

***Ficus* seed dispersal guilds: ecology, evolution and
conservation implications**

MICHAEL J. SHANAHAN

Submitted in accordance with the requirements for the degree of Doctor of Philosophy

The University of Leeds
Centre for Biodiversity and Conservation
School of Biology

December 2000

The candidate confirms that the work submitted is his own and that appropriate credit
has been given where reference has been made to the work of others

ACKNOWLEDGEMENTS

Firstly, I wish to thank my supervisor, Dr Steve Compton, for initially turning me on to the genus *Ficus* and for his guidance throughout my doctorate, especially during the write-up period. This research was conducted whilst I was a visiting research fellow at the Institute of Biodiversity and Environmental Conservation (IBEC) at Universiti Malaysia Sarawak (UNIMAS). For my appointment to this post I thank Professor Ghazally Ismail and Dr Stuart Davies and, for administrative help at UNIMAS, Yaziz and Dayang.

Fieldwork conducted in Sarawak was undertaken with permission of the Forest Department Sarawak and for this I thank, in particular, Abdul Abang Hj. Hamid and Sapuan Hj. Ahmad. Logistical support in Lambir was provided by Johan and Mr Abdullah. Canopy studies were greatly aided by permission to use the walkways and towers of the Canopy Biology Program in Sarawak and I wish to acknowledge the assistance of Professor Tohru Nakashizuka and the late Professor Tamiji Inoue. For permission to live in the "American house" in Lambir I am grateful to the Center for Tropical Forest Science (Smithsonian Tropical Research Institute) and in particular, Drs Jim La Frankie and Elizabeth Losos.

My work in Borneo was greatly aided by my first-rate research assistant Siba anak Aji whose constant hard work and high spirits were an inspiration to me. Further assistance was provided by Ruby and Hazel Oakley. Much of my Bornean research would not have been possible without the previous research and assistance of Rhett Harrison, to whom I am highly grateful.

Life in the house in Lambir was made fun and interesting by the presence, at various times, of Rhett Harrison, Igor and Sophie Debski, Matt Potts, Tristram Seidler, Chuck Cannon, Supinda Bunyanavich, Hazel Oakley, Jose Nieto, Lisa de Lissio, Jenn Smith and Tim Laman, Kenta Tanaka, Yoko Inui, Kaori Murase, Kaori Sato, Aya Hatada, Yamauchi, Hideo and Michiko Nakagawa. The generosity and hospitality of my Iban neighbours, particularly Siba and family, Mama Susi, Mama Franklin and Ukat were greatly appreciated, as was all of the *tuak*.

Chapter 6, on the figs of Long Island, was the result of a collaboration with Dr Rhett Harrison (Kyoto University), Ruby Yamuna (University of Papua New Guinea) and Professor Ian Thornton (La Trobe University). I am extremely grateful to Professor Thornton for inviting me to join the National Geographic funded research trip to Long Island. The other participants on the expedition (Simon Cook, Clinton Schipper, Ross Moore, Professor John Edwards, Rose Singadan and William Boen) ensured that we had good laughs and good poker in the face of the various calamities we endured. The management and staff of Jais Aben Resort provided assistance before and after our time on Long Island and sent emergency food supplies. Thanks are also due to the Christensen Research Institute (Madang) for access to their library and the Forest Research Institute in Lae for identification of specimens.

Chapter 7, the global review of fig-eating by vertebrates, was completed in collaboration with Samson So (University of Hong Kong) and made use of unpublished data and other assistance kindly provided by many researchers to whom I am extremely grateful. These are alphabetically, Rauf Ali, Des Allen, Paul Aston, Ramana Athreya, Vidya Athreya, Yves Basset, Mark Bayley, Cornelis Berg, David Bishop, Lien-Siang Chou, Steve Compton, Ed Colijn, Nancy Lou Conklin-Brittain, James Cook, Richard Corlett, Jared Diamond, Ellen Dierenfeld, Françoise Dowsett-Lemaire, Dan Eisikowitch, R. Farrah, Mauro Galletti, Harish Gaonkar, Jennifer Garrison, Marc Gibernau, David Gorchov, Jaco Greeff, Tristan Guillosson, Britta Denise Hardesty, Allen Herre, Dan Hoare, Matt Heydon, Andrew Mack, Carmi Korine, Nick Helme, Ridwan Jafar, Rajah Jayapal, Elisabeth Kalko, Dhanjaya Katju, Ragupathy Kannan, Margaret Kinnaird, Cheryl Knott, Tim Laman, Mark Leighton, Carlos Machado, Tim Male, Kim McConkey, James MacPherson, Vojtech Novotny, James Paterson, Carlos Peres, Andrew Plumtre, Pilai Poonswad, Jackie Pritchard, S.M.A. Rashid, Vernon Reynolds, Monica Romo, Jana Schulz, Scott Silver, Ana Sosa-Asanza, Hugh Spencer, Sam Stier, S. Subramanya, Jingchuan Sun, Vivek Tawari, John Terborgh, Ian Thornton, George Weiblen, Robert Whittaker and David Wilson.

The research was funded largely by the States of Jersey Education Committee to which I am most grateful. I am also grateful for additional funding in the form of a Bat Conservation International Student Scholarship (1998) and Water Chicken Foundation Travel Bursary.

This thesis and publications arising from work described here benefited from discussions with many individuals especially John Altringham, John Grahame, Allen Herre, Dan Hoare, Nick Mawdsley, Jamie Moore and Jo Wong. I am also extremely grateful to Dr Andrew Carter for providing me with a home during the important final two months of my doctorate.

Finally, I would like to thank my parents, Jennifer and John Shanahan, for all their love and support over the years I have spent in Leeds and overseas in the process of creating this thesis.

ABSTRACT

Ficus (Moraceae) is a large plant genus of considerable ecological, evolutionary and conservation interest. This study focused on the interaction between *Ficus* species and the vertebrates that eat their fruit (figs), thereby acting as potential seed dispersers. Specifically, the study considered this interaction with regard to the mechanisms that allow different guilds of sympatric *Ficus* species to attract differentially subsets of frugivore communities.

Fig packaging and presentation was studied in Borneo and on an island off New Guinea, the former study, of 43 *Ficus* species represents the largest ever characterisation of the fruiting ecology of sympatric congeners. The *Ficus* species studied exhibited considerable diversity in the size, colour, texture, height, water content, seed burden and relative yield of their figs. In both sites, figs were eaten by a large proportion of the vertebrate fauna present. However, that frugivores were not equally attracted to each *Ficus* species provided evidence of *Ficus* dispersal guilds. Guild membership was determined by differences in fig packaging and presentation, with fig size, colour and height of presentation being the strongest predictors of frugivore attraction. These traits, and therefore guild membership, showed strong phylogenetic associations. Nonetheless, apparent adaptations to seed dispersers were also documented.

The differential attraction of frugivores means not only that competition for dispersal agents is reduced between guilds but also that guilds of *Ficus* species experience markedly different seed dispersal services from the frugivores they attract. These differences occur in terms of the number and diversity of frugivores attracted, the proportion of figs that are eaten by seed-predatory frugivores and the distance, density and heterogeneity of seed rain. *Ficus* species that attract relatively small subsets of frugivore communities (such as fruit bats, or large arboreal mammals) which are prone to anthropogenic threats face decreased seed dispersal associated with the continuing decline of these frugivores. Dependence for dispersal on subsets of frugivore communities also means that *Ficus* species differ in their abilities to colonise degraded habitats. A 12 month study of the phenology of fig production in the Bornean field site demonstrated that fig crops are initiated year-round and are thus a valuable resource for fruit-eating animals. However, patterns of fig production were not equal between *Ficus* species (because of a lack of pollination for some) and, so, the availability of the fig resource varied for the different animal groups attracted to each of the *Ficus* guilds.

Globally, figs are eaten by at least ten percent of all bird species and six percent of all mammal species, many of which are capable of dispersing *Ficus* seeds. That these frugivores also disperse the seed of many other plant species appears to support the suggestion that *Ficus* species are of great conservation status. However, the 'keystone resource' epithet applied to figs as a whole need to be re-assessed as I show that, because of fig-frugivore partitioning, *Ficus* species are not equal resources for vertebrate frugivores.

TABLE OF CONTENTS

ACKNOWLEDGEMENTS	i
ABSTRACT	iii
TABLE OF CONTENTS	iv
LIST OF FIGURES	viii
LIST OF TABLES	x
PAPERS ARISING FROM THIS THESIS	xii
DECLARATION	xiii
GLOSSARY	xiv
CHAPTER 1	
GENERAL INTRODUCTION	
1.1 THE BIOLOGY OF <i>Ficus</i> SPECIES	1
1.2 MUTUALISM AND CO-EVOLUTION	2
1.3 FRUGIVORY AND SEED DISPERSAL	2
1.4 FRUIT SYNDROMES AND ECOLOGICAL GUILDS	3
1.5 THE SCOPE OF THIS THESIS	4
CHAPTER 2	
DESCRIPTION OF STUDY SITES	
2.1 LAMBIR HILLS NATIONAL PARK, SARAWAK, MALAYSIA	5
2.2 LONG ISLAND, PAPUA NEW GUINEA	5
CHAPTER 3	
PACKAGING AND PRESENTATION OF BORNEAN FIGS	
3.1 INTRODUCTION	7
3.2 METHODS	7
3.2.1 Sampling	7
3.2.2 Fig design and presentation	8
3.2.3 Data analysis	8
3.3 RESULTS	8
3.3.1 Species studied	8
3.3.2 The diversity of fig design and presentation	9
3.3.3 Associations between traits	18
3.3.4 Fruit syndromes	24
3.4 DISCUSSION	28
3.4.1 The diversity of fig design and presentation	28
3.4.2 Differences between monoecious and dioecious figs	28
3.4.3 Fruit syndromes in <i>Ficus</i>	28
CHAPTER 4	
SEED DISPERSAL GUILDS IN A BORNEAN <i>Ficus</i> COMMUNITY	
4.1 INTRODUCTION	31
4.2 METHODS	31
4.2.1 Sampling	31
4.2.2 Identification of frugivores	31
4.2.3 <i>Ficus</i> dispersal guilds	31
4.3 RESULTS	32
4.3.1 Sampling effort	32
4.3.2 Vertebrate frugivore diversity	32
4.3.3 <i>Ficus</i> dispersal guilds	40
4.3.4 Determinants of <i>Ficus</i> guild membership	49
4.4 DISCUSSION	52
4.4.1 The diversity of fig-eaters	52
4.4.2 <i>Ficus</i> dispersal guilds	52
4.4.3 The predictive power of fruit traits	53
4.4.4 Implications for competition	53
4.4.5 Implications for seed dispersal	53
4.4.6 Conclusion	54
CHAPTER 5	
<i>Ficus</i> DISPERSAL GUILDS AND FIG PHENOLOGY	
5.1 INTRODUCTION	55

5.2 METHODS	55
5.3 RESULTS	56
5.4 DISCUSSION	62
CHAPTER 6	
<i>Ficus</i> DISPERSAL GUILDS AND THE COLONISATION OF VIRGIN ISLANDS IN PAPUA NEW GUINEA	
6.1 INTRODUCTION	63
6.2 METHODS	63
6.3 RESULTS	64
6.4 DISCUSSION	71
CHAPTER 7	
FIG-EATING BY VERTEBRATE FRUGIVORES: A GLOBAL REVIEW	101
7.1 INTRODUCTION	101
7.2 METHODS	102
7.3 RESULTS	103
7.3.1 The quality of the dataset	103
7.3.2 Who eats figs?	103
7.3.3 Are fig-eaters effective seed-dispersers?	110
7.3.4 <i>Ficus</i> fruit syndromes and dispersal guilds	129
7.4 DISCUSSION	130
7.4.1 The quality of the dataset	130
7.4.2 Who eats figs?	131
7.4.3 Why are there so many fig-eaters?	132
7.4.4 Are fig-eaters effective seed-dispersers?	134
7.4.5 <i>Ficus</i> fruit syndromes and dispersal guilds	134
7.4.6 Figs as keystone resources	135
7.4.7 The value and limitations of this database	136
CHAPTER 8	
GENERAL DISCUSSION	139
8.1 Fig packaging and presentations	139
8.2 Patterns of frugivore attraction	140
8.3 Ecological and conservation implications of <i>Ficus</i> seed dispersal guilds	142
8.4 Conclusions	143
REFERENCES	145
APPENDIX 1	
VERTEBRATES OF LAMBIR HILLS NATIONAL PARK	187
APPENDIX 2	
FIG VARIABLES USED IN THE CALCULATION OF PULP WATER CONTENT, RELATIVE YIELD AND SEED BURDEN	197
APPENDIX 3	
VERTEBRATE SPECIES AND GENERA FROM LAMBIR HILLS NATIONAL PARK FOR WHICH FIG-EATING HAS BEEN RECORDED, IN ADDITION TO THOSE OBSERVED IN THIS STUDY	198
APPENDIX 4	
FIG SIZE INDICES	199
APPENDIX 5	
<i>Ficus</i> SPECIES AND THEIR KNOWN FRUGIVORES	200
APPENDIX 6	
FIG-EATING SPECIES AND THE FIGS THEY CONSUME	210

DECLARATION

This thesis involved collaborations with Rhett Harrison (RH), Ruby Yamuna (RY) and Samson So (SS).

Chapter 6.

Some of the collections of *Ficus* specimens on Long Island and Motmot were made by RH and RY. RH also made valuable suggestions to the text of the chapter, which has been submitted for publication as: Shanahan, M., Harrison, R. D., Yamuna, R., Boen, W. & Thornton, I. W. B. (in review). Colonisation by *Ficus* species of a devastated volcanic island (Long Island, Papua New Guinea) and the emergent islet in its caldera lake. *Journal of Biogeography*.

Chapter 7.

SS located some of the records of fig-eating by vertebrates used in Chapter 7 and Appendices 5 and 6, and submitted for publication as: Shanahan, M. & So, S. (in review). Fig-eating by vertebrate frugivores: a global review. *Biological Reviews*. Other, unpublished, data were donated by a number of additional researchers listed in the thesis acknowledgements.

PAPERS ARISING FROM THIS THESIS

The following papers have arisen directly from the research documented in this thesis:

1. SHANAHAN, M. & Compton, S. (2000). Fig-eating by Bornean treeshrews (*Tupaia* spp.): evidence for a role as seed dispersers. *Biotropica* 32, 759-764.
2. SHANAHAN, M. & Compton, S. G. (2001). Vertical stratification of figs and fig-eaters in a Bornean lowland rainforest: how is the canopy different? *Plant Ecology* [in the press] [presented by S. Compton as an oral paper at the European Science Foundation Tropical Forest Canopies Meeting in Oxford, December 1998]
3. SHANAHAN, M. & Debski, I. (in press). Vertebrates of Lambir Hills National Park, Sarawak, Malaysia. *Malayan Nature Journal*
4. SHANAHAN, M., So, S., Compton, S. & Corlett, R. (in press). Fig-eating by vertebrate frugivores: a global review. *Biological Reviews*.
5. Schipper, C., SHANAHAN, M., Cook, S. & Thornton, I. W. B. (in press). Colonisation of an exploded island volcano (Long I, Papua New Guinea) and the emergent island, Motmot, in its caldera lake. III. Birds. *Journal of Biogeography*.
6. SHANAHAN, M., Harrison, R. D., Yamuna, R., Boen, W. & Thornton, I. W. B. (in press). Colonisation of an exploded island volcano (Long I, Papua New Guinea) and the emergent island, Motmot, in its caldera lake. V. Colonisation by figs. *Journal of Biogeography* [presented as an oral paper at the Sixth International Conference on Fig Biology, Cape Town, September 2000]
7. SHANAHAN, M. & Compton, S. G. (in review). Fruiting strangler figs reveal declines in large frugivores in a protected Bornean rain forest. *Conservation Biology*
8. SHANAHAN, M. & Compton, S. G. (in prep.). *Ficus* seed dispersal guilds in a Bornean lowland rain forest [presented as an oral paper at the Sixth International Conference on Fig Biology, Cape Town, September 2000]
9. SHANAHAN, M. & Compton, S. G. (in prep.). Interactions between invertebrates and *Ficus* species in a Bornean lowland rain forest.

GLOSSARY

assemblage	the frugivore species that feed upon a <i>Ficus</i> species' ripe fig crop and potentially disperse the species' seeds
cauliflorous	describes the presentation of figs on a tree's main trunk rather than on leafy branches
dispersal guild	A group of plant species that attract the same frugivore species as potential seed dispersers
fig	The hollow, urn-like reproductive structure produced by all <i>Ficus</i> species. The fig is lined by tiny flowers and acts firstly as an inflorescence and following pollination and seed developed as a fruit (see syconium)
frugivore	any animal that consumes fruit
fruit syndromes	covarying fruit character complexes associated with the attraction of subsets of frugivore communities as seed dispersers e.g. 'bird fruits' being red, soft and small
geocarpic	describes the presentation of fruit on runners that originate at the base of a tree and may even travel below the soil
growth form	The physical form of a plant. Among <i>Ficus</i> species, growth forms exhibited include free-standing trees, hemi-epiphytes , shrubs and climbers
guild	A group of coexisting species that use resources in a very similar manner and (potentially) compete for these shared resources to a greater extent with members of the same guild than with members of other guilds. See dispersal guild
hemi-epiphyte	the term for the growth form of <i>Ficus</i> individuals that germinate in canopy microsites on host trees (and are thus epiphytes) before sending aerial roots down to the ground. These individual are often called strangler figs
keystone species	one whose impact on its community is large and disproportionately large to its abundance (Power <i>et al.</i> , 1996)
phenology	the study of periodic biological phenomena, in this case the production of fig crops
seed dispersal	the movement of seeds away from the parent tree (Janzen, 1983d)
seed predator	an animal that feeds on, and therefore kills, seeds
strangler fig	term for some hemi-epiphytic <i>Ficus</i> species capable of killing their host tree and becoming free-standing as a result
syconium	The botanical term for the fig. Henceforth, in accordance with Janzen's (1979) convention, the terms 'fruit' and 'fig' shall be used in place of the term syconium

CHAPTER 1

GENERAL INTRODUCTION

“Wicked fig-tree, equality puzzle, with your self-conscious secret fruits”
D.H. Lawrence: Bare Fig-Trees
Lawrence (1928)

This study is concerned with the interactions between fruit-producing plants and fruit-eating animals. Specifically, the study focuses on a single diverse plant genus of conservation importance, the fig plants (*Ficus* spp; Moraceae), in an attempt to understand how and why plant species have evolved disparate seed dispersal strategies, and what the implications of this diversity are. This chapter serves to introduce the concepts relevant to the thesis and to summarise the considerations of each subsequent chapter.

1.1 THE BIOLOGY OF *Ficus* SPECIES

With c. 750 species exhibiting a variety of growth forms that includes shrubs, trees, climbers, epiphytes and hemi-epiphytic stranglers, *Ficus* is arguably the world’s most diverse woody plant genus (Corner, 1988; Berg, 1989). The characteristic *Ficus* inflorescence (the fig) is remarkably uniform in structure. Differences do occur, however, in terms of the way that figs are packaged and 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 the leaf axils (Corner, 1988). Furthermore, two breeding systems, monoecy and functional dioecy occur among *Ficus* species, with half the individuals of dioecious species producing figs that contain no, or very few, seeds (Anstett *et al.*, 1997). *Ficus* is distributed largely in the tropics and subtropics and can be divided, taxonomically, into two main groups (Table 1.1). One group, comprising the subgenera *Urostigma* and *Pharmacosycea*, consists of about 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 c. 350 species in subgenus *Ficus* are dioecious (Corner, 1965; Berg, 1989). Corner's (1965) classification is currently under revision by Professor C. Berg but is retained for the purposes of this thesis.

Ficus species are, perhaps, best known for their relationship with pollinating wasps (Hymenoptera, Agaonidae) which, with few exceptions (see Michaloud *et al.* 1996), are species-specific (Wiebes, 1979). The following description of fig pollination draws upon the work of Galil and Eisikowitch (1968, 1969). Tiny, pollen-bearing, female wasps enter the fig through a narrow, bract-covered passage (the ostiole) and pollinate the miniature flowers lining the inner surface. The wasp simultaneously attempts to lay eggs by inserting its ovipositor down the styles. Ovaries on which an egg is deposited form a gall, within which the wasp larvae feed and develop. Ovaries missed by the wasp but which receive pollen develop into seeds normally. Approximately one month later the adult wasps emerge from their galls and mate inside the fig. The females then collect pollen and depart in search of a fig in which to oviposit. Meanwhile the natal fig softens, sweetens and often changes colour to form the characteristic fig fruit (Galil & Eisikowitch, 1968, 1969). In dioecious figs the life cycle differs slightly in that there are separate male and female trees. In male trees the female flowers are modified to receive a wasp egg, and usually only wasps and pollen are produced. In female trees the wasps enter the fig but are unable to lay eggs because the flower styles are too long or fragile and the shape of their stigmas makes oviposition difficult. The wasps therefore fail to reproduce and only seeds develop (Galil, 1973).

Table 1.1 Subgenera and sections of *Ficus*. Approximate numbers of species in each section taken from Berg (1989), following Corner's (1965) classification.

subgenus	section	n species
<i>Ficus</i>	<i>Adenosperma</i>	23
<i>Ficus</i>	<i>Ficus</i>	60
<i>Ficus</i>	<i>Kalosyce</i>	20
<i>Ficus</i>	<i>Neomorphe</i>	6
<i>Ficus</i>	<i>Rhizocladus</i>	55
<i>Ficus</i>	<i>Sinosycidium</i>	1
<i>Ficus</i>	<i>Sycidium</i>	104
<i>Ficus</i>	<i>Sycocarpus</i>	81
<i>Pharmacosycea</i>	<i>Oreosycea</i>	50
<i>Pharmacosycea</i>	<i>Pharmacosycea</i>	20
<i>Sycomorus</i>	<i>Sycomorus</i>	13
<i>Urostigma</i>	<i>Americana</i>	120
<i>Urostigma</i>	<i>Conosycea</i>	65
<i>Urostigma</i>	<i>Galoglychia</i>	75
<i>Urostigma</i>	<i>Leucogyne</i>	2
<i>Urostigma</i>	<i>Malvanthera</i>	20
<i>Urostigma</i>	<i>Stilpnophyllum</i>	1
<i>Urostigma</i>	<i>Urostigma</i>	20
	total	736

Unpollinated figs are eventually aborted and the production of fig fruit is therefore dependent on the presence of pollinator wasps. Conversely, the wasp is only able to reproduce inside a fig. Moreover the wasp has a very short adult life span, usually just one or two days (Kjellberg *et al.*, 1988; Compton *et al.*, 1994a) and is therefore dependent on the presence of receptive figs when it emerges.

Because of each fig species' need to maintain a supply of these pollinator wasps, ripe figs can be found year-round and so have been described as 'keystone resources' in those tropical forests where they are capable of sustaining frugivores through lean periods of low fruit availability (Leighton & Leighton, 1983; Terborgh, 1986; Lambert & Marshall, 1991; but see Gautier-Hion & Michaloud, 1989; Borges, 1993 for evidence to the contrary). The extirpation of such keystone resources is predicted to precipitate a cascade of further extinction (Terborgh, 1986).

The diversity of *Ficus* species is reflected in that of the range of animals recorded eating figs. These include; fishes, lizards, tortoises, civets, bears, birds, primates, treeshrews, rodents, deer and fruit bats (e.g. Ridley, 1930; Baker & Baker, 1936; van der Pijl, 1957; McClure, 1966; Hnatiuk, 1978; Mondolfi, 1989; Traveset, 1990; Emmons, 1991; Heydon & Bulloh, 1997; Horn, 1997). This list is by no means exhaustive but serves to illustrate Janzen's (1979) contention that figs provide an important dietary component for more animal species than the fruit of any other tropical genus. Many, although not all, of these frugivores act as *Ficus* seed dispersers. A detailed global review of fig eating and seed dispersal forms the penultimate chapter of this thesis.

1.2 MUTUALISM AND COEVOLUTION

Ecological interactions between species can be classified according to the relative benefits to each participant and when both participants benefit the interaction is termed a mutualism. Mutualism generally involves the provision of a service by one participant in return for a payment by the other. Janzen (1985b) identified the four main types of mutualism in nature to be harvest mutualisms (e.g. the cellulose-digesting gut flora of termites), pollination mutualisms, protection mutualisms (e.g. many ant-plant relationships) and seed dispersal mutualisms. Both facultative and obligate mutualisms exist and in the latter case interactions tend to be specific relationships, involving just a pair (or closely related set) of interactants (Janzen, 1985b). Diffuse mutualisms, in which groups of participants interact with each other, also occur. Relationships between *Ficus* species and their specific pollinator wasps are examples of the former type of mutualisms (although molecular studies of some *Ficus* species suggest that the one-one relationship is not universal; D. Molbo, pers. comm.). Conversely, the mutualistic interactions that occur between groups of *Ficus* species and groups of frugivores are of a diffuse nature.

The interactants in mutualisms (as in other ecological relationships) often exhibit traits that appear to have evolved under selection from the mutualist, and vice versa. Such coevolution (Ehrlich & Raven, 1964; Janzen, 1980) is more likely between members of obligate, and specific (i.e. one to one) mutualisms. 'Diffuse coevolution' (*sensu* Janzen, 1980) may occur between suites of species or populations that exert selective pressure in concert. However, as Janzen (1980) warns, coevolution and mutualism are not synonymous and many adaptations considered to be coevolved may have already been present before the initiation of a given mutualism. Rather, such traits may simply limit the nature of interactions possible in a given situation. Multi-species mutualisms have not necessarily evolved as a mutualism but may be cases of what Janzen (1985a) calls 'ecological fitting', simply an ability for species that happen to co-occur to interact in a certain way without having had a shared evolutionary history.

This study considers the mutualism of frugivory and seed dispersal in which plants provide a payment, in the form of fleshy fruit, to animals that eat the said fruit and, in doing so, disseminate the seeds within. In the following sections I review the ecology of seed dispersal and introduce the proposed coevolutionary aspects of this interaction.

1.3 FRUGIVORY AND SEED DISPERSAL

Seed dispersal has been defined as 'the movement of seeds away from the parent tree' (Janzen, 1983d), and can be mediated by gravity, wind, ocean currents, or the foraging activities of seed- or fruit-eating animals. Of the latter form of seed dispersal a distinction can be made between exozoochory, whereby seeds become attached to the external parts of an animal only to be later deposited and endozoochory, dispersal resulting from ingestion and subsequent regurgitation or defecation of seeds. The study is concerned with endozoochory, to which the remainder of this section shall be devoted.

Between 50 and 90% of the woody plants in tropical forests produce fleshy fruits as attractive rewards to potential vertebrate seed-dispersers (Frankie *et al.*, 1974; Fleming, 1979; Howe and Smallwood, 1982). Clearly, this ecological interaction is sufficiently widespread to be assumed important in structuring tropical forest communities and maintaining biodiversity. Beyond aiding the natural maintenance of biodiversity, the dispersal of seeds by fruit-eating animals has the potential to ameliorate anthropogenic damage by facilitating regeneration of disturbed forest (e.g. Whittaker & Jones, 1994).

Frugivores can disperse seeds in a number of ways. Seeds may be ingested and later regurgitated or defecated (true endozoochory). Alternatively, whole fruits or portions thereof may be carried and dropped by foraging frugivores. Finally seeds may be discarded during feeding and dropped without having been ingested and before being transported away from the tree. This is, nonetheless, still classed as seed dispersal according to Janzen's (1983d) definition. Once a seed has been dispersed by one of the above processes, its dissemination may not be complete, as secondary dispersal may follow the initial movement. Any species feeding on fallen fruit or seeds have potential to act as secondary dispersers, the most commonly cited examples for *Ficus* species being ants (Roberts & Heithaus, 1986; Athreya, 1996; Laman, 1996b). Indeed, some studies suggest that fig seeds have structures (elaiosomes) that are adaptations to secondary dispersal by ants (Kaufmann *et al.*, 1991).

Seed dispersal through frugivory has been described or proposed for a wide variety of vertebrates, including fruit bats, carnivores, fish, lizards, frogs, primates, tortoises, birds (both volant and flightless), elephants, extinct megafaunal mammals, rodents and deer (e.g. Ridley, 1930; van der Pijl, 1957; Janzen & Martin 1982; Fialho, 1990; Willson, 1993; Yumoto *et al.*, 1995). The currencies of this mutualism are fruit pulp provided in return for seed-dispersal services. In human terms, if payment is offered in advance of a job's completion a customer is exposed to capricious cowboys and con-artists. Similarly, because fruit-pulp rewards can be eaten before the act of seed dispersal, plants are prone to experience a variable seed dispersal service from their associated frugivores. Indeed, vertebrate seed-predators, e.g. parrots (Janzen, 1981; Jordano, 1983) and pulp thieves (Howe & Vande Kerckhove, 1981) are able to take advantage of fruit produced without contributing to seed dispersal. In reality, the distinction between outright seed-predators and beneficial dispersers is not clear (Janzen, 1971) as animals' effects on seeds are not of a binary (destroy all or disperse all) nature. An example serves to illustrate some of the complexity involved in elucidating

a given frugivore's role in seed dispersal. *Treron* and *Chalcophaps* pigeons in South-East Asia are widely cited as seed-predators (e.g. Cowles and Goodwin, 1959; Crome, 1975). Nonetheless, small proportions of ingested *Ficus* seeds can survive gut passage of Emerald Doves (*C. indica*), and some Thick-Billed Green-Pigeons (*T. curvirostra*) lack the gizzard grit that assists their seed destruction (Lambert, 1989c). 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 potential to outweigh the disadvantages of low seed survival.

The proposed advantages of seed-dispersal (as opposed to seeds falling below parent trees) include direction to specific germination micro-habitats, colonisation of new areas, and avoidance of density-related predation and competition near the source tree (Janzen, 1970; Howe & Smallwood, 1982; Dirzo & Domínguez, 1986). These suggested advantages prompted ecologists' attempts to define characteristics of hypothetically ideal dispersal agents. Among these are the removal of seeds from the vicinity of source plants, their delivery (unharmful) to habitats suitable for germination and growth, and crop visitation on a regular basis (McKey, 1975; Howe & Estabrook, 1977). Because so many frugivore taxa disperse seeds, the ways in which they differ in this role is of interest. For example, Fleming and Sosa (1994) suggest that rather than their deposition of seeds in appropriate sites, mammalian contributions to seed-dispersal are a function of large numbers of fruit eaten and distances moved. Conversely, Compton *et al.* (1996) argued that mammals provided a higher quality dispersal service compared to birds' high quantity. Are these taxonomic generalisations valid or do frugivores vary as seed dispersers for different reasons such as size, ability to fly or commitment to frugivory? Indeed, are variations in seed dispersal dependent on plant traits rather than those of frugivores?

In order to address such questions and make genuine comparisons of differential contributions to seed-dispersal, a conceptual framework is required which considers the range of relevant interacting factors, whilst also allowing development of standard methodologies for systematic and comparative study. Such a framework was suggested by Schupp (1993), partly in response to increasingly perplexing uses of terminology to describe animals' roles as seed-dispersers. Schupp rationalised the semantic confusion with the introduction of the concept of seed-dispersal 'effectiveness', the product of quantitative and qualitative components, i.e.,

$$\text{Effectiveness} = (\text{Quantity}) \times (\text{Quality}),$$

in which 'Quantity' represents the number of seeds dispersed and 'Quality' the likelihood of a dispersed seed producing a new reproductive adult.

In Schupp's (1993) framework, the two components of seed-dispersal effectiveness are further subdivided into a hierarchy of more easily studied constituents (Figure 1.1). The quantity of seeds dispersed by a given frugivore depends on the number of visits made to the fruiting plant and the number of seeds dispersed per visit. The former depends on the species' abundance, its reliability of visitation and its diet, whilst the latter is conditional 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 distance, direction, habitat and microsite of seed-placement as well as the 'dispersal environment', i.e. the number and species identity of seeds co-dispersed.

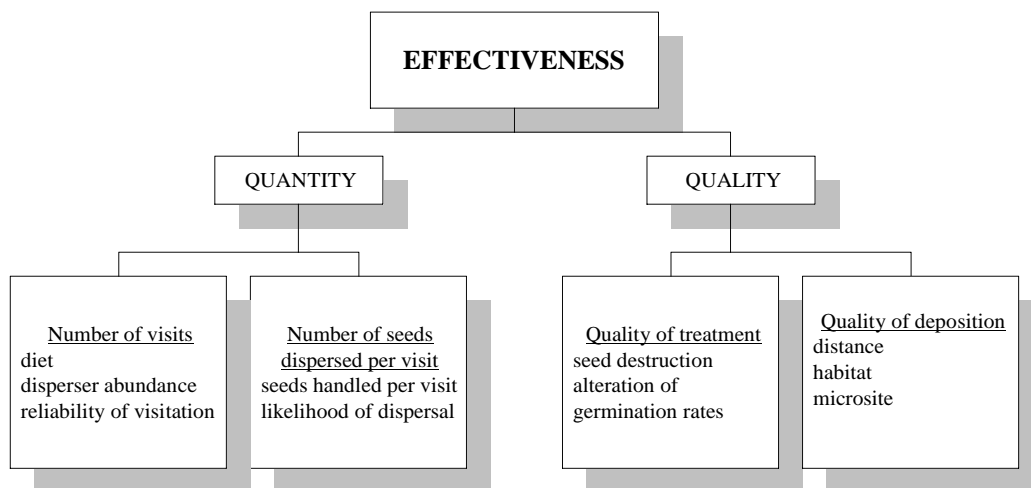


Figure 1.1 The components of seed dispersal effectiveness (based on Schupp, 1993).

1.4 FRUIT SYNDROMES AND ECOLOGICAL GUILDS

There exists among frugivores and the plant species the fruit of which they eat a pattern of subdivision such that a given frugivore does not feed upon all sympatric fruit species, nor is a given plant fed upon by all frugivores present. Rather, it is convenient to consider the interacting species in terms of ecological guilds (*sensu* Root, 1967). Guilds may be defined as functional groups of coexisting species that use resources in a very similar fashion (Joern and Lawlor, 1981). Central to the guild concept is the notion that members of a given guild interact relatively strongly with each other and relatively weakly with members of other guilds. Such interaction usually takes the form of competition. Ecological guilds have been identified, described or proposed for (amongst others) grasshoppers, insect pollinators, lizards and woodland birds (Pianka, 1973; Ulfstrand, 1977; Joern & Lawlor, 1981; Momose & Inoue, 1994). Similarly, one may recognise guilds of frugivore species sharing, and competing for, certain types of fruit resource (e.g. Smythe, 1986). As a corollary, the plant species fed upon may be considered

to share (and compete for) a disperser resource, in the form of their attendant frugivores (Wheelwright, 1985). Such dispersal guilds are of central interest in this thesis.

Guild membership is likely to be largely determined by the interplay between frugivore foraging ecology and plants' fruiting ecology. Considerable interspecific diversity exists in the manner in which fleshy fruits are packaged and presented. The most obvious sources of variation are size, colour, and shape. However, similar variety exists in numerous other fruit traits, including seed size and number, pulp: seed ratio, fruit position, synchrony of ripening and nutrient content (Ridley, 1930; van der Pijl, 1982; Herrera, 1981, 1987; Snow & Snow, 1988). Studies of these fruit characteristics suggest the existence of fruit syndromes, covarying character complexes proposed to have evolved in response to selection by broad frugivore guilds (e.g. Ridley, 1930; van der Pijl, 1957; O'Dowd and Gill, 1986). For example, 'bird-fruits' are classically described as being small, brightly coloured and presented amongst foliage (Ridley, 1930; Turcek, 1963; Snow, 1981; van der Pijl, 1982) whilst 'bat-fruits' are commonly green, odoriferous and presented away from the foliage (van der Pijl, 1957; Marshall, 1985). Syndromes of fruit-traits have also been recognised in relation to other frugivore guilds including rodents, primates, ungulates and carnivores (e.g. Ridley, 1930; Gautier-Hion *et al.* 1985; Herrera, 1989; Yumoto *et al.*, 1995). However, traits that encourage the attraction of certain frugivore taxa over others are not necessarily coevolved. Rather, observed traits may occur because of selection pressures related to other aspects of plant species' biology, or phylogenetic constraint (Wheelwright & Orians, 1982; Bremer & Eriksson, 1992; Fischer & Chapman, 1993; Jordano, 1995).

Two *Ficus* guilds have been recognised on Barro Colorado Island, Panama (Kalko *et al.*, 1996; Korine *et al.*, 2000). The first guild comprises species with green figs that are attractive to bats and the second group of species produced red figs attractive to birds. 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. Preliminary fieldwork (Shanahan, 1997) suggested that among Bornean *Ficus* species different groups of species are fed upon and thus dispersed by different groups of frugivores and that the dispersal guild structure is more complex in Borneo than in the Neotropics. Further investigations of these putative *Ficus* and frugivore guilds form the central theme of this thesis.

1.5 THE SCOPE OF THIS THESIS

Targets of conservation-oriented ecological research of seed-dispersal by frugivorous animals include the identification of important seed-dispersers and fruit resources, the examination of the structure of the seed-dispersal mutualism across broad taxonomic groups, and the development of informed management strategies. From an evolutionary perspective, understanding how frugivores vary in their relative contributions to seed-dispersal is important in terms of understanding the development and maintenance of their mutualism with fruiting plants. The following general questions form the central themes of this thesis.

1. How do *Ficus* species vary in the packaging and presentation of their fig fruit?
2. How is variety linked to *Ficus* breeding systems (monoecy and dioecy) and taxonomy?
3. Are fig traits correlated?
4. Which vertebrate species eat figs?
5. Are these vertebrates effective seed dispersers?
6. What fig traits influence the size and composition of frugivore assemblages attracted to crops of different *Ficus* species?
7. Are the concepts or fruit syndromes and dispersal guilds applicable to *Ficus* species?
8. What are the implications of the existence of *Ficus* seed dispersal guilds?
9. Are *Ficus* species of keystone importance to fruit-eating vertebrates?

Chapter 2 describes the study sites, Lambir Hills National Park (Sarawak, Malaysia) and Long Island (Papua New Guinea), where original field data presented here were collected. The majority of the fieldwork was undertaken at the former site and is presented in Chapters 3 - 5.

Chapter 3 details the diversity of fig packaging and presentation in Lambir Hills National Park. In this chapter I make comparisons between monoecious and dioecious *Ficus* species and seek evidence of fruit syndromes among the species studied. In Chapter 4 I identify the frugivore assemblages attracted to different *Ficus* species and describe the *Ficus* dispersal guild structure. In Chapter 5 I compare patterns of fig production and ripening over one year and draw comparisons between *Ficus* species with different breeding systems and in different dispersal guilds.

The data presented in Chapter 6 was collected on Long Island. This chapter focuses on the colonisation anew of a volcanic island by *Ficus* species and their vertebrate dispersers. Chapter 7 is a global review of fig eating and *Ficus* seed dispersal by vertebrate frugivores and brings together the data collected in Borneo and New Guinea with that from the literature. Chapter 8 serves as a synthesis of the data presented in the preceding chapters and raises suggestions for future research in this field.

CHAPTER 2

DESCRIPTION OF STUDY SITES

Peel a fig for your friend, and a peach for your enemy
Spanish Proverb
(Condit, 1947)

Fieldwork was conducted primarily in Lambir Hills National Park, Sarawak, Malaysia with additional research undertaken on Long Island, Papua New Guinea. Supplementary observations and measurements were also made at a number of additional localities: UNIMAS campus and Rumah Aji longhouse, Sarawak and Jais Aben resort, Madang, Papua New Guinea.

2.1 LAMBIR HILLS NATIONAL PARK, SARAWAK, MALAYSIA

Between March and September 1998 and January and September 1999 fieldwork was conducted in Lambir Hills National Park (4° 20' N, 113°50' E; altitude 150 - 465 m), 30 km south of Miri in Sarawak's Fourth Division on the island of Borneo (Figure 2.1). The 6952 ha park (hereafter Lambir) was gazetted in 1982 and is surrounded by areas with extensive anthropogenic disturbance (logging concessions, oil palm plantations and secondary forest, the result of shifting cultivation; Watson, 1985). Lambir's proximity to the oil-town of Miri and its trails and waterfalls make it Sarawak's most heavily visited national park (Anon., 1995).

Ashton and Hall (1992) provided a detailed description of Lambir's forest structure. The park's vegetation is predominantly Mixed Dipterocarp Forest (MDF), named after the dominant tree family, Dipterocarpaceae, which comprises 80 % of the canopy and emergent trees. A second vegetation type, *kerangas* or heath forest, occurs in small pockets on the highest land. The forest canopy reaches 40 m in height whilst emergent trees are up to 70 m tall (Inoue & Hamid 1995). The dominance of the dipterocarp family belies the diversity of the flora. Lambir has the highest tree diversity of any locality yet described, with 1175 species over 1 cm dbh (diameter at breast height) identified in a 52 ha plot (LaFrankie *et al.*, 1995). Lambir is particularly rich in *Ficus* species having 80 recorded species and varieties (R. Harrison pers. comm.). Two main soil types occur at Lambir; a coarse, nutrient-poor humult derived from sandstone and a fine clay-shale derived udult of higher nutrient content. Certain tree species' distributions appear to coincide exclusively with one or other type (LaFrankie, 1995; Palmiotto *et al.*, 1995).

Mean annual rainfall in Lambir exceeds 5000 mm (Inoue & Hamid, 1994). Every four to six years, however, a pronounced dry period occurs due a change in the Southern trade winds, a fluctuation generated by the El Niño Southern Oscillation (ENSO). Such drought may play a role in triggering general flowering events (Inoue & Hamid, 1995). These flowering events, unique to South-East Asia, entail nearly all dipterocarp species together with species from many other families coming heavily into flowering (see Sakai *et al.*, 1999). Such an event is followed, some months later, by abundant fruiting. No clear annual rainfall pattern occurs in the park (Sakai *et al.*, 1999) but during this study an extreme drought occurred during which pollinators of some *Ficus* species became locally extinct (Harrison, 2000).

Two large research plots have been established at Lambir (Inoue & Hamid, 1994; Lee *et al.*, 1995). The Forest Dynamics Plot was established in 1990 as a joint research venture between the Forest Department Sarawak, Harvard University, Center for Tropical Forest Science at the Smithsonian Tropical Research Institute, and a number of Japanese universities including Ehime, Osaka City and Kyoto (Lee, 1995). Measuring 52 ha in area, the plot's position was chosen to maximise the heterogeneity sampled and to include both of Lambir's soil types (LaFrankie, 1995). All trees over 1 cm dbh (diameter at breast height = 1.3 m) were tagged, measured, mapped and identified (Lee, 1995). Upon completion of the first phase of identification in 1995, 1175 tree species had been recorded, more than in any comparable plot thus far examined (La Frankie *et al.*, 1995).

The eight hectare Canopy Biology Plot was established in 1991 under the banner of the Canopy Biology Research in Sarawak (CBRS) program. Canopy research is facilitated by the presence of nine walkways, (totalling 300 m in length) connecting tree towers constructed around large dipterocarp trees (*Dryobalanops lanceolata* and *Dipterocarpus pachyphyllus*) that reaching heights of 50 and 55 m above the forest floor (Inoue & Hamid, 1995; Inoue *et al.*, 1995; Yumoto & Inoue, 1995).

Over 360 vertebrate species (including 237 bird and 63 mammal species) have been recorded in Lambir (Shanahan & Debski, in press; Appendix 1). However, the park is currently depauperate in larger frugivorous animal species, a probable consequence of the park's small size, proximity to disturbance and the illegal hunting that occurs within its boundaries. In particular, primates, civets, flying foxes and hornbills appear to occur at lower densities than in previously studied Malesian forests (McClure, 1966; Medway & Wells, 1971; Leighton, 1982; Lambert, 1990).

2.2 LONG ISLAND, PAPUA NEW GUINEA

Between 27 June and 7 July 1999 research was undertaken on Long Island (5° 20' S; 147° 10'E), 50 km off the coast of Madang province, Papua New Guinea (Figure 2.2). Volcanic in origin, much of Long Island was destroyed in a catastrophic eruption that occurred in about 1645 (Zielinski *et al.*, 1994). The volcanic activity formed a caldera 13 km in diameter where the main volcano summit had been. The eruption's pyroclastic flows and mud slides left deposits up to 30 m thick whilst layers of compacted ash up to 4 m thick covered the rest of the island (Pain *et al.*, 1981). Almost certainly Long Island's macrobiota was eradicated; the upper layers of deposits contained no plant remains (Pain *et al.*, 1981). Long Island's present land biota has therefore arrived since the eruption and its terrestrial ecosystem is no more than about 350 years old.

Over time a freshwater lake (Lake Wisdom) formed in Long's caldera. Renewed volcanic activity in the early 1950s built up deposits that broke the surface as a series of temporary islands in the southern part of the lake. One island, Motmot, which had emerged by 1968, persisted. Between 1969 and 1973 the island grew through further volcanic activity which included lava emissions that ensured its permanence. Motmot is now some 300 m in diameter and about 60 m high, and very sparsely vegetated, its infant terrestrial ecosystem being no more than three decades old. Motmot's biota is composed of over-water colonists that have travelled at least 5 km, presumably mostly from the ring of Long Island which surrounds the lake.

Lake Wisdom's surface is 190 m above sea level and the caldera cliff walls rise some 200 to 300 m above this. There are two mountains on the caldera plateau, Mount Réaumur (1280 m) in the north and Cerisy Peak (1112 m) in the south. The plateau is

now, as it was in 1925 (Evans, 1939), covered with an open, apparently fairly young, even-age forest with very little undergrowth and a scattering of large older trees. The soil is extremely porous. Cloud forest occurs above about 750 m on the two mountains. After Long's eruption people resettled the island and a total of about 1000 people now live in five small coastal villages. In the coastal lowlands savannah woodland is mixed with rain forest and areas of secondary growth, and large areas have been cleared for gardens and coconut plantations (Ball & Hughes, 1982).

Long Island has a tropical moist climate. Mean annual rainfall has been estimated from records maintained at Umboi Island to the east and on the New Guinea coast, and comments made by administrative officers, as about 2800 mm (Ball & Glucksman, 1978). Rainfall is greater on the two mountains than in the lowland forests. Seasonal variation appears to be greater than on the mainland. The dry season is longer and drier, extending from April to November. The low rainfall combined with 'over-drained' soils results in fairly frequent droughts during prolonged dry seasons, when foliage may wither and leaf fall may occur (Ball & Hughes, 1982).

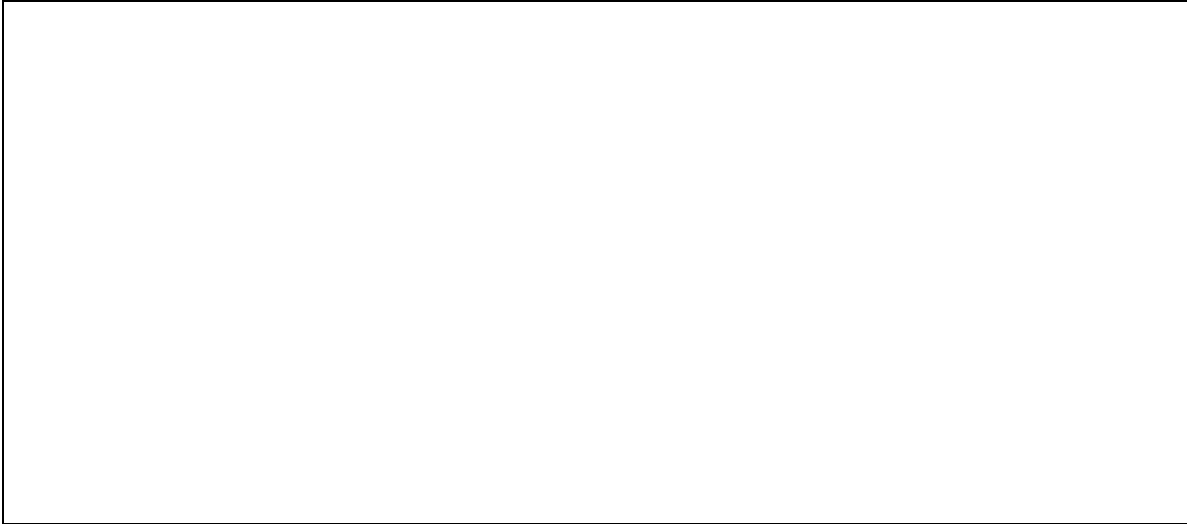


Figure 2.1. The location of Lambir Hills National Park, Sarawak, Malaysia. Redrawn from Inoue & Hamid (1994).

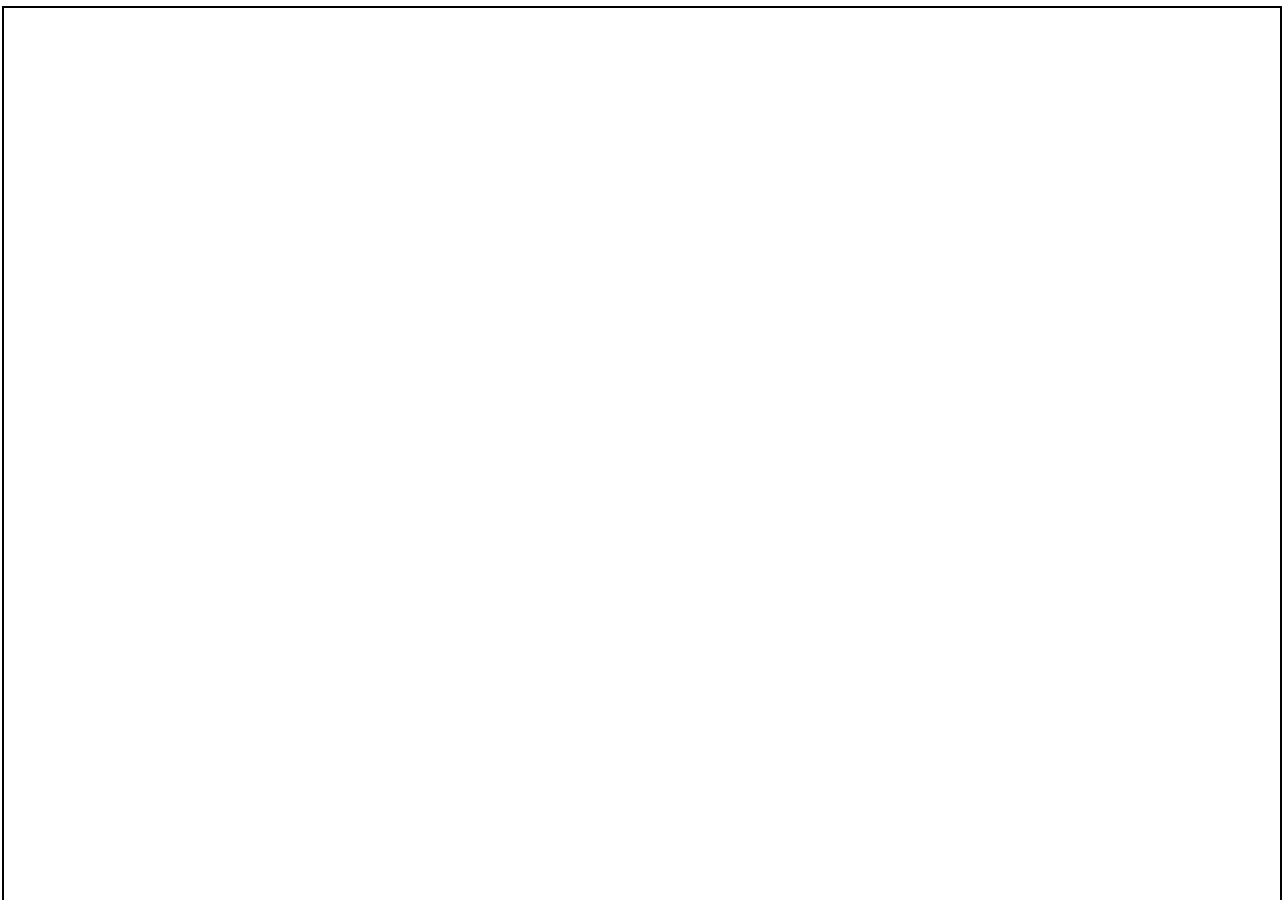


Figure 2.2. Long Island and Motmot. Sampling sites are numbered 1-8. 1 = main camp (short stature forest along the shore of Lake Wisdom, 200 m a.s.l.), 2 = crater rim (400 m a.s.l.), 3 = disturbed coastal habitat, 4 = cultivated land around Matapun village, 5 = small stream, 6 = dry river bed, 7 = Cerisy Peak (200-600 m), 8 = Cerisy Peak (600 - 890 m). Redrawn from Specht *et al.* (1982).

CHAPTER 3

PACKAGING AND PRESENTATION OF BORNEAN FIGS

"The Fici of Borneo show quite a series of adaptations, both in their shape and size, to varied biological conditions, and well deserve special attention"
Beccari (1904)

3.1 INTRODUCTION

There is considerable interspecific diversity in the manner in which fleshy fruits are packaged and presented (Ridley, 1930; van der Pijl, 1982; Herrera, 1981, 1987; Snow & Snow, 1988). Whilst the most obvious sources of variety are size, shape and colour, numerous other traits also vary between species. These include seed size and number, crop size, fruit protection, pulp: seed ratio, fruit position, synchrony of ripening and nutrient content. Figs are not strictly fruit but hollow, urn-shaped inflorescences lined with tiny uniovulate flowers (Verkerke, 1989). The mature ovaries are the true fruits but are often called seeds (Verkerke, 1989). As these 'seeds' mature, figs undergo physical and chemical changes such that latex decreases and sugars increase, and they may also swell and change colour. Thus, at maturity, figs are infructescences that are functionally fruits capable of attracting vertebrate frugivores as seed dispersers.

Between 50 and 90 % of woody plant species in tropical forests produce fleshy fruit that attract potentially seed dispersing vertebrate frugivores (Frankie *et al.*, 1974; Fleming, 1979; Howe & Smallwood, 1982). However, the provision of the reward in advance of the act of seed dispersal exposes this mutualism to cheats in the form of seed-predators or pulp thieves (Howe & Vande Kerckhove, 1981; Janzen, 1981; Jordano, 1983). Plants are therefore under selective pressure to attract genuine, quality dispersers and as such may be expected to exhibit adaptations associated with the attraction of assemblages of frugivores that best meet the plant's needs in terms of seed dispersal. Knowledge of *Ficus* species' germination requirements is limited beyond generalisations such as the need for hemi-epiphytic *Ficus* seeds to be deposited in canopy microsites on host trees (Laman, 1995).

Studies have identified numerous fruit traits capable of interacting with frugivores and thus determining which species will be able to consume the fruit. These include seed size (Levey, 1987), accessibility (Moermond & Denslow, 1983), morphology (Moermond *et al.*, 1986), fruit size (Jordano, 1995) and fruit colour (Willson & Whelan, 1990). Investigations of such fruit characteristics have proposed suites of covarying character complexes, or fruit syndromes, associated with the attraction of discrete subsets of frugivore communities and reflecting their sensory abilities and foraging behaviour (e.g. O'Dowd & Gill, 1986; Ridley 1930; Turcek, 1963; Snow, 1981; van der Pijl 1982, Janson, 1983). Thus, birds tend to be attracted to red or black fruits that are often small and unprotected whilst fruit bats tend to feed on larger, dull and odorific fruits often presented away from the foliage (van der Pijl, 1957; Snow, 1981). However, other selective pressures such as defence against pathogens and insect seed predators, are also likely to be involved in determining the way in which a species packages and presents its fruit. For *Ficus* species, further complexity arises from the fact that figs function initially as inflorescences and subsequently as fruit. Additional constraints are therefore imposed by the requirements of the pollinator wasps that reproduce within figs. For example, these wasps are temperature sensitive and fig size influences cooling rates and, therefore, wasp survival (Patiño *et al.*, 1994). Furthermore, coevolution (even of a diffuse nature, *sensu* Janzen, 1980) between plants and their dispersers is made less likely by the difference in generation times between the two groups of interactants and the provision of the pulp reward before the service of seed dispersal (Wheelwright & Orians, 1982). Similarity between plant species' fruit characters may therefore be due to common ancestry rather than parallel and convergent evolution. This non-adaptive argument is supported by evidence from Bremer & Eriksson (1992) who suggested that the evolution of types of fleshy fruit among the large tropical family Rubiaceae were moulded by changes in the disperser fauna in the early Tertiary, but that subsequent faunal shifts have had little effect on fruit characters. Jordano (1995) studied 910 angiosperm species and showed that phylogeny explained 61 % of the variance in 16 fruit traits whilst Fischer & Chapman (1993) concluded that fruit character complexes (syndromes) independent of phylogeny were rare. Conversely, Janson (1983) studied 238 fleshy fruit species in Peru and concluded that phylogenetic constraint to fruit size, colour and protection were minimal and that adaptation to distinct disperser groups may be more important.

The diversity of *Ficus* (see Chapter 1) makes the genus ideal for studies of interspecific patterns of fruit design and presentation, their ecological and evolutionary determinants and their implications because all *Ficus* species share a common ancestry and a basic common fruit structure, the fig. In this chapter I examine the *Ficus* flora of the main field site, Lambir Hills National Park, in order to demonstrate, firstly, the diversity of fig design and presentation. I then examine the applicability of the concept of fruit syndromes and identify fig design characters that appear to be characteristic of the genus as a whole. I also explore differences in fruiting ecology between monoecious and dioecious *Ficus* species, and between groups of species with different phylogenetic affinities. Such differences are of both ecological and evolutionary interest and may be relevant to the evolution of dioecy in *Ficus*.

3.2 METHODS

3.2.1 Sampling

The locations of hundreds of *Ficus* individuals in Lambir Hills National Park were known in advance through the doctoral research censuses of R. D. Harrison (1999) and a pilot study conducted in 1997 (Shanahan, 1997). Additional *Ficus* individuals were located during an initial surveying period in April 1998. An effort was made to include individuals of all growth forms (hemi-epiphytic, climbers, freestanding trees) and patterns of fig-placement (geocarpic, cauliflorous, among leafy branches) in this study. Species were identified by reference to botanical keys (Corner, 1965; Kochummen, 1983; Primack, 1983) and to Harrison's specimens, previously matched to those in herbaria in Kuching and Singapore. Regular phenological censuses of over 500 *Ficus* individuals (see Chapter 5) allowed trees that were producing crops to be identified. A wide range of species was observed, rather than a few intensively, and consequently sample sizes per *Ficus* species are low. For dioecious species, only female (seed-producing) individuals were considered.

3.2.2 Fig design and presentation

To characterise the attributes of the figs, for each species found fruiting, a sample of 10 to 40 ripe figs was collected either directly from the plant, with the use of a grab-stick or from the freshly fallen fruit knocked down by feeding animals. The design components (Herrera, 1981; Snow and Snow, 1981) of each species' figs were recorded as follows. Each fig was weighed (fresh mass) and its equatorial diameter and length (from the point of attachment to ostiole) were measured. Figs were then separated into their pulp and seed (for monoecious figs this included flowers, galls and insects) components, which were then separately re-weighed. These parts were then dried to constant weight in a drying oven (24 hours at 105° F sufficed) and dry weights were taken. Once the floral parts were dry, the number of seeds present was counted. The measurements taken allowed the derivation of the following additional statistics:

$$\text{Pulp water content} = ((\text{pulp wet mass} - \text{pulp dry mass}) / \text{pulp wet mass}) \times 100$$

$$\text{Seed burden} = (\text{wet floral mass} / \text{total wet mass}) \times 100$$

$$\text{Relative yield} = (\text{dry pulp mass} / \text{total wet mass}) \times 100$$

Seed burden is a measure of the amount of 'ballast' in a fruit (Snow & Snow, 1981), and in figs is comprised not only of the total mass of seeds, but also that of flowers, which in monoecious species will often have contained wasps. Relative yield is a measure of the amount of dry, largely nutritive matter (Herrera, 1981), expressed as a percentage of the total fig wet mass.

At the level of individual trees, the following crop characteristics were recorded. Fig placement was recorded as cauliflorous, axillary, or geocarpic (see Chapter 1). Crop size was either counted directly or estimated by counting the number of figs on typical branches and then extrapolating to total numbers per tree. The degree of synchrony of fig ripening was described with an index derived by calculating the percentage of the crop that was ripe. Fig colour (at maturity) was classed as either red (including orange), green/yellow or brown. Fig pulp and coats were classed as firm if not easily punctured by the thumbnail (otherwise soft) and the presence or absence of a detectable odour was also noted. Following the forest stratification classification of Yamakura (1992), to which Lambir's forest corresponds, vertical crop placement was classed as either; 1: shrub layer (0 - 2.5 m), 2: understorey (2.5 - 12.5 m), 3: subcanopy (12.5 - 27.5 m), 4: canopy (27.5 - 42.5 m) or 5: emergent (> 42.5 m). A crop-height index was calculated as the percentage of the crop in each of these height classes, multiplied by the class numbers (one to five). These figures were then summed to give a range from 100 (all figs in the shrub layer) to 500 (all figs in the emergent layer). Although a proportion of the figs produced by some geocarpic *Ficus* species may be subterranean, they were considered to have a height of zero metres, rather than a negative value.

3.2.2 Data analysis

Chi-squared tests were used to compare the relative numbers of dioecious and monoecious species studied to those occurring in the study site's total *Ficus* flora as well as that of Borneo as a whole. Such tests were also used to compare the sampled species to those in the park and in Borneo with respect to membership of each *Ficus* section. Following Zar (1996), Yates' correction was used in chi-squared tests with only one degree of freedom. Spearman correlation coefficients were calculated to seek associations between pairs of fig packaging and presentation traits and analyses of covariance (ANCOVA, with fig mass as the covariate) were used to compare fig design characteristics of monoecious and dioecious *Ficus* species. Where appropriate variables were log transformed to normalise distributions. Principal components analysis (PCA) was used to identify suites of covarying characters (fruit syndromes). PCA reduces multivariate data distributions to newly derived axes that maximally explain variation in the dataset. Furthermore, the analysis identifies the strength and direction of each factor's contribution to these new axes. In this analysis fig mass, seed number, relative yield, crop size and crop height index were log transformed to normalise their distributions. PCA was also used to confirm intraspecific consistency in fig design characters for species where data were collected from multiple individuals. With the exception of the chi-squared tests, which were performed using Excel 97 (Microsoft, 1997), all statistical tests were carried out using the SYSTAT package (SPSS, 1997).

3.3 RESULTS

3.3.1 Species studied

Measurements of fruit and crop characteristics were made for the 43 *Ficus* species listed in Table 3.1. The species studied represent over 50 % of the study site's total *Ficus* flora (Harrison, 1997) and approximately one-third of the *Ficus* flora of Borneo (Corner, 1965). Monoecious and dioecious *Ficus* species are represented in approximately the same proportions as found in the total park and Borneo fig floras (χ^2 using Yates' correction = 0.06 and 0.51, respectively; d.f. = 1, no significant differences). When the relative numbers of species in each *Ficus* section are compared, there is no significant difference between the species studied and the total fig community of Lambir ($\chi^2 = 3.18$, d.f. = 8, n.s.) but a significant difference when compared to the total Bornean flora ($\chi^2 = 16.4$, d.f. = 8, $p < 0.05$). This is due to the over-representation in the Lambir samples of hemi-epiphytes in *Ficus* section *Conosycea* (χ^2 using Yates' correction = 4.37, d.f. = 1, $p < 0.025$). Aside from this difference, the composition of species described here is therefore characteristic of that occurring at larger spatial scales. Due to limitations imposed by access, time of fruiting, and differences in the number of known individuals, the species were not sampled equally and for eight species data were collected from a single individual (Table 3.1). Intraspecific consistency in fig design characters was confirmed with a principal components analysis (Figure 3.1) which justified the use of combined data from different individuals in the creation of species' means used elsewhere in the thesis.

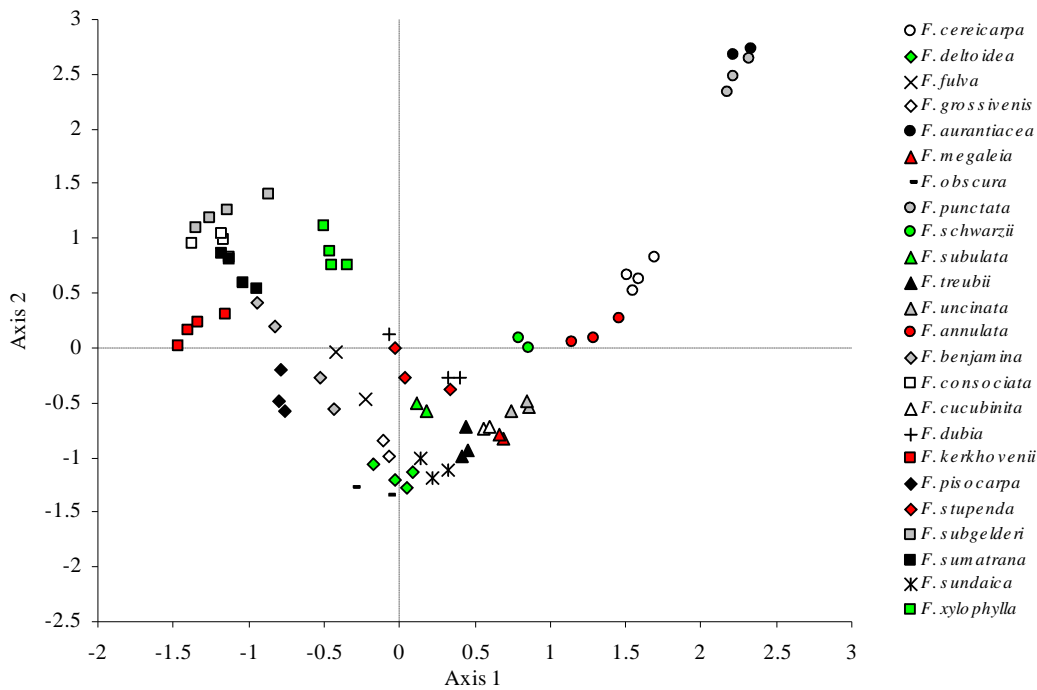


Figure 3.1. Principal components analysis based on fig design characters for *Ficus* species for which more than one individual was sampled (see Table 3.3 for n). The newly-derived axes demonstrate intraspecific consistency in fig design characters.

3.3.2 The diversity of fig design and presentation

Lambir's *Ficus* species exhibit considerable diversity in the manner in which their figs are presented. Crop-level fruiting attributes of each species are summarised in Table 3.2. Among the species sampled were six geocarpic tree species that present figs on runners originating near the base of the tree trunk. Three species were cauliflorous trees that presented their figs on the main trunk in the lower strata of the forest. The remaining species produced figs in the leaf axils and/or on the branches behind leaves. This last group includes species that present their figs in all strata of the forest, from the shrubby *Ficus deltoidea* to *F. callicarpides*, found climbing on emergent trees over 40 metres above the forest floor. Fig colour ranged from dark brown-yellow in *F. cereicarpa*, through green-yellow (*F. annulata*, *F. schwarzii*, *F. condensa*) to figs that ripened from orange to red or purple (see Figure 3.2). Crop sizes ranged from under 50 in some geocarpic species and the shrub *F. deltoidea* to many thousands among the hemi-epiphytic fig species (Table 3.2). The degree of synchrony of fig ripening varied from 3.03 % in *F. aurata* to 44.1 % in *F. deltoidea* (Table 3.2). There was no significant difference in this measure of synchrony between dioecious and monoecious species (Mann-Whitney $U = 172.5$, $p > 0.05$). Although some figs of *F. annulata*, *F. schwarzii*, *F. condensa*, *F. uncinata*, *F. sarawakensis* and *F. xylophylla* were scented, odour was found to be an unreliable trait in that it was detected inconsistently by the human nose.

The fig design components of the 43 *Ficus* species studied are presented in Table 3.3. Interspecific variation among these characters is summarised in Table 3.4 and Figure 3.3. The modal size class of both fig length and diameter was 10-15 mm (Figure 3.3a-b), though distributions of these characters were right-skewed by the small number of species with figs up to five times larger in either dimension (e.g. *Ficus aurantiacea*, *F. cereicarpa*, *F. punctata*). Most species' figs were globose although some were elongate and some were broader than they were long (Figure 3.3c). Fig mass varied over three orders of magnitude from 0.04 g in *Ficus lanata* to 48.5 g in *F. aurantiacea* (Figure 3.3d). Although, Lambir's figs generally had a large number of tiny (0.5 - 2 mm long) seeds, *Ficus deltoidea* was exceptional in having an average of four, considerably larger (5.6 mm) seeds (Figure 3.3e, Table 3.4, 3.5). Pulp water content ranged from 40.2 % to 90.8 % (modal class 85 - 90 %), relative yield from 6.41 to 24.8 % (modal class 5 - 10 %) and seed burden from 13.2 % to 60.8 % (modal class 20 - 25 %; Figure 3.3 f-h). Figure 3.4 compares these values to those of non-*Ficus* fruits in Hong Kong (Corlett, 1996), England (Snow & Snow, 1988), and Spain and undisclosed Neotropical sites (Herrera, 1981). The 43 *Ficus* species studied show similar ranges for these characters as are exhibited between diverse combinations of families elsewhere. The distributions of pulp water content and relative yield of Lambir's figs appear similar to those of non-fig fruits, whilst seed burden appears to be generally higher in the figs.

Table 3.1. Taxonomy, nomenclature and breeding systems of *Ficus* species studied (following Corner 1965). N.B. *Ficus obscura* is normally observed as a climber and *F. acamptophylla* usually occurs as a hemi-epiphyte (Corner, 1965; Harrison, 1997), but this was not the case for the individuals studied.

