Breeding-season biology of the Puerto Rican Bullfinch (Loxigilla portoricensis)

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Breeding-season biology of the
Puerto Rican Bullfinch (*Loxigilla portoricensis*)

by

Amber N. M. Wiewel

A thesis submitted to the graduate faculty
in partial fulfillment of the requirements for the degree of

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ABSTRACT

I studied the Puerto Rican Bullfinch (*Loxigilla portoricensis*), a frugivorous island endemic, in two sites in southwestern Puerto Rico in 2009 and 2010. I modeled nest survival of 37 nests to better understand the effects of several biological factors on daily nest survival. Predation was the most important cause of nest failure. Six models, all including some measure of fruit abundance, received approximately equal support. Constant, linear, and quadratic time trends in nest survival during seasons were all supported in these top six models. Results suggested that *Coccoloba microstachya* fruit abundance had a significant negative relationship, *Bursera simaruba* fruit abundance had a weak positive relationship, and *Bourreria succulenta* fruit abundance had a nearly significant positive relationship with nest survival. I radio-tracked bullfinches and estimated the breeding season home ranges and core areas of 17 adults. Median home range and core area for both sites were $31.4 \pm 30.0$ ha and $13.2 \pm 15.7$ ha, respectively. Home ranges and core areas did not differ in size between males and females or between pre-nesting and nesting periods. These findings increase our understanding of the breeding-season biology of the bullfinch, and will ultimately help inform future studies and conservation efforts of bullfinches and other passerines in southwestern Puerto Rico.
CHAPTER 1
INTRODUCTION

The Caribbean island of Puerto Rico experienced major deforestation during the first half of the 20th century. About 94% of the land had been cleared by the early 1900s (Franco et al. 1997, Kennaway and Helmer 2007). An economical shift from agriculture to industry from about 1930 to 1950 resulted in an increase in forest acreage to about 35% of the island (Birdsey and Weaver 1987); however, an increasing human population is reversing this trend through urbanization (López et al. 2001).

Puerto Rico has a long history of ornithological study (Wiley 1996), yet little is known about many of the breeding bird species found on the island (Acevedo and Restrepo 2008). Additionally, the island lacks comprehensive monitoring and conservation plans, important components of ensuring the continued existence of biodiversity on the island. Conservationists are faced with the challenges of protecting and improving bird habitat while urban expansion threatens secondary forests across the island (López et al. 2001).

Most funding for wildlife management and conservation in Puerto Rico is allocated to game species and species threatened by extinction (García et al. 2005). The Puerto Rico Comprehensive Wildlife Conservation Strategy (CWCS) was initiated in 2003 to determine the population status and distribution of native wildlife species not facing extinction or considered game species so that priority actions and proactive management can be implemented. The CWCS has identified Species of Greatest Conservation Need (SGCN) for Puerto Rico. These species are either considered at risk of extinction or are data deficient, meaning that there is not enough information for an assessment of risk of extinction. The
Puerto Rico Department of Natural and Environmental Resources is concerned about data deficient species, and thus the CWCS emphasizes research on this group (García et al. 2005).

The Puerto Rican Bullfinch (*Loxigilla portoricensis*) is a SGCN because it is poorly studied and is considered data deficient (García et al. 2005). This 32-g, non-migratory passerine of the family Emberizidae is endemic to the Puerto Rican archipelago. Although the bullfinch is relatively common in suitable habitats across Puerto Rico except in the eastern coastal area of the island (Raffaele 1989), reductions in range and overall population size are suspected (García et al. 2005).

Little biological information has been published about the bullfinch other than brief descriptions of reproductive and nesting habits (Bowdish 1901), stomach contents (Wetmore 1916), nest descriptions and range (Danforth 1931), general habits and nest descriptions (Biaggi 1983), and foraging ecology (Cruz 1980 and 1987, Pérez-Rivera 1994, Carlo et al. 2004, Saracco et al. 2005). Bullfinches are thought to be most common in dense mountain forests but are also found in lower forests with thick undergrowth, thick brushy areas, coffee plantations, and infrequently in mangroves (Raffaele 1989, García et al. 2005). They have also been noted to be an open-canopy or edge species (Recher 1970, Pagán 1995, Wunderle et al. 1992). Bullfinches are primarily frugivorous although they do consume other plant and animal matter (Wetmore 1916, Pérez-Rivera 1994, and Carlo et al. 2004). They are considered a foraging generalist based on behavioral flexibility in foraging site preferences, food consumption, and foraging methods (Pérez-Rivera 1994).

As part of a larger project of avian monitoring and conservation in southwestern Puerto Rico, I studied bullfinches during the breeding seasons of 2009 and 2010. Southwestern Puerto Rico lies in the precipitation rain shadow of the Cordillera Central
mountain range, and is largely covered by subtropical dry forest, also known as limestone forest (Ewel and Whitmore 1973). This forest type is the third largest of the island’s six major life zones. It is also the driest life zone of Puerto Rico, yet these dry forests are richer in bird species diversity than any of the wetter forests of the island.

Dry forests are more threatened and less protected than moist and wet forests throughout the world (Gerhardt 1993). In Puerto Rico, the dry southern coast was one of most heavily impacted areas during the early 1900s, because it was suitable land for agriculture and charcoal production (Murphy and Lugo 1986). By the 1940s, only about 5% of the entire southern coast remained as intact forest (Wadsworth 1950). Currently, forest covers about 23% of the dry forest zone (Ramjohn 2004). One of the largest tracts of dry forest remaining in Puerto Rico is Guánica State Forest, located on the south western coast of the island. It has been suggested that Guánica may be the best remaining example of natural vegetation in the subtropical dry forest life zone in the world (Ewel and Whitmore 1973), and it was designated as a United Nations Biosphere Reserve in 1981 in recognition of this status (Lugo et al. 1996). Additionally, Guánica is considered a Critical Wildlife Area (CWA) by the CWCS (García et al. 2005). For these reasons, Guánica State Forest is a priority for research and conservation efforts. The gaps in our knowledge of the biology of many species, particularly endemics such as the bullfinch, need to be addressed before further habitat loss or degradation occurs, and Guánica serves as an important and valuable habitat for this.

The objectives for this study were to document information pertaining to the breeding biology of the bullfinch and gain a better understanding of which factors influence nest survival (Chapter 2), and to quantitatively describe home ranges of adult bullfinches during
the breeding season (Chapter 3). The results presented here can be considered an important
and novel contribution to the knowledge of Puerto Rican Bullfinch biology.

**LITERATURE CITED**

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CHAPTER 2

NEST SURVIVAL AND BREEDING BIOLOGY OF THE PUERTO RICAN BULLFINCH

(LOXIGILLA PORTORICENSIS) IN SOUTHWESTERN PUERTO RICO

A manuscript to be submitted to Condor

Amber N. M. Wiewel, Stephen J. Dinsmore, and Jaime A. Collazo

ABSTRACT

Breeding biology information, including nest survival estimates, are lacking for many nesting species in Puerto Rico. We studied the Puerto Rican Bullfinch (*Loxigilla portoricensis*), a frugivorous island endemic, and modeled daily nest survival to better understand the effects of several biological factors on daily nest survival. In 2009 and 2010 we monitored 37 bullfinch nests in two sites in southwestern Puerto Rico. Predation was the most important cause of nest failure. Six models, all including some measure of fruit abundance, received approximately equal support. Constant, linear, and quadratic time trends in nest survival during seasons were all supported in these top six models. Results suggested that *Coccoloba microstachya* fruit abundance had a significant negative relationship, *Bursera simaruba* fruit abundance had a weak positive relationship, and *Bourreria succulenta* fruit abundance had a nearly significant positive relationship with nest survival. Under the top model, daily nest survival rates for each site and nest stage ranged from 0.63—0.92% in 2009 and 0.63—0.99% in 2010. This information on nest survival and factors that influence it increases our understanding of the breeding biology of the bullfinch, and will ultimately help inform future studies and conservation efforts in southwestern Puerto Rico.
INTRODUCTION

Nest survival estimates are an essential component of modeling avian demographics, and therefore are important for monitoring populations, estimating growth patterns, evaluating management practices, and addressing the need for conservation efforts. Furthermore, information on nest survival can be used to evaluate the health of a habitat (Howell et al. 1996, Larison et al. 2001), and to assess the accuracy of indices of productivity produced by methods other than nest monitoring (Feu and McMeeking 1991, Nur and Geupel 1993, Bart et al. 1999). However, nest survival data are lacking for many species, particularly those in the Neotropics (Robinson et al. 2000).

