



Efficiency of the call-broadcast method for detecting two Caribbean-endemic columbid game species

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Abstract

The white-crowned Pigeon (WCPi), *Patagioenas leucocephala*, and the scaly-naped Pigeon (SNPi), *P. squamosa*, are two Caribbean endemic species of patrimonial and cynegetic interest. Although both species are under the threat of habitat destruction and hunting pressure, population trends remain undocumented in a large part of their geographical range. Here, we used both the “auditory and visual” and “call-broadcast” census methods to assess the occurrence and relative abundance of both species in Guadeloupe (French West Indies). The call-broadcast method was found to be more efficient as it reduced the problem of “false absence” while increasing the probability of detection. Results from our surveys showed that both WCPis and SNPis were at low density and showed complete habitat segregation. SNPis were only encountered in rainforest, whereas WCPis could be observed at count stations located in dry and swamp forests, mangroves, agricultural lands and wet meadows. We recommend the use of the call-broadcast method for monitoring the two species on islands where they occur at low density, under which conditions distance sampling may be poorly reliable. The general relevance of the call-broadcast method to other species of pigeons and doves deserves further attention, especially to document population trends in elusive game species of conservation interest.

Keywords Call-broadcast · Monitoring · *Patagioenas leucocephala* · *Patagioenas squamosa* · Playback · Point counts

Introduction

The genus *Patagioenas* includes 19 different species of New World pigeons (Johnson et al. 2010; del Hoyo et al. 2014; BirdLife International 2020), of which five are of conservation concern (Walker 2007; BirdLife International 2020). In the Caribbean region, the white-crowned Pigeon (WCPi), *P. leucocephala*, and the scaly-naped Pigeon (SNPi), *P. squamosa*, are considered, respectively,

as near-threatened and least-concern in the IUCN Red List (BirdLife International 2016a, b), being both threatened by habitat destruction, climate change, intensive (legal and illegal) hunting pressure as well as harvesting of squabs (Hay 2008; Latta et al. 2010; Latta 2012; Rivera-Milán et al. 2014, 2016; BirdLife International 2016a, b). Although quantitative data are lacking, an overall decline in population size for both species is suspected (Raffaele et al. 1998; Hay 2008). The WCPi’s natural range extends from the Florida Keys (USA) and Bahamas to a part of the Lesser Antilles (up to Saint-Lucia), also including the coasts of Central America and the Cayman Islands (Gibbs et al. 2001; Bancroft et al. 2020). In contrast, the SNPi’s natural range includes all the Antilles islands, plus the islands off the coast of Venezuela in the south (Gibbs et al. 2001; Baptista et al. 2020). At the regional scale, both species are considered as vagrant (Bancroft et al. 2020; Baptista et al. 2020; Cambrone et al. 2021). These closely related arboreal species are mainly frugivorous and are supposed to play an important role in forest regeneration (Pérez-Rivera 1978; Strong and Bancroft 1994; Ware 1997; Strong and Johnson 2001). According to Gibbs et al.

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(2001), WCPi tend to occupy coastal, lower-lying forests such as swamp forests, mangroves or dry evergreen forests, whereas SNPi are mostly found in upland and inland moist forests. However, so far, no quantitative data exist on habitat partitioning by the two species in sympatry. In addition, for both species, data on demographic trends and local abundance are scarce and limited to a few islands (Rivera-Milán 1996; Brooks et al. 2002; Acevedo and Restrepo 2008; Hay 2008; Florida Fish and Wildlife Conservation Commission 2013; Rivera-Milán et al. 2014, 2016).

In the French West Indies, data about the spatial distribution and ecology of these two popular game species is presently limited to observations made by wildlife officers from the *Office Français de la Biodiversité* (formerly *Office National de la Chasse et de la Faune Sauvage*) and local ornithologist associations. The SNPi is observed year-round in the French Antilles. The species is moderately abundant in Guadeloupe, following a marked decline during the twentieth century associated with intensive hunting pressure (especially on La Désirade, small Eastern island of the Guadeloupe archipelago; Pinchon 1976; Feldmann 1998). In contrast, the abundance of the WCPi in Guadeloupe varies seasonally, with a peak from April to December and a recent increase in the number of reported observations (Delcroix et al. 2016). Based on this information, the IUCN local status of two species has been recently reconsidered, with the WCPi being reclassified as endangered in Guadeloupe and vulnerable in Martinique, while the SNPi remained of least concern in Guadeloupe but was reclassified as near-threatened in Martinique (IUCN France et al. 2012, 2020). There is little information on the breeding status of the two species in Guadeloupe and Martinique, apart from anecdotal observations of pairs, nest construction behaviour, reproductive attempts and juveniles (Delcroix et al. 2016 for the WCPi). Further evidence suggestive of local reproduction comes from the regular presence of juveniles in the hunting bags of local hunters (a reliable source of information for demographic monitoring; Christensen and Fox 2014). The closest important breeding areas (> 70 km) to Guadeloupe and Martinique is Antigua for the WCPi and Montserrat and Dominica for the SNPi.

In the absence of quantitative data on the demography of both species in Guadeloupe and Martinique, and considering a recent population genetic study suggesting the existence of one single panmictic population of SNPi at the regional scale (Cambrone et al. 2021), reliable estimates of population abundance are fundamental to identify population fluctuations and changes. Refined estimates of population density, such as those obtained through mark–recapture methods, are available but can be time-consuming and expensive to implement (Thompson 2013; Turlure et al. 2018). In addition, capture of wild birds can be a source of stress and/or trauma, thus limiting its use when dealing with sensitive and/or threatened

species (Powell and Proulx 2003; Pauli et al. 2010). Consequently, game bird populations are often monitored using relative abundance indices, obtained from index counts or hunting statistics (e.g., Cattadori et al. 2003; Evans et al. 2007; Lande et al. 2010; Tillmann et al. 2012; Small et al. 2012; Guillemain et al. 2016; Cretois et al. 2020). Although both indices suffer from some limitations (Rosenstock et al. 2002; Christensen 2005), their combined use can provide improved information on population status (Soininen et al. 2016).

In Guadeloupe, data on hunting bags have been regularly collected by the *Office Français de la Biodiversité* for several years, whereas surveys of WCPi or SNPi populations have been seldom conducted. Indeed, the secretive behaviour of both species and their tendency to perch on trees high in the canopy makes the estimation of their local abundance difficult. It is therefore of particular importance to preliminarily assess the performance of census methods in order to obtain, in the future, reliable estimates of the local abundance of the two species in Guadeloupe, and, possibly, in other Caribbean islands. Two main methods are currently used in surveys of forest bird species. The first and more conventional method simply consists in detecting birds by sight and/or by hear along a point or line transect (i.e., auditory/visual method). The second method adds the broadcasting of calls of the species of interest to induce behavioural responses, such as vocalisations or movements, from nearby individuals, such that they become easier to detect (i.e., call-broadcast method). The use of call-broadcast has proved to be an efficient method to census various bird species, through increasing the number of detections per unit of sampling effort, reducing the problem of false absence and decreasing temporal variation in detection probability (Sutherland et al. 2004; Sutherland 2006).

The call-broadcast method could be particularly suitable to survey population of *Patagioenas* species, as Kirkpatrick et al. (2007) found that the probability of detecting a cooing band-tailed pigeon, *P. fasciata*, increased by 27% compared to auditory surveys. However, this method comes with some limitations. First, the type of habitat or the weather conditions may alter sound propagation (from the loudspeaker to birds), such that the efficiency of the method may vary according to local conditions (Schieck 1997; Buckland et al. 2005; Simons et al. 2007; Pacifici et al. 2008; Yip et al. 2017). More importantly, the method may lead to overestimate population size if birds are attracted to the calls and move around the observer, thus increasing the risk of double counting (Buckland et al. 2008; Fuller et al. 2012). However, Fuller et al. (2012) showed that this potential bias can be accounted for in statistical analyses and concluded that the method appears especially useful for the survey of elusive forest birds, at least to better ascertain their occurrence in various habitats.

In this context, the main aim of this study was to compare the efficiency of the “auditory and visual” (AV) and

“call-broadcast” (CB) census methods for estimating the presence and the relative abundance of both *P. leucocephala* and *P. squamosa* in Guadeloupe. In addition, we analysed the dominant vegetation type associated with the presence and relative abundance of each species, and assessed to what extent the two species occur in similar habitats. Based on results previously obtained with the congeneric *P. fasciata fasciata* (Kirkpatrick et al. 2007), we expected that the CB method would enhance our ability to detect and improve the estimation of relative abundance of both *P. squamosa* and *P. leucocephala*. Furthermore, we expected that each species would be detected in transects dominated by different vegetation formations, based on previous observations in other Caribbean islands (Bancroft et al. 2020; Baptista et al. 2020).

