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Density and abundance of the Black-billed Streamertail (*Trochilus polytmus scitulus*) in eastern Jamaica

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Abstract The Jamaican endemic Streamertail (*Trochilus polytmus*) is divided into two subspecies, the Red-billed Streamertail (*T. p. scitulus*). The Black-billed Streamertail occupies less than 600 km² in the John Crow and Blue Mountains of eastern Jamaica, yet appears to be locally common. However, a formal population assessment is needed to better assess its conservation status. In February 2014, I conducted a point count survey (n = 530) and used distance sampling around the perimeter of the John Crow Mountains and in the southeastern portion of the Blue Mountains to estimate density and abundance of the Black-billed Streamertail population. The probability of detection within 40 m (mean ± SE) estimated under the model with the lowest AIC score was 0.105 ± 0.012 , density was 955 ± 122 individuals/km², and global abundance was $314,100 \pm 40,267$ individuals within the 329 km² survey area. Some problems were detected with model fit. An independent calculation using the variable circular plot method yielded a smaller global abundance estimate of 108,017 individuals. Both methods indicate that the population is much larger than previously thought, and support the current IUCN status of Least Concern. Continued monitoring of this important endemic is recommended to better understand habitat preferences and future population trends.

Keywords Black-billed Streamertail, conservation status, distance sampling, population survey, *Trochilus polytmus scitulus*, variable circular plot method

Resumen Densidad y abundancia de *Trochilus polytmus scitulus* en el este de Jamaica—La especie *Trochilus polytmus*, endémica de Jamaica, está dividida en dos subespecies. *T. p. polytmus* y *T. p. scitulus*. Esta última ocupa menos de 600 km² en las montañas John Crow y Blue Mountains del este de Jamaica y parece ser todavía localmente común. Sin embargo, se necesita llevar a cabo una evaluación formal de la población para evaluar mejor su estado de conservación. En febrero de 2014, llevé a cabo un muestro de puntos de conteo (n = 530) y empleé el método de muestros de distancia alrededor del perímetro de las montañas John Crow y en la parte sureste de las Blue Mountains para estimar la densidad y abundancia de la población de esta subespecie. La probabilidad de detección dentro de los 40 m (media ± ES) estimada según el modelo con la puntuación AIC más baja fue de 0,105 ± 0,012, la densidad fue de 955 ± 122 individuos/km² y la abundancia global fue de 314.100 ± 40.267 individuos dentro del área de muestreo de 329 km². Se detectaron algunos problemas con el ajuste del modelo. Un cálculo independiente utilizando el método de parcelas circulares de radio variable arrojó una estimación de abundancia global más pequeña de 108.017 individuos. Ambos métodos indican que la población es mucho mayor de lo que se pensaba anteriormente y respaldan el estado actual de la UICN de Preocupación Menor. Se recomienda el monitoreo continuo de esta importante endémica para comprender mejor las preferencias de hábitat y las futuras tendencias poblacionales.

Palabras clave estado de conservación, muestreo de distancia, muestreo poblacional, parcelas circulares de radio variable, Trochilus polytmus scitulus

Résumé Densité et abondance du Colibri à bec noir (*Trochilus polytmus scitulus*) dans l'est de la Jamaïque—Le Colibri à tête noire (*Trochilus polytmus*), une espèce endémique de Jamaïque, comprend deux sous-espèces: le Colibri à tête noire (à bec rouge) *T. p. polytmus* et le Colibri à tête noire (à bec noir) *T. p. scitulus*. Le Colibri à bec noir occupe moins de 600 km² dans les John Crow et Blue Mountains, dans l'est de la Jamaïque mais semble être localement commun. Cependant, une évaluation rigoureuse de

Louisiana State University Museum of Natural Science, 119 Foster Hall, Baton Rouge, LA 70803, USA; Department of Vertebrate Zoology, MRC-116, National Museum of Natural History, Smithsonian Institution, PO Box 37012, Washington, DC 20013, USA; e-mail: caroline.duffie@gmail.com la population est nécessaire pour mieux connaître son état de conservation. En février 2014, un relevé par points (n = 530) a été réalisé et la méthode d'échantillonnage par distance sampling a été utilisée dans les John Crow Mountains et la partie sud-est des Blue Mountains pour estimer la densité et l'abondance de la population de l'espèce. La probabilité de détection à moins de 40 m (moyenne ± ET) estimée dans le modèle avec le score d'AIC le plus bas était de 0,105 ± 0,012, la densité de 955 ± 122 individus/km² et l'abondance globale de 314.100

