Journal of Caribbean Ornithology

RESEARCH ARTICLE

Vol. 34:88–98. 2021

Abundance and density estimates of landbirds on Grenada

Eleanor S. Devenish-Nelson   Howard P. Nelson

Photo: Howard Nelson

BirdsCaribbean

Journal of Caribbean Ornithology
jco.birdscaribbean.org ISSN 1544-4953 https://doi.org/10.55431/ jco.2021.34.88-98
RESEARCH ARTICLE Vol. 34:88–98. 2021
BirdsCaribbean
birdscaribbean.org

Abundance and density estimates of landbirds on Grenada

Eleanor S. Devenish-Nelson[*1] and Howard P. Nelson[2,3]

Abstract Throughout the Caribbean, resident landbirds have been subject to proportionately limited research compared to migrant species. In Grenada in particular, there is uncertainty about the status of several regional endemics, including the Grenada Flycatcher (*Myiarchus nugator*) and the Lesser Antillean Tanager (*Stilpnia cucullata*). We conducted distance sampling point counts (n = 199) in forested and agricultural habitats across Grenada in 2018 and 2019 to estimate the distribution and relative abundance of resident bird species (n = 1,235 detections). For species with more than 30 observations, we estimated species density using hierarchical distance models, including site-specific habitat covariates of land cover and elevation. We detected over 90% (n = 32) of the previously recorded landbird species during our surveys. Species turnover was low compared to a similar survey conducted in the 1980s, with a difference of four species between the two studies. These differences could be attributed to recent introductions, seasonality, sampling intensity, or other methodological differences between these studies. We had sufficient observations to estimate density for nine resident species, including the endemic Antillean Crested Hummingbird (*Orthorhyncus cristatus*; 1.68 ind./ha), Lesser Antillean Tanager (1.02 ind./ha), Lesser Antillean Bullfinch (*Loxigilla noctis*; 0.73 ind./ha), and Grenada Flycatcher (0.59 ind./ha). Our results provide an important baseline for future monitoring and conservation work, including monitoring the impacts of climate change, provision of ecosystem services, or land use change.

Keywords avian conservation, Caribbean, distance sampling, endemic, habitat use, hierarchical population model, population density, species turnover

Resumen Estimaciones de abundancia y densidad de aves terrestres en Granada • En todo el Caribe, las aves terrestres residentes han sido objeto de investigaciones relativamente más limitadas que las especies migratorias. En Granada, en particular, existen dudas sobre el estado de varias especies endémicas regionales, como *Myiarchus nugator* y *Stilpnia cucullata*. En 2018 y 2019 llevamos a cabo puntos de conteo con muestreo de distancia (n = 199) en hábitats boscosos y agrícolas de toda Granada para estimar la distribución y la abundancia relativa de las especies de aves residentes (n = 1.235 detecciones). Para las especies con más de 30 observaciones, estimamos la densidad utilizando modelos de distancia jerárquica, que incluyeron covariables de hábitat sitio específicas de la cobertura del suelo y la elevación. Durante nuestros muestreos detectamos más del 90% (n = 32) de las especies de aves terrestres registradas previamente. El recambio de especies fue bajo en comparación con un estudio similar realizado en la década de 1980, con una diferencia de cuatro especies entre ambos. Estas diferencias podrían atribuirse a introducciones recientes, estacionalidad, intensidad de muestreo u otras diferencias metodológicas. Recopilamos suficientes observaciones para estimar la densidad de nueve especies residentes, incluyendo el endémico *Orthorhyncus cristatus* (1,68 ind./ha), *Stilpnia cucullata* (1,02 ind./ha), *Loxigilla noctis* (0,73 ind./ha) y *Myiarchus nugator* (0,59 ind./ha). Nuestros resultados proporcionan una línea base importante para futuros trabajos de monitoreo y conservación, incluido el seguimiento de los impactos del cambio climático, la prestación de servicios ecosistémicos o el cambio de uso del suelo.

Palabras clave Caribe, conservación de aves, densidad poblacional, endémico, modelo jerárquico de población, muestreo de distancia, recambio de especies, uso del hábitat

Résumé Estimation de l'abondance et de la densité des oiseaux terrestres sur l'île de la Grenade • Dans l'ensemble de la Caraïbe, les oiseaux terrestres sédentaires ont fait l'objet de recherches relativement plus limitées que les espèces migratrices. En particulier sur l'île de la Grenade, il existe une incertitude quant au statut de plusieurs espèces endémiques régionales, notamment le Tyran bavard (*Myiarchus nugator*) et le Caliste dos-bleu (*Stilpnia cucullata*). Nous avons réalisé des dénombrements ponctuels par distance sampling (n = 199) dans des habitats forestiers et agricoles à travers la Grenade en 2018 et 2019 pour estimer la répartition et l'abondance relative des espèces d'oiseaux sédentaires (n = 1235 détections). Pour les espèces ayant fait l'objet de plus de 30 observations, nous avons estimé la densité spécifique à l'aide de modèles de distance hiérarchiques, incluant les covariables d'habitat propres au site que sont la couverture végétale et l'altitude. Nous avons détecté plus de 90 % (n = 32) des espèces d'oiseaux terrestres précédemment enregistrées au cours de nos comptages. Le renouvellement des espèces était faible par rapport à un dénombrement

*Corresponding author: [1]Department of Biomedical Sciences, University of Edinburgh, Teviot Place, Edinburgh, EH8 9AG, UK; e-mail: ellie.devenish@ed.ac.uk. Full list of author information is available at the end of the article.

similaire réalisé dans les années 1980, avec une différence de quatre espèces entre les deux études. Cette variation pourrait être attribuée à des introductions récentes, à la saisonnalité, à l'intensité de l'échantillonnage ou à d'autres différences méthodologiques entre ces comptages. Nous avons fait suffisamment d'observations pour estimer la densité de neuf espèces sédentaires endémiques, dont le Colibri huppé (*Orthorhyncus cristatus* ; 1,68 ind./ha), le Caliste dos-bleu (1,02 ind./ha), le Sporophile rouge-gorge (*Loxigilla noctis* ; 0,73 ind./ha), et le Tyran bavard (0,59 ind./ha). Nos résultats constituent une base de référence importante pour les futurs travaux de suivi et de conservation, notamment pour les suivis des conséquences du changement climatique, de la fourniture de services écosystémiques ou du changement d'utilisation des terres.

Mots clés Caraïbes, conservation des oiseaux, densité de population, distance sampling, endémisme, modèle hiérarchique de population, renouvellement des espèces, utilisation de l'habitat

The insular Caribbean is a global biodiversity hotspot (Bellard *et al.* 2014) with avian richness that includes over 600 species, one third (approximately 170 species) of which are endemic to this region (Devenish-Nelson *et al.* 2017, Raffaele *et al.* 2020). Despite this diversity and endemism, resident birds have been subject to proportionally little research compared to migratory birds in the region (Latta 2012, Devenish-Nelson *et al.* 2017, Devenish-Nelson *et al.* 2019). Thus, as a group, published data derived from field surveys on the status of these island species remains limited (Devenish-Nelson *et al.* 2017, Devenish-Nelson *et al.* 2019). Inadequate human and financial resources in regional governments and NGOs (Kaiser-Bunbury *et al.* 2015), the accelerating anthropogenic degradation of natural habitats (Portillo-Quintero and Sánchez-Azofeifa 2010, Holdschlag and Ratter 2013), and the threat of climate change (Bellard *et al.* 2014) challenge the systematic collection of field data to inform conservation efforts of these species. In this context, basic science and monitoring is urgently needed to inform management and conservation actions for these Caribbean species and their habitats to ensure their long-term survival.

