

Frugivory and factors influencing visitation by birds at 'Balo' (*Plocama pendula* Ait., Rubiaceae) plants in the Canary Islands¹

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Abstract: We present results of a three-year study on the frugivory, foraging behavior and factors influencing bird preference visits among conspecific fruiting shrubs of the 'Balo' (*Plocama pendula*), an endemic plant of low xerophytic zones in the Canary Islands. Only four bird species were recorded eating fruits of the 20 individual plants studied, including two seed disperser species, *Sylvia melanocephala* (frequency of visits, FV = 64.8%) and *Sylvia conspicillata* (FV = 20.9%), one seed predator (*Serinus canarius*, FV = 12.6%), and one pulp consumer (*Parus caeruleus*, FV = 1.7%). The number of visits/hour by the two warbler species (1.65) was significantly higher than that of the seed predator (0.28) in the three years. However, visitation rates by dispersers decreased from 1993 to 1995 while a higher visitation rate was observed in 1995 for seed predators. Foraging rates (number of fruits consumed/visit) of seed predators ($\bar{x} = 19.2$) was higher than for legitimate birds than for seed predators. Legitimate dispersers tended to select plants in well-developed shrub cover sites, with a low crop size of neighboring conspecifics and a high individual crop size. Visitation rate by the seed predator species to the plants was significantly correlated with fruit crop size and the presence of high numbers of seeds per fruit.

Keywords: frugivory, bird foraging, seed dispersers, seed predators, *Plocama*, *Sylvia*, *Serinus*, *Parus*.

Résumé : Nous présentons les résultats d'une étude d'une durée de trois ans sur la capture des fruits du 'Balo' (*Plocama pendula*), un arbuste endémique des zones xérophytiques des Îles Canaries. Nous avons analysé le comportement de récolte des oiseaux, ainsi que les facteurs influençant leur préférence de visite des arbustes. Seulement quatre espèces d'oiseaux ont mangé des fruits sur les 20 arbustes étudiés : celles-ci incluaient deux espèces qui disséminent les graines de façon efficace, *Sylvia melanocephala* (fréquence des visites : FV = 64,8 %) et *Sylvia conspicillata* (FV = 20,9 %), une espèce qui consomme les graines (*Serinus canarius*, FV = 12,6 %) et une espèce qui mange la pulpe des fruits (*Parus caeruleus*, FV = 1,7 %). La fréquence des visites faites par *Sylvia* spp. (1,65 visite/heure) était significativement plus élevée que celle faite par *Serinus* (0,28 visite/heure). Cependant, le taux de visite de *Sylvia* spp. a diminué de 1993 à 1995, alors qu'un taux de visite plus élevé était observé en 1995 chez *Serinus*. Le taux de récolte (fruits consommés/visite) de *Serinus* ($\bar{x} = 19,2$) était plus élevé que celui de *Sylvia* spp. ($\bar{x} = 3,3$). Lors de la récolte de la nourriture, les oiseaux du genre *Sylvia* choisissaient plus fréquemment que ceux du genre *Serinus*. *Sylvia* spp. avaient tendance à sélectionner des plantes qui avaient une forte production de fruits, mais dont les voisins avaient une faible production et ce, dans des sites dont le couvert arbustif était dense. Le taux de visite de *Serinus* était significativement corrélé au nombre de fruits produits par l'arbuste et à la présence d'un grand nombre de graines par fruit.

Mots-clés : disséminateurs de graines, prédation sur les fruits, prédateurs de graines, *Plocama*, *Sylvia*, *Serinus*, *Parus*.

Introduction

Studies dealing with interactions between vertebrate frugivores and fleshy-fruited plants have focused on the selective role of vertebrates upon fruit or plant traits (*i.e.*, dispersal syndromes), assuming that these systems are coevolved (Howe & Estabrook, 1977; Herrera, 1981). Since Janzen (1980) defined the term coevolution, most contributions have approached the study of frugivory without examining the spectra of requirements proposed for the occurrence of this phenomenon. This lack is a consequence of the great number of constraints that influence mutualistic fruit-bird interactions (Wheelwright & Orians, 1982; Howe, 1984; Herrera, 1985; 1986; Jordano, 1987a). In this respect, the high diversity of vertebrate seed dispersers using a particular fruit species in different ways deserves mention (Howe & Vande Kerckhove, 1979; Davidar & Morton, 1986;

Malmberg & Willson, 1988; Herrera, 1995 and references therein), as well as the variations in temporal (Willson & Whelan, 1993; Jordano, 1992, 1994, 1995) and spatial (Moore & Willson, 1982; Manasse & Howe, 1983; Guitián *et al.*, 1992; Jordano, 1992, 1994) patterns of fruit removal.

It has been demonstrated that frugivorous bird species do not forage at random (Foster, 1990; Sallabanks, 1993; Traveset, 1994). Both intrinsic (*i.e.*, fruit size, fruit pulpiness, crop size) and extrinsic factors (*i.e.*, vegetation cover of the neighboring plants, crop sizes of the neighboring conspecific plants) have been mentioned as important for attracting frugivorous birds (see Sallabanks, 1993 and references therein). Crop size has been frequently reported as one of the most important factors used by birds to select fruiting plants (Howe & Vande Kerckhove, 1979; Howe, 1981; Jordano, 1982; Martín, 1985; Davidar & Morton, 1986; Murray, 1987; Foster, 1990; Sallabanks & Courtney, 1993; Willson & Whelan, 1993; Herrera *et al.*, 1994; Alcántara *et al.*, 1997). Other variables have also been considered important:

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vegetation structure around the plant (Moore & Willson, 1982; Piper, 1986; Thébaud & Debussche, 1992), neighboring crop size (Manasse & Howe, 1983; Sargent, 1990), and fruit traits such as seed size or number of seeds per fruit (Howe & Vande Kerckhove, 1980; Herrera, 1981; Howe, 1981; Herrera *et al.*, 1994). Furthermore, Howe (1979), Foster (1990), and Guitián, Munilla & Guitián (1994), have all studied the risk of predation as an important modulator of the duration of frugivores visits, the consumption rate of fruits, and its relation to visit rates, respectively. All the previously mentioned factors show both spatial and temporal variations that must influence visit rates.

