

A BIRD COMMUNITY OF LOWLAND RAINFOREST IN NEW GUINEA. 6 FORAGING ECOLOGY AND COMMUNITY STRUCTURE OF THE AVIFAUNA

H.L. BELL

Department of Zoology, University of New England, Armidale, NSW 2351

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SUMMARY

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The foraging ecology and community structure of 83 co-existing species at Brown River, Papua New Guinea, were analysed. Obligate carnivores, mostly insectivorous, are much more diverse in foraging behaviour than are facultative carnivores. Overlap between insectivorous species may be lower than in similar but depauperate communities in Australian rainforests. Herbivores are separated mostly by differences in weight. Carnivores do not conform to current theory on size-differences between co-existing congeners. It is suggested that the two opposing views, explaining the richness of tropical avifaunas, are both correct. For herbivores the abundance of resources permits wide overlaps between species. For carnivores the complex habitat permits many species to co-exist by finely dividing the habitat.

INTRODUCTION

The great diversity of the tropical biota is well-known. MacArthur & MacArthur (1962) argued convincingly that bird species diversity closely matched the complexity of forest structure but modified their view for the tropics, repeating an earlier statement (Klopfer & MacArthur 1961), that the abundant resources of tropical forests permitted more species to co-exist with wide overlaps in their niches. This accords with other theories (Krebs 1972) on biotic diversity in the tropics, e.g. the Predation Hypothesis of Paine (1966) and the Productivity Hypothesis of Connell & Orias (1964).

The opposing view (e.g. Mayr 1969) is that there are more species of birds in tropical forests because there they can fill a greater number of, but more finely-divided, niches, and thus co-exist. Various theories which support this view are that environmental stability allows more species to evolve in the tropics (Fischer 1960) and adapt to specialized niches (Krebs 1972), that competition is stronger in the tropics and as a result niches are narrower (Dobzhansky 1950) and that spatial heterogeneity (e.g. the various levels of a rainforest canopy) permits niche diversity (MacArthur 1965). Studies of community organization in tropical rainforests may be useful in determining the validity of these two opposing views.

Attention has been paid to community organization of rainforest avifaunas only in comparatively recent years (e.g. Orians 1969; Karr 1971; Pearson 1977). In New Guinea Terborgh & Diamond (1970) reported on niche overlaps of nectarivores and frugivores, Frith *et al.* (1976) gave data on the diets of fruit-pigeons, and

Croxall (1977) studied the foraging of some fifty species of insectivores. Crome (1975, 1978) reported on the closely-related but relatively depauperate bird communities of Australian rainforests in North Queensland.

I made a study of the vertical distribution of a bird community in lowland rainforest, at the Three Mile Experimental Plot, Brown River, Papua New Guinea, from December 1975 to November 1977 (Bell 1982a, b, c, d). The opportunity was taken to record also data on feeding, the substrates foraged upon and the foraging methods used by birds. Some additional data were collected outside the study but in the same general area, and are included.

Here, in the final paper of this series, I analyse the partitioning of resources among those species for which sufficient data were collected and attempt to show which factors are most important in the structuring of the bird community at Brown River.

STUDY AREA AND METHODS

The study area, of 2.5 ha, described by Bell (1982a), was reasonably undisturbed lowland rainforest. The mean annual rainfall is 2010 mm (data from Port Moresby Regional Forestry Office), the majority of which falls between December and June. Of 165 species of birds recorded about 110 were resident; additionally there were 19 more species known to occur in the immediate area. The forest conformed to the description of lowland rainforest by Richards (1952), with a canopy at *ca* 30-35 m with a few emergents, a sparser sub-canopy at 8-25 m and an understorey at *ca* 0-8 m.

I visited the site for at least thirty-six hours each month in 1975/76 and for twenty-four hours each month in 1976/77, observations being evenly spaced between 06:00 and 18:00. All birds seen were recorded by one of eleven height categories

(Bell 1982c), one record being one bird at the height where first seen. In addition, if time and visibility permitted, I recorded foraging data. Where animal prey was captured or sought I noted height, substrate and foraging methods used. Substrates were: ground, air (for aerial feeding), trunk, branch, leaf, logs/stumps, vines (those pendant from the canopy), termitaria, cane-grass, palm-fronds and debris (dead leaves caught up in branches or root buttresses). Foraging methods were: sallying (both bird and prey in flight), snatching (bird flying to take a perched prey), hovering (a form of snatching) and gleaning (both bird and prey perched). One datum was one move from one perch or position to another, or a flight from and back to the same perch.

Where plant material was taken I noted height and type of food eaten. Types of food were fruit (those with fleshy pericarps), seeds (including hard woody fruits), nectar (from flowers) and lichen/fungi (for the Pygmy Parrots *Micropsitta* spp). No particular attempt was made to identify plant species but if known the species and the colour and estimated size of fruits were recorded. Where more than one species congregated in the same flowering or fruiting tree, I recorded the number of each species present, if time permitted. It must be stressed that foraging data other than height were taken opportunistically and may be biased. For example, where a large and stationary party of one species was observed, I had ample time to take foraging data. Where only a fleeting view was obtained there was no such opportunity. Thus any differences in foraging which may result from the size of the flock involved would not be revealed by my data.

For each pair of species indices of overlap were calculated using Schoener's (1968) equation:

$$\alpha = 1 - \frac{1}{2} \sum_{i=1}^s Pxi - Pyi /$$

where α = overlap and Pxi and Pyi are the frequency of species x and y in Category i . For carnivores (including mixed-feeders that take both animal and plant food) indices were calculated for four factors: mean weight (taken from Bell 1982a), foraging height, substrate (including food taken in herbivory), and foraging method. For herbivores (including the same mixed-feeders) I calculated only three indices: mean weight, foraging height and type of food. I omitted foraging method, which would have all been 'gleaning', for herbivorous feeding. There were insufficient data to divide fruit, seeds or nectar by plant species, which would be necessary for a more precise study than that attempted by me.

For each pair of species the indices (three for herbivores and four for carnivores) were combined into a single index of overlap. If each index was independent of the others then a product or geometric mean could be used, if dependent it would be the arithmetic mean. There is probably a high degree of dependence between indices. For example, frugivores are usually in the top of the canopy where most fruit occurs while feeders of the air 'substrate' must also be salliers in foraging method. For this reason an arithmetic mean of the three, or four, indices of overlap was used (see Cody 1974).

Two matrices were constructed, one for the thirty-one species of obligate and twenty-three of facultative carnivores, and the other for the twenty-nine obligate and twenty-three facultative herbivores. The matrices were constructed according to Unweighted Pair Group Mean Analysis (Sneath & Sokal 1973) as cited by Cody (1974). From these matrices dendograms illustrating community organization were drawn. For the matrices the sexes of the Frilled Monarch *Arses telescopthalmus* were treated as separate species because they differ strikingly in their ecology (Bell 1982e). Both bronze-cuckoos *Chrysococcyx* spp., both cuckoo-doves *Macropygia* spp., and all four honeyeaters *Meliphaga* spp. were treated as single species

because they are hard to identify in the field. Species largely or wholly confined to secondary vegetation (Bell 1982d) are included.

Nomenclature, as for previous papers in this series, conforms to Rand & Gilliard (1967), modified by Recommended English Names for Australian Birds (RAOU 1977).

RESULTS

There were eighty-three species on which sufficient data were collected for analysis. About another thirty species were resident on the study site. These were not necessarily less abundant but in some cases were merely more difficult to observe. Of the eighty-three, there were eleven groups of congeners: swiftlets *Collocalia* spp (2), pittas *Pitta* spp (2), fantails *Rhipidura* spp (4-5), monarch flycatchers *Monarcha* spp (3), cuckoo-shrikes *Coracina* spp (2-4), manucodes *Manucodia* spp (2), honeyeaters *Xanthotis* spp (2), fruit-doves *Ptilinopus* spp (6-8), imperial pigeons *Ducula* spp (3-5), ground-doves *Chalcophaps* spp (2), mynas *Mino* spp (2) and the three genera referred to earlier that were grouped as a single species (the second number in brackets includes species present but not included in the analysis). Important groups unrepresented, because of lack of data, are raptors (12), megapodes (2) and myzomelid honeyeaters (3). Three species were regular wintering migrants, the Dollarbird *Eurystomus orientalis*, Rainbow Bee-eater *Merops ornatus* and Black-faced Monarch *Monarcha melanopsis*.

