

## Migrant birds are the main seed dispersers of blackberries in southern Spain

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Between-habitat variation in fruit production and bird attributes enhancing seed ingestion and removal were studied to describe the avian seed-dispersal system of blackberries (*Rubus ulmifolius*, Rosaceae) in southern Spain.

Migrant birds were largely responsible for seed dispersal. Among 20 passerine species recorded feeding on fruits, five removed the bulk of seeds: *Sylvia atricapilla* (29.6% of 897 visits recorded), *Erithacus rubecula* (15.2%), *S. borin* (14.7%), *S. melanocephala* (10.1%) and *Turdus merula* (7.7%). During an average day  $\approx$  32400 seeds left a parent clone through the activity of these species.

Seed production was density-dependent, being maximum in high-density situations. Seed removal (i.e., fruit consumption) from individual clones was dependent on crop size, habitat occupied and ripening phenology. Clones ripening a small crop later in the season and/or in low-density habitats had a lower fraction of the crop consumed than did those producing huge crops in high density habitats and/or synchronously with autumn bird migration.

The small, passerine birds presumably contributed to the bulk of seed dispersal because they (1) feed on *Rubus* fruits extensively, (2) showed high visit rates and removed a very high fraction of the seed crop from parent clones, (3) did not damage the seeds nor drop them beneath the parent clone and (4) performed species-specific flights to apparently safe sites for the plant, thus enhancing its colonizing ability.

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Исследовали топические различия в продукции плодов и населении птиц, потребляющих и разносящих семена, с целью анализа системы распространения семян ежевики *Rubus ulmifolius* Rosaceae, птицами в южной Испании. Перелетные птицы активно участвуют в распространении семян. Среди 20 видов воробьиных, у которых зарегистрировано питание плодами, 5 распространяют основную массу семян: *Sylvia atricapilla* (29,6% из 897 зарегистрированных посещений), *Erithacus rubecula* (15,2%), *S. borin* (14,7%), *S. melanocephala* (10,1%), и *Turdus merula* (7,7%). В среднем за день примерно 32400 семян уносятся с родительских клонов в результате активности этих видов птиц. Продукция семян зависит от плотности и достигает максимума в случаях очень высокой плотности. Изъятие семян (то-есть, потребление плодов) с отдельных клонов зависит от величины урожая, характера местообитания и фенологии созревания. В клонах, дающих небольшой урожай и в более позднее время и/или в местообитаниях с более низкой плотностью потребляется меньшая часть урожая, чем в тех, где созревает высокий урожай при высокой плотности и/или синхронно с началом осеннего перелета птиц.

Маленькие воробьиные птицы по-видимому распространяют основную часть семян, т.к. они 1. активно питаются плодами ежевики, 2. часто посещают растения и изымают весьма значительную часть урожая семян с родительских клонов, 3. не повреждают семена и не выбрасывают их рядом с родительскими клонами, 4. осуществляют видоспецифичные полеты в относительно безопасные для растений местообитания и таким образом способствуют их колонизации.

## 1. Introduction

Fleshy-fruit production by plants and fruit-eating by birds are prominent behaviours in both the tropics (Snow 1971, Morton 1973) and temperate areas (McAtee 1947, Turcek 1961). Closely coevolved relationships have been proposed mainly among tropical plants and birds, apparently reciprocally specialized in mutual exploitation for seed dispersal and fruit-food gathering. Extra-tropical plants and birds have been viewed as exemplifying, at the opposite extreme, loose relationships based on mutually opportunistic behaviours (McKey 1975, Howe and Estabrook 1977). However, this theoretical background was built up on the basis of scanty field evidence, in particular from temperate habitats. Thus, several discrepancies with initial predictions on fruit-bird interactions arose when data on non-tropical systems begun to emerge (Frost 1980, Herrera and Jordano 1981, Herrera 1981c).

Most of the initial work on bird-plant coevolution for seed-dispersal lacks documentation of the actual dependence between the system's components, and only infrequently have variations in plant and bird traits related to the dispersal process been studied to clarify selective forces operating upon the system. Bird activity may generate relevant selective pressures on fruiting phenologies (Snow 1965, Thompson and Willson 1979), crop sizes (Howe and Kerckhove 1979) and fruit characteristics (Herrera 1981a, Howe and Kerckhove 1981), thus influencing the overall reproductive pattern of the plant.

I deal here with between-habitat variation in fruit production and fruit features of blackberries, *Rubus ulmifolius* (Schott), in Southern Spain. Clones of *R. ulmifolius*, henceforth referred to as *Rubus*, are commonly found along creeks and water courses, often spreading by vegetative expansion over relatively mesic sites in man-made disturbed areas (e.g., Abrahamson 1975). The considerable within- and between-habitat variation in stem and leaf form, flower features and fruit size and seediness showed by species within the genus *Rubus*, was long ago quoted by Darwin (1859) as an instance of variation in natural populations.

I try to describe the avian seed-dispersal of this shrub and those traits of the bird species that provide removal of the seeds from the parent plant and enhance colonization of new habitat patches.

## 2. Study area

Field work was conducted at Finca El Bañuelo, Provincia de Córdoba, south-central Spain (37° 55'N, 4° 48'W) between 22 Jul and 25 Nov 1978. Mean annual rainfall during the dry period (from Jun through Sep) is 82.0 mm, and 575.4 mm during the humid period (rest of the year). Mean temperature of the hottest and coldest months are 26.6°C (Jul) and 7.9°C

(Dec) (data from the meteorological station of Espiel-Central Térmica, 20 km NNW of El Bañuelo).

The study area is located in a small valley at 500 m a.s.l., with the lower parts in olive-tree culture and orchards. In the uncultivated portions of this zone, *Rubus* grows in dense thickets along a small, seasonal stream. Scattered individuals of *Ulmus* sp., *Rosa* sp., *Crataegus monogyna* (Jacq.), *Ficus carica* (L.), *Celtis australis* (L.) and *Tamus communis* (L.) can also be found in this habitat, which is hereafter named the Grove. A portion of the Grove (referred to as Burned habitat) is an old field recovering from a recent burning in Aug 1977 and *Rubus* clones are there sparsely distributed among some fig and olive trees. The surrounding hillsides are covered by closed Mediterranean oak forest vegetation (Forest habitat hereafter), with *Quercus suber* (L.), *Q. rotundifolia* (Lam.) and *Q. faginea* (Lam.) forming the tree stratum, mixed with reforested *Pinus pinea* (L.). The undergrowth is composed mainly of *Cistus* spp. shrubs and sparsely distributed fleshy-fruit producing species, mainly *Viburnum tinus* (L.), *Arbutus unedo* (L.), *Pistacia lentiscus* (L.), *P. terebinthus* (L.), and *Lonicera implexa* (Aiton). The *Rubus* is found scattered on the lower parts of the hillside, close to the Grove.

