

Seed dispersal and fitness determinants in wild rose: Combined effects of hawthorn, birds, mice, and browsing ungulates

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Summary. Factors not directly related to either the plants or their avian seed-dispersal agents are ultimately responsible for the sign and magnitude of the average contribution of seed vectors to the fitness of *Rosa canina* plants in southern Spain. Coexistence with simultaneously fruiting *Crataegus monogyna*, reproductive depression caused by browsing ungulates, and seed predation by mice, are some of these factors. Disperser behaviour may either enhance, depress, or be neutral to *Rosa* fitness depending on the relative importance of the reproductive depression caused by browsing ungulates (pre-dispersal) and mice (post-dispersal). The contribution of seed vectors to *Rosa* fitness is largely independent of their dispersal-related traits and out of the control of the parent plants. Environmental constraints external to the plant – seed disperser interaction seem therefore to impose very restrictive limits on the maximum degree of adaptedness attainable by dispersal-related plant traits, thus operating against coevolution.

Introduction

Interest in the evolutionary ecology of seed dispersal by vertebrates has grown steadily in recent years following seminal contributions by Snow (1971) and McKey (1975). Theoretical formulations of the evolutionary interactions between plants and vertebrate dispersers have been followed by numerous field studies aimed at testing derived expectations (see Howe and Smallwood 1982 for a review). In the light of coevolutionary theory (Ehrlich and Raven 1964; Gilbert and Raven 1975), most recent field studies and theoretical models have examined the interaction between plants and vertebrate frugivores separately from other coexisting organisms in the same habitats (but see, e.g., Harper 1977; Janzen 1977, 1982, 1983). Tests of predictions from plant-disperser coevolutionary models have often had limited success (e.g., Frost 1980; Fleming 1981; Herrera 1981a; Herrera and Jordano 1981; Jordano 1982; Moore and Willson 1982), and the theory should be modified to account for the variety of plant-disperser interactions observed in nature.

Two implicit, yet crucial, assumptions of plant-disperser coevolutionary models are that: (1) dispersal-related factors affecting plant fitness have an important heritable component; and (2) the combined selective pressures exerted on dispersal-related plant traits by non-disperser organisms are small relative to those exerted by dispersers alone. Selective

pressures exerted by dispersers on dispersal-related plant traits could hardly result in observable adaptations if they are offset (or reversed) by stronger pressures from non-disperser organisms influencing plant fitness and/or if dispersal-related determinants of plant fitness are largely non-heritable (Herrera 1984c). These assumptions have not been critically tested to date, but some evidence tends to suggest that they may often be unjustified (Janzen 1982, 1983; Herrera 1982a, 1984a, e; Manasse and Howe 1983; Manzur and Courtney in press).

Seed dispersal of wild rose by frugivorous birds, and its complex relation to browsing mammals, granivorous rodents, and coexisting hawthorn, are investigated in this paper. The objectives are: (1) to compare the relative importance of disperser and non-disperser organisms in determining dispersers' contribution to wild rose fitness; and (2) to evaluate the extent to which observed seed dispersal patterns should be attributed to selection of dispersers on heritable wild rose traits.

Natural history of plants

Wild rose (*Rosa canina* aggr.) and hawthorn (*Crataegus monogyna*; called *Rosa* and *Crataegus* hereafter) are understory species of pine forests at 1,300–1,600 m elevation in the Sierra de Cazorla, southern Spain. When growing in isolation, *Rosa* forms dome-shaped bushes, but develops a climbing habit when growing beneath other plants providing adequate support for its hooked, ascending stems. *Crataegus* plants are most commonly large multi-stemmed shrubs (3–4 m height) with the lowermost branches spreading close to the ground. *Rosa* bushes are very often rooted beneath *Crataegus*; climbing stems ascend through the *Crataegus* crown, and terminal foliage (and fruits) emerge at the outer surface.

Fruiting phenology and seed dispersal agents of *Rosa* and *Crataegus* are virtually identical. Observations in Cazorla over 1978–1983 indicate that both species quickly ripen all fruits from mid to late September, 2–3 weeks before beginning to shed leaves, but fruit consumption by birds and seed dispersal mostly take place in November–February and are due mainly to *Turdus merula* (Herrera unpubl.). Ripe fruits are red in both species, and are virtually identical in size, shape, relative mass of pulp and seeds, and nutritive value of the pulp (Table 1; see Herrera 1981a, 1982b, for methods). They differ greatly in the concentration of tannins in the pulp (much higher in *Rosa*), and slightly in

Table 1. Average characteristics of *Rosa canina* and *Crataegus monogyna* fruits. See Herrera (1981a, 1982b) for methods and further details^a

	Fresh fruit			Dry fruit		Pulp constituents									
	Length	Width	Mass	Seed mass	Pulp mass	Lip-ids	Pro-tein	NDF	Ash	K	Ca	Na	Mg	P	Tannins ^b
<i>Rosa canina</i>	15.0	9.2	675	103	189	2.8	4.3	15.2	5.1	1.10	0.52	0.08	0.03	0.04	+++
<i>Crataegus monogyna</i>	12.1	9.3	652	124	171	2.3	2.5	16.7	4.3	1.25	0.44	0.03	0.06	0.05	+