Approximately 36 resident landbird species inhabit the island of Grenada (Raffaele *et al.* 2020). The avian assemblage of Grenada has been subject to little research, with the exception of studies conducted in the 1980s (Wunderle 1981, Wunderle 1985), those of the Critically Endangered endemic Grenada Dove (*Leptotila wellsi*; Rusk 2017), and a more recent study of anthropogenic habitats (Williams *et al.* In Review). While the status of the Grenada Dove has been well-documented (Rivera-Milán *et al.* 2015, Rusk 2017), other regional endemic species are less well studied. The Grenada Flycatcher (*Myiarchus nugator*) and the Lesser Antillean Tanager (*Stilpnia cucullata*) are regional endemic species found only in Grenada and St. Vincent and the Grenadines (Raffaele *et al.* 2020). Both species are classified as Least Concern according to the IUCN Red List (IUCN 2020). However, the population size of both species remain unquantified and the Grenada Flycatcher population is thought to be declining due to habitat degradation (IUCN 2020). Neither species is considered endangered and they have historically received little attention (Devenish-Nelson *et al.* 2017). Similarly, while the regional endemic Antillean Crested Hummingbird (*Orthorhyncus cristatus*) and Green-throated Carib (*Eulampis holosericeus*) have a wider distribution among the Caribbean islands (Raffaele *et al.* 2020), their population trends remain unknown (IUCN 2020) and very few published ecological studies have examined these species (Devenish-Nelson *et al.* 2017, Devenish-Nelson *et al.* 2019). Although these regional endemics are often considered locally abundant within their range (Raffaele *et al.* 2020), such common species are increasingly at risk of undergoing more rapid declines than rarer species (Julliard *et al.* 2004, Inger *et al.* 2015, Xu *et al.* 2016). In the absence of basic measures of abundance and population size, rapid declines in such species populations (Wintle *et al.* 2010) can go undetected.

The current gaps in knowledge of the resident bird species on Grenada are of particular concern given the vulnerability of the island to climate change and anthropogenic disturbance (Simpson *et al.* 2012). Hurricanes, which can have substantial impacts on birds and their habitats (Wiley and Wunderle 1993), are predicted to increase in intensity due to climate change (Knutson *et al.* 2019). Since the last widespread landbird survey in the 1980s, Grenada has been hit by the Category 3 Hurricane Ivan in 2004 and Category 2 Hurricane Emily in 2005, resulting in extensive damage and habitat destruction (Rusk 2009). The pressures on terrestrial habitats are also increasing, with considerable land use change since the 1980s due to tourism and housing development (Government of Grenada 2016). Such threats present significant challenges for bird conservation given the limited land area of small islands such as Grenada.

Here, we present the results of an island-wide survey of resident terrestrial bird species on Grenada. To our knowledge, there are no recent island-wide published estimates of resident bird species densities or their relationship with forest habitat; therefore, those estimated in our study fill an important gap and establish a baseline for future monitoring and conservation work. We also provide a brief comparison of avian assemblages on Grenada with those from Wunderle's (1985) study.

Methods

Study Location

Grenada (12°07'N, 61°41'W) is the most southerly island of the Lesser Antilles chain in the Caribbean (Fig. 1), with a total land area of 344 km² and maximum elevation of 840 m. The human population (~111,000) is concentrated in urban areas in the south and approximately 23% of the island is currently under forest cover (high elevation, evergreen, semi-evergreen, and deciduous seasonal forest and woodland; Rusk 2009). Natural vegetation ranges from xeric and drought-deciduous forests to evergreen and cloud forests, with seasonal evergreen and semi-deciduous forests having the highest areas of cover

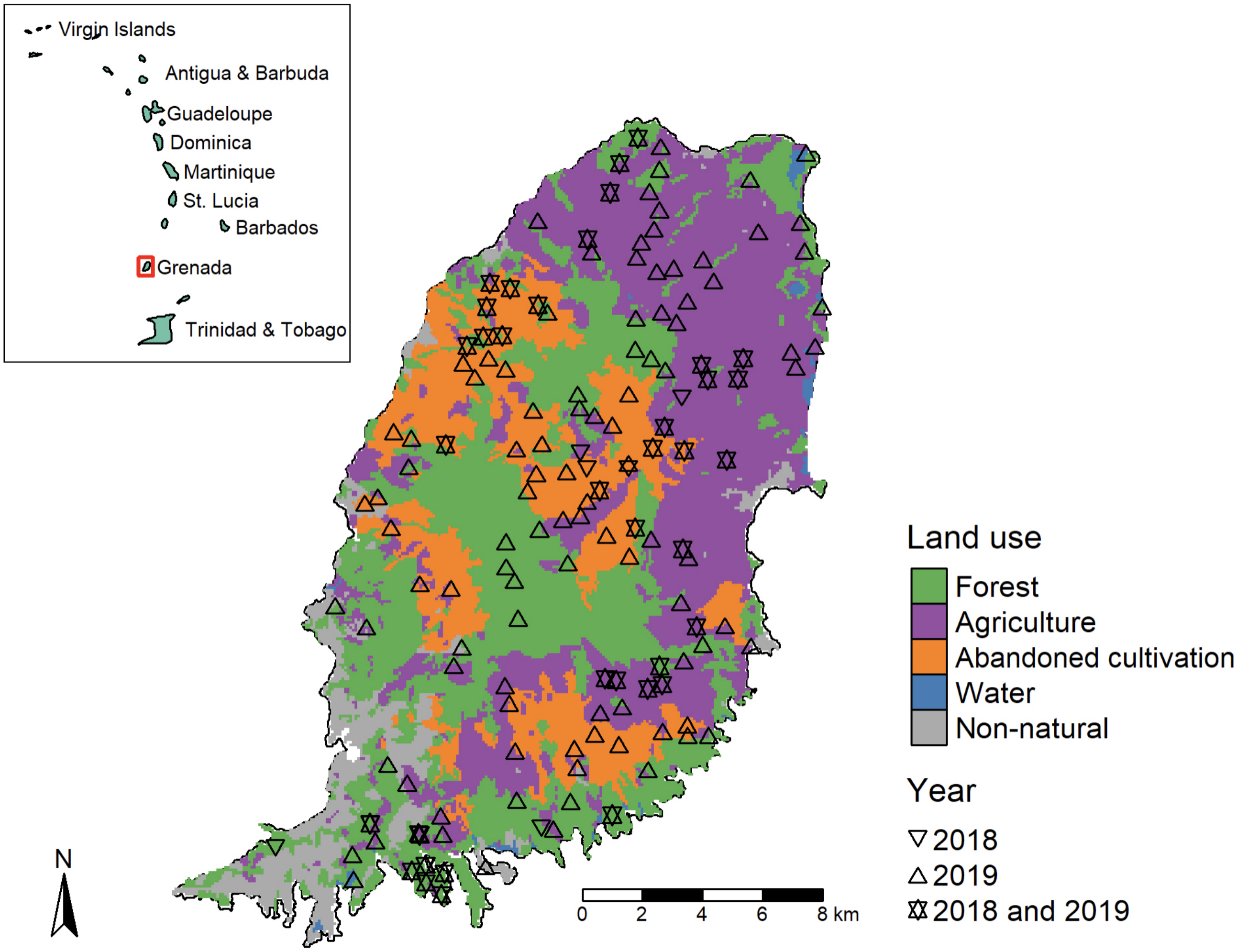

Fig. 1. Map of Grenada showing land use and survey points from 2018 and 2019 (inset shows the position of Grenada in the Lesser Antilles). Source: 2009 land use data (GIS Unit, Ministry of Agriculture, Lands, Forestry and Fisheries, Government of Grenada).

