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Ed.

Habitat-shaping, host plant use by a hemiparasitic shrub, and the importance of gut fellows

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The mutualistic interaction between vertebrate-dispersed (endozoochorous) plants and the animals which disperse their seeds has, at least in theory, the potential to promote evolutionary modifications of the participant organisms. This aspect has attracted considerable attention in recent years, particularly from those attempting to test expectations derived from coevolutionary approaches (see Wheelwright and Orians 1982, Howe 1984, Herrera 1985c, 1986 for reviews). This prevailing emphasis on evolutionary consequences has in some way distracted the attention of researchers from other implications that, although admittedly non-evolutionary in nature, may have a significant role in setting the scenario for evolutionary processes. I include in this category those processes directly resulting from the plant-animal interaction that modify the environment where the interaction occurs in such a way that relevant details of the interaction are, as a consequence, also modified. One example is the potential "habitat-shaping" ability of frugivorous birds. By eating the fruits of preferred species in the preferred proportions, and thus co-ordinately dispersing their seeds, these animals may in the long run modify their local habitats (or re-constitute them in "improved" versions elsewhere) with regard to characteristics that are influential on their interplay with fruiting plants (e.g., the nutritional configuration or the spatial arrangement of the multispecies local fruit supply) (see Herrera 1985b for a more detailed discussion of this idea). If such processes are reasonably continuous or predictable, a sort of mutual reinforcement will eventually connect the plant-disperser interaction and the environment where it takes place. The persistent occurrence of the interaction changes the environment, which in turn modifies some details of the interaction.

This hypothesis may be tested by examining whether some observed characteristic of the habitat (or of the plant-disperser interaction) may simultaneously be interpreted as cause and effect of some particular feature of a plant-disperser interaction (or of the habitat where it takes place). Herrera (1984c) provided the elements for such a test (and supporting evidence for the hypothesis) for the relation between seed dispersal patterns of wild rose *(Rosa canina)* and the spatial distribution of this species in relation to coexisting hawthorn *(Crataegus monogyna)* fruiting plants, although the results were then not explicitly interpreted in the present context. Here, I examine host plant use by *Osyris quadripartita* (Santalaceae), a hemiparasitic shrub, at two southwestern Spanish localities (El Viso and Doñana; see Herrera in press b for descriptions), and relate it to some aspects of its seed dispersal by frugivorous birds. The natural history, ecology and reproductive biology (including seed dispersal) of *O. quadripartita* have been described in detail by Herrera (1984d, 1985a, in press a,b). It is a root hemiparasitic, evergreen shrub inhabiting coastal mediterranean scrublands in the southern half of the Iberian Peninsula, where it parasitizes a variety of evergreen and summer-deciduous woody species. Its fruits are one-seeded drupes, produced over an extended portion of the year, but mostly in autumn-winter. Seeds are dispersed by several species of passerine frugivorous birds. *Sylvia atricapilla* (a 18-g body mass warbler) is the main dispersal agent at the single locality where seed dispersal has been investigated in detail (El Viso; Herrera 1984a, in press a).

O. quadripartita is an obligate hemiparasite. Seedlings may survive for up to one year on their own resources, but eventually die if they fail to establish haustorial connections with a host. It is often possible in the field to identify confidently the host of an adult *O. quadripartita* plant. Surveys were conducted at the two study sites, and the proportional utilization (as hosts) by *O. quadripartita* of coexisting woody species was determined (see Herrera in press b for details on methods). The relative abundance of potential hosts in the habitat was assessed by their proportional cover, as estimated from intercepts on linear transects (totalling 300 m and 600 m in El Viso and Doñana, respectively). Results are summarized in Tab. 1. *O. quadripartita* generally parasitizes shrubs of other species which, like itself, produce fleshy fruits and whose seeds are dispersed by frugivorous birds (91.9% and 82.6% of host plant records in El Viso and Doñana, respectively; Tab. 1). Furthermore, at both sites species with fleshy fruits are parasitized significantly more often than expected from their relative abundance in the habitat (percent cover) (Chi-square=54.2, df=1, P<<0.001, for El Viso; Chi-square=7.8, df=1, P=0.005 for Doñana).

The composition of the diet of frugivorous birds was studied in El Viso over a 4-year period, by examination of fecal samples obtained from mist-netted birds (Herrera 1984a). For *Sylvia atricapilla,* the main seed disperser of *O. quadripartita* at the locality, a total of 316 samples were examined, 118 of which (37.3%) had remains (skins and/or seeds) of *O. quadripartita* fruits. Only in 12.2% of the samples where it occurred was *O. quadripartita* the only fruit species present. In the remaining 87.8% of cases, fruit remains of *O. quadripartita* occurred along with seeds or skins of up to five different plant species simultaneously. This indicates, first, that individual birds most often ingest *O. quadripartita* fruits shortly after or before eating the fruits of one or several different species (given the very short retention time of fruits in the gut of this species; Herrera 1984b, Jordano 1987). And secondly, that individual *O. quadripartita* seeds most often "travel" in the gut of its dispersal agent as part of a multispecies seed package, and thus eventually land quite close to one or several heterospecific seeds ("gut fellows").

