REPRODUCTION OF EASTERN BLUEBIRDS (*SIALIA SIALIAS*) IN RELATION TO FARMLAND MANAGEMENT AND FOOD RESOURCES IN NORTH-CENTRAL FLORIDA

By

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A THESIS PRESENTED TO THE GRADUATE SCHOOL
OF THE UNIVERSITY OF FLORIDA IN PARTIAL FULFILLMENT
OF THE REQUIREMENTS FOR THE DEGREE OF
MASTER OF SCIENCE

UNIVERSITY OF FLORIDA

2008

To my parents, Joe and Linda DeLuca

ACKNOWLEDGMENTS

The USDA Southern Region Sustainable Agricultural Research and Education (SSARE) graduate student grants program funded this research, in part, with additional funding from the Department of Wildlife Ecology and Conservation. K.E. Sieving helped enormously with the design, implementation, and presentation of this research. P.C. Frederick and S.K. Robinson provided insight into research design and valuable comments on earlier drafts of this manuscript. M.C. Christman and R.J. Fletcher provided much-appreciated statistical advice. J. Altman, A. Arner, K. Church, C. Lord, S. Hicks, I. Stark, and J. Teagarden contributed significantly as volunteer field technicians.

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Abstract of Thesis Presented to the Graduate School
of the University of Florida in Partial Fulfillment of the
Requirements for the Degree of Master of Science

REPRODUCTION OF EASTERN BLUEBIRDS (SIALIA SIALIAS) IN RELATION TO FARMLAND MANAGEMENT AND FOOD RESOURCES IN NORTH-CENTRAL FLORIDA

By

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December 2008

Chair: Kathryn E. Sieving
Major: Wildlife Ecology and Conservation

Conservation ornithologists cannot responsibly promote farmlands as avian habitat without first evaluating the effects of farmlands on avian populations. In 2007, we examined the effects of land management (reduced-impact farms [e.g., organic], conventional farms, and natural control areas) on the reproductive success and breeding behavior of the Eastern Bluebird (*Sialia sialis*). Farmland bluebirds began breeding earlier and produced more clutches and eggs than bluebirds in natural areas, but they produced the same number of fledglings over the breeding season. Differences in reproductive parameters between reduced-impact and conventional farms were minor. In 2008, we explored the mechanistic hypothesis that land management influences arthropod prey availability, which in turn influences bluebird reproductive success and breeding behavior. Prey was more bountiful but more unstable on farms over the course of the breeding season; prey biomass during the early breeding season was inversely correlated with first-egg-date; and higher variation in prey biomass inversely correlated with hatchling production during first broods. In comparison to natural areas, farmlands (especially reduced-impact) appeared to provide suboptimal but not necessarily poor habitat for breeding bluebirds. Future research should incorporate survivorship, mortality, and the effects of predation and human disturbance.

CHAPTER 1
GENERAL INTRODUCTION

Promoting farmlands as bird habitat may at first seem attractive to both conservation planners and farmers (Jacobson et al. 2001; Green et al. 2005; Fischer et al. 2008). However, we cannot responsibly encourage habitat management to increase birdlife on farmlands without first evaluating the suitability of farmland habitats in terms of bird population viability and health. Nevertheless, a variety of motivations exist to increase birdlife on farms: Government and consumers are pushing for biodiversity-friendly food-production on farmlands (Grankvist and Beal 2001; Wild Farm Alliance 2005); farmers often appreciate and foster non-pest birdlife on their lands (Jacobson et al. 2003); and as agricultural conversion of natural habitat continues to escalate, conservation planning processes increasingly identify farmlands as necessary to provide sufficient habitat for the protection of viable wildlife populations and communities (Tilman et al. 2001; Fischer et al. 2008). However, ecologists have only recently begun to understand how farmland management (e.g., organic and sustainable farming [i.e., "reduced-impact"] vs. conventional farming techniques) influences the composition, sustainability, and health of non-pest bird communities that use farmlands (Hole et al. 2005; Jones and Sieving 2006). For example, researchers have yet to compare avian reproductive success among conventional farms, reduced-impact farms, and natural open lands. However, such comparisons are needed to gauge the quality of farmlands as habitat for sustaining healthy bird communities. Work presented here addresses this goal and provides insights regarding the potential for avian conservation on farmlands.

Chapter 2 presents a comparative analysis of the effects of land management on the reproductive success and breeding behavior of Eastern Bluebirds (*Sialia sialis*). Reduced-impact farms and conventional farms served as treatment groups and natural areas served as a control.

We compared measures of reproductive success and breeding behavior among these land-management types, including: clutch, egg, hatchling, and fledgling production; nestling body condition and growth status; and first-egg-date, incubation period, and interbrood lapse. We did not detect major differences between bluebird reproduction on reduced-impact and conventional farms. However, farmland bluebirds (in general) began breeding earlier and produced more clutches and eggs than bluebirds in natural areas, but they produced the same number of fledglings over the breeding season.

In Chapter 3, we addressed the potential for food as a mechanism underlying these patterns. We assessed whether arthropod prey resources for bluebirds varied between farms and natural control areas, and whether prey resource differences between land management types were correlated with reproductive success and breeding behavior. We sampled arthropod prey using two distinct transect methods, and we used the data to calculate prey biomass and biomass-stability indices. Dependent variables included clutch production, first-clutch egg and hatchling production, and first-egg-date. The amount of prey available in the early breeding season inversely correlated with first-egg-date. Prey resources were greater in amount but more unstable on farms. Prey instability inversely correlated with first-clutch hatchling production, and farmland bluebirds produced fewer first-clutch hatchlings than those in natural control areas. In comparison to natural areas, farmlands (especially reduced-impact) appeared to provide suboptimal but not necessarily poor habitat for breeding bluebirds.

In Chapter 4, we address if "wildlife-friendly farms" are really wildlife-friendly. We recommend that future research focus on the effects of farm management on survivorship, mortality, and habitat preference in addition to reproductive success, thereby allowing researchers to assess whether farms serve as habitat sources, sinks, or even ecological traps. We also recommend studying differences in predation among farms and natural areas, as well as the effects of human disturbance on farmland wildlife. Finally, we suggest that future research occur over a larger spatial scale with a focus on open-land species of conservation concern.

CHAPTER 2
EFFECT OF LAND MANAGEMENT ON THE REPRODUCTIVE SUCCESS OF A SONGBIRD OF OPEN LANDS

Introduction

Farmland as Wildlife Habitat

Agricultural lands can be managed for both food and biodiversity production, and there is increasing pressure on many farmers to do so. The U.S. Department of Agriculture has released guidelines that require attention to biodiversity protection on organic farms (Wild Farm Alliance 2005). Moreover, increasingly health- and environmentally-conscious consumers are creating market demands for produce branded with biodiversity-friendly certifications (e.g., Smithsonian-certified bird-friendly coffee; Grankvist and Beal 2001). Farmers themselves also show interest in increasing biodiversity on their lands. A survey of family farmers in North-central Florida indicated that most of them think that birds could help control insect pests and that they would like to attract such birds to their farms (n=26 organic farms, 50 conventional; Jacobson et al. 2003). Finally, as global agricultural expansion is projected to replace upward of one billion hectares of natural habitat during the next fifty years, conservationists are increasingly eyeing farmlands as critical habitat to augment insufficiently small protected areas (Tilman et al. 2001, Fischer et al. 2008). The argument is that if agriculture can provide some use to many species and suitable habitat for a few, then it could serve as an ecological buffer around natural areas to boost their biodiversity-holding capacity (Phillips 2002).

Natural habitats and landscape mosaics that are fragmented by agriculture, however, often do not sustain healthy ecological communities. For example, various studies from different biomes document high rates of nest failure for many interior-forest obligate birds in fragments surrounded by agriculture (Ford et al. 2001, Rodewald and Yahner 2001*a* and *b*, Albrecht 2004, Knutson et al. 2004, Peak et al. 2004, Tewksbury et al. 2006). Fragments suffer higher rates of exotic species invasion and nest predation (Rodewald and Yahner 2001*b*, Tewksbury et al. 2006) and generally diminished species richness and evenness of native communities (Rodewald and Yahner 2001*b*). Though farmlands may create population sinks or ecological traps for forest-requiring species (e.g., Wood Thrush [*Hylocichla mustelina*], Fauth 2001, Zuria et al. 2007), current thinking is that they may provide suitable habitat for species that can tolerate, or that prefer, lands where native ecosystems have been cleared for human land uses involving natural resource production (e.g., for food or fiber). Indeed, a central focus in conservation research is to characterize the potential values of "wildlife-friendly farms" (Green et al. 2005, Fischer 2008) and farming landscapes more generally as biodiversity buffers (Daily et al. 2001, Sekercioglu et al. 2007).

Farm Management and Avian Reproductive Success

Avian reproductive success typically appears to be higher on organic and other reduced-impact farms than on conventional farms (see Table 2-1 for definitions, Patnode and White 1991, Hatchwell et al. 1996, Wilson et al. 1997, Bishop et al. 2000*a* and *b*, Brickle et al. 2000, Mayne et al. 2004 and 2005, Bouvier et al. 2005, Britschgi et al. 2006, Hart et al. 2006 – but see Graham and Desgranges 1993). Such variation suggests that some conventional farming operations may not provide useful or productive habitats for native birds, because reproductive success is one of the strongest indicators of habitat quality (Hall et al. 1997). However, such variation also suggests that farm management techniques can be developed to improve both species richness and habitat quality for native species on agricultural lands.

It is not enough to implement management techniques that simply increase wildlife use or species richness; suitable on-farm habitats must also provide critical resources that sustain or augment robust reproduction and population health (Hall et al. 1997). Ecological traps can easily be created on farms if species are attracted to use on-farm habitats for foraging (e.g., Jones and

Sieving 2006) or for reproduction (e.g., Mols and Vissar 2002) but suffer greater mortality or depressed reproduction as a result (Schlaepfer et al. 2002). To offer greater understanding of how habitat quality for native birds can vary on farms, we focused this study on the cavity-nesting Eastern Bluebird (*Sialia sialis*), an aesthetically popular species of open lands known to consume pest insects (Jones et al. 2005). We erected nest-boxes and compared reproductive success and nestling health among conventional and reduced-impact farms and natural control areas (see Table 2-1 for definitions). Our design allowed assessment of bluebird reproductive success on farmlands under different management regimes against reproduction of birds breeding in supposedly high-quality, natural habitat. Detailed analysis of bluebird reproductive parameters allowed us to addresses potential negative aspects of farmland bird conservation efforts involving nest-box provisioning on farmlands.

Research Design

We tested the hypothesis that land management affects Eastern Bluebird (*Sialia sialis*) reproductive success, breeding behavior, and nestling health in a comparative-observational study design. Reduced-impact farms and conventional farms represented treatment groups, and natural areas served as controls (Table 2-1). We placed approximately 100 nest boxes evenly across both farm treatments and 30 nest boxes in natural control areas. For nests established in these boxes, we monitored traditional indicators of avian reproductive success, including: production of clutches, eggs, hatchlings, and fledglings; hatching success; and nestling body condition and pre-fledging growth status (Clark and Martin 2007, Jakob et al. 1996). Since bluebirds lay multiple broods per breeding season (Gowaty and Plissner 1998), we monitored all nest attempts on study sites in 2007 so that we could account for expected declines in reproductive success measures that typically occur over the course of multiple broods over the course of a full breeding season (Slagsvold 1984, Smith et al. 1987, Tinbergen 1987, Gustafsson et al. 1994, Richner et al. 1995, Deerenberg et al. 1997, Nilsson and Svensson 1996, Raberg et al. 1998). We also documented key breeding behaviors known to influence reproductive success, including first-egg-date, interbrood lapse, and incubation period (see Table 2-1, Blanco et al. 2003, Hepp et al. 2006, Moller 2007).

A potential mechanism underlying differences in reproductive success and breeding behavior across treatments could be due to differences in food abundance, quality, and predictability, and/or the direct effects of pesticides. Because reduced-impact farms lack powerful, synthetic pesticides while also using mixed-crop planting methods, they may promote the species richness and abundance of arthropods, providing greater protein-rich food resources necessary for breeding birds than conventional farmlands (Feber et al. 1997, O'Leske et al. 1997, Jones et al. 2005, Britschgi et al 2006, Jones and Sieving 2006). The limited use or absence of pesticides on reduced-impact farms may also prevent negative, direct effects of pesticides seen on some conventional-farms (e.g., Patnode and White 1991, Bishop et al. 2000*a* and *b*, Mayne et al. 2004 and 2005, Bouvier et al. 2005). Though we do not test these mechanisms with measures of insects and pesticides in this study, previous work supports the operating assumption that food resources and direct pesticide effects are likely mechanisms underlying differences in reproductive success and breeding behavior, and that both factors vary predictably across our treatment and control sites (Patnode and White 1991, Korpimaki 1992, Phillips et al. 1996, Bishop et al. 2000*a* and *b*, Valkama et al. 2002, Mayne et al. 2004 and 2005, Bouvier et al. 2005, Davis et al. 2005, Lindstrom et al. 2005). We therefore predicted that bluebirds on reduced-impact farms would produce more clutches, eggs, hatchlings, and fledglings than bluebirds on conventional farms, and that their nestlings would be in better body condition and more advanced development just prior to fledging, suggesting a higher probability for post-fledging survival (Blanco et al. 2003, Hepp et al. 2006, Jakob et al. 1996).

To our knowledge, we are the first to compare the reproductive success of open-land birds on reduced-impact and conventional farmlands to the same species breeding in natural habitats of comparable vegetative structure. Therefore, predictions concerning reproductive success of bluebirds on farms versus our natural control areas were not obvious, though it seemed reasonable to expect that reproduction on reduced-impact farms would be closer to natural areas than conventional farms. However, an important subsidy that farmers provide is irrigation and fertilizer, and this may affect bluebird reproductive success and behavior. The late-winter planting season in Florida typically falls within the dry season (NOAA 2008); irrigation and fertilizer during this period artificially supports plant growth, which in turn could spur flushes of invertebrate prey on farms before natural areas. Since early flushes of food resources are common proximate causes of nesting initiation in breeding birds (Martin 1987, Nooker et al. 2005, Pimentel and Nilsson 2007), we predicted that bluebirds may start breeding earlier on farms than natural areas, and this could influence subsequent reproductive success measures (Elmberg et al. 2005, Nemeckova et al. 2008, Verhulst and Nilsson 2008).

Methods

Study Species

The Eastern Bluebird is a charismatic, primarily insectivorous, ground-gleaning, secondary cavity-nester of open lands. Females lay multiple broods and are the only parent that incubates, though males feed incubating females (Gowaty and Plissner 1998). Because of the species' penchant for using nest-boxes, bluebird reproduction is commonly studied and monitored by ornithologists and lay birders alike. The species was once uncommon in North America, but its populations have grown considerably due to community-based conservation efforts involving nest-box provisioning. However, it remains threatened in parts of its range (Gowaty and Plissner 1998). It is a logical choice as a study-species because 1) it is one of the three most common species found foraging on farmlands in North-central Florida (Jones et al. 2005), 2) it specializes on arthropods throughout the entire year (Gowaty and Plissner 1998), and 3) it takes readily to nest-boxes that can be strategically placed in different habitats for comparative analyses (Gowaty and Plissner 1998).

Study Sites and Nest-Box Placement

We conducted this research in North-central Florida (Alachua and Putnam Counties) during the entire breeding season of 2007 (February-August). We erected nest-boxes on six conventional farms, eight reduced-impact farms, and at four natural control areas within the Ordway-Swisher Biological Station property (> 3760 ha in area, see Table 2-1 for descriptions). Bluebird nest boxes have been provided and monitored in this protected area since the mid 1990's with sustained high levels of nest box occupancy and reproductive success (KES, *personal observation*). Most reduced-impact farms were USDA-certified organic operations or were managed in line with organic standards (but without certification). Cropping systems used in this study and that are characteristic of the region are described fully in Jacobson et al. (2003) and Jones et al. (2005). We asked growers about their use of synthetic pesticides before the beginning of field work. Three of eight reduced-impact farmers used synthetic pesticides (only one used insecticides), but they did so sparingly, only on certain crops at certain times. All participating conventional farmers applied insecticides and other pesticides on the entirety of their crops in multiple applications (for beans, corn, strawberries, tobacco, and/or melons, depending on the farm; we did not ask farmers the exact types or amounts of pesticides that they used).

No nest-box was placed less than 70 m from its nearest neighbor. Nest-boxes on farms were placed within 5 m of the edges of farm-fields (barren, fallow, or with active crop growth), and within at least 300 m of fields with actively growing crops at some point in the season. Nest-boxes in all treatments were within 50 m of protective cover and perching substrates used by bluebirds (e.g., hedgerows, windbreaks, forest). In order to control for predation, we mounted nest-boxes on narrow, metal poles (approximately 1.5 m high). We greased the poles when birds laid eggs and maintained these grease barriers throughout nesting (USDA Natural Resources Conservation Service 1999). If predators overcame this deterrence, then signs left in the grease or on the boxes allowed detection of predation events. We eliminated data from predated nests from statistical analyses as appropriate.

