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Selective pressures on fruit seediness: differential predation of fly larvae on the fruits of Berberis hispanica

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Developing *Berberis hispanica* Boiss & Reuter berries are heavily attacked by a single species of fly larvae which feed on seed contents. There is a steady increase in fruit attack incidence with increasing number of seeds in the fruit, and individual developing seeds have a greater average probability of escaping predation when single in fruits (0.688) than when two (0.379) or more (0.120) are together in the same berry. With increasing fruit seediness, larval food increases and larval mortality decreases. Differential predation on differently-seeded fruits apparently results from higher larval survival in multi-seed fruits, which in turn has selected for differential oviposition among fruit classes by female flies. The proportions of differently-seeded fruits are linearly correlated with the estimated number of surviving seeds per mass unit of pulp expenditure, suggesting that *B. hispanica* plants are probably adjusting the distribution of seeds among fruit classes to maximize absolute number of surviving seeds through accounting simultaneously for predation risk and pulp costs. Mean number of seeds per fruit was found to be greater in a population which did not suffer fly attack, but no difference existed with regard to average pre-abortion seed number per fruit. Fly predation on fruits and seeds of *B. hispanica* seems therefore to influence fruit seediness through seed abortion-mediated plant responses.

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Молодые плоды *Berberis hispanica* Boiss a.Renter подвергаются сильному нападению личинок единственного вида мухи, питающихся содержимым семян. Установлено увеличение повреждаемости плодов с увеличением числа семян в каждом из них; отдельные развивающиеся семена имеют большую вероятность уцелеть от нападения вредителей, если они единичны (0,688), нежели развиваются по-два (0,379) или более (0,120) в одном плоде. С увеличением семенной продукции плода увеличивается запас пищи личинок, и смертность их падает. Дифференциальное хищничество на плодах с разным числом семян вероятно приводит к более высокой выживаемости личинок в плодах с многочисленными семенами, которые, в свою очередь, отбираются самками мух при избирательной яйцекладке на разных классах плодов. Соотношение плодов с разным числом семян имеет линейную зависимость с числом развивающихся семян в расчете на единицу массы мякоти; это показывает, что у *B. hispanica* распределение семян в плодах разных классов адаптировано к максимизации абсолютного количества развивающихся семян с учетом одновременно возможности повреждений и издержек мякоти. Среднее число семян в плодах больше в популяциях, которые не испытывают нападения мух, но при этом не найдены различия средних значений числа недоразвившихся семян в разчете на один плод. Повреждения мухами плодов и семян *B. hispanica* по-видимому влияют на семенную продукцию в результате реакции растений, выражающейся в недоразвитии семян.

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Introduction

Seed dispersers have been ordinarily invoked as the most obvious selective agents for dispersal-related traits of vertebrate-dispersed plants. Fruiting patterns, fruit architecture and nutritive quality of fruit pulp, among others, are adaptations on the part of plants to increase vertebrate-mediated seed dispersal success (e.g., Snow 1971, McKey 1975, Howe and Estabrook 1977, Thompson and Willson 1979, Herrera 1981, 1982a). Factors other than disperser pressures may also evolutionarily shape plant features intimately associated with the seed dispersal process. Among these, fruit predators may become prominent selective agents on vertebrate-dispersed plants (Herrera 1982b). I show in this note that fly larvae have the potential to be strong selective agents on the architecture of the fruits of *Berberis hispanica* Boiss & Reuter, a bird-dispersed shrub, through selectively destroying the seeds of fruits differing in seed number.

Plant natural history, study sites, and methods

Berberis hispanica (Berberidaceae) is a deciduous thorny shrub found in limestone mountains of southern Spain above about 1000 m a.s.l. The present study was conducted in the Roblehondo area, Sierra de Cazorla (Jaén province, southern Spain), at 1300 m a.s.l. Plants grow there on rocky soils of a north-facing slope dominated by pine-juniper woodland (see Herrera and Jordano 1981 for a detailed description of the site). In Roblehondo, *B. hispanica* generally initiates leaf-flushing in early May and flowering takes place from early May through early June. Developing fruits are seen on plants from late May. The earliest ripe fruits are found by early August, and by late August-early September all fruit crops have already matured (observations in the period 1979–1982). Ripe fruits, which are eaten by several species of avian dispersers (mainly *Turdus* spp.), are 9.3 ± 0.5 mm (mean ± SD) long, 5.4 ± 0.7 mm wide, and have a dry mass of 50.7 ± 12.2 mg (N = 20).

