Inter-Relationships Between Type, Size and Colour of Fruits and Dispersal in Southern African Trees

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Summary. The indigenous angiosperm tree flora (1,340 species) of southern Africa was analysed for type, size and colour of fruits and class of biotic dispersal agent (consumer). Species producing fleshy (drupes and berries) and dry (pods, capsules and nuts) fruits account for 52% and 47%, respectively, of the flora. The flora contains about 2.5 times as many berry-producing as drupe-producing species. Based on a log-linear model, fruit type, consumer and fruit size are dependent statistically on each other, whereas fruit colour depends on both fruit size and consumer type acting independently of each other. Drupes and berries are consumed by birds and mammals, with berries being favoured by both birds and mammals. At least 23% (307 species) of the flora apparently depends predominantly on birds for seed dispersal. Drupes and berries favoured by birds tend to be small and brightly coloured (red or black), whereas those eaten mainly by mammals tend to be large and dull (yellow or green). Relatively few fleshy fruits are brown. Pods, capsules and nuts tend to be brown or green. Birds apparently tend to avoid eating green fruits. The notion that green coloration has evolved to enhance crypsis and/or to signal unpalatability in unripe fruit to reduce premature exploitation is questioned. Green as a cryptic colour is incompatible with the demonstrated mammalian selection of this colour, while to function aposematically a stronger contrast colour may be required.

Introduction

Plant species which rely on animals for seed dispersal produce fruits whose characteristics vary in relation to the type of animal agent involved (Snow 1971). Amongst a host of fruit characteristics, fruit type and seed size (McKey 1975; Stiles 1980) and fruit colour (Turcek 1963) have been isolated for special study. Here we report quantitative information on the inter-relationships between fruit type, size and colour in the indigenous angiosperm tree flora of southern Africa in order to make a preliminary assessment of the flora's dependence on birds as seed dispersers. We also discuss aspects of the evolution of fruit characteristics which facilitate avian-based dispersal of seeds.

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Methods

The fruits of 1,340 species of trees were classified according to type (drupe, berry, pod, capsule or nut), colour when ripe (white, red, orange, yellow, green, brown, and blue/black), and size (length in mm), using information taken from Palmer and Pitman (1972, 1973), van Wyk (1972–1974), Palmer (1977) and Coates Palgrave (1977). This information, together with data in Phillips (1927, 1931), Chapin (1932–1954), White (1962), Liversidge (1965), Huntley (1965), Skead (1965) and Oatley (1969), was used in the following categorizations: (a) species whose fruits are known to be eaten frequently by birds (variable BIRD); (b) species congeneric with those in the preceding allocation and whose fruits apparently are palatable to birds and, thus, are likely to be eaten at least occasionally by birds (BIRD 2); (c) species whose fruits are known to be eaten by mammals (MAMMAL); and, (d) all other tree species (OTHER).

Chi-square tests were used to identify relationships between fruit type and classes of consumers, fruit type and colour, and consumer class and colour. Our null hypotheses were that fruit type and consumer, fruit type and colour, and consumer and colour are independent of one another ($P < 0.05$). A computer program (BMDP P2F) was used to isolate sequentially larger contributions (i.e. cells) to the 'χ^2', until the remaining part of the contingency table showed no row-column effects (Fienberg 1972; Brown 1974, 1977a). A new table of expected values was calculated at each step.

We used the Kruskal-Wallis one-way analysis of variance (BMDP P3S) to test for fruit size and fruit type variation amongst consumer and colour classes, with the null hypothesis that fruit size amongst the consumer classes could be the result of sampling from the same population for each of the fruit and colour classes ($P < 0.05$). Conventional analysis of variance necessitates data to be distributed normally with a small variance (s^2). Although our gamma distribution of fruit sizes could be normalized (Manly 1976), a high variance persisted and, therefore, we applied distribution free tests.

