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Photo: Claude Fletcher

A Special Issue on the Status of Caribbean Forest Endemics

Forest disturbance has negative consequences for the persistence of Jamaica's threatened and endangered bird species in Cockpit Country

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Abstract Cockpit Country is a globally important area for Jamaica's threatened and endangered bird species. But habitat disturbance and degradation due to lumber and yam stick extraction, small-scale agriculture, and bauxite mining threaten to disrupt the sensitive ecological processes that maintain both the species and the habitat. Analysis of anthropogenic forest disturbance and point count survey data for birds suggests an association between forest disturbance and bird distribution patterns in Cockpit Country. Threatened and endangered birds such as Plain Pigeon (*Patagioenas inornata exigua*), Crested Quail-Dove (*Geotrygon versicolor*), and Jamaican Blackbird (*Nesopsar nigerrimus*) had greater association with undisturbed forest than species of least conservation concern such as Common Ground-Dove (*Columbina passerina*) and Gray Kingbird (*Tyrannus dominicensis*). Although the observed distribution patterns revealed a suite of bird species that could be utilized for monitoring forest disturbance, the approach used in this study needs to be better developed before implementation in Cockpit Country. The results also have implications for the persistence of threatened and endangered bird species given the lack of clarity about boundaries, proper forest management and enforcement, and ongoing efforts to mine bauxite in the area.

Keywords birds, Cockpit Country, endangered, forest disturbance, threatened

Resumen El disturbio forestal tiene consecuencias negativas para la subsistencia de las aves amenazadas y en peligro de Jamaica en Cockpit Country—Cockpit Country es un área de importancia mundial para las especies de aves amenazadas y en peligro de Jamaica. Sin embargo, la degradación y el disturbio de hábitat producto de la tala y la extracción de ñame, la agricultura a pequeña escala y la explotación de bauxita amenazan con interrumpir los sensibles procesos ecológicos que mantienen tanto a las especies como al hábitat. El análisis de los disturbios forestales por causas antropogénicas y los datos de muestreos de puntos de conteo de aves sugiere una asociación entre el disturbio forestal y los patrones de distribución de aves en Cockpit Country. Especies amenazadas y en peligro como *Patagioenas inornata exigua*, *Geotrygon versicolor* y *Nesopsar nigerrimus* tuvieron una mayor asociación con bosques no perturbados que especies de menor preocupación como *Columbina passerina* y *Tyrannus dominicensis*. Aunque los patrones de distribución observados revelan que podría utilizarse un grupo de aves para el monitoreo del disturbio forestal, el enfoque empleado en este estudio necesita ser desarrollado mejor antes de su implementación en Cockpit Country. Los resultados también tienen implicaciones para la subsistencia de especies de aves amenazadas y en peligro dada la falta de claridad sobre los límites, la aplicación de la ley la presencia de un manejo forestal adecuado, así como los esfuerzos en curso para la extracción de bauxita en el área.

Palabras clave amenazadas, aves, Cockpit Country, disturbio forestal, en peligro

Résumé Conséquences négatives des perturbations des forêts pour le maintien des espèces d'oiseaux menacées et en danger à Cockpit Country en Jamaïque—Cockpit Country est une aire d'importance mondiale pour les espèces d'oiseaux menacées et en danger de la Jamaïque. Toutefois, la perturbation et la dégradation des habitats en raison de l'exploitation du bois et de l'igname, l'agriculture à petite échelle et les mines de bauxite menacent de modifier les processus écologiques sensibles qui maintiennent les espèces et les habitats. L'analyse des perturbations d'origine anthropique de la forêt et des comptages des oiseaux par points suggère l'existence d'un lien entre la perturbation de la forêt et les modèles de répartition des oiseaux à Cockpit Country. Les oiseaux menacés et en danger comme le Pigeon simple (*Patagioenas inornata exigua*), la Colombe versicolore (*Geotrygon versicolor*), et le Carouge de la Jamaïque (*Nesopsar nigerrimus*) sont plus fortement associés à la forêt non perturbée que les espèces dont la conservation est moins préoccupante telles que la Colombe à queue noire (*Columbina passerina*) et le Tyran gris (*Tyrannus dominicensis*). Bien que les schémas de répartition observés aient mis en évidence une série d'espèces d'oiseaux qui permettrait de suivre les perturbations forestières, l'approche utilisée dans cette étude doit être développée davantage avant une mise en œuvre à

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Cockpit Country. Les résultats ont également des implications pour le maintien des espèces d'oiseaux menacées et en danger, compte tenu du manque de clarté quant aux limites, à la bonne gestion des forêts, et à l'application des lois, ainsi qu'aux efforts actuels d'extraction de la bauxite dans la région.

Mots clés Cockpit Country, espèces en danger, espèces menacées, oiseaux, perturbation des forêts

Islands generally have limited area and specialized habitats that support their floral and faunal diversity (McArthur and Wilson 1967, Whittaker 1998). Island species often display characteristics of small populations with restricted ranges, and are thus often susceptible to extinction from human exploitation, predation, disease, competition, climatic change, and habitat alteration (McArthur and Wilson 1967, Lack 1976, Christian *et al.* 1996, Lewis *et al.* 2011).

Habitat disturbance is potentially the most important factor threatening the preservation of viable bird populations (Lawton and May 1995). Species are thought to be sensitive to forest disturbance when their abundance and fitness in remnant forest patches change as the surrounding landscape is fragmented (Walters 1998, Kennedy *et al.* 2010). Habitat degradation often accompanies habitat fragmentation, producing adverse effects that are independent of landscape structure (Lynch and Whigham 1984, Saunders *et al.* 1991). Habitat degradation reduces the size of the area occupied by island species (Saunders *et al.* 1991, Steadman 1997). The smaller the population and area occupied by island species, the more susceptible these populations are to the effects of predation, disease, competition, further habitat alteration, hurricane and storm damage, and climate change (Whittaker 1998, Root *et al.* 2003).

The region identified in Jamaica as “Cockpit Country” was so named because the landform reminded British colonists of the arenas used for cock fighting. Cockpit Country, encompassing

approximately 500 km², represents a portion of the spinal karst limestone forest that stretches across north-central Jamaica, bounded along its periphery by a ring of agriculture and human settlements (Fig. 1; Eyre 1995, Koenig *et al.* 2000). This area represents the largest, relatively intact remnant of what was once a contiguous wet limestone forest across central areas of the island. Cockpit karsts comprise steep-sided, bowl-shaped, closed depressions separated by roughly conical peaks. Cockpits average from 100 m to 120 m in depth and walls generally slope from 30° to 40° (Asprey and Robbins 1953). The highest rainfall totals in Cockpit Country occur in the central core, which receives approximately 2,500–3,800 mm annually, with rainfall diminishing towards the periphery where it averages 1,750–2,500 mm (Barker and Miller 1995).

