OIKOS 36: 51–58. Copenhagen 1981

# Fruit variation and competition for dispersers in natural populations of Smilax aspera

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Herrera, C. M. 1981. Fruit variation and competition for dispersers in natural populations of *Smilax aspera*. – Oikos 36: 51–58.

The berries of *Smilax aspera* L. (Liliaceae), a woody climber of mediterranean scrub, may have either one, two or three seeds. One-seed fruits have the largest, and three-seed the smallest, pulp/seed ratio, so differently-seeded fruits have a differential feeding value to birds feeding on them. In Andalusia, southern Spain, the overall proportions of fruits with different seed number was found to vary between populations as well as between individuals of the same population. *S. aspera* fruiting season overlaps extensively with the fruiting period of many other species and all of them share the same few species of bird dispersers. It was then hypothesized that inter-population variation in fruit seed numbers was related to interspecific competition among plants for dispersers. To test this hypothesis, twelve populations of *S. aspera* were sampled for fipe fruits. For each sample, the proportions of one-, two- and three-seed fruits were determined, and a set of environmental variables was recorded at each sampling locality. Multiple stepwise regression analysis shows that the best single predictor of the mean number of seeds per fruit is the number of plant species bearing fruits simultaneously and equally or more abundant than *S. aspera*. Assuming that the intensity of competition among plant species for dispersers must be roughly proportional to the number and population sizes of competitor species, these results suggest that inter-population variation in the number of seeds per fruit is actually related to variation in competitive pressures, provided that 1) dispersers are in short supply, 2) dispersers select to some extent the most profitable fruits, and 3) number of seeds has some genetic component. Evidence supporting these three assumptions is presented, thus suggesting that observed variation in fruit seed numbers must be attributed to interspecific competition for dispersers among plants.

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Ягоды *Smilax aspera* L. (Liliaceae), древесного вьющегося средиземноморского кустарника, могут иметь 1, 2 и 3 семечка. Односемечковые ягоды-самые крупные, 3-семечковые - самые мелкие. Соотношение объемов мякоти и семечек у таких плодов различно, и они имеют разную питательную ценность для потребляющих их птиц. В Андалузии (южная Испания) соотношение плодов с различным числом семян варьирует в разных популяциях, так же как и у отдельных растений одной популяции. Период плодоношения *S. aspera* сильно перекрывает периоды плодоношения многих других видов растений, и все они используют одних и тех же птиц для распространения семян. Была затем предложена гипотеза о том, что внутрипопуляционные различия количества семян в плоде связаны с межвидовой конкуренцией растений за распространителей. Для проверки этой гипотезы были собраны зрелые плоды у растений из 12 популяций *S. aspera*. В каждой пробе определены соотношения 1-, 2- и 3-семечковых плодов, отмечены различия внешних факторов в местообитаниях каждой популяции. Проведение математического анализа методом множественной регрессии показало, что единственный и лучший индикатор среднего числа семян в плоде - число видов растений, плодоносящих одновременно, плотность которых такая же или более высокая, чем у *S. aspera*. Предполагается, что интенсивность конкуренции за распространителей семян между разными видами растений может быть в общих чертах пропорциональной числу и размерам популяций конкурирующих видов. Полученные результаты показали, что межпопуляционные различия в количестве семян в плоде фактически пропорциональны прессу конкуренции. Отсюда следует, что: 1. число распространителей ограничено; 2. распространители проявляют умеренную избирательность в отношении плодов; 3. число семян определяется генотипом растения. Приводятся доказательства этих трех положений, таким образом, установлено, что наблюдаемые различия числа семян в плодах должны зависеть от условий межвидовой конкуренции зв распространителей семян между растениями.

