

Foraging Ecology of Birds in an Upland Tropical Rainforest in North Queensland

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Abstract

Vertical distribution of herbivores, mixed feeders and insectivores in an upland tropical rainforest reflected variation of foods present in different strata. Arboreal insectivores utilized the widest range of strata because of a wider distribution of arthropod foods. Differential utilization of vertical strata was the most important factor to bring about niche differentiation, not only between the three feeding categories but between species within each of the categories. Species whose vertical ranges were similar were segregated by differential utilization of foraging sites, by foraging behaviours and/or by food resources. Seasonal migration, variation in diet and shifts in vertical foraging levels, and/or diurnal variation of foraging times, resulted in a finer partitioning of resources between those species whose niches greatly overlapped.

Introduction

Avian foraging assemblages of Australasian lowland tropical rainforests have been analysed quantitatively by Bell (1977, 1982a, 1982b, 1982c) and Crome (1978), but no similar data are available for upland rainforests. Studies on the foraging ecology of tropical rainforest birds elsewhere in the world have been summarized by Pearson (1977, and references therein). Previous studies clearly emphasized the importance of differential utilization of strata, foraging sites and behaviours, and food resources as mechanisms for partitioning tropical rainforest avian communities. The aim of this study was to show which factors were important in bringing about ecological segregation between species in an upland rainforest community and whether different factors operated seasonally or diurnally. Particular attention was given to the arboreal insectivores that were diverse and abundant in my study area (see below). I compared my findings for this upland foraging assemblage with those of Crome (1978) for a lowland community.

The study was carried out in the Paluma Range in north Queensland, from August 1978 to April 1979. The study area was located in tropical upland rainforest, approximately 875 m altitude, at 19°00'S., 146°10'E., some 7 km north of Paluma township and approximately 80 km north of Townsville. Mt Spec is the highest peak on the range, at 1019 m. The rainforest ranges from about 600 to 1000 m in altitude, although extending to lower altitudes in deeper gullies. Tracey (1982) classified the vegetation community in the Mt Spec area as simple notophyll vine forest. Rainfall and temperature fluctuate seasonally (Table 1; data of C. B. Frith). The wet season is from December to March, and the dry from April to November. Daily temperatures are highest during the wetter months.

I deal only with species I observed foraging during the period of study and, therefore, with not all the species recorded on the Paluma Range (see Griffin 1974). The majority of birds

I saw foraging, however, are those which are common residents of upland tropical rainforests, and so they are used here to characterize the foraging assemblage as a whole. Nomenclature is in accordance with the R.A.O.U. (1978).

Methods

Seventy-one transect walks, each covering a distance of 4 km in 4 h, were taken from August 1978 to April 1979. I made eight transect walks each month, at approximately equal intervals throughout each month, except during April when I was able to complete only seven walks. Each month I started four walks in the morning and four in the afternoon. No walks were made during heavy rains or winds. Time of starting out depended upon weather, especially during the wetter months when there was often early morning and/or late afternoon cloud mists. Thus, morning walks started between 0630 and 0730 h, and afternoon walks between 1300 and 1400 h.

Each walk commenced at a central point and radiated out 1 km along one of two tracks which I refer to as tracks 1 and 2. From the central point I walked 1 km along track 1 and back again, and then 1 km along track 2 and back again; or vice versa. This 'back-tracking' did not appear to affect my records of foraging, as 51.3% and 51.8% of observations were made on the outward walk along tracks 1 and 2 respectively, and 48.7% and 48.2% on the way back. To avoid biasing my observations in any way, in each month I took track 1 first on two morning and two afternoon walks, and track 2 first on the other walks.

Track 1 is relatively flat and well defined, devoid of litter and vegetation, about 5 m across and at about 800 m altitude. It was originally cleared as an access road to a logging camp. Track edges are fringed with grasses and the red ash *Alphitonia petrei*. The rainforest canopy edge extends in places over the track (about 20% coverage). Track 2, once an old snigging track, is now an ill defined, leaf-littered and slightly overgrown path about 1–3 m across. It rises up a hillside from about 800 m to 900 m altitude. Rainforest, consisting of tall mature trees, fringes the track and its canopy extends well over it (about 70% coverage). Visibility into the forest is better from track 2 than track 1. Foraging observations along the two tracks were compared (see Appendix).

During each walk I recorded foraging height, site and behaviour (see below) of each bird. Whenever possible, foods eaten (fruit, nectar, arthropod or other) were noted. Each different food item eaten by the same bird (i.e. a mixed feeder) was counted as a separate record. Similarly, more than one individual of a species foraging at the same food source were counted as separate records. According to the main diet of a species, based on personal observations, Kikkawa and Webb (1967), Crome (1978) and Readers Digest (1976), I divided the birds into three main feeding categories: herbivores (mostly frugivores); mixed feeders feeding on fruit, nectar and/or arthropods; and insectivores feeding mostly on arthropods.

Bill lengths of species whose foraging height, site and behaviour were similar were compared as an index of the range of size of prey that may be eaten (see Crome 1978).

Foraging Height

Vertical stratification of tropical rainforest varies according to vegetation structure and complexity (Richards 1952); and for the purpose of the present study a classification based on that of Longman and Jenik (1974) was found most applicable (see Table 2).

The Shannon-Weaver function was applied to determine vertical foraging distribution of each species:

$$H' = - \sum p_i \ln(p_i), \quad (1)$$

where H' is the foraging height diversity; p_i the proportion of observations in category i , and s the number of categories. Significant differences between foraging heights of feeding categories as a whole and between selected species were evaluated by χ^2 tests.

Foraging Site and Behaviour

Fifteen foraging sites were recognized (Table 3); the first 13 correspond with those of Crome (1978), and my 14th and 15th correspond with Crome's 15th and 16th. Crome's site 14, fan palms, does not apply to my area. Foraging site diversity was calculated by means of equation (1).

The same eight categories of foraging behaviour defined and used by Crome (1978) were followed, to allow meaningful comparisons between Australian lowland and upland foraging assemblages.

Overall Use of Habitat for Foraging

Foraging records of 23 of the 39 species observed on transect walks (see Appendix) were large enough to permit detailed analysis. For each pair of 23 species overlap indices for foraging height and for foraging site were calculated by means of the Rekkonen Index:

$$\alpha = 1 - \frac{1}{2} \sum_{i=1}^s |px_i - py_i|, \quad (2)$$

where α is overlap, and px_i and py_i are the frequencies of observations of species x and y in category i .

For each pair of species the two indices, one for foraging height (α_{ht}) and one for foraging site (α_s) were combined into a single index of overlap, referred to as the structural overlap (see Cody 1974) by the equation:

$$\alpha_{st} = (\alpha_{ht} + \alpha_s)/2, \quad (3)$$

where α_{st} is structural overlap, α_{ht} overlap with respect to height, and α_s overlap with respect to site. A species-by-species matrix utilizing the indices of structural overlap was used to construct a community dendrogram, as described by Cody (1974).

For pairs of species whose foraging height and foraging site indices were high, overlap of foraging behaviour was also calculated by equation (2).

Table 1. Rainfall, temperature and insect biomass data for the Paluma Range, north Queensland

Month	Rainfall (mm)		Temp. (°C), 1978-81		Mean insect biomass 1978-79 (g)
	1978-79	1969-80 mean	Mean max.	Mean min.	
Aug.	91	51	17.8	10.7	1.3
Sept.	114	57	20.2	12.5	2.6
Oct.	136	91	21.9	14.3	8.2
Nov.	100	111	23.1	16.3	21.2
Dec.	214	474	25.0	17.7	16.6
Jan.	838	638	23.8	18.3	43.5
Feb.	515	559	25.2	19.1	23.6
Mar.	522	463	25.2	17.6	8.1
Apr.	170	162	20.8	16.1	6.2
May	44	126	20.5 ^A	14.7 ^A	—
June	85	49	18.5 ^A	11.9 ^A	—
July	31	24	17.2 ^B	10.3 ^B	—

^A 1980 only. ^B 1979 and 1980.

Seasonal Changes in Foraging

Foraging observations made during the dry months of August–November were compared with those of the wet months from December to March; 32 transect walks were made during each 4-month period. Data for April 1979 were excluded from the analysis, as this month marked the beginning of a new dry season.

The number of foraging observations for mixed feeders and for insectivores during the dry and wet months were compared by χ^2 tests. Data for herbivores were too few to permit meaningful analysis and comparisons. The frequency distributions of foraging records for foraging height, site and behaviour during dry and wet months were compared by χ^2 tests, when applicable. For those species showing significant seasonal differences in foraging sites, changes in the diversity of foraging sites were compared by means of equation (1).

Insects were collected in the study area each month (six samples for August 1978, and eight for each subsequent month to April 1979) by C. B. Frith using light traps, and his monthly values of insect biomass in grams dry weight are presented in Table 1 to examine whether seasonal changes in insect densities were reflected in birds' foraging activities.

Diurnal Changes in Foraging

The 12 hours from 0630 h to 1829 h were divided into six 2-h periods. The total number of hours in each period was not uniform, as I spent more time observing birds foraging during early morning and late afternoon than at midday. The 2-h periods and the number of hours observation per period were as follows: 0630–0829 h, 49 h 15 min; 0830–1029 h, 72 h; 1030–1229 h, 22 h 45 min; 1230–1429 h, 32 h 45 min; 1430–1629 h, 70 h; 1630–1829 h, 37 h 25 min.

Data are presented as frequencies and expressed graphically (Figs 4–9). For each feeding category and selected species data were compared by χ^2 tests, when applicable.

Results

Analysis of Foraging

I recorded 52 species (16 non-passerines and 36 passerines) foraging during the study period; 43 were observed during transect walks and nine at random (see below). The monthly records of 39 of the 43 species are summarized in the Appendix. The foraging activities of the other four species, *Prionodura newtoniana*, *Ptilonorhynchus violaceus*, *Ailuroedus dentirostris* and *A. melanotis*, are not included as they are being investigated separately by C. B. Frith. Of the 39 species, six (15.4%) were herbivores, 11 (22.2%) mixed feeders, and 22 (56.4%) insectivores. Nine species were predominantly terrestrial foragers (one herbivore, one mixed feeder and seven insectivores) and 30 arboreal foragers (five herbivores, nine mixed feeders and 16 insectivores) (see Appendix). In total 2448 foraging observations for these 39 species were made during transect walks: 65 (2.7%) were of herbivores, 278 (11.4%) of mixed feeders and 2105 (85.9%) of insectivores. Twenty-four species were commonly observed foraging and represented 2380 (97.6%) of the total number of foraging records. One of these species, *Merops ornatus*, was observed foraging seasonally, mostly at some distance above the canopy on its northwards and southwards migrations (see Appendix). The remaining 23 species are common residents throughout the year, with the exception of *Rhipidura rufifrons* that migrated during drier months (from April to August–September). Data for these 23 species are analysed individually (see below; Tables 2–4; Fig. 1). The remaining 15 of the 39 species were rarely observed foraging; this was indicative of their relative sparsity within the study area (Appendix).

