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Cover Photograph: Pearly-eyed Thrasher (*Margarops fuscatus*) photographed in the Luquillo Mountains of Puerto Rico. Photograph © Jerry Bauer.

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Abstract - *Margarops fuscatus* (Pearly-eyed Thrasher) is recognized for its vagility, dispersal ability, aggressive behavior, opportunistic diet, high reproductive potential, and ability to inhabit marginal habitats. Given these traits, we predicted that thrasher post-hurricane site occupancy and abundance in the first post-hurricane year (2018) after hurricanes Irma and María (2017) would change with elevation, forest type, and vegetation damage. To document the hurricanes' effects on thrasher site occupancy and abundance along an elevation gradient (150–1074 m a.s.l.) in the Luquillo Experimental Forest (LEF), we compared point-count results obtained before the hurricanes (1998, 2005) and after the hurricanes (2018). We estimated thrasher occupancy with a single-season model and abundance with an *N*-mixture single-season model, with year as a covariate in all models. Elevation (with a quadratic effect) was the most important covariate for site occupancy and abundance estimation. Occupancy across 110 count sites decreased from 0.77 (0.03 SE) in 1998 to 0.50 (0.03) in 2005 to 0.37 (0.03) in 2018 after the hurricanes. Abundance estimates decreased from an average of 11 (0.75 SE) individuals/site in 1998 to 4.39 (0.37) in 2005 and 2.33 (0.19) in 2018. Occupancy and abundance were highest at mid-elevation (400–800 m) sites in all years, and there was no evidence of a shift in elevational range after the 2 hurricanes in 2018. Despite post-hurricane occupancy and abundance declines, the Pearly-eyed Thrasher remains a potential threat as a predator and competitor of endangered wildlife in mid-elevation forests in the LEF.

Introduction

The Caribbean has a high frequency of tropical cyclones, including tropical storms and hurricanes (Bhatia et al. 2019, Goldenberg et al. 2001, Walker et al. 1991). These tropical cyclones (hurricanes hereafter) can significantly affect ecosystem structure and function and may occur with sufficient frequency to play an important role in structuring biotic communities (Odum and Pigeon 1970, Walker et al. 1991, Zimmerman et al. 1996). In 2017, two major hurricanes affected the island of Puerto Rico. Hurricane Irma passed ~80 km northeast of the island on 6 September 2017 as a category 5 (Saffir–Simpson scale) storm with wind

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speeds approaching 300 km/h. On 20 September 2017, Hurricane María landed on southeastern Puerto Rico and crossed diagonally over the island, exiting on the northwest coast as a category 4 storm with maximum sustained winds of ~250 km/h. Hurricane María was the most intense hurricane recorded in Puerto Rico for almost 90 years (García-Rivera et al. 2018). Compared to category 3 Hurricane Hugo in 1989, vegetation damage caused by Hurricane María tripled stem breakage and doubled tree deaths (Uriarte et al. 2019).

We expected these hurricanes to affect bird populations, both directly and indirectly (Wiley and Wunderle 1993). Although direct mortality from hurricanes may cause occupancy and abundance declines, it is the indirect effects that may have the longest-lasting effects on bird populations due to changes in food resources and habitat alterations (Wiley and Wunderle 1993). However, the responses of some bird populations to hurricanes may be species-specific (Lloyd et al. 2019, Rittenhouse 2010). In the long term, for example, certain species may benefit from these disturbances, depending on forest type and other habitat traits (Arendt 2006, Campos-Cerqueira and Aide 2021, Lloyd et al. 2019, Tejeda-Cruz and Sutherland 2005).

A species that is expected to benefit over the long term from hurricanes is *Margarops fuscatus* (Vieillot) (Pearly-eyed Thrasher, hereafter Thrasher), which has the potential to adapt to different habitats, especially in non-competitive situations (Arendt 2006). Thrashers are widely distributed and can colonize human-inhabited islands and disturbed habitats with few potential competitors (Arendt 2006, Arendt et al. 2019). The species is an opportunistic forager with an omnivorous diet composed of a variety of foods, including diverse fruits and various invertebrates and vertebrates (Arendt 2006, Rollé 1965). The Thrasher possesses a relatively large body, which gives it an advantage over its smaller interspecific competitors when it comes to physical combat over food resources and nesting sites (Arendt 2006). As a competitor and predator, the Thrasher threatens endangered species, including various species of frogs, lizards, and birds (Arendt 2006, Snyder et al. 1987). The Thrasher is a species of concern for managers of the endangered *Amazona vittata* Boddaert (Puerto Rican Parrot) because it competes for nest cavities and preys on parrot eggs and nestlings (Arendt 2000, Snyder et al. 1987, US Fish and Wildlife Service 1999).

Given the Thrasher's opportunistic diet, dispersal ability, and colonization of species-poor habitats, we expected a post-hurricane shift in habitats or sites occupied in response to vegetation damage. Several studies have documented shifts in habitat, sites, or elevation after hurricanes by various bird species (Arendt 1990, Wunderle 1995, Wunderle et al. 1992), including post-hurricane site shifts by Thrashers (Arendt 2006; Askins and Ewert 1991, 2020; Wunderle 1995). Some post-hurricane site shifts by birds are believed to be associated with resource or habitat differences in resistance to storm damage or recovery rates (Wiley and Wunderle 1993). Birds with broad elevational distributions may shift elevation after a hurricane as they respond to elevational gradients in storm damage or resource recovery. Shifts in the Thrasher's elevational distribution in the Luquillo Mountains (150–1074 m

a.s.l. m) of Puerto Rico following Hurricane Maria were expected as a result of the higher storm damage to vegetation at higher elevations (Feng et al. 2020, Hu and Smith 2018, Van Beusekomet al. 2018) and the likelihood of slower recovery rates typical of high-elevation vegetation (Walker et al. 1996, Weaver 1990). Therefore, after Hurricane Maria, we expected the Thrashers to move from their preferred mid-elevation palo colorado forest (Arendt 2006, Campos-Cerqueira et al. 2017, Pagán 1995) to other forest types or elevations. The objective of this study was to quantify the effects of the 2017 hurricanes on Thrasher site occupancy and abundance in the first year (2018) after the hurricanes, relative to baseline surveys in 1998 and 2005 along an elevational gradient in the Luquillo Mountains. Results from this study are relevant for understanding the response and resilience of the Thrasher to major hurricanes, with implications for the conservation of endangered species threatened by the Thrasher.

