

A MEDITERRANEAN BIRD DISPERSER ASSEMBLAGE : COMPOSITION AND PHENOLOGY IN RELATION TO FRUIT AVAILABILITY

Max DEBUSSCHE and Paul ISENMANN

*Centre d'Ecologie Fonctionnelle et Evolutive,
(Centre L. Emberger), C.N.R.S., Route de Mende, B.P. 5051,
F-34033 Montpellier Cedex, France*

Among the bird species which feed on fleshy fruits, Herrera (1984) distinguished those which consume either the pulp or the seeds (the « pulp-predators » and « seed-predators ») and the seed-dispersers which restitute seeds able to germinate by regurgitation or in their droppings (the « legitimate » fruit-eaters of Snow, 1971). Assemblages of numerous seed-dispersers (« dispersers » hereafter) exist in temperate zones and disperse seeds almost continuously throughout the year, with a marked peak in the autumn, which may extend into winter in Europe (e.g. Herrera, 1984 ; Jordano, 1984 ; Snow and Snow, 1988) and in North America (e.g. Thompson and Willson, 1979 ; Skeate, 1987).

In this context the present study, dealing with a plant-bird system in Mediterranean France, has been carried out to examine the composition of the disperser assemblage, and the seasonal co-occurrence of both disperser abundance and fruiting. The following questions were addressed :

1) Are Mediterranean assemblages of dispersers different from other temperate zone assemblages ? Herrera (1984) noted that the bird assemblage of southern Spain shows a higher proportion of small-sized species. He suggested that the dense vegetation structure, the mild climate and the abundance of energy-rich fruits are favourable to these small-sized species.

2) Is the seasonal co-occurrence of dispersers and fruiting most influenced by birds or by plants ? Thompson and Willson (1979) suggested that « the fruiting phenology of mid-latitude plants with fleshy fruits appears to have been selected primarily by the seasonal patterns of avian frugivore availability and the probability of destruction of ripe fruit before dispersal ». Likewise, Snow and Snow (1988) suggested that the fruiting phenology is essentially the result of the selective pressure exerted by the dispersers. Herrera (1984), however, considered that if « predominant autumn-winter fruiting may be interpreted as the result of the greater availability of potential dispersers », it may also be the consequence of the low number of pests on ripe fruits during that period, of regional climatic features, and of physiological characteristics of plants. Similarly, Skeate (1987) suggested that physiological factors governing the ripening process may play an important role in determining the fruiting period, thus reducing the role of dispersers as selective agents on fruiting phenology.

Our study was carried out in a patchy environment of Holm Oak (*Quercus ilex*) coppice, garrigues and old fields in the suburbs of Montpellier by mist-netting birds, surveying bird species presence, collecting the seed rain of fleshy-fruited plants and monitoring their fruiting phenology.

STUDY SITE AND METHODS

STUDY SITE

The 2.5 ha large study site was situated on our laboratory campus at the edge of a 100 ha *Quercus ilex* wood containing scattered stands of *Pinus halepensis*, in the suburbs of Montpellier in Mediterranean France (43° 39' N/03° 51' E ; 60 m a.s.l.). The vegetation on the study site is patchy and is dominated by a 5-7 m high *Q. ilex* coppice ca. 50 year old (31 % of the area). The well-developed woody understorey mainly consists of *Viburnum tinus*. In the clearings of the coppice (3 % of the area), there are 1-2 m high garrigues with *V. tinus*, *Pistacia lentiscus* and *Quercus coccifera*; the scarce grassy layer is dominated by *Brachypodium retusum* and *Bromus erectus* (coppice with its clearings = « coppice » hereafter). At the edge of the coppice, the same vegetation as in the clearings occurs mixed with *Rhus coriaria* clumps and scattered *Ulmus minor* (22 % of the area) (« ecotone » hereafter). The neighbouring old fields (20 % of the area) exhibit a rich flora consisting of numerous annual *Gramineae* and *Leguminosae* such as *Avena sterilis*, *Bromus* spp. and *Medicago* spp. (« old field » hereafter). The oldest of these fields (15 years after the last ploughing) are invaded by scattered individuals of *Rubus ulmifolius*, *Pyracantha coccinea* and *Prunus dulcis*. Regularly mowed swards with isolated trees and shrubs cover 13 % of the site. Building and roads cover 11 %.

The climate is Mediterranean and sub-humid with cool winters (see Daget, 1977). The mean annual rainfall is 857 mm; the mean of the maxima of the warmest month is 28.7 °C and the mean of the minima of the coldest month is 0.6 °C (Debussche and Escarre, 1983). Snow cover on the soil rarely lasts more than 1 or 2 days per year.

BIRDS

The birds were trapped with 6 m and 12 m long mist nets. Four mist nets (A, B, C, D) were used from August 1981 to April 1983 and from February 1984 to August 1984, during 94 days at time intervals as regular as possible (8.4 ± 3.8 days) depending on the meteorological conditions (absence of strong wind and rainfall have been a prerequisite). These four mist nets were placed in order to take into account the vegetation gradient crossing the dense *Q. ilex* coppice towards the old fields. Mist net A was located in the closed dense coppice; mist net B in a narrow gap of the dense coppice; mist net C in a clearing within the coppice; mist net D in an ecotonal situation at the coppice edge. In addition, two other mist nets (E and F) were used. Mist net E, located among isolated trees, was working during 8 days between July and September 1982; mist net F, located

in an old field, was working during 16 days from October to February in 1982-1983 and 1983-1984. Mist nets were visited once an hour. The comparison between mist-nets is expressed in captures per 10 m/100 h mist-net.

Each captured bird was retained during 10 minutes in a cloth bag before being banded, measured, weighed and released. The droppings collected in a bag were examined under a microscope at 50 x magnification ; the fruit remains were identified using a complete collection of the fruits of the region as a reference.

On each of the 94 days where mist-netting took place, all the bird species observed on 3 zones of the study site (coppice, ecotone and old field) were censused during a 10 minute period each hour.

PLANTS

The availability of ripe fruits was studied at 10-day intervals on 21 plant species from June 1981 to May 1982 and on 24 plant species from May 1982 to May 1983. Twenty nine plant species were present on the study site. The sample consisted in 3-6 individuals per species with a sub-sample of 2-3 marked branches on each individual plant. Each branch bore about a dozen fruits. At the beginning and at the end of the fruiting period of a given species, periods with short supply of fruits were defined as those during which less than 10 % of the total crop consisted of ripe fruit with intact pulp. The central period is called « maximum crop » hereafter.

The phenology of seed dispersal was studied by collecting seeds with traps whose bottom consisted in 1 mm meshed metallic trellis. Their height was of 0.15 m and their surface either of 0.5 m² or of 0.25 m². Six sets of such seed traps were used (total area : 39.75 m²). Their locations were chosen in order to take into account the various plant communities and the vegetation structure gradient. Set 1 was entirely located in the dense and high coppice ; set 2 was in the dense coppice with some gaps ; set 3 cross-checked coppice clearings ; set 4 was under isolated trees near the edge. Two sets (5 and 6) were located both under and outside the cover of 2 isolated individuals of *Prunus dulcis*, a pioneer tree species in the old field.

