

BIRD ECOLOGY IN TEMPERATE RAINFOREST

by

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Submitted in fulfilment of the requirements
for the degree of Master of Science.

UNIVERSITY OF TASMANIA

May, 1978.

ACKNOWLEDGEMENTS

The author wishes to thank the following :

Professor B. Johnson, Dr I.S. Wilson and Mr A.R. Rose for encouragement and guidance.

Dr D. Ratkowski for advice on similarity analysis and for undertaking the computer analysis.

Dr H.F. Recher for much stimulating discussion concerning various aspects of censusing.

DECLARATION

Except as stated herein this thesis contains no material which has been accepted for the award of any other degree or diploma in any university, and that, to the best of my knowledge and belief, the thesis contains no copy or paraphrase of material previously published or written by another person, except where due reference is made in the text of the thesis.

J. G. Thomas

ABSTRACT

Temperate rainforest, dominated by species of Nothofagus, the Antarctic Beech, occurs in South America, Australia and Tasmania, New Zealand, and in New Guinea and some south-west Pacific Islands.

In Tasmania both habitat types and bird species are distributed along a xeric-mesic gradient. The relationships between the habitats have been established by similarity analysis. The number of bird species decreases along the xeric-mesic gradient and no species is restricted to temperate rainforest. Bird species diversity, equitability, dominance index and relative bird density have been determined along this gradient and the effect of foliage height diversity and per cent vegetation cover has been studied. Temperate rainforests in Chile, Tasmania and New Zealand have comparable bird species diversities, equitabilities and dominance indices. The one Patagonian site for which data are available appears to be atypical.

The structure of the Tasmanian temperate rainforest bird community, which consists of more species than hitherto reported, was determined from measurements of patch preference, vertical stratification and feeding behaviour. A sequential method, which can include any number of niche dimensions, was used to determine niche structure and was applied to temperate rainforest communities in other regions. Similarities in niche occupation patterns in Fagus-Acer and Nothofagus forests are high and show evidence of parallel evolution.

There is considerable evidence that Nothofagus forests generally have never been important as a source of bird species and have been unimportant in the evolution of the class.

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PREFACE

Temperate rainforest, dominated by Nothofagus spp., occurs in Tasmania, south-eastern Australia, New Guinea and some south-west Pacific islands, New Zealand and South America and pollen analysis has shown that it formerly occurred in Antarctica.

The present study was prompted by two well-known observational facts. Firstly, in Tasmania no species of bird is restricted to temperate rainforest and, secondly, this forest supports fewer bird species than do other Tasmanian forest habitats. Any attempt to explain these facts must be concerned with aspects of bird ecology along the xeric-mesic gradient which, in Tasmania, largely determines the composition and structure of the vegetation.

Studies of this type, in recent years, have received much impetus from the work of the late Robert MacArthur and his disciples. Many of MacArthur's ideas remain controversial and some are largely unsupported by observational data. Nevertheless, MacArthur has brought a sense of unity to studies of community structure and its dependence on environmental factors and competition. The approach adopted in this study is broadly in the MacArthur tradition.

Nomenclature follows Condon (1975) for non-passerines and Schodde (1975) for passerines except that the Scrubtit is retained in the monotypic genus Acanthornis and the Brown Scrubwren is treated as being specifically distinct. Scientific names are given in Appendix 1.

CHAPTER 1

GENERAL INTRODUCTION

1.1 INTRODUCTION

Although published accounts of birds in temperate rainforest are very few they deal with widely separated localities in South America, New Zealand, Australia and Tasmania. A critical review of the literature is a necessary precursor to deciding the scope of the present study. The three main aspects covered in this review are : 1) the number of bird species and individuals, 2) bird species diversity, and 3) niche occupation and parallel evolution.

1.2 NUMBER OF SPECIES AND INDIVIDUALS

The numbers of bird species inhabiting Nothofagus forests in Chile, Patagonia and Tasmania appear remarkably similar (Table 1). If the various areas of Nothofagus forest have similar structures they would be expected, on the theory developed by MacArthur and his co-workers, to hold similar numbers of species (MacArthur and MacArthur 1961, Cody 1968). However, it is possible that area effects and the vagaries of sampling are important. The Chilean total is derived from an area of 16.5 acres, the Patagonian total from c. 19 acres, and the New Zealand South Island total from seven sites varying in area from 16 to 100 acres, mainly from limited visits. The New Zealand North Island total was obtained over a period of time from an unspecified area. The anomalous Australian total was obtained from an unspecified area in the New England National Park with many visits over a period of time. This may well account for the greater number of species. However, only 24 species were classed as "regular and abundant". The Tasmanian total is based mainly on scanty published data and, in my experience, underestimates the

TABLE 1. The numbers of bird species recorded in southern hemisphere Nothofagus forests.

LOCALITY	NO. OF SPECIES	REFERENCE
Chile	18	Cody (1970)
Patagonia	19	Vuilleumier (1972)
New Zealand-North Is.	21	Caughley (1962)
New Zealand-South Is.	21	Kikkawa (1966)
Australia	24 ⁽¹⁾ -32 ⁽²⁾	Kikkawa <u>et al.</u> (1965)
Tasmania	17	Ridpath & Moreau (1966)

(1) Classed as abundant and regular

(2) Total species recorded.

number of species. In an attempt to resolve the effect of area, if it exists, the number of species recorded in censuses in Chile, Patagonia and New Zealand have been plotted against log. area in Figure 1. A straight line ($S = 9.6 + 1.53 \log A$) was fitted by least squares. However, the value of the correlation coefficient, 0.1619, was not significant. Visual examination of Figure 1 suggests that a straight line could be fitted if the Chilean point and the one abnormally species-poor New Zealand point were omitted. When this is done, there is a linear relation between S, the number of species and log area (A), (Simpson 1964), $S = 8.07 \log A - 0.475$. The correlation coefficient, 0.8382, is significant at the 0.02 probability level. It is concluded that area effects are important but that other effects, at present unknown, also influence the number of species.

Direct comparison of the numbers of species found in Nothofagus forest and some other forest habitats is possible for all localities except Chile. When the habitats are arranged along the xeric-mesic gradient, starting with the most xeric, the figures given in Table 2 are obtained. The New Zealand South Island figures are based on Figure 10 in Kikkawa (1966) which includes a total of 25 species. However, in Table XV of the same paper 32 species are listed as occurring in "native forest". Of the species included in Table XV but "missing" from Figure 10, three species of Kiwi, the Weka and Morepork are shown in Figure 11 as occurring in Nothofagus forest and its edge. (In Appendix 4 of his paper Kikkawa lists only the South Island and Stewart Island Kiwis, both as subspecies of Apteryx australis. Falla et al. (1966) recognise three species, all of which may occur in Nothofagus forests although their

FIGURE 1. Species-area effects. The points relate to censuses of small areas of temperate rain-forest reported in the literature.

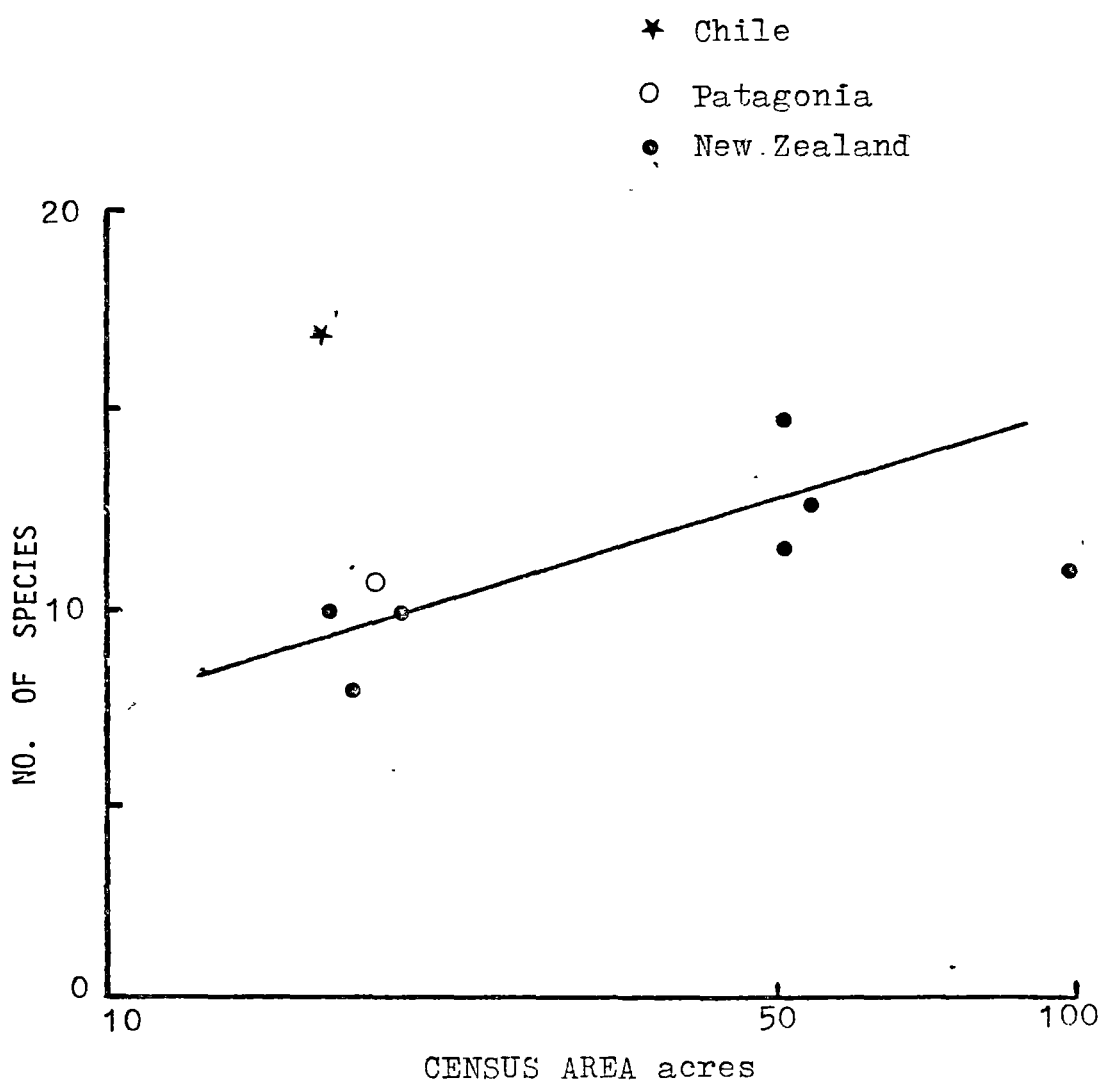


TABLE 2. The numbers of bird species in Nothofagus and other forest habitats (sources as in Table 1). For each locality, the habitats are arranged along the xeric-mesic gradient, the more-xeric habitats being listed first.

LOCALITY	HABITAT	NO. OF SPECIES
Patagonia	Mesophyte forest	19
	<u>Nothofagus</u> forest	19
New Zealand-North Is.	Hardwood forest	18
	<u>Nothofagus</u> forest	21
New Zealand-South Is.	Low hardwood forest	18
	<u>Podocarpus</u> forest	19
	<u>Nothofagus</u> forest	21
Australia (New England)	Grassy forest	26*
	Wet sclerophyll forest	62*
	<u>Nothofagus</u> forest	24*
Tasmania	Dry sclerophyll forest	59
	Wet sclerophyll forest	46
	<u>Nothofagus</u> forest	17

* Species classed as "abundant and regular".

present ranges may not overlap). In the text Kikkawa lists the Australian Harrier as occurring in Nothofagus forest, the Weka as occurring in Nothofagus and Podocarpus forests and the Morepork as occurring in Nothofagus, Podocarpus and low hardwood forests. Thus the totals given for South Island habitats should be treated with reserve.

There appears to be little difference in the number of species occurring in forest habitats in Patagonia and New Zealand. In direct contrast, Australian and Tasmanian Nothofagus forests have fewer species of birds than other forest habitats and the differences are far too great to be the result of sampling vagaries. The number of species decreases towards the mesic end of the xeric-mesic gradient.

Ridpath and Moreau (1966) provide a comprehensive, if subjective, list of the habitat preferences of Tasmanian birds. Although the choice of habitats and allotment of habitat preferences to the individual species require modification, it is shown that no species is restricted to temperate rainforest, i.e. to Nothofagus forest. Similarly, no species recorded by Kikkawa et al. (1965) in Nothofagus forest in the New England National Park is completely absent from all other habitats. In Patagonia, all species listed by Vuilleumier (1972 Table 2) as occurring in rainforest are also listed as occurring in mesophytic and/or montane forests. These forests contain Nothofagus but are structurally different to temperate rainforest. In Chile : "within a limited geographic area, species are extremely widespread and are found in a wide selection of habitats within this range" (Cody 1970 p. 458). In New Zealand, Kikkawa (1966

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p.255) states : "Since the distribution of these species (common land birds) in various forest types is only little known, the classification of habitats used in Table XV is necessarily very broad, yet it shows a wide ecological distribution of common woodland species of both indigenous and naturalized birds, suggesting that these species occupy a variety of habitats with widely overlapping ranges".

Thus, it seems that few, if any, species of birds are restricted to Nothofagus forests although some in South America may be restricted to habitats such as steppe and montane forest that contain Nothofagus.

One problem facing bird ecologists is the delineation of habitats. Among ecologists in general there is still argument whether habitats should be regarded as discrete entities or as a continuum. The continuum concept appears to be gaining ground although some habitats, e.g. pine plantations, are discrete entities and the general idea certainly may be conceptually useful (see, for example, Krebs 1972).

Kikkawa (1968) used similarity analysis to assess the habitat preferences of birds in northern New South Wales. His results, which grouped temperate rainforest with other wet-adapted habitats (sub-tropical rainforest and wet sclerophyll forest), strongly support the continuum concept. A preliminary similarity analysis of the habitat preferences of Tasmanian birds grouped temperate rainforest with the other wet-adapted habitats - wet sclerophyll (eucalypt) forest, mixed Eucalyptus/Nothofagus forest and sub-alpine (eucalypt) forest (see Chapter 2.3).

Just as habitats can be arranged along the xeric-mesic gradient so can birds. Because birds do not "recognise" the transition from wet sclerophyll to Nothofagus forest or Nothofagus to sub-alpine forest, this study is concerned with aspects of avian ecology along the xeric-mesic gradient. In terms of habitat this can be taken primarily as the sequence

dry sclerophyll - wet sclerophyll - mixed forest -

Nothofagus forest - sub-alpine forest

as modified by soil, drainage and (particularly) fire frequency. The transition from Nothofagus to sub-alpine forest may be determined by altitude and temperature gradient rather than by effective rainfall (Chapter 2.2). Dry sclerophyll forest is included because it is the habitat which supports the largest number of bird species in south-eastern Australia and Tasmania and may be important as a source of species (Brereton and Kikkawa 1963). One aim of the present work is to investigate why the number of species decreases along the xeric-mesic gradient.

Darwin (1845) was the first to remark on the paucity of birds in the dark damp rainforests of Tierra del Fuego. Ridpath and Moreau (1966) make similar comments with respect to Tasmanian rainforests. These are, of course, subjective assessments.

Quantitative data are provided by Cody (1970, 1973) for Chile, Vuilleumier (1972) for Patagonia and Kikkawa (1966) for New Zealand (Table 3). The Patagonian value was obtained from a single site and agrees well with the mean value obtained from seven New Zealand sites, bearing in mind the

TABLE 3. Bird density in Nothofagus forests and in some other forest habitats (sources as for Table 1).

LOCALITY	HABITAT	BIRD DENSITY Pairs/100 acres
Chile	<u>Nothofagus</u> forest	294
Patagonia	Mesophytic forest	216
	<u>Nothofagus</u> forest	106
New Zealand- South Is.	Low hardwood forest	175-600, mean 411
	<u>Podocarpus</u> forest	150-188, mean 166
	<u>Nothofagus</u> forest	70-175, mean 123

uncertainties involved in extrapolating the results obtained from censuses of small areas (up to 100 acres). The Chilean result gives a considerably higher density.

No comparable figures are available for Australia and Tasmania. The number of pairs can be calculated (Table 4) for wet and dry sclerophyll forest in New South Wales from figures given by Recher (1969) and for dry sclerophyll forest in Tasmania by Recher et al. (1971) and Thomas (1974). The figures given in Tables 3 and 4 tend to confirm that bird density is lower in Nothofagus forests than in forests with lower rainfall (i.e. on the xeric side of the xeric-mesic gradient). However, bird density in Chilean Nothofagus forest is much greater than in similar Patagonian and New Zealand forests.

1.3 BIRD SPECIES DIVERSITY

Bird species diversity (BSD) can be calculated from the Shannon-Wiener function

$$H = - \sum_{i=1}^n p_i \log_e p_i \quad (1)$$

This function has been used extensively and weights each species according to its relative abundance. Thus, in equation (1) the p_i are the proportions of individuals belonging to each of the n species and H is the measure of diversity.

Cody (1970) obtained a value for H of 2.49 for a 16.5 acre plot of Chilean Nothofagus forest and Vuilleumier (1972) obtained a value of 1.43 for a 7.5 hectare plot of Patagonian Nothofagus forest. These values differ markedly.

No comparable values of BSD have been published for

TABLE 4. Bird density in some Australian and Tasmanian habitats.

LOCALITY	HABITAT	NO. OF SPECIES	BIRD DENSITY Pairs/100 acres
New South Wales	Wet sclerophyll forest	1	290
	Dry sclerophyll forest	2	300-500 mean 400
Tasmania	Dry sclerophyll forest	8	230-575 mean 336

Nothofagus forests in New Zealand, Australia and Tasmania. However, Kikkawa (1966) gives the results of censuses of seven sites in New Zealand Nothofagus forests, ranging from 16 to 100 acres, from which BSD values can be calculated. Values range from 1.97 to 2.44 with a mean of 2.21. BSD appears to be somewhat lower in New Zealand than in Chile although we have only a single value for Chile and this is comparable to the most diverse New Zealand site. BSD in New Zealand is markedly greater than it is in Patagonia.

In Patagonia BSD decreases along the xeric-mesic gradient - 2.14 for mesophytic forest, 1.43 for Nothofagus forest.

BSD values have been calculated along the xeric-mesic gradient for New Zealand from data in Kikkawa (1966), Table 5. BSD appears to increase along the xeric-mesic gradient although the differences in mean values are small.

BSD values for Australian and Tasmanian sclerophyll forests have been calculated (Table 6) from the data of Recher (1969) and Thomas (1974). It appears that BSD decreases along the xeric-mesic gradient, at least between dry and wet sclerophyll forests.

Taking all the data into consideration, it is not possible to predict with any certainty the way BSD varies along the xeric-mesic gradient, if indeed there is a general "rule".

BSD is made up of two components, a) the number of species S , and b) the equitability of the distribution of individuals among the species (Lloyd and Ghelardi 1964). A measure of equitability is given by

TABLE 5. BSD values for New Zealand habitats.

HABITAT	NO. OF SITES	BSD	
		RANGE	MEAN
Low hardwood forest	3 (3 years)	1.86 - 2.45	2.09
<u>Podocarpus</u> forest	6	1.62 - 2.39	2.19
<u>Nothofagus</u> forest	7	1.97 - 2.44	2.21

TABLE 6. BSD values for some Australian habitats.

HABITAT	LOCALITY	BSD	
		RANGE	MEAN
Dry sclerophyll/heath ecotone	N.S.W.		2.13
Dry sclerophyll forest	N.S.W.		2.70
	Tasmania	2.78-2.82	2.80
Wet sclerophyll forest	N.S.W.		2.33

$$\text{Equitability} = H / \log_e S \quad (2)$$

where H is BSD as given by equation (1).

Equitability values calculated for Chilean, Patagonian, Australian and Tasmanian habitats are given in Table 7. Apart from Patagonian habitats, equitability values are clustered around 0.88 to 0.93.

There is a close correlation between BSD and habitat diversity in temperate North America (MacArthur and MacArthur 1961, MacArthur 1964). Recher showed that the same correlation applied to Australian habitats ranging from coastal heath to wet sclerophyll forest. Habitat diversity is measured by foliage height diversity (FHD) which is determined by the proportions of the total foliage area which fall within the horizontal layers 0 - 0.6, 0.6 - 7.6 and >7.6 m above the ground. Biologically, these layers correspond to the herb, shrub and tree layers (MacArthur and MacArthur 1961).

In some tropical areas censuses conform to the northern temperate and Australian relation only if the vegetation profiles are subdivided into four rather than three layers - 0 - 0.6, 0.6 - 7.6, 7.6 - 15.3 and >15.3 m above the ground (MacArthur et al. 1966). These layers correspond to the herb, shrub and two layers of trees.

Cody (1970) suggests that a better fit is achieved for his Chilean data if the vegetation profiles are subdivided into four layers. Chilean habitats, like those in the tropics, support a greater within-habitat diversity which Cody attributes to individuals being more equitably distributed among the species rather than there being more

TABLE 7. Equitability components of BSD.

LOCALITY	HABITAT	EQUITABILITY
Chile	<u>Nothofagus</u> forest	0.88
Patagonia	Mesophytic forest	0.97
	<u>Nothofagus</u> forest	0.60
Australia	Dry sclerophyll forest	0.93
	Wet sclerophyll forest	0.88
Tasmania	Dry sclerophyll forest	0.89, 0.91, 0.93

species.

Recher's work in Australia suggests that the more xeric habitats, up to and including wet sclerophyll forest, should be subdivided into three layers. There is no obvious reason why this should not apply also to the more mesic habitats although mixed Eucalyptus/Nothofagus forest could be exceptional because of its structure with N. cunninghamii forming a closed canopy with an emergent stratum of tall eucalypts. It follows from Cody (1970) that, if birds divide Nothofagus forests in the same way, regardless of locality, it may be necessary to subdivide Australian and Tasmanian Nothofagus forests into four layers. However, the point for Nothofagus forest in Chile falls closer to the regression line of MacArthur et al. (1966) if FHD is calculated on the basis of three layers. Similarly, the fit for N. antarcticus dwarf forest is not improved greatly if the vegetation is divided into four rather than three layers (Cody 1970 Fig. 2).

Vuilleumier (1972) suggests that BSD in Patagonia is greater in less diverse mesophytic forest than in more diverse and dense Nothofagus forest. Vuilleumier relies on a subjective assessment of habitat diversity and appears to place undue reliance on plant species diversity which is not a good indicator of BSD (MacArthur 1964). Vuilleumier further implies, from Ridpath and Moreau's (1966) data, that Tasmanian Nothofagus forest is more diverse than wet sclerophyll forest which, in turn, is more diverse than dry sclerophyll forest. There is no justification for this as Nothofagus forest is structurally simpler than sclerophyllous forests, at least in Tasmania.

1.4 NICHE OCCUPATION AND PARALLEL EVOLUTION

If, other things being equal, BSD is determined mainly by FHD (Cody 1974), forests of similar structure should contain about the same number of species, independent of geographical location and the origins of the avifaunas concerned. Cody (1973) has examined the extent to which bird niches in beech forests show similarities in response to parallel selective forces.

In his comparison, Cody includes both the northern hemisphere beech-maple, Fagus-Acer, and the southern hemisphere beech, Nothofagus, forests. This can be criticised on the grounds that Fagus and Acer are deciduous whereas Nothofagus is evergreen over much of its range and exclusively so in Australia and Tasmania. This is not an entirely valid criticism if the structure of the two formations is similar in terms of FHD and the censuses are undertaken when leaves are present. However, it is not clear whether the structures of the individual forests considered by Cody are similar. Thus, Cody states : "All census areas are alike in that the predominant tree species are beech (Fagus or Nothofagus), other broad-leaf deciduous trees are present (e.g. Acer), and a dense understory of bush-type vegetation slows the progress through the forest for the observer (bamboo-grass Sasa in Japan, the bamboo Chusquea in Chile, cutting grass-Gahnia in Tasmania, and so on)". Apart from the question of whether the dominant trees are deciduous, Cody has obviously mis-read Ridpath and Moreau's (1966) description of Tasmanian Nothofagus forest for they state that the floor is virtually clear apart from in gullies (in which Gahnia does occur) - however see Chapter 2.2. It is, therefore, uncertain whether

Cody is comparing like with like.

In the actual comparison of niche occupation patterns there are errors in transcription (e.g. the Pink Robin is omitted from Tasmania although included as a rainforest species by Ridpath and Moreau); New Zealand rainforests are credited with more species than are listed by Kikkawa (1966); and it is not clear on what authority Australian and Tasmanian species were allocated to the various niches. Cody's contribution illustrates Culver's (1976) assessment of the "MacArthur tradition" of looking for and explaining "the broad patterns of community organisation, often at the expense of detail". I believe Cody's approach to be justified in that it provides a working hypothesis. One of the aims of the present study is to supply some of the detail.

Cody concludes that there are obvious qualitative similarities among the species lists although there are some anomalies. This is hardly surprising in view of the crudeness of some of the data used and possible differences in structure, productivity, historical factors, chance effects, and the effect of basing the comparison on the results of censuses of small areas of different sizes.

1.5 MISCELLANEOUS ASPECTS

References to birds in other areas of Nothofagus forest are very few indeed and many are anecdotal.

In the Otway Range of Victoria Nothofagus forest occupies gullies in wet sclerophyll forest. Emison et al. (1975) list the birds "recently recorded in the area and an

indication of the habitats in which they are likely to occur". A total of 35 species is listed for wet sclerophyll forest but only two, Olive Whistler and Pink Robin, are listed for Nothofagus forest.

Kikkawa (1968) gives additional lists for Nothofagus forest at Barrington Tops and Point Lookout in New South Wales. These lists are incomplete but include eight species additional to those given by Kikkawa et al. (1965) for Point Lookout in the New England National Park.

In New Guinea, Nothofagus forest is confined mainly to altitudes between 2,000 and 3,000 m but can occur at much lower altitudes, e.g. at Lake Kutuba c. 800 m (Schodde and Hitchcock 1968). According to Ridpath and Moreau (1966) these forests "appear to have quite an extensive avifauna". Hitchcock (1964) lists 15 species from undisturbed "primary beech and mixed montane forest". Hitchcock states : "while some species are restricted to certain vegetation zones (e.g. Ducula chalconota and Microeca papuana to primary beech forest), others have adapted to a wide spectrum of ecological niches, with an altitudinal range of up to 3,000 feet". The New Guinea avifauna is characterised by species having patchy distributions including species confined to "mountain islands". Analysis of distributional patterns of New Guinea birds have concentrated on altitudinal ranges rather than on habitats (e.g. Diamond 1972). It can be concluded that Nothofagus forests in New Guinea support a diverse avifauna and that some species are restricted to this habitat. Further, it appears that some species replace related species by one-to-one competitive exclusion.

1.6 SCOPE OF PRESENT WORK

Chapters 2 to 5 are concerned with the avifauna of Tasmanian temperate rainforest. Tasmanian habitats are described in terms of the xeric-mesic gradient and the habitat preferences of Tasmanian birds (Chapter 2). The species comprising the avifauna of temperate rainforest are established in Chapter 3 and their adaptations discussed. Chapter 4 is concerned with the affect of the xeric-mesic gradient on factors such as bird species diversity, bird density, dominance and equitability. Niche overlaps along three niche dimensions are presented in Chapter 5, the community dendrogram is derived and a sequential method is used, permitting the inclusion of any number of niche dimensions, to determine niche structure.

The avian communities of mainland Australian and New Zealand rainforests are discussed in Chapter 6 and compared in Chapter 7. The question of niche structure and parallel evolution in northern hemisphere Fagus-Acer forests and southern hemisphere Nothofagus forests is also considered in Chapter 7.

In Chapter 8 the origins and evolution of the Tasmanian avifauna, with particular reference to the importance of temperate rainforest, are considered in the context of current theories of speciation in Australia. This is extended in Chapter 9 to a consideration of the importance of southern hemisphere temperate rainforests in the evolution of avian species.

The major findings of the study are brought together and discussed in Chapter 10.

CHAPTER 2

TASMANIAN HABITATS

2.1 INTRODUCTION

It has long been recognised (e.g. Gentilli 1949) that the distribution of birds depends more on certain features of the vegetation rather than on the climatic factors which have produced the vegetational features. However, the distribution of plant species is affected directly by climate and climate indirectly controls the distribution of birds.

Although Tasmania is a small island, 26,000 square miles, with a cool maritime climate it has rainfall regimes ranging from 500 mm to >3,050 mm a year (Figure 2). Rainfall is distributed more or less evenly throughout the year and under these climatic conditions climatic moisture factors control the habitats (Gentilli 1949) along a largely unidirectional gradient, the xeric-mesic gradient. Strictly, it is the effective rainfall that controls the vegetation. Effective rainfall represents the moisture balance (precipitation versus evaporation) and is computed from monthly rainfall and temperature data. Temperate rainforest is the expected climax in the super-humid effective rainfall zone (Figure 3) which has an annual effective rainfall of >128 with no dry season. Although the correlation between annual rainfall (Figure 2) and vegetation (Figure 4) is good, largely because there are no dry seasons, it is effective rainfall, which is affected by factors such as altitude and aspect, which must be invoked to account for much of the small-scale mosaic of habitats that occurs in Tasmania that is not fire induced. The presence of gully corridors of rainforest in dry sclerophyll forest can be explained in this way.

