SURVIVAL RATES OF FEMALE WHITE-TAILED DEER ON AN INDUSTRIAL FOREST FOLLOWING A DECLINE IN POPULATION DENSITY

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Abstract.—With white-tailed deer (*Odocoileus virginianus*) populations at historically high levels throughout many North American forests, many current management activities are aimed at reducing deer populations. However, very little information exists on the ecology of low-density white-tailed deer populations or populations that have declined in density. We examined survival and cause-specific mortality rates in a white-tailed deer population that recently experienced a substantial (>50 percent) decline in population density on an industrial forest in central West Virginia. We monitored 57 adult female deer from August 2006 to April 2008, documenting 18 mortalities. Annual survival was 0.810 (0.733–0.894), similar to results found before population decline. Annual cause-specific mortality rates were 0.119 (0.062–0.177) for anthropogenic mortality and 0.071 (0.029–0.113) for natural mortality. The increase in anthropogenic mortality likely resulted from changes in harvest regulations and access to our study area. Our results support previous work suggesting that adult survival rates in ungulates are robust to changes in population density and indicate that density-dependent mechanisms were not acting upon adult survival in this population during our study.

INTRODUCTION

White-tailed deer (*Odocoileus virginianus*) are keystone herbivores in much of North America and can influence many aspects of ecosystem dynamics (Russell et al. 2001). Although the recovery of the white-tailed deer is one of the great success stories in wildlife management, many populations are at levels impacting other aspects of the biota and are deleterious for sustained, healthy ecosystem function (Cote et al. 2004). Overabundant deer populations can affect forested ecosystems in several ways, including reducing the abundance and diversity of understory vegetation and limiting forest regeneration (Rossell et al. 2005, Russell and Fowler 2004, Tilghman 1989). These alterations to the plant community can affect other wildlife by reducing the amount of suitable habitat or forage available for insects (Allombert et al. 2005), birds (McShea et al. 1995), and small mammals (Horsley et al. 2003). Additionally, overabundant deer populations tend to be characterized by animals in poorer physical condition (Keyser et al. 2005b) with higher rates of parasite prevalence than herds at lower density (Eve and Kellogg 1977). Wildlife managers now must implement strategies that

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minimize the biological impacts of these overabundant populations (Brown et al. 2000). Attempts to reduce deer populations by using techniques such as controlled public hunts (Kilpatrick and Walter 1999, McDonald et al. 2007), small-scale removal of family groups (McNulty et al. 1997, Miller et al. 2010), contraceptive and fertility treatments (Locke et al. 2007), or other techniques have had varying degrees of success.

Relatively little information exists on how these management actions affect deer population characteristics. Density-dependent responses in home-range size (Henderson et al. 2000, Kilpatrick et al. 2001), habitat use (Kie and Bowyer 1999), and recruitment (Keyser et al. 2005a) have been observed in white-tailed deer. Studies of mule deer (*O. hemionus*) in Colorado (Bartmann et al. 1992, White and Bartmann 1998) and red deer (*Cervus elaphus*) in Europe (Clutton-Brock et al. 1987) suggest that population density also may affect fawn survival, although this pattern has not often been reported in white-tailed deer (McCullough 1979, Patterson et al. 2002). Despite this abundance of research examining the effects of population density on white-tailed deer, virtually no information exists to address whether adult survival exhibits density-dependent patterns. McCullough (1979, 1990) suggested that adult survival rates are robust to changes in population density in white-tailed deer, but little empirical evidence exists on such relations to confirm this assertion.

Understanding how population density may affect survival rates in white-tailed deer is important for developing sound natural resource management plans, particularly in forested landscapes. Our objectives were to identify patterns in adult female survival and mortality rates in a white-tailed deer population that had recently undergone a substantial reduction in population size (>50 percent). We hypothesized that adult female survival rates would be higher than those reported before population reduction because of per-capita increases in resource availability.

