

JOURNAL OF AVIAN BIOLOGY

Article

Trophic strategies of two sympatric endemic pigeons in insular ecosystems: a framework for understanding spatiotemporal frugivory interactions

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Journal of Avian Biology

2021: e02803

doi: 10.1111/jav.02803

Subject Editor: Tomas Carlo

Editor-in-Chief: Jan-Åke Nilsson

Accepted 21 July 2021



Pigeons are considered to play key ecological roles in frugivory and seed dispersal. They have colonised numerous oceanic islands and diversified into several species in sympatry. How these species coexist in similar niches is poorly understood although dietary separation is among the mechanisms suggested to avoid trophic overlap. We investigated the trophic ecology of the two endemic *Columba* species co-occurring in the laurel forest and thermosclerophyllous relicts of two of the Canary Islands. This study includes diet description in spatiotemporal terms, its relationship with fruit availability and seed treatment in 10 study areas established on La Palma and La Gomera. We used non-invasive DNA analysis to identify the faeces of the two congeneric species and microhistological methods to examine their diets. The degree of trophic overlap was evaluated by niche similarity and breadth indices. Molecular faecal sampling determined the spatiotemporal distribution of both pigeons to identify their areas of coexistence. These frugivorous pigeons' diets did not differ concerning the main plant species, but they diverged quantitatively in the proportions and parts of plants consumed. Lauraceae fruits were their staple foods although Rhamnaceae and some Fabaceae and Solanaceae were also important. Both pigeons showed selective preferences for some fruits. Significant spatiotemporal variations in their diets were observed along with a general tendency to increase fruit intake at its ripening times. Our results suggest that different trophic strategies facilitate the coexistence of these frugivorous columbids. These pigeons act as seed dispersers and/or predators depending on seed features (size and hardness), and this may have valuable implications for their conservation.

Keywords: Canary Islands, *Columba bollii*, *Columba junoniae*, diet, ecological role, seed predation and dispersal

Introduction

Oceanic islands are widely known to be valuable model systems for evolutionary and ecological studies (Gillespie 2007). Their biota is the result of overseas colonisation and local diversification, which are influenced by diverse factors such as organismal



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traits and the islands' geographical and environmental settings (Paulay 1994, Whittaker 1998, Graham et al. 2017). High levels of endemism, specialisation, relictualism and extinction characterise these faunas and floras (Losos and Ricklefs 2009, Cartwright 2019).

Pigeons, although distributed worldwide, have considerably diversified on islands (Baptista et al. 1997, Lapedra et al. 2013). Their high dispersal abilities, linked to other behavioural and physiological adaptations, may have additionally contributed to their wide distribution, leading to several species in sympatry (Steadman 1997, Cibois et al. 2017). One example is that of Bolle's *Columba bollii* and white-tailed *C. junoniae* laurel pigeons, two endemic frugivorous species co-occurring throughout most of their distribution range in the laurel forests of the western Canary Islands (Martín et al. 2000). Nevertheless, while *C. bollii* is found almost exclusively in this forest, *C. junoniae* preferentially occupies the steepest areas of its lower limit, in addition to remnants of thermosclerophyllous 'thermophilous' woodland and even pine forest (Martín et al. 2000, Nogales et al. 2009). This suggests that the now relictual thermosclerophyllous woodland was the ancestral habitat of *C. junoniae* (Martín et al. 2000). The decline and fragmentation of the insular arboreal formations were due mainly to human activities (del Arco et al. 2010), which probably led these pigeons to co-occur in the remaining present-day secondary habitats (Martín et al. 2000). How species with similar niches coexist is a highly complex and heterogeneous problem in ecology (Gordon 2000). However, according to Pianka (1969), variations in any of the three basic niche dimensions (spatial, temporal and dietary) would imply overlap avoidance (Gause 1934).

The spatial and temporal segregation between *C. bollii* and *C. junoniae* populations is not well understood. However, *C. bollii* appears to be more gregarious, nomadic and with a larger population size at a regional level than *C. junoniae*. They both show spatiotemporal fluctuations in their populations (Martín and Lorenzo 2001, Hernández 2007a, b). Both pigeons seem to breed throughout the year although with a maximum nesting period in March–May for *C. bollii* and April–July for *C. junoniae* (Martín et al. 2000). Regarding dietary composition, occasional field observations showed that they include a diversity of flowers and leaf buds in their diets, like other frugivorous columbids (Emmerson 1985). However, the importance of each food item should be evaluated by more reliable methods such as non-invasive faecal analysis (Ralph et al. 1985). In any case, when congeneric species co-occur as in our study, a preliminary faecal DNA analysis would be required to determine the target species involved (Marrero et al. 2008).

Given that food resources are fundamental for animals, trophic ecology research is considered a central theme in the coexistence of species (Sartore and Reis 2013, Lanszki et al. 2020). Indeed, the trophic coexistence strategies used by some sympatric frugivorous species on islands have been described, mainly mammals such as bats and primates (Trehwella et al. 2001, Wright et al. 2011, Hadi et al. 2012).

Here, we focussed on this issue in two sympatric frugivorous columbids inhabiting native forests.

The evergreen laurel forest partly evolved from pre-adapted plant taxa from the Mediterranean, Macaronesia itself, and the tropics during Plio-/Pleistocene and late Miocene (Kondraskov et al. 2015). Lauraceae is the most representative plant family. In this forest, around 15 fleshy-fruited arboreal species display an endozoochorous (mostly ornithochorous) syndrome (Arteaga et al. 2006). The thermosclerophyllous woodland is a diverse series of plant communities dominated by one or several arboreal species of Mediterranean-North African affinities (Fernández-Palacios et al. 2008). In addition to the endemic pigeons (the largest in body size), blackbird *Turdus merula* and European robin *Erithacus rubecula* are the main frugivores in the laurel forest (Martín et al. 2000, Nogales et al. 2016). It is important to note that frugivorous pigeons are strongly involved in plant colonisation and restoration. Through defecation or regurgitation of seeds, they act as important seed dispersal vectors (Corlett and Hau 2000). Therefore, understanding the ecological roles of these columbids will aid in conservation efforts.

