



Research Article

Reduction in Meso-Mammal Nest Predators Improves Northern Bobwhite Demographics

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ABSTRACT Nest predation is the major cause of nest failure in northern bobwhites (*Colinus virginianus*; i.e., bobwhites). Control of mid-sized mammalian nest predators (i.e., meso-mammals) is often conducted to increase reproductive success on lands managed for bobwhites. Nest predation by meso-mammals, however, is only one part of a complex predator-prey trophic system. There is limited understanding of the effect of nest predators on bobwhite demographics, which creates uncertainty about the efficacy of nest predator control. We quantified demographic effects on bobwhite populations from reducing meso-mammals on 4 study areas managed for bobwhites in northern Florida and southwestern Georgia, USA, during 2000–2006. After 1 year of pre-treatment monitoring (2000), we reduced meso-mammal nest predator abundance through trapping over 3-year intervals, March to September, on 2 sites using a crossover design. Efficacy of trapping was demonstrated by a 43% reduction in scent station visitation rates of meso-mammals. Meso-mammal control increased all demographic metrics including a 30% increase in nesting propensity, a 10% increase in nest success, and a 43% increase in chicks produced. Despite significant regional variation in breeding season survival rates, this equated to an average 18% increase in autumn density on trapped sites. Decision-makers should weigh the tradeoffs between bobwhite population goals and costs of meso-mammal control, where those that value maximum bobwhite density and reduced annual variation should likely implement control of meso-mammals. © 2019 The Wildlife Society.

KEY WORDS *Colinus virginianus*, Florida, Georgia, nest, northern bobwhite, population, predation, predator control, reproduction, survival.

The effect of meso-mammals on northern bobwhite (*Colinus virginianus*; i.e., bobwhite) populations has been debated for nearly a century (Errington and Stoddard 1938, Guthery and Beasom 1977, Hurst et al. 1996, Rollins and Carroll 2001) and researchers have examined effects of their control on bobwhite populations with varying results (Beasom 1974, Guthery and Beasom 1977, Palmer et al. 2005, Jackson et al. 2018). Lacking, however, are manipulative experiments designed to dissect the influence of meso-mammal predators

on demographic rates contributing to population change. Furthermore, the possible confounding effects of site and the mediating effects of predator context (i.e., site-specific abundance, species of predators) have not been addressed.

Nest predators are the predominate cause of nest failure in bobwhites (Stoddard 1931, Staller et al. 2005, Rader et al. 2007) and Staller et al. (2005) reported that meso-mammals accounted for 57% of nest predation on lands managed for bobwhites in Florida and Georgia, USA, whereas other predators, principally snakes, ants, and small mammals, accounted for the remainder of known failures. Sandercock et al. (2008) used population modeling to impute that adult survival was the primary factor affecting population trends rather than variation in productivity in mostly declining populations. McConnell et al. (2018), however, indicated that recruitment was more important than survival in a stable population. Thus, managers often reduce meso-mammals in

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an attempt to increase reproductive success of bobwhites for purported increases in autumn recruitment and abundance (Stoddard 1931, Côté and Sutherland 1997, Newton 1998). Meso-mammal control is only effective on a portion of the predator community, providing an opportunity for other predators to compensate for meso-mammal predation of nests and negate removal actions (Smith et al. 2010, Ellis-Felege et al. 2012). Further, population growth rates are weakly sensitive to nest success because bobwhites are prolific renesters and have multiple broods; however, nesting propensity depends on the timing and magnitude of female mortality rates that vary within and among nesting seasons (Burger et al. 1995*b*). Collectively these contingencies create doubt as to the efficacy of meso-mammal control for managing bobwhite populations. From a broader perspective of game bird ecology, research demonstrating positive results from nest predator control on game bird populations has been conducted in agricultural areas with fragmented habitat, or boreal forest ecosystems, both of which have relatively simple trophic systems (Marcström et al. 1988, Tapper et al. 1996, Newton 1998, Holt et al. 2008). Bobwhites in the southeastern United States exist in a complex trophic system relative to previous studies that may influence the efficacy of predator control. Meso-mammal control is a relatively common management practice in the southeastern United States on lands (~0.5 million ha) sustaining wild bobwhites at high densities (i.e., >2.5 bobwhite/ha), but empirical evidence to support it is limited. Thus, understanding the effect of meso-mammal control on bobwhite demographics in complex trophic systems through robust experimentation will improve conservation of game species while cultivating an informed resource manager community.

In a similar system Jackson et al. (2018) reported support for the predation limitation hypothesis (i.e., predators limiting bobwhite reproductive productivity). They reported that reducing meso-mammal abundance was correlated to increased nesting propensity, nest success, and chicks produced; however, it suffered a few important shortcomings. Because of the observational nature, they were unable to experimentally control for intrinsic site effects that may confound treatment effects and were unable to randomly assign treatments to sites. Furthermore, they were unable to determine the effect of predator removal on autumn density, the metric of greatest interest to many stakeholders. Thus, we extend that work using a multi-year crossover experiment with meso-mammal control as the main treatment. We relied on the predation limitation hypothesis as a possible explanation for ecological phenomena but were more interested in treatment effect sizes in the context of informing management decisions. We predicted meso-mammal control would increase 3 reproductive parameters (nesting propensity, nesting success, *per capita* chick production rate) and autumn bobwhite density when compared to control sites with no trapping of meso-mammal predators. We also report breeding season survival because of this parameter's implications for nesting productivity and populations (Sandercock et al. 2008).

