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FEEDING BEHAVIOUR AND ECOLOGY OF NEW GUINEA RAINFOREST INSECTIVOROUS PASSERINES

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The New Guinea avifauna is particularly rich in small to medium-sized insectivorous species, most belonging to the families Muscicapidae, Sylviidae and Pachycephalidae. While in Papua/New Guinea, between October 1971 and January 1972, detailed observations were made of such species in rainforest habitats, in an attempt to shed light on the role of feeding ecology and behaviour in interspecific competitive relationships, in particular between species in polytypic genera. Much more extensive studies of this nature have been conducted in temperate regions, notably by MacArthur (1958) and subsequent extensions of his work (e.g. Morse 1967a, 1970), but, with the exception of Orians (1969), Karr (1971) and Snow & Snow (1971), similar quantitative work in truly tropical areas has hardly yet been attempted.

The island of New Guinea lies between latitudes 0°–11° S and longitudes 130°–151° E, having an overall length of c. 2500 km and a maximum width of c. 750 km. The dominant topographical feature is the central mountain cordillera extending the length of the island; the greatest height is reached in West Irian (Mt Carstenz, c. 5000 m), but a number of peaks in Papua/New Guinea exceed 4000 m. Extensive Pleistocene glaciation has occurred with a snowline at least 1000 m lower than at present (Bik 1972, Löffler 1972).

About 80% of the c. 780 000 km² land area is covered with rainforest, and the majority of the avifauna is restricted to this habitat. Several classifications of the New Guinea vegetation have been proposed (Lane-Poole 1925, Brass 1941, 1964, Robbins 1958) which differ in detail but are in reasonable agreement as to the major plant associations. The rainforests show a basic pattern of altitudinal zonation in physiognomy and floristics. The principal formations are Lowland, Midmontane, Lower Montane, Upper Montane and Subalpine forests.

The principal avifaunal discontinuity occurs at about 1500 m (Rand & Gilliard 1967), 'lowland' species occurring below and 'upland' species above this altitude. There are areas where lowland species penetrate to higher altitudes (e.g., at Karimui (Diamond 1967, 1972)), and places where upland species may descend as low as 1000 m (e.g. Vogelkop peninsula), but in general few species are common both above and below 1500 m.

Meteorological events are controlled by the northwest monsoon (December to March/April), which brings wet weather, and the southeast monsoon (June to October), which brings dry weather but with local rains wherever it meets prominent relief barriers.

STUDY AREAS

Within three main areas of field work—Port Moresby, Wau and Central Highlands—localities were chosen to include typical examples of the range of forest associations (Fig. 1). At each locality observations were made only in virtually undisturbed climatic climax rainforest.

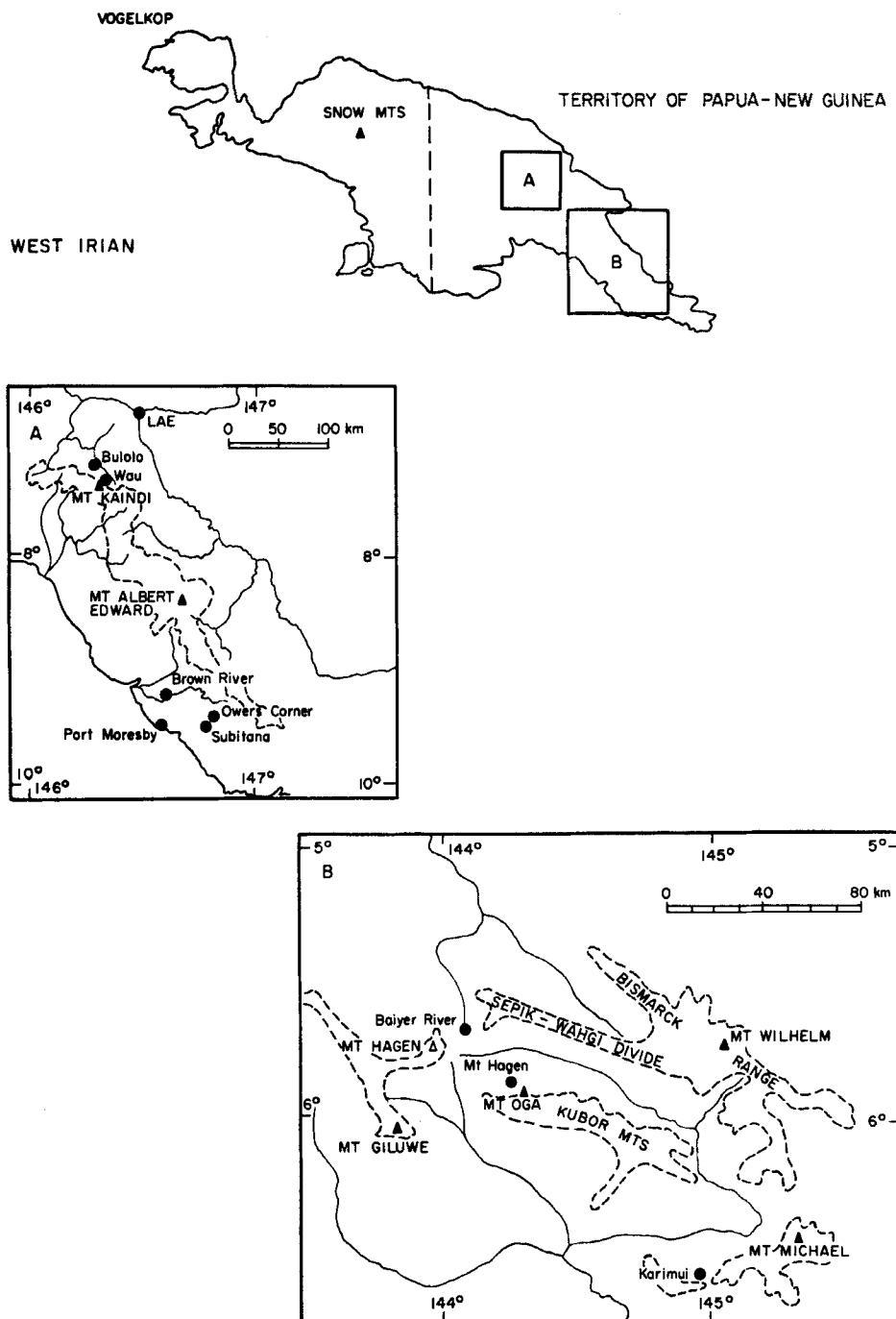


FIGURE 1. Map of New Guinea with insets showing location of study areas and places mentioned in the text.

PORt MORESBY AREA

A good description of most aspects is to be found in Mabbutt *et al.* (1965), on which my account relies heavily.

1. Brown River

On the stable flat alluvial plains of this area, between 5 and 15 m above sea level, tall *Celtis-Pometia* evergreen forest dominates. This has a dense upper closed canopy (canopy B of Richards', 1952, terminology) at 30–35 m with a discontinuous canopy of emergent crowns (canopy A of Richards) rising to at least 40 m. The lower tree layer (Richards' canopy C) is rather open with scattered rattans and palms. In the lowest lying sections, this forest grades into a slightly deciduous *Spondias-Celtis* forest with a main canopy at 35 m, isolated emergents to 40–45 m and a very dense lower layer. The average annual rainfall can be calculated (see Fitzpatrick 1965) as c. 152 cm, most falling in December–April and little in May–August. Mean monthly temperature is 27 °C, with less than 1.5 °C variation from the mean in any month. Relative humidity is fairly constant throughout the year, varying diurnally between 78% at 09.00 hrs and 68% at 15.00 hrs (Fitzpatrick 1965).

2. Subitana

Low hills (500–600 m) on the Sogeri Plateau, forested with evergreen *Castanopsis-Elaeocarpus* forest, often strongly dominated by *Castanopsis* but with local patches of prominent Dipterocarpaceae. The forest has a fairly open canopy at 30–40 m, very isolated emergents and a somewhat poorly differentiated lower canopy layer. Average annual rainfall is 361 cm, least falling between June and August, but fairly evenly spread throughout the year.

3. Owers Corner

The forest in the lower parts is closely similar to that at Subitana, and rainfall regimes are probably similar. On higher ground (700–800 m) the *Castanopsis-Elaeocarpus* forest is mixed with *Lithocarpus-Elaeocarpus* forest which has a greater species diversity and more clearly demarcated canopy layers.

WAU AREA

Some aspects, particularly botanical and related to Mt Kaindi, were described by Brass (1964).

1. Mt Kaindi (2360 m)

In the areas where field work was carried out, primary forest is only found above c. 1800 m. *Castanopsis-Quercus* Midmontane oak forest extends from 1800 to c. 2000 m; between 1950 and 2150 m *Nothofagus grandis* beech forest takes over, replaced near the summit by flat-topped mixed *Nothofagus* forest. All three forest types are rich in epiphytic growth and similar in structure, with a main canopy at c. 30 m, rather few emergents, and a clear lower canopy layer. Mean annual rainfall at 2000 m is 272 cm, fairly evenly spread but most falling in May–August.

2. Wau-Bulolo gorge (900 m)

The forest is principally Midmontane oak but intermingled, especially on ridges, are extensive stands of the gymnosperm *Araucaria klinkii*.

CENTRAL HIGHLANDS

In the Purari or Central Highlands observations were made in the western part surrounding the Wahgi Valley (Fig. 1). Here, in many places, primary forest only commences above 2450–2750 m, the frost-dictated upper limit of cultivation. The reports by Perry *et al.* (1965) and Haantjens *et al.* (1970) are invaluable sources of information on many aspects of the Central Highlands. Brass (1964) provided a good introduction to Mt Wilhelm (4580 m); other important general accounts are to be found in Mayr & Gilliard (1954), Gyldenstolpe (1955) and Sims (1956). Diamond (1972) has presented a comprehensive survey of the Central Highlands avifauna.

1. Baiyer River

Forest in the Baiyer River Bird of Paradise Sanctuary (1200 m) is principally *Lithocarpus* oak with a closed canopy at 30 m, frequent emergents to 35 m, a distinct lower canopy, shrubby undergrowth but rather sparse ground cover. Mean annual rainfall is 259 cm, May–October being the driest months though seasonality is not pronounced.

2. Mt Oga (2750 m)

An outlying spur of the Kubor range, Mt Oga is a moderately to steeply sloping limestone plateau surrounded by 60–180 m cliffs. The primary Lower Montane forest, which begins at 2150 m, has a closed canopy at 30 m, frequent higher emergents, a fairly distinct lower canopy layer, mainly woody shrub undergrowth and rich herbaceous ground cover. Broadleaf trees dominate in the main canopy, with local nearly pure stands of *Nothofagus*, but some gymnosperms are also present.

3. Mt Wilhelm

All field work was carried out in and around the Pindaunde Valley and the approaches to this from Keglsugl on the eastern slopes of the mountain (see Brass 1964 and Wade & McVean 1969). In this area there are no vestiges of forest below 2570 m. Fairly undisturbed mixed broadleaf-gymnosperm Lower Montane forest occurs between 2630 m and 3000 m. The closed canopy is at c. 30 m with some taller, mainly gymnosperm (*Papuacedrus* and *Podocarpus*) emergents, and sub-canopy and rich woody undergrowth strata are discernible. Trees are rich in epiphytes and there is an abundant ground flora.

At about 3050 m a very steep 'jump-up' rises to the terminal moraine of the Pindaunde Valley at 3300 m. The structure of the Upper Montane forest on this slope is basically a single tree layer of crooked small-leaved trees with dense crowns at 10–20 m, with a rich undergrowth and ground cover. Between 3400 and 4000 m discontinuous patches of Subalpine forest occur. This has a dense canopy layer between 7·5 and 9 m, an undergrowth of multi-stemmed, large-leaved shrubs and sparse ground cover. Mean annual rainfall at Keglsugl (2400 m) is 231·4 cm, while at 3480 m it is 300 cm, May–August being the driest months (McVean 1968).

4. Mt Hagen

Field work at this locality was concentrated on the south-facing slopes of the mountain. Apart from an area of essentially coniferous (*Podocarpus*, *Dacrycarpus*, *Papuacedrus*) Lower Montane forest at 2450–2750 m on the southwest slope, there is little undisturbed forest below 2750 m. Mixed broadleaf-conifer occurs between 2750 m and 3250 m and both this and the coniferous forest are structurally similar to the Lower Montane forest on Mt Wilhelm. The transition from this tall (25–30 m) forest to the low canopy (15 m) of the gnarled small-leaved Upper Montane trees at c. 3250 m is striking and quite rapid. Patches of Subalpine forest occur above the line of continuous timber. Mount Hagen town (1680 m), 35 km to the southeast, the nearest point for which climatic data are available, has a mean annual rainfall of 260 cm, the driest months being May–August, though seasonality is not very marked. The range of mean monthly temperature is only 17·4 °C–18·9 °C but the average diurnal range is about 7 °C. Relative humidity is about 88% at 09.00 hrs and 67% at 15.00 hrs; mean cloud cover is 0·7 (Haantjens *et al.* 1970).

Although the study areas covered a wide variety of forest types it seems that the basic structure of all, except the Upper Montane forest, is sufficiently similar to allow observations on the vertical foraging preferences of birds to be considered together. In Lowland and Midmontane forests it is possible reliably to distinguish a closed main canopy, frequent taller emergents, a lower canopy stratum, a shrubby/woody undergrowth layer and the ground cover. In Lower Montane forest the sub-canopy layer is sometimes less well defined. Upper Montane forest is clearly distinct with its single canopy layer, undergrowth and ground cover.

The pattern of rainfall at all localities is also broadly similar, and it is probably reasonable to assume that this is reflected in a similar seasonal regime in new leaf-growth of plants and the likely correlated increase in insect abundance.

SPECIES STUDIED

The New Guinea avifauna contains some 90 species which are probably nearly exclusively insectivorous and live in primary rainforest. About 80 belong to Muscicapidae (in the broad sense), including 61 warblers Sylviidae, flycatchers Muscicapidae and whistlers Pachycephalidae (all in the restricted sense). Of these, 52 have been recorded from the study areas or their vicinity, and 50 actually observed in the field form the basis of this study (Appendix 1).

METHODS

Two aspects of the relationship between the birds and their insect prey were recorded, namely foraging behaviour and preferred feeding stations.

