



Studies on Neotropical Fauna and Environment

ISSN: (Print) (Online) Journal homepage: https://www.tandfonline.com/loi/nnfe20

Levels of genetic differentiation and gene flow between four populations of the Scaly-naped Pigeon, Patagioenas squamosa: implications for conservation

Christopher Cambrone , Frank Cézilly , Rémi Wattier , Cyril Eraud & Etienne Bezault

To cite this article: Christopher Cambrone, Frank Cézilly, Rémi Wattier, Cyril Eraud & Etienne Bezault (2021): Levels of genetic differentiation and gene flow between four populations of the Scaly-naped Pigeon, Patagioenas squamosa: implications for conservation, Studies on Neotropical Fauna and Environment, DOI: 10.1080/01650521.2021.1878765

To link to this article: https://doi.org/10.1080/01650521.2021.1878765



View supplementary material 🕝

1	-0-	
ш		

Published online: 14 Feb 2021.



Submit your article to this journal 🕑



View related articles 🗹



則 View Crossmark data 🗹

ORIGINAL ARTICLE

Taylor & Francis

Check for updates

Levels of genetic differentiation and gene flow between four populations of the Scaly-naped Pigeon, *Patagioenas squamosa*: implications for conservation

Christopher Cambrone Oa,b,c, Frank Cézilly Ob,c,d, Rémi Wattier Ob, Cyril Eraude and Etienne Bezault

^aBiologie des Organismes et Écosystèmes Aquatiques (BOREA) UMR MNHN/SU/UNICAEN/UA/CNRS/IRD/UA, Université des Antilles, Pointe à Pitre, Guadeloupe (F.W.I); ^bUMR CNRS 6282 Biogéosciences, Université de Bourgogne-Franche Comté, Dijon, France; ^cCaribaea Initiative, Université des Antilles, Pointe-à-Pitre, Guadeloupe; ^dUniversité d'Etat d'Haïti, Port-au-Prince, Haiti; ^eOffice Français de la Biodiversité, Unité Avifaune Migratrice, Chizé, France

ABSTRACT

Island-endemic columbid species are particularly vulnerable to environmental degradation, extreme climatic events, and interactions with exotic species. The situation might be even more critical in the case of exploited species, where legal hunting and poaching can severely affect population dynamics. Here we document for the first time the genetic structure of the Scaly-naped Pigeon, *Patagioenas squamosa*, a Caribbean-endemic columbid species of cynegetic interest, over a large part of its range. Using both mitochondrial DNA and nuclear markers (microsatellites), we investigated gene flow, genetic diversity, and genetic structure among four islands populations originating from Puerto-Rico, Guadeloupe, Martinique and Barbados. We found evidence for a significant genetic differentiation only between the Barbados and the three other populations, consistent with the fact that the Barbados population originated from a few captive individuals escaped from a rooftop aviary in Bridgetown about 100 years ago. Given the absence of genetic differentiation between Puerto Rico and the French Antilles, our results suggest that, apart from Barbados, the species may mainly consist of a single large, homogeneous population. We discuss the relevance of our findings in relation to management and conservation issues.

ARTICLE HISTORY

Received 19 February 2020 Accepted 17 January 2021

KEYWORDS

Caribbean islands; Columbiformes; genetic diversity; microsatellites; mitochondrial DNA; management unit

Introduction

It is now widely accepted that genetic diversity is crucial for the persistence of wildlife populations as low diversity results in both low individual fitness and reduced adaptability of populations in the face of environmental changes (Frankham 2005; Evans & Sheldon 2008). Accordingly, over the last 30 years, molecular and conceptual tools from population genetics and phylogeography have been increasingly used in conservation biology (Soulé & Mills 1998; Hedrick 2001; Russello et al. 2020). Population genetics and phylogeography are particularly helpful to determine the evolutionary and geographic boundaries of species, subspecies and populations (Haig et al. 2006, 2011; Garnett & Christidis 2007; Haig & D'Elia 2010). Defining such units is of prime importance to assess extinction risk, to prioritize conservation actions and identify the relevant spatial and temporal scales at which they should be conducted (Haig et al. 2011). This is especially true for species occurring in archipelagos, for which different populations may face

CONTACT Christopher Cambrone Schristopher.cambrone@yahoo.com Supplemental data for this article can be accessed here.

different selection pressures because of contrasted anthropogenic, biotic or abiotic influences between islands (Clegg et al. 2002; Illera et al. 2007; Hoeck et al. 2010).

In addition, island endemic species are often characterized by restricted habitat range and smaller population sizes resulting in lower genetic diversity than mainland species, such that they are more exposed to inbreeding depression and, ultimately, face a higher risk of extinction (Frankham 1998, 2005; Brooks et al. 2002). Consequently, ecological disturbances and environment changes that are globally occurring, such as deforestation, urbanization, introduced pathogens, and competition and predation pressures from invasive species, particularly affect island endemic species (Walsh et al. 2012; Treglia et al. 2013; Ferrer-Sánchez & Rodríguez-Estrella 2014; Ortega et al. 2015; Dornburg et al. 2016; Palmas et al. 2017; Turvey et al. 2017). This is particularly true of bird species, with 80% of all avian species having become extinct since 1600 being island endemics (Manne et al. 1999). The

^{© 2021} Informa UK Limited, trading as Taylor & Francis Group

situation might be even more critical in the case of exploited species, where legal and illegal hunting can severely affect population dynamics (Juillet et al. 2012; Carvalho et al. 2015). In that context, genetic information, including genetic diversity and genetic structure, is of prime importance for delimiting meaningful management units, and developing relevant conservation policies of island game bird species accordingly.

Endemic columbid species can play an important ecological role in island ecosystems through their capacity to disperse seeds over long distances (Shanahan et al. 2001; Bucher & Bocco 2009). However, they are particularly vulnerable to environmental degradation, extreme climatic events, predation, and hunting pressure (Walker 2007; Carvalho et al. 2015; Collar 2015; Stirnemann et al. 2018). Preservation and restoration of forest habitats, sustainability of hunting pressure and control of introduced predators are therefore the main priorities for the management of island columbid species (Walker 2007). However, at a regional scale, information about the degree of connectivity between different island populations is also necessary to understand population structure (Young & Allard 1997; Monceau et al. 2013), movements (Strong & Bancroft 1994), and the role of columbids in the intra- and inter-island transfer of seeds and ecosystem functioning (McConkey et al. 2004; Buelow et al. 2018).