Although the Caribbean island of Puerto Rico has a long history of ornithological study, breeding information is lacking for many nesting species, especially endemics (Wiley 1996). Historically a forested island, about 94% of the land had been cleared by the early 1900s (Franco et al. 1997, Kennaway and Helmer 2007). Substantial reforestation has occurred, but the forests and associated wildlife species are now threatened by urban expansion (López et al. 2001) and invasive species (Garcia et al. 2005). The rate of habitat destruction and the high susceptibility of island species to anthropogenic habitat changes (Acevedo and Restrepo 2008) make Puerto Rico a priority for research and conservation efforts. The gaps in our knowledge of the biology of many species, especially endemics, need to be addressed before further habitat degradation or loss occurs.

The Puerto Rican Bullfinch (*Loxigilla portoricensis*, hereafter bullfinch), a member of the family Emberizidae, is endemic to Puerto Rico. It is relatively common in forests, thick brushy areas, and coffee plantations throughout most of the island of Puerto Rico (Raffaele 1989, García et al. 2005). Despite its regular distribution over the island, reductions
in its range and island-wide population are suspected (García et al. 2005). Furthermore, many biological aspects of bullfinches are poorly understood, including the breeding biology of the species. Little published literature exists on this topic aside from brief descriptions of nests and nesting habits (Bowdish 1901, Wetmore 1916) and clutch size and productivity (Gleffe et al. 2006), all of which are based on very small sample sizes.

In addition to increasing our knowledge of life history characteristics of the bullfinch and estimating its nest survival, it is important to learn how nest survival may vary with factors such as time, nest stage, nest height, precipitation, and resource availability. Annual variation in nest survival may result from factors such as fluctuations in predator numbers and changes in regional weather patterns (Dinsmore et al. 2002). Temporal shifts in predator communities, weather patterns, changes in behaviors of adults and young, and a host of other factors may contribute to variation in nest survival within seasons (Klett and Johnson 1982, Grant et al. 2005). Stage-specific differences in nest survival may be observed because parental behavior, and thereby conspicuousness of nests, can change with stage (Best and Stauffer 1980, Martin et al. 2000). Nest height may influence nest survival by causing variation in predation risk in relation to how accessible nests are to the predominant nest predators of the habitat (Filliater et al. 1994, Schmidt et al. 2008). Because research was conducted in a very seasonal environment, we were also interested in examining the influence of precipitation on nest survival; for example, rainfall may alter nest predator foraging behavior (Morrison and Bolger 2002) or prohibit adults from foraging adequately for themselves or nestlings.

Although the diet of the bullfinch is varied, it is a primarily frugivorous species and seems to prefer fruit when it is available (Wetmore 1916, Pérez-Rivera 1994, Carlo et al.)
The diet of nestling bullfinches is unknown, but most primarily frugivorous bird species feed large quantities of animal matter to their young, at least during the early portion of the nestling stage (Breitwisch et al. 1984). In many frugivorous species, though, the need for protein decreases as nestlings gain the ability to thermoregulate and parents transition into feeding them a diet with a higher fruit content (Breitwisch et al. 1984); therefore, it is likely that nestling bullfinches are fed fruit to some extent. The abundance of fruit resources could then potentially have an effect on nest survival by influencing what nestlings are fed and the amount of time adults spend away from the nest while foraging (Crawford et al. 2006, Boulton et al. 2008). Finally, fruit abundance may also influence predator behavior (Schmidt 1999). For example, omnivorous nest predators may spend less time searching for nests when fruit resources are high.

We report data collected during two breeding seasons on the nesting habits and nest survival of the Puerto Rican Bullfinch. Our objectives were to describe characteristics of their breeding biology and to model daily nest survival to better understand the effects of several biological factors on daily nest survival. This information will increase our understanding of the breeding ecology of an endemic passerine and will ultimately aid conservation efforts for this and other species in the subtropical dry forests of Puerto Rico.

METHODS

STUDY AREA

We studied Puerto Rican Bullfinches in two tracts of subtropical dry forest (Ewel and Whitmore 1973, sensu Holdridge 1967) in southwestern Puerto Rico: Guánica State Forest (17°58′N, 66°52′W; hereafter Guánica) and La Jungla (17°57′N, 66°57′W; Fig. 2.1). On average these two sites receive 750 to 860 mm of precipitation per year, but inter-annual
variation is high and droughts occur regularly (Ewel and Whitmore 1973, Faaborg and Arendt 1995). The forests, comprised of arborescent cacti and deciduous, semi-deciduous, and evergreen shrubs and trees, grow on shallow limestone soils that have little capacity for retaining water (Ewel and Whitmore 1973). Trees are generally <10m in height (Faaborg et al. 2007) and <10 cm in diameter at breast height (Murphy and Lugo 1986).

Most of the 4015-ha Guánica tract has been protected since 1919 by the Puerto Rico Department of Natural and Environmental Resources (DNER), but a peripheral unit of the forest was not added until 1948 (Colon and Lugo 2006). The forest was designated a United Nations Biosphere Reserve in 1981 in recognition of its status as one of the best remaining subtropical dry forests in the world (Lugo et al. 1996). Approximately half the reserve is mature, uncut vegetation, while the other half consists of second-growth, most of which is less than 100 years old, in various stages of regeneration (Lugo et al. 1996). Regenerating areas were used in the past for charcoal production, grazing, subsistence agriculture, tree plantations (mostly *Swietenia mahogoni*) and logging, and human residential areas and roads (Colon and Lugo 2006).

The La Jungla tract consists of roughly 615 ha and is located 8 km west of Guánica. It has been under the protection of the DNER for approximately ten years as a disjunct tract of the Guánica reserve, although it is not regularly monitored by DNER personnel. The land use history of La Jungla is not documented in as great detail as for Guánica, but it includes grazing, charcoal production, and some human residential use (Lugo et al. 1996, Pérez-Martinez 2007). Similarly to Guánica, the vegetation is in varying stages of regeneration, although some areas seem to be in significantly earlier stages of succession at La Jungla (A. Wiewel, pers. obs.).
Nest Survival

We searched for and monitored bullfinch nests from April to July of 2009 (Guánica) and 2010 (Guánica and La Jungla). Nest searching efforts were focused in four discrete 25 ha plots in Guánica and in a contiguous 100 ha plot in La Jungla, but we also monitored nests found opportunistically outside of these defined nest-searching plots. In both sites, the plots encompassed a range of forest ages. We located nests by observing breeding behavior in birds and by systematically searching in appropriate vegetation. Once a nest was found, flagging tape with directions to the nest was attached to vegetation at least 5 m from the nest. We monitored nests approximately every 3-5 days. Nests located higher than 2 m were checked by a small mirror mounted on a rod or a narrow plumbing snake camera (Ridgid microEXPLORER® Digital Inspection Camera). We considered nests depredated if there were signs of predation or if nestlings disappeared before day 14, which was the expected time of fledging. A nest was considered successful if nestlings were observed in the nest up until potential fledging dates and fledglings were observed near the nest on subsequent days. After each nest succeeded or failed we measured the height of the nest from the ground to the top of the nest rim to the nearest 0.1 m, and height, width, and depth of the nest structure to the nearest 0.1 cm.

Precipitation

We used daily precipitation data collected from two locations, one corresponding with each site. For Guánica we used data collected at a location central to the nest searching plots, courtesy of the DNER (M. Canals, pers. comm.). For La Jungla we used data from a U.S. Weather Bureau station located in the town of Ensenada (17°58’N, 66°56’W), approximately 4 km east of the La Jungla site (National Climatic Data Center 2010).
FRUIT ABUNDANCE

We systematically established 20 fruit monitoring stations in Guánica (five in each of the four nest plots) and 18 fruit monitoring stations in La Jungla to measure fruit abundance during the 2009 and 2010 breeding seasons. Because a complete list of fruit species consumed by bullfinches was not available, we developed a list of local species to monitor based on findings of previous studies (Wetmore 1916, Pérez-Rivera 1994), personal observations of the foraging of bullfinches and other frugivorous birds, and recommendations made by knowledgeable botanists and ornithologists. This resulted in a list of 46 species of trees and cacti known or very likely to be food sources for bullfinches in the dry forest (Appendix). Although fruiting vines and shrubs are also likely to provide food for bullfinches, we restricted focal species to trees and cacti.

