# **Population characteristics of a central** Appalachian white-tailed deer herd

# Tyler A. Campbell, Benjamin R. Laseter, W. Mark Ford. and Karl V. Miller

**Abstract** Reliable estimates of white-tailed deer (Odocoileus virginianus) population parameters are needed for effective population management. We used radiotelemetry to compare survival and cause-specific mortality rates between male and female white-tailed deer and present reproductive data for a high-density deer herd in the central Appalachians of West Virginia during February 1999–May 2002. We recorded 343 winter deer captures. Our capture rate of 78 fawns/100 adult females was similar to visual observations of known fawns and adult female deer during winter. In-utero reproductive rates of adults  $(\ge 1$  year old) was 138 fawns:100 iemales, based on a sample of 44 female deer. We radiomonitored 148 female and 43 male deer during the 3-year study. Yearling male annual mortality rates for human-induced and natural mortality were 0.63 (SD=0.09) and 0.12 (SD=0.12), respectively. Conversely, among yearling females. annual mortality rates for human-induced and natural mortality were 0.09 (SD=0.06) and 0.05 (SD=0.03), respectively. Adult male annual mortality rates for human-induced and natural mortality were 0.73 (SD=0.16) and 0.00, respectively, whereas adult female annual mortality rates for human-induced and natural mortality were 0.04 (SD=0.01) and 0.08 (SD=0.02), respectively. Our observed survival, mortality, capture, and reproductive data are characteristic of a population shaped by moderate fawn recruitment and excessive harvest of yearling male deer. We recommend a reduction in female deer to promote forest regeneration and protect biodiversity in this region. We believe this can best be achieved by liberalizing antierless harvest regulations, through hunter education and corporate landowner incentive programs.

Key words Appalachians, mortality, Odocoileus virginianus, recruitment, reproduction, survival, white-tailed deer

, •

Current annual forest removals in West Virginia are >12,000,000 m<sup>3</sup> of sawtimber and pulpwood (United States Department of Agriculture Forest Service 2004), a level which approximates that of the large, widespread harvests at the turn of the twentieth century (Stephenson 1993b). Forest management and wood production are a valuable mainstay of the state's and region's economy (Spencer 1997, Adams et al. 2000). Likewise, this

portion of the central Appalachians, particularly the eastern one-third of the state, is regarded as an important biodiversity hotspot within the Appalachians and among all temperate forested ecosystems (Stephenson 1993a, Chaplin et al. 2000. Roberston and Hull 2003, Ford et al. 2005). From a natural resource management perspective, the conservation of biodiversity and management of economically valuable and ecologically sustainable

Wildlife Society Bulletin 2005, 33(1):212-221

Address for Tvier A. Campbell, Benjamin R. Caseter, and Karl V. Miller: Warnell School of Forest Resources, University of Georgia. Athens, GA 30602, USA: present address for Camphell: NWRC, Texas Field Station, Texas A&M University-Kingsville, MSC 218 "00 University Blvd., Kingsville, "N 78363-8202; e-mail: Mierialcampbell@aphislusdal.gov.: Address for W. Mark Ford: United States Department of Agriculture, Forest Service, Northeastern Research Station, Box 404, Parsons, WV 26287, USA

forests can be complementary activities within the central Appalachians (Fredericksen 1998). However, sustaining these outputs either singly or in concert is complicated by forest system stressors such as atmospheric acid deposition (Adams 1999), exotic insect and disease pathogens (Stipes 1999, Souto and Shields 2000, Davidson et al. 2001), and white-tailed deer (*Odocoileus virginianus*) herbivory (deCalesta 1994, Fredericksen 1998, Horsley et al. 2003) that are occurring in the central Appalachians. For wildlife biologists, white-tailed deer herbivory impacts to ecosystem processes and forest management activities are of paramount interest and concern in this region.

After the near extirpation of white-tailed deer populations from West Virginia during the early 1900s, populations increased due to buck-only hunting regulations, increases in favorable habitat, and restocking efforts (Allen and Cromer 1977). Throughout the last half of the twentieth century. West Virginia had liberal buck harvests with comparatively conservative doe harvests. Populations have increased in some locations to a point where forest damage is apparent (Michael 1987, 1992). On corporate forest lands, altered or failed woody regeneration is common (Tilghman 1989, Horsley et al. 2003). To promote healthier ecosystems and balanced deer populations, harvest regulations have been altered to increase the harvest of female deer. However, in comparison with other southeastern states, antlerless harvest in West Virginia is low (37% of total, Annual Meeting of the Southeast Deer Study Group 2003) and likely insufficient to stabilize deer herds in the near future (J. L. Crum, West Virginia Division of Natural Resources, personal communication). In West Virginia this is due partly to decreasing resident and nonresident hunter recruitment, coupled with a stable to decreasing human population. No sex-, age-, or cause-specific estimates of survival and mortality rates exist for white-tailed deer in West Virginia, hindering biologists' efforts.

Reliable estimates of survival mortality, and reproductive rates are requisite to understanding and managing deer populations (Caughley 1976, Eberhardt 1985, Dusek et al. 1989). Radiotelemetry provides an in-depth evaluation of the timing, causes, and degree of mortality (Heisey and Fuller 1985, Nelson and Mech 1986). Herein, we compared survival and cause-specific mortality rates between male and female white-tailed deer using radiotelemetry and present reproductive and

recruitment data for a high-density deer herd that is in conflict with land management in the central Appalachians of West Virginia.

