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NEST SURVIVAL AND BREEDING BIOLOGY OF THE PUERTO RICAN BULLFINCH (*LOXIGILLA PORTORICENSIS*) IN SOUTHWESTERN PUERTO RICO

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ABSTRACT.—Breeding biology information, including nest survival estimates, are lacking for many nesting species in Puerto Rico. We studied the endemic Puerto Rican Bullfinch (*Loxigilla portoricensis*), and modeled daily nest survival to better understand the effects of several factors on daily nest survival. In 2009 and 2010 we monitored 37 bullfinch nests at two sites in southwestern Puerto Rico. Predation was the most important cause of nest failure. Ten nest survival models received approximately equal support. No temporal trends in nest survival were supported over others. Results suggested that available fruit is important for successful nesting, increased precipitation is related to higher nest survival, nest survival varied by site, and increased nest height is related to lower nest survival in bullfinches. Under the top model, daily nest survival rates for each site and nest stage ranged from 0.83–0.86% in 2009 and 0.80–0.93% 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. Received 8 November 2012. Accepted 29 July 2013.

Key words: breeding biology, bullfinch, frugivory, *Loxigilla*, nest survival, Puerto Rico.

The endemic Puerto Rican Bullfinch (*Loxigilla portoricensis*), a frugivorous species of the family Emberizidae, is common in forests and brushy areas throughout most of Puerto Rico (Raffaele 1989, García et al. 2005). However, many aspects of its life history are poorly understood, including its breeding biology. Little published literature exists on this subject aside from brief descriptions of nests, nesting habits, and clutch size (Bowdish 1901, 1903; Wetmore 1916; Gleffe et al. 2006), each of which is based on only a few observations.

The genus *Loxigilla* is endemic to the Caribbean and contains three species in addition to the Puerto Rican Bullfinch: the Greater Antillean Bullfinch (*L. violacea*) of the Bahamas, Hispaniola, Jamaica, and Turks and Caicos; the Lesser Antillean Bullfinch (*L. noctis*), inhabiting Lesser Antillean Islands from the Virgin Islands south to Grenada, except for Barbados; and the Barbados Bullfinch (*L. barbadensis*), found only on Barbados. Much like the Puerto Rican Bullfinch, the other three species of bullfinches are poorly studied. All *Loxigilla* species are primarily frugivorous (Wetmore 1916, Danforth 1939, Lack

1976, Adolph and Roughgarden 1983) and consume fruit from a wide variety of native and introduced plant species (Greenlaw 1990). All species are described as constructing domed or globular nests and laying clutches of 2–3 eggs (Bowdish 1903, Raffaele and Roby 1977, Bond 1993). Beyond this, little useful information exists for comparison among species.

Despite its widespread distribution over the island of Puerto Rico, reductions in range and overall population of the Puerto Rican Bullfinch (hereafter bullfinch) are suspected (García et al. 2005). Studies of this species are needed to improve upon knowledge of its life history, as well as factors that may be contributing to population declines. Our objectives were to describe characteristics of the breeding biology of the bullfinch and to estimate its nest survival, a parameter that 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 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 placement may influence nest survival by

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causing variation in predation risk in relation to how accessible nests are to predominant nest predators of the habitat (Filliater et al. 1994, Schmidt et al. 2008). Precipitation may influence resource availability, 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 appears to prefer fruit when it is available (Wetmore 1916, Pérez-Rivera 1994, Carlo et al. 2004). The diet of nestling bullfinches is unknown, but most frugivorous bird species feed large quantities of animal matter to their young, especially during the early portion of the nestling stage (Breitwisch et al. 1984). As nestlings gain the ability to thermoregulate, their protein demand typically decreases and parents transition into provisioning a greater proportion of fruit. Therefore, it is likely that nestling bullfinches are fed insects initially but are also fed fruit to some extent. The availability of fruit resources could then affect nest survival by influencing adult condition and behavior, such as the time spent away from the nest while foraging (Crawford et al. 2006, Boulton et al. 2008). To a lesser extent, fruit availability also probably influences what and how much nestlings are fed, as well as predator behavior (Schmidt 1999). For example, nest predators with an omnivorous diet may spend more time searching for nests, or come across more nests by chance, when fruit resources are lower.

