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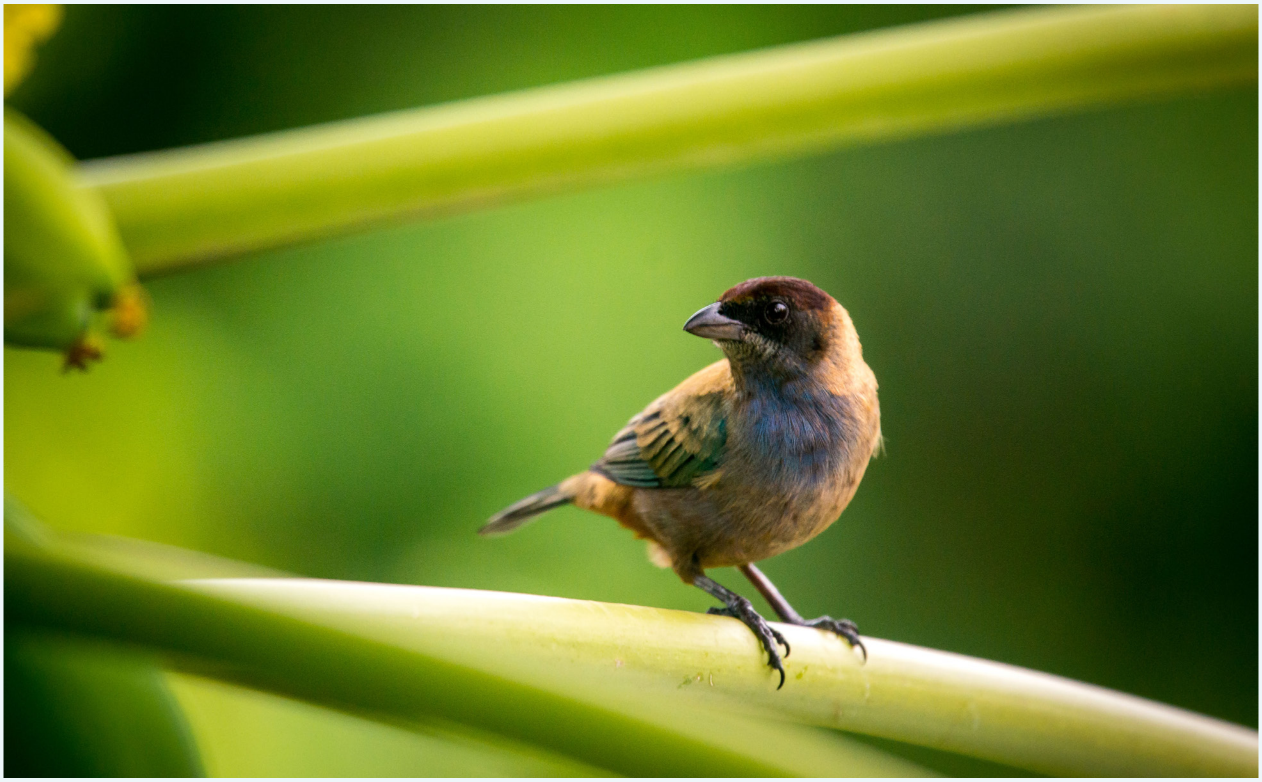

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Avian use of anthropogenic and natural habitats in a Small Island Developing State

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Cover Page: Lesser Antillean Tanager (*Stilpnia cucullata*) on 17 November 2015 in Bathway, St. Patrick, Grenada. Photograph by Paulson Des Brisay.

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Abstract

Avian species on Small Island Developing States (SIDS) are at particular risk from agricultural and urban expansion and climate change. However, creating appropriate management and mitigation actions for SIDS is challenging because ecological and conservation data are often unavailable. To better understand natural and anthropogenic habitat use by resident bird species in a small Neotropical SIDS, we conducted a systematic, community-wide survey of the distribution, diversity, and abundance of Grenada's land birds. Higher densities of most species were found in anthropogenic cultivated and secondary grasslands, while cloud and secondary forests had lower densities of most species. Nonetheless, cloud and secondary forests were selected by some species of conservation concern, such as the regionally endemic Lesser Antillean Tanager (*Tangara cucullata*), Grenada Flycatcher (*Myiarchus nugator*), and all nectarivores. Nectarivores tended to avoid urban habitats. Our results suggest that many avian species in Grenada make significant use of low-intensity agricultural and rural landscapes, and such habitats should be considered in the conservation of avian communities. Conservation of resident land-bird communities across this region will require maintaining a habitat mosaic of natural and anthropogenic habitat types, and collaboration among a wide range of government and non-governmental stakeholders.

Keywords

agriculture, conservation, Grenada, habitat selection, island, terrestrial

Resumen

Uso por parte de las aves de hábitats antropogénicos y naturales en un pequeño estado insular en desarrollo • Las especies de aves en los Pequeños Estados Insulares en Desarrollo (SIDS) corren un riesgo particular debido a la expansión agrícola y urbana y al cambio climático. Sin embargo, la creación de medidas de manejo y mitigación apropiadas para los SIDSs es un desafío porque a menudo no se dispone de datos ecológicos y de conservación. Para comprender mejor el uso del hábitat natural y antropogénico por parte de las especies de aves residentes en un pequeño SIDS neotropical, realizamos un muestreo sistemático a escala comunitaria sobre la distribución, diversidad y abundancia de las aves terrestres de Granada. Las densidades más altas de la mayoría de las especies se encontraron en pastizales secundarios y cultivados por el hombre; mientras que los bosques nublados y secundarios tuvieron densidades más bajas de la mayoría de las especies. No obstante, algunas especies de interés para la conservación, como *Tangara cucullata* endémica de la región, *Myiarchus nugator* y todos los nectarívoros, eligieron los bosques nublados y secundarios. Los nectarívoros tendieron a evitar los hábitats urbanos. Nuestros resultados sugieren que muchas especies de aves en Granada hacen un uso significativo de los paisajes rurales y agrícolas de baja intensidad y tales hábitats deben ser tenidos en cuenta en la conservación de las comunidades de aves. La conservación de las comunidades de aves terrestres residentes en esta región requerirá el mantenimiento de un mosaico de tipos de hábitats naturales y antropogénicos y la colaboración entre un amplio abanico de agentes gubernamentales y no gubernamentales.

Palabras clave

agricultura, conservación, Granada, isla, selección de hábitat, terrestre

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Résumé

Utilisation des milieux anthropiques et naturels par les oiseaux dans un petit État insulaire en développement • Les oiseaux des petits États insulaires en développement (SIDS) sont particulièrement menacés par l'expansion agricole et urbaine ainsi que par le changement climatique. Dans ces États, il est toutefois difficile de mettre en place des mesures de gestion et d'atténuation appropriées, car les données sur l'écologie et la conservation sont rarement disponibles. Pour mieux comprendre l'utilisation des milieux naturels et anthropiques par les espèces d'oiseaux sédentaires dans un SIDS néotropical, nous avons mené une étude systématique à l'échelle de la communauté sur la répartition, la diversité et l'abondance des oiseaux terrestres de la Grenade. Pour la plupart des espèces, les densités observées étaient plus élevées dans les zones cultivées et les prairies secondaires, et plus faibles dans les forêts humides d'altitude et les forêts secondaires. Toutefois, certaines espèces dont l'état de conservation est préoccupant – comme le Caliste dos-bleu (*Tangara cucullata*), endémique à l'échelle régionale, le Tyran bavard (*Myiarchus nugator*), ainsi que tous les nectarivores – préféraient les forêts humides d'altitude et les forêts secondaires. Les nectarivores avaient tendance à éviter les milieux urbains. Nos résultats montrent que de nombreuses espèces d'oiseaux de la Grenade utilisent de manière non négligeable les milieux ruraux comprenant des zones d'agriculture peu intensive, et que ces habitats devraient être pris en compte dans la conservation des communautés d'oiseaux. La conservation des communautés d'oiseaux terrestres sédentaires dans cette région requiert le maintien d'une mosaïque de milieux naturels et anthropiques, ainsi qu'une collaboration entre un large éventail d'acteurs gouvernementaux et non gouvernementaux.

Mots clés

agriculture, conservation, Grenade, île, sélection de l'habitat, terrestre

Human disturbance is one of the most significant threats to global avian biodiversity (Rapoport 1993). Many previous studies suggest that sites with less anthropogenic disturbance generally support greater avian abundance and richness (McKinney *et al.* 2010, Ntongani and Andrew 2013, Kang *et al.* 2015, Simon and Okoth 2016, but see Lepczyk *et al.* 2008) and more unique avian species (Fontúrbel *et al.* 2015, Simon and Okoth 2016). In disturbed landscapes, avian species abundance and richness often decline as land-use intensity increases (Elsen *et al.* 2017), as such disturbances often create fragmented landscapes and more forest edges (Strausberger and Ashley 1997), which are ideal habitat for brood parasitic species such as Shiny Cowbirds (*Molothrus bonariensis*; Dominguez *et al.* 2015). However, the relationship between anthropogenically disturbed habitats and biodiversity have largely come from studies based in temperate, continental regions, as opposed to more tropical island ecosystems.

