Exclusive frugivory and seed dispersal of *Rhamnus alaternus* in the bird breeding season

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Abstract

We studied avian frugivory and seed dispersal in a dioecious shrub, *Rhamnus alaternus*, focusing on the quantitative and qualitative components of effectiveness. The study took place at three locations in the northeast of the Iberian Peninsula, and examined bird behaviour, intensity of feeding, and the consequences for seedling emergence. The coincidence between the bird breeding season and fruit ripening of *R. alaternus* in the absence of other ripe fruit, generates a monospecific interaction. The extant frugivorous species were mainly legitimate seed dispersers and their abundance was low. *Sylvia melanocephala* and *S. undata* were the most important at one site whereas *S. atricapilla*, *Erithacus rubecula* and *Turdus merula* predominated at the other two sites. Fruit handling took place directly on the branches. Bird species used microhabitats differently as first post-feeding perch, which usually was a short distance away. The low density of frugivorous birds in all localities, among others factors, resulted in satiation of the disperser community and many mature fruits unconsumed. Both adults and juveniles feed upon the plants and their foraging patterns are similar. Adults of *S. melanocephala* were observed to feed fruit to nestlings and consequently a second phase of dispersal potentially arises from the transport of fecal sacs. Pulp removal and passage through the digestive tract increased the probability of seedling emergence. This plant-dispersal interaction has important consequences, both positive and negative for the plant. Positively, the fruiting of *R. alaternus* at a time when other ripe fruits are not available avoids interspecific competition for seed dispersers. In addition, a low density of seed rain may reduce intraspecific competition. Negatively, the low density and small size of the breeding frugivorous bird community limit fruit handling and removal away from the parent plants, while the territorial behaviour of birds at that time of the year reduces the potential distances of seed dispersal.

Introduction

Seed dispersal is the process of seed transportation from the mother plant to another place, and thus plays a key role in the subsequent recruitment of new plants (Herrera 2002). When considering dispersal by frugivores, the process of seed dispersal and the seedfall pattern can affect seed viability, seed survival, germination, emergence, survival and growth of new plants (Izhaki et al. 1991; Traveset and Willson 1997; Alcántara et al. 2000). The contribution of

frugivores to plant fitness depends on both the quantity and quality of seed dispersal (Schupp 1993; Jordano and Schupp 2000). The quantity of dispersal is determined primarily by the number of visits to the plant and the number of seeds consumed on each visit. The quality of dispersal is based on treatment in the digestive tract that the seeds receive and the conditions into which seeds are deposited. In this sense, the 'legitimate seed dispersers' swallow whole fruits and either regurgitate or defecate the seeds intact; and differ from 'Pulp consumers' that handle the pulp of the fruits from branches but do not disperse the seeds away from the origin plant (Herrera 1984a; Jordano and Schupp 2000). Combination of quantity and quality indicates whether a frugivore species is a legitimate disperser for a particular plant species (Alcántara et al. 2000; Jordano and Schupp 2000).

We used the Evergreen Buckthorn (*Rhamnus alaternus* L.), a common shrub or small tree in shrublands and woodlands of the Mediterranean region, to explore the patters of frugivory and seed dispersal by birds during spring-early summer in the Mediterranean region. Fruits of this plant species mature very early in comparison with the greater part of fleshy fruit plants in autumn-winter, overlapping with the breeding season of potential frugivores and disperser birds. In Europe, the mutualistic interaction of frugivory and seed dispersal occurs all year, but mainly during autumn and winter when the ripening of fruits coincides with bird migration (Herrera 1984a; Snow and Snow 1988). For this reason, the seed dispersal of the evergreen buckthorn has received little attention (but see Debussche and Isenmann 1983, 1989; Herrera 1984a; Sunyer 1994; Gulías et al. 2004). Even so, the process has been studied in other species that mature fruits in a similar period (Jordano and Schupp 2000; Hampe 2001; Traveset et al. 2003). This early ripening is a differential case that distances from the majority of fleshy fruits plants and that will influence on the relation with the frugivorous birds. In this study, we examined frugivorous and seed dispersing birds on *R. alaternus*, in particular their behaviour, seasonality and intensity of feeding, and the consequences for seedling emergence. The primary issues addressed in our study are: (1) Which are the most important frugivorous and seed dispersal bird species of *Rhamnus alaternus* in the study areas (2) Do the characteristics of the frugivorous community in this period limit the intensity of the seed dispersal? (3) What are the effects of the bird–plant interaction on seedling emergence? and (4) How can the relationship affect the qualitative and quantitative components of the dispersal effectiveness?

Methods

Plant species and study areas

The evergreen buckthorn (*Rhamnus alaternus* L.) is a perennial and dioecious shrub or small tree which is common in shrublands and woodlands of the Mediterranean region up to 1200 m a.s.l. The flowering period begins in January and finishes in May (Herrera 1984a; Aronne and Wilcock 1994). The yellowish flowers produce nectar and pollen stimulating pollination by bees and flies, although wind pollination also occurs (Dafni and O'Toole 1994; Gulías et al. 2004). Drupes (fruits) mature from April to August (Bas 2001), are black (4.9–9.9 × 4.5–8.1 mm (width × length); Herrera 1987; Bas et al. 2002) and they have 2–5 seeds with one endocarp per seed (Bas et al. 2002).