Cockpit Country is particularly rich in avian diversity compared to other old-growth forest patches on the island (Koenig *et al.* 2000). At least 65 of Jamaica's 67 resident breeding land birds have been reported from the area, including 28 of the island's 29 endemic species (BirdLife International 2017). The area represents the largest remaining fragment of the Black-billed (*Amazona agilis*) and Yellow-billed Parrots' (*A. collaria*) historical ranges (Davis 2002). Both occur sympatrically in considerable numbers (Davis 2002), and the area is also one of the strongholds of Black-billed Parrots on the island (Koenig *et al.* 2000). Cockpit Country is considered to be important habitat for a number of Jamaica's other threatened and endangered species

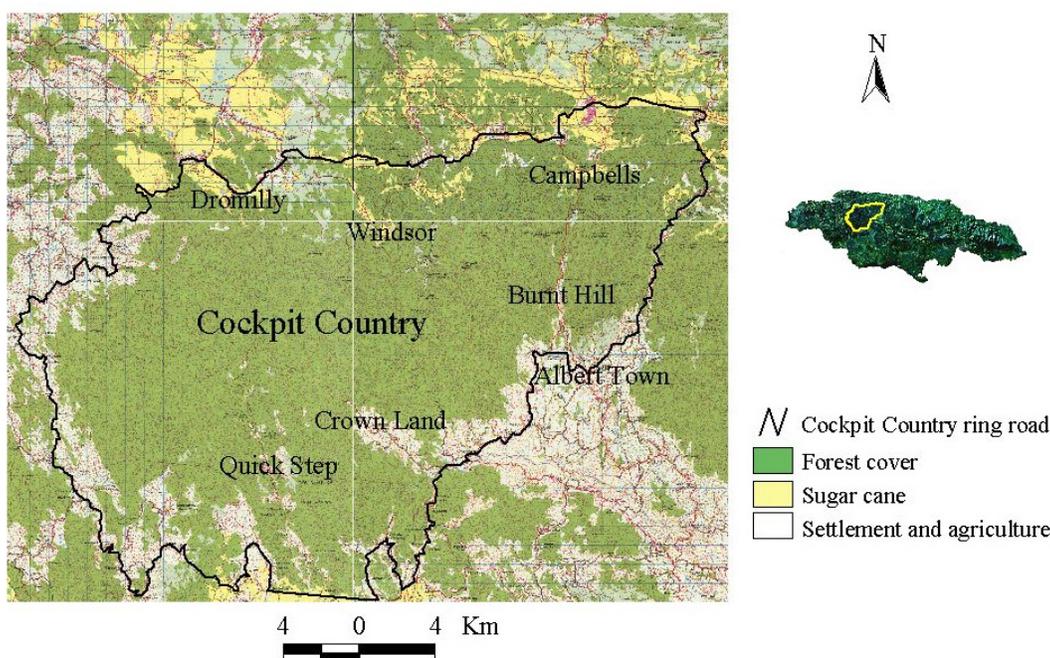


Fig. 1. Cockpit Country in its regional context surrounded by agriculture and other human development.

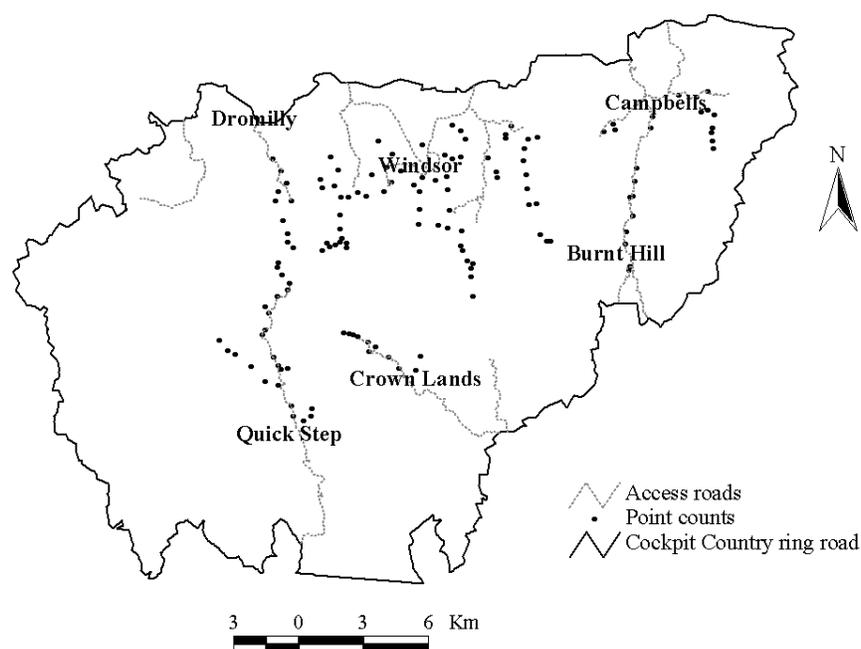


Fig. 2. Main access roads and the distribution of sample points in Cockpit Country, Jamaica.

and subspecies including Plain Pigeon (*Patagioenas inornata exigua*), Ring-tailed Pigeon (*P. caribaea*), Crested Quail-Dove (*Geotrygon versicolor*), Blue Mountain Vireo (*Vireo osburni*), and Jamaican Blackbird (*Nesopsar nigerrimus*), the latter considered to be the most threatened Jamaican endemic species (Raffaele *et al.* 1998, Haynes-Sutton *et al.* 2009). Additionally, Cockpit Country was one of the last known habitats for the now extinct Golden Swallow (*Tachycineta euchrysea euchrysea*; Graves 2014, Proctor *et al.* 2017).