In this study, we quantified the diet of both pigeons in well-conserved native forests located on two islands of the Canary archipelago (La Palma and La Gomera). We also evaluate their trophic coexistence and describe their spatiotemporal frugivory strategies. Thus, the main aims were to 1) study the diet and respective feeding patterns of each pigeon species by microhistological analysis after previously using non-invasive DNA faecal analysis, 2) assess the spatiotemporal patterns of their diets and evaluate if their diet composition is influenced by fruit availability, 3) evaluate the degree of trophic overlap to understand how these two large-bodied frugivorous species coexist in insular forests and 4) examine the ecological roles of both species as seed dispersers/predators.

Material and methods

Study areas

This study was conducted in well-conserved native forests on La Palma (708 km²) and La Gomera (369 km²), islands harbouring the highest numbers of pigeons of these two species in the Canary archipelago (Martín et al. 2000) (Fig. 1). On La Palma, fieldwork was carried out from January 2006 to January 2007 in Barranco del Agua, a deep ravine occupying 74.6 ha in the northeast of the island. The two main habitats for these pigeons are found here: 1) a fragmented thermosclerophyllous woodland at Los Aguales (100 m a.s.l.) and 2) a dense humid laurel forest at Espigón Atravesado (750 m a.s.l.), within the Natural Park of Las Nieves. On La Gomera, the study was undertaken from May 2007 to May 2008 in eight laurel forest areas named La Hoya del Tión, Meriga, Los Pajaritos, Hierba Huerto, Los Sanguinos, Cañada de Don Pedro, Ancón Negro and La Piedra Encantada, within Garajonay National Park. The differences in orientation,

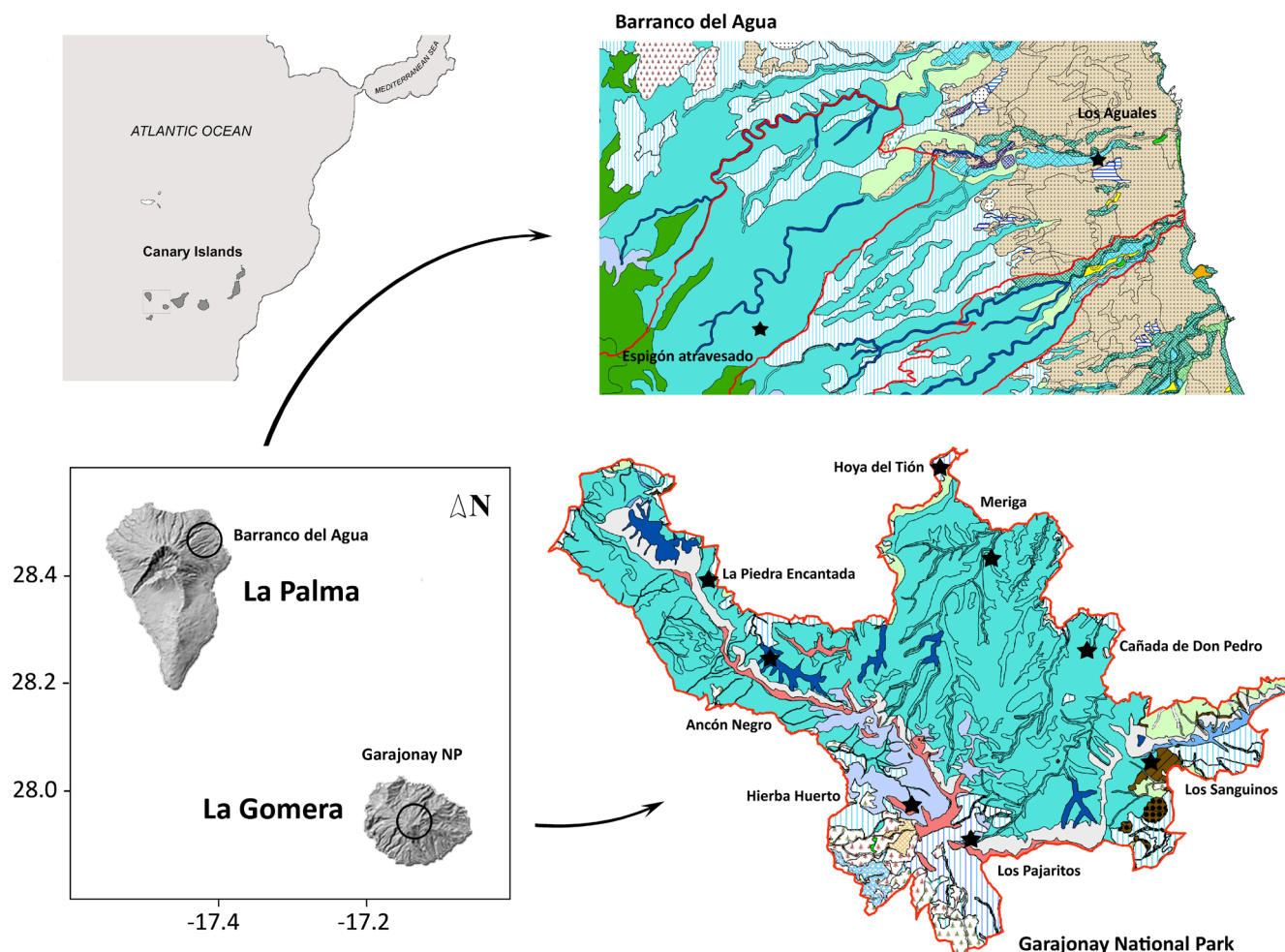


Figure 1. Geographic location of the study areas.

elevation or slope of the terrain determine the variation in plant composition within these study areas.