The study was conducted during April–August 1995–1999 at three sites in Catalonia, northeast Spain. Two of these areas, Mas de la Figuera (FIG) and Aigua Blanca (VALL), are situated at Les Gavarres massif (41°54′ N 02°56′ E, 185 and 295 m a.s.l., respectively). The third area, Aixart d'en Pi (MONT), is located at El Montgrí massif (42°05′ N 03°11′ E, 95 m a.s.l.). The climate is mediterranean, with a mean annual rainfall of 625 mm, a monthly minimum temperature in January (7.5 °C), and a maximum in July–August (24 °C). The vegetation at all sites is dominated by sclerophyllous Mediterranean species: Les Gavarres is a cork oak forest dominated by *Quercus suber*, *Q. ilex*, *Pinus pinea*, *P. pinaster*, and an understorey composed of *Arbutus unedo*, *Erica arborea* and *Cistus monspeliensis* in siliceous substrate. El Montgrí is a calcareous shrubland made up of *Q. coccifera*, *Rosmarinus officinalis*, *C. albidus*, *Brachypodium retusum*, and isolated *P. halepensis*, *Olea europaea* and *Q. ilex*.

Bird communities and frugivorous birds

We captured birds with mist nets (72 m of net/day on average) for 32 days along the breeding seasons 1995–1999 at the three study locations. Birds were marked with colour rings and their depositions (excrements or regurgitations) were collected individually in bags after keeping the birds approximately for 45 min. The presence/absence of *Rhamnus alaternus* seeds, endocarps and pulp was later determined in the laboratory (for methods see Bas et al. 2002). To estimate the composition of the bird community we used point counts at FIG and VALL, because the dense cover and scarcity of pathways made observer movement and visibility very difficult. Four point counts were repeated four times each, along the breeding seasons between 1995 and 1999. We recorded the occurrence of all bird species heard or seen in an area of around 5 ha per point count. Bird densities were measured at MONT, where plant cover was much lower, using the mapping method in a plot of 12.5 ha in 1997–1999 (with an average of 10 census days/breeding season). This method allowed to infer absolute densities of breeding pairs from the territory boundaries obtained from mapping male song posts and movements of colour-ringed birds (Bibby et al. 1992).

Bird behaviour

We studied bird behaviour during fruit ripening in 1997 and 1998 at MONT. The open vegetation allowed birds to be easily followed. During hours of high frugivore activity (early morning and late afternoon) on 24 different days (between June 2 and July 28), birds were followed by means of focal sampling (Altmann 1974). Sampling was based on seven randomly chosen *R. alaternus* female plants. The observer, immobile and hidden at a distance of 15–30 m, recorded complete visits with binoculars (10×40). We omitted the partial observations (not complete visits) and those of birds arriving when a focal bird was being followed. We recorded biological, spatial and temporal, and behavioural variables. Biological variables were species, sex and age (adult or first year). Spatial/temporal variables were arrival and exit directions (east sector = 45°–135°, south = 135°–225°, west = 225°–315°, north = 315°–

45°), total time spent in the plant, plant or microhabitat used as first perch after leaving the fruiting plant, and distance to the first perch. First perch was classified as *P. halepensis*, *O. europaea*, another *R. alaternus*, continuous shrubland (small shrubs), ground/rock/herbaceous plants, and others (isolated plants including *Q. ilex*, *Phillyrea latifolia* and *Pistacia lentiscus*). Behavioural variables were the number and fate of handled fruits: (a) ingested or swallowed in the plant, (b) carried away from the tree in the bill, (c) pecked in the plant without falling, (d) fallen or dropped underneath the plant, and (e) non-successful attempts (touched but not detached from the branches). Finally, we recorded the foraging technique of the fruits (perched or in flight).

Temporal patterns of seed rain and seed dispersal

We approached this in two ways depending on the study area. In MONT, depositions were obtained in the mist-net captures, and the number of seeds and presence of pulp were recorded individually in the laboratory. At Les Gavarres, however, due to the low number of samples, a transect route of 300 m was sampled four times in 1997 and again in 1998. Depositions with remains of any fruit were collected directly from the ground to supplement those from mist-net captures. In this case, seeds were not directly counted because of potential seed removal by ants and rodents (Bas 2001). Instead, we counted the number of endocarps, which are not removed because they are not attractive to these animals. Since there is one seed per endocarp the number of endocarps represents the number of seeds. The presence of material from other plant species was also valued. Temporal pattern of seed rain was measured by placing trays underneath female plants during the years 1996–1999. The 800 cm^2 trays had a metallic mesh of 8 mm that prevented the entry of rodents. We placed either one or two trays, depending on the plant's size (20–40 trays per area per year), beneath female plants. Contents of trays were collected every 10–15 days for later analysis in the laboratory. The entire endocarps coming from depositions (blackish) were counted separately from those fallen from the branches (non-blackish). Simultaneously, all fruits of 1–2 marked branches of these same individual

plants were counted in order to contrast seed removal with temporal fruit ripening. The first count on marked branches was considered the initial production of each branch.

Effects of birds on seedling emergence

The effect on seedling emergence by pulp removal and of passage through the birds' digestive tract was evaluated. A total of 75 ingested seeds (from net-captured S. melanocephala), 75 seeds extracted from ripe fruits, and 75 entire ripe fruits were planted in sterilised soil at about 2 cm depth. The containers were placed in a glasshouse and watered periodically once a week; seedlings were censused every week during 6 months until no emergences were recorded.

Statistical analysis

Non-parametric statistical analyses were used for the analysis of depositions, visit times and post-feeding behaviour (Mann–Whitney test). Also, we used the χ^2 of comparison of frequencies and Spearman's rank correlation test for the comparison of the variables. Data are reported as means ($\pm$ s.e) and range.