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± 40.267 individus dans la zone des relevés de 329 km². Certains problèmes ont été détectés dans l'ajustement du modèle. Un calcul indépendant utilisant la méthode appelée variable circular plot method a donné une estimation de l'abondance globale plus réduite de 108.017 individus. Les deux méthodes indiquent que la population est beaucoup plus importante qu'on ne le pensait auparavant et confirment le classement de l'état de conservation par l'UICN dans la catégorie Préoccupation mineure. Le suivi continu de cette espèce endémique importante est recommandé afin de mieux comprendre ses préférences en matière d'habitat et les tendances futures de sa population.

Mots clés Colibri à bec noir, distance sampling, état de conservation, étude de la population, *Trochilus polytmus scitulus*, variable circular plot method

Two subspecific forms of the endemic Streamertail (*Trochilus polytmus*) occur on Jamaica. The Black-billed Streamertail (*T. p. scitulus*) is geographically restricted to the extreme eastern end of the island (Brewster and Bangs 1901, Gill *et al.* 1973, Graves 2015). It is replaced to the west by the Red-billed Streamertail (*T. p. polytmus*) and the two are known to hybridize (Gill *et al.* 1973, Graves 2015). The males of both species possess the velvet black crests, emerald gorgets, and elaborate tail plumes from which their common name is derived (Fig. 1), but are distinguished by bill color, which is jet black in the Black-billed Streamertail, and coral red in the Red-billed Streamertail. Despite its much smaller geographic range, the Black-billed Streamertail is currently classified by the IUCN as Least Concern (BirdLife International 2016). However, a formal population survey is needed to more rigorously assess its population status.

The Black-billed Streamertail's range in the John Crow and Blue Mountains is composed primarily of wet montane forest and surrounding coastal lowlands (Gill *et al.* 1973). In the north of the range, the species occupies the north-facing slopes of the John Crow Mountains east of the Río Grande Valley; this area receives the highest levels of precipitation in Jamaica (Gill *et al.* 1973). Along Jamaica's southern coast, it is found east of the Morant River Valley. The Red-billed Streamertail is widely distributed across most of the rest of the island (Bond 1936, 1956). Where



Fig. 1. Male Black-billed Streamertail in adult plumage perched near Cunha Cunha Pass Trail in Portland Parish, Jamaica. Photograph by Caroline Judy.

their ranges meet in the Río Grande Valley, they form a narrow zone of hybridization (Gill *et al.* 1973, Graves 2015). Some researchers view these sister taxa as separate species and suggest that they may represent a rare example of *in situ* speciation on a small island (Coyne and Price 2000); Jamaica is less than 11,000 km². The distributional limits of the two subspecies and the geographic boundaries of their hybrid zone are well characterized (Gill *et al.* 1973, Coyne and Price 2000). However, the evolutionary mechanisms that maintain their phenotypic, and arguably, genotypic distinctiveness in the face of ongoing hybridization are unknown and currently under investigation (Graves 2009a, 2009b, Lance *et al.* 2009, McCormack *et al.* 2012, Graves 2015).

Both the male and the female Black-billed Streamertail produce call notes (Schuchmann 1977). The Black-billed Streamertail call is a simple, repeated, high-pitched note that can be heard up to 200 m away, depending on habitat features. The typical male song is a squeaky, trilling vocalization (Schuchmann 1977, 1980). In addition, the fluttering wing feathers of adult males produce a shrill whirring noise (Gosse 1847, Clark 2008). This fluttering is detectable at close range (i.e., within 15 m). Little is known about female song, and females do not produce the whirring noise in flight.

