

DIET OF THE ENDEMIC MADEIRA LAUREL PIGEON AND FRUIT RESOURCE AVAILABILITY: A STUDY USING MICROHISTOLOGICAL ANALYSES

PAULO OLIVEIRA¹, PATRICIA MARRERO² AND MANUEL NOGALES^{2,3}

¹Parque Natural da Madeira, Quinta Bom Sucesso, Caminho do Meio, 9050 Funchal, Madeira, Portugal

²Departamento de Biología Animal (Zoología), Universidad de La Laguna, 38206, Tenerife, Canary Islands, Spain

Abstract. We studied the temporal diet variation of the endemic Madeira Laurel Pigeon (*Columba trocaz*) and fruit resource availability in the laurel forests of northwestern Madeira Island, during 1996 and 1997. We studied a total of 224 fecal samples using microhistological methods and conducted surveys of fruiting phenology throughout a year. Fruits (pulp and seeds) represented 57% of the optical fields analyzed. Leaves and flowers constituted 38% and <1% respectively. Over 33 plant species were identified in the fecal samples. Fruits of *Ocotea foetens*, *Laurus azorica*, *Persea indica*, and *Ilex canariensis* (fruits and leaves) were the most frequently detected food items. Most seeds were defecated intact (*Ilex canariensis*, *Myrica faya*, *Visnea mocanera*, *Ocotea foetens*, and *Apollonias barbujana*), except in the case of *Laurus azorica* where most were damaged. The diet showed a marked seasonal variation. Fruits constituted the major component of the diet in winter and autumn, whereas leaves were frequent in spring and summer. The presence of fruits in the diet was concordant with their availability, and leaves and flowers became important when fruits were scarce. This fact suggests that the Madeira Laurel Pigeon is capable of dietary switching, corresponding to temporal variations in food resource availability. This microhistological technique shows promise for study of the diets of pigeons and other herbivorous bird species.

Key words: *Columba trocaz*, diet, fruit phenology, islands, laurel forest, microhistological analysis, seasonality.

Dieta de *Columba trocaz* y Su Relación con la Disponibilidad de Frutos: Un Estudio Realizado Mediante Análisis Microhistológicos

Resumen. Se estudió la dieta estacional de *Columba trocaz* y la disponibilidad de frutos en los bosques de laurisilva de la zona noroeste de la Isla Madeira, durante 1996 y 1997. Se analizó un total de 224 excrementos mediante métodos microhistológicos, y se realizó un seguimiento estacional de la disponibilidad de frutos, por medio de transectos, a lo largo de un año. Los frutos (pulpa y semillas) representaron un 57% de los campos ópticos analizados; las hojas y las flores constituyeron un 38% y <1%, respectivamente. Más de 33 especies fueron identificadas en los excrementos; restos de frutos de *Ocotea foetens*, *Laurus azorica*, *Persea indica* e *Ilex canariensis* (tanto frutos como hojas) resultaron ser los más frecuentemente detectados. La mayoría de las semillas fueron defecadas intactas (*Ilex canariensis*, *Myrica faya*, *Visnea mocanera*, *Ocotea foetens* y *Apollonias barbujana*), excepto en el caso de *Laurus azorica*, donde la mayoría de ellas aparecieron dañadas. La dieta mostró un marcado carácter estacional, constituyendo los frutos el componente más importante en invierno y otoño, mientras que las hojas fueron más abundantes en primavera y verano. La presencia de frutos en los excrementos fue concordante con su disponibilidad, adquiriendo una mayor relevancia las hojas y las flores cuando la producción de los frutos fue escasa. Este hecho sugiere que *C. trocaz* exhibe una alta flexibilidad en la dieta, aprovechando aquellos recursos que son estacionalmente abundantes. Los resultados obtenidos en estos análisis microhistológicos ofrecen un aceptable nivel de fiabilidad para ser utilizados en estudios sobre dieta de palomas y, probablemente, extensibles a otras aves herbívoras.

INTRODUCTION

The relict laurel forests of the Macaronesian archipelagos harbor three endemic pigeons, one

from Madeira (Madeira Laurel Pigeon [*Columba trocaz*]) and two from the Canaries (Bolle's Laurel Pigeon [*Columba bollii*] and White-tailed Pigeon [*Columba junoniae*]; Bannerman 1963, Bannerman and Bannerman 1965, Goodwin 1983). These species are considered ancient elements of the Macaronesian avifauna (Volsøe

Manuscript received 25 October 2001; accepted 19 July 2002.

³Corresponding author. E-mail: mnogales@ull.es

1955). The Madeira Laurel Pigeon (called “pombo trocaz” in Madeira) is mainly restricted to the laurel forest areas of the humid, mountainous northern slopes of Madeira Island. Since the discovery of this island in 1420, much of the forest has been cleared for agriculture and timber. The laurel forest cover has been estimated at 15 000 ha (about 20% of the total 737 km² of the island surface; Costa Neves et al. 1996). The population size of the Madeira Laurel Pigeon has been estimated as 10 400 birds (Oliveira et al. 1999). Although there has been some research on status (Zino and Zino 1986), distribution (Jones 1990), and habitat preferences (Jones et al. 1988, Oliveira and Jones 1995), little is known about the pigeon's diet. In the case of the Madeira Laurel Pigeon, most of the diet information is based on descriptive and observational data (Harcourt 1851, Godman 1872, Sarmiento 1948), listing mainly the consumption of fruits belonging to trees characteristic of the laurel forest (*Laurus azorica*, *Ocotea foetens*, *Myrica faya*) and the leaves and flowers of flowering plants (*Phyllis nobla*, *Apium nodiflorum*, *Nasturtium officinale*; Zino 1969, Zino and Zino 1986, Oliveira and Jones 1995, Oliveira 1999).

A similar herbivorous diet has been recorded for other forest pigeons both in continental areas (Band-tailed Pigeon [*Columba fasciata*] from western North America, Neff 1947; Common Wood Pigeon [*Columba palumbus*] from England, Snow and Snow 1988; Nilgiri Wood Pigeon [*Columba elphinstonii*] from India, Gibbs et al. 2001), and islands (Henderson Island Fruit Dove [*Ptilinopus insularis*] from Henderson Island, Polynesia, Brooke and Jones 1995; Chatham Island Pigeon [*Hemiphaga novaeseelandiae*] from Chatham Island, New Zealand, Powlesland et al. 1997; Bolle's Laurel Pigeon and White-tailed Pigeon from the Canary Islands, Martín et al. 2000). Direct observation of feeding is widely used to assess pigeon diets, but is subject to observational bias (Snow and Snow 1988, Rosenberg and Cooper 1990). Like many other pigeons, the Madeira Laurel Pigeon is very shy, and feeding observations have to be made from a distance, usually through twigs and foliage. Ralph et al. (1985) suggested that fecal samples are a less biased method to assess diet, and fecal samples can be obtained without disturbing the birds.

