

More Examples of Fruiting Trees Visited Predominantly by Birds of Paradise

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Summary: Based on observations at Varirata National Park, Papua New Guinea, we document and characterise two Papuan tree species in the mahogany family (Meliaceae) whose fruit were consumed only by birds of paradise (family Paradisaeidae), and a third tree of the nutmeg family (Myristicaceae) whose fruit were predominantly consumed by birds of paradise. These three plant species exhibited differing degrees of forager specificity, with the Raggiana Bird of Paradise *Paradisaea raggiana* being the numerically dominant forager at all three plants (80% to 97% of all for-

aging records). All three plants produce structurally protected fruit. By contrast, parallel observations of avian foraging at two foodplants with structurally unprotected fruit documented visitation by diverse frugivore assemblages, more typical of previous studies of foraging at tropical fruiting trees. These data reinforce earlier field observations of restricted paradisaeid foraging assemblages at selected tree species in a forest in the uplands of the northern watershed of Papua New Guinea, and point to the existence of what may be a specialised plant/frugivore syndrome.

Although initial studies of tropical forest communities stressed the intricacy of plant-animal interactions as a key component of these systems (Ehrlich & Raven 1964; Janzen 1966; McKey 1975), more recent analyses (Herrera 1982; Wheelwright & Orians 1982; Schemske 1983; Howe 1984, 1993) have indicated that tight, co-evolved mutualisms are, in fact, relatively rare. Recent field studies of vertebrate-mediated seed dispersal, most of which have been conducted in the neotropics (e.g. McDiarmid et al. 1977; Howe 1982; Wheelwright et al. 1984; Levey 1987), have typically highlighted the diffuse nature of this form of plant-animal interaction. In many instances, even the foodplants with the most morphologically complex fruits have been shown to attract a considerable range of foragers (Howe 1984), often from several or many vertebrate families (Wheelwright & Orians 1982). The oft-cited example of the endemic Mauritius tree *Calvaria major* that purportedly depended on a single bird (the now extinct Dodo *Raphys cucullatus*) for mechanical processing of the seed and its subsequent dispersal (Temple 1977), was based on a hypothetical association rather than direct field observation. We know of no published cases describing plant species dispersed by a single animal species. The tight mistletoe-flowerpecker interactions postulated by Davidar are not supported by published field data (Ali 1931; Docters van Leeuwen 1954; Davidar 1978, 1987).

In his review of the literature of vertebrate fruit for-

aging and dispersal, Howe (1984) reported that the taxonomically most restricted dispersal systems documented involve birds of paradise (Paradisaeidae) and several species of rainforest trees in New Guinea (Beehler 1983, 1988; Pratt & Stiles 1985). In these, a small suite of species of birds of paradise served as the sole or dominant foragers and dispersers. In those papers it was argued that certain Melanesian forest trees may depend upon a single taxonomic group, the Paradisaeidae, for dispersal of their seeds.

A major weakness of the initial field observations of both Beehler and Pratt & Stiles is that they were made at a single locality, Mount Missim, Morobe Province, Papua New Guinea (PNG). Were these results simply a product of limited sampling? In addition, nutritional content of the fruit of the specialised foodplants was not presented in these preliminary studies. These data are useful for testing the predicted relationships between fruit morphology, fruit nutrition, and specialised foraging systems (McKey 1975; Pijl 1983; Beehler 1983, 1989). Most relevant to this particular study, it was predicted that plants producing nutritionally rich fruit in structurally protected woody capsules (exemplified in Papua New Guinea by species of Meliaceae and Myristicaceae) would be dispersed by a small subset of the animal frugivores in the environment. By contrast, small, nutritionally poor, unprotected fruit (exemplified