Data Collection

We monitored nest-boxes approximately every four days, when we recorded how many eggs and/or nestlings were in the nest, and the estimated age of nestlings (using the criteria of Gowaty and Plissner 1998). We consider a bird's first day of life as age, "Day 1." We identified a pair's second or third clutch if it was laid within the same box (typically the case) or if it was within 300 m of the pair's last nest-box and 1-3 weeks after the pair's last brood fledged. Confusion with neighboring pairs within a site was easily prevented because pairs would normally re-nest in the same box and neighbors typically had non-concurrent nesting cycles.

We calculated first-egg-date, incubation period, and interbrood lapse from these data (see Table 2-1 for definitions). Earlier first-egg-dates should correlate with higher clutch production over the breeding season, as bluebirds will presumably have more time to lay more clutches. Shorter incubation periods correlate with higher nestling quality (Blanco et al. 2003, Hepp et al. 2006). Eggs should take less time to hatch when females spend more time on the nest, and females should spend more time on the nest when they are able to forage more efficiently, they are fed more often by their mates, and/or food resources are better. Birds that take less time to re-nest may exhibit higher reproductive success, so interbrood lapse may serve as another indicator of the quality of breeding habitat (Moller 2007). We only included pairs that fledged at least one nestling from their first clutch in the calculation of interbrood lapse.

We uniquely identified nestlings by painting nail-polish on their claws during each visit. After approximately 6 days of age, we tagged them with unique color band-combinations. We recorded a nestling's weight (+/- 1.0 g) and left-tarsus length (+/- 0.1 mm, measured from the distal end of the tarsus to the second scale, counting toward the claws) at each visit. We recorded wing cord (+/- 0.5 cm) and the length of both tarsi at the pre-fledging stage (i.e., at or above 14 days of age). We calculated nestling Body Condition Index (BCI) and pre-fledging body-growth index (BGI) from these data (see Table 2-1). Both measures are standard indicators for nestling quality (Jakob et al. 1996, Navara et al. 2005). We classified nestlings into six categories, as follows: 3 days < Category 1 < 5 days < Category 2 < 8 days < Category 3 < 10 days < Category 4 < 12 days < Category 5 < 14 days. Category 6 included nestlings at or above 14 days of age, and BGI analysis only included nestlings from this category.

Statistical Analysis

Analyses were conducted using general linear and generalized linear mixed models in SAS 9.1 (see Table 2-2 for model descriptions). Whenever using a normal distribution, we first ensured that data met assumptions of normality using q-q plots and those of homoscedasticity using Levene's Test. We used Tukey's test for pairwise comparisons (alpha=0.05). We used the Kenward-Roger method for calculating degrees of freedom.

All but one pair of bluebirds in the natural control failed to produce three clutches, and many birds in the farm treatments laid three. We therefore conducted two types of analyses for the clutch-level and nestling-level data (Tables 2-1 and 2-2). "All-treatments" analyses included all three treatments, with just clutches/broods 1 and 2, and "Farms-only" analyses included only conventional and reduced-impact farms (i.e., we eliminated the only pair of natural control birds that laid a third clutch), with all three clutches/broods included. Two pairs on conventional and reduced-impact farms laid a fourth clutch, but we could not analyze these data at the clutch- or nestling-level (see Table A-1 for raw data). We could not nest bluebird pairs by site-ID in our models; covariance matrices necessary for analysis could not be calculated due to insufficient data at the site-level (e.g., several sites only had 1-3 nesting pairs; Table A-2). However, if there is high between-site variation within each treatment category, any land management differences that are observed should be very strong, making our analyses conservative in nature.

Results

Season-Level Reproductive Success and Breeding Behavior

Twelve of twenty models produced significant results (alpha=0.05; see Table 2-3 for detailed results of all models). First-egg-date was earlier and interbrood lapse shorter on farms, in general, than on natural control areas (Figure 2-1; Table 2-3). First-egg-date and land management were both related to season-level production of eggs. Earlier first-egg-dates corresponded with bluebirds that produced more eggs over the breeding season (Figure 2-2; Table 2-3), and both farm treatments hosted birds that laid more eggs than in the natural control area (Figure 2-3; Table 2-3). Although not statistically significant, the production of 3 clutches by many farmland bluebirds versus 2 by those on natural sites appears to be a biologically significant difference in clutch production (Table 2-3), as the production of third clutches requires a greater expenditure of time and energy for egg production and incubation. Many pairs of bluebirds went on to lay a third clutch on reduced-impact and conventional farms (Table 2-3). On the contrary, only one pair of bluebirds in the natural control area produced a third clutch (and this was only its second brood).

Clutch-Level Reproductive Success and Breeding Behavior

As mentioned earlier, we ran two different types of clutch-level analyses, one with all treatments but just the first two clutches (All-treatments analysis), and another with just farm treatments compared across the first three clutches (Farms-only analysis). All-treatments analyses that land management correlated with hatchling production and hatching success, with bluebirds on conventional farms producing significantly fewer hatchlings and exhibiting significantly lower hatching success than those in natural control areas (Figure 2-3; Tables 1-4 and 1-5). Bluebirds on reduced-impact farms incubated for significantly less time (Figure 2-4; Table 2-3) compared to bluebirds on natural control areas. Second clutches, regardless of land management, took less time to incubate than first clutches (Figure 2-4; Table 2-3). Bluebirds on reduced-impact farms also produced fewer fledglings in their second clutch than in their first (Figure 2-3; Table 2-3).

Farms-only analyses revealed the following patterns for birds nesting on conventional and reduced impact farms. Clutch-order correlated with hatchling and fledgling production, with bluebirds on both farm types producing significantly fewer hatchlings and fledglings in their third clutch than their first (Figure 2-3; Table 2-3). Hatching success was also much lower in third than first clutches (Figure 2-3; Table 2-3). Farms-only results confirmed and extended the all-treatments results in regard to the correlation of clutch-order and incubation period; second and third clutches took significantly less time to incubate than first clutches (Figure 2-4; Table 2-3).

Nestling-Quality Indicators

The only significant nestling-level result came from Farms-only analysis of BCI. Nestlings from second and third broods exhibited significantly lower body condition than those from first broods (Figure 2-5; Table 2-3).

Discussion

Farmland Bluebirds Begin Nesting Earlier

Land management clearly affects the reproductive success and breeding behavior of Eastern Bluebirds. Bluebirds in both farm treatments laid their eggs much earlier than those in natural control areas, confirming a central prediction about the possibility that farm management (e.g., presence of irrigation, fertilizer, crop vegetation, and/or different prey resources) could spur earlier breeding. Also, pairs that produced their first clutch earlier went on to produce more clutches over the breeding season, confirming a pattern we assumed would occur based on previous documentation of the reproductive advantage of early nesting (Figures 1-1 and 1-2; Table 2-3; Elmberg et al. 2005, Nemeckova et al. 2008, Verhulst and Nilsson 2008). It is likely that differences in prey availability during the months of February and March may have driven earlier first-egg-dates, though we did not test that mechanism in this study. These months corresponded to the dry season of our study region, when natural areas lacked green vegetation and moisture (NOAA 2008; JJD *personal observation*). Most participating farmers grew crops year-round on our farmland study sites, except July to September, and most of them irrigated and fertilized their fields throughout the dry season (JJD *personal observation*). The earlier presence of green vegetation due to fertilizer and water on farms may have allowed arthropod prey populations to approach adequate levels to spark earlier breeding in Eastern Bluebirds on these lands (Martin 1987, Nooker et al. 2005, Pimentel and Nilsson 2007). However, despite an earlier start and a greater production of clutches and eggs on farms, net fledgling production of farmland birds was no different than birds nesting on natural areas.

Farmland Bluebirds Reproduce Less Efficiently

First-egg-date and land management both affected clutch production (and consequently, total egg production; Figures 1-2 and 1-3; Table 2-3). Bluebird pairs in both farm treatments produced more eggs over the breeding season than bluebirds in natural control areas (Figure 2-3; Table 2-3). However, bluebirds in all land management groups ended up producing statistically similar numbers of hatchlings and fledglings at the season-level of analysis (Figure 2-3; Table 2-3). While our models did not detect a treatment-by-clutch-order interaction in hatching success, we did detect significant declines in hatching success and fledgling production over the course of the 2007 breeding season on the two farmland treatments (Figures 1-3 and 1-5; Table 2-3). Given that over the entire breeding season of 2007, 24-30% of eggs on farms were produced in third and fourth clutches (versus only 4% of eggs produced after the second clutch on natural control areas), a significant decline in hatching success with clutch order on farms explains how relatively greater seasonal clutch and egg production on farms did not result in greater fledging success on farms relative to natural areas (Table 2-4). Thus, on farmlands in our study, an early start on breeding did not result in greater seasonal production of young as has been observed in various avian taxa in natural habitats (Elmberg et al. 2005, Nemeckova et al. 2008, Verhulst and Nilsson 2008).

The mechanism behind this relative reproductive inefficiency is likely to be linked to differences in availability or access to prey resources on farms in comparison to natural areas. As crops are sowed and harvested and the fallowing of fields waxes and wanes, arthropod communities may cycle more dramatically on farms than on natural sites (Nebel and Wright 1993). Alternatively, the day-to-day activity of farmers may induce reproductive inefficiency on farms. Perhaps the noise and/or movement of people, tractors, and trucks near nest-sites disturb breeding bluebirds on farms, thereby decreasing reproductive success (Yasue and Dearden 2006).

Bluebird Reproductive Behavior and Offspring Quality

Bluebirds in both farm treatments exhibited a shorter interbrood lapse than those in natural control areas (Figure 2-1; Table 2-3), and in all-treatments analyses we found that bluebirds on reduced-impact farms spent much less time incubating than those in natural control areas (Figure 2-4; Table 2-3). Both shorter interbrood lapse and shorter incubation times have been linked to higher quality offspring, suggesting that the greater effort of bluebirds on farms may result in similar numbers of young, but young of higher quality (at least early in the breeding season; Blanco et al. 2003, Hepp et al. 2006, Moller 2007).

To date, few studies have examined the effects of interbrood lapse on reproductive success, but Moller (2007) detected an inverse correlation between interbrood lapse and the strength of nestling immunity in first broods of Barn Swallows (*Hirundo rustica*), another cavity-nesting passerine of open lands. This finding suggests that first-brood nestlings in both farm treatments may have had higher immunocompetency than their natural counterparts, resulting in a survival advantage for the young birds (Moller 2007). However, extrapolation is not straightforward because 1) no causal link has been established between interbrood lapse and immunocompetency (only correlation) and 2) in our study, various other factors could reasonably affect immunocompetency. For example, the use of chemical pesticides on conventional farms may actually compromise nestling immunocompetency, neutralizing or overriding any potential effects of a shorter interbrood lapse (Patnode and White 1991, Bishop et al. 2000*a* and *b*, Mayne et al. 2004 and 2005, Bouvier et al. 2005). However, while we cannot conclude anything without data on immunocompetency of bluebird young in our study, we can propose a hypothesis that farmland bluebird breeding behavior (in this case rapid re-nesting) may be able to offset lower reproductive efficiency over the season by increasing the quality of nestlings, especially those produced early in the breeding season.

On the same theme, shorter incubation periods have been linked to the production of higher quality young; specifically, hatchlings with greater residual reserves and potentially increased survival (Blanco et al. 2003, Hepp et al. 2006). All-treatments analysis revealed that bluebirds on reduced-impact farms exhibited shorter incubation periods than those in natural control areas. Since a) the dataset in this analysis was dominated by nestlings from first broods, b) BCI values of first-brood nestlings were relatively high (Figure 2-4; Table 2-3), and c) incubation period has been shown to have an inverse relationship with nestling quality (Blanco et al. 2003; Hepp et al. 2006), we think that bluebirds from first broods on reduced-impact farms may have been of higher quality than their counterparts in natural control areas. If true, then this may offset, at least in part, the negative fitness effects of reproductive inefficiency on reduced-impact farms.

We cannot find much support to extend such conclusions to second and third broods on farms. Bluebirds incubating second and third broods did so for less time than first broods (Figure 2-4; Table 2-3). However, unlike nestlings from first broods, body condition indices of second- and third-brood nestlings were very low (Figure 2-5; Table 2-3). This indicates that these nestlings were of poor quality (Jakob et al. 1996) and that their relatively shorter incubation periods had more to do with environmental factors (as opposed to somatic or parental care factors). Indeed, later clutches may have taken less time to incubate because of higher ambient temperatures that can speed development during incubation (Hepp et al. 2006) but may also degrade embryo health (Londono et al. 2008).

Despite breeding behavior that suggests that farmland bluebirds might have produced some higher quality offspring than bluebirds in natural areas, we think it is highly unlikely overall. First, our statistical models did not detect a significant interaction between treatment and BCI, nor did clutch-order have an effect in all-treatments analysis – broods 1 and 2 showed no difference in nestling body condition. Second, when we restricted clutch-level analyses to only farms (looking across all clutches), we found that farmland nestlings from second and third broods exhibited much lower body condition than those from first broods (Figure 2-5). Altogether, this suggests that bluebirds in natural control areas produced high-quality nestlings in both of their broods, but farmland bluebirds only produced high-quality nestlings in their first broods. Since over half of all farmland offspring were produced in second and third broods (49 of 85 on conventional farms and 90 of 161 on reduced-impact farms), any immunocompetency or other survival advantages possibly conveyed to farmland fledglings earlier in the breeding season via shorter incubation or inter-brood periods are unlikely to outweigh the effects of such a high proportion of nestlings in relatively poor body condition.

Finally, according to life-history theory, prior reproductive effort lowers a female's body condition which, in turn, negatively affects the development of eggs and the survival of nestlings in future breeding attempts (Slagsvold 1984, Smith et al. 1987, Tinbergen 1987, Gustafsson et al. 1994, Richner et al. 1995, Deerenberg et al. 1997, Nilsson and Svensson 1996, Raberg et al. 1998). The declines in hatching success, hatchling production, and nestling BCI of farmland bluebirds in later clutches are all in line with basic predictions based on life-history theory (Figures 1-3 and 1-5; Table 2-3). But these declines were only evident or detectable in farmland birds because they laid so many clutches during the 2007 season. These same declines in life history parameters would likely have been observed on natural areas had bluebirds nesting there not stopped after their second clutches. Due to the necessity of nesting more times later in the season to boost overall offspring production on farmlands, predictable late season declines in egg viability and offspring BCI weighed more heavily on season-level reproductive success measures. Bluebirds on farms worked harder for (at best) the same, or very likely worse, results than bluebirds breeding on natural areas. This was especially true for bluebirds on conventional farms, given that clutch-level analyses revealed that these birds exhibited much poorer hatching success and produced many fewer hatchlings than bluebirds in natural control areas, especially in their second clutch (Figure 2-3; Table 2-4).

Differences between Reduced-Impact and Conventional Farms

Bluebird reproductive success or breeding behavior did not differ substantially between reduced-impact and conventional farms. Bluebirds on conventional farms produced significantly fewer hatchlings than those in natural control areas at the clutch-level of analysis, but such a difference was not detectable for bluebirds on reduced-impact farms (Tables 2-3 and 2-4). Bluebirds on reduced-impact farms took significantly less time to incubate their early clutches than bluebirds in natural control areas, but bluebirds on conventional farms did not (Figure 2-4; Table 2-3), potentially indicating that first-brood nestlings on reduced-impact farms were of especially high quality (see above). However, we did not detect significant advantages of reduced-impact over conventional farms as avian breeding habitat, in terms of nestling production or condition, whereas other studies have (Patnode and White 1991, Hatchwell et al. 1996, Wilson et al. 1997, Bishop et al. 2000*a* and *b*, Brickle et al. 2000, Mayne et al. 2004 and 2005, Bouvier et al. 2005, Britschgi et al. 2006, Hart et al. 2006 – but see Graham and Desgranges 1993).

Farms as Suitable Habitat for Eastern Bluebirds

One season of data cannot fully address the question of whether farmlands in North-central Florida should be considered high quality habitat for breeding Eastern Bluebirds. High quality (or suitable) habitat has been defined in various ways (Hall et al. 1997), but the most essential elements include provision of critical needs (cover, food, water, and resources for reproduction) sufficient to sustain viable populations (productivity exceeds mortality) over time (Van Dyke 2005). Only a full sample of annual variation in environmental and demographic parameters affecting health and productivity can indicate whether lifetime fitness of bluebirds nesting on farms is sufficient to sustain healthy populations. The magnitude and direction of annual variation in weather, food availability, and associated reproductive success varies greatly among years for a variety of bird species (Korpimaki 1992, Phillips et al. 1996, McCleery et al. 1998, Rodl 1999, Valkama et al. 2002, Davis et al. 2005, Lindstrom et al. 2005). Rainfall in 2007 for North-central Florida was well below the normal range of rainfall values for the region (Table A-3; FAWN 2008). Relative reproductive output on farms versus natural areas may vary in degree and direction along with rainfall variation (e.g., McCleery et al. 1998). Based on this study, we therefore conclude that in one relatively dry year, reproductive output (number of offspring per pair) can be similar on farms and natural areas in this region (though farmland birds invested greater reproductive effort) and overall nestling quality may have been lower on farms.

