

Frugivores and fruit syndromes: differences in patterns at the genus and species level

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Fischer, K. E. and Chapman, C. A. 1993. Frugivores and fruit syndromes: differences in patterns at the genus and species level. – *Oikos* 66: 472–482.

Comparative studies have suggested that fruit traits, such as color, size, and protection, have evolved as covarying character complexes (“dispersal syndromes”) in response to selection by frugivorous dispersers. However, many comparative studies of disperser-specific syndromes have used species as sampling units, a method which implicitly assumes that character complexes evolve *de novo* in each species. This approach overestimates the number of times a character complex has evolved because covariation that results from common ancestry (plesiomorphy) is confounded with covariation across independent lineages (convergence). We compiled data on fleshy fruit traits from five regional floras to test the hypothesis that fruit traits form character complexes which covary independently of phylogeny (i.e. across lineages). Our results suggest that such character complexes are rare, and that analyses of covariation among these character complexes are extremely sensitive to the investigator’s choice of sampling unit. When syndromes derived from observations of the foraging behavior of frugivores are analyzed using species as sampling units, our data show significant associations among traits at four out of five locations. In contrast, when genera are used as sampling units, there is no significant association among traits at any of the sites. Theories of coevolution between fruits and frugivores have proposed that fruit morphology is a response to selective pressures exerted by frugivorous birds and mammals. If these frugivores have shaped fruit morphology into dispersal-related character complexes or syndromes, then traits associated with a syndrome should be absent or much reduced in frequency in regions lacking that guild of dispersers. To test this prediction, we examined the flora of New Guinea, which lacks primates and other diurnal mammalian frugivores, and found no difference in the frequency of traits associated with dispersal by diurnal mammals.

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Most tropical rainforest trees produce fruits that are consumed by animals and are thought to rely on frugivores for seed dispersal (Frankie et al. 1974, Howe 1986, Dowsett-Lemaire 1988). Comparative studies (Ridley 1930, Turcek 1963, van der Pijl 1969, Snow 1981, Janson 1983, Knight and Siegfried 1983, Pratt and Stiles 1985, Wheelwright and Janson 1985, Herrera 1986, Howe 1986, Dowsett-Lemaire 1988) have suggested that fruit traits, such as color, size, and protection, have evolved as covarying character complexes (“dispersal syndromes”) in response to selection by frugivorous dispersers (Table 1). However, seed dispersal

studies have produced little empirical support for tight coevolutionary relationships between plants and their seed dispersers (Howe and Smallwood 1982, Wheelwright and Orians 1982, Herrera 1984, 1985, 1986, Howe 1984). These findings have been attributed to factors which limit the potential for mutualistic coevolution between plants and their animal dispersers, including: asymmetries in the relationship between plants and their dispersers, inequalities in the evolutionary life spans of plant and animal taxa, differences in generation lengths of plants and their dispersers, extensive gene flow between plant populations, weak selective

Accepted 8 May 1992

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Table 1. Bird and mammal fruit syndromes based on observations of frugivore foraging behavior derived from the literature. Note: 1) the variability in syndromes ascribed to the same disperser guild in different geographic regions, 2) the variability in the extent to which syndromes are subdivided by disperser guilds (e.g. mammal vs arboreal mammal), and 3) the variability in the composition of guilds in different regions (e.g. bird vs mammal in Peru, in contrast to birds and monkeys in Gabon and Malawi).

Bird fruit syndromes

Site/Type	Size*	Form	Color	Protection	Source
Peru	≤ 14 mm	not given	red, black, mixed, blue, white, purple	none	Janson 1983
Gabon	< 5 g	berry, drupe, capsule	purple, red	thin or dehiscent	Gauthier-Hion et al. 1985
Costa Rica	not given	juicy, persistent	bright	not given	Wheelwright et al. 1984
Montane New Guinea	$\mu = 11.6$ range 3–28	figs, capsule and drupe	mixed, white, green, pink, yellow, red, purple, orange	none or dehiscent	Beehler 1982
Southern Africa	“small”	pod, capsule, drupe, berry	red, black	dehiscent or none	Knight and Siegfried 1983
Malawi	“small” ~ 3–50 mm	berries, drupes, capsules	black, green, orange, red, yellow, blue, brown, white, purple	none, dehiscent, protected	Dowsett-Lemaire 1988
Highly frugivorous	large, > 10 mm long	aril, drupe	blue, black	dehiscent, unprotected	Howe 1986, Howe and Westley 1988
Partly frugivorous	< 10 mm long	aril, berry drupe	black, blue, orange, red, white	not given	Howe 1986, Howe and Westley 1988
Generalized frugivores	“small”	berry, drupe, capsule, aril	none given	none	Snow 1981
Specialized frugivores	“large”	berry, drupe, capsule, aril	none given	none or dehiscent	Snow 1981

