Survival of Rural and Urban White-Tailed Deer in Missouri

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Abstract: Information on survival rates and causes of mortality are important to understanding white-tailed deer *(Odocoileus virginianus)* population dynamics and implementing appropriate management practices. We examined sex- and age-specific survival rates for three Missouri white-tailed deer populations that represented agricultural, forest, and urban landscapes. Except for males on Woods Farm (forest site), we observed no differences in age-specific or annual survival for male or female deer >6 months of age. For this exception, greater yearling than adult survival was attributed to deer harvest strategies that emphasized harvest of adult males. On the two rural study sites, hunting-related mortality accounted for 66% and 61% of female mortalities and 82% and 97% of male mortality. On the urban site, mortality was evenly distributed within a calendar year and collisions with vehicles accounted for most mortality (males 66%–86%; females 79%–81%), essentially replacing hunting mortality with overall annual survival rates similar to the rural sites.

Key words: Missouri, mortality, *Odocoileus virginianus*, radiotelemetry, survival

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In recent years, white-tailed deer populations have increased in rural settings as well as in metropolitan areas which have suitable green space (McAninch 1995). Increased human-deer conflicts have prompted changes in management emphasis (Conover et al. 1995). Restrictive hunting seasons have given way to liberalized harvest to control numbers (Woolf and Roseberry 1998, Brown et al. 2000). Currently, in most states, white-tailed deer overabundance is a more vexing management issue than underabundance (McShea et al. 1997, Warren 1997).

Deer management has become more complex because both underharvest and overharvest can generate public dissatisfaction. Also, the scale at which deer management occurs has become more variable. Increasingly, deer management decisions must be made on both regional and local scales. Urban settings, where traditional management activities may be prohibited by local ordinances, further complicate herd management and monitoring.

Understanding the factors that influence white-tailed deer populations is an essential component of management. Accurate input parameters are necessary for population models to forecast population effects resulting from regulation or policy change (Walters and Gross 1972, Roseberry and Woolf 1991). Model parameters most affecting change include reproductive and mortality rates (Medin and Anderson 1979), and nonhunting mortality is a significant unknown parameter in population management (Nelson and Mech 1986). Recent deer research in Missouri has focused on collecting information for input into regional population models (Hansen et al. 1996, 1997). Our objective was to determine survival rates of white-tailed deer in agricultural, forested, and urban/suburban landscapes in Missouri.

Study Area

Our study encompassed three areas that represented agricultural, forested, and urban landscapes in Missouri. Thomas Hill study area (TH) served as the agricultural area. TH, located within the Glaciated Plains Natural Division (Thom and Wilson 1980), covered 709 km^2 in Randolph and Macon counties in north-central Missouri. Topography was gently rolling with row-crop agriculture common along river bottoms, pasture on hillsides, and cleared uplands and scattered unmanaged forest. About 14% of the area was forested, 38% in row crops, 43% in pasture and the remainder mostly in water or city/commercial use (Giessman et al. 1986, Pauley 1991). Surface mining for coal was common before 1993; mined land in various stages of succession from reclaimed grassland to closed canopy forest dominated parts of the study area. TH included a 2,000-ha reservoir surrounded by a 2,246-ha public area managed by the Missouri Department of Conservation (MDC) and a 983-ha reservoir surrounded by a 742-ha unhunted state park. The balance was comprised of private ownerships ranging from <1 ha to 1,970 ha. Simulated fall deer densities for the deer management unit (DMU) in which TH was located averaged 5.6/km^2 of total area during the study period 1989–1993 (L. P. Hansen, Missouri Department of Conservation, unpublished data).

During the study, all TH hunters could obtain up to two permits to take deer (only one of which could be antlered) during a 9-day firearms season or an 18-day muzzleloading firearms season; around 70% of hunters obtained both permits. Archers could harvest 2 deer of either sex during an 83-day archery season. Approximately 6% of the study area was open to public hunting and generally received heavy hunting pressure. Root et al. (1988) reported hunting activity of 1.3 hours/ha/day during the firearms deer season on a Missouri public area similar to TH. Hunting activity on private land on TH varied from none to heavy. For the DMU in which TH was located, hunter densities averaged 1.8/km^2; total harvest for 1989–1993 averaged 1.2 deer/km^2 with female harvests averaging 0.5/km^2.

