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Partial meso-mammal predator removal positively affects northern bobwhite reproduction

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Perceived changes in predator–prey dynamics along with documented declines of northern bobwhite *Colinus virginianus* have created a renewed interest from biologists and managers about the role meso-mammals play in shaping bobwhite population trajectories. Therefore, we evaluated the efficacy of meso-mammal trap and removal (MMTR) at reducing meso-mammal activity and increasing bobwhite reproductive success; thus testing the predation limitation hypothesis. During 1999–2006, we monitored bobwhite reproduction on 11 sites in three states across the southeastern United States. Combined, there were 37 site–year combinations when MMTR occurred and 20 combinations when it did not occur. We conducted 57 predator surveys and calculated an index of meso-mammal activity (i.e. predator index), for each site, as the average number of station visits per night by raccoons *Procyon lotor*, nine-banded armadillos *Dasypus novemcinctus*, Virginia opossums *Didelphis virginiana*, bobcats *Lynx rufus* and foxes *Vulpes vulpes*, *Urocyon cinereoargenteus*. The average predator index (predator visits per trap night) across sites was 0.13. We collected bobwhite reproductive information from a total of 3935 radio-tagged bobwhites resulting in 2499 nests. We used generalized linear mixed models to evaluate the relationships between MMTR, predator activity, and bobwhite reproduction. The mean predator index for non-trapped sites was 0.21 (95% CLs: 0.18, 0.24) compared to 0.10 (95% CL: 0.07, 0.13) for trapped sites. Bobwhite nests were 1.33 times (Odds ratio, 95% CL: 1.09, 1.62) more likely to be successful on trapped sites than non-trapped sites. Meso-mammal trap and removal had a positive effect on nests per hen ($\beta_{trapped} = 0.25 \pm 0.06$; 95% CL: 0.13, 0.37), broods per hen ($\beta_{trapped} = 0.37 \pm 0.08$; 95% CL: 0.21, 0.53), and chicks per hen ($\beta_{trapped} = 1.09 \pm 0.52$; 95% CL: 0.07, 2.11). Our results show that MMTR reduces meso-mammal activity and positively affects bobwhite reproduction.

Predation is the largest source of mortality among avian populations (Ricklefs 1969, Martin 1993, Thompson 2007, Conner et al. 2010). Early avian life stages are particularly vulnerable to predation mortality (O'Conner 1991, Coté and Sutherland 1997). High levels of nest predation can limit avian recruitment and reduce population growth (Cowardin et al. 1985). Because ground-nesting birds are particularly susceptible to nest predation by meso-mammals (Rogers and Heard 2000, Jimenez and Conover 2001), managers are often interested in manipulating this predator community to enhance avian reproduction and population densities (Coté and Sutherland 1997, Ellis-Felege et al. 2012). Manipulation could include numerical changes to predator population size (e.g. removal via trapping) or behavioral changes to modify the functional relationship between prey and predator (Holling 1959). However, the efficacy of predator manipulation is predicated on predation being a limiting factor for the population, that is, the predation limitation hypothesis.

Under the predation limitation hypothesis, a reduction in predation should increase population rate of growth or population metrics such as survival or reproduction. Managers have implemented both indirect and direct techniques, such as habitat alteration and meso-mammal trap and removal (MMTR), to reduce predator numbers and increase avian recruitment (Lokemoen 1984, Jimenez and Conover 2001). Although MMTR is often considered a controversial management tool (Messmer and Rohwer 1996, Ellis-Felege et al. 2010), it is commonly used in gamebird and waterfowl management (Potts 1986, Coté and Sutherland 1997). Seasonal predator removal has been shown to increase nest success above levels necessary for population maintenance in upland nesting ducks (Cowardin et al. 1985, Garrettson and Rohwer 2001, Pieron et al. 2013). Seasonal predation control has also proven effective at increasing brood size, production of young, and subsequent breeding populations of grey partridge *Perdix perdix* and ground-nesting moorland birds (Tapper et al. 1996, Fletcher et al. 2010).

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However, uncertainty surrounds the existence of relationships between meso-mammal activity and northern bobwhite *Colinus virginianus* reproductive success, as well as the efficacy of MMTR as a management tool for improving reproductive success. There is a consensus in the literature regarding the efficacy of predator removal for enhancing bird populations (Coté and Sutherland 1997, Smith et al. 2010); however, the literature is scant for bobwhite in particular – only two studies included in Smith et al. (2010). Predator trapping for bobwhite is a unique case of predator removal because of the diverse predator community that depredate their nests with snakes contributing a significant portion (~29%; Staller et al. 2005). Generally, snakes cannot legally be removed as part of a trapping program potentially reducing or negating its effectiveness through compensation on some sites (Ellis-Felege et al. 2012). However, Palmer et al. (2005) did find a positive effect of meso-mammal predator removal on bobwhite nest success.

