



## Original Article

# Effects of Breeding Chronology on White-tailed Deer Productivity in Alabama

MARK A. TURNER,<sup>1</sup> *School of Forestry and Wildlife Sciences, Auburn University, Auburn, AL 36849, USA*

WILLIAM D. GULSBY, *School of Forestry and Wildlife Sciences, Auburn University, Auburn, AL 36849, USA*

STEPHEN S. DITCHKOFF, *School of Forestry and Wildlife Sciences, Auburn University, Auburn, AL 36849, USA*

WILLIAM N. GRAY, II, *Alabama Division of Wildlife and Freshwater Fisheries, 3520 Plaza Drive, Enterprise, AL 36330, USA*

CHRISTOPHER W. COOK, *Alabama Division of Wildlife and Freshwater Fisheries, 8211 McFarland Blvd West, Northport, AL 35476, USA*

**ABSTRACT** Following declines in white-tailed deer (*Odocoileus virginianus*) populations during the 19th century, many areas throughout the southeastern United States were restocked from various sources. As a result, some populations remain genetically distinct, and phenotypic traits of source populations, including breeding chronology, have been conserved. For example, average conception dates vary by  $\geq 60$  days between populations within some Alabama, USA, counties. Although deer have achieved and maintained sustainable densities across much of the southeastern United States for several decades, it is unclear whether this restocking legacy has demographic consequences relevant to management. Therefore, we analyzed a data set containing information on 270 yearling (1.5 yr old) and 2,116 adult ( $\geq 2.5$  yr old) female deer collected during 1995–2017 to determine potential effects of breeding chronology on *in utero* productivity. Parameter estimates from a generalized linear mixed model indicated yearling productivity decreased approximately 16% (95% CL = 0–29%) for each 30-day increase in mean site-specific parturition date. We did not observe a similar relationship for adults. We believe the relationships we observed for yearlings may result from an interaction between parturition and plant phenology. Specifically, on sites with relatively late parturition dates, fawns are born near the end of the growing season when suboptimal nutritional conditions may negatively affect productivity during their first year of life. Variation in reproductive output of large ungulates is primarily driven by young females, so managers should be aware that productivity of late-breeding deer populations may be less than average, especially if those populations are behaving in a density-dependent manner. In addition, these findings emphasize the importance of considering the potential demographic implications of wildlife translocations resulting from differences in timing of life-history traits. © 2019 The Wildlife Society.

**KEY WORDS** Alabama, breeding dates, chronology, *Odocoileus virginianus*, parturition, productivity, reproduction, restocking, translocation, white-tailed deer.

In general, breeding and parturition among species is timed to coincide with environmental conditions that maximize fitness (Greig 1979). White-tailed deer (*Odocoileus virginianus*) breeding chronology is primarily influenced by photoperiod (Diefenbach and Shea 2011), with most deer populations in the United States breeding as day length decreases during the autumn. Subsequently, fawning occurs during late spring to early summer, allowing adequate time for growth and development prior to the onset of winter. However, breeding occurs later in winter in portions of several southeastern states including Alabama (Lueth 1955), Mississippi (Jacobson et al.

1979), and Louisiana, USA (Roberson and Dennett 1966). Differences in breeding dates observed across relatively small geographic scales within these states are likely a result of restocking efforts—the genetic legacy of restocking have been well-documented (Leberg et al. 1994, Leberg and Ellsworth 1999, DeYoung et al. 2003, Gray 2004, Budd et al. 2018). It has been hypothesized that these differences in chronology have been maintained over several decades through maternal inheritance, where female offspring inherit breeding chronology from their dam (Sumners et al. 2015).

Given that female deer are philopatric, there are examples of populations within the same county that have maintained disparate breeding dates >50 years postrestocking. For example, in Barbour County, Alabama, breeding occurs as early as November on Eufaula National Wildlife Refuge and as late as February on Barbour County Wildlife

Received: 5 November 2018; Accepted: 4 July 2019  
Published: 22 November 2019

<sup>1</sup>E-mail: mat0073@auburn.edu

Management Area despite that these sites are separated by only 30 km (Gray 2004). Thus, it is possible for 2 deer within the same age class (i.e., born during the same calendar year) and county to have birth dates that differ by as much as 3 months, which can significantly affect morphology. Specifically, fawning date significantly affects body mass and antler size of yearling males, with later-born males having smaller antlers and reduced body mass (Knox et al. 1991, Shea et al. 1991, Vanderhoof 1991, Jacobson 1995, Gray et al. 2002). Gray et al. (2002) hypothesized that these findings were related not only to the fact that earlier-born males were simply older and had more time for growth, but also that later-born males were at a nutritional disadvantage during their birth year as a result of plant phenology. Specifically, both crude protein and digestibility of forage plants decline as the growing season progresses and plants mature (Short 1975, Buxton 1996). Nonetheless, there is some evidence to suggest the negative effects of later fawning dates on body mass and antler size diminish as males reach older age classes (Vanderhoof 1991).

