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AVIAN REPRODUCTION AND THE CONSERVATION VALUE OF SHADED COFFEE PLANTATIONS

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Resumen. – Reproducción de aves y el valor de las plantaciones de café de sombra para la conservación. – Las plantaciones de café de sombra han sido exaltadas por su valor para la conservación de aves. La mayoría de los estudios enfatizan los beneficios a las aves migratorias Neotropicales. Menos se conoce sobre como las aves residentes utilizan las plantaciones. En Puerto Rico, se ha planteado que las plantaciones de café de sombra sirvieron como un refugio para aves de bosques durante periodos de deforestación extensa, reduciendo así las tasas de extinción. Se considera implícito en dicha hipótesis que las plantaciones de café albergan poblaciones reproductivas. A tales efectos, nosotros reportamos actividad reproductiva y productividad de aves residentes en cafetales de sombra desde 1997 al 1999 y las comparamos con información similar proveniente de bosques secundarios. Encontramos 253 nidos en cafetales y 97 en bosques secundarios. Algunas de las especies con mayor número de nidos fueron las endémicas *Todus mexicanus* (53), *Chlorostilbon maugaeus* (27), *Melanerpes portoricensis* (16), y *Anthracothorax viridis* (12). La depredación y el abandono de nidos fueron responsables, cada uno, por 38% de los nidos perdidos. No hubo diferencias ($P < 0.05$) en la proporción de nidos exitosos entre bosques secundarios y cafetales de sombra para miembros de Vireonidae, Emberizidae, y Trochilidae. Igualmente, no hubo diferencias en el promedio de volantones por intento de anidación entre hábitat para cuatro especies con suficientes datos. Aunque no documentamos el paradero de los volantones (e.g., dispersión, supervivencia), nuestros hallazgos le brindan apoyo a la hipótesis de refugio porque la composición de especies reproduciéndose y su productividad fueron similares entre hábitat. Esa capacidad de productividad, sin embargo, esta asociada a los sustratos de anidación provistos por estrato de sombra, no al estrato de arbustos o plantas de café.

Abstract. – Shaded coffee plantations have been heralded for their conservation value to avifauna. Most studies emphasize benefits to Neotropical migrants. Less is known about how resident species use plantations. It has been hypothesized that in Puerto Rico shaded coffee plantations served as a refuge for resident forest avifauna during periods of widespread deforestation, lowering extinction rates. Implicit in this hypothesis is that shaded coffee plantations harbor breeding populations. Accordingly, we report on reproductive activity and productivity of resident avifauna in plantations and compared them with similar data from secondary forests in Puerto Rico from 1997 to 1999. We found 253 nests in coffee plantations and 97 in secondary forests. Some of the most common nesting species were the endemics *Todus mexicanus* (53), *Chlorostilbon maugaeus* (27), *Melanerpes portoricensis* (16), and *Anthracothorax viridis* (12). Predation and

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nest abandonment each accounted for 38% of nest failures. The likelihood of nest success did not differ between secondary forest and coffee plantations for vireos, tanagers and hummingbirds. Similarly, the average number of young per nest attempt did not differ between habitat types for four species with sufficient data. Although the fate of fledglings (e.g., dispersal, survival) was not assessed, our findings lend support to the refugia hypothesis because the composition of resident species found nesting in shaded coffee plantations and secondary forests and their productivity were similar. The production capacity of shaded coffee plantations, however, is dependent on nesting substrates provided by the shade vegetation layer, not the understory or coffee trees. *Accepted 14 January 2006.*

Key words: Agroecosystem, avian reproduction, Caribbean, conservation, Puerto Rico, shaded coffee plantation.

INTRODUCTION

Shaded coffee plantations have received a great deal of attention in recent years by conservation biologists. Unlike many other agricultural practices, shaded coffee plantations have been heralded as an example of land use compatible with conservation (e.g., Ricklefs 1992, Robbins *et al.* 1992, Petit *et al.* 1995, Jones *et al.* 2002, Rappole *et al.* 2003). Avian communities use them because they contain a wide range of resources, similar to those found in secondary forests (Petit *et al.* 1995, Wunderle & Latta 1998, Carlo *et al.* 2004). Coffee grows well in full sun and under shade trees or forest cover (Moguel & Toledo 1999). However, due to their structural complexity and associated resources, shaded coffee plantations support greater biodiversity than pure coffee stands growing in full sun (Faminow & Rodriguez 2001, Donald 2004).