The macroscopic analysis of fecal samples has been used to describe the diet of many spe-

cies, including pigeons (Innis 1989, Powlesland et al. 1994). However it is likely that this approach produces a strong bias toward those items that, due to their greater digestive resistance (e.g., seeds and hard leaves), are present in the macroscopic fraction of the sample in higher proportions.

We used a microhistological analysis of fecal samples, which may allow less biased quantification of the diet. Microhistological techniques have been widely and satisfactorily used on studies of herbivorous mammals (Sherlock and Fairley 1993, Mohammad et al. 1995) but much less frequently on frugivorous birds (Jordano and Herrera 1981, Herrera 1998). Our aim was to study the diet composition of the Madeira Laurel Pigeon, its seasonal variation, the relationship between the abundance of fruits and their consumption, and the digestive treatment of seeds of each plant species, and also to evaluate the reliability of the microhistological methods in these kinds of studies. Furthermore, the status of this pigeon as an island endemic suggests that this species may have coevolved with this unique habitat and may play an important role as seed disperser or predispersal seed predator, depending on the species of seed.

METHODS

STUDY AREA

The volcanic Madeiran Archipelago is located in the eastern Atlantic about 900 km from Europe (Iberian Peninsula) and some 630 km from the African continent (33°10'N, 15°50'W). The study area is located in Ribeira da Janela, a deep and extensive ravine in the northwestern part of Madeira Island. Rainfall averages >1700 mm per year (Sjögren 1972). As a result of elevational variation (from sea level to 1300 m), many different forest types occur in this valley. At higher altitudes heathers (*Erica* spp.) and shrubs such as *Vaccinium padifolium* dominate, while the lowland vegetation is a well-developed closed-canopy forest. There are about 3366 ha of indigenous, well-preserved forest (Costa Neves et al. 1996), characterized by trees up to 30 m tall, mainly *Ocotea foetens*. Other common trees are *Laurus azorica*, *Myrica faya*, *Persea indica*, and *Clethra arborea*. The understory is dominated by species such as *Teline maderensis*, *Genista tenera*, *Phyllis nobla*, and *Rumex maderensis*. Some exotic species such as *Cytisus*

scoparius, *Cytisus striatus*, and *Ageratina adenophora* are widely distributed. At the mouth of the valley there are human settlements, agricultural fields, and exotic forest.

PIGEON DIET

Data collection. Fieldwork was carried out from spring 1996 through winter 1997. We collected a total of 224 fresh fecal samples along three previously selected path-transects that crossed representative areas of the forest at altitudes of 250, 500, and 750 m. The combined length of the paths was 9200 m (3200, 3900, and 2100 m, respectively), and they were located approximately 7 km apart. In order to avoid seasonal sampling bias, we collected fresh fecal samples along the three paths during several visits in each of four seasons (March–May: $n = 58$ samples, June–August: $n = 39$, September–November: $n = 64$, and December–February: $n = 63$). Due to the high abundance of birds in this study area and their large movements we assumed that pseudoreplication in fecal samples was not significant. Because of the proximity of the paths in this steep area and the pigeons' large movements we did not study spatial variation of diet within the valley. We avoided collecting fecal samples of other species because pigeon feces are larger (no other vegetarian bird species of similar size [~ 463 g] inhabits the study area) and often characteristically shaped (spiral on an edge) when recent. Samples were frozen until they were analyzed.

Fecal analysis. Plant food items were often unidentifiable macroscopically, so we used microhistological methods based on plant epidermal resistance to herbivore digestion (Chapuis 1979). Prior to analysis, every fecal sample was dispersed in water and cleared by the addition of two drops of sodium hypochlorite. From this mixture, we placed approximately 50 μL under a microscope, where we randomly selected 50 optical fields at 10 \times magnification from each fecal sample. In each optical field we scored the presence or absence of each plant item. Epidermal tissues were identified by comparison with a reference collection of leaves, stems, flowers, fruits, and seeds of 139 species from the Ribeira da Janela laurel forest, including trees, shrubs, herbs, and ferns.

Fecal samples were present in three forms: (1) plant material unidentifiable macroscopically, (2) plant material identifiable macroscopically,

and (3) plant material partially identifiable macroscopically. To quantify the proportion of each plant item present, we applied different methods depending on these distinct types: for type 1 we studied 50 randomly selected optical fields in each sample; for type 2 we transformed the percentage of volume of the macroscopic fraction of each item to optical fields (considering a total of 50 optical fields per fecal sample) by a simple extrapolation; and for type 3 we estimated the percentage of the macroscopic fraction and transformed it to optical fields, and studied the remainder (up to 50 optical fields) in the microscopic fraction of the sample. This procedure allowed us to obtain a common unit (number of optical fields) to compare the data. At the end of the analyses ($n = 224$ fecal samples), we had viewed a total of 11 200 optical fields, including those obtained from the transformation of the macroscopic fractions.

Many seeds were damaged by passage through the digestive tract, so we were unable to quantify the number of seeds present in each fecal sample. Therefore, we recorded whole or damaged seeds of each species only as present or absent, once per fecal sample, and our frequency of occurrence data reflect this level of precision.

FOOD RESOURCE AVAILABILITY

Phenology of fruits from the five main tree species of the forest, *Laurus azorica*, *Ocotea foetens*, *Persea indica*, *Apollonias barbudana*, and *Myrica faya* (Costa Neves et al. 1996), was described by first estimating the proportion of trees of each species with ripe fruits, multiplying this by an index of fruit abundance in trees containing ripe fruit, and then multiplying by the dominance of the tree species in the forest, to make the index comparable across species. We only counted ripe fruits because based on our field observations and some stomach contents, pigeons do not eat unripe fruits. Data were collected by walking along the same forest paths used in fecal-sample collection, and establishing sampling units approximately every 300 m. At each point we collected data for the two nearest trees with visible canopies for each of the five main species of the forest. A minimum of 208 trees were sampled in each season.