Unfortunately, considerably less research has focused on effects of fawning date on the female segment of deer populations. Females are primary drivers of deer population growth; factors affecting female body condition and, ultimately, productivity are of great interest to deer researchers and managers. For example, it is well-documented that yearling females are less productive than adults (Verme 1969, Roseberry and Klimstra 1970, Nixon 1971, Jones et al. 2010), but yearling productivity increases as body mass increases (Strickland et al. 2008, Karns et al. 2014).

Although fawning dates affect morphology of male deer, and age and body condition of female deer affect productivity, to our knowledge the link between fawning date and productivity of female deer has not been investigated. Although it seems logical that later-born females would exhibit decreased productivity in the same manner that males do antler size, productivity of female white-tailed deer is a highly conserved trait that is maintained via adjustments to growth rate or body size (Simard et al. 2008). Diefenbach and Shea (2011) suggested that such a relationship may exist, but did not offer quantitative evidence of the phenomenon. If parturition date does influence productivity, it is most likely to be evident for yearling females because productivity of this age class is more sensitive to nutritional conditions than for adults (Verme 1969, Strickland et al. 2008).

We lacked information on the relationship between timing of parturition and female productivity, and the obvious implications of reduced productivity for deer population growth; therefore, we analyzed a data set containing information on female deer collected throughout Alabama to evaluate the relationship between fetal counts and site-specific parturition dates. We predicted that females collected from sites with later-than-average parturition dates would have reduced fetal counts compared with those from sites with earlier-than-average parturition dates, and differences in fetal counts would be most apparent in yearling females. In addition, we predicted that females collected

from sites with later average parturition dates would have lower body mass compared with those from sites with earlier average parturition dates if nutritional availability at birth was driving this relationship.