The results of all these tests were used to 'summarize' the data and produce a simplified four-way table of relationships between colour (C), size (S), consumer (E), and fruit type (F). With such multi-dimensional tables, it is conventionally necessary to test a large number of two-dimensional contingency tables (colour/size, colour/consumer,

Table 1. Contingency table of fruit types and consumer classes; values in parentheses are expected frequencies. 11 species could not be categorized for analysis

Consumer class	Fruit type					Total
	POD	CAPSULE	NUT	DRUPE	BERRY	
BIRD	0 (36.66)	23 (66.37)	0 (29.29)	79 (47.61)	178 (99.44)	280
BIRD2	1 (8.77)	16 (15.88)	0 (7.16)	31 (11.39)	19 (23.80)	67
MAMMAL	1 (7.20)	4 (13.04)	0 (5.88)	6 (9.35)	44 (19.53)	55
OTHER	172 (121.37)	272 (219.72)	142 (99.05)	110 (157.64)	231 (329.23)	927
Total	174	315	142	226	472	1,329

Table 2. Summary of the steps for sequentially removing cells and isolating sources of significance in Table 1. Step 0 indicates the overall chi-square (χ^2) of the table, and further steps summarize the significance of the table with the select removal of individual cells that contribute most to the observed value. The last step indicates the stage where there are no row-column relationships

Step	Row	Column	χ^2	d.f.
0	n/a	n/a	371.63***	12
1	OTHER	POD	272.77***	11
2	OTHER	NUT	174.06***	10
3	OTHER	CAPSULE	46.46***	9
4	BIRD2	BERRY	15.14	8

*** $P < 0.001$

colour/fruit type, size/consumer, size/fruit type, and consumer/fruit type) which each constitute a marginal total of the multi-dimensional contingency table. The large number of tests that need investigation has led researchers to suggest the nesting of tests (Goodman 1969) with each test representing an hypothesis, or a method which can integrate selected hypotheses into a single analysis (Kendall 1980). A multi-dimensional contingency table analysis (Fienberg 1970, 1977) has been developed which tests all variables (colour, size, consumer and fruit type) simultaneously, finds relationships between all variables and removes all unimportant relationships. This is achieved by fitting a hierarchical log-linear model to the cell frequencies. The logarithm of the expected frequency is written as an additive function to the main effects (λ) and interactions in a manner similar to the usual analysis-of-variance model. A normal two-dimensional ($n \times m$) contingency table for a chi-square analysis is defined by two effects (e.g. colour and size) and a single interaction. Provided that a maximum likelihood statistic (G^2) is used for a goodness of fit (see Appendix 1) in lieu of Pearson's statistic (χ^2), a two-dimensional contingency table analysed as a multi-dimensional contingency analysis will yield identical results. A four-way classification of inter-relationships of colour (C), size (S), fruit consumed by biotic agents (E) and fruit type (F) may be defined by the following model

$$
\begin{aligned}
\log_e F_{ijkl} = {} & \theta + \lambda_i^C + \lambda_j^S + \lambda_k^E + \lambda_l^F \\
& + \lambda_{ij}^{CS} + \lambda_{ik}^{CE} + \lambda_{il}^{CE} + \lambda_{jk}^{SE} + \lambda_{jl}^{SF} + \lambda_{kl}^{EF} \\
& + \lambda_{ijk}^{CSE} + \lambda_{ijl}^{CSF} + \lambda_{jkl}^{SEF} + \lambda_{ikl}^{CEF} \\
& + \lambda_{ijkl}^{CSEF} .
\end{aligned}
$$

This is a saturated model and if fitted to the data will produce results that are identical to the original data set. It may also be noted that the suffix i is associated with the C classification, the suffix j with the S classification and so on, while the term λ_i^C will represent the contribution of C to the i th row of the table. The term λ_{ij}^{CS} represents the single interaction of effects λ_i^C and λ_j^S (Fienberg 1970, 1977; Kendal 1980). The word effect (λ) is used in the statistical sense, and it in no way establishes the positive existence of causal relationships among the variables. Indeed, we model our data on the assumption of causality to see how well any model fits our observed data. The smaller the G^2 value, the better the fit of the model. However, we attempt to fit the most parsimonious model that adequately explains the variation in the data (Williams 1976a), using the BMD P3F computer program (Brown 1977b).