Schuchmann (1999) speculated that there were approximately 12 pairs/km² of Red-billed Streamertails in the Blue Mountains and 3-6 pairs/km² of Black-billed Streamertails in the vicinity of Port Antonio (Portland Parish) and Bath (St. Thomas Parish), although the year(s) and season(s) on which these estimates were based are unspecified. Wunderle et al. (1992) reported that prior to Hurricane Gilbert in 1988, population densities of the Red-billed Streamertail were 0.77 individuals per census point in montane cloud forest habitats, with lower densities in other habitats and at lower elevations. While Schuchmann's (1999) observations suggest that the population density of the Blackbilled Streamertail may be lower than that of the Red-billed Streamertail, the lack of current population information for either subspecies limits comparisons. The smaller range size and potentially lower density of the Black-billed Streamertail may make it more susceptible to population declines related to habitat disturbance. In this study, I conducted a point count survey and used conventional distance sampling methods (Buckland et al. 2001) to provide a rigorous assessment of population density and global abundance of the Black-billed Streamertail.

Methods

The point count survey protocol was field-tested in January 2014 on a Red-billed Streamertail population in Trelawny Par-

ish. I then conducted a survey of the Black-billed Streamertail population over 19 days (5–23 February 2014) in Portland and St. Thomas Parishes between 0615 and 1800. The rough terrain and limited access to large regions within the range of the Black-billed Streamertail prevented the use of a randomized survey design. I conducted the point count survey along roads, community footpaths, and forestry trails. Roughly 90% of the survey was conducted via a four-wheel drive vehicle. I traveled on foot along community footpaths in a few areas where there were no larger roads. I spaced the survey points at least 200 m apart in order to minimize counting the same bird at multiple consecutive census points.

I surveyed primary and secondary montane rain forest, gardens, orchards, landscaped residential areas, mixed agricultural areas such as shaded coffee groves, forested perimeters of banana and coconut plantations, taro fields, pasturelands, and patchworks of small agricultural plots near homesteads. A point count station was considered suitable if it supported at least 10% forest cover (visually estimated) within a 15 m radius of the station. Additionally, stations had to be located within 10 m of a tree that was at least 10 m high. These criteria helped to exclude poor habitat areas such as large monocultures of sugar cane and other crops, open pastures, and fallow fields. I also avoided surveying near town centers, churches, schools in session, or noisy homesteads where human activities hindered the survey effort.

After arriving to a point, I recorded the date, time of day, geographic coordinates, and elevation using a Garmin® Vista HCx GPS (Garmin International, Inc., Olathe, KS, USA). I made notes on the weather conditions and habitat features, including visible nectar sources. After these data were recorded, at least two observers (CDJ and one other) scanned the area for Black-billed Streamertails using Nikon Monarch 8×42 binoculars (Nikon, Tokyo, Japan) during a 3-min counting period. The horizontal distance to each detected individual was measured or estimated using a Simmons® LRF 6oo rangefinder (Simmons, Overland Park, KS, USA) or a Garmin® Vista HCx GPS and recorded in a field notebook. After the counting window, additional notes on nectar sources were also recorded, as well as the presence of other nectar-feeding birds. Finally, digital photographs were taken to further document habitat features.

We detected individuals visually and aurally (fluttering, calling, or singing), and for each detected Streamertail, I noted whether the detection was visual or aural. In regions that were geographically within or near the zone of sympatry, I spent additional effort to identify each individual as a Black-billed Streamertail, Red-billed Streamertail, or putative hybrid. I also recorded details on sex, molt, and behavior when possible. These data were used collectively to determine the minimum number of Blackbilled Streamertail individuals at each point.

The survey area encompassed most of the known geographic range for the Black-billed Streamertail (Fig. 2). I constructed a minimum convex polygon (MCP) around all survey points using the minimum bounding geometry tool in ArcGIS software version 10.2 (Esri, Redlands, CA, USA). The total area of the resulting MCP was 453 km². I assessed the habitat suitability within the MCP using the LU1998 coverage layer available from the Forestry Department (www.forestry.gov.jm/resources/maps). I designated regions as "unsuitable" that were described in the LU1998 coverage layer as "tree crops, shrub crops, sugar cane, and banana." While small agricultural areas and the tree-lined edges of large agricultural fields were suitable for the Blackbilled Streamertail, the deforested areas were not. Removing these areas from the MCP yielded an adjusted area of 422 km². I also used 2012 Google Earth Pro (Google, Mountain View, CA, USA) satellite images of Portland and St. Thomas Parishes to identify additional areas of deforestation. Visual inspection of Google satellite images revealed that an additional 15–20% of the MCP may be deforested or otherwise heavily impacted. Therefore, I conservatively set the size of the survey area to be 329 km², or 80% of the adjusted land area within the MCP.

