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RESEARCH ARTICLE

Distance sampling survey and abundance estimation of the critically endangered Grenada Dove (*Leptotila wellsi*)

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ABSTRACT

The Grenada Dove (*Leptotila wellsi*) is critically endangered; its abundance, as estimated by territory mapping, ranges from 68 to 91 calling males (or 136–182 individuals, assuming a census of paired males). However, an accurate census is unlikely in dry and moist forests, unpaired males may be more detectable than paired males, and sex ratio may be male biased. Because methodology can limit the value of monitoring, we used a systematic grid of survey points and distance sampling to estimate abundance (density and population size), accounting for covariates that may influence detection. Time of day was the most important covariate (e.g., individuals were detected at larger distances early than late in the morning). Density was negatively influenced by disturbance level (deforestation) and positively influenced by food abundance and vegetation cover (leguminous trees). None of the covariates caused extreme heterogeneity; and conventional and multiple-covariate analyses generated similar detection and density estimates, which suggests that model selection was of secondary importance for abundance inferences. Detection probability (mean ± SE) was 0.166 ± 0.031 (95% confidence interval [CI]: 0.114–0.242) within 340 m, density was 0.021 ± 0.004 individuals ha^{-1} (95% CI: 0.014–0.030), and population size was 160 ± 30 individuals (95% CI: 107–229) in 7,621 ha. Although spatial distribution was slightly clumped (dispersion parameter: $\hat{b}\sim 1.31$), we recommend surveying 150 points twice between late July and early August for abundance coefficient of variation (CV) $\leq$0.15, even if spatial distribution becomes more clumped (e.g., $b = 2.5$). More survey data are needed to better understand spatial and temporal density variation, test hypotheses about survey design (e.g., road bias in density estimation) and Grenada Dove ecology (rainfall, food, cover, and density correlations), and evaluate management actions (predator removal in nesting areas). With <250 Grenada Doves in the survey region, our data highlight the precarious conservation status of this island endemic, and the urgent need for effective management and targeted monitoring.

Keywords: abundance, distance sampling, Grenada Dove, *Leptotila wellsi*

Muestreo de distancia y estimación de abundancia de la Paloma de Granada (*Leptotila wellsi*) en peligro de extinción crítico

RESUMEN

La Paloma de Granada (*Leptotila wellsi*) está en peligro de extinción crítico; su abundancia, estimada usando el método de mapeo de territorios, alcanzando de 68 a 91 machos cantando (o 136–182 palomas, asumiendo un censo de machos apareados). Sin embargo, un censo es poco probable en bosques secos y húmedos; los machos no apareados pueden ser más detectables que los machos apareados; y la proporción sexual puede estar sesgada en favor de los machos. Porque la metodología puede limitar el valor del monitoreo, usamos una cuadrícula sistemática de puntos y el método de muestreo de distancia para estimar abundancia (densidad y tamaño poblacional), tomando en cuenta covariables que pueden influenciar la detección. La hora del día fue la covariable más importante (p.ej., las palomas fueron detectadas a mayor distancia más temprano que tarde en la mañana). La densidad fue influenciada negativamente por el nivel de disturbio (deforestación), y positivamente por la abundancia de comida y la cobertura vegetacional (árboles leguminosos). Ninguna de las covariables causó heterogeneidad extrema; y los análisis convencionales y multiple-covariados generaron estimados similares de detección y densidad, sugiriendo que la selección de modelos tuvo una importancia secundaria sobre las inferencias de abundancia. La probabilidad detección (median ± ES) fue 0.166 ± 0.031 (intervalo de confianza de 95% [CI]: 0.114–0.242) en 340 m la densidad fue 0.021 ± 0.004 palomas ha^{-1} (0.014, 0.030), y el tamaño poblacional fue 160 ± 30 palomas (107, 229) en 7,621 ha. Aunque la distribución estuvo ligeramente aglomerada (parámetro de dispersión: $\hat{b}\sim 1.31$), recomendamos muestrear 150 puntos dos veces entre finales de julio y principios de agosto para un CV de abundancia $\leq$ 0.15, aunque la distribución espacial sea más aglomerada (p.ej., $b = 2.5$). Más datos de muestreo son necesarios para entender mejor la variación espacial y temporal de densidad, examinar hipótesis de diseño de muestreo (p.ej., sesgo de camino en la estimación de densidad) y de ecología de la paloma (correlaciones entre lluvia, comida, cobertura, y densidad), y la evaluación de acciones de manejo (la remoción de depredadores en áreas de nidificación). Con menos de 250 palomas, nuestros datos ponen en relieve el estado precario de conservación de esta especie endémica isleña, y la urgente necesidad de un manejo efectivo .y un monitoreo orientado.