## 3. Methods

### 3.1. The plants

The position of *Rubus* clones exceeding 0.2 m<sup>2</sup> in basal area were mapped and 19 clones of three sizes (small, <10 m<sup>2</sup>, medium, 10–100 m<sup>2</sup> and large, >100 m<sup>2</sup>) were marked in the three habitats. Basal area and volume were estimated for each clone assigning a geometrical figure and taking the corresponding measurements (Walsberg 1977). Fruit crop was estimated from direct raceme counts in small and medium-sized clones and the number of fruits produced was calculated as: Total number of racemes × mean number of fruits raceme<sup>-1</sup> (the last figure calculated from a sample of marked racemes, see below). The fruit crop of large clones was estimated as: (mean number of racemes m<sup>-2</sup> of exposed surface) × total exposed surface (calculated from the above measurements) × (mean number of fruits raceme<sup>-1</sup>) if a direct count of racemes was impracticable. Mean no. of racemes m<sup>-2</sup> was obtained by regular sampling of the clone's surface with a frame 1 m<sup>2</sup> and recording the number of racemes included in the frame in each of 20 counts per clone.

Fruit characteristics were determined for a sample of fruits taken from six clones of the three habitats. Fresh fruits were weighed individually to the nearest 0.01 g and then desiccated for 24 h at 100°C to obtain dry weights and number of seeds fruit<sup>-1</sup>. Seed dry weight of individual fruits was calculated from the regression of mean seed dry weight for individual clones vs. mean no. seeds fruit<sup>-1</sup>: seed dry weight = 0.005–6.45 · 10<sup>-5</sup> no.

seeds fruit<sup>-1</sup> ( $r_s = -0.857$ ,  $P < 0.01$ ,  $n = 8$ ). This allowed an estimation of individual seed weights for fruits of a given seediness, as it was extremely difficult to separate pulp from seeds due to the small size of the drupelets. Thus, total seed dry weights (i.e. seed loads) were obtained by multiplying the estimated seed weights by the known seediness, pulp dry weights being obtained by subtraction of seed loads from fruit dry weights.

At the beginning of the fruiting period a total of 6625 potential fruits (171 racemes) were marked in 12 clones, either as buds, flowers or unripe fruits. From 22 Jul through 24 Nov 1978, 20 counts (once a week) were carried out on marked racemes, recording the number of buds, flowers, and unripe, ripe, unripe-desiccated, ripe-desiccated, pecked and pecked-desiccated fruits in each raceme.

### 3.2. The birds

Data on bird activity in relation to *Rubus* were obtained by mist-netting and by direct observation of individual clones. Mist nets were operated weekly between 19 Aug and 4 Nov, yielding 708 net-hours. Nets were situated among *Rubus* shrubs in the three habitats and remained open from dawn to dusk. Nets were emptied hourly and birds caught were measured, weighed and released. Net, hour of capture and side of the net in which the bird was found were recorded as well. Samples of the gastrointestinal content were obtained by flushing physiological sodium chloride water solution through the digestive tract (Moody 1970). Faecal samples were stored individually in filter paper and air-dried for later analysis. Percent sample volume made up by animal and vegetable matter was estimated visually to the nearest 10%. Fruit skins were identified by comparison of microscopic slides with a reference collection of skin microphotographs (see Herrera and Jordano 1981 for details).

Direct observations were carried out at a clone (G2, see below) in the Grove from a hide 10 m away on the side of the clone facing the Forest hillside. Five half-hour observation periods were distributed throughout the daylight hours in weekly censuses between 6 Sep and 9 Nov and the identity of all birds flying to and/or from the plant was recorded. Whenever possible, flight directions (along the Grove or to the Forest) of birds leaving the clone and the relative location of the first perch utilized ('distant', if >20 m away or 'close', if <20 m away) and its identity (*Rubus* or a perch above *Rubus*, or another species) were also recorded. Additional observations were carried out on clones M5 and P1, with smaller fruit crops (see Results), for 3.5 and 3.0 h respectively. The number of bird visits d<sup>-1</sup> was calculated from mean visits h<sup>-1</sup>, allowing for 12 h of daylight during the period of field work.

Between the half-hour census periods time was devoted to observing the feeding behaviour of individual

birds at *Rubus*. Whenever possible, the following data were recorded: (1) total time the bird was under observation (either in completely or partially observed visits), (2) total time the bird remained stationary, (3) number of fruits pecked, (4) number of pecks made in the observation period and (5) method of taking fruit (see Results). In each attempt (peck) the birds ingest an unknown number of drupelets, each one containing one seed. To estimate the average number of seeds taken during a visit I first calculated the number of seeds min<sup>-1</sup>, scaling specific feeding rates (pecks min<sup>-1</sup> and pecks fruit<sup>-1</sup>) with respect to *T. merula* average feeding rate (30 seeds peck<sup>-1</sup> and 120 seeds min<sup>-1</sup>) and taking 30 seeds fruit<sup>-1</sup> as the average seediness for fruits from the clone G2:

$$\text{Seeds min}^{-1} (\text{species } i) = \text{Seeds min}^{-1} (T. \textit{merula}) \times \frac{\text{pecks min}^{-1} (T. \textit{merula})}{\text{pecks min}^{-1} (\text{sp. } i)}$$

These ratios are equivalent to weight ratios among the species involved, allowing for the calculation of seeds min<sup>-1</sup> for each species, provided body weight is significantly correlated with measures of feeding rates (see Results). I then estimated seeds visit<sup>-1</sup> for the species *i* from data on visit length and seeds min<sup>-1</sup>. This provides a way to accurately estimate seed ingestion rates for birds feeding on multi-seeded fruits (such as polydrupes, e.g., McDiarmid et al. 1977) for which *one* peck does not represent *one* whole fruit ingested and *one* seed processed.

## 4. Results

### 4.1. The plant population

The *Rubus* population at El Bañuelo is characterized by an abundance of small, 5–10 m<sup>3</sup>, vegetatively expanding clones with crop sizes between 10<sup>2</sup> and 10<sup>3</sup> fruits and some clones with extremely large crops (10<sup>5</sup>–10<sup>6</sup> fruits on clones of 100–1000 m<sup>3</sup>). The clones are distributed on a narrow corridor along the stream course and lower parts of the adjacent hillside (see below). Both clonal size and density are higher in the Grove, where medium-sized (≈250 m<sup>3</sup>) and large (≈1100 m<sup>3</sup>) clones are common. In both the Forest and Burned habitats, only medium (30–70 m<sup>3</sup>) and small (<10 m<sup>3</sup>) clones can be found probably because increased shading and depth of water table and the recent disturbance have limited *Rubus* expansion in these areas.

Fruit crop increases with clone size ( $r_s = 0.86$ ,  $P < 0.01$ ,  $n = 18$ ) but for a given size, crops of the Grove clones are much greater than those of the Forest and Burned habitats. Thus, among the small clones found in the study area, those growing in the Grove consistently had crop sizes >10<sup>3</sup> fruits vs. <700 fruits on clones of the same size found in the Forest and Burned habitats. For a given clone size, fruit production is maximum in the Grove while for a given crop size, clone size is maximum in the Forest and Burned habitats.

