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Quantity, Quality and the Effectiveness of Seed Dispersal by Animals

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Quantity, quality and the effectiveness of seed dispersal by animals

Eugene W. Schupp
Savannah River Ecology Laboratory, Drawer E, Aiken, SC 29802, USA; Present address: Department of Range Science and The Ecology Center, Utah State University, Logan, UT 84322-5230, USA

Abstract

Disperser effectiveness is the contribution a disperser makes to the future reproduction of a plant. Although it is a key notion in studies of seed dispersal by animals, we know little about what determines the effectiveness of a disperser. The role of the present paper is to review the available information and construct a hierarchical framework for viewing the components of disperser effectiveness.

Effectiveness has both quantitative and qualitative components. The quantity of seed dispersal depends on (A) the number of visits made to the plant by a disperser and (B) the number of seeds dispersed per visit. The quality of seed dispersal depends on (A) the quality of treatment given a seed in the mouth and in the gut and (B) the quality of seed deposition as determined by the probability that a deposited seed will survive and become an adult. In this paper I review the ways disperser behavior, morphology and physiology can influence these major components of disperser effectiveness, and when data permit present preliminary analyses of relationships among components.

Introduction

Central to studies of the ecological and evolutionary consequences of seed dispersal by animals is the notion that species of dispersers differ in their effectiveness (McKey 1975, Howe & Estabrook 1977, Snow 1981, Wheelwright & Orians 1982, Levey 1987). Effectiveness, the contribution a disperser makes to plant fitness, depends on the quantity of seed dispersed and the quality of dispersal provided each seed (Herrera & Jordano 1981). Progress is being made towards understanding the attributes of effective dispersers and the extent to which effectiveness varies among species (e.g., Davidar 1987; Reid 1989; Izhaki *et al.* 1991), but many questions remain unanswered. For example, are there highly effective dispersers that maximize both the quantity and the quality of dispersal, or are all deficient in some way? Is quantity or quality more important in determining the effectiveness of dispersal? Are species of dispersers inherently of high or low quality, or does quality differ with plant species dispersed, habitat or year? These and other critical questions have only begun to be addressed. The primary role of this paper is to consolidate the available information and to provide a framework for addressing disperser effectiveness. Note that the same approach is useful for other mutualisms as well (Herrera 1987, 1989a).

Disperser effectiveness

Many important terms in the literature of seed dispersal have been inconsistently applied. 'Effi-

ciency,' for example, has referred to the number of seeds dispersed (Coates-Estrada & Estrada 1988), the quality of dispersal (Reid 1989) and the product of the two (Howe & Estabrook 1977). Just as frequently, several terms have been used for the same concept; 'quality' (McKey 1975; Levey 1987), 'reliability' (Howe & Estabrook 1977), 'goodness' (Janzen 1983b) and 'efficiency' (Howe & Estabrook 1977; Fialho 1990) have all been used more or less as synonyms of effectiveness as defined here. A useful framework for studying the effectiveness of seed dispersal must be built on a logical and consistent terminology. Table 1 presents a hierarchical outline of the major factors likely to influence effectiveness, suggesting the most appropriate terms.

Disperser effectiveness is ideally defined in terms of the contribution a disperser makes to the future reproduction of a plant. As such, the best measure is the number of new adult plants produced by the dispersal activities of a disperser, relative to the number produced by others. Because reliable estimates of the production of new adults can be very difficult, this is to a large extent only a heuristic definition at present. An empirical measure based on seedlings (Reid 1989) is far more tractable and may be nearly equivalent in many systems. In others, however, an emphasis on seedlings may prove misleading. The consequences of a particular pattern of seed dispersal can last far beyond the seedling stage: nearness to conspecifics can affect tropical tree growth even in the 8–16 cm DBH size class (Hubbell & Foster 1990) and differences in *Prunus mahaleb* growth and survival across a range of microhabitats are evident at least up to the size of first reproduction (Schupp, E. W., unpubl. data). Studies of effectiveness will be more difficult, but more enlightening, if viewed as presented here. The key lies in incorporating thorough analyses of plant demography into seed dispersal studies.

Empirically, we will consider:

Effectiveness = (Quantity) × (Quality) ,

where quantity is the number of seeds dispersed and quality is the probability that a dispersed seed will produce a new reproductive adult. The quan-

tity of dispersal is a function of (A) the number of visits made by a disperser and (B) the number of seeds dispersed per visit (Table 1). The quality of dispersal is a function of (A) the quality of treatment in the mouth and gut and (B) the quality of seed deposition (Table 1). Each of these components is in turn influenced by aspects of the biologies of the animal dispersers and the plants being dispersed.

Note that for both dispersal agents and plants, the present definition allows effectiveness to be considered at the scale of individuals, populations, or species. All levels will be addressed, but the following sections will primarily consider disperser populations interacting with plant populations.

Quantity of seed dispersal

Discussion of patterns of variation in the quantity of seed dispersal focuses on 16 data sets covering 15 species of trees, shrubs and vines from the eastern United States, Mexico, Central America and Spain (Fig. 1). Studies are limited to those

Table 1. A hierarchical outline of the major components of disperser effectiveness.