Field-site Description

The study was conducted in the Luquillo Experimental Forest (also known as El Yunque National Forest) in northeastern Puerto Rico (Fig. 1). The Luquillo Experimental Forest (LEF) is the largest protected area (115 km²) with primary forest on the island and has been well studied by ecologists (Harris et al. 2012), including studies of the effects of hurricanes and other disturbances on forest ecosystems (Zimmerman et al. 2020). The LEF includes most of the Luquillo Mountains, which have a maximum elevation of 1074 m a.s.l. and have substantial effects on abiotic

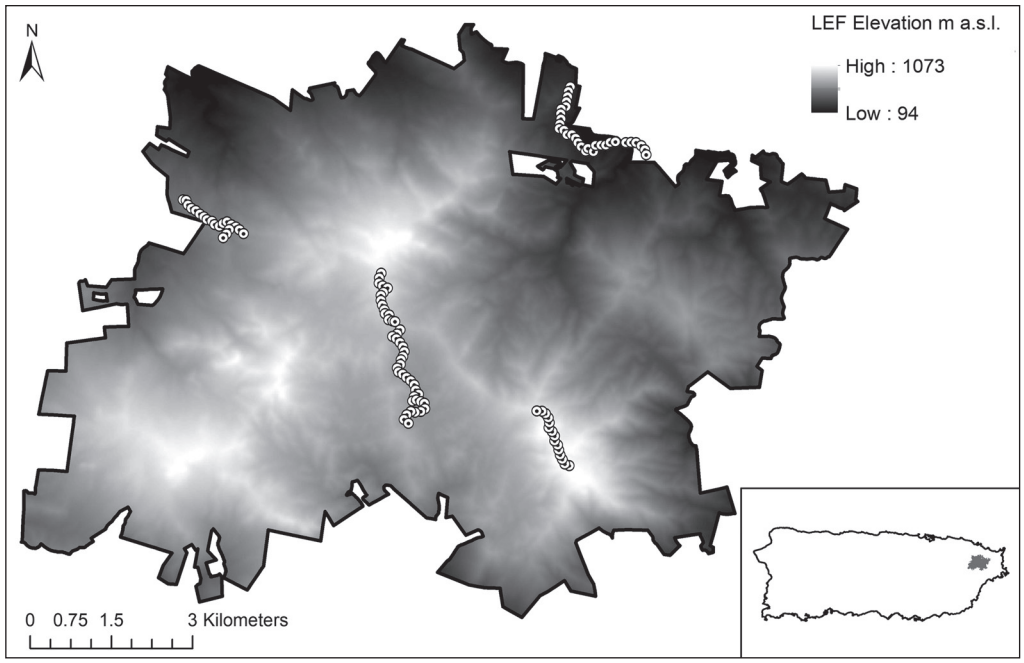

Figure 1. Map of the Luquillo Experimental Forest and its location in northeastern Puerto Rico (grey area in the inserted map). Circles represent all sites sampled for Pearly-eyed Thrashers. Different grayscale colors represent differences in elevation (m a.s.l.)

factors (temperature, rain, humidity) and the biota (Weaver and Gould 2013). Temperature differs by 7 °C for mean maximum values between low and high sites but annually varies little with elevation for mean monthly temperatures (3–3.5 °C), whereas annual rainfall varies from an average of 2450 mm/yr in the lowlands to 4000 mm/yr at higher elevations (Harris et al. 2012). The LEF has 5 ecological life zones: subtropical moist forest, subtropical wet forest, subtropical rainforest, lower montane wet forest, and lower montane rain forest (Ewel and Whitmore 1973). It also has 4 main forest types, approximately stratified by elevation (Wadsworth 1951): (1) tabonuco forest, which is dominated by *Dacryodes excelsa* Vahl. (Tabonuco) and occurs at 150–600 m, predominantly in the subtropical moist and wet forests; (2) palo colorado forest, characterized by the *Ternstroemia luquillensi* Krug & Urb. (Palo Colorado [note this common name has also occasionally been applied to a different species, *Cyrilla reacemiflora* L., much more commonly known as Swamp Cyrrilla]), occurs at 600–950 m and predominates in lower montane wet and rain forest; (3) elfin forest, is a short-stature forest with gnarled trees covered in epiphytes and is confined to peaks and ridge tops. It occurs above 950 m principally in the lower montane rain forest; and (4) sierra palm forest or palm brake, in which *Prestoea acuminata* var. *montana* (Graham) A.J. Hend. & Galeano (Sierra Palm) dominates on steep and eroded slopes at higher elevations and is interspersed between elfin and palo colorado forests.

Methods

Bird surveys

Pre-2017. Thrasher surveys were conducted along the elevation gradient in the LEF using the fixed-radius point-count method of Hutto et al. (1986) from 1989 to 1997, and a distance sampling method (Buckland et al. 1993) from 1998 to 2006 (Arendt et al. 2013*)*. For our research, however, we only used surveys from 1998 and 2005. We used data from these 2 years because of the absence of hurricanes, as well as to allow time (>6 yr) for recovery from Hurricane Hugo in September 1989 and Georges in September 1998. In addition, counts in 1998 and 2005 occurred monthly from March to August, coinciding with the post-hurricane survey period of 2018. The Arendt et al. (2013) surveys included 130 georeferenced points separated by a minimum distance of 100 m and located along 6 trails or roads within the LEF: East Peak (15 points), Mt. Britton (15), Icacos (30), Palo Hueco (30), Catalina (10), and Route 988 (30). However, in 1998 there were only 80 points available because the Route 988 points were established in 1999 after Hurricane Georges. In 2005, we used results from 110 points to match those available in 2018 (see below). At each point, a single observer recorded Thrasher audio and visual detections for 10 minutes between 05:00 and 10:30 hours, and visually estimated detection distances to a visible or vocalizing individual or the center of a cluster of conspecific individuals (Thomas et al. 2010).

