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Bridled Quail-dove *Geotrygon mystacea* population assessment after hurricanes Irma and Maria, St. Eustatius, Caribbean Netherlands

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Summary

Structural vegetation damage and food limitation are important effects of major hurricanes, particularly for fruit/seed-eating, forest-dependent Caribbean birds with restricted distributions and small populations, such as the Bridled Quail-dove *Geotrygon mystacea*. Motivated by the lack of abundance estimates, corrected for detection probability, we conducted distance-sampling surveys inside and outside the Quill National Park each May in 2016-2019. Detection mode was the most important covariate, with others receiving no support from the data. Detectability of available single individuals and clusters of individuals within 60 m of transect centrelines averaged 0.957 ± 0.114 standard error for audio detections, 0.434 ± 0.052 for visual detections, and 0.693 ± 0.064 for detection modes combined. Availability averaged 0.475 ± 0.138 and the product of detectability and availability averaged 0.329 ± 0.098. Density averaged 1.459 ± 0.277 individuals ha^{-1} and population size averaged 642 ± 122 individuals in 440 ha. Density did not differ along and away from forest trails, but was higher inside than outside the park and at elevations within 201-400 m than 100-200 m and 401-600 m. Density declined by 76% after hurricanes Irma and Maria in 2017. We suggest that major hurricanes together with free-ranging livestock overgrazing degraded foraging habitats, limited food supply, and caused a population bottleneck. Our methodology can be implemented across the distribution range to assess population status and trends and evaluate the result of management actions at key conservation sites. Bridled Quail-dove populations probably were declining on most islands before the 2017 hurricanes and population status warrants revision.

Keywords: Bridled Quail-Dove, distance sampling, hurricanes, population assessment, St. Eustatius

Introduction

The intensity of hurricanes is increasing in the warming waters of the wider Caribbean (Goldenberg *et al.* 2001, Webster *et al.* 2005, Biasutti *et al.* 2012). The 2017 Atlantic hurricane season was the fifth most active on record, with six major hurricanes (i.e. category 3-5 on the Saffir-

Simpson scale), including hurricanes Irma (cat. 5, max. wind speed 285 km h^{-1}) and Maria (cat. 5, max. wind speed 280 km h^{-1}; www.nhc.noaa.gov/). The most evident direct effect of major hurricanes to mature forests is structural vegetation damage (Brokaw and Walker 1991, Boose *et al.* 2004, Eppinga and Pucko 2018). However, food limitation is an important indirect effect, particularly for fruit/seed-eating, forest-dependent Caribbean birds, such as quail-doves in the genus *Geotrygon* (Askins and Ewert 1991, Waide 1991, Wauer and Wunderle 1992, Wiley and Wunderle 1993, Wunderle 1995, Boal 2018). Together with other natural and anthropogenic disturbances (e.g. droughts, fires, volcanic activity, unsustainable hunting, non-native invasive species, habitat loss and degradation), major hurricanes can increase the risk of extirpation or extinction of Caribbean birds with restricted distributions and small populations (Rivera-Milán *et al.* 2003, 2005, 2015, 2016, 2018, Wiley *et al.* 2004, Beissinger *et al.* 2008, Şekercioğlu *et al.* 2012, Oppel *et al.* 2014).

The Bridled Quail-dove *Geotrygon mystacea* (Figure 1) is a regional endemic with a distribution range stretching from Puerto Rico to St. Lucia (Raffaele *et al.* 1998, Boal 2011, BirdLife International 2008, 2016). Although survey-based abundance estimates are lacking across the distribution range, Bridled Quail-dove populations tend to be small and scattered, and probably were declining on most islands before the 2017 hurricanes (McNair *et al.* 2005, Platenberg *et al.* 2005, Boal 2011, 2018, Gemmill 2015, BirdLife International 2008, 2016). To our knowledge, the only survey-based abundance estimates, corrected for at least one component of detection probability (Buckland *et al.* 2001, 2015, Nichols *et al.* 2009), were published by Boal (2018) for Bridled Quail-doves on Guana Island, British Virgin Islands, in October 2014 and August 2015. Therefore, we conducted distance-sampling surveys inside and outside the boundaries of the Quill National Park on the island municipality of St. Eustatius, Caribbean Netherlands, each May in 2016-2019.

