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IMPACTS OF RED IMPORTED FIRE ANTS ON NORTHERN BOBWHITE NEST SURVIVAL

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ABSTRACT

Invasive species are a large management issue because of extensive environmental and economic damage. The red imported fire ant (RIFA, *Solenopsis invicta*) is an invasive species of growing concern in wildlife management in the United States because of its increasing distribution, difficulty to suppress, and aggressive predation on native invertebrates, herpetofauna, birds, and small mammals. Managers of the northern bobwhite (*Colinus virginianus*) have questioned the direct impact of RIFA on bobwhite nest success, particularly the factors that might influence the level of nest predation. We hypothesized that RIFA predation on northern bobwhite would vary by location and correlate with drier weather conditions. To test our hypothesis we analyzed bobwhite nest data gathered from 3 properties in the southeastern United States. The nest data are part of a larger research effort on bobwhites, collected by Tall Timbers Research Station and the Albany Quail Project using radiotelemetry from 1992 to 2015. Over these 23 years we tracked bobwhites and located nests ($n = 3,207$) daily to determine nest fate (success or failure) based on field sign and evidence attributed to specific causes of mortality. We used the nest-survival model in Program MARK to estimate nest survival. Average nest survival varied annually for the Albany and Tall Timbers study areas, respectively. The overall effect of RIFAs on nest survival was generally small, with an average annual loss in Albany of 5.13% (range = 0–15.59%) and 2.17% in Tall Timbers (range = 0–5.83%), but in some years was as high as 15.6%. Greater losses occurred late in the breeding season when it was typically drier and the loss rate in general was higher on the drier of the 2 study sites. Despite the relatively small direct impact on nesting success demonstrated, indirect effects of RIFAs on bobwhite populations are poorly understood at present. Quantifying the influence of indirect factors, such as soil type and habitat disturbance, on RIFA abundance and the subsequent impact on bobwhites, will provide additional insight to the ecological interaction with a highly pervasive and expanding invasive species and help inform management options.

One of the greatest conservation threats worldwide is the spread of invasive species, given their large economic and environmental cost to individual flora and fauna and to the integrity of ecosystems as a whole (Pyšek and Richardson 2010). In the United States alone, the estimated economic loss from invasive species is >US $1.1 billion annually (Allen et al. 2004). Beyond the economic impact of invasive species, they are a leading cause of animal extinction (Clavero and García-Berthou 2005) and have been linked to decreasing biodiversity and impairment of ecosystem services worldwide (Pejchar and Mooney 2009, Pyšek and

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Richardson 2010). Preventing the establishment or slowing the spread of invasive species, evaluating their effects on ecosystems, and determining appropriate management responses to invasion are high priorities for wildlife managers globally (Lowry et al. 2013).

An invasive species of particular concern in North America is the red imported fire ant (RIFA(s), *Solenopsis invicta*). Red imported fire ants are a prime example of an invasive species benefitting from changing land-use practices and anthropogenic disturbance (e.g., pastures, mowed areas near roadways, disking; Tschinkel 1988, Camilo and Phillips 1990, Plowes et al. 2007). Native to South America, this species was introduced into the United States during the 1930s or 1940s (Callcott 2002). The widespread availability of highly disturbed land enabled RIFA's rapid population expansion in the southern United States, despite a 1953 U.S. Department of Agriculture quarantine intended to slow its spread. The species has become established in >128 million ha in 13 southern U.S. states and Puerto Rico, as well as in other Caribbean islands, Mexico, Australia, and China (Morrison et al. 2004, Zhang et al. 2007). Under current climatic conditions RIFA has the potential to continue expanding its U.S. distribution northward within southern states and in the Pacific Coast region to Washington State (Korzukhin et al. 2001, Morrison et al. 2004), with even further northward expansions possible under a 21st century climate-warming scenario (Morrison et al. 2005). This historical establishment and continued expansion of RIFA is of urgent conservation concern. Red imported fire ants reach high densities, are highly aggressive, and are omnivorous, giving them potential to impact species ranging from agricultural crops (Jetter et al. 2002), to invertebrates, to vertebrates including herpetofauna, mammals, and birds (Allen et al. 2004). Among vertebrate wildlife species, ground-nesting birds in particular may be at risk of negative population-level effects of RIFA predation (Wojcik et al. 2001, Allen et al. 2004).