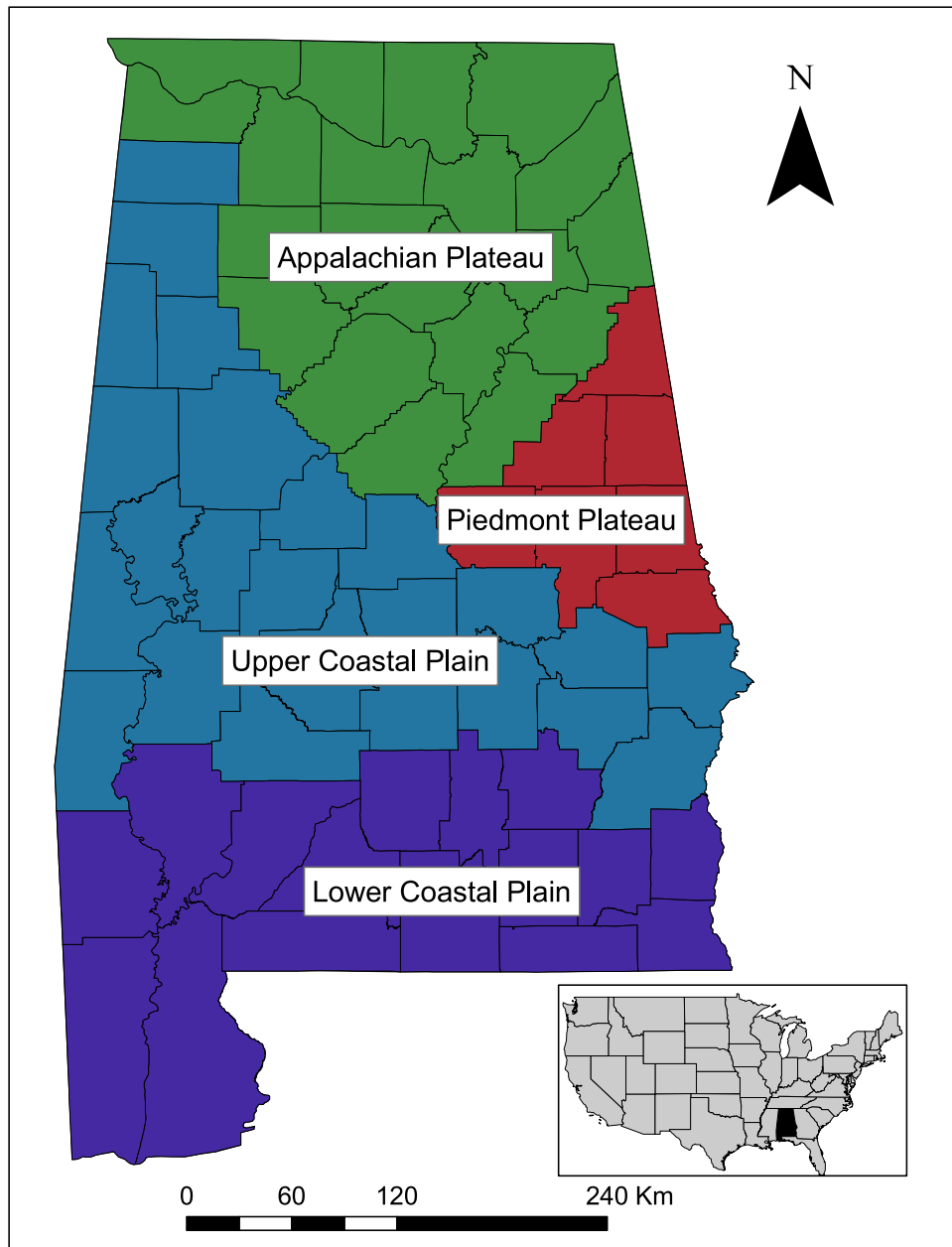
## STUDY AREA

We sampled deer from 48 of 67 counties in Alabama. The number and delineation of physiographic regions in Alabama differs among sources, so we used expert opinion from state deer biologists to divide the state into regions most likely to differ with regard to deer morphometrics (Fig. 1). The Appalachian Plateau was characterized by soils derived from sandstone or shale. Elevation ranged from approximately 90–400 m. Flatter areas of the Appalachian Plateau had row-crop agriculture, but most areas were too steep for cropping. The Piedmont Plateau was characterized by red, clayey subsoils and sandy or clay loam surface layers. Elevation typically ranged from 210 to 300 m and pasture and forest were predominate land-cover types. The Lower Coastal Plain was characterized by loamy or clayey subsoils with sandy loam or loam surface layers. Most of the area was forested and elevations ranged from approximately 60 to 300 m. The Upper Coastal Plain mostly consisted of the Blackland Prairie or “Black Belt” and characterized by soils derived from alkaline, Selma chalk, or acid marine clays. Topography was level to undulating and elevation was approximately 60 m. Soybean (*Glycine max*) was the main row-crop in this area, but timber production and pasture were predominant land-cover types (Mitchell and Loerch 2008). Alabama’s climate was subtropical with a mean annual temperature of 17.3°C and mean annual rainfall of 140.4 cm (National Oceanic and Atmospheric Administration 2017).

## METHODS

### Deer Collection

We collected deer during late winter to early summer from 1995 to 2017 as part of a statewide investigation of white-tailed deer breeding chronology in Alabama. We collected deer via sharpshooting from vehicles and elevated blinds over bait. Following recovery, we transported deer to a nearby processing facility or processed them in the field. We recorded the mass and age of each deer and the number, sex, and age of each fetus for pregnant females. We estimated deer age using tooth replacement and wear patterns (Severinghaus 1949), and aged fetuses based on a 198-day gestation according to Hamilton et al. (1985). We classified each female in the data set as either a yearling (1.5 yr old) or adult ( $\geq 2.5$  yr old), based on their age at the time of conception. We did not analyze productivity data from deer bred as fawns. We calculated the average site-specific parturition date at each collection site where  $\geq 10$  adult females were sampled based on fetal ages from those deer. We conducted deer collections as part of a statewide reproductive survey by the Alabama Department of Conservation and Natural Resources, Division of Wildlife, supported by Federal Aid in consecutive Wildlife Restoration Grant’s AL-W-35-45 through AL-W-35-64. We



**Figure 1.** Map of physiographic regions of Alabama, USA, used as covariates in models estimating the effects of mean parturition date on female white-tailed deer (collected during 1995–2017) on in utero productivity. The number and delineation of physiographic regions in Alabama differs among sources, so we used expert opinion from state deer biologists to divide the state into regions most likely to differ with regards to deer morphometrics.

conducted all collections in adherence to the 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education (Sikes et al. 2016).