Here we report nesting habits and nest survival of the bullfinch from two breeding seasons in southwestern Puerto Rico. This information will increase our understanding of the breeding ecology of an endemic passerine and will ultimately aid future studies and 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 coastal tracts of subtropical dry forest (Ewel and Whitmore 1973) 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. 1). From 1955–2010, these sites received, on average, 790 mm of rain per year (National Climatic Data Center 2010), but inter-annual variation is high and droughts occur regularly (Ewel and Whitmore 1973). The

region is characterized by a distinct dry season from December to April, and a wet season spanning approximately late April to June or July, with another peak in rainfall from September to October (Faaborg 1982). The short, dense forests grow on shallow limestone soils that have little capacity for retaining water (Ewel and Whitmore 1973). Most of the 4,015-ha Guánica tract has been protected since 1919 with peripheral units added later (Colon and Lugo 2006). The forest is recognized as one of the highest quality remaining subtropical dry forests in the world (Lugo et al. 1996). Approximately half the reserve is mature, uncut vegetation; the other half consists of second-growth in various stages of regeneration (Lugo et al. 1996). The La Jungla tract, consisting of about 615 ha, is 8 km west of Guánica. It has been protected since approximately 2000 as a disjunct tract of the Guánica reserve. Much of the vegetation is in earlier stages of succession, with less mature forest overall, compared to Guánica (ANMW, pers. obs.). The land-use history of the sites includes charcoal production, grazing, subsistence agriculture, tree plantations (mostly *Swietenia mahogoni*) and logging, and human residential areas and roads (Lugo et al. 1996, Colón and Lugo 2006, Pérez-Martínez 2007).

Nest Survival.—We searched for and monitored bullfinch nests from April–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 single 100-ha plot in La Jungla, but we also monitored nests found opportunistically outside of these defined plots. In both sites, nest plots encompassed a range of forest ages. We monitored nests approximately every 3–5 days and determined if each nest failed (did not fledge any young) or succeeded (fledged ≥ 1 young). We checked nests above head height using either a small mirror or a plumbing camera attached to a telescoping handle. When a nest failed, we attempted to determine cause of failure, such as destroyed eggs and nest or an empty nest (indicating predation), or cold eggs or dead nestlings (indicating abandonment). After each nest failed or succeeded, 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 and width 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

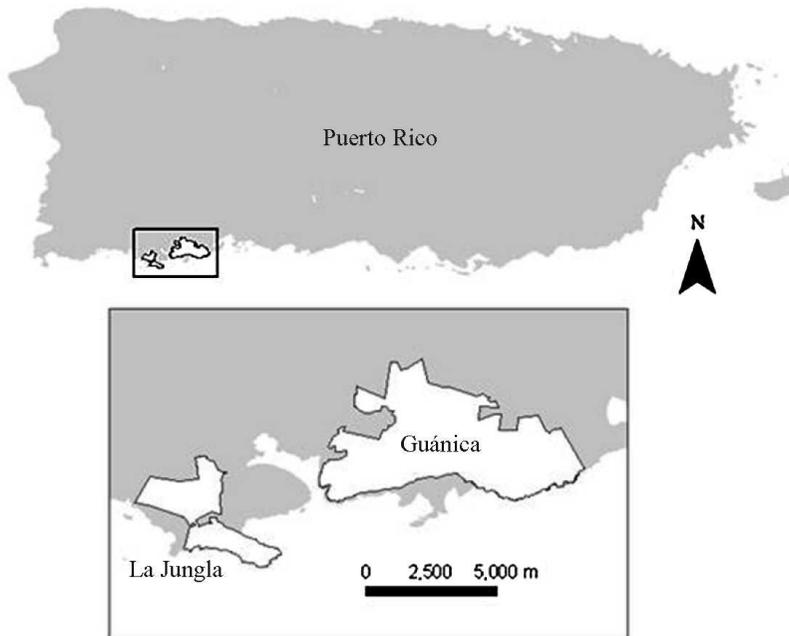


FIG. 1. Map of the study area. The inset map indicates the two study sites, La Jungla ($17^{\circ} 57' N$, $66^{\circ} 57' W$) and Guánica ($17^{\circ} 58' N$, $66^{\circ} 52' W$), and the location of each within southwestern Puerto Rico.