We excluded predation as a potential factor (see Methods), so the best explanation for differences between our treatments lies in food resources (Korpimaki 1992, Phillips et al. 1996, Valkama et al. 2002, Davis et al. 2005, Lindstrom et al. 2005). In particular, the earlier first-egg-dates that we observed on farms were probably due to earlier prey availability (Martin 1987, Nooker et al. 2005, Pimentel and Nilsson 2007). Irrigation and fertilizer inputs causing early-season presence of green crop vegetation (in February-April) may instigate earlier and faster pest (prey) population growth on farms than natural areas; the latter typically continue to be exposed to dry season conditions until late May in this region (NOAA 2008). Higher food availability during the early breeding season may also serve as the mechanism behind shorter incubation periods and interbrood lapses that we observed on reduced-impact farms (e.g., Nooker et al. 2005).

Farmland bluebird pairs may reproduce less efficiently because prey populations may be more volatile on farms. Farm-fields constantly change; farmers plant and harvest crops and leave certain fields fallow while they till others. Such an unstable vegetative landscape may cause prey populations that rely on crops or fallow fields to go through population explosions and crashes (Nebel 1993). In a companion study, we explore hypotheses that farming affects prey resources and, in turn, avian reproductive success (see Chapter 3).

Lastly, assessing the suitability of farmland habitats requires a large spatial scale perspective. Our results suggest that if bluebirds were constrained to breed on farmlands over their lifetimes, then the higher effort associated with more broods per season would reduce lifetime fitness. Life history theory indicates that higher current reproductive effort should decrease future reproductive output and parental survival (Slagsvold 1984, Smith et al. 1987, Tinbergen 1987, Gustafsson et al. 1994, Richner et al. 1995, Deerenberg et al. 1997, Nilsson and Svensson 1996, Raberg et al. 1998). Under this theory, we would expect that bluebirds in natural areas will exhibit greater future reproductive success and survive longer because they produced the same number of fledglings with less effort (Figure 2-1; Table 2-3). However, we have no reason to suspect that bluebird populations are restricted to breeding on farms in North-central Florida because 1) natal philopatry in this species is less than 15% (Gowaty and Plissner 1998), 2) the landscape in the region maintains a high proportion of area in uncultivated and natural habitats, and 3) most farms are too small to support self-sustaining populations (Jones et al. 2005, Jones and Sieving 2006). Thus it is likely that in this region, bluebirds do not currently suffer population-level effects of reduced reproductive efficiency, such as we detected, over the long term.

Future Research and Management Recommendations

This study is among the first to compare Eastern Bluebird reproduction on natural versus human-managed lands (Mayne et al. 2004 and 2005, LeClerc et al. 2005, Stanback and Seifert 2005, Kight and Swaddle 2007). Only in the comparison of natural habitats to human-managed lands can we understand how land management affects native species. Many studies have documented occupancy and use of farmlands by birds (e.g., Daily et al. 2001, Jones and Sieving 2006), foraging activity (e.g., Jones et al. 2005, Sekercioglu et al. 2007) and reproductive success on farmland habitats (e.g., Sekercioglu et al. 2007). Others have shown how wild birds can improve agricultural productivity through consumption of insect pests (Greenberg et al. 2000, Mols and Visser 2002, Phillips 2002, Hooks et al. 2003, Jones et al. 2005, Borkhataria et al. 2006). However, true integration of bird conservation with agricultural production must go further than simply attracting more species to farmlands and promoting biodiversity for the purpose of promoting food production. We must document that farming systems can provide good quality habitat for wild birds. Future research addressing these issues should 1) occur at the largest scales practical, in order to capture population-level implications of land management; 2) occur over several years if possible; 3) assess food resource and mortality factors associated with land management regimes; and 4) compare, as we did, reproductive performance on farms against performance on naturally-occurring suitable habitats with long histories of occupancy and successful reproduction of the species in question. It is not enough to document wildlife use of human-dominated landscapes; fostering true integration of wildlife conservation in land management schemes requires documentation of population viability (Hall et al. 1997).

That being said, farmland managers must increasingly provide habitat for displaced wildlife of open lands as agricultural conversion of natural habitats continues to rise (Tilman et al. 2001). Biodiversity conservation on agricultural lands is increasingly considered an important component of large-scale conservation planning worldwide (Green et al. 2005, Fischer et al. 2008). Farmlands are thought to provide buffers around natural areas, softening the influences of more urbanized environments on natural ecosystem processes and wildlife populations by providing productive habitat for some species and at least marginal uses for other species that may depend on natural areas but can utilize more damaged ecosystems for some resources (Phillips 2002).

In summary, our research suggests that farmlands in general provide suboptimal but productive habitat for breeding bluebirds, at least in dry years (but see discussion of our study's limitations above). However, our research is consistent with other findings that suggest that not all agricultural lands can provide buffers of equal value to wildlife (Hole et al. 2005). Eastern Bluebirds on conventional farms produced fewer hatchlings than those on natural control areas at the clutch-level of analysis (Tables 2-3 and 2-4), and they did not exhibit advantages over natural control areas in terms of incubation period (as was the case for those on reduced-impact farms; see above; Figure 2-4 and Table 2-3). Prior research generally confirms that bird populations fare better on reduced-impact farms than on conventional farms (Hole et al. 2005). We therefore recommend that reduced-impact farms receive priority over conventional farms in regard to conservation efforts geared toward the augmentation of avian biodiversity on farmlands or the incorporation of farmlands as buffer habitat for protected areas.

Table 2-1. List of terms and definitions

Term	Definition
Reduced-impact farms	Non-orchard farms with a variety of different crops mixed row by row; Host a low ratio of crop to non-crop vegetation in the landscape; Lack powerful, synthetic pesticides
Conventional farms	Non-orchard monocultures (acres of field, and therefore several bluebird territories [Gowaty and Plissner 1998] are planted with just one crop); Host a high ratio of crop to non-crop vegetation in the landscape; Frequently treated with insecticides and other pesticides
Natural control areas	Abandoned farm-fields/pastures with a mixture of native and non-native vegetation, within a matrix of long-leaf pine (*Pinus palustris*) and mesic and hydric hardwood forest; An evolutionarily historic habitat of the Eastern Bluebird (Gowaty and Plissner 1998)
Clutch	A set of eggs laid by a breeding pair of birds; Eastern Bluebirds lay multiple clutches per breeding season
Brood	A clutch that produced at least one hatchling
Hatchling	A nestling hatched from an egg
Fledgling	A hatchling that presumably survived and left (i.e., fledged) its nest
First-egg-date	The date that the first egg of the first clutch of a pair was laid; Calculated under assumption that females lay one egg per day and that they do not lay eggs past 1100 hours EST (Gowaty and Plissner 1998); An earlier first-egg-date may correlate with greater clutch production
First-egg-day	A translation of first-egg-date, for purposes of statistical analysis and presentation; "Day 1" corresponds to February 1st
Incubation period	The period between the time when the last egg of a clutch was laid and its eggs hatched (Gowaty and Plissner 1998); A shorter incubation periods may indicate higher quality of breeding habitat
Interbrood lapse	The period between the time that the first clutch hatched and the first egg of the second clutch was laid; A shorter interbrood lapse may indicate higher quality of breeding habitat
BCI	Nestling body-condition index; Calculated from the residual of the regression of ln(weight) on ln(tarsus length); Higher values correspond to nestlings with greater body condition
BGI	Nestling pre-fledging body-growth index; calculated from the residual of the regression of ln(weight) on ln(wing cord) (Jakob et al. 1996); Higher values correspond to more developed nestlings that presumably have a better chance of survival
Pair-ID	Unique identification given to a pair of bluebirds
Brood-ID	Unique identification given to one of potentially several broods of a pair of bluebirds

Table 2-2. Description of statistical models

Analysis Level	Purpose	Dependent Variables	Fixed Effects	Random and Repeated Effects
Season-level	Analyze reproductive success at the coarsest scale (i.e., over the entire breeding season)	First-egg-date; Interbrood lapse; Total # clutches*, eggs*, hatchlings*, and fledglings* produced over the entire breeding season	Land management (reduced-impact farms, conventional farms, natural control areas); first-egg-date also included in analyses of clutch and egg production	None
Clutch-level (All-treatments)	Analyze clutch-by-clutch reproductive success; Includes all treatment groups; Limited to first two clutches, as only one pair in the natural control group laid a third clutch	# Eggs*, hatchlings*, and fledglings* produced; Hatching success*; Incubation period	Land management (reduced-impact farms, conventional farms, natural control areas); clutch-order; land-management*clutch-order	Pair-ID nested by Land Management
Clutch-level (Farms-only)	Analyze clutch-by-clutch reproductive success; Includes clutches 1-3, but only but limited to reduced-impact and conventional farms	Same as above	Same as above, but land management groups restricted to reduced-impact farms and conventional farms	Same as above
Nestling-level (All-treatments)	Analyze clutch-by-clutch nestling BCI and BGI; Includes all treatment groups; Limited to first two clutches	BCI and BGI of a randomly selected nestling from each brood; BGI recorded once at or above 14 days of age (pre-fledging stage); BCI measured several times throughout development	Land management (reduced-impact farms, conventional farms, natural control areas); brood-order; land-management*brood-order; age-class, land-management*age-class also included in BCI analysis	Pair-ID nested by Land Management for analyses of BCI and BGI; Nestling-ID nested by Pair-ID by Land Management also included for analysis of BCI
Nestling-level (Farms-only)	Analyze clutch-by-clutch nestling BCI and BGI; Includes 1st-3rd clutches, but only but limited to reduced-impact and conventional farms	Same as above	Same as above, but land management groups restricted to reduced-impact farms and conventional farms	Same as above

* Indicates a model that assumed a binomial, rather than normal, distribution. Incubation period analyses replaced clutch-order with brood-order (definitions in Table 2). "All-treatments" analysis of incubation period did not include land-management*brood-order in the model, as the model would have been overparameterized. We did not analyze clutch-level fledging success because the dataset did not meet necessary convergence criteria.

Table 2-3. Results

Analysis Level	Model ID	Dependent Variable	Independent Variable	Num. DF	Den. DF	F Value	*p*-value	Sig. post-hoc results
SL	1	First-egg-day	LM	2	43	5.90	0.0054	RIF,CF<NC
	2	Interbrood Lapse	LM	2	35	9.32	0.0006	RIF,CF<NC
	3	Clutches	LM	2	43	0.95	0.3934	
			FED	1	43	3.59	0.0650	
	4	Eggs	LM	2	43	4.04	0.0012	NC<RIF, CF
			FED	1	43	12.04	0.0246	see Figure 2-3
	5	Hatchlings	LM	2	49	1.95	0.1550	
	6	Fledglings	LM	2	37	1.11	0.3409	
CL (AT)	7	Eggs	LM	2	55	0.41	0.6654	
			CO	1	84	0.55	0.4616	
			LM*CO	2	84	0.34	0.7140	
	8	Hatchlings	LM	2	44	2.63	0.0836	CF<NC
			CO	1	85	0.12	0.7296	
			LM*CO	2	85	2.83	0.6460	
	9	Hatching Success	LM	2	45	3.47	0.0396	CF<NC
			CO	1	85	0.35	0.5566	
			LM*CO	2	85	3.60	0.0317	CF.2<NC.2
	10	Fledglings	LM	2	40	2.18	0.1265	
			CO	1	81	1.46	0.2304	
			LM*CO	2	81	3.40	0.0382	RIF.2<RIF.1
	11	Incubation Period	LM	2	43	4.63	0.0151	RIF<NC
			BO	1	34	14.38	0.0006	2<1
NL (AT)	12	BCI	LM	2	62	0.06	0.9376	
			BO	1	259	1.63	0.2035	
			AC	5	266	1.52	0.1840	
			LM*BO	2	258	1.74	0.1784	
			LM*AC	10	264	1.73	0.0744	
	13	BGI	LM	2	34	0.74	0.4862	
			BO	1	22	0.29	0.5980	
			LM*BO	1	22	0.52	0.4793	
CL (FO)	14	Eggs	LM	1	36	1.32	0.2582	
			CO	2	79	2.55	0.0847	
			LM*CO	2	79	0.39	0.6774	
	15	Hatchlings	LM	1	27	2.74	0.1094	
			CO	2	81	5.49	0.0058	1<3

Table 2-3 Continued.

Analysis Level	Model ID	Dependent Variable	Independent Variable	Num. DF	Den. DF	F Value	p-value	Sig. post-hoc results
CL (FO)	15	Hatchlings	LM*CO	2	81	0.81	0.4463	
	16	Hatching Success	LM	1	26	1.66	0.2086	
			CO	2	81	3.32	0.0410	1<3
			LM*CO	2	81	0.67	0.5159	
	17	Fledglings	LM	1	27	2.91	0.0998	
			CO	2	76	5.65	0.0052	1<3
			LM*CO	2	76	2.24	0.1130	
	18	Incubation Period	LM	1	30	2.62	0.1163	
			BO	2	42	7.20	0.0020	2<1; 3<1
			LM*BO	2	42	0.93	0.4036	
NL (FO)	19	BCI	LM	1	34.4	0.58	0.4512	
			BO	2	272	5.12	0.0066	2<1; 3<1
			AC	5	263	0.96	0.4413	
			LM*BO	2	272	0.63	0.5351	
			LM*AC	5	263	0.82	0.5366	
	20	BGI	LM	1	19.8	0.11	0.7487	
			BO	2	36	2.06	0.1426	
			LM*BO	2	36	0.30	0.7417	

Only the details of significant post-hoc comparisons are presented (alpha=0.05). SL=Season-level, CL=clutch-level, NL=nestling-level; AT=All-treatments, FO=Farms-only; LM=land management; CO=clutch order; BO=brood-order; RIF=reduced-impact farm, CF=conventional farm, NC=natural control. Numbers in last column signify first, second, or third clutch or brood.

Table 2-4. Effect of land management and clutch order on hatching success

Land Management	Clutch 1	Clutch 2	Clutch 3	Clutches 1 and 2	Total
Control	0.78	0.93	.	0.86	0.86
Conventional	0.66	0.60	0.51	0.63	0.59
Reduced-Impact	0.80	0.66	0.64	0.73	0.70

Proportions represent number hatchlings divided by number of eggs produced per clutch.

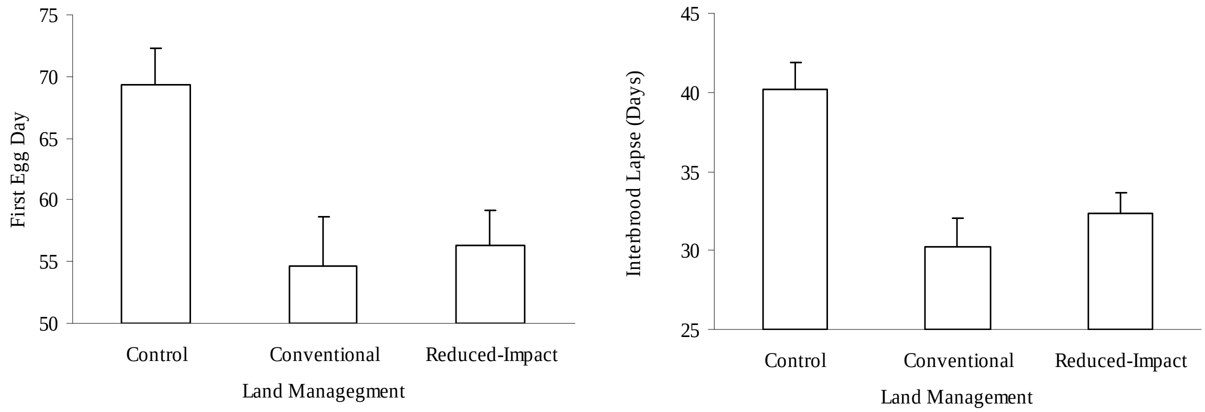

Figure 2-1. Effect of land management on first-egg-day and interbrood lapse. A first-egg-day value of "1" corresponds to 1 February 2008. Farms, in general, hosted bluebirds that exhibited significantly lower first-egg-days and shorter interbrood lapses than natural control areas (alpha=0.05). Error bars indicate 1 SE.

