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Foraging ecology of an assemblage of birds in lowland rainforest in northern Queensland

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Abstract

This paper presents an analysis of the foraging ecologies and hence means of partitioning resources amongst the twenty-eight most conspicuous species of birds in lowland tropical rainforest at Lacey's Creek, North Queensland. The height and site of foraging and the type of behaviour used by the species were compared. The height at which species foraged appeared to be more important for separating species than the site of foraging or the behaviour used. There appeared to be a greater proportion of species with generalized foraging behaviour at Lacey's Creek than in bird communities in the neotropics. Frugivorous species had very similar foraging ecologies but there were differences in the species of fruit eaten by some species. There were seasonal shifts in foraging by some species. It is postulated that the relative shortage of terrestrial species at Lacey's Creek compared with highland forest in North Queensland is due to the harsh dry season in the lowlands. The structure of this bird community appeared to be strongly affected by seasonality of climate.

Introduction

In most coexisting groups of birds there are interspecific differences in the use of resources (space, food, etc.) available in the habitat. These differences are usually interpreted as having evolved in response to interspecific competition for limited resources and as being necessary for continuing coexistence (but see Cole 1960). The means whereby birds inhabiting forest partition resources amongst themselves include interspecific territoriality; time-sharing; and different predatory strategies, the height and nature of the substrate foraged upon and in the sizes of prey consumed (see e.g. Stallcup 1969; Earhart & Johnson 1970; Willson 1970; Lack 1971; Snow & Snow 1971; Williamson 1971; Cody & Walter 1976).

Patterns of partitioning resources appear to be central to the concept of the structure of communities (Diamond 1975) and their analyses provided the basic data for Cody's (1974) stimulating monograph on community organization.

Most studies of differential use of resources, whether within an entire community, or simply between pairs of congeners, have been carried out in the temperate regions, but much attention has also been paid to the very diverse avian communities in neotropical rain forests (Orians 1969; Karr 1971; Pearson 1971, 1975; Lovejoy 1975). Australia's tropical rainforests have been neglected in this respect. Harrison (1962) briefly compared avian communities in Queensland with those in Malaya, while Kikkawa & Webb (1967) and Kikkawa (1974) examined the distribution of broad patterns of use of habitat between avian communities of different forest types.

This study is an attempt to analyse the ways resources are partitioned amongst the most conspicuous species of a large community of birds in lowland rainforest in North Queensland. These data are used to characterize the community and to determine what factors may be important in structuring it.

Study area

The study area was a tract of mixed mesophyll vine forest (Webb 1968) in the Lacey's Creek

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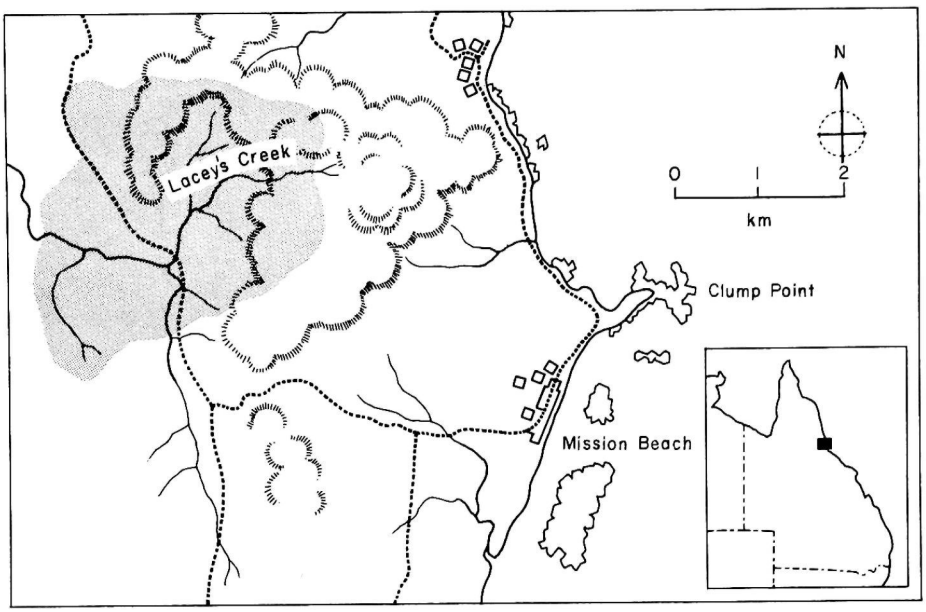

FIG. 1. Location of the study area.

area near Mission Beach, 50 km south of Innisfail (Fig. 1). This forest type is distinguished by having some species that are deciduous in the dry season, by leaf sizes that fall into the mesophyll class, and by few ferns and moderate numbers of woody lianes and epiphytes. In local areas of impeded drainage there are many fan palms (*Licuala* sp.). The forest has been disturbed by logging and cyclones. It has an uneven canopy, 12 to 18 m high, with emergents up to 25 m. There are patches with a dense understorey of saplings, shrubs and vines; and species of *Acacia*, characteristic of disturbed areas, are common and conspicuous. Features of the vegetation are listed in Table 1.

Rainfall is seasonal with a wet season from December–January to April–May, and temperatures are high throughout the year (Table 2).

Methods

Composition of the community

All species of birds seen or captured in mist nets were recorded on monthly visits from May 1971 to April 1972. No identifications were made on the basis of call alone.

Analysis of foraging

During each monthly visit searches for foraging birds were made during the early mornings

TABLE 1. Features of the vegetation of a sample of the study area at Lacey's Creek

Area of sample (hectares)		0.49
Number of tree species		104
Number of individuals		997
Tree species diversity (H')*		3.997
Minimum number of species contributing 50% of the total basal area of trunks		10
Acacia on sample area as	(1) Percentage of individuals	5.1
	(2) Percentage of total basal area	21.3
Species with fleshy fruits (%)		59
Individuals with fleshy fruits (%)		60

N.B. Only trees >10 cm girth at breast height were counted.
*$H' = -\Sigma p_i \ln p_i$, p_i = proportion of individuals in the ith species. The sample is a composite from three transects.