Accepted 21 April 1980

## 1. Introduction

Plant-pollinator and plant-disperser coevolved systems may generate competition for animal agents among plants. This was suggested long ago by Darwin (1859), who pointed out the likely competition among mistletoe plants (*Viscum* L.) for their main dispersal agent (*Turdus viscivorus* L.), and the same argument has recently been adduced to explain some patterns observed in nature. The staggering of flowering and fruiting seasons has been explained as a mechanism preventing competition among plants for pollinators (e.g. Mosquin 1971, Heinrich and Raven 1972, Heithaus 1974, Frankie 1975, Reader 1975, Stiles 1975, 1977, Heinrich 1976) and dispersal agents (Snow 1965, 1971, Smythe 1970) respectively. However, in environments where temporal partitioning has apparently not been possible, competition among plants may have other effects. I present here some evidence from Andalusia, southern Spain, suggesting that competition for dispersers from other fruit-bearing plant species can alter fruit features in natural populations of *Smilax aspera* L. (Liliaceae)

## 2. The plants

*Smilax aspera* is a woody climber whose black berries begin to ripen in late September and remain on the plant until about the following March. Berries are nearly spherical in shape, about 7 mm in diameter and may have either one, two or three seeds. Fruits of all types are found on any individual plant, and the overall proportions of fruits with different seed numbers vary substantially between populations and appreciably between individuals within a population (see below). Fruits with different seed numbers are fairly easily distinguishable by sight with some practice, since they differ in size and, more importantly, in cross-section: one-seed are circular, two-seed elliptical and three-seed rounded-triangle-shaped. *S. aspera* is mostly found in relatively undisturbed areas, where it coexists with a variable constellation of other fruit-bearing plant species.

There is an almost total overlap among all these plant species in their fruiting seasons (autumn-early winter, Tab. 1), and the great majority of them show the syndrome of bird diaspores (Pijl 1969). Only *Arbutus unedo* L. and *Juniperus phoenicea* L. appear to show adaptations for dispersal by mammals (e.g. smell, no permanent attachment) and I have found their seeds in

Tab. 1. Fruiting and flowering seasons of southern Spanish plant species found to bear ripe, fleshy fruits during the fruiting period of *Smilax aspera,* and their main fruit characteristics. Only those species equal or more abundant than *S. aspera* in at least one study locality have been listed. All fruiting and most flowering dates are based on own observations. Some flowering dates were taken from Willkomm and Lange (1861–80), Polunin (1969) and Polunin and Smythies (1973).

| No. | Species | Flowering period | fruiting period | diameter (mm) | fresh weight (g) | % water | pericarp/ seeds |
|---|---|---|---|---|---|---|---|
| 1 | *Juniperus phoenicea* L. (Cupressaceae) | Feb–Apr | Oct–Jan | 9.7 | 0.49 | 38.6 | 10.7 |
| 2 | *Osyris quadripartita* Salzm. (Santalaceae) | Mar–Jul | Sep–Aug | 7.3 | 0.24 | 58.3 | 0.3 |
| 3 | *Rosa* sp. (Rosaceae) | Apr–May | Sep–Dec | 9.2 | 0.65 | 55.2 | 1.8 |
| 4 | *Crataegus monogyna* Jacq. (Rosaceae) | Mar–Apr | Sep–Nov | 9.3 | 0.68 | 57.2 | 1.4 |
| 5 | *Pistacia lentiscus* L. (Anacardiaceae) | Mar–May | Sep–Jan | 5.3 | 0.06 | 60.1 | 0.9 |
| 6 | *Daphne gnidium* L. (Thymelaeaceae) | May–Oct | Sep–Mar | 5.1 | 0.10 | 82.0 | 1.1 |
| 7 | *Myrtus communis* L. (Myrtaceae) | May–Jun | Nov–Jan | 8.5 | 0.39 | 72.4 | 1.7 |
| 8 | *Arbutus unedo* L. (Ericaceae) | Nov–Dec | Nov–Jan | 17.7 | 2.44 | 71.4 | 5.4 |
| 9 | *Olea europaea* L. (Oleaceae) | May–Jun | Nov–Jan | 8.8 | 0.62 | 49.8 | 0.4 |
| 10 | *Phillyrea angustifolia* L. (Oleaceae) | Mar–Apr | Aug–Oct | 5.2 | 0.08 | 47.8 | 0.5 |
| 11 | *Rubia peregrina* L. (Rubiaceae) | May–Jul | Oct–Jan | 6.1 | 0.10 | 76.9 | 1.1 |
| 12 | *Viburnum tinus* L. (Caprifoliaceae) | Mar–May | Oct–Jan | 5.4 | 0.10 | 29.5 | 1.0 |
| 13 | *Smilax aspera* L. (Liliaceae) | Oct–Nov | Sep–Feb | 7.3 | 0.19 | 70.1 | 0.6 |
| 14 | *Ruscus aculeatus* L. (Liliaceae) | Jan–Apr | Nov–Jan | 14.0 | 1.36 | 64.3 | 0.6 |

mammal droppings (mainly carnivores, Herrera unpubl.). Fruit characteristics of plant species in Tab. 1 are fairly similar, percent water content being the most variable feature.