Methods

Study sites

We compared the efficiency of the AV and CB survey for assessing the presence and abundance of both *P. leucocephala* and *P. squamosa* in Guadeloupe (Fig. 1). This archipelago, located in the Lesser Antilles, consists of two main islands climatically, geologically and ecologically different (Rousteau 1996). The eastern part, Grande-Terre island, is the oldest and flattest, with a calcareous soil occupied by fragmented evergreen and semi-deciduous forests. The Basse-Terre island, to the west, is mountainous and largely covered by tropical rainforest. The two islands are separated by a sea inlet called Rivière Salée, where mangroves and swamp forests are concentrated (Fig. 1, Rousteau 1996), making Guadeloupe suitable for the two *Patagioenas* species (Gibbs et al. 2001; Bancroft et al. 2020; Baptista et al. 2020).

Survey design

The study was conducted over two consecutive years, 2016 and 2017. We defined location of transects using aerial photographs and topographic maps, complemented by a mapping of the vegetation of Guadeloupe from *Géoportail* and *Google Earth*. As we aimed at comparing two detection methods, we optimized our sampling effort by positioning the transects in places where each species is known to occur. To that end, we assessed the likely presence/absence of the two pigeon species from observations made by local hunters (a reliable source of information for demographic monitoring; e.g., Lande et al. 2010; Tillmann et al. 2012; Christensen and Fox 2014; Cretois et al. 2020), wildlife officers and data available from ebird (<https://ebird.org>; Callaghan and Gawlik 2015; Callaghan et al. 2017; Walker and Taylor 2017; Fletcher et al. 2019). Twelve different line transects were considered across

Guadeloupe to study both species between April and May 2016 (Fig. 1), each one including 10 count stations, regularly separated by 300. Such a distance reduces the risk of spatial autocorrelation between sampling points (Thomas et al. 2010). Transects' observations were replicated twice (R1: 11 to 27 April 2016 and R2: 28 April to 18 May 2016) in the morning, starting at sunrise, and twice again in the evening, finishing just at sunset, the two periods corresponding to the time at which columbid species are usually the most active (Robbins 1981a; Rivera-Milán et al. 2015). For each replication, the order of transect visits was independently randomized for the morning surveys and for the afternoon surveys. Therefore, a given transect was not systematically visited in the morning and the afternoon on the same day. At each count station, the observer always started with the AV method for a 5-min period, followed by a period during which the calls of the two species were broadcasted one after the other, for a 5-min duration each, and during which cues of the presence of individuals were recorded. During the CB method, the order of presentation of the two species call was systematically reversed between each count station and replication. At each count station, and for each detection method, all individuals seen and heard were recorded, corresponding here to our estimate of relative abundance. For each species, the same 38-s recording was diffused twice for each session of CB method, at the beginning and once again after 150 s. Calls were obtained from “Oiseaux des Antilles” (CEBA/Fremaux et Associés), modified and cleaned (i.e., removing background noise) using the free software Audacity. Calls were broadcasted in four major directions (N, E, S, W) through a Bluetooth-connected nomadic speaker (4 W, Philips BT2600) and a smartphone at the maximum volume without distortion noises. We did not perform surveys during strong rainy weather in order to reduce biases due to altered propagation of calls (from loudspeaker to birds and from birds to the observer) or reduced activity of individuals (Robbins 1981b; Buckland et al. 2005; Overton et al. 2005). We also recorded the global meteorological condition prevailing during each transect survey, according to four categories, from best to worst: “sunny”, “cloudy”, “overcast” or “scattered rains”.

Based on the results obtained in 2016 (see below) and in order to increase detection rate and, hence, statistical power, a decision was made to conduct a more intensive survey in 2017, focusing exclusively on transects where WCPi were likely to be detected. To that end, we added to the survey design five new transects and decided to remove two transects surveyed in 2016, where no pigeon had been detected (transects 14 and 16, as represented in Fig. 1 and Supplementary materials Table S2). The survey protocol was conducted in the same way as the year before, except that only the call of the WCPi was broadcasted. In addition, three replications were performed later in the season,

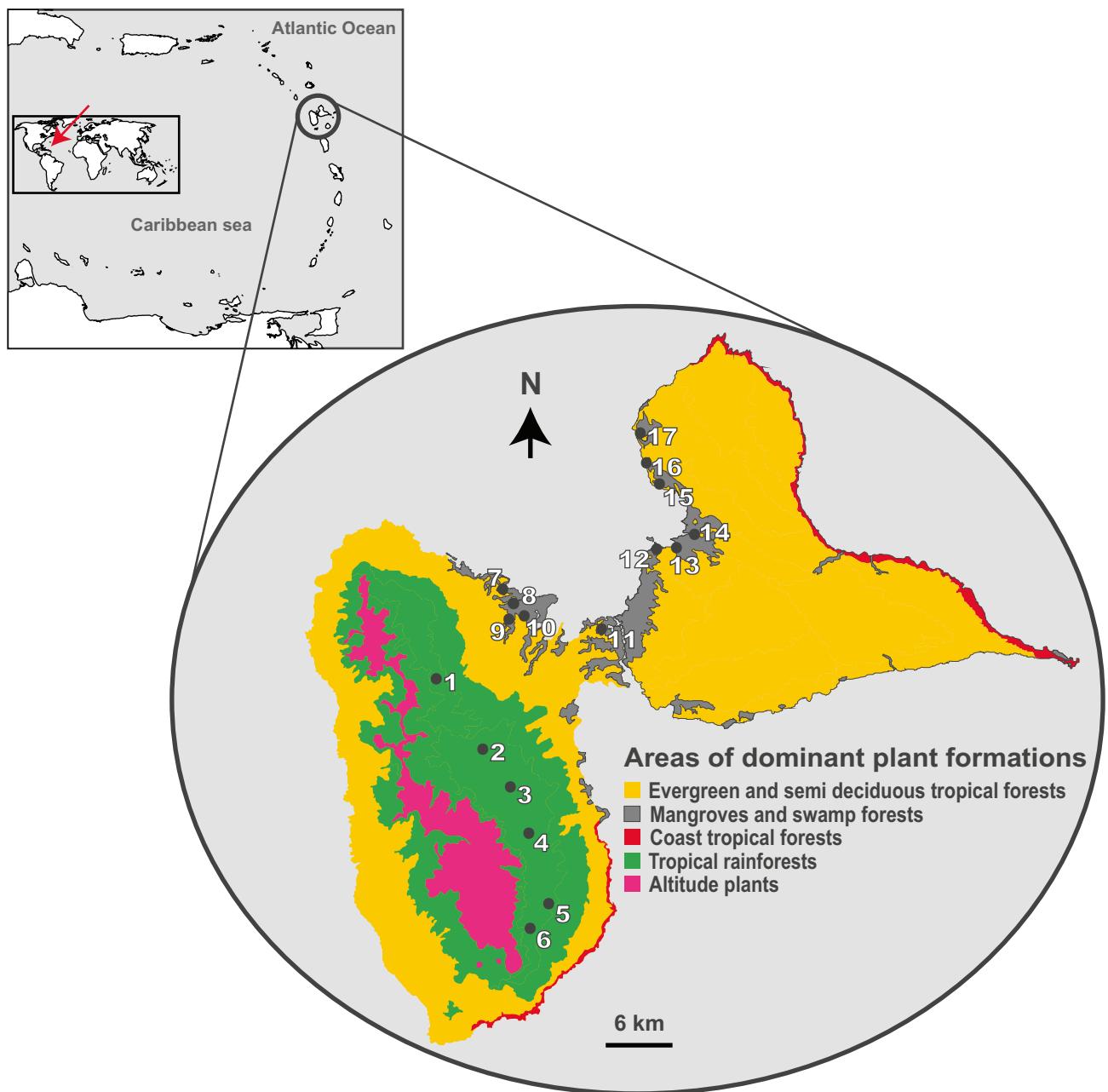


Fig. 1 Map of Guadeloupe, simplified from Rousteau (1996), indicating main vegetation types and the location of transects represented by dots. GPS locations are indicated in Table S2. The red arrow represents the location of the Caribbean region into a world map

in the morning and in the late afternoon, instead of two in 2016 (R1: 1 to 17 May, R2: 22 May to 24 June and R3: 27 June to 11 July). Similar to 2016, the circumstances of detection (Table 1) were recorded for all detected individuals, excepted for the “scanning flight” which was only recorded for the WCPi during the second and third replicates in 2017. Concerning SNPis, scanning flight and “perching” were not recorded because it was difficult to detect such behaviours in response of the broadcasted call, as all individuals were detected in closed and dense tropical rain forest, contrary to

WCPis. Circumstances of detection were determined from the first cue allowing the observer to detect the bird.

