# Frugivory and seed dispersal by birds in Hong Kong shrubland

RICHARD T. CORLETT

Faecal samples were collected from birds caught in mist-nets in secondary shrubland during the winter fruiting peak. Additional records of frugivory came from visual observations of feeding birds. Forty-two shrubland bird species (22 residents, 20 migrants) ate some fruit and at least 92 fruit taxa were eaten by birds. The most important seed-dispersal agents were the Red-whiskered Bulbul *Pycnonotus jocosus*, the Light-vented *Bulbul P. sinensis* and the Japanese White-eye *Zosterops japonicus*. These were the commonest species and were all highly frugivorous during the winter. All three species are resident but populations of *P. sinensis* and *Z. japonicus* may be boosted by migrant birds in winter. The other major frugivores were resident species of laughingthrush *Garrulax* and *Leiothrix*, and migrant robins (*Luscinia*, *Tarsiger*) and thrushes *Turdus*.

## INTRODUCTION

Hong Kong (22°17'N 114°09'E) consists of part of mainland South China and several adjacent islands. The climate is exceptionally seasonal for the tropics, with cool, dry winters and hot wet summers (Fig. 1). The mean annual rainfall is approximately 2,500 mm at the study site (R. D. Hill pers. comm.). The flora has some subtropical characteristics but the resident fauna is almost entirely tropical (Dudgeon and Corlett 1994). Hong Kong's six million human population is concentrated on the limited natural flat land, extended by coastal reclamation. Most of the rest of the territory consists of steep and rugged hills. Several millennia of human impact, intensified over the last few hundred years, has reduced the original forest cover of Hong Kong to a few, isolated remnants in ravines and other protected places. The rest of the vegetation is secondary: mostly grassland and shrubland which, with protection from fire, has developed locally into secondary forest.

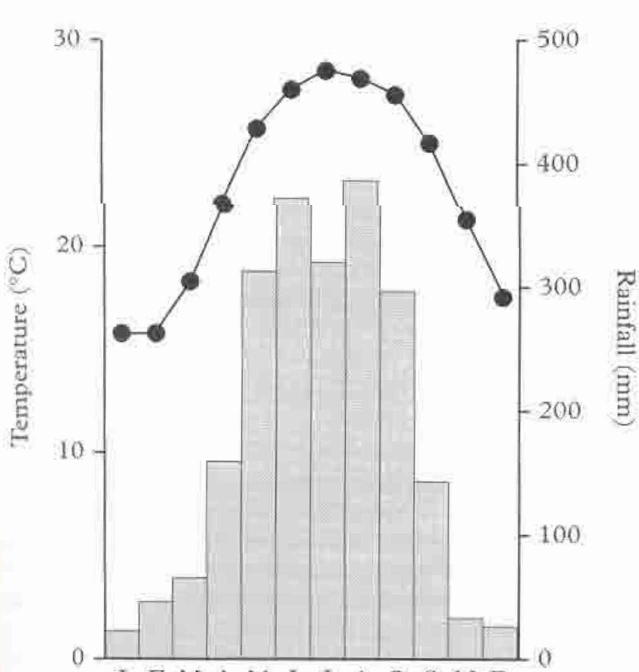


**Figure 1.** Seasonality of mean monthly temperature (dots) and rainfall (bars) in Hong Kong.

The majority of woody plant species in Hong Kong are dispersed by birds (Corlett 1996). There are approximately 490 species with fleshy fruits in the Hong Kong flora (which totals about 1,850 angiosperm species), although most of these are rare and a few species are dispersed by mammals. The woody component of the shrubland and secondary forest consists of approximately 200 widespread species, of which 86% have fleshy fruits and at least 85% of these are known or inferred to be bird-dispersed. The fruit preferences of frugivorous birds may therefore have exerted a strong influence on the species composition of these communities.