Mammal fruit syndromes

Site/Type	Size*	Form	Color	Protection	Source
Peru	> 14 mm	none given	brown, green, white, yellow	present	Janson 1983
Gabon	5–50 g	berry, drupe, capsule	bright red, orange, yellow	not significant	Gauthier-Hion et al. 1985
Southern Africa	“large”	pod, capsule, drupe, berry	yellow, green	not given	Knight and Siegfried 1983
Malawi	“variable” $\bar{x} = 15$ range ~ 4–100	berry, drupe, capsule	red, purple, green, orange, brown, yellow, white	none, protected, dehiscent	Dowsett-Lemaire 1988
Arboreal	“large”	aril, compound	green, brown, orange, white, yellow	often dehiscent	Howe 1986, Howe and Westley 1988
Aerial	“large”	various	green, yellow	not given	Howe 1986, Howe and Westley 1988
Hoarding	none given	nuts	brown	thick walls, indehiscent	Howe and Westley 1988
Terrestrial	none given	nuts, pods or capsules	green, brown	indehiscent	Howe and Westley 1988

* width in mm, unless noted otherwise.

pressures on dispersers, ecological variables outside the control of the parent plant (e.g. influence of other fruiting plants, numbers and kinds of seeds in feces), unpredictability of germination sites, secondary dispersal subsequent to deposition by the primary disperser, morphological similarities among dispersers, and lack of evolutionary plasticity in fruit traits (Wheelwright and Orians 1982, Howe 1984, Herrera 1985, 1986, Loiselle 1990). In addition, fruit traits may represent a response to other selection pressures or may perform more than one function. For example, it has been suggested that green fruits reduce the energetic costs of reproduction through photosynthesis (Wheelwright and Janson 1985, Cipollini and Levey 1991) or that red fruit colors provide protection from arthropod predators through crypsis (Willson and Thompson 1982).

The objectives of this study are to examine the degree to which plants have evolved predictable, disperser-specific syndromes and to determine the consequences of using different taxa as sampling units when analyzing comparative data to test for the existence of dispersal syndromes. If syndromes have evolved in response to selection by frugivorous dispersal agents then 1) convergent evolution should produce character complexes that covary across lineages among plants that share dispersers and 2) regions that lack a particular group of dispersal agents (e.g. diurnal mammals) should show a low frequency of traits associated with dispersal by that guild. We first assess these predictions by testing the hypothesis that fruit traits covary across taxa. To do this we examine the effects of using species and genera as sampling units: if syndromes are the result of convergent evolution, patterns should persist whether genera or species are used as sampling units. Second, in order to make our statistical tests more stringent, we use two "consensus" color syndromes (consensus definitions of bird and mammal fruit colors derived from the literature; see Table 1), to determine whether size and protection covary with these color syndromes as predicted by observations of frugivores' foraging behavior. Finally, we test the specific prediction that character complexes associated with a given frugivore guild should decrease in frequency when that guild is absent.

Choosing the appropriate taxonomic level for analysis poses the problem of what to consider an independent evolutionary event (Huey 1987, Pagel and Harvey 1988, 1989, Gittleman and Kot 1990). Many comparative studies present analyses that use species as sampling units, a method which implicitly assumes that the character complexes in question evolved independently in each species of a given clade. It is unlikely that all species within a genus are independent with respect to fruit morphology, and therefore analyses using species as sampling units are likely to inflate estimates of the number of times a particular character complex evolved. Without accurate phylogenies, use of higher taxa becomes problematic because including polyphyletic taxa in analyses overestimates within-taxon var-

iability and may underestimate the number of evolutionary transitions between character states. In addition, a lack of accurate phylogenies for the taxa in question renders comparative analyses insensitive to the direction and sequence of character transformation (Donoghue 1989).

Because we lack accurate phylogenies for the plants in question, we treated genera as monophyletic groups and assumed that each character complex represented in the genus evolved no more than once within that genus. For example, given a genus containing five species with unprotected red fruits and two species with unprotected black fruits, each complex (unprotected-red and unprotected-black) would be counted as having evolved once.

Genera may be more appropriate sampling units than species or higher taxa (e.g. families) for attempting to identify coevolved dispersal syndromes because 1) genera are more likely to be monophyletic than higher taxa; 2) use of genera as sampling units prevents speciose taxa from dominating the analyses; 3) traits shared among species within a genus are likely to be the result of common descent rather than convergence (see also Janson 1983). Our assumption, that each character complex evolved only once within a genus is based on the premise that within a monophyletic clade the most likely evolutionary pathway is that which minimizes the number of transitions (i.e. that evolution tends toward parsimony). Use of genera as sampling units is not a panacea: because genera are related to one another, assuming that traits evolve *de novo* within genera and that genera are independent within families can overestimate the number of times each character complex evolved; however, analyses using genera as sampling units inflate estimates of the number of evolutionary events far less than does the use of species as sampling units.