FORAGING BEHAVIOUR

Three basic feeding techniques were recognized. The most easily defined of these is 'flycatching' (the capture, by a bird on the wing, of flying insects). 'Gleaning' is defined here as the opposite, i.e., the capture of insects not in flight by birds not on the wing. The intermediate category 'flycatcher-gleaning' is defined as the capture, by a bird on the wing, of insects not in flight. It was usually possible to assign a bird's feeding technique to these three categories without difficulty; exceptions are noted later.

Several species, or groups of species (especially flycatchers), have reasonably distinctive patterns of feeding behaviour which might permit further subdivision of the three main categories. Some patterns are fairly constant, and are described later, but others are more variable, much less easy to define and difficult to categorize under field conditions. It was felt that use of these three fairly clear-cut conditions is preferable in a preliminary investigation.

FEEDING STATIONS

Five horizontal feeding strata were recognized, coinciding with the vegetation layers described earlier:

- H = closed forest canopy and isolated emergent crowns above this,
- M = middle forest storey, below main canopy and above lower canopy,
- L = lower forest storey,
- U = undergrowth (shrubs and saplings),
- G = ground and herbaceous ground cover.

The different strata were usually easily recognizable in Lowland, Midmontane and Lower Montane forest. In Upper Montane forest, however, it was impossible to distinguish a middle forest storey and even the division of the canopy into H and L components was somewhat artificial.

Three vertical feeding zones were also recognized:

- I = inner (central) third of tree, i.e., trunk, large branches and central foliage,
- M = middle third of tree, i.e., chiefly small branches, large branchlets and associated foliage.
- O = outer (peripheral) third of tree, i.e., chiefly small branchlets, twigs and associated foliage.

Of these, somewhat arbitrary, categories the middle zone was the least easy consistently to recognize.

The concept of inner, middle and outer zones is not meaningful for the undergrowth and ground cover and only two vertical subdivisions of these were recognized:

- I = inside of bushes in undergrowth; within dense ground cover,
- O = outside of bushes in undergrowth; in very light ground cover, or in the open.

The activities of flycatchers pose a special problem for both horizontal and vertical categorization. Unlike all other species, their activities cannot be localized by reference to the part of the vegetation where they capture an insect. Not only do flycatchers feed in the interstitial air space between trees but it is often impossible to be sure at what stage in a sallying flight or dive an insect is secured. Accordingly the concept of vertical feeding zones is redundant for practical purposes for flycatchers and the horizontal feeding strata related here to the observed location of perches from which insect-catching sallies were made.

All observations used here refer to adult (i.e., neither fledgling nor obviously juvenile) male or female (only *Gerygone palpebrosa*, *Eugerygone rubra*, *Monarcha chrysomela*, *Arses telescopthalmus*, *Pachycephala schlegelii* and *P. soror* are noticeably sexually dimorphic) individuals of certain specific identification.

Sources of error inherent in this analysis can be summarized as follows:

(a) Forest storeys M and L were sometimes difficult to distinguish and this may result in incorrect assignment of observations.

(b) The middle vertical vegetation zone was sometimes hard to recognize and the occurrence of species in it probably underestimated.

(c) The incidence of flycatcher-gleaning was probably underestimated for two reasons. Firstly, identification of species seen only in flight is often difficult. Whereas flycatchers can usually be watched back to a perch and gleaners move steadily and fairly predictably through the foliage, flycatcher-gleaners often pass right across the field of vision and cannot be re-localized, resulting in a much higher proportion unidentified. For instance, at least two species of *Pachycephala* flycatcher-glean in forest edge habitats, and one or two unidentified individuals were also seen to do this inside forest. Secondly, with very small birds (especially *Sylviidae*) it was often impossible to be certain whether the rather frequent hops through the foliage were merely changes of feeding site or whether each hop was also terminated by plucking an item of food from a leaf or twig (i.e., small-scale flycatcher-gleaning). To simplify matters such species were regarded only as gleaners and the frequency of hopping estimated to provide a guide to a potential extent of flycatcher-gleaning.

(d) The occurrence of species in the canopy must inevitably have been underestimated as the small birds which form the bulk of the canopy species are hard to see and even harder to identify. In upland areas there is some compensation in that the slope of the ground often affords good views of the canopy but this is less true of lowland areas, in particular the flat Brown River site.

OVERLAP AND DIVERSITY INDICES

Differences between species in utilization of the habitat for foraging were calculated by determining the overlap index (R_0) using an equation derived from information theory (Horn 1966):

$$R_0 = \frac{(x_1 + y_1) \log (x_1 + y_1) - \sum x_1 \log x_1 - \sum y_1 \log y_1}{(X + Y) \log (X + Y) - X \log X - Y \log Y}$$

where X and Y are the total number of observations of species X and Y and x_1 and y_1 are the respective number of observations, of species X and Y, in the i th foraging category. The overlap indices for all pairs of species in each habitat are set out in Appendix 2.

The use of a diversity index, also derived from information theory (Shannon & Weaver 1949), enables the degree to which species concentrate their foraging within certain stations to be assessed. In the equation

$$H = - \sum_{i=1}^s P_i \log P_i,$$

H represents the diversity found in the sample, s is the number of foraging stations and P_i the proportion of observations made in category i . All values are expressed as the ratio $\bar{J} = H/H_{\text{max}}$ (Pielou 1966) where H_{max} represents the situation in which utilization of all stations is equal. Species with restricted foraging ranges ('specialists') will receive low \bar{J} values, those with wider foraging ranges ('generalists') high values. The foraging diversity index of each species is given in Appendix 1.

Because both indices are mainly useful in comparative situations, their employment in this paper is restricted to examining trends and comparing the relationships between species in different genera or in different habitats.

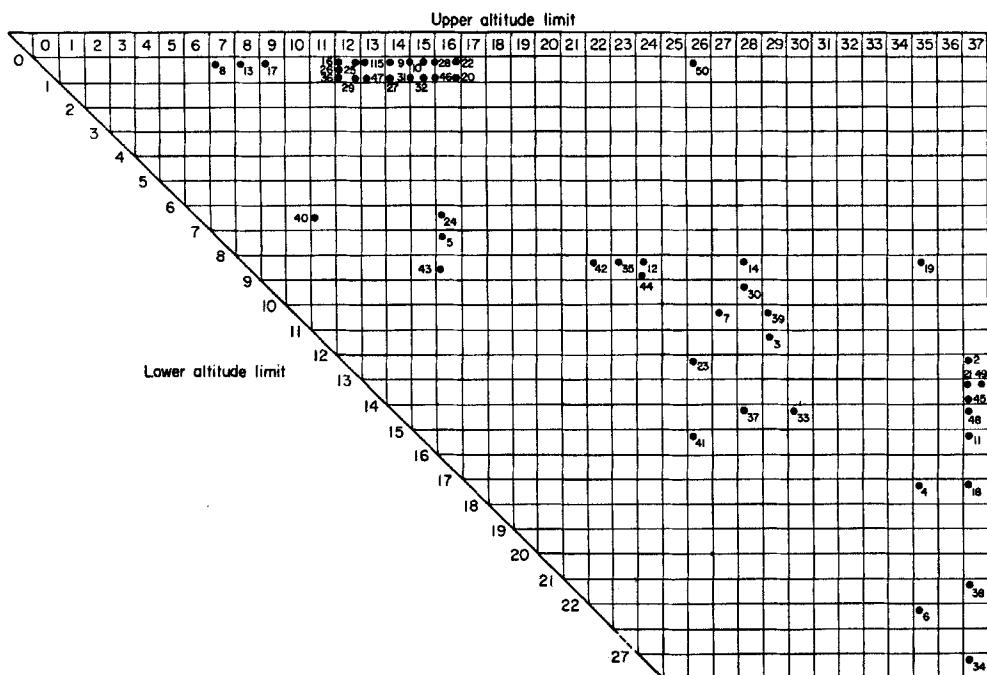
RESULTS

ALTITUDINAL RANGE

In the presentation and analysis of the data on the 50 species observed the initial priority is to determine which have the potential to co-occur. The geographical ranges of all are widespread and broadly coincide, but their altitudinal preferences do not. Reference has already been made to the principal avifaunal discontinuity at c. 1500 m, with lowland species below and upland species above, this altitude. An attempt was made to assign each species to either of these categories, on the basis of personal observation and citation in

the literature (especially Diamond 1969, 1972, Gilliard & LeCroy 1961, 1966, 1967, 1968, 1970, Greenway 1966, Gyldenstolpe 1955, Hartert 1930, Hartert *et al.* 1936, Junge 1939, 1953, Mayr 1931, Mayr & de Schauensee 1939, Mayr & Gilliard 1954, Mayr & Rand 1937, Mees 1964, Ogilvie-Grant 1915, Rand 1942a, b, Rand & Gilliard 1967, Ripley 1964, Schodde & Hitchcock 1968, Sims 1956, Stein 1936, Stresemann 1923). The alternative and preferable procedure—to ascertain the precise altitude range of each species in each study area—was impossible in the field and could not be done from the literature. Diamond's (1972) study, in the Karimui area on the southern flank of the Central Highlands, is the only accurate survey of this kind yet carried out in New Guinea. His work suggests that there are instances of altitudinal replacement that will be unrecognized by the simpler classification I have used. In some cases (e.g., *Sericornis spilodera/S. arfakianus* and *Tregellasia leucops/Microeca papuana*) the records from elsewhere in New Guinea confirm the situation at Karimui, but in other cases (e.g., *Peneothello signatus* and *P. cyanus/Pachycephalopsis poliosoma*) the species do not seem to show so clear altitudinal replacement elsewhere in New Guinea. In these circumstances I have preferred to adopt the simpler, more general analysis that must necessarily underestimate the occurrence of altitudinal replacement and to note in the text (and in Appendix 2) which species pairs appear to have altitudinal isolating mechanisms not taken into account.

The indicated maximum altitudinal ranges are presented in Figure 2. This analysis must tend to overestimate any species' normal range, as it includes records from areas where mountain forest penetrates into lowland altitudes (e.g., in the Vogelkop) and the fewer areas where Lowland forest is known to reach the lower mid-mountain slopes, but usually below 1500 m (e.g., Baiyer River, Karimui). Some records are based on specimens brought in by natives which may have been caught above or below a particular expedition camp.



It is still not difficult to assign most species to an altitude category. Thus all with an upper altitude limit of 1600 m are unequivocally lowland birds, and those in the far right hand column, with species 4, 6, 33, 37 and 41 are upland birds, none occurring anywhere below 1200 m.

The remaining 12 species show less clear-cut distributions. *Phylloscopus trivirgatus* (12), *Tregellasia leucops* (35), *Pachycephalopsis poliosoma* (42) and *Pachycephala soror* (44) seem to be truly intermediate species having an altitude range (800 m–2200/2400 m) extending across the main discontinuity. *Myiolestes megarhynchus* (50) has a most unusual range (0–2600 m). *Sericornis perspicillatus* (3) is also essentially an intermediate species though it clearly overlaps more with upland species, e.g., *S. papuensis* (4) and *S. nouhuysi* (2).

The remaining species fall into two groups. *Peltops montanus* (14) and *Machaerirhynchus nigrippectus* (30) have long been recognized as the upland members of species pairs with,

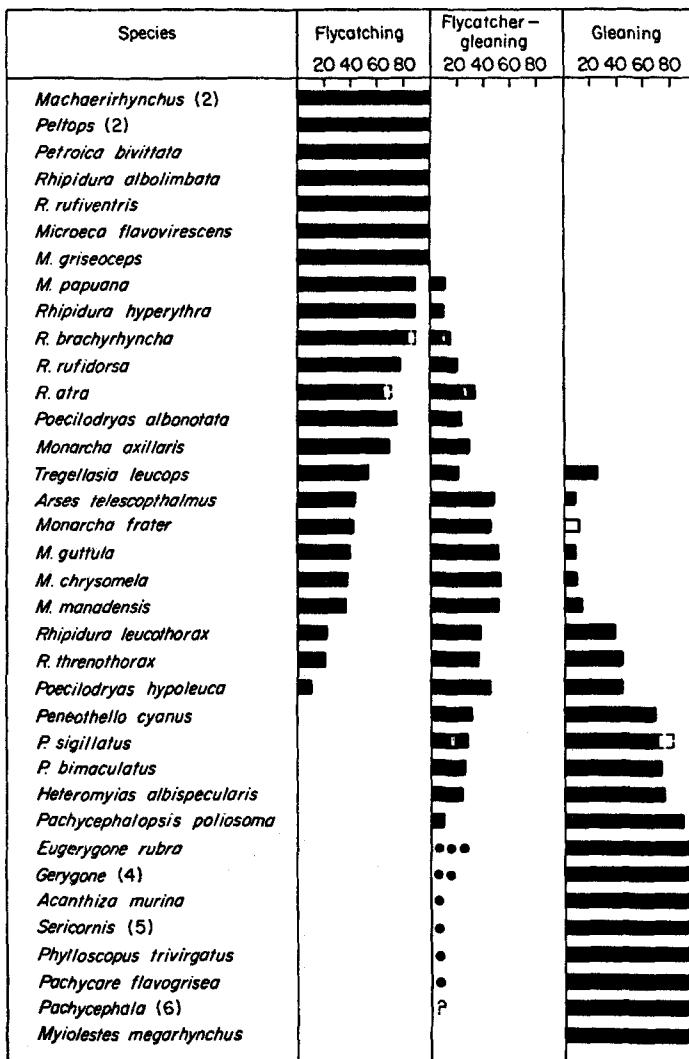


FIGURE 3. Percentage use of each feeding technique. Dotted margins show values for Upper Montane forest, where different. Figures in parentheses give number of species in a genus having identical values. Solid circles suggest the likely extent of flycatcher-gleaning (see text).

respectively, *P. blainvillii* (13) and *M. flaviventer* (29), and must be regarded as essentially upland species even though in places they may range somewhat lower (but without overlap). *Gerygone cinerea* (7), *Rhipidura atra* (19) and *Monarcha axillaris* (23) are all well-known as typically upland species and in the rare cases where they have been recorded down to c. 1000 m there appears to be no altitudinal overlap with lowland congeners. The altitude zone(s) to which each species is assigned is set out in Appendix 1.