The index of fruit abundance was a categorical variable based on a previous survey that established "typical" fruit density per ha of fo-

TABLE 1. Results of pairwise feeding trials carried out to determine whether the main components of the diet of the Madeira Laurel Pigeon are evident in feces at similar rates. Pigeons were force-fed equal amounts of each food item; results are presented as the number of optical fields (of a 10× microscope; out of 100 optical fields) in which the food item appeared.

Feeding trials Species 1 vs. species 2	Number of optical fields containing		χ^2_1
	Species 1	Species 2	
<i>Ocotea foetens</i> vs. <i>Ilex canariensis</i> (fruits)	34	26	0.3
<i>Laurus azorica</i> vs. <i>Persea indica</i> (fruits)	47	20	4.9*
<i>Laurus azorica</i> vs. <i>Apollonias barbujana</i> (fruits)	89	97	0.1
<i>Visnea mocanera</i> vs. <i>Myrica faya</i> (fruits)	16	32	2.1
<i>Aspalathium bituminosum</i> vs. <i>Phyllis nobla</i> (leaves)	96	74	1.2
<i>Aspalathium bituminosum</i> vs. <i>Cytisus striatus</i> (leaves)	68	63	0.04
<i>Phyllis nobla</i> vs. <i>Rumex maderensis</i> (leaves)	72	54	1.0
<i>Brassica oleracea</i> (leaves) vs. <i>Cytisus striatus</i> (flowers)	73	90	0.7

* $P < 0.05$.

liage for each species. The typical density was based on mean numbers of fruits in 1-m² quadrats taken from between 52 (*Apollonias barbujana*) and 206 (*Ocotea foetens*) trees. Using these data as a baseline, we placed trees into three fruit abundance categories (low, medium, and high). Low abundance meant that the tree had less than half of the mean number of fruit per m² previously estimated. A high abundance meant that the tree had more than double the mean number of fruits per m². The final estimate of fruit abundance for each species was calculated as the mean of the fruit abundance scores, multiplied by the “typical density,” multiplied by the proportion of trees with ripe fruit and the proportional dominance of that species in the forest. This index provided an estimate of the number of fruits of each species per ha of forest.

FEEDING TRIALS

Feeding trials were carried out to establish the reliability of the microhistological method and particularly to assess the bias introduced by the possible differential digestibility of food items. Two Madeira Laurel Pigeons were kept in outdoor cages and force-fed with different pairwise combinations of foods (fruits, leaves, and flowers) normally present in the diet (Table 1). Birds were also fed plants that, although not present in the fecal samples, were known to be part of pigeon diet (pers. obs.). This was done to confirm that their absence in the diet was due to sampling effect, rather than total destruction of the epidermis during digestion. We fed pigeons 3 g of each item, every 4 hr of daylight. Each pairwise combination was given three consecu-

tive times; water and grit were continuously available. After finishing with the three consecutive trials of each combination of food we collected at least one fecal sample per individual for analysis. Sample size of optical fields for this group of fecal samples was doubled ($n = 100$ per fecal sample) in order to increase the accuracy of the results.

STATISTICAL ANALYSIS

We present fecal-sample data in two ways: the percentage of all 11 200 optical fields studied that contained a particular species (total percentage), and the mean \pm SE number of optical fields containing a particular species per fecal sample, calculated only from fecal samples in which the species was present (mean percentage). The first measure indicates the incidence of a particular plant species in the diet of this population of Madeira Laurel Pigeons. The second measure indicates the prevalence of a particular plant species in diets of individuals that were able to acquire it. We evaluated the bias of the first measure by calculating Pearson’s correlation coefficient between total percentage of optical fields and simple percent occurrence in the fecal samples.

Chi-square contingency analysis was conducted to test for seasonal differences in the occurrence of particular plant items in the fecal samples. General seasonal variation of the total percentages of optical fields (arcsine transformation) between species and seasons was analyzed by two-way ANOVA. Similarity or overlap in Madeira Laurel Pigeon diets between the drier (spring and summer) and rainier (autumn

and winter) seasons was evaluated using the Morisita index of similarity for percentage of optical fields in fecal samples (Krebs 1989). Niche breadth (using total percentages of optical fields) was evaluated using the standardized Levins' and Hurlbert's niche-breadth indices, where a value close to 0 indicates dietary specialization, and a value close to 1 indicates a broad diet (Krebs 1989). Levins' niche breadth considers all kinds of food items (fruits, leaves, and flowers) while Hurlbert's niche-breadth considers only fruits (available and consumed). Furthermore, Hurlbert's niche breadth incorporates the proportion of the main five fruit-tree species available in each season. Due to the high similarity observed on the results of this index between the two rainy seasons (autumn and winter) and also between the two dry seasons (spring and summer), we pooled similar seasons and calculated Hurlbert's niche breadth for the rainy season and the dry season only. Seasonal relationship between availability of fruits (number of fruits per ha) and percentage of fruits in optical fields was studied by a simple regression analysis for each of the main five fruit species.

The feeding trials were analyzed with chi-square tests, comparing the proportion of each food type in the pairwise comparison that was found in the feces. If the microhistological analyses are reliable, the two food items of each feeding trial should appear in statistically equal proportions. After confirming a high similarity between the contents of the fecal samples yielded by each pigeon in relationship with the different food items (two-way ANOVA, $P > 0.05$), the results from the two animals were pooled. All statistical analyses were performed using SPSS 10.0 (SPSS Inc. 1999).

RESULTS

FEEDING TRIALS

For seven of eight combinations of items fed to captive pigeons, the two food types were present in the feces in statistically similar proportions (Table 1). Therefore, birds did not appear to digest the main components of their diet differently and these results strongly validate the data obtained in the following analyses. The only exception, in a total of 16 food items given, was *Persea indica* fruits, which appeared about 41% less frequently than was expected.

DIET COMPOSITION

The diet of the Madeira Laurel Pigeon included over 33 plant species (Table 2), but at least 80% of the fecal samples contained only one or two plant species. Fruits (pulp and seeds) represented about 57% of all optical fields, leaves about 38%, and flowers <1%. Fruits of *Ocotea foetens*, *Ilex canariensis*, and *Laurus azorica* were the most important sources of food for the pigeons, comprising more than 54% of the optical fields. *Persea indica* was present in 7.5% of all optical fields; however, feeding trials indicated its frequency could have been underestimated by about 41%. Using this correction, its total percentage of optical fields could be as high as 11%. Additionally, *Aspalathium bituminosum*, *Teline maderensis*, *Phyllis nobla*, and an unidentified herbaceous species were found in more than 8% of the samples.