Here we document the extent of genetic structure and gene flow in the Caribbean-endemic Scaly-naped Pigeon (Patagioenas squamosa) using both mitochondrial DNA and nuclear markers (microsatellites). The species' natural range includes both the Greater and the Lesser Antilles and extends to Florida in the north and to the islands off the coast of Venezuela in the south (Del Hoyo et al. 1997). Although the species is a year-round resident throughout much of its range (Nellis et al. 1984; Levesque et al. 2011; García-Quintas & Isada 2014; Rodríguez Batista et al. 2014; Madden et al. 2015), it occurs only seasonally on some islands (Paice & Speirs 2010) and is a vagrant on Jamaica. In addition, individuals can move between islands, particularly following extreme climatic events (Rivera-Milán 1995). The Scaly-naped Pigeon was introduced in Barbados in the early twentieth century, after about 25 individuals escaped from captivity from a rooftop aviary in Bridgetown (Buckley et al. 2009). This arboreal and frugivorous pigeon has a diverse diet and is supposed to play an important role in forest regeneration (Pérez-Rivera 1978). Although the species is currently considered of least concern in the IUCN red list, data on population size, demographic trends and movements of individuals between islands are scarce. Still, the species is exposed to intensive hunting pressure over a large part of its distribution area and is under the threat of ongoing

habitat loss and fragmentation (Wiley 1985; Brooks et al. 2002; Acevedo & Restrepo 2008). According to Raffaele et al. (1998), the species has largely declined in the West Indies, except in Puerto-Rico thanks to the regeneration of secondary forests from abandoned agricultural lands (but see Case & Hughes 2011). In addition, climate change in the Caribbean, with a likely increase in extreme climatic events, such as hurricanes (O'Brien et al. 1992; Wiley & Wunderle 1993; Boose et al. 2004) and an overall rainfall reduction (Bhardwaj et al. 2018), may also put the species at risk in the near future. Therefore, using both mitochondrial and nuclear makers, we assess the extent of genetic differentiation and that of gene flow between four different islands spread over the geographical range of the species. In addition, we compare our results with previous estimates of the genetic structure of other columbid species of contrasted conservation status.

Materials and methods

Sample collection and DNA extraction

Biological samples were obtained between 2009 and 2012 from four different islands: Puerto-Rico (PR), Guadeloupe (GUA), Martinique (MAR) and Barbados (BAR) (Figure 1 and Table S1). Birds in GUA and MAR were collected only during the hunting season, such that birds were not necessarily local breeders. Depending on the island, various types of biological samples were taken from live individuals (blood, feathers) or from individuals shot by local hunters (liver, legs). Liver samples and blood were placed in a storage buffer (70% ethanol and 30% Tris-EDTA buffer pH 8), whereas legs were deep-frozen and feathers were stored in envelopes with silica-gel.

From liver and toe samples, DNA extraction was carried out from small pieces (about 1 cm2) of tissues. In the case of feathers samples, the calamus tip (2–3 mm in length) was used. For each blood sample, 100 μ L were centrifuged at 4000 rpm, at 4°C, during one minute in order to separate the plasma (the supernatant) from the red blood cells. Then, all samples were overnight incubated with 200 μ L of Queen Lysis Buffer (Tris 10 mM, EDTA 10 mM, NaCl 10 mM, n-lauroylsarcosine 1%; Seutin et al. 1991) and 5 μ L of Proteinase K at 55°C. DNA was thereafter extracted according to a standard phenol-chloroform method, as described by Hillis et al. (1996).

Mitochondrial DNA amplification and sequencing

We amplified a mitochondrial DNA (mtDNA) gene coding for the Cytochrome c Oxidase subunit I (COI) from 111 scaly-naped pigeons, by using



Figure 1. Map of the Caribbean archipelago, with the sampled islands in black. Island names are followed by their acronym used in the present study and parenthesis include sampling sizes for mtDNA and microsatellite analyses, respectively.

reverse and forward primers described by Kerr et al. (2007): BirdF1 (5'-TTCTCCAACCACAAAGACATT GGCAC-3') and VertebrateR1 (5'-TAGACTTCTGG GTGGCCAAAGAATCA-3'). The 50 µL PCR mixture contained 200 µmol/L dNTP, 1X Buffer (HotMasterTM Taq Buffer, 5 PRIME), 0.25 U Taq (HotMasterTM Taq DNA Polymerase, 5 PRIME) and 200 nmol/L R and F primers. The PCR reaction, performed within a Biorad DNA Engine Peltier Thermal Cycler (Bio-Rad Laboratories, Inc.), began by an initial denaturating at 94°C for 1 min. 30 s, following by 34 thermal cycles consisted of: 94°C for 30 s 53°C for 45 s, and 65°C for 45 s, ended by a final extension at 65°C for 10 min. The quality of amplifications was assessed on 2% agarose electrophoresis gel. Thereafter, PCR products were purified by adding two enzymes: Exonuclease I (EXOI) at a final concentration equals to 2 U per PCR product, and Shrimp Alkaline Phosphatase (SAP) at a final

concentration equals to 1 U per PCR product. These enzymes were incubated for one hour at 37°C to be activated, and were deactivated through an incubation at 80°C during 10 min. All samples were externally sequenced by Macrogen Inc. (Republic of Korea) on an Applied Biosystems 3730xl DNA Analyzer sequencer (Applied Biosystems), carried out according to a protocol of Big Dye Sequencing.

Microsatellite amplification and genotyping

A total of 128 individuals were genotyped at seven microsatellite loci developed specifically for *P. squamosa* (Barker et al. 2011): PsA130, PsC11, PsC101, PsC120, PsC128, PsD2 and PsD5. The 10 μ L PCR mixture consisted of 200 μ mol/L dNTP, 1X Buffer (HotMasterTM Taq Buffer, 5 PRIME), 0.25 U Taq (HotMasterTM Taq DNA Polymerase, 5 PRIME), 200 nmol/L R and F primers, and 200 nmol/L of

Fluochrome 700 or 800. The PCR thermal condition consisted of an initial denaturing period at 94°C for 5 min., following by 35 thermal cycles including: 94°C for 40 s, 53°C for 30 s, and 65°C for 1 min., ended by a final extension at 65°C for 5 min. Microsatellite alleles were visualized on 6.5% acrylamide 25 cm long and 0.25 mm thick gels on a LICOR 4000 L automated sequencer.

Mitochondrial data analysis

Sequences were manually aligned using MEGA 5 software (Tamura et al. 2011). Molecular diversity indices such as haplotype diversity (h), average number of nucleotide differences between haplotypes (π), number of polymorphic sites (S), Nucleotide diversity (k), and pairwise island differentiation (Φ_{ST}) were estimated with ARLEQUIN 3.5 software (Excoffier & Lischer 2010). Φ_{st} is a F_{ST} analogue for mtDNA sequences and corresponds to the molecular distance between populations based on the number of pairwise differences between haplotypes. These values were estimated with 50 000 permutations and 5% nominal level was adjusted for multiple comparisons with Benjamini-Yekutieli step up procedure (BY; Benjamini & Yekutieli 2001; Narum 2006), resulting in α_{BY} = 0.0204. A minimum spanning network was constructed through POPART 1.7 software (Bandelt et al. 1999; Leigh & Bryant 2015) based on pairwise absolute distances between haplotypes. Neutrality and demographic history tests such as Tajima's D test (Tajima 1989) and Fu's F_S test (Fu & Li 1993) were performed, as well as the more conservative square differences statistic (SSD, mismatch distribution), to compare the observed distribution of the number of nucleotide differences between haplotype pairs to that expected under the null hypothesis of sudden expansion, using 10 000 bootstraps (Rogers & Harpending 1992; Harpending et al. 1993; Fahey et al. 2012). These analyses were also performed with ARLEQUIN 3.5.