Figure 2 also shows up two other points. The discontinuity near 1500 m is further emphasized by the fact that, although many lowland species have their ceiling at between 1200 and 1600 m, the next altitude ceiling for a species is 2200 m, a gap of 600 m. Fourteen species have an upper altitude limit between 2200–3000 m but the remaining 12 are found right up to the treeline at 3500–3700 m. The gap between these two groups emphasizes that only 12 of the 26 upland species occur in the structurally much simpler Upper Montane forest.

FEEDING BEHAVIOUR AND ECOLOGY

The percentage use of each of the three insect-catching techniques by each species in all lowland and lower mountain forests is shown by the solid bars in Figure 3. The circles indicate the relative potential for employment of small-scale flycatcher-gleaning by certain small species (see above). The dotted lines indicate the percentage use of each technique in the upper mountain forest, where this differs. Figures in brackets indicate that more than one species in a genus have identical technique utilization values.

Figures 4–6 present details of the percentage of feeding activity for each vertical and horizontal station. The mid-mountain (LU of Appendix 1) species are repeated in both lowland and upland categories and a few other species (*Poecilodryas albonotata*, *Tregellasia leucops*, *Monarcha axillaris*) appear more than once to facilitate comparison with either their close relatives or species with similar feeding patterns. Figure 5 enables the vertical distribution of the gleaning and flycatcher-gleaning habits to be assessed separately for the 14 species which exhibit both techniques.

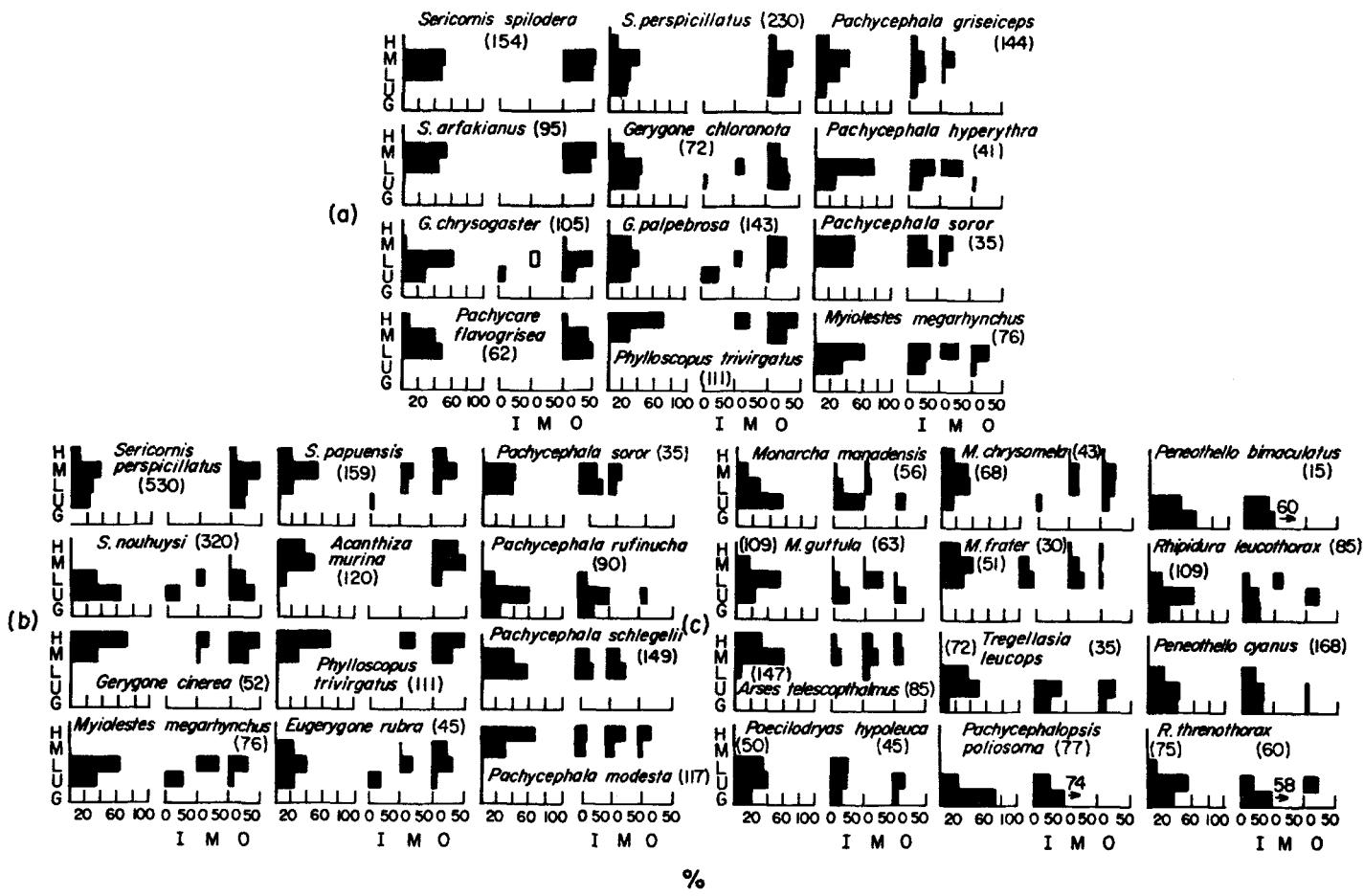
Finally Figure 7 summarizes, in diagrammatic form, some of the foraging relationships of the species in each of the three major altitude habitat divisions.

SPECIES COMPARISONS

Using the information presented in the figures and appendices it is possible to examine the role that feeding behaviour and ecology may play in reducing competition between related species of geographically and altitudinally coexisting rainforest insectivores.

Although the main emphasis is placed on the relationships between congeneric species it is probably quite unrealistic to assume that effective competition will not exist between species in closely related and/or structurally and functionally rather similar genera. Indeed Willis (1966) and Morse (1967b) have shown that species in different families may be in effective competition to the extent that their foraging behaviours are strongly influenced.

Clearly genera should contain species more similar to one another than to those in other genera but there are several cases, noted earlier, where generic distinctions are uncertain (e.g., thicket-flycatchers) and other cases where they are based on characters of uncertain relevance to function and ecology (e.g., wing-formulae in *Sericornis* and *Gerygone*). It is important therefore to consider cases where competition may exist between species in different genera and, to facilitate comparison between text and figures, the three basic foraging technique groups (which do have quite strong underlying taxonomic homogeneity) are considered separately.



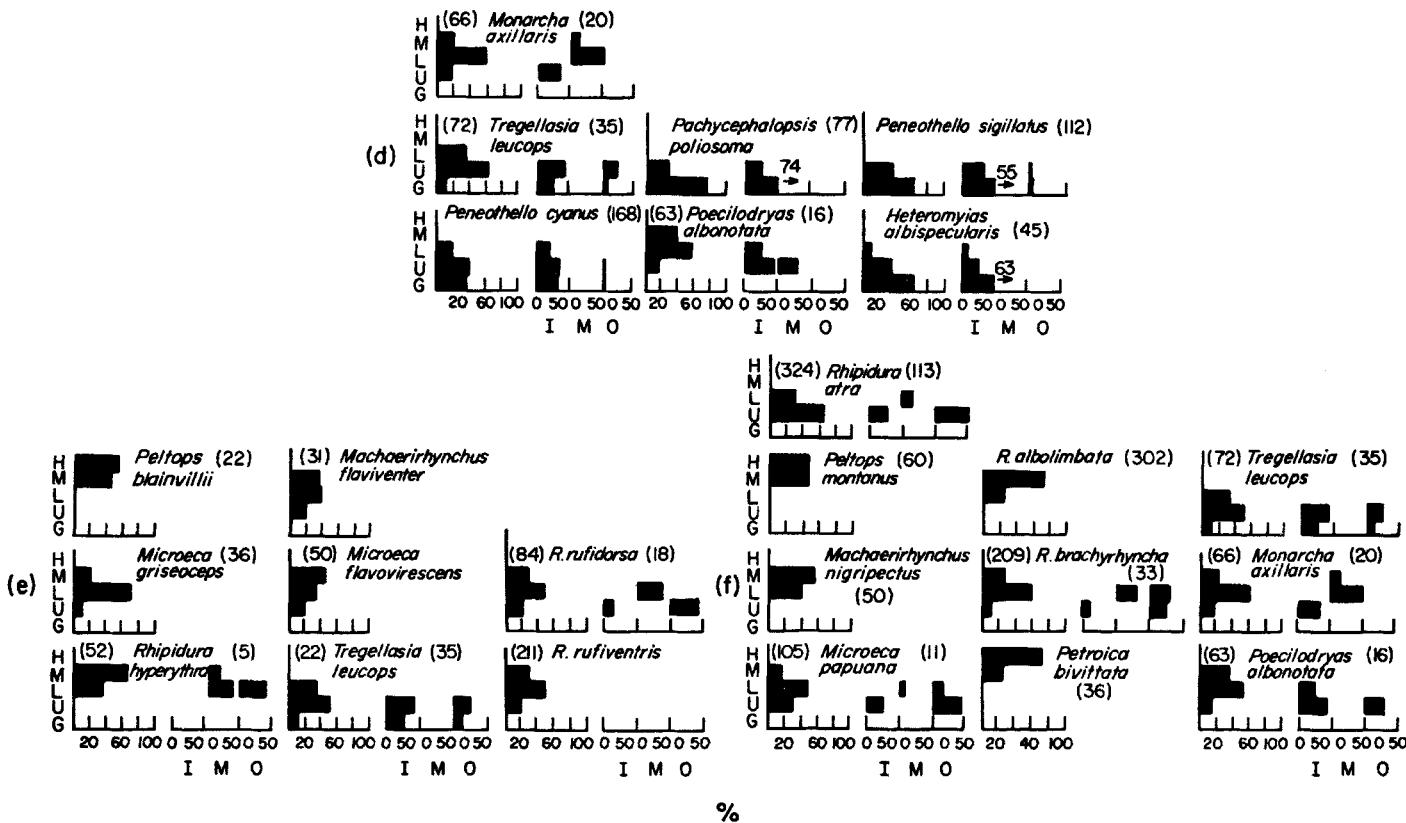


FIGURE 4. Percentage vertical and horizontal distribution of feeding activity. Figures in parentheses give overall number of observations. Vertical forest zone categories (I, M, O) comprise only gleaning and flycatching-gleaning records; hence an additional sample size is indicated. Further details in text. (a) Lowland gleaners. (b) Upland gleaners. (c) Lowland flycatcher-gleaners. (d) Upland flycatcher-gleaners. (e) Lowland flycatchers. (f) Upland flycatchers.

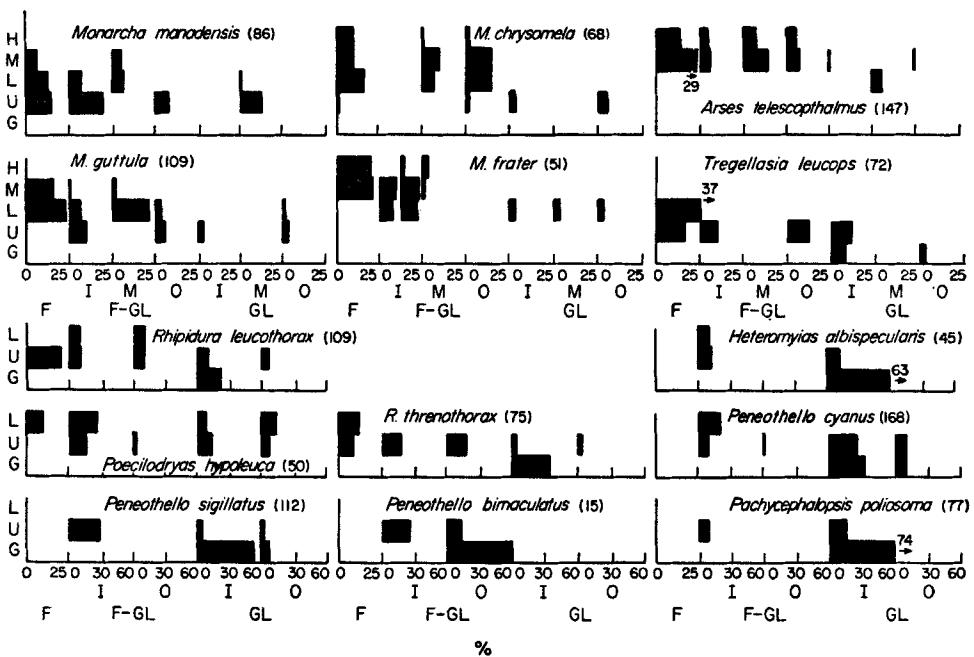


FIGURE 5. Lowland and upland species using both gleaning and flycatcher-gleaning techniques: conventions as Figure 4.

