



## Management and Conservation Article

# Effects of Mesopredators on Nest Survival of Shrub-Nesting Songbirds

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**ABSTRACT** Although nest predation is often the single largest source of mortality in avian populations, manipulative studies to determine predator impacts on nest survival are rare, particularly studies that examine impacts of mid-size mammalian predators (hereafter, mesopredators) on nest survival of shrub-nesting birds. We quantified nest survival and identified nest predators of shrub-nesting songbirds within 4 large (approx. 40-ha) exclosures and 4 control sites within a longleaf pine (*Pinus palustris*) ecosystem. During 2003–2006, we located and monitored 535 shrub nests (222 with videography) for 4,804 nest-days to quantify daily nest survival and document predation events. We found no support for a treatment effect, suggesting mesopredators had little impact on daily nest survival (0.9303 in controls and 0.9260 in exclosures) of shrub-nesting songbirds. For the 5 most commonly monitored species, daily nest survival within species was constant. Our analysis suggested that shrub nests were most vulnerable during the nestling stage and presence of cameras on nests increased survival with the increase in survival being more pronounced during the incubation stage. We filmed 107 nest predation events, identifying predators at 88 nests. Of these 88 nests, snakes caused 33%, red imported fire ants (hereafter fire ants, *Solenopsis invicta*) 28%, raptors 17%, corvids 8%, mesopredators 6%, and small mammals 8% of nest predations. Cause-specific nest predation in controls and exclosures did not differ from expectation, providing evidence that compensatory predation did not occur. Nest predators differed from expectation with regard to nest stage; fire ants and raptors only depredated nests during the nestling stage. Presence of cameras had no effect on nest abandonment. Fire ants were the most prevalent nest predator, and nest predation by fire ants was only observed on nestlings, potentially reducing likelihood of re-nesting. Magnitude and timing of fire ant predation suggests that fire ants may be the most influential nest predator of shrub-nesting birds within the longleaf pine ecosystem. Our data suggest that controlling mesopredators will have no effect on nest success of shrub-nesting birds within longleaf pine forests.

**KEY WORDS** avian productivity, longleaf pine ecosystem, mesomammal, nest success, *Pinus palustris*, predator control, predator exclosure, red imported fire ant, shrub-nesting bird, *Solenopsis invicta*.

Nest predation is often the single largest source of mortality in songbirds (Ricklefs 1969, Martin 1993, Schmidt and Whelan 1999, Heske et al. 2001, Thompson 2007). However, studies that experimentally manipulate predator populations to assess predator impacts on songbird nest survival are rare (Dion et al. 1999, Fontaine and Martin 2006, White et al. 2008) relative to studies measuring habitat effects on songbird nest survival (Filliater et al. 1994, Moorman et al. 2002) or identifying nest predators (Picman and Schriml 1994, Pietz and Granfors 2000, Thompson and Burhans 2003). In contrast, studies that manipulated predator populations to evaluate predator effects on game bird nest survival are relatively common, with most finding positive effects (Tapper et al. 1996, Garrettson and Rohwer 2001). As a result, predator control is sometimes considered as a viable option for enhancing game bird populations (Tapper et al. 1996, Rollins and Carroll 2001, Pearse and Ratti 2004, West and Messmer 2004, Staller et al. 2005).

When assessing potential impacts of lethal predator control on songbird nest survival, it is tempting to extrapolate results from game bird studies to songbirds. However, empirical studies suggest that a greater diversity of predator species prey on songbird nests than on game birds (Soderstrom et al. 1998, Dion et al. 2000). This is likely because most songbirds are smaller than game birds, have altricial instead of precocial nestlings, and have eggs that are much smaller than game bird eggs. Thus, the same predators that impact game birds can

depredate songbird nests, but songbird nests can additionally experience significant depredation from small mammals (Ettel et al. 1998, Dion et al. 1999, Drever et al. 2000). Therefore, generalizing game bird response to predator control to songbirds should be avoided because predator control can lead to complex trophic interactions (Courchamp et al. 1999), resulting in deleterious effects on songbirds. Such deleterious effects may be particularly pronounced if control of large predators leads to an increase in smaller predators that prey on songbird nests, such as predicted by the mesopredator release hypothesis (Rogers and Caro 1998, Courchamp et al. 1999, Crooks and Soulé 1999).