(Helmer *et al.* 2008). Of this forested land, 9% is under formal or informal protection (Helmer *et al.* 2008). Almost 30% of the island is used for mixed woody agriculture, such as nutmeg and cocoa, predominantly at mid-elevations (Helmer *et al.* 2008). The climate is tropical, with a dry (January to May) and rainy season (June to December) and 30-yr annual precipitation cycle estimates ranging from 4,000 mm in the mountains to 1,500 mm in coastal areas (Rusk 2009).

Data Collection

We conducted distance sampling point count surveys (Buckland *et al.* 2001) in forested and agricultural habitats across the island of Grenada to determine the distribution and relative abundance of resident terrestrial bird species. Waterbird and raptor species were recorded but not included in our analyses. We used a 2009 land use map of Grenada (provided by the GIS Unit, Ministry of Agriculture, Lands, Forestry and Fisheries, Government of Grenada) to identify the location of habitat types on the island (excluding residential areas), which we overlaid with a 1-km² systematic grid system in ArcGIS 10.4 (Esri, 80 New York Street, Redlands, California 92373, USA). We randomly sampled survey points within these 1-km² cells, with distances between survey points at a minimum of 500 m to avoid double counting. We chose sample cells to maximize accessibility (e.g., public land, road network) and the number of sites which could be surveyed in a field season. Surveys were conducted in May during the transition period between the end of the dry season and the start of the wet season. We surveyed 52 points between 14 and 24 May 2018, and 147 points between 12 and 29 May 2019, with 38 of these points sampled in both years (Fig. 1). Logistical constraints prevented all survey sites from being sampled twice across both years.

We conducted 10-min unlimited radius point counts at each location between 0600 and 1100 (Lee and Marsden 2008, Matsuoka *et al.* 2014, Rivera-Milán *et al.* 2015). Two observers recorded all birds detected both aurally and visually from a fixed location for a specific time period. During the point counts, we recorded the following parameters for each visual encounter: species, distance from the observer, angle from the observer, and abundance. To avoid double counting individuals, we did not record angle and distance to birds for aural observations, since detectability can be highly influenced by background noise and dense vegetation (Pacifici *et al.* 2008). We estimated site habitat covariates for each location, including elevation (based on a Digital Elevation Model provided by the GIS Unit, Ministry of Agriculture, Lands, Forestry and Fisheries, Government of Grenada) and land cover, determined by the fractional land cover at a 100-m resolution, derived from global remote sensing data downloaded from the Copernicus Global Land Service (Buchhorn *et al.* 2019). Year-site covariates recorded during each point count included date, time of day, rain (presence or absence), and wind speed (continuous).

Data Analysis

We used a chi-square test to compare the relative abundance estimates from our study with those reported from a survey in 1981 by Wunderle (1985). For each study, we defined an index of relative abundance as the sum of each species' presence across all point counts (following Wunderle 1985) and standardized this by the total number of species presences. We treated the index from the Wunderle study as the expected frequencies and that from our study as the observed frequencies. Only species reported during both studies were included in this analysis. For context, Wunderle (1985) conducted 20-min counts in the morning during the wet season in November 1981, recording all species heard or seen within an unlimited radius, with the exception of raptors and waterbirds. His survey consisted of 10 observation periods per habitat, with points at least 100 m apart, and covered nine habitat types (90 counts), defined as secondary grassland, secondary scrub, young secondary forest, old secondary forest, mature lowland forest, cloud forest, savanna, mangrove forests, and residential (Wunderle 1985). With the exception of mangrove forest and residential parklands, our study covered the same habitat types and many similar locations as this 1981 survey. In our analysis, we excluded raptors and waterbirds to be consistent with Wunderle's (1985) survey.

We used hierarchical distance sampling models (Kéry and Royle 2015) to analyse our distance sampling data to determine detectability and density estimates (individuals/ha). We fit density models that account for imperfect detection using the 'gdistsamp' function in the *unmarked* package (Fiske and Chandler 2011) in R 4.0.3 (R Core Team 2020). This model extends generalized distance sampling models (Royle *et al.* 2004) to include variation in abundance and detection as functions of the habitat covariates. We estimated density only for those species with more than 30 visual observations, to avoid uncertainty associated with small sample sizes. Distance data were binned into 10-m intervals and distances were right-truncated at the 95th percentile (Buckland *et al.* 2001). We considered point count stations to be the sampling units and used a 'stacked' data structure that treated each site-year combination as an independent unit, conditional on the explicit habitat variables (Kéry and Royle 2015). By essentially modelling a single season, this structure assumes populations are closed within seasons but open across years. This method is applicable when sample sizes are small or temporal replication is limited and improves computational performance, although it may underestimate some of the variability in abundance (Burnett and Roberts 2015, Fuller *et al.* 2016, Nareff *et al.* 2019, Roberts *et al.* 2019).

We evaluated the fit of both Poisson and negative binomial abundance null models, with half-normal and hazard rate keys for the detection function, using Akaike's Information Criteria (AIC) to determine the most appropriate model structure for each species (Burnham *et al.* 2002). We tested the effect of site and site-year covariates on the detection probability (p) and of habitat covariates on density estimates (λ). We standardized all numeric covariates by rescaling and centering to improve convergence of the optimization algorithm (Kéry and Royle 2015). We tested numeric covariates for collinearity using the Variance Inflation Factor (VIF), excluding those with a VIF > 10 (Dormann *et al.* 2013). We first constructed models of the detection process, keeping λ constant, while exploring how year, Julian date, time of day, and wind affected detection probability. Rain was not included as a covariate due to very low precipitation occurring during the survey. We then explored the influence of the site-specific habitat covariates of land cover and elevation on density estimates. In initial analyses, we included the Copernicus Global Land Service (CGLS) land cover data of cropland cover, herbaceous vegetation, shrubland, and forest cover. However, since CGLS forest cover data had a VIF > 10, we replaced the forest cover layer with data from Global Forest Watch (Hansen *et al.* 2013). This ensured all covariates had a VIF < 2. To avoid overparameterized models, we included a maximum of two covariates in each model to estimate both p and λ, testing each possible combination of covariates.

In the final step, we constructed a candidate set of models for density that included the detection covariates; to avoid overparameterization we included a maximum of one covariate for p and two covariates for λ, testing all possible combinations. We kept availability (Φ) constant for all models. We assessed model fit using AIC and to account for model selection uncertainty, all models with ΔAIC < 6 were considered to be competitive (Richards 2005). We included only detection covariates from detection models with ΔAIC < 6 in the final models. For all competitive models, we assessed their goodness of fit by examining the Freeman–Tukey statistic from a parametric bootstrap approach with 200 simulations (Kéry and Royle 2015) using the 'parboot' function in *unmarked*. We estimated density (individuals/ha) from the most competitive model and estimated confidence intervals with 200 simulations using the 'parboot' function.