Tab. 1. Characteristic features of *Rubus ulmifolius* fruits in the three habitats studied. Means  $\pm$  one s.d., sample size in parentheses. Seed load = seed weight  $\times$  no. seeds fruit<sup>-1</sup>, seed weight being estimated from regression of seed weight (mean values for individual clones) on no. seeds fruit<sup>-1</sup> (see Methods). a = dry weight (g).

	Grove	Forest	Burned habitat
Fresh weight (g) .....	0.81 $\pm$ 0.31 (99)	0.49 $\pm$ 0.26 (10)	0.52 $\pm$ 0.29 (31)
Dry weight (g) .....	0.20 $\pm$ 0.08 (99)	0.16 $\pm$ 0.07 (10)	0.15 $\pm$ 0.07 (31)
Percent water .....	75.5 $\pm$ 3.8 (99)	63.4 $\pm$ 7.9 (10)	67.9 $\pm$ 8.3 (31)
Seed weight (g $\times 10^{-3}$ ) .....	2.6 $\pm$ 0.4 (21)	1.8 $\pm$ 0.2 (15)	4.2 $\pm$ 0.5 (15)
No. seeds fruit <sup>-1</sup> .....	33.5 $\pm$ 14.1 (99)	30.0 $\pm$ 14.0 (10)	11.8 $\pm$ 7.1 (31)
Seed load <sup>a</sup> .....	0.08 $\pm$ 0.01 (82)	0.07 $\pm$ 0.02 (10)	0.04 $\pm$ 0.02 (31)
Pulp load <sup>a</sup> .....	0.14 $\pm$ 0.09 (99)	0.10 $\pm$ 0.08 (10)	0.11 $\pm$ 0.05 (31)
Percent pulp .....	64.0 $\pm$ 19.7 (99)	53.9 $\pm$ 23.6 (10)	69.5 $\pm$ 8.9 (31)

#### 4.2. Fruits

The unripe fruits are green and take on a purple-red coloration just before ripening, preceding the jet-black colour of the ripe polydrupes. They are 15.4  $\pm$  2.4 mm long and 15.6  $\pm$  1.8 mm wide (n = 28) and have a variable number of drupelets inserted on a dry receptacle. Fruits average in the study area 0.73  $\pm$  0.33 g fresh weight and 0.19  $\pm$  0.08 g dry weight, with 73.1  $\pm$  6.7% water content (whole fruit). Mean seed weight is 3.2  $\pm$  0.9 mg and there are 28.8  $\pm$  15.5 seeds fruit<sup>-1</sup>. Thus, the average fruit contains 94.2 mg of pulp dry-weight, representing 12.9% of the fresh fruit.

There is a high variability in fruit characteristics between the three habitats studied (Tab. 1). These divergences appear as the results of fruit design-related compromises: fruit seediness is inversely related to seed weight ( $r_s = -0.82$ ,  $P < 0.01$ ,  $n = 9$ ) and positively related both to pulp dry weight ( $r_s = 0.58$ ,  $P < 0.05$ ,  $n = 9$ ) and fruit weight ( $r_s = 0.77$ ,  $P < 0.001$ ,  $n = 9$ ). Thus, fruits in the Burned habitat have seed loads similar to the Grove fruits (Tab. 1), but half the seed number and double the individual seed weight. Fruits of the Forest occupy an intermediate position along the gradient, with seediness and seed size similar to the Grove fruits. On the other hand, Grove fruits offer a greater absolute amount of pulp to the dispersers (141.1

mg dry wt fruit<sup>-1</sup>) than Burned habitat fruits (105.6 mg fruit<sup>-1</sup>) but the relative amounts of pulp fruit<sup>-1</sup> are similar in the three habitats (Tab. 1,  $t \leq 1.50$ ,  $P > 0.2$ , for the three possible comparisons).

Patterns of between-habitat variation in fruit characteristics were investigated by means of multiple group discriminant analysis (BMDP7M, see Dixon 1975). Results are summarized in Tab. 2. Fruit size and seediness are positively associated to Canonical Variable I and both relative weight of pulp and water content have negative loads on it. This axis accounts for major differences between Grove and Burned habitat fruits. Ca-

Tab. 2. Summary of statistics from multiple-group discriminant analysis performed on characteristics of *Rubus ulmifolius* fruits grouped by habitats. For each variable, F values when entering the discriminant function at the corresponding step are given.

	Step	F <sup>a</sup>	Canon. coeff. I	Canon. coeff. II
Fresh weight .....	4	2.27	4.565	0.310
Dry weight .....	5	2.27	-26.280	4.535
Percent water .....	1	41.18*	-0.004	-0.181
Pulp load .....	6	1.74	15.520	-0.498
Percent pulp .....	3	31.14*	-0.076	0.054
No. seeds/fruit .....	2	25.92*	0.085	0.040
Constant .....			2.320	14.790

\*:  $P < 0.001$

a: 2 and 142 d.f.

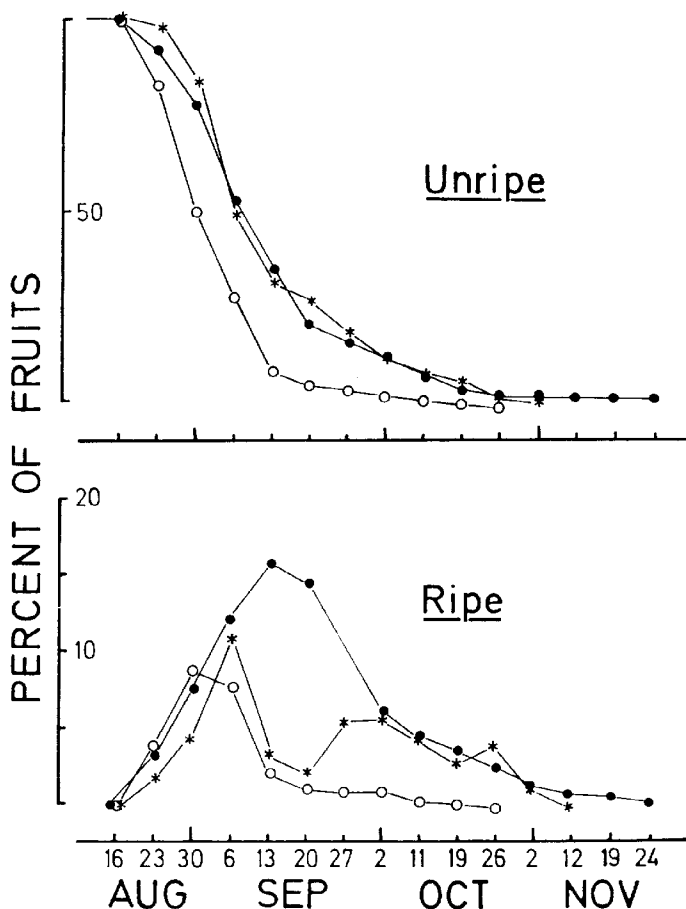


Fig. 1. Phenologies of fruit production of *Rubus ulmifolius* in three different habitats. Dots, Grove; asterisks, Forest, and open circles, Burned habitat. Values are percentages of  $N = 6625$  fruits marked on 12 plants.

nonical Variable II is presumably generated by variation within the Forest sample; water content and pulp weight have negative loads on it. The three possible pairwise comparisons with respect to fruit features resulted significant,  $F = 32.8$ ,  $F = 9.4$  and  $F = 13.6$  for Grove-Burned, Grove-Forest and Forest-Burned habitat respectively, all  $P < 0.001$ , 6 and 142 df. The point to be emphasized here is that variables involved in divergences of fruit characteristics are those that represent the major compromises from the plant's perspective when designing its fruits, namely seediness, pulp weight and water content.