Because studies of the effects of mid-sized mammalian predators (hereafter, mesopredators) on nest survival of songbirds are rare (Heske et al. 2001), we initiated an experiment to address this topic. Specifically, we were interested in determining if mesopredators had any effect, either positive through suppression of smaller predators or negative via direct nest predation, on nest survival of songbirds. We chose to exclude mesopredators because these species can be operationally harvested and are often targeted for predator control in this region. Further, all are known nest predators. We chose to measure nest survival of shrub-nesting songbirds because we assumed that tree-nesting songbirds would be less susceptible to mesopredators and less susceptible to the smaller predators that may be suppressed by mesopredators (e.g., cotton rats, *Sigmodon hispidus*), because shrub-nesting songbird nests would be available to the same suite of nest predators (i.e., all are

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altricial and have about the same length of exposure to predators, and all nests were within 2 m of the ground surface), because tree-nests would have been more difficult to monitor, and because nest density of ground-nesting songbirds on our study area was deemed insufficient to meet perceived sample sizes within available study plots. Our primary objective was to quantify daily nest survival and identify nest predators of shrub-nesting songbirds in areas where mesopredators were excluded and in control areas with no restrictions on mesopredator movements. Although we focused on quantifying mesopredator impacts on shrub-nesting birds in general, we also quantified effects of mesopredators on the most commonly encountered shrub-nesting species.

From the onset of our study, we understood that there were 3 possible responses of songbird nest survival to reduction of mesopredator populations. First, songbird nest survival may increase; greater nest survival within mesopredator exclosures relative to controls would be interpreted as evidence for this response. This result would suggest that predator control may be a viable option for managing songbird populations. Second, mesopredator reduction could result in decreased nest survival in songbirds, suggesting that complex trophic interactions were occurring (Courchamp et al. 1999); lower nest survival within mesopredator exclosures relative to controls would provide evidence for this response. Under this scenario, mesopredator reductions would clearly be ill-advised for songbirds, and the deleterious effects of mesopredator removal on songbird nest survival should be considered when contemplating mesopredator reduction with the objective of benefiting other species. Finally, mesopredator reduction may have no effect, either positive or negative, on songbird nest survival for 1 of 2 reasons: 1) because mesopredators are ecologically unimportant relative to songbird nest survival or 2) nest predation by mesopredators may be compensatory in nature (Crabtree and Wolfe 1988, Greenwood et al. 1998, Jones et al. 2002). Support for a compensatory predation hypothesis would be warranted if nest survival did not vary between mesopredator exclusion and control sites and if mesopredators are significant nest predators in control sites but not in exclusion sites; otherwise, the evidence would favor the hypothesis that mesopredators are biologically insignificant predators of songbird nests and that no complex trophic interactions between mesopredators and songbird nest survival were occurring.

## STUDY AREA

Our research took place on Ichauway, the 12,000-ha outdoor research site of the Joseph W. Jones Ecological Research Center in Baker County, Georgia, USA. The site included approximately 7,250 ha of longleaf pine stands (*Pinus palustris*). Other forest types included slash (*Pinus elliottii*) and loblolly pine (*Pinus taeda*) forests, mixed pine and hardwood forests, lowland hardwood hammocks, oak barrens, and cypress-gum (*Taxodium ascendens*-*Nyssa biflora*) limesink ponds (Boring 2001). Upland sites were subject to prescribed burns on an approximate 2-year

rotation. This burn regime resulted in a relatively sparse mid-story, and kept hardwoods, primarily oaks (*Quercus* spp.), largely restricted to the shrub layer (i.e., ht <2 m); as a result, various upland oak species were the most common species used for nesting (approx. 60%) by the birds we studied. Ichauway was surrounded almost exclusively by center-pivot irrigated agricultural land. We chose 8 sites, each approximately 40 ha, to serve as study plots. All study plots were dominated by longleaf pine in the overstory and native groundcover in the understory. We randomly assigned 4 of these plots to receive mesopredator exclusion.