Results

We detected a total of 32 terrestrial landbird species (Table 1) across both years of surveys (n = 199 sites), of which 25 species were detected visually (n = 1,167). Most individuals were observed at less than 50 m (mean = 26.8 m, SD = 25.86 m), with a maximum observed distance of 295 m. The most commonly detected species were the Scaly-naped Pigeon (*Patagioenas squamosa*), Bananaquit (*Coereba flaveola*), Gray Kingbird (*Tyrannus dominicensis*), Spectacled Thrush (*Turdus nudigenis*), Lesser Antillean Tanager, and Tropical Mockingbird (*Mimus gilvus*) (Table 1). We recorded all species detected by Wunderle (1985) during our surveys, except for the Blue-black Grassquit (*Volatinia jacarina*). Our study also recorded the Yellow Warbler (*Setophaga petechia*), Antillean Euphonia (*Chlorophonia musica*), and Orange-winged Parrot (*Amazona amazonica*), which were not reported by Wunderle (1985). Notable differences between our observations and those in the earlier study were a higher than expected relative abundance of Gray Kingbird and lower than expected relative abundance of Rufous-breasted Hermit

Table 1. Total number of aural and visual detections of landbirds during point count surveys on Grenada in May 2018 and 2019.

Common Name	Scientific Name	Attribution	Number of Detections
Scaly-naped Pigeon	*Patagioenas squamosa*		386
Common Ground Dove	*Columbina passerina*		45
Ruddy Quail-Dove	*Geotrygon montana*		6
Grenada Dove	*Leptotila wellsi*	island endemic	3
Zenaida Dove	*Zenaida aurita*		47
Eared Dove	*Zenaida auriculata*		43
Smooth-billed Ani	*Crotophaga ani*		10
Mangrove Cuckoo	*Coccyzus minor*		44
Gray-rumped Swift	*Chaetura cinereiventris*		15
Rufous-breasted Hermit	*Glaucis hirsutus*		7
Green-throated Carib	*Eulampis holosericeus*	regional resident endemic	17
Antillean Crested Hummingbird	*Orthorhyncus cristatus*	regional resident endemic	105
Orange-winged Parrot	*Amazona amazonica*	introduced resident	48
Caribbean Elaenia	*Elaenia martinica*		11
Yellow-bellied Elaenia	*Elaenia flavogaster*		67
Grenada Flycatcher	*Myiarchus nugator*	regional resident endemic	105
Gray Kingbird	*Tyrannus dominicensis*		195
Black-whiskered Vireo	*Vireo altiloquus*		40
Caribbean Martin	*Progne dominicensis*	regional breeding endemic	2
House Wren	*Troglodytes aedon*		63
Cocoa Thrush	*Turdus fumigatus*		13
Spectacled Thrush	*Turdus nudigenis*		179
Tropical Mockingbird	*Mimus gilvus*		132
Antillean Euphonia	*Chlorophonia musica*	regional resident endemic	2
Shiny Cowbird	*Molothrus bonariensis*	introduced resident	19
Carib Grackle	*Quiscalus lugubris*		11
Yellow Warbler	*Setophaga petechia*		1
Lesser Antillean Tanager	*Stilpnia cucullata*	regional resident endemic	146
Bananaquit	*Coereba flaveola*		384
Black-faced Grassquit	*Melanospiza bicolor*		54
Lesser Antillean Bullfinch	*Loxigilla noctis*	regional resident endemic	100
Yellow-bellied Seedeater	*Sporophila nigricollis*		6

(*Glaucis hirsutus*) and Carib Grackle (*Quiscalus lugubris*) in our study (Fig. 2). The relative abundance of endemic species remained similar between the two studies, with the exception of the Antillean Crested Hummingbird's relative abundance, which was lower than expected in our study (Fig. 2).

We estimated density for the species with more than 30 visual detections (Table 2), including the regional endemic Grenada Flycatcher, Lesser Antillean Tanager, Antillean Crested Hummingbird, and Lesser Antillean Bullfinch. We fit models with a Poisson detection function using a hazard rate key for all species apart from the Spectacled Thrush and Tropical Mockingbird, which were fit with a half-normal function. All covariates had a VIF < 2. Of the species for which we estimated density, the Bananaquit had the highest density (Table 2). Bananaquit density had a negative relationship with crop and shrub cover (Table 2). The Antillean Crested Hummingbird had the highest density of the endemic species included in our analyses, increasing with both crop cover and elevation (Table 2). Of the other regional endemic species, density of Grenada Flycatchers had a negative relationship with elevation and a positive relationship with shrub cover (Table 2), while the Lesser Antillean Tanager was more commonly observed in higher elevation forests. The Lesser Antillean Bullfinch had a positive relationship with both shrub and herbaceous cover (Table 2).

Discussion

Across both years of our survey, we detected approximately 90% of the extant resident landbird species recorded for Grenada (Raffaele *et al.* 2020). Our species assemblage is similar to Wunderle (1985), who reported 30 species in 1981. Differences