Microsatellite data analysis

MICROCHECKER 2.2.3 was used to identify potential genotyping errors due to null alleles, scoring errors due to stuttering, and large allelic dropout, using 10,000 iterations and Bonferroni correction (Van Oosterhout et al. 2004). The number of alleles per locus (N_a), observed heterozygosity (H_0), expected heterozygosity in Hardy-Weinberg equilibrium (H_E ; Nei 1978) and the deviation from Hardy-Weinberg equilibrium (HWE; Guo & Thompson 1992) were performed with Arlequin 3.5, considering 1,000,000 Markov chain

steps and 100,000 dememorisation steps. Inbreeding coefficient (F_{IS}) was calculated in *FSTAT* 2.9.3 (Goudet 1995) by independently taking each island and at the regional scale. Since some loci included null alleles (Table S2), islands paiwise F_{ST} value were first computed using FREENA (Chapuis & Estoup 2007). However, corrected values of pairwise F_{ST} , which excluded null alleles, were not significantly different than those including them (Table S3). Uncorrected values of pairwise F_{ST} were therefore used to visualize pairwise island differentiation, using *FSTAT* 2.9.3. Nominal significance level (5%) was adjusted with BY's correction.

Population structure was also visualized using an individual-based Bayesian clustering method, as implemented in STRUCTURE 2.2.3 (Pritchard et al. 2000), and using principal coordinate analysis (PCoA), as implemented in GENALEX 6.41 (Peakall & Smouse 2006). STRUCTURE assigns individuals into K optimal region groups according to their genetic similarity. To that end, and to determine the optimal number of genotype clusters (K), we ran simulations using the admixture and correlated allele frequencies models by programming ten independent runs for K values ranging from 1 to 6 and a burn-in length of 30,000 followed by 100,000 Markov chain Monte Carlo. Thereafter, the optimal number of genotype groups (*K*) was estimated using the R (version 3.6.2; R Core Team 2019) package CORRSIEVE (version 1.6-8; Campana et al. 2011) by following the ad hoc statistic ΔK method described by Evanno et al. (2005). Clusters were finally visualized using DISTRUCT 1.1 (Rosenberg 2004).

Scaly-naped pigeons were not historically present in Barbados but were imported by local pigeon fanciers (Buckley et al. 2009). Therefore, we used *BOTTLENECK* 1.2.02 (Piry et al. 1999) to detect distortions in the distribution of alleles frequencies due to a recent founder effect (Luikart et al. 1998), considering the single-step mutation model (SSM), known to be more appropriate for microsatellites loci (Di Rienzo et al. 1994; Piry et al. 1999).

Results

Mitochondrial polymorphism

We obtained 624 bp long COI sequences for the 111 samples of Scaly-naped Pigeon, revealing five haplotypes (H_1 - H_5) associated with polymorphism at four single nucleotides (Tables 1 & Tables 2). Haplotype and nucleotide diversities at the local and regional scale are presented in Table 2. The haplotypic network (Figure

Table 1. Occurrences and percentage of COI haplotypes revealed in each island (H_R = total number of haplotypes per island; N = sample size). Sequences of haplotypes are available in GenBank database (Accession codes: MW411793-97).

		•			,
	PR	GUA	MAR	BAR	All islands
H ₁	28 (100%)	24 (82.76%)	13 (76.47%)	37 (100%)	102 (91.89%)
H ₂	-	3 (10.34%)	3 (17.65%)	-	6 (5,41%)
H₃	-	1 (3.45%)	-	-	1 (0.90%)
H ₄	-	1 (3.45%)	-	-	1 (0.90%)
H₅	-	-	1 (5.88%)	-	1 (0.90%)
H _R	1	4	3	1	5
Ν	28	29	17	37	111

2) presents the relationship between the five different mitochondrial haplotypes detected across the 111 studied pigeons. GUA had the highest haplotype richness ($H_R = 4$), followed by MAR ($H_R = 3$). PR and BAR presented only one haplotype (H_1), which was the most abundant at the local and regional scale (Tables 1 & Tables 2 and Figure 2). Exclusive haplotypes were found in both GUA (H_3 and H_4) and MAR (H_5). H_2 , found in both GUA and MAR, was the second most frequent haplotype (Table 1 & Figure 2). Pairwise island mtDNA Φ_{ST} values (Table 3), revealed differentiation between BAR and both GUA and MAR, and between MAR and PR.

We first carried out independent demographic scenario tests for islands showing polymorphism (GUA and MAR), and thereafter carried out the same tests at the regional scale. Results from these tests were in accordance with a demographic stability for MAR (Tajima's D = -0.0697, P = 0.239; Fu's F_S = -0.6240, P = 0.224 and SSD = 0.00870, P = 0.046). For GUA, results from Fu's F_S test supported a within-island demographic expansion (Fu'F_S = -2.194, P = 0.021), whereas both Tajima's D and mismatch distribution tests were in agreement with demographic stability (Tajima's D = -1.350, P = 0.069 and SSD = 0.00228, P = 0.032). All of the demographic scenario tests clearly

supported a demographic expansion at the regional scale (Tajima's D = -1.544, P = 0.015; Fu's F_S = -4.919, P = 0.001 and SSD = 0.000322, P = 0.101).

Microsatellite polymorphism

Genotyping of 128 individuals resulted in a total of 73 alleles (Mean ± SD: 10.429 ± 3.359 alleles per locus), with an average of observed heterozygosity equals to 0.731 ± 0.145 over all loci and at the regional scale (Table 2). We found no difference in terms of number of alleles (Friedman- χ^2 = 2.766, df = 3, *P* = 0.429), allelic richness (Friedman- χ^2 = 6.6, df = 3, *P* = 0.086) and observed heterozygosity between populations (Friedman- χ^2 = 3.514, df = 3, *P* = 0.319; Tables 2 & S4). Global F_{IS} was estimated at -0.0560. The basic summary statistics of genetic variation within different islands are presented in Supplementary Table S4.

All island pairwise F_{ST} values for BAR were significantly different from zero (F_{ST} ranging from 0.0496 to 0.0594), whereas all other values were not, suggesting a moderate level of differentiation between BAR and the three other islands (Table 3). This result was in accordance with results based on *STRUCTURE* analysis (Figure 3) and PCoA (Figure 4). In both analyses, GUA, MAR and PR seemed to form a homogenous group, whereas BAR appeared to be genetically isolated. PCoA result was based on the first and second axes that, respectively, explained 22.66% and 21.23% of the overall variance in microsatellite data.

Based on *BOTTLENECK* analysis, we found that BAR was significantly in deficiency of heterozygosity under the single-step mutations model (Wilcoxon rank test: P = 0.0391; Table 4). At the regional scale, no excess or deficiency of heterozygosity was highlighted.

Table 2. Genetic characteristics of sampled islands, based on the mtDNA COI sequence. See Figure 1 for island acronyms. Variables are: Sample size (N), Number of polymorphic sites (*S*), Haplotypic diversity (*h*), Average number of nucleotide differences between haplotypes (π), Nucleotide diversity (average over loci, *k*), (\bar{N}_a) average number of alleles per microsatellite loci, observed and expected heterozygosity (*Ho* and *He*, respectively) and the inbreeding coefficient (*Fis*); s.d. = standard deviation.