Although there is an extensive overlap in fruiting seasons between *S. aspera* and the remaining species, this is not so for their flowering periods. *S. aspera* flowers in October, overlapping only with one species (*A. unedo,* Tab. 1). These two are the only woody plants flowering in autumn in southern Spanish shrublands.

## 3. Dispersers

In Andalusia, the predominant autumn-winter fruiting season coincides with the arrival of several widespread passerine bird species which largely feed on fruits in the mediterranean shrublands where *S. aspera* is found.

Among several hundred stomachs analyzed of fifteen bird species commonly found in winter in relatively undisturbed habitats of southern Spain, only four species had intact seeds of plant species listed in Tab. 1 in more than 10% of the stomachs analyzed (Tab. 2). These species appear to be the only regular dispersers of the plant species forming mediterranean shrublands and producing fleshly fruits. Their importance seems to be unequal, *Sylvia atricapilla* L. being the most significant disperser. This species is also the main consumer of *S. aspera* berries and it must be considered its main disperser, although *E. rubecula* and *S. melanocephala* also feed on these berries to some extent. All these birds void intact seeds and Tab. 2 suggests that most plant species in Tab. 1 share the same few disperser species.

The extensive overlap in fruiting seasons of many plant species in the study area, together with the low number of disperser species, suggested the possibility of competition among plants for dispersal agents. Interpopulation variations in number of seeds of *S. aspera* fruits was hypothesized to be related in some way to the existence of competition, and this hypothesis was tested in a field investigation, the results of which are presented here.

## 4. Testing the competition hypothesis

### 4.1. Methods

Twelve populations of *S. aspera* were sampled for ripe fruits during autumn-winter 1977–78, the localities being distributed throughout Andalusia across a broad range of environmental conditions. In each locality, fruits were collected from as many plants as possible. Each sample of fruit was oven dried at 90°C during 24 h. A subsample was taken at random from each sample, and all the fruits were individually weighed to the nearest 0.0001 g. Dry weights of seed(s) and pericarp were also determined for every individual fruit in the subsample. For each whole sample, proportions of one-, two- and three-seed fruits were determined.

A set of environmental variables was recorded at each sampling locality (symbols used below and extreme values of the samples in parentheses): latitude (LAT, 36°32′–38°6′), longitude (LONG, 2°50′–6°38′), altitude a.s.l. (AASL, 10–1100 m), mean annual rainfall (MAR, 480–1500 mm), autumn rainfall (AR, 190–610 mm), total number of coexisting plant species bearing ripe fruits simultaneously with *S. aspera* (NS1, 1–7), number of plant species bearing fruits simultaneously and equally or more abundant (percent cover) than *S. aspera* (NS2, 1–5). LAT and LONG were converted to minutes and expressed in the analyses in hundred of minutes units. An eight variable added was the mean euclidean distance from *S. aspera* berries to the fruits of equally or more abundant coexisting species (MED, 0.60–2.78), as a measure of dissimilarity. The fruit of every plant species was characterized by sample averages of diameter, fresh weight, percent water content and the ratio of pericarp to seed(s) weight (Tab. 1). Then the distance from *S. aspera* berries to every other plant species' fruit was computed by standard procedures (e.g. Sneath and Sokal 1973) and the average for each locality was obtained.

Further fruit samples and supplementary information on intra-population variation in fruit seed numbers were obtained in locality no. 7 (see a list of localities in Tab. 4) during the autumns of 1977 and 1978.

