

# Fig-eating by vertebrate frugivores: a global review

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## ABSTRACT

The consumption of figs (the fruit of *Ficus* spp.; Moraceae) by vertebrates is reviewed using data from the literature, unpublished accounts and new field data from Borneo and Hong Kong. Records of frugivory from over 75 countries are presented for 260 *Ficus* species (approximately 30% of described species). Explanations are presented for geographical and taxonomic gaps in the otherwise extensive literature. In addition to a small number of reptiles and fishes, 1274 bird and mammal species in 523 genera and 92 families are known to eat figs. In terms of the number of species and genera of fig-eaters and the number of fig species eaten we identify the avian families interacting most with *Ficus* to be Columbidae, Psittacidae, Pycnonotidae, Bucerotidae, Sturnidae and Lybiidae. Among mammals, the major fig-eating families are Pteropodidae, Cercopithecidae, Sciuridae, Phyllostomidae and Cebidae. We assess the role these and other frugivores play in *Ficus* seed dispersal and identify fig-specialists. In most, but not all, cases fig specialists provide effective seed dispersal services to the *Ficus* species on which they feed. The diversity of fig-eaters is explained with respect to fig design and nutrient content, phenology of fig ripening and the diversity of fig presentation. Whilst at a gross level there exists considerable overlap between birds, arboreal mammals and fruit bats with regard to the fig species they consume, closer analysis, based on evidence from across the tropics, suggests that discrete guilds of *Ficus* species differentially attract subsets of sympatric frugivore communities. This dispersal guild structure is determined by interspecific differences in fig design and presentation. Throughout our examination of the fig-frugivore interaction we consider phylogenetic factors and make comparisons between large-scale biogeographical regions. Our dataset supports previous claims that *Ficus* is the most important plant genus for tropical frugivores. We explore the concept of figs as keystone resources and suggest criteria for future investigations of their dietary importance. Finally, fully referenced lists of frugivores recorded at each *Ficus* species and of *Ficus* species in the diet of each frugivore are presented as online appendices. In situations where ecological information is incomplete or its retrieval is impractical, this valuable resource will assist conservationists in evaluating the role of figs or their frugivores in tropical forest sites.

*Key words*: *Ficus*, frugivory, keystone resources, fruit syndromes, seed dispersal guilds.

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## I. INTRODUCTION

With approximately 750 species exhibiting a variety of growth forms that includes shrubs, trees, climbers, epiphytes and hemi-epiphytic stranglers, *Ficus* (Moraceae) is arguably the world's most diverse woody plant genus (Corner, 1988; Berg, 1989). Furthermore, two breeding systems, monoecy and dioecy, occur among *Ficus* species, with half the individuals of dioecious species producing figs that contain no, or very few, seeds (Anstett, Hossaert-McKey & Kjellberg, 1997). *Ficus* is distributed largely in the tropics and subtropics and can be divided, taxonomically, into two main groups (Corner, 1965; Berg, 1989). One group, comprising the subgenera *Urostigma* and *Pharmacosycea*, consists of approximately 370 species, all of which are monoecious. The second group comprises the subgenera *Ficus* and *Sycomorus*. Whilst the 13 or so *Sycomorus* species are monoecious, all but three of the approximately 350 species in subgenus *Ficus* are dioecious (Berg, 1989).

*Ficus* species are, perhaps, best known for their relationship with pollinating wasps (Hymenoptera, Agaonidae) which, with relatively few exceptions (see Michaloud, Carriere & Koobi, 1996), are species-specific (Wiebes, 1979). In monoecious *Ficus* species, the need to maintain a supply of pollinator wasps means that ripe figs can be found year-round (although some seasonality in crop production may occur, e.g. Windsor *et al.*, 1989). This, together with the exceptionally large crops of many monoecious *Ficus* species, has led to these figs being described as 'keystone resources' in tropical forests, potentially sustaining frugivores through lean periods of low fruit availability (Leighton & Leighton, 1983; Terborgh, 1986; Lambert & Marshall, 1991; Kinnaird, O'Brien & Suryadi, 1999; Korine, Kalko & Herre, 2000). Particularly high calcium levels in figs add further importance to their role in the diets of tropical frugivores (O'Brien *et al.*, 1998a), and the extirpation of such keystone resources has been predicted to precipitate a cascade of further extinction (Terborgh, 1986). However, research in Africa and India has suggested that, because of low *Ficus* densities and lower fruit production, the importance of figs is not universal (Gautier-Hion & Michaloud, 1989; Borges, 1993; Patel, 1996, 1997).

Two decades ago Janzen (1979) published a seminal paper on *Ficus* and, in helping to publicise this fascinating group of plants, helped lay the foundations for today's diversity of fig studies in field and laboratory sites worldwide. In his coverage of frugivory and seed dispersal Janzen (1979) asked, 'Who eats figs?'. He answered this question with a single word, 'Everybody', and stated that figs are an important dietary component for more animal species than the fruit of any other tropical genus. Here, we review the literature in an attempt to judge the accuracy of this contention. We assess the role of fig-eaters as potential seed dispersers and consider the extent of dietary overlap between fig-eating birds, fruit bats and non-volant mammals. We examine the keystone resource epithet applied to figs in tropical forests and identify vertebrate species that specialise on, or are highly reliant upon, figs as a dietary resource.

Vertebrate frugivores are not the only agents of *Ficus* seed dispersal. Invertebrates, including ants, dung beetles, snails and hermit crabs are known to consume fig fruits or seeds, thereby having impacts on *Ficus* seed dispersal (Kaufmann *et al.*, 1991; Athreya, 1996; Laman, 1996; Davis & Sutton, 1997; Shanahan, 2000; Staddon, 2000). Dispersal by floating on water has been suggested for a number of riverine *Ficus* species including *F. hispida*, *F. scabra* (Ridley, 1930) and, in particular, *F. cyathistipula*, the figs of which have a thick, spongy wall that provides buoyancy (Berg & Wiebes, 1992). However, in this review we concentrate solely on the interactions between *Ficus* species and vertebrates.

## II. METHODS

The dataset comprises field data collected by S. S. in Hong Kong (So, 1999), and by M. S. in Lambir Hills National Park, Sarawak, Malaysia (Shanahan, 2000), a literature review and unpublished data contributed by other researchers (see Acknowledgements). The data comprise accounts of which frugivore species consume figs, which *Ficus* species they consume, how frugivores handle figs and whether or not they are likely to be effective seed

dispersers, and how important figs are to the frugivores in question. The data gathered were assembled in a database where each *Ficus* and frugivore species was given a unique alpha-numerical code. Frugivore taxonomy and nomenclature were updated to follow Sibley & Monroe (1990, 1993) and Corbett & Hill (1991) for birds and mammals, respectively. Other frugivores are named in the source literature. Redundant *Ficus* synonyms are abundant in the literature and were eliminated using the classifications of Berg & Weibes (1992) and Corner (1965) for African and Indo-Australian figs, respectively. The taxonomy of the Neotropical fig flora is less well understood and is complicated by the existence of 'species-complexes' (Berg, 1989). For this region we use names approved by Prof. C. C. Berg (personal communication). For analytical purposes we took a conservative approach to the array of *Ficus* taxa found in the literature. Thus, varieties and formally undescribed forms of existing species have been subsumed into their parent taxa. However, in view of the likelihood of future taxonomic revisions, any such inclusions are noted. A number of *Ficus* species names encountered in the literature could not be located using the sources mentioned above. These species are excluded from any analysis although, for completeness of coverage, their frugivory records are included in the Appendices, available online at <http://go.to/figs>.

### III. RESULTS

#### (1) The quality of the dataset

Data on frugivory were gathered for 345 *Ficus* taxa, which, after rationalisation of nomenclature, represent 260 'good' *Ficus* species (approximately 30% of currently recognised species; Appendix 1: available at <http://go.to/figs>). The quality of the data and existence of biases may be assessed with respect to geographical provenance, *Ficus* taxonomy and the types of study from which the data were accumulated.

The dataset is global in provenance, featuring records from 78 countries or equivalent territories. Table 1 indicates, for each of the three major biogeographical regions and selected constituent territories, the number of known *Ficus* species and the percentage of these that are included in this review. The species included in our coverage represent between 28.9 and 59% of the *Ficus* species

known from Neotropical, Afrotropical and Indo-Australian floras. The small *Ficus* flora of Australia is best represented, with records of frugivory available for 28 (84.8%) of the 33 native *Ficus* species. Using Berg's (1989) classification of *Ficus* for comparison, a second, taxonomic, bias in the literature is revealed (Table 2). Sections *Conosycea*, *Galoglychia* and *Malvanthera* are over-represented whilst sections *Ficus*, *Adenosperma* and *Oreosycea* are under-represented. Overall, monoecious species are over-represented. Finally, the quality of the literature may be assessed with respect to the types of study from which the data were accumulated. Nearly 500 sources of data were used (Table 3). The majority of these were casual observations (42.2%) or records reported in other reviews, field guides, etc. (20.5%). The remaining data sources fall into two classes: studies of animals' diets (27.5%) and observations of frugivores visiting fruit crops (9.8%). In each case, the majority of studies were taxonomically restricted with respect to the frugivores considered. Only eight studies (1.6% of the total data sources) considered birds, fruit bats and arboreal mammals simultaneously.

#### (2) Who eats figs?

The diversity and widespread distribution of *Ficus* is reflected in the variety of animals that have been recorded feeding on figs. In total, records of fig consumption were found for 1274 bird and mammal species (Appendix 2: available at <http://go.to/figs>). These comprise 990 bird species in 374 genera and 54 families and 284 mammal species in 153 genera and 38 families (Tables 4, 5). Additionally, figs have been recorded in the diets of less obvious frugivores, such as fish and reptiles (Table 6).

The extent of fig-eating in these frugivore families can be assessed in a number of ways. Tables 4 and 5 show, for each family, the percentage of genera and species for which fig-eating records exist. These figures overemphasize the extent of fig-eating in families with small numbers of genera and/or species (e.g. Hypocoliidae, Psophiidae, Casuariidae). An alternative index of the propensity for fig-eating within a given family can be derived from the product of these percentages and the respective number of genera and species for which fig-eating records were actually obtained. Thus, if all members of all frugivore families ate figs then the families with most species and genera would have the highest values for these indices. Among birds, fig-eating is

Table 1. *The number of Ficus species from each biogeographical region (and selected constituent territories) included in the dataset. Regional species totals are taken from Berg & Wiebes (1992) for Afrotropical figs, Berg (1989) for Neotropical figs and Corner (1965) for Indo-Australian figs*

Region	Total <i>Ficus</i> species	<i>Ficus</i> species in review	% of total represented
Neotropical	145	42	28.9
Afrotropical	105	62	59.0
Madagascar	24	10	41.7
Indo-Australian	473	156	32.9
India	43	27	62.8
Borneo	133	76	56.3
New Guinea	138	41	29.7
Australia	33	28	84.8

most widespread in the parrot (Psittacidae) and pigeon (Columbidae) families (Fig. 1). Among mammals it is in families of primates, squirrels and fruit bats that fig-eating is most frequently recorded (Fig. 2).

The relative effects of numbers of genera in a family and numbers of species per genus can be overcome by standardizing the values for the indices used in Figs 1 and 2 against maxima of 1000 and taking the mean of the two indices. Fig. 3 uses these mean standardised propensity values to identify the frugivore families which interact most strongly with the genus *Ficus* either as a consequence of having many fig-eating genera and species or by consuming the fruits of many *Ficus* species. The division of each axis into quartiles allows each family to be placed into one of four classes based on the extent of their interaction with *Ficus*. The majority of frugivore families (72 out of 92) are placed in the lowest quartile on each axis. Only the parrot (Psittacidae) family is placed in both axes' upper quartile. This figure identifies the families that are likely to have the strongest evolutionary interaction with *Ficus* species on a global scale.

A geographical bias is evident in this figure. The Neotropical fig fauna (approximately 145 species) is small compared to that of the Indo-Australian region (approximately 473 species; Table 1). Further, Old World frugivore families have widespread distributions. The imbalance in the distribution of *Ficus* and of frugivore families may account for the fact that Neotropical fruit bats (Phyllostomidae) and monkeys (Cebidae) have lower values on the  $x$  axis

than their Old World counterparts (Pteropodidae and Cercopithecidae) which occur in the African, Indo-Malayan and (in the case of the Pteropodidae) Australo-Papuan regions. The outlying position of the Lybiidae shows that whilst there are many species and genera of fig-eating African barbets there are relatively few fig species known from their diet. This may simply represent a gap in the literature. However, Africa also has relatively few *Ficus* species when compared to the Indo-Australian region. The lybiid barbets are confined to Africa whereas all of the other bird families with higher  $x$  axis values occur in the Indo-Australian region as well as Africa or the Neotropics, and are thus exposed to a greater range of fig species.

For the *Ficus* species in the dataset an average of 12.3 frugivore species have been recorded. The range however is considerable. For more than half of the *Ficus* species covered here fewer than six frugivore species have been recorded (Fig. 4). Conversely, eight *Ficus* species have more than 50 recorded frugivores (Fig. 4, Table 7). This disparity does not necessarily indicate that most *Ficus* species attract few frugivores regularly. Rather, there exists considerable bias caused by differing extents to which *Ficus* species have been observed (due to, for example, their abundance or accessibility), the relative rarity of studies of frugivore attraction to *Ficus* crops (Table 3), and the fact that figs are often recorded in animal diets simply as '*Ficus* spp.', rather than species identifications being made. Nonetheless, research in Borneo, for which these biases were overcome, has shown that some *Ficus* species with very large figs do indeed attract small assemblages of mammalian frugivores (Shanahan & Compton, in press).

