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Abstract: Most state wildlife agencies collect harvest data to inform management decisions. However, these data are typically considered across relatively short time periods and are rarely revisited. We present a case study using historical records to investigate potential agents (i.e., harvest, predation, and forest change) influencing the declining white-tailed deer (*Odocoileus virginianus*) population in the north Georgia mountains. We used long-term black bear *(Ursus americanus)* and deer harvest data, and indices of forest stand conditions from 1979–2015 on eight Wildlife Management Areas (WMAs) in the north Georgia mountains. During 1979–2015, harvest of male and female deer declined by 85% and 97%, respectively. Over the same time period, mean yearling male deer body weight increased by 21%, mean antler diameter increased by 62%, and mean antler beam length increased by 92%. We observed a 97% reduction in availability of early successional forests (0–10 years old) and a 53% increase in volume of large diameter (>27.9 cm) oak species, suggesting increasing homogeneity/maturation of forest stands across all eight WMAs. Concomitantly, the U.S. Forest Service increased the acreage under prescribed fire management from 2,916 to 5,629 ha during 2003–2015. Black bear populations grew at an annual rate of 1.07 for males and 1.08 for females. Our analyses indicated that despite the reduction in early successional habitats as illustrated by the reduction in young forests (0–10 years old), deer condition indices have improved suggesting that a habitat-driven change in fecundity was not the likely primary driver of the deer population decline. However, increasing fawn predation, coupled with a decline in available fawning cover may be reducing recruitment rates and should be investigated as potential causes for the observed population decline. Our research also illustrates the importance of maintaining long-term data, especially the value offered to evaluate trends over time.

Key words: black bear, forest conditions, Georgia, *Odocoileus virginianus*, white-tailed deer

White-tailed deer (*Odocoileus virginianus*) were extirpated from the north Georgia Mountains by 1895 due primarily to hunting (Jenkins 1952); although timber harvesting and extensive landscape conversion (i.e., row crops in valleys and pastoral use in the uplands) were significant contributors. In 1928, restocking efforts were initiated on the Blue Ridge Wildlife Management Area (WMA; Webb 1956), and by 1940, the first managed deer hunt was held with 111 hunters participating and 21 males and 3 female deer harvested (hunter success = 18.9%; Webb 1956). By 1953, deer populations on Blue Ridge WMA continued to increase and the estimated density was 7 deer/km² (Webb 1956). Populations continued to expand regionally until the early 2000s when deer harvest and hunter success rates began to decline rapidly (C. Killmaster, Georgia Department of Natural Resources-Wildlife Resources Division [DNR-WRD], unpublished data). Currently, deer populations remain low on WMAs in north Georgia with estimated densities ranging from 1.9–3.9 deer/km² (S. Frazier, Georgia DNR-WRD, personal communication). Reasons for the population decline are speculative.

Therefore, we used long-term deer harvest records, trends in forest conditions, and predator population data (e.g., black bear [*Ursus americanus*]) to evaluate factors potentially influencing declines in deer populations.

Predation by black bears, bobcats (*Lynx rufus*), and coyotes (*Canis latrans*) is a common source of mortality of white-tailed deer neonates (e.g., Vreeland et al. 2004, Campbell et al. 2005, Kilgo et al. 2010, Shuman et al. 2017) and can consequently influence recruitment (Chitwood et al. 2015). For example, using a modeling approach, Chitwood et al. (2015) demonstrated that in low-density deer populations with high fawn predation rates, protecting females from harvest may not offset declines in recruitment. Georgia Department of Natural Resources-Wildlife Resources Division (Georgia DNR-WRD) has limited harvest of females on WMAs in north Georgia, but these management changes did not reverse the deer population decline (C. Killmaster, Georgia DNR-WRD, unpublished data). Since 1979, black bear populations have increased across north Georgia with annual growth rates ranging from 1.108

to 1.113 (Little et al. 2017). Although, Georgia DNR-WRD lacks population trend data on bobcats and coyotes in north Georgia populations have purportedly increased over much of the eastern United States (Gompper 2002, Kilgo et al. 2010, Roberts and Crimmins 2010).