	PR	GUA	MAR	BAR	All islands
Mitochondrial polymorphi	ism				
N	28	29	17	37	111
S	0	3	2	0	4
h ± s.d.	0	0.313 ± 0.106	0.404 ± 0.130	0	0.154 ± 0.0456
$\pi \pm s.d.$	0	0.330 ± 0.341	0.426 ± 0.405	0	0.157 ± 0.219
k ± s.d. (x 10 ⁻³)	0	0.529	0.683	0	0.252
Microsatellite polymorphis	sm				
Ν	32	36	28	32	128
$\overline{N}_a \pm s.d.$	7.714 ± 3.352	8.286 ± 3.251	8.000 ± 2.380	7.143 ± 1.773	10.429 ± 3.359
H _o	0.766 ± 0.174	0.758 ± 0.200	0.718 ± 0.205	0.683 ± 0.135	0.731 ± 0.145
He	0.783 ± 0.134	0.777 ± 0.160	0.769 ± 0.173	0.695 ± 0.122	0.774 ± 0.137
F _{is}	0.0181	0.0162	0.0691	0.0244	0.056



Figure 2. Minimum spanning network of 111 haplotypes for a 624 bp sequences of mtDNA COI. Each circle represents a haplotype and its size is proportional to the number of individuals sharing this haplotype. One continuous segment represents one nucleotidic difference. Colors indicate the origin of individuals and its proportion, the relative abundance of individuals sharing the same haplotype and originating from the same location.

Table 3. Pairwise island mtDNA Øst values (below diagonal) and microsatellite *Fst* values (above diagonal) of Scaly-naped Pigeon for four Caribbean islands. Significant values considering *BY's* correction (α BY = 0.0204) are in bold (NS = not significant; * = P < 0.0204; *** = P < 0.00408; *** = P < 0.000408).

	PR	GUA	MAR	BAR
PR	-	0.0124 ^{NS}	0.0165 ^{NS}	0.0496*
GUA	0.0903 ^{NS}	-	0.0079 ^{NS}	0.0586*
MAR	0.201*	-0.0254 ^{NS}	-	0.0594*
BAR	0.000 ^{NS}	0.112**	0.242**	-

Discussion

Genetic diversity

Based on mtDNA analysis, we found an overall relatively low haplotype (h = 0.154) diversity across the four Caribbean islands populations, compared to other island-endemic columbid species that was estimated using the control region gene. These species include the 'critically endangered' Red-headed Wood Pigeon Subspecies, *Columba janthina nitens* (h = 0.12; Ando et al. 2014), the 'endangered' Pink Pigeon *Nesoenas mayeri* (h = 0.45; Swinnerton et al. 2004), the two subspecies of the 'near threatened' Plain Pigeon (*P. inornata wetmorei* with h = 0.48 and *P. i. inornata* with h = 0.59; Young & Allard 1997), the 'near-threatened' New

Zealand Pigeon Hemiphaga novaeseelandiae (h = 0.623; Goldberg et al. 2011) and the 'least-concern' Emerald Dove Chalcophaps indica (h = 0.94; Kirchman & Franklin 2007). The level of haplotype diversity across islands has been influenced by the absence of mtDNA polymorphism in Barbados and Puerto-Rico. Indeed, haplotype diversity values for Guadeloupe and Martinique was h = 0.313 and h = 0.404, respectively. These values are still low compared to what has been previously reported for other columbid species, but in accordance with the Caribbean-endemic and 'least concern' Zenaida Dove, Zenaida aurita (h = 0.404; calculated from Monceau et al. 2013) for which the same mtDNA gene was used. A similar pattern was also visible from the average nucleotide diversity across loci and the average number of nucleotides differences between haplotypes (Young & Allard 1997; Kirchman & Franklin 2007; Goldberg et al. 2011; Ando et al. 2014). The absence of haplotype polymorphism in Barbados was in accordance with what we expected (influence of founder effect, see below), but less so for Puerto-Rico, which is known to harbor a large population with more than 260,000 scalynaped pigeons (Rivera-Milán et al. 2014). This lack of diversity across Puerto Rico samples might have been influenced by the fact that captures were conducted in



Figure 3. Genetic structure of populations of the Scaly-naped Pigeon using Bayesian inference through *STRUCTURE* analysis. (a) and (b) represent results from simulation to determine the optimal number of genotype clusters (K) according to the method describes by Evanno et al. (2005). Error bars represents standard deviations over ten runs. (c) represents results from *STRUCTURE* analysis carried out with maximum-likelihood centered at K = 2 genotype clusters. Each individual is represented by a single vertical bar, partitioned into K colored segments that represent its estimated population membership fractions. Individuals are grouped by population on the x-axis. Population codes are given in Figure 1.

a restricted area within the island (i.e. two separated sites distant from 8 km, Cidra and Comerio municipalities), thus increasing the probability of collecting related individuals, in the case of a geographically structured population.

Contrary to mtDNA diversity, genetic diversity based on the seven microsatellite markers was in accordance with what we expected. All islands showed similar values of observed heterozygosity, with Barbados showing the lowest value (PR: $H_{\rm O} = 0.77$, GUA: $H_{\rm O} = 0.76$, MAR: $H_{\rm O} = 0.72$ and BAR: $H_{\rm O} = 0.68$). In addition, the average observed heterozygosity across the four islands (0.731) was in accordance with its IUCN conservation status, since quite similar to the value reported for the Zenaida Dove (0.725; Monceau et al. 2013). In contrast, this value was clearly higher than the one found for the critically endangered redheaded Wood Pigeon ($H_{\rm O} = 0.04$; Ando et al. 2014).



Figure 4. Principal coordinate analysis (PCoA) based on the genetic distance matrix constructed through seven microsatellite markers from 128 Scaly-naped Pigeons. Diagrams on the right side and at the top represent the density and the distribution of points according to the y-axis (Coord. 1) and the x-axis (Coord. 2), respectively.

Table 4. Wilcoxon signed rank test for mutation-drift equilibrium estimated based on seven microsatellite loci to assess a variation in term of heterozygosity (*H*) due to demographic events such as a bottleneck or a founder effect.