## Study area

Our study was conducted on the MeadWestvaco Corporation's Wildlife and Ecosystem Research Forest (MWWERF) in Randolph County, West Virginia (38º42'N, 80º3'W), which was established in 1994 to assess the influence of industrial silviculture on ecological and ecosystem processes in the central Appalachians. The 3,360-ha MWWERF occurred in the Unglaciated Allegheny Mountain and Plateau Physiographic province within the central Appalachians where precipitation averaged from 170-190 cm/year and elevations ranged from 740-1,200 m (Smith 1995). Forest cover was primarily an Allegheny hardwood-northern hardwood rype (Ford and Rodrigue 2001). Silviculturally, the WMMERF was intensely managed, with even-aged regeneration methods dominating. Preharvest white-tailed deer densities during our study were estimated as 12-20 decr/km<sup>2</sup> (Langdon 2001). Abomasal parasite counts suggested the deer population was at nutritional carrying capacity (Fischer 1996). The MWWERF was open to hunting under West Virginia Division of Natural Resources harvest regulations, with access via foot-travel. Recent and ongoing research have determined that white-tailed deer were serving as a primary ecological agent shaping plant species diversity, abundance, and structure on the MWWERF (B. Collins, Savannah River Ecology Laboratory, personal communication, Collins 2004). Indirect impacts to biota, such as ground-nesting songbirds, have been noted (Weakland 2000).

## Methods

We captured deer from January through April (1999-2001) using modified Clover traps (Clover 1954) and rocket nets (Hawkins et al. 1968) baited with corn. We immobilized, ear-tagged, and radiocollared (Advanced Telemetry Systems, Isanti, Minn.) deer upon capture. We used both physical restraint and chemical (2.2 mg xylazine hydrochloride/kg body weight) immobilization techniques. For chemically immobilized deer, we used <sup>1</sup><sub>2</sub> intravenous and <sup>1</sup><sub>2</sub> intranuscular injections of yohimbine hydrochloride (0.3 mg/kg body weight) as a reversal agent. Radiocollars were equipped with 8hour mortality sensors. We aged deer by tooth eruption, replacement, and wear (Severinghaus 1949). All capture and handling procedures were approved by the University of Georgia's Institutional Animal Care and Use Committee (Permit No. A2002-10119-0).

We monitored each deer  $\geq 3$  times/week from its release, until it died, the study terminated (1 June 2002), or it was censored. We censored deer when they dropped their collars or the collar battery expired. When mortality signals were detected, we located the carcass via homing and conducted a necropsy to determine cause. Predation was identified following procedures in Wade and Bowns We determined starvation from visual (1984). inspections of femur marrow (Verme and Ullrev 1984). Disease was inferred following Davidson and Nettles (1997). Collars from harvested animals commonly were left at the property gates with a note, turned in to the field station, left with the gut pile, or taken home with hunters.

We recorded all visual observations of deer during vehicular travel on the MWWERF, noting age (fawn, adult [ $\geq$ 1 year old], or unknown), sex (male, female, or unknown), group size, and tag numbers when possible. We calculated monthly ratio of fawns:100 adult females for known age and sex observations only. We determined age-specific inutero reproductive rates (fetuses/doe) from 3 does necropsied in 2000, 2 does necropsied in 2001, and 39 does necropsied in 2002. Median and mode conception dates were both 16 November (range= 4 November-23 December). We acquired and examined all female reproductive tracts from January-March.

We determined survival and cause-specific mortality rates from telemetry data for fawns, yearlings, and adults (>2 years old) with MICROMORT (Heisev and Fuller 1985). For all analyses we assumed a 1 June birthday of each cohort. We divided the year into 3 seasons: summer (1 June-30 September), autumn (1 October-31 December), and winter (1 January-31 May). We grouped mortality sources as either natural (starvation, predation, or disease) or human-induced (legal harvest, wounding loss, illegal harvest, or vehicular trauma). Our analyses considered the exposure days of censored deer through the day of censoring (Vangilder and Sheriff 1990). We did not include deer that died of natural causes  $\leq 21$  days after capture in the analyses, to avoid inclusion of deer vulnerable to predation due to capture myopathy (Beringer et al. 1996).

We pooled data from all 3 years to increase sample sizes of males, thereby facilitating meaningful between-sex comparisons (Van Deelen et al. 199<sup>+</sup>). To validate pooling of data from the 3 years, we used 2-tailed Z-tests to compare mortality rates within females among years. Similarly, we used 2-tailed Z-tests to compare mortality rates among ages, between sexes, and among seasons (Heisey and Fuller 1985) on pooled data. To maintain experiment-wise error rate of  $\alpha = 0.05$ , we compared related tests following Bonferroni correction (Sokal and Rohlf 1995).

. .

We estimated survival of fawns from birth to capture (i.e., recruitment age) using change-in-ratio (CIR) estimators (Paulik and Robson 1969). We defined a deer capture as any capture of an individual deer not previously captured within the current trapping year (i.e., recaptures within a trapping year were not included). Time 1 ratios were estimated from capture data, survival estimates, and inutero reproductive estimates. Specifically, we estimated the total number of fawns born to female deer by 1) adding the estimated number of deaths (via vearling and adult survival rates from Junc-December) to the age-specific number captured (this yielded an estimated number of vearling and adult females alive at birth), 2) multiplying the age-specific number of females alive at birth and estimated age-specific in-utero reproductive rates (this vielded an age-specific estimate of fawns born), and 3) summing the age-specific estimates of fawns born across ages. We obtained Time 2 ratios directly from capture data and validated them with observational data.