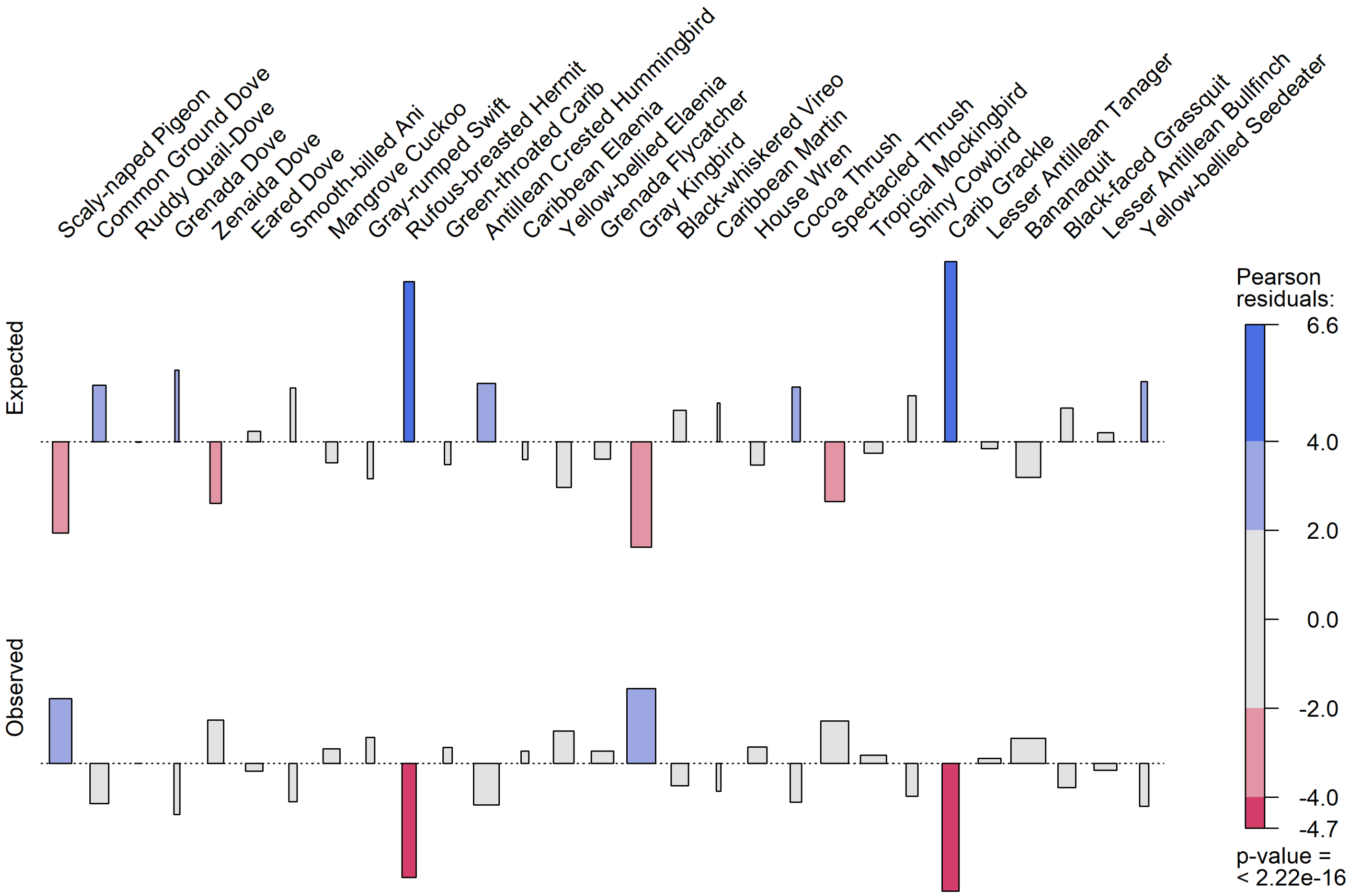

Fig. 2. Pearson residuals of expected (Wunderle 1985) and observed (this study) relative abundance of species, ordered taxonomically. Positive residuals are indicated in blue, negative residuals in red.

in the species observed between these two periods could be attributed, in part, to the timing of the studies. While we conducted our surveys during May, Wunderle conducted his in November, which may explain our lack of observations of the Blue-black Grassquit, as they are known to migrate outside of the breeding season (Raffaele *et al.* 2020). However, it is also worth noting that Wunderle only observed this species in the southwest part of the island (Mt. Hartman, Pt. Saline, and Grand Anse), which has been subject to considerable habitat loss and modification since the 1980s (J. Wunderle pers. comm.). Recent increases in certain species, such as the Yellow-bellied Seedeater (*Sporophila nigricollis*) (A. Jeremiah pers. comm.), as well as the introduction of the Orange-winged Parrot (see below), may explain the new species added to the observed assemblage in our study. As found nearly 40 yr ago (Wunderle 1985), widespread generalists, including a number of regional endemics, were the species most commonly detected in our study. Given the significant habitat destruction and fragmentation caused by Hurricane Ivan (Rusk 2009, Nelson *et al.* 2015), the limited species turnover since the 1980s may indicate some resiliency in the avian community.

The comparison between our study with Wunderle's (1985) should be interpreted with caution. The differences in the timing of the surveys between the two studies make it difficult to draw direct comparisons, particularly as we conducted our study during the dry to wet seasonal transition and Wunderle (1985) surveyed during the wet season. In terms of survey effort, Wunderle's (1985) sample effort was 1,800 observation-minutes across 90 survey points, while in our study, we sampled 199 points with 1,990 observation-minutes of survey effort. Considering this, the survey effort across the two studies was comparable. As such, there remains value in presenting this comparison given the paucity of such surveys for Grenada and that our survey followed a similar method and included many of the same areas as this earlier study. Observed differences in relative species abundance between these two studies could be attributed in part to variation in survey methods or timing. The earlier study included a wider range of habitats, such as residential areas and mangroves, which could account for greater observations of species that are adapted to urban areas or mangrove edges (e.g., Carib Grackles). Fluctuating species abundance can be driven by seasonal shifts in habitat use, such as documented for the Antillean Crested Hummingbird (Schuchmann and Boesman 2020), meaning that comparing data between different seasons could mask any real temporal changes in abundance. However, temporal changes in the abundance of some species may represent real changes in relative abundance due to climate change, habitat degradation, or interspecific competition, and demand further attention. For example, in Puerto Rico, hummingbirds

Table 2. Density estimates and detection probabilities derived from visual detections of nine resident landbirds on Grenada in May 2018 and 2019.

					Covariates from Best-Fitting Models[b]						
			Density		Density (λ)				Detection (p)		
Species	Observa-tions	Detection Probability	Birds/ha	95% CI[a]	Crop	Elevation	Shrub	Herb	Time	Date	Wind
Antillean Crested Hummingbird	97	0.27	1.68	0.91–3.76	+	+			–		
Grenada Flycatcher	63	0.15	0.59	0.10–1.60		–	+			+	
Gray Kingbird	110	0.08	0.69	0.33–1.16		–					–
Spectacled Thrush	66	0.18	0.49	0.32–0.77			–				–
Tropical Mockingbird	77	0.41	0.28	0.02–0.69		–					–
Lesser Antillean Tanager	126	0.19	1.02	0.44–3.09		+				+	
Bananaquit	328	0.43	4.00	2.36–5.41	–		–				+
Black-faced Grassquit	44	0.28	0.68	0.16–1.58		+		+	+		
Lesser Antillean Bullfinch	66	0.22	0.73	0.35–1.52			+	+			+

[a] confidence interval
[b] "+" and "–" indicate a positive and negative relationship, respectively.

such as the Antillean Crested Hummingbird have been slow to recover after Hurricanes Irma and Maria (J. Wunderle pers. comm.) and long-term changes in avian abundance in the Virgin Islands have been attributed to the impacts of hurricanes, land use change, and range expansions (Steadman *et al.* 2009). The limitations with our comparison highlight the need for regular, island-wide surveys to understand patterns in abundance.

Many regional endemic species were abundant and detected in all the habitats that we surveyed across the island. The Antillean Crested Hummingbird was the most abundant endemic species in our survey and was also a commonly observed species by Wunderle (1985). Although there are no published density estimates for this species across its range, it has also been noted as being more abundant at times than Bananaquits on Mustique Island in the Grenadines (Paice and Speirs 2010). The Antillean Crested Hummingbird has one of the most widespread distributions of the regional endemics found on Grenada, and throughout its range—from Puerto Rico to Grenada—it is commonly observed across all habitats and elevations (Chavez-Ramirez and Tan 1993, Shepherdson 2018). However, habitat use by the Antillean Crested Hummingbird appears to vary between islands. This variation may be due to inter-island variation in hummingbird assemblages (Lack 1973). Our models suggested that density of the Antillean Crested Hummingbird increased with both crop cover and elevation, consistent with other recent observations (Williams *et al.* In Review). This may reflect dietary requirements, which shift throughout the year, and possible elevational migration (Schuchmann and Boesman 2020). The Lesser Antillean Tanager was another abundant endemic species observed in our survey, which Wunderle (1985) also detected at reasonably high frequencies. Although this species was previously reported to be common at all elevations on Grenada (Raffaele *et al.* 2020), in our study, this tanager was more abundant at higher elevations, which is consistent with other recent observations on Grenada (Williams *et al.* In Review) as well as records from St. Vincent (Hilty *et al.* 2020). It is unclear whether this reflects an elevational preference or a preference for undisturbed forest that, on Grenada, is found at higher elevations. Notably, since we were unable to sample some high elevation areas due to accessibility constraints, these densities may be underestimates. The Lesser Antillean Bullfinch is an abundant endemic species and our results indicate that their density increased with shrub and herbaceous cover, which is consistent with known habitat preferences (Raffaele *et al.* 2020). We observed the endemic Grenada Flycatcher throughout the island, as did Wunderle (1985), and it was more widely distributed across all habitat types than in the rest of its range on St. Vincent and the Grenadines (Paice and Speirs 2010). However, density for this species increased at lower elevations and with increasing shrub cover, corresponding with its known preference for lowland shrub (Raffaele *et al.* 2020), as also found by recent surveys on Grenada (Williams *et al.* In Review). This species had lower densities than the other endemics reported here, which may reflect a higher degree of habitat specialization or competition with conspecifics, such as on Mustique Island, where this flycatcher was limited by the presence of Gray Kingbirds (Paice and Speirs 2010). It is also important to note that the lowland habitat favored by the Grenada Flycatcher is subject to substantial development pressure (Simpson *et al.* 2012).