Among the 38% of all optical fields that contained leaves, 61% came from herbs and shrubs, 27% from native trees (mainly *Ilex canariensis*: 9.6% of optical fields), and 9% came from introduced trees (mainly *Malus domestica* and *Prunus persica*).

There was a strong correlation between total percentage of optical fields and frequency of occurrence in the fecal samples ($r = 0.95$, $P < 0.001$), indicating that plant species were not inordinately clumped in particular samples.

SEASONAL VARIATION OF THE DIET

The diet showed a significant variation among the four seasons (two-way ANOVA, $F_{1,32} = 11.05$, $P < 0.01$; Table 2). Pigeon diet varied subtly between the drier (spring and summer) and rainier (autumn and winter) seasons, with medium overlap or similarity in food items between seasons (Morisita Index, $C_\lambda = 0.59$).

In spring, leaves of *Ilex canariensis*, *Aspalathium bituminosum*, and an unidentified herbaceous plant were the principal food in the diet, found in more than 55% of optical fields. The diet in summer contained more plant species (at least 22) than the other seasons (at least 16 in each), with only *Laurus azorica* (fruits) and *Aspalathium bituminosum* (leaves) appearing in >12% of optical fields. Fruits of *Laurus azorica*, *Ocotea foetens* and *Persea indica* dominated the feces in autumn (~72% of optical fields). In winter, fruits of *Ocotea foetens* and *Ilex canariensis* were the principal species in the diet, present in more than 80% of optical fields. Fruits

TABLE 2. Diet and seasonal variation pattern of the Madeira Laurel Pigeon in Ribeira da Janela, Madeira. Values are expressed as percentage of 50 optical fields observed in each fecal sample and as mean \pm SE percentage of optical fields containing the item, calculated only for fecal samples in which the item was present. *Component apparently underestimated; corrected percentage is shown in parentheses. Plant part mainly used: f = fruit, l = leaves, fw = flowers; tr = trace amount (<0.05%).

Family Species	Total % occurrence				Optical fields					
	Total				Mean % \pm SE (per fecal sample)					
	Spring	Summer	Autumn	Winter	Total	Spring	Summer	Autumn	Winter	Total
Lauraceae										
<i>Apollonia barbijana</i> (f)	1.0	5.1	3.1	0.2	2.2	60 \pm 0	55 \pm 37	67 \pm 49	10 \pm 0	54 \pm 38
<i>Laurus azorica</i> (f, l)	5.1	20.7	38.4	1.3	16.2	74 \pm 47	81 \pm 41	67 \pm 38	84 \pm 0	76 \pm 38
<i>Ocotea foetens</i> (f, l)	5.8	0.6	18.1	44.6	19.3	56 \pm 36	12 \pm 8	50 \pm 46	61 \pm 35	56 \pm 38
<i>Persea indica</i> * (f)	—	5.3	15.2	7.8	7.5 (10.5)	—	68 \pm 55	61 \pm 46	82 \pm 38	67 \pm 44
Aquifoliaceae										
<i>Ilex canariensis</i> (f, l)	25.1	3.7	6.8	35.8	19.2	58 \pm 36	49 \pm 49	72 \pm 35	35 \pm 32	44 \pm 35
Theaceae										
<i>Visnea mocanera</i> (f)	1.4	7.2	—	—	1.6	40 \pm 49	56 \pm 43	—	—	51 \pm 41
Myricaceae										
<i>Myrica faya</i> (f, l, fw)	0.7	2.6	1.6	0.1	1.1	21 \pm 27	50 \pm 57	53 \pm 46	4 \pm 2	32 \pm 37
Oleaceae										
<i>Picconia excelsa</i> (f)	—	1.3	—	—	0.2	—	50 \pm 0	—	—	50 \pm 0
Myrtaceae										
<i>Eucalyptus globulus</i> (l, fw)	—	—	—	1.4	0.4	—	—	—	45 \pm 49	45 \pm 49
Fabaceae										
<i>Aspalathium bituminosum</i> (l)	13.7	12.3	tr	0.8	5.9	40 \pm 33	48 \pm 40	1 \pm 0	25 \pm 6	40 \pm 34
<i>Cytisus</i> sp. (l)	—	0.9	—	—	0.2	—	18 \pm 18	—	—	18 \pm 18
<i>Teline maderensis</i> (l)	3.7	3.2	3.0	1.4	2.8	27 \pm 26	76 \pm 31	24 \pm 33	35 \pm 30	32 \pm 31
Gen. spp. indeterminate (l)	16.6	—	—	1.9	4.8	60 \pm 24	—	—	9 \pm 13	36 \pm 32
Rubiaceae										
<i>Phyllis nobla</i> (l)	3.7	6.6	4.3	2.2	4.0	43 \pm 39	51 \pm 23	34 \pm 40	70 \pm 17	44 \pm 34
Rosaceae										
<i>Malus domestica</i> (l)	3.5	8.8	—	—	2.4	100 \pm 0	68 \pm 27	—	—	77 \pm 27
<i>Prunus persica</i> (l)	—	5.1	—	—	0.9	—	100 \pm 0	—	—	100 \pm 0
Vitaceae										
<i>Vitis vinifera</i> (l)	6.9	—	—	—	1.8	57 \pm 27	—	—	—	57 \pm 27

TABLE 2. Continued.

Family Species	Total % occurrence					Optical fields				
	Total					Mean % ± SE (per fecal sample)				
	Spring	Summer	Autumn	Winter	Total	Spring	Summer	Autumn	Winter	Total
Ericaceae										
<i>Erica scoparia</i> (l)	0.1	—	tr	0.3	0.1	5 ± 0	—	1 ± 0	4 ± 4	4 ± 3
Chenopodiaceae										
<i>Chenopodium ambrosioides</i> (l)	—	5.1	—	—	0.9	—	100 ± 0	—	—	100 ± 0
<i>Chenopodium</i> sp. (l)	—	0.5	—	—	0.1	—	20 ± 0	—	—	20 ± 0
Lamiaceae										
<i>Bystropogon maderensis</i> (l)	—	1.5	—	—	0.3	—	56 ± 0	—	—	56 ± 0
<i>Micromeria varia</i> (l)	—	2.4	—	—	0.4	—	94 ± 0	—	—	94 ± 0
<i>Prunella vulgaris</i> (l)	—	—	0.1	—	tr	—	—	4 ± 0	—	4 ± 0
Gen. spp. indeterminate (l)	—	1.1	5.1	0.1	1.7	—	22 ± 11	34 ± 32	8 ± 0	30 ± 29
Asteraceae										
<i>Bidens pilosa</i> (l)	—	—	0.5	—	0.1	—	—	32 ± 0	—	32 ± 0
<i>Erigeron karvinskianus</i> (l)	—	—	—	0.6	0.2	—	—	—	24 ± 14	24 ± 14
<i>Sonchus</i> sp. (l)	—	0.1	—	—	tr	—	5 ± 0	—	—	5 ± 0
Poaceae										
Gen. spp. indeterminate (l)	0.1	0.1	—	0.1	0.1	6 ± 0	2 ± 0	—	5 ± 0	4 ± 2
Caryophyllaceae										
<i>Cerastium vagans</i> (l)	—	—	0.2	—	tr	—	—	10 ± 0	—	10 ± 0
Cruciferae										
<i>Arabis caucasica</i> (l)	—	—	tr	—	tr	—	—	1 ± 0	—	1 ± 0
<i>Erysimum bicolor</i> (l)	0.1	—	—	—	tr	8 ± 0	—	—	—	8 ± 0
Pteridophyta	1.9	1.9	—	—	0.8	37 ± 31	37 ± 41	—	—	37 ± 30
Bryophyta	—	—	0.9	0.3	0.3	—	—	6 ± 4	10 ± 7	7 ± 5