Post-2017. From April to August 2018, we surveyed the same 110 points of 2005 (Arendt 2006, Arendt et al. 2013) 3 times between 05:30 and 11:30 hours. All points were surveyed during April–May on the first visit, late June–early July on

the second visit, and late July–early August on the third visit. We did not survey 20 of the original 130 points due to inaccessibility after the 2017 hurricanes. The 2018 surveys differed from those conducted in 1998 and 2005 because we used a team of 2 observers instead of 1, with one observer recording the data and the other measuring detection distances (Rivera-Milán et al. 2014). We measured distances to single Thrashers or clusters with a laser rangefinder (Rivera-Milán et al. 2014) rather than distance estimates as per the pre-2017 surveys. We defined a cluster as 2 or more birds within 10 m of each other. When vocalizing birds could not be visually detected, we measured distances to the nearest horizontal location and grouped detections. We grouped detection distances for vocalizing birds as well as visually detected birds (by an estimate from pre-hurricane counts or rangefinder for post-hurricane counts) using the following distance categories: 0–5, 6–15, 16–25, 26–50, 51–75, 76–100, and >100 m. Based on the distances measured, we truncated the count data at 50 m and defined an area of 0.79 ha (~0.01 km^2) for occupancy and abundance estimations.

Occupancy and abundance modeling

We used single-season occupancy models (Fuller et al. 2016, MacKenzie et al. 2002) to estimate detection probability (p) and occupancy (y) and explored the influence of survey-specific and site-specific covariates in 1998, 2005, and 2018. In addition, we used N-mixture single-season models (Royle 2004) as adapted by Fuller et al. (2016) and Nareff et al. (2019) to estimate detection and abundance (lambda [λ] per survey point and across survey points). This method assumes constant occupancy and abundance (i.e., population closure to births, deaths, immigration, or emigration between survey occasions during April–August 2018), which allowed us to estimate occupancy and abundance assuming count independence between points surveyed each year in 1998, 2005, and 2018 (Fuller et al. 2016, Nareff et al. 2019). Thus, we fitted and compared single-season occupancy models using a Bernoulli distribution, and N-mixture single-season models using a Poisson-binomial distribution. For all possible models, we combined data from the point-count surveys of 1998, 2005, and 2018.

The detection model included the covariates year, ordinal date of the survey (date), the start time of the survey (time), and level of hurricane damage. During the first visit to a point center, the observer subjectively evaluated the hurricane damage within 50 m of the point center by estimating the damage as either: category 0 = none to light damage, or category 1 = medium to high damage. We modeled abundances and occupancy probability as a function of the following covariates: elevation above sea level, percent cover of 4 main forest types (i.e., % tabonuco, % palo colorado, % sierra palm, and % elfin forest) within a 50-mradius, year of survey, and hurricane damage class (only for the year 2018). We used the quadratic effect for elevation and forest type because previous studies have documented quadratic responses of Thrasher distribution along the elevational gradient of the LEF and the covariance of forest types with elevation (Arendt 2006, Campos-Cerqueira et al. 2017). We rescaled all numeric covariates to a mean and standard deviation (SD) of 0 and 1, respectively.

We measured elevation and forest composition for each surveyed point using freely available raster layers. We acquired the elevation data directly from the USGS Digital Elevation Model (DEM) at a 1-m resolution (Gesch and Maune 2007). For the forest composition, we established a grid of 3891 hexagons of 31,000 m^2 over a map of the LEF and the percent of vegetation cover of each forest type using the Puerto Rico GAP Analysis raster layer (Gould et al. 2008). We extracted values for elevation and percentage of each forest type from the cell values of the specific site covariate raster-based layers on the set of survey points and recorded them on an attribute table of the output GIS vector layer.

Model selection

We used a multi-stage model fitting approach that considered 30 potential models (Fuller et al. 2016, Karanth et al. 2011, Nareff et al. 2019). Our analyses differ from those of Fuller et al. (2016) and Nareff et al. (2019) using a secondary-candidate set strategy that fits sub-models independently and combines the top set models from each sub-model for selection in the final stage (Bromaghin et al. 2013, Morin et al. 2020). For model fitting, we used the R package 'Unmarked' (Fiske and Chandler 2011) in R version 4.0.5 (R Core Development Team 2021). First, we assessed the goodness-of-fit of the global model and calculated the overdispersion parameter (ĉ) before evaluating the possible combinations of covariates to select the best models for occupancy and abundance. We used this overdispersion parameter to calculate the quasi-Akaike's information criterion (QAIC) for model selection using the 'AICcmodavg' package (Mazerolle 2020), which is standard practice for dealing with lack-of-fit (Kéry and Royle 2016). When ĉ was close to one, we did not use the QAIC. We calculated the effective sample sizes (*n-ess*) to obtain the corrected Akaike's information criterion (AICc). The goodness-of-fit test indicated overdispersion with ĉ = 3.15 ($P = 0.008$) for the global model of the single-season occupancy model, and therefore we used this value to calculate the QAIC scores for subsequent model selection. For the *N*-mixture single-season model, the goodness-of-fit test (ĉ = 0.99, $P = 0.45$) indicated no overdispersion, which led us to use AIC.

We started our modeling process by choosing the model with the best detection probability. For this, we separately fitted one-factor models with the covariates year, hurricane damage, date, and time of day. Then, we fitted two-factor additive models that included year + hurricane damage, year + date, and year + time, yielding 7 candidate models for thrasher detection (see Table S1 in Supplemental File 1, available online at https://www.eaglehill.us/CANAonline/suppl-files/C237-Wunderle-s1), followed by selecting the best occupancy and abundance models. For this, we again fitted one-factor models for covariates year, hurricane damage, elevation, and each of the 4 forest types: % tabonuco, % palo colorado, % elfin forest, and % sierra palm. We then created two-factor additive models combining the year with the other 6 covariates, repeated with the quadratic forms of the covariate elevation and the percent forest cover for each forest type. These analyses yielded a total of 23 candidate models each for occupancy and abundance (see Tables S3 and S5, respectively, in Supplemental File 1). We compared and selected the best models based on a criterion of $\Delta AICc \leq 2$. Finally,

we plotted the predicted parameter values of Thrasher occupancy and abundance for supported model covariates to examine the changes in pre- and post-hurricane values. Results are presented as means with standard errors (SE) and 95% confidence intervals (CI), using the predicted values for each point and the two-tailed *z*-score to estimate them (Charter 1997). We determined statistical differences by lack of overlap in the 95% CI, but we consider that a <30% overlap in the CIs is still significantly different (Van Belle 2002).

