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Characteristics of vertebrate-dispersed fruits in Hong Kong

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ABSTRACT. Hong Kong has a native angiosperm flora of approximately 1800 species, of which 27% (482 spp.) bear fleshy, presumably vertebrate-dispersed fruits, including 76% of the 337 tree and shrub species and 70% of the 103 climber species. Morphological characteristics were determined for 255 species and nutritional characteristics of the fruit pulp for 153 species. Most fruit species were black (45.1%) or red (24.3%) and 85.9% had a mean diameter <13 mm. Nutritional characteristics varied widely between species with ranges and median values as follows: pulp percentage (range 10.0–99.2%, median 69.2%), water content of pulp (11.1–94.0%, 78%), lipid (0–84.0%, 2.0%), soluble carbohydrate (4–88%, 53%), nitrogen (0.2–3.4%, 0.86%), neutral detergent fibre (1–44%, 14.3%). Fruit development time (50–360 d, 156 d) showed a negative correlation with lipid content, but no significant correlation with fruit or seed size. Principal components analysis of fruit characteristics was dominated by a trend from single-seeded fruits with a thin, lipid-rich pulp layer to multiple-seeded fruits with much, watery, carbohydrate-rich pulp. Bird-dispersed species cover the full range of fruit characteristics except those too large to swallow and too hard to peck bits from. Mammals (bats, civets and/or macaques) are known or suspected to consume most of the fruits too large for birds as well as many bird fruits but none with high-lipid content. Summer fruits (May–September) were significantly larger and had significantly higher seed size and carbohydrate content than winter fruits (November–March). Winter fruits took more than twice as long to develop as summer fruits.

KEY WORDS: birds, China, frugivory, fruit, Hong Kong, mammals, seed dispersal.

INTRODUCTION

Frugivory is a key process in the ecology of tropical forests. Fruits support a high proportion of the vertebrate biomass and the majority of woody plant species are dispersed by animals (Levey *et al.* 1994). Despite this, there has been surprisingly little work done on fruit characteristics in tropical and sub-tropical Asia and the generalizations in the literature are based largely on Neotropical, African and temperate zone studies (Jordano 1995). This paper analyses the characteristics of a large sample of Hong Kong's fleshy fruit flora in order to test the generality of patterns of fruit characteristics observed elsewhere. Fruit–frugivore relationships in Hong Kong are also of special interest because centuries of human impact have left a highly depleted fauna but a surprisingly rich flora: probably a realistic model for the future of most of the tropics. Plant names mostly follow Anonymous (1993) and authorities for the 153 species studied in detail are given in Appendix 1.

THE STUDY AREA

Hong Kong (22° 17′ N, 114° 09′ E) consists of part of mainland China and several adjacent islands, with a total area of 1076 km^2. Although just within the geographical tropics, the thermal climate is more seasonal than typical for this latitude and the flora has a large extra-tropical component, particularly above 400–500 m (Dudgeon & Corlett 1994). Despite almost complete deforestation several centuries ago (Dudgeon & Corlett 1994), a rich tree and shrub flora survived in topographically protected sites and a subset of this now dominates the secondary shrublands and forest which cover, respectively, 16.5 and 9% of the territory (Ashworth *et al.* 1993). The most extensive vegetation type, however, is fire-maintained grassland. Hong Kong's 6.0 million human population is concentrated on the limited natural flat land, extended by coastal reclamation.

Fruit production and frugivory are highly seasonal in Hong Kong. Although some ripe fruit is available year-round, fruit diversity and abundance reaches a maximum in December/January (Corlett 1993). Hong Kong's potential disperser fauna has been depleted by deforestation and hunting (Dudgeon & Corlett 1994). The most highly frugivorous vertebrates in Hong Kong are two species of fruit bat (*Cynopterus sphinx* (Vahl) and *Rousettus leschenaulti* (Desmarest)) which apparently depend largely on five species of figs during the April/May fruit minimum (pers. obs.). At least 35 species of resident (or partly resident) birds and 40 species of migrants probably eat at least some fruit but the major frugivores are resident species of *Pycnonotus*, *Zosterops* and *Garrulax*, and migrant species of *Turdus*, *Luscinia* and *Tarsiger* (Corlett 1992a). *Pycnonotus sinensis* (Gmelin), *P. jocosus* (Linn.) and *Zosterops japonicus* Swinhoe are the most common species and are highly frugivorous in winter. Hong Kong's two civet species (*Paguma larvata* (Hamilton-Smith) and *Viverricula indica* (Gray)) eat a lot of fruit in late summer and winter but are highly selective, concentrating on a dozen fruit species (Goodyer, pers. comm.). The only native primate is *Macaca mulatta* (Zimmerman) and the present-day populations of this species were probably established from released animals (Fellowes 1992). Fruit is a major item in the diet of both this species and the exotic *Macaca fascicularis* (Raffles) established in the same area. The common hillside rat species (*Niviventer fulvescens* (Gray) and *Rattus sikkimensis* (Robinson & Kloss)) also eat some fruit but intact seeds are rarely found in their faeces (Corlett, unpublished). Intact seeds are more frequent in the faeces of the larger, bandicoot rat (*Bandicota indica* (Bechstein)) but this species is now rare in Hong Kong.

METHODS

Fruit type was determined for all the native or naturalized angiosperm and gymnosperm species in Hong Kong, from field observations, herbarium specimens and the taxonomic literature. Ripe fruits were collected from 255 fleshy fruited species between 1989 and 1995, and the following variables recorded: ripe fruit colour, fruit weight, seed number, seed weight, fruit and seed dimensions. Measurements were made on at least 15 fruits (except *Pandanus uropyllus*, for which only five intact fruits were found), chosen to represent the typical size range. Where possible, the fruit development time (estimated as the time between the flowering and fruiting maxima for the species) was also determined.

