



Puerto Rico plain pigeon, scaly-naped pigeon and red-tailed hawk: population dynamics and association patterns before and after hurricanes

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ABSTRACT: Since the 1980s, 3 major hurricanes have made landfall on Puerto Rico: Hugo in September 1989 (Saffir-Simpson scale, category 4), Georges in September 1998 (category 3) and María in September 2017 (category 4). María was the most devastating hurricane since the 3 major hurricanes that occurred in 1899–1932. Major hurricanes can cause severe abundance declines and population bottlenecks by decreasing survival and reproductive rates and increasing predation and competition for limited resources. In April to June 1986–2021, we used distance sampling to estimate abundance and monitor the population dynamics of the endangered Puerto Rico plain pigeon *Patagioenas inornata wetmorei* and the abundant scaly-naped pigeon *P. squamosa* and red-tailed hawk *Buteo jamaicensis*. Here, we fit a Bayesian state-space logistic model with distance sampling abundance estimates to generate posterior estimates of maximum population growth rate and population carrying capacity, and predict abundance in April to June 2020–2030. In addition, we used *N*-mixture and 2-species models to assess association patterns in April to June 2015–2019. The scaly-naped pigeon and red-tailed hawk populations did not decline, or recovered faster from their declines than the plain pigeon population after the hurricanes. The association patterns between species were positive but variable for the 2 pigeon species and negative but variable for the plain pigeon and red-tailed hawk. At lowered abundance (i.e. mean \pm SE estimates $\hat{N} = 1043 \pm 476$ island-wide and $\hat{N} = 522 \pm 157$ at the centre of abundance in the east-central region in April to June 2018–2021), the plain pigeon may become extinct if another hurricane with the path and intensity of María makes landfall on the island during the current decade.

KEY WORDS: Hurricanes · Abundance · Occupancy · Population dynamics · Association patterns · *Patagioenas inornata wetmorei* · *P. squamosa* · *Buteo jamaicensis*

1. INTRODUCTION

Hurricanes can cause abundance declines, give rise to negative interspecific interactions and increase the risk of extinction of Caribbean island birds with restricted distribution ranges and small population sizes

(e.g. see Beissinger et al. 2008). Because of climate change, the frequency of major hurricanes (i.e. Saffir-Simpson scale, categories 3–5) is increasing in the warming waters of the Caribbean region (Goldenberg et al. 2001, Webster et al. 2005, Biasutti et al. 2012). The 2017 Atlantic hurricane season had 6 major hurri-

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canes, including Irma and María, which at maximum intensities reached category 5, with winds exceeding 252 km h^{-1} (US National Oceanic & Atmospheric Administration 2020). On 6 September 2017, Hurricane Irma passed about 100 km off the northeast coast of Puerto Rico, bringing as much as 300 mm of rainfall and category 2 winds in the range of $155\text{--}177 \text{ km h}^{-1}$ affecting mostly the northeastern and east-central regions (US National Oceanic and Atmospheric Administration 2020). Two weeks later, Hurricane María made landfall as a category 4, with as much as 1500 mm of rainfall and winds in the range of $209\text{--}251 \text{ km h}^{-1}$ affecting the whole island (US National Oceanic and Atmospheric Administration 2020).

The most evident direct effect of hurricanes on Caribbean island forests is structural vegetation damage from heavy rains and high-speed winds (Boose et al. 2004, Uriarte et al. 2019, Hall et al. 2020). However, the widespread reduction of vegetation cover from uprooted trees, stem breaks and defoliation can limit food supplies during extended periods of time (e.g. see Wunderle 1995, their Fig. 3), particularly for fruit- and seed-eating birds, such as the endangered Puerto Rico plain pigeon *Patagioenas inornata wetmorei*. Reduced vegetation cover and limited food supplies, in turn, can cause abundance declines and population bottlenecks by decreasing survival and reproductive rates and increasing predation and competition for limited resources (e.g. see Beissinger et al. 2008, their Figs. 5 & 8).

Habitat loss and degradation from agriculture, predation and competition in remaining forest fragments, hunting and the effects of hurricanes San Ciriaco (category 4) in 1899, San Felipe (category 5) in 1928, San Ciprián (category 4) in 1932 and Betsy (category 3) in 1956, may have caused the plain pigeon population bottleneck during the 1920s–1970s (Wetmore 1916, Danforth 1931, Koenig 1953, Pérez-Rivera 1978, Wiley 1985, Miyamoto et al. 1994, Boose et al. 2004). Because of the discovery of a small number of individuals in the east-central region of the island, the US Fish and Wildlife Service listed the plain pigeon as endangered in 1970 (USFWS 1982). Captive breeding was conducted during 1983–2001, with the collaboration of state and federal government agencies and the University of Puerto Rico at Humacao Campus, but reintroduction efforts were mostly unsuccessful for a variety of reasons, including predation by the red-tailed hawk *Buteo jamaicensis* (Ruiz-Lebrón et al. 1995, USFWS 2011).

Concerned about the lack of long-term monitoring and reliable abundance estimates, we initiated island-wide columbid and raptor surveys once per

year beginning in April to June 1986 (Rivera-Milán 1992, 1995a,b, Rivera-Milán et al. 2003a, 2014, 2016). Since then, we have surveyed columbid and raptor populations annually in April to June, except in 2020 due to the coronavirus pandemic. During that time, 3 major hurricanes have made landfall on Puerto Rico: Hugo (category 4) in September 1989, Georges (category 3) in September 1998 and María (category 4) in September 2017. The plain pigeon population recovered after hurricanes Hugo and Georges (see Rivera-Milán et al. 2016, their Fig. 3). However, because María has been the most devastating hurricane to make landfall on the island since the 3 major hurricanes that occurred in 1899–1932 (Boose et al. 2004, Uriarte et al. 2019, Hall et al. 2020), we expected plain pigeon abundance to decline below the lowest estimate since monitoring started, which had occurred in April to June 1990 (Rivera-Milán et al. 2016). Here, we used distance sampling to (1) estimate plain pigeon, scaly-naped pigeon *P. squamosa* and red-tailed hawk abundance island-wide and in the east-central region in April to June 1986–2021, (2) fit a Bayesian state-space logistic model with abundance estimates, (3) generate posterior estimates of maximum population growth rate and population carrying capacity and (4) predict abundance in April to June 2020–2030. We used the Bayesian state-space logistic model to project abundance forward in time to cover a decade, based on the precision of short-term abundance predictions and the time period needed for two 5 yr population status reviews (USFWS 2011, Rivera-Milán et al. 2016). In addition, following recommendations provided in the most recent population status review (USFWS 2011), we repeated the surveys 3 times per year at the centre of abundance of the plain pigeon in the east-central region in April to June 2015–2019. We used *N*-mixture and 2-species models to estimate detection, abundance and occupancy, and to assess association patterns in the east-central region before and after hurricanes Irma and María in September 2017.

While the endangered plain pigeon and the abundant scaly-naped pigeon are similar-sized resident congeners that may compete for limited resources (Pérez-Rivera 1978, Rivera-Milán 1996, 2001, Rivera-Milán et al. 2003b, 2014, 2016), the red-tailed hawk is an abundant resident raptor that preys on both pigeon species (Santana C. & Temple 1988, Rivera-Milán 1995b, Ruiz-Lebrón et al. 1995, Vilella & Nimitz 2012, Vilella et al. 2013, Gallardo et al. 2019). Therefore, mainly because of reduced vegetation cover and limited food supplies after the 2017 hurricanes, we expected plain pigeon detection, abun-

dance and occupancy to be negatively associated with the presence and density of the scaly-naped pigeon and red-tailed hawk, resulting in 'detection δ and species φ interaction factors' (sensu MacKenzie et al. 2004, 2006) below what would have been the case under independent coexistence (i.e. pre-hurricane δ and $\varphi = 1$, post-hurricane φ and $\delta < 1$). However, although predator-prey and competitive interactions may influence community structure and population dynamics (Strong et al. 1984, Begon et al. 1996, Newton 1998), we recognize that alternative explanations about association patterns cannot be excluded with survey-based count data (i.e. pattern does not necessarily relate to process, and correlation or association does not necessarily imply relationship or causation; James & Boecklen 1984, Poling & Hayslette 2006, Cooper et al. 2007). Here, we used the term 'interaction' in a statistical sense, meaning that δ and $\varphi = 1$ would suggest that the 3 species tended to occur independently of each other, based on estimates of detection, abundance and occupancy for the surveyed areas in the east-central region of Puerto Rico in April to June 2015–2019.