Birds are expected to select those plants that maximize their foraging efficiency in terms of energy gained per unit of foraging time (Stephens & Krebs, 1986). According to this theory, one could expect birds to select those plants that maximize foraging rate and minimize the energetic cost and predation risk. These factors may differ among frugivorous bird species having contrasting diets (*i.e.*, pulp or seed) and feeding with different methods (swallowing the fruits whole or discarding the pulp or seeds), spending different amounts of time in visits, varying gut processing rates, forming flocks or foraging individually, segregating foraging sites within plants and habitat requirements, etc. (Herrera, 1984a; Courtney & Sallabanks, 1992; Traveset, 1994).

Oceanic island habitats harbor ideal frameworks for studying this mutualistic interaction due to the lower number of vertebrate frugivorous species (seed dispersers, and seed or pulp predators). These habitats are subjected to lesser temporal fluctuations in migratory bird abundance compared to continental areas, and it is possible to find zones with a small number of fleshy-fruited plants offering fruits simultaneously. The Canary Islands provide the opportunity to study a simple system of a single plant species, *Plocama pendula* (Ait.) 'Balo', and two groups of frugivorous species (birds and lizards). Whereas the Canarian lizard species (*Gallotia spp.*) act as suitable qualitative and quantitative seed dispersers (Valido, 1999), the bird species are involved in different interactions, some of them as seed dispersers and others as fruit predators. Because of this more complex ensemble of interactions, this paper focuses on the avian frugivores of this system. In addition, *P. pendula* is the only shrub that produces small fleshy fruits during the dry summer in our study site.

In this study, we report on the results of three years of fieldwork aimed at studying the general aspects of frugivory, foraging behavior, and factors affecting foraging preferences at *Plocama pendula* plants under the assumption that the different guilds of birds (seed dispersers and seed-predators) probably show differential feeding strategies and ecological requirements. Specifically, we address the following objectives: *i*) to study the frugivorous bird species that are involved in the system, their importance and mode of fruits and seeds handling, *ii*) to assess the foraging behavior of the different bird species under the assumption of the optimal foraging theory, *iii*) to evaluate the potential factors (intrinsic and extrinsic) that are involved in bird visitation rates at plants, and *iv*) to determine the factors influencing bird visitation at plants and variation in patterns during the three years of study.

Material and methods

STUDY AREA AND SPECIES

The volcanic Canary Islands are situated in the Atlantic Ocean some 100 km (at the closest point) from the north-west coast of the African continent (27° 37' to 29° 25' N, 13° 20' to 29° 25' W). The study area is located in Teno Bajo (Barranco de Las Cuevas, 150 m a.s.l.) in the north-western part of Tenerife Island. The climate is typical of dry Canarian coastal habitats, with an annual average temperature of about 21°C and annual average rainfall of 204 mm, mainly during November-January (data from the last 49 years, supplied by the Instituto Nacional de Meteorología de las Canarias Occidentales); the May-September period includes the driest months (rainfall < 3 mm). The vegetation is composed of low and sparse shrub, and is mainly dominated by *Euphorbia spp.*, *Rubia fruticosa* (Ait.), *Periploca laevigata* (Ait.), *Lavandula buchii* (Webb), *Plocama pendula*, and the introduced cactus *Opuntia dillenii* (Ker-Gawl.) Haw. For more information on the study area, see Bramwell (1971) and Valido & Nogales (1994).

The 'Balo', the local name for *P. pendula* (Rubiaceae), is an endemic species of the Canary Islands and is present on the seven main islands, being very common in the riverbeds of the ravines of Tenerife. The 'Balo' occurs in moderate densities, reaching the highest numbers in the ravines (62.7 plants/ha), and the species (up to 4 m high) also grows well, but with lower densities, on the hillsides around the ravines. *P. pendula* flowers during the spring; the fruiting period starts at the beginning of July and finishes by early October. With the exception of fruits produced by the plant *O. dillenii*, an introduced species, no other fleshy fruiting plant species have fruits that ripen during the dry summers of Teno Bajo. *P. pendula* mature fruits vary in the degree of translucency, ranging from a pure tone to roseate translucent. They are round in shape, with a mean diameter of 4.3 mm ($n = 2800$), have one to five small seeds ($\bar{x} = 2.2$, $n = 2800$), and grow in dense terminal clusters.

Fruits of 'Balo' are eaten by the frugivorous birds investigated here and are also heavily consumed by lizards belonging to the endemic genus *Gallotia* (Barquín & Wildpret, 1975; Valido & Nogales, 1994), which are more efficient as seed dispersers than the birds (Valido, 1999). Furthermore, these water-rich fruits (79.4% of the pulp) are consumed by introduced rabbits while they forage on foliage (Nogales, Valido & Medina, 1995) and by the common raven (*Corvus corax* [L.]; Nogales and Hernández, 1994). Nevertheless, consumption by rabbits and ravens is very small when compared to lizards and the passerine birds studied here.

BIRD OBSERVATIONS

Bird visitation was mainly recorded for two weeks in August during the summers of 1993, 1994, and 1995, at the same 20 randomly-selected shrubs. A total of 480 hours (eight hours/shrub/year) of observations were made of bird visitation rates, occurring approximately during the four hours just after sunrise. These 8 hours/year (carried out on clear and warm days) adequately characterized the visitation pattern of each plant and were enough to stabilize the accumulated frequency of bird visits in bivariate plots of number of

bird species *versus* sampling effort (number of observations hours). For each visit observed, we recorded the bird species, visit duration, foraging site (height, external or internal position within the plants), mode of fruit handling (swallow, or consumption of pulp or seeds), number of fruits swallowed or dropped, and number of hops made (an estimate of foraging cost). In addition, agonistic interaction among birds, anti-predator behavior, and presence of raptors (kestrel, *Falco tinnunculus* [L.]; Barbary falcon, *Falco peregrinoides* [Temminck]; sparrowhawk, *Accipiter nisus* [L.]) were also recorded. Bird observations were included in the analyses of visit rates only if they resulted in ingestion of at least one fruit.

Bird species differed in the ways they handled fruits, and, therefore, data for legitimate dispersers and predators were analyzed separately. The two legitimate disperser species, Sardinian warbler *Sylvia melanocephala* (Gmelin), and spectacled warbler *Sylvia conspicillata* (Temminck), plucked and swallowed whole fruits from within the plant. Because of the similarity of fruit treatment, morphology, and behavior, data for these two species were pooled for many statistical analyses. The two predator species, canary *Serinus canarius* (L.), and blue tit *Parus caeruleus* (L.), removed varying amounts of seeds and pulp, respectively. However, analyses include only data for the canary due to the scarcity of visits recorded by the blue tit throughout the study (1.7%).