To illustrate this point, let N be the number of genera per character complex within a family, and let P be the number of species per character complex within a genus. Using genera as sampling units will inflate the number of evolutionary events within a family by a maximum of N for the family's plesiomorphic character complex and by a maximum of $N-1$ for each derived character complex. Analyses of the same family using species as the sampling units will inflate the number of evolutionary events by $(N)(P)$ for the plesiomorphic character complex and $(N-1)(P)$ for each derived character complex within the family. For example, given a family with five genera, each of which has four species that produce brown-husked fruits, the most parsimonious assumption is that brown-husked fruits evolved once and the remaining species inherited this condition as a plesiomorphic trait. If fruits with brown husks are the family's ancestral condition (plesiomorphic), then use of genera as sampling units overestimates the number of evolutionary events by a maximum of N , i.e. 5. Alternatively, if brown-husked fruits are derived (syn-

apomorphic) with respect to the family's ancestral fruit, then we have overestimated the number of times brown husks have evolved by a maximum of $N-1$ or 4. The same analysis, performed using species rather than genera as sampling units, could inflate the estimates of the number of times brown husks evolved by a maximum of $(N)(P)$, i.e. 20, in the plesiomorphic case and by a maximum of $(N-1)(P)$ or 16 in the derived case. Thus, while each analysis risks inflating estimates of the number of times a character complex has evolved, the use of genera reduces by a factor of P the maximum potential error.

In contrast, our assumption that evolution tends toward parsimony may underestimate the number of evolutionary events within the genus (i.e. at the species level). If character complexes are repeatedly derived within genera, then the assumption of parsimony is false and will cause an underestimation of the number of times a character complex has evolved. For example, suppose that a genus contains four species with blue- (A and B) and green-husked (C and D) fruits. Assuming that blue-husked fruits are derived with respect to the genus, the most parsimonious sequence would be that blue-husked fruits evolved once in A and were inherited by (plesiomorphic for) B (i.e. $A \rightarrow B$). Similarly, if green-husked fruits were derived with respect to the genus, the most parsimonious scheme would be if green husks evolved once in C and were subsequently inherited by D (i.e. $C \rightarrow D$). In contrast, if we knew the phylogeny was $C \rightarrow B$, and $A \rightarrow D$, then green-husked fruits would have evolved twice, once in C, and once from the blue-husked condition in D. Likewise, blue-husked fruits would have evolved twice, once in A, and once from the green-husked condition in B. In this case the effect of our assumption of parsimony would be to underestimate the number of times green-husked and blue-husked fruits had evolved.

The effects of these two potential sources of error, assuming that genera are independent and assuming that evolution is parsimonious, are in opposite directions. Overestimating the number of times that a character complex has evolved will mimic syndromes of correlated characters, whereas underestimating the number of evolutionary events may obscure syndromes. In the best of all possible worlds the potential inflation caused by the first assumption would exactly offset the potential under-estimation caused by the second. Although it is unlikely that these factors will balance one another perfectly, there is no reason to believe that the two assumptions, taken together, consistently bias our results. In contrast, analyses using species as sampling units employ the least parsimonious assumptions and increase the risk of overestimating the number of times that a character complex has evolved by a factor of P .

Our second prediction was that regions lacking a guild of dispersal agents (e.g. diurnal mammals) should show a low frequency of traits associated with dispersal by that guild. To test this prediction we examined the

flora of New Guinea. New Guinea offers an ideal test of this prediction because it lacks diurnal mammalian frugivores; although it has frugivorous birds, bats, rodents, and marsupials, the bats, rodents, and marsupials are nocturnal (Lee and Cockburn 1985, Fischer pers. obs.). In addition, there are a number of historical and biogeographical reasons that we would not expect to find fruits adapted for diurnal mammalian dispersal in New Guinea.

New Guinea's biota is derived from two geographic regions: West Malesia (Borneo, Malaya and the lands of the Sunda continental shelf west of Wallace's line) and Sahul (Australia and adjacent islands) (Gressitt 1982a). The majority of plants (van Balgooy 1976, Walker and Hope 1982), invertebrates (Main 1982, Evans 1982, Gressitt 1982b), reptiles, amphibians (Zweifel and Tyler 1982), and birds (Mayr 1988) in New Guinea originated in West Malesia, while most of the mammals are derived from Sahul (Gressitt 1982a). Geologic evidence and the bicentric distribution of some important floristic elements in Malesia suggest that many Malesian plant species reached New Guinea before the collision of Australia with the Sundaic island arcs during the Miocene (Audley-Charles 1987). Indeed, there is palynological evidence for land connections between Australia-New Guinea and Asia as far back as the mid-Cretaceous (Truswell et al. 1987). Thus, a large number of plant taxa were likely to be established in both regions before the arrival of many of the extant mammalian species at either site. In New Guinea, the plant taxa that predate the arrival of diurnal mammalian frugivores in Sunda should be adapted to bird, bat, marsupial, or wind dispersal.