Fruit monitoring stations were circular plots (Denslow et al. 1986, Loiselle 1987) of 7 m in diameter. We determined this plot size after preliminary surveys suggested that it would be an appropriate sampling area considering the average density of focal species and time needed to conduct fruit counts. We marked with numbered aluminum tags up to five trees or cacti of at least 1.5 m height of each focal species at each station (Appendix). If more than five individuals of a species were present, we marked only the five nearest to the center of the station. We visited stations weekly and visually estimated the number of ripe and unripe fruits on each marked individual. Fruit was considered ripe if it was completely mature and unripe if it was completely or partially immature. Each individual was then assigned a separate ripe and unripe fruit abundance index (FAI) based on the following logarithmic scale: 0 = no fruit, 1 = 1-10 fruits, 2 = 11-100 fruits, 3 = 101-1000 fruits, and 4 = 1001-10,000 fruits (following Saracco 2001). Weekly FAIs were summed within each site and
interpolated to provide a daily index at each site during the course of the breeding season. We also summed and interpolated the FAIs separately for the following species: *Amyris elemifera, Bourreria succulenta, Bursera simaruba, Coccoloba microstachya*, and *Crossopetalum rhacoma* (hereafter referred to by genus only). These species were selected because they are known food sources for bullfinches and they are relatively common in both sites; therefore we were interested in examining their relationships with nest survival independent of other species. Although ripe fruits are preferred and we were interested primarily in the ripe fruit abundance, we also wanted to examine the relationship between total (ripe + unripe) fruit abundance because bullfinches were observed eating unripe and partially ripened fruit. Missing values were replaced with the mean values over the rest of the season within a site and year. Missing values primarily occurred during 2009, when formal fruit scoring was not initiated until June.

**Statistical Analyses**

*Nest survival models.* We modeled the daily survival of bullfinch nests, defined as the probability that a nest will survive a single day, using the nest survival model of Dinsmore et al. (2002) as implemented in program MARK (White 2007). This method uses a generalized linear modeling approach based on a binomial likelihood. Dates were scaled so that day 1 was the date when the first nest was found in either year (May 5). For each nest we also included the following explanatory variables: linear and quadratic time trends within year, year, stage, site, nest height, precipitation, ripe FAI, total (ripe + unripe) FAI, total *Amyris* FAI, total *Bursera* FAI, total *Bourreria* FAI, total *Coccoloba* FAI, total *Crossopetalum* FAI, and observer visits. Preliminary analyses suggested that total FAI models performed better than ripe-only FAI models; therefore we used total FAI scores for modeling the five
individual species. We used the logit link function to incorporate covariates in all models. No goodness-of-fit test is available for the nest survival models in program MARK (Dinsmore et al. 2002). We used a hierarchical approach to build the list of candidate models. First we addressed temporal trends in daily nest survival. We assessed temporal variation within season by fitting constant survival, linear time trend, and quadratic time trend models. A linear time trend allows survival to increase or decrease over the season and a quadratic time trend allows survival to follow a curvilinear pattern. To evaluate variation between seasons, we modeled year effects. We also fit a model to nest stage (incubation or nestling) to evaluate potential differences in survival between stages. Next we added the competitive (ΔAIC < 2) time trend models to each individual covariate of site, nest height, precipitation, ripe FAI, total FAI, and individual total FAI for *Amyris, Bursera, Bourreria, Coccoloba,* and *Crossopetalum,* and observer effects. Finally, we combined each competitive time trend with each combination of competitive covariates.

*Model selection.* We ranked the set of candidate models using Akaike’s Information Criterion adjusted for small sample sizes (AIC$_c$; Akaike 1973) and Akaike model weights ($w_i$; Burnham and Anderson 2002) to select the most appropriate models for inference. Values reported in the Results section are means ± SE.

**RESULTS**

**SUMMARY**

Of 43 active bullfinch nests found during 2009 and 2010, 37 had sufficient data for nest survival analyses (Table 2.1). We monitored these nests for 220 exposure days across a 58 d interval (5 May to 2 July). Of the 37 nests used in analyses, 29 failed during incubation, 5 failed during the nestling stage, 2 successfully fledged young, and 1 had an unknown fate.
All unsuccessful nests likely failed due to predation, although we cannot exclude the possibility that abandonment occurred prior to predation in some cases. Additionally, one bullfinch nest was parasitized by a Shiny Cowbird (*Molothrus bonariensis*) but failed before or close to the time of hatching. The two successful nests fledged 2 and 3 nestlings and were both in La Jungla in 2010. Based on these two nests, the incubation period was 14 days and the nestling period was 14 to 15 days. Both nests were visible from trails that were used daily; therefore the nests were observed daily and our observations of the length of the incubation and nestling periods are precise.

Observed clutch sizes ranged from two to four eggs with a mean of 3.08 ± 0.57 (n = 25). Nests ranged from 0.88 to 6.00 m above the ground, with a mean height of 2.4 ± 1.6 m (n = 43). Nest structures were, on average, 160.6 ± 41.3 mm in height (n = 27) and 123.9 ± 21.3 mm wide (n = 25). They varied in shape ranging from slightly domed cup nests to domed nests with side entrances. Nests were usually constructed of palm fronds (*Leucothrinax morrisii*), lignified vascular tissue of cacti (*Cephalocereus* spp.), and various leaves and vines. Additionally, the thin, papery bark of *Bursera simaruba* was frequently used as a lining in the cup of the nest or in between layers of the nest structure.

In 2009 we observed cooperative breeding behavior in bullfinches in Guánica. On multiple occasions we observed family groups consisting of two adults and one to three juveniles, where juveniles were observed collecting nesting material along with adults, and on several occasions were seen adding material to nests.

**NEST SURVIVAL**

In the first step of analysis, all time trend models were competitive (<2 ΔAIC<sub>c</sub>; Table 2.2). Therefore, each of these models was subsequently combined with individual covariates
and combinations of competitive covariates. The results provided approximately equal support for constant, linear, and quadratic time trends in nest survival over the season, and suggested that daily nest survival was related to *Coccoloba*, *Bourreria*, and *Bursera* fruit abundance. Six resulting models were competitive (Table 2.2). Four of these models supported a quadratic time trend. All top models suggested that *Coccoloba* FAI had a significant negative relationship with nest survival. One of these models also suggested that *Bursera* FAI had a weak negative relationship with nest survival, although the coefficient for this model was not significant. Conversely, four of the top models suggested a nearly significant positive relationship between *Bourreria* FAI and nest survival. The overall best-supported model supported constant nest survival and suggested that *Coccoloba* had a significant negative effect ($\hat{\beta}_{Coccoloba} = -1.54$, SE = 0.65, 95% C.L. = -2.81, -0.27) and that *Bourreria* had a weak positive effect ($\hat{\beta}_{Bourreria} = 1.29$, SE = 0.16, 95% C.L. = -0.02, 0.61) on nest survival. Under this model, daily nest survival rates for each site and nest stage ranged from 0.63—0.92% in 2009 and 0.63—0.99% in 2010.

Stage and year effects were not well-supported in the final candidate model set. There was also little support for an observer effect or relationships between nest survival and nest height, precipitation, *Amyris* FAI, and *Crossopetalum* FAI. Models with total FAI (ripe + unripe fruit) tended to be better supported than models with ripe FAI only. Finally, there was support for a nearly significant positive relationship with site, suggesting that nest survival was higher at La Jungla than Guánica.

Using the top model, we predicted nest survival over the nesting period for bullfinches at high and low (mean daily FAI ± 1 SD) abundances of *Coccoloba microstachya*
and Bourreria succulenta (Fig. 2.2). These values were based on the 2010 daily interpolated values of FAI.

**DISCUSSION**

This research has provided valuable information on the breeding biology of the Puerto Rican Bullfinch in southwestern Puerto Rico, including estimates of the length of the incubation and nestling periods, the first known record of a bullfinch nest parasitized by a Shiny Cowbird, and a description of cooperative breeding behavior in juvenile bullfinches. Additionally, this research has produced the first estimates of nest survival for the bullfinch and shed light on factors that influence the species’ nest survival.

