

Opportunism vs. specialization: the evolution of dispersal strategies in fleshy-fruited plants

T. H. Fleming¹, D. L. Venable² & L. G. Herrera M.¹

¹Department of Biology, University of Miami, Coral Gables, FL 33124, USA; ²Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ 85721, USA

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Abstract

In this paper we address two questions concerning the interaction between fleshy-fruited plants and their seed dispersers: (1) What determines optimal disperser coterie size (designated as \hat{C}) and (2) Why does disperser specialization occur along taxonomic lines? We review factors that affect the evolution of \hat{C} and conclude that seed size and disperser quality (designated as Q) are especially important. We present a simple graphical model for determining \hat{C} based on Q and conclude that \hat{C} will be small (i.e. a specialized disperser strategy) when Q declines rapidly with increasing coterie size; \hat{C} will be large when Q declines slowly with increasing coterie size. We construct a model based on fitness set theory to predict that specialization on particular vertebrate taxa (e.g. birds or mammals) will be favored when different disperser taxa are perfectly substitutable or antagonistic (*sensu* Tilman 1982); mixed-taxa coterie are favored when different disperser taxa are complementary. Finally, we predict that when conditions favor taxonomic specialization, plants will evolve bird fruits more often than bat or primate fruits because of the greater species richness of birds compared with bats and primates.

Introduction

The similarity between the title of this paper and the title of Fleming's paper at the 1985 Frugivore and Seed Dispersal symposium ('Opportunism vs. specialization: the evolution of feeding strategies in frugivorous bats') is not coincidental. In that paper, Fleming asked (1) To what extent is diet choice in bats opportunistic or selective and (2) What ecological factors influence bat diet choice and foraging behavior? Similar questions can be asked about plants providing fleshy fruits for frugivores. Just as many frugivorous animals are selective about the fruits they eat, many plants likewise appear to be selective about the animals they 'choose' to consume their fruits and disperse their seeds. Thus, some plants (e.g. mistletoes,

Loranthaceae) appear to have small disperser coterie whereas others (e.g. *Cecropia* and *Ficus*, Moraceae) have much larger disperser coterie. Here we use 'coterie' to denote a group of disperser species.

In addition to differing in the species richness of their disperser coterie, plants also differ in the taxa they use as primary or exclusive dispersers. This specialization is reflected in the existence of dispersal 'syndromes'. Beginning with van der Pijl (1957), the syndrome concept has been widely discussed in the literature (e.g. Gautier-Hion *et al.* 1985; Howe 1986; DeBussche & Isenmann 1989; Herrera 1989). Examples of vertebrate dispersal syndromes are given in Table 1. Bird fruits generally differ from mammal fruits by being small and red, black, or purple in color, lacking a scent

Table 1. Seed dispersal syndromes of vertebrate frugivores. Modified from Howe (1986).

A. Bird fruit syndrome	
Obligate frugivore fruits	Large arillate seeds or drupes; seeds > 10 mm; scentless; rich in lipid or protein; black, blue, green, purple, red
Opportunist fruits	Small or medium-sized arillate seeds, berries, or drupes; seeds < 10 mm; no scent; rich in lipid, protein, sugar or starch; black, blue, orange, red, white
B. Mammal fruit syndrome	
Arboreal frugivore fruits	Large arillate or compound; aromatic, rich in protein, sugar, or starch; brown, green, orange, yellow, white
Aerial frugivore (bat) fruits	Large or small; odorless or musky, often rich in starch or lipid; green, yellow, white or whitish; often pendant
Elephant fruits	Large, tough and indehiscent; fibrous pulp; dull colors; resistant seeds

and a protective husk, and often containing significant amounts of lipids and proteins. Fruit characteristics associated with different dispersal syndromes presumably reflect qualitative as well as quantitative differences in the morphology, physiology, and behavior of potential vertebrate dispersal agents as discussed in detail by Howe (1986) and Schupp (this volume).

It is well-known that these syndromes have many exceptions and that fruit morphological/chemical characteristics are only moderately predictive about which animals disperse particular species of fruit (Heithaus 1982; Howe 1986). Nonetheless, the existence of recognizable 'syndromes' defined by O'Dowd and Gill (1986) as the nonrandom occurrence of combinations of diaspore traits related to the nature of dispersal agents, suggests that many plants indeed specialize on different subsets of animals to disperse their seeds. Instead of producing fruits that are universally attractive to fruit-eating vertebrates, plants often appear to 'aim' their fruits at non-

random subsets of potential dispersers. This raises two important evolutionary questions: (1) What determines optimal disperser coterie size and (2) Why does disperser specialization occur along taxonomic lines?

The purpose of this paper is to explore possible answers to these two questions using theoretical approaches that have not previously been applied to frugivory/dispersal systems. Because birds and mammals are numerically the most important biotic seed dispersers in most contemporary habitats (Howe 1986; Fleming 1991a), we will restrict our discussion to interactions between plants and those two groups of vertebrates. We will proceed by first discussing constraints on the evolution of dispersal strategies and the concept of seed dispersal quality. We will then develop simple models of optimal coterie size and taxon-specific specialization. Our overall conclusions based on this approach are that conditions favoring the evolution of generalized (= opportunistic) dispersal strategies apparently outnumber those favoring taxon-specific strategies, but that when taxon-specificity is favored, birds will be the 'targets' of specificity more often than other groups of vertebrates.

Factors influencing the evolution of fruiting strategies

We begin our discussion of the evolution of dispersal strategies of fleshy-fruited plants by noting that the goal of such a strategy is to maximize the number of surviving, reproducing offspring produced by a plant. Given this goal, an important question then becomes, What determines the coterie size, symbolized as \hat{C} throughout this paper, that maximizes a plant's fitness?