## METHODS

At sites chosen for mesopredator exclusion, we constructed a woven-wire (10 × 20-cm mesh) fence with electric wire attached to E2000 electrical fence chargers (Twin Mountain Fence Company, San Angelo, TX) along the top, middle, and bottom to deter mesopredators from climbing or digging under fences. We left the remaining 4 plots unfenced to serve as controls. At the onset of the study we trapped mammalian predators from within exclosures using a combination of soft-catch (Woodstream Corp., Lititz, PA) and cage (Tomahawk Live Trap Company, Tomahawk, WI) traps. We relocated captured animals just outside of the exclosure in which the animal was captured. Mesopredators targeted for capture included raccoons (*Procyon lotor*), Virginia opossums (*Didelphis virginiana*), striped skunks (*Mephitis mephitis*), gray foxes (*Urocyon cinereoargenteus*), red foxes (*Vulpes vulpes*), coyotes (*Canis latrans*), and bobcats (*Lynx rufus*). To further reduce impacts of mesopredators on nest success, we trapped each exclosure annually during February–April to remove any mesopredators that may have been able to breach the fence. We monitored fences twice weekly for dig-ins and to ensure that the electric wires were functioning.

We used thermal camera surveys (Boonstra et al. 1994) and track counts (Frey et al. 2003) to monitor mesopredator relative abundance within exclosures and control sites. Track-count stations consisted of 5 1 × 2-m areas along the inside edge of exclosures and along the roads serving as boundaries of control sites. We raked stations clean on day 1 and then checked for tracks the following day. We identified any tracks to species and recorded them. Similar to Kuehl and Clark (2002), we did not use an olfactory attractant that may have provided a reward to condition predators to the area; we also used no visual attractant beyond that provided by the disturbed soil. We conducted nighttime thermal camera surveys from roads surrounding exclosure and control sites. We mounted a PALM IR 250 thermal imager (Raytheon, Waltham, MA) in a research vehicle, then drove at approximately 15 km/hour around each plot and recorded the number of mesopredators observed within study. We sampled each plot 3 times/calendar season using both track counts and the thermal imager during 2004–2006.

We searched for nests annually 2003–2006 between 15 April and 15 August. We searched each plot weekly by walking parallel transects with approximately 10 m between transects. We also located nests opportunistically while

monitoring other nests. After locating a nest, we monitored the nest every 3–4 days initially, and then every 2–3 days within a week of the estimated fledging date. Observers minimized disturbance while searching for and monitoring nests by spending the least amount of time possible at a nest, by not approaching a nest if corvids or cowbirds were detected near a nest, by avoiding creation of dead-end trails (i.e., researchers checked a nest and continued walking past the nest), and by using different access routes to the nest on each visit (Ralph et al. 1993). We assigned a number to each nest and recorded bird species and number of eggs or nestlings. We considered a nest as successful if one or more birds successfully fledged. We considered a nest as having fledged if we videotaped young leaving the nest, we saw fledglings near the nest, or if we discovered a monitored nest empty with no sign of predation following estimated fledging date. In the latter case, we assumed the nest fledged because of our frequent monitoring (<3-day interval) near the anticipated fledge date and because snakes were the primary nest predator capable of depredating the nest at this stage without leaving evidence of predation (i.e., snake predation would be the only predation event that we could confuse with fledging). Fire ants (*Solenopsis invicta*) depredated nests following hatching, but these predations were easily detected; in fact, Staller et al. (2005) reported 100% correct identification of fire ant predation on nests. Further, nest videography suggested that snake predations within 3 days of anticipated fledging occurred only in 4 of the 111 nests monitored to this stage or until fledging. We considered nests as preyed upon if we videotaped a predation event, if nest contents were missing or destroyed prior to fledging date, or if there was otherwise evidence of predation (e.g., feathers in vicinity of nest, fire ants in nest, nestling–parent remains, etc.).

We attempted to monitor 10 nests at any given time using time-lapse videography (Thompson et al. 1999, Pietz and Granfors 2000). Nests monitored using videography had an infrared illuminated camera 0.5–1.0 m from the nest such that there was an unobstructed view of the nest. The video recorder was placed approximately 20–25 m from the nest to minimize observer disturbance to nesting birds. We returned daily to retrieve videotapes for later viewing. We filmed video-monitored nests continuously until they fledged, were abandoned, or were depredated. We identified nest predators to species when possible and then grouped them into corvids, raptors, small mammals, mesopredators, snakes, and fire ants for further analyses.