The phenology of fruit production by these plant communities may also have exerted a strong influence on the composition of the bird fauna in Hong Kong. Community patterns of fruiting in secondary shrubland and woodland are highly seasonal, with a maximum in December and a minimum in April (Corlett 1993). Patterns of insect availability have not been studied but are probably the approximate reverse of fruit availability, with a winter minimum and an early summer maximum. Resident fruit-eating birds apparently switch from a relatively high fruit diet in winter to a relatively high insect diet in early summer. Migrant insectivore-frugivores are at peak density between November and March and the winter fruiting maximum in South China may have been a major influence on the evolution of migration patterns in these species.

The principal aim of this study was to identify the bird species responsible for seed dispersal in Hong Kong shrublands. This forms part of a long-term study of the role of seed dispersal in vegetation recovery in the highly degraded landscape of Hong Kong (Corlett 1995, 1996, Corlett and Turner 1997).

## METHODS

Bird names follow Inskipp *et al.* (1996) and plant names follow Corlett (1993). Evidence for frugivory by shrubland birds was obtained in two ways. Faecal samples were collected from birds caught with mist nets at the Kadoorie Agricultural Research Centre (KARC) in the central New

**Table 1.** Frugivorous birds in Hong Kong shrubland.

| **Species** | **No. of faecal samples** | **Percentage with** | | **No. of plant taxa** | | |
|---|---|---|---|---|---|---|
| | | **insects** | **fruit** | **in faeces** | **seen eaten** | **total** |
| GREAT BARBET *Megalaima virens* | 1 | 0 | 100 | 1 | 0 | 1 |
| ASIAN KOEL *Eudynamys scolopacea* | — | — | — | — | 8 | 8 |
| EMERALD DOVE *Chalcophaps indica* | 3 | 33 | 67 | 2 | 0 | 2 |
| RED-BILLED BLUE MAGPIE *Urocissa erythrorhyncha* | — | — | — | — | 5 | 5 |
| GREY TREEPIE *Dendrocitta formosae* | — | — | — | — | 2 | 2 |
| BLACK-BILLED MAGPIE *Pica pica* | — | — | — | — | 1 | 1 |
| BLUE WHISTLING THRUSH *Myophonus caeruleus* | 3 | 33 | 67 | 2 | 7 | 9 |
| ORANGE-HEADED THRUSH *Zoothera citrina* | — | — | — | — | 1 | 1 |
| SIBERIAN THRUSH *Zoothera sibirica* | 1 | 0 | 100 | 1 | 0 | 1 |
| SCALY THRUSH *Zoothera dauma* | — | — | — | — | 4 | 4 |
| GREY-BACKED THRUSH *Turdus hortulorum* | 47 | 67 | 83 | 19 | 8 | 27 |
| JAPANESE THRUSH *Turdus cardis* | 8 | 13 | 100 | 8 | 7 | 15 |
| EURASIAN BLACKBIRD *Turdus merula* | — | — | — | — | 4 | 4 |
| EYEBROWED THRUSH *Turdus obscurus* | 7 | 14 | 100 | 6 | 4 | 10 |
| PALE THRUSH *Turdus pallidus* | 3 | 33 | 100 | 4 | 6 | 10 |
| BROWN-HEADED THRUSH *Turdus chrysolaus* | — | — | | 3 | 3 | |
| DUSKY THRUSH *Turdus naumanni* | 1 | 0 | 100 | 1 | 1 | 2 |
| YELLOW-RUMPED FLYCATCHER *Ficedula zanthopygia* | 14 | 86 | 29 | 3 | 0 | 3 |
| MUGIMAKI FLYCATCHER *Ficedula mugimaki* | 10 | 80 | 60 | 3 | 0 | 3 |
| BLUE-AND-WHITE FLYCATCHER *Cyanoptila cyanomelana* | 3 | 100 | 33 | 4 | 0 | 4 |
| RUFOUS-TAILED ROBIN *Luscinia sibilans* | 40 | 88 | 50 | 14 | 0 | 14 |
| SIBERIAN RUBYTHROAT *Luscinia calliope* | 58 | 97 | 41 | 12 | 0 | 12 |
| ORANGE-FLANKED BUSH ROBIN *Tarsiger cyanurus* | 102 | 96 | 38 | 13 | 3 | 16 |
| ORIENTAL MAGPIE ROBIN *Copsychus saularis* | 2 | 100 | 0 | 0 | 1 | 1 |
| DAURIAN REDSTART *Phoenicurus auroreus* | 2 | 50 | 100 | 3 | 2 | 5 |
| BLACK-COLLARED STARLING *Sturnus nigricollis* | — | — | — | — | 4 | 4 |
| RED-WHISKERED BULBUL *Pycnonotus jocosus* | 528 | 19 | 92 | 41 | 20 | 61 |
| LIGHT-VENTED BULBUL *Pycnonotus sinensis* | 414 | 39 | 96 | 43 | 28 | 71 |
| SOOTY-HEADED BULBUL *Pycnonotus aurigaster* | 11 | 36 | 100 | 9 | 3 | 12 |
| CHESTNUT-FLANKED WHITE-EYE *Zosterops erythropleurus* | 7 | 14 | 100 | 4 | 0 | 4 |
| JAPANESE WHITE-EYE *Zosterops japonicus* | | 642 | 21 | | 41 | 8 |
| JAPANESE BUSH WARBLER *Cettia diphone* | | 7 | 86 | | 3 | 0 |
| MASKED LAUGHINGTHRUSH *Garrulax perspicillatus* | — | — | — | — | 14 | 14 |
| GREATER NECKLACED LAUGHINGTHRUSH *Garrulax pectoralis* | 10 | 70 | 100 | 14 | 2 | 16 |
| HWAMEI *Garrulax canorus* | 72 | 86 | 81 | 14 | 2 | 16 |
| BLACK-THROATED LAUGHINGTHRUSH *Garrulax chinensis* | — | — | — | — | 3 | 3 |
| WHITE-BROWED LAUGHINGTHRUSH *Garrulax sannio* | — | — | — | — | 1 | 1 |
| SILVER-EARED MESIA *Leiothrix argentauris* | 30 | 87 | 97 | 10 | 4 | 14 |
| RED-BILLED LEIOTHRIX *Leiothrix lutea* | 55 | 58 | 96 | 21 | 1 | 22 |
| FIRE-BREASTED FLOWERPECKER *Dicaeum ignipectus* | 3 | 0 | 67 | 1 | 0 | 1 |
| SCARLET-BACKED FLOWERPECKER *Dicaeum cruentatum* | 4 | 0 | 50 | 1 | 1 | 2 |
| FORK-TAILED SUNBIRD *Aethopyga christinae* | — | — | — | — | 1 | 1 |