Before addressing this question, we note that many factors in addition to the characteristics of potential dispersers are involved in the evolution of plant fruiting strategies. For example, the ways in which three factors – establishment site predictability, plant successional status, and plant growth form – influence seed size, a critical factor in fruit choice and fruit availability in birds

and mammals (Wheelwright 1985; Dowsett-Lemaire 1988; DeBussche & Isenmann 1989; Willson *et al.* 1989), is illustrated in Fig. 1. As discussed by Fleming (1988), a seed's size critically influences its mobility and availability to vertebrate consumers. Seed size, in turn, is influenced by a plant's establishment strategy, as discussed by Grime (1979), Willson (1983), and Foster (1986), among others.

Because the number of vertebrate species capable of handling and/or ingesting fruits/seeds is inversely related to diaspore size (Wheelwright 1985; Fleming 1988), seed size and all abiotic and biotic factors influencing seed size (including the size of potential vertebrate dispersers, see below) will automatically have a major influence on \hat{C} (Martin 1985). We suggest that the inverse relationship between fruit/seed size and coterie size should be the null expectation in any discussion of the evolution of \hat{C} in fleshy-fruited plants. Because of their fruit/seed size, some plants will have smaller disperser coterie than others and hence will appear to be more specialized. What is of interest in discussions of the evolution of \hat{C} is variation around the regression line. For example, seeds of *Virola sebifera* and *V. surinamensis* differ considerably in mass (0.7 g vs. 2.0 g, respectively) but have similar small disperser coterie of 7–8 species of birds on Barro Colorado Island, Panama (Howe 1981; Howe & Vande Kerchove

1981). Controlling for the effect of fruit or seed size, why do some plant species have a larger or smaller \hat{C} than expected by chance? Is this variation random or does it conform to a predictable pattern?

Some of the biotic constraints involved in the evolution of the dispersal strategies of fleshy-fruited plants are listed in Table 2. Constraints in the plant column influence diet choice in frugivorous vertebrates and constraints in the animal column can influence the evolution of plant dispersal strategies. For example, as mentioned above, fruit and seed size strongly affect the accessibility of fruit to birds and mammals. Whereas large birds and mammals can handle a wide range of fruit sizes containing either small or large seeds, small species can only handle small fruits containing relatively small seeds. A plant selected to maximize the breadth of its disperser coterie because of its seedling establishment requirements (e.g. a pioneer plant) will be constrained to produce fruits containing many small seeds. Optimal fruit size will also be small (e.g. *Muntingia calabura*, many *Ficus* species) or the fruit must be capable of being eaten and seeds ingested in piecemeal fashion (e.g. *Cecropia* species).

Differences in the body sizes of New World and Old World tropical frugivorous birds and mammals appear to have influenced maximum fruit (and seed?) size in several families of fleshy-

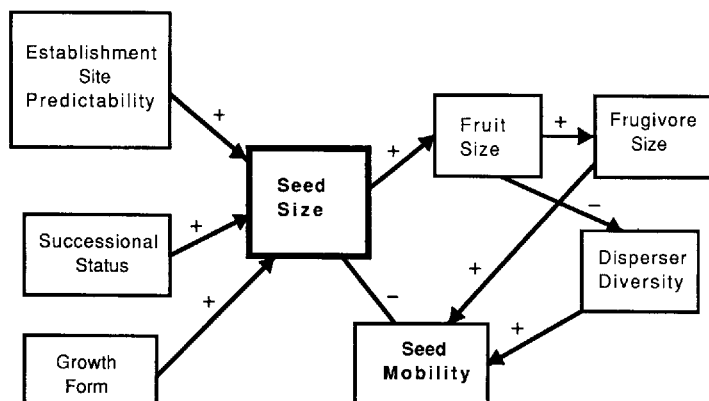


Fig. 1. Diagram indicating some of the factors influencing seed size and the effect of seed size on seed mobility and the diversity of disperser coterie. Plus and minus signs indicate positive and negative correlations, respectively, between variables; the arrow points to the dependent variable in each correlation. Redrawn from Fleming (1988).

Table 2. Biotic constraints in fruit disperser-fruit coevolution.

A. Plant-based constraints	B. Frugivore-based constraints
1. Fruit/seed size	1. Body size (gape width)
2. Degree of seed protection	2. Masticatory morphology
3. Nutritional characteristics/ secondary compounds	3. Digestive physiology
4. Fruit detectability	4. Sensory physiology
5. Fruit accessibility	5. Fruit harvesting behavior
6. Spatio-temporal availability	6. Spatio-temporal availability

Note: Additional constraints on plants but not on animals include effects of seed/seedling predators, pathogens, and competitors.

fruited plants. Fleming *et al.* (1987) reported that maximum sizes of contemporary frugivorous birds, primates, and bats are greater in the paleotropics than in the neotropics. This led A. Mack (unpubl. manuscript) to survey fruit sizes in eight families of plants widely distributed in both the New and Old World tropics. He found that mean fruit size was significantly larger in Old World Moraceae and Anacardiaceae and that the largest genera in the Burseraceae, Lauraceae, Meliaceae, Myristicaceae, Palmae, and Simaroubaceae occurred in the Old World more often than expected by chance. These results suggest that, in addition to the general factors indicated in Fig. 1, fruit size in at least some families of plants is sensitive to selection pressures provided by potential dispersal agents. This kind of animal-influenced plant evolution will influence \hat{C} of tropical plants.