To determine if mesopredator exclosures were effective at excluding predators of interest, we combined all predator encounters using both track counts and thermal imaging data. We then tested the null hypothesis that frequency of observed predator encounters was equal to expected values using a chi-square goodness-of-fit test (Sokal and Rohlf 1981). Because we maintained equal sampling intensity within exclosures and controls, we assumed that predator detection would occur with equal probability within exclosures and controls if predator use was the same in each. Thus, we used half of the total number of

**Table 1.** A priori models explaining the effects of treatment (predator exclusion or control), nest stage (incubation or nestlings), camera monitoring (video camera present or absent), and year on daily nest survival of shrub-nesting songbirds at the Joseph W. Jones Ecological Research Center, southwestern Georgia, USA, 2003–2006. The number of predictor variables ( $K$ ) in each model included the intercept term. Models with lower second order Akaike’s Information Criterion difference ( $\Delta AIC_c$ ) and greater Akaike weight ( $w_i$ ) were more supported by data. Seventeen models with  $w_i \leq 0.00001$  are not reported. We performed analyses using 4,804 nest days.

Model	$K$	$\Delta AIC_c$	$w_i$
Treatment, nest stage, camera, treatment $\times$ nest stage, treatment $\times$ camera, nest stage $\times$ camera, and yr	10	0.0	0.56393
Nest stage, camera, nest stage $\times$ camera, and yr	7	0.5189	0.43506
Nest stage, camera, and yr	6	14.2650	0.00045
Treatment, nest stage, camera, and yr	7	15.7913	0.00021
Camera and yr	5	15.9495	0.00019
Treatment, camera, and yr	6	17.5200	0.00009
Treatment, camera, yr, treatment $\times$ camera	7	18.1396	0.00006

mesopredator encounters as our expected values for both exclosure and control sites.

We partitioned nests into incubation and nestling stages to determine if nest stage affected daily nest survival and to determine if nest stage interacted with mesopredator treatment to affect nest survival. We analyzed daily nest survival as a function of treatment, nest stage, year, and camera presence using the logistic exposure method developed by Shaffer (2004) utilizing PROC GENMOD (SAS Institute Inc., Cary, NC). We developed 24 a priori models to describe daily nest survival (Table 1), and used the second-order Akaike’s Information Criterion ( $AIC_c$ ) to identify the most parsimonious model and to predict variable importance (Burnham and Anderson 2002). These models represented all single-predictor models using treatment (predator exclosure or control), nest stage (eggs or nestlings), and camera (present or absent). We also included all additive combinations of these variables along with all 2-way interactions. Finally, we included year sampled as a predictor and considered all additive combinations of year sampled with other predictors. We did not construct interaction terms with year; rather, we treated year as a blocking factor in an attempt to better quantify treatment, nest stage, and camera effects. Because a well-fit global model suggests that any subset of variables with a lower  $AIC_c$  than the global model will also fit the data (Burnham and Anderson 2002), we used a Hosmer and Lemeshow (2000) test to evaluate goodness-of-fit for the global model. This test involves grouping predicted probabilities into deciles and comparing observed and expected values using a chi-square test. We considered the model with the lowest  $AIC_c$  to be the best model, but considered all models with  $AIC_c < 2.0$  units (i.e.,  $\Delta AIC_c < 2.0$ ) from the best model as the best set of approximating models. We calculated Akaike weights ( $w_i$ ) for each model as an estimate of the probability of the model being the best model of the a priori set. We then developed variable weights by summing model weights for all models

containing the variable. We combined all nests for our primary modeling efforts, but we also developed models of species-specific daily nest survival for species having  $\geq 20$  nests sampled.

We used model averaging to calculate parameter estimates and unconditional standard errors (Burnham and Anderson 2002). We considered predictors useful based on their weight and based on whether or not the 95% confidence interval of the parameter estimate contained zero. Thus, for a predictor to be considered important, it must have high variable weight and a slope that demonstrably differs from zero (Miles et al. 2006, Miller and Conner 2007).