TABLE 2. The climate at Lacey's Creek and a highland area (Herberton)

Month	J	F	M	A	M	J	J	A	S	O	N	D
Innisfail (elevation = 6 m)*												
Rainfall (mm)†	529	599	693	469	301	188	127	114	88	81	148	255
Max. temp. (°C)†	30.2	29.7	28.7	27.6	25.6	23.8	23.2	24.7	25.9	27.3	29.0	29.7
Min. temp. (°C)†	22.9	22.9	22.2	20.3	18.6	16.3	14.9	16.3	17.0	19.2	20.9	22.0
Herberton (elevation = 917 m)												
Max. temp. (°C)‡	28.3	27.7	26.2	24.5	22.9	21.3	21.3	23.4	25.4	27.7	29.3	29.1
Min. temp. (°C)‡	18.0	18.3	17.5	15.5	13.3	10.9	9.5	10.4	11.9	14.2	16.1	17.2

* Nearest meteorological station to Lacey's Creek. † 92-year averages. ‡ 64-year averages.

and late afternoons for 10 to 14 consecutive days. When a foraging bird was encountered its behaviour, height in the vegetation column and foraging site were recorded as indicated below.

The following sources of bias had to be guarded against while collecting these data. Birds low in the forest or in areas of sparse vegetation are more conspicuous than those high in the canopy or in dense vegetation. Some foraging sites such as fan palm leaves are patchily distributed. Birds are easier to see in the dry season than in the wet season. Searches were therefore made extensively and, as far as possible, at random through the forest. A conscious effort was made to search the entire canopy, particularly in the wet season.

Foraging height

It was too difficult to record quickly and accurately the actual heights at which birds foraged in the canopy. Birds were recorded, therefore, as being in one of the following five strata:

I. Ground.
II. Vegetation up to 1 m above the ground.
III. The low canopy from 1 m to one-third the height of the canopy.
IV. The middle canopy from one-third to two-thirds the height of the canopy.
V. The upper canopy from two-thirds to the top of the canopy, including emergents.

The degree of specialization of a species with respect to height of foraging was indexed by the Shannon-Weaver function

$$H' = -\sum_{i=1}^{s} p_i \ln p_i \qquad (1)$$

where H' = diversity (or degree of specialization), p_i = proportion of observations in category i and s = number of categories. Thus, for a species foraging equally over all five vegetational strata, i.e. a perfect height generalist, $H' = 1.609$, whereas for one foraging exclusively in one stratum $H' = 0$.

Foraging site. Sixteen foraging sites were recognized, each one an obvious environmental component. The prey at these sites were arthropods and other small animals except where indicated below. When fruits and seeds were being eaten, they were considered to be a 'site', except for mistletoes where it was usually impossible to determine whether fruits or arthropods were being eaten. These sites were:

(1) Air (flying insects).
(2) Leaves – smaller than 15 × 10 cm, and including twigs and small branches.
(3) Tree trunks.
(4) Branches – > 5 cm diameter.
(5) Large leaves – > 15 × 10 cm, such as those of *Kissodendron australianum* and *Litsea bindoniana*, but not palm leaves.
(6) Dead leaves – occurring in dense bunches.
(7) Dead branch.
(8) Vine – pendant from a limb or crown, but not distinguished if tangled generally in the canopy.
(9) Tangle – a discrete mass of vines, dead vegetation and detritus.
(10) Lawyer tangle – the heavily spined lawyer cane *Calamus moti*, a rattan, forms dense tangles. These tangles were distinguished from (9) because of their armament.
(11) Epiphyte.
(12) Mistletoe – (fruit and insects).
(13) Litter.
(14) Fan palm leaves – *Licuala* sp. is a common palm on the study area, the large (60–80 cm diam.) round, plicated leaves provide a surface for birds to forage on.
(15) Flowers (nectar and arthropods).
(16) Fruits and seeds.

Foraging behaviour. Eight categories of foraging behaviour were recognized:

I. *Flitting* – moving rapidly, often tumbling, over and through the substrate, which appears to be only briefly examined. The prey are probably light, easily disturbed arthropods, some of which may be disturbed by the bird's movements. Sedentary, cryptic prey are likely to be missed. This category tends to grade into the next one, searching, but is usually distinctive.

II. *Searching* – moving more slowly and deliberately than when flitting, searching the substrate more thoroughly and gleaning fruits or insects. Easily disturbed arthropods could perhaps escape this type of hunting. This category is more or less equivalent to the well-known behaviour called gleaning. It also

includes, however, pecking and sallying for distances of a few centimetres over the substrate. It was too hard to distinguish consistently between these types of behaviour, as pecking and short-sallying were rare.

III. *Hovering* – hovering near the substrate and gleaning, pecking or licking up the food item, whether insects, fruit or nectar.

IV. *Sallying* – prey is sighted on a section of substrate remote from the bird, a direct flight is made to the site where the prey is taken, the bird landing at the site or continuing its flight.

V. *Hawking* – flying from the substrate to take a flying insect. This is the only behaviour possible in the foraging site, air.

VI. *Spiralling* – rapidly flying and hopping up and down vines, trunks, branches, etc. disturbing insects and catching them as they fly off.

VII. *Probing* – extracting prey from within thick substrates such as dead limbs and bunches of dead leaves.

VIII. *Scratching* – this is virtually restricted to terrestrial species foraging in litter. It includes gleaning and scraping the substrate to expose prey.

Overlap in foraging behaviour between pairs of species was calculated using equation (2) below.

Overall use of habitat for foraging. The data on foraging heights and sites were combined in an attempt to assess overall differences in foraging ecology between species. The methods used were those outlined by Cody (1974).

For each pair of bird species two indices of overlap, one for foraging height and one for foraging site, were calculated using Schoener's (1968) equation:

$$\alpha = 1 - \tfrac{1}{2} \sum_{i=1}^{s} | Px_i - Py_i | \qquad (2)$$

where α = 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 had to be combined into a single index of overlap (structural overlap). If foraging height and site overlaps were independent variables their product or geometric mean could be used. They are not completely independent however. Biased occurrences include litter and ground; trunks and lower canopy zones; fan palm leaves and middle to low canopy zones, etc. There must also be many other subtle dependencies. For this reason, as outlined more fully in Cody (1974), an arithmetic mean was used:

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

where α_{st} = structural overlap, α_{ht} = overlap with respect to height and α_s = overlap with respect to site.

