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SEED DISPERSAL BY ANIMALS: CONTRASTS WITH POLLEN DISPERSAL, PROBLEMS OF TERMINOLOGY, AND CONSTRAINTS ON COEVOLUTION

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Recent thinking about seed dispersal and the coevolution of fruiting plants and frugivores has been strongly influenced by ideas developed through the study of pollen dispersal by animals. Analogies are commonly drawn between the two systems (Howe 1977; Van der Pijl 1972; Howe and Primack 1975; Howe and Vande Kerckhove 1979; Howe 1979; Howe and De Steven 1979; Howe 1980). Both systems represent coevolved relationships of mutual benefit to plants and animals that involve the dissemination of pollen or seeds and the provision by the plant of some incentive such as nectar or fruit. The evolution of high degrees of mutual dependence and morphological and behavioral specialization, evident in some pollination systems, is assumed also to be likely in certain seed dispersal systems (Howe and Primack 1975; McKey 1975; Howe 1977; Howe and Estabrook 1977). A rich array of evocative metaphors currently used in studies of plant-frugivore interactions ("loyalty," "theft," "reliability," "faithfulness," "reward," and so on; see McKey 1975 and Howe and Estabrook 1977) reflects conceptual biases apparently derived in part from implicit and explicit analogies with pollen dispersal. Although such terms are sometimes useful, they may cloud the true nature of fruit-frugivore interactions.

Pollen and seed dispersal are fundamentally dissimilar, particularly in most characteristics likely to influence choice of diet and foraging itineraries by animal vectors, and patterns of production of pollen and fruit by plants. The purpose of this paper is threefold: (1) to outline clearly the relevant differences between pollen and seed dispersal, (2) to indicate some of the problems of using terminology borrowed from studies of pollen dispersal to describe seed dispersal systems, and (3) to consider the factors that may explain the virtual absence of obligate mutualisms in seed dispersal systems (Howe and Vande Kerckhove 1979). Because of our greater familiarity with avian frugivores and their importance in theoretical and empirical studies of seed dispersal, most of our references deal principally with birds. Future work on seed dispersal by mammals, ants, reptiles, and fish may offer new insights.

THE THEORY OF FRUIT-FRUGIVORE COEVOLUTION

Snow (1971) first considered the consequences of evolutionary interactions between fruiting plants and the frugivores that disperse their seeds and recognized the unique attributes of fruit as a food resource. Relative to other "prey," fruit has evolved to be generally accessible, conspicuous, and easily digestible in order to attract seed dispersers (Snow 1971). Following Snow's contribution, McKey (1975) proposed a model of plant-frugivore coevolution to explain the variety of strategies plants use to disperse their seeds in which he introduced the concept of dispersal quality. At one extreme, some plants produce many small, nutritionally poor fruits that attract a wide variety of "poor quality" dispersers. Alternatively, others produce a smaller number of large, nutritionally superior fruits whose seeds are dispersed by a limited number of species delivering "high dispersal quality." Quality refers to seed size carried and the probability that a seed removed from a plant is deposited in viable condition in a site suitable for germination and establishment (McKey 1975). A number of recent studies, both theoretical (Morton 1973; Howe and Estabrook 1977; Howe 1979; Thompson and Willson 1979; Fleming 1979) and empirical (Smith 1975; Howe 1977; McDiarmid et al. 1977; Thompson and Willson 1978; Howe and De Steven 1979; Howe and Vande Kerckhove 1979; Howe 1980; Howe 1981; Snow 1981) have refined hypotheses, evaluated some predictions, and provided observations on fruit removal rates and behavior of frugivores at fruiting trees.

Central to current theory is the proposition that frugivores differ in behavioral and ecological traits that affect their suitabilities as seed dispersers. If so, under certain circumstances (e.g., predictable ecological requirements for seeds) natural selection is expected to lead to the mutual interdependence and tight association of individual plant species with "one particularly effective disperser" (Howe 1977), or a small number of obligate frugivores (McKey 1975; Howe and Primack 1975; Howe and Estabrook 1977). However, empirical studies have generally failed to discover either highly coevolved frugivores or plants adapted to exclude all but a single disperser, as in some (though much fewer than generally appreciated) pollen dispersal systems. The lack of plant-frugivore counterparts to specialized pollination systems, such as orchids (Dressler 1968; Dodson 1975) or *Dalechampia* (Armbruster and Webster 1979) and euglossine bees, or yucca species and the moth *Tegeticula* (Powell and Mackie 1966), is striking (see also Galil 1977; Sazima and Sazima 1978; Thien 1969). The majority of studies of birds, at least, have documented instead a tremendous diversity of frugivores at fruiting trees (Eisenmann 1961; Land 1963; Willis 1966; Diamond and Terborgh 1967; Jenkins 1969; Leck 1969; Haverschmidt 1971; Cruz 1974; Wheelwright et al., in prep.).