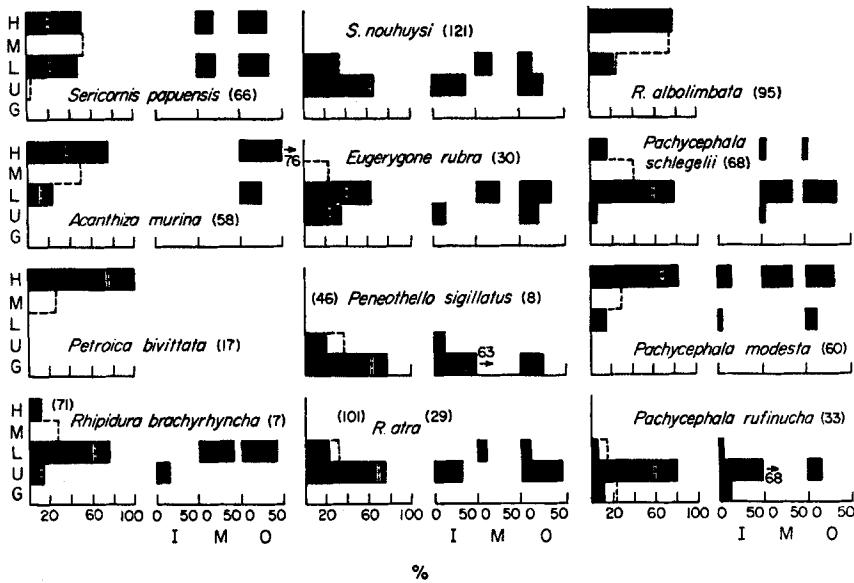
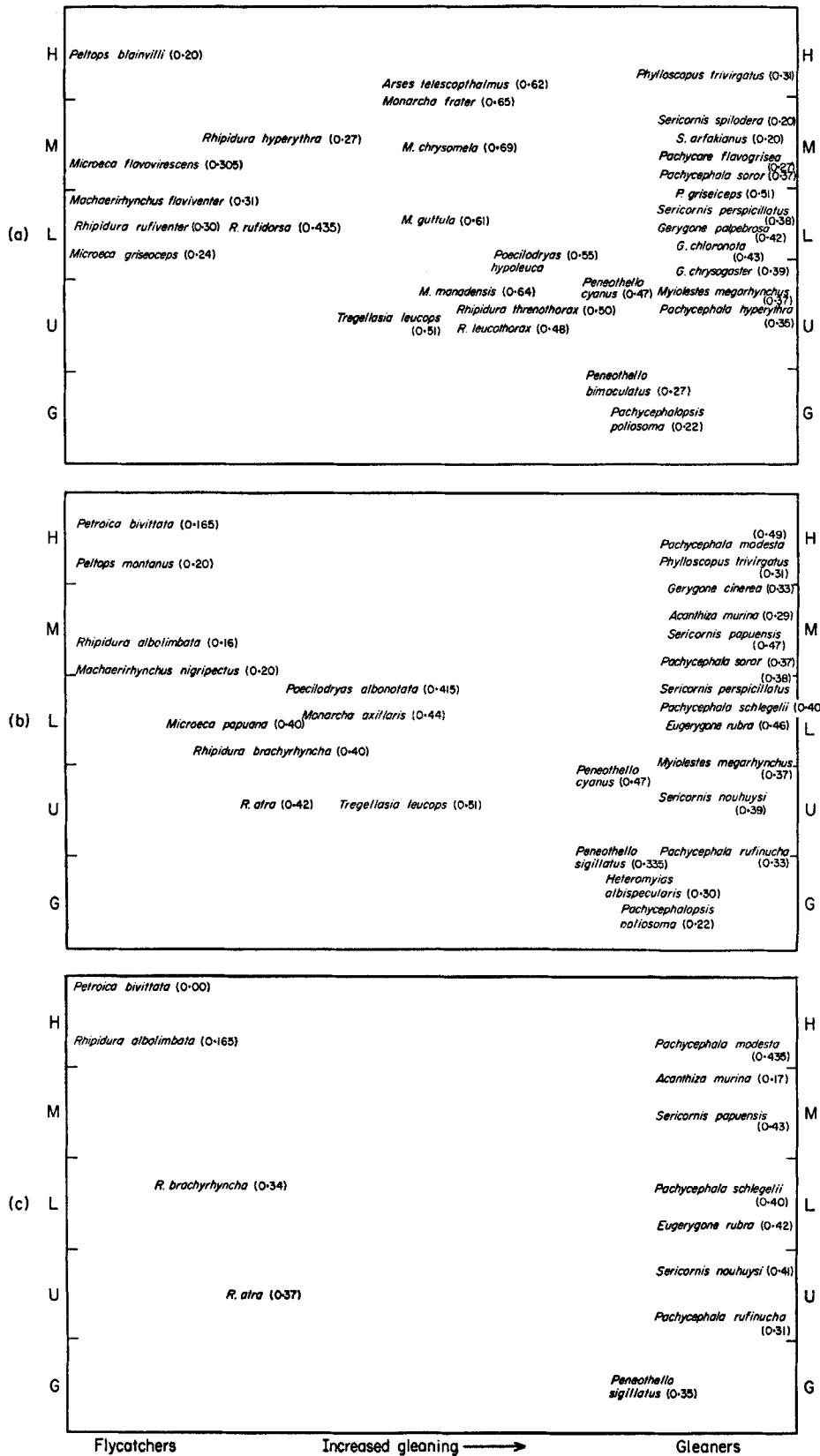


FIGURE 6. Percentage vertical and horizontal distribution of feeding activity for Upper Montane forest species. The dotted lines indicate the pattern of the same species in Lower Montane forest.

FIGURE 7. Diagrammatic representation of feeding behavioural and spatial relationships of species studied. Figures in parentheses are foraging diversity values. (a) Lowland forest species. (b) Lower Montane forest species. (c) Upper Montane forest species. [see opposite]



Flycatchers

Increased gleaning →

Gleaners

INTRAS- AND INTER-GENERIC

Gleaners

The small warblers in the genera *Sericornis*, *Gerygone*, *Acanthiza*, *Phylloscopus* and *Eugerygone* are rather similar in behaviour and general ecology (the first three are very close taxonomically), foraging actively and systematically (less so in *Gerygone* and least in *Eugerygone*) interspersed with short hops (more frequent in the less systematic foragers) and often in flocks.

In the uplands the larger, heavy-billed *S. nouhuysi* is fairly distinct from its smaller, lighter-billed congeners in favouring the lower storey and undergrowth, confirming Diamond's (1969, 1972) view of the ecological relationships within the genus. It also forages in the inner and middle zones of the vegetation; *S. papuensis* which has similar tendencies having a much higher vertical foraging preference, while *S. perspicillatus* is confined to the outer parts of trees. The last two species have similar vertical profiles and Diamond (1972 and *in litt.*) found they replaced each other altitudinally at Karimui and in southeast New Guinea, where records (Mayr & Rand 1937) suggested they might overlap.

Acanthiza and *Gerygone cinerea* forage consistently higher than any *Sericornis* and are totally distinct from *S. nouhuysi*. Their strong preference for outer twigs further reduces competition with *S. papuensis*. *S. perspicillatus* would show considerable overlap with *Acanthiza* but the two do not seem to overlap altitudinally. *G. cinerea* is fairly distinct from the former in its preference for the upper forest stratum, seems altitudinally segregated from *Acanthiza*, but must have great overlap with *Phylloscopus trivirgatus* (which also does not occur with *Acanthiza*). The least common species, *Eugerygone rubra*, must overlap considerably with the three *Sericornis* species (especially *S. papuensis* and *S. nouhuysi*, between which its feeding station preferences are roughly intermediate) but much less with *Acanthiza*, *Phylloscopus* and *G. cinerea*.

In the lowlands the three *Sericornis* species show very considerable mutual overlap, foraging largely in outer twigs, although *S. perspicillatus*, which is 30% heavier than the other two, alone forages in the undergrowth. Diamond (1969, 1972) suggested, and all literature records for areas with at least two species would confirm this, that *S. arfakianus*, *S. spilodera* and *S. perspicillatus* replace each other in an altitudinal series. The foraging diversity of the lowland *Sericornis* species is significantly less ($P = 0.05$, see Table 1) than that of the upland species. This situation is atypical and is not easily interpreted. The three lowland *Gerygone* species foraging mainly in outer twigs and branchlets show very similar patterns, differing only in their proportionate use of middle and lower stories and the undergrowth. All species are sometimes found in second growth and although *G. chloronota* seems to have a somewhat patchy distribution it is not clear how they avoid competition.

The differences in foraging pattern between the species of the two genera are not great but it is noteworthy that the *Sericornis* (*S. perspicillatus*) whose foraging most resembles *Gerygone* species is the one that overlaps least altitudinally. In general *Gerygone* species forage lower and more often in the inner and middle portions of trees than *Sericornis* species. The high degree of overlap remaining is more explicable when it is remembered that the three lowland *Sericornis* species form an altitudinally segregated series and that *G. chloronota* is rather local in occurrence; it is unlikely that more than three out of six species coexist at any one locality. The canopy preference of the remaining small gleaner, *Phylloscopus trivirgatus*, must achieve considerable segregation from the six species above—and it is almost certainly altitudinally isolated from *S. arfakianus*.

Both in the lowlands and uplands these warblers comprise the bulk of the small birds gleaning for insects. The average weight of all species is just over 9 g (including *S. nouhuysi* which is a third heavier than any other species) and this must be largely cor-

related with their ecological separation from the large gleaners of the Pachycephalidae. Both warblers and whistlers utilize a similar range of horizontal strata but the heavier whistlers (*Pachycephala* species, *Myiolestes megarhynchus*: average weight 28 g) forage principally in the inner parts of trees leaving the outer foliage to the warblers. *Pachycare flavogrisea* is 50% heavier than most warblers yet also seems confined to the outer areas of trees. It would be interesting to know what small-scale differences in feeding behaviour might exist, as a consequence of its heavier weight, when foraging on small twigs.

Most forest whistlers are usually solitary, quite noisy, slow moving (but rather often changing perches) species of the inner zones of the middle strata of the forest. Particularly in modified habitats (forest edge, second growth, subalpine scrub, etc.), and perhaps sometimes in forest, flycatcher-gleaning and even flycatching techniques are used. *P. rufinucha* is very different, being much larger, with a longer tarsus, predominantly a species of dense undergrowth and foraging more on the ground than in the lower forest storey. These habits resemble the thicket-flycatchers with which it has been classified.

Diamond (1972) noted that the remaining five species form a broadly overlapping altitude sequence such that *P. griseiceps* includes most of the range of *P. hypertyhra*, *P. soror* straddles part of the range of this and *P. schlegelii* and the latter includes most of *P. modesta*'s range. He suggested that vertical foraging relationships may permit this degree of overlap with *P. griseiceps* above *P. hypertyhra* above *P. soror* above *P. schlegelii* and *P. modesta* above *P. schlegelii*. My study confirms and extends some facets of these relationships. Of upland species *P. modesta* forages significantly higher than *P. soror* and *P. schlegelii* which are almost identical but the available evidence indicates that the latter two species are the pair most nearly replacing each other altitudinally.

In the lowlands the situation is less clear cut. *P. griseiceps* has the greatest vertical range, from undergrowth to canopy, being the only species seen in the top forest storey. *P. hypertyhra* is chiefly found in the lower storey, but also in the undergrowth; *P. soror* which only partly overlaps both species, being intermediate. This seems to be the only case in which my field observations disagree with those of Diamond (who apparently found the reverse foraging preferences). Unlike him, I did not record both species at any one locality, and absence and presence of potentially competing species may well affect the foraging strata occupied. Clearly some separation is achieved by the above combinations of altitude and foraging differences but it is not known what, if any, other factors may also be involved.

Myiolestes megarhynchus resembles a large, rather shy, *Pachycephala*, periods of moderate gleaning activity alternating with quite lengthy motionless perching. Ecologically it is very similar to *P. hypertyhra* in the lowlands and intermediate between *P. soror*/ *P. schlegelii* and *P. rufinucha* in the uplands.

Flycatcher-gleaners

There are two principal groups, the monarch and thicket-flycatchers and a small number of additional species, that show substantial use of flycatcher-gleaning techniques.

Apart from *M. axillaris*, all monarch flycatchers are active, noisy and usually solitary but conspicuous species, often seen 'bounding' through lowland forests. Flycatching, flycatcher-gleaning and gleaning techniques are all used, and each species occurs to some extent in all tree zones (and usually in a wide range of strata, though never in the ground cover). *M. manadensis* is the least active perhaps relating to its preference for feeding stations low in the vegetation column, and *M. chrysomela* the most active perhaps allied to its showing the greatest vertical feeding range in the genus. *Arses telescopthalmus* has the distinctive habit of occasionally clinging to tree-trunks.

M. axillaris not only is the sole upland species but alone in the genus seems to rely greatly on flycatching and was not observed to glean for insects. Behaviourally it is

restless and active, raising and slightly spreading its long tail and drooping its wings in a manner reminiscent of *Rhipidura*.

The remaining species are all rather similar ecologically. *Arses*, and to a lesser extent *M. frater*, seem commonest in the upper two forest strata, setting them apart from *M. manadensis* (mainly inner portion of lower storey and undergrowth) and to a smaller degree *M. guttula*, *M. chrysomela* being intermediate. The five species are particularly interesting in showing quite substantial overlap yet in nearly every case a distinct preference, not usually shared by another, for a particular stratum. They also show the highest values for foraging diversity of any species (see Appendix 1) and it seems surprising that only the rather different *M. axillaris* occurs in upland forest as they do not seem to be replaced ecologically in this habitat (compare Fig. 7, a and b).

The closely related thicket-flycatchers (genera *Poecilodryas*, *Peneothello*, *Heteromyias*, *Pachycephalopsis*) form a natural group related, through *Tregellasia leucops*, to the typical *Microeca* flycatchers and ecologically, if not taxonomically, through *Pachycephala rufinucha* and *P. tenebrosa* to the whistlers. All, except *Poecilodryas albonotata*, are shy, skulking species of undergrowth and ground cover. Individuals remain motionless for long periods, characteristically perched sideways, with body horizontal, on a tree-trunk or sapling stem. From such a perch a quick pounce is made to catch an insect before flying to a fresh (occasionally the same) perch. Most species are at least equally common on the ground where they make rapid (often food gathering) hops across open areas or glean sporadically in dense cover.

Poecilodryas albonotata is clearly set apart by its habit of flycatching from an upright perch in the middle and lower storey (cf. Rand 1942b, Diamond 1972), although it occasionally flycatcher-gleans from a sideways perch in the understorey. It is noteworthy, however, that *Poecilodryas hypoleuca* very occasionally flycatches and has a high foraging diversity value for a thicket-flycatcher, though in other ways its habits seem typical of this group.

With this partial exception all the undergrowth dwelling thicket-flycatchers show very similar foraging patterns, with *Peneothello cyanus* spending less time on the ground than the others. Diamond (1972), based on his field work at Karimui, suggested that *Poecilodryas hypoleuca*, *Pachycephalopsis poliosoma*, *Peneothello cyanus* and *P. sigillatus* are strictly segregated altitudinally, with the rather locally distributed species *Peneothello bimaculatus* and *Poecilodryas placens* essentially fitting in the altitude gap between *P. hypoleuca* and *Pachycephalopsis*. *P. hypoleuca* is certainly found in low altitude Lowland forest, but has been recorded up to 1000 m and must overlap in places with *Peneothello bimaculatus*. A combination of different altitude preferences and rather different feeding habits should, however, provide good segregation. Other well-attested altitude separations, in spite of some overlap in total altitude range, probably exist between *Pachycephalopsis* and *Heteromyias albicularis*, and *Heteromyias* and *Peneothello sigillatus*. At Karimui (Diamond 1972) and Mt Albert Edward (Mayr & Rand 1937) *P. sigillatus* and *P. cyanus* did not overlap but in the Snow Mts a 600 m overlap seems to exist (Rand 1942b). In general, however, the two species do seem to replace one another. The evidence is not so compelling for the replacement of *Pachycephalopsis* by *P. cyanus*. In southeast New Guinea (Mayr & Rand 1937) the former occurs from 770–2450 m, the latter from 950–2400 m; in the Snow Mts *P. cyanus* ranged between 1800–2800 m and *Pachycephalopsis* was found at 2200 m. There is also substantial overlap between *P. cyanus* and *Heteromyias* and *Pachycephalopsis* only partly alleviated by the first spending more time in the lower storey and undergrowth, the others more on the ground. *P. bimaculatus* and *Pachycephalopsis* must also overlap altitudinally to some extent. Further investigation of the general biology of these thicket-flycatchers would be of the greatest interest.

