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Responses of Female White-tailed Deer Home-Ranges to Increased Resource Availability

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Abstract - Management strategies designed to reduce the negative impacts of overabundant *Odocoileus virginianus* (White-tailed Deer) populations on forest regeneration may be influenced by changes in both population density and timber harvest. However, there is conflicting evidence as to how such changes in per capita resource availability influence home-range patterns. We compared home-range patterns of 33 female White-tailed Deer from a low-density population at a site with abundant browse to patterns of a sample of >100 females prior to a 75% reduction in population density and a doubling in timber harvest area. Home-range and core-area sizes were approximately 3 times larger than were found prior to population decline and timber harvest increase, consistent with predictions related to intraspecific competition. We also observed greater site fidelity than previously exhibited, although this may be an artifact of increased home-range sizes. Our results support previous research suggesting that White-tailed Deer home-range size is inversely related to population density and is driven, in part, by intraspecific competition for resources. Relationships among population density, resource availability, and home-range patterns among female White-tailed Deer appear to be complex and context specific.

Introduction

Variability in the size of an animal's home range, i.e., the area used during everyday activities (Burt 1943), is a function of numerous biotic and abiotic factors. Although intrinsic factors such as mating system may influence seasonal patterns in home-range size (Clutton-Brock 1989), intraspecific competition for resources directly affects home-range size (Burt 1943, Sanderson, 1966). In many species, individual home-range size is inversely related to population density (Brown 1969, Getz 1961). This relationship is generally explained as a function of habitat quality, with high-density populations occurring in areas with more resources available and thereby requiring less movement to meet energetic or other resource requirements. Additionally, free distribution in habitat selection would also lead to an inverse relationship between population density and home-range size due to territorial

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interactions (Fretwell and Calver 1969). However, population density is not always monotonically related to habitat quality such that areas with higher population density equate to areas with higher habitat quality (VanHorne 1983). In highly philopatric species, such as *Odocoileus virginianus* Zimmerman (White-tailed Deer, hereafter Deer), it has been suggested that population density and home-range size are directly related (Kilpatrick et al. 2001, Tiersen et al. 1985). These discrepancies in hypothesized relationships make it difficult to predict the relationship between population density and home-range patterns in any individual population.

Although the effects of population density on Deer recruitment (Keyser et al. 2005a), physical condition (Garroway and Broders 2005, Keyser et al. 2005b), and herbivory (Miller et al. 2010), are well known and generally consistent, their effects on space-use patterns are inconsistent, especially in forested landscapes. For example, on coastal islands in South Carolina, seasonal home-range sizes of suburban Deer increased in response to a 50% reduction in population density (Henderson et al. 2000). Similarly, home-range sizes of *O. virginianus clavium* Barbour and Allen (Florida Key Deer) decreased as population densities increased (Lopez et al. 2005). Conversely, Deer in suburban Connecticut decreased their annual home-range sizes immediately after the implementation of a herd reduction program (Kilpatrick et al. 2001). Studies of female Deer herds in enclosures have found an inverse relationship between population density and home-range size (Williams and DeNicola 2002). In a forested landscape in the Adirondacks of New York, McNulty et al. (1997) found that home-range size did not change in response to a localized removal of 80% of the female Deer in their study population, but did find that levels of philopatry decreased at moderate to relatively low population density exhibited in their study area (6–12 Deer/km^2). Populations occurring at higher density or that have undergone a more substantial change in density may exhibit different patterns. For example, populations occurring at higher densities should experience greater levels of intraspecific competition among individuals for finite resources than those at low density, and thus may be expected to exhibit greater responses to reductions in population size. However, McNulty et al. (1997) remains one of the only studies to address the effects of population density on both home-range size and patterns of philopatry.

Population density can affect home-range patterns by changing the availability of resources or through the amount and intensity of intraspecific interactions. An increase in resource availability, as would occur after a reduction in population size, should lead to a decrease in home-range size because animals can obtain the required amount of resources over a smaller area (Kilpatrick et al. 2001). Conversely, reducing population size may also decrease aggressive intraspecific interactions, which could result in increasing home-range size (e.g., Henderson et al. 2000). Because the effects of changes in resource availability on White-tailed Deer home-range sizes are relatively unknown, we contrasted home-range sizes and levels of philopatry in a population prior to and following a >75% reduction in Deer density and an independent doubling in the amount of forage availability in a forested landscape of the Central Appalachians of West Virginia. Our objectives were to determine how: (1) seasonal home-range and core-area sizes and (2) inter-annual site fidelity changed in response to reduced population density and increased timber harvest. We hypothesized that home-range and core-area sizes would decrease due to a presumed increase in per-capita resource availability resulting from both a reduction in population density and increase in timber harvest, and that philopatry would increase due to a reduced need for extensive movements to acquire resources.

