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BREEDING SEASON SURVIVAL AND REPRODUCTION IN A HIGH-DENSITY BOBWHITE POPULATION: A CASE STUDY

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ABSTRACT

The demographic behavior of northern bobwhite (*Colinus virginianus*; hereafter, bobwhite) populations at high densities could provide important insights into why bobwhite populations fluctuate. Therefore, we documented breeding season demographics of bobwhites to understand how prebreeding density influenced reproductive effort and postbreeding density on an intensively managed property in Leon County, Florida, USA, 2002–2006. We estimated prebreeding bobwhite density each April using multi-observer strip-transects and postbreeding densities each November using covey call grid surveys. We radio-tagged 217 bobwhites in March and located bobwhites at least 5 days/week, 15 April–30 September to determine vital rates. Prebreeding density ranged from 1.5–8.6 birds/ha, peaking in 2002, declining through 2005, then increasing in 2006. Breeding season survival was 0.55, 0.17, 0.20, and 0.59, and nesting rate was 0.47, 0.67, 0.80 and 0.89, 2002–2005, respectively. Postbreeding density ranged from 5.2–13.6 birds/ha, also peaking in 2002 and declining through 2004 before increasing beginning in 2005 and 2006. High breeding season survival and nesting success (>0.55) resulted in greater chick production during periods of population growth. Nesting rate was inversely related to prebreeding density. Declines in bobwhite nesting rate at high prebreeding densities appeared to regulate population growth near population peaks. Lower adult survival and nesting success appeared to cause population declines. We suggest density-dependent intraspecific competition limited population growth at high bobwhite densities by reducing nesting rate while predation of adults and nests explained population fluctuations.

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Key words: *Colinus virginianus*, demographics, density, nesting, northern bobwhite, population, quail, reproduction, survival

Modern management of northern bobwhite (*Colinus virginianus*; hereafter, bobwhite) on some private lands in the southeastern United States sustains bobwhite populations at relatively high densities (Palmer and Sisson 2017), but population fluctuations remain common. Intensive management (Palmer and Sisson 2017) to reduce the effect of limiting factors and infrequent episodes of severe weather provides for population stability and the opportunity to sustain high densities. On managed lands in the Red Hills and Albany regions of northern Florida, USA and Southwest Georgia, USA, bobwhite populations are commonly sustained at >3 quail/ha because managers apply techniques that reduce limiting factors (Palmer and Sisson 2017, Terhune et al. 2017). Management actions, such as habitat management, predation management, and supplemental feeding, collectively moderate density-dependent and -independent factors that

limit population growth. Under these management scenarios bobwhite populations may reach postbreeding densities of 8–12 quail/ha (Kellogg et al. 1972; Dimmick et al. 1982; Palmer and Sisson, unpublished data). These high densities may last ≥ 2 years before moderating to more typical densities of 3–6 quail/ha. This raises the question of why we do not see even higher densities (i.e., population growth peaks) if management provides abundant usable space, low predation pressure, and abundant food resources. Further, can managers influence factors responsible for the observed negative density dependence to maintain populations at high densities for longer?

High densities are observed on managed quail ranches in the southwestern United States during periods of adequate rainfall and moderate temperatures (Lehman 1984). Declines in populations following peaks are attributed to recurring

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drought cycles and extreme heat (Lehman 1984, Guthery et al. 1988, Hernández et al. 2005). In the southwestern portion of the bobwhite's range, severe droughts impact quail recruitment, providing a clear explanation for bobwhite population declines. However, elsewhere in the bobwhite range, populations fluctuate because of a combination of density-independent and -dependent factors (Stoddard 1931, McConnell et al. 2018). Adult survival and recruitment are both important to explaining bobwhite population dynamics (Roseberry and Klimstra 1979, Sandercock et al. 2008, Demaso et al. 2013, McConnell et al. 2018). For declining populations, survival explained more variation in population growth than recruitment (Sandercock et al. 2008), and for stable populations recruitment was more important than survival, although both were important (McConnell et al. 2018). These studies examined long-term datasets, but no studies have monitored prebreeding and postbreeding densities along with breeding season demographics in an effort to determine which parameters were sensitive to bobwhite density and the mechanisms that limit postbreeding populations.