Subgenus	Section	Species name and authority	Breeding system	Growth form	n individuals
<i>Ficus</i>	<i>Ficus</i>	<i>F. aurata</i> Miq.	Dioecy	tree	1
<i>Ficus</i>	<i>Ficus</i>	<i>F. deltoidea</i> Jack	Dioecy	shrub	4
<i>Ficus</i>	<i>Ficus</i>	<i>F. fulva</i> Reinw. Ex Bl.	Dioecy	tree	8
<i>Ficus</i>	<i>Ficus</i>	<i>F. brunneo-aurata</i> Corner	Dioecy	tree	2
<i>Ficus</i>	<i>Kalosyce</i>	<i>F. aurantiacea</i> Griff.	Dioecy	climber	3
<i>Ficus</i>	<i>Kalosyce</i>	<i>F. punctata</i> Thunb.	Dioecy	climber	15
<i>Ficus</i>	<i>Kalosyce</i>	<i>F. sarawakensis</i> Corner	Dioecy	climber	4
<i>Ficus</i>	<i>Rhizocladus</i>	<i>F. callicarpides</i> Corner	Dioecy	climber	2
<i>Ficus</i>	<i>Rhizocladus</i>	<i>F. grossivenis</i> Miq.	Dioecy	climber	4
<i>Ficus</i>	<i>Rhizocladus</i>	<i>F. lanata</i> Corner	Dioecy	climber	2
<i>Ficus</i>	<i>Rhizocladus</i>	<i>F. urnigera</i> Miq.	Dioecy	climber	1
<i>Ficus</i>	<i>Sycidium</i>	<i>F. obscura</i> Bl.	Dioecy	tree	2
<i>Ficus</i>	<i>Sycidium</i>	<i>F. rubroscupidata</i> Corner	Dioecy	climber	1
<i>Ficus</i>	<i>Sycidium</i>	<i>F. sinuata</i> Thunb.	Dioecy	climber	2
<i>Ficus</i>	<i>Sycidium</i>	<i>F. subulata</i> Bl.	Dioecy	climber	2
<i>Ficus</i>	<i>Sycidium</i>	<i>F. uniglandulosa</i> Wall. Ex. Miq	Dioecy	tree	1
<i>Ficus</i>	<i>Sycocarpus</i>	<i>F. cereicarpa</i> Corner	Dioecy	tree	6
<i>Ficus</i>	<i>Sycocarpus</i>	<i>F. condensa</i> King	Dioecy	tree	1
<i>Ficus</i>	<i>Sycocarpus</i>	<i>F. geocharis</i> Corner	Dioecy	tree	1
<i>Ficus</i>	<i>Sycocarpus</i>	<i>F. megaleia</i> Corner	Dioecy	tree	3
<i>Ficus</i>	<i>Sycocarpus</i>	<i>F. schwarzii</i> Koord.	Dioecy	tree	6
<i>Ficus</i>	<i>Sycocarpus</i>	<i>F. stolonifera</i> King	Dioecy	tree	2
<i>Ficus</i>	<i>Sycocarpus</i>	<i>F. treubii</i> King	Dioecy	tree	4
<i>Ficus</i>	<i>Sycocarpus</i>	<i>F. uncinata</i> Becc.	Dioecy	tree	3
<i>Ficus</i>	<i>Sycocarpus</i>	<i>F. near uncinata</i>	Dioecy	tree	2
<i>Urostigma</i>	<i>Conosycea</i>	<i>F. acamptophylla</i> Miq.	Monoecy	climber	1
<i>Urostigma</i>	<i>Conosycea</i>	<i>F. annulata</i> Bl.	Monoecy	hemi-epiphyte	4
<i>Urostigma</i>	<i>Conosycea</i>	<i>F. benjamina</i> L.	Monoecy	hemi-epiphyte	7
<i>Urostigma</i>	<i>Conosycea</i>	<i>F. callophylla</i> Bl.	Monoecy	hemi-epiphyte	1
<i>Urostigma</i>	<i>Conosycea</i>	<i>F. consociata</i> Bl.	Monoecy	hemi-epiphyte	5
<i>Urostigma</i>	<i>Conosycea</i>	<i>F. cucurbitina</i> King	Monoecy	hemi-epiphyte	3
<i>Urostigma</i>	<i>Conosycea</i>	<i>F. dubia</i> Wall. Ex King	Monoecy	hemi-epiphyte	5
<i>Urostigma</i>	<i>Conosycea</i>	<i>F. kerkhovenii</i> Val.	Monoecy	hemi-epiphyte	5
<i>Urostigma</i>	<i>Conosycea</i>	<i>F. pellucido-punctata</i> Griffith	Monoecy	hemi-epiphyte	2
<i>Urostigma</i>	<i>Conosycea</i>	<i>F. pisocarpa</i> Bl.	Monoecy	hemi-epiphyte	5
<i>Urostigma</i>	<i>Conosycea</i>	<i>F. stricta</i> Miq.	Monoecy	hemi-epiphyte	2
<i>Urostigma</i>	<i>Conosycea</i>	<i>F. stupenda</i> Miq.	Monoecy	hemi-epiphyte	6
<i>Urostigma</i>	<i>Conosycea</i>	<i>F. subcordata</i> Bl.	Monoecy	hemi-epiphyte	3
<i>Urostigma</i>	<i>Conosycea</i>	<i>F. subgelderii</i> Corner	Monoecy	hemi-epiphyte	6
<i>Urostigma</i>	<i>Conosycea</i>	<i>F. sumatrana</i> Miq.	Monoecy	hemi-epiphyte	4
<i>Urostigma</i>	<i>Conosycea</i>	<i>F. sundaica</i> Bl.	Monoecy	hemi-epiphyte	3
<i>Urostigma</i>	<i>Conosycea</i>	<i>F. xylophylla</i> Wall. ex Miq.	Monoecy	hemi-epiphyte	6
<i>Urostigma</i>	<i>Conosycea</i>	<i>F. retusa</i> L.	Monoecy	hemi-epiphyte	2

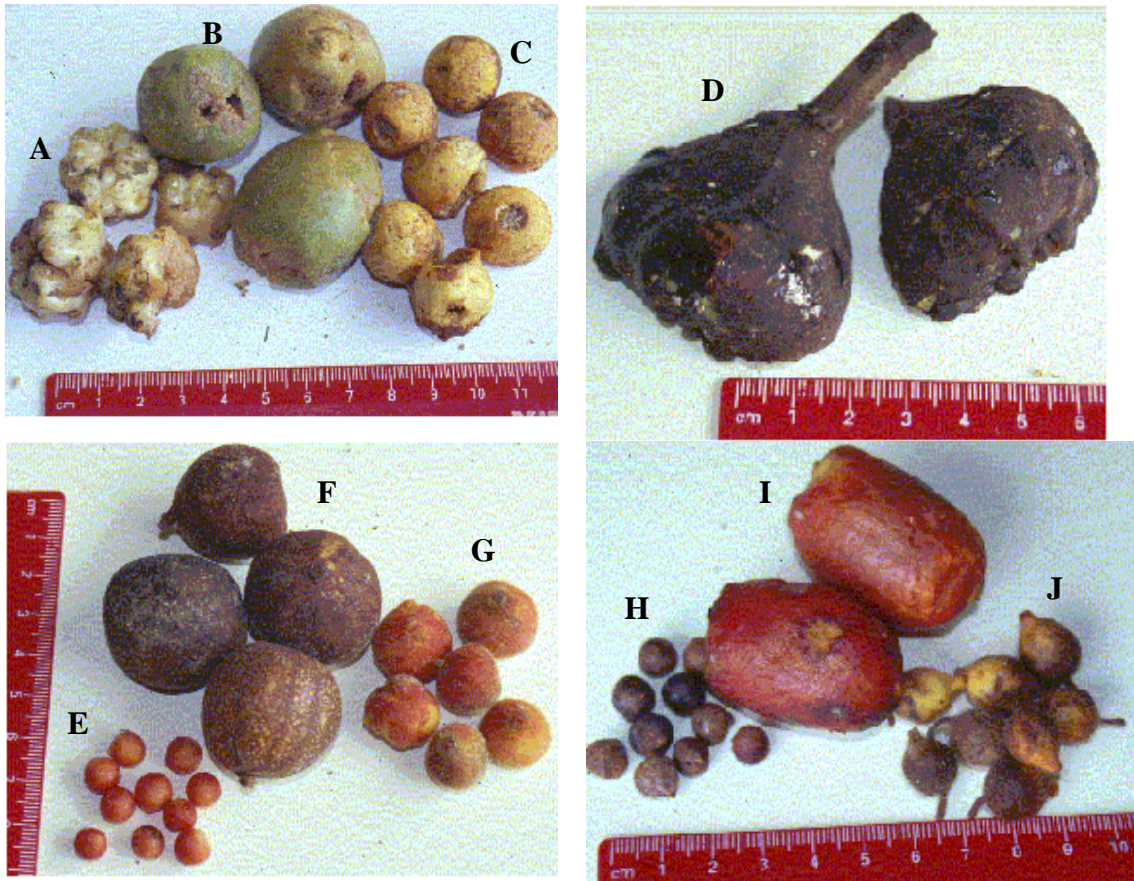


Figure 3.2. Examples of figs from Lambir Hills National Park. A = *Ficus* near *uncinata*, B = *F. annulata*, C = *F. sumatrana*, D = *F. cereicarpa*, E = *F. obscura*, F = *F. sarawakensis*, G = *F. fulva*, H = *F. benjamina*, I = *F. xylophylla*, J = *F. grossivenis*.

Table 3.2. Fig presentation (crop-level fruit characters) of the 43 *Ficus* species studied. Index of synchrony indicates the percentage of a crop that was ripe each day.

<i>Ficus</i> species	Fig placement	Fig colour	Total crop size		Index of synchrony	Crop height (m)		Crop height index
			range	mean		minimum	maximum	
<i>F. aurata</i>	axillary	orange-red	750-2000	1260	3.03	4	8	200
<i>F. brunneo-aurata</i>	axillary	orange-red	1850-3900	2820	4.61	3	14	210
<i>F. callicarpides</i>	axillary	red	240-7200	3693	4.87	32	45	450
<i>F. condensa</i>	cauliflory	green-yellow	43-75	60	26.8	0.9	4.5	150
<i>F. cereicarpa</i>	cauliflory	brown-yellow	43-120	71	10.1	0.25	3.5	115
<i>F. deltoidea</i>	axillary	red	10-32	20	44.1	0.5	0.9	100
<i>F. fulva</i>	axillary	orange-red	1500-5000	3237	6.39	2.56	8.8	195
<i>F. grossivenis</i>	axillary	orange-red	7500-14000	10300	3.50	23	28	360
<i>F. geocharis</i>	geocarpic	red	6-12	9	27.8	0	0.40	100
<i>F. aurantiacea</i>	axillary	red	18-142.75	62	3.21	6	25	300
<i>F. urnigera</i>	axillary	orange	170-560	332	7.23	1.3	2.4	200
<i>F. lanata</i>	axillary	orange-red	2400-5000	3270	6.12	6	20	220
<i>F. megaleia</i>	geocarpic	red	4-12	7	24.3	0	0.22	100
<i>F. obscura</i>	axillary	orange-red	3000-6000	4553	6.84	0.25	2.3	115
<i>F. punctata</i>	axillary	red	12-76	42	4.29	3.6	22.3	255
<i>F. rubroscapitata</i>	axillary	orange-red	430-1200	806	13.7	1.3	2.4	200
<i>F. sarawakensis</i>	axillary	red-purple	75-300	168	7.03	6.10	19	245
<i>F. schwarzii</i>	cauliflory	yellow-green	55-200	108	18.6	0.75	4.5	140
<i>F. sinuata</i>	axillary	orange	350-1100	676	19.2	2	8	200
<i>F. stolonifera</i>	geocarpic	red	17-32	25	12.9	0	0.21	100
<i>F. subulata</i>	axillary	orange-red	1500-4500	2920	10.7	0.5	12	175
<i>F. treubii</i>	geocarpic	pale brown	90-310	199	5.03	0	0.16	100
<i>F. uncinata</i>	geocarpic	dark red	19-34	28	8.61	0	0.36	100
<i>F. near uncinata</i>	geocarpic	white-green	8-30	18	7.92	0	0	100
<i>F. uniglandulosa</i>	axillary	orange	1100-3200	2360	8.47	2	5	190
<i>F. acampophylla</i>	axillary	orange-red	1000-2500	1640	15.2	0.5	1.9	100
<i>F. annulata</i>	axillary	yellow-green	970-3000	1723	4.64	7	16	280
<i>F. benjamina</i>	axillary	orange-red	35000-85000	58800	5.95	19	32	365
<i>F. callophylla</i>	axillary	orange-red	10000-25000	16000	9.38	22	26	395
<i>F. consociata</i>	axillary	orange-red	8000-21000	12600	14.3	28	36	400
<i>F. cucurbitina</i>	axillary	orange-red	8900-21000	13780	17.4	27	33	415
<i>F. dubia</i>	axillary	red-purple	4000-9000	6820	5.87	27	33	410
<i>F. kerkhovenii</i>	axillary	orange-red	44000-75000	54800	10.9	26	37	445
<i>F. pellucido-punctata</i>	axillary	orange-red	14500-21000	18100	17.1	22	26	385
<i>F. pisocarpa</i>	axillary	orange-red	12000-67500	32700	6.12	26	32	400
<i>F. retusa</i>	axillary	red	1200-7500	3910	20.5	28	32	400
<i>F. stricta</i>	axillary	orange-red	5000-13000	8600	11.6	25	35	405
<i>F. stupenda</i>	axillary	orange-red	11000-16700	13440	13.2	31	38	390
<i>F. subcordata</i>	axillary	red-purple	10375-15000	13115	14.5	30	38	440
<i>F. subgelderii</i>	axillary	orange	12000-24000	18800	17.0	32	35	390
<i>F. sumatrana</i>	axillary	orange	17500-22000	19513	9.74	33	41	400
<i>F. sundaica</i>	axillary	orange-red	2300-6000	18800	8.65	28	32	380
<i>F. xylophylla</i>	axillary	orange-red	17400-22000	19580	9.19	20	36	390

Table 3.3 Design characteristics of ripe figs. All values are mean \pm standard error. Raw data used to calculate seed burden, relative yield and pulp water content are presented in Appendix 2.

<i>Ficus species</i>	Diameter (mm)	Length (mm)	Wet mass (g)	Pulp proportion (%)	Relative yield (%)	Pulp water content (%)	Seed burden (%)	Seed number	Fig coat texture	Fig pulp texture	n figs, n individuals
<i>F. aurata</i>	10.87 \pm 0.119	10.74 \pm 0.109	0.481 \pm 0.028	71.06 \pm 1.062	16.55 \pm 1.931	76.61 \pm 2.927	28.87 \pm 1.062	383.1 \pm 15.47	soft	soft	10, 1
<i>F. brunneo-aurata</i>	12.88 \pm 0.243	12.79 \pm 0.236	1.042 \pm 0.048	64.27 \pm 0.545	8.714 \pm 0.578	86.42 \pm 0.924	35.73 \pm 0.545	470.6 \pm 14.23	soft	soft	10, 1
<i>F. callicarpides</i>	4.152 \pm 0.076	4.171 \pm 0.065	0.044 \pm 0.003	56.37 \pm 3.141	24.05 \pm 1.731	56.29 \pm 3.686	43.63 \pm 3.795	12.00 \pm 0.699	soft	soft	10, 1
<i>F. condensa</i>	20.04 \pm 0.458	19.01 \pm 0.361	3.274 \pm 0.179	80.07 \pm 0.859	14.78 \pm 0.501	81.49 \pm 0.753	19.93 \pm 0.859	1185 \pm 45.49	soft	soft	10, 1
<i>F. cereicarpa</i>	42.83 \pm 0.862	41.78 \pm 0.862	43.28 \pm 1.778	81.99 \pm 0.632	7.491 \pm 0.422	90.83 \pm 0.582	18.01 \pm 0.632	1326 \pm 53.92	firm	firm	10, 4
<i>F. deltoidea</i>	8.989 \pm 0.396	9.493 \pm 0.299	0.486 \pm 0.048	59.18 \pm 1.608	7.875 \pm 0.814	86.83 \pm 1.245	40.82 \pm 1.608	4.000 \pm 0.494	soft	soft	10, 4
<i>F. fulva</i>	17.72 \pm 1.036	15.89 \pm 0.676	2.511 \pm 0.315	65.56 \pm 1.415	10.63 \pm 1.012	83.67 \pm 1.659	34.44 \pm 1.415	476.3 \pm 21.32	soft	soft	23, 2
<i>F. grossivenis</i>	11.21 \pm 0.152	12.44 \pm 0.395	0.438 \pm 0.026	62.81 \pm 1.916	10.34 \pm 0.958	83.71 \pm 1.109	37.23 \pm 1.916	226.1 \pm 16.13	soft	soft	39, 2
<i>F. geocharis</i>	19.59 \pm 0.966	16.85 \pm 0.894	9.788 \pm 0.292	75.54 \pm 1.404	7.168 \pm 0.211	90.51 \pm 0.237	24.51 \pm 1.404	582.7 \pm 23.72	soft	soft	10, 1
<i>F. aurantiacea</i>	51.84 \pm 2.578	52.33 \pm 2.865	48.55 \pm 3.053	74.84 \pm 1.381	8.591 \pm 0.362	88.54 \pm 0.411	25.16 \pm 1.381	6559 \pm 578.1	soft	soft	17, 2
<i>F. umigera</i>	7.096 \pm 0.148	7.254 \pm 0.118	0.265 \pm 0.011	50.47 \pm 0.838	20.76 \pm 2.633	58.97 \pm 4.921	49.57 \pm 1.029	56.12 \pm 7.311	soft	soft	13, 1
<i>F. lanata</i>	3.273 \pm 0.113	3.626 \pm 0.227	0.041 \pm 0.003	49.65 \pm 3.003	27.31 \pm 1.928	40.21 \pm 7.367	50.84 \pm 3.246	11.18 \pm 0.818	soft	soft	19, 1
<i>F. megaleia</i>	17.13 \pm 0.387	14.19 \pm 0.475	8.832 \pm 0.319	75.47 \pm 1.404	7.168 \pm 0.211	90.47 \pm 0.237	24.52 \pm 1.404	576.5 \pm 16.04	soft	soft	10, 2
<i>F. obscura</i>	7.018 \pm 0.133	7.186 \pm 0.187	0.351 \pm 0.022	54.79 \pm 0.612	7.694 \pm 0.815	86.03 \pm 1.408	45.21 \pm 0.572	51.27 \pm 2.795	soft	soft	28, 2
<i>F. punctata</i>	48.61 \pm 1.934	47.62 \pm 2.202	46.75 \pm 2.986	74.84 \pm 1.381	8.591 \pm 0.362	88.54 \pm 0.411	25.16 \pm 1.381	6323 \pm 921.9	firm	soft	17, 3
<i>F. rubroscupidata</i>	5.262 \pm 0.389	5.428 \pm 0.418	0.073 \pm 0.003	40.77 \pm 4.241	6.413 \pm 0.631	83.01 \pm 1.181	60.78 \pm 4.022	14.15 \pm 0.809	soft	soft	10, 1
<i>F. sarawakensis</i>	20.80 \pm 0.569	22.03 \pm 0.372	6.603 \pm 0.411	72.24 \pm 0.678	7.945 \pm 0.328	88.98 \pm 0.493	27.76 \pm 0.678	1140 \pm 91.05	soft	soft	10, 2
<i>F. schwarzii</i>	23.80 \pm 1.137	23.57 \pm 0.834	8.778 \pm 0.438	76.17 \pm 1.005	9.268 \pm 0.411	87.86 \pm 0.444	23.81 \pm 1.005	2364 \pm 211.8	soft	soft	12, 2
<i>F. sinuata</i>	4.580 \pm 0.203	5.113 \pm 0.177	0.069 \pm 0.006	42.13 \pm 1.933	10.07 \pm 0.754	81.38 \pm 1.534	44.62 \pm 2.595	15.92 \pm 0.773	soft	soft	12, 1
<i>F. stolonifera</i>	12.93 \pm 0.622	13.83 \pm 0.869	1.753 \pm 0.187	75.12 \pm 1.342	8.503 \pm 0.822	88.76 \pm 0.918	24.88 \pm 1.342	704.6 \pm 61.35	firm	soft	10, 2
<i>F. subulata</i>	8.117 \pm 0.292	8.645 \pm 0.348	0.492 \pm 0.045	79.25 \pm 1.624	12.36 \pm 0.598	84.21 \pm 0.889	20.75 \pm 1.624	223.9 \pm 12.59	soft	soft	20, 2
<i>F. treubii</i>	13.68 \pm 0.459	14.57 \pm 0.486	1.446 \pm 0.133	77.06 \pm 1.503	8.824 \pm 0.442	88.59 \pm 0.404	22.87 \pm 1.503	505.1 \pm 33.85	firm	soft	36, 3
<i>F. uncinata</i>	21.91 \pm 0.617	20.14 \pm 0.395	4.876 \pm 0.256	75.08 \pm 1.411	7.019 \pm 0.291	90.62 \pm 0.439	24.92 \pm 1.411	1820 \pm 72.89	firm	soft	12, 3
<i>F. near uncinata</i>	24.92 \pm 1.036	18.32 \pm 0.605	4.998 \pm 0.183	79.48 \pm 0.774	9.536 \pm 0.548	87.99 \pm 0.681	20.52 \pm 0.774	1513 \pm 72.19	firm	soft	10, 1
<i>F. uniglandulosa</i>	8.096 \pm 0.197	8.278 \pm 0.201	0.307 \pm 0.011	75.87 \pm 1.576	9.916 \pm 0.746	87.03 \pm 0.801	24.06 \pm 1.576	25.22 \pm 2.267	soft	soft	18, 1
<i>F. acamptophylla</i>	11.64 \pm 0.532	10.47 \pm 0.377	0.637 \pm 0.033	51.46 \pm 1.518	14.61 \pm 0.845	71.53 \pm 1.604	48.54 \pm 1.518	182.2 \pm 8.546	soft	soft	10, 1
<i>F. annulata</i>	28.29 \pm 0.503	33.33 \pm 0.612	33.53 \pm 1.124	86.86 \pm 0.451	8.939 \pm 0.215	89.67 \pm 0.249	13.14 \pm 0.451	127.3 \pm 3.787	soft	soft	38, 3
<i>F. benjamina</i>	9.457 \pm 0.205	10.07 \pm 0.173	0.322 \pm 0.014	57.92 \pm 1.692	15.92 \pm 1.339	72.92 \pm 1.897	42.08 \pm 1.692	175.3 \pm 19.68	soft	soft	110, 5
<i>F. callophylla</i>	10.63 \pm 0.158	10.54 \pm 0.142	0.783 \pm 0.033	67.67 \pm 1.712	22.35 \pm 0.945	66.85 \pm 1.485	32.33 \pm 1.712	144.9 \pm 6.325	soft	soft	10, 1
<i>F. consociata</i>	12.07 \pm 0.123	10.96 \pm 0.156	0.893 \pm 0.028	66.22 \pm 0.953	24.83 \pm 0.587	62.29 \pm 1.023	33.78 \pm 0.953	109.2 \pm 7.276	soft	soft	105, 4
<i>F. cucurbitina</i>	17.22 \pm 0.968	34.98 \pm 2.049	7.768 \pm 0.364	80.13 \pm 0.786	8.891 \pm 0.284	88.91 \pm 0.314	19.87 \pm 0.786	243.3 \pm 10.62	soft	soft	36, 2
<i>F. dubia</i>	21.37 \pm 0.502	27.81 \pm 0.895	8.028 \pm 0.398	80.81 \pm 0.973	13.28 \pm 0.641	83.47 \pm 0.928	19.22 \pm 0.973	246.9 \pm 11.51	soft	soft	26, 3
<i>F. kerkhovenii</i>	9.848 \pm 0.164	10.73 \pm 0.207	0.452 \pm 0.019	48.06 \pm 2.821	15.25 \pm 0.635	66.49 \pm 2.037	51.94 \pm 2.821	122.1 \pm 5.621	soft	soft	79, 4
<i>F. pellucido-punctata</i>	9.169 \pm 0.536	11.75 \pm 0.694	0.707 \pm 0.048	74.94 \pm 1.287	15.45 \pm 0.697	79.25 \pm 1.014	25.06 \pm 1.287	128.5 \pm 7.924	soft	soft	16, 1
<i>F. pisocarpa</i>	12.13 \pm 0.187	12.03 \pm 0.177	1.138 \pm 0.034	47.13 \pm 1.372	12.41 \pm 0.564	73.64 \pm 0.959	52.87 \pm 1.372	186.4 \pm 39.47	soft	soft	35, 3
<i>F. stupenda</i>	29.38 \pm 0.823	36.12 \pm 1.185	14.79 \pm 0.901	66.68 \pm 1.782	12.98 \pm 0.943	80.61 \pm 1.119	33.32 \pm 1.782	144.9 \pm 6.113	soft	soft	18, 3
<i>F. subcordata</i>	30.63 \pm 0.759	45.53 \pm 1.019	17.12 \pm 1.101	69.17 \pm 1.885	10.92 \pm 0.498	84.25 \pm 0.466	30.83 \pm 1.885	223.1 \pm 6.576	soft	soft	12, 1
<i>F. subgelderii</i>	10.74 \pm 0.188	13.55 \pm 0.269	0.989 \pm 0.087	67.53 \pm 1.343	23.22 \pm 1.132	65.74 \pm 1.346	28.24 \pm 2.531	143.4 \pm 4.582	soft	soft	99, 5
<i>F. sumatrana</i>	15.62 \pm 0.446	15.54 \pm 0.504	1.361 \pm 0.116	62.85 \pm 1.695	23.57 \pm 1.776	61.94 \pm 3.554	37.15 \pm 1.695	121.9 \pm 10.07	soft	soft	35, 4
<i>F. sundaica</i>	12.71 \pm 0.335	13.22 \pm 0.453	1.204 \pm 0.049	70.87 \pm 1.762	8.272 \pm 0.654	88.14 \pm 1.091	29.13 \pm 1.762	84.87 \pm 3.993	soft	soft	38, 3
<i>F. retusa</i>	6.848 \pm 0.239	7.223 \pm 0.174	0.309 \pm 0.011	56.75 \pm 1.826	11.12 \pm 0.977	80.15 \pm 1.873	43.25 \pm 1.826	27.32 \pm 2.266	soft	soft	22, 1
<i>F. xylophylla</i>	24.76 \pm 0.365	33.42 \pm 0.689	7.523 \pm 0.688	75.74 \pm 1.343	20.74 \pm 2.334	72.61 \pm 3.121	24.26 \pm 1.343	326.8 \pm 13.68	soft	soft	63, 4
<i>F. stricta</i>	21.14 \pm 0.901	23.58 \pm 1.393	3.132 \pm 0.357	61.69 \pm 0.915	9.784 \pm 1.527	83.93 \pm 2.685	38.31 \pm 0.915	140.7 \pm 3.777	soft	soft	20, 1

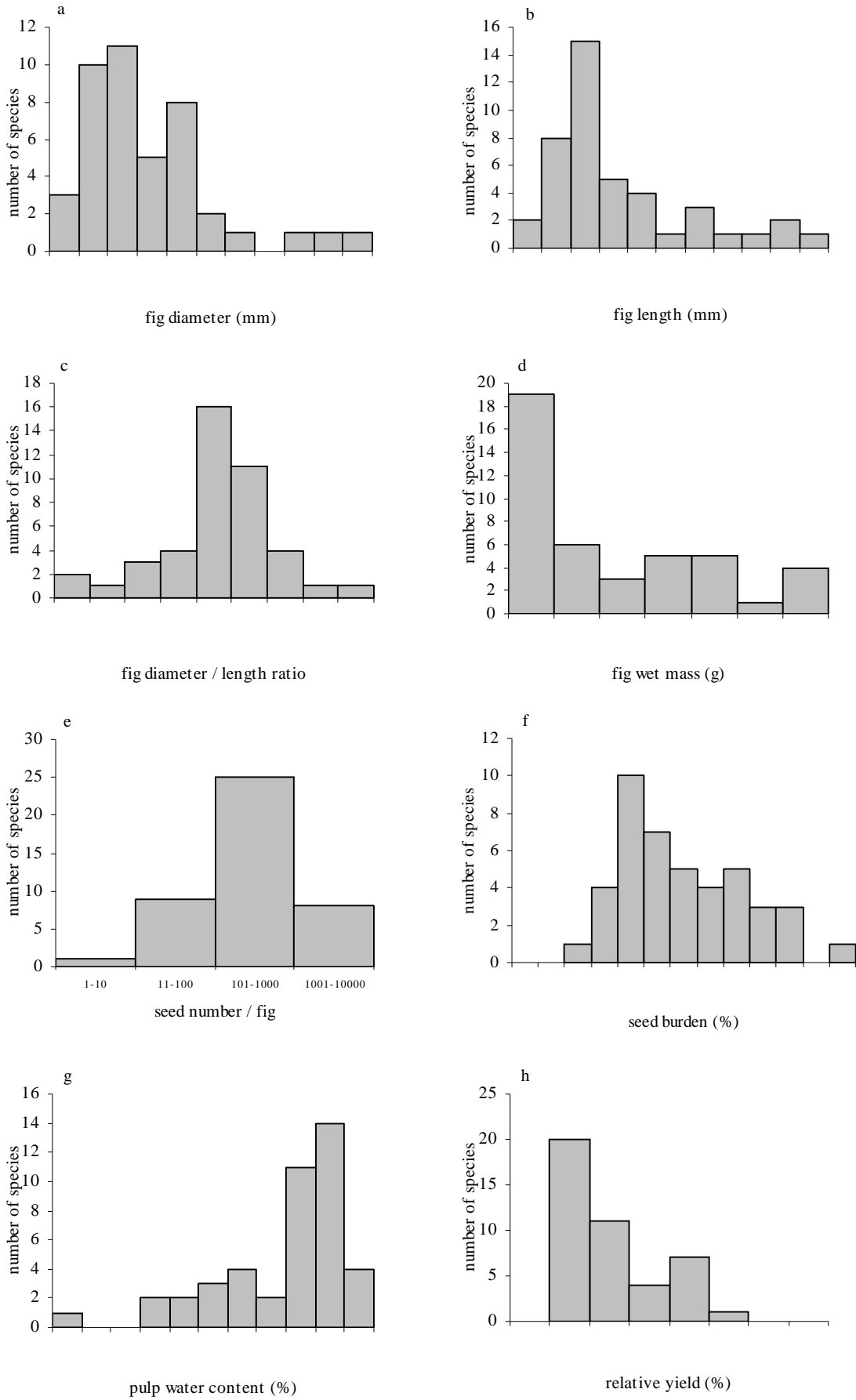


Figure 3.3. Frequency distributions of fig design components for 43 *Ficus* species in Lambir Hills National Park. Note the use of geometric scale for fig wet mass and logarithmic scales for seed number.

Table 3.4. Summary of interspecific variation in fig design components.

Design component	Minimum	Maximum	Mean (\pm S.D.) across 43 species
Fig diameter (mm)	3.27 (<i>F. lanata</i>)	51.9 (<i>F. aurantiacea</i>)	16.77 \pm 11.2
Fig length (mm)	3.62 (<i>F. lanata</i>)	52.3 (<i>F. aurantiacea</i>)	18.11 \pm 12.2
Fig wet mass (g)	0.04 (<i>F. lanata</i>)	48.5 (<i>F. aurantiacea</i>)	6.893 \pm 12.5
Seed number	4 (<i>F. deltoidea</i>)	6559 (<i>F. aurantiacea</i>)	685.1 \pm 1390
Pulp water content (%)	40.2 (<i>F. lanata</i>)	90.8 (<i>F. cereicarpa</i>)	79.73 \pm 11.4
Seed burden (%)	13.2 (<i>F. annulata</i>)	60.8 (<i>F. rubrocupidata</i>)	67.04 \pm 11.7
Relative yield (%)	6.41 (<i>F. rubrocupidata</i>)	24.8 (<i>F. consociata</i>)	12.79 \pm 5.79

Table 3.5. Seed size of some *Ficus* species in Lambir Hills National Park (data from Shanahan, 1997)

<i>Ficus</i> species	mean length (mm) \pm S.D.	n seeds
<i>F. annulata</i>	1.78 \pm 0.081	20
<i>F. aurata</i>	1.18 \pm 0.038	13
<i>F. callophylla</i>	1.61 \pm 0.124	20
<i>F. cereicarpa</i>	0.75 \pm 0.066	13
<i>F. consociata</i>	1.55 \pm 0.147	42
<i>F. deltoidea</i>	5.60 \pm 0.293	11
<i>F. fulva</i>	1.24 \pm 0.156	13
<i>F. grossivenis</i>	1.26 \pm 0.078	18
<i>F. kerkhovenii</i>	1.57 \pm 0.147	20
<i>F. megaleia</i>	0.82 \pm 0.099	24
<i>F. obscura</i>	2.05 \pm 0.151	10
<i>F. pisocarpa</i>	1.73 \pm 0.126	20
<i>F. punctata</i>	1.56 \pm 0.105	20
<i>F. sarawakensis</i>	1.77 \pm 0.182	14
<i>F. schwarzii</i>	1.06 \pm 0.097	16
<i>F. sinuata</i>	0.77 \pm 0.092	20
<i>F. stolonifera</i>	0.66 \pm 0.051	17
<i>F. stupenda</i>	1.51 \pm 0.363	20
<i>F. subulata</i>	0.94 \pm 0.068	20
<i>F. subgelderi</i>	1.59 \pm 0.165	20
<i>F. sumatrana</i>	1.62 \pm 0.118	20
<i>F. treubii</i>	0.78 \pm 0.044	20
<i>F. uncinata</i>	0.82 \pm 0.061	12
<i>F. uniglandulosa</i>	0.74 \pm 0.084	10

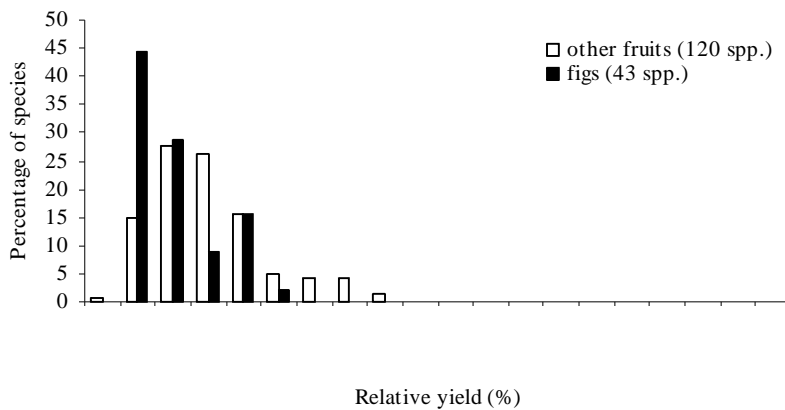
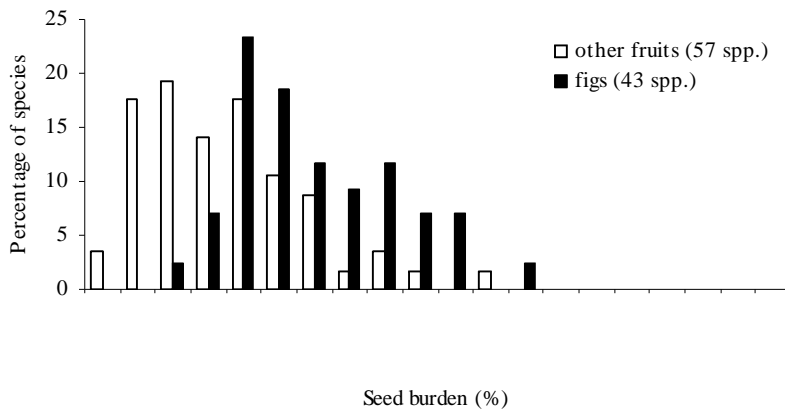
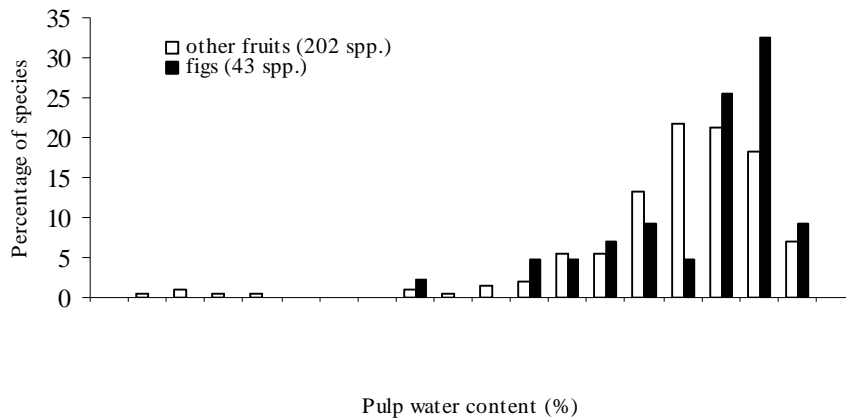


Figure 3.4. Comparison of 43 Bornean *Ficus* species with non-fig fruits. a) fig pulp water content compared with 202 non-*Ficus* species from England (Snow & Snow, 1988) and Hong Kong (Corlett, 1996), b) fig seed burden compared with 57 non-*Ficus* species in 35 genera and 21 families from England (Snow & Snow, 1988), c) fig relative yield compared with 120 non-*Ficus* species in 64 genera and 38 families from Spain, undisclosed Neotropical sites (Herrera, 1981) and England (Snow & Snow, 1988).

3.3.3 Associations between traits

Many of the fig traits measured are significantly correlated (Table 3.6). This is an expectation in the case of correlations between derived variables and their component design characteristics. Linear relationships between fig wet mass and wet and dry masses of pulp and floral components are, also, unsurprising (Figure 3.5). Two *Ficus* species (*F. annulata* and *F. cereicarpa*) did not conform to this pattern because their figs had a greater proportion of watery pulp than those of other species (Table 3.3). Dioecious figs have higher wet pulp mass ($F = 7.26$, $p < 0.05$) and wet floral mass ($F = 43.9$, $p < 0.01$) and lower dry pulp mass ($F = 15.4$, $p < 0.01$) and dry floral mass ($F = 15.2$, $p < 0.01$) than monoecious figs (analysis of covariance with fig wet mass as the covariate).

Figure 3.6 illustrates relationships between fig size (measured as fig wet mass) and other traits of interest, and reveals some differences between monoecious and dioecious figs. Seed burden appears to decrease with increasing fig size in both groups of figs (Figure 3.6a). Among dioecious species, fig size is strongly correlated with seed number ($r_s = 0.82$, $n = 25$, $p < 0.01$), whilst in monoecious species seed number is remarkably constant across a wide range of fig sizes (Figure 3.6b). The outlying position of *Ficus deltoidea* in Figure 3.6b is due to this species' production of small numbers of uncharacteristically large seeds (Table 3.5). Pulp water content is also positively correlated with fig size in figs of each breeding system (Figure 3.6c; Table 3.6). Highly significant negative relationships exist between crop size and fig mass in both monoecious and dioecious *Ficus* species (Table 3.6, Figure 3.6d) but in neither group is there a significant correlation between fig size and crop height (Figure 3.6e). Figures 3.6d and 3.6e reveal that monoecious figs tend to be produced in the canopy and in larger crops whilst dioecious species present generally smaller crops of figs across a wider vertical range, but fruit mainly in the lower strata of the forest (see also Figure 3.7). The outlying position of the monoecious *Ficus acamptophylla* in Figure 3.6e is due to the sampling of a single individual which was growing as a low climber, rather than a hemi-epiphyte, the more common growth form of this species (Dr. R. Harrison, pers. comm.). Differences between the two *Ficus* breeding systems were further revealed by analyses of covariance using size as a covariate (with seed number, wet mass and crop size all log transformed to normalise their distributions). Namely, for any given size of fig, dioecious species have more seeds ($F = 7.707$, $p < 0.01$), more watery pulp ($F = 7.549$, $p < 0.01$), smaller crop sizes ($F = 66.65$, $p < 0.01$) and lower relative yield ($F = 9.139$, $p < 0.01$) than their monoecious counterparts. It should be noted, however, that two of the highest relative yields were recorded from dioecious species that produce tiny figs (Figure 3.6f). No monoecious species in the study produced figs this small.

Strong, significant negative correlations exist between relative yield and pulp water content in both monoecious ($r_s = -0.92$, $n = 18$, $p < 0.01$) and dioecious ($r_s = -0.77$, $n = 25$, $p < 0.01$) fig species (Figure 3.8a). This is to be expected as relative yield is a measure of the contribution of dry pulp to overall mass and increased water content will drive this value down in figs when other variables are constant. Relative yield was significantly positively correlated with crop size among dioecious figs but not among monoecious species (Table 3.6, Figure 3.8b). Relationships can also be detected when other measures of the level of investment in 'reward' are used. In dioecious species the dry mass of pulp increases with seed number (a function of both traits being strongly correlated with fig mass) in a manner best described by the power function $y = 0.0012x^{0.8379}$ ($r^2 = 0.813$, $n = 25$, $p < 0.01$; Figure 3.9). However, no such relationship between fig size and seed number exists among monoecious figs, because seed number varied so little across monoecious species. In monoecious (but not dioecious) figs the amount of dry pulp per seed increases with fig mass (Figure 3.10). This relationship is best described by the linear function $y = 0.0066x + 0.0004$ ($r^2 = 0.944$, $n = 18$, $p < 0.01$). That fig size and crop size are (generally) inversely related in monoecious *Ficus* species (Figure 3.6e) and that there is no relationship between fig size and seed number in these species (Figure 3.11) means that large-cropped monoecious species tend to have less pulp per seed (Figure 3.12). There was no relationship between reward (relative yield) and ballast (seed burden) in either monoecious or dioecious figs (Table 3.6; Figure 3.13).

To summarise the factors related to the amount of reward available to potentially seed-dispersing frugivores, this relative yield increases with fig size but is greater in monoecious figs than dioecious figs of a given size. Among the latter, relative yield increases with crop size and crop height but such relationships were not detected among monoecious species.

Table 3.6. Spearman correlation coefficients for fig design and presentation characters of a) 18 monoecious and b) 25 dioecious *Ficus* species. Dark shading denotes correlation significant at the 0.01 level (two-tailed), light shading denotes correlations significant at the 0.05 level (two-tailed). N.B. Crop size = total crop size, not ripe crop size.

a)

MONOECIOUS	Fig length	Fig wet mass	Pulp wet mass	Floral wet mass	Pulp proportion	Pulp dry mass	Floral dry mass	Relative yield	Pulp water content	Seed burden	Seed number	Crop height	Crop size
Fig diameter	0.91	0.96	0.91	0.97	0.49	0.88	0.93	-0.37	0.48	-0.46	0.43	0.17	-0.54
Fig length	X	0.95	0.94	0.95	0.61	0.91	0.95	-0.35	0.49	-0.61	0.44	0.27	-0.39
Fig wet mass		X	0.96	0.95	0.65	0.93	0.93	-0.40	0.56	-0.63	0.39	0.17	-0.51
Pulp wet mass			X	0.90	0.74	0.94	0.95	-0.31	0.51	-0.74	0.35	0.08	-0.58
Floral wet mass				X	0.46	0.90	0.92	-0.37	0.46	-0.46	0.48	0.25	-0.58
Pulp proportion					X	0.68	0.59	-0.21	0.51	-0.99	0.27	-0.10	-0.48
Pulp dry mass						X	0.91	-0.10	0.31	-0.69	0.44	0.13	-0.63
Floral dry mass							X	-0.30	0.45	-0.59	0.42	0.09	-0.58
Relative yield								X	-0.92	0.16	-0.05	-0.10	-0.14
Pulp water content									X	-0.45	0.18	0.02	0.00
Seed burden										X	-0.27	0.12	0.48
Seed number											X	0.12	-0.16
Crop height												X	0.34
Crop size													X

b)

DIOECIOUS	Fig length	Fig wet mass	Pulp wet mass	Floral wet mass	Pulp proportion	Pulp dry mass	Floral dry mass	Relative yield	Pulp water content	Seed burden	Seed number	Crop height	Crop size
Fig diameter	0.99	0.96	0.95	0.95	0.67	0.94	0.94	-0.39	0.73	-0.67	0.95	-0.23	-0.58
Fig length	X	0.95	0.94	0.94	0.66	0.95	0.94	-0.37	0.71	-0.66	0.95	-0.19	-0.57
Fig wet mass		X	0.99	0.98	0.67	0.97	0.97	-0.49	0.79	-0.66	0.90	-0.29	-0.65
Pulp wet mass			X	0.97	0.72	0.98	0.96	-0.48	0.81	-0.72	0.90	-0.31	-0.65
Floral wet mass				X	0.57	0.96	0.97	-0.54	0.79	-0.57	0.89	-0.29	-0.67
Pulp proportion					X	0.69	0.60	-0.13	0.60	-0.99	0.66	-0.51	-0.48
Pulp dry mass						X	0.97	-0.34	0.71	-0.68	0.92	-0.22	-0.62
Floral dry mass							X	-0.40	0.72	-0.59	0.88	-0.25	-0.67
Relative yield								X	-0.77	-0.32	-0.32	0.47	0.51
Pulp water content									X	-0.60	0.67	0.67	-0.64
Seed burden										X	-0.66	0.51	0.49
Seed number											X	-0.19	-0.54
Crop height												X	0.67
Crop size													X

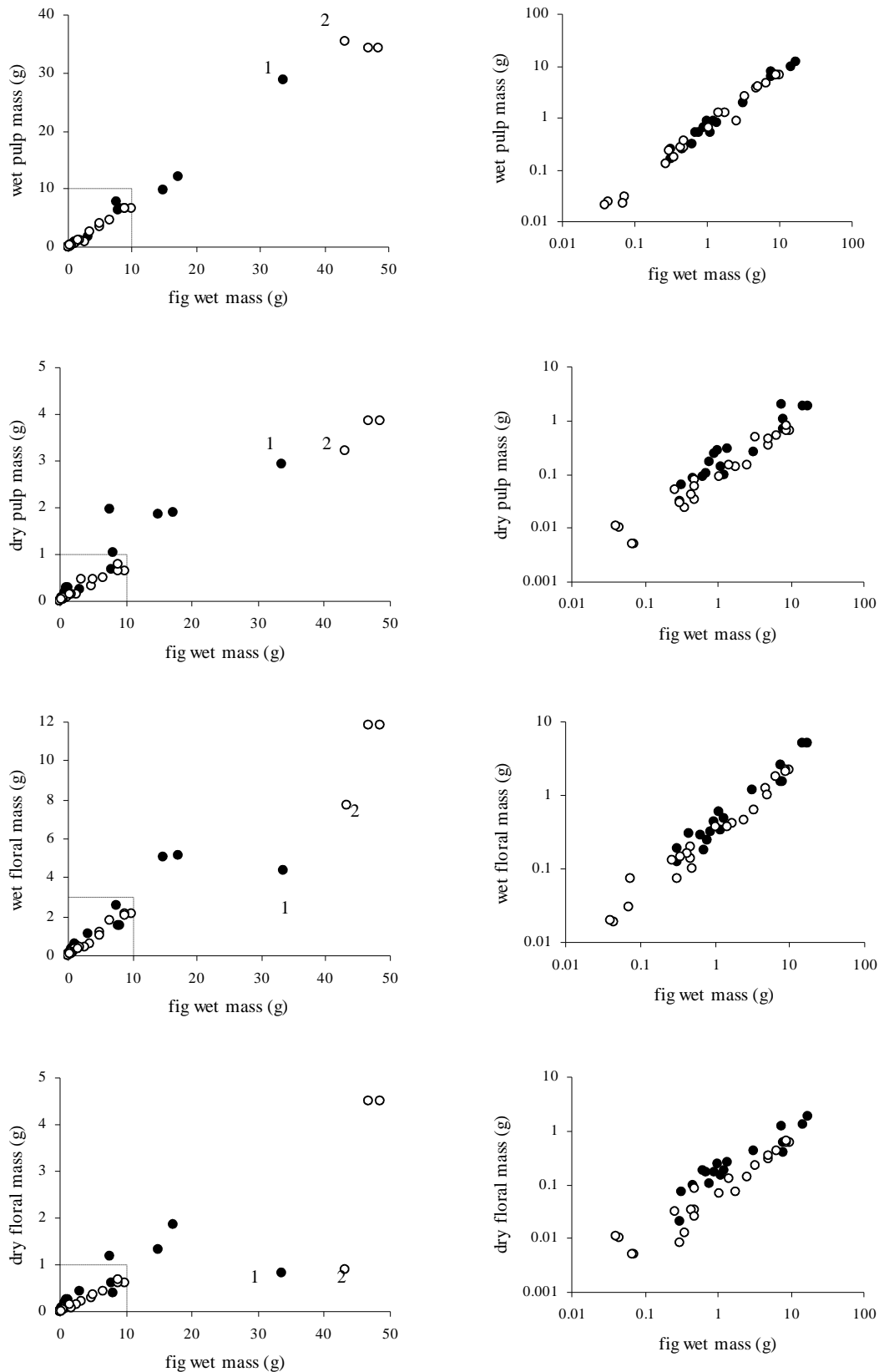


Figure 3.5. Inter-relationships among size-based fig characters. Filled circles = monoecious species, open circles = dioecious species. 1 = *Ficus annulata*, 2 = *F. cereicarpa*. For each chart in the left column the area enclosed with a broken line has been enlarged and displayed with log axes in the right column. Dioecious figs have higher wet pulp mass ($F = 7.26$, $p < 0.05$) and wet floral mass ($F = 43.9$, $p < 0.01$) and lower dry pulp mass ($F = 15.4$, $p < 0.01$) and dry floral mass ($F = 15.2$, $p < 0.01$) than monoecious figs (analysis of covariance with fig wet mass as the covariate).

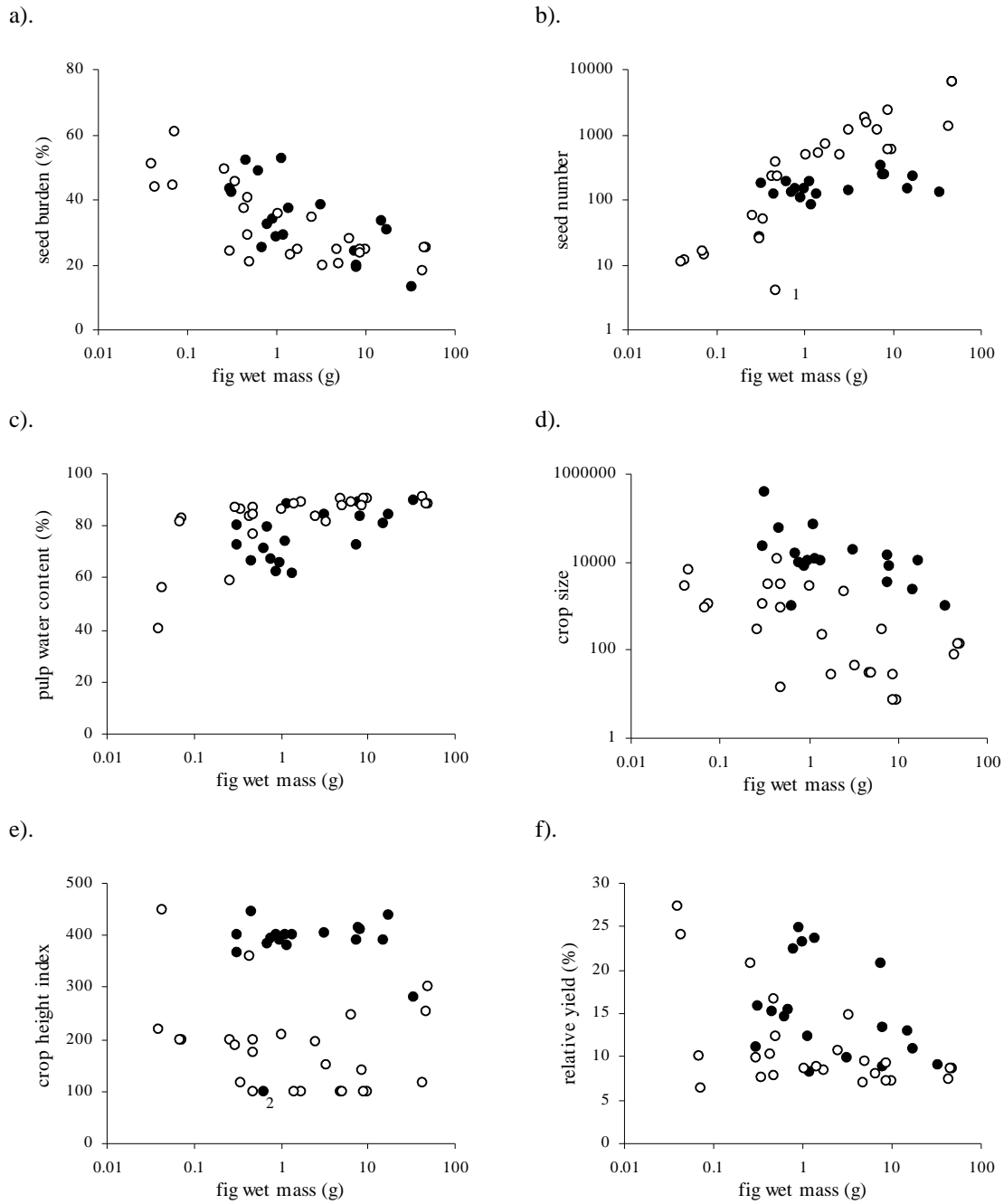


Figure 3.6. Relationships between selected fig design components and fig wet mass. Note the use of log scales in some figures. Filled circles = monoecious species, open circles = dioecious species. 1 (Figure 5b) = *Ficus deltoidea*. 2 (Figure 5e) = *Ficus acamptophylla*.

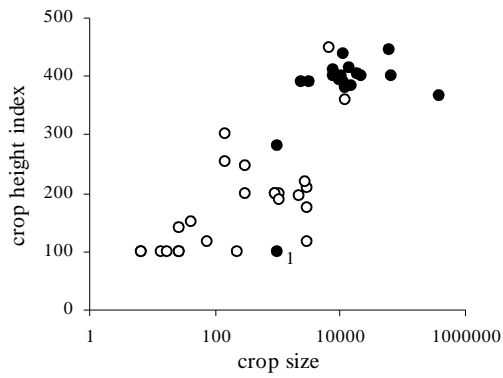


Figure 3.7. The relationship between mean crop size and crop height in monoecious (filled circles) and dioecious (open circles) *Ficus* species. Note the use of a log scale for crop size. 1 = *Ficus acantophylla*.

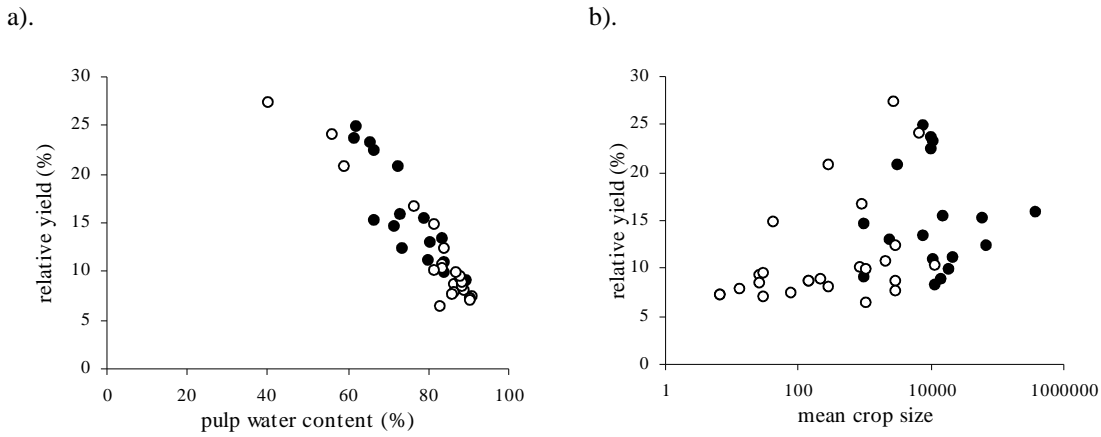


Figure 3.8. Relationships between selected fig traits and relative yield. Note the use of a log scale in part b. Filled circles = monoecious species, open circles = dioecious species.

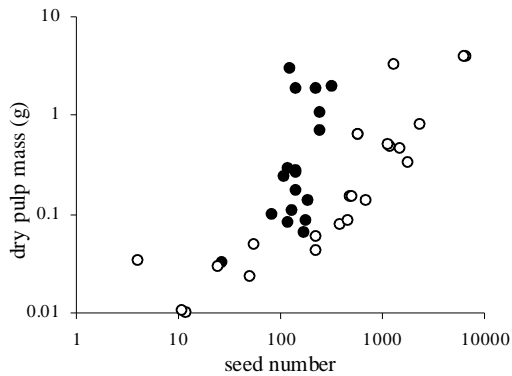


Figure 3.9. The relationship between dry pulp mass (g) and seed number in monoecious (filled circles) and dioecious (open circles) figs.

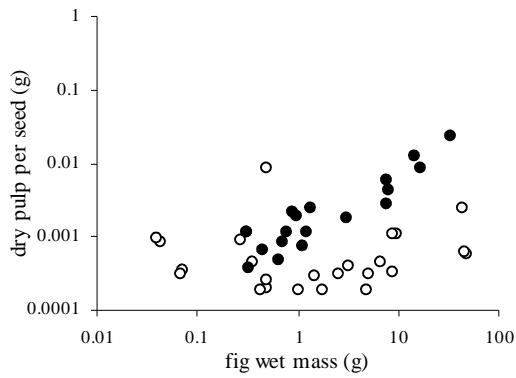


Figure 3.10. The relationship between dry pulp per seed (g) and fig wet mass in monoecious (filled circles) and dioecious (open circles) figs.

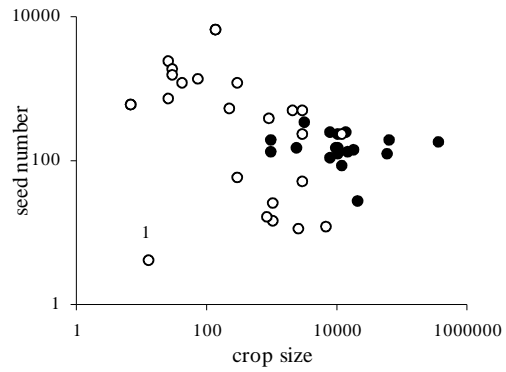


Figure 3.11. The relationship between crop size and number of seeds per fig in monoecious (filled circles) and dioecious (open circles) *Ficus* species. The outlier (1) is *F. deltoidea*

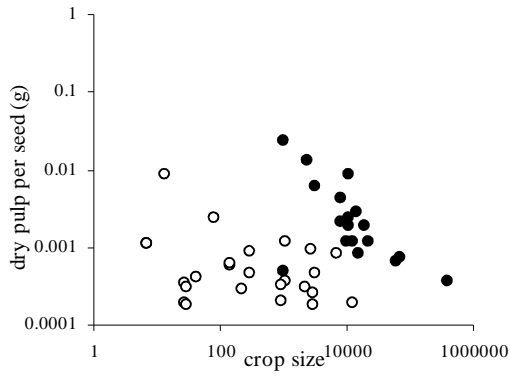


Figure 3.12. The relationship between dry pulp per seed (g) and crop size in monoecious (filled circles) and dioecious (open circles) figs.

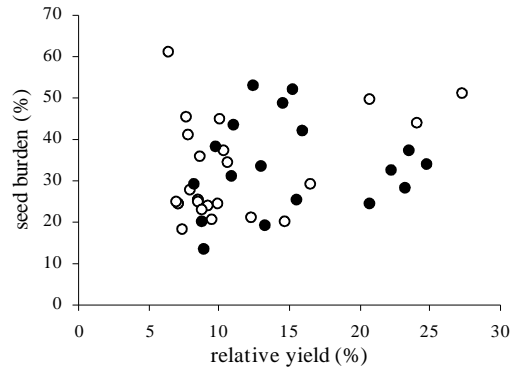


Figure 3.13. The relationship between relative yield and seed burden in monoecious (filled circles) and dioecious (open circles) figs.

3.3.4 Fruit syndromes

As already shown, many of the fig traits considered are highly inter-correlated. General patterns of covariation of fig traits were revealed by principal components analysis (PCA). Ideally, such analyses use only traits that are not inter-correlated. Whilst most traits selected were sufficiently independent, this was not entirely possible because some traits were correlated in monoecious but not dioecious species (Table 3.6). Thus, the PCA results emphasise differences (nonetheless genuine) between the two breeding systems. The first PCA analysis used fig design characters only (as opposed to crop level characters) and created two new axes (Figure 3.14). Axis one separated species primarily on the basis of fig mass, seed burden and pulp water content whilst seed number was the most important trait contributing to axis two. Although not included in the analysis, species' scores on the two PCA axes varied significantly with fig colour and breeding system (Table 3.7). Red figs (monoecious and dioecious) were, on average, smaller, less watery and with a higher seed burden than those of other colours (barring *F. annulata*, all dioecious). Monoecious figs tended to have less watery pulp and fewer seeds than dioecious figs.

Table 3.7. Summary of one-way ANOVA tests for heterogeneity of PCA (using fig design characters) axis scores among groups of *Ficus* species, based on qualitative variables.

Qualitative variable	ANOVA <i>F</i> value	
	Axis 1	Axis 2
Fig colour	11.39**	0.933 ^{NS}
Breeding system	0.268 ^{NS}	12.94**

** $p < 0.01$; ^{NS} not significant

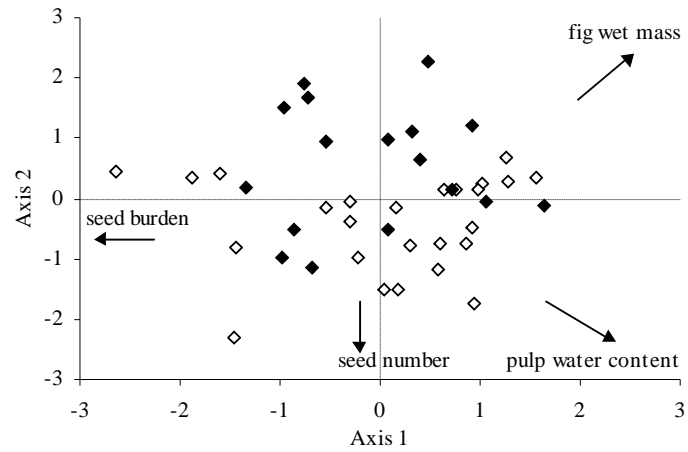
The second PCA analysis also incorporated crop height and size and emphasised the differences between monoecious and dioecious species noted earlier (Figure 3.15). The former tended to produce larger crops, at a greater height than did dioecious species. Fig colour also showed a strong association in this analysis (Table 3.8). Non-red figs were, on average, presented in the lower strata of the forest and in smaller crops than those of red figs. However, these traits (fig colour and breeding system) are also inter-related. Figure 3.16 shows the distribution of members of each *Ficus* section on the scatterplot produced by the second PCA (Figure 3.15). Not only are the monoecious species (section *Urostigma*) closely associated but so, by and large, are the members of each of the dioecious sections. Thus, *Sycocarpus* species produce large figs, in small crops that are low in the vertical structure of the forest. *Sycidium* and *Rhizocladus* species tend to have small figs but differ in that the latter are produced in greater numbers and higher in the canopy. *Kalosyce* figs are the largest under study whilst members of section *Ficus* are the least extreme of any section, clustering around the origins of both axes. These results suggest that phylogeny is an important determinant of the way in which *Ficus* species package and present their figs.

Table 3.8. Summary of one-way ANOVA tests for heterogeneity of PCA (using fig design and crop characters) axis scores among groups of *Ficus* species, based on qualitative variables.

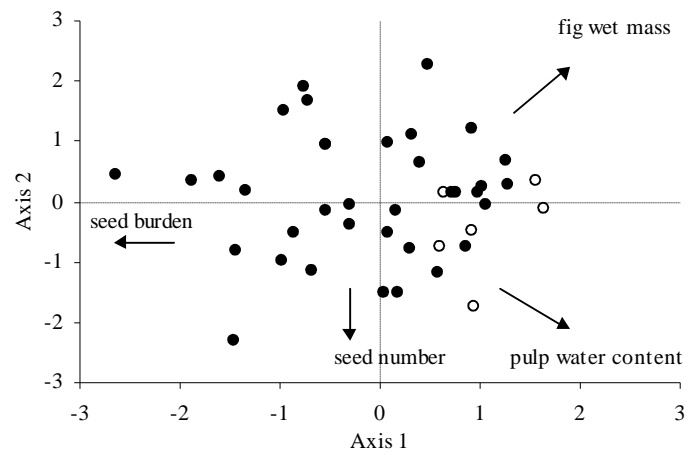
Qualitative variable	ANOVA <i>F</i> value	
	Axis 1	Axis 2
Fig colour	14.46**	0.004 ^{NS}
Breeding system	12.51**	20.49**

** $p < 0.01$; ^{NS} not significant

a).



b).

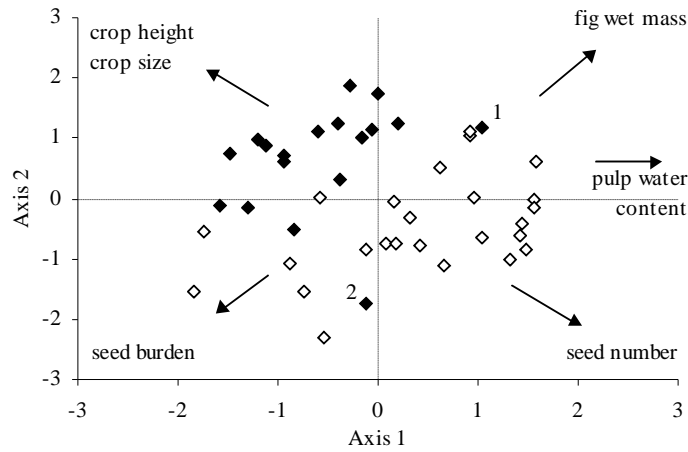


c).

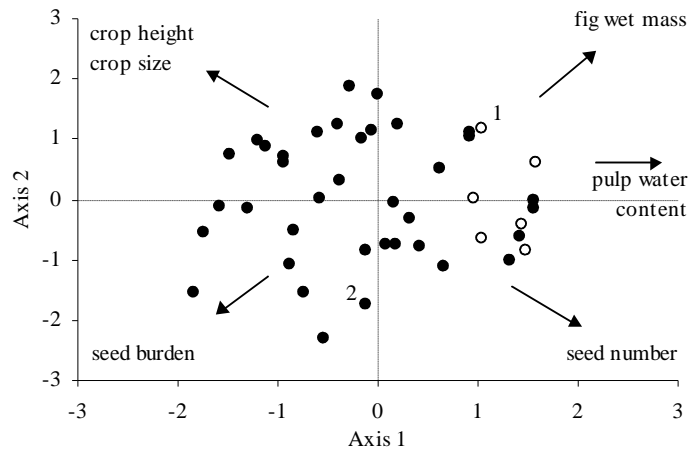
	Standardised factor coefficients	
	Axis 1	Axis 2
Fig wet mass	0.402	0.248
Pulp water content	0.362	-0.300
Seed number	0.006	-0.847
Seed burden	-0.395	-0.036
Percentage of total variance explained	55.7	28.8

Figure 3.14. PCA scatterplots for 43 *Ficus* species in Lambir Hills National Park based on fig mass, seed number, seed burden and pulp water content. a). Monoecious and dioecious species are represented by filled and open diamonds, respectively. b). Circles are filled for species with red figs and open for those with green or brown figs. c). Only two axes were derived by the PCA and the standardised factor coefficients listed indicate the direction in which each trait influences species' positions on the plot. 1 = *Ficus annulata*, 2 = *Ficus acamptophylla*.

a).



b).



c).

	Standardised factor coefficients	
	Axis 1	Axis 2
Fig wet mass	0.231	0.400
Pulp water content	0.277	0.084
Seed number	0.114	-0.428
Seed burden	-0.249	-0.296
Crop size	-0.286	0.186
Crop height index	-0.243	0.362
Percentage of total variance explained	48.1	27.7

Figure 3.15. PCA scatterplots for 43 *Ficus* species in Lambir Hills National Park based on fig mass, seed number, seed burden, pulp water content, crop height and crop size. In a) monoecious and dioecious species are represented by filled and open diamonds, respectively. In b) circles are filled for species with red figs and open for those with green or brown figs. c) Only two axes were derived by the PCA and the standardised factor coefficients listed indicate the direction in which each trait influences species' positions on the plot. 1 = *Ficus annulata*, 2 = *Ficus acamptophylla*.

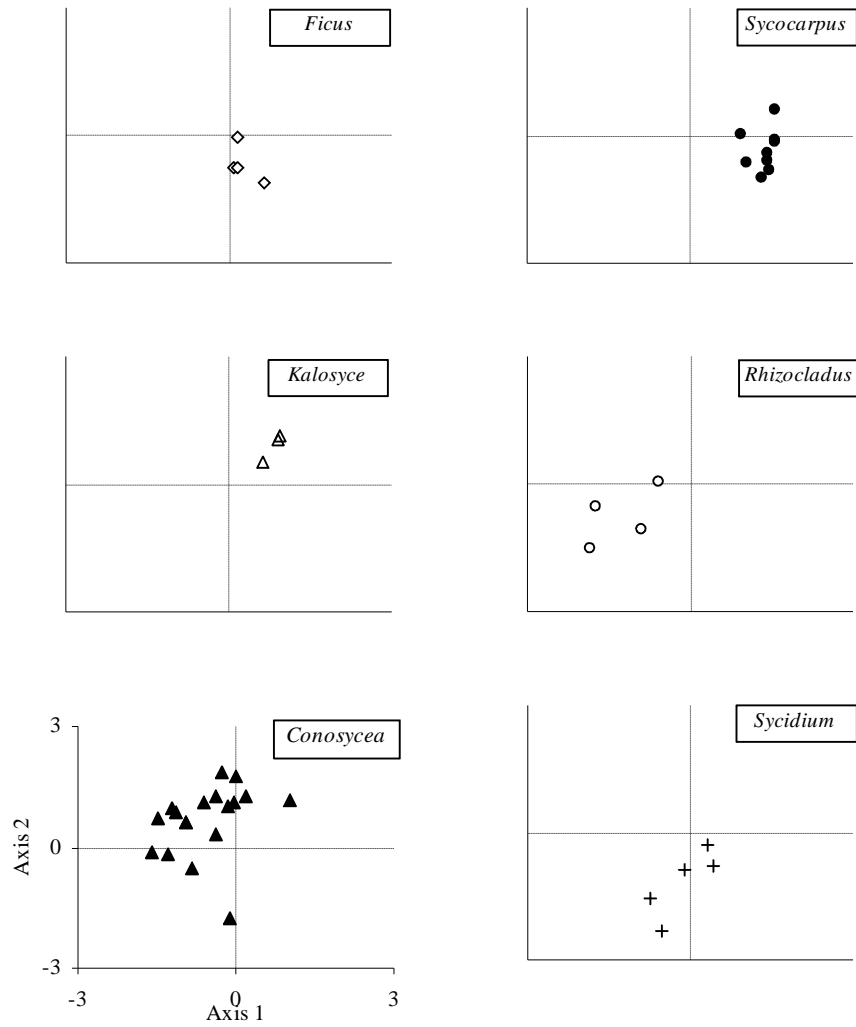


Figure 3.16. PCA scatterplot redrawn from Figure 3.15 to illustrate the distribution of members of each *Ficus* section.

3.4 DISCUSSION

3.4.1 The diversity of fig design and presentation

These results illustrate the great diversity of fruiting strategies displayed by *Ficus* species in Lambir Hills National Park. This variety reflects the fact that Borneo is a centre of diversity for the genus *Ficus*. Thus all of the growth forms reported for the genus, as well as representatives of both monoecious and dioecious breeding systems were included in this study which, covering 43 *Ficus* species, is probably the largest ever characterisation of the fruiting ecology of sympatric congeners. Kalko *et al.* (1996) considered 12 *Ficus* species in Panama but these were all monoecious and the only fruit characters they considered were colour, wet weight, size class and synchrony of ripening.

The species studied are representative of the Bornean *Ficus* flora in general and exhibit much of the diversity in fig packaging and presentation that has been reported for the genus as a whole (Corner 1965, 1988). This diversity occurs in traits associated with the presentation of fig crops as well as with the design and packaging of the figs themselves. While fig colour, crop size and crop height were highly variable, structurally, the figs of each species were more uniform (with generally soft coat and pulp, high water content, low relative yield and high pulp proportion and many small seeds). In spite of these generalisations, the species studied still exhibit variety, in terms of seed burden, pulp water content and relative yield, of a similar order to that shown across diverse families and a range of latitudes studied elsewhere (Herrera, 1981; Snow & Snow, 1988, Corlett, 1996; see Figure 3.4).

Many fig traits are determined by the size of a species' figs. The amount of ballast (seed burden) decreases with size because the pulp proportion increases. This increase in pulp volume is associated with an increase in water content of pulp in large figs. Thus, although large figs have less ballast than smaller figs they are not necessarily more nutritious because a greater proportion of their volume is water. A trade-off, reflecting costs of producing large figs, is suggested by the inverse relationship between crop size and fig size in both monoecious and dioecious *Ficus* species. Such a pattern is expected if data from non-*Ficus* species are indicative (Bazzaz & Grace, 1997).

3.4.2 Differences between monoecious and dioecious figs

Although some characters are relatively consistent throughout the genus, differences do exist between monoecious and dioecious figs. The former tended to have similar numbers of seeds regardless of fig size whereas in dioecious figs seed number was greater in larger figs. This is paradoxical since female flower number correlates positively with fig size in monoecious figs (Herre, 1989). This consistency of seed number is intriguing. It is probably not compensated for by increasing seed size, given that seed burden falls progressively in larger figs. These patterns are opposite to those observed in Panama where Herre (1989) recorded a positive relationship between fig size and seed number. The implication in Lambir is that there is progressively greater emphasis on male reproductive function in larger figs. Larger figs receive more foundress pollinator wasps than small figs. This increase in foundress number means that each foundress will produce fewer offspring on average and selects for a less female-biased sex ratio in the wasp offspring (Herre, 1989). Male wasps cannot disperse *Ficus* pollen and so in order for Lambir's monoecious species with large figs to produce the same number of pollen carriers as would occur in figs with fewer foundresses, they may commit a higher proportion of their flowers to wasp production, thereby producing fewer seeds than expected. Given that flower number scales with fig size the other alternative is that fewer of the flowers are 'used' at all in larger figs.

The large size of hemi-epiphytes predisposes them to having large crops, the figs of which tend to be relatively small. In hemi-epiphytic species that produce smaller crops of larger figs the amount of dry pulp per seed is greater because of the consistency of seed number across species. The greater relative yield of monoecious figs arises because only a certain proportion of their ovules become seeds whilst half are consumed by wasps. These weigh considerably less than seeds and, in any case, have mostly departed the fig by the time of ripening. Thus, in monoecious but not dioecious species, the investment in pulp per seed increases with fig size.

The monoecious species' large crops, presented high in the forest strata reflect the fact that all monoecious species studied were hemi-epiphytes. Dioecious species were generally smaller individuals and although present throughout the vertical structure of the forest, tended to present their fruit in the understorey and subcanopy. The degree of synchrony of crop ripening varied across both monoecious and dioecious species. Generally, between five and ten percent of a crop was ripe on a given day. Thus most crops persisted between ten and 20 days. However, while monoecious species produced discrete crops those of dioecious species tended to overlap (see Chapter 5).

3.4.3 Fruit syndromes in *Ficus*

That fig traits covary allows the recognition of fruit syndromes, though it must be noted that these exist in multi-dimensional hyperspace and are not discrete but operate as continua. They are created by the trade-offs in fig size and number, differences in fig height ruled by growth form, and the distribution of fig colour across species. These syndromes have strong phylogenetic associations. Growth form is strongly linked to phylogeny and determines presentation with respect to height and maximum crop size (which, in turn, is linked to fig size). One exception to the phylogenetic conservatism is *Ficus annulata*, which unlike the rest of the hemi-epiphytes studied, had green figs and may therefore be expected to attract different vertebrate frugivores as potential seed dispersers than other monoecious species. Indeed, as shown in the following chapter, *F. annulata* attracted fruit bats whereas the other monoecious species were fed upon by birds and arboreal mammals.

The function of a fig as an inflorescence as well as a fruit means that figs do not act solely as a reward and attractant to frugivores. In terms of the function of a fig in the seed dispersal mutualism it is important to distinguish between advertisement characters that attract potentially seed dispersing animals and reward characters that are offered as 'payment in advance' for seed dispersal services. In the *Ficus* species studied, most of the variability between figs is in the advertisement rather than the reward. This may be because the reward is constrained also by the role of fig as an inflorescence whereas presentation is more strongly linked to phylogenetic differences in growth form. However, even fig size, an important trait in terms of both reward and advertisement, is influenced by the behaviour and physiological requirements of pollinator wasps. It is interesting to know whether these generalisations hold elsewhere.