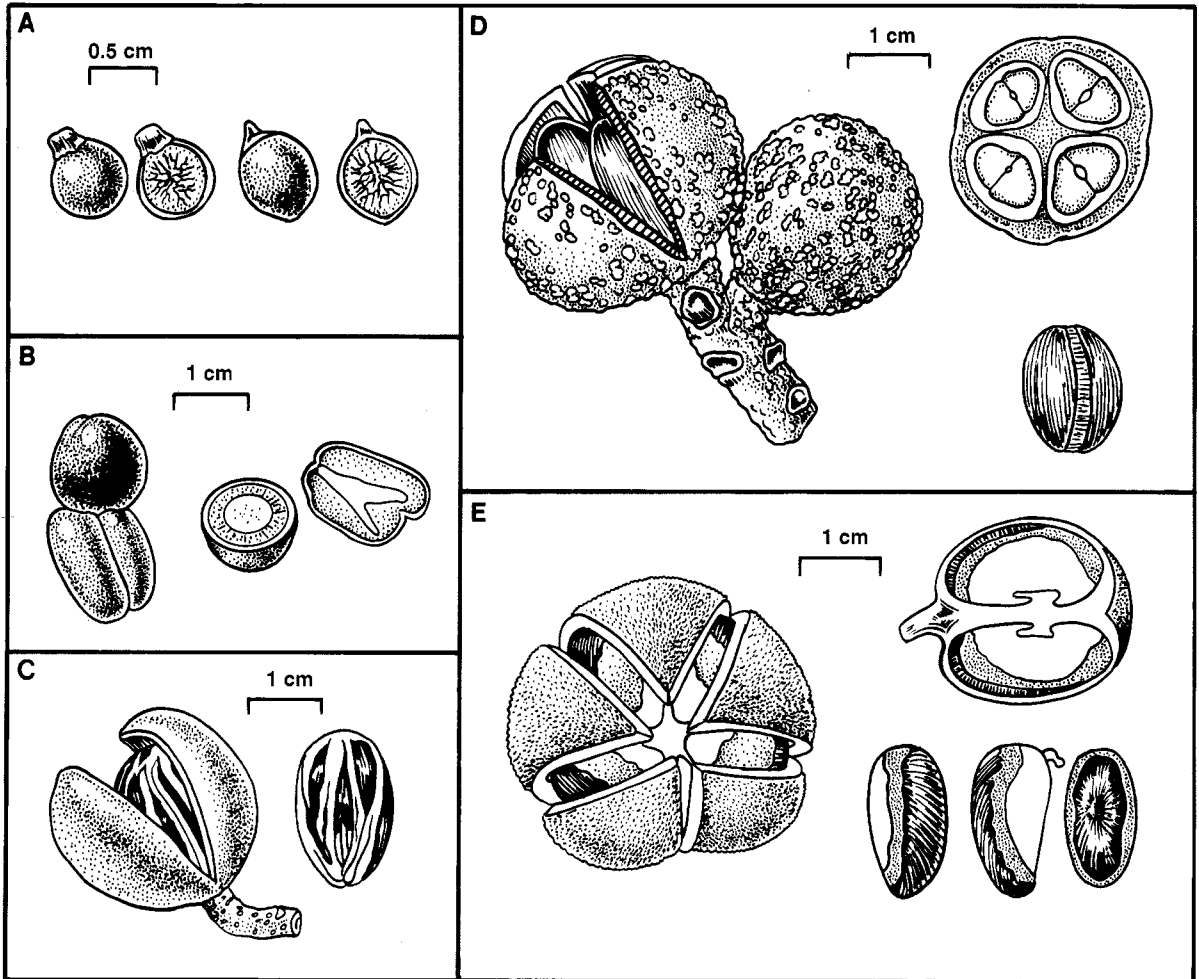


Figure 1 Fruit of the five focal plant species. A. *Ficus cf. obliqua*. B. *Podocarpus nereifolius*. C. *Myristica* species '#008'. D. *Dysoxylum peltigrewianum*. E. *Chisocheton lasiocarpus*. Drawn by Alice Tangerini.

by the figs in PNG) would be dispersed by a broad subset of animal foragers.

In order to examine the relationship between fruit nutrition and morphology vs forager specificity, we present the results of observations at five species of fruit tree at a second location in Papua New Guinea.

Study site and methods

During June–July 1989, April–August 1990, September 1991 and February 1992, as part of a study of the biology of the Raggiana Bird of Paradise *Paradisaea rag-*

giana, we monitored diurnal foraging at five rainforest fruiting tree species at Varirata National Park, Papua New Guinea (9°27'S, 147°21'E; 820 m asl). This site is c. 250 km south of the site of the original bird-plant studies (Mount Missim, 1480–1750 m asl), in the southern (as opposed to northern) watershed, and at a lower elevation. The new field site thus represented a biogeographically and ecologically distinct sampling area (Diamond 1972; Pratt 1982).

We focused on fruiting trees that were used by the Raggiana Bird of Paradise. Based on our knowledge of Papuan bird/fruit tree systems from earlier fieldwork

Table 1 Summary data on foodplants.