2. MATERIALS AND METHODS

2.1. Distance sampling

We surveyed 1400 points island-wide once per year in April to June 1986–2021, including 247 points that were surveyed 3 times per year in the east-central region during 2015–2019 (see Fig. 1 in Rivera-Milán et al. 2016). The surveys covered 7490 km² island-wide and 1100 km² in the east-central region. We did not survey heavily urbanized and industrialized areas or primary roads (e.g. expressways). We located on-road points systematically with random starts along secondary and tertiary roads (e.g. paved and unpaved roads in rural areas). Off-road points were located systematically with random starts at a minimum distance of 200 m from the nearest roads. Minimum distance was 400 m between off-road points and 800 m between on-road points. We used 2-observer teams to meet the following distance sampling assumptions: (1) certain detection of pigeons and hawks at the point centres (i.e. $g[0] = 1$), (2) detection at their initial locations, (3) correct distance measurements and (4) unbiased cluster size estimation (Buckland et al. 2001).

Two observers remained side by side at the point centres for 6 min, with 1 observer mainly recording the data and the other observer mainly measuring the distances to single birds or the geometric centre of

clusters. We defined a cluster as 2 or more individuals of the same species within 10 m of each other, showing similar behaviour (e.g. perching). We used 6 min counts to increase the probability of pigeons and hawks becoming available for detection (e.g. calling). Whenever possible, we measured distances to the nearest metre with rangefinders. However, when we were not able to measure the distances to the nearest metre, distances were measured to the nearest locations and detections were allocated to categories 0–15, 16–30, 31–45, 46–60, 61–90, 91–120, 121–180, 181–240, 241–340 or 341–440 m (Rivera-Milán et al. 2003a, 2014, 2015, 2016).

We used distances to the nearest metre and category midpoints for the analysis of grouped and ungrouped distance data (Buckland et al. 2001). The second and third distance sampling assumptions (see above) were relaxed with 2 observers operating as a team and the use of distance categories (Buckland et al. 2001, Burnham et al. 2004). Regarding the first and fourth assumptions (see above), it was unlikely that 2 experienced observers missed pigeons or hawks at the point centres during 6 min counts, and detections were mostly of single birds or small clusters during the surveys (Rivera-Milán et al. 2003a, 2014, 2016). Flying pigeons and hawks were not included in density estimates, unless we measured the distances to their initial locations, before any movement. To minimize responsive movement, which usually was away from the point centres, we did not implement a settling period before count initiation. We conducted the surveys during 06:30–10:00 and 15:30–19:00 h. Survey effort accounted for the number of visits per point each year (Buckland et al. 2001).

We modelled detection probability as a function of distance r and covariates represented by vector \mathbf{z} (i.e. $g[r, \mathbf{z}]$; Marques et al. 2007). Density was estimated as:

$$\hat{D} = \frac{n\bar{s}}{2\pi k\hat{P}(\mathbf{z}_i)} \quad (1)$$

where \hat{D} is the number of individuals km⁻², n is the number of single and cluster detections, \bar{s} is the average cluster size, which was used for density estimation when cluster detection was not size biased, and k is the number of points. When cluster detection was size biased, we used the size-bias regression method (Buckland et al. 2001), or included cluster size as a covariate in the models. After exploratory data analysis with distances grouped and ungrouped for each species separated and years separated or combined (Buckland et al. 2001, 2015, Marques et al. 2007), we right-truncated the distance data at $w = 120$ m. Detection probability was estimated as:

$$\hat{P}(z_i) = \frac{2}{w^2} \int_0^w r \hat{g}(r, z_i) dr \quad (2)$$

We estimated population size by extrapolating density estimates from the surveyed area (i.e. $k\pi w^2$) to the survey region (i.e. $\hat{N} = \hat{D} \times A$, where $A = 7490 \text{ km}^2$ island-wide or 1100 km^2 for the east-central region). We used nonparametric bootstrapping to estimate detection and abundance standard errors (SEs) (Buckland et al. 2001).

We evaluated the fit of uniform, half-normal and hazard-rate detection models with the Kolmogorov-Smirnov test and Cramer-von Mises family tests (Burnham et al. 2004). Based on minimization of Akaike's information criterion (AIC or AIC corrected for small sample size, AIC_c ; Burnham & Anderson 1998) and model flexibility and robustness (Buckland et al. 2001, 2015), we selected the hazard-rate key function without series expansion to explore the effects of the following categorical or continuous covariates: cluster size (≥ 2 individuals), detection mode (0 = audio, 1 = visual), detection time (0 = 0–3 min, 1 = 4–6 min), time of day (minutes after 06:30 h and minutes before 19:00 h), point location (0 = on road, 1 = off road), life zone (0 = dry, 1 = moist, 2 = wet), 2-observer team (11 teams, designated 0–10), month (0 = April, 1 = May, 2 = June), year (0–34) and vertical and horizontal vegetation cover and food availability for the pigeons on trees, shrubs and vines within 60 m of the point centres (0 = open forest canopy and understorey, none with fruits or seeds, 1 = low, 2 = low-medium, 3 = medium-high, 4 = high; or 0 = none-low, 1 = medium-high).

After the 6 min counts, the 2 observers moved around the point centres as much as needed to determine if nearby pigeons or hawks were missed, verify any problematic distance measurements and reach a consensus about vegetation cover and food availability within 60 m. For more information about the diet of the 2 pigeon species, see Pérez-Rivera (1978), Rivera-Milán (1996, 2001) and Rivera-Milán et al. (2003b). We post-stratified the distance data of each species by year (e.g. pre-hurricane 0 = 2015–2017, post-hurricane 1 = 2018–2021), vegetation cover and food availability (0 = none-low, 1 = medium-high), and used the 2-tailed z-statistic to test for significant differences ($p < 0.05$) in detection and density estimates (Buckland et al. 2001). We used the programs DISTANCE version 7.3.1 (Thomas et al. 2010) and R version 3.6.3 (R Development Core Team 2020), and the R package 'DISTANCE' version 1.0.2 (Miller et al. 2019). Results are presented as means with bootstrapped SEs.

2.2. N-mixture and two-species models

Based on AIC_c (Burnham & Anderson 1998), we selected the Poisson-binomial mixture model (Royle & Nichols 2003, Royle 2004, MacKenzie et al. 2006) to estimate detection probability P_{ij} and abundance λ at 247 points R that were surveyed 3 times per year in the east-central region during 2015–2019. The points were surveyed once in 2021. We defined the repeated counts C_{ij} as conditionally independent binomial random variables with detection and abundance at point i and time j (i.e. P_{ij} , N_{ij}), and integrated likelihood:

$$L(\lambda, P_{ij} | C_{ij}) = \prod_{i=1}^R \left\{ \sum_{N_i=\max(C_i)}^{\infty} \left(\prod_{j=1}^J \text{Binomial}(C_{ij} | N_{ij}, P_{ij}) \right) \text{Poisson}(N_{ij} | \lambda) \right\} \quad (3)$$

We used an additive normal random effect to account for extra-Poisson variation in abundance. For example, $\log(\lambda_{ij}) = \beta_0 + \beta_1(x_{ij}) + \beta_2(y_{ij}) + \varepsilon_{ij}$ for covariates x_{ij} and y_{ij} , with error $\varepsilon_{ij} \sim \text{Normal}(0, \sigma_{\lambda_{ij}}^2)$. We used a logistic regression model to account for extra-binomial variation in detection probability. For example, $\text{logit}(P_{ij}) = \beta_0 + \beta_1(x_{ij}) + \beta_2(y_{ij}) + \varepsilon_{ij}$, for covariates x_{ij} and y_{ij} , with error $\varepsilon_{ij} \sim \text{Normal}(0, \sigma_{P_{ij}}^2)$. We expected plain pigeon abundance and detection estimates to be negatively associated with the point-level density estimates of the scaly-naped pigeon and red-tailed hawk (i.e. $\hat{D}_{ij} = \hat{\lambda}_{ij} / \pi w^2$, where $w = 120 \text{ m}$). We standardised the density estimates (i.e. $z = [\text{raw score} - \text{mean score}] / \text{SD}$), and evaluated the fit of Poisson-binomial mixture models with Pearson's χ^2 test (MacKenzie et al. 2006). With the most basic Poisson-binomial mixture model (i.e. $\lambda[.]$, $P_{ij}[.]$), we assumed (1) constant abundance during the 2 wk survey periods per year in April to June 2015–2019 (i.e. population closure), (2) constant detection (i.e. the same for all individuals of each species at point i and time j) and (3) no false positives (e.g. no double-counting at point i and time j).

In addition, we treated the point-level count data as non-detection or detection (i.e. 0 or 1), and used 2-species models to estimate species φ and detection δ interaction factors:

$$\hat{\varphi} = \frac{\hat{\Psi}^{AB}}{\hat{\Psi}^A \hat{\Psi}^B} \quad (4)$$

and:

$$\hat{\delta} = \frac{\hat{P}_j^A}{\hat{P}_j^A \hat{P}_j^B} \quad (5)$$

where ψ^A is the probability of occupancy by the plain pigeon (i.e. species A), regardless of occupancy by the scaly-naped pigeon or red-tailed hawk (i.e. species B); ψ^B is the probability of occupancy by B , re-

ardless of occupancy by A ; and ψ^{AB} is the probability of AB co-occupancy (MacKenzie et al. 2004, 2006). P_j^A is the probability of detection for A during the j^{th} survey, given AB presence; P_j^B is the probability of detection for B during the j^{th} survey, given AB presence; and P_j^{AB} is the probability of AB co-detection during the j^{th} survey, given AB presence (MacKenzie et al. 2004, 2006).