Our objectives were to determine the efficacy of MMTR in the context of typical management on properties managed for bobwhite. We hypothesized support for the predation limitation hypothesis as tested through predator removal. We predicted that removal of meso-mammals would increase bobwhite reproductive output. This hypothesis is plausible on these sites because habitat is managed intensively and resources (i.e. food and cover) are not likely limiting bobwhite reproduction (Stribling and Sisson 2009, Burger et al. 1998, Palmer and Wellendorf 2007, Terhune et al. 2007), leaving the possibility of predation as a limiting factor more likely. Furthermore, we were interested in understanding how the residual meso-mammal community (i.e. post-trapping) may impact bobwhites. We hypothesized that MMTR effectively eliminates the numerical relationship between predator abundance and bobwhite reproduction metrics. Under this hypothesis we predict no negative relationship between bobwhite reproduction metrics and predator abundance for trapped sites would exist. This hypothesis is not only novel in the predator trapping literature – as no other authors investigated the effects of residual predators – it has management implications because, if supported, no additional predator removal in these systems is warranted that year as predation is no longer a dominant limiting factor. Lastly, we were interested in evaluating the utility of a commonly used scent-station survey, known as the predator index, as a tool to determine predation pressure of a site.

Material and methods

Study area

We studied the relationships between the predator index, MMTR, and bobwhite reproductive demographics at 11 sites in Florida, Georgia and Alabama during 1999–2006. Sites ranged from 1012 ha to 10 927 ha and averaged 4541 ha (Table 1). All study sites were located in the southeastern Coastal Plain and were privately owned with a long history of bobwhite management. Study sites practiced a consistent management program that included maintaining low basal area timber (e.g. 3–9 m^2 ha^{-1}), two year prescribed fire interval, and other mechanical vegetation treatments including mowing, roller-chopping, seasonal disking, and herbicide application. Supplemental feed was broadcast at a rate of 0.06–0.13 metric tons ha^{-1} on all sites. Tall Timbers and the Red Hills plantations were comprised of 80% loblolly *Pinus taeda*, and shortleaf pine *P. echinata* with associated early-successional ground cover vegetation and longleaf pine *P. palustris* with associated wiregrass *Aristida stricta* ground cover. Harwood hammocks were interspersed throughout the Red Hills study sites and comprised 10% of the area. Annually disked fallow fields ranging from 0.4 to 1.2 ha in size covered the remaining 10% of the study sites (Staller et al. 2005, Ellis-Felege et al. 2012). Georgia sites were dominated by upland pine forests (80%) consisting of loblolly, longleaf, and slash *Pinus elliotti* pine. Ground cover vegetation consisted of bunch grasses (*Andropogon* spp.), wiregrass, blackberry *Rubus* spp., goldenrod *Solidago* spp., partridge pea *Chamaecrista fasciculata* and ragweed *Ambrosia artemisiifolia.* Rotational fallow fields ranging from 0.41–2.43 ha in size were interspersed throughout the study sites and covered the remaining 20% of the area (Terhune et al. 2006, 2010, Sisson et al. 2009). Alabama sites consisted of low density pine forests comprised of shortleaf, longleaf, loblolly and slash pine with associated early successional plant communities, covering approximately 70% of the area. Annually disked fallow fields were scattered throughout the sites and ranged from 0.5–3.0 ha in size covering approximately 16% of the area. The remaining 14% of the area was comprised of thinned hardwood forests (Crouch 2010). Meso-mammal trap and removal using box and leg-hold traps occurred throughout the bobwhite breeding season every year during the study on five sites. Six sites had some or all years during the study when meso-mammal trap and removal did not take place. Combined, there were 37 site–year combinations monitored when MMTR occurred and 20 combinations when it did not occur (Table 1). Typical trap density ranged from one trap per 8 hectares to one trap per 20 hectares. The number of meso-mammals removed was recorded for 12 site–year combinations and ranged from 243–737 and averaged 430 meso-mammals removed annually per site.

Table 1. Study sites where meso-mammal activity indices, bobwhite reproductive demographics, and trap years were monitored in Georgia, Florida and Alabama, USA, 1999–2006.

Site	Size (ha)	Years monitored	Years trapped
Tall Timbers	1619	2000–2006	2004–2006
Red Hills plantation 1	8100	2002–2005	2002–2005
Red Hills plantation 2	1214	2000–2006	2001–2003
Albany plantation 1	8094	1999–2006	1999–2006
Albany plantation 2	1400	2000–2006	2001–2003
Albany plantation 3	1400	2000–2006	2004–2006
Albany plantation 4	4452	1999–2004	1999–2004
Georgia plantation 1	1012	2003–2004	2003–2004
Georgia plantation 2	10 927	2003–2004	2003–2004
Alabama plantation 1	1619	2003–2005	
Alabama plantation 2	10 117	2003–2006	2004–2006

