ARE TROPICAL FRUITS MORE REWARDING TO DISPERSERS THAN TEMPERATE ONES?

Although studies relating to avian frugivory date back to several decades (e.g., Wetmore 1914; Wood 1924; Schuster 1930), evolutionary implications of seed dispersal by birds have begun to be recognized only recently (Snow 1965, 1971; Janzen 1970; McKey 1975; Regal 1976). Most field investigations undertaken to elucidate reciprocal adaptations between plants and their dispersers have been conducted in tropical habitats (e.g., Snow 1965; Howe and Primack 1975; Foster 1977; Howe 1977; McDiarmid et al. 1977; Howe and Steven 1979; Howe and Vande Kerckhove 1979, 1980; Howe 1981; Frost 1981). Models and predictions have been elaborated on the basis of resulting field evidence which relate features of seed dispersal performed by the birds to aspects of plant fruiting strategy—crop size, fruiting phenology, fruit quality—(Snow 1965, 1971; McKey 1975; Howe and Estabrook 1977; Howe 1979). The quality of dispersal has been suggested to bear an important relationship to the nutritional reward offered by the plant in form of fruit pulp. Large seeds dispersed by "specialist" avian frugivores are apparently associated with pulps of high lipid and/or protein content, and this finding, among others, has been interpreted as evidence supporting close coevolutionary interactions between these large-seeded plants and their efficient, reliable dispersers (Snow 1970; Snow 1971; McKey 1975; Howe and Estabrook 1977). Most detailed tropical studies have analyzed systems of that kind (Snow 1962*c*; Snow 1970, 1972, 1977; Howe and Primack 1975; McDiarmid et al. 1977; Howe 1977; Howe and Vande Kerckhove 1980; Howe 1981) in which high-reward fruits were involved, while only a few studies deal with less "specialized" avian frugivores and their food plants (Snow 1962*a*, 1962*b*; Snow and Snow 1971). The notion may thus be construed that specialized, rich-fruit-based systems are particularly common in the tropics, as opposed to temperate habitats where environmental limitations have perhaps been responsible for the evolution of mostly "unspecialized," poor-fruit-based plant-bird systems (Snow 1971; Morton 1973; Howe and Estabrook 1977). Previous studies also appear to suggest that temperate fruits are much less rewarding to birds than tropical ones (Snow 1971; White 1974).

Several recent studies do not completely support the view that temperate bird-plant systems are unspecialized, and adaptations for efficient dispersal have also been demonstrated in these frugivore-poor habitats (Livingston 1972; Thompson and Willson 1979; Herrera 1981, 1982; Herrera and Jordano 1981). As nutritional reward contained in fruits has often been considered a variable indicative of coevolutionary properties of plant-bird systems, I will examine in this note how tropical and temperate fruits compare with regard to this variable. Especially, I try to show that (1) the potential profitability inherent to a fruit does not only depend on the quality of its pulp; (2) despite having far richer pulps, tropical fruits are probably not much more rewarding than temperate ones to birds feeding on them; and (3) an explanation for the richer pulps associated with large-seeded

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tropical fruits may not require the consideration of close coevolution between plants and dispersers.

In most studies, pulp quality has implicitly been equated with fruit profitability to the disperser, and the former variable has been the only one dealt with when analyzing the coevolutionary implications of fruit profitability (e.g., Snow 1962*c*, 1971; Morton 1973; White 1974; Howe and Estabrook 1977). I consider endozoochorous seeds in which the whole fruits are ingested by the disperser and the seeds are eventually regurgitated or defecated in undamaged condition (Van der Pijl 1972). The net measurable gain obtained by a disperser after ingesting and processing a single fruit unit is a certain amount of dry material $P(1 - W)$, where P is the fresh weight of any nutritive structure accompanying the seeds (e.g., pericarp or aril), and W is the percent water content of fresh pulp. In the fruit, this dry material is diluted by water and useless seed volume. The seeds pass through the digestive tract (or part of it, in the case of birds that regurgitate seeds) without providing nutrients, and during their transit time load the bird with extra weight and occupy a space which could accommodate nutritious material. It is obvious that seed volume must enter in the calculations of fruit profitability since it impairs the benefits derived from the pulp. Time of permanence of seeds within the digestive tract is a further variable affecting the profitability of fruits. Nevertheless, while seed volume is a feature inherent to the fruit itself, transit time is to the disperser involved, since the same fruit may be processed differently by various disperser species (e.g., Howe 1977; Herrera and Jordano 1981). I will now analyze fruit characteristics only, and return later to the point of transit time of seeds through the birds.