A ground-nesting species of frequent concern is the northern bobwhite (*Colinus virginianus;* hereafter, bobwhite [Allen et al. 2004]). Even prior to RIFA invasions, native fire ants (*S. geminata*) were known as a source of bobwhite mortality and nest loss during pipping (Stoddard 1931, Travis 1938). The accidental introduction and rampant spread of RIFAs stimulated research on their potential effects on bobwhite and other wildlife (Johnson 1961, Simpson 1976). Bobwhites are negatively affected by RIFAs via direct nest predation (Myers et al. 2014), reduced chick survival through harassment (Allen et al. 2004), and competition for similar food resources (Williamson et al. 2002). In the case of nest predation, the majority of studies indicate that the pipping stage, or soon afterward, is when chicks are most vulnerable to RIFA predation (Mueller et al. 1999, Staller et al. 2005). This observation holds true for other taxonomic groups that have an altricial–precocial spectrum as well. For instance, both altricial (e.g., American alligator [*Alligator mississippiensis*], Reagan et al. 2000) and precocial (e.g., loggerhead turtle [*Caretta caretta*; Allen et al. 2001] reptiles are affected by RIFA.

Recent studies have compared impacts of polygyne vs. monogyne varieties of imported fire ants (Macom and Porter 1996) and evaluated their response to specific management actions (Forbes et al. 2002). Studies have also documented a severe impact of RIFA on bobwhite in the Southwest, particularly in Texas (Mueller et al. 1999, Allen et al. 2004). The impact seen in Texas is largely attributed to the high density of polygyne RIFAs, where colonies have multiple queens and ≥3 RIFA density than is observed in monogyne RIFAs (Macom and Porter 1996). High RIFA density in Texas could explain the high predation rates on bobwhite in those areas (Allen et al. 2004). Polygyne RIFAs are found in the Southeast but at much lower densities than are present in Texas (Porter 1992).

Although RIFAs can negatively affect individual bobwhite and have the potential to contribute to landscape-scale population declines, considerable uncertainty remains about long-term average rates of RIFA-caused mortality and the amount and causes of spatial and temporal variability in these mortality rates. This uncertainty reduces the ability of managers to identify the conditions (i.e., when and where) under which RIFA effects on bobwhite warrant higher concern. At within-region scales, RIFA occurrence and activity are affected by site disturbance history, hydrology, and climate (Porter and Tschinkel 1987, Tschinkel 1988). There are likely other factors that influence RIFA that are, as of yet, not well-quantified. Spatial variation in density and other factors presumably could produce variation in RIFA impacts on bobwhite but there has been little work assessing the relative effects of disturbance history and other factors on such variation. Anecdotal evidence suggests that RIFA foraging behavior is altered by moisture or lack thereof, such that severe droughts can trigger more aggressive foraging behavior because the ants are unimpeded by rainfall events and at the same time are driven to seek sources of moisture (Porter and Tschinkel 1987, LeBrun et al. 2012). However, potential interannual variation in RIFA-caused mortality rates, such as differences between drought and nondrought years, are poorly understood because assessing such temporal variation requires long-term data sets.

Given the need for better understanding of variability in RIFA impacts on bobwhite, our goal was to quantify the impact of RIFA on bobwhite nest survival using a long-term data set from the Albany Quail Project and Tall Timbers Research Station and Land Conservancy and to evaluate impacts of RIFAs in relation to geographic location, year, and season. Based upon this goal and the existing literature, we hypothesized that RIFA predation 1) would vary significantly by location and 2) would increase during drier periods. We expected our results to have direct relevance to numerous bobwhite managers in our study region, where bobwhite hunting and conservation are a focus of many landowners, and to help improve understanding of RIFA–bobwhite interactions throughout their area of overlap in the United States.