## Results

We recorded 343 captures of white-tailed deer. Fawns were the dominant age class, representing 41.7% (n=143) of all captures. Females were the dominant sex class, comprising -5.8% (n=260) of all captures. Adult male deer were notably scarce, representing only 1.5% (n=5) of all captures (Figure 1). The ratio of fawns:100 adult ( $\geq$ 1 year old) females at capture was -8.

Overall in-utero reproductive rates of yearling and adult females were 138 fawns:100 females (51 fawns per 37 yearling and adult females). Reproductive rates were greater for adults than yearlings. We observed no evidence of breeding by female fawns (n=7), and 1 adult had 3 femses inutero.



Figure 1. Population profile from white-tailed deer captures (Jan–Apr, n = 343) on the MeadWestvaco Wildlife and Ecosystem Research Forest, West Virginia from 1999–2002. Slashed areas plus respective shaded areas are the estimated number of fawns born to female deer captured (from in utero reproductive rates) assuming a 50:50 sex ratio at birth.

We made 8,497 visual observations of known fawns and adult female deer. Ratios of fawns:100 adult females were low in June, increased during winter, and then declined in April and May (Figure 2). During January-April (i.e., during captures), the ratio of fawns:100 adult females observed did not differ from the ratio obtained from capture data (Figure 2), thereby supporting use of capture ratios in CIR analyses.

From capture data. age-specific reproductive rates, and estimates of female survival probabilities (see below), we estimated fawns and breeding females alive at Time 1 as 274 and 199, respectively. Fawns and breeding females at Time 2 were 143 and 183, respectively. From these data, we estimated the probability of fawns surviving from birth to capture as 0.57. This estimate suggested that fawns experienced greater mortality from June-December than from Januarv-May (0.15 and 0.20 for female and male fawns. respectively;Table 1).

We radiomonitored 148 female and 43 male deer from 1 June 1999 through 31 May 2002. Throughout the study, 16 females (14 adults, 2 yearlings, 0 fawns) and 11 males (0 adults, 9 yearlings, 2 fawns) were censored. We observed 66 mortality events, 35 within females (23 adults, 6 yearlings, 6 fawns) and 31 within males (5 adult, 19 yearlings, 7 fawns). Predation was the primary mortality source for females. Coyotes (*Canis latrans*) killed



10 females, black bears (Ursus americanus) killed 3 females, and unidentified predators killed 3 females Three females died of unknown natural causes. 2 of starvation, and 2 of disease. Human-induced mortality accounted for 12 female deaths. Within this category, 8 deer died from legal harvest, 3 from wounding loss, and 1 deer was harvested illegally. Legal harvest was the primary source of mortality within males, accounting for 22 of 31 deaths. One male died from wounding Natural mortality loss. events accounted for 8

Figure 2. Mean (SE) monthly ratio of tawns (100 adult temales from visual observations m = 8.497) on the MeadWestvaco Wildlife and Ecosystem Research Forest. West Virginia from 1999–2002. Slashed horizontal line is the ratio at capture (78 tawns:100 hoult remains). Triangle in june is the estimated ratio at birth (from in utero reproductive rates). Squares are the estimated ratio from spotlight counts conducted in August. October, and fanuary from Langdon 2001.

# 216 Wildlife Society Bulletin 2005, 33(1):212-221

	Tracking	interval			Radio			Survival	rates	Mortalit	v rates <sup>r</sup>
Ciass	Season	Length	Sev	n	davs	Censored	Dier	Rate!?	95% Cl	Natural	Human
Fawr	Wintei	151	Ļ.	58	5,607	0	6	0.85	0.75-0.97	0.15	
			M	36	3,406	2	5	0.80	0.660.9	0.20	
Yearling	Summer	122	F	4 j	5,031	1	1	0,98	0.93-1.00	0.02	
			M	31	3,538	2	0	1.00			
	Autumn	92	ŕ	41	3,609	0	4	0.90	0.82-1.00		0.10
			M	30	1,608	5	19	0.30	0.20-0.55	0.03	0.63
	Winter	151	F	44	5,892	1	1	0.9.7	0.93-1.00	0.03	
			M	8	980	2	2	0.72	0.48-1.00	0.27	
	Annual		F					0.86	0.760.97	0.05	0.09
			м					0.25	0.13-0.47	0.12	0.63
Adult	Summer	122	F	181	21,924	1	1	0.99	0.98-1.00	0.01	
			М	6	732	υ	0	1.00			
	Autumn	92	۴	190	16,298	0	13	0.93	0.89-0.97	0.03	0.04
			M	б	349	· 0	5	0.22	0.080.84		0.73
	Winter	151	F	218	28,626	13	9	0.95	0.92-0.98	0.05	
			М	1	151	0	0	1.00			
	Annual		F					0.88	0.84-0.93	0.08	0.04
			м					0.22	0.08-0.85		0.73

Table : White-tailed deer survival and mortality rates for summer (May–Sep), autumn (Oct–Dec), winter (Jan–Apr), and annualis (Jun–May) on the MeadWestvaco Wildlife and Ecosystem Research Forest, West Virginia from 1999–2002.

<sup>a</sup> Number of total deer records in the interval with data from 1999-2002 pooled.