A model of optimal disperser coterie size

Any model of optimal disperser coterie size must ultimately explain some pattern in nature. However, with our currently limited database, we know relatively little about how actual or optimal Cs are distributed among and within species of fleshy-fruited plants in most communities. Are they normally or log-normally distributed among species? Are extremely broad- or narrow-niched species exceptional or are they common? Do patterns in tropical communities differ qualitatively from those in non-tropical communities? Izhaki (unpubl. manuscript) reviewed available data on the size of disperser coterie of bird-dispersed plants

and reported that coterie size in temperate plants ($\bar{x} = 8.6$ species, range = 1–31 species) was about half as large as that of tropical plants ($\bar{x} = 14.6$, range = 1–43). Similar questions can be asked within species of fleshy-fruited plants; what is the shape of the curve relating \hat{C} to lifetime fitness? Given the 'diffuse' nature of plant-frugivore interactions (Fleming 1991a), it is likely that \hat{C} varies considerably in space and time (both geological and contemporary) for many plant species. Because of this variation, the answer to the question, What is \hat{C} for plant species *i*?, must often (always?) be location- and time-dependent.

With this caveat in mind we suggest that within a subset of potential vertebrate dispersers (determined by factors in column A of Table 2), \hat{C} will be determined by patterns of variation in seed dispersal quality (Q) among dispersers. For purposes of this paper, we will define Q for disperser species *j* and plant species *i* as $Q_{ij} = r_{ij} \times p_{ij}$ where r_{ij} = the proportion of seeds of *i* removed by *j* and p_{ij} = the proportion of seeds of dispersed by *j* that establish as seedlings. These will be called 'removal' and 'dispersal effectiveness', respectively, for short. Note that r_{ij} depends on the abundance of species *j* and the attractiveness or availability of fruits of *i* to *j*. It may also vary with the species composition of the coterie due to competitive interactions among dispersers. Dispersal effectiveness, p_{ij} , depends on the foraging movements and seed handling behavior of *j*.

Thus, the total number of seeds of species *i* effectively dispersed (a measure of *i*'s fitness) is

$$W_i = F_i \sum_{j=1}^C Q_{ij} = F_i Q_i(C)$$

where F_i is the total number of seeds produced per plant of species *i* per season and $Q_i(C)$ is the dispersal quality of the entire coterie consisting of C members.

Another way of expressing a disperser's Q_{ij} is to determine the proportion of established seedlings of species *i* that it dispersed. Whichever way it is measured, Q_{ij} will be very difficult, if not impossible, to measure for most species (but see Reid 1989). It should be noted that our terminol-

ogy differs somewhat from that of Schupp (this volume). Our Q_{ij} is called 'effectiveness' and our p_{ij} is called 'quality' by Schupp.

Just as \hat{C} is likely to vary among plant species, Q_{ij} is also likely to vary among vertebrate frugivores in a community. We currently have little information on how Q_{ij} varies among species (Is it normally-distributed or right- or left-skewed?). Are some birds or mammals likely to be consistently high (or low) quality dispersers across plant species? Current information (Levey 1986 and Schupp, this volume) suggests that within disperser species, Q_{ij} is likely to vary considerably across plant species. For instance, Chestnut-mandibled toucans (*Ramphastos swainsonii*) are excellent dispersers of the seeds of *Virola surinamensis* but are very poor dispersers of seeds of *Tetragastris panamensis* in Panama (Howe 1990). Some seeds ingested by the howler monkey *Alouatta palliata* (e.g. *Agonandra macrocarpa*, *Muntingia calabura*) are killed by gut passage whereas others (e.g. *Bursera simaruba*, *Cupania guatemalensis*) are not (Chapman 1989).

Plant fitness can also be expressed as the product of the total number of seeds removed times the mean proportion effectively dispersed, both of which are functions of coterie size, C (and coterie membership). The number of seeds of species i removed by C disperser species equals F_i times the total proportion of seeds removed, $r_{i\text{ tot}}(C)$, which equals $\sum_{j=1}^C r_{ij}$. The mean proportion of these seeds that are effectively dispersed is

$$\bar{p}_i(C) = \frac{\sum_{j=1}^C r_{ij} p_{ij}}{\sum_{j=1}^C r_{ij}}$$

This proportion can be thought of as the probability that a removed seed will be effectively dispersed, averaged over all dispersers. Plant fitness can then be expressed as

$$W_i = F_i \Sigma r_{ij} \cdot \frac{\sum_{j=1}^C r_{ij} p_{ij}}{\sum_{j=1}^C r_{ij}} = F_i r_{i\text{ tot}}(C) \cdot \bar{p}_i(C)$$

where

$$Q_i(C) = r_{i\text{ tot}}(C) \cdot \bar{p}_i(C)$$

is the seed dispersal quality of the entire coterie.

Fitness is composed of multiplicative components which, if converted to logarithms, can be expressed as a sum for the purpose of making a simple graphical model. Thus,

$$\ln W_i(C) = \ln F_i + \ln r_{i\text{ tot}}(C) + \ln \bar{p}_i(C).$$

Since F_i is not determined by coterie size or membership, we can find the fitness-maximizing coterie size by concentrating on the components of dispersal success, i.e. the combined dispersal quality of the entire coterie,