STUDY AREA

We conducted our study on the MeadWestvaco Wildlife and Ecosystem Research Forest (MWERF) in central Randolph County, West Virginia. The 3,413-ha site occurs in the Unglaciated Allegheny Mountain and Plateau physiographic province and ranges in elevation from 734 to 1,180 m. Average annual precipitation on the site ranges between 170 and 190 cm with an average snowfall >300 cm/year. The majority of the site was logged initially between 1916 and 1928 and at the beginning of our study comprised primarily maturing, second-growth northern hardwood-Allegheny hardwood forests (Keyser and Ford 2005). These forests were dominated by American beech (*Fagus grandifolia*), black cherry (*Prunus serotina*), sugar maple (*Acer saccharrum*), red maple (*A. rubrum*), yellow birch (*Betula allegheniensis*), and northern red oak (*Quercus rubra*). Higher-elevation areas were dominated by red spruce (*Picea rubens*) and eastern hemlock (*Tsuga canadensis*) communities. At lower elevations, other species such as American basswood (*Tilia americana*), black birch (*B. lenta*), and yellow-poplar (*Liriodendron tulipifera*) also were present. Throughout much of the area, the understory was dominated by greenbrier (*Smilax* spp.) and mountain laurel (*Kalmia latifolia*), with dense rosebay rhododendron (*Rhododendron maximum*) prevalent in riparian areas. Hay-scented fern (*Dennstaedtia punctilobula*) also was abundant throughout the understory due to excessive herbivory from historically high white-tailed deer densities (Keyser and Ford 2005). Between 2000 and 2008, more than 500 ha of forest have been harvested on the MWERF, of which 75 percent were clearcut and 25 percent were deferment cuts and marked selection cuts. Harvest units have averaged 34.7 ha since the mid-1990s, with most harvests conducted in the dormant season.

We conducted four population surveys between October 2005 and October 2007 along a predetermined 35-km survey route that provided adequate spatial coverage of the study area. We used a distance sampling approach to estimate population density (Buckland et al. 2001). Population density estimates from individual surveys ranged from 1.2/km^2 (95-percent confidence interval [CI]: 0.4 - 4.1) to 2.6/km^2 (95-percent CI: 1.1 - 5.7). Similar methods were used during four surveys conducted between August 2000 and May 2001 (Langdon 2001). Density estimates from these previous surveys ranged from 8.3/km^2 (95-percent CI: 6.8 - 10.0) to 10.7/km^2 (95-percent CI: 8.2 - 13.8) (Langdon 2001), indicating a decrease in population density of >50 percent. This decrease was most likely the result of research activities, which removed 100 animals between 2002 and the time of our study (Crimmins, unpublished data; Miller et al. 2010) and limited recruitment (B. Miller, unpublished data). Increases in coyote (*Canis latrans*) and black bear (*Ursus americanus*) populations throughout the region and locally may have limited deer recruitment, as both these predators are known to prey upon deer neonates in the central Appalachians (Vreeland et al. 2004).

METHODS

We captured deer by using modified clover traps (Clover 1954) baited with whole-kernel corn. Upon capture, we restrained and chemically immobilized deer by using an intramuscular injection of xylazine HCl at a dosage of 2.2 mg/kg body weight. Deer were aged yearling or adult by using tooth wear and replacement patterns (Severinghaus 1949). All animals in the study were adult (≥6 months old) females. Once sedated, deer were fitted with mortality-sensitive radio-collars (model M2600, Advanced Telemetry Systems, Ishanti, MN) and numbered plastic ear tags (PermaFlex 7341, National Band and Tag, Newport, KY). We administered a 50 percent intramuscular, 50 percent subcutaneous injection of yohimbine HCl as an antagonist (Wallingford et al. 1996). We released deer at the capture site and monitored them until they were ambulatory. All capture and handling methods were in accordance with the guidelines of the American Society of Mammalogists (Gannon and Sikes 2007) and the Animal Care and Use Committee of West Virginia University (ACUC #05-0706). We located deer ≥1 day each week from August 1, 2006 to April 30, 2008. We monitored status (dead/alive) from the ground using a TRX-2000S receiver (Wildlife Materials, Murphysboro, IL) and a 3-element Yagi antenna (SteppIR Antennas Inc., Bellevue, WA). When a mortality signal was detected, we immediately located the carcass and attempted to determine cause of death. We categorized death as natural (e.g., starvation, predation) or human-induced (anthropogenic).

We estimated annual survival using the Kaplan-Meier method with a staggered entry design (Pollock et al. 1989). We used a recurrent time design to evaluate survival and cause-specific mortality (Fieberg and DelGiudice 2009). We used a competing risks approach to estimate cause-specific mortality rates (anthropogenic vs. natural) by developing cumulative incidence functions for each mortality source to account for temporal changes in the risk set (Heisey and Patterson 2006). Our analyses were conducted using the R programming language (R Development Core Team 2008).