FIGURE 2. Rainfall map of Tasmania

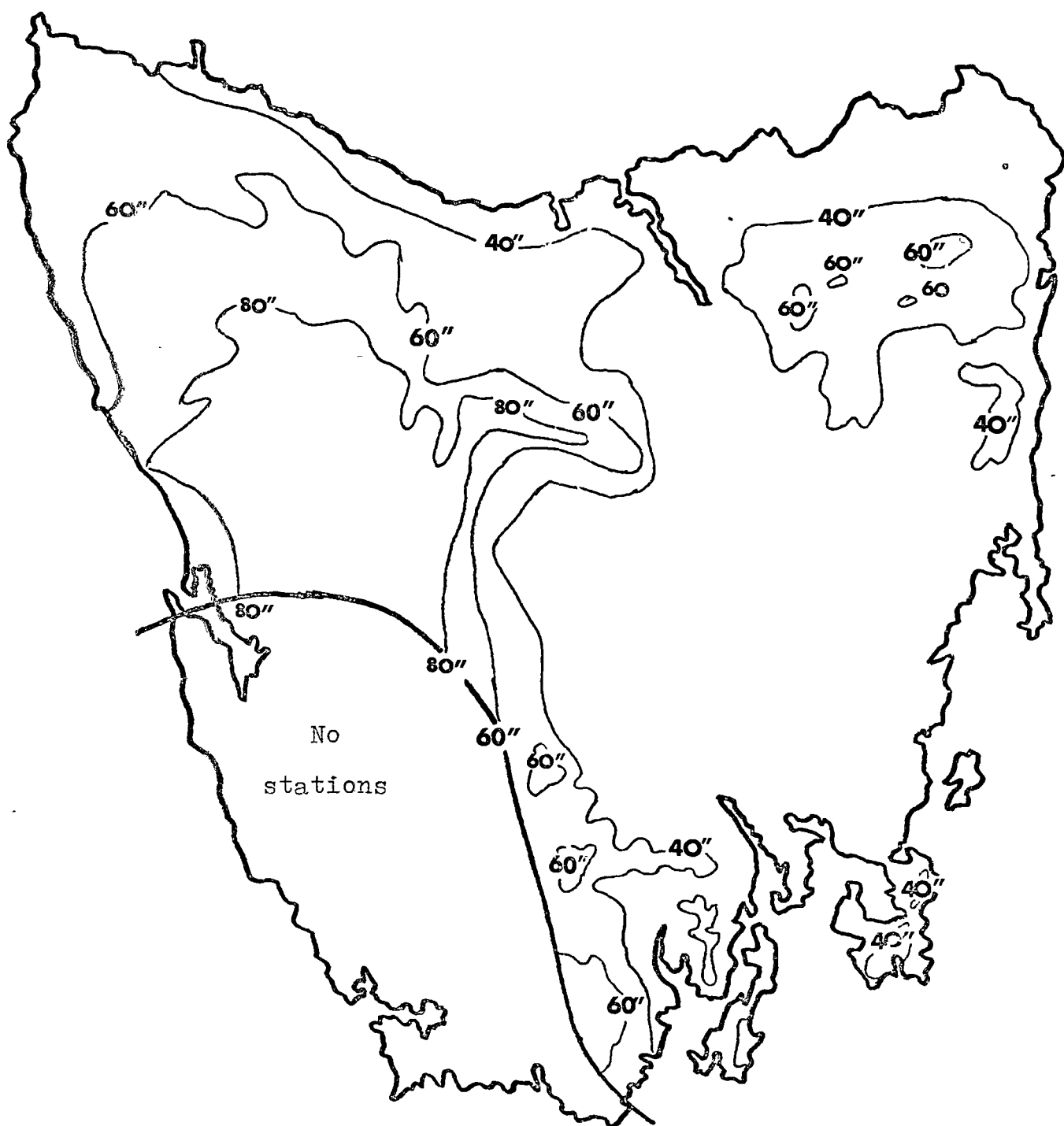


FIGURE 3. Effective rainfall map of Tasmania (modified from Gentilli 1972)

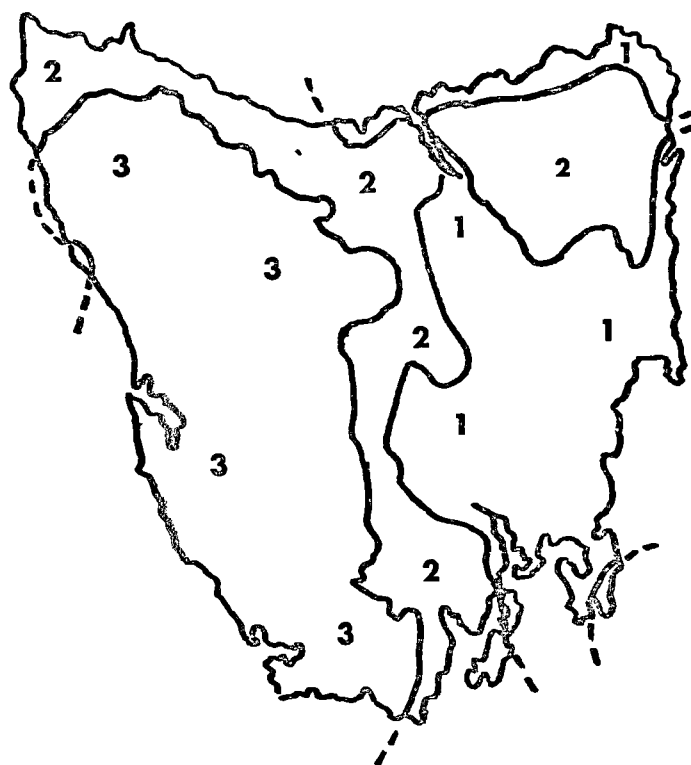
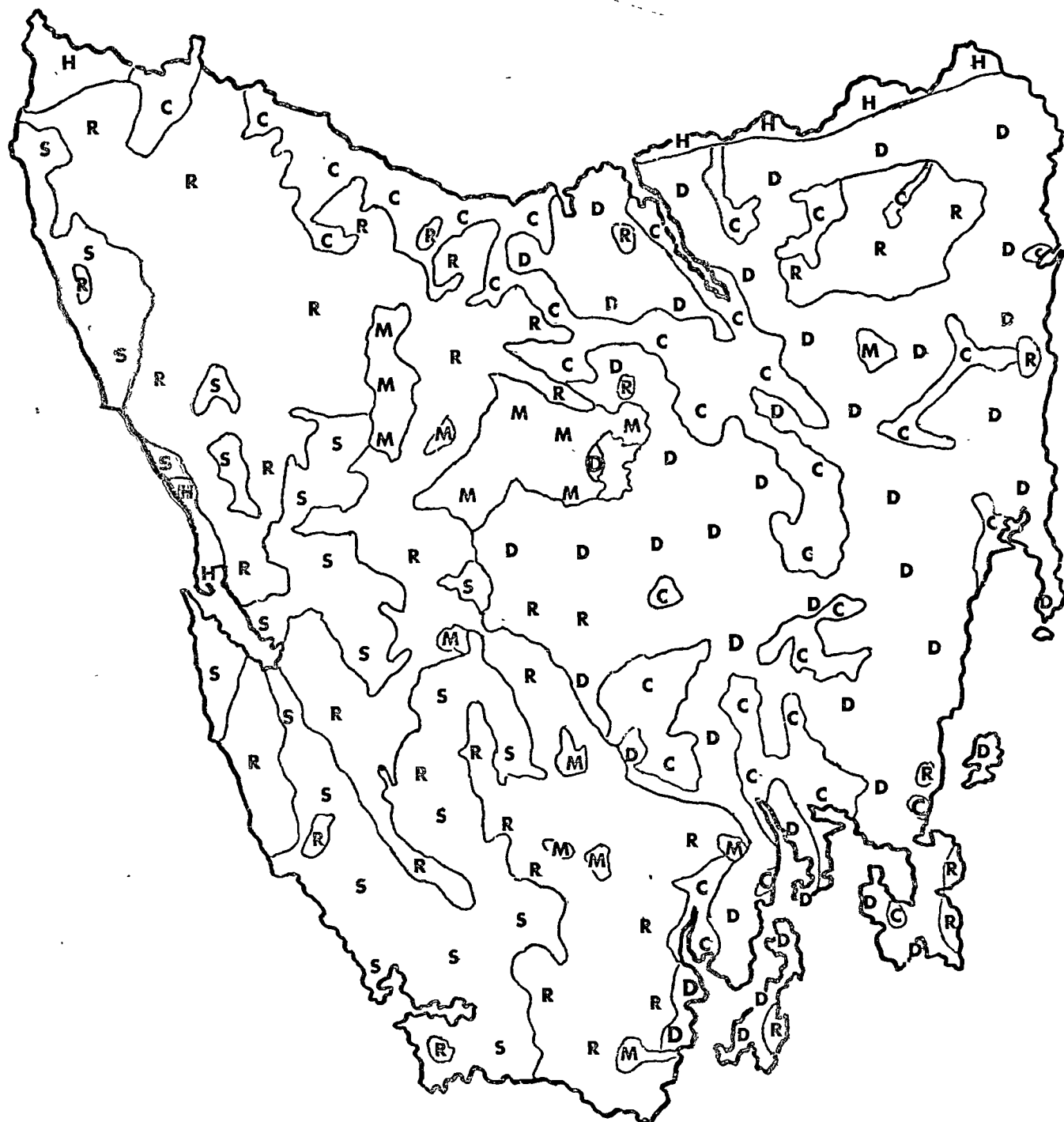


FIGURE 4. Vegetation of Tasmania (after Jackson 1965).

- C - cleared land
- D - dry sclerophyll forest
- H - coastal heath
- M - moorland
- R - temperate rainforest (including wet sclerophyll forest)
- S - sedgeland



Temperate rainforest occurs in South America, New Zealand, Australia, New Caledonia and some other south-west Pacific islands, and New Guinea as well as in Tasmania. The dominant trees are species of Nothofagus and the forests are often referred to as Nothofagus forests. I prefer the term temperate rainforest as other trees, e.g. Dacrydium, Podocarpus, Phyllocladus, may be dominant locally.

2.2 TASMANIAN HABITATS AND THE XERIC-MESIC GRADIENT

There is much evidence that the number of bird species, strictly bird species diversity, is determined largely by the structure of the vegetation (MacArthur and MacArthur 1961, Recher 1969 and many others). Tasmanian habitats are distributed along a largely unidirectional climatic gradient (Jackson 1965, 1968, 1973).

Figure 4 is the vegetation map of Tasmania most often quoted by ornithologists (e.g. Ridpath and Moreau 1966, Keast 1970). Comparison of Figure 4 with the map of rainfall (Figure 2) shows that the unidirectional climatic gradient is dependent largely on rainfall. It would be more accurate to correlate vegetation with effective rainfall (Gentilli 1949) which depends on local factors such as aspect, soil, drainage, etc., and which can change rapidly in a short distance, even along slight rainfall gradients. This results in Tasmanian habitats occurring in a mosaic pattern which, in turn, would be expected to determine the local distribution of bird species within Tasmania. The mosaic has been accentuated further by the use of fire by both aboriginal and European man.

It is possible to classify vegetation in many ways, often in minute detail. However, the important determinant which must not be lost sight of is : how does the structure of the vegetation affect bird distribution ? Experience has shown that quite coarse divisions can be used without loss of precision. The divisions used in this study were chosen mainly in accordance with the habitat classification of Ridpath and Moreau (1966) which has been used subsequently by other workers (e.g. Green 1977). However, three major modifications have been made.

Ridpath and Moreau, following Jackson (1965), consider wet sclerophyll forest to be an ecotone between dry sclerophyll forest and temperate rainforest. However, wet sclerophyll forest varies widely in structure and composition and I have divided it into three categories : wet sclerophyll forest, mixed forest and wet scrub. Wet sclerophyll forest is eucalypt forest with a dense shrub and/or low tree layer with few if any mature N. cunninghamii. Mixed forest (Gilbert 1959) has a substantial proportion of N. cunninghamii and other rainforest trees in the tree understory with an emergent stratum of tall eucalypts. The inclusion of wet scrub, which includes the "wet mallee" of Jackson (1965), in wet sclerophyll forest seems unsatisfactory because the dominant eucalypts of wet sclerophyll forest (e.g. E. obliqua, E. delegatensis, E. regnans) are tall trees which may grow to a height of 90 m whereas E. nitida, the dominant tree of wet scrub, is much smaller, 12 - 20 m, and may have several stems arising from an underground lignotuber. A further reason for treating wet scrub as a distinct habitat is that Ridpath and Moreau consider wet sclerophyll forest

forest as a warm-dry adapted habitat. The distribution of E. nitida, as given by Jackson (1965) under the name E. simmondsii, and its often intimate association with wet tussock sedgeland (button grass plains) suggests that wet scrub should be considered a cold-wet adapted habitat and separated from both wet sclerophyll and mixed forests.

Low-altitude heath (here termed coastal heath), savannah woodland, temperate rainforest, dwarf mountain forests and shrubberies (here termed dwarf coniferous forest) and sub-alpine forest, as defined by Ridpath and Moreau, are retained. Wet tussock sedgeland and high moors were treated by Ridpath and Moreau as if they were "pure" habitats. Wall (1972) has pointed out that watercourses in moorland contain scrub, often dominated by eucalypts, and if this is included the number of bird species inhabiting moorland increases. Similarly, sedgeland contains patches of scrub, often dominated by E. nitida, Banksia marginata, and Leptospermum lanigerum. The bird species associated with these patches of scrub increase the number of species occurring in sedgeland. As the present concern is with macro- rather than micro-habitats, and because moorland and sedgeland occur commonly as a mosaic interspersed with patches of scrub, they have been extended to allow for this and the inevitable edge effects.

A brief description of habitats follows. Where this classification differs from that of Ridpath and Moreau, their name is given in brackets. The structural classification is that of Specht (1970).

COASTAL HEATH (Low-altitude heath)

Mainly in the north, west and east. Consists of a stunted shrub complex of Eucalyptus spp., Banksia marginata, Casuarina, Hakea, Leptospermum spp. with a dense low shrub layer, particularly of Epacridaceae and Leguminosae. Probably results from a long history of burning the original eucalypt forest and not a climax formation.

SAVANNAH WOODLAND

Woodland, low woodland, open-woodland and low open-woodland. Eucalyptus pauciflora or E. viminalis are usually the dominant trees in plains of native grasses which, over large areas, have been converted to improved pastures. Has been extended by the clearing of dry sclerophyll forest.

DRY SCLEROPHYLL FOREST

Mainly open-forest and low open-forest. Eucalyptus forest which is the dominant vegetation from sea-level to 500 m where the rainfall is 550 - 800 mm. The open shrub layer is short with a tendency to xeromorphism.

WET SCLEROPHYLL FOREST

Tall open-forest, open-forest and low open-forest. Eucalyptus forest usually extending from 250 - 900 m in areas where the rainfall is 800 - 1300 mm. There is a tree understory and/or a well-developed shrub layer.

MIXED FOREST

Areas where eucalypts are sparsely emergent, forming a tall open-forest, from a closed-forest understory, mainly of rainforest species including Nothofagus cunninghamii. A fire determined disclimax which occurs in many areas where temperate rainforest would be expected to be the climatic climax (Jackson 1965).

TEMPERATE RAINFOREST

Tall closed-forest, closed-forest and low closed-forest,

tall open-forest, open-forest and low open-forest. Dominated by the Antarctic Beech Nothofagus cunninghamii and includes restricted areas where other trees, e.g. Dacrydium franklinii (Huon Pine), Phyllocladus aspleniifolius (Celery-top Pine) and Acacia melanoxylon (Blackwood), may be locally dominant. In closed-forest the light entering may be so reduced that much of the floor is clear apart from a few cryptograms, e.g. Blechnum spp. Elsewhere, well-developed shrub layers are present, including Horizontal Anodopetalum biglandulosum and Cutting Grass Gahnia psittacorum. Lesser trees of local importance include Leatherwood Eucryphia lucida and Native Laurel Anopterus glandulosa. Occurs mainly in the west and north-east from sea-level to 1200 m where the rainfall exceeds 1040 mm. Good descriptions of temperate rainforest and the importance of fire in determining its distribution are given by Crowden et al. (1976) and Kirkpatrick (1977).

SUB-ALPINE FOREST

Open-forest, dominated by Eucalyptus spp. and occurring from 900 - 1200 m. Often stunted, forming tall-shrubland, with a rich shrub layer.

DWARF CONIFEROUS FOREST (Dwarf mountain forest and mountain shrubberies)

Closed-scrub and low closed-forest. Dominated by endemic conifers that may reach 10 m high. Often as a closed-scrub community in moorland. Occurs above 1000 m.

MOORLAND (High moors)

Occurs above 900 m. Mountain tops have a grassland community dominated by Snow Grass Poa caespitosa but lower down Astelia bog is common on peaty soils. Often in intimate association with dwarf coniferous forest and wet scrub along watercourses.

WET SCRUB (Wet sclerophyll forest)

Tentatively, wet scrub contains two formations recognised by Kirkpatrick (1977) : closed-scrub and eucalypt woodland. Closed-scrub consists of areas dominated by Acacia dealbata, A. melanoxylon, A. mucronata, Banksia marginata, Leptospermum lanigerum, L. scoparium, L. nitidum, Melaleuca ericifolia, M. squarrosa and Phebalium squameum. Eucalypt woodland comprises woodland, low-woodland, open-woodland and low open-woodland dominated by E. nitida, with an understory of heath or sedgeland. Bauera rubbides may be plentiful in both formations. Often in intimate association with sedgeland. Occurs mainly in the west.

SEDGELAND (Wet tussock and hummock sedgelands and moors)

Includes areas of closed-sedgeland dominated by button grass Gymnoschoenus sphaerocephalus, eucalypt-dotted heaths, and communities dominated by Leptocarpus tenax, Diplarrhena moraea, Gleichenia dicarpa. Also includes areas of heathy sedgeland and areas of tall and low shrublands. Other species that may be locally dominant include Sprengelia incarnata, Baeckea leptocaulis, Melaleuca squarrosa, M. squamea and Banksia marginata.

2.3 HABITAT PREFERENCES OF TASMANIAN BIRDS

2.3.1. INTRODUCTION

The only comprehensive list of the habitat preferences of Tasmanian birds is that of Ridpath and Moreau (1966) who emphasized that much more work on the status of individual species in each habitat is needed. They stressed particularly that published records for cold-wet adapted habitats, which cover about one third of the island, are "very meagre".

It is apparent now that, although the cold-wet adapted habitats have an impoverished avifauna, the extent of impoverishment is much less than suggested by Ridpath and Moreau (pers. obs., Newman 1972 et seq.).

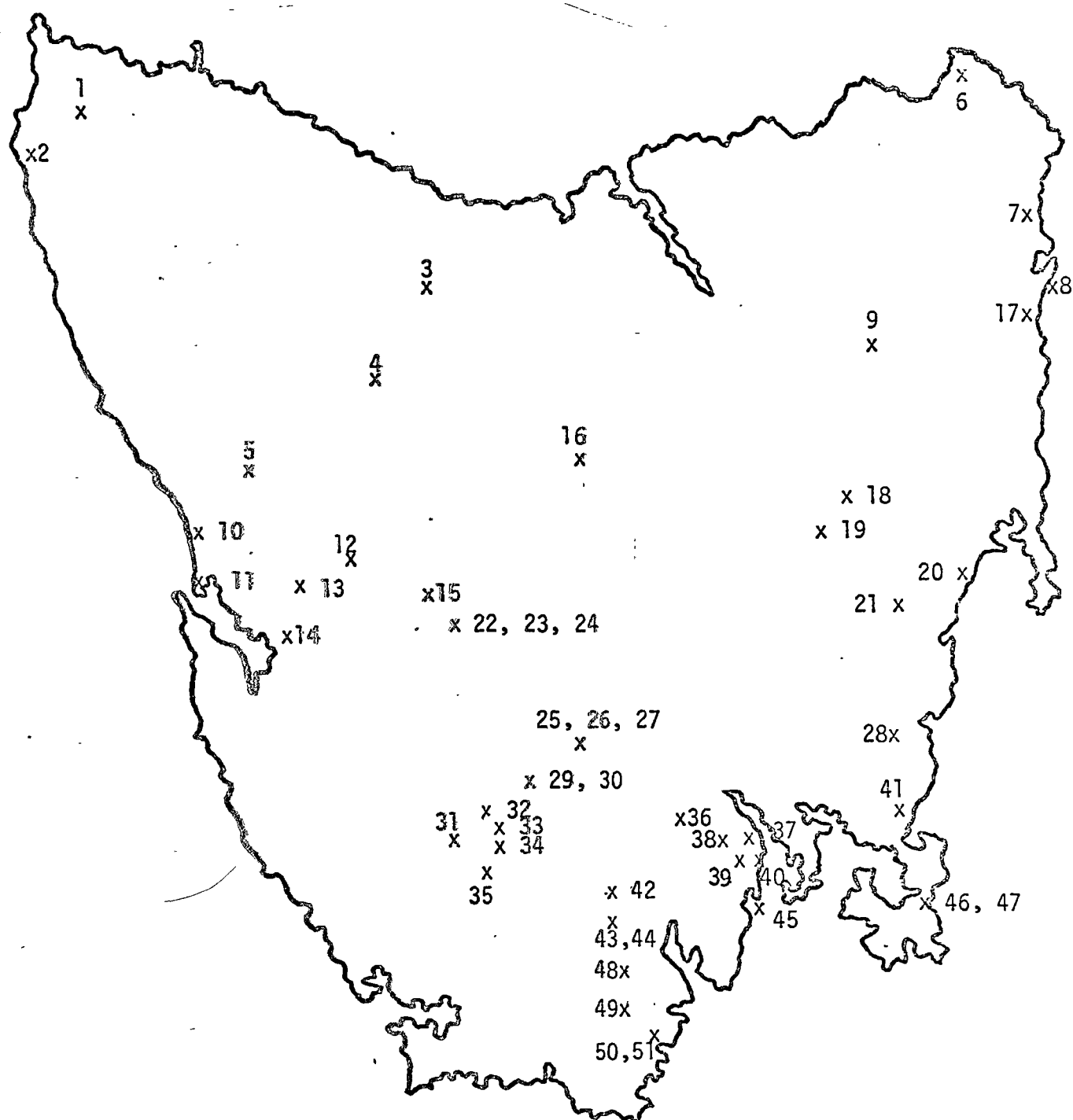
Kikkawa (1968) applied similarity analysis using centroid sorting with the information statistic as coefficient to determine the association of bird species and habitats in northern New South Wales and Queensland (part). Although the choice of clustering algorithm remains subjective, this type of analysis removes much of the subjectivity normally associated with the determination of habitat preferences. The linear similarity measure chosen for treating my Tasmanian data, with suppression of joint absences, is one of the options available in GENSTAT, a programme in the C.S.I.R.O. computing network. The two methods of similarity analysis should produce essentially similar results.

2.3.2. AREAS AND METHODS

Species lists were compiled for 53 sites (Figure 5) which are listed in Appendix 2. Sites were visited for various lengths of time, ranging from a single visit of a few hours to a two-year intensive study. Additional observations in the literature and supplied by other observers were included. Sites varied in area, depending largely on the continuity and structure of the vegetation.

Sites were chosen in accordance with the habitat classification developed in Chapter 2.2. Non-forest habitats, e.g. sedgeland and moorland, were included because of the mosaic pattern of Tasmanian habitats which allows movement

FIGURE 5. Location of sites included in similarity analysis.



between habitats and the importance of edge effects.

2.3.3. NEAREST NEIGHBOURS ANALYSIS

For each habitat, each species was coded '2' if it occurred in more than 50 per cent of the lists for that habitat, '1' if present in ≤ 50 and > 0 per cent of the lists and '0' if not recorded in any list (Appendix 3). The overall percentage similarity, i.e. averaged over all species, is given by

$$\text{Similarity \%} = \sum_{k=1}^n \left\{ 1 - |x_{ik} - x_{jk}| / r \right\} \frac{100}{n} \quad (3)$$

where x_{ik} and x_{jk} are the coded scores for species k in the habitats i and j respectively, r is the range (in this case 2) and n is the total number of species for which x_{ik} and x_{jk} are not both zero. Where $x_{ik} = x_{jk} = 0$, the k th species is ignored.

The results are given as a similarity matrix in Table 8 from which a closest neighbours table (Table 9) has been compiled.

The cluster coastal heath, savannah woodland and dry sclerophyll forest is fairly tight, since for each habitat the first two nearest neighbours are the other members of the same group. Similarly, wet sclerophyll forest, mixed forest, temperate rainforest and sub-alpine forest are very closely associated, as for each habitat the first three nearest neighbours are the other members of the same group. Sedgeland and wet scrub also have members of this group as their near neighbours. Dwarf coniferous forest does not

TABLE 8. Similarity matrix for Tasmanian habitats.

H A B I T A T	S I M I L A R I T Y % *										
	1	2	3	4	5	6	7	8	9	10	11
Coastal heath (1)	-										
Savannah woodland (2)	62.8	-									
Dry sclerophyll (3)	61.7	53.3	-								
Wet sclerophyll (4)	51.7	37.7	50.8	-							
Mixed forest (5)	49.2	38.8	48.4	89.2	-						
Rain forest (6)	42.5	35.2	35.6	63.5	68.9	-					
Sub-alpine forest (7)	52.5	40.2	46.6	72.5	67.5	64.3	-				
Dwarf coniferous forest (8)	33.3	31.6	25.4	30.8	36.8	48.2	44.1	-			
Wet mallee (9)	50.0	36.8	40.5	59.0	59.0	50.0	59.5	38.7	-		
Sedgeland (10)	61.0	50.8	50.8	58.8	56.9	57.6	63.3	47.8	61.7	-	
Moorland (11)	48.2	46.9	39.5	44.2	47.6	48.7	53.8	50.0	45.9	59.2	-

* The numbers refer to the habitats listed in column 1

TABLE 9. Tasmanian habitats - closest neighbours table.

Figures in brackets are percentage similarity.

	1	2	3	4
1. Coastal heath	savannah woodland (62.9)	dry sclerophyll (61.7)	sedgeland (61.0)	sub-alpine forest (52.5)
2. Savannah Woodland	coastal heath (62.9)	dry sclerophyll (53.3)	sedgeland (50.8)	moorland (46.9)
3. Dry sclerophyll	coastal heath (61.7)	savannah woodland (53.3)	wet sclerophyll (50.8)	sedgeland (50.8)
4. Wet sclerophyll	mixed forest (89.2)	sub-alpine forest (72.5)	rain forest (63.5)	wet mallee (59.0)
5. Mixed forest	wet sclerophyll (89.2)	rain forest (68.9)	sub-alpine forest (67.5)	wet mallee (59.0)
6. Rain forest	mixed forest (68.9)	sub-alpine forest (64.3)	wet sclerophyll (63.5)	sedgeland (57.6)
7. Sub-alpine forest	wet sclerophyll (72.5)	mixed forest (67.5)	rain forest (64.3)	sedgeland (63.3)
8. Sedgeland	sub-alpine forest (63.3)	wet mallee (61.7)	coastal heath (61.0)	moorland (59.2)
9. Wet mallee	sedgeland (61.7)	sub-alpine forest (59.5)	wet sclerophyll (59.0)	mixed forest (59.0)
10. Moorland	sedgeland (59.2)	sub-alpine forest (53.8)	dwarf coniferous forest (50.0)	rain forest (48.7)
11. Dwarf coniferous forest	moorland (50.0)	rain forest (48.2)	sedgeland (47.8)	sub-alpine forest (44.1)

really have any close neighbours as moorland is only 50 per cent similar. One reason for this is that dwarf coniferous forest is a species-poor habitat.