I. Quantity of seed dispersal
  A. Number of visits
    1. abundance of disperser
    2. diet
    3. reliability of visitation

  B. Number of seeds dispersed per visit
    1. number of seeds handled per visit
    2. probability of dispersing a handled seed

II. Quality of seed dispersal
  A. Quality of treatment
    1. destroy or pass seeds intact
    2. alter percent or rate of germination

  B. Quality of deposition
    1. movement patterns
      a. habitat and microsite selection
      b. rate and directionality of movement
    2. deposition patterns
      a. rate and pattern of deposition
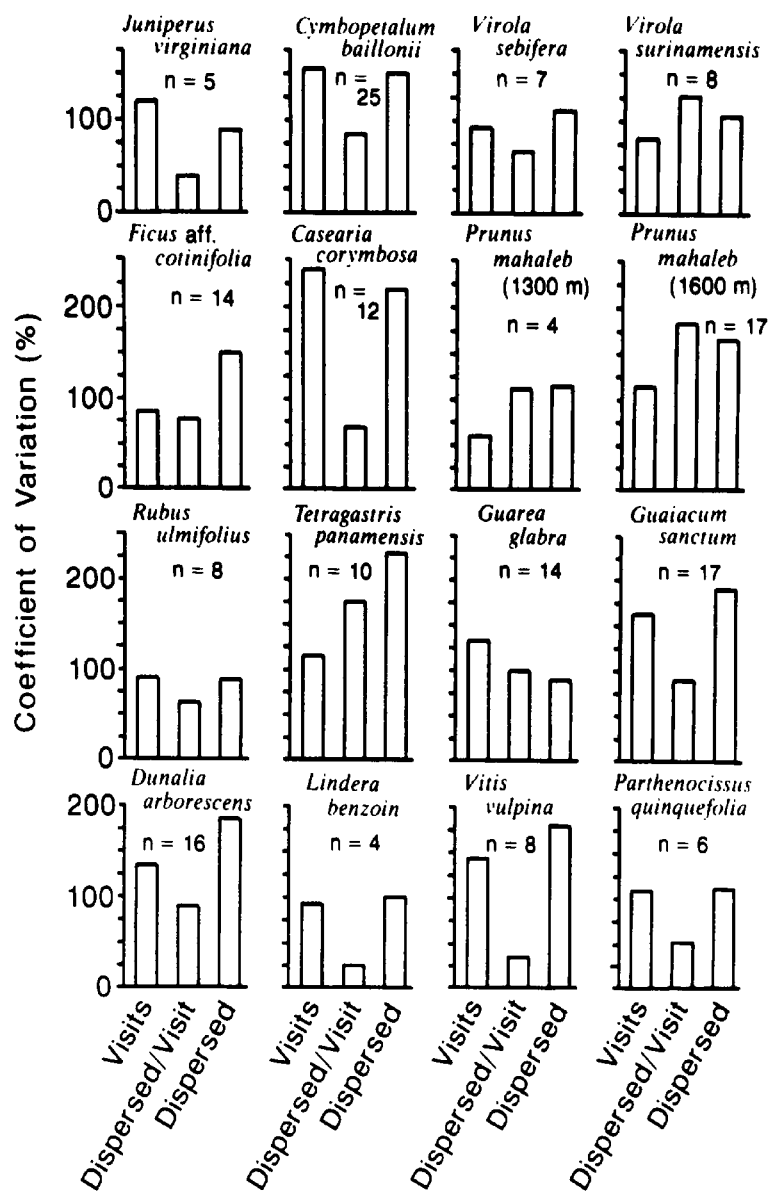   b. seed (diet) mixing

Fig. 1. Among-species variability in the quantitative traits of dispersal exhibited by the disperser assemblages visiting 16 species of plants. Shown are coefficients of variation for the number of visits, the number of seeds dispersed per visit and the total number of seeds dispersed. See text for details on the data sets. n = the number of species of dispersers used. Sources are: *Juniperus virginiana* (Holthuijzen & Sharik 1985), *Cymbopetalum baillonii* (Coates-Estrada & Estrada 1988), *Virola sebifera* (Howe 1981), *Virola surinamensis* (Howe & Vande Kerckhove 1981), *Ficus* aff. *cotinifolia* (Coates-Estrada & Estrada 1986), *Casearia corymbosa* (Howe & Vande Kerckhove 1979), *Prunus mahaleb* at 1300 m elevation (Herrera & Jordano 1981), *P. mahaleb* at 1600 m elevation (Jordano, P. & Schupp, E. W., unpubl. data), *Rubus ulmifolius* (Jordano 1982), *Tetragastris panamensis* (Howe 1980), *Guarea glabra* (Howe & De Steven 1979), *Guaiacum sanctum* (Wendelken & Martin 1987), *Dunalia arborescens* (Cruz 1981), and *Lindera benzoin*, *Vitis vulpina* and *Parthenocissus quinquefolia* (Malmborg & Willson 1988).

with reasonable estimates of the number of visits, the number of seeds 'dispersed' per visit and the total number of seeds 'dispersed' by individual species of dispersers. The accuracies of estimates vary, as do definitions of 'visits' and 'dispersal,' so generalities must be considered tentative.