	SMN	1
POPULATIONS	H deficiency	H excess
PR	0.961	0.0547
GUA	0.766	0.289
MAR	0.469	0.594
BAR	0.0391*	0.973
ALL ISLANDS	0.148	0.945

Genetic structure

Genetic diversity metrics based on both mtDNA and nuclear markers were indicative of genetic depletion in Barbados compared to the three other studied populations, suggesting that this population experienced a recent historical demographic event such as a bottleneck or founder event, a more or less longterm geographical isolation or a combination of these phenomena. This hypothesis was supported by the *BOTTLENECK* analysis (conducted using the stepwise mutation model), which provided evidence for heterozygosity deficiency, suggestive in the present case, of a founder effect. This recent historical demography event broadly explained the observed genetic structure. Indeed, Barbados was strongly differentiated from

Guadeloupe and Martinique based on haplotype frequencies (0.112 and 0.242, respectively). In contrast, Barbados was not differentiated from Puerto-Rico, since both populations exclusively consisted of the same haplotype (H_1) . For the same reason, Puerto-Rico was differentiated from Martinique, whereas, using microsatellite markers, differentiation was only observed between Barbados and the other islands. This pattern was in accordance with results obtained with STRUCTURE and the PCoA analyses, from which two genetic groups were identified, separating individuals from Barbados from those from Martinique, Guadeloupe and Puerto-Rico. This genetic structure could be explained by: (i) the emergence of the Barbados population from a few individuals imported by local pigeon fanciers (i.e., founder effect), (ii) the geographic context of the Barbados island, which is relatively isolated compared to other islands from the Antillean Arc (i.e. restricted gene flow) and (iii) genetic drift, which may be intensified by the two previous phenomena.

In contrast, Martinique, Guadeloupe and Puerto-Rico were not differentiated or structured, what suggests that these islands could be inter-connected by effective migrants and regular movements. This pattern contrasts to some extent with what has been observed in two other Caribbean-endemic columbid species. In the Zenaida Dove, limited gene flow was observed between eight Caribbean islands, even at very short distance like, for instance, between Martinique and Saint-Lucia (Monceau et al. 2013). Interestingly, the latter study also observed a strong divergence between Barbados and the other islands. In the congeneric Plain Pigeon, P. inornata, restricted gene flow was observed between Puerto-Rico and the Dominican Republic, although the extent of genetic differentiation between the two populations suggests that they may correspond to two sub-species (Young & Allard 1997). However, the observed pattern of genetic structure is in accordance with several other studies on columbids, which highlighted the peculiar aspect of the evolution of this family in a biogeographic context of insularity (Santiago-Alarcon et al. 2006; Kirchman & Franklin 2007; Seki et al. 2007; Goldberg et al. 2011; Ando et al. 2014). Indeed, most columbid species have conserved a strong flying ability contrary to most other island-endemic terrestrial birds (Bollmer et al. 2005; Petren et al. 2005; Kawakami et al. 2008). For instance, the White-crowned Pigeon, P. leucocephala, the phylogenetically closest species to the Scaly-naped Pigeon (Johnson et al. 2010), is known to perform daily movements between breeding areas and foraging sites by flying over 50 km, and can fly up to 150 km over water to reach another Caribbean island in order to track food resources and/or suitable environmental conditions (Wiley 1979; Wiley & Wiley 1979; Rivera-Milán 1992; Bancroft et al. 2000; Strong & Johnson 2001; Meyer & Zimmerman 2006; Florida Fish and Wildlife Conservation Commission 2013), such as for avoiding hurricanes (Wiley & Wunderle 1993; Ries et al. 2018). Hurricanes are known to affect avian community and population dynamics by mainly disturbing feeding and breeding habitats (Rittenhouse et al. 2010; Jenouvrier 2013). Due to the inherent strong ability to fly of most of Columbidae, the high frequency of hurricane events in the Caribbean region may induce movements of individuals, potentially homogenizing the allelic pool over the different island populations, as observed in the present study. Therefore, if movements of individuals between islands are frequent and philopatry is low, it is possible that the whole species actually consists of a single large population.

At the geological timescale, results from historical demographic analyses suggest a recent demographic expansion of the Scaly-naped Pigeon population at the regional scale. The Scaly-naped Pigeon might have had a restricted range during the glacial maxima, while population expanded after the Last Glacial Maximum. The same pattern of expansion was found for the New Zealand Pigeon (Wallis & Trewick 2009; Goldberg et al. 2011).

Implications for the management of the species

The Scaly-naped Pigeon is facing several threats such as habitat loss, legal and illegal hunting, exotic predators and climate change. There is a relatively high hunting pressure within its range of distribution, but monitoring data are lacking (Raffaele et al. 1998; Latta et al. 2010; Latta 2012; Rivera-Milán et al. 2014). In Puerto-Rico, where studies are particularly concentrated, it has been argued that the species requires the development of a sustainable harvest strategy at the local level (Case & Hughes 2011). However, given our results and the strong flying ability of Columbiformes, the insular Caribbean (to the possible exception of Barbados) could be considered as an evolutionarily significant unit (ESU) or management unit (MU; Moritz 1994; Paetkau 1999; Zink 2004), emphasizing the need for conservation effort to be undertaken at the regional rather than local scale. To that end, further sampling could be carried out in other Caribbean islands to confirm the genetic structure of the species at the regional scale evidenced in the present study. In addition, other methods could be used to distinguish between historic and contemporary gene flow, and to identify recently diverged population for an effective conservation management of the species (Paetkau 1999; Palsboll et al. 2006; Whitehead 2010; Esteban et al. 2016). For instance, Paetkau (1999) criticized the unique use of genetic data for MUs recognition and advised to combine it with movement data such as Mark-Recapture, telemetry, or GPS tracking data. Using such methods would indeed be valuable to detect contemporary migration/dispersal due to, for instance, current anthropogenic disruptions (Esteban et al. 2016).

Lay summary

- No genetic differentiation between Puerto-Rico, Guadeloupe and Martinique.
- Possibly one large population of Scaly-naped Pigeon at the Caribbean regional scale.
- Significant founder effect in the Barbados population, consistent with its introduced origin.

Acknowledgments

We are grateful to Mr Steve Devonish, Director of the Natural Heritage Department, for granting us the permission

to capture Scaly-naped Pigeons in Barbados, and Nicole Atherley and Sébastien Motreuil for help in catching and processing birds. We thank Francisco J. Vilella for providing samples from Puerto-Rico, and Patrick Asselin de Beauville, Jean-François Maillard, Anthony Levesque, Georges Tayalay (Fédération des chasseurs de Martinique) and local hunters for providing samples from Martinique and Guadeloupe. We also thank Pierre Leclercq for help with genetic analyses at an earlier stage of the study.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

CC was funded by a doctoral grant from the Conseil Régional de la Guadeloupe and Caribaea Initiative.

ORCID

Christopher Cambrone D http://orcid.org/0000-0001-9928-4178

Frank Cézilly b http://orcid.org/0000-0003-2673-6713 Rémi Wattier b http://orcid.org/0000-0001-5772-4681 Etienne Bezault b http://orcid.org/0000-0001-7172-6480