Distance Sampling

Distance sampling allows rigorous estimation of density in the face of variability in detection (Buckland *et al.* 2001). A key assumption is that points are located at random with respect to the birds, such that changes in the number of birds observed with increasing distance from the point can be interpreted as changes in detectability, rather than density. More specifically, distance sampling uses the distribution of the observed distance

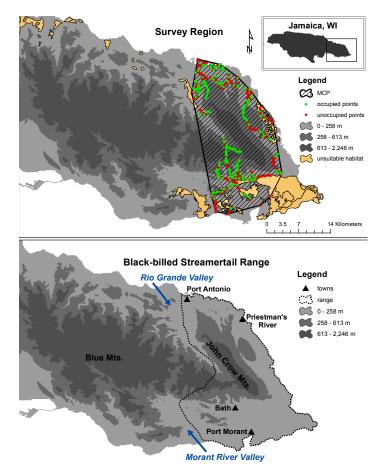


Fig. 2. Top: Survey Region. The shaded polygon represents the minimum convex polygon (MCP) drawn around points where Black-billed Streamertails were detected. Bottom: Black-billed Streamertail Range. The exact area of transition from the Black-billed Streamertail to the Red-billed Streamertail in the Blue Mountains is uncertain.

es to estimate a detection function g(y), which is the probability of detecting a bird at distance y. This function can then be used to estimate the average probability of detecting a bird within distance w of the point, denoted P_a . Given an estimate of P_a , bird density can be estimated as

$D = n/aP_a$

where *n* is the number of birds detected and *a* is the size of the covered region. Finally, abundance can be estimated by extrapolation of the estimated density within the covered region to the larger study area.

I evaluated the fit of the uniform, half-normal, and hazard-rate detection models with quantile-quantile plots and goodness-offit tests (Buckland *et al.* 2001) to six data filters corresponding to three data types (ungrouped, grouped using five equal cutpoints away from favored numbers, grouped using eight equal cutpoints), and two distance truncation schemes (w = 40 m, no truncation). Model selection was made using the Akaike's Information Criterion (AIC; Akaike 1973), and precision was estimated analytically (see details in Fewster *et al.* 2009, Thomas *et al.* 2010). All analyses were implemented in the Distance 7.2 software (Thomas *et al.* 2010).

Variable Circular Plot Method

I used the variable circular plot method (Reynolds *et al.* 1980) to provide an independent calculation of density and abundance for the Black-billed Streamertail population. I summarized the detections by their horizontal distances in 5 m bands around the point (i.e., at 5, 10, 15, 20 m, etc.). I then calculated the density of detections in each band by dividing the number of detections by the area of that band. The inflection point, or the distance at which detection densities decline more than 50%, serves as a guideline for drawing the effective census radius, beyond which observations are discarded (additional details in Reynolds *et al.* 1980). The calculation for density is based on only observations that fall within the effective census radius. Finally, I estimated abundance as the product of density, occupancy rate (proportion of points that were occupied vs. unoccupied), and the size of the survey region.