A measure of the relative yield RY of a fresh fruit in terms of dry nutritious material obtainable by the disperser may be described as

$$\mathrm{RY} = \frac{\mathrm{P}(1 - \mathrm{W})}{\mathrm{P} + \mathrm{n}\cdot\mathrm{s}} = \frac{(1 - \mathrm{W})}{1 + \mathrm{n}\cdot\mathrm{s}/\mathrm{P}} \tag{1}$$

where n = number of seeds per fruit and s = fresh weight of a single seed. RY is a profitability component indicative of how much dry material will be gained per weight unit of whole fruit ingested and processed. The overall profitability OP depends also on the nutritive quality d of the dry material eventually extracted from the fruit. It may be described by $\mathrm{OP} = \mathrm{RY} \cdot d$, where d denotes the relative richness (on a weight to weight basis) of dry pulp in some valuable substance (e.g., fat, protein), and OP is the quantity of such substance which will be recovered by the disperser after processing a weight unit of fresh fruit. This magnitude represents an estimate of the maximum amount of nutrients obtainable; actual profitability values will depend in every case on pulp digestibility and assimilative efficiency of the frugivore (see e.g., Westoby [1974] and Milton [1979] for discussions of profitability in vertebrate herbivores).

OP is made up of two distinct factors: a "chemical" component d, and a "design" or "aspect" component RY, the latter depending on seed/pulp weight ratio and water content of fresh pulp. It is then possible to envisage fruits differing in nutrient quality of pulps but having similar overall profitability owing to concurrent variation in RY values.

Values of RY, *d*, and OP for bird-dispersed fruits from neotropical habitats were gathered from the available literature and are listed in table 1. The *d* was taken as the relative richness of dry pulp in crude lipid and protein combined, the two apparently most relevant nutritional components in fruits' pulps (Snow 1971; McKey 1975; White 1974). Information necessary to compute RY was available for 21 species, whereas *d* values could be gathered for 41 species. Only for 15 species were *d* and RY figures simultaneously available thus allowing for the computation of OP. The nontropical area selected for comparison was Andalusia, in southern Spain, for which RY was obtained for 69 species, *d* for 56 species, and OP for 55 species of bird-dispersed plants based on my own unpublished data and information in Herrera (1982). Southern Spanish data are representative of plants occupying both lowland and montane mediterranean scrub and woodland habitats. Resulting figures for Spanish plants are shown in table 2, and the neotropical-Spanish comparison is presented in table 3.

As expected on the basis of previous comparisons (Snow 1971; White 1974), tropical fruits have pulps much richer in lipid-plus-protein content (*d*) than southern Spanish species, but they also differ markedly by having significantly lower values of "design" profitability (RY). The resulting overall profitability (OP), however, does not statistically differ between areas. This indicates that although tropical fruits are mainly *d*-profitable and temperate ones are predominantly RY-profitable, both groups of species have similar inherent potential profitabilities to dispersers in terms of dry weight of lipid-plus-protein obtainable per weight unit of fresh fruit ingested and processed. This result is not an artifact derived from many neotropical species having only partial data (table 1), for average *d*-figures were similar for species with complete and partial data (28.0% vs. 29.3%, $t = 0.2$, $P > .4$).