Results

Bird communities and frugivorous birds

Bird species richness was similar in the three areas, and most species were passerines (Table 1). The communities were especially similar in the two areas of Les Gavarres (VALL and FIG), with both having the same abundant species: *Sylvia melanocephala*, *S. atricapilla*, *Erithacus rubecula* and *Turdus merula*. In contrast, the MONT site was strongly dominated by *S. melanocephala* and *S. undata*. Most species at MONT, including the two dominants, had similar densities, based on territory mapping, across the three years of the study (Table 1). Bird densities (breeding pairs/ 10 ha) were significantly correlated with the number of captures ($r = 0.89$, $p < 0.001$, $n = 20$ species) and depositions were obtained from most of the captured birds (Table 1). Although

the number of frugivorous species detected on *R. alaternus* was similar across sites, these species was different. Similarly, the frequency of appearance of *R. alaternus* (seeds per deposition) differed, being highest at MONT (Table 1). In *S. melanocephala*, for example, depositions of *R. alaternus* were much more frequent in MONT than in Les Gavarres ($\chi^2 = 5.67$, $p = 0.02$, $n = 265$). Pulp appearance was extremely rare, and depositions generally had at least one seed of *R. alaternus* (98% in Les Gavarres and 97% in MONT) (Table 1). In Les Gavarres, *S. atricapilla* (mean $\pm$ s.e. $= 3.9 \pm 3.0$ seeds/deposition, range 1–11, $n = 17$) deposited more seeds per defecation than *S. melanocephala* (mean $\pm$ s.e. $= 2.1 \pm 1.3$ seeds/deposition, range $= 1$– 5, $n = 28$) (Mann–Whitney test, $U = 592$, $p = 0.002$, $n = 45$). At MONT, however, *S. melanocephala* (mean $\pm$ s.e. $= 2.8 \pm 2.0$, range $= 1$–8, $n = 140$) and *S. undata* (mean $\pm$ s.e. $= 2.1 \pm 1.3$, range $= 1$–6, $n = 35$) did not differ significantly (Mann–Whitney test, $U = 1919$, $p = 0.15$, $n = 175$). Other species of plants sporadically appeared (two depositions with *Bryonia cretica dioica* at VALL, one with *Lonicera implexa* at FIG, and four with *Rubus ulmifolius* at VALL and FIG). In MONT we never found depositions with seeds other than *R. alaternus*.

Bird behaviour

We recorded 230 visits from three different bird species to the female plants, *S. melanocephala*, *S. undata* and *Saxicola torquata*, at MONT (Table 2). There were more visits from *S. melanocephala* adults than *S. undata* adults ($\chi^2 = 36.9$, $p < 0.05$, $n = 222$) (Table 2). The birds handled a total of 380 fruits, and only in 3.9% of the visits no fruit were handled. Up to seven fruits per visit were observed to be handled (*S. undata*), mainly from a branch (Table 2, Figure 1), and most handled fruits (71.6%) were either partially or totally ingested. The frequency of feeding methods that resulted in seed movement away from plants (swallowed vs. carried in the bill) did not differ between the two dominant species, *S. melanocephala* and *S. undata*, ($\chi^2 = 0.04$, $p = 0.85$, $n = 257$). The ratio of 'visits without and with carried fruit in the bill' was 2:1 in adults of *S. melanocephala*, whereas it was 6.7:1 in juveniles. Similarly, there was no preferred direction of flight when leaving a fruiting tree; birds arrived and departed from all

Table 1. Number of captures with mist nets at three locations, breeding pairs (BP) in 10-ha-study plot of MONT (average of the 3 years), and number of collected depositions (DP), with Rhamnus seeds (RS) and with Rhamnus pulp (RP).

Bird species	Mist net captures			Mapping MONT	Depositions					
	Number of captures				Gavarres			Montgrí		
	VALL	FIG	MONT	BP/10 ha	DP	RS	RP	DP	RS	RP
Anas platyrhynchos			*	0.30						
Alectoris rufa	*									
Phasianus colchicus			*							
Columba palumbus	*	*	*	0.13						
Cuculus canorus	*	*	*							
Clamator glandarius			*	0.06						
Dendrocopos major		*								
Troglodytes troglodytes	2	1			3	0	0			
Erithacus rubecula (+)	10	18			25	2	0			
Luscinia megarhynchos	7	*	6	0.13	4	0	0	4	0	0
Saxicola torquata (+)			7	1.46				4	0	1
Turdus merula (+)	7	8	6	0.26	11	1	0	4	1	0
Hippolais polyglotta	1		1					1	0	0
Sylvia undata (+)			82	6.83				61	35	2
Sylvia cantillans (+)	1	3	1		4	1	0	1	0	0
Sylvia melanocephala (+)	11	47	242	7.30	57	28	0	208	140	2
Sylvia atricapilla (+)	16	24			36	17	0			
Phylloscopus bonelli	1				1	0	0			
Phylloscopus collybita		1			1	0	0			
Regulus ignicapillus	2	5			7	0	0			
Aegithalos caudatus	2	*			1	0	0			
Parus cristatus			*	0.20						
Parus ater	*		*	0.06						
Parus caeruleus (+)	6	1			7	0	1			
Parus major	1	1	2	0.20	2	0	0	2	0	0
Certhia brachydactyla	*	*								
Oriolus oriolus	*									
Lanius senator			4	0.53				1	0	0
Garrulus glandarius	*	1								
Serinus serinus	*	*	*	0.40						
Carduelis chloris		1								
Carduelis carduelis			3	0.93				2	0	0
Carduelis cannabina			1	0.40				1	0	0
Emberiza cirlus	*	*	4	0.13				3	0	0
Total captures	67	111	359	19.46	159	49	1	292	176	5
Species richness	22	20	20							