Acorn mast production is an important factor influencing deer populations in the southern Appalachian Mountains (Wentworth et al. 1992, Ryan et al. 2004). In particular, yearly variations in acorn abundance can influence deer weight, antler development, fecundity, and fawn survival (Wentworth et al. 1992). Additionally, indices of herd health (i.e., body weights, antler size) are positively correlated with the amount of young and mid-successional forests, especially in years following poor mast crops (Ford et al. 1997). Acorn production is also critically important to many other wildlife species (e.g., McShea and Schwede 1993, Ryan et al. 2004, McDonald et al. 2005, Whitaker et al. 2005). Recent research has reported declines in oak abundance in some regions (Fei et al. 2011, Greenburg et al. 2011, Dey 2014) due to changes in climate, forest management practices, and introduced pests and pathogens (McShea et al. 2007, Speer et al. 2009). Many forests dominated historically by oaks are converting to shade-tolerant and fire-intolerant species (e.g., red maple [*Acer rubrum*]; McShea et al. 2007, Nowacki and Abrams 2008, Fei et al. 2011). Concomitantly, stand-level species richness is declining throughout much of the eastern forests and will likely continue to decline as numerous fire-adapted plants are replaced by a limited set of shade-tolerant fire-sensitive species (Nowacki and Abrams 2008). These shifts in the composition and structure of forests may negatively impact deer habitat quality.

We used 37 years of long-term data to evaluate the following: (1) deer harvest trends to assess the validity and magnitude of population decline; (2) black bear population growth rates; and (3) forest stand age and volume as indices to changing habitat conditions through time in north Georgia. Our goal was to utilize long-term trends in these data to evaluate potential factors affecting deer populations and direct future research activities.

Study Area

Our study was conducted on eight separate Georgia DNR-WRD WMAs (total area: 993 km²) within the Chattahoochee National Forest (CNF) in north Georgia (Figure 1), which is managed by the U.S. Forest Service (USFS). The WMAs include Blue Ridge, Chattahoochee, Chestatee, Cohutta, Cooper's Creek, Rich Mountain, Swallow Creek, and Warwoman. These WMAs were located in the Blue Ridge physiographic province and were characterized by mountainous terrain with elevations ranging from 550–1530 m. The WMAs were also located in the southern portion of the Blue Ridge Ecoregion in the temperate broadleaf and mixed forests bi-
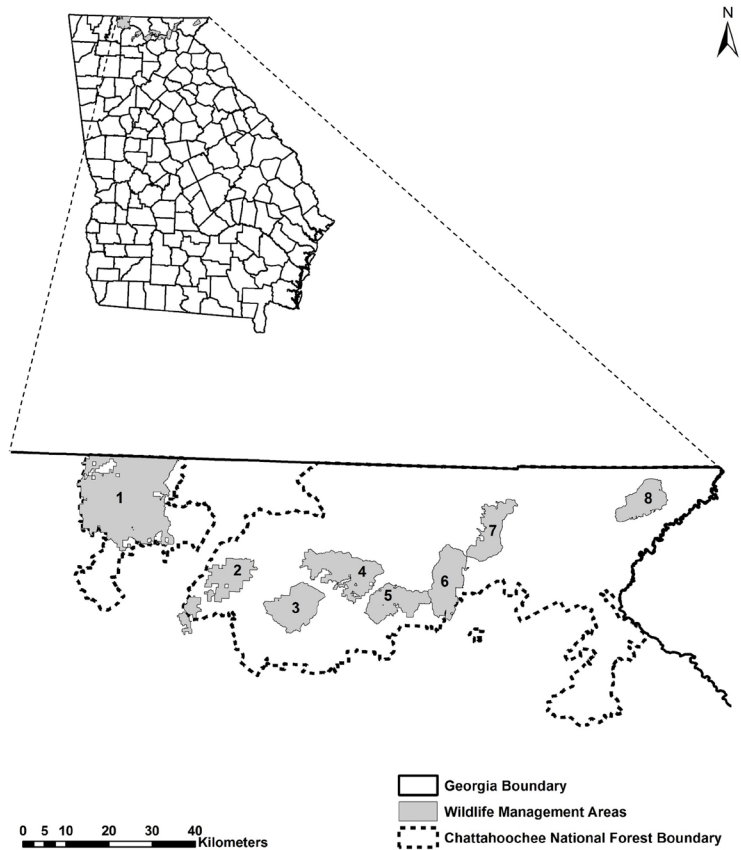

Figure 1. Wildlife management areas used in study (Blue Ridge WMA [1], Rich Mountain [2], Blue Ridge [3], Cooper's Creek [4], Chestatee [5], Chattahoochee [6], Swallow Creek [7], and Warwoman [8]) located in north Georgia.

ome (Omernik 1987). Cove hardwood communities occurred in sheltered concave landforms and north-facing slopes to an elevation of approximately 1,200 m. Cove hardwoods, floristically rich and mesic communities, were dominated by yellow-poplar (*Tulip poplar*), northern red oak (*Quercus rubra*), yellow buckeye (*Aesculus flava*), and American basswood (*Tilia americana*).

