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Alexander L. Jackson
Tall Timbers Research Station

D. Clay Sisson
Tall Timbers Research Station

Justin A. Rectenwald
Tall Timbers Research Station

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MEASURING MULTIPLE DEMOGRAPHIC RATES IN TWO POPULATIONS OF NORTHERN BOBWHITE

Alexander L. Jackson[1]
Tall Timbers Research Station and Land Conservancy, Livingston Place, 1583 Livingston Road, Greenville, FL 32331, USA

D. Clay Sisson
Tall Timbers Research Station and Land Conservancy, Albany Quail Project, 5765 Pigeon Road, Newton, GA 39870, USA

Justin A. Rectenwald
Tall Timbers Research Station and Land Conservancy, Albany Quail Project, 5765 Pigeon Road, Newton, GA 39870, USA

ABSTRACT

Demographic rates of northern bobwhite (*Colinus virginianus*; hereafter, bobwhite) may vary spatially and temporally, and understanding the significance of these individual rates to population performance is critically important to bobwhite management. We present descriptive evidence from 2 populations that were simultaneously monitored from 2015–2020 that suggests different demographic rates can be more important to population performance than other demographic rates within the same region. Our objective was to understand the relative importance of various demographic rates to population performance in separate and seemingly stable populations. We monitored bobwhite seasonal survival and reproductive demographics on 2,475 bobwhites via radio-telemetry and estimated fall density using fall covey counts. Both sites maintained high densities (i.e., ≥3.45 birds/hectare) and remained relatively stable throughout the study period. On one site in the Red Hills region near Monticello, Florida, USA, bobwhite experienced comparatively low seasonal survival, but higher reproduction, including more frequent multiple-brood production. One hundred and twenty-nine kilometers away on a study site near Albany, Georgia, USA, bobwhite demonstrated consistently higher survival and lower reproductive output, including less multiple-brooding compared to the Red Hills population. This suggests, at a minimum, that compensatory or density-dependent reproduction may be occurring in these populations and regional population dynamics can vary locally even among stable populations.

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Key words: *Colinus virginianus*, density dependence, Florida, Georgia, multiple-brooding, northern bobwhite, productivity, survival

A common objective in wildlife research is identifying the relative influence of multiple demographic parameters on population stability. Identifying and prioritizing these life stages for management may improve population performance. Much research has centered around demographic sensitivity of northern bobwhite (*Colinus virginianus*; hereafter, bobwhite) populations including components of fecundity (DeVos and Mueller 1993, Burger et al. 1995) and survival (Curtis et al. 1988, Robinette and Doerr 1993, Madison et al. 2002). The first major comprehensive review and sensitivity analysis of both fecundity and survival utilizing telemetry information from field studies throughout the bobwhite range (Sandercock et al. 2008) concluded that adult over-winter survival had the greatest contribution to population growth. Conversely, recruitment was found to be the most important demographic variable for population persistence in a Florida, USA, bobwhite population (McConnell et al. 2018). Initially, demographic sensitivity was thought to vary regionally depending on climate, with adult survival more important in southern latitudes and reproduction driving northern populations (Folk et al. 2007). More recently, in New Jersey, USA, reproductive parameters were shown to be the driving force and management actions to increase over-winter survival and reproduction were recommended (Williams et al. 2012). Further research is needed to determine which demographic rates influence regional and local bobwhite populations to better inform parameter-based management and influence long-term population persistence.