Results

We made 256 Thrasher detections at 65 of 80 points during the 1998 surveys, 107 Thrasher detections at 43 of 110 points during the 2005 surveys, and 47 Thrasher detections at 27 of 110 points during the 2018 surveys. The global single-season occupancy and N-mixture models included covariates year, ordinal date, start time, and hurricane damage in the detection sub-model. The top detection model included the year and ordinal date of the surveys (see Table S1 in Supplemental File 1). The β coefficients from the top model for year and ordinal dates showed a negative slope. However, the 95% confidence intervals of the detection estimates indicated that there were differences between visits (dates), but not between years (see Table S2 in Supplemental File 1). Thrasher detection probabilities were equivalent during the first survey visit of both pre-hurricane years, 1998 (0.70, 95% CI = 0.68–0.73) and 2005 (0.70, 95% CI = 0.68–0.72), but declined after the 2017 hurricanes in 2018 (0.55, 95% CI = 0.53–0.58). However, no differences in detectability were found among the years during the second visit (1998: 0.48, 95% CI = 0.46–0.51; 2005: 0.48, 95% CI = 0.45–0.50; 2018: 0.44, 95% CI = 0.41–0.47) and during the third visit (1998: 0.27, 95% CI = 0.25–0.29; 2005: 0.28, 95% CI = 0.27–0.30; 2018: 0.27, 95% CI = 0.25–0.29). Overall, mean detectability for all years (1998, 2005, and 2018) declined across the 3 visits from the first visit (0.65, 95% CI = 0.63–0.67) to the second visit (0.47, 95% CI = 0.44–0.47) and the third visit (0.27, 95% CI = 0.26–0.29).

The global occupancy and abundance models included year, hurricane damage, elevation, tabonuco forest, palo colorado forest, sierra palm forest, elfin forest, and the quadratic effect for the last 5 covariates. Model selection results for occupancy probability indicated that the best model included year and elevation with a quadratic term (see Table S3 in Supplemental File 1). The top model estimates for occupancy probability across sites in each year were 0.77 ± 0.03 SE (95% CI = 0.71–0.83) in 1998, 0.50 ± 0.03 (95% CI = 0.44–0.57) in 2005, and 0.37 ± 0.03 (95% CI = 0.31–0.43) post-hurricane in 2018. These values showed a difference across all years. The relationship between elevation and occupancy probability was similar (positive parabolic) across years, but with different values between years of occupancy probability (e.g., Ψ = a + year -1.1 [0.6] + elevation -0.2 [0.2] + elevation^2 -2.3 [0.3] in Fig. 2A). The highest values of occupancy probability were in the mid elevations (~400–800 m) in the 3 years with 0.95 ± 0.01 (95% CI = 0.94–0.96) in 1998, 0.87 ± 0.01 (95% CI = 0.86–0.88) in 2005, and 0.71 ± 0.01 (95% CI = 0.69–0.72) post-hurricane in 2018 (see Table S4 in Supplemental File 1).

As found for occupancy model selection results, abundance indicated that the best model included year and elevation with a quadratic term (see Table S5 in Supplemental File 1). The top model estimates for the abundance across sites in each year were 11 ± 0.75 SE (95% CI = 9.53–12.46) in 1998, 4.39 ± 0.37 (95% CI = 3.68–5.11) in 2005, and 2.33 ± 0.19 (95% CI = 1.95–2.71) post-hurricane in 2018. These values showed a difference across all years as found for occupancy. Also, the relationship between elevation and abundance was similar to occupancy (positive parabolic) and different across years (e.g., λ = a + year - 0.5 [1.5] + elevation 0.7 [0.2] + elevation^2 - 1.9 [0.2] in Fig. 2B). Furthermore, as with occupancy,

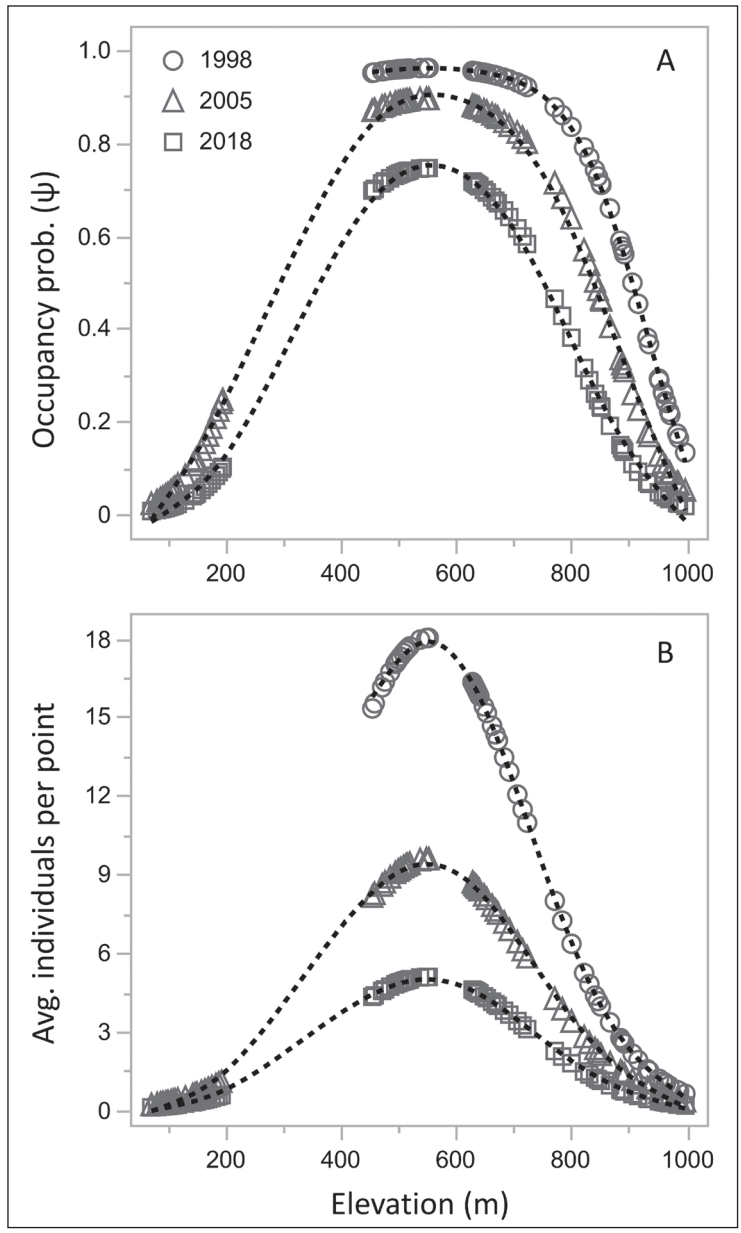

Figure 2. Pearly-eyed Thrasher means modeled for (A) site occupancy probability and (B) site abundance along an elevational gradient in 1998 (circles, n = 80 points), 2005 (triangles, n = 110 points), and 2018 (squares, n = 110 points) in the Luquillo Experimental Forest, PR.

the highest values of abundance were in the mid-elevations (~400–800 m) in the 3 years with 15.83 ± 0.27 SE (95% CI = 15.30–16.37) in 1998, 8.40 ± 0.13 (95% CI = 8.15–8.66) in 2005, and 4.46 ± 0.08 (95% CI = 4.31–4.61) after the hurricanes in 2018 (see Table S6 in Supplemental File 1).

