Invasive Ants Alter Foraging and Parental Behaviors of a Native Bird

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Abstract

Introduced species can exert outsized impacts on native biota through both direct (predation) and indirect (competition) effects. Ants frequently become established in new areas after being transported by humans across traditional biological or geographical barriers, and a prime example of such establishment is the red imported fire ant (*Solenopsis invicta*). Introduced to North America in the 1930s, red imported fire ants are now firmly established throughout the southeastern United States. Although these invasive predators can dramatically impact native arthropods, their effect on vertebrates through resource competition is essentially unknown. Using a paired experimental design, we compared patterns of foraging and rates of provisioning for breeding eastern bluebirds (*Sialia sialis*) in unmanipulated (control) territories to those in adjacent (treated) territories where fire ants were experimentally reduced. Bluebirds inhabiting treated territories foraged nearer their nests and provisioned offspring more frequently than bluebirds inhabiting control territories with unmanipulated fire ant levels. Additionally, nestlings from treated territories were in better condition than those from control territories, though these differences were largely confined to early development. The elimination of significant differences in body condition toward the end of the nestling period suggests that bluebird parents in control territories were able to make up the food deficit caused by fire ants, potentially by working harder to adequately provision their offspring. The relationship between fire ant abundance and bluebird behavior hints at the complexity of ecological communities and suggests negative effects of invasive species are not limited to taxa with which they have direct contact.

Introduction

Understanding the biotic and abiotic factors that structure communities of organisms lies at the heart of ecological research. Competition has long been proposed to rank among the most important factors that shape communities of plants and animals, but with the exception of a few communities such as invertebrates living in rocky intertidal habitats (Gurevitch et al. 1992), competition has been difficult to demonstrate in natural environments within communities consisting of highly co-evolved species. The introduction of a new species to an established community presents an opportunity to observe the process of community structuring in action. The negative impacts of introduced species – from the standpoint of conservation biologists – typically represent successful competition by the introduced species in displacing native species.

The negative impacts of invasive ants on native fauna have been relatively well documented over the last 20 yr (Wojcik et al. 2001; Holway et al. 2002; Allen et al. 2004). Invasive ant species can disrupt native ecosystems through both direct effects on individual organisms (biting, stinging, and envenomization) and via a suite of competitive effects upon

native taxa. Numerous studies have shown direct competition between invasive ants and various native arthropod groups (Gibbons & Simberloff 2005), but the secondary effects that introduced ants can have on native insectivorous vertebrates are beginning to attract the attention of conservation biologists and behavioral ecologists (Allen et al. 2001; Suarez & Case 2002; Davis et al. 2008). These secondary impacts can manifest through direct resource competition between introduced ants and native insectivores (Allen et al. 2001) or through the disruption of the ecological communities that vertebrates depend on (Suarez et al. 2000; Suarez & Case 2002; Davis et al. 2008).

Recently, O'Dowd et al. (2003) documented dramatic multi-trophic effects of the invasive yellow crazy ant (*Anoplolepis gracilipes*) on the ecological community (including crustaceans, scale insects, and trees) of an isolated island in Oceania. In a follow-up study, Davis et al. (2008) explored the specific impacts of these same ants on avian communities and found that in habitats colonized by the ants, several native birds were less abundant, had reduced reproductive success, and altered their foraging behavior. Understanding the effects that invasive species have on native communities is integral for mitigating the negative effects of these alien invaders, which is all the more important for invasive species that are predicted to continue spreading.

The red imported fire ant (*Solenops invicta*) is an invasive ant that is widely recognized to pose a threat to local ecosystems. Fire ants, accidentally introduced to southern Alabama in the 1930s, have spread over a broad area of the southeastern United States (Buren et al. 1974), and there is concern that this species could spread globally (Morrison et al. 2004). Fire ants prey upon native arthropods and can greatly reduce local arthropod abundance and diversity as they colonize an area (Porter & Savignano 1990; but see Morrison 2002). Thus, fire ants represent a serious ecological problem (Williams 1994) because they disrupt natural food webs (Vinson 1994) and negatively impact native flora (Lach 2002) and fauna (Porter & Savignano 1990; Allen et al. 2004). Despite specific investigations of the direct impacts of fire ants on native taxa (Langkilde 2009; reviewed in Allen et al. 2004), a better understanding of the multi-level trophic effects that fire ants can have on natural ecosystems is integral for prioritizing any conservation practices designed to mitigate disturbances caused by fire ant invasion.