[1] *E-mail: ajackson@talltimbers.org*

The ability of northern bobwhites to produce multiple broods (i.e., multiple-brooding) in a single nesting season contributes to high levels of productivity. In fact, second broods may be an important factor for population recovery following periods of extreme lows (Stanford 1972). However, the frequency of multiple-brooding in northern bobwhite populations is not well understood and its significance to population stability likely varies both spatially and temporally. While multiple-brooding was once considered a rare, perhaps nonexistent, trait among bobwhite (Stoddard 1931), radio-telemetry observations from across the range suggest multiple-brooding may be more common than previously thought (Sermons and Speake 1987, Taylor 1991, Curtis et al. 1993, DeVos and Mueller 1993, Suchy and Munkel 1993, Burger et al. 1995, Sisson 2017). Nonetheless, it has been postulated that the relative contribution of multiple-brooding under average nest success has little effect on fall populations (Guthery and Kuvlesky 1998), and that triple brooding is rare and does not contribute significantly to recruitment (Sandercock et al. 2008, Sisson 2017). We compared brood production as a component of reproductive effort between two stable populations, in addition to rates of nest incubation, breeding season survival, over-winter survival, and fall density. Our objective was to demonstrate that not all seemingly stable bobwhite populations persist under the same demographic assumptions by comparing reproductive effort and survival probabilities of 2 bobwhite populations. We predict that varying demographic parameters likely drive different populations and these parameters can vary by site, region, and year.

STUDY AREA

Bobwhite demographics were monitored on 2 large, intensively managed wild bobwhite plantations in the southeastern United States. One study site was Livingston Place, a 3,683-hectare property owned by Tall Timbers located in the Red Hills region near Monticello, Florida and one study site was a 6,000-hectare privately owned property located in the Upper Coastal Plain physiographic region near Albany, Georgia, USA (Figure 1). Both study sites have managed bobwhite habitat with frequent prescribed fire, intensive timber management, seasonal disking of fallow fields, roller-chopping and mowing, supplemental feeding and meso-predator control programs (Yates et al. 1995, Burger et al. 1998, Terhune et al. 2007, Sisson et al. 2009, Sisson and Terhune 2017, Rectenwald et al. 2021). Both sites consisted of low-density (3–9 m^2/ha) upland pine forests composed of loblolly (*Pinus taeda*), slash (*P. elliottii*), shortleaf (*P. echinada*), and longleaf (*P. palustris*) pine with an herbaceous understory maintained by frequent prescribed fire. Seasonally disked fallow fields dominated by ragweed (*Ambrosia* spp.) were scattered across the properties and covered 10–20% of the total upland area. Mid-rotation pines and pine snags were intentionally removed on the Albany site to reduce avian predator habitat. Isolated wetlands and associated drain habitat make up 770 hectares dispersed throughout Livingston Place. Agricultural fields and hardwood hammocks accounted for the remaining area.

METHODS

Bobwhite fall density, over-winter survival, and breeding season demographics were monitored from 2015–2020 on both study sites. Fall density (birds per hectare) was determined from early morning covey calls using a 24.3-hectare grid count technique (Wellendorf et al. 2004, Terhune 2017, Howell et al. 2021). Livingston Place had 5 grids and the Albany study site had 10 grids. Grids were distributed across the landscape to most accurately monitor areas dominated by habitat representative of the uplands. Grid counts were conducted by 4 observers per grid, each at the mid-point of a side connecting the corners of the grid. Observers counted coveys calling from within the grid and calculated grid density (i.e., birds per hectare) as the total number of coveys calling within the grid, multiplied by the average covey size of the site, divided by grid area. Overall density of the site was determined as the average density across all grids.

Bobwhites were trapped twice each year (Oct–Nov and Mar–Apr) using wire funnel traps baited with cracked corn or grain sorghum (Stoddard 1931). All captured birds were classified by sex and age, weighed, and leg banded and a