Not only do many bird species feed on the fruit of a single plant species, but also they may represent up to 13 families (McDiarmid et al. 1977). Even the "specialized," high reward fruits of some Lauraceae (McKey 1975) may have their seeds dispersed by more than 17 species of birds from at least eight families (Wheelwright, in prep.). Morphologically as well as taxonomically, birds feeding on the fruits of the same tree may be quite different (Ricklefs 1977; Wheelwright et al., in prep.).

The discovery of assemblages of many species of diverse frugivores, rather than limited associations, spawned a deprecating terminology to refer to species presumed to be poor dispersers: "opportunists, exploiters" (McKey 1975), "fruit thieves" (Howe and Estabrook 1977), and "parasites" (Janzen 1977). Such metaphors reflect the expectations of the theory more than they do the actual effects of the frugivores; data do not yet exist to evaluate accurately the effectiveness of dispersal by different species. Despite the fact that many studies purport to deal with seed dispersal, most report only observations on who removes fruit, how regular they are as visitors, and, in some cases, whether or not they destroy seeds. The above terminology obscures the fact that frugivores represent a continuum in terms of the number of seeds each species deposits in suitable sites and the probability that it gives an individual seed favorable treatment.

SEED DISPERSAL VERSUS POLLEN DISPERSAL

Pollen dispersal differs from seed dispersal in several fundamental respects that prevent comparable precision in seed dispersal (table 1). First, pollen has a very specific "target," the stigma of a conspecific flower. These flowers are usually easily recognized because of their distinctive colors, scents, and morphology. In contrast, a seed's "objective," a site suitable for germination, establishment, and ultimately reproduction, is more difficult to characterize in space and time. Appropriate sites for seeds have few distinguishing features perceptible by frugivores, although frugivores may preferentially frequent certain habitat types. On a gross scale, some habitat types (flood plains, riverbanks) may be predictable (Howe and Estabrook 1977), but within them sites for seeds are not. Moisture, sunlight, soil nutrients, seed and seedling predators, herbivores, fungal associates, allelopaths, and other subtle factors determine whether a site is a good one for a seed. Moreover, conditions may easily change and characteristics of a site at the time a seed is deposited may be poor indicators of future quality.

Second, pollen dispersal differs from seed dispersal in the temporal availability of suitable sites. Anther dehiscence and pollen dispersal are coordinated with stigma receptivity in synchronously flowering populations, but opportunities for successful seedling establishment (e.g., light gap formation) may occur randomly in time and space (Poore 1967; Knight 1975; Hartshorn 1978).

Third, flowering plants benefit from habitat specificity and sequential visitation of conspecific plants by their pollen vectors because visits to flowers of other species may result in pollen transfer to inappropriate "targets" and consequent waste of pollen. A similar advantage has been suggested for fruiting plants when host-specific frugivores carry seeds to the habitats occupied by conspecific plants (Howe and Primack 1975; Howe and Estabrook 1977). Yet, if species-specific seed and seedling predation is greater near conspecific trees (Janzen 1970; Connell 1971), selection should not favor specialized diets and movements by dispersers between trees of the same species. Moreover, the presence of an adult conspecific plant is not necessarily evidence of an appropriate site for a seed, particularly in the case of shade-intolerant plants, which comprise the majority of canopy species in some tropical forests (Hartshorn 1978) where up to 90% of plant species are animal dispersed (Frankie et al. 1974). Once a tree reaches the canopy, its shade