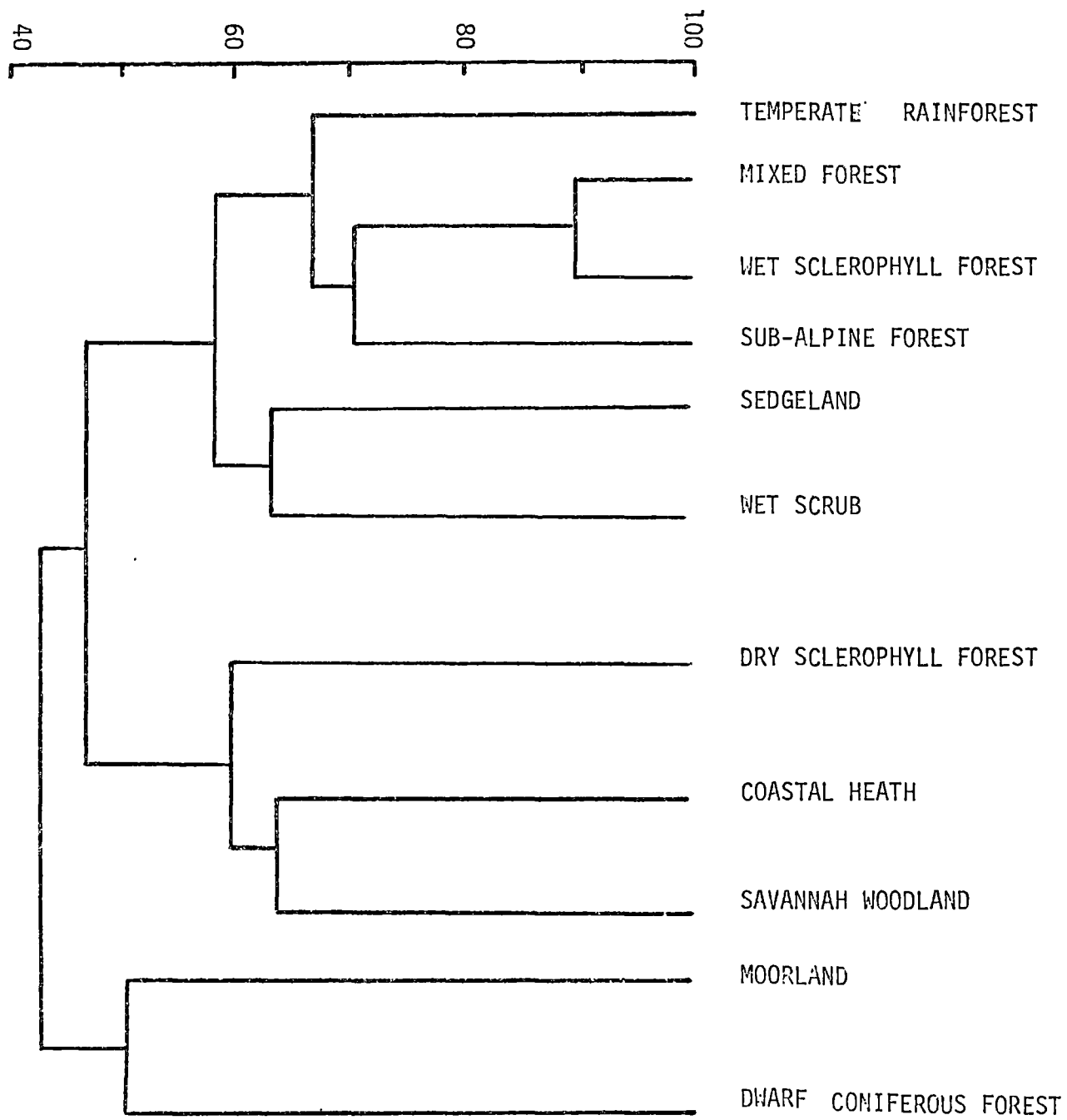
Similarity analysis shows that there is no justification for separating wet sclerophyll and mixed forests (89.2 per cent similarity) whereas separation of wet scrub from both (59.0 per cent similarity) appears justified. Wet scrub has sedgeland as its nearest neighbour.

Kikkawa (1968, 1974) recognised three habitat systems in northern New South Wales. These were obtained from a hierarchical classification (dendrogram) of habitats and bird species. A dendrogram (Figure 6) was constructed using cluster analysis from the similarity matrix of Tasmanian habitats. This produced four groups :

- Tall semihumid formations : coastal heath, savannah woodland,
dry sclerophyll forest
- Tall wet formations : wet sclerophyll forest, mixed forest,
temperate rainforest, sub-alpine forest
- Low wet formations : sedgeland, wet scrub
- Low alpine formations : moorland, dwarf coniferous forest.

The first two formations are comparable to similar formations (tall semiarid and tall wet) in northern New South Wales (Kikkawa 1974). Tasmania has no equivalent to the low semiarid formations of northern New South Wales. This group consists mainly of sites west of the New England Tablelands and includes a group of 19 species restricted to "shrub savannah and other inland semiarid formations" which, from the distribution maps in Slater (1970, 1974), appear to

FIGURE 6. Hierarchical classification of Tasmanian habitats.



have Eyrean rather than Bassian affinities. There is no equivalent in northern New South Wales to the low wet and low alpine formations of Tasmania.

In both northern New South Wales and Tasmania, similarity analysis groups the tall wet formations, including temperate rainforest, together. This means that the similarities between, say, wet sclerophyll forest and temperate rainforest are high and any differences noted by a field observer are most likely concerned with the different numbers of species occurring in the two habitats : in Tasmania, wet sclerophyll forest has 35 species of which 25 are common, compared to temperate rainforest with 25 species of which only 14 are common (Appendix 3). Few, if any, species are restricted to temperate rainforest.

In northern New South Wales, similarity analysis groups both temperate and subtropical rainforests in tall wet formations. This suggests a common origin for the bulk of the avifaunas of these two habitats (see Chapter 6.4).

CHAPTER 3

BIRDS OF TASMANIAN TEMPERATE RAINFOREST

3.1 INTRODUCTION

In this chapter the birds comprising the avifauna of Tasmanian temperate rainforest is established from field observations. The food, adaptations for breeding, habitat preferences and Tasmanian and Australian distributions of rainforest birds are discussed.

3.2 NUMBER OF SPECIES

The similarity analysis described in the previous chapter included species lists from five sites in temperate rainforest. Data for a further ten sites were obtained. The locations of the 15 rainforest sites are shown in Figure 7 and the species lists are given in Appendix 4.

Species occurring in one or two lists were classed as 'rare', in three to seven lists as 'uncommon', in eight to eleven lists as 'common', and in more than eleven lists as 'very common'. While this division into categories is somewhat arbitrary, the method should be applicable generally and provides a more objective method of determining habitat preferences than is normally used, e.g. Ridpath and Moreau (1966). Moreover, Appendix 4 can be expanded by including more sites and up-dated as additional species are added to existing site lists. Thus, any required degree of accuracy can be achieved. This is particularly important for 'uncommon' species as some of these, such as raptors and owls, may prove to be widespread throughout temperate rainforest although present at low density and having a large home range.

FIGURE 7. Location of sites for which species lists were obtained in temperate rainforest.



The results of the present analysis are given in Table 10. Seven species are rare (or occasional), five uncommon, six common and eleven very common. If the 50 percentum rule is applied, seventeen species can be classed as 'common' and a further twelve as 'occurring'. These figures are considerably higher than the six 'common' and eleven 'occurring' quoted by Ridpath and Moreau.

In the similarity analysis (Chapter 2.3) only five rain-forest sites were included. The 50 percentum rule was applied to determine the status of each species in each habitat. If the 15 sites included in Appendix 4 had been included, this would have necessitated the following changes of status for species in temperate rainforest

'Absent'	to 'occurring'	- 4 species
'Occurring'	to 'common'	- 4 species
'Common'	to 'occurring'	- 1 species

These are minor changes only and have little effect on the similarity analysis. The 'new' values are :

Temperate rainforest - mixed forest 78.9 % similarity

Temperate rainforest - wet sclerophyll forest
71.2 % similarity

Mixed forest - wet sclerophyll forest 81.8 % similarity

Probably the species classed as 'rare' in Table 10 are little more than vagrants, or occasional visitors to temperate rainforest and do not breed there to any extent. The species concerned are considered below.

Wedge-tailed Eagle Feeds mainly on the ground on vertebrates including carrion. Prey is located visually while circling over its home range which is very large and, given the mosaic pattern of habitats in Tasmania, would include patches of rainforest. The structure of rainforest is unsuited to the

TABLE 10. Status of species in Tasmanian temperate rainforest.

RARE (7 species)

Wedge-tailed Eagle
 Sulphur-crested Cockatoo
 Fan-tailed Cuckoo
 Yellow Wattlebird
 Strong-billed Honeyeater
 Spotted Pardalote
 Striated Pardalote

UNCOMMON (5 species)

Grey Goshawk
 Brush Bronzewing
 Spotted Owl
 Flame Robin
 Forest Raven

COMMON (6 species)

Yellow-tailed Black Cockatoo
 Shining Bronze Cuckoo
 Scaly Thrush
 Golden Whistler
 Yellow-throated Honeyeater
 Eastern Spinebill

VERY COMMON (11 species)

Green Rosella
 Pink Robin
 Olive Whistler
 Grey Shrikethrush
 Grey Fantail
 Brown Scrubwren
 Scrubtit
 Tasmanian Thornbill
 Crescent Honeyeater
 Silvereye
 Black Currawong

mode of foraging although some food items could be obtained in clearings in the forest. Is best classified as an occasional visitor from neighbouring habitats.

Fan-tailed Cuckoo The few records of this species, which is migratory, suggest that it is an occasional, or even accidental, visitor to rainforest. Breeds in neighbouring habitats (mixed forest, wet sclerophyll forest and wet scrub).

Yellow Wattlebird Is nomadic outside the breeding season. Largely confined, as a breeding species, to the humid and subhumid effective rainfall zones. The few records from temperate rainforest appear to be of nomadic individuals. Not known to breed in rainforest.

Strong-billed Honeyeater Occurs in all effective rainfall zones but is not known to breed in temperate rainforest. Although mainly a bark feeder it is known to visit flowering leatherwoods which flower after the breeding season. Most occurrences appear to be of nomadic flocks.

Spotted Pardalote During the breeding season is confined to the subhumid and humid effective rainfall zones. At other times may form small nomadic flocks which may visit the per-humid zone although it has been recorded infrequently far from the boundary between the perhumid and humid zones.

Striated Pardalote Occurs throughout all effective rainfall zones but as a breeding species is restricted to eucalypt dominated habitats (Newman 1976, Thomas 1977). Migratory. Probably only occurs accidentally in rainforest or as a result of post-breeding dispersal.

Of the species classed as 'uncommon' in Table 10, the Flame Robin has been recorded only occasionally in temperate rainforest, mostly outside the breeding season. As it is an

altitudinal migrant it can be ignored as a rainforest species. The remaining four 'uncommon' species are widely distributed in temperate rainforest although mainly occurring at low density.

Twentyone species, including four classed as 'uncommon', are considered to be associated regularly with temperate rainforest and to constitute the Tasmanian rainforest avifauna (Table 11). Each species is now considered under the headings : Food, Breeding Adaptations, Habitat, Tasmanian Distribution, and Australian Distribution.

3.3 FOOD

There have been very few systematic studies of the food of Australian birds. In considering the relations of birds to their environment it is necessary to know what kinds of food are eaten by each species. In establishing this for birds inhabiting Tasmanian temperate rainforest, reliance has had to be placed on general statements in the standard reference works (Leach 1958, Cayley 1959, Ridpath and Moreau 1966, Frith 1969). Unfortunately, these do not quote their sources of information and, presumably, are based on personal observations augmented by published data, particularly papers such as those by Lea and Gray (1935-6) and McKeown (1944). Because of the reliance on personal observations these generalised statements are largely subjective and, because of this, may be misleading.

There are two papers dealing with gut contents of Tasmanian, including King Island, birds (Green 1966, Green and McGarvie 1971). Relevant data from these papers are

TABLE 11. The avifauna of Tasmanian temperate rainforest.

1. Grey Goshawk
2. Brush Bronzewing
3. Yellow-tailed Black Cockatoo
4. Green Rosella
5. Shining Bronze Cuckoo
6. Spotted Owl
7. Scaly Thrush
8. Pink Robin
9. Olive Whistler
10. Golden Whistler
11. Grey Shrike-thrush
12. Grey Fantail
13. Brown Scrubwren
14. Scrubtit
15. Tasmanian Thornbill
16. Yellow-throated Honeyeater
17. Crescent Honeyeater
18. Eastern Spinebill
19. Silvereye
20. Black Currawong
21. Forest Raven

given in Appendix 5, augmented by recent data for mainland birds (Rose 1973, Mathiessen 1973). It is unlikely that the main kinds of foods eaten by any species will change markedly throughout its range and the inclusion of mainland data is justifiable.

The following main kinds of food are recognised : vertebrates (carnivores), invertebrates (insectivores), seeds (graminivores), fruits and berries (frugivores), nectar (nectarivores) and omnivores. For each species, my assessment of the main kinds of food is given in brackets (Appendix 5).

Apart from a few highly specialised feeders, in general, birds are opportunistic feeders that eat all suitable items encountered (MacArthur 1958, MacArthur and Wilson 1967, Cody 1968, Thomas and Dartnall 1971). This is amply confirmed by the gut analyses given in Appendix 5 and summarised in Table 12. In spite of the small numbers of each species examined, beetles (Coleoptera) are eaten by at least eleven of the twentyone species - Spotted Owl, Scaly Thrush, Olive Whistler, Golden Whistler, Grey Shrike-thrush, Grey Fantail, Brown Scrubwren, Scrubtit, Yellow-throated Honeyeater, Black Currawong and Forest Raven. Weevils Curculionidae are eaten by at least six species : Scaly Thrush, Olive Whistler, Grey Shrike-thrush, Yellow-throated Honeyeater, Black Currawong and Forest Raven. These two examples, and the numbers of species taking each item would be increased markedly if more birds were examined, demonstrate clearly that there is considerable overlap in diet. Even though there may well be differences in the size of items eaten by the various species, there is no justification

TABLE 12. Foods eaten by Tasmanian temperate rainforest birds.

TABLE 12. Foods of Tasmanian temperate rainforest birds. x - from stomach content analysis.
(x) - general statements. ✓ - visual observation.

SPECIES	Plants				Vertebrates			Invertebrates														
	Leaves, Stalks, Etc.	Seeds	Berries/Fruits	Nectar	Reptiles/Amphibians	Birds	Mammals	Mollusca	Crustacea	Myriapoda	Arachnida	Blatiodea	Isoptera	Mantodea	Dermaptera	Orthoptera	Hemiptera	Coleoptera	Diptera	Lepidoptera	Hymenoptera	Others Unspecified
Grey Goshawk					(x)	(x)	(x)															
Brush Bronzewing		x	(x)																			
Yellow-tailed Black Cockatoo		(x)	(x)	(x)																		(x)
Green Rosella	✓	x	(x)														✓					
Shining Bronze Cuckoo																				x		
Spotted Owl							x				x	x				x		x		x		
Scaly Thrush	x								(x)	x	x							x	x	x		x
Pink Robin																						(x)
Olive Whistler	x	x										x						x	x			(x)
Golden Whistler			(x)															x	x			(x)
Grey Shrike-thrush					x	x				x	x	x		x	x	x	x	x		x	x	
Grey Fantail																	x	x	x	x	x	
Brown Scrubwren	x	x										x	x					x	x	x	x	
Scrubtit											x							x				x
Tasmanian Thornbill																						(x)
Yellow-throated Honeyeater				✓							x							x		x		
Crescent Honeyeater				✓															x	x		
Eastern Spinebill			✓	✓																✓		(x)
Silvereye		x	x								x						x				x	
Black Currawong		x									x			x		x	x	x	x	x		
Forest Raven	x	x	x		x	x	x	x	x	x	x					x	x	x	x	x		

for separating species on the basis of diet other than in terms of kinds of food, e.g. seeds, invertebrates, etc., eaten.

Karr (1971) attempted a comparison of food-habit distributions of several forest areas. Table 13 compares the results obtained in the present study with Karr's Table 12. To avoid split allocations, species classed as taking invertebrates and some form of vegetable matter, e.g. nectar, have been classed as omnivores. Moreau (1966) subdivided avifaunas in a somewhat different way : omnivores added one half species to frugivore and insectivore. The data in Table 13 have been reworked in this way (Table 14).

The five tropical lowland forests have avifaunas with very similar food-habit distributions (Table 14) :

Graminivores	0 - 4 %
Frugivores	22 - 28 %
Insectivores	72 - 76 %

One of these forests is an Australian tropical rainforest (Harrison 1962). The lower montane forest in Costa Rica shows a marked increase in the proportion of frugivores whereas this category decreases in the temperate deciduous forest in Illinois. This latter forest appears to have the same proportion of frugivores as temperate rainforest in Tasmania. However, reference to Table 13 shows that neither forest possesses any specialist frugivores (see below).

The most interesting comparison is between the Tasmanian rainforest and the African montane forests because these two habitats are ecological counterparts for the continents of

TABLE 13. Food-habits distribution in selected forest habitats.

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TABLE 13: Food-habits distribution in percentage of total species and number of species in selected forest studies.

HABITAT (Location)	REFERENCE	FOOD HABITS					No. of Species
		Gramini- vore	Frugi- vore	Omni- vore	Insecti- vore	Carni- vore	
Lowland forest (Panama)	Karr 1971	0	11	25	62	2	56
Four lowland forests (Costa Rica)	Orians 1969	0	19	8	72	1	61
Two lowland forests (Africa)	Moreau 1966	4	22	-	72	-	115
Lowland forest (Malaya)	Harrison 1962	0	14	24	57	6	306
Lowland forest (Australia)	Harrison 1962	0	14	22	52	12	117
Two lower montane forests (Costa Rica)	Orians 1969	0	34	7	59	0	29
Six montane forests (Africa)	Moreau 1966	9	25	-	63	-	44
Temperate deciduous forest (Illinois)	Karr 1968	3	-	19	76	3	32
Temperate rainforest (Tasmania)	Present study	9	0	24	62	5	21

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TABLE 14. Food-habits distribution in selected forest habitats : data from Table 13 recalculated to conform with the method used by Moreau (1966).

HABITAT (LOCATION)	FOOD-HABITS %		
	<u>GRAMINIVORE</u>	<u>FRUGIVORE</u>	<u>INSECTIVORE</u>
Lowland forest (Panama)	0	24	76
Four lowland forests (Costa Rica)	0	23	77
Two lowland forests (Africa)	4	22	72
Lowland forest (Malaya)	0	28	72
Lowland forest (Australia)	0	28	72
Two lower montane forests (Costa Rica)	0	38	62
Six montane forests (Africa)	9	25	63
Temperate deciduous forests (Illinois)	3	10	87
Temperate rainforest (Tasmania)	10	12	78

Australia and Africa (Keast 1974). The Tasmanian rainforest is much poorer in fruit-eating species than its African counterpart and, as pointed out above, the Tasmanian forest has no specialist frugivore. The 12 per cent shown in Table 14 as belonging to this category arises from allocating each of the five species of omnivore $\frac{1}{2}$ species to frugivore and $\frac{1}{2}$ species to insectivore. In fact, two of the five omnivores take nectar and invertebrates, not fruit and invertebrates.

While useful in indicating major differences, such as the paucity of frugivores in Tasmanian temperate rainforest, this type of analysis should not be pursued too rigorously because of probable differences in judgements of the categories into which species should be placed.

3.4 BREEDING ADAPTATIONS

3.4.1 INTRODUCTION

The breeding adaptations of birds have been reviewed comprehensively by Lack (1968). As is usual in studies of this kind, the emphasis is on groups of related species or species with some common attribute(s) rather than on communities. Consideration of the adaptations for breeding of species forming a well-defined community can be rewarding for the insight provided into the environmental factors within which the community exists. The breeding adaptations of rainforest species, as far as they are known, are summarised in Appendix 6 and discussed below.

3.4.2 PAIR BOND

All species are monogamous.

3.4.3. NESTING DISPERSAL

All species are solitary nesters.

The Crescent Honeyeater may sometimes nest in loose colonies as Sharland (1958) writes that they nest in "considerable numbers in the one patch of forest or scrub". At Pottery Road, near Hobart, it nests at high density in restricted areas where there is a well-developed low shrub layer. Its patchy distribution may be determined by availability of suitable nest sites. However, in temperate rainforest it is widely distributed and occurs at high density.

3.4.4 NEST TYPE

Nest types are :

Open (cup)	14
Domed	3
Hole	3
None	1 (parasitic cuckoo)

Of particular interest is the absence of small hole-nesting species such as pardalotes. It is not known whether this is due to a lack of suitable nesting holes or whether the species concerned are excluded from temperate rainforests because of a lack of suitable foods.

3.4.5 NEST SITE

Nest sites were divided into the following categories : ground, herb/low shrub layer, shrub, tree and parasitic (Table 15). By combining ground and herb/low shrub layer

TABLE 15. Comparison of nest sites in Tasmanian temperate rainforest and dry sclerophyll forest.

NEST SITE	<u>RAINFOREST</u>		<u>DRY SCLEROPHYLL</u>	
	<u>NO.OF SPECIES</u>	<u>%</u>	<u>NO.OF SPECIES</u>	<u>%</u>
Ground	0	0	2	4
Herb/low shrub	5	23	12	22
Shrub	$7\frac{1}{2}$	36	$13\frac{1}{2}$	25
Trees	$4\frac{1}{2}$	21	$13\frac{1}{2}$	25
Hole	3	14	9	17
Parasitic	1	5	4	7

into a single category, the herb layer, the relative importance of the three vegetation layers (herb, shrub and tree) recognised by MacArthur and MacArthur (1961) in providing nesting sites can be assessed :

Herb	5 species
Shrub	$7\frac{1}{2}$ species
Tree	$4\frac{1}{2}$ species

The comparable figures for Tasmanian dry sclerophyll forest are 14, $13\frac{1}{2}$ and $13\frac{1}{2}$ species (Thomas 1976).

The proportions of species using the various nest sites in temperate rainforest and dry sclerophyll forest are somewhat similar. The main difference is the larger proportion of species nesting in the shrub layer in rainforest (Table 15).

3.4.6. EGG-LAYING INTERVAL IN SMALL PASSERINES

Courtney and Marchant (1971) have suggested that all Acanthiza thornbills lay successive eggs at 48-hour intervals. Presumably the Tasmanian Thornbill lays at 48-hour intervals. The egg-laying routine of the Scrubtit, whose generic status is questionable, is not known. Laying at intervals in excess of 24-hours is very unusual in small passerines.

3.4.7 CLUTCH-SIZE

The distribution of mean clutch-size for species breeding in Tasmanian temperate rainforest (based on Sharland 1958) is compared in Table 16 to that given for temperate rainforest, subtropical rainforest and wet sclerophyll forest combined in Kikkawa (1974) for northern New South Wales. Kikkawa's values were based on Leach (1958) and Cayley (1966). Kikkawa considers these sources to be "reasonable and accurate", a

TABLE 16. Distribution of mean clutch-size in Tasmanian rainforest and wet formations in Northern New South Wales.

MEAN CLUTCH-SIZE	<u>TASMANIA</u>		<u>NEW SOUTH WALES</u>	
	<u>NO.OF SPECIES</u>	<u>%</u>	<u>NO.OF SPECIES</u>	<u>%</u>
1	0	0	8	10
1.1 - 2	3	15	18	23
2.1 - 3	7	35	31	40
3.1 - 4	8	40	12	15
4.1 - 5	1	5	5	6
5.1 - 6	1	5	0	0
6.1 - 7	0	0	2	3
7.1 - 8	0	0	2	3

statement that is open to some doubt. I do not believe that this type of data is accurate enough to justify the use of statistical tests of significance. They may be accurate enough to show possible trends.

The distributions of mean clutch-sizes for both Tasmania and northern New South Wales are sufficiently skewed to make the median or modal clutch-size preferable to the mean when making the comparison :

Median clutch-size : Tasmania	3.05
New South Wales	2.1 - 3.0
Modal clutch-size : Tasmania	3.1 - 4.0
New South Wales	2.1 - 3.0

In both comparisons Tasmania has the larger clutch-size.

This may be because :

- 1) Clutch-size increases with latitude. There is little evidence in support of this in south-eastern Australia (Courtney and Marchant 1971, Thomas 1974).
- 2) The inclusion of subtropical rainforest in the wet formations of northern New South Wales has depressed the values obtained, or
- 3) The data used in compiling the two distributions may be misleading.

Kikkawa found that mean clutch-size for his wet formations was smaller than in both tall and low semiarid formations in northern New South Wales. This led him to state : ".....the distribution of mean clutch-sizes in the wet formations is characteristic of tropical forest birds. Skutch (1949, 1967) considers that the small clutch-size of tropical forest birds is below the feeding capacity of parents which would attract predators and hence the rate of predation at the

nest", and "It is interesting to note that in subtropical Australia the wet formation birds tend to have characteristics of tropical forest birds with increased frugivory and reduced clutch-size. Their phylogenetic affinities with tropical species (Keast 1961, Kikkawa and Pearse 1969) are probably responsible for such tendencies". One should, perhaps, add to this last statement "if they exist".

It is necessary to consider Kikkawa's views because many species occur in temperate rainforest in both Tasmania and New South Wales (Chapter 6.4) and breeding biology must be determined, to some extent at least, by the environment.

Although Skutch did make the point about decreased predation, his main argument is that reduced clutch-size is a device whereby the recruitment rate is adjusted to the mortality rate. This involves group selection for which there really is little convincing evidence. While I accept Lack's (1954, 1966) theory of maximum reproduction, I believe that he is wrong in claiming that clutch-size is determined by the number of young that the parents can feed. I hold the view that clutch-size is determined by the amount of food available to the laying female, as Lack admits is the case for species with nidifugous young. Any reduction in clutch-size in the wet formations of northern New South Wales and Tasmania can be equally well accounted for on the basis of lower productivity of these habitats. Ridpath and Moreau (1966) suggest that Tasmanian temperate rainforest has fewer birds than sclerophyll forests because of a general shortage of foods.

There is some evidence that predation may not be as important in determining clutch-size as Skutch and Kikkawa suggest. Predation of eggs and young of the tropical Black and White Manakin is proportionately the same even though the female visits the nest four times as frequently during the nestling stage (Snow 1962, Lack 1966). The male is promiscuous and never visits the nest.

As was shown earlier in this chapter, Tasmanian temperate rainforest has no specialist frugivorous species. Although Kikkawa claims that a greater proportion of frugivores is "clearly a feature of wet formation birds" in northern New South Wales he admits that "The contrast of the proportion of frugivores is not very great".

I believe that the available evidence does not justify the sweeping conclusions drawn by Kikkawa.

3.4.8 OTHER ADAPTATIONS

- 1) One species, the Grey Goshawk, shows pronounced sexual size dimorphism, with the female being much larger than the male. The male feeds the incubating female and the nestlings. Presumably, the smaller size of the male enables him to obtain smaller prey more efficiently at a time when it is likely to be more abundant than larger items. Goshawks appear to breed when newly-fledged small passerines are available
- 2) Two species, the Brown Scrubwren and Tasmanian Thornbill, have 'helpers at the nest'. Both species occur almost invariably in small parties, which are almost certainly family groups, throughout the year. The main function of the

non-breeding helpers is to assist in feeding nestlings and, particularly, fledgelings. In this way, the breeding pair are released from parental responsibilities once the young leave the nest and can, when environmental conditions permit, start a second clutch before the young from the previous clutch have reached independence. There is no evidence that the incidence of 'helpers at the nest' is higher in temperate rainforest than it is in other Tasmanian habitats and it may even be less : 10 per cent of species compared to 15 per cent in mixed forest, 17 per cent in wet sclerophyll forest and 16 per cent in dry sclerophyll forest.

3) Only one brood parasite, the Shining Bronze Cuckoo, occurs regularly in Tasmanian temperate rainforest.

3.4.9 SUMMARY

Compared to dry sclerophyll forest, temperate rainforest has far fewer species of birds and proportionately fewer species that nest colonially or have 'helpers at the nest'. This suggests that temperate rainforest is the harsher environment (see Chapter 4.9) but that the resources are basically, but not always, predictable and evenly distributed. Proportionately the two habitats have the same number of small passerines that lay successive eggs at 48-hour intervals. I hold that clutch-size is determined by the ability of the female to obtain sufficient food to form the eggs and prolonged intervals between successive eggs to be an adaptation to a sparse food supply.

I have suggested a possible reason for small clutch-size in the tall wet formations of northern New South Wales is

that the low productivity of these formations makes it difficult for the laying female to obtain sufficient food to form a larger clutch. In the case of temperate rainforest harshness should be equated with low productivity associated with climatic conditions and stability. Breeding can still be seasonal as has been shown by Nix (1976). Temperate rainforest may resemble tropical forests in one way : the flush of insects during the breeding season may be less than in less climatically stable habitats and this would account for the smaller clutch-size of birds breeding in these habitats without having to invoke adjusted reproductive rates and group selection.

3.5 HABITAT PREFERENCE

The habitat preferences of the 21 species considered to breed regularly in Tasmanian temperate rainforest are given in Table 17. No species is restricted to temperate rainforest and two-thirds of the species occur also in dry sclerophyll forest, where many are common, at the other end of the xeric-mesic gradient.

3.6 DISTRIBUTION WITHIN TASMANIA

The Tasmanian distributions of the 21 species are shown in Appendix 7 (from data in the Atlas Project of the Bird Observers' Association of Tasmania).

Tasmanian habitats are distributed along lines dictated by a largely unidirectional climatic gradient (Jackson 1965, 1968, 1973). Tasmanian habitats are influenced by elevation,

TABLE 17. Status of rainforest species in other Tasmanian forest habitats. DS dry sclerophyll, WS wet sclerophyll, MF mixed forest, TRF temperate rainforest, SAF sub-alpine forest, DCF dwarf coniferous forest. XX - common, X - uncommon.