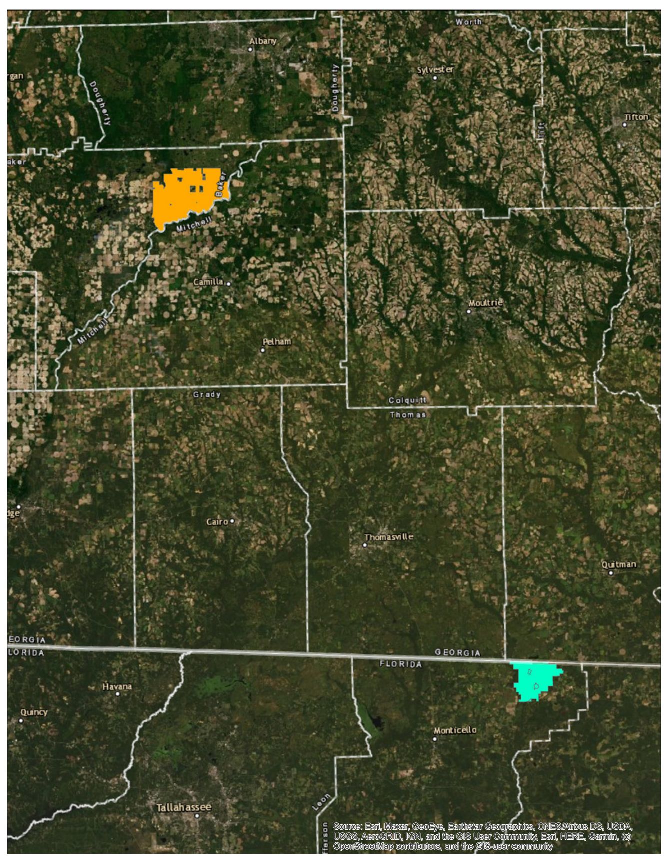

Fig 1. Locations of study sites at Livingston Place (blue), Florida, USA, and near Albany (orange), Georgia, USA.

subset of birds weighing ≥132 g (<5% of body weight) were fitted with 6.2 g necklace-style radio transmitters equipped with motion-sensitive switches (Holohil Systems, Ltd., Carp, Ontario, Canada) and released at the capture site. The radio-tagged sample of bobwhite was evenly distributed across season, site, and year (i.e., ≥50 radio-tagged birds per season, site, and year). Bobwhite over-winter survival was monitored via radio-telemetry from 1 October–31 March. Radio-tagged birds were tracked ≥2 times/week and survival was estimated weekly using the Kaplan-Meier staggered entry method for each site and each year (Kaplan and Meier 1958, Pollock et al. 1989). Bobwhite breeding season demographics were monitored 1 April–30 September using radio-telemetry to track individuals ≥3 times/week. Bobwhite nest success was monitored during incubation after adults were tracked to identical locations on consecutive days. Nests were checked daily until success (≥1 egg hatched) or failure (Taylor et al. 1999, Ellis-Felege et al. 2012). We were specifically interested in nests per hen, double nests per hen, triple nests per hen, and the corresponding brood production. We quantified the number of nests incubated per hen, as well as the frequency of double and triple nesting attempts. We also quantified the number of nests hatched per hen and the frequency of successful double and triple nests. We followed the strict definition provided by Sisson (2017) for double and triple broods as second and third broods hatched from the same hen.

RESULTS

Average fall population density on the Livingston Place study site from 2015–2020 was 3.85 birds/hectare (standard error [SE] = 0.25, range = 3.45–4.20). The population growth rate (i.e., λ) on Livingston Place averaged 0.99 (SE = 0.06, range = 0.88–1.21). Over-winter survival on Livingston Place was calculated from 749 radio-tagged bobwhite and was 0.45 (SE = 0.04, range = 0.33–0.56), resulting in a derived spring density averaging 1.81 birds/hectare (SE = 0.15, range = 1.38–2.33; Table 1). Average fall population density on the Albany study site was 6.18 birds/hectare (SE = 0.45, range = 4.69–7.17). The population growth rate (i.e., λ) on the Albany site averaged 1.14 (SE = 0.11, range = 0.88–1.37). Mean over-winter survival from 600 radio-tagged bobwhite was 0.63 (SE = 0.03, range = 0.53–0.68) and mean spring density was 3.60 birds/hectare (SE = 0.34, range = 2.22–4.45; Table 2).