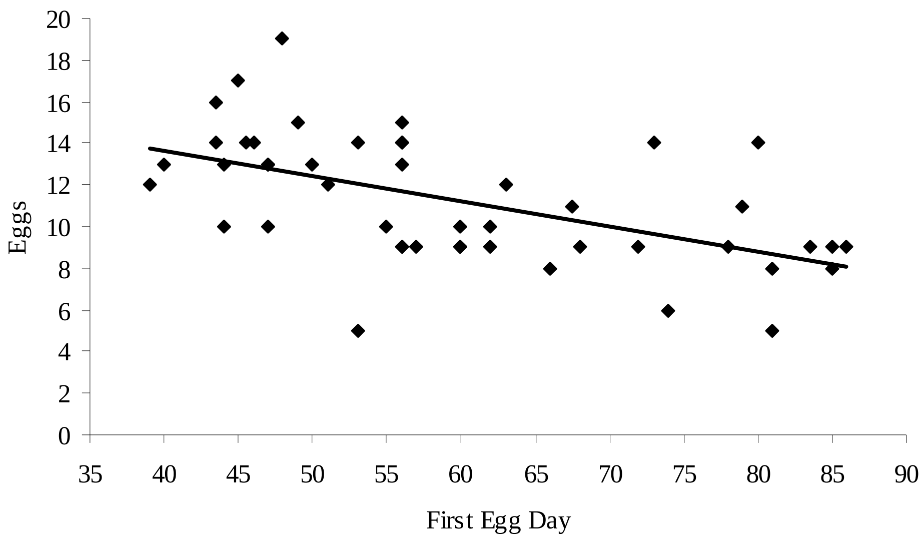

Figure 2-2. Effect of first-egg-day on season-level production of eggs. A first-egg-day value of "1" corresponds to 1 February 2008.

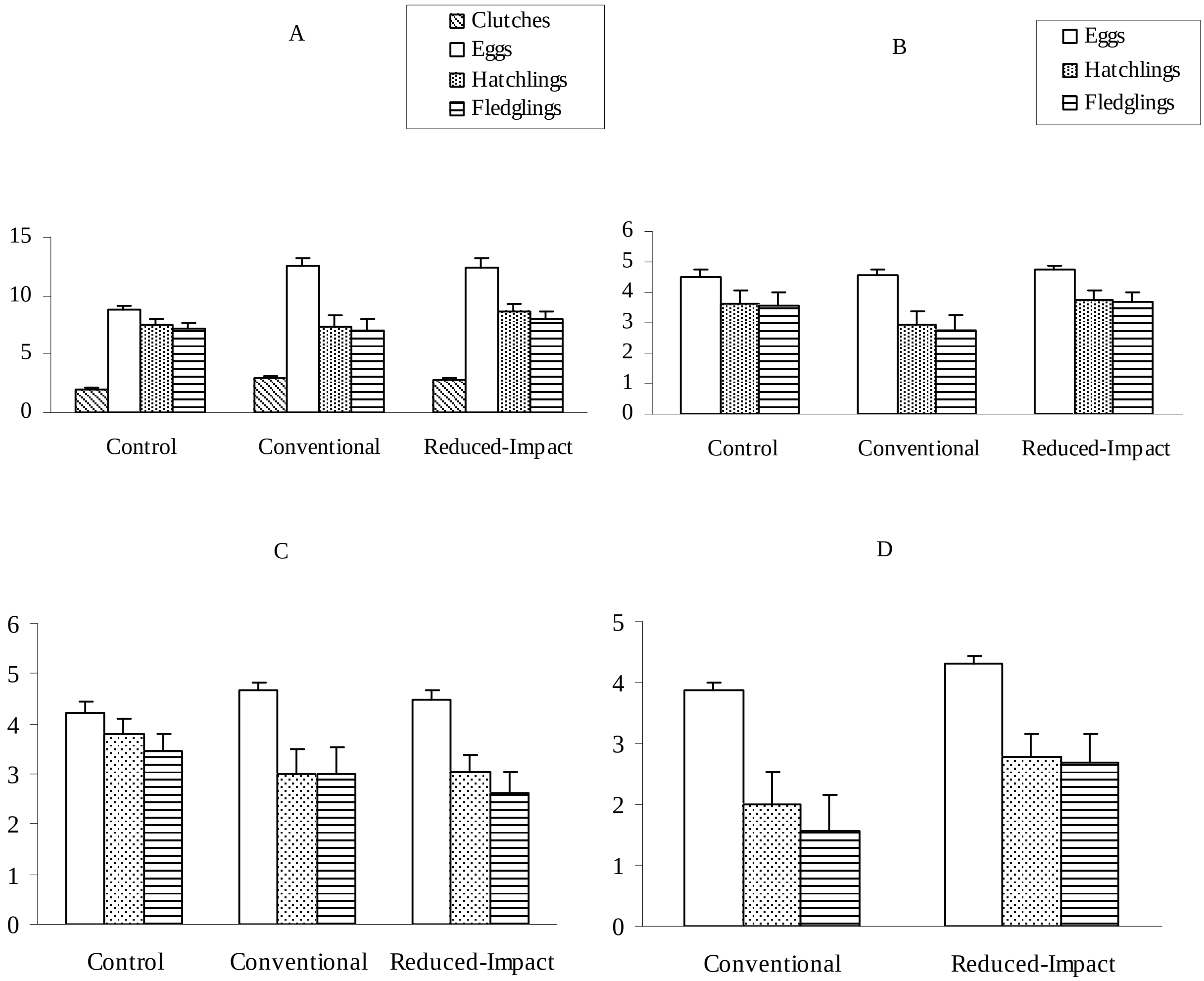

Figure 2-3. Effect of land management on bluebird reproductive success. Y-axis indicates mean numbers of clutches, eggs, hatchlings or fledglings per nest. Panels indicate A) season-level reproductive success, B) first-clutch reproductive success, C) second-clutch reproductive success, and D) third-clutch reproductive success. Error bars indicate 1 SE.

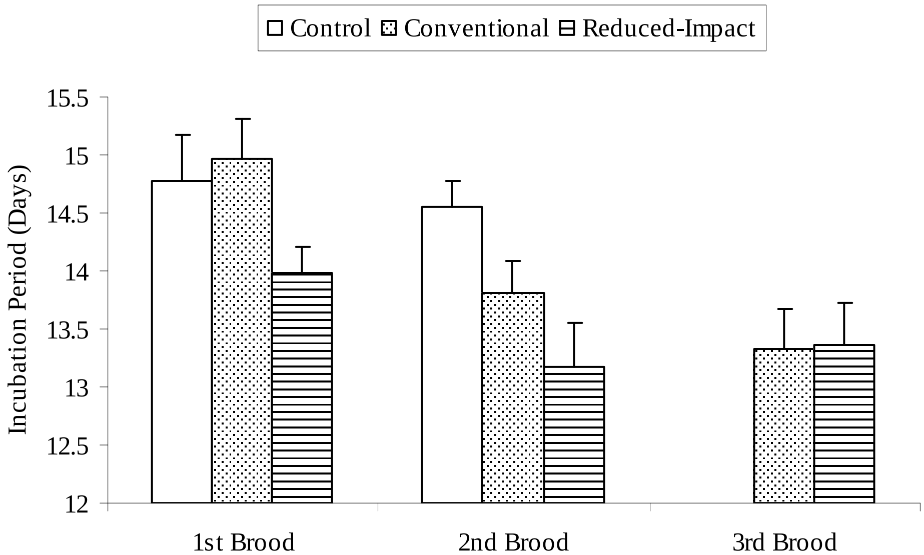

Figure 2-4. Effect of land management and brood-order on incubation period. Bluebirds on reduced-impact farms incubated for significantly less time than those in natural control areas. Second and third broods took significantly less time to incubate than first broods (alpha=0.05). Error bars indicate 1 SE.

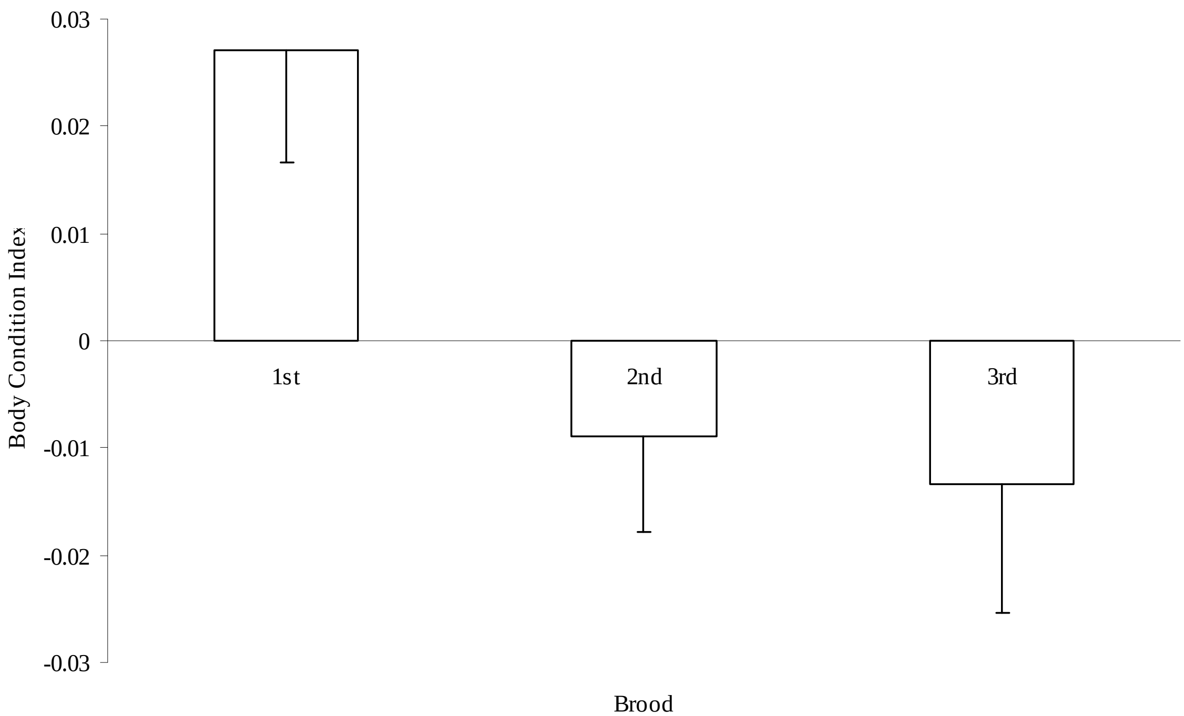

Figure 2-5. Effect of brood order on nestling body condition index (BCI). First-brood BCI was significantly higher than second- or third-brood BCI (alpha=0.05). This analysis only included nestlings from farms. Error bars indicate 1 SE.

CHAPTER 3
REDUCED-IMPACT FARMING, PREY BIOMASS, AND THE REPRODUCTIVE SUCCESS OF EASTERN BLUEBIRDS (*SIALIA SIALIS*)

Introduction

Wildlife-Friendly Farming

"Wildlife-friendly farming" has recently gained the attention of ecologists, conservationists, and policy-makers (Green et al. 2005, Fischer et al. 2008, Scherr and McNeely 2008). From systems producing coffee to broccoli, the maintenance and even enhancement of native biodiversity on farmlands is under study (Greenberg et al. 2000, Daily et al. 2001, Mols and Visser 2002, Phillips 2002, Hooks et al. 2003, Jones et al. 2005, Borkhataria et al. 2006, Jones and Sieving 2006, Sekercioglu 2007). Simultaneously, agricultural policies around the world are changing to reflect increasing awareness of the needs for biodiversity conservation on farmlands (Fischer et al. 2005, Wild Farm Alliance 2005), potential benefits that native species provide in some systems (e.g., pest control; Greenberg et al. 2000, Mols and Visser 2002, Phillips 2002, Hooks et al. 2003, Jones et al. 2005, Borkhataria et al. 2006), and consumer desires to buy foods produced using environmentally sound practices (Grankvist & Beal 2001). In general, fostering appropriate (non-pest) native species on farmlands appears to have few or no negative economic or ecological effects on food production (Hole et al. 2005, Scherr and McNeely 2008), and landscapes dominated by "ecoagriculture" may even benefit the public (from aesthetics and ecological services to recreation; Scherr and McNeely 2008).

However, while attracting wildlife to farms is not difficult, especially in landscapes supporting significant amounts of native habitat (Jones and Sieving 2006), it is important to determine if organic and other "wildlife-friendly" farms provide suitable breeding habitat for wildlife. Even agriculture-dominated lands with interspersed remnants of native habitat (i.e., "soft matrix" – Green et al. 2005) may not support viable populations independent of native, source populations (Sekercioglu et al. 2007). Therefore, assessments of farms from a conservation perspective should make a distinction between wildlife use versus sustainable production of wildlife populations and communities on farmlands. Only in this way can ecology inform natural resource policy and land management decisions that best support wildlife-friendly farming or other conservation-minded, multiple-use alternatives (e.g., “land-sparing”; Fischer et al. 2008).

Effects of Food Resources on Avian Reproduction

For example, no research has addressed the question that if we attract birds to farms, do these birds eat well enough to support their health, survival, and reproduction? Quantity of food available in early spring is a common proximate cue for breeding birds (Martin 1987, Nooker et al. 2005, Pimentel and Nilsson 2007). Reduced-impact farms in North-central Florida typically grow crops continuously through fall, winter, and spring, and part of summer (but not in July-September; JJD *personal observation*). The presence of green vegetation (i.e., crops), subsidized by irrigation and fertilizer on farms, may support arthropod prey populations that may not otherwise exist during the dry season (NOAA 2008), thereby allowing bluebirds on farms to begin reproduction earlier than those in natural areas.

The quality, quantity, and stability of food resources have been shown to affect reproductive success in a variety of bird taxa (Korpimaki 1992, Phillips et al. 1996, Valkama et al. 2002, Davis et al. 2005, Lindstrom et al. 2005). We observed in previous research that farmland pest insect populations appeared to vary dramatically, as farm-fields shifted between being planted or harvested, or being tilled versus left fallow (JJD *personal observation*; see also Nebel 1993). Although long-term prey biomass may be greater on farms than in natural areas (due to resource subsidies and higher peak insect population sizes), the instability of food resources may also be greater on farms than natural open lands. When insect populations crash because of crop harvest, mowing, or tilling, this may decrease reproductive success as parents may have more difficulty feeding themselves or their nestlings at key (and unpredictable) times during the reproductive cycle (Korpimaki 1992, Phillips et al. 1996, Valkama et al. 2002, Davis et al. 2005, Lindstrom et al. 2005). Truly wildlife-friendly farms should host stable food resources of adequate quantity and quality to sustain viable wildlife populations. Nevertheless, researchers have yet to compare the quality, quantity, or stability of food resources on supposedly wildlife-friendly farms in relation to natural open lands.

Avian Reproduction on Wildlife-friendly Farmlands

In a previous study conducted in 2007 (Chapter 2), we compared the reproductive success of Eastern Bluebirds (*Sialia sialis*) nesting on natural control areas, conventionally-managed farms, and reduced-impact (organic and other low-input systems) farms in North-central Florida. Reduced-impact farms in 2007 could generally be described as “wildlife-friendly" from a habitat perspective; they were planted with a variety of crops in a patchwork of fallow fields, with interspersed tree islands, windbreaks, hedgerows, and nearby forest patches. Furthermore, many reduced-impact farms were managed under the requirements for USDA-organic certification (Green et al. 2005, Fischer 2008).

The most important result of our research was that bluebirds began nesting much earlier on both types of farms and therefore raised more clutches on farms than in natural areas (3 on average versus 2), yet bluebirds on farms and natural areas produced similar numbers of nestlings over the breeding season. Greater within-season breeding effort can decrease lifetime reproduction and adult survival (Slagsvold 1984, Smith et al. 1987, Tinbergen 1987, Gustafsson et al. 1994, Richner et al. 1995, Deerenberg et al. 1997, Nilsson and Svensson 1996, Raberg et al. 1998). Our previous findings therefore suggest that even reduced-impact farms may not be as wildlife-friendly as expected (Green et al. 2005, Hole et al. 2005, Fischer et al. 2008). Food resources of lower quality, quantity, or stability may have caused this lower reproductive efficiency on farms. In order to fully address the goal of our research program – to explore wildlife-friendly farming from the conservation perspective – addressing whether such farms provide high quality habitat that supports reproduction adequate to support viable populations – we conducted a follow-up study to address whether differences in food resources underlie differences in bluebird reproductive success and breeding behavior. Given that conventional farm management involves high inputs of pesticides and fertilizers and is not considered as wildlife-friendly as organic farms (Hole et al. 2005), we encouraged bluebird nesting only on natural control areas and organic (or organically managed) farms.

Research Design

In 2007, we established a causal link between land management and various measures of reproductive timing and success (dashed arrow, Figure 3-1). Here we test the hypotheses that food resources affect bluebird reproduction (solid arrow, Figure 3-1) and that land management affects food resources (solid arrow, Figure 3-1), thereby linking land management to reproduction through the mechanism of food-resource effects. We controlled for the effects of nest predation in our research, enabling us to focus on the effects of prey availability on reproduction (see Methods). We recognize two components of bluebird prey availability: biomass of known prey present in foraging microhabitat used by bluebirds, and the stability of said prey biomass. Using a comparative observational design, we monitored bluebird reproduction and sampled arthropod populations on reduced-impact vegetable farms and natural control areas in North-central Florida. We monitored first-egg-date and number of clutches produced per pair over the season, but we limited our analyses of reproductive success to first clutches.