There are only four other species, analysed here, which are ecologically and behaviourally rather similar. *Pachycephala rufinucha* is of similar size and weight to the heaviest

thicket-flycatchers and in vertical and horizontal foraging preferences it is very similar to those species it overlaps (*P. cyaneus*, *P. signatus*, *Pachycephalopsis poliosoma*, *Heteromyias*). The only obvious distinction is that the whistler is a gleaner whilst the flycatchers show at least some flycatcher-gleaning, but overlap must still be substantial. The species with most overlap, *Pachycephalopsis poliosoma*, may, however, be nearly separated by altitudinal preference.

The extensive flycatching and flycatcher-gleaning of *Tregellasia leucops* (typically sallying from a lower storey or undergrowth perch, often adopting the stance of a true thicket-flycatcher) coupled with preferred foraging strata ensures segregation from *P. bimaculatus*, *Pachycephalopsis* and *Heteromyias* with which it overlaps altitudinally and *P. signatus* (from which it is virtually altitudinally isolated) but it is less distinct from *P. cyaneus* and *Poecilodryas albonotata*, between whose habits it is intermediate. It probably only overlaps, however, the bottom part of the range of these species.

Like *Tregellasia* the lowland flycatchers *Rhipidura leucothorax* and *R. threnothorax* are smaller and lighter than thicket-flycatchers and also catch some food by flycatching. This and their greater tendency to forage in the outer parts of vegetation may provide some reduction in competition with *P. hypoleuca* and *Tregellasia* (which have, on average, slightly higher vertical preferences) and *P. bimaculatus*, and perhaps also with *Pachycephalopsis* and *P. cyaneus* in the bottom half of the altitude range of these two species.

In their gleaning habits in the undergrowth and on the ground the thicket-flycatchers are complementary to the warblers and whistlers of the higher vegetation levels. When flycatcher-gleaning they utilize distinctly lower strata than the monarch flycatchers and these two groups can also be regarded as complementary in the lowlands. In the uplands there is no similar ecological complement to the thicket-flycatchers.

Flycatchers

All mainly flycatching species belong to the Muscicapidae but several genera are involved and there are recognizable distinctions in flycatching behaviour. It is uncertain what role these may play in achieving additional relief from competition, though it is always possible that the various techniques produce a bias towards the capture of certain kinds of insects.

Opportunities for avoiding overlap in feeding stations are most restricted in this group. This is partly because it was not practicable further to subdivide the flycatching habit (see Methods) and also because flycatching activities are mainly conducted in the upper three forest strata, only occasionally in the undergrowth and *Rhipidura leucothorax* alone was seen to make a sally from the ground. The empty space at the bottom left corner of Figure 7, a-c, also testifies to this. It is also notable that with species using both flycatching and flycatcher-gleaning the latter technique is mostly used in the lowest strata, particularly in the undergrowth (e.g., in *Tregellasia leucops*, *Poecilodryas albonotata*, *Rhipidura atra*, *R. brachyrhyncha*, *R. hyperythra*, *R. rufiventris*).

The regular use of tree-top perches for flycatching sallies is confined to the two large (c. 30 g), altitudinally replacing *Peltops* species and the small (9 g) *Petroica bivittata*. The remaining species are of much the same weight (9-16 g), though differing widely in relative body proportions.

Diamond (1972) visualized niche segregation in forest *Rhipidura* essentially as follows. Four species foraging mainly in forest under-storey, *R. leucothorax* preferring lowland forest edge, *R. threnothorax* lowland forest interior, *R. atra* at middle altitudes, replaced higher up by *R. brachyrhyncha*, the latter two species also foraging in the middle storey. Of the remaining species *R. albolineata* and *R. hyperythra* feed in middle and upper storeys, and replace each other altitudinally, *R. rufidorsa* feeds in middle and lower storeys often at lower altitudes than *R. hyperythra*, and *R. rufiventris*, which co-occurs with the

latter two, prefers forest edge habitats. My data here support much of this interpretation and introduce several additional features. *R. leucothorax* and *R. threnothorax* are set clearly apart by their solitary, skulking behaviour, frequenting dense undergrowth and ground cover and extensive use of gleaning and flycatcher-gleaning techniques. Although *R. leucothorax* is more often outside dense forest than *R. threnothorax* they can both be seen in very similar situations inside forest, although the latter may have a slight preference for damper microhabitats.

The remaining fantails are conspicuous with a distinctive lively flycatching technique. *R. rufiventris* and *R. rufidorsa* have nearly identical foraging profiles but *R. rufidorsa*, unlike *R. rufiventris*, not infrequently flycatcher-gleans for food. Both species forage lower in the vegetation column than *R. hyperythra* (which is behaviourally intermediate) but there is still considerable overlap. Again, although *R. rufiventris* has a greater tendency to occur near the forest edge it is also seen well inside forest.

Of the three upland species, *R. atra* regularly occurs at lower altitudes than the others, but does co-exist with them (albeit in much smaller numbers), at least in some areas, up to the tree-line. In addition to any difference in altitude preference *R. atra* also more often flycatcher-gleans than the others and this is correlated with its preference for the undergrowth. *R. brachyrhyncha*, which sometimes flycatcher-gleans, chiefly occurs in the lower storey and *R. albolineata*, which was only seen flycatching, prefers the middle forest storey. These differences are further accentuated in Upper Montane forest (Fig. 6).

There is a significant ($P = < 0.05$, see Table 1) decrease between the values of overlap indices for lowland and lower montane *Rhipidura* species. This may be correlated with the decreased complexity of habitat at higher altitudes.

It remains now to consider the relationships between *Rhipidura* species and *Microeca* species, *Machaerirhynchus* species, and also *Monarcha axillaris*, *Poecilodryas albonotata* and *Tregellasia leucops*. In the lowlands *R. hyperythra*, *R. rufiventris* and *Tregellasia* also flycatcher-glean, the last having a lower foraging preference and also gleaning for food. *Machaerirhynchus flaviventer* is very similar to *R. rufiventris* and it is not known how the considerable potential competition may be modified by the greater weight of the latter, minor differences in insect catching behaviour and the rather obvious differences in bill proportions. (Both *Machaerirhynchus* species have a shallow bill whose width is nearly as great as the exposed culmen length, whereas in *Rhipidura* the bill is deeper and its width only one-half to two-thirds the exposed culmen length.) The two very similar lowland *Microeca* species also share the middle storeys with the various *Rhipidura* species, seemingly differing mainly in their quiet and rather inactive behaviour. Diamond (1972) suggested that *M. flavovirens* (flat lowlands) is basically altitudinally segregated from *M. griseocephala* (foothills), although he noted that both have been taken at sea level in the Fly River delta (Rand 1942a). While the very sparse data indicate that this might hold for some areas, it was not the case on the southern slopes of the Mt Albert Edward where the first Archbold expedition found *M. flavovirens* between sea level and 770 m and *M. griseocephala* between 40 and 1250 m (Mayr & Rand 1937).

In the uplands there is an exact parallel involving the three *Rhipidura* species, *Machaerirhynchus nigripectus*, and *Microeca papuana*. *Tregellasia leucops* only overlaps extensively with *Microeca papuana* (which is morphologically a link between the two genera) but there are strong indications of altitudinal segregation. In addition *Monarcha axillaris* and *Poecilodryas albonotata*, both showing some flycatching, as well as their more usual flycatcher-gleaning technique, are present. They have vertical preferences somewhat higher than *Tregellasia*, which also gleans, but very similar to *Microeca papuana*. The restless *Monarcha* is rather different behaviourally from the quiet *Microeca* and *Poecilodryas* and the latter is over twice as heavy as the other two, though it is uncertain what influence this has on flycatching techniques. There is also extensive potential competitive overlap between *P. albonotata*, *Monarcha axillaris* and *R. brachyrhyncha*.

though each is successively twice as heavy as the next, and the monarch probably only partially overlaps altitudinally the fantail, to which it is behaviourally very similar.

In conclusion, it is possible that a combination of more subtle behaviourally and morphologically derived feeding differences may have importance in reducing the apparently extensive potential competition between many species that catch insects by flycatching.

INTERFAMILIAL

It is perhaps fitting to round off this section by very briefly noting a number of other, less closely related, species which are potential competitors with the warblers, flycatchers and whistlers analysed here. Although many small honeyeaters Meliphagidae glean for insects inside the forest they are mostly also quite extensively frugivorous and it does not seem appropriate to discuss them. Nearly all relevant, fundamentally insectivorous species belong also to the Muscicapidae (*sens. lat.*) i.e., the thrushes Turdidae, babblers Timaliidae and wren warblers Maluridae (all *sensu* Rand & Gilliard 1967).

The three forest species of Maluridae—*Clytomyias insignis* Rufous Wren Warbler, *Chenorhamphus grayi* Broad-billed Wren Warbler, *Todopsis wallacei* Wallace's Wren Warbler—were not observed, but apparently glean in the undergrowth of lower forest storey where they move slowly often with tail cocked over the back (Rand & Gilliard 1967).

The three forest thrushes—*Oreocincla dauma* Scaled Ground Thrush, *Amalocichla incerta* Lesser New Guinea Thrush, *A. sclateriana* Greater New Guinea Thrush—and nine species of Timaliidae (all except *Pomatostomus isidori* Rufous Babbler separated as Orthonychiae by Deignan 1964) are all ground-living (and often rare or local) birds. When more is known about them, some at least may prove to be omnivorous rather than basically insectivorous.

Of the remaining babblers, *Ifrita kowaldi* Blue-capped Babbler is essentially like a tree-creeper in habits and *Pomatostomus isidori* is a large (75 g) species of the middle storeys of Lowland forest. The three species of mouse-babbler *Crateroscelis*, which have (Mayr & Amadon 1951, Diamond 1972) been considered to belong to the Maluridae (and hence much closer relatives of the species considered here—especially if Mayr & Amadon are followed in including *Sericornis*, *Gerygone* and *Acanthiza* also within the Maluridae), are small, rather wren-like birds with long tarsi (longer in relation to weight than any other forest insectivore), gleaning insects in the undergrowth and ground cover.

The relationships between the ground and near-ground dwelling thrushes, babblers, thicket-flycatchers, mouse-babblers and pittas (Pittidae), constitute a problem of great interest. Although some of these c. 25 species seem very rare and/or geographically highly restricted and others may be segregated by altitude preferences, little is known about how the remainder avoid competing in their seemingly restrictive habitat of ground, ground cover and low undergrowth. It is intended to present some circumstantial evidence elsewhere (Croxall in prep.) but it is noticeable that the species seem to fall into a number of groups on weight and tarsal length characters.

Within the more widespread lowland species three groups may be distinguished:

- (i) small birds (<20 g) with medium-short tarsi (20–25 mm): *Crateroscelis murina*,
- (ii) medium birds (25–35 g) with medium tarsi (25–30 mm): thicket-flycatchers,
- (iii) large birds (50–90 g) with medium-long tarsi (30–40 mm): pittas and orthonychid 'babblers', including two *Eupetes* species, which segregate altitudinally.

Amongst the commoner and fairly widespread upland species four groups may be distinguished:

- (i) small birds (<20 g) with medium tarsi (25–30 mm): *Crateroscelis robusta*,
- (ii) medium birds (20–35 g) with medium tarsi (25–35 mm): thicket-flycatchers,

- (iii) moderately large birds (35–50 g) with long tarsi (40–50 mm): *Amalocichla*, *Melampitta* and timaliid babblers,
- (iv) large birds (>75 g) with medium tarsi (30–35 mm): *Eupetes leucostictus*.

It is, however, not yet clear what the functional and ecological significances, if any, of these groupings might be.

HABITAT COMPARISONS

The data already presented, together with the numerical values for overlap and foraging diversity indices derived from them, enable certain aspects of the foraging behaviour of Lowland, Lower Montane and Upper Montane forest species to be compared.

LOWLAND: LOWER MONTANE FOREST

Although the foraging diversity indices (Appendix 1) are not significantly greater ($P = > 0.1$, Mann-Whitney U-test) for Lowland species (mean = 0.40) than for those in Lower Montane forest (mean = 0.355) there is nevertheless a trend to decreased values in the upper habitat (Table 1), which continues into the Upper Montane forest habitat (mean = 0.32), when species within a genus or broadly similar grouping are considered.

TABLE 1

Comparison of foraging diversity between genera and generic groups in different habitats. Figures are mean group foraging diversity with number of species in parenthesis. Overlap values for the species within a group were compared for L/LM and LM/UM habitats as above

	L	LM	UM
<i>Sericornis</i>	0.26 (3)*	0.415 (3)	0.42 (2)
<i>Sericornis/Acanthiza/Gerygone</i>	0.34 (6)	0.37 (5)	0.33 (3)
<i>Rhipidura</i> ¹	0.335 (3)	0.33 (3)	0.31 (3)
<i>Monarcha</i>	0.64 (5)	0.44 (1)	—
Thicket-flycatchers ²	0.40 (5)	0.37 (5)	0.35 (1)
<i>Pachycephala</i>	0.41 (3)	0.37 (3)	0.38 (3)

Notes: * Statistically significant at $P = 0.05$.

¹ Excluding *Rhipidura threnothorax* and *R. leucothorax*.

² Including *Tregellasia leucops*.

The number of species in each genus are really too small to expect individual trends to be significant, so it is particularly surprising that the one significant trend (*Sericornis*) is a reversal of the general trend. It is tempting to explain the general trend to reduction of foraging diversity with altitude as a response to some aspect of the decreased complexity of the montane forests (even though the same broad vegetation divisions can still be recognized) forcing birds to concentrate their foraging within a smaller number of categories. The exception shown by *Sericornis*, if real, is difficult to understand and I can only suggest that the absence of some element of direct competition enables Lower Montane forest *Sericornis* species to expand their foraging activities. The only evidence supporting this is that there are only five Lower Montane species in the *Sericornis*—*Acanthiza*—*Gerygone* complex (with eight species-pairs of competitive overlaps, taking intrahabitat altitudinal exclusion into consideration) compared with six Lowland species (with 11 overlaps).