Data for foraging height are not given here but have been presented previously (Bell 1982c).

Foraging Substrate

Table I gives the frequency of foraging, by substrates foraged upon, for carnivores. I stress that the samples in many cases are quite small, reflecting the opportunistic nature of their collection. However, a pattern is discernible in the use of the main groups of substrate; air, ground, bark (including trunks and branches) and leaves. There is a group of aerial feeders, five obligatorily so (three swifts, a dollarbird and bee-eater), two 'flycatchers' predominantly so and three other flycatchers which include aerial feeding as an important part of their ecology. There are three obligate ground-foragers (a rail and two pittas), four species that were seen predominantly on the ground (two kingfishers, the Eupetes and a fantail) and two (the Babbler and the Wren-warbler) for which ground foraging is important. Only one species foraged frequently on trunks, the male (but not the female) Frilled Monarch. Of the seventeen primarily arboreal species only seven foraged upon bark more than on leaves. Three species frequently rummaged among debris caught up in bushes, the Rufous Babbler, Blue Wren-warbler and the Little Shrike-thrush.

TABLE I

Percentage frequency of foraging, by substrate, of carnivores at Brown River (n: no. of foraging moves, number of individual birds in parenthesis; *: mostly in secondary vegetation).

Species	Ground	Air	Trunk	Branch	Leaf	Palm-frond	Log/stump	Vine	Debris	Termitarium	Grass	n
<i>Gymnocrex plumbeiventris</i>												
Bare-eyed Rail	100											20 (5)
<i>Chrysococcyx</i> spp												
Bronze-cuckoos			12	36	52							24 (4)
<i>Hemiprocne mystacea</i>												
Moustached Swift	100											60 (60)
<i>Collocalia vanikorensis</i>												
Lowland Swiftlet	100											50 (50)
<i>Collocalia esculenta</i>												
Glossy Swiftlet	100											50 (50)
<i>Syma torotoro</i>												
Yellow-billed Kingfisher	73	9			18							22 (11)
<i>Tanysiptera galatea</i>												
Common Paradise Kingfisher	60			10	24	6						30 (13)
<i>Merops ornatus</i>												
Rainbow Bee-eater	100											30 (7)
<i>Eurystomus orientalis</i>												
Dollarbird	100											30 (5)
<i>Pitta erythrogaster</i>												
Red-bellied Pitta	100											35 (5)
<i>Pitta sordida</i>												
Black-headed Pitta	100											45 (4)
<i>Eupetes caeruleescens</i>												
Lowland Eupetes	90						10					20 (10)
<i>Pomatomostomus isidori</i>												
Rufous Babbler	26		14	2	14	17		5	15	7		255 (27)
<i>Todopsis cyancephala</i> *												
Blue Wren-warbler	17				17	34	16			17		30 (6)
<i>Gerygone chrysogaster</i>												
Yellow-bellied Gerygone		1		23	76							120 (10)
<i>Peltops blainvillii</i>												
Lowland Peltops		73		9	18							111 (17)
<i>Rhipidura threnothorax</i>												
Sooty Thicket Fantail	49				43		3	5				61 (10)
<i>Rhipidura rufifrons</i>												
Grey-breasted Rufous Fantail	10	1		27	62							73 (8)
<i>Rhipidura hyperythra</i>												
Chestnut-bellied Fantail		11	5	63	21							100 (20)
<i>Rhipidura rufiventris</i>												
Northern Fantail		71	5	20	3			1				89 (25)
<i>Myiagra alecto</i> *												
Shining Flycatcher								3	2			18 (38 (11))
<i>Monarcha melanopsis</i>												
Black-faced Monarch												32 (13)
<i>Monarcha guttula</i>												
Spot-wing Monarch		13		16	63			8				63 (10)
<i>Monarcha chrysomela</i>												
Black & Yellow Monarch		3		12	85							92 (7)
<i>Arses telescopthalmus</i>												
Frilled Monarch ♂	2	2	30	18	35	1		11	1			322 (81)
Frilled Monarch ♀		20	3	21	47	1		3	5			100 (32)
<i>Machaerirhynchus flaviventer</i>												
Yellow-breasted Boatbill		41		41	17							46 (5)
<i>Microeca flavovirescens</i>												
Olive Microeca Flycatcher		31	3	38	29							69 (7)
<i>Poecilodryas hypoleuca</i>												
Black & White Flycatcher	8	4	8	38	42							24 (11)
<i>Pachycephala simplex</i>												
Grey Whistler		4		39	56			2				124 (10)
<i>Colluricinclla megarhyncha</i>												
Little Shrike-thrush	3		5	22	28		2	6	35			87 (10)

Table II gives the frequency for mixed-feeders (those which take both animal and plant food). There are no specialized aerial or ground foragers, although the two megapodes would fit into the latter category had they been included. Eleven of the twenty-three species are predominantly herbivorous, five of them being mainly nectarivorous (two lorikeets, a sunbird and two honey-eaters), and six being mainly frugivorous (two birds of paradise, an oriole, a catbird, the *Meliphaga* group and a starling). The high incidence of nectarivory shown for the Metallic Starling may appear surprising but I often saw them congregating at flowering *Brachychiton* spp. In a special category is the highly-specialized Buffy-faced Pygmy Parrot which appears to feed on termites, lichens and fungi. For their insectivorous foraging, eight species favour bark and thirteen leaves. The bark-foragers tend to be larger birds (birds of paradise, Drongo and the Long-billed Honeyeater). Three of these specialize to some extent on rotting wood, the Pygmy Parrot (presumably after fungi and/or termites), the Magnificent Riflebird (which chisels away dead branches) and the Long-billed Honeyeater (which slides its long bill into crevices of dead wood). Two species, the Grey-bellied Longbill and Black Flowerpecker, took insects out of spider webs. One, the King Bird of Paradise, showed a preference for hanging lianas. Two, the Babbler Honeyeater and Rusty Pitohui, rummaged among debris, not surprisingly, because both follow the Rufous Babbler which forages likewise (Bell 1983).

Table III gives foraging substrate, in fact main food taken, for obligate herbivores. Differentiation between fruit and seeds was often not possible, particularly for ground-foragers, and I have arbitrarily divided their observations equally between fruits and seeds. In reality the mix probably differed between species, e.g. Crome (1975) found that the Brown Cuckoo-dove *Macropygia amboinensis* in Queensland consumed 81% fruit and 19% seeds. Of the thirty species, nineteen are virtually obligate frugivores (i.e. > 90% fruit-eating), one is virtually an obligate nectarivore, two eat both fruit and nectar and eight both fruit and seeds. Some samples are small and in others the data are drawn from many individuals clustered at comparatively few flowering or fruiting trees.

Foraging Method

Table IV shows the frequency of observations of differing methods of foraging by carnivores. Obviously, the five obligatorily aerial feeders referred to earlier were also obligate salliers. Three small insectivores (Peltops, Boatbill and Northern Fantail) were predominantly salliers and others, the female Frilled Monarch and Olive Microeca Flycatcher, sallied substantially. Only three species hovered to any great degree, the Gerygone, Shining Flycatcher and Black and Yellow Monarch. The

two kingfishers and the Black and White Flycatcher were virtually obligate snatchers, while the Peltops, Boatbill and Olive Microeca Flycatcher snatched more than gleaned. Seventeen species were predominantly gleaners (i.e. > 60%), three ground-foragers being obligatorily so.

The mixed-feeders, as shown in Table V, were almost all simple gleaners, even for the insectivorous part of their foraging. The Spangled Drongo, almost entirely insectivorous, sallied and hovered to a high degree, illustrating the all-round versatility typical of its genus. Several nectarivores hovered frequently at flowers, although the Grey-bellied Longbill also hovered at spider's webs.

Weights

Weights are given, for carnivores in Table IV, for mixed-feeders in Table V and for herbivores in Table III. The mean weights of species by feeding-class, in my study, (Bell 1982a) were: carnivores, 38.8 g; mixed-feeders, 74.0 g; herbivores, 160.0 g (but note that these values include species additional to those in Tables III, IV and V). Of note are the numbers of syntopic congeners of similar weight including ground-doves, fantails, monarchs and honeyeaters.