Methods

Study area

We conducted our study in the MeadWestvaco Wildlife and Ecosystem Research Forest (MWERF) in central Randolph County, WV (Fig. 1). The 3413-ha site is located in the Unglaciated Allegheny Mountain and Plateau physiographic province (Fenneman 1938) and ranges in elevation from 734 m to 1180 m. Average annual precipitation ranged between 170 cm and 190 cm with an average snowfall >300 cm/year (National Oceanic and Atmospheric Administration 1998–2002). The majority of the site was comprised of second-growth northern hardwood–Allegheny hardwood forests (Keyser and Ford 2005). Forests were dominated by *Fagus grandifolia* Ehrhart (American Beech), *Acer rubrum* L. (Red Maple), *A. saccharum* Marshall (Sugar Maple), *Liriodendron tulipfera* L. (Yellow Poplar), and *Prunus serotina* Ehrhart (Black Cherry). Other common species included *Betula alleghenienis* Britton (Yellow Birch), *Tilia americana* L. (American Basswood), *B. lenta*

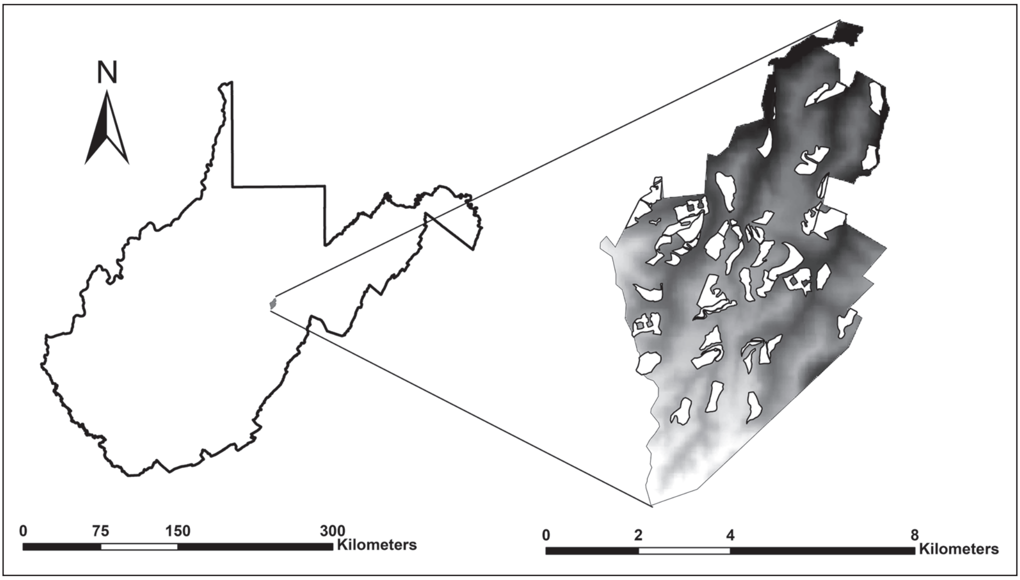

Figure 1. MeadWestvaco Wildlife and Ecosystem Research Forest (MWERF), Randolph County, WV. Solid white polygons represent regenerating clearcuts (0–15 years since harvest) during study period, 2006–2008.

L. (Black Birch), and *Quercus rubra* L. (Northern Red Oak). Higher-elevation areas were dominated by *Picea rubens* Sargent (Red Spruce) and *Tsuga canadensis* Carriere (Eastern Hemlock) communities. Throughout much of the area, the understory was composed of *Smilax* spp. (greenbrier) and *Kalmia latifolia* L. (Mountain Laurel), with dense *Rhododendron maximum* L. (Rosebay Rhododendron) prevalent along riparian areas. *Dennstaedtia punctilobula* Moore (Hay-scented Fern) also was abundant throughout the understory due to excessive herbivory from historically high Deer densities (Keyser and Ford 2005). Since 2000, more than 500 ha of the MWERF have been harvested (Campbell et al. 2006).