$$\ln Q_i(C) = \ln r_{i\text{ tot}}(C) + \ln \bar{p}_i(C).$$

If disperser species are added to the coterie in their order of decreasing quality (Q_{ij}), then $\bar{p}_i(C)$ will usually decline with C whereas the total proportion of seeds removed ($r_{i\text{ tot}}(C)$) will generally increase with C . When the logs of $\bar{p}_i(C)$ and $r_{i\text{ tot}}(C)$ are plotted against $\log C$, \log dispersal success of plant species i can be calculated graphically as the sum of the two curves (Fig. 2). The coterie size favored by selection (\hat{C}) will be the one with the highest sum. \hat{C} can be thought of as the coterie size for which the fitness increase from having more seeds dispersed equals the fitness decrease from lowering the effectiveness of their dispersal. That is, another species should be added to the coterie as long as the increase in the proportion of seeds removed is greater than the reduction in the mean effectiveness of dispersal ($\Delta \ln r_{i\text{ tot}}(C) > -\Delta \ln \bar{p}_i(C)$; cf. Venable 1992; Lloyd & Venable 1992). An easy way to think of logarithms here is as proportional changes; thus \hat{C} is the coterie size at which the proportional increase in seed removal that could be achieved by adding more species to the coterie is exactly balanced by the proportional decrease in the effectiveness of dispersal that would result.

The model predicts that \hat{C} will be small (a specialized disperser strategy) when the mean

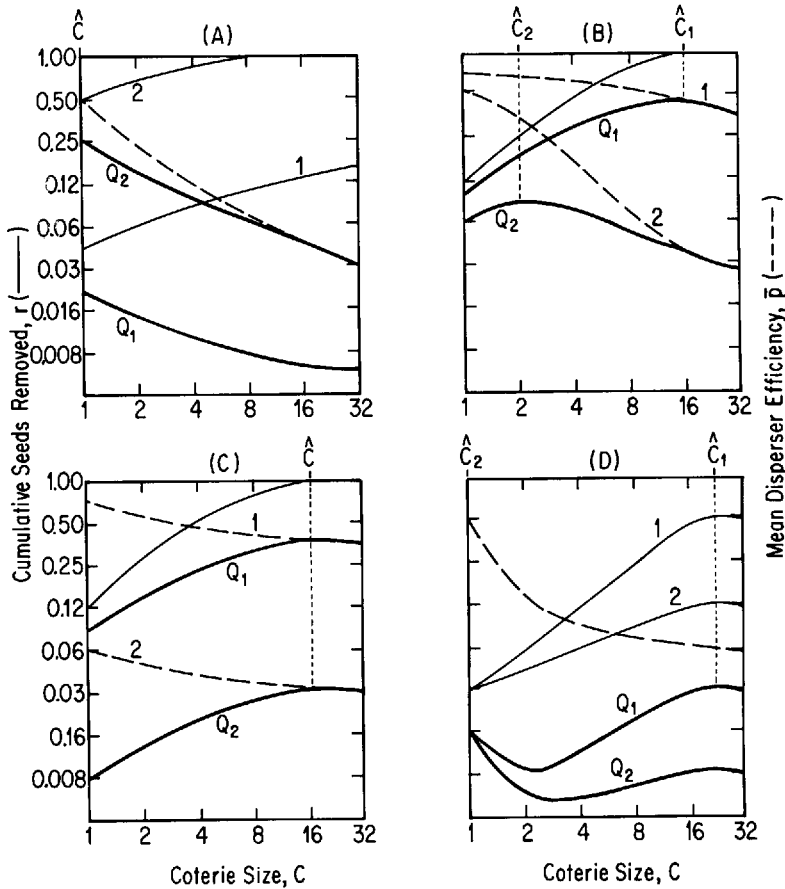


Fig. 2. Graphical models for predicting optimal disperser coterie size (\hat{C}) as a function of the cumulative proportion of seeds removed (r) and the proportion of seeds effectively dispersed (\bar{p}) by different disperser species ranked by their seed dispersal quality. Curves marked Q indicate overall plant fitness. Optimal coterie size (\hat{C}) is that coterie at which Q is greatest. Numbers = 1 & 2 refer to specific cases. See text for further explanation.

dispersal effectiveness tends to decline faster than seed removal increases with increasing C . Conversely, \hat{C} will be large (a generalized or opportunistic disperser strategy) when removal increases faster than the mean dispersal effectiveness declines.

The former case could occur if seeds are generally unattractive or dispersers rare so that the proportion of the fruit crop removed ($\ln r_{i\text{tot}}(C)$) increases only slowly with C (Fig. 2A, case 1). The mean dispersal effectiveness curve would decline rapidly if only one or a few species are very effective dispersers, and \hat{C} would be small. The same prediction of disperser specialization would hold if seeds were very attractive and the dispersers abundant, but again with only a few species

being very effective at dispersing the seeds they remove (Fig. 2A, case 2). In the first case, adding species to the coterie does not improve the proportion of seeds removed much because the potential dispersers are not very attracted (or abundant) and the increment in seed removal is low relative to the reduced effectiveness of dispersal. In the second case, adding species does not improve removal very much because the first species already removes most of the seeds.

It is important to note that we have added the two curves in a downward direction treating 1.0 as the origin. This is because both $\bar{p}_i(C)$ and $r_{i\text{tot}}(C)$ are proportions with values between 0 and 1. Thus their logarithms are negative and adding them gives a more negative value (just as

multiplying a seed removal fraction of 0.5 by an effective dispersal fraction of 0.5 gives a smaller proportion, 0.25, of the seeds that are both removed and effectively dispersed).

Also notice that, in this model, a specialized dispersal coterie can only be favored if dispersers interfere with each other's seed removal or dispersal effectiveness. Even if a second species had a zero dispersal effectiveness, it could not lower total dispersal quality of the coterie unless it had a negative effect on the seed removal or dispersal efficiencies of the better quality dispersers.