The specialist-generalist paradigm in seed dispersal ecology suggests that figs with their many small seeds, are 'generalist' fruits, predicted to attract large and diverse assemblages of non-specialised frugivores that will provide a poor seed dispersal service that is compensated for by the large number of seeds and frugivores involved (Snow, 1971; McKey, 1975; Howe, 1993). Generally figs are structurally unprotected and do not limit the frugivores that can eat them. Furthermore, they have watery pulp

and have a low relative yield, suggesting that rewards are low. Having many small seeds is also seen as characteristic of 'Low Investment Trees' (Howe, 1977, 1993). Whilst these generalisations apply to all of the *Ficus* species studied they are more marked in the monoecious species, which invest simultaneously in male and female function. This stands to reason as a proportion of any investment made by monoecious species will be lost as the ovules are used by the wasp larvae instead. Females of dioecious *Ficus* species do not have this problem.

In spite of *Ficus* species having classic generalist (soft, many seeds, low reward per seed) fruits, the variety of colour, crop size and placement suggest that some structure exists in the attraction of frugivores. This subject forms the theme of the next chapter.

CHAPTER 4

SEED DISPERSAL GUILDS IN A BORNEAN *Ficus* COMMUNITY

"many naturalists have not had the time or inclination to record what visits different species of figs in different parts of the forest, or even to keep the observations separate for different species of wild figs. A fig is not a FIG is not a fig."
Janzen (1979)

4.1 INTRODUCTION

The structure, accessibility, size, colour and other traits of fruits impose limitations with respect to the range of animals that are able to eat them, and thus act as potential seed dispersers. Studies of fleshy-fruited plant species and the animals that consume their fruit have identified syndromes of fruit characteristics associated with the attraction of subsets of frugivore communities. Birds tend to favour relatively small, soft (unprotected) fruits that are frequently red or black (Ridley, 1930; Turcek, 1963; Janson, 1983; Gautier-Hion *et al.*, 1985). Fruit eaten by fruit bats are often dull green or brown, odorous, sugary, and exposed away from the foliage on leafless branches, peduncles or are cauliflorous (van der Pijl, 1957; Marshall, 1985). Herrera (1989) described fruit characteristics associated with the attraction of carnivorous mammals in southern Spain; these included being scented, falling to the ground quickly and being red/orange, brown or black in colour. Fruit traits associated with the attraction of large rodents (fibrous, large with few, well protected seeds), squirrels (dull, dry, fibrous, few seeds, variable size), ruminants (heavy, rarely red or purple), elephants (large size, dull colour), and primates (bright colour, 5-50 g mass) have also been described (Gautier-Hion *et al.*, 1985; Yumoto *et al.*, 1995).

Great diversity in the manner in which figs are packaged and presented has been demonstrated for the genus *Ficus* in Lambir Hills National Park (Chapter 3) and in Borneo in general (Corner 1965). This diversity, together with the widely-cited year-round production of figs in the region (e.g. Leighton & Leighton, 1983; Lambert, 1987; Lambert & Marshall, 1991), suggest not only that figs will be available to a wide range of frugivores, but also that some structure exists in the frequency of interactions between different figs and fig-eaters.

The classic fruit syndromes described in the literature suggest that birds will feed upon red figs and that fruit bats preferentially eat green figs (e.g. Ridley, 1930; van der Pijl, 1957; Snow, 1981). Indeed, Kalko *et al.* (1996) and Korine *et al.* (2000) observed this pattern on Barro Colorado Island, Panama. However, the *Ficus* community studied by these authors comprised just 12 species, all of which are monoecious. The greater diversity of *Ficus* in Borneo, in terms of breeding system, growth form and species number (Corner, 1965; Chapter 3), and the wider range of potential seed dispersers suggest a more complex system of fig-frugivore partitioning.

Such partitioning has implications for interspecific competition and species coexistence, differential seed dispersal and potential for regeneration. Furthermore, structure to the distribution of frugivore use of different *Ficus* species will necessitate a re-evaluation of the keystone resource concept applied to 'figs' as a whole. Detection of associations between *Ficus* fruit characters and frugivore taxa may allow the competing hypotheses of a) coevolutionary change between plants and dispersers and b) phylogenetic constraint in determining fig packaging and presentation to be examined.

In this chapter I identify the fig eating fauna of the main field site, Lambir Hills National Park, Sarawak. I seek to determine whether there are guilds of *Ficus* species that share (and potentially compete for) discrete subsets of the frugivore community and relate my findings to the diversity of fig design and presentation, vertical stratification of figs and frugivores and phylogenetic constraints.

4.2 METHODS

4.2.1 Sampling

Ficus individuals with ripe crops were located and identified as described in Chapter 3. Again, efforts were made to include individuals of all growth forms (hemi-epiphytic, climbers, freestanding trees) and fruit-production patterns (geocarpy, cauliflory, axillary) in this study. For dioecious species only female trees were considered.

4.2.2 Identification of frugivores

Ficus crops with ripe fruit were selected for the observation of frugivory on the basis of their visibility, the criterion being that at least half of the fruit crop could be seen. Observations of frugivory were made during one to three hour sessions divided into a series of scan samples of five minutes duration. During each of these, the identities and numbers of each frugivore species observed eating figs were recorded. Frugivores were identified by reference to MacKinnon and Phillips (1993) and Payne *et al.* (1985) for birds and mammals, respectively. Each crop was observed during both day and night with observation sessions usually beginning at 6 a.m. and 7 p.m., respectively; and continuing until crops of each species had been observed for 20 hours, with an approximately 60:40 time allocation in favour of diurnal observations. Crops in the canopy were viewed from adjacent ridges or from tree towers, ladders or canopy walkways. Diurnal observations were made using 8 × 32 binoculars or a 25 × telescope that aided species identifications at fig crops away from the walkways and towers. Nocturnal observations were made by spotlighting and the use of a Retron night-vision scope. Since mist netting of fruit bats was not permitted, identification to species of these frugivores was not possible. As an alternative, morphological differences in palatal imprints found at feeding sites were used to distinguish two bat taxa, (see RESULTS). The differences in methodology of recording frugivore visits are not of major concern since all analyses were based on readily comparable data (frugivore species' proportional contributions to overall feeding observations at any given crop; see below).

4.2.3 *Ficus* dispersal guilds

The degree of overlap between *Ficus* species in the attraction of frugivores was measured using Horn's (1966) adaptation of Morisita's index which ranges from 0 (no overlap) to 1 (total overlap) and is calculated as

$$C = \sum x_i y_i / (\sum x_i^2 + \sum y_i^2)$$

where x_i = the proportion of feeding records for fig species x made by frugivore i and y_i = proportion of feeding records for fig species y made by frugivore i . As a measure of *Ficus* niche breadth (in terms of fig eaters) and frugivore niche breadth (with respect to the range of *Ficus* species they utilise), Simpson's index (see Ulfstrand, 1977) was calculated as

$$B = \frac{1}{\sum_i^n p_i^2}$$

where p_i represents the proportion of observations falling in the i th of n categories and B can range from 1 to n . The index describes not only the richness (species number) of either figs in the diet of frugivores or frugivores attracted to *Ficus* species, but also the degree of evenness of species' contribution to total observations.

Two methods were used to identify *Ficus* seed dispersal guilds using data on the proportional contributions of each frugivore species to overall feeding visits at each *Ficus* species. Firstly, detrended correspondence analysis (using the Fortran program DECORANA; Hill, 1979) was used to differentiate guilds of frugivores and *Ficus* species. Correspondence analysis reduces data from multidimensional distributions to newly derived axes that explain maximum variation in the dataset. Being a form of reciprocal averaging, DECORANA produces two plots, one that positions frugivores with similar diets together and one that groups *Ficus* species that attract similar frugivore assemblages. The *Ficus* dispersal guild structure was also graphically represented using hierarchical cluster analysis (single linkage, Euclidean distance) of the same dataset using the SYSTAT package (SPSS, 1997).

4.3 RESULTS

4.3.1 Sampling effort

Nearly 700 hours were spent observing ripe crops of 34 *Ficus* species (Table 4.1), approximately 42 % of the field site's *Ficus* community (Harrison, 1997, 1998) and 25 % of that of Borneo (Corner, 1965). Bronstein and Hoffman (1987) point out that, because of spatial and temporal variation in frugivory, observations of single crops may not be informative. In this study, factors such as rarity, and timing and visibility of crops limited observations of frugivory. For a number of dioecious species, the absence of pollinator wasps meant that no ripe crops were produced for part of the year (see Chapter 5). For these reasons sample sizes per species were small (Table 4.1). Spatial and temporal variation in the attraction of frugivores to the species studied here is discussed later. Examination of inter-crop differences in frugivore attraction for the *Ficus* species for which the largest sample sizes were obtained suggest that small samples were sufficient to make conclusions about *Ficus*-frugivore interactions *in this site and at the time of the study*. Figure 4.1 shows that observing additional crops did not markedly increase the total number of species recorded feeding on given *Ficus* species' figs. Furthermore, frugivore species that were added to the total list by observing additional crops contributed relatively little to total feeding visits and the same frugivore species dominated feeding visits across crops of each of the *Ficus* species examined (Table 4.2). For these reasons data from different individuals of each *Ficus* species were combined for the following analyses.

4.3.2 Vertebrate frugivore diversity

Sixty-nine vertebrate taxa were recorded eating figs (Table 4.3). Species accumulation curves suggest that the majority of the frugivores present in the area that were capable of feeding on a given *Ficus* species' figs were observed (Figure 4.2). The observed fig eating community comprised 49 bird species in 13 families and 20 mammal species in 10 families (Table 4.3). Fig-eaters included obligate frugivores (e.g. fruit bats and fruit pigeons), more generalist feeders (e.g. treeshrews, leafbirds and bulbuls) and opportunists such as the Magpie Robin (*Copsychus saularis*) and Maroon-breasted Philentoma (*Philentoma velatum*) that are primarily insectivorous (MacKinnon & Phillips, 1993). Although observations of fruit bats were infrequent, readily observable differences in the size of palatal imprints suggest that at least two bat species fed on figs (Figure 4.3, 4.4). Based on skull sizes of Bornean bats (Payne *et al.*, 1985), the large palatal imprints are likely to have been made by *Pteropus vampyrus*. Four smaller fruit bat species (*Penthetor lucasii*, *Balionycteris maculata*, *Chironax melanocephala* and *Cynoptyrus brachyotis*) have also been recorded from the park (Shanahan & Debski, in press; Appendix 1). The provenance of the smaller palatal imprints cannot, therefore, be determined beyond being from non-*Pteropus* fruit bats.

The vertebrate fauna of Lambir (Shanahan & Debski, in press; Appendix 1) includes further species that are known to eat figs (or have congeners that do so) but which were not recorded doing so during this study (Appendix 3). These include obligate frugivores, omnivores and opportunists. Reasons for not having recorded these species are likely to include their rarity, small size, nocturnal habits or infrequency of frugivory. On the basis of these records from the literature, I estimate that 44.4 - 73.02 % of mammal species and 29.9 - 41.8 % of birds recorded from the park are likely to include figs in their diet (Table 4.4).

Whilst seven hornbill species and three genera of primates have been recorded in the park (see Shanahan & Debski, in press; Appendix 1) observations of these taxa were infrequent or non-existent. Tables 4.5 and 4.6 show, for 20 *Ficus* species for which data exist from other sites in the region (Shanahan & So, in review; Chapter 7), which of Lambir's hornbill and primate species have been recorded eating their figs. It is evident that observations of hornbills and primates were less frequent than might have been expected. Indeed, I failed to record hornbills at eight of the *Ficus* species they are known to consume. Fifteen of the *Ficus* species studied have been recorded in the diets of Lambir's hornbills either in this study or elsewhere. This suggests a total of 105 (7 × 15) *Ficus* - hornbill interactions are possible. However, only 17 (16.2 %) were recorded here, whereas 60 (57.1 %) have been recorded elsewhere. The Helmeted Hornbill (*Buceros vigil*), although recorded from the area, was not observed at any *Ficus* crops. For primates the discrepancy is even greater. Monkeys and gibbons, historically recorded in the park, were not observed at crops of 15 *Ficus* species known from their diets. Nineteen of the *Ficus* species described here have been recorded from the diets of Lambir's three primate genera. Whilst 41 (71.9 %) of a possible 57 (19 × 3) *Ficus* - primate interactions have

been recorded elsewhere only 4 (7.02 %) were observed here. Indeed, no observations were made of Bornean Gibbon (*Hylobates muelleri*), Banded Langur (*Presbytis melalophos*) or Hose's Langur (*P. hosei*).

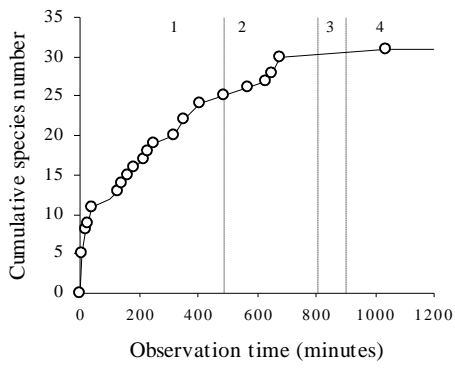
Similarly, fruit bats are known to eat figs of many hemi-epiphytic *Ficus* species but (with the exception of *F. annulata*) were not observed to do so in this study. A large day roost of 130 *Pteropus vampyrus* bats was observed in the park for just two days. Apart from a three week period during which small numbers (< 30) of these bats were observed departing on foraging trips at dusk, the species was not observed during 18 months spent in the field. Observations of smaller fruit bats were also infrequent. This may be related to the general mortality and crop failure (due to local pollinator extinction) of a favoured food, *F. schwarzii* figs, during a period of intense drought (Harrison, 2000).

It would appear that these avian and mammalian frugivores are either locally extinct, present at very low densities, or were simply not spatio-temporally coincident with ripe fig crops during the study. Nonetheless, the 75 ha under study contain the park's highest density of *Ficus* (Dr. R. Harrison, pers. comm.) and the species accumulation curves (Figure 4.2) suggest that sufficient observations were made to record *Ficus* species' assemblages of potential dispersers. Therefore, although a greater local abundance of hornbills, primates and fruit bats feeding on the figs in question would have altered the findings reported here, the results still apply to this particular site.

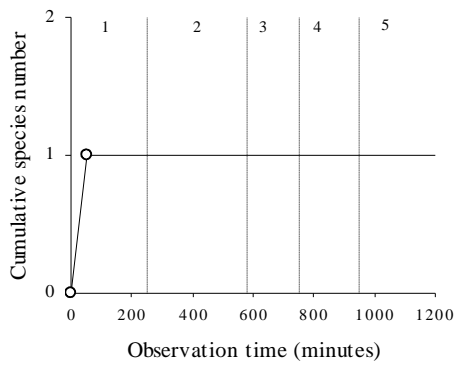
Table 4.1. Sampling effort for observation of frugivory at *Ficus* crops (no two crops from the same tree were monitored).

<i>Ficus</i> species	n individuals	observation time (hours)
<i>F. acamptophylla</i>	1	20
<i>F. annulata</i>	4	20
<i>F. aurantiacea</i>	3	20
<i>F. aurata</i>	1	20
<i>F. benjamina</i>	4	20
<i>F. callicarpides</i>	2	20
<i>F. callophylla</i>	1	20
<i>F. cereicarpa</i>	3	20
<i>F. condensa</i>	2	20
<i>F. consociata</i>	2	20
<i>F. dubia</i>	3	20
<i>F. fulva</i>	2	20
<i>F. geocharis</i>	2	20
<i>F. kerkhovenii</i>	4	20
<i>F. megaleia</i>	2	20
<i>F. obscura</i>	2	20
<i>F. pisocarpa</i>	3	20
<i>F. punctata</i>	4	20
<i>F. sarawakensis</i>	2	20
<i>F. schwarzii</i>	5	20
<i>F. sinuata</i>	1	20
<i>F. stolonifera</i>	2	20
<i>F. stricta</i>	2	20
<i>F. stupenda</i>	3	20
<i>F. subcordata</i>	2	20
<i>F. subgelderi</i>	2	20
<i>F. subulata</i>	2	20
<i>F. sumatrana</i>	3	20
<i>F. sundaica</i>	2	20
<i>F. treubii</i>	3	20
<i>F. uncinata</i>	2	20
<i>F. 'near' uncinata</i>	1	20
<i>F. uniglandulosa</i>	1	20
<i>F. xylophylla</i>	3	20
TOTAL	81	680

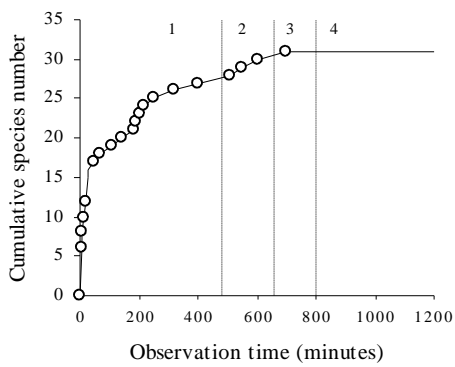
a). *F. benjamina*



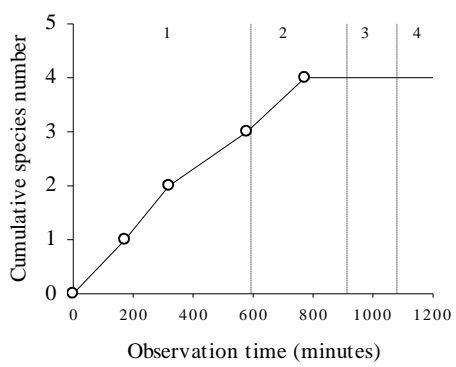
b). *F. schwarzii*



c). *F. kerkhovenii*



d). *F. punctata*



e). *F. annulata*

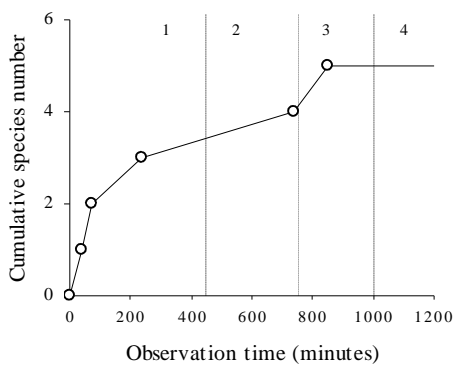


Figure 4.1. Species accumulation curves for frugivore species recorded at crops of five *Ficus* species. Dashed lines demarcate crops on different individuals (numbered 1-5). Note that y-axis scales vary.

Table 4.2. Comparisons of frugivore attraction between crops of the five *Ficus* species with the greatest sampling effort in terms of numbers of crops observed. Scientific names of frugivores appear in Table 4.3. *See text and Figures 4.3 and 4.4.

<i>Ficus</i> species	Frugivore species	Percentage of all feeding visits at crop number				
		1	2	3	4	5
<i>F. schwarzii</i>	non- <i>Pteropus</i> fruit bat*	100	100	100	100	100
<i>F. benjamina</i>	Thick-billed Green-Pigeon	26	23	22	31	-
	Red-eyed Bulbul	21	22	19	16	-
	Brown Barbet	8	14	13	11	-
	Prevost's Squirrel	8	8	8	6	-
	Fairy Bluebird	5	7	9	5	-
	Red-throated Barbet	4	4	4	7	-
	Red-crowned Barbet	5	7	5	6	-
	Other species	23	15	20	18	-
	sum	100	100	100	100	-
<i>F. annulata</i>	Large Flying Fox	54	59	54	36	-
	non- <i>Pteropus</i> fruit bat*	39	33	44	64	-
	Binturong	7	0	0	0	-
	Red-crowned Barbet	0	0	2	0	-
	Prevost's Squirrel	0	8	0	0	-
	sum	100	100	100	100	-
<i>F. punctata</i>	Pig-tailed Macaque	66	43	64	73	-
	Long-tailed Macaque	11	23	0	5	-
	Prevost's Squirrel	23	23	28	16	-
	Giant Squirrel	0	11	8	6	-
	sum	100	100	100	100	-
<i>F. kerkhovenii</i>	Thick-billed Green-Pigeon	32	30	39	33	-
	Brown Barbet	17	14	11	15	-
	Red-eyed Bulbul	8	13	12	12	-
	Prevost's Squirrel	13	13	5	9	-
	Fairy Bluebird	2	4	9	3	-
	Red-throated Barbet	5	8	5	7	-
	Red-crowned Barbet	9	6	4	7	-
	Other species	14	12	15	13	-
	sum	100	100	100	100	-

Table 4.3. Vertebrate species recorded eating figs in Lambir Hills National Park. **Tupaia minor* and *T. gracilis* are virtually indistinguishable in the field (Payne *et al.* 1985) and are treated as a single species here. Nomenclature follows Payne *et al.* (1985) for mammals and MacKinnon & Phillipps (1993) for birds.

Class	Order	Family	Species	
MAMMALIA	Scandentia	Tupaiaidae	Lesser/Slender Treeshrew <i>Tupaia minor/gracilis</i> *	
			Common Treeshrew <i>Tupaia glis</i>	
	Primates	Cercopithecidae	Large Treeshrew <i>Tupaia tana</i>	
			Long-tailed Macaque <i>Macaca fascicularis</i>	
	Chiroptera	Pteropodidae	Pig-tailed Macaque <i>Macaca nemestrina</i>	
			Large Flying Fox <i>Pteropus vampyrus</i>	
	Artiodactyla	Tragulidae	non- <i>Pteropus</i> fruit bat species	
			Lesser Mouse-Deer <i>Tragulus javanicus</i>	
	Carnivora	Suidae	Bearded Pig <i>Sus barbatus</i>	
			Bornean Yellow Muntjac <i>Muntiacus atherodes</i>	
	Rodentia	Viverridae	Binturong <i>Arctictis binturong</i>	
			Muller's Rat <i>Sundamys muelleri</i>	
		Muridae	Long-tailed Porcupine <i>Trychus fasciculata</i>	
			Earspot Squirrel <i>Callosciurus adamsi</i>	
		Hystricidae	Giant Squirrel <i>Ratufa affinis</i>	
			Plantain Squirrel <i>Callosciurus notatus</i>	
	Sciuridae	Prevost's Squirrel <i>Callosciurus prevosti</i>		
		Low's Squirrel <i>Sundasciurus lowi</i>		
				unidentified small flying squirrel (not <i>Petaurista</i>)
				Red Giant Flying-Squirrel <i>Petaurista petaurista</i>
AVES	Piciformes	Bucerotidae	White-crowned Hornbill <i>Aceros comatus</i>	
			Wreathed Hornbill <i>Aceros undulatus</i>	
			Rhinoceros Hornbill <i>Buceros rhinoceros</i>	
			Asian Black Hornbill <i>Anthracoceros malayanus</i>	
			Bushy-crested Hornbill <i>Anorrhinus galeritus</i>	
			Wrinkled Hornbill <i>Aceros corrugatus</i>	
		Megalaimidae	Red-crowned Barbet <i>Megalaima rafflesii</i>	
			Red-throated Barbet <i>Megalaima mystacophanus</i>	
			Blue-eared Barbet <i>Megalaima australis</i>	
			Brown Barbet <i>Calorhamphus fuliginosus</i>	
			Asian Koel <i>Eudynamis scolopacea</i>	
			Long-tailed Parakeet <i>Psittacula longicauda</i>	
			Blue-crowned Hanging-Parrot <i>Loriculus galgulus</i>	
			Pink-necked Green-Pigeon <i>Treron vernans</i>	
	Cuculiformes	Cuculidae	Little Green-Pigeon <i>Treron olax</i>	
			Large Green-Pigeon <i>Treron capellei</i>	
	Pstittaciformes	Pstittacidae	Jambu Fruit Dove <i>Ptilinopus jambu</i>	
			Green Imperial-Pigeon <i>Ducula aenea</i>	
	Columbiformes	Columbidae	Emerald Dove <i>Chalcophaps indica</i>	
			Thick-billed Green-Pigeon <i>Treron curvirostra</i>	
			Black Magpie <i>Platysmurus leucopterus</i>	
			Slender-billed Crow <i>Corvus enca</i>	
			Maroon-breasted Philentoma <i>Philentoma velatum</i>	
			Green Broadbill <i>Calyptomena viridis</i>	
			Dark-throated Oriole <i>Oriolus xanthonotus</i>	
			Greater Green Leafbird <i>Chloropsis somnerati</i>	
			Blue-winged Leafbird <i>Chloropsis cochinchinensis</i>	
			Fairy Bluebird <i>Irene puella</i>	
	Passeriformes	Corvidae	Lesser Green Leafbird <i>Chloropsis cyanopogon</i>	
			Magpie Robin <i>Copsychus saularis</i>	
			Orange-bellied Flowerpecker <i>Dicaeum trigonostigma</i>	
		Eurylaimidae	Yellow-rumped Flowerpecker <i>Prionochilus xanthopygius</i>	
			Scarlet-breasted Flowerpecker <i>Prionochilus thoracicus</i>	
Irenidae		Crimson-breasted Flowerpecker <i>Prionochilus percussus</i>		
		Yellow-vented Bulbul <i>Pycnonotus goiavier</i>		
Muscicapidae		Nectariniidae	Streaked Bulbul <i>Ixos malaccensis</i>	
			Hook-billed Bulbul <i>Setornis criniger</i>	
			Yellow-bellied Bulbul <i>Alophoixus phaeocephalus</i>	
			Grey-cheeked Bulbul <i>Alophoixus bres</i>	
			Olive-winged Bulbul <i>Pycnonotus plumosus</i>	
			Red-eyed Bulbul <i>Pycnonotus brunneus</i>	
	Puff-backed Bulbul <i>Pycnonotus eutilotus</i>			
	Hairy-backed Bulbul <i>Tricholestes criniger</i>			
	Black-headed Bulbul <i>Pycnonotus atriceps</i>			
	Spectacled Bulbul <i>Pycnonotus erythrophthalmos</i>			
Buff-vented Bulbul <i>Iole olivacea</i>				
Pycnonotidae	Cream-vented Bulbul <i>Pycnonotus simplex</i>			
	Hill Myna <i>Gracula religiosa</i>			
	Brown Fulvetta <i>Alcippe brunneicauda</i>			
		Sturnidae		
		Sylviidae		

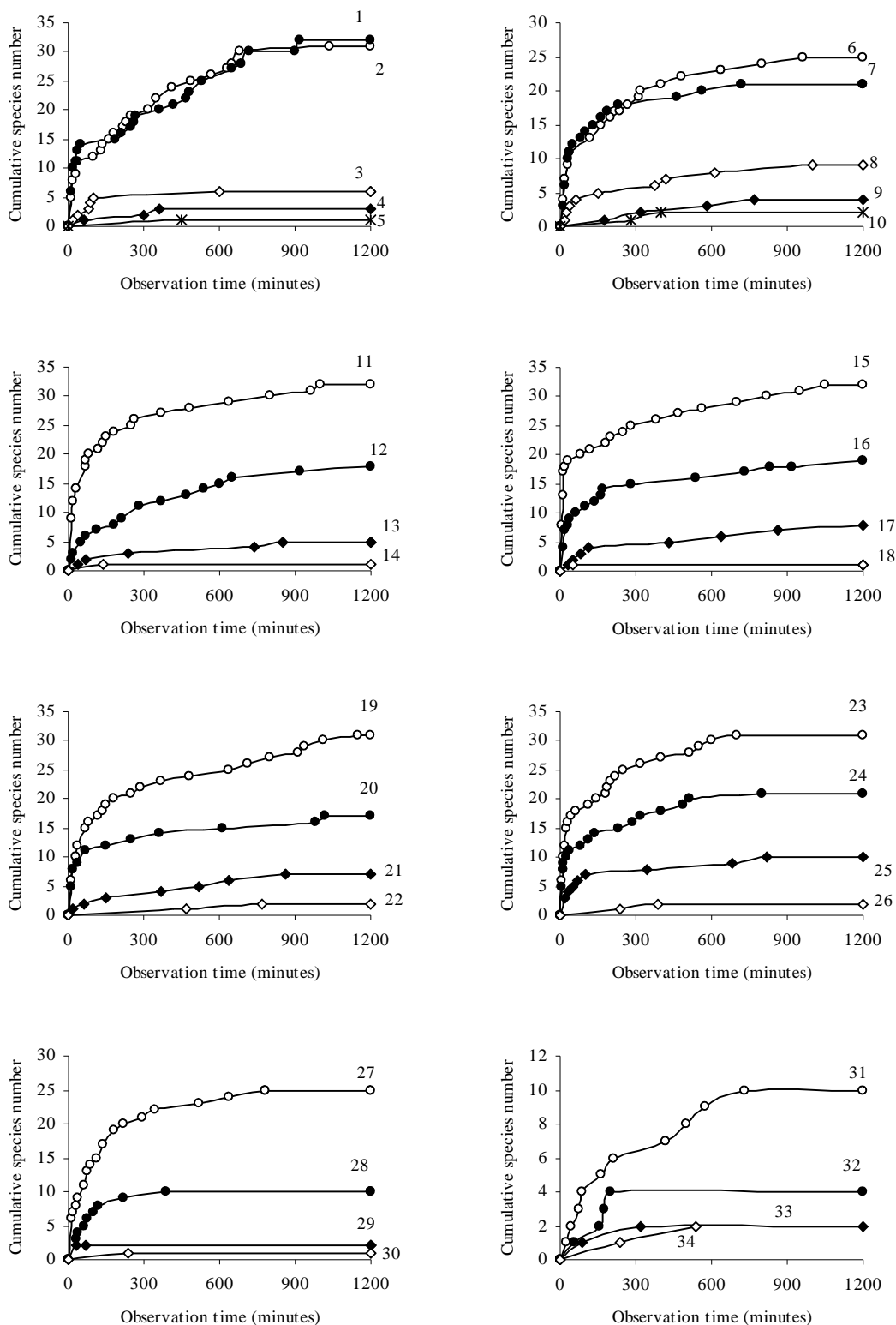


Figure 4.2. Species accumulation curves for frugivore assemblages feeding on *Ficus* species' crops in Lambir Hills National Park. 1 = *F. pisocarpa*, 2 = *F. benamina*, 3 = *F. uniglandulosa*, 4 = *F. treubii*, 5 = *F. aurantiacea*, 6 = *F. stricta*, 7 = *F. consociata*, 8 = *F. obscura*, 9 = *F. punctata*, 10 = *F. geocharis*, 11 = *F. stupenda*, 12 = *F. fulva*, 13 = *F. annulata*, 14 = *F. sarawakensis*, 15 = *F. subcordata*, 16 = *F. sumatrana*, 17 = *F. aurata*, 18 = *F. schwarzii*, 19 = *F. callophylla*, 20 = *F. sundaica*, 21 = *F. sinuata*, 22 = *F. stolonifera*, 23 = *F. kerkhovenii*, 24 = *F. dubia*, 25 = *F. xylophylla*, 26 = *F. megaleia*, 27 = *F. subgeldereri*, 28 = *F. subulata*, 29 = *F. condensa*, 30 = *F. cereicarpa*, 31 = *F. acamptophylla*, 32 = *F. uninata*, 33 = *F. callicarpides*, 34 = *F. near uncinata*.

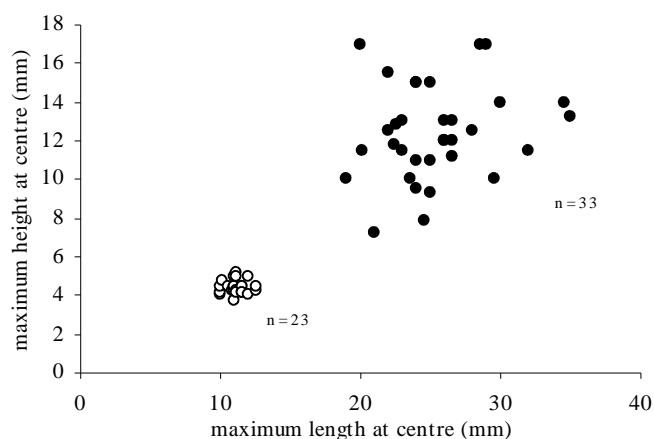


Figure 4.3. Morphological differences in fruit bat palatal imprints. Filled circles = *Pteropus vampyrus*, open circles = non-*Pteropus* fruit bats



Figure 4.4. Palatal imprints assumed to be those of *Pteropus vampyrus* (below) and non-*Pteropus* fruit bats (above)

Table 4.4. Potential fig eating fauna of Lambir Hills National Park Total bird and mammal figures from Shanahan & Debski (in press; Appendix 1).

	Birds		Mammals		
	n	%	n	%	
Total number of species	237		63		
Species recorded eating figs in this study (Table 4.2)	49	20.7	20	31.7	
Additional species recorded eating figs elsewhere (Appendix 3)	22		8		
	Total	71	29.9	28	44.4
Additional species with fig eating congeners (Appendix 3)	28		18		
	Total	99	41.8	46	73.02
Total number of genera	145		42		
Genera recorded eating figs in this study (Table 4.2)	31	21.4	15	35.7	
Genera recorded eating figs elsewhere (Appendix 3)	23		11		
	Total	54	37.2	26	61.9

Table 4.5. *Ficus* species fed upon by Lambir Hills National Park's seven hornbill species in Lambir (L) and elsewhere (E; Shanahan & So, in review; Chapter 7).

<i>Ficus</i> species	Hornbill species							Total species recorded			
	<i>A. galeritus</i>	<i>A. comatus</i>	<i>A. corrugatus</i>	<i>A. undulatus</i>	<i>A. malayanus</i>	<i>B. rhinoceros</i>	<i>B. vigil</i>	Lambir		Elsewhere	
								n	%	n	%
<i>F. acamptophylla</i>	E	E		E	E	E		0	0	5	71.4
<i>F. aurantiacea</i>				E	E			0	0	2	28.6
<i>F. benjamina</i>				E	E	E	E	0	0	4	57.1
<i>F. callophylla</i>				E	L, E			1	14.3	2	28.6
<i>F. consociata</i>	E				E			0	0	2	28.6
<i>F. dubia</i>	E		E	L, E	L, E	E	E	3	42.9	6	85.7
<i>F. kerkhovenii</i>	L, E		E	E	E	E	E	1	14.3	6	85.7
<i>F. sinuata</i>							E	0	0	1	14.3
<i>F. pisocarpa</i>	E		L		L, E	E		2	28.6	3	42.9
<i>F. stricta</i>					L, E			1	14.3	1	14.3
<i>F. stupenda</i>	E	E	E	L, E	L, E	E	E	2	28.6	7	100
<i>F. subcordata</i>		L	L	L	L, E	L, E	E	5	71.4	3	42.9
<i>F. subgelderii</i>				E	E	E		0	0	3	42.9
<i>F. sumatrana</i>	E				E	E		0	0	3	42.9
<i>F. sundaica</i>	E	E		E	E	E	E	0	0	6	85.7
<i>F. xylophylla</i>	E		E	L, E	L, E	E	E	2	28.6	6	85.7

Table 4.6. *Ficus* species fed upon by Lambir Hills National Park's three primate genera in Lambir (L) and elsewhere (E; Shanahan & So, in review; Chapter 7).

<i>Ficus</i> species	Primate genera			Total genera recorded			
	<i>Macaca</i>	<i>Presbytis</i>	<i>Hylobates</i>	Lambir		Elsewhere	
				n	%	n	%
<i>F. annulata</i>	E	E	E	0	0	3	100
<i>F. aurantiacea</i>	L, E	E	E	1	33.3	3	100
<i>F. benjamina</i>	E		E	0	0	2	66.7
<i>F. callophylla</i>			E	0	0	1	33.3
<i>F. consociata</i>	E		E	0	0	2	66.7
<i>F. dubia</i>	L, E	E	E	1	33.3	3	100
<i>F. fulva</i>			E	0	0	1	33.3
<i>F. kerkhovenii</i>	E		E	0	0	2	66.7
<i>F. obscura</i>	E		E	0	0	2	66.7
<i>F. pisocarpa</i>	E		E	0	0	2	66.7
<i>F. schwarzii</i>		E		0	0	1	33.3
<i>F. sinuata</i>			E	0	0	1	33.3
<i>F. stricta</i>	E	E	E	0	0	3	100
<i>F. stupenda</i>	L, E	E	E	1	33.3	3	100
<i>F. subcordata</i>	L, E	E	E	1	33.3	3	100
<i>F. subulata</i>	E	E		0	0	2	66.7
<i>F. sumatrana</i>	E	E	E	0	0	3	100
<i>F. sundaica</i>	E		E	0	0	2	66.7
<i>F. xylophylla</i>	E		E	0	0	2	66.7

4.3.3 *Ficus* dispersal guilds

Frugivore species did not feed on all the figs present nor did any single *Ficus* species attract all frugivores present. Indeed, only 414 (17.4%) of 2380 possible *Ficus* - frugivore interactions shown in Table 4.7 were observed. The total number of frugivores a *Ficus* species attracted to a crop varied from one to 32. Species accumulation curves for each *Ficus* species generally reached a plateau within the period of observation (Figure 4.2) indicating that the observed differences in assemblage sizes are valid and not artefacts of uneven sampling. Thus it appears that a structure exists within the fig-frugivore relationships. The monoecious *Ficus* species (with the exception of the low climber *F. acamptophylla*, all hemi-epiphytes) attracted more frugivores (Mann-Whitney $U_{(2) 19, 15} = 11$, $p < 0.01$) and had a wider niche breadth (Mann-Whitney $U_{(2) 19, 15} = 28$, $p < 0.001$) than the dioecious species which included climbers and free standing trees (Figure 4.5). The number of species' figs eaten by a given frugivore ranged from one to 17. The frugivores that fed upon the most *Ficus* species were generally birds (Figure 4.6) but this pattern was not statistically significant (Mann-Whitney $U_{(2) 19, 15} = 537.5$, $p = 0.128$, n.s.). Furthermore, bird species' B values for dietary breadth were not significantly higher than those of mammalian frugivores (Mann-Whitney $U_{(2) 48, 18} = 527.5$, $p = 0.167$, n. s.).

When comparing the degree of overlap in frugivore attraction (Table 4.8) it can be seen that in the majority (72.72%) of pairwise comparisons, overlap is minimal (Morisita index values under 0.100, the average of all values). Furthermore, no Morisita value greater than 0.498 was obtained - no two *Ficus* species had as much as 50 % overlap in frugivore attraction (in terms of frugivore species' proportional contributions to overall feeding visits). The comparisons of most interest are those where above average overlap was revealed. Approximately one fifth (21.21 %) of species pairs had overlap values between 0.2 and 0.5. The different degrees of overlap between *Ficus* species pairs suggests non-random frugivore attraction with a guild structure whereby the potential disperser resource is shared to a greater extent by some *Ficus* species than by others.

Detrended correspondence analysis (DECORANA) of the proportional contributions of each frugivore species to overall visits at each of the 34 *Ficus* species under study allows the illustration of groups of frugivores of similar importance to groups of *Ficus* species (Figure 4.7a). Thus, the five species of ground-foraging mammal form a tight cluster, as do the two species of fruit bat. Although the diverse bird community's values are more widely spread, the majority of species (32) form a tight cluster and were only observed feeding in the canopy. However, plots for the bulbuls occur throughout the distribution of avian plots (Figure 4.7a), indicating that this family exhibited the greatest variety of fig preference. Among the arboreal mammals the nocturnal Binturong (*Arctictis binturong*) clusters with the fruit bats, and the two primates cluster together but the squirrels and treeshrews, like the birds, are more dispersed. The parallel analysis separates groups of *Ficus* species for which each individual frugivore species make similar contributions to overall feeding visits (Figure 4.7b). With the exception of *F. annulata* (which attracted bats and is associated with the trees *F. condensa* and *F. schwarzii*) and *F. subcordata* (which received proportionally more visits from monkeys), the hemi-epiphytic species form a tight cluster. Conversely, the plots for freestanding trees and climbers are highly divergent. Two climbers (*F. aurantiacea* and *F. punctata*) are positioned at the extreme right of the plot by virtue of their attraction of arboreal mammals (monkeys and squirrels) only. The eigenvalues of the DECORANA axes are both low (axis one = 0.026, axis two = 0.014) indicating that much of the variance is not explained, although this is unsurprising with such a large (34 × 66) data matrix and when overlap in (proportional) frugivore attraction between *Ficus* species was generally low (Table 4.8).

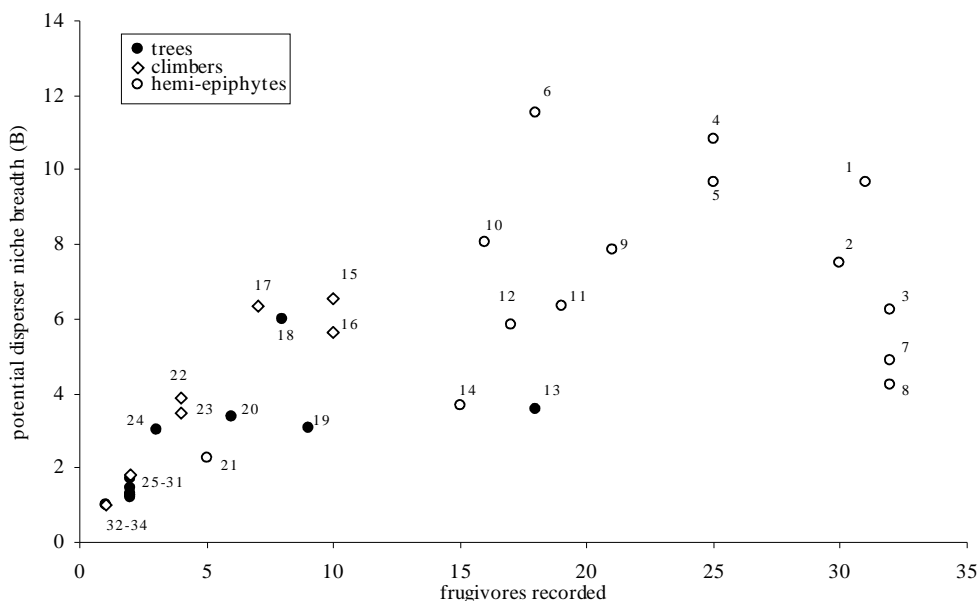


Figure 4.5. Niche breadth (the diversity, measured using Simpson's index B , of potential dispersers) and total frugivore assemblage size for 34 *Ficus* species. The monoecious, hemi-epiphytic *Ficus* species attracted more frugivores (Mann-Whitney $U_{(2)19,15} = 11$, $p < 0.01$) and had a wider niche breadth (Mann-Whitney $U_{(2)19,15} = 28$, $p < 0.001$) than climbers and trees which, with the exception of *Ficus acamptophylla*, are dioecious. 1 = *F. pisocarpa*, 2 = *F. benjamina*, 3 = *F. stupenda*, 4 = *F. subgelderii*, 5 = *F. stricta*, 6 = *F. callophylla*, 7 = *F. kerkhovenii*, 8 = *F. subcordata*, 9 = *F. dubia*, 10 = *F. consociata*, 11 = *F. sumatrana*, 12 = *F. sundaica*, 13 = *F. fulva*, 14 = *F. xylophylla*, 15 = *F. subulata*, 16 = *F. acamptophylla*, 17 = *F. sinuata*, 18 = *F. aurata*, 19 = *F. obscura*, 20 = *F. uniglandulosa*, 21 = *F. annulata*, 22 = *F. punctata*, 23 = *F. callicarpides*, 24 = *F. treubii*, 25 = *F. aurantiacea*, 26 = *F. condensata*, 27 = *F. stolonifera*, 28 = *F. megaleia*, 29 = *F. uncinata*, 30 = *F. near uncinata*, 31 = *F. geocharis*, 32 = *F. schwarzii*, 33 = *F. cereicarpa*, 34 = *F. sarawakensis*.

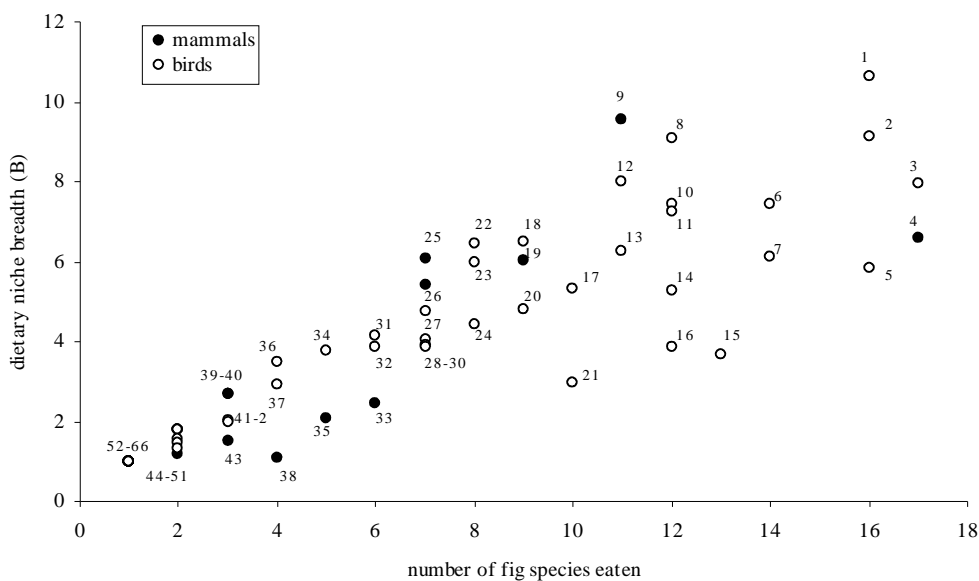


Figure 4.6. Dietary breadth (Simpson's B) and numbers of fig species eaten by avian and mammalian frugivores. The frugivores that fed upon the most *Ficus* species were generally birds but this pattern was not statistically significant because some birds ate only a few species of figs (Mann-Whitney $U_{(2)19,15} = 537.5$, $p = 0.128$, n. s.). Furthermore, bird species' B values for dietary breadth were not significantly higher than those of mammalian frugivores (Mann-Whitney $U_{(2)48,18} = 527.5$, $p = 0.167$, n. s.). 1 = Red-crowned Barbet, 2 = Greater Green Leafbird, 3 = Red-eyed Bulbul, 4 = Prevost's Squirrel, 5 = Brown Barbet, 6 = Red-throated Barbet, 7 = Fairy Bluebird, 8 = Orange-bellied Flowerpecker, 9 = Lesser/Slender Treeshrew, 10 = Yellow-rumped Flowerpecker, 11 = Blue-eared Barbet, 12 = Blue-winged Leafbird, 13 = Green Broadbill, 14 = Puff-backed Bulbul, 15 = Thick-billed Green-Pigeon, 16 = Olive-winged Bulbul, 17 = Buff-vented Bulbul, 18 = Hill Myna, 19 = Earspot Squirrel, 20 = Spectacled Bulbul, 21 = Large Green-Pigeon, 22 = Scarlet-breasted Flowerpecker, 23 = Yellow-bellied Bulbul, 24 = Yellow-vented Bulbul, 25 = Common Treeshrew, 26 = unidentified terrestrial rodent, 27 = Streaked Bulbul, 28 = Grey-cheeked Bulbul, 29 = Asian Black Hornbill, 30 = Lesser Green Leafbird, 31 = Hairy-backed Bulbul, 32 = Black-headed Bulbul, 33 = Giant Squirrel, 34 = Crimson-breasted Flowerpecker, 35 = Plantain Squirrel, 36 = Black Magpie, 37 = Wreathed Hornbill, 38 = Pig-tailed Macaque, 39 = Lesser Mouse-Deer, 40 = Large Treeshrew, 41 = Green Imperial-Pigeon, 42 = Little Green-Pigeon, 43 = Large Flying Fox, 44 = Binturong, 45 = Wrinkled Hornbill, 46 = Asian Koel, 47 = Brown Fulvetta, 48 = Blue-crowned Hanging-Parrot, 49 = Slender-billed Crow, 50 = Long-tailed Parakeet, 51 = non *Pteropus* fruit bat species, 52 = Muller's Rat, 53 = Low's Squirrel, 54 = Long-tailed Macaque, 55 = small flying squirrel, 56 = Red Giant Flying Squirrel, 57 = White-crowned Hornbill, 58 = Rhinoceros Hornbill, 59 = Bushy-crested Hornbill, 60 = Pink-necked Green-Pigeon, 61 = Hook-billed Bulbul, 62 = Cream-vented Bulbul, 63 = Maroon-breasted Philentoma, 64 = Magpie Robin, 65 = Jambu Fruit-Dove, 66 = Dark-throated Oriole.

Table 4.8. Overlap between *Ficus* species in terms of the frugivores they attract. Numbers in cells are Morisita Index (C) values. *Ficus* species have been ordered to graphically maximise association of high C values.

	<i>F. annulata</i>	<i>F. condensa</i>	<i>F. schwartzii</i>	<i>F. callophylla</i>	<i>F. subgeldereri</i>	<i>F. stricta</i>	<i>F. pisocarpa</i>	<i>F. consociata</i>	<i>F. dubia</i>	<i>F. benjamina</i>	<i>F. sumatrana</i>	<i>F. stupenda</i>	<i>F. sundaica</i>	<i>F. kerkhovenii</i>	<i>F. subcordata</i>	<i>F. xylophylla</i>	<i>F. punctata</i>	<i>F. aurantiacea</i>	<i>F. treubii</i>	<i>F. geocharis</i>	<i>F. near uncinata</i>	<i>F. stolonifera</i>	<i>F. megaleia</i>	<i>F. uncinata</i>	<i>F. cerei-carpa</i>	<i>F. subulata</i>	<i>F. sinuata</i>	<i>F. aurata</i>	<i>F. acamptophylla</i>	<i>F. fulva</i>	<i>F. uniglandulosa</i>	<i>F. obscura</i>	<i>F. callicarpides</i>	<i>F. sarawakensis</i>	Row maximum			
<i>F. annulata</i>	X	0.489	0.394	0.007	0.008	0.003	0.006	0.010	0.012	0.007	0.005	0.007	0.004	0.003	0.001	0.009	0.014	0.015	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.004	0.000	0.000	0.000	0.001	0.000	0.000	0.000	0.000	0.489		
<i>F. condensa</i>		X	0.443	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.443	
<i>F. schwartzii</i>			X	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>F. callophylla</i>				X	0.416	0.417	0.460	0.397	0.414	0.401	0.407	0.403	0.398	0.383	0.328	0.324	0.026	0.021	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.066	0.017	0.000	0.056	0.126	0.032	0.095	0.108	0.100	0.460		
<i>F. subgeldereri</i>					X	0.341	0.363	0.450	0.311	0.374	0.341	0.352	0.327	0.332	0.245	0.255	0.030	0.024	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.109	0.026	0.009	0.010	0.151	0.046	0.129	0.192	0.179	0.450		
<i>F. stricta</i>						X	0.447	0.318	0.370	0.447	0.416	0.419	0.421	0.385	0.350	0.326	0.017	0.014	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.028	0.007	0.012	0.117	0.219	0.066	0.170	0.153	0.061	0.447		
<i>F. pisocarpa</i>							X	0.367	0.430	0.442	0.461	0.455	0.457	0.435	0.400	0.395	0.027	0.021	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.064	0.004	0.019	0.064	0.137	0.037	0.101	0.080	0.061	0.461		
<i>F. consociata</i>								X	0.345	0.368	0.361	0.450	0.356	0.362	0.291	0.315	0.042	0.035	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.068	0.004	0.001	0.052	0.110	0.030	0.100	0.142	0.161	0.450		
<i>F. dubia</i>									X	0.364	0.408	0.382	0.403	0.356	0.345	0.377	0.036	0.027	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.098	0.001	0.003	0.034	0.084	0.019	0.051	0.028	0.016	0.408		
<i>F. benjamina</i>										X	0.462	0.463	0.453	0.429	0.378	0.388	0.040	0.034	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.060	0.027	0.015	0.157	0.284	0.095	0.217	0.093	0.082	0.463			
<i>F. sumatrana</i>											X	0.485	0.483	0.475	0.443	0.452	0.014	0.013	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.059	0.006	0.000	0.082	0.175	0.050	0.134	0.071	0.075	0.485			
<i>F. stupenda</i>												X	0.482	0.483	0.449	0.451	0.047	0.043	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.035	0.002	0.004	0.074	0.154	0.045	0.127	0.095	0.109	0.483			
<i>F. sundaica</i>													X	0.475	0.450	0.451	0.014	0.012	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.057	0.002	0.008	0.077	0.164	0.047	0.127	0.065	0.063	0.475			
<i>F. kerkhovenii</i>														X	0.463	0.461	0.013	0.011	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.023	0.005	0.006	0.060	0.121	0.041	0.108	0.117	0.136	0.463			
<i>F. subcordata</i>															X	0.454	0.094	0.115	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.016	0.000	0.004	0.032	0.070	0.020	0.061	0.056	0.074	0.454			
<i>F. xylophylla</i>																X	0.033	0.032	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.036	0.000	0.000	0.037	0.088	0.024	0.068	0.040	0.054	0.088			
<i>F. punctata</i>																	X	0.364	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.364			
<i>F. aurantiacea</i>																		X	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000		
<i>F. treubii</i>																			X	0.329	0.306	0.299	0.261	0.260	0.250	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.329			
<i>F. geocharis</i>																				X	0.498	0.479	0.480	0.480	0.476	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.498		
<i>F. near uncinata</i>																					X	0.488	0.489	0.490	0.488	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.490		
<i>F. stolonifera</i>																						X	0.491	0.492	0.491	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.492	
<i>F. megaleia</i>																							X	0.489	0.493	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.493	
<i>F. uncinata</i>																								X	0.495	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.495
<i>F. cerei-carpa</i>																									X	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>F. subulata</i>																										X	0.166	0.171	0.090	0.049	0.047	0.006	0.012	0.000	0.171			
<i>F. sinuata</i>																											X	0.280	0.352	0.117	0.327	0.175	0.038	0.000	0.352			
<i>F. aurata</i>																												X	0.345	0.114	0.341	0.174	0.000	0.000	0.345			
<i>F. acamptophylla</i>																													X	0.333	0.456	0.327	0.000	0.000	0.333			
<i>F. fulva</i>																														X	0.266	0.405	0.001	0.000	0.266			
<i>F. uniglandulosa</i>																															X	0.287	0.000	0.000	0.287			
<i>F. obscura</i>																																X	0.033	0.049	0.049			
<i>F. callicarpides</i>																																	X	0.242	0.242			
<i>F. sarawakensis</i>																																		X	0.000			
Column maximum	0.000	0.489	0.443	0.007	0.416	0.417	0.460	0.450	0.430	0.447	0.462	0.485	0.483	0.483	0.463	0.461	0.094	0.364	0.000	0.329	0.498	0.488	0.491	0.492	0.495	0.109	0.166	0.280	0.352	0.333	0.456	0.405	0.192	0.242	0.498			

comparisons		
Overlap	n	%
none	271	48.3
0-0.9 %	35	6.2
1-9 %	103	18.4
10-19%	34	6.1
20-29 %	14	2.5
30-39%	44	7.8
40-49%	60	10.7
≥ 50 %	0	0.0

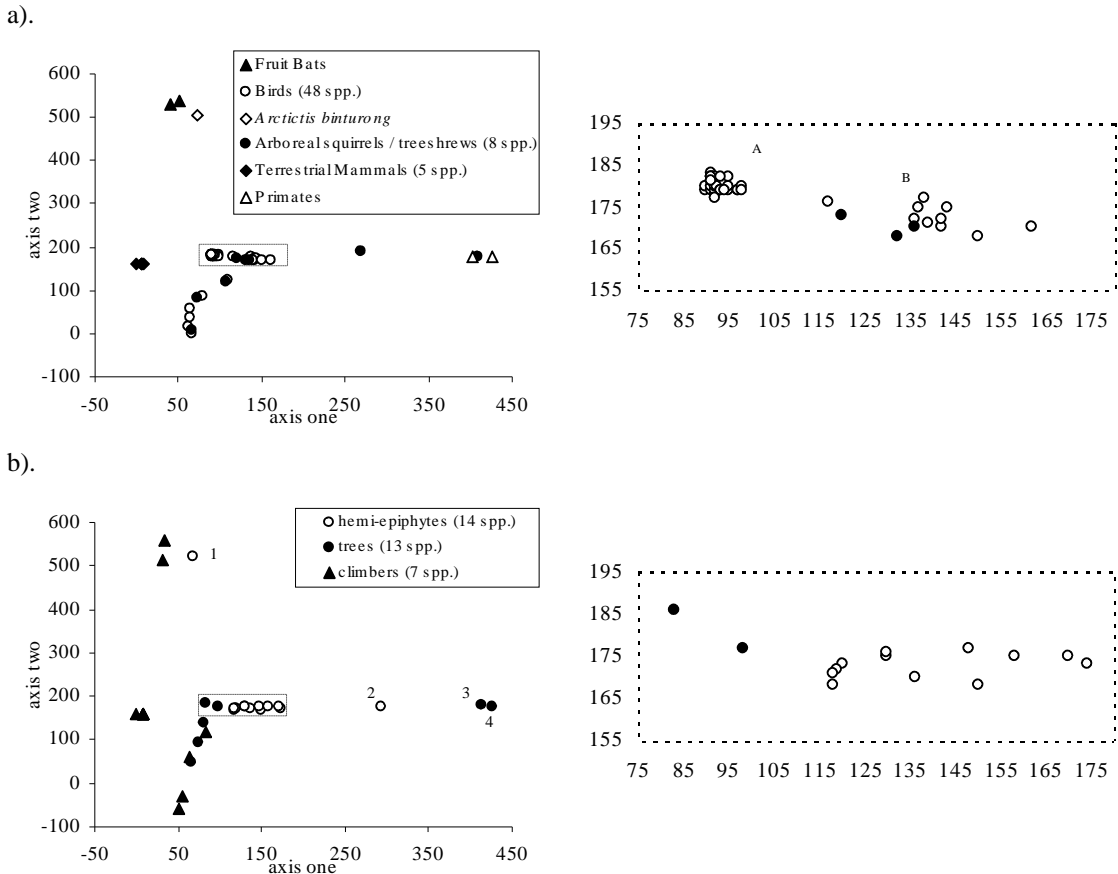


Figure 4.7. DECORANA scatterplots for a) 66 frugivore species based on individual frugivore species' proportional contributions to overall fig visitation for each fig species and b) for 34 *Ficus* species based on individual frugivore species' proportional contributions to overall fig visitation for each fig species. Eigenvalues are 0.026 and 0.014 for axes one and two, respectively. 1 = *Ficus annulata*, 2 = *F. subcordata*, 3 = *F. aurantiacea*, 4 = *F. punctata*. Note that in each chart many points overlap so blow-up boxes have been used to show the distribution of data points where they are densest. The majority (32) of the bird species form a tight cluster (marked A in the blow-up box in Figure 4.7a). The more dispersed cluster (B) comprises four barbet species, slender-billed crow, fairy blue bird, asian koel, black magpie, and two bulbul species. Bulbuls, present in both cluster A and B as well as being represented by all of the avian plots outside of the blow up box, thus exhibit the greatest variety of fig choice of the bird families observed.

The two DECORANA plots and the output of a cluster analysis (Figure 4.8) allow the identification of putative dispersal guilds, which I have given names reflecting the frugivores they most frequently attracted (Table 4.8). The three most distinct guilds, comprising a total of twelve *Ficus* species, were those attracting only terrestrial mammals, only arboreal mammals or largely fruit bats, respectively. With the exception of *F. annulata*, all members of these three guilds are dioecious species. Apart from a single, short observation of Red-crowned Barbet (*Megalaima rafflesii*) eating figs of *F. annulata*, no birds were recorded visiting the crops of these twelve fig species. Conversely, feeding visits to the remaining 22 *Ficus* species were dominated by birds, with arboreal mammals (especially squirrels and treeshrews) also observed. The outlying position of *F. subcordata* in Figure 4.7 is due to the relatively high number of feeding visits contributed by Pig-tailed Macaques (*Macaca nemestrina*) but the species is included within the 'bird/arboreal mammal guild' on the basis of the contributions of birds (85.6 % of all feeding visits). For two bird-attracting *Ficus* species (*F. sarawakensis* and *F. callicarpides*), observations of frugivory were rare and the cluster analysis excluded them from the groups it created. The *Ficus* species attracting birds and arboreal mammals can be divided into two guilds: one attracting canopy frugivores and one attracting understorey frugivores. Just three bird families dominated avian frugivory. Together, bulbuls (Pycnonotidae), barbets (Megalaimidae) and pigeons (Columbidae) accounted for an average (\pm S.D.) of 78.1 ± 9.21 % of all feeding visits. The dichotomy between understorey and canopy guilds arose because pigeons were never observed feeding in the understorey and barbets were only recorded there infrequently (Figure 4.9).

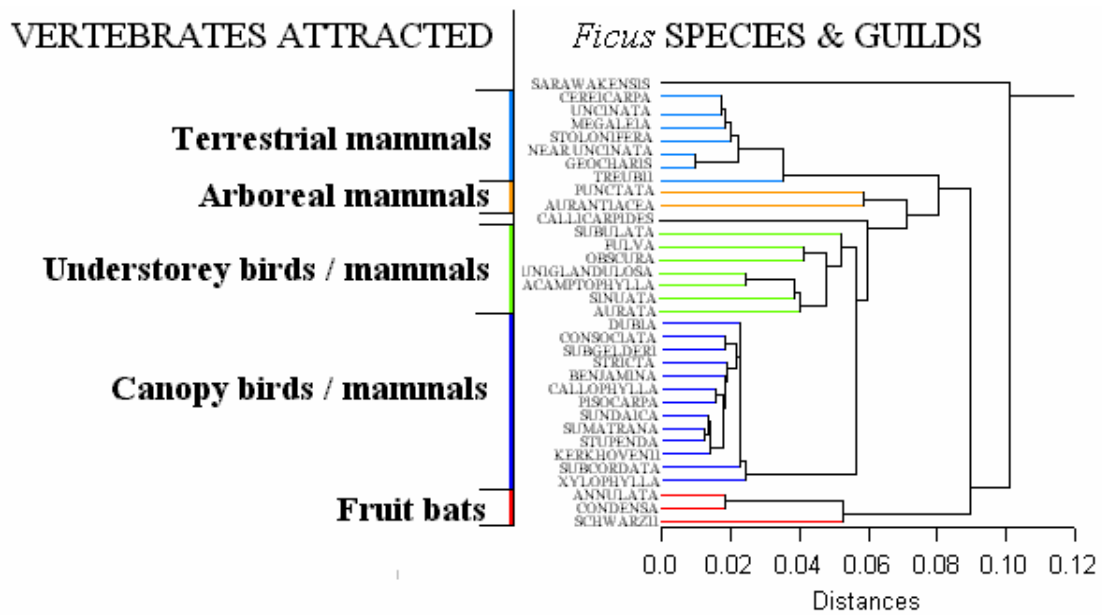


Figure 4.8. Hierarchical cluster analysis of 34 *Ficus* species based on proportional contributions to overall frugivory by vertebrate frugivores in Lambir Hills National Park.

Table 4.9. Summary of *Ficus* seed dispersal guilds in Lambir Hills National Park.

Dispersal guild	Frugivores recorded	Monoecious <i>Ficus</i> species in guild	Dioecious <i>Ficus</i> species in guild
1. Fruit bat attracting guild	Largely fruit bats. Also Binturong, Red-crowned Barbet and Prevost's Squirrel	<i>F. annulata</i>	<i>F. condensa</i> <i>F. schwarzii</i>
2. Arboreal mammal attracting guild	Primates and squirrels		<i>F. aurantiacea</i> <i>F. punctata</i>
3. Terrestrial mammal attracting guild	Mouse-deer, terrestrial rodents and Large Treeshrew		<i>F. cereicarpa</i> <i>F. geocharis</i> <i>F. megaleia</i> <i>F. stolonifera</i> <i>F. treubii</i> <i>F. uncinata</i> <i>F. 'near' uncinata</i>
4. Understorey bird/arboreal mammal attracting guild	Birds, squirrels and treeshrews	<i>F. acamptophylla</i>	<i>F. aurata</i> <i>F. fulva</i> <i>F. sinuata</i> <i>F. subulata</i> <i>F. uniglandulosa</i> <i>F. obscura</i>
5. Canopy bird/arboreal mammal attracting guild	Birds, squirrels, treeshrews and primates	<i>F. callophylla</i> <i>F. pisocarpa</i> <i>F. sundaica</i> <i>F. xylophylla</i> <i>F. subcordata</i> <i>F. dubia</i> <i>F. stupenda</i> <i>F. kerkhovenii</i> <i>F. stricta</i> <i>F. benjamina</i> <i>F. sumatrana</i> <i>F. consociata</i> <i>F. subgelderi</i>	
not determined	Birds		<i>F. sarawakensis</i> <i>F. callicarpides</i>

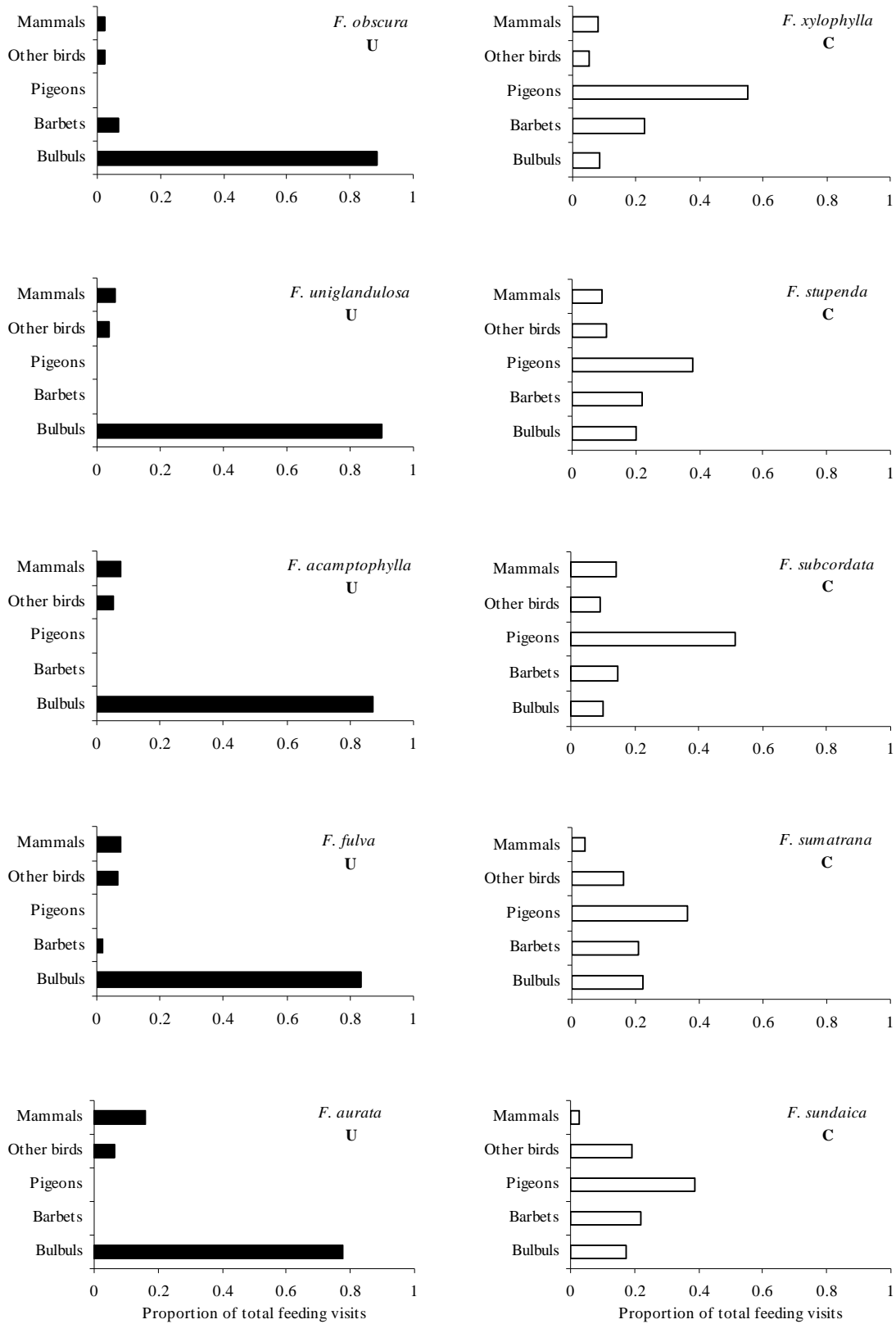


Figure 4.9. Proportional contributions of frugivore taxa to overall feeding visits to individual *Ficus* species attracting birds and mammals. *Ficus* species attracting understory foragers are represented by solid bars and the symbol U. *Ficus* species attracting canopy foragers are represented by open bars and the symbol C. Continued on next page.

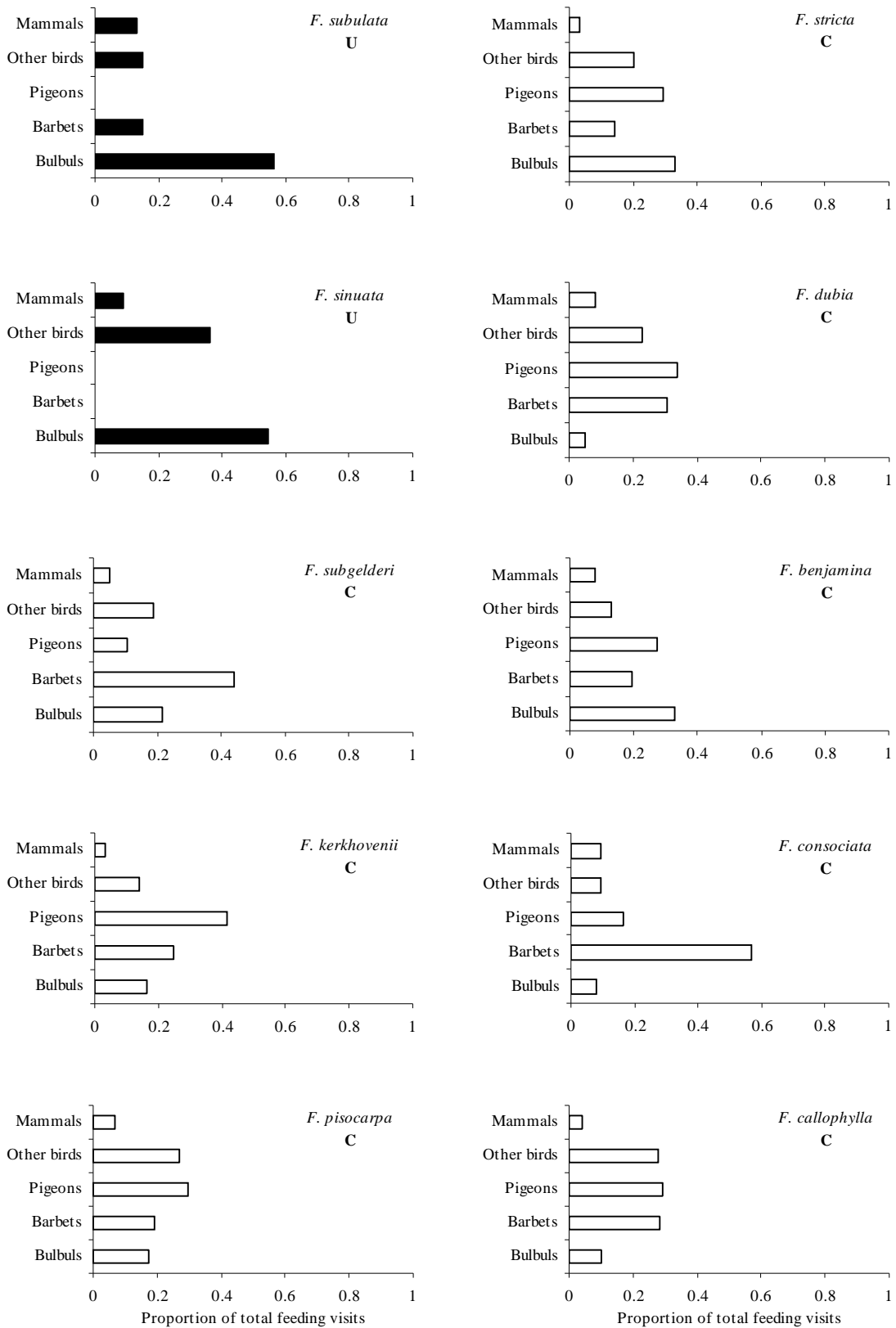


Figure 4.9. continued from previous page.

4.3.4 Determinants of *Ficus* dispersal guild membership

Fig packaging and presentation

All species attracting birds or arboreal mammals had figs that ripened a shade of red. Conversely, the bat-attracting *Ficus* species all had green figs. Among the species attracting terrestrial mammals both red and non-red figs were produced. Odour was inconsistently detected (Chapter 3), although four of the six species for which a fig odour was detected attracted mammals (*F. annulata*, *F. condensata*, *F. schwarzi*, *F. uncinata*) and the former three species attracted primarily fruit bats. Of the other species for which a fig odour was detected, *F. xylophylla* attracted birds and mammals while a single species of bird (Brown Barbet, *Calorhamphus fuliginosus*) was observed feeding on figs of *F. sarawakensis*. *Ficus* dispersal guild membership was also strongly associated with the fig design and presentation traits other than colour (Figure 4.10). On the whole, figs that attracted primarily mammals tended to be larger, more seed-rich, presented in lower forest strata and to have more watery pulp than those visited predominantly by birds.