searching plots, courtesy of the DNER (M. Canals, pers. comm.). For La Jungla we used data from a U.S. Weather Bureau station in the town of Ensenada, approximately 4 km east of the La Jungla site (National Climatic Data Center 2010).

Fruit Abundance.—We systematically established 20 fruit monitoring stations at Guánica (five in each of the four nest plots) and 18 fruit monitoring stations at La Jungla to measure fruit abundance during the 2009 and 2010 breeding seasons. No known comprehensive list of fruit species consumed by the Puerto Rican Bullfinch exists. Most studies of frugivory in the bullfinch have occurred in wetter forests of Puerto Rico (Cruz 1980, Saracco 2001, Carlo et al. 2004), but see Pérez-Rivera (1994). Because plant species turnover is high between different habitats, foraging observations in wet forests are not very useful for developing a list of species consumed in the dry forest. Therefore, we had to rely on personal observations along with several publications to develop a list of 46 species of fruiting trees and cacti known or likely to be consumed by the bullfinch (Wetmore 1916; Lack 1976; Pérez-Rivera 1994; A. Morales Pérez, pers. comm.; J. Sustache, pers. comm.; and ANMW, pers. obs.).

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 required to conduct fruit counts. We marked up to five trees or cacti of at least 1.5-m height of each focal species at each station. 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 = 101–1,000 fruits, and 4 = 1,001–10,000 fruits (following Saracco 2001). Although ripe fruits are preferred (ANMW, pers. obs.) 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 also observed eating unripe and partially ripened fruit.

Weekly FAIs were summed within each site and we used linear interpolation to provide a daily index at each site during the course of the breeding season. In 2009, fruit scoring was not initiated until early June. Missing values from May were replaced with the mean values over the rest of the season within a site and year.

Statistical Analyses.—We modeled the daily survival of nests of bullfinches, 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 5 May, the date the first nest was found in either year, was set as day 1. For each nest we also included the following explanatory variables: linear and quadratic time trends within year, year, nest stage (incubation or nestling), site, nest height, precipitation, ripe FAI, total (ripe + unripe) FAI, and observer visits. 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. To evaluate variation between 2009 and 2010, 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 modeled each individual covariate of site, nest height, precipitation, ripe FAI, total (ripe + unripe) FAI, and observer effects. Preliminary analyses suggested that total FAI models performed better than ripe-only FAI models; therefore, we only used total FAI scores in subsequent models. Finally, we added the competitive ($\Delta\text{AIC} < 2$) time trend models to each of the individual covariates.

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 are means \pm SE.

RESULTS

Nesting Biology.—Of 43 active bullfinch nests found during 2009–2010, 37 had sufficient data

for nest survival analyses (Table 1). We monitored these nests for 220 exposure days across a 58-day interval (5 May–2 Jul). 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 appeared to have failed because of predation. We did not observe any evidence of nest abandonment, but we cannot exclude the possibility that abandonment occurred prior to predation in any failed nests. The two successful nests fledged 2 and 3 nestlings and were both in La Jungla in 2010. Both of these nests were located prior to the initiation of incubation and were observed on the day of fledging. The incubation period was 14 days and the nestling period was 14–15 days. During June 2010, one bullfinch nest at La Jungla was parasitized by a Shiny Cowbird (*Molothrus bonariensis*). The nest initially contained three bullfinch eggs and was later observed with one bullfinch egg and one Shiny Cowbird egg before it subsequently failed. Additionally, we were unable to determine what adult bullfinches were feeding nestlings, as the nesting adults tended to be extremely secretive. We attempted to observe nests from a distance, but the thick vegetation of the dry forest obscured views and adults rarely returned to nests while observers were within sight.