We compared observed frequency of predation within exclosures and controls for identified nest predators to their expected frequencies using a chi-square goodness-of-fit test (Sokal and Rohlf 1981). We calculated expected frequencies by summing the number of nest days monitored using videography in exclosures and controls and calculating the proportion of nest days monitored with videography in each. We then calculated the expected frequency of cause-specific predation by multiplying the number of nest predations by a given predator by these proportions. We performed a similar analysis to determine if cause-specific predation occurred as expected relative to nest stage (incubation or nestling). In the latter analysis, we calculated expected cause-specific predations based on the proportion of video-monitored nest days in incubation and nestling stages as in Liebezeit and George (2002). We used a chi-square test of independence (Sokal and Rohlf 1981; PROC FREQ, SAS Institute Inc.) to determine if nest abandonment was independent of whether or not the nest was monitored using videography.

Because they are common in the literature and easily understood, we provided Mayfield (1975) estimates of nest success, daily nest survival, and the 95% confidence interval for daily nest survival (Johnson 1979) for both mesopredator exclusion and control sites. To calculate Mayfield (1975) estimates of nest success, we assumed that successful nests were exposed to predation for 26 days (i.e., time from first egg to fledge is 26 days following) and raised the estimate of daily nest success to the 26th power (Baicich and Harrison 1997, Twedt et al. 2001).

## RESULTS

We removed 56 Virginia opossums, 9 raccoons, 3 striped skunks, 2 bobcats, and 2 gray foxes from within exclosures. Of these removals, 49% occurred at the onset of the study. We removed remaining animals during annual trapping efforts prior to nesting season. Of those captures following the initial removal, all but 2 (one bobcat and one striped skunk) were Virginia opossums. Our monitoring suggested that mesopredator use of exclosures was less than in controls ( $\chi^2 = 33.33$ ,  $df = 1$ ,  $P < 0.001$ ), with 44 mesopredator detections (25 raccoons, 7 opossums, 9 bobcats, and 3 coyotes) in controls and only 4 detections (one raccoon, one opossum, one bobcat, and one coyote) in exclosures between 13 July 2004 and 31 July 2006.

During the avian nesting seasons of 2003–2006, we located 535 active nests and monitored them for 4,804 nest

**Table 2.** Model-averaged parameter estimates, their unconditional standard errors, and 95% confidence intervals for parameters used to predict daily nest survival of shrub-nesting songbirds during the 2003–2006 nesting seasons in southwestern Georgia, USA. Reference categories with parameter estimates of zero are not presented.

Effect	Coeff.	SE	95% CI
Intercept	3.398	0.241	2.916 to 3.880*
Treatment (control)	0.268	0.283	-0.299 to 0.834
Stage (eggs)	0.562	0.251	0.060 to 1.064*
Camera (absent)	-0.464	0.220	-0.905 to -0.024*
Yr (2003)	-0.581	0.190	-0.961 to -0.201*
Yr (2004)	-0.920	0.181	-1.282 to -0.557*
Yr (2005)	-0.827	0.169	-1.165 to -0.489*
Treatment $\times$ Stage (control, egg stage)	-0.293	0.315	-0.923 to 0.336
Treatment $\times$ Camera (control, no camera)	-0.074	0.174	-0.423 to 0.275
Stage $\times$ Camera (egg stage, no camera)	-0.936	0.245	-1.425 to -0.446*

\* Indicates 95% CI does not contain zero.

days. Our global model predicting daily nest survival suggested that the model satisfactorily fit the data ( $\chi^2 = 4.04$ ,  $df = 8$ ,  $P = 0.85$ ). The global model was the best model of the a priori set ( $w_i = 0.5639$ ; Table 1), but it was only slightly better than the model containing nest stage, camera, year, and the nest stage  $\times$  camera interaction ( $w_i = 0.4351$ ). There was virtually no support for remaining models ( $\Delta AIC_c > 14$  in all cases). Model-averaged parameter estimates suggested that intercept, nest stage, camera, nest stage  $\times$  camera interaction, and year had parameter estimates that did not include zero in the 95% confidence interval (Table 2); thus, these were the only variables useful for predicting daily nest survival.