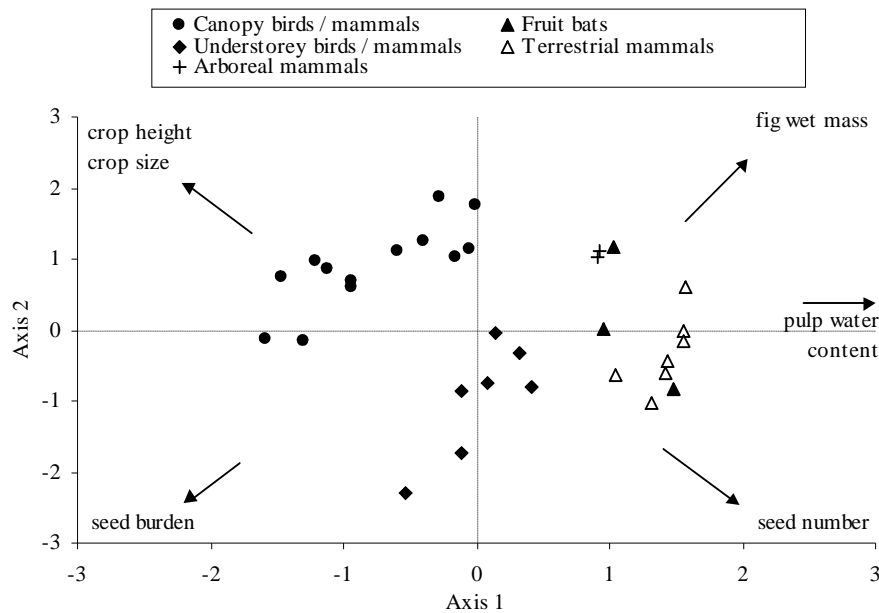


Figure 4.10. Principal components scatterplot based on fig packaging and presentation. Redrawn from Chapter 3 to show positions of members of each putative dispersal guild.

Among the *Ficus* species attracting birds and arboreal mammals, the number of frugivore species visiting crops ranged from six (*F. uniglandulosa*) to 32 (*F. stupenda*, *F. subcordata*). Generally, assemblage sizes were greater for species presenting their crops in the canopy rather than in the understorey. However, crop height does not necessarily determine assemblage size, as relationships between assemblage size and both crop size and fig size were also apparent (Figure 4.11). Multiple regression analysis allows confounding effects of correlated fruit characteristics to be partly controlled for (e.g. Janson, *et al.* 1986). Such a model, explaining 76 % of variation in assemblage size ($F = 16.91$, $p < 0.01$, $R^2 = 0.76$), revealed assemblage size to be significantly (positively) related to crop size ($t = 2.372$, $p = 0.031$) and fig mass ($t = 3.645$, $p = 0.002$) but not to the height of fig crops ($t = 0.382$, $p = 0.708$). Among these *Ficus* species as fig mass increases fig shape becomes considerably elongate rather than round (Figure 4.12; two-tailed Spearman rank correlation coefficient $r_s = -0.447$, $n = 21$, $p < 0.05$).

That crop height should be associated with frugivore attraction is a fairly obvious product of vertical stratification of frugivore species. Whilst, terrestrial mammals have no choice but to forage on the figs produced on the forest floor, the results imply that at least some volant frugivores do not use the fig resources presented in the understorey. Indeed, examining the degree of overlap in frugivore attraction between the two guilds fed upon by birds and arboreal mammals reveals that the majority of these frugivores are confined to the canopy whereas only two (Large Tree Shrew, *Tupaia tana* and Plantain Squirrel, *Callosciurus notatus*) were observed only in the understorey (Figure 4.13).

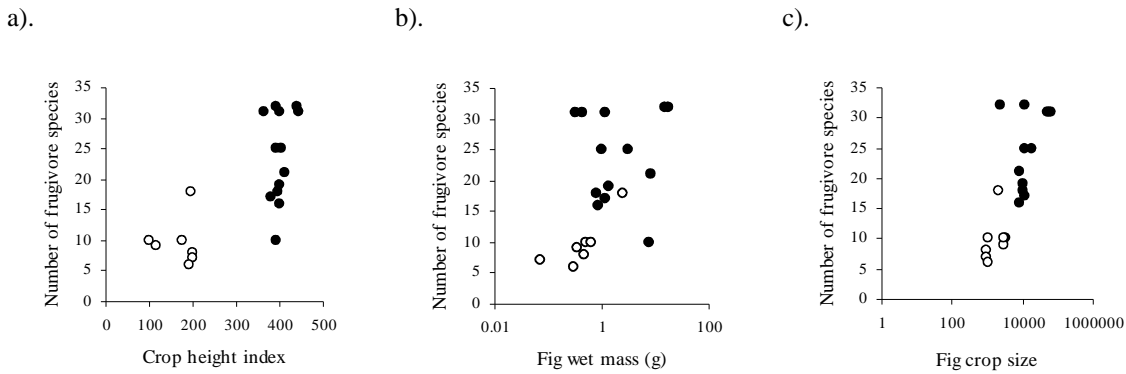


Figure 4.11. The relationship between the number of frugivore species attracted and a) crop height, b) fig wet mass and c) crop size in the two guilds of *Ficus* species attracting birds and arboreal mammals. Filled circles = canopy birds/arboreal mammals guild, open circles = understorey birds/arboreal mammals guild. Note the use of log scales in b and c.

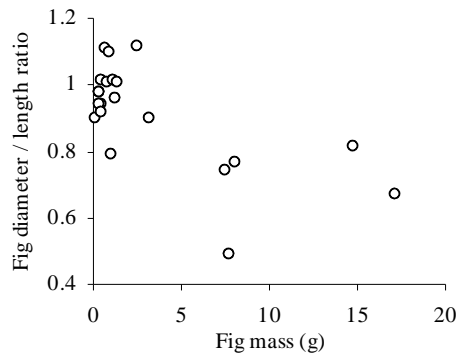


Figure 4.12. The relationship between fig mass and shape among bird-attracting *Ficus* species.

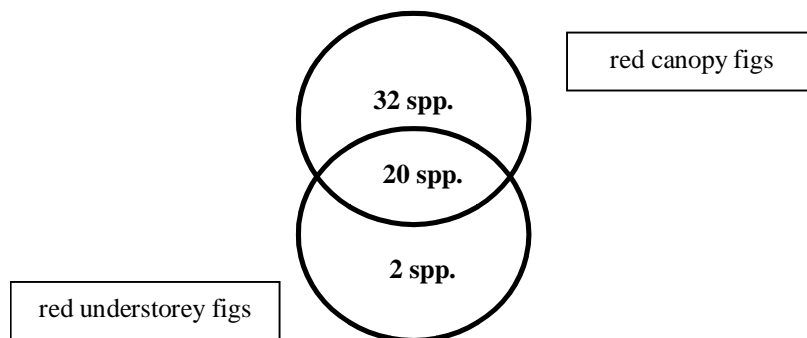
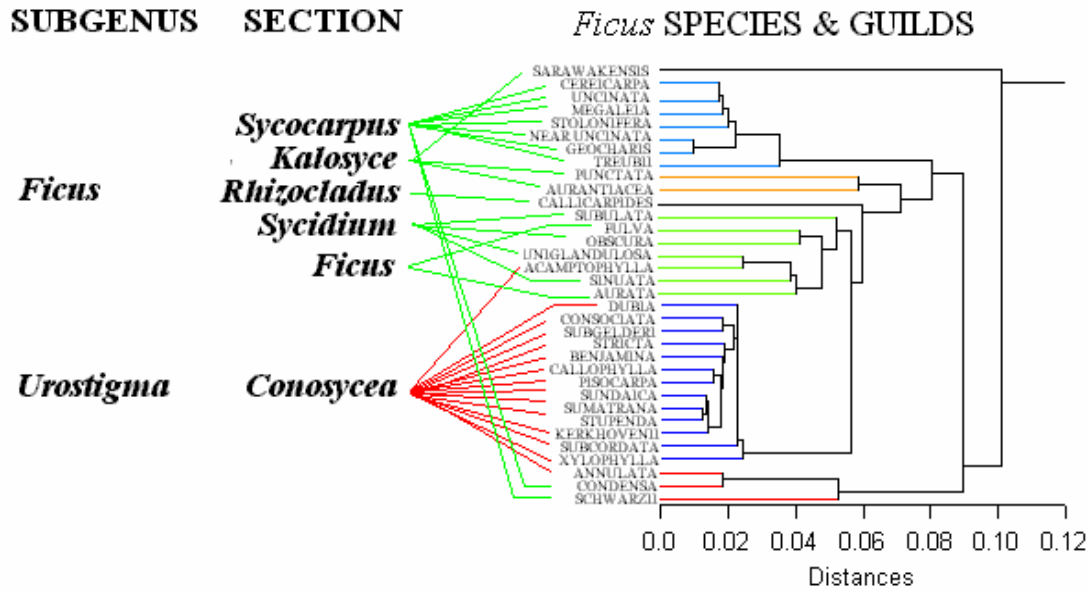


Figure 4.13. The extent of overlap in frugivore attraction between bird and arboreal mammal-attracting *Ficus* species presenting red figs in the canopy and those doing so in the understorey.

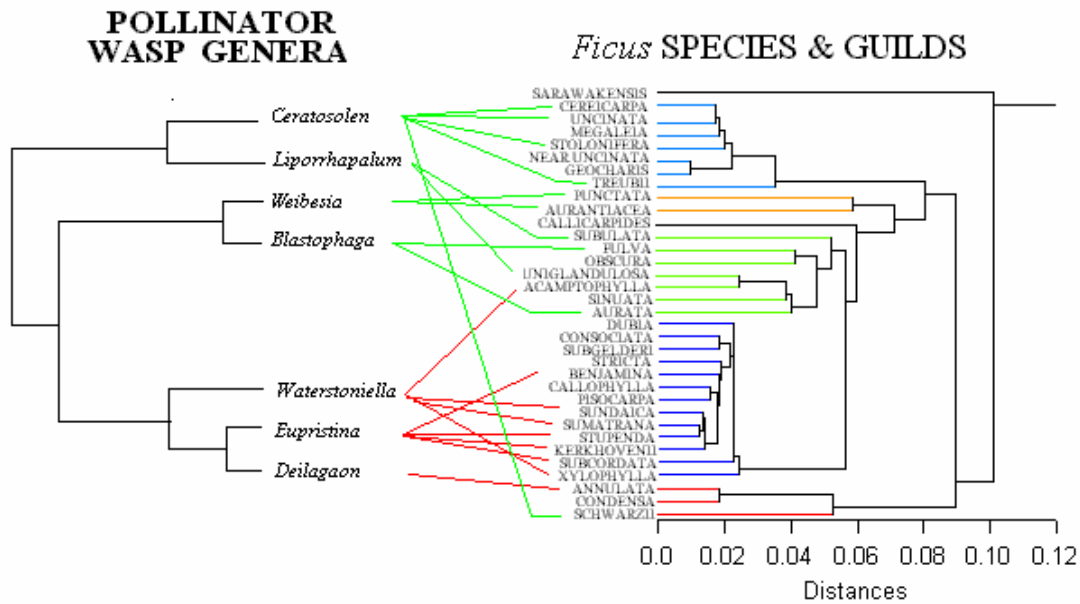
Phylogenetic constraint

Ficus dispersal guild membership is determined largely by fig design and presentation, which in turn are conservative characters in that they are largely governed by phylogeny (Chapter 3). All but one of the twelve *Ficus* species in the three non-avian dispersal guilds are dioecious as are all but one of the species fed upon largely by understorey birds, whilst all of the hemi-epiphytes attracting birds and arboreal mammals are monoecious. Figure 4.14 illustrates the phylogenetic associations of the five *Ficus* guilds identified, expressed in terms of a) *Ficus* subgenera and sections (Corner, 1965; based on plant morphology) and b) the phylogeny of pollinator wasps (based on Dr. J. Cook's unpublished analysis of mitochondrial DNA). Both methods have their drawbacks: Corner's phylogeny is more subjective than a genetic analysis and although based largely on floral characters did use growth form and traits such as geocarpy and cauliflory to determine relationships amongst species. The plant phylogeny

based on the genetic method assumes that pollinator wasps and *Ficus* species share a one-to-one evolutionary past. Furthermore, not all the identities of pollinators of the *Ficus* species under consideration here are not yet known (Wiebes, 1994). Nonetheless, both comparisons suggest a high degree of congruence between *Ficus* dispersal guild membership and phylogeny. However, a number of *Ficus* species occur in guilds with distantly related species. By virtue of having relatively large, green figs *Ficus annulata*, although a monoecious hemi-epiphyte, joins *F. condensa* and *F. schwarzii* (both dioecious trees) in the guild attracting fruit bats. *Ficus acamptophylla*, also monoecious, associates with dioecious species attracting understory birds and arboreal mammals. This is because the individual of *F. acamptophylla* considered here was a low climber rather than a hemi-epiphyte (as is more common for this species; Corner, 1965; R. Harrison, pers. comm.).



a)



b)

Figure 4.14. Phylogenetic associations of members of each *Ficus* seed dispersal guild. a) based on Corner's (1965) classification of *Ficus* and b) on Dr J. Cook's (unpublished) phylogeny of pollinator wasps. Lines linking *Ficus* sections or wasp genera with *Ficus* species are coloured green for dioecious *Ficus* species and red for monoecious species.

4.4 DISCUSSION

4.4.1 The diversity of fig-eaters

These results highlight the diversity of frugivores that eat figs in Lambir. That these species included obligate frugivores, omnivores and opportunist fruit eaters reflects both the abundance and diversity of the fig resource and the ease with which it is handled, even by species without apparent adaptations to a fruit diet. Observations of pteropodid bats (*Pteropus* in particular), hornbills, primates and civets were less frequent than might be predicted from the literature (e.g. Chivers, 1980; Marshall, 1985; Lambert, 1987; Rabinowitz, 1991). In Borneo these large frugivores are prone to the effects of habitat destruction and hunting (Johns, 1983, 1987; Bennett *et al.*, 1997; MacKinnon *et al.*, 1996), and the apparent depauperacy of such species in Lambir Hills National Park is of conservation concern (Shanahan & Compton, in review). The infrequency of observations of understory fruit bats may be linked to the failure, over much of the study period, for *Ficus schwarzi* figs to be pollinated (see Chapter 5). Other, generally small, vertebrate species recorded from the field site and known to eat figs or have fig eating congeners were also not recorded visiting fig crops during this study (Shanahan & Debski, in press; Shanahan & So, in review; Chapter 7). My lack of observations of these additional species may be due to their rarity, small size, secretive and/or nocturnal habits or infrequency of frugivory.

4.4.2 *Ficus* dispersal guilds

While the range of frugivore species observed eating figs in Lambir lends credence to reports of their dietary importance (Janzen, 1979), my data show that all *Ficus* species are not equal in terms of their suitability for particular frugivores. Monoecious *Ficus* species tended to attract larger assemblages of frugivores and had a wider niche breadth with respect to the animals attracted than did dioecious species. This reflects the higher biomass and species richness of frugivores foraging in the canopy, where the majority of monoecious species presented their figs (Wong, 1986; Fleming *et al.*, 1987). The extent of overlap between *Ficus* species in terms of the frugivores attracted to their crops (and their proportional contributions to overall feeding visits) was generally low (< 50 %; Table 4.8). However, the degree of similarity of frugivore attraction was not evenly distributed across all the matrix of species pairs (Table 4.8). Rather, *Ficus* species exist in guilds within each of which frugivores are shared to a greater extent than with species from other guilds.

The *Ficus* dispersal guild structure is determined by the interaction of fig traits (colour, height, and size) with aspects of the vertebrates' ecology, size, sensory capabilities, locomotory ability and behaviour. For example, birds are known to have good colour vision (Hartwig, 1993) and, in agreement with earlier studies (e.g. Ridley 1930; van der Pijl 1982; Turcek 1963; Gautier-Hion *et al.*, 1985), the figs they ate were all red or orange in colour, in stark contrast to the green foliage amongst which they were presented. These figs were also eaten by diurnally foraging mammals: primates (which have trichromatic colour vision; Jacobs, 1996), treeshrews and squirrels; whilst green, odorous figs were taken by the nocturnal fruit bats and Binturong *Arctictis binturong*. Figs with firm coats were generally eaten by mammals rather than birds, the lack of teeth in which presumably precluding this.

When related to the assemblages of frugivores attracted to fig crops, differences in fruit characteristics largely reflect classically recognised fruit syndromes (Ridley, 1930; van der Pijl, 1957; Snow, 1981). However, the consumption of a given fruit by one or more frugivore species does not necessarily imply that the fruit is adapted to those frugivores (see Janzen, 1985b). Rather, shared means of fig packaging and presentation may simply reflect common ancestry rather than coevolutionary responses to efficient vertebrate seed dispersers. Indeed, the fig traits identified as being important determinants of *Ficus* guild membership show strong phylogenetic associations. *Ficus annulata* is of special interest because, unlike the other 14 monoecious species under study that have red figs, it produces green figs that are fed upon primarily by fruit bats. This apparent colour change in ripe figs may be an evolutionary response to seed dispersal by fruit bats. *Ficus annulata*'s closest relative, *F. depressa* (Corner, 1965), also has green figs (M. Shanahan, pers. obs.), thus it appears to be through shared ancestry that this clade attracts primarily fruit bats.

The observed elongation of figs with increasing mass among those species attracting primarily avian frugivores would be favoured by selection as it allows a greater diversity of birds to swallow figs of a given volume than if the figs were spherical (see Mazer & Wheelwright, 1993). This helps explain why frugivore assemblage size increases with fig size among bird-attracting figs rather than large size limiting consumption. Furthermore, the soft texture of most figs means that a greater size range of frugivore species can eat figs of a given size than would be the case if their fruits needed to be swallowed whole, rather than pecked/bitten open. Nonetheless, swallowing may be the most efficient means of fig harvesting and it is likely that *Ficus* dispersal guilds have substructures determined by fig size and frugivore gape width. Indeed, among sympatric *Treron* pigeons and *Megalaima* barbets Lambert (1989b) and New World fruit bats (Kalko *et al.*, 1996) relationships have been found between the size of these frugivores and that of the figs they preferentially ate.

Investigations of fruit characters in *Ficus* are complicated by the fact that figs act initially as inflorescences, before becoming dispersal units. Selection pressures generated by the pollinators of the trees cannot, therefore, be ignored and I urge caution in the interpretation of the adaptive significance of fig structure, especially as formal comparative analyses utilising the phylogenies of the plants have not yet been conducted.

Vertical stratification of figs and frugivores is clearly an important factor structuring the variety of dispersal guilds in Lambir, especially as different *Ficus* species require their seed to be deposited at different heights above the ground (i.e. hemi-epiphytes requiring canopy germination microsites; Laman, 1995). Spatial (i.e. vertical) constraints on frugivore mobility limit the potential disperser assemblages available to species producing fruit in a given forest stratum. Thus *Ficus* species of the 'terrestrial mammals guild' present their figs at or near ground level and are not fed upon by the volant or arboreal frugivores observed at the other guilds (although one might expect ground birds, such as pheasants, to also feed on these geocarpic figs). The three *Ficus* species in the 'fruit bat guild' presented their figs in the understory and subcanopy. Francis (1990, 1994) reports that in Peninsular Malaysia fruit bat abundance is highest in subcanopy, but greater in the canopy than the understory. Elsewhere, fruit bats have been recorded feeding on the figs of hemi-epiphytic *Ficus* species, including some of those discussed here (Shanahan & So, in review; Chapter 7). In spite of the difficulties posed by nocturnal observations, fruit bats are noisy feeders and are easily detected (M. Shanahan pers. obs.). The lack of observations of large canopy feeding fruit bats suggest that local populations at the study site are artificially low, probably due to hunting. Among the *Ficus* species attracting birds and arboreal mammals, canopy-fruiting individuals have the potential to attract dispersers in greater number, of larger body size and of greater species diversity than those in the understory do. This reflects the higher avian frugivore biomass in the canopy and

the fact that the understorey of Malaysian forests is particularly depauperate in frugivorous birds (Wong, 1986; Fleming *et al.*, 1987). Of the frugivores observed feeding on figs in the understorey only two species (Large Treeshrew *Tupaia tana* and Plantain Squirrel, *Callosciurus notatus*) were recorded solely in the understorey. The remainder (20 species, including all birds observed feeding in the understorey) are essentially a subset of those found foraging in the canopy.

Although these results apply to the site and time period of this study, spatial and temporal variation in frugivore attraction are likely to occur. For example, at sites with more intact primate and hornbill faunas patterns of *Ficus* crop visitation might be manifestly different. In terms of temporal variation, I posit that infrequent observation of fruit bats was not normal and that their contribution to total feeding visits at fig crops may have been greater before the drought of 1998.

4.4.3. The predictive power of fruit traits

These findings suggest that fig traits can be used to predict dispersal guild membership without observations of frugivory. Figure 4.15 is redrawn from Figure 4.10 to include *Ficus* species for which frugivores were not recorded or for which *Ficus* guild membership was not satisfactorily determined. Thus, based on Figure 4.15 and the colour of ripe figs (Chapter 3), I predict that *F. pellucido-punctata*, *F. cucurbitina* and *F. grossivenis* will attract canopy birds and mammals, and that *F. brunneo-aurata* and *F. deltoidea* will attract birds and mammals foraging in the understorey. *Ficus sarawakensis*, for which a single observation of avian frugivory was observed, is positioned close to the species that attracted arboreal mammals suggesting that mammals rather than birds are the principal frugivores for this species. The positioning, between the guilds attracting understorey and canopy birds and mammals, of a number of species with red figs suggests that more complexity exists among these *Ficus* species and their frugivores than has been revealed in this study. Some of these species (e.g. *F. callicarpides*, *F. lanata*, *F. retusa*) present very small figs high in the canopy. I predict that they predominantly attract the smaller canopy-foraging birds, and thus represent the extreme of a continuum, the opposite end of which is represented by species with large figs (e.g. *F. xylophylla*, *F. stupenda*, *F. subcordata*) that tended to attract larger frugivores.

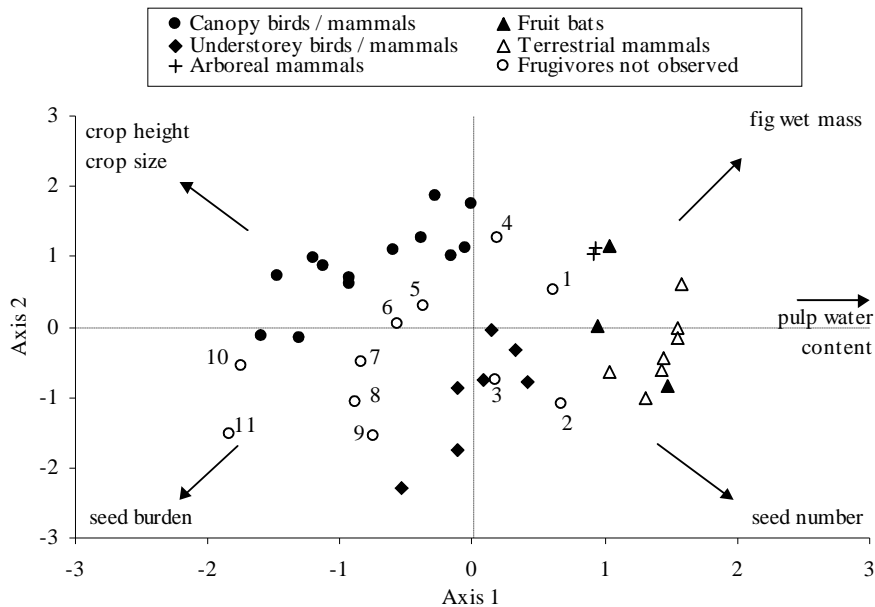


Figure 4.15. Principal components scatterplot based on fig packaging and presentation. Redrawn from Figure 4.10 to include *Ficus* species for which frugivores were not observed or for which guild membership was not satisfactorily determined: 1 = *F. sarawakensis*, 2 = *F. deltoidea*, 3 = *F. brunneo-aurata*, 4 = *F. cucurbitina*, 5 = *F. pellucido-punctata*, 6 = *F. grossivenis*, 7 = *F. retusa*, 8 = *F. urnigera*, 9 = *F. rubroscupidata*, 10 = *F. callicarpides*, 11 = *F. lanata*.

4.4.4 Implications for competition

Interspecific competition among *Ficus* species has already been circumvented to a degree by their species-specific pollination system and the variety of their growth habits. These characteristics have been used to explain the high species packing of *Ficus* in tropical forests (Janzen, 1979). Similarly, competition for dispersers between *Ficus* species and members of other genera is also reduced by the *Ficus* species' year-round fruiting phenology which contrasts that of non-*Ficus* species in Malaysian forests (Medway, 1972; Corlett, 1984; Yumoto & Inoue, 1995; Sakai *et al.*, 1999). Intra-generic competition may potentially be relatively more important in *Ficus*, but any competition for dispersers should be weakened by the diversity of fruiting strategies they display. However, for species occurring at very low densities, such as many hemi-epiphytes, only by offering a resource similar to that of other species can populations of specialists, such as hornbills (see Chapter 7) be maintained. The expectation is therefore that competition for dispersers will be greater within than between guilds. Such competition will be circumvented to a certain degree by the asynchronous fruiting phenology exhibited by the *Ficus* species under study (Chapter 5).

4.4.5 Implications for seed dispersal

The differential attraction of frugivores has major implications for the patterns of seed dispersal that *Ficus* species will experience. The role of frugivorous animals in *Ficus* seed dispersal is reviewed in Chapter 7, where I show that virtually all fig

eating animals are likely to act as seed dispersers to a greater or lesser extent. This includes species such as *Treron* pigeons which although considered to be seed-predatory have been demonstrated to pass a small proportion of *Ficus* seeds intact (Lambert, 1989c).

Hemi-epiphytic *Ficus* species require their seeds to be deposited in canopy microsites and Laman (1996a) estimated that, per fruiting episode, there is only a 1 % chance of a single hemi-epiphytic fig seed reaching a 'safe' site for germination at a distance of 60 metres from its source. Even if no frugivore foraging in the canopy is particularly adept at fig seed dispersal, production of vast crops and attraction of large assemblages of diverse frugivores may function as a bet-hedging trait, maximising the likelihood of a single seed being dispersed. The seed rain generated will exhibit homogeneity because of the variety of sizes (and therefore dispersal distances) of frugivores attracted. In Malaysian forests, frugivorous birds in the canopy are, on average, larger than those in the understorey (Wong, 1986; M. Shanahan, pers. obs.). Large frugivores need to eat more than smaller ones and so may be more reliable fruit removers. They also travel further (Schoener, 1968; Milton & May, 1976) and have longer gut transit times for figs (Lambert 1989b; Chapter 7) so should be more likely to move fig seeds further away from their source. Furthermore, large-bodied birds appear to be either restricted to the canopy or not to descend with any regularity into the lower forest strata. For example, the largest avian frugivores in this study (hornbills, pigeons, mynas and crows) were never observed feeding on figs in the understorey. This is important to canopy-germinating hemi-epiphytes as smaller, vertically transient birds will 'waste' any seeds they defecate below the canopy.

In contrast to the patterns described above, seed rain about understorey bird/mammal-dispersed *Ficus* individuals is likely to be more leptokurtic because of the generally small size of frugivores attracted. That pigeons were never observed foraging at such *Ficus* crops suggests that a greater proportion of seeds escape seed predation than is the case for the hemi-epiphytes.

Ficus species that attracted primarily fruit bats will experience yet another pattern of seed dispersal. Small pteropodid bats (e.g. *Cynopterus*) have been shown to forage using 'trap-lining' behaviour along regular travel paths (Nair *et al.*, 1999). Seed dispersal may therefore be spatially non-random, but occur along such routes, as suggested by the common occurrence of *F. schwarzii* alongside streams and trails (which may be used by the bats for navigation). Whilst small fruit bats carry fruit to feeding roosts, larger species (i.e. *Pteropus*) will consume figs *in situ* and are likely to disperse seeds with greater homogeneity in their long foraging flights.

Geocarpic *Ficus* species probably experience high levels of seed predation from the murid rodents and deer they attract. Treeshrews also feed on these species and have been demonstrated to pass fig seed in a germinable state (Shanahan & Compton, in press a). The small crops of these *Ficus* species and high risk of seed predation may be reflected in the frequency of vegetative reproduction by runners by species in this guild.

Finally, the *Ficus* species producing very large figs and relying on arboreal mammals for seed dispersal may be expected to experience a patchy dispersal of seeds, by virtue of the large body size (and so large defections and long-distance movements) of the primates that dominated feeding visits. In the future these *Ficus* species may experience reduced seed dispersal as primate populations are apparently declining in the study site (Table 4.6; Shanahan & Compton, in review).

4.4.6 Conclusion

Whilst demonstrating the diversity of figs and that of the animals that eat them, I have shown that a system of fig and/or disperser partitioning exists. This dispersal guild structure is determined by differences in fig packaging and presentation, vertical stratification of figs and frugivores, and phylogenetic constraints. Beyond promoting species co-existence through the reduction of competition and resulting in markedly different seed dispersal patterns, the dispersal guild structure observed has certain other implications. Firstly, because each *Ficus* species' figs are not suitable for all frugivores in a given area the keystone resource concept applied to 'figs' as a general resource type needs to be re-assessed. Secondly, *Ficus* species' reliance on particular subsets of frugivore communities for seed dispersal suggests they will differ in their ability to colonisation degraded landscapes. These subjects are examined in Chapters 5 and 6, respectively, whilst additional implications of the dispersal guild structure are considered in the general discussion chapter (Chapter 8).

CHAPTER 5

Ficus DISPERSAL GUILDS AND FIG PHENOLOGY

"All thy strong holds shall be like fig trees with the first ripe figs:
if they be shaken, they shall even fall in to the mouth of the eater"
Nahum 3:12 (Old Testament)

5.1 INTRODUCTION

The importance of figs as a dietary resource for frugivorous vertebrates arises not only because the fruits are of a design that is edible by a wide array of (not necessarily specialised) foragers but also because of the phenological patterns of fig production. Generally, in tropical forests, seasonal patterns of fruit production exist with one or two annual peaks in the availability of ripe fruit (e.g. Medway, 1972; Frankie *et al.*, 1974). Such peaks are usually related to climatic factors, especially rainfall patterns. In Bornean dipterocarp forests a different pattern of temporal availability of fruit occurs with nearly all dipterocarp species (Dipterocarpaceae; the dominant family) as well as species in many other families coming into fruit over a period of a few months in some years but not others (Sakai *et al.*, 1999). Such general fruiting events occur with a periodicity of between four and ten years and may be linked to El Niño Southern Oscillation (ENSO) events (Inoue & Hamid, 1995).

Tropical *Ficus* species, however, tend not to conform to either of these patterns. Rather, at the population level, figs are produced year-round and individuals are capable of producing more than one crop per year (Janzen, 1979). Classically, *Ficus* phenology entails individuals producing synchronously ripening crops but exhibiting asynchrony between individuals. However, many exceptions to the classical pattern are being described, particularly among dioecious *Ficus* species. These exceptions include between-individual synchrony observed in seasonal environments (e.g. Patel, 1996; Spencer *et al.*, 1996) and within-individual asynchrony induced by seasonality (e.g. Cook & Power, 1996) and/or a poor pollination environment (e.g. Bronstein & Patel, 1992). Despite this variation, figs are often available year round and are therefore a reliable food source for frugivorous animals, especially during times of general food scarcity (e.g. Foster, 1982; Leighton & Leighton, 1983; Windsor *et al.*, 1989). Furthermore, these crops can be very large, comprising hundreds of thousand of figs (Lambert & Marshall, 1991). For these reasons figs have been described as 'keystone resources' in tropical forests (Terborgh, 1986; Lambert & Marshall, 1991). However, studies in Africa and India have suggested that this generalisation is not universal but depends on frugivore mobility, *Ficus* density and the synchrony of fig production (Gautier-Hion *et al.*, 1986; Borges, 1993; Patel, 1997). Furthermore, as demonstrated by the previous chapters, not all frugivores in a given area can take advantage of the figs of any given *Ficus* species. Unfortunately, many researchers treat figs as a uniform resource rather than considering differences in terms of their suitability for frugivores, between species or guilds of species (Terborgh, 1986; McKey, 1989; Nason *et al.*, 1998). In Panama two such guilds of *Ficus* species have been described (Kalko *et al.*, 1996) while in Borneo five dispersal guilds are recognised (Chapter 4).

In this chapter I present phenological data for 56 species in the *Ficus* community of the main field site, Lambir Hills National Park, Sarawak, (see Chapter 2). I seek differences between monoecious and dioecious species and interpret patterns of fig production and resource availability to frugivores in light of the dispersal guild structure described in the previous chapters. The production of crops of ripe figs that can be utilised by vertebrate frugivores depends on immature figs being pollinated by their specific agaonid wasps. During an extreme drought between January and March 1998, many *Ficus* individuals died and local extinction of pollinating wasps of several dioecious species was observed (Harrison, 2000). Here, I demonstrate the recovery of these pollinator populations. Finally, I consider the applicability of the keystone resource concept to figs in Lambir Hills National Park.

5.2 METHODS

The fruiting patterns of 527 individuals of 56 *Ficus* species were monitored for one year (September 1998 - August 1999). Some of these individuals had been located and mapped previously by Harrison (1999) whilst the remainder were located during initial fieldwork in April 1998. In total approximately 75 ha of forest were included in the surveys. The plants under study were divided into nine census routes and visited at ten-day intervals (for dioecious *Ficus* species only female plants were observed). During each census visit, two phenological characteristics were recorded following the methods of Harrison (1999). Firstly, crop size was either counted directly or estimated by counting the number of figs on representative branches and then extrapolating to total numbers. Following Leighton (1993), crop size was recorded using a field code based on an exponential scale with each order of magnitude divided into three equally sized classes (see Table 1). Secondly, the ripeness of figs and degree of synchrony of ripening was recorded by assessing the proportion of figs in a crop that were ripe. Data collection on the size of *Ficus* individuals and on their density within the study area was also planned. However, this work was not possible because of restrictions on research activity imposed by the Sarawak Biodiversity Council in September 1999.

Temperature does not vary greatly annually in Lambir Hills National Park (Sakai *et al.*, 1999), and rainfall is likely to be the most significant environmental variable related to fig production. In order to investigate this putative relationship, daily rainfall data were acquired from Telekom Malaysia, who operate a weather station inside Lambir Hills National Park. Spearman correlation coefficients between the proportion of individuals with figs at each census and total rainfall over the preceding ten, 20, 30 and 60 days were then calculated.

While the timing of *Ficus* reproductive activity across the year is of interest, from the point of view of vertebrate frugivores it is the proportion of individuals with *ripe* figs that is significant. Thus, annual patterns of total and ripe fig production were compared between *Ficus* breeding systems and between dispersal guilds identified in Chapter 4. For some species included in this survey, observations of frugivory were not made, yet fruit characters or records from the literature suggest dispersal guild membership. However, to avoid making unnecessary assumptions, only those species for which dispersal guild membership was directly determined in Chapter 4 are included in guild-based analyses.

Table 5.1. Field codes used in the recording of fig crop sizes.

Field recording code	Crop size
0	0
0A	1-3
0B	4-6
0C	7-9
1A	10-39
1B	40-69
1C	70-99
2A	100-399
2B	400-699
2C	700-999
3A	1000-3999
3B	4000-6999
3C	7000-9999
4A	10000-39999
4B	40000-69999
4C	70000-99999
5A	100000-399999
5B	400000-699999
5C	700000-999999

5.3 RESULTS

Of the 528 *Ficus* individuals under study approximately half (257, 48.7%) failed to produce any figs during the year. Of the 271 individuals which did fruit (Table 5.2), between seven and 62 plants were observed with figs at any one time (Figure 5.1). The individuals that failed to fruit were, in general, smaller than their fig-producing counterparts, but forced early departure from the field site meant that measurements could not be made to confirm this.

Figs were present throughout the study period and the proportion of individuals with figs at any one time (excluding those individuals that failed to fruit during the study) showed relatively little variability (Figure 5.1). The mean (\pm S.D.) percentage of all fruiting individuals with figs at any one time was 13.8 ± 5.01 (Figure 5.1; Table 5.3). The proportions of monoecious ($n = 149$) and dioecious ($n = 122$) plants with crops at each census were significantly correlated ($r_s = 0.65$, $n = 39$, $p < 0.001$). However, a higher proportion of dioecious species had figs than monoecious species in all but five of the 39 censuses (Mann-Whitney $U = 1202$, $n = 39$, $p < 0.001$).

Rainfall varied seasonally in the study site. Most months had *c.* 300 mm rain whilst January 1999 had more than double this amount and March, June and, in particular, April 1999 were less wet (Figure 5.2). In stark contrast, just 138.5 mm of rain fell during the preceding drought months of January to March 1998 (source: Telekom Malaysia). No correlation was found between the number of individuals with figs and total precipitation over the ten, 20, 30 or 60 days prior to each phenology census (Table 5.3).

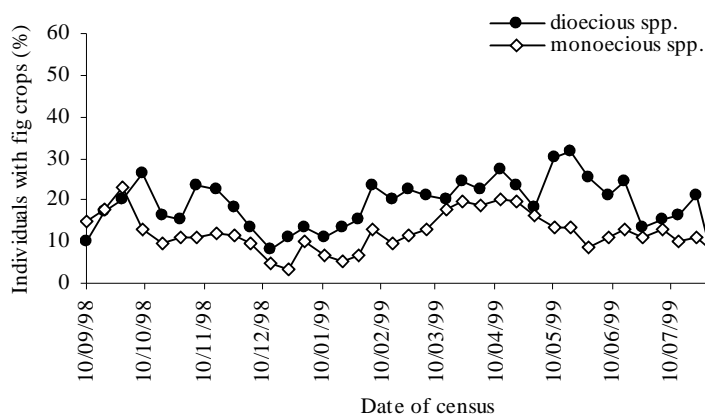


Figure 5.1. Fig crop production by 271 *Ficus* individuals over one year. Solid circles = dioecious species (122 individuals). Open diamonds = monoecious species (149 individuals).

Table 5.2. *Ficus* species producing figs during the phenology censuses. n = number of individuals that produced figs during the study. Dispersal guilds (where identified in Chapter 4) are denoted as AM = arboreal mammals, CAN = canopy birds/mammals, FB = fruit bats, TM = terrestrial mammals, US = understorey birds/mammals.

	<i>Ficus</i> species	dispersal guild	n
Subgenus <i>Urostigma</i> (monoecious)	<i>F. acamptophylla</i>	US	1
	<i>F. annulata</i>	FB	3
	<i>F. benjamina</i>	CAN	7
	<i>F. binnendykii</i>		12
	<i>F. callophylla</i>	CAN	1
	<i>F. consociata</i>	CAN	3
	<i>F. cucurbitina</i>		6
	<i>F. delosyce</i>		4
	<i>F. drupacea</i>		5
	<i>F. dubia</i>	CAN	5
	<i>F. kerkhovenii</i>	CAN	14
	<i>F. microcarpa</i>		10
	<i>F. paracamptophylla</i>		1
	<i>F. pellucido-punctata</i>		1
	<i>F. pisocarpa</i>	CAN	6
	<i>F. retusa</i>		2
	<i>F. stricta</i>	CAN	1
	<i>F. stupenda</i>	CAN	10
	<i>F. subcordata</i>	CAN	6
	<i>F. subgelderii</i>	CAN	14
	<i>F. sumatrana</i>	CAN	3
	<i>F. sundaica</i>	CAN	5
<i>F. superba</i>		1	
<i>F. xylophylla</i>	CAN	22	
	Unidentified species		6
Subgenus <i>Ficus</i> (dioecious)	<i>F. aurantiacea</i>	AM	13
	<i>F. beccarii</i>		1
	<i>F. callicarpides</i>		4
	<i>F. cereicarpa</i>	TM	2
	<i>F. fulva</i>	US	15
	<i>F. grossivenis</i>		7
	<i>F. heteropleura</i>		1
	<i>F. lanata</i>		1
	<i>F. near uncinata</i>	TM	2
	<i>F. obscura</i>	US	4
	<i>F. punctata</i>	AM	11
	<i>F. rubroscupidata</i>		2
	<i>F. sarawakensis</i>		6
	<i>F. schwarzii</i>	FB	15
	<i>F. sinuata</i>	US	2
	<i>F. stolonifera</i>	TM	3
	<i>F. subulata</i>	US	2
	<i>F. treubii</i>	TM	17
	<i>F. trichocarpa</i>		2
	<i>F. uncinata</i>	TM	1
	<i>F. uniglandulosa</i>	US	1
<i>F. villosa</i>		1	
	Unidentified species		9

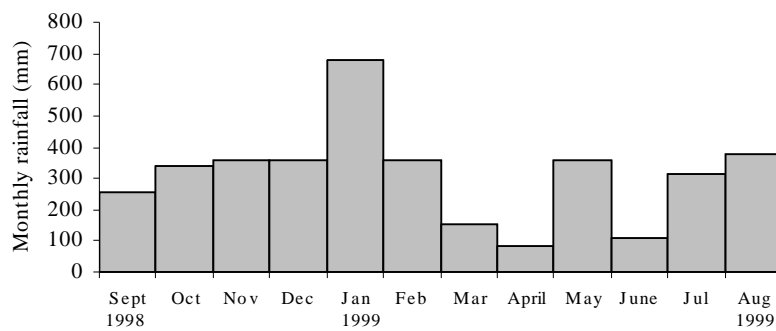


Figure 5.2. Monthly rainfall over the year of the phenology census.

Table 5.3. The proportion of *Ficus* individuals fruiting during each phenology census and correlations (one-tailed Spearman rank, $n = 39$) between fig phenology and rainfall for all *Ficus* species (271 individuals), monoecious species (149) and dioecious species (122).

<i>Ficus</i> species	mean \pm S.D.	% with figs per census		correlation with total rainfall over previous			
		maximum	minimum	10 days	20 days	30 days	60 days
All species	13.81 \pm 5.01	22.6	4.01	-0.009, n.s.	-0.078, n.s.	-0.118, n.s.	-0.143, n.s.
Monoecious	11.57 \pm 4.95	22.9	3.38	0.082, n.s.	0.036, n.s.	0.010, n.s.	-0.172, n.s.
Dioecious	18.04 \pm 6.89	31.8	3.64	-0.059, n.s.	-0.153, n.s.	-0.151, n.s.	-0.130, n.s.

Although figs were being produced year-round, ripe fig crops were not distributed evenly over the sampling period (Figure 5.3). Whereas the proportion of monoecious individuals with ripe crops appears to vary randomly over the year, that of dioecious species showed a markedly different pattern. During the first half of the phenology census between zero and two percent of dioecious individuals bore ripe figs at a given point in time. In contrast, during the second half of the survey, this proportion was between two and five percent. This dichotomy arose because in the first half of the study many crops of dioecious species were aborted because they were not pollinated (see below). Although a greater proportion of dioecious than monoecious individuals bore figs in a given census (Figure 5.1) during the second half of the study, when pollination had resumed there was no significant difference in the proportion of monoecious and dioecious individuals with ripe figs (Figure 5.3; Mann-Whitney $U = 183$, $n = 19$, n.s.).

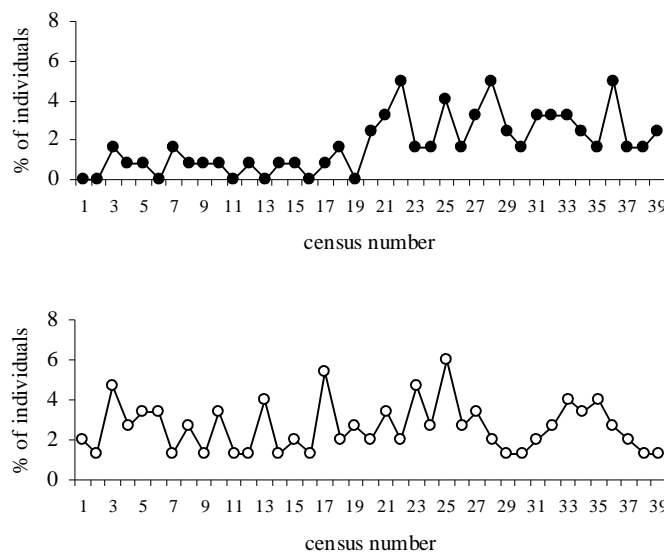


Figure 5.3. The proportion of fruiting *Ficus* individuals with ripe crops at each census. Filled circles = dioecious species. Open circles = monoecious species.

Figure 5.4 demonstrates inter- and intraspecific aseasonality of fig production using data from selected *Ficus* species for which the larger sample sizes (no. of individuals with crops) were obtained and which represent the range of growth forms and dispersal guilds exhibited by the genus. Two patterns are immediately obvious. Firstly, the presence of figs does not imply that a resource is available for frugivores. Ripe figs are present on considerably fewer individuals at any given time than are unripe figs. Nonetheless, for most of the species illustrated figs were present on some of the individuals during virtually all of the censuses. Secondly, despite regularly producing figs, some species (as shown by the charts for *F. schwarzii*, *F. aurantiacea*, *F. punctata* and *F. treubii*) produced no ripe crops during the first half of the study. These species are all dioecious and all suffered local pollinator extinctions during the extreme drought of January - March 1998 (Harrison, 2000). It would appear that pollinator wasps had not recovered until about one year later. In fact, given a period of *c.* two months between pollination and fig ripening, I estimate that some pollinators had returned by early January 1999 for *F. punctata* and *F. treubii*, late February 1999 for *F. schwarzii*, and late March 1999 for *F. aurantiacea*.

When *Ficus* species within each of the putative seed dispersal guilds described in Chapter 4 were analysed separately the average proportion of individuals with fig crops at each census was of a similar order to that of all *Ficus* species (Table 5.4, Figure 5.5). In both the guild attracting primarily fruit bats (Figure 5.5a) and the one attracting arboreal mammals (Figure 5.5b) there was a peak of fig production in May 1999 and a period during which no individuals had figs in December 1998. For the remaining guilds, the proportion of individuals with figs was less variable although isolated peaks were observed in September 1998 and October 1998 for the guilds attracting terrestrial mammals (Figure 5.5c) and understorey birds and mammals (Figure 5.5d), respectively.

Although fig production occurred across the year in each of the five *Ficus* dispersal guilds, the proportion of trees with ripe figs differed greatly (Figure 5.6). Ripe figs of monoecious hemi-epiphytes that attracted canopy birds and mammals were observed during nearly all censuses. Crops attractive to birds and mammals in the understorey were available in approximately half of the censuses, with the fluctuating pattern observed probably due to the small sample size (only 25 individuals compared with, for example, 97 individuals in the guild attracting canopy birds and mammals). For the remaining three guilds virtually no ripe figs were observed during the first half of the year. The data for the guild attracting fruit bats and terrestrial mammals were largely from *F. schwarzii* and *F. treubii*, respectively. Both of these species, as well as the two species in the guild attracting arboreal mammals (*F. punctata* and *F. aurantiacea*), suffered local pollinator extinction in the drought of 1998 (Harrison, 2000).

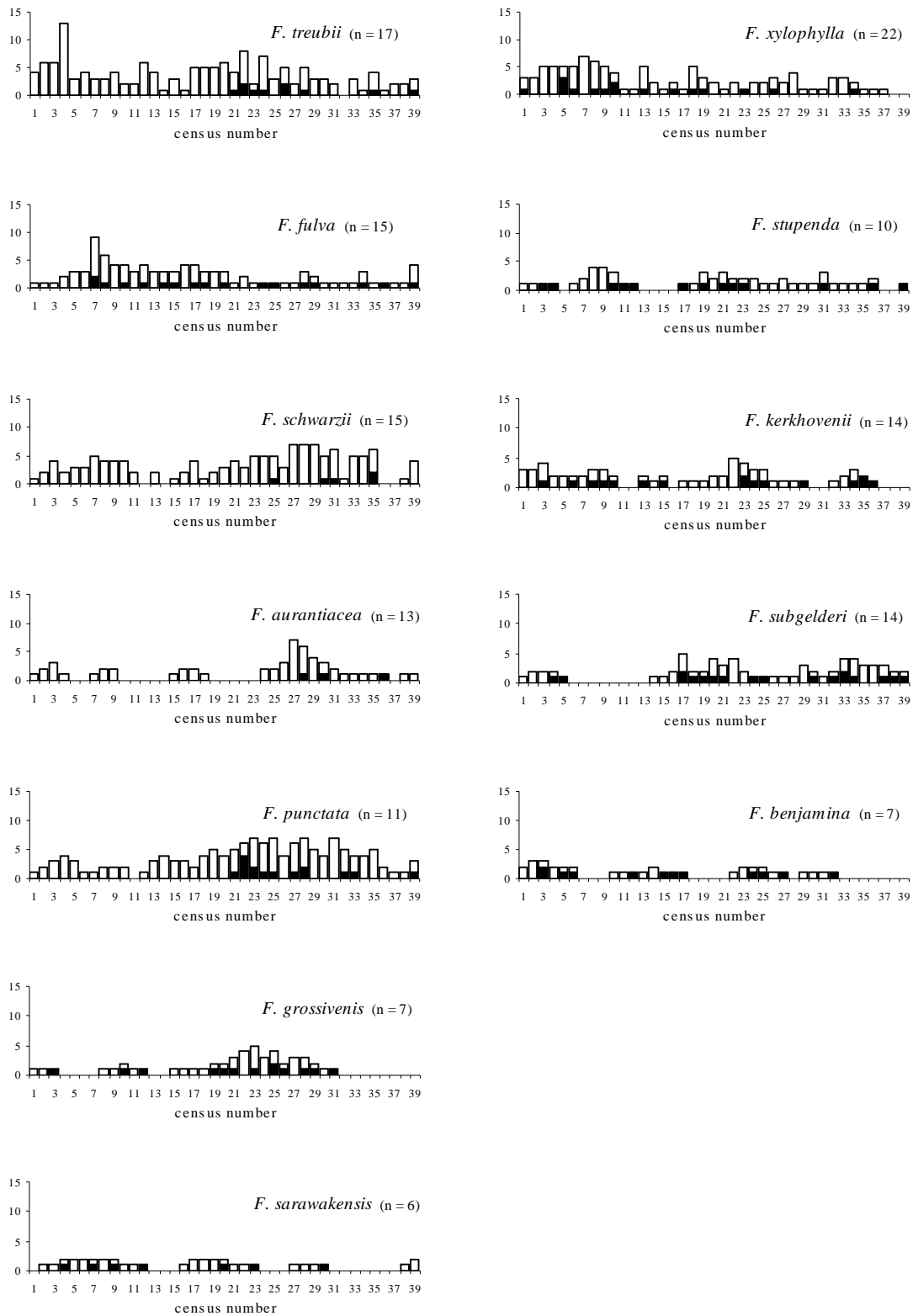


Figure 5.4. Fruiting phenologies of *Ficus* species selected on the basis of largest sample sizes (number of fruiting individuals). Census number 1 began 10 September 1998, census number 39 began 28 August 1999. Open column = unripe crop, filled column = ripe crop. Species in the left column are all dioecious whilst those in the right column are all monoecious.

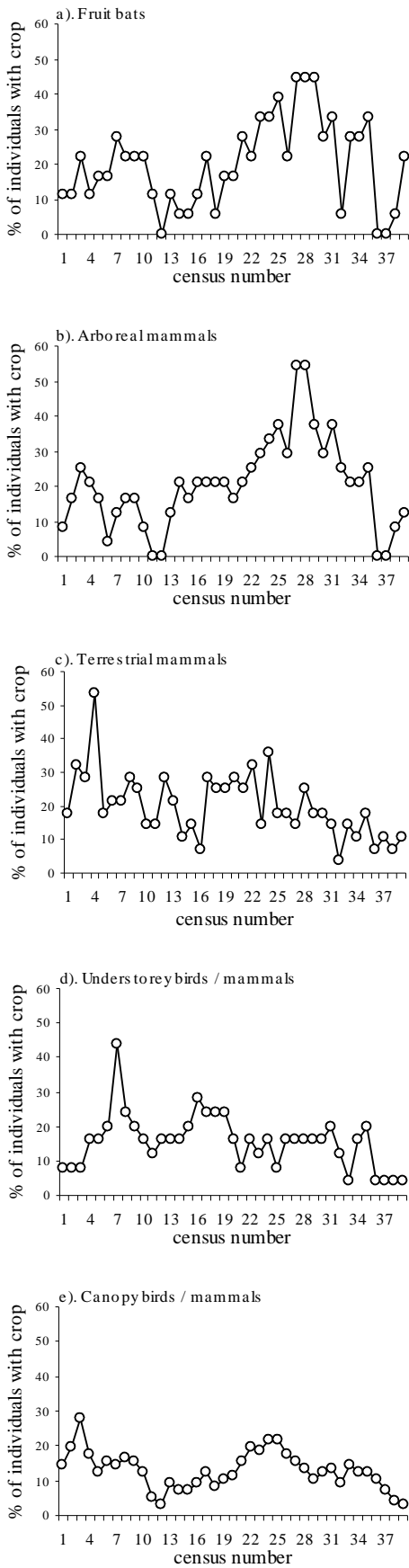


Figure 5.5. Phenology of fig crop production by *Ficus* individuals in each of the five dispersal guilds identified in Chapter 4. Census 1 = 10 September 1998, census 39 = 28 August 1999.

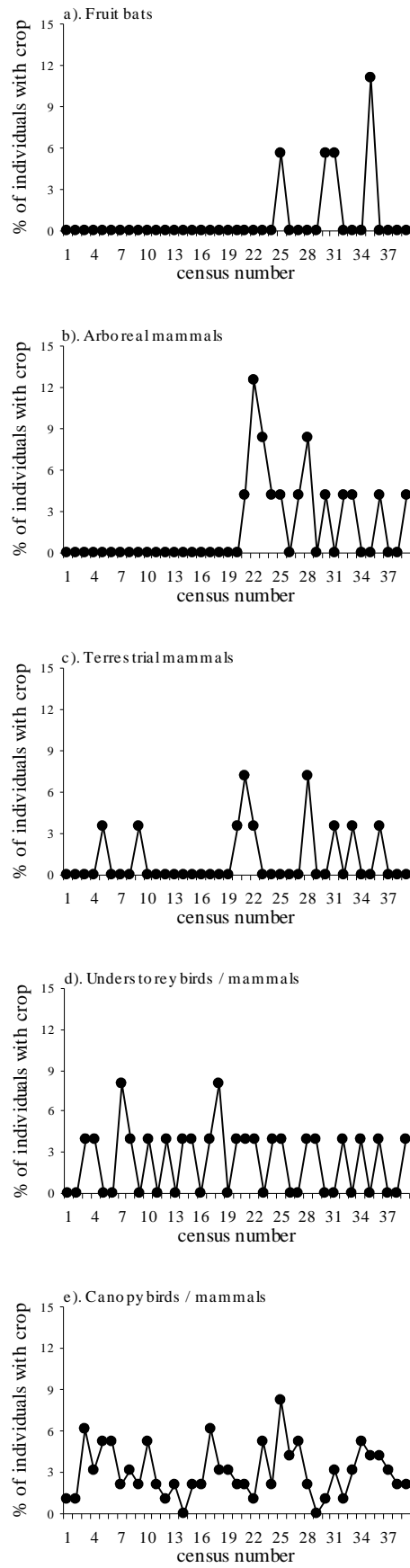


Figure 5.6. Phenology of ripe fig crop production by *Ficus* individuals in each of the five dispersal guilds identified in Chapter 4. Note that the y-axis scale differs from that in Figure 5.5.

5.4 DISCUSSION

Fig crops were produced year round in Lambir Hills National Park. The phenology of fig production was effectively continuous both within and between species and, as also noted by Lambert & Marshall (1991), appears not to be related to rainfall (which, during this study, was typical for the site; Sakai *et al.* 1999). However, evidence of relationships between the annual fruiting phenology of monoecious and dioecious *Ficus* species suggests that common cues may promote changes in fruiting intensity across the *Ficus* community. These, if genuine, remain unclear and require further investigation.

Figs may remain receptive for up to five weeks (Ware & Compton, 1994; Khadhari *et al.*, 1995). The greater proportion of dioecious than monoecious individuals with crops may therefore have been because in the absence of pollinators figs may stay on the tree for longer 'waiting' before eventually being aborted. However, the pattern was still apparent after pollinators for the majority of species had returned and may be more likely to reflect the tendency for dioecious species to have frequent, small crops whilst monoecious species produced larger crops with a greater interval between crops. For some dioecious species not only do crops ripen with the greatest degree of asynchrony (Chapter 3) but also new fig crops are initiated before the previous cohort is ripe. Crops are therefore not discrete but overlap and relatively few figs are available on a given day. Such fruiting phenology may favour animals with trap-lining foraging behaviour (using regular travel paths and tracking the availability of ripe fruits within a relatively small area). These animals include small, understory-foraging frugivores with relatively limited mobility such as bulbuls and small fruit bats (e.g. Nair *et al.*, 1999). In contrast, the monoecious hemi-epiphytes produce large, discrete crops, generally visible above the forest canopy and, thus, capable of drawing in frugivores from a wide area. These frugivores include nomadic species (e.g. pigeons and hornbills) that undertake relatively long-range movements in search of large patches of ripe fruit (Leighton & Leighton, 1983; Kinnaird *et al.*, 1996).

Inter and intraspecific asynchrony of fig crop production was evident among those species for which sufficiently large samples were obtained. However, the presence of figs does not imply the presence of a resource for vertebrate frugivores. Indeed, many crops of dioecious species were aborted during the first half of the study because their figs had not been pollinated. Pollinators had become locally extinct during the severe drought of January - March 1998 which affected much of northern Borneo (Harrison, 2000). Dispersal of wasps from unaffected *Ficus* populations further south, in numbers sufficient to be observed in this study, took approximately one year. Long-distance movement of monoecious *Ficus* species' wasps recorded in Panama (Nason *et al.*, 1998) and rapid recovery of Florida's monoecious fig-wasp populations following extirpation by Hurricane Andrew (Bronstein & Hossaert-McKey, 1995) suggest that such limited dispersal may only be a feature of pollinators of dioecious figs (Dr. R. Harrison, pers. comm.). However, the pollinators of at least some dioecious species disperse in the same way as those of monoecious species (Compton *et al.*, 2000) and these differences in colonisation may result from smaller numbers of wasps being produced, and thus fewer individuals travelling long distances. The lack of *Ficus schwarzi* figs during the first half of the year may have contributed to the small number of observations of understory-foraging fruit bats during the course of this thesis. For the animals feeding on figs in the other guilds that exhibited reduced fig production through the failure of pollination, the lack of figs may have been less important. Arboreal and terrestrial mammals will have been able to feed upon the figs of hemi-epiphytic *Ficus* species, either directly or as fallen fruit, during this time. Foraging activities of bats are also likely to have occurred across a greater spatial scale than those of other mammalian frugivores and it is possible that migrations in search of figs elsewhere took place.

The year-round initiation of crops suggests that, in times when figs do not experience pollen limitation, figs within each of the five dispersal guilds identified in Chapter 4 will be produced year-round. Thus, figs would be available, throughout the year, to all of the major groups of frugivores present in the park. In contrast, the majority of other fleshy-fruited species in Lambir Hills National Park reproduce principally during a mass fruiting episode (Sakai *et al.*, 1999), an event that did not coincide with this study. This availability of figs when other fruit are scarce is one of the reasons for them having been described as keystone resources (Terborgh, 1986). Figs may therefore be expected to be an important food resource to vertebrates in the park, especially outside of these community reproductive episodes. However, differences between *Ficus* species (principally in terms of crop size and periodicity) and between frugivores (with respect to their dietary breadth) suggest that figs will differ in their importance as a resource to frugivores. The monoecious, hemi-epiphytic species (to which the keystone resource concept has generally been applied) produce large crops which feed not only volant and arboreal frugivores (Chapter 4) but also provide a resource (their copious fallen figs) for terrestrial foragers such as deer and pigs (Balasubramanian & Bole, 1993; Heydon & Bulloh, 1997). In contrast, the species in the remaining four *Ficus* guilds identified in Chapter 4 are largely dioecious species that attract taxonomically narrow subsets of the frugivore community to generally smaller fig crops. The keystone concept is potentially less applicable to such *Ficus* species because they are important to fewer frugivore taxa. Furthermore, most animals that feed on these dioecious species also eat the figs of hemi-epiphytes, either directly (as in the case of primates, fruit bats and the majority of bird species that were observed in the understory) or as fallen fruit (as in the case of those terrestrial mammals recorded feeding on geocarpic figs). Whereas fruit bats and certain birds (barbets, pigeons, hornbills) are almost entirely frugivorous, the terrestrial mammals observed feeding upon *Ficus cereicarpa* and the geocarpic species are more generalist foragers. Thus it seems likely that even during times of low fruit abundance in the forest these animals will not necessarily rely upon the figs of this dispersal guild. Rather, non-fruit foods and fallen figs of hemi-epiphytic species are likely to contribute a greater proportion of their diet during these periods. Unfortunately, vertebrate responses to the drought were not monitored in the park, or elsewhere in Borneo.

Most of the volant and arboreal frugivores recorded in the understory also forage in the canopy, and are thus able to take advantage of the crops of hemi-epiphytes as well as dioecious plants in the understory. For dedicated understory frugivores, however, non-fig fruit are not only rare but also exhibit seasonal peaks in abundance (Wong, 1983). The *Ficus* guild attracting understory birds and mammals may be of special importance to a small proportion of the animals (e.g. bulbuls, flowerpeckers, plantain squirrel) recorded feeding there.

The results presented here indicate that in terms of being a resource for frugivores research must confirm that fig crops fully develop to maturity. Furthermore, because a given *Ficus* species' figs are not equal resources for all frugivores in a given area, any disruption to the production of ripe figs (i.e. pollinator extinction) will impact of frugivore taxa differentially. Resilience to pollinator extinction can also be added Lambert and Marshall's (1991) list of reasons why monoecious *Ficus* species can be keystone resources in tropical forests.

CHAPTER 6

FICUS DISPERSAL GUILDS AND THE COLONISATION OF VIRGIN ISLANDS IN PAPUA NEW GUINEA

"It cannot be assumed, therefore, however obvious the general method, that all fig-plants have equal means of dispersal and establishment.....much more specific investigation is required"
Corner (1958)

6.1 INTRODUCTION

Events that sterilise areas of tropical forests allow ecologists the opportunity to gain insights into the processes of colonisation, succession and assembly of these diverse biological communities. Such knowledge is of increasing value given the extent of anthropogenic disturbance to these habitats in modern times. Natural biological extirpation events vary in scale from small fires and landslides to catastrophic volcanic eruptions. While the former may not extinguish all life, leaving, for example, seed banks or invertebrate refugia, the sterilising power of the latter, forces the colonisation to begin completely anew.

This chapter considers the colonisation of Long Island, Papua New Guinea by *Ficus* species and their associated dispersers and pollinating wasps. Long Island, 50 km from the coast of New Guinea, is volcanic in origin and underwent a catastrophic eruption in c. 1645 that is likely to have eradicated all life (see Chapter 2). A 13 km diameter lake formed in the volcano's caldera where, in 1968, a new island (Motmot) that began forming in the 1950s was made permanent by renewed volcanic activity and lava flow.

Opportunities to study the colonisation of tropical islands sterilised by volcanic activity are rare. The best documented of such colonisation processes in the tropics is that following the eruption of Krakatau island (Indonesia) in 1883, and subsequent emergence of Anak Krakatau in 1930 (Thornton, 1997). The importance of *Ficus* species (Moraceae), and their vertebrate seed dispersers, in the colonisation of the Krakatau Islands has been described by Whittaker & Jones (1994) and Thornton *et al.* (1996). It is interesting, therefore, to see if *Ficus* species play a similar role in the regenerative process at other sites in the tropics. During 15 days on Long Island and Motmot the colonisation of these islands by *Ficus* species and their associated animals was investigated.

With c. 750 species exhibiting a variety of growth forms that includes shrubs, trees, climbers, epiphytes and hemi-epiphytic stranglers, *Ficus* is arguably the world's most diverse woody plant genus (Corner, 1988; Berg, 1990). The characteristic *Ficus* inflorescence (the fig) is remarkably uniform in structure but differences occur in the way that figs are packaged and presented. Crops range from tens to millions of red, green, brown or black figs which can be geocarpic (on ground level runners), cauliflorous (growing directly from the stem or trunk) or produced in the leaf axils (Corner, 1988). Furthermore, two breeding systems, monoecy and dioecy occur among *Ficus* species. The diversity of *Ficus* is reflected in the fact that virtually all fruit-eating animals in the tropics include figs in their diet (Shanahan & So, in review; Chapter 7).

The pools of potential colonists to Long Island are in New Guinea and New Britain (Figure 1.1). Over 170 *Ficus* species are known from these islands (Corner, 1965), with New Guinea's *Ficus* flora being one of the world's most diverse. Dr. G. Weiblen (unpublished) has produced a list of 55 *Ficus* species of Madang Province, Papua New Guinea. Given its similar latitude and proximity to Madang, members of this subset of the New Guinea *Ficus* flora would be those most likely to have colonised Long Island. Potential dispersers for *Ficus* in the study area include birds, fruit bats, the introduced Grey Cuscus (*Phalanger orientalis*) and feral pigs (Ball & Hughes, 1982).

In contrast to the relatively diffuse nature of relationships between fig trees and dispersers each *Ficus* species has a specific agaonid wasp (Hymenoptera; Agaonidae) pollinator (Wiebes, 1979; though see Michaloud *et al.*, 1996 for exceptions). The production of fig fruit is therefore dependent on the presence of pollinator wasps. Conversely, the wasp is only able to reproduce inside a fig (see Galil, 1973; Janzen, 1979). Moreover the wasp has a very short adult life span, usually just one day (Kjellberg *et al.*, 1988) and is therefore dependent on the presence of receptive figs when it emerges. Thus in very small fig populations, such as on islands, stochastic extinction of the pollinator wasp is possible (Bronstein *et al.*, 1990; Kameyama *et al.*, 1999). Also, even if the pollinating wasp is present, low pollination levels may be the norm if colonisation rates from mainland populations are low (Compton *et al.*, 1994). Therefore, the stability of the pollinating wasp population and pollination success of a *Ficus* species will ultimately depend on the *Ficus* species' population size, colonisation rate (dispersal ability) of pollinator wasps and the frequency of fruiting by *Ficus* individual (Kameyama *et al.*, 1999). *Ficus* species with different combinations of these characters may therefore differ in their ability to colonise islands.

The fig story is one in which disparate taxa are inextricably linked - the population size and characteristics of the fig trees affects pollinator wasp presence. This in turn affects seed set and fruit ripening, which then influences frugivore attraction and ultimately influences the dispersal of seeds and expansion of a fig species' range. All three groups of organisms must therefore be considered if the colonisation of a virgin island by these fascinating plants is to be understood.

6.2 METHODS

Ad hoc searches for *Ficus* individuals were undertaken, with efforts concentrated in known habitats (forest edge, watercourses, light gaps). Species were identified by reference to Weiblen's (unpubl.) guide to the figs of Madang Province, and Corner's (1965) key. Leaf and, when possible, fig samples were collected and deposited in the Forest Research Institute, Lae, where confirmatory identifications were made by institute staff. Sampling was conducted in eight distinct sites on Long Island (Chapter 2). In contrast to the *ad hoc* sampling employed on Long Island, Motmot was surveyed in its entirety.

The attributes of ripe figs were characterised in the following manner (with only female figs considered for dioecious species). Between 10 and 40 figs were collected from representative ripe crops, either directly from the plant or as freshly fallen fruit. An index of fig size was calculated as the product of fig length (basal to apical dimension) and the square of the equatorial

diameter. Elsewhere, this index has been demonstrated to show a strong, significant correlation with wet mass of figs and is of use in situations where weighing of figs is not practical (Appendix 4). Crop size was either counted directly or estimated by counting the number of figs on representative branches and then extrapolating to total numbers. Fig colour and the presence or absence of a noticeable odour was noted. The placement of the figs (cauliflorous or axillary) and whether they were sessile or stalked was recorded and, in the case of the latter, stalk length was measured. Finally, estimations to the nearest metre were made of the maximum and minimum heights above ground level at which figs were presented.

Colonisation by pollinating wasps was confirmed by observation of wasps inside figs or by the discovery of seeds or galls in mature figs. Placing immature figs in gauze bags (male figs only in dioecious species) allowed wasps to be collected upon emergence and later identified through reference to Boucek (1988).

Frugivorous vertebrates present on Long Island and Motmot were identified by mist-netting, live-trapping for small terrestrial mammals, and *ad hoc* search sampling (see Cook *et al.*, in review; Schipper *et al.*, in review). Fig eating was confirmed by observing ripe crops and recording the identities of species seen eating figs.

The *Ficus* species recorded on Long Island and Motmot were compared with floras available for the Madang region (G. Weiblen, unpublished) and New Guinea as a whole (Corner, 1965). Chi-squared tests with Yates' correction were used to compare the relative numbers of monoecious and dioecious fig species and of members of different sections of the genus (Corner, 1965). *Ficus* dispersal guilds were identified by comparing the proportion of New Guinea bird and fruit bat genera known to eat Long Island's figs for which fig eating records exist for each *Ficus* species on Long Island, using data from this study or the review of Shanahan & So (in review). Canonical discriminant analysis (CDA) was performed to investigate which of the fruit attributes (fruit size, stalk length, crop size and maximum and minimum crop height) were associated with the putative dispersal guilds and whether differences between guilds were significant. CDA provides multivariate axes (canonical variables) for discrimination of groups, clarifying the differences between groups by reducing the number of variables (SAS Institute Inc., 1985; procedure CANDISC). Crop size was log transformed to make it conform to an approximately normal distribution and fruit colour, as a binary variable, was not included in the analysis but its distribution amongst the groups was compared subsequently.

6.3 RESULTS

Thirty *Ficus* species were recorded on Long Island with seven of these having also colonised Motmot (Table 6.1). Additionally, *F. cf. caulocarpa* was recorded on Motmot but not observed on Long Island, although for analytical purposes I assume it is present. Long Island's *Ficus* species exhibit much of the range of diversity of habit, breeding system and means of fruit production known from the genus. Freestanding trees (especially *F. nodosa*, *F. wassa*, and *F. septica*) were abundant around the main camp and lake shore whilst the hemi-epiphytes (notably *F. virens* and *F. virgata*) were more common in the closed forest of the crater rim. Climbing figs, however, were rare on Long Island. Only one individual *F. subulata* was located, despite specific searches for species with this habit.

The *Ficus* species that have succeeded in colonising Long Island are largely a subset of those known from the Madang area of Papua New Guinea (Corner, 1965; G. Weiblen unpublished). The relative numbers of monoecious and dioecious species do not differ significantly from those in the Madang area (Yates corrected $\chi^2 = 0.689$, d.f. = 1, n.s.) or in New Guinea as a whole (Yates corrected $\chi^2 = 2.97$, d.f. = 1, n.s.). Considering the taxonomy of the colonising fig species it appears that members of each *Ficus* section are present on Long Island in proportions equivalent to those in the source areas of Madang or New Guinea (Table 6.2). The only statistically significant difference is that no members of section *Rhizocladus* have colonised in spite of this section accounting for over one fifth of New Guinea's *Ficus* flora (Yates corrected $\chi^2 = 8.52$, d.f. = 1, $p < 0.05$).

Pollinator presence was confirmed for the 16 *Ficus* species found fruiting on Long Island, either by collection of wasps or by observation of seed or galls in mature figs. Only one instance of pollinator limitation was observed. A single female individual of *F. congesta* var. *chalmersii* found during the ascent of Cerisy Peak had unpollinated figs that were in the process of being aborted.

Fruit characteristics of ripe crops of the 16 *Ficus* species observed fruiting on Long Island are presented in Table 6.1, along with supplemental data from trees on the mainland and from literature sources. Long Island's figs exhibit great diversity in terms of size (diameter ranged from 5 mm in *Ficus prasinicarpa* to over 40 mm in *F. sterrocarpa*), placement (cauliflorous or axillary), crop size and vertical placement. In terms of ripe fig colour, two groups of *Ficus* species can be recognised, those producing orange-red-purple figs and those producing yellow-green-brown figs. Odour was found to be an inconsistent trait as it could not be reliably assessed and is not considered further.