Faecal sampling and molecular identification

Pigeon faecal samples were collected seasonally using translucent plastic sheets placed below perches around natural watering points in each study area (Marrero 2009, Hernández-Dávila et al. 2014). In each season of the year (spring: March–May, summer: June–August, autumn: September–November and winter: December–February), all study areas were visited twice. The plastic sheets were cleaned for the next season once the fresh faecal samples were removed. A maximum of 20 independent faecal samples/season/study area (to reduce pseudo-replication) were individually labelled and stored at -20°C .

Faecal samples of *C. bollii* and *C. junoniae* are similar in morphology and composition but distinguishable from those of other animals. Species-level assignment was based on improved DNA extraction from rectal mucosa cells shed on the faeces externally (to reduce PCR inhibition) and an RFLP test on a short sequence (196–197 base pairs) of

the control region of mtDNA (Marrero et al. 2008, 2009). This faecal genetic analysis also provided information about pigeon occurrence and habitat use. It can be the basis for abundance estimates in the study areas throughout the year (Nogales et al. 2009).

Diet analysis

Once the samples were identified at the species level by DNA, their contents were analysed by microhistological methods. Based on the identification of epidermal tissues, this is a common tool used for many wildlife species (Herrera 1998, Hewitt and Messmer 2000, Scasta et al. 2016). Oliveira et al. (2002) applied it to study the seasonal diet variation of the endemic Madeira laurel pigeon (*C. trocaz*), the closest relative of *C. bollii* (Dourado et al. 2014). Feeding tests with *C. trocaz* in captivity confirmed this technique's high accuracy level (Oliveira et al. 2002).

Each sample was disaggregated in about 500 μl distilled water in a petri dish, and from this mixture, two drops were examined under a microscope at 10 \times magnification. Plant epidermal fragments from 10 separate optical fields per slide

were identified using photomicrographs, camera lucida drawings and microhistological keys prepared from permanent reference samples (Marrero and Nogales 2005). Occasionally, higher magnifications were used to facilitate identification. This procedure was repeated five times, analysing 50 optical fields per faecal sample. Material recognisable at macroscopic level, such as whole plant leaves and seeds, was initially identified by comparison with herbarium specimens and later microscopically verified when necessary. As a prior approach, the state in which seeds were found in the faeces (intact or damaged) was recorded per sample to determine the role of pigeons in seed dispersal.

Fruit availability

The composition, phenology and relative abundance of the most common tree species were evaluated to establish the spatiotemporal relationship between fleshy fruit availability and consumption by pigeons. Data were collected by walking along a 500 m transect in each of the 10 study areas, twice per season. All trees with a diameter at breast height (DHB) threshold >10 cm located within 2 m from one side of the transect were monitored using binoculars. The presence/absence of flowers and fruits and the number of ripe fruits of each tree species per hectare estimated in the tree canopies were noted, for phenological characterisation of each habitat. Although the results obtained in this type of sampling do not indicate the actual fruit availability in the habitat (Blake et al. 1990), they provide a rough estimate of their relative abundance.

Data analysis

Dietary data are presented in two ways: 1) the percentage of all optical fields analysed that contained a particular species (total percentage), 2) the mean \pm SE number of optical fields containing a particular species per faecal sample, calculated only from those samples in which the species was present (mean percentage). Evaluated by Pearson's correlation coefficient, the first measure indicates the relative importance of a plant species in the diet of these pigeon populations. Using a correlation matrix, this statistical test explored the association between the simple occurrence percentage in each faecal sample and the total percentage of optical fields in the sample set (Oliveira et al. 2002). The second measure shows a species' prevalence in the diets of individuals that consumed it.

Categorical data analysis was conducted to test for spatiotemporal differences in the occurrence of particular plant items in the faecal samples. Before statistical analyses, the total percentages of optical fields with each plant species in the diet (dependent variables) were arcsine transformed to achieve normality. The relationship between diet composition (response variables) and the seasons and study areas/islands, and all interactions between them (fixed factors), were subjected to multivariable analysis of variance (MANOVA) for each pigeon species. The spatiotemporal variation of the main plant species in the diet was evaluated

with a one-way analysis of variance. The influence of these two factors (seasons and study areas/islands) on the diet was assessed using separate ANOVA type I (applying the posteriori Scheffé test for comparisons) and principal component analysis (PCA). Student's post-hoc t-tests were conducted from results generated from univariate ANOVA. In addition, hierarchical clustering analysis compared the diet between study areas on each island, using the inter-group linkage method and the squared Euclidean distance interval. The likelihood ratio test was applied to examine differences in consumption of the fruits, leaves and flowers of each plant species by each pigeon species. The Student's t-test compared diets of the two pigeon species for each independent sample. A simple regression analysis assessed the seasonal relationship between the percentage of fruits in optical fields and fruit availability.

The Manly–Chesson index was calculated to evaluate food preferences (Manly et al. 1993), using the proportion of a fruit species in the diet and its availability on the trees. Values ranged from $<1/k$ (food avoidance) to $>1/k$ (food preference), with k food types available. Diet similarity or overlap between the two pigeon species was evaluated using the Morisita index while niche breadth was assessed using standardised Levins' and Hurlbert's niche-breadth indices (Krebs 1989). Values ranged from 0 (low similarity and dietary specialisation) to 1 (high similarity and broad diet). Levins' niche breadth considers all kinds of food items (fruits, leaves and flowers) while Hurlbert's refers only to fruits (available and consumed) and incorporates the proportion of the main five fruit-bearing tree species available during each season (Krebs 1989). All the statistical analyses were carried out using the SPSS 27.0 (SPSS Inc. 2020) and Canoco 4.5 (Ter Braak and Šmilauer 2002) programs.

