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Distribution, Abundance, and
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Crow, *Corvus jamaicensis*

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Distribution, Abundance, and Conservation Status of the Jamaican Crow, *Corvus jamaicensis*

Gary R. Graves^{1,2,*} and Brian K. Schmidt¹

Abstract - The arrival of West Nile virus in Jamaica has raised concerns about the conservation status of the endemic *Corvus jamaicensis* (Jamaican Crow), which has been largely restricted to the interior highlands since the 17th century. We conducted an island-wide survey of Jamaican Crow populations using playback of crow vocalizations from 2008 through 2013. Crows were detected at 370 of 1432 playback sites, mostly in the interior highlands of St. Ann and Trelawny parishes where they are locally common. Crows were absent from the Blue Mountains and from a broad band spanning the entire southern coast. Some crows were found in moderately undisturbed limestone forest in Cockpit Country and in the John Crow Mountains, but the majority was observed in anthropogenic habitats, including the patchworks of agriculture, second-growth forest, and pasture that characterize rural landscapes in Jamaica. Preliminary population estimates of <2900 individuals indicate the Jamaican Crow is one of the rarer passerine species in the Western Hemisphere.

Introduction

The endemic *Corvus* spp. (crows) of the West Indies represent a remarkable island radiation that has been largely overlooked by evolutionary biologists, biogeographers, and conservationists. Four or five species are recognized, depending on the taxonomic authority (AOU 1998, Garrido et al. 1997, Olson and Hilgartner 1982). This paper concerns the historic and current geographic range and conservation status of *Corvus jamaicensis* Gmelin (Jamaican Crow; Fig. 1). As far as is known, this small crow evolved in situ and has never occurred outside Jamaica (10,991 km²). In contrast, at least 3 other species of West Indian crows once occurred on multiple islands. *Corvus leucognaphalus* Daudin (White-necked Crow) formerly occurred on Puerto Rico and St. Croix, Virgin Islands (Wetmore 1927), but is now restricted to Hispaniola, where fragmented populations are declining (Keith et al. 2003, Wiley 2006). The widespread *Corvus nasicus* Temminck (Cuban Crow) remains common in Cuba (Garrido and Kirkconnell 2000) and in the Caicos Islands, but fossils show that it once occurred widely in the Bahamas (Olson and Hilgartner 1982). The Hispaniolan and Cuban populations of *Corvus palmarum* Württemberg (Palm Crow) are often considered to be conspecific (AOU 1998, Bond 1956). Other authorities, however, have classified *C. palmarum* as the Hispaniolan Palm Crow and identified *Corvus minutus* Gundlach (Cuban Palm Crow) as specifically distinct because of substantial differences in voice, behavior,

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Figure 1. Territorial *Corvus jamaicensis* (Jamaican Crow) responding to playback of vocalizations.

plumage color, and size (Cory 1892, Garrido et al. 1997, Keith et al. 2003, Ridgway 1904). The geographic range of the Hispaniolan Palm Crow has contracted, but the species remains locally common in Haiti and the Dominican Republic (Keith et al. 2003). The Cuban Palm Crow has evidently been rare and locally distributed for the past century (Barbour 1943, Garrido and Kirkconnell 2000, Garrido et al. 1997). Fossils from New Providence show that palm crows once occurred in the central Bahamas (Olson and Hilgartner 1982). In sum, the geographic ranges of at least 3 of the 5 species of West Indian crows have undergone significant contraction since the arrival of humans.

We were prompted to initiate an island-wide survey of the Jamaican Crow by the recent discovery of West Nile virus in Jamaica birds (Dupuis et al. 2003) and the high mortality rate observed in North American corvids exposed to the virus. Here, we provide the first comprehensive review of the distribution and abundance of the Jamaican Crow.

Historical distribution of the Jamaican Crow

Historical records (pre-1900) of the Jamaican Crow (hereafter also referred to simply as “crow”; all other species of crows are specifically named) are sparse, geographically vague, and can be adequately summarized in a few paragraphs (Browne 1756, Gosse 1847, March 1863, Scott 1893, Sloane 1725). Hans Sloane (1725:298) reported the crow during his visit to Jamaica from 1687 to 1688, the first literature reference that can be identified to this species:

“It frequents the Mountains, where it loves to be always making chattering noise, different from that of any of the European Crows. It is very much in the north-side of the Island.”

Browne (1756:473–474) added:

“This bird is a native of Jamaica, and very common in the cooler inland woody parts, though seldom seen in the more open savannas. They are extremely cautious and watchful, very noisy, and seem to imitate the sounds of most syllables in every language, in their gabblings.”

The definitive early account was provided by Gosse (1847:209–211), whose wonderfully baroque narrative again emphasized the highland distribution of the crow:

“In the wildest parts of the mountain regions of Jamaica, where the perilous path winds round a towering cone on the one hand, and on the other looks down into a deep and precipitous gully; or where a narrow track, choked with tree-ferns on which the vertical sun looks only at noon-day, leads through the dark and damp forest ... the traveller is startled by the still wilder tones of the Jabbering Crow. So uncouth and yet so articulate, so varied in the inflexions of their tones, are these sounds, that the wondering stranger can with difficulty believe he is listening to the voice of a bird, but rather supposes he hears the harsh consonants, and deep guttural intonations of some savage language. ... In some parts of the mountains they are not uncommon, though their loquacity would induce us to think them more numerous than they are,

for we rarely see more than two or three at once ... They scarcely ever desert the solitudes of the mountains; two thousand feet is the lowest limit at which I have known them, with two exceptions. The one is that in certain lofty woods surrounding the extensive morass in the Saltspring Pen, near Black river, I have heard the voices of these birds clamorously uttered, in the latter part of November. The other instance occurred behind Pedro Bluff, but little above the level of the sea, where I heard this bird in June.”

March (1863:300), who was based in Spanish Town, gave no information on the geographic range of the crow, although he apparently traveled to highland areas in St. Ann, St. Mary, and Manchester parishes (Graves 2013) where the crow is found today. His account of colonial breeding suggests that his crow information was obtained from specious second-hand sources:

“They build in company like rooks, on the loftiest forest trees, and are then very fierce. I have for several years endeavored to induce the settlers in the vicinity of their breeding trees to procure me eggs of this species, but they have always declined, fearing an encounter with the parent birds.”