Chemical analysis was carried out on the fruit flesh of 153 species. This included almost all the commonest species and some less common species, for which enough ripe fruit could be obtained, chosen to represent as wide a taxonomic and morphological range as possible. The nutritional variables measured for the fruit pulp were: water content, total nitrogen (Kjeldahl), total lipids (Soxhlet) and total water-soluble carbohydrate (Allen 1989). For 107 species, neutral detergent fibre (Goering & Van Soest 1970) was also determined. All analyses were done on pooled samples from at least six plants, with the exception of *Artocarpus hypargyreus*, *Calamus* sp., *Carallia brachiata*, *Eriobotrya fragrans*, *Lindera megaphylla*, *Osmanthus marginatus*, *Pandanus urophyllus*, *Uvaria calamistrata* and *Uvaria grandiflora*, for which only two to five fruiting plants were available. In most cases, the final figures are the means of three analyses for nitrogen and carbohydrate, two for water and one for lipid (which required large amounts of fruit), but all unusual or extreme values were checked by repeat analysis. No attempt was made to look at variation within species. Although the limitations of all these analyses as measures of nutritional value are well documented (Martinez del Rio & Restrapo 1993, Simons & Bairlein 1990), insufficient is known about the digestive physiology of birds and other frugivores to propose practical alternatives. The methods used have the merit of comparability with previous studies.

Information on the dispersal agents for the plant species studied was obtained from the following observations: identification of seeds in >3000 faecal samples from birds caught with mist nets, with the aid of a comprehensive reference collection (Corlett, unpublished); direct observations of feeding by bird species known to pass seeds intact; direct observations of feeding by fruit bats; identification of seeds in civet scats; direct observation and faecal analysis for macaques. Most observations are my own.

Most of the variables measured have highly skewed distributions so the median value is given instead of the mean. The means reported in the literature of, for instance, lipid content in a fruit flora, have little ecological relevance and are very sensitive to extreme values. For the same reason, non-parametric statistics are used for comparisons. For the principal components analysis, transformations of the data to meet the assumptions of parametric analyses had negligible effect on the results so untransformed data, except for seed size, were used for ease of interpretation. Seed size was log-transformed because of its very wide range (1–2600) and because the resulting range of values is probably a better measure of 'seediness', as experienced by a frugivore.

Jordano (1995) has shown that phylogenetic relatedness explains a large proportion of the total phenotypic variance in fruit characteristics. The intentions of this paper are primarily descriptive but the influence of phylogenetic affinity was reduced by ensuring that no genus contributed more than seven species (*Ilex*, *Ficus*) and no family more than 13 species (Lauraceae) to the total data set.

RESULTS

Hong Kong has a native angiosperm flora of approximately 1800 species (Anonymous 1993, with additions and corrections), of which at least 482 species (27%) bear fleshy, presumably vertebrate-dispersed, fruits. Fifteen species of naturalized exotics also have fleshy fruits (Corlett 1992b) but have been excluded from this study. In addition, the seeds of three native gymnosperms (*Amentotaxus argotaenia*, *Podocarpus neriifolia* and *Gnetum montanum*) are fleshy. Of the native tree and shrub flora for which fruit type could be reliably determined (442 species), the proportion with fleshy fruits (76%) is much higher than for the angiosperm flora as a whole. For native climbers, 70% of the 148 species with known fruit type bear fleshy fruits.

Morphological characters of the fruit and seed were determined for 255 native species (53% of the total native, vertebrate-dispersed, fruit flora) and are summarized in Figure 1. The distribution of fruit and seed sizes is highly skewed. The largest fleshy fruit in Hong Kong is that of coastal *Pandanus odoratissimus* but, although the flesh is considered edible, I have no evidence that this species is dispersed by animals in Hong Kong and it is excluded from this account. The largest non-coastal fruit species is *Pandanus urophyllus* (*c.* 700 g) but, since the drupes separate quite easily in the ripe fruit and are apparently removed by mammals individually, I have treated the drupe as the dispersal unit. The largest fruit removed from the plant as a single unit is that of the climber *Melodinus suaveolens* (164 g). The smallest fleshy fruits are produced by a sedge, *Carex baccans* (0.0044 g). Median fruit weight for the species investigated was 0.36 g and 85.9% of fruit species had a mean diameter <13 mm. Seed weight ranged from 3×10^{-5} g to 2.7 g. Median seed weight was 0.059 g and 95.1% had a mean diameter <10 mm. Fruits of most species (56.1%) had a single seed. The commonest fruit colour is black (45.1% of the species examined), followed by red (24.3%). Bicolour displays – usually black on red – are widespread and two common species (*Sapium discolor* and *Rhus succedanea*) have brightly coloured senescent foliage at the time when the relatively inconspicuous fruits are ripe.

Nutritional characteristics of the fruit flesh varied widely among the 153 species studied (Figure 1; Appendix 1). Pulp mass as a percentage of fruit mass ranged from 10.0% to 99.2%, with a median of 69.2%. Water content ranged from 11.1% to 94.0%, with a median of 78.0%. Lipid contents as a percentage of dry weight were highly skewed, ranging from undetectable by the methods