In Puerto Rico, shaded coffee plantations may have helped conserve resident avifauna by becoming an increasingly predominant component of the island's forest cover during the 19th and early 20th centuries (up to 90%; Birdsey & Weaver 1982, Brash 1987). Forest cover in Puerto Rico decreased dramatically from when the island was colonized in the 1500s through the 1930s, when only 6–15% of the forested cover remained (Wadsworth 1945, 1950). Although 85–94% of the island had been deforested, fewer avian species went extinct than was expected based on a forest area-species relationship (Brash 1987). Brash (1987) hypothesized that many avian species used shaded coffee plantations as refugia, and together with relict forest fragments, served to increase the total area of usable habitat, thus reducing the number of extinctions. Implicit in Brash's (1987) refugia hypothesis is that shaded coffee plantations must have supported successful reproduction.

Avian studies in coffee plantations, while numerous, have focused on population abundances and foraging behavior of birds, particularly of Neotropical migrants (e.g., Robbins *et al.* 1992, Greenberg *et al.* 1997a & b, Wunderle & Latta 1998, Komar in press). To our knowledge, no study has quantified reproductive success of resident forest birds in shaded coffee plantations (see Komar in press for review). Lindell & Smith (2003) estimated nest success of resident species in Costa Rica, but the work compared success among sun plantations, pastures and understory forest. Indeed, data on breeding productivity are scarce throughout the tropics (Bock & Jones 2004). Site-specific reproductive rates are necessary to fully evaluate the functional role of forested habitats (see Van Horne 1983, Martin 1992). Two recent studies examined the use of shaded coffee plantations by resident birds in Puerto Rico, but these focused on the ecological services provided by resident avian species, specifically the contribution of insectivorous species as bio-controls of coffee pests (Borkhataria

2001, Borkhataria *et al.* in press), and the effect of plant species composition on habitat use and foraging behavior of resident frugivores (Carlo *et al.* 2004).

Here we report various measures of reproductive activity in shaded coffee plantations and secondary forests in north-central Puerto Rico from 1997 to 1999. Specifically, we report the number of breeding species, number of active nests per species, two expressions of breeding productivity (proportion of successful nests and number of chicks fledged per nesting attempt), and primary causes of nest failure. Our working hypotheses were that, to serve as refugia, plantations should harbor a similar suite of nesting species as secondary forests (i.e., not a unique segment of the community), and that breeding productivity should not differ between plantations and secondary forests.

STUDY AREA

We conducted field work in seven secondary forests (45 ha) and three shaded coffee plantations (12 ha) located between the municipalities of Ciales and Utuado in north-central Puerto Rico. Secondary forest study areas were Cialitos (18°15’N, 66°31’W, 550 m), Niña Grande (18°15’N, 66°32’W, 550 m), Tres Picachos (18°14’N, 66°34’W, 700 m), Caguana (18°17’N, 66°43’W, 430 m), Cordillera (18°19’N, 66°31’W, 350 m), Frontón (18°19’N, 66°33’, 300 m), and Dominguito (18°29’N, 66°43’W, 100 m). The three shaded coffee plantations were located in the township of Ciales, two in Frontón (18°18’N, 66°32’, 350 m, 18°17’N, 66°33’, 300 m), and the third in Cialitos (18°15’N, 66°33’W, 650 m). Study areas were selected randomly (pool of candidate sites) and were embedded in a landscape matrix of > 75% forest cover to avoid markedly fragmented forest landscapes (Collazo & Groom 2000).

We treated all secondary forests, growing in either karstic (limestone) or volcanic (lateritic) soils, as a broad, functional category to address the question of interest. Although we acknowledge that plant composition might differ between forests growing in both types of soils (Collazo & Groom 2000, Carlo *et al.* 2003, Sustache 2004), to our knowledge no member of the resident avian community required a nesting substrate that could not be found in either secondary forest type (Collazo & Groom 2000). Common tree species in the secondary forests (volcanic soils) included *Schefflera morototoni, Cecropia schreberiana, Alchornea latifolia, Ocotea* spp.*, Inga vera, Andira inermis, Guarea guidonia, Casearia arborea*, and *Cordia sulcata*. Common trees in forests on karstic soils included *Casearia guianensis*, *Clusia rosea, Bucida buceras, Tetrazygia elaeagnoides, Bursera simaruba, Casearia decandra, Eugenia biflora*, and *Coccoloba* spp.

