Space Use and Survival of Male White-tailed Deer in a Bottomland Hardwood Forest of South-central Louisiana

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Abstract: White-tailed deer (*Odocoileus virginianus*) are an important economic and recreational resource in Louisiana. A basic understanding of population dynamics is essential to ensure sound management, but baseline information in Louisiana is lacking. Our objectives were to estimate space use, survival, and causes of mortality for a managed white-tailed deer population in southern Louisiana. We radio-marked 11 yearling (1.5 yr old) and 26 adult males (\geq 2.5 yr old) during 2007–2008. Home ranges (95%) for adult males during spring, summer, and fall were 153.9, 70.4, and 118.0 ha, respectively, and were 119% and 68% larger during spring and fall than summer. Yearling males used 169% larger home ranges during spring (231.6 ha) than summer (86.1 ha), and maintained 50% larger home ranges than adults in spring. Survival estimates for adult males during spring, summer, and fall were 100%, 95%, and 55%, respectively. Mean annual survival for adult males was 53%. No mortalities were observed in spring or summer for 1.5-yr-old males, but harvest records indicated 1.5-yr-old males were being harvested at a rate approaching 20% of the annual male harvest. Mean annual mortality rates for adult males from harvest (40%) were greater than for non-harvest sources of mortality (16%). Home ranges were smaller than previously reported; thus, we suggest that landowners managing small (<300 ha) landholdings may be able to improve herd dynamics in conjunction with protection of young males.

Key words: bottomland hardwood forests, Louisiana, space use, survival, mortality, home range, core area, Odocoileus virginianus, management

Proc. Annu. Conf. Southeast. Assoc. Fish and Wildl. Agencies 63:1-6

Numerous studies have detailed home range and survival for white-tailed deer herds throughout the United States, but such information is lacking for populations in Louisiana, particularly in bottomland forests which comprises 25% of Louisiana's forested land. The fertile soils of the Mississippi Alluvial Valley (MAV) produce diverse and nutritious vegetation that support some of the highest carrying capacities of white-tailed deer in the southeast (Murphy and Noble 1972). Much of Louisiana's bottomland forests were lost through intensive logging or conversion to agriculture (Stanturf et al. 2001). However, bottomland forests are being restored through conservation and reforestation programs. As additional bottomland forests are restored, these areas will increase available habitat for white-tailed deer populations.

As interest on both private and public lands moves toward data-intensive management, so will the desire and need for regional population demographic data such as home range, survival, and cause-specific mortality. Improving our understanding of space use within bottomland systems is important for developing management regimes with implications for management unit size. In addition, survival and mortality patterns within a population may reveal much about harvest intensities. In Louisiana, younger males are protected from harvest through the use of age or antler restrictions; thus, other sources of mortality may be more influential in shaping recruitment of males to older age classes. Our objectives were to estimate home range and core area size, determine seasonal and annual survival rates, and quantify cause-specific mortality of white-tailed deer in a bottomland hardwood forest of southcentral Louisiana.