Assumptions of the nest survival model in MARK are that nests can be correctly aged, nest fates are correctly determined and are independent, daily survival rates are homogeneous, and nest discovery and monitoring do not influence survival. We did not model the effects of age because several nests could not be accurately aged. The other assumptions were met appropriately, as nest fates were usually easily determined, nests were dispersed over the landscape sufficiently to assume independence, and estimated survival rates were assumed to apply equally among nests. The final assumption, that nest checks do not influence survival, was of concern because nest failure rates were so high. Although most studies have found no significant effects of nest checks (e.g., Nichols et al. 1984), others have provided evidence that disturbing nests during nest checks may provide cues or enhance existing cues used by predators to find nests (e.g., Westmoreland and Best 1985). We tested for a change in nest survival in the interval following a visit to a nest by modeling nest visits as individual covariates in MARK; this model was poorly supported and suggests that nest checks did not influence survival our study. Additionally, it is important to note that we were
unable to incorporate daily nest survival estimates during the egg-laying stage into our overall estimate of nest survival because we had little data from this stage. Therefore, our nest survival estimates are probably biased high because they only include the incubation and nestling stages.

Most or all nest failure observed during this study was due to predation. Other studies have reported low estimates of nest survival or success in the tropics (Ricklefs 1969, Skutch 1985, Robinson et al. 2000), and in particular that nest predation is often the most important cause of nest loss in the tropics (Martin 1996). The most frequent nest predator in Guánica and La Jungla was likely the Pearly-eyed Thrasher (*Margarops fuscatus*). This omnivore is an avid nest predator, and has been observed depredating bullfinch nests (Arendt 2006). Additionally, we observed one bullfinch nest in Guánica that was probably depredated by a Pearly-eyed Thrasher (A. Wiewel, pers. obs.). Other likely nest predators that occur regularly at Guánica and La Jungla include Red-legged Thrushes (*Turdeus plumbeus*), Puerto Rican racers (*Alsophis portoricensis*), anole lizards (*Anolis* spp.), black rats (*Rattus rattus*), small Indian mongoose (*Herpestes javanicus*), feral cats (*Felis catus*), and green iguanas (*Iguana iguana*).

Top models provided support for constant, linear, and quadratic time trends in nest survival during the 2009 and 2010 season. Therefore it is unclear if there was a predominant time trend in nest survival in 2009 or 2010. Larger sample sizes may help to clarify this issue. Our models also suggested that nest survival was slightly higher at La Jungla than Guánica. These sites are only 8 km apart, are both coastal forest tracts, and presumably experience similar climatic and weather conditions. Although the vegetation is shorter and scrubbier at La Jungla, both sites are characterized by the same general forest structure and
nearly the same plant species composition. Two notable differences between La Jungla and Guánica were in relative amounts of fruit produced and numbers of Pearly-eyed Thrashers. Weekly fruit scores were consistently lower at Guánica even though the average number of trees per fruit station was similar between sites (A. Wiewel, pers. obs.). However, the lack of a strong relationship between FAIs and nest survival does not support the idea that lower fruit abundance at Guánica may have had a negative influence on nest survival. Additionally, Pearly-eyed Thrashers were infrequently captured in mist nets and detected by point count surveys in La Jungla relative to in Guánica (M. E. Kornegay, pers. comm.). The much lower density of Pearly-eyed Thrashers in La Jungla may have contributed to higher survival of bullfinch nests.

Both total and ripe FAIs showed weak positive trends in relation to nest survival. However, total FAI was better supported than ripe FAI, indicating that including the abundance of unripe fruit in addition to ripe fruit is an important consideration when assessing resource availability for bullfinches. A significant relationship between fruit abundance and nest survival may have been less detectable because nest failures were probably all or nearly all due to predation rather than starvation or abandonment. The inclusion of too many species in the analysis of total fruit, potentially including species not used by bullfinches, could have weakened this relationship as well. We expected to see a stronger positive relationship between fruit abundance and survival during the nestling stage. In this study the sample size was particularly small for the nestling stage because most nests failed during incubation. Analyzing additional years of nest survival and fruit phenology data, particularly with larger sample sizes of nests in the nestling stage, might reveal a stronger relationship between fruit abundance and nest survival. Finally, less inference can be
made between nest survival and fruit abundance in 2009 because there were so many missing values.

Relationships between nest survival and fruit abundance were well-supported for three fruit species: *Coccoloba, Bourreria,* and *Bursera.* *Bourreria* FAI had a positive relationship with nest survival. Contrary to our expectations, however, top models suggested negative relationships between nest survival and *Coccoloba* and *Bursera* FAIs. This may be a spurious result as an artifact of testing a large number of models. Yet these models outperformed the intercept-only model, which suggests that there may be some true relationship, whether direct or indirect, between nest survival and fruit abundance. A potential explanation is that *Coccoloba* or *Bursera* fruiting is correlated with some other unmeasured factor that negatively affects nest survival. An alternative idea is that increases in *Coccoloba* or *Bursera* fruit influences nest predator behavior such that predators are more likely to encounter nests, perhaps while searching for *Coccoloba* fruit (Schmidt 1999).

Because fruiting is ephemeral and quite patchy in the dry forest, it also possible that we did not include a large enough sample size of trees. Although sample sizes were relatively large for most fruit species, many individuals never fruited during the course of our monitoring. Therefore, perhaps even larger fruit plots or more fruit plots are needed to detect stronger relationships between fruit abundance and nest survival.

Despite the low nest survival observed in this study, bullfinches persist in southwestern Puerto Rico. This suggests that the species has a relatively high adult survival rate, as is widely assumed for tropical birds (e.g., Ricklefs 1969, 1997, Johnston et al. 1997). Indeed, a long-term mist netting study in Guánica reports that the annual apparent survival of adults from 1989 to 2010 was 0.714 (J. Faaborg, pers. comm.). This estimate may be biased
low because birds that disperse out of the study area cannot be accounted for and are considered dead. Furthermore, the Guánica study has produced a number of records for bullfinches that are 9 to 12 years of age (J. Faaborg, pers. comm.), which is relatively long-lived for small passerines.

Wetmore (1916:124) reported that bullfinches “nest rather irregularly throughout the year.” This observation may be the result of recording nests throughout most of the year in the wetter forests of Puerto Rico, where seasonality is much less pronounced. In the dry forests of southwestern Puerto Rico, most birds restrict their breeding to the spring and early summer rainy season of approximately April to July. During the dry season that spans roughly December to April, resources are probably too limiting for birds to successfully rear young in most years. However, we suspect that bullfinches do breed opportunistically in the dry forest. In January to March 2009, juvenile bullfinches were regularly captured in mist nets (J. Toms, pers. comm.) and multiple family groups including juvenile bullfinches were observed (A. Wiewel, pers. obs.). Several rainfall events, including one unusually large event, occurred in January 2009, which probably initiated this breeding activity. Taking into consideration the adult survival rates and longevity of bullfinches, it is not surprising that these birds may be able to breed when conditions are favorable and perhaps forego breeding when conditions are less suitable.

The cooperative breeding behavior we observed in 2009 in Guánica was restricted to nest material collection and nest building by juvenile bullfinches. These birds were likely young produced by the associated adult pair during the previous breeding occasion. No further cooperative breeding behavior was observed, but it should be noted that bullfinches are extremely secretive breeders and do not normally build nests, incubate, or feed nestlings
while observers are near. Therefore we do not know if juveniles actually contribute to feeding nestlings or any other breeding efforts. This behavior was only observed in 2009, following the rainy January that seemed to have initiated early breeding in bullfinches that year. The fact that we did not observe cooperative breeding behavior in 2010 suggests that breeding was not attempted, or at least not successful, in January to February of 2010, when conditions were more typical (drier) than the previous year.

The results presented here shed light on the life history of a relatively long-lived tropical island endemic, the Puerto Rican Bullfinch. It is particularly interesting that nest survival was lower in Guánica, the forest tract that receives significantly greater protection and is considered the best or one of the best remaining subtropical dry forests in the world (Lugo et al. 1996). Perhaps this is indicative of the habitat needs of the bullfinch. Habitat disturbance may be important for the bullfinch, a species that evolved on a small island that experiences regular disturbances in the form of hurricanes and other stochastic events. Furthermore, southwestern Puerto Rico historically experienced regular flooding and landslides (Lugo et al. 1996).

There is a clear need for additional research on the breeding biology of this species. Additional nest survival studies would increase sample sizes and yield information on nest survival over a variety of weather conditions, which seems particularly important for the seasonal and drought-subjected southwestern region of Puerto Rico. Frugivory studies of the bullfinch in southwestern Puerto Rico would confirm which fruiting species are consumed by bullfinches in the dry forest and would thus help tease apart relationships between fruit abundance and nest survival. Moreover, some fruit species may only be important to birds in some seasons or some years (Blake and Loiselle 1990), which further emphasizes the need
for more years of nest survival and fruit abundance data. Predictions of nest survival at varying levels of fruit abundance, such as those in Fig. 2.2, may be useful for formulating hypotheses which could be tested by studies in which fruit abundance is manipulated while nest survival is monitored. It would also be useful to quantitatively determine which nest predators play the most important roles in depredating bullfinch nests. This would have particularly interesting implications if any non-native predators such as cats, iguanas, mongoose, or rats caused a significant number of predation events.