STUDY AREA

We studied nest predation and bobwhites from 2000 to 2006 on 4 study areas including Tall Timbers Research Station (TTRS) in Leon County, Florida (1,568 ha; 30° 39' 35" N, 84° 13' 33" W), Pebble Hill Plantation (PH) in Thomas and Grady Counties, Georgia (1,246 ha; 30° 46' 22" N, 84° 5' 35" W), and Pinebloom Plantation in Baker County, Georgia (31° 24' 42" N, 84° 22' 45" W). Pinebloom was divided in half as Pinebloom East (PBE; 1,400 ha) and Pinebloom West (PBW; 1,400 ha). A 600-ha buffer area comprised mainly of a cypress (*Taxodium distichum*) swamp separated PBE and PBW. Tall Timbers and PH are 12 km apart and within the Red Hills physiographic region of the gulf coastal plain. Pinebloom Plantation was located 93 km north of TTRS in the Dougherty plain of southwestern Georgia. Topography on our study areas was flat to gently rolling with elevations of 27–85 m above mean sea level. Our study areas were <150 km of the Gulf of Mexico and experienced relatively mild winters and hot humid summers with average annual temperature of 20°C, average monthly maximum temperatures during summer (May–Sep) of 33–36°C, and average minimum temperatures during winter (Nov–Feb) of 2–9°C. The growing season of the region was approximately 280 days and annual rainfall averaged 127–152 cm/year.

Our study areas were located in a region of approximately 240,000 ha of land mostly managed for wild bobwhites. All study areas were primarily comprised of mature upland pine forests dominated by loblolly (*Pinus taeda*), slash (*P. elliottii*), and shortleaf (*P. echinata*) pine with associated old-field ground cover vegetation (Carr et al. 2010). Pebble Hill also had some areas of longleaf pine (*P. palustris*) with associated wiregrass-dominated (*Aristida stricta*) ground cover. These areas were managed through annual burning of 50–65% of upland pine forests, fallow field management, and supplemental feeding (Palmer and Sisson 2017). Hardwood drains, hammocks, and cypress domes were interspersed across the landscape. On the Thomasville-Tallahassee study sites, PH had a greater amount and interspersed of hardwood drains than TTRS. On the Baker county sites, PBW had more hardwood hammock and cypress domes than PBE. Low intensity hunting occurred on these properties removing <10% of autumn populations each year. Collectively, this management scheme was commonly practiced on managed bobwhite lands across the Southeast.

METHODS

We conducted the study over a 7-year period during 2000–2006. We measured baseline bobwhite demographics during 2000. We implemented a blocked repeated-measures design with a built-in crossover to control for variability due to site. As such, 1 site in each of the 2 geographical regions received meso-mammal removal during 2001–2003 (PBE and PH), whereas we did not trap in the remaining 2 sites (PBW and TTRS). We switched trapping during 2004–2006 to PBW and TTRS and did not trap on PBE and PH. We followed the trapping, handling, euthanizing, and marking procedures

approved by University of Georgia's Institutional Animal Care and Use Committee (permits numbers A2001-10100-0, A2004-10109-c1, and A3437-0).

Meso-Mammal Trapping and Response to Removal

Based on literature identifying primary nest predators using video surveillance, target meso-mammal species included bobcats (*Lynx rufus*), coyotes (*Canis latrans*), gray fox (*Urocyon cinereoargenteus*), nine-banded armadillos (*Dasyurus novemcinctus*), Virginia opossums (*Didelphis virginiana*), and raccoons (*Procyon lotor*; Staller et al. 2005). We did not manipulate other significant nest predators on the study areas, including snakes and red imported fire ants (*Solenopsis invicta*; Staller et al. 2005). To reduce abundance of meso-mammals during the breeding season of bobwhites, we employed 4 full-time United States Department of Agriculture (USDA)-Wildlife Services personnel to trap daily March through September. At any one time, we deployed approximately 100 box traps and 30 leg-hold traps (number 1-3/4, double-spring, offset) at each site. We geo-referenced trap locations and recorded trap type, date, and species. We dispatched target animals following USDA-Wildlife Service's protocols and froze carcasses for determination of age, diet, and various parasite and disease assays (Schoch 2003, Lang 2008).

We assessed meso-mammal predator population response to trapping using scent station indices. We conducted scent station surveys each year during the first 2 weeks of October and selected a 5-day period without rainfall. We visited scent stations each morning of the survey and identified predators to species using footprints. A scent station consisted of a 1-m ring of sand, treated with mineral oil, with a single fatty acid scent tablet (USDA Pocatello Supply Depot, Pocatello, ID, USA) placed at the center of the sand ring (Linhart and Knowlton 1975). We randomly placed 30–40 scent stations along unimproved roads at an approximate density of 1 station/25 ha such that stations were at minimum 0.5 km apart. Unimproved road coverage on our study area was high (~1 km/20 ha) so that scent stations were well distributed across the properties. The nest predator index was the probability that ≥ 1 of the target meso-mammal species visited a scent station per day, calculated as the number of predators observed divided by the number of scent station nights multiplied by the number of target meso-mammal species included in the index. Including the number of target species in the denominator constrains the index between 0 and 1. We recognize that scent station indices are a crude index to abundance and activity of meso-mammals, although we assume the technique is suitable for detecting temporal trends of common meso-mammals (Sargeant et al. 1998, 2003). Previous research in the southeastern United States has demonstrated the utility of scent stations for indexing meso-mammal abundance (Sumner and Hill 1980, Lincombe et al. 1983, Leberg and Kennedy 1987) and a linkage of our predator index with bobwhite reproductive success has been previously demonstrated on our study areas (Staller et al. 2005). A common concern with scent station indices is that they are not corrected for detection rates that may be low

and also vary over time and by land cover type. To minimize these effects we standardized the time of year we conducted surveys and placed scent stations in the same land cover type across our study areas. The scent station index was correlated ($r=0.71$, $P<0.001$) to occupancy of scent stations, corrected by site- and year-specific detection rates, by the same suite of meso-mammals, thus providing additional support that the scent station methodology was adequate for indexing trends in meso-mammal abundance and activity on our study areas (Ellis-Felege et al. 2010).

Bobwhite Population and Demographic Responses

Bobwhite capture and telemetry methodology.—We captured bobwhites in wire walk-in funnel traps (Stoddard 1931) in January (TTRS and PH only), March–April, and October–November. We completely covered bobwhite funnel traps with vegetation to reduce predation and stress of captured bobwhites. Each year, we evenly distributed traps across the study area at a trap density of ≥ 1 trap/5 ha across the upland portions of the study areas. We checked traps beginning at sunset each day. We aged, sexed, and banded bobwhites with uniquely numbered aluminum leg-bands. We selected a subsample of 3–5 bobwhites from each covey for radio-tagging using pendant-style transmitters weighing 6 g and equipped with mortality switches (American Wildlife Enterprises, Tallahassee, FL, USA) or motion sensitive switches (Holohil Systems, Ontario, Canada). We released all bobwhites in a covey, or portion thereof, at their capture location simultaneously.