We investigated demographic rates associated with bobwhite populations at or near peak densities (i.e., carrying capacity) and what demographic rates explained declines from peak densities. We estimated prebreeding and postbreeding population density of bobwhites on an intensively managed quail property and breeding season survival, nesting rate, clutch size, and nesting success to determine how these variables related to prebreeding densities. Further, we provide a broader regional perspective from 19 sites in which we had postbreeding densities and nesting data to explore the relationships we found from our main study site. Though this study is observational, we believe it provides the first demographic-based evidence of intraspecific competition that could be further explored through research. Our results and subsequent findings could be expected to improve population modeling efforts.

STUDY AREA

We studied bobwhite population dynamics on a 380-ha portion of a 3,300-ha private quail hunting property in the Red Hills region of Leon County, Florida, USA, 2002–2006. The property was primarily composed (>95%) of pine (*Pinus* spp.) savanna, frequently burned with a stocking density <12 m² of basal area and with <5% fields and no hardwood drains or hammocks. Approximately 60% of the property was burned each year of the study with the 40% unburned portion distributed in small 5- to 10-ha patches of cover. We mapped the unburned habitat patches using hand-held geographic positioning units (Trimble Geospatial, Inc., Sunnyvale, CA, USA) each year of the study. The groundcover comprised a mixture of grasses, forbs, and shrubs typical of post-agriculture successional “old field” vegetation in the Red Hills region (Carr et al. 2010). Collectively, prescribed fire and mechanical treatments were used to maintain groundcover vegetation with suitable composition and structure for bobwhites while also

facilitating hunting access. Supplemental feeding occurred year-round on the property by spreading >174 L/ha/yr (~2 bushels/acre) of sorghum or corn (or both) broadcast into bobwhite habitat along roads or dedicated feeding trails (or both) spread evenly throughout the property. Mesomammal nest predators were reduced using live-traps throughout the year and periodically using leg-hold trapping methods during the furbearer trapping season. The property was divided into half-day hunting courses. Our study area covered 2 hunting courses. Hunting pressure was relatively low with each course hunted no more than 5 times/season. Harvest rates were <10% of the estimated fall population. The management and hunting staff recorded the number of unique coveys flushed per day of hunting throughout the study.

METHODS

We determined spring densities of bobwhites on the study area each April by conducting multi-observer transect flush counts (Dimmick et al. 1982). We used 12–15 observers walking parallel to one another along 8 randomly selected transect lines bisecting the study area. Observers were spaced approximately every 3 meters and remained parallel while walking the transects. Observers at each end of the line georeferenced the transect boundaries using global position units to estimate actual area flushed. We set the number of transects to achieve a minimum sampling intensity of 15% coverage of the study area. When quail were flushed, the total observed was recorded and their destination was noted to avoid double counting.

We determined the likelihood of flushing a bobwhite from radio-tagged quail on the study area during the survey. An independent observer monitored the location and movements of radio-tagged bobwhites within the transect area and recorded whether a radio-tagged bobwhite was observed or not. Detectability was calculated by dividing the total number of observed radio-tagged bobwhites by the total number of radio-tagged bobwhites within the transect during the surveys.

To estimate prebreeding density, we first calculated a naïve estimate of density of bobwhite in burned and unburned patches by dividing the number of bobwhite flushed in burned and unburned areas by the area of burned and unburned surveyed, respectively. This naïve estimate was adjusted by dividing it by our estimate of detectability to calculate burned and unburned habitat-specific densities. Habitat-specific densities were then multiplied by area of burned and unburned habitat on the study area to determine an overall estimate of bobwhite population size and density of bobwhite on the study area.

We estimated postbreeding autumn densities each October and November by counting coveys during early-morning covey call counts on 6 12.1-ha grids randomly placed on the study area (Wellendorf et al. 2004, Wellendorf and Palmer 2005) or an approximately 20% sampling intensity. We used smaller than normal 24.3-ha grids to aid in identifying individual coveys. At each grid, 4 observers stationed at the

mid-point of each side recorded the time and location of each calling covey inside the grid during peak calling times, which occurred approximately 15–25 minutes before sunrise. Once locations of coveys were identified, coveys within the grid were flushed with the assistance of bird dogs to determine an average covey size. We used estimated calling rates, covey counts, and average covey size to determine postbreeding densities following Wellendorf et al. (2004).