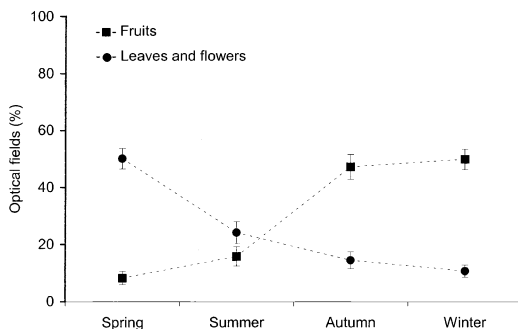


FIGURE 1. Seasonal variation of the presence of fruits (filled squares), and leaves and flowers (filled circles), in the diet of the Madeira Laurel Pigeon during 1996–1997. Points expressed as mean \pm SE percentage of occurrences of the food item in 50 microscope optical fields per fecal sample.

(pulps and seeds), leaves, and flowers were used differentially among the seasons ($\chi^2_6 = 64.0$, $P < 0.001$). Fruits (all from trees) were the major component in the diet during autumn (77% of optical fields) and winter (85%), while leaves and flowers constituted the main component in spring (74%) and summer (55%; $\chi^2_3 = 61.9$, $P < 0.001$; Fig. 1).

RESOURCE USE AND FRUIT AVAILABILITY

Levins' niche breadth, B , (including fruits, leaves, and flowers) was clearly narrower in the rainy seasons (autumn and winter, $B = 0.22$ and 0.13 , respectively) than in the drier ones (spring and summer, $B = 0.36$ and 0.44 , respectively). This suggests that the Madeira Laurel Pigeon showed a tendency to dietary specialization when fruit resources were abundant, but changed to a broad food spectrum when fruits were scarce. However, considering only fruit availability using Hurlbert's niche breadth (B'), the niche was broader for the rainy seasons ($B' = 0.66$) than the drier seasons ($B' = 0.10$). These results are logical since fruits were more available in autumn and winter (Fig. 2). The abundance of fruits in each season was closely correlated with their consumption by the pigeons (total percentages) for all studied fruit species (Fig. 2; all $r^2 > 0.67$, all $P < 0.05$).

SEED DIGESTIVE TREATMENT

Madeira Laurel Pigeons ate but did not damage the seeds of *Ilex canariensis* ($n = 28$ fecal samples), *Myrica faya* ($n = 4$), and *Visnea moczneri* ($n = 6$). Seeds of other species were some-

times damaged during digestion, including *Ocotea foetens* (damaged in 6 of 25 fecal samples), *Apollonias barbujana* (2 of 7 samples), *Persea indica* (8 of 19 samples) and especially *Laurus azorica* (23 of 28 samples). (These sample sizes differ from those in Fig. 2 because they include only samples that contained seeds.)

DISCUSSION

DIET COMPOSITION

Our findings indicate that the Madeira Laurel Pigeon's diet is largely frugivorous, although leaves and flowers are also well represented in spring and summer. *Ocotea foetens*, *Laurus azorica* and *Persea indica* were used in proportion to their importance, dominance, and density in the forest (Costa Neves et al. 1996), and *Ocotea foetens* produced fruits all year round. However, the same explanation cannot be applied to *Ilex canariensis*, which contributes modestly to the composition and structure of the laurel forest of Madeira, especially in our study area, where it has a patchy distribution.

Our data agree with most of the descriptive literature on the diet of the Madeira Laurel Pigeon, which suggests that the main food sources are fruits of *Laurus azorica*, *Ocotea foetens*, and *Myrica faya* (Bannerman and Bannerman 1965, Zino 1969, Zino and Zino 1986). When feeding on the ground, pigeons also eat the flowers and leaves of *Sonchus* spp., *Apium nodiflorum*, *Nasturtium officinale* (Zino and Zino 1986), and *Phyllis nobla* (Oliveira and Jones 1995). Personal field observation also showed that pigeons feed on other plants, such as *Rumex maderensis*, *Plantago major*, and *Nasturtium officinale*, which did not appear in the microhistological analysis. The other two endemic pigeons from the Macaronesian islands, the Bolle's Laurel and White-tailed Pigeons of the Canary Islands, are also frugivorous, eating a wide range of fruits and some leaves and flowers (Hernández et al. 1999, Martín et al. 2000). A varied vegetarian diet has also been described for two other forest fruit pigeons, the Chatham Island Pigeon (Pearson and Climo 1993, Powlesland et al. 1997) and White-crowned Pigeon (*Columba leucocephala*; Bancroft and Bowman 1994). Furthermore, our data agree with the findings that lauraceous fruits are important in the diet of some species of pigeons (Crome 1975).