Like most developing regions around the world, the Caribbean islands have experienced high extinction rates (Wunderle Jr. 2008), and immediate conservation efforts such as, but not restricted to, protected reserves are needed to mitigate species loss across this region. Caribbean bird species face numerous conservation threats including the introduction of invasive species such as the small Indian mongoose (*Urva auropunctata*; Martin 2007, Choudhary *et al.* 2013), habitat loss due to urbanization and tourism (Lack and Lack 1973, Henderson and Berg 2006, Rusk 2009), and natural disasters such as hurricanes (Wunderle Jr. 2008). This suggests that both anthropogenic and natural disturbances are likely to influence Caribbean species and subspecies, many of which are endemic or have restricted ranges. Western conservation strategy often focuses on implementing protected reserves where land clearing and hunting are forbidden (e.g., Pasquier 1980). Such protected reserves are a critical part of conservation technique in tropical forested landscapes because a 90% deforestation of a tropical forest can result in a loss of 50% of biodiversity (Terborgh 1992), and the impacts of biodiversity loss due to human land development can persist for decades (Hansen *et al.* 2005, Hernandez 2016). On Small Island Developing States (SIDS), it may be insufficient to rely solely on protected reserves to conserve tropical forest biodiversity because anthropogenic land uses adjacent to protected reserves can decrease the benefit of protected reserves (e.g., in search of economic opportunities, humans living adjacent to protected areas may enter reserves; Vandermeer and Perfecto 2013).

One promising approach to enhance the effect of protected reserves on biodiversity in developing tropical islands is to consider the value of agroforestry systems (here, defined as agricultural systems including trees, such as cocoa, mango, nutmeg, or other tree products) to biodiversity. Agroforestry systems vary tremendously in many aspects related to the production and harvesting of human food—such as crop type and diversity (Harvey and Villalobos 2007, Hernández *et al.* 2013) and planting and harvesting methods (Harvey and Villalobos 2007)—but many agroforestry systems have had positive impacts on avian communities in the Caribbean compared to secondary forest (Arnold *et al.* 2021, Exantus *et al.* 2021). For example, urban agroforestry systems in Haiti were critical habitats for two vulnerable endemic species, namely the White-necked Crow (*Corvus leucognaphalus*) and Hispaniolan Parrot (*Amazona ventralis*), and Haiti's agroforestry had similar species richness and diversity compared to urban secondary forests (Exantus *et al.* 2021). Additionally, on Trinidad, cacao agroforests were important for habitat generalists, while secondary forests were important for habitat specialist species (Arnold *et al.* 2021). Tropical cacao and banana agroforestry systems have had positive effects on avian and bat communities by serving as essential habitats for a diversity of species, including some forest-dependent fauna (Harvey and Villalobos 2007).

Although agriculture and forestry often have negative impacts on bird communities on continents (Moorman and Guynn 2001, Vickery *et al.* 2001, Şekercioğlu 2002, Green *et al.* 2005, Phillips *et al.* 2005), agroforestry systems in tropical islands may provide valuable habitat for some species, primarily habitat generalists (Cox and Ricklefs 1977). Tropical island agroforestry systems may be a valuable animal habitat type as agricultural practices in developing countries are typically less intensive, less

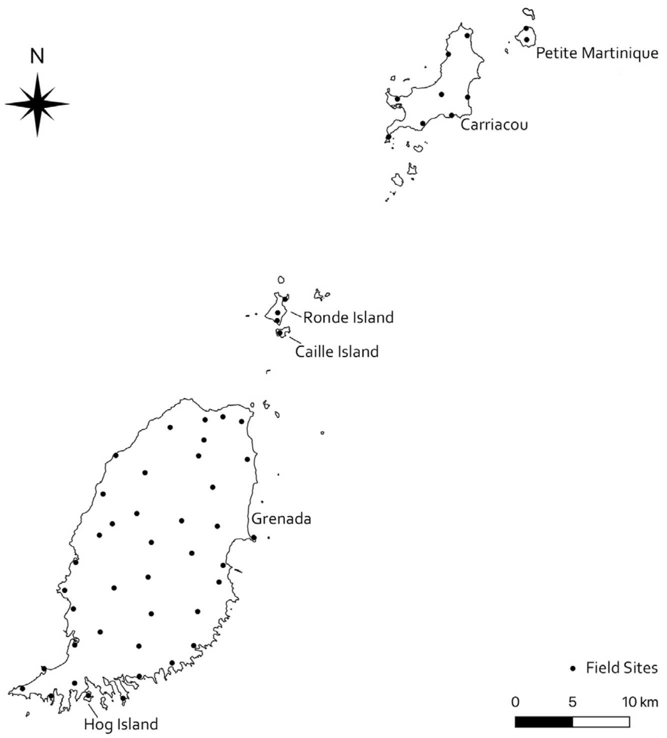

Fig. 1. Map showing the location of our 54 field sites across the six islands surveyed across Grenada in 2017. Map created using QGIS (2019).

mechanized, involve less use of external inputs such as fertilizer and pesticides, and take place on smaller habitat patches (Finegan and Nasi 2004, Hernández *et al.* 2017); these agroforestry features may result in fewer negative impacts on birds in these regions (Perfecto and Vandemeer 2008, Hernández *et al.* 2013, Greenler and Ebersole 2015). Thus, in order to understand the impacts of agriculture on birds on Caribbean islands, we must examine in-situ impacts rather than extrapolating expected impacts from research conducted in other regions.

Grenada is a tropical SIDS located in the southernmost region of the Caribbean archipelago. Like most developing islands around the world, Grenada faces numerous ecological and economic challenges due to its small size, isolation from other regions, and lack of infrastructure. Island ecosystems like Grenada are typically fragile and vulnerable and are particularly sensitive to climate change and natural disasters, while also experiencing the consequences of pressures from external economic systems and high levels of poverty (UN-OHRLLS 2011). Together, these factors can result in significant or unpredictable risks to the wildlife that inhabit Grenada and other tropical countries. Species with restricted ranges on Grenada and in developing countries are particularly vulnerable to extinction (Holdaway *et al.* 2001, Gaston and Fuller 2009, De Lima *et al.* 2011, Devenish-Nelson *et al.* 2019). Considering that the densities of critically endangered terrestrial species are 14 times greater on islands than on continents, the risk of island extinctions are amplified (Tershy *et al.* 2015). Additionally, extinction risks are likely to increase with climate change (Benning *et al.* 2002, Gillespie *et al.* 2008), causing birds on islands to be of significant conservation concern. In fact, island endemics constitute 90% of the birds that have historically gone extinct (Johnson and Stattersfield 1990). However, despite these significant risks, relatively little ecological research has been conducted on endemic birds in SIDS, such as those in the Caribbean (Devenish-Nelson *et al.* 2019).

As such, our aim was to provide baseline data to serve as a foundation for monitoring changes in avian abundance and distribution and to quantify the effects of ecological changes in land-use types and vegetation structure on avian communities. This baseline data will be essential for determining the conservation status and risk of extinction of all terrestrial avian species on Grenada, except the Critically Endangered Grenada Dove (*Leptotila wellsi*) and the Endangered Grenada Hook-billed Kite (*Chondrohierax uncinatus mirus*), which have already been systematically censused (Thorstrom and McQueen 2008, BirdLife International 2021).

Thus, we carried out systematic surveys across the entirety of the country of Grenada to determine the impacts of agriculture, forestry, and urbanization on terrestrial birds in Grenada. We included all terrestrial resident species and all habitat types in our study design, taking care to also include the habitat types of restricted-range and endemic species such as the Grenada Flycatcher (*Myiarchus nugator*) and Lesser Antillean Tanager (*Tangara cucullata*), which are particularly vulnerable to habitat conversion (Oostra *et al.* 2008), as well as including habitat types of the Shiny Cowbird, a species that expanded its range across the Caribbean that may decrease productivity of native species (Cruz *et al.* 1985, Sackmann and Reboreda 2003, Dominguez *et al.* 2015).

Methods

Study Area

This study was conducted throughout the country of Grenada and included all three permanently inhabited oceanic islands: Grenada (12°08'N, 61°40'W), Carriacou (12°28'N 61°26'W), and Petite Martinique (12°31'N 61°23'W) along with some largely uninhabited offshore islands including Caille Island (12°17'14.5"N 61°34'52.7"W), Ronde Island (12°18'08.8"N 61°35'06.6"W), and Hog Island (11°59'58.1"N 61°44'17.9"W) (Fig. 1). Carriacou is located 37 km north of Grenada, Petite Martinique is located 6 km east of Carriacou, and the offshore islands (except Hog Island) are located between Grenada and Carriacou (Fig. 1; Rusk 2009). Grenada has a total area of 311 km², Carriacou has a total area of 32 km², and Petite Martinique has a total area of 2.37 km² (Rusk 2009, Government of Grenada 2018).