Campbell et al. (2004) investigated the spatial ecology of Deer in the MWERF during 1999–2002. At the time of that study, approximately 5% of the study area was comprised of regenerating clearcuts (forest stands harvested within 15 years), and the density of the Deer population was 12–20/km^2 (Langdon 2001). During our study (2006–2008), approximately 14% of the study area was comprised of regenerating clearcuts and the density of the Deer population was 1.2–2.6/km^2 (Crimmins et al. 2013). Thus, the Deer population in the MWERF experienced an increase in resource availability both through a reduction in the size of the population and an increase in the absolute amount of forage (Miller et al. 2009). The causes for the observed population decline were a combination of regional population declines, likely resulting from historic overabundance and increasing predator populations, and localized management actions that occurred between the conclusion of the study by Campbell et al. (2004) and the onset of our study (Crimmins et al. 2012, Miller et al. 2010).

Deer capture and monitoring

We captured Deer from January through March of 2005–2007 using modified Clover traps (Clover 1954) baited with whole-kernel corn. We immobilized Deer with an intramuscular injection of xylazine HCl (Sedazine, Fort Dodge Animal Health, Fort Dodge, IA) at 2.2 mg/kg estimated body weight. We classified Deer age as yearling (≤1.5 years) or adult (>1.5 years) according to tooth eruption and wear patterns (Severinghaus 1949). We fit female Deer with VHF radio-collars equipped with an 8-h mortality switch (Advanced Telemetry Systems, Isanti, MN). We placed a uniquely numbered plastic ear tag on each animal for visual identification (National Band and Tag, Newport, KY). We reversed sedation with a 50% intramuscular and 50% subcutaneous injection of yohimbine HCl (Yobine, Lloyd Laboratories, Shenandoah, IA) at 0.3 mg/kg (Wallingford et al. 1996). All capture and handling methods were in accordance with the Animal Care and Use Committee of West Virginia University (IACUC# 05-0706).

We attempted to locate Deer once per day, 3–4 d/week using biangulation (Mech 1983) or triangulation (White and Garrott 1990) from May 2006 to April 2008. We used 3-element hand-held Yagi antennas and a TRX-1000 receiver (Wildlife Materials, Murphysboro, IL) to locate collared animals. We recorded azimuths from ≥2 geo-referenced stations ($n = 499$) located throughout the MWERF with a maximum of 15 min between azimuths to reduce the effect of animal movement on location accuracy (Schmutz and White 1990). Our telemetry methods were identical to those used by Campbell et al. (2004). We assessed the accuracy of our telemetry locations by placing 10 collars at geo-referenced locations throughout the study area during July 2006 and collecting bearings from ≥10 of our geo-referenced stations to each collar. We augmented telemetry locations with visual locations of radio-collared animals identified via numbered ear tags recorded throughout the year. Preliminary analyses indicated that our results were insensitive to the time of day when we gathered locations (Barber-Meyer and Mech 2014).

Statistical analyses

We generated seasonal home-range and core-area estimates using the fixed-kernel method (Seaman and Powell 1996) with a least-squares cross-validated bandwidth and reference grid-cell size (Gitzen et al. 2006, Kernohan et al. 2001). We used 95% and 50% volume contours to define home ranges and core areas, respectively. We calculated seasonal home ranges and core areas for animals with ≥30 locations in a season (Seaman et al. 1999). We defined seasons as summer (May–September), fall (October–December), and winter (January–April). All of our home-range estimation procedures followed Campbell et al. (2004). We detected no differences in home-range size between years (2006–2007 vs. 2007–2008) and subsequently pooled data between years. We tested for seasonal differences in mean home-range size and core-area size using an analysis of variance model with season as a treatment effect. We compared variability in home-range and core-area sizes between seasons using 2-sided F-tests with Bonferroni corrections. We estimated seasonal philopatry following Lesage et al. (2000) by calculating the overlap in home-range and core-area polygons for individual Deer in successive years. Using t-tests, we compared our seasonal home-range and core-area size estimates and philopatry measurements to those previously found for high density Deer populations (Campbell et al. 2004). We pooled our data across age classes for all analyses. Because we pooled data across age classes, the values we present for those observed at high population-density differ from those presented in Campbell et al. (2004), wherein results were presented separately for each age class.