Bobwhite reproductive demographics

We captured bobwhites using funnel traps baited with cracked corn or grain sorghum (Stoddard 1931), in January,

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April, October and November, depending on site. We checked traps each night beginning at sunset and captured bobwhites were aged, sexed, and birds ≥132 g were fitted with 6.0 g necklace-style radio transmitters equipped with mortality switches (American Wildlife Enterprises, Tallahassee, FL, USA) or motion-sensitive switches (Holohil Systems, ON, Canada) (Mueller et al. 1988, Terhune et al. 2007). We released bobwhites at the capture site immediately following the event and radio-handicapping was shown to have not occurred on these study sites (Palmer and Wellendorf 2007, Terhune et al. 2007). Radio-telemetry monitoring for this study was part of a larger effort to track bobwhite demographics across the region. We monitored bobwhite non-breeding season survival from 1 October to 14 April using radio-telemetry ≥3 times per week. We monitored bobwhite reproduction from 15 April to 30 September using radio-telemetry ≥3 times per week to locate nests and determine nest fate. Bobwhites found in identical locations on consecutive days and/or were immobile for consecutive days were assumed to be incubating, thus, nest monitoring only included incubation and occurred daily until success (≥1 egg pips) or failure (Taylor et al. 1999, Ellis-Felege et al. 2012). We found nests early in incubation (~1–3 days from onset) because of frequent telemetry, thus, the number of exposure days were consistent among nests. The number of eggs hatched per successful nest were counted the day of hatch because nests were checked daily and hatch date was identified immediately; therefore, daily nest monitoring ensured accurate data collection of bobwhite reproductive metrics.

Predator index

Scent-station surveys are a widely used method of developing indices of predator activity for a variety of mammalian species (Wood 1959, Linhart and Knowlton 1975, Diefenbach et al. 1994, Ellis-Felege et al. 2010). Bobwhite managers utilize scent-station surveys to estimate activity levels of raccoons *Procyon lotor*, nine-banded armadillos *Dasypus novemcinctus*, Virginia opossums *Didelphis virginiana*, bobcats *Lynx rufus* and foxes *Urocyon cinereoargenteus and Vulpes vulpes*, as these species are bobwhite nest predators (Stoddard 1931, Rollins and Carroll 2001, Staller et al. 2005). Meso-mammal trap and removal occurred during the bobwhite breeding season (April–September) and beginning in October management priorities shift to hunting season preparation (i.e. vegetation manipulation via roller chopping and mowing). Therefore, we conducted surveys in October of each year immediately following bobwhite nesting season and cessation of MMTR. Stations consisted of a 1.0 m diameter area cleared of debris and covered with a mixture of sand and mineral oil to provide a substrate for tracks. A single fatty-acid scent (FAS) tablet was used as a scent lure, placed in the center of the station (Linhart and Knowlton 1975), and replaced if the tablet was removed. The mineral oil is mixed in a bucket with sand to create the tracking substrate prior to the creation of the scent-station. Additional mineral oil is not added to the station after it is created; however, additional sand–oil mixture may be added if deemed necessary. We placed stations along roads or other linear features (e.g. firebreaks) and located approximately 500 meters apart with 30–40 stations per site. Surveys occurred daily for five days unless a rain event occurred during this period. Rain events caused tracks to be unreadable; therefore, additional days were added to the survey to account for survey days lost to rain events. Surveys were conducted by experienced observers capable of accurately identifying meso-mammal tracks. After a station was checked, animal tracks were erased and additional sand was added as needed. The predator index was determined by dividing the total number of target species visitations by the total number of scent-station nights at the end of the survey. For example, 40 scent-stations run for 5 nights would equal 200 operative scent-station nights, thus, 20 target species visitations, would result in a predator index of 0.1.

Model construction

We used generalized linear-mixed models (GLMMs) to evaluate our hypotheses regarding relationships between predator removal and predator activity (i.e. the predator index); and predator removal and bobwhite reproduction metrics. A linear model with a Gaussian error term was used to model the effect of trapping on the predator index. We treated site as a random effect and the effect of trapping as a binary predictor (i.e. yes or no) in all models. We used four bobwhite reproduction metrics as response variables. Nest success, defined as at least one successful egg hatched in nest, was modeled using a logit link with a binomial error term. Nests hen^{-1} was modeled using a log link with a Poisson error term where the number of nests for a respective site was the response variable and the number of hens alive on 15 April was an offset. Our continuous tracking of females allowed us to detect most nests initiated per hen. Similarly, broods hen^{-1} was modeled with the same model structure except the response variable was total number of hatched nests for a respective site. Chicks hen^{-1} was modeled using a linear model with a Gaussian error term where the response variable was derived as the product of the average clutch size for a site and the number of successful nests divided by the number of hens alive on 15 April. Our chicks hen^{-1} metric is analogous to fecundity; however, it includes both male and female chicks. All models were fitted using the lme4 package in program R (R ver. 3.3.1, <www.r-project.org> accessed 15 January 2016).