References

- Acevedo MA, Restrepo C. 2008. Land-cover and land-use change and its contribution to the large-scale organization of Puerto Rico's bird assemblages. Divers Distrib. 14:114–122.
- Ando H, Ogawa H, Kaneko S, Takano H, Seki S-I, Suzuki H, Horikoshi K, Isagi Y. 2014. Genetic structure of the critically endangered Red-headed Wood Pigeon *Columba janthina nitens* and its implications for the management of threatened island populations. Ibis. 156:153–164.
- Bancroft GT, Bowman R, Sawicki RJ. 2000. Rainfall, fruiting phenology, and the nesting season of white-crowned pigeons in the upper Florida Keys. Auk. 117:416–426.
- Bandelt HJ, Forster P, Rohl A. 1999. Median-joining networks for inferring intraspecific phylogenies. Mol Biol Evol. 16:37–48.
- Barker FK, Bell JJ, Bogdanowicz SM, Bonatto SL, Cezilly F, Collins SM, Dubreuil C, Dufort MJ, Eraud C, Fuseya R, et al. 2011. Permanent genetic resources added to molecular ecology resources database 1 June 2011–31 July 2011. Mol Ecol Resour. 11:1124–1126. doi:10.1111/j.1755-0998.2011.03068.x.
- Benjamini Y, Yekutieli D. 2001. The control of the false discovery rate in multiple testing under dependency. Ann Stat. 29:1165–1188.
- Bhardwaj A, Misra V, Mishra A, Wootten A, Boyles R, Bowden JH, Terando AJ. 2018. Downscaling future climate change projections over Puerto Rico using a non-hydrostatic atmospheric model. Clim Change. 147:133–147.
- Bollmer JL, Whiteman NK, Cannon MD, Bednarz JC, de Vries T, Parker PG. 2005. Population genetics of the Galápagos Hawk

(*Buteo Galapagoensis*): genetic monomorphism within isolated populations. Auk. 122:1210–1224.

- Boose ER, Serrano MI, Foster DR. 2004. Landscape and regional impacts of hurricanes in Puerto Rico. Ecol Monogr. 74:335–352.
- Brooks TM, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Rylands AB, Konstant WR, Flick P, Pilgrim J, Oldfield S, Magin G, et al. 2002. Habitat loss and extinction in the hotspots of biodiversity. Conserv Biol. 16:909–923.
- Bucher EH, Bocco PJ. 2009. Reassessing the importance of granivorous pigeons as massive, long-distance seed dispersers. Ecology. 90:2321–2327.
- Buckley PA, Massiah EB, Hutt MB, Buckley FG, Hutt HF. 2009. The birds of Barbados. Tring (UK): British Ornithologists' Union.
- Buelow CA, Baker R, Reside AE, Sheaves M. 2018. Nutrient subsidy indicators predict the presence of an avian mobile-link species. Ecol Indic. 89:507–515.
- Campana MG, Hunt HV, Jones H, White J. 2011. CorrSieve: software for summarizing and evaluating Structure output. Mol Ecol Resour. 11:349–352.
- Carvalho M, Fa JE, Rego FC, Lima RFD, Santos G, Palmeirim JM. 2015. Factors influencing the distribution and abundance of endemic pigeons on São Tomé Island (Gulf of Guinea). Bird Conserv Int. 25:71–86.
- Case DJ, Hughes SJ. 2011. Priority information needs for Band-tailed Pigeons, Zenaida doves, White-tipped Doves and Scaly-naped Pigeons: a funding strategy. Developed for the Association of Fish and Wildlife Agencies by the Migratory Shore and Upland Game Bird Support Task Force. p. 16.
- Chapuis M-P, Estoup A. 2007. Microsatellite null alleles and estimation of population differentiation. Mol Biol Evol. 24:621–631.
- Clegg SM, Degnan SM, Moritz C, Estoup A, Kikkawa J, Owens IPF. 2002. Microevolution in island forms: the roles of drift and directional selection in morphological divergence of a passerine bird. Evolution. 56:2090–2099.
- Collar NJ. 2015. Natural history and conservation biology of the Tooth-billed Pigeon (*Didunculus strigirostris*): a review. Pacific Conserv Biol. 21:186–199.
- Del Hoyo J, Elliott A, Sargatal J, Cabot J. 1997. Handbook of the birds of the world. Vol. 4, Sandgrouse to cuckoos. Barcelona: Lynx Edicions.
- Di Rienzo A, Peterson AC, Garza JC, Valdes AM, Slatkin M, Freimer NB. 1994. Mutational processes of simple-sequence repeat loci in human populations. Proc Natl Acad Sci. 91:3166–3170.
- Dornburg A, Lippi C, Federman S, Moore JA, Warren DL, Iglesias TL, Brandley MC, Watkins-Colwell GJ, Lamb AD, Jones A. 2016. Disentangling the influence of urbanization and invasion on endemic geckos in tropical biodiversity hot spots: a case study of *Phyllodactylus martini* (*Squamata: Phyllodactylidae*) along an urban gradient in Curaçao. Bull Peabody Museum Nat Hist. 57:147–164.
- Esteban R, Verborgh P, Gauffier P, Giménez J, Martín V, Pérez-Gil M, Tejedor M, Almunia J, Jepson PD, García-Tíscar S, et al. 2016. Using a multi-disciplinary

approach to identify a critically endangered killer whale management unit. Ecol Indic. 66:291–300. doi:10.1016/j. ecolind.2016.01.043.

- Evanno G, Regnaut S, Goudet J. 2005. Detecting the number of clusters of individuals using the software structure: a simulation study. Mol Ecol. 14:2611–2620.
- Evans SR, Sheldon BC. 2008. Interspecific patterns of genetic diversity in birds: correlations with extinction risk. Conserv Biol. 22:1016–1025.
- Excoffier L, Lischer HEL. 2010. Arlequin suite ver. 3.5: a new series of programs to perform population genetics analyses under Linux and Windows. Mol Ecol Resour. 10:564–567.
- Fahey AL, Ricklefs RE, Latta SC, DeWoody JA. 2012. Comparative historical demography of migratory and nonmigratory birds from the Caribbean Island of Hispaniola. Evol Biol. 39:400–414.
- Ferrer-Sánchez Y, Rodríguez-Estrella R. 2014. Man-made environments relationships with island raptors: endemics do not cope with habitat changes, the case of the island of Cuba. Biodivers Conserv. 24:407–425.
- Florida Fish and Wildlife Conservation Commission. 2013. A species action plan for the White-crowned Pigeon *Patagioenas leucocephala*. Tallahassee (FL): Florida Fish and Wildlife Conservation Commission.
- Frankham R. 1998. Inbreeding and extinction: island populations. Conserv Biol. 12:665–675.
- Frankham R. 2005. Genetics and extinction. Biol Conserv. 126:131-140.
- Fu YX, Li WH. 1993. Statistical tests of neutrality of mutations. Genetics. 133:693–709.
- García-Quintas A, Isada AP. 2014. Effects of migrations on the nestedness structure of bird assemblages in cays of the Jardines de la Reina archipelago, Cuba. Anim Biodivers Conserv. 37:127-139.
- Garnett ST, Christidis L. 2007. Implications of changing species definitions for conservation purposes. Bird Conserv Int. 17:187–195.
- Goldberg J, Trewick SA, Powlesland RG. 2011. Population structure and biogeography of Hemiphaga pigeons (*Aves: Columbidae*) on islands in the New Zealand region. J Biogeogr. 38:285–298.
- Goudet J. 1995. FSTAT (Version 1.2): a computer program to calculate F-statistics. J Hered. 86:485–486.
- Guo SW, Thompson EA. 1992. Performing the exact test of Hardy-Weinberg proportion for multiple alleles. Biometrics. 48:361–372.
- Haig SM, Beever EA, Chambers SM, Draheim HM, Dugger BD, Dunham S, Elliott-Smith E, Fontaine JB, Kesler DC, Knaus BJ, et al. 2006. Taxonomic considerations in listing subspecies under the U.S. Endangered Species Act. Conserv Biol. 20:1584–1594. doi:10.1111/j.1523-1739.2006.00530.x.
- Haig SM, Bronaugh WM, Crowhurst RS, D'Elia J, Eagles-Smith CA, Epps CW, Knaus B, Miller MP, Moses ML, Oyler-McCance S, et al. 2011. Genetic applications in avian conservation. Auk. 128:205–229. doi:10.1525/ auk.2011.128.2.205.
- Haig SM, D'Elia J. 2010. Chapter 2: avian subspecies and the U.S. Endangered Species Act. Ornithol Monogr. 67:24–34.
- Harpending HC, Sherry ST, Rogers AR, Stoneking M. 1993. The genetic structure of ancient human populations. Curr Anthropol. 34:483–496.