The seeds were collected every 1 to 3 days from 18 December 1981 to 20 May 1983. To be sure that no seeds were predated between each seed removal, each month marked seeds were left over the seed traps for a week, and none of them disappeared. The collected seeds only came from bird droppings as no mammal scats were ever found in the traps (see Debussche and Isenmann, 1989).

RESULTS

BIRD SURVEY

During the study 57 bird species were recorded, 32 of which were trapped giving a total of 846 captures (Appendix I). Thirteen species were mostly residents and 26 species mostly winter visitors (see Blondel, 1969). Sixteen species were found as breeders on the study site during the period considered. Thirty four were censused at least 5 times and 23 less than 5 times. The latter were either present in

very low densities on the study site (e.g. *Accipiter nisus*, *Aegithalos caudatus*) or just checked as migrants during a brief stop-over (e.g. *Phylloscopus trochilus*, *Turdus torquatus*).

The greatest number of species was recorded in the coppice (43), then the ecotone (38) and the old field (28). Among the 34 species censused at least 5 times, 12 were encountered more often in the coppice than in the two other habitats (e.g. *Regulus ignicapillus*, *Parus major*), 6 more often in the ecotone (e.g. *Fringilla coelebs*, *Carduelis serinus*), and 10 more often in the old field (e.g. *Carduelis chloris*, *Anthus pratensis*).

Following Herrera (1984), we divided the 57 species recorded among 4 classes : 1) non frugivorous species, 2) seed-dispersers, 3) pulp-predators, 4) seed-predators (Appendix I). Twenty nine species consumed one or the other part of a fruit (see Debussche and Isenmann, 1983, 1985a, 1985b, 1989, this paper, and references quoted in Appendix I) of which 8 ate and destroyed the seeds, 5 ate the fruit pulp but did not swallow the seeds and 19 were dispersers releasing, after ingestion, seeds able to germinate. Among the latter 14 were small-sized (< 25 g) and 5 were medium-sized (> 75 g) (see Debussche and Isenmann, 1989). Among the 10 most frequently recorded species (frequency > 75 %), 6 were dispersers. The high frequency of contacts with dispersers was also reflected by the high number of captures (Appendix I) : the 3 most frequently caught species were small-sized dispersers and represented 61 % of the captures (*Sylvia atricapilla*, *Erithacus rubecula*, *Sylvia melanocephala*). Fifteen of the 32 mist-netted species were dispersers ; they represented 597 out of 846 captures (70.6 %).

DISPERSERS IN TIME AND SPACE

The dispersers' abundance varied throughout the annual cycle (Fig. 1). These variations were slight in the case of *S. melanocephala* ; the slightly lower numbers noticed in winter and in early spring were attributed to movements towards coastal lowlands or milder areas, and the maximum at the beginning of summer was due to post-breeding dispersal. *E. rubecula* was only present from September to April (see also Debussche and Isenmann, 1985a) with a maximum of captures between October and January. *S. atricapilla* was recorded all the year round ; the small breeding population was considerably increased between September and March by relatively poorly site-attached migrants and wintering birds (Debussche and Isenmann, 1984 ; see also Rodriguez de los Santos *et al.*, 1986). The other small-sized dispersers captured, which involve species with different phenological status, were caught all the year round but with a summer maximum largely due to *Luscinia megarhynchos*. The medium-sized dispersers captured, represented by *Turdus philomelos* and *Turdus merula*, were absent during the summer (see also Debussche and Isenmann, 1985b).

The three most frequent small-sized dispersers were trapped in all available habitats but their capture numbers depended on the mist net location (Fig. 2). The largest number of *S. atricapilla* and *S. melanocephala* was trapped at the edge (ecotone) of the *Q. ilex* coppice (mist net D) and the smallest number of both species in the dense closed coppice (mist net A). On the contrary the largest number of *E. rubecula* was caught in the dense closed coppice (mist net A) and the smallest number in the large clearing (mist net C).

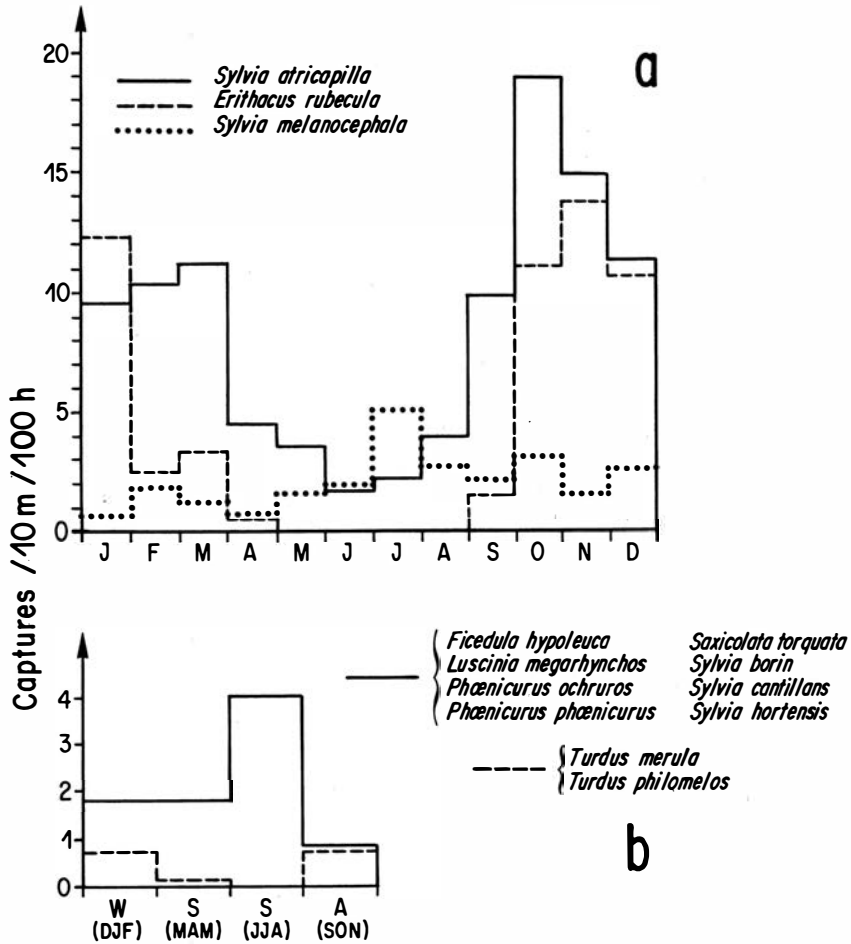


Figure 1. — Abundance of dispersers for 1982 as estimated by mist net captures (mist nets A-D); a: monthly values for the 3 dominant bird species, b: seasonal values for 2 groups (small-sized and medium-sized) of less frequent ones.