STUDY AREA

The Albany Quail Project study site was composed of 2 adjoining private bobwhite hunting plantations in Baker and Dougherty counties of southwest Georgia. One 8,094-ha property served as the headquarters of the project, the second property was 4,400 ha with a similar history and management program to the first (Sisson et al. 2009, Sisson and Stribling 2009). The 2 properties were embedded in a 120,000-ha landscape of similar properties. The sites consisted of small basal area (9.2–13.8 m^2/ha), old-field pine forests (80%) in an open pine–grassland structure maintained through commercial thinning, prescribed fire (50–70% of the areas burned each year), with small fallow fields throughout the area. The majority of the timber was longleaf pine (*Pinus palustris*) and slash pine (*P. elliottii*), with scattered hardwoods such as live oak (*Quercus virginiana*), southern red oak (*Q. falcata*), and water oak (*Q. nigra*). Herbaceous cover was predominantly warm season grasses, such as broomsedge (*Andropogon* sp.), annual broad-leaved forbs, and legumes. Both properties were converted to agricultural fields in the 1800s; however, after agriculture was abandoned in the 1900s these lands were seeded back to pine and native vegetation maintained by prescribed fire. The average growing season for the duration of this study was 15 March to 31 November (varies with weather), with an average temperature of 76° F (24° C). The average annual precipitation for Albany was 127 cm, with an average of approximately 74 cm during the bobwhite breeding season.

Topography on both Albany properties was relatively flat with little to no hardwood drains. Quail estimates for these sites in recent years have averaged approximately 5 birds/ha (Sisson et al. 2009). For further site descriptions, see Terhune et al. (2007).

Tall Timbers was located in Leon County, Florida, embedded in an approximately 161,874-ha landscape of other bobwhite management properties. Like the Albany properties, Tall Timbers was largely old field vegetation and consisted of 1,568 ha of old-field pine forests (66%) of loblolly pine (*P. taeda*) and shortleaf pine (*P. echinata*), interspersed with hardwood drains and hammocks (12%) and small fallow fields (13%; see Palmer et al. 2012). Pine forests maintained an open pine–grassland structure through prescribed fire (50% burned annually). Herbaceous ground cover was a mix of warm season grasses, legumes, and forbs (Hammond 2001). Quail estimates for this site in recent years have averaged approximately 3.75 birds/ha. The average growing season was 15 March to 31 October (varies with weather), with an average temperature of 78° F (26° C) and an average annual precipitation for Tall Timbers of 158 cm, with an average of approximately 91 cm during the bobwhite breeding season.

Soils on the Albany sites were of the Orangeburg–Lucy–Grady and Norfolk–Wagram–Grady soil associations, which were predominantly sandy-loam textured soils with moderate permeability and low natural fertility (Palmer et al. 2012). Soils on Tall Timbers are of the Fuquay–Orangeburg–Faceville soil association, characterized by well-drained, moderately fertile, fine-loam soils with varying amounts of sand and clay (Palmer et al. 2012). The Orangeburg series was common in both Albany and Tall Timbers sites but otherwise there were no shared soil families, meaning soils between sites varied in characteristics such as horizonation, mineral composition, and permeability.

METHODS

From 1992 to 2015, we captured bobwhites during October and November (autumn trapping period), January (winter trapping, only on Tall Timbers), and March–April (spring trapping period) using confusion-style funnel traps baited with milo and/or cracked corn (Stoddard 1931). We covered traps with brush (e.g., fresh-cut pine boughs) to minimize stress on captured birds and to conceal them from avian predators. We classified captured bobwhites by age and sex, weighed and tagged all birds, and radiotagged a subset of birds weighing ≥132 g with a 6-g necklace-style radiotransmitter equipped with an activity switch (Holohil Systems Ltd., Carp, Ontario, Canada). We used necklace-style transmitters because they do not influence body mass dynamics or physiology of captive birds (Corteville 1998, Hernandez et al. 2004) and their effect on survival of bobwhites is negligible (Palmer and Wellendorf 2007, Terhune et al. 2007).

We located radiotagged individuals ≥3 times weekly during the breeding season (1 Apr–1 Oct) using the homing method (White and Garrott 1990, Kenward 2001). We approached birds to within 25 m to minimize location and vegetation classification errors and we recorded locations using ArcView® software (Environmental Systems Research Institute, Inc., Redlands, CA, USA).

Inactive birds, determined via an activity switch, were assumed to be incubating hens if observed in the same area on 2 consecutive days. We approached inactive hens and marked their location with flagging tape at a distance of 3–10 m to monitor the fate of the nest daily from a distance >15 m. We used a Global Positioning System (Garmin V Plus; Garmin Ltd., Olathe, KS, USA) and/or aerial imagery to delineate and archive nest locations. We counted the number of eggs in a nest when the incubating hen was off the nest. We monitored nests daily and determined daily fate categorized as abandoned, successful, or unsuccessful. An unsuccessful nest was any nest in which ≥1 egg was destroyed and the adult bird did not return to incubate the remaining clutch. An abandoned nest was one in which the hen did not complete incubation and all eggs were still intact. Abandoned nests (typically research induced) were excluded from analyses. This caused no bias in the RIFA analysis because nests observed with RIFA were classified as a failure, not an abandoned nest. A successful nest included those in which ≥1 egg hatched. We identified nest predators by video camera (when available) or by sign or tracks left at the nest. Despite known biases associated with assigning nest mortality by sign or tracks, video-surveillance research showed that RIFA depredations almost always were correctly classified by field staff based on presence of RIFA (Staller et al. 2005).