In total 1427 records (58.3%) for 35 species were recorded along track 1 and 1021 (41.7%) for 32 species along track 2. Twenty-eight species were common to both tracks; the other species, rarely sighted on either track, were those uncommon within the area. The larger number of observations along track 1 was mainly due to the large numbers of sightings for *Rhipidura fuliginosa* in the more open sunlit situation. Differences between the two tracks were not considered sufficiently significant to warrant further discussion.

The nine additional species observed during random observations, which are not subsequently discussed, were the herbivores *Ptilinopus superbus*, *Lopholaimus antarcticus*, *Columba leucomela*, *Chalcophaps indica*, *Trichoglossus chlorolepidotus*, *Alisteris scapularis* and *Dicaeum hirundaceum*, and the insectivores *Arses kaupi* and *Chrysococcyx pyrrhophanus*.

Foraging Height

Overall there was a fairly broad use of strata (see Table 2 for H' values); 15 species were height generalists with a foraging height diversity of 1.0 or greater, and eight were height specialists with a foraging height diversity of 0.6 or less. Frequency distributions of foraging observations for the three feeding categories and the 23 species over seven strata are given in Table 2. The vertical distribution of feeding categories was not uniform and apart from some terrestrial foragers no species was confined to one stratum.

Herbivores were height specialists limited mainly to the canopy (5 and 6), where the largest number of species and individuals were observed foraging, and to the ground (1).

More species and individuals of mixed feeders occurred in the canopy (5) and subcanopy (4) than at other levels. The predominantly nectarivorous mixed feeders were height specialists, foraging among the flowering canopy. The mixed feeder *Alectura lathami* was also a height specialist. Other mixed feeders with a more varied diet, however, were height generalists, foraging over a much wider range of strata (Table 2). Species and individuals of insectivores were well represented in the lower part of the canopy (51), subcanopy (4), understorey (3) and ground (1). Arboreal-foraging insectivores were height generalists and terrestrial-foraging

Table 2. Frequency distributions of foraging observations on 23 species of birds in different rainforest strata, and foraging height diversity (H')

Key to strata: 1, ground (soil, litter); 2, herb layer, up to 1 m above ground (ferns, grasses, seedlings); 3, understorey, 1–5 m (tree ferns, shrubs, saplings, trunks, climbing plants); 4, subcanopy, 5–10 m (tree ferns, small trees, lower canopy of larger trees, trunks, climbing plants); 51, lower half of canopy, 10–17.5 m, and 5u, upper half of canopy, 17.5–25 m (canopy of larger trees, climbing plants, epiphytes); 6, emergents, above 25 m (crowns of tall emergents, climbing plants, epiphytes)

Species	H'	Percentage frequency in stratum No.:						
		1	2	3	4	51	5u	6
<i>Coracina lineata</i>	0.3	—	—	—	—	—	20.0	80.0
<i>Platycercus elegans</i>	1.2	—	—	—	3.8	28.6	42.9	25.5
<i>Lichenostomus frenatus</i>	1.4	—	—	1.6	17.3	37.0	29.9	14.2
<i>Ptilinopus magnificus</i>	0.6	—	—	—	—	5.9	82.3	11.8
<i>Clamacteris minor</i>	1.5	—	—	13.8	24.1	24.1	31.1	6.9
<i>Colluricinclla boweri</i>	1.5	1.2	1.2	9.4	32.9	31.8	18.8	4.7
<i>Ptiloris victoriae</i>	1.3	—	—	7.7	13.8	30.8	44.6	3.1
<i>Pachycephala pectoralis</i>	1.5	—	—	14.9	31.3	25.4	25.4	3.0
<i>Rhipidura fuliginosa</i>	1.6	0.4	7.0	13.2	18.4	34.5	24.4	2.1
<i>Meliphaga lewinii</i>	1.2	—	10.0	—	30.0	10.0	50.0	—
<i>Acanthorhynchus tenuirostris</i>	1.1	—	—	—	30.0	30.0	40.0	—
<i>Macropygia amboinensis</i>	1.1	10.0	—	—	10.0	60.0	20.0	—
<i>Gerygone mouki</i>	1.4	—	2.4	23.2	21.2	35.4	17.9	—
<i>Tregellasia capito</i>	1.4	14.3	22.9	31.4	28.6	—	2.8	—
<i>Sericornis magnirostris</i>	1.2	—	13.6	45.4	29.3	11.7	—	—
<i>Rhipidura rufifrons</i>	1.3	10.7	16.0	34.6	29.6	9.4	—	—
<i>Psophodes olivaceus</i>	1.1	66.6	11.8	11.8	5.9	3.9	—	—
<i>Sericornis citreogularis</i>	0.3	92.4	6.2	1.0	0.2	0.2	—	—
<i>Poecilodryas albispecularis</i>	0.3	92.7	5.5	1.8	—	—	—	—
<i>Emblema temporalis</i>	0.7	48.5	51.5	—	—	—	—	—
<i>Alectura lathami</i>	0.4	84.6	15.4	—	—	—	—	—
<i>Crateroscelis gutturalis</i>	0.4	89.0	11.0	—	—	—	—	—
<i>Orthonyx spaldingi</i>	0	100.0	—	—	—	—	—	—
Herbivores								
No. of species		2	—	—	2	4	5	2
No. of individuals		2	—	—	2	18	34	9
Mixed feeders								
No. of species		2	3	2	7	4	7	3
No. of individuals		29	18	7	41	73	83	27
Mixed feeders								
No. of species		11	11	14	11	12	7	6
No. of individuals		765	130	291	299	359	213	48

insectivores were height specialists (Table 2). *Rhipidura fuliginosa* was the only species observed foraging at all strata. Terrestrial-foraging insectivores represented 36.3% of the total number of foraging observations of this feeding category.

Mixed feeders and insectivores used a wide range of arboreal strata (Table 2); but mixed feeders foraged significantly higher than insectivores ($P < 0.001$). The relative use of strata by the two mixed feeders *Lichenostomus frenatus* and *Ptiloris victoriae* was significantly different ($\chi^2_4 = 12.817$, $P < 0.02$). The three insectivores *Pachycephala pectoralis*, *Colluricincla*

Table 3. Frequency distributions of foraging observations on 23 species of birds at different types of site, and foraging site diversity (H')

Key to types of site: 1, air (flying insects); 2, leaves < 15 by 10 cm, twigs and small branches; 3, treestrunks; 4, branches > 5 cm diameter; 5, leaves > 15 by 10 cm; 6, dense bunches of dead leaves; 7, dead branches; 8, pendant vines; 9, tangle of vines and dead vegetation; 10, lawyer vine, *Calamus* spp.; 11, epiphytes; 12, mistletoe (fruits and insects); 13, leaf litter; 14, flowers (nectar and arthropods); 15, fruits and seeds

Species	H'	Percentage frequency at site No.:														
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Arboreal: Herbivores																
<i>Ptilinopus magnificus</i>	0	—	—	—	—	—	—	—	—	—	—	—	—	—	100.0	
<i>Macropygia amboinensis</i>	0.64	—	—	—	—	—	—	—	—	—	—	—	10.0	10.0	—	80.0
<i>Platycercus elegans</i>	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	100.0
Mixed feeders																
<i>Coracina lineata</i>	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	100.0
<i>Meliphaga lewinii</i>	0.67	—	60.0	—	—	—	—	—	—	—	—	—	—	—	40.0	—
<i>Lichenostomus frenatus</i>	1.25	1.6	44.9	1.6	—	4.7	1.6	—	—	—	—	—	0.8	—	40.1	4.7
<i>Acanthorhynchus tenuirostris</i>	1.19	10.0	40.0	—	—	—	—	—	—	—	—	—	10.0	—	40.0	—
<i>Emblema temporalis</i>	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	100.0
<i>Ptiloris victoriae</i>	1.72	—	—	15.4	18.5	—	1.5	21.5	4.6	3.1	—	—	—	—	3.1	32.3
Insectivores																
<i>Tregellasia capito</i>	1.71	20.0	31.3	22.9	—	8.6	—	—	5.7	2.9	—	—	8.6	—	—	
<i>Pachycephala pectoralis</i>	1.11	4.5	73.0	3.0	6.0	6.0	—	1.5	1.5	—	3.0	—	1.5	—	—	
<i>Colluricinclla boweri</i>	1.22	—	68.1	2.4	5.9	10.5	1.2	—	2.4	5.9	1.2	1.2	—	1.2	—	
<i>Rhipidura rufifrons</i>	1.41	17.3	58.7	1.3	—	6.7	—	—	4.0	6.7	—	—	5.3	—	—	
<i>R. fuliginosa</i>	0.79	75.0	19.9	0.2	0.8	0.96	—	0.2	0.2	0.8	0.58	—	—	0.96	0.4	
<i>Sericornis magnirostris</i>	1.65	0.5	43.0	7.8	1.0	20.6	2.0	1.0	1.5	15.2	7.4	—	—	—	—	
<i>Gerygone mouki</i>	1.00	—	83.4	—	0.9	6.6	—	0.9	—	6.3	—	—	1.9	—	—	
<i>Climacteris minor</i>	0.42	—	—	88.0	10.3	—	—	1.7	—	—	—	—	—	—	—	
Terrestrial: Mixed feeder																
<i>Alectura lathami</i>	0.43	—	—	—	—	—	—	—	—	—	—	—	84.6	—	15.4	
Insectivores																
<i>Poecilodryas albispectoralis</i>	0.18	—	—	1.8	—	—	—	—	—	—	1.8	—	—	96.4	—	
<i>Orthonyx spaldingii</i>	0	—	—	—	—	—	—	—	—	—	—	—	—	100.0	—	
<i>Psophodes olivaceus</i>	1.0	—	7.8	9.8	—	—	7.8	—	0	3.9	—	—	—	70.7	—	
<i>Crateroscelis gutturalis</i>	0.35	—	—	—	—	—	—	11.0	—	—	—	—	—	89.0	—	
<i>Sericornis citreogularis</i>	0.34	0.2	1.9	—	0.2	—	—	3.9	—	0.6	0.2	—	0	93.0	—	

boweri and *Gerygone mouki* foraged mostly in the canopy (5) and subcanopy (4). There was no significant difference between the relative use of strata by *P. pectoralis* and *C. boweri* ($\chi^2_4 = 4.281$, $P > 0.03$) but these species foraged overall higher than *G. mouki* ($P < 0.05$). *Tregellasia capito* and *Sericornis magnirostris* both foraged mostly among lower vegetation (strata 2–4) but *S. magnirostris* more frequently higher than *T. capito* ($P < 0.001$). *P. pectoralis*, *C. boweri* and *G. mouki* each foraged significantly higher than either *T. capito* or *S. magnirostris* ($P < 0.001$); *Rhipidura fuliginosa* foraged significantly higher than congener *R. rufifrons* ($P < 0.001$); *Climacteris minor* foraged at the same height as *P. pectoralis*, *C. boweri* and *G. mouki* but its foraging site and behaviour were quite different.