- Hedrick PW. 2001. Conservation genetics: where are we now? Trends Ecol Evol. 16:629-636.
- Hillis DM, Moritz C, Mable BK, Olmstead RG. 1996. Molecular systematics. Sunderland (MA): Sinauer Associates.
- Hoeck PEA, Bollmer JL, Parker PG, Keller LF. 2010. Differentiation with drift: a spatio-temporal genetic analysis of Galápagos mockingbird populations (*Mimus* spp.). Philos Trans R Soc B Biol Sci. 365:1127–1138.
- Illera JC, Emerson BC, Richardson DS. 2007. Population history of Berthelot's pipit: colonization, gene flow and morphological divergence in Macaronesia. Mol Ecol. 16:4599-4612.
- Jenouvrier S. 2013. Impacts of climate change on avian populations. Global Change Biol. 19:2036–2057.
- Johnson KP, Clayton DH, Dumbacher JP, Fleischer RC. 2010. The flight of the Passenger Pigeon: phylogenetics and biogeographic history of an extinct species. Mol Phylogenet Evol. 57:455–458.
- Juillet C, Choquet R, Gauthier G, Lefebvre J, Pradel R. 2012. Carry-over effects of spring hunt and climate on recruitment to the natal colony in a migratory species. J Appl Ecol. 49:1237–1246.
- Kawakami K, Harada S, Suzuki T, Higuchi H. 2008. Genetic and morphological differences among populations of the Bonin Islands White-eye in Japan. Zoolog Sci. 25:882–887.
- Kerr KCR, Stoeckle MY, Dove CJ, Weigt LA, Francis CM, Hebert PDN. 2007. Comprehensive DNA barcode coverage of North American birds. Mol Ecol Notes. 7:535–543.
- Kirchman JJ, Franklin JD. 2007. Comparative phylogeography and genetic structure of Vanuatu birds: control region variation in a rail, a dove, and a passerine. Mol Phylogenet Evol. 43:14–23.
- Latta S, Rimmer C, Keith A, Wiley J, Raffaele HA, McFarland K, Fernandez E. 2010. Birds of the Dominican Republic and Haiti. Princeton (NJ): Princeton University Press.
- Latta SC. 2012. Avian research in the Caribbean: past contributions and current priorities. J Field Ornithol. 83:107–121.
- Leigh JW, Bryant D. 2015. POPART : full-feature software for haplotype network construction. Methods Ecol Evol. 6:1110-1116.
- Levesque A, Duzon F, Mathurin A, Chiffard J. 2011. Liste des oiseaux de la Guadeloupe (6ème édition). Grande-Terre, Basse-Terre, Marie-Galante, les Saintes, la Désirade, Îlets de la Petite-Terre. Rapport AMAZONA n° 30.
- Luikart G, Allendorf FW, Cornuet JM, Sherwin WB. 1998. Distortion of allele frequency distributions provides a test for recent population bottlenecks. J Hered. 89:238-247.
- Madden H, Hensen R, Piontek S, Walton S, Verdaat H, Geelhoed SC, Stapel J, Debrot AO. 2015. New bird records for the island of St. Eustatius, Dutch Caribbean, with notes on other significant sightings. J Caribb Ornithol. 28:28–34.
- Manne LL, Brooks TM, Pimm SL. 1999. Relative risk of extinction of passerine birds on continents and islands. Nature. 399:258–261.
- McConkey KR, Meehan HJ, Drake DR. 2004. Seed dispersal by Pacific pigeons (*Ducula pacifica*) in Tonga, Western Polynesia. Emu. 104:369–376.
- Meyer KD, Zimmerman GM. 2006. Foraging habitats, winter residency, survival, and philopatry of adult white-crowned

pigeons in the lower Florida Keys. Final Report. Tallahassee (FL): Florida Fish and Wildlife Conservation Commission

- Monceau K, Cézilly F, Moreau J, Motreuil S, Wattier R. 2013. Colonisation and diversification of the Zenaida Dove (*Zenaida aurita*) in the Antilles: phylogeography, contemporary gene flow and morphological divergence. PLoS One. 8:e82189.
- Moritz C. 1994. Defining 'Evolutionarily Significant Units' for conservation. Trends Ecol Evol. 9:373–375.
- Narum SR. 2006. Beyond Bonferroni: less conservative analyses for conservation genetics. Conserv Genet. 7:783–787.
- Nei M. 1978. Estimation of average heterozygosity and genetic distance from a small number of individuals. Genetics. 89:583–590.
- Nellis DW, Dewey RA, Hewitt MA, Imsand S, Philibosian R, Yntema JA. 1984. Population status of zenaida doves and other columbids in the Virgin Islands. J Wildl Manage. 48:889–894.
- O'Brien ST, Hayden BP, Shugart HH. 1992. Global climatic change, hurricanes, and a tropical forest. Clim Change. 22:175–190.
- Ortega N, Price W, Campbell T, Rohr J. 2015. Acquired and introduced macroparasites of the invasive Cuban Treefrog, *Osteopilus septentrionalis*. Int J Parasitol Parasites Wildl. 4:379–384.
- Paetkau D. 1999. Using genetics to identify intraspecific conservation units: a critique of current methods. Conserv Biol. 13:1507–1509.
- Paice MR, Speirs R. 2010. The avifauna of Mustique Island (St Vincent and the Grenadines). J Caribb Ornithol. 23:61-84.
- Palmas P, Jourdan H, Rigault F, Debar L, De Meringo H, Bourguet E, Mathivet M, Lee M, Adjouhgniope R, Papillon Y, et al. 2017. Feral cats threaten the outstanding endemic fauna of the New Caledonia biodiversity hotspot. Biol Conserv. 214:250–259. doi:10.1016/j.biocon.2017.08.003.
- Palsboll PJ, Berube M, Allendorf FW. 2006. Identification of management units using population genetic data. Trends Ecol Evol. 22:11–16.
- Peakall R, Smouse PE. 2006. GENALEX 6: genetic analysis in Excel. Population genetic software for teaching and research. Mol Ecol Notes. 6:288–295.
- Pérez-Rivera RA. 1978. Preliminary work on the feeding habits, nesting habitat and reproductive activities of the Plain Pigeon (*Columba inornata wetmorei*) and the Red-necked Pigeon (*Columba squamosa*), sympatric species: an analysis of their interaction. Science-Ciencia. 3:89–98.
- Petren K, Grant PR, Grant BR, Keller LF. 2005. Comparative landscape genetics and the adaptive radiation of Darwin's finches: the role of peripheral isolation. Mol Ecol. 14:2943–2957.
- Piry S, Luikart G, Cornuet J-M. 1999. BOTTLENECK: a computer program for detecting recent reductions in the effective size using allele frequency data. J Hered. 90:502–503.
- Pritchard JK, Stephens M, Donnelly P. 2000. Inference of population structure using multilocus genotype data. Genetics. 155:945–959.
- R Core Team. 2019. R: a language and environment for statistical computing. Available from: https://www.r-project.org/
- Raffaele HA, Wiley J, Garrido O, Keith A, Raffaele J. 1998. A Guide to the Birds of the West Indies. Princeton (NJ): Princeton University Press.