By counting the number of times that *O. quadripartita* is found in individual fecal samples with each of the locally coexisting, woody (for consistency with host plant records), fleshy fruit-producing species, and then dividing the resulting figures by their sum, I computed a set of relative indices of "coexistence in feces" (ICF). Values obtained are, in ascending order, 0% *(Arbutus unedo, Rhamnus alaternus),* 1.0% *(Lonicera implexa),* 1.9% *(Daphne gnidium),* 3.9% *(Rhamnus lycioides),* 13.6% *(Myrtus communis, Phillyrea angustifolia),* and 66.0% *(Pistacia lentiscus).* These figures are closely correlated with the proportion of host plant records contributed by each of these species (Tab. 1) (r=0.974, N=8, P<0.001). The frequency with which *O. quadripartita* parasitizes one fleshy fruit-producing species is thus directly proportional to the frequency with which the seeds of the two species co-occur in the feces of their shared bird disperser. Two different, although not mutually exclusive mechanisms may account for this highly significant correlation: (1) After being dispersed together, the seeds of *O. quadripartita* and those of its accompanying species produce seedlings that grow close together, and the young *O. quadripartita* plant establishes early in its life a parasitic association with the similarly young plant of the other species (host-parasite pairs are even-aged). (2) The frequency of association

Tab. 1. Host plants of *Osyris quadripartita* at two southwestern Spanish localities, and their relative abundaces in the habitats (% cover).

	El Viso		Doñana	
	% Hosts (N=111)	% Cover	% Hosts (N=86)	% Cover
Non-endozoochorous species:				
Rosmarinus officinalis	2.7	8.6	8.1	9.0
Erica spp.	1.8	0.2	2.3	0.7
Quercus coccifera	3.6	12.5		
Cistus libanotis			2.3	6.7
Ulex minor			1.2	0.2
Cytisus grandiflorus			1.2	0.1
Stauracanthus genistoides			2.3	0.1
Others	0.	22.1	0.	14.9
Total	8.1	43.4	17.4	31.7
Endozoochorous species:				
Pistacia lentiscus	56.8	18.0		
Phillyrea angustifolia	23.4	6.1		
Daphne gnidium	0.9	0.5		
Myrtus communis	9.9	8.2		
Rhamnus lycioides	0.9	1.7		
Juniperus phoenicea			74.4	52.8
Corema album			8.2	3.6
Others	0.	22.1	0.	11.9
Total	91.9	56.6	82.6	68.3

of *O. quadripartita* with other species in bird feces is proportional to the frequency with which the dispersers forage for fruits in shrubs of these other species shortly after or before ingesting *O. quadripartita* fruits. Consequently, ICF values are indicative of the differential probabilities with which previously ingested *O. quadripartita* seeds will be defecated beneath other species' crowns. In this case, the parasitic relationship would be established between a seedling of the parasite and the heterospecific adult plant under which it germinated (uneven-aged host-parasite pairs).

I do not have any evidence either supporting or falsifying (1) above, but I do have for testing (2). If mechanism (2) holds, *O. quadripartita* should tend to parasitize female plants of dioecious species more often than conspecific males. In these species, only females produce fruits and have the ability to act as "frugivore attractors" and hence an increased likelihood of receiving under their crowns bird defecations containing heterospecific seeds. *P. lentiscus,* the main host species in El Viso, is such a dioecious species. Its sex ratio in the locality does not depart significantly from 1:1 (48.3% of individuals are female, N=145; Chi-square=0.17, P=0.68). Among *P. lentiscus* plants which are parasitized by *O. quadripartita*, the sex ratio is significantly biased in favour of females (67.5% of plants; G=4.74, df=1, P=0.029). When it parasitizes *P. lentiscus,* therefore, *O. quadripartita* is found on females more frequently than expected from the proportional abundance of this sex in the host population. This result is thus consistent with mechanism (2) above. Furthermore, it replicates in an intraspecific context the finding presented earlier, that *O. quadripartita* parasitizes fleshy fruit-producing species much more frequently than species with other seed dispersal methods (Tab. 1).