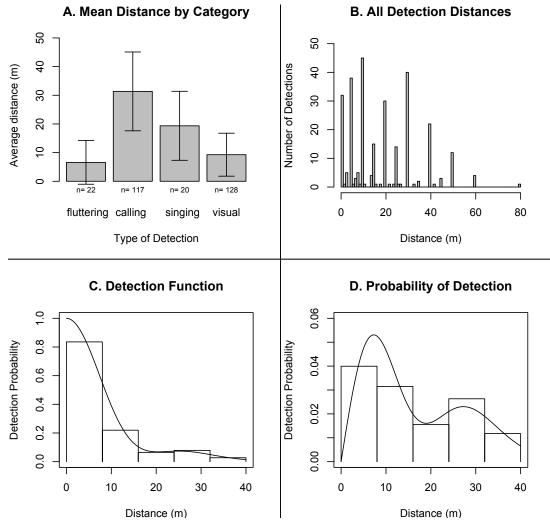


Fig. 3. (A) Mean distance to detected Black-billed Streamertails in four detection categories: fluttering, calling, singing, and visual. Number (*n*) of detections in each category is given. (B) Histogram of ungrouped distance data. Tendency to round to favored distances ("heaping") is apparent, as is rounding near to zero ("spiking"). Some evidence for over-dispersion at mid-range distances is also apparent. (C) Detection function fitted to data using a half-normal key model plus cosine adjustments. (D) Probability of detection.



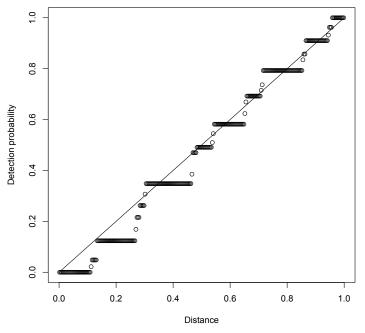


Fig. 4. Quantile-quantile plot corresponding to the fit of a half-normal detection function model with cosine adjustments. "Stepped" appearance relates to heaping at favored distances, and more detections than expected near g(o) suggest poor model fit.

Results

Distance Sampling

We detected a total of $_{287}$ individuals at $_{530}$ survey points. Aural detections ($n = _{159}$) constituted $_{55\%}$ of all detections (Fig. 3A). Fluttering detections occurred at the closest mean distance from the point (6.6 m), and calling detections occurred at the farthest mean distance ($_{31.4}$ m). The maximum detection distance was 80 m, considerably greater than the second largest distance, 60 m. As is common for point count surveys, there was a long tail of distribution; the median detection distance was 15 m.

Visual inspection of the data revealed a signal for an excess of observations at zero distance from the point ("spiking") which indicates rounding to zero. There was also a strong pattern of favored numbers ("heaping"), and appearance of over-dispersion (Fig. 3B), suggesting the data should be grouped into intervals for reliable analysis. Truncation of distances to 40 m removed 21 or 7.3% of observations from the dataset. Truncation improved reliability of the goodness-of-fit tests by increasing the expected values in the largest distance intervals, although it reduced precision (Tables 1 and 2).

The data filter with five equal cutpoints and truncation at 40 m had cutpoints away from favored numbers (Buckland *et al.* 2001; Thomas *et al.* 2010); therefore, it appears better suited to my dataset given the strong evidence for heaping. Of the models tested for this data filter, the half-normal key model with cosine adjustments had the lowest AIC score (Tables 1 and 2). The *p*-values associated with the χ^2 goodness of fit tests were significant across models for this data filter, but three orders of magnitude lower for the half-normal key model with cosine adjustments ($\chi^2 = 5.14$, df = 1, *p* = 0.023). The quantile-quantile plot (Fig. 4) revealed poor fit near to zero, such that more empirical detections were made than predicted by the model. Heaping was also apparent in the quantile-quantile plot.

Based on the data filter with five equal cutpoints away from favored numbers and truncation at 40 m, and the half-normal model with cosine adjustments, the probability of detection (mean \pm SE) was 0.105 \pm 0.012 (Cl: 0.084–0.131) within 40 m, the density was 955 \pm 122 (Cl: 43–227) individuals/km², and global abundance was 314,100 \pm 40,267 (Cl: 251,720–391,930) individuals within the 329 km² survey area. The detection function and the probability of detection plotted over histograms of the data are presented in Figs. 3C and 3D, respectively.

Table 1. Summary of AIC values for two truncation values, w = 40, and w = largest observation. The data were analyzed ungrouped and with two different groupings: five intervals of equal widths with cutpoints away from favored values, and eight intervals of equal widths. For each data type, an asterisk indicates which model had the smallest AIC score. Failed models are indicated by "n.a."