While φ and $\delta = 1$ would suggest independent co-occupancy and co-detection (i.e. $\psi^{AB} = \psi^A \times \psi^B$ and $P_j^{AB} = P_j^A \times P_j^B$), φ and $\delta < 1$ would suggest negative and φ and $\delta > 1$ would suggest positive co-occupancy and co-detection. We also estimated the probability of occupancy and detection of A during the j^{th} survey, given A presence but B absence (denoted ' b ') (i.e. ψ^{Ab} and P_j^{Ab}). With φ and $\delta < 1$, we would expect ψ^{Ab} and $P_j^{Ab} > \psi^{AB}$ and P_j^{AB} ; that is, higher plain pigeon occupancy and detection with scaly-naped pigeon and red-tailed hawk absence than presence at the surveyed points. For additional information about the formulation of 2-species models, see MacKenzie et al. (2004, 2006). We used the single-season Poisson-binomial mixture and 2-species models as implemented in the program PRESENCE version 2.13.6 (Hines 2020) and the R package 'UNMARKED' version 1.1.0 (Fiske & Chandler 2011). Results are presented as means with bootstrapped SEs.

2.3. Bayesian state-space logistic model

We modelled the population dynamics of the plain pigeon, scaly-naped pigeon and red-tailed hawk with the standard logistic equation (Runge et al. 2009, Rivera-Milán et al. 2014, 2016):

$$N_{t+1} = N + r_m N_t \left(1 - \left[\frac{N_t}{K} \right] \right) - M_t \quad (6)$$

where r_m is the maximum intrinsic rate of population growth, K is the population carrying capacity, N_t is the true unknown abundance state of the population, and M_t is the total number of human-induced deaths in year t . $M_t = N_t \times m_t$, where m_t is the mortality rate between year t and $t + 1$. We generated mortality rates randomly as part of the Markov chain Monte Carlo (MCMC) algorithm with uniform distributions (e.g. $m \sim \text{Uniform}[0.01, 0.10]$ for the plain pigeon and red-tailed hawk to account for illegal hunting; and $m \sim \text{Uniform}[0.05, 0.50]$ for the scaly-naped pigeon to account for legal and illegal hunting; Rivera-Milán et al. 2014, 2016). We re-parameterized the unknown abundance state as a proportion of population carrying capacity (i.e. N_t/K) to reduce the autocorrelation

of MCMC samples. We assumed that the error of state model predictions ϵ was lognormally distributed with mean 0 and estimated standard deviation σ_p . Based on this reparameterization, we projected abundance forward in time with:

$$P_{t+1} = \left(P_t + r_m P_t [1 - P_t] - \frac{M_t}{K} \right) e^{\epsilon_t} \quad (7)$$

We modelled the abundance proportion of the first year using a lognormal distribution with mean P_0 and variance $\sigma_{P_0}^2$:

$$P_1 \sim \text{Lognormal}(P_0, \sigma_{P_0}^2) \quad (8)$$

While the process model in the state-space formulation accounted for our incomplete understanding of pigeon and hawk population dynamics, we related true abundance state to the distance sampling abundance estimates and SEs to account for observation variance (Knappe 2008). That is, we specified that abundance y_t and observation variance $\sigma_{t,o}^2$ were estimated from the surveys. Because the distribution of abundance estimates tends to be positively skewed, we assumed a lognormal distribution for $\sigma_{t,o}^2$ (Buckland et al. 2001). We transformed abundance estimates to the natural logarithm scale by transforming the bootstrapped SEs to the standard deviations (SDs) of the corresponding lognormal distribution. To complete the observation model of the state-space formulation, we related true unknown abundance state (i.e. $N_t = P_t \times K$) and estimated abundance with:

$$\log(y_t) = \log(P_t K) + \mu_t \quad (9)$$

where:

$$\mu_t \sim \text{Normal}(0, \sigma_{t,o}^2) \quad (10)$$

We assumed equal mortality for all individuals of each species, regardless of age and sex class. We also assumed additive mortality from natural and human-induced disturbances, although the model formulation allowed for compensation through linear density-dependent population growth (Runge et al. 2009, Rivera-Milán et al. 2014, 2016). We estimated unobserved population parameters and unknown abundance states under the assumption of conditional independence for each time step. We specified uniform prior distributions with wide but biologically realistic ranges. For example, in the case of the plain pigeon island-wide (see Rivera-Milán et al. 2016, their Table 1), $r_m \sim \text{Uniform}(0.01, 1)$, $K \sim \text{Uniform}(10\,000, 100\,000)$, and the mean of initial abundance on the log scale $P_0 \sim \text{Uniform}(-2, 0)$. For the SDs of process error and initial annual abundance proportion, we also used uniform priors (e.g. σ_p and $\sigma_{t,o}^2 \sim \text{Uniform}[0, 2]$).

To generate parameter posterior distributions, we ran the program JAGS version 4.3.0 (Plummer 2003) with the R package 'R2JAGS' version 0.5–7 (Su & Yajima 2015). We generated 250 000 iterations and used the first 50 000 iterations for a burn-in period. We thinned 3 Markov chains by 25 to obtain samples of 8000 iterations. We checked for convergence of the MCMC algorithm with trace plots and node summary statistics (e.g. Brooks-Gelman-Rubin diagnostic statistic R), and made posterior predictive checks of model fit with Bayesian p -values (Gelman & Hill 2007). Results are presented as means \pm SDs and medians with 2.5th and 97.5th percentiles.

3. RESULTS

3.1. Distance sampling

Overall, we made 803 plain pigeon detections (Fig. 1), 33 817 scaly-naped pigeon detections (Fig. 2), and 1624 red-tailed hawk detections (Fig. 3) at the 1400 points that were surveyed in April to June 1986–2021. The hazard-rate key function without series expansion fit the distance data of the plain pigeon (e.g. range of Cramer-von Mises family tests $0.70 < p \leq 0.80$; Fig. 1), scaly-naped pigeon ($0.60 < p \leq 0.70$; Fig. 2) and red-tailed hawk ($0.80 < p \leq 0.90$; Fig. 3). Vegetation cover had a negative effect and was the most important detection covariate for the plain pigeon ($\beta \pm \text{SE} = -0.24 \pm 0.06$), scaly-naped pigeon ($\beta = -0.82 \pm 0.04$) and red-tailed hawk ($\beta = -0.46 \pm 0.03$). Other covariates, such as point location ($\Delta\text{AIC}_c \geq 3.68$), 2-observer team ($\Delta\text{AIC}_c \geq 4.31$) and year ($\Delta\text{AIC}_c \geq 5.71$), received less support from the distance data of the 3 species. For the plain pigeon, detection probability averaged 0.38 ± 0.06 in none–low vegetation cover and 0.22 ± 0.05 in medium–high vegetation cover ($z = 2.05$, $p = 0.04$). For the scaly-naped pigeon, detection probability averaged 0.35 ± 0.03 in none–low vegetation cover and 0.27 ± 0.02 in medium–high vegetation cover ($z = 2.22$, $p =$

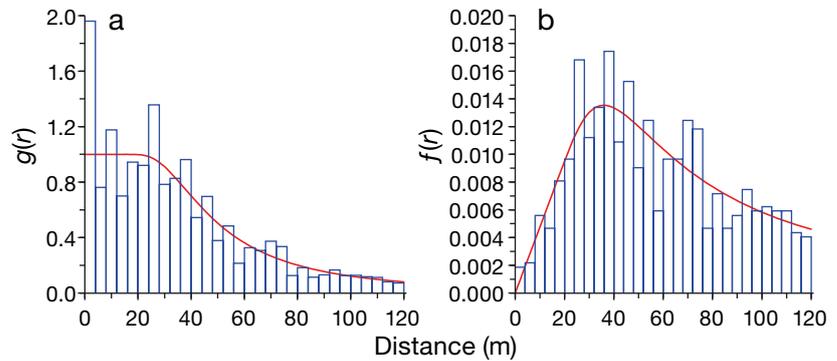


Fig. 1. Plain pigeon (a) detection probability $g(r)$ and (b) probability density function $f(r)$ based on the hazard-rate key function without series expansion and 803 detections made at the 1400 points surveyed on Puerto Rico in April to June 1986–2021