Northern hardwoods occurred on north-facing slopes and sheltered headwater ravines above cove hardwood communities at mid- to higher elevations (>1,200 m) and across a variety of aspects and landforms at the highest elevations. These communities were dominated by yellow birch (*Betula alleghaniensis*), black birch (*Betula lenta*), American beech (*Fagus grandifolia*), and northern red oak often with dense understory of rosebay rhododendron (*Rhododendron maximum*) on the most mesic sites and striped maple (*Acer pensylvanicum*) and flame azalea (*Rhododendron calendulaceum*) on the less mesic sites. Montane streamside communities were characterized by eastern hemlock (Tsuga canadensis)-white pine (*Pinus strobus*) overstories and dense understories of rosebay rhododendron.

Upland hardwood communities occurred throughout all elevations on submesic to xeric sites. Dominant overstory species included: northern red oak, white oak (*Q. alba*), black oak (*Q. velutina*), hickories (*Carya spp.*), red maple (*Acer rubrum*), and blackgum (*Nyssa sylvatica*). Shrub layers of American chestnut (*Castanea dentata*), Fraser's magnolia (*Magnolia fraseri*), and rosebay rhododendron often were present in mesic upland hardwood sites, whereas more xeric sites were dominated by mountain laurel. Mixed-pine hardwood communities occurred on exposed ridges and side slopes with southern or southwestern aspects throughout. Although variable across site moisture regimes, aspect, elevation, and disturbance histories, these communities were dominated by chestnut oak (*Q. montana*), scarlet oak (*Q. coccinea*), blackgum, red maple, and various montane yellow pines (*Pinus spp.*). Thick growth of mountain laurel (*Kalmia latifolia*), smilax (*Smilax spp.*), or highbush blueberry (*Vaccinium corymbosum*) often occurred in understories (NRCS-Georgia Soil Survey 2017).

Methods

Deer harvest data

We obtained deer harvest data collected by state biologists stationed at each WMA check station from 1979–2015. Biologists collected hunter name, harvest date, sex, estimated age (1.5, 2.5, and ≥3.5 years; Severinghaus 1949), weight, and antler measurements (i.e., beam diameter, beam length, antler spread, and total number of antler points). All deer harvested on the WMA were required to be checked. Hunters were permitted to harvest deer with archery, firearms, and/or muzzleloader equipment depending on the season. For our data analysis, we excluded archery harvest data due to limited harvest each year and the lack of mandatory check-in for hunters in that portion of the season. Deer harvest regulations varied across the eight WMAs based on the year and weapon type: firearms (males: = 4.1 days, SE = 0.06; females: = 0.6 days, SE = 0.04) and muzzleloader (males: = 3.5 days, SE = 0.08; females: = 3.1 days, SE = 0.12). In 1993, Georgia experienced an extreme snow event (NOAA 2017) and Georgia DNR-WRD subsequently closed female deer harvest for the next two years to reduce potential impacts of winter mortality on long-term population growth (K. Kammermeyer, Georgia DNR-WRD, personal communication).

To evaluate harvest trends over time, we pooled harvest data from all eight WMAs: (1) by deer harvested with firearms and muzzleloaders, (2) by sex, and (3) by year. We chose to pool the data because we observed similar harvest trends across WMAs. We then evaluated whether a monotonic trend existed using the nonparametric Mann-Kendall test using package 'Kendall' in program R (R Core Team 2013, McLeod 2015). This test is useful in examining environmental time series because there are no assumptions regarding the underlying distribution of the data, it can handle missing values, and it tests for a trend without the need to specify whether the trend is linear or nonlinear (Libiseller and Grimvall 2002, Yue and Wang 2004). However, an important assumption of the Mann-Kendall test is the absence of serial correlation. We tested for serial correlation using the autocorrelation (acf) and partial autocorrelation functions (pcf) in the 'Kendall' package. We generated figures of harvest trends for males and females, the average number of harvest days available per year, and standardized harvest (number of male deer harvested/total number of hunters) from 1979–2015. Georgia DNR-WRD required hunters to check-in only one time during the hunting period; therefore, we report hunting pressure as the total number of hunters/year rather than the number of hunter-days/year.

Yearling male body mass and antler size are sensitive to environmental factors (Ashley et al. 1998, Keyser et al. 2005, Simard et al. 2014). Therefore, we investigated the effects of forest conditions on body mass (kg) and antler size (beam diameter [mm] and beam length [cm]) of yearling males harvested on the eight WMAs from 1979–2015. We conducted a Mann-Kendall test using package 'Kendall' in program R to evaluate whether a monotonic trend existed in these condition indices (R Core Team 2013, McLeod 2015). We were only able to report standard errors for data from 2002–2015 because sample sizes were unavailable prior to this time period.

Bear harvest data and population trends

Bear hunting was concurrent with muzzleloader and firearms seasons for deer with a limit of 1 bear/hunter from 1979–2010 and 2 bears/hunter from 2011–2015. Harvest of a female with cubs or any bear weighing <34 kg (live-weight) or use of bait was prohibited throughout the study period. Registration of harvested bears was mandatory and Georgia DNR-WRD personnel recorded data from all harvested bears including sex and weight (Little et al. 2017). Georgia DNR-WRD personnel also extracted a premolar for aging using cementum annuli (Willey 1974).