Discussion

Thrasher detection probability varied with the covariate ordinal date as expected because Thrashers are more readily detected during their breeding season when they are most vocal (Arendt 2006). In the absence of hurricanes, the Thrasher breeding season in the LEF occurs from January to July (Arendt 2006, Beltrán et al. 2010). However, during the first breeding season following hurricanes, nesting may be delayed until April, as documented after both Hurricanes Hugo and Georges (Arendt 2006). Consistent with post-hurricane delayed nesting was our finding that Thrasher detections during the first visit in April–May 2018 were lower than detections during the first visits of the 1998 and 2005 surveys. As previously found by Arendt (2006), post-hurricane nesting was not extended to compensate for delayed breeding. We found no evidence of increased detections during the second visits (June–early July) and third visits (July–early August). Delayed and reduced breeding after hurricanes has been related to vegetation damage and limited food supply, mainly the fruits of *Prestoea acuminata* var. *montana* (Arendt 2006, Thompson-Baranello 2000, Wunderle 1999), which are important for Thrasher reproduction in the LEF (Arendt 2006, Beltrán et al. 2010).

Our pre-hurricane surveys also indicated that the LEF Thrasher population declined between 1998 and 2005, as evidenced by a 35% decrease in site occupancy and a 60% decline in abundance. Although this Thrasher decline was previously reported by Arendt (2006), the cause has not been determined. Although it is uncertain if the LEF Thrasher population continued to decline in site abundance after 2005, Thrasher site occupancy as measured by passive acoustic monitoring along the elevation gradient in the LEF in 2015 by Campos-Cerqueira et al. (2017) and in 2016 by Campos-Cerqueira and Aide (2021) was comparable to our 2005 occupancy values. For example, our 2005 Thrasher site occupancy value (0.50 ± 0.09 SE), was similar to the 2015 value (0.51 ± 0.11) and the 2016 value (0.49 ± 0.11), even after a 2015–2016 drought.

We can make potential estimates of the relative magnitude of post-hurricane declines in Thrasher occupancy and abundance using our 2005 values as a baseline, assuming the values did not change before the 2017 hurricanes. This is a reasonable assumption for the occupancy estimate given the occupancy estimates for 2015 and 2016 found by Campos-Cerqueira et al. (2017) and Campos-Cerqueira and Aide (2021); however, we are uncertain if average site abundance changed between 2005 and 2016 because abundance was not determined in those years. Nonetheless, the Thrasher population likely declined by ~26% in occupancy (i.e., 0.50 occupancy in 2005 to 0.37 in 2018) and by ~47% in abundance (i.e., 4.39 abundance in 2005 to 2.33 in 2018) after the 2017 hurricanes. Although there are no other pre- vs. post-hurricane studies of Thrasher numbers in the LEF for comparison, we note that the

annual survival of breeding Thrashers in the palo colorado forest decreased by 47% in the first breeding season after Hurricane Hugo (i.e., 89% annual survival in 10 non-hurricane years to 42% annual survival in the first year after Hurricane Hugo; Arendt 2006). The post-Hugo decline in annual survival suggests that mortality plays an important role relative to emigration in Thrasher population site declines after hurricanes. Despite uncertainty as to how well the post-hurricane decline in Thrasher annual survival (47% after H. Hugo) directly relates to a decline in site abundance (47% after H. Maria), it appears that the post-hurricane decline values were similar. The magnitude of the post-hurricane decrease in Thrasher site occupancy and abundance in the LEF is similar to declines recorded in other bird species after major hurricanes (e.g., Askins and Ewert 2020; Campos-Cerqueira and Aide 2021; Rivera-Milán et al. 2021, 2022).

Despite our finding of Thrasher declines in site occupancy and abundance in the LEF from 1998 to 2005 to 2018, the maximum values for these 2 measures were found at 400–800 m elevational for all years. Similarly, Campos-Cerqueira et al. (2017) found that Thrasher site occupancy was highest at 450–850 m in the LEF and that the elevational range had contracted from 1998 to 2015 with a significant decrease in site occupancy only at the upper elevation limit. Maximum site occupancy values for LEF Thrashers occurred at 400–800 m elevation in 2016, despite a severe 2015–2016 drought, and in 2019 after 2 years of recovery from the 2017 hurricanes (Campos-Cerqueira and Aide 2021). Thus, despite overall elevation-wide changes in Thrasher site occupancy and abundance, some associated with extreme weather events, Thrashers continued to remain most abundant in the mid-elevation wet forest of the LEF. The preference for this mid-elevation zone by the Thrasher, primarily a secondary-cavity nester (Arendt 2004), has been attributed to the availability of cavities and the Thrasher's tendency to nest in large trees in the palo colorado forest type in the proximity of sierra palm forest for access to fruit (Arendt 2006, Beltrán et al. 2010, Thompson-Baranello 2000).

In contrast to our predictions, we found no evidence for post-hurricane shifts in elevation by Thrashers in the LEF, at least in the first year after the 2017 hurricanes. By the second year (2019) after the hurricanes, however, site occupancy estimates in the LEF indicated that Thrashers had shifted farther up the mountain (Campos-Cerqueira and Aide 2021). Perhaps this shift was associated with increased foraging opportunities, as Thrasher nesting at high elevations in the LEF is minimal (at least in the absence of hurricanes), owing to high rates of nest failures resulting from egg pathogens (Cook et al. 2003, 2004). Several other factors may have also contributed to the 2019 movement into higher-elevation sites. For instance, Thrasher reproduction performance may have increased in the second post-hurricane breeding season after the 2017 hurricanes, as occurred after other hurricanes. In the second breeding season after Hurricane Hugo, Arendt (2006) found that Thrasher breeding was initiated earlier than normal, resulting in an abnormally high number of successive clutches per female, attributable to increased primary productivity in the second year after the hurricane (Scatena 1998). This increased reproductive output may have contributed to the Thrasher movement to higher elevations. In addition, vegetation recovery likely was delayed at higher

elevations as a result of greater vegetation damage than at lower elevations after Hurricane Maria (Feng et al. 2020, Hu and Smith 2018) and slower growth rates of vegetation at high elevations (Weaver 1990, Walker et al. 1996). Slower vegetation recovery at high elevations, in turn, may have delayed the availability of Thrasher food resources.