*, Birds detected with point counts and not captured with mist nets. +, species with Rhamnus fruits on depositions.

directions (arrivals: N = 25%, E = 30%, S = 29% and O = 16%; departures: N = 20%, E = 34%, S = 16% and O = 30%). Neither did adults and juveniles differ in their arrival and departure directions considering all visits (S. melanocephala: $\chi^2 = 1.48$, $p = 0.22$, $n = 128$; S. undata: $\chi^2 = 1.16$, $p = 0.28$, $n = 94$). However, the adult S. melanocephala that carried the fruits in the bill did coincide in their arrival and departure trajectories ($\chi^2 = 5.4$, $p < 0.05$, $n = 78$). These birds depart back in the direction from which they came. All birds stayed on the plant a short time (< 60 s mainly)

(Table 2), without any differences between the main species (Mann–Whitney test, $U = 5884$, $p = 0.78$, $n = 222$). The number of handled fruits depended on the visit time for S. melanocephala ($r = 0.23$, $p = 0.01$, $n = 128$), but did not for S. undata ($r = 0.04$, $p = 0.68$, $n = 94$).

Sylvia melanocephala and S. undata did not differ in the identity of perches first used after leaving a Rhamnus. Both species predominantly used Olea and continuous shrubland ($\chi^2 = 2.31$, $p = 0.13$, $n = 196$). S. undata also used open ground and other Rhamnus plants, though not very often (Figure 2).

Table 2. Foraging behaviour of the three frugivorous species at MONT (*n* and range are given in parentheses).

		Sylvia melanocephala	*Sylvia undata*	*Saxicola torquata*
Foraging visits (%)		55.6 (128)	40.9 (94)	3.5 (8)
Age of frugivore on the visits (%)	Adult birds	60.9 (78)	19.1 (18)	75.0 (6)
	First year	39.1 (50)	80.9 (76)	25.0 (2)
Time (s) /visit (mean ± s.e.)		32.7 ± 18.7 (6–92)	33.9 ± 24.0 (5–154)	54.4 ± 29.1 (30–100)
Visits with handled fruits		124	89	8
Foraging technique (%)	Perched	100.0 (124)	100.0 (89)	75.0 (6)
	In flight	0.0 (0)	0.0 (0)	25.0 (2)
Number of handled fruits		198	172	10
Handled fruits/visit (mean ± s.e.)		1.5 ± 0.8 (0–4)	1.8 ± 1.2 (0–7)	1.2 ± 0.5 (1–2)
Fate of the handled fruits (%)	Removed away	82.8 (164)	58.1 (100)	80.0 (8)
	Fallen beneath	3.6 (7)	2.3 (4)	0.0 (0)
	Non-successful	13.6 (27)	39.6 (68)	20.0 (2)
Number of fruits removed away/visit (mean ± s.e.)		1.3 ± 0.6 (0–4)	1.1 ± 0.5 (0–2)	1.0 ± 0.8 (1–2)
Types of removed away fruits (%)	Swallowed	82.3 (135)	77.0 (77)	75.0 (6)
	Carried in the bill	17.7 (29)	16.0 (16)	0.0 (0)
	Pecked	0.0 (0)	7.0 (7)	25.0 (2)
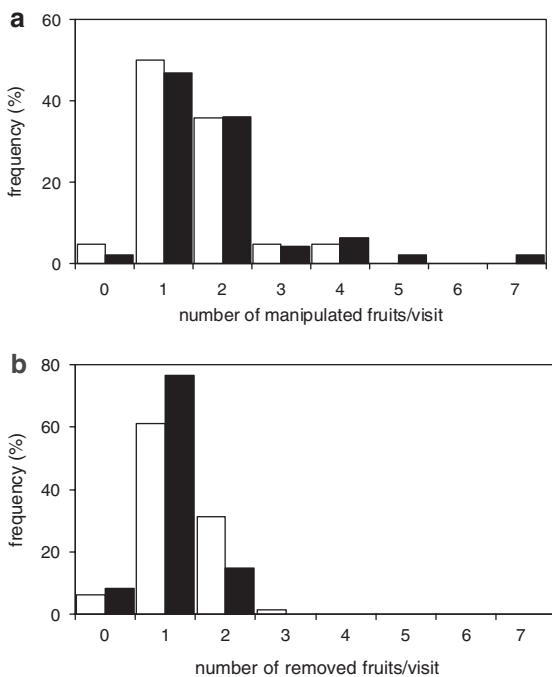
Figure 1. (a) Proportion of handled fruits/visit and (b) removed fruits/visit from the plant (*Sylvia melanocephala*, white columns; *Sylvia undata*, dark columns). Date from MONT.