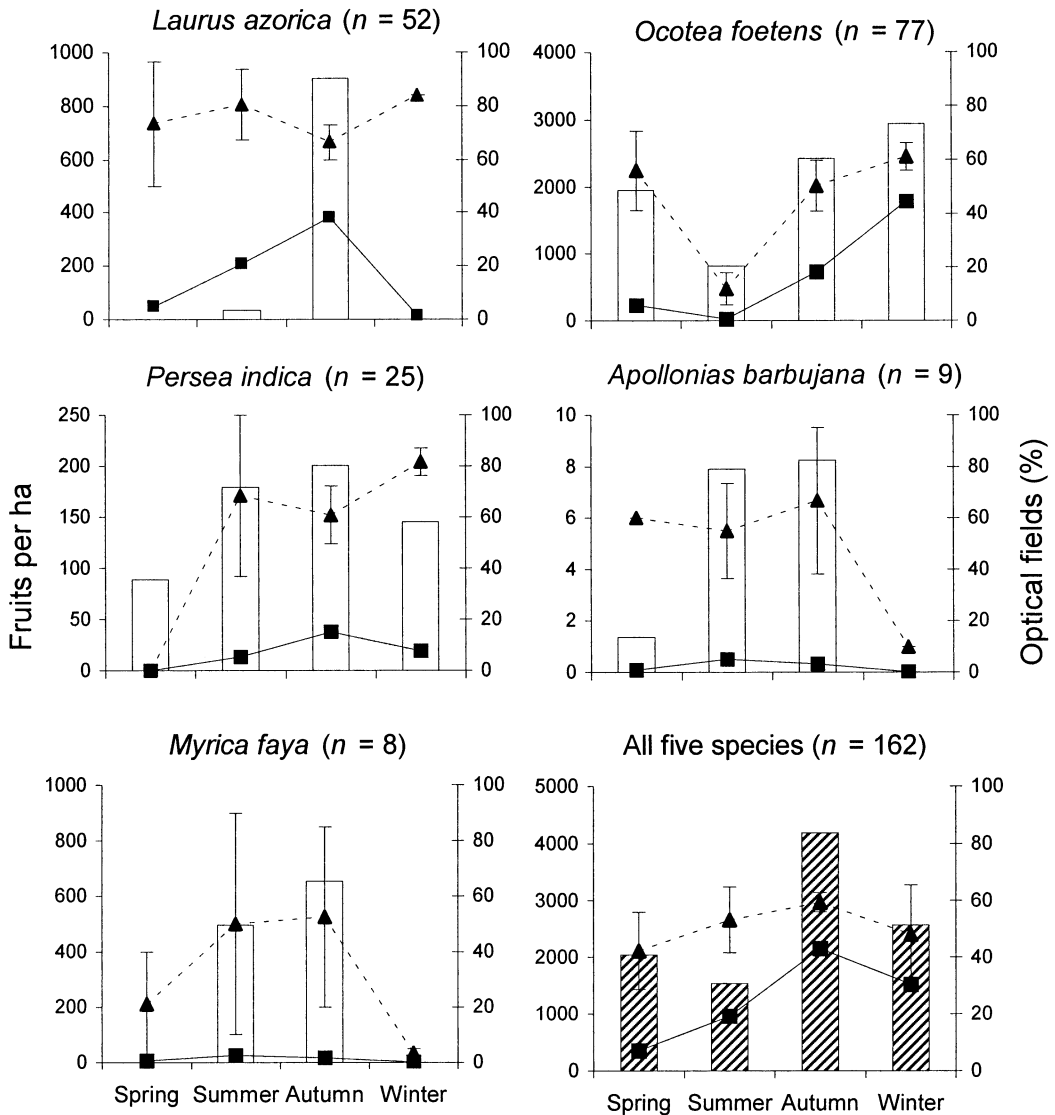


FIGURE 2. Relationship between fruit abundance and diet of the Madeira Laurel Pigeon in Ribeira da Janela, Madeira, from spring 1996 to winter 1997. Triangles and dashed lines represent mean \pm SE percentage of occurrences of the food item in 50 microscope optical fields per fecal sample. Squares and solid lines represent total percentage of all optical fields scanned. Bars represent the estimated number of fruits available per ha of forest. Sample sizes indicate the number of fecal samples containing fruit or seeds of the indicated species, and were used to calculate the mean \pm SE percentages.

SEASONAL VARIATION IN DIET AND AVAILABILITY OF FRUITS

The diet of the Madeira Laurel Pigeon showed a clear seasonal variation. When forest fruit production was at its highest in autumn and winter, fruits were heavily consumed. During autumn *Laurus azorica*, *Ocotea foetens*, and *Persea indica* were very important in the diet; through-

out this period the overall fruit production of the forest, including *Laurus azorica* and *Persea indica*, was at its maximum. In winter, fruits of *Ocotea foetens* and *Ilex canariensis* were intensively consumed, also in concordance with their abundance.

In spring leaves assumed a more important role in the diet, namely those of *Ilex canariensis*,

Aspalthium bituminosum, and an unidentified herbaceous species. This is presumably a result of the low fruit production in the forest at that time. The high diversity of leaf species in the diet reached its maximum during the summer, when at least 22 species were identified in the fecal samples, and fruit production reached its minimum.

These patterns of resource use suggest that Madeira Laurel Pigeons, which live in a limited area and habitat, are dietarily flexible and exploit each food resource as it becomes available. This flexibility in diet was demonstrated by the strong seasonal changes in niche breadth. Hurlbert's index and the positive correlation between percentage of optical fields and availability of fruits indicated that niche breadth was determined by food availability. According to Levins' niche, Madeira Laurel Pigeons narrow their diets in response to a high availability of fruits, and they broaden their diet to include other plant parts when fruits are scarce. These observations suggest an evolutionary relationship between this pigeon and highly variable plant resources.

A study of habitat use carried out simultaneously at the same site (Oliveira et al., unpubl. data) corroborated the seasonal patterns observed in the diet. When the total abundance of fruits in the forest decreased, birds shifted from the trees to the ground and shrub layers. This occurred in late spring and early summer, exactly when *Ocotea foetens* fruits reached their lowest abundance.

In a wider geographic context, Innis (1989) showed that foraging habits of fruit pigeons in subtropical forests in Australia were largely opportunistic; the birds used whatever fruits were available. Frith et al. (1976) and Crome (1975) identified the same pattern for several Australian Columbidae species.

The use of other parts of plants by fruit pigeons when fruit is in short supply has been documented for other species such as the Chatham Island Pigeon (Powlesland et al. 1997). Furthermore the consumption of some leaves and herbs all year round, even when fruit production is high, implies that these foods could supply important diet components. This strategy of using complementary food sources is present among frugivores generally (Jordano 1988, Izhaki and Safriel 1989, Sallabanks and Courtney 1992) and has already been described for other fruit pigeons, namely the White-crowned Pigeon

(Bancroft and Bowman 1994) and the Chatham Island Pigeon (Powlesland et al. 1997).