Number of visits

Differences among disperser species in the number of visits made to a plant can be due to differences in abundance, diet, and reliability of visitation (Table 1). Species of dispersers differ extensively in local abundances (Fleming *et al.* 1977; Greenberg 1981; Herrera 1984, 1988; Thomas 1991); in one study, net captures of common avian dispersers of *Rubus ulmifolius* varied from four for *Sylvia melanocephala* to 184 for *S. atricapilla* (Jordano 1982). Such large differences in abundances contribute to differences in visitation.

Disperser species also differ in the importance of fruit in the diet and in the choice of individual fruit species. Species within local assemblages (Jordano 1982; Herrera 1984), families (e.g., Phyllostomatidae; Fleming 1988) and even genera (e.g., *Sylvia*; Jordano 1987) show continuous variation from near total frugivory to the addition of occasional fruits to a diet of insects, vertebrates, pollen or nectar. Frugivorous species also differ in which species of fruit they consume. In Panama (Howe & DeSteven 1979; Howe 1980, 1981, 1986b; Greenberg 1981), an Illinois woodlot (Malmborg & Willson 1988), west Africa (Gautier-Hion *et al.* 1985) and southern Spain (Herrera 1989b) frugivorous species differed in the use of available fruits. Disperser size (Jordano 1987) and digestive physiology (Martinez del Rio & Restrepo, this volume), fruit presentation (Moermond & Denslow 1985), concentrations of nutrients (Fleming 1988) and chemical deterrents (Howe & Vande Kerckhove 1981), and the packaging (Murray *et al.*, this volume) and passage rates (Sorensen 1984) of seeds have all been implicated in fruit choice. Regardless of the causes, choice will play a role in determining visitation.

Disperser reliability spans a range of temporal and spatial scales. Temporally, a reliable disperser dependably visits plants throughout the day, the season and the years. Variation among species of dispersers has been observed at all scales. Kantak (1981) noted that some Mexican birds fed on fruit throughout the day, but others fed only part of the day. At La Selva, Costa Rica *Tityra semifasciata* was the only disperser that reliably visited *Casearia corymbosa* throughout the season, and consequently was the most abundant visitor overall (Howe 1977). Reliability on the scale of years can take several forms. A disperser may be abundant one year and absent the next, as in the periodic southern invasions of Waxwings (*Bombycilla garrulus*) beyond their normal wintering range (Snow & Snow 1988). Species may be reliably present each year, but unreliably abundant. In southern Spain, autumn abundances of the birds *Erithacus rubecula* and *Sylvia atricapilla* varied more than four-fold over nine years (Herrera 1988). Similarly, the disperser assemblage of *Virola surinamensis* in Panama was consistent over four years, but relative abundances of the species differed significantly (Howe 1986b). Even if a disperser is reliably present and abundant each year, it may be an unreliable visitor due to year-to-year shifts in fruit choice (Malmborg & Willson 1988).

Spatially, a reliable disperser will dependably visit all individuals of all populations throughout the range of the plant species. As with temporal reliability, variation among seed dispersers exists at all scales. Observing 14 *Virola sebifera* in Panama, Howe (1981) recorded three disperser species visiting all trees and four visiting only three or fewer trees. On a larger scale, disperser assemblages differed for *Casearia corymbosa* in wet and dry forests in Costa Rica (Howe 1977; Howe & Vande Kerckhove 1979), and for *Prunus mahaleb* at 1300 m and 1600 m elevation in the Sierra de Cazorla of Spain (Herrera & Jordano 1981; Jordano, P. & Schupp, E. W., unpubl. data). At the largest scale, the geographical range of a disperser may or may not (Wheelwright 1988; Jordano, this volume) encompass the range of a plant species it disperses.

Patterns of variation in disperser abundances, diets and reliabilities of visitation combine to yield overall patterns of visitation to fruiting plants. In all systems studied, species of seed dispersers differed in the number of feeding visits made (Fig. 1); coefficients of variation for the 16 data sets range from 59–239% with a median of 114%.

Though extensive, these estimates of variation are minimal. Restricting the data sets to dispersal agents for which feeding (dispersal) rate information existed biased the data against rare visitors, decreasing the CV's. Additionally, while published lists of dispersers reliably record abundant visitors, they lack some to many infrequent visitors. Rarefaction may be useful for estimating the degree of completeness of sampling (P. Jordano, pers. comm.), but increased effort should add at least a few species to most lists (see Wheelwright *et al.* 1984), increasing estimates of variation. The rate at which increased sampling adds new species will depend on whether the added effort is at the same trees, new trees or new populations.

Fig. 2 shows the proportion of the total visits made by individual disperser species to representative tree species with small (*Prunus mahaleb*,

1300 m elevation), medium (*Virola sebifera*) and large (*Dunalia arborescens*) disperser assemblages. In large assemblages (> 10 disperser species), most species make few visits, while several make over half of all visits. With smaller assemblages there are proportionally fewer species of infrequent visitors, but most visits are still made by a few species.