Elsewhere, Thrashers have shown various post-hurricane population site shifts. For example, and in contrast to our 2018 LEF findings, post-Hurricane Maria Thrasher site occupancy significantly increased from baseline occupancy estimates as expected in mid- to high-elevation sites (median = 760 m, min–max = 5–1297 m) in the Cordillera Central of Puerto Rico within 4 months following the two 2017 hurricanes (Lloyd et al. 2019). This finding may reflect a post-hurricane increase in Thrasher home-range size or wandering as Thrashers searched more widely for food, the latter a behavior observed for several months in the LEF shortly after Hurricane Hugo (Arendt 2006, Wunderle 1995). Our 2018 LEF Thrasher occupancy results may differ from the 2018 results from the Cordillera Central found by Llyod et al. (2019) for 2 reasons. First, the 2018 sampling occurred at slightly different times (January–March 2018 for Llyod et al. [2019] and April–August 2018 in this study). Second, and possibly most importantly, the LEF was struck by 2 hurricanes, in contrast to the Cordillera Central, which was distant from Hurricane Irma's path and little affected by Irma.

We found no evidence that our covariates for hurricane vegetation damage or forest type were associated with Thrasher site occupancy or abundance after the hurricanes. The absence of covariation of site occupancy or abundance with vegetation damage may be attributable to its subjective assessment by different observers as a categorical covariate where the value of 0 showed no or minor damage and the value of 1 showed medium or high damage. It is possible that the low precision of this covariate affected its choice in the models, especially in different forest types. For instance, a heavily damaged sierra palm forest (score 1) may have had little mortality of Sierra Palms but suffered many lost most palm fronds that were replaced quickly. By contrast, a heavily damaged tabonuco or palo colorado forest site (score 1) may have suffered tree mortality (e.g., due to trunk snap, wind throw) and loss of large canopy branches, thereby retarding canopy closure for many years (Zimmerman et al. 2021).

The forest type covariate was based on classification into 1 of 4 forest types based mostly on the predominant tree species. However, as recognized by Heartsill-Scalley (2012), there are several weaknesses in using the forest-type classification scheme to characterize vegetation variation along the elevational gradient in the LEF. For example, cloud cover and topography influence the distribution and density of plant species across the LEF elevational gradient (Barone et al. 2008, Silver et al. 1999). Even within a forest type or particular span of elevations, differences in topography may result in differences in plant species composition, reflecting variations in nutrients, moisture, and edaphic conditions (Heartsill-Scalley 2012). Moreover, the forest-type classification does not include differences in plant age, stature, or disturbance history and stand succession, which may vary within a forest type (Chazdon 2008, 2010).

Despite post-hurricane declines in average site occupancy and site abundance, overall Thrasher distribution along the elevational gradient was resistant to the 2017 hurricanes, maintaining peak values at ~400–800 m in the first (2018) and second years (2019; Campos-Cerquiera and Aide 2021) following the hurricanes. The Thrasher's post-hurricane fidelity to habitats within this elevational span, which encompasses palo colorado and palm forest types, suggests that Thrasher competition and predation remain a threat to sensitive animal populations in this zone even in the aftermath of hurricanes.

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Literature Cited

Arendt, W.J. 1990. Impact of Hurricane Hugo on the Monserrat Oriole, other forest birds, and their habitat. Final Report on file at the USDA Forest Service, Institute of Tropical Forestry, Sabana Research Field Station, Luquillo, PR, USA. 41 pp.

Arendt, W.J. 2000. Impact of nest predators, competitors, and ectoparasites on Pearly-eyed Thrashers, with comments on the potential implications for Puerto Rican Parrot recovery. Ornitologia Neotropical 11:13–63.

Arendt, W.J. 2004. Open- and cavity-nesting traits merge in the evolution of an avian supertramp, the Pearly-eyed Thrasher (*Margarops fuscatus*). Ornitologia Neotropical 15:455–465.

Arendt, W.J. 2006. Adaptations of an avian supertramp: Distribution, ecology, and life history of the Pearly-Eyed Thrasher (*Margarops fuscatus*). General Technical Report 27. US Department of Agriculture, Forest Service, International Institute of Tropical Forestry, Luquillo, PR, USA. 416 pp.

Arendt, W.J., S.S. Qian, and K.A. Mineard. 2013. Population declines of the Elfin-woods Warbler (*Setophaga angelae*) in eastern Puerto Rico. Bird Conservation International 23(2):136–146.

Arendt, W.J., M.M. Paulino, L.R. Paulino, M.A. Tórrez, and O.P. Lane. 2019. Colonization of Hispaniola by the Pearly-eyed Thrasher, *Margarops fuscatus* (Vieillot). Urban Naturalist 23:1–24.

Askins, R.A., and D.N. Ewert. 1991. Impact of Hurricane Hugo on bird populations on St. John, US Virgin Islands. Biotropica 23:481–487.

Askins, R.A., and D.N. Ewert. 2020. Resistance and resilience of Virgin Islands bird populations following severe hurricanes. Wilson Journal of Ornithology 132:898–910.

Barone, J.A., J. Thomlinson, P.A. Cordero, and J.K. Zimmerman. 2008. Metacommunity structure of tropical forest along an elevational gradient in Puerto Rico. Journal of Tropical Ecology 24:525–534.

Beltrán, J.W., J.M. Wunderle Jr., and W.J. Arendt. 2010. Changes in home range of breeding and post-breeding male Pearly-eyed Thrashers in the Luquillo Mountains of Puerto Rico. Ornitologia Neotropical 21:409–423.

Bhatia, K.T., G.A. Vecchi, T.R. Knutson, H. Murakami, J. Kossin, K.W. Dixon, and C.E. Whitlock. 2019. Recent increases in tropical cyclone intensification rates. Nature Communications 10:1–9.

Bromaghin, J.F., T.L. McDonald, and S.C. Amstrup. 2013. Plausible combinations: An improved method to evaluate the covariate structure of Cormack–Jolly–Seber mark–recapture models. Open Journal of Ecology 3:11–22.