TABLE 1
GENERAL DIFFERENCES BETWEEN POLLEN DISPERSAL AND SEED DISPERSAL

	Pollen Dispersal	Seed Dispersal
Suitable site for dispersal	stigma of conspecific flower	site appropriate for germination and establishment
Characteristics of site as predictors of suitability	distinctive: color, shape, etc.; often apparent at a distance	unpredictable: many subtle factors involved; present characteristics often poor indicators of future quality
Temporal pattern of suitable sites	synchronous with pollen dispersal	unpredictable: often independent of habitat type or phenology of conspecific plants
Advantage for plant of diet and habitat specificity by animal vector	high: most pollen lost if visits to other species of plants intervene between visits to conspecifics	low: presence of adult conspecific plant often an unsuitable site because of density-dependent seed predation or different habitat requirements of seed and tree
Ability of plant to direct animal vectors to suitable site	high: incentives (nectar, pollen, etc.) provided at suitable site	low: no incentive for frugivore to deposit seed in favorable site; seed represents heavy and space-consuming ballast that is profitably discarded as quickly as possible.

has changed the favorable microhabitat that allowed its own establishment as a seed and seedling.

Perhaps the most fundamental distinction between pollen dispersal and seed dispersal systems is the ability of the plant to manipulate the behavior of the animal vector. Flowering plants can control pollinators' movements to a greater extent by providing nutritional (Baker and Baker 1975) and reproductive (Dodson 1975) incentives at the appropriate site (flower) for pollen transfer. There is, in effect, "payment upon delivery." There is no similar incentive for seed dispersers to drop seeds in appropriate places. Fruiting plants suffer the costs of "advance payment": Once frugivores have stripped seeds of their nutritious fruit, there is no further advantage in carrying the "ballast" (Snow 1971) which, unlike pollen, may be heavy and space consuming. Hence, rapid regurgitation or defecation of the seed benefits the disperser, irrespective of its advantage to the plant. For both pollinators and frugivores, the delayed return benefits of "altruistic" pollen or seed dispersal (such as future increases in local flower or fruit availability) may be discounted (see also Howe and Estabrook 1977).

Given these limitations, to what degree might plants be able to manipulate their potential seed dispersers? It has been suggested that morphological, chemical, and phenological characteristics of plants and their fruits may induce frugivores to leave fruiting trees after consuming few fruits. Among the conceivable incentives are limited levels of fruit production (Howe 1977), mild toxicity, nutritional

inadequacy of fruits, bulky or slowly digestible fruits, and structural modifications of the plant to increase the risk of predation. Whether these are "adaptations" or consequences of other life history demands (defense against fungal, bacterial, or insect fruit and seed parasites; limitations of energy or nutrients; photosynthetic considerations, etc.) remains uncertain at this point. In any event, plants cannot direct the dispersal of seeds to a particular location with a degree of exactness comparable to pollen dispersal, though possibly they could favor animal vectors with particular behaviors (Docters van Leeuwen in McKey 1975), habitat preferences, or probabilistic patterns of seed dispersal (Smith 1975; Howe 1977; Howe and Primack 1975).

Thus, environmental unpredictability and the difficulty of directing seed vectors, even if suitable sites were "knowable," constrain seed dispersal systems from achieving the precision and specialization of some pollen dispersal systems.

"SPECIALIZATION" IN PLANT-FRUGIVORE INTERACTIONS

Just as comparisons with pollen dispersal have led to unrealistic expectations about coevolved mutualisms in seed dispersal systems, imprecise and inconsistent terminology has affected theoretical developments and interpretation of empirical observations. For example, the term "specialist" is used frequently with respect to fruit-frugivore interactions. Basically the term refers to the use of only a portion of the total array of available resources. No organism is a pure generalist, using all potential resources in proportion to their availability, but, because species differ in the extent to which they are selective in resource use, the term "specialist," even though it is inevitably imprecise, is useful for comparing species.

A first source of confusion arose because the degree to which a frugivore should be considered a "specialist" has been assessed by different criteria: being totally or mostly frugivorous (Snow 1971); feeding only fruit to its nestlings ("total frugivory"; Morton 1973); relying solely on fruit as its source of protein and lipids (McKey 1975); and being an animal that is "totally dependent on fruit for food for at least part of its life and which invariably voids or regurgitates seeds in viable condition" (Howe and Estabrook 1977, p. 818). Snow (1981) defines a specialist in terms of the quality and size of the fruits it eats. The bearded bellbird (*Procnias averano*) is often cited as the archetypal "specialist" (McKey 1975), despite the fact that it actually feeds on at least 40–50 species of fruit (Snow 1970) and probably insects and lizards as well (based on personal observations of its congener *P. tricarunculata* and other tropical frugivores). All of the above notions have value, but the use of a single term to refer to such disparate characteristics is certain to foster continued confusion. It would be preferable to use more precise terms to refer to particular patterns of resource use, such as "principally frugivorous." Moreover, the term "specialist" is totally inappropriate when applied to characteristics unrelated to resource use, such as dispersal quality.