Territories, on a northwest-facing slope at 220-260 m a.s.l. The vegetation of the netting site is more or less closed secondary shrubland, 1-3 m in height, with scattered trees. The dominant shrubs, in order of abundance, are *Rhodomyrtus tomentosa*, *Litsea rotundifolia*, *Eurya chinensis*, *Ilex asprella*, *Melastoma sanguineum* and *Aporusa dioica*. The commonest trees are: *Cratoxylum cochinchinense*, *Sapium discolor*, *Rhus hypoleuca*, *Schefflera octophylla*, *Ilex rotunda*, *Evodia lepta*, and *Bridelia tomentosa*. The mist netting was done between late August and May, 1989-1995, by other people (listed in the Acknowledgements) with the aim of ringing as many birds of as many species as possible. Netting effort, in terms of days and numbers of nets used, was concentrated in the peak period for migrant birds (late October to mid December) which overlapped substantially with the main fruiting period at the site (Corlett 1993). This sampling pattern is likely to maximize the number of bird species found eating fruit but it exaggerates the importance of fruit in their annual diets and the widely varying sample sizes make comparisons between months difficult. Faecal samples were collected and examined systematically only for bird species thought likely to consume fruit. However, many samples from a wide range of other species were also examined superficially in the field to check for evidence of frugivory. Several species (all flycatchers and *Cettia* warblers) were added to the systematic list after superficial examination had revealed frugivory.