We monitored radio-tagged bobwhites 3 times/week 1 October through 14 April, and daily during the breeding season, 15 April to 30 September. We located bobwhites by homing (White and Garrott 1990) and we plotted their locations on maps. When bobwhites were at the same location on consecutive visits, we assumed they were incubating a nest. We checked incubating bobwhites daily, including weekends, until nest fate occurred. We determined clutch size when the incubating adult was on recess from the nest site. We considered a nest as successful when ≥ 1 chick fledged. We included male- and female-incubated nests in our estimate of nesting success to maximize sample size of nests. We tracked bobwhites with broods daily until 21 days post-hatch.

Measuring reproductive productivity.—We estimated nesting propensity by summing all nests for each population in each breeding season then used an offset (radio-tagged sample of females at the beginning of the breeding season, 15 Apr each year) in the Poisson regression model to derive a *per capita* rate of nesting propensity. Although we recognize the importance of male-incubated nests (Burger et al. 1995a), we ignored male contributions in our *per capita* productivity ratios because of insufficient sample sizes of radio-tagged males in some sites and years; therefore, we analyzed only female contributions to productivity.

Autumn bobwhite abundance.—We conducted covey call grid counts during October and November each year to estimate bobwhite density following methods described by Wellendorf and Palmer (2005). We applied approximately

30% sampling intensity, which resulted in conducting 12 500-m × 500-m grids/site. This method minimizes errors caused by judging distance to calling coveys (Rusk et al. 2010) because >1 observer records each covey. To maintain consistency, we used a core group of 8 observers each year of the project (Rusk et al. 2010). Following the call count, we located coveys in the grid with the aid of bird dogs and flushed coveys to determine covey size. Density (bobwhite/ha) was based on the estimated number of coveys, adjusted by the estimated covey calling rate (Wellendorf et al. 2004) and average covey size divided by the number of hectares sampled.

Breeding season survival rates.—We estimated breeding season survival using staggered-entry Kaplan–Meier method (Pollock et al. 1989) to determine site-specific and across-site (i.e., regional) trends in survival rates, and used a simple correlation coefficient to relate breeding survival to nesting propensity and nesting success. Regional trends in survival rates and their effect on nesting propensity provided context for interpreting treatment effects (Sandercock et al. 2008). We included male and female radio-tagged bobwhites in estimating breeding season survival because it was more important to maintain adequate sample sizes for Kaplan–Meier estimates than it was to determine sex-specific survival (Palmer et al. 2007). We right censored bobwhites that experienced radio-failure. Previous research demonstrated that radio-tagging bobwhites did not bias survival estimates on our study areas (Palmer and Wellendorf 2007, Terhune et al. 2007, Sisson et al. 2010).

Statistical Analyses

We used Bayesian hierarchical models to analyze the effects of predator trapping on the 4 key bobwhite demographics (i.e., nest success, nest propensity, chick production, autumn density) and the predator index. We used the same set of candidate models for each response variable to explore the effects of treatment, baseline, site, and carryover (Table 1). Carryover effects in crossover designs occur when the condition of a subject during the first treatment influences the effect of that subject during the second treatment (Littell et al. 1996). In our case a carryover effect could have occurred if meso-mammal control reduced predator abundance following the crossover of treatments. Although we assumed meso-mammals re-colonized our study sites between

breeding seasons, thereby minimizing carryover effects, we recognized the predator index and bobwhite demographics were potentially influenced by carryover. Therefore, we assessed carryover using a period × treatment interaction, with periods following trapping sessions, 2001–2003, and 2004–2006.

We modeled each demographic metric using the most appropriate statistical distribution. We modeled nest success using a logit link and binomial distribution in a success or failure data structure. Similarly, we modeled predator activity using a binomial distribution where the numbers of successes indicated visitation (i.e., track of species detected on a given night) and the trials were the product of the number of stations and days surveyed. We modeled nest propensity and chick production using log link and Poisson distribution. For example, the most general model for response (Y_i ; i.e., observed value) of nest propensity (λ_i ; i.e., expected value) to meso-mammal control was as follows:

$$Y_i \sim \text{Poisson}(\lambda_i), \text{ where}$$

$$(\lambda_i) = \beta_1 + \beta_2 \times \text{period}_i + \beta_3 \times T_i + \gamma_1 \times \alpha_{\text{site}_i}^{\text{random}}$$

$$+ (1 - \gamma_1) \times \alpha_{\text{site}_i}^{\text{fixed}} + \gamma_2 \times \beta_4 \times B_i$$

$$+ \log(\text{number of females}_i)$$

$$\alpha_{\text{site}_i}^{\text{random}} \sim \text{Normal}(0, \sigma_{\text{site}}^2)$$

$$\alpha_{\text{site}_i}^{\text{fixed}} \sim \text{Normal}(0, 10^{-3}),$$

for $i = 1, 2, \dots, N$ where N represents number of observations. The effects of period and treatment are represented with 2 indicator variables, period_i and T_i for observation i . We modeled site in 2 ways: as a random effect, denoted $\alpha_{\text{site}_i}^{\text{random}}$, and a fixed effect, denoted $\alpha_{\text{site}_i}^{\text{fixed}}$. Baseline effects, B_i , were incorporated in some models. Following Ntzourfras (2009), our model structure used binary indicator variables, γ_1 (0 = fixed effects and 1 = random effects) and γ_2 (1 or 0 depending on the inclusion of a baseline measurement). We used uninformative priors for each of the fixed effects, β_i , where the mean is centered on zero and precision (i.e., inverse of variance) is small, $\text{Normal}(0, 10^{-3})$.

We estimated chick production as a derived variable as the product of expected nest success, nest propensity, and mean clutch size for each observation as follows:

Table 1. Model structures and Deviance Information Criterion (DIC) values for models testing the effects of predator removal on the relative abundance (predator index) of meso-mammals and northern bobwhite nest success, nesting propensity, and autumn density on 4 sites in northern Florida and southwest Georgia, USA, with nest predator control applied using a crossover design, 2000–2006.