We positively identified 16 species of shrub-nesting birds, but only 5 species (northern cardinals [*Cardinalis cardinalis*], eastern towhees [*Pipilo erythrophthalmus*], brown thrashers [*Toxostoma rufum*], blue grossbeaks [*Guiraca caerulea*], and indigo buntings [*Passerina cyanea*]) had a sufficient number of nests ( $>20$ ) monitored to warrant analysis of nest survival at the species level. Although the best predictive model varied by species, the only predictor in any model with a parameter estimate that did not contain zero in the 95% confidence interval was the intercept term. Thus, daily nest survival for these 5 species taken individually was constant. Mayfield estimates of daily nest survival and associated confidence intervals further corroborate a lack of impact of mesopredator presence on nest survival (Table 3).

We monitored 222 nests using time-lapse videography and filmed 107 predation events. Predators of 19 nests (11 in controls, 8 in exclosures) could not be identified because of technical difficulties (e.g., predation event moved the camera, camera failure prior to predation event, disturbance due to weather, etc.). Snakes were responsible for 29 (15 in controls, 14 in exclosures), fire ants for 25 (10 in controls, 15 in exclosures), raptors for 12 (6 in controls, 6 in exclosures), corvids for 10 (4 in controls, 6 in exclosures), mesopredators for 5 (all in controls), and small mammals for 7 (3 in controls, 4 in exclosures) of the 88 identified nest predations. Because small mammals and mesopredators

**Table 3.** Mayfield nest success estimates (S), daily nest survival (DNS), and associated 95% confidence intervals for shrub-nesting songbirds in a longleaf pine ecosystem in southwestern Georgia, 2003–2006.

Species	Treatment <sup>a</sup>	N <sup>b</sup>	Nest days	Failed nests	Lower CI	DNS	Upper CI	S
All	Control	323	2,898	202	0.921	0.930	0.940	0.153
	Exclosure	212	1,906	141	0.914	0.926	0.938	0.134
Northern cardinal	Control	105	1,071	58	0.932	0.946	0.960	0.235
	Exclosure	77	773	47	0.922	0.939	0.956	0.196
Brown thrasher	Control	25	214	17	0.884	0.921	0.957	0.116
	Exclosure	21	183	16	0.872	0.913	0.954	0.093
Eastern towhee	Control	57	547	33	0.920	0.940	0.960	0.199
	Exclosure	16	147	9	0.900	0.939	0.978	0.194
Blue grosbeak	Control	22	301	5	0.969	0.983	0.998	0.647
	Exclosure	16	186	10	0.914	0.946	0.979	0.237
Indigo bunting	Control	14	165	11	0.895	0.933	0.971	0.166
	Exclosure	11	120	6	0.911	0.950	0.989	0.264

<sup>a</sup> Exclosure = mesopredator exclusion treatment, Control = no predator exclusion.

<sup>b</sup> N = no. of nests monitored.

rarely depredated nests, we combined their observed and expected frequencies for the goodness-of-fit test to determine if nest predators depredated nests as expected relative to exclosures and controls. Cause-specific nest predations in controls and exclosures did not differ from expectation ( $\chi^2 = 7.70$ ,  $df = 11$ ,  $P = 0.766$ ), despite the observation that mesopredators only preyed on nests in control sites.

In our analysis of cause-specific predation relative to nest stage, snakes were responsible for 29 (9 during incubation and 20 during nestling), fire ants for 25 (all during nestling), raptors for 12 (all during nestling), corvids for 10 (3 during incubation, 7 during nestling), mesopredators for 5 (4 during incubation, one during nestling), and small mammals for 7 (4 during incubation and 3 during nestling) of 88 identified nest predations. As in the previous analysis, we combined small mammals and mesopredators for the goodness-of-fit test to determine if nest predators depredated nests as expected relative to incubation and nesting stages. Cause-specific nest predations differed from expectation with regard to nest stage ( $\chi^2 = 53.84$ ,  $df = 11$ ,  $P < 0.001$ ), largely because fire ants and raptors only preyed on nests during the nestling stage.