Number of seeds dispersed per visit

The number of seeds dispersed per visit is the product of the number of seeds handled and the probability a handled seed is dispersed (Table 1). A key characteristic affecting both is handling method. Classifications of handling methods have been initiated for bats (Bonaccorso & Gush 1987)
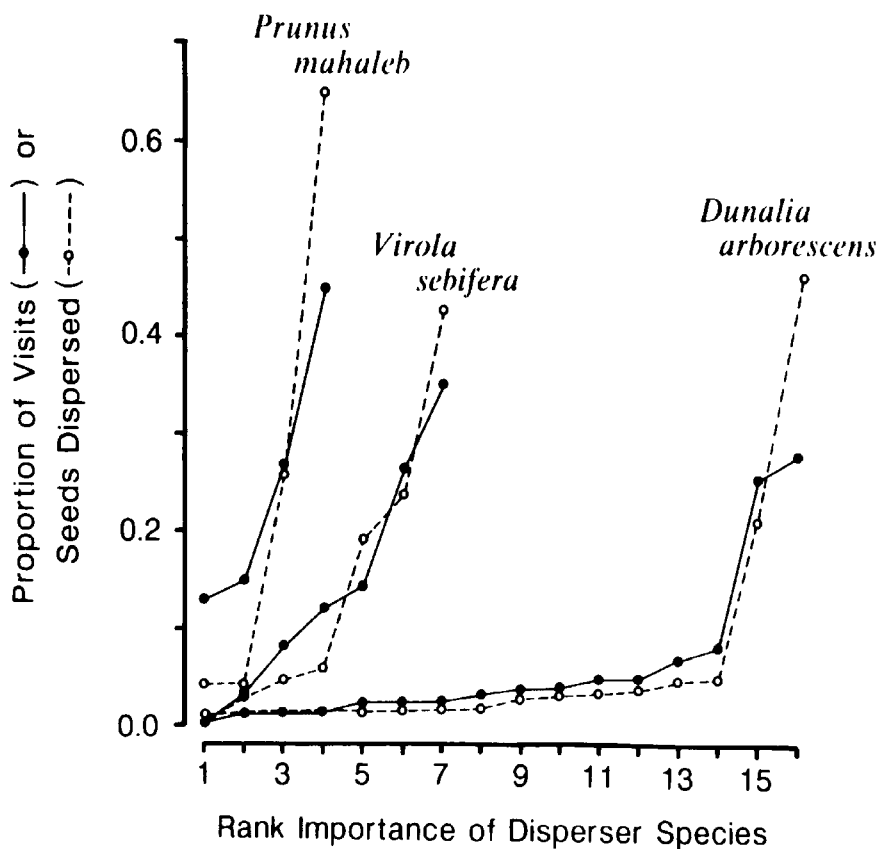

Fig. 2. The proportion of visits made by a species and the proportion of total seeds dispersed by a species, with dispersal agents ranked from smallest to largest proportions (rank importance of disperser species). Representative small, medium and large disperser assemblages are shown. See Fig. 1 legend for sources of data.

and primates (Corlett & Lucas 1990), but I will focus on birds, for which more information is available. Frugivorous birds may be categorized as 'swallowers,' 'mashers' or 'biters' (Trainer & Will 1984; Moermond & Denslow 1985; Foster 1987; Levey 1987).

Swallowers may reject plucked fruits, but generally swallow fruits and included seeds whole so they have a relatively high probability of dispersing handled seeds. Mashers manipulate the fruit in the mouth and ingest juice and pulp along with a variable number of seeds; the proportion swallowed decreases from 1.0 for very small-seeded species to 0.0 for large-seeded species (Levey 1987). Consequently, mashers should have a high probability of dispersing small seeds, but a low probability of dispersing large seeds. Biters remove bits of pulp by biting or pecking a fruit that is either still attached or plucked and held against a branch. Seeds are not swallowed, and are only rarely dispersed when a biter carries the fruit to another tree for feeding. Larger species are more likely to be swallowers, while smaller species tend to be mashers or biters (Trainer & Will 1984; Foster 1987; Snow & Snow 1988).

At least for swallowers, the number of fruits handled per visit roughly increases with disperser size (Howe & De Steven 1979; Jordano 1982; Murray 1988). For dispersers of equivalent size, however, handling method should be a major determinant of the maximum number of fruits that can be handled in a feeding bout. Since they reject seeds and much of the attached pulp, biters will fill the gut less rapidly and potentially handle more seeds per visit than a swallower. This expected pattern may, however, be counteracted by the longer handling times per fruit for biters (Levey 1987). Mashers should be intermediate, but more like swallowers when feeding on small-seeded species and more like biters when feeding on large-seeded fruits (Levey 1987).

The potential number of seeds dispersed per visit is further modified by the length of a visit. Staying in a tree longer will result in more seeds being handled, but also more being regurgitated or defecated beneath the parent (Howe 1981; Pratt & Stiles 1983). Most dispersers leave a feeding tree quickly, however, because of aggressive displacement (Herrera & Jordano 1981; Howe 1981), fear of predators (Howe 1979; Snow & Snow 1988; Fleming 1988) or as part of an intentional diet-mixing strategy (Jordano 1987, 1988; Loiselle 1990). Few dispersers appear to stay in a tree long enough to regurgitate or defecate seeds from that feeding bout (Wheelwright 1991), but for those with longer visit lengths, gut processing becomes an important trait. A swallowed seed may be regurgitated or defecated; regurgitation is most likely for large seeds and small dispersers (Johnson et al. 1985). Gut passage time for defecation varies considerably (Herrera 1984; Jordano 1987) but is almost always longer than for regurgitation (Johnson et al. 1985; Levey 1986, 1987). Given the same visit length, then, a disperser that regurgitates may be less likely to disperse seeds than one that defecates.

