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# Frugivory and seed dispersal by vertebrates in the Oriental (Indomalayan) Region

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## ABSTRACT

Current knowledge of frugivory and seed dispersal by vertebrates in the Oriental Region is summarized. Some degree of frugivory has been reported for many fish and reptile species, almost half the genera of non-marine mammals and more than 40 % of bird genera in the region. Highly frugivorous species, for which fruit dominates the diet for at least part of the year, occur in at least two families of reptiles, 12 families of mammals and 17 families of birds. Predation on seeds in fleshy fruits is much less widespread taxonomically: the major seed predators are colobine monkeys and rodents among the mammals, and parrots, some pigeons, and finches among the birds. Most seeds in the Oriental Region, except near its northern margins, are dispersed by vertebrate families which are endemic to the region or to the Old World. Small fruits and large, soft fruits with many small seeds are consumed by a wide range of potential seed dispersal agents, including species which thrive in small forest fragments and degraded landscapes. Larger, bigger-seeded fruits are consumed by progressively fewer dispersers, and the largest depend on a few species of mammals and birds which are highly vulnerable to hunting, fragmentation and habitat loss.

*Key words:* Asia, birds, frugivory, mammals, Oriental Region, seed dispersal, seed predation.

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## I. INTRODUCTION

Seed dispersal by vertebrates is a key process in the dynamics of natural vegetation and in vegetation recovery after human impact (Corlett, 1995). As deforestation and fragmentation increase and as global warming alters regional weather patterns, many species will have to migrate to survive. In these circumstances, dispersal limitation of plant distributions will become an increasingly serious problem (Primack & Miao, 1992). Thus, loss of dispersal agents may, in the long term, be as serious a threat to tropical plant diversity as deforestation (Bond, 1994). Vertebrates which depend on fruit for a significant part of their diet may, in turn, be vulnerable to changes in fruit supply resulting from deforestation, logging (Leighton & Leighton, 1983), and the influence of climatic change on plant phenology (Corlett & LaFrankie, 1998).

Studies of frugivory and seed dispersal in tropical Asia have concentrated on primates, fruit bats and a few families of birds, but many other vertebrates consume some fruit and disperse some seeds. Degraded Asian landscapes typically lack many of the best-studied dispersal agents, such as gibbons and

hornbills, increasing the significance of those which remain. Even a preliminary assessment of the likely impact of disperser losses on plants and changes in fruit supply on animals requires information on which animal species eat fruit and disperse seeds. However, the information which exists is scattered in numerous, often obscure, sources.

The aim of this report is to provide an overview of frugivory and seed dispersal by vertebrates in the entire Oriental (or Indomalayan) Region. This region was chosen for review because it has, except near its margins, a fairly uniform flora and fauna at higher taxonomic levels: similar habitats in different parts of the region share many of the same families and genera of plants and animals. I have defined it in the broadest sense, approximately following Corbet & Hill (1992) and Inskipp, Lindsey & Duckworth (1996) (who both call it the Indo-malayan Region), to include: Pakistan, India, Nepal and Bhutan below the Himalayan treeline at approximately 3000 m; Sri Lanka; Bangladesh; Burma; China below 3000 m and south of 35 °N; Yakushima and the Ryukyu Islands; and the whole of South-east Asia, including Sulawesi, the Lesser Sunda Islands, Timor, and the Moluccas (Fig. 1).

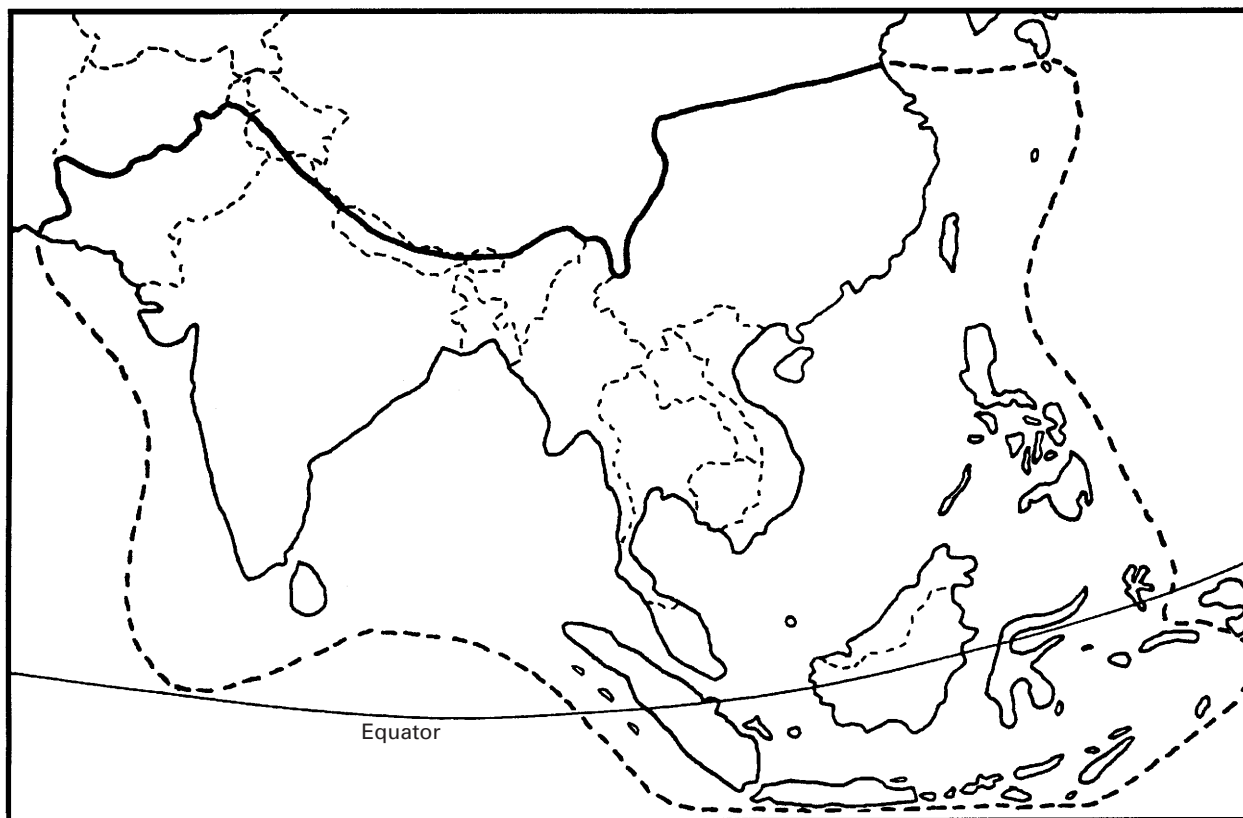


Fig. 1. Boundary of the Oriental Region as defined in this paper (modified from Corbet & Hill, 1992).

Pakistan and, particularly, south-eastern China are transitional to the Palearctic Region, while the islands from Sulawesi to the Moluccas are transitional to the Australian Region. Alternative boundaries, especially with the Palearctic, are equally arbitrary, and inclusion of these marginal areas ensures a more complete treatment of the Oriental fauna, without adding many non-Oriental families or genera. As defined, the region supports one-quarter of the world's bird species (approximately 2462 spp., including the endemic families Megalaimidae and Irenidae) and almost a quarter of the world's non-marine mammal species (approximately 1000 spp., including the endemic Tupaiidae, Hylobatidae and several smaller, non-frugivorous families).

On the plant side, I have only considered fleshy fruits: those which provide an obvious reward to dispersal agents. As Janzen's (1984) foliage-as-fruit hypothesis suggests, almost any herbivore may disperse small-seeded species, with no obvious adaptations on either side. On the animal side, I have included known and suspected seed predators, if they take seeds from fleshy fruits, since it is likely that many seed predators disperse at least some seeds. I

have omitted invertebrates because there is virtually no literature from the region to review.

## II. METHODS

I searched the literature for the answer to four major questions about Oriental vertebrates. Do they eat fruit? Do they defecate, regurgitate, spit or drop potentially viable seeds away from the parent plant? Are they significant seed-dispersal agents? What fruit and/or seed characteristics influence their choice of fruit? Most often, only the first question can be answered directly, but probable answers to the others can sometimes be inferred from comparisons with similar and/or related taxa, or from the morphology of the mouth and digestive system. The literature varies in clarity and quality. I have largely avoided general accounts which list diets without giving the source of information. Instead, I have, as far as possible, used reports of feeding observations, stomach contents or faecal analysis. Information is presented at the generic level or above, unless enough is known to show significant differences between species. Records from outside

the region were only used where either they applied to a species also found within the region, or where there was reason to believe that the observation applied to the whole genus. Classification and nomenclature follows Corbet & Hill (1992) for mammals, Inskipp *et al.* (1996) (which is very similar to Monroe & Sibley, 1993) for birds, and the individual sources for fish and reptiles.

### III. FISH

Most fruits which fall into the water will be eaten eventually and there are many accounts of frugivory by fish in the Oriental region. Fish eat fruits which fall from riverbank trees (Khoo *et al.*, 1987) or in seasonally flooded forest (Roberts, 1993; Roberts & Baird, 1995). In North Borneo, for instance, 'the plop of a fruit or flower hitting the surface is often followed by the strike of a fish... usually *Puntius bulu*' (Inger & Chin, 1962). There has been no study, however, of the fate of the seeds in these fruits comparable to the work done in the much more extensive, seasonally inundated forests of Amazonia (Kubitzi & Ziburski, 1994). Many fish species of tropical Asian headwater streams seem to be indiscriminately euryphagous, taking whatever drops into the water (Lowe-Connell, 1987), but the major reported frugivores are large Cyprinidae (*Leptobarbus*, *Puntius*, *Puntioplites*, *Tor*) and catfish (*Clarias*, *Pangasius*) (Inger & Chin, 1962; Khoo *et al.*, 1987; Roberts, 1993; Roberts & Baird, 1995; MacKinnon *et al.*, 1996). Cyprinids have neither oral teeth nor stomachs, unlike the neotropical frugivorous Characidae, but the pharyngeal jaws are probably as effective in masticating plant tissues (Sibbing, 1991). I have found no information on what proportion, if any, of ingested seeds is defecated intact.

A wide range of fruit taxa have been reported to be consumed by fish, including riverine or swamp species of *Aglaiia*, *Artabotrys*, *Dysoxylum*, *Gonystylus*, *Hydnocarpus*, *Pandanus*, *Quassia*, *Sandoricum* and *Syzygium* (Ridley, 1930; van der Pijl, 1982; Khoo *et al.*, 1987; Roberts, 1993; Mabberley, Pannell & Sing, 1995; Roberts & Baird, 1995). Many of these are large fruits (2–4 cm diameter) and it is possible that dispersal by fish is obligatory. Interestingly, several taxa (*Dysoxylum angustifolium*, *Hydnocarpus*, *Quassia*) are reported to render the fish inedible or, in the case of *Leptobarbus hoevenii* feeding on ripe fruits of *Hydnocarpus*, both intoxicated and inedible! (Banarescu & Coad, 1991). Fish also consume, however,

many species which are clearly not specially adapted to fish dispersal, such as *Ficus variegata*, which is largely dispersed by bats.

### IV. AMPHIBIANS AND REPTILES

There have been no reports of frugivory among Oriental amphibians. Most reptiles are carnivorous, but numerous turtles and lizards are at least partly herbivorous and several species are known or suspected to play a role in seed dispersal (Moll & Jansen, 1995 and references therein). Unfortunately, there have been very few studies of the diet of wild reptiles in the Oriental region and a willingness to eat fruit in captivity – usually peeled, soft fruit – is probably not a reliable guide to natural behaviour.

Some of the Asian softshell turtles, in the family Trionychidae, may eat fruit occasionally, but this has not been reported for Oriental species. In contrast, the semi-aquatic Emydidae – the most diverse turtle family in the region – includes many species which will eat fruit, at least in captivity (in the genera *Annamemys*, *Cuora*, *Hardella*, *Heosemys*, *Hieremys*, *Kachuga*, *Ocadia* and *Sacalia*) and several which prefer it (Ernst & Barbour, 1989). *Heosemys silvatica*, a rare terrestrial species from the forests of south-west India, is reported to feed on fallen fruits of *Dillenia pentagyna*, *Cordia obliqua* and the jackfruit, *Artocarpus heterophyllus* (Vijaya, 1982). Jackfruit is also said to attract *Indotestudo forsteni* (= *Geochelone travancorica*), a terrestrial tortoise in the family Testudinidae (Vijaya, 1982). Fallen fruits also appear to be a major food item for other tortoises in the region, including other species of *Indotestudo*, *Geochelone* and *Manouria* (Ernst & Barbour, 1989). Most turtles and tortoises simply gulp their food down, reducing the likelihood of seed damage, but detailed studies will be needed to determine if seed dispersal by this group is of any significance to the plants involved.

Many lizards will eat small amounts of fruit in captivity (Staniszewski, 1990) and a few species in many families (including the Agamidae, Gekkonidae, Lacertidae, Scincidae and Varanidae, of those which occur in the Oriental region) are thought to eat fruit regularly in the wild and, in a few cases, to be significant in seed dispersal (Whitaker, 1987; Auffenberg, 1988). In southern Luzon, the Philippines, seven of 11 sympatric skink (Scincidae) species ate some fruits, suggesting that frugivory may be common among Asian forest-dwelling skinks (Auffenberg & Auffenberg, 1988). Fruits made up 6.5%

and 11.6%, respectively, of the diet in the large, arboreal species *Dasia grisea* and *Lamprolepis smaragdina*. 'Fruit and seeds' also made up 35% of the stomach contents of four individuals of the widespread *Mabuya multifasciata* caught on the Krakatau Islands (Iwamoto, 1986). However, with one notable exception, there have been no detailed studies of frugivory by lizards in the Oriental region. The exception is a remarkable varanid, Gray's Monitor Lizard (*Varanus olivaceus*), which inhabits the rainforests of southern Luzon (Auffenberg, 1988; from which all the following information is taken). No other varanid lizard is known to eat fruit in the wild, although *Varanus prasinus* will take some in captivity (Sprackland, 1992).

Gray's Monitor is one of the largest living lizards, attaining lengths of over 1.5 m and weights approaching 10 kg. When young it is completely carnivorous but fallen fruits form approximately half of the adult diet. It is a highly selective frugivore, eating only 4% of the local fruit flora and only in a state of perfect ripeness. Fruit genera consumed are: *Dracontomelum*, *Uvaria*, *Canarium* (three spp.), *Garcinia*, *Sandoricum* (naturalized), *Ficus*, *Malaisia*, *Caryota*, *Corypha*, *Livistona*, *Pandanus* and *Grewia*. The monitors eat fruits with diameters in the range 1–5 cm, the upper limit being set, apparently, by the adult throat diameter. Most are one-seeded. Otherwise, there are no obvious shared characters. The list includes both sugary and lipid-rich fruits, all major fruit types, and a range of colours. Larger fruits with a hard rind are punctured and crushed before swallowing but seeds pass through (in approximately 3 days) undamaged to the faeces, which are often deposited on bare ground. *Varanus olivaceus* may be a locally important dispersal agent for *Canarium* spp., which are eaten by few other vertebrates, and possibly *Pandanus*.