<sup>b</sup> Rate adjusted for small sample size bias (Heisey and Fuller 1985).

<sup>c</sup> Rate determined by Heisey and Fuller (1985). Natural mortality included predation, starvation, and disease.

male deaths; 4 males died from coyote predation, 2 from unidentified predators, 1 from starvation, and 1 from bobcat (*Felis rufus*) predation. We observed no vehicular trauma mortality.

Natural (0.07-0.12) and human-induced (0.05-0.07) mortality rates within females did not differ among years (all P > 0.35), suggesting minimal weather or harvest-regulation effects and validating our pooling of data. Survival rates peaked during summer and were minimal during autumn for all

Table 2. Comparison of white-tailed deer annual cause-specific mortabity rates for sex and age classes on the MeadWestvaco Wildlife and Ecosystem Research Forest. West Virginia from 1999–2002. Standard deviations are reported in parentheses.

Class	Males	Females	7 Statistic	P.value0
			2 5/100-101	7 Value,
Yearlings				
Human	0.63 (0.09)	0.09 (0.06)	5.48	< 0.001
Natural	0.12 (0.07)	0.05 (0.03)	1.06	0.289
Aduits				
Human	0.73 (0.16)	0.04 (0.01)	4.37	:0.001
Natural	0.00 (0.00)	0.08 (0.02)	+.03	< 0.001

\* To maintain an experiment-wise error rate of  $\alpha = 0.05$ , related tests were compared with an adjusted  $\alpha = 0.0125$  (Sokal and Rohl) (1995).

sex and age classes (Table 1). Yearling females had a 63% greater probability of annual survival than yearling males (Table 1). Similarly, adult females had a 66% greater probability of annual survival than adult males (Table 1). Annual human-induced mortality was greater for yearling and adult males than females (Table 2). Annual natural mortality was greater in adult females than adult males but did not differ within yearlings (Table 2).

in a start of the start of the

During winter mortality rates were similar between males and females within both fawns (Z= 0.51, P=0.61) and yearlings (Z=1.48, P=0.14). However, adult females had greater (Z=-3.06, P= 0.002) mortality rates in winter than adult males. Mortality rates during autumn were greater for yearling (Z=5.93, P<0.001) and adult (Z=4.19, P< 0.001) males than females. No differences occurred between males and females within yearling (Z=-1.01, P=0.31) and adult (Z=-1.00, P= 0.52) summer mortality rates.

Female adult and yearling annual cause-specific mortality did not differ for human-induced (Z = -1.08, P = 0.28) or natural (Z = 0.79, P = 0.45) mortality. Similarly, comparisons between adult and yearling males revealed no differences for human-

induced (Z=0.58, P=0.56) and natural (Z=-1.88, P=0.06) mortality.

We observed no differences in comparisons between summer mortality rates of adult and yearling females (Z = -0.76, P = 0.45), summer mortality rates of adult and yearling males (Z=0.00, P=1.00), autumn mortality rates of adult and yearling females (Z = -0.53, P = 0.60), and autumn mortality rates of adult and yearling males (Z=0.39, P=0.70). Within females, no differences in mortality rates occurred during winter between adults and yearlings (Z=0.72, P=0.47), between adults and fawns (Z=-1.77, P=0.08), or between yearlings and fawns (Z=-2.02, P=0.04). Within males, we observed no differences in mortality rates during winter between adults and yearlings (Z=-1.66, P=0.10) or between yearlings and fawns (Z=0.37, P=0.71). However, male fawns had greater (Z=2.50, P=0.01) mortality rates than adult males during winter.

# Discussion

Ricca et al. (2002) compared annual survival rates among white-tailed deer populations throughout North America. Within hunted populations, adult ( $\geq 1$  year old) male survival rates were greatest in southern Texas (0.65-0.74, DeYoung 1989) and least in northern Michigan (0.22-0.25, Van Deelen et al. 1997). Our observed adult male annual survival rates (0.22-0.23) represent the lowest range among those reported. Adult ( $\geq 1$  vear old) female survival rates within hunted populations were greatest in northeastern Minnesota (0.79-0.80, Nelson and Mech 1986) and northern Michigan (0.77-0.89, Van Deelen et al. 1997) and least in Montana (0.43-0.83, Dusek et al. 1989). Similarly, our observed adult female annual survival rates (0.86-0.88) represent the highest range among those reported and were similar to or exceeded unhunted populations (Ricca et al. 2002).

Estimates of neonate and young fawn survival are scarce, particularly within the eastern United States. Recently, however, Vreeland (2002) reported that fawn survival from birth to recruitment age (posthunting season) in Pennsylvania ranged from 0.28-0.59, depending on the study area and year. Our estimate of fawn survival from birth to capture  $(0.5^{--})$  was consistent with Vreeland (2002) and, similarly, we suspect that coyotes, black bears, and bobcats preved upon neonate and young fawns during the summer months because these predators also killed older deer during the months that followed. The primary human-induced mortality factor influencing white-tailed deer population ecology in north-central West Virginia is the differential harvest between sexes (Table 1). This finding is not unique to this region (Van Deelen et al. 1997). Langdon (2001) reported pre-hunting season adult ( $\geq$ 1 year old) sex ratios (male:female) for spotlight and camera surveys on the MWWERF as 7:100 and 26:100, respectively. Others have attributed skewed sex ratios directly to male-biased hunting (Nelson and Mech 1981, Dusek et al. 1989, Nixon et al. 1991).