FRUIT AND SHRUB CHARACTERISTICS

A total of 2800 randomly-selected fruits (40-50 fruits/plant/year) were sampled for measurements. We weighed fresh fruits and seeds using a balance to the nearest 0.1 mg, the diameter was measured with calipers to the nearest 0.1 mm, and the seeds were counted. Dry mass was obtained by drying the fruits in an oven (45-50°C) until constant mass was achieved. Fruit color ($n = 200-250$ fruits/plant/year) was recorded directly on the plants by establishing two categorical types (translucent and roseate). Infestation fruit rate by insects might influence fruit choice; therefore, to study this aspect in the different plants, 200 fruits from each shrub were randomly sampled in 1995 at the end of the study and dissected under a magnification lens (10x).

Plant cover and maximum height were measured. Furthermore, crop size of each plant was estimated by extrapolating counts of fruits on 50 standard bunches, to the whole plant. These estimates were carried out by the same person to avoid bias, and in plants with small crops (less than 3000) all fruits were counted.

During the study, we observed that foraging birds tended to hide inside the plant when predators were present nearby. Therefore, to study the relationship between foliage density and predation risk upon visiting birds, we took four photographs/plant/year to assess the relative degree of foliage cover of each plant. After installing a cardboard target (12 cm × 12 cm) in the center of the shrub, pictures were taken from each of the four cardinal points, at a distance of 1.5 m and a height of 1.70 m. A grid was overlapped on each photograph which allowed a visual estimation of the relative percentage of foliage cover in each of 10 grid squares. This method gave an estimation of the foliage density of each plant and was carried out by the same person to avoid biases.

MICROHABITAT CHARACTERISTICS

In order to characterize the microhabitat where each plant was situated, we used the point-intercept technique. Two perpendicular lines (10 m long) were traced from the center of the 20 plants, oriented towards the four cardinal directions; a scaled stick was held vertically on the ground at one meter intervals to determine the presence or absence of escarpment, stones, bare ground, or shrubs at different heights (25, 50, 75, 100, and 150 cm). Crop sizes of neighboring plants were only measured in the third year, and only plants situated within 25 m were considered.

DATA ANALYSES

Univariate and bivariate statistical analyses were performed and non-parametric tests were used when the requirements of parametric tests were not met, even after data transformation (Zar, 1984; Siegel, 1990). Due to the high number of analyses carried out (bird visitation, foraging rates, fruit and shrub characteristics, and microhabitat), the different tests are indicated in each case where they were performed and also the kind of transformation applied. In order to reduce the variables describing fruit traits (diameter, percentage of water, number of seeds, fruit mass, pulp mass, and pulp mass ratio) and microhabitat characteristics (percentages of escarpment, stones, bare ground, and shrubs at different heights: 25, 50, 75, 100 and 150 cm), two different Principal Component Analyses (PCA) with varimax rotation were performed. Factor scores from the main two components of both analyses were used as single variables in subsequent analyses. In order to obtain the most consistent and simple model, a multiple regression analysis (stepwise) was performed (Pedhazur, 1982). We considered visit rates of the legitimate dispersers and seed predators as two dependent and different variables, and as independent variables: fruit crop size, percentage of foliage density, fruit color (percent of translucent fruits), percentage of seeds damaged, crop size of the neighbor conspecific plants, the first two components of the PCA performed on fruit traits, and the other two components of the PCA that define the microhabitat. In order to increase the sample size in the stepwise regression analysis, we considered the visit rate data pooled for the three years ($n = 60$ plants). The main problem for simultaneously studying the general plant visitation pattern is the non-statistical independence of data and the existence of between-year variance. To remove this variation, we estimated residuals from one-way ANOVA analyses for each variable (intrinsic and extrinsic) with year as the main effect. These residuals were included as new variables in the stepwise regression analyses, and the variables were normalized prior to analyses.

Results

BIRD VISITATION

A total of 925 feeding visits were recorded during the study period, and only four bird-species visited the 20 plants selected in the study area. Most of the visits (85.7%) were made by seed dispersers (64.8% for *Sylvia melanocephala* and 20.9% for *S. conspicillata*), whereas the seed predator (*Serinus canarius*) and the pulp consumer (*Parus caeruleus*) showed lower values (12.6% and 1.7% respectively; Table I). Apart from the four species observed

TABLE I. Number of feeding visits by bird species to *Plocama pendula* shrubs during the study period. Seed dispersers: Smel = Sardinian warbler (*Sylvia melanocephala*) and Scons = spectacled warbler (*Sylvia conspicillata*); Fruit predators: Pcac = blue tit (*Parus caeruleus*; pulp consumer) and Scan = canary (*Serinus canarius*; seed predator); V/hr = number of bird visits per hour

Year	Frugivorous birds				Seed dispersers		Fruit predators		Total	
	Smel	Scons	Pcac	Scan	Visits	V/hr	Visits	V/hr	Visits	V/hr
1993	270	114	9	28	384	2.29	37	0.22	421	2.51
1994	227	70	4	5	297	1.85	9	0.06	306	1.90
1995	102	9	3	84	111	0.72	87	0.57	198	1.29
Total	599	193	16	117	792	1.65	133	0.28	925	1.93

consuming fruits at the 20 plants monitored, Spanish sparrow (*Passer hispaniolensis* Temminck) and blackbird (*Turdus merula* L.) were occasionally seen feeding upon this fruit species in other shrubs (one and two occasions, respectively).

Number of visits/hour made by the Sardinian warbler was significantly higher than those carried out by the spectacled warbler and the canary in all three years combined (one-way ANOVA, $F_{2,177} = 17.61$, $p < 0.001$) and when analyzed separately by years ($p < 0.05$). However, no statistical difference was detected in 1995 between the Sardinian warbler and the canary (Scheffé test, $p > 0.05$) but a significant difference was seen between the canary and the spectacled warbler in the same year ($F_{2,57} = 4.35$, $p = 0.017$, Scheffé test, $p < 0.05$; Table I).

The number of visits/h by legitimate disperser species decreased from 1993 to 1995 (RANOVA: Sardinian warbler, $F_{2,38} = 7.84$, $p = 0.001$; Spectacled warbler, $F_{2,38} = 3.95$, $p = 0.028$). A different trend, reaching a maximum in the last year, was observed in the case of the seed predator ($F_{2,38} = 7.46$, $p = 0.002$, Scheffé test, $p < 0.05$). No significant differences were detected among years for pulp consumers ($F_{2,32} = 0.82$, $p = 0.44$).