Grenada is geographically characterized by mountainous terrain and contains a diverse range of habitat types (Wunderle Jr. 1985, Koper and Grieef 2016). Forested habitats include secondary forests of varying ages, and montane, mature lowland, cloud, and mangrove forests (Wunderle Jr. 1985). Non-forest-dominated habitats include secondary scrub, secondary grassland, and savanna (Wunderle Jr. 1985). Anthropogenic habitats include pastures, urban areas, and cultivated areas, including small row crop patches (e.g., okra *Abelmoschus esculentus*, string bean *Phaseolus vulgaris*, lettuce *Lactuca sativa*, corn *Zea mays*, tomato *Solanum lycopersicum*, watermelon *Citrullus lanatus*, sweet potato *Ipomoea batatas*, cucumber *Cucumis sativus*, and bell pepper *Capsicum annuum*) and larger, diverse agroforest communities consisting of mixed species (e.g., pigeon pea *Cajanus cajan*, *Citrus* sp., soursop *Annona muricata*, papaya *Carica papaya*, breadfruit *Artocarpus altilis*, mango *Mangifera indica*, banana *Musa* sp., cocoa *Theobroma cacao*, and nutmeg *Myristica fragrans*) (Wunderle Jr. 1985, Helmer *et al.* 2008). Both Carriacou and Petite Martinique have rich fertile soil that has resulted in extensive deforestation for agriculture and free-grazing livestock farming (i.e., goats, cows, sheep, and donkeys) following European colonization (Peters 2015). Forested areas on Carriacou include seasonal evergreen forest, deciduous forest, dry thorn scrub, and mangroves (Rusk 2009, Crask 2012).

Grenada has 35 recorded species of terrestrial resident bird species, including frugivores, granivores, nectarivores, insectivores, omnivores, and one carnivore (Wunderle Jr. 1985). We categorized each of our focal species into dietary guilds using species diet information from the Cornell Lab of Ornithology Birds of the World electronic database (Baptista *et al.* 2020a, 2020b, 2020c, Chantler and Boesman 2020, Cody 2020, Collar 2020, Fraga 2020, Goodrich *et al.* 2020, Hilty and Christie 2020, Hinkelmann *et al.* 2020, Johnson 2020, Joseph 2020, Lowther and Post 2020, Quinn and Startek-Foote 2020, Rising 2020, Rising and Jaramillo 2020, Rising *et al.* 2020, Schuchmann and Boesman 2020, Smith and Jackson 2020, Telfair II 2020, Hilty *et al.* 2022). All focal species of this study are residents, which are much more common than terrestrial migrants on this island. For the purposes of this study, we had sufficient data to analyze habitat use by 21 species. Grenada is home to the Critically Endangered Grenada Dove and the Endangered Grenada Hook-billed Kite. Near-endemic or restricted range species include the Lesser Antillean Tanager, Grenada Flycatcher (Bangs 1907, Lack and Lack 1973, Bierregaard 1994, Thorstrom and McQueen 2008, Rusk 2009), and the Lesser Antillean Bullfinch (*Loxigilla noctis*) (Lack and Lack 1973).

Study Design and Field Sites

A previous study on detectability (here defined as the probability of detecting birds that are available for detection) of Grenada's land birds (Bergen *et al.* 2023) informed our study design. We ran surveys at 54 different sites from June to October 2017 during the rainy season (World Bank Group 2020), which corresponded with most land bird's breeding seasons and when birds were most likely to sing (Bergen *et al.* 2023). Field sites were distributed among the different islands with more sites on the larger islands, as follows: Grenada 39, Carriacou 8, Ronde Island 3, Petite Martinique 2, Caille Island 1, and Hog Island 1. Field sites were distributed to reflect all habitat types across the islands and included three Important Bird Areas (IBAs) on Grenada, namely Grand Etang, Mount Hartman, and Perseverance Dove Sanctuary. The IBAs were identified as such based on the presence of seven Lesser Antillean restricted-range avian species (Rusk 2009). Field sites also included key inland and coastal habitats (e.g., Woburn Bay mangrove forests, Levera wetlands, forests, and mixed secondary growth vegetation) as well as agricultural areas, urban sites, and other developed areas. Adjacent field sites were separated by at least 3 km to ensure each site was independent and to evenly cover all geographic locations within the islands. We conducted a second survey at some field sites (*n* = 6 out of 54 field sites) when unfavorable weather interrupted our first survey in order to standardize our field method and to yield better estimates of abundance of particular species at those sites (Ralph *et al.* 1995).

Data Collection Method

Double and Single Observer Surveys.—For most surveys (*n* = 42) we conducted point counts by applying the dependent double-observer method (Nichols *et al.* 2000, Forcey *et al.* 2006), using the methods described by Hutto *et al.* (1986) with slight modifications (Cook and Jacobson 1979, Nichols *et al.* 2000). In this method, two observers visit each point count plot. A primary observer identifies all birds seen or heard, while the secondary observer records the primary observer's observations as well as the birds that were missed by the primary observer. The primary and secondary observer switch roles among point count plots, thus allowing the perceptibility (here defined as the percent of birds available for detection that were detected by observers) to be estimated (Nichols *et al.* 2000).

We conducted double-observer surveys at 42 field sites (Grenada *n* = 34 sites, Carriacou *n* = 5 sites, Petite Martinique *n* = 2 sites, Hog Island *n* = 1). The remaining sites were surveyed using the single observer method as field assistants were unable to assist with these surveys (e.g., offshore islands).

Field Methods

***Point Count Surveys.*—**For each field site, we conducted 8 point count surveys (25-m radius); each point count location was separated by 100 m to reduce chances of double-counting individuals. However, we conducted fewer than a full set of 8 different point count locations at 6 of the 54 sites due to wind or rain interruptions. A total of 454 point counts were conducted across 54 field sites.

Each point count survey was conducted for 5 min. Point count surveys were only conducted on days with winds < 20 km/h and without rain (Ralph *et al.* 1995). Survey locations were recorded using a GPS unit (Garmin Etrex 20X). Observer(s) conducted point count surveys during either of two time sampling periods: 1) from dawn until 1000 ("AM"), or 2) from 1630 until dusk ("PM"). For almost all of our focal species, the relative abundance of individuals detected during surveys conducted during each of these periods does not differ significantly (Bergen *et al.* 2023). One survey on Caille Island continued until noon due to the inaccessibility of the island at other times, and to avoid unfavorable weather.

Habitat Structure and Land Use.—We visually recorded the percentage of habitat types and land uses within each 25-m radius point count plot following avian surveys (Table 1). Some 25-m radius point count plots included more than one habitat type; in these cases, we visually estimated the percent of the plot that contained each habitat type, and assigned the percentage of each habitat type as the habitat variable used in subsequent analyses. We then compared densities of each species among ten habitat types (Table 2) and eight anthropogenic land types (Table 3). Habitat types used are defined in Table 1.

Statistical Analyses

***Perceptibility.*—**We used the program DOBSERV (Nichols *et al.* 2000), a computer program designed to calculate perceptibility of each species using the dependent double-observer sampling methods described above. We ran six separate models to test whether detection probability differed by observer, among species, or by feeding guild (e.g., frugivores, where specific feeding guilds included two or more species that are assumed to have equal detection probability; Nichols *et al.* 2000). Each species or feeding guild had at least 10 individuals, which is the minimum number of individuals required for analyses in DOBSERV (Nichols *et al.* 2000). We selected the model for subsequent analyses by comparing the difference in Akaike's Information Criterion (AIC) value (Wagenmakers and Farrell 2004). Specifically, we compared the delta AIC (Δ_i) values (Wagenmakers and Farrell 2004, Mazerolle 2006). All candidate models selected had a Δ_i value < 7, as 7 is considered the highest threshold for suitable candidate models (Mazerolle 2006). We selected candidate model P(S,I) for all perceptibility analyses (Table 5). To calculate Δ_i, we used the following formula:

$$\Delta_i = \text{AIC}_i - \min \text{AIC}$$

where min AIC is the AIC value of the "best" model, and AIC_i is the AIC value for model *i* (Richards 2005, Mazerolle 2006; Table 5).

Habitat-specific Double Observer Method.—To evaluate whether perceptibility differed among habitat types, we used DOBSERV (Nichols *et al.* 2000) to calculate perceptibility within each of four broad habitat categories: 1) forested habitats (montane, mature lowland, secondary, cloud, and mangrove forests, and secondary scrub); 2) cultivated habitats (cocoa, nutmeg trees, farmlands, and cultivated areas); 3) urban habitats (airports, urban areas, apartments, houses, stadiums, parks, and business buildings); and 4) open area (secondary grasslands, savannas, and pastures). The difference in Δ_i values were used to select the model that best fit our data, and all candidate models selected had a Δ_i value < 7 (Wagenmakers and Farrell 2004, Richards 2005, Mazerolle 2006).

Habitat use.—We used R 3.3.3 to conduct General Linear Models (GLM) as residuals followed non-normal distributions (Bates *et al.* 2015, Bates and Maechler 2017, R Core Team 2017, Wickham *et al.* 2017, Bartoń 2018). To determine the appropriate distribution for each species, we compared fit of Gaussian, Poisson, and negative binomial distributions using QQ plots, histograms, and deviance/df ratios as appropriate. If none of these distributions fit the data, we concluded that we had insufficient data to model relative abundance of that species and dropped that species from further analyses. We included time of day and date as fixed variables to control for the potential impacts of these variables on perceptibility, but as they were not the focus of our study, we do not discuss them in the text. We had sufficient data to assess habitat use by 21 of Grenada's 35 resident bird species (Appendix Table 1).