Species	Family	Fruit type	Fruit size ¹	Edible part	% Lipid	% Protein	% Carbohydrate	Crop size
<i>Ficus cf. obliqua</i>	Moraceae	Berry	5x6-6x7	Same	5	5	1.6	>100 000
<i>Podocarpus nereifolius</i>	Podocarpaceae	Drupe	12x27-13x32	Same	0.7	3.5	15.7	16 000
<i>Myristica</i> 'spp. #008'	Myristicaceae	Dehiscent capsule	18x24-20x26	8x14-11x17	57	6	1.9	100-200
<i>Chisocheton lasiocarpus</i>	Meliaceae	Dehiscent capsule	21x21-31x31	8x14-11x25	60	10.5	1	400
<i>Dysoxylum peltigrewianum</i>	Meliaceae	Dehiscent capsule	15x16-25x26	9x18-10x20	35	13	6.6	2000-3000

¹ All measurements in mm.

(Beehler 1983, 1988; Pratt 1983; Pratt & Stiles 1985), we selected a series of tree species that by fruit morphology we predicted would exhibit one of two distinct patterns of avian frugivore use, one with many forager species visiting the plant, the other with few. By comparing the avian assemblages visiting trees of these two plant types, we hoped to demonstrate that the restricted forager subset visiting the plants with structurally protected fruit was but a small subset of active fruit-eaters in the forest at the time and not just a sampling artifact.

The focal plant species (Table 1, Fig. 1) were as follows: *Ficus cf. obliqua*, an emergent strangler fig of the section *Xylosyca*, with structurally unprotected fruit (Fig. 1a), monitored in 1989 and 1990; *Podocarpus nereifolius* (Podocarpaceae), a large canopy tree with structurally unprotected fruit (Fig. 1b), monitored in 1990; *Myristica* sp. #008 (Myristicaceae), a common understory tree with structurally protected fruit (Fig. 1c), monitored in 1989; *Dysoxylum cf. peltigrewianum* (Meliaceae), a medium-to-large canopy tree with structurally protected fruit (Fig. 1d), monitored in 1990 and 1991; and *Chisocheton cf. lasiocarpus* (Meliaceae), an understory tree with structurally protected fruit (Fig. 1e), monitored in 1990 and 1992. The latter three species produce structurally protected arillate woody capsules postulated to be typical 'bird of paradise fruit' by Beehler (1983).

Our selection of focal species and the timing of our observations were limited by the availability of trees producing ripe fruit. In PNG forests, few trees produce ripe fruit at any one time and many species produce fruit only every second or third year. Within the limitations of our field seasons, it was thus impossible for us to construct an 'experiment' where trees with particular

characteristics fruited side-by-side at the same time. Nonetheless, we monitored trees from a single patch of forest no more than a kilometre in diameter.

Published observations on Papuan frugivores and nectarivores indicate that the avian foragers will disregard typical microhabitat preferences to forage on favoured food resources (Beehler 1994).

Observations at fruit trees were made by the authors and several field assistants, as follows: 1989 (JPD, BMB, Bulisa Iova, Mark Laska), 1990 (JPD, BMB, William E. Davis, Jill Heath, David Heath, Bulisa Iova, Michael Lucas), 1991 (Bulisa Iova) and 1992 (Bulisa Iova).

For all five foodplants, birds are the primary or exclusive foragers and dispersers. We did not monitor the fate of fruit that fell to the ground below the parent tree, nor did we study incidental dispersal by terrestrial seed predators (mostly invertebrates and rodents). For the *Ficus* strangler, we documented incidental nocturnal foraging by the pteropodid bat *Dobsonia moluccensis*, and at both the *Ficus* and the *Podocarpus* we would expect additional incidental seed predation by several marsupial taxa (e.g. *Phalanger* and perhaps *Pseudocheirus*). Only birds are known to be regular foragers and dispersers of the foodplants with structurally protected fruit (Pratt & Stiles 1985; Beehler 1983, 1988).

For each of the five focal plant species, we documented:

(1) The birds visiting each tree species. We included only instances in which foragers entered the plant to feed on fruit, following the methods outlined in Beehler (1983). For each species we attempted to accumulate at least 100 separate forager visits. For *Myristica*, we observed at six fruiting individuals; for *Dysoxylum* and

Ficus, two individuals; and for the two other tree species, a single individual each. For each tree species, Shannon-Weiner indices of diversity are provided for each forager assemblage.