## V. MAMMALS

### (1) Marsupalia

#### (a) *Phalangeridae*

Among the marsupials which penetrate the eastern margins of the Oriental Region, only the cuscuses are likely to have any significance as frugivores. There are few hard data on the diets of oriental cuscuses but all of them probably eat at least some fruit. In Sulawesi, the Small Cuscus, *Stigococcus celebensis*, is reputedly a nocturnal frugivore, while the Bear Phalanger, *Ailurops ursinus*, although largely folivorous, eats some fruit (Whitten, Mustafa & Henderson, 1987; Kinnaird, 1995). The Moluccan

Cuscus, *Phalanger ornatus*, of the North Moluccas, has been found eating the 'fleshy outer covering' of cultivated nutmegs (Flannery, 1995). Nothing has been reported on seed fates, but the impoverished mammalian faunas of these islands may increase the significance of these marsupials as dispersal agents.

### (2) Insectivora

#### (a) *Erinaceidae*

The Insectivora is the most carnivorous of terrestrial mammal orders, but frugivory has been reported for several members of the hedgehog family, Erinaceidae, within the Oriental Region. The consumption of fallen fruit has been reported for species of *Hemiechinus* and *Paraechinus* (Roberts, 1977; Prakash, 1994). Whittow, Gould & Rand (1977) report that captive Moon Rats (*Echinosorex gymnurus*) ate various fruits and that wild individuals ate oil palm fruits, while Davis (1962) found fruit in one of seven stomach contents he examined. The Lesser Gymnure, *Hylomys suillus*, has also been reported to eat some fruit (Nowak, 1991; IUCN, 1995).

### (3) Scandentia

#### (a) *Tupaiaidae*

Although treeshrews were long considered primarily insectivorous, Emmons (1991) has shown that, for four *Tupaia* spp. at least, fruit is an important part of the natural diet. Fruit has also been reported as part of the wild or captive diets of some species in the genera *Dendrogale*, *Ptilocercus* and *Urogale* (Lim, 1967; Lekagul & McNeely, 1977; Luckett, 1980; Rabor, 1986; IUCN, 1995). The Madras Treeshrew, *Anathana ellioti*, probably also eats some fruit (Roonwal & Mohnot, 1977). Treeshrews seem curiously ill-adapted for frugivory and can only deal with soft fruits (Emmons, 1991). These are processed in the mouth in a similar way to fruit bats, with only the juice and soft pulp swallowed, while the skin, fibres and seeds are spat out in wads. Like bats, the food transit time is very short, with mean times to first defecation of marker dye of 20 min in *Tupaia minor* and 57 min in *T. tana*. Among the 11 fruit species recorded by Emmons (1991) as eaten, seven were figs. It seems unlikely that treeshrews are significant dispersers for these small, soft 'bird fruits' in habitats with an intact vertebrate fauna. Most species appear to be tolerant of some degree of human disturbance (IUCN, 1995), however, and they can reach very high densities in disturbed and fragmented habitats (Corlett & Lucas, 1995). Emmons, Nias & Briun

(1991) also suggest they may be major dispersers of *Rafflesia keithii*, which has huge, indehiscent fruits with numerous tiny seeds in an oily pulp.

#### (4) Dermoptera

##### (a) *Cynocephalidae*

Although it has been suggested that the flying lemurs (two *Cynocephalus* spp.) may eat some soft fruit, which they will accept 'reluctantly' in captivity (MacDonald, 1984), there seems to be no field evidence for this and they appear to be primarily folivores (Wischusen, Ingle & Richmond, 1994).

#### (5) Chiroptera

##### (a) *Pteropodidae*

By comparison with most other mammalian frugivores, the Old World fruit bats have received a lot of attention in the literature, but most studies have been superficial and nothing at all is known about the ecology of most species. This is unfortunate because the fruit bats are not only abundant and taxonomically diverse in the Oriental Region, but also extremely varied ecologically (Flannery, 1995). Although some taxa may be entirely nectarivorous, and some may even be opportunistically insectivorous (Courts, 1997), the majority apparently subsist largely or entirely on fruits. Pteropodids typically land on the plant and very large fruits (relative to the bat) are eaten piecemeal while still attached. The treatment of smaller fruits seems to depend on bat size. With small bat species, either a single fruit is plucked or, for smaller fruits, the bat clambers around, using the enlarged thumb claw, to pluck several (Fleming, 1993). The bat then usually flies away to a feeding roost, 20–200 m from the fruiting tree in the species studied, where the fruit or fruits are processed (Marshall, 1983; Phua & Corlett, 1989; Bhat, 1994; Izhaki, Korine & Arad, 1995). Small fruit bats can fly with more than their own weight in fruit and the larger species can carry more than 200 g (van der Pijl, 1982), but the larger bat species seem more likely to process fruit in the fruiting tree (Roberts, 1977; Richards, 1990; Utzurrum, 1995; R. T. Corlett, unpublished observations). Utzurrum (1995) contrasted the 'shuttling' feeding behaviour of small bats with the 'sit and feed' behaviour of large species (> 150 g). Richards (1990), however, proposed a 'raiders versus residents' model for long-distance dispersal of large fruits and seeds by species of large bats in tropical Australia,

whereby individuals, raiding feeding territories established early in the night, carry fruits away to avoid aggression.

Fruit processing is complex. The rind, if present, is usually removed first and large seeds are also dropped before the remainder is taken into the mouth. After thorough mastication, the pulp is pressed between the tongue and the palate, the juice is swallowed, and the rest discarded as a fibrous wad. The fate of the seeds depends on bat, fruit and seed characteristics. Very little is known about differences between bat species in their treatment of the same fruits, but one obvious influence is bat size: a large *Pteropus* can fly off with a whole mango while a small *Cynopterus* will simply bite off pieces of the flesh *in situ*. For fruits which are removed from the plant, seed fate seems to be influenced by both seed size and pulp texture. Most large seeds are dropped under feeding roosts by all species, although some may also be dropped, apparently by accident, in flight. Some or all of the smallest seeds may be ejected in the fibrous wad, but others may be swallowed with the juice: the threshold for seed swallowing is reported as less than 4 mg for *Rousettus* in Israel (Izhaki *et al.*, 1995), less than 2.4 mm diameter for 35 g *Cynopterus* in Singapore (Phua & Corlett, 1989), and less than 3.2 mm diameter for a 600 g *Pteropus conspicillatus* in Australia (Richards, 1990). The proportion of seeds swallowed seems to be greatest for fruits with semi-fluid interiors (Phua & Corlett, 1989) or very slippery seeds (Utzurrum & Heideman, 1991).

Figs are the food taxon most frequently mentioned in the Oriental fruit bat literature. Other families which feature prominently are the Anacardiaceae, Guttiferae, Myrtaceae, Palmae and Sapotaceae (Marshall, 1985; Fujita & Tuttle, 1991). Although the pteropodids as a whole consume a huge variety of fruits, there is a distinct 'bat fruit' syndrome – medium to large, drab colour, strong odour, held away from the foliage (Marshall, 1983). In all areas, there appear to be species dispersed only by bats, with the exception, probably, of near the northern limits of their distribution, in the northern Ryukyus, where the reported diet of *Pteropus dasymallus* consists of fruit species also eaten by birds (Funakoshi, Watanabe & Kunisahi, 1993). Moreover, fruit bats appear to be 'sequential specialists' (Mickleburgh & Carroll, 1994), eating only a small fraction of the available fruit species at a time.

Pteropodids are clearly very important dispersal agents for many taxa throughout the region and perhaps the most important vertebrate dispersers on many oceanic islands, where they are the only



animals capable of carrying large-seeded fruits (Mickleburgh & Carroll, 1994). Their habit of defecating and, occasionally, dropping seeds in flight is probably particularly important in the revegetation of large cleared areas (Phua & Corlett, 1989; Mickleburgh & Carroll, 1994). However, the paucity of hard data on seed dispersal by pteropodids in the Oriental Region suggests a need for caution at this stage. Pteropodid feeding strategies have clearly evolved to minimize the transport of indigestible seeds so these are often not carried far. Flannery (1995) also points out the great diversity of ecological niches occupied by pteropodids, giving as an example the large and complex teeth of *Pteralopex* spp., which enable them to crack the nuts of *Canarium* spp.

Pteropodids are threatened by habitat destruction and hunting (Utzurum, 1992; Mickleburgh & Carroll, 1994). The large species (e.g. *Pteropus*, *Acerodon*) are already in serious decline throughout the region and many populations have been eliminated or are only a fraction of their former size. Many of the less well-known small species may be equally vulnerable, but some (particularly *Cynopterus* spp.) thrive in human-dominated landscapes (Phua & Corlett, 1989; Utzurum, 1992).

## (6) Primates

### (a) *Loridae*

The lorises are reported to be basically carnivorous but also to eat some fruit, both in the wild and in captivity (Lekagul & McNeely, 1977; Nowak, 1991). There is no published information on seed fates, but it seems unlikely that these slow-moving animals are major dispersal agents.

### (b) *Cercopithecidae-Cercopithecinae*

The macaques (*Macaca* spp.) of the Oriental Region are generally frugivorous and at least partly arboreal, but their importance in seed dispersal is unclear (Ridley, 1930; Lucas & Corlett, 1998). Ripe fruit appears to be the preferred food of all species, when it is available, and forms the major component of the diet of tropical forest macaques (Lucas & Corlett, 1991, 1998; DeClue, 1992; Shailly, 1993; Krishnamani, 1994; Kinnaird, 1995). Macaques eat a great variety of fruit taxa, by no means confining themselves to the so-called 'primate fruits': those with large seeds, orange-brown colour, and a protective rind (Lucas & Corlett, 1991; Leighton, 1993; Mabblerley *et al.*, 1995).

A detailed study of the Long-tailed Macaque, *Macaca fascicularis*, in Singapore showed that the fate of seeds in ripe, fleshy fruits was determined largely by seed size (Corlett & Lucas, 1990). Only the smallest seeds (< 3 mm diameter) were regularly swallowed: larger seeds were spat out or, in the case of some very large ones, were dropped without ever entering the mouth. The macaques in this study also destroyed some seeds in the mouth but most of these were the dry fruits of Fagaceae and various wind-dispersed species. No other macaque species has been investigated in this detail but a similarly seed-size dependent range of seed fates has been observed in Rhesus Macaques, *Macaca mulatta*, in Hong Kong (Dudgeon & Corlett, 1994), Tibetan Macaques, *M. thibetana*, in Sichuan, China (Zhao, 1996), and Japanese Macaques, *M. fuscata*, on Yakushima Island (Yumoto, Noma & Maruhashi, 1998).

Seed-spitting will only lead to effective seed dispersal if the seeds have been carried away from the parent plant. The likelihood of this happening in macaques is increased by the presence of cheek pouches. These are used to store fruit – peeled with the incisors if necessary – which are then processed as the monkey moves (Lucas & Corlett, 1998; Yumoto *et al.*, 1998). As a result, while many seeds will usually be spat out under the fruiting tree, a proportion are carried away and spat elsewhere, usually one at a time (Corlett & Lucas, 1990; Yumoto *et al.*, 1998). Swallowed seeds will be carried further, but, since these are almost all very small, they are deposited clumped together in the faeces.

In tropical forests with intact vertebrate faunas, most of the fruit taxa eaten by macaques are probably more efficiently dispersed by other frugivores. In human-dominated landscapes, however, the more tolerant macaque species (*M. fascicularis*, *M. mulatta*, *M. radiata*; DeClue, 1992) thrive as long as they are not directly persecuted and are often the largest surviving wild vertebrates in these areas. These tolerant species can live in tiny forest patches, use young secondary forest, cross open ground and eat a wide variety of foods. In such areas, macaques are probably the only dispersal agents for many protected and/or large-seeded fruit species.

### (c) *Cercopithecidae-Colobinae*

In contrast to the macaques, the Asian colobine monkeys are mostly specialist feeders on leaves and seeds (Bennett & Davies, 1994). Mature, fleshy fruits are generally avoided, because a high content of simple sugars may upset the complex digestive

system (Waterman & Kool, 1994). It is usually assumed therefore, that all seeds eaten are destroyed. The Proboscis Monkey, *Nasalis larvatus*, eats many fruits, but these are mostly unripe and/or non-fleshy and no intact seeds were found in over 100 faecal samples examined (Yeager, 1989). Some colobines, however, such as the Hanuman Langur, *Semnopithecus entellus* (Roberts, 1977; Bennett & Davies, 1994), and the Capped Langur, *Presbytis pileata* (Feeroz, Islam & Kabir, 1994), do eat considerable quantities of ripe fruit at some sites. Where the diet includes ripe figs (*Ficus* spp.) and other small-seeded species, it seems unlikely that all seeds are broken or digested, but the seeds that colobines are most likely to disperse intact are those which least need primates for dispersal.

#### (d) *Hylobatidae*

With the exception of the Siamang, *Hylobates syndactylus*, in Malaysia (Raemaekers, 1979), and the Black Gibbon, *H. concolor* (Lan, 1993; Sheeran, 1993), which eat a higher proportion of leaves, gibbons are highly frugivorous (Chivers & Raemaekers, 1986; Feeroz *et al.*, 1994; Palombit, 1997). In comparison with other primates, they are very selective feeders, concentrating on a relatively small proportion of the available fruits (Chivers & Raemaekers, 1986; Ungar, 1995). Figs (*Ficus* spp.) are a major part of the diet in many species (Gittins, 1982; Kappeler, 1984; Srikosamatara, 1984; Feeroz *et al.*, 1994; Palombit, 1997) and, although a wide variety of fruit types are consumed, small, unprotected fruits seem to be preferred when available (Gittins, 1982; Ungar, 1995). Ungar (1994) suggests that large fruits which require extensive preparation with the incisors may be less attractive, because of the need for gibbons to keep their hands free for support and locomotion.

Fruits are usually swallowed whole, or with the rind removed first, if necessary, the seeds are excreted intact in the faeces (Chivers & Raemaekers, 1986), and are mostly viable (Whittington & Treesucon, 1991). The faeces of Kloss Gibbons (*H. klossii*) usually shatter before reaching the ground (Whitten, 1982), so the seeds are less clumped than would otherwise be the case. Some larger seeds, however, may be dropped or spat out while feeding (Gittins, 1982; Chivers & Raemaekers, 1986; Pannell & Koziol, 1987; Whittington & Treesucon, 1991). Gibbons are probably important seed dispersal agents where they survive, but all species have suffered from habitat destruction and hunting.