Hypothesis testing

We fitted models with the effect of trapping in the model and compared it to a null model to test the predation limitation hypothesis. We split the data into two datasets – one with site–year combinations when trapping occurred and one with site–year combinations when trapping did not occur – to test the effect of residual predators. We fitted two models for each of these datasets – one model to test the effect of residual predators (i.e. predator index) and a null model. That is, in each model set, one model had the effect of residual predators and the other had no effect of residual predators. Competing models were constructed using R and evaluated using likelihood ratio tests (LRT) to compare null and alternative models.

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Results

We collected bobwhite reproductive information from a total of 3935 radio-tagged bobwhites ($\bar{x}$ = 69 site^{-1}, SD = 31.37) across 8 years (1999–2006), resulting in 2499 nests ($\bar{x}$ = 44 site^{-1}, SD = 24.11). Nest success ranged from 0.29 to 0.72 among sites and averaged 0.52 (SD = 0.11). The number of nests per hen ranged from 0.22 to 1.92 and averaged 0.71 (SD = 0.32). Broods per hen averaged 0.37 (SD = 0.21) with a range of 0.06 to 1.02 and the number of chicks per hen averaged 4.09 (SD = 2.42) and ranged from 0.42 to 11.52 (Table 2). The mean predator index was 0.13 (range = 0.03–0.38, SD = 0.08) with a species indices proportion of 0.061 raccoons (range = 0–0.27, SD = 0.06), 0.024 nine-banded armadillos (range = 0–0.09, SD = 0.02), 0.017 Virginia opossums (range = 0–0.11, SD = 0.02), 0.021 bobcats (range = 0–0.08, SD = 0.02), and 0.008 foxes (range = 0–0.03, SD = 0.008; Table 3).

Trapping was effective at reducing predator activity. The model containing the trap effect was supported by the LRT (χ^2 = 34.95, df = 1, p < 0.001). The model predicted mean predator index for non-trapped sites was 0.21 (95% CLs: 0.18, 0.24) compared to 0.10 (95% CL: 0.07, 0.13) for trapped sites. The lack of variability surrounding the predator index across trapped sites (residual variance = 0.0023) suggests that trap effort had similar effects on predator activity across sites.

We found support for the predation limitation hypothesis among all bobwhite reproduction metrics. The nest success model containing the trap effect was supported by the LRT (χ^2 = 7.59, df = 1, p = 0.006). Nests were 1.33 times (odds ratio, 95% CL: 1.09, 1.62, β = 0.29 ± 0.10) more likely to be successful on trapped sites than non-trapped sites (Fig. 1). Mean nest success on trapped sites was 0.56 (95% CL: 0.52, 0.59) and mean nest success on non-trapped sites was 0.48 (95% CI: 0.43, 0.53, Fig. 1). The nests hen^{-1} model containing the trap effect was also supported by the LRT (χ^2 = 19.45, df = 1, p < 0.001) – for every 100 hens they produced 14 more nests on trapped sites (β = 0.25, 95% CL: 0.13, 0.37, Fig. 2). The broods hen^{-1} model containing the trap effect was supported by the LRT (χ^2 = 24.81, df = 1, p < 0.001) – for every 100 hens they produced 12 more broods (β = 0.37, 95% CL: 0.21, 0.53, Fig. 3). Lastly, the chicks hen^{-1} model containing the trap effect was supported by the LRT (χ^2 = 4.16, df = 1, p = 0.041) – for every 100 hens they produced 109 more chicks on trapped sites (β = 1.09, 95% CL: 0.07, 2.11, Fig. 4).

We found support for the residual predator hypothesis using the trapped site–year data subset, i.e. our predictions were supported in each case. We found no relationship between residual predators and nest success (β = –0.36, 95% CL: –3.14, 2.42), the hypothesis was not supported over the null model (χ^2 = 0.065, df = 1, p = 0.798; Fig. 5). The nests hen^{-1} model supported our hypothesis even though the null was rejected (χ^2 = 16.04, df = 1, p < 0.001; Fig. 6), because we did not find a negative effect between residual predators and nests hen^{-1} (β = 2.92, 95% CL: 1.52, 4.32). Concomitantly, with broods hen^{-1} our hypothesis was supported (χ^2 = 7.37, df = 1, p = 0.007; Fig. 7), because we did not find a negative effect between residual predators and broods hen^{-1} (β = 2.72, 95% CL: 0.79, 4.64). Furthermore, we did not find a negative effect between residual predators and chicks hen^{-1} among trapped sites (β = 5.56, 95% CL: –8.77, 19.89) and this model was not selected over the null, (χ^2 = 0.605, df = 1, p = 0.437; Fig. 8).

Table 2. Summary statistics of monitored bobwhite metrics among study sites in Georgia, Florida and Alabama, USA, 1999–2006.