Palabras clave: Abundancia, *Leptotila wellsi*, muestreo de distancia, Paloma de Granada

INTRODUCTION

The Grenada Dove (*Leptotila wellsi*; Figure 1) was thought to be nearly extinct in the 1960s (Devas 1970). At present, this island endemic is listed as critically endangered by the International Union for Conservation of Nature (Rusk 2008). Habitat loss and degradation due to forest clearing for agriculture, cattle grazing, and urban development; catastrophic natural events, such as Hurricane Ivan in 2004; and predation by introduced mammals are major conservation threats (Rusk 2008). However, survey data are needed to estimate population abundance, establish population-based conservation objectives to increase or maintain demographic sustainability and ecological viability (Tear et al. 2005, Sanderson 2006), and assess population response to environmental disturbances and management actions (B. L. Rusk personal observation).

Territory mapping was used to estimate Grenada Dove (hereafter "dove") abundance intermittently between 1987 and 2007; the most recent abundance estimates range from 68 to 91 calling males (or 136–182 individuals, assuming a census of paired males in dry and moist forests; B. L. Rusk personal observation). However, detection is likely imperfect in dry and moist forests and may change before and after hurricanes, leading to erroneous abundance inferences (Rivera-Milán 1995a, 1995b, 1999). Pairing status, stage of the nesting cycle, weather conditions, and other factors may influence calling activity. For example, unpaired males may call more often and be more detectable than paired males during the breeding season (Baskett 1993). Additionally, sex ratio may be male biased in a small and range-restricted dove population (Donald 2007).

Recognizing that population monitoring has to be reliable and cost effective, we collected survey data in a manner that would facilitate the combination of point-transect distance sampling with time-removal and repeated-count survey methods (Buckland et al. 2001, 2004, Burnham et al. 2004, Marques et al. 2007, Sillett et al. 2012, Amundson et al. 2014). Here, we will concentrate on point transects and conventional and multiple-covariate modeling frameworks, which are widely used to assess the status and trends of columbid populations (Rivera-Milán et al. 2003a, 2014, Newson et al. 2008, Small et al. 2012). In July 2013, we conducted a range-wide population survey of the Grenada Dove using a systematic grid of points and distance sampling to estimate abundance (density and population size), accounting for survey and site-specific covariates that may influence detection probability. We use the data to test hypotheses about survey design (e.g., density differs along and away from roads; Marques et al. 2010) and ecological factors (density differs at points with low and high food abundance; Rivera-Milán et al. 2003a); and provide recommendations to standardize data collection, meet method assumptions, and estimate abundance with precision (desired coefficient of variation [CV] ≤ 0.15) for management evaluation and targeted monitoring (Nichols and Williams 2006).

Study Area

The survey region covered 7,621 ha (Figure 2). We established a systematic grid of 180 points separated by 400 m in primary habitat and 1,000 m in potential habitat (P. J. Rivera-Lugo personal observation). Logwood (*Haematoxylum campechianum*), gumbo limbo (*Bursera simaruba*), black loblolly (*Pisonia fragrans*), strongbark (*Bourreria succulenta*), and wild tamarind (*Leucaena leucocephala*) were among the most common trees in the survey region.

METHODS

Conventional distance sampling is based on estimation of a detection function, $\hat{g}(r)$ in the case of points, which decreases with distance (r) and is needed to estimate probability of detection in the surveyed area. By definition, $g(r)$ is the conditional probability of detecting a single dove or cluster of doves, given distance (r) from the center of a survey point (Buckland et al. 2001).