(2) Fruit crop size, estimated using the method outlined in Beehler (1985).

(3) Fruit morphology, all physical aspects of the fruit/seed/aril package relevant to the forager. Samples of each fruit were preserved in ethanol and as botanical specimens deposited in the herbaria of the University of Papua New Guinea and the United States National Museum.

(4) Dimensions of the edible portion; length and diameter of 20 samples were measured for each species.

(5) Macronutrient content of the edible portion. We collected fresh fruits and removed the seed and inedible portions, and sun-dried the pulp or edible aril for analysis. After initial drying, these samples were then frozen for the remainder of the study season, subsequently dried in a low temperature oven and then tested for dry weight content of lipid, protein and total nonstructural carbohydrate by the University of Alaska Plants and Soils Analysis Laboratory, Palmer, Alaska, USA.

Finally, we provide for the Raggiana Bird of Paradise, at each tree species, the binomial probability of observing at least the recorded number of visits by chance alone (see Appendix 1 for further discussion of this statistical test). This offers a statistical indication of specificity of forager assemblages visiting each tree.

Results

Frugivore use

The forest habitats of Varirata National Park support an avian frugivore assemblage of at least 38 bird species. In addition, there are eight bird species that can be classified as arboreal seed predators (Coates 1985, 1990; Beehler et al. 1986; Beehler 1988).

The foodplants with unprotected fruit were visited by a total of 30 avian forager species (Table 2, Appendix 2). These included 29 fruit-eaters and a single seed eater (the parrot *Alisterus chloropterus*). These plants were visited by all four birds of paradise recorded in the park's forest habitats, yet paradisaeid foragers constituted only 16% of the forager visits to these two plant species with unprotected fruit.

By contrast, the three species of plants with protected fruit were visited by only seven species of foragers; four birds of paradise and three fruit-doves of the genus

Ptilinopus (Table 2, Appendix 2), none of these are seed predators. Visits by birds of paradise constituted 97% of the forager visits to these three foodplants.

The two mahoganies, *Chisocheton* cf. *lasiocarpus* and *Dysoxylum* cf. *pettigrewianum*, were visited only by birds of paradise. For *Dysoxylum*, the Raggiana Bird of Paradise constituted 97% of the avian visits to the tree; for *Chisocheton*, the Raggiana visits constituted 85% of the visits (Table 2).

Fruit morphology and nutrition

The two foodplants with structurally unprotected fruit can be swallowed whole by foraging birds without manipulation. In contrast, the three 'specialised' foodplants produce fruit that is protected within an inedible woody husk; the arillate seed must be prised from the dehiscent capsule. This dichotomy in fruit morphology parallels a dichotomy in measures of the nutritional content of the sample fruit. The combined protein+lipid content of the two unprotected fruits is 10% (*Ficus*) and 4.2% (*Podocarpus*), while that of the structurally protected fruits contain 48% (*Dysoxylum*), 63% (*Myristica*), and 70.5% (*Chisocheton*) (Table 1). The plants with structurally protected fruit produced a forager reward five to 17 times richer in lipid and protein than the generalist foodplants.

Discussion

Our five plant species constitute too small a sample to provide useful insight on the importance of size of the edible portion of the fruit to the development of specific patterns of forager use. Our data, and additional unpublished data, indicate that the size of structurally unprotected fruits varies considerably among plant species in New Guinea. Fruit size, *per se*, can influence which species of foragers will visit a foodplant (Pratt & Stiles 1985). Smaller drupes and berries can be visited by any and all Papuan frugivores. Large drupes are taken primarily by fruit-pigeons, cassowaries and fruit-bats.

Structurally protected fruits, in general, attract a distinct assemblage of foragers, most or all of which will also opportunistically visit the plants with unprotected fruit (Pratt & Stiles 1985). Seed (or edible portion) size of the structurally protected fruits varies considerably (Table 1) but usually is large relative to the size of the entire fruit, or in comparison to the edible part of the fruit. These foodplants produce large-seeded fruits with small but highly nutritious rewards, whereas the un-

Table 2 Summary data on avian foraging.