Foraging Site

Foraging site diversity (H') and frequency distributions of foraging observations at different foraging sites for the 23 species are given in Table 3. Obviously there was a basic separation of site use between herbivores and insectivores, mixed feeders overlapping with both categories (Table 3).

Foraging site diversity of *Lichenostomus frenatus* was greater than that of *Meliphaga lewinii* or *Acanthorhynchus tenuirostris*; the lower foraging site diversity of *A. tenuirostris* relating to its predominantly nectarivorous diet. Other mixed feeders, *Coracina lineata* and *Emblema temporalis*, were only observed eating fruits and seeds respectively ($H' = 0$) but presumably use other sites when hunting arthropods as indicated in the literature (Readers Digest 1976). *Ptiloris victoriae* utilized a wide range of foraging sites ($H' = 1.72$) including tree trunks and branches, and in this respect its foraging site overlapped with *Climacteris minor*.

Foraging site diversity of terrestrial-foraging insectivores was obviously low, except that of *Psophodes olivaceus* which often foraged in sites other than leaf litter (Table 3) and in higher strata (Table 2). *Pachycephala pectoralis*, *Colluricincla boweri* and *Gerygone mouki* foraged mainly among leaves (78.0%); *Rhipidura rufifrons* and *Sericornis magnirostris* from leaves (63.0%) and also from air (17.3%) and vines (15.2%) respectively; and *Tregellasia capito* from air, leaves and tree-trunks (> 20.0% per site). Foraging site diversity of *R. fuliginosa* and *Climacteris minor* were low (Table 3); and their main foraging sites (air and trunks respectively) ecologically segregated them from other arboreal insectivores.

Foraging Behaviour

Searching was the main behaviour of all herbivores, six species of mixed feeders and eight species of insectivores. Frequency distributions of foraging observations in the different behavioural categories for the 23 species are given in Table 4. The mixed feeder *Ptiloris victoriae* searched for fruits but probed for arthropod foods. *Alectura lathami* and *Orthonyx spaldingii*, unlike the other terrestrial foragers that mainly searched for food, scratched among leaf litter. Foraging behaviours of the two fantails differed; *Rhipidura rufifrons* foraged mostly by flitting and *R. fuliginosa* by hawking (Table 4). Behaviours of the two robins also differed; *Poecilodryas albispectoralis* mostly sallied from vertical perches down onto the leaf litter, whereas *Tregellasia capito* foraged by searching, sallying and hawking, depending upon foraging site. *Climacteris minor* searched and spiralled when hunting foods. Utilization of different behaviours was important in contributing to niche differentiation between some species, particularly arboreal foraging insectivores.

Overall Use of the Habitat for Foraging

The dendrogram resulting from the indices of structural overlap (foraging height + site) for the 23 species is illustrated in Fig. 1. No two species were identical in their overall use of habitat. Structural overlap values between several species were high, and these species are grouped together (Fig. 1, groups A–C).

Group A consisted of three species of herbivores and one species of mixed feeder. Structural overlap values between *Ptilinopus magnificus*, *Platycercus elegans* and *Coracina lineata* were high because they foraged mostly in the canopy; but between these and *Macropygia amboinensis* structural overlap values were relatively lower, because this species was also observed foraging near to, or on, the ground (Table 2). *Coracina lineata* foraged mostly on fruits of strangler fig *Ficus destruens* (90·0% of all observations).

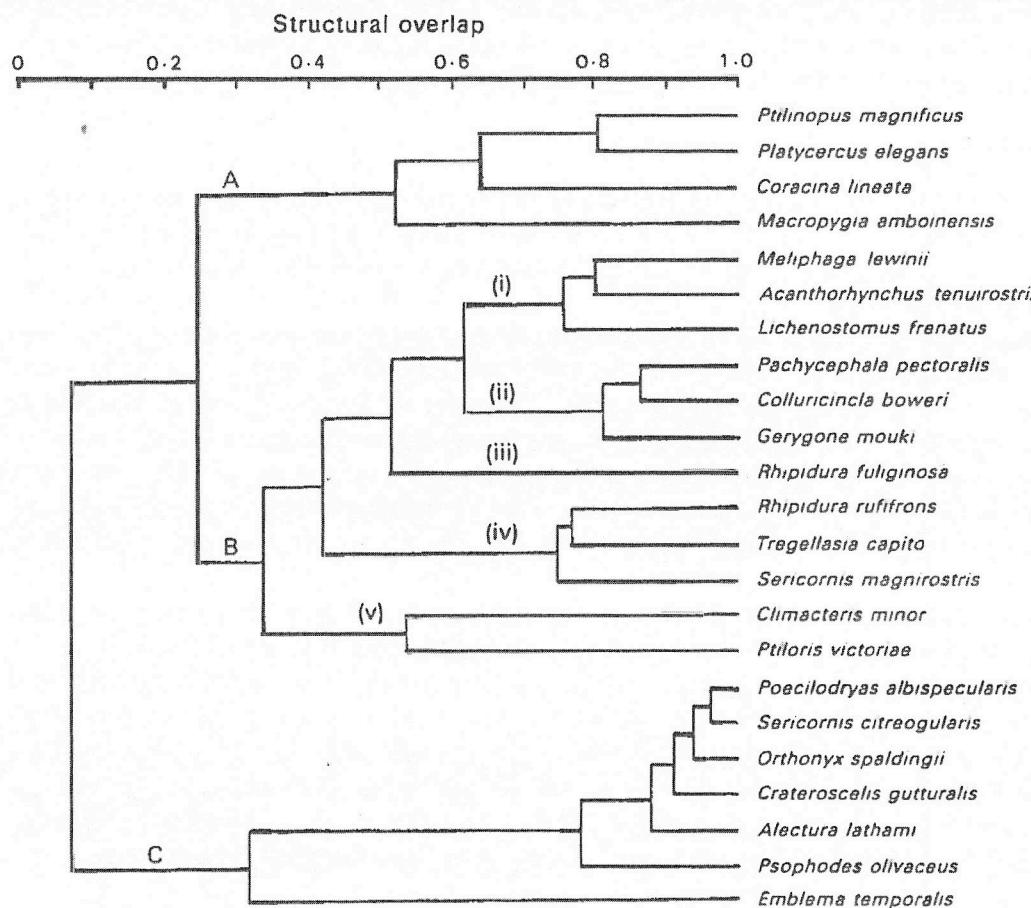


Fig. 1. Dendrogram of structural overlap for 23 species of birds in upland tropical rainforest. A-C, main groups; (i)-(iv), subgroups.

Group B consisted of four species of mixed feeders and eight species of insectivores that foraged predominantly in the canopy, subcanopy and understorey (Fig. 1), and was divided into subgroups i-v (Fig. 1). Structural overlap values between species within each subgroup were high and were not, therefore, segregated to any significant degree by foraging height and site. For these species (subgroups i, ii and iv) indices of behavioural overlap and ratios of bill lengths were compared (Table 5).

Structural and behavioural overlap values between the three species of honeyeaters (subgroup i) were high (Fig. 1) and bill lengths similar (Table 5). Differential utilization of food resources possibly segregated these species, as *Acanthorhynchus tenuirostris* was observed foraging mostly on nectar or arthropods whereas *Meliphaga lewinii* and *Lichenostomus frenatus* foraged on fruit as well* as flowers (mostly flowers of pandanus *Freycinetia excelsa*[†]) and insects.

**M. lewinii* was observed foraging on fruits during random observations, not during transect walks.

[†] Since this study I have observed *L. frenatus* eating the soft fleshy orange inner bracts about the base of the pandanus inflorescence. During this investigation 60·0% of the 40·1% of foraging site records at flowers for *L. frenatus* were at pandanus. I record foods eaten at flowers as nectar and/or arthropods (Table 3) but it is possible that the bracts were also being eaten. Similarly, *M. lewinii* and *P. victoriae*, which also foraged at pandanus, may have been eating these bracts.

Pachycephala pectoralis, *Colluricincla boweri* and *Gerygone mouki* (subgroup ii) were closely associated with the honeyeaters (Fig. 1) because of similarities in use of strata (Table 2), and use of sites when honeyeaters foraged on arthropods (Table 3). Although structural and behavioural overlap values between these three arboreal foraging insectivores were high, their bill lengths differed (Table 5), which may result in their utilizing different sizes and/or types of arthropod foods. Moreover, the limited differential use of strata (see above) may further contribute to niche differentiation. *Rhipidura fuliginosa* (subgroup iii) was closely linked with subgroups i and ii because of similarities in foraging height (Table 2) rather than foraging site (Table 3). Foraging site and behaviour were the main factors to partition this fantail from the other seven arboreal insectivores in group B.