Two plantations (Frontón) were traditional polycultures (see Moguel & Toledo 1999). The third one, Cialitos, was nearly 70% traditional polyculture, with the remaining 30% considered a rustic plantation. We believe that plantations in this study captured many of the conditions that prevailed in the island historically. It is likely that many plantations started as “rustic” (planting coffee trees under native forest), but were transformed into traditional polycultures as the canopy was modified to meet shade and growing coffee needs by selective cuts and favoring of nitrogen-fixing trees (e.g., *Inga vera*). Shade trees at Cialitos included *Inga vera, Inga laurina, Andira inermis, Cecropia schreberiana, Schefflera morototoni, Ocotea* spp.*, Alchornea latifolia, Cordia sulcata.* The canopy of the Frontón plantations was comprised predominantly of *I vera, I. laurina,* and *A. inermis.* The understory shrubs in all plantations included *Miconia* and *Psychotria* spp., and some banana and citrus trees. Within each coffee study site there were also abandoned or “non-active” patches of coffee overgrown by secondary montane forest, and in one of the Frontón sites, a patch (< 0.5 ha) had elements that resembled a commercial polyculture (e.g., large gaps in shade layer).

METHODS

We established a flagged grid system (30 m x 30 m) to assist in locating nests in each of the 10 study sites. Plots were as large as possible within each study site avoiding edges between secondary forests and plantations (= 30 m from edges; see *http://pica.wru.umt.edu/BBIRD/*). Study sites ranged in size from approximately 4 to 9 ha with coffee plantations being approximately 4 ha each. Each plot was surveyed for active nests from January through June from 1997 to 1999. Searches were conducted from sunrise to 10:00 h, every 2 to 3 days, throughout the entire grid. Monitoring protocols followed those described by Martin & Guepel (1993, see also *http://pica.wru.umt.edu/BBIRD/*). Once an active nest was encountered, location (with reference to the grid within each plot), nest height, type (open cup vs. cavity), and nesting tree/shrub were recorded. Nests were subsequently monitored every 2 to 3 days. During each visit, we recorded clutch size, or number and approximate age of nestlings. If a nest failed, we recorded the probable cause of failure (e.g., predation, weather). A nest was considered successful if one or more individuals fledged. Breeding productivity was expressed as the number of individuals fledged per nesting attempt. We did not report Mayfield survival estimates because sample sizes for most species were too small and many species nested in the canopy, precluding accurate determination of nest content on every visit. Thus, our estimates should be regarded as apparent nesting success (Williams *et al.* 2001).

We report the most frequently used nesting substrates in each habitat type and mean nest height (SE). If the nesting substrate was a plant species, we classified it as native or introduced (exotic) according to Francis & Liogier (1991). We tested for differences in nesting success between habitat types in two ways. First, we tested the broader question of whether the likelihood of nest success (successful or not) was related to forest (habitat) type using a logistic regression model, as the response was binary (PROC GENMOD, SAS 2000). A successful nest was one that fledged at least one chick. The model's fixed effect was habitat type. The model was adjusted to appropriately test the effect of habitat on the response variable. Site was the primary experimental unit, and in the model, treated as a random effect. The model included a repeated/subject = site statement. The "repeated" statement accounted for both the random aspect of sites and observations within site. Observations (nests) were assumed to be correlated within a site, but independent among sites. A compound symmetry (cs) was used as the correlation structure for the model. Because the two coffee plantations in Frontón were in close proximity (separated by a paved road), we treated them as one plantation in this and all subsequent analyses to minimize problems of pseudoreplication. To increase sample sizes, but cognizant of the importance of preserving taxonomic relatedness for valid inferences (e.g., Martin *et al.* 2000), we restricted analyses to pooled data of two species in each of three families. These were hummingbirds [Trochilidae; Puerto Rican Emerald (*Chlorostilbon maugaeus)* and Green Mango (*Anthracothorax viridis*)], vireos [Vireonidae; Puerto Rican Vireo (*Vireo latimeri)* and Black-whiskered Vireo (*V. altiloquus*)], and tanagers [Emberizidae; Puerto Rican Spindalis (*Spindalis portoricensis*) and Antillean Euphonia (*Euphonia musica*)].