- Ries L, Neupane N, Baum KA, Zipkin EF. 2018. Flying through hurricane central: impacts of hurricanes on migrants with a focus on monarch butterflies. Anim Migr. 5:94–103.
- Rittenhouse CD, Pidgeon AM, Albright TP, Culbert PD, Clayton MK, Flather CH, Huang C, Masek JG, Radeloff VC. 2010. Avifauna response to hurricanes: regional changes in community similarity. Global Change Biol. 16:905–917.
- Rivera-Milán FF. 1992. Distribution and relative abundance patterns of columbids in Puerto Rico. Condor. 94:224–238.
- Rivera-Milán FF. 1995. Detectability and population density of scaly-naped pigeons before and after Hurricane Hugo in Puerto Rico and Vieques Island. Wilson Bull. 107:727–733.
- Rivera-Milán FF, Boomer GS, Martínez AJ. 2014. Monitoring and modeling of population dynamics for the harvest management of scaly-naped pigeons in Puerto Rico. J Wildl Manage. 78:513–521.
- Rodríguez Batista D, Arias Barreto Á, Ruiz Rojas E, editors. 2014. Fauna terrestre del archipiélago de Sabana-Camagüey, Cuba. La Habana: Editiorial Academia. p. 444.
- Rogers AR, Harpending HC. 1992. Population growth makes waves in the distribution of pairwise genetic differences. Mol Biol Evol. 9:552–569.
- Rosenberg NA. 2004. DISTRUCT: a program for the graphical display of population structure. Mol Ecol Notes. 4:137-138.
- Russello M, Amato G, DeSalle R, Knapp M. 2020. Conservation genetics and genomics. Genes. 11:318.
- Santiago-Alarcon D, Tanksley SM, Parker PG. 2006. Morphological variation and genetic structure of Galapagos Dove (*Zenaida galapagoensis*) populations: issues in conservation for the Galapagos bird fauna. Wilson J Ornithol. 118:194–207.
- Seki S-I, Takano H, Kawakami K, Kotaka N, Endo A, Takehara K. 2007. Distribution and genetic structure of the Japanese Wood Pigeon (*Columba janthina*) endemic to the islands of East Asia. Conserv Genet. 8:1109–1121.
- Seutin G, White BN, Boag PT. 1991. Preaservation of avian blood and tissue samples for DNA analyses. Can J Zool. 69:82–90.
- Shanahan M, So S, Gompton SG, Gorlett R. 2001. Fig-eating by vertebrate frugivores: a global review. Biol Rev. 76:529–572.
- Soulé ME, Mills SL. 1998. Population genetics: no need to isolate genetics. Science. 282:1658–1659.
- Stirnemann RL, Stirnemann IA, Abbot D, Biggs D, Heinsohn R. 2018. Interactive impacts of by-catch take and elite consumption of illegal wildlife. Biodivers Conserv. 27:931–946.
- Strong AM, Bancroft GT. 1994. Postfledging dispersal of White-crowned Pigeons: implications for conservation of deciduous seasonal forests in the Florida Keys. Conserv Biol. 8:770–779.
- Strong AM, Johnson MD. 2001. Exploitation of a seasonal resource by nonbreeding plain and white-crowned pigeons: implications for conservation of tropical dry forests. Wilson Bull. 113:73–77.
- Swinnerton KJ, Groombridge JJ, Jones CG, Burn RW, Mungroo Y. 2004. Inbreeding depression and founder diversity

among captive and free-living populations of the endangered Pink Pigeon *Columba mayeri*. Anim Conserv. 7:353–364.

- Tajima F. 1989. Statistical method for testing the neutral mutation hypothesis by DNA polymorphism. Genetics. 123:585–595.
- Tamura K, Péterson D, Peterson N, Stecher G, Nei M, Kumar S. 2011. MEGA5: molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. Mol Biol Evol. 8 (10):2731–2739.
- Treglia ML, Valiulis J, Leavitt DJ, Fitzgerald LA. 2013. Establishment of the Puerto Rican Ground Lizard (*Ameiva exsul: Teiidae*), on St. Croix, U.S. Virgin Islands: a threat to native fauna. Caribb J Sci. 47:360–365.
- Turvey ST, Kennerley RJ, Nuñez-Miño JM, Young RP. 2017. The Last Survivors: current status and conservation of the non-volant land mammals of the insular Caribbean. J Mammal. 98:918–936.
- Van Oosterhout C, Hutchinson WF, Wills DPM, Shipley P. 2004. MICRO-CHECKER: software for identifying and correcting genotyping errors in microsatellite data. Mol Ecol Notes. 4:535–538.
- Walker JS. 2007. Geographical patterns of threat among pigeons and doves (*Columbidae*). Oryx. 41:289–299.
- Wallis GP, Trewick SA. 2009. New Zealand phylogeography: evolution on a small continent. Mol Ecol. 18:3548–3580.

- Walsh JC, Venter O, Watson JEM, Fuller RA, Blackburn TM, Possingham HP. 2012. Exotic species richness and native species endemism increase the impact of exotic species on islands. Glob Ecol Biogeogr. 21:841–850.
- Whitehead H. 2010. Conserving and managing animals that learn socially and share cultures. Learn Behav. 38:329–336.
- Wiley JW. 1979. The White-Crowned Pigeon in Puerto Rico: status, distribution, and movements. J Wildl Manage. 43:402–413.
- Wiley JW. 1985. Bird conservation in the United States Caribbean. In: Temple SA, editor. Bird Conservation 2. Madison: University of Wisconsin Press. p. 107–159.
- Wiley JW, Wiley BN. 1979. The biology of the White-crowned Pigeon. Wildl Monogr. 64:3–54.
- Wiley JW, Wunderle JM. 1993. The effects of hurricanes on birds, with special reference to Caribbean islands. Bird Conserv Int. 3:319–349.
- Young DL, Allard MW. 1997. Conservation genetics of the Plain Pigeon *Columba inornata* in Puerto Rico and the Dominican Republic. Mol Ecol. 6:877–879.
- Zink RM. 2004. The role of subspecies in obscuring avian biological diversity and misleading conservation policy. Proc R Soc B Biol Sci. 271:561–564.