We used past literature to inform our density calculation (Bayne *et al.* 2008). To calculate density of species, we used the following formula:

density = total observations of each individual species at each point count / perceptibility of each individual species

We compared densities of birds among the five islands we surveyed, then among natural and anthropogenic habitats. We used separate GLM models to compare, 1) resident land bird habitat use among specific habitat categories (montane, mature lowland, secondary, cloud, and mangrove forests; secondary scrub; secondary grassland; savanna; pasture; other cultivated), and 2) among specific anthropogenic land uses (farmland, cocoa, nutmeg, residential, airport, stadium, industrial, park; for further information regarding habitat types, see Table 1). All analyses were conducted separately by species, but where appropriate, we also discuss impacts of habitat on each feeding guild.

Results

Perceptibility

Δ_i ranged from 0 to 86.84 with one candidate model, P(S,I), falling below threshold 7 (Mazerolle 2006; Table 6). Double-observer analyses suggest that perceptibility of focal species was generally high and ranged from 57% to 100% with a mean perceptibility of 84% (SD = 0.10; SE = 0.02 [Appendix Table 2]). 32% of species (10 out of 31 species) had a perceptibility > 0.91, 48% (15 out of 31 species) had perceptibility ranging between 0.81 to 0.86, 13% (4 out of 31 species) had perceptibility ranging between 0.73 to 0.76, and 7% (2 out of 31 species) had perceptibility < 0.59 (Common Ground Dove [*Columbina passerina*], perceptibility of 0.58, and Mangrove Cuckoo [*Coccyzus minor*], perceptibility of 0.57). For the following analyses, we did not analyze species with < 10 observations or species with perceptibility < 0.73, because > 0.70 is considered average perceptibility for experienced observers (Bart 1985). Because perceptibility was generally high, we chose not to adjust our results for detectability, as this can increase, rather than decrease, bias (Johnson 2008, Efford and Dawson 2009). However, we recognize that our analyses thus underestimate density, as perceptibility is less than 1.0, and should be considered as relative rather than absolute measures of density. We also included fixed variables in our models to account for potential variation in detectability due to time of day and date.

Habitat-specific Perceptibility.—Both forested and cultivated habitat Δ_i ranged from 0 to 44.84 and 0 to 11.86, respectively, and had 3 candidate models [P(S,I), P(.,I), and P(G,I)] below threshold 7 (Mazerolle 2006; Table 5). Both urban habitats and open area Δ_i range from 0 to 77.41 and 0 to 64.85, respectively, and had 1 candidate model, P(S,I) below threshold 7 (Mazerolle 2006; Table 5). Double-observer analyses of focal species showed that detectability was high and ranged from 89% to 100% among different habitat types, with a mean perceptibility of 96% (SD among means = 0.03; Appendix Table 3). In virtually all cases, the confidence interval for each habitat type included mean perceptibility for all other habitat types, indicating no significant difference in perceptibility among habitat types for any focal species (Appendix Table 3).

Variation Among Islands

Most species had higher densities on Grenada than on the smaller islands (Table 4), including the Shiny Cowbird, a brood parasite. Few species had lower densities on Grenada compared to the smaller islands. Specifically, 1) Antillean Crested Hummingbirds (*Orthorhyncus cristatus*) had lower densities on Grenada compared to Caille and Ronde Island and Petite Martinique; 2) Bananaquits (*Coereba flaveola*), Gray-rumped Swifts (*Chaetura cinereiventris*), and Smooth-billed Anis (*Crotophaga*

Table 1. Land use classification, determined through in-person visits to each point-count plot, used to evaluate habitat selection by birds in Grenada. All land use classifications were considered in our analysis (see Results section). All land use data were collected as the % of each specific land use type observed within each 25-m radius point count plot.

Land Use	Land Use Measurement at Each Point Count
Agriculture	
Farmland	habitat use analyses (see Table 2), further divided into pasture or cultivated
Cocoa-dominated	one of the agroforestry types
Nutmeg-dominated	one of the agroforestry types
Pasture	graminoid-dominated, grazed by livestock
Cultivated	non-woody row crops
Residential	
House(s)	anthropogenic habitats
Apartment(s) / Hotel(s)	complexes
Transport	
Road(s)	pavements with asphalt, unpaved, or concreted passage[a]
Airport	facilities, structures, or fenced property
Recreational	
Stadium	facilities, structures, or fenced property
Park	facilities, structures, or fenced property
Commercial/Industrial	
Business(es)	business place(s)
Factories	facilities, structures, or fenced property
Natural/naturalized	
Montane forest	mountainous
Mature lowland forest	low elevations
Secondary forest	regrown since cultivation; includes high abundance of exotic and/or cultivated tree crop species
Cloud forest	close to mountain peaks, unlikely to have been cultivated historically
Mangrove forest	including coastal wetlands
Secondary scrub	mix of shrub, graminoid, and occasional trees
Secondary grassland	regrown grassland
Savanna	contains significant abundance of both graminoid and tree vegetation

[a] allows the passage of four-wheel motor vehicles

ani) had lower densities on Grenada compared to Caille Island and Ronde Island; 3) Scaly-naped Pigeons (*Patagioenas squamosa*) and Black-faced Grassquits (*Tiaris bicolor*) had lower densities on Grenada compared to Carriacou and Petite Martinique; and 4) Tropical Mockingbirds (*Mimus gilvus*) and Carib Grackles (*Quiscalus lugubris*) had lower densities on Grenada compared to Petite Martinique (Table 4).

Habitat Types

38% (8 out of 21 species) of our focal species, including Shiny Cowbirds, had higher abundances in sites with more cultivated and secondary grassland, whereas several species avoided sites with higher extents of cloud and secondary forests (29% and 24%, *n* = 6 and 5 out of 21 species, respectively; Table 2). Effects of habitat type on abundance varied among feeding guilds. Granivores had lower densities in sites with more secondary and cloud forests, while nectarivores had higher densities in secondary and cloud forests (Table 2). Frugivores, granivores, and insectivores had higher densities in sites with more secondary grasslands, whereas nectarivores had lower densities in sites with more secondary grasslands. Both nectarivores and granivores had higher densities in sites with more cultivated habitats. Omnivores, insectivores, nectarivores and frugivores all had higher densities in mangrove forests (Table 2). Both species of hummingbirds selected similar habitat types; Antillean Crested Hummingbirds and Rufous-breasted Hermits (*Glaucis hirsutus*) had higher densities in sites with more secondary and cloud forests, savanna, pasture, and cultivated habitat, and Rufous-breasted Hermits also selected sites with montane forests (Table 2).

Restricted-range species used a diversity of habitat types (Table 2). Grenada Flycatchers were found in higher densities in sites with more mature lowland, secondary, and mangrove forests, and secondary scrub (Table 2), while Lesser Antillean Tanagers were found in higher densities in cloud forests. Both Grenada Flycatchers and Lesser Antillean Tanagers were also found in higher densities in cultivated habitats. Lesser Antillean Bullfinches had lower densities in sites with more mature lowland and cloud forests, savannas, secondary scrub, and cultivated habitats.

Anthropogenic land uses

Densities of almost half of all focal species (48%, 10 out of 21 species) increased with abundance of farmland, and many species had higher densities in sites with more residential habitats (43%, 9 out of 21 species). Fewer species had higher densities in sites that were dominated by airport structures (19%, 4 out of 21 species), cocoa trees (14%, 3 out of 21 species), nutmeg trees (14%, 3 out of 21 species), or commercial buildings (14%, 3 out of 21 species).

Shiny Cowbirds were detected in higher densities in sites that were more urban or residential. Both species of hummingbirds had higher abundances in agricultural sites, but Antillean Crested Hummingbirds were more abundant in sites with more farmlands and cocoa trees, while Rufous-breasted Hermits were more abundant in sites with more nutmeg trees (Table 3). All nectarivores avoided urban habitats with higher proportions of residential buildings, airport facilities, or commercial build-

Table 2. Use of habitat types by land birds on Grenada in 2017. For visualization purposes, significant positive parameter estimates are bold, significant negative parameter estimates are not bold, and non-significant differences are not shown ($p > 0.05$). ID = insufficient data. Habitat types were measured as the percentage present within each 25-m radius point count plot. All response variables were modeled using a Poisson distribution.

Feeding Guilds of Species	Statistical Parameter	Montane Forest	Mature Lowland Forest	Secondary Forest	Cloud Forest	Mangrove Forest	Secondary Scrub	Secondary Grassland	Savanna	Pasture	Cultivated
Carnivores											
Broad-winged Hawk	Beta	ID				ID	−0.021	ID	ID		
(*Buteo platypterus*)	SE	ID				ID	0.010	ID	ID		
Frugivores											
Scaly-naped Pigeon	Beta	ID	−0.012	0.012	−0.023	0.022	0.011	0.008	0.011		−0.010
(*Patagioenas squamosa*)	SE	ID	0.003	0.001	0.007	0.002	0.001	0.002	0.002		0.002
Zenaida Dove	Beta	ID	ID		ID	ID		ID	ID	ID	
(*Zenaida aurita*)	SE	ID	ID		ID	ID		ID	ID	ID	
Granivores											
Black-faced Grassquit	Beta			−0.010	−0.022	ID		0.013		0.017	0.008
(*Melanospiza bicolor*)	SE			0.004	0.008	ID		0.004		0.006	0.002
Eared Dove	Beta			−0.031	ID	ID	−0.009			ID	
(*Zenaida auriculata*)	SE			0.007	ID	ID	0.003			ID	
Yellow-bellied Seedeater	Beta	ID			ID	ID		0.020	ID	ID	
(*Sporophila nigricollis*)	SE	ID			ID	ID		0.006	ID	ID	
Insectivores											
Cattle Egret	Beta	ID	ID		ID		0.008	0.041		ID	−0.010
(*Bubulcus ibis*)	SE	ID	ID		ID		0.004	0.004		ID	0.005
Gray-rumped Swift	Beta	0.031		−0.031	ID			0.039		ID	0.032
(*Chaetura cinereiventris*)	SE	0.008		0.009	ID			0.006		ID	0.003
Grenada Flycatcher	Beta		0.020	0.014		0.030	0.025		ID		0.020
(*Myiarchus nugator*)	SE		0.007	0.006		0.009	0.006		ID		0.005
House Wren	Beta	ID			ID	0.013	0.006				
(*Troglodytes aedon*)	SE	ID			ID	0.005	0.003				

Table 2 cont.