Assuming that the selective pressures associated with the coevolutionary process involving a plant and its dispersers are able to promote some modifications in OP-value of fruits, and that in most instances the trend will be one of increasing it (Herrera 1981; Howe and Vande Kerckhove 1980), then a plant's response to these selective pressures may be directed to increasing *d*, RY, or both (Herrera 1981, unpubl. MS). Variation in these parameters must primarily be limited by the combined action of three sets of factors relating to (1) seed load per fruit, (2) geometrical, scaling effects, and (3) fruit size.

Seed load.—Tropical fruits tend to have larger seed loads than temperate ones. In the sample of species dealt with here, mean dry weight of seeds per fruit (± 1 SE) for neotropical species in table 1 with available data is 505 ± 259 mg ($n = 15$, range 6–3,914 mg), while corresponding figures for southern Spanish species in table 2 are 74 ± 101 mg ($n = 69$, range 3.5–698 mg). These differences are mainly due to the addition of a set of large-seeded species in the neotropical sample which is absent from the temperate one. Since large-seeded tropical forest trees have most likely evolved seed size independently of their relationships with dispersal agents, seed size thus represents a constraining starting point for the evolution of fruit architecture (Snow 1971).

Scaling effects.—As it may readily be derived from expression (1) above, for low values of $n \cdot s$ (fruits with small seed loads), only very slight changes in P

TABLE 1

Nutritional Features of Fruits from Neotropical Bird-Dispersed Plants

Species	*d**	RY†	OP‡	Reference§
Anacardiaceae				
Tapirira guianensis	12	...	...	1
Apocynaceae				
Stemmadenia donnell-smithii	74.9	9.8	7.3	4
Araliaceae				
Didymopanax morototoni	45	...	...	2
Boraginaceae				
Cordia nitida	31.9	...	...	3
Burseraceae				
Dacryodes sp.	35	...	...	1
Protium tenuifolium	14.6	...	...	3
Tetragastris panamensis	4.8	28.1	1.3	3
Connaraceae				
Connarus panamensis	24.3	7.8	1.9	3
Rourea glabra	62.2	12.7	7.9	3
Lauraceae				
Cinnamomum elongatum	53	...	...	1
Nectandra salicina	51.8	13.0	6.7	5
Ocotea oblonga	30	...	...	1
Ocotea wachenheimii	48	...	...	1
Ocotea canaliculata	42	...	...	1
Leguminosae				
Schwarzia simplex	24.6	...	...	3
Loranthaceae				
Phoradendron sp.	58.5	...	...	3
Melastomaceae				
Miconia sp.	12.0	...	...	3
Mouriri parvifolia	10.0	37.4	3.7	3
Moraceae				
Cecropia exima	...	5.8	..	3
Ficus nitida	10.9	9.7	1.1	3
Ficus sp.	12.9	...	...	3
Ficus sp.	11.6	...	...	3
Musaceae				
Heliconia mouriri	49.8	...	...	3
Myristicaceae				
Virola nobilis	18.8	15.9	3.0	3
Virola sebifera	59.3	13.0	7.7	8
Virola surinamensis	65.6	...	...	9
Myrsinaceae				
Ardisia revoluta	12.9	10.1	1.3	6
Myrtaceae				
Eugenia nesiotica	7.5	9.0	.7	3

(*Continued*)

TABLE 1 (*Continued*)

