

VARIATIONS IN SPINDLE *EUONYMUS EUROPAEUS* CONSUMPTION BY FRUGIVOROUS BIRDS DURING THE FRUITING SEASON

Ángel HERNÁNDEZ*

SUMMARY.—*Variations in Spindle Euonymus europaeus consumption by frugivorous birds during the fruiting season.*

Aims: The main aim of this study was to investigate the small scale spatio-temporal variations (during a fruiting season in different microhabitats) in Spindle *Euonymus europaeus* fruit consumption by birds. Specifically, variations were tested taking into consideration the configuration of the visiting assemblages, visit frequency, amount of fruit consumed per visit, and methods of taking the fruits.

Location: A 1 km² plot situated in the Torío river valley (900-1000 m a.s.l.), León province, NW Spain.

Methods: Four plants with a maximum distance of 0.5 km between them situated in different microhabitats were used to study fruit consumption. The sampling unit was the feeding visit. The number of fruits eaten by each bird during each feeding visit and the method of taking the fruit were also recorded. The persistence of ripe fruit in all the plant species with fleshy fruits was checked weekly, and data was obtained on the seasonal availability of insects and other invertebrates. Bibliography was consulted for quantitative data on fleshy fruit availability and bird density in the area during the study period. The statistical analyses included the chi-square association test (χ^2), Poisson rates test (z), t -test, Mann-Whitney U -test, and Kruskal-Wallis test (K).

Results: Considering the overall data (330 feeding visits), the species that most frequented the Spindles were the Blackcap *Sylvia atricapilla* (40.6%), Robin *Erithacus rubecula* (33.9%), and Song Thrush *Turdus philomelos* (13.6%). Significant differences in the visiting assemblages were recorded among the shrubs. The larger bird species consumed significantly more fruits per feeding visit than the smaller ones (Song Thrush: 11.9 fruits/visit, $n = 45$ visits; Blackcap: 4.2, $n = 134$; Robin: 3.0, $n = 112$). The amount of fruits eaten by some species per visit and the removal method used varied significantly among plants and temporally.

Conclusions: Spatio-temporal changes were probably related to the characteristics of each microhabitat, plant physiognomy, bird movements, and temporal changes in food accessibility and energy demand. The variations observed in the frugivorous avian assemblages within both bird species and species groups (disperser and non-disperser), though the latter differences were subtle and non-significant, could affect Spindle local demography.

Key words: Birds, *Euonymus europaeus*, foraging methods, frugivory, fruit removal, spatio-temporal variations, Spindle.

RESUMEN.—*Variaciones en el consumo de Bonetero Euonymus europaeus por aves frugívoras durante la temporada de fructificación.*

Objetivos: El objetivo general del trabajo fue investigar las variaciones espacio-temporales de pequeña escala (durante una temporada de fructificación en microhábitats diferentes) en el consumo de frutos de Bonetero *Euonymus europaeus* por aves. Concretamente, se analizaron variaciones en la configuración de los gremios de aves, frecuencia de visita, cantidad de frutos consumidos por visita, y métodos de coger los frutos.

Localidad: Una parcela de 1 km² situada en el valle del río Torío (900-1000 m s.n.m.), provincia de León, NO España.

Métodos: Para estudiar el consumo de frutos se utilizaron cuatro plantas en microhábitats diferentes con una distancia máxima entre ellas de 0,5 km. La unidad de muestreo fue la visita de alimentación. Se consideró también la cantidad de frutos consumidos por visita de alimentación y el método de coger los frutos. La persistencia de frutos maduros en todas las especies de plantas con frutos carnosos fue comprobada semanalmente, y se obtuvieron datos sobre la disponibilidad estacional de insectos y otros invertebrados. Se consultó bibliografía para obtener información cuantitativa sobre disponibilidad de frutos carnosos y densidad de aves en el área durante el periodo de estudio. Los análisis estadísticos incluyeron el test de asociación chi-cuadrado (χ^2), test de tasas de Poisson (z), test de la t , test de Mann-Whitney (U), y test de Kruskal-Wallis (K).

Resultados: Teniendo en cuenta los datos globales (330 visitas de alimentación), las especies que visitaron con mayor frecuencia los Boneteros fueron la Curruca Capirotada *Sylvia atricapilla* (40,6%), el Petirrojo *Erit-*

* Departamento de Ciencias Agroforestales, Escuela Técnica Superior de Ingenierías Agrarias, Universidad de Valladolid, E-34004 Palencia, España. e-mail: ahernan@agro.uva.es

hacus rubecula (33,9%), y el Zorzal Común *Turdus philomelos* (13,6%). Las diferencias registradas entre plantas en los gremios visitantes fueron significativas. Las especies de aves más grandes consumieron significativamente más frutos por visita que las más pequeñas (Zorzal Común: 11,9 frutos/visita, $n = 45$ visitas; Curruca Capirotada: 4,2, $n = 134$; Petirrojo: 3,0, $n = 112$). La cantidad de frutos comidos por visita por algunas especies y el método de coger los frutos variaron significativamente entre plantas y temporalmente.

Conclusiones: Los cambios espacio-temporales descritos estuvieron relacionados probablemente con las características de cada microhábitat, la fisonomía de las plantas, los movimientos de las aves, y los cambios temporales en la accesibilidad del alimento y en la demanda energética. Las variaciones observadas en los gremios de aves frugívoras tanto a nivel de especie como de grupos de especies (dispersantes y no dispersantes), aunque estas últimas diferencias fueron sutiles y no significativas, podrían afectar a la demografía local del Bonetero.