We modeled detection as a function of distance and other covariates represented by vector $\mathbf{z}$ (i.e. $g[r, \mathbf{z}]$; Marques et al. 2007), and we estimated density as

$$\hat{D} = \frac{n\bar{s}}{2\pi k\hat{P}(\mathbf{z}_i)}$$

where $\hat{D}$ is the number of doves per hectare; n is the number of single and cluster detections; $\bar{s}$ is the sample mean, which can be used as an unbiased estimator of average cluster size when cluster detection is not size biased;

FIGURE 1. When a Grenada Dove is flushed from a perch by an approaching observer, it will fly a short distance to another perch or to the ground and walk slowly away to find cover. Grenada Doves can also be seen singly or in small clusters drinking water and foraging on the ground in forested areas. Photo credit: Greg R. Homel, Natural Encounters

and k is the number of survey points. We truncated the distance data ($w = 340$ m) and estimated detection probability as

$$\hat{P}(\mathbf{z}_i) = \frac{2}{w^2}\int_0^w r\hat{g}(r, \mathbf{z}_i)dr$$

When cluster detection was size biased ($P < 0.15$), $\log(s_i)$ was regressed on $\hat{g}(r_i)$ to estimate the value of expected cluster size [$\hat{E}(s)$] where $\hat{g}(r_i) = 1$, and $\hat{E}(s)$ instead of $\bar{s}$ was used to estimate density (Buckland et al. 2001). A team of 2 observers surveyed all points, with 1 observer (F.F.R.-M.) measuring detection distances, and the other (F.B., F.S., or B.L.R.) recording the data. The observers remained side by side for 6 min, measuring distances from points to doves detected singly or the geometric center of clusters. A cluster was defined as $\geq$2 doves 10 m from each other, showing similar behavior (e.g., walking on the ground).

A 6-min count increased the chance of detecting calling doves visually, facilitating distance measurements with rangefinders. However, when calling doves were not seen, we measured distances to the nearest horizontal locations and used distance categories (0–15, 16–30, 31–45, 46–60, 61–90, 91–120, 121–180, 181–240, 241–340, and 341–440 m; Rivera-Milán et al. 2003b, 2014). Moving doves were not included in density estimates unless their initial locations were ascertained during or after the count. The points were visited in the morning (0630–1100 hours) and afternoon (1530–1900 hours). Survey effort accounted for 2 visits made to 79 points (Buckland et al. 2001).

FIGURE 2. Map of the island of Grenada (area ~34,400 ha; 12.00°N, 61.78°W), showing the survey region, which covered 7,621 ha. Green circles are for survey points where Grenada Doves were detected during July 19–31, 2013.

We evaluated the fit of uniform, half-normal, and hazard-rate detection models with quantile–quantile plots and goodness-of-fit tests (Burnham et al. 2004). Model selection was based on Akaike's Information Criterion corrected for small sample sizes (AIC$_c$; Buckland et al. 2001). Models with AIC$_c$ $<$ 2 were considered to be equally supported by the data. On the basis of model fit and precision (observed density CV $<$ 0.20), we selected the half-normal key function without series expansion for multiple-covariate analysis. As an alternative to covariate analysis, we used the same key function and post-stratified the data, for example, by point location (1 = along, 2 = away from road) and used the Z statistic to compare density estimates (null hypothesis [H_0]: $\hat{D}_1 = \hat{D}_2$; Buckland et al. 2001:84–86).

We used rangefinders and binoculars to determine canopy height, vegetation cover, and food abundance within 60 m of point centers, and disturbance level from conservation

TABLE 1. Half-normal detection models with and without covariates fitted to the Grenada Dove survey data collected during July 19–31, 2013.

Covariate [a]	K [b]	ΔAIC_c	$\hat{P}$	SE	$\hat{D}$	SE
Time of day [c]	2	0.00	0.166	0.031	0.021	0.004
Time of day	2	2.65	0.171	0.033	0.020	0.003
Vegetation cover	2	3.16	0.185	0.031	0.019	0.003
Canopy height	2	3.49	0.198	0.038	0.017	0.004
No covariate [d]	1	4.40	0.183	0.031	0.019	0.003
Detection time	2	4.88	0.193	0.032	0.018	0.003
Point location	2	5.58	0.197	0.032	0.017	0.003
Disturbance level	2	5.60	0.197	0.032	0.017	0.003
Food abundance	2	5.66	0.197	0.032	0.017	0.003
Forest type	2	5.71	0.197	0.032	0.017	0.003
Detection mode	2	5.72	0.197	0.032	0.017	0.003
Cluster size	2	5.75	0.198	0.032	0.017	0.003

[a] Time of day (minutes after sunrise or before sunset; or 1 = 0630–0900, 1631–1900, 2 = 0901–1100 hours), cluster size ($\geq$2 doves), detection time (1 = 0–3, 2 = 4–6 min), canopy height (1 = below 5 m, 2 = above 5 m), point location (1 = along, 2 = away from road), forest type (1 = dry, 2 = moist), detection mode (1 = heard only, 2 = heard and seen or seen only), vegetation cover, food abundance, and disturbance level (1 = 0–50% [none–low], 2 = 51–100% [medium–high]).