Cockpit Country's Forest Reserve status initially offered the area some formal legal protection from habitat degradation, but a lack of enforcement, lack of clarity about boundaries, general attitudes towards the use of government lands, small-scale agriculture, and timber and yam stick extraction continue to degrade this site (Varty 1991, Barker and Miller 1995, Newman *et al.* 2014, Williams-Raynor 2015). However, since the area was proposed as a suitable candidate for World Heritage Site status (Eyre 1995), there have been mounting efforts to conserve and preserve this unique ecosystem from the increasing threat of bauxite mining (Williams 2008, Thompson 2013, Newman *et al.* 2014, Williams-Raynor 2015, Douglas 2016). Jamaica has rich bauxite deposits, and since the 1950s, the industry has made substantial contributions in revenue and employment to the Jamaican economy (Berglund and Johansson 2004). Bauxite extraction, however, typically involves strip-mining, which destroys native vegetation resulting in the loss and degradation of habitat and negative impacts on bird demography (Berglund and Johansson 2004, Kennedy 2009, Kennedy *et al.* 2011).

Understanding how habitat destruction and degradation impact bird populations is critical for the development of effective conservation strategies for these species. Study of a species' population and distribution within spatially isolated habitats such as Cockpit Country can provide important insights into what these changes could mean for the avian occupants (Whit-

taker 1998). Species occupying large habitat fragments may be cushioned from extinction processes, but they may be lost from isolated habitats if adequate conservation programs are not implemented (Preston 1962, McArthur and Wilson 1967, Rosenzweig 1995).

In Jamaica, systematic studies of the distribution and abundance patterns of land bird species have rarely been conducted (but see Davis 1998, Douglas 2001). The result is that conservation decisions are often based on data gleaned from anecdotal observation, for example, Jamaica's National Ecological Gap Assessment Report (Ecological Working Group 2009). The aim in this paper is to assess how forest disturbance levels impact land bird distribution patterns in Cockpit Country and the implications for the persistence of the bird community.

Methods

Parrot Surveys

Taking topographical considerations and parrot behavioral traits into account, a modified point transect method was used to survey *Amazona* parrots in Cockpit Country (Snyder *et al.* 1987, Bibby *et al.* 1992). Existing trails and roads were used as transects to establish 140 points across Cockpit Country (Fig. 2). In this region, roads and trails typically run along the edge of or at the bottom of cockpit depressions. A depression, with its rim of limestone hills, defined the survey area around each point (the sample unit—average 0.1 km²), thereby allowing the observer to focus on territorial birds in that restricted space. It was determined from field observations that vocalizing parrots were easily distinguishable up to 300 m away from observers. Points, therefore, were spaced 500 m apart along transects to eliminate the possibility of counting territorial pairs from adjacent depressions. Some trails were fairly straight whereas others doubled back on themselves because of the irregular topography. In such cases, points were spaced more than 500 m apart to minimize

double counting errors and give observers a relatively good view of the area being surveyed so that territorial parrots could be more easily located.

Counts of territorial parrots were made for 2.5 hr at each point from either 0700 to 0930 or 1600 to 1830 during the breeding season (March to June) when birds establish breeding territories and are not flocking and flying off to feeding areas in edge habitat. These periods corresponded to the peak times of counter-calling between territorial parrot pairs and to peak activity of nesting pairs (e.g., food transfer; Koenig 1999), and thus, represented the periods of highest detectability. An ethogram was developed (based on all-day observations of parrots in and adjacent to their nest stands) to describe parrot behavior qualitatively so that territorial behaviors could be distinguished from the general parrot activity within the sample unit (Davis 2002). Parrots were determined to be a territorial pair once they remained in one location and counter-called vigorously with another pair for 30 min or more during the count period (Koenig 1999). All territorial pairs heard or observed during the count period were assigned a unique number and their activities within the sample unit were followed and noted on data sheets. These precautions were taken to eliminate counting a pair more than once. All parrot flocks observed during the count period were also noted on the data sheets. An effort was made to count parrots in different locations across Cockpit Country within the same month. Additionally, all observers counted parrots in the same location throughout the study period. These precautions were taken to guard against any disparity in Yellow-billed and Black-billed Parrot territorial behavior as the breeding season progressed across Cockpit Country. It was observed that parrot territorial activity can change because of early nest failure or early fledging, and that Yellow-billed Parrots can be more sensitive to human observers than Black-billed Parrots are in nesting territories (Koenig 1999).

The counting of territorial parrot pairs in Cockpit Country during the 1998 and 1999 parrot breeding seasons was accomplished by three observers—HD, Noel Snyder, and Daville Holmes. All observers were evaluated as to their ability to distinguish between the two species visually and vocally. This was done by cross-checking and correcting observer identification during simultaneous observation from vantage points where both species were easily identified visually. All observers counted parrots in the same region of Cockpit Country during the same time period.

Of the 140 points sampled, HD counted 83 and the two other observers 57 (Snyder $n = 5$; Holmes $n = 52$). Seven points were re-surveyed in the 1999 parrot breeding season with more than 80% accuracy (observations at six of the seven points produced the same number of territorial pairs as when first sampled). However, re-surveying all points was not possible during the 1999 breeding season because of time constraints, the number of available observers, and the extensive area that was to be covered during the short study period.

Surveys for Other Bird Species

Other bird species were counted using simple point count methodology (counts of all birds seen or heard within the same sample unit defined for the parrot surveys) at each of the 140

points (Bibby *et al.* 1992). Point counts were conducted for 10 min, where all birds seen and heard were recorded using standard Alpha codes developed by the USGS Bird Banding Laboratory (Pyle *et al.* 1997). Point counts were conducted along transects between 1 day and 1 week following the initial parrot count. Counts were conducted between 0600 and 1000, with start time depending on the time it took to hike to some sites. All counts were conducted in the breeding season (March to June).

Vegetation Assessment

Mueller-Dombois and Ellenberg's (1974) Point-Centered Quarter Method (PCQM) was used to determine absolute tree (trunk ≥ 15 cm circumference at breast height [CBH]) density and total and mean basal area at 49 of the 140 sample units. Logistic considerations did not permit an assessment of the vegetation structure within each sample unit. Thus, sites were selected to give an approximate representation of the vegetation structure across the 140 sample units in Cockpit Country. A 100-m transect was established running east to west from the center of each point count location. For sites in the middle of cleared depressions, transects were laid out on hills to the east within the sample unit. Where points were directly on trails, transects were laid out 20 m or more off the trails. Four quarters were established at 10-m intervals along the tape. The distance from the center to the midpoint of the nearest tree in each quarter was measured and its height estimated to the nearest meter. The CBH (1.5 m from the ground) for each of the selected trees was measured, and this was used to calculate the diameter at breast height (DBH).