	DS	WS	MF	TRF	SAF	DCF
Grey Goshawk		X	X	X	X	
Brush Bronzewing		XX	XX	X	X	
Yellow-tailed Black Cockatoo	X	XX	XX	XX	X	X
Green Rosella	XX	XX	XX	XX	X	X
Shining Bronze Cuckoo	XX	XX	XX	XX	XX	
Spotted Owl	X	X	X	X	X	
Scaly Thrush		XX	XX	XX		
Pink Robin		XX	XX	XX	X	
Olive Whistler		XX	XX	XX	XX	X
Golden Whistler	XX	XX	XX	XX	X	
Grey Shrike-thrush	XX	XX	XX	XX	XX	
Grey Fantail	XX	XX	XX	XX	X	
Brown Scrubwren	XX	XX	XX	XX	XX	X
Scrubtit		XX	XX	XX	XX	X
Tasmanian Thornbill		XX	XX	XX	XX	XX
Yellow-throated Honeyeater	XX	XX	XX	XX	XX	
Crescent Honeyeater	XX	XX	XX	XX	XX	XX
Eastern Spinebill	XX	XX	XX	XX	X	
Silvereye	XX	XX	XX	XX	XX	
Black Currawong	X	XX	XX	XX	XX	XX
Forest Raven	XX	XX	XX	X	XX	X

soil, drainage, aspect and past history of burning and present a mosaic rather than the large continuous blocks suggested by published small-scale vegetation maps such as Figure 4 which is based on Jackson (1965). While Tasmanian habitats are correlated broadly with rainfall (cf. Figures 2 and 4), effective rainfall, which depends on soil, drainage, etc., is a more meaningful determinant of habitat (Gentilli 1949). A generalised effective rainfall map, based on Gentilli (1972) but with additional small humid areas (presence of Nothofagus) is given in Figure 3.

Comparison of the bird species maps (Appendix 7) with that of effective rainfall shows that none of the 21 species of birds occurring in temperate rainforest is restricted to one effective rainfall zone and that many occur in all three zones (Table 18).

To some extent the distribution maps of Appendix 7 reflect the distribution of observers. The maps are, for example, biased towards the south-eastern part of the island. Consequently, the maps do not indicate the relative abundance of a species in the three effective rainfall zones. This can be obtained by dividing Tasmania into 100 km squares and expressing the number of 10 km squares in each 100 km square in which a species has been recorded as a percentage of the number of 10 km squares within the same 100 km square in which the most recorded species, the Forest Raven, has been recorded. Tasmania was divided roughly into 100 km squares as shown in Figure 8. The results of this analysis are presented in Appendix 8 and shown schematically in Figure 9.

TABLE 18. Status of species breeding in Tasmanian temperate rainforest in the effective rainfall zones.

XX - common and widespread. X - uncommon or local.

SPECIES	<u>EFFECTIVE RAINFALL ZONE</u>		
	<u>PERHUMID</u>	<u>HUMID</u>	<u>SUBHUMID</u>
Grey Goshawk	XX	XX	
Brush Bronzewing	XX	XX	
Yellow-tailed Black Cockatoo	XX	XX	XX
Green Rosella	XX	XX	XX
Shining Bronze Cuckoo	XX	XX	XX
Spotted Owl	XX	XX	XX
Scaly Thrush	XX	XX	
Pink Robin	XX	XX	
Olive Whistler	XX	XX	X
Golden Whistler	XX	XX	XX
Grey Shrike-thrush	XX	XX	XX
Grey Fantail	XX	XX	XX
Brown Scrubwren	XX	XX	XX
Scrubtit	XX	XX	
Tasmanian Thornbill	XX	XX	X
Yellow-throated Honeyeater	XX	XX	XX
Crescent Honeyeater	XX	XX	XX
Eastern Spinebill	XX	XX	XX
Silvereye	XX	XX	XX
Black Currawong	XX	XX	X
Forest Raven	XX	XX	XX

FIGURE 9. Abundance of species, compared to that of the most recorded species, in the '100 km squares' of Figure 8. Data from B.O.A.T. Atlas project.

GREY GOSHAWK	BRUSH BRONZEWING	YELLOW-TAILED BLACK COCKATOO
12 7 10	20 15 7	52 44 35
28 2 0	50 7 8	72 34 39
14 9	29 15	92 53
20 8 6	35 17 10	62 57 42
GREEN ROSELLA	SHINING BRONZE CUCKOO	SPOTTED OWL
94 71 53	12 24 13	8 22 17
100 73 76	31 12 20	22 7 9
112 92	39 32	29 22
97 85 74	22 25 22	15 19 16
SCALY THRUSH	PINK ROBIN	OLIVE WHISTLER
12 15 3	40 22 13	46 27 13
31 12 5	34 30 12	63 36 7
33 17	67 22	72 23
22 20 8	37 40 16	54 45 14
GOLDEN WHISTLER	GREY SHRIKE-THRUSH	GREY FANTAIL
44 34 22	66 54 50	84 63 60
56 29 31	75 68 71	97 59 63
82 61	96 83	88 90
50 48 38	70 73 68	90 70 71
BROWN SCRUBWREN	SCRUBTIT	TASMANIAN THORNBILL
38 48 30	20 5 3	36 39 15
69 46 35	31 32 5	94 56 11
94 36	61 10	90 37
54 63 34	26 33 6	60 60 21
YELLOW-THROATED HONEYEATER	CRESCENT HONEYEATER	EASTERN SPINEBILL
54 46 37	40 24 25	22 22 25
91 77 68	100 59 44	60 25 36
96 90	112 73	65 58
72 73 65	70 65 47	41 37 40
SILVEREYE	BLACK CURRAWONG	
34 39 43	76 17 25	
66 39 32	94 73 41	
66 63	108 49	
50 48 46	85 66 38	

Several species have a predominantly western distribution : Grey Goshawk, Brush Bronzewing, Yellow-tailed Black Cockatoo, Scaly Thrush, Pink Robin, Olive Whistler, Brown Scrubwren, Scrubtit, Tasmanian Thornbill, Crescent Honeyeater and Black Currawong. These eleven species are predominantly birds of the perhumid and humid zones. Most also occur in the sub-humid zone where, as breeding species, they are restricted to areas where the vegetation resembles wet sclerophyll. Typically, they occur in wet gullies and other shaded areas where the effective rainfall is higher than in the surrounding habitat, which usually is dry sclerophyll forest.

The occurrence of the 21 species on six of the larger off-shore islands is listed in Appendix 9.

3.7 AUSTRALIAN DISTRIBUTION

The Australian distributions of species occurring in Tasmanian temperate rainforest, as given by Slater (1970, 1974), are shown in Appendix 10. Where a Tasmanian endemic species is replaced on the mainland by another species with which it forms a superspecies (Green Rosella/Crimson Rosella, Brown Scrubwren/White-browed Scrubwren, Yellow-throated Honeyeater/White-eared Honeyeater, Black Currawong/Pied Currawong) the distribution of the latter is shown.

Two species present special difficulties. The Tasmanian Thornbill obviously is closely related to the Brown Thornbill which also occurs in Tasmania although not in rainforest. The Australian distribution of the Brown Thornbill is included in Appendix 10 as it appears to occupy a similar niche in

mainland temperate rainforest to the one occupied by the Tasmanian Thornbill (see Chapter 6). The Scrubtit may be the ecological counterpart of the mainland Large-billed Scrubwren (Schodde 1975) and the distribution of this species is included in Appendix 10.

The Australian distribution of Tasmanian temperate rainforest species is essentially : coastal regions in south-eastern and eastern Australia. The northern limit is variable, suggesting replacement by species whose origin is further north, which could include New Guinea.

A few species have isolated populations in south-western Australia. Only two species, Spotted Owl and Grey Fantail, occur throughout Australia..

CHAPTER 4

RESOURCE DIVISION ALONG THE XERIC-MESIC GRADIENT

4.1 INTRODUCTION

As indicated in Chapter 1, a survey of the literature showed that it is by no means clear how bird species diversity (BSD) varies along a xeric-mesic gradient. The work reported here aims at establishing the variation in BSD in Tasmanian forested habitats when these are arranged along the xeric-mesic gradient.

The data obtained can also be used to compare BSD and number of species in widely separated temperate rainforests. They can be used further to compare relative densities of birds along the Tasmanian xeric-mesic gradient and in establishing the ranges of individual species along this gradient.

4.2 METHODS

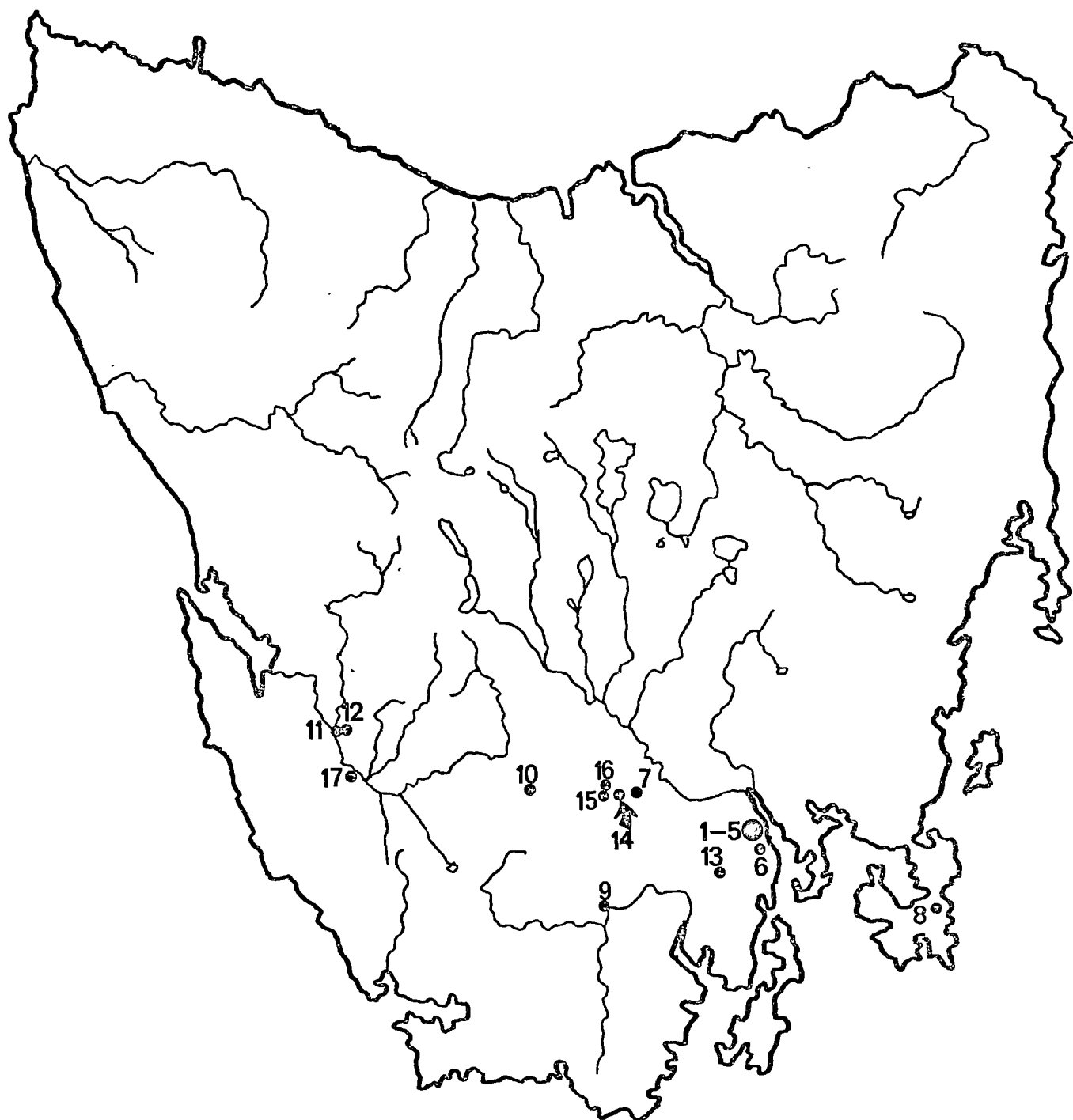
Seventeen sites were chosen, comprising :

- 3 sites in dry sclerophyll forest (Nos. 1 - 3)
- 1 site in an area with an abrupt change from dry to wet sclerophyll forest (5)
- 1 site in a wet sclerophyll gully in dry sclerophyll forest (4)
- 3 sites in wet sclerophyll forest (6 - 8)
- 2 sites in mixed forest (9, 10)
- 3 sites in temperate rainforest (11, 12, 17)
- 3 sites in sub-alpine forest (13 - 15)
- 1 site in dwarf coniferous forest (16)

The locations of these sites are shown in Figure 10.

The determination of BSD requires that some form of census

FIGURE 10. Location of census sites.



of a small area be made. Because the structure of the various Tasmanian habitats varies markedly, different habitats have different visibilities and afford various degrees of freedom of movement for the observer. Some habitats, such as those with areas of dense Bauera or Horizontal, are almost impenetrable except along existing tracks.

Several methods of censusing are possible, but most are not equally applicable to all habitats. The classical method of mapping territories (Enemar 1959), used by Thomas (1974) in dry sclerophyll forest, cannot be used in habitats where movement of the observer is severely restricted. Netting has been used in such habitats (e.g. Pattemore and Kikkawa 1975) but large ground-frequenting species, species whose home range is much larger than the census area and canopy frequenting species are often 'missed'. Netting is not effective in the more open habitats. Karr (1971) used a mixture of both methods.

For the present work a method was devised that could be used in all habitats. A transect was selected and marked out at 50 m intervals. Each transect was walked at least eight times and the presence of species was recorded on each traverse for each of the 50 m intervals in which they were seen or heard. Censuses were undertaken during the breeding season which was taken as October - December in the most xeric habitats and November - January in the rest. These are one month earlier than the periods calculated by Nix (1976) in which the vegetation growth index is at its maximum and which he predicts coincide with the periods

of maximum breeding activity. Breeding seasons were chosen from past experience although it should be noted that in 1976-7, when most of the censuses were taken, breeding was later than in most years (pers. obs. O.M.G. Newman pers. comm). Censuses made outside the breeding season are of limited value because of the mobility of many bird species and a pronounced tendency for individuals of many species to congregate at places of locally high food density.

Additionally, foliage profiles were measured along each transect using the method devised by Karr (1968). The presence/absence of foliage was recorded at 0, 0.5, 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16-20, 21-30, 31-40, 41-50, and so on, feet above the ground. The foliage profiles constructed from these simple measurements were used to calculate the per cent vegetation cover and foliage height diversity (FHD).

4.3 RESULTS

The full census results are given in Appendix 11 and the vegetation profiles in Appendix 12. The results are summarised in Table 19.

4.4 BIRD SPECIES DIVERSITY

There are problems associated with the analysis of results of this kind, the major one being the choice of a measure of diversity. A variety of indices has been proposed but the most commonly used measure of BSD is the Shannon-Wiener information statistic H (MacArthur and MacArthur 1961, Cody

TABLE 19. Results of censuses along the Tasmanian xeric-mesic gradient - summary. Full results are given in Appendix 11 (bird censuses) and Appendix 12 (foliage profiles).

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TABLE 19

Summary of Tasmanian census results

HABITAT	SITE			F H D	PER CENT. COVER			BIRD SPECIES	B.S.D.	RELATIVE DENSITY
	NO.	LOCATION			2. - LAYER	3. - LAYER	4. - LAYER			
Dry Sclerophyll (open)	1	Pottery Road	D	0.9718		108		25	2.6244	1.929
" "	2	" "	A	1.0984		76		21	2.5080	4.178
" "	3	" "	C	1.0664		75		25	2.7223	4.083
Dry → Wet Sclerophyll	5	" "	B	1.0088		78		24	2.6267	4.620
Wet Sclerophyll gully	4	" "	E	1.0826		120		22	2.7314	5.180
Wet sclerophyll	6	Myrtle Gully		1.0304		147		26	2.7812	6.410
" "	7	Mt. Field		1.0165		88 →	124	17	2.5514	5.962
" "	8	Clemes Peak		0.9139		139		22	2.6987	3.583
Mixed Forest	9	Tahune		0.9978		83 →	118	19	2.6843	3.938
" "	10	Tim's Track		0.9622		113		20	2.6059	3.700
Temperate rainforest	11	Gordon River	A	0.9865		78 →	102	17	2.362	4.100
" "	12	" "	B	0.9254	112 ←	221		16	2.239	3.900
" "	17	Olga Camp		1.0266				18	2.6398	6.781
Sub-alpine forest	13	Neika		1.0270		107		17	2.3276	3.922
" " "	14	Beattie's Tarn		1.0468		122		19	2.3876	5.000
" " "	15	Lake Dobson		1.0906		89		18	2.3323	3.857
Dwarf Coniferous forest	16	Pandanni Grove		0.8442		97		6	1.6004	2.500

1968, Recher 1969, Wiens 1969, Karr and Roth 1971, Thomas 1974 and many others). H is given by equation (1). Recently, Taylor et al. (1976) have criticised the use of H on the grounds that it overemphasises the contribution of the more common species to the value of BSD. This is certainly true where one species is very much more abundant than all others (Thomas unpubl. data). However, it may not be such a serious criticism where, in comparing different geographical areas or habitats, the equitability components (Lloyd and Ghelardi 1964) are similar.

Variation in H along the xeric-mesic gradient is summarised in Table 20 and shown schematically in Figure 11.

BSD reaches a maximum in wet sclerophyll forest. Temperate rainforest has lower BSD than the more xeric habitats, including mixed Nothofagus - Eucalyptus forest, and somewhat higher BSD than the more cold-adapted Eucalyptus sub-alpine forest. Dwarf coniferous forest has very low BSD.

4.5 COMPARISON OF BSD IN VARIOUS TEMPERATE RAINFORESTS

It is possible to compare the value of H obtained for Tasmanian temperate rainforest with those given in, or calculated from, the literature for temperate rainforests in other parts of the southern hemisphere. This is done in Table 21.

The values for Chile and Tasmania are comparable. The mean value of H for the South Island of New Zealand is somewhat lower although the most diverse site has a value of H comparable to the value for the one Chilean site and the Tasmanian mean. Differences could arise from differences in

TABLE 20. Bird species diversity and number of species in Tasmanian habitats arranged along the xeric-mesic gradient.

HABITAT	NO.OF SITES	NO.OF SPECIES		BSD	
		RANGE	MEAN	RANGE	MEAN
Dry sclerophyll forest	3	21-25	24	2.508- 2.722	2.618
Wet sclerophyll forest	4	17-26	21.8	2.551- 2.781	2.691
Mixed forest	2	19-20	19.5	2.606- 2.684	2.645
Temperate rain- forest	3	16-18	17	2.239- 2.640	2.414
Sub-alpine forest	3	17-19	18	2.328- 2.388	2.349
Dwarf coniferous forest	1		6		1.600

FIGURE 11. Bird species diversity along the Tasmanian xeric-mesic gradient.

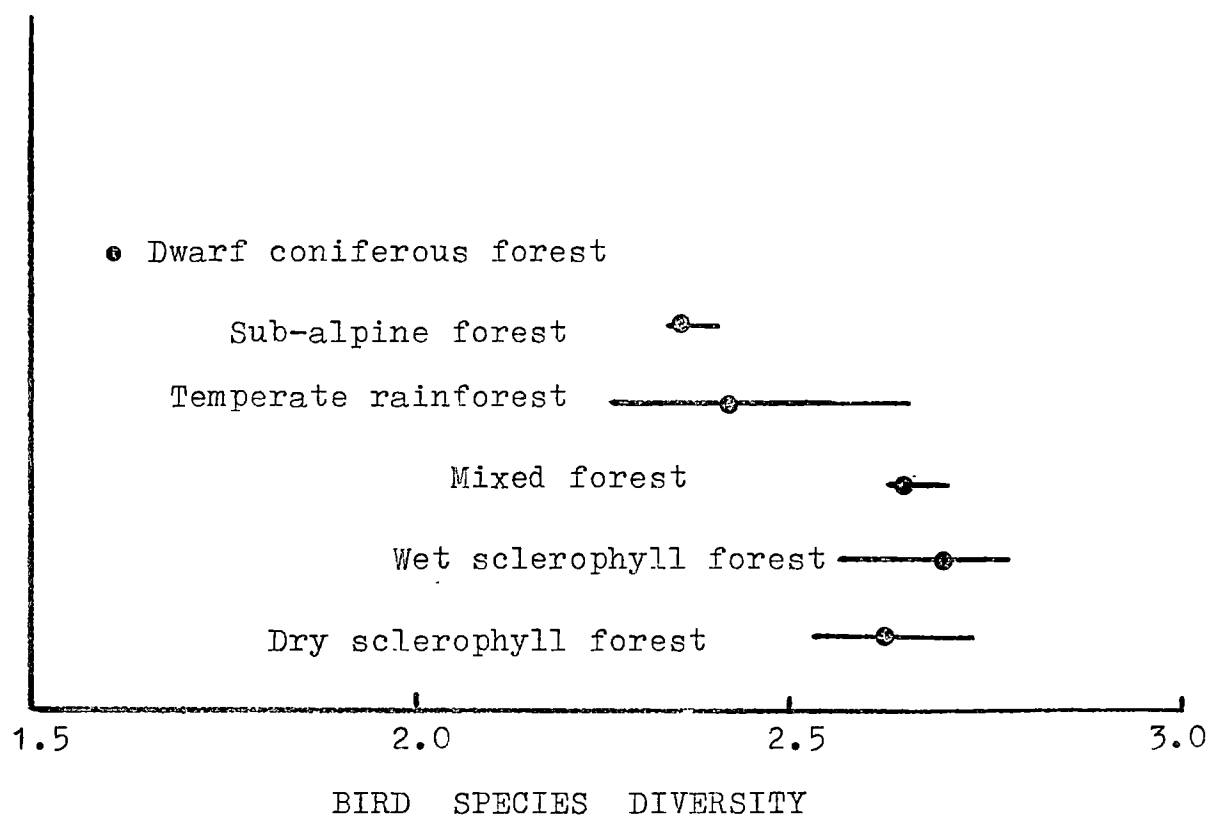


TABLE 21. Comparison of BSD in southern hemisphere
temperate rainforests.

LOCALITY	NO.OF SITES	BSD		SOURCE OF DATA
		RANGE	MEAN	
Chile	1		2.49	Cody (1970)
Patagonia	1		1.43	Vuilleumier (1972)
New Zealand-South Is.	1		2.65	Caughley (1962)
New Zealand-North Is.	7	1.97-2.44	2.21	Kikkawa (1966)
Tasmania	3	2.24-2.64	2.41	This study

census techniques used by the workers concerned. It is not entirely clear how Caughley (1962) arrived at his values for the abundance of species in temperate rainforest in the North Island of New Zealand. It appears that his technique underestimates the importance of the more abundant species and this could well account for the abnormally high value of BSD calculated from his data. It is unlikely that differences in method of censusing alone can account for the low value of H for Patagonia.

The equitability component of BSD, calculated from equation (2), is

Chile	1 site	0.88
Patagonia	1 site	0.60
N.Z. North Is.	1 site	0.92
N.Z. South Is.	7 sites	0.86 - 0.95 (mean 0.92)
Tasmania	3 sites	0.81 - 0.91 (mean 0.85)

Possibly the equitability component varies from region to region but is fairly constant within a region, e.g. New Zealand. It would appear that New Zealand temperate rainforest has slightly greater equitability than Tasmanian temperate rainforest on average although there is considerable overlap if the values for the individual sites are considered. The Chilean value falls within the ranges for both New Zealand and Tasmania. The low value for Patagonia arises because a single species accounts for 37 per cent of the census and this accounts for the low value of BSD obtained by Vuilleumier (1972).

4.6 NUMBER OF SPECIES ALONG THE XERIC-MESIC GRADIENT

The number of species declines steadily towards the

mesic end of the xeric-mesic gradient (Table 20). However, sub-alpine forest has slightly more species than temperate rainforest, possibly because it is a Eucalyptus dominated habitat.

4.7 RELATIVE DENSITY ALONG THE XERIC-MESIC GRADIENT

The census method used allows relative, but not absolute, density to be calculated. Relative bird density is calculated from

$$\text{Relative density} = \frac{\text{total records}}{\text{no. of traverses} \times (\text{transect length}/50)} \quad (4)$$

Relative densities are included in Table 19. Mean densities for the various habitats are given in Table 22.

From the most open dry sclerophyll relative density increases, reaching a maximum in wet sclerophyll. Wet sclerophyll forest, including mixed forest, is often regarded as an ecotonal disclimax between dry sclerophyll forest and temperate rainforest (Jackson 1965). Maximum relative density occurs in sites with the greatest per cent vegetation cover (Table 19), in this case with a well-developed shrub layer. It is not surprising that relative density decreases from this maximum, the decrease starting in the more mesic wet sclerophyll sites. There is considerable variation in relative density between sites in the same habitat. Two sites, Olga Camp and Beattie's Tarn, have higher relative densities than would be expected from the densities recorded at other sites in the same habitats. If these sites are excluded, there is little difference in bird density in mixed forest, temperate rainforest and sub-alpine forest. Dwarf coniferous forest has low relative density as well as having few species

TABLE 22. Mean relative bird densities for Tasmanian
habitats along the xeric-mesic gradient.

<u>HABITAT</u>	<u>MEAN RELATIVE DENSITY</u>
Open dry sclerophyll forest (1 site)	1.929
Dry sclerophyll forest (2)	4.130
Dry-wet sclerophyll forest (1)	4.620
Wet sclerophyll forest (4)	5.284
Mixed forest (2)	3.819
Temperate rainforest (3)	4.927
Sub-alpine forest (3)	4.260
Dwarf coniferous forest (1)	2.500

and low BSD.

Surprisingly, the highest relative density recorded was for a site (Olga Camp) in temperate rainforest. The relative densities and number of species recorded do not support Ridpath and Moreau's (1966) view that there is a paucity of birds in Tasmanian temperate rainforest.

That some species may occur at high densities in temperate rainforest is shown by an estimated density of Crescent Honeyeaters at Sir John Falls Camp on the Lower Gordon River of $330 \pm \text{S.D. } 77$ per 40 hectares in the 1976 breeding season. This value was derived from sound records using the formula derived by Gates (1969)

$$N = n (2n - 1) A / 2 L \sum r \quad (5)$$

where

N = density

n = number of individuals

A = area

L = transect length

r = distance of individual from observer

The standard deviation S.D., is given by

$$\text{var } (N) = \left[\frac{n}{2L/A\lambda} \right] \left[\frac{3n - 2}{2(n-1)(2L/A\lambda)} - 1 \right] \quad (6)$$

where

$$\lambda = (2n - 1) / \sum r \quad (7)$$

Even if the estimated density is out by a factor of two, the density is still high at c. 180 per 40 hectares.

The use of equation (5) is restricted to species which are distributed evenly throughout the census area (Poole 1974).

This appears to be so for the Crescent Honeyeater. λ may be considered to represent the 'visibility' of a species and should be constant for a species that is evenly dispersed even though overall density may vary markedly.

The Gates formula was applied to records of all species obtained from a transect undertaken in wet sclerophyll forest at Myrtle Gully, the results of which are included in Appendix 11. The λ values obtained at Sir John Falls and Myrtle Gully, 0.029 and 0.023 respectively, are sufficiently similar to justify the assumption of even dispersal. The λ values obtained at Myrtle Gully tend to clump around 0.017 - 0.033 for large or very vocal species and 0.100 - 0.120 for the small less conspicuous species.

4.8 EQUITABILITY OF TASMANIAN HABITATS

It has been shown that there are differences in BSD, number of species and relative density of individuals in the different habitats. It remains to compare the equitability components of BSD. This is done in Table 23 for the individual sites. All values lie between 0.81 and 0.91, a fairly narrow range.

Wet sclerophyll forest, mixed forest and dwarf coniferous forest have higher equitability components than the other habitats, as summarised in Table 24. This implies that individuals are slightly more evenly distributed among the species in wet sclerophyll, mixed and dwarf coniferous forests than they are in the other habitats. However, individual sites may show higher equitability than other

TABLE 23. Equitability component of BSD for Tasmanian sites.

<u>SITE</u>	<u>EQUITABILITY</u>
1. Pottery Road D	0.81
2. Pottery Road A	0.82
3. Pottery Road C	0.85
4. Pottery Road E	0.88
5. Pottery Road B	0.83
6. Myrtle Gully	0.85
7. Mount Field	0.90
8. Clemes Peak	0.89
9. Tahune	0.91
10. Tim's Track	0.87
11. Gordon River A	0.83
12. Gordon River B	0.81
13. Neika	0.82
14. Beattie's Tarn	0.81
15. Lake Dobson	0.81
16. Pandanni Grove	0.89
17. Olga Camp	0.91

TABLE 24. Mean equitability component of BSD for Tasmanian habitats

<u>HABITAT</u>	<u>EQUITABILITY</u>
Dry sclerophyll forest	0.83
Wet sclerophyll forest	0.88
Mixed forest	0.89
Temperate rainforest	0.85
Sub-alpine forest	0.81
Dwarf coniferous forest	0.89

sites in the same habitat as is shown by the value obtained in temperate rainforest at Olga Camp.

In all Tasmanian habitats the large equitability component and its generally small range for a particular habitat suggests that H , as given by the Shannon-Wiener function, may be a reasonable measure of species diversity.

4.9 DOMINANCE

A different way of looking at equitability is to consider the contribution of the two most abundant species to the total census. McNaughton and Wolf (1970) define dominance index (DI) as

$$DI = (Y_1 + Y_2) / Y \quad (8)$$

where Y_1 and Y_2 are the abundance of species 1 and 2, the two most abundant species, and Y is the total for all species. The mean values of DI for Tasmanian habitats are given in Table 25 and shown schematically in Figure 12.