Palabras clave: Aves, Bonetero, *Euonymus europaeus*, frugivorismo, métodos de coger los frutos, recolección de frutos, variaciones espacio-temporales.

INTRODUCTION

Very few studies have examined patterns of spatial and temporal variations of the mutual relationships between species of animal-dispersed plants and their vertebrate counterparts (Herrera, 2002). The qualitative and quantitative research of these variations is essential since to a certain extent the features involved of plants and animals change with natural selection depending on the intensity of their relationships, and, furthermore, the demography of plants with fleshy fruits varies according to distinct spatio-temporal scenarios in which relationships with disperser and non-disperser frugivorous vertebrates are different (Herrera & Pellmyr, 2002; Levey *et al.*, 2002).

It is known that the efficiency and dispersal patterns of frugivorous bird species differ depending on their physiological, morphological and behavioural characteristics (Jordano, 1992; Traveset, 1994; Wenny & Levey, 1998; Loiseille & Blake, 1999; Herrera, 2002), but information on changes in composition, structure and visit frequency in frugivorous avian assemblages affecting plant species is still scarce (Guitián *et al.*, 1992; Laska & Stiles, 1994; Nogales *et al.*, 1999; Jordano & Schupp, 2000; Restrepo *et al.*, 2002).

The general objective of this paper is to investigate the small scale spatio-temporal variations (during a fruiting season in different microhabitats) in Spindle *Euonymus europaeus* fruit consumption by birds. Specifically, variations were tested taking into consideration 1) the configuration of the visiting assemblages, 2) visit frequency, 3) amount of fruit consumed per visit, and 4) methods of taking the fruits.

The potential effects of these variations on dispersal success and their importance as selective pressure for population differentiation of the Spindle are only very slightly discussed since further research is needed. The study also contributes to our knowledge of the natural history of the Spindle, as to date only Sorensen (1981) and Snow & Snow (1988) have examined its dispersal biology; and Kollmann *et al.* (1998) and Kollmann & Grubb (1999) have analyzed its post-dispersal survival.

STUDY AREA AND METHODS

General description of the study area

The study area covers 1 km² and is situated in the Torío river valley (30TTN9434 U.T.M. coordinates, 900-1000 m a.s.l., León province, NW Spain). It is part of the Supramediterranean bioclimatic stage in the Mediterranean biogeographic region. The landscape is a mosaic of riparian woodland, hedges, irrigated pastureland, scrub and Pyrenean Oak *Quercus pyrenaica* woods (Hernández & Alegre, 1991; Martín-Larrañaga, 1997).

The plant

The Spindle is an Euroasiatic shrub or small tree, up to 4-6 m tall, and belongs to the family Celastraceae. In Spain it inhabits hedges or clear woods, preferably in fresh, deep soils in the north of the country (López, 1988). In the study area it is not abundant on the edge of the Pyrenean Oak woods and is more common in

hedges (8% occurrence frequency, Hernández & Alegre, 1991), and may display ripe fruit between late October and early February. Its fruit is capsular-shaped and has a long pedicel; when ripe it is pink and opens up revealing three or four seeds covered in a fleshy, orange aril. Each arillate seed measures 4.5-5.0 mm in diameter and 6.0-7.5 mm in length, and from now on will be called "fruit" because it is the unit taken by a feeding bird. The aril pulp is very rich in lipids (36% of the dry weight, Snow & Snow, 1988). The Spindle fruits are eaten by typical seed-disperser birds that swallow them whole and by others that peck at the pulp (Sorensen, 1981; Snow & Snow, 1988). Although the seed is soft and easily opened, it is not consumed by seed-predator birds, probably because of its high toxicity (Snow & Snow, 1988) but is, however, eaten by rodents (Kollmann *et al.*, 1998; Hernández, 1999).

Methods

Four plants with a maximum distance of 0.5 km between them situated in different microhabitats were used to study Spindle fruit consumption by birds:

Plant A. Height: 4.5 m; maximum width: 4.8 m. In a rough scale of density of fruits from 1 (very low density) to 5 (very high density) this plant reached 5. Located on the edge of a narrow irrigation ditch; on one side of the ditch there was a large Poplar *Populus x canadensis* plantation with tall trees and on the other side irrigated pasture; on the edge of the ditch, 25 m on both sides of the Spindle shrub, there were predominantly Hazels *Corylus avellana* but also Dog Roses *Rosa canina*, Hawthorns *Crataegus monogyna*, Black Poplars *Populus nigra*, Willow Trees *Salix fragilis* and Pyrenean Oaks.

Plant B. Height: 4.6 m; maximum width: 3.0 m. Density of fruits: 2. Located on the edge of a Pyrenean Oak wood. Pastureland predominated in a 25 m radius around the Spindle shrub, with some Blackthorns *Prunus spinosa* and a few Pyrenean Oaks and Hawthorns.

Plant C. Height: 3.8 m; maximum width: 3.5 m. Density of fruits: 2. Situated in a hedge with irrigated pasture on both sides. Within the line of the hedge, 25 m on either side of the Spindle shrub, Hazels and Elders *Sambucus ni-*

gra predominated. There were also some Dog Roses, Hawthorns, Blackthorns, Brambles (*Rubus ulmifolius* and *R. caesius*), Privets *Ligustrum vulgare*, Guelder Roses *Viburnum opulus* and Black Poplars.

Plant D. Height: 4.2 m; maximum width: 2.5 m. Density of fruits: 4. The plant had the same type of location and accompanying plants as plant C, but situated in a wider, denser hedge.