Plant species	No. of foraging records	Avian families	No. of species	Shannon-Weiner Index	% visits by BOPs ¹	% by most common forager species ²	Chance ³ probability
<i>Ficus cf. obliqua</i>	561	11	28	1.24	16	12	> 0.1
<i>Podocarpus nereifolius</i>	113	4	12	0.959	16	24	> 0.1
<i>Myristica</i> sp.	44	2	6	0.378	84	77	< 0.001
<i>Chisocheton lasiocarpus</i>	199	1	3	0.229	100	85	< 0.001
<i>Dysoxylum peltigrewianum</i>	395	1	3	0.065	100	97	< 0.001

¹ BOP = bird of paradise. ² In all cases but for *Podocarpus*, the single most common forager (by number of visits) is the Raggiana Bird of Paradise. ³ Probability of observing, by chance, this number of foraging visits by the Raggiana Bird of Paradise (see Appendix 2).

protected fruits have a relatively larger amount of less nutritious edible portion. Not all structurally protected fruits in New Guinea are consumed predominantly by birds of paradise (E.D. Brown & M.G. Hopkins unpubl. data); this may be related to fruit size, degree of fruit dehiscence, the shape and thickness of the husk, and the placement of the fruit on the branch.

From a study of foodplants and vertebrate frugivory at a humid forest site in Peru, Janson (1983) concluded that foodplants produce fruit with morphologies that appear to be specifically adapted to either mammalian or avian seed dispersers. The results of our study provide further evidence that in New Guinea, certain tree species may produce fruit taken by a single taxonomic group: the birds of paradise.

A number of researchers provide cogent arguments why seed-dispersal systems are unlikely to develop into tight coevolved mutualisms (Herrera 1982; Wheelwright & Orians 1982). Hurdles to these mutualisms include: (a) noncongruence of geographic ranges of plant and animal; (b) weak selective pressures of dispersers upon their foodplants; (c) longer generation times and slower species turnover with respect to plants; and (d) the advantages to the plant of using a broad range of dispersers.

Whereas we agree with these theoretical constraints, we offer our field observations of apparent counterexamples for consideration. Are there ways in which our examples surmount the constraints? Perhaps some characteristics of the birds in question, and some peculiarities of the Papuan biota, may permit a degree of specialisation not seen in dispersal systems in other biogeographic realms (for detailed arguments see Beehler 1983, 1988, 1989).

Several traits of the Raggiana Bird of Paradise make it a 'safe' mutualist. The species is both widespread and abundant from the lowlands to about 1400 m above sea level, inhabiting both forest and forest-edge. It is apparently an excellent disperser because it does not damage the seeds of the fruit it consumes, it takes only a few fruits per foraging bout and it does not loaf in foraging trees — producing a more even seed rain (Pratt 1983; Beehler 1988, 1989). It forms a part of the *Paradisaea apoda* superspecies that inhabits all of New Guinea and several satellite islands. We assume that these allo-species are equally appropriate dispersers for these specialised foodplants, and thus where the Raggiana is replaced by its sister-form, the latter serves in its stead as the local disperser of seeds for these foodplants. We also believe that the dispersal system has 'back-up' players — secondary dispersers (in the Varirata system represented by the Magnificent Bird of Paradise *Cicinnurus magnificus* and Magnificent Riflebird *Ptiloris magnificus*), which in the absence of *Paradisaea* species may disperse a portion of the seeds of these foodplants. All these species can gain access to structurally protected fruits using their strong and dexterous bills and feet (one presumes originally adapted for scansorial arthropod foraging).

The three morphologically specialised plant species we found at Varirata have nearly identical counterpart species at the Mount Missim study site (see Beehler 1983: Fig 1J, 1L and *Myristica subaluata*, illustrated in Cooper & Forshaw 1977). We thus see very similar morphologies in taxonomically and geographically distinct plant forms.

What peculiarity of the Papuan region might permit the evolution of plants that rely on birds of paradise for

seed dispersal? We believe the absence of most arboreal placental mammals that elsewhere serve as seed predators may have opened the door to the evolution of a foraging/dispersal system that in other regions would be evolutionarily precarious. These structurally protected fruits would be easily accessible to arboreal squirrels that are present in neotropical and south-east Asian forests. In addition, the presence of a primate fauna, usually with taxa that serve both as generalised dispersers and seed predators, would hinder the evolution of fine-tuned systems between plants and birds of paradise. Local primate faunas usually include generalist species that have the ability to invade nearly any fruit dispersal system (Terborgh 1983).

We believe that additional study of these Papuan dispersal systems will provide useful information on the dynamics of restricted bird-plant frugivore systems. The data we present here are incomplete but suggestive. We look forward to future field studies that rigorously test the nature of the paradisaeid-fruit relationship in various habitats in New Guinea, Australia and the Northern Moluccas.