Model	$(\gamma_1, \gamma_2)^a$	Period effect	Site effect	Baseline	Carryover	DIC			
						Nest success	Nesting propensity	Autumn density	Predator index
1	(0,0)	Yes	Fixed	No	No	135.5	177.8	271.0	206.6
2	(1,0)	Yes	Random	No	No	135.5	177.2	271.7	206.5
3	(0,1)	Yes	Fixed	Yes	No	135.5	177.8	272.5	206.8
4	(1,1)	Yes	Random	Yes	No	136.1	177.5	374.1	207.5
5	(1,1)	Yes	Random	Yes	Yes	136.4	177.4	347.3	207.2

^a Binary indicator variables for the treatment effect, γ_1 (0 = fixed effect and 1 = random effect) and γ_2 (1 or 0 depending on the inclusion of a baseline measurement).

$$Chick\ production_i = (nest\ success_i \times \lambda_i \times clutch\ size_i)$$

The nest success and nest propensity values are expected values from their respective values thus contain all of the uncertainty from those models. We summarized the expected chick production for each treatment as the expected mean among each treatment.

We fitted models using Markov-chain Monte Carlo (MCMC) simulation with Gibbs sampling to estimate random variable marginal distributions from the joint probability distribution. We implemented models using JAGS and the jagsUI package in R (Plummer 2003, R Development Core Team 2014). We conducted 25,000 MCMC iterations using 3 chains with a burn-in of 1,000, and thinned by a factor of 5. We checked convergence using visual inspections of trace plots and the Gelman-Rubin statistic \hat{R} (Gelman and Rubin 1992, Gelman et al. 2004). We used Deviance Information Criterion (DIC) to rank each set of models for each demographic metric, where the lower the value the better the model fits the data (Spiegelhalter et al. 2002). We used Bayesian P -values as probability statements about the treatment effect (i.e., predator control) being greater than the control. Values close to 0.5 suggest no difference in parameter estimates, whereas values of ≥ 0.9 suggest differences that can be interpreted as a 90% probability the parameter value of interest is greater than another.

RESULTS

The model including the effects of period and treatment as fixed effects with site as a random effect was in general the best-supported model across all candidate sets according to DIC (model 2; Table 1). Other models were competitive, but we chose to keep the model structure consistent throughout because the random effect of site allowed inference to be unconditional on site and the parameter estimates were virtually identical across all competitive models. All parameters converged according to visual inspection and \hat{R} (Table 2).

Meso-Mammal Reduction

We removed meso-mammals from PBE ($n = 1,310$) and PH ($n = 836$) during 2001–2003, and PBW ($n = 1,366$) and TTRS ($n = 1,436$) during 2004–2006 (Fig. 1). Opossums ($n = 2,293$), raccoons ($n = 1,497$), and armadillos ($n = 954$) accounted for 94.1% of the target meso-mammals removed. The predator index demonstrated greater meso-mammal

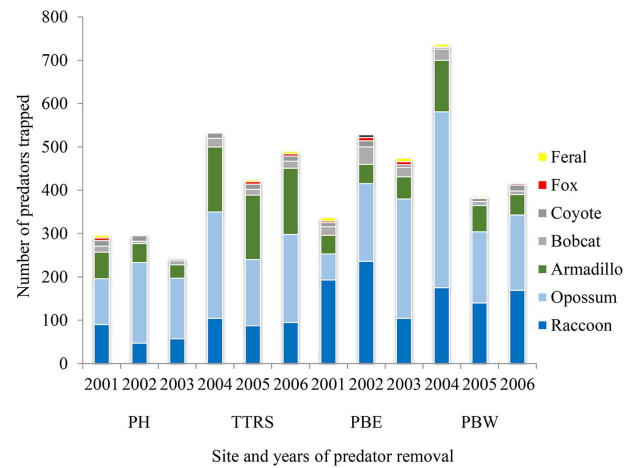


Figure 1. Number of meso-mammal nest predators removed during a 6-year crossover removal study in northern Florida and southwest Georgia, 2000–2006. Pebble Hill (PH) and Pinebloom East (PBE) had meso-mammal predators removed during 2001–2003, whereas Tall Timbers (TTRS) and Pinebloom West (PBW) had removal during 2004–2006. Feral includes feral domestic dogs and cats.

abundance at PBE (0.03 ± 0.1 [SD]) and PBW (0.03 ± 0.1) than at TTRS (0.02 ± 0.14) or PH sites (0.02 ± 0.14 ; Fig. 2). The probability that trapping and removal reduced predator activity relative to the control was 1.0 (Bayesian P -value). Predator activity reflected via scent stations on trapped sites was 1.93 times less (odds ratio, 95% credible interval (CrI) = 1.70, 2.23) than on non-trapped sites, resulting in a reduction of predator activity by 43%. Expected predator activity was 0.04 on trapped sites (CrI = 0.02, 0.06) and 0.07 (CrI = 0.03, 0.11) on non-trapped sites.

Northern Bobwhite Response

We radio-tagged 4,015 bobwhites during 2000 to 2006: 662 at PBE, 638 at PBW, 1,920 at TTRS, and 795 at PH. Study sample size of radio-tagged females entering the reproductive season (15 Apr) each year used to estimate nesting productivity was 280, 267, 723, and 339 at PBE, PBW, TTRS, and PH, respectively. Annual sample sizes for females entering the nesting season averaged 40.0, 38.1, 103.3, and 48.4 females on PBE, PBW, TTRS, and PH, respectively. Total samples for males entering the nesting season were, 164, 182, 323, and 108 on PBE, PBW, TTRS, and PH, respectively. Annual sample sizes for males entering the nesting season averaged 23.4, 26.0, 46.1, and 15.4, males on PBE, PBW, TTRS, and PH, respectively.

Table 2. Parameter estimates and 95% credibility intervals for models testing the effects of predator removal on the relative abundance (predator index) of meso-mammals and on northern bobwhite nest success, nesting propensity, and autumn density on 4 sites in northern Florida and southwest Georgia, USA, with nest predator control applied using a crossover design, 2000–2006. Nest success and predator index parameter estimates are on the logit scale, nest propensity estimates are on the log scale, and autumn density on the normal scale.