During November and December 1996 and January 1997 the birds feeding on the Spindle fruit were directly observed for 55 and a half hours distributed over 19 days. I established two time periods (autumn period 1: 15th November-14th December, 10 observation days; winter period 2: 15th December-14th January, 9 observation days). Morning (08.00-12.00 hours, solar time) was initially distinguished from afternoon (13:00-17:00 hours, solar time) to assess the possible effect of hour of the day, but statistical analyses did not show differences in this respect, so morning and afternoon were considered as a whole. The minimum observation time for each plant during each stage of the day and period of time was 4 hours (except for plant B, which was 1-3 hr; however, two of the three species feeding on this plant during the total 7 hr observation time were detected in both stages of the day and in both periods of time, and carried out 63 of the total 64 recorded feeding visits). There were no data available for Spindle shrubs C and D during period 2 because these plants had no fruit from mid December onwards.

The sampling unit was the feeding visit, that is, each visiting bird was checked for the consumption of at least one fruit (Snow & Snow, 1988). I also recorded the number of fruits eaten by each bird during each feeding visit, as well as the method of taking the fruit (normally perched, in flight, hanging; simplified version from Moermond & Denslow, 1985). The birds were observed from positions that were hidden by vegetation, at a distance of 30-40 m.

In order to determine the availability of other food resources the persistence of ripe fruit in all the plant species with fleshy fruits was checked weekly. The principal European frugivorous bird species are partially insectivorous (Cramp, 1988, 1992), so data was obtained on the seasonal availability of insects and other invertebrates in the study area from Hernández *et al.*

(1993) (systematic sampling) and by rough appreciation of their activity during November 1996-January 1997. Martín-Larrañaga (1997) was consulted for quantitative data on fleshy fruit availability and bird density in the study area from November 1996 to January 1997. Additional information on bird communities of the study area can be found in Hernández & Alegre (1991). Meteorological data provided by the Centro Meteorológico Territorial de Castilla y León came from the La Robla station (León province), very near the study area and at the same altitude.

The statistical analyses followed Fowler *et al.* (1998) and included the chi-square association test (χ^2) (variations in frugivorous avian assemblages considering number of feeding visits, and variations in the methods of taking fruit considering number of fruits consumed), Poisson rates test (z) (variations in feeding visit rate), t -test, Mann-Whitney U -test and Kruskal-Wallis test (K) (variations in the number of fruits consumed per feeding visit). I used the non-parametric U and K tests to compare averages, except the parametric t -test to compare two samples with more than 20 observations in any of them. The critical values were $P < 0.05$ (significant) and $P < 0.01$ (highly significant).

RESULTS

A total of 10 bird species consuming 1,577 Spindle fruits on 330 feeding visits were recorded (Tables 1 and 2). The species that most frequented the Spindles were the Blackcap *Sylvia atricapilla* (*Sa*) (40.61% of total feeding visits), Robin *Erithacus rubecula* (*Er*) (33.94%) and Song Thrush *Turdus philomelos* (*Tp*) (13.64%).

Temporal and spatial variations in the frugivorous avian assemblages and temporal changes in feeding visit rate

When feeding visits carried out by the different bird species were considered, significant temporal differences between periods in the assemblages were recorded for plant A ($\chi^2 = 33.94$, $df = 8$, $P < 0.01$) but not for plant B ($\chi^2 = 0.97$, $df = 2$, $P > 0.05$). With regard to

spatial differences (among plants), significant differences were observed in both periods (period 1: $\chi^2 = 76.47$, $df = 24$, $P < 0.01$; period 2: $\chi^2 = 31.55$, $df = 6$, $P < 0.01$). In general terms, throughout the entire study period plant A was visited predominantly by *Er*, though values for *Sa* and *Tp* were considerable; plant B was visited predominantly by *Sa*; plant C by *Sa*, though values for *Er* were high; and plant D by *Er* (Table 1).

In spite of the spatio-temporal changes detected when the different avian species were considered separately, no significant differences between periods or among plants were observed when two groups, the disperser and non-disperser species, were considered without distinguishing species ($P > 0.05$ in all cases). The mean value for feeding visits by the non-disperser birds, considering each plant and period, was 5.42% ($SD = 4.15$, range = 0.00-11.60, $n = 6$). All the non-disperser birds observed consumed pulp, especially the Great Tit *Parus major* (*Pm*) and there was no record of any of the birds opening the seeds. The non-disperser birds usually pecked at the pulp of the fruits on the plant without removing it or removing and holding it on a branch under the foot. However, on two occasions *Pm* carried the fruit to different places, 4 and 20 m away from the plant, where it ate the pulp and could therefore have acted as a potential short distance disperser.

Considering all the frugivorous bird species, there was a significant temporal increase in the rate of feeding visits to plant A, from 0.93 visits/10 min in period 1 to 1.34 in period 2 ($z = -2.59$, $P < 0.05$), whilst visits to plant B decreased significantly from 2.17 to 1.27 respectively ($z = 2.13$, $P < 0.05$), and the main species of visiting birds showed the same tendencies (Table 1).