Results

Fruit Type and Consumer

Species producing fleshy fruits account for 52% of the indigenous tree flora, whereas 47% of the species possess dry fruits (pods, capsules and nuts), of which 11% contain arillate seeds. Further, at least 23% of the tree flora would seem to rely on birds for seed dispersal. We reject the null hypothesis of independence between fruit type and consumer; variable OTHER being an 'extreme contribution' to the overall significance of the χ^2 value (Tables 1 and 2). Most species bearing pods, capsules and nuts occur in the group OTHER; these species being mainly wind dispersed (anemochorous). Berries, in both BIRD and MAMMAL categories, and drupes, in the BIRD2 category, exceed expected frequencies, reflecting an apparent selection for species with fleshy fruits by these animals. A re-analysis of these data, with OTHER removed entirely, indicates that although berries have higher than expected frequencies for MAMMAL and BIRD categories, only the higher than

Table 3. Contingency table of fruit types and colour classes; the values in parentheses are expected frequencies. 184 species could not be categorized for analysis

Fruit colour	Fruit type					Total
	POD	CAPSULE	NUT	DRUPE	BERRY	
WHITE	4 (6.93)	24 (9.47)	7 (4.57)	7 (8.68)	6 (18.36)	48
RED	41 (40.74)	41 (55.62)	15 (26.83)	72 (50.98)	113 (107.82)	282
ORANGE	2 (14.30)	4 (19.53)	1 (9.42)	29 (17.90)	63 (37.85)	99
YELLOW	20 (24.99)	35 (34.12)	13 (16.46)	23 (31.28)	82 (66.15)	173
GREEN	6 (14.74)	35 (20.12)	11 (9.71)	13 (18.44)	37 (39.00)	102
BROWN	58 (31.64)	70 (43.19)	58 (20.84)	14 (39.59)	19 (83.74)	219
BLACK	36 (33.66)	19 (45.95)	5 (22.17)	51 (42.13)	122 (89.09)	233
Total	167	228	110	209	442	1,156

Table 4. Summary of the steps for sequentially removing cells and isolating sources of significance in Table 3. Step 0 indicates the overall chi-square (χ^2) of the table, and further steps summarize the significance of the table with the select removal of individual cells that contribute most to the observed value. The last step indicates the stage where there are no row-column relationships

Step	Row	Column	χ^2	d.f.
0	n/a	n/a	346.07***	24
1	BROWN	BERRY	228.17***	23
2	BROWN	DRUPE	168.32***	22
3	WHITE	CAPSULE	132.33***	21
4	GREEN	CAPSULE	97.80***	20
5	BLACK	NUT	82.89***	19
6	YELLOW	CAPSULE	72.26***	18
7	ORANGE	POD	61.13***	17
8	ORANGE	NUT	49.71***	16
9	WHITE	NUT	41.67***	15
10	ORANGE	CAPSULE	32.68**	14
11	RED	NUT	25.39*	13
12	BLACK	CAPSULE	18.43	12

* $P<0.05$ ** $P<0.01$ *** $P<0.001$

Table 5. Contingency table of consumer classes and fruit colour; the values in parentheses are expected frequencies. 184 species could not be categorized for analysis

Fruit colour	Consumer class				Total
	BIRD	BIRD2	MAMMAL	OTHER	
WHITE	10 (11.09)	0 (2.70)	0 (2.28)	38 (31.93)	48
RED	72 (65.13)	17 (15.86)	6 (13.42)	187 (187.59)	282
ORANGE	39 (22.87)	9 (5.57)	9 (4.71)	42 (65.86)	99
YELLOW	44 (39.96)	10 (9.73)	17 (8.23)	102 (115.08)	173
GREEN	14 (23.56)	2 (5.74)	11 (4.85)	75 (67.85)	102
BROWN	14 (50.58)	3 (12.31)	5 (10.42)	197 (145.68)	219
BLACK	74 (53.82)	24 (13.10)	7 (11.09)	128 (155.00)	233
Total	267	65	55	769	1,156

expected frequency for drupes in BIRD2 was isolated through the sequential cell removal technique. This suggests that fruit types for BIRD2 differ markedly from those in BIRD and MAMMAL, and may explain why the fruits of the BIRD2 species have not been observed to be eaten frequently.

Fruit Type and Colour

The null hypothesis of independence between colour and type of fruit is rejected (Tables 3 and 4). The brown berry and the brown drupe both have far higher expected than observed frequencies. The white capsule and the green capsule both have greater observed than expected frequencies, whereas orange has a relatively lower than expected fre-

quency. No particular colour appears to predominate in pods, but the frequency of orange again is lower than expected. Frequencies of red, orange and black nuts are lower than expected, and there is a greater frequency of white nuts than expected.