A species by species matrix of indices of structural overlap was constructed for the twenty-seven species and species pairs (see below) used in this analysis. To facilitate its interpretation the matrix was subjected to Unweighted Pair Group Mean Analysis (Sneath & Sokal 1973). This is an agglomerative, hierarchical, clustering analysis involving the calculation of average similarities between a candidate unit or cluster and an extant cluster, weighting each unit equally.

Ecological isolation between frugivores. Frugivores may show interspecific differences in the species of fruit eaten, so overlaps between frugivores with respect to this were calculated using eqn (2).

Seasonal changes in foraging. To examine seasonal differences the data were divided into those collected in the wet (December to April) and those in the dry (May to November) seasons. The frequencies of foraging records for height and site in each season were compared by χ^2 tests, after combining categories to eliminate zeros. For those species showing significant seasonal differences in the use of foraging sites, changes in the diversity of foraging sites were compared using eqn (1).

Results

Composition of the community

Seventy-four species of birds were recorded in the study area.* The families with the greatest representation were the Muscicapidae with twelve species, the Columbidae with eight, and the Cuculidae with six. However, birds of the former two families were numerous and conspicuous whereas those of the latter were rare. There were surprisingly few species of honeyeaters (Meliphagidae) on the plot,

*This list is available as a separate publication from the author on request.

neither were there any tree creepers (Climacteridae).

Six species are migratory: the Grey and Rufous Fantails are present from April to September, the Koel from October to April, Shining Starlings from August to March, White-tailed Kingfishers from November to March and Scrub Turkeys from January to May with a few sporadic sightings in the dry season. In addition the frugivores and omnivores are nomadic to varying degrees, following fruit and flowers.

Analysis of foraging

Reasonable samples of foraging activity were obtained for thirty-six species of the community. Detailed analyses of foraging by the Cassowary and the seven fruit pigeons have been presented elsewhere (Crome 1975, 1976), and this information will be drawn upon below where appropriate. A total of 3109 observations of foraging were recorded for the remaining twenty-eight species. Two of these, the Lesser Lewin and Graceful Honeyeaters are very difficult to consistently identify in the field so the data for both have had to be combined.

Foraging height. The frequency distribution of foraging observations are given in Table 3.

There are some obvious interspecific differences, e.g. the Grey Fantail forages higher than its congener the Rufous Fantail ($\chi^2_{(d.f.=2)} = 70.5$, $P < 0.001$), and the Fairy Warbler forages higher than the similar sized Large-billed Scrub-wren ($\chi^2_{(d.f.=3)} = 67.9$, $P < 0.001$). There is in general, however, much overlap. For example all the observations of the White Cockatoo, Barred Cuckoo-shrike and White-eared Flycatcher were in stratum V. Those of the Koel and Macleay Honeyeater spread more or less evenly over the three canopy strata

TABLE 3. The frequency of foraging observations in different strata of the rainforest (%)

Species	Number of observations	Stratum				
		I	II	III	IV	V
White Cockatoo	93					100
Barred Cuckoo-shrike	41					100
White-eared Flycatcher	30					100
Fig Parrot	21				14	85
Spotted Catbird	21				19	81
Figbird	480			2	13	85
Varied Triller	73		2	9	19	70
Shining Starling	400			13	18	69
Dusky Honeyeater	148			20	29	51
Grey Fantail	81		1	11	42	46
Silvereye	47			22	32	46
Pied Flycatcher	88			23	53	24
Mistletoebird	44			16	50	34
Victoria Riflebird	43			21	44	35
Fairy Warbler	80		2	11	61	26
Koel	21			33	33	34
Macleay Honeyeater	75	1		35	30	34
Boat-billed Flycatcher	75		3	36	49	12
Spectacled Flycatcher	204		3	43	40	14
Lesser Lewin/Graceful Honeyeater	210		16	27	27	30
Grey Whistler	133		3	35	29	33
Rufous Shrike-thrush	140	10	7	30	32	21
Rufous Fantail	194	18	18	29	24	11
Large-billed Scrub-wren	151	2	8	59	26	5
Pale-yellow Robin	89	13	14	43	23	7
Northern Chowchilla	64	90	10			
Noisy Pitta	63	100				
Number of observations	**3109**	**184**	**121**	**641**	**774**	**1389**

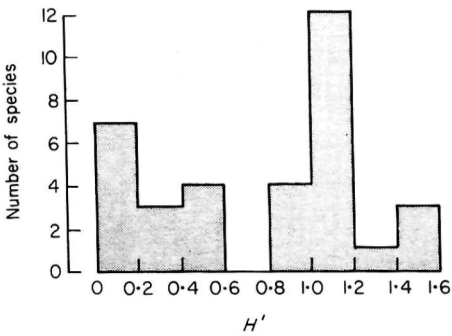

FIG. 2. Distribution of the indices of specialization in foraging height for birds at Lacey's Creek (this figure includes data for the seven species of fruit pigeon).

($\chi^2_{(d.f.=2)}$ = 0.2, N.S.), and those of the Boat-billed and Spectacled Flycatcher mostly in the middle to lower strata ($\chi^2_{(d.f.=3)}$ = 2.1, N.S.). Overall there was a fairly broad use of foraging strata with 59% of species, including fruit pigeons, with an H' of 0.8 or more (Fig. 2).

Within the canopy there is a trend for heavier birds to forage higher than lighter ones (Fig. 3). Thus stratum II is used mostly by birds of 5–10 g and by no bird heavier than 35 g, except the Northern Chowchilla. In strata III and IV the modal weight is 10–15 g but there is a lot of foraging by heavier birds (30+g). This use by heavier birds increases from stratum III where 23% of foraging is by birds heavier than 30 g to stratum (IV) where 32% is by these heavier birds ($\chi^2_{(d.f.=1)}$ = 18.59, $P < 0.001$). Finally, the upper canopy, stratum V is used mostly by heavy birds.