Observed clutch sizes of bullfinches ranged from 2–4 eggs with a mean of 3.1 ± 0.6 ($n = 25$). Nests ranged from 0.9 to 6.0 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 open cups to domed nests with side entrances. Nests were usually constructed of dry palm fronds (*Leucothrinax morrisii*), lignified vascular tissue of cacti (*Cephalocereus* spp.), and 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.

During May and June 2009, we observed cooperative breeding behavior in bullfinches in Guánica. On several occasions we observed family groups consisting of two adults and 1–3 juveniles, where juveniles were observed collecting nesting material along with adults and on several occasions were seen adding material to nests. In two territories, we also observed three bullfinches, all in adult plumage, collecting nest

TABLE 1. The total number of nests of Puerto Rican Bullfinches (*Loxigilla portoricensis*) from two subtropical dry forest sites (Guánica and La Jungla) in southwestern Puerto Rico during 2009–2010 used in nest survival analyses.

Year	No. nests	Guánica		La Jungla	
		Incubation	Nestling	Incubation	Nestling
2009	9	9	2	–	–
2010	28	4	0	23	6
Totals	37	13	2	23	6

material together. No additional cooperative behavior such as feeding nestlings was observed, and no cooperative behavior was observed in 2010.

Nest Survival.—In the first step of analysis, all time trend models were competitive ($<2 \Delta AIC_c$; Table 2). Therefore, each of these models was combined with individual covariates. Ten resulting models were competitive and provided approximately equal support for constant and quadratic time trends in nest survival over the season (Table 2). The top model, although weak and insignificant, does suggest that fruit availability has a positive relationship with nest survival ($\hat{\beta}_{FAI_{total}} = 0.007$, SE = 0.004, 95% CL = -0.001, 0.015). Similarly, the variables site and precipitation each show weak, positive relationships with nest survival in two of the top models. Nest height, conversely, shows a weak, negative relationship with nest survival. Linear time trend, stage and year effects were not well supported in our models and there was little evidence of observer effects on nest survival. Under the top model, daily nest survival rates for each site and nest stage ranged from 0.83–0.86% in 2009 and 0.80–0.93% in 2010. Nest success was 0.012 (95% CL = 0.001, 0.071) for Guánica in 2009, and 0.044 (95% CL = 0.007, 0.147) for La Jungla in 2010. We defined nest success as the probability of surviving a consecutive 14-day incubation period and a 14-day nestling period, beginning 24 May (the mean date of initiation of incubation in both years) and using mean values for all covariates. Nest success could not be estimated for Guánica in 2010, because we had no nestling stage data from that site and year.

DISCUSSION

This study has provided valuable information about the breeding biology of the Puerto Rican Bullfinch in southwestern Puerto Rico, including estimates of the length of the incubation and nestling periods and a preliminary description of

cooperative breeding behavior in juvenile or helper bullfinches. Additionally, this research has produced the first estimates of nest survival for the bullfinch and shed light on several factors that may influence the species' nest survival. It is important to note that, because of our small sample sizes and lack of strong results, we are not making inferences about direct causes of nest mortality; instead, we are interested in examining patterns in nest survival.

Most or all nest failure observed during this study resulted from predation. Other studies have reported low estimates of nest survival or success in the tropics (Ricklefs 1969, Skutch 1985, Robinson et al. 2000, Ryder et al. 2008, Newmark and Stanley 2011), and in particular that nest predation is often the most important cause of nest loss in the tropics (Sargent 1993, Martin 1996). We think the most frequent nest predator in Guánica and La Jungla was the Pearly-eyed Thrasher (*Margarops fuscatus*). This omnivorous species is an avid nest predator, and has been observed depredating bullfinch nests (Arendt 2006). We also observed one bullfinch nest in Guánica as it was detected by a Pearly-eyed Thrasher, and soon after it was found to be depredated (ANMW, pers. obs.). Other potential, although less probable, nest predators occurring at Guánica and La Jungla include Red-legged Thrushes (*Turdus plumbeus*; Oberle 2000); Puerto Rican racers (*Borikenophis portoricensis*; Pérez and Laboy 1996); anole lizards (*Anolis* spp.), one of which was observed depredating the nest of a Bananaquit (*Coereba flaveola*) during our study (ANMW, pers. obs.), small Indian mongoose (*Herpestes javanicus*; Vilella 1998), green iguanas (*Iguana iguana*; Lazell 1973), feral cats (*Felis catus*) and black rats (*Rattus rattus*; Woodworth 1999, Arendt 2000).