Woods Farm (WF) study area, selected as the forested area, was 91 km^2 in the Ozark Natural Division (Thom and Wilson 1980) in Crawford and Phelps counties. The area was mostly oak-hickory (*Quercus* spp and *Carya* spp) forest with steep to nearly level topography. Forest soils were thin and stony but the area contained a series of broad fertile bottomland fields. WF included two large private tracts (1,268 ha) where access was limited and three publicly-owned areas totaling 2,991 ha. Simulated fall deer densities for the DMU incorporating WF averaged 3.9/km^2 total area during the study period 1993–1996. Although DMU deer populations were low, deer densities on some portions of WF were high, approaching 25/km^2 (Haroldson 1999).

WF was in a deer management unit with restrictive harvest opportunities. Only one deer could be harvested during the firearms or muzzleloading firearms seasons and approximately 50% of the hunters were restricted to antlered deer. Archery regulations were identical to those on TH. In the DMU incorporating WF, total harvest averaged 0.7 deer/km^2 during 1993–1996 with female harvests averaging 0.2/km^2. Hunter densities averaged 1.7/km^2.

The Town and Country (TC) study area was a 67-km^2 suburban area in St. Louis county. TC had a mix of affluent housing developments interspersed with green space, including a 230-ha county park. Major cover types were residential (44%), wooded (27%), and open (17%). Developed commercial properties, open water, and construction sites composed 12% of the study area (J. Beringer, Missouri Department of Conservation, unpublished data). TC was intersected with roads including multi-lane highways with high-speed traffic. Aerial surveys of TC conducted during the study indicated deer densities averaged 22/km^2 total area during winter. Ordinances against the discharge of firearms or bows on TC prohibited legal deer harvest on most of the study area. Some deer dispersed to areas open to hunting and were legally taken by hunters. Others were taken by hunters on the study area in spite of the ordinances. In both cases the deer were classified as deer taken during the legal hunting season.

Methods

We captured deer with rocket nets and modified Clover traps (Beringer et al. 1999) from December through March 1988 to 1992, 1993 to 1996, and 1997 to 1999 on TH, WF, and TC, respectively. Capture efforts generally were distributed throughout each study area. We blindfolded, manually restrained (in some cases sedated with a 2.4:1 mixture of ketamine and xylazine) and aged captured deer as fawn (<1 year) or adult (≥ 1 year) based on body size and, for males, antler development. All deer received numbered metal ear tags (Salt Lake Stamp Co., Salt Lake City, Utah). Most females and some males received motion-sensitive radio transmitters on a 4-h switch (Advanced Telemetry Systems, Inc., Isanti, Minnesota, Lotek Engineering, Newmarket, Ontario, or Telonics, Inc., Mesa, Arizona). Most deer received intramuscular injections of procaine penicillin G (Universal Cooperatives, Minneapolis, Minnesota) or liquamycin (Pfizer Laboratories, New York, New York) to reduce the risk of infection caused by capture and processing.

Radiomarked deer were located 2–3 times per week with 4-element antennas mounted on vehicles and attached to a scanning receiver. We used aircraft with mounted antennas to search for missing deer or to locate deer that moved off study areas. We immediately located deer with transmitters in mortality mode and, if dead, conducted a field necropsy to determine cause of death. Deer mortalities with no apparent cause were submitted to the Veterinary Medical Diagnostic Laboratory at the

University of Missouri, Columbia, for necropsy. Often, deer carcasses had been moved by predators or scavengers, preventing the transmitter from switching to mortality mode. Near complete consumption of the deer prevented us from determining the cause of death in many of these cases.