FRUITING AND SEED RAIN PHENOLOGY

The highest numbers of fruiting species were recorded from September to the beginning of December both in 1981 ($n = 12-15$) and 1982 ($n = 13-18$) (Fig. 3). The same periods were concerned when considering the native species alone, with a peak of availability through September-November (1981) and through October-November (1982) (Fig. 3). The seeds of 38 fleshy-fruited plant species (among them 13 alien and cultivated species) were collected at the study site (Appendix II). Although *Arum italicum*, *Crataegus azarolus* and *Sorbus domestica* were fleshy fruited plants present at the study site, though represented by few individuals, their seeds were never recorded. On a per week basis, the highest number of

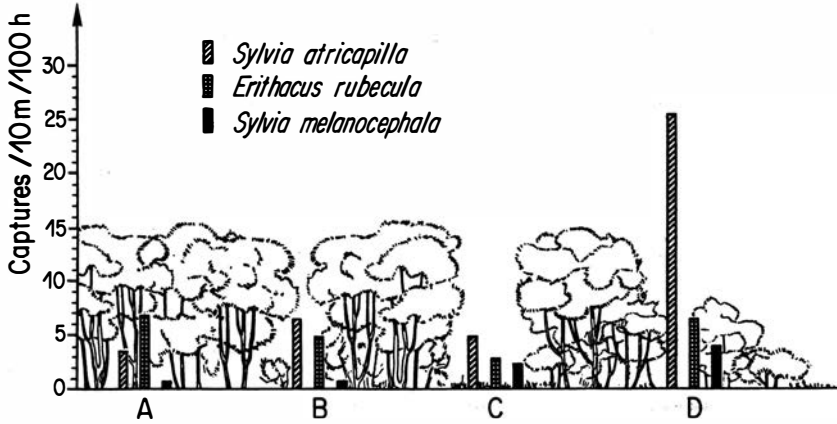


Figure 2. — Abundance of the 3 dominant dispersers for 4 mist net locations (A-D) as estimated by mist net captures. The locations are arranged along a gradient of vegetation structure.

dispersed plant species ($n = 10-15$) was recorded from October to January (Fig. 4). The maximum number of native species ($n = 9-13$) was dispersed from September to January, with a peak in the first week of October (Fig. 4), and alien and cultivated species ($n = 4-5$) from November to January.

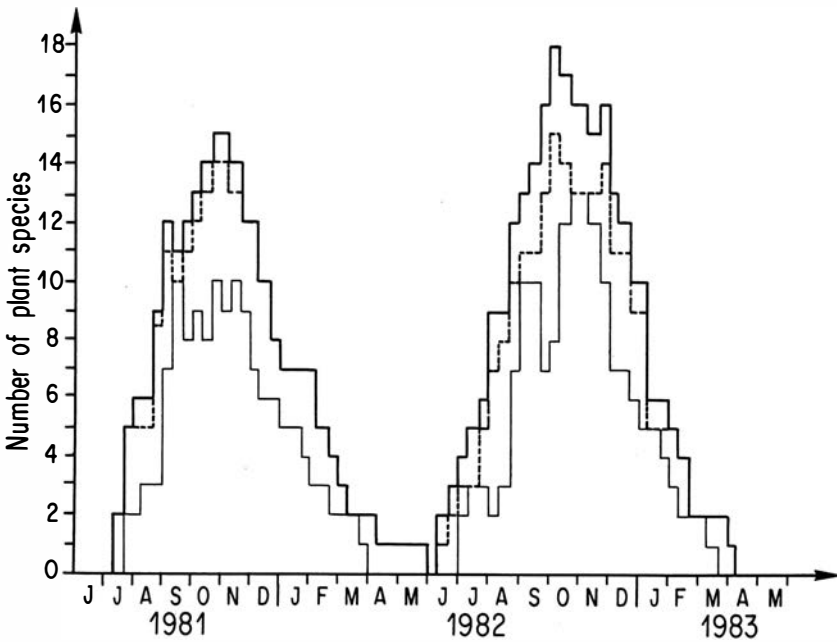


Figure 3. — Number of fruiting plant species (solid line), number of fruiting native plant species (dashed line) and number of fruiting native plant species with maximum crop (thin line) observed per 10 day-period.

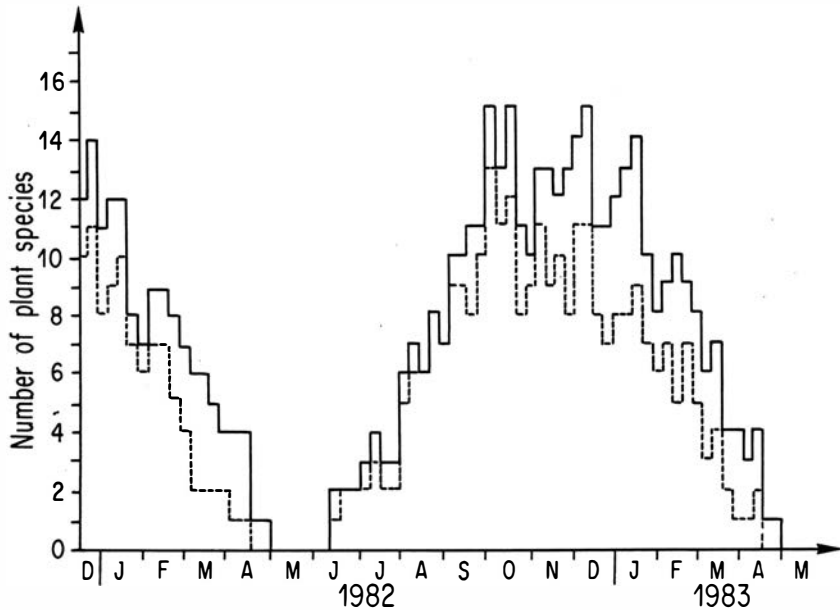


Figure 4. — Number of plant species (solid line) and number of native plant species (dashed line) whose seeds were collected per week.

When considering the whole set of fleshy fruited plants, there is no discrepancy between fruiting phenology and seed rain phenology. Four seed rain phenologies with characteristic peaks could be distinguished (Fig. 5): 1) summer and early autumn (e.g. *Sambucus nigra*, *Rubus ulmifolius*, *Ficus carica*), 2) autumn and winter (e.g. *Rhus coriaria*), 3) early winter (e.g. *Hedera helix*, *Viburnum tinus*), 4) late winter (e.g. *Cotoneaster horizontalis*, *Pyracantha coccinea*).

The number of consumed fruits, obtained by computing the collected seed rain and the mean number of seeds per fruit (see Appendix II) strongly varied throughout the annual cycle. The peak in autumn and at the beginning of winter and the minimum in spring were obvious (Fig. 6). The amount of consumed fruits showed a significant linear correlation with the consuming biomass (see Salt, 1957 and Blondel, 1969; bird weights are given in Debussche and Iseemann, 1989) of the captured dispersers (significance tested with r ; $p < 0,01$) (Fig. 6).