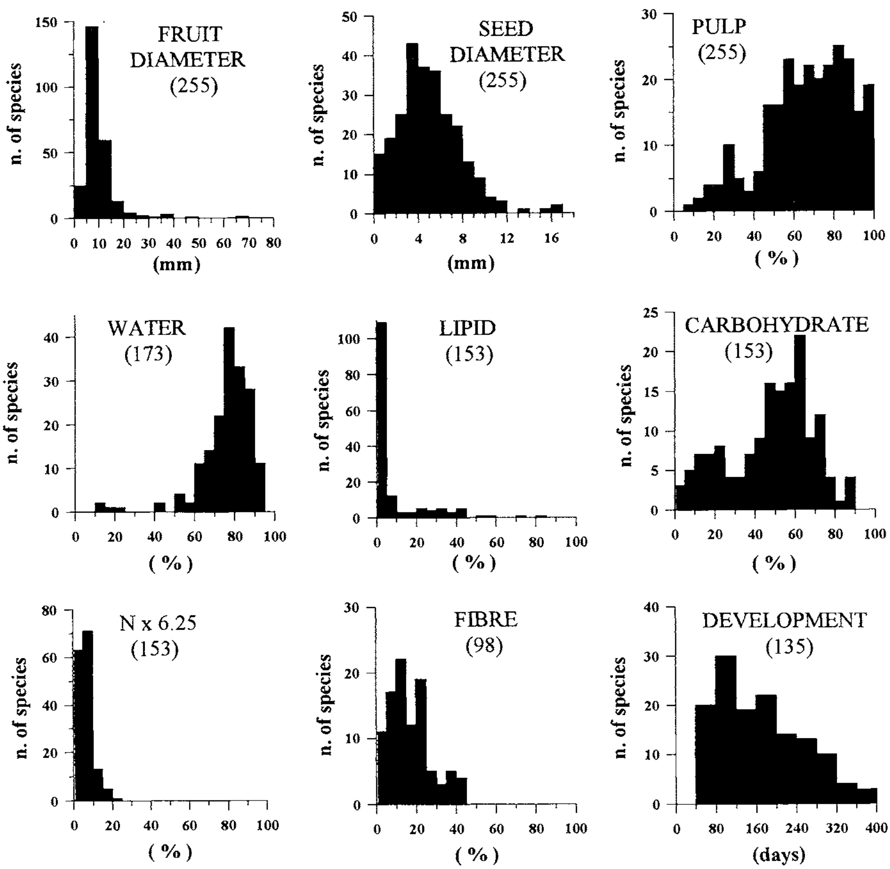

Figure 1. Frequency distribution of fruit characteristics of Hong Kong species: with pulp as percentage of fruit mass; water as percentage of pulp wet weight; lipid, soluble carbohydrate, nitrogen (×6.25) and fibre as percentages of pulp dry weight; and development time in days from anthesis to ripe fruit.

used to 84.0%, with a median of only 2.0% (mean 8.7%). Most high-lipid (>15% lipid) fruits were in the families Lauraceae and Euphorbiaceae, but 10 other families were represented. Soluble carbohydrate content showed a similar range to lipid, from 4% to 88%, but the distribution is much less skewed and the median was 53%. Nitrogen contents were considerably lower, with a range of 0.2% to 3.4% and a median of 0.86%. Using the standard multiplication factor of 6.25 this is equivalent to 1.3–21.3% protein. Among the 107 species for which neutral detergent fibre was measured, the lowest value was less than 1% (in *Strychnos angustifolia*, from which the inedible peel was removed before analysis), the highest was 44% and the median was 14.3%.

Median fruit development time for the 135 species in which it was determined (Appendix 1) was 156 d, with a range of 50 d to 360 d. Development time showed no significant correlation with fruit or seed size, or any other morphological variable measured, but was negatively correlated with lipid content (Spearman's rank correlation coefficient $r_s = 2.25$, $n = 110$, $P < 0.05$).

Table 1. Principal components analysis of 153 fruiting species in Hong Kong: eigenvector loadings of eight variables on the first three components.

Variable	PC1	PC2	PC3
Fruit diameter	−0.202	0.380	−0.698
Seed diameter	0.154	0.747	−0.140
Log_{10} seed number	−0.283	−0.413	−0.543
Pulp	−0.466	−0.167	−0.059
Water	−0.420	0.150	0.122
Lipid	0.463	−0.182	−0.260
Carbohydrate	−0.465	0.120	0.167
Nitrogen	0.178	−0.170	−0.291

The principal components analysis summarizes the major patterns of variation in fruit characteristics (Table 1; Figure 2). For this analysis, diameter (the widest point perpendicular to the long axis) is used as the measure of fruit and seed size most relevant to a frugivore and seed number was log-transformed. Fibre content was omitted because it was determined for fewer species than the

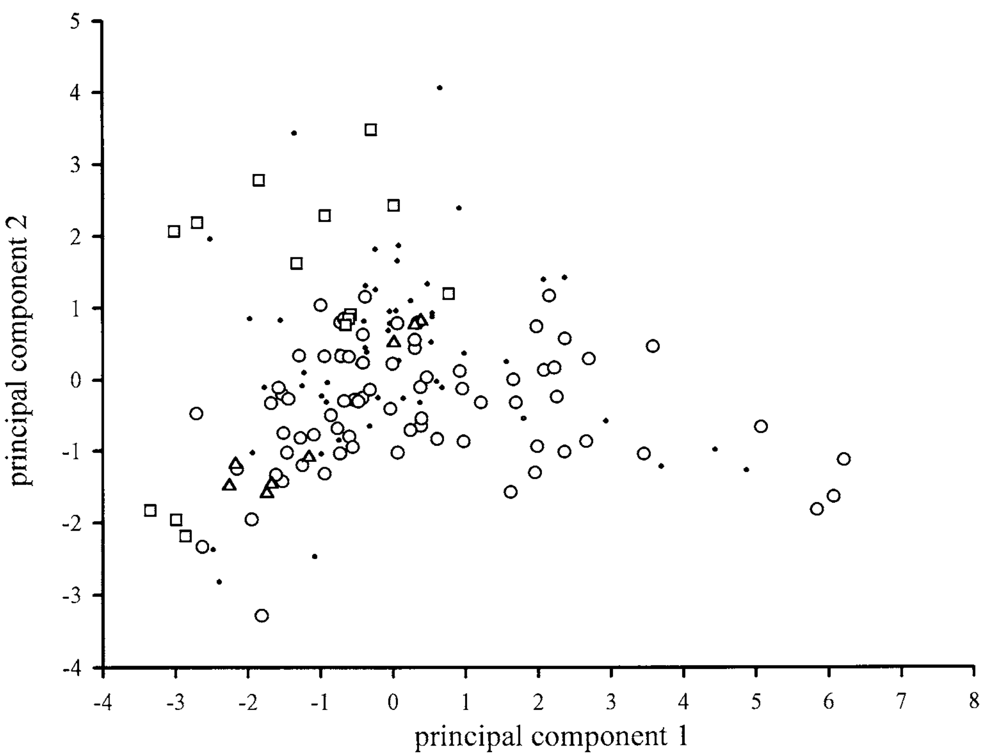

Figure 2. Principal components analysis of Hong Kong fruit characteristics (variables in Table 1) showing species known to be dispersed by mammals (squares), birds (circles), both (triangles) and with unknown dispersal agent (dots).

other attributes. It was not significantly correlated with any other attribute in pairwise tests. Although the details of the PCA output are sensitive to which variables are included, the major trends are robust. Moreover, clear separation of taxonomic groups on the plot suggests that this arrangement is biologically meaningful. The first two principal components account for 59.2% of the variance in the fruit attributes.