Coterie size should vary inversely with the variance in dispersal effectiveness. This is because variation in dispersal effectiveness steepens the mean dispersal effectiveness curve (Fig. 2B, cf. cases 1 and 2). If all dispersers are similar in effectiveness, the mean dispersal effectiveness curve will be flat. Dispersers can be either ineffective or highly effective and have low variance and a flat mean effectiveness curve (Fig. 2C, cases 1 and 2). This should select for large dispersal coterie as long as the seed removal curve is steeper.

Consider one last example that illustrates several important points not touched on above. Suppose the potential disperser community contains one species that does not remove very many seeds but is highly effective at depositing those removed in favorable sites. All of the other potential dispersers remove even fewer seeds, have a negative effect on seed removal by the first species, and have very low effectiveness at depositing seeds they do remove in favorable sites (Fig. 2D). For a plant with this set of potential dispersers, there may be two coterie sizes that are local optima, depending on parameter values. One local optima will be to specialize on the effective disperser; the other will be to be a generalist. The latter is a local optimum as long as some coterie sizes exist for which the increments in proportion of seeds dispersed are greater than the continued reduction in mean dispersal effectiveness. Whether the generalist strategy is a global optimum or not depends on how much the large coterie can increase the proportion of seeds effectively dispersed (Fig. 2D, cf. cases 1 and 2).

Regardless of whether the generalist or special-

ist strategy is the global optimum, there is likely to be a fitness valley between them. This creates a role for phylogenetic conservatism and rapid punctuated evolution in fruit biology. A specialist species would not be favored to become somewhat more generalist, even if the highly generalized strategy were the global optimum (Fig. 2D, case 1). Likewise, selection would not favor a slightly less generalized generalist, even if the specialist were the global optimum (Fig. 2D, case 2). Only macro-mutations affecting traits that influence fruit attractiveness or availability to frugivores could permit plants to cross the fitness valley.

This model provides a graphical tool for thinking about the evolution of coterie size. It predicts how coterie size should evolve with different communities of dispersers having different distributions of removal proportions and dispersal effectivenesses. Many scenarios not discussed here could be analyzed, yielding predictions that might not be easy to derive otherwise. The key idea is to think in proportional changes. We have presented some simple examples of predictions that can be generated with this model but have not explored it exhaustively here.

Taxon-specific disperser specialization

The existence of fruit syndromes implies that selection has favored the evolution of specialization along taxonomic lines. Why should fruit syndromes exist? Are the qualitative and quantitative characteristics listed in Table 2 different enough between birds and mammals to favor the evolution of taxonomically specialized dispersal strategies?

Here we develop a graphical model for determining the dispersal strategy that maximizes a plant's fitness when it has two (or more) vertebrate taxa to 'choose' from as its seed dispersers. First we plot the proportion of a plant's seeds removed by each of two groups of dispersers (e.g. birds and mammals) for different fruit designs (Fig. 4a). Seed removal is defined as in the previous section, so that r_{ib} and r_{im} are the propor-

tions of the F_i seeds of plant species i that are removed by birds and mammals, respectively. These points are bounded by a *removal constraint curve*. Each point in the stippled area represents the bird and mammal removal fractions that result from a particular feasible fruit design. For each point below the removal constraint curve, some aspect of fruit design could be improved to give greater seed removal by one disperser without any cost in terms of seed removal by the other. All such changes should be favored by natural selection, leading to fruit designs that fall along the constraint curve. Points on the constraint curve are at the design limit where no further improvement in fruit removal by either taxon can be attained without a reduction in removal by the other taxon, thus the negative slope. Such tradeoffs are due to differences between birds and mammals in size, food-gathering morphology, digestive physiology, and sensory physiology (e.g. Table 2; Shupp, this volume; Martinez del Rio and Restrepo, this volume). That is, fruits that are more attractive to birds owing to their color, nutrient composition, time of ripening (e.g. day vs. night), etc. will be less attractive to mammals and vice versa.

This model is similar to the one presented in the previous section. There we dealt with several to many disperser species (without regard to taxonomy) but only discussed in a general way the fact that adding an additional disperser may reduce seed removal or effectiveness of animals already in the coterie. In the present model, we will explicitly graph these interactions and consider how changes in fruit design increase or decrease seed removal by various actual or potential dispersers (though our 2 dimensional graphical approach only deals with 2 disperser species or 2 taxa at a time).

As mentioned previously, seed removal is determined partly by the attractiveness of the fruit, and thus by the constraints listed in Table 2, and partly by the relative abundance of the potential dispersers (Fig. 3). If, for example, it is difficult to design a fruit that attracts birds but is easy to design one that attracts mammals, then the removal constraint curve will tend to have a shall-

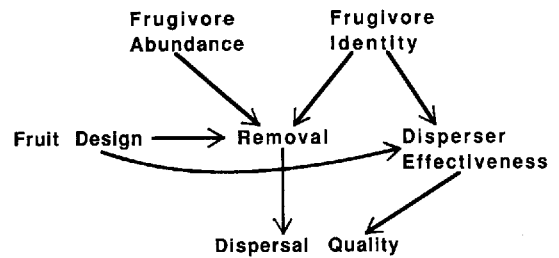


Fig. 3. Schematic plot of the interaction of factors affecting the dispersal quality experienced by a fleshy-fruited plant attracting vertebrate frugivores.

low slope. If birds are more abundant than mammals, it may be easier to obtain higher removal proportions with birds than with mammals. This would generate a steep removal constraint curve (e.g. Fig. 4A).