We tracked 526 radio-tagged hens on Livingston Place and 600 hens on the Albany site to estimate breeding season survival, annual survival, nest production, and brood production. On Livingston Place, breeding season survival averaged 0.32 (SE = 0.03, range = 0.23–0.42) across all years, resulting in an average annual survival of 0.15 (SE = 0.02, range = 0.09–0.23; Table 1). We found 422 nests and documented 258 broods on Livingston Place. Annual nests per hen averaged 0.75 (SE = 0.06, range = 0.51–0.91) and annual broods hatched per hen averaged 0.46 (SE = 0.05, range = 0.30–0.67). Of the 422 nests, 104 were double incubations by hen (i.e., 0.20 double nests/hen) and 24 were triple incubations by hen (0.05 triple nests/hen). Similarly, 49 broods were double broods (0.09 double broods/hen), and 4 were triple broods (0.01 triple broods/hen; Table 3). On the Albany site, average breeding season survival was 0.42 (SE = 0.03, range = 0.36–0.51), resulting in average annual survival of 0.26 (SE = 0.02, range = 0.21–0.36; Table 2). We found 333 nests and documented 171 broods. Overall annual nests per hen averaged 0.50 (SE = 0.03, range = 0.40–0.58) and annual broods hatched per hen averaged 0.26 (SE = 0.01, range = 0.20–0.30). Of the 333 nests, 67 were double incubations by hen (0.11 double nests/hen) and 9 were triple incubations by hen (0.02 triple nests/hen). We found 11 double broods (0.02 double broods/hen) and there were no triple broods (Table 3).

Table 1. Northern bobwhite (*Colinus virginianus*) density and seasonal survival estimates for the Livingston Place study site in the Red Hills region, Florida, USA, 2015–2020.

Metric	Mean	Standard error	Minimum	Maximum
Fall density (birds/ha)	3.85	0.25	3.45	4.20
Over-winter survival	0.45	0.04	0.33	0.56
Spring density (birds/ha)	1.81	0.15	1.38	2.33
Breeding season survival	0.32	0.03	0.23	0.42
Annual survival	0.15	0.02	0.09	0.23
Growth rate (λ)	0.99	0.06	0.88	1.21

Table 2. Northern bobwhite (*Colinus virginianus*) density and seasonal survival estimates for the Albany, Georgia, USA, study site, 2015–2020.

Metric	Mean	Standard error	Minimum	Maximum
Fall density (birds/ha)	6.18	0.45	4.69	7.17
Over-winter survival	0.63	0.03	0.53	0.68
Spring density (birds/ha)	3.60	0.34	2.22	4.45
Breeding season survival	0.42	0.03	0.36	0.51
Annual survival	0.26	0.02	0.21	0.36
Growth rate (λ)	1.14	0.11	0.88	1.37

Table 3. Number of radio-tagged northern bobwhite (*Colinus virginianus*) hens and associated reproductive parameters from the Livingston Place (Red Hills region, Florida, USA) and Albany, Georgia, USA, study sites, 2015–2020.

Metric	Livingston Place	Albany
Radio-tagged hens	526	600
Total nests	422	333
Nests per hen	0.75	0.50
Double nests per hen	0.20	0.11
Triple nests per hen	0.05	0.02
Total broods	258	171
Broods per hen	0.46	0.26
Double broods per hen	0.09	0.02
Triple broods per hen	0.01	0.00

DISCUSSION

As an r-selected species, northern bobwhite have adopted a flexible mating system to maximize potential productivity and to offset high annual mortality (Burger et al. 1995). However, the relative contributions of reproduction and survival to population growth remain unclear. As intensive research over the past 3 decades has added insight to detailed demographic information, modern modeling efforts have been improved through more accurate demographic parameterization, allowing for a more thorough investigation (Curtis et al. 1988, DeVos and Mueller 1993, Guthery et al. 2000, Madison et al. 2002, Sandercock et al. 2008, McConnell et al. 2018). Although adult survival probabilities and reproductive effort are both important contributions to population growth (Guthery et al. 2000, Folk et al. 2007, Sandercock et al. 2008), site-specific differences in risk among varying age-classes may favor specific population demographics to achieve population stability.