Our first objective was to estimate abundance (i.e. density $\hat{D}$ and population size $\hat{N}$), corrected for changes in two components of detection probability (i.e. observer detectability $\hat{P}_d$ and Quail-dove availability $\hat{P}_a$), before and after hurricanes Irma and Maria in September 2017. Second, we compared density estimates at transects inside and outside the boundaries of the Quill National Park, as well as along and away from forest trails and three elevation categories within the larger Quill study area. Because of anthropogenic disturbances in foraging habitats (e.g. free-ranging livestock; Debrot *et al.* 2015, Madden 2020), we hypothesized that density estimates would be higher on transects inside than outside the park and away from than along forest trails. In addition, because Quail-doves prefer mature forests and can track changes in fruit/seed production and abundance (Waide 1991, Stouffer and Bierregaard 1993, Wunderle 1995, Rivera-Milán 1996, Steadman *et al.* 2009, Boal 2018), we hypothesized that density estimates would be higher on transects in middle elevations (range = 201-400 m) with semi-evergreen and evergreen forests (canopy heights > 8 m) than at transects in lower and upper elevations (range = 100-200 and 401-600 m) with semi-deciduous and deciduous-mixed forests (canopy height < 8 m; Van Andel *et al.* 2016). Third, we compared pre-hurricane density estimates from the study area in May 2016 and 2017 with Boal's (2018) density estimates for Guana Island in October 2014 and August 2015. Survey-based abundance estimates, corrected for detection probability, provide much-needed quantitative baselines for assessments of population status and trends on other key conservation sites across the distribution range (e.g. Important Bird Area VG001 on Great Tobago, VI007 on St. John, GP002 on Guadeloupe, KN001 on St. Kitts, and LC002 on St. Lucia; BirdLife International 2008, www.ebird.org/home).

Methods

Study area

St. Eustatius (2,100 ha) has two volcanic centres separated by lowlands inhabited by humans (Collier and Brown 2008, Van Andel *et al.* 2016). Our study area (440 ha) included the Quill National Park (220 ha; Figure 2), which is one of two designated Terrestrial Protected Areas and

Figure 1. Bridled Quail-dove *Geotrygon mystacea* at the Quill National Park, St. Eustatius, Caribbean Netherlands.

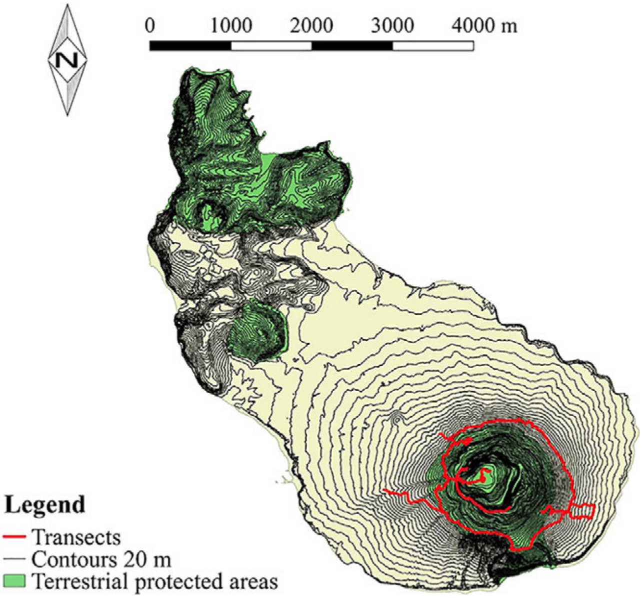

Figure 2. Map of St. Eustatius showing 20-m elevation contour lines, terrestrial protected areas, and the paths of transects surveyed inside and outside the boundaries of the Quill National Park in May 2016-2019. The study area (440 ha) is within the Quill Important Bird Area AN008 (470 ha; 17°29′ N, 62°58′W; Collier and Brown 2008).

Figure 3. Bridled Quail-dove typical foraging habitat at the Quill study area.

Important Bird Areas (Collier and Brown 2008) managed by St. Eustatius National Parks Foundation. The Quill is a dormant stratovolcano that rises to 602 m (Collier and Brown 2008). The floristic diversity of the study area includes 617 vascular plants (Axelrod 2017). The vegetation of the study area is similar to other islands across the distribution range of the Bridled Quail-dove (Rivera-Milán 1996, Rivera-Milán *et al.* 2003, Gemmill 2015, Steadman *et al.* 2009, Van Andel *et al.* 2016, Boal 2018).