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

TABLE 2. Models considered for analyzing daily nest survival for Puerto Rican Bullfinches (*Loxigilla portoricensis*) with corresponding number of parameters (K), ΔAIC_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, individual covariates were modeled and competitive time trends were combined with individual covariates. The AIC_c value for the top-ranked time trend + covariate model was 127.96. 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.

Model	ΔAIC_c	w_i	K	Deviance
Time Trend Models				
Constant	0.00	0.29	1	126.63
Quadratic	0.28	0.26	3	122.83
Year	0.88	0.19	2	125.48
Linear	1.42	0.14	2	126.02
Stage	1.85	0.12	2	126.45
Best Time Trends + Covariates				
Constant + Total FAI	0.00	0.09	2	123.91
Quadratic + Site	0.59	0.07	4	120.39
Constant + Site	0.61	0.07	2	124.52
Constant + Precipitation	0.94	0.06	2	124.84
Quadratic + Precipitation	1.32	0.05	4	121.11
Constant + Height	1.44	0.05	2	125.34
Constant + Ripe FAI	1.71	0.04	2	125.62
Quadratic + Total FAI	1.82	0.04	4	121.61
Linear + Total FAI	1.94	0.04	3	123.80
Quadratic + Height	1.95	0.04	4	127.75

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 in 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.

Top nest survival models primarily provided support for constant and quadratic time trends; therefore, it is unclear if there was a predominant time trend in nest survival in 2009 and 2010. Although a large number of nest survival models received approximately equal support and no covariates were statistically significant, the results seem biologically appropriate and would likely be strengthened with larger sample sizes and more years of data. Collectively, the top models suggest that available fruit is important for successful nesting, increased precipitation is related to higher nest survival, nest survival was higher at La Jungla than at Guánica, and increased nest height is related to lower nest survival.

The positive relationships between nest survival and the variables precipitation and fruit availability were unsurprising. Increased precipitation was probably related to increased resource availability, whether fruit resources or other resources that we did not measure, such as insect abundance. 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 all or nearly all due to predation rather than starvation or abandonment and because we had very small sample sizes for the nestling stage, the stage in which we expect survival to be most affected by resource availability. Furthermore, fruiting is spatially and temporally ephemeral in the dry forest, and some fruit species may only be important to birds in some seasons or years (Blake et al. 1990). This emphasizes the need for more years of nest survival and fruiting phenology data. Finally, less inference can be made between nest survival and fruit abundance in 2009, because there were missing values in that year.

During 2010, nest survival was slightly higher at La Jungla than Guánica. These sites are only 8 km apart, are both coastal forest tracts, and experience similar 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 amounts of fruit produced and density 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 (ANMW, unpubl. data). However, as the relationship between FAI and nest survival was weak, we can only suggest that the lower fruit abundance at Guánica may have negatively impacted nest survival. Additionally, Pearly-eyed Thrashers were infrequently captured in mist nets and detected by point count surveys in La Jungla compared to in Guánica (Kornegay 2011). The much lower density of Pearly-eyed Thrashers in La Jungla may have contributed to higher survival of bullfinch nests at that site. Finally, our results suggest that higher nests had slightly lower nest survival. This might indicate that the Pearly-eyed Thrasher searches for nests higher in the canopy.