A second problem arises with respect to the concept of a "specialized dispersal system." Specialization in plant-animal mutualisms has two components that must be distinguished. A fruiting plant, for example, may specialize with regard to its seed dispersers: Its seeds may be principally dispersed by only one or

a few of the array of potential frugivores. A fruit-eating animal, in turn, may be a specialist by restricting the major part of its diet to a small subset of the fruits available. In principle, therefore, a plant could specialize on a few generalist dispersers, just as a frugivore could specialize on a plant dispersed by many species. Moreover, there is no a priori reason to expect a strong correlation between the degree of specialization and the importance of a plant to a frugivore and vice versa. A frugivore may be very important to a plant in a situation where neither the plant nor the frugivore is a specialist (e.g., the tree *Casearia corymbosa* [= *C. nitida*] and the masked tityra, *Tityra semifasciata*; Howe and Primack 1975; Howe 1977; also Noble 1975).

Pollen and seed dispersal systems differ in the extent to which plants benefit from specialization, either in terms of being dispersed by a limited number of potential dispersers or attracting diet-specific animal vectors. In the case of flowering plants, entrained pollinators reduce the incidence of hybridization and wasted investment in lost pollen and inviable seeds, and increase the amount of pollen delivered to suitable sites. Pollination by species-specific vectors allows the persistence and reproduction of plants when population densities are low (Baker and Hurd 1968; Janzen 1971). Because of the relative precision of pollen transfer, natural selection can favor the evolution of complex flowers that exclude or discourage organisms unlikely to transfer pollen to conspecific stigmas with little adverse effect on pollination success. Not surprisingly, there are examples of flowers that attract only one or a few pollinators with narrow diets ("specialize on specialists"; see references above).

The potential values to plants of having only a few kinds of seed dispersers depend on both treatment of seeds and the way they are deposited into the environment. If only a single frugivore species regularly visits a plant, most of the plant's seeds receive similar treatment. Either seeds will be regurgitated or, if they pass through the digestive tract, they will encounter similar chemical and physical conditions (McKey 1975). Therefore, an optimal seed coat just sufficient to withstand the abrasion received by the seed in the gut of the frugivore, but not so tough as to inhibit subsequent germination or cause waste of resources in the construction of unnecessarily strong coats, can evolve. Birds that rely on fruits for all or nearly all of their nutritional needs are believed to have soft-lined gizzards (McKey 1975), and many of them regurgitate seeds. However, it is likely that soft-lined gizzards evolved to avoid digestion of toxic, thin-coated seeds rather than to provide gentle treatment to the seeds, and regurgitation is advantageous because it quickly reduces the indigestible ballast carried by the frugivore.

In general, the smaller the number of species of frugivores that visit a plant species, the fewer the habitat types in which its seeds are likely to be deposited. However, within those habitats, suitable sites for seed germination and seedling establishment may arise unpredictably. Because of seed dormancy or seedling longevity, sites may be occupied long before they arise (Howe 1980). Therefore, unless there are strong temporal correlations between the sites visited by a particular disperser and the present or future availability of suitable sites, the potential advantage of having only a restricted set of seed dispersers may not be realized (Howe 1977).

Set against these possible advantages of restricting the array of frugivores regularly visiting a plant, there are a number of advantages likely to be associated with attracting many kinds of dispersers. First, the larger the number of species of frugivores, the greater the number of dispersing individuals and the larger the number of fruits that can be removed from the tree per day (Snow 1971). Since fruits may often rot on trees or fall to the ground without having been consumed (personal observation; Howe 1981), there are often situations in nature when having more visitors would probably be beneficial.

Second, a fruit capable of being dispersed by a variety of frugivores is not limited to the habitat or general geographical range of any single disperser (a restriction in some pollination systems; Baker and Hurd 1968) and can expand its distribution to colonize new sites (Hamilton and May 1977).