Foraging site. The frequencies of foraging at different sites are presented in Table 4. There was a basic separation between frugivores and insectivores but within the latter group few specialized in foraging on sites other than leaves. The Pied Flycatcher specialized on trunks, the Macleay Honeyeater on bunches of dead and/or large leaves, and the Mistletoebird on mistletoe. The Large-billed Scrub-wren, Rufous Shrike-thrush and Victoria Riflebird foraged widely over a variety of sites, the Riflebird using dead branches to a considerable extent. There was little foraging on epiphytes and Fan Palm leaves.

Overall the differential use of foraging sites does not appear to be of great importance in the ecological separation of this assemblage.

Foraging behaviour. The majority of non-terrestrial species are searchers. Only six species of flycatchers specialize in other forms of foraging behaviour. Four of these are flitters, the Pale Yellow Robin is a sallier and the Pied Flycatcher a highly specialized spiraller. All the frugivores, including the fruit pigeons are searchers, and, although honeyeaters occasionally hover to take fruit elsewhere (personal observation), searching was the only method of taking fruit observed during this study. For a further comparison the behaviour of the remaining species at Lacey's Creek can be broadly classified from general knowledge. Of the sixty-seven non-terrestrial species in the assemblage, forty-four are searchers and only thirteen are definitely known to specialize in other types of behaviour (Table 6).

It seems therefore that this community is basically composed of searchers. If 'searching' could be subdivided further into, e.g. 'gleaning', 'pecking' and 'short-sallying' more differences could become obvious. This is unlikely, at least among those species studied in detail, because any species specializing in 'pecking' or 'short-sallying' would have been obviously distinguishable.

Overall use of habitat for foraging. The dendrogram resulting from UPGMA of the indices of structural overlap is presented in Fig. 4. The analysis shows three major groups – the two terrestrial species, a group of seven frugivores, with which, of course, the fruit pigeons would group, and the remaining insectivores and omnivores. Within this insectivore/omnivore group there is a main group of seven species with high structural overlap (Boat-billed Flycatcher to Silvereye in Fig. 4) successively joined by the remaining species. No two species were identical in their overall use of the habitat but several were very close and apparently not ecologically segregated by foraging height and site. These include six frugivores (the Koel separates out well on foraging height) to be discussed later, the two terrestrial species, the Pale Yellow Robin and Rufous Fantail, and the group of seven insectivores/omnivores.

The Noisy Pitta and the Northern Chowchilla probably eat different sizes or types of food items. Thus, the Chowchilla is 1.62 times heavier and has a proportionally narrower,

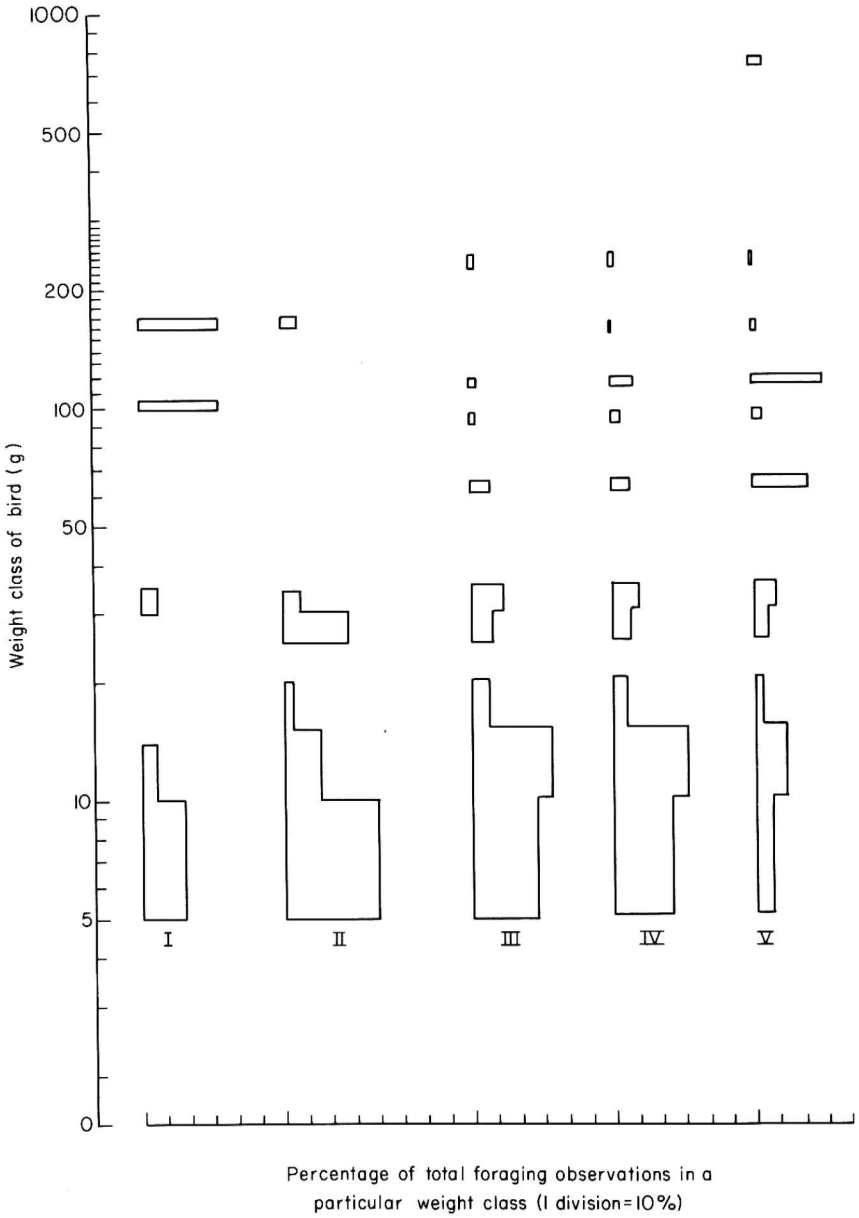

FIG. 3. Distribution of weights of foraging birds in each stratum. (N.B. weight of the Lesser Lewin Honeyeater is used to represent the Lesser Lewin/Graceful Honeyeater combination).