[b] Number of parameters in the model.

[c] $\text{AIC}_c = 103.35$ for the half-normal key function with no series expansion and with time of day defined as a continuous covariate.

[d] Half-normal key function without series expansion and no covariate (Buckland et al. 2001:41–49).

threats within 200 m. We did not include a settling period before starting the counts (Lee and Marsden 2008). After finishing the counts, we moved around point centers as much as needed to measure problematic distances, determine whether we had missed any doves, identify plants bearing fruits or seeds, and reach a consensus about canopy height (1 = below 5 m, 2 = above 5 m), vegetation cover, food abundance, and disturbance level (1 = 0–50% [or none–low], 2 = 51–100% [or medium–high]; Rivera-Milán 1996, 1999, 2001, Rivera-Milán et al. 2003a, 2014). Google Earth Pro, version 7.1 (http://www.google.com/enterprise/mapsearth/) was used to complete our assessment of disturbance from forest clearing (e.g., due to urban development). Mammalian predators, garbage dump sites, forest fires, and hunting activity were also recorded as conservation threats. Time of day was defined as a discrete and continuous covariate (Marques et al. 2007). Additional information about covariates is provided in Table 1.

Population size was estimated by extrapolating estimated density to the survey region ($\hat{N} = \hat{D} \times A$, where $A =$ 7,621 ha). Equation 7.17 in Buckland et al. (2001:246) was used to calculate the number of survey points needed to estimate abundance with precision (desired CV $\leq$ 0.15) when spatial distribution was random ($b = 1$) or clumped ($b = 2$–3). Dispersion parameter was estimated as $\hat{b} \sim n \times (\text{CV}[\hat{D}])^2$. We used program DISTANCE version 6.0, Release 2 (Thomas et al. 2010). Results are means ± SE, with 95% CI in parentheses.

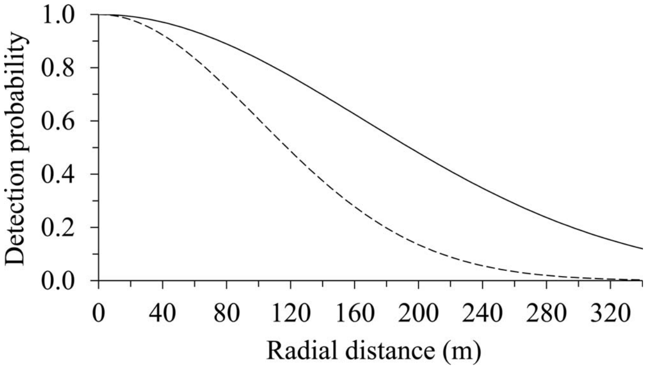

FIGURE 3. Detection probability of the Grenada Dove presented as a function of distance and time of day. Detection was modeled using the half-normal key function without series expansion and time of day as a continuous or factor covariate (solid line: 0630–0900, 1631–1900 hours; dashed line: 0901–1100, 1530–1630 hours).

RESULTS

We detected 33 doves (n) within 340 m of point centers. We discarded 5 dove detections within 341–440 m (i.e. 13% after data truncation), and 3 dove detections beyond 440 m (maximum detection distance). Four doves were detected at 3 new locations in the south and southeast of the island (Figure 2). Encounter rate (n/survey effort) was 0.209 ± 0.004 (0.201–0.218). Average cluster size was 1.091 ± 0.067 (1.000–1.236), but detection tended to be size biased ($r_{31} = -0.28$, $P = 0.09$). Expected cluster size was 1.002 ± 0.041 (1.000–1.088). To simplify detection models ($K \leq 2$; Table 1), we used expected cluster size in multiple-covariate analyses.