Results

From the molecular analysis, a total of 345 faecal samples were identified for La Palma, 200 (58%) for *C. bollii* and 145 (42%) for *C. junoniae*. In contrast, for La Gomera, 200 (78.1%) of 256 identified samples were assigned to *C. bollii* and 56 (21.9%) to *C. junoniae*. *Columba bollii* was detected in all the study areas on La Palma, with a significantly greater abundance in laurel forest, $G_1 = 101.090$, $p < 0.001$, and on La Gomera. Otherwise, *C. junoniae* was significantly detected in the thermosclerophyllous woodland areas of La Palma while it was present in only five of the eight laurel forest study areas on La Gomera. Thus, faecal sampling confirmed co-occurrence of the two pigeon species in seven of the ten study areas. Nevertheless, seasonal population fluctuations of both pigeons were also detected.

The dietary content of the identified faeces was analysed by examining 30 050 optical fields, of which 17 250 (57.40%) were from La Palma samples and 12 800 (42.60%) from La Gomera. Pearson's correlation coefficient indicated that faecal analysis was representative of the diet ($r_p = 0.985$; $p < 0.001$ for *C. bollii*, and $r_p = 0.964$; $p < 0.001$ for *C. junoniae*).

Diet of Bolle's laurel pigeon

Its diet included over 25 plant species, but the fruits of *Laurus nobilis* were the fundamental plant resource. This pigeon is predominantly frugivorous, but includes leaves of trees and shrubs (Fig. 2). Invertebrates from orders Araneae, Coleoptera, Julida, Acari, Opiliones and Hymenoptera and Class Chilopoda appear to be a limited resource. At least 84% of the faecal samples contained only one or two plant species.

Diet composition (Supporting information) showed significant spatiotemporal variation between islands and seasons for all plant species (Wilks' Lambda=70.813, $p < 0.001$). In winter and spring, *L. nobilis* fruits were crucial (56% of the total optical fields), whereas, in summer and autumn, there was high consumption of *Rhamnus glandulosa* (18.4%) (Supporting information). Figure 3 shows that this variation was based on fluctuating ingestion of fruits, leaves and flowers ($G_6=912.304$; $p < 0.001$). Fruits were important all year round, but less so when *C. bollii* ate more leaves (mainly those of *R. glandulosa* – 15.2% and *Ilex canariensis* – 12.8%) in summer and autumn. In general, it consumed a higher proportion of leaves of *R. glandulosa* ($G_1=1861.720$; $p < 0.001$) and *I. canariensis* ($G_1=110.178$; $p=0.057$) than their fruits, but preferred *Bituminaria bituminosa* seeds to its leaves ($G_1=124.075$; $p < 0.001$).

Columba bollii diet was relatively similar in composition on both islands although more diverse on La Palma (with about 24 plant species) than on La Gomera (14) (Supporting information). Furthermore, spatiotemporal variation in diet was observed among islands (Wilks' Lambda=3.054, $p < 0.001$ for La Palma and 2.194, $p < 0.001$ for La Gomera) and between study areas within each island, with significant differences for both La Palma (Supporting information) and La Gomera. The hierarchical clustering analysis among the eight study areas of La Gomera distinguished the diet similarity into two groups: 1) areas located in margin areas and 2) areas within the laurel forest (Supporting information). The PCA showed that diet was similar in spring and winter, highlighting *L. nobilis* and more diverse in autumn and summer (Supporting information).

Diet of the white-tailed laurel pigeon

Its basically frugivorous diet (Supporting information) was composed of at least 21 plant species, with *B. bituminosa*, *Apollonias barbuja*, *R. glandulosa* and some unidentified Solanaceae species as basic food items (Fig. 2). About 72% of faecal samples contained plant remains from only one or two species.

Spatiotemporal study of the diet showed significant differences (Wilks' Lambda=2.809; $p=0.001$). In general,