**LITERATURE CITED**


Table 2.1. The total number of Puerto Rican Bullfinch (*Loxigilla portoricensis*) nests from two subtropical dry forest sites in southwestern Puerto Rico during 2009-2010 used in nest survival analyses.

<table>
<thead>
<tr>
<th>Year</th>
<th>No. nests</th>
<th>Guánica</th>
<th>La Jungla</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Incubation</td>
<td>Nestling</td>
</tr>
<tr>
<td>2009</td>
<td>9</td>
<td>9</td>
<td>2</td>
</tr>
<tr>
<td>2010</td>
<td>28</td>
<td>4</td>
<td>0</td>
</tr>
<tr>
<td>Totals</td>
<td>37</td>
<td>13</td>
<td>2</td>
</tr>
</tbody>
</table>
Table 2.2. Models considered for analyzing daily nest survival of Puerto Rican Bullfinch nests (Loxigilla portoricensis) with corresponding number of parameters (K), $\Delta$AIC$_c$ values, and Akaike weights ($w_i$) for model selection. The table illustrates the hierarchical approach to model building. In the first step, time trend models were considered. The AIC$_c$ value for the top-ranked time trend model was 128.65. In the next step, competitive time trend models were combined with covariates. The AIC$_c$ value for the top-ranked time trend + covariates model was 123.80. Only competitive (<2$\Delta$AIC$_c$) models are presented. Analyses were based on 220 days of nest monitoring at 37 nests in two subtropical dry forest sites in southwestern Puerto Rico during 2009-2010.

<table>
<thead>
<tr>
<th>Model</th>
<th>$\Delta$AIC$_c$</th>
<th>$w_i$</th>
<th>K</th>
<th>Deviance</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Time Trend Models</strong></td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Constant</td>
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<td>0.29</td>
<td>1</td>
<td>126.63</td>
</tr>
<tr>
<td>Quadratic</td>
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<td>0.26</td>
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<td>122.83</td>
</tr>
<tr>
<td>Year</td>
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<td>125.48</td>
</tr>
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<td>Linear</td>
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<td>0.14</td>
<td>2</td>
<td>126.02</td>
</tr>
<tr>
<td>Stage</td>
<td>1.85</td>
<td>0.12</td>
<td>2</td>
<td>126.45</td>
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<tr>
<td><strong>Best Time Trends + Covariates</strong></td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Constant + <em>Coccoloba</em> + <em>Bourreria</em></td>
<td>0.00</td>
<td>0.13</td>
<td>3</td>
<td>117.70</td>
</tr>
<tr>
<td>Quadratic + <em>Coccoloba</em> + <em>Bourreria</em></td>
<td>0.71</td>
<td>0.09</td>
<td>5</td>
<td>114.27</td>
</tr>
<tr>
<td>Quadratic + <em>Coccoloba</em> + <em>Bursera</em></td>
<td>1.01</td>
<td>0.08</td>
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</tr>
<tr>
<td>Linear + <em>Coccoloba</em> + <em>Bourreria</em></td>
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</tr>
<tr>
<td>Quadratic + <em>Coccoloba</em> + <em>Bursera</em> + <em>Bourreria</em></td>
<td>1.64</td>
<td>0.06</td>
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<td>113.09</td>
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<tr>
<td>Quadratic + <em>Coccoloba</em></td>
<td>1.76</td>
<td>0.06</td>
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<td>117.39</td>
</tr>
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</table>
Figure 2.1. Map of the study area in southwestern Puerto Rico indicating the two study sites, La Jungla and Guánica.
Figure 2.2. Predicted nest survival values (± 95% confidence limits) for the 28-day nesting (incubation + nestling) period of the Puerto Rican Bullfinch (*Loxigilla portoricensis*) in southwestern Puerto Rico, given varying values of fruit abundance for two tree species. Values were generated using estimates from the top nest survival model (Constant survival + *Coccoloba* FAI + *Bourreria* FAI; Table 2.2). Average abundances represent the daily mean indices of total (ripe + unripe) fruit abundance observed in 2010 for *Coccoloba microstachya* and *Bourreria succulenta*. Low and high abundances represent the daily mean index of total (ripe + unripe) fruit abundance ± 1 SD. Because the low value (mean – 1 SD) was negative, 0.00 was used as the low value for both species.
APPENDIX

Total list of fruiting tree and cactus species used in counts of fruit abundance indices (FAIs) in subtropical dry forest in southwestern Puerto Rico. For each site, the number of 7 m diameter plots containing at least one individual of the species, and the total number of individuals (up to five per plot), are shown.

<table>
<thead>
<tr>
<th>Species</th>
<th>Guánica No. plots (n=20)</th>
<th>Guánica No. individuals</th>
<th>La Jungla No. plots (n=18)</th>
<th>La Jungla No. individuals</th>
</tr>
</thead>
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<td>Amyris elemifera</td>
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<td>49</td>
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<td>18</td>
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<tr>
<td>Antirhea lucida</td>
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<td>0</td>
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<td>Bucida buceras</td>
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<td>14</td>
<td>3</td>
<td>10</td>
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<td>Bursera simaruba</td>
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<td>23</td>
<td>8</td>
<td>13</td>
</tr>
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<td>Canella winterana</td>
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<td>2</td>
<td>4</td>
<td>6</td>
</tr>
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<td>Capparis flexuosa</td>
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<td>2</td>
<td>2</td>
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<tr>
<td>Capparis hastata</td>
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<td>0</td>
<td>0</td>
</tr>
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<td>1</td>
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<td>2</td>
</tr>
<tr>
<td>Cassine xylocarpa</td>
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<td>1</td>
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<td>Cephalocereus royenii</td>
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<td>2</td>
<td>4</td>
<td>18</td>
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<td>Coccoloba diversifolia</td>
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</tr>
<tr>
<td>Coccoloba krugii</td>
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<td>Coccoloba microstachya</td>
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<td>14</td>
<td>43</td>
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<td>Colubrina arborescens</td>
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<td>23</td>
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<td>65</td>
</tr>
<tr>
<td>Erithalis fruticosa</td>
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<td>5</td>
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<td>Erythroxylum areolatum</td>
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<td>Eugenia xerophytica</td>
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<td>Guaiacum sanctum</td>
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<td>Guapiira discolor</td>
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<td>Gymnanthes lucida</td>
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<td>Chr 3</td>
<td>Chr 4</td>
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<td>----------------------------------------</td>
<td>-------</td>
<td>-------</td>
<td>-------</td>
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<td><em>Hylocereus trigonus</em></td>
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<td><em>Jacquinia berteroi</em></td>
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<td>8</td>
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<td><em>Polygala cowellii</em></td>
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<td><em>Randia aculeata</em></td>
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<td><em>Reynosia vivesiana</em></td>
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<td><em>Schaefferia frutescens</em></td>
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<td><em>Zanthoxylum flavum</em></td>
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</table>
CHAPTER 3

BREEDING-SEASON HOME RANGE OF THE PUERTO RICAN BULLFINCH

(*LOXIGILLA PORTORICENSIS*) IN SOUTHWESTERN PUERTO RICO

A manuscript to be submitted to *Journal of Caribbean Ornithology*

Amber N. M. Wiewel, Stephen J. Dinsmore, and Jaime A. Collazo

ABSTRACT

We radio-tracked Puerto Rican Bullfinches, a frugivorous island endemic, in dry forest of southwestern Puerto Rico. We estimated the breeding season home ranges and core areas of 17 adult bullfinches. The median home range was $31.4 \pm 30.0$ ha, and the median core area was $13.2 \pm 15.7$ ha. Home ranges and core areas did not differ in size between males and females or between pre-nesting and nesting periods. We propose that this relatively large home range size illustrates the need of bullfinches to make forays from core areas to search for ripe fruit, a patchy resource in the dry forest. These findings contribute to the knowledge of a poorly understood tropical species and will further the conservation of bullfinches and other frugivorous passerines of Puerto Rico.