Habitat characterisation

After having mapped all count stations using Google Earth, we drew a circle with a radius of about 125 m (accuracy of measurements (mean \pm SD) 125.45 m \pm 0.28) from the centre of each count station. We chose this distance according to our survey methodology (see above) assuming that

Table 1 Details and explanations of circumstances of detection recorded during surveys

Circumstances of detection level 1	Circumstances of detection level 2	Explanations	Recorded for	
			SNPi (2016)	WCPi (2017)
Seen	Seen	The bird was already perched near to the count station	No*	Yes
	Flight	The bird was seen flying next to or distant to the count station	Yes	Yes
	Perching	The bird came to perch near to the count station	No*	Yes
Heard	Heard	The bird was detected through its callings	Yes	Yes
Scanning flight		<ul style="list-style-type: none"> • The bird deviated from their straight flight line to come near the count station to perch or not • Or, it took off its perch during the counting to fly over the count station to perch not far away • Or, it took off its perch performing a flight over the count station before going away from the observer. 	No*	Yes

*The circumstance of detection was recorded during the survey, but no pigeon was detected in these way

a 300-m distance between count stations significantly reduces the risk of spatial autocorrelation and that of double counting between successive count stations by the observer (Thomas et al. 2010). In addition, we estimated the sound propagation of call-broadcast using both a sound meter (measure of sound intensity à 25 m) and observer hearing capacity (maximum distance broadcast detection). The intensity of bird's song broadcasts played by the speaker was standardized at a level/volume about 60 dB as measured at 25 m distance of the source. This sound intensity allowed us to distinguish the bird calls from background noise at a distance between 100 and 150 m, depending on the vegetation type surrounding the loudspeaker and level of background noise in the environment. Previous studies based on domestic pigeons' hearing capacity (e.g., Schwartzkopff 1955; Kreithen and Quine 1979; Heffner et al. 2013) suggest that columbids have a shorter hearing distance than humans. Circles of vegetation determination were imported in *Géoportail* (French web platform for national geographic information; Institut National de l'Information Géographique et Forestière—IGN, 2006), in order to characterize vegetation from aerial photographs (2013). We mapped the vegetation surrounding each count station according to the major vegetation types occurring in Guadeloupe (Fig. 1): tropical rainforest, mangrove, swamp forest, dry forest (i.e., evergreen and semi-deciduous tropical forest) and others (i.e., all non-forest structures such as agricultural lands, wet meadows, sea or habitations; Supplementary materials Table S1 and S2). The identification of vegetation types was achieved from the different texture and green colours in aerial photographs (see an example in Supplementary materials Fig. S5). Vegetation types were subsequently confirmed by direct observations in the field. We then estimated for each circle around each count station the absolute and relative surface covered by each vegetation type using the surface area tool in the *Géoportail* platform.

Data analysis

All calculations, models and statistical tests were performed using the R software 3.6.2 (R Core Team 2019). For inference statistics, significance level was set at 0.05. In 2016, our statistical power was too low for the WCPi (see Supplementary materials Table S4). Therefore, analyses on SNPis were based on data collected in 2016, whereas analyses on WCPis relied on data collected in 2017. We assessed the reproducibility of our data from pairwise Spearman's correlation tests for each species and each detection method. We adjusted *p* values for repetitive tests by using Benjamini–Yekutieli's correction (Benjamini and Yekutieli 2001). Confidence intervals (CIs) for effect sizes were determined through 10,000 bootstraps.

White-crowned pigeon We calculated the diversity of habitat (*Hd*) using the Shannon index for each count station:

$$Hd = - \sum p_h \times \log_2(p_h)$$

where p_h is the proportion of habitats. We relied on a principal component regression in order to manage colinearity between variables describing habitats (proportions of each habitat type at count station and *Hd*; Supplementary materials Table S1), using the R package *FactoMineR* 2.2 (Husson et al. 2020) to reduce variation in habitats to two principal components (PC1 and PC2).

We used generalized linear mixed models (GLMMs; Bolker et al. 2009; Stroup 2012) in order to compare the detection methods using both relative abundance and presence/absence data. We considered PC1 and PC2, meteorological conditions (including sunny/cloudy vs. overcast/scattered rains) and time of day (coded as morning vs. afternoon) as explanatory variables interacting with detection methods in order to assess their influence on the effectiveness of the CB method. We thereafter relied on two other GLMMs using data obtained through the CB method in order to assess to what extent PC1, PC2, meteorological conditions and time of day

could explain changes in the presence/absence or abundance of WCPis. We also considered PC1 and PC2 interacting with other variables. We relied on random effect models, such as GLMMs, to avoid pseudoreplication (Harrison et al. 2018) as our sampling scheme consisted of three temporal replications. For all models, we then considered replica nested within station ID as random effect parameters. GLMMs were fitted with Poisson distribution (log link) for the estimated relative abundance data and with binomial error distribution (logit link) for presence/absence data. We ran models using the R package *glmmTMB* 1.0.0 (Brooks et al. 2017). Because our dataset based on relative abundance included many zeros, we tested our GLMMs for zero inflation compared to a Poisson distribution (Zuur et al. 2010; Bolker 2020) using the R package DHARMA 0.2.7 (Hartig 2020). We relied on quantile–quantile and goodness-of-fit plots using the same R package for verifying GLMM assumptions and detecting deviations from the expected distribution. Model selection was performed using the R package MuMIn 1.6 (Barton and Barton 2019) and based upon the adjusted Akaike’s information criteria (AIC_c, Burnham and Anderson 2002). We considered models having $\Delta\text{AIC}_c \leq 2$ as equivalent for explaining variations of the presence or relative abundance of the species (Burnham and Anderson 2002; Arnold 2010). In order to assess the importance of model parameters, we relied on full-model averaging to estimate coefficients (β_i) of model parameters and their 85% confidence intervals (85% CI) (Burnham and Anderson 2002; Arnold 2010), counted as effect size (Galipaud et al. 2017). Model parameters that did not overlap zero were considered meaningful. Among the top ranked models (i.e., having $\Delta\text{AIC}_c \leq 2$), we selected the model including the meaningful parameters according to the full-model averaging procedure (Arnold 2010). We also relied upon the variable model-averaged absolute of the *t* statistics, which consists in dividing the absolute coefficient estimate of model parameter (β_i) with their standard deviation, so as to estimate the relative importance of each model parameter (Cade 2015; Galipaud et al. 2017). We also used the R package MuMIn 1.6 to calculate marginal R^2 (R^2_m) and conditional R^2 (R^2_c) values of the selected models, based on the delta method, to see to what extent fixed effect parameters and fixed effects combined with random effect parameters of models explained variation of the response, respectively (Nakagawa and Schielzeth 2013; Nakagawa et al. 2017). Based on presence/absence data, we also performed a McNemar change test in order to assess the ability of the CB method to detect pigeons when the AV method failed to do so. In order to assess the influence of call-broadcasting on the behaviour of WCPis, we assessed to what extent the circumstances of detection of individuals (circumstances of detection levels 1 and 2; Table 1) were dependent upon the method of detection used, using a Fisher’s exact test and associated odds ratio.

Scaly-naped pigeon The survey strategy used in 2016 implied to broadcast the song of the two species at each count station. Therefore, we assessed whether the broadcasting order of calls impacted our ability to detect SNPis. To that end, we calculated the matched-pair rank biserial correlation coefficient, r_c (King et al. 2018), using the R package *rcompanion* 2.3.25 with the “none” zero method, which takes into account null pairs (Mangiafico 2020). Calculated effect size based on the relative abundance estimated when the intraspecific CB was played first vs. the opposite was compared based on 95% CI (Cumming and Finch 2005). The same procedure was performed for presence/absence data using the *Cohen’s g* (C_g) as effect size (Cohen 1988).

Results aiming at comparing detection methods were obtained using the same procedures used for the WCPi. However, we did not include any habitat variable in GLMMs as the species was only found in tropical rainforests, such that only meteorological conditions and time of day interacting with detection method were considered. Besides, we assessed to what extent these variables could explain changes in abundance or the presence/absence of SNPis between count stations. In order to assess the influence of call-broadcasting on the behaviour of SNPis, we assessed to what extent the circumstances of detection of individuals (circumstances of detection level 1; Table 1) were dependent on the method of detection used, using a Fisher’s exact test.

Comparison between species We performed interspecific comparisons in order to see whether the effectiveness of call-broadcasting differed between species and between interspecific and intraspecific call-broadcasting, by relying on the r_w and C_g effect sizes and their 95% CI. In order to assess interspecific attraction to calls, we relied on data obtained in 2016 for the WCPi, despite low statistical power resulting from weak abundance. We also compared the circumstances of detection level 1 (seen vs. heard; Table 1) between the two species using a Fisher’s exact test and associated odds ratio. Habitat segregation between the two species was directly estimated from visual inspection of barplots as the observed pattern was obvious.