Feeding Guilds of Species	Statistical Parameter	Montane Forest	Mature Lowland Forest	Secondary Forest	Cloud Forest	Mangrove Forest	Secondary Scrub	Secondary Grassland	Savanna	Pasture	Cultivated
Nectarivores											
Antillean Crested Hummingbird	Beta			0.007	0.010				0.120	0.020	0.015
(*Orthorhyncus cristatus*)	SE			0.003	0.003				0.005	0.005	0.002
Bananaquit	Beta	0.006		0.006		0.007		−0.031	−0.007		0.008
(*Coereba flaveola*)	SE	0.003		0.001		0.003		0.005	0.003		0.001
Rufous-breasted Hermit	Beta	0.060	ID	0.023	0.047	ID	ID	ID	0.046	0.043	0.045
(*Glaucis hirsutus*)	SE	0.008	ID	0.007	0.006	ID	ID	ID	0.011	0.113	0.007
Omnivores											
Carib Grackle	Beta	ID		−0.026	ID	0.023	0.021	0.020			
(*Quiscalus lugubris*)	SE	ID		0.118	ID	0.007	0.004	0.007			
Gray Kingbird	Beta	−0.018	−0.016		−0.017						
(*Tyrannus dominicensis*)	SE	0.008	0.005		0.004						
Lesser Antillean Bullfinch	Beta		−0.014		−0.028		−0.018		−0.015	ID	−0.003
(*Loxigilla noctis*)	SE		0.005		0.008		0.004		0.005	ID	0.002
Lesser Antillean Tanager	Beta		ID		0.019	ID					0.009
(*Stilpnia cucullata*)	SE		ID		0.004	ID					0.003
Shiny Cowbird	Beta	ID			ID		−0.010	0.027		0.024	−0.009
(*Molothrus bonariensis*)	SE	ID			ID		0.005	0.006		0.007	0.004
Smooth-billed Ani	Beta	ID	ID		ID	ID		0.019		ID	
(*Crotophaga ani*)	SE	ID	ID		ID	ID		0.009		ID	
Spectacled Thrush	Beta	ID			−0.020			−0.008	−0.015		0.004
(*Turdus nudigenis*)	SE	ID			0.004			0.004	0.005		0.001
Tropical Mockingbird	Beta	ID	−0.074	−0.017	−0.060	0.007	0.004				−0.017
(*Mimus gilvus*)	SE	ID	0.018	0.003	0.017	0.003	0.002				0.002

Table 3. Resident land bird densities in anthropogenic land types in Grenada in 2017. For visualization purposes, significant positive parameter estimates are bold, significant negative parameter estimates are not bold, and non-significant differences are not shown ($p > 0.05$). ID = insufficient data. Habitat types were measured as the percentage present within each 25-m radius point count plot. All response variables were modeled using a Poisson distribution.

Feeding Guilds of Species	Statistical Parameter	Farmland	Cocoa	Nutmeg	Residential	Airport	Stadium	Business	Park
Carnivores									
Broad-winged Hawk	Beta					ID	ID		ID
(*Buteo platypterus*)	SE					ID	ID		ID
Frugivores									
Scaly-naped Pigeon	Beta	−0.018		−0.174	−0.012	ID		0.008	ID
(*Patagioenas squamosa*)	SE	0.002		0.022	0.002	ID		0.003	ID
Zenaida Dove	Beta					ID	ID	ID	ID
(*Zenaida aurita*)	SE					ID	ID	ID	ID
Granivores									
Black-faced Grassquit	Beta	0.006	0.008		−0.005	−0.052			
(*Melanospiza bicolor*)	SE	0.001	0.002		0.002	0.014			
Eared Dove	Beta	0.019	−0.119		0.021		ID		ID
(*Zenaida auriculata*)	SE	0.003	0.027		0.004		ID		ID
Yellow-bellied Seedeater	Beta	0.008			0.028	0.029	ID		ID
(*Sporophila nigricollis*)	SE	0.004			0.005	0.011	ID		ID
Insectivores									
Cattle Egret	Beta	−0.013			−0.036	0.047	ID	ID	ID
(*Bubulcus ibis*)	SE	0.006			0.010	0.005	ID	ID	ID
Gray-rumped Swift	Beta	0.041			0.016	0.057	ID		ID
(*Chaetura cinereiventris*)	SE	0.003			0.006	0.007	ID		ID
Grenada Flycatcher	Beta					ID	ID		ID
(*Myiarchus nugator*)	SE					ID	ID		ID
House Wren	Beta				0.017	ID	ID		
(*Troglodytes aedon*)	SE				0.003	ID	ID		

Table 3 cont.

Feeding Guilds of Species	**Statistical Parameter**	**Farmland**	**Cocoa**	**Nutmeg**	**Residential**	**Airport**	**Stadium**	**Business**	**Park**
Nectarivores									
Antillean Crested Hummingbird	Beta	0.001	0.126			ID		−0.034	
(*Orthorhyncus cristatus*)	SE	0.002	0.004			ID		0.015	
Bananaquit	Beta	0.006	0.008		−0.005	−0.052			
(*Coereba flaveola*)	SE	0.001	0.002		0.002	0.014			
Rufous-breasted Hermit	Beta			0.054	−0.064	ID	ID		ID
(*Glaucis hirsutus*)	SE			0.008	0.017	ID	ID		ID
Omnivores									
Carib Grackle	Beta						ID		ID
(*Quiscalus lugubris*)	SE						ID		ID
Gray Kingbird	Beta				0.006			0.013	
(*Tyrannus dominicensis*)	SE				0.002			0.004	
Lesser Antillean Bullfinch	Beta	0.008			0.008	ID			ID
(*Loxigilla noctis*)	SE	0.002			0.003	ID			ID
Lesser Antillean Tanager	Beta	0.009		0.023	0.012	ID	ID	−0.167	ID
(*Stilpnia cucullata*)	SE	0.003		0.008	0.004	ID	ID	0.079	ID
Shiny Cowbird	Beta				0.021	ID			ID
(*Molothrus bonariensis*)	SE				0.005	ID			ID
Smooth-billed Ani	Beta	0.014				0.048	ID		ID
(*Crotophaga ani*)	SE	0.005				0.016	ID		ID
Spectacled Thrush	Beta	0.008	−0.015	0.022	0.008				ID
(*Turdus nudigenis*)	SE	0.005	0.005	0.004	0.002				ID
Tropical Mockingbird	Beta	−0.010	−0.042	−0.026				0.008	ID
(*Mimus gilvus*)	SE	0.002	0.009	0.010				0.004	ID

Table 4. Comparisons of relative density of all land bird species that we had sufficient data to study, per 25-m radius plot between Grenada and other islands, in 2017. Significant positive parameter estimates (abundances are higher on Grenada) are bold, significant negative parameter estimates are not bold, and non-significant differences are not shown ($p > 0.05$). ID = insufficient data. NP = Not present. All response variables were modeled using a Poisson distribution. Scientific names for species are in Appendix 2.

Feeding Guilds of Species	Statistical Parameter	Carriacou	Petite Martinique	Ronde Island	Caille Island
Carnivores					
Broad-winged Hawk	Beta	NP	NP	NP	NP
(*Buteo platypterus*)	SE	NP	NP	NP	NP
Frugivores					
Scaly-naped Pigeon	Beta	**1.968**	**1.438**		ID
(*Patagioenas squamosa*)	SE	**0.101**	**0.128**		ID
Zenaida Dove	Beta			NP	NP
(*Zenaida aurita*)	SE			NP	NP
Granivores					
Black-faced Grassquit	Beta	**0.500**	**1.204**	NP	NP
(*Melanospiza bicolor*)	SE	**0.188**	**0.217**	NP	NP
Eared Dove	Beta			NP	NP
(*Zenaida auriculata*)	SE			NP	NP
Yellow-bellied Seedeater	Beta	NP	NP	−2.915	NP
(*Sporophila nigricollis*)	SE	NP	NP	0.949	NP
Insectivores					
Cattle Egret	Beta	−3.279	NP	NP	NP
(*Bubulcus ibis*)	SE	0.600	NP	NP	NP
Gray-rumped Swift	Beta	−0.759	NP	**2.189**	NP
(*Chaetura cinereiventris*)	SE	0.207	NP	**0.205**	NP
Nectarivores					
Antillean Crested Hummingbird	Beta		**0.692**	**0.481**	**0.670**
(*Orthorhyncus cristatus*)	SE		**0.229**	**0.239**	**0.314**
Bananaquit	Beta	**0.348**			**0.523**
(*Coereba flaveola*)	SE	**0.082**			**0.152**
Rufous-breasted Hermit	Beta	NP	NP	NP	NP
(*Glaucis hirsutus*)	SE	NP	NP	NP	NP

ings. Lesser Antillean Bullfinches and Lesser Antillean Tanagers had higher densities in sites with more farmlands and residential building sites, whereas Lesser Antillean Tanagers had lower abundances in sites with more commercial buildings (Table 3). Lesser Antillean Tanagers also had higher densities in sites that were more agricultural with higher proportions of nutmeg trees.