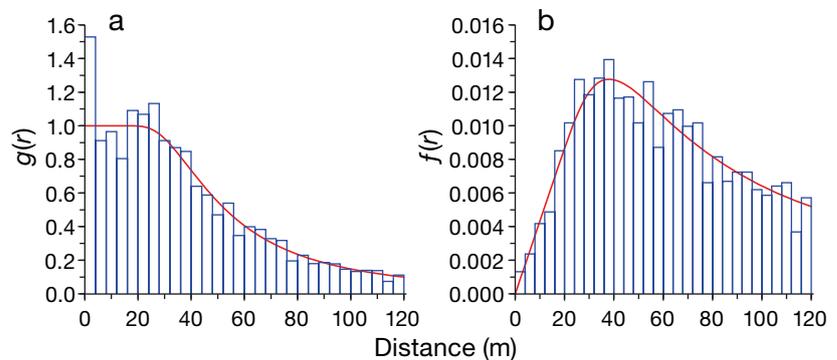


Fig. 2. Scaly-naped pigeon (a) detection probability $g(r)$ and (b) probability density function $f(r)$ based on the hazard-rate key function without series expansion and 33 817 detections made at the 1400 points surveyed on Puerto Rico in April to June 1986–2021

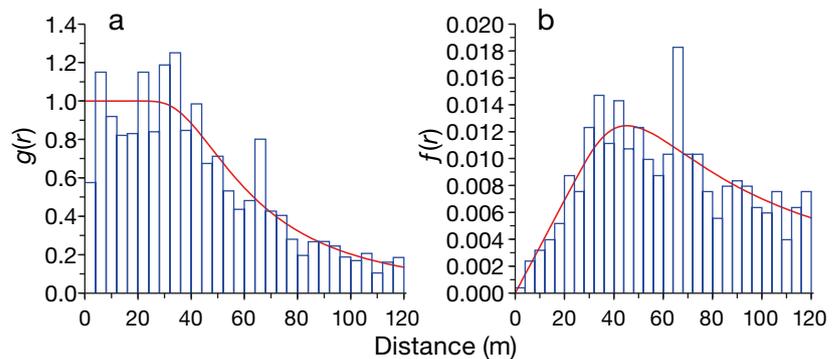


Fig. 3. Red-tailed hawk (a) detection probability $g(r)$ and (b) probability density function $f(r)$ based on the hazard-rate key function without series expansion and 1624 detections made at the 1400 points surveyed on Puerto Rico in April to June 1986–2021

0.03). For the red-tailed hawk, detection probability averaged 0.54 ± 0.10 in none–low vegetation cover and 0.26 ± 0.03 in medium–high vegetation cover ($z = 2.68$, $p = 0.01$). Overall, detection probability averaged

0.30 ± 0.02 for the plain pigeon (Fig. 1), 0.32 ± 0.01 for the scaly-naped pigeon (Fig. 2) and 0.40 ± 0.03 for the red-tailed hawk (Fig. 3).

Overall, plain pigeon density and population size averaged 2.66 ± 0.94 km⁻² and 20 456 ± 6697 island-wide (Table 1, Fig. 4a), and 5.43 ± 1.81 km⁻² and 6149 ± 2226 in the east-central region (Table 1, Fig. 4b). Plain pigeon density and population size declined island-wide ($z = 2.25, p = 0.03$) and in the east-central region ($z = 2.58, p = 0.01$) after Hurricane Hugo in 1989. Plain pigeon abundance did not decline significantly island-wide ($z = 1.74, p = 0.08$) or in the east-central region ($z = 1.89, p = 0.06$) after Hurricane Georges in 1998 (Table 1, Fig. 4). However, between 2017 and 2018 (i.e. before–after hurricanes Irma and

María), plain pigeon density and population size declined from 1.60 ± 0.70 km⁻² and 11 984 ± 5129 to 0.10 ± 0.05 km⁻² and 749 ± 354 island-wide ($z = 2.14, p = 0.03$; Table 1, Fig. 4a), and from 3.90 ± 1.70 km⁻² and 4257 ± 1822 to 0.50 ± 0.10 km⁻² and 550 ± 110 in the east-central region ($z = 2.00, p = 0.05$; Table 1, Fig. 4b). Plain pigeon abundance was at the lowest level ever estimated since monitoring started in 1986, and remained low during 2018–2021 (Table 1, Fig. 4). After the 1989, 1998 and 2017 hurricanes, plain pigeon abundance was higher at the points with medium–high than none–low vegetation cover ($z > 2.30, p < 0.02$) and food availability ($z > 2.09, p < 0.04$).

Overall, scaly-naped pigeon density and population size averaged 37.19 ± 5.88 km⁻² and 278 780 ± 44 117 island-wide (Table 2, Fig. 5a), and 42.95 ± 8.03 km⁻² and 47 080 ± 8854 in the east-central region (Table 2, Fig. 5b). Scaly-naped pigeon density and population size did not decline island-wide or in the east-central region after hurricanes Hugo in 1989 and Georges in 1998 ($z < 1.17, p > 0.24$; Table 2, Fig. 5). However, between 2017 and 2018, scaly-naped pigeon density and population size declined from 53.90 ± 5.10 km⁻² and 403 711 ± 38 199 to 30.30 ± 2.79 km⁻² and 226 947 ± 20 879 island-wide ($z = 3.99, p < 0.001$; Table 2, Fig. 5a), and from 67.80 ± 12.07 km⁻² and 74 580 ± 13 275 to 29.20 ± 4.38 km⁻² and 32 120 ± 4818 in the east-central region ($z = 3.08, p = 0.002$; Table 2, Fig. 5b). Scaly-naped pigeon abundance returned to pre-hurricane levels in 2019 (Table 2, Fig. 5). After the 1989, 1998 and 2017 hurricanes, scaly-naped pigeon abundance was higher at the points with medium–high than none–low vegetation cover ($z > 2.38, p < 0.02$) and food availability ($z > 2.19, p < 0.03$).

Overall, red-tailed hawk density and population size averaged 2.49 ± 0.57 km⁻² and 18 787 ± 4197 island-wide (Table 3, Fig. 6a), and 1.63 ± 0.41 km⁻² and 1844 ± 468 in the east-central region (Table 3, Fig. 6b). After the 1989 and 1998 hurricanes, red-tailed hawk abundance did not decline significantly island-wide or in the east-central region ($z < 1.58, p > 0.11$; Table 3, Fig. 6). Red-tailed hawk density and population size island-wide averaged 2.81 ± 0.73 km⁻² and 21 066 ± 5498 in 2017, and 1.93 ± 0.52 km⁻² and 14 456 ± 3860 in 2018 ($z = 0.98, p = 0.33$; Table 3, Fig. 6a). However, in the east-central region, red-tailed hawk density and population size averaged 2.20 ± 0.53 km⁻² and 2420 ± 581 in

Table 1. Plain pigeon distance sampling abundance estimates with bootstrapped SEs island-wide and in the east-central region of Puerto Rico in April–June 1986–2021. For the island-wide estimates, density (\hat{D}) = ind. km⁻² at 1400 surveyed points, and population size (\hat{N}) = ind. 7490 km⁻². For the east-central region, \hat{D} = ind. km⁻² at 247 surveyed points, and \hat{N} = ind. 1100 km⁻²

Year	Island-wide				East-central region			
	\hat{D}	SE	\hat{N}	SE	\hat{D}	SE	\hat{N}	SE
1986	0.70	0.20	5018	1260	1.20	0.30	1320	331
1987	1.50	0.30	11535	2445	3.10	0.70	3410	723
1988	1.60	0.40	11984	2696	2.10	0.50	2310	520
1989	1.40	0.30	10411	2613	3.40	0.90	3740	939
1990	0.50	0.20	3745	1393	1.00	0.40	1100	409
1991	1.30	0.40	9363	3286	2.30	0.80	2530	888
1992	2.30	0.90	17227	6426	4.30	0.90	4740	1768
1993	2.40	0.90	17602	6548	3.40	0.15	3740	1391
1994	4.60	1.60	34454	11749	6.20	2.10	6820	2326
1995	4.10	1.20	30709	9305	5.70	1.70	6270	1900
1996	8.10	2.40	60669	18140	8.10	2.40	8910	2664
1997	7.50	2.70	56175	20240	12.80	3.80	13770	4961
1998	10.20	3.20	76398	23968	20.20	6.50	22220	6971
1999	3.70	1.90	27713	14231	7.20	2.30	7920	4067
2000	4.10	1.50	30709	11235	8.10	3.00	8910	3260
2001	5.80	1.80	43442	13482	15.50	4.70	17050	5291
2002	4.00	1.40	29960	10486	11.00	3.70	12100	4235
2003	3.30	1.20	24717	8988	9.00	3.40	9900	3600
2004	1.80	0.80	13482	5992	5.10	2.30	5610	2493
2005	1.60	0.60	11984	4494	4.90	1.50	5390	2021
2006	1.80	0.80	13482	5963	5.20	2.30	5720	2530
2007	1.90	0.90	14231	6582	8.00	3.70	8800	4070
2008	3.20	1.20	23968	9205	6.50	1.00	8079	3103
2009	3.60	1.30	26964	4494	7.20	1.10	7920	2904
2010	3.10	0.90	23219	2459	5.10	0.70	5610	1716
2011	2.40	0.90	17602	3389	5.10	2.00	5578	2203
2012	1.60	0.60	11984	3286	3.90	1.50	4257	1633
2013	0.80	0.40	5992	2969	2.60	1.30	2849	1412
2014	1.90	0.80	14445	1388	4.40	1.70	4836	1915
2015	1.40	0.60	10446	4387	3.50	1.50	3896	1636
2016	1.50	0.60	11235	4752	3.70	1.60	4081	1726
2017	1.60	0.70	11984	5129	3.90	1.70	4257	1822
2018	0.10	0.05	749	354	0.50	0.10	550	110
2019	0.08	0.03	599	237	0.40	0.10	440	110
2021	0.24	0.11	1781	839	0.50	0.20	550	265