The first principal component (40.4% of the variance) has a high positive loading for lipid content and high negative loadings for pulp percentage, water content, carbohydrate content and the logarithm of seed number (Table 1). Fruit species with high scores on this axis are single-seeded with a thin, lipid-rich pulp layer, such as *Sapium* spp., *Mallotus paniculatus*, *Celastrus hindsii* and *Ternstroemia gymnanthera*. Fruits with low scores are multiple-seeded, with much, watery, carbohydrate-rich pulp, such as *Ficus* spp., *Lasianthus chinensis* and *Artocarpus hypargyrea*. The second principal component (18.9% of the variance) basically represents a gradient of increasing size but, because seed size has a higher loading than fruit size, tiny-seeded large fruits, such as *Ficus variegata*, have relatively low scores. The third principal component (14.9% of the variance; not illustrated) has high positive scores for seed number and fruit size.

Overlaying the known dispersal agents on the PCA plot (Figure 2) reveals two, overlapping, dispersal syndromes. The 83 species known to be dispersed by birds cover the full range of fruit morphology and chemistry with the exception of the largest fruits. A gape limit of 13–14 mm for the commonest avian dispersers is supported by field observations and cage experiments. Within this size range, 74.5% of the fruit species are black or red. The only larger fruits consumed by these birds are soft enough for pieces to be pecked out. Seed dispersal only occurs in these cases if the seeds are small and numerous, as in Hong Kong's commonest shrub species, *Rhodomyrtus tomentosa* (mean fruit diameter 14.3 mm). Several less common birds with larger gapes eat some fruit and it is possible that some larger fruits are at least partly dispersed by birds. However, all the larger fruits in the sample studied here are known or suspected to be dispersed by mammals (bats, civets and/or macaques; Appendix 1). The majority are yellow, brown or green in colour, have high pulp percentages and high carbohydrate contents. An inedible peel is present in *Calamus* spp., *Fortunella hindsii*, *Garcinia oblongifolia* and *Strychnos angustiflora*. Only *Choerospondias axillaris* falls to the ground undamaged when ripe. Mammals also consume some smaller fruits eaten by birds but none of these have a high-lipid content.

Fruit characteristics were compared between species fruiting in the cool, dry winter (November–March) – the period when migrant insectivore–frugivores are in Hong Kong – and in the hot, wet summer (May–September). Most species fruited in winter (Corlett 1993). Summer fruits were significantly larger than winter fruits and had significantly higher seed size and carbohydrate content (Mann–Whitney, Table 2). Summer fruits also had a higher percentage of pulp and less fibre, although this was only marginally significant

Table 2. Seasonal variation in fruit characteristics of Hong Kong species, with Mann–Whitney tests of difference between fruits ripening in winter (November–March) and those in summer (May–September). n = 89 winter fruits and 43 summer fruits, except for fibre content (n = 62 and 24, respectively) and development time (n = 68 and 34).

Variable	Median		P =
	Winter	Summer	
Fruit diameter (mm)	7.8	9.8	0.0054
Seed diameter (mm)	4.7	5.7	0.023
Seed number	1.0	1.0	0.32
Pulp (%)	63.6	71.4	0.068
Water (%)	76.8	79.2	0.56
Lipid (%)	2.0	3.0	0.17
Carbohydrate (%)	47.0	61.0	0.013
Nitrogen (%)	0.9	0.9	0.91
Fibre content (%)	16.5	13.4	0.087
Development (days)	194.0	86.5	<0.00001

($0.10 < P < 0.05$). Winter fruits had a median development time (194 d) more than twice as long as summer fruits (87 d). No other measured characteristic showed any significant difference between the seasons.

DISCUSSION

The proportion of the Hong Kong flora with fleshy, animal-dispersed fruits (27%) is low for the wet tropics (Levey *et al.* 1994). This is undoubtedly the result of deforestation, which has replaced forest, dominated by predominantly animal-dispersed trees, shrubs and climbers, by grassland with few fleshy fruits (Dudgeon & Corlett 1994). There were probably many extinctions among the woody flora and it is doubtful that much of the current 'native' herbaceous flora could have survived in a forested landscape. Selective extinction may also be part of the explanation for the small proportion of large fruits in the flora (14.1% of species >13 mm diameter) compared with the equatorial forests of south-east Asia (Corlett, unpublished data). Large-fruited species are poorly dispersed by the surviving fauna and may be particularly vulnerable to repeated cycles of deforestation. An additional factor, however, has probably been the exclusion from Hong Kong, by occasional periods of extreme low temperature (Corlett 1992c), of some large-fruited families, such as the Burseraceae and Myristicaceae, which are important in forests further south.

The predominance of black and red, usually in that order, as fruit colours, seems to be a universal feature of fruit floras (Willson & Whelan 1990) and the general patterns of fruit nutritional characteristics in Hong Kong are similar to those reported elsewhere. The great variation in lipid content, with few high-lipid fruits and a strong negative correlation between lipid and carbohydrate contents, has been found in studies from all over the world (Debussche *et al.* 1987, French 1991, Gautier-Hion *et al.* 1985, Herrera 1987, Johnson *et al.* 1985, Jordano 1992, Wheelwright *et al.* 1984). One interesting exception is the study by Eriksson & Ehrlen (1991), in central Sweden (latitude 59° N), where no fleshy fruit species in the local flora had >15% lipid and there was no significant correlation between lipid and carbohydrate. This is one extreme of a rather weak latitudinal gradient in reported mean lipid content, with the highest values from the tropics (French 1991). The mean lipid content of the fruits studied in Hong Kong (8.7%) is closer to those reported for the temperate zone than for the tropics but, as discussed earlier, means of highly skewed distributions are very sensitive to outliers.

Variations in carbohydrate content are more difficult to compare because of the variety of analytical methods used. However, it is clear that soluble carbohydrate is the normal reward for dispersers, except in high-lipid fruits. In contrast, mean nitrogen contents are low in all reported studies and there seems to be no data on the nutritional significance of the occasional species with high-nitrogen pulp (such as *Brucea javanica* in Hong Kong).

The absence of a significant correlation between fruit development time and fruit and seed morphology suggests that development time is not constrained by development needs but is a result of independent selective pressures on flowering and fruiting times. This is supported by the observation that the very similar fruits of congeneric species sometimes have very different development times in Hong Kong (Corlett 1993). This phenological flexibility within genera contrasts strongly with the conservatism of fruit morphology and chemistry.