Third, plants that rely on many species to disperse their seeds may have a lower probability of extinction if a single disperser becomes extinct or becomes very rare (Howe 1977; Howe and Vande Kerckhove 1979; Temple 1977; Gilbert 1980). However, the evolution of such "bet-hedging" strategies has yet to be supported by genetic models of natural selection at the level of the individual (Slatkin and Maynard Smith 1979). High rates of population turnover, probably even greater in the tropics where many species have low population densities and poor dispersal abilities (Willis 1974), may mean that fruiting plants are rarely in association long enough with specific frugivores to evolve tight obligate mutualisms even if they were favored over the short term.

Fourth, even though the mean probability of seed survival might be lower in seed distributions produced by dispersers of many species than in distributions produced by a single high quality disperser, natural selection could favor attracting many dispersers rather than a single one (fig. 1). Whether or not the right-hand tail of the seed distribution curve generated by many dispersers lies further to the right than that generated by a single disperser depends, of course, on the relative availabilities of dispersers and on their behavior. But since a tree may produce hundreds to millions of seeds during its lifetime, each with an extremely low probability of survival (given the fact that each plant leaves, on average, one offspring in an equilibrial forest), counting on a single disperser may be analogous to Williams' (1975) assessment of asexual reproduction: the multiple purchase of the same lottery ticket.

Unfortunately, testing this hypothesis directly is extremely difficult. Of the many seeds produced, finding the surviving seedlings is difficult. Knowing their parents and their dispersers seems almost hopeless. Although the probability of survival of any one seed is extremely low, whether or not the possibility of improving that probability is favored by natural selection depends on the value of alternative uses of energy by the plant. For adult plants that have reached the canopy or their normal full size, alternative uses of energy or nutrients should normally have very low marginal values, favoring heavy investments in reproduction even when the marginal value of increments to reproductive investments are as low as they normally must be for most plants. The real meaning of "waste" in seed dispersal (Howe 1980) is therefore unclear.

Viewing the problem from the point of view of frugivores also suggests that under most circumstances eating a variety of fruits, plus animal foods as well,

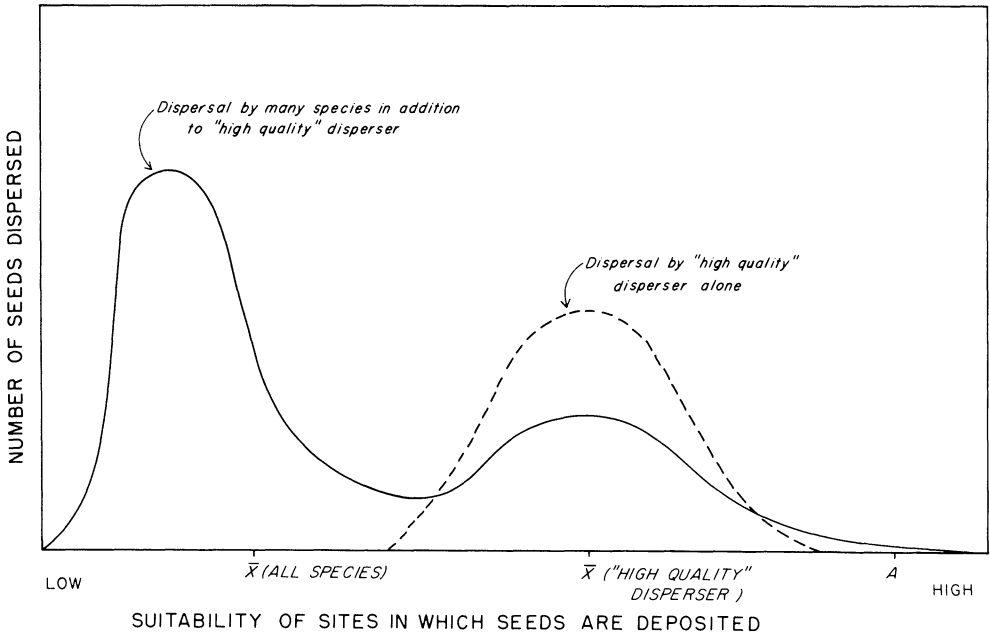


FIG. 1. Suitability of seed dispersal by a wide assemblage of dispersers (solid line), versus by a single "high quality" disperser (dashed line). If only those seeds deposited in the best sites (to the right of point A) are likely to survive, natural selection will favor the attraction of a diverse disperser assemblage in spite of its lower mean dispersal quality (cf. Williams 1975).