Of 57 nests that we classified as abandoned, we monitored 20 using time-lapse videography. Nest abandonment was independent ( $\chi^2 = 1.14$ ,  $df = 1$ ,  $P = 0.28$ ) of whether or not we monitored nests using videography. Moreover, 10 video-monitored nests were abandoned following  $\geq 5$  days of monitoring, providing evidence that initial placement of cameras did not cause abandonment.

## DISCUSSION

Our study represents one of the few studies to experimentally manipulate mesopredator populations while monitoring effects on songbird nest survival. Our data suggest that mesopredators have little impact, either positive or negative, on nest survival of songbirds. If we double the number of nests depredated by mesopredators to compensate for our mesopredator exclosure treatment, we would expect mesopredators to depredate approximately 11% of nest, having similar impact as small mammals, corvids, and raptors and less than half the impact of either snakes or fire ants.

Our study relied on our ability to greatly reduce mesopredator use in our exclosures; we suggest this was accomplished but with occasional mesopredator trespass. We attributed most mesopredator trespass to fence failures associated with storm events (e.g., tree across fence, power outage, etc.) or to small Virginia opossums passing through the fence mesh. We suggest that our annual trapping efforts were effective in removing these animals prior to nesting season each year. Indeed, our data indicate that exclosures reduced mesopredator abundance well below that of controls and below that reported in many predator control studies. For example, Frey et al. (2003) reported that they annually removed 50–75% of the mesopredators on their study plots and that the number of animals removed annually did not decline, suggesting that lethally removed predators were replaced annually by immigration or recruitment. Meckstroth and Miles (2005) indicated that monthly removal of mesopredators resulted in almost no detectable difference in mesopredator abundance relative to control sites. Chessness et al. (1968), Marcstrom et al. (1988), Harding et al. (2001), and Pearse and Ratti (2004) reported little decline in predators removed from year to year on their study sites, suggesting that recolonization to pre-trapping levels occurred annually. Garretson and Rohwer (2001) also removed predators and reported that number of predators removed remained relatively constant from year to year and number of predators on removal and control sites did not differ during the second year of the study, indicating any long-term reduction in predator numbers did not occur.

Our nest survival estimates were within the range of studies reported elsewhere. Twedt et al. (2001) reported daily nest survival rates of 0.91–0.95 for a number of passerines in Louisiana forests. Similarly, Rodewald (2002) reported daily survival rates ranging from 0.92 to 0.99. Filliater et al. (1994) studied northern cardinals and reported a daily nest survival rate associated with incubation and nestling stages of 0.939, which is very similar to our estimates for this species. Nolan (1963) reported that apparent nest success averaged 21.2% for 11 species nesting in a deciduous scrub habitat in Indiana. Although this is slightly greater than our Mayfield estimates, estimates of apparent nest success are often greater than

estimates derived by extrapolating daily survival rates (Jehle et al. 2004).

Others indicated that mesopredators seldom depredate nests of songbirds (Liebezeit and George 2002, Moorman et al. 2002, Stake and Cimprich 2003). However, complex trophic interactions have been hypothesized (Rogers and Caro 1998, Courchamp et al. 1999, Rogers and Heard 2000), suggesting that removal or exclusion of mesopredators may have unintended consequences. Our data suggest that daily nest survival was not affected by excluding mesopredators. In fact, nest survival rates actually were slightly lower in exclosures than in controls. Therefore, we suggest that mesopredators had little direct or indirect effect on nest survival of shrub-nesting birds on our study site. Moreover, because cause-specific nest predation did not differ between treatment and control sites, compensatory predation (Crabtree and Wolfe 1988, Greenwood et al. 1998, Jones et al. 2002) did not occur.

Lower daily survival rates of nestlings have been attributed to increased adult activity associated with caring for nestlings (Skutch 1949, Martin et al. 2000). However, Martin et al. (2000) point out that lower nestling survival relative to incubation is often observed because of poor nest site selection. During our study, we found daily nest survival during the nestling stage to be lower than during the incubation stage. However, we suggest that decreased nest survival during the nestling stage is best explained by additional predation from fire ants and raptors during this stage, because prior to hatching, nests were not depredated by these predators.