Seasonal variations in fruit characteristics have not been quantified previously for tropical fruit floras and temperate zone studies have produced inconsistent results (Eriksson & Ehrlen 1991). The differences in morphology and chemistry reported here reflect the summer fruiting of several species from largely equatorial genera (e.g. *Artocarpus*, *Garcinia*, *Uvaria*) with large, large-seeded, pulpy, carbohydrate-rich fruits. The large seasonal difference in fruit development time is because most winter-fruiting species flower early in the year and fruit the next winter while almost all the summer-fruiting species flower and fruit during the same summer.

All woody vegetation in Hong Kong today is dominated by species with fruits which can be consumed by two of the commonest avian dispersal agents, *Pycnonotus sinensis* and *P. jocosus* (Corlett 1992a). Most of the species known or suspected to be dispersed by mammals share a syndrome of characters: relatively large size, yellow, brown or green coloration, high pulp percentage, high carbohydrate content and low lipid. Some or all of these have been reported as characteristic of mammal fruits elsewhere (Debussche & Isenmann 1989, Herrera 1989, Howe 1986, Willson 1993). Debussche & Isenmann (1989) suggest that the preference for lipid-poor fruits is in order to avoid associated secondary compounds. There are, as yet, insufficient data to distinguish between the fruit types preferred by different mammal species in Hong Kong. Data for bat dispersal, in particular, are very incomplete and the seasonality of fruit production must limit specialization by these obligate frugivores. However, several common plant species do seem to be completely dependent on mammals other than bats for dispersal. These mammal species are currently being eliminated over vast areas of southern China (and adjacent parts of tropical Asia) by hunting and trapping, largely for food. Further research is urgently needed so that we can understand the consequences of this rapid defaunation before it is too late.

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LITERATURE CITED

ALLEN, S. E. 1989. *Chemical analysis of ecological materials* (2nd edition). Blackwell, Oxford.

ANONYMOUS. 1993. *Check list of Hong Kong plants.* Agriculture and Fisheries Department, Hong Kong.

ASHWORTH, J. M., CORLETT, R. T., DUDGEON, D., MELVILLE, D. S. & TANG, W. S. M. 1993. *Hong Kong flora and fauna: computing conservation.* Worldwide Fund for Nature, Hong Kong.

CORLETT, R. T. 1992a. Seed dispersal by birds in Hong Kong shrubland. *Memoirs of the Hong Kong Natural History Society* 19:129–130.

CORLETT, R. T. 1992b. The naturalized flora of Hong Kong: a comparison with Singapore. *Journal of Biogeography* 19:421–430.

CORLETT, R. T. 1992c. The impact of cold and frost on the terrestrial vegetation of Hong Kong. *Memoirs of the Hong Kong Natural History Society* 19:133–135.

CORLETT, R. T. 1993. Reproductive phenology of Hong Kong shrubland. *Journal of Tropical Ecology* 9:501–510.

DEBUSSCHE, M., CORTEZ, J. & RIMBAULT, I. 1987. Variation in fleshy fruit composition in the Mediterranean region: the importance of ripening season, life-form, fruit type and geographical distribution. *Oikos* 49:244–252.

DEBUSSCHE, M. & ISENMANN, P. 1989. Fleshy fruit characters and the choices of bird and mammal seed dispersers in a Mediterranean region. *Oikos* 56:327–338.

DUDGEON, D. & CORLETT, R. T. 1994. *Hills and streams: an ecology of Hong Kong.* Hong Kong University Press, Hong Kong.

ERIKSSON, O. & EHRLEN, J. 1991. Phenological variation in fruit characteristics in vertebrate-dispersed plants. *Oecologia* 86:463–470.

FELLOWES, J. R. 1992. *Hong Kong macaques.* World Wide Fund for Nature, Hong Kong.

FRENCH, K. 1991. Characteristics and abundance of vertebrate-dispersed fruits in temperate wet sclerophyll forest in southeastern Australia. *Australian Journal of Ecology* 16:1–13.

GAUTIER-HION, A., DUPLANTIER, J. M., EMMONS, L., FEER, F., HECKESTWEILER, P., MOUNGAZI, A., QURIS, R. & SOURD, C. 1985. Fruit characters as a basis of fruit choice and seed dispersal in a tropical forest vertebrate community. *Oecologia* 65:324–337.

GOERING, H. K. & VAN SOEST, P. J. 1970. *Forage fiber analysis.* USDA, Agricultural Handbook No. 397.

HERRERA, C. M. 1987. Vertebrate-dispersed plants of the Iberian peninsula: a study of fruit characteristics. *Ecological Monographs* 57:305–331.

HERRERA, C. M. 1989. Frugivory and seed-dispersal by carnivorous mammals, and associated fruit characteristics, in undisturbed Mediterranean habitats. *Oikos* 55:250–262.

HOWE, H. F. 1986. Seed dispersal by fruit-eating birds and mammals. Pp. 123–190 in Murray, D. R. (ed.). *Seed dispersal.* Academic Press, Sydney.

JOHNSON, R. A., WILLSON, M. F., THOMPSON, J. N. & BERTIN, R. I. 1985. Nutritional values of wild fruits and consumption by migrant frugivorous birds. *Ecology* 66:819–827.

JORDANO, P. 1992. Fruits and frugivory. Pp. 105–156 in Fenner, M. (ed.). *Seeds: the ecology of regeneration in plant communities.* CAB International, Wallingford.

JORDANO, P. 1995. Angiosperm fleshy fruits and seed dispersers: a comparative analysis of adaptation and constraints in plant–animal interactions. *American Naturalist* 145:163–191.

LEVEY, D. J., MOERMOND, T. C. & DENSLOW, J. S. 1994. Frugivory: an overview. Pp. 282–294 in McDade, L. A., Bawa, K. S., Hespenheide, H. A. & Hartshorn, G. S. (eds). *La Selva: ecology and natural history of a neotropical rain forest.* University of Chicago Press, Chicago.

MARTINEZ del RIO, C. & RESTRAPO, C. 1993. Ecological and behavioural consequences of digestion in frugivorous animals. *Vegetatio* 107/108:205–216.

SIMONS, D. & BAIRLEIN, F. 1990. Neue Aspekte zur zugzeitlichen Frugivorie der Gartengrasmucke (*Sylvia borin*). *Journal für Ornithologie* 131:381–401.

WHEELWRIGHT, N. T., HABER, W. A., MURRAY, K. G. & GUINDON, C. 1984. Tropical fruit-eating birds and their food plants: a survey of a Costa Rican lower montane forest. *Biotropica* 16:173–192.