Table 4. Frequency distributions of foraging observations on 23 species of birds, according to behaviour

Key to behaviours: Fl., flitting; Se., searching; Ho., hovering; Sa., sallying; Ha., hawking; Sp., spiralling; Pr., probing; Sc., scratching

Species	Fl.	Se.	Ho.	Percentage frequency				
				Sa.	Ha.	Sp.	Pr.	Sc.
Arboreal: Herbivores								
<i>Ptilinopus magnificus</i>	—	100·0	—	—	—	—	—	—
<i>Macropygia amboinensis</i>	—	100·0	—	—	—	—	—	—
<i>Platycercus elegans</i>	—	100·0	—	—	—	—	—	—
Mixed feeders								
<i>Coracina lineata</i>	—	100·0	—	—	—	—	—	—
<i>Meliphaga lewinii</i>	—	100·0	—	—	—	—	—	—
<i>Lichenostomus frenatus</i>	—	96·0	0·8	2·4	0·8	—	—	—
<i>Acanthorhynchus tenuirostris</i>	—	90·0	—	—	10·0	—	—	—
<i>Emblema temporalis</i>	—	84·9	—	15·1	—	—	—	—
<i>Ptiloris victoriae</i>	—	44·6	—	—	—	—	55·4	—
Insectivores								
<i>Tregellasia capito</i>	—	37·1	5·7	37·1	20·1	—	—	—
<i>Pachycephala pectoralis</i>	1·5	77·6	—	11·9	9·0	—	—	—
<i>Colluricincla boweri</i>	—	95·3	—	4·7	—	—	—	—
<i>Rhipidura rufifrons</i>	61·4	16·0	—	5·3	17·3	—	—	—
<i>R. fuliginosa</i>	25·0	1·4	0·2	2·5	70·9	—	—	—
<i>Sericornis magnirostris</i>	—	97·0	10·0	2·0	—	—	—	—
<i>Gerygone mouki</i>	0·9	84·5	4·0	12·7	0·5	—	—	—
<i>Climacteris minor</i>	—	34·5	—	—	—	65·5	—	—
Terrestrial: Mixed feeders								
<i>Alectura lathami</i>	—	15·1	—	—	—	—	—	84·9
Insectivores								
<i>Poecilodryas albispectoralis</i>	—	1·8	—	96·4	—	—	—	1·8
<i>Orthonyx spaldingii</i>	—	—	—	—	—	—	—	100·0
<i>Psophodes olivaceus</i>	—	100·0	—	—	—	—	—	—
<i>Crateroscelis gutturalis</i>	—	100·0	—	—	—	—	—	—
<i>Sericornis citreogularis</i>	—	99·6	—	0·2	0·2	—	—	—

Tregellasia capito, *Rhipidura rufifrons* and *Sericornis magnirostris* (subgroup iv) linked with subgroups i–iii because of similarities in foraging sites (Table 3) rather than foraging heights (Table 2). Structural overlap between these three species was high, but behavioural overlap values low (Table 5). As there was little difference between their bill sizes (Table 5), foraging behaviour was an important mechanism in ecologically segregating them. The structural overlap value between *Climacteris minor* and *Ptiloris victoriae* (subgroup v) was high because they used similar height and sites (Tables 2, 3), but differences in their behaviours (Table 4), bill lengths and diets clearly partitioned resource use.

Group C consisted of six terrestrial foragers, one being a mixed feeder and five insectivores (Fig. 1). The mixed feeder, *Emblema temporalis*, is loosely associated with

group C because I only observed it foraging on grass seeds on, or near to, the ground (Fig. 1). Structural overlap between species in this group was high. The larger size of *Alectura lathami* and its mixed diet clearly segregated it from the smaller insectivorous species. *Poecilodryas albispecularis* foraged mostly among leaflitter, as did the other insectivores in this group, but by a totally different behaviour (Table 3). Behavioural overlap value between *Sericornis citreogularis* and *Crateroscelis gutturalis* was high, but the slightly longer bill of the fern wren (Table 5) may result in at least partial utilization of different arthropod foods. Moreover,

Table 5. Structural and behavioural overlaps, and bill length, among groups of species that overlap considerably in their use of habitat

Bill length is given as the mean \pm standard deviation of N measurements. S.O., structural overlap; B.O., behavioural overlap; B.R., ratio of the longer to the shorter bill

Species	<i>N</i>	Bill length (mm)	<i>L. frenatus</i>	<i>A. tenuirostris</i>
<i>Meliphaga lewinii</i>	6	23.6 ± 1.6	S.O.	0.800
			B.O.	0.908
			B.R.	1.21
<i>Lichenostomus frenatus</i>	41	26.8 ± 1.4	S.O.	0.763
			B.O.	0.900
			B.R.	1.06
<i>Acanthorhynchus tenuirostris</i>	16	28.5 ± 1.64		
<i>Pachycephala pectoralis</i>	17	16.1 ± 2.14	<i>C. boweri</i>	<i>G. mouki</i>
			S.O.	0.809
			B.O.	0.909
<i>Colluricinclla boweri</i>	40	26.5 ± 1.03	B.R.	1.38
			S.O.	0.815
			B.O.	0.892
<i>Gerygone mouki</i>	7	11.8 ± 0.61	B.R.	2.26
<i>Tregellasia capito</i>	20	14.8 ± 0.55	<i>R. rufifrons</i>	<i>S. magnirostris</i>
			S.O.	0.652
			B.O.	0.401
<i>Rhipidura rufifrons</i>	32	14.1 ± 0.59	B.R.	1.02
			S.O.	0.746
			B.O.	0.192
<i>Sericornis magnirostris</i>	61	15.1 ± 1.49	B.R.	1.07
<i>Orthonyx spaldingii</i>	6	23.9 ± 1.09	<i>P. olivaceus</i>	
			S.O.	0.687
			B.O.	0
<i>Psophodes olivaceus</i>	5	22.8 ± 0.95	B.R.	1.05
<i>Crateroscelis gutturalis</i>	28	19.9 ± 0.86	<i>S. citreogularis</i>	
			S.O.	0.941
			B.O.	0.996
<i>Sericornis citreogularis</i>	70	15.3 ± 1.9	B.R.	1.3

S. citreogularis, unlike *C. gutturalis*, followed, and thus benefited from, flocks of foraging logrunners; and also foraged at higher strata around its nests during the breeding season. Foraging behaviours of the two similar-sized insectivores *Orthonyx spaldingii* and *Psophodes olivaceus* were quite different (Table 4), and *P. olivaceus* also foraged at higher levels (Table 2).

Seasonal Fluctuations in Foraging

Monthly foraging records for the 39 species and for each feeding category are summarized in the Appendix; as are the total number of species and individuals of each feeding category for dry and wet months.

Species diversity of foraging mixed feeders was highest during February and March, due to the presence of *Phylidonyris nigra*, *Myzomela obscura* and *M. sanguinolenta* that moved into the forest from the forest edge when a notably large number of tree species were flowering. Similarly, *Emblema temporalis* was only observed foraging during the wetter months when grasses seeded (Appendix). A significantly larger number of individuals of mixed feeders were observed foraging during the wetter months than during the drier period ($P < 0.001$). Species diversity of insectivores was similar during both periods (see Appendix). A larger number of individuals was recorded during the wet months when there was a notable increase in insect abundance (Table 1), but this seasonal difference was not significant ($\chi^2_3 = 5.315$, $P > 0.1$). Fewer individuals of mixed feeders and insectivores were observed feeding during August, when temperatures, rainfall and insect biomass were at their lowest (Table 1).

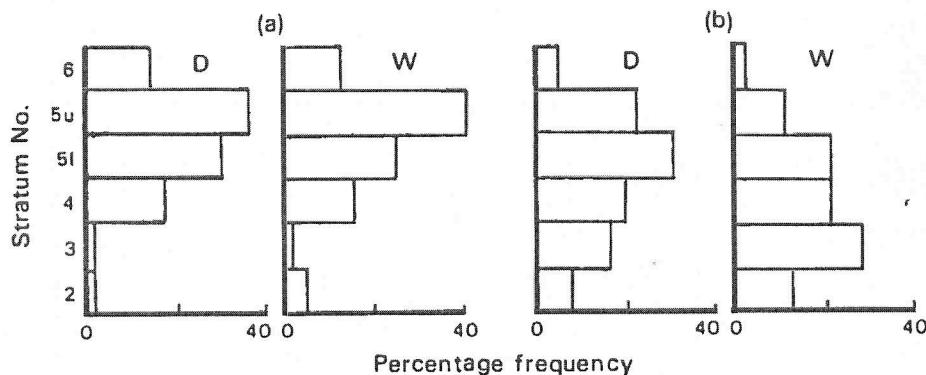


Fig. 2. Percentage frequency distributions of foraging observations in arboreal strata 2–6 during dry (D) and wet (W) months. (a) Mixed feeders, 97 and 122 observations in the dry and wet respectively. (b) Insectivores, 544 and 671 observations in the dry and wet respectively.

Seasonal Effects on Foraging Height, Site and Behaviour

Frequency distributions of foraging observations of mixed feeders and insectivores in arboreal strata 2–6 for dry and wet months are given in Fig. 2. The larger number of records noted for *Emblema temporalis* during the wet (see Appendix) were excluded, because when they were included results indicated an overall trend downwards by all mixed feeders during this period.

There was no significant difference between the height at which mixed feeders foraged during dry and wet months ($\chi^2_3 = 4.35$, $P = 0.5$). *Lichenostomus frenatus* and *Ptiloris victoriae*, whose foraging records represented 79.6% and 57.2% of the total number of mixed feeder records during dry and wet months respectively, showed no significant changes in height (*L. frenatus* $\chi^2_3 = 2.2028$, $P > 0.7$; *P. victoriae* $\chi^2_3 = 1.008$, $P > 0.5$). There was, however, a significant difference between the height at which insectivores foraged during dry and wet months ($P < 0.001$), due to a downward trend during the wetter period (Fig. 2). Frequency distributions of foraging observations for eight insectivores at different strata for dry and wet months are given in Fig. 3. These eight species represented 61.7% and 57.6% of total insectivore records during dry and wet months respectively. Apart from *Tregellasia capito*, they tended to forage at lower levels during the wet (Fig. 3). For species whose sample size per stratum was large enough for a χ^2 test to be meaningfully applied, this downward shift was significant for *Colluricinclla boweri* ($\chi^2_3 = 13.32$, $P < 0.01$), *Rhipidura fuliginosa* ($\chi^2_3 = 14.75$,

$P < 0.02$) and *Sericornis magnirostris* ($\chi^2_3 12.85, P < 0.01$), but less so for *Gerygone mouki* ($\chi^2_3 7.233, P < 0.1$).