The second set of analyses was species-

TABLE 1. Checklist, mean clutch size and breeding productivity (± SD) of resident species in secondary forests and shaded coffee plantations in north-central Puerto Rico, 1997-1999. Breeding productivity is defined as young/nest attempt. Breeding productivity was compared for 4 species (bold) using ANOVA. NE = not visible/estimable, * = endemic species, n = sample size.

Species	Habitat	n	Clutch size (SD)	Productivity (SD)
Buteo jamaicensis	Coffee	1	NE	0.00
Falco sparverius	Coffee	2	2.50 (0.71)	2.00 (0.0)
	Secondary	1	NE	1.00
Columba squamosa	Coffee	2	2.00	1.00 (1.41)
Geotrygon montana	Coffee	2	2.00 (0.0)	2.00 (0.0)
	Secondary	15	1.87 (0.35)	1.07 (0.96)
Zenaida asiatica	Coffee	3	2.00 (0.0)	1.33 (1.15)
*Megascops nudipes**	Secondary	1	1.00	0.00
*Saurothera vieilloti**	Coffee	1	2.00	0.00
	Secondary	4	2.00 (0.0)	1.00 (1.15)
Coccyzus minor	Secondary	1	3.00	2.00
*Anthracothorax viridis**	Coffee	10	2.00 (0.0)	1.40 (0.97)
	Secondary	2	2.00 (0.0)	0.00 (0.0)
*Chlorostilbon maugaeus**	Coffee	17	1.94 (0.24)	**1.18 (0.95)**
	Secondary	10	1.50 (0.53)	**0.80 (0.92)**
*Melanerpes portoricensis**	Coffee	14	NE	0.71 (1.20)
	Secondary	2	5.00	1.50 (2.12)
*Todus mexicanus**	Coffee	33	2.45 (0.51)	**1.97 (0.85)**
	Secondary	20	2.42 (0.69)	**1.80 (1.06)**
*Myiarchus antillarum**	Coffee	3	3.00	1.33 (1.15)
	Secondary	3	3.00 (0.0)	2.33 (0.58)
Tyrannus caudifasciatus	Coffee	6	2.67 (0.52)	1.83 (1.17)
	Secondary	1	3.00	2.00
Tyrannus dominicensis	Coffee	13	2.73 (0.47)	1.46 (1.27)
*Contopus portoricensis**	Coffee	2	3.00 (0.0)	2.50 (0.71)
	Secondary	4	2.50 (0.58)	2.50 (0.58)
Mimus polyglottos	Coffee	1	3.00	0.00
	Secondary	2	3.00 (0.0)	1.50 (2.12)
Margarops fuscatus	Coffee	2	NE	1.00
	Secondary	4	3.00	1.00
Turdus plumbeus	Coffee	5	3.00	0.60 (0.89)
	Secondary	3	NE	0.67 (1.15)
Vireo altiloquus	Coffee	13	2.67 (0.65)	**1.23 (0.93)**
	Secondary	3	2.67 (0.58)	**1.33 (1.15)**
*Vireo latimeri**	Coffee	2	3.00 (0.0)	3.00 (0.0)
	Secondary	7	2.75 (0.5)	1.14 (1.46)
Euphonia musica	Coffee	15	2.22 (0.44)	0.87 (0.99)
	Secondary	2	NE	2.00
Coereba flaveola	Coffee	78	2.38 (0.66)	**1.24 (1.29)**
	Secondary	9	2.50 (0.53)	**0.89 (1.36)**
*Spindalis portoricensis**	Coffee	4	3.67 (0.58)	2.25 (2.06)
	Secondary	1	3.00 (0.0)	0.00

TABLE 1. Continued.