We addressed the following specific hypotheses and predictions. H1: Food resources (measured in terms of prey biomass and stability) affect first-egg-date, clutch production, and reproductive success (i.e., first-clutch egg and hatchling production). Predictions for H1 include: a) higher prey biomass and stability just prior to the onset of breeding will correlate with earlier first-egg-dates, b) greater prey biomass through the season will correlate with higher clutch production and reproductive success, and c) less variation in prey biomass through the season will correlate with higher clutch production and reproductive success. H2: Land management affects food resources (prey biomass and stability). Predictions for H2 include: a) farms will host higher prey biomass but b) lower prey stability than natural control areas. Since these hypotheses were proposed to explain the results of Chapter 2, we assumed for this study that patterns of reproductive success in relation to land management observed in 2007 (Chapter 2) would be similar in 2008. In 2007, farmland bluebirds began breeding earlier and produced more clutches than those in natural control areas, and first-clutch egg and hatchling production were similar on farms and natural areas. We monitored bluebird reproductive behavior and output in order to verify whether these patterns persisted in 2008.

Methods

Study Species, Study Sites, and Nest-Box Placement

The Eastern Bluebird is a charismatic, primarily insectivorous, multiple-brooded, ground-foraging, secondary cavity-nester of open lands (Gowaty & Plissner 1998). We conducted our research on three USDA-certified organic farms and one organically managed (i.e., in process of certification) farm in Alachua County, Florida, and six natural control areas within the >3760 ha Ordway-Swisher Biological Station in adjacent Putnam County. All farms exhibited the typical heterogeneous structure of wildlife-friendly farms (Green et al. 2005, Jones et al. 2005, Jones and Sieving 2006, Fischer 2008). Natural control areas consisted of abandoned pasture in the process of natural restoration, with a mixture of native and non-native grasses and shrubs, within a landscape of long-leaf pine (*Pinus palustris*) and both mesic and xeric hardwood forests (Gowaty and Plissner 1998).

We monitored 31 nest-boxes on 4 reduced-impact farms and 32 boxes in 6 natural control sites, beginning in mid-February. No nest-box was placed less than 70 m from its nearest neighbor. Nest-boxes on farms were placed within 5 meters of the edges of farm-fields (barren, fallow, or with active crop growth), and within at least 200 m of fields with actively growing crops at some point in the season. Nest-boxes in all treatments were within 50 m of protective cover and perching substrates used by bluebirds (e.g., hedgerows, tree islands, windbreaks, forest). In order to control for predation, we mounted nest-boxes on narrow, metal poles (approximately 1.5 m high) and kept the poles greased (USDA Natural Resources Conservation Service 1999).

Prey Surveys

We sampled arthropod populations on an approximately weekly basis between February 17th (12 days before the first clutch of the season was laid) and June 1st. We conducted two types of transects, both 20 m long: “grasshopper-walk” (GW) and “walk-brush” (WB) surveys. The purpose of GW surveys was to count large mobile arthropods (e.g., Orthoptera, Lepidoptera, Odonata) that move dramatically when approached and therefore are easy to see. GW transects were located in microhabitat with the tallest herbaceous vegetation available during a given visit to each of the areas. On farms, we did not conduct GW surveys in actively growing crops, but rather in field edges or fallow fields with weeds. We conducted GW surveys by walking at 1 pace per second for 10 m while recording all arthropods that moved or were readily visible within approximately 1 m on either side of the observer, avoiding double-counting.

The purpose of WB surveys was to target smaller, ground-dwelling arthropods, and those animals inhabiting low, actively growing herbaceous vegetation, including crops. In natural control areas, WB surveys were conducted in herbaceous vegetation, and on farms they were conducted between crop rows (principally leafy vegetables such as kale, cabbage, broccoli, collared greens, etc.; see Jones et al. 2005). We conducted the first 10 m of WB surveys in the same manner as GW surveys. During the second 10 m, we bent low, brushed vegetation with our hands, and looked under leaves and plants, in the middle of the vegetation layer, and on top of vegetation, within 1 m to either side of the transect line. Time to complete brushing varied depending on arthropod abundance (our aim was to conduct a thorough search), as the time it took to count and classify arthropods and record data increased as we encountered more arthropods.

We developed these sampling methods based on Gardiner et al. (2005) in order to sample prey that were frequently taken from foraging microhabitats commonly used by bluebirds nesting on the study sites (JJD unpublished data). Adult Orthoptera and Lepidoptera larvae were the principal prey items identified in previous observations (though many smaller prey could not be identified), and bluebirds frequently foraged in crops, fallow fields, and field edges within 100m of the nesting site, but also flew further away (to unobservable locations off site; JJD unpublished data). Previous research confirms these patterns (Gowaty and Plissner 1998).

By conducting WB transects between crop rows and GW surveys in fallow vegetation surrounding farm fields (and in the most similar microhabitat available in natural control areas) we assessed representative food resources available to bluebirds on both types of land management. After bluebirds began nesting, we conducted prey surveys within 100 m of nests in each site in appropriate foraging habitats. To maintain independence of samples, observers avoided using any transect more than once. We selected transect locations subjectively on each visit to sites, by looking for those areas with vegetation that was most dense and actively growing (greenest), assuming that such vegetation would attract the kind of herbivorous prey that bluebirds target. We conducted at least two (up to 8) of each type of transect (GW and WB) at each visit to a site – the number of transects per site was proportional to the number of boxes clustered at each site (box number varied from 3 to 10 per site).

We only recorded arthropods that were greater than 0.5 cm in length. We classified arthropods into 6 size categories (0.5-1 cm, 1-2 cm, 2-3 cm, 4-5 cm, 5-6 cm, and 6 or more cm). Five different observers conducted arthropod surveys. We monitored cloud cover, temperature, and wind speed during sample periods to insure some degree of standardization of conditions. We conducted surveys between 0800 and 1630 hours, EST. We did not conduct surveys during rain events or when winds reached more than 15 km/hr. We conducted surveys in exposed (unshaded) microhabitats with full insulation and avoided the coldest periods during the day (early morning).

Prey Indices

We summarized prey data for three distinct time periods for use in statistical analyses. "Pre-breeding" prey indices represented food resources that were available just before and during nest initiation; data were used from all transects sampled between February 17th (more than one week before the earliest first-egg-date) and March 13th (the mean observed first-egg-date on farms, the treatment with the earlier mean first-egg-date). "First-clutch" prey indices were calculated to represent the food available to pairs during their first clutch of the 2008 season. Specifically, we based first-clutch prey indices on those transects sampled between the two weeks before and the two weeks after the average first-egg-date at each site (i.e., different time periods were used for different sites). Finally, "Season-long" prey indices were calculated using data from the entire arthropod sampling period (i.e., mid-February to early June) spanning both first and second brood attempts across all study sites.

For these three time periods, two types of indices were calculated for both GW and WB data. For each 20m survey, we calculated a "prey biomass index," one for each type of sampling method (GW or WB), equal to the absolute number of prey items encountered during a survey multiplied by the mean prey-size. We then averaged these data on a site-by-site basis for each time period (pre-breeding, first-clutch, or season-long) and both survey type (GW or WB). In addition, we quantified prey biomass stability using the coefficients of variation across transect during each of these time periods and for both survey types.

Monitoring Bluebird Reproduction

We monitored the nesting activity of Eastern Bluebirds, at different levels of intensity, during the entire breeding season of 2008 (February-August). We recorded nest-construction status, number of eggs, and number of hatchlings at each visit to a nest-box. Before bluebirds laid their first clutches, we monitored nest-boxes once or twice per week in order to estimate first-egg-date within two days' accuracy (over 85% were determined to the exact date; assuming bluebirds lay one egg every 24 hours and do not lay past 1100 hours; Gowaty & Plissner 1998). We define first-egg-date as the day that the first egg of the first clutch of a pair was laid. First-egg-date was translated into first-egg-day, with Day 1 equal to February 1st (e.g., a first-egg-day value of 27 would be equal to February 27th and a value of 29 would equal March 1st). After the majority of first clutches were laid, we visited sites once per week, and after early June (when first clutches were finishing), we reduced visitation rates to between 10 – 15 days between visits, with some longer periods (up to 3 weeks at the end of the season). Visits were more frequent early in the breeding season to establish precise estimates of first-egg-dates and food availability in the early breeding season (for testing H1 and verifying whether reproductive success in the first clutch reflected 2007 patterns with respect to farms versus natural areas). By continuing to visit sites throughout the breeding season (though less often) we could assess long-term (season-long) prey biomass and variability, and determine clutch produciton. The typical Eastern Bluebird nesting cycle lasts 28 days (Gowaty and Plissner 1998), so we visited nests often enough to be able to calculate the total number of clutches and mean number of nestlings produced per pair over the breeding season. Poles that secured the nest-boxes above ground were continually greased to prevent predation (as in Chapter 2). We identified predation events by marks left by predators on boxes, nests, and grease. We accordingly removed predated nests from analyses.

Statistical Analysis

In testing statistical hypotheses, we used sites as replicates. Based on previous observations (JJD), we assumed different pairs nesting within the same site foraged in unpredictable, often overlapping territories. Furthermore, we conducted prey surveys at various locations spread across each site, not around each nest-box. That is, we did not conduct prey surveys around particular breeding pairs (and we could not do so before breeding began, anyway). We therefore analyzed data on a site-by-site (not pair-by-pair) basis. This limited our sample size (n=4 farms and 6 natural control areas), so we used nonparametric analyses to avoid making assumptions about underlying distributions that we were unable to identify. We used the Spearman Correlation Index to test H1, and the Mann-Whitney U Test to test both H2 and predictions concerning assumed patterns of reproductive success (see first five columns in Table 3-1 for details of analytical methods; data analyzed in SPSS 16.0).

Results

Prey Availability

Pre-breeding GW prey biomass inversely correlated with first-egg-date (Spearman R=-0.770; p=0.009; Figure 3-2; Table 3-1), but pre-breeding WB prey biomass did not. None of the other GW or WB prey biomass indices was correlated with first-egg-date (Table 3-1). No prey biomass indices were correlated with season-long clutch production or first-clutch egg production (Table 3-1). First-clutch GW prey biomass, WB prey biomass, and GW instability were unrelated to first-clutch hatchling production (Table 3-1), but first-clutch WB instability was inversely correlated with first-clutch hatchling production (Spearman R=-0.654; p=0.040; Figure 3-3; Table 3-1). Season-long GW and WB prey biomass were higher and more unstable on farms than in natural control areas (p<0.02; Figure 3-4; Table 3-1). Pre-breeding and first-clutch prey indices did not vary significantly between farms and natural areas.

Land Management and Bluebird Reproduction

Confirming results obtained in the previous year (Chapter 2), farmland bluebirds began breeding earlier than those in natural control areas (p=0.038; Figure 3-2; Table 3-1), but land management was not clearly related to clutch or first-clutch egg production (Figure 3-3; Table 3-1). In contrast to 2007 patterns, farmland bluebirds produced a similar number of clutches but significantly fewer first-clutch hatchlings than those in natural control areas (p=0.010; Figure 3-5; Table 3-1). Confirming 2007 patterns, bluebirds that began breeding earlier produced more clutches (p=0.027; Figure 3-6; Table 3-1).

Discussion

Prey Availability as a Mechanism for Earlier First-Egg-Dates

The hypothesis that prey availability may influence first-egg-date was confirmed. Bluebirds in habitat with higher pre-breeding GW biomass began breeding earlier. As in 2007, bluebirds on farms in 2008 exhibited earlier first-egg-dates than those in natural control areas. This finding is in line with other work showing that the abundance of food resources determines the onset of avian reproduction (Martin 1987, Nooker et al. 2005, Pimentel and Nilsson 2007) and provides a reasonable mechanism to explain earlier first-egg-dates on farms (Figure 3-2; Table 3-1). Even though we were unable to detect a difference in prey biomass between farms and natural areas during the pre-breeding period, farms did support greater prey biomass over the course of the breeding season (Feb to June; Figure 3-4; Table 3-1), providing partial support for predictions under H2. It is likely that ability to detect pre-breeding prey differences between farms and natural areas was limited because many fewer surveys went into the calculation of pre-breeding indices (less than 10 surveys per site) than into long-term indices. In addition, small sample sizes may have also limited power (n=6 natural control areas and 4 farms). Given that previous research shows that early breeding in birds is related to early food availability (Martin 1987, Nooker et al. 2005, Pimentel and Nilsson 2007), and that farms in our study produced more prey biomass over the season than natural areas, we suggest that land management likely influenced first-egg-date in our study via differences in pre-breeding prey biomass (Figures 3-2 and 3-4). This hypothesis should be re-tested with a more rigorous sampling regime by sampling more farms at a higher rate during the pre-breeding period.

Prey Biomass Instability and Hatchling Production

Prey biomass and instability indices did not correlate with either clutch production or first-clutch egg production. However, prey instability was linked to first-clutch hatchling production and was significantly higher on reduced-impact farms where significantly fewer hatchlings were produced (Figures 3-3 and 3-4; Table 3-1). Bluebirds in sites with less stable WB prey biomass produced fewer hatchlings (Figure 3-3; Table 3-1). Farms exhibited significantly higher WB prey instability over the course of the season than natural control areas (and first-clutch WB prey instability tended to be higher on farms; Figure 3-4; Table 3-1). Because first-clutch prey indices were calculated based on fewer sampling periods than season-long indices (as for pre-breeding indices, see above), the power of statistical tests relating first-clutch prey availability to first-clutch reproduction was likely to be limited in this study. Given the marked season-long differences in prey biomass stability on farms, however, we conclude that land management could very likely influence hatchling production through the mechanism of prey instability (Figures 3-3 and 3-4). Unstable food resources affect reproductive success for a variety of birds (Korpimaki 1992, Phillips et al. 1996, Valkama et al. 2002, Davis et al. 2005, Lindstrom et al. 2005). Specifically, our data show that first-clutch reproductive output was lower not because hatchlings died, but because eggs did not hatch (i.e., we observed “dead eggs” in nests after viable eggs hatched). Perhaps prey instability caused female bluebirds on farms to spend more time off of the nest in search of prey, thereby decreasing their time spent incubating eggs. Alternatively, prey instability may have prevented females from gaining the proper nutrition to produce viable eggs (Martin 1987).

Our detection of prey biomass instability on farms could be explained by prey population cycles generated by typical farming dynamics. Water and fertilizer subsidies can create artificially high arthropod populations, and harvest and field fallowing activities can cause abrupt drops in arthropod biomass (Nebel et al. 1993). Moreover, we may have detected higher overall mean prey biomass on farms simply because of the artificially high population explosions on farms that unsubsidized natural areas did not experience. Without more detailed measures of where individual bluebird pairs foraged during specific portions of their nesting cycle, and the availability of prey in foraging sites, we cannot explain more about how or why farmland bluebirds suffered lower hatchability in this study. However, the fact that farms had greater overall prey biomass suggests that bluebirds are exceptionally sensitive to fluctuations in spatio-temporal distribution of their prey and that improving farmlands for wildlife conservation may require improvements in the stability of food resources (Korpimaki 1992, Phillips et al. 1996, Valkama et al. 2002, Lindstrom et al. 2005).

First-egg-date and Season-level Clutch Production

Though farmland bluebirds began breeding earlier than those in natural control areas, clutch production over the season was not different between farms and natural areas (Figure 3-3; Table 3-1). This contrasts with 2007 results from the same study system, when farmland bluebirds nested earlier and produced more clutches than bluebirds on natural areas, resulting in a significantly greater overall reproductive effort on the part of farmland birds (Chapter 2). In light of current results, the contrast in patterns of relative production of clutches and reproductive effort between years appears most closely linked to first-egg date (Figure 3-6).

Based on 2007 data alone, we concluded that higher clutch production was probably coupled to farming. However, farmland bluebirds in 2008 did not produce more clutches than their natural counterparts (Figure 3-6; Table 3-1). This may have resulted because bluebirds on natural areas began breeding much earlier in 2008 than 2007 (approximately two weeks earlier; Figure 3-5). Since the difference between clutch production on farms and natural areas disappeared in 2008, it may be that the extra two weeks of early breeding was enough to allow bluebirds in natural control areas to “catch up” to farmland bluebirds in terms of clutch production. Indeed, the mean first-egg-date of bluebirds in natural control areas in 2008 corresponded to the mean first-egg-date of bluebirds on farms in 2007 (Figure 3-5).

Furthermore, land management was correlated with prey biomass and stability (Figure 3-4; Table 3-1) but not to clutch production, and prey biomass and stability did not correlate with season-long clutch production. Only first-egg-date was related to season-long clutch production (in both 2007 and 2008). Finally, previous research on Eastern Bluebirds across North America confirms this finding in demonstrating that as latitude increases, first-egg-date increases and clutch production consequently decreases (Gowaty and Plissner 1998).

The difference in first-egg-date between 2007 and 2008 could be related to rainfall levels. Substantially more rain fell in the study region in 2008 than in 2007 and probably influenced the earlier onset of breeding (Table A-3; FAWN 2008). Rainfall levels in both years (2007 and 2008) fell outside the 95% confidence interval for rainfall levels in the past eight years (with 2008 falling above and 2007 below the upper and lower bounds; Table A-3). In other words, rainfall in the months when bluebirds began breeding (February-April) was more than twice as high in 2008 than 2007 (Table A-3). Higher rainfall in the early months of breeding may have stimulated the growth of green vegetation, which consequently may have sparked earlier increases in pre-breeding prey biomass (which we have shown correlates with earlier first-egg-dates, which in turn correlate with higher clutch production; Nooker et al. 2005, Pimentel and Nilsson 2007).