We radio-tagged quail on the study area during March using 5.5 g necklace-style transmitters with 12-month battery life (American Wildlife Enterprises, Monticello, FL, USA) to determine breeding season demographics. We located bobwhites 5 days/week during the breeding season to determine breeding season survival, nesting, clutch size, and nesting success. Bobwhites that survived until 15 April of each year were considered the “breeding population” and radio-tagged bobwhites alive at this point were used to determine the per capita nesting and brood rearing estimates for each year. To remove the effects of survival rate on per capita nesting, nesting rate was determined as the proportion of hens that survived the nesting season to incubate at least one nest. We estimated breeding season survival (15 Apr–30 Sep) using the Kaplan-Meier staggered entry method (Pollock et al. 1989).

Each October of the study, we conducted a mesomammal scent station survey to estimate the nest predator activity and abundance on the property (Jackson et al. 2018). We randomly placed 15 scent stations along the roads system throughout the property. Scent stations were monitored for 3 consecutive days and total number of mesomammal nest predators observed divided by 45 station-days was used to assess predator activity. A predator index <0.15 indicates that predators are not likely to significantly reduce nesting success on similarly managed properties (Jackson et al. 2018).

Regional Nesting and Density Study

We monitored bobwhite population density and reproductive effort on 19 properties where bobwhites were being radio-tracked from 1998 to 2020. Eighteen of these sites were private quail hunting properties located within the Albany, Georgia to Tallahassee, Florida region and as such were managed similarly to our primary study area. Each site was monitored between 1 and 5 years. Management intensity varied across sites. Primary differences were that some sites had greater pine basal area, others had more hardwood basal area, and some did not conduct predator management. However, all were specifically managed for bobwhite and as such had sustainable quail populations. These properties provided a range of bobwhite densities from which to assess the relationship of density and bobwhite nesting activity.

Depending on the size of the study site (100–2,000 ha) we conducted 1–12 covey call grids/site to provide an estimate of bobwhite postbreeding density. Covey call grids were conducted during October and November each year using similar methods as for our focal area. We grouped each site and year combination into 3 categories: those with fall densities <3.7 quail/ha, those

with 3.7–6.2 quail/ha, and those with >6.2 quail/ha to represent low, medium, and high bobwhite densities. These densities correspond to below-average to average, above average, and well above average bobwhite densities for intensively managed properties in this region.

We considered each site and year combination as independent for our analyses. We justify independence of site and year combinations as annual changes to predator abundance, weather, and alternative prey-base that influence bobwhite populations independently from year to year on our study areas (Ellis-Felege et al. 2012, Palmer et al. 2019). We graphed the relationship between bobwhite density and nests per hen determined from a radio-tagged sample to examine the relationship between bobwhite abundance and per capita nesting. Significance of the differences was tested using a basic ANOVA.

RESULTS

Prebreeding and Postbreeding Density

We counted 737, 356, 198, 99, and 113 bobwhites during flush counts, April 2002–2006, respectively. Forty-four radio-tagged individuals were within transects during flush counts, of which 39 (89%) were observed, one held and was not flushed, and 2 moved out of the survey path before we encountered them. Prebreeding densities peaked in 2002 at 8.6 quail/ha and then declined to 7.1 quail/ha in 2003, 3.7 quail/ha in 2004, and 1.5 quail/ha in 2005 before increasing to 2.7 quail/ha in 2006.

Postbreeding densities were highest in 2002 at 13.6 quail/ha, then declined to 6.2 quail/ha in 2003 and 5.4 quail/ha in 2004. Postbreeding densities then increased to 6.9 quail/ha in 2005 and increased again to 10.3 quail/ha in 2006. Hunting success was highly correlated to bobwhite densities ($r = 0.92$, $P = 0.02$) with an average of 64 coveys seen per day in 2002, declining to 26 coveys/day in 2005, and increasing to 42 coveys/day in 2006.

Nest Predator Index

The predator index was highest in 2002 at 13.8%. The predator index ranged between 5% and 8.4% from 2003 to 2006. The relative abundance of predators was approximately equally distributed among raccoons (*Procyon lotor*), Virginia opossum (*Didelphis virginiana*), nine-banded armadillos (*Dasyurus novemcinctus*), and bobcats (*Lynx rufus*).

Breeding Season Demographics

We radio-tagged 217 bobwhites between 2002 and 2005 to determine breeding season demographics (Table 1). A total of 181 bobwhites (144 females) were utilized to develop breeding season statistics. Survival was highest in 2002 and 2006 and was significantly lower in 2003 and 2004. This resulted in lower nests per hen in 2003 and 2004. Nevertheless, nesting rate for surviving hens was greatest in

Table 1. Breeding season demographics for radio-tagged northern bobwhites (*Colinus virginianus*; $n = 144$) on an intensively managed quail hunting property, Leon County, Florida, USA, 2002–2005.