#### (e) *Hominidae*

The Orang Utan, *Pongo pygmaeus*, is the largest arboreal frugivore in the region. Orang Utans eat large amounts of fruit of many different types (Rodman, 1977; Rijksen, 1978; Galdikas, 1982, 1988; Campbell, 1992; Djojosedharmo & van Schaik, 1992), including more large fruits than are eaten by sympatric primate species (Ungar, 1995). Seeds may be spat, broken or swallowed and defecated intact. Orang Utans can exert greater seed-breaking forces than other primates (Lucas, Peters & Arrandate, 1994), but Galdikas (1982) found intact seeds in 94% of faecal samples in Kalimantan, with a median of 111 seeds per defecation, while Rijksen (1978) found seeds in 44% of samples in Sumatra. The faeces often scatter as they drop from the canopy, thus reducing clumping of seeds. Individual Orang Utans may differ in the way they handle large seeds (Rijksen, 1978) and one individual may process seeds of the same species in multiple ways within one feeding session (Galdikas, 1982). Faeces from one individual may thus contain intact and broken seeds from the same plant species. Seeds which are not swallowed may be transported up to 75 m before being spat out (Galdikas, 1982).

Galdikas (1982) argues that Orang Utans are very important seed dispersal agents and suggests that some plant species may be largely dependent on them for dispersal. This seems unlikely, since none of the species mentioned is confined within the present range of Orang Utans, but there are Pleistocene records of these apes from Java, Vietnam and South China (Corbet & Hill, 1992) so they may have been more important in the past.

### (7) *Carnivora*

#### (a) *Canidae*

Many canids have very varied diets, with fruit a seasonally important component. The most highly frugivorous species in the Oriental Region is the Raccoon Dog, *Nyctereutes procyonoides*, which has unusually short legs for a canid and teeth which are not specialized for a carnivorous diet (Sasaki & Kawabata, 1994). Fruit is important year-round in the diet of Palearctic *Nyctereutes* populations in central and southern Japan, although the frequency of fruit remains in scats varies seasonally (Ikeda, 1985, 1986; Sasaki & Kawabata, 1994). Fruit genera consumed include *Actinidia*, *Morus*, *Myrica*, *Prunus*, *Rubus*, *Stauntonia* and *Vitis*. Although Raccoon Dogs can climb, most fruit seems to be taken from the

ground. Seeds are passed intact in the faeces but many individuals tend to use the same place to defecate, which must reduce their value as seed dispersal agents.

The Asiatic jackal, *Canis aureus*, is an opportunistic feeder which eats significant amounts of fruit. In Bangladesh, India and Pakistan, the jackal eats fallen fruits of several species, including those dropped by feeding langurs, and seeds of *Cassia fistula*, *Salacia chinensis*, *Syzygium cumini* and other species have been found sprouting from the scats (Ridley, 1930; Schaller, 1967; Roberts, 1977; Newton, 1986; Poche *et al.*, 1987; Balasubramanian & Bole, 1993). The wolf, *Canis lupus*, now eliminated from most of its previous Asian range, is, in contrast, highly carnivorous, although occasional fruit consumption has been reported from north-west India (Prakash, 1994) and other parts of its huge range (Papageorgiou *et al.*, 1994). Fruit is seasonally dominant in the diet of some populations of the Red Fox, *Vulpes vulpes* (Roberts, 1977; Debussche & Isenmann, 1989) and both the Bengal Fox, *Vulpes bengalensis*, and Blanford's Fox, *Vulpes cana*, also eat some fruit (Roberts, 1977). The Dhole, *Cuon alpinus*, seems to be the least frugivorous of Asian canids, but Cohen *et al.* (1978) found one scat in 150 examined to be composed entirely of *Zizyphus jujuba* and Shrestha (1997) says that it takes fallen fruit of *Aegle marmelos* in Nepal.

#### (b) *Ursidae*

Apart from the Polar Bear, the ursids are predominantly herbivorous and fruit is a major dietary item for most species. Relatively little is known about the diet of the Sun Bear, *Ursus malayanus*, but it is reported to eat a wide range of fruit (Ridley, 1930; Cranbrook, 1991). The Sloth Bear, *Ursus ursinus*, is also highly frugivorous for several months of the year, although insects are more important in the total annual diet at most sites (Gopal, 1991; Gokula & Varadarajan, 1995; Baskaran, Sivaganesan & Krishnamoorthy, 1997; Joshi, Garshelis & Smith, 1997). Wild fruits eaten by this species include *Aglaia*, *Dillenia*, *Diospyros*, *Ficus*, *Grewia*, *Madhuca*, *Phoenix*, *Rhus*, *Syzygium* and *Zizyphus*. The largely Palaearctic Asiatic Black Bear, *Ursus thibetanus*, eats mostly fruit when it is available (Schaller, 1969; Roberts, 1977; Gao, 1987; Reid *et al.*, 1991). Fruits eaten include *Actinidia*, *Aralia*, *Celtis*, *Cornus*, *Cotoneaster*, *Elaeagnus*, *Litsea*, *Machilus*, *Morus*, *Prunus*, *Rubus*, *Schisandra*, *Sorbus* and *Zizyphus*. All three bear taxa can climb trees but also feed on fallen fruit. A

fourth species, the Brown Bear, *Ursus arctos*, which occurs on the northern boundary of the region, also eats some fruit (Roberts, 1977).

Numerous intact seeds are found in bear faeces and they may be significant dispersal agents for some large-seeded taxa. North American Black Bears, *Ursus americana*, swallow small fruits unchewed, defecate even large seeds viable and undamaged, and can travel long distances in a day, which may make them important dispersers for some species (Rogers & Applegate, 1983; Maehr, 1984). In the Oriental Region, however, most species reported to be eaten by bears, particularly in the north of the region, are also taken by birds, which probably provide a higher quality of dispersal as the seeds are partitioned into numerous small faecal deposits, rather than dropped in large clumps. All three bear species are in decline in most of their ranges as a result of habitat destruction and hunting.

The Giant Panda, *Ailuropoda melanoleuca*, is also largely herbivorous, but occasional fruit consumption is only mentioned in one of the several recent accounts of its diet (Gao *et al.*, 1987).

#### (c) *Ailuridae*

The Red Panda, *Ailurus fulgens* is largely folivorous but also eats fruits, particularly those of *Sorbus* spp. (Gao *et al.*, 1987; Yonzon, 1993; Laidler & Laidler, 1996).

#### (d) *Mustelidae*

Seasonal frugivory is widespread among the mustelids, particularly the martens (*Martes* spp.) (Gao *et al.*, 1987; Clevenger, 1994). The Stone Marten, *Martes foina*, which penetrates the northern boundaries of the Oriental Region, is highly frugivorous at many sites in Europe (Genovesi, Secchi & Boitani, 1996), as is the Japanese Marten, *Martes melampus*, on Tsushima Island (Tatara & Doi, 1994). The largely Oriental Yellow-throated Marten, *M. flavigula*, is also reported to eat some fruit (Lekagul & McNeely, 1977; Roberts, 1977; Gao *et al.*, 1987; Shrestha, 1997). In contrast, the weasels, *Mustela*, are usually considered specialist carnivores, but *M. sibiric*, which enters the Oriental Region from the north, consistently ate fruit on Tsushima Island, Japan, including *Ficus*, *Rhus*, *Rubus*, *Stauntonia* and *Viburnum* (Tatara & Doi, 1994). Nothing seems to be known about the diet of the tropical weasels. Of the other mustelids, the Eurasian Badger, *Meles meles*, which occurs in the north of the region, is a generalist, with fruit a major component of diet in

most European studies (Roper, 1994). Less is known about the diets of the largely Oriental Ferret-badgers, *Melogale* spp., but they are also reported to eat some fruit (Gao *et al.*, 1987; Nowak, 1991; Chuang & Lee, 1997; Shrestha, 1997). Fruits (*Lonicera*, *Rubus*, *Smilax*) occurred in eight of 57 stomachs of the Hog-badger, *Arctonyx collaris*, examined in Shaanxi, China (Zheng *et al.*, 1988). The Honey Badger, *Mallivora capensis*, is largely carnivorous but also eats ripe fruits of *Zizyphus* in Pakistan (Roberts, 1977). Little is known about the diet of the stink badgers, *Mydaus*, and the otters are apparently strict carnivores.

Some mustelids certainly disperse large numbers of intact seeds (e.g. Pigozzi, 1992, for *Meles meles*), but the little available dietary information suggests that they mainly consume small fruit species which are available to many other vertebrates, including birds. Many species are hunted, but, where this is not a problem, most mustelids seem to be tolerant of considerable human disturbance.

#### (e) *Viverridae*

Of all the Oriental carnivores, the civets are the most consistently frugivorous. Many species are largely arboreal and probably all the terrestrial viverrids can and do climb trees. Fruit is recorded in the diets of all genera except *Prionodon* and the little-known *Chrotogale* (Ridley, 1930; Lekagul & McNeely, 1977; Novak, 1991). The most frugivorous species seem to be the palm civets (*Paguma*, *Paradoxurus*) and the Binturong (*Arctictis*), which have teeth less specialized for carnivory than the other genera (Cranbrook, 1991). In Hong Kong, where fruit availability varies seasonally, *Viverricula indica* switches from a largely carnivorous diet in spring and summer to a largely frugivorous one in autumn and winter (Dudgeon & Corlett, 1994). Similar diet seasonality has been reported for other species in seasonal areas (Rabinowitz, 1991; Joshi, Smith & Cuthbert, 1995; Chuang & Lee, 1997).

Civets can harvest fruits in a tree or vine without waiting for them to fall, have wide gapes, swallow fruits more or less whole, travel long distances, and defecate seeds intact, often selecting open sites to do so (Bartels, 1964; Auffenberg, 1988; Gruezo & Soligam, 1990; Rabinowitz, 1991; Dudgeon & Corlett, 1994; Emmons, 1995). Some species may repeatedly re-use the same 'latrines', however, and all appear to be highly selective in their choice of fruit, concentrating on only a few species at a time (Auffenberg, 1988; Gruezo & Soligam, 1990; Bala-

subramanian & Bole, 1993; Dudgeon & Corlett, 1994; Joshi *et al.*, 1995). In Hong Kong, these preferred fruits are all sugar- rather than lipid-rich, and mostly relatively large (Corlett, 1996). Fruits with an inedible rind are avoided in Hong Kong but some are reported to be eaten elsewhere (Leighton & Leighton, 1983; Pannell & Koziol, 1987). Although a wide range of fruit species have been recorded in viverrid diets in the region as a whole, certain taxa are particularly common on published lists, including palms (*Caryota*, *Phoenix*, *Pinanga*), Annonaceae, figs and both wild and cultivated coffee (*Coffea* spp.). For at least some of these, it seems likely that civets are the major dispersal agents.

A few viverrid species (e.g. *Paguma larvata*, *Paradoxurus hermaphroditus*, *Viverricula indica*) are tolerant of human impact, as long as they are not actively hunted, and appear to thrive in degraded landscapes. Most others, however, are highly vulnerable to habitat destruction and all species have been eliminated by hunting in many areas (Schreiber *et al.*, 1989).

#### (f) *Herpestidae*

Although most Oriental literature suggests that mongooses eat little or no fruit (e.g. Lekagul & McNeely, 1977; Roberts, 1977; MacDonald, 1984), there are very few field data on diets from the region. Balasubramanian & Bole (1993) reported that the Indian Grey Mongoose, *Herpestes edwardsii*, ate some fruit in India, but only swallowed the pulp, dropping the seeds under the parent plant. The Short-tailed Mongoose, *H. brachyurus*, is also reported to eat small amounts of fruit in Borneo (Davis, 1962). On a northern Mediterranean island, in contrast, fruit made up half the winter diet of the introduced Small Asian Mongoose, *H. javanicus*, with the seeds ending up in the faeces (Cavallini & Serafini, 1995).

#### (g) *Hyaenidae*

The Striped Hyaena, *Hyaena hyaena*, whose range extends from Africa into the western part of the region, is mostly a scavenger and predator, but also eats some fruit (Roberts, 1977; MacDonald, 1984). Indeed, it is notorious in Israel for destroying fruit crops, including melons, dates, grapes and apricots (Nowak, 1991).

#### (h) *Felidae*

The felids are the most predatory family in the Carnivora, with teeth adapted for seizing and cutting

prey (Nowak, 1991). Tigers are reputed to like durians and fallen wild mangoes (Ridley, 1930), although the same has been said about almost the entire Malayan mammal fauna at some time or other! In eastern China, the Leopard Cat, *Prionailurus (Felis) bengalensis*, is reported to consume some fruit, including the sarcotesta-covered seeds of *Ginkgo biloba*, which are passed intact in the faeces (Gao *et al.*, 1987; Tredici, Ling & Yan, 1992).

## (8) Proboscidea

### (a) Elephantidae

There has been no detailed study of frugivory and seed dispersal by the Asian Elephant, *Elephas maximus*, but there is plenty of evidence that wild elephants will eat fruit when it is available, that seeds are defecated intact, and that some seeds later germinate in the dung (Ridley, 1930; Lekagul & McNeely, 1977; Mukhtar, 1994; Davison, 1995). A fondness for the large fruit of wild mangos (*Mangifera* spp.) is widely reported. Mangos are picked up from the ground with the trunk, but elephants will also knock down small trees or shake larger ones to obtain ripe fruit (Lekagul & McNeely, 1977). Large seeds may sometimes be spat out rather than swallowed (Davison, 1995). The only common feature of the fruits reported to be eaten by elephants is their relatively large size, but there is no evidence that they are exclusive dispersers of any plant species, in contrast to the more frugivorous African Elephant (Feer, 1995). Asian elephants are now rare or extinct over most of their historical range.

## (9) Perissodactyla

### (a) Tapiridae

The Malayan Tapir, *Tapirus indicus*, has been reported to be largely folivorous but Williams (1978) found seeds and fruit parts in most fecal deposits examined and considered them potentially important seed dispersal agents.

### (b) Rhinocerotidae

The three Asian rhinoceros species are all reported to eat some fallen fruit, although very few plant species are named in the literature. The Indian Rhinoceros, *Rhinoceros unicornis*, may be the major dispersal agent for *Trewia nudiflora* in Chitwan, lowland Nepal (Dinerstein & Wemmer, 1988; Dinerstein, 1991). Seeds took 3–7 days to pass through the gut of captive rhinos and manuring with dung significantly

increased seedling growth. This rhino species also ingested a variety of other fleshy fruits, most of which were less than 1 cm diameter (Dinerstein, 1991). The Javan Rhinoceros, *Rhinoceros sondaicus*, is reported to disperse seeds of *Pandanus* species and *Dillenia aurea* (Ammann, 1985 cited in Payne, 1995), while the Sumatran Rhinoceros, *Dicerorhinus sumatrensis*, is said to be especially fond of wild mangos (*Mangifera*) (Hubback, 1939, Lekagul & McNeely, 1977). The faeces are full of intact mango seeds in season and seedlings grow out of old dung piles (Hubback, 1939). Cubitt, Whitten & Whitten (1992) claim that certain tree species produce seeds which must pass through a rhino gut to germinate, and suggest that many wild mango species may be in this category.