DISCUSSION

BIRD ASSEMBLAGE

Nineteen species of dispersers (38 % of the passerines recorded at the study site) and 12 species of fruit-predators (they include the pulp- and seed-predators and 24 % of the passerines) were recorded on the study site. Three small-sized

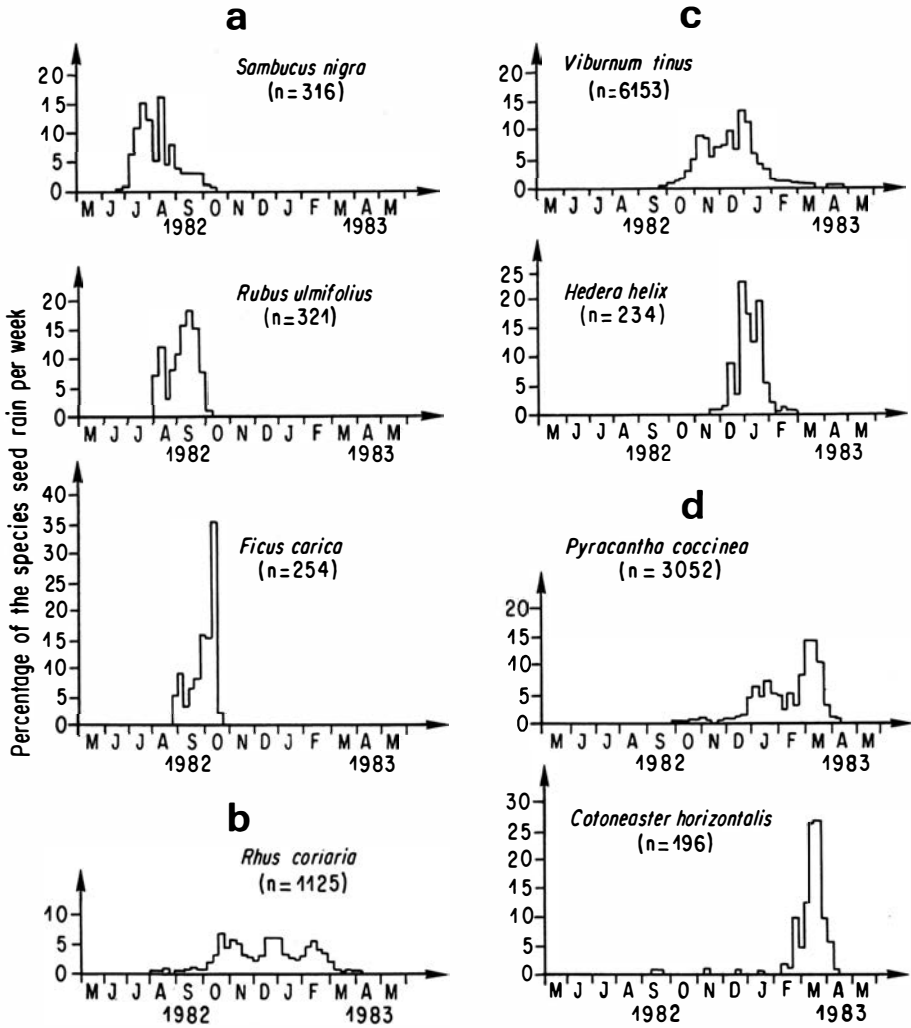


Figure 5. — Examples of seed rain phenology per week ; a : summer-early autumn, b : autumn-winter, c : early winter, d : later winter.

passerines (*Sylvia atricapilla*, *S. melanocephala* and *Erithacus rubecula*) were by far the major dispersers. *Turdus merula* and *T. philomelos* were the two most frequent medium-sized dispersers. The small-sized (< 30 g) *Parus major*, *P. caeruleus*, *Fringilla coelebs*, *Carduelis carduelis* and *C. chloris* were the major fruit-predators on the study site. In the maquis of Corsica, a Mediterranean island, the main dispersers were the same 5 bird species as those found in the present study (Debussche *et al.*, 1990). In the scrublands of southern Spain, composition and structure of the bird assemblage were rather similar (Herrera, 1984 ; Jordano, 1984, 1985). Herrera (1984) found that, in the bird community he

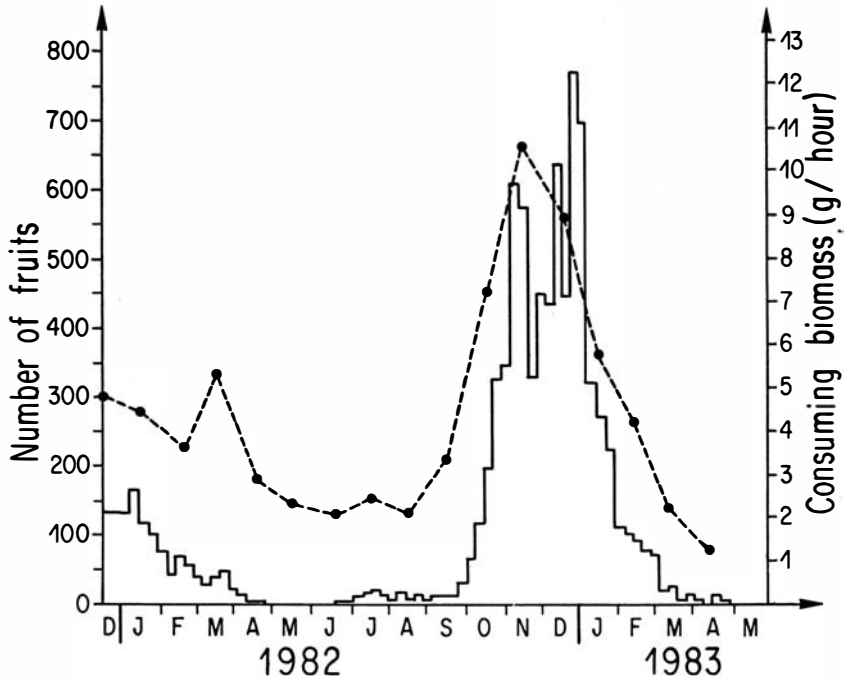


Figure 6. — Number of fruits consumed and disperser consuming biomass over time (groups of seed traps 1, 2 and 3 and mist nets A-D are only concerned because of their close vicinity). Number of fruits (entire line) is computed for each week from the number of seeds collected and the average number of seeds per fruit. Consuming biomass (dashed line) involves the monthly means of captures.

studied, there were 34 % of dispersers and 29 % of fruit-predators. Fourteen dispersers were found in both areas, and the 3 major species were the same (*S. atricapilla*, *S. melanocephala* and *E. rubecula*). Only 5 fruit-predators occurred at both locations, with again *P. major*, *P. caeruleus* and *C. chloris* as important species in these scrublands. Jordano (1984, 1985) found 43 % of dispersers and 23 % of fruit-predators on his study site. Fifteen dispersers were in common and again the 3 same above mentioned species were the most important ones, accompanied in this study by *Sylvia borin*, *T. merula* and *T. philomelos*. Ten fruit-predators were in common.