### (3) Are fig-eaters effective seed dispersers?

For the relationship between *Ficus* species and frugivorous vertebrates to be mutualistic the animals must provide an effective seed dispersal service in return for the nutriment paid, in advance, in the form of fig pulp, inside which the numerous small seeds are embedded. Frugivore effectiveness in seed dispersal has both qualitative and quantitative components (Schupp, 1993). The quantity of seeds dispersed by a given frugivore depends on the number of visits made to a fruiting plant and the number of seeds dispersed per visit. The former depends on the frugivore's abundance, its reliability of visitation and the importance of fruit (and figs in particular) in its diet, while the latter is conditional

Table 2. Comparison of (a) relative numbers of monoecious and dioecious *Ficus* species, and (b) relative numbers of species in each *Ficus* section known globally and covered by this review. Monoecious species are over-represented ( $\chi^2 = 13.9$ , D.F. = 1,  $P < 0.001$ ). Three sections (marked >) are over-represented in the review: *Conosycea* ( $\chi^2 = 8.49$ , D.F. = 1,  $P < 0.01$ ), *Galoglychia* ( $\chi^2 = 9.89$ , D.F. = 1,  $P < 0.01$ ) and *Malvanthera* ( $\chi^2 = 4.92$ , D.F. = 1,  $P < 0.05$ ). Three sections (marked <) are under-represented: *Adenosperma* ( $\chi^2 = 9.01$ , D.F. = 1,  $P < 0.01$ ), *Ficus* ( $\chi^2 = 4.73$ , D.F. = 1,  $P < 0.05$ ) and *Oreosycea* ( $\chi^2 = 5.15$ , D.F. = 1,  $P < 0.05$ ). All  $\chi^2$  tests used Yates' correction for one degree of freedom (Zar, 1996)

		Global <sup>a</sup>		This study		
		N	% of total	N	% of total	
(a) Breeding system						
Monoecious		389	52.9	172	66.2	>
Dioecious		347	47.1	88	33.8	<
(b) <i>Ficus</i> taxonomy						
Subgenus	Section					
<i>Ficus</i>	<i>Adenosperma</i>	23	3.13	0	0	<
<i>Ficus</i>	<i>Ficus</i>	60	8.15	11	4.23	<
<i>Ficus</i>	<i>Kalosyce</i>	20	2.72	4	1.54	
<i>Ficus</i>	<i>Neomorphe</i>	6	0.82	4	1.54	
<i>Ficus</i>	<i>Rhizocladus</i>	55	7.47	13	5.00	
<i>Ficus</i>	<i>Sinosycidium</i>	1	0.14	0	0	
<i>Ficus</i>	<i>Sycidium</i>	104	14.1	35	13.5	
<i>Ficus</i>	<i>Sycocarpus</i>	81	11.1	21	8.08	
<i>Sycomorus</i>	<i>Sycomorus</i>	13	1.77	7	2.69	
<i>Pharmacosycea</i>	<i>Oreosycea</i>	50	6.79	8	3.08	<
<i>Pharmacosycea</i>	<i>Pharmacosycea</i>	20	2.72	5	1.92	
<i>Urostigma</i>	<i>Americana</i>	120	16.3	37	14.2	
<i>Urostigma</i>	<i>Conosycea</i>	65	8.83	40	15.4	>
<i>Urostigma</i>	<i>Galoglychia</i>	75	10.2	46	17.7	>
<i>Urostigma</i>	<i>Leucogyne</i>	2	0.27	2	0.77	
<i>Urostigma</i>	<i>Malvanthera</i>	20	2.72	15	5.77	>
<i>Urostigma</i>	<i>Stilpnophyllum</i>	1	0.14	1	0.38	
<i>Urostigma</i>	<i>Urostigma</i>	20	2.72	11	4.23	
Total		736		260		

<sup>a</sup> Berg (1989) after Corner (1965).

on the number of seeds handled at each visit and their probability of being dispersed. Quality of seed dispersal is contingent upon the treatment received by seeds and the quality of their subsequent deposition. Seed treatment includes the level, if any, of seed destruction and the alteration of germination rates. Deposition quality depends on the distance, direction, habitat and microsite (especially important for canopy-germinating hemi-epiphytes; Laman, 1995) of seed dispersal as well as the 'dispersal environment', i.e. the number and identity of species co-dispersed with and, thus, potentially competing with a given *Ficus* species' seeds at the seedling stage (Schupp, 1993). Thus, frugivores' propensity for fig-eating, feeding methods,

effects of ingestion on seed viability and germination rates, distance moved (in terms of frugivore mobility and gut passage time), and patterns of deposition can be used to identify the major *Ficus* seed dispersers. Rather than covering in detail the full range of fig-eaters, we concentrate the emphasis in this section on the major fig-eating families identified in Figs 1–3. In the course of this coverage we also attempt to identify fig specialists. Sources of fig-eating records mentioned in the following treatments of each frugivore order are presented in Appendix 2 (see <http://go.to/figs>). Where presented, general dietary information comes from Perrins (1990) and Novak & Paradiso (1983) for birds and mammals, respectively.

Table 3. Sources of fig-eating records

Type of study	Number of sources	% of total
Reviews, field guides, compendia, etc.	100	20.5
Casual observations	206	42.2
Dietary study	134	27.5
Birds	32	6.56
Fruit bats	22	4.51
Non-volant mammals	77	15.8
Reptiles	3	0.61
Plant-centred study	48	9.84
Birds only	24	4.91
Fruit bats only	1	0.20
Non-volant mammals only	1	0.20
Birds & fruit bats	3	0.61
Birds & non-volant mammals	11	2.25
Non-volant mammals & fruit bats	0	0.00
Birds, non-volant mammals & fruit bats	8	1.64

(a) *Birds*(i) *Struthioniformes*

The flightless cassowaries (*Casuarius* spp.; Casuariidae) occur in New Guinea and Australian rain forests where they subsist largely on fallen fruit. Figs are eaten by *C. benneti* in New Guinea and by *C. casuarius* in Australia and fig seeds are defecated in a viable state (Stocker & Irvine, 1983; Cooper & Cooper, 1995; Y. Bassett, personal communication). In Africa, Ostrich (*Struthio camelus*; Struthionidae) has been recorded eating the introduced *Ficus carica* (Cramp, 1977). Ratites have long gut passage times (1–2 days to a week for Emu, *Dromaius novaehollandiae*; Willson, 1989) and will, therefore, carry seeds long distances. However, the sizeable defecations of these birds will result in large clumps of seeds. Further, all seeds will be deposited on the ground and, for hemi-epiphytic *Ficus* species, therefore wasted.

(ii) *Craciformes*

Members of the family Cracidae are the Neotropic's ecological equivalents of the Old World galliforms (see below), which they largely replace in the New World. Figs are known from the diets of *Crax* and *Mitu* currasows, *Ortalis* chachalacas, and guans in the genera *Chamaepetes*, *Penelope* and *Pipile* and are considered to be a favoured food of *Pipile albipennis* (del Hoyo, Elliot & Sargatal, 1994). Cracids tend to be terrestrial foragers, although Galetti *et al.* (1997) mention *Pipile jacutinga* staying for up to 10 days in fruiting *Ficus enormis* trees. Large *Penelope* guans have gut transit times of 15–45 min

and, for *Virola surinamensis* (Myristicaceae) seeds, Howe, Schupp & Westley (1985) predicted dispersal distances of 50 m or more, based on the birds' movements. Salvin's Currasow (*Mitu salvini*) retains food for considerably longer (mean 3 h 15 min) but destroyed 92–94% of *F. sphenophylla* seeds ingested whilst those passed in faeces failed to germinate (Yumoto, 1999). This supports the statement of Galetti *et al.* (1997) that although other cracids are generally important seed dispersers, the currasows (*Crax* and *Mitu* spp.) tend to be seed predators.

Among the megapodes (Megapodiidae) of the Australo-Papuan region there is a single record of *Megapodius eremita* feeding on cauliflorous figs in New Guinea (Jones *et al.*, 1995). Nothing is known of the importance of figs to this family or the fate of seeds ingested.

(iii) *Galliformes*

Most records of fig consumption by galliforms are for members of the pheasant family (Phasianidae) in the genera *Afropavo*, *Caloperdix*, *Francolinus*, *Galloperdix*, *Gallus*, *Lophura*, *Pavo*, *Polyplectron*, *Rollulus* and *Syrnaticus*. Other fig-eating galliforms include *Odontophorus* wood-quail (Odontophoridae) and *Acryllium* guinea-fowl (Numididae). Members of this order are omnivorous terrestrial feeders and are generally shy and difficult to observe in the field. It is therefore likely that galliform species are under-represented in this review. Nevertheless, they are likely to provide poor seed-dispersal services to the *Ficus* species whose figs they consume because in the few cases where specific figs are known from the diets of these birds, the *Ficus* species in question are hemi-epiphytes,

Table 4. *Fig-eating birds (families listed alphabetically). Nomenclature follows Sibley & Monroe (1990)*

Family	Genera			Species		
	Total	Fig-eaters	%	Total	Fig-eaters	%
Ardeidae	20	1	5	65	1	1.5
Bombycillidae	4	1	25	8	1	12.5
Bucerotidae	8	8	100	54	40	74.1
Casuariidae	2	1	50	4	2	50
Centropodidae	1	1	100	30	1	3.3
Cisticolidae	14	1	7.1	119	1	0.8
Coliidae	2	1	50	6	2	33.3
Columbidae	40	25	62.5	310	125	40.3
Coraciidae	2	1	50	12	1	8.3
Corvidae	127	43	33.9	647	99	15.3
Cracidae	11	6	54.6	50	8	16
Crotophagidae	2	1	50.	4	1	25
Cuculidae	17	8	47.1	79	8	10.1
Dacelonidae	12	1	8.3	61	1	1.6
Eopsaltriidae	14	1	7.1	46	1	2.2
Eurylaimidae	8	4	50.	14	6	42.9
Fringillidae	240	40	16.7	993	89	8.9
Hypocoliidae	1	1	100	1	1	100
Indicatoridae	4	1	25	17	1	5.9
Irenidae	2	2	100	10	6	60
Laniidae	3	1	33.3	30	2	6.7
Laridae	28	1	3.6	129	1	0.8
Lybiidae	7	7	100	42	34	80.9
Megalaimidae	3	3	100	26	20	76.9
Megapodiidae	6	1	16.7	19	1	5.3
Melanocharitidae	3	1	33.3	10	4	40
Meliphagidae	42	12	28.6	182	23	12.6
Motmotidae	6	2	33.3	9	2	22.2
Muscicapidae	69	14	20.3	449	38	8.5
Musophagidae	5	5	100	23	15	65.2
Nectariniidae	8	6	75	169	25	14.8
Numididae	4	1	25	6	1	16.7
Odontophoridae	4	1	25	6	1	16.7
Paridae	7	2	28.6	65	4	6.15
Passeridae	57	10	17.5	386	19	4.9
Phasianidae	45	11	24.4	177	18	10.2
Philepittidae	2	1	50	4	1	25
Picidae	28	11	39.3	215	22	10.2
Pittidae	1	1	100	31	1	3.2
Psittacidae	80	42	52.5	358	122	34.1
Psophiidae	1	1	100	3	1	33.3
Ptilonorhynchidae	7	5	71.4	20	11	55
Pycnonotidae	21	16	76.2	137	62	45.3
Rallidae	34	2	5.9	142	2	1.4
Rhamphastidae	9	4	44.4	55	8	14.6
Sittidae	2	1	50	25	1	4
Steatornithidae	1	1	100	1	1	100
Struthionidae	1	1	100	1	1	100
Sturnidae	38	22	57.9	148	64	43.2
Sylviidae	101	15	14.9	552	32	5.8
Trogonidae	6	3	50	39	6	15.4



Table 4 (cont.)

Family	Genera			Species		
	Total	Fig-eaters	%	Total	Fig-eaters	%
Tyrannidae	146	19	13	537	36	6.7
Vireonidae	4	1	25	51	3	5.9
Zosteropidae	13	2	15.4	96	13	13.5
Passerines	1510	215	14.2	7028	543	7.7
Non-passerines	547	159	29.1	2644	447	16.9
Total birds	2057	374	18.2	9672	990	10.2

requiring canopy germination microsites. Although some galliforms are tree-roosting, the terrestrial habits of most galliforms preclude such directed dispersal. Furthermore, pheasants and their allies have muscular, grit-filled gizzards that are likely to damage ingested seeds (Krefting & Roe, 1949; Corlett, 1998*b*). Reflecting this, only 5.8% of *F. prolixa* seeds recovered from the faeces of *Gallus gallus* germinated (Staddon, 2000).

(iv) *Piciformes*

There are scattered records of figs being eaten by woodpeckers (Picidae) in the genera *Celeus*, *Colaptes*, *Dendrocopos*, *Dinopium*, *Dryocopos*, *Meiglyptes*, *Melanerpes*, *Picoides* and *Piculus*. Woodpeckers are generally insectivorous and probably only take figs opportunistically. However, some Neotropical *Melanerpes* species appear to be more highly frugivorous and are more frequently observed eating figs (Stiles and Skutch, 1989; Winkler, Christie & Nurney, 1995).

A degree of dietary specialisation towards fig-eating appears to occur in many species of Asian barbets (*Megalaima*, *Calorhamphus*, *Psilopogon* spp; Megalaimidae) and 20 of the family's 26 species are confirmed fig-eaters. Barbets are amongst the most frequently observed fig-eaters in Borneo, India and Peninsular Malaysia where they generally feed on canopy-fruited hemi-epiphytes but also descend to lower forest strata (Ridley, 1930; Wells, 1982; Kannan, 1994; Grimmett, Inskipp & Inskipp, 1998; Balasubramanian, Narendra Prasad & Kandavel, 1998; Shanahan & Compton, in press). Lambert's (1989*a*) radio-tracking study showed that *M. henricii* and *C. fuliginosus* travel up to 700 m in search of ripe fig crops and that the former species spent 71–85% of its time foraging at them. Fruit-handling methods vary depending on fig size, thus Brown Barbets (*Calorhamphus fuliginosus*) can swallow small (7 mm

diameter) *Ficus obscura* figs whole, need to mash the larger (11 mm) figs of *F. subgelderii*, but can only peck at those (30 mm) of *F. subcordata* (M. Shanahan, personal observation). Other barbets are larger and all have large gapes for their size suggesting that many seeds will be ingested in each feeding bout. Gut passage times for barbets are short (20–35 min for *Megalaima haemacephala*; Lambert, 1989*b*), implying short dispersal distances, although Laman (1994) reported that barbets disperse significant quantities of fig seeds beyond 60 m from the source tree. Figs of 43 *Ficus* species are known to be consumed by Asian barbets and these birds are likely to be important seed dispersers for the genus.

Similarly, numerous African barbets (Lybiidae) in the genera *Buccanodon*, *Gymnobucco*, *Lybius*, *Pogoniulus*, *Stactolaema*, *Trachyphonus* and *Tricholaema* also eat figs (Appendix 2: see <http://go.to/figs>) and some, such as *Lybius dubius*, are thought to feed chiefly on figs (Robbins, 1993). Short feeding visits (< 10 m for *Lybius torquatus* and < 5 m for *Pogoniulus pusillus*) and defecation of viable seeds suggest that these barbets are significant fig seed dispersers in Africa (Compton, Craig & Waters, 1996).

Fig consumption is somewhat less widespread in the Neotropical toucan family (Rhamphastidae) with *Rhamphastos*, *Aulacorhynchus*, *Pteroglossus* and *Semnornis* species recorded feeding on a small number of fig species. deFigueiredo (1996*b*) considers *Rhamphastos toco* to be a fig specialist, although other members of the family show little preference for figs when other fruits are available (Wheelwright *et al.*, 1984). Toucans have gut transit times of 10–25 min and, for *Virola surinamensis*, Howe *et al.* (1985) predicted dispersal distances of 50 m or more. Bronstein & Hoffman (1987), however, noted that *Aulacorhynchus prasinus* spent up to 23 min in a fruiting fig tree, defecating many seeds *in situ*. Conversely, Coates-Estrada & Estrada (1986) recorded shorter

Table 5. *Fig-eating mammals (families listed alphabetically). Nomenclature follows Corbet & Hill (1991)*

Family	Genera			Species		
	Total	Fig-eaters	%	Total	Fig-eaters	%
Bovidae	46	6	13.0	127	6	4.7
Callithricidae	5	2	40	19	3	15.8
Canidae	11	2	18.2	35	4	11.4
Cebidae	11	6	54.6	45	14	31.1
Cercopithecidae	15	9	60	80	34	42.5
Cervidae	13	4	30.8	38	7	18.4
Cheirogaleidae	5	2	40	7	2	28.6
Dasyproctidae	3	1	33.3	14	1	7.1
Didelphidae	14	5	35.7	75	5	6.7
Echimyidae	14	2	14.3	45	2	4.4
Elephantidae	2	2	100	2	1	50
Herpestidae	18	2	11.1	39	2	5.1
Hominidae	1	1	100	1	1	100
Hylobatidae	1	1	100	9	8	88.9
Hystriidae	3	2	66.7	11	3	27.3
Indriidae	3	1	33.3	5	1	20
Lemuridae	5	4	80	11	7	63.6
Lorisidae	8	1	12.5	15	1	6.7
Macropodidae	10	3	30	49	5	10.2
Muridae	246	6	2.4	1160	6	0.5
Mustelidae	22	5	22.7	64	5	7.8
Peramelidae	7	2	28.6	18	4	22.2
Petauridae	8	4	50	23	5	21.7
Phalangeridae	5	3	60	21	5	23.8
Phyllostomidae	51	16	31.4	152	35	23
Pongidae	3	3	100	4	3	75
Potoroidae	5	1	20	10	1	10
Procaviidae	3	2	66.7	8	2	25
Procyonidae	6	3	50	13	3	23.1
Pteropodidae	40	20	50	162	47	29
Sciuridae	49	13	26.5	254	29	11.4
Suidae	5	3	60	8	4	50
Tapiridae	1	1	100	4	2	50
Tayassuidae	2	1	50	3	1	33.3
Tragulidae	2	2	100	4	2	50
Tupaiidae	5	1	20	16	4	25
Ursidae	7	4	57.1	8	4	50
Viverridae	18	7	38.9	35	8	22.9
Total mammals	1066	153	14.4	4327	284	6.6

feeding visits of 7.2 and 5.0 min for *Pteroglossus torquatus* and *Ramphastos sulfuratus*, respectively. The role of toucans in *Ficus* dispersal remains unclear but as small *Cecropia* (Cecropiaceae) seeds pass intact through the gut (Olson & Blum, 1968), it seems likely that the similarly small fig seeds will do so too.