## (10) Artiodactyla

### (a) Suidae

Fallen fruit probably forms part of the diet of all wild pig species (*Sus* spp.) in Asia (Diong, 1973, Lekagul & McNeely, 1977; National Research Council, 1983; Payne, Francis & Phillipps, 1985; Nowak, 1991; Laman, 1996; Shrestha, 1997). The Bearded Pig, *Sus barbatus*, travels long distances in huge herds in search of fallen fruit (Cranbrook, 1991). The role of pigs in seed dispersal is less clear. They probably destroy the seeds of most species they consume (Ridley, 1930; Leighton & Leighton, 1983) or feed only on the fleshy parts, leaving the seeds near the parent tree (Payne, 1995), but some intact seeds from fleshy fruits, including *Ficus*, *Manilkara* and *Zizyphus*, are found in pig faeces (Balasubramanian & Bole, 1993; Grice, 1996). The fruits consumed by pigs are already lost to arboreal frugivores, so any additional dispersal is a bonus to the parent plant.

Fallen fruit is also reported to form an important part of the diet of the Babirusa, *Babyrussa babyrussa* (MacDonald, 1984; Cubitt *et al.*, 1992). There is no published information on seed fate, but if seeds are dispersed this may be more significant in Sulawesi, with its impoverished mammal fauna, than dispersal by pigs in Sundaland and on the Asian mainland.

### (b) Tragulidae

Both species of mouse-deer (*Tragulus*) are highly frugivorous (Lekagul & McNeely, 1977) and, indeed, probably dependent on an easily digestible, fruit-based diet (Heydon & Bulloh, 1997). Galdikas (1982) reported that both feed on fruits dropped by feeding Orang Utans. Harrison (1962) found 'large seeds' in all three stomachs of *T. javanicus* that he

examined, showing that seeds can avoid destruction in the mouth and may, therefore, be dispersed intact. The Indian Chevrotain, *Moschiola meminna*, is also reported to eat fallen fruits (Shrestha, 1997).

(c) *Moschidae*

I can find no record of frugivory by the Musk Deer, *Moschus berezovskii*, in the Oriental Region, but small amounts of fruits are consumed by other Musk Deer populations (Green, 1987).

(d) *Cervidae*

Fallen fruits are probably eaten by all species of deer which have access to them. In the Oriental Region, there are reports of fruit consumption by species of *Cervus* (Ridley, 1930; Lekagul & McNeely, 1977; Brockelman, 1985; Dinerstein, 1989, 1991; Khan, 1994), *Axis* (Roberts, 1977; Johnsingh, 1981; Blouch & Atmosoedirdjo, 1987; Dhungel & O'Gara, 1991; Dinerstein, 1989, 1991; Khan, 1994; Moe & Wegge, 1994), *Muntiacus* (Lekagul & McNeely, 1977; Roberts, 1977; Sheng & Lu, 1982; Dinerstein, 1989) and *Elephodus* (Sheng & Lu, 1982). A particularly wide range of fruit genera have been reported in the diet of *Axis* spp., including *Callicarpa*, *Diospyros*, *Elaeocarpus*, *Ficus*, *Grewia*, *Irvingia*, *Syzygium*, *Xeromphus* and *Zizyphus*. Chital, *Axis axis* and, to a lesser extent, other species are said to wait under foraging monkey troops for fallen fruit.

Payne (1995) suggests that deer, like pigs, either destroy seeds in the mouth or spit them out near the parent tree. Ridley (1930) stated that seeds of fleshy fruits are not defecated but 'disgorged during rumination'. Some seeds from fleshy fruits, however, certainly do end up in the faeces of a variety of deer species (Dinerstein, 1989; Balasubramanian & Bole, 1993) and some large seeds may be effectively dispersed in the mouth (Brockelman, 1985). It seems likely that only small or exceptionally tough or toxic seeds are regularly dispersed, but, as with pigs, any fruits consumed by deer are already lost to more effective dispersal agents so their impact is unlikely to be negative.

(e) *Bovidae*

As with the deer, the importance of fruit in bovid diets seems to depend largely on access. Some fruit from the ground or accessible bushes is known to be eaten by at least the following genera; *Bos* (Ridley, 1930; National Research Council, 1983; Dinerstein & Wemmer, 1988), *Bubalus* (National Research

Council, 1983; Whitten *et al.*, 1987; Shrestha, 1997), *Boselaphus* (Roberts, 1977; Sankar & Vijayan, 1992; Khan, 1994), *Antelope* (Balasubramanian & Bole, 1993), *Gazella* (Loggers, 1991: in the Middle East) and *Hemitragus* (Nowak, 1991: in the Middle East). Fallen fruits appear to be most important in the diet of the forest bovids, the Gaur (*Bos gaurus*) (Ridley, 1930; Dinerstein & Wemmer, 1988; National Research Council, 1983), the Banteng (*Bos javanicus*) (National Research Council, 1983), and the most forest-adapted species, the Lowland Anoa (*Bubalis depressicornis*) and Mountain Anoa (*B. quarlesi*) (Whitten *et al.*, 1987; Nowak, 1991). The anoas are reported to eat, especially, fallen figs (National Research Council, 1983). The faeces of both wild and domestic cattle contain viable seeds from fleshy fruit (Balasubramanian & Bole, 1993; Payne, 1995; Grice, 1996), but there is no information on how seeds of different sizes are treated or the significance of any bovid in seed dispersal.

## (11) Rodentia

(a) *Sciuridae*

The squirrels of the Oriental Region have a great diversity of diets but most species seem to eat some fleshy fruit and/or the seeds they contain. Fruits seem to be particularly important to the giant squirrels (*Ratufa*) (Harrison, 1962; Lekagul & McNeely, 1977; MacKinnon, 1978; Payne, 1980; Borges, 1993), and species of *Funambulus* (Roberts, 1977; Mishra & Gautam, 1992; Balasubramanian & Bole, 1993; Balasubramanian, 1995), *Callosciurus* (Harrison, 1962; Lekagul & McNeely, 1977; Payne, 1980; Leighton & Leighton, 1983; Chou, Lin & Mole, 1985), *Sundasciurus* (Lekagul & McNeely, 1977; MacKinnon, 1978; Leighton & Leighton, 1983), *Lariscus* (Whitten, 1981) and *Rheithrosciurus* (Leighton & Leighton, 1983). The smaller flying squirrels (e.g. *Hylopetes*, *Iomys*, *Petaurillus*) seem to be mostly frugivorous, while the larger species (especially *Petaurista*) eat more leaves, although some fruit is still eaten (Harrison, 1962; Muul & Lim, 1978; Rabor, 1986; Lee, Progulske & Lin, 1986).

Unfortunately, the literature often does not make a clear distinction between consumption of the pulp and the seeds. While most species seem to destroy most seeds, often discarding the flesh, the most detailed studies also report that, in some fruits, the pulp only is eaten and the seed dropped (Payne, 1980; Leighton & Leighton, 1983; Ando, Shiraishi & Uchida, 1984; Mishra & Gautam, 1992; Balasubramanian & Bole, 1993). The Indian Palm

Squirrel, *Funambulus palmarum*, eats the pulp and seeds together in small-seeded fruits (Balasubramanian, 1995). *Callosciurus prevosti* seems to specialize on lipid-rich fruit flesh, although it also eats some seeds (Leighton & Leighton, 1983; Becker, Leighton & Payne, 1985).

Seed dispersal by squirrels could happen in several ways. First, seeds could be swallowed and defecated intact. Although there is no direct evidence for this in the literature, it seems unlikely that squirrels can destroy all the seeds in fruits such as figs. Emmons *et al.* (1991) suggest that *Callosciurus notatus* and other squirrels may be important dispersal agents for *Rafflesia keithii*, which has large, indehiscent fruit with numerous, tiny seeds in the oily pulp. Secondly, seeds could be deliberately cached and subsequently forgotten. Caching has rarely been reported for Oriental squirrels, but this may well reflect a lack of detailed field observations for most species. The widespread *Callosciurus erythraeus* scatter-hoards seeds in the surface soil, at least in Taiwan (Chou *et al.*, 1985) and *Sundasciurus hippuris* apparently does the same in Borneo (Leighton & Leighton, 1983). Other reports of caching by tree squirrels all probably refer to temporary caching of seeds or fruits above ground (Becker *et al.*, 1985). Seeds may also be dispersed when a squirrel transports a seed or fruit away from the parent plant in the mouth. This is common behaviour in some species (Becker *et al.*, 1985) and would result in dispersal if the seed is subsequently dropped, either deliberately or accidentally (Ridley, 1930).

It is not possible to assess the role of squirrels in seed dispersal on the evidence currently available. Even if they are of little or no importance in intact forest, some squirrel species are among the last forest vertebrates to survive in forest fragments and degraded landscapes.

#### (b) *Muridae*

Very little is known about the diets of Oriental rats and mice, and most species for which there is information seem to be highly opportunistic (Harrison, 1962). Many species, particularly forest specialists, are reported to eat fleshy fruits and/or the seeds within them (Harrison, 1962; Musser, 1982; Payne *et al.*, 1985; Rabor, 1986). Seed fates, however, have rarely been determined, although it is generally assumed that murids are primarily seed predators. Scatter-hoarding has not been reported in any Oriental murid, in contrast to the situation in Neotropical forests, where large, scatter-hoarding

caviomorph rodents are important seed-dispersal agents (Forget, 1990). Seed dispersal may also occur *via* ingestion and defecation. Although this possibility seems to have been largely ignored in the Oriental literature, intact small seeds (< 3 mm) are often found in the faeces of all three non-urban rat species in Hong Kong, particularly those of the Large Bandicoot-rat, *Bandicota indica* (Corlett, 1996).

#### (c) *Hystriidae*

Fallen fruits are reported in the diets of all three porcupine genera (Lekagul & McNeely, 1977; Roberts, 1977; Payne *et al.*, 1985). Although there is no published information on seed fate, it seems likely that some small seeds escape destruction in the mouth by chance.

### (12) *Lagomorpha*

#### (a) *Leporidae*

Fruit has been reported in the diets of the Ryukyu Rabbit, *Pentalagus furnessi* (Nowak, 1991) and the Indian Hare, *Lepus nigricollis* (Prakash, 1994). Small seeds are common in the faeces of rabbits in Europe (Malo & Suarez, 1995) so it is possible that some are dispersed by the Oriental species.

## VI. BIRDS

### (1) *Non-passerines*

#### (a) *Megapodiidae*

The megapodes are confined to the eastern margins of the region where they have an almost perfectly complementary distribution to the phasianids (Jones, Dekker & Roselaar, 1995). The Oriental species are ground foragers, consuming invertebrates and some fallen fruits (Ridley, 1930; Elliott, 1994; Jones *et al.*, 1995). The Australian Bush Turkey, *Alectura lathami*, is reported to crush in its gizzard most of the seeds of the prickly pear (*Opuntia*) fruits it eats (Elliott, 1994), but there is no information on seed fate in Oriental megapodes. All species are increasingly threatened by overexploitation and habitat destruction (Elliott, 1994; Jones *et al.*, 1995).

#### (b) *Phasianidae*

Fruit appears to be at least a seasonal component in the diet of most Oriental pheasants, partridges and grouse (e.g. Mason and Maxwell-Lefroy, 1912; Ridley, 1930; Smythies, 1960; Cheng, 1978; Han,

Lan & Zheng, 1989; Roberts, 1991; de Juana, 1994) and it is important year round to some tropical forest species (Payne, 1980; Davison, 1981 *a, b*; McGowan, 1994). Most phasianids feed on the ground, but, in addition to fallen fruit, many species take fruit from bushes, climbers or trees (McGowan, 1994). Although most fruits reported as eaten are small and/or soft (e.g. *Ficus*, *Rubus*, *Ribes*), some species can eat large, large-seeded fruits: the Great Argus (*Argusianus argus*) can swallow whole fruits of up to 21 mm diameter (Davison, 1981 *b*).

In view of the paucity of understorey frugivores in Asian tropical forests (Karr, 1980; Wong, 1986), phasianids are potentially important, but there is very little information on the fate of the seeds in the fruits they consume. Most species which eat fleshy fruits also eat dry seeds and fruits (grains, acorns etc.) or other tough vegetable matter which must be ground up with grit in the muscular gizzard before digestion, but it is likely that at least a proportion of seeds will escape damage. In Hawaii, the introduced Common Pheasant (*Phasianus colchicus*) and Chukar (*Alectoris chukar*) – both Oriental species – disperse viable seeds of native, woody dicotyledons in their droppings (Cole *et al.*, 1995), while the Kalij Pheasant (*Lophura leucomelanos*) appears to be an important disperser of exotic plant pests (Lewin & Lewin, 1984). Almost all Oriental phasianids are in decline and many species are threatened with extinction as a result of hunting and habitat destruction (McGowan, 1994).

#### (c) *Anatidae*

Several members of this family (particularly in the genera *Anas*, *Anser* and *Cygnus*) consume some small fruits in the Palaearctic (Cramp & Simmons, 1977), but there are no reports of frugivory by the same species in the Oriental Region.

#### (d) *Picidae*

Although the woodpeckers are specialists in the excavation of wood, many species also eat some fruit (Mason & Maxwell-Lefroy, 1912; Ali & Ripley, 1983; Askins, 1983; Roberts, 1992; Chang *et al.*, 1996). Most of the reports of fruit in the diet of Oriental woodpeckers, however, refer to small and/or soft fruits, particularly figs (Mason & Maxwell-Lefroy, 1912; Wells, 1975; Roberts, 1991), which are well-dispersed by more abundant bird species that are less sensitive to human impacts than are the woodpeckers, several of which require large areas of forest to survive (Round, 1988).

#### (e) *Megalaimidae*

The barbets are among the most highly frugivorous birds in the region, west of Wallace's Line. Several species seem to feed largely on figs, for which they must be major dispersal agents (Ridley, 1930; McClure, 1966; Ali & Ripley, 1983; Leighton & Leighton, 1983; Lambert, 1989 *b*; Roberts, 1991; Laman, 1994), but barbets also eat lipid-rich capsular fruits (Leighton & Leighton, 1983). Fruits are swallowed whole and barbets have wide gapes for their size (Leighton, 1982). Montane species generally have smaller bills, which may reflect the generally smaller size of fruits in montane forest (Davison, 1992). With a few exceptions, barbets are forest birds, although they are more tolerant of fragmentation and disturbance than are some other groups of avian frugivores (Round, 1988).

#### (f) *Bucerotidae*

All hornbills eat some animal food, but the Oriental species are all largely frugivorous (Mason & Maxwell-Lefroy, 1912; Kemp, 1995). The larger species are the largest avian frugivores in the region and can handle fruits which are too big for any other bird (Leighton, 1982, 1986; Kannan, 1994; Kemp, 1995). Some species can also force open capsular fruits before they dehisce naturally (Leighton & Leighton, 1983). Hornbills may be the only dispersal agents for some large, capsular fruits with lipid-rich arils, such as those produced by many Meliaceae and Myristicaceae (Leighton, 1986), but most species also eat large amounts of smaller, mostly sugar-rich fruits, and figs dominate the diet of some (Leighton, 1982; Roberts, 1991; Kannan, 1994; Kemp, 1995; Kinnaird, O'Brian & Suryadi, 1996).