Though infrequently observed, natural mortality was primarily from predation. Coyotes accounted for 61% (14 of 23) of all known natural mortality events and 78% (14 of 18) of all known predation events, including 7 adults. As in New Brunswick (Whitlaw et al. 1998), covotes were the primary predator of adult deer. Traditionally, coyotes have been considered opportunistic predators (Bekoff 1977, Van Vuren and Thompson 1982). However, recent work in southern Alberta suggests that covotes regularly participate in group hunts, specifically for deer when alternate prev is not available (Lingle 2000). Our observations from mortality sites suggest that multiple coyotes participated in deer kills. Black bear predation occurred in summer or early autumn and was not limited to fawns.

Summer mortality was notably low for each age and sex class but similar to summer mortality for adult deer in New Brunswick (Whitlaw et al. 1998). In agricultural regions of Illinois, Nixon et al. (1991) found the highest summer mortality rates within yearling females (0.15); however, all summer mortalities within their study were human-induced. Van Deelen et al. (1997) reported the highest summer mortality rates within yearling males (0.16), with half of the mortalities from starvation and half from unknown causes. We observed only 2 summer mortalities, both from natural causes and within females (Table 1). Low natural mortality rates within yearlings and adults during summer suggest adequate nutrition for maintenance, enhanced hiding cover, and the possibility that predators were using alternate prey (Lingle 2000). Our estimate of fawn survival from June-December suggests these alternate prey likely included neonate and young fawns. Autumn mortality of both yearlings and adults reflect selection by hunters for male deer. The greatest seasonal mortality rates for all age and sex classes were observed for adult males during autumn, which is a finding not unique to our study area (Nixon et al. 1991). Winter mortality within

# 218 Wildlife Society Bulletin 2005, 33(1):212-221

fawns was less than observed in northern Michigan (Van Deelen et al. 1997) and northeastern Minnesota (Nelson and Mech 1986), but greater than east-central Illinois (Nixon et al. 1991). Van Deelen et al. (1997) observed winter mortality rates of 0.20 and 0.00 for adult and yearling males. respectively. This relationship was reversed in our study. However, only 1 adult male survived into the winter, thus limiting meaningful comparisons. Our observed winter mortality rate for yearling males (0.27) was less than reported from east-central Illinois (Nixon et al. 1991). However, 2 of 3 reported winter mortalities within vearling males from Nixon et al. (1991) were human-induced, whereas all of ours were from natural causes. High natural winter mortality within yearling males may suggest nutritional deficits and corresponding increase in vulnerability to predators (Nelson and Mech 1986).

Our data illustrate the limitations of in-utero reproductive measures (counts of corpora lutea early in gestation or fetuses later in gestation) as indicators of population health. McCullough (1979) demonstrated that while both reproductive and recruitment rates are density dependent, they follow differing curves. Therefore, it may be inappropriate to manage deer populations for maximum reproductive output because the associated increases in fawn mortality may result in decreases in net recruitment rates. Because winter is the most nutritionally stressful season for deer in the central Appalachians and reproductive rates are indicators of health prior to the breeding season (Wentworth et al. 1990, Gee et al. 1994, Kroll and Jacobson 1995), we do not recommend in-utero reproductive measurements as the sole indicator of population health in this region. Without estimates of recruitment (a function of reproductive and survival rates) and other population measures, reproductive rates do not provide reliable management information.

Many wildlife managers use visual observations collected incidentally or methodically (e.g., from spotlight count data) to generate estimates of recruitment or the "fawn crop" (Gee et al. 1994, Kroll and Jacobson 1995) without considering biases associated with the temporal detectability or behavior of deer (McCullough et al. 1994). Using spotlight counts, McCullough (1982) found biases in the fawn:adult female ratio in every month except April, with the ratio being underestimated from June-March. Similarly, Langdon (2001) found a markedly smaller ratio of fawns:adult females in October than in January, despite the low incidence of harvested adult females. Consequently, the traditional timing of spotlight counts (i.e., prehunting season) may not generate reliable estimates of recruitment. Our data and Langdon (2001) suggest that in the central Appalachians of West Virginia recruitment rates may be most reliably estimated from observational or spotlight count data collected from February–April, the months when our capture ratios were similar to the other estimates or extrapolations.

Population status and health should be indexed through direct comparisons of reproductive and recruitment rates. Comparisons of reproductive data (as a measure of prior nutritional condition and an estimate of fawn production) and recruitment data (collected during winter months with minimal bias) could be expressed as a crude fawn survival rate (% fawns:100 adult females born that reached recruitment age). Changes in crude fawn survival rates can guide management recommendations independent of density estimates because both reproductive and recruitment rates are functions of density relative to carrying capacity (McCullough 1979).