Metric	Mean	SD	Minimum	Maximum
Bobwhite nests	43.84	24.11	11.00	108.0
Nest success	0.518	0.109	0.286	0.723
Nests hen^{-1}	0.705	0.316	0.215	1.922
Broods hen^{-1}	0.374	0.207	0.062	1.021
Chicks hen^{-1}	4.092	2.415	0.422	11.52

Table 3. Summary statistics of scent-station surveys among study sites in Georgia, Florida and Alabama, USA, 1999–2006.

Metric	Mean	SD	Minimum	Maximum
Predator index surveys	0.132	0.077	0.030	0.375
Raccoon	0.061	0.061	0.000	0.265
Nine-banded armadillo	0.024	0.019	0.000	0.096
Virginia opossum	0.018	0.020	0.000	0.115
Bobcat	0.021	0.019	0.000	0.085
Fox	0.008	0.008	0.000	0.03

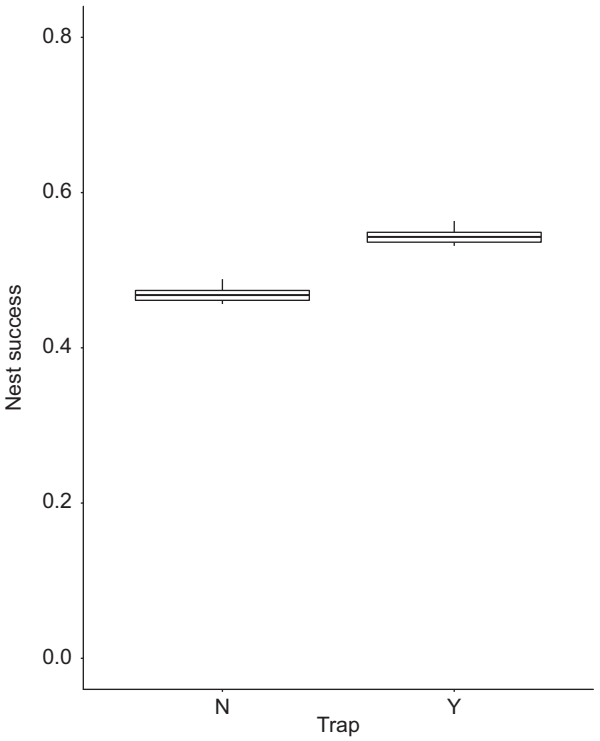


Figure 1. Predicted bobwhite nest success on trapped study sites versus non-trapped study sites in Georgia, Florida and Alabama, USA, 1999–2006. Median nest success value depicted by the center lines of each box plot, 75% upper quartiles represented by the upper bounds of each box, 25% lower quartiles represented by the lower bounds of each box,and associated outliers.

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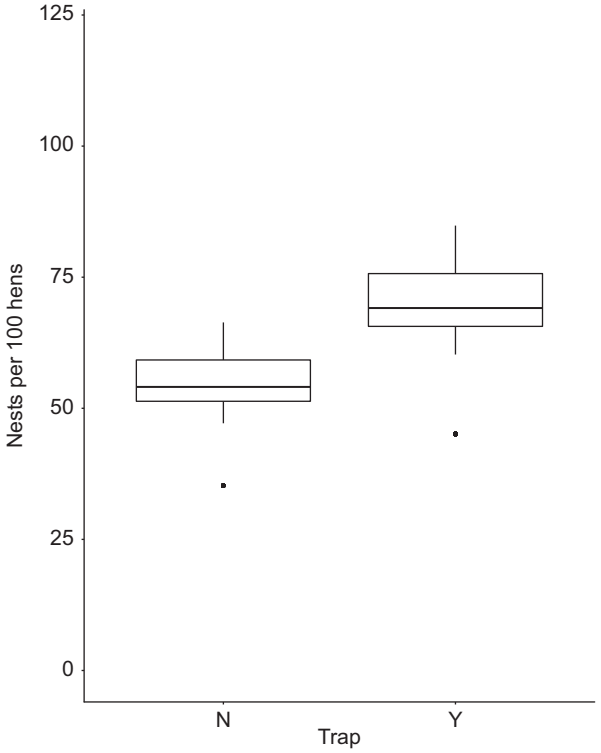


Figure 2. Predicted number of nests per 100 hens on trapped study sites versus non-trapped study sites in Georgia, Florida and Alabama, USA, 1999–2006. Median number of nests per 100 hens depicted by the center lines of each box plot, 75% upper quartiles represented by the upper bounds of each box, 25% lower quartiles represented by the lower bounds of each box, and associated outliers.