Tab. 2. Frequency of occurrence of fruit remains and seeds in stomach contents of four passerine species in southern Spain, and plant species (numbers refer to Tab. 1) of which seeds or skins were found in stomachs or droppings. Birds and droppings were collected from October through March in shrublands of southern Spain. The four species shown are those which, within a larger species sample, had intact seeds in more than 10% of the stomachs analyzed.

| Bird species | Stomachs | | | Plant species present |
|---|---|---|---|---|
| | N | % with fruit remains | % with seeds | |
| *Sylvia atricapilla* L. | 15 | 93.3 | 53.3 | 2, 3, 5, 6, 7, 8, 9, 10, 11, 12, 13 |
| *Erithacus rubecula* L. | 21 | 90.5 | 42.9 | 2, 5, 7, 8, 9, 10, 11, 12, 13 |
| *Sylvia melanocephala* Gm. | 18 | 83.3 | 27.8 | 2, 5, 6, 7, 8, 9, 10, 11, 13 |
| *Turdus merula* L. | 14 | 57.1 | 14.3 | 2. 3, 5, 7, 8, 9, 10, 13 |

### 4.2. Intra-population variation in fruit characteristics

*S. aspera* forms usually large aggregations where individuals are found closely intermixed and hardly recognizable, thus it was difficult to undertake an extensive investigation on inter-individual differences in fruit characteristics. In locality no. 7 five individuals could be adequately sampled (two in 1977, three in 1978), and their entire fruit crops collected. The two most distant plants (P1 and S2) were about 70 m apart, the closest ones (S3 and S2) only 3 m. The five individuals were of about the same size, and were growing on horizontal terrain of identical soil type.

Inter-individual differences observed in the proportions of fruits with different seed numbers (Tab. 3) are statistically significant (Chi-square = 56.3, df = 8, $p \ll 0.001$), individuals differing in the proportions of the three fruit types. When the fruits of the five individuals are pooled in a single sample, the resulting proportions are strikingly similar to the overall population figures for 1977 (Tab. 4) obtained by sampling a much larger number of individuals (not including either P1 or P2) (Chi-square = 0.13, df = 2, $p > 0.90$). Comparing the overall population proportions for 1977 with the proportions resulting from combining fruits of S2, S3 and NN (1978), the difference does not reach statistical significance (Chi-square = 3.68, df = 2, $p > 0.10$). These results tend to suggest that overall population proportions of fruits with different seed numbers remain fairly constant from year to year, and demonstrate that significant inter-individual variability exists within populations. Furthermore, overall population figures seem to reflect adequately the combined effects of intra-individual variance in number of seeds per fruit and inter-individual differences in mean number of seeds.

The mean percentage of individual fruits represented by the pericarp (on a dry weight basis) decreases from one- through three-seed fruits (Fig. 1). Within any population of *S. aspera,* one-seed berries provide relatively most food material and least seed mass per fruit, the opposite being true for three-seed berries. In other words, within populations one-seed fruits would be expected to be the most profitable ones to the birds eating *S. aspera* berries, since they provide the greatest proportion of useful, nutritious material and the least of useless ballast. Accordingly, individual plants with high frequency of one-seed fruits should be favoured in each population.

Tab. 3. Proportions of fruits with different numbers of seeds in five individuals of *Smilax aspera* in locality no. 7. N = number of fruits.

| Individual | Year | N | Frequency (percent) | | |
|---|---|---|---|---|---|
| | | | 1-seed | 2-seed | 3-seed |
| P1 | 1977 | 438 | 63.5 | 33.8 | 2.7 |
| P2 | 1977 | 285 | 50.2 | 36.1 | 13.7 |
| S2 | 1978 | 79 | 59.5 | 34.2 | 6.3 |
| S3 | 1978 | 57 | 87.7 | 10.5 | 1.8 |
| NN | 1978 | 128 | 60.9 | 28.9 | 10.2 |