Although it is not now possible to dissect out the relative contributions of handling method, visit length and seed processing, disperser species do vary in the number of seeds dispersed per visit (Fig. 1). Coefficients of variation range from 26–183% with a median of 80%. The variation is less than in the number of visits made, but important.

Quantity of seed dispersal: reprise

Species vary greatly in the total number of seeds dispersed (Fig. 1); the median CV is 130.5% and the range from 88–229%. As with the number of visits, the distributions of total numbers of seeds dispersed tend to be skewed; a few species disperse many seeds but most disperse a small to moderate number (Fig. 2).

Two relationships are of further interest. First, do the quantitative traits covary such that species that make many visits tend to also disperse many seeds per visit? The answer appears to be no. Of the 16 data sets, the number of visits was significantly correlated with the number of seeds dispersed per visit only in Guaiacum sanctum $(r_s = .690, n = 17, p < 0.005)$. The typical disperser is deficient in one way or the other.

Second, what is the major determinant of the

quantitative importance of a disperser to a plant? The number of visits a disperser makes appears to be a slightly better predictor of the total quantity of seed dispersed than is the number of seeds dispersed per visit (Table 2). Spearman rank correlations involving the number of visits were generally larger and more likely to be significant than correlations involving the number of seeds dispersed per visit. This suggestive trend does not mean that the number of seeds dispersed per visit is a trivial component of dispersal, however.

Quality of seed dispersal

The quality of seed dispersal is a function of (A) the quality of seed treatment in the mouth and gut and (B) the quality of seed deposition, or probability a deposited seed survives and produces a new adult (Table 1). Wheelwright and Orians (1982) suggested that differences among species in the quality of dispersal may be relatively small, but this need not be true. Dispersers vary in seed treatment, and in the size, shape and heterogene-

ity of seed shadows produced (Willson 1986), and there are many opportunities for some attribute of a disperser to affect the probability of a seed safely completing the long, perilous passage to adulthood.

Quality of treatment

Seed treatment can affect the quality of dispersal by destroying seeds or by altering patterns of germination (Table 1). Although in reality one grades into the other, they will be discussed as distinct effects. In some dispersal systems, seed processing in the bill or mouth is detrimental; seed-eating birds (Coates-Estrada & Estrada 1986) and mammalian carnivores (Herrera 1989b) feeding on fruit crush variable numbers of seeds while swallowing the remaining undamaged. Effects of treatment in the gut, however, are probably more pervasive.

Species of frugivorous birds that are usually considered 'legitimate' seed dispersers seldom damage seeds during gut passage (Howe 1986a). In contrast, seed-eating birds destroy vast quan-

Table 2. Spearman rank correlation coefficients for correlations between estimates of the total number of seeds dispersed by a species and either the number of seeds dispersed per visit or the total number of visits made for the 16 species of plants in Fig. 1. n = number of disperser species used in analyses. * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

Species	n	Correlation between total # seeds dispersed and	
		# dispersed/visit (r_s)	# visits (r_s)
Juniperus virginiana	5	− 0.700	0.900
Cymbopetalum bailonii	25	0.470*	0.729***
Virola sebifera	7	0.714	0.714
Virola surinamensis	8	0.833*	0.695
Ficus aff. *cotinifolia*	14	0.975***	0.642*
Casearia corymbosa	12	− 0.149	0.965***
Prunus mahaleb	4	0.800	0.800
Prunus mahaleb	17	0.320	0.867***
Rubus ulmifolius	8	0.714	0.905**
Tetragastris panamensis	10	0.406	0.828**
Guarea glabra	14	0.026	0.882***
Guaiacum sanctum	17	0.905***	0.913***
Dunalia arborescens	16	0.493	0.532*
Lindera benzoin	4	0.949	0.800
Vitis vulpinia	8	0.814*	0.898**
Parthenocissus quinquefolia	6	0.406	0.928*

tities in the grinding gizzard, but pass some in viable condition (Lambert 1989); the proportion destroyed varies with both bird and seed species (Krefting & Roe 1949). Less data are available for mammals, but it appears that at least some monkeys pass most to all seeds in a viable condition while ungulates often destroy substantial quantities (Howe 1986a). *Tapirus bairdii* and feral horses and cows destroyed, respectively, 78%, 44–83% and 14–21% of the *Enterolobium cyclocarpum* seeds ingested (Janzen 1981, 1982). The differences are at least partly a function of the length of time seeds are retained in the gut.

Studies of germination have focused on comparisons of germination with and without ingestion by dispersers. Of interest here, however, are the few studies that address the effects of different disperser species on germination of a given plant species. In 12 of 49 'trials,' species of dispersers differed significantly in their effects on percent germination (Holthuijzen & Sharik 1985; Reid 1989; Barnea *et al.* 1990, 1991; Izhaki & Safriel 1990). Lieberman & Lieberman (1986) presented a complex study of 16 fruit species and six animal species and reported no overall effect of animal species, but several figures in their paper are suggestive of a difference for some plant species. As with the destruction of seeds, differences among species in effects on percent germination may result from differences in gut retention (Barnea *et al.* 1991).