In addition to the well-documented negative effects on the arthropod groups that they prey upon (Porter

& Savignano 1990; Calixto et al. 2006), fire ants can also harm native vertebrate fauna. Most studies examining the effects of fire ants on reptiles, mammals, and birds have focused primarily on the direct impacts from predation and envenomization (reviewed in Allen et al. 2004). However, because fire ants can dramatically alter arthropod communities on a local level (Porter & Savignano 1990; Eubanks et al. 2002), their abundance could also influence the foraging strategies and success of insectivorous animals.

To date, few studies have focused on the indirect impacts of fire ants on insectivorous vertebrates. Lymn & Temple (1991) found decreased numbers of loggerhead shrikes (*Lanius ludovicianus*) following invasion by fire ants, but Yosef & Lohrer (1995) found no effect of fire ant abundance on prey capture rates or breeding success of this same species of shrike. An experimental study conducted by Allen et al. (2001), however, found increased arthropod diversity and abundance, as well as increased shrike abundance, in sites treated to reduce fire ants. While correlative studies can provide an important framework for understanding fire ant impacts, experimental procedures like the one conducted by Allen et al. (2001) provide a more convincing demonstration of the specific impacts of fire ants on insectivorous birds. For example, a recent experimental study by Ligon et al. (2011) showed that fire ant abundance can reduce hatching success, diminish the likelihood of re-nesting, and alter offspring sex-ratio of eastern bluebirds (*Sialia sialis*). Given the known impact of fire ants on vertebrate and invertebrate taxa, coupled with the predicted global spread of fire ants (Morrison et al. 2004), more experimental studies of the competitive interactions between fire ants and native insectivores are needed.

Eastern bluebirds are cavity-nesting passerine birds that are common throughout eastern North America (Gowaty & Plissner 1998). They are an ideal species for examining the effects of fire ants on vertebrate foraging strategies and success because (1) they are insectivorous [relying on many of the same invertebrates that fire ants feed upon (Hays & Hays 1959; Tennant & Porter 1991)]; (2) they inhabit the fields and pastures in which fire ants are often abundant (Tschinkel 2006); and (3) they readily use man-made nest boxes for reproduction, which greatly facilitates detailed study of their reproductive biology (Gowaty & Bridges 1991; Siefferman & Hill 2007). Use of nest boxes makes it relatively easy for researchers to measure nestling growth and fledging success, as well as to observe feeding behavior in the open environments favored by bluebirds. If fire ants compete with

bluebirds for resources, then we expect bluebirds in areas with high concentrations of foraging fire ants to experience greater difficulty in obtaining sufficient arthropod food items than bluebirds in habitats with low-fire ant abundance. Competitive interactions between bluebirds and fire ants are likely exacerbated when the food demands of bluebirds are highest, namely during the nesting period when adult bluebirds must forage for themselves as well as rapidly growing offspring.

To test the idea that localized fire ant abundance influences bluebird foraging and reproductive behavior, we created plots with experimentally reduced fire ant abundance. We then compared the provisioning rates, foraging behaviors, and offspring quality of bluebirds in these treated, low-fire ant territories to those of bluebirds in adjacent control territories with unmanipulated, high-fire ant levels. Based on the impacts fire ants can have on local arthropod abundance (Porter & Savignano 1990), we expected (but did not explicitly measure) an increased abundance of (non-fire ant) arthropods within the areas treated for fire ants. We predicted that such an increase in potential food items would result in a higher proportion of bluebird foraging attempts being conducted in the area treated around the nest box. Additionally, we predicted that bluebirds in control territories with high densities of foraging fire ants would be forced to forage farther from their nest boxes (owing to a reduction in available food items) than those individuals in treated habitats with fewer fire ants and that these changes in foraging behavior would cause bluebirds in control territories to provision their offspring at lower rates. Consequently, we also predicted that nestlings from control territories with high-fire ant abundance would exhibit poorer body condition than their counterparts in treated territories with reduced fire ant competition.