We obtained insufficient observations to estimate density for several endemics detected during our surveys. Detection rates were low for the Grenada Dove, likely due to its very localized distribution (Rusk 2017). We detected two Antillean Euphonia, which is considered localized and hard to detect (V. Francis pers. comm.). These individuals were both observed at high elevation sites near Clabony Sulphur Springs, which is consistent with their status on other islands as a rare, high elevation habitat and dietary specialist (Pérez-Rivera 1991). This species is also sensitive to hurricane disturbance, with significant declines after Hurricane Irma observed in Puerto Rico (Lloyd *et al.* 2019). We also detected Caribbean Martin (*Progne dominicensis*)—a regional breeding endemic that is present on Grenada in May—but as with previous observations (Wunderle 1985, see also eBird records), this species was not abundant. We detected relatively few Green-throated Carib across the island, with this species being less abundant than the Antillean Crested Hummingbird, as also noted on other islands (Madden and van Zanten 2020). However, our observations suggest that this species is locally abundant and tended to occur at higher elevations. While Green-throated Carib occur throughout Grenada, they are thought to display elevational or seasonal migration on the island (A. Jeremiah pers. comm.), which may explain the patterns in our observations of this species. Indeed, Neotropical hummingbird species exhibit similar seasonal, elevational migration, driven in part by resource availability (Rappole and Schuchmann 2003). Two regional endemics documented on Grenada (Raffaele *et al.* 2020)— the Purple-throated Carib (*Eulampis jugularis*) and Scaly-breasted Thrasher (*Allenia fusca*)— were not detected during this study and are thought to be either extremely rare or extirpated on the island (V. Francis pers. comm.).

We also estimated density for several non-endemic resident species. Our density estimates for Bananaquits across different habitats are consistent with previous estimates for Grenada; reported as 2 (thorn-scrub) to 12 (coconut plantations) individuals per ha (Wunderle 1984), though our survey did not include all habitat types documented in this earlier study. Bananaquits are one of the most abundant species throughout the Caribbean (Paice and Speirs 2010, Wolff *et al.* 2018, Madden and van Zanten 2020). The Gray Kingbird, another common species across the region, is more abundant in open habitats at lower elevations (Smith and Jackson 2020). This pattern appears to be evident on Grenada, with density decreasing with elevation in our study. The Black-faced Grassquit (*Melanospiza bicolor*) is a fairly common resident and our density estimates for Grenada were similar to that reported on other islands (Lloyd and Slater 2011, Wolff *et al.* 2018). For this species, our models suggested that density increased with elevation, and although they were not observed by Wunderle (1985) at higher elevations, they occur at high elevations on some islands (Rising 2020). That their abundance increased with herbaceous cover, as previously observed on Grenada (Wunderle 1985) and in Puerto Rico (Wolff *et al.* 2018), is unsurprising given that they are an open-habitat granivore. Here, it is worth noting that our sampling methodology, which maximized accessibility, could potentially lead to overestimates of such edge species, although our estimates correspond with published densities. The Spectacled Thrush decreased with shrub cover, which is consistent with its preference for forested habitat (Wunderle 1985, Raffaele *et al.* 2003), and the Tropical Mockingbird occurred at low densities on Grenada, declining with elevation. Wunderle (1985) observed the Tropical Mockingbird at fairly high frequency, but not at higher elevations, suggesting that our results may reflect the need to survey wider habitat types, including residential areas. Species with insufficient observations to estimate density typically included those that were more likely to be detected aurally, such as the Scaly-naped Pigeon and House Wren (*Troglodytes aedon*), those that occur at low densities, such as the Yellow-bellied Seedeater, or those that are habitat specialists, such as the Rufous-breasted Hermit, Ruddy Quail-Dove (*Geotrygon montana*), and Cocoa Thrush (*Turdus fumigatus*).

Given the vulnerability of islands to invasive species (Cassey 2003) and the frequent introduction of non-native avian species throughout the insular Caribbean (Wiley and Wunderle 1993, Cassey *et al.* 2015), Grenada has comparatively few established non-native bird species. The Rock Pigeon (*Columba livia*), long-established in the Caribbean, including on Grenada (Raffaele *et al.* 2020), was not detected in this survey, probably due to the types of habitats surveyed and low densities of this species. The Shiny Cowbird (*Molothrus bonariensis*) has spread naturally throughout much of the Caribbean and has been established on the island since at least 1901 (Post and Wiley 1977). We detected this species at low abundances across the island, suggesting the population has not increased substantially since the study by Wunderle (1985). A more recent addition to the Grenadian avifauna is the Orange-winged Parrot, thought to have originated from aviary releases in the late 1980s (Massiah and Frost 2003). We mainly detected this species at mid-level elevations in forested habitats, and although visual detections were insufficient for density analyses, this species now appears to be widely established on the island. The Channel-billed Toucan (*Ramphastos vitellinus*) also escaped from captivity in the 1980s but did not become widely established (Massiah and Frost 2003). We did not observe this species during our surveys, and though there are a few recent records in eBird (eBird 2021); if this species is still present on the island it is rare and localized (Raffaele *et al.* 2020).

This study makes an important contribution to our knowledge of bird abundance and distribution on the island of Grenada. Our results suggest that the bird assemblage on Grenada is fairly stable and we provide density estimates for several of Grenada's regional endemic species. In particular, the density estimates of the Grenada Flycatcher, Antillean Crested Hummingbird, Lesser Antillean Tanager, and Lesser Antillean Bullfinch represent a significant contribution to our knowledge of these important regional endemic species. However, these estimates are limited to one season in two consecutive years and this, together with a lack of density estimates from across their distributions, prevent us from detecting spatial and temporal changes. Further, detection of many species was too low to estimate density, which limits our ability to explore community composition and dynamics. Long-term monitoring is vital to be able to detect such patterns, which is particularly important for the conservation of island species in light of climate change and the increasing threat of hurricanes, as well as for understanding ecosystem functioning.

Acknowledgments

We are grateful to Anthony Jeremiah, Chief Forestry Officer (Ag.) of the Grenada Forestry and National Parks Department, Government of Grenada for valuable support, and to Michael Mason of the Land Use Division, MALFF, who was generous with his time, data, and advice. We thank Vaughan Francis for his insightful discussions and local knowledge, and Joe Wunderle for constructive comments. We thank three anonymous reviewers for their comments which greatly improved this manuscript. This project was funded in part by the Percy Sladen Fund.

Title Page Illustration

Grenada Flycatcher (*Myiarchus nugator*) at Mt. Hartman on 18 May 2016. Photograph by Howard Nelson.

Author Information

[1]Department of Biomedical Sciences, University of Edinburgh, Teviot Place, Edinburgh, EH8 9AG, UK; e-mail: ellie.devenish@ed.ac.uk; [2]Fauna and Flora International, David Attenborough Building, Pembroke Street, Cambridge, CB1 3QZ, UK; e-mail: howard.nelson@fauna-flora.org; [3]Department of Geography, University of Cambridge, Downing Place, Cambridge, CB2 3EN, UK

Literature Cited

Bellard, C., C. Leclerc, and F. Courchamp. 2014. Impact of sea level rise on the 10 insular biodiversity hotspots. Global Ecology and Biogeography 23:203–212.