RESULTS

We monitored 57 adult female deer beginning August 1, 2006. During our study, which ended April 30, 2008, we documented 18 mortality events: 12 anthropogenic and 6 natural. Limited sample sizes prevented robust comparisons of survival within age classes; therefore, we present data pooled across age classes. Annual survival was 0.810 (0.733 - 0.894), with most mortalities occurring during fall

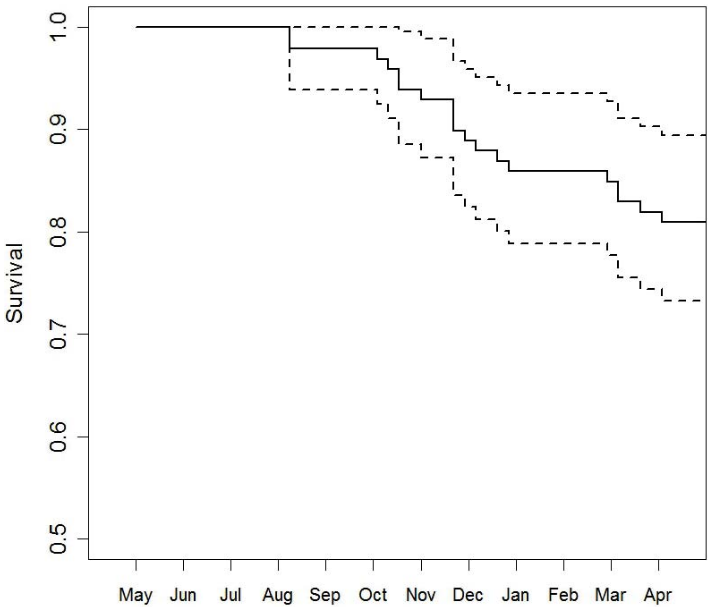

Figure 1.—Annual Kaplan-Meier survival function for white-tailed deer on the MeadWestvaco Wildlife and Ecosystem Research Forest, West Virginia, 2006-2008. Dotted lines represent 95-percent confidence intervals.

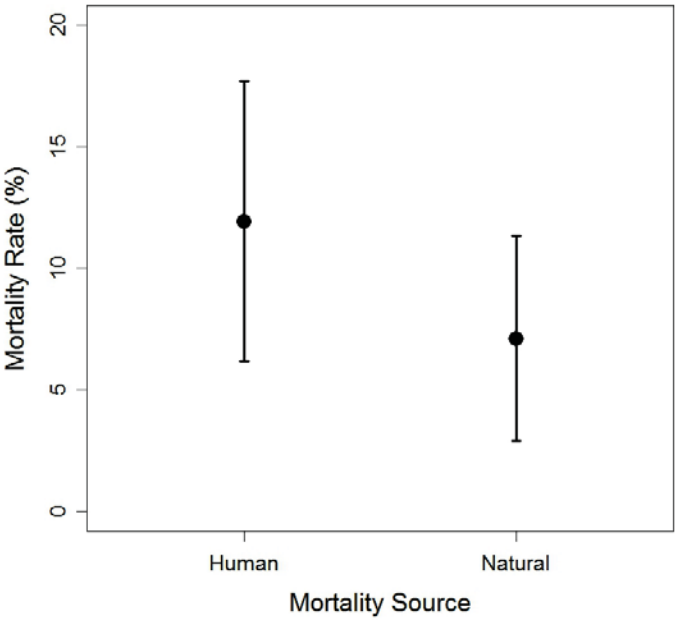

Figure 2.—Annual cause-specific mortality rates for white-tailed deer on the MeadWestvaco Wildlife and Ecosystem Research Forest, West Virginia, 2006-2008. Error bars represent 95-percent confidence limits.

(October - December) hunting season (Fig. 1). Anthropogenic (0.119) and natural (0.071) mortality rates did not differ based on overlapping 95-percent confidence intervals (Fig. 2). Natural mortalities occurred throughout the calendar year, whereas anthropogenic mortalities were concentrated in fall, coincident with hunting season. Of the 12 anthropogenic mortalities, 9 occurred during the legal hunting season (approximately October - December) and 3 occurred in the spring when the season was closed.