Data Type	Model (Key + Adjustment)	<i>w</i> = 40			w = largest observation		
		Number of Parameters			Number of Parameters		
		Key	Adjustments	AIC	Кеу	Adjustments	AIC
Ungrouped	Half-normal + cosine	1	3	3,503.8	1	4	3,831.8
	Half-normal + Hermite	1	0	n.a.	1	0	n.a.
	Uniform + cosine	0	4	3,300.6*	0	5	3,660.1*
	Hazard-rate + cosine	2	0	3,311.3	2	0	3,738.1
Grouped	Half-normal + cosine	1	2	820.3*	1	2	644.6*
(5 equal)	Half-normal + Hermite	1	0	896.4	1	0	700.1
	Uniform + cosine	0	4	823.2	0	2	789.7
	Hazard-rate + cosine	2	0	827.2	2	0	650.8
Grouped	Half-normal + cosine	1	4	1,048.2	1	4	848.1*
(8 equal)	Half-normal + Hermite	1	0	1,204.6	1	0	934.9
	Uniform + cosine	0	5	1,061.7	0	5	888.5
	Hazard-rate + cosine	2	0	1,038.4*	2	0	864.8

Table 2. Summary of the estimated density (*D*) and the coefficient of variation (*cv*) for two truncation values (*w*). The data were analyzed ungrouped and with two different groupings: five intervals of equal widths with cutpoints away from favored values, and eight intervals of equal widths. For each data type, an asterisk indicates the model with the smallest AIC score. Models that failed are indicated by "n.a."

Data Type	Model (Key + Adjustment)	Truncation					
		w = 4	40 m	w = largest observation			
		D	cv (%)	D	cv (%)		
Ungrouped	Half-normal + cosine	1,107.9	14.0	703.1	11.0		
	Half-normal + Hermite	n.a.	n.a.	n.a.	n.a.		
	Uniform + cosine	880.8*	12.0	410.0*	49,069.0		
	Hazard-rate + cosine	23,071.2	19.0	14,654.2	2,095,096.0		
Grouped	Half-normal + cosine	954.7	13.0	553.9*	10.0		
(5 equal)	Half-normal + Hermite	401.1	9.0	313.0	9.0		
	Uniform + cosine	889.8*	15.0	163.7	8.0		
	Hazard-rate + cosine	2,329.3	75.0	428.0	13.0		
Grouped	Half-normal + cosine	1,940.6	12.0	850.2	11.0		
(8 equal)	Half-normal + Hermite	452.9	9.0	315.7	8.0		
	Uniform + cosine	1,372.2	11.0	468.9	9.0		
	Hazard-rate + cosine	9,214.3*	102.0	792.2*	20.0		

Variable Circular Plot

Following the methods in Reynolds *et al.* (1980), I summarized detections by 5 m bands around the points. The inflection point occurred at 10 m (Fig. 5). Because of the issue with spiking, I conservatively set the effective census radius to 20 m, leaving a total of 187 individuals at 145 points with radius 20 m, or 1,026 individuals/km² of occupied habitat. Given an occupancy rate of 32%, the calculation for abundance was 108,017 individuals within the 329 km² survey region.

Discussion

In the current study, the Black-billed Streamertail density estimated by distance sampling (955 individuals/km²) and the variable circular plot method (1,026 individuals/km²) are roughly two orders of magnitude higher than a previous estimate of 3–6 pairs/km² (Schuchmann 1999). The difference could reflect population growth, seasonal effects, survey methods, or any combination of these three factors. Black-billed Streamertail occurrence in habitats such as gardens and churchyards suggests that they adapt well to human modifications of the landscape, and their populations may actually be increasing in low- and midelevations where agriculture and urban areas are expansive. The ability of the Red-billed Streamertail to feed on a wide variety of introduced nectar sources such as Syzygium jambos and Spathodea campanulata was noted by Lack (1976). Throughout the survey period, I frequently witnessed the Black-billed Streamertail feeding on these and other introduced plants. Hence, human activities, in some cases, may serve to enhance habitat quality for the Black-billed Streamertail by increasing the availability of nectar sources.