INTRODUCTION

Home ranges are considered the areas within available habitat where organisms concentrate their daily activities (Feldhammer et al. 2004). All of an animal’s routine necessities, such as shelter and food, must be found within the home range; therefore, home range size is an important indicator of the resource requirements of an animal (Perry and Garland 2002). The size of a home range may be determined by factors such as resource availability, season, habitat, and life-history traits (e.g., Kelt and Van Vuren 2001, Ober et al. 2005, Volampeno et al. 2011). Relatively few studies of home ranges have been conducted...
on tropical birds (Beltrán et al. 2010), even though it has been suggested that, in general, tropical species may differ in extent of territoriality and home range compared to temperate zone species. For example, Karr (1971) reported large and overlapping home ranges in many tropical forest species of Panama, in contrast to smaller and more strongly defended home ranges of temperate forest species of Illinois. Willson et al. (1973) suggested that large home ranges in tropical birds may be necessitated by the occurrence of patchily distributed resources such as fruiting trees. In the dry forests of southwestern Puerto Rico, fruit is indeed a spatially and temporally ephemeral resource (Murphy and Lugo 1986a; A. Wiewel, unpubl. data). This region experiences a regular dry season from about December to April, as well as frequent droughts (Ewel and Whitmore 1973, Faaborg 1982). Therefore, frugivorous birds of southwestern Puerto Rico may be expected to have relatively large home ranges.

The Puerto Rican Bullfinch (*Loxigilla portoricensis*), a non-migratory passerine of the family Emberizidae, is endemic to the Puerto Rican archipelago. The species inhabits forests, brushy areas, and coffee plantations throughout most of Puerto Rico, and is a common species of the dry forests of southwestern region of the island. It is primarily a frugivorous species, although it does also consume invertebrates (Wetmore 1916, Pérez-Rivera 1994, Carlo et al. 2004). The Puerto Rico Department of Natural and Environmental Resources’ Comprehensive Wildlife Conservation Strategy (CWCS) considers the bullfinch a Species of Greatest Conservation Need under the classification of Data Deficient (García et al. 2005). This category identifies species whose status is of concern but for which data to support a current classification (i.e. endangered or threatened) are lacking. The CWCS specifically calls for conducting research to study home ranges, among other important biological factors, of these species, to aid in developing conservation and management plans.
Many components of the life history of the bullfinch are missing from scientific knowledge, including information on home ranges. To our knowledge, no information exists on the size or other characteristics of home ranges for the bullfinch. Because it is a frugivorous species, it may be expected to have a relatively large home range for its body size (Schoener 1968), particularly in the dry forest. Here, we report results from a study of home ranges in Puerto Rican Bullfinches in dry forest of southwestern Puerto Rico. We focused our study during the breeding season, which typically extends from April to June in the dry forest. Specifically, we estimated the breeding-season home range and core area sizes of adult bullfinches. We also tested for differences in home ranges and core areas between males and females and between pre-nesting and nesting periods. We use the definition of home range as the extent of an area with a defined probability of occurrence of an animal, during a specified time period (Kernohan et al. 2001).

**METHODS**

**STUDY AREA**

We captured, marked, and radio-tracked bullfinches in two tracts of subtropical dry forest (Ewel and Whitmore 1973, *sensu* Holdridge 1967) in southwestern Puerto Rico: Guánica State Forest (17°58′N, 66°52′W; hereafter Guánica) and La Jungla (17°57′N, 66°57′W; Fig. 3.1). Approximately half of the 4015-ha Guánica tract is mature, uncut vegetation, while the remainder consists of second-growth forest in various stages of regeneration (Lugo et al. 1996). The elevation of the study area at Guánica ranges from approximately 100 to 200 m. The La Jungla tract is located about 8 km west of Guánica. It consists of roughly 615 ha and ranges in elevation from approximately 0 to 75 m.
On average the study sites receive 750 to 860 mm of precipitation per year, but inter-
annual variation is high and droughts occur regularly (Ewel and Whitmore 1973, Faaborg
and Arendt 1995). The forests, comprised of arborescent cacti and deciduous, semi-
deciduous, and evergreen shrubs and trees, grow on shallow limestone soils that have little
capacity for retaining water (Ewel and Whitmore 1973). Trees are generally <10m in height
(Faaborg et al. 2007) and <10 cm in diameter at breast height (Murphy and Lugo 1986b).

**Radio Telemetry**

We radio-tracked bullfinches from May to June 2009 in Guánica, and from March to
July 2010 in La Jungla. Bullfinches were captured using mist nets placed along trails in the
study sites and were usually processed, including banding and radio-tagging, in ≤10 min.
Twelve bullfinches were radio-tagged in 2009 (model A2415; Advanced Telemetry Systems,
Isanti, MN, USA) and 30 bullfinches were radio-tagged in 2010 (models BD-2 and BD-2N;
Holohil Systems Ltd., Carp, ON, Canada). Transmitters ranged in weight from 0.5 g to 0.75 g
and had estimated lifespans of 18 to 28 days, although some transmitter batteries exceeded
their nominal lifespans. In 2009 bullfinches were initially outfitted by gluing transmitters to
the skin of the interscapular region using a nontoxic cyanoacrylate adhesive. After
determining that these transmitters were quickly falling off birds, subsequent transmitters
were attached with 1-mm diameter elastic thread using a modified version of Rappole and
Tipton’s (1991) figure-eight thigh-harness. This harness method was used for the remainder
of 2009 and all of 2010. Harnesses added about 0.2 g to the weight of each transmitter,
resulting in total weights of 0.7 to 0.95 g. Radio-tagged bullfinches ranged in weight from 25
to 35 g; therefore even the heaviest transmitters added <4% of the total body weight to the
smallest birds, which falls under the recommended maximum addition of 5% of the body
weight (Naef-Daenzer et al. 2001). Following their release, outfitted birds were observed to ensure that normal movements were not inhibited. Only adult bullfinches were radio-tagged except for three juvenile birds that received transmitters in 2009. These three juveniles were not used in analyses; therefore the following methods and results apply to adult bullfinches only.

The majority of bullfinches that were radio-tagged could not be sexed at the time of capture because they were not in breeding condition. We used a linear discriminant analysis (LDA) based on a set of known-sex bullfinches to separate males and females on measures of wing chord and weight, and then developed a rule to assign the sex to unknown-sex individuals. The LDA rule determined the sex of a set of 59 known-sex individuals with 97% accuracy.

Outfitted birds were radio-tracked using scanning receivers (model R410, Advanced Telemetry Systems, Isanti, MN) and three-element, hand-held Yagi antennas. Following the detection of a signal, a bearing was recorded. Due to the topography of the study sites and the dense vegetation, bounced signals were frequently detected in addition to true signals. We attempted to discern the true signal, but occasionally the two signals could not be distinguished. In these cases, both signals were recorded and the true signal was subsequently chosen based on the directionality of the remaining signals recorded during the same radio-tracking session. If the true signal could not be determined, both bearings were removed from the dataset.

In 2009, birds were radio-tracked once daily by a single observer from permanent ground stations. In 2010, birds were initially radio-tracked twice daily from permanent ground stations established throughout the 100 ha plot in La Jungla. Five telemetry towers
were constructed in early April 2010. The tower platforms stood approximately 4.9 m above
ground, which was sufficient to raise antennas above the canopy and allowed signals to be
detected from greater distances. Following construction of the towers, birds were radio-
tracked twice daily from a combination of towers and ground stations. The twice-daily radio-
tracking during 2010 consisted of a morning session (between 0900 and 1230 hours) and an
afternoon session (between 1530 and 1900 hours). During each session, two observers
simultaneously radio-tracked birds from a series of towers and ground stations.

We estimated angular error of signals by placing transmitters in known locations.
Naïve observers then recorded bearings to the test transmitters using the same protocol as
described above. To get a measure of mean angular error that did not include extremely
erroneous bearings (such as null or bounced signals), we visually assessed the bearings for
each location and removed outliers in a standardized manner. An average error was then
calculated for each site in LOAS™ (Ecological Software Solutions LLC 2010). This error
test also allowed us to test the ground stations to determine which ones were in locations that
minimized signal bounce. The worst performing ground stations were removed from
subsequent tracking sessions.

Using the same methods as described above, we visually assessed the bearing sets for
all birds and removed outlier bearings. Locations for each bird were estimated by
triangulation using the maximum likelihood estimator (MLE; Lenth 1981) in LOAS™.
Because we were concerned about outliers we also estimated locations using the Andrews
estimator (Lenth 1981), which is more robust to outliers. The two estimators yielded similar
results, suggesting that few or no significant outlier bearings remained in the dataset, and we
used MLE for subsequent analyses. The mean angular error estimates calculated above were used in estimating locations.