Dispersers may also alter germination rate (Izhaki & Safriel 1990), and some detected differences in percent germination may simply reflect differences in germination rate on the scale of years. The consequences of altering the speed of germination are likely complex. Potential effects include changes in the length of exposure to post-dispersal seed predators and in the probability of encountering ephemeral seedling microsites.

Quality of deposition

This topic is usually discussed in terms of the probability a seed will be deposited in a suitable site (McKey 1975; Howe & Estabrook 1977; Herrera & Jordano 1981; Wheelwright & Orians 1982). Sites are not simply suitable or unsuitable, however; they vary continuously with respect to seed survival, germination, and seedling growth and survival (Janzen 1983a). Further, the suitability of a site may differ for seeds and seedlings (Schupp & Frost 1989). Seed dispersal should not be viewed in terms of the probability of hitting the right spot, but rather in terms of the creation of a continuous array of survival probabilities, each associated with a dispersed seed.

Wheelwright & Orians (1982) suggested that species of dispersers differ relatively little in quality because suitable sites for dispersal are unpredictable in space and time, and no seed has much of a chance of surviving to produce a new adult. It is true that locations of 'suitable' sites are unpredictable (Schupp 1988a; Whelan *et al.* 1991), but some sites are predictably associated with higher probabilities of survival than are others (Schupp *et al.* 1989). It is also true that the probability of any seed producing a new adult is exceedingly small, but the range of probabilities represented by the different seeds in a population may span orders of magnitude. There are ample opportunities for dispersers to vary substantially in the seed shadows they produce, and consequently in the distributions of survival probabilities they create.

Of interest in this section are attributes of seed dispersers that determine 'where' seeds fall in the broad sense: the biotic and physical conditions into which seeds are deposited. I will consider movement patterns and deposition patterns (Table 1). Though not a clear dichotomy, this distinction will facilitate the discussion.

The major movement pattern affecting where seeds fall is habitat selection. Although they are habitat generalists in a relative sense, dispersers select among habitats on a variety of scales (Herrera 1985). Selection can occur between treefall gaps and forest understory (Charles-Dominique 1986; Hoppes 1988; Levey 1988; Malmborg & Willson 1988; Thomas 1991), between mature and second growth patches (McDiarmid *et al.* 1977; Thomas 1991), or along moisture and vege-

tation gradients (Karr & Freemark 1983). On a more local scale, species of frugivorous birds differ in post-feeding microhabitat use (Sorensen 1981; Jordano 1982; Izhaki *et al.* 1991; Schupp, E. W., unpubl. data, see Fig. 3). At an even smaller scale, species of ants can differ in the types of substrates to which they disperse seeds (Horvitz 1981, Horvitz & Schemske 1986). The habitats and microsites in which seeds are deposited vary in suitability to plants. The characteristics of the physical environment that influence habitat selection by dispersers also influence the probability of a seed surviving, germinating and growing to adulthood (Augspurger 1983; Sork 1985, 1987; Murray 1988; Schupp 1988a, b; Willson 1988; Schupp & Frost 1989; Alvarez-Buylla & Martinez-Ramos 1990; Howe 1990; Vazquez-Yanes & Orozco-Segovia 1990; Willson & Whelan 1990; Fisher *et al.* 1991; Whelan *et al.* 1991).
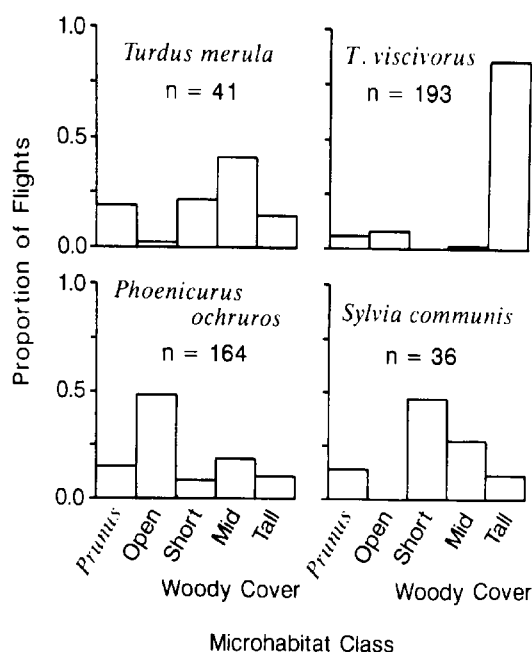
The size, shape and density of a seed shadow