Table 6.1. *Ficus* species recorded on Long Island (L) and Motmot (M). Nomenclature follows Corner (1965). Growth form: T = tree, HE = hemi-epiphyte, C = climber. Breeding system: D = dioecious, M = monoecious. Fig placement: A = axillary, C = cauliflorous. Data from this study unless otherwise noted. Fig size index calculated as $(\text{length} \times \text{diameter}^2) / 100$

Subgenus	Section	Species name and authority	Growth form	Locality	Breeding system	Ripe fig colour	placement	diameter mm (mean \pm S.D.)	length mm (mean \pm S.D.)	peduncle	fig size index	crop size	crop height
<i>Ficus</i>	<i>Adenosperma</i>	<i>F. adenosperma</i> Miq.	T	L	D	green ¹	A/t ³	10.24 \pm 0.932 ¹	8.8 \pm 0.92 ¹	5.74 \pm 1.11 ¹	9.23	15000 ¹	2 - 12 m ¹
<i>Ficus</i>	<i>Adenosperma</i>	<i>F. mollior</i> Benth.	T	L	D	green	A/C	16.34 \pm 1.103	16.16 \pm 0.994	6.86 \pm 0.581	43.15	5000	1 - 5 m
<i>Ficus</i>	<i>Neomorphe</i>	<i>F. nodosa</i> Teysm. et Binn.	T	L, M	D	green	C	27.91 \pm 3.48	26.44 \pm 3.64	9.83 \pm 1.87	205.96	2500	1 - 5 m
<i>Ficus</i>	<i>Neomorphe</i>	<i>F. variegata</i> Bl.	T	L	D	green/dark red	C	27.31 \pm 1.41	24.66 \pm 1.33	22.47 \pm 1.47	183.90	1000	2 - 4 m
<i>Ficus</i>	<i>Sycidium</i>	<i>F. copiosa</i> Steud.	T	L, M	D	yellow	C	29.07 \pm 4.31	28.25 \pm 4.11	20.1 \pm 2.02	245.64	1200	1 - 6 m
<i>Ficus</i>	<i>Sycidium</i>	<i>F. gul</i> Laut. et K. Schumm.	T	L	D	orange ³	A/t ³	6 - 9 ⁴	no data	3 - 18 ⁴	no data	no data	no data
<i>Ficus</i>	<i>Sycidium</i>	<i>F. melinocarpa</i> Bl.	T	L, M	D	orange-red	A	8.21 \pm 0.57	8.17 \pm 0.55	4.95 \pm 1.15	5.51	4000	10 - 16 m
<i>Ficus</i>	<i>Sycidium</i>	<i>F. porphyrochaete</i> Corner	T	L	D	no data	C ³	5 - 12 ⁴	no data	0 - 2 ⁴	no data	no data	no data
<i>Ficus</i>	<i>Sycidium</i>	<i>F. subulata</i> Bl.	C	L	D	orange ²	A ²	8.12 \pm 1.304 ²	8.65 \pm 1.56 ²	2.73 \pm 0.647 ²	5.70	4500 ²	1 - 10 m ²
<i>Ficus</i>	<i>Sycidium</i>	<i>F. tinctoria</i> Forst.f.	HE	L	D	orange-red	A	10 - 17 ⁴	no data	present	no data	12000	10 - 20 m
<i>Ficus</i>	<i>Sycidium</i>	<i>F. trachypison</i> K. Schum.	T	L	D	orange-red	A	7.23 \pm 0.56	7.15 \pm 0.599	sessile	3.74	5500	12 - 20 m
<i>Ficus</i>	<i>Sycidium</i>	<i>F. virgata</i> Reinw. ex Bl.	HE	L, M	D	orange-red	A	8.44 \pm 0.95	8.15 \pm 1.11	sessile	5.81	18000	12 - 16 m
<i>Ficus</i>	<i>Sycidium</i>	<i>F. wassa</i> Roxb.	T	L, M	D	pink	C	11.01 \pm 1.34	10.89 \pm 1.18	14.11 \pm 3.6	13.20	2000	1 - 7 m
<i>Ficus</i>	<i>Sycocarpus</i>	<i>F. botryocarpa</i> Miq.	T	L	D	yellow-green ³	C	20 - 50 ⁴	no data	present ³	no data	no data	no data
<i>Ficus</i>	<i>Sycocarpus</i>	<i>F. congesta</i> Roxb.	T	L	D	yellow ³	C	25.82 \pm 3.16	24.9 \pm 1.97	17.75 \pm 0.979	166.00	1200	1 - 5 m
<i>Ficus</i>	<i>Sycocarpus</i>	<i>F. itoana</i> Diels	T	L	D	yellow-green	C	34.28 \pm 1.69	32.08 \pm 2.05	57.8 \pm 6.54	376.98	2500	3 - 10 m
<i>Ficus</i>	<i>Sycocarpus</i>	<i>F. microdictya</i> Diels	T	L	M	red	A	9.48 \pm 1.20	8.57 \pm 1.07	3.38 \pm 0.95	7.70	2000	6 - 10 m
<i>Ficus</i>	<i>Sycocarpus</i>	<i>F. papuana</i> Corner	T	L	D	no data	C ⁴	20 - 30 ⁴	no data	no data	no data	no data	no data
<i>Ficus</i>	<i>Sycocarpus</i>	<i>F. septica</i> Burm.f.	T	L, M	D	green	C	29.96 \pm 5.82	20.67 \pm 2.98	8.53 \pm 3.87	185.53	300	1 - 8 m
<i>Ficus</i>	<i>Sycocarpus</i>	<i>F. cf. hispidooides</i> S. Moore	T	L	D	green-brown	C	34.55 \pm 2.19	25.06 \pm 1.4	14.66 \pm 2.3	299.14	450	1 - 8 m
<i>Pharmacosycea</i>	<i>Oreosycea</i>	<i>F. pachystemon</i> Warb.	T	L	M	no data	A/C	no data	no data	no data	no data	no data	no data
<i>Pharmacosycea</i>	<i>Oreosycea</i>	<i>F. polyantha</i> Warb.	T	L	M	no data	A	18 - 30 ⁴	no data	no data	no data	no data	no data
<i>Urostigma</i>	<i>Conosycea</i>	<i>F. benamina</i> L.	T, HE	L, M	M	red-purple	A	9.28 \pm 1.09	9.64 \pm 1.19	sessile	8.30	*	*
<i>Urostigma</i>	<i>Conosycea</i>	<i>F. drupacea</i> Thunb.	HE	L	M	orange-red ³	A ³	15 - 25 ⁴	12 - 20 ⁴	sessile ³	no data	no data	-30 m
<i>Urostigma</i>	<i>Malvanthera</i>	<i>F. glandifera</i> Summerh.	HE	L	M	no data	A	10 - 35 ⁴	10 - 18 ⁴	sessile	no data	no data	no data
<i>Urostigma</i>	<i>Malvanthera</i>	<i>F. hesperidiiformis</i> King	HE	L	M	no data	A	> 35 ⁴	no data	10 - 50 ⁴	no data	no data	no data
<i>Urostigma</i>	<i>Malvanthera</i>	<i>F. sterrocarpa</i> Diels	HE	L	M	no data	A	40 - 50 ⁴	70 - 110 ⁴	present ³	no data	no data	no data
<i>Urostigma</i>	<i>Malvanthera</i>	<i>F. xylosicia</i> Diels.	HE	L	M	red	A	13.13 \pm 0.91	25.78 \pm 1.81	4.43 \pm 0.74	44.44	3500	10 - 17 m
<i>Urostigma</i>	<i>Urostigma</i>	<i>F. prasinicarpa</i> Elm.	HE	L	M	red	A	5 - 8 ⁴	no data	1 - 2.5 ⁴	no data	no data	no data
<i>Urostigma</i>	<i>Urostigma</i>	<i>F. virens</i> Ait.	HE	L	M	orange-red	A	10.3 \pm 1.11	9.43 \pm 0.99	1.55 \pm 0.53	10.00	18000	15 - 20 m
<i>Urostigma</i>	<i>Urostigma</i>	<i>F. cf. caulocarpa</i> Miq.	T	M	M	no data	A	5 - 8 ⁴	no data	1 - 4 ⁴	no data	no data	no data

¹ data from Madang (M. Shanahan, unpublished data), ² data from Sarawak (Chapter 4), ³ data from Weiblen's unpublished flora. ⁴ data from Corner (1965). * one individual was a free standing tree with 6000 figs presented between 2.5 and 3.5 m, another was a hemi-epiphyte with figs presented between 20 and 25 m and a crop of 20000 figs.

Table 6.2. Comparison of *Ficus* breeding systems and taxonomy on Long Island, Motmot and the mainland. No significant difference exists in the relative numbers of monoecious and dioecious species between Long and Madang (χ^2 with Yates' correction = 0.689) or New Guinea (χ^2 with Yates' correction = 2.07). Regarding taxonomy, the only significant difference is the lack of *Rhizocladus* species on Long compared to New Guinea (χ^2 with Yates' correction = 8.52, $p < 0.05$). Small expected frequencies for Motmot's *Ficus* species prevent statistical comparison with potential source areas.

	New Guinea ^a		Madang area ^b		Long Island		Motmot	
	n species	% of total	n species	% of total	n species	% of total	n species	% of total
a). Breeding system								
Monoecious	38	25.9	17	30.9	12	38.7	2	25
Dioecious	109	74.2	38	69.1	19	61.3	6	75
b). <i>Ficus</i> section								
<i>Adenosperma</i>	17	11.6	5	9.09	2	6.45	0	0
<i>Neomorphe</i>	4	2.72	3	5.45	2	6.45	1	12.5
<i>Sycidium</i>	28	19.1	14	24.5	9	29.1	4	50.0
<i>Sycocarpus</i>	23	15.7	12	21.8	7	22.6	1	12.5
<i>Oreosycea</i>	11	7.48	7	12.7	2	6.45	0	0
<i>Conosycea</i>	10	6.81	5	9.09	2	6.45	1	12.5
<i>Malvanthera</i>	9	6.12	3	5.45	4	12.9	0	0
<i>Urostigma</i>	5	3.44	2	3.66	3	9.68	1	12.5
<i>Rhizocladus</i>	32	21.8	4	7.27	0	0	0	0
<i>Kalosyce</i>	2	1.36	0	0	0	0	0	0
<i>Ficus</i>	3	2.04	0	0	0	0	0	0
<i>Sycomorus</i>	3	2.04	0	0	0	0	0	0
Total	147		55		31		8	

^adata from Corner (1965), ^bdata from G. Weiblen (unpublished)

Table 6.3. *Ficus* species recorded on Motmot since its appearance in 1968. ? indicates a dubious identification. Numbers in parentheses indicate numbers of individuals recorded in 1999.

<i>Ficus</i> species	year			
	1971 ^a	1972 ^a	1988 ^b	1999
<i>F. pungens</i> Reinw. ex Bl.	?			
<i>F. benjamina</i> L.	?	*		* (6)
<i>F. virgata</i> Reinw. ex Bl.		?	*	* (1)
<i>F. glaberrima</i> Bl.			*	
<i>F. opposita</i> Miq.			*	
<i>F. wassa</i> Roxb.				* (21)
<i>F. septica</i> Burm. f.				* (1)
<i>F. nodosa</i> Teysm. et Binn.				* (1)
<i>F. cf. caulocarpa</i> Miq.				* (1)
<i>F. copiosa</i> Steud.				* (2)
<i>F. melinocarpa</i> Bl.				* (2)
Total <i>Ficus</i> species present	2	2	3	8

^aBall & Glucksman 1975, ^bOsborne & Murphy 1989

Thirty-one years after its appearance in Lake Wisdom, Motmot is now occupied by eight *Ficus* species, of which two are monoecious and six are dioecious (Table 6.2). Small expected frequencies for Motmot prevent statistical comparison with potential source areas. Despite the relatively large number of *Ficus* species for an island of its size and successional state, one species, *F. wassa*, accounts for almost two-thirds of the individuals (Table 6.3). Table 6.3 illustrates the colonisation of Motmot by *Ficus* species since its emergence. Ball & Glucksman (1975) and Osborne & Murphy (1989) identified three *Ficus* species that have not been recorded since or from Long Island itself. It is likely that Ball & Glucksman's *F. ? pungens* and Osborne & Murphy's *F. opposita* were misidentified individuals of *F. nodosa*, a species on Motmot with superficially similar leaves. That Osborne and Murphy failed, in 1988, to record *F. benjamina* (a species present in 1972 and 1999) is also noteworthy. The large *F. benjamina* tree on Motmot is likely to be more than ten years old and, if so, was probably misidentified as *F. glaberrima* (both species are in subgenus *Urostigma*, section *Conosycea*; Corner, 1965), a species not recorded by this survey or in Weiblen's Madang flora.

Most fig individuals on Motmot are small and likely to be immature. Three small crops, two of *Ficus wassa* and one of *F. nodosa*, were observed but the figs were not pollinated. The large freestanding *F. benjamina* individual is the largest plant on Motmot and is of sufficient size to be producing crops of figs numbering in their thousands.

Thirty-six species of potentially or actually fig eating vertebrates have been recorded on Long Island (Table 6.4). More detailed coverage of these and other colonists can be found elsewhere (Schipper *et al.*, in review; Cook *et al.*, in review). On Motmot the only living frugivore recorded was the Melanesian Scrubfowl (*Megapodius eremita*). However, the skull of an *Aplonis* starling was found, indicating that it had either been killed there or brought from Long Island by a raptor. Table 6.4 indicates which *Ficus* species are eaten by each frugivore species or their congeners, on Long Island or elsewhere. Long Island's *Ficus* species occur in the diets of 44 genera of volant New Guinea birds and eight genera of New Guinea bats (Shanahan & So, in review; Chapter 7). When the proportions of these genera for which fig consumption is recorded are plotted across fig species it becomes possible to identify three putative dispersal guilds (Figure 6.1). The first comprises seven fig species for which very few avian genera are recorded but between one and eight fruit bat genera are recorded (i.e. arbitrarily <10 % of bird genera but >10 % of bat genera) and for which I assume dispersal is primarily effected by bats. The second group includes six *Ficus* species for which both avian and fruit bat genera are well represented (> 10 % of both bird and bat genera recorded). Finally, for eight species only avian frugivores are known, but records for this group are too sparse for conclusions about their overall dispersal strategy to be drawn. Members of the bat-dispersed guild are all dioecious, whilst both monoecious and dioecious species are included in the other two groups.

In order to assess whether these putative dispersal guilds can be separated on the basis of the mode of fruit presentation, canonical discriminant analysis was performed using fruit size, stalk length, crop size and maximum and minimum crop height as variables. It was possible to include only the 18 *Ficus* species for which adequate data had been collected (data from Long Island for 16 species, and from other localities for the remaining two; Table 6.1). For 14 of these species identities of frugivores are known (Table 6.4). Overall, there was a highly significant difference between the putative guilds (Wilk's $\lambda = 0.0624$, $p < 0.01$). However, when Mahalanobis distances between guilds were calculated the bat-dispersed guild was significantly different from each of the other two (bat vs. bird and bat, $F = 18.8$, $p < 0.01$; bat vs. bird, $F = 12.7$, $p < 0.01$), but these were not significantly different from each other (bird and bat vs. bird, $F = 0.04$, $p > 0.05$). On the basis of the fruit characters considered here, the latter two putative guilds should be considered as a single group.

The scatterplot of the first (CAN1) and second (CAN2) canonical variables illustrates this result clearly with the putative bat-dispersed figs all positioned to the right side of the plot. CAN 1 and CAN 2 accounted for 99.8 % and 0.2 % of the variance between guilds, respectively. The contributions of each fig character to CAN1 and CAN2 are shown in terms of their standardised canonical coefficients in Figure 6.2. Thus, of the variables considered, the major determinants of guild membership are fig size and crop height. Furthermore all members of the putative bat guild had green-yellow figs, whilst all of those in the other two putative guilds had orange-red-purple figs.

The four *Ficus* species for which frugivores are not known were classified with the bird and bird-and-bat dispersed species. However, two of these species (*F. adenosperma* and *F. mollior*) have green figs and appear to cluster away from the other species. Strong predictions about the identities of their dispersers cannot be made. The outlying position of point 19 may reflect the fact that it represents a freestanding individual of *F. benjamina*, the normal habit of which is hemi-epiphytic (Corner, 1988).

Table 6.4. Potential fig seed dispersers of Long Island and Long Island figs known from their diet. I = data from this study, X = record from literature. C = congener recorded eating figs (data from Shanahan & So; in review; Chapter 7). Nomenclature follows Sibley & Monroe (1990) for birds and Corbet & Hill (1991) for mammals. Faunal list compiled from this study and Coultas (1933-35), Diamond (1974, 1981), Ball & Glucksman (1975), Cook *et al.* (in review) and Schipper *et al.* (in review).

	<i>F. nodosa</i>	<i>F. variegata</i>	<i>F. copiosa</i>	<i>F. gul</i>	<i>F. melinocarpa</i>	<i>F. tinctoria</i>	<i>F. trachypison</i>	<i>F. virgata</i>	<i>F. wasa</i>	<i>F. botryocarpa</i>	<i>F. congesta</i>	<i>F. itoana</i>	<i>F. septica</i>	<i>F. hispidoides</i>	<i>F. benjamina</i>	<i>F. drupacea</i>	<i>F. hesperidiiformis</i>	<i>F. sterrocarpa</i>	<i>F. xylosicia</i>	<i>F. prasinicarpa</i>	<i>F. virens</i>	<i>F. caulocarpa</i>	Any <i>Ficus</i> species
BIRDS																							
<i>Megapodius eremita</i>																							X
<i>Gallus gallus domesticus</i>																							X
<i>Amaurornis olivaceus</i>																					C		X
<i>Macropygia amboinensis</i>					C	C	C	C	C														X
<i>Macropygia mackinlayi</i>					1	X	X	1	C												1		1
<i>Chalcophaps stephani</i>															C								C
<i>Gallilolumba beccarii</i>										C													C
<i>Ptilinopus iozonus</i>						X	X	C	C						C			C	C				X
<i>Ptilinopus insolitus</i>						C	C	C	C						1			C	C				1
<i>Ptilinopus solomonensis</i>						X	X	1	C						1			1	1	1			1
<i>Ducula pistrinaria</i>									C						C						1		1
<i>Ducula bicolor</i>									C						X						X		X
<i>Eudynamis scolopacea</i>								1							X				1	1	1		1
<i>Trichoglossus haematodus</i>						1	X								X				1	X			1
<i>Lorius hypoinochrous</i>								C															C
<i>Charmosyna placentis</i>							X																C
<i>Cacomantis variolosus</i>																							C
<i>Scythrops novaehollandiae</i>																							X
<i>Pitta sordida</i>																							C
<i>Coracina tenuirostris</i>																							C
<i>Monarcha cinerascens</i>							1																X
<i>Aplonis cantoroides</i>						C	X	C	C						C			C	C				X
<i>Aplonis metallica</i>						1	C	1	1						1			1	1	1			1
<i>Nectarinia jugularis</i>									C														C
<i>Zosterops griseotincta</i>		C			1		1	1							1			1	1	1			1
<i>Erythrura trichroa</i>																							C
MAMMALS																							
<i>Phalanger orientalis</i>	X	X	X			X	X	1					X										1
<i>Nyctimene albiventer</i>	X	X	X			X	X	X					X										X
<i>Nyctimene cephalotes</i>	C	C	C			C	C	C					C										C
<i>Pteropus conspicillatus</i>	X	C				X		X	C					C						X			X
<i>Macroglossus minimus</i>	X	X	X			X	X	X	X	X													X
<i>Melonycteris melanops</i>									1														1
<i>Sus scrofa</i>															X								X
<i>Rattus praetor</i>		C											C										C
<i>Rattus exulans</i>		C											C										C
REPTILES																							
<i>Varanus indicus</i>																							C
OTHER NEW GUINEA FRUGIVORES																							
(ABSENT FROM LONG ISLAND)																							
Volant bird genera	1	2	2	6		9	12	19	1	2	5	9	1	1							5	4	
Fruit bat genera	3	4	4			4	2	4	1	4	2												
Arboreal mammal genera	2	2	3			3	3	3	2	1													

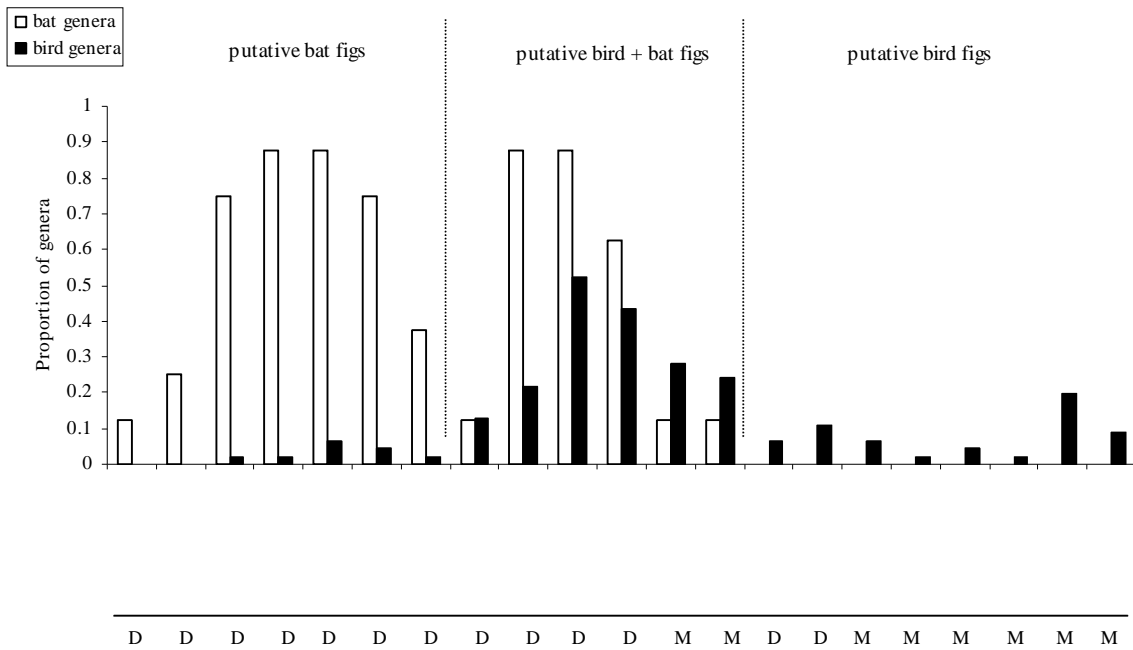


Figure 6.1. The proportion of New Guinea volant bird and fruit bat genera that are known to eat Long Island's figs for which frugivory has been recorded at individual *Ficus* species. Data from this study and Shanahan & So (in review; Chapter 7). M and D indicate monoecious and dioecious species, respectively.

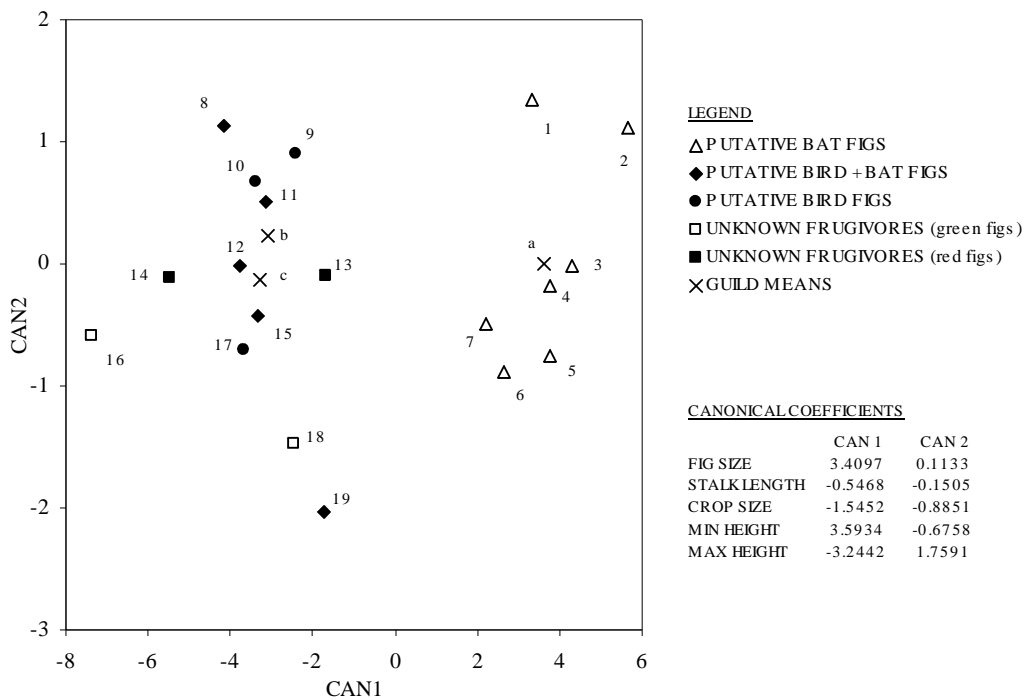


Figure 6.2. Scatterplot of the first (CAN1) and second (CAN2) axes of the canonical discriminant analysis based on fruit attributes (fig size, fig stalk length, crop size and maximum and minimum crop height) of the figs of Long Island. The putative bat-dispersed species (open triangles) are significantly different from the putative bird & bat dispersed species (black diamonds; $F = 18.8, p < 0.01$) and the putative bird-dispersed species (black circles; $F = 12.7, p < 0.01$). However, no significant difference was detected between the latter two guilds ($F = 0.04, p > 0.05$). Putative guild means are indicated by \times (a = bat figs, b = bird figs, c = bird and bat figs). 1 = *F. septica*, 2 = *F. hispidioides*, 3 = *F. itoana*, 4 = *F. copiosa*, 5 = *F. variegata*, 6 = *F. nodosa*, 7 = *F. congesta*, 8 = *F. trachypison*, 9 = *F. xylosicia*, 10 = *F. melinocarpa*, 11 = *F. benjamina* (hemi-epiphytic), 12 = *F. virens*, 13 = *F. microdictya*, 14 = *F. subulata*, 15 = *F. wassa*, 16 = *F. adenosperma*, 17 = *F. virgata*, 18 = *F. mollior*, 19 = *F. benjamina* (freestanding tree). *F. benjamina* is represented twice because of the two different growth forms observed.

6.4 DISCUSSION

In the approximately 350 years since Long Island's biota was eradicated, 31 species of *Ficus* (a little over half of those known from the Madang area) have colonised the island. The lack of *Rhizocladus* climbers may simply reflect a West-East decline in the numbers of these species across the island of New Guinea - only four of New Guinea's 32 *Rhizocladus* species are known from Madang (G. Weiblen, unpublished).

The facts that 16 *Ficus* species were located on Long Island with ripe figs in only 15 days, and that half of the island's land-bird species eat figs or have congeners that do so support claims that figs are an exceptionally important resource in regenerating tropical forests (Whittaker & Jones, 1994; Thornton *et al.*, 1996). However, fig species are not equal in terms of their suitability for particular frugivores. The analyses suggest two distinct *Ficus* dispersal guilds: one comprising species using primarily bats for dispersal and one fed upon by a range of bird and bat species. The former present their large, dull green or yellow figs in the lower storeys of the forest whilst the latter produce bright orange or red figs that are available throughout the vertical structure of the forest. Compared to the green/yellow figs, the red/orange figs occur across a greater size range and include smaller-sized figs.

These observations mirror those made in diverse *Ficus* communities in Panamá (Korine *et al.*, 2000) and Sarawak (Chapter 4) and support the classical concepts of fruit syndromes and seed dispersal guilds (e.g. van der Pijl, 1957; 1982). However, it should be noted that bats do not feed exclusively on green fruits. Rather than specifically attracting bats, it appears that the large green fruits of *F. nodosa*, *F. copiosa*, etc. are excluding birds. This contention is supported by the case of *F. wassa* which, like the primarily bat-dispersed species, is cauliflorous and produces its relatively large figs in the understorey, but has red rather than green figs and attracts a diverse range of birds (as well as bats) in New Guinea (Yves Bassett, pers. comm; Figure 6.1). All seven of Long's *Ficus* species that are primarily bat-dispersed are dioecious. The tendency for fig species that rely upon mammalian dispersers to be dioecious has also been observed in Sarawak (Chapter 4).

Whilst the existence of covarying character traits may be seen as evidence of diffuse coevolution between figs and their dispersers, phylogenetic constraints should not be ignored. A comprehensive phylogeny of *Ficus* has yet to be published and, therefore, no rigorous comparative analysis can be undertaken at this stage. However, it is noteworthy that the seven members of the putative bat guild hail from three different *Ficus* sections (*Neomorphe*, *Sycidium* and *Sycocarpus*) and that red-fruited, bird-attracting species also occur in two of these (*Sycidium* and *Sycocarpus*).

Against this framework of seed dispersal guilds, three distinct patterns of *Ficus* seed dispersal are occurring in the Long Island system: dispersal from the mainland to Long, dispersal within Long itself, and dispersal from Long to Motmot.

Fig seeds have been demonstrated to pass intact through the guts of *Pteropus*, *Ducula* and *Ptilinopus* species (e.g. Crome, 1975; Lambert, 1989; Uzzurum & Heideman, 1991; Shilton *et al.* 1999). Based on flight capabilities and gut passage times Thornton *et al.* (1996) concluded that members of these genera and *Aplonis* starlings were the most likely agents of fig seed dispersal to the Krakatau archipelago, Indonesia.

The Krakatau islands were sterilised in 1883 and lie 32 - 41 km from their sources of colonists (Sumatra and Java, respectively). It is probable that species in these genera are the only members of Long Island's fauna capable of retaining seeds in their guts on reaching Long Island from the mainland. The smaller fig eating birds, with shorter gut passage times and lesser flight capabilities, are more likely to defecate over the sea. Small bats may, however, be able to retain seeds for longer than previously thought. Shilton *et al.* (1999) demonstrated that small *Cynopterus* fruit bats can retain *Ficus* seeds for over 12 hours. The smaller fruit bats of Long Island may therefore also be capable of long-distance seed dispersal.

The potential agents of *Ficus* range expansions on Long Island itself comprise some 35 species of birds and mammals and one lizard. Although *Varanus olivaceus*, a relative of Long Island's Mangrove Monitor (*V. indicus*), has been recorded eating figs in the Philippines (Auffenberg, 1988) I do not expect these lizards to be important fig seed dispersers. Likewise, some of the bird species (e.g. *Monarcha cinerascens*, *Pitta sordida* and *Cacomantis variolosus*) are primarily insectivorous (Beehler *et al.*, 1996) and probably eat figs only rarely and contribute little to fig seed dispersal. The ground-doves in the genera *Chalcophaps* and *Macropygia* are generally considered to be seed-predatory (Corlett, 1998) and are likely to destroy a proportion of *Ficus* seeds, in spite of their small size. Although I could find no information on the fate of fig seeds ingested by Long's parrot species other members of this family are known to destroy fig seeds (Janzen, 1981; Jordano, 1983), as do passerids (Compton *et al.*, 1996), represented on Long Island by *Erythrura trichroa*.

Based on their propensity for fig eating and passage of intact fig seeds the most important vectors of fig seeds on Long Island are likely to be *Ptilinopus* and *Ducula* fruit-doves, *Aplonis* starlings, *Zosterops griseotincta*, *Eudynamis scolopacea* and *Phalanger orientalis* and fruit bats in the genera *Pteropus*, *Nyctimene*, *Macroglossus* and *Melonycteris*.

On Long Island there was evidence of the presence of pollinators for all *Ficus* species that were found fruiting. The pollinating wasps of these species are thus capable of at least occasional long-distance dispersal enabling them to colonise Long Island. The high densities of many *Ficus* species found in surveys of Long Island would suggest that their populations are large enough to maintain their pollinators and have high levels of pollination success. Studies from elsewhere suggest that many dioecious fig species fruit frequently (Corlett, 1987; Corlett, 1993; Chou & Yeh, 1995; Harrison *et al.*, 2000; Harrison, in prep) and can therefore support their pollinator populations with a relatively small number of trees (Kameyama *et al.* 1999). Of the 20 dioecious *Ficus* species on Long Island, 12 were observed with pollinated figs and for a number of species (e.g. *F. nodosa*, *F. variegata*, *F. congesta*, *F. copiosa*, *F. wassa*) figs were found on several individuals. It is interesting that the crops of *F. nodosa* and *F. wassa* found on Motmot were not pollinated. In some frequently-fruiting dioecious *Ficus* species pollinators rarely disperse far (Harrison, 2000; in prep). Similar dispersal abilities of pollinators of Motmot's *Ficus* species will limit the ability of trees on Long Island to pollinate individuals on Motmot. Thus, dioecious *Ficus* species on Motmot may be strongly pollen limited until there are sufficient mature male individuals to maintain the pollinator population after a rare colonisation event. Most monoecious *Ficus* species produce crops much more infrequently (Bronstein *et al.*, 1990; Harrison, 2000) and of the 11 monoecious species present on Long Island only four were found fruiting. In only one of these, *F. benjamina*, was more than one (actually two) found with figs. However, regular pollinator dispersal distances in at least some monoecious species are very long (Nason *et al.*, 1998), and frequent long-distance pollination appears to be achievable if other instances of rapid recolonisation of wasps after local extirpation events (Bronstein & Hossaert-McKey, 1995; Harrison 2000) are indicative.

Figs are known to have reached Motmot within three years of its creation and now eight species are present on the island. Currently, seed-dispersing frugivores have little reason to visit Motmot since there are few mature fruit trees. Dispersal of *Ficus* seeds to the island therefore probably results from rare over-flights and occasional roosting by seed-bearing frugivores. Because

of the threat posed by the frequently observed diurnal raptors, birds may be less likely than fruit bats to fly over Lake Wisdom on foraging trips. The relative importance of fruit bats over birds in the very early stages of colonisation is further suggested by the fact that five of Motmot's *Ficus* species (and 25 of the 35 individuals) are known from the diets of fruit bats. This pattern was also evident in the colonisation of the Krakatau archipelago by fig trees (Thornton *et al.*, 1996). The discovery of skeletal remains of *Aplonis* starlings suggests that raptors may be bringing fig seeds to Long Island and Motmot in the guts of their prey items (see Zann *et al.*, 1990). Finally, some *Ficus* species may be water-borne colonists. Ball & Glucksman (1975) found *F. benjamina* seeds on the shore of Motmot in 1972 and *F. virgata* figs were observed floating in Lake Wisdom during this study. However patches of high temperature in the water around Motmot (Osborne & Murphy 1989) may kill some of these floating seeds. Furthermore, *Ficus* plants were not observed growing as shore plants as would be expected if such dispersal were successful.

Colonisation of virgin habitat requires not only that seeds arrive but that they germinate and the resulting plants survive to reach maturity. Motmot is still very sparsely vegetated, the majority of the island being covered with lava flows, ash and scoria. Most of the island is likely to be inhospitable to a *Ficus* seedling. The dioecious *Ficus* plants on Motmot are all small shrubs, generally around the fringes of the island and, therefore, presumably in the least water-stressed environment available. The craters, cliff faces and ash and scoria beds also have a scattering of individuals, again presumably due to favourable microclimates. However, in the lava flows very few individuals have become established. As the vegetation gradually claims more of the island, with the concurrent development of better soils and more hospitable microhabitats, more of the fig seeds arriving on the island can be expected to establish. With the development of better soils and more hospitable microclimates, vegetation on Motmot will gradually cover a higher proportion of the island and more *Ficus* arrivals will become established.

Most of the monoecious *Ficus* species on Long Island are hemi-epiphytes. Their colonisation of Motmot is therefore limited, not only by seed dispersal, but also by a total lack of potential host trees. Exceptions are those species capable of adopting a freestanding habit, as represented on Motmot by *F. caulocarpa* and *F. benjamina*. Hemi-epiphytes endure extreme water stress during their seedling, epiphytic, stage (Holbrook & Putz, 1996) and this would appear to pre-adapt some species to colonising lava or other inhospitable environments (Corner, 1988). The big *F. benjamina* individual is in the middle of a lava field near the centre of the island and yet is the largest plant on the island. Other saplings of *F. benjamina* and *F. caulocarpa* also appeared to be well established.

Despite having arrived on Motmot, the *Ficus* species there are currently unlikely to be capable of increasing their numbers except by the arrival of further seeds from Long Island. Apart from the single large *F. benjamina*, all *Ficus* individuals on Motmot are small and probably immature. Moreover, given the small number of fruiting individuals it seems unlikely that pollinator populations on the island will become permanently established for some years. If pollinator dispersal from Long Island is limiting, as suggested by the unpollinated figs of *F. nodosa* and *F. wassa*, the fig community may take some time to become established. On Anak Krakatau it took 34 years for *Ficus* species to mature (Zann *et al.*, 1990). The *F. benjamina* tree in the centre of Motmot is certainly big enough to produce large crops of fruit. A similar individual observed on the coast of Long Island had c. 6000 figs. Also, as mentioned above, the pollinators of many monoecious species appear capable of long-distance dispersal (Nason *et al.*, 1996). The presence on Motmot of five *F. benjamina* saplings, clearly much younger than the large tree, raises the possibility that they originated from seeds from this tree, especially as *F. benjamina* was not particularly common on Long Island itself. As the single large fruit tree on the island, this *F. benjamina* individual could play a disproportionately important role in the colonisation of Motmot, not only through dispersing its own seeds but by increasing and prolonging the visits of frugivores from Long Island. Until the regular production of mature, pollinated fig crops begins on Motmot there will be little reason for volant frugivorous to visit the island. Motmot's flora remains in an early successional state (Harrison *et al.* in prep.) but following fig maturation on Motmot a rapid increase in the numbers of fleshy-fruited plant species colonising the island can be expected.

This study suggests that *Ficus* species are not equally able to colonise virgin land. One source of variation is in the frugivores that they rely upon as seed dispersers because of differences in fig size and presentation. Reliance on limited subsets of a frugivore community, such as fruit bats alone, for dispersal exposes plant species to risks should their narrow groups of dispersers decline in range or population, as is occurring to many fruit bat species in the Old World (Mickleburgh *et al.*, 1992). Differences in phenology, population and fig wasp longevity and dispersal are also important factors in determining successful colonisation by *Ficus*. In spite of the dispersal guild structure described here it appears that fruit bats can eat red or green figs at various heights in the forest. This, and the fact that most *Ficus* species and individuals on Motmot are known from the diets of bats, suggests that fruit bats are of exceptional importance to seed dispersal and early rain forest regeneration in the Old World tropics. The abundance and variety of ripe figs observed during this short study suggest that *Ficus* is an important resource in regenerating forest, a resource capable of attracting a diversity of frugivores likely to disperse seeds of other plant species and thus encourage succession and community assembly.

CHAPTER 7

FIG EATING BY VERTEBRATE FRUGIVORES: A GLOBAL REVIEW

"No more shall the mite and the gall-making blight
The fruit of the fig tree devour,
Of thrushes one troop on their armies shall swoop
And clear them all off in an hour"

Aristophanes: The Birds
(Condit, 1947)

7.1 INTRODUCTION

With c. 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 *et al.*, 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 about 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 c. 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 *et al.*, 1996), are species-specific (Weibes, 1979). In monoecious *Ficus* species, the need to maintain a supply of pollinator wasps means that ripe figs can be found year-round. 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 *et al.*, 1999). 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; Patel, 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 world-wide. In his coverage of frugivory and seed dispersal Janzen 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 (Janzen, 1979). In this chapter I review the literature in an attempt to judge the accuracy of this contention. I 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. I 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, 1996b; Davis & Sutton, 1997; Staddon, 2000; M. Shanahan, unpublished data). Dispersal by water has been suggested for a number of riverine *Ficus* species including *F. hispida*, *F. scabra* (Ridley, 1930) and, in particular, *F. cythastipula*, the figs of which have a thick, spongy wall that provides buoyancy (Berg & Wiebes, 1992). However, in this review I concentrate solely on the interactions between *Ficus* species and vertebrates.

7.2 METHODS

The dataset comprises field data collected in Lambir Hills National Park, Sarawak, Malaysia (Chapter 4), a literature review, and unpublished data contributed by other researchers (see ACKNOWLEDGEMENTS). The data comprises 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 and Monroe (1990; 1993) and Corbett and Hill (1991) for birds and mammals, respectively. Other frugivores are named as in the source literature. Redundant *Ficus* synonyms are abundant in the literature and were eliminated using the classifications of Berg & Wiebes (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 I use names approved by Prof. Berg (pers. comm.). For analytical purposes I 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.

7.3 RESULTS

7.3.1 THE QUALITY OF THE DATASET

Data on frugivory were gathered for 313 *Ficus* taxa, which, after rationalisation of nomenclature, represent 238 'good' *Ficus* species (~30 % of currently recognised species; Appendix 5). 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 73 countries or equivalent territories. Table 7.1 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 this coverage represent between 28.9 and 47.4 % 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 (84.4 %) of the 33 native fig species. Using Corner's (1965) classification of *Ficus* for comparison a second, taxonomic, bias in the literature is revealed (Table 7.2). Sections *Conosycea* and *Malvanthera* are over-represented whilst sections *Ficus*, *Adenosperma* and *Oreosycea* are under-represented. Overall, monoecious species are over-represented. Finally, the quality of literature may be assessed with respect to the types of study from which the data were accumulated. Over 450 sources of data were used (Table 7.3). The majority of these were casual observations (43.6 %) or records reported in other reviews, field guides, etc. (21.4 %). The remaining data sources fall into two classes: studies of animals' diets (25.1 %) and observations of frugivores visiting fruit crops (9.91 %). In each case, the majority of studies were taxonomically restricted with respect to the frugivores considered. Only eight studies (1.79 % of the total data sources) considered birds, fruit bats and arboreal mammals.

7.3.2 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 1236 bird and mammal species (Appendix 6). These comprise 977 bird species in 369 genera and 53 families and 277 mammal species in 149 genera and 37 families (Table 7.4, 7.5). Additionally, figs have been recorded in the diets of less obvious frugivores, such as fish and reptiles (Table 7.6).

The extent of fig eating in these frugivore families can be assessed in a number of ways. Tables 7.4 and 7.5 show, for each family, the percentage of genera and species for which fig eating records exist. These figures overemphasise the extent of fig eating in families with small numbers of genera and/or species (e.g. Hypocoliidae, Psophiidae, and Casuariidae) for which 100 % of species of genera eat figs. 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 most widespread in the parrot (Psittacidae) and pigeon (Columbidae) families (Figure 7.1). Among mammals it is in families of primates, squirrels and fruit bats that fig eating is most frequently recorded (Figure 7.2).

The relative effects of numbers of genera in a family and numbers of species per genus can be overcome by standardising the values for the indices used in Figures 7.1 and 7.2 against maxima of 1000 and taking the mean of the two indices. Figure 7.3 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 of 90) 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 (c. 145 species) is small compared to that of Indo-Australian region (c. 473 species; Table 7.1). 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 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 12.9 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 (Figure 7.4). Conversely, eight *Ficus* species have more than 50 recorded frugivores (Figure 7.4, Table 7.7).

Table 7.1. 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	44	41.9
Madagascar	24	10	41.7
Indo-Australian	473	152	32.1
India	43	27	62.8
Borneo	133	75	55.6
New Guinea	138	41	29.7
Australia	33	28	84.8

Table 7.2. Comparison of a) relative numbers of monoecious and dioecious *Ficus* species and b) relative numbers of species in each *Ficus* section globally and covered by this review. Monoecious species are over-represented (Yates corrected $\chi^2 = 10.72$, d.f. = 1, $p < 0.01$). Two sections are over-represented in the review: *Conosycea* (Yates corrected $\chi^2 = 10.5$, d.f. = 1, $p < 0.01$) and *Malvanthera* (Yates corrected $\chi^2 = 6.22$, d.f. = 1, $p < 0.05$). Three sections are under-represented: *Adenosperma* (Yates corrected $\chi^2 = 8.31$, d.f. = 1, $p < 0.01$), *Ficus* (Yates corrected $\chi^2 = 4.43$, $p < 0.05$) and *Oreosycea* (Yates corrected $\chi^2 = 4.08$, d.f. = 1, $p < 0.05$).

	Global ^a		This study		
	n species	% of total	n species	% of total	
a). breeding system					
Monoecious	389	52.9	154	64.7	
Dioecious	347	47.1	84	35.3	
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	4.62
<i>Ficus</i>	<i>Kalosyce</i>	20	2.72	4	1.68
<i>Ficus</i>	<i>Neomorphe</i>	6	0.82	4	1.68
<i>Ficus</i>	<i>Rhizocladus</i>	55	7.47	12	5.04
<i>Ficus</i>	<i>Sinosycidium</i>	1	0.14	0	0
<i>Ficus</i>	<i>Sycidium</i>	104	14.1	33	13.9
<i>Ficus</i>	<i>Sycocarpus</i>	81	11.1	20	8.40
<i>Sycomorus</i>	<i>Sycomorus</i>	13	1.77	6	2.52
<i>Pharmacosycea</i>	<i>Oreosycea</i>	50	6.79	8	3.36
<i>Pharmacosycea</i>	<i>Pharmacosycea</i>	20	2.72	5	2.10
<i>Urostigma</i>	<i>Americana</i>	120	16.3	37	15.6
<i>Urostigma</i>	<i>Conosycea</i>	65	8.83	39	16.4
<i>Urostigma</i>	<i>Galoglychia</i>	75	10.2	31	13.1
<i>Urostigma</i>	<i>Leucogyne</i>	2	0.27	2	0.84
<i>Urostigma</i>	<i>Malvanthera</i>	20	2.72	15	6.30
<i>Urostigma</i>	<i>Stilpnophyllum</i>	1	0.14	1	0.42
<i>Urostigma</i>	<i>Urostigma</i>	20	2.72	10	4.20
	total	736		237	

^aBerg (1989) after Corner (1965)

Table 7.3. Sources of fig eating records.

Type of study	number of sources	% of total
Reviews, field guides, compendia, etc.	97	21.4
Casual observations	198	43.6
Dietary study	114	25.1
birds	30	6.61
fruit bats	20	4.41
non-volant mammals	64	14.1
Plant-centred study	45	9.91
birds only	21	4.63
fruit bats only	1	0.22
non-volant mammals only	1	0.22
birds & fruit bats	4	0.88
birds & non-volant mammals	10	2.20
non-volant mammals & fruit bats	0	0
birds, non-volant mammals & fruit bats	8	1.76

Table 7.4. 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
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	97	14.9
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	37	15.4	993	85	8.6
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	33	78.6
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	37	8.2
Musophagidae	5	5	100	23	15	65.2
Nectariniidae	8	6	75	169	25	14.8
Numidae	4	1	25	6	1	16.7
Odontophoridae	4	1	25	6	1	16.7
Paridae	7	2	28.6	65	3	4.6
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	21	55.3	148	63	42.6
Sylviidae	101	15	14.9	552	32	5.8
Trogonidae	6	3	50	39	6	15.4
Tyrannidae	146	19	13	537	34	6.3
Vireonidae	4	1	25	51	3	5.9
Zosteropidae	13	2	15.4	96	13	13.5
PASSERINES	1510	215	14.2	7028	531	7.6
NON-PASSERINES	547	154	28.2	2644	446	16.9
TOTAL BIRDS	2057	369	17.9	9672	977	10.1

Table 7.5. Fig eating mammals (families listed alphabetically). Nomenclature follows Corbet & Hill (1991).

Family	GENERA			SPECIES		
	Total	Fig-eaters	%	Total	Fig-eaters	%
Bovidae	46	4	8.7	127	4	3.2
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	32	40
Cervidae	13	4	30.8	38	7	18.4
Cheirogaleidae	5	1	20	7	1	14.3
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
Hylobatidae	1	1	100	9	7	77.8
Hystricidae	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	149	13.9	4327	277	6.4

Table 7.6. Other (non-avian, non-mammalian) fig-eaters. Fig species consumed are listed in Appendix 6.

	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>	Ridley, 1930
	Machaca	<i>Brycon guatemalensis</i>	Horn, 1997
	Fish	species not named	Verkerke, 1987; Corlett, 1998b
	Fish	<i>Pterodoras granulosus</i>	Conceicao de Souza, 1994

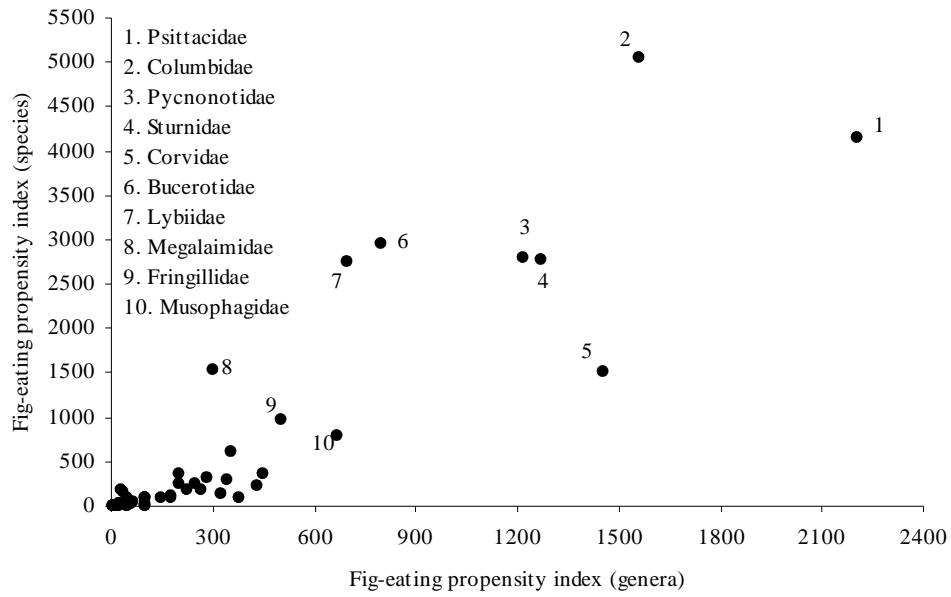


Figure 7.1. 'Fig eating propensity' of 53 avian frugivore families. Each index is calculated as the percentage of genera/species in a family that are known to eat figs multiplied by the actual number of genera/species recorded eating figs.

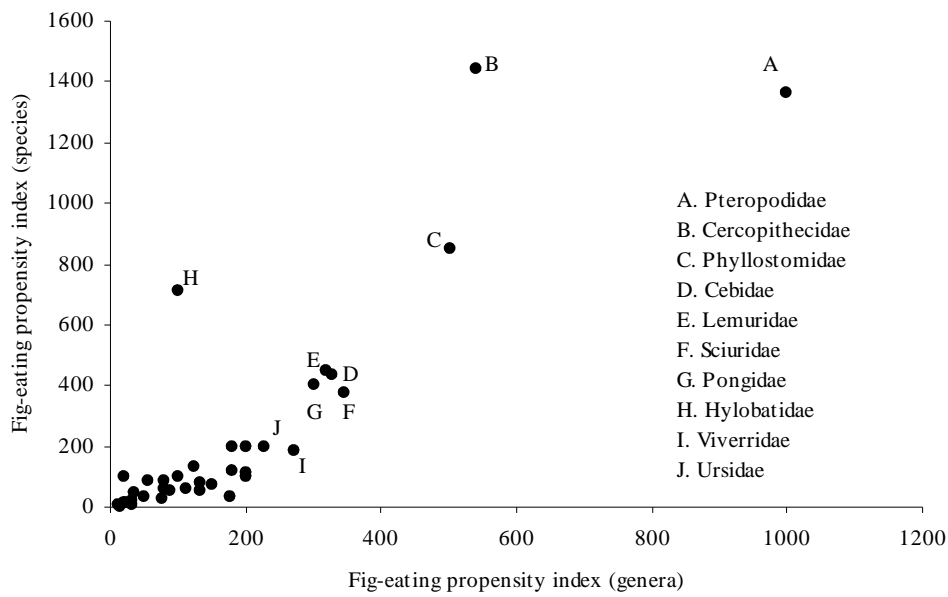


Figure 7.2. 'Fig eating propensity' of 37 mammalian frugivore families. Each index is calculated as the percentage of genera/species in a family that are known to eat figs multiplied by the actual number of genera/species recorded eating figs.

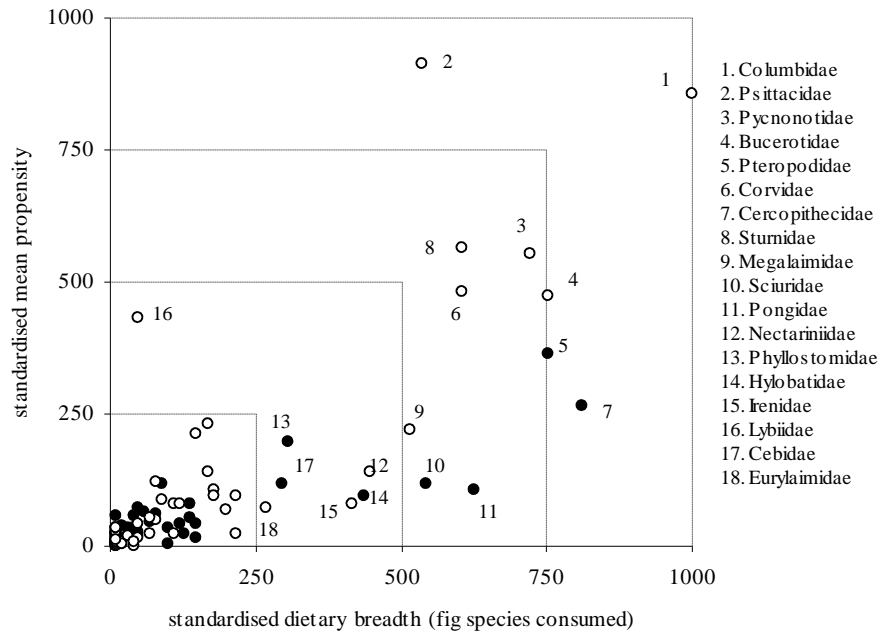


Figure 7.3. An illustration of the frugivore families for which the *Ficus*-frugivore interaction is most widespread. Each frugivore families' propensity for fig eating (mean of standardised indices from Figures 7.1 & 7.2) is plotted against the number of *Ficus* species known to be consumed by that family's members (standardised against 1000 for the Columbidae which are known to consume figs of 90 *Ficus* species; see appendices). Broken lines mark the quartiles. Closed circles = mammal families, open circles = bird families.

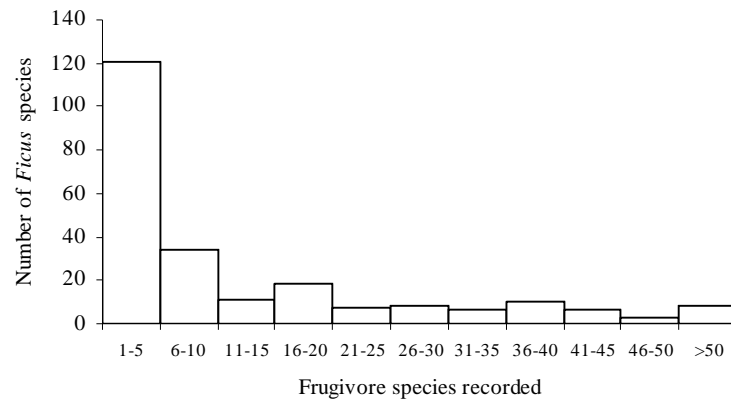


Figure 7.5. Frequency distribution of the number of frugivore species recorded for each species of *Ficus* in the review

Table 7.7. Top ten *Ficus* species in terms of number of frugivore species recorded eating their figs (see Appendix 5)

<i>Ficus</i> species	Region	Number of known frugivore species
<i>F. microcarpa</i>	Indo-Malayan, Australo-Papuan, Neotropical (introduced)	196
<i>F. virens</i>	Indo-Malayan, Australo-Papuan	90
<i>F. benjamina</i>	Indo-Malayan, Australo-Papuan, Neotropical (introduced)	82
<i>F. cotinifolia</i>	Neotropical	72
<i>F. drupacea</i>	Indo-Malayan, Australo-Papuan	63
<i>F. pertusa</i>	Neotropical	55
<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

7.3.3 ARE FIG-EATERS EFFECTIVE SEED DISPERSERS?

For the relationship between *Ficus* species and frugivorous 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 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 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, I concentrate the emphasis in this section on the major fig eating families identified in Figures 7.1-3. In the course of this coverage I also attempt to identify fig specialists. Sources of fig eating records mentioned in the following treatments of each frugivore order are presented in Appendix 6. Where presented, general dietary information comes from Perrins (1990) and Novak and Paradiso (1983) for birds and mammals, respectively.

Birds

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, pers. comm.). 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.

Craciformes

Members of the family Cracidae are the Neotropics' 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* curassows, *Ortalis* chachalacas and guans in the genera *Chamaepetes*, *Penelope* and *Pipile* and are considered to be a favoured food of *Pipile albipennis* (del Hoyo *et al.*, 1994). Cracids tend to be terrestrial foragers, although Galetti *et al.* (1997) mention *Pipile jacutinga* staying for up to ten days in fruiting *F. enormis* trees. Large *Penelope* guans have gut transit times of 15 - 45 minutes and, for *Virola surinamensis* (Myristicaceae) seeds, Howe *et al.* (1985) predicted dispersal distances of 50 m or more. Salvin's Curassow (*Mitu salvini*) retains food for considerably longer (mean 3 h 15 m) 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 curassows (*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.

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 *Syrmaticus*. Other fig eating galliforms include *Odontophorus* wood-quail (Odontophoridae) and *Acryllium* guineafowl (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, 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, 1998b). Reflecting this, only 5.8 % of *F. prolixa* seeds recovered from the faeces of *Gallus gallus* germinated (Staddon, 2000).

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 *et al.*, 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 fruiting hemi-epiphytes but also descend to lower forest strata (Ridley, 1930; Wells, 1982; Kannan, 1994; Grimmer *et al.*, 1998; Balasubramanian *et al.*, 1998; Shanahan & Compton, in press b). Lambert's (1989a) 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) *F. 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, unpublished data). 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 minutes for *Megalaima*

haemacephala; Lambert 1989b), 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 6) 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 suggests that these barbets are significant fig seed dispersers in Africa (Compton *et al.*, 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. de Figueiredo (1996b) 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 minutes 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 minutes in a fruiting fig tree, defecating many seeds in situ. Conversely, Coates-Estrada & Estrada (1986) recorded shorter feeding visits of 7.2 and 5.0 minutes 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*; Indicatoridae), a species that usually feeds on wax and insects (Fry *et al.*, 1988).

Bucerotiformes

Hornbills (Bucerotidae) occur in Africa (*Ceratogymna* and *Tockus* spp.) and South-East Asia (*Aceros*, *Annorhinus*, *Anthracoseros*, *Buceros*, *Ocyeros* and *Penelopides* 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 7.8). 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 *et al.*, 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 *Ficus 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 minutes (*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.

Table 7.8. 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	Kinnaird & 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 %	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>Anthracoseros 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)

Trogoniformes

The trogon family (Trogonidae) is pan-tropical but whilst the palaeotropical species are largely insectivorous, 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 Resplendent Quetzal (*Pharomachrus mocinno*) and four *Trogon* species. In Mexico *Trogon aurantiiventris* spent 32.4 % of its time visiting fig crops (Kantak, 1979). Neotropical trogons have wide gapes (*P. mocinno* 21 mm, *T. aurantiiventris* 19 mm) that facilitate the swallowing of relatively large figs whole (Wheelwright *et al.*, 1984). Howe *et al.* (1985) report gut transit times of 10-25 min for *Trogon* species.

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*; Daceloniidae) 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.

Coliiformes

Two *Colius* mousebird species (Coliidae) are known to eat figs and disperse viable seeds following short (c. three minutes) 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 *et al.*, 2001). Mousebirds are obligate frugivores and probably disperse fig seeds.

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 (2000) reported the koel eating up to 68 *F. 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 SE Asia. Other records of fig eating exist for cuckoos in the genera *Cacomantis*, *Coua*, *Cuculus*, *Microdynamis*, *Phaenicophaeus* and *Surniculus* (Appendix 6)

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.

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, 1988; Corlett, 1998b). 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.

Musophagiformes

The turacos (*Corythaëola*, *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, of which over 60 % fail to germinate (Compton *et al.*, 1996).

Strigiformes

The nocturnal Oilbird (Steatornithidae) eats figs in its native Trinidad (del Hoyo *et al.*, 2000). The species' role in *Ficus* seed dispersal is not clear. Thornton *et al.* (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.

Columbiformes

The pigeon family (Columbidae) has a world-wide 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.*, 1976b). 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 (~ 3 hours) in the fruiting fig tree (M. Shanahan, pers. obs.). However, their gut transit times are long relative to those of other avian frugivores (up to 420, 480, 530, and 720 minutes for *Ducula bicolor*, *Treron vernans*, *T. curvirostra* and *Chalcophaps indica*, respectively; Lambert, 1989c; Thornton *et al.*, 1996). Furthermore, pigeons fly fast and over considerable distances (speeds of 55 km h⁻¹ in *T. vernans*, 80 km h⁻¹ in *Streptopelia* spp; flight ranges of 100 km in *D. bicolor*, 800 km in *C. indica* and 44 km day⁻¹ 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 review).

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*, *Gallinolumba*, *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 1989c). 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, 1989c).

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.

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 review). Hall (1987) showed that Lanner Falcon (*Falco biarmicus*; Falconidae) dispersed seeds of two *Ficus* species in pellets composed of avian prey.

Passeriformes

Together the passerines account for 58.3 % of genera and 54.4 % of species recorded eating figs (Table 7.4). However, the majority of these records are for members of just four families: Corvidae (97 spp.), Fringillidae (85 spp.), Sturnidae (63 spp.) and Pycnonotidae (62 spp.). Rather than deal with each passerine family in detail I cover here only those I consider to be of most interest with respect to *Ficus* seed dispersal.

Corvidae

In Sibley & Monroe's (1990) classification the Corvidae includes a number of bird groups previously treated as separated 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 *F. 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 *et al.*, 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 %), *Pariotia lawesii* (19 %) and *Cicinnurus magnificus* (9 %). Sixteen percent of visits to *F. cf. obliqua* were made by birds-of-paradise (Beehler & Dumbacher, 1996) and their generally high propensity for fig eating suggest 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 (< three min for *Oriolus cruentus* feeding on *F. vasculosa* in Malaysia, five minutes maximum for *O. larvatus* on *F. burtt-davyi* in South Africa; Wells, 1982; Compton *et al.*, 1996). Lambert (1989b) recorded fig seed retention times in the range 2 - 250 minutes 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 (*Pitohiu* spp.) drongos (*Dicrurus* spp.), ioras (*Aegithina*), a *Telophorus* bushshrike, a *Platysteira* wattle-eye and a *Batis* species (Appendix 6). 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.

Fringillidae

Eighty-five species of fringillid in 37 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 Emberizidae, *Saltator*, *Cardinalis*, *Caryothraustes*, *Cyanocompsa*, *Pheuticus* 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 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 *F. luschnathiana*, respectively (de Figueiredo, 1996b). 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* (de Figueiredo *et al.*, 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* & *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.

Sturnidae

Starlings are found across the tropics and 63 species in 21 genera are known to eat figs. The nomadic Hill Myna (*Gracula religiosa*) feeds on the figs of 19 hemi-epiphytic species throughout its range, and passes seeds after 5 - 76 minutes (Lambert, 1989b). This species accounted for up to 50 % of avian feeding visits to *Ficus* crops in Peninsular Malaysia (Lambert, 1989b). Following ingestion by *Acridotheres* mynas, seeds of *F. benghalensis* were passed after 18 - 44 minutes and showed improved germination (Midya & Brahmachary, 1991). *Ficus* seed dispersal distances of > 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 hours for *Sturnus vulgaris*, suggesting considerable dispersal distances.

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; M. Shanahan, pers. obs.). Bulbul gut passage times have been measured at 5 - 47 minutes (Lambert, 1989b; Barnea *et al.*, 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 understorey *Ficus* trees that fail to attract larger frugivores. For such trees in Sarawak, bulbuls were responsible for about 80 % of all feeding visits (Shanahan & Compton, in press b). The ability of many bulbul species to survive in anthropogenically degraded landscapes suggests that they are important agents of forest regeneration (Corlett 1998b)

Irenidae

The leafbirds (*Chloropsis* spp.) and Fairy Bluebird (*Irene puella*) are major fig-eaters in the Indo-Malayan region where they feed largely on hemi-epiphytes in the canopy but are also observed to descend to the understorey or forest edge (McClure, 1966; Lambert, 1987; 1989; Chapter 4). 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.

Zosteropidae

At least twelve *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 1998a) 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 *F. 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*.

Tyrannidae

Neotropical figs are eaten by at least 34 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. Katak (1979) reported that visits to fig crops accounted for 46 - 74 % of all feeding visits by tyrannids, regardless of the availability 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.

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 *F. 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*. Defaecation 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*, *Cossypha caffra* in South Africa, and, in China, *Phoenicurus aureus* and *Chaimarrornis leucocephalus*. These birds are largely insectivorous and are unlikely to play a great role in *Ficus* seed dispersal.

Ptilonorhynchidae

Seven 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.

Sylviidae

In the subfamily Sylviinae, species of babbler (tribe Timaliini) and warbler (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 *F. sumatrana* figs available (McClure, 1966)

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 specialised 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-davyi* 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).

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 these nectariniids.

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*.

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 6). Compton *et al.* (1996) found no intact seeds in the faeces of *Ploceus bicolor* following consumption of *F. burtt-davyi*.

Eurylaimidae

The Green Broadbill (*Calyptomena viridis*) is a highly frugivorous species that shows 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 30.7-62.4 % 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.).

Other families

Finally, among the passerines there are records of fig eating by several vireo species (*Vireo* spp; Vireonidae), Grey Hypocolius (Hypocoliidae), Common Fiscal (*Lanius collaris*; Laniidae) Noisy Pitta (*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.

Mammals

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. Medellin (1994) estimated mean dispersal distances of under 15 metres 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 than 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.

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 *F. reflexa* and *F. lutea* figs. Gut passage times of captive lemurs vary between 1.7 (*Varecia*) and 4.75 (*Lemur catta*) hours (Cabre-Vert & Feistner, 1995), suggesting dispersal of seeds away from the source tree. Madagascan figs are also eaten by the indris (Indriidae) and dwarf 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* (1.5 to 4 hours; Zhang & Wang, 1995), *Ateles* (4.4 ± 1.5 h; Milton, 1981) and *Alouatta* (20.4 ± 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 (Delfer & Defler, 1996) and by Howler Monkeys (*Alouatta*), with the latter elevating the likelihood of fig seed germination (Estrada & Coates-Estrada, 1986; de Figueiredo, 1993).

Also in the Neotropics, figs are eaten by marmosets and tamarins (*Callithrix* and *Saguinus* spp; Callithricidae). These small primates are omnivorous and probably make relatively little contribution to *Ficus* seed dispersal.

The large family of Old World Monkeys (Cercopithecoidea) includes at least 32 species that eat figs. Among the colobine monkeys (subfamily Colobinae) figs are eaten by about 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 six percent of the diet of *Presbytis thomasi*; Ungar 1995). Conversely, among the subfamily Cercopithecoinae (*Cercocebus*, *Cercopithecus*, *Erythrocebus*, *Macaca*, *Miopithecus* and *Papio* spp.), fig eating appears to be more widespread. Lieberman *et al.* (1979) found that *F. platyphylla* seeds were the second most abundant of 59 seed species found in

baboon (*Papio*) dung, accounting for 29% of all seeds. However, in South Africa, *P. anubis* has been observed feeding on immature figs of *F. ingens* (S. Compton, pers. comm.). 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. In 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 Gibbons (*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 (~45 %) feeding on figs than their mainland counterparts. Gibbon gut passage times exceed 21 hours 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).

Finally, 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 ten 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 *F. 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 gut (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).

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* & *Viverricula* spp.). The arboreal Binturong (*Arctictis binturong*) particularly favours figs and may be a specialist forager (Leighton & Leighton, 1983; Payne *et al.*, 1985). Gruezo & Soligam (1990) found that *F. 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 three hours in the gut (M. Shanahan, unpublished data). Civet daily movements have been measured by Rabinowitz (1991) for *Paradoxurus* (2.8 km) and *Paguma* (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. Seeds of *F. consociata* were dispersed at least 200 metres by Sun Bear (*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 (*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.

Scandentia

The 16 species of treeshrews (Tupaiaidae) are confined to South-East Asia. *Tupaia* species consume a range 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, in press a). Treeshrews make short visits to fig crops (< 5 min) and are apparently rapidly satiated (Shanahan, pers. obs.). In a captive trial seeds of *F. montana* were passed (mean 60.6 seeds per faeces) between 33 and 63 minutes after ingestion in a readily germinable state (Shanahan & Compton, in press a).

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 gram fruits 200 metres; 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 (M. Shanahan, unpublished data) and in faeces. Gut passage times of 12-70 minutes have been recorded for *Pteropus*, *Ptenochirus*, *Nyctimene*, *Lissonycteris*, *Epomops* and *Rousettus* species (Wolton *et al.*, 1982; Tedman & Hall, 1985; Uzzurum & 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* (Uzzurum & Heideman, 1991) and by *Pteropus voeltzkowi* (Entwistle & Corp, 1997). However, it has been suggested that bats differentially ingest viable seeds (Uzzurum & Heideman, 1991). Pteropodid bats fly fast and far and have been implicated in the dispersal of *Ficus* seeds across distance greater than 50 km (Thornton *et al.*, 1996; Shanahan *et al.*, in review).

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 *et al.* (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. *Artibeus jamaicensis* bats (considered fig specialists; Janzen, 1979) can carry whole figs, weighing 6-20% of their body weight, hundreds of metres to feeding roosts (Morrison, 1978; August, 1981). 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 metres. Like their Old World counterparts, Neotropical fruit bats have been demonstrated to elevate *Ficus* germination rates by ingesting seeds (Fleming & Heithaus, 1981).

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.

Hyracoidea

Hyraxes (*Procavia* and *Dendrohyrax* species; Procaviidae) have been recorded eating figs in Africa. However, Greeff & Whiting (1999) found that *P. capensis* killed many *F. cordata* seeds through mastication.

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.

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 (Chapter 4), 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 positively correlated with the density of hemi-epiphytic *Ficus* species and for six months of the year figs were the only fruit eaten.

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; M. Shanahan, pers. obs.) Furthermore, *Ratufa*, *Callosciurus* and *Tamiops* squirrels were recorded eating unripe figs by Poonswad *et al.* (1998a) in Thailand. Eight 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 *et al.*, 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 *F. burtt-davyi* survived passage through African murids but experienced reduced germination rates (Compton *et al.*, 1996).

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 and Whiting (1999) showed that the lizard *Platysaurus broadleyi* passes seeds of *F. cordata* intact and defecated 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 these lizards may be important seed dispersers.

7.3.4 *Ficus* FRUIT SYNDROMES & 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 *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 (Figure 7.5). Despite the patterns of overlap observed, for more than half of the fig 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.

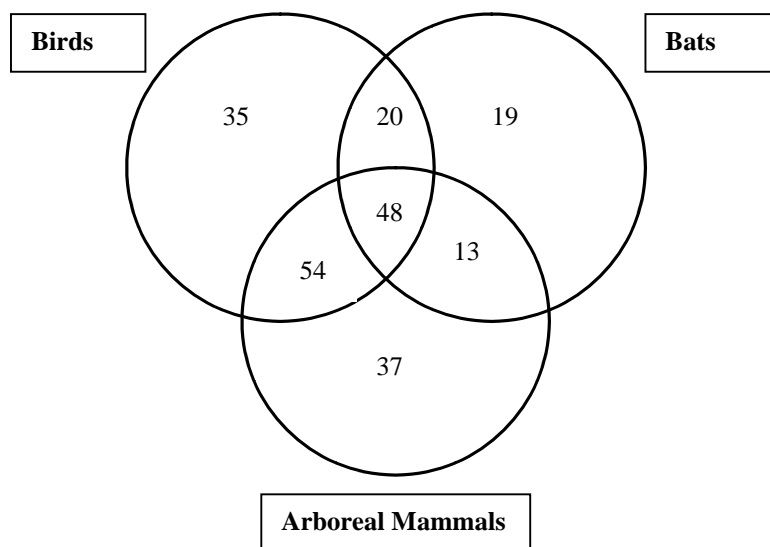


Figure 7.5. Overlap between major frugivore guilds (geocarpic *Ficus* species are excluded, as are ground-foraging birds and mammals for which records of fig eating mostly pertain to the consumption of fallen fruit or geocarpic figs). Numbers = number of *Ficus* species consumed by each frugivore guild. 40.9 % of the *Ficus* species are known from diet of only one guild, 37.7 % are eaten by two guilds of frugivores and 21.3 % are eaten by members of all three guilds. Overlap is greater between birds and arboreal mammals (44.4 % of *Ficus* species shared) than birds and bats (30.2 %) or bats and arboreal mammals (27.1 %).

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 7.4) but exist for four tropical sites. In a detailed study of 34 *Ficus* species and 69 frugivore species in Borneo a *Ficus* dispersal guild structure has been demonstrated (Chapter 4). Three guilds of *Ficus* species attracted 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 subguilds. Guild membership was determined by largely phylogenetically determined differences in fig colour, size and height above ground (Chapter 4; Shanahan & Compton, in press b).

Similarly, Chapter 5 describes two major guilds of *Ficus* colonists to Long Island, Papua New Guinea, a volcano that erupted catastrophically in the 17th 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 green figs that are attractive to bats and the second group of species produced red figs attractive to birds. Finally, in the Philippines, Hamann and 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 all dioecious whilst those attracting both birds and mammals included dioecious and monoecious species (Chapters 4 and 6; Shanahan & Compton, in press b; Shanahan *et al.*, in review).

7.4 DISCUSSION

7.4.1 THE QUALITY OF THE DATASET

Records of frugivory were accumulated for 238 *Ficus* species, a respectable proportion (~ 30 %) of the world's total *Ficus* flora. With 41.9 % of species included, the African figs are best represented in the dataset. The lower coverage of Neotropical species

(26.2 %) is due in part to the conservative approach adopted here when faced with the complicated taxonomy of New World figs. With 27.5 % 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.

7.4.2 WHO EATS FIGS?

The animals known to eat figs include ten percent of the world's bird species (18 % of genera) and six percent of the world's mammals (14 % of genera). Despite the depth of coverage of this review these figures are minima and considerably more members of less well studied frugivore taxa are also expected 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 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 90 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 one 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 the 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*, *Ptilinopus* & *Lopholaimus* 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* & *Lopholaimus* pigeons, Asian Koel, Channel-billed Cuckoo, fig-parrots (*Cyclopsitta*, *Psittaculirostris*), and the Green Figbird (*Sphecotheres viridis*), Vulturine Parrot (*Psittichas 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 specialism 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. An alternative explanation is 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 the bulbuls, woodpeckers, mouse-birds, cuckoos, turacos, cracids, pheasants and many families of passerine birds. Mammalian generalists include treeshrews, 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.