Each bird, after removal from the net, was placed in a separate cloth bag for 15-60 minutes, during which time most individuals of most species defecated. The birds were then identified, described, weighed, ringed and released. Any faeces left in the bag were scraped into separate, labelled tubes for examination in the laboratory. When I was not present myself, faecal samples were more likely to be collected if they were large, which would be expected to favour evidence of frugivory. However, there was no evidence of such a bias when these samples were compared with those I collected myself. Seeds were identified and counted under a dissecting microscope, with the help of a large reference collection (deposited in the University of Hong Kong Herbarium, HKU). An attempt was also made to identify fruit skins and other remains but this was possible only in a minority of cases. Finally, a visual estimate was made of the percentage, by volume, of plant remains (largely fruit) and animal remains (largely insects) in the sample. This procedure may underestimate the importance of animal foods in the diet because soft-bodied invertebrates and the soft parts of insects may be completely digested or unrecognisable. These data are only used qualitatively here.

The number of faecal samples collected for each frugivorous species is an approximate reflection of the relative abundance of the species in the total catch. The three commonest bird species are under-represented, however, because, on some days when only a single ringer was present, faecal samples were collected only from the rarer species, omitting either the white-eye or it and the two common bulbuls. Species also differed considerably in the proportion of individuals from which faecal samples were obtained. No records were kept of this but, of the more abundant species, the two *Leiothrix* species were the most reliable producers of faecal samples and the Grey-backed Thrush the least.

Additional records of frugivory came from direct visual observations of birds consuming fruit. Most of these were made during other fieldwork in various parts of Hong Kong, either by chance, or by watching fruiting plants for periods of 5-30 minutes. These data are used only qualitatively here and observations of birds and plant species which do not occur in shrubland are excluded.

## RESULTS

Twenty-nine bird species captured at KARC (12 residents, 17 winter visitors or passage migrants) produced at least one faecal sample containing intact seeds (Table 1). An additional 13 species found in shrubland (10 residents, 3 winter visitors) were observed eating fruit at least once. Sixty fruit taxa (probably representing at least 65 species) were identified from the 2,088 faecal samples examined from these birds and an additional 32 shrubland fruit species were seen to be eaten by shrubland birds.

The most important shrubland frugivores were the Japanese White-eye and the Light-vented and Red-whiskered Bulbuls (Table 1). These were the commonest birds at KARC and the most frequently observed frugivores in shrubland elsewhere in Hong Kong (Corlett unpublished). All three were highly frugivorous over the period of study (>92% of samples of each species contained fruit remains and <22% contained insects) and were almost entirely frugivorous during the November-January fruiting peak (>97% contained fruit, <10% insects). The diet of the Japanese White-eye was less diverse than the two bulbul species, presumably because a number of common fruits are larger than the maximum gape of these small birds. All three species are residents but the populations of the Japanese White-eye and Light-vented Bulbul may be boosted by migrant birds in winter. A more detailed comparison of the monthly diets of these three species will be made in a subsequent paper.

**Table 2.** The number of bird species recorded consuming the major bird-fruits in the shrubland at KARC, based on faecal analysis and direct observations.

| Plant species | Bird species (number) |
|---|---|
| *Bridelia tomentosa* | 12 |
| *Eurya chinensis* | 19 |
| *Evodia lepta* | 15 |
| *Ilex pubescens/I. rotunda* | 10 |
| **Lantana camara* | 13 |
| *Litsea rotundifolia* | 10 |
| *Melastoma candidum/M. sanguineum* | 9 |
| *Microcos paniculata* | 10 |
| *Psychotria rubra* | 14 |
| *Psychotria serpens* | 12 |
| *Rhodomyrtus tomentosa* | 12 |
| *Rhus chinensis/R. hypoleuca* | 15 |
| *Sapium discolor* | 14 |
| *Schefflera octophylla* | 22 |