Results

We found significant and positive correlations between replications within each species and each detection method ($P < 0.05$ for all correlations, see Supplementary materials Table S3 for detailed results), indicating that the relative abundance at each count station was, on average, reproducible over our replications. For the two species, statistical power and number of counts per replication and detection method are presented in Supplementary materials Table S4.

Overall, we detected more individuals when using the CB method compared to when using the AV one for both species, with 134 vs. 59 WCPis and 118 vs. 67 SNPis, respectively. For both species, encounter rates (number of detections/min ± SD) were relatively low, but significantly higher for the SNPi for each detection method. We detected 0.054 ± 0.130 SNPis per min against 0.022 ± 0.087 WCPis per min using the AV method (Wilcoxon’s test, $W = 72,033$; $P < 0.001$) and 0.098 ± 0.165 against 0.050 ± 0.155 using CB method, respectively ($W = 77,842$; $P < 0.001$). The proportion of birds heard or seen differed significantly between the two species (*P. squamosa*: heard = 155, seen = 30; *P. leucocephala*: heard = 91, seen = 102; Fisher’s exact test, $P < 0.001$). In addition, the efficiency of the intraspecific CB method did not differ between the two species when assessing their presence/absence, whereas it was more effective for the SNPi when considering relative abundance (Fig. 2).

The vegetation pattern at point stations where SNPis were observed differed markedly from that of point stations where WCPis were observed (Fig. 3). SNPis were only detected at count stations dominated by tropical rainforests, located in the Basse-Terre island of the Guadeloupe archipalego, whereas the WCPi was found in the Grande-Terre and Basse-Terre island, at count stations characterized by more diverse vegetation types, including mangrove, swamp forests, dry forests and non-forest habitat.

Principal component regression reduced variation in vegetation cover to two principal components, PC1 and PC2, explaining 43.11% and 33.2% of the total variation, respectively (Table 2 and Supplementary materials Fig. S1). Larger values of PC1 represented count stations dominated by dry forest with large values of Hd, while lower values define count stations dominated by non-forest vegetation structure. For PC2, larger values represented count stations dominated by swamp forest, while lower values corresponded to those dominated by mangrove.

For all GLMMs, we included random effect parameters (i.e., replica nested within station ID) in order to explain variation in the presence/absence and the relative abundance of birds among and within count stations as the mere use of fixed effect parameters resulted in a poor R^2_m for the two species, contrary to R^2_c (i.e., $R^2_m < R^2_c$; Supplementary materials Table S5 and S7). Quantile–quantile plots and goodness-of-fit tests showed no evidence of problems with fit (Supplementary materials Figs. S2, S3 and S4).

White-crowned pigeon

The CB method improved significantly the detection of WCPis over the AV method (McNemar change test, $X^2 = 17$, $df = 1$, $P < 0.001$). We compared 17 logistic regression models to compare the efficiency of the detection method and the

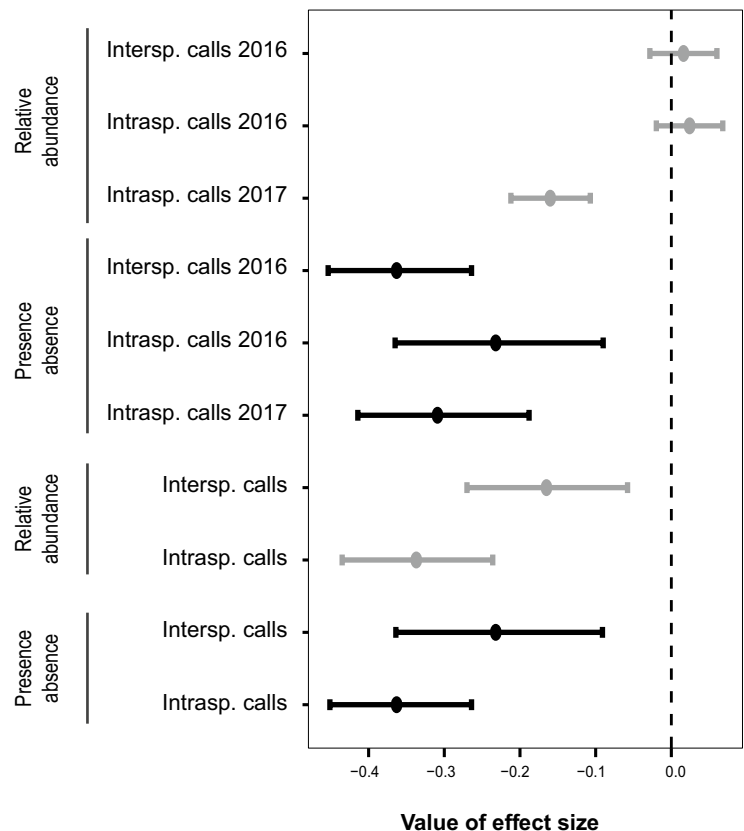
Fig. 2 Effect size values based upon the relative abundance (r_c in grey) and presence/absence (C_g in black) for both the WCPi and the SNPi. Error bars indicate the 95% CI. Significant negative values corresponds to AV < CB



P. leucocephala



P. squamosa



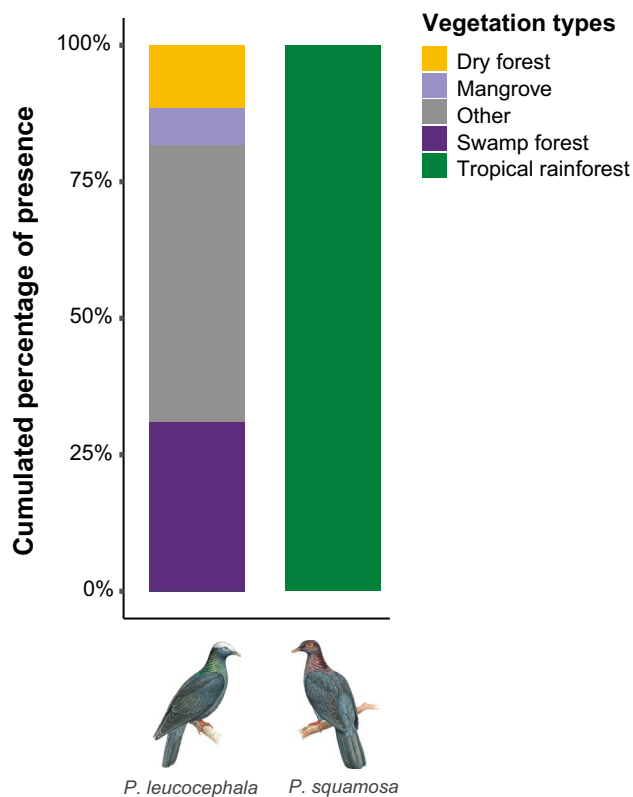


Fig. 3 General patterns of vegetation at count stations where SNPIs and WCPis were detected in Guadeloupe during the survey

influence of several variables on the detection of the presence of the species (Table 3 (A)). The top ranked model included the detection method and its interaction with PC2, with the first variable having the largest influence on the detection of WCPis. As expected, the CB method was positively associated with the presence of the species ($\bar{\beta}_{CB}$ [85% CI] = 1.284 [0.678; 1.890]; Table 4 (A)). Besides, the estimated probability of detection was significantly higher when using the CB method than when using the AV one (AV [85% CI] = 0.010 [0.004; 0.021], CB [85% CI] = 0.028 [0.014; 0.054]; Fig. 4A).

Table 2 Factor loadings of the four habitats on the components 1 (PC 1) and 2 (PC 2). Bold values refer to loading values larger than |0.50| for each principal component. See Supplementary materials Fig. S1 for PCA plots

Habitats	PC 1	PC 2
Other	-0.938	-0.123
Mangrove	0.491	-0.665
Swamp forest	0.231	0.905
Dry forest	0.666	-0.013
Hd	0.888	0.035
Eigenvalues	2.406	1.333
Cumulative variance %	43.107	74.770

The presence of pigeons was also positively associated, but to a lesser extent, to the interaction between the detection method and PC2 ($\bar{\beta}_{AV:PC2}$ [85% CI] = 0.445 [0.246; 0.776] and $\bar{\beta}_{CB:PC2}$ [85% CI] = 0.267 [0.049; 0.564]; Table 4 (A)). Regardless of the method used, the probability of detection tended to be higher at count stations dominated by swamp forest compared to those dominated by mangrove, where it dropped to about zero (Supplementary materials Fig. S6).