Year	n	Number of hens	Number of nests	Nesting rate ^a	Nests per hen	Number of renesters ^b	Nesting success	Clutch size	Survival rate
2002	39	31	18	0.47	0.58	3	0.61	13.8	0.55
2003	45	32	11	0.67	0.34	0	0.36	13.7	0.20
2004	46	42	17	0.80	0.40	1	0.7	13.1	0.17
2005	51	39	34	0.89	0.87	10	0.51	13.1	0.59

^a Number of hens that survived 14 April–15 September to incubate at least one nest.

^b Number of hens to incubate more than one nest.

2004 and 2005 and corresponds to the lower observed spring densities. Conversely, nesting rate was lowest in 2002 and 2003 when prebreeding densities were >7 quail/ha (Figure 1). Clutch size was consistent across all years. Nesting success was lowest in 2003, but we had a low sample size during that year due to low survival; otherwise nest success was >0.50 . We observed the highest level of double clutching in 2005 when prebreeding density was lowest (Table 1).

Regional Nesting and Density

We had 50 site and year combinations for which we had monitored an adequate radio-tagged sample of hens to assess nesting activity and also obtained an estimate of postbreeding densities. Of the 50 site and year combinations, 24, 17, and 9 were in the low, medium, and high quail density categories, respectively. Nests per hen was related to density and averaged 0.77 (standard error [SE] = 0.049), 0.85 (SE = 0.071) and 0.61 (SE = 0.066) for the low, medium, and high quail density categories ($F_{2,47} = 2.61$, $P = 0.08$; Figure 2).

DISCUSSION

We believe that this is the first study to document bobwhite prebreeding and postbreeding densities along with breeding season behavior of bobwhites at the individual level to assess population dynamics and investigate density dependence. Previous studies have measured prebreeding or postbreeding densities (or both) but did not have individual-based estimates of reproductive behavior to dissect which parameters were most sensitive to density. Studies have relied on population-level parameters such as percent summer gain, age ratios, and total nests found relative to prebreeding season abundance on the study areas (Roseberry and Klimstra 1972, Dimmick et al. 1974, Guthery et al. 1988). Given our findings, it is interesting that these studies found that nest production largely explained postbreeding densities of bobwhites more than other reproductive variables. More recent and robust analyses of long-term band-recapture data derived estimates of productivity (McConnell et al. 2018) and found evidence for density-dependent recruitment and survival. What has been missing, and a value of our study, was individual-based

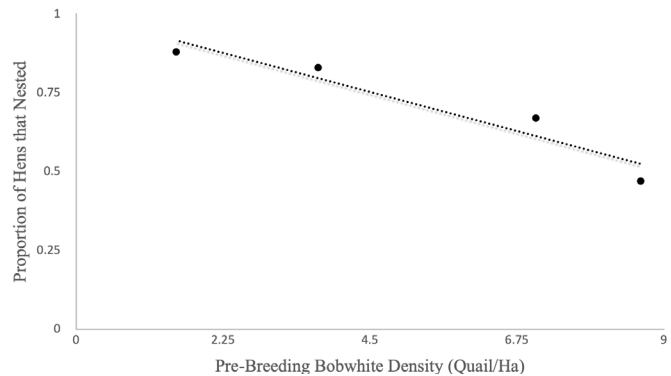


Fig. 1. Relationship between northern bobwhite (*Colinus virginianus*) prebreeding density (quail/ha) and nesting rate (proportion of hens to survive the nesting season to incubate at least one nest) on a privately managed quail hunting property, Leon County, Florida, USA, 2002–2005.