Materials and Methods

During the spring of 2009, we tested the effects of fire ant abundance on a banded population of eastern bluebirds in Alabama, USA. Bluebirds in this population nest in wooden boxes placed along the edges of open-field habitats, and these nest boxes are typically at the center of all-purpose territories defended by bluebirds during the breeding season. Because differences in habitat quality and local resource abundance are likely to contribute to differences in reproductive success and behavior between bluebirds inhabiting different territories, we used a paired experimental design in an attempt to control for such variation in

territory quality. In early 2009, prior to the breeding season, we selected 28 pairs of adjacent nest boxes, hereafter territory dyads, used by bluebirds in previous years. We also incorporated one additional dyad of new nest boxes (never before used by bluebirds) into the study. Territory dyads were selected for their proximity (boxes within 150 m of one another) and habitat homogeneity. We used rough definitions of habitat homogeneity when assigning members of dyads and looked for pairs of nest boxes that existed in similar habitat types. We placed nest boxes into the same experimental dyad only if they were within 150 m of one another and were both located (1) in open fields; (2) near forest edges; or (3) near water. To ensure that inherent differences between territories could not explain any observed differences in bluebird behavior or success between treated and control territories (see Fire Ant Treatment and Measurement below), we analyzed the reproductive success of bluebirds in a subset of territory dyads (n = 13) from previous years. We found that the reproductive success of bluebirds did not differ between territories that, in the current study, became control territories and those that were eventually treated for fire ants ($t_{12} = -0.35$, p = 0.73).

We monitored each nest box from Mar. to July 2009 to determine when a given nest was in use, to identify when eggs hatched and to obtain morphological measurements of growing nestlings. Unoccupied boxes were monitored every 3 d until a bluebird pair began building a nest in a given box. From that point, we monitored the box daily until four eggs were laid or bluebirds stopped laying for three consecutive days. Fourteen days after the fourth egg (or last egg) of a given clutch was laid, we returned to the box to check for signs of hatching (and every day thereafter if eggs did not hatch on that day). Nestlings were then measured at 2, 8, and 14 d of age (hatch day = day 0). As a measure of nestling body condition, we used residuals from ordinary least squares linear regressions of body mass against tarsus (Schulte-Hostedde et al. 2005).

Fire Ant Treatment and Measurement

In conjunction with another study measuring the effects of fire ants on the reproductive success of bluebirds (Ligon et al. 2011), we assessed the impact of fire ants on the foraging and feeding behavior of bluebirds by suppressing fire ants on one randomly chosen territory in each dyad using commercially available, ant-specific hydramethylnon bait (Amdro; American Cyanamid, Wayne, NJ, USA). Amdro bait is an ideal

means to control fire ants in experimental plots without impacting other arthropods because it attracts foraging fire ants but is largely ignored by other insects (Eubanks et al. 2002). Foraging fire ants find the bait and bring it back to their mound, where the poison is spread throughout the colony. Direct effects of Amdro application on the bluebirds were assumed to be negligible because (1) this compound is largely ignored by non-ant arthropods; (2) bluebirds only rarely consume ants (Pinkowski 1978); and (3) the National Pesticide Information Center technical fact sheet on hydramethylnon classifies the compound as 'slightly toxic to practically non-toxic when ingested by birds' (NPIC 2002).

In each treated territory, we used hand-operated dispensers to spread the Amdro fire ant bait (approximately 0.45 kg per territory) over all available fire ant habitats (which excluded roads and ponds) within a 40 m radius around the nest box in that territory. The treated area within each territory, therefore, typically covered approximately 5024 m^2, which represents roughly 25% of an average eastern bluebird territory (Krieg 1971; Gowaty & Plissner 1998). We chose this 40 m radius because we wanted to influence only the fire ant population in the area nearest the nest box in a given territory while eliminating the possibility that fire ants in adjacent control territories were affected. We treated territories in late March and early April, before most bluebirds at our study site began to breed, but after males had already settled and begun to defend territories. The timing of our bait application eliminated the likelihood that observed differences in bluebird behavior or reproductive success between treated and untreated plots arose as a result of preferential settlement by superior individuals on treated territories. Additionally, the application of axle grease to nest box poles prevented the loss of any bluebird nests because of direct fire ant predation.