Specific, temporal and spatial variations in the number of fruits consumed per feeding visit

Significant interspecific differences were observed in plant A during both periods: *Tp* always consumed more fruits per visit than *Er* or *Sa* (period 1: $K = 33.53$, $df = 2$, $P < 0.01$; period 2: $K = 67.88$, $df = 2$, $P < 0.01$), but this was not the case for plants B, C and D in any of the periods (*Er* and *Sa* were compared; $P >$

TABLE 1

Feeding visits and amount of Spindle *Euonymus europaeus* fruit consumed by birds on each visit. Period 1: 15 November-14 December 1996; Period 2: 15 December 1996-14 January 1997. FV/t (FC/FV): feeding visits per 10 min; in brackets mean amount of fruit consumed per feeding visit. TFV: total feeding visits for each frugivorous bird species. TFC: total fruit consumed for each frugivorous bird species. *Er*: *Erithacus rubecula*. *Sa*: *Sylvia atricapilla*. *Tp*: *Turdus philomelos*. *Tv*: *Turdus viscivorus*. *Ti*: *Turdus iliacus*. *Tm*: *Turdus merula*. *Po*: *Phoenicurus ochruros*. *Pc*: *Parus caeruleus*. *Pm*: *Parus major*. *Ac*: *Aegithalos caudatus*. D: seed-disperser species. PC: pulp-consumer species. g: approximate weight of each bird species in grams (taken from Cramp, 1988, 1992; Cramp & Perrins, 1993). Plants C and D lacked fruit during Period 2.

[*Visitas de alimentación de aves y cantidad de frutos consumidos por visita a Boneteros Euonymus europaeus. Periodo 1: 15 de noviembre-14 de diciembre de 1996; Periodo 2: 15 de diciembre de 1996-14 de enero de 1997. FV/t(FC/FV): visitas de alimentación/10 min; entre paréntesis cantidad de frutos consumidos por visita de alimentación. TFV: total de visitas de alimentación para cada especie de ave frugívora. TFC: total de frutos consumidos por cada especie de ave frugívora. D: especie dispersante de semillas. PC: especie consumidora de pulpa. g: peso aproximado en gramos de cada especie de ave (tomado de Cramp, 1988, 1992; Cramp & Perrins, 1993). Las plantas C y D no tuvieron frutos durante el periodo 2.*]

| | Period 1 [Periodo 1] | | | | Period 2 [Periodo 2] | | TFV | TFC | TFC/TFV |
|-----------------------|----------------------------------|----------------------------------|----------------------------------|----------------------------------|----------------------------------|----------------------------------|-----|-----|---------|
| | Plant A [Planta A] 870 min | Plant B [Planta B] 120 min | Plant C [Planta C] 540 min | Plant D [Planta D] 540 min | Plant A [Planta A] 960 min | Plant B [Planta B] 300 min | | | |
| | FV/t (FC/FV) | FV/t (FC/FV) | FV/t (FC/FV) | FV/t (FC/FV) | FV/t (FC/FV) | FV/t (FC/FV) | | | |
| <i>Er</i> (D) (16 g) | 0.27 (3.00) | 0.25 (2.67) | 0.22 (2.50) | 0.20 (2.54) | 0.58 (3.30) | 0.20 (2.33) | 112 | 337 | 3.01 |
| <i>Sa</i> (D) (19 g) | 0.22 (4.53) | 1.92 (2.09) | 0.28 (3.27) | 0.11 (2.00) | 0.42 (6.82) | 1.03 (3.00) | 134 | 561 | 4.19 |
| <i>Tp</i> (D) (70 g) | 0.32 (9.89) | | 0.05 (6.33) | | 0.14 (17.07) | | 45 | 535 | 11.89 |
| <i>Tv</i> (D) (120 g) | | | 0.02 (6.00) | | | | 1 | 6 | 6.00 |
| <i>Ti</i> (D) (60 g) | 0.03 (9.00) | | 0.02 (3.00) | | | | 4 | 30 | 7.50 |
| <i>Tm</i> (D) (90 g) | 0.03 (3.33) | | | 0.05 (2.00) | 0.03 (6.33) | | 9 | 35 | 3.89 |
| <i>Po</i> (D) (16 g) | | | | | 0.01 (3.00) | | 1 | 3 | 3.00 |
| <i>Pc</i> (PC) (11 g) | 0.02 (3.00) | | | | 0.03 (1.67) | | 5 | 11 | 2.20 |
| <i>Pm</i> (PC) (18 g) | | | 0.05 (3.33) | 0.02 (2.00) | 0.12 (3.33) | 0.03 (4.00) | 17 | 56 | 3.29 |
| <i>Ac</i> (PC) (8 g) | 0.02 (1.50) | | | | | | 2 | 3 | 1.50 |

0.05 in all cases). *Er* showed no significant differences between periods in plants A or B ($P > 0.05$ in both plants), but *Sa* and *Tp* did: higher values were recorded during period 2 for both plants (*Sa*-plant A: $t = 3.50$, $df = 57$, $P < 0.01$; *Sa*-plant B: $t = 1.89$, $df = 52$, $P < 0.05$; *Tp*-plant A: $t = 3.49$, $df = 40$, $P < 0.01$). Significant differences among plants affected *Sa* during both periods: the highest values always corres-

ponded to plant A (period 1: $K = 19.38$, $df = 3$, $P < 0.01$; period 2: $t = 6.91$, $df = 69$, $P < 0.01$), and not *Er* ($P > 0.05$ in both periods). *Er* consumed 3.01 fruits/visit ($SD = 1.20$, range = 1-6, $n = 112$ visits), *Sa* 4.19 ($SD = 2.70$, range = 1-13, $n = 134$) and *Tp* 11.89 ($SD = 7.06$, range = 2-32, $n = 45$) throughout the entire study period and considering all the plants as a whole (Table 1).