The flight distances to the first perch (mean ± s.e.) were generally short (Figure 2; *S. melanocephala*: 21.0 ± 17.7 m, range = 1–75, n = 128; *S. undata*: 13.9 ± 13.0 m, range = 1–60, n = 94; and *S. torquata*: 16.2 ± 10.3 m, range = 5–30, n = 8). *S. melanocephala* had greater distances than *S. undata* (Mann–Whitney test, $U = 4682$, $p = 0.004$, $n = 222$) (Figure 2). These differences remained when considering microhabitats. In continuous scrubland of *Quercus coccifera*, *S. melanocephala* showed a mean distance ± s.e = 22.2 ± 12.5 m (range = 1–75, n = 60) and *S. undata* = 8.4 ± 7.2 m (range = 1–25, n = 34) (Mann–Whitney test, $U = 730$, $p = 0.02$, $n = 94$). In *Olea europaea*, *S. melanocephala* showed a mean distance ± s.e = 23.7 ± 12.4 m (range = 5–75, n = 54) and *S. undata* = 17.7 ± 15.4 m (range = 2–60, n = 48) (Mann–Whitney test, $U = 842$, $p = 0.002$, $n = 102$).

Temporal patterns of seed rain and seed dispersal

The seed rain of *R. alaternus* resulting from bird dispersal occurred between mid May and the end of August. Depending on the area and the year, dispersal period lasted 51–96 days with a mean of 68.5 days (±15.6) (Figure 3). Along the period, birds dispersed 50% of the seeds over 36.1 ± 20.1 days (mean ± s.e., range = 13–56 days, n = 7), with a maximum dispersion on the 42.3 ± 17.5 days (mean ± s.e., range = 16–66 days, n = 7). The length of the seed dispersal period did not depend on the size of the initial production on marked branches of each area ($r = 0.13$, $p = 0.79$, $n = 7$) and on the start date of dispersion ($r = -0.16$, $p = 0.73$, $n = 7$). The number of seeds dispersed in a given location can vary greatly among years (Figure 4). The number of seeds dispersed in a year did not depend on the initial production of fruits on marked branches ($r = 0.68$,
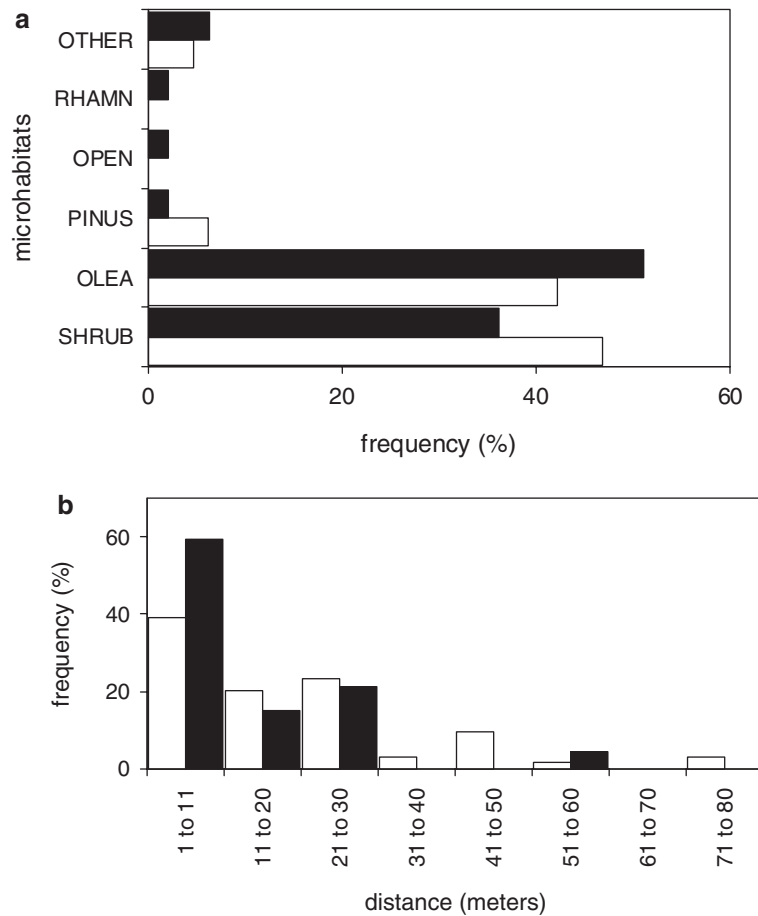
Figure 2. (a) Use of the different microhabitats as the first perch of the main bird species (*Sylvia melanocephala*, white columns; *Sylvia undata*, dark columns) (SHRUB = shrubland, PINUS = *Pinus halepensis*, OLEA = *Olea europaea*, RHAMN = *Rhamnus alaternus* different from the foraged plant, OPEN = ground, rock and herbaceous plants, OTHER = isolated plants including *Quercus ilex*, *Phillyrea latifolia* and *Pistacia lentiscus*) and (b) distances from the female plant to the first perch used (*Sylvia melanocephala*, white columns; *Sylvia undata*, dark columns).

$p = 0.09$, $n = 7$ cases). The number of seeds dispersed in a given period was, however, positively correlated to the number of fruits available in that period; $p < 0.05$ for seven cases: FIG (1996, 1997, 1998), VALL (1996, 1998), and MONT (1998, 1999). Seed deposition clearly differed between two areas (Figure 5): MONT with 3.6 ± 1.9 seeds/deposition (mean ± s.e.; range = 1–8, 172 depositions with 1747 seeds) and Les Gavarres (FIG-VALL) with 9.1 ± 9.0 seeds/deposition (mean ± s.e, range = 1–69, 191 depositions with 456 seeds) (Mann–Whitney test, $U = 4407$, $p = 0.00$).