Buckland , S.T. , D.R. Anderson, K.P. Burnham, and J.L. Laake. 1993 Distance Sampling: Estimating Abundance of Biological Populations. Chapman and Hall, London, UK. 446 pp.

Campos-Cerqueira, M., and T.M. Aide. 2021. Impacts of a drought and hurricane on tropical bird and frog distributions. Ecosphere 12:e03352.

Campos-Cerqueira, M., W.J. Arendt, J.M. Wunderle Jr., and T.M. Aide. 2017. Have bird distributions shifted along an elevational gradient on a tropical mountain? Ecology and Evolution 7:9914–9924.

Charter, R.A. 1997. Confidence interval procedures for retest, alternate-form, validity, and alpha coefficients. Perceptual and Motor Skills 84:1488–1490.

Chazdon R. 2008. Chance and determinism in tropical forest succession. Pp. 384–408, *In* W.P. Carson and S.A. Schnitzer (Eds.). Chapter 23. Tropical Forest Community Ecology. Blackwell Publishing Ltd.,West Sussex, UK. 536 pp.

Chazdon R. 2010. Composition and dynamics of functional groups of trees during tropical forest succession in northeastern Costa Rica. Biotropica 42:31–40.

Cook, M.I., S.R. Beissinger, G.A. Toranzo, R.A. Rodríguez, and W.J. Arendt. 2003. Trans-shell infection by pathogenic microorganisms reduces the shelf life of non-incubated bird's eggs: A constraint on the onset of incubation? Royal Society of London. Series B: Biological Science 270:2233–2240.

Cook, M.I., S.R. Beissinger, G.A. Toranzo, R.A. Rodríguez, and W.J. Arendt. 2004. Microbial infection affect egg viability and incubation behavior in a tropical passerine. Behavioral Ecology 16:30–36.

Ewel, J.J., and J.L. Whitmore. 1973. The ecological life zones of Puerto Rico and the US Virgin Islands. Research Paper ITF-018. USDA Forest Service, Institute of Tropical Forestry, Luquillo, PR, USA. 72 pp.

Feng, Y., R.I. Negrón-Juárez, and J.Q. Chambers. 2020. Remote sensing and statistical analysis of the effects of hurricane María on the forests of Puerto Rico. Remote Sensing of Environment 247:111940.

Fiske, I., and R. Chandler. 2011. Unmarked: An R package for fitting hierarchical models of wildlife occurrence and abundance. Journal of Statistical Software 43:1–23.

Fuller, A.K., D.W. Linden, and J.A. Royle. 2016. Management decision-making for Fisher populations informed by occupancy modeling. Journal of Wildlife Management 80:794–802.

García-Rivera, J.E., A.P. Marrero, and W.M. Latalladi. 2018. General Surgery Residency Program response plan to Hurricane Maria in Puerto Rico. Journal of the American College of Surgeons 227: S219.

Gesch, D.B., and D. Maune. 2007. Digital elevation model technologies and applications: the DEM user's manual. American Society for Photogrammetry and Remote Sensing 2:99–118.

Goldenberg, S.B., C.W. Landsea, A.M. Mestas-Nuñez, and W.M Gray. 2001. The recent increase in Atlantic hurricane activity: Causes and implications. Science 293:474–479.

Gould, W.A., C. Alarcón, B. Fevold, M.E. Jiménez, S. Martinuzzi, G. Potts, M. Quinones, M. Solórzano, and E. Ventosa. 2008. The Puerto Rico Gap Analysis Project volume 1: Land cover, vertebrate species distributions, and land stewardship. General Technical Report IITF-39. USDA Forest Service, Institute of Tropical Forestry, Luquillo, PR, USA. 165 pp.

Harris, N.L., A.E. Lugo, S. Brown, and T. Heartsill-Scalley. 2012. Luquillo Experimental Forest: Research history and opportunities. Experimental Forest and Range EFR-1. USDA Forest Service, Washington, DC. 152 pp.

Heartsill-Scalley, T. 2012. Vegetation. Pp. 64–72, *In* N.L. Harris, A.E. Lugo, S. Brown, and T. Heartsill-Scalley (Eds.). Luquillo Experimental Forest: Research history and opportunities. Experimental Forest and Range EFR-1. USDA Forest Service, Washington, DC. 152 pp.

Hu, T., and R.B. Smith. 2018. The impact of Hurricane Maria on the vegetation of Dominica and Puerto Rico using multispectral remote sensing. Remote Sensing 10:827–847.

Hutto, R.L., S.M. Pletschet, and P. Hendricks. 1986. A fixed-radius point-count method for nonbreeding and breeding season use. The Auk 103:593–602.

Karanth, K.U., A.M. Gopalaswamy, N.S. Kumar, S. Vaidyanathan, J.D. Nichols, and D.I. MacKenzie. 2011. Monitoring carnivore populations at the landscape scale: Occupancy modeling of Tigers from sign surveys. Journal of Applied Ecology 48:1048–1056.

Kéry, M., and J.A. Royle. 2016. Applied Hierarchical Modeling in Ecology: Analysis of Distribution, Abundance, and Species Richness in R and BUGS. Academic Press, Cambridge, MA, USA 789 pp.

Lloyd, J.D., C.C. Rimmer, and J.A. Salguero-Faría. 2019. Short-term effects of hurricanes Maria and Irma on forest birds of Puerto Rico. PLoS ONE 14:e0214432.

MacKenzie, D.I., J.D. Nichols, G.B. Lachman, S. Droege, J.A. Royle, and C.A. Langtimm. 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology 83:2248–2255.

Mazerolle, M.J. 2020. Model selection and multimodel inference using the AICcmodavg package. R package version 3.2.0. Available online at http://CRAN.R-project.org/package=AICcmodavg.

Morin, D.J., C.B. Yackulic, J.E. Diffendorfer, D.B. Lesmeister, C.K. Nielsen, J. Reid, and E.M. Schauber. 2020. Is your ad hoc model selection strategy affecting your multimodel inference? Ecosphere 11:e02997.

Nareff, G.E., P.B. Wood, D.J. Brown, T. Fearer, J.L. Larkin, and W.M. Ford. 2019. Cerulean Warbler (*Setophaga cerulea*) response to operational silviculture in the central Appalachian region. Forest Ecology and Management 448:409–423.

Odum, H.T., and R.F. Pigeon. 1970. A tropical rain forest: A study of irradiation and ecology at El Verde, Puerto Rico. Division of Technical Information, US Atomic Energy Commission, Washington, DC. 289 pp.