SEED DIGESTIVE TREATMENT

Most of the seeds of *Ocotea foetens* and *Apollonias barbuiana* present in the fecal samples passed unharmed through the digestive tracts of the birds. However, almost half of the *Persea indica* seeds and most of *Laurus azorica* present in the fecal samples were damaged. These data suggest that pigeons act as legitimate seed dispersers for the first two species. Given that *Ocotea foetens* is the only fruit consistently present throughout the year (Oliveira and Jones 1995, this study), it is probable that pigeons disperse more of their seeds than of the other tree species. The other seed species present in the fecal pellets (*Ilex canariensis*, *Myrica faya*, and *Visnea mocanera*) were smaller in size and more compact, and showed a high resistance to digestion; these data suggest that the Madeira Laurel Pigeon is a potential dispersal agent. Determining the role of Madeira Laurel Pigeons as seed dispersers of several fleshy-fruit tree species will require more specific experiments, including the effect of digestion on seed viability and germination. In other geographical insular areas, such as Polynesia, pigeons play an important role as seed dispersal agents (Steadman and Freifeld 1999).

VALIDATION OF THE MICROHISTOLOGICAL METHOD

Differential digestibility and rates of passage through the digestive tract may introduce some bias in the analysis of fecal samples (Rosenberg and Cooper 1990). However, Rosati and Bucher (1992) have suggested that the impact on the estimated botanical composition will rarely cause significant alterations in diet estimates. Other authors have suggested microhistological methods as a suitable alternative technique for studying avian diets (Jordano and Herrera 1981, Herrera 1998).

In order to validate the results obtained in this study, we performed parallel feeding trials. When we fed birds known amounts of different components of the diet (in different combinations), we generally recovered them in the fecal samples in about the same proportions as expected. Plants that we knew were eaten by the Madeira Laurel Pigeon, but that were absent or in a very low frequency in our fecal samples

(e.g., leaves from *Rumex maderensis* and *Cytisus striatus*), were nevertheless found in the feeding trial fecal samples in the expected proportions. Moreover, despite the greater digestibility of the flower soft tissues, feeding trials showed that they are likely to appear in feces in the same proportion as the other parts of the plants. This strongly validates our conclusions on the composition and seasonal changes in the diet.

In the light of these findings we suggest that the microhistological techniques and procedures described here provide an acceptable level of accuracy, that they are appropriate for the study of herbivorous pigeon diet, and that they may be extensible to other bird species that consume abundant plant food.

CONSERVATION AND MANAGEMENT IMPLICATIONS

The findings of this study contribute to the understanding of the relationship between a vulnerable endemic bird species and its relict forest habitat. Conservation of the species depends on preserving all habitat types required to meet their resource needs throughout the year. Nowadays, with the Madeiran laurel forest well protected, habitat loss and degradation is no longer a threat for the species. However, the knowledge that pigeons use many flowering plants, which occur more abundantly on the edges of the forest, can be used to redefine the conservation value of these areas.

On the other hand, illegal hunting, poisoning, and unpopularity of the Madeira Laurel Pigeon due to the damage it causes to crops, is the present major threat for this species. The information presented here may help to understand the proximate factors which lead to the seasonal use of these areas and may help find a solution to this problem.

ACKNOWLEDGMENTS

This paper is dedicated to the memory of Luis Monteiro, who devoted the last years of his life to a great task on the bird research of the neighboring Azores archipelago. He is an important source of encouragement and inspiration for this and other parts of our work. Stephen Browne, Martin Jones, Derek Gruar, Miguel A. Hernández, the managing editor (Hugh Powell), the editor (David Dobkin) and two anonymous referees read and made useful suggestions that helped to improve the manuscript. Isamberto and Roberto Silva helped us to collect and identify several plants, and Félix M. Medina, Guillermo Hernández,

Francisco Sánchez, Miguel A. Hernández, Martinho Pirs, and Celia and Juan J. Marrero collected fruits. Henrique Costa Neves encouraged us to undertake this study and gave logistical support. María Candelaria Martín, Dília Menezes, and Emanuel Spínola shared some days with us in the field and in the laboratory. Thomas Dellinger and Pedro Oromí provided important technical logistic support. Luisa Fernandes facilitated the development of this research with her kind hospitality. This paper was partially financed by the Parque Natural da Madeira (E.C. Life project) and by a grant from the Universidad de La Laguna awarded to Manuel Nogales.

LITERATURE CITED

- BANCROFT, G. T., AND R. BOWMAN. 1994. Temporal pattern in diet of nestling White-crowned Pigeons: implications for conservation of frugivorous columbids. *Auk* 111:844–852.
- BANNERMAN, D. A. 1963. Birds of the Atlantic islands, vol. 1. A history of the birds of the Canary Islands and of the Salvages. Oliver and Boyd, Edinburgh, UK.
- BANNERMAN, D. A., AND W. M. BANNERMAN. 1965. Birds of the Atlantic islands. Vol. 2. A history of the birds of Madeira, the Desertas and the Porto Santo Islands. Oliver and Boyd, Edinburgh, UK.
- BROOKE, M. DE L., AND P. JONES. 1995. The diet of the Henderson Fruit Dove *Ptilinopus insularis*. I. Field observations of fruit choice. *Biological Journal of the Linnean Society* 56:149–165.
- CHAPUIS, J. L. 1979. Evolution saisonnière du régime alimentaire d'*Oryctolagus cuniculus* dans différents types d'habitats, en France, p. 743–761. In K. Myers and C. D. MacInnes [EDS.], *Proceedings of the world lagomorph conference*. University of Guelph, ON, Canada.
- COSTA NEVES, H., A. V. VALENTE, B. FAVILA, I. SILVA, J. C. MARQUES, N. GOUVEIA, P. SILVA, AND P. OLIVEIRA. 1996. Laurissilva da Madeira. Caracterização quantitativa e qualitativa. Secretaria Regional de Agricultura, Florestas e Pescas. Parque Natural da Madeira, Funchal, Portugal.
- CROME, F. H. J. 1975. The ecology of fruit pigeons in tropical Northern Queensland. *Australian Wildlife Research* 2:155–185.
- FRITH, H. J., F. H. J. CROME, AND T. O. WOLFE. 1976. Food of fruit-pigeons in New Guinea. *Emu* 76: 49–58.
- GIBBS, D., E. BARNES, AND J. COX. 2001. Pigeons and doves. A guide to the pigeons and doves of the world. Pica Press, Mountfield, UK.
- GODMAN, F. 1872. Notes on resident and migratory birds of Madeira and the Canaries. *Ibis* 2:209–224.
- GOODWIN, D. 1983. Pigeons and doves of the world. Cornell University Press, New York.
- HARCOURT, E. 1851. A sketch of Madeira. John Murray, London.
- HERNÁNDEZ, M. A., A. MARTÍN, AND M. NOGALES. 1999. Breeding success and predation on artificial nests of the endemic pigeons Bolle's Laurel Pigeon *Columba bollii* and White-tailed Laurel Pi-