Parameter	β	Nest success			Nest propensity			Autumn density			Predator index		
		\bar{x}	Lower	Upper	\bar{x}	Lower	Upper	\bar{x}	Lower	Upper	\bar{x}	Lower	Upper
Intercept	1	0.02	-0.32	0.38	-0.41	-0.64	-0.17	3.35	2.44	4.23	-2.73	-3.36	-2.12
Period	2	-0.14	-0.41	0.12	-0.24	-0.38	-0.11	-0.52	-0.85	-0.18	-0.02	-0.16	0.14
Treatment	3	0.20	-0.07	0.47	0.26	0.12	0.39	0.45	0.12	0.79	-0.66	-0.80	-0.53

Nest success and nesting propensity.—During the 7 years of the study, we found 1,271 bobwhite nests, of which 1,083 and 188 were incubated by females and males, respectively. Six hundred and seventy nests successfully hatched ≥ 1 chick, including 52.7% and 53.7% of female- and male-incubated nests, respectively. Predation accounted for 537 of 601 nest failures from predation of the nest ($n = 479$) or mortality of the incubating bird ($n = 58$). Sixty-four nests were abandoned during incubation. Observed nesting propensity (nests/female) averaged 0.67 ± 0.03 (SE) with a low of 0.43 in 2004 at PH and a maximum of 1.08 at PBE in 2001 (Table 3).

Overall, nesting propensity was greater on trapped sites (0.87; CrIs = 0.68, 1.09) than on non-trapped sites (0.67; CrIs = 0.53, 0.83), representing about a 30% increase in nesting by females on trapped sites compared to non-trapped sites (Bayesian P -value 1.00). The random effect of site (α_{site}^{random}) was 0.04 ± 0.04 ($\bar{x} \pm SD$).

Nests in treated sites were 1.2 times (odds ratio, CrI = 0.94, 1.59) more likely to be successful than control nests. Predicted nest success was 55.7% (CrI = 46.5, 64.5) in treated sites and 50.1% (42.0, 59.4) in control sites. The Bayesian P -value for the treatment effect was 0.94. The random effect of site (α_{site}^{random}) was 0.08 ± 0.10 (SD).

Chick production.—Observed chicks/female averaged 3.82 ± 0.30 (SE) across all sites and years and ranged from a low of 1.58 chicks/female at PH in 2000 to a high of 8.10 chicks/female at PBE in 2001. We found meso-mammal control had a positive effect on chick production with an expected 5.30 (CrIs = 4.70, 5.90) chicks/female for trapped sites and 3.70 (CrIs = 3.20, 4.20) for control sites (Fig. 3). Meso-mammal control increased chicks/female by 1.6 chicks (CrIs = 0.78, 2.40), or a 43% increase in chicks produced.

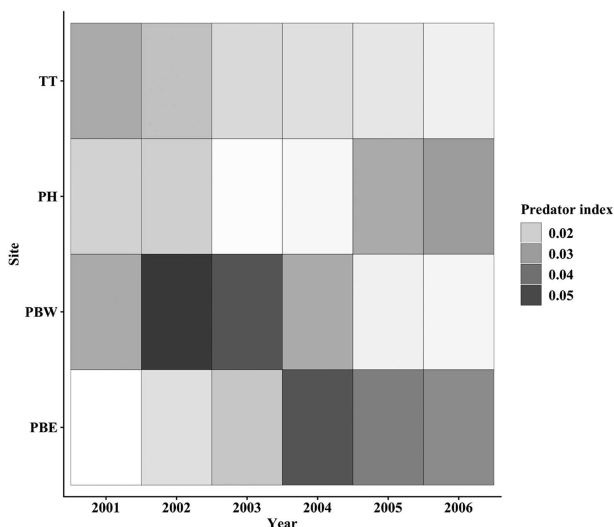


Figure 2. The observed predator index during a 6-year crossover removal study in northern Florida and southwest Georgia, USA, 2000–2006. Pebble Hill (PH) and Pinebloom East (PBE) had meso-mammal predators removed during 2001–2003, whereas Tall Timbers (TT) and Pinebloom West (PBW) had removal during 2004–2006.

Breeding season survival.—Breeding season survival of adult bobwhites averaged 0.37 ± 0.024 (SE) across all sites and years and ranged from a low of 0.15 at PBE in 2005 to a high of 0.58 at TTRS in 2002. There was a regional trend of higher survival rates during 2001–2002 and lower survival rates from 2003–2005 with an increase in 2006 (Fig. 4). Nesting propensity was related ($r_{26} = 0.59$, $P = 0.001$) to breeding season survival. Nesting success was not correlated with breeding season survival ($r_{26} = 0.10$, $P = 0.60$).

Bobwhite abundance.—Observed autumn density averaged 2.6 ± 0.22 (SE) birds/ha across all sites and years and ranged from a low of 0.8 birds/ha at PH in 2000 to 5.2 birds/ha at PBE in 2003. Expected autumn density on trapped sites (3.30 birds/ha, CrI = 2.50, 4.12) was higher than non-trapped sites (2.80 birds/ha, CrI = 1.97, 3.63). The Bayesian P -value for the treatment effect was 1.00. This equated to a difference of 0.50 birds/ha (CrI = 0.32, 0.67), or an 18% increase in autumn density relative to the control (Fig. 5).

DISCUSSION

We demonstrated that consistent effort in meso-mammal control enhances reproductive performance of an important game bird. Using a crossover design with spatial and temporal replicates, we found support for the predation limitation hypothesis such that predator removal effectively reduced predator activity and positively influenced population response of bobwhites. We believe that observed increases in reproductive performance provide opportunity to increase fall abundance in bobwhite populations and reduce annual swings in fall abundance inherent to the species.