#### 4.3. Phenology

Flowering began in late May and fruiting lasted until late Nov. Ripe fruits appeared in the marked racemes on 11 (Grove) and 23 (Forest and Burned habitat) Aug but they were seen elsewhere in the study area as early as 2 Aug. Ripe fruits were available in the area for three months (Fig. 1) and  $65.8 \pm 33.6$  d ( $n = 12$ ) on marked clones, the ripening period for individual fruits being approximately 35–40 d. Ripening of 50% of the total fruit crop took place between 2 and 30 Sep, with a peak of 13.5% in 13 Sep. The ripening phenologies were very similar in the three habitats. Ripening rates (Fig. 1) were not significantly different between habitats ( $D \leq 0.27$ , for the three possible comparisons,  $P > 0.2$ , Kolmogorov-Smirnov test), however, the peak availability of ripe fruits in the Burned habitat occurred about two weeks before the peak in the Grove. The mean ripening rate in this habitat was  $19.0\%/wk^{-1}$ , somewhat faster than the  $16.0\% wk^{-1}$  of the Grove and  $14.8\% wk^{-1}$  of the Forest.

Total potential fruit crops (either as buds, flowers or unripe fruits) experience different losses during the flowering and ripening processes, either in the flowering stage (bud predation or desiccation), ripening stage (desiccation of unripe fruits, seed predation) or dispersal stage (ripe fruit dried on the plant, ingestion by seed predators, fungus attack). Estimates of losses in differ-

ent habitats are given in Tab. 3. Both in the Grove-Forest and in the Forest-Burned habitat comparisons, fruit losses during the ripening process (green-dried fruits) and dispersal stage (ripe-dried fruits) were similar, but significantly greater in the Burned habitat than in the Grove ( $U = 1$ ,  $P = 0.016$  and  $U = 2$ ,  $P = 0.032$ , for the two stages respectively, Mann-Whitney U-test). On the other hand, the crop fraction taken by potential dispersers was greater in the Grove than in the other two habitats (Tab. 3). Correlates between mid-date of the interval when 50% of the mature fruits are available and crop losses during the ripening and dispersal stages show that clones fruiting later lost greater proportions of their fruits in the dispersal stage ( $r_s = 0.60$ ,  $P < 0.05$ ,  $n = 12$ ) and there is a marginally significant trend for early fruiting clones having greater losses during the ripening period ( $r_s = -0.48$ ,  $P \approx 0.05$ ). These facts suggest that directional selective pressures may be operating to synchronize the ripening phenologies towards the time when dispersal success (fruit consumption) is greater.

#### 4.4. The principal species of birds. Seasonal dynamics

Among the 32 passerine species recorded in the area during the study period, only 20 were seen actually feeding on *Rubus* fruits. Most of these species were autumn passage migrants that peaked in abundance between mid-Sep and early Oct, reaching 95 birds/100 net-hours. *Sylvia borin* (Bodd.), *Ficedula hypoleuca* (Pall.), *S. communis* (Lath.), *Luscinia megarhynchos* (Brehm) and *Hippolais pallida* (Hempr. and Eh.) were the main members of an 'early group' of migrants. Other species, rarely observed at *Rubus*, included *S. cantillans* (Pall.), *S. conspicillata* (Temm.), *Saxicola torquata* (L.) and *Phoenicurus phoenicurus* (L.). *S. borin* was the principal species in this group, reaching 51 birds/100 net-hours on 16 Sep (Fig. 2). From early Oct throughout Nov, I recorded a second peak of 'late migrants' reaching 256 birds/100 net-hours by 13 Oct. The main species in this group were *S. atricapilla* (L.) (peak

Tab. 3. Fruit losses during different phases of the fruiting process. For each habitat, figures indicate overall crop fraction lost as well as maxima and minima recorded for individual clones.

	Number of plants	Number of fruits <sup>a</sup>	Percent lost during ripening <sup>b</sup>	Percent not consumed <sup>c</sup>	Percent consumed
Grove .....	5	4816	4.2 (0–37.9)	7.7 (0.6–18.8)	88.0 (54.5–93.6)
Burned habitat .....	4	499	56.3 (3.7–87.0)	1.2 (0–3.5)	42.5 (12.2–96.3)
Forest .....	3	488	12.3 (0–35.2)	8.2 (0–14.8)	79.5 (64.7–97.0)
Total study area .....	12	5803	9.4	7.2	83.4

a: remaining after flowering (see Methods).

b: unripe-dried fruits.

c: ripe-dried fruits.

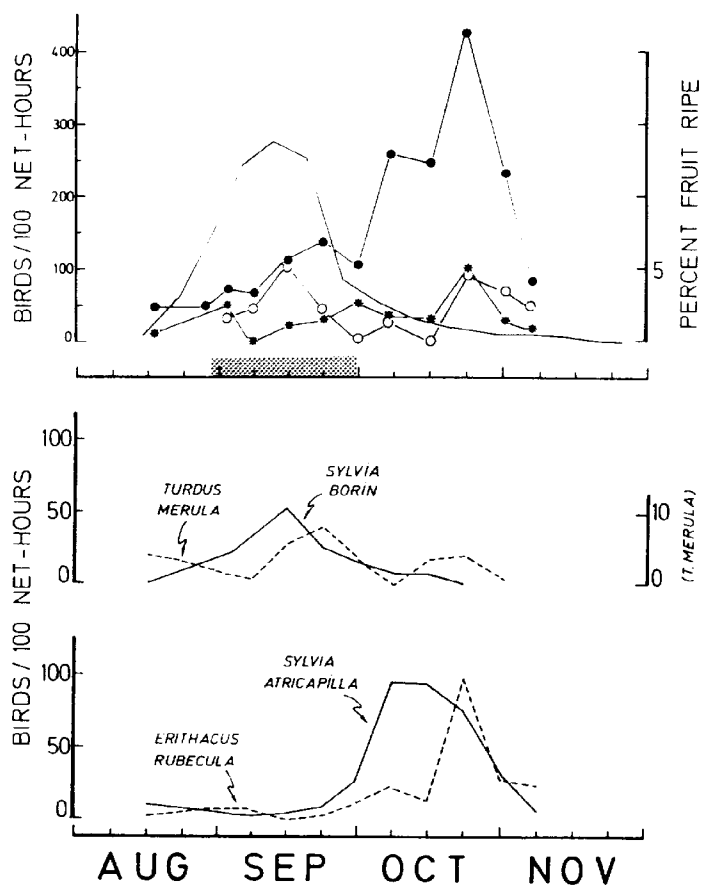


Fig. 2. Bird capture rates in the three habitats (symbols as in Fig. 1) and percent fruit crop ripe (all the study area, continuous line). The dotted area denotes the time interval when 50% of the ripe fruit was available. Bottom: patterns of temporal abundance (capture rates) of the four principal species.