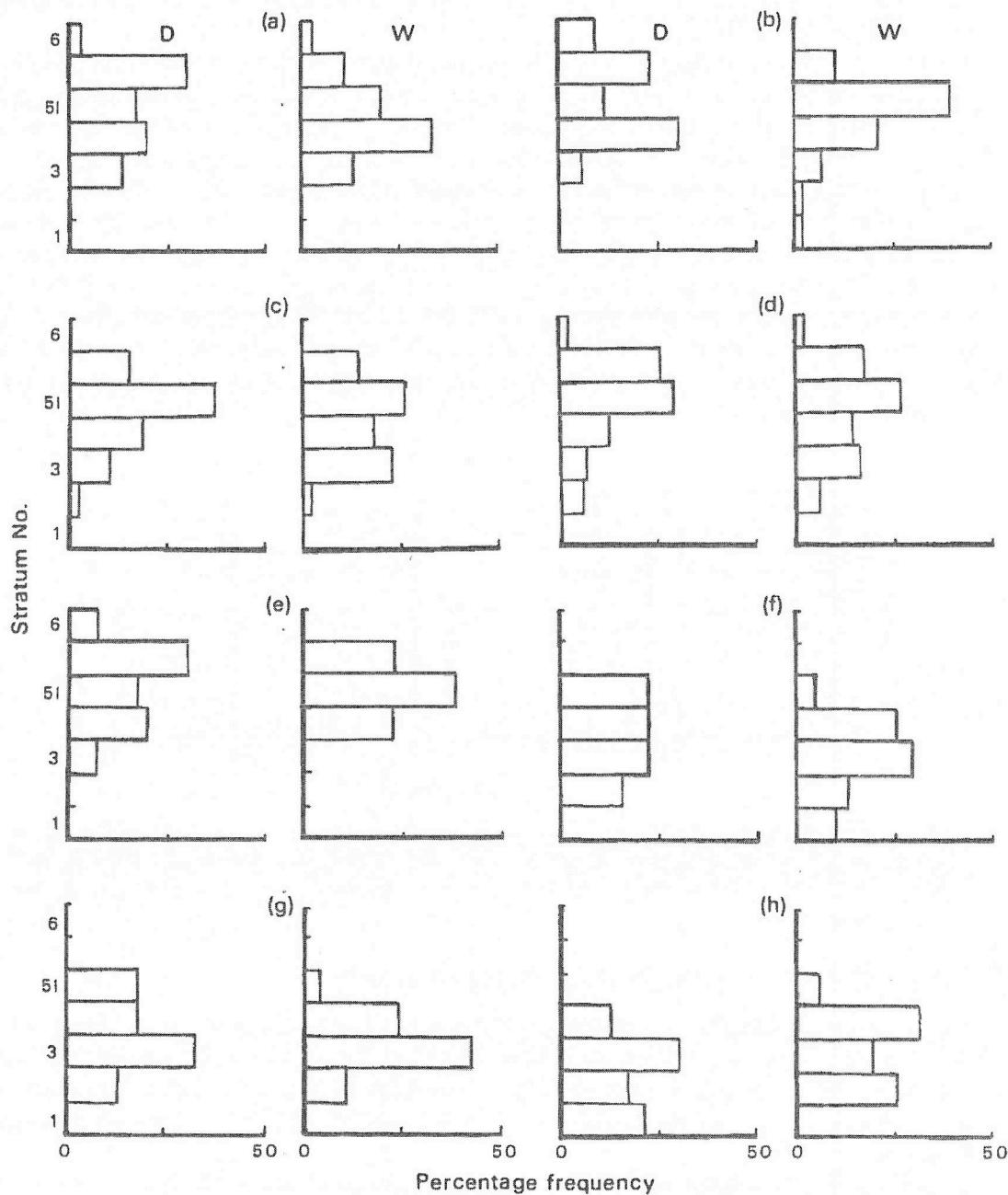


Fig. 3. Percentage frequency distributions of foraging observations on eight species of insectivores in strata 1–6 during dry (D) and wet (W) months. Species and sample sizes:

	Dry	Wet		Dry	Wet
(a) <i>Pachycephala pectoralis</i>	25	36	(e) <i>Climacteris minor</i>	33	11
(b) <i>Colluricincla boweri</i>	35	44	(f) <i>Rhipidura rufifrons</i>	15	58
(c) <i>Gerygone mouki</i>	93	110	(g) <i>Sericornis magnirostris</i>	58	123
(d) <i>Rhipidura fuliginosa</i>	226	232	(h) <i>Tregellasia capito</i>	19	13

Seasonal changes in the use of foraging sites is given in Table 6 for two mixed feeders and eight insectivore species. The relative use of sites by *L. frenatus* and *P. victoriae* differed between dry and wet months (Table 6). *L. frenatus* changed its diet significantly from a predominantly herbivorous diet during the dry months (78.0%) to a mainly insectivorous

diet (75.0%) during the wet months ($\chi^2 30.97, P < 0.001$). *P. victoriae* ate mostly insects during both dry (73.7%) and wet (54.8%) months, and although it foraged more on fruit during the wet this diet change was not significant ($\chi^2 3.829, P > 0.1$). The relative use of main foraging site(s) by six of the eight insectivores was similar during both dry and wet periods (Table 6); although foraging site diversity increased during the wet months because

Table 6. Seasonal changes in the use of types of foraging site by 10 species of birds, and in foraging site diversity (H')

For key to types of site, see Table 3. N , number of individuals seen. For the most commonly used sites, the percentage frequency distribution is given in parentheses

Species	Season	N	Sites used and percentage frequencies	H'
<i>Lichenostomus frenatus</i>	Dry	59	2(28.1), 3, 12, 14(59.3), 15	1.036
	Wet	52	1, 2(59.6), 5, 14(25.0)	1.030
<i>Ptiloris victoriae</i>	Dry	19	3(26.3), 4(15.8), 7(31.6), 9, 14(10.5), 15(10.5)	1.636
	Wet	31	3, 4(29.0), 7(16.1), 9, 15(38.7)	1.299
<i>Tregellasia capito</i>	Dry	19	1(15.8), 2(26.3), 3(31.6), 5(10.5), 13(15.8)	1.533
	Wet	13	1(23.1), 2(38.4), 3(15.4), 9(15.4), 10(7.7)	1.480
<i>Pachycephala pectoralis</i>	Dry	25	1, 2(68.0), 3, 4(12.0), 5, 8	0.892
	Wet	36	1, 2(72.0), 3, 4, 5, 7, 10, 12	1.121
<i>Colluricinclla boweri</i>	Dry	35	2(77.0), 4, 5(11.4), 8, 11	0.817
	Wet	44	2(63.5), 3, 4, 5(11.4), 6, 9, 10, 13	1.284
<i>Rhipidura rufifrons</i>	Dry	15	1(26.7), 2(66.6), 10	0.804
	Wet	7	1(15.5), 2(58.7), 3, 5, 9, 10, 13	1.355
<i>R. fuliginosa</i>	Dry	226	1(86.4), 2(9.3), 3, 4, 5, 7, 13, 14	0.555
	Wet	232	1(65.2), 2(29.4), 4, 5, 8, 9, 10, 13	0.886
<i>Sericornis magnirostris</i>	Dry	57	1, 2(63.0), 3, 5(14.0), 9, 10(10.6)	1.071
	Wet	123	2(39.8), 3, 4, 5(26.1), 6, 7, 8, 9(13.1), 10	1.611
<i>Gerygone mouki</i>	Dry	93	2(89.4), 4, 5, 9	0.438
	Wet	110	2(80.0), 5, 7, 9, 12	0.753
<i>Chincasteris minor</i>	Dry	33	3(97.0), 4	0.033
	Wet	12	3(75.0), 4(16.7), 7	0.772

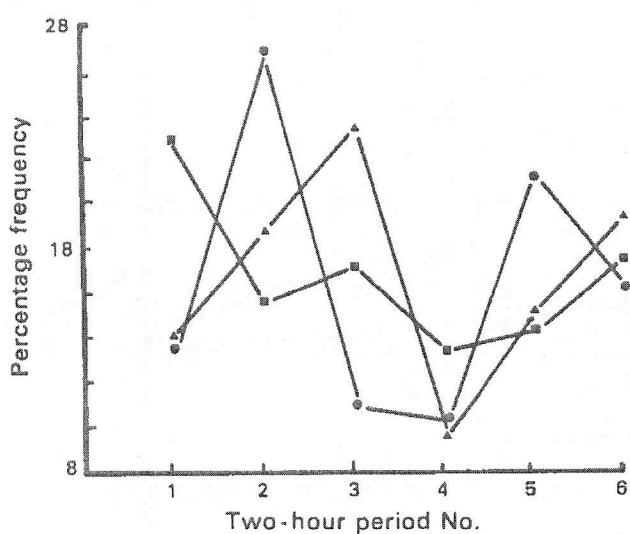


Fig. 4. Percentage frequency distributions of foraging observations during 2-hour periods throughout the day. ● Herbivores ($n = 65$). ▲ Mixed feeders ($n = 278$). ■ Insectivores ($n = 2105$). Periods: 1, 0630–0829 h; 2, 0830–1029 h; 3, 1030–1229 h; 4, 1230–1429 h; 5, 1430–1629 h; 6, 1630–1829 h.

of a greater utilization of sites such as tangle and/or vines (Table 6), this increase was too small to be significant. *Rhipidura rufifrons* and *R. fuliginosa* foraged more among leaves than from air when it was wetter, but this shift in site use was significant only for *R. fuliginosa* (*R. rufifrons*, $\chi^2 0.353, P > 0.5$; *R. fuliginosa*, $\chi^2 30.412, P < 0.001$).

As the relative use of foraging behaviours changed little between dry and wet months for the mixed feeders and insectivore species (Table 6), data for each period are not presented separately. Fantails foraged more by flitting rather than hawking during the wet, due to a

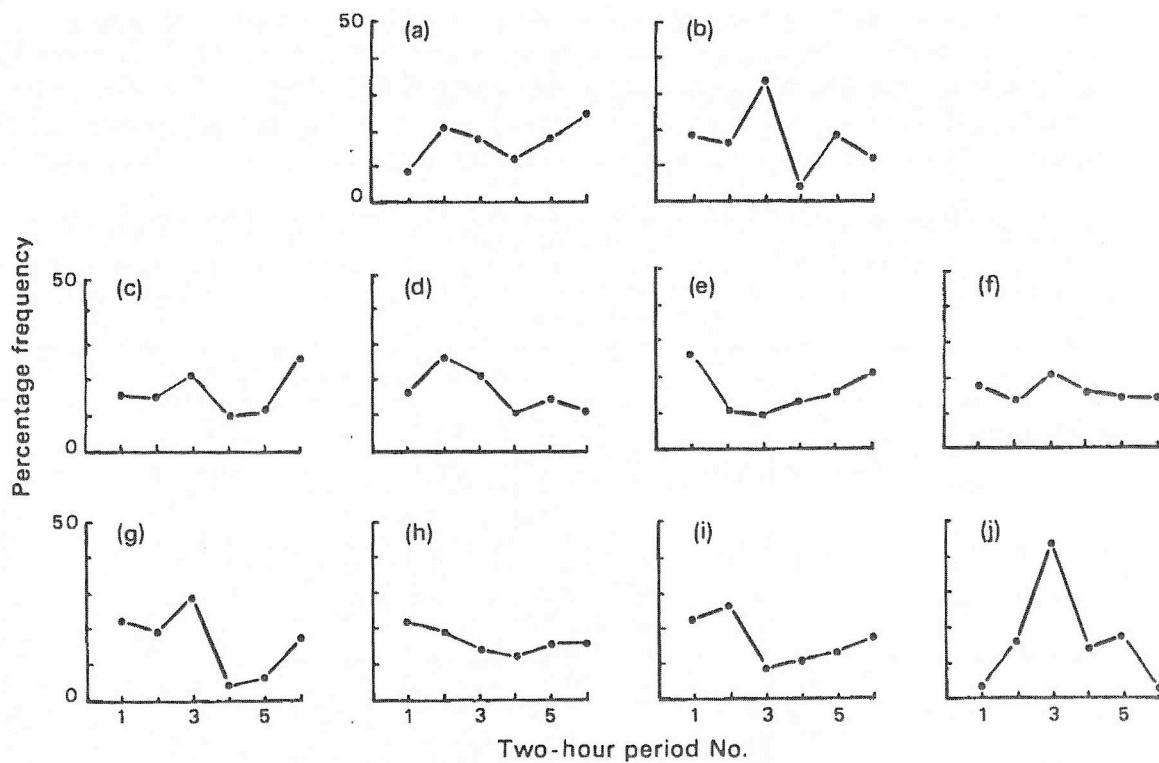


Fig. 5. Percentage frequency distributions of foraging observations on two species of mixed feeders and eight species of insectivores during 2-hour periods throughout the day. Periods as in Fig. 4. Species and sample sizes:

(a) <i>Lichenostomus frenatus</i>	127	(f) <i>Rhipidura fuliginosa</i>	517
(b) <i>Ptiloris victoriae</i>	65	(g) <i>Climacteris minor</i>	65
(c) <i>Pachycephala pectoralis</i>	67	(h) <i>Rhipidura rufifrons</i>	75
(d) <i>Colluricinclla boweri</i>	85	(i) <i>Sericornis magnirostris</i>	205
(e) <i>Gerygone mouki</i>	212	(j) <i>Tregellasia capito</i>	35

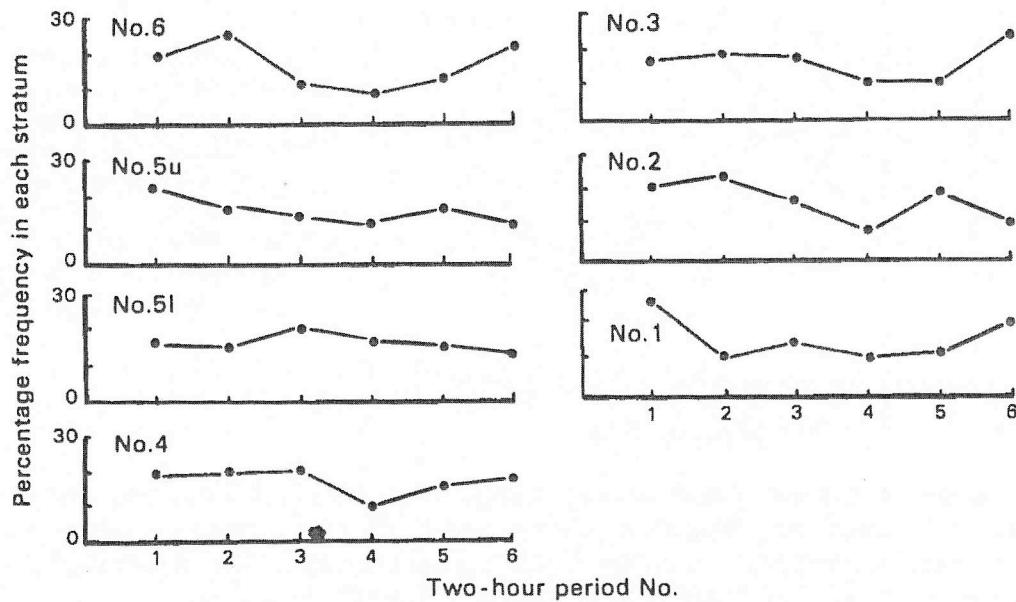


Fig. 6. Percentage frequency distributions of the total number of foraging observations during each 2-hour period throughout the day in each stratum. Periods as Fig. 4. Sample sizes: stratum 1, 1652; 2, 148; 3, 298; 4, 342; 5u, 450; 6, 84.

shift in site use (see above) but this change was significant only for *R. fuliginosa* (*R. rufifrons*, $\chi^2_1 2.278$, $P > 0.1$; *R. fuliginosa*, $\chi^2_1 22.80$, $P < 0.001$).

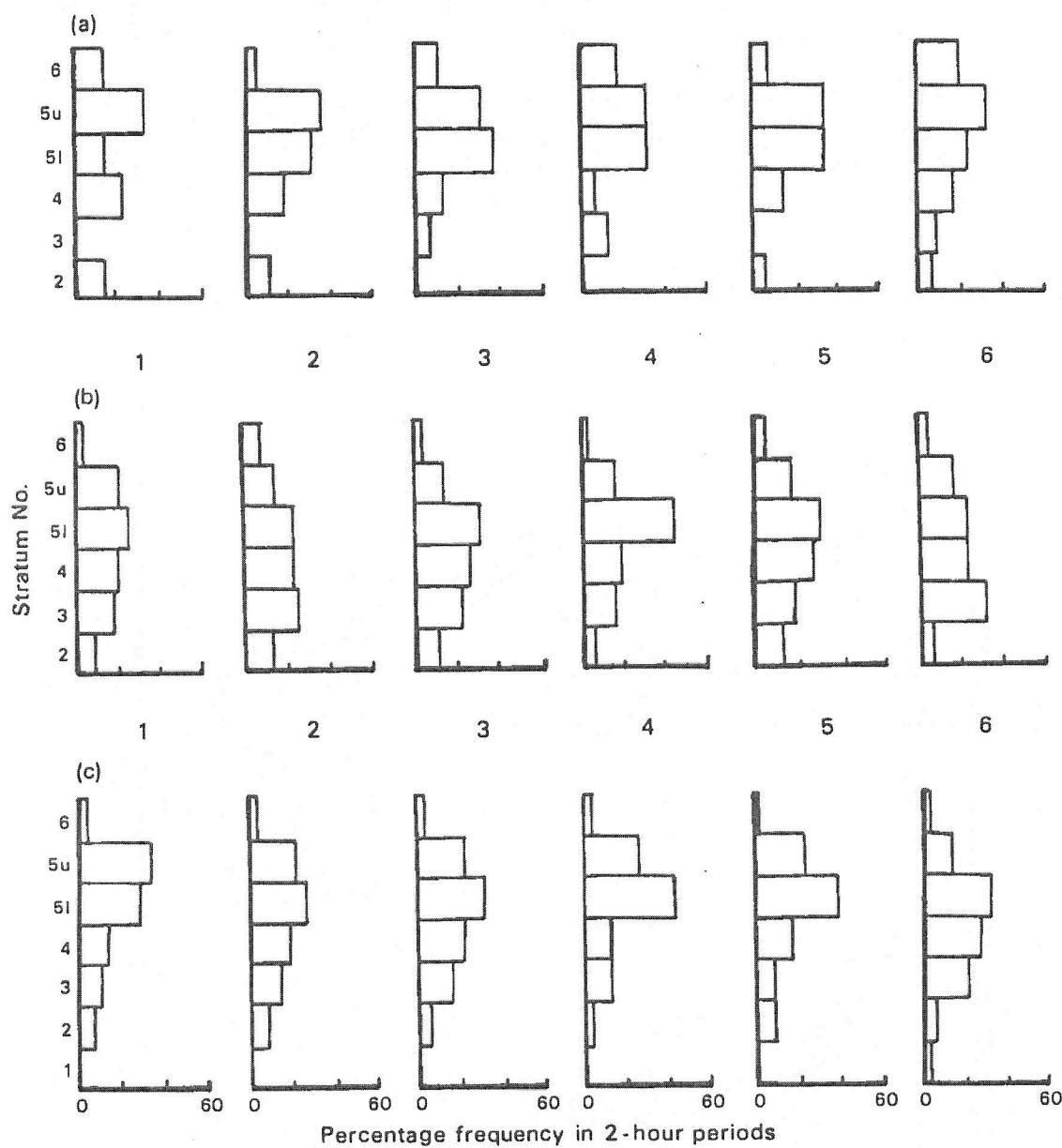


Fig. 7. Percentage frequency distributions of foraging observations in strata 2–6 during each 2-hour period throughout the day. (a) Mixed feeders. (b) Insectivores. (c) *Rhipidura fuliginosa*. Sample sizes for each period:

	1	2	3	4	5	6
(a)	34	73	26	16	60	40
(b)	276	360	113	128	290	173
(c)	98	121	53	60	122	63

Diurnal Fluctuations in Foraging

Herbivorous birds foraged mainly during mid-morning (0830–1029 h) and mid-afternoon (1430–1629 h) (Fig. 4). Mixed feeders foraged mostly during the mid-morning as well as the later morning (1030–1229 h) and during the later afternoon (1630–1829 h) (Fig. 4). Diurnal fluctuations of mixed feeders were mostly those of *Lichenostomus frenatus* and

Ptiloris victoriae (Fig. 5), whose foraging records represented 69.0% of the total mixed feeder observations. There was no significant difference between the foraging times of these two mixed feeders ($\chi^2_5 9.503, P > 0.1$). Interestingly, there was no significant difference between the diurnal times the mixed feeders foraged on insects and on flowers and fruits ($\chi^2_5 7.272, P > 0.2$).