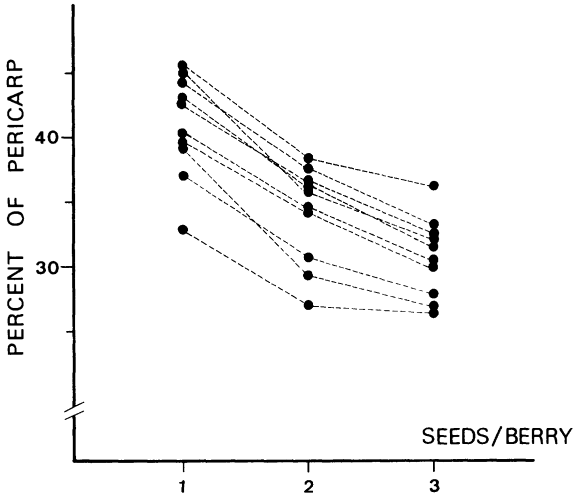

Fig. 1. Mean percentage of whole fruit represented by the pericarp (on a dry weight basis) in one-, two- and three-seed berries in ten southern Spanish populations of *Smilax aspera.* Lines connect points from the same population. Data from localities no. 2 and 9 (Tab. 4) are missing.

### 4.3. Inter-population variation in fruit characteristics

Observed differences between populations regarding frequency distributions of the three fruit types are highly significant (Tab. 4; Chi-square = 435.4, df = 22, $p \ll 0.001$), the null hypothesis tested being that all populations have the same relative frequencies of the three fruit types. Taking as dependent variable the mean number of seeds per fruit in each population (MNSPF), a multiple stepwise regression analysis was run on the data, the eight independent variables being those referred to in Methods. Results are shown in Tab. 5. The best single predictor of MNSPF is NS2 (number of plant species bearing fruit simultaneously and equally or more abundant), which alone explains 69.2% of the variance of MNSPF attributable to independent variables. LONG and AASL were also significant variables, together accounting for 24.6% of the explained variance. In all, these three variables account for 93.8% of MNSPF explained variation.

Multiple regression analyses may produce misleading results if independent variables are highly correlated among themselves and thus having similar effects. However, in the present analysis this effect must be unimportant, due to (1) the mean of absolute values of all pairwise correlation coefficients among independent variables is 0.421 ± 0.0504 (s.e.), (2) in pairwise correlations, NS2, the best predictor of MNSPF, is significantly related only to NS1 ($r = 0.609$, $p < 0.05$), but

Tab. 4. Locality characteristics and relative frequency of fruits with different numbers of seeds in populations of *Smilax aspera* in southern Spain. See Methods for symbols. In locality no. 7, figures in parentheses represent a supplementary sample of unripe fruits (see Discussion).

| Locality | Environmental variables | | | | | | | | Sample size | Frequency (percent) | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | LAT | LONG | AASL | MAR | AR | NS1 | NS2 | MED | | 1-seed | 2-seed | 3-seed |
| 1. Linares (Huelva) | 37°53′ | 6°38′ | 650 | 1046 | 405 | 4 | 3 | 2.78 | 153 | 71.2 | 26.8 | 2.0 |
| 2. Constantina (Sevilla) | 37°50′ | 5°37′ | 600 | 601 | 241 | 5 | 1 | 1.28 | 1141 | 37.3 | 43.0 | 19.7 |
| 3. Doñana (Huelva) | 36°58′ | 6°28′ | 10 | 606 | 262 | 1 | 1 | 0.60 | 147 | 33.3 | 42.9 | 23.8 |
| 4. Algaida (Cádiz) | 36°52′ | 6°18′ | 10 | 606 | 262 | 5 | 5 | 1.47 | 95 | 73.7 | 24.2 | 2.1 |
| 5. Ubrique (Cádiz) | 36°32′ | 5°36′ | 800 | 1190 | 437 | 2 | 2 | 1.09 | 289 | 44.6 | 43.6 | 11.8 |
| 6. Aznalcázar (Sevilla) | 37°15′ | 6°13′ | 20 | 568 | 249 | 5 | 4 | 0.98 | 172 | 82.0 | 16.3 | 1.7 |
| 7. Viso (Sevilla) | 37°27′ | 5°44′ | 50 | 530 | 235 | 6 | 4 | 1.74 | 750 | 60.4 | 32.9 | 6.7 |
| | | | | | | | | | (152) | (74.4) | (24.3) | (1.3) |
| 8. Cabra (Córdoba) | 37°30 | 4°28′ | 600 | 679 | 275 | 3 | 2 | 1.33 | 649 | 36.7 | 43.4 | 19.9 |
| 9. Cardeña (Córdoba) | 38°3′ | 4°17′ | 350 | 480 | 189 | 2 | 1 | 0.89 | 357 | 23.3 | 50.1 | 26.6 |
| 10. Adamuz (Córdoba) | 38°6′ | 4°32′ | 350 | 480 | 189 | 4 | 3 | 1.42 | 773 | 42.8 | 44.2 | 13.0 |
| 11. Cazorla-1 (Jaén) | 38° | 2°50′ | 900 | 1500 | 614 | 7 | 3 | 2.78 | 494 | 43.3 | 37.9 | 18.8 |
| 12. Cazorla-2 (Jaén) | 37°58′ | 2°53′ | 1100 | 1500 | 614 | 4 | 4 | 2.24 | 641 | 51.0 | 37.6 | 11.4 |