Second, it is unlikely that Sundaic plants with fruits adapted for non-volant mammalian dispersal have colonized New Guinea because of the persistent oceanic barriers between New Guinea and the Sunda shelf. The major land masses reached positions close to those they currently occupy approximately 15 million years ago (Whitmore 1987). Although sea levels fluctuated considerably during the Plio-Pleistocene, substantial barriers to dispersal between Sundaland and New Guinea persisted. It is probable that most plant taxa that reached New Guinea during this period did so with volant dispersers (i.e. birds, bats, and wind). Thus, in New Guinea we expect that character complexes associated with dispersal by diurnal mammalian frugivores should be under-represented relative to those character complexes associated with bird and bat dispersal.

Methods

Data on fruit size, color, and structural protection were collected from the published literature and floras: Guiana (van Roosmalen 1985); Malaya (Whitmore 1972, 1973, Ng 1978); New Guinea (Womersley 1978,

Table 2. For each site we list the total number of genera, the mean number of character states found within a genus, the proportion of genera with either protected or unprotected fruits, the proportion of genera with both protected and unprotected fruits, the proportion of genera with fruits of only one color, the proportion of genera with fruits in two color categories, the proportion of genera with fruits in three color categories, the proportion of genera with fruits in four color categories, and the proportion of genera with fruits in five color categories.

	Guiana	Uganda	Malaya	New Guinea	Panama
No. of Genera	132	24	64	35	59
Mean character states/genus	2.6	2.4	2.3	2.5	2.7
Genera w/1 protection state	92.1%	100%	87.8%	77.8%	86.7%
Genera w/2 protection states	7.9%	0%	12.2%	22.2%	13.3%
Genera w/1 color	11.2%	10%	34.1%	22.2%	30.0%
Genera w/2 colors	36.0%	50%	24.4%	50.0%	30.0%
Genera w/3 colors	39.3%	3%	24.4%	16.7%	20.0%
Genera w/4 colors	11.2%	10%	14.6%	5.6%	20.0%
Genera w/5 colors	2.2%	0%	2.4%	5.6%	0%

Henty 1981, Johns 1987); Panama (Croat 1978, Chapman pers. obs.) and Uganda (Hamilton 1981 and Chapman pers. obs.). Fruits were classified as structurally protected if the exocarp was greater than 3 mm thick or described as thick, leathery, coriaceous, or woody. Fruits with spines, stinging hairs or other forms of mechanical defense were also considered to be protected. Only non-dehiscent, fleshy fruits were considered since botanists do not employ uniform criteria in describing dehiscent fruit. Color was assigned based on descriptions of ripe material only. If more than one color was listed for a ripe fruit (e.g. red or black when ripe) the species was listed in both color categories. If more than one color was present on ripe individual fruits, then the fruit was classified as having mixed colors and was excluded from our analysis. Fruit size was based on published measures of the diameter of fresh, ripe specimens. When a range of values was given, the mean for the range was used.

The color and protection state of fruit in each species within a genus was tabulated and each unique occurrence was scored. Each color and each category of protection is considered a character state; color and protection, together, form a character complex. When a genus contained species with different character states, each character complex was scored as evolving once within that genus. Thus, if a genus contained species producing brown, husked fruits and species producing orange, husked fruits, the character complexes orange-husked and brown-husked were each scored as having evolved once within that genus. Analyses performed with species as sampling units employed the same procedures.

The mean size of fruits in each character complex was determined for each region. The mean size of fruits within each genus was also determined and ANOVA was used to compare the generic means of the character complexes within regions.

We used G-tests to determine whether color and protection were associated among the tabulated genera and species within each geographic location. Following

these analyses, fruit colors were consolidated into two categories corresponding to a consensus definition of bird (red, pink, blue, black and purple) and mammal (orange, yellow, green, brown) color syndromes (Table 1). The data were then analyzed using G-tests to determine whether color (bird or mammal) and protection were associated among the tabulated taxa within each geographic location. This analysis was performed twice, once with genera as the sampling units, and once with species as the sampling units. If sample sizes were less than 50, G-tests were adjusted for small sample size using Williams' correction (Sokal and Rohlf 1981).

These data are not without shortcomings. Floristic accounts of fruit color and size are usually based on field data; however, fruit construction is often analysed using herbarium specimens which differ in their state of preservation and the extent to which relevant characters such as husk thickness are preserved. Nonetheless, these problems are unlikely to act in a consistent fashion that would bias our results.