We divided the year into three survival periods: summer (1 June to 30 September), fall–early winter (1 October to 15 January) and winter–spring (16 January to 31 May) corresponding with important demographic events for Midwestern deer (Nixon et al. 1991), including parturition in summer, the hunting season in fall–early winter, and dispersal and migrations during winter–spring. We used the program STAGKAM (Kulowiec 1989) which uses a Kaplan-Meier staggered entry approach to estimate seasonal and annual survival rates (Pollock et al. 1989). We assumed the probability of being censored was independent of a deer's fate (Vangilder and Sheriff 1990) and included censored deer in the analyses. We used log-rank tests (Pollock et al. 1989) to compare annual, seasonal, sex-specific, and age-specific differences in survival.

To eliminate bias associated with capture-related mortalities, we excluded deer dying within 30 days of capture from the analysis. We considered a deer lost when a transmitter signal was not obtained for two consecutive flights. Although some lost deer were eventually observed or appeared in the legal deer harvest, for our analyses these deer were censored on the date the signal was lost (Pollock et al. 1989).

Monitored deer were advanced into the next older age class on 1 June of each year. Although most deer were not separated into yearling ($\geq$1 year and $<$2 years of age) or adult ($\geq$2 years of age) age classes at capture, we were able to conduct survival analyses for these age classes. Deer were first captured at $>$6 months of age; therefore, we compared survival of fawn ($>$6 months and $<$1 year of age), yearling, and adult deer during winter–spring. However, we compared only survival of yearling and adult deer during summer and fall–early winter.

Hunting was a major mortality factor on TH and WF. On TH we interviewed most landowners to determine hunting pressure distribution and to identify exposure of marked deer to hunting. Locations with multiple hunters during the firearms season were classified as hunted while those properties with no or very restricted hunting were classified as unhunted. Home ranges of deer often included both hunted and unhunted properties. Based on the proportion of locations in each, females were classified as inhabiting primarily hunted or unhunted land. Deer using hunted or unhunted properties equally or occupying properties for which the hunting status was not known were excluded from the analysis.

Results

We radiomarked 530 female (253, 146, and 131 on TH, WF, and TC, respectively) and 236 male (37, 76, and 123 on TH, WF, and TC, respectively) white-tailed deer. Of females, 66 died as a result of capture (Beringer et al. 1996) and were excluded from the analyses, resulting in 217, 136, and 120 monitored females on the TH, WF, and TC, respectively; 26 males died as a result of capture, leaving 36, 69, and 105 monitored males on TH, WF, and TC, respectively. Excluding capture-related deaths, we recorded 120 male and 166 female mortalities.

Firearms hunting was the most important mortality factor for females on TH and WF (Table 1). Hunting-related mortality accounted for 66% and 61% of female mortalities on TH and WF, respectively. Other female mortality factors on TH were illegal kill (11%), unknown factors (11%), and deer-vehicle accidents (8%). Illegal kill also was important on WF (9% of female mortality) but only one deer-vehicle accident occurred. On WF 14% of female mortality was attributed to disease primarily during summer 1996 when a mild outbreak of epizootic hemorrhagic disease killed several radiomarked females (Beringer et al. 2000). Otherwise, disease incidence on WF and TH was low (Table 1). Conversely, most (90%) female mortality on TC involved collisions with vehicles (Table 1).

Survival distributions, seasonal survival estimates, and annual survival estimates for females did not differ between age classes (log likelihood tests, $P > 0.05$) on any study area for any year, so we grouped age classes for further analyses. Seasonal survival patterns were similar on TH and WF for all years with fall survival lower ($P < 0.05$) than summer and winter–spring survival. There were no differences between summer and winter–spring survival (Table 2). On TC survival rates of females did not differ among seasons ($\chi^2 = 1.4$, df = 2, $P = 0.50$ and $\chi^2 = 2.1$, df = 2, $P = 0.35$ for 1997–98 and 1998–99, respectively). Survival did not differ among years for TH or TC but survival on WF was lower in 1995–96 than in 1994–95 ($\chi^2 = 3.7$, df = 1, $P = 0.05$). A change in female harvest management strategies on two large private ownerships on WF may account for this difference (Table 2).