The quality of the vegetation within all 140 sample units was visually appraised on a 1 to 4 scale of forest disturbance—1 for undisturbed forest, 2 for minimally disturbed forest, 3 for mostly disturbed forest, and 4 for very disturbed forest—according to predefined criteria. These criteria were (a) the presence of large clearings, (b) evidence of past logging activity, (c) evidence of present logging activity, (d) evidence of past agricultural activity, and (e) evidence of present agricultural activity. On this scale, 1 represented none of the above criteria; 2 represented (b), (c), or both; 3 represented (b), (c), (d), or a combination of these; and 4 represented all of the above criteria.

Analyses

The computer software CANOCO version 2.1 (Braak 1988) was used to perform a canonical correspondence analysis (CCA) on the data. CCA is a direct multivariate gradient analysis capable of detecting and relating species composition and distribution patterns to measured environmental variables (Palmer 1993). CCA arranges species, sites, and environmental variables along axes that represent a composite of environmental gradients. CCA statistically distinguishes which of the measured environmental variables are important in influencing bird composition and distribution in Cockpit Country. The relative importance of the axes in explaining species distribution patterns is expressed as eigenvalues and numbered according to diminishing importance, with the first CCA axis having the highest eigenvalue.

The analysis was performed using the forest abundance matrix of 44 species across 140 sample units and a matrix of four environmental variables across the same sites. The environmen-

Table 1. Eigenvalues, biplot scores of the environmental variables, and percent variance accounted for by the four axes derived from the CCA.

Axis	Eigenvalue	% Variance Accounted for by the Axis	Biplot Scores			
			East	North	Disturbance	Elevation
1	0.07	56.4	0.73	0.81	2.56 ^a	-1.37 ^a
2	0.03	21.0	1.46 ^a	0.72	0.14	0.75
3	0.02	16.3	0.19	1.19 ^a	-0.05	-0.71
4	0.008	6.3	-0.31	-0.17	0.19	0.48 ^a

^aHighest absolute biplot scores contributing most to explaining each axis. Therefore, axis 1 expresses disturbance and elevation, axis 2 expresses a west to east direction, axis 3 expresses a south to north direction, and axis 4 weakly expresses elevation.

tal variables were forest disturbance (using the qualitative scale described above), elevation, X coordinates expressing an easterly direction, and Y coordinates expressing a northerly direction. The coordinates were included because preliminary assessment of the data seemed to suggest bird distribution patterns were associated with different locations in Cockpit Country. Several species were excluded from the analysis because they occurred at too few points and were likely to mask distribution patterns among habitat specialists (Appendix 1). Spearman rank correlation was used to correlate CCA site scores with data on vegetation structure (tree density, tree height, and mean basal area) for the 49 sample units at which vegetation was measured.

The results were then represented graphically—species as points and environmental variables as arrows—with ordination diagrams, following Braak (1988). ArcView GIS 3.0 (Esri, Redlands, CA, USA) was also used to analyze the spatial abundance patterns of bird species in relation to the first two CCA axes, to further elucidate their influence on bird species distribution patterns.

Results

The first two CCA axes accounted for 77.4% of the variation explained by the analysis, while the third and fourth axes together accounted for 22.6% (Table 1). The following interpretation of the results is therefore restricted to the first two axes. The biplot scores for the environmental variables permitted interpretation of the axes (Table 1). Axis 1 expressed forest disturbance and to a lesser degree elevation. Since the two scores had opposite signs, the forest was less disturbed in higher elevation areas of Cockpit Country. Axis 2 mainly expressed an eastern direction, and to a lesser degree a northern direction and elevation. Thus, high axis 2 scores indicate eastern and north-eastern locations at somewhat high elevations.

The results of the CCA were used to create an ordination diagram as a biplot of species scores and environmental variables (Fig. 3). In order to reduce crowding and create space for plotting the points with less extreme values, axes were restrained in the diagram. Therefore, some species that fall outside the range of values plotted were shown along the edges in the diagram. Bird species with low (negative) axis 1 scores (Fig. 3) were best represented at undisturbed sites. These include Plain Pigeon, Crested Quail-Dove, Jamaican Pewee (*Contopus pallidus*), Blue Mountain Vireo, Rufous-throated Solitaire (*Myadestes genibar-*

bis), White-eyed Thrush (*Turdus jamaicensis*), Arrowhead Warbler (*Setophaga pharetra*), and Jamaican Blackbird. Conversely, bird species with high (positive) axis 1 scores were best represented at disturbed sites. These include Common Ground-Dove (*Columbina passerina*), Jamaican Mango (*Anthracothorax mango*), Green-rumped Parrotlet (*Forpus passerinus*), Sad Flycatcher (*Myiarchus barbirostris*), Gray Kingbird (*Tyrannus dominicensis*), Loggerhead Kingbird (*T. caudifasciatus*), Yellow-faced Grassquit (*Tiaris olivaceus*), and Black-faced Grassquit (*T. bicolor*).

Axis 2 most strongly reflects a west to east direction, and to a lesser degree south to north and elevation. Thus, bird species such as Yellow-billed Parrot and Yellow-faced Grassquit had their greatest abundance in the east and were towards the top of the ordination diagram (Fig. 3). On the other hand, those species with greatest abundance in the west—e.g., Jamaican Lizard-Cuckoo (*Coccyzus vetula*), Loggerhead Kingbird, and Greater Antillean Bullfinch (*Loxigilla violacea*)—were found towards the bottom of the figure. Both *Amazona* parrot species had negative axis 1 scores relatively close to zero, with Yellow-billed Parrot having a more negative axis 1 score and achieving greatest abundance in the east, while Black-billed Parrot appeared to be more abundant in western Cockpit Country. Several species with axis 1 and 2 scores that were intermediate and close to zero showed no abundance differences related to disturbance or location and were found clustered towards the center of the ordination diagram (Fig. 3). These include the Chestnut-bellied Cuckoo (*Coccyzus pluvialis*), Jamaican Crow (*Corvus jamaicensis*), White-chinned Thrush (*Turdus aurantius*), Bananaquit (*Coereba flaveola*), and Jamaican Oriole (*Icterus leucopteryx*).