Statistical Analysis

We estimated daily survival rate (DSR) for bobwhite nests and evaluated competing models explaining variation in nest survival using the nest survival model in Program MARK (White and Burnham 1999). We modeled our binomially distributed data (nest fate = 1 if failed and 0 if successful) with a user-defined, logit-link function while simultaneously considering the effects of time (day of year and year effect; linear and quadratic time trends; T and TT), year (modeled as individual groups: 1992–2015), group (predation type: red-imported fire ants, other), and site (Albany, Tall Timbers). For our data, we standardized 15 April as Day 1 and numbered nest observations sequentially thereafter until Day 191 (10 Sep), the final day of nesting activity during our study (see Dinsmore et al. 2002, Rotella et al. 2004). We coded each individual nest with the following pieces of required information to input into Program MARK (see White and Burnham 1999, Dinsmore et al. 2002): 1) the day the nest was found (k), 2) the last day the nest was checked and known alive (l), 3) the last day the nest was checked (m), and 4) the nest fate (f). Additionally, we used indicator variables to assign individual nest encounters to group-specific covariates as outlined above (i.e., year, group, site, and treatment type). We incorporated a measure of dryness into nest survival analysis using the Keetch–Byram Drought Index (KBDI), whereby KBDI values of 0–200 indicate substantial soil moisture, KBDI values of 200–400 indicate beginning stages of drought and moderate dryness, KBDI values of 400–600 indicate drought conditions, and KBDI values of 600–800 indicate severe drought and extremely dry conditions.

We used an information-theoretic approach (Akaike 1973, Anderson et al. 2000, Anderson and Burnham 2002) to evaluate the set of candidate models with the best model determined by Akaike's Information Criterion adjusted for small sample bias (AIC_c; Wedderburn 1974, Anderson and Burnham 2002). We considered the model with the smallest AIC_c value the best given the data and considered the relative plausibility of each model via Akaike weights (w_i; Anderson et al. 2000, Anderson and Burnham 2002), where the best approximating model in the candidate set has the greatest Akaike weight. When appropriate, we used model-averaging (Akaike 1974, 1978; Anderson and Burnham 2002) to obtain daily survival and estimated nest survival as the product of DSR across the 23-day incubation period. To derive additional inference and render direct covariate-specific comparison, we report beta coefficients, their standard errors and 95% confidence intervals, and effect size for variables of interest (e.g., site, treatment); and, for comparison with other studies, we report the derived estimates of DSR (with associated 95% CI).

RESULTS

Between 1992 and 2015, we found 3,207 nests on Albany ($n = 1,822$) and Tall Timbers Research Station ($n = 1,385$) study sites, with an average of 134 nests found each year (range = 35–307; Table 1). Average annual loss

of nests to RIFA on Albany sites was 5.13% (range = 0–15.59%) and on Tall Timbers was 2.18% (range = 0–5.38%). Three models received support in explaining the variation in nest survival but one model (an interaction between site and predator-type) was overwhelmingly supported more than the others (Table 2).

The most-supported model included site and non-RIFA predators and the top 3 models all included non-RIFA predators. Comparatively, the models ranked next best (which incorporated RIFAs) received no support, suggesting that RIFA explained relatively little variation in nest survival compared with other nest predators (Table 2). The inclusion of year was not supported and explained very little variation in our data with the exception of 2 years on the Albany sites ($\beta_{1993} = -0.606$; 95% CI = $-1.199, -0.014$ and $\beta_{2007} = -0.640$; 95% CI = $-1.218, -0.063$) and 2 years on the Tall Timbers site ($\beta_{2011} = -0.464$; 95% CI = $-0.861, -0.066$ and $\beta_{2013} = -0.491$; 95% CI = $-0.913, -0.070$); these 4 years had the lowest nest survival in their respective sites (Fig. 1).