If foraging overlap values (Appendix 2, Table 2) are examined, there is again no statistically significant difference when all Lowland and Lower Montane species are compared ($P = > 0.1$, Mann-Whitney U-test) but there is a similar trend to a decrease in overlap with increasing altitude within generic groupings. Both for *Rhipidura* species

and the *Sericornis*—*Acanthiza*—*Gerygone* complex, this trend is significant ($P = 0.05$, Mann-Whitney U-test). The explanation for these and the general trend may well be similar to that advanced above for the decrease in foraging diversity.

It is interesting that in both Lowland and Lower Montane forest the species of Pachycephalidae show significantly less overlap amongst themselves than do species in other groups (for details see Tables 1 and 2) but it is not clear why the large gleaners should be more 'spaced-out' than other groups. The very high mean value for those Muscicapidae remaining after thicket- and monarch flycatchers are removed is derived from lack of subdivision of the flycatching technique comparable to the division of flycatcher-gleaning and gleaning techniques into vertical strata and horizontal zones.

TABLE 2

Comparison of foraging overlap and diversity between various genera and generic groups in different habitats. First pair of figures are mean group overlap without (left) or with (right) adjustment for altitude segregation within major habitat category. Figures in parentheses are the number of overlap values in the group. L/LM and LM/UM habitats are compared using Mann-Whitney U-test

	L	LM	UM
<i>Sericornis</i>	0.90/0 (3/0)*	0.56/0.56 (3/3)	0.40 (1)
<i>Sericornis</i> / <i>Acanthiza</i> / <i>Gerygone</i>	0.78/0.68 (15/11)*	0.59/0.45 (10/8)	0.52 (3)
<i>Rhipidura</i> ¹	0.84/0.84 (3/3)*	0.30/0.30 (3/3)	0.41 (3)
<i>Monarcha</i>	0.5 /0.5 (10/10)	—	—
Thicket-flycatchers ²	0.67/0.53 (10/6)	0.55/0.47 (15/9)	—
<i>Pachycephala</i>	0.69/0.45 (3/3)	0.35/0.22 (6/6)	0.22 (3)

Notes: * Statistically significant at $P = 0.05$.

¹ Excluding *Rhipidura threnothorax* and *R. leucothorax*.

² Including *Tregellasia leucops*.

The whistler and thicket-flycatcher species also show no significant decrease in overlap, as groups, between Lowland and Lower Montane forest. Both Sylviidae and the remaining Muscicapidae show a significant decrease ($P = 0.05$ and $P = 0.002$, respectively). Presumably this indicates that, on average, the species in the latter two groups effectively contracted their niche, this perhaps being correlated with the general trend to reduction in foraging diversity. In contrast, the whistler and thicket-flycatcher species maintain on average, similar overlap relationships with each group. In comparison with the other two groups they are effectively expanding their niches while maintaining their 'spacing'. It may be significant that the whistlers, and at least some of the thicket-flycatchers, have higher than average foraging diversity values and may thus (as generalists) be in the best position to benefit from the absence of the high foraging diversity monarch flycatchers in the Lower Montane habitat.

LOWER MONTANE: UPPER MONTANE FOREST

The feeding behaviour and foraging areas of the twelve species that are common to Lower and Upper Montane forest can be compared in these two structurally distinct habitats (Fig. 11). It is clear that nearly every species shows a reduction in its foraging range in the Upper Montane forest. In general terms, its foraging in one vertical stratum is increased at the expense of the foraging in the others. It might be expected that species not foraging in the middle zone of Lower Montane forest (missing in Upper Montane forest) would not show this trend. Indeed *Sericornis nouhuysi* does show very little difference but, in contrast, *Pachycephala rufinucha*, *Rhipidura atra* and *Peneothello sigillatus* all show a clear increase in foraging in one stratum. This implies that even

species not directly affected by the most obvious structural change in the habitat (there are almost certainly more subtle changes that do affect them directly) respond to the change in foraging stations of the species which are directly affected, presumably through competitive interactions.

It could still be a possibility that the overall trend might be an artefact introduced by the reduction in the number of available foraging stations consequent on the loss of the middle storey. This can be investigated using the foraging diversity indices, as those values are a function of the number of available foraging categories and are thus directly comparable in the two habitats. The tendency to reduced foraging diversity in the upper habitat is then shown to be highly significant ($P = < 0.005$, Wilcoxon matched pairs test).

We can also examine the foraging overlaps between the twelve species common to both habitats. This is not such a clear-cut test since what is being measured, in a sense, is whether the twelve species are better 'spaced-out' from one another in Upper Montane forest than they are in the Lower Montane forest. In the latter habitat, however, they are in the company of up to 14 other species which will inevitably create competitive pressures of their own, unrelated to those created by the species that occur in both habitats. There is still a distinct trend towards reduced overlap in Upper Montane forest which is, however, not significant ($P = > 0.1$, Wilcoxon matched pairs test). Even then the comparison is not fully realistic as the reduction of foraging categories (from 31 to 24) has artificially made it proportionately more difficult for species to maintain an equal overlap index. If the Upper Montane forest overlap values are corrected in proportion to the foraging category reduction then the overlap between pairs of species in the Upper Montane forest is just significantly less ($P = 0.07$, Wilcoxon matched pairs test) than the overlap between the same pairs of species in the Lower Montane forest. This confirms the earlier suggestion that species can respond to changes in the foraging areas of other species by modifying their own feeding activities.

The relative reduction in foraging diversity and overlap must together play a part in maintaining some level of segregation from competition between the species in Upper Montane forest. Thus, considering the small gleaners, *Acanthiza* still shows considerable overlap with *Sericornis papuensis* but differs in its greater use of the upper stratum and restriction to the outer portions of the vegetation. *S. nouhuysi* remains mainly in the undergrowth but must still overlap *Eugerygone*. The larger gleaning species (still complementary to the smaller ones) maintain substantial separation, *Pachycephala modesta* mainly in the uppermost storey, *P. schlegelii* in the lower storey and *P. rufinucha* in the undergrowth. *Peneothello sigillatus*, virtually only a gleaner in this habitat, is the common species of the ground cover.

The remaining species can all be considered as flycatchers; only two species show any (at most 30%) flycatcher-gleaning. Separation is well maintained, with *R. atra* predominantly (though rather sparse) in the undergrowth, *R. brachyrhyncha* in the lower storey and *R. albolineata* in the upper storey, which it shares with the smaller *Petroica bivittata*. The latter is quiet and unobtrusive making frequent brief sallies whereas the fantail is ubiquitous and indulges in the complex flycatching behaviour typical of the genus.

SPECIES COMPOSITION AND ALTITUDE

The foraging diversity indices, together with the figures, in particular Figure 7, a, b, c, can also be used to compare the nature, as defined by their utilization of feeding stations, of the species present in the three main habitat categories.

One point that emerges clearly from this comparison is that species are not completely randomly distributed with respect to the foraging diversity values. The species at the margins of Figure 7, while showing a considerable range of values, include nearly all those with really low diversity indices. Conversely the central area of the figures nearly only

contains species with diversity values much higher than the average. This distribution is hardly surprising because these figures diagrammatically portray one aspect of foraging diversity, that of the foraging technique, and give a rough indication of average vertical position (though not a real demonstration of vertical range), but cannot represent the third dimension of horizontal position. A reasonable conclusion seems that whereas the marginal columns of 'true' flycatchers and gleaners include both specialist (low diversity index) and generalist (high diversity index) species, the central area contains generalists.

This finding is of particular interest when Figure 7, a, b and c are compared. Considering first Figure 7, a and b, the reduction in species diversity from 31 Lowland to 26 Lower Montane species is accompanied by little change in the number of species in the marginal columns (i.e., 4 'true' flycatchers and 12 'true' gleaners in each) so that the reduction is due to the disappearance of species (by the above definition, generalists) from the central area. Furthermore the species that disappear, in the sense either of no longer occurring, or not being directly ecologically replaced, in the Lower Montane forest are those with the highest foraging diversity indices viz., five *Monarcha* species, two *Rhipidura* species and *Poecilodryas hypoleuca*.

Because the overall distribution of diversity index values are not significantly different ($P = > 0.1$) between the two habitats there is presumably a slight expansion in the foraging diversity of some species or replacement species—particularly perhaps whistlers and thicket-flycatchers—though not enough to obscure the existence of a general tendency to decreased foraging diversity. Equally it is clear that no species in Lower Montane forest expand their foraging activities to take over the role filled by the *Monarcha* flycatchers in the Lowlands.

Comparison of Figure 7, b and c, shows the process taken a stage further. With the substantial species diversity reduction from 26 to 12 in Upper Montane forest there are still two 'true' flycatchers and seven 'true' gleaners with the other three species remote from the central area. Again the species not replaced are those with much higher than average foraging diversity values, e.g., *Tregellasia leucops*, *Peneothello cyanus*, *Monarcha axillaris* and *Poecilodryas albonotata*—there are only two Lower Montane species with higher values than these. As in the previous comparison the decrease in foraging diversity is not significant ($P = > 0.1$) when all species are compared but there is clearly no tendency for species to expand their foraging activities to duplicate the habits of *Tregellasia leucops*, *Poecilodryas albonotata* and *Monarcha axillaris* in the Lower Montane forest.

In short there seems to be a distinct tendency for certain types of generalist species—chiefly those with 'intermediate' (flycatcher-gleaning) foraging patterns—to disappear at progressively higher altitudes in forest. There are two likely explanations for this situation. On the one hand the flycatcher-gleaning niche may be filled at higher altitudes by species unrelated to those considered here. The only real candidates might be the mainly insectivorous (partly frugivorous) small and medium-sized honeyeaters of the genera *Ptiloprora*, *Oreornis* and perhaps even the larger *Melidectes* species. At least some of these species occasionally flycatcher-glean (perhaps rather clumsily) and many are particularly common at higher altitudes.

On the other hand environmental parameters, such as changes in habitat structure or prey availability may be primarily responsible. Orians (1969) has shown that an important difference between temperate and Neotropical avifaunas is the much greater number of tropical species that catch insects by hovering (in which category he includes both truly hovering species such as hummingbirds Trochilidae and species that would be flycatcher-gleaners in my terminology). Although such species are very common in Lowland forests they are among the first to disappear as the altitude increases. He also suggests that two factors may be largely responsible for this situation.

It is noted that gleaning species are restricted in leaf-foraging to what they can reach from branches, twigs and perhaps petioles of larger leaves. In Lowland forest this will

leave many central areas of the predominantly large leaves in this habitat 'unexploited', and hence particularly available for the flycatcher-gleaners. Since average leaf size decreases with increasing altitude the amount of unexploited leaf area for the flycatcher-gleaners will similarly decline.

The second factor is related to the fact that species feeding by hovering seem to prefer to take larger insects, at least than the gleaning species. Janzen (quoted in Orians 1969: 790) has found that there are fewer large insects per unit area in Neotropical Montane forest than in the Lowland forest. Thus it must become increasingly difficult for species dependent on catching large insects to maintain themselves at higher altitudes.

The situation in New Guinea appears to parallel this. Thus the altitude distribution of flycatcher-gleaners is similar to that of the Neotropical hovering species, and there exists a similar gradient in leaf-size. In addition it appears that in New Guinea *Pachycephala* species (gleaners) of similar size to *Monarcha* species (flycatchers-gleaners) were consistently taking smaller prey. This may be correlated directly with their feeding techniques, the nearly continuously mobile gleaners snapping up anything within reach, more or less irrespective of size, whereas the flycatcher-gleaners (and flycatchers) keeping watch from a perch may, whenever possible, select items offering a good return for the energy expended in capturing them.

In view of all this it seems reasonable to accept that a reduction in the abundance of preferred diet, a disappearance of much of the favoured foraging niche and perhaps also competition from less closely related species which also sometimes use flycatcher-gleaning (but have more catholic dietary preferences), all combine to restrict the opportunities in Upland forests for species that are neither sallying flycatchers nor gleaners.

CONCLUSIONS

After a preliminary analysis of one aspect of the biology of some members of an avifauna rather poorly known from the ecological and behavioural point of view, it is perhaps unwise to draw many firm conclusions, beyond stating that the use of different feeding methods and stations is of considerable importance in enabling otherwise very similar species to co-exist.

Comparison of species morphological measurements with their feeding patterns does suggest the existence of some correlations (although there appear to be fairly frequent exceptions). Particularly within genera there seems a general tendency for heavier species to forage either nearer the central areas of trees or nearer the ground, and for species with longer tarsi to feed closer to the ground. Weight restrictions seem less important for flycatchers, many of which have notably long wings and/or tails. Amongst relatives, larger-billed species appear to feed nearer the ground and/or nearer the inner zones of the foliage. The relationships between all these, and other, morphological factors and foraging techniques and stations is very complex and a detailed analysis is to be presented elsewhere (Croxall in prep.).

This study does emphasize, however, that whether differences in species foraging patterns are examined from the standpoint of feeding behaviour, or vertical and horizontal habitat divisions, many gradations of behaviour are observed and nearly all foraging areas are utilized, usually by several species. Thus in Lowland forest 29, and in Lower Montane forest 23, out of the 31 foraging categories are used; in Upper Montane forest 18 out of 24 are utilized. The occurrence of unused, or little used, stations is either due to restrictions placed by the habitat on the employment of certain techniques—e.g., flycatching and flycatcher-gleaning from the ground and the scarcity of flycatchers in the undergrowth—or to the absence of species using a particular technique and/or foraging area—e.g., the lack of ecological counterparts, in Lower and Upper Montane forest, to the Lowland *Monarcha* flycatchers. In contrast the absence of species totally confined to the ground can

probably be traced to competition from exclusively ground-dwelling members of the Turdidae and Timaliidae.