should normally be favored. Very few plants fruit throughout the year, and few are common in more than a limited part of their range. Moreover, most frugivores (with the exception of ants) are moderate-sized, relatively long-lived organisms that cannot package their annual cycle within a single fruiting season the way that many pollinators do. Not surprisingly, a number of large, principally frugivorous birds undergo marked seasonal movements during the year in response to local variations in fruit abundance (personal observation). Few dispersers are constantly reliable in the sense of McKey (1975) and Howe and Estabrook (1977).

Also, frugivores that may provide high quality dispersal at one time of the year may not do so at other times. The obligately frugivorous oilbird (*Steatornis caripensis*) roosts and nests in caves where most of the seeds it ingests are deposited (Snow 1962); bellbirds and manakins typically drop seeds beneath display perches during the breeding season (personal observation). Although they probably give all seeds gentle treatment, they are usually low quality dispersers at such times in terms of the sites where they deposit seeds.

CONSTRAINTS ON COEVOLUTION

We have argued that finely tuned mutualistic relationships in seed dispersal systems should be rare for the following reasons: (1) the inability of the plant to provide incentives for precision in seed dispersal; (2) the relatively small dif-

ferences among frugivores in seed dispersal quality; (3) the unpredictability and difficulty of recognition of suitable targets for seeds; (4) the potential advantages of having a broad assemblage of dispersers; and (5) the nature of life cycles of frugivores. There may also be evolutionary constraints on developing a restricted assemblage of seed dispersers (cf. Janzen 1977). For example, in Costa Rica's lower montane wet forest, both mountain robins (*Turdus plebejus*) and white-throated robins (*T. assimilis*), as well as many other species, feed on lauraceous fruits. The habitat preferences and foraging patterns of the two species differ markedly (personal observation). They may also differ in some measure of dispersal quality, yet it is difficult to imagine what adaptations a plant could use to exclude the poorer disperser without barring its morphologically similar congener as well. Classes of dispersers could be favored by altering fruit size (McKey 1975; Howe and Estabrook 1977), height of presentation (L. Best, in prep.), firmness of attachment, color, nutrition and many other features. These traits, however, are likely simply to reduce the diversity of visitors (possibly excluding some good dispersers), not to limit it to a single species.

Equally important may be the influence of spatial heterogeneity and gene flow (Howe and Vande Kerckhove 1979). Geographical regions differ in the proportion of habitat types and the pool of available dispersers. Even over relatively short distances totally different frugivores may feed on the fruits of the same tree species. Thus, if there is gene flow between populations of a tree species, it may not evolve adaptations to exclude poor dispersers in one area because the same tree in another place is visited by a different group of birds. Gene flow probably constrains coevolution of one-to-one mutualisms in pollination systems as well.

Under what conditions would one expect to find highly coevolved mutualisms between fruiting plants and frugivores? Two accounts document obligate mutualisms (from the plant's perspective; Rick and Bowman 1961; Temple 1977). Interestingly, both of these associations occur on islands, where environments are relatively uniform, faunas are impoverished, and populations are isolated from the homogenizing influence of gene flow.

SUMMARY

Theoretical and empirical research on frugivory and seed dispersal has been influenced by concepts derived from the study of pollination. In particular, explicit and implicit analogies between seed dispersal and pollen dispersal have led to the expectation, under certain conditions, of the evolution of obligate, species-specific relationships between fruiting plants and the animals that disperse their seeds. The two systems differ in important respects, however. Plants benefit by directing pollen dispersers to a definite, recognizable "target," a conspecific flower, and they can provide incentives at flowers which serve to attract potential pollinators. In effect, there is "payment upon delivery" of the pollen. In contrast, for seeds the target (an appropriate site for germination and establishment) is seldom readily discernible, and dispersal beneath a conspecific plant may actually be undesirable. Another important difference is that frugivores are "paid in advance." Because of these differences and others, the outcomes of coevolution

of fruiting plants and frugivores are expected to be different than those of flowering plants and flower visitors. There are therefore problems with drawing analogies between the two systems and using terminology derived from studies of pollination to design and interpret studies of seed dispersal.