Effects of birds on seedling emergence

The emergence of plants began 8 weeks after sowing for both forceps-manipulated pulp-free and ingested seeds, but delayed until 14 weeks in seeds inside the pulp of intact fruits. Seeds removed from pulp with forceps had higher emergence percentages (44.0%) than seeds in intact fruits (17.8%) ($\chi^2 = 15.8$, $p < 0.001$), but lower than seeds that had passed through bird digestive tracts (70.7%) ($\chi^2 = 14.9$, $p < 0.001$).

Discussion

Monospecific frugivory and seed dispersal

Frugivory and seed dispersal by birds during the spring-summer had a strongly monospecific character in the studied areas. The almost exclusive availability of *R. alaternus* fruit in this period
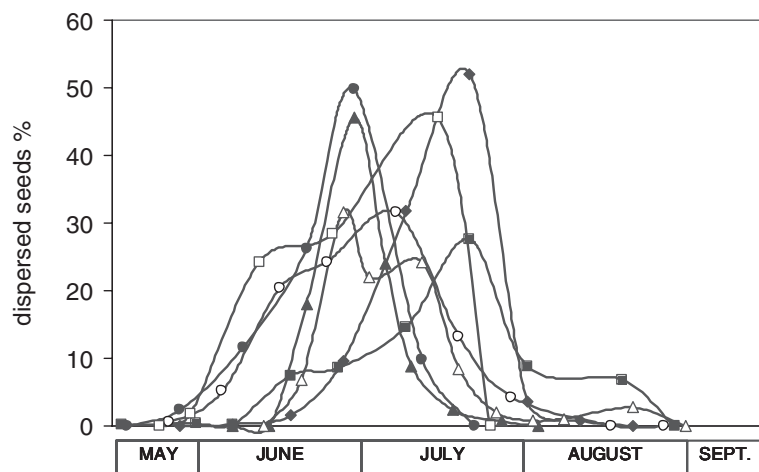
Figure 3. Temporal patterns of dispersed seeds collected at the sites over different years (white circles = MONT 1998, black circles = MONT 1999, white triangles = FIG 1996, black triangles = VALL 1996, white squares = FIG 1997, black squares = VALL 1998, black rhomb = FIG 1998).
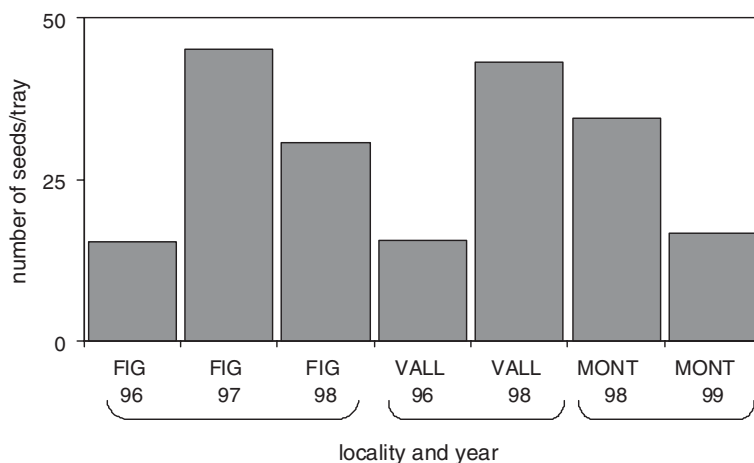
Figure 4. Intensity of the seed fall at the locations from different years. Mean number of dispersed seeds/tray (FIG = Mas de la Figuera, VALL = Aigua Blanca , MONT = Aixart d'en Pi).

(Herrera 1984a; Aronne and Wilcock 1994; Bas 2001) results in a monospecific seed rain. This is opposite to the situation in autumn and winter, when the majority of fleshy fruits ripe and seed rain is mixed even within single depositions (Herrera 1984a). Only 7–13% of the species in the south of Spain (Herrera 1984a), 12% in the Eastern Mediterranean (Izhaki and Safriel 1985) and 33% in the temperate zones of Europe (Snow and Snow 1988) ripen during spring-summer. Other congeners such as *R. lycioides, R. saxatilis, R. catharticus, R. frangula, R. alpina, R. pumila* and

R. ludovici-salvatoris have similar fruiting phenology patterns (pers. obs.). In the Western Mediterranean, specifically, monospecific frugivory during bird breeding seasons has been noted in *R. frangula* (*Frangula alnus*) (Hampe 2001) and *R. ludovici-salvatoris* (Traveset et al. 2003).

The number of frugivorous birds was low in all the three locations, especially in MONT. This low diversity in the reproductive season is typical for scrublands in the Mediterranean (Blondel 1969). Whereas *S. melanocephala* and *S. atricapilla* were the main frugivores in the Gavarres,