Similar to Stake and Cimprich (2003), we found no evidence that presence of video cameras affected the probability of nest abandonment; rather, we observed that presence of cameras increased daily nest survival, with the increase being more pronounced during the incubation stage. In the absence of videography, nest predators are often misidentified (Pietz and Granfors 2000, Staller et al. 2005); therefore, we did not attempt to identify nest predators unless video cameras were present. Thus, we could not determine if presence of cameras simply affected overall nest predation rates or if they also affected the ratio of predator species that depredated nests. As a result, we do not know if video-monitored and non-video-monitored nests were depredated by similar predator communities. However, we suggest that mesopredators were not selectively avoiding video-monitored nests and that our conclusions regarding mesopredator impact on nest survival are warranted because nest survival of video-monitored nests was no greater in controls than in exclosures (i.e., there was no evidence of a camera  $\times$  treatment effect).

Our results suggest that shrub-nesting songbirds are less impacted by mesopredators than reported for game birds (see reviews in Coté and Sutherland 1997, Heske et al. 2001), because we rarely observed mesopredators to prey on eggs or nestlings of shrub-nesting birds. These data are in agreement with a separate study on our site in which we collected videography on 41 nest predation events on shrub-nesting birds (L. M. Conner, Joseph W. Jones Ecological

Research Center, unpublished data) and observed only one mesopredator (a raccoon) destroying a nest.

Snakes are well documented as nest predators (Thompson and Burhans 2003, Staller et al. 2005), and we expected snake predation during our study. Thompson and Burhans (2003) observed snakes to be the dominant nest predator during their study, and they videotaped 5 different species of snakes depredating nests. Although we combined all snake species in our analyses, we positively identified at least 5 species of snakes (gray rat snakes [*Elaphe spiloides*], red rat snakes [*Elaphe guttata*], eastern kingsnakes [*Lampropeltis getula*], black racers [*Coluber constrictor*], and eastern coachwhips [*Masticophis flagellum*]) and at least one unknown species depredating nests. If we partition snake predations by snake species, fire ants become the primary nest predator of shrub-nesting songbirds on our study site. Stake and Cimprich (2003) also reported snakes as the most common predator of black-capped vireo (*Vireo atricapillus*) nests in Texas. However, during their study only 2 snake species were identified. If snake predation had been partitioned by species, fire ants would have had the same impact on black-capped vireo nests as the top snake predator (Stake and Cimprich 2003).

Fire ant predation of bird nests is commonly reported in studies of nest survival within the fire ant's geographical range (Allen et al. 2004). Nest losses to fire ants can be great; for example, fire ants were responsible for 58% of nest predations in Mississippi cottonwood (*Populus deltoides*) plantations (Twedt et al. 2001). Similar to Stake and Cimprich (2003), we did not observe fire ants depredating intact eggs. However, Staller et al. (2005) observed fire ants forming a mound over northern bobwhite (*Colinus virginianus*) nests. Thus, timing of nest susceptibility to fire ant predation apparently differs between shrub- and ground-nesting species; ground-nesters are more susceptible during incubation, whereas shrub-nesters are more vulnerable during the nestling stage.

Adult birds that lose nests late in the nesting cycle are less likely to renest than birds losing nests early in the nesting cycle (Montgomerie and Weatherhead 1988). Because fire ants were responsible for more nest losses than any other nest predator species and because they destroyed nests later in the nesting cycle, we suggest that fire ants are the most significant nest predator of shrub-nesting birds in our study system. However, it is unknown whether or not magnitude of fire ant predation actually results in a population level response in any of the bird species monitored.

## MANAGEMENT IMPLICATIONS

Our data suggest that mesopredator control had no effect, either positive or negative, on shrub-nesting birds. Therefore, control of mesopredators is not likely to benefit shrub-nesting birds in this system. We suggest that consideration of impacts on shrub-nesting birds when evaluating mesopredator control programs may not be critical within longleaf pine ecosystems. We documented red imported fire ants as frequent nest predators. This species is an exotic, invasive species and we believe more effort should be put

forth to control fire ant populations. Additional research on whether fire ant control will increase nest survival on shrub-nesting species is warranted.

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