Surprisingly for such huge birds, only the smallest seeds (less than approximately 5 mm diameter) are defecated and larger seeds are regurgitated intact (Leighton, 1982; Kemp, 1995). Fruit processing in the gut is slow, with both regurgitation and defecation occurring, on average, an hour or more after the fruit was swallowed (Leighton, 1982; Kemp, 1995). A large hornbill can carry up to 500 g of fruit (Kinnaird *et al.*, 1996) and many species have huge home ranges and fly long distances in the course of a day (Kemp, 1995). Many hornbills will enter secondary forest and plantations (Mitra & Sheldon, 1993), and some will cross open areas to visit isolated forest patches (Kemp, 1995). Ultimately, however, the survival of almost all species is dependent on the existence of large areas of forest,



making them extremely vulnerable to deforestation and fragmentation (Kemp, 1995).

(g) *Trogonidae*

The Oriental trogons seem to be almost entirely insectivorous, but Diard's Trogon (*Harpactes diardii*) eats some figs (Lambert, 1989b) and all three Indian species (*Harpactes*) have also been reported to eat some fruit (Ali & Ripley, 1983).

(h) *Coraciidae*

The European Roller (*Coracias garrulus*) is reported to eat figs occasionally in the Mediterranean Region (Cramp, 1985), but I can find no records of frugivory by this otherwise insectivorous family in the Oriental Region.

(i) *Halcyonidae*

There is a single record of the Banded Kingfisher, *Lacedo pulchella*, eating figs in Thailand (Brockelman, 1982).

(j) *Cuculidae*

Fruit consumption has been reported for almost all the Oriental cuckoo genera (Legge, 1880; Mason & Maxwell-Lefroy, 1912; Smythies, 1960; Ali & Ripley, 1983; Barker & Vestjens, 1989; Cheng, Xian & Guan, 1991; Roberts, 1992), but, in most cases, this seems to be a relatively minor component of the diet. The major exceptions are the Asian and Australian Koels (*Eudynamys scolopacea*, *E. cyanocephala*), which are largely frugivorous (Legge, 1880; Mason & Maxwell-Lefroy, 1912; Bell, 1984a; Barker & Vestjens, 1989; Cheng *et al.*, 1991; Corlett & Ko, 1995; Balasubramanian, 1996), while both the Channel-billed Cuckoo (*Scythrops novaehollandiae*) (Barker & Vestjens, 1989) and the Drongo Cuckoo (*Surniculus lugubris*) (Legge, 1880; Cheng *et al.*, 1991) are, at least, consistent consumers of fruit. The Red-faced Malkoha (*Phaenicophaeus pyrrhocephalus*) has been reported to live 'almost exclusively on fruit' (Legge, 1880), apparently on the basis of both stomach contents and observations, but most other authors contradict this. Legge (1880) also described the Blue-faced Malkoha, *Phaenicophaeus viridirostris*, as largely frugivorous in Sri Lanka. Other malkohas are reported to eat fruit occasionally (Wells, 1975; Ali & Ripley, 1983; Cheng *et al.*, 1991).

The Asian Koel has an exceptionally wide gape (> 2 cm) for its body size and can swallow palm

fruits that other open-country birds in Hong Kong avoid (Corlett & Ko, 1995), but koels regurgitate large seeds (Legge, 1880; Corlett & Ko, 1995), which, together with their extreme reluctance to leave a fruiting tree (Pratt, 1984; R. T. Corlett, unpublished observations), may reduce dispersal distances.

(k) *Centropodidae*

Although basically carnivorous, the Greater Coucal, *Centropus sinensis*, is reported to eat fruit occasionally (Ali & Ripley, 1983; Roberts, 1992) and a coucal, *Centropus* sp., has been seen eating figs (Wells, 1975).

(l) *Psittacidae*

With the exception of the lorries and lorikeets (*Chamosyna*, *Eos*, *Lorius*, *Psitteuteles*, *Trichoglossus*), which are pollen- and nectar-feeding specialists, largely confined to the eastern margins of the region, most parrots in the Oriental Region feed mostly on seeds and fruits. Frugivory is reported in the genera *Alisterus*, *Cacatua*, *Eclectus*, *Geoffroyus*, *Loriculus*, *Psittacula* and *Psittinus* (Mason & Maxwell-Lefroy, 1912; Wells, 1975; Ali & Ripley, 1983; Whitten *et al.*, 1987; Barker & Vestjens, 1989; Cheng *et al.*, 1991). Although some parrots destroy many seeds from fleshy fruits in the beak or gizzard (Leighton & Leighton, 1983; Mishra, Bhatnagar & Sharma, 1987; Wells, 1988; Saini, Dhindsa & Toor, 1994), it is not clear from the available evidence that this is the case for all parrots and all seeds. Figs are prominent in reported diets for several species of *Loriculus* and *Psittacula* (Mason & Maxwell-Lefroy, 1912; Wells, 1975; Ali & Ripley, 1983; Lambert, 1989b) and the destruction of all the small, hard seeds would be hard to achieve. This is apparently done, however, by the Orange-chinned Parakeet (*Brotogeris jugularis*) in Costa Rica (Janzen, 1981) and, in India, the Rose-ringed Parakeet, *Psittacula krameri*, cracks individual guava seeds in the bill (Saini *et al.*, 1994). Some species of lory and lorikeet also eat some fruit (Bell, 1984a; Cannon, 1984; Barker & Vestjens, 1989) and their reduced and simplified digestive systems would presumably allow rapid passage of any seeds which are not destroyed in the bill.

(m) *Columbidae*

Most pigeons and doves in the region feed largely on fruit and/or seeds (Smythies, 1960; Ali & Ripley, 1983; Goodwin, 1983; Cheng *et al.*, 1991; Roberts,

1991) and Ridley (1930) considered them the most important avian seed dispersal agents, but the species differ widely in the proportion of fleshy fruits eaten and in the fate of the seeds they consume. Some, such as *Geopelia* and most *Streptopelia*, feed largely on dry seeds and fruits (Ali & Ripley, 1983), while, at the other extreme, *Ducula*, *Ptilinopus* and *Treron* eat almost entirely fleshy fruits (Payne, 1980; Leighton & Leighton, 1983; Ali & Ripley, 1983; Lambert, 1989a; Cheng *et al.*, 1991). The genus *Columba* includes both largely granivorous and largely frugivorous species (Ali & Ripley, 1983; Roberts, 1991).

The granivorous columbids probably destroy most of the seeds they swallow in their muscular gizzards (Cowles & Goodwin, 1958; Goodwin, 1983; Okamoto, 1994). However, in Europe, the Common Wood Pigeon, *Columba palumbus*, defecates intact some seeds from fleshy fruits (Snow & Snow, 1988) and both the Rock Pigeon, *C. livia*, and the Eurasian Collared Dove, *Streptopelia decaocto*, are said to regurgitate some large seeds (Hofstetter, 1954 cited in Cowles & Goodwin, 1958). It is possible that these birds adjust their grit intake and/or the muscular action of the gizzard to avoid damaging toxic seeds (Snow & Snow, 1988).

The genera *Macropygia*, *Reinwardtoena*, *Chalcophaps* and *Gallicolumba*, with various proportions of fleshy fruit in their diets, also have the grinding gizzard and long, narrow intestines of seed predators (Diamond *et al.*, 1977; Goodwin, 1983). However, a small proportion of fig seeds survive gut passage intact in the Emerald Dove, *Chalcophaps indica* (Lambert, 1989a; Corlett, 1998), and it is likely that the proportion of a particular seed species which is destroyed will depend on its characteristics, including size, hardness and toxicity. Despite being highly frugivorous, the Green Pigeons, *Treron* spp., are also seed predators, grinding up the seeds of the figs that many specialize on (Cowles & Goodwin, 1958; Ali & Ripley, 1983; Leighton & Leighton, 1983; Lambert, 1989a). However, some *Treron* species eat a wide range of other fruits, in addition to figs, and the fate of other seed types may be different: Balasubramanian (1996) found many uninjured seeds of *Manilkara hexandra* and *Zizyphus oenophia* under roosting sites of *Treron bicincta*. Even with figs, a few seeds occasionally pass through intact (Lambert, 1989a).

The Nicobar Pigeon, *Coloenas nicobarica*, feeds on fallen fruit and seeds, and uses its thick-walled, muscular stomach lined with horny plates, together with swallowed stones, to grind up large and extremely hard seeds (Diamond *et al.*, 1977; Ali &

Ripley, 1983). Some large-seeded fruits are eaten by both Nicobar Pigeons and Imperial Pigeons, with the former destroying the seeds and the latter defecating them intact (Goodwin, 1983).

In contrast to all the other Oriental columbids for which information is available, the Imperial Pigeons, *Ducula* spp., the Fruit Doves, *Ptilinopus* spp., and the Mountain Pigeons, *Gymnophaps* spp., have thin-walled gizzards and short, wide guts, through which even large seeds can pass undamaged (Goodwin, 1983; Lambert, 1989a). Ali & Ripley (1983) describe the Green Imperial Pigeon, *Ducula aenea*, as having 'a gape and gullet enormously extensible, ridiculously large nutmegs [*Myristica*] being swallowed entire, two or three being accommodated in the crop at a time – a seemingly impossible physical feat'. One individual of the Torresian Imperial Pigeon *Ducula spilorrhoa* in Darwin, Australia, swallowed 98 g of palm fruits in 3 min (Healey, 1992). Imperial Pigeons are among the largest frugivores in the forest and can feed on large, lipid-rich fruits which few other birds can handle (Leighton & Leighton, 1983): up to 4 cm diameter, for the Green Imperial Pigeon, *Ducula aenea* (Ali & Ripley, 1983).

Those pigeons which have been tested retain seeds longer than do most other frugivorous birds in the region (20–530 min for *Ptilinopus*) (Lambert, 1989a). Combined with the apparently nomadic habits of many species, this must make the fruit specialists almost perfect dispersal agents, while even those species which destroy most seeds may be significant in long-distance dispersal). Moreover, many pigeons can make use of secondary or disturbed habitats, and even the forest species appear able to disperse between fragments (Round, 1988).

#### (n) *Otididae*

Fruit consumption is recorded for all but one (*Tetrax tetrax*) of the bustard species which spend at least part of the year in the Oriental Region, although it is a minor component for most (Ali & Ripley, 1983; Collar, 1996; Mason & Maxwell-Lefroy, 1912). The Indian Bustard, *Ardeotis nigriceps*, however, depends largely on fruit, particularly *Zizyphus*, for part of the year and defecates seeds intact (Bhushan & Rahmani, 1992).

#### (o) *Gruidae*

A small amount of fruit consumption has been recorded for both the Common Crane, *Grus grus*, and

the Hooded Crane, *G. monacha*, although not in the Oriental Region (Cramp, 1980; Archibald & Meine, 1996).

(p) *Rallidae*

Rails normally feed on invertebrates and seeds of herbaceous plants, but the White-breasted Waterhen, *Amaurornis phoenicurus*, eats fleshy fruits occasionally in Hong Kong (R. T. Corlett, unpublished observations), as does the Water Rail, *Rallus aquaticus*, in Pakistan (Roberts, 1991), and the Common Moorhen, *Gallinula chloropus*, elsewhere (Ali & Ripley, 1983; Taylor, 1996). Many species are hard to observe so it is possible that frugivory is more widespread among rails than reported.

(q) *Pteroclididae*

The sandgrouse feed largely on seeds and shoots of herbaceous plants, but the Painted Sandgrouse, *Pterocles indicus*, is also reported to eat some fruit (Ali & Ripley, 1983).

(r) *Scolopacidae*

Many shorebirds in this family eat varying amounts of small fruits in their breeding ranges in the Palaearctic (Cramp, 1983) but there are no records of frugivory by the same species when they are in the Oriental Region.

(s) *Laridae*

The Black-headed Gull, *Larus ridibundus*, which is a winter visitor to the Oriental Region, eats cherries, olives, figs, *Cinnamomum camphora* and a variety of other fruit species in the Palaearctic (Cramp, 1983; Micali, 1986).

(t) *Accipitridae*

The hawks and their relatives generally feed on vertebrates and large insects, but there are reliable records of the consumption of small fruits by the Pacific Baza, *Aviceda subcristata* (Bell, 1984b; Debus, 1994), and Roberts (1991) states that 'other authors' (not named) have recorded frugivory by the Oriental Honey-buzzard, *Pernis ptilorhynchus*. The Black Kite, *Milvus migrans*, includes a high proportion of oil palm fruits (*Elaeis guineensis*) in its diet in Ivory Coast, West Africa, even feeding them to its young (Thiollay, 1994), but there are no reports of it doing so in Asia.

(u) *Ardeidae*

The ardeids are almost entirely carnivorous, but Cattle Egrets (*Bubulcus ibis*) have been seen eating figs from a tree in India (Chaturvedi, 1993).

## (2) *Passerines*

(a) *Pittidae*

The pittas are ground-foraging, forest insectivores. Fruit consumption has been reported for the Rusty-naped Pitta, *Pitta oatesi*, in China, where it formed 20% of the stomach contents of five birds (Zheng, 1985), and 'hard round large seeds' were found in the stomach of a Garnet Pitta, *Pitta granatina*, in Borneo (Smythies, 1960). Lambert & Woodcock (1996) suggest that pittas only eat fruits infested by insects, but offer no evidence for this. It would not be surprising if occasional consumption of fallen fruit has been overlooked in other species.

(b) *Eurylaimidae*

The Green Broadbill (*Calyptomena viridis*) is a medium-sized, specialist forest frugivore, which eats a wide variety of fruits, including figs (Lambert, 1989b), palms (Payne, 1995), and lipid-rich capsular fruits (Leighton & Leighton, 1983; Pannell & Koziol, 1987). It has a very large gape for its size and can swallow whole fruits 20 mm in diameter, regurgitating large seeds (Lambert & Woodcock, 1996). The related Hose's Broadbill (*C. hosii*) and Whitehead's Broadbill (*C. whiteheadi*) are also reported to be highly frugivorous (Smythies, 1960; Davison, 1992; Lambert & Woodcock, 1996). The other broadbills are described as primarily carnivorous, but several of them eat fruit occasionally, particularly figs (Smythies, 1960; Wells, 1975; Zheng, 1985; Pannell & Koziol, 1987; Lambert & Woodcock, 1996).

(c) *Meliphagidae*

The honeyeaters are confined largely to Australia and New Guinea, but several species enter the eastern margins of the Oriental Region and one, the Brown Honeyeater, *Lichmera indistincta*, has crossed Wallace's Line to Bali. Honeyeaters have diets composed of various combinations of nectar, insects and fruits, with fruit more important in the tropical rainforest species (Salomonsen & Ford, 1985). the Helmeted and Little Friarbirds (*Philemon buceroides* and *P. citreogularis*), which occur in the Oriental

Region, eat some fruit in Australia (Barker & Vestjens, 1990), as do myzomelas (*Myzomela* spp.) in Papua New Guinea (Diamond *et al.*, 1989).