Because inferential statistics are techniques designed primarily to reject a false null hypothesis, rather than to confirm it or to test its reliability, it is important to determine the statistical power of a test if confirmation of a null hypothesis is required (Cohen 1988). Power tests are often used to determine the ability of a given statistical test to detect type II error or the probability of failing to reject a false null hypothesis. For statistical tests where the null hypothesis is of particular interest, power analyses should be used to ensure that the power of the test ($1-\beta$) is as large as possible and β is minimized (Sokal and Rohlf 1981). The larger $1-\beta$, the smaller the probability that one has failed to reject a false null hypothesis. The power of a test is determined, in part, by the size of the difference or the "effect size" one wishes to detect. Effect size is the difference between the distribution posited by the null hypothesis (in our analyses, no association between character states) and that posited by the alternative hypothesis (i.e. reliability of retaining some association between character states). As the effect size to be detected becomes smaller, the

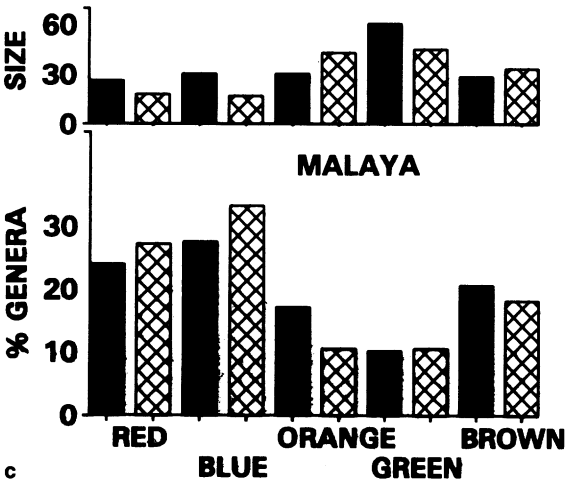
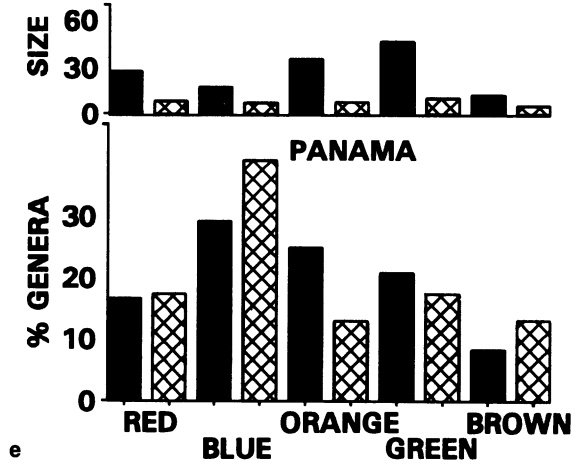
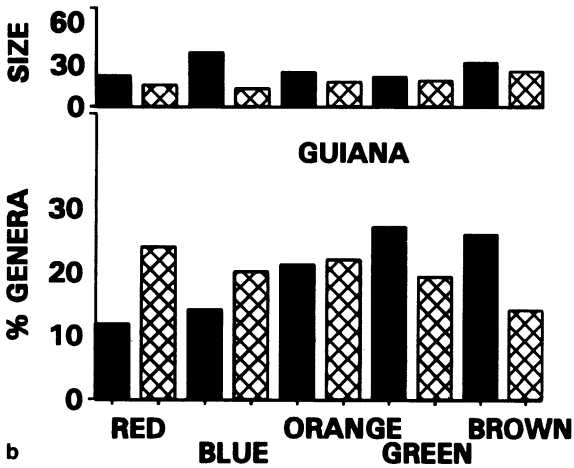
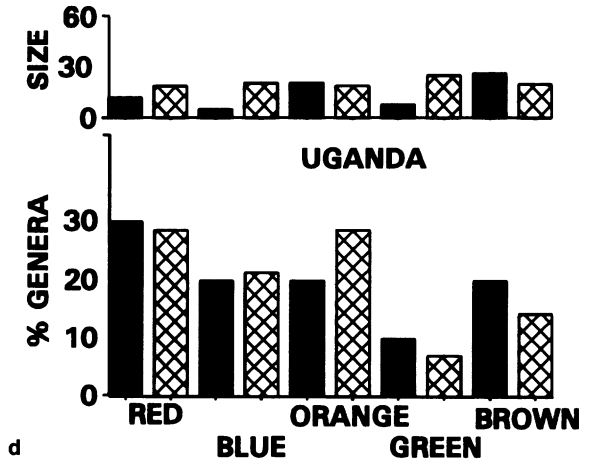
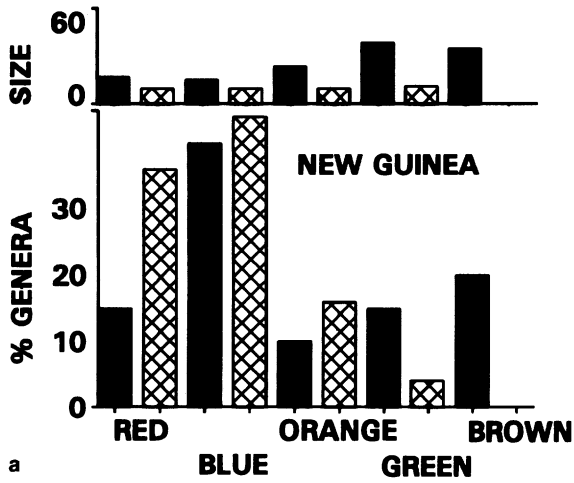


Fig. 1. The proportion of genera containing species in each character complex for the five regions. These proportions may sum to more than 100 because genera may have species in more than one character complex. The mean diaspore size (in mm) for each character complex is given above the histogram. Solid bars indicate protected complexes; hatched indicate unprotected complexes.