To assess the effectiveness of our fire ant treatments, we monitored the abundance of foraging fire ants by trapping them in 50 ml screw-top plastic vials (BD Biosciences, San Jose, CA, USA) baited with 2.5 cm sections of hot dog. We placed baited vials on the ground and shaded them with opaque plastic plates mounted on 16-gauge wire. After 30 min, we capped the vials that were frozen upon return to the laboratory to allow quantification of fire ants at a later time. For each territory, we placed vials 20 m from the nest box at the four cardinal and four intermediate directions (15.3 m apart) when suitable habitat existed at these locations. Although the topographical characteristics (such as open water or hard-surfaced roads) of some territories prevented us from deploying

all eight baited vials, we attempted to deploy the maximum number of appropriately spaced vials in suitable fire ant habitat. We divided the total number of fire ants captured at a given territory by the number of vials deployed, to get an average number of ants captured per vial. We measured fire ant abundance when nestling bluebirds were 5–12 d old, approximately 3–6 wk after we applied the hydramethylnon bait.

Bluebird Behavior

To determine whether fire ants impact the provisioning rates of eastern bluebirds, we recorded the rate of feeding attempts made by pairs of bluebird parents to their offspring when the nestlings were 11 d old (±1 d). We compared the rate at which chicks were provisioned in unmanipulated control territories to the rate chicks were provisioned in adjacent treated territories. We had to rely on fewer territory dyads than were initially identified and treated because one or both nest boxes (control or treated) in 12 territory dyads were unoccupied by breeding bluebirds.

To examine our prediction that bluebirds facing different levels of competition with fire ants would direct their foraging efforts in different locations, we conducted detailed observations of bluebird foraging behavior in 20 different territories (10 territory dyads) during the nestling stage of reproduction. For each territory that we observed, we recorded the location of five foraging attempts per pair, per observation period. We used a telescope, binoculars, and a laser range-finder to pinpoint the location and distance of each foraging attempt, as well as the distance between ourselves and the nest box. We also used a triangular protractor to estimate the angle separating the two points. Using trigonometric functions, we were later able to determine the distance between the observed foraging locations and the nest box.

During each observation period, we monitored foraging behavior until we had observed five foraging attempts or 1 h had elapsed, whichever occurred first. In each observation period, one of us (RAL) was stationed near enough to the nest box on the territory to observe foraging behavior, but far enough away to minimize disturbance to the foraging bluebirds (approximately 25–40 m). The location of foraging attempts was recorded irrespective of the sex of the parent observed, although the sex of foraging individual was recorded. We did not analyze foraging behavior separately based on the sex of the individual observed because male and female bluebirds (members of a breeding pair) typically foraged and perched near one another. We felt that the high degree of cor-

relation between the foraging locations of males and females, coupled with the fact that male and female eastern bluebirds use many of the same foraging perches (Pinkowski 1977), made it unnecessary to analyze their behavior separately.

We were able to observe the foraging behavior twice during the nestling stage for each of 14 territories (seven dyads); but for six territories (three dyads) we were able to observe foraging behavior only once. For each territory, we obtained a mean foraging distance (from the nest box on that territory) and determined the proportion of foraging attempts observed that occurred within 50 m of the nest box. We focused on foraging attempts within 50 m because we applied hydramethylnon bait within 40 m of each nest box (treated territories), but foraging fire ants from just outside of this area very likely encountered the ant bait and brought it back to their colonies as well.

Statistics

We used paired t-tests to analyze differences in fire ant abundance between treated and control territories, as well as to compare differences in average for-aging distances of adult bluebirds in these different territory types. Additionally, the data pertaining to the portion of feeding attempts conducted within 50 m of the home nest box met the assumptions required for the paired t-tests we used to analyze them. Specifically, these proportional data were normally distributed (Shapiro–Wilk normality test, $W = 0.95$, p value = 0.40), and proportions from control and treated territories had equal variances (F-test comparing two variances, $F = 1.38$, $p = 0.64$). In addition to paired t-tests, we also used a repeated measures mixed model (PROC MIXED in SAS 9.2; SAS Institute Inc., Cary, NC, USA), with nest box as a random effect, to examine whether nestling body condition varied as a function of age, territory type (treated vs. control), or the interaction of the two.