It is perhaps surprising that any land bird population on Jamaica or elsewhere in the Caribbean could thrive given the frequency and severity of hurricanes occurring there. Documented declines of several Caribbean bird species have occurred as a result of hurricanes and major storms (Raffaele 1977, Jeggo and Taynton 1980, Smith and Temple 1982, but see Varty 1991). However, Hurricane Gilbert, which devastated parts of Jamaica in 1988, did not cause drastic population declines for several species of land birds surveyed, at least in the short-term (Varty 1991). Wunderle *et al.* (1992) compared population densities of land birds on Jamaica before and after the hurricane, and showed that nectarivorous and frugivorous bird populations (including the Red-billed Streamertail) had sharper declines in local density after Hurricane Gilbert than did insectivorous bird



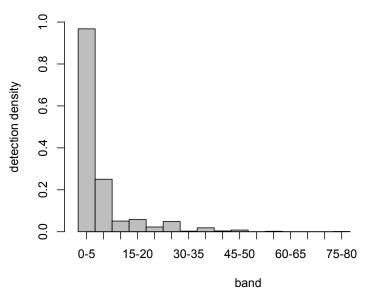


Fig. 5. Detection densities per 5 m band away from points. The inflection point of Reynolds *et al.* (1980) occurs at 10 m.

populations. However, the general pattern among localities was idiosyncratic: mean number of birds declined in two montane habitats, but increased in two lowland sites, and stayed the same in the remaining five lowland sites (Wunderle et al. 1992). Movement, rather than mortality, may have caused the majority of the change in local abundance. Black-billed Streamertail populations might be resilient to the adverse effects of hurricanes if they are able to move away from areas of heavy defoliation to avoid starvation. Given their high vagility and generalist foraging strategy (feeding on a wide variety of flowering plants), this is likely to be the case. Post-hurricane observations of the Blackbilled Streamertail in neighboring St. Andrew Parish (or approximately 20–25 km west of the known distribution) suggest they were either blown or flew out of their typical range in order to find nectar (Gosse Bird Club 1988, 1989). However, more studies are needed to better understand the impacts of human activity and natural disturbances on Black-billed Streamertail densities in different habitats.

The reliability of density and abundance estimates obtained with conventional distance sampling methods depends heavily on whether or not the data meet four key assumptions. First, distance modeling assumes that birds on the point are certain to be detected. Failure to detect all birds at zero distance from the point will result in a negative bias in the estimate of density and abundance (Buckland *et al.* 2001, 2008). The montane wet forests of the John Crow and Blue Mountains, like all tropical forests, have a complex vertical structure and low light levels. Both sexes can be fairly camouflaged against a green background in low light conditions. The inconspicuously plumed females can be especially difficult to detect. Therefore, I cannot rule out the possibility that some birds at zero distance from the point were missed.

Second, objects must be detected at their initial location. The mathematical theory underlying distance sampling assumes that random movement of objects does not occur. In reality, all birds move, which creates a bias because the probability of detection is a non-increasing function of distance from the point. Objects moving at random are more likely to be detected when moving closer to the point, leading to an under-estimate of distance and a positive bias in density estimation. In point counts, where the observer is stationary, overestimation due to random movement is especially problematic (Buckland et al. 2001). Some published studies have shown that density estimates can be inflated by as much as a factor of 10 due to these random effects (Bibby et al. 2000). A snapshot approach, in which distances to detected birds are measured in a snapshot moment (Buckland et al. 2001, Buckland 2006, Buckland et al. 2008), may help mitigate the positive bias caused by random and responsive movement during the counting period. This approach may prove effective for future surveys of the Black-billed Streamertail.

Movement of objects can also be non-random in response to the observer. Response to the observer may take the form of movement towards or away from the observer. Responsive movement away from the observer would lead to under-estimation of density, whereas movement toward the observer would lead to over-estimation of density (Bibby *et al.* 2000, Buckland 2006, Thomas *et al.* 2010). During my point count survey, Blackbilled Streamertail did not tend to exhibit highly evasive behavior, such as flushing in reaction to human activity. For example, in most cases, individuals that were singing continued to sing, foraging birds continued to feed, and dominant individuals appeared to be completely consumed with chasing away competitors, thus paying the human observers scant attention. For the current study, bias arising from evasive movement might be small, although bias arising from random movement could be large.