Similarly, when comparing the 17 models based upon relative abundance, the detection method was included in the three top ranked models (Table 3 (A)). The full-model averaging procedure retained the model including the detection method, the interaction between detection method and PC2 and the interaction between detection method and meteorological conditions (Table 4 (A)). As expected, the use of the CB method was positively associated with relative abundance ($\bar{\beta}_{CB}$ [85% CI] = 0.862 [0.506; 1.218]; Table 4 (A)), with a higher averaged predicted relative abundance when using the CB method compared to when using the AV one (AV [85% CI] = 0.018 [0.010; 0.033]; CB [85% CI] = 0.040 [0.023; 0.071]; Fig. 4B). The interaction between detection method and PC2 was also positively related to the predicted relative abundance ($\bar{\beta}_{AV:PC2}$ [85% CI] = 0.243 [0.141; 0.561] and $\bar{\beta}_{CB:PC2}$ [85% CI] = 0.222 [0.120; 0.522]; Table 4 (A)), suggesting to be higher at count stations dominated by swamp forests and dropping to almost zero in habitats dominated by mangrove, regardless of the detection method considered (Supplementary materials Fig. S6). Meteorological conditions had also an influence on our ability to detect the species using the CB method, with a higher relative abundance on sunny days compared to overcast days (Fig. 5A).

Overall, the proportion of pigeons seen or heard was independent of the detection method used (Fisher's test, $P=0.100$, odds ratio [95% CI] = 1.603 [0.309; 1.166]; Fig. 6A). However, the proportion of WCPis detected according to "circumstances of detection level 2" (see Table 1) was found to vary with the detection method (Fisher's test, $P=0.020$; Supplementary materials Fig. S7). Besides, scanning flights were only observed when using the CB method (Fisher's test, $P<0.001$; Supplementary materials Fig. S7). Finally, there was no significant difference in terms of response between interspecific (i.e., SNPI) and intraspecific calls when comparing count data in 2016 (r_c), and when comparing presence/absence (C_g) data in 2016 and 2017 (Fig. 2).

When comparing the 47 models consisting in assessing variation in the relative abundance or presence of WCPis, obtained with the CB method, in relation to environmental conditions at count stations and sessions, top ranked models included PC1, PC2, meteorological conditions, and time of day (Table 5A). However, only PC2 was meaningful and positively associated to both the presence and the relative abundance of the species, according to the full-model averaging procedure ($\bar{\beta}_{PC2}$ [85% CI] = 0.188 [0.040; 0.525] and

Table 3 Model selection results for comparing detection methods, for (A) the WCPi and (B) the SNPi. No habitat parameters are used for *P. squamosa* because all transects are in homogeneous habitat. Only models having $\Delta AIC_c < 2$ are listed. Other models are in Supplementary materials Table S5

	Response	Models	<i>k</i>	$-2\ln L$	ΔAIC_c	w_i
(A)	PA	DM + DM:PC2 ^a	6	-273.204	0.000	0.436
		Full	12	-271.283	8.372	0.007
		Null	3	-283.860	15.256	-0.000
	RA	DM + DM:PC2 ^b	6	-405.638	0.000	0.265
		DM + DM:PC2 + DM:W	8	-404.175	1.129	0.151
		DM	4	-408.613	1.909	0.102
		Full	12	-402.576	6.090	0.013
		Null	3	-423.577	29.821	-0.000
		DM	4	-408.613	1.909	0.102
(B)	PA	DM ^c	4	-237.655	0.000	0.577
		DM + DM:W	6	-236.415	1.613	0.257
		Full	8	-236.150	5.213	0.043
		Null	3	-248.586	19.829	-0.000
	RA	DM + DM:Tot ^d	6	-342.999	0.000	0.304
		DM + DM:W	6	-343.082	0.166	0.280
		DM	4	-345.140	0.189	0.277
		Full	8	-341.726	1.582	0.138
		Null	3	-352.926	13.727	-0.000
		DM	4	-345.140	0.189	0.277
		Full	8	-341.726	1.582	0.138
		Null	3	-352.926	13.727	-0.000

Full models were (A) DM + PC1:DM + PC2:DM + W:DM + Tod:DM and (B) DM + W:DM + Tod

RA relative abundance, PA presence/absence, DM detection method (AV vs. CB), PC1 principal component 1, PC2 principal component 2 (see Table 2), W meteorological conditions (sunny/cloudy vs. overcast/scattered rains), Tod time of day (i.e., AM vs. PM), $-2\ln L$ the 2log likelihood, *k* number of model parameters, w_i Akaike weight

^aAIC_c = 558.486

^bAIC_c = 823.355

^cAIC_c = 483.394

^dAIC_c = 698.175

$\bar{\beta}_{PC2}$ [85% CI] = 0.220 [0.080; 0.481], respectively; Supplementary materials Table S8).

Scaly-naped pigeon

The order of presentation of intraspecific calls did not affect response to stimulus (intraspecific broadcasting played first: r_w [95% CI] = -0.203 [-0.379; -0.023], played second: r_w [95% CI] = -0.310 [-0.502; -0.107]). Therefore, subsequent analyses were performed without including the order of intraspecific call-broadcasting during the 2016 sampling scheme.

As for the WCPi, the CB method significantly improved the detection of pigeons over the AV one (McNemar change test, $\chi^2 = 24$, *df* = 1, $P < 0.001$). The influence of detection method and that of other variables was further assessed through the comparison of five models (Table 3 (B)). Based on the presence of SNPis at count stations, top ranked models included detection method and its interaction with meteorological conditions as model parameters. However, the full-averaged model procedure showed that detection method was the only meaningful parameter (Table 4 (B)). For this species as well, the CB method was positively associated with the presence of the species at count stations ($\bar{\beta}_{CB}$ [85% CI] = 1.564 [0.604;

2.525]; Table 4 (B)). Indeed, the probability of detection was higher when using the CB method than the AV one (AV [85% CI] = 0.096 [0.061; 0.149]; CB [85% CI] = 0.267 [0.193; 0.363]; Fig. 4C). When restricting the analysis to data obtained through the CB method, meteorological conditions and time of day failed to explain variations in the presence of the species across and within counts station (Table 5 (B) and Supplementary materials Table S8).

Based upon relative abundance, the detection method was the most important parameter, with its interaction with meteorological conditions and its interaction with time of day (Table 3 (B)). However, the time of day parameter was not meaningful according to the full-averaged model procedure, what led us to only consider the detection method and its interaction with meteorological conditions. These two parameters were in fact positively associated with the relative abundance at count stations ($\bar{\beta}_{CB}$ [85% CI] = 0.915 [0.182; 1.647] and $\bar{\beta}_{AV:W}$ [85% CI] = 0.370 [0.108; 1.663]; Table 4 (B)). The use of the CB method resulted in a higher relative abundance of SNPis compared to the AV one (AV [85% CI] = 0.149 [0.109; 0.203]; CB [85% CI] = 0.270 [0.203; 0.360]; Fig. 4D). The averaged predicted relative abundance was significantly higher in sunny conditions when using the AV method, whereas there was no such difference

when using the CB method (Fig. 5B). In addition, the effectiveness of the CB method was meaningful regardless of meteorological conditions. GLMMs aiming at assessing to what extent relative abundance could be associated with environmental features did not reveal meaningful parameters (Table 5 (B) and Supplementary materials Table S8).

The proportion of SNPis seen or heard was independent of the detection method (Fisher's test, $P = 1.000$, odds ratio [95% CI] = 1.023 [0.409; 2.456]), even when the interspecific CB was used (Fisher's test, $P = 0.700$; Fig. 6B). In addition, there was no difference in the efficiency of the CB method between intraspecific and interspecific calls (i.e., WCPi calls), in terms of presence data. However, the use of the CB method resulted in a significantly higher estimate of abundance when using intraspecific calls compared to when using interspecific calls (Fig. 2).