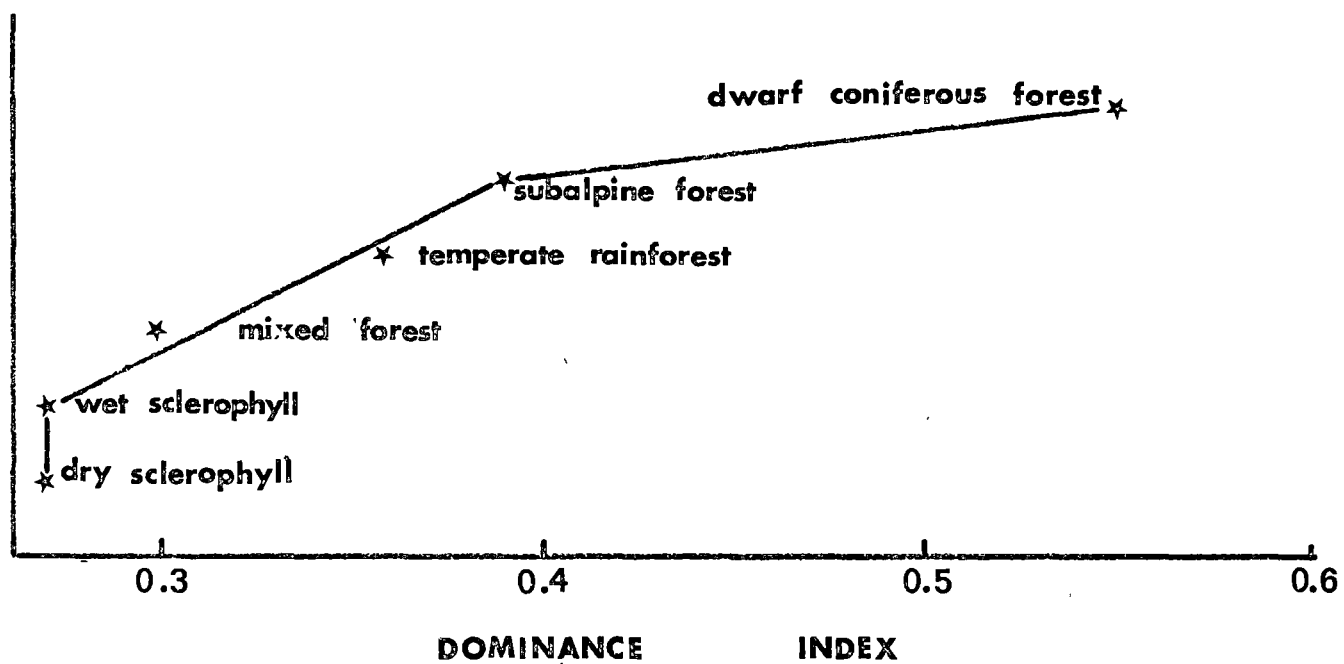
Dominance index increases along the xeric-mesic gradient. McNaughton and Wolf relate dominance to the 'harshness' of the environment in both shrub-grass and avian communities. Karr (1971) has shown that the mean dominance index is higher in temperate environments than in tropical ones and implies that temperate environments are harsher than tropical environments. The present study indicates that the more-mesic Tasmanian habitats are harsher than the more-xeric habitats (see also Chapter 3.4.7). Harsher environments may have greater diurnal and/or seasonal fluctuations, greater hydrologic fluctuations, or lower productivity.

The one species that contributes to the high value of DI

TABLE 25. Mean dominance index for Tasmanian habitats.

<u>HABITAT</u>	<u>DOMINANCE INDEX</u>
Dry sclerophyll forest	0.27
Wet sclerophyll forest	0.27
Mixed forest	0.30
Temperate rainforest	0.36
Sub-alpine forest	0.39
Dwarf coniferous forest	0.50

FIGURE 12. Dominance index along the Tasmanian xeric-mesic gradient.



for temperate rainforest, sub-alpine forest and dwarf coniferous forest is the Crescent Honeyeater (see census results in Appendix 11). Surprisingly, Ridpath and Moreau (1966) do not list the Crescent Honeyeater as occurring in temperate rainforest.

The dominance index can be calculated for the southern hemisphere Nothofagus forests :

Chile	0.35
Patagonia	0.51
New Zealand- South Is	0.38

The values for Tasmania, Chile and New Zealand are similar but the Patagonian value is considerably higher, which agrees with the equitability components of BSD, where the Patagonian value differs markedly from the others.

4.10 BIRD DISTRIBUTION ALONG THE XERIC-MESIC GRADIENT

Appendix 13 shows the distribution of species along the xeric-mesic gradient. Appendix 13 is based on the census results in Appendix 11. However, it is well known that as the area censused is increased the greater the number of species that are recorded. To allow for this, species recorded just outside the actual census area and additional species recorded in the census area during the breeding season are included in Appendix 13. Records from outside the census area were included only if the habitat was similar to that of the census area. The breeding season was as defined previously.

Appendix 13 is essentially similar to Appendix 3 and clearly confirms that no species of bird is restricted to temperate

rainforest in Tasmania.

4.11 BIRD SPECIES DIVERSITY AND HABITAT

MacArthur and MacArthur (1961) related BSD to foliage height diversity FHD with spectacular success for North American habitats. They divided the vegetation into three layers : 0 - 2, 2 - 25 and >25 feet and calculated both BSD and FHD using the Shannon-Wiener function. Recher (1969) showed subsequently that the same relation held for northern New South Wales and unpublished work by the University of Tasmania Zoology Department showed that it held also for Tasmanian habitats. The Australian and Tasmanian work was restricted to low-altitude habitats dominated by eucalypts.

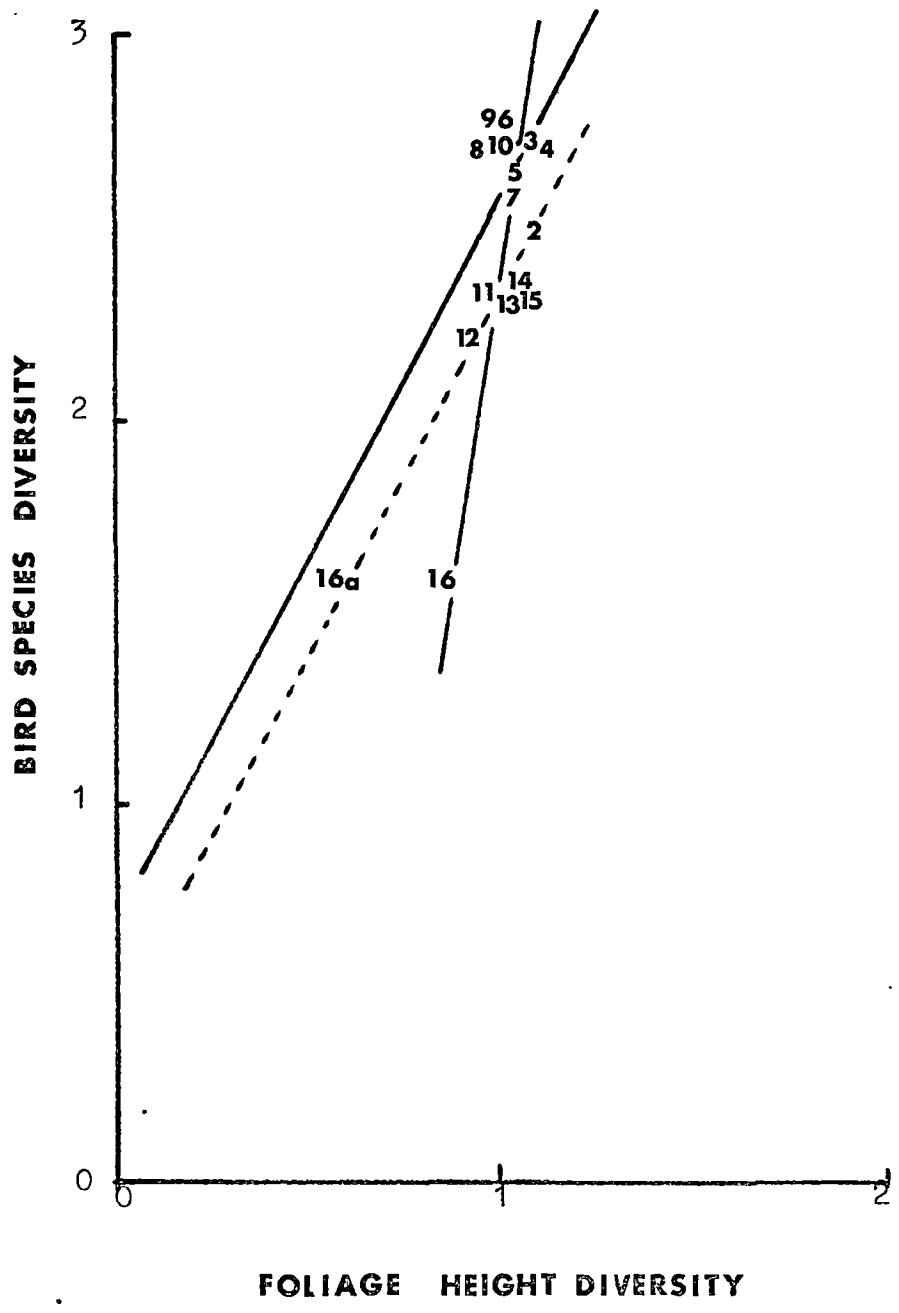
Botanically the three layers correspond to the herb, shrub and tree layers. It seems logical that BSD, however measured should depend on the relative extents of these three layers. In some habitats, e.g. wet sclerophyll forest it is by no means obvious where each layer begins and ends. This problem has obviously been encountered by others who have used different height intervals to those used originally by MacArthur and MacArthur (1961). Thus, Karr and Roth (1971) used 0 - 2, 2 - 20 and >20 feet. I suggest that exact height intervals need not be used. Rather, each habitat should be divided according to its actual structure. A 'herb' layer extending to five feet may be more meaningful in wet sclerophyll forest but a herb layer of only two feet appears more meaningful in many areas of dry sclerophyll forest.

FHD of Tasmanian habitats was calculated using the intervals 0 - 2, 2 - 20 and > 20 feet. BSD has been plotted

against FHD in Figure 13. The points fall into three groups : close to the regression line obtained by MacArthur et al. (1966) for North American habitats; somewhat below the regression line; well below the regression line. With one exception (Point 2) the points lying below the regression line relate to the more-mesic habitats temperate rainforest, sub-alpine forest and dwarf coniferous forest. Only one point from this group of habitats falls close to the regression line. A straight line has been fitted by eye to the Tasmanian points. This has a much steeper slope than the regression line of MacArthur et al. and gives a negative intercept, which is unrealistic.

Bearing in mind that points obtained previously for sclerophyllous Tasmanian habitats fall close to the regression line, an alternative explanation can be offered : the regression of BSD on FHD has the same slope for the xeric and mesic habitats but has different intercepts. The suggested slope of the BSD v FHD relation for the more mesic habitats is shown in Figure 13 as a dashed line parallel to the original regression line of MacArthur et al. The regression line obtained by Karr and Roth (1971) for data from Illinois (North America) and Panama is also parallel to the original regression line but the intercepts are different. Cody (1970) found that BSD is underestimated by the original regression for Chilean habitats. Cody obtained a better fit if Chilean habitats were divided into four layers, although his point for Nothofagus forest fell closer to the regression line if this habitat was divided into three layers. There is no suggestion that the more-mesic Tasmanian habitats should be divided into four layers as this would move the points

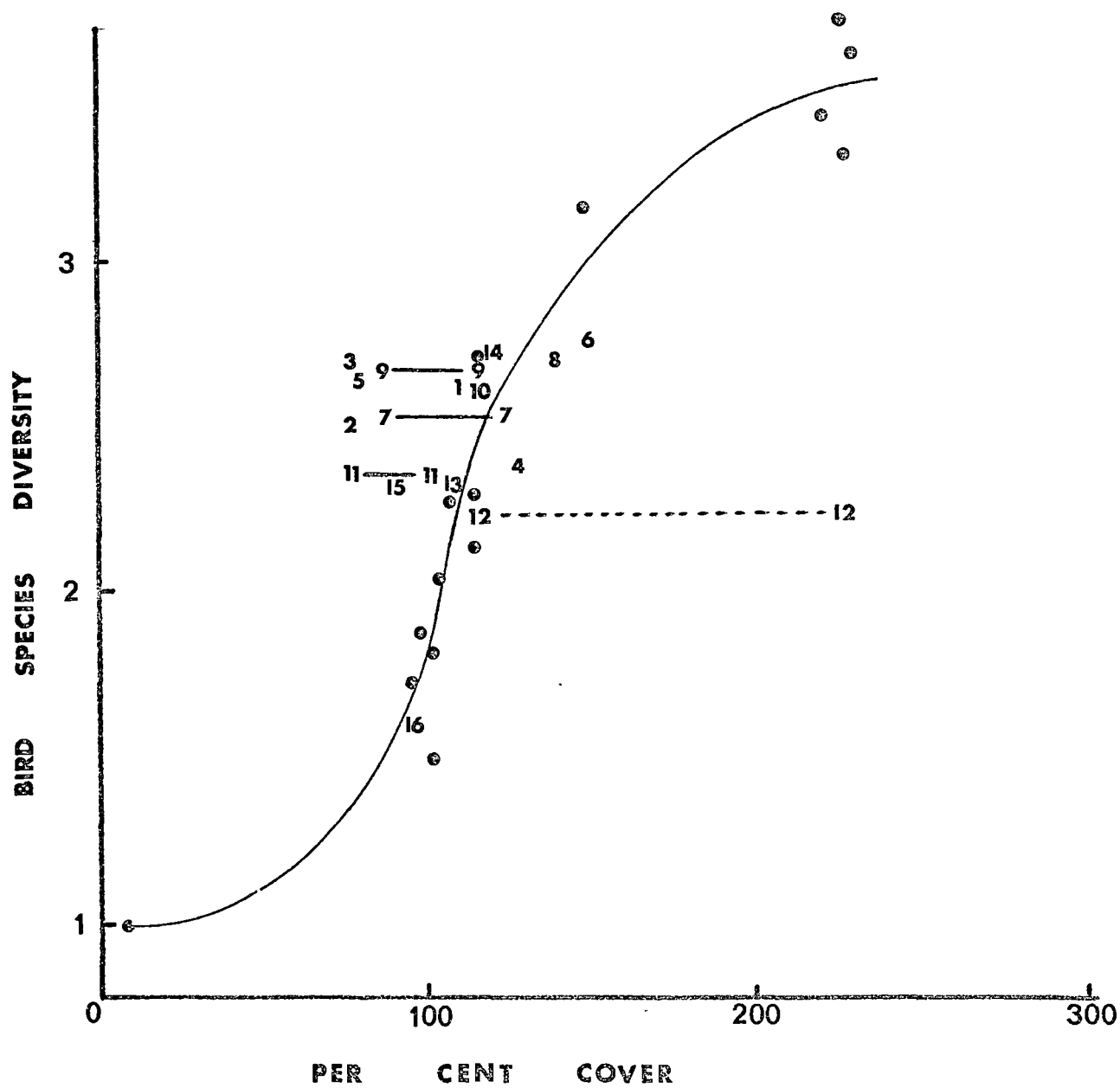
FIGURE 13. The relation between bird species diversity and foliage height diversity. The regression line is that due to MacArthur et al. (1966)



further from the regression line. The possibility that birds divide Tasmanian temperate rainforest into two layers, as they do on Puerto Rico, an island (MacArthur et al. 1966) should be examined. Points 11 and 12 can be brought closer to the original regression line if the vegetation is divided into two layers. However, the layers are different for the two sites : 0 - 20 and >20 feet for site 11 (Gordon River A) and 0 - 8 and >8 feet for site 12 (Gordon River B). As these sites are structurally very different (Appendix 12) this may be justified and the possibility that birds divide temperate rainforest into two layers cannot be discounted. To resolve this point would require large masses of data. The point (site 16) falling well below the original regression line can be brought closer (to 16a in Figure 13) if this site (Pandanni Grove) is divided into two layers.

Following Margalef (1958), Karr and Roth (1971) showed that there was a sigmoidal relation between BSD (as measured by the information statistic) and per cent vegetation cover. This relation overcomes any problem associated with using the information statistic for determining FHD, while still using it to calculate BSD. However, the problem of choosing the vegetation layers remains. In spite of this, it was felt to be worthwhile to compare the results of the present study with those of Karr and Roth using the same height divisions, viz. 0 - 2, 2 - 20 and >20 feet. Per cent vegetation cover is the sum of per cent covers in each layer over all layers of vegetation. The results are given in Figure 14 which includes Karr and Roth's data. The agreement is reasonably good with the exception of sites 2, 3, 5, 7, 9, 11 and 12. Sites 7 and 9 essentially have a four-layer structure with an emergent

FIGURE 14. The relation between bird species diversity and per cent vegetation cover.

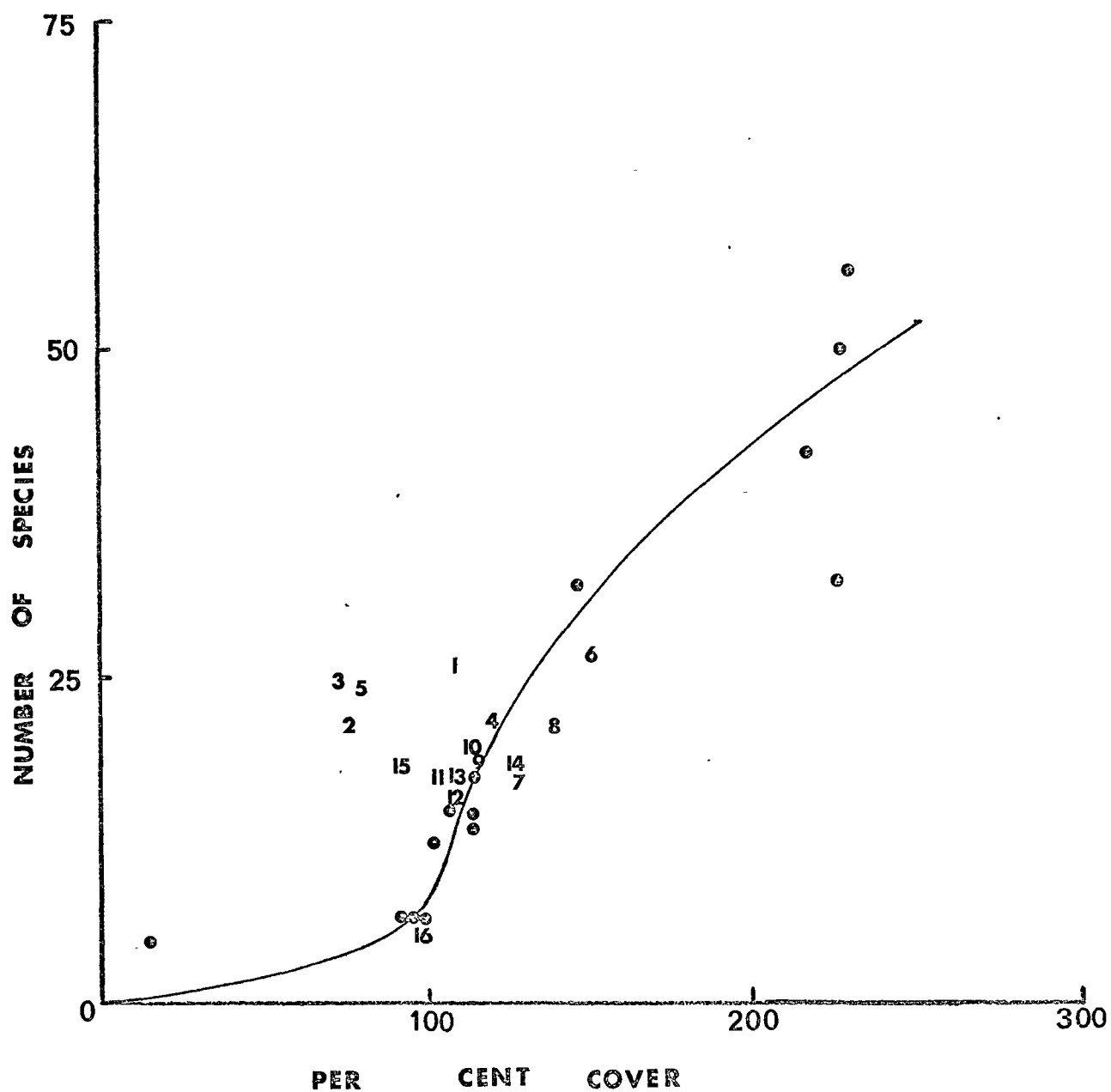


stratum of eucalypts. Site 11 (Appendix 12) can also be considered as having a four-layer structure with an emergent stratum of over-mature Nothofagus cunninghamii. In considering the regression of BSD on FHD it was shown that there was no reason to treat Tasmanian habitats as having four layers and that site 11 could consist of two layers. This paradox can be resolved if it is assumed that the presence of a sparse emergent stratum of tall trees depresses the per cent cover in the tree layer, giving rise to a smaller value of the total per cent vegetation cover. As suggested previously, site 12 could be considered as having only two layers (the herb and shrub layers consisting of tangled Horizontal and Cutting Grass). When these sites are treated in this way, the points fall closer to the line, as indicated in Figure 14.

Site 5 includes a sharp change from dry to wet sclerophyll forest and this may well be the reason why it lies above the line. The remaining sites, 2 and 3, are in dry sclerophyll forest that has been modified by past burning and inhomogeneity (better called patchiness) probably accounts for these sites having more species than predicted. A lack in precision in sampling patchy sites may be a contributing factor.

So far the information statistic has been used to determine BSD. To avoid the criticism that has been levelled at this measure, a different measure of diversity can be used. One such measure is simply the number of species, as suggested by Recher (1971). Figure 14 has been replotted in Figure 15 with number of species replacing BSD. Bearing in mind the uncertainties of determining the exact number of species

FIGURE 15. The relation between bird species numbers and per cent vegetation cover.



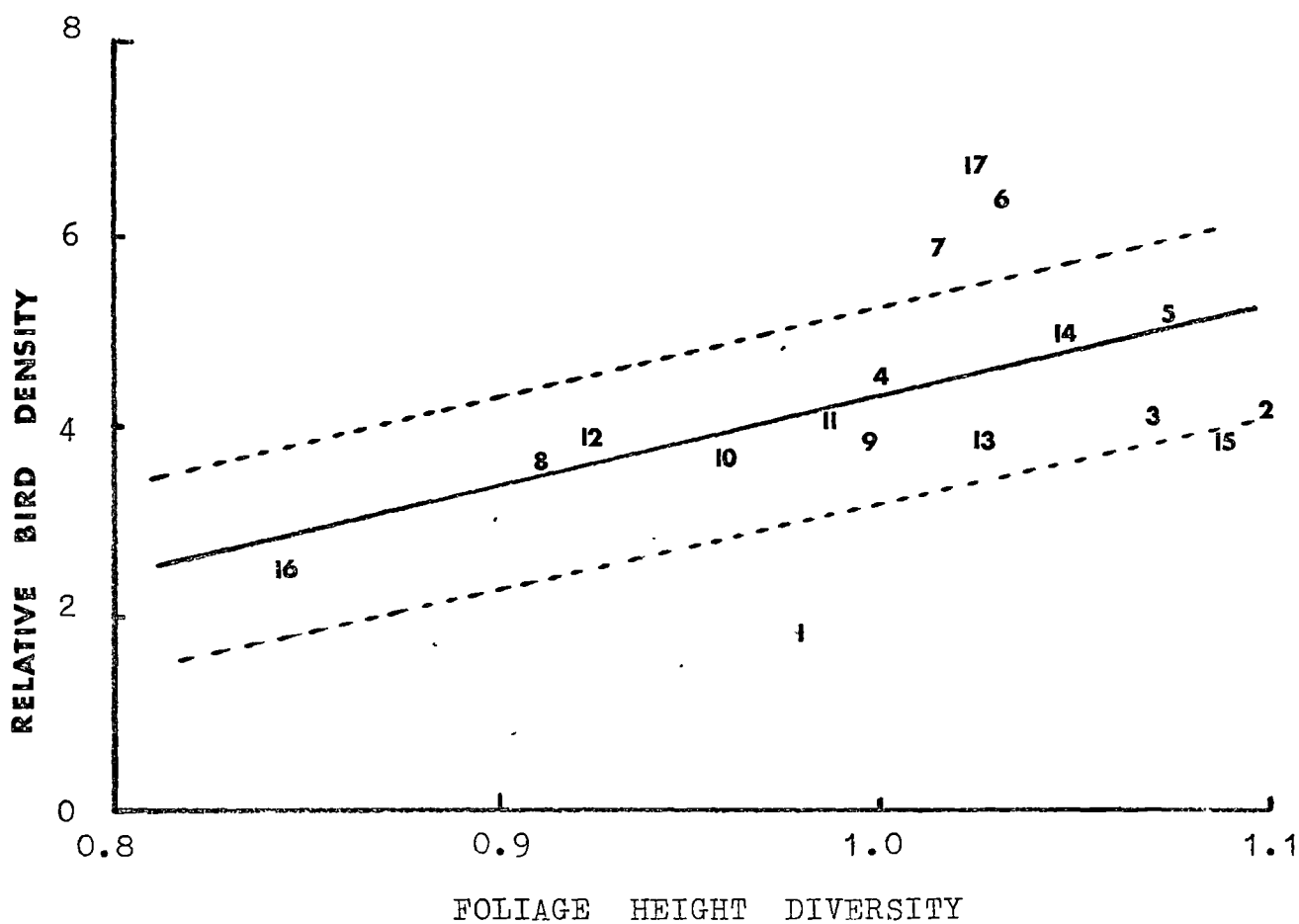
and per cent cover, particularly in patchy environments, the agreement is reasonably good apart from sites where the vegetation cover exceeds 200 per cent. Again, the dry sclerophyll sites 2 and 3 and the mixed dry-wet sclerophyll forest site 5 lie above the line. As was suggested for BSD, this probably results from patchiness.

Karr and Roth (1971) considered sites along a successional gradient ranging from bare ground to mature forest and concluded that with the addition of the first shrubs, diversity begins to increase more rapidly with a peak rate when both shrub and tree layers are being added. After that an asymptote is reached with only slight increases in diversity up to about 230 per cent vegetation cover, which is the region in which Figure 15 shows most scatter. Comparison of Figures 14 and 15 shows that per cent cover is correlated with both BSD and number of species for the more-mesic Tasmanian habitats but, from the data of Karr and Roth, the correlation between BSD and vegetation cover may be closer when the vegetation cover exceeds 200 per cent. The greater scatter at high vegetation cover in Figure 15 implies that more species are being added but that they are present at low densities and thus have little effect on BSD. It seems preferable to use BSD rather than number of species alone as the measure of diversity in spite of the criticism this has incurred. Number of species is, of course, important.

4.12 RELATIVE BIRD DENSITY AND FHD

Relative bird density is plotted against FHD in Figure 16. Most points lie in a narrow band showing that relative

FIGURE 16. The effect of foliage height diversity on relative bird density.



density increases with increasing FHD. As shown in Figure 16, the linear relation between relative density and FHD almost reaches significance at the 0.05 level. That other environmental factors may be important is shown by the few points that fall outside the band.

4.13 BIRD SPECIES DIVERSITY, NUMBER OF SPECIES AND EQUITABILITY

BSD is plotted against number of species in Figure 17. The data used are from this study (Table 19) and Table 1 of Karr and Roth (1971). An additional point 'x' has been added to show the effect of patchiness. Point 'x' (Dyynyrne) was obtained from a transect along the edge of a wet sclerophyll area that bordered an area of urban (cleared) land. In addition to showing any affect arising from patchiness, 'x' will also include any edge effects. The combined effect is that Dyynyrne is species-rich, as expected. Apart from this, there is good correlation between BSD and number of species. For $BSD > 3.25$, the addition of rare species has little influence on BSD and considerable scatter can result.