7.4.3 WHY ARE THERE SO MANY FIG-EATERS?

To understand why there are so many fig-eaters I 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 constricted 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 (Chapter 3), 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, 1989b; Rogers *et al.*, 1990; Borges, 1993; Conklin & Wrangham, 1994; Chapter 3). Conversely, Ko *et al.* (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. 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) 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). 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 *et al.*, 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.*, 1998a). 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 constraint 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 the 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.

7.4.4 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 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 the 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, *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 suggest that even small 'peckers' will ingest some seeds. However, large animals produce large droppings exposing seed dispersed thus to risks of clumping (competition in germination/seedling stage and risk of discovery by seed predators).

7.4.5 *Ficus* FRUIT SYNDROMES & DISPERSAL GUILDS

The specialist-generalist paradigm in seed dispersal 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, there are others which 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 dioecious, dull (green/brown) and tend to be much larger than those eaten by birds, which can be dioecious or monoecious and tend to ripen red. 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 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, with their good colour vision (Hartwig, 1993) tend to eat red figs, conspicuously displayed among green foliage. Colour is less important to nocturnal foragers and although Neotropical bats favoured 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. 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 depressed, that *Ficus* species experience differential seed dispersal services (Chapter 4) and thus differ in their ability to colonise degraded landscapes (Shanahan *et al.*, in review). Individual *Ficus* species are also of differing importance to frugivore species and so the keystone 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.

7.4.6 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". I have already demonstrated that the figs are available to, and eaten by, an diverse range of vertebrate species. Based on the data accumulated in this review and published species lists Table 7.8 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 Selva, Costa Rica 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.

Table 7.9. Proportions of tropical bird or terrestrial mammal faunas that eat figs or have congeners that do so. Sources of species totals: ¹McDade *et al.* (1994), ²Milliken & Ratter (1998), ³Struhsaker (1997), ⁴Langrand (1990), ⁵Shanahan & Debski (in press), ⁶Payne *et al.*, (1985), ⁷Schipper *et al.* (in review).

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

^asee Appendix 6

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 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 a 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 on Barro Colorado Island, Panama (Foster, 1982a, 1982b; Windsor *et al.*, 1989) and within Kalimantan, Borneo (Leighton & Leighton, 1983). 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. Nonetheless, the individual *Ficus* species that attract the greatest numbers of frugivores (and thus can be expected to be of greatest conservation value) can be identified from the data presented in Appendix 5.

7.4.7 THE VALUE AND LIMITATIONS OF THIS DATABASE

The database assembled has several potential applications. Much of the data collected here comes from zoologists' description 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 to identify dietary overlap of their study animals with other groups of frugivores. Knowledge of the frugivore species that eat the 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 depauperacies of certain frugivore taxa (Shanahan & Compton, in review).

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. 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 on 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).

CHAPTER 8

GENERAL DISCUSSION

"Every fruit has its secret, the fig is a very secretive fruit"

D.H. Lawrence
Lawrence (1928)

The aim of this thesis was to examine interactions between *Ficus* species (Moraceae) and vertebrate frugivores. Specifically, I examined the influence of fig packaging and presentation on patterns of frugivore attraction, the ecological and evolutionary determinants of *Ficus*-frugivore interactions and the ecological and conservation implications of the patterns identified. In this chapter I summarise and synthesise the findings of the previous chapters.

8.1 Fig packaging and presentation

I have demonstrated considerable diversity in the manner in which *Ficus* species package and present their figs in Lambir Hills National Park, Sarawak (Chapter 3) and on Long Island, Papua New Guinea (Chapter 6). This variety was manifest in the figs themselves (in terms of fig colour, odour, size, coat and pulp texture, seed number, pulp water content, pulp:seed ratio, etc.) as well as at the crop level (i.e. crop size, crop height, fig placement and synchrony of fig ripening). In spite of this diversity a number of traits were characteristic of figs in general. These including having many small seeds (with the exception of *F. deltoidea*), a soft texture, high pulp water content, low relative yield (proportional contribution of dry pulp to total fig mass) and a high pulp proportion.

A number of differences in fig characters were apparent between monoecious and dioecious *Ficus* species in Lambir Hills National Park (Chapter 3). Some of these differences arise because, as well as producing seeds, monoecious figs have a male sexual function realised through the rearing of pollinating wasps. That a proportion of potential seeds are lost to wasp larvae during their development means that, compared to female dioecious figs, monoecious figs of a given size have a higher relative yield; because the pollinating wasps produced instead of seeds are lighter than seeds and, regardless, have usually all departed the fig at the time of ripening. While seed number and fig size were strongly correlated among dioecious species, seed number varied little among monoecious species. The failure of large monoecious figs to produce more seeds may be related to the biology of pollinator wasps. In larger figs more pollen-bearing female wasps enter to oviposit and will thus produce fewer offspring on average. A less female-biased sex ratio in the offspring will therefore be selected for. Since male wasps cannot disperse *Ficus* pollen, monoecious species with large figs may be forced to commit more flowers to the production of wasps rather than seeds in order for the same number of pollen carriers as would occur in figs with fewer foundresses. Monoecious species also had larger crops than dioecious species, a function of monoecious species being large hemi-epiphytes whereas dioecious species were small trees, climbers and shrubs.

Many fig traits were highly inter-correlated, a reflection perhaps of the constraints imposed by the fig's functions as an inflorescence, pollinator brood chamber and 'fruit' capable of attracting seed-dispersing frugivores. Covariation among fruit traits allowed the recognition of two broad fruit syndromes: red figs were, on average, smaller, less watery and had a greater seed burden than those of other colours, which also tended to be presented in the lower strata of the forest and in smaller crops. This dichotomy was driven by the differences between monoecious and dioecious figs (all but one of the monoecious species studied had figs that ripened red and were presented in the higher strata of the forest). Thus fig characters show strong phylogenetic associations. Indeed, among the dioecious species studied, members of each *Ficus* section exhibited shared similar patterns of fig production (e.g. cauliflory and geocarpy among *Sycocarpus* species and extremely large figs in *Kalosyce* species).

8.2 Patterns of frugivore attraction

The diversity of figs is mirrored in that of the animals that were recorded eating them in the two field sites (Chapters 4 and 6) and globally (Chapter 7). Fig eating animals include obligate frugivores (indeed, fig specialists), generalist foragers and opportunists that probably only eat figs rarely. 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 (from ground level to the canopy) and because figs are generally soft and, therefore, easily consumed. Particularly high levels of calcium have also been found in figs and have been cited as a factor contributing to the diversity of frugivores recorded eating figs (O' Brien *et al.*, 1998a).

That figs are generally structurally unprotected, have many small seeds and a low relative yield supports the generalisation that *Ficus* species are 'Low Investment Trees' (McKey, 1975; Howe, 1993). However, this classification may not be relevant as it predicts that *Ficus* species will attract low-quality dispersers that are generalist feeders. Whilst many generalists do eat figs, the majority of species attracted to *Ficus* crops are likely to disperse seeds. Furthermore, many fig eating species appear to be specialised on figs and are important dispersers (Chapter 7). Certain frugivore species have been demonstrated to increase fig seed germination rates or proportions following ingestion. Whilst some species such as *Treron* pigeons are known to destroy a proportion of fig seeds ingested the large number of figs they eat suggests that some will nonetheless be dispersed to microsites favourable for germination (Lambert, 1989c).

Ficus species differed in the number and identity of frugivore species attracted to their crops and a given *Ficus* species' figs were not an equal resource for all frugivores present. Rather, evidence of fig-frugivore partitioning was observed in both Sarawak (Chapter 4) and Long Island (Chapter 6). Whereas five dispersal guilds were identified in Lambir Hills National Park (Chapter 4) only two guilds were suggested by data collected on Long Island (Chapter 6). These were guilds of *Ficus* species attracting bats or both birds and bats as potential seed-dispersers. The three additional guilds observed in Sarawak, but not on Long Island were those attracting a) terrestrial mammals, b) arboreal mammals or c) understorey birds and arboreal mammals. Whilst the former two *Ficus* guilds are likely to occur on the mainland of New Guinea their member species are unlikely to colonise Long Island because their dispersers can only get there if brought by humans. A distinction between *Ficus* species

attracting birds in the canopy and those doing so in the understorey was not detected in the study of Long Island's *Ficus* community. This probably reflects the limited resolution and short time-scale of the study rather than a genuine absence of such a structure.

This system of *Ficus* dispersal guilds was mediated by the interaction of frugivore foraging ecology and physiology and fig fruit characters, themselves largely constrained by phylogeny. Species with red figs attracted predominantly birds but also arboreal mammals. Conversely, *Ficus* species with green or yellow figs in both field sites tended to attract primarily fruit bats. These observations reflect the classically described fruit syndromes (e.g. Ridley, 1930; van der Pijl, 1957). Thus, diurnally-foraging frugivores with colour-vision fed on red figs, the colour of which contrasts with that of the green foliage amongst which they are produced. The nocturnal fruit bats and binturong (*Arctictis binturong*) took advantage of green figs, the dull colour of which may be more conspicuous in moonlight. Data from the literature indicate that fruit bats are also able to take advantage of red figs, including those of many hemi-epiphytes. This suggests that odour cues, not necessarily perceptible to human noses, may be used to locate such crops. Figs with thick coats were consumed by mammals and it appears that most birds, lacking teeth, are unable to access the pulp of these figs. Among the *Ficus* species that attracted primarily birds, there was a relationship between fig size and shape such that small figs were more or less spherical and larger figs were elongate. Had these large figs also been spherical the number of bird species capable of swallowing them (or even manipulating them using the beak) would be lower than that observed for the elongate figs.

These observations suggest plant adaptations to favourable dispersers. However, the strong phylogenetic associations of members of each *Ficus* dispersal guild suggest that common ancestry rather than evolutionary responses to the observed faunal assemblages explains much of the patterns of fig fruit characters described here. Indeed, vertical stratification of figs and fig-eaters is of great importance in the determination of *Ficus* dispersal guild membership and the height at which figs are presented is controlled by *Ficus* growth form, which in turn is governed by phylogeny.

Nonetheless, evidence was found of some *Ficus* species exhibiting fruit characters or patterns of frugivore attraction markedly different from those of close relatives. For example, in Lambir Hills National Park *Ficus annulata* produced green figs and attracted primarily fruit bats whereas the other monoecious hemi-epiphytes studied produced red figs that were consumed by birds and arboreal mammals. Thus, in terms of fig characters and frugivore attraction, *F. annulata* is associated with dioecious *Ficus* species that also produced green, bat-attracting figs. Similarly on Long Island, members of the fruit bat dispersed guild of *Ficus* species hailed from three different *Ficus* sections (*Neomorpha*, *Sycocarpus* and *Sycidium*), in two of which (*Sycocarpus* and *Sycidium*) species with bird-attracting red figs also occur.

The relative importance of phylogenetic constraint and evolutionary responses to the actions of favourable dispersers in moulding *Ficus* fruit characteristics remains unclear. However, any co-evolution between frugivores and figs is likely to be of a diffuse nature (sensu Janzen, 1980) as opposed to the specific, one to one evolution that has occurred between *Ficus* species and their pollinator wasps. Furthermore, recent molecular research has estimated the origin of the fig-fig wasp mutualism to have occurred c. 90 million years ago (Machado *et al.*, 2000). The oldest known fossils of the major frugivore families studied in this thesis are all considerably more recent (e.g. pigeons and parrots, c. 20 mya; passerine birds, c. 55 mya; bats, 45 mya; Old World monkeys c. 16 mya; Olson, 1985; Benefit & McCrossin, 1997; Cooper & Penny, 1997). The early fossil record for birds and mammals is notoriously poor, and therefore unreliable, and molecular evidence suggests that many modern avian and mammalian orders pre-dated and survived the Cretaceous-Tertiary mass extinction 65 million years ago (Cooper & Penny, 1997; Kumar & Hedges, 1998). Nonetheless, *Ficus* is a more ancient genus and was being dispersed long before the frugivore families recognised today arose. Many of the fig traits associated with the attraction of, say, birds or fruit bats, may therefore have pre-dated their present day dispersers and current associations between *Ficus* guilds and frugivore taxa may be examples of ecological fitting (sensu Janzen, 1985a) rather than the result of shared evolutionary history.

8.3 Ecological and conservation implications of *Ficus* seed dispersal guilds

The implications of the *Ficus* dispersal guild systems identified are numerous. In the first instance competition for seed dispersers between *Ficus* species in different guilds can be expected to be depressed whilst that between species within guilds may be accentuated. However, even within dispersal guilds competition is made less likely by the pattern of between individual asynchrony in crop production pattern that is exhibited by *Ficus* species (Chapter 5).

Another of the main implications of frugivore partitioning between plant species is that the seed dispersal services they experience are likely to differ depending on which frugivores are attracted. Frugivores differ qualitatively and quantitatively in their effectiveness as seed dispersers (Schupp, 1993). However, measuring aspects of disperser effectiveness presents some problems as plant germination requirements (e.g. light, soil, water, substrate) are difficult to assess, as are the role of distance and density in seed and seedling mortality (Janzen, 1983d). Furthermore, the fate of seeds ingested by frugivores is often unknown and frugivores may be genuine dispersers for some plant species but not others. The main way in which seed dispersal will differ for members of different *Ficus* guilds is that the number and diversity of frugivore species attracted will determine differences in seed rain distance and density and in the diversity of microsites where seeds are deposited.

As shown by the data collected on Long Island *Ficus* species differ in their ability to colonise new areas and thus expand ranges. This has implications not only for the colonisation of islands such as Long but also for rain forest regeneration following disturbance such as fire or logging.

Reliance upon limited subsets of frugivore communities not only limits *Ficus* species' dispersal in the way described above but exposes them to risks should their seed-dispersing frugivores decline in range or population size. Species reliant on fruit bats or primates are probably at the greatest risk as these animal groups are in decline in the regions of the study sites (Mickleburgh *et al.*, 1992; Shanahan & Debski, in press). Such species may experience genetic consequences as have recently been reported for the Neotropical tree *Inga ingoides* deprived (due to hunting) of its monkey seed disperser (Pacheco & Simonetti, 2000). Although large birds, such as hornbills, are also in decline (Bennett *et al.*, 1997), the *Ficus* species that are dispersed by them also attract numerous smaller bird species capable of seed dispersal (Chapter 4).

The existence of *Ficus* dispersal guilds also has a bearing on the application of the 'keystone resource' epithet to figs. Loosely, a keystone resource is one whose loss from an ecosystem is predicted to precipitate a cascade of further extinction. Since Paine (1966, 1969) introduced the term, there have been many and varied applications of the keystone species concept, prompting Power *et al.* (1996) to rationalise the resulting confusion by formally defining a keystone species as one "...whose impact on its community or ecosystem is large and disproportionately large relative to its abundance". The concept was first

applied to *Ficus* species by Leighton & Leighton (1983) in Borneo, and Terborgh (1983, 1986) in Peru, because of their year-round fruiting phenology and presence during times of general fruit scarcity which suggested the potential to sustain frugivores that also disperse seeds of many non-*Ficus* species. Indeed, Terborgh (1986) stated "Remove figs from the [Peruvian Amazon] ecosystem and one could expect it to see it collapse." Lambert and Marshall (1991) described the 'keystone characteristics' of hemi-epiphytic *Ficus* species in Peninsular Malaysia to be their phenology, large crop sizes, ease of harvesting and relative numerical abundance of *Ficus* individuals. In spite of Power *et al.*'s (1996) keystone definition being species based, Mawdsley *et al.* (1998) recognised that "the keystone role of figs is not through individual species but is a collective property of groups of species within the genus owing to the general feeding habits of fig-eating frugivores".

That figs are eaten, year-round, by so many vertebrate species (Chapter 7), many of which are seed dispersers of both *Ficus* and many other non-*Ficus* species, supports Janzen's (1979) claim that *Ficus* is the most important plant genus for tropical frugivores. However, it does not follow that all *Ficus* species are disproportionately important in maintaining the diversity of tropical forests. The keystone resource concept has been applied largely to monoecious *Ficus* species, which account for only c. 50 % of the genus. The keystone characteristics identified by Lambert and Marshall (1991) are not found in all *Ficus* species nor are all fig-eating animals capable of exploiting the fig resource at a given time or place. Indeed, as Borges (1993), in India, and Gautier-Hion and Michaloud (1986), in Gabon, demonstrated, ripe fig crops may occur at sufficiently low densities to preclude visitation by all but the most mobile frugivores. Furthermore, the existence of *Ficus* dispersal guilds means that a given species' figs are not an equally important resource to all frugivores in a given area. Finally, in order for figs to fulfil the keystone role attributed to them, the animals feeding upon them must be reliant on the figs for at least part of the year during which other fruit resources are in limited supply.

Figs were produced year-round in Lambir Hills National Park, yet *ripe* crops of all species were not available throughout the year (Chapter 5). Pollen limitation due to the local extinction of pollinator wasps of a number of dioecious species meant that, even though figs are capable of remaining receptive for a number of weeks (Compton & Ware, 1994; Khadhari *et al.*, 1995), crops were aborted during the first half of the phenology census. These species were prominent members of the three dispersal guilds that attracted mammalian frugivores and it is possible that the absence of the fig resource had negative impacts on the populations of these vertebrates.

In light of the above considerations, before application of the keystone resource concept, future research must take into account the availability of non-*Ficus* resources, *Ficus* density, fig phenology, and frugivore mobility before confirming that the figs in question are suitable for, available to, and required by the frugivores in question.

A further conservation implication of the *Ficus* dispersal guild structure I have described here is the differential resilience of *Ficus* growth forms to anthropogenic disturbance. In Indo-Malayan primary forests the distributions of dioecious species (especially trees) are often limited to disturbed areas, edges and the banks of streams (Corner, 1988; Heydon & Bulloh, 1997; M. Shanahan, pers. obs.). Heydon and Bulloh (1997) showed that densities of freestanding *Ficus* trees were greater in logged forests whilst Johns (1987) has shown that *Ficus* hemi-epiphytes are rarer in such habitats. Indeed, because hemi-epiphytes often grow on valuable timber trees they foresters may cut or poison them (Lambert 1991; Mawdsley *et al.*, 1998). Noting this differential resilience of *Ficus* species to anthropogenic disturbance Mawdsley *et al.* (1998) questioned whether figs in disturbed habitats perform the same ecological functions as forest *Ficus* species. The present research from Borneo indicates that this is not the case with, for example, the majority of fig-eating birds feeding only on canopy fruiting hemi-epiphytic *Ficus* species as opposed to the smaller bird-dispersed *Ficus* species that are common in secondary regrowth (Chapter 4). The role of growth form and breeding system in determining which frugivores are able to take advantage of *Ficus* species' figs suggests that ability of disturbed habitats to support frugivore populations will certainly differ from, and may be severely compromised when compared to, that observed in primary forests. A second difference in function between figs in mature forest and in disturbed habitats exists because, by attracting frugivores, *Ficus* individuals have been demonstrated to act as 'recruitment foci' (e.g. Slocum & Horvitz, 2000) for seeds dispersed by the animals they attract. They may therefore encourage regeneration of disturbed sites and are potential tools of forest restoration. The differential attraction of seed-dispersing frugivores to ripe fig crops suggests that the number and species composition of both *Ficus* and non-*Ficus* seeds dispersed by these frugivores around members of different *Ficus* dispersal guilds will be markedly different. *Ficus* species (and guilds) will therefore play different roles in promoting rain forest regeneration through the attraction of seed-dispersing frugivores to their crops.

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 *et al.*, 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 *et al.*, 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 *et al.*, 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 (Chapter 5), an interesting area of research exists.

8.4 Conclusions

This study has demonstrated that figs are fed upon by an exceptional range of vertebrate frugivores, particularly birds and mammals, throughout the range of the genus *Ficus*. However, the figs of a given *Ficus* species are not equally suitable to all frugivores in a given area. As shown by data collected from distinct *Ficus* and frugivore communities in Borneo and Papua New Guinea, a dispersal guild structure exists within the genus *Ficus*. This system of fig and/or disperser partitioning is determined

largely by differences in fig packaging and presentation (in which phylogeny plays a major part). Beyond promoting species co-existence through the reduction of competition the dispersal guild structure observed has certain other implications. Firstly, members of each guild are likely to experience markedly different seed dispersal services from the subsets of the frugivore community they attract. Secondly, because each *Ficus* species' figs are not suitable for all frugivores in a given area the application of the 'keystone resource' concept to figs needs to be re-assessed. Thirdly, a *Ficus* species' reliance on a particular subset of a frugivore community for seed dispersal means that its dispersal will be limited not only by the movements but also by the continued presence of the relevant frugivore species). Finally, the differential resilience of *Ficus* species to anthropogenic disturbance suggests that *Ficus* communities in pristine and recovering habitats will differ considerably in their ability to support and attract seed-dispersing vertebrate frugivores.

The diversity of *Ficus* (and the wide range of habitats in which its members occur) lends itself to confusion about the conservation importance of figs, particularly with regard to the keystone resource concept. As Janzen (1979) pointed out "a fig is not a FIG is not a **fig**" and the conservation value of one *Ficus* species may not be reproduced by the next. 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 (for the reasons cited by 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.

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 and added to 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.

REFERENCES

- ADLER, G. H. (2000). Tropical tree diversity, forest structure and the demography of a frugivorous rodent, the spiny rat (*Proechimys semispinosus*). *Journal of Zoology* **250**, 57-74.
- AGAMI, M. & WAISEL, Y. (1988). The role of fish in the distribution and germination of seeds of the submerged macrophytes *Najas marina* L. and *Ruppia maritima* L. *Oecologia* **76**, 83-88.
- ALL, S. (1996). *The Book of Indian Birds. Salim Ali Centenary Edition*. Oxford University Press, Oxford, UK.
- ALTMANN, J. (1974). Observational study of behaviour: sampling methods. *Behaviour* **49**, 227-267.
- ALVAREZ, T. & GONZALEZ, Q. L. (1970). Analisis polinico del contenido gastrico de murcielagos Glossophaginae de Mexico. *Anales de la Escuela Nacional de Ciencias Biologicas, Mexico* **18**, 137-165.
- ANON. (1995). At a glance: Lambir Hills National Park. *Inside CTFs. Center for Tropical Forest Science of the Smithsonian Tropical Research Institute* **Fall 1995**, 6.
- ANSTETT, M.-C., HOSSAERT-MCKEY, M. & KJELLBERG, F. (1997). Figs and fig pollinators: evolutionary conflicts in a coevolved mutualism. *Trends in Ecology and Evolution* **12**, 94-99.
- ANSTETT, M.-C., MICHALOUD, G. & KJELLBERG, F. (1995). Modelling the persistence of small populations of strongly interdependent species: the case of figs and fig wasps. *Conservation Biology* **11**, 204-213.
- ASHTON, P. S. & HALL, H. (1992). Comparisons of structure among mixed dipterocarp forests of north-western Borneo. *Journal of Ecology* **80**, 459-481.
- ATHREYA, V. R. (1993). Fruiting strangler figs (genus *Ficus*, subgenus *Urostigma*) and temporal variation in visitation of their avian frugivores in a tropical evergreen forest in the Western Ghats, India. M.Sc. thesis., Pondicherry University, Pondicherry, India.
- ATHREYA, V. R. (1996). Are ants secondary dispersers of fig seeds in Indian forests? *Journal of the Bombay Natural History Society* **93**, 595-596.
- ATHREYA, V. R. (1997). Trees with a difference: the strangler figs. *Resonance* **2**, 67-74.
- AUFFENBERG, W. (1988). *Gray's Monitor Lizard*. University of Florida Press, Florida, USA.
- AUGUST, P. V. (1981). Fig fruit consumption and seed dispersal by *Artibeus jamaicensis* in the llanos of Venezuela. *Biotropica* **13**, 70-76.
- AYENSU, E. S. (1974). Plant and bat interactions in West Africa. *Annals of the Missouri Botanical Garden* **61**, 702-727.
- BAKER, H. G. & HARRIS, B. J. (1957). The pollination of *Parkia* by bats and its attendant evolutionary problems. *Evolution* **11**, 449-460.
- BAKER, J. R. & BAKER, Z. (1936). The seasons in a tropical rain forests. Part 3. The fruit bats. *Journal of the Linnean Society of London, (Zoology)* **40**, 123-141.
- BALASUBRAMANIAN, P. (1996). Interactions between fruit-eating birds and bird-dispersed plants in the tropical dry evergreen forest of Point Calimere, South India. *Journal of the Bombay Natural History Society* **93**, 428-441.
- BALASUBRAMANIAN, P. & BOLE, P. V. (1993). Seed dispersal by mammals at Point Calimere Wildlife Sanctuary, Tamil Nadu. *Journal of the Bombay Natural History Society* **90**, 33-44.
- BALASUBRAMANIAN, R., NARENDRA PRASAD, S. & KANDAVEL, K. (1998). *Role of Birds and Bird-dispersal in the Natural Regeneration of Forest Plants in Tamil Nadu*. Salim Ali Centre for Ornithology and Natural History, Coimbatore, India.
- BALL, E. E. & GLUCKSMAN, J. (1975). Biological colonisation of Motmot, a recently-created tropical island. *Proceedings of the Royal Society of London Series B* **190**, 421-442.
- BALL, E. E. & GLUCKSMAN, J. (1978). Limnological studies of Lake Wisdom, a large New Guinea caldera lake with a simple fauna. *Freshwater Biology* **8**, 455-468.
- BALL, E. E. & HUGHES, I. M. (1982). Long Island, Papua New Guinea - People, resources and culture. *Records of the Australian Museum* **34**, 463-525.
- BANACK, S. A. (1996). Flying foxes, genus *Pteropus*, in the Samoan Islands: interaction with the forest communities. Ph.D. thesis., University of California, USA.
- BANCROFT, G. T. & BOWMAN, R. (1994). Temporal patterns in diet of nestling white-crowned pigeons: implications for conservation of frugivorous columbids. *Auk* **111**, 844-852.
- BARKER, R.D. & VESTJENS, W. J. M. (1989). *The Food of Australian Birds I. Non-passerines*. CSIRO, Melbourne, Australia.
- BARKER, R.D. & VESTJENS, W. J. M. (1990). *The Food of Australian Birds II. Passerines*. CSIRO, Melbourne, Australia.
- BARLOW, C. & WACHER, T. (1997). *A Field Guide to Birds of the Gambia and Senegal*. Yale University Press, New Haven, USA.
- BARNEA, A., YOM-TOV, Y. & FRIEDMAN, J. (1991). Does ingestion by birds affect seed germination? *Functional Ecology* **5**, 394-402.
- BARTELS, M. (1929). Kiara-gasten. *De Tropische Natuur* **18**, 37-42.
- BAZZAZ, F. A. & GRACE, J. A. (1997). *Plant Resource Allocation*. Academic Press, London, UK.
- BECCARI, O. (1904). *Wanderings in the Great Forests of Borneo*. Archibald Constable and Co. Ltd., London, UK.
- BECKER, P., LEIGHTON, M. & PAYNE, J. B. (1985). Why tropical squirrels carry seeds out of source crowns. *Journal of Tropical Ecology* **1**, 183-186.
- BECK-KING, H., VON HELVERSEN, O. & BECK-KING, R. (1999). Home range, population density, and food resources of *Agouti paca* (Rodentia: Agoutidae) in Costa Rica: A study using alternative methods. *Biotropica* **31**, 675-685.
- BEDGOOD, G. W. (1970). Bird notes from East Gippsland. *Australian Bird Watcher* **3**, 252-265.
- BEEHLER, B. (1983). Frugivory and polygamy in birds of paradise. *Auk* **100**, 1-12.
- BEEHLER, B. M. (1987). Ecology and behavior of the Buff-tailed Sicklebill (Paradisaeidae, *Epimachus albertisi*). *Auk* **105**, 48-55.
- BEEHLER, B. M. (1989). The birds of paradise. *Scientific American* **261**, 67-73.
- BEEHLER, B. M. & DUMBACHER, J. P. (1996). More examples of fruiting trees visited predominantly by birds of paradise. *Emu* **96**, 81-88.
- BEEHLER, B. M., PRATT, T. K. & ZIMMERMAN, D. A. (1986). *Birds of New Guinea*. Princeton University Press, New Jersey, USA.
- BENEFIT, B. R. & MCCROSSIN, M. L. (1997). Oldest known Old World monkey skull. *Nature* **388**, 368-371.
- BENNETT, E. L., NYAIOI, A. J. & SAMPUD, J. (1997). Hornbills *Buceros* spp. and culture in Northern Borneo: can they continue to co-exist? *Biological Conservation* **82**, 41-46.
- BERG, C. C. (1989). Classification and distribution of *Ficus*. *Experientia* **45**, 605-611.
- BERG, C. C. & WIEBES, J. T. (1992). *African fig trees and fig wasps*. North-Holland, Amsterdam.
- BERNEY, F. (1906). Field notes on the birds of the Richmond District, North Queensland. *Emu* **6**, 41-47.
- BHAT, H. R. (1994). Observations on the food and feeding behaviour of *Cynopterus sphinx* Vahl (Chiroptera, Pteropodidae) at Pune, India. *Mammalia* **58**, 363-370.
- BINGHAM, C. T. (1897). The Great Indian Hornbill in the wild state. *Journal of the Bombay Natural History Society* **11**, 308-310.
- BINSTEAD, G. (1977). Food of the Western Bowerbird in the Chichester Range, W. A. *Western Australian Naturalist* **14**, 77.
- BIRKINSHAW, C. R. (1999). The importance of the black lemur (*Eulemur macaco*) for seed dispersal in Lokobe Forest, Nosy Be. In *New Directions in Lemur Studies* (ed. B. Rakotosamimanana, H. Rasamimanana, J. Ganzhorn and S. M. Goodman), pp. 189-199. Kluwer Academic, New York, USA.
- BLANFORD, W. T. (1870). *Observations on the Geology and Zoology of Abyssinia*. MacMillan & Co., London, UK.
- BORGES, R. M. (1993). Figs, Malabar giant squirrels and fruit shortages within two tropical Indian forests. *Biotropica* **25**, 183-190.
- BOUCEK, Z. (1988). *Australasian Chalcidoidea (Hymenoptera)*. C. A. B. International, Wallingford, Oxon, UK.
- BRADBURY, J. W. (1981). The evolution of leks. In *Natural Selection and Social Behaviour* (ed. R. D. Alexander and O. W. Tinkle), pp. 138-169. Chiron Press, New York, USA.
- BRAVO, S. P., KOWALEWSKI, M. M. & ZUNINO, G. E. (1995). Dispersión y germinación de semillas de *Ficus monckii* por *Alouatta carya*. *Boletín Primatológico Latinoamericano* **5**, 27-30.
- BRAVO, S. P. & ZUNINO, G. E. (1998). Effects of black howler monkey (*Alouatta caraya*) seed ingestion on insect larvae. *American Journal of Primatology* **45**, 411-415.
- BREGULLA, H. L. (1992). *Birds of Vanuatu*. Anthony Nelson, Oswestry, UK.
- BREITWISCH, R. (1983). Frugivores at a fruiting *Ficus* vine in a southern Cameroon tropical wet forest. *Biotropica* **15**, 125-128.
- BREMER, B. & ERIKSSON, O. (1992). Evolution of fruit characters and dispersal modes in the tropical family Rubiaceae. *Biological Journal of the Linnean Society* **47**, 79-95.
- BRONSTEIN, J. L., GOUYON, P. H., GLIDDON, C., KJELLBERG, F. & MICHALOUD, G. (1990). The ecological consequences of flowering asynchrony in monoecious figs: a simulation study. *Ecology* **71**, 2145-2156.
- BRONSTEIN, J. L. & HOSSAERT-MCKEY, M. (1995). Hurricane Andrew and a Florida fig pollination mutualism: resilience of an obligate interaction. *Biotropica* **27**, 373-381.
- BROOKS, D. M., BODMER, R. E. & MATOLA, S. (1997). *Tapirs - Status survey and conservation action plan*. IUCN, Gland, Switzerland.
- BROCKELMAN, W. Y. (1982). Observations of animals feeding in a strangler fig, *Ficus drupacea*, in southeast Thailand. *Natural History Bulletin of the Siam Society* **30**, 33-44.
- BRONSTEIN, J. L. & HOFFMAN, K. (1987). Spatial and temporal variation in frugivory at a neotropical fig, *Ficus pertusa*. *Oikos* **49**, 261-268.
- BRONSTEIN, J. L. & PATEL, A. (1992). Causes and consequences of within-tree phenological patterns in the Florida strangling fig, *Ficus aurea* (Moraceae). *American Journal of Botany* **79**, 41-48.
- BROSSET, A. & ERARD, C. (1986). Les oiseaux des regions forestieres du Nord-Est Gabon. Volume I. Ecologie et comportement des especes. *Revue d'Ecologie (la Terre et la Vie)* **supplement 3**.

- BUCHANAN, R. A. (1989). Pied currawongs (*Strepera graculina*): their diet and role in weed dispersal in suburban Sydney, New South Wales. *Proceedings of the Linnean Society of New South Wales* **111**, 241-255.
- BURBIDGE, A. (1985). *The Regent Parrot: a report on the breeding distribution and habitat requirements along the Murray River in South-Eastern Australia*. Australian National Parks and Wildlife Service Report Series No 4. National Parks and Wildlife Service, Canberra, Australia.
- BUTLER, W. H. (1971). Yellow Figbird in Western Australia. *Western Australian Naturalist* **12**, 21.
- CABRE-VERT, N. & FEISTNER, A. T. C. (1995). Comparative gut passage times in captive lemurs. *The Dodo* **31**, 76-81.
- CAIN, A. J. & GALBRAITH, I. C. J. (1956). Field notes on the birds of the eastern Solomon Islands. *Ibis* **98**, 100-134.
- CANNON, C. E. (1984). The diet of Lorikeets *Trichoglossus* spp. in the Queensland-New South Wales border region. *Emu* **84**, 16-22.
- CARR, G. W. (1993). Exotic flora of Victoria and its impact on indigenous biota. In *Flora of Victoria* (ed. D. B. Foreman and N. G. Walsh), pp. 256-294. Inkata Press, Melbourne, Australia.
- CARVALHO, C. T. (1960). Sobre os hábitos alimentares de phillostomeídeos (Mammalia, Chiroptera). *Revista de Biologia Tropical* **9**, 53-60.
- CATERALL, C. P. (1985). Winter energy deficits and the importance of fruit versus insects in a tropical island bird population. *Australian Journal of Ecology* **10**, 265-279.
- CHANDLER, L. G. (1915). Figs eaten by Butcherbird. *Emu* **15**, 51.
- CHAO, J., KOH, C., FANG, K., CHEN, Y. & YEH, W. (1993). Feeding on plants by the Red-bellied Tree Squirrel *Callosciurus erythraeus* in Taipei Botanical Garden. *Bulletin of the Taiwan Forestry Research Institute, New Series* **8**, 39-50.
- CHAPIN, J. C. (1954). The birds of the Belgian Congo. Part IV. *Bulletin of the American Museum of Natural History* **75B**, 1-846.
- CHAPMAN, C. A. (1989). Primate seed dispersal: the fate of dispersed seeds. *Biotropica* **21**, 148-154.
- CHARLES-DOMINIQUE, P., ATRAMENTOWICZ, M., CHARLES-DOMINIQUE, M., GERARD, H., HLADIK, A., HLADIK, C. M. & PREVOST, M. F. (1981). Les mammifères frugivores arboricoles nocturnes d'une forêt guyanaise: inter-relations plantes-animaux. *Revue d'Ecologie (La Terre et la Vie)* **35**, 341-435.
- CHATURVEDI, N. (1993). Dietary of the cattle egret *Bubulcus coromandus* (Boddaert). *Journal of the Bombay Natural History Society* **90**, 90.
- CHENG, C. (1996). *Nature Reserves of Guangdong Province*. Guangdong Tourism Publishing House, Guangdong, China.
- CHIMCHOME, V., VIDHIDHARM, A., SIMCHAREON, S., BUMRUNGSRI, S. & POONSWAD, P. (1998). Comparative study of the breeding biology and ecology of two endangered hornbills species in Huai Kha Khaeng wildlife sanctuary, Thailand. In *The Asian Hornbills: Ecology and Conservation* (ed. P. Poonswad), pp. 111-136. Biodiversity Research and Training Program, National Center for Genetic Engineering and Biotechnology, Bangkok, Thailand.
- CHIVERS, D. J. (1977). The feeding behaviour of Siamang (*Symphalangus syndactylus*). In *Primate Ecology: Studies of Feeding and Ranging Behaviour in Lemurs, Monkeys and Apes* (ed. T. H. Clutton-Brock), pp. 335-382. Academic Press, London, UK.
- CHIVERS, D. J. (1980). *Malayan Forest Primates. Ten Years Study in Tropical Rain Forest*. Plenum Press, New York, USA.
- CHOU, L. S. & YEH, H. M. (1995). The pollination ecology of *Ficus aurantiaca* var. *parvifolia*. *Acta Zoologica Taiwanica* **6**, 1-12.
- CHUANG, S.-A. & LEE, L.-L. (1997). Food habits of three carnivore species (*Viverricula indica*, *Herpestes urva* and *Melogale moschata*) in Fushan Forest, northern Taiwan. *Journal of Zoology* **243**, 71-79.
- CHURCH, R. J. (1997). Avian frugivory in a subtropical rainforest: Eleven years of observations in Lamington National Park. *The Sunbird* **27**, 85-97.
- CLELAND, J. B., MAIDEN, J. H., FROGGART, W. W., FERGUSON, E. W. & MUSSON, C. T. (1918) *The Food of Australian Birds*. New South Wales Department of Agricultural Science Bulletin No 15. N.S.W. Department of Agricultural Science, Sydney, Australia.
- CLEMENT, P., HARRIS, A., DAVIS, J. (1993). *Finches and Sparrows, an identification guide*. Christopher Helm, London, UK.
- COATES, B. J. (1985). *The Birds of Papua New Guinea including the Bismarck Archipelago and Bougainville. Volume 1. Non-Passerines*. Dove Publications, Alderley, Queensland, Australia.
- COATES, B. J. (1990). *The Birds of Papua New Guinea including the Bismarck Archipelago and Bougainville. Volume 2. Passerines*. Dove Publications, Alderley, Queensland, Australia.
- COATES, B. J. & BISHOP, K. D. (1997). *A Guide to the Birds of Wallacea*. Dove Publications, Alderley, Queensland, Australia.
- COATES-ESTRADA, R. & ESTRADA, A. (1986). Fruiting and frugivores at a strangler fig in the tropical rain forest of Los Tuxtlas, Mexico. *Journal of Tropical Ecology* **2**, 349-357.
- COCKRUM, E. L. & BRADSHAW, G. R. (1963). Notes on mammals from Sonora, Mexico. *Amer. Mus. Novit.* **2138**, 1-9.
- COMPTON, S. G., CRAIG, A. J. F. K. & WATERS, I. W. R. (1996). Seed dispersal in an African fig tree: birds as high quantity, low quality dispersers? *Journal of Biogeography* **23**, 553-563.
- COMPTON, S. G., ELLWOOD, M. D. F., DAVIS, A. J. & WELCH, K. (2000). The flight heights of chalcid wasps (Hymenoptera, Chalcidoidea) in a lowland Bornean rain forest: fig wasps are the high fliers. *Biotropica* **32**, 515-522.
- COMPTON, S. G. & MCCORMACK, G. (1999). The Pacific banyan in the Cook Islands: Have its pollination and seed dispersal mutualisms been disrupted, and does it matter? *Biodiversity and Conservation* **8**, 1707-1705.
- COMPTON, S. G., RASPLUS, J.-Y. & WARE, A. B. (1994a). African fig wasp parasitoid communities. In *Parasitoid Community Ecology* (ed. B. A. Hawkins and W. Sheehan), pp. 343-368. Oxford University Press, Oxford, UK.
- COMPTON, S. G., ROSS, S. J. & THORNTON, I. W. B. (1994b). Pollinator limitation of fig tree reproduction on the island of Anak Krakatau (Indonesia). *Biotropica* **26**, 180-186.
- CONCEICAO DE SOUZA-STEVAUX, M., NEGRELLE, R. R. B. & CITADINI-ZANETTE, V. (1994). Seed dispersal by the fish *Pterodoras granulosus* in the Parana river basin, Brazil. *Journal of Tropical Ecology* **10**, 621-626.
- CONDIT, I. J. (1947). *The Fig*. Chronica Botanica Co., Waltham, Mass., USA.
- CONKLIN, N. L. & WRANGHAM, R. W. (1994). The value of figs to a hind-gut fermenting frugivore: a nutritional analysis. *Biochemical Systematics and Ecology* **22**, 137-151.
- COOK, J. M. & POWER, S. A. (1996). Effects of within-tree flowering asynchrony on the dynamics of seed and wasp production in an Australian fig species. *Journal of Biogeography* **23**, 487-493.
- COOK, S., SINGADAN, R., THORNTON, I. W. B. (in review). Colonisation of an island volcano, Long I, Papua New Guinea, and an emergent island, Motmot, in its caldera lake: a nested natural experiment. IV. Mammals, Reptiles and Amphibia. *Journal of Biogeography*.
- COOPER, A. & PENNY, D. (1997). Mass survival of birds across the Cretaceous-Tertiary boundary: molecular evidence. *Science* **275**, 1109-1113.
- COOPER, H. M. (1958). Currawongs on Kangaroo Island. *South Australian Ornithologist* **22**, 5-6.
- COOPER, W. & COOPER, W. T. (1995). *Fruit of the Rain Forest. A Guide to the Fruit in Australian Tropical Rain Forests*. Blackie, London, UK.
- CORBET, G. B. & HILL, J. E. (1991). *A World List of Mammalian Species*. Oxford University Press, Oxford, UK.
- CORLETT, R. T. (1984). The phenology of *Ficus benjamina* and *Ficus microcarpa* in Singapore. *Journal of the Singapore Academy of Science* **13**, 30-31.
- CORLETT, R. T. (1987). The phenology of *Ficus fistulosa* in Singapore. *Biotropica* **19**, 122-124.
- CORLETT, R. T. (1993). Sexual dimorphism in the reproductive phenology of *Ficus grossularioides* Burm. f. in Singapore. *Malayan Nature Journal* **46**, 149-155.
- CORLETT, R. T. (1996). Characteristics of vertebrate dispersed fruits in Hong Kong. *Journal of Tropical Ecology* **12**, 819-833.
- CORLETT, R. T. (1998a). Frugivory and seed dispersal by birds in Hong Kong scrubland. *Forktail* **13**, 23-27.
- CORLETT, R. T. (1998b). Frugivory and seed dispersal by vertebrates in the Oriental (Indomalayan) Region. *Biological Reviews* **73**, 413-448.
- CORLETT, R. T. & LUCAS, P. W. (1990). Alternative seed-handling strategies in primates - seed-spitting by long-tailed macaques (*Macaca fascicularis*). *Oecologia* **82**, 166-171.
- CORNER, E. J. H. (1965). Check list of *Ficus* in Asia and Australasia, with keys to identification. *Garden's Bulletin, Singapore* **21**, 1-186.
- CORNER, E. J. H. (1988). *Wayside Trees of Malaya, Volume 2. 3rd edition*. United Selangor Press, Kuala Lumpur, Malaysia.
- COULTAS, W. F. (1933-35). *Journal and letters of William F. Coultas, Vol IV, Whitney South Sea Expedition, October 1933 - March 1935*. Unpublished, in American Museum of Natural History, New York, USA.
- COWLES, G. S. & GOODWIN, D. (1959). Seed digestions by the fruit eating pigeon *Treron*. *Ibis* **101**, 253-254.
- CRAIG, R. J. (1996). Seasonal population surveys and natural history of a Micronesian bird community. *Wilson Bulletin* **108**, 246-267.
- CRAMP, S. (1977). *Handbook of the Birds of Europe, the Middle East and North Africa. (The Birds of the Western Palearctic.) Vol. I. Ostrich to Ducks*. Oxford University Press, Oxford, UK.
- CRAMP, S. (1983). *Handbook of the Birds of Europe, the Middle East and North Africa. (The Birds of the Western Palearctic.) Vol. III. Waders to Gulls*. Oxford University Press, Oxford, UK.
- CRAMP, S. (1985). *Handbook of the Birds of Europe, the Middle East and North Africa. (The Birds of the Western Palearctic.) Vol. IV: Terns to Woodpeckers*. Oxford University Press, Oxford, UK.
- CRAMP, S. (1988). *Handbook of the Birds of Europe, the Middle East and North Africa. (The Birds of the Western Palearctic.) Vol. V. Tyrant Flycatchers to Thrushes*. Oxford University Press, Oxford, UK.
- CRAMP, S. (1992). *Handbook of the Birds of Europe, the Middle East and North Africa. (The Birds of the Western Palearctic.) Vol. VI. Warblers*. Oxford University Press, Oxford, UK.
- CRAMP, S. & PERRINS, C. M. (1993). *Handbook of the Birds of Europe, the Middle East and North Africa. (The Birds of the Western Palearctic.) Vol. VII. Flycatchers to Shrikes*. Oxford University Press, Oxford, UK.
- CRAMP, S. & PERRINS, C. M. (1994). *Handbook of the Birds of Europe, the Middle East and North Africa. (The Birds of the Western Palearctic.) Vol. VIII. Crows to Finches*. Oxford University Press, Oxford, UK.

- CRANBROOK, EARL OF & EDWARDS, D. S. (1994). *A Tropical Rainforest. The Nature of Biodiversity at Belalong, Brunei*. Royal Geographic Society & Sun Tree Publishing, UK and Singapore.
- CROME, F. H. J. (1975). The ecology of fruit pigeons in tropical north Queensland. *Australian Wildlife Research* **2**, 155-185.
- CROME, F. H. J. (1978). Foraging ecology of an assemblage of birds in lowland rainforest in north Queensland. *Australian Journal of Ecology* **3**, 195-212.
- CROUTHER, M. M. (1985). Some breeding records of the common koel *Eudynamis scolopacea*. *Australian Bird Watcher* **11**, 49-56.
- CRUZ, A. (1980). Avian feeding assemblages in Puerto Rico. *Caribbean Journal of Science* **15**, 21-27.
- CUMMING, G. S. & BERNARD, R. T. F. (1997). Rainfall, food abundance and timing of parturition in African bats. *Oecologia* **111**, 309-317.
- DATE, E. M., FORD, H. A. & RECHER, H. F. (1991). Frugivorous pigeons, stepping stones and weeds in northern New South Wales. In *Nature Conservation 2. The Role of Corridors* (ed. D. A. Saunders and R. J. Hobbs), pp. 241-245. Surrey Beatty & Sons, Chipping Norton, New South Wales, Australia.
- DAVIS, A. J. & SUTTON, S. L. (1997). A dung beetle that feeds on figs: implications for the measurement of species rarity. *Journal of Tropical Ecology* **13**, 759-766.
- DAWS, G. & FUJITA, M. (1999). *Archipelago. The Islands of Indonesia*. University of California Press, Berkeley, USA.
- DECKER, B. S. (1989). Effects of habitat distribution on the behavioural ecology and demographics of the Tana River red colobus (*Colobus badius rufomitratu*). Ph.D. thesis, Emory University, Atlanta, USA.
- DEFIGUEIREDO, R. A. (1993). Ingestion of *Ficus enornis* seeds by howler monkeys *Alouatta fusca* in Brazil: effects on seed germination. *Journal of Tropical Ecology* **9**, 541-543.
- DEFIGUEIREDO, R. A. (1996a). Complex interactions in nature: parrotlet feeding on fig fruits lessens seed dispersal and gene flow. *Ciencia e Cultura: Journal of Brazilian Association for Advancement of Science* **48**, 282-283.
- DEFIGUEIREDO, R. A. (1996b). Vertebrates at neotropical fig species in a forest fragment. *Tropical Ecology* **37**, 139-141.
- DEFIGUEIREDO, R. A., MOTTA JR, J. C. & VASCONCELLOS, L. A. D. S. (1995). Pollination, seed dispersal, seed germination and establishment of seedlings of *Ficus microcarpa*, Moraceae, in southeastern Brazil. *Revista Brasileira de Biologia* **55**, 233-239.
- DEFLER, T. R. & DEFLER, S. B. (1996). Diet of a group of *Lagothrix lagothericha lagothericha* in southeastern Colombia. *International Journal of Primatology* **17**, 161-190.
- DEL HOYO, J., ELLIOT, A. & SARGATAL, J. (1994). *Handbook of the Birds of the World. Volume 2. New World Vultures to Guineafowl*. Lynx Edicions, Barcelona, Spain.
- DEL HOYO, J., ELLIOT, A. & SARGATAL, J. (1997). *Handbook of the Birds of the World. Volume 4. Sandgrouse to Cuckoos*. Lynx Edicions, Barcelona, Spain.
- DEL HOYO, J., ELLIOT, A. & SARGATAL, J. (2000). *Handbook of the Birds of the World. Volume 5. Barn Owls to Hummingbirds*. Lynx Edicions, Barcelona, Spain.
- DEL HOYO, J., ELLIOT, A. & SARGATAL, J. (2001). *Handbook of the Birds of the World. Volume 6. Mousebirds to Hornbills*. Lynx Edicions, Barcelona, Spain.
- DEW, J. L. & WRIGHT, P. (1998) Frugivory and seed dispersal by four species of primates in Madagascar's eastern rain forest. *Biotropica* **30**, 425-437.
- DIAMOND, J. M. (1974). Colonization of exploded volcanic islands by birds: the supertramp strategy. *Science* **184**, 803-806.
- DIAMOND, J. M. (1976). Preliminary results of an ornithological exploration of the islands of Vitiaz and Dampier Straits, Papua New Guinea. *Emu* **76**, 1-7.
- DIAMOND, J. M. (1981). Reconstitution of bird community structure on Long Island, New Guinea, after a volcanic explosion. *National Geographic Society Research Report 1972* **1**, 191-204.
- DINERSTEIN, E. (1979). An ecological survey of the Royal Karnali-Bardia Wildlife Reserve, Nepal. Part II. Habitat / animal interactions. *Biological Conservation* **16**, 265-300.
- DINERSTEIN, E. (1986). Reproductive ecology of fruit bats and the seasonality of fruit production in a Costa Rican cloud forest. *Biotropica* **18**, 307-318.
- DINERSTEIN, E. (1987). Deer, plant phenology, and succession in the lowland forests of Nepal. In *Biology and Management of the Cervidae* (ed. C. M. Wemmer), pp. 272-288. Smithsonian Institution Press, Washington, D. C., USA.
- DIRZO, R. & DOMÍNGUEZ, C. A. (1986). Seed shadows, seed predation and the advantages of dispersal. In *Frugivores and Seed Dispersal* (ed. A. Estrada and T. H. Fleming), pp. 237-249. Junk, Dordrecht, Netherlands.
- DOCTERS VAN LEEUWEN, W. M. (1935). The dispersal of plants by fruit-eating bats. *Gardens Bulletin, Straits Settlement* **9**, 58-63.
- DOWSETT-LEMAIRE, F. (1988). Fruit choice and seed dissemination by birds and mammals in the evergreen forests of upland Malawi. *Revue d'Ecologie (La Terre et la Vie)* **43**, 251-285.
- DOWSETT-LEMAIRE, F. (1990). Eco-ethology, distribution and status of Nyungwe Forest birds (Rwanda). Tauraco Research Report **3**, 31-85.
- DOWSETT-LEMAIRE, F. (1996). Avian frugivore assemblages at three small-fruited tree species in the forests of northern Congo. *Ostrich* **67**, 88-89.
- DUPONT, J. E. & RABOR, D. S. (1973). Birds of Dinagat and Siargao, Philippines. *Nemouria* **10**, 1-111.
- EBY, P. (1998). An analysis of diet specialization in frugivorous *Pteropus poliocephalus* (Megachiroptera) in an Australian subtropical rainforest. *Australian Journal of Ecology* **5**, 443-456.
- EGLOFF, B. J. & SPECHT, J. (1982). Long Island, Papua New Guinea: Aspects of the prehistory. *Records of the Australian Museum* **34**, 427-446.
- EHRlich, P. R. & RAVEN, P. H. (1964). Butterflies and plants: a study in coevolution. *Evolution* **18**, 386-608.
- ELANGOVAN, V., MARIMUTHU, G. & KUNZ, T. H. (1999). Temporal patterns of individual and group foraging behaviour in the short-nosed fruit bat, *Cynopterus sphinx*, in South India. *Journal of Tropical Ecology* **15**, 681-687.
- EMMONS, L. H. (1980). Ecology and resource partitioning among nine species of African rain forest squirrels. *Ecological Monographs* **50**, 31-54.
- EMMONS, L. H. (1991). Frugivory in treeshrews (*Tupaia*). *American Naturalist* **138**, 642-649.
- ENTWISTLE, A. C. & CORP, N. (1997). The diet of *Pteropus voeltzkowi*, an endangered fruit bat endemic to Pemba Island, Tanzania. *African Journal of Ecology* **35**, 351-360.
- ESTRADA, A. & COATES-ESTRADA, R. (1986). Frugivory by howling monkeys (*Alouatta palliata*) at Los Tuxtlas, Mexico: dispersal and fate of seeds. In *Frugivores and Seed Dispersal* (ed. A. Estrada & T. H. Fleming), pp 93-104. Junk, Dordrecht, Netherlands.
- EVANS, G. (1939). The characteristic vegetation of recent volcanic islands in the Pacific. *Bulletin of Miscellaneous Information, Botanic Gardens, Kew* **1939**, 43-44.
- EVANS, P. G. H. (1979). Status and conservation of the Seychelles black parrot. *Biological Conservation* **16**, 233-240.
- FAN, Z. (1990). *Zhong Guo Niao Lei Zhong Bie Gai Yao*. Liao Ning Science Press, Beijing, China.
- FEARE, C. & CRAIG, A. (1998). *Starlings and Mynas*. Christopher Helm, London.
- FIALHO, R. F. (1990). Seed dispersal by a lizard and a treefrog - effect of dispersal site on seed survivorship. *Biotropica* **22**, 423-424.
- FISCHER, K. E. & CHAPMAN, C. A. (1993). Frugivores and fruit syndromes: differences in patterns at the genus and species level. *Oikos* **66**, 472-482.
- FITZPATRICK, J. W. (1983). *Tyrannus melancholicus* (Tirano Tropical, Pecho Amarillo, Tropical Kingbird). In *Costa Rican Natural History* (ed. D. H. Janzen), pp. 611-613. University of Chicago Press, Chicago, USA.
- FLANNERY, T. (1995). *Mammals of New Guinea. Revised and Updated Edition*. Cornell University Press, New York, USA.
- FLANNERY, T. F. (1994). *Possums of the World. A Monograph of Phalangerioidea*. GEO in association with the Australian Museum, Sydney, Australia.
- FLEMING, T. H. (1979). Do tropical frugivores compete for food? *American Zoologist* **19**, 1157-1172.
- FLEMING, T. H. (1981). Fecundity, fruiting pattern, and seed dispersal in *Piper amalago* (Piperaceae), a bat-dispersed tropical shrub. *Oecologia* **51**, 42-46.
- FLEMING, T. H. (1983). *Carollia perspicillata* (Murcielago Candelario, Lesser Short-tailed Fruit Bat). In *Costa Rican Natural History* (ed. D. H. Janzen), pp. 457-458. University of Chicago Press, Chicago, USA.
- FLEMING, T. H., BREITWISCH, R. & WHITESIDES, G. H. (1987). Patterns of tropical vertebrate frugivore foraging diversity. *Annual Review of Ecology and Systematics* **18**, 91-109.
- FLEMING, T. H. & HEITHAUS, E. R. (1981). Frugivorous bats, seed shadows and the structure of tropical forests. *Biotropica* **13** (suppl.), 45-53.
- FLEMING, T. H., HEITHAUS, E. R. & SAWYER, W. B. (1977). An experimental analysis of the food location behaviour of frugivorous bats. *Ecology* **58**, 619-627.
- FLEMING, T. H., HOPPER, E. T. & WILSON, D. E. (1972). Three Central American bat communities: structure, reproductive cycles, and movement patterns. *Ecology* **53**, 555-569.
- FLEMING, T. H. & SOSA, V. J. (1994). Effects of nectarivorous and frugivorous mammals on reproductive success of plants. *Journal of Mammalogy* **75**, 845-851.
- FORSYTH, J. E. & COOPER, W. T. (1981). *Australian Parrots. 2nd (revised) edition*. Lansdowne, Melbourne, Australia.
- FORSYTH, J. M. & MULLER, K. A. (1978). Annotated list of birds observed at Iron Range, Cape York peninsula, Queensland, during October 1974. *Australian Birdwatcher* **7**, 171-194.
- FOSTER, R. B. (1982a). Famine on Barro Colorado Island. In *The Ecology of a Tropical Forest. Seasonal Rhythms and Long-term Changes* (ed. E. G. Leigh Jr, A. S. Rand and D. M. Windsor), pp. 210-212. Smithsonian Institution Press, Washington D.C., USA.
- FOSTER, R. B. (1982b). The seasonal rhythm of fruitfall on Barro Colorado Island. In *The Ecology of a Tropical Forest. Seasonal Rhythms and Long-term Changes* (ed. E. G. Leigh Jr, A. S. Rand and D. M. Windsor), pp. 151-172. Smithsonian Institution Press, Washington D.C., USA.
- FRAGASO, J. M. V. (1997). Tapir-generated seed shadows: scale-dependent patchiness in the Amazon rain forest *Journal of Ecology* **85**, 519-529.

- FRANCIS, C. M. (1990). Trophic structure of bat communities in the understory of lowland dipterocarp rain forest in Malaysia. *Journal of Tropical Ecology* **6**, 421-431.
- FRANCIS, C. M. (1994). Vertical stratification of fruit bats (Pteropodidae) in lowland dipterocarp rainforest in Malaysia. *Journal of Tropical Ecology* **10**, 523-530.
- FRANKIE, G. W., BAKER, H. G. & OPLER, P. A. (1974). Comparative phenological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. *Journal of Ecology* **62**, 881-919.
- FRITH, C. B. & BEEHLER, B. M. (1998). *The Birds of Paradise*. Oxford University Press, Oxford, UK.
- FRITH, H. J. (1952). Notes on the pigeons of the Richmond River, N.S.W. *Emu* **52**, 89-99.
- FRITH, H. J. (1957). Food habits of the topknot pigeon. *Emu* **57**, 341-345.
- FRITH, H. J. (1982). *Pigeons and Doves of Australia*. Rigby, Melbourne, Australia.
- FRITH, H. J., MCKEAN, J. L. & BRAITHWAITE, L. W. (1976a). Sexual cycles and food of the doves *Streptopelia chinensis* and *Streptopelia senegalensis* in Australia. *Emu* **76**, 15-24.
- FRITH, H. J., WOLFE, T. O. & BARKER, R. D. (1976b). Food of eight species of Columbidae, in the genera *Geopelia*, *Phaps*, *Geophaps* and *Petrophassa*. *Australian Wildlife Research* **3**, 159-171.
- FROST, P. G. H. (1988). Fruit-frugivore interactions in a South African coastal dune forest. *Acta XVII Congressus Internationalis Ornithologi* **3**, 1179-1184.
- FRY, C. H., KEITH, S. & URBAN, E. K. (1988). *The Birds of Africa. Volume III*. Academic Press, London, UK.
- FUENTES, A. (1996). Feeding and ranging in the Mentawai Island langur (*Presbytis potenziani*). *International Journal of Primatology* **17**, 525-548.
- FUJITA, M. S. & TUTTLE, M. D. (1991). Flying foxes (Chiroptera: Pteropodidae): threatened animals of key ecological and economical importance. *Conservation Biology* **5**, 455-463.
- FULLER, O. (1942). English starling eating olives. *South Australian Ornithologist* **16**, 44.
- FUNAKOSHI, F., WATANABE, H. & KUNISAKI, T. (1993). Feeding ecology of the northern Ryukyu fruit bat, *Pteropus dasymallus*, in a warm-temperate region. *Journal of Zoology* **230**, 221-230.
- FWS. (1992). *Endangered and Threatened Species of the Southeastern United States (The Red Book). FWS Region 4*. Fish and Wildlife Service, Washington D.C., USA.
- GALDIKAS, B. M. F. (1988). Orangutan diet, range, and activity at Tanjung Puting, Central Borneo. *International Journal of Primatology* **9**, 1-35.
- GALETTI, M., MARTUSCELLI, P., OLMOS, F. & ALEIXO, A. (1997). Ecology and conservation of the jacutinga *Pipile jacutinga* in the Atlantic Forest of Brazil. *Biological Conservation* **82**, 31-39.
- GALETTI, M. & MORELLATO, L. P. C. (1994). Diet of the large fruit-eating bat *Artibeus lituratus* in a forest fragment in Brasil. *Mammalia* **58**, 661-665.
- GALETTI, M. & PEDRONI, F. (1994). Seasonal diet of capuchin monkeys (*Cebus apella*) in a semideciduous forest in south-east Brazil. *Journal of Tropical Ecology* **10**, 27-39.
- GALETTI, M., PEDRONI, F. & MORELLATO, L. P. C. (1994). Diet of the brown howler monkey *Alouatta fusca* in a forest fragment in southeastern Brazil. *Mammalia* **58**, 111-118.
- GALIL, J. (1973). Pollination in dioecious figs: pollination of *Ficus fistulosa* by *Ceratosolen hewitii*. *Gardens Bulletin, Singapore* **26**, 303-311.
- GALIL, J. & EISIKOWITZ, D. (1968). On the pollination ecology of *Ficus sycomorus* in East Africa. *Ecology* **49**, 259-269.
- GALIL, J. & EISIKOWITZ, D. (1969). Further studies on the pollination ecology of *Ficus sycomorus* L. (Hymenoptera, Chalcidoidea, Agaonidae). *Tijdschrift voor Entomologie* **112**, 1-13.
- GANZHORN, J. U. (1988). Food partitioning among Malagasy primates. *Oecologia* **75**, 436-450.
- GARBITT, N. (1999). *Mammals of Madagascar*. Pica Press, Surrey, UK.
- GARDNER, A. L. (1977). Feeding Habits. In *Biology of the Bats of the New World Family: Phyllostomidae. Part 2* (ed. R. J. Baker, J. K. Jones and D. C. Carter), pp. 293-335. Special Publications of The Museum, Texas Tech University. Number 13. Texas Tech Press, Lubbock, Texas, USA.
- GARTLAN, J. S. & STRUHSACKER, T. T. (1972). Polyspecific associations and niche separation of rain-forest anthropoids in Cameroon, West Africa. *Journal of Zoology* **168**, 221-266.
- GATTER, W. (1997). *Birds of Liberia*. Pica Press, East Sussex, UK.
- GAUTIER-HION, A. (1980). Seasonal variation of diet related to species and sex in a community of Cercopithecus monkeys. *Journal of Animal Ecology* **49**, 237-269.
- GAUTIER-HION, A., EMMONS, L. H. & DUBOST, G. (1980). A comparison of the diets of three major groups of primary consumers of Gabon (primates, squirrels and ruminants). *Oecologia* **45**, 182-189.
- GAUTIER-HION, A., HECKETSWEILER, P., SOURD, C., TIOLLAY, J. M., ROUSILHON, C., QURIS, R., DECOUX, J. P., DUBOST, G., DUPLANTIER, J. M., ERARD, C., EMMONS, L., FEER, F. & MOUNGAZI, A. (1985). Fruit characters as a basis of fruit choice and seed dispersal in a tropical forest vertebrate community. *Oecologia* **65**, 324-337.
- GAUTIER-HION, A. & MICHALOUD, P. (1989). Are figs always keystone resources for tropical frugivorous vertebrates? A test in Gabon. *Ecology* **70**, 1826-1833.
- GINIGE, P. (1998). Notes on some observations of the habitats and biology of hornbills in Sri Lanka. In *The Asian Hornbills: Ecology and Conservation* (ed. P. Poonswad), pp. 33-48. Biodiversity Research and Training Program, National Center for Genetic Engineering and Biotechnology, Bangkok, Thailand.
- GILBERT, L. E. (1980). Food web organisation and conservation of neotropical diversity. In *Conservation Biology: An Evolutionary-Ecological Perspective* (ed. M. E. Soulé and B. A. Wilcox), pp. 11-34. Sinauer, Sunderland, Mass., USA.
- GITTINS, L. E. & RAEMAEEKERS, J. J. (1980). Siamang, lar and agile gibbons. In *Malayan Forest Primates. Ten Years Study in Tropical Rain Forest* (ed. D. J. Chivers), pp. 63-105. Plenum Press, New York, USA.
- GLANZ, W. E., THORINGTON JR, R. W., GIACALONE-MADDEN, J., HEANEY, L. R. (1982). Seasonal food use and demographic trends in *Sciurus granatensis*. In *The Ecology of a Tropical Forest. Seasonal Rhythms and Long-term Changes* (ed. E. G. Leigh Jr, A. S. Rand and D. M. Windsor), pp. 239-252. Smithsonian Institution Press, Washington D.C., USA.
- GOODMAN, S. M., GANZHORN, J. U. & WILMÉ, L. (1997). Observations at a Ficus tree in Malagasy Humid Forest. *Biotropica* **29**, 480-488.
- GOODWIN, G. G. & GREENHALL, A. M. (1961). A review of the bats of Trinidad and Tobago. Description, rabies infection and ecology. *Bulletin of the American Museum of Natural History* **122**, 187-302.
- GOODWIN, D. (1983). *Pigeons and Doves of the World, 3rd edition*. Cornell University Press, Ithaca, N.Y., USA.
- GORCHOV, D. L., CORNEJO, F., ASCORRA, C. F. & JARAMILLO, M. (1995). Dietary overlap between frugivorous birds and bats in the Peruvian Amazon. *Oikos* **74**, 235-250.
- GOULD, J. (1865). *Handbook to the birds of Australia*. J. Gould, London, UK.
- GRAHAM, C. H., MOERMOND, T. C., KRISTENSEN, K. A. & MVUKIYUMWAMI, J. (1995). Seed dispersal effectiveness by two bulbuls in *Masea lanceolata*, an African montane forest tree. *Biotropica* **27**, 476-486.
- GRAHAM, D. L. (1996). Interactions of understory plants and frugivorous birds in a lowland Costa Rican forest. Ph.D. thesis, University of Miami, Miami, USA.
- GREEFF, J. M. & WHITING, M. J. (1999). Dispersal of Namaqua Fig (*Ficus cordata cordata*) seeds by the Augrabies Flat Lizard (*Platysaurus broadleyi*). *Journal of Herpetology* **33**, 328-330.
- GREEN, R. J. (1993). Avian seed dispersal in and near subtropical rainforests. *Wildlife Research* **20**, 535-557.
- GREENHALL, A. M. (1956). The food of some Trinidad fruit bats (*Artibeus* and *Carollia*). *Journal of the Agricultural Society of Trinidad and Tobago* **869**, 1-23.
- GREWAL, B., MONGA, S. & WRIGHT, G. (1993). *Birds of India, Bangladesh, Nepal, Pakistan and Sri Lanka: A Photographic Guide*. Guidebook Company Limited, Hong Kong.
- GRIMMETT, R., INSKIPP, C. & INSKIPP, T. (1998). *Birds of the Indian Subcontinent*. Christopher Helm, London, UK.
- GRUEZO, W. S. & SOLIGAM, A. C. (1990). Identity and germination of seeds from feces of the Philippine Palm Civet (*Paradoxurus philippensis* Jourdan). *Natural History Bulletin of the Siam Society* **38**, 69-82.
- HAILEY, A. (1997). Digestive efficiency and gut morphology of omnivorous and herbivorous African tortoises. *Canadian Journal of Zoology* **75**, 787-794.
- HALL, G. (1987). Seed dispersal by birds of prey. *Zimbabwe Science News* **21**, 2.
- HALL, K. R. L. (1965). Behaviour and ecology of the wild Patas monkey, *Erythrocebus patas*, in Uganda. *Journal of Zoology* **148**, 15-87.
- HAMANN, A. & CURIO, E. (1999). Interactions among frugivores and fleshy fruit trees in a Philippine submontane rainforest. *Conservation Biology* **13**, 766-773.
- HAMILTON, W. J. I. (1986). Namib Desert baboon (*Papio ursinus*) use of food and water resources during a food shortage. *Madoqua* **14**, 397-407.
- HARRISON, R. D. (1996). The ecology of the fig - fig wasp mutualism in a lowland tropical forest in Sarawak, Malaysia. M.Sc. thesis, Center for Ecological Research, Kyoto University, Kyoto, Japan.
- HARRISON, R. D. (1997). The *Ficus* flora of Lambir Hills National Park, Sarawak. In *General Flowering of Tropical Rainforests in Sarawak* (ed. T. Inoue and A. A. Hamid), pp. 86-95. Center for Ecological Research, Kyoto University, Kyoto, Japan.
- HARRISON, R. D. (1998). Guide to the *Ficus* flora of Lambir Hills National Park, Sarawak. Unpublished report.
- HARRISON, R. D. (1999). Phenology and wasp population dynamics of several species of dioecious fig in a lowland tropical rain forest in Sarawak, Malaysia. Ph.D. thesis, Center for Ecological Research, Kyoto University, Kyoto, Japan.
- HARRISON, R. D. (2000). Repercussions of El Niño: Drought causes extinction and the breakdown of mutualism in Borneo. *Proceedings of the Royal Society of London Series B*, **267**, 911-915.
- HARRISON, R. D. (in prep.). Phenology and wasp production dynamics of two species of dioecious fig in a lowland tropical forest in Sarawak.
- HARRISON, R. D., YAMAMURA, N. & INOUE, T. (2000). The phenology of a common roadside fig in Sarawak. *Ecological Research*, **15**, 47-61.