Indications for Lower Reproductive Success on Farms

Results of this study reveal another contrast with our 2007 findings. In 2007, farmland birds bred earlier, raised more clutches but achieved equal numbers of fledged young per pair, leading us to conclude that while reproductive efficiency was lower on farms; net reproductive success in the same season was equal. In 2008, bluebirds in natural control areas produced similar numbers of clutches as farmland bluebirds (Figure 3-3; Table 3-1), presumably because farmland bluebirds lost the relative advantage of being able to nest just enough earlier to lay more clutches than control birds. It is also possible that overall food abundance on natural areas in the drier year (2007) was low enough to discourage late-season clutches, limiting them to only two clutches for the season (Chapter 2).

We did not conduct monitoring activities intensely enough to describe the reproductive success of second and third clutches in this study (see Methods). However, it is possible that the reproductive success of later clutches on farms was much poorer in 2008 than 2007, and than bluebirds in natural control areas in 2008. Second and third clutches met worse fates than first clutches on farms in 2007 (Chapter 2). One could reasonably extrapolate this pattern to 2008 bluebirds, as life-history theory expects decreased reproductive success in successive clutches, and this pattern is frequently observed in avian species (Slagsvold 1984, Smith et al. 1987, Tinbergen 1987, Gustafsson et al. 1994, Richner et al. 1995, Deerenberg et al. 1997, Nilsson and Svensson 1996, Raberg et al. 1998). Nevertheless, we cannot conclude anything definitively about the season-level reproductive success of bluebirds in 2008 without actual data on second and third clutches.

It appears that farms serve as suboptimal but productive habitat for breeding bluebirds during especially dry years like 2007 (Chapter 2; Table A-3; FAWN 2008), as farmland bluebirds were able to match the net reproductive success of bluebirds in natural control areas (albeit they exerted more effort; Chapter 2). During years with especially high rainfall, however, the quality of farmlands as breeding habitat for bluebirds dropped relative to natural areas. In years with high rainfall levels (like 2008), birds on natural areas appeared to be able to lay as many clutches as farmland birds and exhibit higher reproductive success (Figure 3-3). Our data suggested that arthropod prey resources may be a crucial factor in determining this pattern, as high biomass was correlated with earlier first-egg-dates (which in turn determined the number of clutches produced per season) and high instability with reduced hatchling production (Figure 3-2 and 3-3). Bluebirds on natural areas were exposed to lower prey biomass (by both GW and WB indices) but still did better than farmland birds that had more biomass available but with much less predictability. Previous research further corroborates that volatile food resources lead to lower reproductive success (Korpimaki 1992, Phillips et al. 1996, Valkama et al. 2002, Lindstrom et al. 2005).

However, we would make these conclusions with stronger inference had we conducted this research on more farms and natural sites over a broader spatial and temporal extent: We monitored bluebirds on few farms and natural control areas within a limited geographic domain (North-central Florida), our natural control areas may have exhibited some spatial autocorrelation (as they were spread throughout one large reserve), and our research occurred over just two breeding seasons. Given that the vast majority of natural habitat development is from natural lands to agriculture (Tilman et al. 2001), and that habitat development is the primary threat to wildlife conservation (Van Dyke 2003), conservation biologists are increasingly hoping that farmlands may serve as productive habitat for songbirds and other wildlife species adapted to open lands (Green et al. 2005, Fischer et al. 2008). However, indications of low avian reproductive success in our study system and similar systems (Sekercioglu et al. 2007) suggest that more empirical research into the effects of supposedly "wildlife-friendly" farms on wildlife reproductive success would be prudent before we promote them as conservation lands.

Table 3-1. Results

Model ID	Hypothesis/Assumption Addressed	Analysis Type	Dependent Variable	Independent Variable	Test Statistic	*p*-value	Sig. post-hoc results
1	H1	Spearman	First Egg Day	Pre-breeding GW Prey Biomass	-0.479	0.009	*
2	H1	Spearman		Pre-breeding WB Prey Biomass	-0.515	0.128	
3	H1	Spearman	Clutch Production	Long-term GW Prey Biomass	0.291	0.415	
4	H1	Spearman		Long-term WB Prey Biomass	0.550	0.100	
5	H1	Spearman		Long-term GW Prey Instability	0.291	0.415	
6	H1	Spearman		Long-term WB Prey Instability	0.045	0.901	
7	H1	Spearman	First-clutch Egg Production	First-clutch GW Prey Biomass	-0.359	0.309	
8	H1	Spearman		First-clutch WB Prey Biomass	-0.334	0.345	
9	H1	Spearman		First-clutch GW Prey Instability	-0.486	0.154	

Table 3-1 Continued

Model ID	Hypothesis/Assumption Addressed	Analysis Type	Dependent Variable	Independent Variable	Test Statistic	p-value	Sig. post-hoc results
10	H1	Spearman		First-clutch WB Prey Instability	-0.164	0.650	
11	H1	Spearman	First-clutch Hatchling Production	First-clutch GW Prey Biomass	0.232	0.518	
12	H1	Spearman		First-clutch WB Prey Biomass	0.110	0.762	
13	H1	Spearman		First-clutch GW Prey Instability	-0.110	0.762	
14	H1	Spearman		First-clutch WB Prey Instability	-0.654	0.040	*
15	H2	Mann-Whitney U	Pre-breeding GW Prey Biomass	Land Management	-1.066	0.352	
16	H2	Mann-Whitney U	Pre-breeding WB Prey Biomass	Land Management	-1.066	0.352	
17	H2	Mann-Whitney U	Long-term GW Prey Biomass	Land Management	-2.345	0.019	RIF>NC
18	H2	Mann-Whitney U	Long-term WB Prey Biomass	Land Management	-2.345	0.019	RIF>NC
19	H2	Mann-Whitney U	Long-term GW Prey Instability	Land Management	-2.345	0.019	RIF>NC

Table 3-1 Continued

Model ID	Hypothesis/Assumption Addressed	Analysis Type	Dependent Variable	Independent Variable	Test Statistic	p-value	Sig. post-hoc results
20	H2	Mann-Whitney U	Long-term WB Prey Instability	Land Management	-2.558	0.010	RIF>NC
21	H2	Mann-Whitney U	First-clutch GW Prey Biomass	Land Management	-0.426	0.762	
22	H2	Mann-Whitney U	First-clutch WB Prey Biomass	Land Management	0.000	1.000	
23	H2	Mann-Whitney U	First-clutch GW Prey Instability	Land Management	-1.066	0.352	
24	H2	Mann-Whitney U	First-clutch WB Prey Instability	Land Management	-1.706	0.114	
25	A1	Mann-Whitney U	First Egg Day	Land Management	-2.132	0.038	RIF<NC
26	A1	Mann-Whitney U	Clutch Production	Land Management	-1.137	0.352	
27	A1	Spearman		First Egg Day	-0.692	0.027	*
28	A1	Mann-Whitney U	First-clutch Egg Production	Land Management	-0.535	0.610	
29	A1	Mann-Whitney U	First-clutch Hatchling Production	Land Management	-2.582	0.010	RIF<NC

*See Figures 3-1, 3-3, and 3-6. Dependent variables averaged on a site-by-site basis, as sites (not breeding pairs) were our replicates (see Table B-1 for detailed site-by-site data and Table B-2 for definitions). n=6 natural control areas and 4 farms when land management serves as the independent variable of a model. n=10 sites (with land management treatments lumped) in all other models.

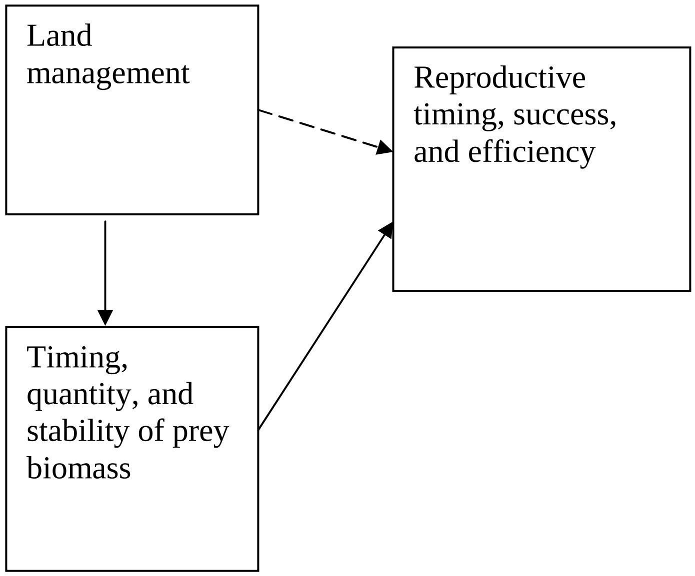

Figure 3-1. Design logic for Chapter 3. Using a comparative-observation study design, we tested the hypotheses that prey availability affects bluebird reproduction and that land management affects prey availability (solid arrows). We also tested the assumption that land management affects reproductive success and behavior (dashed arrows), based on results of a previous study (Chapter 2).

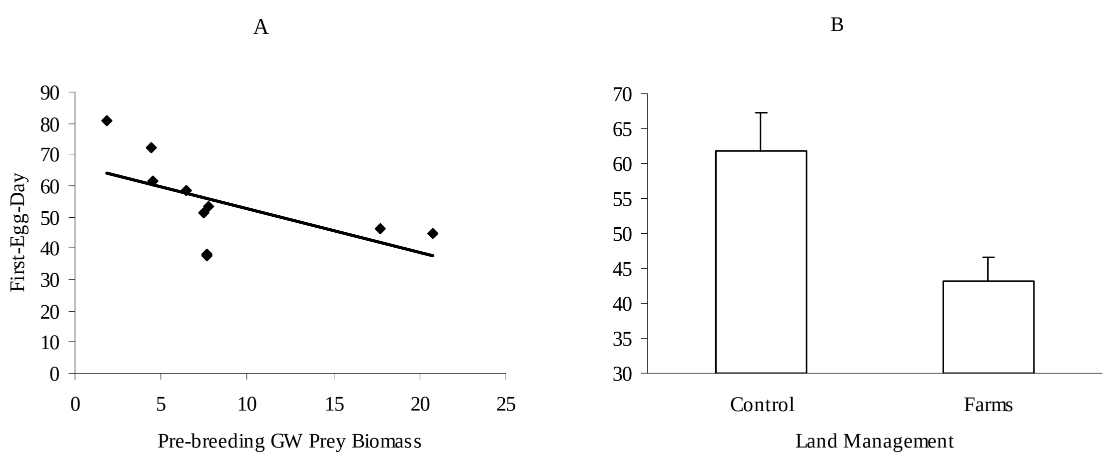

Figure 3-2. Effect of land management and pre-breeding GW prey biomass on first-egg-day. A) Effects of land management. B) Effects of pre-breeding GW prey biomass. Error bars represent 1 SE.

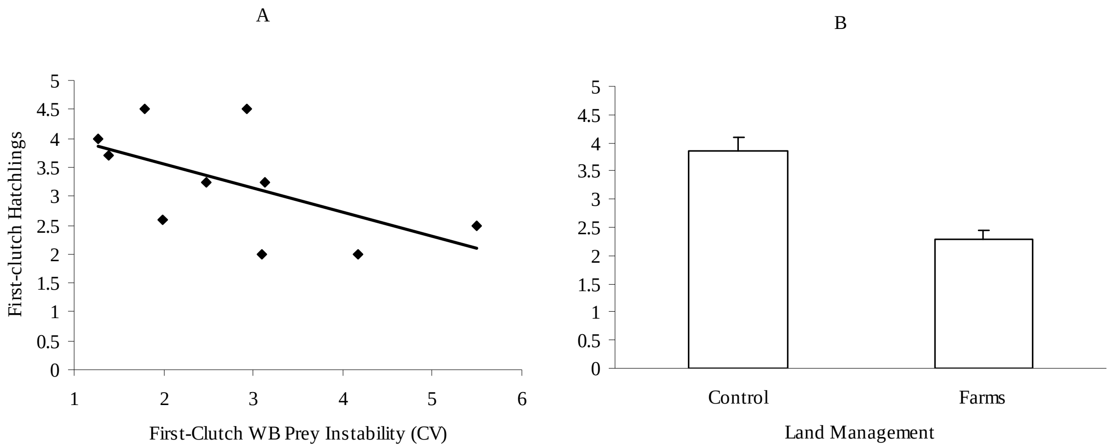

Figure 3-3. Effect of first-clutch WB prey instability (CV) and land management on first clutch hatchling production. A) Effects of first-clutch WB prey instability. B) Effects of land management. Error bars represent 1 SE.

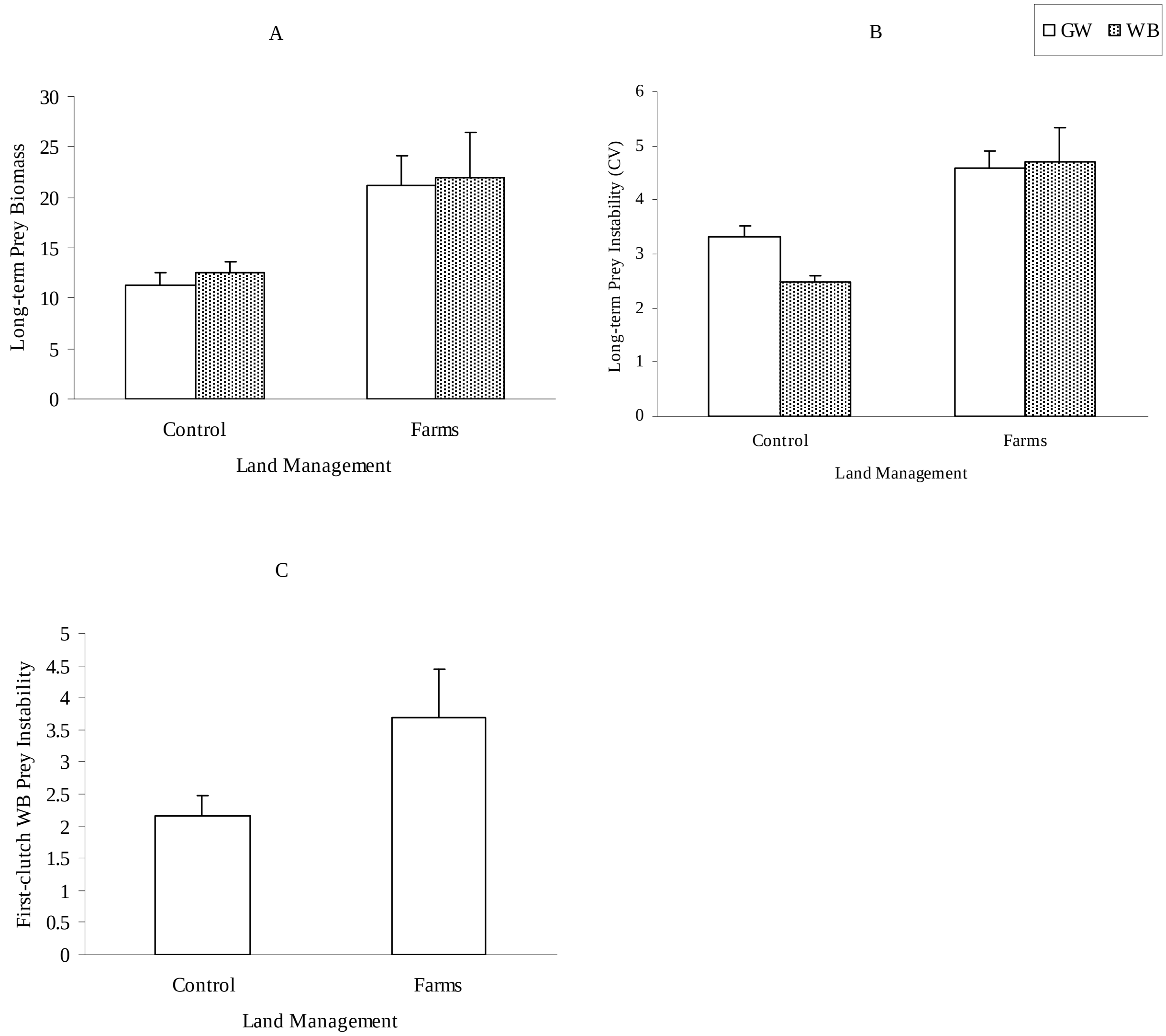

Figure 3-4. Effect of land management on long-term prey biomass, long-term prey instability (CV), and first-clutch WB prey instability. A) Effects on long-term prey biomass. B) Effects on long-term prey instability. C) Effects on first-clutch WB prey instability. "GW denotes "grasshopper walk" surveys, and "WB" denotes "walk-brush" surveys. Error bars represent 1 SE.