Finally, there is a record of fig consumption by the Scaly-breasted Honeyguide (*Indicator variegatus*; In-

dicatoridae), a species that usually feeds on wax and insects (Fry, Keith & Urban, 1988).

(v) *Bucerotiformes*

Hornbills (Bucerotidae) occur in Africa (*Ceratogymna* and *Tockus* spp.) and South-east Asia (*Aceros*, *Annorhinus*, *Anthracoceros*, *Buceros*, *Ocyrceros* and *Penelo-*

Table 6. Other (non-avian, non-mammalian) fig-eaters. Fig species consumed are listed in Appendix 2 (<http://go.to/figs>)

	Common name	Scientific name	Reference
Reptiles	Aldabran Giant Tortoise	<i>Geochelone gigantea</i>	Hnatiuk (1978)
	Tortoises	<i>Geochelone carbonaria/denticulata</i>	Moskovits (1998)
	Black River Turtle	<i>Rhinoclemmys funerea</i>	Moll & Jansen (1995)
	Cape Flat lizard	<i>Platysaurus capensis</i>	Whiting & Greeff (1997)
	Flat Lizard	<i>Platysaurus broadleyi</i>	Whiting & Greeff (1999)
	Gray's Monitor Lizard	<i>Varanus olivaceus</i>	Auffenberg (1988)
	Jesus Christ Lizard	<i>Basiliscus basiliscus</i>	van Devender (1983)
	Culebra Island Giant Anole	<i>Anolis roosevelti</i>	FWS (1992)
	Ctenosaur	<i>Ctenosura similis</i>	Roberts & Heithaus (1986)
	Fish	Catfish	<i>Clarius major</i>
Machaca		<i>Brycon guatamalensis</i>	Horn (1997)
Fish		species not named	Verkerke (1987); Corlett (1998b)
Fish		<i>Pterodoras granulosus</i>	Conceicao de Souza-Stevaux <i>et al.</i> (1994)

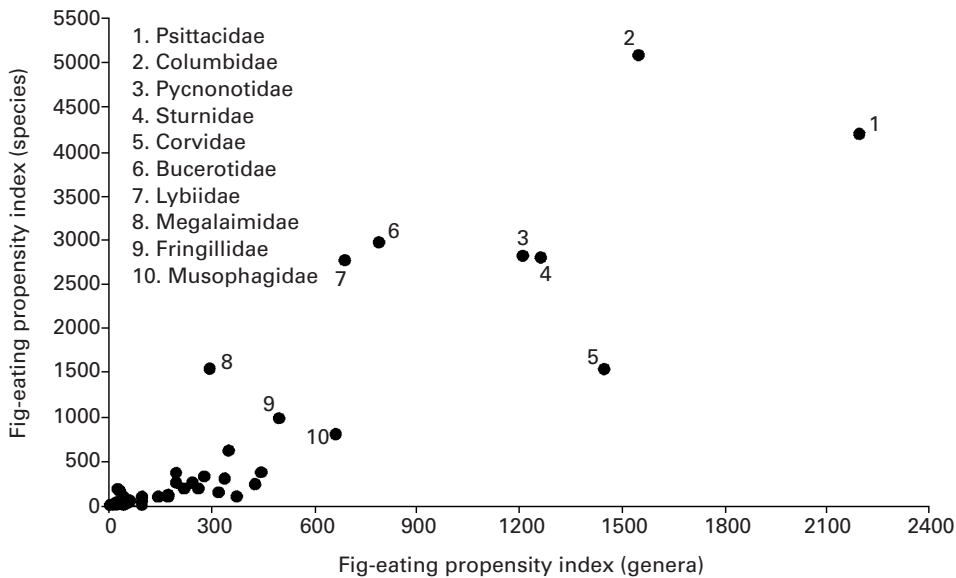


Fig. 1. ‘Fig-eating propensity’ of 54 avian frugivore families. Each index is calculated as the percentage of genera/species in a family that are known to eat figs multiplied by the actual number of genera/species recorded eating figs.

*pides* spp.). Figs are known to be eaten by 40 of the family’s 54 species but feature especially heavily in the diet of Asian hornbills (Table 8). Hornbills undertake long daily movements (13 km by *Aceros cassidix*; Kinnaird *et al.*, 1996; 14.4 km by *Buceros bicornis*; Poonswad & Tsuji, 1994) and may be capable of tracking the spatio-temporal availability of figs (Kinnaird, O’Brien & Suryadi, 1996). The large size of hornbills implies high levels of fruit and seed intake (*Buceros rhinoceros* consumed 27 *Ficus binnendykii* figs per minute; Leighton, 1982), and their wide gapes allow even large figs to be swallowed whole. Indeed, Brockelman (1982) noted that

hornbills were the only birds capable of eating *F. drupacea* figs whole. Although hornbills regurgitate large seeds, the small *Ficus* seeds are defecated – gut transit times for fig seeds have been measured as 30 min (*Buceros bicornis*; Lambert, 1989b) and Whitney *et al.* (1998) showed that hornbills defecate fig seeds intact. Together, these observations suggest that hornbills are important dispersers of *Ficus* species.

(vi) Trogoniformes

The trogon family (Trogonidae) is pan-tropical but whilst the palaeotropical species are largely in-

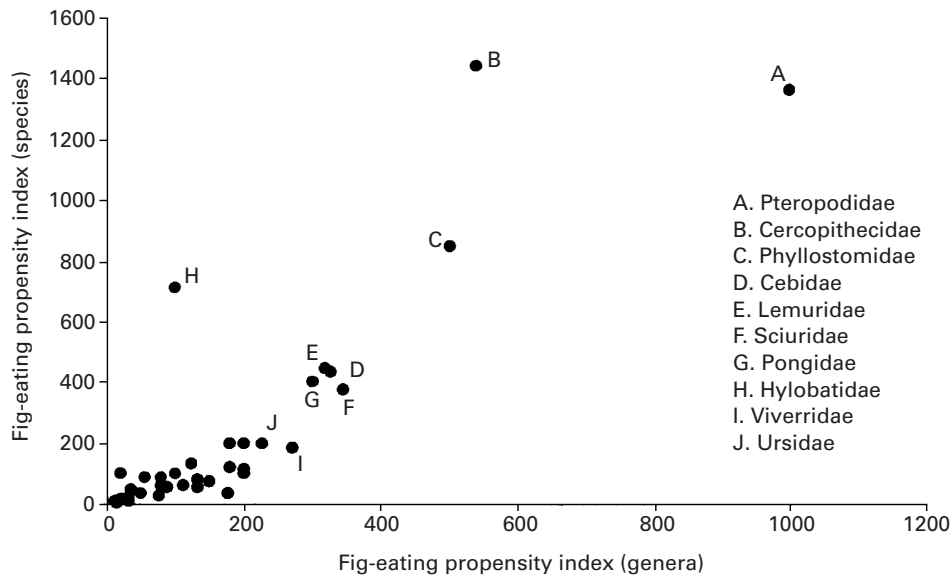


Fig. 2. ‘Fig-eating propensity’ of 38 mammalian frugivore families. Each index is calculated as the percentage of genera/species in a family that are known to eat figs multiplied by the actual number of genera/species recorded eating figs.

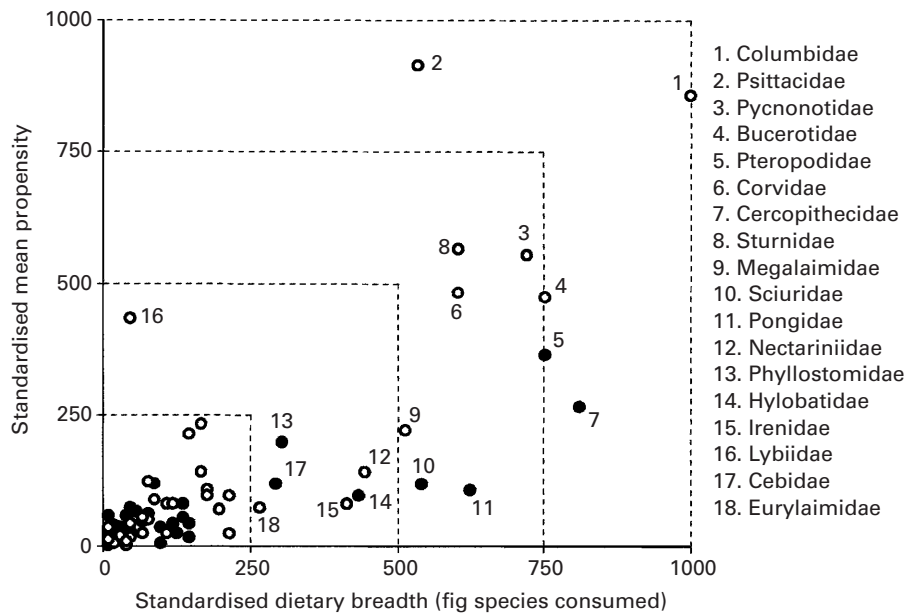


Fig. 3. An illustration of the frugivore families for which the *Ficus*-frugivore interaction is most widespread. Each frugivore family’s propensity for fig-eating (mean of standardised indices from Figs 1 and 2) is plotted against the number of *Ficus* species known to be consumed by each frugivore family’s members (standardised against 1000 for the Columbidae which are known to consume figs of 90 *Ficus* species; see Appendices available at <http://www.go.to/figs>). Broken lines mark the quartiles. Filled circles = mammal families, open circles = bird families.

sectivorous, frugivory is more widespread among the neotropical species. There is just a single record of fig-eating by *Harpactes diardii* in Malaysia (Lambert, 1989b) so it is probable that Old World trogons consume figs too infrequently to have any significant

role in seed dispersal. In the New World, figs are recorded from the diets of the Resplendant Quetzal (*Pharomachrus mocinno*) and four *Trogon* species. In Mexico, *Trogon aurantiiventris* spent 32.4% of its time visiting fig crops (Kantak, 1979). Neotropical tro-

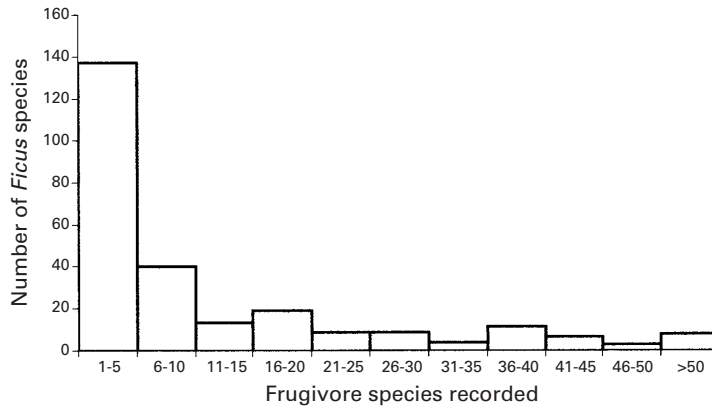


Fig. 4. Frequency distribution of the number of frugivore species recorded for each species of *Ficus* in the review

Table 7. Top ten *Ficus* species in terms of number of frugivore species recorded eating their figs (see Appendix 1, available at <http://go.to/figs>)

<i>Ficus</i> species	Region	Number of known frugivore species
<i>F. microcarpa</i>	Indo-Malayan, Australo-Papuan, Neotropical (introduced)	200
<i>F. virens</i>	Indo-Malayan, Australo-Papuan	90
<i>F. benjamina</i>	Indo-Malayan, Australo-Papuan, Neotropical (introduced)	84
<i>F. cotinifolia</i>	Neotropical	82
<i>F. drupacea</i>	Indo-Malayan, Australo-Papuan	63
<i>F. pertusa</i>	Neotropical	57
<i>F. stupenda</i>	Indo-Malayan	53
<i>F. sumatrana</i>	Indo-Malayan	52
<i>F. kerkhovenii</i>	Indo-Malayan	50
<i>F. pisocarpa</i>	Indo-Malayan	49

Table 8. Importance of figs in the diet of Asian hornbills. Nomenclature has been updated to follow Sibley & Monroe (1990)

Hornbill species	Role of figs	Reference
Knobbed Hornbill <i>Aceros cassidix</i>	81% of fruit biomass	Kinnaid & O' Brien (1999)
White-crowned Hornbill <i>Aceros comatus</i>	47.9% of diet	Tsuji (1996)
Rufous-necked Hornbill <i>Aceros nipalensis</i>	17.9% of diet	Chimchome <i>et al.</i> (1998)
Wreathed Hornbill <i>Aceros undulatus</i>	53% of diet	Poonswad <i>et al.</i> (1988)
Writhed-billed Hornbill <i>Aceros waldeni</i>	Over one-third of food at nest	Kauth <i>et al.</i> (1998)
Helmeted Hornbill <i>Buceros vigil</i>	Nearly 100% of fruits eaten	Leighton (1982)
Rhinoceros Hornbill <i>Buceros rhinoceros</i>	93% of female diet at nest	Johns (1987)
Great Hornbill <i>Buceros bicornis</i>	57.2% of diet	Poonswad <i>et al.</i> (1988)
	53.7% of diet	Tsuji (1996)
	80% of visits to fruit trees were to figs	Kannan (1994)
Oriental Pied-Hornbill <i>Anthracoceros albirostris</i>	35.3% of diet	Poonswad <i>et al.</i> (1988)
	24.5% of diet	Tsuji (1996)
Brown Hornbill <i>Anorrhinus tickelli</i>	21.5% of diet	Poonswad <i>et al.</i> (1988)

gons have wide gapes (*P. mocinno* 21 mm, *T. aurantiiventris* 19 mm) that facilitate the swallowing of relatively large figs whole (Wheelwright *et al.*,

1984). Little is known of the role of trogons in seed dispersal. Howe *et al.* (1985) report gut transit times of 10–25 min for *Trogon* species and it is likely that

*Ficus* seeds survive gut passage, especially among the queztl and the larger *Trogon* species, which are more frugivorous than smaller species (Remsen, Hyde & Chapman, 1993).