Using ArcView GIS to map bird species distributions in relation to axis 1 and 2 facilitated the spatial interpretation of bird distribution patterns in Cockpit Country (Fig. 4). More than 50% of axis 1 high scores occurred in the low-elevation north-central region and the majority of the axis 1 low scores occurred at mid-to high-elevation sites towards the interior of Cockpit Country. When species abundance for each count was mapped, several species that have a strong association with undisturbed forests were found to attain their greatest abundance in the area of low scores—axis 1 low—for axis 1 (e.g., Plain Pigeon; Fig. 5a). Conversely, several species known to have a strong association with disturbed and open habitats had their greatest abundance outside the area of low scores for axis 1 (e.g., Black-faced Grassquit; Fig. 5b). Black-billed Parrot numbers were similar inside and

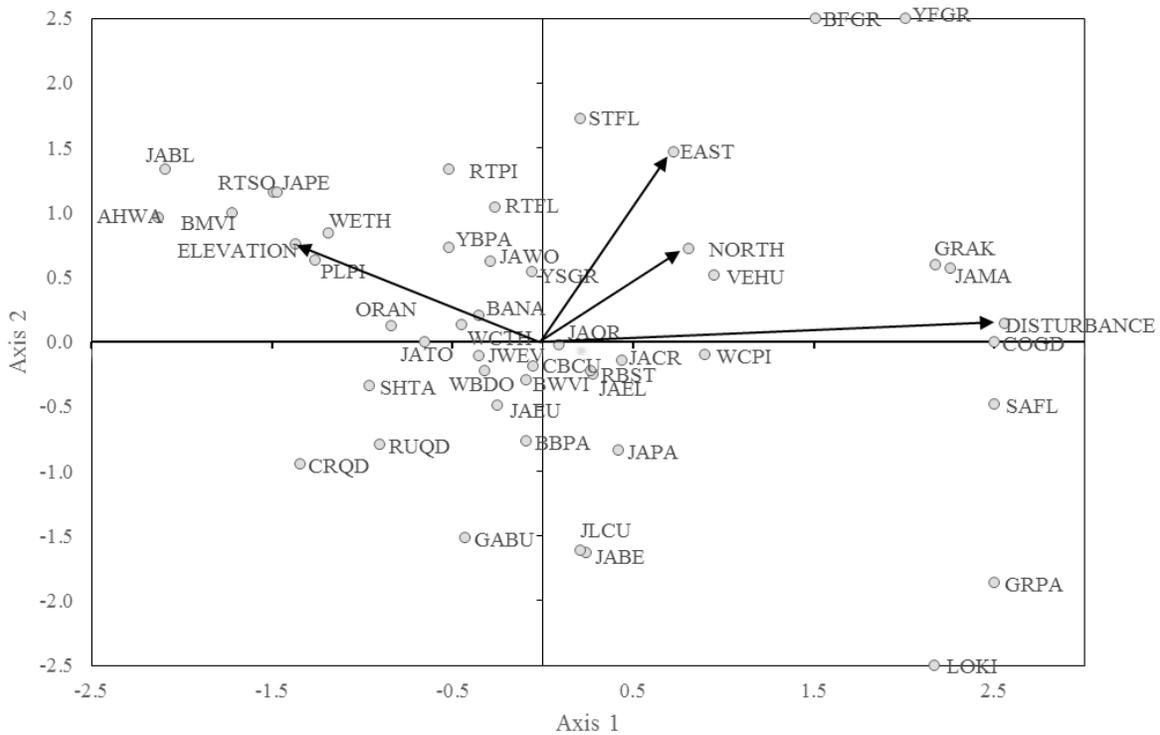


Fig. 3. CCA ordination diagram of 44 bird species and four environmental variables (arrows) from point counts in Cockpit Country, Jamaica. Arrowhead Warbler (AHWA), Bananaquit (BANA), Black-billed Parrot (BBPA), Black-faced Grassquit (BFGR), Blue Mountain Vireo (BMVI), Black-whiskered Vireo (BWVI), Chestnut-bellied Cuckoo (CBCU), Common Ground-Dove (COGD), Crested Quail-Dove (CRQD), Greater Antillean Bullfinch (GABU), Gray Kingbird (GRAK), Green-rumped Parrotlet (GRPA), Jamaican Becard (JABE), Jamaican Blackbird (JABL), Jamaican Crow (JACR), Jamaican Elaenia (JAEL), Jamaican Euphonia (JAEU), Jamaican Mango (JAMA), Jamaican Oriole (JAOR), Olive-throated Parakeet (JAPA), Jamaican Pewee (JAPE), Jamaican Tody (JATO), Jamaican Woodpecker (JAWO), Jamaican Lizard-Cuckoo (JLCU), Jamaican Vireo (JWEV), Loggerhead Kingbird (LOKI), Orangequit (ORAN), Plain Pigeon (PLPI), Streamertail (RBST), Rufous-tailed Flycatcher (RTFL), Ring-tailed Pigeon (RTPI), Rufous-throated Solitaire (RTSQ), Ruddy Quail-Dove (RUQD), Sad Flycatcher (SAFL), Jamaican Spindalis (SHTA), Stolid Flycatcher (STFL), Vervain Hummingbird (VEHU), Caribbean Dove (WBDO), White-crowned Pigeon (WCPI), White-chinned Thrush (WCTH), White-eyed Thrush (WETH), Yellow-billed Parrot (YBPA), Yellow-faced Grassquit (YFGR), and Yellow-shouldered Grassquit (YSGR).

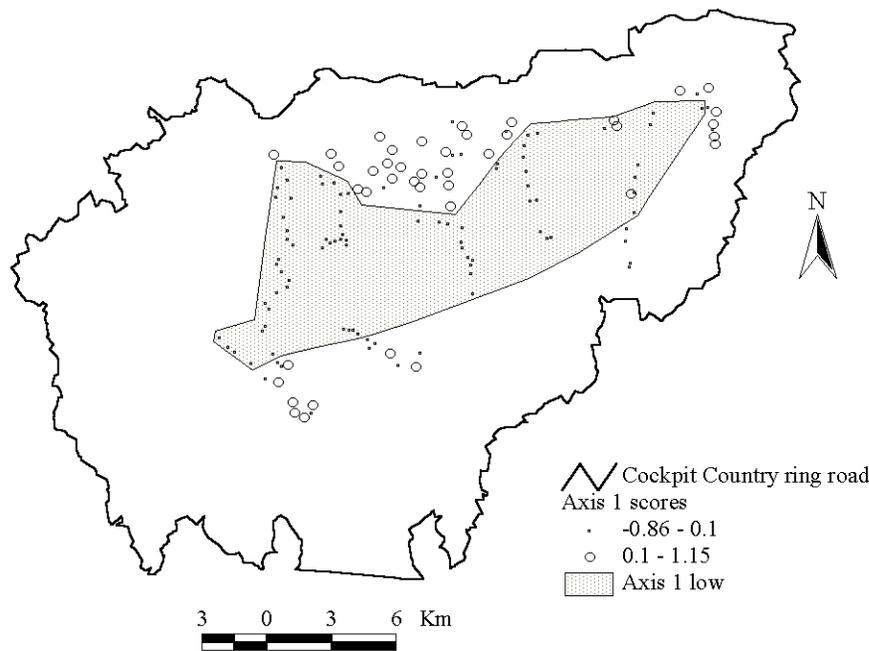


Fig. 4. The main region of low axis 1 scores derived from a CCA of the point count data collected in Cockpit Country, Jamaica.