Results

From May 2006 to April 2008, we collected 5252 locations from 35 individuals. Of those, 33 had a sufficient number of locations (≥30) to generate at least one seasonal home-range, resulting in 111 seasonal home ranges using a total of 4768 locations. Telemetry error in our trials of geo-referenced collars was minimal (mean = 1.1°, $n = 120$). The number of seasonal home-ranges calculated per individual ranged from 1 to 6. We were able to estimate seasonal philopatry from 15, 10, and 12 individuals in summer, fall, and winter, respectively. Our analysis of variance indicated that mean home-range size was similar among seasons ($F_2 = 2.84$, $P = 0.06$), as was mean core-area size ($F_2 = 1.73$, $P = 0.18$) (Table 1). Home-range size was less variable among individuals during winter than summer ($F_{40,34}$ = 3.20, $P < 0.01$) or fall ($F_{32,34}$ = 3.31, $P < 0.01$) (Table 1). Variability in home-range size was similar in summer and fall ($F_{32,40}$ = 0.966, P = 0.93) (Table 1). Similarly, core-ranges were less variable in winter than summer ($F_{40,34}$ = 3.60, $P < 0.01$) or fall ($F_{32,34}$ = 3.44, $P < 0.01$) (Table 1). As with home ranges, variability in core-area size was similar in summer and fall ($F_{32,34}$ = 1.05, P = 0.88; Table 1).

Home-range estimates were larger after the reduction in Deer density and increase in timber harvest than prior to reduction in density and increase in timber harvest during summer ($t_{43.68}$ = 6.55, $P < 0.001$), fall ($t_{35.76}$ = 5.60, $P < 0.001$), and winter ($t_{71.51}$ = 3.69, $P < 0.001$) (Table 1). Similarly, core-area estimates were also significantly larger in summer ($t_{43.68}$ = 6.236, $P < 0.001$), fall ($t_{35.76}$ = 5.475, $P < 0.0001$), and winter ($t_{71.51}$ = 5.463, $P < 0.0001$) than prior to population reduction (Table 1). In general, seasonal home-range and core-area estimates were 2–4 times greater than previously observed for Deer populations with high densities (Table 1; Campbell et al. 2004).

Home-range philopatry did not differ among seasons (F = 1.57, df = 2; P = 0.22; Table 2). Home-range philopatry was higher at low population-density than at high population-density in summer (t = 4.084, df = 64.48; $P < 0.0001$), fall (t = 10.134, df = 47.47; $P < 0.0001$), and winter (t = 9.277, df = 80.87, $P < 0.0001$) (Table 2). Core-area philopatry differed among all seasons (F = 50.63, df = 2; $P < 0.001$), with the highest values in fall and lowest in winter (Table 2). Core-area philopatry at low density was similar to that at high density in summer (t = -1.20, df = 70.24; P = 0.23), but was greater in fall (t = -13.31, df = 19.61, $P < 0.001$) and winter (t = -2.58, df = 28.43; P = 0.02) (Table 2).

Table 1. Mean seasonal core-area (CA) and home-range (HR) sizes in hectares (95% CI) of female White-tailed Deer on the MeadWestvaco Wildlife and Ecosystem Research Forest during periods of high (1999–2002) and low (2006–2008) population density. Data from 1999–2002 was recalculated from Campbell et al. (2004).

	1999–2002			2006–2008		
Season	*n*	Core area	Home range	*n*	Core area	Home range
Summer	165	18.0 (15.4–20.6)	99.5 (84.1–114.9)	42	87.4 (65.7–109.0)	389.7 (304.2–475.2)
Fall	162	18.6 (13.7–23.5)	104.9 (82.2–127.7)	33	89.7 (64.7–114.6)	383.4 (288.6–478.3)
Winter	177	26.1 (20.5–31.7)	152.1 (117.7–186.5)	36	64.6 (51.9–77.2)	267.6 (216.9–318.4)

Table 2. Mean seasonal core-area (CA) and home-range (HR) philopatry (95% CI), as measured in percent overlap between years, of female White-tailed Deer on the MeadWestvaco Wildlife and Ecosystem Research Forest during periods of high (1999–2002) and low (2006–2008) population density. Data from 1999–2002 was recalculated from Campbell et al. (2004).