Discussion

Information on both the WCPi and the SNPi is scarce, and all studied populations so far are restricted to the Florida Keys, the Greater-Antilles or the US Virgin Islands (e.g., Strong et al. 1994; Rivera-Milán 1996; McNair 2008;

Fig. 4 Averaged probability of detection and relative abundance for A, B WCPis and C, D SNPis, respectively, predicted from the selected GLMMs, including all significant parameters for both relative abundance and presence/absence (Table 3). Error bars corresponds to the 85% CI

Rivera-Milán et al. 2014, 2016). No study so far had been conducted on populations located in the southern part of the distribution areas of these species. In the Lesser Antilles, the two species are exposed to hunting pressure, with little or no regulation (Hay 2008). In addition, population sizes or trends of the two species are not monitored and no standardized methods have been developed so far to that end (Hay 2008; Florida Fish and Wildlife Conservation Commission 2013). The CB method is of particular interest to improve the ability to detect birds when population density is low, and when dealing with shy and secretive species (Sutherland 2006; Fuller et al. 2012). Although numerous studies have pointed out its effectiveness for various bird species, such as waterbirds (Allen et al. 2004; Conway and Nadeau 2005; Conway and Gibbs 2005; Rehm and Baldassarre 2007), partridges (Kasprzykowski and Goławski 2009; Jakob et al. 2010; Warren et al. 2018;

Table 4 Averaged coefficient estimates (β_i), their standard error (SE) and the relative importance of parameters (RI) determined from the full-averaged model procedure performed upon models aiming at comparing detection methods (Table 3). (A) is for the WCPi and (B) for the SNPi. Due to the number of parameters, we listed parameters having RI > 0.30. Supplementary materials Table S6 presented all of them. In bold are significant effect (95% CI not overlapping zero), and see Table 3 for abbreviations

	Responses	Parameters i	β_i [95% CI]	SE	RI
(A)	PA	Intercept	-5.035 [-6.067; -4.004]	0.716	
		DM	1.284 [0.678; 1.890]	0.421	3.048
		DM(A/V):PC2	0.445 [0.246; 0.776]	0.243	1.836
		DM(C-B):PC2	0.267 [0.049; 0.564]	0.196	1.364
		DM(C-B):PC1	-0.145 [-1.082; 0.017]	0.309	0.468
		DM(A/V):PC1	-0.093 [-0.951; 0.264]	0.268	0.349
		DM(A/V):Tod	0.090 [-0.175; 1.009]	0.256	0.349
		RA	Intercept	-4.337 [-5.111; -3.562]	0.538
	DM		0.862 [0.506; 1.218]	0.247	3.487
	DM(A/V):PC2		0.243 [0.141; 0.561]	0.203	1.198
	DM(C-B):PC2		0.222 [0.120; 0.522]	0.188	1.176
	DM(A/V):W		-0.171 [-0.918; -0.013]	0.294	0.581
	DM(C-B):W		-0.087 [-0.546; 0.075]	0.173	0.500
	DM(C-B):PC1		-0.128 [-0.917; 0.006]	0.266	0.480
	DM(A/V):PC1		-0.106 [-0.867; 0.111]	0.247	0.428
	(B)	PA	Intercept	-0.915 [-1.496; -0.335]	0.403
DM			-.564 [-2.525; -0.604]	0.667	2.346
DM(A/V):W			0.234 [-0.203; 1.764]	0.517	0.453
DM(CB):W			-0.121 [-1.137; 0.328]	0.334	0.363
RA		Intercept	-1.412 [-1.805; -1.020]	0.272	
		DM	-0.915 [-1.647; -0.182]	0.509	1.798
		DM(A/V):W	0.370 [0.108; 1.663]	0.559	0.663
		DM(A/V):Tod	0.165 [-0.001; 0.747]	0.253	0.651
		DM(CB):Tod	0.104 [-0.037; 0.506]	0.171	0.607

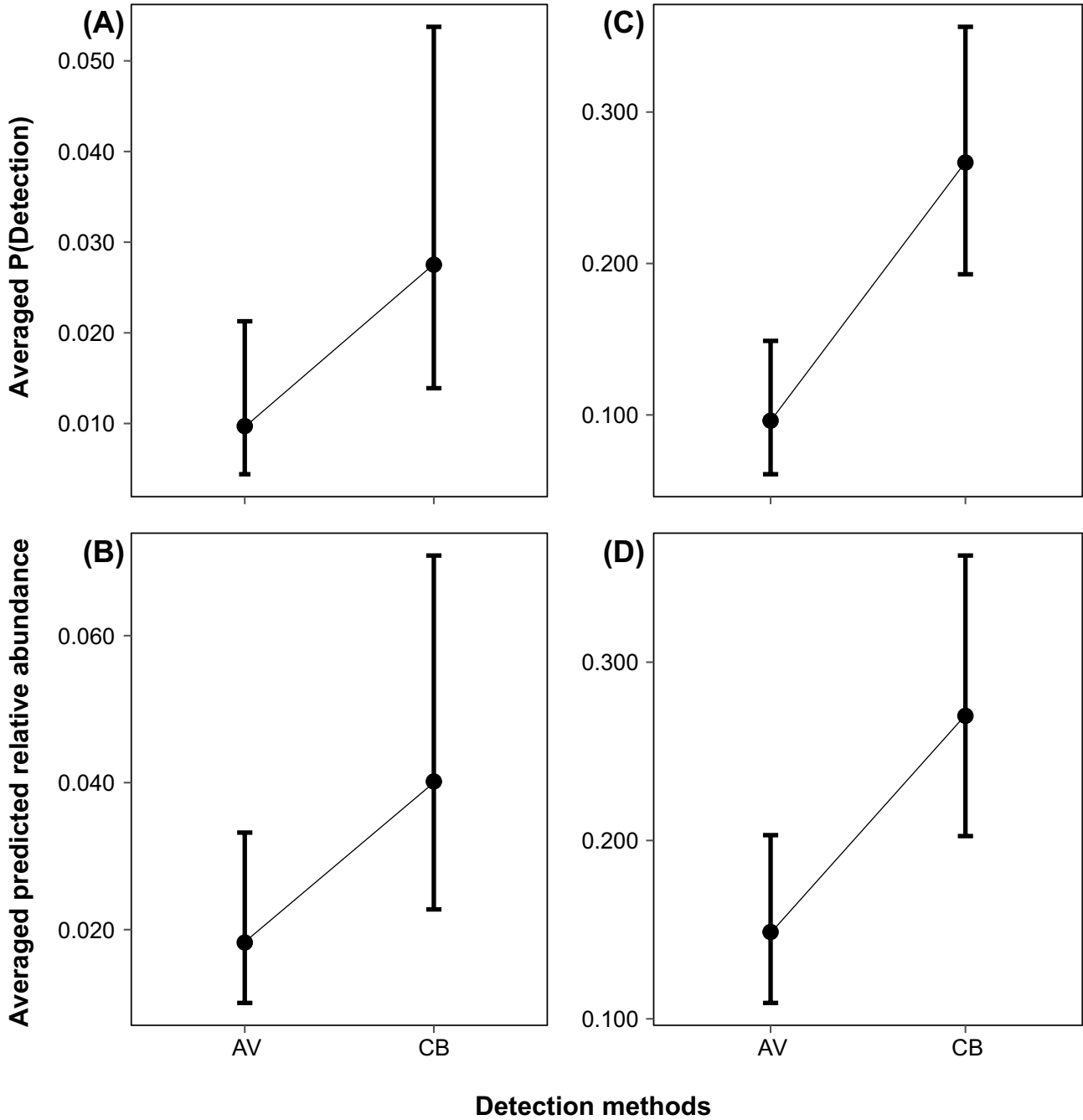
Variables are sorted by the relative importance