### Data Analysis

We were interested in quantifying the relationship between mean parturition date and fetal productivity; however, we also expected variation in productivity due to physiographic region, sampling location, and year. Thus, we used the lme4 package to fit a generalized linear mixed model to these data in the Program R software version 3.5.1 (Bates et al. 2015, R Core Team 2018). Specifically, we treated average parturition date and physiographic region as fixed effects, and

site nested within year as a random effect. The response variable was a count (i.e., no. of fetuses), so we used Poisson regression with a logit link. Female productivity and body mass are typically related, so we also quantified the relationship between mean parturition date and female body mass using the nlme package in the R software (Pinheiro et al. 2017). We used the same model structure as for the productivity analysis, but added Julian date of collection as a fixed effect to account for differences in body mass due to this factor. We expected responses to differ between age classes (i.e., yearling and adult), so we modeled each age class separately. We set  $\alpha = 0.05$  for all statistical tests. To aid in interpretation of results, we back-transformed and scaled parameter estimates generated via Poisson regression,

and used the effects package in the R software to graphically display the effect of parturition date on parameters of interest (Fox and Hong 2009).

## RESULTS

The final data set included 270 yearling and 2,116 adult females representing 77 collection sites across 48 Alabama counties. On average, site-specific parturition dates were calculated from 27.4 adult females. The overall mean for parturition date was 24 July (range = 16 May–24 Aug). Parturition date was a significant predictor of yearling productivity, which decreased approximately 16% (95% CL = 0–29%) for each 30-day increase in mean parturition date (Table 1). Based on the effects plot, yearling productivity increased 1.7 times from the latest to the earliest site-specific parturition date we observed (Fig. 2). We did not observe a relationship between mean parturition date and yearling body mass (Table 2). Yearling females from the Piedmont Plateau and Lower Coastal Plain tended to have lower body mass compared with those from the Appalachian Plateau, but mass was similar for yearling females from the Appalachian Plateau and the Upper Coastal Plain (Table 2).

There was no evidence to suggest a relationship between adult productivity or body mass and parturition date (Tables 1, 2). However, adult females from the Lower Coastal Plain and Piedmont Plateau had lower body mass than those from the Appalachian Plateau. Body mass was similar between adult females from the Appalachian Plateau and the Upper Coastal Plain. Finally, adult female body mass increased with Julian date of collection (Table 2).

**Table 1.** Back-transformed (from log link) and scaled (where indicated) parameter estimates ( $\beta$ ), 95% confidence limits (LCL–UCL),  $z$ -values, and probability the coefficient differs from 0 ( $\Pr(>|z|)$ ;  $P$ ) for models predicting the effects of mean parturition date on fetal counts of yearling (1.5-yr-old) and adult ( $\geq 2.5$ -yr-old) white-tailed deer collected across Alabama, USA, between 1995 and 2017.

	$\beta$	95% LCL	95% UCL	$z$	$P$
Yearlings					
Intercept <sup>a</sup>	3.82	1.20	11.32	2.34	0.019
Parturition date <sup>b</sup>	0.84	0.72	1.00	-1.98	0.048
Lower Coastal Plain <sup>c</sup>	1.10	0.78	1.55	0.56	0.573
Piedmont Plateau <sup>d</sup>	0.64	0.36	1.07	-1.60	0.110
Upper Coastal Plain <sup>e</sup>	0.98	0.75	1.28	-0.16	0.877
Adults					
Intercept	1.29	0.91	1.82	1.45	0.148
Parturition date	1.05	0.99	1.10	1.67	0.095
Lower Coastal Plain	0.93	0.84	1.02	-1.49	0.136
Piedmont Plateau	0.94	0.81	1.10	-0.72	0.470
Upper Coastal Plain	1.04	0.96	1.12	0.85	0.394

<sup>a</sup> Estimate for females in the Appalachian Plateau with earliest observed mean parturition date.

<sup>b</sup> Estimated proportional change in no. of fetuses for each 30-day increase in mean parturition date.

<sup>c</sup> Lower Coastal Plain physiographic region.

<sup>d</sup> Piedmont Plateau physiographic region.

<sup>e</sup> Upper Coastal Plain physiographic region.