* exotic

Most of the other important shrubland frugivores belong to one of two groups of related species, the resident *Garrulax* and *Leiothrix* or the migrant *Luscinia*, *Tarsiger* and *Turdus*. Among the first group, the commonest species is the Hwamei, for which most faecal samples contained both fruit and insects. The limited observations of other laughingthrush species in Hong Kong suggest that they may have similar diets. The two *Leiothrix* species, the Silver-eared Mesia and Red-billed Leiothrix, were highly frugivorous over the study period. The three common robins: Siberian Rubythroat *Luscinia calliope*, Rufous-tailed Robin *L. sibilans* and Orange-flanked Bush Robin *Tarsiger cyanurus* consumed insects more often than fruit during the study period, but the larger Grey-backed Thrush was largely frugivorous, as were, probably, the other, less common thrush species, although the sample sizes were small. Among the minor species, the most interesting records of frugivory are those for the Blue-and-white Flycatcher *Cyanoptila cyanomelana*, Mugimaki Flycatcher *Ficedula mugimaki*, and Yellow-rumped Flycatcher *F. zanthopygia*. In contrast, superficial examination of many faecal samples from several species of *Phylloscopus* warblers showed no evidence of frugivory, although related species consume some fruit elsewhere (e.g. Jordano 1987).

Fourteen fruit taxa were consumed by eight or more bird species (Table 2). The number of bird species recorded as consuming a particular fruit species depends not only on the characteristics of the fruit itself but also on its fruiting period in relation to bird migration and the fruiting phenology of other plant species. The plant species consumed by most bird species included the shrubland dominants at KARC, *Eurya chinensis*, *Litsea rotundifolia*, *Melastoma sanguineum* and *Rhodomyrtus tomentosa*, and the most common winter-fruiting trees in the vicinity, *Bridelia tomentosa*, *Evodia lepta*, *Microcos paniculata*, *Rhus* spp., *Schefflera octophylla* and *Sapium discolor*. Of the other common woody species at the site, *Cratoxylum* is wind-dispersed while *Ilex asprella* and *Aporusa dioica* fruit in summer, when fewer species of frugivores are present and no birds were captured. Fruits of both species are consumed by bulbuls and probably other birds. All but five of the 60 fruit taxa identified from faecal samples were consumed by more than one bird species.

Individual faecal samples contained seeds of 1-5 plant species. The proportion of multispecies samples (as a percentage of all samples containing more than one seed) ranged from 20.0% in the largely insectivorous Orange-flanked Bush Robin to 84.0% in the highly frugivorous Red-billed Leiothrix. However, these samples were collected from bags in which a bird had been held for up to one hour and some may represent more than one defecation.

The two common bulbuls were observed to sometimes regurgitate large seeds (larger than 9-10 mm diameter) in the field. Other bird species may also regurgitate seeds, or drop them during fruit processing in the beak, but this was never observed in the field. Regurgitated seeds could not be distinguished consistently from defecated ones in the samples collected from the bird bags. Since regurgitated seeds spend less time inside the bird, the sampling method may have underestimated the importance of large-seeded plant species in the diet.

Seed recovered from faecal samples of birds in Table 1 were almost all undamaged. It was not possible to test the viability of most seeds because the samples were stored frozen but small samples of seeds from fresh faecal samples showed no loss of viability in comparison with seeds extracted directly from fruits. Faecal samples of most known seed predators (species of *Lonchura*, *Emberiza*, and *Streptopelia*), in contrast, never contained intact seeds. Two samples from the Emerald Dove *Chalcophaps indica*, did, however, contain some undamaged seeds, although this bird usually destroys most seeds in its muscular gizzard (Lambert 1989).

## DISCUSSION

The bird-fruit interactions in Hong Kong shrubland invite comparison with studies in the Mediterranean shrublands of southern Spain (Herrera 1984) and the mixed hardwood forest of northern Florida (Skeate 1987). Although these sites are at higher latitudes than Hong Kong (38°N and 30°N, respectively), and have different rainfall seasonality, they both have mild winters, an autumn-winter fruiting peak and large populations of over-wintering frugivores. However, at both sites, resident frugivores are relatively unimportant, in contrast to Hong Kong.