In the models incorporating an effect of RIFA, variation in nest survival was best explained by site and a linear time trend (Table 2). Red imported fire ants depredated more nests on Albany sites (DSR = 0.996, SE = 0.001) compared with Tall Timbers sites (DSR = 0.998, SE = 0.001) for all years combined (Fig. 2) and DSR for those nests depredated by RIFAs was higher than those depredated by all other nest predators combined. Red imported fire ants decreased daily nest survival and survival decreased linearly with the progression of the season ($\beta_T = -0.002$; 95% CI = $-0.003, -<0.001$; $\beta_{RIFAs} = -0.721$; 95% CI = $-0.929 -0.513$) such that nest survival was lower at the end of the season compared with early in the nesting season. The KBDI influenced nest survival in a curvilinear relationship, such that lower DSRs were observed at low KBDI (<200) levels and high KBDI (>400) levels ($\beta_{KBDI} = -0.170$; 95% CI = $-0.290, -0.050$; $\beta_{KBDI^2} = -0.438$; 95% CI = $-0.630, -0.250$; Fig. 3). Keetch–Byram Drought Index levels were on average higher on Albany sites compared with Tall Timbers; high levels of KBDI (≥ 425 and ≥ 370) in Albany and Tall Timbers, respectively, were associated with increased nest failure (Fig. 4).

DISCUSSION

Our results supported the first hypothesis that RIFA predation would vary by location. Bobwhite nest loss due to RIFA fluctuated between geographic locations, with the Albany sites having more nest mortality than Tall Timbers (Fig. 2). Our results indicate that the direct impact of RIFA predation on bobwhite nest survival generally is low at our 2 study sites, with only 4% average loss for the sites combined. However, predation was greater in some years and on some areas of the study region. The reason for the disparity between nest mortality by site in our study is unclear but could be due to subtle vegetation differences related to either or both soil characteristics and local climate affecting RIFA densities and/or their impact on bobwhite nests. For

Table 1.   Northern bobwhite nest success at Albany, Georgia, and Tall Timbers Research Station (TTRS), Florida, USA, study sites during 1992–2015.

Year	Albany			TTRS			Total
	n(succ)[a]	n(dep)[b]	n(total-PL)[c]	n(succ)	n(dep)	n(total-TTRS)[d]	Total
1992	33	30	63				63
1993	10	25	35				35
1994	53	38	91				91
1995	41	31	72				72
1996	47	37	84				84
1997	56	35	91				91
1998	54	50	104				104
1999	92	88	180	12	17	29	209
2000	124	91	215	46	46	92	307
2001	64	38	102	31	35	66	168
2002	30	43	73	86	40	126	199
2003	49	41	90	34	35	69	159
2004	35	33	68	42	22	64	132
2005	28	28	56	41	16	57	113
2006	24	31	55	59	38	97	152
2007	23	28	51	34	22	56	107
2008	33	37	70	63	40	103	173
2009	25	13	38	64	39	103	141
2010	21	27	48	37	30	67	115
2011	30	19	49	38	56	94	143
2012	37	23	60	59	28	87	147
2013	35	18	53	29	44	73	126
2014	12	10	22	41	53	94	116
2015	31	21	52	62	46	108	160
TOTAL	987	835	1,822	778	607	1,385	3,207

[a] No. of successful northern bobwhite nests.
[b] No. of depredated northern bobwhite nests.
[c] Total no. of nests in the Albany study area.
[d] Total no. of nests in the TTRS study area.

Table 2.   Model selection results for analysis of nest survival of northern bobwhites on Albany, Georgia, and Tall Timbers Research Station, Florida, USA, during 1992–2015.

Model[a]	ΔAIC_c[b]	w_i[c]	Model L	K[d]	Deviance
S + Site + non-RIFA + Site × non-RIFA	0.0	0.998	1.000	4	10,085.9
S + Site + non-RIFA	13.2	0.001	0.001	3	10,101.1
S + non-RIFA	14.3	0.001	0.001	2	10,104.1
S + T + RIFA	2,585.2	0.000	0.000	3	12,673.1
S + T + TT + RIFA	2,585.8	0.000	0.000	4	12,671.7
S + Site + T + RIFA	2,587.2	0.000	0.000	4	12,673.0
S + RIFA + KDBI + KDBI × KDBI	2,589.2	0.000	0.000	4	12,675.0
S + RIFA + KDBI	2,590.0	0.000	0.000	3	12,677.9
S + RIFA	2,591.0	0.000	0.000	3	12,678.9
S + Site + RIFA	2,591.1	0.000	0.000	3	12,679.0
S + Site + RIFA + Site × RIFA	2,592.9	0.000	0.000	4	12,678.8
S + KDBI	2,594.0	0.000	0.000	2	12,683.9
S + T	2,621.5	0.000	0.000	2	12,711.4
S + T + TT	2,622.5	0.000	0.000	3	12,710.4
S.	2,626.3	0.000	0.000	1	12,718.2
S + Site	2,628.3	0.000	0.000	2	12,718.2