Buchhorn, M., B. Smets, L. Bertels, M. Lesiv, N.E. Tsendbazar, M. Herold, and S. Fritz. 2019. Copernicus Global Land Service: Land Cover 100m: epoch 2015: Globe. Dataset of the global component of the Copernicus Land Monitoring Service 2019.

Buckland, S.T., D.R. Anderson, K.P. Burnham, D.L. Thomas, and J.L. Laake. 2001. Introduction to Distance Sampling: Estimating Abundance of Biological Populations. Oxford University Press, Oxford, UK.

Burnett, R.D., and L.J. Roberts. 2015. A quantitative evaluation of the conservation umbrella of Spotted Owl Management Areas in the Sierra Nevada. PLoS ONE 10:e0123778.

Burnham, K.P., and D.R. Anderson. 2002. Model Selection and Multi-Model Inference: a Practical Information-Theoretic Approach. Springer-Verlag, New York.

Cassey, P. 2003. A comparative analysis of the relative success of introduced land birds on islands. Evolutionary Ecology Research 5:1011–1021.

Cassey, P., M. Vall-Llosera, E. Dyer, and T.M. Blackburn. 2015. The biogeography of avian invasions: history, accident and market trade. Pp. 37–54 *in* Biological Invasions in Changing Ecosystems (J. Canning-Clode, ed.). De Gruyter Open Poland, Warsaw, Poland.

Chavez-Ramirez, F., and S.S. Tan. 1993. Habitat separation and arthropod resource use in three Lesser Antillean hummingbirds. Condor 95:455–458.

Devenish-Nelson, E.S., D.E. Weidemann, J.M. Townsend, and H.P. Nelson. 2017. The role of a regional journal as a depository for valuable ornithological data as demonstrated by Caribbean forest endemic birds. Journal of Caribbean Ornithology 30:75–87.

Devenish-Nelson, E.S., D.E. Weidemann, J.M. Townsend, and H.P. Nelson. 2019. Patterns in island endemic forest-dependent bird research: the Caribbean as a case-study. Biodiversity and Conservation 28:1885–1904.

Dormann, C.F., J. Elith, S. Bacher, C. Buchmann, G. Carl, G. Carré, J.R.G. Marquéz, B. Gruber, B. Lafourcade, P.J. Leitão, T. Münkemüller, C. McClean, P.E. Osborne, B. Reineking, B. Schröder, A.K. Skidmore, D. Zurell, and S. Lautenbach. 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography 36:027–046.

eBird. 2021. Channel-billed Toucan. eBird: an Online Database of Bird Distribution and Abundance. eBird, Ithaca, NY. ebird.org/species/chbtou1.

Fiske, I., and R. Chandler. 2011. unmarked: an R package for fitting hierarchical models of wildlife occurrence and abundance. Journal of Statistical Software 43:1–23.

Fuller, A.K., D.W. Linden, and J.A. Royle. 2016. Management decision making for fisher populations informed by occupancy modeling. Journal of Wildlife Management 80:794–802.

Government of Grenada. 2016. Grenada National Land Policy: Providing for Sustainable Land Management and Ecosystem Resilience. Government of Grenada, Grenada.

Hansen, M.C., P.V. Potapov, R. Moore, M. Hancher, S.A. Turubanova, A. Tyukavina, D. Thau, S.V. Stehman, S.J. Goetz, T.R. Loveland, A. Kommareddy, A. Egorov, L. Chini, C.O. Justice, and J.G.R. Townshend. 2013. High-resolution global maps of 21st-century forest cover change. Science 342:850–853.

Helmer, E.H., T.A. Kennaway, D.H. Pedreros, M.L. Clark, H. Marcano-Vega, L.L. Tieszen, T.R. Ruzycki, S.R. Schill, and C.M.S. Carrington. 2008. Land cover and forest formation distributions for St. Kitts, Nevis, St. Eustatius, Grenada and Barbados from decision tree classification of cloud-cleared satellite imagery. Caribbean Journal of Science 44:175–198.

Hilty, S., J. del Hoyo, N.J. Collar, and G.M. Kirwan. 2020. Lesser Antillean Tanager (*Stilpnia cucullata*), version 1.0. *In* Birds of the World (J. del Hoyo, A. Elliott, J. Sargatal, D.A. Christie, and E. de Juana, eds.). Cornell Lab of Ornithology, Ithaca, NY. doi.org/10.2173/bow.leatan1.01.

Holdschlag, A., and B.M.W. Ratter. 2013. Multiscale system dynamics of humans and nature in The Bahamas: perturbation, knowledge, panarchy and resilience. Sustainability Science 8:407–421.

Inger, R., R. Gregory, J.P. Duffy, I. Stott, P. Voříšek, and K.J. Gaston. 2015. Common European birds are declining rapidly while less abundant species' numbers are rising. Ecology Letters

18:28–36.

International Union for Conservation of Nature (IUCN). 2020. IUCN Red List of Threatened Species. Version 2020.1. iucnredlist.org.

Julliard, R., F. Jiguet, and D. Couvet. 2004. Common birds facing global changes: what makes a species at risk? Global Change Biology 10:148–154.

Kaiser-Bunbury, C.N., F. Fleischer-Dogley, D. Dogley, and N. Bunbury. 2015. Scientists' responsibilities towards evidence-based conservation in a Small Island Developing State. Journal of Applied Ecology 52:7–11.

Kéry, M., and J.A. Royle. 2015. Applied Hierarchical Modeling in Ecology: Analysis of Distribution, Abundance and Species Richness in R and BUGS, Vol. 1: Prelude and Static Models. Academic Press, Cambridge, MA.

Knutson, T., S.J. Camargo, J.C.L. Chan, K. Emanuel, C.H. Ho, J. Kossin, M. Mohapatra, M. Satoh, M. Sugi, K. Walsh, and L. Wu. 2019. Tropical cyclones and climate change assessment: Part I: detection and attribution. Bulletin of the American Meteorological Society 100:1987–2007.

Lack, D. 1973. The numbers of species of hummingbirds in the West Indies. Evolution 27:326–337.

Latta, S.C. 2012. Avian research in the Caribbean: past contributions and current priorities. Journal of Field Ornithology 83:107–121.

Lee, D.C., and S.J. Marsden. 2008. Adjusting count period strategies to improve the accuracy of forest bird abundance estimates from point transect distance sampling surveys. IBIS 150:315–325.

Lloyd, J.D., C.C. Rimmer, and J.A. Salguero-Faría. 2019. Short-term effects of hurricanes Maria and Irma on forest birds of Puerto Rico. PLoS ONE 14:e0214432.

Lloyd, J.D., and G.L. Slater. 2011. Abundance and distribution of breeding birds in the pine forests of Grand Bahama, Bahamas. Journal of Caribbean Ornithology 24:1–9.

Madden, H., and A. van Zanten. 2020. Monitoring of terrestrial avifauna in six habitats on St. Eustatius, Caribbean Netherlands, 2009–2017. Caribbean Journal of Science 50:23–36.

Massiah, E.B., and M.D. Frost. 2003. Is Channel-Billed Toucan (*Ramphastos vitellinus*) established on Grenada? Journal of Caribbean Ornithology 16:68–69.

Matsuoka, S.M., C.L. Mahon, C.M. Handel, P. Sólymos, E.M. Bayne, P.C. Fontaine, and C.J. Ralph. 2014. Reviving common standards in point-count surveys for broad inference across studies. Condor 116:599–608.