In modern Hong Kong, the rich winter-fruiting shrub flora and the rich fauna of winter-resident frugivorous birds are interdependent but there is no evidence for tight co-evolution. The common frugivores consume a very wide range of fruits and the common fruiting plants have a wide range of potential dispersal agents. The lack of specialization is not surprising because the present vegetation is a result of human impact over the last few centuries and, before then, bird-fruit relationships must have been very different. The dominant plants of the shrubland and secondary forest would have been rare or absent in the primeval forested landscape and the resident bird fauna must also have been very different. However, the primeval forest would also have had a winter fruit maximum, judging by the phenology of the surviving tree flora, so patterns of winter migration by fruit-eating birds may have been similar in the past, even if the species involved may have changed.

The apparent matching of bird and fruit characteristics in the Hong Kong shrubland community is probably a result of "selection" by the bird fauna from the regional species pool, i.e. only species which can be dispersed by the surviving avifauna (or by wind or, in a few cases, civets) have been able to participate in secondary succession. This hypothesis is supported by the presence of a much wider range of fruit sizes and types in the flora as a whole than in the secondary shrubland and forest (Corlett unpublished data). Much of the tree flora may no longer be effectively dispersed.

All the seeds recovered from bird droppings at KARC came from plant species which are found commonly in shrubland, although some were trees which are also important in the later stages of forest succession. All the plant species recorded are found within 150 m of the netting site. The presence of intact seeds in faecal samples is evidence for seed dispersal but the relative effectiveness of different bird species as dispersal agents will also depend, in a complex way, on the number of seeds per defecation, patterns of movement within and between habitats, preferred defecation positions and other factors. The high proportion of faecal samples which contain more than one species of fruit can be interpreted in at least two, contradictory, ways. It can be seen as evidence of lack of discrimination between fruit species, with the birds simply consuming the nearest available fruit after movements triggered by fear of predators (Howe 1979). Alternatively, it can be interpreted as evidence that the birds are attempting to balance their nutrient intake or limit ingestion of fruit-specific toxins (White and Stiles 1990). In secondary vegetation, where the composition of the plant community is itself, to a large extent, a consequence of the fruit choices of past bird communities, observation alone cannot hope to distinguish between these two explanations.

Bulbuls of various species are dominant or important frugivores and seed dispersers of open, secondary vegetation throughout tropical and subtropical Asia, as well as much of Africa, and the Middle East, and have been widely introduced in similar environments outside their natural range (Lever 1987). Their relatively large maximum gape widths for their size (12-13 mm in birds 190 mm long for the Hong Kong species) permit them to consume a wide range of fruits and the extremely flexible diets of many species (including nectarivory and flycatching in Hong Kong) enables them to survive in areas where fruit abundance varies seasonally.

Species of *Zosterops* are also important insectivore-frugivores throughout tropical and subtropical Asia, Africa and Australasia, and the Japanese White-eye has been introduced in the Hawaiian islands, where it is now the most abundant land bird (Lever 1987). Limited maximum gape-size (c. 8 mm in Japanese White-eye) must reduce their significance as seed dispersal agents, but the small size of individual defecations may be of benefit to small-seeded species.

The obvious importance of the three commonest shrubland bird species does not mean that less common species are of no significance in seed dispersal. Less common species may be the major dispersal agents for fruits too large for the bulbuls and for plants confined to the shaded understorey, which none of the three most abundant bird species normally enter. This is difficult to assess from the results of this study as almost all fruits in the main study area were within the gape limit of all species except the Japanese White-eye and there is no well-developed understorey. Interactions between rare birds and rare plants may be of crucial importance for conservation but are inherently difficult to study.

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*Richard T. Corlett, Department of Ecology and Biodiversity, The University of Hong Kong, Pokfulam Road, Hong Kong.*