NS1 is nonsignificantly related to MNSPF, and (3) the most significant cross-correlations among independent variables are found within the group made up of AR, MAR, AASL and LONG, neither of which bear significant relations to MNSPF in pairwise correlations.

*S. aspera* is a dioecious species, thus necessarily outcrossed, and pollination success might be important to the number of seeds set per fruit. Quantitative data on possible variation in pollination success among populations are not available, but the virtual absence of overlap with other species in flowering season (Tab. 1) tends to suggest that variations in pollination success, if any, are not due to competitive interactions, but rather to other locality-specific attributes (e.g. insect diversity, climatic features) which presumably have been accounted for, to an unknown extent, by the independent variables used.

Coefficients in the regression equation show that as NS2 increases, MNSPF decreases. Both LONG and AASL also bear a negative relationship to MNSPF, the effect of the latter being greatest in the easternmost, highest localities when the effect of NS2 has been removed. Apart from this geographical trend, the analysis shows that in those plant communities rich in fruit-bearing plants, individual *S. aspera* berries have, on average, fewer seeds than in species-poor communities, and hence are more beneficial to the birds which exploit them.

Tab. 5. Results of multiple stepwise regression of MNSPF on eight environmental variables. Only variables contributing to $R^2$ by more than 0.001 are shown, listed in the order they enter the equation (see Methods for symbols). Only those coefficients in equation referring to significant variables, appearing after the third step, are shown.

| Variable | Increase in $R^2$ | F | P | Coefficient in equation |
|---|---|---|---|---|
| NS2 | 0.692 | 22.51 | <0.001 | –0.187 |
| LONG | 0.201 | 16.97 | <0.001 | –0.287 |
| AASL | 0.045 | 5.86 | <0.05 | –0.0002 |
| LAT | 0.010 | 1.39 | n.s. | – |
| MED | 0.002 | 0.25 | n.s. | – |
| MAR | 0.009 | 1.14 | n.s. | – |

There is a considerable inter-population variation in the percentage represented by the pericarp with respect to the whole fruit (Fig. 1), due to variation in both weight of pericarp and size of seeds. To investigate possible environmental correlates of these two variables, regression was again used. In independent trials, I successively selected as the dependent variable the dry weight of pericarp in one-, two- and three-seed berries, as well as dry weight of seed(s) in each of these fruit types. The independent variables were those referred to in Methods. None of these analyses revealed any statistically significant relationship, so the inter-population variation in seed size and weight of pericarp must be related to some unknown factor not accounted for here.

## 5. Discussion

The pericarp produced by any fruit-bearing plant is an 'investment' directed to obtain a benefit, namely the dispersal of one or several seeds (Snow 1971, McKey 1975). Quantity and quality of pericarp (amount invested) must bear some relation to the amount of benefit received. Plant species dispersed by obligate specialists which generate high-quality dispersal (Type 1, Howe and Estabrook 1977) usually produce a very nutritious flesh, thus providing a high reward to the disperser. In non-tropical areas, plants dispersed by opportunists predominate (Type 2, Howe and Estabrook 1977), dispersers shifting their diets temporarily to fruits when the availability of the most preferred resources falls below a critical threshold (Berthold 1976).