FORAGING RATES

The seed predator showed higher consumption rates (number of fruits consumed/visit) compared to legitimate dispersers (one-way ANOVA, $F_{2,350} = 71.99$, $p < 0.001$) and no significant differences were observed between the two warbler species (Scheffé test, $p > 0.05$). Canaries spent significantly more time in plants per visit (one-way ANOVA, log transformation, $F_{2,212} = 32.11$, $p < 0.001$) and also showed slightly higher foraging rates ($\bar{x} \pm SD = 6 \pm 3.1$ fruits/minute, $n = 35$) than seed dispersers ($\bar{x} \pm SD = 5.1 \pm 3.4$ fruits/minute, $n = 310$; $F_{2,344} = 7.76$, $p = 0.0035$). Significant differences were observed between the two warbler species (Scheffé test, $p < 0.05$). Hopping rate was higher for legitimate dispersers compared with seed predators (one-way ANOVA, $F_{2,344} = 49.1$, $p < 0.001$; Scheffé test, $p < 0.05$; Figure 1).

Similar fruit foraging rates were observed for the warbler species in each year (1993: $\bar{x} \pm SD = 5.2 \pm 3.4$ fruits/minute, $n = 109$; 1994: 4.6 ± 2.9 fruits/minute, $n = 145$; and 1995: 6 ± 3.9 fruits/minute, $n = 56$) and only one significant difference was detected between 1994 and 1995 (one-way ANOVA, logarithm transformation, $F_{2,307} = 3.23$, $p = 0.040$, Scheffé test, $p < 0.05$). With respect to the seed predators, significant differences were found among years (1993: $\bar{x} \pm SD = 5.1 \pm 2.5$ fruits/minute, $n = 12$; 1994: 2.0 ± 1.5 fruits/visit, $n = 3$; and 1995: 7.7 ± 2.7 fruits/visit, $n = 20$; one-way ANOVA, logarithm transformation, $F_{2,32} = 12.49$, $p < 0.001$, Scheffé test, $p < 0.05$).

The foraging rate (fruits/minute) of the disperser species was not correlated with fruit crop size (Pearson correlation coefficient; $r_p = 0.10$, $p = 0.52$, $n = 39$). However, the rates at which these birds consumed fruits (range: 4.02-7.02 fruits/minute) differed significantly among shrubs (one-way ANOVA, logarithm transformation, $F_{11,318} = 2.59$, $p = 0.0036$), using only the 12 plants with at least 10 observations of foraging rates.

FRUIT CHARACTERISTICS

The five main fruit characteristics (diameter, fresh mass, quantity of water in pulp, number of seeds/fruit, and color) are shown in Table II. Diameter and fresh mass were the only variables that presented significant variation among years and all fruit traits were correlated (Table III).

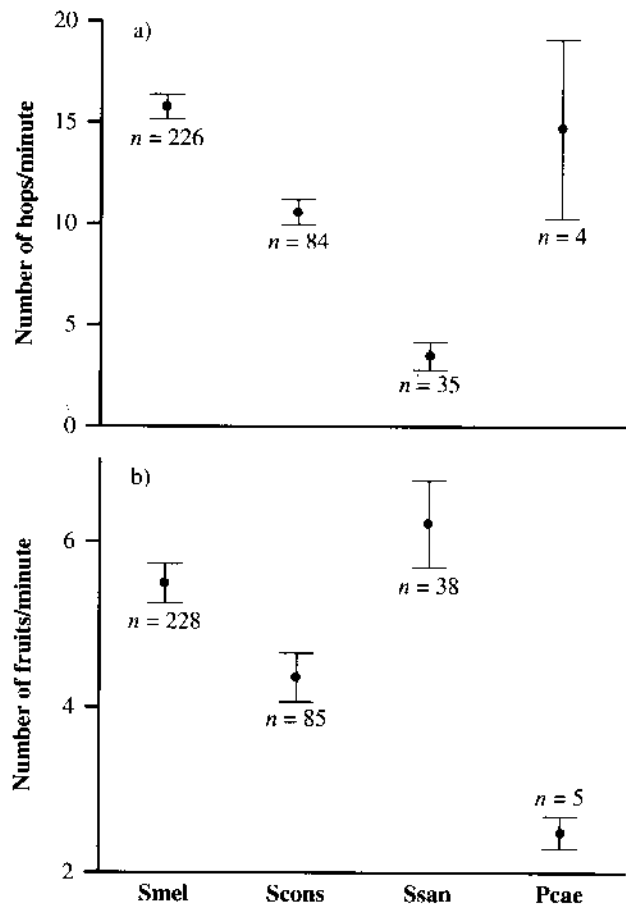


FIGURE 1. a) Mean (\pm SE) of hops/minute observed in the bird species that consumed fruits of *Plocama pendula*. b) Mean (\pm SE) of foraging rates (number of fruits consumed/minute). (Smel: Sardinian warbler *Sylvia melanocephala*, Scons: spectacled warbler *Sylvia conspicillata*, Ssan: canary *Serinus canarius*, Pcac: blue tit *Parus caeruleus*. Number of size observations is indicated).

TABLE II. Descriptive statistics ($\bar{x} \pm SD$) of the main fruit characteristics of *Plocama pendula* (50 fruits/plant/year)

Fruit traits	1993	1994	1995	F	p
Diameter	4.3 ± 0.3	4.1 ± 0.3	4.4 ± 0.3	8.21	0.001
Fresh mass (g)	0.05 ± 0.01	0.04 ± 0.01	0.05 ± 0.01	4.35	0.020
Water in pulp (%)	80.1 ± 2.5	79.3 ± 0.6	79.1 ± 2.5	2.28	0.116
Number of seeds/fruit	2.2 ± 0.3	2.3 ± 0.3	2.2 ± 0.4	1.37	0.266

Adjusted probability values for results of ANOVA (repeated measures).

TABLE III. Correlation matrix of (log-transformed) fruit characteristics of *Plocama pendula*. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Pulp ratio: pulp/seed weight

Fruit Traits	% of water in pulp	Fruit diameter	Fresh weight	Seed weight	Pulp weight	Pulp ratio
% of water						
Fruit diameter	0.270*					
Fresh weight	0.293*	0.839***				
Seed weight	0.007	0.159	0.143			
Pulp weight	0.294*	0.837***	0.999***	0.108		
Pulp ratio	0.295**	0.617***	0.673***	-0.511***	0.694***	

To reduce the number of these correlated fruit characteristics, two components were obtained from PCA analysis. These factors explained 80.5% of the total variance and can be summarized as follows. Factor I (hereafter FI-F) was positively related to fruit size and Factor II (hereafter FII-F) was a gradient of seed load (Table IV).