Nareff, G.E., P.B. Wood, D.J. Brown, T. Fearer, J.L. Larkin, and W.M. Ford. 2019. Cerulean Warbler (*Setophaga cerulea*) response to operational silviculture in the central Appalachian region. Forest Ecology and Management 448:409–423.

Nelson, H.P., E.S. Devenish-Nelson, M. Geary, A. Lawrence, and B.L. Rusk. 2015. Report on the re-sampling of the 2004 vegetation plots of the dry forest Grenada Dove (*Leptotila wellsi*) habitat. Unpublished report. Forestry and National Parks Department, Government of Grenada, St. George's, Grenada.

Pacifici, K., T.R. Simons, and K.H. Pollock. 2008. Effects of vegetation and background noise on the detection process in auditory avian point-count surveys. Auk 125:600–607.

Paice, M.R., and R. Speirs. 2010. The avifauna of Mustique Island (St. Vincent and the Grenadines). Journal of Caribbean Ornithology 23:61–84.

Pérez-Rivera, R.A. 1991. Change in diet and foraging behavior of the Antillean Euphonia in Puerto Rico after Hurricane Hugo. Journal of Field Ornithology 62:474–478.

Portillo-Quintero, C.A., and G.A. Sánchez-Azofeifa. 2010. Extent and conservation of tropical dry forests in the Americas. Biological Conservation 143:144–155.

Post, W., and J.W. Wiley. 1977. The Shiny Cowbird in the West Indies. Condor 79:119–121.

R Core Team. 2020. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. R-project.org.

Raffaele, H.A., J. Wiley, O.H. Garrido, A. Keith, and J.I Raffaele. 2003. Birds of the West Indies. Princeton University Press, Princeton, NJ.

Raffaele, H.A., J. Wiley, O.H. Garrido, A. Keith, and J.I. Raffaele. 2020. Birds of the West Indies. 2nd edn. Princeton University Press, Princeton, NJ.

Rappole, J.H., and K.L. Schuchmann. 2003. Ecology and evolution of hummingbird population movements and migration. Pp. 39–51 *in* Avian Migration (P. Berthold, E. Gwinner, and E. Sonnenschein, eds.). Springer-Verlag, Berlin Heidelberg, Germany.

Richards, S.A. 2005. Testing ecological theory using the information-theoretic approach: examples and cautionary results. Ecology 86:2805–2814.

Rising, J.D. 2020. Black-faced Grassquit (*Melanospiza bicolor*), version 1.0. *In* Birds of the World (J. del Hoyo, A. Elliott, J. Sargatal, D.A. Christie, and E. de Juana, eds.). Cornell Lab of Ornithology, Ithaca, NY. doi.org/10.2173/bow.bkfgra.01.

Rivera-Milán, F.F., P. Bertuol, F. Simal, and B.L. Rusk. 2015. Distance sampling survey and abundance estimation of the critically endangered Grenada Dove (*Leptotila wellsi*). Condor 117:87–93.

Roberts, L.J., R. Burnett, J. Tietz, and S. Veloz. 2019. Recent drought and tree mortality effects on the avian community in southern Sierra Nevada: a glimpse of the future? Ecological Applications 29:e01848.

Royle, J.A., D.K. Dawson, and S. Bates. 2004. Modeling abundance effects in distance sampling. Ecology 85:1591–1597.

Rusk, B.L. 2009. Grenada. Pp. 229–234 *in* Important Bird Areas in the Caribbean: Key Sites for Conservation (D.C. Wege and V. Anadon-Irizarry, eds.). BirdLife International, Cambridge, UK.

Rusk, B.L. 2017. Long-term population monitoring of the Critically Endangered Grenada Dove (*Leptotila wellsi*) on Grenada, West Indies. Journal of Caribbean Ornithology 30:49–56.

Schuchmann, K.L., and P.F.D. Boesman. 2020. Antillean Crested Hummingbird (*Orthorhyncus cristatus*), version 1.0. *In* Birds of the World (J. del Hoyo, A. Elliott, J. Sargatal, D.A. Christie, and E. de Juana, eds.). Cornell Lab of Ornithology, Ithaca, NY. doi.org/10.2173/bow.anchum1.01.

Shepherdson, J.P. 2018. Observations of territorial behavior of the Antillean Crested Hummingbird (*Orthorhyncus cristatus*) on St. Eustatius. Journal of Caribbean Ornithology 31:48–50.

Simpson, M.C., J.F. Clarke, D.J. Scott, M. New, A. Karmalkar, O.J. Day, M. Taylor, S. Gossling, M. Wilson, D. Chadee, H. Stager, R. Waithe, A. Stewart, J. Georges, N. Hutchinson, N. Fields, R.

Sim, M. Rutty, L. Matthews, S. Charles, and A. Agosta G'meiner. 2012. The CARIBSAVE Climate Change Risk Atlas (CCCRA), Grenada, DFID, AusAID and The CARIBSAVE Partnership, Barbados, West Indies.

Smith, G.A., and J.A. Jackson. 2020. Gray Kingbird (*Tyrannus dominicensis*), version 1.0. *In* Birds of the World (A.F. Poole and F.B. Gill, eds.). Cornell Lab of Ornithology, Ithaca, NY. doi.org/10.2173/bow.grykin.01.

Steadman, D.W., J.R. Montambault, S.K. Robinson, S.N. Oswalt, T.J. Brandeis, A.G. Londoño, M.J. Reetz, W.M. Schelsky, N.A. Wright, J.P. Hoover, J. Jankowski, A.W. Kratter, A.E. Martinez, and J. Smith. 2009. Relative abundance, habitat use, and long-term population changes of wintering and resident landbirds on St. John, US Virgin Islands. Wilson Journal of Ornithology 12:41–53.

Wiley, J.W., and J.M. Wunderle. 1993. The effects of hurricanes on birds, with special reference to Caribbean islands. Bird Conservation International 3:319–349.

Williams, R.J.T., M.H. Warrington, and N. Koper. In Review. Avian use of anthropogenic and natural habitats in a Small Island Developing State.

Wintle, B.A., M.C. Runge, and S.A. Bekessy. 2010. Allocating monitoring effort in the face of unknown unknowns. Ecology Letters 13:1325–1337.

Wolff, P.J., B.A. DeGregorio, V. Rodriguez-Cruz, E. Mulero-Oliveras, and J.H. Sperry. 2018. Bird community assemblage and distribution in a tropical, urban ecosystem of Puerto Rico. Tropical Conservation Science 11:1–10.

Wunderle, J. 1985. An ecological comparison of the avifauna of Grenada and Tobago, West Indies. Wilson Bulletin 97:356–365.

Wunderle, J.M. 1984. Mate switching and a seasonal increase in polygyny in the Bananaquit. Behaviour 88:123–144.

Wunderle, J.M. 1981. An analysis of a morph ratio cline in the Bananaquit (*Coereba flaveola*) on Grenada, West Indies. Evolution 35:333–344.

Xu, Y., S. Lin, J. He, Y. Xin, L. Zhang, H. Jiang, and Y. Li. 2016. Tropical birds are declining in the Hainan Island of China. Biological Conservation 210:9–18.

Cite this article as:

Devenish-Nelson, E.S., and H.P. Nelson. 2021. Abundance and density estimates of landbirds on Grenada. Journal of Caribbean Ornithology 34:88–98. https://doi.org/10.55431/ jco.2021.34.88-98