Species	Habitat	n	Clutch size (SD)	Productivity (SD)
Icterus dominicensis	Coffee	6	3.25 (0.50)	1.67 (1.03)
	Secondary	1	NE	2.00
Tiaris olivacea	Coffee	4	2.50 (1.00)	0.00 (0.0)
Tiaris bicolor	Coffee	5	2.20 (0.45)	1.00 (1.41)
	Secondary	1	2.00	2.00
*Loxigilla portoricensis**	Coffee	9	3.33 (0.50)	2.00 (1.22)

specific tests to determine if breeding productivity (number of chicks/nest attempt) differed between habitat (forest) types using an ANOVA (PROC MIXED, SAS 2000). Model terms were similar to the previously described model. Habitat was the fixed effect and site was treated as a random effect. The "repeated" statement in the model accounted for both the random aspect of site and assumed correlation among observations (nests) within site. The correlation structure for the model was compound symmetry (cs). Species-specific analyses were restricted to the Puerto Rican Emerald (endemic, open nest), Puerto Rican Tody (*Todus mexicanus*; endemic, cavity nest), Black-whiskered Vireo (seasonal resident, open nest), and Bananaquit (*Coereba flaveola*; resident, globular nest). Data for these species met minimum sample size requirements and homogeneity of variance assumption (Levene's tests, P = 0.05). We also used this ANOVA model to test for differences in mean nest height between habitat types. Lastly, we tested whether the likelihood of nest failure due to predation or other causes was related to habitat type using a logistic regression model (PROC GENMOD, SAS 2000). Model terms were the same as those described for testing for nesting success. As with breeding productivity, we restricted tests to the same three families highlighted above and to the Bananaquit, the species with the largest sample size.

RESULTS

We recorded a total of 28 nesting species and 350 nests throughout the study—253 (72%) in coffee plantations and 97 in secondary forest study sites. Twenty-six species were recorded in coffee plantations as compared to 22 in secondary forests. Nests of 20 species were recorded in both habitat types. Two species, the Puerto Rican Screech-Owl (*Megascops nudipes*) and Mangrove Cuckoo (*Coccyzus minor*), were recorded exclusively in secondary forests, whereas six species were recorded only in coffee plantations (Table 1). Of 11 endemic species recorded, 10 were found nesting in each of the two habitat types. As noted above, the screech-owl was not recorded in the shaded coffee plantations whereas the Puerto Rican Bullfinch (*Loxigilla portoricensis*) was not recorded in our secondary forest study sites. Nesting activity peaked between March and April for most species, with the exception of the Puerto Rican Woodpecker (*Melanerpes portoricensis*, Fig. 1*)*, whose nesting activity started in January and extended through April. Species with the greatest overall number of nests were the Bananaquit (87), Puerto Rican Tody (53), Puerto Rican Emerald (27), Antillean Euphonia (17), and Puerto Rican Woodpecker (16).

Thirty-two species of plants were used as nesting substrates during the study. Of these, 21 were native to Puerto Rico. The number of