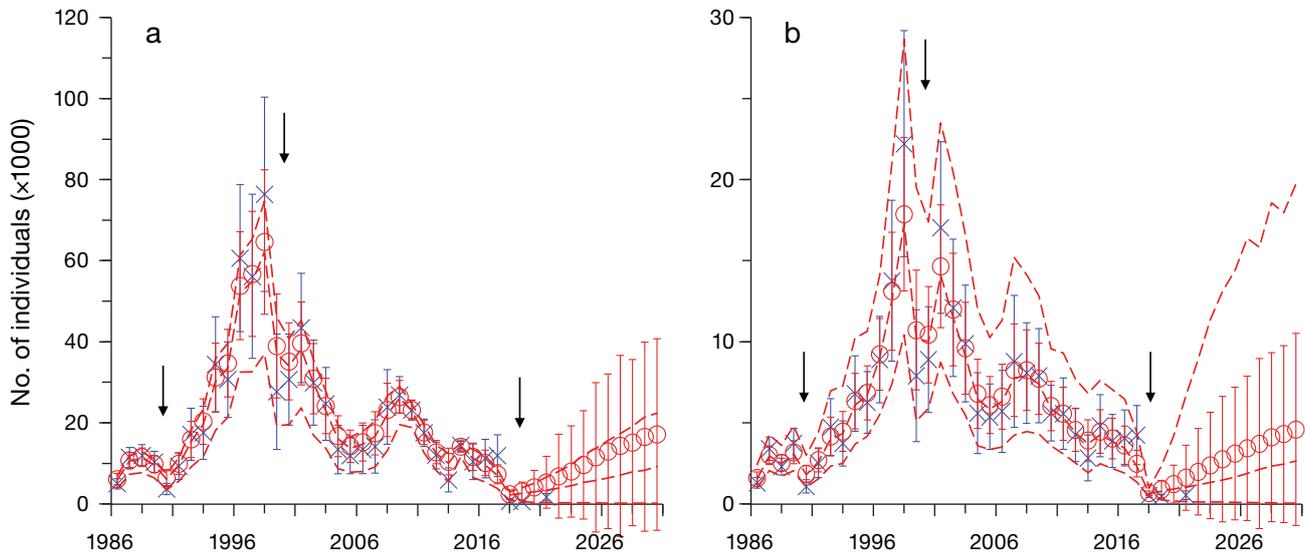


Fig. 4. Plain pigeon distance sampling abundance estimates with bootstrapped SEs (crosses with vertical lines) in April to June 1986–2021, and Bayesian state-space logistic model means and SDs (circles with vertical lines) with medians and 2.5–97.5th percentiles (dashed lines) and predicted abundance (a) island-wide and (b) in the east-central region of Puerto Rico in April to June 2020–2030. The arrows point to post-hurricane abundance estimates in April to June 1990, 1999 and 2018. Surveys were not conducted in 2020

2017, and $1.00 \pm 0.31 \text{ km}^{-2}$ and 1100 ± 341 in 2018 ($z = 1.96$, $p = 0.05$; Table 1, Fig. 6b). After the 1989, 1998 and 2017 hurricanes, red-tailed hawk abundance was higher at the points with medium–high than none–low vegetation cover ($z > 2.42$, $p < 0.02$).

3.2. N-mixture and two-species models

The most basic Poisson-binomial mixture model fit the plain pigeon count data collected at the 247 points that were surveyed 3 times per year in the east-central region in April–June 2015–2019 (range of Pearson's $\chi^2 = 0.62$ –2.13, $df = 7$, $p = 0.95$ –0.99; range of AIC_c values = 709.46–837.37). More complex models (e.g. λ [pigeon + hawk density], P_{ij} [pigeon + hawk density]; range of Pearson's $\chi^2 = 0.61$ –1.98, $df = 7$, $p = 0.96$ –0.99; range of ΔAIC_c values = 0.52–0.62) were informative but increased the SEs of detection and abundance estimates. As a result, there was a positive but variable association between the plain pigeon and scaly-naped pigeon point-level density estimates (range of beta coefficients $\beta = 0.24$ –0.70, $SE = 0.20$ –0.50) and detection estimates ($\beta = 0.26$ –0.56, $SE = 0.22$ –0.41), and there was a negative but variable association between the plain pigeon and red-tailed hawk point-level density estimates ($\beta = -1.06$ to -1.22 , $SE = 0.97$ –1.11) and detection estimates ($\beta = -1.02$ to -1.27 , $SE = 0.84$ –1.10). The Poisson-binomial mixture models and dis-

tance sampling hazard-rate models generated similar abundance estimates for the east-central region during 2015–2019. For example, based on the Poisson-binomial mixture models, population size averaged 543 ± 237 for the plain pigeon, $42\,807 \pm 1417$ for the scaly-naped pigeon and 1353 ± 96 for the red-tailed hawk in 2018 and 2019. For comparison with the distance sampling abundance estimates, see Tables 1–3.

Based on the 2-species models, plain pigeon occupancy averaged 0.32 ± 0.03 , scaly-naped pigeon occupancy averaged 0.91 ± 0.04 , and red-tailed hawk occupancy averaged 0.68 ± 0.14 at the points that were surveyed in the east-central region during 2015–2019. Co-occupancy ψ^{AB} averaged 0.48 ± 0.05 for the plain pigeon and scaly-naped pigeon, and 0.19 ± 0.08 for the plain pigeon and red-tailed hawk. That is, the species interaction factor φ averaged 1.66 ± 0.25 for the plain pigeon and scaly-naped pigeon, and 0.90 ± 0.43 for the plain pigeon and red-tailed hawk. Plain pigeon detection probability, given both pigeon species presence, averaged 0.37 ± 0.11 . Scaly-naped detection probability, given both pigeon species presence, averaged 0.69 ± 0.03 . Red-tailed hawk detection probability, given plain pigeon and red-tailed hawk presence, averaged 0.70 ± 0.15 . Co-detection (P_j^{AB}) averaged 0.37 ± 0.06 for the plain pigeon and scaly-naped pigeon, and 0.17 ± 0.06 for the plain pigeon and red-tailed hawk. That is, the detection interaction factor δ averaged 1.42 ± 0.49 for

Table 2. As in Table 1, but for scaly-naped pigeon

Year	Island-wide				East-central region			
	\hat{D}	SE	\hat{N}	SE	\hat{D}	SE	\hat{N}	SE
1986	7.30	1.76	54677	13166	14.60	3.27	16060	3597
1987	8.40	1.80	62916	13501	16.80	3.71	18480	4084
1988	16.30	4.00	122087	29970	16.30	3.91	17930	4303
1989	20.90	5.14	156541	38480	21.80	5.38	23980	5923
1990	32.50	8.52	243425	63786	25.20	6.25	27720	6875
1991	15.20	3.68	113848	27539	18.20	4.08	20020	4484
1992	15.40	3.94	115346	29482	25.40	6.27	27940	6901
1993	25.06	4.51	187723	33792	30.10	6.77	33110	7450
1994	31.25	6.07	234030	45489	32.50	7.64	35750	8401
1995	38.00	8.80	284656	65941	38.00	8.40	41805	9239
1996	39.16	8.76	293338	65638	39.16	8.66	43080	9521
1997	37.85	9.12	283523	68338	37.85	7.57	41639	8328
1998	40.10	10.16	300349	76134	50.00	12.00	55000	13200
1999	53.20	12.30	398468	92145	40.30	9.39	44330	10329
2000	50.40	8.07	377496	60435	50.40	8.01	55440	8815
2001	45.50	5.95	340795	44557	45.50	7.28	50050	8008
2002	46.00	6.96	344540	52162	46.00	7.27	50600	7995
2003	26.00	4.28	194740	32043	52.00	7.96	57200	8752
2004	32.70	5.70	244923	42696	65.40	11.71	71940	12877
2005	45.30	6.54	339297	48984	45.30	7.11	49830	7823
2006	31.80	6.48	238182	48571	63.60	12.53	69960	13782
2007	45.90	6.53	343791	48921	61.80	10.07	67980	11081
2008	41.20	5.75	308603	43053	51.30	9.49	56430	10440
2009	41.20	3.50	308588	26215	41.20	8.12	45320	8928
2010	53.60	4.98	401427	37293	53.60	9.43	58955	10376
2011	52.91	5.05	396281	37792	52.91	10.58	58199	11640
2012	52.22	5.11	391135	38292	44.40	6.75	48840	7424
2013	43.33	5.58	324560	41771	43.33	7.89	47665	8675
2014	35.27	2.77	264150	20726	70.53	13.12	77587	14431
2015	41.98	3.29	314438	24620	64.00	10.18	70400	11194
2016	40.87	6.71	306129	50289	61.80	10.20	67980	11217
2017	53.90	5.10	403711	38199	67.80	12.07	74580	13275
2018	30.30	2.79	226947	20879	29.20	4.38	32120	4818
2019	47.70	4.77	357273	74783	38.90	6.22	42790	6846
2021	64.00	6.46	479360	48415	62.90	9.88	69190	10863

the 2 pigeon species, and 0.64 ± 0.33 for the plain pigeon and red-tailed hawk.