In southern England, however, the assemblage of frugivorous birds studied by Snow and Snow (1988) was quite different. While 6 fruit-predators were in common (with mostly *Paridae* and *Fringillidae* species), there were only 9 dispersers in common. *E. rubecula* and *S. atricapilla* were still the major species, but the importance of medium-sized dispersers strongly increased. *T. merula* and *T. philomelos* were joined by *T. iliacus*, *T. pilaris*, *T. viscivorus* and *Sturnus vulgaris*. The major role played by the *Turdus* species among the frugivorous birds in England was also emphasized by Sorensen (1981). In Europe, dispersers are chiefly represented by the *Sylviidae* and the *Turdidae*, and by *Bombycilla garrulus* (see Glutz von Blotzheim and Bauer, 1985), the latter being restricted to Northern Europe. Fruit-predators are mainly represented by *Fringillidae* and *Paridae*.

The paramount role played by medium-sized dispersers was also noted by several authors in eastern North America, with birds of the families *Turdidae*, *Mimidae*, *Bombycillidae* and *Picidae* whatever the latitude (e.g. Stiles, 1980 ; Hohlthuijzen, 1983 ; Willson, 1986 ; Skeate, 1987).

Therefore, the whole set of shrublands and open evergreen woodlands of the Mediterranean Basin are characterized by a shift towards the small-sized dispersers. As small birds have higher metabolic and energetic requirements with decreasing temperatures (Kendeigh, 1970 ; Kendeigh *et al.*, 1977), the relatively mild winter of the Mediterranean climate may explain this shift (Herrera, 1984). However, Skeate's (1987) study showed that there is hardly any difference in the structure of bird assemblages (dominance of medium-sized birds) between Florida and the northern areas of the United States (e.g. Stiles, 1980), apparently contradicting this explanation. It is likely that vegetation history and structure may provide an alternative explanation. Extensive shrubland areas whose limits fluctuated with glaciations and which existed long before human interference, have led to a rich speciation in the Mediterranean *Sylvia* species (Blondel and Farré, 1988). In this genus, we have recorded 3 species, one of which was among the major fruit consumers at our study site : *S. melanocephala*, *S. hortensis* and *S. cantillans*. The medium-sized dispersers, dominated by the genus *Turdus* and *Sturnus vulgaris* in Europe, mainly forage on the ground in rather open herbaceous habitats, forested habitats, and cultivated areas (orchards, vineyards,...) (Glutz von Blotzheim and Bauer, 1988). The fruits consumed by these medium-sized birds are diverse (e.g. Guitian, 1984 ; Tejero *et al.*, 1984 ; Debussche and Isenmann, 1985b, 1989 ; Théry, 1989). As fruit accessibility plays a major role in fruit choice (Denslow and Moermond, 1982, Moermond *et al.*, 1986), the very dense intricate structure of many Mediterranean shrublands from the ground level up to height of 2-3 m is not particularly suited for the usual foraging behaviour of these medium-sized species (Herrera, 1984). Moreover, many fleshy-fruited shrubs generally have poorly developed twigs and branchlets that hinder perching by birds of such a size (Herrera, 1984). Herrera's explanation is strengthened by the fact that, in the vicinity of our study area, the few dense deciduous forests dominated by *Quercus pubescens* with a poor understorey, as well as grasslands with fringing hedges and patchy woodlands, are regularly visited in large numbers by four to five *Turdus* species and more rarely by *Sturnus vulgaris* (Debussche, pers. obs.).

SEASONAL SUCCESSION OF FRUITING AND DISPERSERS

At the species level, the comparison of the beginning of fruiting periods, and dispersal-consumption periods, along a latitudinal gradient at low elevation is documented from Andalusia to Sweden by 10 pairs of dates involving 10 plant species (see Herrera, 1984 ; Snow and Snow, 1988 ; Eriksson and Ehrlén, 1991) (Table I). In 5 cases the dates of fruiting, or dispersal-consumption, are identical (difference < 15 days) and for the 5 other cases the dates are later at higher latitudes than at lower ones (Table I). In Andalusia, fruiting period begins later at higher elevations than at lower ones for 5 plant species out of the 6 plant species observed at both sites (Table I). Though a few plant species (*Crataegus monogyna*, *Prunus spinosa*, *Rosa canina*) ripen their fruit at the same date across a large range of their distribution area, the fruiting phenology of a majority of plants (9 out

TABLE I

Comparison of the beginnings of the ripening and dispersal periods between Montpellier, Andalusia (after Herrera, 1984), England (after Snow and Snow 1988) and Sweden (after Eriksson and Ehrlén 1991).

	Andalusia (A)		Montpellier (lat. : 43°39'N)	England (A) (lat. : 51°50'N)	Sweden (A) (lat. : 58°50'N)
	Lowland site (lat. : 37°24'N) (alt. : 100 m) Fruiting	Highland site (lat. : 37°59'N) (alt. : 1 150 m) Fruiting	Fruiting (B) (1981-82, 1982-83)	Dispersal (C) (1982-83)	Consumption
<i>Arbutus unedo</i>	Nov. 8	Oct. 15			
<i>Crataegus monogyna</i>			Aug. 20, Aug. 10		Aug. 25
<i>Daphne gnidium</i>	Aug. 1	Sep. 8			
<i>Hedera helix</i>			Dec. 1, Nov. 20	Nov. 19	Dec. 20
<i>Lonicera implexa</i>	Aug. 15	Sept. 15	Jul. 20, Aug. 1		
<i>Phillyrea angustifolia</i>	Aug. 1	Aug. 15			
<i>Pistacia lentiscus</i>	Sep. 22	Oct. 8	Oct. 10, Oct. 1	Sep. 24	
<i>Prunus spinosa</i>			Sep. 1, Aug. 20		Sep. 1
<i>Rhamnus alaternus</i>	May 22		Jul. 10, Jun. 10	Jun. 11	
<i>Rosa canina</i>		Sep. 8	Sep. 1, Sep. 1		Nov. 15
<i>Rubia peregrina</i>	Aug. 8	Oct. 22	Sep. 20, Oct. 10	Oct. 15	
<i>Sambucus nigra</i>			(?), Jun. 20	Jun. 18	Aug. 1
<i>Smilax aspera</i>	Jul. 15		Sep. 1, Aug. 20	Sep. 10	

(A) : as phenological data are presented by Herrera (1984), Snow and Snow (1988) and Eriksson and Ehrlén (1991) in diagrammatic form we have visually estimated the dates when not mentioned in their texts.

(B) : (?) : absence of observation.

(C) : plant species with more than 30 collected seeds are only considered.

of 13) is significantly delayed at higher latitudes and at higher altitudes, *i.e.* due to climatic conditions. This latitudinal trend is in contradiction with Stiles' (1980) and Snow and Snow's (1988) expectations. These specific phenological patterns may be explained by the physiology of the plants, without any intervention of the selective pressures of dispersers.