Community Organization of Carnivores

Figure 1 is a dendrogram depicting the community organization of carnivores, obligate and facultative together, based on overlaps in height, substrate, foraging method and mean weight. Of nine steps of dichotomy shown, five result mainly from differences between species in vertical distribution, two by the substrate foraged upon, one by the foraging method used and one by differences in weight.

If one examines each cluster of species in Figure 1, starting from the top, separating mechanisms in each cluster are discernible. The first cluster, of above-canopy aerial foragers, comprises species of diverse size and morphology, although the two swiftlets sort out only by weight (6 and 11 g). A small cluster of nectarivorous birds includes one small sunbird and two large lorikeets, but one of the latter, the Dusky-orange Lory, merely irrupts in large numbers only in times of plenty. The next cluster is a large one of fairly large birds of the canopy, all mixed-feeders, although two, the Drongo and Starling, are only marginally so. Within this group each closely-overlapping pair is usually of two unrelated species of differing morphologies. The exception is the Trumpet Manucode/Raggiana Bird of Paradise combination, but the latter species is more insectivorous. The next cluster is of fairly large birds of the understorey, of greatly disparate habits (see Tables

TABLE II

Percentage frequency of foraging, by substrate, of mixed-feeding species at Brown River (n: no. of foraging moves, number of individual birds in parenthesis).
*: mostly in secondary vegetation.

Species	Ground	Air	Trunk	Branch	Leaf	Palm-frond	Log/stump	Vine	Debris	Fruit	Nectar	Others	n
<i>Pseudeos fuscata</i>						5 (pupae)				95			300 (300)
Dusk-orange Lory													200 (200)
<i>Trichoglossus haematodus</i>						5 (pupae)				95			
Rainbow Lorikeet													
<i>Micropsitta pusio</i>	21	59											46(17)
Buffy-faced Pygmy Parrot													
<i>Lalage leucomela</i>	9	52	22							17			
Varied Triller													
<i>Coracina melanotos</i>	3	24	26							47			156 (50)
Black Cuckoo-shrike													
<i>Pitohui ferruginea</i>	1	7	5	23	6				3	17	38		188 (25)
Rusty Pihoihi													
<i>Aplonis metallica</i>						3				67	30		200 (50)
Metallic Starling													
<i>Oriolus szalayi</i>	22	17	16	31					8	6			45 (14)
Brown Oriole													
<i>Dicrurus hottentottus</i>	6	13	7	34					40				72 (7)
Spangled Drongo													
<i>Manucodia atter</i> *	24	24	20						24				144 (65)
Glossy-mantled Manucode													
<i>Manucodia keraudrenii</i>	5	12	7	22					25	6	27		8 (rotten wood) 150 (30)
Trumpet Manucode													
<i>Ptiloris magnificus</i>	7	13	22						8	2	63		3 (rotten wood) 156 (42)
Magnificent Riflebird													
<i>Cicinnurus regius</i>	25	25							5		50		20 (4)
King Bird of Paradise													
<i>Paradisea raggiana</i>	6	6									88		48 (10)
Raggiana Bird of Paradise													
<i>Ailuroedus buccoides</i>	22	26	11						15	4	22		54 (16)
White-eared Catbird													
<i>Nectarinia sericea</i>	11	24	5	2					5	2	47		128 (25)
Black Sunbird													
<i>Timeliopsis griseigularis</i>	14	11	19						5	32	19 (rotten wood)		88 (21)
Babbler Honeyeater													
<i>Toxorhamphus lilocephalus</i>	3	8	29						19	41			113 (20)
Grey-bellied Longbill													
<i>Meliphaga spp.</i>	7	18							5	70			41 (11)
Honeyeater													
<i>Melanocharis nigra</i>	6	18							1	42	32		21.9 (40)
Black Flowerpecker													
<i>Xanthotis polygramma</i>	34	19	4							39	4 (spider web)		105 (41)

TABLE III

*Percentage frequency of foraging, by substrate, of herbivores at Brown River (n: no. of individuals;
: mostly in secondary vegetation).

Species	Fruit	Nectar	Seeds	n	Weight (g)
<i>Ptilinopus superbus</i>					
Superb Fruit-Dove	100			ca.100	122
<i>Ptilinopus coronulatus</i>					
Little Coroneted Fruit-Dove	100			ca.700	77
<i>Ptilinopus iozonus</i>					
Orange-bellied Fruit-Dove	100			ca.900	115
<i>Ptilinopus nanus</i>					
Small Green Fruit-Dove	95	5		20	47
<i>Ptilinopus perlatus</i>					
Pink-spotted Fruit-Dove	100			50	210
<i>Ptilinopus magnificus</i>					
Wompoo Fruit-Dove	100			33	189
<i>Ducula mulleri</i>					
Mullers Imperial Pigeon	100			10	800
<i>Ducula ruficaster</i>					
Purple-tailed Imperial Pigeon	100			19	436
<i>Ducula zoeae</i>					
Zoe Imperial Pigeon	100			20	590
<i>Gymnophaps albertisii</i>					
Mountain Pigeon	100			ca. 50	259
<i>Macropygia</i> spp					
Cuckoo-doves	50		50	21	140
<i>Reinwardtoena reinwardtsii</i>					
Great Cuckoo-dove	50		50	10	209
<i>Chalcophaps indica</i> *					
Emerald Dove	50		50	12	116
<i>Chalcophaps stephani</i>					
Stephen's Ground Dove	50		50	12	118
<i>Gallicolumba rufigula</i>					
Red-throated Ground Dove	50		50	15	130
<i>Trugon terrestis</i>					
Thick-billed Ground Dove	50		50	9	390
<i>Chalcopsitta scintillata</i>					
Greater Streaked Lory	67	33		ca. 70	200
<i>Domicella lory</i>					
Black-capped Lory	33	67		ca. 80	190
<i>Charmosyna placentis</i>					
Yellow-fronted Blue-capped Lory	10	90		ca.100	34
<i>Opopsitta guillemetti</i>					
William's Fig Parrot	80		20	18	31
<i>Geoffroyus geoffroyi</i>					
Red-cheeked Parrot	85		15	20	148
<i>Larius roratus</i>					
Eclectus Parrot	100			11	454
<i>Alisterus chloropterus</i>					
Papuan King Parrot	90		10	9	156
<i>Microdynamis parva</i>					
Black-capped Koel	100			20	43
Black-capped Koel					
<i>Eudynamis scolopacea</i>	100			8	294
<i>Campochaera sloetii</i>					
Orange Cuckoo-shrike	100			32	42
<i>Coracina boyeri</i>					
Boyers Cuckoo-shrike	100			ca.300	64
<i>Mino anais</i>					
Golden-breasted Myna	100			21	144
<i>Mino dumontii</i>					
Yellow-faced Myna	100			ca.100	217

TABLE IV

Percentage frequency, by foraging method used, of carnivores at Brown River (n: no. of foraging moves, no. of individual birds in brackets) and mean weights of species.

Species	*Sallying	Hovering	Snatching	Gleaning	n	Mean weight (g)
Bare-eyed Rail				100	20 (5)	?300
Bronze-cuckoos				100	24 (4)	20
Moustached Swift	100				60 (60)	11
Lowland Swiftlet	100				50 (50)	11
Glossy Swiftlet	100				50 (50)	6
Yellow-billed Kingfisher	9		73	18	22 (11)	37
Common Paradise Kingfisher			95	5	30 (13)	50
Rainbow Bee-eater	100				30 (7)	30
Dollarbird	100				30 (5)	126
Red-bellied Pitta				100	35 (5)	87
Black-headed Pitta				100	45 (5)	65
Lowland Eupetes				100	20 (10)	49
Rufous Babbler				100	255 (27)	70
Blue Wren-warbler				100	30 (6)	13
Yellow-bellied Gerygone	1	20		79	120 (10)	8
Lowland Peltops	73		27		111 (17)	30
Sooty Thicket Fantail				100	61 (10)	18
Grey-breasted Rufous Fantail	1			99	73 (8)	10
Chestnut-bellied Fantail	11	3	8	78	100 (20)	11
Northern Fantail	71	1	21	7	89 (25)	15
Shining Flycatcher		24	24	52	38 (11)	24
Black-faced Monarch				93	32 (13)	23
Spot-wing Monarch	13	8	18	61	63 (10)	16
Black & Yellow Monarch	3	18		79	92 (7)	14
Frilled Monarch ♂	2	6	19	73	300 (81)	15
Frilled Monarch ♀	20	3	16	61	100 (32)	15
Yellow-breasted Boatbill	41		31	28	46 (5)	11
Olive Microeca Flycatcher	30	9	49	12	69 (7)	15
Black & White Flycatcher	4	4	88	4	24 (11)	18
Grey Whistler	4	11	27	58	124 (10)	21
Little Shrike-thrush				100	87 (10)	32

* includes above-canopy aerial feeding

TABLE V

Percentage frequency, by foraging method used, of mixed-feeding species at Brown River (n: no. of foraging moves, no. of individual birds in brackets) and mean weights of species.