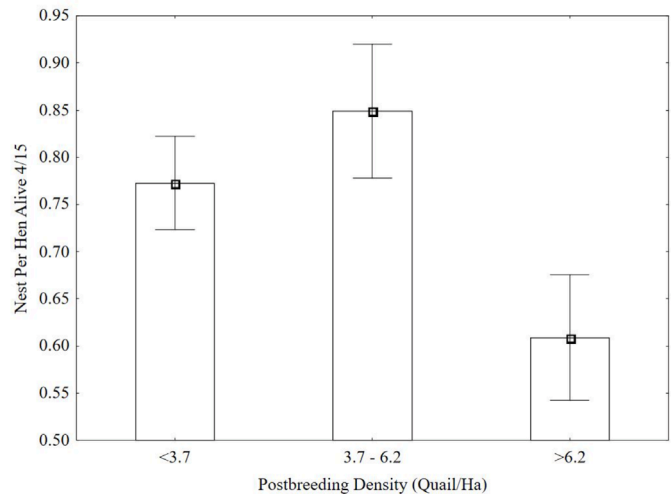


Fig. 2. Mean number of nests per hen alive on 15 April from radio-tagged sample of northern bobwhites (*Colinus virginianus*) on 19 properties (50 site and year combinations) grouped by bobwhite postbreeding densities as measured from covey call grids, October and November, 1999–2020. Properties were mainly located in the Albany, Georgia, USA and Tallahassee, Florida, USA region.

behavior from radio-tagged individuals, providing insight into bobwhite reproductive behavior that explained observed changes in population-level parameters and apparent density-dependent relationships.

We utilized strip-transect flush counts to estimate prebreeding density. We observed a greater proportion of radio-tagged bobwhites during our flush counts than previously reported. Dimmick et al. (1982) reported flushing 50% of radio-tagged coveys with observers spread 20 m apart. Janvrin et al. (1991) observed 56% of individuals and 61% of coveys with observers 10 m apart and reported an average flush distance of 5 m from observers. We maintained a closer distance between observers, which improved detection. The higher density of bobwhites on the study area, the timing of flush counts after covey break-up in spring, and the relatively open habitat conditions contributed to observed detection and provided reliable estimates of prebreeding density.

Of the parameters measured, we observed lower nesting rate of hens in years with higher prebreeding densities on our intensive study site, and across multiple sites we observed lower overall per capita nesting rate by hens when bobwhite densities were highest. We believe this is the first study to document a negative relationship between nesting rate of individual hens and bobwhite breeding densities. The low nesting rate observed at high density occurred despite other population parameters remaining above-average, such as nesting success and breeding season survival. This is counter to the logic that for r-selected species, such as the bobwhite, density dependence is more important at low densities than high densities (Fowler 1981). We suspect that strategic management of habitat, predation, and food resources moderates density-dependent factors typically found in the bobwhite (Guthery and Shaw 2012). This also suggests that bobwhites in our study exhibited lower nest production at high densities due to some form of intraspecific competition for space, as food and cover were likely maximized, and predator abundances were minimized through management.

Roseberry and Klimstra (1972) suggested that low nesting rates observed on their study areas were a result of habitat loss or unfavorable weather conditions, or a combination thereof. In our study, none of these conditions occurred, yet less than half of the hens that survived the nesting season were observed to have incubated a nest following the peak in prebreeding densities and only 67% of hens nested in the year with the second highest prebreeding density. The cause of low nesting rate could have been some factor other than intraspecific competition. For instance, it is possible that we failed to count hens that initiated nests but never reached incubation due to predators depredate their nests during egg-laying. However, we do not believe this is the case as we did not observe characteristics and behaviors we would expect to see when predators depredate nests during egg-laying. For instance, when nesting initiation is limited by predators, we would expect to see low nesting success as well (Staller et al. 2005). However, nesting success was high during the study and was 61% during the year with greatest prebreeding

density and lowest nesting rate. Breeding season survival also peaked during the year with the highest prebreeding density, indicating low overall predation pressure. Further, if hens were losing nests during pre-incubation, but surviving the nesting season, we would have expected to see reneesting later in the nesting season. Finally, nest predators were maintained at low levels by trapping, and scent station surveys confirmed low activity and abundance on the study area (Jackson et al. 2018). Snakes can also be a significant nest predator (Staller et al. 2005, Ellis-Felege et al. 2012). However, snakes often fail to depredate the entire nest and tend to depredate nests during the incubation phase (Staller et al. 2005). We did not witness low nesting success, high reneesting, partial depredateations by snakes, or low adult survival during years with the highest prebreeding and postbreeding densities, suggesting that nest predation was not limiting nesting on our study area.