The only early record from eastern Jamaica was from Priestmans River, Portland Parish (Scott 1893:178):

“These birds were not uncommon at a point known as Egg Hill about three miles inland from Priestman’s River and about one thousand feet in altitude. Here, in a practically unsettled wilderness, I procured some six or eight individuals at various times, and this was the only point where I observed them.”

The first post-1900 summary described the Jamaican Crow as “found only in the wilder parts of the mountains” (Bangs and Kennard 1920). The vast majority of subsequent reports, including more than 50 undocumented sight records published in the Gosse Bird Club Broadsheet (1963–1998) and its successor, the BirdLife Jamaica Broadsheet (1998–2014), also originated from the interior highlands (Cruz 1971, Danforth 1928, Graves 2009a, Haynes-Sutton et al. 2009, Jeffrey-Smith 1956, Lack 1976). The overall impression gleaned from recent records (post-1963) is that the Jamaican Crow can be dependably observed at about a dozen locations in north-central and western Jamaica and in the John Crow Mountains. It appears to be absent or rare in the remainder of the island, including the accessible portions of the Blue Mountains. BirdLife International listed the conservation status of the Jamaican Crow as “least concern” (BirdLife International 2014), based on a pair of dated references (Madge and Burn 1994, Stotz et al. 1996), which in turn appear to be based on 60-year-old anecdotes (Jeffrey-Smith 1956). Haynes-Sutton et al. (2009) listed the species as “locally common” and included a map that showed a continuous geographic range along the entire northern versant of Jamaica.

Field-site Description

Jamaica has a relatively high population density (251 people/km²; World Bank 2015). Thirty-one percent of the land area is currently covered with forest, and only

8% (88,000 ha) is classified as primary forest (Food and Agriculture Organization of the United Nations 2010). Point-count surveys for Jamaican Crows were conducted island-wide in 13 of 14 Jamaican parishes. Surveyed habitats included wet and dry limestone forest, lower-montane rainforest, mangroves, gardens and orchards, landscaped suburban gardens, shaded coffee plantations, pasturelands with scattered old-growth trees, pine plantations, tree-lined roads traversing pasturelands, church yards, riverine gallery forest, reclaimed bauxite mines, and patchworks of secondary woodland, bamboo, agricultural scrub, pasture, and sugarcane, banana, and coconut plantations. No surveys were conducted in sugarcane monocultures or low-stature ruinate scrub where crows have never been observed. Topography at survey points varied from level floodplains to knife-like ridges above steep slopes ($>70^\circ$). Surveys were restricted to sites with $>15\%$ canopy cover, broadly defined, and at least some trees or palms >10 m in height. The latter constraint was instituted because Jamaican Crows have never been recorded in habitats lacking a substantial number of taller trees. Most survey sites were located along quiet rural roads, with fewer sites along primary roads, 4-wheel drive tracks, and foot trails.

Methods

Surveys with playback broadcast

We learned basic information about the natural history and distribution of Jamaican Crows from 1994 to 2008 while conducting fieldwork on *Limnothlypis swainsonii* (Audubon) (Swainson's Warbler; Graves 1996, Winker and Graves 2008) and the hummingbirds *Trochilus polytmus* L. (Red-billed Streamertail) and *T. scitulus* (Brewster & Bangs) (Black-billed Streamertail) (Graves 2009b, 2009c, 2015; Harvey et al. 2015; Lance et al. 2009; McCormack et al. 2011). Jamaican Crows defend large year-round territories against the incursion of their neighbors (G.R. Graves and B.K. Schmidt, unpubl. data; S. Koenig, Windsor Research Centre, Trelawny Parish, Jamaica, unpubl. data). Although vocalizing crows are difficult to overlook, singletons as well as territorial pairs can be remarkably quiet and secretive and may be easily missed during standard 5–10-minute census periods. We quickly learned that the only effective way to survey crows was with the aid of playback broadcast of crow vocalizations. Playback vastly increases the detectability of territorial avian species (see Ralph and Scott 1981). Singletons, pairs, and family groups of the Jamaican Crow respond strongly to playback from distances as great as 400 m. Crows typically fly toward the playback while uttering raucous yodels and caws and often circle the sound source. Effective broadcast distance is attenuated in valley bottoms, but repeated playback trials indicated that most, if not all individuals, within 300 m of the playback source can be detected in all landscapes. This assumption was validated by the behavior of crows (50–400 m from playback source) that were spotted before playback commenced. We conservatively estimated the effective survey radius to be 300 m, thereby sweeping an area of ~ 0.28 km² (600 m in diameter). Crows reported here were all observed within 300 m of the survey point. We measured distances and tree heights with a Bushnell® laser rangefinder (model 20-1354).

Playback was broadcast from a dual-speaker boombox (77 dB at 20 m) at each survey site. The playback recording consisted of a mixture of caws and yodels made by an agitated pair of crows in response to playback. Speakers were rotated every 5–10 s. We tried two different playback protocols. The first consisted of 2 minutes of playback, followed by a minute of silence, another minute of playback, and a final minute of silence. The second method consisted of 3 minutes of playback followed by 2 minutes of silence. These similarly effective protocols were alternated during the first survey day in December 2008, but afterward the simpler second playback protocol was used. Playback efficiency was reduced when wind speeds exceeded 20 km/h, probably because the effective range of the broadcast was attenuated. Thus, an additional 30 s of playback was broadcast when wind or traffic noise was excessive. Crow response appeared to be undiminished during periods of mist or light rain. However, we suspended surveys when wind speeds exceeded 25 km/h or when rain was heavier than drizzle. Playback was paused as soon as crows responded. If 2 or more crow territories occurred within the effective range of the playback, vocalizing crows frequently perched in sentinel trees near presumed territorial boundaries. In those cases, we took additional time after the survey period to observe territorial interactions and to determine whether pairs were accompanied by a third or fourth individual. We took notes after each survey period.

We conducted surveys during the non-breeding season (30 November–17 December) from 2008 through 2013. Some crows in Trelawny Parish begin staging for communal roosting in late afternoon (16h45–18h00). Roosting crows depart at dawn (06h00–06h22) and rapidly return to their day territories (Graves 2009a). For that reason, surveys were restricted to mid-day (07h15–15h30). Both authors were present at each survey site.