TABLE 4. The frequency of foraging observations at different sites

Species	Foraging station															
	Air	Leaves	Trunks	Branches	Large leaves	Dead leaves	Dead branches	Vines	Tangles	Lawyer tangles	Epiph-ytes	Mistle-toes	Litter	Fan palm leaves	Flowers	Fruits and seeds
White Cockatoo																100
Barred Cuckoo-shrike		10														90
White-eared Flycatcher	5	95														
Fig Parrot																100
Spotted Catbird		5							5							90
Figbird		7														93
Varied Triller		46		11			1	3	1			1				37
Shining Starling		5														95
Dusky Honeyeater		64		1	2			4				3			26	
Grey Fantail	22	74	4													
Silvereye		81			5						2					12
Pied Flycatcher	1		53	40				6								
Mistletoebird	2	36			5		5				2	48				2
Victoria Riflebird		5	5	10		2	19		5	14	2			5		33
Fairy Warbler	1	88			5	1		1	1	3						
Koel																100
Macleay Honeyeater	3	7			21	34			5	8				1	16	5
Boat-billed Flycatcher	4	95				1										
Spectacled Flycatcher	2	75			2	1		2	3	10	3			2		
Lesser Lewin/ Graceful Honeyeater		44	2		2			3			1	9			18	21
Grey Whistler	1	80		8	3		1	2	2		1	1			1	
Rufous Shrike-thrush	4	32	12	10		4		4	10	10	3		10	1		
Rufous Fantail	4	70	3	1				1	4	1			16			
Large-billed Scrub-wren		41	5	1	4	7	1	8	14	16	2		1			
Pale-yellow Robin	3	77	5	1					1	1			12			
Northern Chowchilla		2							8				90			
Noisy Pitta													100			

Number of observations as in Table 3.

TABLE 5. The frequency of foraging observations in different behavioural categories

Species	Foraging behaviour							
	Flitting	Searching	Hovering	Sallying	Hawking	Spiralling	Probing	Scratching
White Cockatoo		100						
Barred Cuckoo-shrike		100						
White-eared Flycatcher	25	70			5			
Fig Parrot		100						
Spotted Catbird		100						
Figbird		100						
Varied Triller	2	98						
Shining Starling		100						
Dusky Honeyeater		83	17					
Grey Fantail	74				22	4		
Silvereye	2	98						
Pied Flycatcher					1	99		
Mistletoebird		81	17		2			
Victoria Riflebird		75					25	
Fairy Warbler		98	1		1			
Koel		100						
Macleay Honeyeater		77			3		20	
Boat-billed Flycatcher	50	10	1	35	4			
Spectacled Flycatcher	59	37		2	2			
Lesser Lewin/ Graceful Honeyeater		96				4		
Grey Whistler	3	86	3	7	1			
Rufous Shrike-thrush	3	93			4			
Rufous Fantail	90	2	4		4			
Large-billed Scrub-wren		100						
Pale-yellow Robin		34		63	3			
Northern Chowchilla		10						90
Noisy Pitta								100

Number of observations as in Table 3.

TABLE 6. General classification of foraging behaviour of all species on the study area

Behaviour	Numbers of species specializing in each behavioural category		
	Species studied in detail	Others	Total
Flitting	4	0	4
Searching	20*	24	44
Hovering	0	0	0
Sallying	1	6	7
Hawking	0	1	1
Spiralling	1	0	1
Probing	0	0	0
Scratching	2	5	7
Unknown	0	10	10

*N.B. The Lesser-Lewin and Graceful Honeyeater considered separately.