## Management implications

Our observed survival, mortality capture, and reproductive data are characteristic of a population shaped by moderate fawn recruitment and excessive harvest of vearling male deer. We recommend a reduction in female deer to promote forest regeneration in harvested stands and to protect and conserve mature forest community components, such as vernal woodland, herbaceous flora, or understory vegetative cover necessary for ground-nesting neotropical migratory songbirds. Failure to respond to white-tailed deer overabundance on the MWWERF and throughout the central Appalachians of West Virginia may produce alternative steadystate forest conditions of low economic utility and reduced wildlife and biodiversity values (deCalesta and Stout 1997, Stromayer and Warren 1997, Waller and Alverson 1997, Pedersen and Wallis 2004), Van Deelen et al. (1997) noted that in northern Michigan, differential mortality rates between sexes were the product of male-biased hunting regulations and recommended increasing antierless permits to relieve hunting pressure on males. Likewise, we recommend that state wildlife agencies within this region continue to liberalize anderless deer seasons. Because many hunters in the central Appalachians are not willing to harvest antlerless deer, being comfortable with the traditional deer management paradigm of buck-only hunting, we recommend that educational programs (via state wildlife agencies, extension services, and private organizations) continue to be directed at hunters who are reluctant to harvest antlerless deer (e.g., see Alt 2003). These programs should clearly outline the ecological and biological need and benefits of harvesting female deer (e.g., see Hamilton et al. 1995). Furthermore, we recommend that corporate landowners pursue cooperative agreements with hunters, implementing incentive (e.g., earn-abuck) programs to encourage hunters to harvest female deer.

Acknowledgments. Financial support was provided by the MeadWestvaco Corporation and the United States Department of Agriculture's, National Research Initiative Program (grant 00-35101-9284). Editorial comments to earlier drafts of this manuscript were graciously provided by R. J. Warren, J. P. Carroll, and R. L. Hendrick. We are indebted to the 30 field technicians who assisted in data collection and J. L. Crum, P. D. Keyser, and D. A. Osborn for their logistical assistance. Deer were captured and handled under the auspices of Scientific Collection Permits 43-1999. 16-2000, 2001.008, and 2002.009 from the West Virginia Division of Natural Resources.

#### Literature cited

- ADAMS, M. B. 1999. Acidic deposition and sustainable forest management in the central Appalachians. Forest Ecology and Management 122:17-28.
- ADAMS, M. B., J. A. BURGER, A. B. JENKINS, AND L. ZELAZNY. 2000. Impacts of harvesting and atmospheric pollution on nutrient depletion of eastern U.S. hardwood forests - Forest Ecology and Management 138, 501–519.
- ALLEN, T. J., AND J. I. CROMER. 19<sup>--</sup>. White-tailed deer in West Virginia. Wildlife Resources Division Bulletin Number<sup>--</sup>. West Virginia Department of Natural Resources, Charleston, USA.
- Art, G. L. 2003. The role of deer hunting providing an environmental/ecological service to society and its possible implications to the future of hunting. Proceedings of the Annual Southeastern Deer Study Group 26:13
- ANNUAL MEETING OF THE SOUTHEAST DEER STUDY GROUP. 2003. Southeastern deer harvest summaries for the 2001–2002 season. Proceedings of the Annual Southeastern Deer Study Group 26:52–57.
- BEKOFE M. 1977 Canus latrans Mammal Species 79:1-9.
- BERINGER, J., L. P. HANSEN, W. WILDING, J. FISCHER, AND S. L. SHERIFT 1996. Factors affecting capture invopathy in white-tailed

deer Journal of Wildlife Management 60:375-380.

- CAUGHLEY, G. 1976. Wildlife management and the dynamics of ungulate populations. Applied Biology 1:183–246
- CHAPTEN, S. J., R. A. GERRARD, H. M. WATSON, I. L. MANTER, AND S. R. FLACK 2000. The geography of imperiment: targeting conservation towards cruical biodiversity areas. Pages 159–200 in B. A. Stein, L. S. Kunner, and J. S. Adams, editors. Precious heritage: the status of biodiversity in the United States Oxford University Press, New York, New York, USA.
- CLOVER, M. R. 1954. A portable deer irap and catch-net California Fish and Game 40:367-373.
- COLLINS, R. J. 2004. The effects of prescribed fires, canopy gaps and deer herbivory on tree species composition impleations for succession theory. Dissertation, University of Pittsburgh, Pittsburgh, Pennsylvana, USA.
- DAVIDSON, C. B., K. W. GOTISCHALK, AND J. E. JOHNSON 2001 European gypsy moth (*Lymantra dispar* L.) outbreaks: a review of the literature. United States Department of Agriculture Forest Service, Northeastern Research Station. General Technical Report NE-278. Newtown Square. Pennsylvania, USA.
- DAVIDSON, W. R., AND V. F. NETTLES 1997. Field manual of wildlife diseases in the southeastern United States. Second edition Southeastern Cooperative Wildlife Disease Study, University of Georgia, Athens, USA.
- DECALESTA, D. 5. 1994 Deer and diversity in Allegheny hardwood forests: managing an unlikely challenge. Landscape and Urban Planning 28:47–53.
- DECALESTA, D. S., AND S. L. STOUT. 1997. Relative deer density and sustainability: a conceptual framework for integrating deer management with ecosystem management. Wildlife Society Bulletin 25:252-258.
- DEYOUNG, C. A. 1989. Mortality of adult white-tailed deer m south Texas. Journal of Wildlife Management 53:513–518.
- DUSEN, G. L., R. J. MACKIE, J. D. HERRIGES, AND B. B. COMPTON. 1989 Population ecology of white-tailed deer along the lower Yellowstone River. Wildlife Monographs 104.
- EBERHARDT, L. L. 1985. Assessing the dynamics of wild populations. Journal of Wildlife Management 49:997-1012.
- FISCHER, J. R. 1996. White-tailed deer herd health check on the Westvaco Wildlife and Ecosystem Research Forest Southeastern Cooperative Wildlife Disease Study, Final Report to the West Virginia Division of Natural Resources. Charleston, USA.
- FORD, W. M., T. S. MCCAY, M. A. MENZEL, W. D. WEBSTER, C. H. GREENBERG, J. F. PAGELS, AND J. F. MERRITT. 2005. Influence of elevation and forest type on shrew community assemblage and species distribution in the central and southern Appalachian Mountains. In J. F. Merritt and S. B. Churchfield, editors Second International Congress of the Biology of the Soricidae. Carnegie Museum of Natural History Special Publication. In press
- FORD, W. M., AND J. L. RODRIGUE. 2001. Soricid abundance in partial overstory removal harvests and riparian areas in an industrial forest landscape of the central Appalachians. Forest Ecology and Management 152: 159–168.
- FREDERICKSEN,T.S. 1998. Impacts of logging and development on central Appalachuan forests. Natural Areas Journal 18, 175–178
- GEE, K. L., M. D. PORTER, S. DEMARAIS, F. C. BRYANT, AND G. VAN VREIDE 1994. White-tailed deer: their toods and management in the Cross Timbers. Second edition. samuel Roberts Noble Foundation Publication. Ardmore, Oklahoma, USA.