Species	Sallying	Hovering	Snatching	Gleaning	n	Mean weight (g)
Dusk-orange Lory				100	300 (300)	149
Rainbow Lorikeet				100	200 (200)	122
Buffy-faced Pygmy Parrot				100	58 (20)	11
Varied Triller	9	5	5	81	46 (17)	27
Black Cuckoo-shrike	3			97	156 (50)	55
Rusty Pitohui				100	188 (25)	94
Metallic Starling				100	200 (50)	61
Brown Oriole			12	88	30 (5)	96
Spangled Drongo	22	19	7	52	108 (17)	76
Glossy-mantled Manucode		6		94	45 (14)	208
Trumpet Manucode				100	72 (7)	161
Magnificent Riflebird				100	150 (30)	175
King Bird of Paradise				100	144 (65)	52
Raggiana Bird of Paradise				100	156 (42)	177
White-eared Catbird				100	20 (4)	138
Black Sunbird		10		90	48 (10)	8
Babbler Honeyeater				100	54 (16)	32
Grey-bellied Longbill		20		80	128 (25)	11
Long-billed Honeyeater				100	88 (21)	36
Tawny-breasted Honeyeater	3			97	113 (20)	39
Spotted Xanthotis				100	41 (11)	20
<i>Meliphaga</i> spp				100	219 (40)	22
Black Flowerpecker		3		97	105 (41)	13

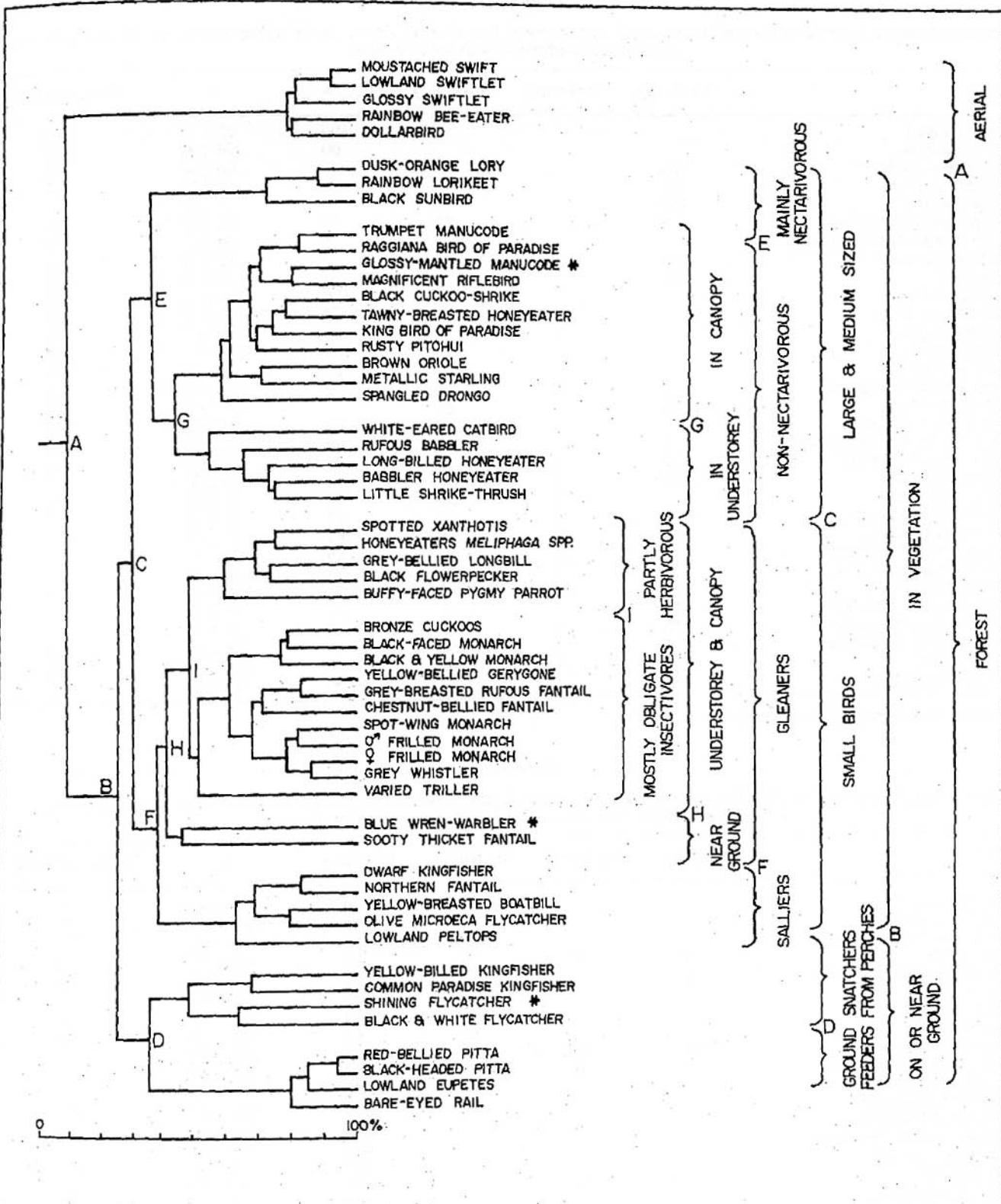


Figure 1. Dendrogram depicting the community organization of carnivorous bird species at Three Mile Plot, Brown River. (*: primarily found in secondary vegetation).

I and II). Following them is a group of small, primarily nectarivorous, mixed-feeders. Next comes a fairly tight and large cluster of small insectivores, which will be separately discussed later. After them is a cluster of predominantly salliers which sort out between themselves mainly on height (Bell 1982c). Then comes a cluster of snatchers which forage close to the ground, one kingfisher and one flycatcher snatching from the ground and another of each mainly from the foliage. Lastly, there is the cluster of obligate ground-foragers. The Eupetes turn over litter, the Rail stabs into the ground, but the two pittas present a problem. They forage, and breed, side by side, although there is a weight difference (65 to 87 g).

The community organization of the small (i.e. < 32 g) insectivores is shown again in Figure 2, this time without the other carnivorous species. This includes the large group referred to in the preceding paragraph, plus a few other species. They divide into four main clusters. On its own is a single species, the Peltops, which is a sallier of emergents and the higher canopy; followed by a group of sallier/snatchers; a large one of mainly gleaners species and a small one of two that forage on or near the ground. Table VI sums up the main sorting factors within the small insectivores, including additionally the Fairy Gerygone *Gerygone palpebrosa* for which the foraging method used is estimated only. For each factor, (height, substrate and foraging method used) the category given is the one for which there were the most observations for each species. Such a crude

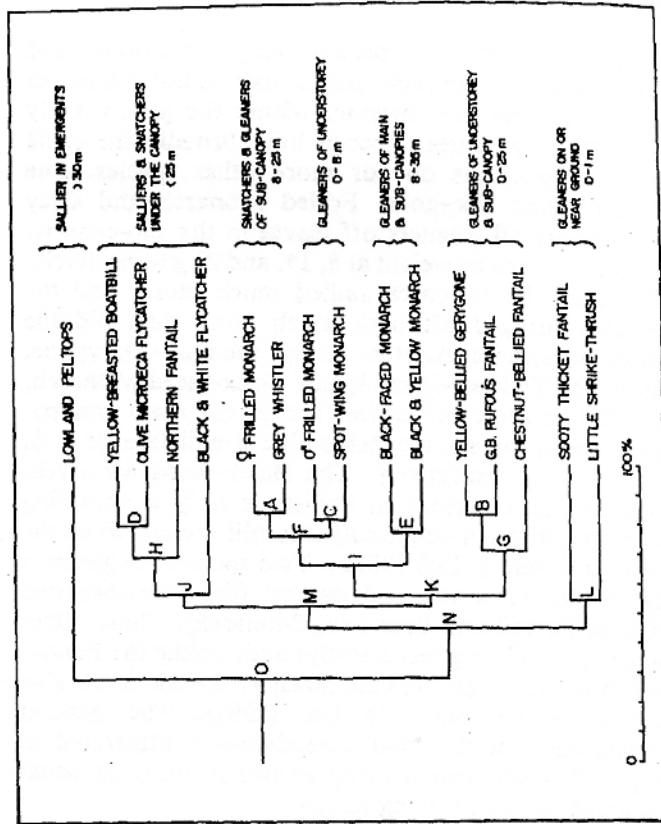


Figure 2. Dendrogram depicting the community organization within small (< 32 g) insectivorous birds of primary forest at Three Mile Plot, Brown River.