^a Linear measurements are expressed in mm, masses in mg, and pulp constituents as g/100 g dry pulp. NDF = neutral-detergent fiber

^b Determined on a semi-quantitative scale by comparison of protein-precipitating activity with a series of tannic acid test solutions. Successive scores on the scale represent a 10-fold difference in protein-precipitating activity/mass unit of substance (R.C. Soriguer, unpubl.)

some mineral elements. *Rosa* pulp contains a higher concentration of carotenoids and vitamin C than *Crataegus* (Goodwin and Goad 1971; Mapson 1971; Font Quer 1980). *Rosa* fruits have long pedicels (3–15 cm) and are borne singly or in small loose racemes at the extreme of long, nearly vertical flexible stems. Those of *Crataegus* have short pedicels (1–3 cm) and are presented in small axillary clusters adjacent to short (2–4 cm), spiny-tipped lateral branchlets. *Rosa* 'fruits' (in fact they are not true fruits, as they are derived from the enlarged hypanthium, not the ovary) lack an abscission layer and, if uneaten, persist on the plant for many months after ripening until they eventually rot and decay in spring. Ripe *Crataegus* fruits fall to the ground over most of the autumn–winter period, although at a slow rate.

Study sites and methods

Most field work was carried out from 27 December 1982 to 5 January 1983 at three localities (Valdehillos, Nava de San Pedro, Nava del Espino) in the Sierra de Cazorla (southeastern Spain, Jaén province; see Fernández Galiano 1960; Polunin and Smythies 1973; Otero et al. 1978, for general descriptions) located within a radius of 2.5 km. Supplementary information on general aspects of plants' dispersal ecology come from my 5-year experience with fruiting plants and avian frugivores in the area (see, e.g., Herrera 1981b, 1982b, 1984b, d; Herrera and Jordano 1981). Vegetation in Valdehillos and Nava del Espino was open *Pinus nigra* forest with a sparse understory of *Berberis hispanica*, *Rosa canina*, *Crataegus monogyna* (except at Nava del Espino), *Quercus ilex* and *Quercus faginea*. Plants grow there on rocky soils of north-facing (Nava del Espino, 1,350 m elevation) and west-facing (Valdehillos, 1,450 m) slopes. Vegetation in Nava de San Pedro (1,280 m) was on a narrow floodplain and adjacent rocky foothills, and consisted of a mosaic of pine forest similar to the other sites, successional scrub, and young pine plantations.

During this study snow cover (from recent snowfalls) was virtually complete at Valdehillos and Nava del Espino, and patchy at Nava de San Pedro. Days were generally sunny, and minimum daily temperature remained below -5°C . These conditions are representative of winter regional climate.

Mist-netting and direct observations on avian frugivores revealed that *Turdus merula* was the single species feeding on fruits at the three sites. Feces presumably from this spe-

cies were collected from the snow surface at all sites, and the number and species of seeds present recorded.

Post-dispersal seed distribution was studied in detail at Valdehillos. Forty linear transects (20 m) were laid out there in three parallel series according to a stratified design, and cover of woody species was assessed from the length of intercepts determined by vertical projections. Occurrence of *Turdus* feces within 20 cm on either side of transects was recorded, as well as their position relative to plant cover and number and species of seeds they contained. Judging from the dates of the last snowfalls, bird feces examined integrated information from the 10–12 days preceding study dates.

Height and standing fruit crops were determined for all *Rosa* bushes within a 250 × 500 m plot (enclosing the transects mentioned earlier), as well as their position relative to other plants (growing alone or climbing on *Crataegus* or other species). Plants from all woody species intercepting the transects were examined for climbing *Rosa* bushes. I do not know what fraction of crops had already been removed from *Rosa* plants by the study dates. Taking account of the very low removal rates found from December to April (see below), and of the fact that consumption of *Rosa* fruits by birds begins around November and is maximal in December–January (Herrera unpubl.), it may be assumed that birds had removed a negligible fraction of fruits prior to the study, and that standing crops observed are representative of actual crop sizes. Differences shown later in average standing crops of *Rosa* plants growing under different conditions might have resulted from differential fruit consumption by dispersers, but results presented below reveal that any biases of the winter standing crop estimates fall on the conservative side.