- geon *Columba junoniae* in the laurel forest of Tenerife (Canary Islands). *Ibis* 141:52–59.
- HERRERA, C. M. 1998. Long-term dynamics of Mediterranean frugivorous birds and fleshy fruits: a 12-year study. *Ecological Monographs* 68:511–538.
- INNIS, G. J. 1989. Feeding ecology of fruit pigeons in subtropical rainforests of south-eastern Queensland. *Australian Wildlife Research* 16:365–394.
- IZHAKI, I., AND U. N. SAFRIEL. 1989. Why are there so few exclusively frugivorous birds? Experiments on fruit digestibility. *Oikos* 54:23–32.
- JONES, M. J. 1990. A survey of the distribution and habitat preferences of the Long-toed Pigeon, *Columba trocaz* in Madeira. *Boletim do Museu Municipal do Funchal* 42:71–86.
- JONES, M. J., K. HAMER, J. HILL, M. V. HOUNSOME, P. JEPSON, L. A. LACE, H. READ, AND C. TURTLE. 1988. A survey of the distribution and habitat preferences of the Long-toed Pigeon, *Columba trocaz* in Madeira. International Council for Bird Preservation. Study report 32. Cambridge, UK.
- JORDANO, P. 1988. Fruit choice and variation in body condition of frugivorous warblers in Mediterranean scrubland. *Ardea* 76:193–209.
- JORDANO, P., AND C. M. HERRERA. 1981. The frugivorous diet of Blackcap populations *Sylvia atricapilla* wintering in southern Spain. *Ibis* 123:502–507.
- KREBS, C. J. 1989. *Ecological methodology*. Harper Collins, New York.
- MARTÍN, A., M. A. HERNÁNDEZ, J. A. LORENZO, M. NOGALES, AND C. GONZÁLEZ. 2000. Las palomas endémicas de Canarias. Consejería de Política Territorial y Medio Ambiente del Gobierno de Canarias and SEO/BirdLife, Santa Cruz de Tenerife, Spain.
- MOHAMMAD, A. G., R. D. PIEPER, J. D. WALLACE, J. L. HOLECHEK, AND L. W. MURRAY. 1995. Comparison of fecal analysis and rumen evacuation techniques for sampling diet botanical composition of grazing cattle. *Journal of Range Management* 48:202–205.
- NEFF, J. A. 1947. Habits, food, and economic status of the Band-tailed Pigeon. USDI Fish and Wildlife Service. North American Fauna 58. Washington, DC.
- OLIVEIRA, P. 1999. A conservação e gestão do Madeira Laurel Pigeon Trocaz na Madeira. *Pardela* 9:3–6.
- OLIVEIRA, P., AND M. JONES. 1995. Population numbers, habitat preferences and the impact of the Long-toed Pigeon, *Columba trocaz*, on agriculture. *Boletim do Museu Municipal do Funchal* 4:531–542.
- OLIVEIRA, P., M. JONES, D. CAIRES, AND D. MENEZES. 1999. Population trends and status of the Madeira Laurel Pigeon, *Columba trocaz*. *Bird Conservation International* 9:387–395.
- PEARSON, P. E., AND G. C. CLIMO. 1993. Habitat use by Chatham Island Pigeons. *Notornis* 40:45–54.
- POWLESLAND, R. G., P. J. DILKS, I. A. FLUX, A. D. GRANT, AND C. J. TISDALL. 1997. Impact of food abundance, diet and food quality on the breeding of the fruit pigeon, Parea *Hemiphaga novaeseelandiae chathamensis*, on Chatham Island, New Zealand. *Ibis* 139:353–365.
- POWLESLAND, R., A. GRANT, P. DILKS, I. FLUX, AND M. BELL. 1994. Some aspects of the ecology and breeding biology of Parea on Southern Chatham Island, July 1993–April 1994. *Science and Research Series* 82. Wellington, New Zealand.
- RALPH, C. P., S. E. NAGATA, AND C. J. RALPH. 1985. Analysis of droppings to describe diets of small birds. *Journal of Field Ornithology* 56:165–174.
- ROSATI, V. R., AND E. H. BUCHER. 1992. Seasonal diet of the Chacoan Cavy (*Pediolagus salinicola*) in the western Chaco, Argentina. *Mammalia* 56:567–574.
- ROSENBERG, K. V., AND R. J. COOPER. 1990. Approaches to avian diet analysis. *Studies in Avian Biology* 13:80–90.
- SALLABANKS, R., AND S. P. COURTNEY. 1992. Frugivory, seed predation, and insect-vertebrate interactions. *Annual Review of Entomology* 37:377–400.
- SARMENTO, A. A. 1948. Vertebrados da Madeira. I. Junta Geral do Distrito Autónomo, Funchal, Portugal.
- SHERLOCK, M. G., AND J. S. FAIRLEY. 1993. Seasonal changes in the diet of red deer *Cervus elaphus* in the Connemara National Park. *Biology and environment. Proceedings of the Royal Irish Academy* 93:85–90.
- SJÖGREN, E. 1972. Vascular plant communities of Madeira. *Boletim do Museu Municipal do Funchal* 26:45–125.
- SNOW, B., AND D. SNOW. 1988. *Birds and berries*. T and AD Poyser, London.
- SPSS INC. 1999. *SPSS for Windows*, Release 10.0. SPSS Inc., Chicago.
- STEADMAN, D. W., AND H. B. FREIFELD. 1999. The food habits of Polynesian pigeons and doves: a systematic and biogeographic review. *Ecotropica* 5:13–33.
- VOLSØE, H. 1955. The breeding birds of the Canary Islands. II. Origin and history of the Canarian avifauna. *Videnskabelige meddelelser fra Dansk Naturhistorik Forening* 117:117–178.
- ZINO, P. A. 1969. Observations sur *Columba trocaz*. *L'Oiseau et la Revue Française D'Ornithologie* 39:261–264.
- ZINO, F., AND P. A. ZINO. 1986. An account of the habitat, feeding habits, density, breeding and need of protection of the Long-toed Pigeon, *Columba trocaz*. *Bocagiana* 88:1–16.