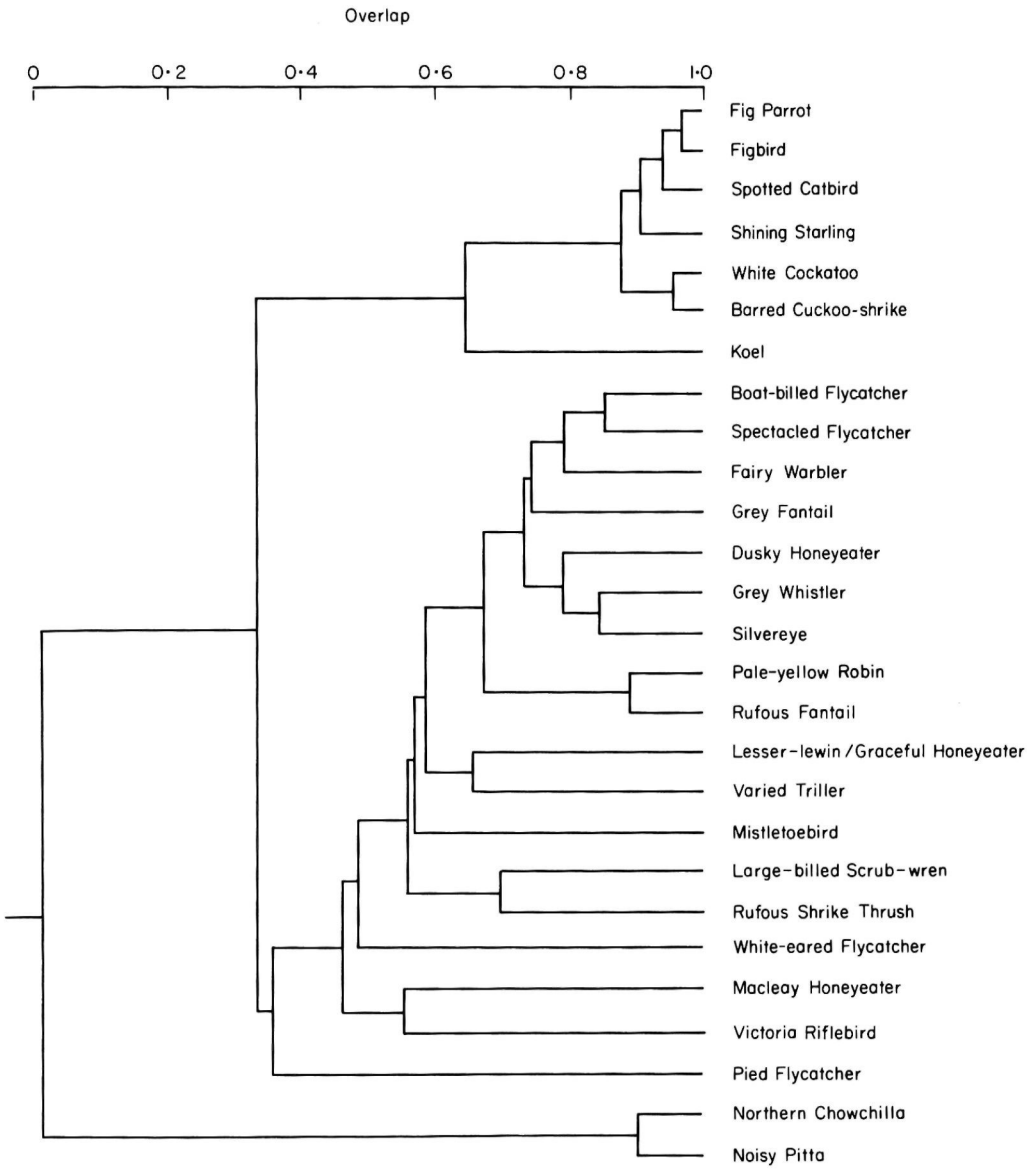

FIG. 4. Unweighted Pair Group Mean Analysis (U.P.G.M.A.) of structural overlap amongst birds at Lacey's Creek.

heavier bill (length/width = 2.64 as opposed to 3.44) than the Pitta so perhaps may be able to handle larger prey and sort through heavier débris. The Pale Yellow Robin and Rufous Fantail use different foraging behaviour, the former sallying and gleaning, the latter flitting (behavioural overlap = 0.05).

The final group of similar species includes four flycatchers, a warbler and two omnivores. The matrices of overlap of habitat use, behaviour and bill length for these species are presented for further examination (Table 7). Bill length is included as an index of the range of size of prey that may be eaten. Several species pairs are strikingly different in behaviour, e.g. Grey Fantail and Dusky Honeyeater, and some differ in bill length by a factor of almost two. The mean behavioural overlap between all species pairs is 0.44 compared to a mean structural overlap of 0.73.

TABLE 7. Overlap in overall use of habitat, behaviour, and bill size amongst a group of species that overlap considerably in use of habitat

	Spectacled Flycatcher	Fairy Warbler	Grey Fantail	Dusky Honeyeater	Grey Whistler	Silvereye
Boat-billed Flycatcher	0.845 *0.64* 1.15	0.745 *0.12* 1.39	0.725 *0.54* 1.55	0.625 *0.11* 1.24	0.800 *0.22* 1.11	0.565 *0.12* 1.32
Spectacled Flycatcher		0.575 *0.38* 1.20	0.625 *0.61* 1.35	0.655 *0.37* 1.44	0.820 *0.44* 1.04	0.735 *0.39* 1.15
Fairy Warbler			0.775 *0.01* 1.12	0.665 *0.83* 1.73	0.770 *0.88* 1.25	0.775 *0.98* 1.05
Grey Fantail				0.623 *0* 1.93	0.745 *0.04* 1.4	0.815 *0.02* 1.11
Dusky Honeyeater					0.765 *0.86* 1.38	0.805 *0.83* 1.65
Grey Whistler						0.840 *0.88* 1.19

Roman type = Overlap in overall use of habitat.
Italic type = behavioural overlap.
Underlined type = ratio of bill lengths (larger/smaller).

High values of structural overlap however are not consistently associated with low behavioural overlaps (Spearman Rank Correlation Coefficient = 0.33, N.S.) but there is a significant correlation between high structural overlap and low differences in size of the bill ($r_s = 0.56$, $P < 0.01$). This suggests that these species may differ in the size and type of prey they take.

Ecological isolation between frugivores. The fruit pigeons partition resources by nomadism and by eating different fruits (Crome 1975). The fruits eaten by the six frugivores studied here are presented in Appendix I. It is impossible to compare all these species because of the large numbers of species of fruits and the small samples for some of the species of birds. However, since the large samples for the White Cockatoo, Shining Starling and Figbird allow these species to be compared with the fruit pigeons, overlaps in species of fruit eaten between these species are presented in Table 8. Overlap is low between all species pairs, suggesting that the use of different fruits, and possibly, of course, nomadism, may be important factors for ecological isolation amongst them.

Seasonal changes in foraging. Table 9 shows

TABLE 8. Overlap between frugivores with respect to species of fruit eaten*

	Shining Starling	Figbird	Wompoo Pigeon	Purple-crowned Pigeon	Red-crowned Pigeon	Brown Pigeon
White Cockatoo	0.05	0.049	0.04	0	0.05	0.05
Shining Starling		0.213	0.091	0.323	0.5	0.15
Figbird			0.515	0.163	0.297	0.291
Wompoo Pigeon				0.327	0.05	0.076
Purple-crowned Pigeon					0.021	0.116
Red-crowned Pigeon						0.391

*The values for overlap between fruit pigeons are for data collected during the period of this study and differ from the data collected over 3 years and reported in Crome (1975).