The removal constraint curve is not necessarily straight, and its degree of curvature has an important effect on the superiority of a specialist vs. a generalist dispersal syndrome. If the curve bows inward, a generalist syndrome will have a lower total seed removal ($r_{i\text{ tot}} = r_{ib} + r_{im}$) than could be achieved by specializing on one (or perhaps either) of the disperser taxa. The curvature is determined by such factors as the competitive interactions between birds and mammals for fruit and by how different the specialized bird and mammal dispersal syndromes are. For example, if birds and mammals undergo interference competition, the line will bow toward the origin. Following the terminology of Tilman (1982) and others, such a curve can be called an 'antagonistic removal constraint'. If the dispersers experience some kind of mutualistic interaction, perhaps by inadvertently warning each other about predators while feeding, the line would bow out (i.e. a 'complementary removal constraint'). If an attractive mammal fruit is very different in design from an attractive bird fruit, it may be that an intermediate fruit design will not result in much seed removal by either group. This would result in an antagonistic curve bowed in towards the origin. If the two syndromes are not very different, intermediate designs may result in considerable removal by both groups and a complementary removal curve.

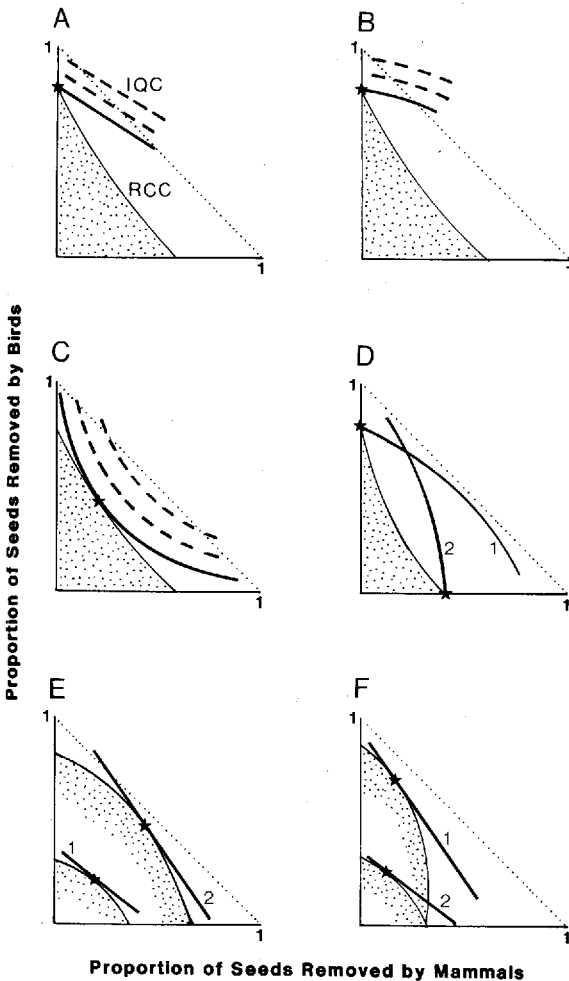


Fig. 4. Graphical models for predicting the optimal disperser strategy (*i.e.* specialization on one taxon or on a mixture of taxa) in fleshy-fruited plants. Axes indicate the proportion of a plant's seed crop removed by either birds or mammals. The solid light lines represent removal constraint curves (RCC). The solid heavy and dashed lines represent lines of constant disperser effectiveness (*i.e.* isoquality curves, IQC). The dotted line indicates maximum seed removal. Stars indicate the optimal disperser strategy. Numbers 1 & 2 refer to specific cases. See text for further explanation.

As discussed in our previous model, seed removal does not necessarily translate directly into dispersal quality because taxa may differ in their effectiveness at transporting seeds to sites favorable for establishment (Shupp, this volume). Specifically, the dispersal quality of a particular disperser j for plant species i has been defined as

$$Q_{ij} = r_{ij} \times p_{ij} \text{ and the dispersal quality of plant species } i \text{ due to the entire coterie is given by } Q_i(C) = \sum_{j=i}^C r_{ij} \times \bar{p}_{ij}.$$

We can translate removal proportions into dispersal quality by adding to our graph a plot of *isoquality curves* which connect the removal proportions that yield equal dispersal quality. In the case of bird vs. mammal dispersal, such an isoquality curve is given by $Q_i(C) = r_b p_b + r_m p_m = K$ where K is a given constant dispersal effectiveness and which can be related to fitness by

$W_i = F_i Q_i(C) = F_i K$. There will be a family of isoquality curves parallel to one another, each with a different dispersal quality K . As total seed removal increases, the K curves will move farther from the origin (Fig. 4A). Such curves are sometimes called *indifference curves* because a plant should be indifferent to the set of removal proportions specified by particular isoquality curves (and corresponding fruit design) because they all generate the same fitness.

The fundamental question for the evolution of dispersal syndromes is, Which fruit design gives the highest K and thus the highest fitness? This can be ascertained by determining the highest K isoquality curve that intersects the removal constraint curve (the heavy solid line in Fig. 4A). The one with highest K will always be tangent to the removal constraint curve (or touch it at the boundary where it meets one of the axes), and the best fruit design will be the one associated with the seed removal proportions at this point. This type of graphical analysis is similar to fitness set analysis (Levins 1968) and to the approach used by Tilman (1980, 1982) and others (e.g. Rapport 1971; Covich 1972) in foraging theory. The graphical and algebraic techniques for such models are well developed (cf. Venable & Brown 1988; Lloyd & Venable 1992).