(vii) *Coraciiformes*

Among the highly insectivorous/carnivorous Coraciiformes there exist single records of fig-eating for European Roller (*Coracias garrulus*; Coraciidae) and Banded Kingfisher (*Lacedo pulchella*; Dacelonidae) and two records for motmots (*Momotus momota* and *Eumomota superciliosa*; Motmotidae). Little is known of the role these birds may play in fig seed dispersal but the importance of figs in their diets is likely to be very low.

(viii) *Coliiformes*

Two *Colius* mousebird species (Coliidae) are known to eat figs and disperse viable seeds following short (approximately 3 min) feeding visits (Fry *et al.*, 1988; Compton *et al.*, 1996). Gut passage times of Red-naped Mousebird (*Urocolius macrourous*) have been measured at 6–18 min (del Hoyo, Elliot & Sargatal, 2001). Mousebirds are obligate frugivores and probably disperse fig seeds.

(ix) *Cuculiformes*

Although many cuckoos (Cuculidae) include some fruit in their diet they tend to be largely insectivorous. However, two species are highly frugivorous and warrant attention. The Asiatic Koel (*Eudynamis scolopacea*) occurs from India to Australia and has been recorded eating the figs of 17 *Ficus* species. The species has a wide gape (> 2 cm) allowing large figs to be swallowed whole. So (1999) reported the koel eating up to 68 *Ficus virens* figs before regurgitating a pellet containing seeds. Such regurgitation of seeds, coupled with the koel's disinclination to vacate fruiting trees may limit dispersal distances. The Channel-Billed Cuckoo (*Scythops novaehollandiae*) also favours fruit, especially figs (Coates & Bishop, 1997). This large cuckoo has a massive bill and may be an ecological equivalent of the hornbills of South-east Asia. Other records of fig-eating exist for cuckoos in the genera *Cacomantis*, *Coua*, *Cuculus*, *Microdynamis*, *Phaenicophaeus* and *Surniculus* (Appendix 2, see <http://go.to/figs>).

There are also records of fig-consumption by Smooth-billed Ani (*Crotophaga ani*; Crotophagidae) in Brazil and a coucal (*Centropus* sp.; Centropodidae)

in Malaysia. Both of these species are highly insectivorous/carnivorous and probably contribute minimally to fig seed dispersal.

(x) *Psittaciformes*

The large parrot family (Psittacidae) has a pan-tropical distribution and 122 species in 42 genera are known to eat figs. Members of the genera *Cyclopsitta* and *Psittaculirostris* have the common name fig-parrots, and some degree of specialism on figs is suggested for these species together with some *Agapornis* lovebirds, *Amazona finschii*, *Loriculus* species and *Psittacula columboides* (Juniper & Parr, 1998; Corlett, 1998*b*). Mack & Wright (1998) suggest that the Vulturine Parrot (*Psittichas fulgidus*) is an extreme fig specialist, one that eats the pulp of a small number of thick-walled figs in New Guinea where it may act as a keystone mutualist by making seeds accessible to smaller, potentially seed-dispersing, birds. Parrots' powerful beaks and muscular gizzards tend to destroy seeds, even small ones such as those of *Ficus*. Janzen (1981) reported destruction of *F. ovalis* seeds by *Brotogeris jugularis*. Similarly, in Jordano's (1983) study, seed-predatory parrots destroyed 78% of *F. cotinifolia* seeds. Furthermore, parrots' strong bills allow them to open unripe figs that have yet to soften and may contain immature seeds. The extent of fig-eating by parrots suggests that although these birds may destroy the majority of fig seeds ingested, small numbers may survive and be dispersed.

(xi) *Musophagiformes*

The turacos (*Corythaeola*, *Musophaga* and *Tauraco* spp.; Musophagidae) are confined to Africa where they subsist on a highly frugivorous diet that includes the figs of at least 15 *Ficus* species, which are often swallowed whole (Compton *et al.*, 1996; Barlow & Wacher, 1997). The birds have been shown to make long-duration feeding visits to fruiting trees and defecate fig seeds intact (Compton *et al.*, 1996). Although in Compton *et al.*'s (1996) study over 60% of fig seeds recovered from turaco faeces failed to germinate, this value was not significantly different from that of control seeds and it is likely that turacos are genuine *Ficus* seed dispersers.

(xii) *Strigiformes*

The nocturnal Oilbird (Steatornithidae) eats figs in its native Trinidad (del Hoyo, Elliot & Sargatal,

2000). The species' role in *Ficus* seed dispersal is not clear. Thornton, Compton & Wilson (1996) hinted that Barn Owl (*Tyto alba*; Tytonidae) had the potential to disperse *Ficus* seeds in the pellets regurgitated following consumption of rodent or avian prey.

(xiii) *Columbiformes*

The pigeon family (Columbidae) has a worldwide distribution and, after the parrots, has more fig-eaters than any other frugivore family (125 species in 25 genera). Some pigeons are highly reliant upon figs at least for part of the year. Leighton & Leighton (1983) and Lambert (1991) suggested that *Treron* pigeons in the Indo-Malayan region are fig specialists. In Australia, Innis (1989) reported the proportion of foraging activity spent on figs to be 75.1% for *Lopholaimus antarcticus*, 75.2% for *Ptilinopus regina* and 89% for *P. magnificus*. In New Guinea, figs are proposed to be the most important food for frugivorous pigeons (Frith *et al.*, 1976*b*). Among Neotropical pigeons, *Columba nigrirostris* was the most important frugivore of *F. cotinifolia* in Mexico, responsible for 33% of avian fig removal (Coates-Estrada & Estrada, 1986). In Florida, figs accounted for 17% of the diet of *Columba leucocephala*, but when other fruits were available figs were largely ignored (Bancroft & Bowman, 1994).

Flocking, nomadic pigeons are capable of sustained flight and can probably track spatial and temporal variation in fig availability. In Malaysia, Wells (1999) noted a local decline in *Ducula badia* numbers when ripe figs were scarce. Pigeons are capable of consuming large numbers of figs in a single feeding visit and often stay for a long time (approximately 3 h) in the fruiting fig tree (Shanahan, 2000). However, their gut transit times are long relative to those of other avian frugivores (up to 420, 480, 530, and 720 min for *Ducula bicolor*, *Treron vernans*, *T. curvirostra* and *Chalcophaps indica*, respectively; Lambert, 1989*c*; Thornton *et al.*, 1996). Furthermore, pigeons fly fast and over considerable distances (speeds of 55 km h<sup>-1</sup> in *T. vernans*, 80 km h<sup>-1</sup> in *Streptopelia* spp.; flight ranges of 100 km in *D. bicolor*, 800 km in *C. indica* and 44 km day<sup>-1</sup> in *Columba leucocephala*; Bancroft & Bowman, 1994; Whittaker & Jones, 1994; Thornton *et al.*, 1996). Pigeons are thus capable of long-distance seed dispersal. Indeed, columbids have been implicated in the early colonisation of exploded volcanic islands in Indonesia (Krakatau; Thornton *et al.*, 1996) and New Guinea (Long Island; Shanahan *et al.*, in press).

Many pigeon species favour hard fruit and grains over fleshy fruits and upon eating figs act as seed predators, destroying seeds with their muscular, grit-filled gizzards. Such species include members of the genera *Chalcophaps*, *Columba*, *Gallicolumba*, *Macropygia*, *Reinwardtoena*, *Streptopelia* and *Treron* (Cowles & Goodwin, 1959; Crome, 1975; Goodwin, 1983). Nonetheless, small proportions of ingested *Ficus* seeds can survive gut passage of Emerald Doves (*Chalcophaps indica*), and some Thick-billed Green-Pigeons (*Treron curvirostra*) lack the gizzard grit that assists fig seed destruction (Lambert, 1989*c*). These birds' long seed-retention times and flight ability suggest that the minority of seeds surviving ingestion will be dispersed a considerable distance from their source – a premium that has the potential to outweigh the disadvantages of low seed survival. For other species, notably those in the genera *Ducula*, *Lopholaimus* and *Ptilinopus*, the gizzard is weak and lacks grit, and *Ficus* seeds are passed intact (Cowles & Goodwin, 1959; Innis, 1989; Lambert, 1989*c*).

(xiv) *Gruiformes*

In the Neotropics, three *Ficus* species are recorded from the diet of an unidentified trumpeter (*Psophia* sp.; Psophiidae) whilst, in the Old World, fig-eating has been recorded for the Purple Swampphen *Porphyrio porphyrio* and White-breasted Waterhen (*Amaurornis phoenicurus*). Members of this largely terrestrial order probably make little contribution to *Ficus* dispersal.

(xv) *Ciconiiformes*

Within this diverse order there are individual records of Black-headed Gull (*Larus ribidibundus*; Laridae) and Cattle Egret (*Bubulcus ibis*; Ardeidae) eating figs. Both of these families are carnivorous and these records represent rare events. The role of gulls and egrets in *Ficus* seed dispersal is thus of little interest. Although they have not been recorded eating figs, birds-of-prey have been implicated in *Ficus* seed dispersal by virtue of their ejection of pellets or carriage of frugivore carcasses bearing fig seeds (Thornton *et al.*, 1996; Shanahan *et al.*, in press). Hall (1987) showed that Lanner Falcon (*Falco biarmicus*; Falconidae) dispersed seeds of two *Ficus* species in pellets composed of avian prey.

(xvi) *Passeriformes*

Together, the passerines account for 57.5% of genera and 54.8% of species recorded eating figs (Table 4). However, the majority of these records are for members of just four families: Corvidae (99 spp.),

Fringillidae (89 spp.), Sturnidae (64 spp.) and Pycnonotidae (62 spp.). Rather than deal with each passerine family in detail we cover here only those we consider to be of most interest with respect to *Ficus* seed dispersal.

#### (A) *Corvidae*

In Sibley & Monroe's (1990) classification, the Corvidae includes a number of bird groups previously treated as separate families but now considered as tribes. The true crows (tribe Corvini) are omnivorous opportunists and have been recorded eating figs throughout the tropics. Even when other fruits were available, figs comprised 23.1% of the diet of Brown Jay (*Psilhorinus morio*) in Mexico (Kantak, 1979). The same species was responsible for up to 20% of *Ficus pertusa* fig removal and made short feeding visits (1.8 min) that imply seed dispersal away from the source tree. Crows are capable of long-distance flights and gut passage times are long (10–25 h for *Cyanocorax yncas*; Proctor, 1968, up to 1000 min for *Corvus macrorhynchos*; Thornton *et al.*, 1996) making long-distance seed dispersal possible. However, the effects of ingestion on seeds are not clear. In the Canary Islands, *Corvus corax* regurgitated pellets of up to 980 *F. carica* seeds (Nogales, Hernández & Valdés, 1999). However, *F. carica* is not fertile in the Canaries and the effects of ingestion could not be ascertained.

Birds-of-paradise (tribe Paradisaeini) eat figs in New Guinea and Australia and some species are considered to be fig specialists. Beehler (1989) and Frith and Beehler (1998) estimated the proportion of diet comprised of figs for *Manucodia chalybata* (93%), *M. keraudreni* (80%), *Paradisea rudolphi* (57%), *P. raggiana* (36%), *Parotia lawesii* (19%) and *Cicinnurus magnificus* (9%). Sixteen percent of visits to *Ficus* cf. *obliqua* were made by birds-of-paradise (Beehler & Dumbacher, 1996) and their generally high propensity for fig-eating suggests that birds-of-paradise are important seed dispersers. The third corvid tribe of special interest is the Oriolini, comprising fig-eating cuckoo-shrikes (*Coracina* spp.), minivets (*Pericrocotus* spp.) and Old World orioles (*Oriolus* and *Sphecotheres* spp.). Thirteen *Oriolus* species have been recorded feeding on African and Indo-Australian *Ficus* species whilst 11 *Ficus* species are known to be eaten by the aptly named Green Figbird (*Sphecotheres viridis*). Short feeding visits have been recorded for orioles (< 3 min for *Oriolus cruentus* feeding on *F. vasculosa* in Malaysia, 5 min maximum for *O. larvatus* on *F. burtt-davyi* in South Africa; Wells, 1982;

Compton *et al.*, 1996). Lambert (1989*b*) recorded fig seed retention times in the range 2–250 min for *O. chinensis*. It is likely then that orioles disperse seeds away from the source tree and these birds have been cited as valid *Ficus* dispersers in India (Balasubramanian, 1996) and the Krakatau archipelago (Thornton *et al.*, 1996).

Other fig-eating corvids include currawongs (*Strepera* spp.), pitohuis (*Pitohui* spp.), drongos (*Dicrurus* spp.), ioras (*Aegithina*), a *Telophorus* bush-shrike, a *Platysteira* wattle-eye and a *Batis* species (Appendix 2, see <http://go.to/figs>). With the exception of the currawong (for which figs can provide up to 50% of the diet; Buchanan, 1989), these species are more heavily reliant on animal food and are unlikely to have major impacts on *Ficus* dispersal.

#### (B) *Fringillidae*

Eighty-nine species of fringillid in 40 genera are known to eat figs (Table 4). Many fringillids are predominantly seed-eaters that use powerful bills to crack open seeds before ingestion. Even tiny *Ficus* seeds are likely to be destroyed by these birds (e.g. in subfamily Fringillinae, *Serinus* and *Carpodacus* spp.; in tribe Cardinalini, subfamily Emberizibae, *Saltator*, *Cardinalis*, *Caryothraustes*, *Cyanocompsa*, *Pheucticus* and *Passerina* spp.).

The tanagers (tribe Thraupini, subfamily Cardinalini) are more highly frugivorous and high levels of reliance on figs have been reported. In Mexico, figs comprised 57.3 and 99.4% of the diets of *Euphonia affinis* and *E. hirundinacea*, respectively (Kantak, 1979) and are the favoured food of *Tangara icterocephala*, *T. gyrola*, *Thraupis palmarum* and *Piranga bidentata* in Costa Rica (Stiles & Skutch, 1989). In Brazil, *Thraupis sayaca*, *Pitangus sulphuratus* and *Dacnis cayana* contributed 30, 15 and 13% of avian visits to *Ficus luschnathiana*, respectively (deFigueiredo, 1996*b*). In Costa Rica, *Piranga ludoviciana* was responsible for removing 10.1% of the figs in a *F. cotinifolia* crop (Jordano, 1983) and *T. sayaca* contributed 21% of all avian visits to introduced *F. microcarpa* (deFigueiredo, Motta & Vasconcellos, 1995). Tanagers make short feeding visits to fig crops (< 5.2 min for *P. ludoviciana*, *P. rubra*, *P. olivacea*, *Cyanerpes cyanea* and *E. hirundinacea* feeding on *Ficus cotinifolia*; Jordano, 1983, Coates-Estrada & Estrada, 1986, and 7.4–8.5 min for *Euphonia luteicapilla*, *Thraupis episcopus* and *Chlorophonia occipitalis* eating *Ficus pertusa*; Bronstein & Hoffman, 1987). Whilst the fate of fig seeds is not known, mistletoe (Viscaceae) berries are ingested and successfully dispersed by *Euphonia*



species (Raffaele *et al.*, 1998). Fig seeds are therefore likely to be ingested and, given tanagers' propensity for fig consumption and short feeding visits, are likely to be dispersed away from the parent tree.

The fig-eating icterids (tribe Icterini) include species of *Dives*, *Icterus*, *Molothrus* and *Quiscalus*. Their role in fig seed dispersal is probably slight as they apparently prefer non-fig fruits. In Mexico, when other fruits were available, figs made up only 3.4 and 11.1% of fruit crop visitations by *I. galbula* and *Dives dives*, respectively, whilst sympatric *Icterus* species ignored figs completely (Kantak, 1979).