The relation between BSD and number of species was explored further for temperate rainforest. Figure 18 was based on the present study, Caughley (1962), Cody (1970), Vuilleumier (1972) and Tables II, III, IV and VII (all of which include counts in temperate rainforest) in Kikkawa (1966). Each point is represented by a number which is the equitability component of BSD. The plot can be divided into zones, separated by parallel linear boundaries, according to the

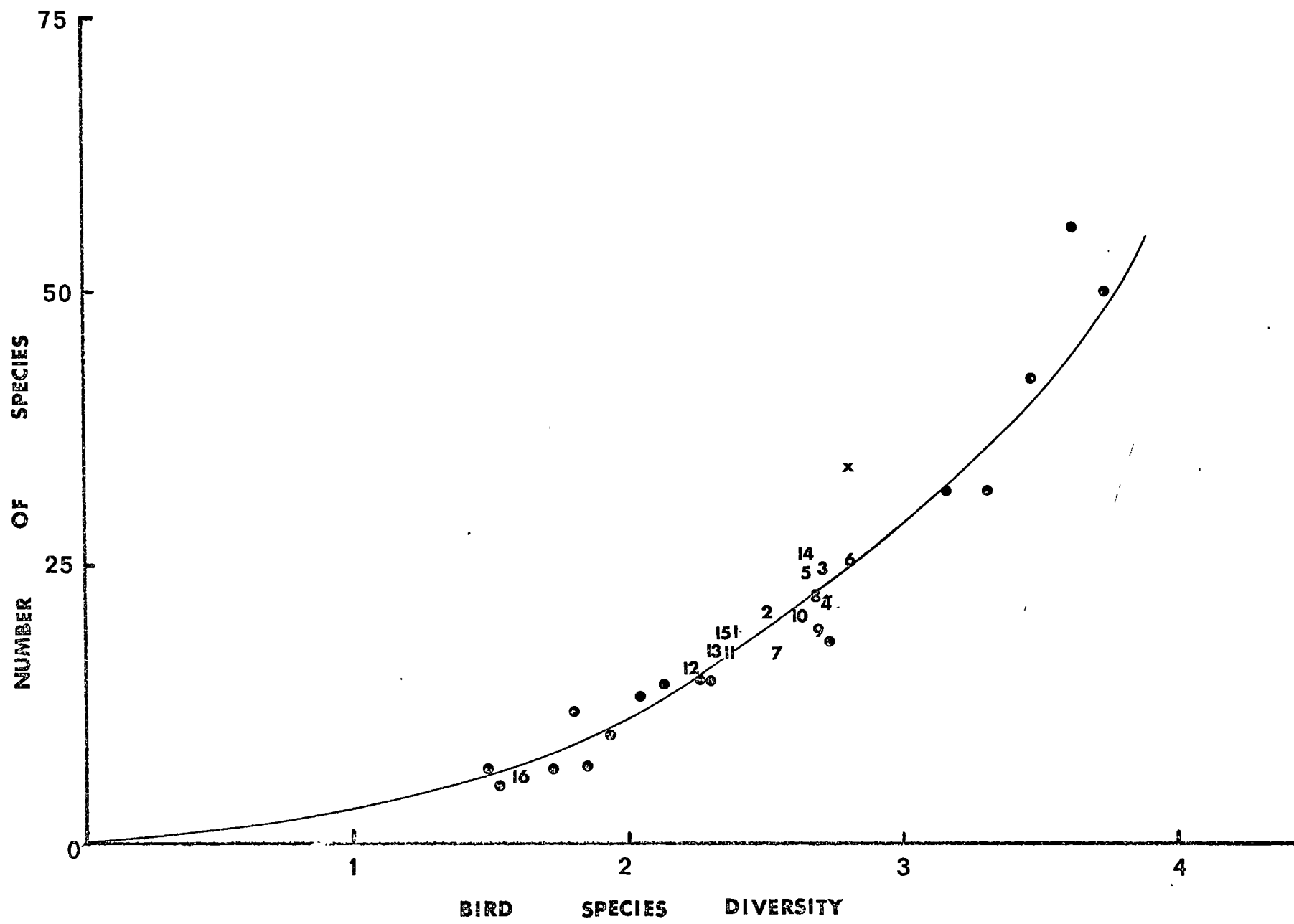


FIGURE 17. Bird species diversity and number of species.

FIGURE 18. Number of species, species diversity and equitability.

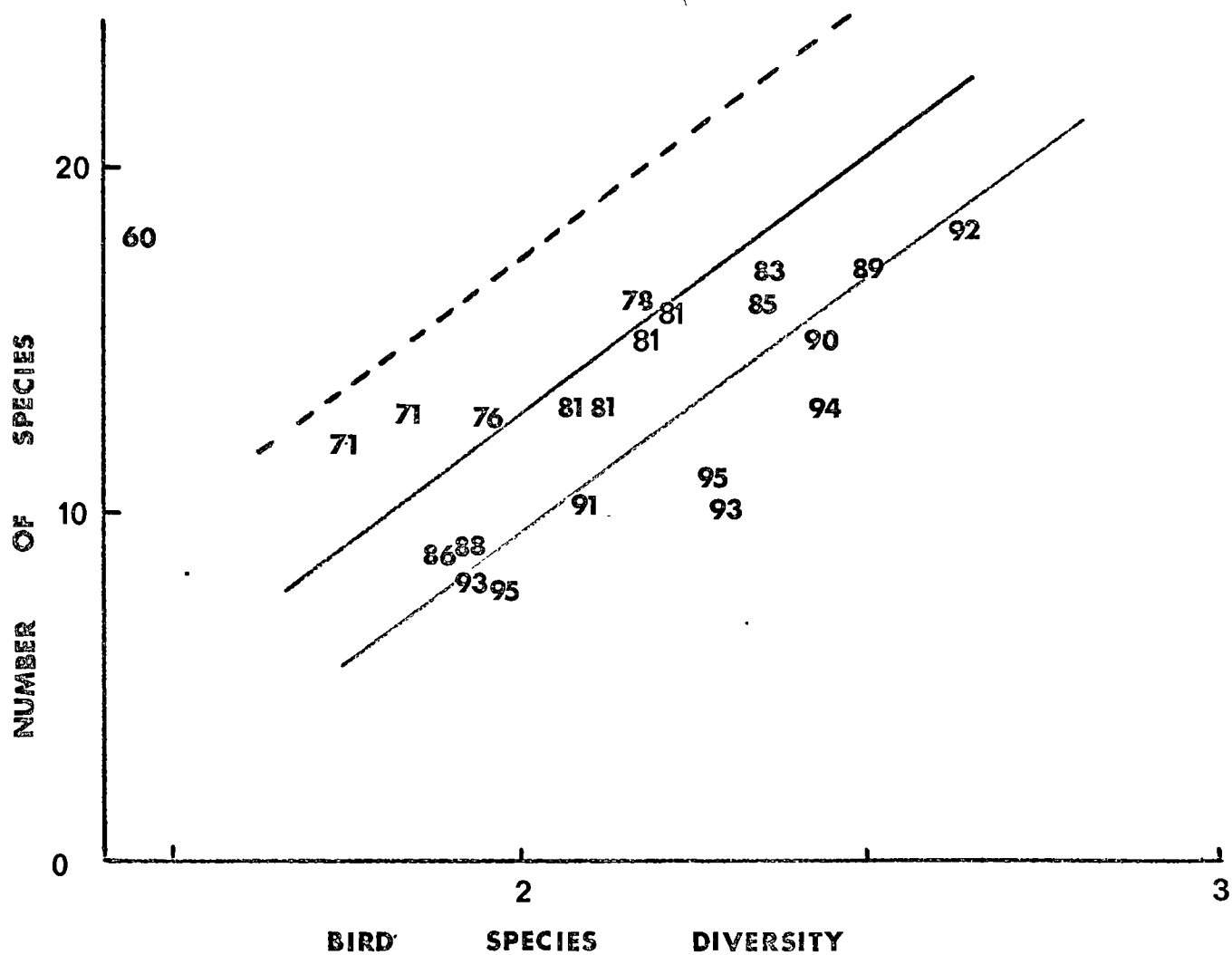
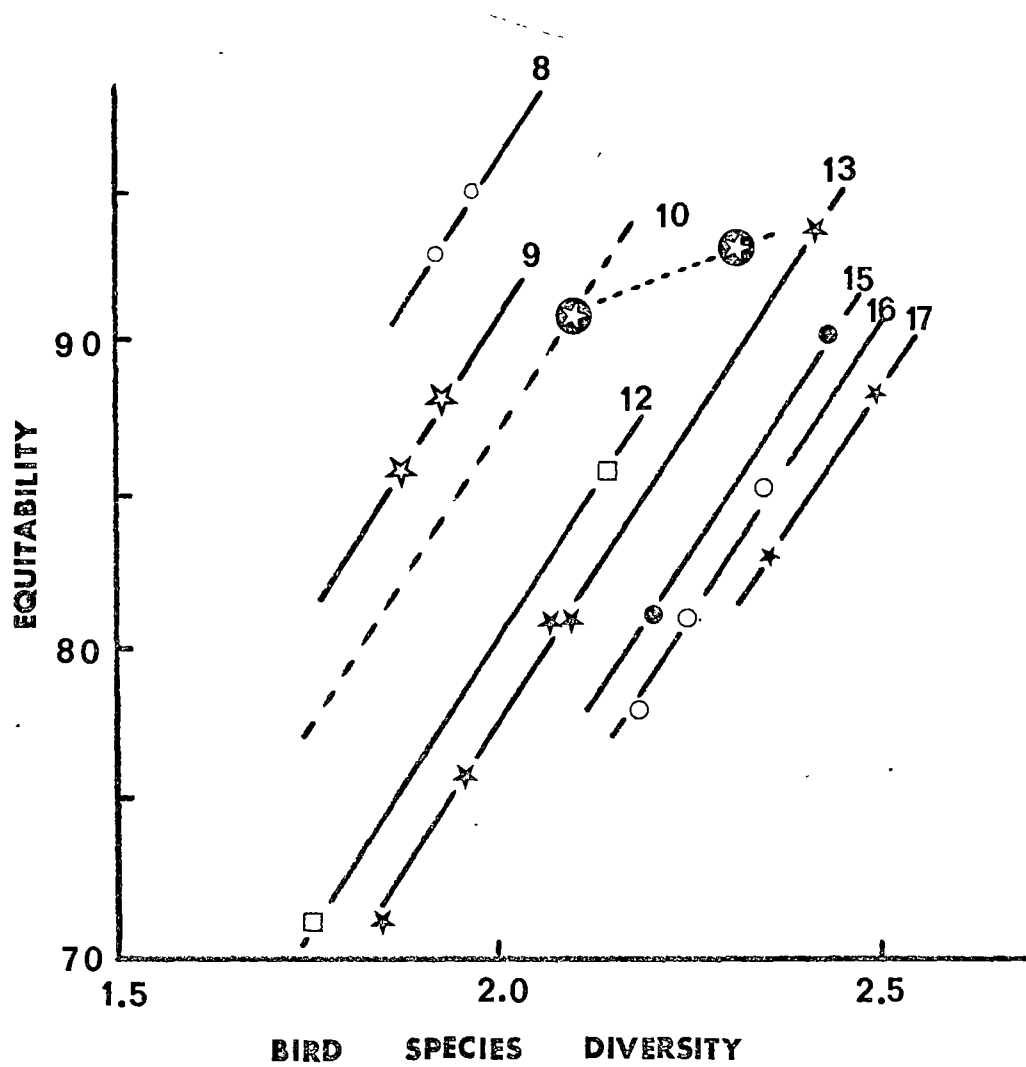


FIGURE 19. The effect of varying equitability and number of species on species diversity.



magnitude of the equitability component. Thus, it is justified to use the information statistic to compare species diversity provided that the equitability components are similar.

If equitability is plotted against BSD, as in Figure 19, the result is a series of parallel straight lines for the various values of S (number of species). For a given number of species, BSD increases as equitability increases.

Tramer (1969) found that differences in BSD between a wide range of breeding bird censuses (267) in North America were closely related to the number of species while the equitability component remained constant. This finding does not hold for temperate rainforest where both the number of species and the equitability component vary. It is preferable, therefore, to specify diversity by both the information statistic and the number of species rather than by either alone. When both are known, the equitability can be read directly from Figure 19. In this way, differences in diversity can be apportioned between differences in the number of species and differences in the distribution of individuals among the species.

CHAPTER 5

COMMUNITY STRUCTURE

5.1 INTRODUCTION

One of the fundamental questions of ecology is : how do species in a community manage to coexist ? Put another way : how similar can coexisting species be ? These aspects are considered in this chapter for Tasmanian temperate rainforest.

5.2 VERTICAL STRATIFICATION AND FEEDING BEHAVIOUR IN COOL - WET FORESTS

It was shown in Chapter 2.3 that there is considerable similarity between the avifaunas of wet sclerophyll forest, mixed forest and temperate rainforest. The main differences are due to the decrease in the number of species towards the mesic end of the xeric-mesic gradient. It is not unreasonable to assume that the manner in which birds exploit their environment remains sensibly constant within these habitats. This point was checked for several species by comparing the vertical stratification and feeding behaviour of a number of species in wet sclerophyll, mixed and temperate rainforests. These comparisons are made in Appendix 14 for vertical stratification and Appendix 15 for feeding behaviour. Percent similarities were calculated for each species pair from the formula devised by Schoener (1968)

$$\alpha_{xy} (D) = \left\{ 1 - \frac{1}{2} \sum_{i=1}^n |P_{x,i} - P_{y,i}| \right\} \cdot 100 \quad (9)$$

where $\alpha_{xy} (D)$ is the overlap between species x and y along niche axis D and the $P_{x,i}$ are the proportional occurrence of species x in each of the divisions of D, in this case vegetation layers and feeding sites. The results are given in Table 26.

TABLE 26. Similarities in vertical stratification and feeding behaviour of birds in wet sclerophyll forest, mixed forest and temperate rainforest.

SPECIES	HABITAT PAIRS	SIMIL. %	SPECIES	HABITAT PAIRS	SIMIL %
<u>VERTICAL STRATIFICATION</u>			<u>FEEDING BEHAVIOUR</u>		
Brown Scrubwren	WS-MF	98	Brown Scrubwren	WS-MF	90
	MF-TRF	88		MF-TRF	87
	WS-TRF	90		WS-TRF	87
Scrubtit	WS-MF	94	Scrubtit	WS-MF	83
	MF-TRF	90		MF-TRF	82
	WS-TRF	93		WS-TRF	73
Tasmanian Thornbill	WS-MF	81	Tasmanian Thornbill	WS-MF	83
	MF-TRF	83		MF-TRF	92
	WS-TRF	89		WS-TRF	75
Grey Fantail	WS-MF	94	Grey Fantail	WS-MF	79
	MF-TRF	93		MF-TRF	78
	WS-TRF	98		WS-TRF	83
Crescent Honeyeater	WS-MF	91	Pink Robin	WS-MF	79
	MF-TRF	62	Golden Whistler	WS-MF	88
	WS-TRF	68	Strong-billed Honeyeater	WS-MF	85
Green Rosella	WS-MF	80	Silvereye	WS-MF	95
Pink Robin	WS-MF	81			
Olive Whistler	WS-MF	80			
Striated Pardalote	WS-MF	99			

WS = wet sclerophyll forest

MF = mixed forest

TRF = temperate rainforest

For species that occur in all three habitats the mean similarities are :

Vertical stratification :

wet sclerophyll - mixed forest	92 %
mixed - temperate rainforest	83 %
wet sclerophyll - temperate rainforest	88 %

Feeding behaviour :

wet sclerophyll - mixed forest	84 %
mixed - temperate rainforest	85 %
wet sclerophyll - temperate rainforest	80 %

When the smallness of some of the samples is taken into account, the above figures confirm that there is little change in vertical stratification and feeding behaviour in the three formations. The differences found can be accounted for by the vagaries of sampling, particularly as birds are opportunistic feeders and results (especially for small samples) may be influenced by local transient abundances of food. It follows that little precision will be lost if data obtained in all three habitats are combined.

5.3 NICHE OVERLAPS

Communities can be understood in terms of niche dimensions along which species become segregated through competitive interactions. While niches are multi-dimensional, most communities appear to exist in three, or at the most four, such dimensions (Cody 1974). The niche dimensions that are considered usually are horizontal habitat separation, which I prefer to call patch preference, vertical stratification and differences in food and feeding behaviour.

5.3.1 PATCH PREFERENCE α_H .

The data on the occurrence of species at 15 sites in temperate rainforest reported in Appendix 3 were used to calculate overlaps in patch preference. Equation (9) was used with the $P_{x,i}$ being the proportion of sites in which one or both of the species being compared occurred. The resulting overlaps are detailed in Appendix 16.

5.3.2 VERTICAL STRATIFICATION α_V

Vertical stratification was determined by recording the vegetation layer (herb, shrub or tree) in which a bird was first located (Table 27). Niche overlaps, α_V , as calculated from equation (9) are recorded in Appendix 17.

Thomas (1974) has given vertical height distributions for the Brown Scrubwren, Scrubtit and Tasmanian Thornbill for the breeding season. Mean heights were

Brown Scrubwren	1.2 ft
Scrubtit	10.1 ft
Tasmanian Thornbill	19.5 ft

A similar study during the non-breeding season gave mean heights of

Brown Scrubwren	0.8 ft
Scrubtit	10.2 ft
Tasmanian Thornbill	20.2 ft

Thus, there is little evidence of seasonal change.

5.3.3 FEEDING BEHAVIOUR α_F

Feeding behaviour was determined by recording the feeding

TABLE 27. Vertical stratification. Combined data from wet sclerophyll, mixed and temperate rainforests.

SPECIES	NO.OF OBS	OCCURRENCE %		
		HERB	SHRUB	TREE
Brush Bronzewing	20	100	0	0
Yellow-tailed Black Cockatoo	45	16	31	53
Green Rosella	133	10	22	68
Shining Bronze Cuckoo	14	0	84	14
Scaly Thrush	100	80	20	0
Pink Robin	101	15	83	2
Olive Whistler	88	15	78	7
Golden Whistler	28	0	14	86
Grey Shrike-thrush	63	10	17	73
Grey Fantail	349	13	60	27
Brown Scrubwren	336	86	14	0
Scrubtit	101	23	76	1
Tasmanian Thornbill	376	11	72	17
Yellow-throated Honeyeater	237	5	48	48
Crescent Honeyeater	385	8	50	42
Eastern Spinebill	12	33	50	17
Silvereye	131	9	52	39
Black Currawong	24	25	17	58
Forest Raven	38	24	8	68

zone(s) in which feeding movements were made. Records were restricted to five per individual. The feeding zones used were : air (hawking); ground, herb layer; litter lying on the ground but excluding fallen leaves; trunks; branches; twigs; foliage; flowers (whether seeking nectar, pollen or insects). The results are given in Table 28 and the calculated overlaps in Appendix 18.

5.4 NICHE OVERLAPS AND THE COMMUNITY MATRIX

α_H, α_V and α_F can be regarded as partial competition coefficients in the Volterra competition equations. The problem of combining the partial coefficients into a single coefficient has been discussed by Cody (1974). He assumed that species differ in each niche dimension separately and that coexistence can be achieved by species pairs exceeding some threshold of minimum ecological difference. This led him to propose two measures of niche overlap :

'Summation alpha', $\underline{\alpha}$, which is given by

$$\underline{\alpha} = \sum^k (\alpha_R) / k = (\alpha_H + \alpha_V + \alpha_F) / 3 \quad (10)$$

and 'product alpha', $\underline{\alpha}$, given by

$$\underline{\alpha} = \Pi^k (\alpha_R) = \alpha_H \cdot \alpha_V \cdot \alpha_F \quad (11)$$

Both $\underline{\alpha}$ and $\underline{\alpha}$ lie between 0 and 1.

For niche dimensions that are quite independent, product alpha gives the best estimate but when niche dimensions are nonindependent, summation alpha is the more accurate estimator. Both $\underline{\alpha}$ and $\underline{\alpha}$ have been calculated, using the data in Appendices 16, 17 and 18. Values of $\underline{\alpha}$ are given in the form of a

TABLE 28. Feeding behaviour. Combined data from wet

sclerophyll, mixed and temperate rainforest.

A = air, G = ground, H = herb, Li = litter,

Tr = trunk, B = branch, Tw = twig, L = leaf,

F = flowers.

	N	OCCURRENCE %								
		A	G	H	Li	Tr	B	Tw	L	F
Brush Bronzewing	28		100							
Yellow-tailed Black Cockatoo	31		6		16	23	55			
Green Rosella	81		9			7	6	33	23	21
Shining Bronze Cuckoo	62			2	3	15	68	5	8	
Scaly Thrush	67		88	3	9					
Pink Robin	159	8	39	1	9	15	15	4	9	
Olive Whistler	118	1	8	18	4	5	5	7	53	
Golden Whistler	62	2				2		8	88	
Grey Shrike-thrush	94		12		3	49	34	1	1	
Grey Fantail	850	47	4	1	4	4	3	12	25	+
Brown Scrubwren	783	+	27	14	49	4	3	1	2	
Scrubtit	550	+	1	5	6	47	35	2	3	
Tasmanian Thornbill	1284	1	+	1	+	6	10	19	63	
Yellow-throated Honeyeater	384	9	4		1	37	26	11	9	4
Crescent Honeyeater	465	8	2	1	1	35	15	16	9	14
Eastern Spinebill	1040	8	+	2	1	1	+	3	12	73
Silvereye	224			+	2				94	4
Black Currawong	27		100							
Forest Raven	21		100							

community matrix in Appendix 19. Similarly, values of $\underline{\alpha}$ are also given in Appendix 19. Both were calculated because it is quite uncertain whether niche dimensions are independent in temperate rainforest.

The data for \underline{a} were used to construct the community dendrogram given in Figure 20. The strategy used, Group Average, weights the similarity in proportion to the number of members in each group. Thus, in calculating the similarity, upon fusion of a 6-member group with a 2-member group, with some third group, the similarity of the third group is obtained by taking $\frac{3}{4}$ of the similarity with the larger group and adding $\frac{1}{4}$ of the similarity with the smaller group. This differs from the method used by Cody who took the straight arithmetic average of the groups under consideration, irrespective of the number of items in each group - a procedure that is virtually obsolete (D. Ratkowski pers. comm.).

The distribution of \underline{a} is shown in Figure 21, while Figure 22 shows the distribution of $\underline{\alpha}$. The observed distributions of niche overlaps can be compared with distributions generated from random associations of numbers with the same range as niche overlap (0 - 1) as given by Cody (1974). These 'expected' distributions are also included in Figures 21 and 22. The expected distribution of summation alpha was generated by summing three numbers independently chosen from a flat distribution with range 0 - 1; by the central limit theorem, this produces a normal looking curve, with its mean at 0.50. The expected distribution for product alpha is obtained by taking the products of three numbers drawn with

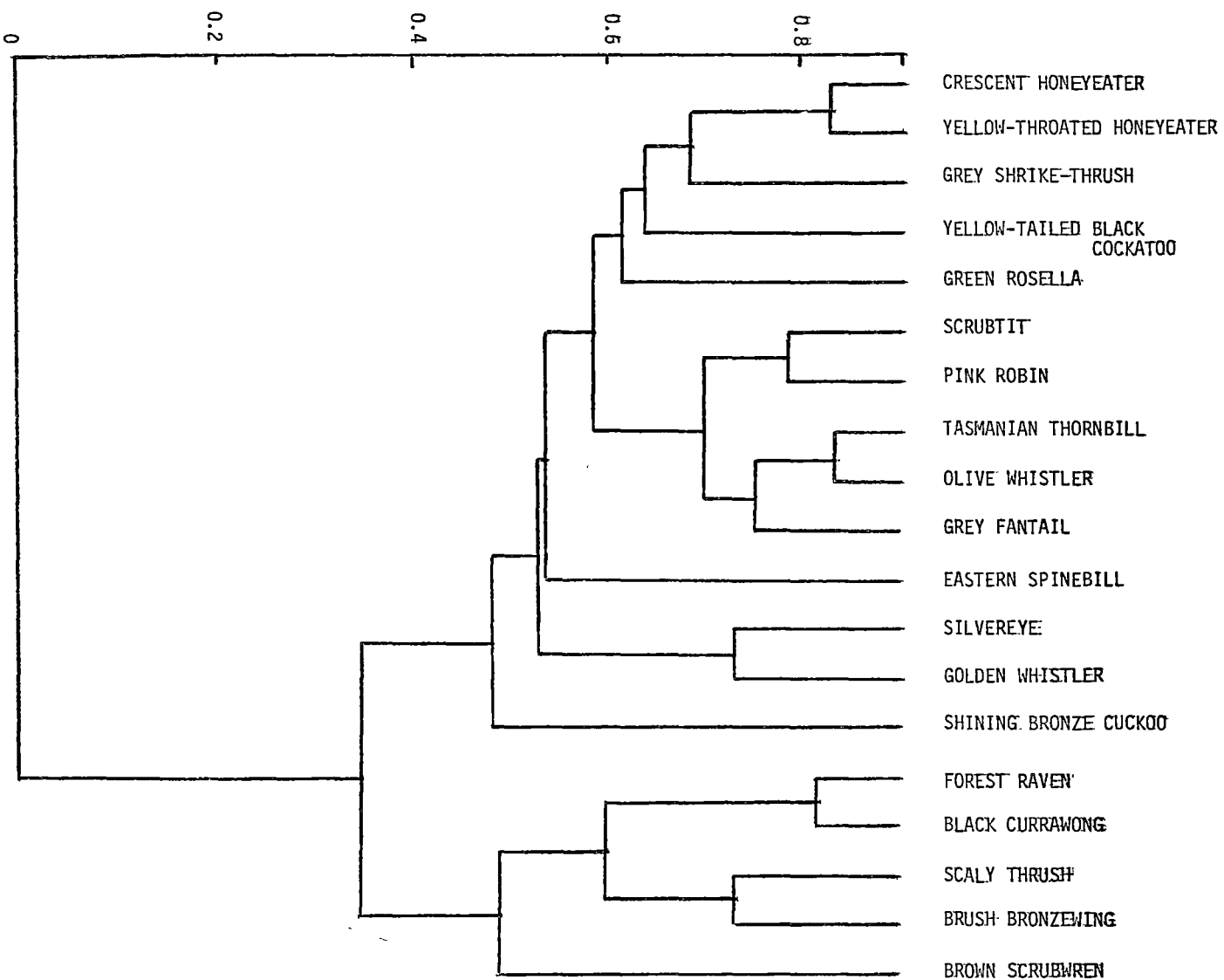


FIGURE 20. Hierarchical classification of species in Tasmanian temperate rainforest.

FIGURE 21. Distribution of summation alpha.

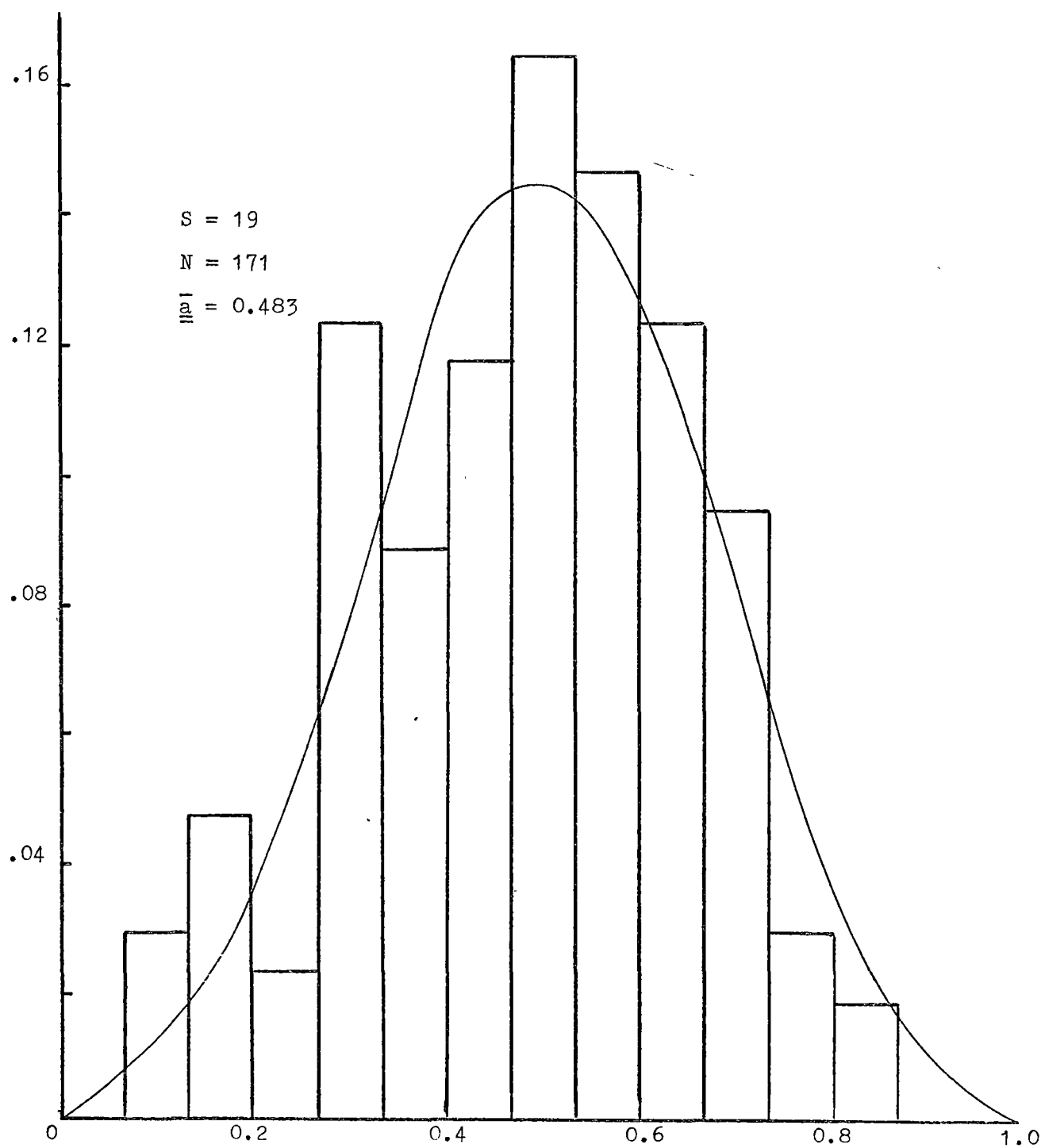
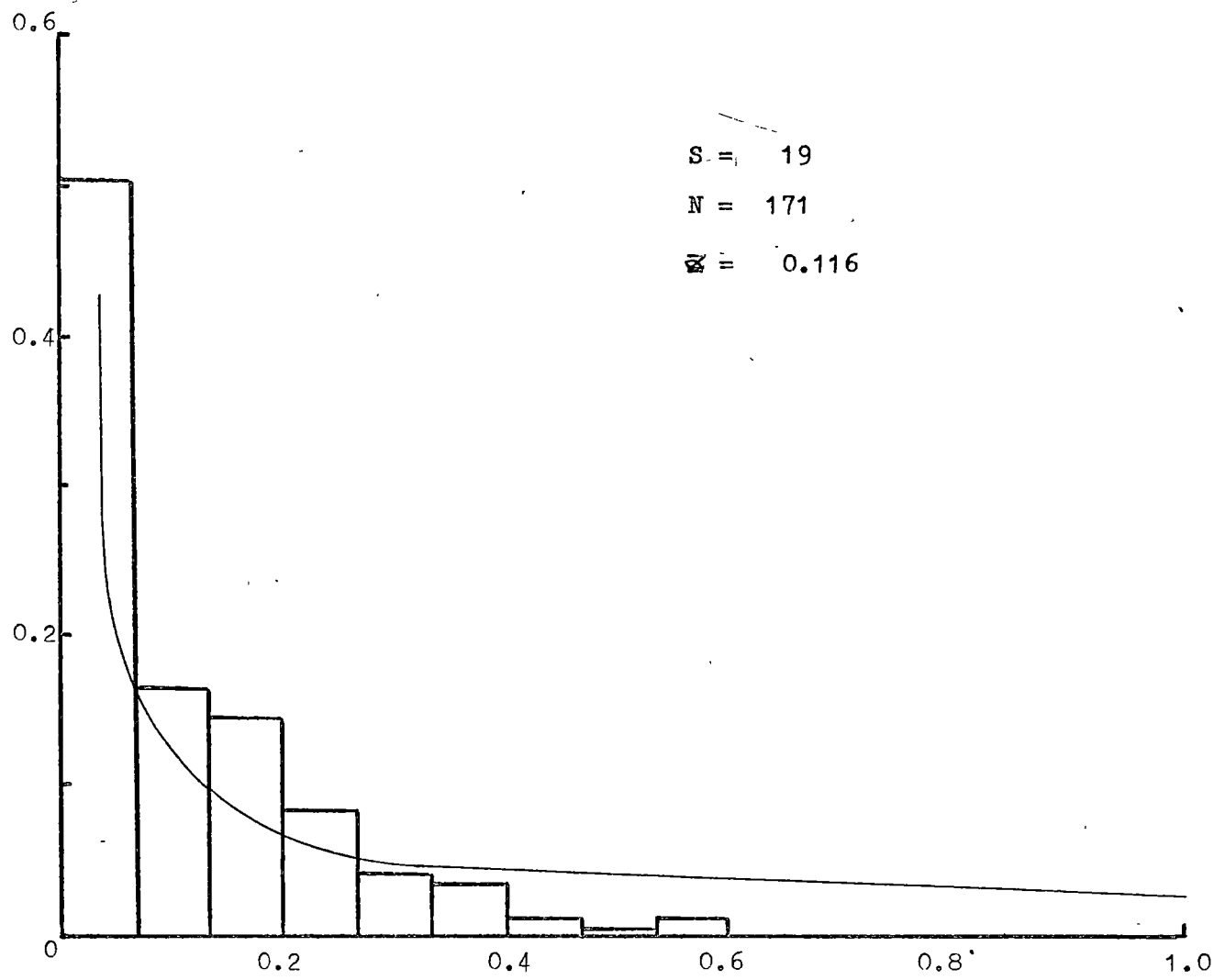


FIGURE 22. Distribution of product alpha.



equal probabilities from the same flat distribution range 0 - 1. This yields a curve with one-half of the products less than $(0.5)^2 = 0.125$, and half in the long tail above 0.125.