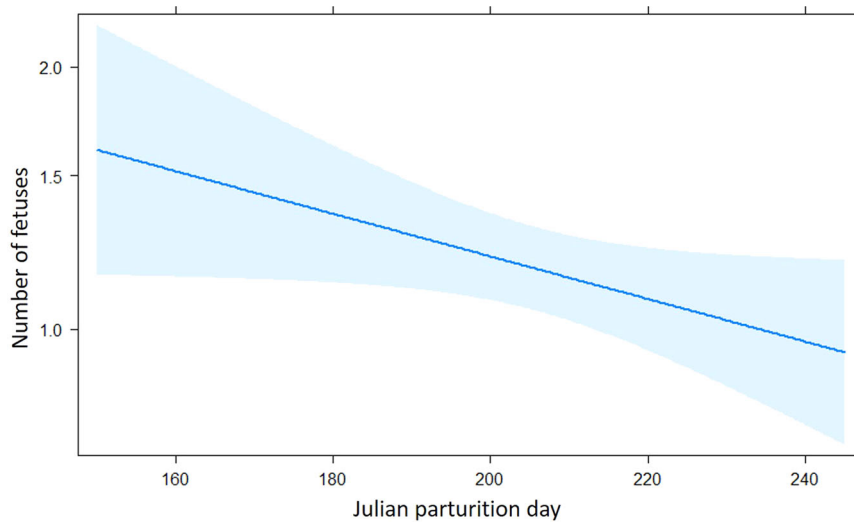
## DISCUSSION

Unlike the negative relationship between antler score of yearling male deer and parturition date others have observed (e.g., Vanderhoof 1991, Gray et al. 2002), age alone is not sufficient to explain the relationship we observed between parturition date and yearling female productivity. Breeding chronology is maternally inherited (Summers et al. 2015), so later-born females also breed later, meaning all females in our study were bred at approximately the same relative age. Instead, the late-born yearling females in our study may have been less productive because they are born near the end of the growing season, when crude protein content and digestibility of forage plants are lower, placing them at a nutritional disadvantage (Short 1975, Buxton 1996, Glow and Ditchkoff 2017).

However, our study was not designed to address this hypothesis, and if the decreased yearling productivity we observed was nutritionally driven, we also expected to find a negative effect of increasing parturition date on yearling body mass, which we did not. This may be explained by the fact that female deer adopt a strategy that favors their own survival, reproductive potential, and growth over that of their offspring when nutrient availability is limited (Therrien et al. 2007). Thus, yearling females from late-breeding populations may have sacrificed reproductive output during their first year of life to preserve body mass and future reproductive output (Simard et al. 2008). Considering our data, this strategy appears effective because productivity was similar among populations with disparate breeding dates for adult females.

Decreased productivity of any age class can result in decreased fawn recruitment and affect population growth rates. However, it is questionable how a decrease in yearling productivity affects overall recruitment, given that adults are inherently more productive than yearlings. Nonetheless, physically immature but reproductively active females of large herbivore species may be the most important demographic to consider because variation in survival and reproductive output are greatest within younger age classes (Gaillard et al. 2000). Therefore, it seems plausible that the decrease in yearling productivity we observed may affect population growth, although we were unable to examine the population-level effects in the current study. Further, because population density also affects fecundity of young females (Gaillard et al. 2000), it is reasonable to presume that negative effects of reduced yearling productivity in late-breeding populations would be further exacerbated in populations behaving in a density-dependent manner.

A variety of factors influence the breeding dates of white-tailed deer, but we believe most of the observed variation in breeding dates in Alabama is a legacy of restocking. Specifically, 82% of the deer used to restock Alabama came from source populations in Clarke, Sumter, and Marengo counties in the southwestern portion of the state, where deer breed in late January to early February (Allen 1965). This breeding pattern remains evident across portions of the state where deer from this area were restocked (Gray 2004).



**Figure 2.** Plot predicting fetal counts of yearling (1.5-yr-old) female white-tailed deer in Alabama, USA, relative to the average parturition date at the site where they were collected. Deer were collected from 1995 to 2017. Bands represent 95% confidence limits.