- HARRISON, R. D., SHANAHAN, M., YAMUNA, R. & THORNTON, I. W. B. (in review). Colonisation of an island volcano, Long I, Papua New Guinea, and an emergent island, Motmot, in its caldera lake: a nested natural experiment. II. Vascular plants. *Journal of Biogeography*.
- HARTWIG, H-G. (1993) The central nervous system of birds: A study of functional morphology. In *Avian Biology. Vol IX* (ed. D. S. Farner, J. R. King and K. C. Parkes), pp. 1-119. Academic Press, London, UK.
- HEALEY, C. (1992). Abundance, diet and roosting defaecations of the Torresian Imperial-Pigeon *Ducula spilorrhoa* in Darwin. *Corella* **16**, 107-110.
- HEITHAUS, E. R., FLEMING, T. H. & OPLER, P. A. (1975). Patterns of foraging and resource utilisation in seven species of bats in a seasonal tropical forest. *Ecology* **56**, 841-854.
- HERBST, L. H. (1986). The role of nitrogen fruit pulp in the nutrition of the frugivorous bat *Carollia perspicillata*. *Biotropica* **18**, 39-44.
- HERRE, E. A. (1989). Coevolution of reproductive characteristics in 12 species of New World figs and their pollinator wasps. *Experientia* **45**, 637-647.
- HERRERA, C. M. (1981). Are tropical fruits more rewarding to dispersers than temperate ones? *American Naturalist* **118**, 896-907.
- HERRERA, C. M. (1987). Vertebrate-dispersed plants of the Iberian Peninsula: A study of fruit characteristics. *Ecological Monographs* **57**, 305-331.
- HERRERA, C. M. (1989) Frugivory and seed dispersal by carnivorous mammals, and associated fruit characteristics in undisturbed Mediterranean habitats. *Oikos* **55**, 250-262.
- HEYDON, M. J. & BULLOH, P. (1997). Mousedeer densities in a tropical rainforest: the impact of selective logging. *Journal of Applied Ecology* **34**, 484-496.
- HIDE, R. L., PERNETTA, J. C. & SENABE, T. (1984). *Exploitation of wild animals. The Research Report of the Simbu Land Use Project, Vol. 4*. South Simbu: Studies in Demography, Nutrition, and Subsistence. I. A. S. E. R., Port Moresby, Papua New Guinea.
- HIGGINS, P. J. (1999). *Handbook of Australian, New Zealand and Antarctic Birds. Volume 4. Parrots to Dollarbird*. Oxford University Press, Melbourne, Australia.
- HIGGINS, P. J. & DAVIES, S. J. F. (1996). *Handbook of Australian, New Zealand and Antarctic Birds. Volume 3. Snipe to Pigeons*. Oxford University Press, Melbourne, Australia.
- HILL, M. O. (1979). *DECORANA - a Fortran program for detrended correspondence analysis and reciprocal averaging*. Cornell University, Ithaca, New York, USA.
- HIRAIWA-HASEGAWA, M. (1990). Role of food sharing between mother and infant in the ontogeny of feeding behaviour. In *The Chimpanzees of the Mahale Mountains: Sexual and Life-history Strategies* (ed. T. Nishada), pp. 267-275. University of Tokyo Press, Tokyo, Japan.
- HLADIK, C-M. (1977). A comparative study of the feeding strategies of two sympatric species of leaf monkeys: *Presbytis senex* and *Presbytis entellus*. In *Primate Ecology: Studies of Feeding and Ranging Behaviour in Lemurs, Monkeys and Apes* (ed. T. H. Clutton-Brock), pp. 324-353. Academic Press, London, UK.
- HLADIK, C-M. (1981). Diet and the evolution of feeding strategies among forest primates. In *Omnivorous Primates* (ed. R. S. O Harding and G. Telai), pp. 215-254. Columbia University Press, New York, USA.
- HNATIUK, S. H. (1978). Plant dispersal by the Aldabran giant tortoise *Geochelone gigantea* (Schweigger). *Oecologia* **36**, 345-350.
- HOLBROOK, N. M. & PUTZ, F. E. (1996). From epiphyte to tree: differences in leaf structure and leaf water relations with the transition in growth form in eight species of hemi-epiphytes. *Plant Cell and Environment* **19**, 631-642.
- HOLMES, G. (1987). *Avifauna of the Big Scrub Region*. New South Wales National Parks and Wildlife Service, Sydney, Australia.
- HOLMES, G. (1990). The biology and ecology of Coxen's fig parrot. *Royal Australian Ornithological Union Report* **65**, 1-34.
- HORN, H. S. (1966). Measurement of "overlap" in comparative ecological studies. *American Naturalist* **100**, 419-425.
- HORN, M. H. (1997). Evidence for dispersal of fig seeds by the fruit-eating characid fish *Brycon guatemalensis* Regan in a Cost Rican tropical rain forest. *Oecologia* **109**, 259-264.
- HOWE, H. F. (1977). Bird activity and seed dispersal of a tropical wet forest tree. *Ecology* **58**, 539-550.
- HOWE, H. F. (1983). *Rhamphastos swainsonii* (Dios Tede, Toucan de Swainson, Chestnut-mandibled Toucan). In *Costa Rican Natural History* (ed. D. H. Janzen), pp. 603-604. University of Chicago Press, Chicago, USA.
- HOWE, H. F. (1990). Seed dispersal by birds and mammals: implications for seedling demography. In *Reproductive Ecology of Tropical Forest Plants* (ed. K. S. Bawa and M. Hadley), pp. 191-218. UNESCO & Parthenon Publishing Group, Paris, France.
- HOWE, H. F. (1993). Specialised and generalised dispersal systems: where does 'the paradigm' stand? *Vegetatio* **107/108**, 3-13.
- HOWE, H. F. & ESTABROOK, G. F. (1977). On interspecific competition for avian dispersers in tropical trees. *American Naturalist* **111**, 817-832.
- HOWE, H. F., SCHUPP, E. W. & WESTLEY, L. C. (1985). Early consequences of seed dispersal for a neotropical tree (*Viola surinamensis*). *Ecology* **66**, 781-791.
- HOWE, H. F. & SMALLWOOD, J. (1982). Ecology of Seed Dispersal. *Annual Review of Ecology and Systematics* **13**, 201-228.
- HOWE, H. F., & VANDE KERCKHOVE, G. A. (1979). Fecundity and seed-dispersal of a tropical tree. *Ecology* **60**, 180-189.
- HUME, I. D. (1998). *Marsupial Nutrition*. Cambridge University Press, New York, USA.
- HUME, I. D., JAZWINSKI, E. & FLANNERY, T. F. (1993). Morphology and function of the digestive tract in New Guinea possums. *Australian Journal of Zoology* **41**, 85-100.
- HUTCHINS, B. R. & LOVELL, R. H. (1985). *Australian Parrots*. Avicultural Society of Australia, Melbourne, Australia.
- IDANI, G. (1986). Seed dispersal by Pygmy Chimpanzees (*Pan paniscus*): A preliminary report. *Primates* **27**, 441-447.
- INNIS, G. J. (1989). Feeding ecology of fruit pigeons in subtropical rainforests of South-east Queensland. *Australian Wildlife Research* **16**, 365-394.
- INNIS, G. J. & MCEVOY, J. (1992). Feeding ecology of Green Catbirds (*Ailuroedus crassirostris*) in subtropical rainforests of south-eastern Queensland. *Wildlife Research* **19**, 317-329.
- INOUE, T. & HAMID, A. A. (1994). *Plant reproductive systems and animal seasonal dynamics: Long-term study of dipterocarp forests in Sarawak*. Center for Ecological Research, Kyoto University, Kyoto, Japan.
- INOUE, T. & HAMID, A. A. (1995). The canopy biology program in Sarawak. *Inside CFS. Center for Tropical Forest Science of the Smithsonian Tropical Research Institute Fall 1995*, 7.
- INOUE, T., YUMOTO, T., HAMID, A. A., LEE, H. S. & OGINO, K. (1995). Construction of a canopy observation system in a tropical rainforest of Sarawak. *Selbyana* **16**, 24-35.
- ISLAM, M. A. & FEEROZ, M. M. (1992). Ecology of the Hoolock Gibbon. *Primates* **33**, 451-464.
- ISLER, M. L. & ISLER, P. R. (1999). *The Tanagers. Natural history, distribution, and identification*. Smithsonian Institution Press, Washington, D. C., USA.
- JACKSON, S. W. (1910). Additional notes on the Tooth-billed Bower-Bird (*Scenopactes dentiostria*) of North Queensland. *Emu* **10**, 81-88.
- JACOBS, G. H. (1996). Primate photopigments and primate color vision. *Proceedings of the National Academy of Sciences of the United States of America* **93**, 577-581.
- JACOBSON, N. H. G. & DUPLEISS, E. (1976). Observations on the ecology and the biology of the Cape fruit bat *Rousettus aegyptiacus leachi* in the Eastern Transvaal. *South African Journal of Science* **72**, 270-273.
- JANSON, C. H. (1983). Adaptation of fruit morphology to dispersal agents in a neotropical forest. *Science* **219**, 187-189.
- JANSON, C. H., STILES, E. W., WHITE, D. W. (1986). Selection on plant fruiting traits by brown capuchin monkeys: a multivariate approach. In *Frugivores and Seed Dispersal* (ed. T. H. Fleming and A. Estrada), pp. 82-92. Junk, Dordrecht, Netherlands.
- JANZEN, D. H. (1970). Herbivores and the number of tree species in tropical forests. *American Naturalist* **104**, 501-528.
- JANZEN, D. H. (1971). Seed predation by animals. *Annual Review of Ecology and Systematics* **2**, 465-492.
- JANZEN, D. H. (1979). How to be a fig. *Annual Review of Ecology and Systematics* **10**, 13-51.
- JANZEN, D. H. (1980). When is it coevolution? *Evolution* **34**, 611-612.
- JANZEN, D. H. (1981). *Ficus ovalis* seed predation by an orange-chinned parakeet (*Brotogeris jugularis*) in Costa Rica. *Auk* **98**, 841-844.
- JANZEN, D. H. (1983a). *Canis latrans* (Coyote). In *Costa Rican Natural History* (ed. D. H. Janzen), pp. 456-457. University of Chicago Press, Chicago, USA.
- JANZEN, D. H. (1983b). *Eira barbara* (Tolumuco, Tayra). In *Costa Rican Natural History* (ed. D. H. Janzen), pp. 469-470. University of Chicago Press, Chicago, USA.
- JANZEN, D. H. (1983c). *Odocoileus virginianus* (Venado, Venado Cola Blanca, White-tailed Deer). In *Costa Rican Natural History* (ed. D. H. Janzen), pp. 481-483. University of Chicago Press, Chicago, USA.
- JANZEN, D. H. (1983d). Seed and pollen dispersal by animals: convergence in the ecology of contamination and sloppy harvest. *Biological Journal of the Linnean Society* **20**, 103-113.
- JANZEN, D. H. (1985a). On ecological fitting. *Oikos* **45**, 308-310.
- JANZEN, D. H. (1985b). The natural history of mutualism. In *The Biology of Mutualism* (ed. D. H. Boucher), pp. 40-99. Oxford University Press, New York, USA.
- JANZEN, D. H. & MARTIN, P. S. (1982). Neotropical anachronisms: the fruits the gomphotheres ate. *Science* **215**, 19-27.
- JARMAN, H. (1953). The R.A.O.U. campout in central Australia. *Emu* **53**, 169-185.
- JOERN, A. & LAWLOR, L. R. (1981). Guild structure in grasshopper assemblages based on food and microhabitat resources. *Oikos* **37**, 93-104.
- JOHNS, A. D. (1981). Observations on nesting behaviour in the rhinoceros hornbill, *Buceros rhinoceros*. *Malayan Nature Journal* **35**, 173-177.
- JOHNS, A. D. (1983). Tropical forest primates and logging: can they co-exist? *Oryx* **17**, 114-118.
- JOHNS, A. D. (1987). The use of primary and selectively logged forest by Malaysian hornbills (Bucerotidae) and implications for their conservation. *Biological Conservation* **40**, 179-190.
- JOHNSGARD, P. A. (1999). *The Pheasants of the World*. Smithsonian Institution Press, Washington, D.C., USA.
- JONES, D. N., DEKKER, R. W. R. J., ROSELAAR, C. S. & PERLO, B. V. (1995). *The Megapodes*. Oxford University Press, Oxford, UK

- JONES JR, J. K., CHOATE, J. R. & CADENA, A. (1972). Mammals from the Mexican state of Sinaloa. II. Chiroptera. Occasional Papers of the Museum of Natural History, University of Kansas **6**, 1-29.
- JORDANO, P. (1983). Fig-seed predation and dispersal by birds. *Biotropica* **15**, 38-54.
- JORDANO, P. (1995). Angiosperm fleshy fruits and seed dispersers: a comparative analysis of adaptation and constraints in plant-animal interactions. *American Naturalist* **145**, 163-191.
- JOSHI, A. R., GARSHELIS, D. L. & SMITH, J. L. D. (1997). Seasonal and habitat-related diets of sloth bears in Nepal. *Journal of Mammalogy* **78**, 584-597.
- JOSHI, A. R., SMITH, J. L. D. & CUTHBERT, F. J. (1995). Influence of food distribution and predation pressure on spacing behaviour in palm civets. *Journal of Mammalogy* **76**, 1205-1212.
- JULIEN-LAFFERIERE, D. (1993). Radiotracking observations on ranging and foraging patterns by kinkajou (*Potos flavus*) in French Guiana. *Journal of Tropical Ecology* **9**, 19-32.
- JUNIPER, T. & PARR, M. (1998). *Parrots. A Guide to the Parrots of the World*. Pica Press, Sussex, UK.
- KALINA, J. (1988). Ecology and behaviour of the Black-and-white Casqued Hornbill (*Bycanistes subcylindricus*) in Kibale Forest, Uganda. Ph.D. thesis., Michigan State University, USA.
- KALKO, E. K. V., HERRE, E. A. & HANDLEY, C. O. J. (1996). Relation of fig fruit characteristics to fruit-eating bats in the New and Old World tropics. *Journal of Biogeography* **23**, 565-576.
- KAMEYAMA, T., HARRISON, R. D. & YAMAMURA, N. (1999). Persistence of fig wasp population and evolution of dioecy: a simulation study. *Researches on Population Ecology* **41**, 243-252.
- KANG, N. (1992). Radiotelemetry in an urban environment: a study of mynas (*Acridotheres* spp.) in Singapore. In *Wildlife Telemetry. Remote monitoring and tracking of animals* (ed. I. G. Priede and S. M. Swift), pp. 179-232. Ellis Horwood, Chichester, UK.
- KANNAN, R. (1994). Ecology and conservation of the Great Pied Hornbill in the Western Ghats of Southern India. Ph.D. thesis, University of Arkansas, USA.
- KANTAK, G. E. (1979). Observation on some fruit-eating birds in Mexico. *Auk* **96**, 183-186.
- KAPLIN, B. A., MUNYALIGOGA, V., MOERMOND, T. C. (1998). The influence of temporal changes in fruit availability on diet composition and seed handling in blue monkeys (*Cercopithecus mitis doggetti*). *Biotropica* **30**, 56-71.
- KAPPELER, M. (1984). Diet and feeding behaviour of the Moloch Gibbon. In *The Lesser Apes. Evolutionary and Behavioural Biology* (ed. H. Preuschoft, D. J. Chivers, W. Y. Brockelman and N. Creel), pp. 242-257. Edinburgh University Press, Edinburgh, UK.
- KAUFMANN, J. H. (1983). *Nasua narica* (Pizote, Coati). In *Costa Rican Natural History* (ed. D. H. Janzen), pp. 478-480. University of Chicago Press, Chicago, USA.
- KAUFMANN, S., MCKEY, D. B., HOSSAERT-MCKEY, M., HORVITZ, C. C. (1991). Adaptations for a two-phase seed dispersal system involving vertebrates and ants in a hemi-epiphytic fig (*Ficus microcarpa*, Moraceae). *American Journal of Botany* **78**, 971-977.
- KAUTH, M., ENGEL, S., LASTIMOZA, L. L. & CURIO, E. (1998). Observations on the breeding biology of the Writhed-billed Hornbill (*Aceros waldeni*) in the Philippines. *Journal of Ornithology* **139**, 475-483.
- KAWAMICHI, T. & KAWAMICHI, M. (1979). Spatial organisation and territoriality of tree shrews (*Tupaia glis*). *Animal Behaviour* **27**, 381-393.
- KAYS, R. W. (1999). Food preferences of kinkajou (*Potos flavus*): a frugivorous carnivore. *Journal of Mammalogy* **80**, 589-599.
- KEITH, S., URBAN, E. K. & FRY, C. H. (1992). *The Birds of Africa. Volume IV*. Academic Press, London, UK.
- KEMP, A. (1995) *The Hornbills*. Oxford University Press, Oxford, UK.
- KHADHARI, B., GIBERNAU, M., ANSTETT, M.-C., KJELLBERG, F. & HOSSAERT-MCKEY, M. (1995). When figs wait for pollinators: the length of fig receptivity. *American Journal of Botany* **82**, 992-999.
- KINGDON, J. (1971). *East African Mammals. An Atlas of Evolution in Africa. Volume I*. Academic Press, London, UK.
- KINGDON, J. (1974). *East African Mammals. An Atlas of Evolution in Africa. Volume II Part A (Insectivores and Bats)*. Academic Press, London, UK.
- KINGDON, J. (1977). *East African Mammals. An Atlas of Evolution in Africa. Volume III Part A (Carnivores)*. Academic Press, London, UK.
- KINGDON, J. (1979). *East African Mammals. An Atlas of Evolution in Africa. Volume III Part B (Large Mammals)*. Academic Press, London, UK.
- KINNAIRD, M. F. & O'BRIEN, T. G. (1993). Preliminary observation on the breeding ecology of the endemic Sulawesi Red-knobbed Hornbill. *Tropical Biodiversity* **1**, 107-112.
- KINNAIRD, M. F. & O'BRIEN, T. G. (1999). Breeding ecology of the Sulawesi Red Knobbed Hornbill *Aceros cassidix*. *Ibis* **141**, 60-69.
- KINNAIRD, M. F., O'BRIEN, T. G. & SURYADI, S. (1996). Population fluctuation in Sulawesi Red-knobbed Hornbill *Aceros cassidix*: tracking figs in space and time. *Auk* **113**, 431-440.
- KINNAIRD, M. F., O'BRIEN, T. G. & SURYADI, S. (1999). The importance of figs to Sulawesi's imperiled wildlife. *Tropical Biodiversity* **6**, 5-18.
- KITAMURA, S. (2000). Seed dispersal by hornbills in a tropical rain forest in Khao Yai National Park, Thailand. M.Sc. thesis, Graduate School of Science, Kyoto University, Kyoto, Japan.
- KJELLBERG, F., DOUMESCHE, B., BRONSTEIN, J. L. (1988). Longevity of a fig wasp (*Blastophaga psenes*). *Proceedings of the Koninklijke Nederlandse Akademie Van Wetenschappen Series C Biological and Medical Sciences* **91**, 117-122.
- KLEIN, L. L. & KLEIN, D. B. (1977). Feeding behaviour of the Columbian Spider Monkey *Ateles belzebuth*. In *Primate Ecology: Studies of Feeding and Ranging Behaviour in Lemurs, Monkeys and Apes* (ed. T. H. Clutton-Brock), pp. 153-141. Academic Press, London, UK.
- KO, I. W. P., CORLETT, R. T. & XU, R.-J. (1998). Sugar composition of wild fruits in Hong Kong, China. *Journal of Tropical Ecology* **14**, 381-387.
- KOCHUMMEN, K. M. (1983). Moraceae. In *Tree Flora of Malaya. Volume 3* (ed. F. S. P. Ng), pp. 135-162. Longman, Kuala Lumpur, Malaysia.
- KOFORD, C. B. (1983). *Felis wiedii* (Tigrillo, Causel, Margay). In *Costa Rican Natural History* (ed. D. H. Janzen), pp. 471-472. University of Chicago Press, Chicago, USA.
- KOHLHAAS, A. K. (1993). Behaviour and Ecology of *Macaca nigrescens*: Behavioural and Social Responses to the Environment and Fruit Availability. Ph.D. thesis, University of Colorado, USA.
- KORINE, C., IZHAKI, I. & ARAD, Z. (1999). Is the Egyptian fruit-bat *Rousettus aegyptiacus* a pest in Israel? An analysis of the bats' diet and implications for its conservation. *Biological Conservation* **88**, 301-306.
- KORINE, C., KALKO, E. K. V. & HERRE, E. A. (2000). Fruit characteristics and factors affecting fruit removal in a Panamanian community of strangler figs. *Oecologia* **123**, 560-568.
- KREFTING, L. W. & ROE, E. I. (1949). The role of some birds and mammals in seed germination. *Ecological Monographs* **19**, 269-286.
- KUMAR, S. & HEDGES, S. B. (1998). A molecular timescale for vertebrate evolution. *Nature* **392**, 917-920.
- LAFRANKIE, J. (1995). Initial findings from Lambir: Trees, soils and community dynamics *Inside CTFS. Center for Tropical Forest Science of the Smithsonian Tropical Research Institute Fall 1995*, 5.
- LAFRANKIE, J. V., TAN, S. & ASHTON, P. S. (1995). *Species List for the 52-ha Forest Dynamics Research Plot Lambir Hills National Park, Sarawak, Malaysia. Miscellaneous Internal Report (2/9/95)*. Center for Tropical Forest Science. Smithsonian Tropical Research Institute, Washington D.C., USA.
- LAMAN, T. G. (1994). The ecology of strangler figs (hemiepiphytic *Ficus* spp.) in the rain forest canopy of Borneo. Ph.D. thesis., Harvard University, Ann Arbor, USA.
- LAMAN, T. G. (1995). *Ficus stupenda* germination and seedling establishment in a Bornean rain forest canopy. *Ecology* **76**, 2617-2626.
- LAMAN, T. G. (1996a). *Ficus* seed shadows in a Bornean rain forest. *Oecologia* **107**, 347-355.
- LAMAN, T. G. (1996b) The impact of seed harvesting ants (*Pheidole* sp. nov) on *Ficus* establishment in the canopy. *Biotropica* **28**:777-781.
- LAMAN, T. G. (1997). Borneo's strangler fig trees. *National Geographic* **191**, 38-55.
- LAMBERT, F. R. (1987). Forest fig phenology and avian frugivores in Malaysia. Ph.D thesis., University of Aberdeen, Aberdeen, UK.
- LAMBERT, F. & WOODCOCK, M. (1996). *Pittas, Broadbills and Asities*. Pica Press, East Sussex, UK.
- LAMBERT, F. R. (1989a). Daily ranging behaviour of three tropical forest frugivores. *Forktail* **4**, 107-116.
- LAMBERT, F. R. (1989b). Fig-eating by birds in a Malaysian lowland forest. *Journal of Tropical Ecology* **5**, 401-412.
- LAMBERT, F. R. (1989c). Pigeons as seed predators and dispersers of figs in a Malaysian lowland forest. *Ibis* **131**, 521-527.
- LAMBERT, F. R. (1990). Some notes on fig-eating by arboreal mammals in Malaysia. *Primates* **31**, 453-458.
- LAMBERT, F. R. (1991). The conservation of fig-eating birds in Malaysia. *Biological Conservation* **58**, 31-40.
- LAMBERT, F. R. & MARSHALL, A. G. (1991). Keystone characteristics of bird-dispersed *Ficus* in a Malaysian lowland rain forest. *Journal of Ecology* **79**, 793-809.
- LAMONT, D. A. (1997). Unpublished M.Sc. Thesis. University of New England, Armidale, NSW.
- LANGRAND, O. (1990). *Guide to the birds of Madagascar*. Yale University Press, New Haven, USA.
- LAWRENCE, D. H. (1928). *The Collected Poems of D. H. Lawrence. Volume 2. Unrhyming Poems*. Martin Secker, London, UK.
- LEE, H. S. (1995). Long term ecological research in Sarawak, Malaysia. *Inside CTFS. Center for Tropical Forest Science of the Smithsonian Tropical Research Institute Fall 1995*, 4.
- LEE, H. S., ASHTON, P. S., OGINO, K. (1995). *Long Term Ecological Research of Tropical Rain Forest in Sarawak Reports of a New Program for Promotion of Basic Sciences. Studies of Global Environmental Change with Special Reference to Asia and Pacific Regions, Vol. 11-3*. Ehime, Japan.
- LEFRANC, N. & WORFDK, T. (1997). *Shrikes. A guide to the shrikes of the world*. Yale University Press, New Haven, USA.
- LEIGHTON, M. (1982). Fruit resources and patterns of feeding, spacing and grouping among sympatric Bornean hornbills (Bucerotidae). Ph.D. thesis, University of California, Davis, USA.
- LEIGHTON, M. (1986). Hornbill social dispersion: variations on a monogamous theme. In *Ecological Aspects of Social Evolution. Birds*

- and Mammals (ed. D. I. Rubenstein and R. W. Wrangham), pp. 108-130. Princeton University Press, New Jersey, USA.
- LEIGHTON, M. (1993). Modeling dietary selectivity by Bornean orangutans: evidence for integration of multiple criteria in fruit selection. *International Journal of Primatology* **14**, 257-313.
- LEIGHTON, M. & LEIGHTON, D. R. (1983). Vertebrate responses to fruiting seasonality within a Bornean rain forest. In *Tropical Rain Forest: Ecology and Management* (ed. S. L. Sutton, T. C. Whitmore, and A. C. Chadwick), pp. 181-196. Blackwell, Oxford, UK.
- LONDON, A. H. (1973). *Neville W. Cayley's Australian Parrots in Field and Aviary*. Angus and Robertson, Sydney, Australia.
- LEPSCHI, B. J. (1997). Food of some birds in southern Australia: Additions to Barker and Vestjens. 2. *Emu* **97**, 84-87.
- LEVEY, D. J. (1987). Seed size and fruit handling techniques of avian frugivores. *American Naturalist* **129**, 471-485.
- LI, G., ZHENG, B. & LIU, G. (1982). *Fauna Sinica, Aves Vol. 13, Passeriformes: Paridae-Zosteropidae*. Science Press, Beijing, China.
- LIEBERMAN, D., HALL, J. B., SWAINE, M. D. & LIEBERMAN, M. (1979). Seed dispersal by baboons in the Shai Hills, Ghana. *Ecology* **60**, 65-75.
- LIU, W. (1996). *Wildlife Resources of Tibet Series (1): Musk and Bear*. China Forestry Publishing House, Beijing, China.
- LONG, M. E. (1999). The shrinking world of hornbills. *National Geographic* **196**, 52-71.
- LORD, E. A. R. (1956). Birds of the Murphy's Creek district, Queensland. *Emu* **56**, 100-128.
- LU, T. C. (1991). *The Rare and Endangered Gamebirds in China*. Fujian Science and Technology Press, Fuzhou, China.
- LU, T. C. & CHANG, W. F. (1993). *Rare and endangered Galliformes of China*. Chung Thai Science and Technology Press, Taipei, Taiwan.
- MACHADO, C. A., JOUSSELIN, E., KJELLBERG, F., COMPTON, S. G. & HERRE, E. A. (2000). Phylogenetic relationships, historical biogeography and character evolution of fig-pollinating wasps. *Proceedings of the Royal Society of London Series B* **268**, 685-694.
- MACK, A. L. & WRIGHT, D. D. (1996). Notes on the occurrence and feeding of birds at Crater Mountain Biological Research Station, Papua New Guinea. *Emu* **96**, 89-101.
- MACK, A. L. & WRIGHT, D. D. (1998). The vulturine parrot, *Psittichas fulgidus*, a threatened New Guinea endemic: notes on its biology and conservation. *Bird Conservation International* **8**, 185-194.
- MACKINNON, J. & PHILLIPS, K. (1993). *A Field Guide to the Birds of Borneo, Sumatra, Java and Bali*. Oxford University Press Inc., New York, USA.
- MACKINNON, K., HATTA, G., HALIM, H. & MANGALIK, A. (1996). *The Ecology of Kalimantan. Indonesian Borneo*. Oxford University Press, Oxford, UK.
- MADGE, S. & BURN, H. (1994). *Crows and Jays. A Guide to the Crows, Jays and Magpies of the World*. Christopher Helm, London, UK.
- MAJNEP, I. S. & BULMER, R. (1990). *Kalam hunting traditions. Working Papers in Anthropology, Archaeology, Linguistics and Maori Studies No 86-91*. University of Auckland, Auckland, New Zealand.
- MARCONDES-MACHADO, L. O., PARANHOS, S. J. & DE MELOS BARROS, Y. (1994). Estrategias alimentares de aves na utilizacao de frutos fe *Ficus microcarpa* (Moraceae) em uma area Antropica. *Iheringia* **77**, 57-62.
- MARINHO-FILHO, J. S. (1991). The coexistence of two frugivorous bat species and the phenology of their food plants in Brazil. *Journal of Tropical Ecology*, **7**, 59-67.
- MARSHALL, A. G. (1985). Old World phytophagous bats (Megachiroptera) and their food plants: a survey. *Zoological Journal of the Linnean Society* **83**, 351-369.
- MARTINS, M. M. & SETZ, E. Z. F. (2000). Diet of buffy tufted-eared marmosets (*Callithrix aurita*) in a forest fragment in southeastern Brazil. *International Journal of Primatology* **21**, 467-476.
- MASON, C. W. & MAXWELL-LEFROY, H. (1912). The food of birds in India. *Memoir of the Department of Agriculture, India* **3**, 1-137.
- MAWDSLEY, N. A., COMPTON, S. G., WHITTAKER, R. J. (1998). Population persistence, pollination mutualisms, and figs in fragmented tropical landscapes. *Conservation Biology* **12**, 1416-1420.
- MAZER, S. J. & WHEELWRIGHT, N. T. (1993). Fruit size and shape: allometry at different taxonomic levels in bird-dispersed plants. *Evolutionary Ecology* **7**, 556-575.
- MCCANN, C. (1934). Notes on the flying fox (*Pteropus giganteus* Brunn). *Journal of the Bombay Natural History Society* **37**, 143-149.
- MCCLURE, H. E. (1966). Flowering, fruiting and animals in the canopy of a tropical rain forest. *Malaysian Forester* **29**, 192-203.
- MCCONKEY, K. R. (1999). Gibbons as seed dispersers in the rain-forests of central Borneo. Ph.D. thesis, University of Cambridge, Cambridge, UK.
- MCCONKEY, K. & GALETTI, M. (1999). Seed dispersal by the sun bear *Helarctos malayanus* in Central Borneo. *Journal of Tropical Ecology* **15**, 237-241.
- MCDADE, L. A., BAWA, K. S., HESPENHEIDE, H. A., HARTSHORN, G. S. (1994). *La Selva: Ecology and Natural History of a Neotropical Rain Forest*. University of Chicago Press, Chicago, USA.
- MCFARLAND-SYMMINGTON, M. (1988). Food competition and foraging party size in the Black Spider Monkey (*Ateles paniscus* Chamek). *Behaviour* **105**, 117-134.
- MCGILP, J. N. (1944). Bird life west of Oodnadatta, South Australia. *South Australian Ornithologist* **17**, 1-8.
- MCGREGOR, R. C. (1909). *A manual of Philippine birds. Galliformes to Eurylaimiformes*. Bureau of Printing, Manila, Philippines.
- MCKEY, D. (1975). The ecology of coevolved seed dispersal systems. In *Coevolution of Animals and Plants* (ed. L. E. Gilbert and P. H. Raven), pp. 159-191. University of Texas Press, Austin, USA.
- MCKEY, D. (1989). Population biology of figs: Applications for conservation. *Experientia* **45**, 661-673.
- MCLENNON, W. (1917). Northern Australian birds. *Emu* **16**, 205-231.
- MEDELLIN, R. A. (1994). Seed dispersal of *Cecropia obtusifolia* by two species of opossums in the Selva Lacandona, Chiapas, Mexico. *Biotropica* **26**, 400-407.
- MEDWAY, LORD. (1972). Phenology of a tropical forest in Malaysia. *Biological Journal of the Linnean Society* **4**, 117-146.
- MEDWAY, LORD. & WELLS, D. R. (1971). Diversity and density of birds and mammals at Kuala Lompat, Pahang. *Malayan Nature Journal* **24**, 238-247.
- MEIJER, W. (1969). Fruit trees in Sabah. *Malayan Forester* **32**, 232-265.
- MEINERTZHAGEN, R. (1954). *Birds of Arabia*. Oliver & Boyd, Edinburgh, UK.
- MENON, S. A. (1993). Ecology and Conservation of the Endangered Lion-tailed Macaque (*Macaca silenus*) in the Landscapes Mosaic of the Western Ghats. Ph.D. thesis, Ohio State University, USA.
- MENZIES, J. I. & PERNETTA, J. C. (1986). A taxonomic revision of cuscuses allied to *Phalanger orientalis* (Marsupialia: Phalangeridae). *Journal of Zoology (London) (B)* **1**, 551-618.
- MERCHANT, J. C. (1983). Agile Wallaby. In *The Australian Museum Complete Book of Australian Mammals* (ed. R. Strahan), pp. 242-243. Angus & Robertson, Sydney, Australia.
- MERRITT, P. G. (1980). Group foraging by Mockingbirds in a Florida stranger fig. *Auk* **97**, 869-872.
- MICHALOUD, G., CARRIERE, S., KOOBI, M. (1996). Exceptions to the one:one relationship between African fig trees and their fig wasp pollinators: possible evolutionary scenarios. *Journal of Biogeography* **23**, 513-520.
- MICKLEBURGH, S. P., HUTSON, A. M. & RACEY, P. A. (1992). *Old World Fruit Bats: An Action Plan for their Conservation*. IUCN, Gland, Switzerland.
- MICROSOFT. (1997). *Excel 97 SR-2*. Microsoft Corporation, Seattle, USA.
- MIDYA, S. & BRAHMACHARY, R. L. (1991). The effect of birds upon the germination of banyan (*Ficus bengalensis*) seeds. *Journal of Tropical Ecology* **7**, 537-538.
- MILLIKEN, W., RATTER, J. A. (1998). *Maraca: the biodiversity and environment of an Amazonian rainforest*. John Wiley and Sons, Chichester, UK.
- MILTON, K. (1981). Food choice and digestive strategies of two sympatric primate species. *American Naturalist* **117**, 496-505.
- MILTON, K. & MAY, M. L. (1976). Body weight, diet and home range area in primates. *Nature* **259**, 459-462.
- MILTON, K., WINDSOR, D. M., MORRISON, D. W. & ESTRIBI, M. (1982). Fruiting phenologies of two neotropical *Ficus* species. *Ecology* **63**, 752-762.
- MITCHELL, A. H. (1994). Ecology of Hose's Langur, *Presbytis hosei*, in Mixed Logged and Unlogged Dipterocarp Forest of Northeast Borneo. Ph.D. thesis, Yale University, New Haven, USA.
- MOERMOND, T. C. & DENSLow, J. S. (1983). Fruit choice in Neotropical birds: effects of fruit type and accessibility on selectivity. *Journal of Animal Ecology* **52**, 407-420.
- MOERMOND, T. C., DENSLow, J. S., LEVEY, D. J. & SANTANA, C. E. (1986). The influence of morphology on fruit choice in neotropical birds. In *Frugivores and Seed Dispersal* (ed. A. Estrada and T. H. Fleming), pp. 137-146. Junk, Dordrecht, Netherlands.
- MOLL, D. & JANSEN, K. P. (1995). Evidence for a role in seed dispersal by two tropical herbivorous turtles. *Biotropica* **27**, 121-127.
- MOMOSE, K. & INOUE, T. (1994). Pollination syndromes in the plant-pollinator community in the lowland mixed dipterocarp forests of Sarawak. In *Plant reproductive systems and animal seasonal dynamics. Long term study of dipterocarp forests in Sarawak* (ed. T. Inoue and A. A. Hamid), pp. 119-141. Center for Ecological Research, Kyoto University, Kyoto, Japan.
- MONDOLFI, E. (1989). Notes on the distribution, habitat, food habits, status and conservation of spectacled bears (*Tremarctos ornatus* Cuvier) in Venezuela. *Mammalia* **53**, 525-544.
- MORRISON, D. W. (1978). Foraging ecology and energetics of the frugivorous bat *Artibeus jamaicensis*. *Ecology* **59**, 716-723.
- MORRISON, D. W. (1980). Efficiency of food utilisation by fruit bats. *Oecologia* **45**, 270-273.
- MOSKOVITS, D. (1998). Population ecology of the tortoises *Geochelone carbonaria* and *G. denticulata* on the Ilha de Maracá. In *Maracá. The Biodiversity and Environment of an Amazonian Rainforest* (ed. W. Milliken and J. A. Ratter), pp. 263-284. John Wiley & Sons Ltd., Chichester, UK.
- NAIR, N. G., ELANGOVAN, V., SRIPATHI, K., MARIMUTHU, G. & SUBBARAJ, R. (1999). Foraging behaviour of the Indian short-nosed fruit bat *Cynopterus sphinx*. *Zeitschrift für Säugetierkunde* **64**, 187-191.
- NARANJO, E. (1995). Hábitos de alimentación del tapir (*Tapirus bairdii*) en un bosque tropical húmedo de Costa Rica. *Vida Silvestre Neotropical* **4**, 32-37.

- NASON, J. D., HERRE, E. A. & HAMRICK, J. L. (1996). Paternity analysis of the breeding structure of strangler fig populations: evidence for substantial long-distance wasp dispersal. *Journal of Biogeography* **23**, 501-512.
- NASON, J. D., HERRE, E. A. & HAMRICK, J. L. (1998). The breeding structure of a tropical keystone resource. *Nature* **391**, 685-687.
- NATIONAL RESEARCH COUNCIL (1983). *Little-known Asian Animals with a Promising Economic Future*. National Academy of Sciences, Washington, D.C., USA
- NEWHAM, A. (1911). Hornbills devouring young paroquets. *Journal of the Bombay Natural History Society* **21**, 263-264.
- NEWTON-FISHER, N. E. (1999). The diet of chimpanzees in the Budongo Forest Reserve, Uganda. *African Journal of Ecology* **37**, 344-354.
- NHAT, P. (1994). Preliminary results on the diet of the red-shanked douc langur (*Pygathrix nemaeus*). *Asian Primates* **4**, 1.
- NOGALES, M., HERNÁNDEZ, E. C. & VALDÉS, F. (1999). Seed dispersal by common ravens *Corvus corax* among island habitats (Canarian Archipelago). *Ecoscience* **6**, 56-61.
- NORTON, J. (1897). Magpies (Black and Grey). *Agricultural Gazette of New South Wales* **8**, 535-537.
- NOVAK, R. M. & PARADISO, J. L. (1983). *Walker's Mammals of the World. 4th Edition*. The Johns Hopkins University Press, Baltimore, USA.
- OATES, J. F. (1977). The Guereza and its food. In *Primate Ecology: Studies of Feeding and Ranging Behaviour in Lemurs, Monkeys and Apes*. (ed. T. H. Clutton-Brock), pp. 276-321. Academic Press, London, UK.
- O'BRIEN, T. G., KINNAIRD, M. F., DIERENFELD, E. S., CONKLIN-BRITTAİN, N. L., WRANGHAM, R. W. & SILVER, S. C. (1998a). What's so special about figs? *Nature* **392**, 668.
- O'BRIEN, T., KINNAIRD, M. F., JEPSON, P. & SETIAWAN, I. (1998b). Effect of forest size and structure on the distribution of Sumba Wreathed Hornbills *Aceros everetti*. In *The Asian Hornbills: Ecology and Conservation* (ed. P. Poonswad), pp. 209-217. Biodiversity Research and Training Program, National Center for Genetic Engineering and Biotechnology, Bangkok, Thailand.
- O'DOWD, D. J., GILL, A. M. (1986). Seed dispersal syndromes in Australian *Acacia*. In *Seed Dispersal* (ed. D. R. Murray), pp. 87-121. Academic Press, Sydney, Australia.
- OKON, E. E. (1977). Functional anatomy of the alimentary canal in the fruit bat *Eidolon helvum* and the insect bat *Tadarida nigrianae*. *Acta Zoologica* **58**, 83-93.
- OLSON, S. L. (1985). The fossil record of birds. In *Avian Biology Vol. 8* (ed. D. S. Farner, J. R. King and K. L. Parkes), pp. 79-238. Academic Press, Orlando, Florida, USA.
- OLSON, S. L. & BLUM, K. E. (1968). Avian dispersal of plants in Panama. *Ecology* **49**, 565-566.
- OLUPOOT, W., WASER, P. M. & CHAPMAN, C. A. (1998). Fruit finding by mangabeys (*Lophocebus albigena*): Are monitoring of fig trees and use of sympatric frugivore calls possible strategies? *International Journal of Primatology* **19**, 339-353.
- OPPENHEIMER, J. R. (1982). *Cebus capucinus*: Home range, population dynamics, and interspecific relationships. In *The Ecology of a Tropical Forest. Seasonal Rhythms and Long-term Changes*. (ed. E. G. Leigh Jr, A. S. Rand and D. M. Windsor), pp. 253-272. Smithsonian Institution Press, Washington D.C., USA.
- OSBORNE, P. L. & MURPHY, R. (1989). Botanical colonisation of Motmot island, Lake Wisdom, Madang Province. *Science in New Guinea* **15**, 57-63.
- OSMASTON, H. A. (1965). Pollen and seed dispersal in *Chlorophora excelsa* and other Moraceae, and in *Parkia filicoidea* (Mimosaceae), with special reference to the role of the fruit bat, *Eidolon helvum*. *Commonwealth Forestry Review* **44**, 96-103.
- PACHECO, L. F. & SIMONETTI, J. A. (2000). Genetic structure of a mimosoid tree deprived of its seed disperser, the spider monkey. *Conservation Biology* **14**, 1766-1775.
- PAIN, C. F., BLONG, R. J. & MCKEE, C. O. (1981). Pyroclastic deposits and eruptive sequences on Long Island, Papua New Guinea. Part 1. Lithology, stratigraphy and volcanology. (Cooke-Ravian Volume of Geological Survey of Papua New Guinea Memoir **10**, 101-107.
- PAINE, R. T. (1966). Food web complexity and species diversity. *American Naturalist* **100**, 65-75.
- PAINE, R. T. (1969). A note on trophic complexity and species diversity. *American Naturalist* **103**, 91-93.
- PALMER, C., PRICE, O. & BACH, C. (2000). Foraging ecology of the black flying fox (*Pteropus alecto*) in the seasonal tropics of the Northern Territory, Australia. *Wildlife Research* **27**, 169-178.
- PALMEIRIM, J. M., GORCHOV, D. L. & STOLESON, S. (1989). Trophic structure of a Neotropical frugivore community: Is there competition between birds and bats? *Oecologia* **79**, 403-411.
- PALMIOTTO, P., VOGT, K. & OLANDER, L. (1995). Nutrient cycling, ecophysiology and habitat heterogeneity. *Inside CTFS. Center for Tropical Forest Science of the Smithsonian Tropical Research Institute Fall 1995*, 6.
- PALOMBIT, R. A. (1997). Inter- and intraspecific variation in the diets of sympatric siamang (*Hylobates syndactylus*) and lar gibbons (*Hylobates lar*). *Folia Primatologica* **68**, 321-337.
- PANG, Y., YOUNG, T. & KANG, B. (1980). *Yunnan Nialolei Minglu*. Yunnan Scientific Press, Yunnan, China.
- PASCHOAL, M. & GALETTI, M. (1995). Seasonal food use by the neotropical ground squirrel *Sciurus ingrami* in southeastern Brazil. *Biotropica* **27**, 268-273.
- PATEL, A. (1996). Variation in a mutualism: phenology and the maintenance gynodioecy in two Indian fig species. *Journal of Ecology* **84**, 667-680.
- PATEL, A. (1997). Phenological patterns of *Ficus* in relation to other forest trees in southern India. *Journal of Tropical Ecology*, **13**, 681-695.
- PATINO, S., HERRE, E. A. & TYREE, M. T. (1994). Physiological determinants of *Ficus* fruit temperature and the implications for survival of pollinator wasp species: comparative physiology through an energy budget approach. *Oecologia* **100**, 13-20.
- PAYNE, J. B. (1979). Synecology of Malayan tree squirrels with special reference to the genus *Ratufa*. Ph.D. thesis, Cambridge University, Cambridge, UK.
- PAYNE, J., FRANCIS, C. M. & PHILLIPPS, K. (1985). *A Field Guide to the Mammals of Borneo*. The Sabah Society & WWF Malaysia, Kota Kinabalu, Malaysia.
- PERES, C. A. (1993). Diet and feeding ecology of saddle-back (*Saguinus fuscicollis*) and moustached (*Saguinus mystax*) tamarins in an Amazonian terra firme forest. *Journal of Zoology* **230**, 567-592.
- PERRINS, C. M. (1990). *The Illustrated Encyclopedia of Birds*. Headline Book Publishing plc., London, UK.
- PHILLIPS, J. F. V. (1928). Turacos *Corythaix corythaix* ("Lourie") in the Knysna forests. *South African Journal of Science* **25**, 295-299.
- PIANKA, E. R. (1973). The structure of lizard communities. *Annual Review of Ecology and Systematics* **4**, 53-74.
- POONSWAD, P., TSUJI, A. & NGARMPONGSAI, C. (1988). A comparative ecological study of four sympatric hornbills (Family Bucerotidae) in Thailand. *Acta XIX congressus Internationalis Ornithologi* **2**, 2781-2791.
- POONSWAD, P., CHUAILUA, P., PLONGMAI, K. & NAKKUNTOD, S. (1998a). Phenology of some *Ficus* species and utilisation of *Ficus* sources in Khao Yai National Park, Thailand. In *The Asian Hornbills: Ecology and Conservation* (ed. P. Poonswad), pp. 227-252. Biodiversity Research and Training Program, National Center for Genetic Engineering and Biotechnology, Bangkok, Thailand.
- POONSWAD, P. & TSUJI, A. (1994). Ranges of males of the Great Hornbill *Buceros bicornis*, Brown Hornbill *Ptilolaemus tickelli* and Wreathed Hornbill *Rhyticeros undulatus* in Khao Yai National Park, Thailand. *Ibis* **136**, 79-86.
- POWER, M. E., TILMAN, D., ESTES, J. A., MENGE, B. A., BOND, W. J., MILLS, L. S., DAILY, G., CASTILLA, J. C., LUBCHENCO, J. & PAINE, R. T. (1996). Challenges in the quest for keystones. *Bioscience* **46**, 609-620.
- POONSWAD, P., TSUJI, A., JIRAWATKAVI, N. & CHIMCHOME, V. (1998b). Some aspects of food and feeding ecology of sympatric hornbill species in Khao Yai National Park, Thailand. In *The Asian Hornbills: Ecology and Conservation* (ed. P. Poonswad), pp. 137-153. Biodiversity Research and Training Program, National Center for Genetic Engineering and Biotechnology, Bangkok, Thailand.
- PRATT, T. K. & STILES, E. W. (1985). The influence of fruit size and structure on the composition of frugivore assemblages in New Guinea. *Biotropica* **17**, 314-321.
- PRICE, M. V. & JENKINS, S. H. (1986). Rodents as seed consumers and dispersers. In *Seed Dispersal* (ed. D. R. Murray), pp. 191-235. Academic Press, Sydney, Australia.
- PRIMACK, R. B. (1983). *Forester's guide to the Moraceae of Sarawak*. Forest Department, Kuching, Sarawak, Malaysia.
- PROCTOR, V. W. (1968). Long-distance dispersal of seeds by retention in the digestive tract of birds. *Science* **160**, 321-322.
- PUTZ, F. E. & APPANAH, S. (1987). Buried seeds, dispersed seeds, and the dynamics of a lowland forest in Malaysia. *Biotropica* **19**, 326-333.
- QURIS, R. (1975). Ecologie et organisation sociale de *Cercopithecus galeritus agilis* dans le Nord-Est du Gabon. Thesis de 3^e cycle, Université de Rennes, Rennes, France
- RABINOWITZ, A. R. (1991). Behaviour and movements of sympatric civet species in Huai Kha Khaeng Wildlife Sanctuary, Thailand. *Journal of Zoology* **223**, 281-298.
- RACEY, P. A. & NICOLL, M. E. (1984). Mammals. In *Biogeography and ecology of the Seychelles Islands* (ed. D. R. Stoddart), pp. 361-364. Junk Press, Leiden, Netherlands.
- RAEMAEKERS, J. (1984). Large versus small gibbons: relative roles of bioenergetics and competition in their ecological segregation in sympatry. In *The Lesser Apes. Evolutionary and Behavioural Biology* (ed. H. Preuschoft, D. J. Chivers, W. Y. Brockelman and N. Creel), pp. 209-218. Edinburgh University Press, Edinburgh, UK
- RAFFAELE, H., WILEY, J., GARRIDO, O., KEITH, A. & RAFFAELE, J. (1998). *Bird of the West Indies*. Christopher Helm, London, UK.
- RANGER, G. (1950). Life of the crowned hornbill. *Ostrich* **21**, 2-13.
- RATCLIFFE, F. N. (1932). Notes on the fruit bats (*Pteropus* spp.) of Australia. *Journal of Animal Ecology* **1**, 32-57.
- REYNOLDS, V. & REYNOLDS, F. (1965). Chimpanzees of the Budongo Forest. In *Primate Behaviour. Field Studies of Monkeys and Apes* (ed. I. De Vore), pp. 368-424. Holt, Reinhart and Winston, New York, USA.
- RIDLEY, H. N. (1930). *The Dispersal of Plants Throughout the World*. L. Reeve & Co., Kent, UK.
- ROBBINS, M. (1993). *Birds of the World*. Dorling Kindersley, New York, USA.

- ROBERTS, J. T. & HEITHAUS, E. R. (1986). Ants rearrange the vertebrate-generated seed shadow of a neotropical fig tree. *Ecology* **67**, 1046-1051.
- ROBERTS, T. J. (1992a). *The Birds of Pakistan, Vol. 1. Regional Studies and Non-Passeriformes*. Oxford University Press, Oxford, UK.
- ROBERTS, T. J. (1992b). *The Birds of Pakistan, Vol. 2. Passeriformes, Pittas to Buntings*. Oxford University Press
- ROBINET, O., BARRE, N. & SALAS, M. (1996). Population estimate for the Ouvea parakeet *Eumyphicus cornutus uvaeensis*: its present range and implications for conservation. *Emu* **96**, 151-157.
- ROGERS, M. E., MAISELS, F., WILLIAMSON, E. A., FERNANDEZ, M., TUTIN, C. E. G. (1990). Gorilla diet in the Lope Reserve, Gabon: A nutritional analysis. *Oecologia* **84**, 326-339.
- ROMO, M. C. (1996). Seasonal variation in fruit consumption and seed dispersal by canopy bats (*Artibeus* spp.) in a lowland forest in Peru. *Vida Silvestre Neotropical* **5**, 110-119.
- ROOT, R. B. (1967). The niche exploitation pattern of the blue-headed flycatcher. *Ecological Monographs* **37**, 317-350.
- ROSE, A. B. (1973). Food of some Australian birds. *Emu* **73**, 177-183.
- RUSSELL, J. K. (1982). Timing of reproduction by coatis (*Nasua narica*) in relation to fluctuations in food resources. In *The Ecology of a Tropical Forest. Seasonal Rhythms and Long-term Changes*. (ed. E. G. Leigh Jr, A. S. Rand and D. M. Windsor), pp. 413-431. Smithsonian Institution Press, Washington D.C., USA.
- SAKAI, S., MOMOSE, K., YUMOTO, T., NAGAMITSU, T., NAGAMASU, H., HAMID, A. A. & NAKASHIZUKA, T. (1999). Plant reproductive phenology over four years including an episode of general flowering in a lowland dipterocarp forest, Sarawak, Malaysia. *American Journal of Botany* **86**, 1414-1436.
- SALAS, L. A. & FULLER, T. K. (1996). Diet of the lowland tapir (*Tapirus terrestris* L.) in the Tabaro Valley, southern Venezuela. *Canadian Journal of Zoology* **74**, 1444-1451.
- SÁNCHEZ-CORDERO, V. & MARTINEZ-GALLARDO, R. (1998). Postdispersal fruit and seed removal by forest-dwelling rodents in a lowland rainforest in Mexico. *Journal of Tropical Ecology* **14**, 139-151.
- SAS INSTITUTE INC. (1985) *SAS User's Guide: Statistics*. SAS Institute Inc., Cary, North Carolina, USA.
- SAUNDERS, C. R. (1985). Interactions between Grey and Purple-crested Louries. *Honeyguide* **31**, 108.
- SCHIPPER, C., SHANAHAN, M., COOK, S. & THORNTON, I. W. B. (in review). Colonisation of an exploded island volcano, Long I., Papua New Guinea, and an emergent island, Motmot, in its caldera lake: a nested natural experiment. III. Birds. *Journal of Biogeography*.
- SCHLEGEL, H. & MULLER, S. (1845). Over drie buideldieren uit de familie der Kengeroe's. In *Verhandelingen over de Natuurlijke over de Geschiedenis de Nederlandsche Overzeesche Bezittingen door de Leden natuurkundige commissie in India andore Schrijvers* (ed. C. J. Temminck), pp. 129-148. Leiden, Netherlands.
- SCHOENER, T. W. (1968). Sizes of feeding territories among birds. *Ecology* **49**, 123-141.
- SCHOLTZ, C. H. (1972). Grey hornbill (R424) feeding on peanuts. *Lanarius* **3**, 3.
- SCHOMBURGK, R. (1848). *Reisen in Britisch-Guiana in dem Jahren 1840-1844. Part 3*. J. J. Weber, Leipzig, Germany.
- SCHULZ, J. (1999). Fruit-eating birds and mammals on Pacific islands. Unpublished B.Sc. thesis, University of Leeds, Leeds, UK.
- SCHUPP, E. W. (1993). Quantity, quality and the effectiveness of seed dispersal by animals. *Vegetatio* **107/108**, 15-29.
- SCOTT, E. & MARTIN, R. F. (1984). Avian consumers of *Bursera*, *Ficus* and *Ehretia* fruits in Yucatan. *Biotropica* **16**, 319-323.
- SHANAHAN, M. (1997). Fruit characters, frugivory and seed dispersal of Bornean figs (*Ficus*, Moraceae). Unpublished MSc thesis, University of Leeds, Leeds, UK.
- SHANAHAN, M. & COMPTON, S. G. (in press a). Fig-eating by Bornean treeshrews (*Tupaia* spp.): evidence for a role as seed dispersers. *Biotropica*
- SHANAHAN, M. & COMPTON, S. G. (in press b). Vertical stratification of figs and fig-eaters in a Bornean lowland rainforest: how is the canopy different? *Plant Ecology*
- SHANAHAN, M. & COMPTON, S. G. (in review). Fruiting strangler figs reveal declines in large frugivores in a protected Bornean rain forest. *Conservation Biology*
- SHANAHAN, M. & DEBSKI, I. (in press). Vertebrates of Lambir Hills National Park, Sarawak. *Malayan Nature Journal*.
- SHANAHAN, M., HARRISON, R. D., YAMUNA, R., THORNTON, I. W. B. (in review). Colonisation of an island volcano, Long I, Papua New Guinea, and an emergent island, Motmot, in its caldera lake: a nested natural experiment. V. Colonisation by figs (*Ficus* species). *Journal of Biogeography*.
- SHANAHAN, M. & SO, S. N. G. (in review). Fig-eating by vertebrate frugivores: a global review. *Biological Reviews*.
- SHILTON, L. A. (1999). Seed dispersal by fruit bats on the Krakatau Islands, Indonesia. Ph.D. thesis, University of Leeds, Leeds, UK.
- SHILTON, L. A., ALTRINGHAM, J. D., COMPTON, S. G. & WHITTAKER, R. J. (1999). Old World fruit bats can be long-distance seed dispersers through extended retention of viable seeds in the gut. *Proceedings of the Royal Society of London Series B* **266**, 219-233.
- SIBLEY, C. G. & MONROE JR, B. L. (1990). *Distribution and Taxonomy of Birds of the World*. Yale University Press, New Haven, USA.
- SIBLEY, C. G. & MONROE JR, B. L. (1993). *A Supplement to Distribution and Taxonomy of Birds of the World*. Yale University Press, New Haven, USA.
- SILVER, S. C., OSTRO, L. E. T., YEAGER, C. P. & DIERENFELD, E. S. (2000). Phytochemical and mineral components of foods consumed by black howler monkeys (*Alouatta pigra*) at two sites in Belize. *Zoo Biology* **19**, 95-109.
- SKINNER, J. D. & SMITHERS, R. H. N. (1990). *The Mammals of the Southern African Subregion*. University of Pretoria, Pretoria, South Africa.
- SLOCUM, M. G. & HORVITZ, C. C. (2000). Seed arrival under different genera of trees in a neotropical pasture. *Plant Ecology* **149**, 51-62.
- SMITH, C. C. (1977). Feeding behaviour and social organisation in howling monkeys. In *Primate Ecology: Studies of Feeding and Ranging Behaviour in Lemurs, Monkeys and Apes* (ed. T. H. Clutton-Brock), pp. 97-126. Academic Press, London, UK.
- SMITH, D. S. & HOOD, C. S. (1981). Preliminary notes on bats from the Bismarck Archipelago (Mammalia: Chiroptera). *Science in New Guinea* **8**, 81-121.
- SMYTHE, N. (1986). Competition and resource partitioning in a guild of neotropical terrestrial frugivorous mammals. *Annual Review of Ecology and Systematics* **17**, 169-188.
- SMYTHIES, B. E. (1960). *Birds of Borneo*. Oliver & Boyd Ltd, Edinburgh, UK.
- SNOW, B. K. & SNOW, D. W. (1971). The feeding ecology of tanagers and honeycreepers in Trinidad. *Auk* **88**, 291-322.
- SNOW, B. & SNOW, D. (1988). *Birds and Berries. A Study of an Ecological Interaction*. T & A.D. Poyser, Calton, UK.
- SNOW, D. W. (1971). Evolutionary aspects of fruit-eating in birds. *Ibis* **113**, 194-202.
- SNOW, D. W. (1980). Regional differences between tropical floras and the evolution of frugivory. *Acta XVII Congressus Internationalis Ornithologi* **1**, 1185-1191.
- SNOW, D. W. (1981). Tropical frugivorous birds and their food plants: a world survey. *Biotropica* **13**, 1-14.
- SNOW, D. (1982). *The Cotingas*. Oxford University Press, Oxford, UK.
- SO, N. H. S. (1999). Birds and figs in Hong Kong. M. Phil thesis. The University of Hong Kong, Hong Kong.
- SOUTHWICK, C. H., BEG, M. A. & SIDDIQI, M. R. (1965). Rhesus monkeys in North India. In *Primate Behaviour. Field Studies of Monkeys and Apes* (ed. I. DeVore), pp. 111-159
- SOWLS, L. K. (1983). *Tayassu tajacu* (Saino, Collared Peccary). In *Costa Rican Natural History* (ed. D. H. Janzen), pp. 497-498. University of Chicago Press, Chicago, USA.
- SPECHT, J., BALL, E. E., BLONG, R. J., EGLOFF, B. J., HUGHES, I. M., MCKEE, C. O. & PAIN, C. F. (1982). Long Island, Papua New Guinea: Introduction. *Records of the Australian Museum* **34**, 407-417.
- SPENCER, H. J. & FLEMING, T. H. (1989). Roosting and foraging behaviour of the Queensland Tube-nosed bat, *Nyctimene robinsoni* (Pteropodidae): Preliminary radio-tracking observations. *Australian Wildlife Research* **16**, 413-420.
- SPENCER, H., WEIBLEN, G. & FLICK, B. (1996). Phenology of *Ficus variegata* in a seasonal wet tropical forest at Cape Tribulation, Australia. *Journal of Biogeography* **23**, 467-475.
- SPSS. (1997). *Systat 7.0 for Windows*. SPSS inc., Chicago, USA.
- SRIKOSAMATARA, S. (1984). Ecology of Pileated Gibbons in South-East Thailand. In *The Lesser Apes. Evolutionary and Behavioural Biology* (ed. H. Preuschoft, D. J. Chivers, W. Y. Brockelman and N. Creel), pp. 242-257. Edinburgh University Press, Edinburgh, UK.
- STADDON, S. (2000). Seed dispersal in the Pacific Banyan *Ficus prolixa*: the effectiveness of frugivores as dispersal agents and the importance of seed disperser mutualisms. M.Sc. thesis, Leeds, UK.
- START, A.N. & FULLER, P. J. (1983). Birds. *Wildlife Research Bulletin, Western Australia* **12**, 94-108.
- STEVENSON, P. R., QUINONES, M. J. & AHUMADA, J. A. (1998). Annual variation in fruiting pattern using two different methods in a lowland tropical forest, Tinigua National Park, Colombia. *Biotropica* **30**, 129-134.
- STILES, F. G. & SKUTCH, A. F. (1989). *A Guide to the Birds of Costa Rica*. Comstock Publishing Associates (Cornell University Press), New York, UK.
- STOCKER, G. C. & IRVINE, A. K. (1983). Seed dispersal by cassowaries (*Casuarus casuarus*) in north Queensland's rainforest. *Biotropica* **15**, 170-176.
- STONES, W. & ROBERTS, H. R. (1935). Zoological results of the Mato Grosso expedition to Brazil in 1931. II Birds. *Proceedings of the Academy of Natural Sciences of Philadelphia* **86**, 363-394.
- STOTT, K. (1947). Notes on the Philippine Brown Hornbill. *Condor* **49**, 35.
- STRUHSAKER, T. (1997). *Ecology of an African Rain Forest: Logging in Kibale and the Conflict between Conservation and Exploitation*. University Press of Florida, Gainesville, USA.
- SUBRAMANYA, S. & PRASAD, J. N. (1994). Yellow-throated bulbul at Horsley Hills. *Journal of the Bombay Natural History Society* **93**, 55-58.
- SUN, C. & MOERMOND, T. C. (1997). Foraging ecology of three sympatric turacos in a montane forest in Rwanda. *The Auk* **114**, 396-404.
- SUSSMAN, R. W. (1975). A preliminary study of the behaviour and ecology of *Lemur fulvus rufus* Audebret 1860. In *Lemur Biology* (ed. I.

- Tattersall and R. W. Sussman, pp. 237-258. Plenum Press, New York, USA.
- SUSSMAN, R. W. (1977). Feeding behaviour of *Lemur catta* and *Lemur fulvus*. In *Primate Ecology: Studies of Feeding and Ranging Behaviour in Lemurs, Monkeys and Apes* (ed. T. H. Clutton-Brock), pp. 1-36. Academic Press, London, UK.
- TAN, K. H., ZUBAID, A. & KUNZ, T. H. (1998). Food habits of *Cynopterus brachyotis* (Muller) (Chiroptera: Pteropodidae) in Peninsular Malaysia. *Journal of Tropical Ecology* **14**, 299-307.
- TANG, C. (1996). *Birds of the Hengduan Mountains Region*. Science Press, Beijing, China.
- TATARA, M. & DOI, T. (1994). Comparative analyses on food habits of Japanese marten, Siberian weasel and leopard cat in the Tsushima islands, Japan. *Ecological Research* **9**, 99-107.
- TAYLOR, H. C. (1978). Capensis. In *Biogeography and Ecology of Southern Africa* (ed. M. J. A. Werger), pp. 171-229. Junk, The Hague, Netherlands.
- TEDMAN, R. A. & HALL, L. S. (1985). The morphology of the gastrointestinal tract and food transit time in the fruit bats *Pteropus alecto* and *P. poliocephalus* (Megachiroptera). *Australian Journal of Zoology* **33**, 625-640.
- TEMME, M. (1979). Notes on the Violet-backed Starling (*Sturnus philippensis*) in Manila / Philippines. *Ornithologische Mitteilungen Göttingen* **31**, 86-87.
- TERBORGH, J. (1983). *Five New World Primates. A Study in Comparative Ecology*. Princeton University Press, New Jersey, USA.
- TERBORGH, J. (1986). Keystone plant resources in the tropical forest. In *Conservation Biology, the Science of Scarcity and Diversity* (ed. M. E. Soule), pp. 330-344. Sinauer, Sunderland, MA, USA.
- TERBORGH, J. & DIAMOND, J. M. (1970). Niche overlap in feeding assemblages of New Guinea birds. *The Wilson Bulletin* **82**, 29-52.
- THOMAS, D. W. (1982). The ecology of an African savanna fruit bat community: Resource partitioning and role in seed dispersal. Ph.D. thesis, University of Aberdeen, Aberdeen, UK.
- THOMAS, H. F. (1957). The starling in the Sunraysia district, Victoria. *Emu* **57**, 151-180.
- THOMPSON, H. & GOODFELLOW, D. (1987). *Common Birds of the Darwin Area*. Sandpiper, Winnellie, Australia.
- THOMSON, D. F. (1935). *Birds of Cape York Peninsula*. H. J. Green, Melbourne, Australia.
- THORNTON, I. (1997). *Krakatau: The destruction and reassembly of an island ecosystem*. Harvard University Press, Ann Arbor, USA.
- THORNTON, I. W. B., COMPTON, S. G. & WILSON, C. N. (1996). The role of animals in the colonisation of the Krakatau islands by fig trees (*Ficus* species). *Journal of Biogeography* **23**, 577-592.
- TINLEY, K. L. (1969). Dikdik, *Madoqua kirkii*, in south-west Africa: notes on distribution, ecology and behaviour. *Madoqua* **1**, 7-33.
- TRAINER, J. M. & WILL, T. C. (1984). Avian methods of feeding in *Bursura simaruba* (Bursuraceae) fruits in Panama. *Auk* **101**, 193-194.
- TRAIL, P. (1994). The phenology of rainforest plants in Tutuila, American Samoa. Unpublished Manuscript. Department of Marine and Wildlife Resources, American Samoa.
- TRAVESET, A. (1990). *Ctenosaura similis* Gray (Iguanidae) as a seed disperser in a Central American deciduous forest. *American Midland Naturalist* **123**, 402-404.
- TRAVESET, A. & WILLSON, M. F. (1997). Effects of birds and bears in seed germination of fleshy fruited plants in temperate rainforests of southeast Alaska. *Oikos* **80**, 89-95.
- TSUJI, A. (1996). *Hornbills. Masters of Tropical Forests*. Sarakadee Press, Bangkok, Thailand.
- TURCEK, F. J. (1963). Colour preferences in fruit and seed-eating birds. *Proceedings XIII International Ornithological Congress 1962, Ithaca, New York*, 285-292.
- TUTIN, C. E. G., WHITE, L. J. T., WILLIAMSON, E. A., FERNANDEZ, M. & MCPHERSON, G. (1994). List of plant species identified in the northern part of the Lope Reserve, Gabon. *Tropics* **3**, 249-276.
- TUTTLE, M. D. (1970). Distribution and zoogeography of Peruvian bats, with comments on natural history. University of Kansas Science Bulletin **49**, 45-86.
- ULFSTRAND, S. (1977). Foraging niche dynamics and overlap in a guild of passerine birds in a south Swedish coniferous woodland. *Oecologia* **27**, 23-45.
- UNGAR, P. S. (1995). Fruit preferences of four sympatric primate species at Ketambe, Northern Sumatra, Indonesia. *International Journal of Primatology* **16**, 221-245.
- URBAN, E. K., FRY, C. H. & KEITH, S. (1986). *The Birds of Africa. Volume II*. Academic Press, London, UK.
- URBAN, E. K., FRY, C. H. & KEITH, S. (1997). *The Birds of Africa. Volume V*. Academic Press, London, UK.
- UTAMI, S. S., WICH, S. A., STERCK, E. H. M. & VAN HOOFF, J. A. R. A. M. (1997). Food competition between wild orangutans in large fig trees. *International Journal of Primatology* **18**, 909-927.
- UTZURRUM, R. B. & HEIDEMAN, P. D. (1991). Differential ingestion of viable vs. non-viable *Ficus* seeds by fruit bats. *Biotropica* **23**, 311-312.
- UTZURRUM, R. C. B. (1995). Feeding ecology of Philippine fruit bats: patterns of resource use and seed dispersal. *Symposium of the Zoological Society of London* **67**, 63-77.
- VAN DER PIJL, L. (1957). The dispersal of plants by bats (Chiropterophily). *Acta Botanica Neerlandica* **6**, 291-315.
- VAN DER PIJL, L. (1982). *Principles of Dispersal in Higher Plants. 3rd Edition*. Springer-Verlag, Berlin, Germany.
- VAN DER ZEE, D. & SKINNER, J. D. (1977). Preliminary observations on samango and vervet monkeys near Lake Sibayi. *South African Journal of Science* **73**, 381-382.
- VAN DEVENDER, R. W. (1983). *Basiliscus basiliscus* (Chisbala, Garrobo, Basilisk, Jesus Christ Lizard). In *Costa Rican Natural History* (ed. D. H. Janzen), pp. 379-380. University of Chicago Press, Chicago, USA.
- VAN SCHAIK, C. P. (1996). Strangling figs: their role in the forest. In: *Leuser: A Sumatran Sanctuary* (ed. C. P. van Schaik and J. Supriatna), pp. 112-120. YABSHI, Depok, Indonesia.
- VAN SCHAIK, C. P. & VAN NOORDWIJK, M. A. (1988). Scramble and contest in feeding competition among female long-tailed macaques (*Macaca fascicularis*). *Behaviour* **105**, 77-98.
- VÁSQUEZ-YANES, C., OROZCO, A., FRANCOIS, G. & TREJO, L. (1975). Observations of seed dispersal by bats in a tropical humid region in Veracruz, Mexico. *Biotropica* **7**, 73-76.
- VELLAYON, S. (1981). The nutritive value of *Ficus* in the diet of the lar gibbon (*Hylobates lar*). *Malaysian Applied Biology* **10**, 177-181.
- VERKERKE, W. (1987). Syconial anatomy of *Ficus asperifolia* (Moraceae), a gynodioecious tropical fig. *Proceeding of the Koninklijke Nederlandse Akademie van Wetenschappen C* **90**, 461-492.
- VERKERKE, W. (1989). Structure and function of the fig. *Experientia* **45**, 612-621.
- VERNON, C. J. (1993). Gluttonous starlings raid Natal mahogany. *Bee-eater* **44**, 9.
- VILLA-R, B. (1967). *Los murcielagos de Mexico*. Instituto de Biología, Universidad Nacional Autónoma de México, Mexico City, Mexico.
- WAIDE, R. B. (1996). Birds. In *The Food Web of a Tropical Rain Forest* (ed. D. P. Reagan and R. B. Waide), pp. 363-398. University of Chicago Press, Chicago, USA.
- WALTON, D. W. & RICHARDSON, B. J. (1989). *Fauna of Australia. Mammalia. Vol. 1B*. Australian Government Publishing Service, Canberra, Australia.
- WARE, A. B. & COMPTON, S. G. (1994). Responses of fig wasps to host plant volatile cues. *Journal of Chemical Ecology* **20**, 785-802.
- WASER, P. (1977). Feeding, ranging and group size in the Mangabey *Cercocebus albigena*. In *Primate Ecology: Studies of Feeding and Ranging Behaviour in Lemurs, Monkeys and Apes* (ed. T. H. Clutton-Brock), pp. 183-222. Academic Press, London, UK.
- WATERHOUSE, R. D. (1997). Some observations on the ecology of the rainbow lorikeet *Trichoglossus haematodus* in Oatley, South Sydney. *Corella* **21**, 17-24.
- WATSON, H. (1985). *Lambir Hills National Park: Resource inventory with management recommendations*. National Park and Wildlife Office, Forest Department, Kuching, Sarawak, Malaysia.
- WAUGH, D. (1995). Action for Buffon's Macaw in Ecuador: a report from the field. *Proceedings of the International Aviculturists Society* January 11-15, 1995.
- WELLS, D. R. (1975). Bird Report: 1972 and 1973. *Malayan Nature Journal* **28**, 186-213.
- WELLS, D. R. (1982). Bird Report: 1974 and 1975. *Malayan Nature Journal* **36**, 61-85.
- WELLS, D. R. (1999). *Bird of the Thai-Malay Peninsula, Vol 1: Non-passerines*. Academic Press, London, UK.
- WHEELWRIGHT, N. T. (1985). Competition for dispersers, and the timing of flowering and fruiting in a guild of tropical trees. *Oikos* **44**, 465-477.
- WHEELWRIGHT, N. T., HABER, W. A., MURRAY, K. G. & GUIDON, C. (1984). Tropical fruit eating birds and their food plants: a survey of a Costa Rican lower montane forest. *Biotropica* **16**, 173-192.
- WHEELWRIGHT, N. T. & ORIAN, G. H. (1982). Seed dispersal by animals: constraints with pollen dispersal, problems of terminology, and constraints on coevolution. *American Naturalist* **119**, 402-413.
- WHITE, F. J. (1998). Seasonality and socioecology: the importance of variation in fruit abundance to Bonobo sociality. *International Journal of Primatology* **19**, 1013-1027.
- WHITE, L. J. T., TUTIN, C. E. G., & FERNANDEZ, M. (1993). Group composition and diet of forest elephants, *Loxodonta africana cyclotis* Matschie 1900, in the Lope Reserve, Gabon. *African Journal of Ecology* **31**, 181-199.
- WHITING, M. J. & GREEFF, J. M. (1997). Facultative frugivory in the cape flat lizard *Platysaurus capensis* (Sauria: Cordylidae). *Copeia* **4**, 811-818.
- WHITING, M. J. & GREEFF, J. M. (1999). Use of heterospecific cues by the lizard *Platysaurus broadleyi* for food location. *Behavioural Ecology and Sociobiology* **45**, 420-423.
- WHITNEY, K. D., FOGIEL, M. K., LAMPERTI, A. M., HOLBROOK, K. M., STAUFFER, D. J., HARDESTY, B. D., PARKER, V. T. & SMITH, T. B. (1998). Seed dispersal by *Ceratogymna hornbills* in the Dja reserve, Cameroon. *Journal of Tropical Ecology* **14**, 351-371.
- WHITTAKER, R. J., JONES, S. H. (1994). The role of frugivorous bats and birds in the rebuilding of a tropical forest ecosystem, Krakatau, Indonesia. *Journal of Biogeography* **21**, 245-258.
- WHITTEN, A. J. (1984). Ecology comparisons between Kloss Gibbons and other small gibbons. In *The Lesser Apes. Evolutionary and Behavioural Biology* (ed. H. Preuschoft, D. J. Chivers, W. Y. Brockelman and N. Creel), pp. 219-227. Edinburgh University Press, Edinburgh, UK.
- WHITTEN, J. E. J. (1981). Ecological separation of three diurnal squirrels in tropical rainforest on Siberut Island, Indonesia. *Journal of Zoology*, **193**, 405-420.