A substantial fraction of developing *B. hispanica* fruits in Roblehondo and other localities at similar elevations are attacked every year (observations from 1979 through 1982) by the larvae of a single species of Tephritid fly. Unequivocal homogeneity in external larval morphology (see Phillips 1946), shape and location of distinctive oviposition scars on the fruit surface (see e.g. Andrés Cantero 1965), and feeding pattern of larvae within the fruits, as well as in the size, position and characteristic shape of larval exit holes (see below), all strongly suggest that a single fly species is involved ("the fly" hereafter). Species composition and taxonomic status of the Sierra de Cazorla Tephritids are very poorly known (see Morgan 1980), let alone host plant selection, and I have been unable so far to rear adult flies from infested *Berberis* fruits, thus unfortunately precluding any attempt at species identification. Nevertheless, provided that a single fly species is involved, naming it is not essential to the main results and interpretations below.

Fly larvae feed exclusively on, and destroy most or all of, seed contents of infested fruits. Seed coats and fruit pulp are not damaged except for indispensable mining for the larvae to get in and out of the fruit. Only one larva is found within each individual infested fruit. Oviposition takes place sometime in June-July and the vast majority of larvae leave the fruits just prior to their ripening to pupate elsewhere. Fruits showing larval exit holes begin to be abundant in the population 2–3 wk before the local peak of fruit ripening. A small fraction of attacked fruits still enclose seed-feeding larvae after ripening. I do not know whether some infested fruits are aborted and shed by parent plants prior to ripening, but large numbers of attacked fruits showing exit holes do ripen on all plants. These remain attached to the plant and their pulp acquires the colour, taste and texture of ripe uninfested fruits.

On 21–22 August 1979 I collected two samples of newly ripe fruits from two *B. hispanica* plants 45 m apart whose size and fruit crops were representative of the local population. One of them was growing beneath a large *Crataegus monogyna* Jacq. tree and was heavily shaded, while the other was exposed to full sunlight. The incidence of fly seed predation in the fruit samples, as judged by the proportion of fruits with larval exit holes, was equivalent to that observed in other plants in the area. Fruits were dissected individually, annotating the number of full-sized seeds (and of small, empty, soft-coated aborted seeds when present). For infested fruits, record was kept of the number of damaged seeds and of the presence of exit holes and live or dead larvae. Results from the two plants sampled were similar in all respects, thus I have combined them in the analyses to follow.

In early October 1982 I sampled a further *B. hispanica* population growing near Nava de Pablo (1700 m a.s.l., 5 km SE of Roblehondo). Ripe fruits were collected from four plants and dissected using the same procedures as above. *B. hispanica* starts flowering there about one month later than in Roblehondo, but timing of fruit ripening does not differ substantially. The flowering-to-fruiting interval in Nava de Pablo is thus substantially shorter than in Roblehondo. Fruits in Nava de Pablo and other localities at similar elevations are totally free from the attack of fly larvae; not a single larval exit hole has been ever observed in fruits from these areas after examination in the field of many fruit crops over several years.

Results and discussion

The following refers throughout to the Roblehondo population unless otherwise stated.

The vast majority of fruits had either one (56.4%) or two (41.9%) seeds, and very few (1.7%) exceeded these figures (Fig. 1). The maximum recorded was a single 4-seed fruit. These data refer exclusively to the number of full-sized, hard-coated seeds, disregarding aborted ones, which were present in 22.4% of the 466 fruits examined.

The incidence of fly-infested fruits (having exit holes and destroyed seeds, or lacking exit holes but containing a live or dead larva) differed greatly among fruits with varying number of full-sized seeds (Fig. 1). The percent of one-seed fruits that were attacked by fly larvae was 31.2%, while corresponding figures for two- and three- or more seed ones were 62.1% and 87.5%, respectively. These differences are highly significant ($G = 50.2$, $df = 2$, $P \ll 0.0001$), demonstrating that there is a steady increase in fruit attack incidence with increasing numbers of seeds in the fruit. Individual fly larvae invariably destroyed all discernible seed contents before leaving a fruit. All of the 282 seeds contained in the 169 fruits that had exit holes had been extensively fed upon by the larvae; not a single seed in an attacked multi-seed fruit survived fly attack. The outcome of predation on seeds in fruits with varying seed numbers is therefore that individual developing seeds have a substantially greater average probability of escaping predation when they occur singly in fruits (0.688) than when two (0.379) or more (0.125) occur in the same fruit.