If the dispersal effectiveness of birds and mammals is invariant with changes in fruit design, the isoquality curves described above will form straight lines given by $r_b = K/p_b - (p_m/p_b)r_m$ when plotted in r_b, r_m space. In this situation, birds and mammals can be considered to be perfectly substitutable dispersers (*sensu* Tilman 1982). The

slope will be determined by the relative effectiveness of birds and mammals. If birds are more effective than mammals, the slope of the curve will be shallow and will intersect the bird removal axis at a low point determined by K/p_b . The opposite situation will hold if mammals are the more effective dispersers.

The intuition behind isoquality curves may be clearer if it is remembered that they tend to function in an inverse fashion to the removal constraint curves. Removal values farther from the origin are 'better', so a steep removal curve means that birds remove more seeds than mammals. In contrast, an isoquality line closer to the origin on the bird axis means that birds are more effective than mammals. This is because the same dispersal quality can be achieved with fewer seeds removed by birds. Thus a slope more shallow than -1 implies that birds are more effective dispersers than mammals. Indeed, the fitness maximum occurs where the 2 curves touch, i.e. where the removal curve is out far enough and an isoquality curve is in far enough that they coincide. Thus, if birds removed more seeds than mammals (giving a steep removal curve such as in Fig. 4A) and birds were also more effective at dispersing removed seeds (yielding a shallower isoquality curve as in Fig. 4A), then the 2 curves will intersect at the left of the graph at a point representing a specialized bird fruit, just as our intuition tells us it should.

Isoquality curves will not be straight lines if disperser effectiveness varies with fruit design. Recall from the previous model that the dispersal quality of an entire coterie can be thought of as the product of the total proportion of seeds removed and the average effectiveness of dispersers, i.e. $Q_i(C) = r_{i\text{ tot}} \times \bar{p}_i$. Thus, if the average dispersal effectiveness is lower at intermediate fruit designs, removal proportions must be higher to maintain the constant dispersal quality of an isoquality curve. In this case, the isoquality curves would bow away from the origin (an 'antagonistic isoquality curve'; Fig. 4B). If average dispersal effectiveness were higher at intermediate fruit designs, then removal proportions would have to be lower to maintain a constant dispersal quality,

and the curves would bow in (a 'complementary isoquality curve'; Fig. 4C). Technically, the condition for an antagonistic isoquality curve is that $p_b + p_m$ is greater for specialized bird and mammal plants than for generalists (the inequality is reversed for complementary isoquality curves, and a straight isoquality curve is generated by constant values of p_b and p_m). Again, the intuition is the reverse of that for the removal constraint curves: an outward bowing isoquality curve is an antagonistic one signifying that it is hard to have high quality dispersal with an intermediate, generalist fruit dispersal strategy.

As an example, consider the following scenario. As a species becomes more specialized for dispersal by birds, not only is the attractiveness to birds and seed removal by birds likely to increase, but also birds may become more effective dispersers of removed fruit. This might result from evolutionary changes in fruit design affecting, e.g. hardness of the endocarp, the production of mucilage on the seed coats, or changes in the laxative properties of the pulp. If other modifications occur when the fruit specializes more on mammals, the effectiveness of mammals might also increase. Under these circumstances, p for specialized bird or mammal fruits would be higher than p for generalized fruits, which would result in an outward bowing (antagonistic) isoquality curve (Fig. 4B).

It is theoretically possible, though unlikely, that increased specialization and increased removal by a disperser taxon might be accompanied by a declining effectiveness of that disperser. For example, if birds and mammals dispersed seeds to different types of safe sites for germination and both types were limited in availability, density dependent mortality might occur among seedlings within each type of safe site. This could result in lower effectiveness as specialization towards one disperser increased. The density effects might be alleviated somewhat by utilizing both types of dispersers in a generalized syndrome that would have a higher \bar{p} , which would result in a complementary isoquality curve (Fig. 4C).

Curved isoquality lines could also result if the effectiveness of two disperser taxa interacted. For

example, the curves might bow in (a complementary effect; Fig. 4C) if dispersal by either taxon alone was not very effective, but successive dispersal by both was highly effective. In this scenario, \bar{p} would be highest with intermediate, more generalized fruits (or perhaps with dual dispersal mechanisms). Possible examples of this include combined bird and ant dispersal (Byrne & Levey, this volume) and combined ballistic and ant dispersal (Beattie 1985).

We have discussed how the biology of frugivore-plant systems outlined in Fig. 3 gives rise to differently shaped removal constraint and isoquality curves. We can now put these curves together to predict how the different factors in Fig. 3 select for taxon-specific or generalized dispersal syndromes. One scenario that we consider likely is that fruit traits favoring attraction and removal by birds may often be sufficiently different from those favoring removal by mammals that intermediate fruits are not very attractive to either and thus experience low seed removal. That is, birds and mammals are antagonistic dispersers. In many habitats birds are more abundant than mammals, which could result in the removal constraint curve intersecting the bird axis at a high removal proportion and a steep removal slope (Fig. 4D). Since specialization on either taxon is likely to increase dispersal effectiveness, the isoquality curve will be antagonistic (bowed out) with its slope depending on the relative effectiveness of birds and mammals. This scenario probably describes many dispersal systems, and it always favors specialization on one taxon over generalization. Which taxon depends on the quantitative interplay of removal and effectiveness. If birds, by virtue of their abundance, tend to remove more seeds than mammals, then specialization on birds will often be favored (Fig. 4D, case 1). Mammals would have to be significantly more effective than birds for mammal fruits to be favored by selection (Fig. 4D, case 2).