We also do not believe that weather or nutrition was limiting during the period. Low nesting rate in some bobwhite populations has been attributed to severe drought conditions (Hernández et al. 2005). The peak in population in our study occurred during a period of near ideal weather conditions for bobwhites and their populations increased throughout the Red Hills region (McConnell et al. 2018, Palmer et al. 2019). Bobwhite were provided with supplemental food, suggesting that energy requirements were at least met at a minimum level, but likely exceeded (Whitelaw et al. 2009).

Analyses of 30 years of data from Tall Timbers determined that both recruitment and annual survival were responsible for population growth (McConnell et al. 2018). Our observational study provides insight into why per capita nesting declines as populations reach carrying capacity. At lower nesting rates, populations can maintain themselves only by sustaining high survival rates. Even though per capita nesting rate declines at high densities, there is still a high amount of per hectare production due to the number of quail on the landscape. As a result, populations can increase, or remain stable at high densities, despite the lower nesting rate. However, as nesting declines due to intraspecific competition, population maintenance becomes more dependent on survival. If some factor causes survival to decline, the population declines. In our study the population declined due to decreasing survival rates the year following the peak density in 2002. We continued to observe low nesting rate the year following the peak as prebreeding densities remained high. Following 2 years of declines due to lower survival, nesting rate increased, resulting in population increases during the last 2 years of the study. This suggests that if survival was not impacted by avian predation, the densities may have remained high for some period of time. But ultimately, with per capita production relatively low, it is only a matter of time until something impacts survival of adults, or young (Palmer and Sisson 2017, Terhune et al. 2019). A decline in populations ultimately results in an increase in productivity through increased nesting of hens and male incubation, and populations begin to recover. Therefore, when management lessens the effects of predation, weather, and habitat on quail populations, we

believe that population growth is limited by reduced nesting propensity of hens. We observed reduced nesting propensity when bobwhite density exceeded approximately 7 quail/ha.

This study documented a declining population due to reduced survival and low nest production. It is important to mention that quail densities were high on this property for 2 years before the beginning of this study. We estimated fall densities >7 quail/ha the year prior (2001) to beginning this project. We have observed other properties, including our main study area in Albany, Georgia, that have sustained high densities for 3–5 years prior to some factor impacting survival (such as avian predation) or reproduction (such as drought) and causing a decline. High density of bobwhites may reduce nesting, but management of food resources, habitat, and predation can maintain high survival and overall reproduction, thereby sustaining high abundances for multiple years. This is counter to the idea that management cannot influence carrying capacity above what is maximized by usable space (Guthery and Shaw 2012).

At lower densities bobwhite nesting rate is higher and nearly every surviving hen is thought to have produced at least one nest. We observed 80% and 89% of surviving hens incubating at least one nest at lower prebreeding densities and populations began to recover. This nesting rate was similar to rates reported by Miller et al. (2012) when prebreeding season quail densities were <3 quail/ha. When prebreeding densities are lower, and populations and conditions favorable, we observe higher male incubation of nests along with high incubation rates by females (Palmer, unpublished data; Palmer et al. 2019; Jackson et al. this volume). The propensity of males to incubate nests during increasing phases provides increased productivity. At high density we predict that male incubation opportunities are lower as fewer hens are producing more than one nest, and based on this study, some hens produce no nests. Additional research is needed to determine what behavioral or physiological differences occur in hens that appear to forgo reproduction versus hens that reproduce normally, and what triggers males to incubate nests.

MANAGEMENT IMPLICATIONS

This study suggests that reproduction of bobwhites is affected by their density and that at postbreeding densities above approximately 7 quail/ha, and prebreeding densities above approximately 4 quail/ha bobwhite, nesting rate declines significantly. While the exact mechanism remains unknown, our results do suggest managers focused on sustaining high postbreeding densities should manage habitat to maximize usable space during the prebreeding and breeding season to uniformly distribute bobwhites across a management area and reduce apparent bobwhite density. Further, for bobwhite translocation, this study suggests that managers avoid releasing too many bobwhites into a small area, but rather spread out the translocated bobwhites at a reasonable (~1 quail/ha) prebreeding density to maximize reproduction. Our study also

shows the importance of maintaining high bobwhite survival to maintain high densities over time. Finally, our study suggests that the nesting rate of hens could be an important vital rate in bobwhites for invoking compensation in response to harvest or removal for translocation. Understanding the degree to which nesting rate may govern regulation near a population carrying capacity has important management implications for harvest and translocation policy. Increasing the harvest and translocation rate in high density populations may be acceptable for sustaining populations at high density when weather conditions are stable and favorable.

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