Study Area

We conducted our research on a 16,000-ha privately-owned bottomland hardwood forest located west of Baton Rouge and east of the Atchafalaya Basin. The eastern end of the study site was approximately 16 km from the Mississippi River Bridge at Baton Rouge with the western end bordered by Bayou Grosse Tete. The area was composed primarily of semi-contiguous bottomland hardwood forest with active logging occurring annually. The most common forest management practice was clear-cutting fashioned in a checker-board pattern with cuts approximately 20 ha each. The forest overstory was dominated by American sycamore (Platanus occidentalis), water oak (Quercus nigra), overcup oak (Q. lyrata), Nuttall oak (Q. texana), elm (Ulmus americana), sweetgum (Liquidambar styraciflua), sugarberry (Celtis laevigata), green ash (Fraxinus pennsylvanicus), baldcypress (Taxodium distichum), and water hickory (Carya aquatica). Midstory species included boxelder (Acer negundo), deciduous holly (Ilex decidua) Drummond red maple (Acer rubrum var. drummondii), persimmon (Diospyros virginiana), tallowtree (Triadica sebifera), and swamp dogwood (Cornus drummondii). Common understory species included yellowtop (Senecio glabellus), rattan vine (Berchemia scandens), greenbrier (Smilax spp.), blackberry (Rubus spp.), trumpet creeper (Campsis radicans), Virginia creeper (Parthenocissus quinquefolia), poison ivy (Toxicodendron radicans), muscadine (Vitis spp.), Japanese honey-suckle (Lonicera japonica), and peppervine (Ampelopsis spp.). Most forest openings (e.g., rights-of-way, logging roads) were planted to food plots, primarily wheat, oats, or clover. Various supplemental feeds (e.g., corn, rice bran, soy beans; primarily available during hunting season) were also accessible to deer on the study site. Baiting for white-tailed deer in Louisiana is a legal and common practice.

Our study area was accessible through improved and unimproved roads. Interstate 10 traversed 12.8 km of the northern portion of the study area, Bayou Choctaw divided the east and west sides of the area, and the Intra-coastal Navigation Canal bordered the southern end of the study area. There were three other primary or secondary paved roads or highways that dissected the study area. The study site was privately owned by a multitude of both small (<200 ha) and large (>200 ha) landowners, with A. Wilbert's Sons, LLC (Wilbert), controlling most (>50%) of the land. Wilbert leased hunting rights on its lands to hunting clubs and also encouraged clubs to join the Choctaw Quality Deer Management (QDM) Cooperative (Co-op). Although clubs leasing lands from Wilbert were strongly encouraged to join the Co-op, privatelyowned hunting clubs and clubs leasing from other landowners surrounding Wilbert land joined the Co-op voluntarily, resulting in approximately 30 hunting clubs participating in a program promoting QDM annually across approximately 16,000 ha. The Co-op's harvest guidelines included a recommendation from the Louisiana Department of Wildlife and Fisheries for antlerless deer harvest of 1 female/20.5 ha with an antler restriction (38.1 cm main beam length and 33.0 cm inside spread) designed to protect younger bucks (\leq 2.5 years). From 1997–2007, the annual average deer harvest on the Co-op was 1169 (range = 996 - 1367).

Hunting seasons spanned 1 October-15 February, with the modern firearm season generally ranging from the second week

in November through the middle of January. One week in December, as well as the remainder of the season, was either archery, primitive weapon, or both. Clubs hunting within the Co-op were informed about the presence of radio-collared deer and asked to treat them like any other in hopes of reducing possible bias in regards to estimating harvest rates. Hunters also were asked to report the harvest of any collared or ear-tagged deer. We assigned cause of death as harvest, natural (disease), or deer-vehiclecollision (DVC). Herd health collections (n=23 females) performed by the Louisiana Department of Wildlife and Fisheries in spring 2007 and 2008 indicated fetus/doe ratios of 1.3 and 1.9 and average weights of 48 kg and 51 kg, respectively

Methods

Capture and telemetry

We captured male white-tailed deer during spring (February– April) 2007 and 2008 with drop nets and dart projectors at permanent bait sites (n = 13). We chemically immobilized each deer with an intramuscular injection (by hand or a pole syringe) of 5 mg/kg Telazol (Fort Dodge Animal Health, Fort Dodge, Iowa) and 2.49 mg/kg Xylazine (Phoenix Scientific, St. Joseph, Missouri) at the dosage of 1 ml per 38.5 kg (Amass and Drew 2006). After processing, deer were intravenously injected with Tolazoline (100 mg/ml, Tolazine; Lloyd Laboratories, Shenandoah, Iowa, at 3.0 mg/kg and released at the capture site.