Further, a 2004 (50 yr after restocking) comparison of mtDNA haplotypes between deer from the source population in Clarke County and those of a population 200 km away in Barbour County, which was restocked with those deer, showed that the populations remained genetically indistinct. In contrast, deer from a mid- to late-November breeding population in Barbour County were genetically distinct from both the Clarke County deer and the late-breeding Barbour County deer (Gray 2004). A Mississippi study that examined mtDNA haplotypes among populations with varying breeding dates similarly concluded that differences in breeding dates could largely be explained

by genetic differences driven by restocking efforts (Sumners et al. 2015).

Nonetheless, white-tailed deer restocking efforts in Alabama were apparently successful in spite of any potential negative demographic consequences—all counties in the state now harbor huntable populations. However, it is also important to recognize that the majority of deer in Alabama were restocked from populations within the state. Had these same deer been used to restock areas with increased winter severity and shorter growing seasons, productivity may have been more negatively affected and restocking efforts less successful. Additionally, the relative importance of life-history trait timing for translocations is dependent on the degree of phenotypic plasticity of the trait in question. For white-tailed deer in the southeastern United States, it is apparent that plasticity of reproductive chronology is low, given that timing of breeding remains consistent between restocked and source populations, even 50 years after restocking. This may be a consistent trend in ungulate species; research on roe deer (*Capreolus capreolus*) showed that birth dates have not shifted to match the increasingly earlier onset of spring, despite the fact that offspring survival increases as parturition date decreases (Plard et al. 2014).

However, it is also possible that breeding chronology of restocked Alabama deer is relatively plastic, but selection pressure (against reduced yearling productivity) is insufficient or not enough time has passed to elicit a response. Additional research on the sensitivity of population growth rates to the range in yearling productivity we observed would not only help elucidate the probability that mean breeding dates will shift earlier, but also provide valuable information to deer managers.

## MANAGEMENT IMPLICATIONS

Our results indicate that yearling female productivity decreased as parturition date (likely influenced by restocking sources) increased. Although we were not able to directly link

**Table 2.** Parameter estimates ( $\beta$ ), 95% confidence limits (LCL–UCL), and *P*-values for models predicting the effects of mean parturition date on body mass (kg) of yearling (1.5-yr-old) and adult ( $\geq 2.5$ -yr-old) white-tailed deer collected across Alabama, USA, between 1995 and 2017.

	$\beta$	95% LCL	95% UCL	<i>P</i>
<b>Yearlings</b>				
Intercept <sup>a</sup>	47	38	56	<0.001
Parturition date <sup>b</sup>	-0.98	-2.6	0.60	0.23
Lower Coastal Plain <sup>c</sup>	-4.1	-6.7	-1.4	0.003
Piedmont Plateau <sup>d</sup>	-4.2	-7.6	-0.8	0.02
Upper Coastal Plain <sup>e</sup>	0.040	-2.1	2.0	0.97
Julian date <sup>f</sup>	0.016	-0.01	0.04	0.24
<b>Adults</b>				
Intercept	41	37	46	<0.001
Parturition date	0.43	-0.4	1.2	0.29
Lower Coastal Plain	-5.8	-7.3	-4.6	<0.001
Piedmont Plateau	-3.3	-5.5	-1.2	0.003
Upper Coastal Plain	1.07	-0.2	2.3	0.10
Julian date	0.050	0.04	0.06	<0.001

<sup>a</sup> Estimate for females in the Appalachian Plateau with earliest observed mean parturition date.

<sup>b</sup> Estimated change in mass for each 30-day increase in mean parturition date.

<sup>c</sup> Lower Coastal Plain physiographic region.

<sup>d</sup> Piedmont Plateau physiographic region.

<sup>e</sup> Upper Coastal Plain physiographic region.

<sup>f</sup> Estimated mass change for each 1-day increase in Julian date of collection.

productivity decreases to population growth rates, deer managers should be aware that growth rates could be lower for late-breeding populations. These findings could be particularly important for some southeastern United States deer populations where fawn survival is already limited by predation. In addition, the suppressed productivity in late-breeding populations may decline further if these populations are acting in a density-dependent manner. Managers of late-breeding populations should also be cautious when implementing intensive female harvest, which could decrease mean female age, thereby increasing the relative importance of yearling productivity. Finally, future restocking efforts should consider factors such as life-history trait timing in addition to genetics when selecting source populations, because they may have demographic consequences.

## ACKNOWLEDGMENTS

Funding for this project was provided by the Wildlife Section of the Alabama Division of Wildlife and Freshwater Fisheries through the Wildlife Restoration Program, which derives monies through an excise tax on sporting arms and ammunition paid by hunters and recreational shooters. We also thank J. Martin for his critical contribution to deer collections. Finally, we thank the Associate Editor and anonymous reviewers for their comments that improved earlier drafts of this manuscript.