Common plants that may be important food sources for the Bridled Quail-dove include *Eugenia* spp., *Samyda dodecandra, Bursera simaruba, Coccoloba swartzi, Capparis* spp., *Ternstroemia peduncularis, Erythroxylum havanense, Maytenus laevigata, Coffea arabica, Ardisia obovata, Zanthoxylum martinicense, Guettarda scabra, Bourreria baccata, Chionanthus compactus, Ficus* spp., and *Ceiba pentandra.* However, although primarily a fruit/seedeater, the Bridled Quail-dove also consumes flowers, molluscs, invertebrates, and small vertebrates (Seaman 1966, Boal 2008, 2011, Steadman *et al.* 2009). Foraging habitats in the study area are characterised by partially closed forests with fallen branches and leaves, as well as bare ground with rocks and exposed soil (Figure 3). The 2017 hurricanes caused severe structural vegetation damage (Figure 4; Eppinga and Pucko 2018).

Distance sampling

Distance sampling is based on estimation of a detection function, $\hat{g}(x)$ in the case of line transects, which decreases with distance x and is needed to estimate detection probability for single individuals or clusters of individuals in the surveyed area (Buckland *et al.* 2001, 2015, Nichols *et al.* 2009). We modelled detection as a function of distance x and covariates represented by vector $\mathbf{z}$ (i.e. $g[x, \mathbf{z}]$; Marques *et al.* 2007, Buckland *et al.* 2015). We estimated density as

Figure 4 Vegetation at the Quill study area before (A) and after (B) hurricanes Irma and Maria in September 2017.

$$\hat{D} = \frac{n\bar{s}}{2wl\hat{P}_a\hat{P}_d(\mathbf{z}_i)},$$

where $\hat{D}$ was the number of individuals ha^{-1}; n was the number of detections of singles or clusters; $\bar{s}$ was the sample mean, which we used as an unbiased estimator of average cluster size, when cluster detection was not size biased; and l was the number of transects per survey occasion in May 2016-2019. After exploratory data analysis (Buckland *et al.* 2001, 2015, Marques *et al.* 2007), we right truncated the distance data (w = 60 m) and estimated detection probability of available singles and clusters as

$$\hat{P}_d(\mathbf{z}_i) = \frac{1}{w}\int_0^w \hat{g}(x, \mathbf{z}_i)\,dx.$$

When cluster detection was size-biased (Pearson's correlation coefficient r, $P < 0.15$), we regressed $\log(s_i)$ on $\hat{g}(x_i)$ to estimate the value of expected cluster size $\hat{E}(s)$ where$\hat{g}(x_i) = 1$;

and we used $\hat{E}(s)$ instead of $\bar{s}$ to estimate density (Buckland *et al.* 2001). We defined a cluster as two or more individuals 10 m from each other, showing similar behaviour (e.g. ground foraging). We used a compass to measure sighting angles and a tape measure or rangefinder to measure detection distances from transect centrelines to singles and cluster centres. When perpendicular distances could not be measured directly, we used sighting angles and radial distances (i.e. perpendicular distances = sine of sighting angles × radial distances). For individuals heard calling but not seen, we measured distances to nearest locations and used the midpoints of distance categories 0–10, 11–20, 21–30, 31–40, 41–50, 51-60 and 61-70 m. Moving individuals were not included in density estimates, unless we measured detection distances to initial locations.

Survey effort L accounted for transect lengths (range 50-165 m) and the number of visits per transect each survey occasion (range 2-10). Because Bridled Quail-doves are year-round residents in the study area, detection probability has two components (i.e. $\hat{P}_{da} = \hat{P}_d \times \hat{P}_a$; Buckland *et al.* 2001, 2015, Nichols *et al.* 2009). Repeated visits to fixed transects per survey occasion allowed us to estimate both components of detection probability using distance sampling and N-mixture models (Royle 2004, MacKenzie *et al.* 2006, Burton and Rivera-Milán 2014). We included availability $\hat{P}_a$ as a multiplier in the density estimator (Buckland *et al.* 2001, Thomas *et al.* 2010, Thomas and Marques 2012). We used nonparametric bootstrapping to estimate detection probability standard errors (Efron and Tibshirani 1993, Buckland *et al.* 2001, 2015).