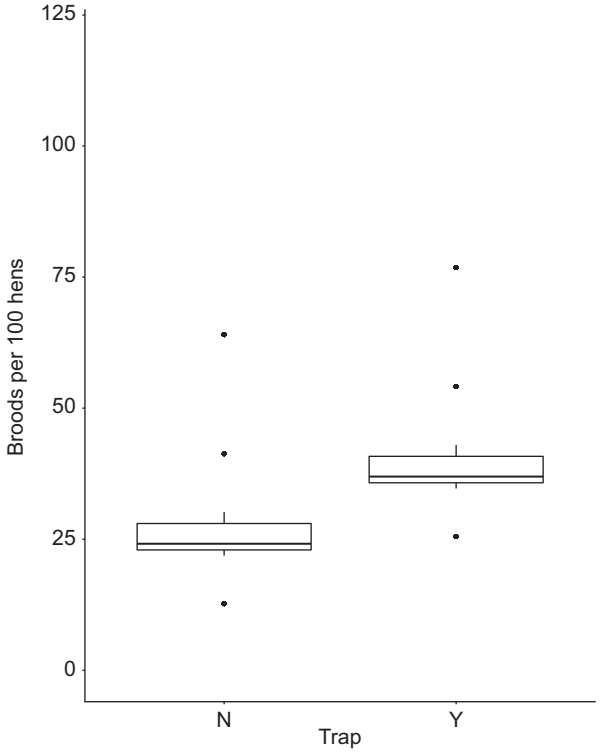


Figure 3. Predicted number of broods per 100 hens on trapped study sites versus non-trapped study sites in Georgia, Florida and Alabama, USA, 1999–2006. Median number of broods per 100 hens is depicted by the center lines of each box plot, 75% upper quartiles represented by the upper bounds of each box, 25% lower quartiles represented by the lower bounds of each box, and associated outliers.

Discussion

We found support that predation limits bobwhite reproduction by reducing nest success, nests hen^{-1}, broods hen^{-1} and chicks hen^{-1}. After controlling for predator removal (i.e. subsetting analysis to only trapped sites), we did not detect a negative relationship between residual predator activity and reproduction suggesting that trapping was effective at reducing predation. We found trapped sites to have a lower average predator index than non-trapped sites, suggesting that MMTR reduces predator activity. Collectively, our results suggest management of meso-predators to improve reproduction is feasible when habitat resources are not deficient, but methods of measuring predator activity need further study.

The predation limitation hypothesis characterizes predation as a limiting factor for prey (e.g. northern bobwhite) populations. Our findings support this hypothesis and are similar to previous studies (Balser et al. 1968, Chesness et al. 1968, Duebbert and Lokemoen 1980, Garrettson and Rohwer 2001), further strengthening the justification and utility of MMTR as a management tool. While nest success alone is a tenuous metric for determining population growth in bobwhite (Etterson et al. 2011, Ellis-Felege et al. 2012), nests hen^{-1}, broods hen^{-1} and chicks hen^{-1} are stronger predictors of reproductive success and population trajectories. Bobwhite population growth is most sensitive to the variation in reproductive demographics (Sandercock 2006, Stahl and Oli 2006); thus, it is reasonable to believe that the increases in reproduction, especially nests hen^{-1}, broods hen^{-1} and chicks hen^{-1}, we observed would lead to population growth. Given that bobwhite populations experience dramatic annual mortality (Stoddard 1931, Rosene 1969, Klimstra and Roseberry 1975, Roseberry and Klimstra 1984, Brennan 1991), increased chick and brood production can help stabilize populations by offsetting local declines due to adult mortality (Sandercock et al. 2008). Increased fecundity (i.e. chicks hen^{-1}) can lead to higher recruitment to the fall, higher fall abundance, and increased breeding densities the following year when overwinter survival remains good (Tapper et al. 1996). In areas where habitat and resources are not limiting, managers can use MMTR to reduce predation pressure and benefit bobwhite productivity.

While MMTR can reduce predation pressure on bobwhite populations, bobwhites and meso-mammals coevolved such that bobwhites themselves, have strategies to mitigate the risk of predation (e.g. cryptic coloration, renesting). However, the loss of apex predators and landscape changes can release and elevate meso-mammal populations to unprecedented levels (Soulé et al. 1988, Crooks and Soulé 1999, Conner and Morris 2015), potentially