Species	*d**	RY†	OP‡	Reference§
Ochnaceae				
Ouratea lucens	15.9	8.8	1.4	3
Olacaceae				
Heisteria concinna	35.1	...	...	3
Heisteria costaricensis	...	8.4	...	3
Palmae				
Bactris cuesa	52	...	...	1
Chamaedora wendlandiana	30.1	8.2	2.5	3
Jessenia oligocarpa	31	...	...	1
Morenia caudata	20.0	5.8	1.2	7
Pinanga kuhlii	...	8.7	...	3
Roystonea regia	11	...	...	3
Phytolaccaceae				
Phytolacca sp.	4.3	...	...	3
Rubiaceae				
Hamelia nodosa	15.2	...	...	3
Faramea occidentalis	21.4	...	...	3
Psychotria limonensis	...	8.6	...	3
Psychotria marginata	...	10.3	...	3
Rutaceae				
Stauranthus sp.	16.7	11.6	1.9	5
Sapindaceae				
Paullinia turbacensis	13.1	...	...	3
Verbenaceae				
Lantana camara	12.7	...	...	3
Zingiberaceae				
Renealmia strobilifera	...	10.9	...	3
Unidentified species	19.7	...	...	3

* Fat plus protein content of dry pulp (percent).

† "Design" profitability, as described in expression (1) in the text (percent).

‡ Overall profitability as described in the text (percent).

§ 1, Snow (1962*c*); 2, Snow (1971); 3, White (1974); 4, McDiarmid et al. (1977); 5, Snow (1977); 6, Foster (1977); 7, Snow (1979); 8, Howe (1981); 9, Howe and Vande Kerckhove (1980).

and/or W are sufficient to alter substantially the design profitability RY of the fruit, whereas above certain threshold values of seed load, very large changes in P and/or W would be necessary to promote even slight modifications in the RY value of the fruit. Similarly, the larger the $n \cdot s/P$ ratio of a fruit, the lower the upper limit set to RY by scaling effects alone (fig. 1). All else being equal, fruits with large relative seed loads would most likely tend to modify OP through changes in *d*, whereas fruits with small seed loads may change either *d* or RY (or any combination) to modify overall profitability. Very simply stated, it appears that fruits with small seed loads relative to total fruit weight have two alternative ways open to modify OP (RY- and *d*-way), whereas fruits with large seed loads have only the *d*-way available.

Fruit size.—Once a plant has evolutionarily "chosen" the way of being bird dispersed, it not only needs to evolve a set of attributes for it (a "syndrome"; Van

TABLE 2

NUTRITIONAL FEATURES OF FRUITS FROM SOUTHERN SPANISH BIRD-DISPERSED PLANTS

Species	*d*	RY	OP
Anacardiaceae			
Pistacia lentiscus	64.3	28.3	18.2
Pistacia terebinthus	63.2	21.7	13.7
Aquifoliaceae			
Ilex aquifolium	7.9	15.2	1.2
Araceae			
Arum italicum	8.8	13.3	1.2
Araliaceae			
Hedera helix	36.9	18.4	6.8
Berberidaceae			
Berberis hispanica	9.4	21.1	2.0
Caprifoliaceae			
Lonicera arborea	5.4	23.1	1.2
Lonicera etrusca	5.8	20.5	1.2
Lonicera implexa	5.2	22.5	1.2
Lonicera periclymenum	...	16.9	...
Lonicera splendida	5.0	21.4	1.1
Sambucus ebulus	...	16.4	...
Sambucus nigra	...	10.4	...
Viburnum lantana	...	16.7	...
Viburnum tinus	25.3	34.7	8.8
Cornaceae			
Cornus sanguinea	31.3	21.3	6.7
Cucurbitaceae			
Bryonia dioica	32.6	12.9	4.2
Cupressaceae			
Juniperus communis	20.5	29.2	6.0
Juniperus oxycedrus	13.0	38.5	5.0
Juniperus phoenicea	19.5	20.2	3.9
Juniperus sabina	19.6	30.9	6.1
Dioscoreaceae			
Tamus communis	7.3	8.1	.6
Empetraceae			
Corema album	8.0	6.6	.5
Ericaceae			
Arbutus unedo	6.6	33.2	2.2
Iridaceae			
Iris foetidissima	...	22.4	...
Lauraceae			
Laurus nobilis	60.6	22.9	13.9
Liliaceae			
Asparagus acutifolius	...	31.8	...
Asparagus albus	...	19.5	...
Asparagus aphyllus	...	17.8	...
Ruscus aculeatus	6.4	14.5	.9
Ruscus hypophyllum	...	5.2	...
Smilax aspera	7.4	13.1	1.0