Finally, *Parula americana* and four *Dendroica* species (tribe Parulini) have been seen to eat figs. Scott & Martin (1984) showed that *Dendroica* species favour non-fig fruits when they are available.

#### (C) *Sturnidae*

Starlings are found across the tropics and 64 species in 22 genera are known to eat figs. The nomadic Hill Myna (*Gracula religiosa*) feeds on the figs of 19 hemiepiphytic species throughout its range, and passes seeds after 5–76 min (Lambert, 1989*b*). This species accounted for up to 50% of avian feeding visits to *Ficus* crops in Peninsular Malaysia (Lambert, 1989*b*). Following ingestion by *Acridotheres mynas*, seeds of *F. benghalensis* were passed after 18–44 min and showed improved germination (Midya & Brahmachary, 1991). *Ficus* seed dispersal distances of more than 100 m have been estimated by So (1999) for *Sturnus* species in Hong Kong. Proctor (1968) recorded extremely long gut passage times of 2–15 h for *Sturnus vulgaris*, suggesting considerable dispersal distances.

#### (D) *Pycnonotidae*

The bulbul family of Africa and Asia includes 62 confirmed fig-eating species in 16 genera. Bulbuls tend to make short feeding visits and fig seeds are defecated or regurgitated in pellets in a viable state (So, 1999; Shanahan, 2000). Bulbul gut passage times have been measured at 5–47 min (Lambert, 1989*b*; Barnea, Yom-tov & Friedman, 1991; Graham *et al.*, 1995). Members of this family have been recorded feeding on 63 *Ficus* species and, in terms of fig seed dispersal, are probably the most important smaller frugivores. However, So (1999) recorded *Pycnonotus jocosus* and *P. sinensis* eating unripe *F. virens* figs in which seeds had yet to develop fully. Bulbuls may be especially important dispersers of small-fruited understory *Ficus* trees that fail to

attract larger frugivores. For such trees in Sarawak, bulbuls were responsible for approximately 80% of all feeding visits (Shanahan & Compton, in press). The ability of many bulbul species to survive in anthropogenically degraded landscapes suggests that they are important agents of forest regeneration (Corlett, 1998*b*).

#### (E) *Irenidae*

The leafbirds (*Chloropsis* spp.) and Fairy Bluebird (*Irene puella*) are major fig-eaters in the Indo-Malayan region where they feed largely on hemiepiphytes in the canopy but are also observed to descend to the understory or forest edge (McClure, 1966; Lambert, 1987, 1989*b*; Shanahan, 2000). McClure (1966) reported that these birds selectively fed on the ripest *F. sumatrana* figs in Malaysia. The Fairy Bluebird has been recorded feeding on 32 fig species throughout its range whilst 15, 21 and 27 *Ficus* species are known from the diets of *C. cochinchinensis*, *C. cyanopogon* and *C. sonnerati*, respectively. Members of this family appear to be somewhat specialised on *Ficus* and are likely to be important seed dispersers, if seeds are passed intact.

#### (F) *Zosteropidae*

At least 12 *Zosterops* species and *Cleptornis marchei* eat figs in the African, Indo-Malayan and Australo-Papuan regions. These small birds have limited gapes (8 mm in *Z. japonica*; Corlett, 1998*a*) and tend to peck at figs rather than swallow them whole. Nonetheless, they remain likely to ingest some seeds. Indeed, Compton *et al.* (1996) demonstrated this in South Africa where *Z. pallidus* made 29% of all visits to *Ficus burtt-davyi* and defecated viable seeds (96.3% germinated,  $N = 54$ ). Short feeding visits (0.5–15 min; Compton *et al.*, 1996) suggest that seeds will be defecated away from source trees and that white-eyes play a role in the dissemination of *Ficus*.

#### (G) *Tyrannidae*

Neotropical figs are eaten by at least 36 tyrannid species in 19 genera (including manakins, cotingas and tyrant-flycatchers). Figs are either eaten whole or pecked at and can be taken from a perch, in sallying flights or by hover-gleaning (Cruz, 1980; Jordano, 1983; Scott & Martin, 1984; Stiles & Skutch, 1989). For at least some species, figs appear to be an important resource. Kantak (1979) reported that visits to fig crops accounted for 46–74% of all feeding visits by tyrannids, regardless of the avail-

ability of non-fig fruits. Tyrannids are fairly small birds with short gut passage times (15 min for *Manacus vitellinus*, 12 min for *Pipra mentalis*; Worthington, 1989) and so dispersal distances are likely to be short.

#### (H) *Muscicapidae*

Many thrushes (subfamily Turdinae) are highly frugivorous and species have been recorded eating figs in the Neotropical, African and Indo-Malayan regions. Whilst some thrushes (e.g. *Zoothera* spp.) are terrestrial foragers, feeding only on fallen fruit, others take figs from a perch or by hover-gleaning (Cruz, 1980). *Turdus* species in Hong Kong selectively took the ripest figs of *Ficus microcarpa* and *F. virens* (So, 1999). Viable fig seeds have been found in the intestine of *T. hortulorum* in Hong Kong (So, 1999), and from the faeces of *T. olivaceus* (93.5% germination,  $N = 31$ ; Compton *et al.*, 1996). In Mexico, Coates-Estrada & Estrada (1986) observed short feeding visits (5–5.6 min) to *F. cotinifolia* by *T. grayi*, *Catharus ustulatus* and *C. mustelina*. Similarly short visits of 6.3–7.6 min were recorded by So (1999) for *Turdus* species feeding on *F. virens* in Hong Kong. Barnea *et al.* (1991) recorded a gut passage time of 21–74 min for *Turdus merula*. Defecation of viable seeds, short visits to fruiting trees and moderate gut passage times suggest that thrushes are genuine dispersers of *Ficus*. However, terrestrial foraging species seem unlikely to defecate seeds in the canopy microsites required by hemi-epiphytic *Ficus* species.

Among the flycatchers (subfamily Muscicapinae) there are records of fig-eating for *Ficedula hypoleuca* in Borneo, *Cossypha caffra* in South Africa, and, in China, *Phoenicurus aureoreus* and *Chaimarrornis leucocephalus*. These birds are largely insectivorous and are unlikely to play a great role in *Ficus* seed dispersal.

#### (I) *Ptilonorhynchidae*

Eight bowerbird species in the genera *Amblyornis*, *Chlamydera*, *Ptilonorhynchus* and *Sericulus* and three catbird species (*Ailuroedus*) are known to eat figs in the Australo-Papuan region. In one study, more than 30% of the food consumed by *Ailuroedus crassirostris* was figs (Innis & McEvoy, 1992). No information could be found on the effects these birds have on seed survival and germination.

#### (J) *Sylviidae*

In the subfamily Sylviinae, species of babblers (tribe Timaliini) and warblers (tribe Sylviini) are both

recorded feeding on figs. Among the former, *Alcippe brunneicauda* was one of the most frequently recorded species visiting figs in Malaysia (Lambert, 1989b) and *Pomatorhinus montanus* was observed to consume selectively the ripest *Ficus sumatrana* figs available (McClure, 1966).

#### (K) *Nectariniidae*

The tiny flowerpeckers (*Dicaeum*, *Prionochilus* spp.) are commonly observed eating figs throughout the Indo-Malayan region. *D. agile* was the most commonly observed frugivore feeding on *Ficus drupacea* in Thailand, with 50–100 individuals in the tree throughout the day (Brockelman, 1982). Their size dictates that flowerpeckers can only peck at all but the smallest of figs and they have been observed to suck pulp out using a pumping action (Wells, 1975). Nonetheless, the design of figs suggests that some seeds will be ingested and dispersed. The short feeding visits of flowerpeckers imply that seeds will be defecated away from the fruiting individual. Figs are also recorded in the diets of sunbirds (*Nectarinia* spp.) and spiderhunters (*Arachnothera* spp.) although the former are highly specialized nectar feeders and the latter are predominantly insectivorous and, as such, cannot be expected to be of great importance to *Ficus* seed dispersal. Indeed, Compton *et al.* (1996) recorded three *Nectarinia* species visiting crops of *F. burtt-davayi* but the birds fed only on exudate from fig wasp exit holes and not on the figs themselves. The sunbirds also dislodged figs whilst foraging, making them unavailable for other, potentially seed-dispersing, frugivores (Compton *et al.*, 1996).

#### (L) *Melanocharitidae*

Four species of berrypecker (*Melanocharis*) eat figs in New Guinea, where they are ecological equivalents of the Indo-Malayan flowerpeckers. Thus, their feeding behaviour and role in seed dispersal are likely to be similar to those of the nectariniids.

#### (M) *Meliphagidae*

Despite nectar being a major dietary component of the Australo-Papuan honeyeaters, 23 species in 12 genera have also been recorded feeding on figs. The relatively simple digestive apparatus associated with nectarivory is unlikely to affect adversely fig seeds ingested and these species are likely to be dispersers of *Ficus*.

(N) *Passeridae*

Passerids tend to be seed eaters but a number of species in the genera *Nigrita*, *Ploceus*, *Passer*, *Nesocharis*, *Erythrura*, *Caryothraustes* and *Malimbus* are known to eat figs (Appendix 2, see <http://go.to/figs>). Compton *et al.* (1996) found no intact seeds in the faeces of *Ploceus bicolor* following consumption of *Ficus burtt-davyi*.

(O) *Eurylaimidae*

The Green Broadbill (*Calyptomena viridis*) is a highly frugivorous species that shows a particular preference for figs. In Malaysia, Lambert (1989a, b) recorded 21 *Ficus* species in the diet of this bird and by radio-tracking individuals showed that they can spend 31–62% of their time visiting fig crops, covering 13–24 ha per week in the process. The species' wide gape allows many *Ficus* species' figs to be swallowed whole, ensuring that seeds are ingested. The species is likely to be an important disperser of *Ficus*. The broadbill family also includes predominantly carnivorous species that have nonetheless been recorded eating figs (*Psarisomus*, *Eurylaimus* and *Cymbirhynchus* spp.).

(P) *Other families*

Finally, among the passerines there are records of fig-eating by several vireo species (*Vireo* spp.; Vireonidae), Grey Hypocolius (Hypocoliidae), Cedar Waxwing (*Bombycilla cedrorum*; Bombycillidae), Common Fiscal (*Lanius collaris*; Laniidae), Noisy Pitta (*Pitta versicolor*; Pittidae), Schlegel's Assity (Philepittidae), Velvet-fronted Nuthatch (*Sitta frontalis*; Sittidae), two tit species (Paridae), an Australian robin (*Poecilodryas placens*; Eopsaltriidae) and a prinia (*Prinia maculosa*; Cisticolidae). Such records are rare and none of these families are likely to play a significant role in *Ficus* dispersal.

(b) *Mammals*(i) *Marsupialia*

Opossums (Didelphidae) eat figs in Neotropical forests but, due to their nocturnal activity, little is known of the extent of fig-eating or the role these animals play in *Ficus* seed dispersal. Medellín (1994) estimated mean dispersal distances of under 15 m for *Cecropia* seeds dispersed by *Philander opossum* and *Didelphis marsupialis*.

The absence of primates east of Wallace's line suggests that marsupials play a greater role in *Ficus* dispersal in Australo-Papuan forests than in the

Neotropics, especially for *Ficus* species with large and/or dull fruits that are not attractive to birds. Although wallabies and tree-kangaroos (Macropodidae), bandicoots (Peramelidae), sugar-gliders (Petauridae), cuscuses (Phalangeridae), and a species of rat-kangaroo (Potoroidae) have all been observed eating figs, very little is known of the importance of figs to these animals or the role they play in *Ficus* dispersal.

(ii) *Primates*

Madagascan figs are eaten by at least four genera of lemurs (*Haplemur*, *Lemur*, *Petterus* and *Varecia* spp.; Lemuridae). Garbitt (1999) states that figs are especially important to *Petterus fulvus* and that 60% of fruit-eating observations for *Varecia variegata* were of consumption of *Ficus reflexa* and *F. lutea* figs. Gut passage times of captive lemurs vary between 1.7 h (*Varecia* spp.) and 4.75 h (*Lemur catta*) (Cabre-Vert & Feistner, 1995), suggesting dispersal of seeds away from the source tree. Madagascan figs are also eaten by the indris (Indriidae) and dwarf and mouse lemurs (Cheirogaleidae) but little is known of their dietary importance to, and likelihood of dispersal by, members of these families. Similarly, there is a single record of fig consumption by Potto Gibbon (*Perodicticus potto*; Lorisidae) on the African mainland (Kingdon, 1971), but it is unlikely that this primarily insectivorous family has a major role to play in *Ficus* seed dispersal.

Fig-eating is widespread amongst New World monkeys of the genera *Alouatta*, *Ateles*, *Callicebus*, *Cebus*, *Lagothrix*, and *Saimiri* (Cebidae). Figs comprise nearly all of the dry season diet of Squirrel Monkeys (*Saimiri sciureus*) at Cocha Cashu, Peru (Terborgh, 1986) and are the most important dry season food item (28.8% by mass) for Mantled Howler Monkeys (*Alouatta palliata*) on Barro Colorado Island, Panama (Smith, 1977). Gut transit times have been recorded for *Cebus apella* (1.5–4 h; Zhang & Wang, 1995), *Ateles geoffroyi* (mean  $\pm$  s.d., 4.4  $\pm$  1.5 h; Milton, 1981) and *Alouatta palliata* (mean  $\pm$  s.d., 20.4  $\pm$  3.5 h; Milton, 1981) and dispersal distances have been predicted for *Alouatta palliata* (100–300 m; Estrada & Coates-Estrada, 1986) and *Ateles belzebuth* (several km; Milton & May, 1976). Fig seeds are defecated intact by Common Woolly Monkeys *Lagothrix lagotricha* (Delfer & Defler, 1996) and by Howler Monkeys (*Alouatta* spp.), with the latter elevating the likelihood of fig seed germination (Estrada & Coates-Estrada, 1986; deFigueiredo, 1993).

Also in the neotropics, figs are eaten by marmosets

and tamarins (*Callithrix* and *Saguinus* spp.; Callitrichidae). These small primates are omnivorous and probably make relatively little contribution to *Ficus* seed dispersal.

The large family of Old World Monkeys (Cercopithecidae) includes at least 34 species that eat figs. Among the colobine monkeys (subfamily Colobinae) figs are eaten by approximately one-third of the species and half of the genera (*Colobus*, *Presbytis* and *Pygathrix*). Nevertheless, figs appear to contribute little overall to the diets of colobine monkeys as they tend to be folivorous (in Sumatra figs accounted for just 6% of the diet of *Presbytis thomasi*; Ungar, 1995). Conversely, among the subfamily Cercopithecinae (*Cercocebus*, *Cercopithecus*, *Erythrocebus*, *Macaca*, *Miopithecus* and *Papio* spp.), fig-eating appears to be more widespread. Lieberman *et al.* (1979) found that *Ficus platyphylla* seeds were the second most abundant of 59 seed species found in baboon (*Papio* spp.) dung, accounting for 29% of all seeds. However, in South Africa, *P. anubis* has been observed feeding on immature figs of *F. ingens* (S. G. Compton, personal observations). In Uganda, *Ficus exasperata* figs were the most frequently eaten fruits for *Cercopithecus mitis*, accounting for 30.8% of all food (Butynski, cited by Gautier-Hion & Michaloud, 1989) whilst in Kenya three fig species contributed 17.6 and 15.9% of the diets of *C. mitis* and *C. ascanius*, respectively. By contrast, in Gabon figs were eaten infrequently by monkeys (Gautier-Hion & Michaloud, 1989). In Sumatra, figs made up 20% of the diet of *Macaca fascicularis* (Ungar, 1995). *Ficus* seeds are smaller than the size threshold shown to be spat by *M. fascicularis* (Corlett and Lucas, 1990) and it is likely that *Ficus* seeds are instead swallowed by all Old World monkeys. Fig seeds pass intact through *Cercocebus albigena* guts (Waser, 1977) and Kitamura (2000) found between seven and 492 (mean = 180.1) *Ficus* seeds in the dung of *M. nemestrina*. Poonswad *et al.* (1998a), however, reported *Macaca nemestrina* to be a partial seed predator, feeding on unripe figs.