However, the composition of the fleshy-fruited flora considerably changes along the considered latitudinal gradient : e.g. not a single species was found both at the lowland study site in Andalusia by Herrera (1984) and at the study site of Eriksson and Ehrlén (1991) in Sweden. This leads us to examine the phenological shifts not only at the species level, but also at the level of the flora as a whole. At Montpellier, the largest number of native species was dispersed in October ; none were dispersed in May. The maximum fruiting period extends from September to November. On a regional scale, around Montpellier, the native plants have their highest fruit availability in October (Debussche, 1988). In Spanish scrublands, the maximum number of fleshy-fruited plants bearing ripe fruits occurs in November-December ; none, or only a few, bear ripe fruits in May and June (Herrera, 1984). In England, the number of plant species whose fruits are consumed is highest in November and lowest in April and May (Snow and Snow, 1988). In Sweden, maximum fruiting occurs in September with no plant species bearing fruits in April and May (Eriksson and Ehrlén, 1991). In Europe, for the latitudes where data are available, fructification is the most abundant and diversified from September to December and the lowest from April to June. The differences in study methods do not allow to ascertain without doubt whether it exists a phenological shift of the peak of fruit availability in relation to latitude as suggested by Snow and Snow (1988). The data suggest, however, that this shift across a latitudinal range of 21° from Sweden to Spain is highly probable, reaching approximately 2 months. In North America, two studies (Thompson and Willson, 1979 and Skeate, 1987) using the same methods, showed that along a gradient of some 10° in latitude the maximum number of fleshy-fruited plants with ripe crops occurred in September in Illinois and in December in Florida. A difference of 16 °C exists between the average temperature of the coldest month in Chicago (Illinois) with - 3 °C and that of Jacksonville (Florida) with 13 °C (see Rudloff, 1981). On the other hand this difference reaches 13 °C between the average temperature of the coldest month for the European study sites (Stockholm : - 3 °C ; London : 4 °C ; Montpellier : 6 °C ; Sevilla : 10 °C ; see Rudloff, 1981). Owing to the well-known climatic difference between the western and eastern sides of continents, it is Scandinavia at about 60° N (hence 18° further north than Illinois) which is the European equivalent of the study site of Thompson and Willson (1979) when considering the average temperature of the coldest month. The latitudinal shift of timing in peak fruit availability is clear in North America and highly probable in Europe, as inferred from the available data. We suggest that this shift is mainly the result of climatic constraints on plants : southwards, mild temperatures in autumn and in winter allow late fruiting in the year, whereas northwards low temperatures and frost prevent fruiting in late autumn and winter.

On our study site, the highest number of dispersers was encountered from October to January, involving a mixture of resident, migrating and wintering species. The lowest number was recorded from May to August with only breeding species present. In southern Spain the highest number of dispersers is also present from October to January in the scrublands, the lowest number occurring slightly

earlier, from April to July (Herrera, 1984 ; Jordano, 1985). In England the peak is in September (Snow and Snow, 1988), *i.e.* earlier than in the Mediterranean area. While some frugivorous species remain in England during winter (Snow and Snow, 1988 ; see also Lack, 1986), this is not true for northern Europe where very few species overwinter (e.g. *Bombycilla garrulus* ; Glutz von Blotzheim and Bauer, 1985 and 1988). In the whole of Europe, many taxonomically diverse species belong to the so-called short-distance migrants for which the Mediterranean region is the main wintering area (Blondel, 1969). Among the passerines the bulk is formed by *Motacillidae*, *Turdidae*, *Sylviidae* and *Fringillidae*. Four out of the 5 predominant dispersers (*Sylvia atricapilla*, *Erithacus rubecula*, *Turdus philomelos* and *T. merula*) are such typical short-distance migrants. These 4 species have populations which breed primarily in forests, to leave them in September-October and invade afterwards in huge numbers the Mediterranean area for about 4-6 months (Blondel, 1969). In North America, short-distance migrants also occur (see e.g. Keast and Morton, 1980 ; Cox, 1985). In Illinois, the maximum number of dispersers is present in September and October and the minimum in winter (Thomson and Willson, 1979). Further south, in Florida, the maximum occurs from October to February and the minimum from May to August (Skeate, 1987). In both continents, at medium latitudes, there is a peak of dispersers in September-October and a winter minimum which is gradually more pronounced northwards. On the contrary, in more southern areas the peak begins in October and continues during part of the winter, while the minimum occurs from the end of spring until summer. Thus, there is a shift of the peak of dispersers' abundance according to latitude which is very similar in duration and timing to the latitudinal shift observed in fruiting peak.

Beside the native plants, two introduced species play a significant role in the system studied : *Pyracantha coccinea* and *Cotoneaster horizontalis*. However, *P. coccinea* is perhaps spontaneous in the French Mediterranean area (Tutin *et al.*, 1968), though doubtfully, even in the Montpellier region (Loret and Barrandon, 1876 ; Fournier, 1977). This species was introduced as an ornamental shrub at least a century ago and became quickly naturalized, fairly frequently, in hedges and old fields (Debussche and Isenmann, 1990). On the other hand, *C. horizontalis* is clearly an alien ornamental shrub of south west Asiatic origin (Tutin *et al.*, 1968) that does not naturalize in our study area (Debussche and Isenmann, 1990). Both species have their dispersal peaks in March, much later than those of the native species, although their fruits are available since late September. This time lag is probably due to competition for dispersal with native species whose fruits are much more rich in lipids, as it is the case with *Hedera helix* and *Viburnum tinus* (with a pulp lipid content of 23 % and 27 % respectively vs. 2 % for *P. coccinea* and *C. horizontalis*) which have their dispersal peaks in December-January. Debussche and Isenmann (1990) hypothesized that the availability of fruits of non-native plants befalling after that of native plants may influence the wintering and the spring migration patterns of the most frugivorous species (e.g. *S. atricapilla*), emphasizing their versatility.

The selective pressures of dispersers might well affect the fruiting phenology, the observed latitudinal shift and the coincidence between periods of high fruit availability and those of dispersers abundance (e.g. Thompson and Willson, 1979 ; Stiles, 1980 ; Snow and Snow, 1988). However, it has also been emphasized that the selective pressures of dispersers were in fact weak and that historical, physiological and phylogenetic constraints on plant species could provide valua-

ble explanations for several features of fruits and fruiting patterns (e.g. Herrera, 1984, 1985, 1986, 1987; Debussche *et al.*, 1987). In the same perspective, we consider that the observed latitudinal shift in fruiting is mainly determined by climatic constraints on plants. The coincidence between high fruit availability and dispersers abundance can then be seen as a simple consequence of the opportunist behaviour of frugivorous birds.

SUMMARY

This study deals with a fleshy-fruited plant-bird dispersal system at a site in Mediterranean France, characterized by *Quercus ilex* coppices, shrublands and old fields. Among the 19 bird dispersers recorded, 14 were of small size (< 25 g), with *Sylvia atricapilla*, *Erithacus rubecula* and *S. melanocephala* accounting for 86.6 % of those caught in mist nets. The importance of small-sized dispersers seems to characterize the Mediterranean shrublands and evergreen woodlands in the whole of the temperate systems.

The highest numbers of dispersers occurred from October to January. The seeds of 38 fleshy-fruited plants (native, cultivated and alien) were collected in seed traps. Seed rain occurred throughout the year except in May, with a maximum fruiting period extending from September to early December and the greatest number of native species being dispersed in October. When we compare our data to those collected in Spain, England and Sweden a shift of the peak of fruit availability in relation to latitude (the higher the latitude the earlier the peak) is very likely in Europe. Such a shift is obvious in the United States. We suggest that 1) this shift is the result of climatic constraints on plants rather than that of the selective pressures of dispersers, and 2) that the coincidence between high fruit availability and dispersers' abundance can simply result from the opportunist behaviour of frugivorous birds.