Browsing ungulates (*Dama dama*, *Capra pyrenaica*, *Ovis musimon*) are abundant in the area and feed on new shoots and terminal foliage of *Rosa* in spring and summer. At these times, the few fruits still remaining on the plants are badly damaged by rot or otherwise, hence the possibility that they disperse seeds can be ruled out. Examination of fecal pellets of the ungulate species above (R.C. Soriguer, unpubl.) has not revealed to date any *Rosa* seed. Height and standing fruit crops were determined for *Rosa* bushes growing within two large ungulate enclosures set up in 1979 (Nava de San Pedro, 3.5 ha; Nava del Espino, 1 ha) and contiguous areas of identical substrate and exposure. Only *Rosa* bushes growing alone were considered in the enclosure (and adjacent) populations sampled, since association with

Table 2. Occurrence (%) of *Rosa* and *Crataegus* seeds in *Turdus* feces^a

	<i>N</i>	<i>Rosa</i> alone	<i>Rosa</i> and <i>Crataegus</i>	<i>Crataegus</i> alone	Other species ^b
<i>Crataegus</i> available					
Nava de San Pedro	19	5.3 (1.0)	21.1 (2.8; 1.3)	73.7 (1.9)	10.5 (4.5)
Valdetrillos	175	4.0 (3.4)	7.4 (2.7; 1.7)	88.6 (1.7)	2.3 (2.0)
<i>Crataegus</i> unavailable					
Nava del Espino	30	100.0 (8.2)	0	0	3.3 (2.0)

^a *N* = number of feces examined that contained seeds. Average number of seeds is shown in parentheses

^b *Juniperus communis*, *Berberis hispanica*, and *Ilex aquifolium*. Seeds of these species most often occurred with *Rosa* or *Crataegus*, hence the sum of percentages in a row exceeds 100

other plants was very infrequent due to past understory management practices (Nava de San Pedro) or to natural causes (Nava del Espino).

Seed-feeding mice, presumably *Apodemus sylvaticus* (the only rodent species captured in the area after continued small mammal trapping; R.C. Soriguer, unpubl.), searched for seeds in *Turdus* feces under *Crataegus* plants, as evidenced by chewed seed coats close to disintegrated feces. Seeds of fallen *Crataegus* fruits are also fed upon after removal of the pericarp, being cracked open in situ or taken to nests. The effect of mice on short-term survival of *Rosa* seeds was examined in Nava de San Pedro. Thirty pairs of clean *Rosa* seed piles, with 10 seeds each (a number in the range of seed numbers in *Turdus* feces), were set out, and examined on two consecutive days. In each pair, one pile was placed under *Crataegus*, close to the base, and the other on open ground at the closest possible position being at least 1 m away from the limit of the vertical projection of the *Crataegus* crown.

Standing fruit crops of *Rosa* plants were counted again at the three study sites on 1–4 April 1983. As every year, most avian dispersers had left the area by that time and the few individuals present were not feeding on fruit. Most fruits present were rotting or damaged in other ways, so should be considered to have failed at dispersal. Enclosed seeds were black or dark brown in color, instead of the normal pale yellow appearance, denoting direct effect of rot.

Results

Seed dispersal

Avian seed dispersers fed largely on *Rosa* and *Crataegus* fruits in the study area (Table 2). Other fruit species were of minor importance; the remains of animal prey were found in less than 10% of feces and always accounted for a negligible-fraction in volume. In the absence of *Crataegus*, fruits of *Rosa* formed the bulk of the diet of birds, but they concentrated on *Crataegus* wherever it was present. *Rosa* fruits were similarly abundant (per habitat surface unit) at the three sites, hence these data reveal a preference of dispersers for *Crataegus*. This preference was not, however, extreme enough to exclude *Rosa* fruits, and seeds of *Crataegus* and *Rosa* often appeared together in feces (Table 2). When coexisting locally, therefore, the two plants share the same dispersers and seed dispersal of *Rosa* is most often simultaneous with that of *Crataegus*.

The heavy reliance of birds on *Crataegus* should be asso-

Table 3. Relative distribution (%) of *Turdus* feces and *Rosa* plants among cover categories in the Valdetrillos plot

Cover category	Percentage ^b	Proportion of <i>Turdus</i> feces cover (N=190)	Proportion of <i>Rosa</i> bushes (N=111)	Proportion ^d of individuals with <i>Rosa</i> associated (sample size)
Open ground ^a	68.2	2.1	44.2	–
<i>Crataegus monogyna</i>	10.4	83.6	34.2	33.6 (131)
<i>Pinus nigra</i>	17.5	7.4	14.4	14.2 (218)
<i>Quercus faginea</i>	1.8	1.1	0.9	10.0 (10)
<i>Berberis hispanica</i>	1.1	0.5	4.5	16.9 (77)
<i>Quercus ilex</i>	1.0	5.3	1.8	16.7 (18)

^a Rocky, grassy or covered by dwarf shrubs

^b Based on length of intercept on linear transects totalling 800 m (see Methods)

^c Based on examination of *Rosa* bushes

^d Based on examination of non-*Rosa* plants

ciated with a relative concentration of their activity on these plants, and a nonrandom pattern of post-dispersal seed distribution is to be expected. *Crataegus* plants covered an estimated 10.4% of the surface of the Valdetrillos plot, yet 83.6% of bird feces were found under these plants (Table 3). Open ground, in contrast, accounted for 68.2% of the surface of the plot, but received only 2.1% of feces. Observed/expected contrasts are far less marked for the remaining cover categories. Of the 44 *Rosa* seeds recovered from *Turdus* feces in the Valdetrillos transects, 77% were under *Crataegus*, and all of them were under large plants bearing fruit crops in excess of 400 fruits. There is therefore a strong post-dispersal concentration of both *Rosa* and *Crataegus* seeds under plants of the latter species, related to a differential habitat use by frugivores that is dictated by their intense preference for *Crataegus* fruits.