DISCUSSION

Our annual survival estimate (0.81, 95-percent CI 0.73–0.89) was similar to what was previously found for this population (0.88, 95-percent CI 0.84–0.93) from 1999 to 2002, when densities were substantially higher (Campbell et al. 2005). This result suggests that adult survival rates in this population are robust to changes in population density. Bartmann et al. (1992) reported that adult survival rates in mule deer (*O. hemionus hemionus*) remained constant after population reduction in Colorado despite density-dependent related changes in fawn survival; they suggested density-dependent survival responses would be observed in adults only if substantial changes in density occurred. Fowler (1981) suggested that density-dependent processes in large mammals are easier to detect the further the population is from carrying capacity. The deer population on our study area exhibited a decrease of a sufficient magnitude (>50 percent) that density-dependent related mechanisms would have been expressed (McCullough 1990). Furthermore, based on abomasal parasite counts (Campbell et al. 2005), the population was at or near nutritional carrying capacity before the decline in density. We also found an increase in overall in-utero reproductive rates from ~1.4 fawns/female from 1999 through 2001 to ~1.6 fawns/female at the time of our study (Campbell et al. 2005; Crum, unpublished data). Thus, based on the starting position of the population, the

>50-percent decrease likely represented a substantial reduction in density relative to carrying capacity. Nevertheless, we were unable to observe any significant changes in adult survival rates, suggesting that density-dependent mechanisms were not operating on this population.

Campbell et al. (2005) reported annual cause-specific mortality rates of 0.04 for anthropogenic mortality and 0.08 for natural mortality using similar analytical methods. Our estimated natural mortality rate of 0.071 was similar to that of Campbell et al. (2005), but our estimated anthropogenic mortality rate (0.119) was substantially greater. The similarity between our estimates of natural mortality is somewhat surprising, as increases in per-capita available resources resulting from decreased density would presumably lead to higher fitness (Fretwell and Lucas 1970). However, the high survival rates (>0.8) exhibited at both high and low densities suggest that resource limitations on our study site never reached a threshold where they affected adult survival (Gaillard et al. 1998). The observed increases in anthropogenic mortality could be the result of changes in human hunting pressure, as ownership changed and subsequent access to our study site increased during our study. Regardless, our results suggest that overall survival rates of adult female white-tailed deer are highly resistant to changes in population density.

The reduction in population density on our study area was likely the result of several factors, including an earlier removal of animals for research purposes over part of the study area (Miller et al. 2010), cumulative habitat degradation from two decades of overabundance that may have limited recruitment, and increased predator populations. Similarly, liberalization in harvest regulations during this time also led to an increase in the local doe harvest. During this time black bear populations increased in the area (Ryan 2009), while anecdotal evidence suggests that coyote populations also increased substantially. These predator populations may have limited recruitment by reducing fecundity and fawn survival (Kilgo et al. 2010). This multitude of factors must be considered, as we may have observed different patterns if the reduction in the deer population on our study site had resulted solely from deer management programs such as regulated harvest that would have a smaller effect on neonate survival or population growth rates.

The consistency of natural mortality rates between the two study periods suggests that other factors such as hunting pressure may influence survival rates more than population density does (Weckerly et al. 2005). In more northern latitudes, winter severity is generally thought to be one of the primary limiting factors for white-tailed deer populations (Garroway and Broders 2005). Although our study site was at latitudes not normally associated with such conditions, its relatively high elevation made the local climate more similar to northern areas with severe winters. Even though we lacked long-term data on winter severity or mast production from our study area, the relatively low observed natural mortality rates suggest that winter weather or mast failures may not have been a substantial contributing factor to adult survival rates in our population during our study period. Similarly, regional mast production estimates suggest that mast production was above average during most of our study (Ryan et al. 2009). However, it is important to note that we were unable to assess fawn survival and recruitment, which are highly susceptible to severe winter conditions.

CONCLUSIONS

Our results suggest that management actions aimed at reducing deer population density can operate under the assumption that adult female survival rates, if high prior to population reduction, will remain fairly constant after population reduction. Indeed, others have concluded that adult survival rates are extremely robust to changes in population density (McCullough 1979, White and Bartmann 1998). Our lack of an observed increase in survival rates, particularly when combined with the minimal change in natural mortality rates, suggests that population control measures may be effective at limiting population growth. Given sufficient lag-time to allow for forest regeneration, such measures may also be effective at limiting herbivory in forested regions subjected to heavy browsing pressure (Crimmins et al. 2010, Miller et al. 2009). However, the potential for increased fecundity and recruitment would need to be carefully assessed before any population control measures were taken, as these factors are more commonly thought to be density-dependent (Keyser et al. 2005a). Our results support previous research suggesting that adult survival rates in ungulates are robust to changes in population density and that density-independent factors may make important contributions to structuring population dynamics in white-tailed deer.

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