Survey site selection

Statisticians recommend a stratified random-sampling design to survey finite populations when complete censuses are impractical or impossible (Borchers et al. 2002, Cochran 1977, Seber 1973). In an ideal world, each Jamaican Crow subpopulation would be sampled independently, site accessibility would be unconstrained by anthropogenic contingencies, and detection probabilities for each age and sex class would be perfectly known at each site. These conditions are rarely achievable for non-colonial birds, especially for poorly known species with large home ranges and secretive behavior (Ralph and Scott 1981).

Although we were able to solve the detectability conundrum with playback, we were compelled to abandon a stratified random-sampling approach for 3 reasons: (1) subpopulation distributions were unknown until the survey was completed, (2) habitat accessibility varied widely across the island, and (3) cultural sensitivities made a priori selection of randomly chosen survey sites impossible. The later factor was especially significant in small hamlets and towns that dot the Jamaican countryside. Crow vocalizations (and playback) are loud and considered by many Jamaicans to be obnoxious. One cannot simply pick a random point on the Jamaican map and expect to conduct a playback survey at that site. We avoided conducting

playback surveys near homes, pedestrians, schools, and church services. Secondary factors for survey site selection included road safety and good sight lines. We adopted a minimum distance criterion for spacing survey sites based on the observed spacing of crow territories in high-density populations in St. Ann Parish. If crows were detected at a survey site, we established subsequent survey sites at least 1000 m away. If no crows were detected at a survey point, we established subsequent survey sites as close as 700 m. We determined distance between survey sites with a GPS receiver.

Results

We conducted 1432 point surveys of crows on 81 field days: 4–16 December 2008 (13 field days), 3–16 December 2009 (14 field days), 2–15 December 2010 (14 field days), 30 November–15 December 2011 (16 field days), 30 November–10 December 2012 (11 field days), and 5–17 December 2013 (13 field days). We surveyed most secondary roads and many of the smaller unpaved tertiary roads in Jamaica. Survey waypoint tracks totaled 10,460 km. The cumulative area surveyed by survey points ($1432 \times 0.28 \text{ km}^2$) was equivalent to 3.7% of the land area of Jamaica (10,991 km^2). Survey sites were located from sea level to 1232 m asl: (i) 0–100 m ($n = 336$ sites); (ii) 101–300 m ($n = 490$ sites); and (iii) >300 m ($n = 606$ sites).

We conducted a disproportionate number of survey points in St. Ann, St. Mary, and Trelawny parishes, where crows reached their highest density and where crow habitat was widespread (Table 1). No surveys were located in the relatively small Kingston Parish (21.8 km^2), which consists primarily of industrial and commercial areas of downtown Kingston. The low density of survey sites (Fig. 2) on the southern coastal plain reflected the sparsity of suitable habitat. Few forest patches with trees tall enough (>10 m) to support crows remain in the southern portions of St. Elizabeth, Clarendon, St. Catherine, and St. Andrew parishes.

Table 1. Distribution of survey sites by parish for *Corvus jamaicensis* (Jamaican Crow).

Parishes	Parish area (km^2)	# of survey sites	Parish area/ # of survey sites	# of surveys with crows	Proportion of survey sites with crows
St. Ann	1213	232	5.23	144	0.62
Trelawny	875	167	5.24	64	0.38
Clarendon	1196	140	8.54	33	0.24
Portland	814	128	6.36	4	0.03
St. Mary	611	117	5.22	31	0.26
Westmoreland	807	96	8.41	15	0.16
St. Catherine	1192	96	12.42	23	0.24
Manchester	830	93	8.92	12	0.13
St. James	595	90	6.61	21	0.23
St. Elizabeth	1212	79	15.34	5	0.06
Hanover	450	70	6.43	16	0.23
St. Thomas	743	66	11.26	0	0.00
St. Andrew	431	58	7.43	2	0.03

We recorded crows at 370 survey sites (25.8% of total) located from sea level to 829 m asl: (i) 0–100 m ($n = 21$ sites), (ii) 101–300 m ($n = 113$ sites), and (iii) >300 m ($n = 236$ sites). Using nearest-neighbor distance (≥ 1 km) as a narrow criterion for defining new localities, we documented territories at more than 300 previously unreported locations. New localities were documented in all 12 parishes in which Jamaican Crows were observed, strong evidence that the distribution and abundance of the species were poorly known before the survey. Most occupied sites occurred at mid-altitudes. The upper altitudinal limit of crow distribution is unknown because relatively few survey sites occurred above 800 m ($n = 28$).

Most occupied sites (59.5%) were defended by a single pair of crows ($n = 220$ sites). Fewer sites (14.6% of those occupied) were occupied by singletons ($n = 54$ sites). Pairs accompanied by a third crow, presumably an immature from the previous breeding season, were observed at 22 sites (5.9% of those occupied). We documented 2 or more crow territories at 74 survey sites (20.0% of those occupied), including 10 sites with at least 1 pair accompanied by a third individual. Extra-pair