Abundance in stable populations may negatively affect recruitment (McConnell et al. 2018). We present data from 2 populations in the same region that achieve moderate stability across simultaneous years in different ways. The Albany population experienced high over-winter survival and high spring densities; therefore, high levels of production were not as necessary to maintain similar densities across years. On Livingston Place, low over-winter survival probabilities resulted in lower spring densities, requiring higher recruitment to maintain similar densities across years. Our results provide additional evidence of density-dependent reproductive effort. Greater nest production, brood production, and frequency of multiple brooding on Livingston Place compared to the Albany site likely reflect density-dependent reproductive effort.

Individual bobwhite have a high propensity to produce multiple nests during the same breeding season (Sandercock et al. 2008). However, population density likely contributes to the frequency of occurrence of this physiological adaptation. We documented lower seasonal survival, annual survival, and densities on Livingston Place compared to the Albany study site. However, overall average number of nests incubated per hen was 40% more on Livingston Place. Multiple-broods occurred every year of the study on Livingston Place, accounting for 21% of total brood production, with triple-brood production in 4 out of the 6 years. While relatively insignificant to fall populations (Guthery and Kuvlesky 1998), the multiple occurrences of triple broods are noteworthy given that Sisson (2017) previously documented only one triple brood occurrence in 25 years (1992–2016) of monitoring the same Albany population discussed in this study. While multiple-brooding occurred in 5 years of the 6-year study in Albany, they accounted for only 6% of total brood production. Therefore, we contend that while survival is important, populations that experience comparatively low levels of seasonal and annual survival, must rely heavily on reproduction to maintain stability from year to year.

The higher level of multiple-brooding in the Livingston Place population is only part of the overall reproductive effort required to overcome lower over-winter survival in Red Hills populations. Per capita reproduction (including multiple nests and broods) on Livingston Place averaged 0.75 ± 0.06 nests/hen and 0.46 ± 0.05 broods/hen, but only 0.50 ± 0.03 nests/hen and 0.26 ± 0.01 broods/hen in Albany (i.e., 40% and 56% difference, respectively). However, further research should investigate the prevalence and importance of male incubation to population performance, as this metric is relatively unknown. Additionally, future investigations should incorporate a metric of brood success to investigate the uncertainty in this period that we did not account for in this descriptive study.

Differences in reproductive effort between the 2 sites may reflect differences in over-winter survival probabilities. Harvest rates are relatively light on both properties, averaging 12% on Livingston Place and 5% in Albany, with most of the additional mortality attributed to avian predation (Rectenwald et al. 2021). The landscape in the Red Hills region has more habitat conducive to avian and mammalian predators and larger surges of migrating raptors in winter (Rectenwald et al. 2021). In addition to landscape differences, the Albany site had intentionally removed avian predator habitat (i.e., mid-rotation pines and pine snags), which had reduced the number of raptors seen on survey routes over time (Rectenwald et al. in press). These practices have not been applied on Livingston Place and a higher percentage of hardwood drains remain intact. Given that the Albany site has both higher over-winter survival and a higher fall density, it is possible that elevating over-winter survival in the Red Hills could increase fall densities in this region. Management actions that increase over-winter survival in the Red Hills may increase fall densities if that is the desired objective.

MANAGEMENT IMPLICATIONS

We provide evidence of differing seasonal survival probabilities and resulting reproductive efforts for 2 distinct bobwhite populations within the same region. While one population experiences high survival and moderate reproduction, the other experiences moderate survival and high reproduction. Increases in reproductive effort may be a compensatory mechanism when over-winter survival is low. However, more data would be needed to determine whether variation within a single population is compensatory over time and how those actions influence population growth. This work demonstrates that demographic rates of seemingly stable populations within the same region may vary and targeting management for a specific demographic can vary spatially and over time. Comprehensive management plans promoting both high over-winter survival and reproductive output are recommended, as it is uncertain when or where one particular demographic might be most important.

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