- WHITTEN, P. L. (1988). Effects of patch quality and feeding subgroup size on feeding success in Vervet monkeys (*Cercopithecus aethiops*). *Behaviour* **105**, 35-52.
- WICKLER, W. & SEIBT, U. (1976). Field studies of the African fruit bat *Epomoporus wahlbergi* (Sundevall) with special reference to male calling. *Zeitschrift für Tierpsychologie* **40**, 345-376.
- WIEBES, J. T. (1979). Co-evolution of figs and their insect pollinators. *Annual Review of Ecology and Systematics*, **10**, 1-12.
- WILES, G. J., ENGBRING, J. & OTOBED, D. (1997). Abundance, biology and human exploitation of bats in the Palau Islands. *Journal of Zoology* **241**, 203-227.
- WILLIAMS, K. D. (1984). The Central American tapir (*Tapirus bairdii* Gill) in northwestern Costa Rica. *Dissertation Abstracts International, B (Science and Engineering)* **45**, 1075.
- WILLSON, M. F. (1989). Gut retention times of experimental pseudoseeds by emus. *Biotropica* **21**, 210-213.
- WILLSON, M. F. (1993). Mammals as seed-dispersers in North America. *Oikos* **67**, 159-176.
- WILLSON, M. F. & WHELAN, C. J. (1990). The evolution of fruit color in fleshy-fruited plants. *American Naturalist* **136**, 790-809.
- WILSON, J. M., STEWART, P. D., RAMANGASON, G. S., DENNING, A. M. & HUTCHINGS, M. S. (1989). Ecology and conservation of the Crowned Lemur, *Lemur coronatus*, at Ankarana, N Madagascar - with notes on Sanford's Lemur, other sympatric and subfossil lemurs. *Folia Primatologica* **52**, 1-26.
- WINDSOR, D. M., MORRISON, D. W., ESTRIBI, M. A., DE LEON, B. (1989). Phenology of fruit and leaf production by 'strangler' figs on Barro Colorado Island, Panama. *Experientia* **45**, 647-653.
- WINKLER, H., CHRISTIE, D. A. & NURNEY, D. (1995). *Woodpeckers: A Guide to the Woodpeckers, Piculets and Wrynecks of the world*. Pica Press, Sussex, UK.
- WODZICKI, K. & FELTEN, H. (1975). The peka, or fruit bat (*Pteropus tonganus tonganus*) (mammalia, Chiroptera), of Nuie Island, Pacific Ocean. *Pacific Science* **29**, 131-138.
- WOLTON, R. J., ARAK, P. A., GODFRAY, H. C. J. & WILSON, R. P. (1982). Ecological and behavioural studies of the Megachiroptera at Mount Nimba, Liberia, with notes on Microchiroptera. *Mammalia* **46**, 419-448.
- WONG, M. (1986). Trophic organisation of understorey birds in a Malaysian dipterocarp forest. *Auk* **103**, 100-116.
- WOODALL, P. F. (1985). Crested and feral pigeons feeding on fig-seeds - commensalism, feeding rates and vigilance. *Emu* **85**, 121-125.
- WORTHINGTON, A. (1982). Population sizes and breeding rhythms of two species of manakins in relation to food supply. In *The Ecology of a Tropical Forest. Seasonal Rhythms and Long-term Changes* (ed. E. G. Leigh Jr, A. S. Rand and D. M. Windsor), pp. 213-225. Smithsonian Institution Press, Washington D.C., USA.
- WORTHINGTON, A. H. (1989). Adaptations for avian frugivory - assimilation efficiency and gut transit-time of *Manacus vitellinus* and *Pipra mentalis*. *Oecologia*, **80**, 381-389.
- WRANGHAM, R. W. (1977). Feeding behaviour of Chimpanzees in Gombe National Park, Tanzania. In *Primate Ecology: Studies of Feeding and Ranging Behaviour in Lemurs, Monkeys and Apes* (ed. T. H. Clutton-Brock), pp. 503-538. Academic Press, London, UK.
- WRANGHAM, R. W., CONKLIN, N. L., ETOT, G., OBUA, J., HUNT, K. D., HAUSER, M. D. & CLARK, A. P. (1993). The value of figs to chimpanzees. *International Journal of Primatology* **14**, 243-256.
- WU, K. (1994). Particular in Sichuan Mammals. Science and Technology Press, Sichuan, China.
- XU, R. X. (1997). *Macaque and I (Chinese)*. Yuan Liu Publication Limited, Taipei, Taiwan.
- XUE, L. (1983). *Birds and Mammals of Hainan*. Science Press, Beijing, China.
- YAMAGIWA, J., MWANZA, N., YUMOTO, T. & MARUHASHI, T. (1994). Seasonal change in the composition of the diet of eastern lowland gorillas. *Primates* **35**, 1-14.
- YAMAKURA, T. (1992). Structure and species diversity. In *Considering of Tropical Forests* (ed. T. Shidei and T. Kira), pp.53-59. Jinbunshoin, Kyoto, Japan.
- YANG, D., LI, C. & YANG, B. (1997). Studies on animal structure and biodiversity on *Ficus* in the tropical rain of Xishuangbanna, China. *Zoological Research* **18**, 189-196.
- YANG, L., WEN, X., HAN, L., YANG, X., SHI, W. & WANG, S. (1995). *The avifauna of Yunnan China*. Yunnan Science and Technology Press, Yunnan, China.
- YU, Y. T. (1998). Migration and stopover ecology of Oriental Reed Warbler *Acrocephalus orientalis* at Mai Po Marshes Nature Reserve, Hong Kong. Unpublished B.Sc. thesis, University of Hong Kong, Hong Kong.
- YUMOTO, T. (1999). Seed dispersal by Salvin's Currawong, *Mitu salvini* (Cracidae), in a tropical forest of Colombia: Direct measurement of dispersal distance. *Biotropica* **31**, 654-660.
- YUMOTO, T. & INOUE, T. (1995). Canopy Biology Program in Sarawak - Long term study of plant phenology and plant-animal interactions in a mixed dipterocarp forest. *Tropics* **4**, 307-315.
- YUMOTO, T., MARUHASHI, T., YAMAGIWA, J. & MWANZA, N. (1995). Seed-dispersal by elephants in a tropical rain forest in Kahuzi-Biega National Park, Zaire. *Biotropica* **27**, 526-530.
- YUMOTO, T., NOMA, N. & MARUHASHI, T. (1998). Cheek-pouch dispersal of seeds by Japanese monkey (*Macaca fuscata yakui*) on Yakushima Island, Japan. *Primates*, **39**, 325-338.
- ZAKARIA, M. (1994). Ecological Effects of Selective Logging in a Lowland Dipterocarp Forest on Avifauna, with Special Reference to Frugivorous Birds Faculty of Life Sciences. Ph.D. thesis, Universiti Kebangsaan Malaysia, Bangi, Malaysia.
- ZANN, R. A., MALE, E. B. & DARJONO. (1990). Bird colonisation of Anak Krakatau, an emergent volcanic island. *Philosophical Transactions of the Royal Society of London B* **328**, 95-121.
- ZAR, J. (1996). *Biostatistical Analysis. Third Edition*. Prentice-Hall, Inc., Upper Saddle River, NJ., USA.
- ZHANG, C., ZHU, X. & PANG, B. (1997). *Birds of China*. China Forestry Publishing House, Beijing, China.
- ZHANG, S.-Y. & WANG, L.-X. (1995). Fruit consumption and seed dispersal of *Ziziphus cinnamomum* (Rhamnaceae) by two sympatric primates (*Cebus apella*) and *Ateles paniscus* in French Guiana. *Biotropica* **27**, 397-401.
- ZHAO, Q., DENG, Z. & XU, J. (1991). Natural foods and their ecological implications for *Macaca thibetana* at Mount Emei, China. *Folia Primatologica* **57**, 1-15.
- ZHAO, Z. J. (1995). *A Handbook of the Birds of China, Vol. 1. Non-passerines*. Jilin Science and Technology Press, Changchun, China.
- ZHENG, B. (1985). *Fauna Sinica, Aves Vol. 8, Passeriformes: Eurylaimidae-Irenidae*. Science Press, Beijing, China.
- ZHENG, G. & WANG, Q. (1998). *China Red Data Book of Endangered Animals: Aves*. Science Press, Beijing, China.
- ZHENG, Z. (1978). *Fauna Sinica, Aves Vol. 4, Galliformes*. Science Press, Beijing, China.
- ZHENG, Z. (1993). *Economic Birds of China. 2nd Edition*. Science Press, Beijing, China.
- ZHENG, Z., LI, D., WANG, Z., WANG, Z., JIANG, Z. & LU, T. (1983). *The Avifauna of Xizang*. Science Press, Beijing, China.
- ZHENG, Z., LONG, Z. & ZHENG, B. (1987). *Fauna Sinica, Aves Vol. 11, Passeriformes: Muscicapidae II. Timaliinae*. Science Press, Beijing, China.
- ZHENG, Z., XIAN, Y. & GUAN, G. (1991). *Fauna Sinica, Aves Vol. 6, Columbiformes, Psittaciformes, Cuculiformes and Strigiformes*. China, Beijing, China.
- ZIELINSKI, G. A., MAYEWSKI, P. A., MEEKER, L. D., WHITLOW, S., TWICKLER, M. S., MORRISON, M., MEESE, D. A., GOW, A. J. & ALLEY, R. B. (1994). Record of volcanism since 7000 B.C. from the GISP2 Greenland ice core and implications for volcano-climate science. *Science* **264**, 948-952.
- ZIMMERMAN, D. A., TURNER, D. A., PEARSON, D. J. (1996). *Birds of Kenya and Northern Tanzania*. Christopher Helm, London, UK.
- ZONA, S. & HENDERSON, A. (1989). A review of animal-mediated seed dispersal of palms. *Selbyana* **11**, 6-21.

APPENDIX 1

Vertebrates of Lambir Hills National Park, Sarawak, Malaysia
(in press, *Malayan Nature Journal*)

M. SHANAHAN^{1,3} & I. DEBSKI^{2,3}

¹Centre for Biodiversity and Conservation, School of Biology, University of Leeds, Leeds LS2 9JT, United Kingdom

²Department of Plant and Soil Science, University of Aberdeen, Cruikshank Building, St. Machar's Drive, Aberdeen AB24 3UU, United Kingdom

³Institute for Biodiversity & Environmental Conservation, Universiti Malaysia Sarawak, 93400 Kota Samarahan, Sarawak, Malaysia.

ABSTRACT

We present a list of vertebrates recorded in Lambir Hills National Park, Sarawak, Malaysia. The list is compiled from published sources, personal observations made by the authors over three years and contributions of unpublished observations by scientists and bird watchers. Our checklist includes 65.6 % more species than the park's last inventory, published in 1985. Excluding fish, which have yet to be considered in any detail, 366 vertebrate species have been recorded in the park to date. These comprise 237 bird species, 63 mammals, 46 reptiles and 20 frogs. Drawing comparisons between the bird fauna recorded in 1985 and that recorded in the late 1990s, we note the increased observation of species normally considered montane/hill forest specialists and of species generally found in open/disturbed habitats. Anthropogenic effects are cited as contributing to these changes in the composition of the avifauna. We identify 23 bird and mammal species for which reliable records have not been made since 1985. Most of these absences can be readily explained but the fates of three species raise conservation concerns. One species, the Helmeted Hornbill (*Buceros vigil*) is considered to have become locally extinct in the park whilst the fates of Great Slaty Woodpecker (*Mulleripicus pulverulentus*) and Banded Langur (*Presbytis melalophos*) are uncertain. Despite the high species diversity, population densities, especially of large species, appear to be low. This is of special concern given the extent of illegal hunting that we have observed in the park.

INTRODUCTION

Lambir Hills National Park (4° 20' N, 113° 50' E; altitude 150 - 465 m), 30 km south of Miri in Sarawak's Fourth Division, was gazetted in 1982. The park comprises nearly 7000 hectares of mixed dipterocarp forest and *kerangas* (heath forest), and annual rainfall exceeds 5000 mm (Inoue & Hamid 1994). Lambir Hills is amongst the most botanically diverse forests in the world (1175 tree species have been identified in a 52 ha plot; La Frankie *et al.* 1995). The forest in Lambir is the subject of major ecological research collaborations between Japanese, American, Malaysian and British scientists (e.g. Inoue & Hamid 1994, Lee *et al.* 1995, Sakai *et al.* 1995). Despite this, an enumeration of the park's vertebrate fauna has not been undertaken since the inventory undertaken upon the park's creation (Watson 1985). Excluding fish, this account recorded 221 vertebrate species.

This paper aims to update the state of knowledge of Lambir's vertebrate fauna, to provide a checklist of species recorded in the park and to identify species for which apparent population declines are of conservation concern.

METHODS

Vertebrate records were accumulated in 1998 and 1999 during doctoral research totally over three-observer years (Debski 2000, Shanahan 2000). In addition to *ad hoc* observations, regular bird-watching sessions and nocturnal searches for frogs, MS spent over 600 hours recording frugivorous vertebrates visiting fruiting fig trees (*Ficus* spp; Moraceae). Tourist bird-watchers and other researchers at the site provided additional records. These records were combined with literature on Lambir's vertebrates (Watson 1985, Bransbury 1993, Abdullah & Hall 1997, Sato 1999) to create a new species list for the park. Two 'sampling periods' can be recognised: a) the initial work of Watson and b) the later records that were all made in the 1990s. To compare the composition of the bird fauna recorded in each of these periods each bird species was allocated to one of three groups based on information in MacKinnon and Phillipps (1993). These were a) species known from closed primary lowland forest, b) species primarily found in secondary forest, forest edge, open habitat or associated with open water, and c) species primarily found in montane or hill forest. A chi-squared test (Sokal & Rohlf 1995) was used to identify differences in the numbers of birds in each of these groups recorded in each period.

RESULTS

Excluding fish, 366 vertebrate species have been recorded from Lambir Hills to date (Table 1, Appendix A). This tally represents a 65.6 % increase in total species number compared to that of the last published list (Watson 1985), whilst the number of mammals recorded has more than doubled. Figure 1 illustrates the proportion of each vertebrate group recorded by Watson (1985) only, by Watson and subsequent observers, and by subsequent observers alone. Forty-five percent of frogs and 37 % of reptiles recorded by Watson have not been recorded since. Conversely, for birds and mammals, the majority of Watson's records have been confirmed, indeed significantly added to. Many of the new additions to Lambir's bird list are species not normally associated with closed primary lowland forest. Rather, they are either montane/hill species or birds of open/disturbed habitats (MacKinnon and Phillipps 1993). Indeed, there is a significant difference in the composition of the avifauna recorded by Watson (1985) and that observed only in the 1990s with respect to known habitat associations of each bird species ($\chi^2 = 18.51$, 3 d.f., $p < 0.01$; Table 2). The proportion of all birds that are generally considered to be hill/montane specialists increased from 1.95 % to 14 % whilst that of species of open or disturbed habitats rose from 33.8 % to 42 %. In spite of the

numerous additions to the park's faunal list, 14 bird species and nine mammals recorded in 1985 have not been observed in recent years (Table 3).

Table 1. Increases (between 1985 and 1999) in total species number recorded in Lambir Hills National Park

	present in 1985 ¹	new records in 1990s	Total	% increase
Frogs	13	7	20	53.9
Reptiles	25	21	48	84
Mammals	29	34	61	117.2
Birds	154	83	237	53.9
total	221	145	365	65.6

¹Watson (1985)

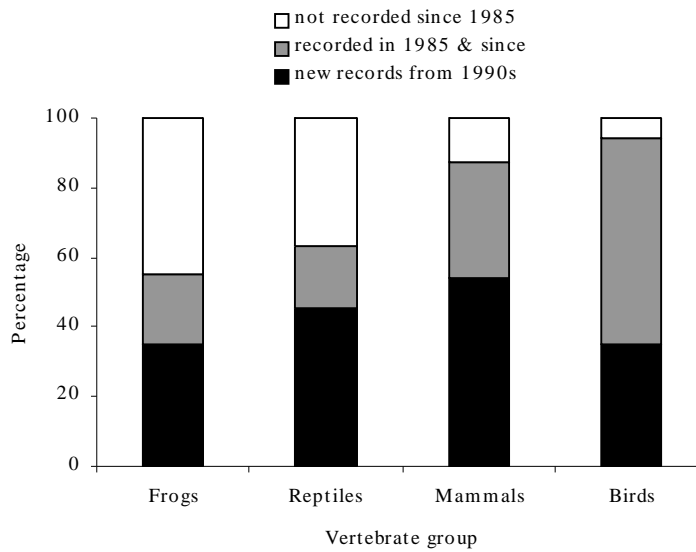


Figure 1. The proportions of Lambir's frogs, reptiles, mammals and birds a) not recorded since Watson's (1985) inventory (white), b) recorded by Watson as well as subsequent observers (grey) and c) not recorded by Watson but seen in the 1990s (black).

Table 2. Comparison of avifauna recorded in 1985 and only in the 1990s. The composition of the new species recorded in the 1990s differs significantly from that recorded by Watson ($\chi^2 = 18.51$, 3 d.f; $p < 0.001$). The proportion of all birds that are generally considered to be hill/montane specialists increased from 1.95 % to 14 % whilst that of species of open or disturbed habitats rose from 33.8 % to 42 %. Species' habitat associations follow MacKinnon & Phillipps (1993).

Habitat	Watson (1985)		species recorded only in the 1990s	
	n	%	n	%
Closed primary lowland forest	99	64.3	36	43
Secondary forest, forest edge, open habitat, and water	52	33.8	35	42
Hill/montane forest	3	1.95	12	14
	TOTAL 154		83	

Table 3. Bird and Mammal species not recorded since Watson's (1985) inventory

Class	Scientific name	Common name
Birds	<i>Anhinga melanogaster</i>	Oriental Darter
	<i>Cacomantis sonnerati</i>	Banded Bay Cuckoo
	<i>Chrysococcyx minutillis</i>	Little Bronze Cuckoo
	<i>Phodilus badius</i>	Oriental Bay Owl
	<i>Caprimulgus macrurus</i>	Large-tailed Nightjar
	<i>Buceros vigil</i>	Helmeted Hornbill
	<i>Indicator archipelagicus</i>	Malaysian Honeyguide
	<i>Mulleripicus pulverulentus</i>	Great Slaty Woodpecker
	<i>Hemicircus concretus</i>	Grey-and-buff Woodpecker
	<i>Malacopteron albugulare</i>	Grey-breasted Babbler
	<i>Kenopia striata</i>	Striped Wren-Babbler
	<i>Pachycephala grisola</i>	Mangrove Whistler
	<i>Anthreptes siparaja</i>	Crimson Sunbird
	<i>Erythrura prasina</i>	Pin-tailed Parrotfinch
Mammals	<i>Tupaia dorsalis</i>	Striped Treeshrew
	<i>Rhinolophus sedulus</i>	Lesser Woolly Horseshoe Bat
	<i>Hipposideros galeritus</i>	Cantor's Roundleaf Bat
	<i>Manis javanica</i>	Pangolin
	<i>Presbytis melalophos</i>	Banded Langur
	<i>Rattus exulans</i>	Polynesian Rat
	<i>Mus castaneus</i>	Asian House Mouse
	<i>Niviventer cremoriventer</i>	Dark-tailed Tree Rat
<i>Trichys fasciculata</i>	Long-tailed Porcupine	

DISCUSSION

Despite its small size and limited altitudinal range Lambir Hills National Park has a high diversity of vertebrates, many of which have been recorded only relatively recently. As well as providing a baseline for future studies, differences between the two distinct sampling periods allow us assess changes in our knowledge of Lambir's complement of different vertebrate groups and to identify possible population declines of conservation concern.

Birds and mammals have been relatively well surveyed, with the majority of Watson's (1985) records having been confirmed in the 1990s. Furthermore many species have been recorded for the first time in the 1990s. Among the birds, many of these new additions to the park list are species normally associated with disturbed/open habitat. We hypothesise that increased habitat heterogeneity associated with human activity (creation of ponds, edges and open habitat) has promoted the observation of such species. An even more marked increase in the number of montane/hill species is evident. Two hypotheses exist to explain this observation. The patterns may simply be artefacts of incomplete knowledge of avian species' distributions. Alternatively, genuine altitudinal shifts of species ranges' may have occurred in recent years, possibly due to habitat disturbance associated with logging in the highlands of Sarawak prompting avian migration to the lowlands.

That ~40 % of frogs and reptiles recorded by Watson (1985) have not been recorded since probably reflects problems of field identification and limited sampling effort compared to that devoted to the observation of birds and mammals. Among the reptiles, these problems appear especially marked for skinks, geckos and flying lizards, which account for 14 of the 17 reptile species not recorded since 1985 whereas 14 of the 21 new reptile records are for snakes. No studies have focused explicitly on frogs or reptiles and little can be concluded about Lambir's total number of species in these groups.

Several explanations exist for the lack of observations of bird and mammal species recorded by Watson (1985). Firstly, a number are nocturnal and thus easily overlooked in the absence of dedicated searches. These include Oriental Bay-Owl, Large-tailed Nightjar, the two bat species, Pangolin and the four rodent species. Other species recorded by Watson do not normally occur in primary lowland forest and are likely to represent opportunistic sightings or have specialised habitat requirements within primary forest (MacKinnon & Phillipps 1993; Payne *et al.* 1985). Thus it is unsurprising that subsequent observers have not noted the following species; Oriental Darter (a riverine species), Grey-and-buff Woodpecker (prefers secondary forest/open habitat), Grey-breasted Babbler (peat swamp and heath forest), Pin-tailed Parrotfinch (bamboo thickets/rice fields), Mangrove Whistler (coast and mangrove specialist). Further species are simply difficult to observe through being rare (Little Bronze Cuckoo,

Malaysian Honeyguide) or having inconspicuous behaviour (Banded Bay Cuckoo, Striped Wren-Babbler). The Crimson Sunbird may have been overlooked because of its small size. For three species, no such explanation can be easily applied. Helmeted Hornbill, Great Slaty Woodpecker and Banded Langur are all large and conspicuous species but none have been recorded in the 1990s. Similarly, the authors only infrequently made sightings of other large vertebrates (other hornbills, deer, pig, civets and other primates) in 1998-1999. Despite spending thousands of hours in the forest, the distinctive calls of Bornean gibbon were heard on only two occasions, and we found no recent evidence (e.g. conspicuous scratch marks) of Sun Bear. Dedicated research is necessary if the status of these animal populations is to be accurately assessed.

Whilst the small size of Lambir Hills National Park implies a low carrying capacity for populations of large vertebrates, a more direct threat can be identified. Illegal hunting regularly occurs within the boundaries of the park. Shotgun blasts were regularly heard and snares, animal carcasses and hunters' camps were occasionally encountered in the forest. Additionally, at night we often observed vehicles from Miri "spotlighting" for vertebrates with powerful torches on the Miri-Bintulu road that dissects the park. Other factors likely to encourage the decline of large vertebrate populations are the degradation of forested land (logging and conversion to oil palm plantation) around the park since 1985.

Lambir Hills National Park's proximity to Miri and its numerous waterfalls make it the most heavily visited national park in Sarawak (Anon 1995). The closeness of human populations also exposes the fauna to the depredations of hunting. Uncontrolled illegal hunting in the park is a major threat to large animals and one that is likely to be revealed in future inventories of the park's vertebrate fauna.

ACKNOWLEDGEMENTS

We are grateful to the following individuals for providing unpublished information; K. & J. Wiggers, Kaori Sato, H & T. Armstrong and Dr. R.D. Harrison. Dr. Indraneil Das provided personal data on frogs and reptiles and clarified nomenclature for these groups. Hazel Oakley assisted in frog surveys. During their time in Lambir, the authors were visiting research fellows at the Institute for Biodiversity and Environmental Conservation at Universiti Malaysia Sarawak. The States of Jersey Education Committee funded MS. ID was funded by the Carnegie Trust for the Universities of Scotland.

REFERENCES

- Abdullah, M. T. & Hall, L. S. 1997. Abundance and distribution of fruit bats and other mammals in the tropical forest canopy in Borneo. *Sarawak Museum Journal* **72**: 63-74.
- Anon. 1995. At a glance: Lambir Hills National Park. *Inside CTFS*. Center for Tropical Forest Science, Smithsonian Tropical Research Institute, vol Fall 1995, p. 6
- Bransbury, J. 1993. *A Birdwatcher's Guide to Malaysia*. 296 pp. Waymark Publishing, Australia.
- Debski, I. 2000. Abundance and co-existence in *Aporosa* (Euphorbiaceae) in two Malaysian rain forests. Ph.D. thesis. University of Aberdeen.
- Inger, R. F. & Steubing, R. B. 1997. *A Field Guide to the Frogs of Borneo*. Natural History Publications, Kota Kinabalu, Malaysia.
- Inoue, T. & Hamid, A. A. 1994. *Plant reproductive systems and animal seasonal dynamics: Long-term study of dipterocarp forests in Sarawak*. Center for Ecological Research, Kyoto University, Japan.
- Inoue, T. & Hamid, A.A. 1995. The canopy biology program in Sarawak. *Inside CTFS*. Center for Tropical Forest Science, Smithsonian Tropical Research Institute, vol Fall 1995, pp 7.
- LaFrankie, J. V., Tan, S. & Ashton, P. S. 1995. *Species List for the 52-ha Forest Dynamics Research Plot Lambir Hills National Park, Sarawak, Malaysia*. Center for Tropical Forest Science, Smithsonian Tropical Research Institute, Washington D.C.
- Lee, H. S., Ashton, P. S. & Ogino, K. 1995. Long Term Ecological Research of Tropical Rain Forest in Sarawak: Reports of a New Program for Promotion of Basic Sciences. *Studies of Global Environmental Change with Special Reference to Asia and Pacific Regions, Vol. 11-3*, Ehime, Japan
- MacKinnon, J. & Phillipps, K. 1993. *A Field Guide to the Birds of Borneo, Sumatra, Java and Bali*. Oxford University Press Inc., New York.
- Payne, J. Francis, C. M. & Phillipps, K. 1985. *A Field Guide to the Mammals of Borneo*. The Sabah Society & WWF Malaysia, Kota Kinabalu.
- Sakai, S., Momose, K., Yumoto, T., Nagamitsu, T., Nagamasu, H., Hamid, A. A. & Nakashizuka, T. 1999. Plant reproductive phenology over four years including an episode of general flowering in a lowland dipterocarp forest, Sarawak, Malaysia. *American Journal of Botany* **86**: 1414-1436.
- Sato, K. 1999. Unpublished MSc thesis. Center for Ecological Research, Kyoto University, Japan.
- Shanahan, M. 2000. *Ficus* seed dispersal guilds: ecology, evolution and conservation implications. Ph.D. thesis. University of Leeds.
- Sokal, R. R. & Rohlf, F. J. 1995. *Biometry*. W. H. Freeman & Co., New York
- Watson, H. 1985. *Lambir Hills National Park: Resource inventory with management recommendations*. National Park and Wildlife Office, Forest Department, Kuching, Sarawak, Malaysia.

Appendix A.

Checklist of vertebrates recorded in Lambir Hills National Park. Nomenclature follows MacKinnon & Phillipps (1993) for birds, Payne *et al.* (1985) for mammals and Inger & Steubing (1997) for frogs. For reptiles we use names provided by Dr Indraneil Das of Universiti Sarawak Malaysia. + indicates new records from the 1990s, 0 indicates species recorded in 1985 and confirmed since, - indicates species recorded in 1985 but not in the 1990s.

	scientific name	common name	
Frogs	<i>Leptobrachium abbotii</i>	Lowland Litter Frog	+
	<i>Bufo divergens</i>	Crested Toad	0
	<i>Metaphrynella sundana</i>	Tree Hole Frog	+
	<i>Occidozyga laevis</i>	Yellow-bellied Puddle Frog	+
	<i>Rana chalconota raniceps</i>	White-lipped Frog	0
	<i>Rana erythraea</i>	Green Paddy Frog	+
	<i>Rana glandulosa</i>	Rough-sided Frog	+
	<i>Polypedates leucomystax</i>	Four-lined Tree Frog	-
	<i>Polypedates macrotis</i>	Dark-eared Tree Frog	-
	<i>Polypedates otitophus</i>	File-eared Tree Frog	-
	<i>Rhacophorus appendiculatus</i>	Friilled Tree Frog	-
	<i>Rhacophorus pardalis</i>	Harlequin Tree Frog	-
	<i>Rana hosii</i>	Poisonous Rock Frog	-
	<i>Rana ingeri</i>	Greater Swamp Frog	+
	<i>Limnonectes kuhlii</i>	Kuhl's Creek Frog	-
	<i>Limnonectes leporina</i>	Giant River Frog	0
	<i>Fejervanya limnocharis</i>	Grass Frog	-
	<i>Rana palavanensis</i>	Smooth Guardian Frog	0
	<i>Rana signata</i>	Striped Stream Frog	-
	<i>Staurois natator</i>	Black-spotted Rock Frog	-
Reptiles	<i>Python curtus</i>	Blood Python	+
	<i>Oligodon octolineatus</i>	Striped Kukri Snake	+
	<i>Tropidolaemus wagleri</i>	Wagler's Pit Viper	0
	<i>Python reticulatus</i>	Reticulated Python	-
	<i>Ramphoiphlops braminus</i>	Brahminy Blind Snake	+
	<i>Xenopeltis unicolor</i>	Sunbeam Snake	-
	<i>Gonyosoma oxycephalum</i>	Red-tailed Racer	0
	<i>Dendrelaphis pictus</i>	Painted Bronzeback	+
	<i>Dendrelaphis formosus</i>	Elegant Bronzeback	+
	<i>Macropisthodon rhodomelas</i>	Blue-necked Keelback	0
	<i>Rhabdophis conspicillata</i>	Speckled Keelback	+
	<i>Xenochropis maculatus</i>	Spotted Keelback	+
	<i>Chrysopelea paradisi</i>	Garden Tree Snake	+
	<i>Ahaetulla prasina</i>	Oriental Vine-Snake	+
	<i>Psammodynaster pictus</i>	Mock Viper	+
	<i>Boiga sp.</i>	Cat-Snake sp.	+
	<i>Bungaris fasciatus</i>	Banded Krait	+
	<i>Naja sumatrana</i>	Sumatran Cobra	+
	<i>Ophiophagus hannah</i>	King Cobra	+
	<i>Ampiesma saravacensis</i>	Sarawak Water Snake	-
	<i>Cyrtodactylus pubisulcus</i>	Grooved bent-toed gecko	-
	<i>Cyrtodactylus consobrinus</i>	Peters' bent-toed gecko	-
	<i>Hemidactylus frenatus</i>	Asian house gecko	0
	<i>Gehyra mutilata</i>	Small-clawed gecko	-
	<i>Cosymbotus craspedotus</i>	Parachute gecko	-
	<i>Cosymbotus platyurus</i>	Flat-tailed gecko	+
	<i>Hemiphyllodactylus typus</i>	Oriental worm gecko	+
	<i>Luperosaurus serricaudatus</i>	Saw-tailed gliding gecko	+
	<i>Gekko smithii</i>	Smith's Gecko	-
	<i>Ptychozoon horsfieldi</i>	Horsfield's gliding gecko	-
	<i>Ptychozoon kuhli</i>	Kuhl's gliding gecko	+
	<i>Bronchocela cristatellus</i>	Green crested Lizard	+
	<i>Draco cornutus</i>	Horned flying lizard	-
	<i>Draco quinquefasciatus</i>	Five-lined Flying Lizard	-
	<i>Draco haematopogon</i>	Red-bearded Flying lizard	-
	<i>Draco melanopogon</i>	Black-bearded flying lizard	-
	<i>Gonocephalus borneensis</i>	Bornean angle-headed lizard	0
	<i>Gonocephalus grandis</i>	Large angle-headed lizard	0
	<i>Varanus salvator</i>	Water monitor	0
	<i>Mabuia multifasciata/rudis</i>	Many-banded/Rough-scaled Brown Skink	-
	<i>Mabuia rugifera</i>	Rough-scaled Skink	-
	<i>Apterygon vittatus</i>	Striped Tree Skink	+
<i>Sphenomorphus variegatus</i>	Variegated Skink	-	

	<i>Tropidophorus brookei</i>	Brooke's water skink	-
	<i>Takydromus sexlineatus</i>	Six-lined grass lizard	+
	<i>Amyda cartilaginea</i>	Malayan softshell turtle	0
Mammals	<i>Suncus etruscus</i>	Savi's pygmy shrew	+
	<i>Tupaia gracilis/T. minor</i>	Slender/Lesser Treeshrew	0
	<i>Tupaia glis</i>	Common Treeshrew	+
	<i>Ptilocercus lowii</i>	Pentail Treeshrew	+
	<i>Tupaia dorsalis</i>	Striped Treeshrew	-
	<i>Tupaia tana</i>	Large Treeshrew	0
	<i>Cynopteryx brachyotis</i>	Short-nosed Fruit Bat	+
	<i>Penthetor lucasii</i>	Dusky Fruit Bat	+
	<i>Balionycteris maculata</i>	Spotted-winged Fruit Bat	0
	<i>Chironax melanocephala</i>	Black-capped Fruit Bat	+
	<i>Pteropus vampyrus</i>	Large Flying Fox	0
	<i>Emballurona monticola</i>	Lesser Sheath-tailed Bat	+
	<i>Rhinolophus sedulus</i>	Lesser Woolly Horseshoe Bat	-
	<i>Rhinolophus trifolius</i>	Trefoil Horseshoe Bat	+
	<i>Hipposideros cervinus</i>	Fawn Roundleaf Bat	+
	<i>Hipposideros galeritus</i>	Cantor's Roundleaf Bat	-
	<i>Manis javanica</i>	Pangolin	-
	<i>Cynocephalus variegatus</i>	Colugo	+
	<i>Nycticebus coucang</i>	Slow Loris	0
	<i>Presbytis hosei</i>	Hose's Langur	+
	<i>Presbytis melalophos</i>	Banded Langur	-
	<i>Macaca fascicularis</i>	Long-tailed Macaque	0
	<i>Macaca nemestrina</i>	Pig-tailed Macaque	0
	<i>Hylobates muelleri</i>	Bornean Gibbon	0
	<i>Ratufa affinis</i>	Giant Squirrel	0
	<i>Callosciurus prevostii caroli</i>	Prevost's Squirrel	0
	<i>Callosciurus notatus</i>	Plantain Squirrel	0
	<i>Callosciurus adamsi</i>	Ear-spot Squirrel	+
	<i>Sundasciurus hippurus</i>	Horse-tailed Squirrel	+
	<i>Sundasciurus lowi</i>	Low's Squirrel	+
	<i>Dremomys everetti</i>	Bornean Mountain Ground Squirrel	+
	<i>Exilisciurus exilis</i>	Plain Pygmy Squirrel	+
	<i>Rheithrosciurus macrotis</i>	Tufted Ground Squirrel	+
	<i>Petaurillus hosei</i>	Hose's Pygmy Flying Squirrel	+
	<i>Petinomys setosus</i>	Temmink's Flying Squirrel	+
	<i>Petinomys vordermanni</i>	Vorderman's Flying Squirrel	+
	<i>Petaurista petaurista</i>	Red Giant Flying Squirrel	0
	<i>Aeromys thomasi</i>	Thomas's Flying Squirrel	+
	<i>Rattus exulans</i>	Polynesian Rat	-
	<i>Mus musculus/castaneus</i>	House Mouse	-
	<i>Rattus tiomanus jalorensis</i>	Malaysian Field Rat	+
	<i>Sundamys muelleri</i>	Muller's Rat	+
	<i>Maxomys rajah</i>	Brown Spiny Rat	0
	<i>Niviventer cremoriventer</i>	Dark-tailed Tree Rat	-
	<i>Maxomys whiteheadi</i>	Whitehead's Rat	0
	<i>Leopoldamys sabanus</i>	Long-tailed Giant Rat	+
	<i>Chiropodomys major</i>	Large Pencil-Tailed Tree-Mouse	+
	<i>Chiropodomys gliroides</i>	Common Pencil-tailed Tree-Mouse	+
	<i>Haeromys margarettae</i>	Ranee Mouse	+
	<i>Trichys fasciculata</i>	Long-tailed Porcupine	-
	<i>Helarctos malayanus</i>	Sun Bear	0
	<i>Aonyx (Amblonyx) cinerea</i>	Oriental Small-clawed Otter	0
	<i>Viverra zangalunga</i>	Malay Civet	+
	<i>Arctitis binturong</i>	Binturong	0
	<i>Paradoxurus hermaphroditus</i>	Common Palm Civet	+
	<i>Hemigalus derbyanus</i>	Banded Palm Civet	0
	<i>Herpestes sp.</i>	Mongoose species	+
	<i>Felis marmorata</i>	Marbled Cat	+
	<i>Sus barbatus</i>	Bearded Pig	0
	<i>Tragulus javanicus</i>	Lesser Mouse-deer	0
	<i>Tragulus napu</i>	Greater Mouse-deer	+
	<i>Muntiacus muntjac</i>	Bornean Red Muntjac	+
	<i>Muntiacus atherodes</i>	Bornean Yellow Muntjac	+
	<i>Cervus unicolor</i>	Sambar Deer	0
Birds	<i>Phalacrocorax carbo</i>	Great Cormorant	+
	<i>Anhinga melanogaster</i>	Oriental Darter	-
	<i>Butorides striatus</i>	Striated Heron	+
	<i>Nycticorax nycticorax</i>	Black-crowned Night-Heron	+

<i>Dupetor flavicollis</i>	Black Bittern	0
<i>Aviceda jerdoni</i>	Jerdon's Baza	+
<i>Pernis ptilorhynchus orientalis</i>	Oriental Honey-Buzzard	+
<i>Haliastur indus</i>	Brahminy Kite	0
<i>Haliaeetus leucogaster</i>	White-bellied Fish-Eagle	0
<i>Spilornis cheela</i>	Crested Serpent-Eagle	0
<i>Accipiter gularis</i>	Japanese Sparrowhawk	+
<i>Accipiter nisus</i>	Eurasian Sparrowhawk	+
<i>Accipiter trivirgatus</i>	Crested Goshawk	0
<i>Ictinaetus malayensis</i>	Black Eagle	0
<i>Hieraautus kiernerii</i>	Rufous-bellied Eagle	+
<i>Spizaetus cirrhatus</i>	Changeable Hawk-Eagle	+
<i>Spizaetus alboniger</i>	Blyth's Hawk-Eagle	+
<i>Spizaetus nanus</i>	Wallace's Hawk-Eagle	+
<i>Microhierax fringillarius</i>	Black-thighed Falconet	0
<i>Falco peregrinus ernesti</i>	Peregrine Falcon	0
<i>Coturnix chinensis</i>	Blue-breasted Quail	+
<i>Rollulus roulroul</i>	Crested Partridge	+
<i>Lophura erythrophthalma</i>	Crestless Fireback	+
<i>Lophura ignita</i>	Crested Fireback	+
<i>Argus argusianus</i>	Great Argus	0
<i>Porzana cinerea</i>	White-browed Crake	+
<i>Amauormis phoenicurus</i>	White-breasted Waterhen	+
<i>Tringa hypoleucos</i>	Common Sandpiper	0
<i>Treron curvirostra</i>	Thick-billed Green-Pigeon	0
<i>Treron olax</i>	Little Green-Pigeon	+
<i>Treron vernans</i>	Pink-necked Green-Pigeon	+
<i>Treron capellei</i>	Large Green Pigeon	+
<i>Ptilinopus jambu</i>	Jambu Fruit-Dove	0
<i>Ducula aenea</i>	Green Imperial-Pigeon	+
<i>Columba livia</i>	Rock Pigeon	+
<i>Streptopelia chinensis</i>	Spotted Dove	+
<i>Chalcophaps indica</i>	Emerald Dove	0
<i>Psittacula longicauda</i>	Long-tailed Parakeet	0
<i>Psittinus cyanurus</i>	Blue-rumped Parrot	0
<i>Loriculus galgulus</i>	Blue-crowned Hanging-Parrot	0
<i>Clamator coromandus</i>	Chestnut-winged Cuckoo	+
<i>Cuculus vagans</i>	Moustached Hawk-Cuckoo	+
<i>Cuculus fugax</i>	Hodgson's Hawk-Cuckoo	+
<i>Cuculus micropterus</i>	Indian Cuckoo	0
<i>Cacomantis sonnerati</i>	Banded Bay Cuckoo	-
<i>Cacomantis merulinus</i>	Plaintive Cuckoo	0
<i>Chrysococcyx maculatus</i>	Violet Cuckoo	0
<i>Chrysococcyx minutillis</i>	Little Bronze Cuckoo	-
<i>Surniculus lugubris</i>	Drongo Cuckoo	0
<i>Eudynamis scolopacea</i>	Asian Koel	+
<i>Phaenicophaeus diardi</i>	Black-bellied Malkoha	+
<i>Phaenicophaeus sumatranus</i>	Chestnut-bellied Malkoha	+
<i>Phaenicophaeus chlorophaeus</i>	Raffle's Malkoha	0
<i>Phaenicophaeus javanicus</i>	Red-billed Malkoha	+
<i>Phaenicophaeus curvirostris</i>	Chestnut-breasted Malkoha	0
<i>Centropus rectunguis</i>	Short-toed Coucal	0
<i>Centropus sinensis</i>	Greater Coucal	0
<i>Centropus bengalensis</i>	Lesser Coucal	0
<i>Phodilus badius</i>	Oriental Bay Owl	-
<i>Otus rufescens</i>	Reddish Scops-Owl	+
<i>Otus lempiji</i>	Collared Scops-Owl	+
<i>Ninox scutulata</i>	Brown Hawk-Owl	0
<i>Strix leptogrammica</i>	Brown Wood-Owl	0
<i>Batrachostomus auritus</i>	Large Frogmouth	+
<i>Batrachostomus stellatus</i>	Gould's Frogmouth	+
<i>Caprimulgus macrurus</i>	Large-tailed Nightjar	-
<i>Collocalia fuciphaga</i>	Edible-nest Swiftlet	+
<i>Collocalia maxima/linchii</i>	Black-nest/Mossy-nest Swiftlet	0
<i>Collacalia esculenta</i>	Glossy Swiftlet	0
<i>Hirundapus giganteus</i>	Brown-backed Needletail	0
<i>Raphidura leucopygialis</i>	Silver-rumped Swift	0
<i>Apus pacificus</i>	Fork-tailed Swift	+
<i>Hemiprocne longipennis</i>	Grey-rumped Treeswift	0
<i>Hemiprocne comata</i>	Whiskered Treeswift	0
<i>Harpactes kasumba</i>	Red-naped Trogon	0
<i>Harpactes diardii</i>	Diard's Trogon	+
<i>Harpactes duvaucelii</i>	Scarlet-rumped Trogon	0

<input type="checkbox"/>	<i>Alcedo atthis</i>	Common Kingfisher	+
<input type="checkbox"/>	<i>Alcedo meninting</i>	Blue-eared Kingfisher	0
<input type="checkbox"/>	<i>Alcedo euryzona</i>	Blue-banded Kingfisher	0
<input type="checkbox"/>	<i>Ceyx rufidorsa</i>	Rufous-backed Kingfisher	+
<input type="checkbox"/>	<i>Pelargopsis capensis</i>	Stork-billed Kingfisher	0
<input type="checkbox"/>	<i>Lacedo pulchela</i>	Banded Kingfisher	+
<input type="checkbox"/>	<i>Actenoides concretus</i>	Rufous-collared Kingfisher	+
<input type="checkbox"/>	<i>Merops viridis</i>	Blue-throated Bee-eater	0
<input type="checkbox"/>	<i>Nyctiornis amictus</i>	Red-bearded Bee-eater	0
<input type="checkbox"/>	<i>Eurystomus orientalis</i>	Dollarbird	0
<input type="checkbox"/>	<i>Anorrhinus galeritus</i>	Bushy-crested Hornbill	0
<input type="checkbox"/>	<i>Aceros comatus</i>	White-crowned Hornbill	+
<input type="checkbox"/>	<i>Aceros corrugatus</i>	Wrinkled Hornbill	0
<input type="checkbox"/>	<i>Aceros undulatus</i>	Wreathed Hornbill	0
<input type="checkbox"/>	<i>Anthracoceros malayanus</i>	Asian Black Hornbill	0
<input type="checkbox"/>	<i>Buceros rhinoceros</i>	Rhinoceros Hornbill	0
<input type="checkbox"/>	<i>Buceros vigil</i>	Helmeted Hornbill	-
<input type="checkbox"/>	<i>Megalaima chrysopogon</i>	Gold-whiskered Barbet	0
<input type="checkbox"/>	<i>Megalaima rafflesii</i>	Red-crowned Barbet	0
<input type="checkbox"/>	<i>Megalaima mystacophanos</i>	Red-throated Barbet	0
<input type="checkbox"/>	<i>Megalaima australis</i>	Blue-eared Barbet	0
<input type="checkbox"/>	<i>Calorhamphus fuliginosus</i>	Brown Barbet	0
<input type="checkbox"/>	<i>Indicator archipelagicus</i>	Malaysian Honeyguide	-
<input type="checkbox"/>	<i>Sasia abnormis</i>	Rufous Piculet	0
<input type="checkbox"/>	<i>Celeis brachyurus</i>	Rufous Woodpecker	+
<input type="checkbox"/>	<i>Picus puniceus</i>	Crimson-winged Woodpecker	0
<input type="checkbox"/>	<i>Picus mentalis</i>	Checker-throated Woodpecker	+
<input type="checkbox"/>	<i>Picus miniaceus</i>	Banded Woodpecker	+
<input type="checkbox"/>	<i>Dinopium rafflesii</i>	Olive-backed Woodpecker	0
<input type="checkbox"/>	<i>Meiglyptes tristis</i>	Buff-rumped Woodpecker	0
<input type="checkbox"/>	<i>Meiglyptes tukki</i>	Buff-necked Woodpecker	0
<input type="checkbox"/>	<i>Mulleripicus pulverulentus</i>	Great Slaty Woodpecker	-
<input type="checkbox"/>	<i>Dryocopus javensis</i>	White-bellied Woodpecker	0
<input type="checkbox"/>	<i>Denrocopus canicapillus</i>	Grey-capped Woodpecker	0
<input type="checkbox"/>	<i>Hemicircus concretus</i>	Grey-and-buff Woodpecker	-
<input type="checkbox"/>	<i>Blythipicus rubiginosus</i>	Maroon Woodpecker	0
<input type="checkbox"/>	<i>Reinwardtipicus validus</i>	Orange-backed Woodpecker	0
<input type="checkbox"/>	<i>Corydon sumatranus</i>	Dusky Broadbill	+
<input type="checkbox"/>	<i>Cymbirhynchus macrorhynchus</i>	Black-and-red Broadbill	+
<input type="checkbox"/>	<i>Eurylaimus javanicus</i>	Banded Broadbill	0
<input type="checkbox"/>	<i>Eurylaimus ochromalus</i>	Black-and-yellow Broadbill	0
<input type="checkbox"/>	<i>Calyptomena viridis</i>	Green Broadbill	0
<input type="checkbox"/>	<i>Pitta baudii</i>	Blue-headed Pitta	+
<input type="checkbox"/>	<i>Pitta nympha</i>	Fairy Pitta	+
<input type="checkbox"/>	<i>Pitta granatina</i>	Garnet Pitta	0
<input type="checkbox"/>	<i>Pitta sordida</i>	Hooded Pitta	+
<input type="checkbox"/>	<i>Hirundo rustica</i>	Barn Swallow	0
<input type="checkbox"/>	<i>Hirundo tahitica</i>	Pacific Swallow	+
<input type="checkbox"/>	<i>Hirundo daurica</i>	Red-rumped Swallow	+
<input type="checkbox"/>	<i>Hemipus hirundinaceus</i>	Black-winged Flycatcher-Shrike	+
<input type="checkbox"/>	<i>Tephrodornis gularis</i>	Large Woodshrike	+
<input type="checkbox"/>	<i>Coracina striata</i>	Bar-bellied Cuckoo-Shrike	+
<input type="checkbox"/>	<i>Coracina fimbriata</i>	Lesser Cuckoo-Shrike	+
<input type="checkbox"/>	<i>Pericrocotus igneus</i>	Fiery Minivet	+
<input type="checkbox"/>	<i>Pericrocotus flammeus</i>	Scarlet Minivet	0
<input type="checkbox"/>	<i>Aegithina viridissima</i>	Green Iora	0
<input type="checkbox"/>	<i>Aegithina tiphia</i>	Common Iora	0
<input type="checkbox"/>	<i>Chloropsis cyanopogon</i>	Lesser Green Leafbird	+
<input type="checkbox"/>	<i>Chloropsis sonnerati</i>	Greater Green Leafbird	0
<input type="checkbox"/>	<i>Chloropsis cochinchinensis</i>	Blue-winged Leafbird	0
<input type="checkbox"/>	<i>Pycnonotus zeylanicus</i>	Straw-headed Bulbul	+
<input type="checkbox"/>	<i>Pycnonotus melanoleucos</i>	Black-and-white Bulbul	0
<input type="checkbox"/>	<i>Pycnonotus atriceps</i>	Black-headed Bulbul	0
<input type="checkbox"/>	<i>Pycnonotus cyaniventris</i>	Grey-bellied Bulbul	0
<input type="checkbox"/>	<i>Pycnonotus eutilotus</i>	Puff-backed Bulbul	0
<input type="checkbox"/>	<i>Pycnonotus goiavier</i>	Yellow-vented Bulbul	0
<input type="checkbox"/>	<i>Pycnonotus plumosus</i>	Olive-winged Bulbul	0
<input type="checkbox"/>	<i>Pycnonotus simplex</i>	Cream-vented Bulbul	0
<input type="checkbox"/>	<i>Pycnonotus brunneus</i>	Red-eyed Bulbul	0
<input type="checkbox"/>	<i>Pycnonotus erythrophthalmos</i>	Spectacled Bulbul	0
<input type="checkbox"/>	<i>Alophoixus bres</i>	Grey-cheeked Bulbul	0
<input type="checkbox"/>	<i>Alophoixus phaeocephalus</i>	Yellow-bellied Bulbul	0
<input type="checkbox"/>	<i>Setornis criniger</i>	Hook-billed Bulbul	+

<input type="checkbox"/>	<i>Tricholestes criniger</i>	Hairy-backed Bulbul	0
<input type="checkbox"/>	<i>Ixos malaccensis</i>	Streaked Bulbul	0
<input type="checkbox"/>	<i>Hypisipetes flavala</i>	Ashy Bulbul	+
<input type="checkbox"/>	<i>Dicrurus annectans</i>	Crow-billed Drongo	+
<input type="checkbox"/>	<i>Dicrurus aeneus</i>	Bronzed Drongo	0
<input type="checkbox"/>	<i>Dicrurus paradiseus</i>	Greater Racket-tailed Drongo	0
<input type="checkbox"/>	<i>Oriolus xanthonotus</i>	Dark-throated Oriole	0
<input type="checkbox"/>	<i>Irena puella</i>	Asian Fairy Bluebird	0
<input type="checkbox"/>	<i>Platylophus galericulatus</i>	Crested Jay	+
<input type="checkbox"/>	<i>Platymurus leucopterus</i>	Black Magpie	0
<input type="checkbox"/>	<i>Corvus enca</i>	Slender-billed Crow	0
<input type="checkbox"/>	<i>Pityriasis gymnocephala</i>	Bornean Bristlehead	0
<input type="checkbox"/>	<i>Sitta frontalis</i>	Velvet-fronted Nuthatch	0
<input type="checkbox"/>	<i>Pellorneus capistratum</i>	Black-capped Babbler	0
<input type="checkbox"/>	<i>Trichastoma rostratum</i>	White-chested Babbler	0
<input type="checkbox"/>	<i>Trichaster bicolor</i>	Ferruginous Babbler	+
<input type="checkbox"/>	<i>Malacocincla malaccense</i>	Short-tailed Babbler	0
<input type="checkbox"/>	<i>Malacopteron magnirostre</i>	Moustached Babbler	+
<input type="checkbox"/>	<i>Malacopteron affine</i>	Sooty-capped Babbler	0
<input type="checkbox"/>	<i>Malacopteron cinereum</i>	Scaly-crowned Babbler	0
<input type="checkbox"/>	<i>Malacopteron magnum</i>	Rufous-crowned Babbler	0
<input type="checkbox"/>	<i>Malacopteron albogulare</i>	Grey-breasted Babbler	-
<input type="checkbox"/>	<i>Pomatorhinus montanus</i>	Chestnut-backed Scimitar-Babbler	0
<input type="checkbox"/>	<i>Kenopia striata</i>	Striped Wren-Babbler	-
<input type="checkbox"/>	<i>Stachyris rufifrons</i>	Rufous-fronted Babbler	+
<input type="checkbox"/>	<i>Stachyris poliocephala</i>	Grey-headed Babbler	+
<input type="checkbox"/>	<i>Stachyris maculata</i>	Chestnut-rumped Babbler	0
<input type="checkbox"/>	<i>Stachyris nigricollis</i>	Black-throated Babbler	0
<input type="checkbox"/>	<i>Stachyris erythroptera</i>	Chestnut-winged Babbler	0
<input type="checkbox"/>	<i>Macronous gularis</i>	Striped Tit-Babbler	0
<input type="checkbox"/>	<i>Macronous ptilosus</i>	Fluffy-backed Tit-Babbler	0
<input type="checkbox"/>	<i>Alcippe brunneicauda</i>	Brown Fulvetta	+
<input type="checkbox"/>	<i>Yuhina zantholeuca</i>	White-bellied Yuhina	0
<input type="checkbox"/>	<i>Erithacus cyane</i>	Siberian Blue Robin	+
<input type="checkbox"/>	<i>Copsychus saularis</i>	Magpie Robin	0
<input type="checkbox"/>	<i>Copsychus malabaricus</i>	White-rumped Shama	0
<input type="checkbox"/>	<i>Copsychus stricklandi</i>	White-browed Shama	+
<input type="checkbox"/>	<i>Trichixox pyrrhopygus</i>	Rufous-tailed Shama	+
<input type="checkbox"/>	<i>Enicurus ruficapillus</i>	Chestnut-naped Forktail	0
<input type="checkbox"/>	<i>Enicurus leschenaulti</i>	White-crowned Forktail	0
<input type="checkbox"/>	<i>Myiophoneus melanurus</i>	Sunda Whistling-Thrush	+
<input type="checkbox"/>	<i>Gerygone sulphurea</i>	Golden-bellied Gerygone	+
<input type="checkbox"/>	<i>Orthotomus atrogularis</i>	Dark-necked Tailorbird	0
<input type="checkbox"/>	<i>Orthotomus ruficeps</i>	Ashy Tailorbird	0
<input type="checkbox"/>	<i>Orthotomus sericeus</i>	Rufous-tailed Tailorbird	0
<input type="checkbox"/>	<i>Prinia flaviventris</i>	Yellow-bellied Prinia	0
<input type="checkbox"/>	<i>Rhinomyias umbratilis</i>	Grey-chested Jungle-Flycatcher	0
<input type="checkbox"/>	<i>Muscicapa sibirica</i>	Dark-sided Flycatcher	+
<input type="checkbox"/>	<i>Muscicapa dauurica latirostris</i>	Asian Brown Flycatcher	0
<input type="checkbox"/>	<i>Muscicapa thalassina</i>	Verditer Flycatcher	0
<input type="checkbox"/>	<i>Ficedula narcissina</i>	Narcissus Flycatcher	+
<input type="checkbox"/>	<i>Cyornis unicolour</i>	Pale-blue Flycatcher	+
<input type="checkbox"/>	<i>Cyornis caerulatus</i>	Large-billed Blue Flycatcher	+
<input type="checkbox"/>	<i>Cyornis superbus</i>	Bornean Blue-Flycatcher	+
<input type="checkbox"/>	<i>Cyornis turcosus</i>	Malaysian Blue-Flycatcher	0
<input type="checkbox"/>	<i>Culicicapa ceylonensis</i>	Grey-headed Flycatcher	0
<input type="checkbox"/>	<i>Rhipidura perlata</i>	Spotted Fantail	0
<input type="checkbox"/>	<i>Rhipidura javanica</i>	Pied Fantail	0
<input type="checkbox"/>	<i>Hypothymis azurea</i>	Black-naped Monarch	0
<input type="checkbox"/>	<i>Philentoma velatum</i>	Maroon-breasted Philentoma	0
<input type="checkbox"/>	<i>Philentoma pyrhopterum</i>	Rufous-winged Philentoma	0
<input type="checkbox"/>	<i>Terpsiphone paradisi</i>	Asian Paradise Flycatcher	0
<input type="checkbox"/>	<i>Pachycephala grisola</i>	Mangrove Whistler	-
<input type="checkbox"/>	<i>Motacilla cinerea</i>	Grey Wagtail	0
<input type="checkbox"/>	<i>Artamus leucorhynchus</i>	White-breasted Wood-Swallow	0
<input type="checkbox"/>	<i>Gracula religiosa</i>	Hill Myna	0
<input type="checkbox"/>	<i>Anthreptes simplex</i>	Plain Sunbird	0
<input type="checkbox"/>	<i>Anthreptes malacensis</i>	Plain-throated Sunbird	0
<input type="checkbox"/>	<i>Anthreptes rhodolaema</i>	Red-throated Sunbird	+
<input type="checkbox"/>	<i>Anthreptes singalensis</i>	Ruby-cheeked Sunbird	0
<input type="checkbox"/>	<i>Hypogramma hypogrammicum</i>	Purple-naped Sunbird	0
<input type="checkbox"/>	<i>Anthreptes siparaja</i>	Crimson Sunbird	-
<input type="checkbox"/>	<i>Arachnothera longirostra</i>	Little Spiderhunter	0

<input type="checkbox"/>	<i>Arachnothera robusta</i>	Long-billed Spiderhunter	0
<input type="checkbox"/>	<i>Arachnothera flavigaster</i>	Spectacled Spiderhunter	+
<input type="checkbox"/>	<i>Arachnothera chrysogenys</i>	Yellow-eared Spiderhunter	0
<input type="checkbox"/>	<i>Arachnothera affinis</i>	Grey-breasted Spiderhunter	+
<input type="checkbox"/>	<i>Prionochilus thoracicus</i>	Scarlet-breasted Flowerpecker	0
<input type="checkbox"/>	<i>Prionochilus maculatus</i>	Yellow-breasted Flowerpecker	0
<input type="checkbox"/>	<i>Prionochilus xanthopygius</i>	Yellow-rumped Flowerpecker	0
<input type="checkbox"/>	<i>Prionochilus percussus</i>	Crimson-breasted Flowerpecker	+
<input type="checkbox"/>	<i>Dicaeum trigonostigma</i>	Orange-bellied Flowerpecker	0
<input type="checkbox"/>	<i>Passer montanus</i>	Eurasian Tree Sparrow	0
<input type="checkbox"/>	<i>Erythrura prasina</i>	Pin-tailed Parrotfinch	-
<input type="checkbox"/>	<i>Lonchura leucogastra</i>	White-bellied Munia	+
<input type="checkbox"/>	<i>Lonchura fuscans</i>	Dusky Munia	0
<input type="checkbox"/>	<i>Lonchura malacca</i>	Black-headed Munia	0

APPENDIX 2

Fig variables (mean \pm SE) used in the calculation of pulp water content, relative yield and seed burden according to the following formulae:

$$\text{Pulp water content} = ((\text{pulp wet mass} - \text{pulp dry mass}) / \text{pulp wet mass}) \times 100$$

$$\text{Seed burden} = (\text{wet floral mass} / \text{total wet mass}) \times 100$$

$$\text{Relative yield} = (\text{dry pulp mass} / \text{total wet mass}) \times 100$$

<i>Ficus species</i>	Wet pulp mass (g)	Wet floral mass (g)	Dry pulp mass (g)	Dry floral mass (g)
<i>F. aurata</i>	0.331 \pm 0.015	0.137 \pm 0.011	0.078 \pm 0.0119	0.033 \pm 0.006
<i>F. brunneo-aurata</i>	0.654 \pm 0.031	0.364 \pm 0.019	0.087 \pm 0.0047	0.066 \pm 0.015
<i>F. callicarpoides</i>	0.025 \pm 0.002	0.019 \pm 0.002	0.009 \pm 7 \times 10 ⁻¹¹	0.009 \pm 7 \times 10 ⁻¹¹
<i>F. condensa</i>	2.616 \pm 0.161	0.639 \pm 0.028	0.476 \pm 0.0225	0.221 \pm 0.011
<i>F. cereicarpa</i>	35.39 \pm 1.423	7.757 \pm 0.382	3.224 \pm 0.1962	0.887 \pm 0.034
<i>F. deltoidea</i>	0.272 \pm 0.024	0.193 \pm 0.023	0.034 \pm 0.0027	0.085 \pm 0.011
<i>F. fulva</i>	0.848 \pm 0.142	0.461 \pm 0.099	0.147 \pm 0.0404	0.138 \pm 0.033
<i>F. grossivenis</i>	0.262 \pm 0.014	0.158 \pm 0.014	0.042 \pm 0.0025	0.033 \pm 0.004
<i>F. geocharis</i>	6.689 \pm 0.343	2.152 \pm 0.128	0.638 \pm 0.0413	0.594 \pm 0.039
<i>F. auriantacea</i>	34.32 \pm 1.966	11.86 \pm 1.303	3.875 \pm 1.3811	4.485 \pm 0.355
<i>F. urnigera</i>	0.129 \pm 0.006	0.127 \pm 0.006	0.05 \pm 0.0042	0.031 \pm 0.003
<i>F. lanata</i>	0.021 \pm 0.003	0.021 \pm 4 \times 10 ⁻⁴	0.011 \pm 4 \times 10 ⁻⁴	0.011 \pm 4 \times 10 ⁻⁴
<i>F. megaleia</i>	6.689 \pm 0.343	2.152 \pm 0.128	0.638 \pm 0.0413	0.593 \pm 0.039
<i>F. obscura</i>	0.172 \pm 0.012	0.143 \pm 0.012	0.024 \pm 0.0024	0.013 \pm 0.002
<i>F. punctata</i>	34.31 \pm 1.966	11.86 \pm 1.303	3.875 \pm 0.1881	4.485 \pm 0.355
<i>F. rubrocospidata</i>	0.031 \pm 0.002	0.073 \pm 0.031	0.005 \pm 3 \times 10 ⁻¹¹	0.005 \pm 3 \times 10 ⁻¹¹
<i>F. sarawakensis</i>	4.654 \pm 0.335	1.771 \pm 0.103	0.509 \pm 0.0382	0.412 \pm 0.027
<i>F. schwartzii</i>	6.595 \pm 0.301	2.088 \pm 0.155	0.793 \pm 0.0293	0.662 \pm 0.029
<i>F. sinuata</i>	0.022 \pm 0.002	0.031 \pm 0.002	0.005 \pm 4 \times 10 ⁻¹¹	0.005 \pm 4 \times 10 ⁻¹¹
<i>F. stolonifera</i>	1.216 \pm 0.112	0.404 \pm 0.043	0.136 \pm 0.0158	0.072 \pm 0.016
<i>F. subulata</i>	0.371 \pm 0.033	0.102 \pm 0.011	0.058 \pm 0.0058	0.025 \pm 0.004
<i>F. treubii</i>	1.289 \pm 0.077	0.378 \pm 0.025	0.148 \pm 0.0115	0.129 \pm 0.021
<i>F. uncinata</i>	3.595 \pm 0.184	1.214 \pm 0.103	0.333 \pm 0.0144	0.288 \pm 0.036
<i>F. near uncinata</i>	3.892 \pm 0.149	1.004 \pm 0.053	0.466 \pm 0.0302	0.345 \pm 0.033
<i>F. uniglandulosa</i>	0.226 \pm 0.009	0.072 \pm 0.006	0.038 \pm 0.0024	0.008 \pm 4 \times 10 ⁻⁷
<i>F. acampthophylla</i>	0.308 \pm 0.015	0.292 \pm 0.018	0.087 \pm 0.0052	0.176 \pm 0.013
<i>F. annulata</i>	28.85 \pm 0.999	4.339 \pm 0.183	2.935 \pm 0.0816	0.818 \pm 0.015
<i>F. benjamina</i>	0.247 \pm 0.013	0.184 \pm 0.016	0.065 \pm 0.0039	0.074 \pm 0.004
<i>F. callophylla</i>	0.513 \pm 0.021	0.247 \pm 0.019	0.167 \pm 0.0091	0.103 \pm 0.008
<i>F. consociata</i>	0.635 \pm 0.026	0.321 \pm 0.013	0.237 \pm 0.0102	0.166 \pm 0.007
<i>F. cucurbitina</i>	6.263 \pm 0.324	1.557 \pm 0.108	0.694 \pm 0.0423	0.591 \pm 0.039
<i>F. dubia</i>	6.488 \pm 0.354	1.524 \pm 0.087	1.043 \pm 0.0391	0.397 \pm 0.024
<i>F. kerkhovenii</i>	0.256 \pm 0.016	0.301 \pm 0.031	0.082 \pm 0.0041	0.097 \pm 0.006
<i>F. pellucidopunctata</i>	0.523 \pm 0.036	0.175 \pm 0.015	0.106 \pm 0.0058	0.165 \pm 0.094
<i>F. pisocarpa</i>	0.513 \pm 0.016	0.579 \pm 0.024	0.134 \pm 0.0053	0.151 \pm 0.007
<i>F. stupenda</i>	9.742 \pm 0.415	5.043 \pm 0.561	1.862 \pm 0.0717	1.321 \pm 0.052
<i>F. subcordata</i>	12.06 \pm 1.118	5.185 \pm 0.347	1.894 \pm 0.1727	1.862 \pm 0.113
<i>F. subgelderi</i>	0.865 \pm 0.081	0.441 \pm 0.049	0.271 \pm 0.0169	0.241 \pm 0.017
<i>F. sumatrana</i>	0.827 \pm 0.082	0.476 \pm 0.035	0.292 \pm 0.0138	0.255 \pm 0.013
<i>F. sundaica</i>	0.836 \pm 0.034	0.342 \pm 0.021	0.097 \pm 0.0078	0.186 \pm 0.009
<i>F. retusa</i>	0.165 \pm 0.009	0.125 \pm 0.007	0.032 \pm 0.0029	0.023 \pm 0.002
<i>F. xylophylla</i>	7.907 \pm 0.749	2.545 \pm 0.287	1.965 \pm 0.0537	1.179 \pm 0.094
<i>F. stricta</i>	1.865 \pm 0.222	1.141 \pm 0.131	0.259 \pm 0.0232	0.422 \pm 0.047

APPENDIX 3

Vertebrate species and genera from Lambir Hills National Park for which fig eating has been recorded in addition to those observed in this study. Lambir faunal list from Shanahan & Debski (in press; Appendix 1). A = record of fig eating exists for animal listed, C = record of fig eating exists for congener of species listed (see Chapter 7). Nomenclature follow MacKinnon and Phillipps (1993) and Payne *et al.* (1985) for birds and mammals, respectively.

Class	Order	Family	Common Name	Scientific name			
MAMMALIA	Scandentia	Tupaidae	Striped Treeshrew	<i>Tupaia dorsalis</i>	C		
	Primates	Cercopithecidae	Banded Langur	<i>Presbytis melalophos</i>	A		
			Hose's Langur	<i>Presbytis hosei</i>	C		
	Chiroptera	Hylobatidae	Bornean Gibbon	<i>Hylobates muelleri</i>	A		
			Lucas's Short-nosed Fruit Bat	<i>Penthetor lucasii</i>	A		
		Pteropodidae	Lesser Dog-faced Fruit Bat	<i>Cynopterus brachyotis</i>	A		
			Black-capped Fruit Bat	<i>Chironax melanocephalus</i>	A		
	Artiodactyla	Tragulidae	Greater Mouse-Deer	<i>Tragulus napu</i>	C		
		Cervidae	Sambar Deer	<i>Cervus unicolor</i>	C		
	Carnivora		Viverridae	Bornean Red Muntjac	<i>Muntiacus muntjak</i>	A	
		Common Palm Civet		<i>Paradoxurus hermaphroditus</i>	A		
	MAMMALIA	Carnivora	Viverridae	Malay Civet	<i>Viverra zangalunga</i>	C	
				Sun Bear	<i>Helarctos malayanus</i>	A	
		Rodentia	Ursidae	unidentified mongoose	<i>Herpestes</i> sp.	C	
			Herpestidae	Polynesian Rat	<i>Rattus exulans</i>	C	
		Rodentia	Muridae	Horse-tailed Squirrel	<i>Sundasciurus hippurus</i>	C	
			Sciuridae	Low's Squirrel	<i>Sundasciurus lowii</i>	A	
		AVES	Galliformes	Phasianidae	Crested Fireback	<i>Lophura ignita</i>	A
					Crestless Fireback	<i>Lophura erythrophthalma</i>	C
			Piciformes	Indicatoridae	Malaysian Honeyguide	<i>Indicator archipelagicus</i>	C
Picidae					Olive-backed Woodpecker	<i>Dinopium rafflesii</i>	C
Bucerotiformes	Bucerotidae		Helmeted Hornbill	<i>Buceros vigil</i>	A		
Coraciiformes	Daceloniidae		Banded Kingfisher	<i>Lacedo pulchela</i>	A		
AVES	Trogoniformes		Trogonidae	Diard's Trogon	<i>Harpactes diardi</i>	A	
				Red-naped Trogon	<i>Harpactes kasumba</i>	C	
				Scarlet-rumped Trogon	<i>Harpactes duvaucelii</i>	C	
				Short-toed Coucal	<i>Centropus rectunguis</i>	C	
	Cuculiformes		Centropodidae	Greater Coucal	<i>Centropus sinensis</i>	C	
				Lesser Coucal	<i>Centropus bengalensis</i>	C	
				Moustached Hawk-Cuckoo	<i>Cuculus vagans</i>	C	
				Indian Cuckoo	<i>Cuculus micropterus</i>	C	
			Cuculidae	Banded Bay-Cuckoo	<i>Cacomantis sonnerati</i>	C	
				Plaintive Cuckoo	<i>Cacomantis merulinus</i>	C	
				Hodgson's Hawk-Cuckoo	<i>Cuculus fugax</i>	C	
				Rock Pigeon	<i>Columba livia</i>	A	
Columbiformes	Columbidae		Spotted Dove	<i>Streptopelia chinensis</i>	A		
			White-breasted Waterhen	<i>Amauormis phoenicurus</i>	A		
Gruiformes	Rallidae		Yellow-bellied Prinia	<i>Prinia flaviventris</i>	C		
AVES	Passeriformes		Cisticolidae	Fiery Minivet	<i>Pericrocotus igneus</i>	A	
				Scarlet Minivet	<i>Pericrocotus flammeus</i>	A	
			Corvidae	Green Iora	<i>Aegithina viridissima</i>	A	
				Common Iora	<i>Aegithina tiphia</i>	A	
				Bar-bellied Cuckoo-Shrike	<i>Coracina striata</i>	A	
				Lesser Cuckoo-Shrike	<i>Coracina fimbriata</i>	C	
				Large Woodshrike	<i>Tephrodornis gularis</i>	C	
				Crow-billed Drongo	<i>Dicrurus annectans</i>	C	
				Bronzed Drongo	<i>Dicrurus aeneus</i>	C	
		Greater Racket-tailed Drongo		<i>Dicrurus paradieus</i>	C		
		Banded Broadbill		<i>Eurylaimus javanicus</i>	A		
		Black-and-yellow Broadbill		<i>Eurylaimus ochromalus</i>	A		
		Muscicapidae		White-rumped Shama	<i>Copsychus malabaricus</i>	C	
				White-browed Shama	<i>Copsychus stricklandi</i>	C	
	Nectariniidae	Rufous-winged Philentoma	<i>Philentoma pyrhopterum</i>	C			
		Plain-throated Sunbird	<i>Anthreptes malacensis</i>	A			
		Yellow-breasted Flowerpecker	<i>Prionochilus maculatus</i>	A			
		Plain Sunbird	<i>Anthreptes simplex</i>	C			
		Red-throated Sunbird	<i>Anthreptes rhodolaema</i>	C			
		Ruby-cheeked Sunbird	<i>Anthreptes singalensis</i>	C			
	Passeridae	Crimson Sunbird	<i>Anthreptes siparaja</i>	C			
		Eurasian Tree Sparrow	<i>Passer montanus</i>	A			
		Pin-tailed Parrot Finch	<i>Erythrura prasina</i>	C			
		Pycnonotidae	Grey-bellied Bulbul	<i>Pycnonotus cyaniventris</i>	A		
			Ashy Bulbul	<i>Hemixos flava</i>	A		
		Sylviidae	Straw-headed Bulbul	<i>Pycnonotus zeylanicus</i>	A		
Black and white Bulbul			<i>Pycnonotus melanoleucos</i>	A			
Chestnut-backed Scimitar-Babbler			<i>Pomatorhinus montanus</i>	A			
Black-capped Babbler			<i>Pellorneum capistratum</i>	C			
REPTILIA		Squamata	Varanidae	Monitor Lizard	<i>Varanus salvator</i>	C	

APPENDIX 4

Fig size indices

In situations where it is not possible to weigh figs an index based on fig length and diameter can be used as a measure of fig size. Using the data collected in Lambir Hills National Park (Chapter 3) I tested a number of different indices to see which was the best predictor of fig mass. Fig index C provided the best approximation of fig mass and was used in the analyses of Chapter 6.

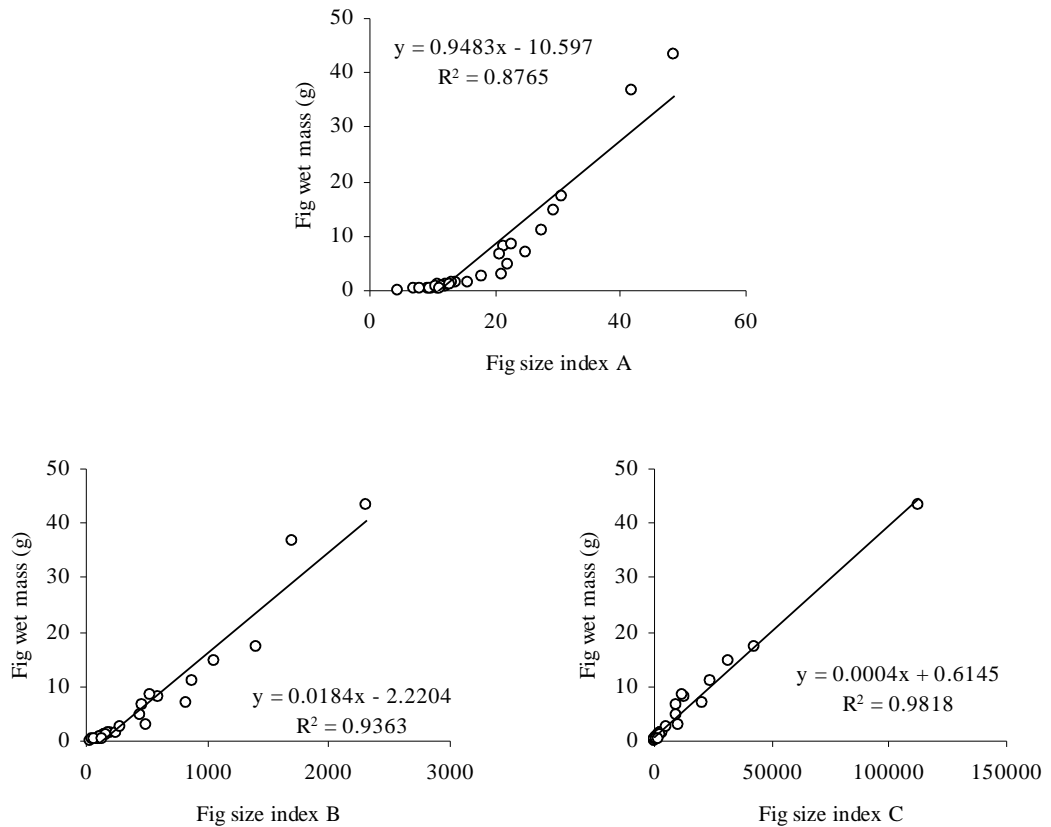


Figure 1. Relationships between fig wet mass and fig size indices. Fig size index A = fig diameter. Fig size index B = diameter \times length. Fig size index C = diameter² \times length.

APPENDIX 5

&

APPENDIX 6

To save space in this edition of the thesis, Appendix 5 (*Ficus* species and their known frugivores) and Appendix 6 (Fig eating vertebrates and the *Ficus* species they consume) have been omitted but can be found in the original format at the following internet sites:

<http://www.geocities.com/mikeshanahan/figs/figreview.html>

or

<http://go.to/figs>