Insectivores foraged predominantly during the early morning (0630–0829 h) and late afternoon (1630–1829 h) (Fig. 4). There was a significant difference between foraging times of mixed feeders and insectivores, insectivores foraging overall earlier and later than mixed feeders ($P < 0.001$; see 'Discussion'). There was considerable variation between the foraging

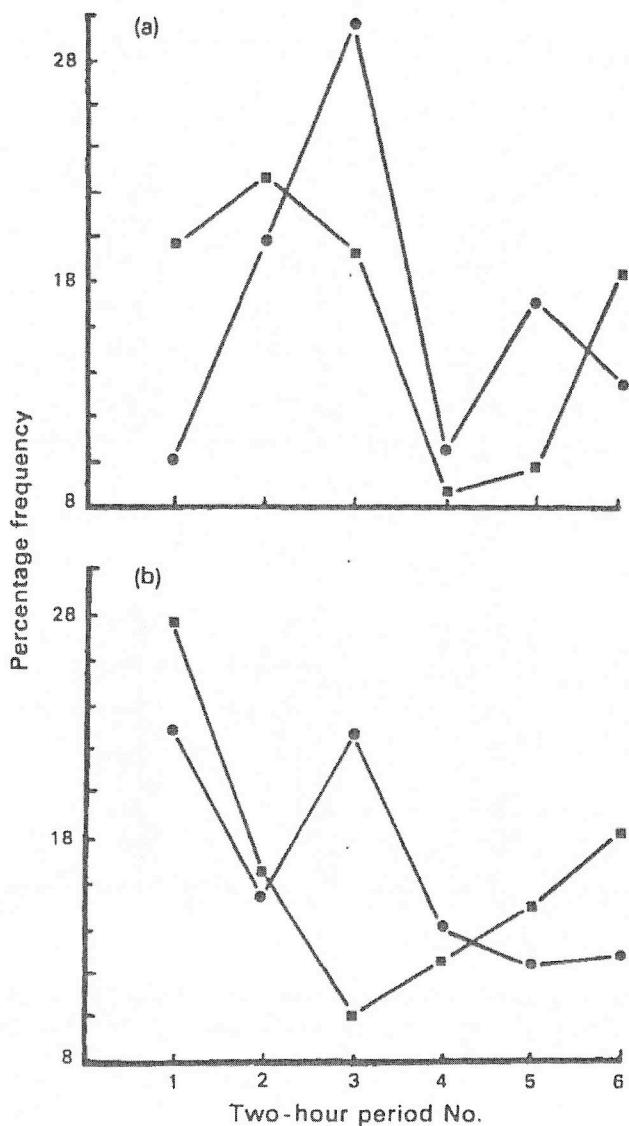


Fig. 8. Percentage frequency distributions of foraging observations during each 2-hour period throughout the day during dry (●) and wet (■) months.
 (a) Mixed feeders, 78 and 145 observations respectively.
 (b) Insectivores, 832 and 1074 observations respectively. Periods as in Fig. 4.

times of the eight insectivore species (Fig. 5). Although there was no significant difference between foraging times of *Pachycephala pectoralis* and *Colluricinclla boweri* ($\chi^2_5 5.185, P > 0.5$), both these species foraged later in the morning than *Gerygone mouki*; however, this difference was only significant between *C. boweri* and *G. mouki* (*P. pectoralis* and *G. mouki*, $\chi^2_5 7.557, P > 0.1$; *C. boweri* and *G. mouki*, $\chi^2_5 17.949, P < 0.001$). The relative foraging times of *Tregallasia capito* and *Sericornis magnirostris* also differed significantly ($\chi^2_5 18.918, P < 0.001$). The two fantails foraged throughout the day with little variation (Fig. 6) and there was no significant difference between their foraging times ($\chi^2_5 2.323, P > 0.8$).

Diurnal Variation in Vertical Distribution

The relative inactivity of foraging during the midday period was reflected in all strata (Fig. 6). Overall frequency distributions of mixed feeders and insectivores foraging at different arboreal strata throughout the day were similar (Fig. 7) and there was no apparent midday shift to lower levels. Sample sizes of individual species at each strata for each of the 2-h periods were too small to analyse individually, apart from those of *Rhipidura fuliginosa*. The relative use of strata by this species was similar throughout the day, except during midday (1230–1429 h), when there was a very slight upward movement (from strata 3 and 4 to 5; Fig. 7); it should be noted that this upward shift was reflected in the overall insectivore frequencies at these strata during this time of day (Fig. 7).

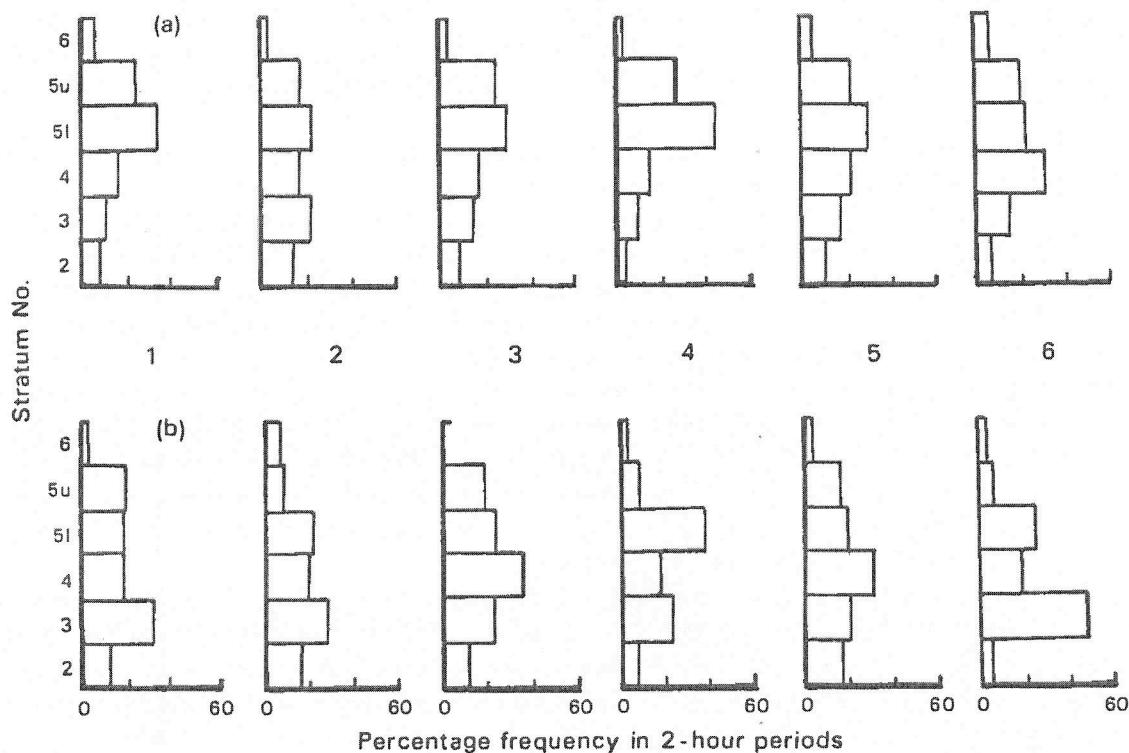


Fig. 9. Percentage frequency distributions of foraging observations on insectivores in strata 2–6 during each 2-hour period throughout the day. (a) Dry months. (b) Wet months. Sample sizes for each period:

	1	2	3	4	5	6
(a)	113	130	49	65	113	66
(b)	160	190	43	51	151	76

Seasonal Fluctuations in the Diurnal Pattern

Mixed feeders and insectivores foraged earlier in the morning and later in the afternoon during the wet months than they did during the drier period (Fig. 8), but this diurnal shift between seasons was significant only for insectivores (mixed feeders, χ^2_5 8.401, $P > 0.1$; insectivores, χ^2_5 24.700, $P < 0.001$). There was a significant difference between the foraging times of mixed feeders and insectivores during both dry (χ^2_5 12.399, $P < 0.05$) and wet (χ^2_5 17.78, $P < 0.01$) months.

Seasonal Fluctuations in the Diurnal Pattern of Vertical Distribution

Frequency distributions of foraging observations at different arboreal strata for each 2-h

period of the day during both dry and wet months are given for insectivores in Fig. 9. The seasonal shift downwards during the wet months (see above) was reflected at every stratal level throughout the day.

Discussion

Results clearly showed that differential utilization of vertical strata was, overall, the most important factor contributing to niche differentiation within an upland tropical rainforest foraging assemblage; they concurred with those of other similar studies (Orians 1969; Karr 1971, 1976; Karr and Roth 1971; Pearson 1971, 1975, 1977; Lovejoy 1974; Croxall 1977; Crome 1978; Beehler 1981; Bell 1982c). Major differences between the vertical distribution of herbivores, mixed feeders and insectivores reflected the availability of food resources in different strata. Thus, the majority of herbivores foraged among the canopy fruit crop, or on fallen fruit on the ground, whereas mixed feeders and especially insectivores utilized a much broader range of strata.

Significantly more mixed feeders foraged in higher strata than insectivores, particularly in the upper part of the canopy where at least the herbivorous part of their diet was concentrated and where they possibly filled the insectivorous niche. Although Elton (1973) and Wolda (1979) recorded a higher biomass of insects in tropical rainforest canopies than in lower strata, Fogden (1972) noted that tropical insect densities in and above the canopy were seasonally more variable than those at lower levels. Karr (1976) suggested the less stable insect foods in the canopy was not as important to mixed feeders as to insectivores; it is possible, therefore, the greater use of lower strata by insectivores in my study area reflected a greater stability of insect foods lower down. Foraging height undoubtedly was a major factor contributing to ecological segregation between mixed feeders and insectivores, but results indicated that other factors operated to bring about a finer partitioning of resources between these two groups: namely, seasonal variations in diets, seasonal vertical shifts in foraging levels, and diurnal variation in foraging times.

There is evidence to suggest that mixed feeders alter their seasonal diets according to the availability of food resources. Bell (1977) suggested that mixed feeders coexisted with insectivores by foraging more on herbivorous foods during dry months when flowers and fruits were apparently more abundant, and on the hyperabundance of insects during the wet months. The significant change in the diet of *Lichenostomus frenatus* from flowers and fruits to insects during the wet supports Bell's contention. The majority of mixed feeders and insectivores began breeding during the latter part of the dry season (September–November) when temperatures, rainfall and insect biomass started to increase. That an increase in rainfall stimulates a greater productivity of leaves, which in turn stimulates an increase in the abundance of herbivorous insects, is well documented for tropical rainforests (Janzen and Schoener 1968; Fogden 1972; Janzen 1973; Willis 1976; Wolda 1977, 1978a, 1978b, 1979; 1980). By the mid-wet, when insects were hyperabundant, birds were feeding nestlings and fledglings, and the increased arthropod biomass may further reduce competition between mixed feeders and insectivores, and also with herbivorous species (i.e. bowerbirds; C. B. Frith, personal communication) that feed young on insect foods during this period.

Mixed feeders showed no significant seasonal vertical shifts, unlike the insectivores that moved to lower strata during the wet. These seasonal vertical movements were reflected at every stratal level throughout the day, were most pronounced between higher strata, i.e. from the canopy down into the subcanopy and understorey, and resulted in a greater exploitation of foraging sites. In Australasian tropical rainforests the opposite situation has been reported (Crome 1978; Bell 1982c), i.e. insectivores shifting upwards during the wet and downwards during the dry. Crome (1978) recorded a greater use of foraging sites at lower strata during the dry and, on the basis of Janzen's (1973) findings, related this to movements of insects into moister lower vegetation during drier, less favourable, periods. Crome suggested that the upward shift in the wet season was due to increased insect abundance in

the canopy during the damper period, and also to the unprofitability of foraging in areas of reduced light intensities at lower strata on overcast days. Bell (1982c), on the other hand, suggested that the downward dry-season shift was due to a partial leaf fall in that season, which caused insectivores to expand their vertical foraging ranges downwards (it should be noted that both Crome's and Bell's lowland forest sites are partly deciduous, unlike my upland area) and, on the basis of Orian's (1969) findings, also due to increased light levels which allowed species to exploit lower areas that were normally too dark for them to utilize.