Type 2 plants depend on the production of large numbers of fruits to attract unspecialized dispersers and fruits have poor-quality pericarps (Howe and Estabrook 1977, McKey 1975).

The temporal overlap in fruiting season of many type-2 plant species taking place in southern Spain during autumn-winter provides opportunist bird dispersers with a broad spectrum of fruit types from which it is possible to select the most profitable ones. At any locality, selection may operate at both inter- and intraspecific levels, favouring either particular plant species or particular individual phenotypes within a population. Thus one may envisage competition for dispersers among type-2 plants if dispersers are in short supply. Plant species and/or phenotypes lower in the ranking of dispersers' preferences would have poorer chances of dispersal and they may be outcompeted by higher-ranking plants. In an intraspecific context, natural selection will favour those genotypes having greater competitive ability (attracting most dispersers) within a given population.

To 'climb' the ranking of dispersers' preferences, a plant species may produce a more nutritious pericarp, increase the amount of pericarp per fruit without altering seed number or, in the case of multiseed fruits, alter the frequency distribution of fruits with different numbers of seeds; or there may be some kind of compromise between these possibilities. In the case of *S. aspera*, if all energy allocated were used to produce one-seed berries only, the total number of fruit produced per plant would be higher and total number of seeds lower, than if all were three-seed fruits (assuming no alterations in pericarp quantity and nutritive value). From an energetic viewpoint, the former situation would lie closer to the dispersers' optimum (highest food/ballast ratio), whereas the latter would stay closer to the plant's optimum (many propagules produced at a low pericarp-investment cost). Actual situations found in nature must represent a compromise between these two counteracting selective forces. It may be hypothesized that the weaker the interspecific competition for dispersers, the more favoured will be those genotypes within a population producing a large proportion of three-seed fruits (greatest number of propagules) and, in turn, the stronger the interspecific competitive pressures the more favoured will be those genotypes having many one-seed berries (superior competitive ability).

It is reasonable to assume that, if the frequency of dispersers is limiting, the intensity of competition for unspecialized dispersal agents must be roughly proportional to the number and population sizes of competitor species. Hence it may be predicted that *S. aspera* populations coexisting with diverse and abundant competitors will tend to have berries with low average seed number, with individual plants of lower mean number of seeds predominating. This is in complete agreement with the results of the multiple regression shown above.

For the previous argument to be valid, it is necessary to demonstrate the three major assumptions, namely a) dispersers are actually in short supply, b) dispersers select to some extent the most profitable fruits, and c) the overall frequency distribution of fruits with different numbers of seeds in a population has some genetic component, individual plants differing in mean number of seeds.

Localities no. 7 and 10 (Tab. 4) were visited at the end of the fruiting season and, in both, many berries of *S. aspera* had became desiccated, while still attached to the plant, by late winter and early spring. Most of them must have spent at least five months on the plant without having been taken by birds. Desiccated fruits of some other coexisting species were also observed by the end of the winter (e.g. *Rubia peregrina, Pistacia lentiscus*), while the abundant fruit crops of other plant species had been totally exhausted by the same dates in these localities (e.g. *Arbutus unedo*). In localities no. 7 and 10 *S. aspera* coexists with 4 and 3 equally or more abundant fruit-bearing species, respectively, being above the mean level of plant competitors (average of twelve localities = 2.75 species). This tends to suggest that in some species-rich localities there is a shortage of dispersers or, at least, that some plant species (*S. aspera* among them) are negatively affected by a relative shortage of dispersers in these species-rich communities.

In locality no. 7, a sample of berries which had not totally ripened was collected in addition to the usual sample of ripe fruits, both samples being taken the same days and from the same plants (Tab. 4). The observed difference between the frequency distributions of berries with different number of seeds is statistically significant (Chi-square = 10.51, df = 1, $p < 0.001$). Among ripe fruits, one-seed berries are underrepresented compared to the unripe sample. As the berries do not fall to the ground but remain attached to the plant throughout the winter, 'missing' fruits among ripe berries may be attributed to feeding activity by birds. This favours the assumption that birds are actually selecting one-seed fruits, although alternative explanations can also be put forwards.