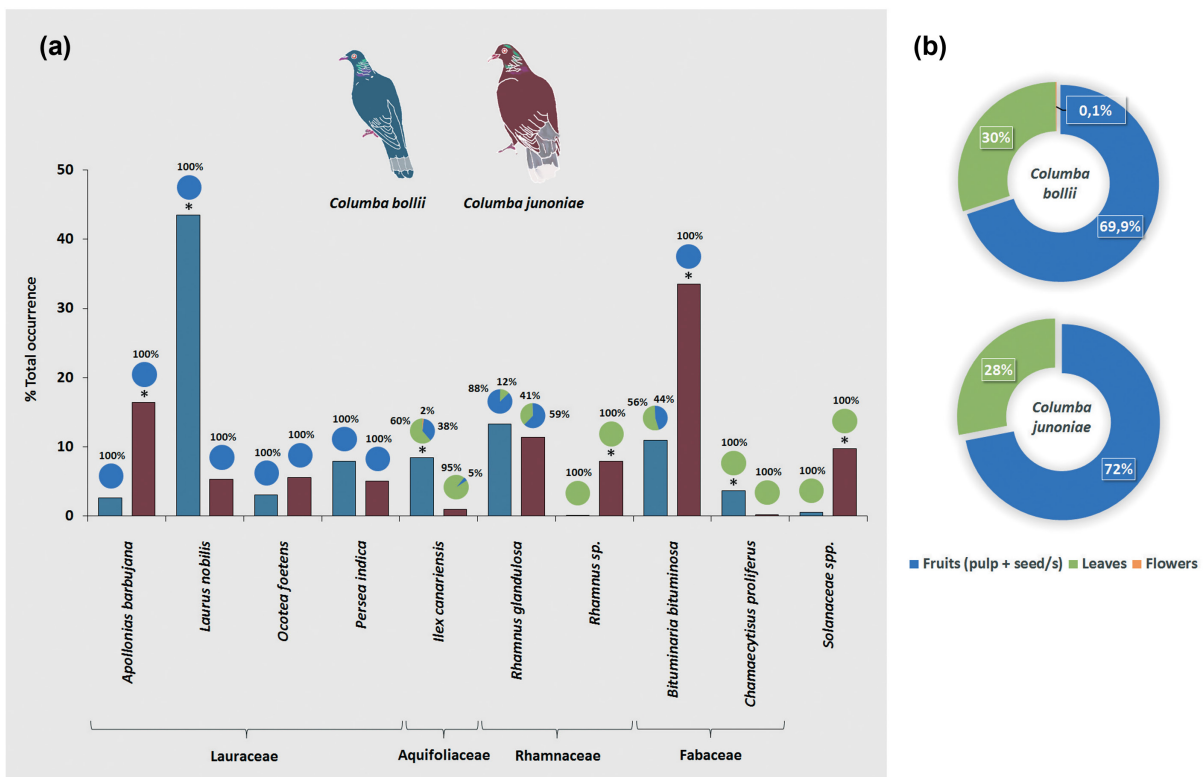


Figure 2. Diet composition of Bolle's laurel pigeon (*Columba bollii*) and white-tailed laurel pigeon (*C. junoniae*). (a) Main food items in the diet of the pigeon species (bars), and percentage of fruits, leaves and flowers (circles) from each plant species consumed. (b) Total percentage of fruits, leaves and flowers in the diet of the pigeon species. Asterisks (*) indicate the significant p-values of the Student's t-test for independent samples.

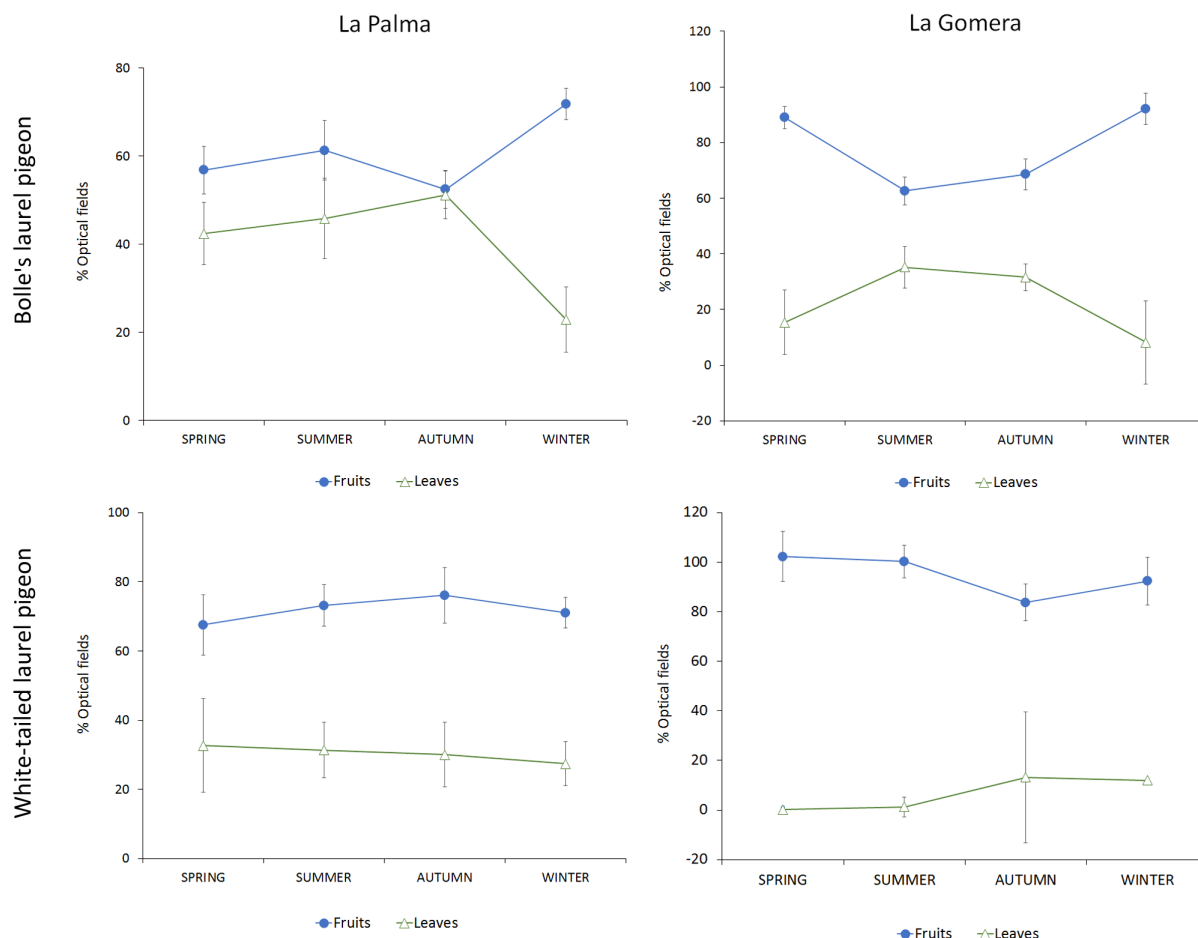


Figure 3. Seasonal variation in the presence of fruits (blue circles) and leaves (green triangles) in the diet of Bolle's and white-tailed laurel pigeons on La Palma and La Gomera. The dots represent the mean and standard deviation of each species' percentage of appearance in the 50 optical fields analysed per sample.

fruits were significantly more consumed than leaves throughout the year ($G_3=38.570$, $p < 0.001$) as shown in Fig. 3. *Columba junoniae* diet was based on the fruits of *B. bituminosa* (33.5% of total optical fields) during all seasons of the year (Supporting information). It consumed more leaves of *I. canariensis* than its fruits ($G_1=42.623$, $p < 0.001$).

Diet composition involved at least 21 plant species on La Palma and only about eight on La Gomera (Supporting information). It was influenced by spatiotemporal variations between islands (Wilks' Lambda=9.952, $p < 0.001$ for La Palma and 5.112, $p < 0.001$ for La Gomera) and study areas within each island, with significant differences for both La Palma (Supporting information) and La Gomera. Although the small sample size of *C. junoniae* did not permit clustering analysis, the PCA showed more *R. glandulosa* in summer, and more *A. barbujana*, *L. nobilis* and *Ocotea foetens* in autumn and winter on La Gomera (Supporting information).