TABLE VI

Generalized foraging habits, and mean weights of small 32 g insectivores at Brown River.

Species	Weight (g)	Main height*	Main substrate	Main foraging method
Yellow-bellied Gerygone	8	Sub-canopy	Leaves	Gleaning
Fairy Gerygone	8	Lower canopy	Leaves?	Gleaning
Grey-breasted Rufous Fantail	10	Lower under-storey	Leaves	Gleaning
Chestnut-bellied Fantail	11	Lower under-storey	Branches	Gleaning
Yellow-breasted Boatbill	11	Upper under-storey	Air	Sallying
Black & Yellow Monarch	14	Lower canopy	Leaves	Gleaning
Frilled Monarch ♂	15	Lower under-storey	Bark	Gleaning
Frilled Monarch ♀	15	Sub-canopy	Leaves	Gleaning
Northern Fantail	15	Lower under-storey	Air	Sallying
Olive Microeca Flycatcher	15	Sub-canopy	Bark	Snatching
Spot-wing Monarch	16	Lower under-storey	Leaves	Gleaning
Sooty Thicket Fantail	18	Ground	Ground	Gleaning
Black & White Flycatcher	18	Lower under-storey	Bark	Snatching
Grey Whistler	21	Sub-canopy	Leaves	Gleaning
Black-faced Monarch	23	Lower canopy	Leaves	Gleaning
Lowland Peltops	30	Upper canopy	Air	Sallying
Little Shrike-thrush	32	Lower under-storey	Debris	Gleaning

* Heights divided into Upper canopy ca > 30 m; Lower canopy ca 25-30 m; Sub-canopy ca 8-25 m; Upper understorey ca 4-8 m; Lower understorey 0-4 m; Ground.

measure, of course, masks many variations and combinations within each species' habits, but still serves to illustrate the fine divisions within the group. Only eight out of seventeen species have broadly the same foraging habits as one or more other species. The Yellow-bellied Gerygone, Frilled Monarch and Grey Whistler are all gleaners off leaves in the sub-canopy, but sort out well by weight at 8, 15, and 21 g respectively. Moreover, the Monarch sallied much more, and the Whistler foraged off bark much more than did the remaining species. Another group, the Fairy Gerygone, Black and Yellow Monarch and Black-faced Monarch, are also gleaners off leaves, but in the main canopy. Once again, there is a considerable size difference at 8, 14 and 23 g respectively. The Black-faced Monarch, very like its congener in habits, is only a wintering migrant, although admittedly it is still present when the other is breeding (Bell 1982b). Two species are gleaners off leaves in lower understorey (the Grey-breasted Rufous Fantail and Spot-wing Monarch). These differ in size (10 and 16 g respectively) and, unlike the Fantail which is almost an obligate gleaner, the Monarch also sallies, hovers and snatches (39%). The general organization of the small insectivores is illustrated in Figure 3, each species being shown in its most usual combination of foraging habits.

Community Organization of Herbivores

Figure 4 depicts the community organization of herbivores, once again including the mixed-feeders. Because herbivory involves merely gleaning as a foraging method, only weight, vertical distribution and substrate are considered. Of the eleven steps of dichotomy shown, five are mainly caused by differences in weights, five by food taken (i.e. substrate) and only one by height.

The community divides into four main groups. There is a large cluster (I) of virtually obligate herbivores, in turn divided into one cluster of nectarivores and three of frugivores which are separated by weight. Next there is a cluster (F) of strongly insectivorous species, tending to divide by the type of herbivory; fruit or nectar-eating. Then there is a small cluster (D) of three very small mixed-feeders, but each of different diets. Last there is a cluster (B) of generally very big obligate herbivores, dividing into ground-feeders and arboreal species, the latter dividing into frugivores and granivores (seed-eaters).

Overlaps appear much higher than for carnivores, even allowing for the smaller number of factors (three against four) built into the matrices. But although there is a whole series of closely-overlapping species pairs, there are explanations of separating mechanisms for each. Two pairs, Red-cheeked Parrot/Golden-breasted Myna and Papuan King Parrot/Wompoo Pigeon,

involve one species (the parrot) which can tear apart large fruits and another which must swallow whole fruits. Five pairs are of species with differing diets, four involving a nectarivore with a frugivore (Black Sunbird/Varied Triller, Tawny-breasted Honeyeater/Black Cuckoo-shrike, Grey-bellied Longbill/Black Flower-pecker and Spotted Xanthotis/*Meliphaga* spp, and one pair the highly-frugivorous Trumpet Manucode and much less so Raggiana Bird of Paradise. Two pairs are of species of similar weights and ecology, but with the first species a continuous resident and the other an irruptive visitor during periods of abundance (Rainbow Lorikeet/Dusk-orange Lory and Pink-spotted Fruit-Dove/Mountain Pigeon). Two pairs separate by size, the Great (209 g) and other cuckoo-doves (90–140 g), and the Muller's (*ca* 800 g) and Rufous-tailed (*ca* 436 g) Imperial Pigeons. Two pairs involve a species of primary forest and one of secondary growth (Magnificent Riflebird/Glossy-mantled Manucode and Emerald Dove/Stephen's Ground Dove). One pair separates mainly by vertical distribution, the Babbler and Long-billed Honeyeaters. Lastly one pair (Small Green Fruit-Dove and Black-capped Koel) involve two similarly-sized birds which both eat figs in the main canopy, but one (the Koel) is very likely a brood-parasite whose young are reared by insectivorous species, and both appear to be sparse.

There is little doubt that overlap would have been lower had I data on the species of plants from which herbivores took nectar, fruit or seeds. To illustrate further possible separating mechanisms between species of seemingly similar ecology, I use data, shown in Table VII, from Frith *et al.* (1976) who analysed the stomach contents of a large series of fruit-doves *Ptilinopus* spp taken at Brown River. I also show in Table VIII my own data on associations, in mixed-species aggregations at the same feeding trees, between the species of fruit-doves. The data from Table VII and VIII are presented as a dendrogram in Figure 5. Figure 5a shows the relationship between species using the data from the community matrix from which Figure 4 was drawn (involving weight, foraging height, and food taken in all cases 100% the same). Figure 5b shows the relationship substituting the overlaps of plant species eaten for the factor of food taken. Figure 5c similarly substitutes with the data on size of fruits taken. Finally Figure 5d uses overlap in feeding associations in lieu of food taken. Some of the samples in Figure 5d are too small, but the frequency of each species in an aggregation corresponds well with the totals seen throughout the study. There may be bias in the data of Frith *et al.* (1976). The primary aim of Frith *et al.*'s collection was to check on breeding condition and overlap in food may in some cases be an outcome of taking, for convenience, many specimens at the same tree. In their data smaller species did appear to take smaller fruits than larger species but