Discussion

In Grenada, anthropogenic cultivated and secondary grasslands had higher densities of most species, while cloud and secondary forests had lower densities of most species except some species of conservation concern, such as the regionally endemic Lesser Antillean Tanager and Grenada Flycatcher. Our findings that many anthropogenic habitats on Grenada are favored by avian species are in contrast with results from continental studies that have generally shown habitats with less anthropogenic disturbance support greater avian abundance and richness (McKinney *et al.* 2010, Ntongani and Andrew 2013, Kang *et al.* 2015, Simon and Okoth 2016; but see Lepczyk *et al.* 2008). Although many anthropogenic habitats were favored on Grenada, we found specific feeding guilds, including nectarivores and granivores, tended to avoid urban habitats. This is also in contrast with results from continental studies that have shown urban habitats support higher abundances of nectarivores and granivores (Davis *et al.* 2012, Davis *et al.* 2015). Thus, our study demonstrates that factors influencing avian diversity on a tropical developing island are different than in more continental habitats, and therefore tropical developing island habitats should

Table 4. cont.

Feeding Guilds of Species	Statistical Parameter	Carriacou	Petite Martinique	Ronde Island	Caille Island
Omnivores					
Carib Grackle	Beta	**0.397**		−0.835	−1.238
(*Quiscalus lugubris*)	SE	**0.171**		0.264	0.442
Gray Kingbird	Beta	−0.548		−1.507	NP
(*Tyrannus dominicensis*)	SE	0.142		0.288	NP
Lesser Antillean Bullfinch	Beta	NP	NP	NP	NP
(*Loxigilla noctis*)	SE	NP	NP	NP	NP
Lesser Antillean Tanager	Beta	NP	NP	NP	NP
(*Stilpnia cucullata*)	SE	NP	NP	NP	NP
Shiny Cowbird	Beta	−2.838	−1.145	NP	NP
(*Molothrus bonariensis*)	SE	0.505	0.505	NP	NP
Smooth-billed Ani	Beta	NP	NP	**1.885**	NP
(*Crotophaga ani*)	SE	NP	NP	**0.713**	NP
Spectacled Thrush	Beta	NP	NP	−3.786	NP
(*Turdus nudigenis*)	SE	NP	NP	0.878	NP
Tropical Mockingbird	Beta	**0.833**		**0.547**	**0.481**
(*Mimus gilvus*)	SE	**0.096**		**0.133**	**0.173**

be considered in the conservation of avian communities across those regions.

As cloud forests have relatively low tree diversity and lower abundances of fruit and flower resources than some lower-elevation habitats (NK pers. obs.), this may account for the lower diversity of bird species seen in our study. Despite their low avian diversity, cloud and secondary forests are important habitats for both the regionally endemic Lesser Antillean Tanager and the Grenada Flycatcher, respectively, and all nectarivores in our study. Our results are consistent with a recent study on Grenada that found higher abundance of Lesser Antillean Tanagers in high elevation forests (Devenish-Nelson and Nelson 2021). Similarly, cloud forests are crucial for conserving endemic birds on Puerto Rico (Acevedo and Restrepo 2008) and amphibians, reptiles, plants, and mammals in Mexico (Almazán-Núñez *et al.* 2018), and secondary forests are important for conserving frogs in Costa Rica (Hilje and Aide 2012).

Higher abundances of certain species in agricultural habitats may also result from an abundance of food resources in farmlands and gardens (defined as plant-dominated cultivated lands closely associated with dwellings) that attract generalist species (Piha *et al.* 2007). Our findings shows that the Lesser Antillean Tanager and Lesser Antillean Bullfinch (restricted range species) were observed in farmlands, as were more widely distributed species, which may be because of the wide availability of resources that may meet the needs of a variety of species. Indeed, one vitally important factor that influences avian species' habitat selection is an abundance of food resources (Schlacher *et al.* 2014, Wolfe *et al.* 2014). For example, avian species likely benefit from an abundance of food resources in low-intensity farmlands (Doxa *et al.* 2010) and agroforestry systems (Schroth *et al.* 2013). Likewise, in Grenada most farming is small-scale, cultivates several species, and is organic (Brierley 1985, Graham 2012), which may support high abundances and diversity of plants and invertebrates (Piha *et al.* 2007). Organic farming, like the type conducted in Grenada on a much smaller scale, is known to support significantly higher abundances and richness of avian species in Europe and Canada compared to the conventional farming across those regions (Christensen *et al.* 1996, Freemark and Kirk 2001). Our results are consistent with past literature that found agroforestry systems containing cocoa habitats provide suitable habitats for an abundance of avian species (Greenberg *et al.* 2000, Reitsma *et al.* 2001, Harvey and Villalobos 2007, Madden and van Zanten 2020). In fact, agroforestry systems have long been recognized for providing habitat for tropical and Caribbean birds (Wetmore 1916, Griscom 1932, Wunderle Jr. and Latta 1996, Arnold *et al.* 2021).

Different ecosystems including mature lowland, mangrove, and secondary scrub were also selected by several Grenadian species, such as the endemic Grenada Flycatcher. Recent surveys on Grenada also found higher densities of the endemic Grenada Flycatcher in lowland habitats (Koper and Grieef 2016, Devenish-Nelson and Nelson 2021), thus demonstrating that mature lowlands are critical habitat for this species. Our results are consistent with other studies that found that both mangrove and mature lowland forests are essential habitat for some specialist species (Round and Brockelman 1998, Nagelkerken *et al.* 2008, Joseph 2020).

Despite the association between abundance of food resources in urban gardens and nectarivore presence (van Heezik *et al.*

Table 5. DOBSERV models used for calculating habitat specific perceptibility (Nichols *et al.* 2000). Only models with delta AIC values < 7 were selected for perceptibility analyses (Wagenmakers and Farrell 2004, Richard 2005, Mazerolle 2006).

	All habitats		Forested habitat		Cultivated habitat		Urban habitat		Open Area	
Model i	**AIC**	**Delta AIC**	**AIC**	**Delta AIC**	**AIC**	**Delta AIC**	**AIC**	**Delta AIC**	**AIC**	**Delta AIC**
P(S,I)	227.09	0	209.51	2.10	187.32	6.35	259.65	0	110.53	0
P(.,I)	295.27	68.18	207.41	0	180.97	0	270.58	10.93	153.76	43.23
P(G,I)	295.27	68.18	207.41	0	180.97	0	270.58	10.93	153.76	43.23
P(S,.)	347.47	120.38	247.89	40.48	190.22	9.25	328.05	68.40	145.13	34.60
P(G,.)	362.27	135.18	252.25	44.84	192.83	11.86	337.06	77.41	175.38	64.85
P(.,.)	362.27	135.18	252.25	44.84	192.83	11.86	337.06	77.41	175.38	64.85

The different models that we ran were as follow: [1] P(.,.): detection probability = same for all observers, species, or groups; [2] P(.,I): detection probability = differs by observer, but same for all species or groups; [3] P(S,.): detection probability = differs by species, but same for all observers; [4] P(G,.): detection probability = differs by group, but same for all observers; [5] P(S,I): detection probability = differs between observers and by species; and [6] P(G,I): detection probability = differs between observers and by groups. Each species or feeding guild had at least 10 individuals, which is the minimum number of individuals required for analyses in DOBSERV (Nichols *et al.* 2000). Delta AIC = AICi – min AIC; where min AIC is the AIC value of the "best" model, and AICi is the AIC value for model i (Richard 2005, Mazerolle 2006).

Table 6. DOBSERV models used for calculating perceptibility (Nichols *et al.* 2000). Only models with delta AIC values <7 were selected for perceptibility analyses (Wagenmakers *et al.* 2004, Richard 2005, Mazerolle 2006).

Model i	AIC	Delta AIC
P(S,I)	273.12	0
P(.,I)	292.96	19.84
P(G,I)	292.96	19.84
P(S,.)	344.78	71.66
P(G,.)	359.96	86.84
P(.,.)	359.96	86.84

The different models that we ran were as follow: [1] P(.,.): detection probability = same for all observers, species, or groups; [2] P(.,I): detection probability = differs by observer, but same for all species or groups; [3] P(S,.): detection probability = differs by species, but same for all observers; [4] P(G,.): detection probability = differs by group, but same for all observers; [5] P(S,I): detection probability = differs between observers and by species; and [6] P(G,I): detection probability = differs between observers and by groups. Each species, or feeding guild had at least 10 individuals, which is the minimum number of individuals required for analyses in DOBSERV (Nichols *et al.* 2000). Delta AIC = AICi – min AIC, where min AIC is the AIC value of the "best" model, and AICi is the AIC value for model i (Richard 2005, Mazerolle 2006).