Results

Fire ant abundance, measured as an average number of ants per collection vial, was significantly lower in territories treated with the hydramethylnon ant bait ($\bar{x} = 38.9 \pm SE\ 11.8$) than in adjacent control territories ($\bar{x} = 128.8 \pm 27.9$; n territory dyads = 16, paired t-test, $t_{15} = 3.2$, $p = 0.006$; Fig.1a). Additionally,
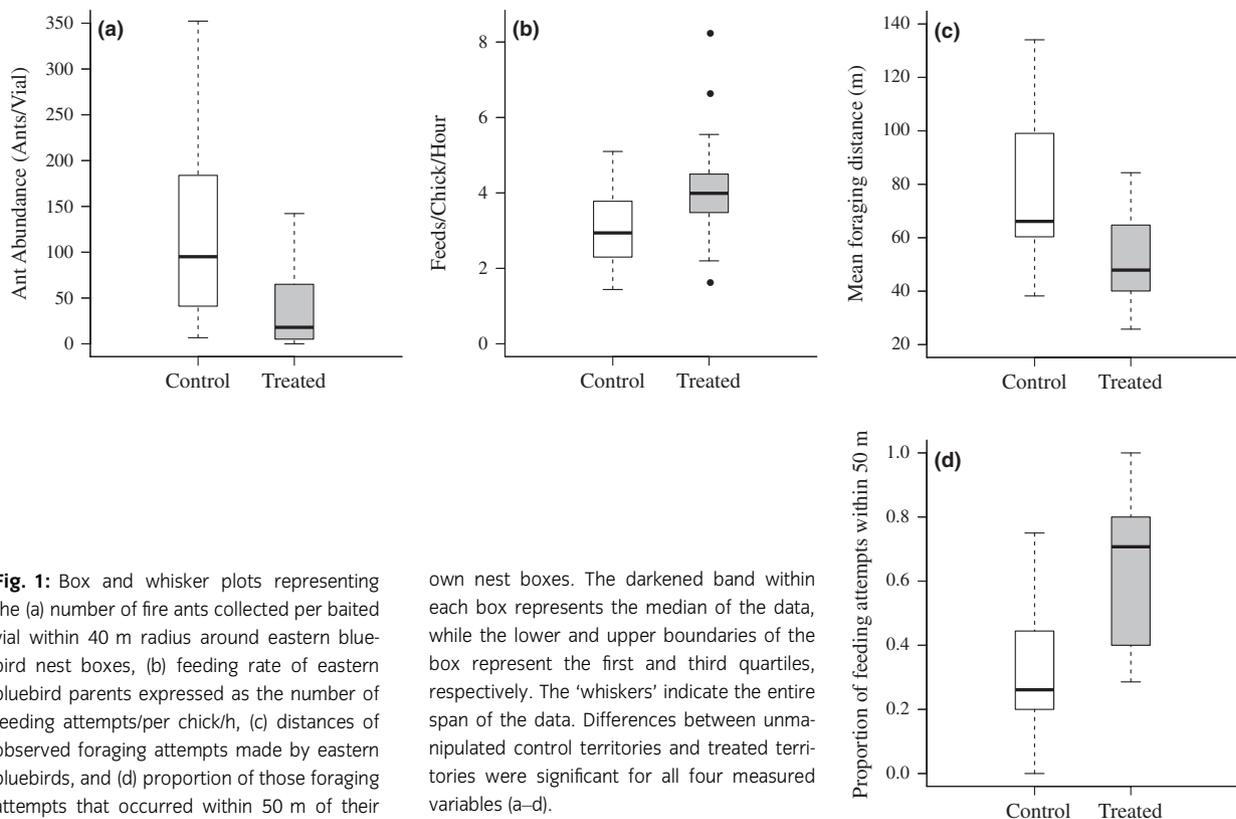

Fig. 1: Box and whisker plots representing the (a) number of fire ants collected per baited vial within 40 m radius around eastern bluebird nest boxes, (b) feeding rate of eastern bluebird parents expressed as the number of feeding attempts/per chick/h, (c) distances of observed foraging attempts made by eastern bluebirds, and (d) proportion of those foraging attempts that occurred within 50 m of their own nest boxes. The darkened band within each box represents the median of the data, while the lower and upper boundaries of the box represent the first and third quartiles, respectively. The 'whiskers' indicate the entire span of the data. Differences between unmanipulated control territories and treated territories were significant for all four measured variables (a–d).