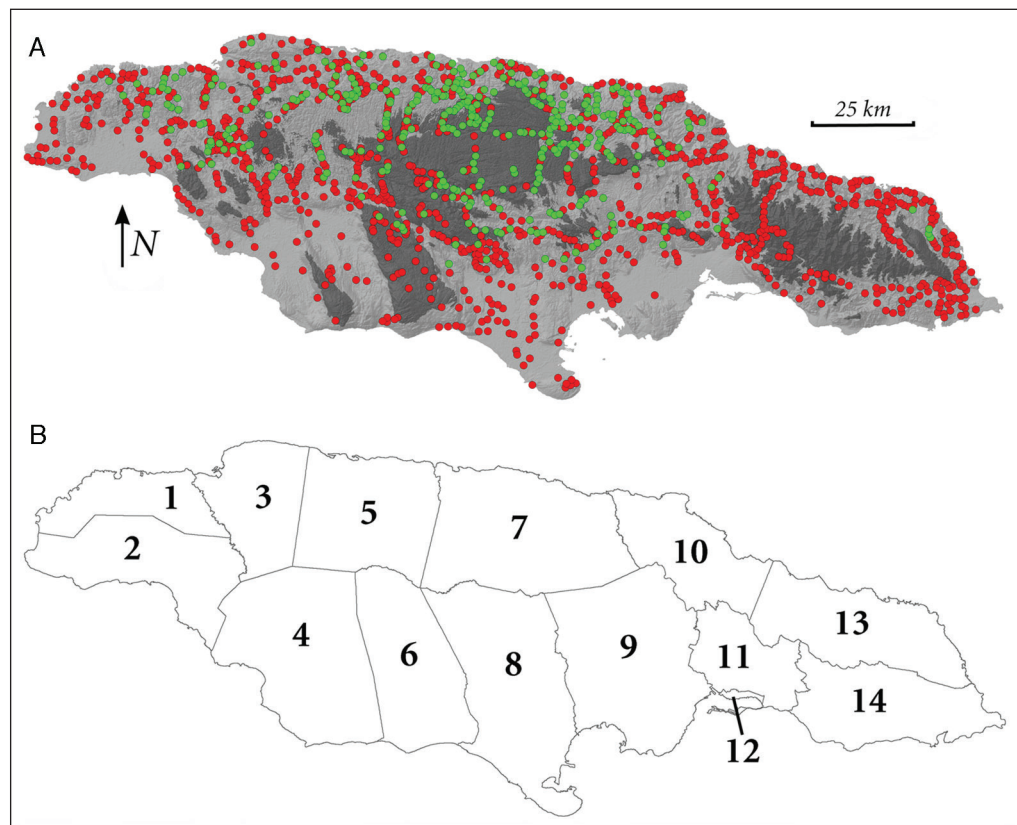


Figure 2. (A) Survey sites for *Corvus jamaicensis* (Jamaican Crow) in Jamaica: (1) green circles (crows present, $n = 370$); (2) red circles (no crows, $n = 1062$). Dark gray shading represents areas > 500 m asl. (B) Jamaican parishes: (1) Hanover; (2) Westmoreland; (3) St. James; (4) St. Elizabeth; (5) Trelawny; (6) Manchester; (7) St. Ann; (8) Clarendon; (9) St. Catherine; (10) St. Mary; (11) St. Andrew; (12) Kingston; (13) Portland; and (14) St. Thomas.

individuals were usually less aggressive but still responded to playback. Only occasionally were we able to study individuals closely enough to determine whether they were immature (characterized by subtly duller plumage). We observed a single instance of a pair accompanied by 2 individuals. In total, we observed pairs accompanied by a third or fourth individual at 33 sites (8.9% of those occupied). We recognized the possibility that supernumerary individuals could represent nest helpers but had no way of differentiating those from lingering offspring from the previous breeding season. It is worth noting that nest helpers or territorial defense by more than a pair has not been reported in the White-necked Crow of Hispaniola (Wiley 2006).

Discussion

Current distributional patterns

The geographic distribution of the Jamaican Crow is centered in north-central Jamaica where it is sparsely distributed but locally common on the northern frontier of Cockpit Country in Trelawny Parish and in the Dry Harbour Mountains in St. Ann Parish (Table 1, Fig. 2). Several surprising aspects of crow distribution surfaced during the survey. First, crows were absent from a broad swath along the southern coast from Negril at the western tip of Jamaica to the eastern terminus of the island in St. Thomas Parish. Of particular note, crows were absent from the May Day Mountains in Manchester Parish, and from the Santa Cruz Mountains (914 m) in St. Elizabeth Parish, possibly because both ranges have been largely deforested. Nor were crows observed on Portland Ridge in Clarendon Parish, which supports the best remaining stands of dry limestone forest in southern Jamaica. With the exception of a recent report from Belmont Beach near Bluefields in Westmoreland Parish (Tate 2010), records reported by Gosse (1847) from Salt Spring Peninsula and Pedro Bluff, both in St. Elizabeth Parish, remain the only credible reports of crows on the southern coast in the past 168 years.

We confirmed the continued presence of a small crow population along the Ecclesdown Road on the eastern flank of the John Crow Mountains and at a single site on the northern end of the same mountain range, all in Portland Parish. These sites lie within a few kilometers of the Priestmans River site where Scott collected specimens in 1891 (Scott 1893).

We failed to find crows during the current survey in the Port Royal Mountains above Kingston or on the accessible lower slopes of the Blue Mountains in St. Thomas and Portland parishes. A review of our field notes and reports in the Gosse Bird Club Broadsheet (1963–1998) and BirdLife Jamaica Broadsheet (1998–2013) revealed 4 extralimital reports of crows from the southern versant of Jamaica. In extreme western Jamaica, a single bird was sighted at Sheffield, near Negril, Manchester Parish (Kristos 2010). In eastern Jamaica, a group of 4–5 crows was twice observed flying high near Hillside in St. Thomas Parish at the base the Blue Mountains (Scofield 1991). Crows were also observed on the trail between Bath and Corn Puss Pass (Siphron 1976), and a single crow was heard near Cuna Cuna Pass (743 m) on 28 March 2006 (G.R. Graves, unpubl. data).

Both passes lie on the ridge that connects the Blue Mountains and John Crow Mountains in St. Thomas Parish.

The paucity of records outside the core distributional range is surprising given the flight capacity of crows. The flight time required to reach any part of the island from the heart of the crow's distribution in St. Ann Parish is no more than a few hours. This suggests that fidelity to breeding territories is high, that natal dispersal distances are limited, and that there is no seasonal migration to the southern coastal plain.

Territory size and habitat preferences of Jamaican Crow

Crow territories were spaced at intervals of 0.95–1.4 km in areas of St. Ann Parish that exhibited the highest population density observed during the survey. This finding suggests that the minimum territory size is roughly 1.0 km². Territory size in thinly populated areas, especially near the range margins may be substantially larger. Our estimate of territory size is significantly larger than that reported for White-necked Crows in Hispaniola (Wiley 2006).