The observed distributions deviate somewhat from the expected distributions. For summation alpha, the overall mean of 0.483 (calculated from the grouped frequency distribution) approaches the expected value of 0.50. Comparison of Figure 21 with the distributions given by Cody (1974) suggests that the mean value of niche overlap increases as the number of species in the community increases. There are minor peaks at low values of \underline{a} (0.2 and 0.3) and the distribution is truncated at about 0.90. The tail of the observed distribution of product alpha falls below the expected distribution and is truncated at \underline{c} . 0.7. These maximum observed values of 0.9 for \underline{a} and 0.7 for \underline{c} may be significant (see following section).

5.5 SEQUENTIAL DETERMINATION OF NICHE STRUCTURE

There is a body of empirical data which suggests that "species must achieve a total difference, in the various ecological categories in which they compete, equivalent to a mean difference in one character of at least 30 - 50 per cent" (MacArthur and Wilson 1967). It must be assumed that there is a limiting degree of similarity beyond which two species cannot coexist indefinitely. In the preceding section it was assumed that species differ in each niche dimension separately and that coexistence is achieved by species pairs exceeding some threshold of minimum ecological difference. If it is now

assumed that the minimum difference is 30 per cent, the simplest way to achieve this is for a species pair to differ by this amount along a single niche dimension. If there is complete overlap along the other two niche dimensions, product alpha should not exceed 0.7 and summation alpha should not exceed 0.9. These criteria are met in Tasmanian temperate rainforest (Figures 21 and 22) but may not be in other habitats (Cody 1974, Thomas in prep.).

Values of α greater than 0.7 and \underline{a} greater than 0.9 could arise

- 1) in a non-equilibrium situation, e.g. where an invading species is replacing an existing species,
- 2) if the three niche dimensions chosen are inadequate to show the full extent of ecological separation, or
- 3) if neither product alpha or summation alpha are appropriate measures.

A corollary of 3) is that α and \underline{a} do not define the mechanisms which enable species to coexist. Certainly this is true.

I have no evidence to suggest that we are dealing with a non-equilibrium situation. However, I do have strong evidence concerning the coexistence of honeyeaters at Pottery Road that supports Rowley's (1973) contention that differences in socio-ecology (Crook 1970a, b) may be necessary for some species pairs to coexist. This throws considerable doubt on the adequacy of using only three niche dimensions.

Cody (1974) concedes that there is an alternative : species pairs may exceed some threshold of minimum ecological difference in a single niche dimension. Again it can be

assumed that this minimum separation is 30 per cent. Clearly, two species do not compete if they eat different foods (e.g. one is graminivorous and the other insectivorous) regardless of how similar they are in all other attributes.

Figure 23 is a representation of niche structure in Tasmanian temperate rainforest that has been constructed by sequentially considering the following

Differences in kinds of food

Differences in methods of locating prey - pursuers
or searchers

Differences in vertical stratification

Differences in foraging zones

Differences in bill size which is correlated with
differences in the size of items eaten (Hespenheide
1971, Cody 1974).

5.6 NICHE STRUCTURE IN DRY SCLEROPHYLL AND TEMPERATE RAINFOREST - A COMPARISON

Dry sclerophyll forest was chosen for this comparison because it is the most species-rich Tasmanian forest habitat. As the xeric-mesic gradient is traversed, the number of species decreases (Table 20). As species packing decreases it might be expected that niche breadths would increase. This was investigated for feeding behaviour of species occurring in both dry sclerophyll and temperate rainforest. Feeding behaviour comparisons for ten species are given in Appendix 20 and per cent similarities, calculated from equation (9), in Table 29. In terms of overall similarity, temperate rainforest resembles dry sclerophyll forest in winter rather

FIGURE 23. Niche structure in Tasmanian temperate rainforest.

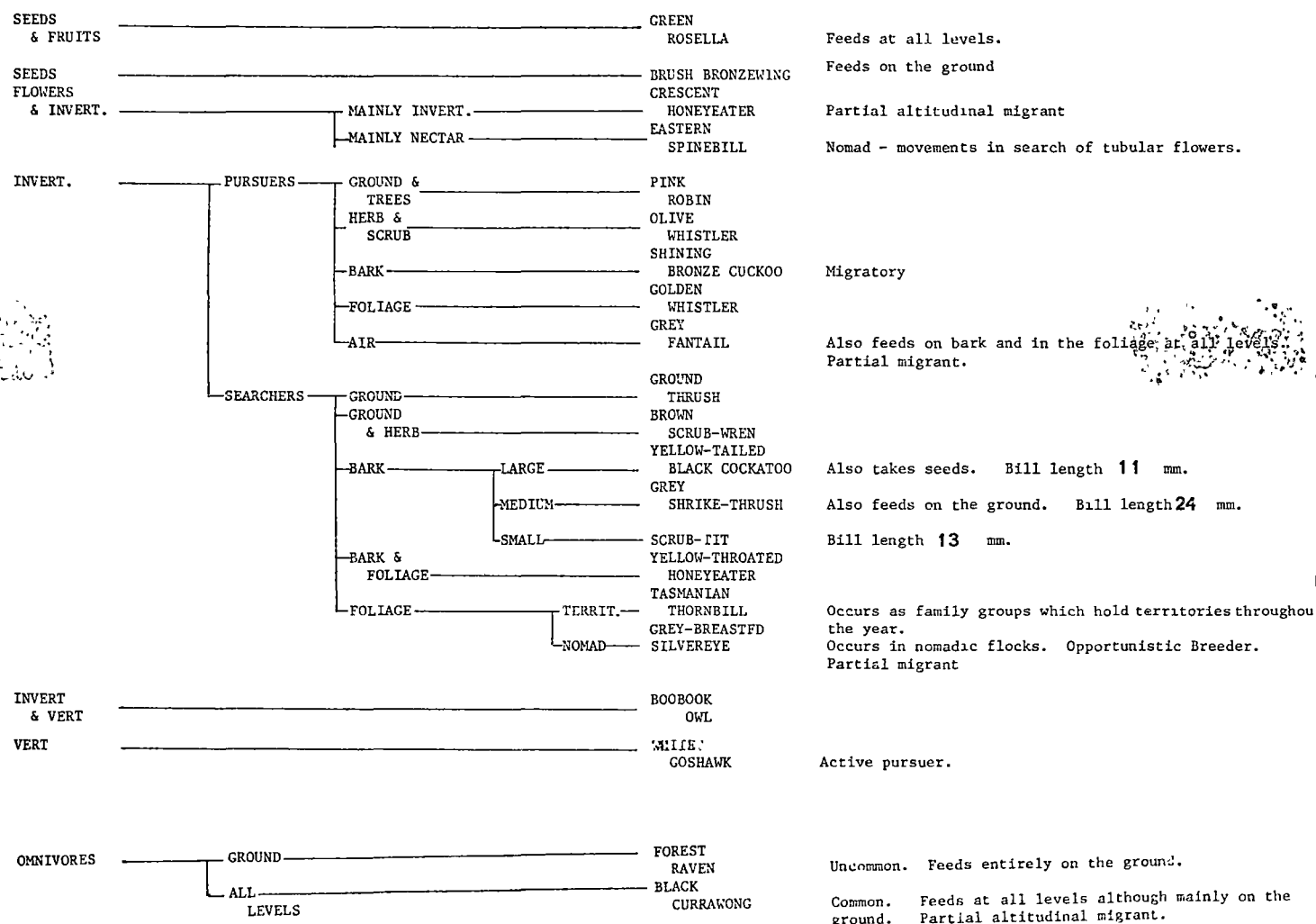


TABLE 29. Feeding behaviour : similarities between dry sclerophyll forest and temperate rainforest (wet formations).

		SIMILARITY %
Green Rosella	Dry sclerophyll (summer) - Wet formations	68
Shining Bronze Cuckoo	Dry sclerophyll (summer) - Wet formations	83
Golden Whistler	Dry sclerophyll (summer) and (winter)	83
	Dry sclerophyll (summer) - Wet formations	86
	Dry sclerophyll (winter) - Wet formations	72
Grey Shrike-thrush	Dry sclerophyll (summer) and (winter)	72
	Dry sclerophyll (summer) - Wet formations	73
	Dry sclerophyll (winter) - Wet formations	93
Grey Fantail	Dry sclerophyll (summer) and (winter)	72
	Dry sclerophyll (summer) - wet formations	86
	Dry sclerophyll (winter) - wet formations	72
Brown Scrubwren	Dry sclerophyll (summer) and (winter)	71
	Dry sclerophyll (summer) - wet formations	73
	Dry sclerophyll (winter) - wet formations	90
Yellow-throated Honeyeater	Dry sclerophyll (summer) and (winter)	82
	Dry sclerophyll (summer) - wet formations	79
	Dry sclerophyll (winter) - wet formations	79
Crescent Honeyeater	Dry sclerophyll (summer) and (winter)	65
	Dry sclerophyll (summer) - wet formations	63

TABLE 29 (cont).

Eastern Spinebill	Dry sclerophyll (winter) -	90
	Wet formations	
Silvereye	Dry sclerophyll (summer)	53
	and (winter)	
	Dry sclerophyll (summer) -	53
	Wet formations	
	Dry sclerophyll (winter) -	70
	Wet formations	

MEAN SIMILARITIES : Dry sclerophyll (summer)

and (winter)	71 %
Dry sclerophyll (summer) -	74 %
wet formations	
Dry sclerophyll (winter) -	79 %
wet formations	

than in summer. This is not surprising because there are fewer species present in dry sclerophyll forest in winter. The greatest difference is the seasonal difference (29 per cent) in dry sclerophyll forest. This suggests that there is some rearrangement of foraging behaviour in winter and, because fewer species are involved, this appears to support the contention that niches are broader as species packing becomes less.

This aspect was investigated further by considering numerical values of niche breadth as calculated from the formula given by Levins (1968)

$$1 / B = \sum p_i^2 \quad (12)$$

where B is niche breadth and the p_i are the proportional frequencies. The results are given in Table 30.

Comparing dry sclerophyll forest in summer with the same habitat in winter, two species show increased foraging range in winter and five show decreased foraging range. Comparing dry sclerophyll forest in summer with temperate rainforest shows that five species show an increased, and three a decreased, foraging range in temperate rainforest. Similarly, five species in temperate rainforest have an increased foraging range, and two a decreased range, compared to dry sclerophyll forest in winter.

It cannot be concluded from these results that foraging range increases generally as the number of species in the community decreases. This seems to be so in temperate rainforest, although there are exceptions (which may be real), but does not apply in dry sclerophyll forest where fewer

TABLE 30. Feeding behaviour : niche breadth in dry sclerophyll and temperate rainforest (wet formations).

SPECIES	NICHE BREADTH IN		
	DRY SCLEROPHYLL (SUMMER)	DRY SCLEROPHYLL (WINTER)	WET FORMATIONS
Green Rosella	2.60	N.D.	4.49
Shining Bronze Cuckoo	1.39	N.D.	2.02
Golden Whistler	1.67	2.37	1.28
Grey Shrike-thrush	2.33	3.10	2.69
Grey Fantail	3.17	1.73	3.29
Brown Scrubwren	4.14	2.64	2.98
Yellow-throated Honeyeater	4.49	3.33	4.24
Crescent Honeyeater	4.48	4.30	4.87
Eastern Spinebill	N.D.	1.73	1.80
Silvereye	2.72	1.81	1.13

N.D. = not determined (few birds present).

species are present in winter. A possible reason for this is that, in dry sclerophyll forest, the abundance of food varies seasonally and species may have to rely more in winter on their specialised foraging behaviour if they are to avoid competitive exclusion. The Grey Fantail can be used to illustrate this. In dry sclerophyll forest in summer, two other specialist aerial hawkers (Satin Flycatcher and Dusky Woodswallow) are present. Because of competition from these species, Grey Fantails may be forced to obtain insects from foliage, etc. (by gleaning and hover-gleaning). Foliage insects are likely to be most abundant at this time and competition with other foliage gleaners can be relaxed. In winter, no other aerial feeders are present and there are fewer Grey Fantails than in summer. Although the number of flying insects will be reduced, sufficient may be present to support the reduced population of Grey Fantails. To account for the foraging behaviour of the Grey Fantail in temperate rainforest it is necessary to assume that flying insects are not abundant enough to allow Grey Fantails to exist, even in the absence of other aerial feeders, without exploiting other sources of insects.

The indication is, then, that some species appear to occupy broader niches in temperate rainforest than they do in dry sclerophyll forest but others may occupy a narrower niche. Other factors, apart from the extent of species packing, appear to be important. If the speculative explanation of niche breadth variation in the Grey Fantail is correct, the environmental factors affecting niche breadth are complex. This is a problem worthy of comprehensive

and detailed study beyond the scope of the present work.

We can compare temperate rainforest and dry sclerophyll forest on the basis of the main kinds of foods eaten by the various species in the two communities. This is done in Table 31 in two ways : (a) where a species eats more than one kind of food, this is shown as such, e.g. 'Fruits and Seeds', and (b) where a species eats more than one kind of food, one species is allocated to each of the kinds of food involved. Table 31 emphasises the importance of invertebrates in both habitats, particularly when split allocations are taken into account. In only two categories, Fruits & Seeds and Invertebrates & Vertebrates, are the numbers of species the same in both habitats. Temperate rainforest has no species that rely on seeds & invertebrates, flowers & invertebrates, nectar, and invertebrates. In only one category, nectar & invertebrates, does temperate rainforest have more species than dry sclerophyll forest, but this does not apply when split allocations are allowed for. About half the missing species rely on invertebrates and the greater proportion of these are pursuers. The actual 'missing' niches are summarised in Table 32.

The indications are that environmental harshness increases along the xeric-mesic gradient with the result that the amount of food, particularly invertebrates, decreases. While there is some rearrangement of niches, species drop out mainly because the number of available niches decreases.

TABLE 31. Comparison of community structure in dry sclerophyll and temperate rainforests according to food.

FOOD	DRY SCLEROPHYLL		TEMP. RAINFOREST	
	NO.OF SPECIES	%	NO.OF SPECIES	%
Fruits & seeds	1	2	1	5
Seeds	4	8	1	5
Seeds & invertebrates	2	4	-	-
Flowers & invertebrates	2	4	-	-
Nectar	2	4	-	-
Nectar & invertebrates	1	2	2	10
Invertebrates-pursuers	16	55	5	62
-searchers	12		8	
Invertebrates & vertebrates	2	4	2	10
Vertebrates	4	8	-	-
Omnivores	5	10	2	10

Fruits	1	2	1	5
Seeds	7	14	2	10
Flowers	2	4	-	-
Nectar	3	6	2	10
Invertebrates	35	69	17	81
Vertebrates	6	12	2	10
Omnivores	5	10	2	10

TABLE 32. 'Missing' niches in temperate rainforest

Graminivores	Native species	1	
	Introduced species	2	
Graminivores/Insectivores Ground feeding		2	
Flower eating/Insectivores Migratory/ nomadic lorikeets		2	
Nectarivores	Honeyeaters	2	
Insectivores (Pursuers)	Nocturnal	2	}
	Brood parasites	3	
	Ground feeding robins	2	
	Foliage gleaners	1	
	Aerial feeders	3	
			11
Insectivores (Searchers)	Ground feeders	2	}
	Foliage gleaners	2	
			4
Carnivores		3	
Omnivores	Native species	2	
	Introduced species	1	

CHAPTER 6

AVIAN ECOLOGY IN AUSTRALIAN AND NEW ZEALAND
TEMPERATE RAINFORESTS

6.1 INTRODUCTION

Temperate rainforest occurs in small isolated pockets on the Australian mainland as well as in New Guinea, New Zealand and South America. Based on short visits to some areas and information in the literature, a comparison can be made between temperate rainforests in different localities.

6.2 OTWAY RANGES, VICTORIA

Emison et al. (1975) list only two species as likely to occur in Nothofagus forest in the Otway Range and Rose (pers. comm.) recorded 13 species during a visit of three days in 1977 during the non-breeding season. The probable reasons for this are the small amount, c. 500 hectares, of temperate rainforest remaining, its linear distribution along gullies and the short amount of time that has been spent in the habitat. The temperate rainforest occurs in wet sclerophyll forest and it is unlikely that there will be major differences in the avifaunas of the two habitats. Emison et al. list 35 species as occurring in the wet sclerophyll forest and this assemblage can be used in comparisons of species composition of Tasmanian and mainland rainforests. Further comparisons should not be made because wet sclerophyll forest is a eucalypt dominated habitat.

6.3 NORTHERN NEW SOUTH WALES

6.3.1 NUMBER OF SPECIES

Some difficulty exists in establishing the avifauna of

temperate rainforest in northern New South Wales. Kikkawa et al. (1965) list 32 species for Point Lookout, made up of
 XX, common and most abundant in temperate rainforest -

1 species

X, regular, but less common or rare 23 species

(X), occasional (or seasonal) occurrence 8 species

The major problem lies in deciding whether a species is occasional, i.e. a visitor from another habitat, in which case it should not be included in the avifauna of temperate rainforest, or occurs seasonally when it should be included in the avifauna if it breeds regularly in temperate rainforest, i.e. is a breeding migrant.

Kikkawa (1968) includes Point Lookout and Barrington Tops in a similarity analysis of the ecological association of bird species and habitats. However, the lists for these sites are incomplete, e.g. an unknown number of species reports in a residual group that is not associated with any habitat group and which includes the Olive Whistler, known to occur in temperate rainforest in northern New South Wales (Kikkawa 1974).

The lists of Kikkawa et al. (1965) and Kikkawa (1968) have been used to compile a provisional avifauna for the temperate rainforests of northern New South Wales (Table 33). In considering each species, allowance has been made for my knowledge of the temperate rainforest avifaunas in Tasmania (Chapter 3.2) and southern Queensland (Chapter 6.4).

The avifauna of temperate rainforest consists of 33 species (Table 33), to which should be added one raptor, almost

TABLE 33. The avifauna of temperate rainforest in northern New South Wales.

1. REGULAR

King Parrot	Eastern Whipbird
Crimson Rosella	Large-billed Scrubwren
Fan-tailed Cuckoo	Yellow-throated Scrubwren
Shining Bronze Cuckoo	White-browed Scrubwren
Spotted Owl	Brown Thornbill
Superb Lyrebird	Striated Thornbill
Scaly Thrush	White-throated Treecreeper
Brown Warbler	Red Wattlebird
Rose Robin	White-eared Honeyeater
Eastern Yellow Robin	Eastern Spinebill
Olive Whistler	Spotted Pardalote
Golden Whistler	Silvereye
Grey Shrike-thrush	Satin Bowerbird
Black-faced Monarch	Green Catbird
Rufous Fantail	Pied Currawong
Grey Fantail	<u>Corvus</u> sp.
Spine-tailed Chowchilla	

2. OCCASIONAL

Sulphur-crested Cockatoo	Red-browed Treecreeper
Kookaburra	Yellow-faced Honeyeater
Flame Robin	Striated Pardalote
Rufous Whistler	

certainly the Grey Goshawk.

6.3.2 NICHE STRUCTURE

The community structure of the avifauna of Tasmanian temperate rainforest was derived in Chapter 5.5. It is not possible to derive the community structure for temperate rainforest in northern New South Wales in the same way because of the lack of quantitative data on foraging behaviour and vertical stratification. However, a less-precise model can be derived using qualitative data in the literature. The relevant information for each of the 34 species is given in Appendix 21 and the derived niche structure in Figure 24.

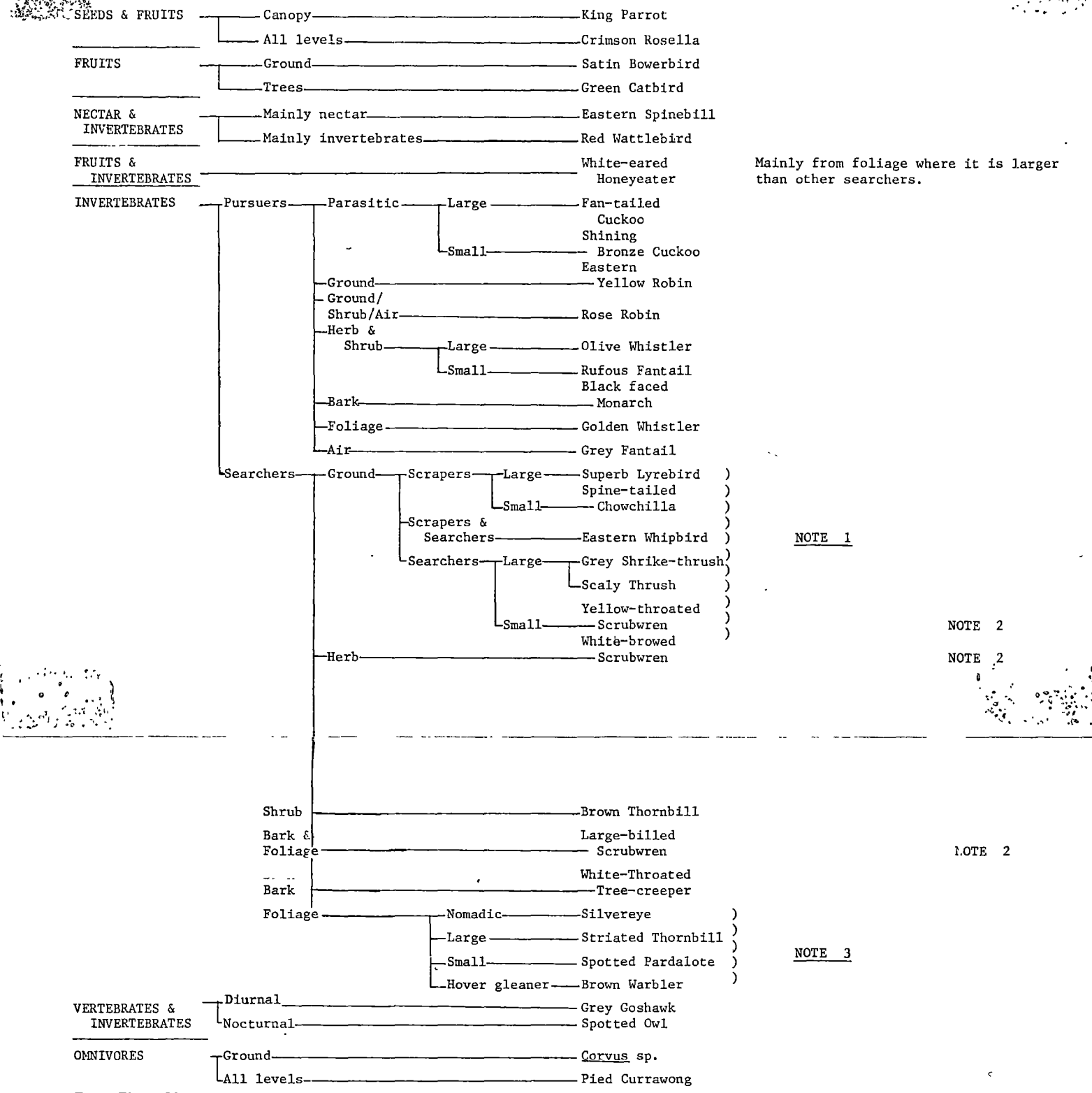
6.4 THE MACPHERSON RANGES, QUEENSLAND

6.4.1 NUMBER OF SPECIES

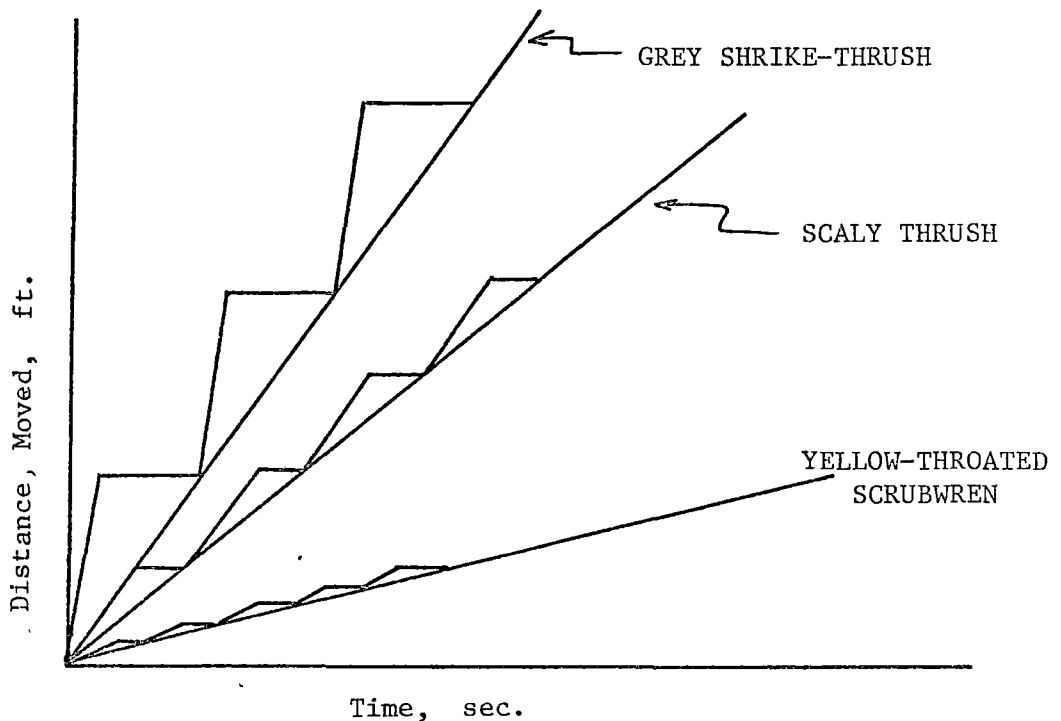
Species recorded in temperate rainforest at Green Mountain in April 1977 and Tullawallal in November 1977 are listed in Appendix 22. Twentyfour species were recorded at Green Mountain and 32 at Tullawallal. This latter figure included several migratory species which would be expected to be absent in April. A total of 38 species was recorded.