bluebird parents inhabiting treated territories fed their offspring at significantly higher rates (feeds/chick/h = 4.2 ± 0.4) than parents in adjacent control territories (feeds/chick/h = 3.0 ± 0.3) with unmanipulated levels of fire ants (paired t-test, n territory dyads = 16, t_{15} = 2.91, p = 0.011; Fig. 1b). We also found that parents in treated territories foraged significantly nearer their nest boxes ($\bar{x}$ = 52.5 m ± 6.2) than parents inhabiting control territories ($\bar{x}$ = 74.4 m ± 9.2; n territory dyads = 10, paired t-test, t_9 = 2.31, p = 0.046; Fig. 1c). Parents in treated territories also focused a higher proportion of their foraging attempts within 50 m of their nest box (64.5% ± 7.8) compared to their counterparts inhabiting control territories (32.2% ± 6.6, paired t-test, n territory dyads = 10, t_9 = 3.41, p = 0.008; Fig. 1d).

Using a repeated measures mixed model, we found that territory type had a significant effect on nestling body condition, with nestlings raised in treated territories exhibiting better body condition ($\bar{x}$ = 0.149 ± 0.097) than nestlings in control territories ($\bar{x}$ = −0.196 ± 0.101; $F_{1,31}$ = 6.02, p = 0.02; Fig. 2). However, there was no significant effect of age on body condition ($F_{2,57}$ = 0.06, p = 0.94), nor any significant interaction between age and territory type ($F_{2,57}$ = 1.69, p = 0.19). The lack of a significant interaction between age and territory type was so surprising,
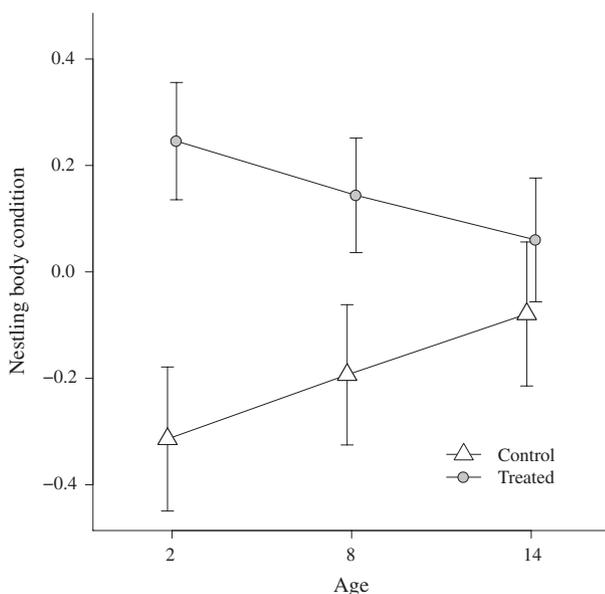

Fig. 2: Body condition (±SEM) of eastern bluebirds nestlings at 2, 8, and 14 d of age. Nestlings were raised in territories experimentally treated to reduce fire ant abundance (gray) or in untreated control territories (white). Body condition scores were calculated from the residuals of mass/tarsus regressions, and the plotted points represent least squares means for body condition at each time point.

given the apparent changes in body condition over time (Fig. 2), that we conducted a separate repeated measures mixed model with only nestling body condition at 2 and 14 d of age. This model uncovered a significant interaction between territory type and age ($F_{1,27}$ = 4.19, p = 0.05), and *post hoc* tests revealed that differences in nestling body condition between treated and control territories were significant at 2 d of age ($F_{1,27}$ = 11.16, p < 0.01), but not 14 d ($F_{1,27}$ = 0.74, p = 0.40).

Discussion

We documented a significant negative effect of introduced fire ants on the foraging and parental behavior of a native insectivorous vertebrate, the eastern bluebird. We found that bluebirds inhabiting territories with experimentally reduced fire ant abundance foraged significantly nearer their nest boxes, conducted a larger proportion of their foraging attempts within 50 m of their nest boxes, and provisioned their offspring at significantly higher rates than bluebirds in adjacent control territories. Additionally, we found a negative effect of fire ant abundance on nestling body-condition – an effect that decreased as nestlings grew.