(*Continued*)

TABLE 2 (*Continued*)

Species	*d*	RY	OP
Loranthaceae			
Viscum album	12.7	19.7	2.5
Viscum cruciatum	20.2	21.1	4.3
Myrtaceae			
Myrtus communis	5.7	17.3	1.0
Moraceae			
Ficus carica	5.8	...	...
Oleaceae			
Jasminum fruticans	12.2	16.5	2.0
Ligustrum vulgare	9.2	11.0	1.0
Olea europaea var. *sylvestris*	49.8	14.6	7.3
Phillyrea angustifolia	5.2	16.1	.8
Phillyrea latifolia	5.5	16.0	.9
Rhamnaceae			
Frangula alnus	...	10.1	...
Rhamnus alaternus	7.7	16.7	1.3
Rhamnus lycioides	6.0	23.4	1.4
Ziziphus lotus	3.5	30.6	1.1
Rosaceae			
Amelanchier ovalis	4.4	35.1	1.5
Cotoneaster granatensis	9.6	15.2	1.5
Cotoneaster integerrimus	...	17.0	...
Crataegus laciniata	5.6	19.4	1.1
Crataegus monogyna	4.8	25.3	1.2
Prunus mahaleb	6.0	12.8	.8
Prunus prostrata	8.7	10.8	.9
Prunus ramburii	4.2	24.2	1.0
Prunus spinosa	6.3	16.0	1.0
Rosa sp. (*canina* group)	7.1	29.0	2.1
Rosa sp.	5.9	27.0	1.6
Rubus ulmifolius	...	18.0	...
Sorbus aria	5.9	37.1	2.2
Sorbus aucuparia	6.2	24.8	1.5
Sorbus torminalis	4.8	38.3	1.8
Rubiaceae			
Rubia peregrina	15.1	12.1	1.8
Santalaceae			
Osyris alba	6.9	19.6	1.4
Osyris quadripartita	7.8	9.4	.7
Solanaceae			
Solanum dulcamara	...	11.6	...
Solanum nigrum	...	4.3	...
Taxaceae			
Taxus baccata	2.6	20.7	.5
Thymelaeaceae			
Daphne gnidium	10.5	9.3	1.0
Daphne laureola	6.7	10.6	.7
Ulmaceae			
Celtis australis	4.7	43.7	2.1
Vitaceae			
Vitis vinifera ssp. *sylvestris*	4.2	20.8	.9

NOTE.—Symbols as in table 1. Nomenclature follows Tutin et al. (1964–1980).

TABLE 3

COMPARATIVE SUMMARY OF NUTRITIONAL FEATURES OF FRUITS FROM TROPICAL AND NONTROPICAL BIRD-DISPERSED PLANTS

	d	RY	OP
Neotropical species	28.8 ± 19.3 (41)	12.1 ± 7.4 (21)	3.3 ± 2.7 (15)
Southern Spanish species	13.4 ± 14.9 (56)	19.9 ± 8.5 (69)	2.9 ± 3.6 (55)
Student's *t*	4.39	3.75	.39
df	95	88	68
P	<.0001	<.001	>.6

NOTE.—Mean ± 1 SD, number of species entering in the computations in parentheses. Symbols as in table 1.