Berry choice experiments were carried out with captive *S. atricapilla* which were offered small bunches of *S. aspera* berries containing a mixture of fruit types. Preliminary results (Herrera unpubl.) suggest the existence of a selection of fruit types by the birds. Pooling the results of several trials in a single set of data, the percentage of total available fruits in each class ingested by the birds were (total fruits offered per class in parentheses) 26.09 (69), 8.82 (34) and 0 (7), for one-, two- and three-seed berries respectively. Difference in number of seeds between ingested and not-ingested fruits is statistically significant (Chi-square = 5.87, df = 1, $p < 0.02$). Consumption decreases from one- through three-seed berries, the birds thus behaving as predicted. As berries with different numbers of seeds are externally recognizable by the human eye on the basis of size and shape, these features can presumably be also used by the birds to distinguish between the various fruit types. The results of these experiments only demonstrate that caged birds ingest a largest proportion of one-seed fruits, without providing evidence on whether net pulp gain per berry is the actual variable being optimized. They support, however, together with the indirect field evidence presented above, the assumption of feeding selectivity by dispersers.

Differences in relative pericarp-richness between one- and three-seed fruits vary between 6.4 and 13.2% (average = 10.24 ± 0.61%) (Fig. 1), so it can be argued that in some localities one-seed berries are not much better than either two- or three-seed ones. The water content of *S. aspera* berries ranges from 69.7 to 72.0% in the populations studied, so to get a significant amount of nutritious material a bird must ingest a large number of fruits. Ten *S. atricapilla* held in captivity and feeding ad libitum on *S. aspera* berries ingested about 60 fruits per bird-day on average, despite a supplement of mealworms to the diet (3.5 g/bird-day) (Herrera unpubl.). The consumption of berries is probably higher in the field, where the animal component in the diet of *S. atricapilla* in winter is usually negligible (Herrera and Jordano unpubl.). In these conditions and provided fruits are not in short supply, even small differences in relative pericarp-richness between one- and three-seed berries within a population must be worth selecting.

The finding reported above that, within the population inhabiting locality no. 7, individual *S. aspera* plants of equivalent size living in a very restricted, homogeneous area, differ significantly in numbers of seeds per fruit, supports the assumption of some genetic component in the control of number of seeds. The year-to-year constancy in overall population frequencies of berries with different numbers of seeds in the same locality, further supports it. The entire fruit crop of plant P1 (Tab. 3) was collected again in 1979 and the percentages of one-, two- and three-seed fruits found were 64.2, 32.1 and 3.7, respectively (n = 212 fruits). These figures are virtually identical to those found the preceding year (Tab. 3) (Chi-square = 0.64, df = 2, $p > 0.70$), suggesting inter-year constancy in mean number of seeds of individuals plants.

The evidence presented strongly supports the proposed hypothesis that interspecific competition among plants is responsible for the observed geographical variation in mean number of seeds of *S. aspera* fruits, through differential dispersal of the various plant seed number-phenotypes mediated by bird selection of fruit types. In all the populations sampled the three fruit types were represented and, since natural selection has not led to the elimination of all but one type, it can be speculated that some mechanism(s) is operating to maintain a balance of the proportions of the three fruit types in each population. Three-seed fruits are the cheapest, and one-seed the most expensive, in terms of fruit pulp and flower accessory structures. Plant economics must be constantly favouring an increase in the number of seeds per fruit, but dispersers which ingest the fruits are favouring a decrease in number. In addition, if competitive pressures faced by a *S. aspera* population are not constant through fruiting seasons, the ideal 'optimally-seeded' fruit will be subject to temporal changes and thus the maintenance of all three fruit types would be advantageous. Annual changes in competitive pressures may originate either from failures in the fruit crop of some competitor(s) or from alterations in the winter population sizes of bird dispersers.

*Acknowledgments* – J. A. Amat, R. C. Soriguer and M. Rodríguez supplied me with several fruit samples. Computer time was generously provided by the Centro de Cálculo, Universidad de Sevilla. My wife, Dori, assisted extensively with field and laboratory work, discussed many aspects of plant-frugivore interactions, criticized several drafts of the manuscript and provided constant encouragement. D. W. Snow and B. Valdés read and commented on an earlier draft. D. H. Janzen provided important doses of moral support.

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