95 birds/100 net-hours on 4 and 14 Oct) and *Erithacus rubecula* (L.) (99 birds/100 net-hours on 21 Oct) (Fig. 2), which are also common overwintering species in southern Spain. Other species in this group were *Turdus philomelos* (Brehm) and *T. iliacus* (L.). Among resident birds, *T. merula* (L.), *S. melanocephala* (Gm.) and *Parus caeruleus* (L.) were the main species in relation to *Rubus*, along with *P. major* (L.), *Passer domesticus* (L.), and *Chloris chloris* (L.), which were irregular visitors.

Tab. 4. Summary of diet composition of the most common bird species at El Bañuelo, from Aug through Nov 1978. Samples were classified in four exclusive classes of vegetable matter content. Figures are percent samples falling in each class.

	N	Animal matter (mean %)	Vegetable matter				Samples with <i>Rubus</i> (pulp or seeds)
			<30%	30-60%	60-90%	>90% (100%)	
<i>Sylvia atricapilla</i> .....	184	2.8	1.2	1.7	4.6	92.5 (23.1)	60.3
<i>Sylvia borin</i> .....	99	4.4	-	2.1	12.6	85.3 (32.6)	65.7
<i>Erithacus rubecula</i> .....	101	51.8	33.3	28.4	16.0	22.2 (2.5)	51.5
<i>Turdus merula</i> .....	22	11.1	-	9.1	27.3	63.6 (22.7)	86.4
<i>Ficedula hypoleuca</i> .....	17	80.6	70.6	23.5	5.9	-	64.7
<i>Luscinia megarhynchos</i> ..	9	74.1	66.7	22.2	11.1	-	44.4
<i>Parus caeruleus</i> .....	9	50.0	33.3	22.2	22.3	22.2	55.6
<i>Sylvia communis</i> .....	7	3.8	-	-	28.6	71.4 (28.6)	85.7
<i>Hippolais pallida</i> .....	7	72.8	57.1	28.6	-	14.3	71.4
<i>Sylvia melanocephala</i> ...	4	47.5	-	75.0	25.0	-	25.0

Bird visits showed a high variation between habitats, as reflected by mist-netting (Fig. 2). Average capture rates were  $149 \pm 113$ ,  $84 \pm 35$  and  $38 \pm 25$  birds/100 net-hours in the Grove, Burned habitat and Forest, respectively. Capture rates were higher in the Grove ( $U = 6$ ,  $P < 0.001$ ;  $U = 10$ ,  $P < 0.001$ ) and similar in the Burned habitat and Forest ( $U = 40$ ,  $P > 0.05$ ). Differential capture rates of the principal species in the three habitats suggest the existence of species-specific habitat preferences. All four species had higher absolute capture rates in the Grove. Only *S. borin* was a regular visitor to the Burned habitat (15.4% of its captures vs.  $< 7\%$  for the remaining species), when crops of *Ficus carica* were ripe there. *E. rubecula* was the commonest species in the Forest (19.4%) but also a large fraction of *T. merula* (37.0%) were netted in this habitat. *S. atricapilla* almost exclusively visited the Grove (94.7%).

#### 4.5. Fruit consumption

The diet of the principal species in the study area is summarized in Tab. 4. There is a marked gradient from a high dependence on fruit for food (*Sylvia* spp., *T. merula*, *E. rubecula*) to an almost complete insectivory (*F. hypoleuca*, *L. megarhynchos*, *H. pallida*).

Fruits of *Rubus* were the most extensively consumed item in the study area. Remains of *Rubus* fruits (either as seeds or pulp) were present in 60.8% of samples, contrasting with an occurrence of other plant species (up to 16) always  $< 20\%$ , with the exception of *F. carica* (see below). *Rubus* seeds ( $n = 2646$ ) accounted for 64.4% of the seeds found in faecal samples ( $n = 4110$ ). *S. atricapilla* samples contained 32.4% of the *Rubus* seeds; 25.3% were found in *T. merula*, 17.9% in *S. borin*, 15.3% in *E. rubecula* and 3.5% in the remaining species. The four species showed frequencies of occurrence of *Rubus* remains greater than 50% (Tab. 4), illustrating their high dependence on fruits of this species. Fruits of other plant species are seldom included in the diet of autumn migrants in the study

area (see Jordano 1981). Only *F. carica* was often present in *S. borin* samples (60.6% occurrence). The fruiting of this tree overlaps with *Rubus* and also coincides with the autumn migration of *S. borin*.

The temporal variation of ripe fruit availability is correlated with the shifts in the diet of the frugivorous birds. Percent vegetable matter increased by mid-Sep coinciding with the ripening of *Rubus* fruits, and continued with little variation throughout the autumn. Maximum presence of *Rubus* in samples of *S. atricapilla*, *S. borin* and *T. merula* (57.3%, 50.0% and 70.0%, respectively) was recorded by early Sep, when 35.6% of the crop was ripe. Together with the decrease in availability of *Rubus* berries there was a general increase in the frequency of occurrence of other fruits. The abundance of *Rubus* fruits decreased by late Sep (<20% crop ripe), and the occurrence of *F. carica* and other plant species increased in the two *Sylvia* (44.0% to 61.9% in *S. borin* and 50.0 to 55.3% in *S. atricapilla*). *S. borin* left the study area by mid-Oct and *S. atricapilla* shifted to consume autumn-winter fruits (e.g., *P. lentiscus*, *O. europaea*; Jordano and Herrera 1981), with occurrence of 73.0% by late Oct, contrasting with 27.0% for *Rubus*. The diet of *E. rubecula* from October throughout the winter consisted mainly of acorn fragments (present in 88.2% of Nov samples) and *V. tinus* fruits (17.6%); these items sharply replaced *Rubus* fruits by late Oct, when <8.0% of the crop was ripe.