The probability of occupancy and detection of the plain pigeon, given plain pigeon presence but scaly-naped pigeon absence, averaged 0.13 ± 0.06 and 0.20 ± 0.09 ; that is, ψ^{Ab} and $P_j^{Ab} < \psi^{AB}$ and P_j^{AB} . However, the probability of occupancy and detection of the plain pigeon, given plain pigeon presence but red-tailed hawk absence, averaged 0.40 ± 0.25 and 0.71 ± 0.20 ; that is, ψ^{Ab} and $P_j^{Ab} > \psi^{AB}$ and P_j^{AB} . The association patterns were similar during 2015–2019. For example, before the 2017 hurricanes, φ and δ averaged 1.16 ± 0.45 and 1.42 ± 0.96 for the 2 pigeon species (i.e. positive but variable associations), and 0.89 ± 0.44 and 0.36 ± 0.19 for the plain pigeon and red-tailed hawk (i.e. negative but variable associations).

3.3. Bayesian state-space logistic model

Markov chains and node summary statistics showed convergence of the MCMC algorithm (e.g. Brooks-Gelman-Rubin diagnostic statistic, range of $R = 1.00$ – 1.01), and Bayesian p-values showed no evidence of model lack of fit (range of $p = 0.29$ – 0.57). Posterior estimates of maximum population growth rate r_m and carrying capacity K for the 2 pigeon species and red-tailed hawk are provided in Table 4. Posterior mean \pm SD estimates of r_m

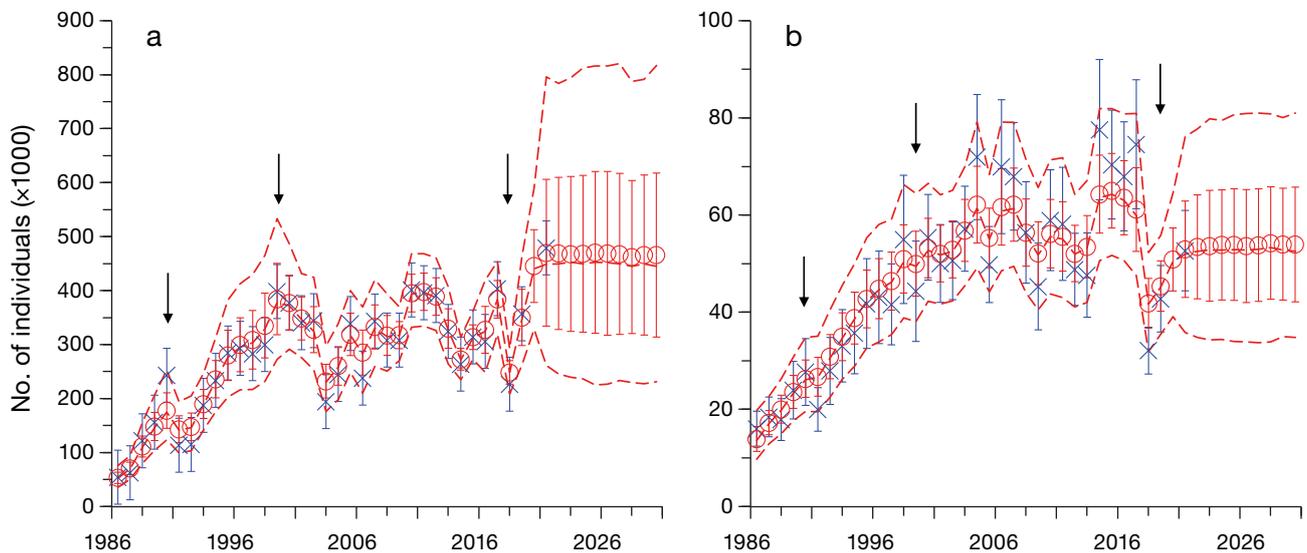


Fig. 5. As in Fig. 4, but for scaly-naped pigeon

Table 3. As in Table 1, but for red-tailed hawk

Year	Island-wide				East-central region			
	\hat{D}	SE	\hat{N}	SE	\hat{D}	SE	\hat{N}	SE
1986	1.67	0.42	12508	3115	1.00	0.28	1104	309
1987	1.80	0.48	13482	3559	1.11	0.31	1221	342
1988	1.90	0.34	14231	2576	1.20	0.32	1320	356
1989	1.88	0.47	14089	3494	1.20	0.31	1320	343
1990	1.30	0.33	9737	2483	0.90	0.19	990	208
1991	1.37	0.31	10246	2346	1.14	0.25	1256	276
1992	1.39	0.35	10381	2626	1.66	0.48	1830	531
1993	1.26	0.29	9405	2173	1.51	0.32	1658	348
1994	1.81	0.35	13573	2633	1.75	0.44	1920	480
1995	2.42	0.48	18129	3608	1.90	0.46	2095	503
1996	2.52	0.55	18910	4085	1.80	0.52	1980	574
1997	2.41	0.47	18027	3497	1.89	0.38	2077	415
1998	2.61	0.65	19541	4866	2.00	0.50	2200	550
1999	1.58	0.34	11805	1826	1.29	0.39	1420	426
2000	1.62	0.47	12108	1986	1.50	0.34	1648	494
2001	1.99	0.36	14905	2683	1.50	0.39	1650	429
2002	2.14	0.60	16029	4472	1.68	0.49	1848	536
2003	2.34	0.47	17527	3540	1.80	0.47	1980	515
2004	2.94	0.74	22043	5577	1.65	0.33	1818	364
2005	2.77	0.55	20747	4108	1.92	0.44	2116	487
2006	2.91	0.60	21796	4512	1.79	0.45	1971	493
2007	3.13	0.70	23451	5277	1.76	0.40	1933	445
2008	3.41	0.71	25527	5310	1.91	0.55	2100	609
2009	3.51	0.70	26275	5255	2.00	0.40	2200	440
2010	3.84	1.11	28728	8331	2.10	0.53	2310	578
2011	3.76	1.02	28175	7607	2.20	0.62	2420	678
2012	3.70	0.70	27712	5265	2.30	0.62	2530	683
2013	3.90	0.78	29210	5871	2.30	0.58	2530	633
2014	3.54	0.72	26517	5409	2.10	0.57	2310	624
2015	3.78	0.81	28299	6056	2.00	0.54	2200	594
2016	3.68	0.91	27552	6805	2.10	0.46	2310	508
2017	2.81	0.73	21066	5498	2.20	0.53	2420	581
2018	1.93	0.52	14456	3860	1.00	0.31	1100	341
2019	1.75	0.43	13121	3188	1.09	0.32	1200	348
2021	2.43	0.45	18222	3389	1.41	0.32	1550	357

and K island-wide were 0.23 ± 0.11 and $49\,235 \pm 6835$ for the plain pigeon, 0.55 ± 0.05 and $534\,134 \pm 40\,216$ for the scaly-naped pigeon, and 0.17 ± 0.10 and $43\,130 \pm 20\,869$ for the red-tailed hawk (Table 4). Posterior mean estimates of r_m and K in the east-central region were 0.26 ± 0.12 and 9725 ± 2793 for the plain pigeon, 0.57 ± 0.06 and $60\,820 \pm 4622$ for the scaly-naped pigeon, and 0.25 ± 0.12 and 2962 ± 999 for the red-tailed hawk (Table 4).