To estimate black bear population growth rates on the eight WMAs, we used Downing's population reconstruction methodology (Downing 1980). Population reconstruction is a technique that uses age-at-harvest data and backward addition of cohorts to estimate minimum population size over time and is commonly used by state agencies for black bear and white-tailed deer population estimation (Davis et al. 2007). The advantage of population reconstruction is that it requires only two primary data (total harvest by year and age-at-harvest by year; Downing 1980) and can be used to identify trends in abundance over time (Tilton 2005). We analyzed sexes separately because harvest mortality may differ

for males and females (Davis et al. 2007). We collapsed ages into five classes: cubs: 0.25–0.75 years old; yearlings: 1–1.75 years old; 2-year-olds: 2–2.75 years old; 3-year-olds: 3–3.75 years old, and ≥4 year-olds. We reconstructed the population from 1979–2014 using program PopRec2011 (Pond and Property, LLC, Newport, Virginia), which uses Downing's (1980) method of population reconstruction. For years of complete reconstructed cohorts, PopRec2011 calculates the annual population growth rate (λ_t) as:

$$\lambda_t = N_{t+1}/N_t$$

where is the total reconstructed abundance in year t. We censored years 2013–2015 due to incomplete cohorts; therefore, our final reconstructed populations were from 1979–2012. Population reconstruction does not account for deaths due to natural mortality, thus reconstructed abundances are underestimates of total population abundance (Davis et al. 2007).

Forest stand and prescribed fire data

To evaluate changes in forest conditions across the study period, we evaluated trends in forest stand age and changes in oak volume by stand size class (small [<12.7 cm], medium [12.7–27.9 cm], and large diameter [>27.9 cm]). We obtained stand age data from the USFS-Chattahoochee-Oconee National Forests Geospatial Database (USFS 2017) and classified stands into seven classes (0–10, 11–20, 21–30, 31–40, 41–50, 51–60, and ≥61 years old) and report the amount (% across all eight WMAs combined) by size class for 1979 and 2015. To evaluate changes in oak volume by stand size class, we used the USFS-Forest Inventory and Analysis program database to calculate the total volume (million m³) of all oak species combined by stand size class for each available inventory from 1982–2014 (USDA-FIA 2017). Our study sites constituted 32.7% of the 3,036 km² CNF and were likely representative of the entire forest.

We obtained prescribed fire data (2003–2015) for our study areas from the CNF fire staff. The majority of the burning occurred during the dormant season (January–early April) and was of low to moderate intensity (J. Wentworth, USFS, personal communication).

Results

From 1979–2015, hunters harvested 18,016 male and 6,450 female deer during the muzzleloader and firearms seasons across the eight WMAs. From 1979–2015, harvest of males and females declined by 84.9% ($\tau = -0.74$, $P < 0.001$, Figure 2a) and 97.0% ($\tau = -0.60$, $P < 0.001$, Figure 2b), respectively, and was consistent across all WMAs. Despite accounting for hunter effort during the same time frame, harvest of males declined by 50% ($\tau = -0.51$, $P < 0.001$, Figure 3) and was consistent across all WMAs. Male
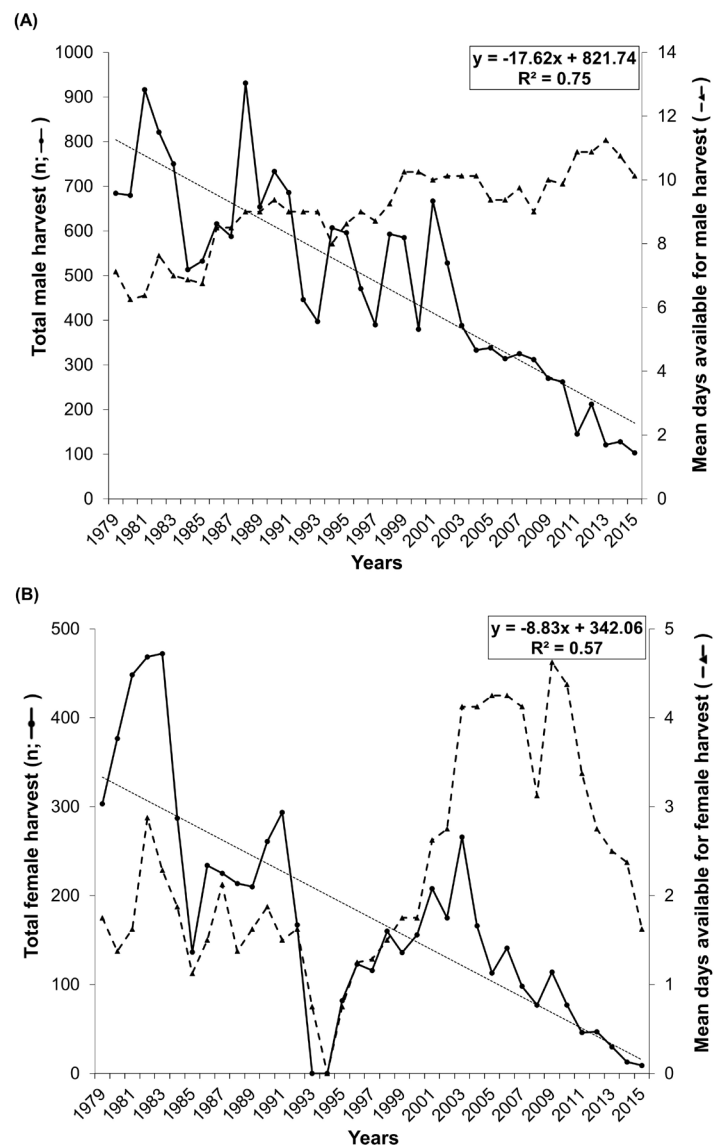