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LITERATURE CITED

- Armbruster, W. S., and G. L. Webster. 1979. Pollination of two species of *Dalechampia* (Euphorbiaceae) in Mexico by euglossine bees. *Biotropica* 11:278–283.
- Baker, H. G., and I. Baker. 1975. Studies of nectar constitution and pollinator-plant coevolution. Pages 100–140 in L. E. Gilbert and P. H. Raven, eds. *Coevolution of animals and plants*. University of Texas Press, Austin.
- Baker, H. G., and P. D. Hurd. 1968. Intrafloral ecology. *Annu. Rev. Entomol.* 13:385–414.
- Connell, J. H. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. Pages 298–312 in P. J. den Boer and G. R. Gradwell, eds. *Proceedings of the Advanced Study Institute on dynamics of numbers in populations*, Oosterbeek, 1970. Centre for Agricultural Publishing and Documentation, Wageningen.
- Cruz, A. 1974. Feeding assemblages of Jamaican birds. *Condor* 76:103–107.
- Diamond, J. M., and J. W. Terborgh. 1967. Observations on bird distribution and feeding assemblages along the Rio Callaria, Department of Loreto, Peru. *Wilson Bull.* 79:273–282.
- Dodson, C. H. 1975. Coevolution of orchids and bees. Pages 91–99 in L. E. Gilbert and P. H. Raven, eds. *Coevolution of animals and plants*. University of Texas Press, Austin.
- Dressler, R. L. 1968. Observations on orchids and Euglossine bees in Panama and Costa Rica. *Rev. Biol. Trop.* 15:143–183.
- Eisenmann, E. 1961. Favorite foods of Neotropical birds: flying termites and *Cecropia* catkins. *Auk* 78:636–638.
- Fleming, T. H. 1979. Do tropical frugivores compete for food? *Am. Zool.* 19:1157–1172.
- Frankie, G. W., H. G. Baker, and P. A. Opler. 1974. Comparative phenological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. *J. Ecol.* 62:881–919.
- Galil, J. 1977. Fig biology. *Endeavour* 1:52–56.
- Gilbert, L. E. 1980. Food web organization and the conservation of neotropical diversity. Pages 11–34 in M. E. Soulé and B. A. Wilcox, eds. *Conservation biology*. Sinauer, Sunderland, Mass.
- Hamilton, W. D., and R. M. May. 1977. Dispersal in stable habitats. *Nature* 269:578–581.
- Hartshorn, G. S. 1978. Tree falls and tropical forest dynamics. Pages 617–638 in P. H. Tomlinson and M. N. Zimmerman, eds. *Tropical trees as living systems*. Cambridge University Press, Cambridge.
- Haverschmidt, F. 1971. Large numbers of birds exploiting a fruit tree in Surinam. *Wilson Bull.* 83:104–105.
- Howe, H. F. 1977. Bird activity and seed dispersal of a tropical wet forest tree. *Ecology* 58:539–550.
- . 1979. Fear and frugivory. *Am. Nat.* 114:925–931.
- . 1980. Monkey dispersal and waste of a neotropical fruit. *Ecology* 61:944–959.