Specific, temporal and spatial variations in the methods of taking the fruits

The interspecific differences for each plant and period of time were consistently significant ($P < 0.01$ in five cases), except for plant B in period 1 ($\chi^2 = 0.07$, $df = 1$, $P > 0.05$). In this case only *Er* and *Sa* visited the plant and took the fruit either normally perched or in flight in similar percentages. In general, *Er* removed the fruit mostly in flight (56.68% of 337 fruits consumed), though the normal perched position was also considerable (43.32%); *Sa* used the normal perched method most (73.97% of 561) but in flight as well (24.24%); *Tp* and other *Turdus* species almost always used the normal perched method (98.84% of 606); *Pm* obtained most of the fruit perched normally (76.79% of 56), although it frequently used the hanging from the perch and in flight methods (14.28% and 8.93% respectively); and the Blue Tit *Parus caeruleus* (*Pc*) mostly hung from the perch (81.82% of 11) (Table 2). The Black Redstart *Phoenicurus ochruros* used the normal perched and in flight methods, and the Long-tailed Tit *Aegithalos caudatus* only hung

from the perch, but the sample size for these two species was very small (three fruits for each).

Intraspecific differences were important in some cases, both temporally and spatially, and affected *Er* and *Sa*. During period 1 *Er* obtained most of the fruit on plant A normally perched, whilst in period 2 in flight was predominantly used ($\chi^2 = 20.76$, $df = 1$, $P < 0.01$). *Sa* increased the proportion of in flight removal in comparison to normally perched, on this same plant and comparing both periods; additionally, in period 2 it used the hanging position ($\chi^2 = 10.36$, $df = 2$, $P < 0.01$). During period 1, *Er* preferred the in flight method on all plants except A, where the normally perched position was predominant ($\chi^2 = 40.82$, $df = 3$, $P < 0.01$); *Sa* used normally perched comparatively more on plant A than on the other plants during both periods (period 1: $\chi^2 = 42.26$, $df = 3$, $P < 0.01$; period 2: $\chi^2 = 24.57$, $df = 2$, $P < 0.01$). No significant spatio-temporal intraspecific differences were observed in other cases for *Er* and *Sa* and in all cases for *Tp*, the Blackbird *Turdus merula* (*Tm*), and *Pm* ($P > 0.05$).

TABLE 2

Methods of taking fruit from the Spindle *Euonymus europaeus* by frugivorous birds. FC/t: fruit consumed per 10 min. P: bird normally perched, F: bird in flight, H: bird hanging from the perch. *Er*, *Sa*, *Tp*, *Tv*, *Ti*, *Tm*, *Po*, *Pc*, *Pm* and *Ac*: as in Table 1. Plants C and D lacked fruit during period 2.

[Métodos de coger los frutos de Bonetero *Euonymus europaeus* por aves frugívoras. FC/t: frutos consumidos/10 min. P: ave posada normalmente, F: ave en vuelo, H: ave posada colgándose. *Er*, *Sa*, *Tp*, *Tv*, *Ti*, *Tm*, *Po*, *Pc*, *Pm* y *Ac*: como en Tabla 1. Las plantas C y D no tuvieron frutos durante el periodo 2.]

| | Period 1 [Periodo 1] | | | | | | | | Period 2 [Periodo 2] | | | | | | |
|-----------|----------------------------------|-----------|-----------|----------------------------------|-----------|----------------------------------|-----------|----------------------------------|-------------------------|----------------------------------|-----------|-----------|----------------------------------|-----------|-----------|
| | Plant A [Planta A] 870 min | | | Plant B [Planta B] 120 min | | Plant C [Planta C] 540 min | | Plant D [Planta D] 540 min | | Plant A [Planta A] 960 min | | | Plant B [Planta B] 300 min | | |
| | P FC/t | F FC/t | H FC/t | P FC/t | F FC/t | P FC/t | F FC/t | P FC/t | F FC/t | P FC/t | F FC/t | H FC/t | P FC/t | F FC/t | H FC/t |
| <i>Er</i> | 0.61 | 0.22 | | 0.25 | 0.42 | 0.05 | 0.50 | 0.15 | 0.37 | 0.79 | 1.13 | | 0.10 | 0.37 | |
| <i>Sa</i> | 0.93 | 0.06 | | 2.00 | 2.00 | 0.55 | 0.35 | 0.22 | | 2.26 | 0.50 | 0.08 | 1.70 | 1.33 | 0.07 |
| <i>Tp</i> | 3.17 | 0.01 | | | | 0.33 | 0.02 | | | 2.45 | 0.04 | | | | |
| <i>Tv</i> | | | | | | 0.11 | | | | | | | | | |
| <i>Ti</i> | 0.31 | | | | | 0.05 | | | | | | | | | |
| <i>Tm</i> | 0.11 | | | | | | | 0.09 | 0.02 | 0.20 | | | | | |
| <i>Po</i> | | | | | | | | | | 0.01 | 0.02 | | | | |
| <i>Pc</i> | 0.02 | | 0.04 | | | | | | | | | 0.05 | | | |
| <i>Pm</i> | | | | | | 0.17 | 0.02 | 0.02 | 0.02 | 0.31 | 0.03 | 0.07 | 0.10 | | 0.03 |
| <i>Ac</i> | | 0.03 | | | | | | | | | | | | | |

Availability of other food resources / Bird communities / Meteorological scenarios

Thirteen (72.22%) of 18 plant species with fleshy fruit displayed ripe fruit during some portion of time of the whole study period, but only seven (38.89%) kept them during the period 2: Spindle, Hawthorn, Dog Rose, Blackthorn, Dogwood *Cornus sanguinea*, Privet and Guelder Rose. Quantitatively, the availability of fleshy fruits decreased from 31.3 to 1.1 (fruits/m²) in November and January, respectively. Seasonal abundance of insects and other invertebrates peaked in summer, progressively decreasing by up to 90% in winter; and their monthly availability also diminished noticeably from November through to January. The most abundant bird species were *Er* and *Tm* in most microhabitats during the whole study period. The mean maximum temperature dropped from 9.7°C in period 1 to 6.4 in period 2, the mean minimum temperature dropped from 0.8 to -2.8 respectively, and the ground was covered with snow during four and 13 days respectively.