**HOME RANGE AND CORE AREA**

We estimated 95% fixed-kernel densities (KDE; referred to hereafter as “home range”) with ABODE (Laver 2008) for ArcGIS (ESRI 2009). We used the biweight kernel form and fixed smoothing of kernels using the least-squares cross-validation (LSCV) technique to select the smoothing factor (bandwidth). This was based on Seaman and Powell’s (1996) conclusion that LSCV fixed kernels outperform adaptive kernels. Kernels had a grid-cell resolution of 25 m and contouring was performed by volume. We used a scaling factor of 1,000,000 and standardized the data using unit variance measures. Horner and Powell (1990) and Powell (2000) recommend that core areas be determined uniquely for each home range rather than based on a 50% probability density. Therefore, for each home range we used ABODE to calculate the core area, defined as the area in which the probability density was significantly greater than expected by a random distribution.

Because this study was initiated before nesting activity began for most bullfinches, we wanted to test for a difference in home range size preceding nesting compared to when birds were actively nesting. Based on our observations of bullfinch nesting behavior and activity in 2010, we split the 2010 data into a pre-nesting period (prior to May 1) and a nesting period (May 1 and later). For most individuals, all location estimates were entirely contained in one of the two periods. If location estimates overlapped both periods, we removed all location estimates in one period if there were insufficient locations to estimate a home range, or split the location estimates into the two periods and estimated a separate home range for each. Data for two individuals were used in both periods, but in the context
of testing for differences in home range size over time we considered these as independent samples between the two periods.

To assess if sample sizes of location estimates were sufficient to estimate home range size (Seaman et al. 1999), we determined the number of locations at which home range size reached an asymptote in ABODE. Each individual’s home range was recalculated after the addition of each randomly added location, and 10 iterations of this process were repeated. Following the methods of Laver (2005), we considered home ranges to have reached an asymptote when the mean simulated home range was first and thereafter consistently within 15% of the final home range size (calculated using all location estimates for an individual). Only individuals whose home ranges reached an asymptote were included in subsequent analyses.

**Statistical Analyses**

We tested home range and core area data for normality using Shapiro–Wilk tests, and for homogeneity of variances between groups using Levene’s tests, in Program R (R Development Core Team 2009). We then log-transformed these data as necessary to meet the assumptions of normality and equal variances. We ran t-tests in Program R to test for differences in mean home range and core area sizes between sexes and between the pre-nesting and nesting periods. We tested for autocorrelation in location data by calculating the ratio of the mean squared distance between successive observations and the mean squared distance from the center of activity \( (\bar{r}^2 / r^2) \) using the Animal Movements extension (Hooge et al. 1999) for ArcView GIS (ESRI 2002). Values reported in the Results section are means ± SD. All statistical tests were significant at \( \alpha = 0.05 \).
RESULTS

RADIO TELEMETRY

We radio-tagged twelve and thirty bullfinches in 2009 and 2010, respectively. In 2009, issues with transmitter loss and failure resulted in a lack of data from that season; therefore most results are from 2010. Of these 42 radio-tagged bullfinches, enough locations were estimated to attempt further analyses for 21 individuals. The home ranges of 17 bullfinches reached asymptotes according to our definition. The number of relocations to asymptote varied greatly by individual (\( \bar{x} = 15.1 \pm 8.4 \) locations, range 6–33 locations). Estimates of mean angular error were 9.87 ± 9.03 (\( n = 84 \) bearings) for Guánica, and 9.29 ± 11.50 for La Jungla (\( n = 29 \) bearings). Of the 17 individuals used in analyses, only four were able to be sexed at the time of capture. The remaining 13 birds were assigned sex using the LDA rule.

HOME RANGE AND CORE AREA

The median size of the home ranges of 17 individuals was 31.4 ± 30.0 ha (range 2.0—117.8 ha), and the median core area was 13.2 ± 15.7 ha (range 1.2—68.8 ha; Table 3.1). The mean percentage of the total home range that made up the core area was 67.4 ± 11.4% (range 45—82%). The mean size of home ranges did not differ between males (median = 24.9 ± 20.0 ha, range 2.0—68.1 ha, \( n = 9 \)) and females (median = 46.7 ± 37.3 ha, range 7.2—117.8 ha, \( n = 8 \), \( t_{15} = 0.94, P = 0.36 \)). The mean size of core areas also did not differ between males (median = 13.2 ± 8.2 ha, range 1.2—28.9 ha, \( n = 9 \)) and females (median = 14.2 ± 21.3 ha, range 2.3—68.8 ha, \( n = 8 \), \( t_{15} = 0.55, P = 0.59 \)). Furthermore, the mean size of home ranges did not change significantly between the pre-nesting (\( \bar{x} = 58.8 \pm 35.3 \) ha, range 20.6—99.1 ha, \( n = 4 \)) and nesting (\( \bar{x} = 36.9 \pm 35.8 \) ha, range 7.2—117.8 ha, \( n = 13 \), \( t_{15} = -1.22, P = \)
0.24) periods. Neither did the size of core areas change significantly between the pre-nesting
($\bar{x} = 21.2 \pm 9.0$ ha, range 15.3—34.5 ha, $n = 4$) and nesting ($\bar{x} = 18.1 \pm 20.7$ ha, range 2.3—
68.8 ha, $n = 13$, $t_{15} = -0.98$, $P = 0.34$) periods (Figs. 3.2 and 3.3).

Thirteen of 17 individuals had mean $t^2/r^2$ ratios >1.5, where a ratio >2 signifies
independence between successive locations and a ratio >1.5 is considered a moderately low
level of autocorrelation (Swihart and Slade 1997).

**DISCUSSION**

**HOME RANGE AND CORE AREA**

In 2009 and 2010, Puerto Rican Bullfinches had median home ranges and core areas
of 31.4 and 13.2 ha, respectively, with considerable variation between individuals (home
range 2—118 ha; core area 1—69 ha) and no differences between sexes or between pre-
nesting and nesting periods. These home range estimates represent the area over which
bullfinches search for resources. In the dry forests of southwestern Puerto Rico, ripe fruit is a
patchy and ephemeral resource. Monitoring of fruit resources in 2009 and 2010 (see Chapter
II) indicates that ripe fruit abundance varied temporally and spatially, even within a short
time scale and local spatial scale. We propose that bullfinches must make significant forays
from their core area to search for ripe fruit, and that some of these movements are captured in
our home ranges estimates.

We did not observe differences between home ranges of males and females, which
suggests that both sexes are foraging for the same resources and otherwise using their habitat
in the same way. We also did not observe a difference in home ranges of the pre-nesting and
nesting periods. However, the pre-nesting telemetry period only captured about one month
before nesting was initiated in most bullfinches. Therefore, this may have not been early
enough in time because bullfinches may have already been settled onto their breeding home ranges and territories with mates by this time. Furthermore, we do not know the actual breeding status of most of the bullfinches we radio-tracked because they were not in breeding condition at the time of capture.

One previous study using radio telemetry in bullfinches has been attempted; the purpose was to use radio-tracking to repeatedly locate and make foraging observations of marked individuals (Collazo and Noble 2007). The authors determined that it was impossible to approach bullfinches without causing them to either fly away or approach observers, which biased the individuals’ locations. Triangulation of locations was most accurate at \( \leq 150 \) m, but at very close ranges the arc from which the birds could be detected was wide. Finally, signal bounce occurred frequently because of the closed canopy, and the authors recommended that elevated platforms be used.

We drew similar conclusions based on our study in southwestern Puerto Rico. In 2009 we attempted to track bullfinches by honing in on their actual location. We found that the dense vegetation made it impossible to quietly move in the forest with radio-tracking equipment, such that the individuals being tracked always flushed before a visual was obtained. We also observed that individuals in very close proximity to the receivers could be detected over nearly 360 degrees, especially when tracking from towers. Conducting radio-tracking from towers in 2010 increased the distance over which birds could be detected, but did not necessarily increase the accuracy of bearings. Furthermore, tracking from towers reduced the number of null signals detected but did not eliminate them.

Our home range and core area size estimates may be biased slightly high because of small numbers of locations per individual and moderately large error rates in bearings.
However, under the methods we used for asymptote analyses, most home ranges reached asymptote at < 30 locations, which is generally accepted as the minimum number of locations required for home range estimates (White and Garrott 1990). This may be because each individual was tracked for such a short period of time (usually 4 weeks) that fewer locations were needed to capture the area of the home range over this timeframe.