#### 4.6. Visit rates

Clones of different size had different visitation rates by

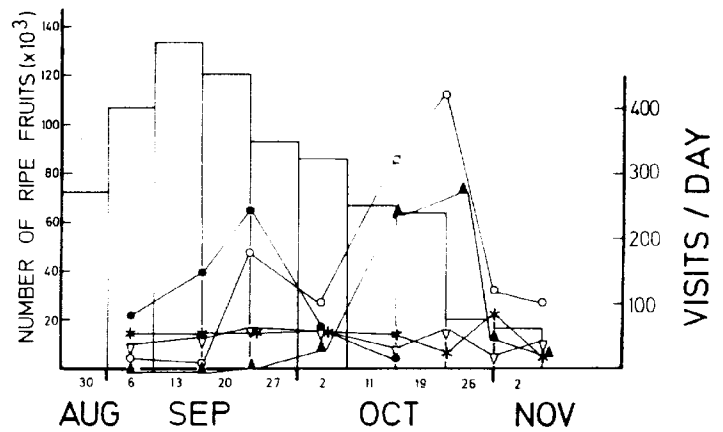


Fig. 3. Temporal variation in fruit production (bars) and bird visitation at clone G2 (see Methods). Open circles: *S. atricapilla*; dots, *S. borin*; filled triangles, *E. rubecula*; asterisks, *S. melanocephala* and open triangles, *T. merula*.

birds. A Grove clone (G2) with a fairly large crop ( $\approx 1.4 \times 10^6$  fruits) had  $487 \pm 208$  ( $n = 8$ ) visits  $d^{-1}$ . Frequency of visits to a medium sized clone in the Burned habitat ( $6.4 \times 10^3$  fruits) and a small clone ( $5.5 \times 10^3$  fruits) of the Grove were  $20 \pm 19$  ( $n = 8$ ) and  $10 \pm 10$  ( $n = 6$ ) visits  $d^{-1}$ , respectively.

*S. atricapilla* and *E. rubecula* were the main visitors at clone G2 (29.6 and 15.2% of 897 visits recorded), followed by *S. borin* (14.7%), *S. melanocephala* (10.1%) and *T. merula* (7.7%) (Tab. 5). Visits by the remaining 15 species made up 22.3%. Different bird species had peak visitation at different dates (Fig. 3). A minor peak of 691 visits  $d^{-1}$  was recorded one week after maximum availability of ripe fruit on the clone ( $1.2-1.3 \times 10^5$  ripe fruits) and was largely due to peak visitation by *S. borin*

Tab. 5. Statistics of fruit consumption for several passerine species observed at *Rubus ulmifolius*. Figures are means  $\pm$  one s.d. (sample size). Body weights are means for mist-netted birds in the study area. Behaviour: G, gleaning, P, perched on the fruit, H, hovering beneath the fruit, S, sallying from a nearby branch.

	Body weight (g)	Behaviour	Length of visit (s)	Pecks $min^{-1}$	Pecks fruit $^{-1}$	Visits $d^{-1}$	Seeds visit $^{-1}$	Percent seeds taken
<i>S. borin</i> .....	21.6	G	79.4 $\pm$ 41.5 (10)	7.1 $\pm$ 5.3 (19)	2.8 $\pm$ 2.2 (19)	110.0	90.8	30.8
<i>S. atricapilla</i> .....	17.9	G, S	59.7 $\pm$ 45.4 (15)	11.9 $\pm$ 7.9 (32)	3.9 $\pm$ 2.3 (32)	180.0	43.4	24.1
<i>S. communis</i> .....	18.0	G	63.1 $\pm$ 38.7 (9)	6.5 $\pm$ 5.9 (21)	2.2 $\pm$ 1.5 (21)	29.6	84.0	7.7
<i>S. melanocephala</i> .....	11.1	G	54.3 $\pm$ 18.5 (7)	12.3 $\pm$ 7.0 (21)	2.8 $\pm$ 1.7 (21)	48.0	36.2	5.3
<i>T. merula</i> .....	68.1	G	-	3.8 $\pm$ 1.8 (4)	1.1 $\pm$ 0.8 (4)	37.5	120.0	13.9
<i>P. caeruleus</i> .....	9.0	P, G	82.0 $\pm$ 42.8 (5)	38.8 $\pm$ 23.9 (5)	16.3 $\pm$ 9.4 (5)	7.2	16.8	0.4
<i>E. rubecula</i> .....	14.3	G, S	72.1 $\pm$ 59.4 (7)	9.7 $\pm$ 8.5 (12)	2.6 $\pm$ 2.8 (12)	93.6	57.7	16.6
<i>F. hypoleuca</i> .....	13.8	H, G	39.0 $\pm$ 26.0 (4)	5.6 $\pm$ 3.5 (4)	1.4 $\pm$ 2.8 (4)	19.8	19.5	1.2

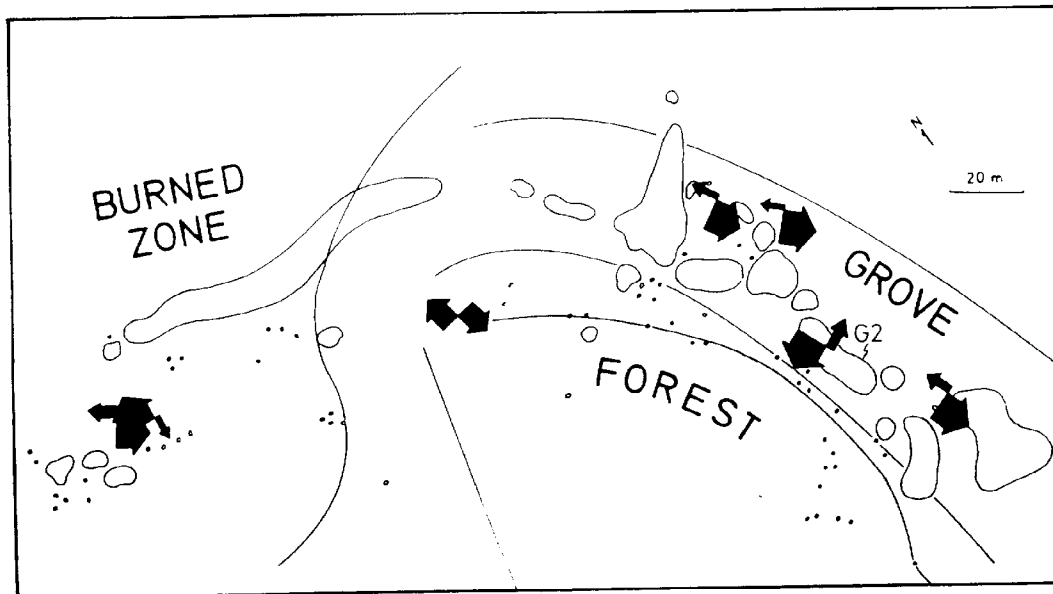


Fig. 4. Map of the study area showing locations of *Rubus* clones along the valley bottom and the major flight pathways as indicated by bird captures in the mist-nets. Each pair of arrows represents percent of captures in each direction. Limits of the three habitats studied and location of the intensively observed clone G2 are also shown.