Post-dispersal seed survival

Crataegus plants are not activity centers only for avian frugivores that disperse seeds. Groups of wild boars (*Sus scrofa*) follow definite paths from one tree to the next, feeding on fallen *Crataegus* fruits but apparently ignoring scattered seeds and bird feces (they destroy all ingested *Crataegus* seeds, as revealed by examination of feces collected in the area during the study dates). Mice (presumably *Apodemus sylvaticus*) also feed on the seeds of fallen *Crataegus* fruits and those contained in bird feces, as noted earlier.

These rodents take advantage of the "rain" of seed-containing bird feces steadily falling from the *Crataegus* crown, and are most likely responsible for most post-dispersal seed mortality. Ground-foraging granivorous birds are very scarce in winter in the study area, and most of them are unable to crack the very hard-coated seeds of *Rosa* and *Crataegus* (the only exception being *Coccothraustes coccothraustes*, extremely infrequent in the area).

After two days, 56.7% of the 30 piles of *Rosa* seeds placed on the ground under *Crataegus* had been found by mice (some or all seeds eaten or removed), while none of those placed slightly away from the *Crataegus* crown was discovered ($P \leq 0.0001$, Fisher test). Under *Crataegus*, 58.0% of seeds initially present ($N=300$) disappeared or were chewed by mice, but none in paired piles away from *Crataegus*. Among the latter, 20% of piles were trampled by large mammals and the seeds scattered and partly buried. Signs of trampling were not observed in piles under *Crataegus*, which must be related to the presence of low, horizontally-spreading spiny branches.

Post-dispersal survival prospects of *Rosa* seeds are therefore much greater away from *Crataegus* as a consequence of decreased mice predation. Increased trampling in open areas may further contribute to differential seed survival. Disintegration of bird feces and partial burial of seeds may render them more difficult to harvest by rodents and facilitate germination and early growth.

Establishment

In the Valdetrillos plot, *Rosa* bushes are not distributed randomly among the six cover categories considered (Table 3). They are associated with *Crataegus* more frequently, and with open ground less frequently, than would be expected on the basis of the relative importance of these cover categories (Chi-square = 70.5, $df=1$, $P \leq 0.0001$). Out of a total of 111 *Rosa* bushes examined, 34.2% were rooted under (and climbing on) *Crataegus* and 44.2% were growing in the open, as compared with relative cover values of 10.4% and 68.2% for these two categories, respectively. Observed-expected differences were small and nonsignificant (Chi-square = 3.8, $df=2$, $P=0.15$) for the remaining four cover categories. That *Rosa* is more frequently associated with *Crataegus* than with any other tree or shrub species is further supported by data from the examination of 454 plants from the five woody species considered in defining cover categories. *Crataegus* plants had *Rosa* bushes associated about twice as frequently as did plants of either of the other species (Table 3), and the difference is statistically significant (Chi-square = 20.5, $df=3$, $P=0.0001$).

Distribution of *Rosa* plants among cover classes bears but a slight resemblance to post-dispersal seed distribution as determined by *Turdus* feces (Table 3), and the difference is highly significant (Chi-square = 100.2, $df=5$, $P \leq 0.0001$). Open ground (2.1% of feces, 44.2% of plants) and *Crataegus* (83.6% of feces, 34.2% of plants) are the cover categories displaying the greatest contrasts between the estimated fraction of *Rosa* seeds received and the proportion of adult *Rosa* plants ultimately associated with them. Much smaller differences exist in the other cover categories. Assuming that seed dispersal conditions prevailing during the establishment of *Rosa* plants in Valdetrillos were similar to those documented in this study (this assumption is discussed later), these data indicate that the probability of successful

germination and establishment of *Rosa* seeds is much greater in open ground than under *Crataegus*, which is consistent with the results of the seed predation experiment reported above.

Growth

Examination of *Rosa* plants in Valdetrillos and elsewhere in Cazorla revealed that the frequency of terminal stem breaks (attributable to mammalian bites) was clearly greatest among individuals growing alone, lowest for those growing in association with *Crataegus*, and intermediate in plants associated with other species. The stiff, spiny, radially-spreading, lowermost horizontal branches of *Crataegus* apparently deterred herbivores to the benefit of associated *Rosa*, whose stems were able to climb through its host plant and avoid serious browsing damage (hooks and spines are soft on the young *Rosa* stems browsed by herbivores, but eventually harden and may potentially have a deterrent function). Plants other than *Crataegus* either fail at "basal protection" (single-trunk trees lacking branches at or below mammalian herbivores' mouth height: *Pinus*, *Quercus*) or at "upwards escape" (low spiny shrubs: *Berberis*). Differences among cover categories in average height of associated *Rosa* plants conform to these observations (3.3 m, 2.7 m, and 1.2 m for bushes associated with *Crataegus*, other plants, and growing alone, respectively; Table 4).