Fruit availability and consumption

At least 12 fleshy-fruited tree species were recorded along transects established in the study areas. In general, *L. nobilis*,

I. canariensis and *Morella faya* were the most abundant species in the forests (Supporting information). Fleshy fruits were produced during most of the year. A general tendency was observed in both pigeons to increase fruit intake at its ripening times (Fig. 4). The comparison of phenological data and diets showed that in general, pigeons consumed fruits and/or leaves of tree species present in each study area. However, some species like *P. indica*, *O. foetens* and *R. glandulosa* were found in samples collected in study areas (mainly on laurel forest edges) where these species were not recorded. The standardised Hurlbert's index indicated that *C. bollii* fed within a broader niche breadth than *C. junoniae* in terms of fruit abundance (Table 1).

Comparison of the two pigeons' diet

The diets of the endemic pigeons were quantitatively different. *Columba bollii* preferentially consumed *L. nobilis*, *I. canariensis* and *Chamaecytisus proliferus* while *C. junoniae* did so with *A. barbujana*, *B. bituminosa* and Solanaceae spp. These significant differences were also observed when the parameter 'island' was included in the analysis. Furthermore,

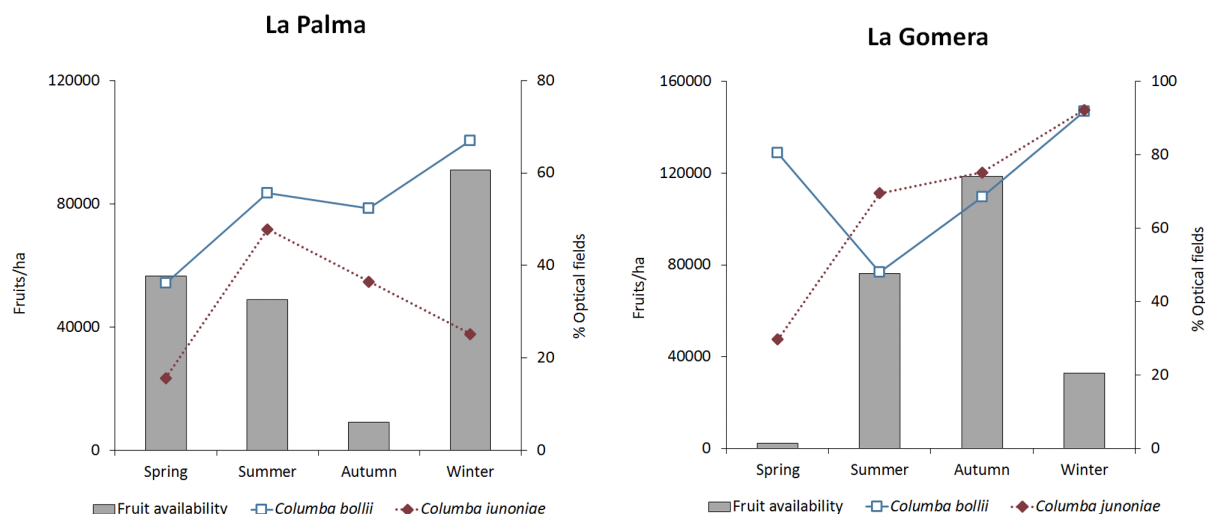


Figure 4. Relationship between fruit availability (bars) and percentage of fruits in the 50 optical fields analysed per sample for Bolle's (white squares) and white-tailed laurel pigeon (black diamonds) in the Canary Islands.

P. indica was ingested more often by *C. bollii* and *O. foetens* by *C. junoniae* on La Gomera (Table 2). The Manly–Chesson index indicated that fruits of *O. foetens* in La Palma and *A. barbujana* in La Gomera were preferred by both pigeon species (Supporting information).

The similarity between diet compositions of the two laurel pigeons can be considered as a medium in level, according to their Morisita's index (Table 1). In any case, Levin's index indicates that both diets tend towards specialisation, whereby in general there are few central species in their composition (Table 1).

Seeds in the faecal contents

In general, small hard seeds like those of *I. canariensis*, *R. glandulosa* and *M. faya* were found apparently intact in the faeces, whereas most seeds of *B. bituminosa* and Lauraceae (larger and softer) were utterly destroyed. However, large seeds were not always destroyed, like some from *L. nobilis* and *P. indica* (Table 3).

Discussion

Faecal DNA sampling revealed the co-occurrence areas of the two pigeon species and the generally low abundance of *C. junoniae* with respect to *C. bollii*, its smaller distribution range in the study areas and its preferential presence in

forest edges and thermosclerophyllous woodland. The non-invasive genetic use of faecal samples, as an efficient method to seasonally document the locations, abundance and habitat use of the Canary pigeons, was verified by Nogales et al. (2009). That study compared faecal sampling with data from census techniques.

Columba bollii and *C. junoniae* showed differentiated feeding behaviours in these shared areas of native Canary Island forests. Despite the pigeons' diets being notably similar concerning the main plant species consumed, they diverged in the proportion in which the food items were eaten, particularly the parts of some plants. Spatiotemporal fluctuations in resources also influenced their diet composition. According to Lanszki et al. (2020), differences in dietary patterns, the flexibility of feeding habits and resource characteristics and availability are described elsewhere as essential factors allowing co-occurrence between species.

Trophic ecology of the pigeons

Fruits are a staple food for these endemic pigeons, those of Lauraceae being primary resources in all seasons and study areas. This plant family acquires importance for frugivorous birds in tropical and sub-tropical forest regions (Frith and Griffith 1952, Crome 1975a, b, Wheelwright 1983, Innis 1989, Solorzano et al. 2000, Ando et al. 2013, Corlett 2017). Its fruits have relatively large seeds and high nutritional quality (rich in carbohydrates and lipids). They, therefore,

Table 1. Indices of trophic overlap and breadth niche in the diet of Bolle's laurel pigeon (*C. bollii*) and white-tailed laurel pigeon (*C. junoniae*).