Figure 2. Total male (A) and female (B) white-tailed deer (*Odocoileus virginianus*) harvest across eight Wildlife Management Areas in north Georgia and mean number of available harvest days by sex, 1979–2015.

harvest was highest and most variable from 1979–2001 ($\tau = -0.39$ $P = 0.009$, Figure 2a); however, harvest only declined by 2.5% during this time period. Male harvest steadily declined from 2002–2015 by 80.5% ($\tau = -0.91$, $P < 0.001$), despite a 42% increase in the mean number of days available to harvest males (Figure 2a) and was consistent across all WMAs. Similarly, female harvest was highest and most variable from 1979–2003 ($\tau = -0.39$ $P = 0.006$), but steadily declined from 2004–2015 by 94.6% ($\tau = -0.84$, $P < 0.001$, Figure 2b) and was found to be consistent across all WMAs.

All yearling male condition indices increased from 1979–2015: mean body weight increased by 21% ($\tau = 0.62$, $P < 0.001$, Figure 4a),
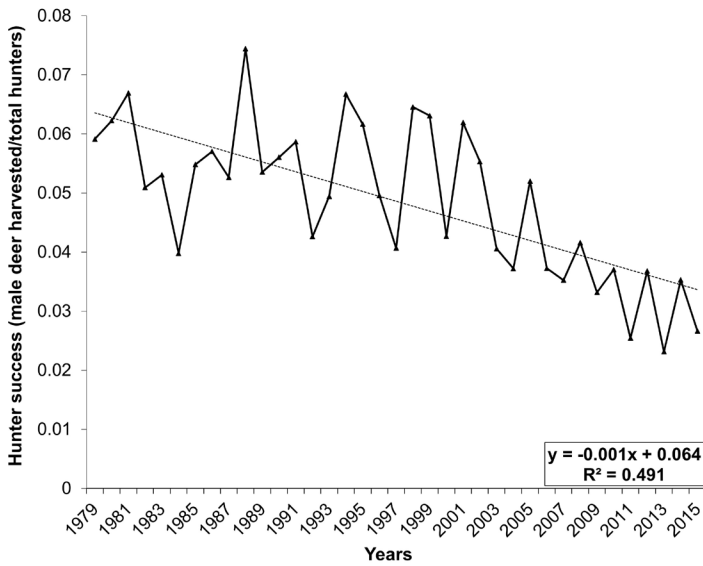
Figure 3. Total male white-tailed deer (*Odocoileus virginianus*) harvest standardized by number of hunters/year across eight Wildlife Management Areas in north Georgia, 1979–2015.

mean antler diameter increased by 62% ($\tau = 0.74$, $P < 0.001$, Figure 4b) and mean antler beam length increased by 92% ($\tau = 0.59$, $P < 0.001$, Figure 4c) and was found to be consistent across all WMAs.

From 1979–2015, hunters harvested 1,119 male and 1,066 female black bears on the eight WMAs. Hunters harvested 22 cubs, 486 yearlings, 328 2-year-olds, 137 3-year-olds, and 146 ≥4 year-old males. Hunters harvested 12 cubs, 217 yearlings, 218 2-year-olds, 139 3-year-olds, and 480 ≥4 year-old females. Annual population growth rate for males and females was 1.07 and 1.08, respectively (Figure 5).