We marked immobilized deer with uniquely numbered Monel ear-tags in both ears (National Brand and Tag Company; Newport, Kentucky), estimated mass and age, and recorded antler measurements. We collared adult (\geq 2.5 years) males with a 400-g mortalitysensitive radio-collar (Mod M2510B; Advanced Telemetry Systems, Isanti, Minnesota) and yearling (1.5 years) males with the same radio-transmitter unit except the unit was mounted on an expandable collar (Mod M4230B; Advanced Telemetry Systems, Isanti, Minnesota) to allow for growth. We aged captured deer using tooth replacement and wear (Severinghaus 1949) and categorized them as 1.5 or \geq 2.5 years of age. Hereafter, 1.5-yr-olds will be referred to as yearlings and \geq 2.5 as adults. All capture and handling methods were reviewed and accepted by the Louisiana State University Agricultural Center Animal Care and Use Committee (Protocol No. A06-07).

We estimated deer locations via triangulation from 3-6 fixed telemetry stations (n = 178) with a hand-held 3-element Yagi antenna and a R2000 receiver (Advanced Telemetry Systems, Inc., Isanti, Minnesota). We located radio-marked deer 1-5 times a week throughout the study. If radio-marked deer could not be located from the ground, we used fixed-wing aircraft to locate the animal. We used a 15-min maximum time interval among triangu-

lation bearings to minimize error associated with deer movement. If we detected a mortality signal or suspected mortality from a lack of movement, we located the deer using homing. We attempted to determine cause of death in the field or transported the carcass to the Louisiana State University Veterinary School for necropsy.

We used Location of a Signal (LOAS, Version 4.0.2.2 beta, Ecological Software Solutions 1999) with the maximum likelihood estimator method (Lenth 1981) to compute spatial coordinates and estimate error ellipses of deer locations. We used estimated locations with error ellipses ≤ 4 ha and separated by >8 hours to maximize accuracy and potential of independence among observations. We estimated telemetry error during both leaf-on (spring and summer) and leaf-off (winter) periods (Withey et al. 2001) with >50 bearings per observer per season taken on dummy radios (n = 10). We placed "dummy" radios at deer neck height and observers were unaware of the location of the dummy radio. Average angle error was $\pm 7.8^{\circ}$.

We divided seasons into spring (15 Feb–31 May), summer (1 Jun–31 Sept), and fall/winter (1 Oct–15 Feb) based on deer biology (pre-fawning, fawning, and breeding seasons, respectively) and hunting seasons within the study area (1 Oct–15 Feb). We determined peak of breeding and range of conception/parturition through the collection of parturient females during March and April 2007 (n=13) and 2008 (n=10). After counting and sexing fetuses, we used forehead-rump length measurements to determine fetus age in days and back-dated to estimate conception date (Hamilton et al. 1985). Based on the conception date, we added 200 days to determine approximate parturition date (Cheatum and Morton 1942).

To determine the minimum number of locations necessary to estimate home range size, we constructed area-observation curves using 9–14 deer/season. We only included radio-marked deer with \geq 15 locations per season in home range analyses based on our area-observation curves. Prior to analysis, we used Animal Space Use 1.1 Beta (Horne 2005) to estimate the smoothing parameter (*h*) based on the likelihood cross-validation method (CV*h*; Silverman 1986). Once we identified *h* for an individual deer within a season, we calculated home range (95%) and core area (50%) contours using the fixed-kernel method (Worton 1989) within the Animal Movement Extension (Hooge and Eichenlaub 2000) in ArcView. We also constructed composite home range and core areas for radio-marked males monitored three complete seasons.

We used a factorial analysis of variance (ANOVA) to test for season by age interactions in home range and core area sizes with PROC MIXED in SAS V9.1 (SAS Institute, 2003). We first used a one-way ANOVA to test for effects of year on home range and core area, and having observed no differences, constructed a factorial ANOVA with season and age effects. We subsequently used LSMEANS to evaluate differences in mean home range and core area sizes by the interaction between age and season. We considered statistical tests significant at P<0.05.