Hunting mortality was greater for males than females on all three study areas (Table 1). Hunting made up 82%, 97%, and 18% of all male mortality on TH, WF, and TC, respectively. Deer-vehicle accidents accounted for 11% of deaths on TH and was the greatest male mortality factor (63%) on the TC, but did not account for any mortalities on WF.

Survival of males did not differ between age classes on TH or TC (log likelihood tests, $P > 0.05$) so their age classes were pooled for further analyses. A hunting strategy on WF that protected yearling males resulted in survival of adult males during fall 1994–95 being lower than that of yearlings ($\chi^2 = 4.7$, $P = 0.03$); therefore, these classes were separated (Table 3). Male survival was lowest in fall on all three study areas ($P > 0.05$). The differences were greatest on TH and WF with mortality more evenly distributed on TC (Table 3).

Initially, most trapping on TH occurred on unhunted areas because deer densities were highest and large numbers of deer could be captured and marked. Starting in 1992 we captured deer in areas that included a mix of hunted and unhunted sites. Therefore, marked deer locations through 1991–92 were mostly on unhunted lands, but later we had larger samples in hunted areas (Table 4). Low sample sizes of radiocollared males precluded comparisons between hunted and unhunted areas, therefore TH comparisons were restricted to females. On TH annual female survival rates were lower on hunted areas during all years except 1991–92 ($\chi^2 = 12.3$, df = 1, $P < 0.01$, $\chi^2 = 11.7$, df = 1, $P < 0.01$, $\chi^2 = 0.4$, df = 1, $P < 0.52$, $\chi^2 = 5.3$, df = 1, $P = 0.02$ for 1989–90, 1990–91, 1991–92 and 1992–93, respectively).

Table 1. Cause of death (%) for male (M) and female (F) white-tailed deer on three Missouri study areas. Agricultural, forest, and urban/suburban landscapes are represented by TH, WF, and TC, respectively. Total number of mortalities are in parentheses.

		TH 1989–1993		WF 1993–1996		TC 1997–1999	
Cause of death	Season	M	F	M	F	M	F
Firearms hunting	Fall	63(17)	58(49)	90(28)	40(17)	2(1)	0
Archery hunting	Fall	15(4)	4(3)	0	14(6)	11(7)	5(2)
Hunting wounding loss	Fall	4(1)	5(4)	7(2)	7(3)	5(3)	0
Total hunting-related		82(22)	66(56)	97(30)	61(26)	18(11)	5(2)
Illegal kill	Summer	0	7(6)	0	2(1)	0	0
	Fall	0	4(3)	0	7(3)	0	0
	Winter–spring	0	0	0	0	0	0
Total illegal kill		0	11(9)	0	9(4)	0	0
Vehicle collisions	Summer	4(1)	1(1)	0	0	14(9)	24(9)
	Fall	4(1)	6(5)	0	0	31(19)	21(8)
	Winter–spring	4(1)	2(2)	0	2(1)	18(11)	45(17)
Total vehicle collisions		11(3)	8(8)	0	2(1)	63(39)	90(34)
Disease	Summer	0	1(1)	0	12(5)	0	0
	Fall	0	2(2)	0	0	0	0
	Winter–spring	0	0	0	2(1)	0	0
Total disease		0	4(3)	0	14(6)	0	0
Caught in fence	Summer	0	0	0	0	0	0
	Fall	0	0	0	0	0	0
	Winter–spring	0	0	0	0	3(2)	0
Total caught in fence		0	0	0	0	3(2)	0
Unknown	Summer	0	4(3)	3(1)	7(3)	2(1)	3(1)
	Fall	7(2)	2(2)	0	2(1)	10(6)	0
	Winter–spring	0	5(4)	0	5(2)	5(3)	3(1)
Total unknown		7(2)	11(9)	3(1)	14(6)	16(10)	5(2)
Total	Summer	4(1)	13(11)	3(1)	21(9)	16(10)	26(10)
	Fall	92(25)	80(68)	97(30)	70(30)	58(36)	26(10)
	Winter–spring	4(1)	7(6)	0	9(4)	26(16)	47(18)