Bobwhite are a short-lived species for which adult survival has been identified as the most important predictor for bobwhite population change (Sandercock et al. 2008). However, bobwhite exhibit a complex mating system with individual variability (including extra-pair copulation, rapid multi-clutching, male incubation, intra-specific nest parasitism, and multiple brooding) to permit recovery from high annual mortality (Brennan 1999, Burger et al. 1995b, Faircloth 2008, Miller et al. 2012). We observed significant regional variation in breeding season survival, which was correlated to nesting propensity. That said, meso-mammal control had minimal effect on adult survival even though predation is the greatest cause of adult mortality (Stoddard 1931, Carroll et al. 2007). We suspect this apparent paradox was from adult mortality being largely a function of avian predation on our study areas (Sisson et al. 2009), and as demonstrated elsewhere (Burger et al. 1995a, 1998). Observed annual variation in adult mortality was linked to regionally scaled conditions such as weather that influenced abundance of avian predators (Holt et al. 2012) on our study areas and cyclical small-mammal abundances that influenced their diet (Norrdahl and Korpimaki 2000). Therefore, processes that affected adult survival were decoupled from meso-mammal control, which mostly reduced predation on nests and young but only marginally affected adults. Because adult survival did not increase with reducing predators, observed population increases were unequivocally a function of increased chick production. This demonstrates, for the

Table 3. Observed demographics (survival 15 Apr–1 Oct, nest success, nests/female alive 15 Apr, chicks/female alive 15 Apr) of 4,015 radio-tagged northern bobwhites and autumn density of bobwhites on 4 sites in northern Florida and southwest Georgia, USA, with nest predator control applied using a crossover design, 2001–2006.

	Site ^a	Year						\bar{x}	SD	\bar{x}	SD	
		2000	2001	2002	2003	2004	2005	2006	2001–2003	2004–2006		
Survival	TTRS	0.48	0.52	0.58	0.31	0.32 ^b	0.43 ^b	0.42 ^b	0.47	0.14	0.39 ^b	0.06 ^b
	PH	0.34	0.35 ^b	0.49 ^b	0.25 ^b	0.21	0.26	0.39	0.36 ^b	0.12 ^b	0.28	0.09
	PBE	0.21	0.31 ^b	0.53 ^b	0.44 ^b	0.27	0.15	0.29	0.43 ^b	0.11 ^b	0.24	0.08
	PBW	0.27	0.31	0.59	0.38	0.45 ^b	0.25 ^b	0.30 ^b	0.43	0.15	0.33 ^b	0.10 ^b
Nest success	TTRS	0.46	0.34	0.60	0.45	0.64 ^b	0.62 ^b	0.58 ^b	0.46	0.13	0.61 ^b	0.03 ^b
	PH	0.33	0.48 ^b	0.47 ^b	0.52 ^b	0.41	0.59	0.41	0.49 ^b	0.02 ^b	0.47	0.10
	PBE	0.41	0.64 ^b	0.58 ^b	0.52 ^b	0.41	0.57	0.39	0.58 ^b	0.06 ^b	0.45	0.10
	PBW	0.47	0.50	0.50	0.37	0.34 ^b	0.35 ^b	0.42 ^b	0.46	0.07	0.37 ^b	0.04 ^b
Nests/female	TTRS	0.94	0.67	0.73	0.45	0.64 ^b	0.48 ^b	0.77 ^b	0.62	0.15	0.63 ^b	0.14 ^b
	PH	0.38	0.57 ^b	1.00 ^b	0.57 ^b	0.43	0.45	0.63	0.71 ^b	0.25 ^b	0.50	0.11
	PBE	0.59	1.08 ^b	0.90 ^b	1.04 ^b	0.55	0.54	0.51	1.01 ^b	0.09 ^b	0.53	0.02
	PBW	0.67	0.57	0.93	0.66	0.83 ^b	0.74 ^b	0.55 ^b	0.72	0.19	0.71 ^b	0.15 ^b
Chicks/female	TTRS	5.12	3.01	5.64	2.09	4.38 ^b	3.65 ^b	5.43 ^b	3.58	1.84	4.49 ^b	0.90 ^b
	PH	1.59	4.78 ^b	5.28 ^b	3.20 ^b	2.55	3.22	2.63	4.42 ^b	1.08 ^b	2.80	0.37
	PBE	2.52	8.10 ^b	4.54 ^b	5.62 ^b	2.26	3.80	2.49	6.09 ^b	1.83 ^b	2.85	0.83
	PBW	3.71	3.14	5.22	2.45	2.90 ^b	2.84 ^b	2.58 ^b	3.60	1.44	2.77 ^b	0.17 ^b
Autumn Density	TTRS	1.70	2.27	4.09	3.13	2.36 ^b	3.25 ^b	3.73 ^b	3.16	0.91	3.12 ^b	0.70 ^b
	PH	0.76	1.84 ^b	2.36 ^b	1.97 ^b	1.74	1.42	2.03	2.06 ^b	0.27 ^b	1.73	0.31
	PBE	3.61	4.35 ^b	4.82 ^b	5.19 ^b	3.56	2.50	1.61	4.79 ^b	0.42 ^b	2.55	0.98
	PBW	2.10	2.08	2.97	1.85	2.82 ^b	2.25 ^b	1.68 ^b	2.30	0.59	2.25 ^b	0.57 ^b

^a Sites include Tall Timbers Research Station (TTRS), Pebble Hill (PH), Pinebloom West (PBW), and Pinebloom East (PBE).

^b Predator control occurred during year or period.

first time, that bobwhite populations can be increased by managing nest predators and reducing their effect on nesting propensity and hatching rates, although variation in adult survival and its influence on populations remains important.