Survival Analysis

We used MARK (White and Burnham 1999) to calculate survival and cause-specific mortality rates for adult males using a known fate model with season as the interval. To estimate mortality rates from non-hunting causes, we determined survival rates when considering only mortalities from either natural or DVCs while censoring all hunting-related mortalities. Conversely, we estimated hunting-related mortality rates by censoring all non-hunting mortalities when estimating survival. We then calculated cause-specific mortality rates by *1-survival*.

We applied two candidate models to determine effects of season on survival. The first model held survival constant across seasons, whereas the second model allowed survival to vary across seasons. We used Akaike's information criterion (AICc), changes in AICc and Δ AICc values, and Akaike weights (AICw) to evaluate model performance and chose the best-fitting model (Anderson et al. 2000). We developed multiple models because survival rates of male white-tailed deer may vary through time due to fall hunting seasons (Fuller 1990, Hewitt et al. 1999, Ditchkoff et al. 2001).

We did not estimate survival and mortality rates for yearly males because of small sample size and timing of capture. Based on the season of capture, 1.5 yr-old males caught in spring moved into the adult cohort at the onset of the subsequent fall (1 Oct.), therefore these animals were considered 2.5 years old during the first fall after their capture. Thus, we report survival of yearling males as the percentage of the radio-marked sample that survived throughout a season.

Results

Space Use

We excluded seasonal home ranges and core areas for 7 males from analyses due to insufficient number of locations during an individual season as a result of censoring. Consequently, our analyses included 116 home ranges and core areas for 36 males. We only included juvenile males in spring and summer analyses of their capture year due to recruitment into the adult age class at the onset of the fall season. The average number of seasons that males were radio-monitored was 3.1.

Home range ($F_{1/114}$ =0.8, P=0.374) and core area ($F_{1/114}$ =0.99, P=0.322) size did not differ among years, thus we pooled data for further analysis. Season and age interacted to affect both home range ($F_{4/111}$ =7.41, P<0.001) and core area ($F_{4/111}$ =4.47, P=0.002;

Table 1. Mean seasonal home range (HR) and core area (CA) size (ha) of adult and yearling radio-marked
male while-tailed deer in Louisiana from 2007 to 2008.

Season	Age	HR size	HR Standard error	CA size	CA Standard error	
Spring	Yearling	231.6	28.3	39.4	5.8	
	Adult	153.9	16.6	25.5	3.4	
Summer	Yearling	86.1	28.3	15.9	5.8	
	Adult	70.4	16.8	13.4	3.4	
Fall	Yearling	n/a	n/a	n/a	n/a	
	Adult	118	16.9	19.8	3.4	
Composite	Yearling	147.5	14.4	16.7	2.4	
	Adult	108.7	32.8	23.7	5.8	

Table 1) sizes. Adults maintained 68% larger home ranges in fall ($t_{111} = 1.99$, P = 0.049) and 119% large home ranges in spring ($t_{111} = 3.52$, P < 0.001) than summer, as well as 90% larger core areas in spring than summer ($t_{111} = 2.53$, P = 0.013). Yearling deer also maintained 169% larger home ranges ($t_{111} = 3.63$, P < 0.001) and core areas (148%; $t_{111} = 2.89$, P = 0.005) in spring than summer, both of which were larger for yearlings than adults (home ranges, $t_{111} = -2.37$, P = 0.020; and core areas, $t_{111} = -2.08$, P = 0.040) in spring.