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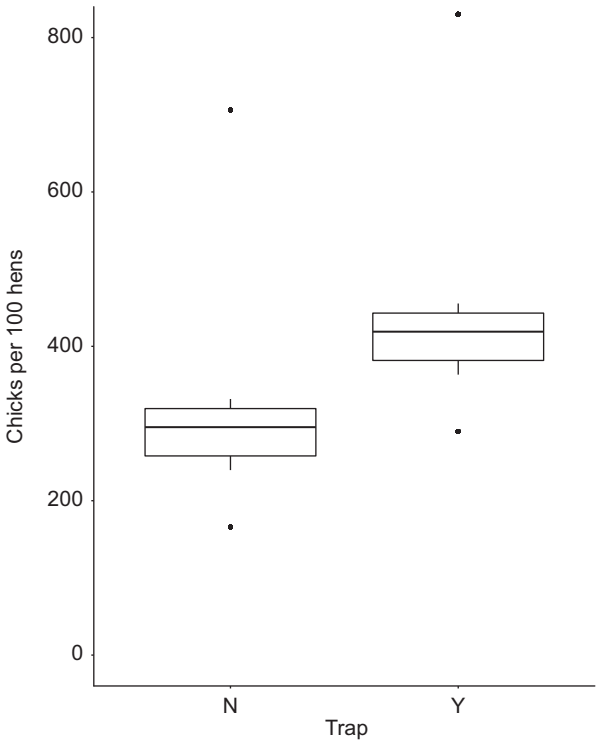


Figure 4. Predicted number of chicks per 100 hens on trapped study sites versus non-trapped study sites in Georgia, Florida and Alabama, USA, 1999–2006. Median number of chicks per 100 hens depicted by the center lines of each box plot, 75% upper quartiles represented by the upper bounds of each box, 25% lower quartiles represented by the lower bounds of each box, and associated outliers.

destabilizing the predator–prey relationship between bobwhites and meso-mammals (Rogers and Heard 2000, Prugh et al. 2009, Conner et al. 2010). Managers focused on promoting bobwhite populations often utilize MMTR to combat perceived negative impacts of elevated meso-mammal populations. However, the goal of MMTR is not to eliminate meso-mammals from a particular site, but rather to reduce them to a level where predation no longer limits reproduction (Ellis-Felege et al. 2010). Meso-mammal trap and removal is effective at reducing meso-mammal populations within a year, but annual implementation is likely required to impede their reestablishment upon cessation of

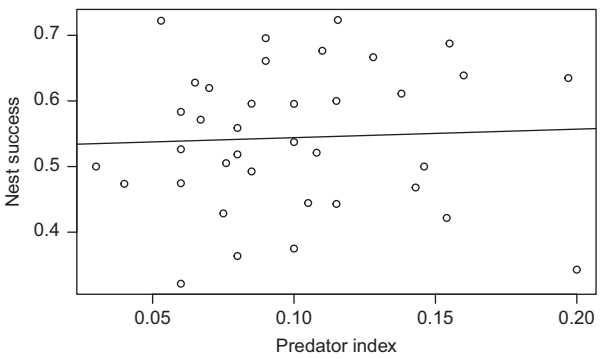


Figure 5. Relationship between nest success and residual predators on trapped study sites in Georgia, Florida and Alabama, USA, 1999–2006.

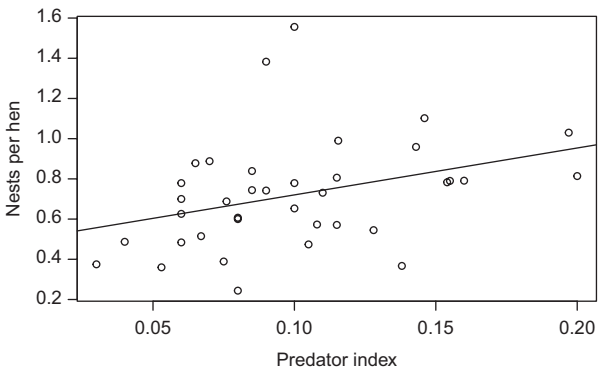


Figure 6. Relationship between nests hen^{-1} and residual predators on trapped study sites in Georgia, Florida and Alabama, USA, 1999–2006.

trapping (Tapper et al. 1996, Ellis-Felege et al. 2010). We demonstrate that MMTR is an effective tool for bobwhite managers, however, it should be used under appropriate conditions within a holistic management regime. That is, MMTR should complement other management actions, as habitat management is fundamental to bobwhite management (Stoddard 1931, Rosene 1969, Brennan 1991).

We found support that trapping reduced meso-mammals to a level that residual predators were not limiting bobwhite reproduction. Thus, the intensity of MMTR in this study was effective at reducing predation pressure within a given year. But, we found positive effects on trapped sites between residual predators and nests hen^{-1}, broods hen^{-1} and chicks hen^{-1}. We postulate that on trapped sites with few residual predators, alternative mechanisms may be driving bobwhite reproductive success. Residual predators may consist primarily of bobcats and foxes, as they may be more wary of novel things in their environment (e.g. traps; Hernandez et al. 1997). Therefore, the positive effects we found between residual predators and bobwhite reproduction may be a result of the predator species remaining on a site post-trapping. Therefore, the effects predicted by our residual predator models could be spurious relationships between residual predators and bobwhite reproduction.