- . 1981. Fruit production and animal activity in two tropical trees. In E. Leigh, Jr., A. S. Rand, and D. M. Windsor, eds. *The ecology of a tropical forest: seasonal rhythms and long-term changes*. Smithsonian Institution, Washington, D.C.
- Howe, H. F., and D. DeSteven. 1979. Fruit production, migrant bird visitation, and seed dispersal of *Guarea glabra* in Panama. *Oecologia* 39:185–196.
- Howe, H. F., and G. F. Estabrook. 1977. On intraspecific competition for avian dispersers in tropical trees. *Am. Nat.* 111:817–832.
- Howe, H. F., and R. B. Primack. 1975. Differential seed dispersal by birds of the tree *Casearia nitida* (Flacourtiaceae). *Biotropica* 7:278–283.
- Howe, H. F., and G. A. Vande Kerckhove. 1979. Fecundity and seed dispersal of a tropical tree. *Ecology* 60:180–189.
- Janzen, D. H. 1970. Herbivores and the number of tree species in tropical forests. *Am. Nat.* 104:501–528.
- . 1971. Euglossine bees as long-distance pollinators of tropical plants. *Science* 171:203–205.
- . 1977. Promising directions of study in tropical animal-plant interactions. *Ann. Mo. Bot. Gard.* 64:706–736.
- Jenkins, R. 1969. Ecology of three species of Saltators with special reference to their frugivorous diet. Unpubl. Ph.D. diss. Harvard University.
- Knight, D. H. 1975. An analysis of late secondary succession in species-rich tropical forest. Pages 53–59 in F. B. Golley and E. Medina, eds. *Tropical ecological systems*. Springer-Verlag, New York.
- Land, H. C. 1963. A tropical feeding tree. *Wilson Bull.* 75:199–200.
- Leck, C. F. 1969. Observations of birds exploiting a Central American fruit tree. *Wilson Bull.* 81:264–269.
- McDiarmid, R. W., R. E. Ricklefs, and M. S. Foster. 1977. Dispersal of *Stemmadenia donnell-smithii* (Apocynaceae) by birds. *Biotropica* 9:9–25.
- McKey, D. 1975. The ecology of coevolved seed dispersal systems. Pages 155–191 in L. E. Gilbert and P. H. Raven, eds. *Coevolution of animals and plants*. University of Texas Press, Austin.
- Morton, E. S. 1973. On the evolutionary advantages and disadvantages of fruit-eating in tropical birds. *Am. Nat.* 107:8–22.
- Noble, J. C. 1975. The effects of emus (*Dromaius novaehollandiae* Latham) on the distribution of the nitre bush (*Nitraria billardieri* DC.). *J. Ecol.* 63:979–984.
- Poore, M. E. D. 1967. The concept of the association in tropical rain forest. *J. Ecol.* 55:460–470.
- Powell, J. A., and R. A. Mackie. 1966. Biological interrelationships of moths and *Yucca whipplei* (Lepidoptera: Gelechiidae, Blastobasidae, Prodoxidae). *Univ. Calif. Publ. Entomol.* 42:1–46.
- Rick, C. M., and R. I. Bowman. 1961. Galapagos tomatoes and tortoises. *Evolution* 15:407–447.
- Ricklefs, R. E. 1977. A discriminant function analysis of assemblages of fruit-eating birds in Central America. *Condor* 79:228–231.
- Sazima, M., and I. Sazima. 1978. Bat pollination of the passion flower, *Passiflora mucronata*, in Southeastern Brazil. *Biotropica* 10:100–109.
- Slatkin, M., and J. Maynard Smith. 1979. Models of coevolution. *Q. Rev. Biol.* 54:233–263.
- Smith, A. J. 1975. Invasion and ecesis of bird-disseminated woody plants in a temperate forest sere. *Ecology* 56:19–34.
- Snow, B. K. 1970. A field study of the bearded bellbird in Trinidad. *Ibis* 112:299–329.
- Snow, D. W. 1962. The natural history of the oilbird (*Steatornis caripensis*) in Trinidad, W.I. II. Population, breeding ecology and food. *Zoologica* 47:199–221.
- . 1971. Evolutionary aspects of fruit-eating by birds. *Ibis* 113:194–202.
- . 1981. Tropical frugivorous birds and their food plants: a world survey. *Biotropica* 13:1–14.
- Temple, S. 1977. Plant-animal mutualism: coevolution with dodo leads to near extinction of plant. *Science* 197:885–886.
- Thien, L. B. 1969. Mosquito pollination of *Habenaria obtusa* (Orchidaceae). *Am. J. Bot.* 56:232–237.
- Thompson, J. N., and M. F. Willson. 1978. Disturbance and the dispersal of fleshy fruits. *Science* 200:1161–1163.
- . 1979. Evolution of temperate fruit/bird interactions. *Evolution* 33:973–982.

- Van der Pijl, L. 1972. Principles of dispersal in higher plants. Springer-Verlag, New York.
- Williams, G. C. 1975. Sex and evolution. Princeton University Press, Princeton, N.J.
- Willis, E. O. 1966. Competitive exclusion in birds of fruiting trees in Western Colombia. *Auk* 83:479-480.
- . 1974. Populations and local extinctions of birds on Barro Colorado Island, Panama. *Ecol. Monogr.* 44:153-169.