model 5 threshold levels (r=–0.01, p=0.96; Fig. 2). No relationship (p >0.05) was found between monthly home range size and monthly IVOMD levels.

DISCUSSION

The relationship between home range size and forage quality was weak. This low correlation likely was due to several factors. Palmetto mast, which accounts for a large proportion of the fall and winter diet when present (Harlow 1961, Harlow and Jones 1965), was unusually abundant at ONF in fall 1990, and was prevalent in fecal pellets of deer from September 1990–March 1991 (JCK, pers. observ.). The correlation between home range size and forage quality may be higher in years of normal palmetto mast abundance. Additionally, deer movements likely were affected by rutting activity (Ozoga and Verme 1975, Hölzenbein and Schwede 1989, Fritzen 1992) and by hunter activity during fall (Downing et al. 1969, Root et al. 1988, Sargent 1992).

Despite low r values, the correlations were significant; seasonal home range size of deer was correlated with the relative nutritional quality of their food resources. In fact, low correlation coefficients for each parameter should be expected, given the number of potential influences on home range size. Although movements by both migratory (Sparrowe and Springer 1970, Garrott et al. 1987) and resident (Michael 1965, Marchinton and Jeter 1967, Downing et al. 1969, Byford 1969, Marchinton and Hirth 1984, Loft 1988) deer populations have been attributed to changing food resources and deer in the South have been shown to reduce intake seasonally (Short et al. 1969), a relationship between forage quality and seasonal fluctuations in home range size has not been quantified previously.

Adult does at Osceola may have responded to a low-level threshold of CP, below which they decreased their home range size with decreasing CP content of forages, and above which they increased their home range size with decreasing P content of forages. The threshold CP level varied over the annual cycle, according to the reproductive state of the deer: maintenance = 6%, gestation = 8%, and lactation = 12%. The predicted negative relationship between home range size and CP above the threshold was not evident. However, this pattern is in accordance with reports that intake is correlated positively with CP below a certain level, but that, above that level, the relationship weakens (Van Soest 1982). The lack of any discernable relationship between home range size and digestibility was suprising due to the demonstrated relationship between digestibility and intake (Ammann et al. 1973), but suggests that digestibility of forages at Osceola is adequate to permit foraging strategies aimed at optimization of CP and P in the diet.

Collectively, these results suggest that when the CP content of deer forages at Osceola drops below the threshold level, deer may respond by reducing home range size, a behaviour potentially adapted to reduce physiological expenditures during periods of nutritional stress. However, when deer are released from this protein restriction, i.e., CP content of forage is adequate, they may be able to concentrate on maximizing P intake; this is accomplished, in part, by increasing home range size as P levels decline.

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