Fruit Colour and Consumer

We reject the null hypothesis of independence between consumer and colour of fruit (Tables 5 and 6). Brown in OTHER appears to be the most significant contribution to the contingency table, and probably reflects anemochor-

Table 6. Summary of the steps for sequentially removing cells and isolating sources of significance in Table 5. Step 0 indicates the overall chi-square (χ^2) of the table, and further steps summarize the significance of the table with the select removal of individual cells that contribute most to the observed value. The last step indicates the stage where there are no row-column relationships

Step	Row	Column	χ^2	d.f.
0	n/a	n/a	140.54***	18
1	BROWN	OTHER	67.41***	17
2	ORANGE	OTHER	53.49***	16
3	RED	MAMMAL	43.09***	15
4	GREEN	BIRD	34.41**	14
5	BLACK	BIRD2	26.40*	13
6	BLACK	BIRD	19.19	12

* $P<0.05$ ** $P<0.01$ *** $P<0.001$

ous elements. Orange has a far lower observed frequency than expected, and, therefore, is more characteristic of the other consumer groups. Green fruits appear not to be taken as frequently as expected in BIRD, whereas for MAMMAL there is a greater than expected frequency for species with green fruits. Birds select species which possess predominantly black fruits, and to a lesser extent orange and red, whereas red in mammals was lower than expected.

Fruit Size and Consumer

In the case of capsules, we accept the null hypothesis that BIRD, BIRD2, MAMMAL, and OTHER come from the same population (Table 7). The drupe and berry size stratification among the consumer classes is pronounced. A comparison between species with drupes and those with berries indicates that for both types, mammals select fruits of similar size (Mann-Whitney U test = 154, $P>0.05$). Birds, however, select species with berries which are larger than drupes (Mann-Whitney U test = 2,775, $P<0.05$). Drupes and berries are also of similar size in our control category BIRD2 (Mann-Whitney U test = 227, $P>0.05$).

Fruit Size and Colour

Fruit size differs in relation to colour in species bearing either berries, drupes or nuts (Table 8). For pods and capsules, we accept the null hypothesis that samples of colour come from the same population. The species with the largest drupes tend to have yellow fruits. Green and orange drupes are also quite large, whereas the smallest are brown or black. Drupes are smaller than berries. The largest berries tend to be white or green. Brown and yellow berries are slightly smaller, and the smallest are black. The largest nuts are red and green. Orange pods tend to be relatively small.

Integration Model

The inter-relationships between fruit type and consumer type, fruit size and colour are integrated in a multi-dimensional contingency table (Tables 9 and 10); only those two fruit types (drupe and berry) which appear to be dependent on animals for dispersal being included. A log-linear model of all these variables is fitted, which adequately explains the data with the fewest effects (λ). Marginal and partial association tests were used to 'screen' the data and to determine which effects, and combination of effects, should be incorporated in the model (Brown 1977b). These tests were highly significant for SE, FE and CS, while CE and SFE were also significant (Table 11). In testing four suites of effects, or models M1–M4, we found M1 to have a non-significant most parsimonious fit (Table 12) and, therefore, may be used to explain the variation in the data. The most significant difference in tests of fit between this and other models was found with M4, and this model appears to be the best fit for the data. The percentage of variation explained by M4 is 69.57%. The final log-linear model applied is

$$\log_e F_{ijkl} = \theta + \lambda_i^C + \lambda_j^S + \lambda_k^E + \lambda_l^F \\ + \lambda_{ij}^{CS} + \lambda_{ik}^{CE} + \lambda_{jk}^{SE} + \lambda_{jl}^{SF} + \lambda_{kl}^{EF} + \lambda_{jkl}^{SEF}.$$

Hence, in this model, fruit size (S) and consumer (E) and fruit type (F) are related and dependent on each other. Colour depends on fruit size and consumer but not on fruit

Table 7. Mean fruit length (mm) for fruit type among four consumer classes; the Kruskal-Wallis statistic (H) indicates significance of inter-consumer variation in fruit length among each of the fruit types

Variable	Statistic	POD	CAPSULE	NUT	DRUPE	BERRY
BIRD	Mean	10.00	58.65	0.00	7.75	13.21
	SD	0.00	205.74	0.00	7.30	7.68
	N	1	23	0	79	176
BIRD2	Mean	0.00	11.36	0.00	12.87	12.67
	SD	0.00	7.35	0.00	12.67	8.76
	N	0	14	0	30	19
MAMMAL	Mean	300.00	88.75	0.00	33.33	36.20
	SD	0.00	76.64	0.00	9.31	28.45
	N	1	4	0	6	44
OTHER	Mean	139.39	42.73	14.22	12.61	21.23
	SD	174.59	97.73	16.18	8.61	23.25
	N	172	230	125	108	227
All	H	n/a	6.76	n/a	55.36*	41.73*