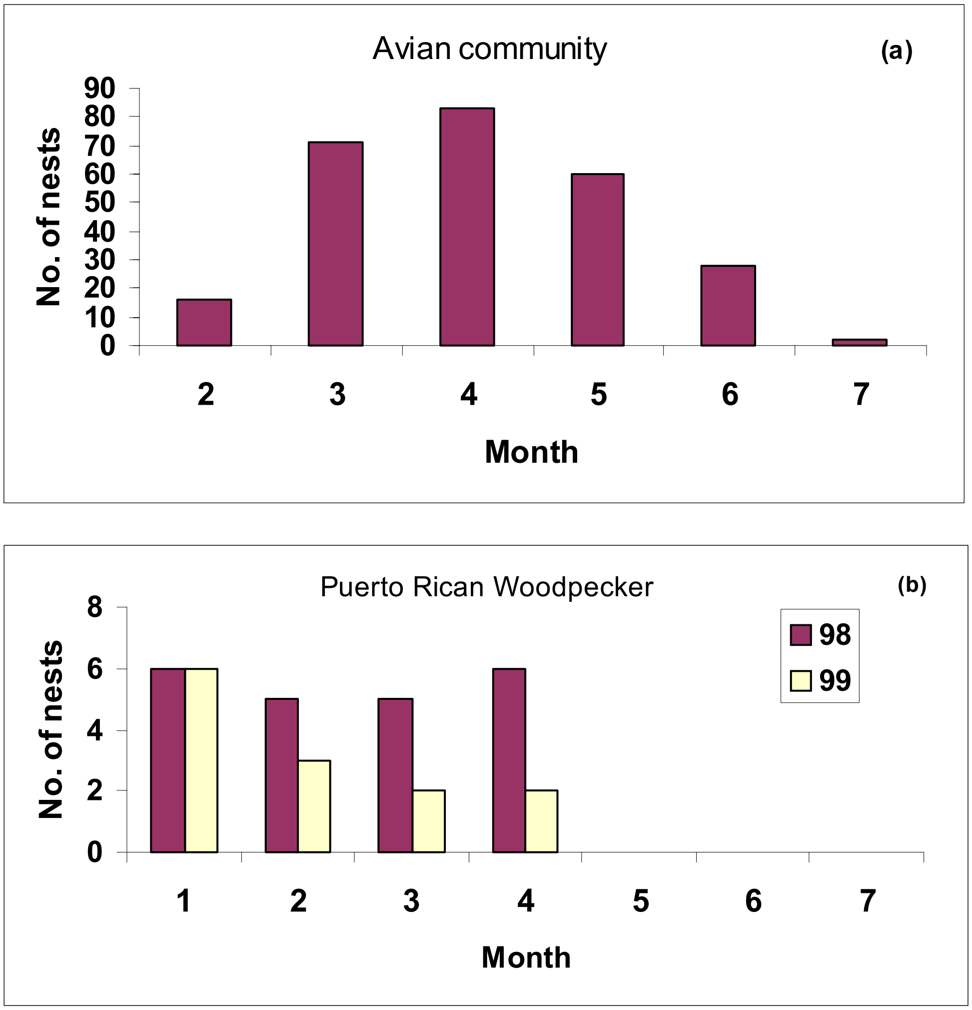

FIG 1. Nesting chronology of the avian community (open nesters only, panel a) in north-central Puerto Rico, 1997-1999. The chronology for the Puerto Rican Woodpecker in 1998 and 1999 is depicted in panel b. Months are coded chronologically by number (e.g., 1 = January, 7 = July).

introduced (exotic) plant species used as nesting substrates was low; 6 in coffee plantations (including coffee trees) and 8 in secondary forest study sites. Twenty-eight plant species were used as nesting substrates in secondary forest study sites. The two most frequently used were *Guarea guidonea* (n = 9) and *Roystonea borinquena* (n = 9), accounting for 26% of the nests. In coffee plantations, 31 plant species were used as nesting substrates (other than coffee). *Inga vera* (n = 28) and *Andira inermis* (n = 21) were the most frequently used, accounting for 24% of nests. Twenty-six percent (66/253) of the nests found in plantations occurred on coffee trees; the majority were nests of Bananaquits and Puerto Rican Emeralds (84%). Average nest height was 7.15 m (0.48 SE) in coffee plantations

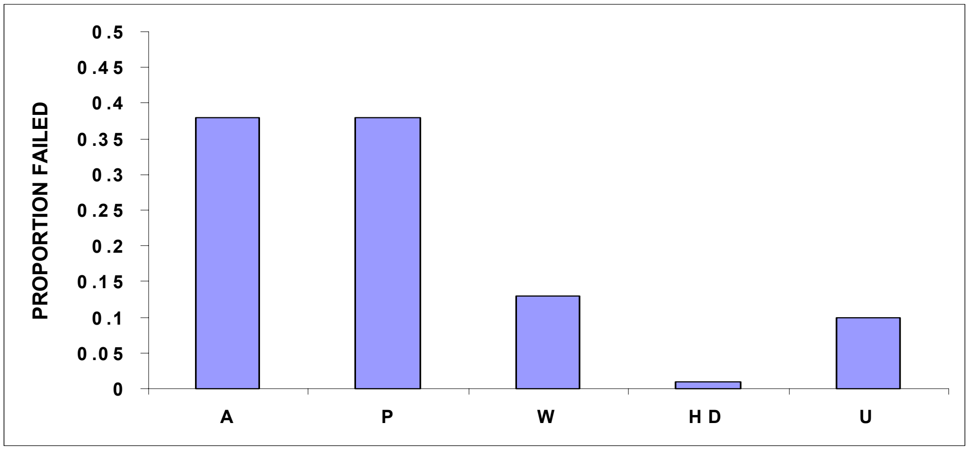

FIG 2. Proportion of nests that failed and causes of failure (N = 135). A = abandonment, P = predation, W = weather, HD = human disturbance, and U = unknown.