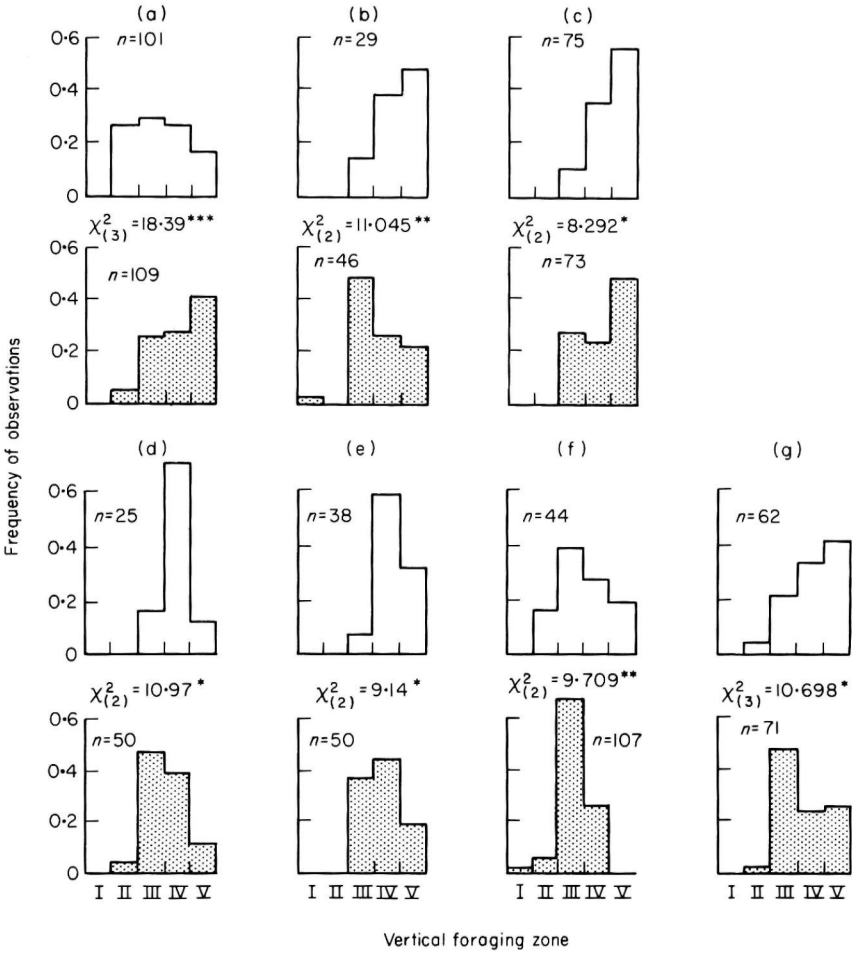

FIG. 5. Seasonal changes in foraging height by birds at Lacey's Creek. The upper histogram (open) is the distribution of foraging in the wet season December to April and the lower (stippled) is that in the dry season May to November. The number in each histogram is the number of observations. (a) Lesser-Lewin/Graceful Honeyeater; (b) Macleay Honeyeater; (c) Dusky Honeyeater; (d) Boat-billed Flycatcher; (e) Pied Flycatcher; (f) Large-billed Scrub-wren; (g) Grey Whistler. *P = 0.5–0.1; **P = 0.1–0.001; ***$P < 0.001$.

that records of foraging were spaced well enough throughout the year to enable seasonal comparisons to be made. Five 'species' showed significant seasonal differences in both foraging height and site, two in height only, and one in site only (Table 10 and Fig. 5). Six of the seven 'species' that changed height did so by foraging higher in the wet season. The Lesser Lewin and Graceful Honeyeater foraged lower. Insectivores generally used fewer foraging sites in the wet season, but honeyeaters used more by increasing their use of fruits and flowers. Thus, the Dusky Honeyeater moved up into blossoming crowns, hence the shift in height. The Lesser Lewin/Graceful Honeyeater moved lower for fruits of wild raspberry (*Rubus* sp.) that grow along clearings.

The Large-billed Scrub-wren and Grey Whistler foraged more on leaves and less on other categories, e.g. lawyer tangles in the wet season, while the Rufous Thrush used vines and trunks more and lawyer tangles less. These shifts in use of sites may be due to the possible rarity of some sites higher in the vegetation. Alternatively the shifts in height may be due to the shifts in site. The Pied Flycatcher foraged more on branches than trunks in the wet season: an obvious correlation with height. The Boat-billed

TABLE 9. Distribution of records through the study period

Period ending	10 May 1971	11 June 1971	9 July 1971	3 Aug. 1971	8 Sept. 1971	13 Oct. 1971	15 Nov. 1971	15 Dec. 1971	12 Jan. 1972	4 Feb. 1972	7 March 1972	5 April 1972
Total number of records	370	361	471	317	96	216	232	215	122	315	225	169
Number of records excluding Figbird and Shining Starling	307	325	270	245	77	128	183	168	112	139	115	160
Total number of species observed*	21	21	18	21	18	21	25	20	17	22	19	20

*The Lesser Lewin and Graceful Honeyeaters are considered as one species.

TABLE 10. Seasonal changes is use of foraging sites by birds at Lacey's Creek

	May – November			December – April			
	Number of categories foraged in	H'	% of foraging in flowers and fruit	Number of categories foraged in	H'	% of foraging in flowers and fruit	χ^2, d.f.
Large-billed Scrub-wren	11	1.858	0	8	1.526	0	23.315, 7**
Pied Flycatcher	4	0.926	0	3	0.7782	0	9.459, 2**
Grey Whistler	8	1.064	0	5	0.3707	1.6	13.535, 3**
Rufous Shrike-thrush	12	2.086	0	8	1.847	0	15.345, 7*
Lesser Lewin/Graceful Honeyeater	9	1.395	28.7	8	1.593	52.7	23.447, 6**
Dusky Honeyeater	6	0.836	8.2	4	1.009	37.3	18.963, 3***

Number of observations as in Fig. 8. *$P = 0.05–0.01$, **$P = 0.01–0.001$, ***$P < 0.001$.

Flycatcher foraged on leaves throughout the year. The Macleay Honeyeater continued to specialize in bunches of dead and/or large leaves throughout the year but foraged more on flowers in the wet season. The shift however was not significant (χ^2 (d.f. = 7) = 7.46, N.S.).

Discussion

The species studied in detail here and in Crome (1975) represent less than half of the total number of species at Lacey's Creek, and the data collected are only samples of their foraging ecologies. None the less they are the commonest species, and so are used here to tentatively characterize the community as a whole.

Foraging height appears to be more important than foraging site or behaviour in separating the insectivores and omnivores. The majority are general foliage searchers, and there appear to be fewer behavioural specialists than in the neotropical areas that have been studied. Orians (1969), for example, presents analyses of foraging behaviour of birds on forest plots in Costa Rica. His category 'gleaning' (seven categories in his Table 5, excluding 'ground gleaning' which appears equivalent to 'scratching'), may be compared to the category 'searching' used in this study. Considering only his five lowland plots, the percentage of species specializing in behaviour other than gleaning ranges from 52% to 66% with a mean of 58%. This compares with a maximum of 40% for Lacey's Creek, assuming that all species unclassified in Table 6 of this paper are not searchers. The proportion would decrease to 35% if 'flitting' were included in searching, as it appears to be in Orian's work. There are many more hoverers (hummingbirds) and probers (woodpeckers) on the Costa Rican plots. Similarly Pearson (1975) demonstrated the abundance of specialists such as hoverers, probers and army ant followers in Amazonian forests.