Average dry mass (± SD) of undamaged seeds in one-seed fruits was 15.1 ± 1.6 mg, and in two-seed fruits 27.8 ± 2.3 mg ($N = 10$ fruits for each class). Individual seeds are thus only very slightly smaller in two-seed fruits. I failed to obtain sufficient numbers of three- and four-seed unattacked fruits to weigh, but examination of the size of their seeds in infested fruits indicates that total seed mass per fruit certainly exceeded that of two-seed ones. There is therefore a steady increase in available larval food with increasing fruit seediness. This fact, and the observation that individual larvae destroyed all the seeds present in a fruit regardless of their number (and hence total seed mass), tend to suggest that larval food is not in excess even in multi-seeded fruits. It may then be hypothesized that differential predation on differently-seeded fruits results from higher larval survival in multi-seeded fruits, which in turn selects for differential oviposition among fruit classes by female flies.

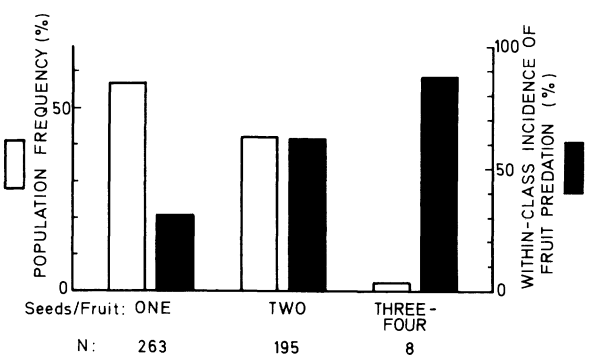

Fig. 1. Frequency of *Berberis hispanica* fruits with different seed number in the sample studied (open bars), and proportion of fruits infested by fly larvae in each of the three fruit classes considered (filled bars).

The frequency of occurrence of dead larvae varied among fruit classes, being greatest in one-seed fruits: 52.9% of the 17 larvae found in one-seed fruits were dead, but only 5.3% of the 19 found in multi-seeded ones ($P = 0.0018$, Fisher exact probability test). The small fraction of infested fruits which contained larvae (17.1%) is a consequence of the fact that by my sampling dates most successful larvae had already left the fruits, as revealed by exit holes. The above figures may accordingly be used to obtain overall estimates of within-fruit larval survival in differently-seeded fruits over the entire growing period, simply by incorporating into the computations the number of fruits showing exit holes and thus, presumably, having produced a successful larva. Larval survival estimates thus obtained are 0.890 and 0.992 for one- and multi-seed fruits, respectively ($N = 82$ and 128 fruits), and the difference is statistically significant ($P = 0.0011$, Fisher test). Larvae therefore survive better in multi-seeded than single-seeded fruits.

Survival figures above are conservative estimates, since any larva still alive within ripe fruits when I sampled them are susceptible to die in the gizzard of a bird eating its host fruit. Since birds do not usually ingest fruit until they are fully ripe, the latest larvae, not having completed their development before fruit ripening, most likely incur great mortality from avian frugivory. Among infested fruits, 75.6% of one-seed and 85.3% of multi-seed showed exit holes ($G = 3.04$, $P = 0.08$). This suggests that larvae developing in multi-seed fruits tend to emerge before, on average, than those in single-seed ones, and are therefore less susceptible to being fed upon by frugivorous birds. Differential timing of larval emergence may result from slower developmental rates and/or later oviposition in one-seed fruits. Whatever the cause, differences in emergence time would further enhance the differential within-fruit survival rates of larvae in differently-seeded fruits shown above. On the other hand, differences among fruit classes in larval food supply will most likely generate differences in size at pupation, which may further increase differential adult fly fitness.