P. lentiscus fruits are the staple food of *S. atricapilla* in El Viso. It occurs in 63% of fecal samples and accounts for 60% of the total number of fruits ingested by this bird species (Herrera 1984a). Its fruits are the most abundant in the habitat, and have a high lipid and protein content but, if consumed singly, are apparently unable to provide a balanced diet to the birds. In addition, the birds regularly ingest the less nutritious fruits of several other "minor" species (*O. quadripartita* among them) which seem essential to maintain a balanced nutrient intake (Herrera 1984a). *O. quadripartita* ranks first among these minor species with regard to both frequency of ingestion and percent of fruits contributed to the diet of *S. atricapilla.* Relative to the other minor species, *O. quadripartita* ranks third in average fruit abundance in the habitat, and sixth, third and first in lipid, protein and total mineral content of fruit pulp (on a dry mass basis), respectively (Herrera 1984a, 1987). Abundance and overall nutritional features of the pulp alone thus do not seem to account for the importance of the fruits of this species in the diet of *S. atricapilla.* The frequent spatial proximity of *O. quadripartita* plants to female shrubs of *P. lentiscus,* the main fruit species in *S. atricapilla*'s diet, may be one contributing factor. *O. quadripartita* is dioecious, and females parasitize *P. lentiscus* much more often than conspecific males (Herrera in press b; this pattern was interpreted in the context of sexual niche partitioning). Accordingly, there is a high proportion of *P. lentiscus–O. quadripartita* host-parasite pairs made up of two female, and thus fruit-producing plants. The spatial proximity of *O. quadripartita* and *P. lentiscus* fruit sources should greatly reduce the locomotion costs of birds foraging for a mixed fruit diet, and thus may explain the disproportionate consumption of *O. quadripartita* fruits relative to their abundance and nutritional characteristics. A critical test of this idea would require direct observations of foraging birds in the field, but the dense vegetation of the El Viso scrubland rendered this impractical.

In summary, as a consequence of the food selection behaviour of *S. atricapilla,* its main seed disperser, *O. quadripartita* seeds are dispersed in multispecies packages rather than singly. This explains the pattern of host use exhibited by this plant parasite: it mostly parasitizes bird-dispersed coexisting species, and these in proportions closely correlated with the frequency of co-occurrence as gut fellows. The frequent close association of female *O. quadripartita* plants with females of *P. lentiscus,* the most preferred *S. atricapilla* fruit plant (and also the most frequent parasite's host and gut fellow), helps to explain the disproportionate incidence of *O. quadripartita* fruits in the diet of this bird. Returning to the hypothesis stated in the introduction, the evidence presented here provides support to the notion of a dynamic feedback connecting the plant-disperser interaction and the structure of the habitat. By recruiting *O. quadripartita* seeds under its preferred fruit source, *S. atricapilla* largely determines host plant use by the parasite and enhances a close spatial association between a minor, yet important fruit species and its preferred fruit plant. In the long run, the expected consequence will be an increase in the proportional use of *O. quadripartita* fruits by *S. atricapilla* relative to other minor species (despite greater abundance or nutritional quality of some of these). This, in turn, will reinforce further the *P. lentiscus–O. quadripartita* host-parasite association. In general, the process will probably result in an improvement of the dispersal prospects of *O. quadripartita* seeds, and make the spatial arrangement of fruit sources in the habitat better suited to the disperser's economy and nutritional requirements.

Mechanisms analogous to the one exemplified here are presumably at work in natural habitats more often than commonly realized (see, e.g., Debussche et al. 1982, 1985, Herrera 1984c, Stiles and White 1986). By shaping the environments where plant-disperser interactions occur, and by influencing the interaction itself, these processes may be directly responsible for some patterns of mutualistic congruency, thus relieving us in these instances from invoking coevolution to interpret them (Herrera 1985b, Janzen 1985). Furthermore, these processes may act as strong proximate "modifiers" of the constellation of selective pressures operating on both plants and dispersers, thus setting the evolutionary scenario for the participants in the mutualistic interaction.

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Size, reproductive potential and fecundity in insects: things aren't as simple as they seem

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It is considered axiomatic for most arthropods that increased weight and/or size results in increased fecundity (Gilbert 1984a), and this has been reported for many insects, especially aphids (Dixon and Wratten 1971, Leather and Wellings 1981, Dixon et al. 1982). However, this relationship may not be as straightforward as it seems, particularly in aphids and Lepidoptera. The accepted weight/fecundity relationship may become less reliable if, as is the case in many studies, the steps between the dependent and independent variables are increased. For example, in many aphid studies, potential fecundity (reproductive potential, i.e. embryo counts or even large embryo counts) is used instead of actual total fecundity to assess adult fecundity (Elliott 1973, Dewar 1977, Bintcliffe and Wratten 1982, Llewellyn and Brown 1985). These short cut fecundity estimates are adequate in those aphids where ovulation ceases after adult moult, e.g. *Drepanosiphum platanoidis* Schr (Leather 1983). In the case of aphids like *Rhopalosiphum padi* (L.) where ovulation continues after the adult moult, the initial estimates of fecundity can be as much as 135% lower than actuality, and this is particularly marked in the smaller individuals (Leather 1983). Thus only the initial rate of reproduction is estimated accurately by large embryo counts and other short cut fecundity estimates.

This should thus be borne in mind when total fecundity estimates are made using such short cuts and are