Alternatively, it may be more appropriate to use a more conservative value for asymptote analysis, such as considering the mean simulated home range as suitable when within 10%, instead of 15%, of the final home range size. Furthermore, the criteria used for home range analysis was based on the final home range size that we estimated, which for many individuals was calculated from < 30 locations and may have biased low anyway. Therefore, we recommend using ≥ 30 locations per individual bullfinch when possible, particularly if radio-tracking occurs over a longer period of time, to ensure proper sampling of locations.

The need to test for autocorrelation in telemetry data has been emphasized (see Laver and Kelly 2008) because a lack of independence in locations may negatively bias estimates of home range size (Swihart and Slade 1985). Although only four individuals in this study were considered to have truly independent successive locations ($r^2/r^2 > 2$), most other individuals did have only moderately autocorrelated location data ($1.5 < r^2/r^2 < 2$). Regardless, sampling at intervals less than the statistical time to independence may not invalidate kernel density estimations (Swihart and Slade 1997). Furthermore, we think that considering biological independence between successive locations is a more meaningful approach in this case. Time to biological independence is described as the amount of time in which an animal can move from one point in its home range to any other point in its home range (Lair 1987), which is a negligible amount of time for a bullfinch. Therefore, we are convinced that the
location estimates that we recorded were, at the very least, biologically independent. Finally, because the transmitters used only lasted for three to five weeks, it would have been impossible to increase the time between successive estimates of locations without significantly decreasing sample sizes. We suggest following the recommendations of Swihart and Slade (1985) to collect one to two locations every 24 hours for each individual and, at a minimum, to ensure that sampling occurs at intervals greater than the time required by bullfinches to describe their home range boundaries (Otis and White 1999).

In a breeding-season study of male Pearly-eyed Thrashers (*Margarops fuscatus*) in Puerto Rico, 95% KDE was used to estimate that males used median home ranges of 2.0 ha and 0.5 ha during incubation and nestling stages, respectively (Beltrán et al. 2010). This is significantly smaller than our estimated median home range of 24.9 ha for male bullfinches during the breeding season. Although the Pearly-eyed Thrasher is larger than the bullfinch and therefore might be expected to have a larger home range, it is an opportunistic omnivore. Consequently, the thrasher may be able to find adequate resources over a smaller area than the bullfinch, a relatively specialized forager by comparison (Schoener 1968). Furthermore, the Pearly-eyed Thrasher was studied in tropical rainforest of northeastern Puerto Rico, a habitat that may support birds on smaller home ranges than the dry forests of southwestern Puerto Rico.

Replication of this study is needed to improve upon the accuracy of our results. This study contains data from primarily one site and one year, although we incorporated home range estimates for two individuals from the previous year at a nearby site. Even though the two sites represented in our study, Guánica and La Jungla, are discontiguous forest tracts, they are only 8 km apart and are both representative habitats of subtropical dry forest in
southwestern Puerto Rico. Additional studies of home range use over the entire year and in different habitats are needed to gain a more comprehensive understanding of home ranges and area requirements in bullfinches. Spatial and temporal changes in home range size would provide information on habitat quality of different forest tracts and changing resource distribution and abundance over time. We suggest that future studies focus on the size and location of home ranges in relation to the availability of important resources and other landscape characteristics, in both dry and wet forests of Puerto Rico. This requires a better knowledge of which resources a truly important to bullfinches. Furthermore, the practicality of these recommendations must be considered. We found the use of telemetry towers beneficial, but these towers require considerable effort to construct, especially when materials must be carried into sites that cannot be accessed by road. Furthermore, the construction of towers requires permission from landowners or agencies and also means that a small area of vegetation must be cleared to build the tower. Alternative ideas are attempting radio-tracking studies of bullfinches in habitats with more clearings or shorter vegetation, such as field and forest matrices, and areas of dry forest nearer to the coast.

These results provide the first estimates of home range in Puerto Rican Bullfinches, a Species of Greatest Conservation Need. This information has important implications for conservation, and will inform management decisions of bullfinches and other frugivorous passerines in Puerto Rico. For example, our home range estimates will be used in conjunction with density and abundance estimates for bullfinches in Guánica and La Jungla to help determine minimum size requirements for protected lands and forest-specific carrying capacity of bullfinches. Additionally, our findings concerning home ranges of bullfinches in
the dry forest may be compared with future studies to make recommendations on habitat requirements for bullfinches.

LITERATURE CITED


Table 3.1. Puerto Rican Bullfinches for which home range analysis was attempted in southwestern Puerto Rico, 2009 (Guánica) and 2010 (La Jungla). Only individuals for which home range reached an asymptote were used in further analyses. ID denotes each individual’s identification number. Home ranges and core areas are in hectares. The percent area of the total home range that was considered core area, the total number of locations used in estimating each home range and core area, and the number of locations at which home range reached an asymptote are provided. No number in the last column signifies that asymptote was not reached.

<table>
<thead>
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<th>ID</th>
<th>Site</th>
<th>Sex</th>
<th>Home Range</th>
<th>Core Area</th>
<th>% Area</th>
<th>Locations</th>
<th>Asymptote</th>
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<td>11.3</td>
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<td>10</td>
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<td>3.5</td>
<td>51</td>
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<td>14</td>
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</tbody>
</table>

^aSex was determined at the time of capture, and supported by results of a linear discriminant analysis rule used to assign sex to unknown-sex individuals based on wing chord and weight.

^bIndividual could not be sexed at the time of capture. Sex was assigned by a linear discriminant analysis rule based on wing chord and weight.
Figure 3.1. Map of the study area in southwestern Puerto Rico indicating the two study sites, La Jungla and Guánica.
Figure 3.2. Core areas (areas in which the probability density was significantly greater than expected by a random distribution) of home ranges during the pre-nesting period (before May 1) in La Jungla, southwestern Puerto Rico, 2010 for one male (a) and females (b). The core area represented 70% of the total home range area of the male and from 45—86% of the total home range areas of the females.
Figure 3.3. Core areas (areas in which the probability density was significantly greater than expected by a random distribution) of home ranges during the nesting period (May 1 and later) in La Jungla, southwestern Puerto Rico, 2010 for males (a) and females (b). The core area represented 55—82% of the total home range areas of the males and from 51—81% of the total home range areas of the females.
CHAPTER 4

GENERAL CONCLUSIONS

In this project, I studied features of the breeding-season biology of the Puerto Rican Bullfinch, an endemic frugivore of Puerto Rico. In Chapter 2, I reported the first estimates of nesting period length in bullfinches, the first known record of a bullfinch nest parasitized by a Shiny Cowbird, and a description of cooperative breeding behavior in juvenile bullfinches. These findings add to our knowledge of bullfinch life history and contribute critical preliminary information to future breeding studies of bullfinches.

Additionally, this research produced the first estimates of nest survival for the bullfinch and shed light on factors that influence the species’ nest survival. Nest survival in bullfinches was constant within season and low during 2009 and 2010, and most or all nest failure was due to predation. Results suggested that nest survival was higher at La Jungla than Guánica, and that fruit availability, at least of certain species, may influence nest survival. I propose that dry forest tracts that are not as mature or not considered as “pristine” as Guánica Forest Reserve, such as La Jungla, may provide equally or more suitable breeding habitat for bullfinches. Furthermore, periodic habitat disturbance may be important for the bullfinch.

In Chapter 3, I reported estimates of home range and core area size for adult bullfinches during the breeding season. Home ranges and core areas were relatively large, varied among individuals, and showed a high degree of overlap. I propose that bullfinches must make significant forays from their core area to search for ripe fruit, and that some of these movements are captured in my home ranges estimates. Additionally, I did not observe differences in home ranges or core areas between sexes or between pre-nesting and nesting
periods. The home range and core area estimates presented here will help inform management decisions for of bullfinches and other frugivorous passerines in Puerto Rico, particularly when considering minimum size requirements for protected forests.

There is a clear need for additional research on the breeding biology of the bullfinch to further clarify relationships between nest survival and factors such as site characteristics and fruit availability. Additional nest survival studies will increase sample sizes and yield information on nest survival over a variety of weather conditions, which seems particularly important for the seasonal and drought-subjected region of southwestern Puerto Rico. Replication of the home range study is also needed to improve upon the accuracy of my results, as well as to test factors that may influence home range size. Additional studies of home range use over the entire year and in different habitats will provide a more comprehensive understanding of home ranges and area requirements in bullfinches.
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