Flies tend to destroy preferentially those seeds which are part of multiple seed packages. By selecting those fruits with larger amounts of larval food to oviposit, female flies improve offspring survival and differentially parasitize those plants producing predominantly multi-

seeded fruits. If *Berberis hispanica* plants have some control on seed number per fruit, as suggested by the abundant occurrence of aborted seeds, and this mechanism is under genetic control, flies may be strong selective agents on fruit seediness. Why are two-seeded fruits, which are subject to 30% more heavy predation, almost as abundant in the population as one-seed ones?

Seeds placed in one-seed fruit have a much greater probability of escaping predation (0.688) than do those in two-seed fruits (0.379), but also have a greater cost to the parent plant in terms of weight of pulp accompanying each seed (25.4 ± 5.8 mg and 16.6 ± 2.6 mg of pulp per seed in one- and two-seed fruits, respectively). Excessive pulp expenditure, as in one-seed fruits, reduces the total number of seeds produced. One-seed fruits are relatively safer from larval attack, but less seeds can be produced in fruits of this kind alone. One should thus expect the plant to balance the total number of seeds surviving fly attack against pulp expenditure (as well as the other forces operating on seediness), and this may be achieved by "manipulating" the distribution of seeds among fruit classes. Using the seed survival and pulp weight data presented above, and a projected figure of 12 mg pulp/seed for three-seed fruits (based on the variation with seed number of pulp/seed ratios observed in other southern Spanish plants with similarly-sized fruits; Herrera unpubl.), the estimated number of surviving seeds per 100 mg of pulp expenditure is 2.71, 2.28 and 1.00 for seeds placed in one-, two- and three-seeded fruits, respectively. These figures are linearly correlated with the proportions of differently-seeded fruits found in the sample analyzed, and the fit is remarkably good in spite of the small number of data points ($r = 0.99989$ and 0.9987, for original and arcsin-transformed percentage data, respectively; $N = 3$, $P < 0.05$). When aborted seeds present in fruits are considered in addition to full-sized ones, the percentages of one-, two- and three- or more seed fruits in the sample become 36.5%, 58.6% and 4.9%, respectively. The correlation of these figures with the expected number of surviving seeds per 100 mg of pulp investment is no longer significant ($P > 0.10$). These results tend to suggest that *Berberis hispanica* plants in Roblehondo probably adjust the distribution of seeds among fruit classes to increase the absolute number of surviving seeds through accounting simultaneously for predation risk and pulp costs. Among fruits which initiated two seeds, fly infestation affected 17.2% of those which aborted one seed ($N = 90$), and 63.4% of those which did not ($N = 183$) ($G = 53.5$, $df = 1$, $P \ll 0.0001$). Among fruits having initiated three or more seeds, percent predation for those which aborted one or more seeds ($N = 14$) and those which did not ($N = 9$) was 35.7% and 88.9%, respectively ($P = 0.016$, Fisher test).

If selective pressures from flies are one of the forces molding fruit seediness, as suggested above, then the average number of filled seeds per fruit may increase in absence of flies. Out of a total of 570 fruits examined from Nava de Pablo, 37.9% had one, 61.9% two, and 0.2% three filled seeds, which differ significantly from Roblehondo figures ($G = 35.6$, $df = 1$, $P \ll 0.0001$) in the predicted direction. A negligible fraction of fruits had aborted seeds (0.9%) or were attacked by seed-eating Lepidopteran larvae (0.9%). Importantly, the two populations studied are similar with regard to the proportion of fruits which initiate one, two and three or more seeds ($G = 0.03$, $df = 1$, $P = 0.86$). These results are consistent with the prediction above and strongly support the role of flies in determining fruit seediness through seed abortion-mediated plant responses.

Conclusion

Although the preceding analyses are based on a limited sample, the results strongly suggest that non-dispersal agents have the potential to become important selective agents in shaping plant features as intimately associated with the seed dispersal process as are the number of seeds and the amount of pulp per fruit. On the other hand, the results allow one to envisage complex evolutionary interactions among seed predators, plants and seed dispersers which have remained unexplored to date. Avian seed dispersers have been shown to select for larger pulp/seed weight ratios, and hence decreased seediness, in fruits (Howe and Vande Kerckhove 1980, Herrera 1981). If they behave similarly in the case of *B. hispanica* fruits, intricate feedback loops may exist, simultaneously involving fruit predators and seed dispersers, which will select synergistically against plant economy favouring an improvement of fruit design from the viewpoint of birds and an impairment for both plants and flies.

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