Lone *Rosa* bushes do not become taller in the absence of browsing ungulates, as revealed by similar average height within and outside exclosures (Table 4). There seems to be a species-specific average height for *Rosa* bushes growing alone (about 1.25 m) which is independent of local growing conditions. This may be due to predetermined stem elongation in absence of contacts with supports for climbing, or bending down of long flexible stems to the ground after failing to contact supporting substrates. These data indicate that the size (as measured by height) of lone *Rosa* plants is not significantly affected by browsing, and that greater size of bushes associated with *Crataegus* or other plants derives from greater development of climbing stems.

Reproduction

(a) *Differences among habitat patches.* Significant differences in standing crop size exist among *Rosa* plants growing under different conditions in Valdetrillos. In association with *Crataegus* they bear an average of 116 fruits, with other species 38 fruits, and growing alone 7 fruits (Table 4). Differential fruit production may result from differences in plant size (standing crop size is linearly related to plant height, Table 4), to differential size-specific fruit production rates, or both. Covariance analysis of regression equations relating crop size to plant height revealed significant heterogeneity ($F=3.79$, $df=2$, 107, $P=0.026$) among regressions corresponding to plants growing with *Crataegus*, other plants, and alone. For any given size, *Rosa* plants growing alone produce the least fruits, those associated with *Crataegus* the most fruits, and those with other species an intermediate number, as indicated by relative values of regression slopes and intercepts (Table 4). This demonstrates that observed differences in average standing crop size are due both to differential size of plants and to differences in size-specific fruit production rates.

Table 4. Standing crop and plant sizes (mean \pm SD) of *Rosa* growing under different conditions

	N	Plant height (m)	Standing crop	Height (x) – Crop size (y) regressions		
				y-intercept	Slope	r ²
Valdehillos						
Associated with <i>Crataegus</i>	38	3.32 \pm 1.25 ^c	116 \pm 135 ^d	– 133	0.75	0.486
Associated with other species	24	2.69 \pm 1.57 ^b	38 \pm 59 ^{e,f}	– 31	0.26	0.466
Growing alone	49	1.22 \pm 0.70 ^a	7 \pm 23 ^h	– 10	0.12	0.366
Nava del Espino						
Within enclosure	100	1.26 \pm 0.49 ^a	28 \pm 56 ^{f,g}	– 50	0.62	0.285
Outside enclosure	100	1.33 \pm 0.60 ^a	11 \pm 25 ^h	– 28	0.29	0.484
Nava de San Pedro						
Within enclosure	65	1.32 \pm 0.47 ^a	115 \pm 140 ^d	– 182	2.23	0.564
Outside enclosure	65	1.27 \pm 0.52 ^a	16 \pm 28 ^{g,h}	– 32	0.38	0.502

Note: Significance of differences between means of the same variable is coded such that entries having some letter in common are not statistically different. In Nava del Espino and Nava de San Pedro all *Rosa* plants considered were growing alone

(b) *Effects of browsing.* Browsing significantly depresses fruit production in *Rosa*, as revealed by differences in average standing crop sizes within and outside enclosures (Table 4). Relative depression was most pronounced in the most favorable growing conditions of Nava de San Pedro (fertile alluvial soils, insolated), where browsed plants had standing crops which were, on average, 86% smaller than those of unbrowsed plants, as compared with a 61% reduction in Nava del Espino (rocky slope, shaded). There is no reason to suspect that the proportion of ripe fruits removed by dispersers prior to the study dates was substantially different within and outside enclosures, hence observed variation must actually reflect differential crop sizes.

Increased fruit production with increasing plant height is significantly steeper within than outside enclosures (Table 4), as revealed by covariance analyses of paired regression equations ($F=41.6$, $df=1$, 127, $P<0.0001$; $F=15.1$, $df=1$, 197, $P=0.0001$; Nava de San Pedro and Nava del Espino, respectively). Although vertebrate herbivory does not affect average height of *Rosa* bushes (growing alone) as noted above, reproductive depression takes place through a reduction in size-specific fruit production rates.

(c) *Browsing \times habitat-patch interaction.* The interaction effect of browsing and habitat-patch type on fruit production could not be investigated directly due to the scarcity of climbing plants within enclosures. Available data, however, provide some indirect evidence.

Average height and standing crop size of lone browsed plants are similar in Nava de San Pedro, Nava del Espino and Valdehillos (Table 4). Significant heterogeneity does exist, however, in the slope and intercept of crop-size/height regressions among these three populations ($F=4.39$, $df=2$, 209, $P=0.014$). These results suggest that there are local differences in size-specific fruit production rates of *Rosa* plants, since abundance of browsing ungulates is similar at the three sites. Inter-population variation in regression slopes for browsed lone plants is closely consistent with a subjective assessment of differential favorability of growing conditions, based on the consideration of elevation, substrate and insolation. Regression slopes are 0.38, 0.29 and 0.12 for Nava de San Pedro (1,280 m, fertile soil, insolated),

Nava del Espino (1,350 m, rocky soil, shaded) and Valdehillos (1,450 m, rocky soil, partly shaded), respectively.