WILLSON, M. F. 1993. Mammals as seed-dispersal mutualists in North America. *Oikos* 67:159–176.

WILLSON, M. F. & WHELAN, C. J. 1990. The evolution of fruit color in fleshy-fruited plants. *American Naturalist* 136:790–809.

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Appendix 1. Characteristics of 153 vertebrate-dispersed fruits from Hong Kong.

Family	Species	Disp. agent[1]	Fruit diam. (mm)	Seed diam. (mm)	Pulp[2] (%)	Water[3] (%)	Lipid[4] (%)	TSC[5] (%)	N[4] (%)	Dev. time[6] (d)
Alan.	*Alangium chinense* (Lour.) Harms.	B	7.9	5.3	71	74	36	16	2.8	80
Anac.	*Choerospondias axillaris* (Roxb.) Burtt & Hill	CM	24.6	15.0	78	82	2	42	0.8	186
	Rhus hypoleuca Champ. ex Benth.	B	4.6	3.5	48	52	22	5	0.6	50
Anno.	*Desmos chinensis* Lour.	B	8.0	5.9	55	62	2	62	0.5	173
	Uvaria calamistrata Hance	mamm	39.6	8.2	90	80	1	84	1.1	—
	Uvaria grandiflora Roxb.	mamm	26.4	7.4	89	85	1	67	1.4	—
	Uvaria microcarpa Champ. ex Benth.	?	13.5	7.4	66	82	1	54	0.9	145
Apoc.	*Alyxia sinensis* Champ.	b	7.3	5.5	44	7	3	31	0.8	—
	Melodinus suaveolens Champ. ex Benth.	M	67.3	6.6	89	74	1	51	0.7	240
	Rauvolfia verticillata (Lour.) Baill	b	7.7	5.5	73	88	6	61	0.9	84
Aqui.	*Ilex asprella* (Hook. & Arn.) Champ. ex Benth.	B	7.7	2.3	84	77	5	78	0.6	60
	Ilex cinerea Champ. ex Benth.	B	7.3	3.0	77	71	1	63	0.9	245
	Ilex hanceana Maxim.	b	6.3	2.6	63	78	1	45	0.6	170
	Ilex memecylifolia Champ. ex Benth.	b	7.0	1.8	88	68	1	60	0.6	262
	Ilex pubescens Hook. & Arn.	B	5.8	1.6	87	77	1	60	0.7	238
	Ilex rotunda Thunb. ex Merr.	B	5.7	1.8	82	76	2	46	0.6	—
	Ilex triflora Bl.	b	9.5	5.0	57	63	1	36	0.7	272
Arac.	*Alocasia macrorrhiza* (L.) Schott	B	7.0	5.6	50	79	1	88	0.5	—
	Pothos chinensis (Raf.) Merr.	b	10.9	8.2	59	88	3	63	2.2	83
Aral.	*Aralia dasyphylla* Miq.	B	5.4	1.9	86	77	2	74	0.7	—
	Dendropanax proteus (Champ.) Benth.	B	8.2	3.2	64	72	12	29	1.0	80
	Eleutherococcus trifoliatus (L.) S. Y. Hu	B	4.4	2.3	50	83	34	12	1.3	—
	Schefflera octophylla (Lour.) Harms.	B	7.8	3.2	53	68	19	40	1.0	94
Aspa.	*Asparagus cochinchinensis* (Lour.) Merr.	B	8.9	4.9	79	80	2	68	0.8	—
Aucu.	*Aucuba chinensis* Benth.	?	13.1	11.2	32	77	1	47	0.7	350
Capr.	*Viburnum odoratissimum* Ker-Gawl.	B	5.4	3.8	68	74	5	63	0.6	126
	Viburnum sempervirens K. Koch	B	5.1	4.5	62	83	2	55	0.4	199
Cela.	*Celastrus hindsii* Benth.	b	5.9	5.3	29	42	40	4	3.0	290
	Euonymus chinensis Lindl.	b	4.9	4.5	20	52	43	5	1.8	243
Chlo.	*Sarcandra glabra* (Thunb.) Nakai	B	6.5	3.4	75	85	14	30	1.3	200
Conn.	*Rourea microphylla* (Hook. & Arn.) Planch.	b	5.7	4.8	43	70	44	12	0.9	175
Conv.	*Liriope spicatus* (Thunb.) Lour.	B	6.5	5.2	45	82	3	51	0.8	100
Daph.	*Daphniphyllum calycinum* Benth.	B	9.9	6.3	75	76	2	54	0.7	244
	Daphniphyllum oldhamii (Hemsl.) Rosenth.	B	7.4	5.0	69	80	1	64	0.8	300
Dill.	*Tetracera asiatica* (Lour.) Hoogland	B	3.5	3.5	30	50	26	11	1.4	148
Eben.	*Diospyros morrisiana* Hance	C	18.7	6.0	78	69	1	51	0.6	220
	Diospyros vaccinioides Lindl.	B	9.4	6.8	56	77	3	45	0.8	165
Elaea.	*Elaeagnus loureiri* Champ.	b	8.3	4.8	75	92	2	47	2.5	100