(d) *Irenidae*

The Asian Fairy Bluebird, *Irena puella*, and Philippine Fairy Bluebird, *Irena cyanogaster*, are both highly frugivorous, eating small fruits, including figs (Mason & Maxwell-Lefroy, 1912; Smythies, 1960; McClure, 1966; Leighton & Leighton, 1983; Rabor, 1986; Lambert, 1989*b*). The leafbirds (*Chloropsis* spp.) all also include fruit, particularly figs, in a more varied diet (Mason & Maxwell-Lefroy, 1912; Smythies, 1960; McClure, 1966; Ali & Ripley, 1983; Zheng, 1985; Rabor, 1986; Lambert, 1989*b*).

(e) *Laniidae*

The shrikes are usually considered to be purely carnivorous, but the Long-tailed Shrike, *Lanius schach*, has been seen eating *Melia* fruits in India (Ali & Ripley, 1983) and there are reports from outside the region of other Oriental species eating some fruit (Cramp & Perrins, 1993).

(f) *Corvidae*

In the classification used here (Inskipp *et al.*, 1996), the Corvidae includes several groups which have previously been classified separately. Frugivory is widespread in the subfamily Corvinae. The Black Magpie, *Platysmurus leucopterus*, is an important, large-gaped consumer of fruit in south-east Asian rainforests (Payne, 1980; Pannell and Koziol, 1987; Lambert, 1989*b*) and the hornbills, can force open lipid-rich fruit capsules before they dehisce naturally (Leighton & Leighton, 1983). Fruit also forms part of the diet of the Crested Jay, *Platylophus galericulatus* (Payne, 1980), the Eurasian Jay, *Garrulus glandarius* (Ali & Ripley, 1983; Roberts, 1992), the magpies (*Cissa*, *Urocissa*, *Cyanopica*, *Pica*) (Goodwin, 1977; Ali & Ripley, 1983; Roberts, 1992; Madge & Burn, 1994), the treepies (*Dendrocitta*, *Crypsirina*) (Mason & Maxwell-Lefroy, 1912; Smythies, 1960; Goodwin, 1977; Ali & Ripley, 1983; Roberts, 1992), the choughs (*Pyrrhocorax*) (Mason & Maxwell-Lefroy, 1912; Roberts, 1992), and the crows (*Corvus*) (Mason & Maxwell-Lefroy, 1912; Ali & Ripley, 1983; Goodwin, 1977; Lambert, 1989*b*; Mishra *et al.*, 1987; Payne, 1980; Roberts, 1992; Thornton, 1996). As well as dispersing seeds internally, many corvids will carry off large fruits in their bills (Cramp and

Perrins, 1994; R. T. Corlett, unpublished observations). The Spotted Nutcracker, *Nucifraga caryocatactes*, is generally a seed predator and will take large seeds from fleshy fruits (Cramp & Perrins, 1994).

The orioles (*Oriolus*) are highly frugivorous and seem to be particularly fond of figs (Mason & Maxwell-Lefroy, 1912; Payne, 1980; Ali & Ripley, 1983; Lambert, 1989*b*; Roberts, 1992; Thornton, 1996), as is the Timor Figbird, *Sphecotheres viridis* (Barker & Vestjens, 1990). Fruit is also significant in the diet of some minivets (*Pericrocotus*) (McClure, 1966; Payne, 1980; Zheng, 1985; Rabor, 1986) and several species of cuckooshrike (*Coracina*) (Smythies, 1960; Ali & Ripley, 1983; Bell, 1984*a*; Roberts, 1992; Zheng, 1985). Two species of triller (*Lalage* spp.) are reported to eat some fruit in the Philippines (Rabor, 1986) and the Varied Triller, *Lalage leucomela*, disperses exotic *Lantana* in Australia (Liddy, 1985). The Black-faced Woodswallow, *Artamus cinereus*, which enters the margins of the Oriental Region, has also been recorded feeding on small fruits in Australia (Eckert, 1989).

There are also scattered records of frugivory among other corvid subfamilies. Some whistlers (*Pachycephala* spp.) are reported to eat a little fruit (Zann, Male & Darjono, 1990; Barker & Vestjens, 1990), as do the ioras (*Aegithina* spp.) (McClure, 1966; Zheng, 1985). The Greater Racket-tailed Drongo, *Dicrurus paradiseus*, has been seen eating figs (Wells, 1975) and the Spangled Drongo, *D. hottentottus*, eats some fruit in New Guinea (Bell, 1984*a*; Mack & Wright, 1996).

It is difficult to make generalizations about such a diverse group, but the Corvidae includes several ecologically tolerant species which survive in human-dominated landscapes. In such areas, they are often among the largest and largest-gaped birds, and even the less frugivorous species may be significant as dispersers of fruits and seeds too large for smaller frugivores (e.g. Mishra *et al.*, 1987).

(g) *Bombycillidae*

Two species of waxwing (*Bombycilla*) are irruptive, frugivorous winter visitors to the northern margins of the Oriental Region (Ali & Ripley, 1983; Roberts, 1992).

(h) *Muscicapidae-Turdinae*

The thrushes of the Oriental Region include both resident species and winter visitors from the Palaearctic, both of which are concentrated in the northern

and montane parts of the region. Fruit is probably a major part of the diet of most species, although there are only scattered records in the literature (Mason & Maxwell-Lefroy, 1912; Smythies, 1960; Ali & Ripley, 1983; Rabor, 1986; Lambert, 1989*b*; Wells, 1990; Davison, 1992; Roberts, 1992; Zheng, Long & Lu, 1995). In Hong Kong, intact seeds were found in most droppings of migratory thrushes (*Turdus* spp.), and species of *Monticola*, *Myophonus* and *Zoothera* also eat fruit in winter (Corlett, 1998). Thrushes make up a significant proportion of the winter bird biomass in many northern or montane habitats and are likely to be important dispersal agents for small and medium-sized fruits.

(i) *Muscicapidae-Muscicapini*

The flycatchers also include both resident and migratory species. Often considered to be entirely insectivorous, fruit forms part of the winter diet of several *Ficedula* species and the Blue-and-white Flycatcher, *Cyanoptila cyanomelana*, in both Borneo and Hong Kong (Smythies, 1960; Corlett, 1998), and is mentioned for species of *Niltava*, *Cyornis* and *Eumyias* in India (Ali & Ripley, 1983), the Large Niltava, *Niltava grandis*, in the Malay Peninsula (Ridley, 1930), the Snowy-browed Flycatcher, *Ficedula hyperythra*, in the Philippines (Rabor, 1986), and the Narcissus Flycatcher, *F. narcissina*, on Yakushima Island (Noma & Yumoto, 1997). Frugivory is probably under-reported in this group.

(j) *Muscicapidae-Saxicolini*

The robins and chats again include both resident and migratory species and are concentrated in the northern part of the region. Fruit consumption has been reported in the genera *Chaimarriornis*, *Cochoa*, *Copsychus*, *Grandala*, *Hodgsonius*, *Luscinia*, *Myiomela*, *Oenanthe*, *Phoenicurus*, *Rhyacornis*, *Saxicola* and *Tarsiger* (Ali & Ripley 1983; Roberts, 1992; Zheng *et al.*, 1995; Corlett, 1998) and probably occurs in others, because most species are not easy to observe. In Hong Kong, overwintering robins (*Luscinia*, *Tarsiger*) are important frugivores in secondary shrublands, eating a wide variety of small fruits and defecating the seeds intact (Corlett, 1998).

(k) *Sturnidae*

The starlings and mynas include both resident and migrant species and both forest specialists and birds of open country habitats. All species for which the

diet is recorded eat a lot of fruit, particularly figs (Legge, 1880; Mason & Maxwell-Lefroy, 1912; Smythies, 1960; Ali & Ripley, 1983; Bell, 1984*a*; Roberts, 1992; Kinnaird, 1995; Balasubramanian, 1996). The large Hill Myna, *Gracula religiosa*, is an important forest frugivore, capable of swallowing fruits up to 23 mm in diameter (Leighton, 1982). It eats lipid-rich capsular fruits as well as figs (Payne, 1980; Leighton & Leighton, 1983; Pannell & Koziol, 1987; Lambert, 1989*b*) and regurgitates large seeds, as does the related Sri Lanka Myna, *G. philogenys* (Legge, 1880). The open country starlings and mynas (*Aplonis*, *Acridotheres*, *Sturnus*), although smaller, are among the largest and most abundant frugivores in many human-dominated Oriental landscapes and are probably major seed dispersal agents (Legge, 1880; Ali & Ripley, 1983; Corlett & Lucas, 1989; Mishra & Singh, 1989; Roberts, 1992).

(l) *Sittidae*

The nuthatches feed largely on invertebrates and, in some species, dry seeds, but in the Palearctic, the European Nuthatch, *Sitta europaea*, sometimes takes seeds or flesh from fleshy fruits (Cramp & Perrins, 1993; Chang *et al.*, 1996) and the Sulphur-billed Nuthatch, *Sitta oenochlamys*, is reported to eat some fruit in the Philippines (Rabor, 1986).

(m) *Paridae*

The tits in the Oriental Region appear to be largely insectivorous, but the Sultan Tit, *Melanochlora sultanea*, eats some figs and other fruits (Mason & Maxwell-Lefroy, 1912; Lambert, 1989*b*) and both seeds and fruits are reported in the diets of several species of *Parus* (Ali & Ripley, 1983; Rabor, 1986; Roberts, 1992). Palearctic tits usually destroy the seeds of fruits they eat or, less often, remove the pulp and leave the seed (Cramp & Perrins, 1993). Seed dispersal could occur if small seeds are swallowed, if larger seeds are rejected after the fruit has been carried from the plant for processing (as tits commonly do), or if the extracted seeds are scatterhoarded in the ground (as some boreal species do) (Cramp & Perrins, 1993).

(n) *Aegithalidae*

Like the true tits, members of this family are reported to be largely insectivorous, but also to take some fruits. The Black-throated Tit, *Aegithalos concinnus*, is reputed to be particularly fond of wild *Rubus* fruits

(Ali & Ripley, 1983). There is no information on seed fates.

(o) *Pycnonotidae*

Fruit forms part of the diet of all bulbul species for which there is information (Mason & Maxwell-Lefroy, 1912; Smythies, 1960; Ali & Ripley, 1983; Zheng, 1985; Rabor, 1986; Roberts, 1992; Balasubramanian, 1996; Corlett, 1998). The proportion of fruit in the diet probably varies widely between species, but, for all the best-studied species, fruit is at least seasonally dominant (Zheng, 1985; Hsu & Lin, 1994; Corlett, 1998). The forest bulbul species are the most important small frugivores at many sites in the region, consuming mostly figs and other sugar-rich fruits (McClure, 1966; Wells, 1975; Leighton & Leighton, 1983; Wong, 1986; Lambert, 1989*b*), but also taking such lipid-rich capsular fruits as *Aglaia* (Pannell & Koziol, 1987). Davison (1992) suggests that montane bulbuls 'stoke up' with sugar-rich, high-energy fruits in the cool early morning and eat a greater variety of foods later in the day.

Some of the forest bulbuls are very tolerant of disturbance (Round, 1988) and a few, widespread bulbul species are often the commonest frugivores in man-made, open-country habitats, including urban areas (Rabor, 1986). In Hong Kong, the Light-vented Bulbul (*Pycnonotus sinensis*) is the dominant frugivore in all major habitats, from forest to urban parks. It is highly frugivorous, particularly in winter, and consumes the full range of fruit types within its gape limit (13–14 mm), defecating (or, sometimes, regurgitating) all seeds intact (Corlett, 1996, 1998). In Central Japan, the Brown-eared Bulbul, *Ixos amaurotis*, consumed 53 spp. of fruits, up to 12 mm diameter, defecating all seeds intact and viable (Fukui, 1995). Two bulbul species were among the earliest avian colonisers of Krakatau, where they are apparently major seed-dispersal agents (Thornton, 1996). Altogether, the available evidence suggests that the bulbuls may be most important seed dispersal agents in anthropogenic open habitats in the Oriental Region.

(p) *Hypocoliidae*

The Grey Hypocolius, *Hypocolius ampelinus*, which is a winter visitor to the north-west of the region, is reported to be largely frugivorous, rejecting larger seeds, but swallowing and defecating small ones (Cramp, 1988; Roberts, 1992; Tiwari, Varu & Himmatsinhji, 1995).

(q) *Zosteropidae*

All white-eyes for which information is available seem to have a mixed diet of insects, fruit and nectar (Smythies, 1960; Li, Zheng & Liu, 1982; Kikkawa, 1985; Roberts, 1992). In South China, the Japanese White-eye, *Zosterops japonicus*, eats largely fruit in winter but is largely insectivorous in summer (Li *et al.*, 1982; Corlett, 1998). The more ecologically tolerant white-eye species are extremely common in some parts of the region. Their small size and limited maximum gape width (approximately 8 mm in *Z. japonicus*) must reduce their general significance as seed dispersal agents, but the small size of individual defecations will reduce seed clumping, making them excellent dispersal agents for those fruit species which they can swallow.

(r) *Sylviidae-Acrocephalinae*

The acrocephaline warblers are, with the muscicapids, the most diverse group of Palaearctic migrants in the Oriental Region, although most genera also have resident species or populations. They are primarily insectivorous, but reports of occasional frugivory outside the breeding season are widespread. The Clamorous Reed Warbler, *Acrocephalus stentoreus*, has been seen to eat fruit while wintering in northern India (Parasharya *et al.*, 1995), the Dusky Warbler, *Phylloscopus fuscatus*, ate figs in the same area (Mason & Maxwell-Lefroy, 1912), and the Japanese Bush Warbler, *Cettia diphone*, eats several types of small fruits while wintering in Hong Kong (Corlett, 1998). A Himalayan resident, the Grey-hooded Warbler, *Seicercus xanthoschistos*, is also reported to eat occasional fruits (Ali & Ripley, 1983). There are also scattered reports of Oriental species of *Acrocephalus*, *Locustella* and *Phylloscopus* eating fruits in the Palaearctic (Cramp, 1992).

(s) *Sylviidae-Garrulacinae*

This sub-family is concentrated in the northern and montane parts of the region. Most of the laughingthrushes and liocichlas for which information is available eat some fruit (Mason & Maxwell-Lefroy, 1912; Smythies, 1960; Ali & Ripley, 1983; Cheng, Long & Zheng, 1987; Islam, 1987; Yen, 1990; Roberts, 1992; Corlett, 1998). Reported diets range from largely insects to largely fruit, but no study has been detailed enough to be sure that these differences are real. In Hong Kong, the laughingthrushes (*Garrulax*) are highly frugivorous in winter, eating a

range of small and medium-sized fruits and defecating the seeds intact (Corlett, 1998).