P. leucocephala



P. squamosa



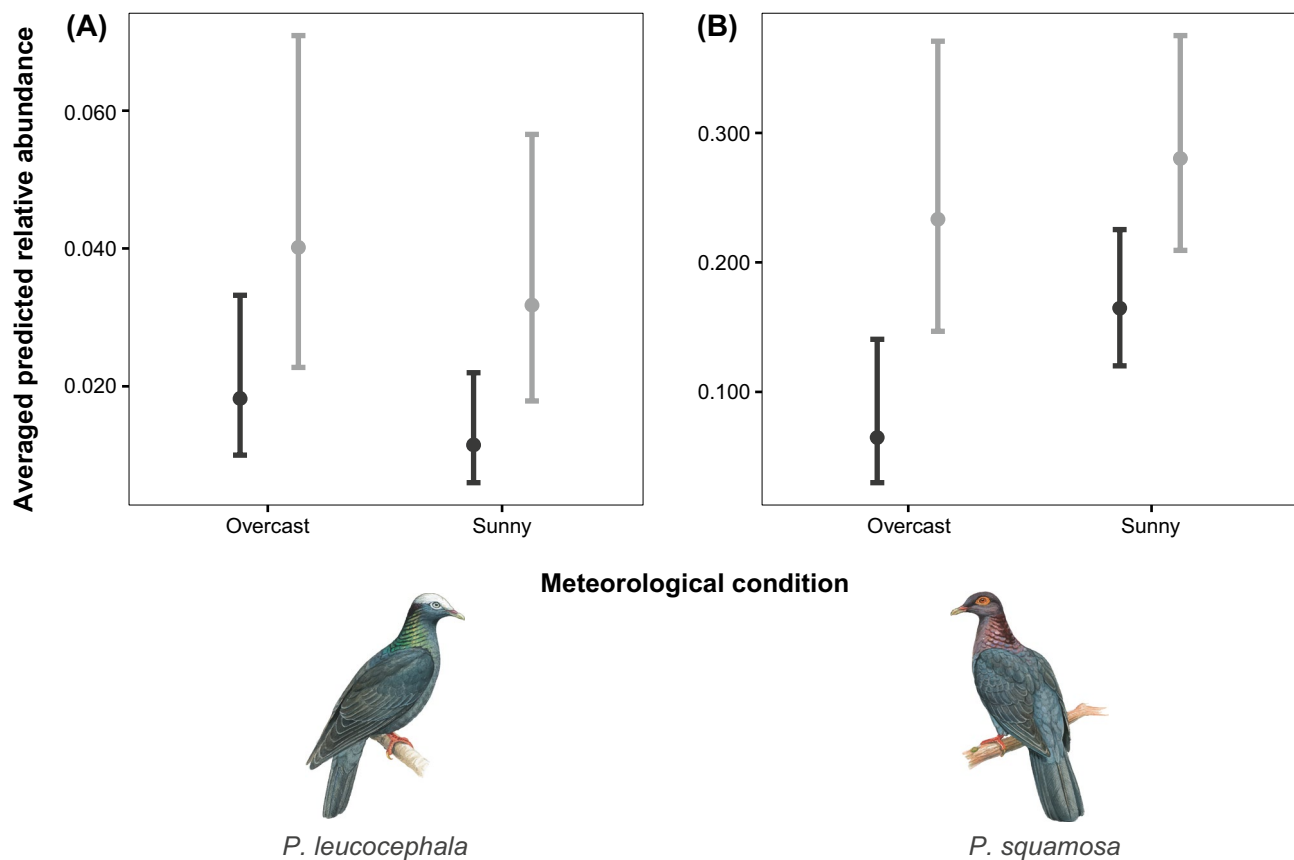


Fig. 5 Averaged relative abundance in relation meteorological conditions for **A** the WCPi and **B** the SNPi, when using AV (black dots and error bars) and CB (grey dots and error bars). GLMMs used

for estimating predicted values included all significant parameters (Table 3). Error bars corresponds to the 85% CI

Chiatante et al. 2020), birds of prey (Barnes et al. 2012; Clewley et al. 2016; van der Horst et al. 2019), passerine species (Boscolo et al. 2006; McNeil et al. 2014; Lewis et al. 2017; Broughton et al. 2018) and other forest birds species (Boscolo et al. 2006; Frieze et al. 2012; Figarski 2017), only one study concerned columbids so far (*P. fasciata fasciata*; Kirkpatrick et al. 2007). The present study is then the second to confirm the benefit of the use of this detection method for the monitoring of *Patagioenas* species. Indeed, our results showed that the CB method improved the probability of detection (as defined by Marsh and Sinclair 1989) through both reducing the problem of false absence and allowing to detect more individuals. This suggests that, for a similar amount of sampling effort, the mere use of the AV method may result in an underestimation of the relative abundance and spatial distribution of the WCPi and SNPi (Duren et al. 2011).

However, some cues of presence induced by the CB method may result in biased population estimates. For instance, during our study, some behavioural responses to CB, especially in WCPis (e.g., coming to perch or performing a scanning flight), did not occur, or more rarely, when using the AV method (e.g.,

St. Clair et al. 1998; Bélisle and Desrochers 2002; Summers and Buckland 2011). Such induced behaviours are not compatible with some methods of population size estimation, such as distance sampling which requires that individuals are detected at their initial location (Buckland et al. 2015; but see Summers and Buckland 2011; Fuller et al. 2012). They were not observed in the SNPi, possibly because the species was only detected in dense rain forests and rarely below the canopy, where its behaviour is more difficult to observe, which may also explain why this species was more often heard than seen, contrary to the WCPi (Brewster and Simons 2009). Therefore, further investigations on behavioural responses to broadcasted calls by SNPis should be carried out before using the method in conjunction with distance sampling to see whether similar behaviours to those exhibited by WCPi occur in this species.

In addition, the CB method may induce sex-biased estimates. Indeed, it is supposed to preferentially induce responses by males (Sutherland 2006). In the absence of both marked sexual dimorphism in both species and knowledge of population sex ratio, we were unable to check this assumption in the field. However, it is likely that both males and females reacted to the broadcasted calls. Indeed, there is

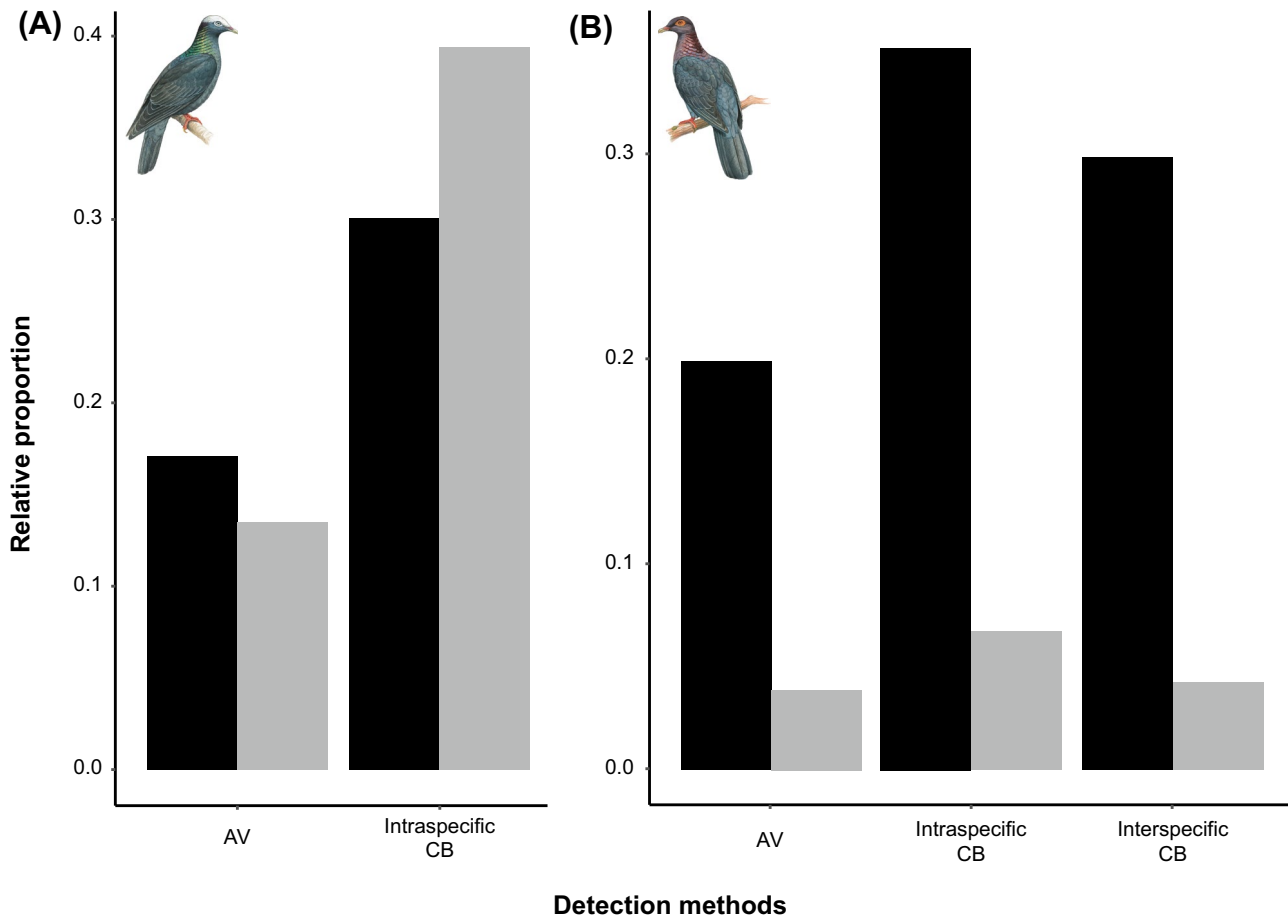


Fig. 6 Relative proportion of **A** WCPis and **B** SNPis according to whether pigeons were detected by visual (grey bars) or hearing cues (black bars), and according to the detection method

evidence that males of both species perform callings at the beginning of the reproductive season to signal their presence to females and attract them (Bancroft et al. 2020; Baptista et al. 2020), suggesting that females usually react to conspecific calls. In addition, female pigeons may respond to playback if they take an active part in defense of the pair territory, irrespective of the sex of intruders, as has been observed in other columbid species (Quinard and Cézilly 2012). In this respect, breeding status may also influence the effectiveness of the call-broadcast method. Response rates to broadcasted calls may be related to the timing of surveys within the breeding season (Kirkpatrick et al. 2005, 2007; Rehm and Baldassarre 2007). For the closely related *P. fasciata fasciata*, Kirkpatrick et al. (2007) suggested that the number of unmated males, which decreased over time during the reproduction season, might be positively correlated to the probability that one individual performed coo-calls in response to conspecific calls in the population. In the present study, we observed significant correlations between each pair of replications based upon the relative abundance of white-crowned and scaly-naped pigeons using

the CB method, suggesting that pigeons responded equally to call-broadcasting over time, possibly because the study period coincided with the first half of the breeding season. Indeed, one WCPi fledgling was observed in the swamp forest habitat during our survey when using CB. This confirms previous anecdotal observations by local ornithologists and confirms that the reproduction of this species, although rare, does occur in Guadeloupe (Delcroix et al. 2016).