	Morisita	Levin		Hurlbert	
	<i>C. bollii</i> versus <i>C. junoniae</i>	<i>C. bollii</i>	<i>C. junoniae</i>	<i>C. bollii</i>	<i>C. junoniae</i>
Total	0.439	0.125	0.228		
La Palma	0.538	0.145	0.193	0.499	0.267
La Gomera	0.409	0.206	0.345	0.363	0.014

Table 2. Comparison of the main food items in the diet of Bolle's laurel pigeon and white-tailed laurel pigeon as percentages of optical fields.

Family species	Total		La Palma		La Gomera	
	t ₅₉₉	p	t ₅₉₉	p	t ₅₉₉	p
Lauraceae						
<i>Apollonias barbujana</i>	-7.501	< 0.001	-6.748	< 0.001	-7.495	< 0.001
<i>Laurus nobilis</i>	11.182	< 0.001	15.251	< 0.001	14.869	< 0.001
<i>Ocotea foetens</i>	-1.744	0.082	-0.824	0.410	-2.021	0.044
<i>Persea indica</i>	1.275	0.203	1.008	0.314	4.054	< 0.001
Aquifoliaceae						
<i>Ilex canariensis</i>	4.066	< 0.001	3.756	< 0.001	4.884	< 0.001
Rhamnaceae						
<i>Rhamnus glandulosa</i>	0.760	0.448	1.780	0.076	-0.294	0.769
Fabaceae						
<i>Bituminaria bituminosa</i>	-8.290	< 0.001	-8.435	< 0.001	-10.116	< 0.001
<i>Chamaecytisus proliferus</i>	-3.058	0.002	4.105	< 0.001	3.645	< 0.001
Solanaceae spp.	-6.452	< 0.001	-5.693	< 0.001	-4.908	< 0.001

constitute energy sources essential for reproduction, moulting, growth and migratory movements (Crome 1975a, Snow 1981, Zino and Biscoito 1993, Bolam 1994). However, most frugivores cannot maintain their body mass on only a fruit-based diet and need to incorporate some additional protein supply (Levey and Martínez del Río 2001, Pryor et al. 2001, Carlo et al. 2012). Although lower in energy, higher in fibre and more likely undesirable chemicals, leaves offer more protein than fruits (Jordano 2000).

Powlesland et al. (1997) found that the protein content of herbaceous leaves and flower buds ingested by the Kereru

(*Hemiphaga novaeseelandiae*), an endemic frugivorous pigeon from New Zealand, was higher than that of tree leaves and fruits. Moreover, Emeny et al. (2009) recorded that this pigeon's diet showed spatiotemporal changes in the consumption of fruits, leaves and flowers. A similar feeding strategy was described in *C. trocaz* (Oliveira et al. 2002). Fruits were consumed in autumn and winter, coinciding with their abundance peaks, whereas leaves became the staple food in spring and summer. Apparently, *C. trocaz* obtains most of its protein intake from leaves of herbaceous plants and shrubs because no invertebrate remains were found in its

Table 3. Fruit and seed production, and seeds in faecal samples of Bolle's laurel pigeon and white-tailed laurel pigeon. Range of undamaged seeds found in each faecal sample (seeds), and percentage of faecal samples containing undamaged seeds (%) in relation to the total number (n) of faecal samples with seeds (intact or damaged) of the plant species.

Family species	Number of seeds/fruit	Fruit length (mm)	Seed length (mm)	Bolle's laurel pigeon			White-tailed laurel pigeon		
				Seeds	Faecal samples with undamaged seeds/total	n	Seeds	Faecal samples with undamaged seeds/total	n
Lauraceae									
<i>Apollonias barbujana</i>	1	18–23	15–20	–	0	8	–	0	59
<i>Laurus nobilis</i>	1	17–22	14–19	1–2	0.5	201	–	0	21
<i>Ocotea foetens</i>	1	27–32	25–28	–	0	18	–	0	18
<i>Persea indica</i>	1	17–23	15–20	1	3.2	31	–	0	22
Aquifoliaceae									
<i>Ilex canariensis</i>	3–5	8–12	5–10	1–10	91.7	12	1	50	2
Rhamnaceae									
<i>Rhamnus crenulata</i>	3–4	4–6	1–4	1	100	1	1	100	1
<i>Rhamnus glandulosa</i>	3–4	6–11	1–4	1–3	85.7	7	1–11	73.3	15
Fabaceae									
<i>Bituminaria bituminosa</i> ¹	1		4–6	–	0	33	1	1.0	104
Gen. spp. indeterminate	–	–	–	–	0	1	–	–	–
Myricaceae									
<i>Morella faya</i>	1	4–11	1–3	1	100	1	–	–	–
Solanaceae									
<i>Solanum nigrum</i>	25–30	3–6	1–2	–	–	–	1	14.3	7
Moraceae									
<i>Ficus carica</i> ²	> 100	30–50	1–2	–	–	–	82	100	1
Amaranthaceae									
<i>Bosea yervamora</i> ³	1	5–6	3–4	–	–	–	1–5	100	3

¹Dry fruit (legume).

²*Ficus carica* has drupes without embryos.

³Undamaged whole fruits of *Bosea yervamora* were found in the faecal samples, each containing one seed.

diet. Leaves of diverse species (mainly Fabaceae) were found in the Canary pigeons' diet. It is well known that legume leaves are rich in protein, and maybe for that reason, Canary herders have used these species since pre-Hispanic times as livestock fodder (Morales Mateos 2003). These plants usually grow in open areas, track sides and rocky zones; this means that *C. bollii* and *C. junoniae* must fly to the forest margins to consume them. Fragmented seeds found in the faeces are also a significant protein source (Janzen 1971, Díaz 1996). The same applies to invertebrates, whether the result of active insectivory or more likely taken accidentally together with plant foods. They could still however be intentional alternative protein resources (Courts 1998).