In short, there exists an immensely complex pattern of interdigitating use of available feeding areas by birds showing a variety of foraging habits. Many examples of this have been cited in the preceding sections. In particular there are several congeneric pairs of species, within a habitat, showing essentially mutually exclusive vertical foraging preferences (e.g., *Sericornis nouhuysi* and *S. papuensis*, *Pachycephala modesta* and *P. rufinucha*, *Rhipidura albolineata* and *R. atra*) and on a more general scale the thicket and monarch flycatchers, with both groups showing similar horizontal preferences but hardly overlapping vertically in the vegetation column. In contrast, the warblers and whistlers, which show very similar vertical foraging ranges are almost exactly complementary in their horizontal preferences: the former occur in the inner and middle tree areas, the warblers on the outer branchlets and twigs. In addition there are many flycatchers and gleaners that show similar preferences in vertical and horizontal feeding stations but differ dramatically in their feeding technique.

These examples should not, however, obscure the fact that the results of the present study seem to show many cases of substantial overlap between pairs of related species. There are though a number of ways in which this analysis may have generated artificially high overlap values.

First it has been assumed that all 50 rainforest species are present in one general locality, between sea level and the timber-line. Tropical rainforest species are well known to have spotty geographical distributions although these are often of a microgeographic nature. It is still possible that many fewer than 50 species co-occur in practice but the evidence of three field studies seems not to support this. On the south slopes of Mt Albert Edward (Mayr & Rand 1937), 44 of the species analysed in this paper were found, with two other rainforest species I did not encounter, and four more were recorded in a disjunct forest area nearer sea level. On the north slopes of the Snow Mts (Rand 1942b) 48 of the 50 species were recorded, with four other forest relatives that I did not record. At Karimui 48 species (plus one other relative that I did not see) were recorded (Diamond 1972). Nearly all the species I have discussed (and/or their close relatives) are thus capable of occurring in the same general area. This cannot, however, exclude the possibility that fewer species than I have predicted may actually co-occur in local parts of this area.

Second there are clearly additional ways in which the behaviour, ecology and the habitat of the birds may be further subdivided. I have already drawn attention to a possible subdivision of the flycatcher-foraging habit and for gleaning species more precise preference for branchlets, twigs, leaves, etc. could perhaps be established. It may become difficult to establish the functional importance of some of these very small-scale differences.

There is also the possibility that species may be distinct in the precise composition of their diet. Presumably feeding behaviour and preferred foraging site inevitably introduce some selection of particular kinds of insect, but it would be difficult to collect adequate data under field conditions to demonstrate the level of significance.

Neotropical rainforest studies (e.g., Orians 1969) have suggested that the undergrowth stratum may be further subdivisible with respect to the foraging activities. In New Guinea, although no species is confined to the undergrowth, it might be possible better to distinguish those which use the ground-cover and lower undergrowth, as opposed to the lower storey and upper undergrowth, if this stratum were subdivided. There are numerous other ways in which habitat might be further subdivided, but it is important that some relevance to vegetation structure should be maintained.

Third, I will have underestimated the incidence of strict altitudinal segregation of species within my broader altitude zones. The importance of altitude exclusion of related species in the tropics has recently been emphasized by Terborgh (1971) who found that, with Peruvian rainforest birds on an altitudinal gradient, major ecotones account for less

than 20%, but altitudinal (competitive) exclusion for 33%, of species distributional limits, the remainder being attributed to gradually changing conditions along the gradient. Diamond (1972) has also sought to demonstrate the ubiquity of altitudinal segregation in New Guinea birds, but although aware of the importance of this mechanism I have basically only applied it in a very simple way (i.e., the division into Lowland and Upland species). There is still insufficient accurate information available as to which species strictly exclude each other (and the situation between pairs of species does not always appear to be the same in different parts of New Guinea), and hence many decisions would be rather arbitrary and subjective. I have noted the cases for which the evidence is nearly unequivocal and made allowances for these in the numerical analyses also (see Appendix 2) and as more information accumulates it will become easier to determine which species are actual, as opposed to potential, competitors. An interesting and important point arises from cases of altitudinal segregation within my two main altitudinal zones. In many cases, as can be seen from Appendix 2, the pairs of species for which all the evidence points to altitudinal segregation are those which show amongst the highest overlap values in the group in question.

This can be tested by comparing, for each species, its values for foraging overlap with the species with which it co-exists with the potential foraging overlap values with those species from contact with which it is excluded by differing altitude ranges. If the mean values for each of two sets of figures are compared (see Appendix 3) most species show a smaller mean overlap with their co-occurring species than they do with those from which they are segregated by altitude. This trend is highly significant ($P = < 0.001$, Wilcoxon matched pairs test), and is precisely what one might expect if the species most similar in foraging habits and preferences were completely segregated whereas less similar species co-exist. This provides a suggestion of positive evidence that the species with the most closely similar requirements cannot co-exist—a fundamental tenet of ecology but one that is most often supported by evidence showing that species with different requirements can co-exist.

Diamond (1972:30) has also made the point that 'the correlation between degree of morphological similarity and strictness of altitude segregation . . . suggests that strict altitude segregation was the first sorting mechanism to develop . . . and that some degree of altitudinal overlap became possible only as further evolution and morphological divergence led to other ecological differences'. I feel an alternative, if related, viewpoint is also possible. I would envisage the altitude overlap between a closely related pair of species, coming together after evolving in isolation, being initially determined by the degree and nature of the ecological (and perhaps behavioural) differences that have been acquired during this isolation. Thus if the two species are virtually identical in habits either one species will eliminate the other or, if it is feasible, strict altitudinal segregation will take place. With less identity in habits a degree of altitudinal overlap may be initially possible but the nature of the continued co-existence of both species will be determined by the subsequent course of evolution of these habits. Thus widening divergence in habits should allow greater altitudinal overlap, whereas no, or even initially very slow, divergence may cause the gradual reduction of the altitude overlap either to a more 'acceptable' level or to strict altitude exclusion. Clearly, whichever way one examines the situation, the end result is that competition between related species determines the nature of their altitudinal contact and is responsible for altitude exclusions.

In summary, I feel, notwithstanding the problems raised above, that the often high degree of overlap shown between related species in this analysis need not necessarily be unusual for tropical insectivorous birds. Clearly the 'acceptable' degree of overlap will be different for each species pair but high overlap values, if not anomalous, may well contribute to the existence of high tropical avian species diversity. It is appropriate to conclude with a few remarks on this.

Pianka (1966) and MacArthur (1969) have reviewed hypotheses put forward to account for the high species diversity in the tropics. Although they note that the various explanations are not mutually exclusive, most attention has centred on the idea that tropical climates are more stable and predictable (Slobodkin & Sanders 1969), allowing species to be packed closer together, i.e., greater overlap or smaller niches (MacArthur & Levins 1967), and that in the more productive tropics what were marginally scarce resources become adequate to support new species (MacArthur 1969).

Rosenzweig (1968) has shown that evapotranspiration, greatest in the tropical lowlands (Holdridge 1967), is clearly correlated with net production and Orians (1969) has noted that, by analogy with altitudinal gradients in the tropics, one might expect that stronger winds, lower absolute insect numbers (and smaller diversity), smaller leaf-size, and other factors, contribute to lower bird (or at least insectivore) species diversity in temperate regions. The role of the structural complexity of the habitat (e.g., foliage height diversity), much discussed by MacArthur (e.g., MacArthur & MacArthur 1961), seems of less certain importance, some studies finding positive correlation (Karr 1968, Karr & Roth 1971) but others failing to find a correlation with species diversity (Howell 1971), while other workers have doubted the underlying reality of the idea (Snow & Snow 1971).

In this study the altitude gradient from the more temperate Upper Montane forest, with least species diversity, to the fully tropical Lowland forest, with greatest species diversity, is accompanied by increases in foraging diversity and overlap. Habitat factors are very likely to influence this and have been discussed earlier, but the trend would seem to be evidence for the view that although tropical species show greater niche overlap they do not necessarily have smaller niches.

As MacArthur (1969) had recognized, with considerable overlap in resources and close packing, tropical species will tend to have more uniform abundance and their existence to become more precarious, causing the spotty geographical distributions. A number of factors may combine to permit high levels of niche overlap and the consequent tight species packing and high species diversity. The pattern demonstrated here, of numerous species whose resource-exploitation niches are interdigitating and multidimensional, may reflect a similarly complex balance of competitive advantages. Any element of seasonality and fluctuation within a largely stable and predictable environment may enable those species exploiting particularly marginal resources to persist for a considerable time before elimination by competitively superior species. It also seems plausible that the tropical environment may be sufficiently lacking in homogeneity to ensure that a resource that is marginal in one area may be sufficient in another. Hence a species gradually displaced in one area may be the superior competitor in another area—at least until its resources in that area are adversely affected by the inevitable fluctuations in the environment. Such a situation, with species, particularly perhaps those dependent on relatively marginal resources, showing differential competitive ability in various parts of their range coupled with slow rates of exclusion and displacement permits tighter packing of species (and maximum efficiency of habitat utilization) than might be predicted if more rigorous competitive exclusion was the rule.

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SUMMARY

Fifty species of insectivorous warblers Sylviidae, flycatchers Muscicapidae and whistlers Pachycephalidae were studied in primary rainforest at various localities in New Guinea. The structure of the various forest types is described and the birds' feeding ecology and behaviour analysed by recognizing three main foraging techniques and five horizontal and three vertical basic structural divisions of the habitats.

Altitudinal ranges of the species are assessed to determine potential co-existence and they are divided into lowland and lower montane groups (either side of the main avifaunal discontinuity at 1500 m) with a third small group occurring in both areas and a fourth group of 12 lower montane species that occur also in the structurally much simpler Upper Montane forest.

The feeding behaviour and ecology of the species within each major habitat are compared, with particular attention to taxonomically related and ecologically similar species. Other important considerations—additional behavioural differences, notable morphological distinctions, altitudinal separation of ranges within the habitat—are also noted.

The likely importance of differences in foraging behaviour and feeding sites for reducing competition between related species is amply demonstrated, members of several pairs and groups of species have nearly mutually exclusive preferences. The overall pattern of habitat utilization is, however, extremely complex with nearly all stations used, in a variety of ways, by several species and there are many instances of substantial similarity between pairs of species, often involving congeners.

The calculation of information theory derived indices of foraging diversity and overlap enables more general comparisons between the altitudinally graded habitats to be made and differences related to current ideas on tropical species diversity.

Between Lowland and Lower Montane forest there is a fairly general trend of reduction in foraging diversity and decrease in the mean overlap between species in many genera and groups. The 12 species that continue into the simpler Upper Montane forest show very significantly reduced foraging diversity (compared with their values in lower montane forest) and also less overlap, indicating a different relationship between these species in the absence of the other Lower Montane forest birds. Together these results suggest that the most tropical (i.e., lowland) species show greatest overlap but do not necessarily have smaller niches.

In progressively higher habitats there is a bias to the disappearance of generalist (high diversity index) species. These mainly use flycatcher-gleaning techniques supporting suggestions that the increase in insectivorous species in the tropics is partly due to exploitation of feeding strategies related to hovering. Habitat and ecological factors influencing this are assessed.

The importance of altitudinal isolating mechanisms is also discussed and, amongst the species studied, both on average and in specific cases, those with the greatest similarities in foraging behaviour and ecology are segregated altitudinally and do not co-exist. It is suggested, however, that substantial overlap between many co-existing tropical species may not be abnormal, but rather an adaptation for ensuring maximum efficiency of habitat utilization in the prevailing environmental conditions of tropical rainforest.

APPENDIX 1

New Guinea rainforest warblers, flycatchers and whistlers. Scientific and vernacular names are from Rand & Gilliard (1967). Species bearing serial numbers were observed during this study

Species	Average adult weight (♂+♀) (g)	Habitat ¹	Foraging ² diversity index (L or U/UM)	Locality ³
Sylviidae				
1. <i>Sericornis spilodera</i> ⁴	Pale-billed Sericornis	11.5	L	0.20
<i>S. beccarii</i>	Beccari's Sericornis	12.7	L	B,P
<i>S. virgatus</i>	Perplexing Sericornis	12.7	L	
2. <i>S. nouhuysi</i>	Large Mountain Sericornis	15.5	U	0.39/0.41
3. <i>S. perspicillatus</i>	Buff-faced Sericornis	8.6	LU	0.38
4. <i>S. papuensis</i>	Papuan Sericornis	10.6	U	0.47/0.43
5. <i>S. arfakianus</i>	Grey-green Sericornis	8.6	L	0.20
<i>S. nigroviridis</i>	Black & Green Sericornis	—	L	W
6. <i>Acanthiza murina</i> ⁴	DeVis Tree Warbler	8.5	U	0.29/0.17
7. <i>Gerygone cinerea</i> ⁴	Grey Gerygone Warbler	7.8	U	0.33
8. <i>G. chrysogaster</i>	Yellow-bellied Gerygone Warbler	7.5	L	0.39
9. <i>G. chloronota</i>	Grey-headed Gerygone Warbler	6.3	L	0.43
10. <i>G. palpebrosa</i>	Black-headed Gerygone Warbler	8.2	L	0.42
11. <i>Eugerygone rubra</i> ⁵	Red-backed Warbler	8.9	U	0.46/0.42
12. <i>Phylloscopus trivirgatus</i>	Leaf Warbler	8.6	LU	0.31
				C,W

APPENDIX 1—continued.