The Jamaican Crow is an omnivorous habitat generalist that feeds on invertebrates, small vertebrates, and a variety of native and introduced fruits (Gosse 1847; Cruz 1971; G.R. Graves and B.K. Schmidt, unpubl. data). The diet is thus similar to that of mainland species of *Corvus* (dos Anjos 2009) and the White-necked Crow of Hispaniola (Wiley 2006). Jamaican Crows occur in relatively dry areas (rainfall <1500 mm/year) on the northern coast of Trelawny and St. Ann parishes but also in the John Crow Mountains, one of the rainiest localities (>4000 mm/year) in the West Indies (Jamaica Meteorological Service 1963). On the other hand, they have never been recorded in the xeric limestone forest of Portland Ridge in Clarendon Parish, or in the Hellshire Hills in St. Catherine Parish.

The vast majority of crows were found in anthropogenic habitats (Fig. 3), including rural gardens near homesteads where most of the woody biomass consists of introduced fruiting or flowering trees (e.g., *Artocarpus altilis* (Parkinson) Fosberg [Breadfruit], *Blighia sapida* K.D. Koenig [Ackee], *Mangifera indica* L. [Mango], *Spathodea campanulata* P. Beauv. [Fountain Tree], *Syzygium malaccense* (L.) Merr. & L.M. Perry [Malaysian Apple]), *Cocos nucifera* L. (Coconut Palm), and *Bambusa vulgaris* Schrad. ex J.C. Wendl. (Common Bamboo). Few crow territories were located in moderately undisturbed limestone forest in Cockpit Country and the John Crow Mountains. Habitat quantification is complicated by large territory size and the variable size, number, and type of habitat patches that may occur within territorial boundaries. For example, a typical territory (1 km²) in the Dry Harbour Mountains in St. Ann Parish may encompass more than 2 dozen discreet woodlots and patches of mixed-crop agriculture and pasturage (Fig. 3B). Introduced fruiting plants were often observed on territories—e.g., *Musa* sp. (banana and plantain) and Ackee. The importance of introduced fruiting plants in the diets of crows is unknown, but it is worth noting that bananas and Ackee are cultivated island-wide in areas with annual rainfall >1000 mm. In several instances, we found crow territories in small towns featuring a mosaic of small-scale agricultural plantings and

fragments of cut-over secondary forest interspersed with goat pastures and the usual assortment of fruiting trees and coconut palms planted close to homesteads. Crows also occurred at several sites on cattle ranches where rural roads were lined with large spreading trees supporting heavy epiphyte loads, on the landscaped



Figure 3. Jamaican Crow territories in anthropogenic habitats in Manchester Parish (A) and St. Ann Parish (B).

grounds of Georgian-period great houses that featured a substantial number of large spreading trees (e.g., *Albizia saman* (Jacq.) F. Muell. [Raintree]), and in reclaimed bauxite mines where hilltop vegetation was largely untouched. Most notably, crows were absent from areas dominated by monocultures of banana, sugarcane, and coconut. There have been no records of crows from Kingston proper during the past 300 years, despite the long presence of landscaped estates and botanical gardens. On the other hand, crows are present in small numbers in the hilly residential areas of Ocho Rios in St. Ann Parish.

Is the range of the Jamaican Crow expanding?

There are no baseline data by which island-wide changes in the crow's geographic range can be quantified. With few notable exceptions, observational continuity in Jamaican localities has been insufficient to document claims of new locality records or range expansion. The best-documented report by a resident observer was communicated from Stewart Town in Trelawny Parish (Jeffrey-Smith 1952). She followed this report with a more extensive account (Jeffrey-Smith 1956:61):

“When 50 years ago, I first went to Trelawny, I was told that the Jabbering Crow was abundant in the hills near Stewart Town, but in inaccessible places. Later I was to learn that this was not strictly so. The birds did live in the remote hills behind Richmond Pen and Belmont, which were then large properties lying between Gibraltar and Stewart Town, not yet cut up into small holdings. However, ‘they come down in September’ to lower levels, driven by drought conditions, for they seem to like the cool, damp recesses of the deep woods. In recent years Jabbering Crows have increased considerably. No longer, in St. Ann, are they confined to Geddes Mountain or the lonelier parts of Lillyfield, but may be seen by the main road between Lumsden and Brown’s Town and near Moneague. In Trelawny they have increased even more rapidly and can be heard at any time at Good Hope near Falmouth, at Sportsman’s Hall or Mahogany Hall, adjoining properties near Jackson Town. ... What governs the movements of these birds? One appreciates the need of water driving them from their mountain fastnesses to lower levels when their natural supply in the wild pines fails. They will then come near human habitations. But, why to one place rather than to another? In Trelawny they were always abundant at Mahogany Hall, and yet never crossed over to Woodlands, and adjoining property, on the Stewart Town area until 1951, when flocks were seen flying across the dividing hill. In the immediate vicinity of Stewart Town, too, they were now to be seen. ... from Mahogany Hall to Quickstep in St. Elizabeth, as the crow flies, is not very far. There in the Cockpit Country they are readily seen. They are well-known at Windsor, Sherwood, Content.”

Jeffrey-Smith (1956) was the principal source for the secondary reference (Madge and Burn 1994) cited by BirdLife International (2014), which concluded that the “population is estimated to be increasing as the species appears to expand its range.” However, the perception of population increase could also reflect

Jeffrey-Smith's (b. 1881–d. 1973) growing awareness of the local distribution of crows and an increase in her leisure time and mobility as her teaching career in Stewart Town drew to a close after World War II. It is difficult to draw conclusions about population trends from anecdotal reports. The suggestion that crows make seasonal altitudinal movements is of interest because this phenomenon has not been conclusively documented elsewhere in Jamaica. It is possible that Jeffrey-Smith did not appreciate the large size of crow territories and confused seasonal exploitation of widely scattered food sources within territories for seasonal altitudinal movements between highland and lowland areas. The communal roosting behavior of crows may have also caused some confusion (Graves 2009a). Daily altitudinal movements associated with roosting behavior have been reported in the White-necked Crow in Hispaniola (Wiley 2006).