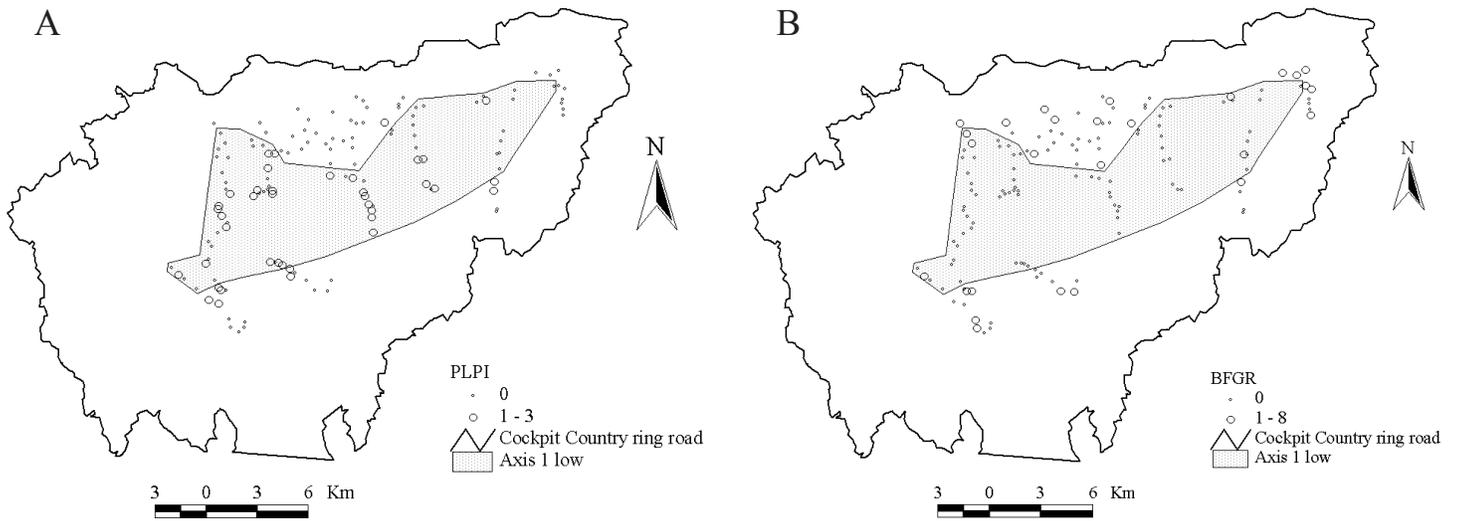


Fig. 5. Distributions of (a) Plain Pigeons and (b) Black-faced Grassquits in relation to CCA axis 1 in Cockpit Country, Jamaica.

outside of the area of low scores for axis 1, with birds concentrated in the north-central areas. On the other hand, Yellow-billed Parrot numbers were slightly greater in the area of low axis 1 scores, with some concentration towards the extreme east of Cockpit Country.

Examining spatial distribution patterns of bird abundance along axis 2 revealed some patterns that were not altogether clear because of the confluence of environmental variables expressed by this axis. Nonetheless, axis 2 scores revealed two areas for spatial analysis: an area of consistently low scores—axis 2 low—in the north-central region and an area of consistently high scores—axis 2 high—in the eastern regions of Cockpit Country. Outside these two distinct areas was a mix of low and high axis 2 scores. Spatial analysis of bird abundance across these two distinct axis 2 areas found clear patterns for several species with axis 1 and 2 scores that were intermediate and close to zero, such as both *Amazona* parrot species. The number of

Yellow-billed Parrots for each count was uniformly high in the axis 2 high area and uniformly low in the axis 2 low area (Fig. 6a). In contrast, the number of Black-billed Parrots for each count was fairly high and uniform in the north-central region and varied elsewhere in Cockpit Country (Fig. 6b). Among bird species typically found in disturbed areas, axis 2 scores seemed to indicate the extent to which these species were restricted towards the periphery of Cockpit Country. Species with low axis 2 scores such as the Loggerhead Kingbird were well represented in the disturbed north as well as utilizing disturbed areas penetrating deep into the Cockpit Country forest interior. On the other hand, species with high axis 2 scores such as Black-faced Grassquit and Yellow-faced Grassquit appeared to be more abundant in peripheral than interior disturbed forest.

The Spearman rank correlation analysis showed that axis 1 scores had a significant negative correlation with tree height, and a non-significant but negative correlation with mean basal