[a] S = ?; Non-RIFA = all predations recorded besides RIFA (RIFA = red imported fire ants predation); T = Linear within-year time trend; TT = quadratic trend; KDBI = Keetch–Byram Drought Index.
[b] Change in AIC_c.
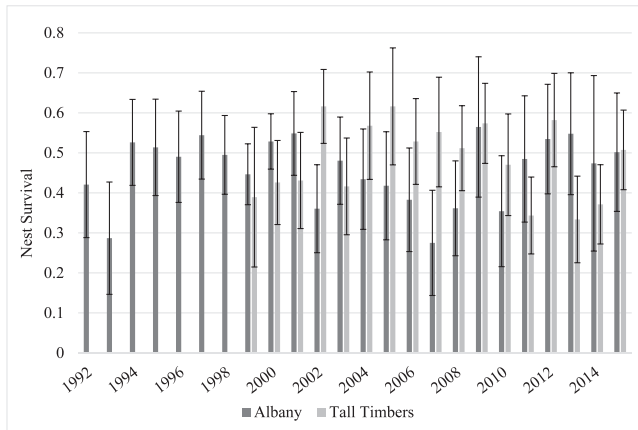[c] AIC_c weight.
[d] The no. of free parameters in the model.

Fig. 1. Northern bobwhite nest survival for Albany and Tall Timbers Research Station, Florida, USA, for 1992–2015.

Fig. 3. Predicted daily survival rate for northern bobwhite nests relative to the Keetch–Byram Drought Index (KBDI) on Albany and Tall Timbers study sites, Florida, USA, during 1992–2015.

example, the Tall Timbers site has more fertile soils and receives approximately 25–38 cm of annual rainfall more than the Albany sites, which may influence vegetation conditions depending on timing and amount of rainfall in a given year.

The nest mortality rates we observed are similar to previous studies in the Southeast, which recorded 5–12% bobwhite nest loss at pipping (Johnson 1961). We observed variation in nest mortality attributed to RIFA among sites, with a 5.13% loss rate in Albany versus only a 2.18% loss rate at Tall Timbers (Fig. 1). Such small loss rates may not be biologically significant; however, in years when nest loss to RIFA is as high as 15.6%, the loss is biologically meaningful. Notably, 20 years prior to the start of our study in the Albany study area, Simpson (1976) found <1% loss to RIFA. Several possibilities exist for the temporal discrepancies between studies, including differing techniques (nest search vs. telemetry), disparate vegetation conditions or management regimes, or possibly differing RIFA densities. Red imported fire ants had only recently infested southern Georgia at that

time (Allen et al. 2000), so it is possible there were fewer colonies during Simpson's study; however, we have no direct data to confirm this. Studies have shown a pattern of bobwhite decline following fire ant invasion in Texas (Allen et al. 1995) as well as in the Southeast (Allen et al. 2000) but did not document a similar relationship in Georgia (Allen et al. 2000). Our studies in Albany likewise have not documented declining populations during these years; bobwhite populations are currently as large as or larger than they have been in 50 years (Sisson and Stribling 2009). This stability could be due to long-term management regimes and abundant food sources for bobwhites. As such, high bobwhite densities may mitigate the overall impact of RIFA on bobwhite populations but additional research is warranted on low-density sites.