The most compelling report of recent range expansion originated from the mountainous suburbs of Kingston, where crows were observed at Stony Hill in St. Andrew Parish in 2005 and perhaps as early as 2003 (Fletcher 2006). Crows had previously been observed as early as 1990 at Castleton in St. Mary Parish, ~14 km north of Stony Hill, but there were no other prior reports from the immediate area of Kingston (Fletcher 1994, 2006). The history of ornithological observation from Stony Hill dates to 1890, when W.E.D. Scott spent 6 weeks observing birds and collecting specimens (Scott 1904). Scott stayed at Constant Spring and Stony Hill but never observed a crow until he traveled to Priestmans River in Portland Parish (Scott 1893). During the current survey of crow populations, we confirmed the presence of crows at 2 sites within 3 km of the city center of Stony Hill (Fig. 2: southeasternmost green circles in St. Andrew Parish) but failed to find crows at more than 2 dozen other survey sites in the foothills overlooking Kingston. While it appears that Jamaican Crows have expanded their range southeastward in the past 20 years, they appear to be rare and thinly scattered in St. Andrew Parish.

Global population size

Because we were unable to conduct a true census (a complete count of all individuals), we will not attempt a detailed analysis of population size. However, in order to obtain a first approximation of population size, we constructed concave polygons around sites where crows were recorded. The small eastern population in the John Crow Mountains was treated separately. The area of the western polygon was 4692 km² (42.7% of the land area of Jamaica). Examination of Google Earth Pro images of Jamaica and ground-truthing of landscapes during the survey suggest that ~60–80% of the area (2815–2753 km²) within the western polygon supported habitat that was at least superficially similar to that found in crow territories. Given a minimum territory size of 1.0 km², the ceiling on the number of crow territories would range from 2815 to 2753. Crows were observed at 366 (42.1%) of 869 strategically spaced survey sites (nearest-neighbor distance > 0.7 km) in suitable habitat within the polygon. Assuming a 42% occupancy rate of survey sites (600 m in diameter), and an average of 1.7 crows/territory, then the population size of the western population likely ranges from 2010 to 2680 individuals.

Much of the John Crow Mountains is inaccessible, but the geographic range of the eastern population is certainly less than 130 km², and perhaps less than 100 km². This suggests a maximum population size of ~200 individuals, assuming that 90% of the area is suitable. Combining estimates from the eastern and western subpopulations, the global population appears to be fewer than 2900 individuals. A more precise estimate may be possible by generating geographically explicit abundance surfaces, but that will depend on a more nuanced understanding of the range boundaries of the eastern and western populations. In any event, the Jamaican Crow appears to be one of the rarer passerine birds of the Western Hemisphere (Collar et al. 1992, Stattersfield and Capper 2000).

Factors limiting geographic range and population size

The causes underlying the crow's current rarity and its historic restriction to the interior highlands are unknown. Factors most frequently implicated in avian population decline and extinction on islands include habitat destruction (Olson and James 1982, Steadman 1995), pathogens (Warner 1968), introduced predators (Galbreath and Brown 2004, Savidge 1987), and hunting and direct human exploitation (Duncan et al. 2002). We briefly address each of these possible factors.

Cultivation of the coastal plain of Jamaica began with the arrival of the Tainos more than 1500 years ago (Rouse 1992), but the extent of land clearing by the Tainos has not been determined. One of the earlier calculations of agricultural clearing after European colonization was provided by Edward Long (1774:350): "land opened, cleared of its wood, and applied to pasturage or cultivation of some sort, the whole may be rated at six hundred thousand acres [2428 km²], without including the savannahs, which may reckoned to add about two hundred and fifty-thousand [1012 km²]." This implies that roughly a third of the island, and presumably most of the lowland forest <100 m asl, was cut over or significantly degraded by the mid-18th century. One could argue that habitat destruction alone was sufficient to explain the restriction of Jamaican Crows to the interior highlands of Jamaica from the 17th through 19th century (Browne 1756, Gosse 1847, Long 1774, Sloane 1725). However, the present-day occurrence of Jamaican Crows in harlequin mixtures of agriculture, pasturage, secondary scrub, and fruiting trees suggests one of 2 things: (1) crows were never restricted to old-growth forests or (2) crows have undergone a relatively recent habitat expansion analogous to that recently observed in breeding populations of Swainson's Warbler in the southeastern United States (Graves 2015). In either case, habitat specialization does not seem to be the cause of the current scarcity of the crow.

Two other potential factors also seem to be less likely explanations for the crow's small global population size. As mentioned earlier, the detection of West Nile virus in Jamaica (Dupuis et al. 2003) was the catalyst for the current survey of crow populations. However, there is no evidence that this pathogen or any other has affected crow populations in the past decade. Predation is more difficult to rule out as a pertinent factor. Jamaican Crows are relatively large (~335 g) and have no known nocturnal or diurnal avian predators (Graves 2009a). Predation

by the nocturnal and arboreal *Epicrates subflavus* Stejneger (Jamaican Boa) is thought to be minimal owing to the selection of thin branches in tall trees by roosting crows (Graves 2009a). However, incubating crows and their nestlings could be vulnerable as suggested by significant Jamaican Boa predation on adult and nestling parrots (Koenig 2001, Koenig et al. 2007). Chronic predation by the arboreal *Rattus rattus* (L.) (Black Rat) may have deleterious effects on populations of most Jamaican land birds (Graves 2013), but the size and aggressive behavior of adult crows may provide some immunity from rat predation on their eggs and nestlings.

Jamaican Crows have long been hunted for food. Sloane (1725:298) noted, “It is counted pretty good meat, but is not much sought after.” This could mean that at the time of his visit to the island (1687–1688) other species (e.g., pigeons, doves, parrots, macaws) were the preferred quarry of hunters or that the crow was good eating but that it was difficult to obtain because of its remote habitat and wild behavior. Browne (1756:474) observed, “They feed generally upon fruits and other vegetable productions, and are frequently served up at table while young.” However, Gosse (1847: 217) remarked, “The flesh is not eaten; but having a curiosity to taste it, I had one broiled. The flesh of the breast was well-tasted and juicy, but so dark, tough, and coarse-grained, that I should readily have mistaken it for beef.”