Table 3. Results for each of the analyses. Analyses are subdivided by region, by how the color of fruits was categorized (colors or consensus syndromes), and by the taxon used as the sampling unit (species or genus). Values for the G-test, P-values, and the power (1-β) of each comparison are provided.

Location	Category	Sampling unit	G-value	P-value	1-β-value
Uganda	colors	species (N=81)	12.99*	<0.025	0.83
		genus (N=24)	1.17	>0.50	0.19
	syndrome	species (N=81)	2.92	>0.05	0.37
		genus (N=24)	0.73	>0.10	<0.17
Malaya	colors	species (N=411)	63.41**	<<0.001	0.90
		genus (N=64)	1.45	>0.50	0.61
	syndrome	species (N=411)	29.35**	<<0.001	>0.99
		genus (N=64)	0.12	>0.50	0.12
New Guinea	colors	species (N=136)	26.18**	<0.001	0.98
		genus (N=35)	9.32	>0.05	0.29
	syndrome	species (N=136)	13.10**	<0.001	0.93
		genus (N=35)	1.14	>0.10	<0.22
Guiana	colors	species (N=570)	51.73**	<<0.001	>0.99
		genus (N=132)	15.49**	<0.005	0.98
	syndrome	species (N=570)	45.93**	<<0.001	>0.99
		genus (N=132)	2.73	>0.05	0.47
Panama	colors	species (N=176)	9.33	>0.05	0.71
		genus (N=59)	1.44	>0.50	0.49
	syndrome	species (N=176)	6.61**	<0.01	0.76
		genus (N=59)	0.41	>0.50	0.12

*significant at $p < 0.05$.

**significant at $p < 0.01$.

power of the test declines and discriminating between null and alternative hypotheses becomes more difficult. In other words the power of a test decays rapidly as the predictions of the alternative and null hypotheses converge, a consequence of the roughly inverse relationship between type I and type II error.

Results

On average each genus contained two to three character complexes (mean across sites = 2.50), indicating flexibility within genera (i.e. at the species level) in the expression of these traits (Table 2). Most species were monomorphic for color; however there was considerable variation in color among species within a genus (\bar{x} = 2.56 colors per genus). Similarly, the size of fruits within a character complex tended to be quite variable (Fig. 1); size often ranged several hundred millimeters within a single character complex. In contrast, protection appeared to be less variable than color or size: on average 11.1% of the genera at each site contained both protected and unprotected fruit species.

When species were used as sampling units, our analyses indicated that color and protection were associated in all locations except Panama (Table 3). In contrast, when genera were used as sampling units, color and protection were not associated in any location except Guiana (Table 3). When consensus syndromes are analyzed using species as sampling units, our data show

significant associations between character states at four out of five locations. In contrast, when genera are used as sampling units, there is no significant association between character states at any of the sites (Table 3). Thus, our first prediction, that if syndromes exist character states should covary independently of phylogeny, appears not to be supported. Our results also suggest that analyses of association among character states are extremely sensitive to the choice of sampling unit.

Our second prediction was that if existing frugivores have shaped fruit morphology into dispersal-related character complexes or syndromes, then traits associated with a syndrome should be absent or much reduced in frequency in regions lacking that guild of dispersers. To test this prediction, we examined the flora of New Guinea, which lacks diurnal mammalian frugivores.

To determine whether character complexes associated with diurnal mammalian dispersal were underrepresented in New Guinea, we first determined which fruit traits are associated with consumption by diurnal mammalian frugivores. The variety of syndromes described in past studies makes it difficult to determine traits consistently associated with diurnal mammalian dispersal. For instance, Gautier-Hion et al. (1985) and Dowsett-Lemaire (1988) unite birds and primates in a single dispersal syndrome, whereas other studies (reviewed by Howe 1986) have described separate bird and mammal syndromes. The consensus syndrome used here is based on Howe's (1986) review, which indicates that fruits consumed by diurnal mammals generally tend to be large, mechanically protected, and green, brown, orange, or yellow in color.