## LITERATURE CITED

- Allen, R. H. 1965. History and results of deer restocking in Alabama. Alabama Department of Conservation and Natural Resources, Division of Game and Fish, Technical Bulletin Number 6, Montgomery, USA.
- Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67:1–48.
- Budd, K., L. K. Berkman, M. Anderson, J. Koppelman, and L. S. Eggert. 2018. Genetic structure and recovery of white-tailed deer in Missouri. *Journal of Wildlife Management* 82:1598–1607.
- Buxton, D. R. 1996. Quality-related characteristics of forages as influenced by plant environment and agronomic factors. *Animal Feed Science Technology* 59:37–49.
- DeYoung, R. W., S. Demarais, R. L. Honeycutt, A. P. Rooney, R. A. Gonzales, and K. L. Gee. 2003. Genetic consequences of white-tailed deer (*Odocoileus virginianus*) restoration in Mississippi. *Molecular Ecology* 12:3237–3252.
- Diefenbach, D. R., and S. M. Shea. 2011. Managing white-tailed deer: eastern North America. Pages 481–500 in D. G. Hewitt, editor. *Biology and management of white-tailed deer*. CRC Press, Boca Raton, Florida, USA.
- Fox, J., and J. Hong. 2009. Effect displays in R for multinomial and proportional-odds logit models: extensions to the effects package. *Journal of Statistical Software* 32:1–24.
- Gaillard, J. M., M. Festa-Bianchet, N. G. Yoccoz, A. Loison, and C. Toigo. 2000. Temporal variation in fitness components and population dynamics of large herbivores. *Annual Review of Ecology and Systematics* 31:367–393.
- Glow, M. P., and S. S. Ditchkoff. 2017. Economic optimization of forage and nutrient availability during stress periods for white-tailed deer. *Journal of the Southeastern Association of Fish and Wildlife Agencies* 4:121–129.
- Gray, W. N., II. 2004. Mitochondrial DNA analysis of white-tailed deer populations found in Clarke, Barbour, and Houston Counties, Alabama. Alabama Department of Conservation and Natural Resources, Division of Wildlife and Freshwater Fisheries, Grant Number W-35, Study 14, Montgomery, USA.
- Gray, W. N., II, S. S. Ditchkoff, M. K. Causey, and C. W. Cook. 2002. The yearling disadvantage in Alabama deer: effect of birth date on development. *Proceedings of the Southeastern Association of Fish and Wildlife Agencies* 56:255–264.
- Greig, J. C. 1979. Principles of genetic conservation in relation to wildlife management in southern Africa. *South African Journal of Wildlife Research* 9:57–78.
- Hamilton, R. J., M. L. Tobin, and W. G. Moore. 1985. Aging fetal white-tailed deer. *Proceedings of the Southeastern Association of Fish and Wildlife Agencies* 39:389–395.
- Jacobson, H. A. 1995. Age and quality relationships. Pages 103–111 in K. V. Miller and R. L. Marchinton, editors. *Quality whitetails: the why and how of quality in deer management*. Stackpole, Mechanicsburg, Pennsylvania, USA.
- Jacobson, H. A., D. C. Guynn, R. N. Griffin, and D. Lewis. 1979. Fecundity of white-tailed deer in Mississippi and periodicity of corpora lutea and lactation. *Proceedings of the Southeastern Association of Fish and Wildlife Agencies* 33:30–35.
- Jones, P. D., B. K. Strickland, S. Demarais, and A. C. Blaylock. 2010. Reproductive characteristics of white-tailed deer in Mississippi. *Southeastern Naturalist* 9:803–812.
- Karns, G. R., A. M. Holland, T. D. Steury, and S. S. Ditchkoff. 2014. Maternal life history of white-tailed deer: factors affecting fetal sex allocation, conception timing, and senescence. *Evolutionary Ecology Research* 16:165–178.
- Knox, W. M., M. O. Bara, and K. V. Miller. 1991. Effect of fawning date on physical development of yearling male white-tailed deer. *Proceedings of the Southeastern Association of Fish and Wildlife Agencies* 45:30–36.
- Leberg, P. L., and D. L. Ellsworth. 1999. Further evaluation of the genetic consequences of translocations on southeastern white-tailed deer populations. *Journal of Wildlife Management* 63:327–334.
- Leberg, P. L., P. W. Stangel, H. O. Hillestad, R. L. Marchinton, and M. H. Smith. 1994. Genetic structure of reintroduced wild turkey and white-tailed deer populations. *Journal of Wildlife Management* 58:698–711.
- Lueth, F. X. 1955. The birth dates of Alabama deer. *Proceedings of the Southeastern Association of Game and Fish Commissioners* 10:129–131.
- Mitchell, C. C., Jr., and J. C. Loerch. 2008. Soil areas in Alabama. *Natural Resources Conservation Service Soils*. <[https://www.nrcs.usda.gov/wps/portal/nrcs/detail/soils/survey/office/ssr7/?cid=nrcs142p2\\_047868](https://www.nrcs.usda.gov/wps/portal/nrcs/detail/soils/survey/office/ssr7/?cid=nrcs142p2_047868)>. Accessed 2 Oct 2018.
- National Oceanic and Atmospheric Administration. 2017. National Centers for Environmental information, Climate at a Glance: U.S. Time Series. <<http://www.ncdc.noaa.gov/cag/>>. Accessed 31 Oct 2017.
- Nixon, C. M. 1971. Productivity of white-tailed deer in Ohio. *Ohio Journal of Science* 71:217–225.
- Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, and R Core Team. 2017. nlme: linear and nonlinear mixed effects models. R Package version 3.1-131. <<https://CRAN.R-project.org/package=nlme>>. Accessed 20 Apr 2018.
- Plard, F., J. M. Gaillard, T. Coulson, A. J. M. Hewison, D. Delorme, C. Warnant, and C. Bonenfant. 2014. Mismatch between birth date and vegetation phenology slows the demography of roe deer. *PLoS ONE* 12(4):e1001828.
- R Core Team. 2018. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <<http://www.R-project.org>>. Accessed 20 Apr 2018.
- Roberson, J. H., Jr., and D. Dennett, Jr. 1966. Breeding season of white-tailed deer in Louisiana. *Proceedings of the Southeastern Association of Game and Fish Commissioners* 20:123–130.
- Roseberry, J. L., and W. D. Klimstra. 1970. Productivity of white-tailed deer on Crab Orchard National Wildlife Refuge. *Journal of Wildlife Management* 34:23–28.
- Severinghaus, C. W. 1949. Tooth development and wear as criteria of age in white-tailed deer. *Journal of Wildlife Management* 13:195–216.
- Shea, S. M., T. A. Breault, and M. L. Richardson. 1991. Relationship of parturition date to antler development and weight of yearling bucks in northwest Florida. *Proceedings of the Annual Meeting of the Southeast Deer Study Group* 14:21.
- Short, H. L. 1975. Nutrition of southern deer in different seasons. *Journal of Wildlife Management* 39:321–329.
- Sikes, R. S., and the Animal Care and Use Committee of the American Society of Mammalogists. 2016. 2016 Guidelines of the American