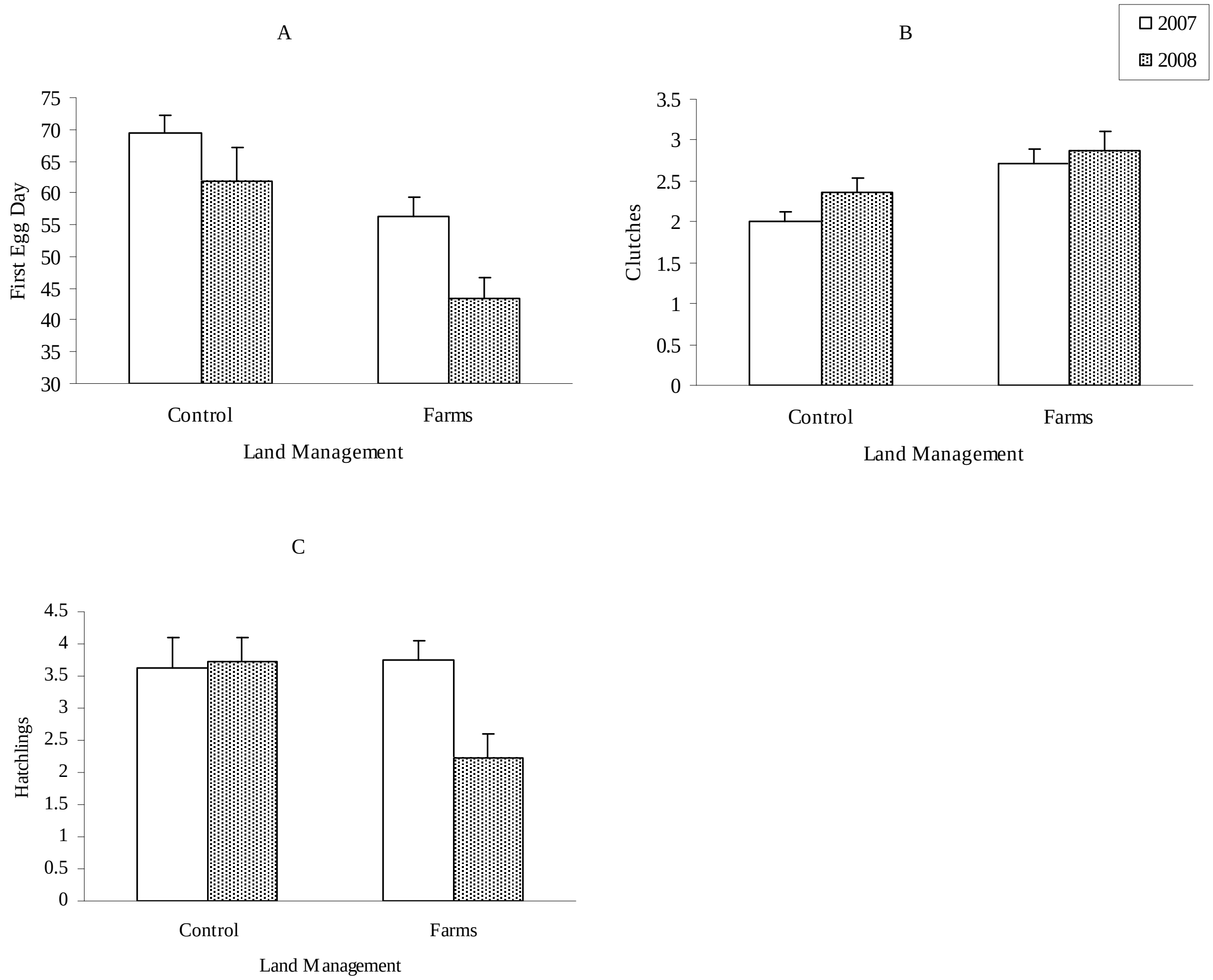

Figure 3-5. Effect of land management on first-egg-day, clutch production, and hatchling production, compared by year. A) Effects on first-egg-day. B) Effects on clutch production. C) Effects on hatchling production. Error bars represent 1 SE.

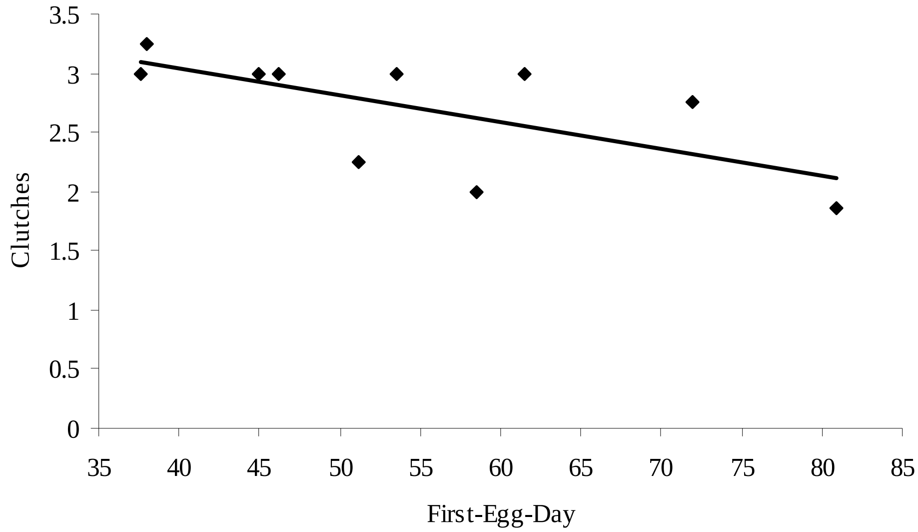

Figure 3-6. Effect of first-egg-day on clutch production

CHAPTER 4
ARE “WILDLIFE-FRIENDLY FARMS” REALLY WILDLIFE-FRIENDLY?

In targeting farmland habitat for biodiversity conservation, policy-makers and natural resource management professionals must choose between two distinct types of farm management, “land-sparing” or “wildlife-friendly” operations. Land-sparing operations entail uniformly planted agricultural lands (i.e., monocultures) that are managed to increase yields through high-intensity inputs of fertilizer and pesticide, while maintaining separate natural reserves for biodiversity conservation. “Wildlife-friendly” operations integrate conservation and farming within more diverse landscapes over a larger area, without necessarily protecting separate reserves (Fischer et al. 2008).

Conservation biologists have recently expressed support for the latter method of land management (e.g., Green et al. 2005, Fischer et al. 2008). However, ecologists are only beginning to examine the potential of farmlands as productive habitat for breeding birds and other wildlife, and results remain inconclusive (e.g., Sekercioglu et al. 2007). Our research also indicates that reduced-impact farms (which could just as well be considered “wildlife-friendly”) do not necessarily provide ideal habitat for farmland wildlife, in contrast to popular notions (Green et al. 2005, Hole et al. 2005, Fischer et al. 2008). Bluebirds on reduced-impact farms produced many more nestlings in poor body condition and reproduced with much less efficiency (i.e., pairs laid more clutches and raised more broods but produced the same number of young) than bluebirds in natural control areas in 2007. Differences were also distinct in the subsequent year (2008); bluebirds produced approximately twice as many first-clutch hatchlings in natural control areas as on farms (a pattern that, if persistent throughout the entire breeding season, would result in lower production of young on farms).

While data presented here may seem to indicate that farms did not provide as excellent breeding habitat as natural areas, farmland bluebirds still produced substantial numbers of offspring. Bluebirds on farms produced more than enough young to replace themselves in both 2007 and 2008 (assuming that most offspring survived after fledging), and they exhibited similar net reproductive success as bluebirds in natural areas in 2007. Although certain measures of reproduction (e.g., reproductive efficiency, nestling health; see above) suggest that farms provide suboptimal breeding habitat in comparison to natural control areas, more research is required to determine whether farmlands are source or sink habitat, or even ecological traps.

Population source habitat occurs where high reproductive success results in a population surplus (i.e., excess reproduction prevents any deleterious effects of mortality on population size). Surplus individuals from source habitat emigrate to sink habitat, where reproduction and survivorship are lower than mortality (Brawn and Robinson 1996, Van Dyke 2003). If most bluebird fledglings survived to adulthood on farms, then farms would have not been sink habitat, and they may have even been source habitat. However, we did not monitor juvenile or adult survival in our study. Future research could measure reproductive output, survivorship, and mortality, thereby verifying if farms serve as source or sink habitat.

The assessment of whether or not farms serve as ecological traps also requires detailed population-level data. An ecological trap is defined as "an environment that has been altered suddenly by human activities, [where] an organism makes a maladaptive habitat choice based on formerly reliable environmental cues, despite the availability of higher quality habitat" (Schlaepfer et al. 2002). In order for farms to be considered ecological traps, bluebirds would have to fare worse on farms than alternative habitat (e.g., natural areas), while simultaneously preferring farms over alternative habitat. Farms certainly are environments that have been altered by human activities, and our results suggest that farms are suboptimal habitat in comparison to natural areas (see above). However, we cannot state that bluebirds make choices in favor of farmland habitat over natural habitat (or vice-versa) because we did not measure habitat preference. Future research could determine if farms act as ecological traps by monitoring bluebird reproductive success, survivorship, and mortality on replicate plots of natural open-lands adjacent to farmlands while quantifying competition levels among bluebirds in both of these treatments (thereby quantifying habitat preference).

We excluded predation from evaluation in our study in order to more precisely assess the potential that food resources varied with land management (see Methods in Chapters 2 and 3). However, this major source of bluebird mortality (Gowaty and Plissner 1998) may differ between farms and natural areas, potentially affecting the habitat quality of farms. Predator communities may differ between farms and natural areas, and predation rates of forest-adapted birds are often high on the edges of agricultural lands (e.g., Rodewald & Yahner 2001*b*, Tewksbury et al. 2006). However, such research is limited to a comparison of conventional farms to reduced-impact farms, or conventional farms to natural areas. No research (to our knowledge; Hole et al. 2005, Scherr and McNeely 2008, Watson et al. 2008) has compared predator communities on natural open lands to those on reduced-impact or conventional farms, while focusing on the reproductive success of birds that have evolved in open landscapes (i.e., those that are appropriately targeted by conservation efforts). Conservation biologists must verify if predation levels are substantially higher or lower on farms in comparison to natural areas before subscribing farmlands as conservation areas.

Human disturbance is another potentially important factor in determining the suitability of farmland habitat for wildlife conservation, as it has been shown to inversely correlate with avian reproductive success (Yasue and Dearden 2006, Kight and Swaddle 2007). Farmer activity rarely subsides during the growing season – this seems especially true on reduced-impact farms, where a variety of crops are grown and harvested at different times, requiring near-constant activity by farmers (JJD *personal observation*). Such disturbance may adversely affect bluebird populations, as bluebird reproductive success has been shown to decrease with an increase in human disturbance (Kight and Swaddle 2007). The effects of human disturbance on farmland wildlife merits further research, as it will aid in the evaluation of the conservation potential of farms.

Spatial scale needs to be considered if research is to obtain comprehensive understanding of the complexities involved with sustaining wild birds and other vertebrates on agricultural lands (Hole et al. 2005). We conducted our research on few farms in North-central Florida, and all of our natural open-land sites were located within one large protected reserve (raising issues of spatial autocorrelation). Furthermore, the Eastern Bluebird is a highly mobile species that is fairly broad in its breeding habitat selection, including habitats not sampled here (e.g., orchards, graveyards, golf courses; Gowaty and Plissner 1998). Research conducted over a greater geographic range, with more replicates, and across a diversity of habitats would further strengthen our ability to assess the value of farms as habitat.

Finally, many native species adapted to open landscapes that inhabit farmlands are of greater conservation concern than bluebirds, and they deserve the attention of future research (e.g., Loggerhead Shrike [*Lanius ludovicianus*; Yosef 1996], Common Ground-Dove [*Columbina passerina*; Bowman 2002], Northern Bobwhite [*Colinus virginianus*; Brennan 1999]). A multi-species approach across a variety of open-land habitats would also improve ecosystem management. It would increase explanatory power while more accurately determining the landscape attributes and appropriate management schemes required for conserving birds of open lands (Lambeck 1997). Furthermore, agro-ecosystem designs that encompass biodiversity protection are among the most challenging and relevant problems in conservation biology (Daily et al. 2001; Hole et al. 2005).

Our research suggests that farms provide suboptimal breeding habitat in comparison to natural areas, yet farmland bluebirds still produced substantial numbers of offspring (see above). By measuring reproductive success alongside survivorship and habitat preference, future research could determine if farms act as habitat sources, sinks, or ecological traps (Brawn and Robinson 1996, Schlaepfer et al. 2002, Van Dyke 2003). Ecologists could further elaborate the effects of farmlands on reproduction, survivorship, and mortality by monitoring predation and human disturbance among farms and natural open lands. Lastly, future research could increase applicability and generality by focusing on open-land communities of priority conservation concern. Without such data, we cannot yet conclude that "wildlife-friendly" farms are truly wildlife-friendly. However, this research is the first to compare avian reproductive success among reduced-impact farms, conventional farms, and natural areas (to our knowledge; Hole et al. 2005, Scherr and McNeely 2008, Watson et al. 2008), and our results certainly illuminate fruitful paths for future research.

APPENDIX A
EFFECTS OF LAND MANAGEMENT ON THE REPRODUCTIVE SUCCESS OF A SONGBIRD OF OPEN LANDS

Table A-1. Raw data for pairs that laid a fourth clutch

Land Management	Brood	Incubation Period	Eggs	Hatchlings	Fledglings
Conventional	3	17.5	4	3	3
Conventional	3	12	4	2	2
Reduced-Impact	4	unknown	4	2	0
Reduced-Impact	would be "3"	n/a	4	0	0

The second column indicates whether the clutch in concern was or would have been the actual third or fourth brood.

Table A-2. Site-level descriptive statistics, presented clutch by clutch

Site-ID*	Clutch	Parameter	Incubation Period	#Eggs	#Hatchlings	#Fledglings	Hatching Success	Fledging Success	First-egg-day	Interbrood Lapse
RIF1	1	Mean	15.50	4.00	3.00	3.00	0.75	1.00	43.50	27.00
		N	1.00	1.00	1.00	1.00			1.00	1.00
		SE	.	.	.	.			.	.
	2	Mean	16.00	3.00	2.00	1.00	0.67	0.50		
		N	1.00	1.00	1.00	1.00				
		SE	.	.	.	.				
	3	Mean	13.00	5.00	3.00	3.00	0.60	1.00		
		N	1.00	1.00	1.00	1.00				
		SE	.	.	.	.				
	Total	Mean	14.83	4.00	2.67	2.33	0.67	0.88		
		N	3.00	3.00	3.00	3.00				
		SE	0.93	0.58	0.33	0.67				
RIF2	1	Mean	14.00	4.67	3.00	3.00	0.64	1.00	60.00	34.50
		N	3.00	3.00	3.00	3.00			3.00	2.00
		SE	0.58	0.33	0.58	0.58			7.00	.
	2	Mean	9.00	3.50	2.00	2.00	0.57	1.00		
		N	1.00	2.00	2.00	2.00				
		SE	.	1.50	2.00	2.00				
	3	Mean	14.00	4.00	1.00	1.00	0.25	1.00		
		N	1.00	1.00	1.00	1.00				
		SE	.	.	.	.				
	Total	Mean	13.00	4.17	2.33	2.33	0.56	1.00		
		N	5.00	6.00	6.00	6.00				
		SE	1.05	0.48	0.67	0.67				
RIF3	1	Mean	14.40	4.60	4.00	3.75	0.87	0.94	64.20	30.60
		N	5.00	5.00	5.00	4.00			5.00	5.00
		SE	0.53	0.40	0.45	0.48			6.39	7.36
	2	Mean	13.60	4.60	3.00	2.80	0.65	0.93		
		N	5.00	5.00	5.00	5.00				
		SE	0.24	0.24	0.55	0.49				
	3	Mean	14.00	4.33	2.33	2.33	0.54	1.00		
		N	2.00	3.00	3.00	3.00				
		SE	1.00	0.33	1.20	1.20				
	Total	Mean	14.00	4.54	3.23	3.00	0.71	0.93		
		N	12.00	13.00	13.00	12.00				
		SE	0.28	0.18	0.39	0.39				
RIF4	1	Mean	14.00	4.75	3.75	3.67	0.79	0.98	47.25	34.67
		N	4.00	4.00	4.00	3.00			4.00	3.00
		SE	0.00	0.25	0.48	0.67			0.25	5.77
	2	Mean	13.75	4.75	2.25	2.25	0.47	1.00		
		N	4.00	4.00	4.00	4.00				
		SE	0.48	0.25	0.63	0.63				
	3	Mean	14.00	4.33	2.00	1.67	0.46	0.83		
		N	3.00	3.00	3.00	3.00				
		SE	1.00	0.33	0.00	0.33				
	Total	Mean	13.91	4.64	2.73	2.50	0.59	0.92		
		N	11.00	11.00	11.00	10.00				
		SE	0.28	0.15	0.36	0.40				