Gibbons (*Hylobates* spp.; Hylobatidae) also eat figs. At a site in Peninsular Malaysia, Gittins and Raemaekers (1980) recorded the percentage of annual feeding time that was spent eating figs to be 22% for Siamang (*H. syndactylus*) and Lar Gibbon (*H. lar*) and 17% for Agile Gibbon (*H. agilis*). Both Siamang and Lar Gibbon selected figs preferentially over other fruit types. In Sumatra, figs composed nearly half of the diet of *H. lar* (Ungar, 1995). Palombit (1997) also noted that Sumatran hylobatids spend about twice as much time (approx-

mately 45%) feeding on figs than their mainland counterparts. Gibbon gut passage times exceed 21 h in captivity (Idani, 1986) suggesting long dispersal distances for defecated seeds. In spite of being apparently good dispersers, gibbons have also been recorded eating unripe figs (Poonswad *et al.* 1998a).

Figs are commonly recorded in the diet of great apes (Pongidae). Orang-utans (*Pongo pygmaeus*) consume at least seven species of figs in Borneo and 10 species in Sumatra, where figs account for 30% of the diet (Ungar, 1995). Leighton (1993) showed that orang-utans preferred figs high in water-soluble carbohydrate and low in phenolics and condensed tannin. In Africa, gorillas (*Gorilla gorilla*) and chimpanzees (*Pan troglodytes*) are known to eat 11 and 15 species of figs, respectively. In Budongo Forest (Uganda), fig seeds were the most common seeds in chimpanzee dung (Wrangham *et al.*, 1994). For both Pygmy Chimpanzees (*Pan paniscus*) and Common Chimpanzees (*P. troglodytes*), figs appear to be eaten year-round and are therefore considered a staple food rather than one used in time of general shortage (White, 1998; Newton-Fisher, 1999). In Uganda, consumption of figs of *Ficus sur* accounted for 33.5% of chimpanzee's dry season feeding time (Newton-Fisher, 1999). Chimpanzees have a long gut passage time (23.6 hours in captivity; Idani, 1986) and are thus likely to disperse fig seeds over long distances. Furthermore, fig seed germination is improved by passage through chimpanzee guts (Wrangham *et al.*, 1994). Chimpanzees may also act as fig seed predators as they are known to eat unripe, as well as ripe, figs (Newton-Fisher, 1999).

Finally, wild figs are eaten by humans in Borneo, Papua New Guinea (M. Shanahan, personal observation), and Africa, where figs of approximately one quarter of the *Ficus* flora occur in human diets (Peters, O'Brien & Drummond, 1992). Given the role of the great apes (Pongidae) in *Ficus* seed dispersal it is likely that forest-dwelling humans are also capable of dispersing fig seeds.

### (iii) Carnivora

Many carnivores include fruit in their diet, at least for part of the year. The most frugivorous carnivores are the civets (Viverridae) which eat figs in Africa (*Nandina* and *Viverra* spp.) and Asia (*Arctogalidea*, *Arctictis*, *Paguma*, *Paradoxurus*, *Viverra* and *Viverricula* spp.). The arboreal Binturong (*Arctictis binturong*) particularly favours figs and may be a specialist forager (Leighton & Leighton, 1983; Payne, Francis & Phillipps, 1985). Gruezo & Soligam (1990) found that *Ficus minahassae* seeds from the faeces of

Philippine Palm Civet (*Paradoxurus philippinensis*) failed to germinate yet seeds of *F. annulata* from the faeces of captive Binturong germinated readily after being retained for over 3 h in the gut (Shanahan, 2000). Civet daily movements have been measured by Rabinowitz (1991) for *Paradoxurus hermaphroditus* (2.8 km) and *Paguma larvata* (2.8 km) and suggest that seeds will be moved some distance from the source tree.

Bears (Ursidae) eat figs in India, Nepal, South America and Borneo. *Ficus consociata* seeds were dispersed at least 200 m by Sun Bears (*Helarctos malayanus*) and germinated but then died (McConkey & Galetti, 1999). North American bears have been shown to be effective seed dispersers, retaining seeds for several hours to one day before defecating them in a viable state and, in some cases, elevating germination rates (Traveset & Willson, 1997). However, the large size of ursid defecations implies that fig seeds dispersed thus will be highly clumped.

In the dog family (Canidae), figs are known from the diets of Red Fox (*Vulpes vulpes*) in Europe, jackals (*Canis adustus* and *C. mesomelas*) in Africa and coyotes (*C. latrans*) in Mexico. Seeds occur in faeces but little more is known of the dogs' contribution to *Ficus* dispersal.

Mongoose (*Herpestes, Galerella*; Herpestidae) and martens and their allies (*Martes, Melogale, Mustela, Eira*; Mustelidae) are known to eat figs but nothing can be concluded about their role in seed dispersal.

There is a record of a captive Margay (*Felis weidii*; Felidae) accepting figs as food (Koford, 1983) but no field records of cats eating figs were found.

Finally, two Neotropical species of Procyonidae consume figs with some regularity. Kays (1999) concluded that *Ficus* is the most important food genus for the highly frugivorous Kinkajou (*Potos flavus*), occurring in 44.9% of faeces and accounting for 24.6% of feeding bouts. Indeed, a quarter of the Neotropical *Ficus* species included in this review are eaten by *P. flavus*. Julien-Laferriere (1993) estimated seed transit times of 45 min to 3 h 35 min indicating that dispersal of seeds away from the source tree is likely. Howe (1990), however, notes that high densities of seeds are defecated beneath Kinkajou sleeping sites and are prone to discovery by seed-predatory insects. Coatis (*Nasua narica*) eat figs of six species but little is known of their role in dispersal.

#### (iv) Scandentia

The 16 species of tree shrews (Tupaiaidae) are

confined to South-east Asia. *Tupaia* species consume a variety of figs ranging from those of geocarpic species, produced on the forest floor, to those of hemi-epiphytes high in the canopy (Kawamichi & Kawamichi, 1979; Emmons, 1991; Shanahan & Compton, 2000). Tree shrews make short visits to fig crops (< 5 min) and are apparently rapidly satiated (Shanahan, 2000). In a captive trial, seeds of *Ficus montana* were passed (mean 60.6 seeds per faeces) between 33 and 63 min after ingestion in a readily germinable state (Shanahan & Compton, 2000).

#### (v) Chiroptera

Fruit constitutes the majority of the diet of all genera of Old World fruit bats (Pteropodidae), save six predominantly nectarivorous genera in the subfamily Macroglossinae (Marshall, 1985). Figs are eaten by at least 47 pteropodid species in 20 genera (including the nectarivorous *Macroglossus* and *Syconycteris*) and for some species figs appear to be an important food source. Eighty-eight percent of oral swabs and faecal samples from *Hypsignathus monstrosus* in Gabon contained fig seeds (Gautier-Hion & Michaloud, 1989). On Anak Krakatau, Indonesia, 90% of bat faeces contained *Ficus* seeds (Shilton, 1999). In Eby's (1998) three-year study of *Pteropus poliocephalus* diet in Australia, figs were consumed in all months. These three examples from separate continents suggest a more general reliance on figs by Old World fruit bats. Figs are either eaten *in situ* or carried in the mouth to a feeding roost some distance away (*Cynopterus brachyotis* can carry 75 g fruits 200 m; van der Pijl, 1957). During feeding fruit pulp is pressed against the palate to extract juices (trituration) before being ejected as a pellet (palatal imprint). Whilst these imprints often contain fig seeds, the seeds' small size allows many to be swallowed with the juice. Fig seeds can therefore be dispersed in three ways: in fruit dropped in flights to feeding roosts, in palatal imprints and in faeces. Gut passage times of 12–70 min have been recorded for *Pteropus*, *Ptenochirus*, *Nyctimene*, *Lissonycteris*, *Epomops* and *Rousettus* species (Wolton *et al.*, 1982; Tedman & Hall, 1985; Utzurrum & Heideman, 1991; but can be much longer, Shilton *et al.*, 1999). Fig seeds survive gut passage and elevated germination rates following passage through bat guts have been recorded for *Ficus chrysolepis* (Utzurrum & Heideman, 1991) and by *Pteropus voeltzkowi* (Entwistle & Corp, 1997). However, it has been suggested that bats differentially ingest viable seeds (Utzurrum & Heideman, 1991). Pteropodid bats fly

fast and far and have been implicated in the dispersal of *Ficus* seeds across distances greater than 50 km (Thornton *et al.*, 1996; Shanahan *et al.*, in press).

Similarly, at least 35 species of Neotropical fruit bats (Phyllostomidae) in 16 genera eat figs. In Peru, fig seeds were the most frequently recorded seeds in the faeces of *Artibeus* bats and figs were eaten by these bats year-round (Romo, 1996). In Panama, Kalko, Herre & Handley (1996) demonstrated a positive relationship between the body mass of fruit bats and the size of the figs on which they forage. At the same site, Korine *et al.* (2000) estimated that individual *Ficus* hemi-epiphytes with small figs can feed 571 bats over two to five nights whilst those with large figs can sustain 834 large bats over the same period. Neotropical fruit bats carry whole figs (weighing 6–20% of their body mass in *Artibeus jamaicensis*) hundreds of metres to feeding roosts (Morrison, 1978; August, 1981). That these feeding roosts are often in the canopy, and that seeds pass intact through bat guts and are defecated in flight suggests that the bats deposit seeds over wide areas as well as in the canopy microsites required by hemi-epiphytic *Ficus* species (Morrison, 1978; Handley, Gardner & Wilson, 1991; Kalko *et al.*, 1996). Gut passage times for phyllostomids appear to be of a similar order to those of pteropodids (e.g. 15–20 min for *Carollia perspicillata*; Fleming, 1981; Fleming & Heithaus, 1981). Fleming (1981) calculated that more than 90% of *Piper* seeds dispersed by *C. perspicillata* were moved more than 50 m to feeding roosts and that some were dispersed over 300 m. Some of the larger Neotropical bats, such as *Artibeus jamaicensis* and *A. literatus* which travel several km per night (Handley *et al.*, 1991), are likely to disperse fig seeds over considerably greater distances. Like their Old World counterparts, some Neotropical fruit bats have been demonstrated to elevate *Ficus* germination rates by ingesting seeds (Fleming & Heithaus, 1981), possibly because gut passage removes the fruit pulp that encourages fungal decay.

(vi) *Proboscidea*

Fig seeds have been recorded in the dung of African elephants (*Loxodonta africana*; Elephantidae) and Indian elephants (*Elephas maximus*) in Thailand. The large size of these defecations and the high numbers of seeds and co-occurring species suggests competition at the germination/seedling stage.

(vii) *Hyracoidea*

Hyraxes (*Procavia* and *Dendrohyrax* species; Procaviidae) have been recorded eating figs in Africa.

However, Greeff & Whiting (1999) found that *P. capensis* killed many *Ficus cordata* seeds through mastication.

(viii) *Perissodactyla*

Two species of tapirs (*Tapirus* spp.; Tapiridae) are recorded eating fallen figs in the Neotropics. Fragoso (1997) estimated dispersal distances for non-*Ficus* seeds to be 2 km. However, Salas & Fuller (1996) reported that *T. terrestris* defecates in water, a behaviour that will have major implications for seed dispersal.

(ix) *Artiodactyla*

Amongst the even-toed ungulates figs are eaten by deer (Cervidae), pigs (Suidae), peccaries (Tayassuidae), cattle (Bovidae) and mouse-deer (Tragulidae). Other than records of *Tragulus* mouse-deer eating geocarpic figs directly from the tree (Shanahan, 2000), these records pertain to the consumption of fallen fruit. Heydon & Bulloh (1997) reported that the density of *T. napu* and overall mouse-deer biomass in a Bornean forest were both positively correlated with the density of hemi-epiphytic *Ficus* species and for six months of the year figs were the only fruit eaten.

(x) *Rodentia*

The majority of records of fig-eating by rodents concern squirrels (Sciuridae), although this probably reflects their greater visibility, arboreality and diurnal activity. Squirrels occur throughout the range of *Ficus* and are known to eat figs wherever they occur. The squirrels have undergone an extensive radiation that has resulted in species foraging at all levels where figs may be presented, from the forest floor to the emergent layer, both during the day and at night (flying squirrels). *Callosciurus* and *Ratufa* squirrels are commonly observed eating figs in the canopy of Malaysian forests where they appear to act as ‘pulp thieves’ (*sensu* Howe & Vande Kerckhove, 1979), stripping the fig pulp away with their teeth and discarding the seed-rich core (Lambert, 1990; Shanahan, 2000). Furthermore, *Ratufa*, *Callosciurus* and *Tamiops* squirrels were recorded eating unripe figs by Poonswad *et al.* (1998a) in Thailand. Eight out of nine African squirrel species studied by Emmons (1980) and *Sciurus granatensis*, a widespread Neotropical squirrel,

cache food. In Malaysia, observations of fruit-caching or carriage by squirrels are relatively rare (Payne, 1979) although provisioning of juveniles is likely since they are not observed to forage (Becker, Leighton & Paine, 1985).

Records of fig-eating from rodent families other than the Sciuridae are less abundant. A handful of rat species (Muridae), porcupines (Hystricidae), two genera of spiny rat (Echimyidae) and Agouti (Dasyproctidae) eat figs. Adler (2000) found a strong correlation between densities of the spiny rat *Proechimys semispinosus* and large-fruited fig trees in Panama. Rodents are generally considered to be seed-predators (Price & Jenkins, 1986). Seeds of *Ficus burtt-davyi* survived passage through African murids but experienced reduced germination rates (Compton *et al.*, 1996).

#### (c) Reptiles and fishes

Compared to their avian and mammalian counterparts, the reptiles and fish recorded eating figs probably contribute very little to *Ficus* seed dispersal. Nonetheless, they may still play a role, especially in extreme situations where other frugivores are depauperate such as on the island of Aldabra where the giant tortoise (*Geochelone gigantea*) disperses *Ficus rubra* and has been implicated in the transport of seeds 400 km from Madagascar (Hnatiuk, 1978). Tortoises and fish have long gut passage times (days rather than hours; Agami & Waisel, 1988; Moll & Jansen, 1995; Hailey, 1997; Horn, 1997) and have been demonstrated to pass fig seeds intact (Moll & Jansen, 1995; Horn, 1997). For riverine *Ficus* species that disperse using water, fish may facilitate upstream dispersal (Horn, 1997). Greeff & Whiting (1999) showed that the lizard *Platysaurus broadleyi* passes seeds of *F. cordata* intact and defaecated them at an average of 120 m from the nearest source tree. The large numbers of lizards foraging together on *F. cordata* figs (mean 30.4, range 8–134; Whiting & Greeff, 1997) and the distance seeds are moved suggest that these lizards may be important seed dispersers.