Although the Jamaican Crow is nominally protected by the Wild Life Protection Act of 1945, it and most other avian endemics are still frequently hunted for food in rural areas. During our recent survey, several residents of St. Catherine, St. Ann, and Trelawny parishes volunteered that crows were frequently eaten and that young were captured and fattened for the stew pot. Few people in rural areas possess firearms and ammunition for hunting. However, slingshots and bird lime, made from the latex-like sap of the Breadfruit, are widely used by boys and men to kill or capture birds. Communal roosting behavior (Graves 2009a) may make crows unusually vulnerable to systematic persecution. Finally, the Jamaican Crow is widely reviled by Jamaicans who live in its restricted geographic range because it is reputed to be a predator of eggs and nests and a pest of bananas, plantains, and the fruit of planted trees, and because the crow’s wild yodeling calls are considered to be both ominous and irritating. Long-term survival of the Jamaican Crow may well hinge on changes in public opinion.

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Literature Cited

- American Ornithologists' Union (AOU). 1998. Check-list of North American Birds. Seventh Edition. Washington, DC, USA. 829 pp.
- Bangs, O., and F.H. Kennard. 1920. A list of the birds of Jamaica. Government Printing Office, Kingston, Jamaica. 18 pp.
- Barbour, T. 1943. Cuban ornithology. *Memoirs of the Nuttall Ornithological Club* 9:1–144.
- BirdLife International. 2014. Species factsheet: *Corvus jamaicensis*. Available online at <http://www.birdlife.org>. Accessed 6 March 2014.
- Bond, J. 1956. Check-list of the Birds of the West Indies. Fourth Edition. Academy of Natural Sciences of Philadelphia, Philadelphia, PA, USA. 214 pp.
- Borchers, D.L., S.T. Buckland, and W. Zucchini. 2002. Estimating animal abundance: Closed populations. Springer-Verlag, London, UK. 314 pp.
- Browne, P. 1756. The Civil and Natural History of Jamaica. Printed for the author, and sold by T. Osborne and J. Shipton, London, UK. 503 pp.
- Cochran, W.G. 1977. Sampling Techniques. Wiley, New York, NY, USA. 428 pp.
- Collar, N.J., L.P. Gonzaga, N. Krabbe, A. Madrono Nieto, L.G. Naranjo, T.A.I. Parker, and D.C. Wege. 1992. Threatened birds of the Americas: The ICBP/IUCN Red Data Book, 3rd Edition, Part 2. International Council for Bird Preservation, Cambridge, UK. 1150 pp.
- Cory, C.B. 1892. Catalogue of West Indian birds. Published by the author, Boston, MA, USA. 163 pp.
- Cruz, A. 1971. Food and feeding behavior of the Jamaican Crow, *Corvus jamaicensis*. *Auk* 89:445–446.
- Danforth, S.T. 1928. Birds observed in Jamaica during the summer of 1926. *Auk* 45:480–491.
- dos Anjos, L. 2009. Family Corvidae (crows). Pp. 494–565, *In* J. del Hoyo, A. Elliott, and D.A. Christie (Eds.). Handbook of the Birds of the World. Vol. 14. Bush-shrikes to Old World Sparrows. Lynx Edicions, Barcelona, Spain.
- Duncan, R.P., T.M. Blackburn, and T.H. Worthy. 2002. Prehistoric bird extinctions and human hunting. *Proceedings of the Royal Society of London B* 269:517–521.
- Dupuis, A.P., P.P. Marra, and L.D. Kramer. 2003. Serologic evidence of West Nile virus transmission, Jamaica, West Indies. *Emerging Infectious Diseases* 9:860–863.
- Fletcher, J. 1994. Jamaican Crow. *Gosse Bird Club Broadsheet* 63:22.
- Fletcher, J. 2006. The Jamaican Crow: Is it increasing its range? *BirdLife Jamaica Broadsheet* 83:12–13.
- Food and Agriculture Organization of the United Nations. 2010. Global forest resources assessment 2010. FAO forestry paper 163, Rome, Italy. 378 pp.
- Galbreath, R., and D. Brown. 2004. The tale of the lighthouse-keeper's cat: Discovery and extinction of the Stephens Island Wren (*Traversia lyalli*) *Notornis* 51:193–200.
- Garrido, O.H., and A. Kirkconnell. 2000. Field Guide to the Birds of Cuba. Comstock Publishing, Ithaca, New York, NY, USA. 253 pp.
- Garrido, O.H., G.B. Reynard, and A. Kirkconnell. 1997. Is the Palm Crow, *Corvus palmarum* (Aves: Corvidae), a monotypic species? *Ornithologia Neotropical* 8:15–21.
- Gosse, P.H. 1847. The birds of Jamaica. Bentley, Wilson and Fley, London, UK. 447 pp.
- Graves, G.R. 1996. Censusing wintering populations of Swainson's Warbler: Surveys in the Blue Mountains of Jamaica. *Wilson Bulletin* 108:94–103.
- Graves, G.R. 2009a. Communal roosting of the Jamaican Crow (*Corvus jamaicensis*) *Journal of Caribbean Ornithology* 22:48–51.