	1999–2002			2006–2008		
Season	*n*	Core area	Home range	*n*	Core area	Home range
Summer	59	40.2 (39.7–40.8)	55.8 (55.3–56.3)	15	44.8 (43.8–45.8)	66.1 (65.1–67.1)
Fall	58	18.2 (17.6–18.8)	41.2 (40.7–41.7)	10	74.0 (72.8–75.1)	69.2 (68.1–70.4)
Winter	83	26.2 (25.8–26.7)	51.2 (50.8–51.6)	12	35.7 (34.6–36.8)	68.8 (67.7–69.8)

Discussion

It is widely recognized that population density can have substantial effects on White-tailed Deer biology (Keyser et al. 2005a, 2005b; Kilpatrick et al. 2001). Understanding how density affects home-range patterns in Deer can aid managers in developing management strategies to minimize disease transmission and herbivory impacts to biodiversity and/or forest resources. Contrary to previous work suggesting that seasonal changes in resource availability can affect space-use patterns in White-tailed Deer (Labisky and Fritzen 1998), we found no evidence of difference in home-range or core-area size among seasons in this study. Although previous research has found similar consistencies among seasonal home-range patterns (e.g., Sargent and Labisky 1995), this result emphasizes that the effects of density on space use can be difficult to predict, particularly when coupled with other factors such as habitat quality and resource abundance. At high population-densities, Deer in the MWERF exhibited seasonal variation in space-use, with larger home ranges and core areas in winter than in summer or fall (Campbell et al. 2004). Changes in resource availability in the MWERF led to species-specific changes in browsing rates (Crimmins et al. 2010, Miller et al. 2009). Thus, seasonal variability in home-range sizes previously observed (Campbell et al. 2004) may have been the result of seasonal-resource limitation at high population densities and lower resource abundance, which would be unlikely to have affected the population during our study due to reduced population density and increased forage abundance. Additionally, we found higher levels of site fidelity at low population densities, suggesting that per capita resource limitation at high densities may have caused Deer to exhibit annual switches in home-range areas in search of adequate resources. However, the increased site fidelity that we observed could be an artifact of increased home-range sizes.

Timber harvesting on our study site led to a nearly 3-fold increase in the area of early successional habitat. An increase in regenerating clearcuts from approximately 5% of the study area in 1999–2002 to nearly 14% in 2006–2008 increased the amount of browse available to deer during spring and summer, a period of high nutritional requirements for lactating females (Ford et al. 1993, Wentworth et al. 1990). Regenerating clearcuts at our study area contained abundant forage compared to mature forest stands (Crimmins et al. 2010), highlighting the ecological importance of this component of the landscape. Home-range and core-area sizes were approximately 300% larger than prior to the population reduction likely due to a combination of reduced population density and increased habitat disturbance. Research in other regions has indicated that population density and habitat patchiness can affect home-range size independently (Ford 1983, Kilpatrick et al. 2001, Lopez et al. 2005). Our finding indicating that Deer had larger home ranges at decreased population densities is contrary to several previous studies (Kilpatrick et al. 2001, McNulty et al. 1997) and supports the theory that decreased intraspecific competition is a driving factor in structuring home-range patterns.

Our finding of increased site fidelity at lowered densities contrasts with previous research focused on socio-spatial patterns in Deer family groups (McNulty et al. 1997). It is possible that these increases in site fidelity were the result of increases in per capita resources, whereby abundant resources reduced the need for exploratory behavior in search for adequate forage. This explanation is supported by previous research at our study area that documented an increase in the abundance of forage following the reduction in Deer population density and increase in timber harvest (Crimmins et al. 2010). Although increases in the availability of resources could lead to the changes in home-range patterns we observed, alternative explanations such as increased predator populations also merit consideration. For example, the substantial increases in *Canis latrans* Say (Coyote) populations that have occurred in the region (Crimmins et al. 2012) could lead to altered space-use patterns by Deer in an attempt to reduce predation risk. Because of the coupled changes in population density and habitat structure that occurred during our study, it is impossible to determine the absolute influence of either factor on the changes in home-range patterns we observed. Additional research to examine changes in habitat-use patterns could further elucidate the mechanisms behind these observed changes in home-range patterns. Previous research has shown that overall browsing rates in the MWERF declined following the Deer population decline and increase in timber harvest, but that browsing rates for forage species generally thought to be preferred by White-tailed Deer showed a negligible decline (Crimmins et al. 2010). This result suggests that increases in home-range size may have been a function of Deer actively searching for preferred food sources over greater areas rather than relying on sub-optimal forage resources within a smaller area. Regardless of the causal mechanism behind the observed changes in home-range patterns, our results suggest that in this region, it may be difficult to successfully implement management strategies designed to reduce White-tailed Deer abundance at a localized scale (Campbell et al. 2004).

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