is further influenced by the directionality and rate of movement away from the fruiting tree, and by the rate and pattern of seed deposition. Some disperser species move directly to other fruiting trees, others to isolated perches (Howe & Primack 1975; Coates-Estrada & Estrada 1988; Fleming 1988). Some move continuously, others intersperse quiescent periods with short periods of rapid movement (Murray 1988). Some fly short distances to a perch for seed processing, others fly longer distances (Cruz 1981; Howe 1986b; Coates-Estrada & Estrada 1988; Schupp, E. W., unpubl. data, see Fig. 4). Overlying these movement patterns are variations in the rate and pattern of seed deposition. Regurgitated seeds are deposited rapidly (Levey 1986), while defecated seeds may be passed in minutes by small birds (Levey 1986), hours to days by monkeys (Milton 1981) or weeks to months by ungulates (Janzen 1982). Seeds may further be deposited singly or in clumps. *Trogon rufus* defecates *Tetragastris panamensis* seeds individually while *Alouatta palliata* defecates them in piles of up to 60 (Howe 1980). Some species deposit the entire gut load in a single defecation, others spread it over several defecations (Izhaki *et al.* 1991). Given that growth and survival depend in some manner on distance from a conspecific adult (Clark & Clark 1984; Howe *et al.* 1985; Coates-Estrada & Estrada 1988; Hubbell & Foster 1990) and on density of conspecific seeds and seedlings (Howe 1980; Webb & Willson 1985; Andersen 1987; Lewis 1987), movement and deposition patterns can have major impacts on the quality of seed deposition.

Diet-mixing by dispersers adds complexity to the local environment facing a dispersed seed (Fleming & Heithaus 1981; Loiselle & Blake 1990). Both the probability of being deposited in a fecal clump with another species and the identity of neighbors in that clump vary with disperser species. Seed species richness is greater in the guts of large than of small sylviid warblers (Jordano 1987), and greater in defecations of Costa Rican mashers than of swallowers (Loiselle 1990). Certain combinations of seeds are found more often than expected by chance, and dispersers

Fig. 3. Differences in distributions of post-foraging microhabitat use for four representative seed dispersers of *Prunus mahaleb* at 1600 m in the Sierra de Cazorla, Spain. Distributions are based on the first destination of a bird after feeding on fruit and leaving the tree (Schupp, E. W., unpubl. data). n = number of flights recorded.
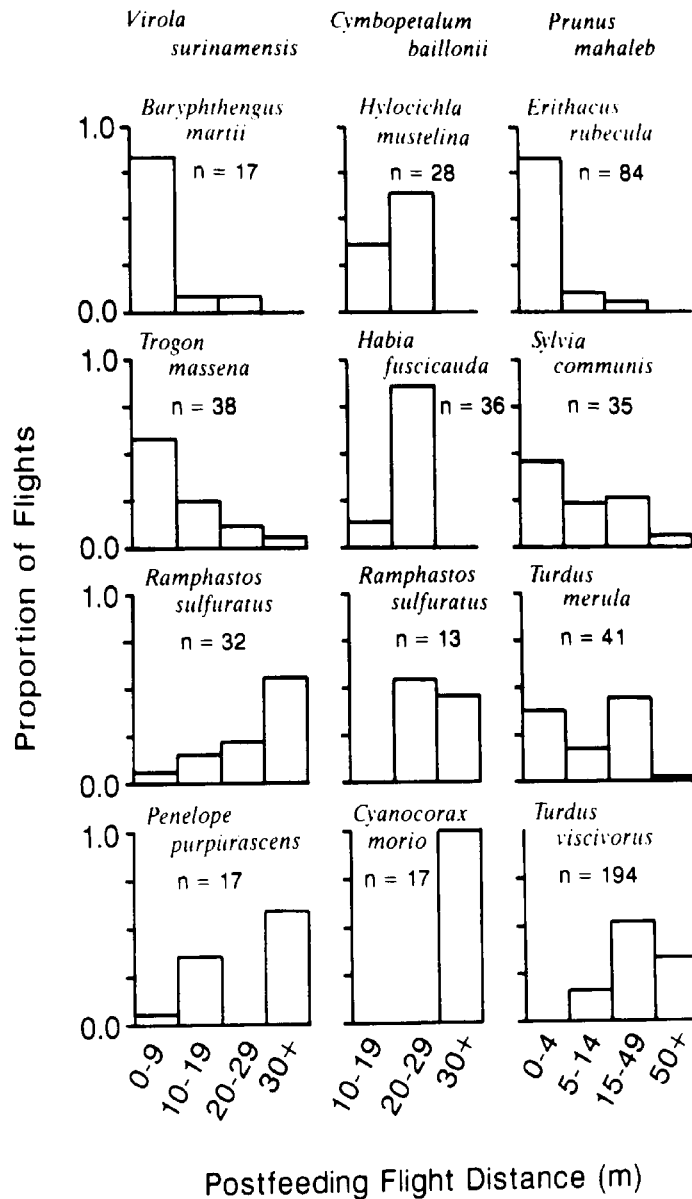
Fig. 4. Distributions of distances flown in first flight from feeding tree for representative bird species dispersing *Virola surinamensis* (Howe 1986b), *Cymbopetalum baillonii* (Coates-Estrada & Estrada 1988) and *Prunus mahaleb* (Schupp, E. W., unpubl. data). n = the number of flights observed for a disperser species.

differ in the combinations generated (Jordano 1988; Loiselle 1990). Interspecific competition among seedlings in these mixed species clumps may be an important factor affecting the quality of deposition. If some species are consistently superior competitors, the vigor of a seedling will partly depend on the identity of its neighbors, a function of the species that dispersed that seed (Loiselle 1990).