der Pijl [1972]), but also has to match external fruit size to the gape width of available potential dispersers. I would thus hypothesize that the relative position of the seed size of a plant with respect to the modal class of gape widths in a habitat would be responsible for the way chosen by the plant to make its fruits worth feeding without impairing dispersal. In particular, large-seeded species whose seeds are well to the right of the modal class of gape widths frequency distribution should tend to keep pericarp thickness to a minimum so as not to displace external fruit size further from the modal class of gape widths. Nevertheless, the possibilities of pericarp thickness among which the plant may select probably decrease precipitously when seed size approaches the right-hand tail of gape-size distribution. Assuming that seed size may not be altered by plant-disperser interactions, a large-seeded plant may at best not increase fruit size excessively, but it may never be able to reduce fruit size below individual seed size. Consequently, large-seeded plants probably cannot allow themselves to add much pulp to seeds, because the resulting large fruit either would not attract dispersers of adequate size or would facilitate the detrimental work of fruit thieves which exploit the pulp and leave the seeds in situ. *Tityra semifasciata* (Cotingidae), a reliable, "specialized" frugivore according to Howe (1977), behaves as a legitimate disperser when it feeds on the arillate seeds of *Casearia corymbosa* (10 × 9 mm, Howe 1977), but when feeding on *Virola surinamensis* arillate seeds (20 mm long), it becomes a fruit thief by dropping seeds below the parent tree and ingesting only the nutritious aril (Howe and Vande Kerckhove 1980). *Casearia* trees were visited by as many as 20 species of legitimate avian dispersers, while the larger-fruited *Virola* trees attracted only six species. In a temperate habitat, Herrera and Jordano (1981) have also documented a determinant role of fruit size to the constitution of the disperser assemblage of *Prunus mahaleb*. Fruit size is not, however, the only variable affecting the disperser assemblage of a fruiting plant. *Virola sebifera* fruits have far smaller seeds than those of *V. surinamensis*, but attract the same species (Howe 1981). The fruits of *Tetragastris panamensis*, primarily dispersed by monkeys, attract more birds than *V. sebifera* or *surinamensis* (Howe 1980), in spite of the fact that the arils and seeds are much larger than those of *V. sebifera*.

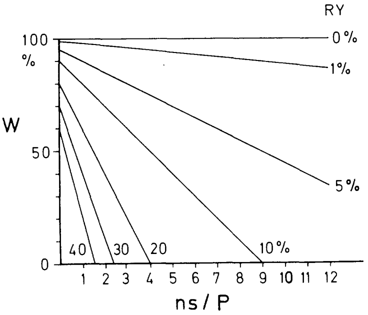

FIG. 1.—Variation in the "design" profitability RY of fruits with changes in percent water content of pulp W and the seed/pulp weight ratio ns/P. The graph was obtained by plotting expression (1) in the text for various RY values. It can be seen that (1) fruits with low ns/P ratios may potentially become highly RY-profitable even while possessing very watery pulps, (2) the maximum possible RY-profitability allowed to a fruit decreases steadily as ns/P increases, and (3) for fruits lying close to the left extreme of the horizontal axis, important changes in RY may be brought about with very slight alterations in W, but as fruits approach the right-hand extreme, changes in W have virtually no effect on RY. All this indicates that the potential for modification of RY decreases substantially as relative seed load per fruit increases.

These considerations point to the conclusion that the rich pulps commonly found in tropical fruits are not necessarily related to close coevolution between large-seeded plants and their "specialized" dispersers (Snow 1970; Snow 1971; McKey 1975; Howe and Estabrook 1977). Simple scaling effects resulting from the increase in seed size of tropical bird-dispersed plants relative to nontropical ones limit the range of possibilities available to fruit architecture. These possibilities are further limited by the available range of disperser gape widths relative to seed size. Temperate plants, being mostly small seeded, have perhaps a broader potential range of alternatives to build up the reward section of their relatively small-sized fruits, since both RY- and *d*-variation appear to be allowed. These geometrical and biological constraints do not deny at all, however, the possibility of birds and plants becoming selective agents on each other and mutually inducing evolutionary changes (coevolution, in the sense of Janzen [1980]), but rather they may serve to establish the feasible ways to coevolution. As suggested by Snow (1973) for some Cotingidae, the disproportionately wide gape of some tropical frugivores probably constitutes an adaptation to feeding on large-seeded fruits.