DISCUSSION

Variations in frugivorous avian assemblages

Frugivorous avian assemblages visiting Spindles differed much more noticeably among plants than temporally in the same plant. This was probably influenced by the microhabitat of each plant. Plant A was protected by the Poplar plantation standing close by, which also gave larger birds, such as *Tp*, access to the Spindle shrub; the dense shrub and arboreal cover found near the irrigated pastureland may explain the great relative importance of *Er*, which was predominant in the study area in winter, along with *Tm*, in this type of vegetation. Plant B, situated on the edge of a sparsely populated Pyrenean Oak wood was not visited by large frugivorous birds and *Sa* was ostensibly more prevalent than *Er*. This was perhaps due to the winter nomadic behaviour and arboreal habits of *Sa* (Cuadrado, 1992; Cramp, 1992; own *unpubl. data*). It could also have been because of the scarce shrub cover available for *Er* to remain more constantly (*Er* is very sedentary and territorial in winter, Cramp, 1988; Cuadrado,

1995). Considering both periods as a whole, although there were significant differences among the four plants ($\chi^2 = 98.61$, $df = 27$, $P < 0.01$), no such differences were observed between plants C and D ($\chi^2 = 10.3$, $df = 6$, $P > 0.05$), which were both situated in hedges between irrigated pasturelands and were visited in particular by *Er* and *Sa*.

Temporal changes in feeding visit rate

Changes observed in feeding visit rate during the entire study period appeared to be the result of the acute decrease in fruit availability on most of the Spindle shrubs at the end of the period. However, plant A, with the highest crop size, maintained a good supply of fruit until early January and this allowed feeding visit frequency to increase in period 2. This increase in fruit consumption was presumably brought on by higher energy demand and practically no animal prey availability, both of which were phenomena linked to adverse weather. Passerines with a vegetal-animal mixed diet in the forest ecosystems of NW Spain commonly increase their fruit consumption during adverse atmospheric conditions (Gutián, 1985). Probably, the concentration of Spindle fruit in a few shrubs during period 2 attracted a great number of frugivorous birds to these feeding sites which are scarce and rich in fats. Plant A was visited predominantly by *Er* and at least three different individuals per day came to it in early January, although *Er* density decreased from 24 birds per 10 ha in November to 6 in January, on average, in the study area (Martín-Larrañaga, 1997).

Variations in the number of fruits consumed per feeding visit

The number of fruits consumed during each feeding visit is usually negatively correlated to the size of the fruit and positively correlated to the size of the bird (Jordano, 1992; Fuentes, 1995a; Jordano & Schupp, 2000; Hampe, 2001). It is therefore logical that *Tp* consumed significantly more Spindle fruits on each visit than *Er* or *Sa*. This is most interesting as the order of importance in the total use of Spindle in relation to feeding visits was not the same as

in relation to the number of fruits consumed ($Sa > Er > Tp$ versus $Sa > Tp > Er$). *Sa* and *Tp* both ate approximately twice as many fruits as *Er*.

Sa was able to consume a significantly different number of fruits per visit depending on the Spindle plant. This could be due to variations in accessibility to the fruits and/or the protection provided by the plant and its surrounding vegetation (the highest values were obtained for plant A, which was the thickest, displayed the highest density of fruits, and was surrounded by dense shrub and woodland cover); however, the influence of greater or less availability of other food in each microhabitat must not be ruled out. Some avian species feeding on the same plant ate more fruits per visit during period 2 than period 1, presumably conditioned by the same factors previously explained regarding the parallel increase in feeding visit frequency. According to Hampe & Bairlein (2000a), energy demand and avoidance of predators can affect the number of fruits consumed by birds during each feeding visit. *Er*, which was the smallest species, was least flexible as regards the amount of fruit ingested per visit and showed no significant differences among plants or periods, therefore underlining the limiting effect of body size.

Variations in the methods of taking fruit

Bearing in mind such traits as size, the morphology of the legs (osteology and myology), foot size, pelvis width, morphology of the wings and wing-loading, *Sa* and *Turdus* spp. must feed preferably normally perched, *Er* in flight, *Pc* in the hanging position and *Pm* normally perched or hanging (Leisler & Winkler, 1985; Tatner & Bryant, 1986; Jordano, 1987; Snow & Snow, 1988; Moreno & Carrascal, 1993). These predictions came true in the study area when the birds took fruit from the Spindle, with noticeable interspecific differences, but also some important intraspecific temporal and spatial variations were observed. In the case of plant A, *Sa* and *Er* used the in flight method more and the normally perched method less in period 2, probably because the remaining fruit was inaccessible to the bird in the normally perched position (see Jordano, 1992; Larrinaga,

1997; Fraga, 1998). Both species used the normally perched position in plant A more than in the other plants, presumably due to the large amount of fruit and branches which were easy to negotiate whilst in the perched position but not in flight.