Which disperser attributes have the greatest impact on the quality of deposition depend on the reason dispersal is advantageous to the plant. Howe & Smallwood (1982) proposed three advantages of dispersal: (1) escape, (2) colonization

and (3) directed dispersal. If escape from the vicinity of the parent is a critical advantage of dispersal, traits promoting movement out of the parent and away from conspecifics will be most important. If colonization of unpredictable disturbances is crucial, characteristics promoting widespread dispersal will have a dominant impact. If specific but predictable conditions are needed for establishment and survival, dispersal directed towards the necessary habitat or microsite will be the crucial characteristic. Adequately assessing which disperser traits are most important requires more detailed knowledge about the consequences of various patterns of seed dispersal than is currently available. Recent studies have, however, supported the notion that the characteristics associated with high-quality deposition are not fixed, but rather depend on the ecology of the plant.

Howe et al. (1985) presented evidence that the quality of deposition of *Virola surinamensis* seeds is largely a function of how far birds fly before perching to process seeds. Murray (1988) suggested that for gap-dependent plants, however, the quality of deposition primarily depends on rates of movement and gut passage; species moving rapidly and depositing seeds over an extended period are most likely to disperse seeds to present and future gaps. Finally, in southeastern Brazil the quality of deposition of *Erythroxylum ovalifolium* seeds is determined by plant microsite requirements. Seeds are dispersed to the moist interiors of terrestrial bromeliads by the frog *Hyla truncata* and to open, sandy soil by the lizard *Tropidurus torquatus* (Fialho 1990); experimental 'dispersal' yielded higher germination and establishment for 'frog-dispersed' than for 'lizard-dispersed' seeds. Empiricists have only begun to address the quality of deposition, but these and other studies demonstrate that innovative approaches can yield exciting insights.

Disperser effectiveness: reprise

Both quantity and quality are critical components of effectiveness, but a paucity of detailed studies hinders an assessment of the relative importance of each at present. Recent studies have begun to yield preliminary answers, however. Reid's (1989) study of dispersal of the mistletoe *Amyema quandang* by the birds *Dicaeum hirundinaceum* and *Acanthagenys rufogularis* is one of the most thorough. *Acanthagenys rufogularis* was less reliable seasonally but more abundant, and as a result was quantitatively more important than *D. hirundinaceum*. Compared to seeds dispersed by *D. hirundinaceum*, those dispersed by *A. rufogularis* were less likely to germinate and less likely to land on a perch, but perches on which they did land were more likely to be suitable. The outcome was no detectable difference between the species in the quality of dispersal. As a consequence, *A. rufogularis* was the more effective disperser because it provided the greater quantity of dispersal.

Quantity does not appear to be the key component of disperser effectiveness in all systems, however. *Phainopepla nitens* was overwhelmingly the most effective disperser of the mistletoe *Phoradendron californicum* because it was both quantitatively and qualitatively superior to either of the other two dispersers at the site (Larson 1991).

Few data exist from systems involving more species of dispersers and less discrete qualities of dispersal sites, but useful preliminary calculations can be made from Howe's work with *Virola surinamensis*. Using data on the quantity of dispersal from Howe & Vande Kerckhove (1981), flight distances from Howe (1986b), and distance-dependent survival from Howe et al. (1985), I estimated both quantitative and qualitative components of disperser effectiveness. This analysis assumed the quality of dispersal was determined by the distance a seed was dispersed, and effectiveness could be represented by the estimated number of 12-wk seedlings produced. Spearman rank correlations suggest effectiveness was related more strongly to the quality ($r_s = 0.90$, $p = 0.10$, $n = 5$) than to the quantity ($r_s = 0.10$, $p > 0.50$, $n = 5$) of dispersal. If the definition of dispersal was relaxed to include all handled seeds to account for the small but real probability of survival beneath the parent, effectiveness was still more strongly correlated with quality ($r_s = 0.93$, $p < 0.05$, $n = 6$) than quantity ($r_s = 0.52$, $p > 0.20$,

n = 6). Despite the crudeness of the analyses, there is evidence that in some systems quality is the dominant component of effectiveness.

Empirical studies of seed dispersal have emphasized the quantity of seeds dispersed by different species, often with the assumption that quantity is a strong correlate of effectiveness. The available evidence suggests, however, that this assumption may frequently be invalid. Investigations of the quantity of dispersal are important, but are not surrogates for studies of effectiveness; more emphasis should be placed on quantifying the consequences of dispersal by different disperser species. Effectiveness can only be evaluated with detailed studies of the natural histories of the interacting organisms; studies that interweave the behavior, morphology and physiology of dispersers with the demography of plants. The present review has revealed many gaps in our knowledge of effectiveness, but has also shown that the answers are not beyond our reach.

Disperser effectiveness: epilogue

This paper has covered characteristics of dispersers that more or less directly determine disperser effectiveness, but more complex relationships exist. The interactions of secondary dispersal agents such as dung beetles (Estrada & Coates-Estrada 1986) and ants (Byrne & Levey, this volume) with the seed shadows produced by vertebrates may greatly alter the effectiveness of primary dispersers. Defense of a fruit source (Snow & Snow 1984) can curtail the number of disperser species contributing to the seed shadow and delay the timing of dispersal. As a consequence of fruit selection based on external traits, disperser species may sometimes disperse different-sized seeds (Jordano 1984), which can in turn influence the success of dispersal. These are but a fraction of the intriguing complexities involved in disperser effectiveness.

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