The proportion of genera with these traits in New Guinea did not differ from the proportion of genera with these traits in the four locations with diurnal mammalian frugivores (Fig. 1). It has been suggested that primates are usually more capable of handling fruits with indehiscent husks than avian frugivores (Howe 1986). We therefore contrasted the number of genera with protected and unprotected fruits at all locations to test the prediction that New Guinea should have fewer protected fruits than areas with primate frugivores. This prediction was not upheld (protection was not significantly associated with location, ($G = 3.03$, $df = 4$, $p > 0.50$, $\beta = 0.06$)). In fact, contrary to prediction, New Guinea had the highest proportion of protected fruits of any location. To test this prediction more rigorously, we performed a pair-wise comparison of genera found in both New Guinea and Malaya ($N = 22$ genera). There was no significant difference between the proportion of protected fruits between the two sites ($G_{adj} = 4.47$, $df = 4$, $p > 0.10$, $\beta = 0.68$). The power of the first comparison (New Guinea vs the other four locations) is sufficient ($1 - \beta = 0.94$) that we can retain the first null hypothesis with relative confidence. Given the G -value and the low power of the second test we can neither accept nor reject the hypothesis that the proportion of protected fruits differs in New Guinea and Malaya; however, it is important to recall that the low power of the second test is, in part, a function of the small sample size ($N = 22$).

Discussion

Dispersal syndromes have been compiled based on observations of frugivores' foraging behavior and diet. These syndromes may reflect frugivores' fruit preferences; however, our results suggest that, with respect to the traits considered, the evidence garnered thus far is inadequate to infer that these traits evolved in response to selective pressures exerted by frugivores. To propose that coevolution between frugivores and fruiting plants has led to the evolution of fruit character complexes we must be able to demonstrate that there have been reciprocal evolutionary changes in the interactants (Janzen 1980). Although incomplete, data from the fossil record demonstrate that dispersal syndromes persist longer than dispersers (Tiffney 1986, Herrera 1989).

Gymnosperms have produced fleshy diaspores that are functionally analogous to fruits since at least the Carboniferous (Herrera 1989). Fleshy angiosperm fruits of modern aspect (e.g. drupes) first appear in the Late Cretaceous (Friis and Crepet 1987), and many modern families are well established by the early to middle Eocene (e.g. Burseraceae, Anacardiaceae, Annonaceae, Lauraceae, Menispermaceae) (Collinson and Hooker 1987). This implies that aspects of fruit morphology have remained relatively constant for millions

of years. Fleshy diaspores have evolved multiple times, in a variety of ecological circumstances (Wing and Tiffney 1987, Herrera 1989). For some traits, however, it seems likely that a succession of frugivore lineages has encountered morphologically similar fruits. This suggests that persistence of some fruit characters depends more on the persistence of plant taxa than on the persistence of specific dispersers (Tiffney 1986) and that some aspects of fruit morphology are exapted (sensu Gould and Vrba 1982) to their current dispersers.

Whether or not fruit traits are the result of coevolution, it is likely that plant - frugivore interactions do influence the fitness of both interactants. Both macroevolutionary and microevolutionary consequences of plant - frugivore interaction have been explored (e.g. Herrera 1989, Janson 1992). For instance, Janson (1992) has proposed that macroevolutionary patterns of change in fruit morphology may be influenced by plant-frugivore interactions. His analysis of transitions among fruit characters, using a Markov model to estimate transition probabilities, indicates that transitions from unhusked to husked forms are more likely than the reciprocal transition. Janson suggests that this may be partly due to differences in the foraging behavior of birds and mammals. Mammals feed on both husked and unhusked fruits, whereas birds feed almost exclusively on unhusked fruits (Janson 1983). This, he suggests, provides a selection pressure favouring the transition from unhusked to husked, while a reciprocal selection pressure associated with avian dispersal is never applied to husked fruits.

Although Herrera (1989) has shown that plant genera with fleshy diaspores are no more speciose than those without fleshy diaspores, our analysis suggests that when only genera with fleshy diaspores are considered some character complexes are more speciose than others (Table 3). In our sample this effect appears to be the result of including speciose genera within which fruit morphology varies little. The radiation of these speciose genera may or may not be related to seed dispersal, but this result raises the questions of 1) whether some kinds of biotic dispersal affect speciation and/or extinction rates, and 2) if they exist, how the effects are generated. To pursue these questions we must first determine whether speciose complexes are actually associated with particular guilds of dispersers, as our analysis of consensus syndromes suggests.

Work which relates the effects of plant - frugivore interactions to the fitness of the interactants can also offer insights into the evolution of dispersal syndromes. In several studies (e.g. Becker and Wong 1985, Howe 1986, Dinerstein and Wemmer 1988, Herrera 1988, Murray 1988, Chapman 1989, Loiselle 1990) the influence of frugivores on the germination and survival of seedlings has been examined; such studies relate dispersal directly to components of plant fitness. Likewise, studies which relate the effects of differences in morphology, physiology, and behavior of plants and frugi-

vores to components of the fitness of the interactants suggest which traits are currently under selection (e.g. Herrera 1982, 1984, Levey 1986, Vasquez-Yanez and Orozco-Segovia 1986, Murray 1987).