Implications

On a macrogeographical scale, frugivorous avian assemblages vary significantly within the same plant species depending on the area (Fuentes, 1995b, for the European context) and there is evidence that plant populations can select adaptations to particular frugivorous avian assemblages from relatively distant localities (Herrera, 1981; Keeler-Wolf, 1988; Hampe & Bairlein, 2000b; Restrepo *et al.*, 2002; but see Herrera, 1995). On a microgeographical scale, assemblages visiting different plants belonging to the same species appear to show significant differences if the habitat is heterogeneous regarding vegetation structure and flora (Gutián *et al.*, 1992; Nogales *et al.*, 1999; Jordano & Schupp, 2000; present study), unlike plants found in similar microhabitats (e.g. Hernández, 1993).

The spatio-temporal differences observed among Spindle shrubs in the visiting avian assemblages imply differences in the methods of taking fruit and in the efficacy and pattern of seed dispersal, that is, the plants are subjected to different selective pressures. This occurs on such a small spatial scale that differentiation among populations linked to distinct microhabitats would be prevented because of the gene flow, as discussed in similar studies (e.g. Gutiérrez *et al.*, 1992; but see Jordano & Schupp, 2000). However, differences within both frugivorous species and species groups (disperser and non-disperser), though the latter variations are subtle and non-significant, influence plant local demography (Jordano, 1995, and references given in his study), and could affect Spindle.

ACKNOWLEDGEMENTS.—I would like to thank Marcelino Fuentes, José Gutiérrez, Arndt Hampe, Carlos Herrera, Pedro Jordano and Alfredo Valido for their valuable comments on the original manuscript.

BIBLIOGRAPHY

- CRAMP, S. (Ed.) 1988. *The Birds of the Western Palearctic, Vol. V*. Oxford University Press. Oxford.
- CRAMP, S. (Ed.) 1992. *The Birds of the Western Palearctic, Vol. VI*. Oxford University Press. Oxford.
- CRAMP, S. & PERRINS, C. M. (Eds.) 1993. *The Birds of the Western Palearctic, Vol. VII*. Oxford University Press. Oxford.
- CUADRADO, M. 1992. Year to year recurrence and site-fidelity of Blackcaps *Sylvia atricapilla* and Robins *Erithacus rubecula* in a Mediterranean wintering area. *Ringing and Migration*, 13: 36-42.
- CUADRADO, M. 1995. Territory characteristics and the attacks against intruders in migrant robins *Erithacus rubecula* wintering in the Mediterranean area. *Ardeola*, 42: 147-160.
- FOWLER, J., COHEN, L. & JARVIS, P. 1998. *Practical Statistics for Field Biology*. Second edition. Wiley. Chichester.
- FRAGA, M. S. 1998. Fruit-feeding behaviour of the European blackbird (*Turdus merula*) on Atlantic ivy (*Hedera hibernica*): variation between sexes and among locations. *Etología*, 6: 41-47.
- FUENTES, M. 1995a. The effect of unripe fruits on ripe fruit removal by birds in *Pistacia terebinthus*: flag or handicap? *Oecologia*, 101: 55-58.
- FUENTES, M. 1995b. How specialized are fruit-bird interactions? Overlap of frugivore assemblages within and between plant species. *Oikos*, 74: 324-330.
- GUITIÁN, J. 1985. Datos sobre el régimen alimenticio de los passeriformes de un bosque montano de la Cordillera Cantábrica occidental. *Ardeola*, 32: 155-172.
- GUITIÁN, J., FUENTES, M., BERMEJO, T. & LÓPEZ, B. 1992. Spatial variation in the interactions between *Prunus mahaleb* and frugivorous birds. *Oikos*, 63: 125-130.
- HAMPE, A. 2001. The role of fruit diet within a temperate breeding bird community in southern Spain. *Bird Study*, 48: 116-123.
- HAMPE, A. & BAIRLEIN, F. 2000a. Nahrungssuche und Vergesellschaftung frugivorer Zug- und Brutvögel. *Journal für Ornithologie*, 141: 300-308.
- HAMPE, A. & BAIRLEIN, F. 2000b. Modified dispersal-related traits in disjunct populations of bird-dispersed *Frangula alnus* (Rhamnaceae): a result of its Quaternary distribution shifts? *Ecography*, 23: 603-613.
- HERNÁNDEZ, A. 1993. Variación temporal en el consumo de frutos de arraclarón (*Frangula alnus*) por aves en el valle del río Torío (Cordillera Cantábrica, NO de España). *Ardeola*, 40: 21-26.
- HERNÁNDEZ, A. 1999. Semillas de bonetero *Euonymus europaeus* consumidas por ratones de campo *Apodemus sylvaticus*. *Galemys*, 11: 41-43.
- HERNÁNDEZ, A. & ALEGRE, J. 1991. Estructura de la comunidad de passeriformes en setos de la provincia de León (NO de España). *Doñana Acta Vertebrata*, 18: 237-250.
- HERNÁNDEZ, A., PURROY, F. J. & SALGADO, J. M. 1993. Variación estacional, solapamiento interespecífico y selección en la dieta de tres especies simpátricas de alcaudones (*Lanius* spp.). *Ardeola*, 40: 143-154.
- HERRERA, C. M. 1981. Fruit variation and competition for dispersers in natural populations of *Smilax aspera*. *Oikos*, 36: 51-58.
- HERRERA, C. M. 1995. Plant-vertebrate seed dispersal systems in the Mediterranean: ecological, evolutionary, and historical determinants. *Annual Review of Ecology and Systematics*, 26: 705-725.
- HERRERA, C. M. 2002. Seed dispersal by vertebrates. In, C. M. Herrera & O. Pellmyr (Eds.): *Plant-Animal Interactions. An Evolutionary Approach*, pp. 185-208. Blackwell Science. Oxford.
- HERRERA, C. M. & PELLMYR, O. (Eds.) 2002. *Plant-Animal Interactions. An Evolutionary Approach*. Blackwell Science. Oxford.
- JORDANO, P. 1987. Frugivory, external morphology and digestive system in Mediterranean sylviid warblers *Sylvia* spp. *Ibis*, 129: 175-189.
- JORDANO, P. 1992. Fruits and frugivory. In, M. Fenner (Ed.): *Seeds. The Ecology of Regeneration in Plant Communities*, pp. 105-156. CABI. Wallingford.
- JORDANO, P. 1995. Spatial and temporal variation in the avian-frugivore assemblage of *Prunus mahaleb*: patterns and consequences. *Oikos*, 71: 479-491.
- JORDANO, P. & SCHUPP, E. W. 2000. Determinants of seed disperser effectiveness: the quantity component and patterns of seed rain for *Prunus mahaleb*. *Ecological Monographs*, 70: 591-615.
- KEELER-WOLF, T. 1988. Fruit and consumer differences in three species of trees shared by Trinidad and Tobago. *Biotropica*, 20: 38-48.
- KOLLMANN, J., COOMES, D. A. & WHITE, S. M. 1998. Consistencies in post-dispersal seed predation of temperate fleshy-fruited species among seasons, years and sites. *Functional Ecology*, 12: 683-690.
- KOLLMANN, J. & GRUBB, P. J. 1999. Recruitment of fleshy-fruited species under different shrub species: control by under-canopy environment. *Ecological Research*, 14: 9-21.
- LARRINAGA, A. R. 1997. Behaviour of redwing (*Turdus iliacus* L.) during feeding on berries of hawthorn (*Crataegus monogyna*). *Etología*, 5: 9-18.
- LASKA, M. S. & STILES, E. W. 1994. Effects of fruit crop size on intensity of fruit removal in *Viburnum prunifolium* (Caprifoliaceae). *Oikos*, 69: 199-202.
- LEISLER, B. & WINKLER, H. 1985. Ecomorphology. *Current Ornithology*, 2: 155-186.
- LEYEY, D. J., SILVA, W. R. & GALETTI, M. (Eds.) 2002. *Seed Dispersal and Frugivory: Ecology, Evolution and Conservation*. CABI. Wallingford.