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Appendix 1 Binomial distribution for probabilities of forager specificity.

The Raggiana Bird of Paradise is an extremely common bird in Varirata National Park and one could argue that this might explain its dominant representation in our feeding records on focal fruit trees. If a fruit tree is visited randomly by all frugivorous birds, then the expected proportion of feeding records by any one species follows the binomial distribution. The probability that this tree will be visited by any one species more than x times out of the total number of feeding records, n , by all species, is given by the equation

$$P(X \geq x | n, p) = \sum_{k=x}^n \binom{n}{k} p^k (1-p)^{n-k}$$

where p_i is the proportion of species i of all potential foragers in the park. If this probability is lower than some arbitrary rejection value, then we can say that the tree is visited by that forager more than expected. Since this test examines one tree at a time, the disparity in observations between trees is irrelevant.

This test assumes that we know the relative frequencies of frugivore species in the park, which we do not know. However, we can estimate of the relative frequencies from the data pooled from all of the trees that we watched. This will necessarily inflate our estimate of the relative abundance of the Raggianas in the park because we focused on trees that are favored by this bird species. This introduces a bias against our rejecting the null hypothesis that feeding is random, thus giving us an extremely conservative test of the deviation from random and the specialisation of the 'bird of paradise trees'. Furthermore, we feel that the test is robust only if the experimenter chooses *a priori* which species should be tested for potential specialisation and the trees doing the specialising are highly sampled. For example, the Wompoo Fruit Dove *Ptilinopus magnificus* would have values less than 0.05 for this test in the *Myristica* but the test is not conservative for *P. magnificus* (the relative proportion of *P. magnificus* from our data is low because we did not target trees that they might preferentially use). We thus present the probabilities only for the Raggiana Bird of Paradise and test only the three putative 'specialist' trees.

Appendix 2 Visits by birds to five species of foodplants at Varirata National Park.

Year observed	Plant species ¹							
	FI 1989	FI 1990	PO 1990	MY 1989	CH 1990	CH 1992	DY 1990	DY 1991
Bird species								
COLUMBIDAE								
<i>Ducula rufigaster</i>		2						
<i>Ducula zoeae</i>		5	8					
<i>Ptilinopus perlatus</i>	26	16	12					
<i>Ptilinopus iozonus</i>	38	12	3					
<i>Ptilinopus superbis</i>	35	26	1	1				
<i>Ptilinopus nanus</i>		12						
<i>Ptilinopus pulchellus</i>	32	24	15	2				
<i>Ptilinopus magnificus</i>	7	2	27	4				
<i>Ptilinopus</i> sp.?		6	4					
<i>Gymnophaps albertisii</i>			19					
PSITTACIDAE								
<i>Lorius lory</i>	2							
<i>Alisterus chloropterus</i>			3					
CAMPEPHAGIDAE								
<i>Coracina caeruleo-grisea</i>		5						
<i>Coracina melaena</i>		6						
<i>Coracina lineata</i>	27							
<i>Coracina boyeri</i>		33						
PACHYCEPHALIDAE								
<i>Pitohui dichrous</i>		13	3					
DICAEIDAE								
<i>Dicaeum pectore</i>		4						
<i>Melanocharis nigra</i>		41						
ZOSTEROPIDAE								
<i>Zosterops atrifrons</i>	10	56						
MELIPHAGIDAE								
<i>Philemon buceroides</i>		25						
<i>Xanthotis flaviventer</i>		2						
<i>Pycnopygius stictocephalus</i>	1	4						
<i>Meliphaga</i> sp.	1	25						
STURNIDAE								
<i>Mino dumontii</i>	20	5						
ORIOOLIDAE								
<i>Oriolus szalayi</i>	9	9						
PTILONORHYNCHIDAE								
<i>Chlamydera cerviniventris</i>	3							
PARADISAEIDAE								
<i>Manucodia chalybatas</i>	6	4	6	1			2	
<i>Ptiloris magnificus</i>		18	1		11	3	6	4
<i>Cicinnurus magnificus</i>		1		2	14	2		
<i>Paradisaea raggiana</i>	18	60	11	34	123	46	280	102
Number of observations per tree	235	416	113	44	148	51	288	106
Number of species observed	15	25	12	6	3	3	3	2

¹ *Ficus* (FI), *Podocarpus* (PO), *Myristica* (MY), *Chisocheton* (CH), *Dysoxylum* (DY).