Mean standing crop size of *Rosa* plants associated with *Crataegus* in Valdehillos is indistinguishable from that of unbrowsed lone plants growing in the most favorable conditions of Nava de San Pedro enclosure, and significantly greater than crop size of unbrowsed lone plants within the Nava del Espino enclosure (Table 4). Assuming conservatively that in the absence of browsing ungulates crop size of lone *Rosa* bushes in Valdehillos would be able to rise to levels similar to those among unbrowsed Nava del Espino plants, these data suggest that association with *Crataegus* would most likely improve *Rosa* reproduction even in absence of ungulates through increasing the number of fruits produced by individual plants. This increase would be due not only to greater plant size derived from the development of the climbing habit, but also to increased size-specific fruit production rate. Crop size/height regression lines are significantly steeper among *Crataegus*-associated plants than among unbrowsed lone plants in Nava del Espino ($F=12.2$, $df=1$, 140, $P=0.007$).

Fruit removal rates

Ripe *Rosa* fruits fall to the ground quite infrequently and standing crop reduction from early winter to early spring may be used to estimate fruit removal rates by birds. Observations and mist-netting at study sites and elsewhere in Cazorla indicate that virtually all fruits removed from plants are ingested by avian seed dispersers. Consumption of *Rosa* fruits by climbing rodents has been reported elsewhere in Europe (Eldridge 1969), but I do not have evidence of this (toothmarks left on fruit pedicels or fruit remains in nest entrances) in the study area. The few fallen *Rosa* fruits are mostly eaten by wild boars which, in contrast to the situation with *Crataegus* noted earlier, defecate seeds undamaged and thus actually perform dispersal. Their role as *Rosa* seed dispersers is probably negligible.

In spring, average standing crop size of *Rosa* plants in Valdehillos growing alone (2 ± 4 fruits; $\bar{X} \pm SD$), associated with *Crataegus* (106 ± 97 fruits), and with other species (36 ± 58 fruits) were but slightly smaller than in winter

(Table 4). Plants growing alone experienced a relative reduction of 71% whereas this was in the range of 5%–8% for the other two groups. In Nava de San Pedro, spring standing crops for plants within (90 ± 102 fruits) and outside (14 ± 27 fruits) the enclosure represent reductions of 22% and 13% relative to winter, respectively. In Nava del Espino, spring standing crops within (16 ± 31 fruits) and outside (8 ± 15 fruits) the enclosure represent reductions of 43% and 27% relative to winter. Substantial fractions of crops thus remained undispersed in 1982–1983, as they had every year since 1978 (rotting fruits were similarly abundant across years on plants in early spring; Herrera unpubl.). Among populations, the greatest relative removal rates occurred in Nava del Espino, where *Rosa* does not coexist with *Crataegus*, a result consistent with the differential occurrence of *Rosa* seeds in bird feces at the three sites (Table 2). In Valdehillos, plants growing alone dispersed a greater proportion of fruits than those associated with either *Crataegus* or other species.

Absolute numbers of fruits dispersed are probably more directly related to plant fitness than estimates of the fraction of crops removed. The difference between winter and spring in average crop size may be used as an estimate of the average number of dispersed fruits per plant. Browsed lone plants in Valdehillos, Nava del Espino and Nava de San Pedro have an average of 5, 3, and 2 fruits dispersed/plant, respectively, similar to the 2 fruits/plant dispersed by Valdehillos plants associated with non-*Crataegus* hosts. Unbrowsed lone plants in Nava de San Pedro and Nava del Espino have an average of 25 and 12 fruits dispersed/plant, respectively. Finally, the estimate for *Rosa* plants associated with *Crataegus* in Valdehillos is 10 fruits dispersed/plant. These figures suggest that, in the presence of browsing ungulates, the association of *Rosa* with *Crataegus* is related to an increase in the number of seeds dispersed. In the absence of browsing mammals, however, lone plants are able to disseminate as many or more seeds than *Crataegus*-associated, browsed plants.

Discussion

Evaluation of results

Presentation of results has been organized to resemble the natural succession of stages in the life cycle of individual *Rosa* plants. This idealized reconstruction could serve as a reasonably valid description of the actual life cycle of *Rosa* if the following assumptions hold true: (1) the nature of documented effects of seed dispersers, browsers, and seed predators on *Rosa* plants has remained unchanged over a time period long enough to encompass several *Rosa* generations; (2) current ecological conditions in the study habitats are representative of those prevailing at the time of establishment of *Rosa* populations currently living there; (3) the life cycle of *Rosa* is relatively short in comparison to that of coexisting species serving as support for climbing individuals, resulting in a greater turnover of *Rosa* individuals relative to host species; and (4) patterns documented by this study are representative of the whole *Rosa* seed dispersal season and do not change substantially between years. Information available supports all these assumptions.