For the two species, we recommend the systematic use of the CB method for monitoring population trends at several point count transects over years using the number of detections as an index of population density, especially in islands where they are at low density. The surveys could be performed in the morning, starting at sunrise, in the evening, finishing at sunset or both, since time of day had no significant influence in our surveys. The interspecific CB tended to be as effective as intraspecific CB, especially in terms of detection of species presence. This might be explained by the fact that the two species have evolved in sympatry in some islands, encouraging the recognition of interspecific calls in context of competition, mutual helping against predators or simply because they

Table 5 Model selection results to see in what extent the presence and relative abundance were associated with count stations features, for (A) the WCPis and (B) the SNPis. Models are based on data collected during intraspecific call-broadcast methods for both the relative abundance (RA) and the presence/absence (PA). Only models having $\Delta AIC_c < 2$ are listed. Other models are in Supplementary materials Table S7. See Table 3 for abbreviations

	Response	Models	k	$-2\ln L$	ΔAIC_c	w_i	
(A)	PA	PC2 ^a	4	-176.549	0.000	0.113	
		PC1 + PC2	5	-175.672	0.282	0.099	
		PC1	4	-176.986	0.873	0.073	
		PC2 + W	5	-176.290	1.518	0.053	
		Tod + PC2	5	-176.356	1.652	0.050	
		PC1 + PC2 + W	6	-175.411	1.806	0.046	
		Tod + PC1 + PC2	6	-175.479	1.941	0.043	
		Full	11	-174.556	10.439	0.001	
		Null	3	-178.175	1.221	0.062	
		RA	PC2 ^b	4	-272.788	0.000	0.085
			PC2 + W	5	-271.856	0.174	0.078
	PC1 + PC2		5	-272.094	0.649	0.061	
	PC1 + PC2 + W		6	-271.157	0.820	0.056	
	Tod + PC2		5	-272.414	1.291	0.044	
	(B)	PA	Tod + PC2 + W	6	-271.443	1.393	0.042
			Tod + PC1 + PC2	6	-271.720	1.948	0.032
Full			11	-269.218	7.286	0.002	
RA		Null	3	-274.909	2.213	0.028	
		Null ^c	3	-149.227	0.000	0.462	
		W	4	-148.821	1.255	0.246	
		Null ^d	3	-216.252	0.000	0.373	
		Tod	4	-215.420	0.404	0.305	
		W	4	-216.012	1.588	0.168	

Full models were PC1 + PC2 + W + Tod + PC1: Tod + PC2: Tod + PC1: W + PC2: W for (A) and W + Tod + W: Tod for (B)

^a $AIC_c = 361.174$

^b $AIC_c = 533.650$

^c $AIC_c = 304.556$

^d $AIC_c = 438.606$

confuse their calls (Møller 1992), which are very similar. For instance, the two species share same nest sites in US Virgin Islands (McNair 2008). However, we recommend to broadcast intraspecific song to monitor population trends. In addition, in order to document spatial or temporal variation in relative abundance, environmental conditions during count events should be taken into account, by considering meteorological conditions and determining vegetation patterns at each count station between each year of survey, especially where natural vegetation landcover is subject to rapid changes due to human activities. To do so, it is possible to follow the same methodology used in this study for characterising vegetation patterns of each count stations, by using Google Earth platform, which regularly updates their aerial photographs. The second option would require more skills in remote sensing technique and would consist in using these methods in addition to geographical information system (GIS) and Google Earth Engine platform to define landcover and analyse changes over years, as explained by Sidhu et al. (2018). Such additional variables might be important as our study showed that the effectiveness

of the CB method may be affected by vegetation type and meteorological conditions, suggesting that a change in terms of number of detections might be the result of a decrease of CB effectiveness due to a change of vegetation in count stations or different meteorological condition over surveys, but not of a change of population density. Indeed, although such effects appeared to be weak in our results, they suggested a lower efficiency of the CB method in swamp forests and in overcast/scattered rain meteorological condition for the WCPi. This might be explained by the fact that swamp forests are essentially used by pigeons as a corridor connecting the nesting (i.e., mangroves or islets off the coast) and foraging habitats (i.e., humid evergreen and semi-deciduous hardwood dry forests; Gibbs et al. 2001; Bancroft et al. 2020). In addition, both the propagation of calls (from loudspeaker to birds and from birds to the observer, Schieck 1997) and the activity of individuals might be reduced under overcast/scattered rain conditions (Robbins 1981b; Buckland et al. 2005; Overton et al. 2005).

As our methodology was initially designed to compare two detection methods, the relevance of our data to habitat selectivity and the spatial distribution of the two species in Guadeloupe is limited. Nevertheless, the two species were never observed together at a given count station, suggesting that they do not occupy the same places in Guadeloupe, at least for the period of the survey. In addition, vegetation patterns at the count stations associated to each species were in accordance with what has been observed in other Caribbean islands. The WCPi was associated with coastal areas: coastal flooded forests and islets off the coast dominated by mangrove and swamp forest, which are usually used as breeding sites, and humid evergreen and semi-deciduous hardwood dry forests in mangrove hinterland, usually used for foraging (Wiley and Wiley 1979; Gibbs et al. 2001; Bancroft et al. 2020). In contrast, the SNPi is more of an upland species, occupying primary and secondary rainforests (Gibbs et al. 2001; Baptista et al. 2020). However, the present study did not report local co-occurrence of the two species in Guadeloupe, contrary to other places where they can occasionally be observed together (Wiley and Wiley 1979; Gibbs et al. 2001; Bancroft et al. 2020).

Management implications

The present study suggests that both species occur at low density in Guadeloupe, compared to what is observed in the Greater Antilles (Rivera-Milán et al. 2014, 2016), even though the SNPi seems to occur at higher density than the WCPi. In addition, we showed that the CB method provides an easy-to-use and standardized tool to estimate population trends across the spatial distribution area of the two species, which might be of use in the future for the monitoring of relative abundance of the two species through time, especially in relation to threats faced by the two species such as habitat degradation, local hunting pressure, climate change and the impact of invasive predators, parasites or competitors (Baptista et al. 2020; Bancroft et al. 2020). However, both species are considered vagrant, easily moving across their distribution area (Wiley 1979; Wiley and Wiley 1979; Rivera-Milán 1992; Bancroft et al. 2000, 2020; Gibbs et al. 2001; Strong and Johnson 2001; Florida Fish and Wildlife Conservation Commission 2013; Baptista et al. 2020). In addition, recent genetic evidence suggests that the SNPi consists in a single panmictic population (Cambrone et al. 2021), whereas corresponding information is still missing for the WCPi. Therefore, local fluctuations in the relative abundance of both species could be a consequence of local demographic processes or irregular movements of individuals between islands, induced by different factors, such as a sudden drop in resources availability, particularly following extreme climatic events such as hurricanes. Indeed, Perdomo-Velázquez et al. (2017) have shown that species

feeding on plant products are more impacted by hurricanes than more generalist or insectivorous ones; hence, SNPis and WCPis may be more prone to move both within and between islands following natural perturbations (Wunderle 1995; Campos-Cerqueira and Aide 2021). Therefore, further investigations on movements of individuals within and between islands are important to better ascertain population trends and identify factors influencing population size and movements. Such investigations, combining population genetics (e.g., Cambrone et al. 2021 for the SNPis) and satellite tracking of individuals would also directly contribute to determine the more suitable management units for the two species.

More broadly, although columbid species are particularly threatened (Devenish-Nelson et al. 2019), especially those living in insular areas (Walker 2007), this group is one of the least studied avian group in ecology and conservation biology. In general, columbid species play however an important ecological role in island ecosystems through their capacity to disperse seeds over long distances (Shanahan et al. 2001; Bucher and Bocco 2009). The relevance of the CB method to other species of pigeons and doves therefore deserves further attention, especially to document population trends and habitat use in elusive species of conservation interest.

Supplementary information The online version contains supplementary material available at <https://doi.org/10.1007/s10344-021-01507-0>.

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Author contribution F.C., E.B. and C.C. conceived the project, design and experiments. C.C. performed the experiments. C.C. and F.C. analysed the data. F.C., E.B. and C.C. wrote and edited the paper.

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Data availability The datasets analysed during the current study are available from the corresponding author on reasonable request.

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