The data on frugivores presented here suggest that the reduction of competition by harvesting different fruits may not be a phenomenon restricted to fruit pigeons (Crome 1975) in the area. If it were more universal there should be some relationship between the diversity of fruits in a large area particularly the more nutritious ones, and the number of frugivores that can be supported. There is some tentative support for this from the work of Kikkawa & Williams (1971) in New Guinea. They found that whereas the numbers of species of insectivores increase with altitude, those of frugivores decrease. This decrease could possibly be the result of a reduction in biomass of fruit available at higher altitudes, but also perhaps to the reduction of the diversity of plants.

Seasonality and the structure and composition of the community

Seasonal changes in the abundance and distribution of invertebrates, changes in cloud cover, and the physical effects of rain possibly caused species to shift their foraging heights and sites seasonally.

Insects in Costa Rican forests with a harsh dry season (Janzen 1973) and in lowland forest in Sarawak (Fogden 1972) are more abundant in the wet season when leaf growth is rapid, the peak in Costa Rica being in the second or third month of the season. In the dry season in Costa Rica insects move into moist refugia (Janzen & Schoener 1968; Janzen 1973). Thus an increase in the abundance of insects in the wet season may reduce competitive pressures between birds foraging on herbivorous insects and allow birds with broad foraging ranges in the dry season to specialize more on leaves in the wet. The shift upwards in the vegetation by some birds may be the result of greater production of herbivorous insects in the upper portions of the canopy where light intensities and hence primary productivity should be higher.

In the dry season, if insects are concentrated in damp refugia such as tangles, birds would have to forage more widely over foraging sites rather than concentrate on leaves.

Light is greatly attenuated at the lower levels of tropical forests. In the wet season with its almost continual heavy cloud, light intensities at these lower levels would be reduced even further (Longman & Jenik 1974). This could have a direct effect on

foraging by increasing the time required to seek and catch prey, and making foraging in dark areas such as tangles and lower strata less profitable. The profitability of these areas may decrease even further in the wet season, since heavy rain reduces the time available for birds to forage (Foster 1974). Rain may also have a direct effect by differentially reducing the abundance of insects at certain foraging sites. Thus the Pied Flycatcher may shift from foraging on trunks to branches as a response to the hypothesized increase of insects in the upper canopy or because the undersides of branches are relatively drier than the sodden trunks and provide more resting sites for insects.

Breeding seasons are also timed with seasonal abundances of food. The fruit pigeons and the Cassowary breed at the end of the dry season when fruit is most abundant (Crome 1975, 1976). Insectivores breed from the end of the dry to the middle of the wet season, when invertebrates should be most abundant (Lavery, Seton & Bravery 1975).

Seasonality may also explain why lowland forest in North Queensland has fewer species and proportionately fewer terrestrial species than the highland forests of the Atherton Tablelands. For example, eighty-three species of birds were recorded from a 0.5 km^2 tract of rainforest on Mt Lewis (altitude = 1000 m) during 1972 (personal observation), nine more than in Lacey's Creek.* Lacey's Creek has seven terrestrial species and Mt Lewis ten. Moreover, Mt Lewis has a species, the Atherton Scrub wren (*Sericornis keri*) that is restricted to the ground and low shrubbery (up to 1.5 m) and three bowerbirds, the Golden Bowerbird (*Prionodura newtoniana*), Satin Bowerbird (*Ptilonorhynchus violaceus*) and Tooth-billed Catbird (*Ailuroedus crassirostris*), that spend much time on or near the ground in the breeding season (September–January), attending bowers and playgrounds. Environmental conditions (food supply or microclimate) in the lowlands may be unsuitable for the development of a large terrestrial or semi-terrestrial community. The dry season is very severe at Lacey's Creek (see Table 1), there are several deciduous species of tree in the forest, and the ground can be so dry that it cracks. The forest at Mt Lewis, however, is simple notophyll to microphyll vine-fern forest (Webb 1968), characterized by trees with small leaves, none or very few deciduous species, and many more ferns and mosses indicating cooler, damper conditions. Temperatures are lower (Table 1) and the days are usually wet and misty. This would lower evapotranspiration and ameliorate the severity of the dry season. Lower temperatures may also reduce breakdown of litter in the wet season. It may be expected, therefore, that there are more terrestrial insects available through the year at Mt Lewis and hence more terrestrial birds can be supported than at Lacey's Creek.

*Copies of these species lists are available as separate publications from the author on request.

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Appendix I. Species of fruit eaten by frugivores; entries are numbers of records

	Species of fruit	Fig Parrot	White Cockatoo	Koel	Barred Cuckoo-Shrike	Shining Starling	Yellow Figbird	Catbird
Arecaceae	*Calamus* sp.				2	10		
Piperaceae	*Piper* sp.			1			8	1
Moraceae	*Ficus destruens*	8		2	15			
	F. leptoclada	1				18	19	
	F. virens				7	11		1
Proteaceae	*Carnarvonia araliifolia*		9					
Loranthaceae	*Notothixos subaureus*					38		
Annonaceae	*Cananga odorata*						61	
Myristicaceae	*Myristica muelleri*			4		16		
Lauraceae	*Endiandra hypotephra*			10				
	Litsea leefeana			1		54	10	
Mimosaceae	*Acacia* sp.		60					
Rutaceae	*Euodia bonwickii*		9					
Meliaceae	*Dysoxylum micranthum*					10	7	
	D. oppositifolium					50	20	
	Melia azedarach						16	
Euphorbiaceae	*Alphitonia whitei*	12			5	6		
Vitaceae	*Cissus sterculifolius*					28	18	1
Elaeocarpaceae	*Elaeocarpus grandis*						110	2
	E. largiflorens						11	
Combretaceae	*Terminalia sericocarpa*				8	10		
Myrtaceae	*Syzygium leuhmannii*					23		
Araliaceae	*Kissodendron australianum*					60		1
	Polyscias elegans						120	4
	P. murrayi		6			21	13	4
Oleaceae	*Linociera ramiflora*			2			8	
	Others		9	1		25	25	6
	Total	**21**	**93**	**21**	**37**	**380**	**446**	**20**