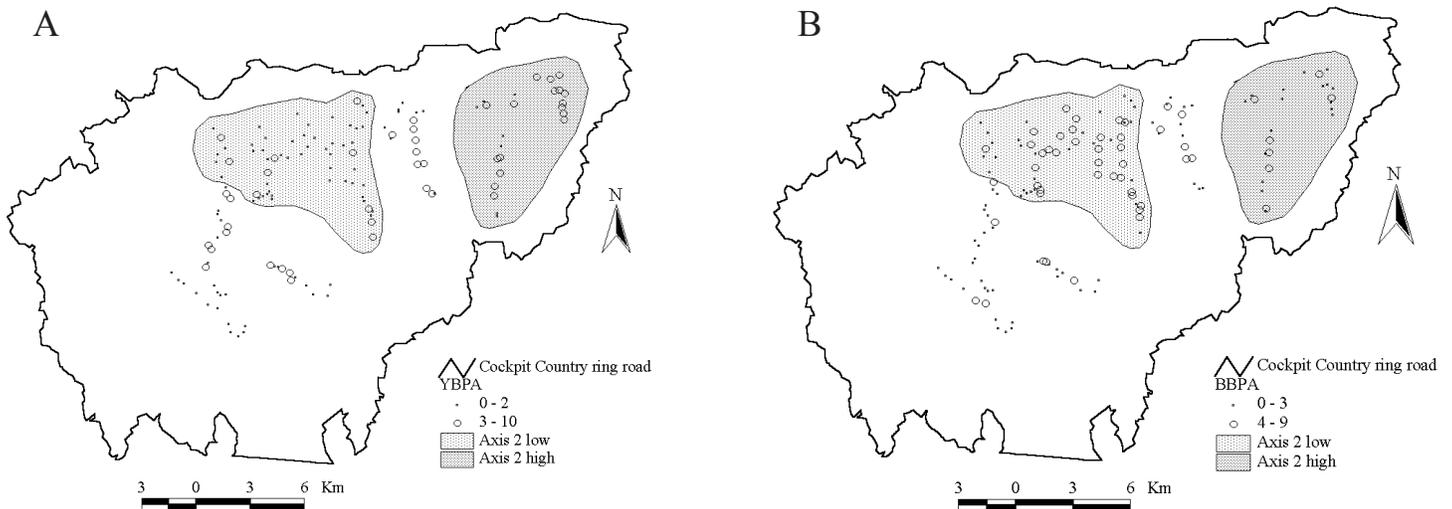


Fig. 6. Distributions of (a) territorial Yellow-billed Parrot pairs and (b) territorial Black-billed Parrot pairs in relation to CCA axis 2 low and high scores in Cockpit Country, Jamaica.

Table 2. Spearman rank correlation of site scores with vegetation structure variables for the first two axes derived from the CCA. *P*-values are given in parentheses. *N* = 49.

Axis	Tree Density	Tree Height	Mean Basal Area
1	0.15 (0.303)	-0.34 (0.017)*	-0.27 (0.061)
2	-0.22 (0.127)	-0.12 (0.453)	-0.04 (0.784)

*Significant negative correlation of tree height with axis 1.

area of trees (Table 2). Axis 2 showed no correlation with vegetation structure variables.

Discussion

Although the results of this study revealed an inter-relatedness of forest disturbance, elevation, and geographical position, it is clear that past and potentially future forest disturbance and degradation in Cockpit Country will have negative consequences for the persistence of many of Jamaica's threatened and endangered bird species. This evaluation of how avian abundance changes along environmental gradients provides important insight into the bird-habitat relationships in Cockpit Country. Forest disturbance had a clear influence on the abundance and distribution patterns of a number of bird species including Plain Pigeon, Jamaican Pewee, Rufous-throated Solitaire, White-eyed Thrush, Arrowhead Warbler, and Jamaican Blackbird. That these species showed the strongest negative response to forest disturbance suggests their reliance and perhaps interdependency on the island's natural forest ecosystems, making the case for preserving natural ecosystems such as Cockpit Country (Eyre 1995, Anadón-Irizarry *et al.* 2012).

Species such as the Jamaican Blackbird, whose populations are now restricted to three "habitat islands," are extreme habitat specialists that are vulnerable to even small-scale forest disturbance (Haynes-Sutton *et al.* 2009, BirdLife International 2017). Due to severe forest disturbance that has reduced the availability of suitable territories, these populations now have diminished dispersal opportunities and are potentially exposed to the effects of climate change, competition, brood parasitism from Shiny Cowbirds (*Molothrus bonariensis*), and possibly extinction in these habitat fragments. The arrival of Shiny Cowbirds on Puerto Rico in the 1970s led to the near extinction of Yellow-shouldered Blackbirds (*Agelaius xanthomus*), were it not for human intervention (Wiley *et al.* 1991, López-Ortiz *et al.* 2002). Despite these threats, the large numbers of Plain Pigeons (Fig. 5a) in undisturbed sections of Cockpit Country suggest the presence of a breeding population since detections were typically of calling birds. This is encouraging for the conservation of this species, now considered threatened throughout its range because of habitat loss, hunting, and predation by introduced mammals (Raffaele *et al.* 1998, Rivera-Milán *et al.* 2003, BirdLife International 2017).

The strong positive association between the distribution patterns of bird species such as Common Ground-Dove, Jamaican Mango, Green-rumped Parrotlet, Gray Kingbird, and Black-faced Grassquit and open disturbed areas of Cockpit Country is not surprising. Forest disturbance and habitat alterations

along the Cockpit Country periphery and at some interior locations (Barker and Miller 1995) appear to have created structural changes in the ecosystem that benefit these species. This suite of birds—a mix of endemic, native, and introduced species—all share common traits of tolerance and preference for open habitat and high levels of forest disturbance (Raffaele *et al.* 1998, Haynes-Sutton *et al.* 2009).

The use of one or more bird species as indicators of habitat quality can serve as an inexpensive but important conservation tool (O'Connell *et al.* 1998, Guilfoyle *et al.* 2009) for monitoring forest disturbance effects since birds are some of the most visible, vocal, and widely distributed of all vertebrate species in Cockpit Country. The results in this study suggest a suite of bird species that demonstrate strong positive and negative responses to forest disturbance that could serve as part of a monitoring program aimed at conservation in Cockpit Country. The ecological traits (e.g., nesting behavior, diet guilds, and habitat associations) found within such a group could make them suitable targets that are easy to assess for monitoring the health of the ecosystem. But, the influence of forest disturbance and other variables on the distribution patterns of many bird species assessed in this study was unclear due to the concurrence of some variables which confounded interpretation of the results, suggesting that the methodology and approach are in need of further development before its application as a monitoring tool.

The distribution and abundance of Black-billed Parrot, as assessed in this study, was not strongly influenced by forest disturbance. This species occurred in the same relative numbers at most sites and was better represented in more disturbed areas of Cockpit Country than Yellow-billed Parrot. On the other hand, Yellow-billed Parrots appeared to show a response to forest disturbance as indicated by the larger number of territorial pairs detected within the Cockpit Country interior. That this observed pattern in Yellow-billed Parrot distribution may be the direct result of forest disturbance finds support in results from the study by Koenig (1999), where Yellow-billed Parrots showed a preference for nesting in trees with larger DBH. Although the Spearman rank correlation analysis of vegetation structure suggests that as forest disturbance became more severe, trees had a tendency to be shorter and have lower mean basal areas, vegetation assessments were not carried out in parrot territories, so the correlation analysis results may not necessarily explain the parrot distribution patterns observed.

The influence of elevation on bird distribution patterns was not easily discernible because of the disproportionate distribution of disturbed sites at low-elevation areas and undisturbed sites at mid- and high-elevation areas in Cockpit Country. This unintended geographic distribution of disturbed and undisturbed sites, a consequence of using existing trails and roads to establish sample units (Fig. 2) because of the rugged and difficult terrain, may have produced the negative relationship between axis 1 and elevation (Table 1), making interpretation of the results difficult.