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 1989–2011 was 0.75 (Faaborg and Wiewel 2010). Furthermore, the Guánica study has produced several age records for bullfinches that are 9–12 years old (Faaborg and Wiewel 2010), which is relatively long-lived for small passerines. It should also be noted that we found and monitored only a small subset of the total bullfinch nests in our study areas. Although we observed very few fledglings produced from nests that we monitored, hatch-year bullfinches were regularly captured in both years during a concurrent mist-netting study that took place within our nest plots (Kornegay 2011). Bullfinch nests vary in detectability, and it is likely that our sample was biased towards nests that were more detectable to both nest predators and human observers. This may have contributed to higher predation rates in our sample than in the overall population of bullfinch nests.

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 species restrict their breeding to the spring and early summer rainy season of approximately late April to July. During the dry season from December to April, resources are probably too limiting for birds to successfully rear young in most years. However, we think that bullfinches do breed opportunistically in the dry forest as well. For example, in January–March 2009, juvenile bullfinches were regularly captured in mist nets (J. Toms, pers. comm.) and multiple family groups including juvenile bullfinches were observed (ANMW, pers. obs.). Several rainfall events, including one unusually large event, occurred in January 2009, which probably initiated this breeding activity. It might be possible that bullfinches and other species attempt to breed again during the shorter annual rainy peak in September and October. Considering 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 bullfinch is not thought to be a frequent victim of nest parasitism by Shiny Cowbirds (Post et al. 1990, Nakamura and Cruz 2000). In the only other known report of parasitism of a bullfinch

nest, Cruz et al. (1989) observed parasitism of one bullfinch nest out of four monitored in southwestern Puerto Rico from 1980–1983. The Lesser Antillean Bullfinch and Barbados Bullfinch have also been observed victims of Shiny Cowbird parasitism (Friedmann 1943, French 1973), although it is likely an infrequent occurrence in these species as well. Therefore, parasitism by Shiny Cowbirds is probably not a significant factor in nest survival of the bullfinch.

The cooperative breeding behavior we observed in 2009 in Guánica was restricted to nest material collection and nest building by helper bullfinches. These birds were likely young produced by the associated adult pair during the previous breeding occasion (Stacey and Koenig 1990). No further cooperative breeding behavior was observed, but it should be noted that bullfinches are secretive breeders and were infrequently observed building or incubating, and never observed feeding nestlings. Therefore, we do not know if helpers contributed to additional breeding efforts. This behavior was only observed in 2009, following the rainy January that seemed to have initiated early breeding in bullfinches that year. Cooperative breeding behavior is observed more frequently in non-migratory species, species with low annual mortality rates, and species living in relatively unchanging environments (Arnold and Owens 1998, Cockburn 2006), all of which are characteristics of bullfinches. Additionally, cooperative breeding is considered a facultative trait in most bird species (Hatchwell and Komdeur 2000) and may not occur every year, or in all breeding pairs or habitats, in bullfinches. Cooperative breeding has been inferred to occur in 9% of species of the family Emberizidae (Cockburn 2006).

The results presented here shed light on the life history of a relatively long-lived tropical island endemic, the Puerto Rican Bullfinch, in southwestern Puerto Rico. We emphasize the need for additional research on the breeding biology of the bullfinch. 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 highly seasonal and drought-subjected southwestern region of Puerto Rico. Foraging studies would help confirm which fruit and insect species are consumed by bullfinches in the dry forest and would aid in developing more detail-specific nest survival studies. As nest predation was our most

frequent cause of nest failure, it may be useful to quantitatively determine which nest predators play the most important roles in depreeding bullfinch nests.

Dry forests of southwestern Puerto Rico historically supported higher bird densities and species diversity than the wetter forests of the island (Kepler and Kepler 1970). Because Guánica is considered one of the most pristine tracts of dry forest remaining in the subtropics (Lugo et al. 1996), we expect that nest survival rates should be relatively high. There is a clear need for determining if the low nest survival rates we observed are typical or if they may be playing a role in suspected and known population declines in the bullfinch and other Puerto Rican endemics (García et al. 2005). No apparent, significant changes in the habitat in Guánica have occurred within the past few decades (Faaborg et al. 2013). This suggests that impacts on nest survival might be occurring at a larger scale, such as through climate change, lack of disturbance to forest habitat, or habitat loss in the matrix surrounding our study area.

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