Elaeo.	*Elaeocarpus chinensis* Hook. f. ex Benth.	B	6.8	4.6	71	57	2	45	0.4	134
	Elaeocarpus sylvestris (Lour.) Poir.	BC	11.0	6.3	74	65	2	52	0.8	153
Eric.	*Vaccinium bracteatum* Thunb.	B	5.1	0.8	98	71	2	44	0.3	131
Euph.	*Antidesma japonicum* Sieb. & Zucc.	b	5.5	3.4	85	90	2	46	0.7	174
	Aporusa dioica (Roxb.) Muell.-Arg.	B	8.4	5.3	80	81	1	54	0.7	104
	Bischofia javanica Bl.	B	14.0	3.4	89	79	2	58	0.3	—
	Bridelia tomentosa Bl.	B	6.4	4.2	74	66	1	66	0.8	104
	Endospermum chinense Benth.	?	15.9	3.6	96	81	4	76	1.1	73
	Macaranga tanarius Muell.-Arg.	B	7.4	4.9	69	70	29	35	0.8	—
	Mallotus paniculatus (Lam.) Muell.-Arg.	B	3.3	3.2	21	11	58	8	1.2	112
	Phyllanthus emblica L.	c	17.5	8.2	88	84	1	20	0.6	194
	Sapium discolor (Benth.) Muell.-Arg.	B	4.6	4.3	28	11	70	4	0.9	150
	Sapium sebiferum (L.) Roxb.	B	6.8	5.9	31	15	84	2	0.4	148
	Securinega virosa (Roxb.) Pax. & Hoffm.	b	7.1	1.3	92	84	2	74	0.6	—
Flac.	*Scolopia saeva* (Hance) Hance	B	7.7	2.5	88	70	1	39	0.7	—
Gnet.	*Gnetum montanum* Markgr.	CM	18.7	11.9	63	75	4	63	1.2	110
Good.	*Scaevola taccada* (Gaertn.) Roxb.	b	10.9	6.0	85	92	1	67	0.5	—
Gutt.	*Calophyllum membranaceum* Gardn. & Champ.	?	10.7	7.9	47	77	4	45	0.4	—
	Garcinia oblongifolia Champ. ex Benth.	M	38.5	10.8	85	83	11	79	0.8	98
Hydr.	*Dichroa febrifuga* Lour.	b	7.8	0.3	96	87	1	58	1.5	214
Laur.	*Cinnamomum camphora* (L.) Presl.	B	9.6	6.7	71	66	23	20	1.3	230
	Cinnamomum parthenoxylum (Jack) Nees	B	8.6	5.7	71	69	29	20	1.2	—
	Cryptocarya chinensis (Hance) Hemsl.	b	11.3	10.1	29	71	8	15	1.6	—
	Lindera megaphylla Hemsl.	?	17.0	11.6	69	77	35	15	1.8	—
	Litsea cubeba (Lour.) Pers.	B	6.3	4.1	75	63	32	9	0.9	207
	Litsea glutinosa (Lour.) C. B. Rob.	B	8.8	6.8	57	70	26	13	1.1	76
	Litsea monopetala (Roxb.) Pers.	B	8.1	6.4	51	75	22	24	2.4	85
	Litsea rotundifolia Hemsl.	B	7.0	5.0	59	78	5	43	1.3	73
	Litsea verticillata Hance	b	10.0	7.4	54	87	2	27	1.1	—
	Neolitsea pulchella (Meissn.) Merr.	b	7.4	6.1	46	82	15	17	1.2	—
	Persea breviflora (Benth.) Pax.	B	10.6	8.3	49	79	22	13	1.3	108
	Persea leptophylla (Hand.-Mazz.) Kosterm.	B	12.3	8.8	62	61	38	24	1.1	—
	Persea oreophila (Hance) Kosterm.	B	10.3	7.7	57	75	33	23	2.0	—
	Persea thunbergii (Sieb. & Zucc.) Kosterm.	B	10.9	8.1	56	64	41	19	1.3	88
	Persea velutina (Champ. ex Benth.) Kosterm.	B	12.4	9.4	45	77	20	15	1.6	84
Loga.	*Strychnos angustiflora* Benth.	c	23.5	13.9	80	83	0	72	0.2	140
Mela.	*Melastoma dodecandrum* Lour.	b	11.6	0.5	99	86	2	53	1.0	68
	Melastoma sanguineum Sims	B	7.3	0.5	60	82	1	64	1.9	148
	Memecylon ligustrifolium Champ.	b	11.7	7.9	63	69	1	46	0.6	290
Meni.	*Cocculus orbiculatus* (L.) DC.	B	6.1	3.9	79	85	2	49	1.2	65
	Diploclisia glaucescens (Bl.) Diels	?	12.0	9.0	71	80	1	61	1.6	85

Appendix 1. *(cont.)*

Family	Species	Disp. agent[1]	Fruit diam. (mm)	Seed diam. (mm)	Pulp[2] (%)	Water[3] (%)	Lipid[4] (%)	TSC[5] (%)	N[4] (%)	Dev. time[6] (d)
Mora.	*Artocarpus hypargyreus* Hance	MC	45.2	7.8	93	79	3	76	0.4	60
	Ficus fistulosa Reinw. ex Bl.	F	19.5	0.6	98	84	1	71	0.4	—
	Ficus hirta Vahl.	B	14.9	0.7	94	82	2	71	1.5	—
	Ficus hispida L. f.	F	26.1	0.8	95	85	3	58	1.7	—
	Ficus microcarpa L. f.	BF	11.0	0.9	99	79	4	53	0.7	—
	Ficus superba Miq.	BFC	11.6	1.0	98	83	2	47	1.0	—
	Ficus variegata Bl.	F	24.8	1.0	95	87	3	56	1.1	—
	Ficus variolosa Lindl. ex Benth.	B	10.3	1.9	88	77	6	65	0.7	—
Myri.	*Myrica rubra* (Lour.) Sieb. & Zucc.	C	18.6	8.8	90	89	0	61	1.1	58
Myrs.	*Ardisia crenata* Sims	B	8.6	6.1	50	84	1	50	0.8	194
	Ardisia punctata Lindl.	b	9.2	6.2	58	91	3	38	0.6	194
	Ardisia quinquegona Bl.	b	8.4	5.7	67	86	2	55	1.1	210
	Embelia laeta (L.) Mez	C	9.1	6.1	69	81	3	64	0.4	154
	Embelia ribes Burm. f.	B	5.1	3.2	75	83	4	58	0.6	158
	Maesa japonica (Thunb.) Moritzi	b	6.8	0.6	96	81	6	39	1.8	306
	Maesa perlarius (Lour.) Merr.	B	6.0	0.7	97	88	3	57	1.0	314
	Myrsine neriifolia Sieb. & Zucc.	b	7.2	4.7	69	82	5	59	0.6	310
Myrt.	*Cleistocalyx operculatus* Merr. & Perry	?	9.8	7.0	51	86	2	30	1.0	54
	Syzygium buxifolium Hook. & Arn.	Cb	9.0	7.3	36	87	1	30	0.6	108
	Syzygium hancei Merr. & Perry	B	9.6	6.2	69	85	2	56	0.4	—
	Syzygium levinei (Merr.) Merr. & Perry	B	10.4	7.4	62	90	2	53	0.8	—
Olea.	*Jasminum lanceolarium* Roxb.	b	8.9	6.7	48	80	2	63	0.8	124
	Ligustrum lucidum Aiton	b	6.2	3.8	66	77	2	41	1.0	—
	Ligustrum sinense Lour.	B	5.4	3.5	63	77	3	60	1.4	340
	Osmanthus marginatus (Benth.) Hemsl.	b	14.2	9.8	60	77	2	50	0.6	—
Palm.	*Calamus* sp.	?	19.6	16.4	33	75	1	66	0.8	—
	Calamus thysanolepis Hance	?	9.8	6.8	68	76	1	64	0.9	—
	Phoenix hanceana Naud.	BC	8.9	7.0	58	67	2	60	0.9	56
Pand.	*Pandanus urophyllus* Hance	c	15.2	10.9	70	87	1	75	0.8	365
Phor.	*Dianella ensifolia* (L.) DC.	B	11.1	3.3	87	88	4	73	0.9	—
Poly.	*Polygonum chinense* L.	B	6.7	2.3	93	94	0	58	1.9	—
Rham.	*Berchemia racemosa* Sieb. & Zucc.	B	5.6	3.1	83	85	2	58	1.2	160
	Sageretia theezans L.	B	7.2	3.7	91	82	2	49	2.0	140
Rhiz.	*Carallia brachiata* (Lour.) Merr.	B	8.1	5.1	62	80	7	58	1.1	134
Rosa.	*Eriobotrya fragrans* Champ. ex Benth.	c	17.9	9.8	83	74	2	22	0.5	—
	Photinia prunifolia (Hook. & Arn.) Lindl.	B	6.3	2.3	84	68	3	27	0.7	258
	Rhaphiolepis indica (L.) Lindl.	B	7.3	5.2	58	64	2	28	0.6	274
	Rhodomyrtus tomentosa (Ait.) Hassk.	BCM	14.3	2.4	91	79	1	62	0.5	110