Quantile–quantile plots and goodness-of-fit tests showed no major problems with the data. For example, when using the half-normal key function without series expansion, the largest difference between the observed and expected distances was not significant (Kolmogorov-Smirnov test: $D_n = 0.16$, $P = 0.50$). The half-normal key function without series expansion and with time of day defined as a continuous covariate provided the best fit to the data (Table 1 and Figure 3). Based on this model, detection probability was 0.166 ± 0.031 (0.114–0.242) within 340 m, density was 0.021 ± 0.004 doves ha^{-1} (0.014–0.030), and population size was 160 ± 30 doves (107–229) in 7,621 ha.

The half-normal key function without series expansion and with time of day defined as a factor covariate ranked second best in the set ($\Delta\text{AIC}_c = 2.65$), with other models receiving less support from the data but generating similar

TABLE 2. Comparison of Grenada Dove density estimates (ha^{-1}) after post-stratification of the distance data collected during July 19–31, 2013.

Stratum	Level	$\hat{D}$	SE	n	Z	P
Disturbance level	1	0.018	0.005	23	2.66	0.01
	2	0.001	0.004	10		
Food abundance	1	0.005	0.002	11	−2.24	0.03
	2	0.015	0.004	22		
Vegetation cover	1	0.005	0.002	10	−2.22	0.03
	2	0.013	0.003	23		
Canopy height	1	0.007	0.002	13	−1.11	0.27
	2	0.011	0.003	20		
Forest type	1	0.008	0.003	14	−0.71	0.48
	2	0.011	0.003	19		
Point location	1	0.011	0.003	21	0.56	0.58
	2	0.009	0.002	12		

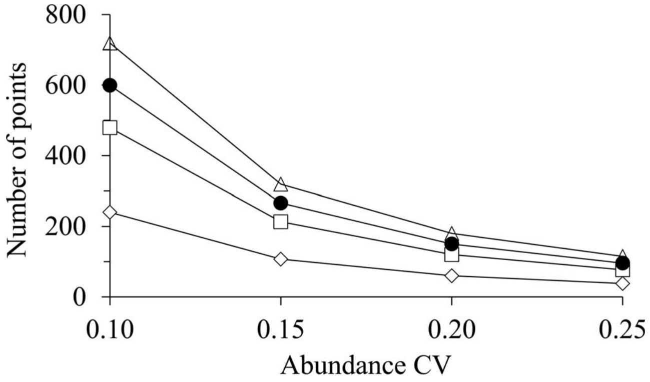

FIGURE 4. Number of survey points needed for abundance CV = 0.10–0.25, when the Grenada Dove spatial distribution is random (diamonds: dispersion parameter [b] = 1) or clumped (squares: b = 2; triangles: b = 3). For survey planning, we assumed that spatial distribution was clumped (circles: b = 2.5).

detection and density estimates (Table 1). The inclusion of covariates in the detection models increased the precision of the density estimator. Density CV was 0.193 for the detection model with no covariate and ranged from 0.162 to 0.188 for the detection models with covariates (Table 1).

Post-stratification analyses indicated that dove density was negatively influenced by disturbance level and positively influenced by food abundance and vegetation cover at survey points (Table 2). Dove density was not influenced by canopy height, forest type, or point location (Table 2). Dove spatial distribution was slightly clumped ($\hat{b} \sim 1.31$). However, we recommend surveying 150 points twice between late July and early August for an abundance CV $\leq$ 0.15, even if spatial distribution becomes more clumped (say, $b = 2.5$; Figure 4). With an encounter rate of 0.209 (0.201–0.218), this survey effort would generate 63 detections (60–65) in the survey region.

DISCUSSION

The reliability of survey data for population monitoring depends greatly on the ability of observers to meet method assumptions. The basic assumptions of distance sampling are (1) perfect detection of doves at point centers (i.e. $g[0] = 1$); (2) distance measurement to initial locations, before responsive movement; (3) accurate count of clustered doves; (4) measurement of detection distances without error; and (5) representative sampling of the survey region (Buckland et al. 2001, 2008).

We did not likely miss doves at or near point centers during 6-min counts (e.g., detection probability $\geq$ 0.868 within 60 m). Doves calling from perches and walking on the ground were conspicuous and did not show much responsive movement when approached, and we were able to measure detection distances to initial locations in most instances. Quantile–quantile plots and goodness-of-fit tests showed little evidence of measurement error (e.g., see Burnham et al. 2004: fig. 11.9). Although most of the detections were of single doves, we were diligent in counting doves in clusters. We established a systematic grid of points and covered the range of dove distribution (Blockstein 1988, 1991, P. J. Rivera-Lugo personal observation, B. L. Rusk personal observation). Therefore, we consider that the basic assumptions of distance sampling were met by having an adequate survey design and using a 2-observer team.