Plain pigeon predicted abundance N_p for 2020–2030 averaged $11\,102 \pm 17\,705$ SD (median = 5955, 2.5–97.5th percentiles = 324–13 803) island-wide and 3034 ± 3942 (median = 1744, 2.5–97.5th percentiles = 115–13 386) in the east-central region (Fig. 4). For the scaly-naped pigeon, N_p averaged $465\,825 \pm 138\,680$ (median = 448 824, 2.5–97.5th percentiles = 244 415–784 155) island-wide and $53\,498 \pm 10\,860$ (median = 52 546, 2.5–97.5th percentiles = 34 917–78 387) in the east-central region (Fig. 5). For the red-tailed hawk, N_p averaged $17\,874 \pm 6120$ (median = 17 171, 2.5–97.5th percentiles = 8043–31 951) island-wide and 1680 ± 463 (median = 1662, 2.5–97.5th percentiles = 865–2691) in the east-central region (Fig. 6).

Predicted abundance was variable mainly due to process variance (i.e. range of σ_o^2 coefficient of variation CV = 0.40–0.73; and range of observation variance σ_o^2 CV = 0.17–0.37). For the plain pigeon, σ_p^2 posterior mean \pm SD

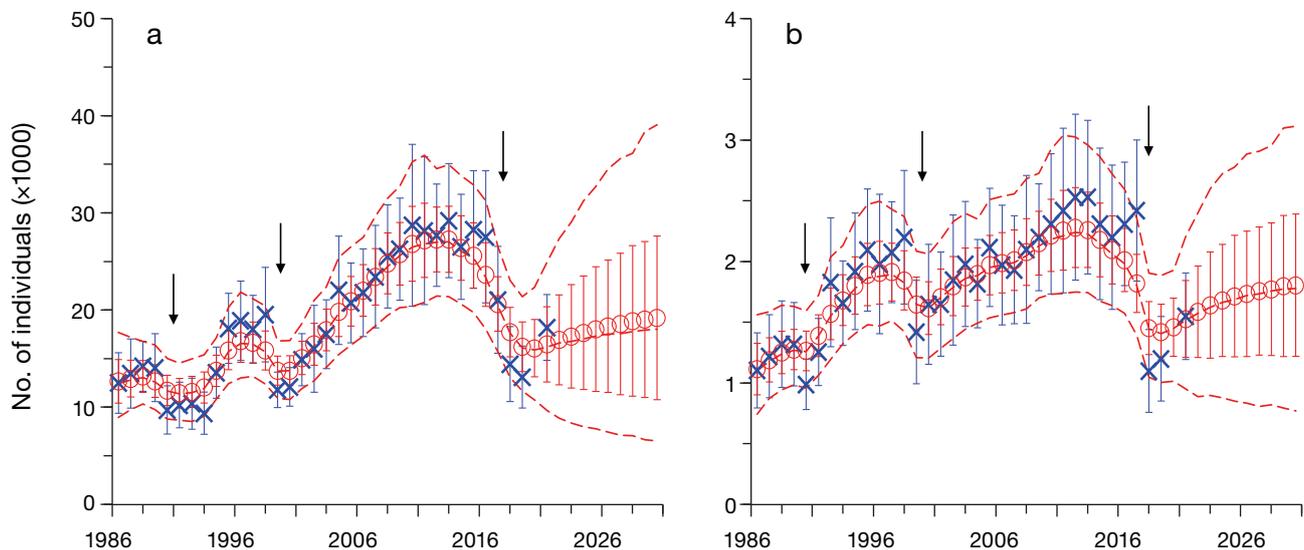


Fig. 6. As in Fig. 4, but for red-tailed hawk

Table 4. Posterior estimates of maximum population growth rate r_m and population carrying capacity K for the plain pigeon, scaly-naped pigeon and red-tailed hawk island-wide and in the east-central region of Puerto Rico in April to June 1986–2021

Island-wide	Species	r_m	SD	Median	2.5 th	97.5 th
	Plain pigeon	0.232	0.113	0.207	0.095	0.295
	Scaly-naped pigeon	0.550	0.046	0.536	0.502	0.676
	Red-tailed hawk	0.165	0.104	0.142	0.028	0.416
Island-wide	Species	K	SD	Median	2.5 th	97.5 th
	Plain pigeon	49 235	16 835	43 628	30 538	58 600
	Scaly-naped pigeon	534 134	40 216	521 415	500 725	640 312
	Red-tailed hawk	43130	20 869	35 540	19 675	92 563
East-central	Species	r_m	SD	Median	2.5 th	97.5 th
	Plain pigeon	0.255	0.124	0.228	0.097	0.562
	Scaly-naped pigeon	0.566	0.061	0.546	0.502	0.735
	Red-tailed hawk	0.249	0.118	0.238	0.065	0.477
East-central	Species	K	SD	Median	2.5 th	97.5 th
	Plain pigeon	9725	2793	9314	5404	15 980
	Scaly-naped pigeon	60 820	4622	60 408	52 980	70 732
	Red-tailed hawk	2962	999	2561	1928	5626

was 0.25 ± 0.11 (median = 0.23, 2.5–97.5th percentiles = 0.10–0.30) island-wide and 0.26 ± 0.10 (median = 0.24, 2.5–97.5th percentiles = 0.11–0.51) in the east-central region. For the scaly-naped pigeon, σ_p^2 posterior mean was 0.07 ± 0.03 (median = 0.06, 2.5–97.5th percentiles = 0.03–0.13) island-wide and 0.03 ± 0.01 (median = 0.02, 2.5–97.5th percentiles = 0.01–0.06) in the east-central region. For the red-tailed hawk, σ_p^2 posterior mean was 0.04 ± 0.02 (median = 0.04, 2.5–97.5th percentiles = 0.01–0.10) island-wide and 0.02 ± 0.01 (median = 0.02, 2.5–97.5th percentiles = 0.001–0.06) in the east-central region.

4. DISCUSSION

The plain pigeon population recovered after the 1989 and 1998 hurricanes, but the most severe abundance decline occurred after the 2017 hurricanes. In contrast, the scaly-naped pigeon and red-tailed hawk populations did not decline, or recovered faster from their declines, than the plain pigeon population after the 1989, 1998 and 2017 hurricanes. That is, the scaly-naped pigeon and red-tailed hawk populations showed more ‘resistance’ and ‘resilience’ (sensu Pimm 1991) than the plain pigeon population. Hugo in 1989 was a stronger hurricane but affected a smaller portion of the island than Georges did in 1998 (see Uriarte et al. 2019, their Fig. 1). However, based on the abundance decline in April to June 1990, we suggested that a hurricane with the intensity of Hugo but

the path of Georges would have been devastating for the plain pigeon population (Rivera-Milán et al. 2003a,b). In September 2017, hurricane Irma brought heavy rains and category 2 winds that affected mostly the northeastern and east-central regions. However, a hurricane with the path and intensity of María had not occurred since the 3 major hurricanes that occurred in 1899–1932 (see Boose et al. 2004, their Table 2 and Fig. 4), and the structural vegetation damage from record-breaking rainfall and category 4 winds was extensive in lowland and highland forests across the island, including the centre of abundance of the plain pigeon in the east-central region (see Hall et al. 2020, their Figs. 1 & 3).

Because of reproductive adaptations and strategies typical of the columbids (e.g. crop-milk production, multiple brooding and extended nesting seasons; Blockstein & Westmoreland 1993), successful reproduction is of key importance for population recovery after major hurricanes (Rivera-Milán 1996, 2001, Rivera-Milán et al. 2003b). However, contrary to the scaly-naped pigeon, which was actively calling and nesting during the 2018–2021 surveys, the plain pigeon was rarely calling and the few nesting attempts we observed were unsuccessful most likely due to nest predators, such as the black rat *Rattus rattus* and pearly-eyed thrasher *Margarops fuscatus*, which were abundant in second-growth forests of the east-central region (Rivera-Milán 1996, 2001, Rivera-Milán et al. 2003b, Ventosa-Febles 2019). In addition, because the detection probability of the plain pigeon and scaly-naped pigeon was higher at the points with none–low than medium–high vegetation cover, the extensive structural vegetation damage caused by the 2017 hurricanes may have increased pigeon exposure and predation rates (Santana C. & Temple 1988, Ruiz-Lebrón et al. 1995, Beissinger et al. 2008, Vilella & Nimitz 2012, Vilella et al. 2013, Gallardo et al. 2019).

Detection, abundance and occupancy estimates suggested positive but variable associations between the plain pigeon and scaly-naped pigeon (i.e. contrary to what we expected, φ and $\delta > 1$), and negative but variable associations between the plain pigeon and red-tailed hawk (i.e. as we expected, φ and $\delta < 1$). Although alternative explanations cannot be excluded

with our survey-based count data (e.g. competitive interactions from exploitation, interference or exclusion; Pérez-Rivera 1978, Poling & Hayslette 2006, Cooper et al. 2007), we suggest that a simple explanation for the positive associations is that both pigeon species responded similarly to hawk predation and foraging resources, converging at localities with medium–high vegetation cover and food availability (James & Boecklen 1984, Rivera-Milán 1995a, 1996, 2001, Rivera-Milán et al. 2003b). As a result, plain pigeon detection and occupancy estimates were higher with scaly-naped pigeon presence than absence at the points surveyed in the east-central region during 2015–2019 (i.e. ψ^{Ab} and $P_j^{Ab} < \psi^{AB}$ and P_j^{AB}). In addition, because both pigeon species were observed flying and feeding together on plants such as the Puerto Rico royal palm *Roystonea borinquena*, day-blooming jasmine *Cestrum diurnum* and princess vine *Cissus verticillata* before–after the 1989, 1998 and 2017 hurricanes, and because similar results were obtained with different datasets (e.g. transect surveys of columbid nests during 1986–1999; see Rivera-Milán 2001, their Fig. 2), we suggest that individual-level competitive interactions with the scaly-naped pigeon had a negligible effect on the plain pigeon population dynamics.