Figure 5. Frequency of depositions containing different number of seeds in Les Gavarres (FIG-VALL, white columns) and MONT (grey columns).
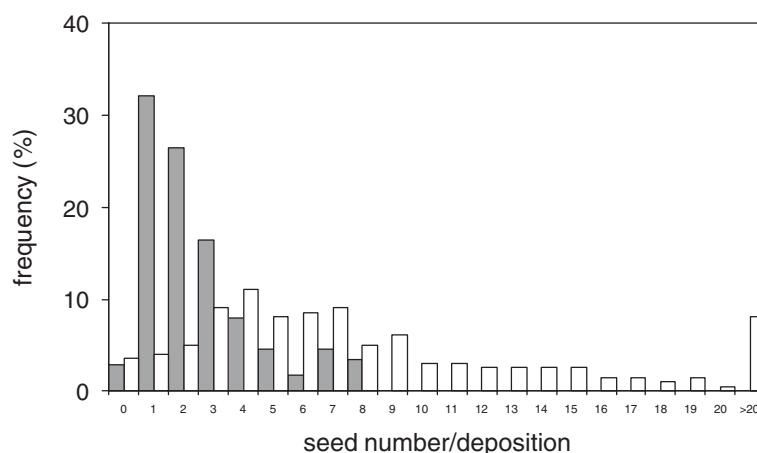
S. melanocephala and *S. undata* take on this role in MONT. *S. melanocephala* eats more fruits in MONT than in the Gavarres, which is probably influenced by the microclimatic conditions. Summer in MONT is more extreme so that the birds have a higher dependency on water and nutrients, available in the pulp of *R. alaternus*. As Herrera (1987) and Izhaki (1992) noted, in comparison to other Mediterranean fleshy fruits this species has high levels of carbohydrates (55–85%), average levels of proteins (4–7%) and low levels of lipids (1%). This deficit in proteins and nitrogen forces frugivores of *R. alaternus* to ingest arthropods in order to compensate for this deficit (personal observation). The high pulp water content (67–72%), however, makes the ingestion of fruits very rewarding. This is reflected in the high fruit use by *S. undata* in MONT, a result that has not been found in other studies (Debussche and Isenmann 1983; Hódar 1994).

While the production of fruits is variable across years (Bas 2001), the community of frugivorous birds did not change in successive years due to territoriality during the breeding season. This stability of the breeding community contrasts with the community during autumn-winter period when there is high interannual variability due to the less predictable climate and resources. Although the stability may have advantages for dispersal, the low density of frugivorous birds during the breeding period (Blondel 1969) results in satiation of the disperser community, the fall of many fruits (ripe and unripe) to the ground

and predation by rodents underneath the plants (Bas 2001) in years of high production. These temporal and spatial fluctuations in fruit production make coevolution of dependences among participants unlikely (Jordano 1994; Herrera 1998; Herrera 2002).

Frugivore types and behaviour of frugivorous birds

Ripe fruits of *R. alaternus* are easily swallowed by frugivorous birds. Although bill size is related to size of fruits that can be consumed (Herrera 1984b; Debussche and Isenmann 1989), even the small bill of *S. undata* poses no problem in ingesting *Rhamnus* fruits. *Sylvia melanocephala*, *S. atricapilla*, *S. cantillans*, *T. merula* and *E. rubecula* have already been described as true seed dispersers (legitimate seed dispersers, Herrera 1984a) of Rhamnaceae in general (Izhaki et al. 1991; Traveset 1992; Hernández 1993; Traveset et al. 2003) or *R. alaternus* in particular (Debussche and Isenmann 1989; Sunyer 1994). Some of the observed dispersers such as *S. undata* and *S. torquata*, have previously been considered of little importance in dispersal (Debussche and Isenmann 1983, 1989; Herrera 1984a; Hódar 1994). In this study, however *S. undata* showed to be very important. *Sylvia sarda*, a species ecomorphologically similar to *S. undata* has, however, been shown to be an important fruit consumer of *R. alaternus* (Sunyer 1994) and *R. ludovici-salvatoris* (Traveset 1992; Gargallo pers. obs.).

The pulp consumer (pulp predator, Herrera 1984a), unlike the seed disperser, rarely moves seeds away from the mother plant. Although sometimes seeds can be dispersed accidentally by pulp consumers (Jordano 1994), the seeds fall underneath the plants (Jordano 1995) and the future plants will compete with the mother plant. The main bird disperser at MONT (*S. melanocephala* and *S. undata*) demonstrated two behavioural patterns: fruits could either be swallowed or carried away in the bill. Fruit swallowing, observed in *S. melanocephala* feeding on *R. alaternus* (Sunyer 1994) and other species (Jordano 1994; Traveset 1994), has not been mentioned for *S. undata*. Fruit carried in the bill, described in other *Sylvia* (*S. atricapilla* and *S. cantillans*) and other genera (Jordano 1994), result in dispersal away from the mother plant. Considering that *R. alaternus* has on average 2.7 viable seeds/fruit (Bas et al. 2002) and the number of fruit removed away per visit, the average number of seeds dispersed by visit was 3.5, 2.9 and 2.7 for *S. melanocephala*, *S. undata* and *Saxicola torquata*, respectively. The aborted seeds (fruits with similar aspect; Bas et al. 2002) did not affect the behaviour of frugivores but reduced the number of viable seeds dispersed (Obeso 1998). Only *S. torquata* took fruits in flight. *Sylvia undata* may appear to be more effective in the dispersal of seeds because it remained more time on female plants, but this is probably because it spends more time searching for and handling fruit.

The main frugivores (*S. melanocephala* and *S. undata*) used the same types of first perches but differed in the distances to these perches, possibly because of the flight behaviours and habitat use of these species. Probably in Gavarres populations, the flight distances would be minor due to the greatest presence of trees. Moreover, two results and one personal observation support the idea that adults of *S. melanocephala* transport fruit to nestlings. First, the higher rate of 'visits without carried in the bill/visits with carried in the bill' in adults than in juveniles suggests that adults are carrying fruits to the young. Second, the arrival and departure directions of the adults coincide, suggesting they are coming from and returning to the nest. Third, we found *R. alaternus* in the analysis of three fecal sacs from nestlings (pulp and seeds) and in two nests (seeds) (personal observation). We also found seeds in a nest previously occupied by *S. undata* (personal observation) which confirms at least a sporadic feeding to nestlings by this species. Regular feeding of fruits to nestlings by adults has been described in other bird species (Snow and Snow 1988). In other Rhamnaceae like *R. frangula*, however, fruit feeding to nestlings has not been detected (Hampe 2001). The feeding of fruits to the nestlings or the recently fledged will result in secondary dispersal (Chambers and Macmahon 1994) by transportation of fecal sacs by the adults from the nests or by movements of the recently full-fledged.