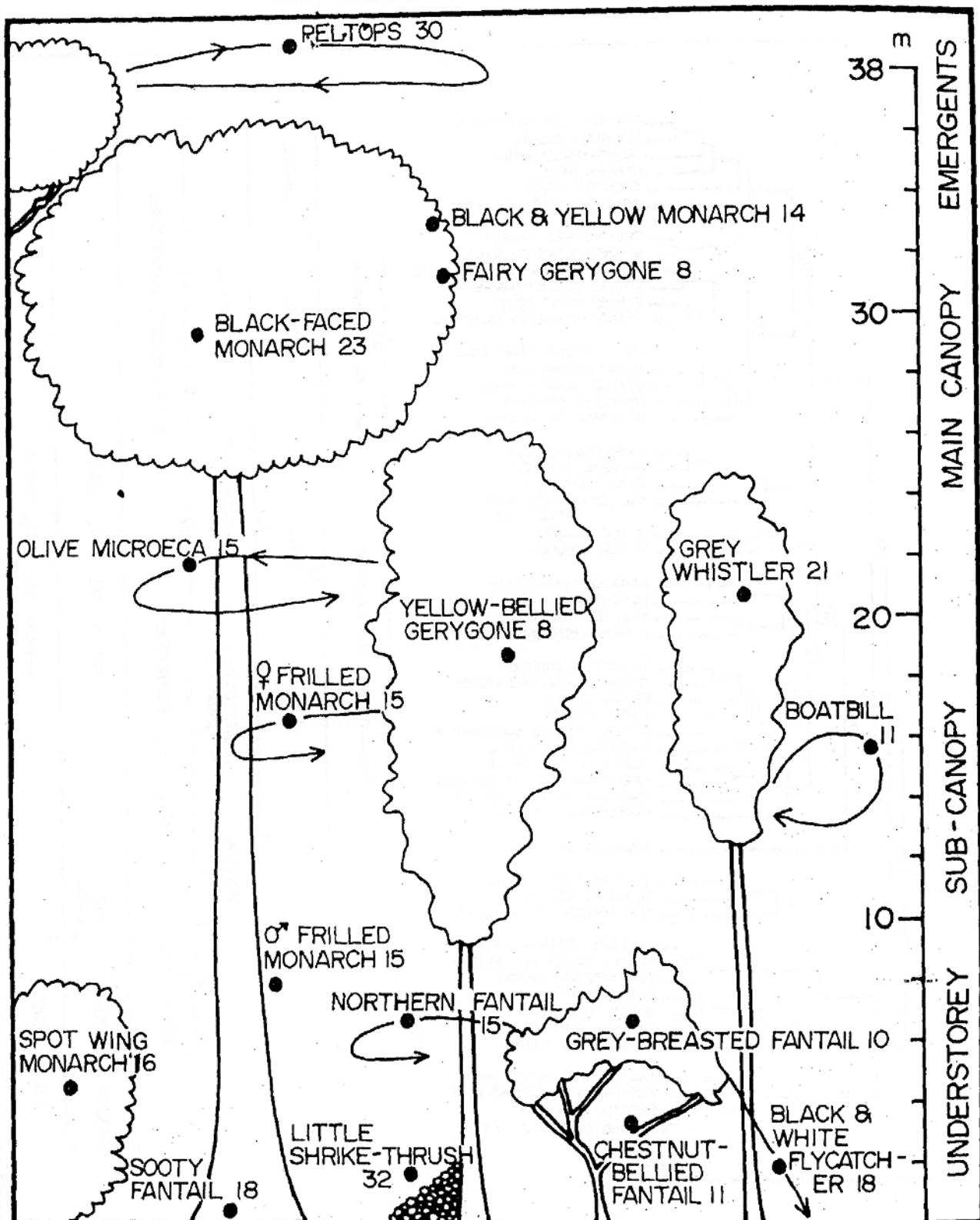


Figure 3. General ecological organization of small (< 32 g) insectivores at the primary forest at Three Mile Plot, depicting for each species the most usual combination of height, substrate and foraging method. Number for each species is mean weight (g).

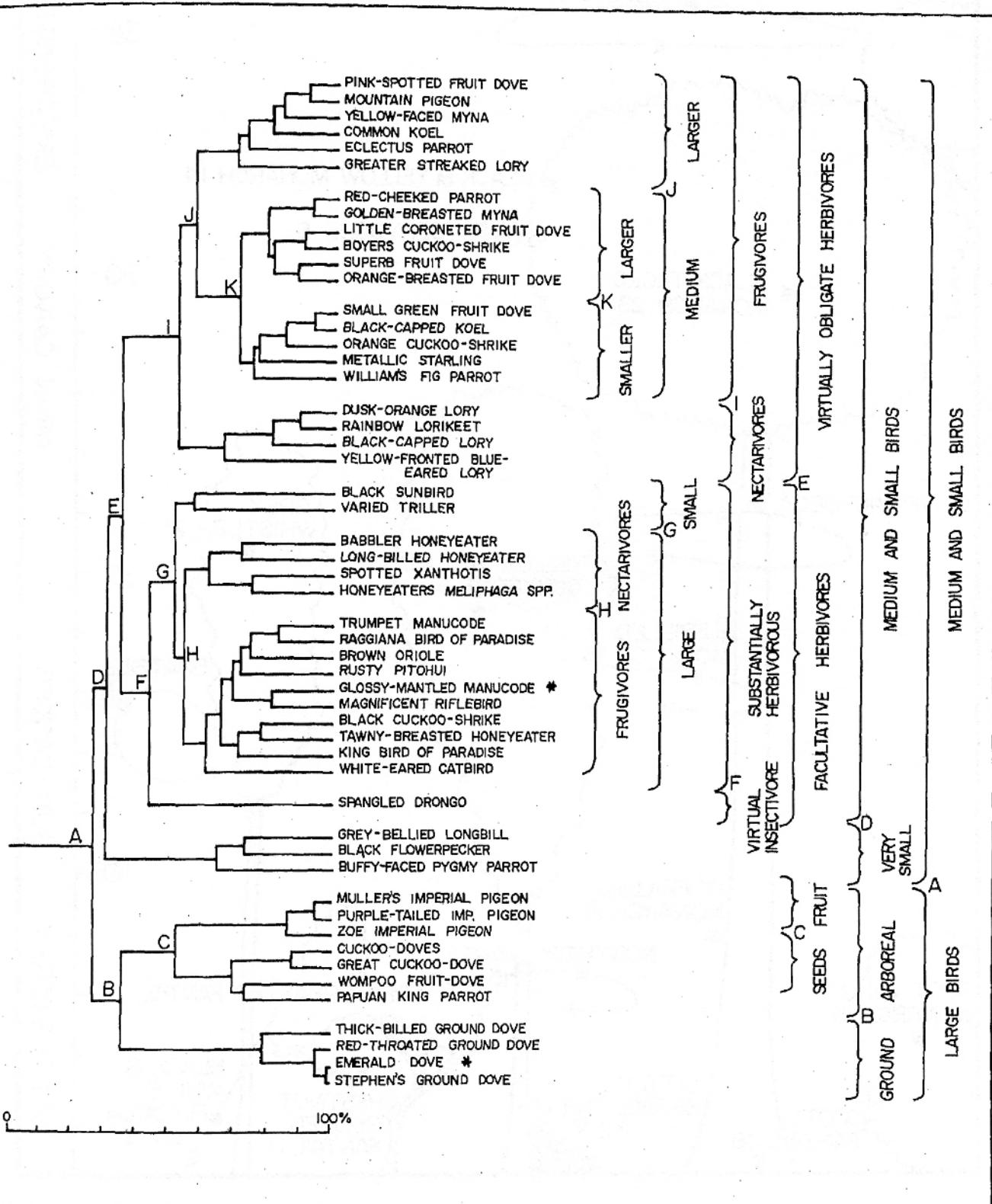


Figure 4. Dendrogram depicting the community organization of herbivorous bird species at Three Mile Plot, Brown River. (*: primarily found in secondary vegetation).

TABLE VII

Percentage overlaps between diets of fruit-doves *Ptilinopus* spp at Brown River (data from Frith et al. 1976). Number on top is overlap by frequency of occurrence of plant species; on bottom overlap by frequency of occurrence of size-ranges of fruits. Number of crops sampled in brackets.