I have been so far concerned with the potential profitability inherent in each kind of fruit, regardless of the procedure used by the dispersers to handle seeds. Transit time of seeds through the bird may change whether seeds are regurgitated or defecated, thus modifying the detrimental effect of seed processing. In southern Spain, *Erithacus rubecula* (body wt 17 g) regurgitates seeds within 6–12 min after fruit ingestion, whereas the similarly sized *Sylvia atricapilla* (18 g) takes between 15–25 min to defecate seeds after feeding (Herrera, unpubl. MS). *Phainopepla nitens* (27 g), a North American frugivore, takes 12–45 min to defecate seeds after feeding (Walsberg 1975). The Central American cotingid *Procnias tricarunculata* (around 150 g) regurgitates seeds about 15 min after feeding (Snow 1977), while the European *Turdus merula* (90 g) may take up to 6 h to defecate seeds (Herrera, unpubl. MS). These data suggest shorter processing times among regurgitating birds, but this is not to say that seeds are not ballast to birds which regurgitate seeds. The latter have been shown to select fruits on the basis of minimizing ingestion of seed mass when feeding on the fruits of *Virola surinamensis* (Howe and Vande Kerckhove 1980), despite the extremely high nutritive value of the pulp, in much the same manner as defecating nontropical birds do when feeding on poor-pulp temperate fruits (Herrera 1981, unpubl. MS). Until physiological studies are conducted on the assimilative efficiency of regurgitating versus defecating birds, it is not possible to discuss on a firm basis the possible improvement in nutrient yield obtained by the former group, although some improvement is likely to occur.

If the two seed handling procedures were unequally common in the two geographical areas compared here, it would imply that the similarly rewarding fruits of both regions could eventually be exploited differentially by their respective disperser assemblages. Among Neotropical frugivores, species in the Cotingidae, Tyrannidae, Trogonidae, and Ramphastidae regurgitate seeds, while most or all of the Pipridae, Turdidae, and Thraupidae usually defecate them. In southern Spain there are at least four important small frugivores which regurgitate all but the smallest seeds (*Erithacus rubecula, Ficedula hypoleuca, Phoenicurus phoenicurus, P. ochruros*), while none of *Sylvia* and *Turdus* species is known to regurgitate. Although it is impracticable to compare their relative proportions, the two seed-processing modalities are present on both areas, including an extremely efficient seed-processor (*E. rubecula*) in southern Spain. But even in the likely case of the regurgitating habit being relatively most common among Neotropical frugivores as a whole, this would only indicate that birds there are more efficient in harvesting nutritious material from the fruits, but not that Neotropical fruits are offering intrinsically better rewards.

Results presented in this note, showing similar inherent profitability to tropical and nontropical fruits and suggesting alternative, noncoevolutionary explanations to the relationship between the large seed loads and high pulp quality characteristic of tropical fruits must be taken as provisional until further studies of fruit quality are conducted in more geographical areas using larger samples of species. While my Spanish sample probably represents well above 80% of the regional bird-dispersed flora, the Neotropical species list is only a tiny fraction of the enormous existing total. In addition, the tropical sample used here is almost certainly biased towards species with the richest pulps. Species in the Palmae and Lauraceae are particularly well represented, while ubiquitous, very diverse families as Rubiaceae and Melastomaceae are at an obvious disadvantage. On the other hand, further aspects not accounted for here that may substantially affect actual fruit profitability include pulp content in undigestible and toxic substances (Janzen 1978). These limitations of both the approach and the Neotropical sample I have used lead me to deliberately avoid discussing further my results, despite the fact that some important questions remain obviously unanswered as, for instance, What is the evolutionary basis for the similar overall profitability inherent to tropical and nontropical fruits? I wish not to add further to the existing hypotheses and generalizations before more hard data on the quality of fruits and the processing efficiency of frugivores has been gathered. I agree with Howe (1979) in that relevant intuition must now await expanded experience.

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