From 1979–2015, the age of forest stands increased across the WMAs (Figure 6). Coverage of the two youngest age classes (0–10 years old and 11–20 years old) was reduced by 95.3% from 6.4% in 1979 to 0.3% by 2015. Concomitantly, forest coverage by stands in the ≥61 year age class increased by 104.7% from 42.8% in 1979 to 87.6% in 2015 (Figure 6). From 1982–2014, oak volume in the CNF increased by 52.8% in the large diameter class (>27.9 cm) whereas oak volume decreased by 73.5% in the small diameter class (<12.7 cm; Figure 7). From 2003–2015, area managed by prescribed fire in the CNF increased from 2,916 to 5,629 ha ($\tau = 0.44$, $p = 0.044$).

Discussion

Trends in white-tailed deer harvest data suggested that deer populations on the eight WMAs in north Georgia declined substantially during the past 37 years. Despite purposeful reductions in antlerless deer harvest to stimulate population growth, deer populations failed to stabilize or increase. Based on morphometric indices of
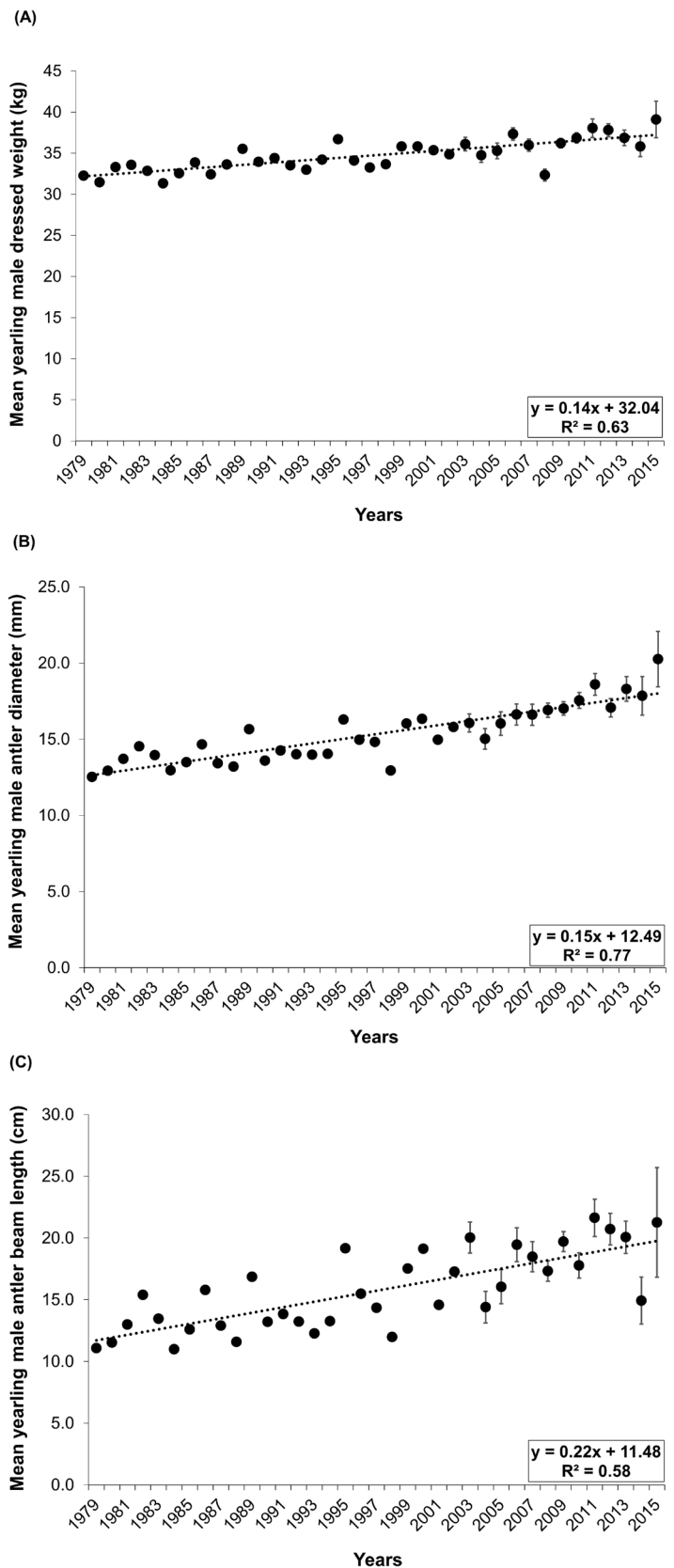