Meso-mammal control increased nesting propensity more than nesting success, as measured using radio-telemetry. Increased nesting propensity by females on treatment sites

could have been a behavioral response to reduced predator abundance. For instance, individual behavioral shifts may follow predator control such that the perceived risk of predation decreased on treatment sites (e.g., landscape of fear concept; Laundré et al. 2001, 2010). Fear response in prey could affect parental care and incur constraints on demography or individual fitness (Dudeck et al. 2017). Behavioral adaptations can be dictated by surrounding conditions and reduction of predators could ostensibly reduce interactions and assuage a fear response, resulting in increased nest propensity. We suspect increased nesting propensity on sites with meso-mammal control could be an

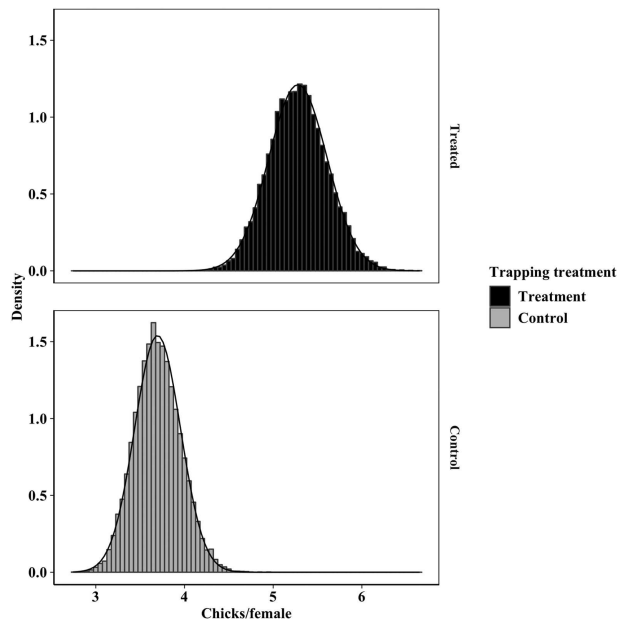


Figure 3. The model-predicted chicks/female for northern bobwhite during a 6-year crossover removal study on 4 sites in northern Florida and southwest Georgia, USA, with nest predator control applied using a crossover design, 2000–2006.

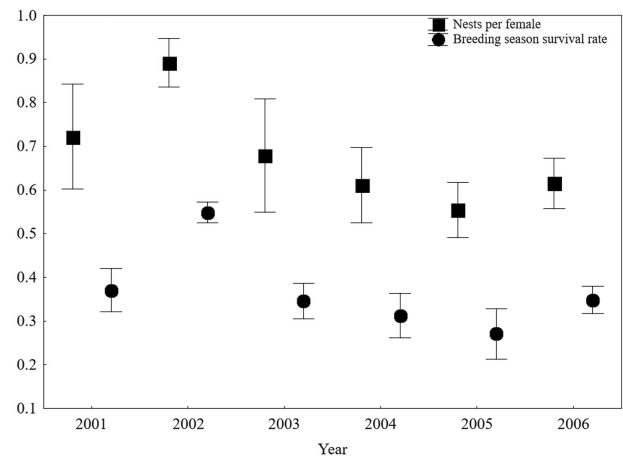


Figure 4. Mean breeding season survival rate of northern bobwhite on 4 sites in northern Florida and southwest Georgia, USA, in relation to number of nests produced by females alive at the beginning of the breeding season, 2000 to 2006.

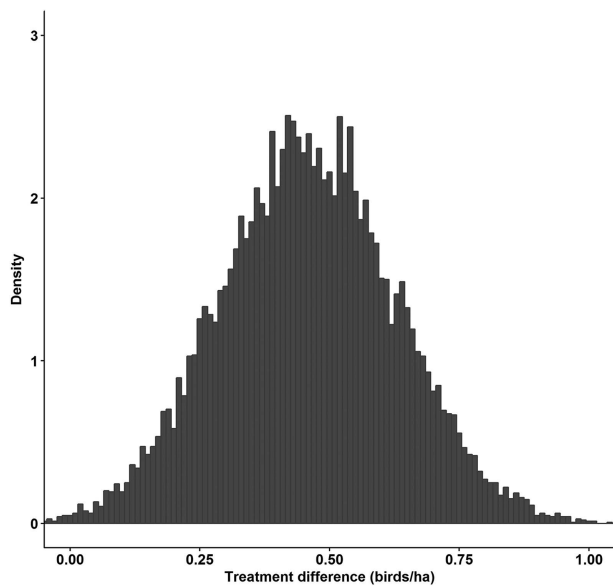


Figure 5. The expected difference in autumn northern bobwhite density (bobwhites/ha) on 4 sites in northern Florida and Southwest Georgia, USA, treated with predator removal versus a control, 2000 to 2006.

artifact of how we measured nesting propensity. Most bobwhite nests in our study were at the onset of incubation and an unknown number of nests were depredated during the laying stage therefore confounding true nest propensity and nesting success. Future research should evaluate whether predator abundance and contextual clues associated with fear response affects reproductive output and nest propensity.

In our study the magnitude of population response varied substantially among sites and years. For instance, bobwhite autumn densities on PH and PBE following 3 years of nest predator management increased by 2.7 (PH) and 1.3 (PBE) relative to pre-trapping means in 2000. However, these sites were trapped during an increasing phase in bobwhite numbers across the region associated with high breeding season survival rates and above average chick survival (T. M. Terhune, Tall Timbers Research Station, unpublished data). Mean bobwhite densities declined on PH by 16% and on PBE by 47% after we ceased removing meso-mammal predators. This decline corresponded with 3 years of general regional declines partially a result of declining breeding season survival we measured on all sites. Contrary to PH and PBE, meso-mammal control on TTRS and PBW began when bobwhite densities were relatively high following the regional increases observed in 2000–2002. However, although bobwhite populations declined subsequent to ceasing meso-mammal trapping on PH and PBE, mean bobwhite populations were constant during the same period on TTRS and PBW despite declining breeding season survival rates on all properties. It appears that increased chick production, as a result of meso-mammal control, helped to forestall declines caused by declining adult survival rates.