The predator index is an effective tool for monitoring predator activity on a site (Best and Whiting 1990, Diefenbach et al. 1994, Ellis-Felege et al. 2010). We detected differences in the predator index between trapped and

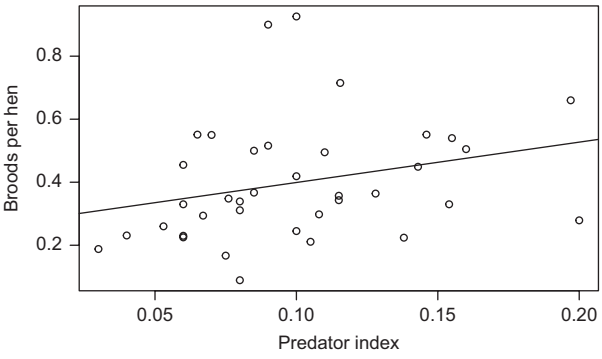


Figure 7. Relationship between broods hen^{-1} and residual predators on trapped study sites in Georgia, Florida and Alabama, USA, 1999–2006.

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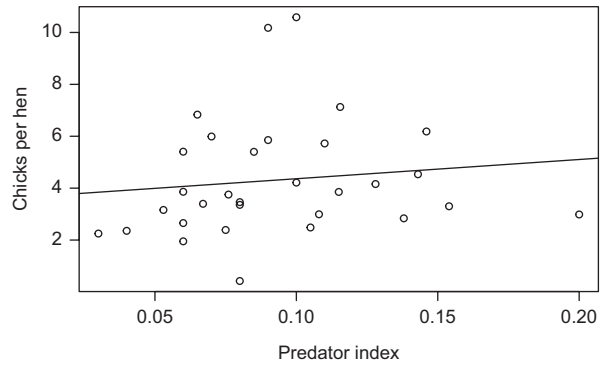


Figure 8. Relationship between chicks hen^{-1} and residual predators on trapped study sites in Georgia, Florida and Alabama, USA, 1999–2006.

non-trapped sites, suggesting it provides value for managers to evaluate the efficacy of trapping programs or determine if predator activity levels warrant trapping. However, the predator index surveys were conducted post-bobwhite breeding season and may not accurately depict actual predator abundance or even predator activity during peak breeding season (Diefenbach et al. 1994). Future studies conducting surveys during the bobwhite breeding season and incorporating detection of meso-predators into the predator index may yield improved estimates and result in stronger predictive power.

While meso-mammal populations impact bobwhite reproduction, the predator index does not account for factors known to impact reproduction. Adult bobwhite survival, for instance, is a critical driver of population performance (Sandercock et al. 2008), and while meso-mammals prey on adults, raptors pose a more significant threat to adult survival (Burger et al. 1998, Rollins and Carroll 2001, Sisson et al. 2009). Similarly, the predator index does not provide a measure of snake activity, which are significant nest predators and known to prey on chicks and adult bobwhites (Stoddard 1931, Staller et al. 2005, Ellis-Felege et al. 2012). Furthermore, heterogeneity in individual fitness, habitat quality, weather, and supplemental feeding can also impact production (Brennan 1991, Doerr and Silvy 2006, Rolland et al. 2011, Tri et al. 2013, Buckley et al. 2015). Therefore, the predator index should be used as a crude predictor of meso-mammal activity and the associated effects differing levels may have on bobwhite reproduction, with the knowledge that additional factors affect overall bobwhite reproductive output and population trajectories.

Our study was conducted on sites with a long history of bobwhite management and maintaining consistently high abundance compared to other areas throughout the range of bobwhites (Stribling and Sisson 2009, Terhune et al. 2007). Therefore, where habitat is limited, meso-mammal populations could be different and the effects of trapping on bobwhite reproduction could be different as well. Furthermore, we only studied the effectiveness of MMTR for a single biological objective – bobwhite reproduction. The impact of MMTR to overall recruitment, population growth rate, and ultimately abundance needs more study to further justify the use and costs of MMTR as a management tool as well as the potential impact on ecosystem health.

Management implications

In areas where habitat is managed intensively and resources (i.e. food and cover) are not likely limited, bobwhite population performance may be limited by meso-mammal predation pressure. As such, managers focused on maximizing bobwhite populations should consider meso-mammal trap and removal as a tool to reduce predation pressure attributed to meso-mammals, especially during habitat restoration phases of management. Given that meso-predators can recolonize rapidly and are capable of high reproduction, annual application of MMTR may be required to mitigate reestablishment of predator communities upon cessation of trapping. We recommend that MMTR programs follow the Best management practices (BMP) trapping guidelines as developed by State wildlife management agencies, The Association of Fish and Wildlife Agencies, and USDA Wildlife Services. Meso-mammal trap and removal should complement other management actions, and be used following or in conjunction with habitat management. The predator index is a simple and easy method for managers to measure meso-mammal activity and can help evaluate the efficacy of trapping programs or determine if trapping is needed. Lastly, the degree to which MMTR will enhance bobwhite recruitment and fall populations, especially in the context of varying spatial arrangements, is unknown and needs further investigation.

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