We evaluated the fit of uniform, half-normal, and hazard-rate detection models with goodness-of-fit tests (e.g. Kolmogorov-Smirnov test D_n, $P < 0.05$); and we used Akaike Information Criterion (AIC) for stepwise model selection (Buckland *et al.* 2001, 2015, Marques *et al.* 2007). We used the half-normal and hazard-rate key functions without series expansions to model the effects of the following covariates: cluster size (continuous, ≥ 2 individuals), detection mode (categorical, 0 = audio, 1 = visual), detection angle (continuous, 0-359°), survey occasion (categorical, 0 = May 2016, 1 = May 2017, 2 = May 2018, 3 = May 2019), time of day (continuous, 07h07-15h05), transect survey time (continuous, end - start time), transect location (categorical, 0 = along, 1 = away trail), transect elevation (categorical, 0 = 100-200, 1 = 201-400, 2 = 401-600 m), horizontal and vertical vegetation cover (categorical, 0 = none-low, 1 = medium-high), and observer (categorical, 0 = HM alone, 1 = HM-FFRM, 2 = HM-KV, 3 = HM-OJ, 4 = HM-AP). We recorded elevation and cover at transect start, middle and end points; and we used the mean and mode for category definition. We modelled quadratic terms for time of day and mean elevation.

We stratified (e.g. 0 = inside, 1 = outside park) and post-stratified (e.g. 0 = May 2016 and 2017, 1 = May 2018 and 2019) the distance data to compare density estimates using the two-sample z test (Buckland *et al.* 2001, 2015, Crawley 2007). We also used the two-sample z test to compare Guana Island density estimates (Boal 2018) with our study area pre-hurricane density estimates. For density comparisons, we accepted statistical significance at $P < 0.05$. We present results as original means and bootstrapped standard errors for all parameter estimates, with 2.5% and 97.5% quantiles provided for population size estimates per survey occasion across the study area (i.e. $\hat{N} = \hat{D} \times \mathrm{A}$, where A = 440 ha). For data analysis, we used programs DISTANCE ver. 7.3 rel. 1 (Thomas *et al.* 2010) and R ver. 3.5.3 (R Development Core Team 2019) with package UNMARKED ver 0.13-2 (Fiske and Chandler 2011).

Results

Overall, we made 141 audio and 105 visual detections on 255 transects in May 2016-2019 (Figure 5a,b). Cluster size $\bar{s}$ averaged 1.024 ± 0.011 and cluster detection was not size biased (Pearson's r = -0.01, df = 244, P =0.43). Encounter rate n/L (i.e. 246/82 000) averaged 0.003 ± 0.0005. Based on goodness-of-fit tests and minimisation of AIC, the hazard-rate key function without series expansion provided the best fit to the distance data (e.g. $D_n = 0.11$, $P = 0.50$; Table 1, Figure 5a). Detection mode was the most important detection covariate, with others receiving no support from the distance data (Table 1, Figure 5b). For survey occasions combined, observer detectability $\hat{P}_d$ averaged 0.957 ± 0.114 for audio detections and 0.434 ± 0.052 for visual detections

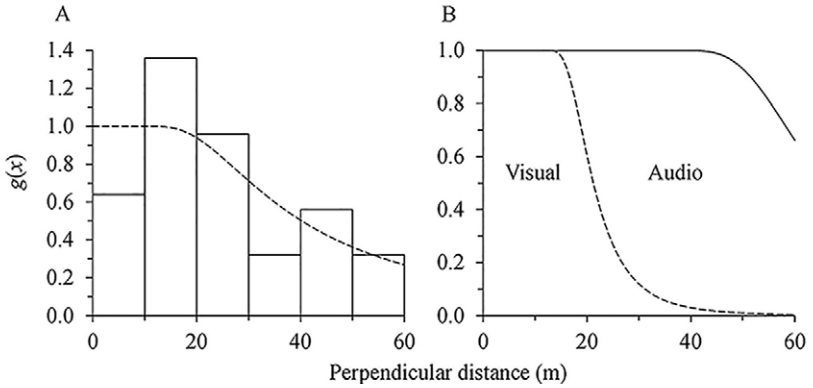

Figure 5. Detection probability $g(x)$ based on the hazard-rate key function without series expansion for audio and visual detections combined (A) and separated (B) of Bridled-Quail doves at transects surveyed in the Quill study area each May in 2016-2019. Distance data right truncated at w = 60 m.

Table 1. Top five-ranked detection models using conventional (CDS) and multiple-covariate (MCDS) distance sampling for Bridled Quail-dove line transect surveys at the Quill study area each May in 2016-2019. Distance data right truncated at w = 60 m.