Seedling emergence

The fruit ingestion of *R. alaternus* by frugivorous birds results in the deposition of clean seeds (without pulp) but enclosed within endocarps (Bas et al. 2002). Endocarps generally release the seeds when dry, but some endocarps never open, preventing seedling emergence (Bas 2001). Pulp covering seeds not only decreases the proportion of seedlings emerging but also slows emergence. These results are not universal, however. Pulp presence in the Rhamnaceae varies in its effects depending on the species. In *Rhamnus palaestinus*, pulp did not affect emergence percent but did delerate it (Izhaki and Safriel 1990). In *Ziziphus mauritiana*, as in this study, pulp decreased and slowed emergence (Grice 1996). In *R. alaternus* in another study (Barnea et al. 1991) and in *R. cathartica* (Archibold et al. 1997) pulp-covered seeds never germinated, indicating the presence of inhibitors in the pulp (Izhaki and Safriel 1990; Barnea et al. 1991), interference with water absorption by the seeds (Debussche 1985), or harmful organisms that grow in the pulp (Traveset and Willson 1997).

Gut passage by frugivores affects emergence beyond the mere removal of pulp. Seeds ingested by birds had a greater probability of emerging than seeds we manually extracted from pulp. The overall increase proportion of ingested seeds in our study coincides with that found Barnea et al. (1991) in *R. alaternus*, and by Izhaki and Safriel (1990) in *R. palaestinus*, although the acceleration onset of germination described by Barnea et al. (1991) in *R. alaternus* was not found here. Such contrasting results have been described in other species (e.g., *Solanum nigrum*; see review in

Traveset 1998). These contrasts can be partially justified by differences in retention time and physiological characteristics of the frugivores (Barnea et al. 1990; Izhaki and Safriel 1990; Clergeau 1992; Traveset et al. 2001). In *R. alaternus*, the effects of retention time were shown by Barnea et al. (1991). Definitively, the pulp removal and digestive treatment coupled with the mechanical opening of the endocarps have positive effects for the plant.

Quantity and quality of the monospecific seed dispersal in Rhamnus

The birds in this system are mainly legitimate dispersers (Herrera 1984a). In order to evaluate disperser contributions to future plant reproduction, however, disperser effectiveness needs to be considered (Schupp 1993). Effectiveness depends on the number of seeds dispersed, as well as on the seed treatment in the digestive tract and the quality of microsites where seeds are deposited.

In *R. alaternus*, the frugivorous interaction can have different quantitative effects. In general, the low density of frugivorous birds in the spring-summer period, together with an abundance of other resources (arthropods), limit the visits to fruiting plants and the removal of fruits from branches (Bas 2001). In addition, because of the small size and low capacity of ingestion (*Sylviidae* mainly) few seeds are dispersed per visit, further reducing dispersal. Thus, the community as a whole appears to have relatively low quantitative effectiveness, resulting in many seeds remaining undispersed. The most quantitatively effective birds were *S. melanocephala* and *S. undata* at MONT, and *S. atricapilla*, *S. melanocephala* and *T. merula* at Les Gavarres (FIG and VAL). On the positive side, because seed dispersal in this period is monospecific, it is probable that more *R. alaternus* seeds are being dispersed than would be if other species were also fruiting simultaneously. Also, the early ripening during spring-summer by itself could indicate an evolutionary advantage of *R. alaternus* in relation to other plants.

Qualitatively, the birds appear to be reasonably effective. Firstly, pulp removal increases seedling emergence, while the endocarps prevent seed destruction in the beak and gut. This seed protection was explained as a system to avoid the loss of seed viability (Izhaki and Safriel 1990), whereas the increased germination was explained as an adaptive mechanism in dry ecosystems where rain is fairly unpredictable (Izhaki and Safriel 1990; Traveset and Willson 1997). Second, the monospecific nature of dispersal may again be advantageous by reducing the interspecific competition (Loiselle 1990). Despite many seeds remaining undispersed, the low density of *Rhamnus* seeds on soil will locally reduce the intraspecific competition of future plants. Moreover, the spatial distribution in small concentrations of seeds under particular microhabitats in spring-summer can modify the overall postdispersal pattern of seed predation by rodents in front of other periods (Herrera 1984c; Whelan et al. 1991; Alcántara et al. 2000). In any case, seed predation by harvester ants (genus *Messor*) would be considered negligible since they mainly occupy open areas (ground or rock; Bas 2001) not used by the frugivores' first perch. Third, the territorial behaviour of these frugivorous passerines during the breeding season reduces the potential distance of dispersal, perhaps making it less likely that seeds will be dispersed far away to unsuitable habitats. Studies on the role of bird dispersers in other species of *Rhamnus* of Europe or the Mediterranean basin that also ripen fruits during this period would be valuable. In addition, the potential role of ants in secondary dispersal of *R. alaternus* (Aronne and Wilcock 1994; Bas 2001) and other Rhamnaceae (Traveset et al. 2003) should be more throroughly investigated.

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