In my study area the majority of arboreal insectivores foraged over a wide range of strata during both dry and wet periods, particularly within the darker lower part of the canopy, subcanopy and understorey, and it was only the relative use of these strata that changed seasonally. Throughout the year, birds foraged in relatively dimly lit vegetation and, moreover, mainly during the early morning or late afternoon when, even during the dry season, the forest was often shrouded in cloud mist. Thus, variation in light intensity was not, apparently, an important factor in seasonal vertical movements of insectivores in my study area, unlike the lowland forests (Crome 1978; Bell 1982c). The effects of heavy rain, which Foster (1974) found reduced time available for foraging, and of the accompanying stronger wet-season winds were notably more severe in the upper canopy than in lower strata. It is feasible that during adverse conditions the insectivores foraged in the more protected lower vegetation where they, presumably, were assured a more stable food source and, in so doing, utilized the lower strata more fully at this time of year; this may be less critical to mixed feeders, or herbivores. The possibility that this wet-season downward shift by insectivores may be a further means of partitioning their resources from those of mixed feeders, and to a lesser extent herbivores, at a time when all three categories fed young on insects, cannot be overlooked.

As is characteristic of avian communities, the majority of birds foraged in early morning and later in the afternoon. During wetter months, when days are longer, birds foraged even earlier and later. Insectivores foraged significantly earlier and later than mixed feeders during both dry and wet periods, and this differential in foraging times may further enable coexistence between them. Mixed feeders showed no significant preference for insectivorous foods or herbivorous foods at different times of the day, nor did they forage mainly on herbivorous foods when the insectivores were most active. Pearson (1971) and Bell (1977, 1982c) found birds in lowland forest foraged more in the lower range of their strata during midday, and related this diurnal vertical shift, as well as the overall midday inactivity, to increased temperatures and light intensities, lack of insect activity, and/or variation in availability of pollen and nectar. Although there was overall midday inactivity in my area, there was no evidence of downward diurnal vertical movement; this may be indicative of a greater stability of climate and food resource in upland tropical forests. *Rhipidura fuliginosa* and *R. rufifrons* were the only species to forage at similar frequencies throughout the day. During the heat of the day, however, *R. fuliginosa* foraged more among denser vegetation (51) than in the lower levels of its range. Pearson (1971) suggested that some insects become active during the hotter part of the day, and perhaps these fantails, that hunt mainly by hawking or flitting, utilized such insect activities.

Although I made no relevant observations during this study, another factor partitioning resources between mixed feeders and insectivores may be utilization of different leaf surfaces. Greenberg and Gradwohl (1980) found insectivores foraged mostly from the underside of leaves, where there was a higher density of insects, whereas mixed feeders selected insects mainly from the upper side; interestingly, they recorded more sightings of upper leaf foraging in the upper canopy where mixed feeders were more abundant.

Differential utilization of foraging height was an important factor in segregating species within each feeding category, but other factors proved to be equally important in segregating species whose use of strata was similar. Crome (1975) found that the presence and

abundance of rainforest pigeons varied with the seasonal fruit crop, and partitioning between them was implemented by differential nomadism and migration as well as by utilization of different species and sizes of fruits. My data for individual species of herbivores were too few to make similar comparisons. The mixed feeder *Coracina lineata* ate almost exclusively fruits of strangler figs, and this isolated it from the canopy foraging herbivores (except bowerbirds; C. B. Frith, personal communication). Diamond (1973) suggested perching-branch size was an important sorting mechanism between closely related fruit pigeons, but no observations of this nature were made during this study.

Vertical foraging ranges of many species of mixed feeders and of insectivores overlapped considerably. There was some evidence to suggest that the three common resident honeyeaters, *Acanthorhynchus tenuirostris*, *Meliphaga lewinii* and *Lichenostomus frenatus*, utilized different food resources, whereas other honeyeater species foraged seasonally and opportunistically within the study area. Species of arboreal insectivores foraged in many strata with considerable overlap between their foraging ranges; this reflected a broad vertical distribution of arthropod foods. Bell (1977), whose findings in New Guinea were similar to those of this study, suggested that this indicated a high degree of competition between the insectivores and a finer partitioning of their resources. Differential utilization of foraging sites, behaviours and foods were important mechanisms in bringing about sharper niche definition between those insectivores whose foraging heights were similar; competition was reduced further during the dry season, when insects were less abundant, by seasonal migration. Furthermore, there was some evidence to indicate that species whose niches were very close staggered their diurnal foraging times, but this particular aspect of the study requires further investigation. Different foraging behaviour, and/or use of different species or sizes of arthropods, were important factors segregating ground foragers.

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Appendix. Numbers of Foraging Records for each Species and Feeding Category Observed August 1978–April 1979

H, herbivore; MF, mixed feeder; I, insectivore. P, species present but not observed foraging. Totals under November and March are accompanied in parentheses by subtotals for the dry (August–November) and wet (December–April) months respectively. Lack of a record may be due to lack of observation rather than to a species' absence

Species	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	Total	Track 1	Track 2
<i>Casuarinus casuarinus</i> (H)	—	—	1	—	P	—	—	P	—	1	—	1
<i>Alectura lathami</i> (MF)	1	P	P	P	I	2	5	4	P	13	6	7
<i>Ptilinopus magnificus</i> (H)	P	11	2	1	P	P	1	2	P	17	12	5
<i>Macrocyptnia amboinensis</i> (H)	I	1	P	3	P	P	2	3	P	10	4	6
<i>Cacatua galerita</i> (H)	P	2	P	P	I	I	P	2	I	7	1	6
<i>Psittaculairostris diophthalma</i> (H)	—	—	—	—	—	—	—	2	—	2	—	2
<i>Platycercus elegans</i> (H)	9	5	P	P	2	P	2	4	6	28	18	10
<i>Chrysococcyx lucidus</i> (I)	I	—	—	—	—	—	—	—	I	2	1	1
<i>Merops ornatus</i> (I)	2	4	3	—	—	—	—	15	P	24	20	4
<i>Pitta versicolor</i> (I)	—	—	—	—	—	I	P	P	—	1	20	—
<i>Coracina papuensis</i> (MF)	—	2	—	—	—	—	P	—	—	1	1	—
<i>C. lineata</i> (MF)	P	8	P	I	—	—	1	—	—	2	2	—
<i>Zosterops dauma</i> (I)	P	1	P	I	I	P	P	I	P	10	9	1
<i>Tregellasia capito</i> (I)	7	5	5	2	2	3	5	3	3	4	1	3
<i>Poecilodryas albispecularis</i> (I)	3	4	I	I	13	21	8	4	P	35	19	16
<i>Pachycephala pectoralis</i> (I)	4	7	8	6	8	9	10	9	P	55	19	36
<i>Colluricinclia boweri</i> (I)	4	10	7	14	7	8	19	10	6	67	55	12
<i>Machaerirhynchus flaviventer</i> (I)	P	P	—	I	—	—	—	—	6	85	46	39
<i>Monarcha melanopsis</i> (I)	—	—	—	—	I	—	I	—	—	1	1	—
<i>M. trivirgatus</i> (I)	—	1	—	P	—	—	P	—	—	2	1	1
<i>Rhipidura rufifrons</i> (I)	—	—	4	11	6	13	15	24	2	75	50	25
<i>R. fuliginosa</i> (I)	24	70	77	55	71	58	57	46	59	517	371	146
<i>Orthonyx spaldingii</i> (I)	24	25	23	5	24	20	8	33	P	200	151	49
<i>Psophodes olivaceus</i> (I)	3	5	2	8	18	3	5	7	P	51	31	20
<i>Crateroscelis gutturalis</i> (I)	2	2	2	2	1	1	1	P	P	11	5	6
<i>Sericornis magnirostris</i> (I)	20	10	13	15	16	29	34	44	24	205	85	120
<i>S. citreogularis</i> (I)	55	40	50	46	70	75	69	47	34	486	135	351
<i>Gerygone mouki</i> (I)	18	24	27	24	21	24	31	34	9	212	166	46
<i>Acanthiza katherina</i> (I)	P	P	P	2	P	P	P	2	1	5	4	1
<i>Climacteris minor</i> (I)	4	13	11	5	2	5	2	2	14	58	43	15
<i>Myiophaga lewini</i> (MF)	2	2	P	P	P	I	3	2	P	10	5	5
<i>Lichenostomus frenatus</i> (MF)	15	21	11	12	11	14	12	15	16	127	72	55
<i>Phylidonyris nigra</i> (MF)	—	—	—	—	—	—	P	3	P	3	3	—

<i>Acanthorhynchus tenuirostris</i> (MF)	1	1	1	1	1	P	1	2	2	10	8	2
<i>Myzomela obscura</i> (MF)	—	—	—	—	—	—	—	—	—	1	—	1
<i>M. sanguinolenta</i> (MF)	—	—	—	—	—	—	—	4	—	4	—	—
<i>Zosterops lateralis</i> (I)	2	2	—	2	—	—	1	—	1	8	8	—
<i>Emblema temporalis</i> (MF)	—	—	—	—	—	8	15	8	2	33	33	—
<i>Ptiloris victoriae</i> (MF)	7	4	2	6	1	8	3	19	15	65	37	28
Herbivores												
No. of species	2	4	2	2 (5)	2	1	3	5 (5)	2	6	4	6
No. of individuals	10	19	3	4 (36)	3	1	5	13 (22)	65	35	30	30
Mixed feeders												
No. of species	5	5	3	4 (7)	5	5	7	8 (10)	4	11	10	7
No. of individuals	25	38	14	20 (97)	15	33	40	57 (145)	36	278	179	99
Insectivores												
No. of species	15	17	14	17 (19)	15	14	15	15 (20)	13	22	21	19
No. of individuals	174	223	233	200 (830)	261	270	266	81 (1078)	197	2105	1034	892
Total No. of species	22	26	19	23 (31)	22	20	25	28 (35)	19	39	35	32
Total No. of individuals	209	280	250	224 (963)	279	304	311	351 (1245)	240	2448	1427	1021