Figure 4. Yearling male white-tailed deer (*Odocoileus virginianus*) condition indicators (mean body weight [A], mean antler diameter [B], and mean antler beam length [C]) across eight Wildlife Management Areas in north Georgia, 1979–2015.
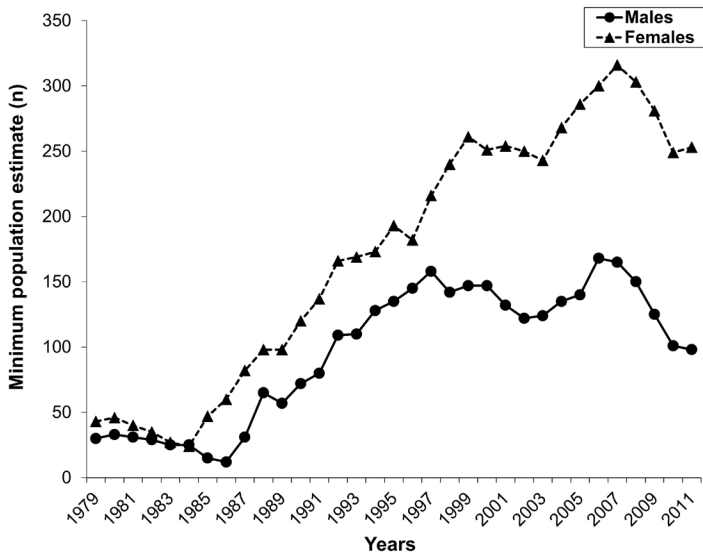
Figure 5. Population reconstruction of male and female black bears (*Ursus americanus*) across eight Wildlife Management Areas in north Georgia, 1979–2012. We censored population estimates for 2013–2015 because age class data were incomplete.
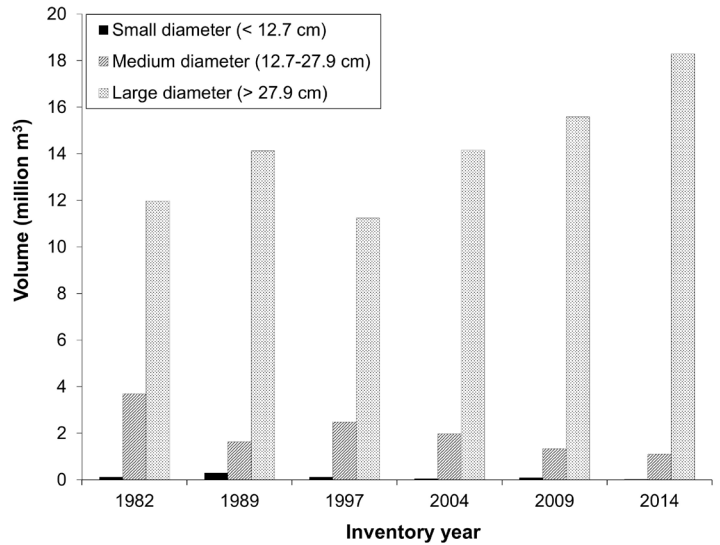

Figure 7. Oak (*Quercus* spp.) volume (million cubic feet) by stand size class (small, <12.7 cm; medium, 12.7–27.9 cm; and large, >27.9 cm) in the Chattahoochee National Forest containing the eight Wildlife Management Areas in north Georgia used in our study, 1982–2014. Forest Inventory Analysis (FIA) data were collected from 1982–2014 by U.S. Forest Service personnel, and sampling frequency varied from 5 to 8 years during this time period.
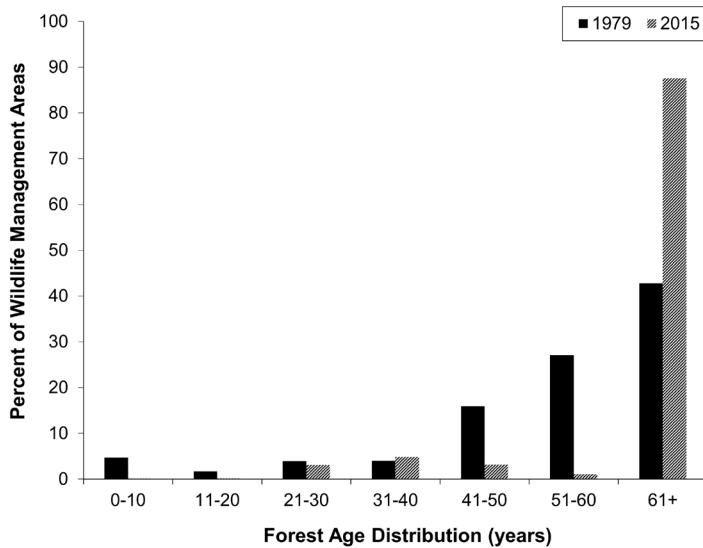

Figure 6. Forest age distribution (%; 0 − ≥61 years old) across eight Wildlife Management Areas in north Georgia, 1979 and 2015.

yearling male deer, the physical condition of deer improved markedly during the same time period despite a decrease in early successional habitat. Concomitantly, black bear populations increased during this same time period, which is supported by data from other state agencies in the southeastern United States (Telesco 2013).