#### (4) *Ficus* fruit syndromes and dispersal guilds

Most species that remove figs directly from the source tree (as opposed to feeding on fallen fruit) can be placed into one of three major frugivore guilds: volant birds, fruit bats or arboreal mammals. Many

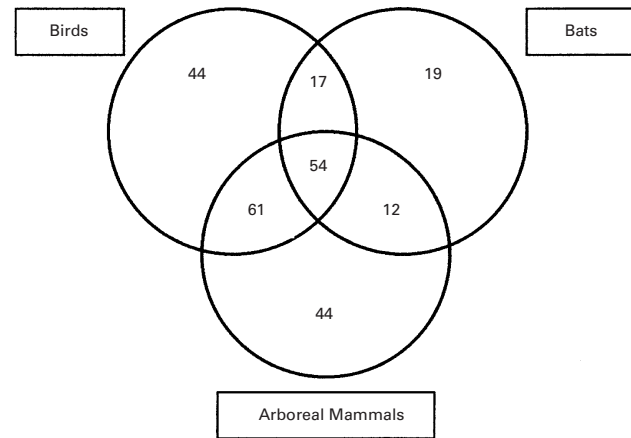


Fig. 5. Overlap between major frugivore guilds (geocarpic *Ficus* species are excluded, as are ground-foraging birds and mammals for which records of fig-eating mostly pertain to the consumption of fallen fruit or geocarpic figs). Numbers = number of *Ficus* species consumed by each frugivore guild. 42.6% of the *Ficus* species are known from diet of only one guild, 35.9% are eaten by two guilds of frugivores and 21.5% are eaten by members of all three guilds. Overlap is greater between birds and arboreal mammals (45.8% of *Ficus* species shared) than birds and bats (28.3%) or bats and arboreal mammals (26.3%).

*Ficus* species' figs are eaten by members of two or more of these guilds, with overlap being greater between birds and arboreal mammals than between either of these guilds and fruit bats (Fig. 5). Despite the patterns of overlap observed, for two-fifths of the *Ficus* species considered, frugivores of only one guild have been recorded. However, this analysis is crude, failing to take into account differences in proportional visitation or fruit removal.

Only detailed studies that simultaneously examine multiple fig species and diverse frugivore taxa can allow the examination of whether individual fig species tend to attract broad subsets (e.g. birds, bats or primates) of frugivore communities as potential seed dispersers, or whether they are equally attractive to all frugivores present. Such studies are lacking (Table 3) but exist for four tropical sites. In a detailed study of 34 *Ficus* species and 69 frugivore species in Borneo, Shanahan (2000) has demonstrated a *Ficus* dispersal guild structure. Three guilds of *Ficus* species attracted (almost exclusively) fruit bats, terrestrial mammals or arboreal mammals, respectively. The remaining fig species attracted diverse assemblages of birds and arboreal mammals but could be divided into two further guilds, one in the canopy and one in the understory. Guild membership was determined by largely phylogenetically determined differences in fig colour, size

and height above ground (Shanahan, 2000; Shanahan & Compton, in press).

Similarly, Shanahan *et al.* (in press) recognised two major guilds of *Ficus* colonists to Long Island, Papua New Guinea, a volcano that erupted catastrophically in the 17<sup>th</sup> century. One guild, with large, dull figs that are presented in the lower storeys of the forest attracted primarily bats whereas both birds and bats were attracted to the second guild, whose figs were red, tended to be smaller and were distributed throughout the vertical strata of the forest.

Two *Ficus* guilds have also been recognised on Barro Colorado Island, Panama (Kalko *et al.*, 1996; Korine *et al.*, 2000). The first guild comprises species with scented green figs that are attractive to bats and the second group of species produces odorless red figs attractive to birds. Additionally, whilst crops of 'bat-figs' ripened synchronously those of *Ficus* species attracting birds exhibited within-crop asynchrony of ripening.

Finally, in the Philippines, Hamann & Curio (1999) found that four *Ficus* species were eaten only by fruit bats whilst, in addition to the bats, *Ficus heteropleura* attracted 13 species of birds.

In each of these examples, different patterns of frugivore attraction were associated with differences in fruit characters. Specifically, green or brown figs tend not to attract avian frugivores and such figs are rarely as small as the smallest bird-dispersed figs. In the Old World, *Ficus* species attracting primarily fruit bats, terrestrial mammals or arboreal mammals were generally dioecious whilst those attracting both birds and mammals included dioecious and monoecious species (Shanahan, 2000; Shanahan & Compton, in press; Shanahan *et al.*, in press).

#### IV. DISCUSSION

##### (1) The quality of the dataset

We have accumulated records of frugivory for 260 *Ficus* species, a respectable proportion (approximately 30%) of the world's total *Ficus* flora. With 59% of species included, the African figs are best represented in the dataset. The lower coverage of Neotropical species (28.9%) is due in part to the conservative approach we adopted when faced with the complicated taxonomy of New World figs. With 32.9% of its *Ficus* species included, the Indo-Australian flora is also under-represented relative to that of Africa. This probably reflects gaps in the

literature for the figs of Sri Lanka, New Guinea and Pacific island groups as well as the region's greater number of dioecious species, which are under-represented in the review. The greater coverage of monoecious species reflects that fact that they tend to be larger and have larger crop sizes than dioecious species. As well as being more conspicuous, monoecious species, especially the hemi-epiphytes (including the over-represented section *Conosycea*) tend to attract larger and more diverse feeding assemblages than their dioecious counterparts and are thus more likely to be the subjects of observation.

##### (2) Who eats figs?

The animals known to eat figs include over 10% of the world's bird species (18% of genera) and over 6% of the world's mammals (14% of genera). Despite the depth of coverage of this review, these figures are minima and we expect considerably more members of less well-studied frugivore taxa also to eat figs. In particular, additional ground birds (e.g. Tinamidae), small rodents, and species endemic to regions under-represented in the literature or occupying inaccessible (e.g. highland) habitats are likely to eat figs. The data accumulated here support Janzen's (1979) contention that figs are an important resource for more animal species than the fruit of any other genus. Indeed, in Zona & Henderson's (1989) review of frugivores of palms, considerably fewer frugivores were identified (86 bird species in 63 genera and 23 families, 70 mammal species in 52 genera and 24 families), in spite of their coverage of 140 taxa in this speciose family (Palmae) rather than a single genus.

Most of the animal species recorded eating figs belong to a handful of the 92 families that include fig-eating species. Predictably, there is a strong relationship between the number of fig-eating species/genera in a family and the number of *Ficus* species' figs that family consumes. Thus we can identify the families that are most likely to have strong ecological and evolutionary interactions with the genus *Ficus*. Globally, these are the parrots (Psittacidae), pigeons (Columbidae), starlings (Sturnidae) and crows and allies (Corvidae). In the Neotropics, these families are joined by New World monkeys (Cebidae) and fruit bats (Phyllostomidae). The other major families of fig-eaters in the African and Indo-Australian regions are bulbuls (Pycnonotidae), starlings (Sturnidae), hornbills (Bucerotidae), Old World fruit bats (Pteropodidae), Old World monkeys (Cercopithecidae), African barbets



(Lybiidae), Asian barbets (Megalaimidae), and squirrels (Sciuridae).

Fig-eating animals can be considered in three broad groups: specialists, generalists and casual consumers of figs. For part of the year, or year-round, fig specialists eat little else and are highly reliant on figs as a dietary resource. In the Indo-Malayan region, some degree of fig specialism has been suggested for hornbills, *Chloropsis* leafbirds, the Fairy Bluebird *Irene puella*, *Treron*, *Ducula* and *Ptilinopus* pigeons, barbets (Megalaimidae), parrots (*Loriculus*, *Psittacula* spp.), gibbons, the Binturong *Arctictis binturong*, and *Pteropus* and *Cynopterus* fruit bats. Australo-Papuan species exhibiting heavy reliance upon, or consumption of, figs include birds-of-paradise (*Manucodia*, *Paradisea*), *Ducula*, *Ptilinopus* and *Lopholaimus* pigeons, Asian Koel, Channel-billed Cuckoo, fig-parrots (*Cyclopsitta*, *Psittaculirostris*), the Green Figbird (*Sphecothebes viridis*), Vulturine Parrot (*Psitttrichas fulgidus*), and *Pteropus* bats. Additional fig specialists in Africa include various primates, some *Agapornis* lovebirds, and fruit bats. In the Neotropics, a degree of fig specialism has been suggested for the Kinkajou (*Potos flavus*), Toco Toucan (*Rhamphastos toco*), certain monkeys (Cebidae) and the fruit bat *Artibeus jamaicensis*. It would appear that specialisation on figs is a more widespread phenomenon in the Old World than in the Neotropics. Snow (1980), considering birds only, also reaches this conclusion and proposed that Neotropical figs may be less nutritious than those in the Old World. We suggest an alternative explanation: that the pattern arises because of the lower diversity of *Ficus* and greater diversity of non-fig fruits (that may be more nutritious than Old World non-fig fruits) in Neotropical forests.

The generalist fig-eaters include bulbuls, woodpeckers, mouse-birds, cuckoos, turacos, cracids, pheasants and many families of passerine birds. Mammalian generalists include tree shrews, certain primates and carnivores. Rather than being heavily reliant on figs, the generalists appear to use figs as a supplement to diets of other fruits, leaves, nectar or animal matter. Nonetheless, there may be times of year where these animals rely on figs to a greater degree.

Casual fig-eaters are generally not frugivorous and probably only eat figs opportunistically. Such species include the gull, shrike, ibis, kingfisher, roller, and motmots recorded eating figs.

This classification of fig-eaters is basic and does not take into account plasticity of frugivore diets. Seasonal diet shifts, variation in local abundance of

figs, and incongruities in the distributions of fig and frugivore species all mean that an animal species that is a fig specialist at one site or time may not be elsewhere. For example, the Neotropical fruit bat *Artibeus jamaicensis* was described by Janzen (1979) as a fig specialist. However, the species also occurs at sites with few *Ficus* species or where figs occur at low densities (Handley *et al.*, 1991). Further research is required to assess more accurately the degree to which frugivore species are specialised on figs as a dietary resource.

### (3) Why are there so many fig-eaters?

To understand why there are so many fig-eaters, we look to the figs themselves and consider what it is about patterns of fig packaging and presentation that makes them so attractive to frugivores. Firstly, the fact that *Ficus* is a widespread genus means that many frugivore species occur within its range. Furthermore, because *Ficus* occurs in each of the major biogeographical regions of the tropics, figs are exposed to diverse groups of birds and mammals which themselves have more restricted ranges (e.g. lemurs of Madagascar, Australasian marsupials). Secondly, figs are 'easy' fruits to handle and consume. Figs are generally unprotected and therefore the range of animals that eats them is not limited to those with powerful bills, teeth or claws. Rather, the soft flesh of figs is accessible to frugivores regardless of size, masticatory apparatus or digestive capability. Exceptions are rare but include some geocarpic species (Shanahan, 2000), and certain members of section *Malvanthera* in New Guinea (Mack & Wright, 1998). However, once opened by parrots, the latter groups of figs are accessible to a range of other bird species (Mack & Wright, 1998). Additionally, figs' small seeds are easily handled, and impose little constraint on frugivores in terms of foraging time and ballast.

Nutritional quality may also contribute to the diversity of fig-eaters recorded. However, there has been some debate in the literature about the nutritional quality of figs. This is because generalisations appear inconsistent and disparate methodologies hinder comparisons (Conklin & Wrangham, 1994). Janzen (1979) stated that figs had a 'high nutrient value' but based this premise, in part, on the fact that many animals eat figs. Milton *et al.* (1982) reported that figs were of lower nutritional value than non-figs in Barro Colorado Island (Panama), whilst in India, Borges (1993) reported a similar pattern, especially with regard to soluble

carbohydrate. Generally, it appears that although protein, carbohydrate and lipid content of figs are variable, they are low (compared to other fruits) and fig fibre and pulp water content tend to be high (Vellayon, 1981; Jordano, 1983; Herbst, 1986; Bronstein & Hoffmann, 1987; Lambert, 1989*b*; Rogers *et al.*, 1990; Borges, 1993; Conklin & Wrangham, 1994; Shanahan, 2000). Conversely, Ko, Corlett & Xu (1998) reported relatively high carbohydrate values for three *Ficus* species in Hong Kong, and Kalina (1988) states that *Ficus exasperata* figs are an excellent protein source. Wendeln, Runkle & Kalko (2000) provided further evidence that figs are not 'cheap' fruit but have high levels of protein, carbohydrate, fibre and minerals. However, *Ficus* species differed in their nutritional value suggesting that a mixed fig diet, rather than any single species, may be required to provide adequate nutrients for Panamanian fruit bats (Wendeln *et al.*, 2000). Much of the confusion over figs' nutritional value may be overcome if future studies are more consistent in methodology and consider only the pulp of ripe figs. Conklin & Wrangham (1994) draw attention to the fact that animals capable of fore- or hind-gut fermentation may be capable of obtaining up to 50% more metabolisable energy from figs and that such digestion of insoluble fibre may explain the widespread occurrence of figs in frugivore diets. O'Brien *et al.* (1998*a*) provide perhaps the most compelling evidence that there is a nutritional basis to the desirability of figs. In a comparison of fig and non-fig species in Belize, Uganda and Indonesia, they demonstrated that figs have over three times as much calcium as non-fig fruits. Such a calcium source may promote eggshell deposition and bone growth (O'Brien *et al.*, 1998*a*). Finally, figs have been suggested to be a potential source of animal protein in the form of larvae of fig pollinator wasps, their parasites and other insects (e.g. Vellayon, 1981). However, as Conklin & Wrangham (1994) note, in ripe figs most fig-wasps will have already departed the fig and the remaining corpses of males and aborted offspring are unlikely to contribute greatly to overall protein levels.

The unorthodox phenology of fig production also contributes to the fact that so many animal species eat figs. Most *Ficus* species occur in tropical forests where the majority of fleshy-fruited plant species share one or two peaks of ripening each year (e.g. Medway, 1972; Frankie, Baker & Opler, 1974). Conversely, *Ficus* species exhibit inter-tree asynchrony in fig production (Milton *et al.*, 1982; Corlett, 1984, 1987; Lambert, 1987; Compton *et al.*, 1996;

Spencer *et al.*, 1996; Patel, 1997; Poonswad *et al.*, 1998*a*). The year-round production of figs is linked to their pollination biology – the short-lived pollinator wasps need to locate receptive figs within one or two days of leaving their natal fig. Thus, figs are available year-round and constitute a reliable food source for frugivorous animals, especially during times of general fruit scarcity. Furthermore, crop sizes of some *Ficus* species and individuals are so high (numbering in their hundreds of thousands) that many frugivore species can forage simultaneously, with, presumably, a relaxation of competition.

One further factor influencing the number of fig-eating species recorded is the diversity of fig design and presentation. Although the fig, due to constraints imposed by acting firstly as an inflorescence, is remarkably uniform in structure, differences do occur in terms of the way that figs are presented. Crops range from tens to millions of red, yellow, orange, green, brown or black figs which can be geocarpic (on ground level runners), cauliflorous (growing directly from the stem or trunk) or produced in leaf axils (Corner, 1988). This diversity exposes different fig species to the foraging activities of highly disparate frugivore taxa and structures sympatric *Ficus* species into dispersal guilds that share (and potentially compete for) subsets of local frugivore communities (see below). Thus, diurnal feeders with colour vision (e.g. birds, primates) are able to locate red figs amongst green foliage whilst at night nocturnal foragers (e.g. fruit bats) are able to locate figs by olfaction and/or echolocation. Diversity in the vertical placement of figs means that they are available to volant, arboreal and exclusively terrestrial foragers (Shanahan & Compton, in press).