* $P<0.05$

Table 8. Mean fruit length (mm) for fruit type among seven colour classes; the Kruskal-Wallis statistic (*H*) indicates significance of inter-consumer variation in fruit length among each of the fruit types

Variable	Statistic	POD	CAPSULE	NUT	DRUPE	BERRY
WHITE	Mean	127.50	22.00	8.71	6.00	53.50
	SD	56.79	26.87	9.64	2.94	52.89
	N	4	24	7	7	6
RED	Mean	145.90	46.66	31.40	13.06	14.21
	SD	143.41	94.21	18.31	10.12	9.65
	N	41	38	15	71	112
ORANGE	Mean	72.50	13.25	25.00	10.48	19.94
	SD	67.18	7.89	0.00	9.90	21.82
	N	2	4	1	29	63
YELLOW	Mean	116.00	43.18	20.00	17.27	21.82
	SD	89.98	144.96	15.65	13.35	21.25
	N	20	34	13	23	82
GREEN	Mean	103.33	48.64	27.09	10.08	37.14
	SD	26.58	77.96	19.68	6.50	24.23
	N	6	33	11	13	37
BROWN	Mean	162.07	62.93	10.25	7.64	24.71
	SD	256.80	11.09	13.32	8.56	13.51
	N	58	69	57	14	17
BLACK	Mean	137.78	68.84	4.00	9.77	12.15
	SD	105.29	225.88	3.00	5.76	12.63
	N	36	19	3	51	120
All	H	3.99	6.61	33.82*	22.84*	84.41*

* $P < 0.05$

Table 9. Categories used in the four-dimensional contingency table for modelling the effects of consumer, fruit type, length (size) and fruit colour on each other

Variable	Symbol	Index	Category number						
			1	2	3	4	5	6	7
Colour	(C)	i	WHITE	RED	ORANGE	YELLOW	GREEN	BROWN	BLACK
Size	(S)	j	<15	15–30	>30				
Fruit	(F)	k	DRUPE	BERRY					
Consumer	(E)	l	BIRD	BIRD2	MAMMAL				

type, whereas the influences of fruit size and consumer on colour are independent of each other.

Discussion

Evolution of Colour of Fleshy Fruit

Our results indicate that species with drupes and berries tend to display particular fruit colours, and that the colours differ according to whether the fruits are eaten predominantly by mammals or birds. Species with yellow, orange and green fruits tend to be favoured by mammals, whereas birds favour black, and to a lesser extent, orange and red fruits. It is generally accepted that large fruits are mammal dispersed (Snow 1971) and, therefore, will have 'mammal colours'. Most mammals have monochrome vision, whereas primates and birds are equipped with colour vision (Hildebrand 1974). Fruit colour probably functions best as an attractant when contrasted against a differently coloured background. The combination of large size and white colour in certain fruits (Table 8) is probably an adaptation for attracting bats, as seed dispersers (van der Pijl 1969b).

The incidence of tree species producing white, orange, yellow or green fruits is much lower in Europe, where red and black fruits predominate for dispersal by birds (Turcek 1963), than in southern Africa. This difference presumably reflects a disproportionate influence of mammals, particularly the relative abundance of primates and fruit bats as seed-dispersers in southern Africa. In southern Africa, the relatively large size of yellow and orange drupes and berries conceivably enhances primate-based dispersal of seeds. Species with smaller, orange fruits might be dispersed mainly by birds.

The results also show that among species with fruits favoured by birds, orange fruits tend to be larger than red and black fruits, in that order. This might be a function of the foraging behaviour of birds of different sizes. Small birds might tend to search for fruits within the cover of

Table 10. Four-dimensional contingency table of consumer, fruit type, length (size) and colour in relation to each other, and arranged in a hierarchy of effects