Discussion

Excluding hunting, survival exceeding 90% on TH and WF was similar to that reported for lower Midwestern deer populations (Nixon et al. 1991, 1994, 2001). In spite of landscape differences, nonhunting mortality of males and females on TH and WF were low with little annual variation during the study periods. Male and female deer on WF were less likely to die from collisions with vehicles than on TH, possibly

Table 2. Seasonal and annual survival of radio collared female white-tailed deer on three Missouri study areas. Agricultural, forest, and urban/suburban landscapes are represented by TH, WF, and TC, respectively.

			Survival		
Study area	Season[a]	Year	*N*[b]	Rate	SE
TH	Winter–spring	1989	37	1.00	0.000
	Summer	1989	31	1.00	0.000
	Fall	1989–90	40	0.86	0.050
	Winter–spring	1990	78	1.00	0.000
	Annual		78	0.86	0.036
	Summer	1990	77	0.96	0.022
	Fall	1990–91	81	0.86	0.035
	Winter–spring	1991	109	0.99	0.010
	Annual		109	0.82	0.033
	Summer	1991	109	0.97	0.016
	Fall	1991–92	103	0.85	0.034
	Winter–spring	1992	132	0.98	0.013
	Annual		132	0.81	0.031
	Summer	1992	129	0.98	0.014
	Fall	1992–93	119	0.86	0.032
	Winter–spring	1993	125	0.98	0.012
	Annual		129	0.83	0.032
	Summer	1993	114	0.99	0.010
	Fall	1993–94	99	0.86	0.035
WF	Winter–spring	1994	63	0.98	0.019
	Summer	1994	63	1.00	0.000
	Fall	1994–95	91	0.94	0.024
	Winter–spring	1995	128	0.99	0.008
	Annual		128	0.94	0.021
	Summer	1995	128	0.98	0.013
	Fall	1995–96	123	0.90	0.027
	Winter–spring	1996	109	0.99	0.009
	Annual		128	0.87	0.030
	Summer	1996	106	0.94	0.022
	Fall	1996–97	100	0.89	0.031
TC	Winter–spring	1997	67	0.92	0.032
	Summer	1997	65	0.91	0.036
	Fall	1997–98	63	0.91	0.034
	Winter–spring	1998	93	0.95	0.023
	Annual		93	0.79	0.039
	Summer	1998	88	0.95	0.022
	Fall	1998–99	84	0.95	0.023
	Winter–spring	1999	80	0.89	0.038
	Annual		88	0.81	0.045

a. Fall survival significantly differed from that in winter–spring and summer ($P < 0.05$). Fall season extends over 2 calendar years through January 15.

b. Number at risk at beginning of period plus number added in staggered entry during the period.

Table 3. Seasonal and annual survival of radio collared male white-tailed deer on three Missouri study areas. Agricultural, forest, and urban/suburban landscapes are represented by TH, WF, and TC, respectively.

Study area	Season[a]	Year	Survival		
			N[b]	Rate	SE
TH	Winter–spring	1992	34	0.97	0.030
	Summer	1992	31	0.97	0.033
	Fall	1992–93	29	0.50	0.107
	Winter–spring	1993	11	0.90	0.095
	Annual		31	0.44	0.109
WF	Winter–spring	1994	15	1.00	0.000
	Summer	1994[c]	29	1.00	0.000
	Fall-yearlings	1994–95	7	0.71	0.144
	Fall-adults	1994–95	9	0.29	0.139
	Winter–spring	1995	16	1.00	0.000
	Annual-yearlings		14	0.63	0.128
	Annual-adults		15	0.29	0.091
	Summer	1995	28	1.00	0.000
	Fall-yearlings	1995–96	10	0.44	0.191
	Fall-adults	1995–96	14	0.18	0.167
	Winter–spring	1996	9	1.00	0.000
	Annual-yearlings		12	0.44	0.125
	Annual-adults		16	0.18	0.118
	Summer	1996[d]	9	1.00	0.000
	Fall-adults	1996–97	9	0.22	0.139
TC	Winter–spring	1997	59	0.84	0.046
	Summer	1997	52	0.86	0.047
	Fall	1997–98	45	0.79	0.054
	Winter–spring	1998	66	0.92	0.033
	Annual		66	0.63	0.050
	Summer	1998	60	0.95	0.028
	Fall	1998–99	57	0.54	0.069
	Winter–spring	1999	27	0.92	0.059
	Annual		60	0.47	0.076