RÉSUMÉ

Nous avons étudié un système plantes à fruits charnus-oiseaux disséminateurs dans une station du Midi de la France, caractérisée par une mosaïque de taillis de Chêne vert, de garrigues et de friches. Parmi les 19 espèces d'oiseaux disséminateurs répertoriées, 14 sont de petite taille (< 25 g) avec *Sylvia atricapilla*, *Erithacus rubecula* et *S. melanocephala* comptant pour 86,6 % des individus capturés. L'importance des disséminateurs de petite taille semble caractériser les garrigues et formations sempervirentes de la région méditerranéenne par rapport aux autres systèmes tempérés.

Le plus grand nombre de disséminateurs est présent d'octobre à janvier. Les graines de 38 espèces de plantes à fruits charnus (spontanées, cultivées et introduites) ont été recueillies dans des collecteurs. La pluie de graines a lieu toute l'année, sauf en mai, avec une période de disponibilité en fruits maximale de septembre à début décembre et un nombre maximal d'espèces spontanées disséminées en octobre. La comparaison de nos données à celles obtenues en Espagne, en Angleterre et en Suède montre qu'un décalage d'environ deux mois du maximum de disponibilité en fruits en fonction de la latitude, est hautement probable en Europe (le maximum étant d'autant plus précoce que l'on va vers le

nord). Ce décalage est certain aux Etats-Unis. Nous suggérons que 1) ce décalage dans le temps est le résultat de contraintes climatiques sur les plantes plutôt que celui d'une pression sélective exercée par les oiseaux disséminateurs et que 2) la coïncidence entre la disponibilité maximale en fruits et l'abondance maximale des oiseaux disséminateurs est tout simplement la conséquence du comportement opportuniste de ces derniers.

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APPENDIX I

Bird species : frequency and abundance at the study site ; feeding habits on fruits and status.

Bird species	Family	Frequency* of observation			Mist-netted		Feeding** habit	Status***
		Q.i.	ec.	o.f.	Captures	Individuals		
<i>Regulus ignicapillus</i>	Sylviidae	A			37	17		W1, W2
<i>Parus major</i> (N)	Paridae	A	B		49	38	P	S, (W1, W2)
<i>Luscinia megarhynchos</i> (N)	Turdidae	A	C	E	18	16	D	M1, M2
<i>Prunella modularis</i>	Prunellidae	A	B	E	51	25		W1, W2
<i>Turdus merula</i>	Turdidae	A	D	C	7	7	D	W1, W2, S
<i>Turdus philomelos</i>	Turdidae	A	C	B	13	13	D	W1, W2
<i>Erithacus rubecula</i>	Turdidae	A	A	B	106	62	D	W1, W2, (S)
<i>Sylvia atricapilla</i> (N)	Sylviidae	A	A	A	336	263	D	W1, W2, S
<i>Sylvia melanocephala</i> (N)	Sylviidae	A	A	A	75	52	D	S
<i>Fringilla coelebs</i>	Fringillidae	B	A		7	7	P,S	W1, W2, S
<i>Parus caeruleus</i>	Paridae	B	C	C	17	15	P	S, (W1, W2)
<i>Carduelis serinus</i> (N)	Fringillidae	C	B	C	4	4	S	W1, W2, S
<i>Hippolais polyglotta</i> (N)	Sylviidae		B		4	4	D1	M1, M2
<i>Carduelis carduelis</i> (N)	Fringillidae	E	B	C	9	9	S	W1, W2, S
<i>Carduelis chloris</i> (N)	Fringillidae	C	C	B	13	13	S	W1, W2, S
<i>Anthus pratensis</i>	Motacillidae		E	B	1	1		W1, W2,
<i>Troglodytes troglodytes</i>	Troglodytidae	C	D		16	9		W1, W2
<i>Certhia brachydactyla</i>	Certhiidae	C	D	E	18	12		S
<i>Passer domesticus</i> (N)	Ploceidae	C	D	E	6	6	P, S	S
<i>Pica pica</i> (N)	Corvidae	C	C	E			D	S
<i>Passer montanus</i> (N)	Ploceidae	D	C		2	2	P, S	S, (W1, W2)

APPENDIX I, *continued*

Bird species	Family	Frequency* of observation			Mist-netted		Feeding** habit	Status***
		Q.i.	ec.	o.f.	Captures	Individuals		
<i>Emberiza cirlus</i> (N)	Emberizidae	E	C	C	7	6	S	S, (W1, W2)
<i>Saxicola torquata</i> (N)	Turdidae	E	C	C	5	3	D	W1, W2, S
<i>Ficedula hypoleuca</i>	Muscicapidae	D	E	C	7	7	D	M1
<i>Phoenicurus ochruros</i> (N)	Turdidae	E	D	C	10	7	D	W1, W2, S
<i>Phoenicurus phoenicurus</i> (N)	Turdidae	E	D	C	5	5	D	M1, M2,
<i>Phylloscopus collybita</i>	Sylviidae	E	D	C	8	7		W1, W2,
<i>Sylvia hortensis</i> (N)	Sylviidae			C	4	3	D	M2
<i>Coccothraustes coccothraustes</i>	Fringillidae	D	E				S	W1, W2
<i>Phylloscopus bonelli</i>	Sylviidae	D	E		2	2		M1, M2
<i>Emberiza calandra</i>	Emberizidae		D	E				W1, W2
<i>Sylvia borin</i>	Sylviidae	E		D	3	3	D	M1
<i>Sylvia cantillans</i>	Sylviidae	E		D	3	3	D	M2
<i>Cisticola juncidis</i>	Sylviidae			D	2	2		S
<i>Accipiter nisus</i>	Accipitridae	E						W1, W2, S
<i>Acrocephalus turdoides</i>	Sylviidae	E						M1, M2,
<i>Aegithalos caudatus</i>	Aegithalidae	E						S
<i>Alcedo atthis</i>	Alcedinidae	E						W1, W2, S
<i>Carduelis spinus</i>	Fringillidae	E						W1, W2
<i>Columba palumbus</i>	Columbidae	E						W1, W2, S
<i>Falco tinnunculus</i>	Falconidae	E						W1, W2, S
<i>Jynx torquilla</i>	Picidae	E						M1, M2
<i>Muscicapa striata</i>	Muscicapidae	E						M1, M2

APPENDIX I, *continued*

Bird species	Family	Frequency* of observation			Mist-netted		Feeding** habit	Status***
		Q.i.	ec.	o.f.	Captures	Individuals		
<i>Parus cristatus</i>	Paridae	E						S
<i>Regulus regulus</i>	Sylviidae	E						W1, W2
<i>Streptopelia decaocto</i>	Columbidae	E						S
<i>Phylloscopus trochilus</i>	Sylviidae	E	E					M1
<i>Acrocephalus scirpaceus</i>	Sylviidae	E		E	1	1	D2	M1, M2
<i>Carduelis cannabina</i>	Fringillidae		E					W1, W2, S
<i>Corvus corone</i>	Corvidae		E					S
<i>Lanius senator</i>	Laniidae		E					M1, M2,
<i>Locustella naevia</i>	Sylviidae		E					M1
<i>Sturnus vulgaris</i>	Sturnidae		E				D	W1, W2, S
<i>Sylvia communis</i>	Sylviidae		E				D	M1
<i>Turdus torquatus</i>	Turdidae		E				D3	W1
<i>Upupa epops</i>	Upupidae		E					M1, M2, W1, W2
<i>Lanius collurio</i>	Laniidae			E				M1

* Q.i., ec., o.f.: *Quercus ilex* coppice, ecotone and olf field, respectively (see Study site and Methods).