2013), all nectarivorous species significantly avoided anthropogenic habitats with residential buildings, airport facilities, or commercial buildings. This contrasts with some previous studies that found hummingbird species positively responded to fragmentation in the Brazilian Amazon (Stouffer and Bierregaard 1995) and urbanization in Mexico (Escobar-Ibáñez and MacGregor-Fors 2015), perhaps because of an abundance of cultivated flowering plants in urban areas. However, in Grenada cultivated flowering plants may differ in species and abundance compared to the Brazilian Amazon and Mexico, demonstrating that as a Small Island Developing State, Grenada may have unique pressures and urban ecosystems compared with larger mainland regions, emphasizing the importance of conducting more research in these regions.

In contrast, Shiny Cowbirds, a brood parasite generalist, had higher abundances in sites with residential development. Higher intensities of residential and industrial development and deforestation on Grenada have created marginal edge habitat, which may explain the higher abundances of Shiny Cowbirds on Grenada than on Carriacou and Petite Martinique. Higher densities of Shiny Cowbirds on Grenada may negatively impact Grenada's terrestrial avifauna as Shiny Cowbirds are brood parasites well-known for reducing species' reproductive success by destroying their host's eggs or killing their host's hatchlings before laying their eggs in their host's nests (Dominguez *et al.* 2015). Our finding is consistent with a previous study that found residential habitats were suitable for Shiny Cowbirds on Grenada (Wunderle Jr. 1985).

The occupation of disturbed habitats by many species in Grenada is in contrast to other studies in temperate, continental habitats that found a decline in avian biodiversity with disturbance (Elsen *et al.* 2017). However, species living on tropical islands face different selective pressures, such that understanding the effects of anthropogenic disturbance on tropical island species require research in-situ rather than extrapolating expected effects from research conducted in temperate zones. Other tropical biodiversity studies have found a positive association between anthropogenically disturbed habitats and agroforestry systems and avian diversity, as also seen in our study. For example, Hernandez (2016) found agroforestry systems combined with protected reserves to be important habitat for avian biodiversity conservation on Hispaniola. Similarly, our results demonstrate the importance of agroforestry systems interspersed with natural and semi-natural habitats to the bird communities of Grenada. Agroforestry can play a vital role in biodiversity conservation (Harvey and Villalobos 2007, Jose 2009, Schroth *et al.*

2013), at least within low-intensity agricultural systems such as those that dominate Grenada's anthropogenically modified landscapes. Our results suggest, therefore, that a mosaic of natural and anthropogenic habitats is needed to conserve biodiversity on Grenada properly, but that further urbanization should be limited to maintain species diversity. However, understanding the factors driving different biodiversity patterns among species and habitat types is nuanced and requires further research.

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Appendix 1. Average density of land birds per plot across all surveyed islands (Grenada, Carriacou, Petite Martinique, Caille Island, Ronde Island) in 2017. Mean = average among islands. AM = density of species surveyed in the morning (dawn to 10:00). PM = density of species surveyed in the evening (16:30 until dusk). ID = insufficient data.

Species	Statistical Parameter	Grenada	Carriacou	Petite Martinique	Caille Island	Ronde Island	Mean	AM	PM
Antillean Crested Hummingbird	Density	1.206	1.360	2.076	1.993	1.709	1.309	1.385	1.185
(*Orthorhyncus cristatus*)	SD	1.579	1.715	2.566	1.004	2.225	1.689	1.631	1.777
Bananaquit	Density	4.797	7.007	4.153	8.307	5.186	5.266	5.030	5.650
(*Coereba flaveola*)	SD	3.515	5.575	3.965	4.777	3.597	4.109	3.715	4.665
Black-faced Grassquit	Density	0.979	1.517	3.074	ID	ID	1.165	1.318	0.931
(*Melanospiza bicolor*)	SD	1.460	2.127	3.148	ID	ID	1.749	1.838	1.580
Broad-winged Hawk	Density	0.185	ID	ID	ID	ID	0.185	0.237	0.092
(*Buteo platypterus*)	SD	0.541	ID	ID	ID	ID	0.541	0.623	0.337
Carib Grackle	Density	0.367	2.418	1.412	0.807	1.268	0.843	0.865	0.809
(*Quiscalus lugubris*)	SD	1.084	2.837	1.455	1.254	1.987	1.804	1.831	1.765
Cattle Egret	Density	0.358	0.037	ID	ID	ID	0.291	0.325	0.224
(*Bubulcus ibis*)	SD	1.811	0.250	ID	ID	ID	1.621	1.777	1.349
Eared Dove	Density	0.647	1.530	1.586	ID	ID	0.859	0.765	1.001
(*Zenaida auriculata*)	SD	1.737	3.412	1.851	ID	ID	2.206	1.946	2.551
Gray Kingbird	Density	1.965	1.351	2.093	ID	0.555	1.768	1.784	1.742
(*Tyrannus dominicensis*)	SD	2.258	1.925	2.072	ID	1.437	2.180	2.062	2.366
Gray-rumped Swift	Density	0.493	0.563	ID	ID	6.968	0.921	0.570	1.501
(*Chaetura cinereiventris*)	SD	1.898	3.657	ID	ID	18.208	5.313	2.076	8.217
Grenada Flycatcher	Density	0.291	0.124	ID	ID	ID	0.026	0.220	0.312
(*Myiarchus nugator*)	SD	0.792	0.510	ID	ID	ID	0.745	0.639	0.883
House Wren	Density	0.706	0.012	ID	ID	ID	0.562	0.668	0.398
(*Troglodytes aedon*)	SD	1.247	0.112	ID	ID	ID	1.146	1.293	0.849
Lesser Antillean Bullfinch	Density	1.263	ID	ID	ID	ID	1.263	1.034	1.664
(*Loxigilla noctis*)	SD	2.017	ID	ID	ID	ID	2.017	1.637	2.509
Lesser Antillean Tanager	Density	0.623	ID	ID	ID	ID	6.228	0.625	0.618
(*Stilpnia cucullata*)	SD	1.046	ID	ID	ID	ID	1.046	1.026	1.084
Rufous-breasted Hermit	Density	0.294	ID	ID	ID	ID	0.294	0.383	0.137
(*Glaucis hirsutus*)	SD	0.874	ID	ID	ID	ID	0.874	1.016	0.507

Appendix 1 cont.

Species	Statistical Parameter	Grenada	Carriacou	Petite Martinique	Caille Island	Ronde Island	Mean	AM	PM
Scaly-naped Pigeon	Density	3.302	15.294	9.028	ID	1.277	5.624	4.641	7.220
(*Patagioenas squamosa*)	SD	7.546	16.748	7.618	ID	4.185	10.895	9.166	13.105
Shiny Cowbird	Density	0.340	0.056	0.300	ID	ID	0.282	0.388	0.121
(*Molothrus bonariensis*)	SD	1.067	0.521	0.930	ID	ID	0.982	1.177	0.534
Smooth-billed Ani	Density	0.169	ID	ID	ID	0.298	0.179	0.155	0.225
(*Crotophaga ani*)	SD	0.612	ID	ID	ID	1.576	0.733	0.770	0.656
Spectacled Thrush	Density	2.564	ID	ID	ID	0.047	2.364	2.122	2.823
(*Turdus nudigenis*)	SD	2.558	ID	ID	ID	0.250	2.548	2.353	2.834
Tropical Mockingbird	Density	1.934	8.691	4.661	7.251	4.661	3.692	3.282	4.359
(*Mimus gilvus*)	SD	2.617	9.675	2.817	6.018	5.883	5.714	4.183	7.536
Yellow-bellied Seedeater	Density	0.352	ID	ID	ID	0.044	0.328	0.346	0.296
(*Sporophila nigricollis*)	SD	0.893	ID	ID	ID	0.233	0.863	0.914	0.760
Zenaida Dove	Density	0.231	0.480	0.329	ID	ID	0.284	0.251	0.335
(*Zenaida aurita*)	SD	0.658	0.927	0.760	ID	ID	0.728	0.656	0.083

Appendix 2. Single observer compared to double observer perceptibility of focal species on Grenada in 2017.