#### (4) Are fig-eaters effective seed dispersers?

Determining which frugivores are the most effective dispersers of *Ficus* seeds is a difficult task that is complicated by the range of germination requirements exhibited by the genus. An animal that provides an effective seed dispersal service to ground-germinating trees and climbers may be totally ineffectual in dispersing the seeds of hemi-epiphytes that require deposition in microsites on suitable host trees (Laman, 1995). Furthermore, differences in faunal composition between sites mean that frugivore species' importance can vary. Whilst quality of dispersal (*sensu* Schupp, 1993) must be concluded case-by-case bearing in mind the requirements of individual *Ficus* species, quantity is more easily compared. In simple terms, species that eat the most

figs have a higher probability of dispersing them. Thus, the putative fig-specialists are of special interest. On the whole, these species are likely to be effective seed dispersers. Not only are their rates of consumption high but, in the case of most primates, fruit bats, hornbills, and *Ducula* and *Ptilinopus* pigeons, they pass fig seeds intact, move them from the parent tree and (in some cases) elevate germination. Conversely, parrots and *Treron* pigeons that specialise on figs may be exploiting the system, destroying the majority of seeds they encounter. For all frugivores, specialists and generalists alike, a number of generalisations can be made that assist in interpreting roles in dispersal. On the whole, large frugivores eat more figs, travel further and retain seeds longer in their guts. Thus, larger fig-eaters are likely to disperse more fig seeds and disperse them greater distances than small fig-eaters. Furthermore, larger frugivores are more likely to ingest seeds as they can eat figs whole, although some small birds do have disproportionately large gapes and the design of figs suggests that even small 'peckers' will ingest some seeds. However, large animals produce large droppings exposing dispersed seeds to risks of clumping (competition in germination/seedling stage and risk of discovery by seed predators). The abundance of frugivores is another important factor. For example, on Barro Colorado Island fruit-eating bats, many regularly eating figs, are estimated to move several million fruits per year (Kalko, 1997). These bats are estimated to consume 28 kg (dry mass) of figs per hectare each year, compared to 20 kg per hectare per year eaten by Mantled Howler Monkeys (*Alouatta palliata*), the other major fig consumer on the island (Milton, 1980; Handley *et al.*, 1991).

##### (5) *Ficus* fruit syndromes and dispersal guilds

The specialist-generalist paradigm in seed dispersal (McKey, 1975; Howe, 1993) predicts that *Ficus* species (with their soft fruit with many, tiny seeds) will attract diverse assemblages of generalist frugivores which will provide a generally poor dispersal service in return for the 'low-quality' fig reward. However, the demonstration of *Ficus* dispersal guilds throughout the tropics challenges this concept.

Whilst some *Ficus* species do indeed attract large and diverse frugivore assemblages comprising disparate taxa such as fruit bats, birds and primates, some of these are not only obligate frugivores but fig specialists. Furthermore, other *Ficus* species appear

to attract smaller subsets of the frugivore community of a given area. Thus, guilds of bat-, primate- and terrestrial-mammal-dispersed *Ficus* species have been described. Moreover, since bats and arboreal mammals also feed on those figs attracting primarily birds, it would appear that the more specialised *Ficus* guilds are excluding avian visitation. In the Indo-Australian region, the figs that fail to attract birds are generally dioecious, dull (green/brown) and tend to be much larger than those eaten by birds, which can be dioecious or monoecious and tend to be red when ripe. By failing to attract birds (many of which are seed-predatory pigeons and parrots), the former may experience a better seed-dispersal service. In monoecious figs, approximately half of the potential seeds are lost to the larvae of pollinating wasps. Such figs may be expected to invest less in the pulp reward for dispersers than do dioecious species for which such seed predation does not occur in female figs. Thus, monoecious species tend to produce large crops of small figs that attract diverse frugivore assemblages whilst dioecious species attract smaller subsets of frugivore communities with relatively small crops of often large figs.

Membership of *Ficus* dispersal guilds is determined by the interaction between fig packaging and presentation characters and the sensory ability and foraging behaviour of vertebrate frugivores. Thus, birds and primates, with their good colour vision (Hartwig, 1993; Jacobs, 1996) tend to eat red figs, conspicuously displayed among green foliage. Colour is less important to nocturnal foragers and although Neotropical bats favour green figs, those in the Old World feed upon both red and green figs. This difference may relate to the disparate biology of the Phyllostomidae and Pteropodidae. The former use olfaction and echolocation to detect food whilst the latter have well-developed visual and olfactory systems but do not echolocate (Kalko *et al.*, 1996). Interspecific differences in fig design and presentation show strong phylogenetic associations suggesting that, in general, similarities result from common ancestry rather than parallel and convergent evolution in response to selective pressures exerted by different frugivore classes.

Implications of the *Ficus* dispersal guild structure are that competition for seed-dispersing frugivores between sympatric *Ficus* species is reduced, that *Ficus* species experience differential seed-dispersal services (Shanahan, 2000) and thus differ in their ability to colonise degraded landscapes (Shanahan *et al.*, in press). Individual *Ficus* species are also of differing importance to frugivore species and so the keystone

Table 9. Proportions of tropical bird or terrestrial mammal faunas that eat figs or have congeners that do so. Sources of species totals: <sup>1</sup>McDade *et al.* (1994), <sup>2</sup>Milliken & Ratter (1998), <sup>3</sup>Struhsaker (1997), <sup>4</sup>Langrand (1990), <sup>5</sup>Shanahan & Debski (*in press*), <sup>6</sup>Payne *et al.* (1985), <sup>7</sup>Schipper *et al.* (*in press*)

Location	Frugivore taxon	Total species	Fig-eating species <sup>a</sup>	% of total	Additional species with fig-eating congeners <sup>a</sup>	Cumulative % of total
La Selva, Costa Rica	Birds	411 <sup>1</sup>	67	16.3	48	29.2
	Mammals	117 <sup>1</sup>	33	28.2	7	33.3
Maraca, Brazil	Birds	442 <sup>2</sup>	38	8.6	63	22.9
	Mammals	91 <sup>2</sup>	15	16.5	11	28.6
Kibale Forest, Uganda	Birds	321 <sup>3</sup>	40	12.5	72	34.9
Ranomafana National Park, Madagascar	Birds	83 <sup>4</sup>	7	8.4	19	31.3
Lambir Hills National Park, Malaysia	Birds	238 <sup>5</sup>	73	30.7	28	42.4
	Mammals	60 <sup>5</sup>	27	45	17	73.3
Borneo	Mammals	2156	41	19.1	34	34.9
Long Island, Papua New Guinea	Land birds	49 <sup>7</sup>	15	30.6	10	51.1

<sup>a</sup> see Appendix 2 (<http://go.to/figs>).

resource concept must not be applied to figs as a whole but to individual species or guilds of species and only in relation to those frugivores capable of consuming their figs.

## (6) Figs as keystone resources

Power *et al.* (1996) defined a keystone species as one "... whose impact on its community or ecosystem is large and disproportionately large relative to its abundance". We have already demonstrated that figs are available to, and eaten by, a diverse range of vertebrate species. Based on the data accumulated in this review and published species lists, Table 9 shows, for well-studied tropical localities, the percentage of total bird and mammal species which are known to eat figs or have congeners that do so. These values range from 23% of birds in La Maraca, Brazil to 73% of mammals at Lambir Hills, Sarawak. Naturally, the enumeration of faunas in tropical sites is difficult, especially with regard to small mammals and bats. Thus, these comparisons remain crude. Nonetheless, it is evident that throughout the tropics considerable proportions of avian and mammalian faunas will be composed of species able to take advantage of figs as a dietary resource. However, a number of criteria must be met before the valid application of the keystone epithet.

Firstly, the existence of *Ficus* dispersal guilds means that the figs of a given *Ficus* species are not equally suitable, as food, for all frugivores in a given

area. Often, the keystone concept is applied to *Ficus* communities as a whole, rather than to individual species or eco-taxonomic units such as dispersal guilds (e.g. Kinnaird *et al.*, 1999). This approach is flawed. With the concept of dispersal guilds in mind, the presence of not only certain discrete types of *Ficus* but also of the frugivores that exploit these guilds must be confirmed. Secondly, as highlighted by Gautier-Hion & Michaloud (1989) and Borges (1993), the density of *Ficus* individuals affects which frugivores are able to exploit the resource. In both India and Gabon, species with small ranges were unable to exploit the widely distributed *Ficus* crops. Thirdly, non-fig food must be in limited supply for some or all the year for figs to be a valuable resource and the density of figs must be such that they can meet the demands such general food shortages create. Such a scenario has been demonstrated in Kalimantan (Leighton & Leighton, 1983) and on Barro Colorado Island, Panama (Foster, 1982*a, b*; Windsor *et al.*, 1989), although in the latter case, figs were also rare for part of the food shortage before reaching peak abundance. Conversely, Patel (1997) showed that peak *Ficus* fruiting coincided with that of non-*Ficus* species at two sites in India. For most other tropical sites, this level of information is not yet available. Considerably more data are required before conclusions can be drawn about the role of *Ficus* in maintaining frugivore populations in tropical forests.

In light of the above considerations, before application of the keystone resource epithet, future

research must take into account the availability of non-*Ficus* resources, *Ficus* density, fig phenology, and frugivore mobility, and confirm that figs are suitable for, available to, and required by the frugivores in question.

The potential role that *Ficus* species play in the conservation of tropical forest biodiversity is complicated by their unique pollination system, given the extent of anthropogenic habitat fragmentation. The species-specific relationship between figs and their pollinator wasps, and the short life spans of the latter, require that figs are available year round for pollinators to breed in. For this reason, populations of *Ficus* individuals numbering in their hundreds are necessary in order to maintain wasp populations (Anstett, Michaloud & Kjellberg, 1995). The low densities of many *Ficus* species indicate that such minimum viable populations (MVPs) occur over large areas, yet many protected areas in South-East Asia are not sufficiently large to meet the demands of Anstett *et al.*'s (1995) model (Mawdsley, Compton & Whittaker, 1998). However, recent research from Panama shows that fig wasps routinely carry pollen over distances of 10 km, indicating that *Ficus* breeding units exist over considerably larger areas than previously thought; in fact of an order of magnitude greater than those of any other plant species (Nason, Herre & Hamrick, 1996, 1998). The implication is that even low density *Ficus* populations may remain reproductively successful, so long as pollen arrives from distant source trees and that, following Mawdsley *et al.*'s (1998) conclusions, it may be necessary to conserve *Ficus* individuals outside of protected areas or even plant new *Ficus* plants there.

The MVP model of Anstett *et al.* (1995) and paternity analysis of Nason *et al.* (1996, 1998) concerned themselves with monoecious *Ficus* species and, as such, there is little reason to assume they will hold true for dioecious species, such are the differences in fig phenology and pollination biology between the two breeding systems. Given the higher population densities of the latter *Ficus* species but the apparent limited ability of their wasps to make regular long-distance pollination flights (Shanahan, 2000), an interesting area of research exists.

In light of the mass of information gathered here, perhaps a better understanding of their conservation importance can be summarised as follows. Functional groups (dispersal guilds) of *Ficus* species have the potential to act as keystone resources to subsets of frugivore communities (comprising generalist and/or specialist species) only if their figs are available

when other resources are scarce, and are accessible to these frugivores in terms of density of *Ficus* individuals and numerical abundance of figs. By attracting and sustaining animals which also feed on, and disperse seeds of, a diverse range of other fruits, *Ficus* guilds may have further roles in maintaining diversity of other plant species and in facilitating regeneration of disturbed habitats. However, these roles are likely to differ considerably between *Ficus* dispersal guilds and habitats. For example, in Borneo whereas large monoecious hemi-epiphytes are likely to be particularly important food resources in mature forests (see Lambert & Marshall, 1991), the smaller, dioecious, species characteristic of secondary growth are probably relatively more important in facilitating the regenerative process than in sustaining frugivore populations.

#### (7) The value and limitations of this database

The database assembled has several potential applications. Much of the data collected here come from zoologists' descriptions of animal diets (without reference to the effects these animals have on *Ficus* dispersal) or plant ecologists' incidental observations of frugivores (without allusion to the importance of figs for the animals). While the interests of the two groups of researchers have traditionally overlapped minimally (Howe, 1993), the information in this review can be used by either group. Furthermore, specialist primatologists, ornithologists and bat biologists can use the appendices (<http://go.to/figs>) to identify dietary overlap of their study animals with other groups of frugivores. Knowledge of the frugivore species that eat figs of a given *Ficus* species allows subsequent observations of the range of visitors to fig crops to be used as a rapid faunal inventory tool such that differences between observed and expected assemblages (based on local or regional faunal lists) may reveal deficiencies of certain frugivore taxa (M. Shanahan & S. G. Compton, in preparation).

Although the database is exceptional in breadth, it is lacking in depth and highlights the potential for future studies of figs and the animals that eat them. This research can be targeted towards the gaps in the literature discussed above. In particular, it is of interest to know not only which animals eat figs of a given species but also how reliable these animals are as potential seed dispersers and how important the figs are in their diets. Studies of any widespread *Ficus* species throughout its range are lacking, so we have

no idea of the extent to which species attract markedly different frugivore assemblages in different parts of their range. Nor do we know the form of the relationship between the size of regional frugivore assemblages, the size of assemblages present at individual crops and its consequences for fig dispersal rates. Such knowledge is pertinent to questions about coevolution between plants and dispersers and the implications of frugivore absence. For example, despite the local extinction of all the native avian frugivores that eat its figs elsewhere, *Ficus prolixa* persists on Mangaia (Cook Islands), presumably aided by dispersal generated by a fruit bat (Compton & McCormack, 1999).

Over two decades ago Janzen (1979) predicted that figs would 'quickly provide that animal-plant interaction in the tropics about which we know the most'. Whilst subsequent study, much of which is synthesised here, has gone some way towards elucidating fig-frugivore interactions, figs remain a fascinating subject in tropical ecology and the potential for considerable further research exists.

## V. CONCLUSIONS

(1) Figs are eaten by an impressive range of vertebrate frugivores, many of which are likely to act as seed dispersers to a greater or lesser degree.

(2) The diversity of fig-eaters arises because of the widespread distribution of *Ficus*, the year-round production of figs, considerable diversity in the manner in which figs are packaged and presented and because figs are easily consumed and have high levels of calcium.

(3) Figs are not equal resources for all frugivores but a system of partitioning exists such that discrete guilds of *Ficus* species share (and potentially compete for) subsets of a given frugivore community. Membership of dispersal guilds is determined by differences in fig packaging and presentation that are, in turn, governed largely by phylogeny.

(4) The 'keystone resource' concept must not be applied to figs without detailed consideration of fig density, frugivore ranging and confirmation that the figs in question are suitable for the frugivores in question.

(5) Gaps in the literature exist for certain frugivore taxa (e.g. ground birds, small rodents), regions (e.g. New Guinea, Sri Lanka), habitats (e.g. highland forests) and *Ficus* taxa (dioecious species in particular and members of sections *Adenosperma*, *Oreosyceae* and *Ficus*, in particular).

(6) There exists considerable potential for future research on the interactions between figs and frugivores.

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