Pagán, M. 1995. Habitat relationships of avian communities on an elevational gradient in the Luquillo Experimental Forest of Puerto Rico. M.Sc. Thesis. University of Puerto Rico, Río Piedras, USA. 99 pp.

R Development Core Team. 2021. R: A language and environment for statistical computing. Version 4.0.5. Available online at http://www.R-project.org. R Foundation for Statistical Computing, Vienna, Austria.

Rittenhouse, C.D., A.M. Pidgeon, T.P. Albright, P.D. Culbert, M.K. Clayton, C.H. Flather, and V.C. Radeloff. 2010. Avifauna response to hurricanes: Regional changes in community similarity. Global Change Biology 16:905–917.

Rivera-Milán, F.F., G.S. Boomer, and A.J. Martínez. 2014. Monitoring and modeling of population dynamics for the harvest management of Scaly-naped Pigeons in Puerto Rico. Journal of Wildlife Management 78:513–521.

Rivera-Milán, F.F., H. Madden, and K. Verdel. 2021. Bridled Quail-dove, *Geotrygon mystacea*, population assessment after hurricanes Irma and Maria, St. Eustatius, Caribbean Netherlands. Bird Conservation International 31:656–667.

Rivera-Milán, F.F., A.J. Martínez, A. Matos, D. Guzmán, C.R. Ruiz-Lebrón, E.A. Ventosa-Febles, and H. Diaz-Soltero. 2022. Puerto Rico Plain Pigeon, Scaly-naped Pigeon, and Red-tailed Hawk: Population dynamics and association patterns before and after hurricanes. Endangered Species Research 47:75–89.

Rollé, F.J. 1965. An observation of heavy predation by Pearly-eyed Thrasher. Wilson Bulletin. 77:296–297.

Royle, J.A. 2004. N-mixture models for estimating population size from spatially replicated counts. Biometrics 60:108–115.

Scatena, F.N. 1998. An assessment of climate change in the Luquillo Mountains of Puerto Rico. Pp. 193–198, *In* R.I. Segarra-García (Ed.). Proceedings of the Third international symposium on tropical hydrology and Fifth Caribbean Islands water resources congress; San Juan, Puerto Rico. American Water Resources Association, Herndon, VA, USA. 268 pp.

Silver, W.L., A.E. Lugo, and M. Keller. 1999. Soil oxygen availability and biogeochemistry along rainfall and topographic gradients in upland wet tropical forest soils. Biogeochemistry 44:301–328.

Snyder, N.F.R., J.W. Wiley, and C.B. Kepler. 1987. The Parrots of Luquillo: Natural History and Conservation of the Puerto Rican Parrot. Western Foundation of Vertebrate Zoology, Los Angeles, CA, USA. 384 pp.

Tejeda-Cruz, C., and W.J. Sutherland. 2005. Cloud forest bird responses to unusually severe storm damage. Biotropica 37:88–95.

Thomas, L., S.T. Buckland, E.A. Rexstad, J.L. Laake, S. Strindberg, S.L. Hedley,J.R.B. Bishop, T.A. Marques, and K.P. Burnham. 2010. Distance software: Design and analysis of distance sampling surveys for estimating population size. Journal of Applied Ecology 47:5–14.

Thompson-Baranello, J.J. 2000. Resource and population modeling of the Puerto Rican Parrot (*Amazona vittata*). M.Sc. Thesis. University of Puerto Rico, Río Piedras, PR, USA. 108 pp.

US Fish and Wildlife Service. 1999. Technical/Agency Draft Revised Recovery Plan for the Puerto Rican Parrot (*Amazona vittata*). USFWS Region 4, Atlanta, GA, USA. 75 pp.

Uriarte, M., J. Thompson, and J. K. Zimmerman. 2019. Hurricane María tripled stem breaks and doubled tree mortality relative to other major storms. Nature Communications 10:1362.

Van Belle, G. 2002. Statistical Rules of Thumb. John Wiley and Sons, Hoboken, NJ, USA. 304 pp.

Van Beusekom, A., N. Álvarez-Berríos, W. Gould, M. Quiñones, and G. González. 2018. Hurricane María in the US Caribbean: Disturbance forces, variation of effects, and implications for future storms. Remote Sensing 10:1386

Wadsworth, F.H. 1951. Forest management in the Luquillo Mountains. Caribbean Forester 12:93–114.

Walker, L.R., D.J. Lodge, and R.B. Waide. 1991. An introduction to hurricanes in the Caribbean. Biotropica 23:313–316.

Walker, L.R., J.K. Zimmerman, D.J. Lodge, and S. Guzmán-Grajales. 1996. An altitudinal comparison of growth and species composition in hurricane-damaged forests in Puerto Rico. Journal of Ecology 84:877–889.

Weaver, P.L. 1990. Succession in the elfin woodland of the Luquillo Mountains of Puerto Rico. Biotropica 22:83–89.

Weaver, P.L., and W.A. Gould. 2013. Forest vegetation along environmental gradients in northeastern Puerto Rico. Ecological Bulletins 54:43–66.

Wiley, J.W., and J.M. Wunderle Jr. 1993. The effects of hurricanes on birds, with special reference to Caribbean islands. Bird Conservation International 3:319–349.

Wunderle, J.M., Jr. 1995. Responses of bird populations in a Puerto Rican forest to Hurricane Hugo: The first 18 months. The Condor 97:879–896.

Wunderle, J.M, Jr. 1999. Pre-and post-hurricane fruit availability: Implications for Puerto Rican Parrots in the Luquillo Mountains. Caribbean Journal of Science 35:249–264.

Wunderle, J.M., Jr., D.J. Lodge, and R.B. Waide. 1992. Short-term effects of Hurricane Gilbert on terrestrial bird populations in Jamaica. The Auk 109:148–166.

Zimmerman, J.K., M.R. Willig, L.R. Walker, and W.L. Silver. 1996. Introduction: Disturbance and Caribbean ecosystems. Biotropica 28(4a):414–423.

Zimmerman, J.K., M.R. Willig, and E.A. Hernández-Delgado. 2020. Resistance, resilience, and vulnerability of social–ecological systems to hurricanes in Puerto Rico. Ecosphere 11:e03159.

Zimmerman, J.K., T.E. Wood, G. González, A. Ramirez, W.L. Silver, M. Uriarte, M.R. Willig, R.B. Waide, and A.E. Lugo. 2021. Disturbance and resilience in the Luquillo Experimental Forest. Biological Conservation 253:108891.