Survival

Our estimates of survival rates were based on 34 adult males. During fall hunting seasons, 14 of 34 adult males (41%) were harvested. Aside from harvest, causes of death for adult males included natural (n=3; one from a bacterial infection and two from unknown causes) and DVC during fall (n=2). One adult male was shot, wounded, and later recovered by field staff. The best approximating model showed survival varying across seasons (AICc=74.7243, $\Delta AICc=0$, and AICw=1). Survival was lower in fall (0.55, SE=0.08; Table 2) than summer (0.95, SE=0.03) and spring (1.00, SE=0.00). Mean annual survival was 0.53 (SE=0.08) during 2007–2009. Mean annual mortality rates from harvest (0.40) were greater than non-harvest (0.16). Cause-specific non-

hunting mortality rates included both natural causes (0.09) and DVCs (0.09). Of the 11 radio-marked yearlings, none suffered mortalities prior to the fall hunting season when they were recruited into the adult age class.

Discussion

Our findings suggest that yearlings used 22%–50% more space than adults seasonally. During spring, increased space use of adults was possibly correlated with late breeding activity, prompting males to search for remaining females in estrous (Kammermeyer and Marchinton 1977, Nelson and Mech 1981, Beier and McCullough 1990). Alternatively, early spring also coincides with the time of depleted resource availability, removal of bait by hunters, and the need for males to recover depleted body reserves lost during breeding. A combination of these factors may force deer, especially males, to increase movements to secure necessary resources.

Decreases in space use during summer are common and likely a response to seasonal increases in forage (Harestad and Bunnell 1979, Beier and McCullough 1990), a reduction in conspecific aggression (Thomas et al 1965), increased aggregation (Hirth 1977), and as a response to extreme weather conditions (Michael 1970). Reduced space use in our study during summer could be a result of strategies designed to conserve energy and mitigate thermoregulatory stress and may indicate that deer are able to meet physiological and nutritional needs in a reduced area (Hellickson et al. 2008), with forage availability that may have exceeded metabolic demand (Harestad and Bunnell 1979). We suspect that abundant early successional habitat (created through clearcutting) juxtaposed with mature forest stands provided deer with a mosaic of forage and thermal cover throughout the summer, allowing deer to reduce space use.

Although movement is expected to vary among individuals and be influenced by numerous environmental, ecological, and behavioral variables (Wiens et al. 1995, Phillips et al. 2004), forest management strategies on our study area likely played a key role in

Table 2. Mean survival and cause-specific mortality rates by age age class for male white-tailed deer in Louisiana from 2007–2008.

Age class	Interval	n	Survival		Cause-specific mortality rate							
			Rate	SE	Hunting ^a	SE	Non-hunting	SE	Natural ^b	SE	Vehicular	SE
Yearling	Spring	11	1.00	n/a	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Summer	11	1.00	n/a	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Adult	Spring	34	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Summer	34	0.95	0.03	0.00	0.00	0.05	0.03	0.05	0.03	0.00	0.00
	Fall	34	0.55	0.08	0.40	0.08	0.13	0.07	0.05	0.04	0.09	0.06
	Annual	34	0.53	0.08	0.40	0.08	0.16	0.07	0.09	0.05	0.09	0.06

a. Hunting = legal harvest and wounding loss

b. Natural = known or unknown natural

influencing space use. By implementing timber management plans that continually stagger stand ages using periodic timber harvests and natural or artificial regeneration, the forest management regime resulted in a forest with abundant early and late successional plant communities. The juxtaposition of these plant communities likely resulted in quality browse and cover distributed in a manner that allowed deer to maintain smaller home ranges than expected.

Our estimates of annual survival closely resemble those reported by Bowman et al. (2007) in Mississippi. When considering only adult males, Bowman et al. (2007) reported annual survival rates ranging from 44%–63%. Although deer populations in Texas are in close proximity geographically, survival rates of 50%–91% adult males in several studies (DeYoung 1989, Heffelfinger et al. 1990, Ditchkoff et al. 2001, Webb et al. 2007) may be inflated because males are often protected from harvest until they reach 4.5 or \geq 5.5 yrs old.