SHRUB CHARACTERISTICS AND MICROHABITATS

Plant height and ground plant cover varied between 1.45-4.0 m and 1.33-22.5 m², respectively, and no correlation among these traits was observed (Pearson correlation coefficient; $r_p = 0.43$, $p = 0.06$, $n = 20$). Significant differences were detected with respect to fruit crop size of the 20 studied plants (1993: $\bar{x} \pm SD = 56\ 591 \pm 59\ 467$; 1994:

TABLE IV. Principal component analysis of the correlation matrix of (log-transformed) traits of *Plocama pendula* fruits and microhabitat variables of the 20 plants studied

FRUIT TRAITS	Factors	
	F1	F2
FACTOR LOADINGS		
Percentage of water	0.414	-0.089
Fruit diameter	0.913	0.075
Fresh weight	0.973	0.046
Seed weight	-0.115	0.979
Pulp weight	0.973	0.011
Pulp ratio	0.730	-0.640
Cumulative percentage of total variance	58.0	80.5
MICROHABITAT VARIABLES		
Escarpment	-0.491	0.161
Rock cover	0.031	-0.994
Bare ground cover	0.225	0.886
Vegetation cover (at < 25 cm height)	0.794	0.431
Vegetation cover (26-50 cm)	0.906	0.225
Vegetation cover (51-75 cm)	0.961	0.073
Vegetation cover (76-100 cm)	0.941	0.151
Vegetation cover (101-150 cm)	0.651	0.432
Cumulative percentage of total variance	56.8	77.9

Factor loadings > 0.50 and < -0.5 are shown in boldface type.

$\bar{x} \pm SD = 34\ 212 \pm 42\ 518$; 1995: $\bar{x} \pm SD = 33\ 001 \pm 38\ 864$; RANOVA test, logarithm transformation, $F_{2,38} = 5.43$, $p = 0.008$). Fruit crop size was positively correlated with foliage density (Pearson correlation coefficient; $r_p = 0.40$, $p < 0.01$, $n = 60$).

Foliage density was different in each of the three years studied (1993: $\bar{x} \pm SD = 69.9\% \pm 21.0$; 1994: $\bar{x} \pm SD = 58.2\% \pm 18.9$; 1995: $\bar{x} \pm SD = 62.2\% \pm 14.6$; RANOVA, $F_{2,38} = 6.21$, $p = 0.005$).

The PCA on microhabitat variables explained 77.9% of the total variance, with two components. Factor I best summarized vegetation cover (hereafter FI-H), while Factor II is related to the substrate (both bare ground and rocky places) around the plants (hereafter FII-H; Table IV).

FACTORS INVOLVED IN BIRD FORAGING PREFERENCES

For seed dispersers, despite the small sample size, shrub density around the plant (FI-H) was the only variable showing a consistent positive relationship with bird visitation among all three years (Spearman correlation coefficient; 1993: $r_s = 0.62$, $p = 0.003$, $n = 20$; 1994: $r_s = 0.46$, $p = 0.041$, $n = 20$; 1995: $r_s = 0.60$, $p = 0.005$, $n = 20$). Pulpiness (FI-F) was consistent in only the last two years (1994: $r_s = 0.51$, $p = 0.021$, $n = 20$; 1995: $r_s = 0.52$, $p = 0.017$, $n = 20$). Factors only occasionally correlated with bird visitation were foliage density (1993: $r_s = 0.47$, $p = 0.035$, $n = 20$), crop size (1995: $r_s = 0.61$, $p = 0.004$, $n = 20$), plant height (1995: $r_s = 0.56$, $p = 0.010$, $n = 20$), and cover (1995: $r_s = 0.55$, $p = 0.011$, $n = 20$).

For the seed predator, visitation rates were significantly related to foliage density (1993: $r_s = 0.44$, $p = 0.049$, $n = 20$; 1995: $r_s = 0.62$, $p = 0.003$, $n = 20$), plant height (1994: $r_s = -0.46$, $p = 0.040$, $n = 20$), seed load per fruit (1995: $r_s = 0.44$, $p = 0.047$, $n = 20$), and fruit crop size (1995: $r_s = 0.51$, $p = 0.021$, $n = 20$).

Analyses based on pooled, three-year data were performed to assess the visitation pattern shown by the two main bird groups. Stepwise regression analysis indicated that legitimate dispersers tended to select those individual plants that presented higher vegetation shrub cover in the surrounding areas, higher fruit crop size, and lower fruit crop size of the neighboring conspecific plants (Table V). In the case of the seed predator, only two variables were selected in the stepwise analysis, namely fruit crop size and FII-F (fruit seediness).

Discussion

BIRD VISITATION AND FORAGING RATES

Few frugivorous bird species visited 'Balo' plants to consume fruits. This contrasts with the much higher number of frugivorous bird species involved in most palearctic continental communities (Herrera & Jordano, 1981; Herrera, 1984b; Snow & Snow, 1988; Debussche & Isenmann, 1989; Fuentes, 1990; Guitián *et al.*, 1992; Traveset, 1994; Jordano, 1994; 1995). This fact suggests the existence of a specific mutualistic interaction between frugivorous birds and fleshy-fruited plants in island habitats such as the Canary Islands. Nevertheless, it is interesting to note the existence of other frugivorous vertebrates on the Canary Islands that play a major role in seed dispersal of *P. pendula*, such as the Canarian endemic lizards belonging to the genus *Gallotia*, which disperse many seeds produced by the 'Balo' (Valido,

TABLE V. Multiple stepwise regression analysis performed between the frequency of visits of the two group of birds (seed disperser and seed predator) as dependent variables, and crop size, density of foliage, seed damage, crop size of the neighbor conspecific fruits, fruit color, and the two PCA factors obtained on the fruit and microhabitat traits, respectively, as independent variables. FIH = Factor I of the PCA on microhabitat characteristics (high cover of shrubs); CROP = Crop size; CRCN = Crop size of conspecific neighbor plants; FIIF = Factor II of the PCA performed on fruit traits (fruit seediness)

Step	Variable	R ²	mult. R	Partial F	P
SEED DISPERSERS					
1	FIH	0.36	0.60	10.18	0.0051
2	CROP	0.53	0.72	9.69	0.0016
3	CRCN	0.64	0.80	9.68	0.0007
Final model: Visit rate = 0.19 FIH + 9.05 × 10 ⁻⁴ CROP - 0.44 CRCN - 0.07					
SEED PREDATORS					
1	CROP	0.31	0.55	0.55	0.0106
2	FIIF	0.51	0.71	0.71	0.0023
Final model: Visit rate = 0.085 CROP + 7.11 FIIF - 1.81 × 10 ⁻¹⁶					

1999). Despite the low number of avian frugivores, the frequency of visits of the different species was highly variable among the three years (Table I). High between-year variation in the composition of avian frugivore assemblages has similarly been found in other systems (Foster, 1990; Willson & Whelan, 1993; Jordano, 1994).