Table A-2 Continued

Site-ID*	Clutch	Parameter	Incubation Period	#Eggs	#Hatchlings	#Fledglings	Hatching Success	Fledging Success	First-egg-day	Interbrood Lapse
RIF5	1	Mean	13.50	6.00	4.00	4.00	0.67	1.00	56.00	38.50
		N	1.00	1.00	1.00	1.00			1.00	1.00
		SE	.	.	.	.			.	.
	2	Mean	10.00	5.00	4.00	0.00	0.80	0.00		
		N	1.00	1.00	1.00	1.00				
		SE	.	.	.	.				
	3	Mean	12.00	4.00	3.00	3.00	0.75	1.00		
		N	1.00	1.00	1.00	1.00				
		SE	.	.	.	.				
	Total	Mean	11.83	5.00	3.67	2.33	0.73	0.64		
		N	3.00	3.00	3.00	3.00				
		SE	1.01	0.58	0.33	1.20				
RIF6	1	Mean	14.50	5.00	3.33	3.33	0.67	1.00	51.83	32.50
		N	2.00	3.00	3.00	3.00			3.00	2.00
		SE	0.00	0.00	1.67	1.67			4.17	0.71
	2	Mean	12.33	4.67	4.33	4.33	0.93	1.00		
		N	3.00	3.00	3.00	3.00				
		SE	0.73	0.33	0.33	0.33				
	3	Mean	13.50	4.00	4.00	4.00	1.00	1.00		
		N	2.00	2.00	2.00	2.00				
		SE	0.50	0.00	0.00	0.00				
	Total	Mean	13.29	4.63	3.88	3.88	0.84	1.00		
		N	7.00	8.00	8.00	8.00				
		SE	0.47	0.18	0.58	0.58				
RIF7	1	Mean	13.75	4.50	4.50	4.50	1.00	1.00	66.75	30.00
		N	2.00	2.00	2.00	2.00			2.00	2.00
		SE	0.25	0.50	0.50	0.50			16.75	7.07
	2	Mean	13.00	4.50	3.50	2.50	0.78	0.71		
		N	2.00	2.00	2.00	2.00				
		SE	1.00	0.50	1.50	2.50				
	3	Mean	13.00	4.00	3.00	3.00	0.75	1.00		
		N	1.00	1.00	1.00	1.00				
		SE	.	.	.	.				
	Total	Mean	13.30	4.40	3.80	3.40	0.86	0.89		
		N	5.00	5.00	5.00	5.00				
		SE	0.37	0.24	0.58	0.93				
RIF8	1	Mean	13.00	5.00	5.00	5.00	1.00	1.00	49.00	33.00
		N	1.00	1.00	1.00	1.00			1.00	1.00
		SE	.	.	.	.			.	.
	2	Mean	13.00	5.00	4.00	4.00	0.80	1.00		
		N	1.00	1.00	1.00	1.00				
		SE	.	.	.	.				
	3	Mean	12.00	5.00	5.00	5.00	1.00	1.00		
		N	1.00	1.00	1.00	1.00				
		SE	.	.	.	.				
	Total	Mean	12.67	5.00	4.67	4.67	0.93	1.00		
		N	3.00	3.00	3.00	3.00				
		SE	0.33	0.00	0.33	0.33				

Table A-2 Continued

Site-ID*	Clutch	Parameter	Incubation Period	#Eggs	#Hatchlings	#Fledglings	Hatching Success	Fledging Success	First-egg-day	Interbrood Lapse
CF1	1	Mean	15.00	4.50	2.00	2.00	0.44	1.00	50.00	25.00
		N	1.00	2.00	2.00	2.00			2.00	1.00
		SE	.	0.50	2.00	2.00			6.00	.
	2	Mean	13.50	5.00	3.50	5.00	0.70	1.43		
		N	2.00	2.00	2.00	1.00				
		SE	0.50	0.00	1.50	.				
	3	Mean		4.00	0.00	0.00	0.00	.		
		N		1.00	1.00	1.00				
		SE		.	.	.				
	Total	Mean	14.00	4.60	2.20	2.25	0.48	1.02		
		N	3.00	5.00	5.00	4.00				
		SE	0.58	0.24	1.02	1.31				
CF2	1	Mean	15.50	4.67	4.00	3.67	0.86	0.92	69.67	37.00
		N	3.00	3.00	3.00	3.00			3.00	3.00
		SE	0.87	0.33	0.58	0.67			8.21	2.18
	2	Mean	13.83	4.00	4.00	4.00	1.00	1.00		
		N	3.00	3.00	3.00	3.00				
		SE	0.17	0.00	0.00	0.00				
	3	Mean	13.00	4.00	4.00		1.00	0.00		
		N	1.00	1.00	1.00					
		SE	.	.	.					
	Total	Mean	14.43	4.29	4.00	3.83	0.93	0.96		
		N	7.00	7.00	7.00	6.00				
		SE	0.52	0.18	0.22	0.31				
CF3	1	Mean	15.00	5.50	1.50	1.00	0.27	0.67	62.50	23.00
		N	1.00	2.00	2.00	2.00			2.00	1.00
		SE	.	0.50	1.50	1.00			16.50	.
	2	Mean	14.00	5.00	1.00	1.00	0.20	1.00		
		N	1.00	2.00	2.00	2.00				
		SE	.	0.00	1.00	1.00				
	3	Mean	13.00	4.00	3.00	3.00	0.75	1.00		
		N	1.00	1.00	1.00	1.00				
		SE	.	.	.	.				
	Total	Mean	14.00	5.00	1.60	1.40	0.32	0.88		
		N	3.00	5.00	5.00	5.00				
		SE	0.58	0.32	0.68	0.60				
CF4	1	Mean	15.50	4.33	3.00	3.00	0.69	1.00	50.67	34.67
		N	3.00	3.00	3.00	3.00			3.00	3.00
		SE	0.76	0.33	1.00	1.00			3.18	5.53
	2	Mean	14.67	4.67	2.00	2.00	0.43	1.00		
		N	3.00	3.00	3.00	3.00				
		SE	0.67	0.33	1.00	1.00				
	3	Mean	14.00	4.00	1.00	1.00	0.25	1.00		
		N	2.00	3.00	3.00	3.00				
		SE	0.00	0.00	0.58	0.58				
	Total	Mean	14.81	4.33	2.00	2.00	0.46	1.00		
		N	8.00	9.00	9.00	9.00				
		SE	0.40	0.17	0.53	0.53				

Table A-2 Continued

Site-ID*	Clutch	Parameter	Incubation Period	#Eggs	#Hatchlings	#Fledglings	Hatching Success	Fledging Success	First-egg-day	Interbrood Lapse
CF5	1	Mean	13.00	3.00	2.00	2.00	0.67	1.00	39.00	34.00
		N	1.00	1.00	1.00	1.00			1.00	1.00
		SE	.	.	.	.			.	.
	2	Mean		2.00	0.00	0.00	0.00	.		
		N		1.00	1.00	1.00				
		SE		.	.	.				
	3	Mean	13.00	3.00	1.00	1.00	0.33	1.00		
		N	1.00	1.00	1.00	1.00				
		SE	.	.	.	.				
	Total	Mean	13.00	2.67	1.00	1.00	0.38	1.00		
		N	2.00	3.00	3.00	3.00				
		SE	0.00	0.33	0.58	0.58				
CF6	1	Mean	14.75	4.50	4.00	4.00	0.89	1.00	42.75	28.00
		N	2.00	2.00	2.00	2.00			2.00	2.00
		SE	0.75	0.50	1.00	1.00			2.75	4.24
	2	Mean	13.25	5.00	4.50	4.00	0.90	0.89		
		N	2.00	2.00	2.00	2.00				
		SE	0.75	0.00	0.50	1.00				
	3	Mean	13.00	4.00	3.50	4.00	0.88	1.14		
		N	2.00	2.00	2.00	1.00				
		SE	1.00	0.00	0.50	.				
	Total	Mean	13.67	4.50	4.00	4.00	0.89	1.00		
		N	6.00	6.00	6.00	5.00				
		SE	0.51	0.22	0.37	0.45				
NC1	1	Mean	15.50	4.50	4.50	4.50	1.00	1.00	69.00	39.50
		N	2.00	2.00	2.00	2.00			2.00	2.00
		SE	1.50	0.50	0.50	0.50			3.00	10.61
	2	Mean	14.25	4.00	4.00	4.00	1.00	1.00		
		N	2.00	2.00	2.00	2.00				
		SE	0.25	0.00	0.00	0.00				
	Total	Mean	14.88	4.25	4.25	4.25	1.00	1.00		
		N	4.00	4.00	4.00	4.00				
		SE	0.72	0.25	0.25	0.25				
NC2	1	Mean	14.38	4.60	3.40	3.20	0.74	0.94	77.40	40.83
		N	4.00	5.00	5.00	5.00			5.00	3.00
		SE	0.24	0.24	0.87	0.86			4.01	2.57
	2	Mean	14.50	4.25	4.00	3.75	0.94	0.94		
		N	4.00	4.00	4.00	4.00				
		SE	0.35	0.25	0.41	0.48				
	Total	Mean	14.44	4.44	3.67	3.44	0.83	0.94		
		N	8.00	9.00	9.00	9.00				
		SE	0.20	0.18	0.50	0.50				

Table A-2 Continued

Site-ID*	Clutch	Parameter	Incubation Period	#Eggs	#Hatchlings	#Fledglings	Hatching Success	Fledging Success	First-egg-day	Interbrood Lapse
NC3	1	Mean	15.25	4.80	4.00	4.00	0.83	1.00	63.80	39.75
		N	4.00	5.00	4.00	4.00			5.00	4.00
		SE	0.43	0.20	0.41	0.41			5.44	7.05
	2	Mean	14.80	4.40	3.80	3.40	0.86	0.89		
		N	5.00	5.00	5.00	5.00				
		SE	0.46	0.24	0.20	0.24				
	Total	Mean	15.00	4.60	3.89	3.67	0.85	0.94		
		N	9.00	10.00	9.00	9.00				
		SE	0.31	0.16	0.20	0.24				
NC4	1	Mean	16.00	3.50	2.50	2.50	0.71	1.00	63.75	41.00
		N	1.00	2.00	2.00	2.00			2.00	1.00
		SE	.	1.50	2.50	2.50			3.75	.
	2	Mean	13.00	5.00	5.00	5.00	1.00	1.00		
		N	2.00	2.00	2.00	1.00				
		SE	2.00	0.00	0.00	.				
	3	Mean	12.50	4.00	4.00	4.00	1.00	1.00		
		N	1.00	1.00	1.00	1.00				
		SE	.	.	.	.				
	Total	Mean	13.63	4.20	3.80	3.50	0.90	0.92		
		N	4.00	5.00	5.00	4.00				
		SE	1.14	0.58	0.97	1.19				

RIF=reduced-impact farm, CF=conventional farm, NC=natural control.

Table A-3. Rainfall patterns in North-central Florida

Parameter	Feb-Apr	Feb-Aug
8-year Mean Rainfall	7.44	10.64
Confidence Interval	2.14	1.89
Lower Bound	5.29	8.75
Upper Bound	9.58	12.53
2007 Mean Rainfall	4.46	9.10
2008 Mean Rainfall	10.74	14.16

Data used from Putnam Hall station of Florida Automated Weather Network (FAWN 2008). Values were calculated from data between February and April (second column) and February and August (third column), between 2001 and 2008.

APPENDIX B

REDUCED-IMPACT FARMING, PREY BIOMASS, AND THE REPRODUCTIVE SUCCESS OF EASTERN BLUEBIRDS (*SIALIA SIALIS*)

Table B-1. Site-level descriptive statistics

Site	Parameter	First Egg Day	Clutches	First-Clutch Eggs	First-Clutch Hatchlings	PB GW Biomass	PB WB Biomass	LT GW Biomass	LT WB Biomass	LT GW Instability	LT WB Instability	C1 GW Biomass	C1 WB Biomass	C1 GW Instability	C1 WB Instability
RIF2	Mean	51.2	2.25	4.8	2.6	7.50	5.59	23.11	18.90	4.70	23.11	6.71	5.57	4.75	4.70
	N	5	4	5	5	.	.	.	.	.	.	.	.	.	.
	Std. Deviation	17.81	0.50	0.45	1.95	.	.	.	.	.	.	.	.	.	.
RIF3	Mean	37.58	3	4.17	2	7.63	11.82	22.30	15.24	13.54	22.30	11.59	19.06	14.52	13.54
	N	6	5	6	6	.	.	.	.	.	.	.	.	.	.
	Std. Deviation	8.30	1.22	0.98	1.10	.	.	.	.	.	.	.	.	.	.
RIF4	Mean	38	3.25	4.5	2	7.69	6.81	13.03	18.39	14.74	13.03	10.38	12.45	8.10	14.74
	N	4	4	4	4	.	.	.	.	.	.	.	.	.	.
	Std. Deviation	9.42	0.96	1	1.83	.	.	.	.	.	.	.	.	.	.
RIF9	Mean	46.25	3	3.5	2.5	17.75	21.00	26.53	35.20	36.53	26.53	22.59	44.20	15.15	36.53
	N	2	2	2	2	.	.	.	.	.	.	.	.	.	.
	Std. Deviation	5.30	0	0.71	2.12	.	.	.	.	.	.	.	.	.	.
NC1	Mean	72	2.75	4.75	3.25	1.88	4.50	11.50	13.65	9.37	11.50	12.56	14.39	3.61	9.37
	N	4	4	4	4	.	.	.	.	.	.	.	.	.	.
	Std. Deviation	11.43	0.96	0.50	2.22	.	.	.	.	.	.	.	.	.	.
NC2	Mean	80.93	1.86	4.29	3.71	1.88	4.50	9.48	9.77	4.15	9.48	15.60	9.00	8.21	4.15
	N	7	7	7	7	.	.	.	.	.	.	.	.	.	.
	Std. Deviation	24.02	0.69	0.76	1.80	.	.	.	.	.	.	.	.	.	.
NC3	Mean	58.5	2	4.25	3.25	6.50	9.06	9.86	10.44	11.35	9.86	4.71	13.19	3.65	11.35
	N	4	3	4	4	.	.	.	.	.	.	.	.	.	.
	Std. Deviation	1.91	0	1.5	2.36	.	.	.	.	.	.	.	.	.	.
NC4	Mean	45	3	4.5	4.5	20.77	15.08	17.29	16.48	8.49	17.29	20.57	22.44	16.76	8.49
	N	2	1	2	2	.	.	.	.	.	.	.	.	.	.
	Std. Deviation	0	.	0.71	0.71	.	.	.	.	.	.	.	.	.	.
NC5	Mean	61.5	3	4	4	4.50	2.17	11.26	11.06	4.67	11.26	12.26	13.65	10.04	4.67
	N	2	2	2	2	.	.	.	.	.	.	.	.	.	.
	Std. Deviation	0.71	0	0	0	.	.	.	.	.	.	.	.	.	.
NC6	Mean	53.5	3	5	4.5	7.75	4.25	8.10	14.06	11.33	8.10	10.72	14.94	8.11	11.33
	N	2	2	2	2	.	.	.	.	.	.	.	.	.	.
	Std. Deviation	3.54	0	0	0.71	.	.	.	.	.	.	.	.	.	.

RIF=reduced-impact farm; NC=natural control area; GW=”grasshopper walk” survey; WB=”walk-brush” survey; PB=pre-breeding; LT=long-term; C1=first-clutch. We used some of the same sites from our previous study, as well as some new sites (see Table A-2).

Table B-2. Chapter 3 definitions

Term	Definition
First Egg Day	The day that the first egg of the first clutch of pair was laid
Clutch Production	The total number of clutches produced per pair
First-clutch Egg Production	The total number of hatchlings produced per pair in the first clutch
First-clutch Hatchling Production	The total number of eggs produced per pair in the first clutch
Pre-breeding	Adjective denoting the time period (when arthropod sampling began and before bluebird breeding began) between February 17th and March 13th (the mean first-egg-date for reduced-impact farms [the land management type with the earlier mean first-egg-date]); This time period is the same for all sites
First-clutch	Adjective denoting the time period between the two weeks before and the two weeks after the mean first-egg-date for a given site; This time period varies site-by-site
Long-term	Adjective denoting the time period between the February 17th and June 1st, the entire period when arthropod sampling occurred; This time period is the same for all sites
Prey Biomass	Absolute number of prey encountered on a transect multiplied by the mean prey length for that transect (see methods for details on determining prey length); Averaged on a site-by-site basis in the calculation of pre-breeding, first-clutch, and long-term prey biomass indices
Prey Instability	The coefficient of variation (CV) of prey biomass; Equal to the standard deviation divided by the square root of the mean; Calculated on a site-by-site basis for pre-breeding, first-clutch, and long-term prey instability indices
GW	Adjective denoting "Grasshopper Walk" surveys; see Methods for details
WB	Adjective denoting "Walk-brush" surveys; see Methods for details

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BIOGRAPHICAL SKETCH

I focus on wildlife (especially bird) species and communities to address problems in applied ecological research, conservation, and natural resources management. I have worked in organismal biology, population and community ecology, agroecology, urban ecology, conservation ornithology, long-term monitoring projects, and the human dimensions of wildlife management. I have worked in a variety of landscapes in North and South America. Study species range from aquatic macroinvertebrates to tapirs. I graduated with a Bachelor of Arts in environmental science and zoology from Miami University of Ohio.