- Graves, G.R. 2009b. Ontogeny of bill color in streamertail hummingbirds. *Journal of Caribbean Ornithology* 22:44–47.
- Graves, G.R. 2009c. Skeletal correlates of body weight in the Black-billed Streamertail (*Trochilus scitulus*) of Jamaica. *Caribbean Journal of Science* 45:1–4.
- Graves, G.R. 2013. Historical decline and probable extinction of the Jamaican Golden Swallow (*Tachycineta euchrysea euchrysea*). *Bird Conservation International* 24:239–251.
- Graves, G.R. 2015. Recent large-scale colonisation of southern pine plantations by Swainson’s Warbler, *Limnothlypis swainsonii*. *Bird Conservation International* 2015:1–14.
- Graves, G.R. 2015. A primer on the hybrid zone of Jamaican streamertail hummingbirds (Trochilidae: *Trochilus*). *Proceedings of the Biological Society of Washington* 128:111–124.
- Harvey, M.G., C.D. Judy, G.F. Seeholzer, J.M. Maley, G.R. Graves, and R.T. Brumfield. 2015. Similarity thresholds used in DNA sequence assembly from short reads can reduce the comparability of population histories across species. *PeerJ* 3:e895; DOI 10.7717/peerj.895.
- Haynes-Sutton, A., A. Downer, and R. Sutton. 2009. *A Photographic Guide to the Birds of Jamaica*. Princeton University Press, Princeton, NJ, USA. 304 pp.
- Jamaica Meteorological Service. 1963. *The rainfall of Jamaica*. Scientific Research Council, Jamaica. 18 pp.
- Jeffrey-Smith, M. 1952. Jabbering Crow (*Corvus jamaicensis*). *Natural History Notes of the Natural History Society of Jamaica* 54–55:127.
- Jeffrey-Smith, M. 1956. *Bird-watching in Jamaica*. Pioneer Press, Kingston, Jamaica. 159 pp.
- Keith, A.R., J.W. Wiley, S.C. Latta, and J.A. Ottenwalder. 2003. *The Birds of Hispaniola*. British Ornithologists’ Union and British Ornithologists’ Club, Tring, Hertfordshire, UK. 293 pp.
- Koenig, S.E. 2001. The breeding biology of Black-billed Parrot, *Amazona agilis*, and Yellow-billed Parrot, *Amazona collaria*, in Cockpit Country, Jamaica. *Bird Conservation International* 11:205–225.
- Koenig, S.E., J.M. Wunderle, and E.C. Enkerlin-Hoeflich. 2007. Vines and canopy contact: A route for snake predation on parrot nests. *Bird Conservation International* 17:79–91.
- Kristos, W. 2010. Jamaican Crow, *Corvus jamaicensis*. *BirdLife Jamaica Broadsheet* 91:21.
- Lack, D. 1976. *Island Biology, Illustrated by the Land Birds of Jamaica*. University of California, Berkeley, CA, USA. 445 pp.
- Lance, S.L., C. Hagen, T.C. Glenn, R.T. Brumfield, K.F. Stryjewski, and G.R. Graves. 2009. Fifteen polymorphic microsatellite loci from Jamaican streamertail hummingbirds (*Trochilus*). *Conservation Genetics* 10:1195–1198.
- Long, E. 1774. *The history of Jamaica or general survey of the ancient and modern state of that island with reflections on its situation, settlements, inhabitants, climate, products, commerce, laws, and government*. Vol. 1. T. Lowndes, London, UK. 628 pp.
- Madge, S., and H. Burn. 1994. *Crows and Jays: A Guide to the Crows, Jays, and Magpies of the World*. Christopher Helm, London, UK. 191 pp.
- March, W.T. 1863. Notes on the birds of Jamaica. *Proceedings of the Academy of Natural Sciences of Philadelphia* 15:283–304.
- McCormack, J.E., J.M. Maley, S.M. Hird, E.P. Derryberry, G.R. Graves, and R.T. Brumfield. 2011. Next-generation sequencing reveals phylogeographic structure and a species tree for recent bird divergences. *Molecular Phylogenetics and Evolution* 62:397–406.
- Olson, S.L., and W.B. Hilgartner. 1982. Fossil and subfossil birds from the Bahamas. *Smithsonian Contributions to Paleobiology* 48:22–56.

- Olson, S.L., and H.F. James. 1982. Fossil birds from the Hawaiian islands: Evidence for wholesale extinction by man before western contact. *Science* 217:633–635.
- Ralph, C.J., and J.M. Scott (Eds.). 1981. Estimating numbers of terrestrial birds. *Studies in Avian Biology* No. 6. 630 pp
- Ridgway, R. 1904. The birds of North and Middle America, Part 3. *Bulletin of the United States National Museum* 50:1–801.
- Rouse, I. 1992. *The Tainos: Rise and decline of the people who greeted Columbus*. Yale University Press, New Haven, CT, USA. 224 pp.
- Savidge, J. A. 1987. Extinction of an island forest avifauna by an introduced snake. *Ecology* 68:660–668.
- Scofield, R. 1991. Jabbering Crow. *Gosse Bird Club Broadsheet* 56:24.
- Scott, W.E.D. 1893. Observations on the birds of Jamaica, West Indies. II. A list of the birds recorded from the island, with annotations. *Auk* 10:177–181.
- Scott, W.E.D. 1904. *The Story of a Bird Lover*. MacMillan, New York, NY, USA. 372 pp.
- Seber, G.A.F. 1973. *The Estimation of Animal Abundance and Related Parameters*. Griffin, London, UK. 506 pp.
- Siphron, J. 1976. Cornpuus Gap birdlife. *Gosse Bird Club Broadsheet* 27:4–5.
- Sloane, H. 1725. *A voyage to the islands of Madera, Barbadoes, Nieves, St. Christophers, and Jamaica; with the natural history of the herbs and trees, four-footed beasts, fishes, birds, insects, reptiles, & c. of the last of those islands*. Vol. 2. Printed by B.M. for the author, London, UK. 499 pp.
- Stattersfield, A.J., and D.R. Capper (Eds.). 2000. *Threatened Birds of the World*. Lynx Editions. Cambridge, UK. 852 pp.
- Steadman, D.W. 1995. Prehistoric extinctions of Pacific island birds: Biodiversity meets zooarchaeology. *Science* 267:1123–1131.
- Stotz, D.F., J.W. Fitzpatrick, T.A. Parker, and D.K. Moskovits. 1996. *Neotropical Birds: Ecology and Conservation*. University of Chicago Press, Chicago, IL, USA. 478 pp.
- Tate, V. 2010. Jamaican Crow, *Corvus jamaicensis*. *BirdLife Jamaica Broadsheet* 91:21.
- Warner, R.E. 1968. The role of introduced diseases in the extinction of the endemic Hawaiian avifauna. *Condor* 70:101–120.
- Wetmore, A. 1927. *The Birds of Porto Rico and the Virgin Islands: Psittaciformes to Passeriformes*. New York Academy of Sciences, New York, NY, USA. 407–598 pp.
- Wiley, J.W. 2006. The ecology, behavior, and conservation of a West Indian corvid, the White-necked Crow (*Corvus leucognaphalus*). *Ornithologia Neotropical* 17:105–146.
- Winker, K., and G.R. Graves. 2008. Genetic structure of breeding and wintering populations of Swainson’s Warbler. *Wilson Bulletin* 120:433–445.
- World Bank. 2015. Population density (people per sq. km of land area). Available online at <http://data.worldbank.org/indicator/EN.POP.DNST>. Accessed 31 March 2015.