(t) *Sylviidae-Timaliini*

The babblers are the most diverse group of birds in the region, making up 6–15 % of all passerine species in scrub or forest habitats west of Wallace's Line, rising to 20 % in the Himalayas (Gaston, 1985). Most species are primarily insectivorous, but some degree of frugivory is widespread – possibly universal – and some species are highly frugivorous for at least part of the year. Most records of frugivory refer to the genera *Actinodura*, *Cutia*, *Heterophasia*, *Leiothrix*, *Minla*, *Pomatorhinus*, *Stachyris*, *Timalia* and *Tuhina* (Mason & Maxwell-Lefroy, 1912; Smythies, 1960; Payne, 1980; Ali & Ripley, 1983; Rabor, 1986; Cheng *et al.*, 1987; Yen, 1990; Roberts, 1992), but this may simply reflect observer effort. In Hong Kong, the Silver-eared Mesia (*Leiothrix argentauris*) and Red-billed Leiothrix (*L. lutea*) are highly frugivorous in winter, eating a wide variety of small fruits and defecating all seeds undamaged (Corlett, 1998). The partly granivorous Jungle Babbler, *Turdoides striatus*, is reported to damage seeds (Saini *et al.*, 1995) but the related Common Babbler, *T. caudatus*, defecates the hard seeds of *Lantana*, at least, intact (Narang, 1986). The abundance of the babblers must make them significant seed dispersal agents for small fruits, at least in the subtropical and montane parts of the region.

(u) *Sylviidae-Sylviini*

Several of the *Sylvia* warblers which winter in the northern Oriental Region eat fruit in autumn and winter (Ali & Ripley, 1983; Cramp, 1992; Roberts, 1992).

(v) *Nectariniidae*

The flowerpeckers (Dicaeini) are tiny birds with diets which consist of various combinations of fruit, invertebrates and nectar (Smythies, 1960; Li *et al.*, 1982; Ali & Ripley, 1983). Some species of both *Dicaeum* and *Prionochilus* appear to be highly frugivorous, eating figs (Wells, 1975; Brockelman, 1982; Lambert, 1989b; McClure, 1966) and a variety of other small fruits (Leighton & Leighton, 1983). Some *Dicaeum* specialize on mistletoe fruits (Loranthaceae and Viscaceae) for which they are highly effective dispersal agents (Reid, 1991). The short digestive tract and reduced gizzard may also make

them effective dispersers of other small fruit species but the very rapid gut passage will result in a tight seed shadow (Murphy *et al.*, 1993). In contrast to the other flowerpeckers, the Thick-billed Flowerpecker, *D. agile*, is reported to strip the pericarp off fruits without swallowing the seed (Roberts, 1992).

The sunbirds (Nectariniini) feed largely on nectar and/or insects but occasional consumption of small fruits has been reported for several species of *Anthreptes* (Smythies, 1960; Thornton, 1996), *Nectarinia* (Smythies, 1960; Hoffman, 1993), and *Hypogramma* (Lambert, 1991), and for some spiderhunters, *Arachnothera* (Smythies, 1960).

(w) *Passeridae*

The sparrows (*Passer* and *Petronia*) are small, largely seed-eating birds, but several species also eat some fruit (Ali & Ripley, 1983; Roberts, 1992). Sparrows in Britain either destroy or drop seeds in the fruit they eat (Snow & Snow, 1988), but I can find no information on seed fate in the Oriental Region. Some accentors (*Prunella*) also take some fruit (Cramp, 1988; Roberts, 1992). Many other passerids are seed eaters, but none is reported to take seeds from fleshy fruits.

(x) *Fringillidae*

The finches (Fringillinae) are a group of small, largely seed-eating birds which are diverse and abundant as migrants and residents along the northern margin of the Oriental Region. Feeding on fleshy fruit has been reported in the genera *Carduelis*, *Carpodacus*, *Coccothraustes*, *Eophona*, *Fringilla*, *Haemato-spiza*, *Loxia*, *Mycerobas*, *Pinicola*, *Pyrrhoplectes*, *Pyrrhula* and *Serinus* (Ali & Ripley, 1983; Roberts, 1992; Clement, 1993) and probably occurs in others. Finches feeding on fleshy fruits generally act as seed predators, destroying the seeds and discarding the flesh (Cramp & Perrins, 1994; Chang *et al.*, 1996). The larger-billed species can crack quite large, hard seeds, while the smaller-billed species can efficiently extract seeds as small as those of *Rubus* and *Sorbus* (Snow & Snow, 1988), but all finches do not destroy all seeds. In Pakistan, for example, the White-winged Grosbeak, *Mycerobas carnipes*, feeding on juniper 'berries', discards the pulp and feeds on the seed, while the Fire-fronted Serin, *Serinus pusillus*, and Common Rosefinch, *Carpodacus erythrinus*, eat only the pulp (Roberts, 1992). The role, if any, of finches in seed dispersal needs further investigation.

The buntings (Emberizinae) are specialist grani-

vores, with most species feeding largely on grass seed, but fleshy fruit is eaten occasionally by the House Bunting, *Emberiza striolata*, and Corn Bunting, *Miliaria calandra*, in Pakistan (Roberts, 1992).

## VII. THE FRUITS

Little work has been done on fruit characteristics in the Oriental Region and this review covers only those aspects which can be related to frugivory by vertebrates: the phenology of fruit production, external protection of the fruit, fruit colour, fruit and seed size, and the nutritional characteristics of the flesh. Other factors, such as accessibility of the fruit, and how firmly the flesh is attached to the seeds, are of undoubted significance but have not been investigated systematically in the region.

### (1) Phenology

Patterns of fruiting phenology within the Oriental Region are varied and complex (Corlett & LaFrankie, 1998). In the subtropics and marginal tropics, winter low temperatures impose more or less regular annual cycles at the individual, population and community level (Shukla & Ramakrishnan, 1982; Newton, 1988; Corlett, 1993). Maximum fruit availability in this zone tends to occur in winter (November–January), coinciding with the influx of partly frugivorous migrant birds from the Palearctic (Corlett, 1993, 1998; Noma & Yumoto, 1997). Even in Hong Kong (22° N), however, several species of fig (*Ficus*) have irregular, subannual fruiting cycles (Corlett & LaFrankie, 1998). For most of tropical Asia, seasonality in rainfall, rather than temperature, is the major ecological factor. Regular, annual cycles are still obvious at the community level, but there is a greater diversity of phenological patterns and more inter-annual variation than further north (Corlett & LaFrankie, 1998). Fruiting maxima are often less sharp, but tend to occur around the beginning of the wet season, typically May–June (e.g. Bhat, 1992; Singh & Singh, 1992; Borges, 1993).

In the relatively aseasonal core of the Asian tropics (most of Sumatra, Borneo and Peninsula Malaysia), there is no regular dry or cold season to synchronize plant phenology and, although almost all studies have detected annual cycles at the community level, these are usually weak and irregular (Ng, 1988; Corlett & LaFrankie, 1998). Seasonality of fruit supply may, however, increase with altitude (Djojosedharmo & van Schaik, 1992).

Inter-annual variation in the lowlands culminates in community-level mass flowering and fruiting at supra-annual intervals: a phenomenon apparently unique to the aseasonal Asian tropics (Appanah, 1993). Although most studies have concentrated on the wind-dispersed Diterocarpaceae, vertebrate-dispersed species from many families and all woody life-forms also participate (Leighton & Leighton, 1983; Corlett, 1990). The spatial extent of this phenomenon varies, in different episodes, from a single valley to the whole of aseasonal west Malesia (Ashton, 1982; Appanah, 1993; Curran, 1994). The result, for frugivores, is that fleshy fruits are rare most of the time, but superabundant at intervals of 2–9 years. As a consequence, vertebrate frugivores in the aseasonal Asian tropics must either have very flexible diets or forage over very large areas (Leighton & Leighton, 1983; Lucas & Corlett, 1991). Not all species, however, have supra-annual fruiting phenologies. Continuous fruiting at the individual level is extremely rare, even among pioneers, but more or less regular annual or biannual cycles are not uncommon, as is fruiting several times a year, with individual plants either synchronized or not at the population level (Corlett & LaFrankie, 1998).

### (2) Protection

‘Protected fruits’, those with a thick, inedible rind, which must be removed to get at the edible fruit flesh, are one extreme of a continuum from thin-skinned fruits with flesh accessible to all, through progressively thicker skins which exclude a progressively wider range of vertebrates. Many species are protected during development and dehiscence spontaneously when ripe, but indehiscent protected fruits are concentrated in a few genera (e.g. *Aglaia*, *Diospyros*, *Garcinia*, *Melodinus*, *Nephelium*) and account for only a few per cent of all fleshy fruit species in the region. In the Oriental Region, such fruits seem to be consumed largely by primates (Leighton & Leighton, 1983; Pannell & Koziol, 1987; Corlett, 1996).

### (3) Colour

Discussion of fruit colour is greatly complicated by the fact that human colour vision is not typical for vertebrates. Many birds have tetrachromatic vision and can discriminate surface colours in the ultra-violet (300–400 nm) region of the spectrum (Tovee, 1995). Human-type trichromatic vision seems to be



confined to the primates, including, probably, all Old World monkeys and apes (Jacobs *et al.*, 1996). All other mammals appear to be dichromats or, if nocturnal, colour-blind. It has been suggested that trichromacy in primates evolved as an adaptation to frugivory, making it easier to detect fruits against a background of leaves (Osario & Vorobyev, 1996).

Local and regional floras are not a reliable source of information on ripe fruit colours because, even if the descriptions are based on fresh material, the fruits are usually collected before they are fully ripe and too soft to preserve. Fruits which are only eaten when black are thus often described as red or orange in the literature. Most ripe, fleshy fruits in Hong Kong are black (often with a waxy bloom) or red (Corlett, 1996) and this is probably true throughout the region. However, the proportion of brown, yellow and green fruits in Hong Kong (15%) – almost all of which are relatively large and mammal-dispersed – is probably lower than at more tropical latitudes, where more fruits are apparently targeted at mammals. Those fruits eaten only or largely by mammals are typically duller-coloured than fruits taken mostly by birds (Leighton & Leighton, 1983; Lambert & Marshall, 1991).

#### (4) Fruit and seed size

Fruit and seed masses vary over more than five orders of magnitude in both equatorial Singapore (Corlett & Lucas, 1990; Metcalfe & Grubb, 1995) and marginally tropical Hong Kong (Corlett, 1996). The smallest fruits in the region have fresh masses around 5 mg while the largest are approximately 1 kg. The largest, however, are compound fruits (*Artocarpus*, *Pandanus*) which are rarely, if ever, harvested in one piece, and the biggest simple fruits, are approximately 150–200 g (e.g. *Mangifera*, *Melodinus*). Seed masses range from approximately 0.02 mg (several genera of Melastomataceae and Rubiaceae) to 5–10 g (some Anacardiaceae, Burseraceae, Lauraceae, Myristicaceae and Palmae).

Both fruit and seed size interact with the characteristics of potential dispersers, with fruit size most critical for many birds if the fruit must be swallowed whole (Leighton & Leighton, 1983). Very small fruits (< 8 mm equatorial diameter) are available to all fruit-eating vertebrates, although large animals may find them uneconomical to harvest, unless high fruit densities or clustering allow intake of many fruits per bite (Welch *et al.*, 1997). Small fruits (8–13 mm) are potentially available to all but a few tiny bird species, such as white-eyes and flower-

peckers. Larger fruits can be swallowed whole by progressively fewer bird species. An equatorial diameter of 22 mm probably excludes all but hornbills, fruit pigeons (*Ducula*, *Ptilinopus*), and the largest pheasants, cuckoos, thrushes, starlings, barbets, babblers and corvids. Diameters above 30 mm probably exclude all birds but hornbills and fruit pigeons, yet such fruits can still be harvested by most fruit-eating mammals. Only the largest fruits are inaccessible to small mammalian frugivores, such as fruit bats, because of size alone.

Fruits from which pieces can be bitten out are potentially accessible to birds too small to swallow them whole, or bats too small to carry them off. If the seeds are small, this may result in seed dispersal. Figs are the most important example of this and, although larger figs generally attract larger frugivores, even the largest figs are eaten by small birds (Leighton & Leighton, 1983; Lambert, 1989*b*). The commonest vertebrate feeding on the 20 mm diameter figs of *Ficus drupacea* in Thailand was the tiny Thick-billed Flowerpecker, *Dicaeum agile*, and only hornbills were seen to swallow the figs whole (Brockelman, 1982).

Seed size strongly influences seed processing in a wide range of vertebrates. Except for seed predators, seeds are unwanted ballast, to be disposed of as quickly as possible. The threshold size above which seeds are regularly dropped, spat or regurgitated without passing through the entire gut is in the 3–5 mm range for animals as big as macaques (Corlett & Lucas, 1990), flying foxes (Richards, 1990), and hornbills (Leighton, 1982), although many smaller animals swallow and defecate much larger seeds. In general, the larger the seed, the fewer the species which regularly defecate it and the shorter the distance it is likely to be dispersed. Small seeds may also escape from seed predators, such as rodents and some birds, where seed breakage occurs in the mouth but, conversely, are probably more vulnerable to destruction in the gut. Small seeds may also receive secondary dispersal (or suffer predation) from ants (Laman, 1994; Athreya, 1996) and in at least some Asian fig species, the individual seeds are covered in a lipid-rich exocarp which survives passage through frugivorous birds and increases attractiveness to ants (Kaufmann *et al.*, 1991).

#### (5) Fruit chemistry

There are few published analyses of fruit flesh in the region and most of these have been fairly crude (Ko, Corlett & Xu, 1998). Even less is known about the

nutritional requirements of wild vertebrates. The discovery that members of the often highly frugivorous Sturnidae-Muscicapidae clade lack the enzyme sucrase (Martinez del Rio, 1990), suggests that more detailed studies of both fruit chemistry and vertebrate digestive physiology could be informative. A principal components analysis of the characteristics of 153 fruit species in Hong Kong (30 % of the total fleshy fruit flora) was dominated by a trend from single-seeded fruits with a thin, lipid-rich pulp layer to multiple-seeded fruits with much watery, sugar-rich pulp (Corlett, 1996). Birds consumed the full range of fruit types, except those too large to swallow and too hard to peck bits from. Mammals (bats, civets and/or macaques) consumed those fruits too large for birds as well as many smaller fruits, but none with high lipid content. Analysis of the sugars in 58 of these fruit species showed that frugivorous birds consumed mostly hexose-dominated fruits while mammals ate both sucrose- and hexose-rich species (Ko *et al.*, 1998).