Spatiotemporal changes in resource availability may influence the regular movements of columbids through forest areas (Moran et al. 2004). Consumption of fruits and leaves from species unrecorded in some of our study areas (mainly growing in forest margins) points to such movements in these Canary pigeons. From observation points and transects, Martín et al. (2000) recorded considerable seasonal fluctuations in pigeon abundance between study areas, which could be related to this feeding strategy. However, the pigeons' preferences towards certain fruit species could also be important. For example, the high proportion of *L. nobilis* in the diet of *C. bollii* could be associated with its abundance in the forest, but other equally abundant fruits like *M. faya* were poorly represented. In contrast, *A. barbujana* and *O. foetens* were heavily consumed, despite their more restricted range. From our spatial analysis showing a clustering between forest margin areas and those located within the laurel forests, pigeons might remain in an area long enough for the content of their diets to reflect the floristic composition of these study areas. Oliveira (2003) observed similar behaviour in *C. trocaz*. When this pigeon found a suitable area, it took advantage of the resources for a long period, before moving on to another area. This feeding behaviour is frequent in birds that depend on resources as variable as fruits (Pyke et al. 1977, Herrera 1985, Levey and Stiles 1992, Powlesland et al. 1997).

The relationship between fruit availability and feeding behaviour

The present results show a comparable seasonal pattern for these pigeons although not as evident as that of *C. trocaz* (Oliveira et al. 2002). The abundance of fruits varies enormously between years and seasons (depending on the rainfall regime) and also between habitats. This generally leads to a heterogeneous, unpredictable distribution in time and space (Levey 1988, Herrera 2002), and such variations influence the dynamics of frugivorous bird communities (Loiselle and Blake 1991). The main six fleshy-fruited species consumed by pigeons showed differing fruiting phenology in the present study. Although in general, fruit consumption was related to the peak of ripe fruit production, the opposite trend was also observed. Several scenarios, not mutually exclusive, could explain this result. From observations in the field, large numbers of fallen fruits remain on the forest floor after their

production peak in the crown of trees has passed, extending their availability period at least until the next season. Moreover, pigeons can move between areas of similar floristic composition but with plants in a slightly more advanced fruiting state. Lastly, pigeons may consume fruits not yet fully ripe.

Ecological roles

The Canary pigeons are the largest frugivorous birds in the laurel forest (*C. bollii*, 35–37 cm and 340–380 g; *C. junoniae*, 37–38 cm and 350–450 g in body size and weight, respectively). These large body sizes mean that the number of fruits they can ingest, along with their digestive tract characteristics, must at least be different from those of other smaller fruit-eating species (such as *T. merula* and *E. rubecula*). From the state in which seeds were found in faecal contents, *C. bollii* and *C. junoniae* both seem to have greater food crushing and processing power than *C. trocaz* (Oliveira et al. 2002). It was also observed that laurel pigeons probably act as seed dispersers of certain plant species and as predators of others, even of the same species. These two interactions (mutualistic seed dispersal versus antagonistic seed predation) play a central ecological role in determining the plant population dynamics (García et al. 2011, Arnan et al. 2012). The morphological and physiological characteristics of avian digestive systems and the size and hardness of seeds are crucial factors in determining the fate of seeds (Pratt and Stiles 1983, Loiselle 1990, Bhattacharyya 1994, Whelan et al. 1998, McConkey et al. 2004). These pigeons can also store fruits in their crop and then regurgitate seeds, free of pulp, under the mother plant or at some distance from it. Therefore, it must be recognised that the global role of pigeons regarding seed removal needs to be studied in detail.

Conclusions

Faecal DNA sampling revealed the co-occurrence areas of the two pigeon species and their habitat use. Quantitative diet analysis based on microhistological methods showed that both frugivorous pigeons consume a diversity of plant species (more than 20) although Lauraceae fruits were their staple foods. Fruits and/or leaves of Rhamnaceae, some Fabaceae and Solanaceae were also important. In general, fruit consumption was related to the peak of ripe fruit production. The two pigeons showed preferences for some fruits. Niche similarity and breadth indices indicated a medium-grade diet similarity, tending towards specialisation. Differential trophic strategies concerning resource availability at different spatiotemporal scales appear to be important factors facilitating their co-occurrence. The ecological role of pigeons as seed dispersers and/or predators could be influenced by some seed features, such as size and hardness. This study shows how understanding spatiotemporal frugivory interactions on oceanic islands has valuable evolutionary and ecological implications, and can contribute to their management and conservation.

Acknowledgements – We thank Ángel Fernández and Antonio Zamorano (Garajonay National Park) and Félix M. Medina (Unidad Insular de Medio Ambiente del Cabildo de La Palma) for providing us with crucial logistical support. We are also grateful to David P. Padilla for help with the fieldwork, Heriberto López for identifying arthropod remains and Javier Romero for making helpful suggestions on the manuscript.

Funding – This study was partially funded by the Organismo Autónomo de Parques Nacionales (80/2005), Ministerio de Medio Ambiente y Medio Rural y Marino of Spain. PM received grant support from Proyectos Intramurales Especiales (2004 3 OE 169) of the Spanish National Scientific Research Council. The manuscript was edited by Guido Jones, currently funded by the Cabildo de Tenerife, under the TFinnova programme supported by MEDI and FDCAN funds.

Author contributions

Patricia Marrero: Conceptualization (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Software (lead); Writing – original draft (lead); Writing – review and editing (equal). **Manuel Nogales:** Conceptualization (equal); Funding acquisition (lead); Investigation (equal); Methodology (equal); Project administration (lead); Supervision (equal); Validation (equal); Visualization (equal).

Transparent Peer Review

The peer review history for this article is available at <<https://publons.com/publon/10.1111/jav.02803>>.

Data availability statement

Data are available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.pnvx0k6n9>> (Marrero and Nogales 2021).

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