Seed predators seemed to display more efficient foraging behavior than the seed dispersers. The canary handled a mean of about six times more fruits per visit, spent three minutes more on each visit, and carried out four times fewer hops per time spent foraging than legitimate dispersers.

If we relate the number of visits and the mean of foraging rates (mean number of handled fruits/visit) in 'Balo' plants by a simple multiplication (Table VI and Figure 1), the seed dispersers handled a higher number of fruits than seed predators (53.8 versus 46.2% respectively; $\chi^2 = 27.8$, $p < 0.001$), but these birds usually consumed only one seed per fruit. Therefore, the canary destroyed only about 45.5% of the total amount of seeds from the fruits that it handled, while the two warbler species dispersed all the seeds from fruits they handled. However, a high percentage (54.5%) of seeds from the fruits handled by the canary were dropped beneath the shrubs or close to them.

Several warbler species belonging to the genus *Sylvia* feed intensively on fleshy fruits (Herrera, 1984b; Jordano, 1987b; 1988; Debussche & Isenmann, 1989). Among them, the spectacled warbler shows a more insectivorous diet despite some researchers reporting the sporadic consumption of fruits (see Cramp, 1992 and references therein). Although this phenomenon seems to be infrequent and not intense in temperate continental habitats, our results from the Canary

Islands indicate that this species consumes fruits frequently (20.9% of the visits in this study). This tendency for birds that inhabit oceanic islands to consume fruits, compared to populations from continental zones, has been mentioned previously (Nogales & Hernández, 1994).

FACTORS INFLUENCING FORAGING PREFERENCES AMONG BIRD SPECIES

Both microhabitat variables (out of control from the parent plant) and fruit-shrub characteristics, which are intrinsic traits of the plants, influence the frequency of visits by frugivorous birds. The traits selected by seed dispersers and predators varied from year to year. The only consistent variable was high shrub density adjacent to fruiting plants (FI-H).

Although the data presented here were obtained over a three-year period, our results suggest that even in a natural system characterized by the presence of a single plant species bearing fleshy fruits and few avian frugivores, there are no clear patterns between the fruit-bird relationship. Similar results have previously been reported in more complex continental ecosystems (Traveset, 1994; Herrera *et al.*, 1994; Jordano, 1994; 1995).

Taking into account the pattern observed for the three years pooled (regression analysis), legitimate seed dispersers tended to select those plants that presented a well-developed surrounding shrub cover (FI-H), a low fruit crop size of neighboring conspecifics, and a high individual fruit crop size. These variables have been reported to be important by other researchers (Moore & Willson, 1982; Manasse & Howe, 1983; Piper, 1986; Malmborg & Willson, 1988; Sallabanks, 1992), indicating that studies of the evolutionary ecology of seed dispersal should consider external influences quite out of the control of parent plants. Microsites with presence of shrubs are very suitable and selected by both species of warbler when foraging (Trujillo, 1992).

During 480 hours of observations, we observed six predation attempts; on four occasions a kestrel (*Falco tinnunculus*) dove at a canary while it was feeding on fruits of 'Balo', and in two other cases a female sparrowhawk (*Accipiter nisus*) tried to catch other bird species. Barbary falcons (*Falco pelegrinoides*) were also seen in the study area. The shy behavior of the Sardinian warbler and spectacled warbler is consistent with the hypothesis that predation attempts are regular events during foraging bouts (Howe, 1979). Although the high density of shrubs in the areas surrounding fruiting 'Balo' plants was an important factor, perhaps related to predation risk, regression analyses did not find the foliage density of shrubs to be important. Our observations of raptors hunting birds were made at those plants with high fruit crop size and which were frequently visited by frugivores.

TABLE VI. Three-year estimations of the number of *Plocama pendula* fruits and seeds handled per visit by the two groups of avian frugivores in the twenty plants studied

Frugivorous birds	Number of visits	Mean number of fruits handled /visit	Estimation of handled fruits	Mean number of seeds handled /fruit	Total estimation of seeds handled
Seed dispersers	792	3.3	2614	2.2	5751
Seed predators	117	19.2	2246	1	2246

The second variable found to be important was fruit crop size, which has been mentioned as a key trait positively influencing bird visitation to fruiting plants in other studies (Howe & Vande Kerckhove, 1979; Howe, 1981; Jordano, 1982; Davidar & Morton, 1986; Herrera, 1988; Foster, 1990; Sallabanks & Courtney, 1993; Willson & Whelan, 1993; Herrera *et al.*, 1994; Alcántara *et al.*, 1997). Birds visiting plants with high fruit crop size could maximize foraging efficiency by reducing travel times between fruits. The third variable found to influence visitation by disperser species was the fruit crop size of the neighboring shrubs, as also reported by Manasse & Howe (1983) and Sargent (1990).

Canary visitation to individual plants was significantly correlated with fruit crop size and the presence of high numbers of seeds per fruit. Both variables are intrinsic and therefore under the genetic control of the parent plant. However, if seed disperser's choices are mostly due to extrinsic factors, then opportunities for coevolutionary-type mutualistic interactions are less likely.