Pine forests in Valdehillos and surrounding areas at similar elevation have been relatively undisturbed by man in historical times. Selective cutting of pines has taken place

a few times in this century, but understory plants have been little affected. There are no records of recent avian or mammalian species extinctions, nor reasons to suspect that seed predators and dispersers have changed in behavior or abundance recently. Wild browsing mammals have greatly increased in abundance in the last few decades following the disappearance of domestic livestock. Nevertheless, this increase has been mostly the reversal of a past reduction due to the introduction of domestic herbivores (mainly goats). Browsing mammals, either wild or domestic, have therefore been present abundantly at least during the last 200 years. Little information is available on the demography of woody plants in the study area, but it supports the third assumption above. Age estimates based on ring counts, along with differential frequency of occurrence of dead or senescent individuals in populations of all species dealt with here suggest a shorter average life span for *Rosa* than for the other species (with the single exception of *Berberis hispanica*; Herrera unpubl.). These observations are consistent with overall demographic patterns of different growth forms (Harper and White 1974). Although this study was conducted over a short time period and a single season, there are no reasons to believe that the patterns observed depart significantly from prevailing conditions. Avian seed dispersers, their marked preference for *Crataegus* fruits, and seed deposition patterns, remain unchanged both within and between fruiting seasons (Herrera unpubl.; J.R. Obeso unpubl.).

Natural selection and Rosa seed dispersal pattern

Regardless of the fitness correlates for *Rosa* plants of disperser behavior and resulting seed dispersal pattern, which will be discussed later, could the observed patterns reasonably be attributed to the action of natural selection? This question may be addressed by considering (1) to what extent heritable *Rosa* traits are responsible for observed patterns, and (2) whether heritable traits relevant to dispersal may be interpreted as actual adaptations.

Coexistence with *Crataegus*, preference of avian frugivores for this species, and their regular consumption of less-preferred *Rosa* fruits, are the factors ultimately determining seed dispersal patterns of *Rosa* in Cazorra. Coexistence with, and dispersers' preference for, *Crataegus* are factors extrinsic to *Rosa* plants and, therefore, nonheritable, hence natural selection can not be responsible for these aspects of *Rosa*'s seed dispersal ecology (I mean, of course, directly responsible). [Preference for *Crataegus* fruits is likely to be due to their greater accessibility resulting from short pedicels and axillary presentation (Denslow and Moermond 1982; Moermond and Denslow 1983), and a much lower concentration of tannins in the pulp (Herrera 1982a)].

It is reasonable to assume that fruiting phenology is under genetic control in *Rosa*; since its seed dispersal pattern depends in part on the simultaneous availability of its fruits and those of *Crataegus*, natural selection might be responsible for fruiting synchronization with *Crataegus*. This cannot be properly tested at present, but seems unlikely in view of the fact that fruit ripening (which is what the plant can control) takes place well before fruit consumption by dispersers, and fruit persistence after ripening will obscure or eliminate inter-individual differences in ripening time. On the other hand, fruit ripening time of *Rosa* coincides with that of many other similarly deciduous species

in the region, including several mammal-dispersed ones (e.g., *Sorbus* spp.; Herrera 1984d), and would be better seen as a constraint imposed by the deciduous habit.

Infrequent, yet consistent, consumption of *Rosa* fruits by birds that rely mostly on *Crataegus* fruits for food may result from the need for adequate amounts of some important nutrients which are required in small amounts, are scarce in *Crataegus*, and readily obtainable from *Rosa* (e.g., carotenoids and vitamin C). The production of these nutrients is probably a heritable trait and might therefore have been selected for, leading to the simultaneous dispersal of both species. This seems unlikely, however, since similarly high content of vitamins and provitamins is also found in the fruits of other *Rosa* species from disparate geographical regions (Goodwin and Goad 1971; Mapson 1971; Font Quer 1980; P. Montserrat, per. comm.), and thus seems a genus-specific feature independent of habitat type and composition of the coexisting fruit-bearing plant assemblage.

I conclude therefore that the general seed dispersal pattern of *Rosa* in Cazorla results from the combination of some factors which are extrinsic (hence not heritable) to the plants, and others which are presumably heritable but that do not seem to have evolved in connection with selective pressures from current dispersers.

Determinants of fitness: Crataegus, birds, mice, and browsing ungulates

Average seed dispersal success (as estimated by the fraction of fruits removed) is higher in *Rosa* populations which do not coexist with *Crataegus*. Where both species coexist, the large *Crataegus* fruit crops (mostly 200–2,000 fruits/plant) are exhausted every year while the smaller *Rosa* crops remain largely uneaten. These facts, along with the preference of avian seed vectors for *Crataegus* fruits, all suggest that the two plants compete in the attraction of a limited supply of avian dispersers and that *Rosa* is competitively inferior to *Crataegus*. The most simple corollary, namely that coexistence with *Crataegus* in the same habitats is detrimental to *Rosa* plants, is not, however, as straightforward as suggested by these data alone.