(240 visits  $d^{-1}$ ) and other trans-saharan migrants on 25 Sep. Maximum visitation (806 visits  $d^{-1}$ ) was recorded when the standing crop was as low as  $6.5 \times 10^4$  ripe fruits. This peak in visit rate was due to the arrival of *S. atricapilla* and *E. rubecula*, reaching 422 and 278 visits  $d^{-1}$ , respectively, on 23 Oct (Fig. 3). *T. merula* and *S. melanocephala* showed a regular visit rate of approximately 35 visits  $d^{-1}$  throughout the fruiting period (Fig. 3).

#### 4.7. Feeding rates

The fruit consumption statistics for the principal species are summarized in Tab. 5. Body weight is positively correlated with the number of seeds ingested visit $^{-1}$  ( $r_s = 0.91$ ,  $P < 0.01$ ,  $n = 8$ ), following: No. seeds visit $^{-1} = 25.67 \pm 1.514$  Body weight. Thus, body weight is a major variable affecting seed ingestion rate at *Rubus*. It is negatively correlated with the number of attempts min $^{-1}$  ( $r_s = -0.71$ ,  $P < 0.05$ , Tab. 5) and the time spent in active search for fruits ( $r_s = -0.62$ ,  $P \approx 0.05$ ).

Foraging behaviour varied between species and apparently influenced ingestion rate and efficiency (Tab. 5). The commonest technique employed was gleaning fruits from a nearby branch or from the same infructescence on which the bird was perched. Gleaners ingested more seeds visit $^{-1}$  than species showing other fruit-harvest techniques ( $U = 2$ ,  $P = 0.057$ , Mann-Whitney U-test), suggesting that gleaning is an efficient technique because it allows a greater ingestion rate (independent of body weight differences) as compared with the more energetically costly sallying or hovering techniques (see Jordano 1981). Sallying to peck the fruit from a nearby branch was employed by *E. rubecula* (33.3% of the observations) and incidentally by *S. atricapilla* (6.3%). Both gleaning and hovering were equally employed by *F. hypoleuca* (50.0% both) and *P. caeruleus* typically hung from the fruit (60.0%) and insistently pecked the drupelets, ingesting only pulp.

I recorded only sporadic intraspecific behavioral interactions with incidental persecutions, among *F. hypoleuca*, *S. atricapilla* and *E. rubecula*. Interspecific attacks were not observed and predation pressure must be very low in the study area, as it is heavily managed and avian predators are rarely observed. Thus, feeding rates reported in Tab. 5 are probably just the result of proximate constraints set up by species-specific body sizes and foraging behaviors.

#### 4.8. Exit flights and seed delivery by birds

It is extremely difficult to know the landing place of a seed ingested by a given bird at *Rubus*, as it is to know which dispersal agent delivered the seed found anywhere on the ground surrounding a *Rubus* clone. However, in an attempt to identify the seed-delivery sites (see Herrera and Jordano 1981 for a similar approach) of the main frugivores at *Rubus*, I recorded three features of the first perches employed by 176 birds leaving the clone G2 after feeding, namely their distance, identity and location (see Methods).

General flight pathways over the study area show a marked directional pattern along the Grove (valley bottom) (Fig. 4), and another one from the Grove to the Forest, up the hillside. Observations of the clone G2 were consistent with these patterns. Exit flights of *S. melanocephala* and *E. rubecula* were preferentially towards the Forest (69.6 and 82.1%, respectively). Moreover, 43.5 and 75.9% of the flights, respectively, were to perches in the Forest, near (<20 m) the parent clone, and not on other *Rubus*. Both *S. borin* and *S. atricapilla* left the clone indifferently in the two directions (50.0 and 52.8% to the Grove, respectively). In 10.3 and 28.1% of the instances, these species perched >20 m from the parent clone, in the Grove, and on plants other than *Rubus*. Other perches favoured (24.1 and 29.8%, respectively) were near the clone, in the Forest, but not on other *Rubus*. *T. merula* left towards



the Grove in 80.0% of the observations, but noteworthy perched >20 m away, in the Grove, and on perches other than *Rubus* (61.1% of the observations).

Birds seemed to actively avoid stopping on another *Rubus* for perch on it after leaving the observed clone. They favoured short distance (<20 m) flights along the Grove or to the Forest, depending upon species.

## 5. Discussion

### 5.1. Variations in fruit production

There exist important between-habitat variations in fruit production and fruit features of individual clones. At high density, dispersers seemed to select for maximum possible crops for each clone size (see Howe and Estabrook 1977) and were responsible for a thorough removal of the seeds (see below). Among Grove clones, crop size is positively related to the fraction of the crop consumed ( $r_s = 0.90$ ,  $p = 0.05$ ,  $n = 5$ ). An escape behavior in response to a highly-crowded situation is predicted by the so-called strawberry-coral model of density-dependent allocation to sexual reproduction (Williams 1975) and is illustrated by the between-habitat differences in reproductive pattern reported for other *Rubus* species (Abrahamson 1975, Kirby 1980). Heavy fruit production in high-density habitats may favour the long-distance dispersal of seeds by the activity of avian frugivores. However, for all the clones pooled fruit consumption is not correlated with crop size ( $r_s = 0.38$ ,  $n = 12$ ), suggesting that, in addition, other factors might be influencing seed removal.

From the disperser's viewpoint, altering seed-related traits in the fruit-design may represent variations in the reward/ballast ratio and must influence fruit choice by birds (e.g., Herrera 1981a, Howe and Kerckhove 1981). However, average pulp load per fruit of individual clones was unrelated to the fraction of the crop consumed ( $r_s = 0.00$ ,  $n = 5$ ) indicating that interclonal variations in absolute reward obtainable per fruit did not apparently influence attractiveness of fruits to dispersers. Most likely other factors may be involved. Thus, for the same time in active foraging, the greater abundance of fruits in the Grove is associated with a greater ingestion rate, probably enhancing the intrinsic reward load in the fruits, and thus influencing disperser foraging behavior in terms of patch selection (Krebs and Cowie 1976, Salomonson and Balda 1977, Green 1978). Differential bird-capture rates in the three habitats are consistent with this observation. Migrant frugivores might favour those habitat patches with higher fruit densities, provided hyperphagia is a widespread syndrome among birds at stopover sites (Blem 1976 and references therein).

From the plant's perspective, increasing seed production represents an increase in seed density by soil surface unit and/or in the proportion of the available soil surface where seeds would arrive, but an increase in

energy invested per seed could also be an alternative way of increasing the proportion of available soil surface where germination and seedling survival would be successful (Stebbins 1971, Smith 1975). Thus, the escape behavior in the Grove habitat is mediated also by production of fruits with many seeds (mean 33.5 vs. 30.0 and 11.8 in Forest and Burned habitats, respectively), this increase in seediness being associated with a decrease in seed size (2.4 vs. 2.7 and 4.4 mg, respectively).

Apparently, the ability to attract dispersers is largely dependent on the clone's mass fruiting pattern (i.e., producing a huge crop in a population of high spatial density). As suggested in the next paragraph, the transient nature of the disperser assembly would favour those clones that show a greater coincidence with their conspecifics in both space and time.