- LOISELLE, B. A. & BLAKE, J. G. 1999. Dispersal of melastome seeds by fruit-eating birds of tropical forest understory. *Ecology*, 80: 330-336.
- LÓPEZ, G. 1988. *La Guía de Incafo de los Árboles y Arbustos de la Península Ibérica*. Segunda edición. Incafo. Madrid.
- MARTÍN-LARRAÑAGA, M. 1997. *Endozoocoria por mirlos y zorzales (Turdus spp.) en un borde de melojar (Quercus pyrenaica) en la provincia de León, España*. Trabajo Fin de Carrera. Escuela Técnica Superior de Ingenierías Agrarias. Universidad de Valladolid. Valladolid.
- MOERMOND, T. C. & DENSLow, J. S. 1985. Neotropical avian frugivores: patterns of behavior, morphology, and nutrition, with consequences for fruit selection. In, P. A. Buckley, M. S. Foster, E. S. Morton, R. S. Ridgely & F. G. Buckley (Eds.): *Neotropical Ornithology*, pp. 865-897. American Ornithologist Union. Washington.
- MORENO, E. & CARRASCAL, L. M. 1993. Leg morphology and feeding postures in four *Parus* species: an experimental ecomorphological approach. *Ecology*, 74: 2037-2044.
- NOGALES, M., VALIDO, A., MEDINA, F. M. & DELGADO, J. D. 1999. Frugivory and factors influencing visitation by birds at «Balo» (*Plocama pendula* Ait., Rubiaceae) plants in the Canary Islands. *Écoscience*, 6: 531-538.
- RESTREPO, C., SARGENT, S., LEVEY, D. J. & WATSON, D. M. 2002. The role of vertebrates in the diversification of New World mistletoes. In, D. J. Levey, W. R. Silva & M. Galetti (Eds.): *Seed Dispersal and Frugivory: Ecology, Evolution and Conservation*, pp. 83-98. CABI. Wallingford.
- SNOW, B. K. & SNOW, D. W. 1988. *Birds and Berries*. Poyser. Calton.
- SORENSEN, A. E. 1981. Interactions between birds and fruit in a temperate woodland. *Oecologia*, 50: 242-249.
- TATNER, P. & BRYANT, D. M. 1986. Flight cost of a small passerine measured using doubly labeled water: implications for energetic studies. *Auk*, 103: 169-180.
- TRAVESSET, A. 1994. Influence of type of avian frugivory on the fitness of *Pistacia terebinthus*. *Evolutionary Ecology*, 8: 1-10.
- WENNY, D. G. & LEVEY, D. J. 1998. Directed seed dispersal by bellbirds in a tropical cloud forest. *Proceedings of the National Academy of Sciences, USA*, 95: 6204-6207.

Ángel Hernández is Professor of Zoology and Wildlife Management at Valladolid University, Spain. He is interested in the ecological relationships of the plants and animals from the temperate woodlands and country areas of northern Spain. The importance of plants with fleshy fruit to the survival and conservation of frugivorous vertebrates, and vice versa, is among his research subjects. At present, he has studied in the field for three years the natural history of the Bullfinch *Pyrrhula pyrrhula* (habitat, food, breeding), a granivorous passerine linked to forest edge and overgrown hedgerows.

[Recibido: 30-04-03]
[Aceptado: 17-05-03]