Seasonal survival rates in our study were considerably higher outside hunting seasons. Elevated survival during spring (100%) and summer (95%) was due to the lack of hunting, although abundant forage and a decrease in interaction-related injuries between individuals (e.g., fighting among males during the breeding season; Thomas et al. 1965) likely contributed. Our spring and summer survival rates were similar to those reported by Bowman et al. (2007). Survival rates were lowest during fall hunting seasons, which also coincided with breeding periods for deer on our study site. Aside from harvest, the loss of nutritional reserves from breeding activity is known to be stressful for males and can lead to increased susceptibility to natural mortality (Warren et al. 1981, Gavin et al. 1984, Hewitt et al. 1999, Ditchkoff et al. 2001). Although the breeding season on our study area was considered late and rather lengthy, we did not observe any natural mortalities during fall or spring.

Although we could not account for potential harvest of yearling old males through monitoring of our radio-collared animals, harvest data from the Choctaw Co-op over the last 10 years indicates yearling males have made up 18% of the total harvest for males. Bowman et al. (2007) reported that hunters often harvested yearling males by mistake, believing them to be females, which could partially be responsible for the harvest rate of yearling males on our study area.

We offer that age-specific survival for males was a function of antler restrictions in place on our study area. Harvest records within the Co-op indicate main beam length and inside spread for 2.5- yr-old males (n = 1491; 1997–2007) average 34.5 and 29.7 cm, respectively. For 3.5-yr-old males (n = 1236; 1997–2007), the same measurements averaged 38.4 and 33.0 cm. Thus, with Co-op antler restrictions set at 38.1 and 33.0 cm for the same two measurements, the average 2.5-yr-old male falls slightly short of the restrictions and the average 3.5-yr-old males harvested within the Co-op just barely meet the minimum requirements. According to the average antler characteristics of male deer found within the Co-op, 1.5-yr-old males and average 2.5-yr-old males should be protected from harvest. However, males in these age classes comprised 60% of the annual buck harvest and males >3.5-years of age (which generally exceed the restriction) comprised only 35% of the annual male harvest. We suspect that survival of males on our study site decreases as males approach the antler restriction, regardless of age.

Deer-vehicle collisions can be a significant source of mortality in some regions (Miller et al. 2003), with incidents usually peaking at the height of breeding season (Allen and McCullough 1976). Both DVCs in this study occurred during fall and involved males of 2.5 and 5.5 years of age. Although only four roads (three twolane paved roads, one Interstate) passed through the study area, vehicular-related mortalities resulted in a probability of males dying from DVCs equal to that of natural mortalities. Thus, it appears that DVCs may be an important source of mortality for mature males on our study area.

Management Implications

Our results indicate that white-tailed deer on our study site maintained much smaller home ranges than populations in other areas of the Southeast. These small home ranges have implications for private landowners who own or manage \leq 300 ha of managed bottomland hardwood forests and highlight the benefits of cooperatives as a useful tool to increase the acreage influenced by management activities. If managing for larger antler size, managers may need to consider ways to decrease harvest rates of adult males. For example, more restrictive antler restrictions or a focus on morphological characteristics may be required to allow males to reach older age classes. The cumulative probability of an adult male ultimately living \geq 4.5 years is minimal; thus, increasing antler restrictions as well as increasing education and commitment to management by cooperating landowners may alleviate some of the current harvest pressure on males.

Acknowledgments

Funding and support were provided by the Louisiana Department of Wildlife and Fisheries; A. Wilbert's Sons, LLC; Acoustical Supplies; the Quality Deer Management Association (QDMA); the South Louisiana Chapter of QDMA; the Bercham Group; Acadian Sportsman's League; Bayou State Bowhunters; the Louisiana Wildlife and Fisheries Foundation; the School of Renewable Natural Resources at Louisiana State University (LSU); and the LSU Agricultural Center. This manuscript was approved for publication by the Director of the Louisiana Agricultural Experiment Station as manuscript number 2009-241-4086.

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