#### 220 Wildlife Society Bulletin 2005, 33(1):212-221

- HAMILION, J., W. M. KNOMAND D. C. GUYNN, JR. (1995). Harvest strategres. Pages (7-57 m K V. Miller and R. L. Marchinton, editors Quality whitetails, the why and how of quality deer management. Stackpole Books, Mechanicsburg, Pennsylvania, USA.
- HAWKINS, R. E., L. D. MARIOGLIO, AND G. G. MONTGOMERY 1968 Cannon-netting deer Journal of Wildlife Management 32, 191–195.
- HEISEN, D. M., AND T. K. FULLER 1985 Evaluation of survival and cause-specific mortality rates using telemetry data. Journal of Wildlife Management 49:668-674.
- HORSEN, S. B., S. L. STOUT, AND D. S. DECALESIA. 2003. White-tailed deer impact on the vegetation dynamics of a northern hardwood forest. Ecological Applications 15:98–118.
- KROLL, J. C., AND H. A. JACOBSON 1995 Starting out. Pages 19–46 in K. V. Miller and R. L. Marchinton, editors - Quality whitetails, the why and how of quality deer management stackpole Books, Mechanicsburg, Pennsylvania, USA.
- LANGDON, C.A. 2001. A comparison of white-tailed deer population estimation methods in West Virginia. Thesis, West Virginia University, Morgantown, USA.
- LINGLE, S. 2000. Seasonal variation in coyote feeding behaviour and mortality of white-tailed deer and mule deer. Canadian Journal of Zoology 78:85–99.
- McCULLOUGH, D.R. 1979. The George Reserve deer herd: population ecology of a K-selected species. University of Michigan Press, Ann Arbor, USA.
- McCULLOUGH, D. R. 1982. Evaluation of night spotlighting as a deer study technique. Journal of Wildlife Management 46: 963-973.
- MCCULLOUGH, D. R., F.W. WECKERIN, P. I. GARCIA, AND R. R. EVETT 1994. Sources of inaccuracy in black-tailed deer herd composition counts. Journal of Wildlife Management 58: 319–329.
- MICHAFL, E. D. 1987. Bark stripping by white-tailed deer in West Virginia. Northern Journal of Applied Forestry 4:96–97.
- MICHAEL, E. D. 1992. Impact of deer browsing on regeneration of balsam fir in Canaan Valley West Virginia. Northern Journal of Applied Forestry 9:89–90.
- NELSON, M. E., AND L. D. MECH. 1981. Deer social organization and wolf predation in northeastern Minnesota. Wildlife Monograph 77.
- NELSON, M. E., AND L. D. MECH. 1986. Mortality of white-tailed deer in northeastern Minnesota. Journal of Wildlife Management 50:691–698.
- NIXON, C. M., L. P. HANSEN, P.A. BREWER, AND J. E. CHELSVIG. 1991. Ecology of white-tailed deer in an intensively farmed region of Illinois. Wildlife Monograph 118.
- PAGLIK, G. J., AND D. S. ROBSON. 1969. Statistical calculations for change-in-ratio estimators of population parameters. Journal of Wildlife Management 53: 1–27.
- PEDERSEN, B. S., AND A. M. WALLIS. 2004. Effects of white-tailed deer herbivory on forest gap dynamics in a wildlife preserve, Pennsylvania, USA. Natural Areas Journal 24:82-94.
- RICCA, M. A., R. G. ANTHONY, D. H. JACKSON, AND S. A. WOLFE. 2002. Survival of Columbian white-tailed deet in western Oregon. Journal of Wildlife Management 66: 1255–1266.
- ROBERSTON, D. P., AND R. B. HULL. 2003. Biocultural ecology: exploring the social construction of the southern Appalachian ecosystem. Natural Areas Journal 23:180–189.
- SEVERINGHAIN, C.A. 1949. Tooth development and wear as criteria of age in white-tailed deer. Journal of Wildlife Management 13:195–216

SMITH D.W. 1995. The southern Appalachian hardwood region.