	Rubus reflexus Ker	BC	11.1	1.3	92	89	1	64	0.9	56
Rubi.	*Antirhea chinensis* (Champ.) Benth. & Hook. f.	b	6.9	3.5	82	78	2	69	0.8	96
	Gardenia jasminoides Ellis	B	12.6	3.3	48	62	34	14	0.6	230
	Lasianthus chinensis Benth.	B	11.5	2.3	97	93	2	88	0.7	74
	Morinda umbellata L.	B	11.3	2.9	80	84	3	41	0.6	52
	Psychotria rubra (Lour.) Poir.	B	8.7	5.0	75	91	2	70	0.8	156
	Psychotria serpens L.	B	6.3	3.1	78	92	2	70	0.8	172
	Tricalysia dubia (Lindl.) Ohwi	B	8.4	3.8	72	80	20	40	1.0	202
Ruta.	*Acronychia pedunculata* (L.) Miq.	B	13.6	7.0	85	74	4	71	0.6	162
	Atalantia buxifolia (Poir.) Oliv.	b	9.8	7.0	55	74	7	45	0.5	—
	Fortunella hindsii (Champ. ex Benth.) Swingle	?	11.5	6.0	77	77	1	47	1.0	—
	Glycosmis parvifolia (Sims) Little	b	10.4	6.3	77	85	0	72	2.1	—
Sant.	*Dendrotrophe frutescens* (Champ.) Danser	bC	11.3	7.0	74	75	2	67	0.8	168
Sapo.	*Sarcosperma laurinum* (Benth.) Hook. f.	b	13.8	9.0	59	85	6	62	0.7	—
Sima.	*Brucea javanica* (L.) Merr.	?	7.1	5.6	54	77	2	19	3.4	244
	Picrasma quassioides (D. Don) Benn.	b	5.9	4.6	45	61	42	5	2.4	68
Smil.	*Heterosmilax japonica* Kunth.	B	9.4	5.0	48	79	2	54	1.0	202
	Smilax china L.	B	7.2	3.3	58	58	1	55	1.0	274
	Smilax corbularia Kunth.	b	10.0	6.6	64	71	3	39	1.1	135
	Smilax lanceifolia Roxb.	b	6.7	4.7	61	70	2	36	1.1	88
Stap.	*Turpinia arguta* Seem.	b	8.6	4.4	83	78	1	57	0.7	264
Ster.	*Sterculia lanceolata Cav.*	B	10.6	9.0	29	62	31	20	2.7	104
Symp.	*Symplocos lucida* (Thunb.) Sieb. & Zucc.	b	10.2	6.5	71	76	3	45	0.6	268
Thea.	*Eurya chinensis* R. Brown	B	5.1	1.1	86	74	1	67	0.4	325
	Eurya nitida Korthals	BC	5.8	1.8	80	70	1	70	0.6	360
	Ternstroemia gymnanthera Sprague	B	6.3	5.8	24	21	52	12	0.7	153
Thym.	*Wikstroemia indica* (L.) C. A. Mey.	B	7.0	3.6	87	81	2	87	0.8	94
	Wikstroemia nutans Champ.	b	9.6	4.5	89	91	1	56	1.1	94
Tili.	*Microcos paniculata* L.	BC	8.8	6.5	45	75	2	58	1.0	170
Ulma.	*Celtis tetrandra* Roxb.	B	6.3	4.6	55	44	3	61	0.7	154
Verb.	*Callicarpa brevipes* Hance	b	5.2	2.5	72	88	2	53	1.3	176
	Callicarpa kochiana Makino	B	4.9	1.0	96	86	1	85	1.1	—
Visc.	*Viscum ovalifolium* DC.	B	6.3	4.1	81	86	7	54	1.3	—
Vita.	*Cayratia corniculata* (Benth.) Gagnep.	b	11.1	4.5	83	89	4	65	1.3	83
Zing.	*Alpinia chinensis* Rosc.	b	8.1	4.4	53	78	4	41	1.3	—
	Alpinia stachyodes Hance	b	8.3	3.7	53	73	6	47	1.2	204

[1] Dispersal agent: upper case – observed, lower case – inferred; B, b = bird, C, c = civet, F, f = fruit bat, M, m = macaque, mamm = unknown mammal.
[2] As a percentage of fruit fresh weight.
[3] As a percentage of pulp fresh weight.
[4] As a percentage of pulp dry weight.
[5] Total soluble carbohydrate, as a percentage of pulp dry weight.
[6] Fruit development time (anthesis to ripe fruit).