a. Fall season extends over 2 calendar years through January 15.

b. Number at risk at beginning of period plus number added in staggered entry during the period.

c. Yearlings and adults separated because of survival differences.

d. Data available only for adults.

Table 4. Fall survival of radio collared female white-tailed deer on hunted and unhunted portions of TH (agricultural study area), 1989–1994.

Fall survival period[a]	Hunted			Unhunted		
	N[b]	Survival	SE	*N*[b]	Survival	SE
1989–90	24	0.80	0.073	16	1.00	0.000
1990–91	37	0.78	0.065	48	0.94	0.013
1991–92	42	0.81	0.058	61	0.88	0.041
1992–93	72	0.79	0.048	47	0.98	0.022
1993–94	71	0.85	0.043	27	0.89	0.060

a. Fall period extends over 2 calendar years through January 15.

b. Number at risk at beginning of period plus number added in staggered entry during period.

because deer on TH were more likely to disperse, often moving long distances. Also, there was a more developed road system on TH so deer were more likely to encounter roads in their movements.

Female survival on the unhunted portion of TH exceeded 90%. This, along with little evidence that deer populations in lower Midwest exhibit density dependence (Nixon et al. 1991), suggests that female hunting mortality on TH, and likely also on WF, was additive to other mortality factors (Bartmann et al. 1992). We were not able to compare survival of males on hunted and unhunted portions of TH but we suspect that, as with females, hunting mortality of males was mostly additive. However, in some unhunted settings males may have higher mortality than females (Ditchkoff et al. 2001). Additive mortality has been suggested in other studies of white-tailed deer (Dusek et al. 1992, Whitlaw et al. 1998). Compensatory mortality likely is rare in deer in the lower Midwest due to mild winters, ready access to food, and deer populations that are maintained well below the biological carrying capacity by hunting. Compensation could occur in other parts of the white-tailed deer range, especially where deer densities approach or exceed carrying capacity (McCullough 1984) or possibly where males are exploited at an extremely high rate.

Causes of deer mortality on TC differed from those on TH and WF. Collisions with vehicles on TC essentially replaced hunting mortality with overall annual survival rates similar to the rural sites. Cornicelli (1992), Witham and Jones (1992), and Swihart et al. (1995) also noted that collisions with vehicles were the most important deer mortality factor on urban study areas. Annual survival varied among these sites, ranging from 0.56 for yearling females at a suburban Chicago, Illinois, site (Witham and Jones 1992) to 0.86 for yearling females in Bridgeport, Connecticut (Swihart et al. 1995).

Results of this and other studies in lower Midwestern states suggest that non-hunting mortality rates are low with little annual variation. Similarly, reproductive rates are generally constant (Hansen et al. 1996). Rural deer populations are most impacted by harvest in Missouri so, given an accurate measure of annual deer harvest, accounting models may be a useful tool for predicting population size and guiding annual deer harvest recommendations. An exception occurs during periodic mortality events, such as outbreaks of epizootic hemorrhagic disease (Fischer et al. 1995, Beringer et al. 2000) when the magnitude of these outbreaks is unpredictable. Modeling can be useful in post-mortem assessments of epizootic hemorrhagic disease impacts (Fischer et al. 1995); however, these assessments may not be practical until several years after the outbreak. Management decisions for areas that have experienced disease outbreaks using models that do not account for this mortality can result in overharvest (Fischer et al. 1995).

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