Consumer (E)	Fruit (F)	Size (S)	Colour (C)						
			1	2	3	4	5	6	7
BIRD	DRUPE	<15	4	24	12	7	5	10	10
		15–30	0	0	0	2	0	0	0
		>30	0	0	2	1	0	0	0
	BERRY	<15	1	36	19	20	2	3	55
		15–30	1	9	4	10	5	1	6
		>30	1	2	1	0	0	0	0
BIRD2	DRUPE	<15	0	3	4	0	0	1	15
		15–30	0	3	0	3	0	0	1
		>30	0	3	0	0	0	0	0
	BERRY	<15	0	7	3	0	0	0	0
		15–30	0	1	0	0	0	0	2
		>30	0	0	1	0	0	0	0
MAMMAL	DRUPE	<15	0	0	0	0	0	0	0
		15–30	0	2	1	0	0	0	0
		>30	0	0	0	2	1	0	0
	BERRY	<15	0	3	6	4	0	1	2
		15–30	0	1	1	6	0	0	3
		>30	0	0	1	5	7	2	1

Table 11. Tests of partial and marginal association for each subset of effects (Brown 1976, 1977b)

Effect	d.f.	Partial[a] association		Marginal[b] association	
		G^2	proba-bility	G^2	proba-bility
C	6	146.41	0.0000		
S	2	214.55	0.0000		
F	1	36.22	0.0000		
E	2	181.84	0.0000		
CS	12	38.36	0.0001	49.91	0.0000
CF	6	15.08	0.0197	12.26	0.0565
CE	12	22.27	0.0346	31.08	0.0019
SF	2	3.97	0.1373	3.21	0.2005
SE	4	52.70	0.0000	63.58	0.0000
FE	2	27.15	0.0000	23.66	0.0000
CSF	12	10.16	0.6017	11.35	0.4990
CSE	24	19.55	0.7220	18.77	0.7643
CFE	12	15.79	0.2011	14.30	0.2818
SFE	4	12.80	0.0123	9.71	0.0456
CSFE	24	13.46	0.9579		

[a] Partial association is calculated as the difference between the full order model and that which excludes only the subset of effects

[b] Marginal association is calculated as the summation of the table over the unspecified indices and then the specified subset of effects are tested to be zero

Table 12. The characteristics of four models derived from the results of partial and marginal association tests. M1 appears the most parsimonious model in explaining relationships between consumer, fruit type, length, and colour. However, tests of difference between this model and the other three models (M2–M4) indicate Model 4 to be the most suitable (see text)

Model		d.f.	G^2	proba-bility	% varia-tion
SE FE CS	M1	96	107.02	0.2078	56.17
SE FE CS CE	M2	84	87.73	0.3960	64.07
SFE CS	M3	90	93.58	0.3772	61.67
SFE CS CE	M4	78	74.29	0.5981	69.57

enhance crypsis (Snow 1971), thus providing some protection against premature exploitation and/or destruction by vertebrate predators. If a signal of unpalatibility is assumed, it becomes debatable whether green provides the necessary visual impact to reinforce conditioned avoidance after birds have experienced the poisonous and/or distasteful nature of fruits of this colour. Unpalatability is advertized by high-contrast colour patterns (aposematic coloration) in many animal classes. It could be argued that the option of evolving high contrast colours in unripe fruit is closed to flowering plants, because evolution has favoured such colours as an attractant for avian frugivores through which effective dispersal of propagules can be achieved. The case against green as a cryptic colour generally is the demonstrated mammalian selection of green berries. If mammals, many of which have monochrome vision, are able to exploit preferentially such fruits, there seems little reason for birds not to do likewise. Thus, greenness, and the associated unpalatability of unripe fruits, could be a consequence of genetic pleiotropy, with no significant cryptic or advertizing function.

Evolution of Colour of Non-Fleshy Fruit

In general, birds and mammals select fleshy fruits ahead of capsules, pods and nuts (Tables 1 and 2). However, tree species with arillate seeds in capsules and pods rely on animals for dispersal, and are believed to represent an early stage in the evolution of zoochory (Corner 1949). Arillate seeds, having bright colours, tend to be dispersed by birds (Skutch 1980); those lacking bright colours are probably dispersed by ants (Berg 1975).

Green capsules occurred at greater than expected frequencies (Tables 3 and 4) and, depending on background and point of observation, may enhance crypsis and, hence, reduce losses due to consumption by browsing mammals. White capsules also occurred at greater than expected frequencies. Many white capsules possess a covering of fine white or transparent hairs which are good reflectors of light, and the fruits may therefore be fairly inconspicuous. The fact that species with orange capsules and pods tend to be very small (Table 8) might be related to a reduction in conspicuousness, providing that this colour is an inescapable consequence of pleiotropy.