Sources of variation influencing the effect of meso-mammal control were largely contextual, uncontrollable, and included cyclic abundance of alternative prey, rainfall

patterns, a distemper outbreak among the meso-mammal population in 2001, and compensation among nest predator guilds (Ellis-Felege et al. 2012). We observed high hispid cotton rat (*Sigmodon hispidus*) abundance (>rats 25/ha) on our study areas during 2001 through 2002, and again during 2005 to 2006 (W. E. Palmer, Tall Timbers, unpublished data). High cotton rat abundances may have reduced the effect size of meso-mammal control as predators switched from bobwhites to more abundant cotton rats, reducing predation rate on nests. Several studies have documented that predators readily switch to alternative prey (Oaten and Murdoch 1975, Akre and Johnson 1979), or shared prey (Norrdahl and Korpimaki 2000), as they become more available. Small mammals, including cotton rats (Schnell 1968), are prone to cyclic fluctuations that vary in magnitude and this periodicity of mass presence of small rodents alters the predator-prey dynamics and reduces the demographic effect from predator control (Korpimaki and Krebs 1996, Abrams and Matsuda 1996). In the Southeast droughts are rarely severe enough to shut down reproductive activity altogether and rainfall patterns explain less variation in population size than in the Southwest (Brennan et al. 1997). Rainfall patterns varied among years, however, potentially influencing recruitment by affecting chick survival (T. M. Terhune, unpublished data). Increased chick fledging rates from meso-mammal control may be expunged by excessive rainfall during brood rearing, such as in 2003 and 2004, reducing fall recruitment and the effect of meso-mammal control. Annual and site-specific variation in chick survival may help explain why a 43% improvement in chick production from meso-mammal control resulted in a lower percent increase in autumn abundance. This also suggests that chick survival may not be as influenced by meso-mammal control as other nesting demographics. Finally, we observed partial compensation by fire ants and certain snake species, which principally occurred on 2 of our study sites (PBE and PH). Increased predation by snakes was possibly a response to changes in habitat availability for snakes and not increased snake populations given the 3-year time frame that meso-mammal control was implemented on each site (Ellis-Felege et al. 2012).

Despite the demographic variation created by these and other factors, we observed increases in recruitment due to reduced nest predation, which resulted in greater bobwhite populations. That said, a positive effect on bobwhite nesting propensity and chick production from meso-mammal control may result in increased bobwhite populations statistically, but the management result may be a reduced rate of population decline in any given year because of factors outside the control of management. Collectively, increased chick production from reducing meso-mammal predation provides a demographic cushion for bobwhites that can help moderate population declines during years with poor conditions and enhance population growth during years of good conditions, thus maximizing bobwhite populations through time.

Bobwhite in the southwestern portion of their range experience substantial weather-related variation in demo-

graphic rates and subsequent autumn population trajectories (Lehmann 1946). Severe droughts and high temperatures can cease egg-laying, reduce hatching rates and chick survival rates and result in severe population declines (Hernandez et al. 2005). Rainfall-related reproductive failures may be 1 reason why effect of meso-mammal control on bobwhite populations varies among studies (Guthery and Beason 1977, Jackson et al. 2018) because increased fledgling rates may not translate into autumn recruitment if chick survival is severely compromised by drought. Additional research on the effect of meso-mammal control on bobwhite demographics in drought-prone regions of the bobwhite range would be useful to determine limits of its efficacy.

Our study areas are located in landscapes managed for sustainable bobwhite populations (Palmer et al. 2002, Stribling and Sisson 2009). To sustain high density bobwhite populations, property managers maximize the availability and quality of habitat to meet the year-round needs of bobwhites through combinations of prescribed fire, open pine canopies, and annual fallow weed fields. As such, the habitat availability and vegetation structure and composition were similar among our study sites because of the use of similar management techniques. In addition, managers on surrounding properties often conduct meso-mammal control, which likely reduces extant predator populations (Jackson et al. 2018). Therefore, the response of bobwhite populations to meso-mammal control may vary on areas with less habitat available or where higher densities of meso-mammals occur. Additional research is needed to elucidate how nest predation affects bobwhite demographics on isolated sites with more fragmented habitat (as in Palmer et al. 2005).

Although our ability to quantitatively assess abundance of predators was limited to an index of predator activity, it proved to be a valuable tool. The predator index demonstrated that we effectively reduced predator activity via removal efforts and that despite intensive trapping effort, extirpation of any species of predator did not occur. As such, the predator index provides a valuable management tool for assessing predator context relative to bobwhite reproductive and population performance at the local scale (Jackson et al. 2018). Relative to other studies investigating bobwhite population response to meso-mammal control, we removed 3 times the number of individual meso-mammals on a per hectare basis (Beason 1974, Guthery and Beason 1977). We also removed about the same number of predators each year of the study and found no carryover effects in our scent station data, indicating that to maintain lower predator abundance and activity requires similar effort each year. Other studies have shown a similar quick recovery of populations of meso-mammal predators (Reynolds and Tapper 1996, Tapper et al. 1996, Newton 1998).

Control of meso-mammals should not take the place of habitat management and should be viewed as 1 component of predation management (Palmer and Sisson 2017). Meso-mammal control is a tool that can be deployed when conditions within a management program warrant its use and habitat conditions are adequate. Although legal in many

parts of the bobwhite range, meso-mammal control may be viewed as controversial by some stakeholders, which could influence implementation. We view bobwhites as an umbrella species (Crosby et al. 2015) where bobwhite management provides habitat for many declining species in the southeastern United States (Brennan et al. 1998). Like bobwhite habitat management, benefits of meso-mammal control accrue to more than bobwhites (Ritchie and Johnson 2009), and include other ground-nesting species, such as gopher tortoise (*Gopherus polyphemus*; Tuberville et al. 2009). Reducing meso-mammal populations using predator control may replace natural control once provided by top predators now extirpated from nearly all of the bobwhite range (Ritchie and Johnson 2009). As such, predator control is a tool that when used should be based on science and used responsibly and humanely, to avoid unnecessary controversy.

MANAGEMENT IMPLICATIONS

Meso-mammal control provides an additional management tool to regulate meso-mammal nest predators that in turn affect bobwhite population abundance. To maximize bobwhite abundance and reduce variation through time, we recommend using the nest predator index to gauge meso-mammal abundance and activity to help guide decisions when considering the need for initiating a meso-mammal reduction program. Predator index values >0.02 would suggest predator activity could be affecting bobwhite demography and warrant predator management. On a typical-sized private management area of 2,000 ha, bobwhite population increases observed in this study in response to trapping would add approximately 1,000 bobwhite to the autumn population, providing opportunity to sustainably harvest an additional 150 to 200 bobwhites. Meso-mammal control requires a significant amount of effort to elicit a response in bobwhite demographics and the magnitude of its effect will vary by site and year in conjunction with factors outside the control of managers.

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