Method	Key[a]	Series[b]	Covariate[c]	AIC	ΔAIC	q[d]
CDS	HR	--	--	1740.31	0	2
	HR	1 CO	--	1743.06	2.75	3
	HR	1 SP	--	1743.25	2.94	3
	HN	1 CO	--	1763.19	22.88	2
	HN	1 HP	--	1764.38	24.07	2
MCDS	HR	--	DM	1740.17	0	3
	HR	--	OB	1745.01	4.84	7
	HR	--	TL	1748.61	8.44	3
	HR	--	ST	1754.18	14.01	3
	HR	--	TE	1758.23	18.06	3

[a] HR = hazard-rate, HN = half-normal key function
[b] COS = cosine, SP = simple polynomial, HP = Hermite polynomial series expansion
[c] OB = observer, DM = detection mode, TL = transect location, ST = starting time, TE = transect elevation.
[d] Number of parameters

(Figure 5b). For detection modes combined, $\hat{P}_d$ averaged 0.693 ± 0.064 (Figure 5a) and ranged from 0.692 ± 0.075 to 0.699 ± 0.086 (Table 2). Effective strip width $E\hat{S}W$ (i.e. $w \times \hat{P}_d$) averaged 41.58 ± 3.84 and ranged from 41.52 ± 4.50 to 41.94 ± 5.16 m. For survey occasions and detection modes combined, Quail-dove availability $\hat{P}_a$ averaged 0.475 ± 0.138 and ranged from 0.410 ± 0.125 to 0.585 ± 0.191 (Table 2). The product of detection components $\hat{P}_{da}$ averaged 0.329 ± 0.098 and ranged from 0.284 ± 0.081 to 0.402 ± 0.103 (Table 2).

For survey occasions and detection modes combined, density ($\hat{D}$ = individual ha^{-1}) averaged 1.459 ± 0.277 and ranged from 0.540 ± 0.211 to 2.361 ± 0.307 (Table 3). That is, population size ($\hat{N}$ = individuals in 440 ha) averaged 642 ± 122 (2.5% and 97.5% quantiles = 449, 913) and ranged from 238 ± 93 (118, 390) to 1039 ± 135 (806, 1339; Table 3). Density declined by 76% between May 2017 and 2018 (i.e. rate of change $\hat{R} = \hat{D}_{2018}/\hat{D}_{2017} - 1 = -0.757 \pm 0.329$; z = 2.67, p = 0.008; Table 3). Density remained low in May 2019 (Table 3).

Table 2. Bridled Quail-dove estimates of detection probability at the Quill study area in May 2016-2019. Distance data right truncated at $w = 60$ m.

Date	$\hat{P}_d$[a]	SE	$\hat{P}_a$[b]	SE	$\hat{P}_{da}$[c]	SE
05/2016	0.687	0.057	0.585	0.191	0.402	0.103
05/2017	0.699	0.086	0.428	0.129	0.299	0.123
05/2018	0.693	0.039	0.479	0.107	0.332	0.083
05/2019	0.692	0.075	0.410	0.125	0.284	0.081

[a] Observer detectability
[b] Quail-dove availability
[c] Product of detection probability components

Table 3. Bridled Quail-dove estimates of density and population size at the Quill study area in May 2016-2019. Distance data right truncated at $w = 60$ m.

Ocassion	$\hat{D}$[a]	SE	$\hat{N}$[b]	SE	2.5%	97.5%
05/2016	2.359	0.354	1038	156	755	1369
05/2017	2.361	0.307	1039	135	806	1339
05/2018	0.575	0.239	253	105	117	552
05/2019	0.540	0.211	238	93	118	390

[a] Individuals hal
[b] Individuals in 440 ha

Density did not differ along (0.683 ± 0.204, $n = 47$) and away (0.776 ± 0.158, $n = 199$) from forest trails ($z = -0.36$, $p = 0.72$). However, density was higher inside (1.216 ± 0.205, $n = 217$) than outside the park (0.244 ± 0.184, $n = 29$; $z = 3.53$, $P = 0.004$). Density also was higher at elevations within 201-400 (1.016 ± 0.181, $n = 197$) than 100-200 (0.120 ± 0.088, $n = 32$) and 401-600 m (0.324 ± 0.127, $n = 17$; all z scores > 3.13, P values < 0.002); but density did not differ between 401-600 and 100-200 m ($z = 1.32$, $P = 0.19$). Lastly, Boal's Guana Island densities for two survey periods combined (reported as 1.48 ± 0.20) did not differ from our study area pre-hurricane densities combined (2.360 ± 0.468; $z = 1.73$, $P = 0.08$; Table 3).