Because foraging parents must repeatedly return to their nests during the period of nestling dependence, they typically use food resources closest to their nests while these resources are available. As a result, birds breeding in low-quality territories exhaust nearby food resources more quickly than birds breeding in high-quality territories and are subsequently forced to travel greater distances to obtain food (Tremblay et al. 2005). The increased travel time expended by parents in low-quality habitats during foraging results in reduced provisioning rates for birds occupying areas with less abundant food resources (Luck 2002; Tremblay et al. 2005). The reduced offspring provisioning rates we observed in control territories supports the prediction that fire ants reduce habitat quality for eastern bluebirds by forcing provisioning parents to travel farther than their counterparts who do not have to compete with fire ants for arthropod food resources.

Not only were there reduced provisioning rates by parents in control territories with more fire ants, but the nestlings in these territories were, on average, in poorer body condition than nestlings from treated territories with fewer ants. The most straightforward explanation for differences in nestling body condition is that the reduced feeding rate exhibited by parents in control territories limited the basic nutrients that

their nestlings required for growth and development. Despite an apparent trend suggesting changes in the relative body condition of control vs. treated nestlings throughout the nestling period (Fig. 2), a significant interaction between nestling age and territory type on bluebird nestling body condition was statistically significant only when evaluating a subset of data (from nestlings at 2 and 14 d of age). We suggest that the trend for large differences between nestlings early in life, but no significant differences toward the end of the nestling period, may have arisen partially as result of differences in egg-quality between control and treated territories. Hatching success is reduced when bluebird parents nest in territories with high-fire ant abundance (Ligon et al. 2011), and the factors that influence hatching rate (such as poor female body condition; Lain & Rajasilta 1999) are also likely to play a role in the body condition of recently hatched offspring. Specifically, female passerine birds in worse body condition tend to lay smaller eggs (Robinson et al. 2010), which can lead to smaller hatchlings (Smith et al. 1993). It is also worth considering the possibility that nestlings from low- and high-ant territories may have also differed in traits other than the readily observable morphological characters that we used to quantify body condition. Nestlings from territories with greater fire ant abundance were fed at lower rates, which can increase stress levels (Rensel et al. 2010), compromise immunocompetence (Saino et al. 1997), and hinder cognitive development (Nowicki et al. 1998). Unfortunately, we did not measure cognition, stress hormones, or immunocompetence of the nestlings in our study.

Managing, mitigating, and ameliorating the negative effects of invasive species requires knowledge of the specific impacts that such introduced taxa have on native species, as well as an understanding of the biological needs of the non-native species. It is our hope that the present manuscript aids in this process by providing a more complete understanding of how fire ants can indirectly affect the reproductive strategies and success of a native insectivorous bird (Ligon et al. 2011). We have previously shown that increased fire ant abundance reduces the seasonal reproductive success of eastern bluebirds (Ligon et al. 2011), and the behavioral changes we have documented here appear to be the proximate mechanisms underlying these larger shifts in seasonal reproductive success. Additionally, the shifts in foraging behavior and the altered offspring provisioning rates we document here are also likely related to the previously documented reduction in hatching success, reduction in the likelihood of re-nesting in a given territory,

and reduction in male/female offspring sex ratios for bluebirds nesting in territories with high densities of fire ants (Ligon et al. 2011). Because parents in control territories fed offspring at lower rates, they may have had to forage for a greater portion of the day to adequately provision their growing young. This would reduce time available for self-maintenance behaviors and could potentially reduce future hatching success (Barbraud & Chastel 1999), alter offspring sex ratios (Whittingham & Dunn 2000), and reduce survival (Siefferman & Hill 2008). To determine the long-term impacts of fire ants on individual bluebird adults, it would be highly informative to analyze survival and return rates of bluebird parents in subsequent years.

Here, we document the proximate-level impacts of resource competition between fire ants and eastern bluebirds in an attempt to explain the larger, ecosystem-level impacts of this invasive species on a native passerine bird. Fire ants negatively influence the seasonal reproductive success of bluebirds at our study site, as well as the likelihood of re-nesting and even offspring sex-ratio (Ligon et al. 2011). Coupled with the results of the present study, these observations demonstrate both the negative impacts of fire ants on the reproductive success and reproductive behavior of eastern bluebirds as well as the mechanisms by which these negative impacts are manifested.

Acknowledgements

Ethical Standards

The authors declare that the present study complies with the current laws of the United States.

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