	Little Coroneted	Orange-bellied	Pink-spotted	Wompoo
Superb (21)	60 59	44 65	46 77	63 79
Little Coroneted (39)		46	45	77
		88	62	66
Orange-bellied (151)			96	45
			75	76
Pink-spotted (62)				46
				86
Wompoo (118)				

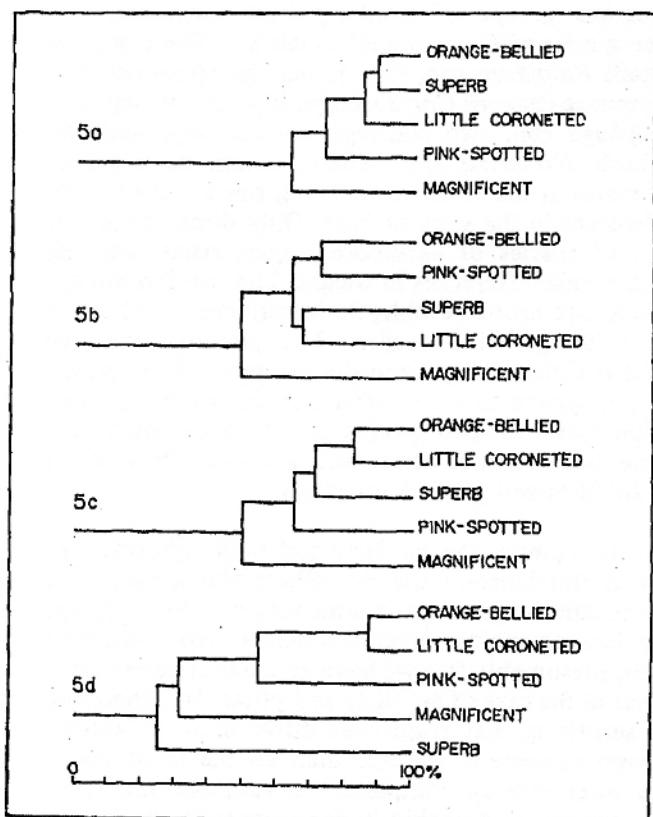


Figure 5. Dendrogram showing relationships between species of resident fruit-doves *Ptilinopus* spp at Three Mile Plot, (a) using factors of weight, height and substrate (100% fruit) as in Figure 4; (b) using weight, height and species of fruit taken (from Frith et al. 1976); (c) using weight, height, and size of fruit taken (from Frith et al.); (d) using weight, height and co-occurrence in same fruiting tree (pers. obs.).

TABLE VIII

Number of associations together in same feeding trees of species of fruit-doves *Ptilinopus* spp at Brown River 1975-77. Number underlined is of the total occurrences for each species feeding with others, not necessarily fruit-doves.

	Superb	Little Coroneted	Orange-bellied	Pink-spotted	Wompoo
Superb	4	2	3	1	1
Little Coroneted		40	38	14	3
Orange-bellied			58	15	4
Pink-spotted				16	1
Wompoo					4
No. of individuals counted throughout study	413	1506	3208	245	584

the authors point out that the year of collection (1968/69) may have had a fruiting pattern different from other years, I found differences between my two years of study. Except for the Wompoo, fruit-doves occurred at substantially the same heights, i.e. in the main canopy, where most fruit occurs (Bell 1982c).

DISCUSSION

Foraging Substrate

Tables I-III show that 38% of species ate mostly fruit or seeds and 20% more ate some fruit. This high proportion of frugivores in New Guinean rainforests compared to those elsewhere has been discussed previously (Bell 1982a). The mainly nectarivorous species were 11% with another 7% partly so. The mainly insectivorous species were 51% with another 14% partly so.

The data presented in Tables I-III are not greatly at variance with such descriptions as have been in the literature (e.g. Rand & Gilliard 1967). However, birds of paradise seemed much more insectivorous than usually implied, e.g. by Schodde (1976). However both samples, of my foraging data, and Schodde's on diet, are quite small. In another study (Bell 1982f) I found the Glossy-mantled Manucode occurring year-round in habitat where fruit was unavailable for many months each year.

Pearson (1977), in a comparison of Pantropical rainforest avifaunas, commented correctly on the seeming paucity of trunk-foragers in New Guinea. My data show more than the one trunk-forager (the Pygmy Parrot) recorded by Pearson (1977). They included the Babbler, male Frilled Monarch, the Drongo, Glossy-mantled Manucode, the Riflebird, the Longbill and the Long-

billed Honeyeater. However, the absence of trunk-feeding specialists such as woodpeckers Picidae or treecreepers Climacteridae is striking. Pearson suggested that in New Guinea the trunk-foraging role may be occupied by animals from classes other than birds, such as the Tiger Beetle *Tricondyla aptera*. I found several species of anglehead lizards *Gonocephalus* spp commonly on trunks, but their ecology is little-known. There are two large vertebrates, the possum *Dactylopsida trivirgata* and the monitor *Varanus prasinus*, which have elongated claws apparently suitable for probing crevices in bark.

Foraging Method

The data presented in Tables IV and V differ greatly from those previously published. Croxall (1977) gives data on fourteen species of the small insectivores that are shown in Table IV. The two sets of data are so different that in some cases it is hard to believe that they relate to the same species. The sample size for Croxall's data is not given, but if it is the same for his data on height, then our respective samples are roughly equal. Of four species shown by Croxall as mainly (90%) sallying (Boatbill, Olive Microeca Flycatcher, Chestnut-bellied and Grey-breasted Rufous Fantails) the extent of sallying observed by me was only 41, 30, 11 and 1% respectively. Two species groups listed as 100% gleaners by Croxall, the gerygones and whistlers, were found by me to forage by other methods, on 21% and 42% of occasions respectively. Clearly, either one of us is mistaken, or birds in some of the other areas visited by Croxall behave differently from those at Brown River.

Table IV shows that the obligate carnivores have a wide range of foraging methods. This is in contrast to the mixed-feeders (Table V). Among the mixed-feeders there is the Drongo, virtually an obligate insectivore which has a wide repertoire of foraging methods, two small nectarivores which hover and a frugivore, the Varied Triller which sallies, hovers and snatches. The rest are all virtually obligate simple gleaners, although it could be argued that some (e.g. the lorikeets) have the ability to hang and thus differ in foraging method from others of their feeding-class. In general, herbivory tends to impose a more stereotyped method of feeding, (i.e. with stationary as opposed to mobile 'prey') thus reducing the options by which species can co-exist by evolving different methods of foraging.

Weight

Hutchinson (1959) emphasized the difference in size of syntopic congeners with his theory that their weight, or size of trophic apparatus, should differ by a ratio of at least 1:1.2. Diamond (1973) illustrated this graphically for the frugivorous pigeons *Ducula* spp and *Ptilinopus*

spp. However, Simberloff & Boecklen (1981) have questioned the representativeness of the data from which the theory is based and my own evidence from Brown River shows that the theory does not apply to the whole bird community. It seems true that the obligate herbivores sort out well by weight, for example the resident *Ptilinopus* spp weigh 47, 77, 115, 122, 198 and 210 g. Two other species were recorded (Bell 1982a) at 70 and 164 g but these were sub-montane vagrants to Brown River. Leaving out other montane visitors (e.g. Little Red Lory *Charmosyna pulchella*, Lilac-collared Parrot *Geoffroyus simplex*) all other groups of obligatorily herbivorous congeners displayed considerable differences in size between species, except the two ground doves *Chalcophaps* spp (116 and 118 g) where one species inhabits the forest and the other secondary growth (Bell 1982d).

The picture with carnivores is quite different. Taking all species known to be present (Bell 1982a) there are numerous groups of similarly-sized congeners. The three species of *Gerygone* all weigh 8 g. There are five fantails *Rhipidura* spp, four monarchs *Monarcha* spp, two bronze-cuckoos *Chrysococcyx* spp, four honeyeaters *Meliphaga* spp, two starlings *Aplonis* spp, and two sunbirds *Nectarina* spp, where, within each group, difference in size is less than 1:1.2, nor are there great differences in the sizes of bills. Only three congeneric pairs of species of carnivores, apart from raptorial, display wide differences in weight. The two *Pitohui* spp include one probable obligate insectivore (79 g) and a larger (94 g) mixed-feeder. The pitohuis, the two swiftlets *Collocalia* spp and the two pittas *Pitta* spp are the only genera to show differences in weight. Of note is that these last two groups are those in which each species uses the same height and the same substrate (air for swiftlets and ground for pittas).