Convergence also offers evidence of past selective pressures. For example, the convergence of morphology and physiology among distantly related taxa of folivores has been adduced as evidence that functional considerations associated with leaf-eating have exerted strong selective pressures on dentition, gut morphology, and physiology (e.g. Grand 1978, Kay and Hylander 1978, Hume 1982). In this study we used data from floristic accounts to examine plant taxa from various families and geographic regions for convergence in several dispersal-related traits (protection, color, and size). Similar studies that examine convergence among fruiting plants and frugivores may offer insights into the selective pressures which have shaped the morphology, physiology, and behavior of the interactants (Howe and Westley 1988). Polymorphic taxa offer a particularly useful group (e.g. Herrera 1989). For example, one approach would be to examine the dispersal of polymorphic plant species in sites with and without key disperser groups. Because polymorphic species are known to have the genetic potential for convergent evolution of a given trait, a priori predictions can be tested by comparing population-level responses to regions with different dispersers.

To determine the range of characteristics that influence plant – frugivore interactions, future research should attempt to quantify the variety of fruit characteristics encountered by dispersers and the variety of dispersers typical for a given syndrome or character-complex. Second, we should continue to extend our analyses of fruit syndromes to include a wider range of fruit traits, such as nutrient content, secondary compounds, crop size, temporal and spatial dispersion, and spatial display of fruits (e.g. Tomback 1983, Manzur and Courtney 1984, Moermond et al. 1986, Herrera 1987, Levey 1988, Loiselle and Blake 1989). These traits could be more important than color and protection in determining frugivore food preferences (Willson et al. 1990). Third, future studies might consider including experiments that evaluate correlative field observations. For example, our results suggest that blue and red unprotected fruits are generally more speciose than other character complexes. This corresponds with syndromes derived from observations of bird foraging behavior (e.g. Howe and Westley 1988); however, in color preference experiments three species of North American frugivorous birds showed no tendency to favour red or black and only a weak tendency to reject yellow (Willson et al. 1990). It would be interesting to know if birds are consuming blue and red fruits in proportion to their abundance relative to other colors, and whether red and blue fruit colors are correlated with other characteristics that do influence fruit choice in birds (Willson and Whelan 1990). Finally, we should continue

attempts to determine the effects of biotic dispersal on micro- and macroevolutionary processes (e.g. Herrera 1989, Janson 1992).

Before evaluating data on fruit syndromes, researchers should examine the extent to which species and genera can be treated as independent units for the purposes of analysis. The current study uses a method which is likely to underestimate the number of evolutionary events at the species level, and to overestimate the number of evolutionary events at the genus level. A more satisfying resolution of this problem will be possible as phylogenies are better understood (Donoghue 1989). Reconstruction of phylogenetic lineages should allow an analysis of the temporal sequence of character transformation in a limited number of plant groups across a range of geographically and ecologically disjunct sites. This approach could address specific questions concerning the evolution of fruit traits in response to selection pressures exerted by frugivorous dispersal agents. Such studies would also facilitate a more complete understanding of the influence of phylogeny. Until phylogenetic information is available, there are a number of methods that estimate phylogenetic effects (Huey 1987, Pagel and Harvey 1988, Bell 1989, Gittleman and Kot 1990) and these should be used to avoid conflating adaptation with ancestry.

Finally, although our analyses suggest that the fruit traits examined here are fortuitously compatible exaptations rather than the results of coevolution (see Janzen 1980), the results offered here *cannot* refute the hypothesis of coevolution between frugivores and their food plants. When genera are used as sampling units, only our analysis of Guiana has sufficient power to reliably confirm the null hypothesis that color and protection are not associated. For all other analyses effect sizes are very small, hence the power required to confirm the null hypothesis can only be achieved with very large ($N > 1000$) sample sizes. These very small effect sizes indicate that the observed distributions differ little from those posited by the null hypothesis in most cases. The effect size required to establish *biological* significance (i.e. to be worth detecting) is beyond the scope of conventional inferential statistics. Rather than relying on statistical methods to determine whether a test is sufficiently powerful to detect the observed effect size, biologists should establish a priori hypotheses about the magnitude of the effect expected on biological grounds and use these as criteria for the power required of a test.

Acknowledgements – We would like to thank both L. Chapman and E. McKenzie for help in all stages of preparation of this manuscript. The Grey Herbarium and the Arnold Arboretum Library Staff provided invaluable assistance in collecting the data. P. Ashton, S. Austad, L. Chapman, R. Cook, C. Herrera, A. Gautier-Hion, D. Holmes, C. Janson, T. Laman, S. Lewis, C. Lindell, E. McKenzie, M. Pagel, J. Phelan, and Hal Stern provided helpful comments on this paper. Portions of this research were supported by a Jacob K. Javits scholarship, Sheldon Fellowship and Wenner Gren Predoctoral Grant to K.F., and National Geographic and USAID grants to C.A.C.

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