Pages 175-225 *m* J.W Barrett, editor. Regional silviculture of the United States. John Wiley and Sons, New York, New York USA

- SOKAL, R. R., AND F.J. ROHEF. 1995. Biometry: Third edition. W.H. Freeman and Company, New York, New York, USA
- SOUTO, D. R., AND K. S. SHIELDS. 2000. Overview of hemloct, health: Pages 76-80 m K A. McManus, K. S. Shields, and D. R. Souto, editors. Proceedings: symposium of sustainable management of hemlock ecosystems in eastern North America. United States Department of Agriculture Forest Service, Northeastern Research station. General Technical Report NE-267. Newtown Square, Pennsylvania, USA.
- SPENCER, A. 1997. Adding value piece by piece. Mountain Promise 7, 4–3.
- STEPHENSON, S. L. 1993a. An introduction to the upland forest region. Pages 1–9 in S. L. Stephenson, editor. Upland forests of West Virginia. McClain. Printing, Parsons. West Virginia, USA.
- STEPHENSON, S. L. 1993b. Upland forest vegetation. Pages 11–34 in S. L. Stephenson, editor Upland forests of West Virginia, McClain Printing, Parsons, West Virginia, USA.
- STIPES, R. J. 1999. Trojan horse in Appalachian forests. Pages 73-79 in R. P. Eckerlin, editor. Proceedings of the Appalachian Biogeography Symposium. Virginia Museum of Natural History Special Publication No. 7, Martinsville, USA.
- STROMAYER, K.A., AND R. J. WARREN 1997. Are overabundant deer herds in the castern United States creating alternative stable states in forest plant communities? Wildlife Society Bulletin 25: 227-234.
- TILGHMAN, N. G. 1989 Impacts of white-tailed deer on forest regeneration in northwestern Pennsylvania. Journal of Wildlife Management 53:524-532.
- UNITED STATES DEPARTMENT OF AGRICULTURE FOREST SERVICE. 2004 Northeastern forest inventory and analysis: West Virginia results. United States Department of Agriculture Forest Service. Northeastern Research Station. Newtown Square. Pennsylvania. USA. Available online at: http://www.fs.fed.us/ ne/fia/states/wv/index.html (accessed 1 May 2004).
- VAN DEELEN, T. R., H. CAMPA, III, J. B. HAUFLER, AND P. D. THOMPSON, 1997. Mortality patterns of white-tailed deer in Michigan's Upper Peninsula. Journal of Wildlife Management 61: 903-910
- VANGILDER, L. D., AND S. L. SHERIFF. 1990. Survival estimation when fates of some animals are unknown. Transactions of the Missouri Academy of Science 24:57–68.
- VAN VUREN, D., AND S. E. THOMPSON, JR. 1982. Opportunistic feeding by coyotes. Northwest Science 56: 131–135.
- VERME, L. J., AND D. E. ULIREY. 1984. Physiology and nutrition. Pages 91-118 in L. K. Halls, editor. White-tailed deer ecology and management Stackpole Books, Harrisburg, Pennsylvania, USA.
- VREELAND, J. 2002. Fawn survival ut Pennsylvania. Pennsylvania Game News 73(9):12-16.
- WADE, D.A., AND J. E. BOWNS. (1984). Procedures for evaluating predation on livestock and wildlife. Texas Agricultural Extension Service, College Station, USA.
- WALLER, D. M., AND W.S. ALVERSON. 1997. The white-tailed deer: a keystone herbivore. Wildlife Society Bulletin 25:217-226.
- WEARLAND, C. A. 2000. Effects of diameter-limit and two-aged timber harvesting on songbird populations on an industrial forest in central West Virginia. Dissertation, West Virginia University, Morgantown, USA.
- WENTWORTH, J. M. A.S. JOHNSON AND P.E. HALE, 3 (990). Influence of

# Deer population characteristics • Campbell et al. 221

acorn use on nutritional status and reproduction of deer in the southern Appalachians – Proceedings of the Annual Conference of Southeastern Association of Fish and Wildlife Agencies 4-0 142–154

WIRTHAW, H.A., W. B. BAHARO, D. L. SAPINC, S. J. YOUNG, R.A. JENKINS, AND G. J. FORBES. (1998). Survival and cause-specific mortality rates of adult white-tailed deer in New Branswick. Journal of Wildlife Management 62: 1535–1544.



*Tyler A. Campbell* (photo) is a research wildlife biologist with the National Wildlife Research Center at the Kingsville, Texas field station. He received a B.S. in wildlife and fisheries man-

agement from Texas Tech University, an M.S. in range and wildlife management from Texas A&M University-Kingsville, and a Ph.D. in forest resources from the University of Georgia. His research has focused on wildlife habitat and nutritional relationships. He has been a member of The Wildlife Society since 1993 and a Certified Associate Wildlife Biologist since 1998. Benjamin R. Laseter is a Ph.D. candidate in the Warnell School of Forest Resources at the University of Georgia. He received his B.S. from the University of Georgia and his M.S. from the University of Memphis. His research interests include social and genetic structure of wildlife populations. W. Mark Ford is a research wildlife biologist with the United States Department of Agriculture Forest Service Northeastern Research Station at the Fernow Experimental Forest in West Virginia. He received his Ph.D. in forest resources from the University of Georgia in 1994. His research focus is on wildlife management and forest community ecology in the southern and central Appalachians. He has been a member of The Wildlife Society since 1987 and a Certified Wildlife Biologist since 1998. Karl V. Miller is a professor of wildlife ecology and management in the Warnell School of Forest Resources at the University of Georgia. He and his students focus their research interests on the interactions among physiology, social behavior, communication, and management of white-tailed deer and on the influence of forest management practices on habitat conditions for game and nongame wildlife in the southeastern United States.

Associate editor: Euler