During the 480 hours of timed watches at fruiting plants, no interspecific aggression and few instances of aggression were observed. Seed dispersers visited plants individually, and did not capitalize on group-associated benefits such as collective vigilance, reduction of individual risk, or confusion effect. However, the canary normally visited plants in flocks. This could be related to the location of feeding activity: the Sardinian warbler and spectacled warbler preferred to feed within the shrubs, whereas the canary normally foraged on the perimeter of bushes. The risk of predation by raptors is thus likely to be higher for the canary than for both warbler species due to their relative position in the plant when foraging. Additionally, the flocking behavior of the canary at feeding may be better suited to increased vigilance and therefore increased chances of predator detection. In contrast, the position of both warbler species is appropriate for escaping from aerial-scanning of raptors. These combined factors may represent temporally constrained, behavioral alternatives for maximizing the use of the fruit resource by these different frugivores throughout the dry summer (Stephens & Krebs, 1986).

The lack of a significant correlation between visitation rates and fruit size could be related to the small 'Balo' fruit size relative to gape width of the birds. Also, the lack of significant correlations between visits by both warbler species and other fruit traits may reflect the great availability of fruits and the fact that, given the small size and mass of a single seed ($\bar{x} = 0.85$ mg), ingestion of seed ballast would not limit ingestion rates of edible pulp. However, the seed selectiveness for the birds studied by Howe & Vande Kerckhove (1980) and Herrera (1981) decreased as the abundance of fruit increased, suggesting that birds were less concerned with quality when presented with quantity (Howe, 1983; Jordano, 1988). In this respect, the flexibility in foraging behavior may promote an important variability of fruits and might help to understand the existence of a few general patterns (Sallabanks, 1993).

Fruits of 'Balo' are an important water source, and during dry summers in the lowland habitats of the Canary Islands could be critical for the water balance and thermoregulation of small passerines. On the other hand, the water percentage

of fruits did not vary among plants, so selection of individual plants might not be expected on this basis.

Despite the fact that some researchers have reported lower consumption of fruits with insect-damaged seeds relative to fruits with non-parasited seeds (Jordano, 1987c; Cipollini & Stiles, 1993), this factor was not important in the 'Balo', probably because of the very low seed infection (1.8%).

Most of the papers published on the factors influencing bird foraging preferences among fruit plants have cited different factors such as fruit crop size, seed size, the number of seeds per fruit, microsite characteristics, etc. The data on 'Balo' presented here suggest a complex avian-plant interaction among characteristics of the surrounding habitat, individual fruit crop size, and fruit production in the neighboring conspecific shrubs.

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Literature cited

- Alcántara, J. M., P. J. Rey, F. Valera, A. M. Sánchez-Lafuente & J. E. Gutiérrez, 1997. Habitat alteration and plant intra-specific competition for seed dispersers: An example with *Olea europaea* var. *sylvestris*. *Oikos*, 79: 291-300.
- Barquín, E. & W. Wildpret, 1975. Diseminación de plantas canarias. Datos iniciales. *Vieraea*, 16: 263-272.
- Bramwell, D., 1971. Studies in the Canary Islands Flora: The vegetation of Punta de Teno, Tenerife. *Cuaderno de Botánica Canaria*, 11: 4-37.
- Cipollini, M. L. & E. W. Stiles, 1993. Fruit rot, antifungal defense, and palatability of fleshy fruits for frugivorous birds. *Ecology*, 74: 751-762.
- Courtney, S. P. & R. Sallabanks, 1992. It takes guts to handle fruits. *Oikos*, 65: 163-166.
- Cramp, S., 1992. Handbook of the Birds of Europe, the Middle East and North Africa. Volume VI. Warblers. Oxford University Press, Oxford.
- Davidar, P. & E. S. Morton, 1986. The relationship between fruit crop size and fruit removal rates by birds. *Ecology*, 67: 262-265.
- Debusche, M. & P. Isenmann, 1989. Fleshy fruit characters and the choices of bird and mammal seed dispersers in a Mediterranean region. *Oikos*, 56: 327-338.
- Foster, M. S., 1990. Factors influencing bird foraging preferences among conspecific fruit trees. *Condor*, 92: 844-854.
- Fuentes, M., 1990. Relaciones entre pájaros y frutos en un matorral del norte de España: Variación estacional y diferencias con otras áreas geográficas. *Ardeola*, 37: 53-66.
- Gutián, J., M. Fuentes, T. Bermejo & B. López, 1992. Spatial variation in the interactions between *Prunus mahaleb* and frugivorous birds. *Oikos*, 63: 125-130.
- Gutián, J., I. Munilla & P. Gutián, 1994. Influencia de los depredadores de aves en el consumo de *Crataegus monogyna* por zorzales y mirlos. *Ardeola*, 41: 45-54.