Nuts are transported and stored by birds and mammals in cool temperate regions experiencing severe winters. Many such nuts are not reclaimed, and thus are dispersed effectively. The winters in southern Africa are probably too mild to promote the widespread evolution of such a system. Red,

trees, whereas large birds search for fruits while on the wing. This implies that fruits taken by large birds require to be more conspicuous, with regard to position in tree as well as colour and size.

Birds evidently avoid eating green fruits (Tables 5 and 6). Green may signal unpalatability (Corner 1949) or

orange and black are poorly represented as colours for nuts; brown being most common (Tables 3 and 4). Since nuts tend to be spherical and of similar size to many bird-selected fleshy fruits (Tables 7 and 8), they could be susceptible to accidental removal for inspection by frugivores. Hence, selection favouring the evolution of a colour (brown) least characteristic of fleshy fruits might be expected. The species with the largest nuts have red and green fruits (Table 8), and generally are produced by anemochorous *Combretum* and *Terminalia* species. The selective advantage attending any coloration in anemochorous fruits would appear to be inconsequential, unless the colour enhances crypsis or functions aposematically. In the case of red nuts, the colour might be advantageous in promoting crypsis in an autumnal-coloured foliage background.

Aposematic coloration, with obligate fruit unpalatability, might have evolved with advantage in anemochorous fruits. However, most of these are brown, and apparently their main defence against predators is the production of very large numbers of propagules and the hard, woody pericarp enclosing the seed (Snow 1971). If the majority of anemochorous species are of more recent origin than those producing fleshy fruits, as van der Pijl (1969a) suggests, the adoption of high-contrast colours by the latter for attracting vertebrate dispersers, chiefly birds and primates, might have precluded aposematic coloration in anemochory.

Evolution of Size of Fruit

Size partitioning of zoochorous fruits is very pronounced, with mammals selecting berries approximately three times the size of those selected by birds (Table 7). This is perhaps surprising, since mammal or bird-based dispersal of a fruit should also depend on the relative softness or hardness of the pericarp. Large fruits having soft pericarps (e.g. some *Ficus* species) can be consumed (in pieces) by even small frugivores, promoting dispersal if the seeds are small. Alternatively, small fruits with hard pericarps (e.g. some *Strychnos* species) will not be consumed easily by birds. The most suitably sized fruits for ornithochory are red or black (Table 8), and both red drupes (the most common drupe colour) and black berries (the most common berry colour) are similar in size.

Evolution of Type of Fruit

Species producing fruits whose seeds are dispersed predominantly by birds or mammals have been classed as specialists (dependent on obligate frugivores) or opportunists (Morton 1973; McKey 1975; Howe and Estabrook 1977). Assuming that all drupes with their single seeds are fruits of specialists and all berries with their multitudes of seeds are fruits of opportunists, the southern African tree flora contains about two and a half times as many opportunist as specialist species. This might be related to the fact that, whereas drupes tend to supply dispersers with proteins and lipids, berries not only are larger (Table 7) but contain relatively more water which could be an important 'reward' for avian dispersers in semi-arid southern Africa. The indehiscent capsules of some species (e.g. *Kigelia*) are eaten by large animals (e.g. hippopotamus) which might disperse their seeds. However, dehiscent capsules which contain arillate seeds are generally an adaptation for biotic dispersal (Skutch 1980). Seeds contained in pods probably are dispersed by ungulates (Lamprey et al. 1974; van der Pijl 1969a), and within the southern African tree flora few species produce pods possessing seeds with well developed arils (Knight & Siegfried unpublished).

Appendix 1

Maximum Likelihood Statistic

For a goodness of fit measure in our multi-dimensional contingency table models, we could have used Pearson's statistic $\chi^2 = \Sigma(O-E)^2/(E)$. However, Pearson's approximation of the maximum likelihood estimate $G^2 = (2\Sigma \log_e O/E)$ is not valid under certain conditions (Williams 1976b). Therefore, the G^2, which is no longer computationally inconvenient to calculate, was used. Brown (1973) has established that G^2 has the advantage of being additive under partitioning, i.e. if M1 and M2 are two models such that the marginals fitted by M1 are a subset of those fitted by M2 then

$$G^2(M1) = G^2(M1\,|\,M2) + G^2(M2).$$

Therefore, this goodness of fit measure is universally used in preference to the normal Pearson's statistic.

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