White-tailed deer populations in the Appalachians are influenced by forage availability and quality, weather, and predators (Wentworth et al. 1992, Johnson et al. 1995, Ford et al. 1997, Ryan et al. 2004, Campbell et al. 2005). In particular, indices of herd health (i.e., body weights, antler size) are positively correlated with the amount of young and mid-successional forests, especially in years following poor mast crops (Ford et al. 1997). The data we examined indicates that early successional forests have essentially disappeared on our study areas. However, all indices we evaluated suggested that the condition of yearling male deer increased over time, which may partly be explained by the increase in area managed by prescribed fire. Despite the lack of early successional habitat, deer are likely able to acquire adequate resources for maintenance and growth due to reduced competition for resources (Ashley et al. 1998, Keyser et al. 2005), thus mitigating any density-dependent effects associated with lack of early successional habitats. Using yearling males as an index (Keyser et al. 2005), we may assume that the condition of adult females was sufficient to maintain normal reproductive levels (Verme 1969, Albon et al. 1983, Sæther and Haagenrud 1983, Hewison 1996, Festa-Bianchet et al. 1998). Thus, a habitat-driven change in fecundity is an unlikely factor in the decline in population trends. Rather, our observed

trends suggest that recruitment rates may have declined over the course of the study. Considering evidence from other Southeastern deer populations (e.g., Kilgo et al. 2012), neonatal predation may be suspected as a factor limiting deer populations in north Georgia. Additionally, the lack of early successional habitat may reduce fawning cover and increase risk of predation for neonates.

Predation is one of the most common sources of mortality of white-tailed deer neonates (Vreeland et al. 2004, Carstensen et al. 2009, Kilgo et al. 2012, Chitwood et al. 2015, Shuman et al. 2017) and black bears have been shown to be effective predators of neonates (Vreeland et al. 2004, Shuman et al. 2017). Since 1979, the estimated minimum population of black bears on our study sites increased 381% from 73 individuals to ≥351. Similarly, recent research has documented high fawn predation rates by coyotes throughout the Southeast (Kilgo et al. 2012, Jackson and Ditchkoff 2013, Chitwood et al. 2015, Nelson et al. 2015, Shuman et al. 2017). Coyotes were extremely rare on the CNF in the 1980s, but have become increasingly common in recent years (K. Kammermeyer, Georgia DNR-WRD, personal communication), although density estimates are lacking. As such, our results suggest predator-induced declines in recruitment as a possible correlate that should receive research attention.

Limits on timber harvests on CNF have reduced the amount of early successional habitats as suggested by decreased small oak volume, and in turn soft mast producing plants and browse available for deer. Adult female deer may need to utilize larger areas and increase the frequency and duration of foraging bouts to procure resources to meet the demands of gestation and lactation (e.g., Crimmins et al. 2015). Previous studies suggested that omnivorous predators, such as coyotes, increase consumption of mammals when soft mast is less abundant (Andelt et al. 1987, Schrecengost et al. 2008). Additionally, habitat characteristics affect distribution, density, and hunting efficacy of predators (Gese et al. 1996, Dijak and Thompson 2000). Decreased landscape heterogeneity (e.g., homogenous forested blocks with few cover types) may increase the likelihood of coyote predation on neonates (Gulsby et al. 2017). We suspect that the reduction in early successional habitats as partly illustrated by the decrease in small oak volume, may lead to reduce fawning cover and/or increased risk of predation.

We believe our long-term data provide strong directional indicators of population and habitat trends through time, and our analyses of these trends suggest plausible causes for the population declines in north Georgia. However, they also emphasize the critical need to obtain information on deer survival, cause-specific mortality, and reproductive rates along with more detailed examination of habitat conditions regionally to understand these changes and the subsequent information needs for managers (Caughley

1976, Eberhardt 1985, Dusek et al. 1989). Likewise, it is important to track the changing predation context; although bear populations have increased dramatically, status and population trends of other predator populations (e.g., bobcats and coyotes) are unknown. Similarly, we lack information on how habitat conditions such as understory vegetation or early successional habitats may influence the probability of survival and subsequent recruitment of fawns. Therefore, population monitoring through time is critical and can help identify important data gaps. However, research-based assessments of current conditions in changing systems are also necessary to verify the drivers of population trajectories and direct management actions.

Management Implications

Despite reductions in antlerless harvest opportunities, the deer populations on these north Georgia WMAs have continued to decline. Georgia DNR-WRD has exhausted most deer-harvest management options to increase deer populations in north Georgia and has satisfied recommended requisites before initiating a neonate deer survival study (Rosenberry et al. 2011). We believe an understanding of the interplay among harvest mortality, predator-induced changes in recruitment, and habitat will be necessary to direct future management of white-tailed deer on these wildlife management areas, and perhaps elsewhere in the southern Appalachians.

Acknowledgments

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