Species	Single Observer	SE	95% CI lower	95% CI upper	Double Observer	SE	95% CI lower	95% CI upper
Antillean Crested Hummingbird (*Orthorhyncus cristatus*)	0.75	0.045	0.66	0.84	0.91	0.025	0.87	0.96
Bananaquit (*Coereba flaveola*)	0.81	0.021	0.77	0.85	0.94	0.010	0.92	0.96
Black-faced Grassquit (*Melanospiza bicolor*)	0.91	0.028	0.86	0.97	0.98	0.010	0.96	0.99
Blue-black Grassquit (*Volatinia jacarina*)	0.83	0.108	0.62	1.04	1.00	0.067	0.87	1.13
Blue-throated Macaw (*Ara glaucogularis*)	0.83	0.108	0.62	1.04	1.00	0.067	0.87	1.13
Broad-winged Hawk (*Buteo platypterus*)	0.92	0.063	0.71	0.96	1.00	0.041	0.92	1.08
Carib Grackle (*Quiscalus lugubris*)	0.93	0.036	0.89	1.03	0.99	0.013	0.96	1.01
Caribbean Elaenia (*Elaenia martinica*)	1.00	<0.0001	1.00	1.00	1.00	0.333	0.35	1.65
Cattle Egret (*Bubulcus ibis*)	0.96	0.036	0.89	1.03	0.99	0.013	0.96	1.01
Common Ground Dove (*Columbina passerina*)	0.58	0.136	0.31	0.85	0.77	0.120	0.54	1.01
Eared Dove (*Zenaida auriculata*)	0.95	0.031	0.89	1.01	0.99	0.009	0.97	1.00
Fork-tailed Flycatcher (*Tyrannus savana*)	0.83	0.108	0.62	1.04	1.00	0.067	0.87	1.13
Gray Kingbird (*Tyrannus dominicensis*)	0.84	0.037	0.76	0.91	0.97	0.013	0.94	0.99
Gray-rumped Swift (*Chaetura cinereiventris*)	0.84	0.063	0.71	0.96	0.98	0.013	0.96	1.01
Green-throated Carib (*Eulampis holosericeus*)	0.83	0.108	0.62	1.04	1.00	0.067	0.87	1.13
Grenada Dove (*Leptotila wellsi*)	0.83	0.108	0.62	1.04	1.00	0.067	0.87	1.13
Grenada Flycatcher (*Myiarchus nugator*)	0.86	0.098	0.66	1.05	0.97	0.032	0.91	1.03
House Wren (*Troglodytes aedon*)	0.97	0.031	0.91	1.03	1.00	0.005	0.99	1.01
Lesser Antillean Bullfinch (*Loxigilla noctis*)	0.85	0.051	0.75	0.94	0.94	0.025	0.90	0.99
Lesser Antillean Tanager (*Stilpnia cucullata*)	0.97	0.027	0.92	1.03	1.00	0.005	0.99	1.00
Mangrove Cuckoo (*Coccyzus minor*)	0.57	0.258	0.07	1.08	0.73	0.248	0.24	1.21
Orange-winged Parrot (*Amazona amazonica*)	1.00	<0.0001	1.00	1.00	1.00	0.000	1.00	1.00
Rufous-breasted Hermit (*Glaucis hirsutus*)	0.81	0.083	0.64	0.97	0.95	0.035	0.88	1.02
Scaly-naped Pigeon (*Patagioenas squamosa*)	0.73	0.037	0.65	0.80	0.93	0.017	0.90	0.97
Shiny Cowbird (*Molothrus bonariensis*)	0.83	0.072	0.69	0.97	0.96	0.027	0.91	1.02

Appendix 2 cont.

Species	Single Observer	SE	95% CI lower	95% CI upper	Double Observer	SE	95% CI lower	95% CI upper
Smooth-billed Ani (*Crotophaga ani*)	0.84	0.153	0.54	1.14	0.96	0.055	0.85	1.07
Spectacled Thrush (*Turdus nudigenis*)	0.75	0.061	0.64	0.87	0.90	0.039	0.82	0.97
Tropical Mockingbird (*Mimus gilvus*)	0.84	0.024	0.80	0.89	0.98	0.007	0.96	0.99
Yellow-bellied Elaenia (*Elaenia flavogaster*)	0.93	0.067	0.80	1.06	0.98	0.021	0.94	1.02
Yellow-bellied Seedeater (*Sporophila nigricollis*)	0.81	0.077	0.66	0.96	0.99	0.012	0.96	1.01
Zenaida Dove (*Zenaida aurita*)	0.76	0.158	0.45	1.07	0.95	0.068	0.82	1.08
Mean	0.84				0.96			
SD	0.10				0.06			
SE	0.02				0.01			

Appendix 3. Comparison of habitat-specific double observer perceptibility of focal species on Grenada in 2017. ID = insufficient data. ^{A} = Mean among habitats. ^{B} = Standard deviation of means among habitats.

	Forested				Urban				Cultivated				Open Area				All Habitats	
Species	Double observer	SE	95% CI lower	95% CI upper	Double observer	SE	95% CI lower	95% CI upper	Double observer	SE	95% CI lower	95% CI upper	Double observer	SE	95% CI lower	95% CI upper	Mean^A	SD^B
Antillean Crested Hummingbird (*Orthorhyncus cristatus*)	0.90	0.03	0.85	0.96	0.91	0.03	0.85	0.96	0.89	0.04	0.82	0.97	0.90	0.03	0.85	0.96	0.90	0.01
Bananaquit (*Coereba flaveola*)	0.92	0.02	0.89	0.95	0.94	0.01	0.92	0.96	0.94	0.02	0.90	0.97	0.95	0.03	0.89	1.00	0.94	0.01
Black-faced Grassquit (*Melanospiza bicolor*)	0.98	0.02	0.93	1.00	0.98	0.01	0.96	1.00	0.98	0.01	0.96	1.00	0.93	0.05	0.84	1.00	0.97	0.02
Broad-winged Hawk (*Buteo platypterus*)	0.96	0.03	0.90	1.00	0.95	0.04	0.87	1.00	0.96	0.03	0.89	1.00	ID	ID	ID	ID	0.96	0.01
Carib Grackle (*Quiscalus lugubris*)	0.97	0.03	0.91	1.00	0.97	0.02	0.93	1.00	0.95	0.09	0.78	1.00	0.98	0.02	0.93	1.00	0.97	0.01
Cattle Egret (*Bubulcus ibis*)	0.99	0.02	0.95	1.00	0.99	0.01	0.97	1.00	0.96	0.03	0.89	1.00	1.00	0.02	0.96	1.00	0.98	0.02
Eared Dove (*Zenaida auriculata*)	1.00	0.06	0.88	1.00	0.99	0.01	0.97	1.00	0.99	0.01	0.97	1.00	1.00	0.00	1.00	1.00	0.99	0.01
Gray Kingbird (*Tyrannus dominicensis*)	0.97	0.02	0.94	1.00	0.97	0.01	0.94	0.99	0.92	0.04	0.85	1.00	1.00	0.01	0.98	1.00	0.96	0.03
Gray-rumped Swift (*Chaetura cinereiventris*)	0.99	0.01	0.97	1.00	0.98	0.01	0.96	1.00	0.99	0.01	0.98	1.00	1.00	0.00	1.00	1.00	0.99	0.01
Grenada Flycatcher (*Myiarchus nugator*)	0.98	0.03	0.91	1.00	0.97	0.03	0.92	1.00	0.95	0.05	0.85	1.00	ID	ID	ID	ID	0.97	0.01
House Wren (*Troglodytes aedon*)	0.99	0.01	0.98	1.00	0.99	0.01	0.98	1.00	0.99	0.01	0.98	1.00	0.93	0.05	0.83	1.00	0.98	0.03
Lesser Antillean Bullfinch (*Loxigilla noctis*)	0.95	0.03	0.89	1.00	0.90	0.05	0.81	1.00	0.95	0.02	0.90	1.00	0.97	0.04	0.90	1.00	0.94	0.03
Lesser Antillean Tanager (*Stilpnia cucullata*)	1.00	0.05	0.90	1.00	0.99	0.01	0.98	1.00	0.99	0.01	0.97	1.00	ID	ID	ID	ID	1.00	0.004
Rufous-breasted Hermit (*Glaucis hirsutus*)	0.93	0.05	0.83	1.00	0.96	0.03	0.91	1.00	0.98	0.02	0.95	1.00	ID	ID	ID	ID	0.96	0.02

Appendix 3 cont.

	Forested				Urban				Cultivated				Open Area				All Habitats	
Species	**Double observer**	**SE**	**95% CI lower**	**95% CI upper**	**Double observer**	**SE**	**95% CI lower**	**95% CI upper**	**Double observer**	**SE**	**95% CI lower**	**95% CI upper**	**Double observer**	**SE**	**95% CI lower**	**95% CI upper**	**Mean**	**SD of means**
Scaly-naped Pigeon (*Patagioenas squamosa*)	0.95	0.01	0.93	0.98	0.93	0.02	0.89	0.97	0.91	0.04	0.84	0.98	0.92	0.03	0.85	0.99	0.93	0.02
Shiny Cowbird (*Molothrus bonariensis*)	0.98	0.02	0.93	1.00	0.97	0.02	0.92	1.00	0.96	0.04	0.89	1.00	0.93	0.05	0.83	1.00	0.96	0.02
Smooth-billed Ani (*Crotophaga ani*)	0.96	0.03	0.90	1.00	0.95	0.04	0.87	1.02	0.96	0.03	0.89	1.00	ID	ID	ID	ID	0.96	0.01
Spectacled Thrush (*Turdus nudigenis*)	0.92	0.05	0.83	1.00	0.91	0.03	0.84	0.97	0.92	0.04	0.85	0.99	0.93	0.05	0.83	1.00	0.92	0.01
Tropical Mockingbird (*Mimus gilvus*)	0.99	0.01	0.97	1.00	0.97	0.01	0.95	0.98	0.99	0.01	0.97	1.00	0.96	0.02	0.91	1.00	0.97	0.01
Yellow-bellied Seedeater (*Sporophila nigricollis*)	0.96	0.05	0.86	1.00	0.97	0.02	0.93	1.00	0.99	0.01	0.97	1.00	ID	ID	ID	ID	0.97	0.02
Zenaida Dove (*Zenaida aurita*)	0.96	0.03	0.90	1.00	0.97	0.04	0.89	1.00	ID	ID	ID	ID	ID	ID	ID	ID	0.97	0.005
Mean	0.96				0.96				0.96				0.96					
SD of means	0.03				0.03				0.03				0.03					