### 5.2. Spatial and temporal coincidences of seeds and dispersers

Several authors have pointed out the importance of spatial and temporal synchronizations in the evolution of temperate bird-plant interactions for seed dispersal (Salomonson 1978, Thompson and Willson 1978, 1979, Baird 1980, Stiles 1980), indicating the existence of selective pressures favouring those plant phenotypes showing maximal coincidence with the peak of frugivore abundance during the autumn migration.

The diet shifts of the late migrant species towards fruits of greater profitability, paralleling a decrease in *Rubus* consumption, may be largely responsible for greater fruit losses among the late ripening individuals, thus selecting for early ripening synchronous with the bulk of autumn migration. The <3% fat and protein content of the *Rubus* pulp (Snow 1971) is to be contrasted with values for *V. tinus*, *P. lentiscus* and *O. europaea* pulps, the main food of overwintering frugivores in mediterranean scrubland (Herrera 1981b, Herrera and Jordano 1981), namely 21.6, 58.8 and 41.9% for fat, respectively, and ranging between 3.7–7.9% for protein. For a typical Model 2 species (Howe and Estabrook 1977) like *R. ulmifolius*, shifting the ripening period and thus avoiding temporal overlap with these species perhaps superior in competitive ability, may represent an adaptive way to increase the dispersers' attraction, rather than increasing the absolute amount of nutritional reward per ingested seed. From an intrapopulation perspective such a directional evolution of ripening phenologies causes synchrony and generates strong intraspecific competition for dispersers, favouring high-fecundity individuals (Howe and Estabrook 1977, present study). Several plant species also bear ripe fruit by late summer and early autumn in undisturbed, non-marginal, mediterranean scrubland (e.g., *Phillyrea angustifolia*, (L.), *Rhamnus* spp., *Osyris* spp.) sharing the same seed-dispersers as *Rubus*. Further study is needed to compare their relationships

with migrant birds and their interspecific interactions for disperser attraction both within- and between-habitat types (i.e., with allopatric species like *Rubus*).

The spatial coincidence seems to be mediated by a certain correspondence between both the plant's and dispersers' habitat selection. *R. ulmifolius* is a characteristic pioneer species of mesic sites in forest borders, secondary succession habitats and marginal areas, usually monopolizing large patches through cloning. The greater abundance of frugivorous birds in these habitat types (Karr 1976, Thompson and Willson 1979, Baird 1980) as compared to dense forest (see Fig. 2) is well documented. The evidence obtained suggests that *Rubus* gets a thorough removal of the crop produced (i.e., 83.4% of the fruits consumed for the overall population) by matching the peak abundance of frugivores both in time and space.

### 5.3. The disperser assemblage

Seed dispersal is a one-way movement (Janzen 1975) in which the dispersers' activity, delivering seeds to safe sites for the plant, is of core importance. Fruit size alone is a major factor determining, particularly on a body size basis, the composition of the disperser assemblage (Herrera and Jordano 1981). Plants producing large, undivided conventional fruits (e.g., berries, drupes) are thought to exclude small frugivores (unable to swallow the whole fruit and process the seeds), while metabolic- as well as accessibility-related factors prevent larger birds from ingesting small fruits (Diamond 1975, Kantak 1979). Producing multi-seeded fruits (like polydrupes and catkins) enables the plant to rely on a greater variety of frugivores, apparently not limited by any size-related factor, the benefit of this increased disperser coterie being an increased colonizing ability (Smythe 1970). Seed ingestion rate (either by swallowing the whole fruit or pecking the drupelets) is determined by body size and foraging behaviour, but for a given bird species, the product of its visit rate by the number of seeds removed per visit determines its overall 'quantity' value from the plant's perspective (Herrera and Jordano 1981). Thus, *T. merula* ingested nearly three times more seeds per visit than *S. atricapilla*, but the latter visited the plant nearly five times more frequently, the final balance favouring it in spite of its four times smaller body size. Thus, approximately 55% of the  $\approx 32400$  seeds leaving the plant during an average day (Tab. 5) are transported by *S. atricapilla* and *S. borin*, largely because of their high visitation rate.

A close coevolutionary relation has usually been proposed between good 'seed-removers' and the plants they visit (McDiarmid et al. 1977, Howe 1977, 1981, Howe and De Steven 1979). Nevertheless, two further variables are thought to determine the actual reliability

of a given disperser to the plant, namely the importance of alternative food (other fruits, insects) in its diet and the quality of the dispersal performed (McKey 1975). The four principal species show extensive frugivory both in different habitat types and throughout the year (Herrera 1981a, Jordano and Herrera 1981, and references therein) and the results presented here reveal a high dependence on *Rubus* fruits among them. I have argued elsewhere (Jordano 1981) that the high content of soluble carbohydrates in *Rubus* fruits may provide a readily metabolizable fuel to avoid a rapid exhaustion of the fat supply in the migratory birds (see Snow 1965, McKey 1975). Also, the high water content of the pulp must be of great importance to avoid water losses during the hot mediterranean summer (Langslow 1976) and may explain the general consumption of *Rubus* fruits among the autumn passage migrants even when they are insectivorous species.

All the species in the *Rubus*-feeding assemblage, with the exception of *C. chloris* and *P. domesticus* which damaged the seeds, apparently were dispersal agents. They performed flights which removed seeds from the parent plant and rarely dropped seeds in situ while pecking. Another quality aspect of the seed dispersal includes the flight patterns and habitat selection of the dispersers, which produce non-random seed shadows over the habitat (Janzen et al. 1976, Howe and Primack 1975, Herrera and Jordano 1981). Species in the *Rubus* disperser assemblage seem to perform a high-quality dispersal of the seeds and probably play a major role in determining the distribution pattern of *Rubus* in the study area. Similar situations have been described both in the tropics, e.g. for *Cecropia*, distributed along creeks by birds (Janzen 1975), and in temperate areas for a mistletoe (*Phoradendron*) distributed along valley bottoms by phainopeplas (Walsberg 1977). The seeds ingested by *S. atricapilla*, *S. borin* and *T. merula* will be mainly delivered along the valley bottom, as they fly predominantly in this direction, and, on the other hand, the short flights of *S. melanocephala* and *E. rubecula* into the Forest may provide a seed stock ready to germinate and colonize the open clearings in this habitat.

The results reported in this paper indicate that migrant birds remove a very high fraction of the seed crop produced by a *Rubus* population, the fruit pulp representing the major food of these birds. This, however, is not enough evidence to support the conclusion that *R. ulmifolius* and migrant birds illustrate a coevolved system for seed dispersal (see Janzen 1980 for a general discussion). The former is distributed over many habitat types in the general region of mediterranean Spain, interacting with rather different sets of dispersers. Autumn migrants, on the other hand, are characterized by their transitory stay, individual birds spending very short time intervals interacting with the plant at stopover sites.

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