In my opinion the swiftlets and pittas illustrate the flaw in Hutchinson's theory. Where two species must use the same height and the same substrate for foraging, then they can avoid competition only by eating different foods, presumably (for we have no data) different-sized insects in the case of swiftlets and pittas. It is therefore not surprising that frugivores differ more in weight, between congeneric species, than do the insectivores. Frugivores overlap completely in substrate i.e. fruit, and overlap considerably in the heights at which they feed, because most of their food is concentrated, either in the canopy, or as fallen fruits on the ground. It is true that certain frugivores may eat fruit in different ways e.g. parrots can chew open large fruits, some honeyeaters feed on fruits that parrots have first opened, and some passerines may be better equipped than pigeons to snap off certain fruits. However, the large arrays of fruit-eating pigeons in New Guinea feed in the same way and at the same heights. To them the only separating

mechanism available is different size and thus, presumably, different sized fruits.

Conversely, insectivores in tropical rainforests have a whole range of options open. Their food is distributed through all levels, and above and below the forest, and it occurs on a wide variety of substrates (e.g. trunks, leaves). Efficient foraging on these substrates requires different morphological adaptations. Therefore, many insectivores, even congeners of the same size, can co-exist, not by eating different foods, but by eating the same food taken in places and by methods not readily available to other species. In general, I believe that Hutchinson's theory applies only where there is no other option than specialization in taking similar foods but of different sizes.

Community Organization of Carnivores

The fine division of the habitat (of the forest levels and substrates) by carnivores accords with MacArthur *et al.* (1966), in that the vertical distribution of birds tended to correspond with the profile of vegetation (see Bell 1982c). However obligate carnivores divided the habitat more by substrate and height than did facultative carnivores, the latter sorting out more by differences in size (see Figs 1 and 4). Among the eighty-three species for which I have foraging data obligate carnivores averaged $21.89 \pm S.D. 14.3$ g, compared to facultative ones, which averaged $77.59 \pm S.D. 63.6$ g.

In general, as shown in Figure 1, of the four factors analysed, i.e. vertical distribution, substrate, foraging method and weight, differences in vertical distribution are the dominant.

My data may be compared with those of Crome (1978), who worked with an avifauna similar to that in New Guinea but with far fewer species. Crome's Table 7 gives overlaps in habitat, behaviour and bill size between seven common species. For five pairs of small insectivorous species I compare Crome's data, in Table IX, against five pairs of the same or similar species at Brown River. Where the species at Lacey's Creek (Crome's area) is absent or not represented by full data at Brown River (Fairy Gerygone, Grey Fantail *Rhipidura fuliginosa* and Spectacled Monarch *Monarcha trivirgata*) I have used, for comparison, a closely-related species of similar ecology to the Australian species. In order to standardize our two sets of data my height categories (Bell 1982c) are adapted to fit Crome's. Crome has more classes of substrate but in general our classifications substantially agree. With behaviour (foraging method) it was necessary to fit Crome's data of eight categories into mine of four (sallying, hovering, snatching and gleaning). Thus Crome's 'flitting', 'spiralling', 'probing' and 'scratching', all of which occurred at Brown River, are included in my 'gleaning', while his 'sallying' equates to my 'snatching'. As shown in Table IX overlaps between species in the depauperate Australian rainforest are higher than those in New Guinea but are significantly so only for foraging behaviour. This suggests that, for insectivores at least, as species diversity increases the trend is for further partitioning to take place through exploiting similar habitat by using different foraging behaviour.

Community Organization of Herbivores

In spite of the plausible explanations, given earlier, for differences in niche among frugivores, I still have

TABLE IX

Comparison of overlaps of habitat (height plus substrate) and foraging method between the same or related species at Lacey's Creek, Queensland (Crome 1978) and Brown River, Papua New Guinea.

Species pair	Overlap		Species pair	Overlap	
	Habitat	Method		Habitat	Method
Yellow-breasted Boatbill/Fairy Gerygone	0.75	0.64	Boatbill/Yellow-bellied Gerygone	0.61	0.29
/Grey Fantail	0.73	0.64	/Chestnut-bellied Fantail	0.74	0.47
/Spectacled Monarch	0.85	0.80	/Spot-wing Monarch	0.54	0.59
/Grey Whistler	0.80	0.79	/Grey Whistler	0.72	0.59
Fairy Gerygone/Grey Fantail	0.78	0.79	Yellow-bellied Gerygone/Chestnut-bellied		
/Spectacled Monarch	0.63	0.97	Fantail	0.64	0.79
/Grey Whistler	0.77	0.91	/Spot-wing Monarch	0.76	0.71
Grey Fantail/Spectacled Monarch	0.63	0.80	/Grey Whistler	0.80	0.80
/Grey Whistler	0.75	0.79	Chestnut-bellied Fantail/Spot-wing Monarch	0.66	0.84
Spectacled Monarch/Grey Whistler	0.82	0.95	/Grey Whistler	0.64	0.33
Means	0.75	0.81	Spot-wing Monarch/Grey Whistler	0.64	0.88
				0.67	0.63

Significant difference between locations, by matched-pairs *t*-test (arcsin transfer of data) (9 d.f.): habitat. n.s.; foraging method, $p < 0.05$.

reservations about them, particularly for pigeons. The samples of fruits taken at Brown River by pigeons (Frith *et al.* 1976) were small, the many specimens containing only limited numbers of identifiable fruits, and, as mentioned earlier, there may have been biases in the collection of specimens. I find it hard to believe from my observations of them, and from the extent to which they forage off the same trees (Table VIII), that the Orange-bellied and Little Coroneted Fruit-Doves (77% of all pigeons seen, out of 26 species) do not eat substantially the same fruits. They differ remarkably only in nesting habits. The Little Coroneted nests within 3 m from the ground, its nest being the most frequently found of all New Guinean rainforest pigeons. Incredibly, in view of its abundance, the Orange-breasted has been found breeding twice only, both times in the top of a canopy. However, nesting site may have little effect on the partitioning of food resources between the two species. Diamond (1973) suggested that smaller fruit-doves can reach outer branches not accessible to heavier species, so the Little Coroneted, when feeding with the Orange-breasted, should be expected to feed more on outer branches. I looked for but found no evidence for this at Brown River, although the very large imperial pigeons *Ducula* spp fed lower in the canopy than did the fruit-doves (Bell 1982c).

Schoener (1982) pointed out that differentiation between species does not have to be the outcome of selection pressures throughout the year. It can result from pressures that operate only in time of scarcity, and it is no coincidence that studies on resource-partitioning (e.g. Zaret & Rand 1971, on fish; Jarman 1971, on large African ungulates; Smith *et al.* 1978, on Galapagos finches) show decreased overlap, i.e. specialization, in such periods. Thus, in periods of scarcity, Diamond's suggestion on use of outer branches by smaller species may well apply. Most of his studies of *Ptilinopus* spp on the mainland of New Guinea were in montane areas, where fruit is much less abundant than in the lowlands (Kikkawa & Williams 1971), but where there can co-exist a range of species similar to, or greater than that at Brown River. There may be as yet hidden, more subtle differences. For example, between the two fruit-doves which feed upon the same types of fruit, one may be more adapted to taking the less ripe fruits, and Crome (1975) found some evidence for this in Queensland.

In spite of the foregoing arguments on how frugivores may partition a resource substantially available to one foraging strategy (gleaning at canopy level), the evidence suggests that frugivores, and to a lesser extent, other herbivores, overlap between species at Brown River to a greater extent than do carnivores, especially the obligate ones.

CONCLUSION

I stress that this analysis is based on small sample sizes of data. Further study, particularly that revealing seasonal and diel changes in feeding habits, will alter the picture portrayed in Figures 1 to 5. Moreover, detailed examination of the species of fruits, seeds and flowers exploited by birds will reveal differences between herbivorous species that may currently seem to closely compete. Against these points, however, is that this analysis gives only part of the story, omitting some thirty more resident species for which data were unavailable. I commend, to those who may have the opportunity to pursue similar studies in New Guinea, the foothill zone (*ca* 300–600 m), because in that zone there is almost the full range of lowland species (or their superspecies equivalents) and in addition many more species of small insectivores than in lowland forests.

Klopfer & MacArthur (1961) suggested that birds in tropical rainforests have wider niches because of abundant resources, whereas Mayr (1969) suggested the opposite; that most species can be packed into tropical forests because the habitat lends itself to division into narrower niches. I believe that, if the bird community at Brown River is structured similarly to those of other Equatorial rainforests, then both views are correct. Klopfer & MacArthur's views hold for herbivores, particularly frugivorous ones, but do not apply to carnivores, in particular the obligate ones. Conversely, Mayr's views hold for carnivores but not so well for herbivores.

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