Discussion

Application of line-transect distance sampling depended on the following basic assumptions: (1) single individuals and clusters of individuals were distributed independently of transects; (2) singles and clusters at transect centrelines were not missed (i.e. $g[0] = 1$); (3) perpendicular distances and/or distance categories were correct; (4) singles and clusters were detected at initial locations; and (5) cluster size estimation was unbiased. Detection probability and abundance estimation were not influenced by transects along and away from forest trails. Transects provided adequate coverage of foraging habitats inside and outside the park and three elevation categories across the study area. We often detected Bridled Quail-doves calling from low branches or while walking slowly ground foraging; and their initial locations were easily spotted before any responsive movement, which was characterised by distinguishable wing beats and/or rustle of leaf litter. Detection mode was the most important covariate, but audio and visual detections did not show extreme heterogeneity in the detection function (e.g. compare our Figure 5b with Figure 3 in Marques *et al.* 2007). The hazard-rate key function without series expansion adequately described audio and visual detections, with nearly a complete count or census (i.e. mean $\hat{P}_d = 0.957$) for calling individuals and sufficiently high detectability (i.e. mean $\hat{P}_d = 0.434$) for non-calling individuals available within 60 m of transect centrelines. In addition, availability remained sufficiently high during survey occasions (i.e. mean $\hat{P}_a = 0.475$), clusters tended to be small (usually ≤ 3 individuals ground foraging), and cluster detection was not size biased. Therefore, we likely met the above-mentioned basic assumptions and estimated abundance unbiasedly.

Contrary to what we hypothesized, density did not differ along and away from forest trails. However, as we hypothesized, density was higher inside than outside the park and at elevations within 201-400 m than 100-200 m and 401-600 m. We suggest that density did not differ along and away from forest trails (usually < 5 m wide), because foraging habitats within 60 m of transect centrelines were similar to forest interior areas, and because trails were narrow and there was little disturbance from park visitors during the surveys (see Figure 3). However, the degradation of foraging habitats by free-ranging livestock (mainly goats) can explain density differences inside and outside the park and three elevation categories. For example, Madden (2020) estimated densities between 3.29 ± 0.82 and 2.84 ± 0.93 goats ha^{-1} at low and high elevations in the study area; and during our surveys, Bridled Quail-doves were not detected in overgrazed areas below 200 m. In addition, we suggest that density was higher within 201-400 than 100-200 and 401-600 m because fruit/seed production and abundance were higher in middle elevation semi-evergreen and evergreen forests than in lower and upper elevation semi-deciduous and deciduous-mixed forests. However, although these are plausible explanations, we did not measure fruit/seed production and abundance, and we agree with Boal (2011, 2018) that research is needed on the diet and foraging habitat preferences of the Bridled Quail-dove, as well as on the effects of free-ranging livestock overgrazing.

The Bridled Quail-dove population declined significantly between May 2017 and 2018 and remained low between May 2018 and 2019. Hurricanes Irma and Maria caused severe structural vegetation damage and high tree mortality (Eppinga and Pucko 2018). Therefore, we suggest that major hurricanes together with free-ranging livestock overgrazing degraded foraging habitats and limited food supply, which, in turn, lowered reproduction and/or survival rates, and caused a population bottleneck in the absence of immigration from nearby islands (Rivera-Milán and Schaffner 2002, Beissinger *et al.* 2008). In addition, nest predators (mainly black rats *Rattus rattus*) were abundant in the study area (Madden *et al.* 2019). Under these circumstances, and considering the life history characteristics of Columbidae (e.g. low survival and high reproductive rates), we recommend control management (e.g. permanent fences and sustained removal) within the park to improve foraging habitats and promote population recovery through successful reproduction (Rivera-Milán 1996, Rivera-Milán *et al.* 2003, Debrot *et al.* 2015, Madden *et al.* 2019, Madden 2020).

Boal's (2018) and our methodologies were similar and can be implemented across the distribution range of the Bridled Quail-dove to assess population status and trends, and monitor population responses to control management actions. However, surveys should be conducted during the peak of calling activity in April-June to maximise Bridled Quail-dove availability and observer detectability (Rivera-Milán *et al.* 2005, 2015, 2016, 2018). Lastly, with the exception of some possible strongholds, such as Guadeloupe's Important Bird Area GP002 (Levesque and Mathurin 2008; www.ebird.org/home), we agree with Boal (2011, 2018) and other researchers that Bridled Quail-dove populations probably were declining on most islands before the 2017 hurricanes and that population status warrants revision (BirdLife International 2016).

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