A, B, C, D, E: observation frequency > 75 %, 50-75 %, 10-50 %, 5-10 % and < 5 % respectively (see Methods).

** P, D, S: pulp-predator, seed-disperser and seed-predator respectively (see Herrera, 1984). Evidences observed by the authors in the Montpellier region excepted: 1, 2, 3, after Olioso *et al.*, 1987, Olioso, *in litt.* and Debussche pers. obs. respectively, concerning neighbouring areas of the French Mediterranean region.

*** M1, M2, S, W1, W2: migrant wintering in tropical zone and breeding outside of the region, migrant wintering in tropical zone and breeding in the region, sedentary and erratic in the Mediterranean zone, Mediterranean wintering migrant and Mediterranean overwintering respectively (after Blondel, 1969). If a species includes populations with different phenological status all of them are given, the less frequent ones in parentheses.

(N) nesting at the study site.

APPENDIX II

Plant species : number of seeds per fruit, fruiting period (1981-82, 1982-83) and dispersal period (1982-83).

Plant species (A)	Family	Seeds per fruit (B)	Fruiting period (C)	Dispersal period (D)
<i>Arum italicum</i> (1)	Araceae	2-3	Jul.-Aug., Jul.-Aug.	
<i>Asparagus acutifolius</i>	Liliaceae	1 (2)	Nov.-Dec., Sep.-Nov.	Oct.-Dec.
<i>Celtis australis</i>	Ulmaceae	1	Oct.-Dec., Sep.-Dec.	Sep.-Mar.
<i>Cornus sanguinea</i> (2)	Cornaceae	1		
<i>Cotoneaster horizontalis</i> (2) (a)	Rosaceae	2		Sep.-Apr.
<i>Crataegus azarolus</i> (1) (a)	Rosaceae	2	(?), Aug.-Nov.	
<i>Crataegus monogyna</i>	Rosaceae	1	Aug.-Dec., Aug.-Dec.	
<i>Ficus carica</i> (2)	Moraceae	1 000-2 000		Aug.-Oct.
<i>Hedera helix</i>	Araliaceae	1-4 (5)	Dec.-Feb., Nov.-Feb.	Nov.-Mar.
<i>Jasminum fruticans</i>	Oleaceae	(1) 2	Aug.-Dec., Aug.-Jan.	
<i>Juniperus oxycedrus</i> (2)	Cupressaceae	2-4		
<i>Laurus nobilis</i>	Lauraceae	1	Oct.-Dec., (s)	
<i>Ligustrum ovalifolium</i> (2) (a)	Oleaceae	(1) 2		
<i>Lonicera implexa</i>	Caprifoliaceae	2-3	Jul.-Nov., Aug.-Oct.	
<i>Lycium barbarum</i> (2) (a)	Solanaceae	15-25		
<i>Mahonia aquifolium</i> (2) (a)	Berberidaceae	1-5		
<i>Melia azedarach</i> (2) (a)	Meliaceae	1		
<i>Morus alba</i> (a)	Moraceae	3-6	(?), Jun.-Aug.	
<i>Olea europaea</i> var. <i>europaea</i> (a)	Oleaceae	1	(s), (s)	
<i>Osyris alba</i>	Santalaceae	1	Jul.-Oct., Jul.-Dec.	
<i>Parthenocissus quinquefolia</i> (2) (a)	Vitaceae	1-3		
<i>Phillyrea latifolia</i>	Oleaceae	1	Aug.-Nov., (s)	
<i>Phytolacca americana</i> (a)	Phytolaccaceae	10	Aug.-Nov., Aug.-Dec.	
<i>Pistacia lentiscus</i>	Anacardiaceae	1	Oct.-Feb., Oct.-Feb.	Sep.-Mar.
<i>Pistacia terebinthus</i>	Anacardiaceae	1	(s), Aug.-Oct.	
<i>Pittosporum tobyra</i> (2) (a)	Pittosporaceae	1		
<i>Prunus spinosa</i>	Rosaceae	1	Sep.-Nov., Aug.-Nov.	
<i>Pyracantha coccinea</i> (a)	Rosaceae	5	(?), Sep.-Jan.	Sep.-Apr.
<i>Rhamnus alaternus</i>	Rhamnaceae	3	Jul.-Sep., Jun.-Aug.	Jun.-Oct.

APPENDIX II, *continued*

Plant species (A)	Family	Seeds per fruit (B)	Fruiting period (C)	Dispersal period (D)
<i>Rhus coriaria</i>	Anacardiaceae	1	Aug.-Feb., Aug.-Feb.	Aug-Apr.
<i>Rosa canina</i>	Rosaceae	10-40	Sep.-Mar., Sep.-Apr.	
<i>Rubia peregrina</i>	Rubiaceae	1 (2)	Sep.-Feb., Oct.-Jan.	Oct.-Mar.
<i>Rubus ulmifolius</i>	Rosaceae	30-50	Jul.-Oct., Jul.-Oct.	Jul.-Oct.
<i>Ruscus aculeatus</i>	Liliaceae	1 (2)	Oct.-May, Oct.-Mar.	
<i>Sambucus nigra</i>	Caprifoliaceae	3	(?), Jun.-Oct.	Jun.-Oct.
<i>Smilax aspera</i>	Liliaceae	1-3	Sep.-Dec., Aug.-Jan.	Sep.-Feb.
<i>Solanum nigrum</i>	Solanaceae	30-50	(?), (?)	
<i>Sophora japonica</i> (2) (a)	Leguminosae	4-8		
<i>Sorbus domestica</i> (1)	Rosaceae	2-4	(?), (?)	
<i>Viburnum tinus</i>	Caprifoliaceae	1	Sep.-Apr., Sept.-Feb.	Sep.-Apr.
<i>Vitis vinifera</i> subsp. <i>vinifera</i> (2) (a)	Vitaceae	1-2		

- (A) : present at the study site and whose seeds were collected at the study site, excepted : (1) present but no seed was collected, (2) absent but their seeds were collected ; (a) : alien and cultivated species in the Montpellier region.
 (B) : obtained at the study site or nearly from 25-60 fruit samples.
 (C) : observed at the study site ; (?) : absence of observation, (s) : too small crop.
 (D) : plant species with more than 30 collected seeds are only considered.