Consider what would happen with two different bird groups such as mashers (tanagers) and gulpers (manakins) (Levey 1986; Stiles and Roselli, this volume). The optimal fruit design for these taxa is likely to be similar enough that many

fruits may be removed if they are of intermediate design. If seed removal is generally low, either because dispersers are uncommon or fruits have low attractiveness (perhaps due to repellent chemistry), then total seed removal ($r_{i\text{ tot}}$) is likely to be higher with intermediate designs, which would result in a strongly complementary (bowed out) removal curve (Fig. 4E, case 1). If seed removal by these 2 taxa is very high, they are likely to compete resulting in a straighter removal curve (total removal cannot be greater than 1 so the removal curve cannot bow out past the dashed line in Fig. 4E). Dispersal effectiveness of these 2 bird taxa is not likely to change much as fruit design changes which leads to a fairly straight isoquality curve. In this scenario, our model predicts that the optimal fruit will be generalized and attractive to both disperser taxa. An exception to this (Fig. 4F) would be if one group had significantly higher removal (case 1) or effectiveness (case 2), in which case specialization might still be favored.

Up to this point we have considered birds and mammals to be homogeneous groups, but this is clearly an oversimplification. In addition to specialization on birds or mammals (e.g. Janson 1983), we expect to see specialization on ecologically and behaviorally similar taxonomic groups within birds and mammals (e.g. Gautier-Hion *et al.* 1985). Groups of birds with unusual ecologies such as oil birds (Steatornithidae) may represent special opportunities involving peculiar fruit designs and high potential returns for specialization. Likewise, plants should be specialists rather than generalists on mammals as different as elephants and bats.

Many other scenarios could be explored. To do this, one must first determine how different ecological and behavioral factors lead to different removal constraint and isoquality curves. These curves can then be used to predict the optimal dispersal syndrome.

These concepts can be related to actual dispersal systems by determining whether or not seed removal and seed wastage increase, remain the same, or decrease when dispersal strategies contain a mixture of taxa compared with when they

are specialized on one taxon. We predict that, because of their morphological, physiological, and behavioral differences, birds and mammals are more likely to have antagonistic removal and iso-quality curves than complementary ones. Because of its importance in determining optimal coterie size and degree of taxonomic specialization and its implications for conservation biology, this is an important topic for future research.

Taxon-specific specialization and fruit-frugivore coevolution

Because birds greatly outnumber bats, primates, and other kinds of mammals in number of species and families (Howe 1986; Fleming *et al.* 1987; Fleming 1991a), the removal constraint curve should be steep and should intersect the bird removal axis at a high point (e.g. Fig. 4A). Yet as more and more bird-dispersed species migrate into or evolve in a community, new plants will be less likely to attract sufficient numbers of birds, and eventually other vertebrates will be able to remove as many or more of their seeds. There should come a point where disperser species are utilized in proportion to their availability (appropriately weighted by their effectiveness). This process should function at the interspecific level much as ideal free distribution theory suggests that individuals should behave within species (e.g. Milinski & Parker 1991). If this idea is correct, we should expect to find plants specializing on birds as their exclusive dispersers more frequently than on mammals whenever taxon-specific dispersal syndromes are favored. Data summarized in Willson *et al.* (1989) for several tropical and subtropical localities generally support this prediction. Except for Gabon, bird or bird-bat fruits outnumber mammal fruits by a factor of at least 2 in South Africa, Australia, and the neotropics. A similar bias towards bird fruits exists in temperate habitats (Stiles 1980; Skeate 1987; Herrera 1989).

This bias towards birds rather than mammals in specialized seed dispersal systems raises an important evolutionary question: To what extent

have the speciation rates of fleshy-fruited plants and their vertebrate dispersers been coupled or uncoupled? Some theoretical models of speciation between mutualistic plants and animals (e.g. Kiestler *et al.* 1984) indicate that coupled speciation is likely. The general feeling among researchers studying fruit-frugivore interactions, however, is that the interaction is too diffuse to promote diversity via coupled speciation (Howe 1984, 1986; Herrera 1985). In the case of one well-studied fruit-frugivore system (*Piper* fruits and *Carollia* bats, Fleming 1988), plant speciation has clearly proceeded independently of bat speciation. In lowland Central America, *Piper* species richness increases from five species in tropical dry forest to nearly 50 species in tropical wet forest whereas *Carollia* diversity only increases from two to three species (Fleming 1985, 1991b; Marquis 1991). Charles-Dominique (this volume) suggests that the association between certain specialized frugivorous birds and mammals and species-rich genera of plants has promoted plant speciation, but he provides no coevolutionary model to explain this process.

Conclusions

We have used a variety of theoretical approaches to address questions of optimal disperser coterie size and degree of disperser-taxon specialization in fleshy-fruited plants. \hat{C} depends on a variety of factors of which fruit/seed size and the seed dispersal quality (Q) of different disperser species appear to be especially important. The way in which Q varies among potential dispersers can influence the evolution of specialized or generalized disperser coterie. We suggest that the degree of taxonomic specialization of a plant's disperser coterie depends on whether different disperser taxa (e.g. birds, mammals) are perfectly substitutable, complementary, or antagonistic (*sensu* Tilman 1982). Taxonomic specialization, as reflected in dispersal 'syndromes', is likely to evolve when disperser taxa are perfectly substitutable or antagonistic. Otherwise, evolution will favor taxonomically-mixed disperser coterie. Fi-

nally, we suggest that plants evolving taxonomically-specialized dispersal strategies should 'target' birds more often than bats or primates because of their greater species richness. Important future work in this area includes determining (1) Q values of frugivores within and among species of plants, (2) whether different taxonomic or ecological groups of dispersers are perfectly substitutable, complementary, or antagonistic, and (3) the extent to which rates of speciation in fleshy-fruited plants and their dispersers are interdependent. In addition to their theoretical importance, each of these topics has important implications for the conservation of biodiversity.

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