and 6.44 m (0.79 SE) in secondary forest study sites. Mean nest heights between habitat types were not significantly different (F = 0.45, d.f. = 1, 8, *P* = 0.52). Nineteen of the 28 nesting species nested in the canopy layer (12.2 ± 0.61 SE, n = 138); the remaining nested in the understory (2.71 ± 0.31 SE, n = 176).

Nest success of individual species across both habitats ranged from 21% to 86%. Nest success exceeded 50% for 16 species. The lowest success rate was recorded for Puerto Rican Woodpeckers, whose success rate in 1998 was 5% (1/21). In 1999, however, nesting success increased to 46% (6/13). Nest success for hummingbirds in coffee plantations was 65% (17/26) as compared to 36% (4/11) in secondary forest sites. For tanagers, nest success was 50% (coffee, 9/18) and 67% (secondary forest, 2/3), and for vireos it was 73% (coffee, 11/17) and 50% (secondary forest, 5/10). An equal proportion (38%) of nest failures was caused by predation and abandonment (Fig. 2). Other causes of nest failure included inclement weather (e.g., wind or rain) and human disturbance (e.g., fires to clear vegetation).

The likelihood of nest success was not related to habitat (forest) type for hummingbirds (χ^2 = 2.08, d.f. = 1, *P* = 0.15), vireos (χ^2 = 1.38, d.f. = 1, *P* = 0.23), and tanagers (χ^2 = 0.20, d.f. = 1, *P* = 0.65). Similarly, there was no difference in the mean number of young per nest attempt for four species (Table 1). The likelihood of nest loss to predation as compared to other causes was not related to habitat type for vireos (χ^2 = 0.85, d.f. = 1, *P* = 0.35) and tanagers (χ^2 = 0.74, d.f. = 1, *P* = 0.38). However, for hummingbirds, a greater proportion of nests were lost to predation than to other causes in coffee plantations compared to secondary forests (66% vs. 14%; χ^2 = 3.70, d.f. = 1, *P* = 0.05). Losses to predation for Bananaquits, the species with the largest sample size, did not differ between habitat types (χ^2 = 0.03, d.f. = 1, *P* = 0.85).

DISCUSSION

Our findings documented that shaded coffee plantations supported reproductive activity of more species (26) than secondary forest study sites (22). Shaded coffee plantations also supported the same number of nesting endemic species (10) as the secondary forest sites. Only two species nesting in secondary forests were not recorded in coffee plantations. Equally important, two expressions of nest success were similar between habitat types. We acknowledge that nest detection in coffee plantations (12 ha) was facilitated by dirt roads and "managed" understory. This may have contributed to the higher number of nests encountered in this habitat type compared to secondary forest, even though a larger area was searched in secondary forests (45 ha). Nonetheless, the density of nests in coffee plantations was arguably high. Productivity from resident birds nesting in shaded coffee plantations could be an important contributor to population maintenance (e.g., *sensu* Pulliam 1988). Although the fate of fledglings (e.g., dispersal, survival) was not assessed, our findings confirmed a fundamental assumption of the refugia hypothesis, namely, there was successful reproduction in shaded coffee plantations by a suite of species similar to that found in secondary forests.

These demographic attributes, coupled with the fact that shaded coffee plantations were more widespread in the past (Birdsey & Weaver 1982) and were managed as rustic plantations and traditional polycultures (Bergard 1983, Miranda-Castro 2004), lend considerable support to the proposition that shaded coffee plantations served as a refuge for resident avian species during periods of widespread deforestation in Puerto Rico. Although shaded coffee plantations could never replace the biodiversity and the ecological processes found in primary forests, in landscapes with dwindling natural forest cover (e.g., Puerto Rico in the 19th century), rustic and traditional polyculture plantations may have provided suitable, alternative habitat for breeding populations and other elements of biodiversity (see Dunn 2004, Donald 2004, Komar in press). This is because agricultural practices retained many floristic and structural elements of the forest they replaced, particularly the shade layer. These elements have been found to influence the presence of and habitat use by foraging resident species (Carlo *et al.* 2004). Foraging studies of migratory species have also highlighted the importance of the floristics and structure of the shade layer (Greenberg *et al.* 2000; Cruz-Angon & Greenberg 2005, Hietz 2005).