The concurrence of variables expressed by axis 2 also made interpretation of bird distribution patterns difficult. The presence of forest and non-forest dependent species along axis 2 suggests that a complex set of environmental factors, not measured in this study, produced the distribution patterns observed. But, it is generally agreed that diversity and abundance of birds

increases with floristic (tree species richness in each stratum) and structural (number of different strata occurring) vegetative diversity (Perfecto *et al.* 2003, Carlo *et al.* 2004), though the specific mechanisms behind the relationship in ecosystems can be complicated and not easily ascertained (Dietsch *et al.* 2007).

Despite inherent deficiencies in this study (e.g., limited assessment of physical and biotic variables and limited coverage and distribution of sample units), the results suggest that forest disturbance in Cockpit Country negatively impacts the abundance and distribution of ecologically sensitive species. Currently, the ecosystem continues to support a biologically diverse bird community, where no species are missing but some populations are rare. However, increasing threats to the integrity of the old-growth forest ecosystem from yam stick and lumber harvesting, bauxite mining, and the still undeclared preserve boundary (Koenig *et al.* 2000, Williams 2008, Williams-Raynor 2015) may inevitably result in the loss of Jamaica's rare and endangered species, since changes outside the natural range of variation in Cockpit Country forests could disconnect the habitat selection stimuli of individual bird species from factors that ultimately determine their success.

Classifying the sample units according to their distance from forest edge could lead to more meaningful interpretation of the results in this study since the distance of suitable habitat from forest edge can influence bird demography (Kennedy *et al.* 2010). Also, since the results demonstrate that ecologically sensitive species will become rare with forest disturbance and these species tend to have poor dispersal ability through degraded matrix habitats (Kennedy and Marra 2010), future studies should incorporate forest edge/matrix assessments in Cockpit Country to better understand how the matrix may act as a barrier to movement of these species between suitable habitats (Saunders *et al.* 1991, Wiegand *et al.* 2005).

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Appendix 1. List of avian species recorded in Cockpit Country during bird surveys in 1998 and 1999. Alpha codes are of species included in the correspondence analysis. Neotropical migrants were not included in the study.

Family	Common Name	Scientific Name	Alpha Code
Columbidae	White-crowned Pigeon	<i>Patagioenas leucocephala</i>	WCPI
	Plain Pigeon	<i>P. inornata</i>	PLPI
	Ring-tailed Pigeon	<i>P. caribaea</i>	RTPI
	Common Ground-Dove	<i>Columbina passerina</i>	COGD
	Crested Quail-Dove	<i>Geotrygon versicolor</i>	CRQD
	Ruddy Quail-Dove	<i>G. montana</i>	RUQD
	Caribbean Dove	<i>Leptotila jamaicensis</i>	WBDO
	White-winged Dove	<i>Zenaida asiatica</i>	
	Zenaida Dove	<i>Z. aurita</i>	
	Mourning Dove	<i>Z. macroura</i>	
Cuculidae	Chestnut-bellied Cuckoo	<i>Coccyzus pluvialis</i>	CBCU
	Jamaican Lizard-Cuckoo	<i>C. vetula</i>	JLCU
Trochilidae	Smooth-billed Ani	<i>Crotophaga ani</i>	
	Jamaican Mango	<i>Anthracothorax mango</i>	JAMA
	Vervain Hummingbird	<i>Mellisuga minima</i>	VEHU
	Streamertail	<i>Trochilus polytmus</i>	RBST
Ardeidae	Cattle Egret	<i>Bubulcus ibis</i>	
Accipitridae	Red-tailed Hawk	<i>Buteo jamaicensis</i>	
Todidae	Jamaican Tody	<i>Todus todus</i>	JATO
Picidae	Jamaican Woodpecker	<i>Melanerpes radiolatus</i>	JAWO
Falconidae	American Kestrel	<i>Falco sparverius</i>	
	Psittacidae	Olive-throated Parakeet	<i>Eupsittula nana</i>
	Green-rumped Parrotlet	<i>Forpus passerinus</i>	GRPA
	Yellow-billed Parrot	<i>Amazona collaria</i>	YBPA
	Black-billed Parrot	<i>A. agilis</i>	BBPA
Tyrannidae	Jamaican Elaenia	<i>Myiopagis cotta</i>	JAEL
	Jamaican Pewee	<i>Contopus pallidus</i>	JAPE
	Sad Flycatcher	<i>Myiarchus barbirostris</i>	SAFL
	Rufous-tailed Flycatcher	<i>M. validus</i>	RTFL
	Stolid Flycatcher	<i>M. stolidus</i>	STFL
	Gray Kingbird	<i>Tyrannus dominicensis</i>	GRAK
	Loggerhead Kingbird	<i>T. caudifasciatus</i>	LOKI
Tityridae	Jamaican Becard	<i>Pachyramphus niger</i>	JABE
Vireonidae	Blue Mountain Vireo	<i>Vireo osburni</i>	BMVI
	Jamaican Vireo	<i>V. modestus</i>	JWEV
	Black-whiskered Vireo	<i>V. altiloquus</i>	BWVI
Corvidae	Jamaican Crow	<i>Corvus jamaicensis</i>	JACR
Turdidae	Rufous-throated Solitaire	<i>Myadestes genibarbis</i>	RTSO
	White-eyed Thrush	<i>Turdus jamaicensis</i>	WETH
	White-chinned Thrush	<i>T. aurantius</i>	WCTH
Mimidae	Northern Mockingbird	<i>Mimus polyglottos</i>	

Appendix 1. cont.

Family	Common Name	Scientific Name	Alpha Code
Fringillidae	Jamaican Euphonia	<i>Euphonia jamaica</i>	JAEU
Parulidae	Arrowhead Warbler	<i>Setophaga pharetra</i>	AHWA
Thraupidae	Bananaquit	<i>Coereba flaveola</i>	BANA
	Yellow-faced Grassquit	<i>Tiaris olivaceus</i>	YFGR
	Black-faced Grassquit	<i>T. bicolor</i>	BFGR
	Orangequit	<i>Euneornis campestris</i>	ORAN
	Greater Antillean Bullfinch	<i>Loxigilla violacea</i>	GABU
	Yellow-shouldered Grassquit	<i>Loxipasser anoxanthus</i>	YSGR
Incertae sedis	Jamaican Spindalis	<i>Spindalis nigricephala</i>	SHTA
Icteridae	Jamaican Blackbird	<i>Nesopsar nigerrimus</i>	JABL
	Greater Antillean Grackle	<i>Quiscalus niger</i>	
	Jamaican Oriole	<i>Icterus leucopteryx</i>	JAOR

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