The doves remained active during the morning and afternoon (e.g., calling loudly and repeatedly from the same perches for prolonged periods, or walking slowly on the ground searching for food under the forest canopy). However, we found that they were more detectable at larger distances during the early morning and late afternoon than during the late morning and early afternoon. We aimed to increase dove availability, and detection given availability, with 2 observers conducting 6-min counts during the morning and afternoon and by repeating visits to survey points in late July, when breeding is starting and calling activity is high (B. L. Rusk personal observation). Most of the density variation (89.8%) was related to factors influencing detection probability. Time of day was the most important covariate influencing detection, and its inclusion in the detection models increased the precision of the density estimator. However, none of the covariates caused extreme heterogeneity in the detection function (e.g., see Marques et al. 2007: fig. 3), and conventional and multiple-covariate analyses generated similar detection and density estimates, which suggests that model selection was of secondary importance for abundance inferences in the survey region (Buckland et al. 2001).

We detected doves outside their primary habitat in the west and southwest, which suggests that they may have dispersed (perhaps after the 2004 hurricane) or may have been missed previously at potential habitat in the south and southeast of the island (Blockstein 1988, 1991, P. J. Rivera-Lugo personal observation, B. L. Rusk personal observation). Dove density was negatively influenced by disturbance level and positively influenced by food abundance and vegetation cover. These probably are important predictors of dove density, but additional survey data are needed to better understand spatial and temporal variation of density in the survey region (Rivera-Milán 1995b, Rivera-Milán et al. 2003b, 2014). Our basic modeling framework can be easily extended to account for the influence of covariates on detection and abundance (e.g., see Sillett et al. 2012, Amundson et al. 2014) and to address hypotheses about ecological factors driving population dynamics more explicitly and with greater precision (Rivera-Milán et al. 2014, F. F. Rivera-Milán personal observation). For example, on the basis of previous studies, we expected rainfall to be positively correlated with vegetation cover and food abundance, which, in turn, should be positively correlated with dove calling, nesting, and density in dry forests; on the other hand, we expected weaker correlations among these variables in moist forests (Rivera-Milán 1995b, 1996, 1999, 2001, B. L. Rusk personal observation). In general, we found doves in dry and moist forests with leguminous trees, such as logwood, forming closed canopies and understories with fallen leaves and branches, shrub–scrub cover, and bare ground with rocks and exposed soil (also see Blockstein 1991). The absence of mammalian predators and the presence of freshwater sources also seemed to be important to the doves (e.g., Mt. Hartman Estate and National Park; B. L. Rusk personal observation).

Surveys conducted along roads may bias detection and density estimation (Marques et al. 2010). However, our survey data indicated that dove detection and density estimates did not differ along and away from roads; and similar results have been obtained for columbids on other Caribbean islands (Rivera-Milán et al. 2014, F. F. Rivera-Milán personal observation). Although the use of roads would greatly facilitate data collection, more surveys are needed to test thoroughly for road bias. Therefore, we recommend using the systematic grid of points and 2 observers to survey 150 points twice between late July and early August. This survey effort would be enough to estimate density with reasonable precision and determine the importance of point location and other covariates.

Moreover, we recommend using abundance estimates, corrected for changes in detection, to determine whether the population is responding to specific management actions, such as the establishment of fenced buffer zones to protect habitat from anthropogenic disturbances, the removal and exclusion of mammalian predators from freshwater and nesting areas, and the restoration of degraded forests with leguminous vegetation to provide cover and food (B. L. Rusk personal observation). Because columbids tend to have low annual survival and high reproductive rates (Rivera-Milán 1996, 1999, Rivera-Milán et al. 2003a, 2014), we suggest that predator removal and habitat protection and restoration should be considered management priorities to increase and maintain demographic sustainability and ecological viability. With <250 Grenada Doves in the survey region, our data highlight the precarious conservation status of this island endemic, as well as the urgent need for effective management and targeted monitoring to meet population-based conservation objectives.

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