In Hong Kong, there is no evidence of the bimodal distribution of characters implied by the frequent division of fruit types into sugar-rich and lipid-rich in the Oriental frugivory literature (e.g. Leighton & Leighton, 1983; Kannan, 1994), although this may partly reflect the absence there of the families Burseraceae, Meliaceae and Myristicaceae, which supply many of the large, lipid-rich fruits at more tropical latitudes. In contrast, correlated morphological and chemical features of Malaysian *Aglaia* (Meliaceae) fruits correspond to two dispersal types: indehiscent, protected fruits with pale-coloured, sugar-rich arils with a characteristic odour, consumed by primates; and dehiscent capsules with red-skinned, odourless, lipid-rich arils, eaten by birds (Pannell & Koziol, 1987). As Mabberley *et al.* (1995) point out, however, the 'primate syndrome' also occurs in some species which grow to the east of Wallace's Line, where primates are absent. For unknown reasons, lipid-rich fruits in general seem to be avoided by Oriental mammals, except for some Lauraceae, which are eaten by macaques in many places (Leighton, 1982; R. T. Corlett, personal observations) and by many other mammals near the northern margins of the region, where fruit is seasonally scarce.

Figs (*Ficus* spp.) are sometimes treated as a distinct fruit type, with a high fibre content and low nutritive value (Raemaekers, 1984; Borges 1993). However, the measured nutrient content of figs depends greatly on the state of ripeness (R. T. Corlett, unpublished data) and I suspect that some researchers have

been less fussy when picking figs (and, indeed, other fruits) for analysis than are most fruit-eating vertebrates. The seed-free flesh of eight, ripe fig species analysed in Hong Kong had a similar range of nutrient contents to other sugar-rich fruits: on a dry mass basis, 45–71 % total soluble carbohydrate, 9–25 % fibre, 2–11 % protein and 1–6 % lipid (Corlett, 1996). The ability of several avian frugivores to live almost entirely on figs (e.g. some green pigeons, barbets and hornbills) suggests that they are nutritionally adequate (Kinnaird *et al.*, 1996) and there is evidence that they are a particularly good source of calcium (O'Brien *et al.*, 1998). Indeed, figs are the only known plant taxon upon which Oriental vertebrates have specialized (Lambert & Marshall, 1991). The great importance of figs to numerous species of Oriental birds, bats and primates, however, reflects more than just their nutritional value, but also their year-round availability as a result of non-synchronous fruiting, even in relatively seasonal climates, their often huge crop size ripening over a short period, and their soft flesh and small seeds, which make them easy to ingest. Figs seem to be particularly important for wide-ranging frugivores during periods of fruit scarcity (Lambert & Marshall, 1991).

Mimetic seeds are brightly coloured, usually red or red and black, seeds which lack any digestible reward for the dispersal agent (van der Pijl, 1982). They are produced by a variety of legume species in the Oriental Region, including *Adenanthera pavonina* and species of *Ormosia*. Although it has been suggested that very hard seeds of this type may be ingested by granivorous birds to act as gizzard grit (Peres & van Roosmalen, 1996), van der Pijl (1982) found that granivores refused *Adenanthera pavonina* while frugivorous barbets accepted them and defecated them intact. This supports his contention that such seeds are mimics of fleshy fruits and achieve dispersal by deceit.

## VIII. DISCUSSION

Some degree of frugivory has been reported for mammals in at least 11 orders (of 14 non-marine orders in the region), 29 families (of 51), 130–150 genera (of 296) and 400–500 species (of 1000). The uncertainty increases at lower ranks because little is known about the diets of rodents. For birds, the figures are at least 13 orders (of 17), 41 families (of 82, but 23 of the families without frugivores are

largely aquatic), 260 genera (of 560) and an estimated 900–1200 species (of 2471). If aquatic and grassland species are excluded, it becomes clear that a majority of bird and mammal species of Oriental forests probably eat at least some fruit. Species from several fish families and at least two orders and seven families (of 26) of reptiles also eat some fruit. Highly frugivorous species, for which fruit is the major component of the diet for at least part of the year, are also widespread, occurring in at least two orders and two families of reptiles, seven orders and 12 families of mammals, and six orders and 17 families of birds. Total frugivory has been suggested for some fruit bats, *Calyptomena* broadbills, and some pigeons, and may occur in other taxa, but no species has been studied in enough detail to confirm this.

That many vertebrates eat at least some fruit is not surprising: small fruits are easy to find, ingest and digest. Only the most extreme specialization of the mouth or gut will make frugivory impossible. The fermentative digestive system of colobines may preclude heavy reliance on fruit (Waterman & Kool, 1994; Cork, 1996), but the only reasonably well-studied terrestrial mammal families in the Oriental Region for which I have found no records of frugivory, are the largely insectivorous pangolins (Manidae), shrews (Soricidae), tarsiers (Tarsiidae) and microchiropteran bats (Microchiroptera). Among bird families, those without Oriental records of frugivory are ecologically more diverse, including: aerial insectivores (Apodidae, Hemiprocnidae, Hirundinidae, Meropidae), birds of prey (Falconidae and most Accipitridae), aquatic birds (including most Ciconiiformes), nocturnal birds (all Strigiformes), and ground-feeders of open habitats (Alaudidae, Turnicidae).

Predation on seeds of fleshy fruits is much less widespread, taxonomically, among Oriental vertebrates than is frugivory, although the number of animal species involved is large. Presumably this reflects the contrast between the relatively soft and undefended fruit flesh and the hard and often heavily defended seeds (or seed plus endocarp) (Corlett & Lucas, 1990). Seed predators must either be highly selective (as are most non-specialists, such as macaques) or highly specialized. The main mammalian seed predators are the colobine monkeys and rodents, plus, probably, the pigs and deer. Among the birds, the parrots, pigeons (in part), finches and, possibly, tits seem to be most important, although seed predation may be under-reported in other families. Most of these species are known or suspected to also disperse some seeds.

For open habitats and the forest canopy, it is unlikely that any major group of seed dispersal agents has been overlooked, but there are few data on frugivory and seed dispersal in the forest understorey, or on the fate of seeds in the fallen fruits consumed by forest ungulates. It must also be emphasized that animals which are of minor significance as part of an intact, mainland forest fauna may be important where the disperser fauna is impoverished by biogeographic isolation (e.g. Sulawesi, small islands in general), climatic extremes (very dry or high altitude habitats) or human impact.

Most of the information available on seed dispersal in the Oriental Region is anecdotal and qualitative. What happens to the seeds in the mouth and digestive system has rarely been recorded and the post-dispersal seed fate has generally been ignored. As a result, although most vertebrates mentioned in this paper probably disperse at least some seeds, any assessment of relative dispersal quality must be largely speculative at this stage.

Dispersal distance is often assumed to be an important component of dispersal quality, although there is surprisingly little evidence for benefits of dispersal much beyond the edge of the parent crown (Okuda *et al.*, 1995; Chapman & Chapman, 1996; He, Legendre & Lafrankie, 1997). Deposition under the parent is most likely for large seeds which are either not swallowed or rapidly regurgitated, but even in hemi-epiphytic fig trees in Borneo, more than half the seed crop fell below the crown (Laman, 1996). For seeds which are dispersed by passage through a vertebrate gut, dispersal distances will be determined largely by the ranging behaviour of the dispersal agent, rather than by gut passage times or travelling speeds, because the theoretical maximum dispersal distance (passage time multiplied by travel speed) typically greatly exceeds the maximum width of the normal daily range. The exceptions are likely to be communally roosting birds and bats, and nomadic or migratory species, which may travel long distances in a more or less straight line. Wide-ranging megaherbivores may sometimes disperse seeds over long distances in forested landscapes, but only birds and fruit bats are likely to bridge the gaps between widely separated forest fragments. Fruit pigeons and hornbills are probably of particular significance because of their wide gapes, fast flight, long gut passage times, and often huge ranges. Fruit pigeons (*Ducula*, *Ptilinopus*) have probably been of particular importance in dispersing large-seeded species across water gaps to Krakatau (Whittaker,

Table 1. *Frugivory and seed dispersal by Oriental vertebrates. Doubtfully frugivorous and biogeographically marginal taxa are excluded. Frugivory: 1, occasional; 2, consistent; 3, fruit seasonally dominant; 4, majority of annual diet. Seed survival refers to proportion of seeds which survive oral processing and, if swallowed, gut passage. Importance is the predicted impact of local extinction of the taxon on plant communities through loss of seed dispersal services: 1–4, minor to major*

Taxon	Frugivory	Seed survival	Importance
<b>Fish</b>			
Cyprinidae	0–3	?	?
Pangasiidae	0–3	?	?
Clariidae	0–3	?	?
<b>Reptiles</b>			
Emyidae	0–3	Most?	?
Testudinidae	0–3	Most?	?
Agamidae	0–2?	Most?	?
Scincidae	0–2	Most?	?
Varanidae	0–3	Most	1
<b>Mammals</b>			
Phalangeridae	1–2	Most?	?
Erinaceidae	0–2	?	?
Tupaiidae	3	Most	1
Pteropodidae	4	Most	4
Loridae	1	Most	1
Cercopithecidae			
Ceropithecinae	3–4	Most	3
Colobinae	1–2	Few	0
Hylobatidae	4	Most	4
Hominidae	4	Most	3
Canidae	1–3	Most	2
Ursidae	3–4	Most	2
Ailuridae	2	Most	1
Mustelidae	1–3	Most	1
Viverridae	0–4	Most	4
Herpestidae	1–2	Most	1
Felidae	0–1	Most	0
Elephantidae	2	Most	2
Tapiridae	2	Most	2
Rhinocerotidae	2	Most	2
Suidae	2	Some	1
Tragulidae	4	Some?	2?
Cervidae	2	Some	2?
Bovidae	1–3	Some	2
Sciuridae	0–4	Few	?
Muridae	0–4	Some	1
Hystriidae	2	Few?	?
Leporidae	1–2	Few?	?
<b>Birds</b>			
Megapodiidae	2	?	?
Phasianidae	2–3	Some	2
Picidae	1	?	?

Megalaimidae	4	Most	4
Bucerotidae	4	Most	4
Trogonidae	1	?	?
Cuculidae	1–3	Most	2
Centropodidae	1	?	?
Psittacidae	4	None?	0
Columbidae			
<i>Ducula, Ptilinopus</i>	4	Most	4
<i>Gymnophaps</i>			
Other genera	1–4	Few	1
Otididae	1–3	Most?	1
Rallidae	1	?	?
Pittidae	1	?	?
Eurylaimidae			
<i>Calypomena</i>	4	Most	3
Other genera	1	?	?
Meliphagidae	2	Most	1
Irenidae	2–3	Most	2
Corvidae	1–3	Most	2
Muscicapidae			
Turdinae	2–3	Most	2
Muscicapinae	1	Most	1
Saxicolini	1–3	Most	2
Sturnidae	2–4	Most	3
Paridae	1–2	Few	?
Pycnonotidae	3	Most	4
Zosteropidae	3	Most	3
Sylviidae			
Acrocephalinae	1	Most	0
Garrulacinae	1–3	Most	2
Timaliini	1–3	Most	3?
Nectariniidae			
Dicaeini	2–4	Most	2
Nectariniini	1	Most	0
Passeridae	0–2	None?	0
Fringillidae	0–4	Few?	0

Jones & Partomihardjo, 1997) and the islands of the tropical Pacific (Steadman, 1997).

On current evidence, it appears that most seeds in the Oriental Region, except near its northern margins, are dispersed by vertebrate families which are either endemic to the region (gibbons, barbets) or to the Old World (pteropodid fruit bats, cercopithecine monkeys, hominids, civets, hornbills, bulbuls, white-eyes, babblers and flowerpeckers). While pigeons are cosmopolitan, the seed-dispersing fruit pigeons are also confined to the Old World tropics. As far as can be determined from the literature, the only vertebrate families which are significant in both the Palaeotropics and the Neotropics are the Corvidae, Muscicapidae and Sturnidae (in the broad sense, which includes both the Old World Sturnini and the New World Mimini, which are

often treated as separate families). Although many major plant families are pantropical, seed dispersal relationships in the Neotropics and Palaeotropics must, to a large extent, have evolved independently for tens of millions of years, which should warn against the indiscriminate application of generalizations derived from one area to the other.

It is clear from this survey that the dispersal of small fruits (and of large, soft fruits with many small seeds) is likely to be highly resilient to any changes in the disperser fauna resulting from human impacts. Through most of the region, even the smallest forest fragments and most degraded landscapes support a range of small frugivorous birds (often dominated by Pycnonotidae and Sturnidae) and bats (often *Cynopterus* spp.). In contrast, the dispersal of large, large-seeded fruits depends on very few vertebrate species, most of which are highly vulnerable to hunting, fragmentation and habitat loss. Large fruit bats, gibbons, elephants, rhinoceroses, hornbills and imperial pigeons have been eliminated from much of their former ranges and are threatened elsewhere. Piles of uneaten fruits, rotting under the parent tree, are a characteristic and depressing feature of forests which have lost all their large vertebrates (Ng, 1983; Corlett & Turner, 1997). Moreover, the consumers of large fruit are not simply interchangeable. Although some big fruits are consumed by a wide range of vertebrates, others are apparently taken only by large birds, primates or large fruit bats, respectively. Whether or not there are fruits dispersed only by large terrestrial herbivores cannot be answered from the available data. Our inability to answer such basic questions shows the urgency of further research on plant-disperser relations in the few areas which still have a more or less intact flora and fauna.

## IX. CONCLUSIONS

(1) Most forest birds and mammals in the Oriental Region probably eat at least some fruit, as do many fish and reptiles (Table 1). Highly frugivorous species, for which fruit dominates the diet for at least part of the year, occur in at least two families of reptiles, 12 families of mammals, and 17 families of birds.

(2) Predation on seeds in fleshy fruits is much more restricted taxonomically. The major seed predators are colobine monkeys and rodents, among the mammals, and parrots, some pigeons, and finches, among the birds.

(3) Most animals which eat fruit probably disperse at least some seeds. Information on seed fates is rarely given in the Oriental literature, but, on current evidence, the most important seed dispersal agents are: among the mammals, pteropodid fruit bats, macaques, gibbons and civets; and among the birds, barbets, hornbills, fruit pigeons, broadbills, corvids, muscicapids, bulbuls, white-eyes, laughing-thrushes, babblers and flowerpeckers. Other groups may be important where the disperser fauna has been impoverished by geographic isolation or human impact.

(4) Patterns of fruiting phenology within the Oriental Region are varied and complex. Where temperature and/or rainfall vary seasonally, there is a more or less regular annual cycle of fruit availability. In the relatively aseasonal core of the Asian tropics, in contrast, fruit availability is low except during periods of mass-fruiting which occur at supra-annual intervals.

(5) Fruit and seed characters within the Oriental Region vary over a huge range, but there is rather little evidence relating this variation to vertebrate preferences and seed fates. Small fruits and large, soft fruits with many small seeds are consumed by a wide range of potential dispersal agents, including species which thrive in small forest fragments and degraded landscapes. Larger, larger-seeded fruits are eaten by progressively fewer potential dispersers, and the largest depend on a few species of mammals and birds which are highly vulnerable to hunting, fragmentation and habitat loss.

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