Regarding predator–prey interactions, because the red-tailed hawk was observed attacking the plain pigeon and scaly-naped pigeon before–after the 1989, 1998 and 2017 hurricanes, we suggest that the pigeons tended to avoid localities with none–low vegetation cover and medium–high hawk density. As a result, plain pigeon detection and occupancy estimates were higher with red-tailed hawk absence than presence at the points surveyed in the east-central region during 2015–2019 (i.e. ψ^{Ab} and $P_j^{Ab} > \psi^{AB}$ and P_j^{AB}). Although the pigeons can respond to hawk audio and visual cues with avoidance and other antipredator behaviours (Burger et al. 1989, Cook et al. 2005, Stephan & Bugnyar 2013), we suggest that additive mortality from predation and human-induced disturbance can influence the population dynamics of both pigeon species (Rivera-Milán et al. 2014, 2016), and increase the risk of extinction of the plain pigeon at lowered abundance levels (i.e. distance sampling mean \pm SE estimates $\hat{N} = 1043 \pm 476$ island-wide and $\hat{N} = 522 \pm 157$ at the centre of abundance in the east-central region in April to June 2018–2021; Table 1, Fig. 4).

In the Bayesian state-space logistic model, the parameter r_m represented the exponential rate of increase of the pigeon and hawk populations from low numbers and under favourable environmental conditions

(i.e. in the absence of natural and human-induced disturbances and with plenty of food and other resources needed to maximize reproductive and recruitment rates; Niel & Lebreton 2005, Runge et al. 2009). In the model, the parameter K represented the abundance levels above which the pigeon and hawk populations tended to decline due to the effects of density dependence (e.g. the size of home ranges and limited space with suitable resources to survive and reproduce; Vilella & Nimitz 2012, Vilella et al. 2013). Although parameters r_m (range of CVs = 0.08–0.63) and K (CVs = 0.08–0.49) and abundance predictions N_p (CVs = 0.30–1.60) were difficult to estimate with precision (e.g. at CVs < 0.20) from survey-based count data collected annually under varying environmental conditions (i.e. future population dynamics may or may not repeat previous ones due to uncertainty from climate change, extreme weather and variation in density-independent and density-dependent responses, resulting in high process variance; Knappe 2008, Knappe & de Valpine 2011, Opper et al. 2014, Sæther et al. 2016), we monitored the recovery of the pigeon and hawk populations from low numbers during a period of natural reforestation of abandoned pasturelands and croplands (Koenig 1953, Brandeis & Turner 2013, Yuan et al. 2017), and before–after severe abundance declines from the landfall of 3 major hurricanes during 1986–2021 (Boose et al. 2004, Uriarte et al. 2019, Hall et al. 2020). Because parameter posterior estimates and abundance predictions were updated annually with survey-based count data, we continued learning from monitoring and modelling, despite imperfect observations of population state (e.g. due to detection probability), partial control over human-induced disturbance (e.g. due to illegal hunting) and incomplete understanding of population dynamics (e.g. due to environmental stochasticity).

In addition, although we made a series of simplifying assumptions (e.g. linear density dependence and equal mortality probability, regardless of age and sex class), the Bayesian state-space logistic model was useful for estimation and prediction, despite differences in life-history characteristics and demographic traits (i.e. columbid early maturity with low survival and high reproductive rates as opposed to raptor delayed maturity with high survival and low reproductive rates). For example, using the demographic invariant method (see Niel & Lebreton 2005, their Eq. 15), and assuming annual survival rates were in the range of 0.40–0.70 for hatch-year and after-hatch year pigeons (Vilella et al. 2013), r_m was in the range of 0.24–0.60; and assuming annual survival rates were in the range of 0.70–0.95 for after-hatch year

and after-second year hawks (Gallardo et al. 2019), r_m was in the range of 0.03–0.24 (for comparison, see the medians and 2.5–97.5th percentiles in Table 4). Likewise, using life-stage survival probabilities and a seasonal matrix model, Gallardo et al. (2019) obtained an intrinsic rate of increase r in the range of 0.05–0.24 for the red-tailed hawk. The model provided an adequate representation of the pigeon and hawk survey-based count data (i.e. Bayesian p-values were within the range of 0.1–0.9; Gelman & Hill 2007), and generated reasonable posterior estimates of K and N_p , including 2020 when surveys were not conducted due to the coronavirus pandemic. The posterior estimates of K overlapped with the distance sampling abundance estimates, and have been used to set population management objectives (Sanderson 2006, Traill et al. 2010, Rivera-Milán et al. 2014, 2016). The posterior estimates of N_p , which accounted for observation and process variance, also provided valuable information about the expected magnitude of the pigeon and hawk population fluctuations during 2020–2030.

Based on our monitoring and modelling results, we suggest that the abundance of the plain pigeon, scaly-naped pigeon and red-tailed hawk increased from low numbers and approached carrying capacity levels during the late 1990s in response to increased foraging and nesting resources in second-growth forests across the island. However, while the abundance of the scaly-naped pigeon and red-tailed hawk continued fluctuating around carrying capacity, we suggest that the abundance of the plain pigeon declined during 2002–2017 as a result of habitat loss and degradation from development, which was widespread in the east-central region (see Martinuzzi et al. 2007, their Fig. 8), and the combined effects of predation and human-induced mortality (Rivera-Milán 1996, Rivera-Milán et al. 2003b, 2016). The plain pigeon has a clutch size of 1 egg instead of the typical columbid clutch size of 2 eggs (Blockstein & Westmoreland 1993), which can limit annual reproductive output and lower maximum population growth rate. The 2.5–97.5th percentiles of r_m ranged from 0.50 to 0.74 for the scaly-naped pigeon and from 0.10 to 0.56 for the plain pigeon. That is, population doubling time ($t = \ln[2]/r_m$) ranged from 0.94 to 1.38 yr for the scaly-naped pigeon and from 1.24 to 7.30 yr for the plain pigeon. Therefore, the plain pigeon population had less ‘demographic vigour’ (sensu Caughley 1977) and was less resilient (Pimm 1991) than the scaly-naped pigeon population to natural and human-induced disturbances.

The plain pigeon population did not recover during the 2018–2021 surveys and may undergo a pro-

longed bottleneck (Miyamoto et al. 1994, Beissinger et al. 2008), which may result in extinction, particularly if human-induced disturbance continues unabated, reproduction remains unsuccessful, and another hurricane with the path and intensity of María makes landfall on Puerto Rico during the current decade. Therefore, in addition to long-term monitoring, which is needed to update the posterior estimates of population parameters and increase the precision of abundance predictions, we recommend to (1) continue predator removal efforts at nesting localities to increase and maintain reproductive success rates above 0.40 ± 0.05 (SE) (Rivera-Milán et al. 2003b, Ventosa-Febles 2019), (2) use radio and satellite telemetry to estimate annual survival rates and quantify movements and resource use (Meyer & Wilmers 2007, Vilella et al. 2013), (3) combine count, telemetry and nesting data using an integrated population modelling framework (Johnson et al. 2010, Oppel et al. 2014) and (4) initiate a captive breeding programme with reintroduction methods similar to the Puerto Rican parrot *Amazona vittata* (White et al. 2005, Earnhardt et al. 2014, Clubb et al. 2015). We also need to minimize human-induced mortality from illegal hunting (Rivera-Milán et al. 2016); and, because most of the island forests are under private ownership (Brandeis & Turner 2013), we need to engage landowners in habitat conservation through programmes such as the Partners for Fish and Wildlife (see www.fws.gov/caribbean/ES/ and www.fws.gov/partners/). We consider the plain pigeon subspecies *Patagioenas inornata wetmorei* a unique conservation unit (Miyamoto et al. 1994, Russello et al. 2010) in need of targeted, question-driven monitoring and evidence-based management (Sutherland et al. 2004, Nichols & Williams 2006, Lindenmayer & Likens 2010), aiming to increase and maintain abundance above the carrying capacity 2.5th percentiles (i.e. >30 000 island-wide and >5000 in the east-central region; Sanderson 2006, Traill et al. 2010, Rivera-Milán et al. 2016).

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