The third assumption of distance modeling is that distances to detected individuals are precisely measured (Buckland et al. 2001, Buckland 2006, Buckland *et al.* 2008, Thomas *et al.* 2010). From Buckland et al. (2001), if distances were underestimated by 10%, then densities would be overestimated by $100 \times (1/0.9^2 - 1)$ = 23%; if distances were overestimated by 10%, then densities would be underestimated by $100 \times (1 - 1/1.1^2) = 17\%$. In the current study, the use of a laser range finder increased the precision of distance estimates to visually detected objects. However, distance estimates for aural detections can only be approximated. Breeding bird surveys conducted in forest habitats can have up to 90% aural detections (Reynolds et al. 1980, Bibby et al. 2000). Somewhat surprisingly, only 55% of Black-billed Streamertail detections were aural, thereby limiting the impact of biased estimation relative to surveys for which there are higher percentages of aural detections. However, biased estimation could still be an issue for this survey. Examining the histogram of detection distances (Fig. 3B), there appears to be some signal for overdispersion, and the probability of detection function (Fig. 3D) tries to fit a smaller peak at around 30 m. Given that hummingbirds do not typically flush, this pattern could be the result of imprecise distance measurements, or an artifact caused by spiking.

Finally, the sampled plots must be representative of the entire region. Generally speaking, surveys conducted along roads and paths constitute a poor survey design and may bias survey data (Marques et al. 2007, but see Rivera-Milán et al. 2015 for an exception). I surveyed primarily along roads and community footpaths rather than using a randomized survey design or grid. If Otaheite apple (Syzygium malaccense), hibiscus (Hibiscus rosa-sinensis), grow stick (Gliricidia sepium), and other major nectar sources are planted preferentially along roads, then Streamertail density may be higher along roads than non-roads and would produce an upward bias in the population estimate. Apart from planted nectar sources, the openness of human modified forests, housing, or agricultural areas might represent a structural advantage for this species. Schuchmann (1999) noted that densities of Streamertails were lower in extremely thick vegetation. In reality, there was no way to avoid this potential source of bias in the present study because of the logistical constraints and the difficult terrain.

Mischaracterization of the larger region can also occur if census points are clustered too tightly together, which can lead to counting the same individuals across multiple census points. While counting the same bird across multiple survey points does not violate the assumptions of distance sampling *per se*, tight clustering can limit the survey's ability to detect variation in density across the larger region. By spacing the survey points at least 200 m apart, I minimized this source of bias. Because I was driving between census points for most of the survey (approximately 90%), instances of double counting were likely rare. Overall the survey points were well spaced throughout the larger region (excluding inaccessible areas; Fig. 2).

The spiking in the Black-billed Streamertail data can indicate a failure of model assumptions or a real biological feature (Thomas *et al.* 2010). Only adult males produce the whirring noise in flight. Therefore, some spiking may have occurred because there are more ways to aurally detect adult males at small distances from the point. Spiking can also arise if animals move toward the observer, although, as discussed above, Streamertails do not tend to display responsive behavior. Finally, rounding errors at small distances can also cause a spike in the data.

The density estimated for the variable circular plot method was based on occupied points only, while the density for the distance methods was based on both occupied and unoccupied points. This fact, together with the issues discussed above for model fit (spiking, rounding, etc.), suggests that the distance sampling analysis may have a positive bias, and the results should be interpreted with caution. The smaller global estimate of total abundance using the variable circular plot, which was adjusted for occupancy rate (108,017 individuals), may be more realistic.

Conclusions and Recommendations

The global estimate for Black-billed Streamertail abundance under both the variable circular plot method and distance methods support the current IUCN status of Least Concern. The more conservative global abundance estimate of 108,017 individuals from the variable circular plot method may be more reliable due to the potential overestimation of abundance in the distance sampling analysis. Ongoing monitoring of Black-billed Streamertail is recommended to better understand population trends, habitat preferences, and the impact of human and natural disturbance events.

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Dedication

This paper is dedicated to Mike Schwartz (1947–2018) for his contributions to Jamaican conservation.

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