The canopy layer harbored the majority of nesting bird species recorded in this study, regardless of forest type. This pattern could be a response to differential predation pressure between canopy and understory layers (Martin 1988, Martin 1993, Collazo & Groom 2000). However, experiments with artificial nests suggest that this is not the case. Predation rates of nests placed at 1–2 m and at 6–10 m off the ground within secondary forests were not significantly different (Gleffe 2005). While our experiments were suited to test for nest location effects (within and between habitats), they do not lend themselves to test all possible factors influencing predation rates (Burke *et al.* 2004, Faaborg 2004, Gleffe 2005). For example, theoretical and field work suggest that multiple stems of the same substrate can benefit nesting species as predators are discouraged by the low encounters relative to the potential nest sites they need to search (Martin & Roper 1988). In this context, the paucity of nesting species in the understory layer of coffee plantations was noteworthy, and so was the low use of coffee trees, the densest nesting substrate. The majority of nests on coffee trees (84%) belonged to the Puerto Rican Emerald and Bananaquits. It was also noteworthy that losses to predation, as compared to other causes, were greater in coffee plantations for hummingbirds than in secondary forest study sites. The quality of shaded plantations, or any other forested habitat, might be improved by identifying and managing for habitat features related to successful reproduction (Martin 1992). This potential, and our results, justify pursuing further studies on predation rates (see Martin 1993). Taken as a whole, however, observed nesting patterns affirmed the value of the shade layer of coffee plantations for reproduction. Our findings also suggest that the presumed role of coffee plantations as refugia may have been more dependent on the layer that provided shade than on the understory, dominated by coffee trees.

Forest cover in Puerto Rico was reduced to 6–10% of its original extent as the island's population and demand for land increased, particularly during the 19th and early 20th centuries (Birdsey & Weaver 1982, Helmer *et al.* 2002). During this time period, much of the island's forest cover was provided by a flourishing coffee industry (Birdsey & Weaver 1982, Brash 1987), an industry that took advantage of and maintained a shade (canopy) layer that resembled primary forests. This habitat component, more than any other, probably contributes the most to the conservation value of shaded plantations for resident avian species in Puerto Rico (this work, Carlo *et al.* 2004). Opportunities for such "functional habitat substitutions" are not as likely in the 21st century. One reason is that forest cover provided by shaded coffee plantations is diminishing in Puerto Rico (only 41% of coffee crops are still grown under shade; US Department of Agriculture 2002). Another reason is that many modern shaded plantations do not necessarily aim at preserving or restoring native forests as their shade layer (Miranda-Castro 2004). The situation is compounded because part of the declining trend is due to conversions to sun coffee plantations, a practice that might exacerbate the potential loss of nesting habitat for forest birds (see Lindell & Smith 2003). Carefully designed studies, particularly studies focusing on parameters influencing fitness (e.g., Martin 1992), are needed before adjudicating similar conservation value to coffee plantations with differing habitat characteristics.

The possible consequence of these trends on resident avian species in Puerto Rico is magnified by the loss of forested lands to human encroachment, which tends to be permanent (e.g., urban sprawl). Therefore, future conservation strategies could strive to increase the number of protected areas of "recovered" secondary forest on the island (Helmer *et. al.* 2002) in combination with the restoration of the native shade canopy of existing and new coffee plantations on private lands (Miranda-Castro 2004). This study, and Carlo *et al.* (2004), highlighted the extensive use of native plants in the shade layer as nesting and foraging substrates. Shade plantations could supplement the functional role of protected areas (e.g., breeding productivity) via integrated conservation and economic goals. Coffee ranks second among the most important international commodities (O'Brien & Kinnaird 2003) and is the third most important crop in Puerto Rico (US Department of Agriculture 2002). Thus, the potential to encourage practices that are advantageous to both birds and coffee growers still exists in Puerto Rico, and elsewhere in coffee-growing regions of the world.

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