Although variation existed in RIFA predation between sites, there was no difference in the non-RIFA mortality agents of nests across sites. There was, however,
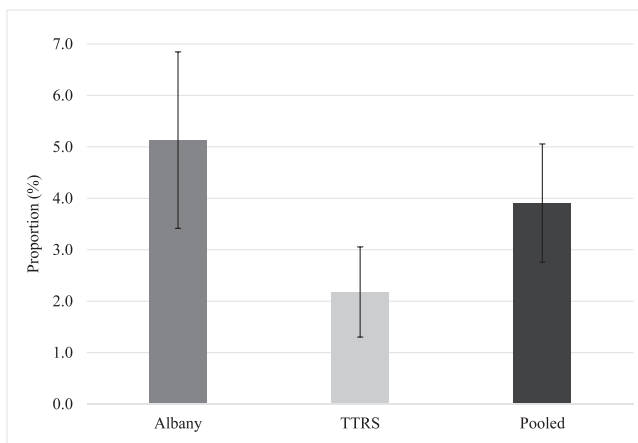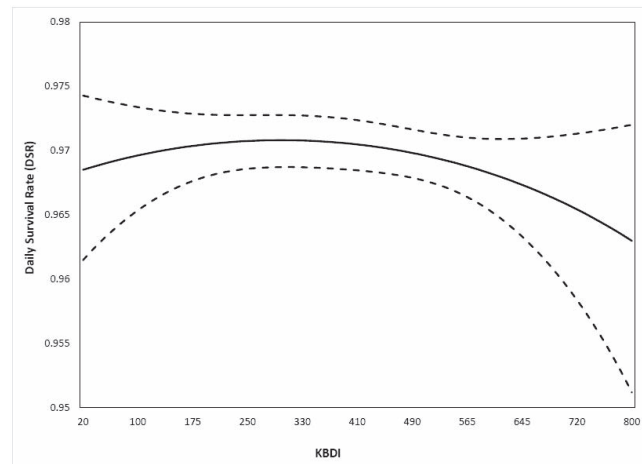

Fig. 2. Average annual proportion of northern bobwhite nests depredated by red imported fire ants on Albany, Tall Timbers Research Station (TTRS), and all sites pooled in Florida, USA for 1992–2015.
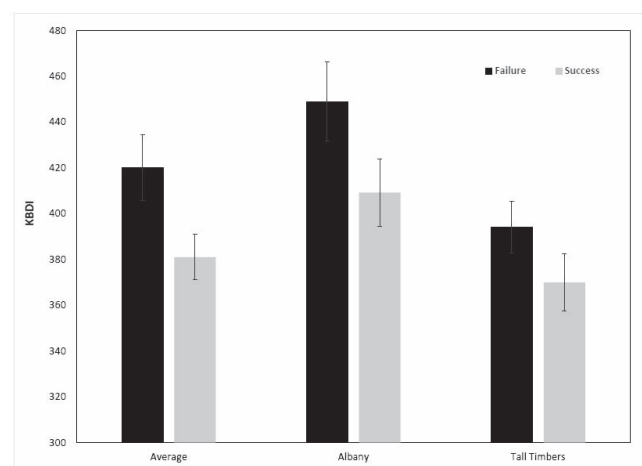

Fig. 4. Northern bobwhite nest survival relative to the Keetch–Byram Drought Index (KBDI) on Albany and Tall Timbers study sites, Florida, USA, during 1992–2015.

a notable difference in the daily survival rates (DSRs) of nests, with those predated by RIFA having higher DSRs than those predated by non-RIFA predators on all sites. Our finding is expected because RIFA typically depredate nests at the pipping stage, thus mainly affecting nests that had survived nearly to hatching. This is significant because it means a greater time investment by the bobwhite parents and when the nest is lost they have less time in the breeding season to renest.

With the exception of fallow field percentage, both study sites employ similar management regimes (i.e., prescribed fire, disking) and land-use history (managed similarly for ≥40yr). Therefore, the lack of variation in other nest mortality agents was not surprising but presumably factors outside of the management regimes must be driving variation in RIFA impacts. Major differences between sites include soil type and climate. Albany sites have sandy soils, while Tall Timbers has loamy, more clay-based soils. However, there is little information on whether RIFA colonization and densities are related to soil types and this could be influencing the variation we observed in our results. Some studies have found no evidence that soil type affects RIFA (Wangberg et al. 1980, Porter et al. 1991); whereas, others suggest that a relationship exists, with sandier soils having slightly higher RIFA abundance than silty or loamy soils (Ali et al. 1986). Interestingly, Ali et al. (1986) conducted their research in an intensive agricultural setting, which may be similar to more intensive fallow field management in the Albany sites compared with the Tall Timbers site in our study. Explicitly testing whether intensive soil disturbance, through farming or fallow field management, in relation to other environmental factors, may expose site-specific conditions facilitating RIFA distribution.