- Society of Mammalogists for the use of wild mammals in research and education. *Journal of Mammalogy* 97:663–688.
- Simard, M. A., S. D. Côté, R. B. Weladji, and J. Huot. 2008. Feedback effects of chronic browsing on life-history traits of a large herbivore. *Journal of Animal Ecology* 77:678–686.
- Strickland, B. K., S. Demarais, and P. D. Gerard. 2008. Variation in mass and lactation among cohorts of white-tailed deer *Odocoileus virginianus*. *Wildlife Biology* 14:263–271.
- Summers, J. A., S. Demarais, R. W. DeYoung, R. L. Honeycutt, A. P. Rooney, R. A. Gonzales, and K. L. Gee. 2015. Variable breeding dates among populations of white-tailed deer in the southern United States: the legacy of restocking? *Journal of Wildlife Management* 79:1213–1225.
- Therrien, J.-F., S. D. Côté, M. Festa-Bianchet, and J. F. Ouellet. 2007. Conservative maternal care in an iteroparous mammal: a resource allocation experiment. *Behavioral Ecology and Sociobiology* 62:193–199.
- Vanderhoof, R. E. 1991. Effects of parturition date on antler development of white-tailed deer. *Proceedings of the Annual Meeting of the Southeast Deer Study Group Meeting* 14:21.
- Verme, L. 1969. Reproductive patterns of white-tailed deer related to nutritional plane. *Journal of Wildlife Management* 33:881–887.

*Associate Editor: Jacques.*