Species		Average adult weight (♂+♀) (g)	Habitat ¹	Foraging ² diversity index (L or U/U/M)	Locality ³
Muscicapidae					
13. <i>Peltops blainvillii</i>	Lowland Peltops Flycatcher	29.9	L	0.20	P
14. <i>P. montanus</i>	Mountain Peltops Flycatcher	33.1	U	0.20	W
15. <i>Rhipidura threnothorax</i>	Sooty Thicket Fantail	17.8	L	0.50	W
16. <i>R. leucothorax</i>	White-breasted Thicket Fantail	15.4	L	0.48	B,P
17. <i>R. rufidorsa</i>	Grey-breasted Rufous Fantail	9.5	L	0.435	P
18. <i>R. brachyrhyncha</i>	Dimorphic Rufous Fantail	9.7	U	0.40/0.34	C
19. <i>R. atra</i>	Black Fantail	11.8	U	0.42/0.37	C,W
20. <i>R. hyperythra</i>	Chestnut-bellied Fantail	11.4	L	0.27	P
21. <i>R. albolineata</i>	Friendly Fantail	10.0	U	0.16/0.165	C
22. <i>R. rufiventris</i>	White-throated Fantail	15.6	L	0.30	P,W
23. <i>Monarcha axillaris</i>	Black Monarch Flycatcher	15.7	U	0.44	C,W
<i>M. rubiensis</i>	Rufous Monarch Flycatcher	—	L		
24. <i>M. frater</i>	Black-winged Monarch Flycatcher	21.5	L	0.65	W
25. <i>M. manadensis</i>	Black & White Monarch Flycatcher	22.5	L	0.64	B,P
26. <i>M. guttula</i>	Spot-wing Monarch Flycatcher	17.3	L	0.61	B,P
27. <i>M. chrysomela</i>	Black & Yellow Monarch Flycatcher	18.4	L	0.69	W
28. <i>Arses telescopthalmus</i> ⁶	Frilled Flycatcher	18.8	L	0.62	P,W
29. <i>Machaerirhynchus flaviventer</i>	Yellow-breasted Flatbill Flycatcher	11.5	L	0.31	B
30. <i>M. nigripectus</i>	Black-breasted Flatbill Flycatcher	10.6	U	0.20	C
31. <i>Microeca griseoceps</i>	Yellow-footed Microeca Flycatcher	12.8	L	0.24	W
32. <i>M. flavovirens</i>	Olive Microeca Flycatcher	15.8	L	0.305	P
33. <i>M. papuana</i>	Papuan Microeca Flycatcher	13.6	U	0.40	C
34. <i>Petroica bivittata</i>	Forest Robin Flycatcher	9.0	U	0.165/0.00	C
35. <i>Tregellasia leucops</i> ⁷	Whitefaced Flycatcher	16.8	LU	0.51	C,W
36. <i>Poecilodryas brachyura</i> ⁸	White-breasted Flycatcher	25.1	L		
36. <i>P. hypoleuca</i>	Black & White Flycatcher	18.7	L	0.55	W
<i>P. placens</i>	Olive-Yellow Flycatcher	25.6	L		
37. <i>P. albonotata</i>	Black-throated Flycatcher	37.2	U	0.415	C
38. <i>Peneothello sigillatus</i> ⁸	White-winged Thicket Flycatcher	22.2	U	0.335/0.33	C
<i>P. cryptoleucus</i>	Grey Thicket Flycatcher	18.9	LU		
39. <i>P. cyaneus</i>	Slaty Thicket Flycatcher	25.3	LU	0.47	C
40. <i>P. bimaculatus</i>	White-rumped Thicket Flycatcher	23.2	L	0.27	W
41. <i>Heteromyias albicularis</i> ⁸	Ground Thicket Flycatcher	32.9	U	0.30	C
<i>Pachycephalopsis hattamensis</i> ⁸	Green Thicket Flycatcher	34.6	LU		
42. <i>P. poliosoma</i>	White-throated Thicket Flycatcher	37.4	LU	0.22	W
Pachycephalidae					
43. <i>Pachycare flavogrisea</i>	Golden-faced Pachycare	16.6	L	0.27	B,W
44. <i>Pachycephala soror</i>	Sclater's Whistler	25.5	LU	0.37	C
45. <i>P. schlegelii</i>	Schlegel's Whistler	22.5	U	0.40/0.40	C
<i>P. lorentzi</i>	Lorentz's Whistler	19.4	U		
<i>P. meyeri</i>	Vogelkop Whistler	19.1	LU		
46. <i>P. griseiceps</i>	Grey-headed Whistler	22.6	L	0.51	P
47. <i>P. hyperythra</i>	Rufous-breasted Whistler	28.1	L	0.35	W
48. <i>P. modesta</i>	Brown-backed Whistler	19.1	U	0.49/0.435	PC,W
49. <i>P. rufinucha</i> ⁹	Rufous-naped Whistler	39.3	U	0.33/0.31	C
<i>P. tenebrosa</i> ⁹	Sooty Whistler	46.0	LU		
50. <i>Myiolestes megarhynchus</i> ¹⁰	Brown Shrike-Flycatcher	36.8	LU	0.37	P,C,W

Notes: ¹ L = Lowland, U = Upland, UM = Upper Montane.

² First figure for Lowland or Lower Montane forest, second for Upper Montane forest.

³ P = Port Moresby, W = Wau, C = Central Highlands, B = Bariyer River.

⁴ The genera *Sericornis* and *Gerygone* are very closely related, technically separable only on minor details of wing formulae, and *Acanthiza* is essentially intermediate between them. These three genera can legitimately be regarded as a single taxonomic unit.

⁵ *Eugerygone rubra* has usually been classified with the Sylviidae (e.g., Rand & Gilliard 1967) but Mayr & Gilliard (1954) suggested, on the basis of its juvenile plumage, that it belongs to the Muscicapidae. As its behaviour is basically that of a warbler it is retained, for convenience, in the former position here.

⁶ *Arses telescopthalmus* is often placed within *Monarcha* (Ripley 1964, Diamond 1972), *M. rubiensis* with a tendency to an eye wattle and neck frill—providing the connecting link. In all other respects *Arses* agrees very well with *Monarcha*, better in fact than *M. axillaris*.

⁷ *Tregellasia leucops* was frequently placed in *Microeca* and *Poecilodryas*; this well testifies to its position intermediate between the two genera.

⁸ *Poecilodryas*, *Peneothello*, *Heteromyias* and *Pachycephalopsis* are conveniently collectively designated as thicket-flycatchers and can be regarded as a single unit, for analytical and comparative purposes, especially as distinctions between the component genera are not at all clear; *Poecilodryas* in particular lacks homogeneity. The group is, in some respects, intermediate between the more typical flycatchers and the Pachycephalidae.

⁹ *Pachycephala rufinucha* (and *P. tenebrosa*) have been considered to belong to *Pachycephalopsis* but do seem better placed as a slightly aberrant element in *Pachycephala*.

¹⁰ *Myiolestes megarhynchus* has been treated as a *Colluricincla* (Diamond 1972). Both genera are closely related to *Pachycephala* and the broader concept of *Colluricincla* creates no problems for the present analysis as the only other member of the genus in New Guinea is not found in rainforest.

APPENDIX 2

Foraging overlap indices (R_0); for method of calculation, see text. Species are identified by serial numbers (cf. Appendix 1) in both axes of the tables, and by name in the vertical axes

		Lower Montane forest species																															
		2	3	4	6	7	11	12	14	18	19	21	23	30	33	34	35	37	38	39	41	42	44	45	48	49	50						
1 <i>Sericornis spilodera</i>		-62	.39	.24	.13	.81	.07	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	<i>Sericornis nouhuysi</i>	2				
3 <i>S. perspicillatus</i>			.68†	.84*	.60	.62	.58	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	<i>S. perspicillatus</i>	3				
5 <i>S. arfakianus</i>				.84*	.78*	.51	.79*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	<i>S. papuensis</i>	4				
8 <i>Eugrygone chrysogaster</i>					.36	.95	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	<i>Acanthiza murina</i>	6				
9 <i>G. chloronota</i>						.25	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	<i>Eugrygone cinerea</i>	7				
10 <i>G. palpebrata</i>							.62	.70*	.62	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	<i>Phylloscopus trivirgatus</i>	11				
12 <i>Phylloscopus trivirgatus</i>								.76	.68†	.78	.85	.85	0	0	.96	.27	.54	.30	.95	0	0	0	0	0	0	0	0	<i>Peltops montanus</i>	12				
13 <i>Peltops blainvillii</i>									.37*	.58	.39	.11	.23	.29	0	.27	.88	.89	.92	.26	.63	.87	.06	.06	.06	0	0	0	<i>Rhipidura brachyrhyncha</i>	18			
15 <i>Rhipidura threnothorax</i>										0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	<i>R. atrata</i>	19				
16 <i>R. leucothorax</i>										0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	<i>R. albolineata</i>	21				
17 <i>R. rufifrons</i>											0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	<i>Monarcha axillaris</i>	23				
20 <i>R. hyperythra</i>											0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	<i>Macærithlyncus nigripectus</i>	30				
22 <i>R. rufiventris</i>											0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	<i>Microeca papuana</i>	33				
24 <i>Monarcha frater</i>												.08	.06	.09	.15	.14	.13	0	.66	0	.18	.34	.36	.24	0	0	0	<i>Tregellasia leucops</i>	35				
25 <i>M. mandarinensis</i>												0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	<i>Poecilodryas albomotata</i>	37				
26 <i>M. guttula</i>													.03	.08	.03	.17	.18	.15	0	.30	.48	.52	.77	.60	.51	.49	0	<i>Peneothello stigmaria</i>	38				
27 <i>M. chrysomela</i>														.05	.03	.05	.12	.13	.12	.04	.71	0	0	.30	.48	.30	.77	.23	<i>Heteromyias albispicularis</i>	41			
28 <i>Arses telescopthalmus</i>															.05	.03	.05	.12	.13	.12	.04	.71	0	0	.30	.48	.30	.77	.23	<i>P. cyanus</i>	39		
29 <i>Macærithlyncus flaviventer</i>																0	0	0	0	0	0	0	0	0	0	0	0	0	0	<i>Pachycephalopsis poliosoma</i>	42		
31 <i>Microeca griseiceps</i>																	0	0	0	0	0	0	0	0	0	0	0	0	0	<i>Pachycephala soror</i>	44		
32 <i>M. flavororescens</i>																		0	0	0	0	0	0	0	0	0	0	0	0	<i>P. schlegelii</i>	45		
33 <i>Tregellasia leucops</i>																		0	0	0	0	0	0	0	0	0	0	0	0	<i>P. modesta</i>	48		
36 <i>Poecilodryas hypoleuca</i>																			.08	.24	.26	.19	0	0	.68	.70	.28	.16	.16	<i>P. rufigularis</i>	49		
39 <i>Peneothello cyanus</i>																				.23	.21	.07	.06	.50*	.50*	.50*	.50*	.50*	<i>Myiolestes megarhynchus</i>	50			
40 <i>P. bimaculatus</i>																					.08	.12	.10	.16	0	0	.81	.63	.66	.32	.59	<i>P. rufinucha</i>	
42 <i>Pachycephalopsis poliosoma</i>																																	
43 <i>Pachycephala flavogrisea</i>																																	
44 <i>Pachycephala soror</i>																																	
46 <i>P. griseiceps</i>																																	
47 <i>P. hyperythra</i>																																	
50 <i>Myiolestes megarhynchus</i>																																	
		1	3	5	8	9	10	12	13	15	16	17	20	22	24	25	26	27	28	29	31	32	35	36	39	40	42	43	44	46	47		
		Lowland forest species																															

Notes: * Complete altitudinal range separation.

† Substantial altitudinal range separation, for related species.

APPENDIX 2—(continued)

	2	4	6	11	18	19	21	34	38	45	48	49	Upper Montane forest species
2 <i>Sericornis nouhuysi</i>	0.40	0.19	0.93	0	0	0	0	0.07	0.33	0.14	0.73		
4 <i>S. papuensis</i>		0.73	0.56	0	0	0	0	0	0.46	0.74	0		
6 <i>Acanthiza murina</i>			0.30	0	0	0	0	0	0.49	0.47	0		
11 <i>Eugerygone rubra</i>				0	0	0	0	0.09	0.47	0.18	0.47		
18 <i>Rhipidura brachyrhyncha</i>					0.49	0.61	0.36	0.06	0	0	0		
19 <i>R. atra</i>						0.12	0	0.15	0	0	0		
21 <i>R. albolineata</i>							0.92	0	0	0	0		
34 <i>Petroica bivittata</i>								0	0	0	0		
38 <i>Peneothello signillatus</i>									0	0	0.30		
45 <i>Pachycephala schlegelii</i>										0.34	0.26		
48 <i>P. modesta</i>											0.05		
49 <i>P. rufinucha</i>													

APPENDIX 3

Comparison of species' mean foraging overlap values with co-occurring species (A) and those altitudinally segregated (B). (Seven species, which occur in both major altitude zones, overlap with all, or nearly all, other species and are excluded)

	A	B		A	B
<i>Sericornis spilodera</i>	0.129	0.233	<i>Monarcha manadensis</i>	0.326	0.285
<i>S. nouhuysi</i>	0.197	0.257	<i>M. guttula</i>	0.340	0.301
<i>S. papuensis</i>	0.228	0.217	<i>M. chrysomela</i>	0.289	0.253
<i>S. arfakianus</i>	0.051	0.329	<i>Arses telescopthalmus</i>	0.189	0.214
<i>Acanthiza murina</i>	0.099	0.234	<i>Machaerirhynchus flaviventer</i>	0.292	0.317
<i>Gerygone cinerea</i>	0.160	0.132	<i>M. nigripectus</i>	0.212	0.355
<i>G. chrysogaster</i>	0.251	0.221	<i>Microeca griseoceps</i>	0.274	0.301
<i>G. chloronota</i>	0.250	0.207	<i>M. flavovirens</i>	0.287	0.316
<i>G. palpebrosa</i>	0.271	0.227	<i>M. papuana</i>	0.234	0.382
<i>Eugerygone rubra</i>	0.239	0.304	<i>Petroica bivittata</i>	0.132	0.197
<i>Peltops blainvillii</i>	0.162	0.256	<i>Poecilodryas hypoleuca</i>	0.229	0.278
<i>P. montanus</i>	0.154	0.298	<i>P. albonotata</i>	0.256	0.380
<i>Rhipidura threnothorax</i>	0.266	0.254	<i>Peneothello signillatus</i>	0.080	0.254
<i>R. leucothorax</i>	0.274	0.215	<i>P. bimaculatus</i>	0.176	0.228
<i>R. rufidorsa</i>	0.311	0.323	<i>Heteromyias albispercularis</i>	0.134	0.250
<i>R. brachyrhyncha</i>	0.239	0.391	<i>Pachycare flavigrisea</i>	0.199	0.185
<i>R. atra</i>	0.169	0.359	<i>Pachycephala schlegelii</i>	0.085	0.099
<i>R. hyperythra</i>	0.255	0.306	<i>P. griseiceps</i>	0.127	0.159
<i>R. albolineata</i>	0.135	0.189	<i>P. hyperythra</i>	0.164	0.158
<i>R. rufiventris</i>	0.266	0.307	<i>P. modesta</i>	0.117	0.055
<i>Monarcha axillaris</i>	0.224	0.353	<i>P. rufinucha</i>	0.194	0.198
<i>M. frater</i>	0.216	0.213			

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