Climate, precipitation, or level of dryness is known to impact RIFA foraging behavior and/or nest depredation rates (LeBrun et al. 2012). Average annual rainfall on Tall Timbers (158 cm) is greater than on Albany (127 cm) sites and Tall Timbers receives 25–38 cm more rainfall than Albany. Albany sites and soils are more drought-prone and also experienced higher rates of depredation at pipping by RIFA (Fig. 2).

The temporal variation we observed supported our second hypothesis that RIFA predation would correlate with warmer, drier climate conditions. Across sites, nest survival decreased relative to time of season and KBDI (level of dryness), which is linked to higher temperatures and less precipitation typical later in the breeding season compared with earlier in the season. Past research has found a connection between higher RIFA predation rates and climate, particularly during drought conditions (LeBrun et al. 2012). Drought conditions and level of dryness (measured by KBDI in our study) was an indicator of nest survival, such that at low levels (<200) and high levels (>400) daily survival rate of nests was low compared with normal levels (200–400 KBDI). It is unclear from our study why this is the case, especially when KBDI is low. We expect, however, that when KBDI levels are low nest depredations by mammals might increase as a result of favorable scent conditions due to increased moisture (Conover 2007). When KBDI is

high and drought conditions persist, lower nest survival and specific loss to RIFA increased in our study (Fig. 4). Notably, annual variation in nest survival in our data only occurred in 4 of 23 years on each study site. During 3 of these 4 years, the KDBI was higher than the long-term average and considered to indicate drought conditions based on the Palmer Drought Index, particularly during the breeding season in 1993 (KBDI = 545) and 2007 (KBDI = 524) for the Albany sites, and 2011(KBDI = 480) and 2013 (KBDI = 245) for Tall Timbers. These years also had the lowest bobwhite nest survival for their respective sites (Fig. 1). In light of declining nest survival throughout the breeding season and KBDI being higher in August and September, the potential impact of RIFA on the late hatch may be biologically relevant, especially during drought years, given that the late hatch can be a purported boon to overall productivity, autumn recruitment, and population growth (T. M. Terhune, unpublished data).

The proportion of direct RIFA nest depredation in our study was similar to previous studies (Johnson 1961, Simpson 1976) but the significant variation of impact between sites and magnitude of nest loss to RIFA relative to KBDI has not been explicitly evaluated. Human disturbance has been linked to RIFA invasions (Tschinkel 1988, King and Tschinkel 2008) and habitat management may influence their expansion. Management practices, such as prescribed burning, have been examined for connections to RIFA density (Forbes et al. 2002), yet their impacts are poorly documented. Examining indirect variables such as geographic location, soil type, climate, and species interactions in relation to bobwhite management practices could reveal connections to RIFA presence or absence and density at a given location. These indirect effects could have negative effects on bobwhite populations, especially if RIFA expansion and mound densities continue to escalate. For example, the hispid cotton rat (*Sigmodon hispidus*) is an important bottom-level prey species, serving as an alternate prey species for predators of bobwhite (Harris 2011). Red imported fire ants depredate cotton rat young, and past studies have recorded alteration in cotton rat behavior and even habitat use when RIFA invade an area (Pedersen et al. 2003). More research is needed to quantify these relationships, which could in turn shed light on indirect influences RIFAs have on bobwhites and other ground-nesting birds. Understanding how environmental factors and land-use practices impact RIFA density, expansion, and behavior will provide valuable knowledge for land managers to determine whether RIFA treatment regimens are necessary for bobwhite conservation.

MANAGEMENT IMPLICATIONS

Although the overall impact of RIFA predation on bobwhite nest survival is low, we found evidence suggesting that these impacts can be site-specific and magnified during drought conditions, especially in conjunction with the late hatch. Therefore, during most years control of RIFA is unnecessary. However, the

impacts of RIFA are more problematic on some sites when soils and climatic conditions are more drought-prone. In these scenarios, RIFA removal may be an option for land managers trying to improve bobwhite populations but more research is warranted to determine whether removal results in lower RIFA abundance and moderates their impact on nest survival. At the moment, the potential cost of directly reducing RIFA populations by treating large acreages may be unrealistic and the potential deleterious impacts on other species are uncertain. Thus, until more information is available, the best management strategy for bobwhite populations is mitigating nest loss to RIFA by increasing productivity with management methods (e.g., vegetation management and other common practices) that have been rigorously tested and validated.

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