- Herrera, C. M., 1981. Fruit variation and competition for dispersers in natural populations of *Smilax aspera*. *Oikos*, 36: 51-58.
- Herrera, C. M., 1984a. Adaptation to frugivory of Mediterranean avian seed dispersers. *Ecology*, 65: 609-617.
- Herrera, C. M., 1984b. A study of avian frugivores, bird-dispersed plants and their interaction in Mediterranean scrublands. *Ecological Monographs*, 54: 1-23.
- Herrera, C. M., 1985. Determinants of plant-animal coevolution: The case of mutualistic dispersal of seeds by vertebrates. *Oikos*, 44: 132-141.
- Herrera, C. M., 1986. Vertebrate-dispersed plants: Why they don't behave the way they should. Pages 5-18 in A. Estrada & T. H. Fleming (ed.), *Frugivores and Seed Dispersal*. Dr W. Junk Publishers, Dordrecht.
- Herrera, C. M., 1988. Plant size, spacing patterns, and host-plant selection in *Osyris quadripartita*, a hemiparasitic dioecious shrub. *Journal of Ecology*, 76: 995-1006.
- Herrera, C. M., 1995. Plant-vertebrate seed dispersal systems in the Mediterranean: Ecological, evolutionary, and historical determinants. *Annual Review of Ecology and Systematics*, 26: 705-727.
- Herrera, C. M. & P. Jordano, 1981. *Prunus mahaleb* and birds: The high-efficiency seed dispersal system of a temperate fruiting tree. *Ecological Monographs*, 51: 203-218.
- Herrera, C. M., P. Jordano, L. López-Soria & J. A. Amat, 1994. Recruitment of a mast-fruiting, bird dispersed tree: Bridging frugivore activity and seedling establishment. *Ecological Monographs*, 54: 315-344.
- Howe, H. F., 1979. Fear and frugivory. *American Naturalist*, 114: 925-931.
- Howe, H. F., 1981. Dispersal of neotropical nutmeg (*Vitellia sebifera*) by birds. *Auk*, 98: 98-99.
- Howe, H. F., 1983. Annual variation in a neotropical seed-dispersal system. Pages 211-227 in S. L. Sutton, T. C. Whitmore & A. C. Chadwick (ed.), *Tropical Rain Forest: Ecology and Management*. Blackwell Scientific Publications, London.
- Howe, H. F., 1984. Constraints on the evolution of mutualisms. *American Naturalist*, 123: 764-777.
- Howe, H. F. & G. F. Estabrook, 1977. On intraspecific competition for avian dispersers in tropical trees. *American Naturalist*, 111: 817-832.
- Howe, H. F. & G. A. Vande Kerckhove, 1979. Fecundity and seed dispersal of a tropical tree. *Ecology*, 60: 180-189.
- Howe, H. F. & G. A. Vande Kerckhove, 1980. Nutmeg dispersal by tropical birds. *Science*, 210: 925-927.
- Janzen, D. H., 1980. When is it coevolution? *Evolution*, 34: 611-612.
- Jordano, P., 1982. Migrant birds are the main seed dispersers of blackberries in southern Spain. *Oikos*, 38: 183-193.
- Jordano, P., 1987a. Patterns of mutualistic interactions in pollination and seed dispersal: Connectance, dependence asymmetries, and coevolution. *American Naturalist*, 129: 657-677.
- Jordano, P., 1987b. Frugivory, external morphology and digestive system in Mediterranean sylviid warblers *Sylvia spp.* *Ibis*, 129: 175-189.
- Jordano, P., 1987c. Avian fruit removal: Effects of fruit variations, crop size, and insect damage. *Ecology*, 68: 1711-1723.
- Jordano, P., 1988. Diet fruit choice and variation in body condition of frugivorous warblers in Mediterranean scrubland. *Ardea*, 76: 193-209.
- Jordano, P., 1992. Fruits and frugivory. Pages 105-156 in M. Fenner (ed.), *Seeds: The Ecology of Regeneration in Plant Communities*. Commonwealth Agricultural Bureau International, Wallingford.
- Jordano, P., 1994. Spatial and temporal variation in the avian-frugivore assemblage of *Prunus mahaleb*: Patterns and consequences. *Oikos*, 71: 479-491.
- Jordano, P., 1995. Frugivore-mediated selection on fruit and seed size: Birds and St. Lucie's cherry, *Prunus mahaleb*. *Ecology*, 76: 2627-2639.
- Malmberg, P. K. & M. F. Willson, 1988. Foraging ecology of avian frugivores and some consequences for seed dispersal in an Illinois woodlot. *Condor*, 90: 173-186.
- Manasse, R. S. & H. F. Howe, 1983. Competition for dispersal agents among tropical trees: Influences of neighbors. *Oecologia*, 59: 185-190.
- Martin, T. E., 1985. Resource selection by tropical frugivorous birds: Integrating multiple interactions. *Oecologia*, 66: 563-573.
- Moore, L. A. & M. F. Willson, 1982. The effect of microhabitat, spatial distribution, and display size on dispersal of *Lindera benzoin* by avian frugivores. *Canadian Journal of Botany*, 60: 557-560.
- Murray, K. G., 1987. Selection for optimal fruit-crop size in bird-dispersed plants. *American Naturalist*, 129: 18-31.
- Nogales, M. & E. C. Hernández, 1994. Interinsular variations in the spring and summer diet of the raven *Corvus corax* in the Canary Islands. *Ibis*, 136: 441-447.
- Nogales, M., A. Valido & F. M. Medina, 1995. Frugivory of *Plocama pendula* (Rubiaceae) by the rabbit (*Oryctolagus cuniculus*) in xerophytic zones of Tenerife (Canary Islands). *Acta Oecologica*, 16: 585-591.
- Pedhazur, E. J., 1982. *Multiple Regression in Behavioral Research*. Harcourt Brace, Jovanovich, Texas.
- Piper, J. K., 1986. Effects of habitat and size of fruit display on removal of *Smilacina stellata* (Liliaceae) fruits. *Canadian Journal of Botany*, 64: 1050-1054.
- Sallabanks, R., 1992. Fruit fate, frugivory, and fruit characteristics: A study of the hawthorn, *Crataegus monogyna* (Rosaceae). *Oecologia*, 91: 296-304.
- Sallabanks, R., 1993. Hierarchical mechanisms of fruit selection by an avian frugivore. *Ecology*, 74: 1326-1336.
- Sallabanks, R. & S. P. Courtney, 1993. On fruit-frugivore relationships: Variety is the spice of life. *Oikos*, 68: 567-570.
- Sargent, S., 1990. Neighborhood effects on fruit removal by birds: A field experiment with *Viburnum dentatum* (Caprifoliaceae). *Ecology*, 71: 1289-1298.
- Siegel, S., 1990. *Nonparametric Statistics for the Behavioral Sciences*. McGraw-Hill, New York.
- Snow, B. & D. Snow, 1988. *Birds and Berries*. T & AD Poyser, Calton.
- Stephens, D. W. & J. R. Krebs, 1986. *Foraging Theory*. Princeton University Press, Princeton, New Jersey.
- Thébaud, C. & M. Debussche, 1992. A field test of the effects of infructescence size on fruit removal by birds in *Viburnum tinus*. *Oikos*, 65: 391-394.
- Traveset, A., 1994. Influence of type of avian frugivory on the fitness of *Pistacia terebinthus*. *Evolutionary Ecology*, 8: 1-10.
- Trujillo, O., 1992. Los silvidos en Gran Canaria. Excmo. Cabildo Insular de GC, Las Palmas de GC.
- Valido, A., 1999. *Ecología de la dispersión de semillas por lagartos endémicos canarios (g. Gallotia, Lacertidae)*. Tesis Doctoral, Universidad de La Laguna, Tenerife, Canary Islands.
- Valido, A. & M. Nogales, 1994. Frugivory and seed dispersal by the lizard *Gallotia galloti* (Lacertidae) in a xeric habitat of the Canary Islands. *Oikos*, 70: 403-411.
- Wheelwright, N. T. & G. H. Orians, 1982. Seed dispersal by animals: Contrasts with pollen dispersal, problems with terminology, and constraints on coevolution. *American Naturalist*, 119: 402-413.
- Willson, M. F. & C. J. Whelan, 1993. Variation of dispersal phenology in a bird-dispersed shrub, *Cornus drummondii*. *Ecological Monographs*, 63: 151-172.
- Zar, J. H., 1984. *Biostatistical Analysis*. Prentice-Hall, London.