When browsing ungulates are present, disadvantages to *Rosa* plants (with regard to relative dispersal success) derived from coexistence with *Crataegus* may be offset by benefits derived from close association with that species. *Rosa* plants climbing on *Crataegus* are able to escape from mammalian browsers, thus avoiding reproductive depression caused by recurrent herbivory. They produce many more fruits (both in absolute terms and relative to plant size) than individuals growing alone or associated with non-*Crataegus* hosts. Even though they have low relative dispersal success (which should be expected from the preference of avian dispersers for the fruits of the host), their large crop sizes enable them to disperse a number of fruits per plant roughly comparable to that dispersed by plants free from mammalian herbivores within artificial enclosures. In the conditions of the study region, therefore, browsing was more detrimental to *Rosa* reproduction (in terms of absolute number of seeds eventually dispersed per plant) than *Crataegus* competition for dispersal agents. Accordingly, it may be argued that any mechanism favoring close association with *Crataegus* and subsequent escape from herbivorous mammals (and increased reproductive

output), will produce a net increase in the fitness of *Rosa* plants.

That mechanism does exist: intense activity of avian seed vectors on the preferred *Crataegus* plants lead most *Rosa* seeds to fall under plants of that species after dispersal and, especially, under the largest ones presumably providing the best support for climbing stems. Nevertheless, the conclusion that avian frugivores are actually enhancing the fitness of *Rosa* plants through concentrating their seeds under *Crataegus* host plants would be correct only in the absence of mice inhabiting the base of *Crataegus*. Most *Rosa* seeds falling under *Crataegus* perish, while most seeds defecated elsewhere survive and have a great chance of becoming an established plant. Seed dispersers are therefore “pumping” *Rosa* seeds into spots of high seed mortality and, in this respect, their activity is detrimental to parent plants; but these places are high-quality post-germination sites, and bird activity is in this sense beneficial to *Rosa*.

How do the expected average reproductive potential of *Rosa* seeds under *Crataegus* and elsewhere compare? Reproductive potential of a newly-dispersed seed is proportional to the product of the probability of becoming an established, reproductive individual and the average number of seeds produced over its lifetime. The first factor is smallest, and the second largest (assuming similar longevities and age-specific reproductive tactics for *Rosa* plants growing under different conditions), under *Crataegus*. Relative estimates may be obtained for the first factor by comparing the proportions of *Rosa* seeds and established plants in each cover category (columns 2 and 3 in Table 3). Assigning an arbitrary value of 1.0 to open ground, the probability of establishment of *Rosa* seeds dispersed under *Crataegus* and under other plants are 0.019 and 0.038, respectively. Relative magnitudes of these estimates seem reasonable in view of the high mouse predation rates recorded after only 2 nights of experiments (dispersal under *Crataegus* may also adversely affect seedling establishment via competition for light and nutrients). The product of these figures and the respective average crop sizes (Table 4) indicates that an average newly-dispersed seed has a slightly smaller reproductive potential under *Crataegus* than elsewhere.

Beyond the particular values of these parameters, which may only be taken as very rough estimates, these analyses serve to show that factors not directly related to a plant and its dispersal agents may be ultimately responsible for the sign and magnitude of the average contribution of seed vectors to the fitness of fruit-bearing plants. Disperser behavior may either enhance, depress, or be neutral to *Rosa* fitness depending on the relative importance of the reproductive depression caused by browsing ungulates (pre-dispersal) and mice (post-dispersal). Provided that both browsing ungulates and granivorous rodents are an ecological constant in the highland ecosystems inhabited by *Rosa* in Cazorla, and that this plant coexists most predictably with *Crataegus* in these habitats, this study demonstrates that the average contribution of seed dispersers to *Rosa* fitness will depend on a delicate balance between the severity of rodent seed predation (that increases the relative value of non-*Crataegus*-covered areas as seed landing places) and browsing mammals (that increase the value of *Crataegus*-covered areas). Even slight year-to-year variation may result in drastic changes in the direction of potential selective pressures of seed dispersers on *Rosa* plants. Furthermore, as the behavior of avian seed vectors relevant to *Rosa* (post-

dispersal seed concentration under *Crataegus*) is the result of a set of factors extrinsic to *Rosa* plants, it may be concluded that the sign and magnitude of the contribution of seed vectors to *Rosa* fitness is largely independent of dispersal-related *Rosa* traits and, therefore, out of the control of the parent plants.

Concluding discussion

This study has shown that the pattern of seed dispersal by birds is actually important in determining the fitness of *Rosa* plants in Cazorla. Nevertheless, dispersal-related factors influencing *Rosa* fitness are largely nonheritable and extrinsic to the plants. On the other hand, the combined effects of coexisting nondisperser organisms (including granivorous rodents, browsing ungulates, and simultaneously fruiting *Crataegus* plants) on the postdispersal reproductive potential of *Rosa* seeds are apparently more important than avian seed vectors themselves in determining the average contribution of seed dispersers to *Rosa* fitness. These results, and those of other recent studies (Janzen 1982, 1983; Manasse and Howe 1983; Herrera 1984c; Manzur and Courtney in press), strongly point to the conclusion that environmental constraints external to the plant-seed disperser interaction usually impose very restrictive limits on the maximum degree of adaptedness attainable by dispersal-related plant traits (see also Howe and Vande Kerckhove 1979; Herrera 1982a; Janzen 1983). These constraints heavily operate against the feasibility of coevolution between species of plants and vertebrate seed dispersers.

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