A comparison of species that have been recorded in wet sclerophyll forest in the Otways (Emison et al. 1975), subtropical rainforest in New South Wales (Kikkawa et al. 1965) and Queensland (Wheeler 1973), and temperate rainforest in New South Wales (Chapter 6.3.1) and Queensland (Appendix 22) is made in Appendix 23. Very few species recorded in

FIGURE 24. Niche structure in temperate rainforest in northern New South Wales.



NOTE 1 This arrangement of ground feeding searchers is somewhat speculative, largely because there is a lack of precise information in the literature. Size differences alone seem enough to separate the Superb Lyrebird and Yellow-throated Scrubwren from each other and from the other species. The Spine-tailed Chowchilla and Eastern Whipbird locate food by scraping among the litter, the Spine-tailed Chowchilla almost exclusively. The Eastern Whipbird also forages in the herb layer and it seems likely that there is a degree of vertical habitat separation. The Scaly Thrush and Grey Shrike-thrush obtain food from the surface although the Scaly Thrush may turn over leaves with its bill and the Grey Shrike-thrush may forage above the ground. The Grey Shrike-thrush may also, in part, be a pursuer. Taxonomically it is placed between the whistlers and the* both of which are pursuers. All, including the Scaly Thrush are placed in the Muscicapidae, the majority of which except the true Thrushes formerly placed in the Turdidae are pursuers. However, in Tasmania the Grey Shrike-thrush has a large bark foraging component and is a searcher. These matters can only be resolved by the collection of comparative numerical data. I would predict that the saw-tooth foraging curve devised by Cody (1968) would separate the various species. For example, I predict that these curves for the searchers would be.



NOTE 2 Comparative numerical data on patch preference, height utilisation and foraging behaviour are required to justify the tentative arrangement proposed.

NOTE 3 This arrangement is tentative. Quantitative data obtained throughout the year are needed.

* Monarch flycatchers.

temperate rainforest do not occur in subtropical rainforest. Some of the exceptions, e.g. Flame Robin and Red Wattlebird, probably are only occasional visitors to temperate rainforest. This is hardly surprising if the two habitats intergrade along a xeric-mesic (or temperature) gradient and species are not restricted to particular habitats.

Of the species occurring in temperate rainforest in New South Wales, 18 (45 per cent) also occur in Tasmania. Of the 38 species occurring in temperate rainforest in Queensland, 16 (42.1 per cent) also occur in Tasmania (Table 34). Twenty-nine species occur in temperate rainforest in New South Wales and Queensland and, of these, 15 (51.7 per cent) occur in Tasmania.

Fifteen species (38.5 per cent) of those occurring in subtropical rainforest in New South Wales occur in Tasmania, but only 22 (31.9 per cent) of the 69 species occurring in subtropical rainforest in Queensland occur in Tasmania. Subtropical rainforest in Queensland appears to have more species than the same habitat in New South Wales.

Table 35 lists the species common to temperate rainforest in New South Wales and Queensland that occur on Tasmania. Four of the 15 species common to temperate rainforest in New South Wales and Queensland that occur in Tasmania listed in Table 35 - Fan-tailed Cuckoo, Brown Thornbill, Spotted Pardalote and Red(Yellow) Wattlebird - are not birds of temperate rainforest in Tasmania (Chapter 3.2). The Fan-tailed Cuckoo and Spotted Pardalote are occasional visitors, as is the Yellow Wattlebird which replaces the Red Wattlebird

TABLE 34. Species occurring in Tasmania also occurring in the Otways (Vic), New England N.P. (NSW) and the Macpherson Ranges (Q'D).

	SPECIES	TOTAL SPECIES ALSO OCCURRING IN TASMANIA	
		NO.	%
Victoria - wet sclerophyll	38	26	68.4
N.S.W. - temperate rainforest	40	18	45.0
subtropical r'forest	39	15	38.5
Q'd - temperate rainforest	38	16	42.1
subtropical rainforest	69	22	31.9

Species common to temperate rainforest in New South Wales
and Queensland : 29

Species common to temperate rainforest in New South Wales
and Queensland that occur in Tasmania : 15

TABLE 35. Species common to temperate rainforest in New South Wales and Queensland that occur in Tasmania.

Crimson Rosella*
Fan-tailed Cuckoo
Shining Bronze Cuckoo
Scaly Thrush
Olive Whistler
Golden Whistler
Grey Shrike-thrush
Grey Fantail
White-browed Scrubwren*
Brown Thornbill
Red Wattlebird*
Eastern Spinebill
Spotted Pardalote
Silvereye
Pied Currawong*

* Replaced in Tasmania by a member of the same superspecies.

in Tasmania. On the other hand, the Brown Thornbill is restricted to the more-xeric habitats and is replaced in the more-mesic habitats, including temperate rainforest, by the endemic Tasmanian Thornbill.

6.4.2 CENSUS AT TULLAWALLAL

A census, 8 x 500 m transects, was made across the subtropical - temperate rainforest interface by the method described in Chapter 4.2 (Appendix 11). The vegetation profile is included in Appendix 12. Along the transect, 0 - 300 m can be taken as high-altitude subtropical rainforest and 400 - 500 m as temperate rainforest, with 300 - 400 m as the ecotone. Several conclusions can be drawn from the census results :

- 1) There is no change in the composition of the avifauna across the interface. (Several additional species were recorded in temperate rainforest outside the actual census).

- 2) Relative density decreases along the xerix-mesic gradient :

Subtropical rainforest	6.000
Temperate rainforest	4.398

Relative density in temperate rainforest at Tullawallal is no higher than it is in temperate rainforest in Tasmania (3.900 to 6.875, mean 4.957 for 3 sites).

6.4.3 VERTICAL STRATIFICATION AT TULLAWALLAL

Limited data on height distribution were obtained at Tullawallal (Table 36).

Some comparisons of height distributions in temperate

TABLE 36. Vertical stratification at Tullawalla.

	N	OCCURRENCE %		
		HERB	SHRUB	TREE
Brown Pigeon	3	0	67	33
Crimson Rosella	74	4	3	93
Scaly Thrush	1	100	0	0
Southern Yellow Robin	3	0	100	0
Golden Whistler	20	5	25	75
Grey Shrike-thrush	10	0	10	90
Black-faced Monarch	23	0	70	30
Rufous Fantail	21	10	80	10
Grey Fantail	2	0	100	0
Spine-tailed Chowchilla	2	100	0	0
Eastern Whipbird	15	67	20	13
Large-billed Scrubwren	5	20	80	0
Yellow-throated Scrubwren	3	0	100	0
White-browed Scrubwren	20	65	35	0
Brown Warbler	4	0	50	50
Brown Thornbill	21	0	100	0
Striated Thornbill	2	0	100	0
White-throated Treecreeper	1	0	0	100
Lewin's Honeyeater	17	0	0	100
Silvereye	3	0	33	67
Satin Bowerbird	3	100	0	0
Green Catbird	2	0	0	100
Paradise Riflebird	1	0	100	0
Pied Currawong	3	0	0	100

rainforest in Queensland and various Tasmanian habitats are made in Table 37 (Golden Whistler and White-browed (Brown) Scrubwren) and Figure 25 (Brown Thornbill). There is no evidence that there is any difference in the height distribution of the Golden Whistler : the Queensland data fall between the values obtained in Tasmanian dry sclerophyll forest in summer and winter.

The White-browed Scrubwren appears to utilise the shrub layer more in Queensland than it does in Tasmania. This agrees with the contention of Ridpath and Moreau (1966) that the Tasmanian form feeds exclusively on the ground whereas the mainland form commonly goes up trees and shrubs. The Tasmanian form also has a longer relative tarsus length (tarsus / wing) of 0.416 as against 0.368 - 0.383 for mainland races (Galbraith and Parker 1969). Terrestrial species tend to have relatively longer legs than arboreal species. However, many more quantitative data are needed for mainland populations before such a difference in vertical stratification can be established unequivocally.

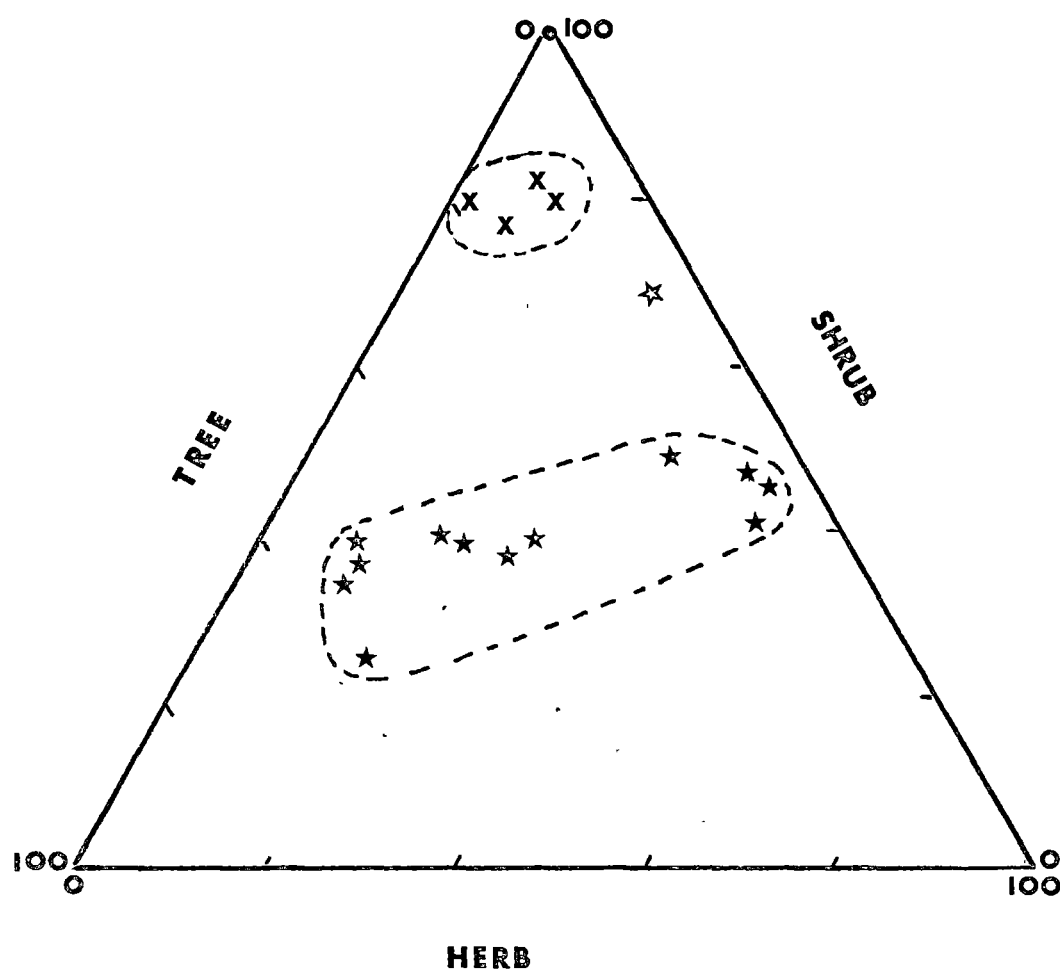
Three scrubwrens, Yellow-throated, White-browed and Large-billed occur in temperate rainforests in Queensland and New South Wales. The Yellow-throated Scrubwren (relative tarsal length 0.410) is terrestrial (Galbraith and Parker 1969, McGill 1970) and the Large-billed Scrubwren (relative tarsal length 0.354 - 0.362) is arboreal (Frith 1969, Galbraith and Parker 1969, McGill 1970, Slater 1974). Apparently, the White-browed Scrubwren occupies an intermediate position. In Tasmania only two scrubwrens, Brown Scrubwren and Scrubtit, occur if indeed the Scrubtit is a scrubwren (see Chapter 8.5).

TABLE 37. Vertical stratification of the Golden Whistler and White-browed (Brown) Scrubwren in temperate rainforest in Queensland and various Tasmanian habitats.

LOCALITY	HABITAT	N	FREQUENCY %		
			HERB	SHRUB	TREE
<u>GOLDEN WHISTLER</u>					
Tasmania	Dry sclerophyll (summer)	4184*	1	18	81
	" " (winter)	4412*	5	32	63
	Wet sclerophyll	19	0	10	90
Queensland	Temperate rainforest	20	5	25	70
<u>WHITE-BROWED (BROWN) SCRUBWREN</u>					
Tasmania	Dry sclerophyll (summer)	5489*	97	3	0
	" " (winter)	2572*	99	1	0
	Wet sclerophyll	237	87	13	0
	Mixed forest	56	89	11	0
	Temperate rainforest	30	77	23	0
Queensland	Temperate rainforest	20	65	35	0
Tasmania	Sub-alpine forest	78	85	15	0

* Seconds, maximum 60 sec. per individual.

FIGURE 25. Vertical stratification of Brown and Tasmanian Thornbills.



TASMANIA

- ★ Brown Thornbill - dry sclerophyll forest (monthly)
- x Tasmanian Thornbill

QUEENSLAND

- Brown Thornbill - temperate rainforest
- ★ Brown Thornbill - subtropical rainforest

The Brown Scrubwren is terrestrial and the Scrubtit arboreal. On the face of it, this appears to be a case of two species on an island replacing three mainland species. However, this may be an oversimplification because the Large-billed Scrubwren does not appear to have the large bark foraging component of the Scrubtit and the wet habitats of the Otway Range only support one scrubwren, the White-browed (Emison et al. (1975), Wheeler 1967). Possibly the small area of temperate rainforest (500 ha) and wet sclerophyll forest (originally 15,000 ha) has behaved as a habitat island as it is isolated from other areas of similar habitat. The situation in Tasmania is complicated further by the absence of mainland specialist bark feeders into whose adaptive zone the Scrubtit has moved.

There is considerable difference in the height distribution of the Brown Thornbill (Figure 25). In Tasmania it uses all three vegetation layers although there is considerable variation from month to month. In Queensland it is largely a bird of the shrub layer rarely venturing into the canopy. The height distribution of the Queensland Brown Thornbill is closer to that of the Tasmanian Thornbill although the latter has a small canopy feeding component. Keast (1970) noted a similar difference in height distribution between Tasmanian and Victorian Brown Thornbills. He attributes this to increased ecological versatility of Tasmanian Brown Thornbills in the absence of canopy feeding Striated and Little Thornbills. This seems an oversimplification because mainland Brown Thornbills occur in different habitats in different localities (Table 38) and the other thornbills do not occur

TABLE 38. Habitat preference of the Brown Thornbill.

LOCALITY	HABITAT	REFERENCE
Queensland - Macpherson Range.	Rainforest and open forest.	Wheeler (1973)
New South Wales - northern.	Significant association with tall wet formations, present in tall dry formations.	Kikkawa (1974)
A.C.T.	Wherever there are trees with a few shrubs.	Frith (1969)
Victoria	All types of forested country.	Wheeler (1967)
Victoria - Otway Range	Wet sclerophyll forest, dry sclerophyll forest, woodland, heath communities, pasture.	Emison <u>et al.</u> (1975)
South Australia	Wooded areas of greater density.	Condon (1968)
Tasmania	Dry sclerophyll forrest	Ridpath and Moreau (1966)
<hr/>		
General	Rainforests and moist forest country generally, wherever undergrowth and ground cover are plentiful. Rain forest, dense moist eucalypt forest.	McGill (1970) Slater (1974)

commonly in all habitats. For example, Little Thornbills are absent from rainforest in southern Queensland and northern New South Wales and the Striated Thornbill is far from common in this habitat. To some extent the height distribution of the Brown Thornbill in Tasmanian habitats is due to the sparseness of the shrub layer.

6.4.4 FEEDING BEHAVIOUR AT TULLAWALLAL

Limited data on foraging behaviour were obtained in temperate rainforest at Tullawallal (Table 39).

The most significant observation was the absence of aerial feeding. Two flycatchers were common but both obtained invertebrates from the vegetation : the Black-faced Monarch mainly from the foliage and the Rufous Fantail from the foliage and from bark (including litter). The similarity in feeding behaviour was only 42 per cent which suggests that a real difference does exist in spite of the limited number of observations. Neither species occurs in temperate rainforest in Tasmania where the common flycatcher is the Grey Fantail. This species does occur in the temperate rainforests of southern Queensland and northern New South Wales but at Tullawallal I found it to be uncommon and greatly outnumbered by the Rufous Fantail. In Tasmania, the Grey Fantail obtains a significant part of its food by aerial hawking in all habitats although it does hover-glean like the Black-faced Monarch and Rufous Fantail.

The Brown Thornbill was found to be almost exclusively a foliage gleaner at the time of my visit although it did

Tullawallal.

C = catkin.

[illegible]

obtain some (3 per cent) of its food from bark. The proportion of food obtained from the foliage is greater than is the case with Tasmanian thornbills, see Table 28.

Crimson Rosellas were numerous in temperate rainforest at Tullawallal where they were feeding on beech catkins in the canopy.

6.4.5 SUBTROPICAL RAINFOREST AT BINNA-BURRA

Limited time was spent in subtropical rainforest and few data were obtained. For completeness, vertical stratification data are given in Table 40 and feeding behaviour data in Table 41. The height data for the Brown Thornbill have been included in Figure 25.

Enough feeding data were obtained for the Brown Thornbill to allow a comparison to be made between its behaviour in subtropical and temperate rainforest (Table 42). Feeding behaviour in the two habitats is similar (81 per cent similarity).

6.4.6 COMPARISON OF THE AVIFAUNAS OF SUBTROPICAL AND TROPICAL RAINFOREST

Kikkawa (1968) lists 53 species as being associated with tropical rainforest (complex mesophyll vine forest and/or mixed mesophyll vine forest) in northern Queensland. Of these, 26 (49 per cent) occur in subtropical rainforest in southern Queensland and northern New South Wales. Only nine species (17 per cent) occur in temperate rainforest.

TABLE 40. Vertical stratification in subtropical rainforest
at Bina-purra.

	N	OCCURRENCE		
		HERB	SHRUB	TREE
Wonga Pigeon	2	2	0	0
Crimson Rosella	5	0	1	4
Noisy Pitta	1	1	0	0
Scaly Thrush	3	3	0	0
Southern Yellow Robin	6	3	3	0
Olive Whistler	5	0	5	0
Golden Whistler	4	0	1	3
Grey Shrike-thrush	3	0	0	3
Spectacled Monarch	2	0	2	0
Rufous Fantail	2	0	2	0
Grey Fantail	2	0	1	1
Spine-tailed Chowchilla	3	3	0	0
Eastern Whipbird	5	5	0	0
White-browed Scrubwren	6	1	5	0
Brown Warbler	2	0	2	0
Brown Thornbill	17	4	12	1
Lewin's Honeyeater	3	0	0	3
Eastern Spinebill	1	0	1	0
Spotted Pardalote	1	0	0	1
Satin Bowerbird	4	3	1	0
Green Catbird	2	0	0	2
Pied Currawong	32	8	4	20

TABLE 41. Feeding behaviour in subtropical rainforest at
Binniburra.

A = air, G = ground, H = herb, Lt = litter,
Tr = trunk, B = branch, Tw = twig, L = leaf.

	N	OCCURRENCE							
		A	G	H	Lt	Tr	B	Tw	L
Wonga Pigeon	5		5						
Noisy Pitta	5		5						
Scaly Thrush	5		5						
Southern Yellow Robin	15		15						
Olive Whistler	10								10
Spectacled Monarch	2								2
Grey Fantail	5						2		3
Spine-tailed Chowchilla	15		15						
Eastern Whipbird	10		10						
White-browed Scrubwren	15		5						10
Brown Warbler	5								5
Brown Thornbill	65	1	5			7		6	46
Eastern Spinebill	5	1							4
Spotted Pardalote	5								5
Satin Bowerbird	15		15						
Australian Regentbird	5		5						
Pied Currawong	40		40						

TABLE 42. Comparison of foraging behaviour of the Brown Thornbill in subtropical and temperate rainforest in southern Queensland.

FEEDING ZONE	FREQUENCY %	
	SUBTROPICAL RAINFOREST	TEMPERATE RAINFOREST
No. of observations	65	60
Air	2	0
Ground	8	0
Herb	0	0
Litter	0	0
Trunk	11	3
Branch	0	0
Twig	9	8
Foliage	70	89

The latitudinal distributions of the 26 species occurring in northern Queensland tropical rainforest and in subtropical rainforests in southern Queensland and northern New South Wales fall into the following broad categories :

1) All eastern Australia and Tasmania (6 species)

Brown Goshawk, Sulphur-crested Cockatoo, Shining Bronze Cuckoo, Spotted Owl, Tawny Frogmouth, Silvereye.

2) All eastern Australia except Tasmania (4 species)

Kookaburra, Rufous Fantail, Mistletoe-bird, Red-browed Finch.

3) Eastern Australia east of Port Philip Bay (4 species)

Brush Cuckoo, Eastern Whipbird, Large-billed Scrubwren, Spangled Drongo.

4) Central eastern Australia (1 species)

Pale Yellow Robin.

5) North-eastern Australia (11 species)

Brush Turkey, Red-crowned Pigeon, Purple-crowned Pigeon, Brown Pigeon, Green-winged Pigeon, Noisy Pitta, Yellow-eyed Cuckoo-shrike, Varied Triller, Spectacled Monarch, Rufous Shrike-thrush.

Thus, of the 73 species recorded in subtropical rainforest in northern New South Wales and southern Queensland (Appendix 23) only 11 (15 per cent) appear to have Torresian origins, i.e. those in category 5). Several of these, e.g. the pigeons, can be classed as 'super-tramps' (Diamond 1974) which are good, if not permanent, colonists.

6.4.7 COMPARISON OF THE AVIFAUNAS OF TEMPERATE AND TROPICAL RAINFOREST

The nine species that occur in both temperate rainforest in

northern New South Wales and southern Queensland and in tropical rainforest in northern Queensland can be treated similarly :

- 1) All eastern Australia and Tasmania (3 species)
Shining Bronze Cuckoo, Spotted Owl, Silvereye.
- 2) All/eastern Australia except Tasmania (1 species)
Rufous Fantail.
- 3) Eastern Australia east of Port Philip Bay (2 species)
Eastern Whipbird, Large-billed Scrubwren.
- 4) Central eastern Australia (0 species)
- 5) North-eastern Australia (3 species)
Brush Turkey, Brown Pigeon, Noisy Pitta.

Only the three species in category 5) have an undoubted Torresian origin and, of these, the Brown Pigeon and Noisy Pitta probably are 'super-tramps'. There can be little doubt that most of the species occurring in Australian temperate rainforests originated (see below) in south-eastern Australia. Similarly, many species occurring in subtropical rainforest in northern New South Wales and southern Queensland originated in south-eastern Australia. The undoubted affinities between the avifaunas of these habitats and that of temperate rainforest reinforce this conclusion.

Several species occurring in both subtropical and tropical rainforests have a widespread distribution (category 1) above) which includes both the present day Bassian and Torresian regions. It is not suggested that these species originated, in the sense that they became distinct from other populations at the specific level, in south-eastern Australia. However, it can be postulated that these species were present in south-eastern Australia at the close of the Pleistocene.

For a species to have originated in south-eastern Australia, a population must have been isolated in a refuge in the area during the late-Pleistocene and/or early-Recent. As conditions 'improved' some time after 10,000 B.P. these species spread out until their expansion was stopped by ecological barriers or competition from other species. Such isolation and radiation may or may not have involved some degree of speciation.

6.4.8 COMMUNITY STRUCTURE

The community structure of temperate rainforest in Queensland was derived in the same way as was that of northern New South Wales. The relevant data for the individual species are as given previously (Appendix 21) or in Appendix 23 for species not occurring in northern New South Wales. The derived community structure is shown in Figure 26.

6.5 NEW ZEALAND

The methods used above were used to derive the community structure in temperate rainforests in New Zealand. Data on feeding behaviour were taken from Goodwin (1967), Newton (1967), Oliver (1955) and Falla et al. (1966).

The community structure for North Island temperate rainforest is given in Figure 27.

The community structure in the temperate rainforests of the South Island is essentially the same except that three species are added and a further species, the Whitehead, is replaced by a closely related species, the Yellowhead. The

FIGURE 26. Niche structure in temperate rainforest in southern Queensland.

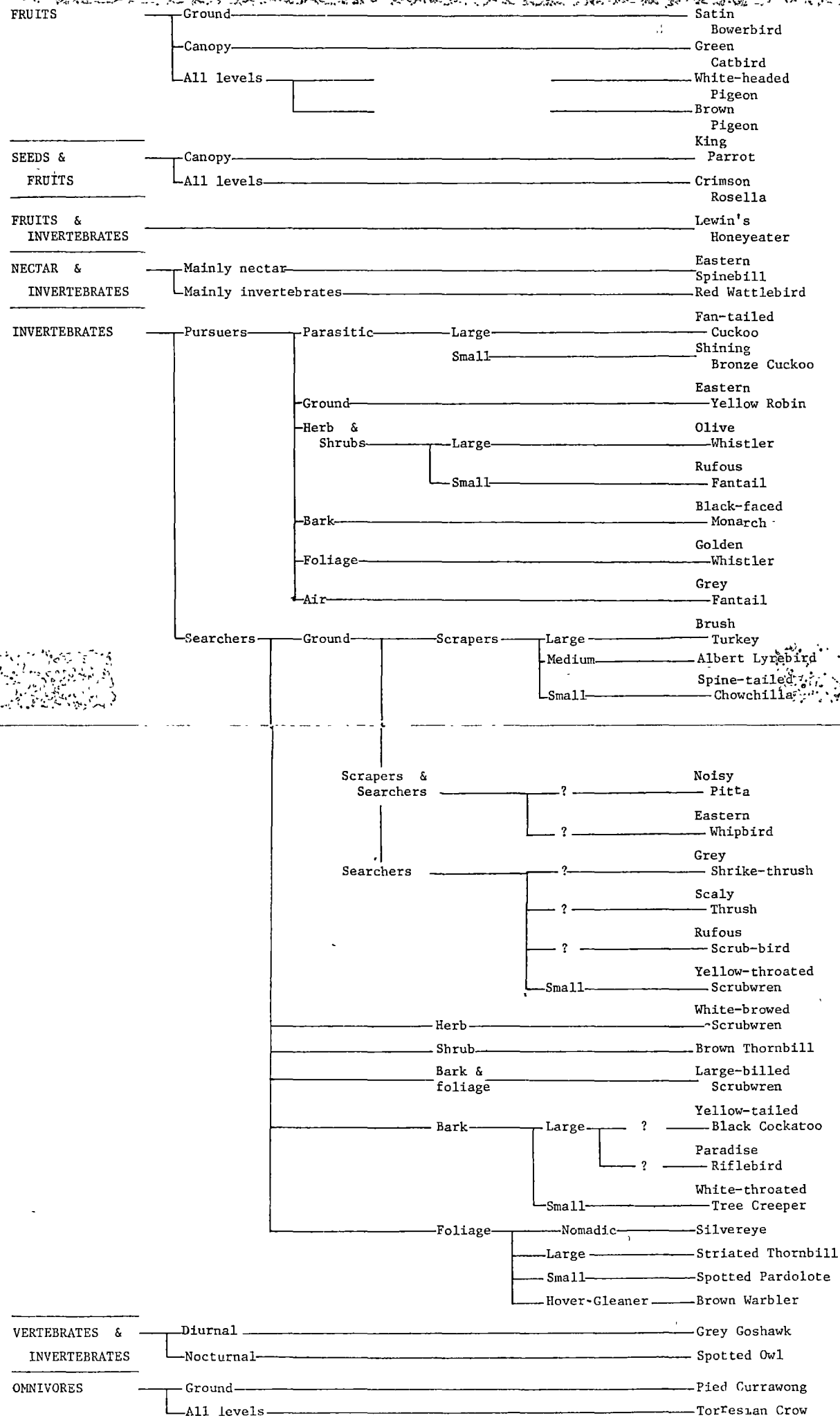


FIGURE 27. Niche structure in temperate rainforest, North
Island of New Zealand.

FIGURE 27

Community structure in temperate rainforest, New Zealand North Island

SEEDS			Redpoll)	
SEEDS & FRUITS			Parakeets)	
SEEDS & INVERTEBRATES			Chaffinch)	NOTE 1
FRUITS			N.Z. Pigeon)	
INVERTEBRATES NECTAR & FRUITS		Large	Tui	Bill 28 mm)	NOTE 2
		Small	Bellbird	Bill 14.8 mm)	
INVERTEBRATES	PARASITIC	Large	Long-tailed Cuckoo	Bill 24 mm)	
		Small	Shining Cuckoo	Bill 10.5 mm)	NOTE 3
	PURSUERS	Ground	Robin)	
		Herb & Shrub	Pied Tit)	NOTE 4
		Air	Fantail)	
	SEARCHERS	Ground	Large	Kiwis	Bill 130 mm)
			Medium	Blackbird	Bill 22 mm)
			Small	Hedge Sparrow	Bill 12 mm)
		Bark	Large	Kaka	Bill 44 mm)
			Small	Rifleman	Bill 11 mm)
		Bark & foliage	Whitehead		Also eats seeds and fruits
		Foliage	Large	Silvereye	Bill 11.2 mm)
			Small	Grey Warbler	Bill 8 mm)
INVERTEBRATES & VERTEBRATES	DIURNAL		N.Z. Falcon		
	NOCTURNAL		Morepork		

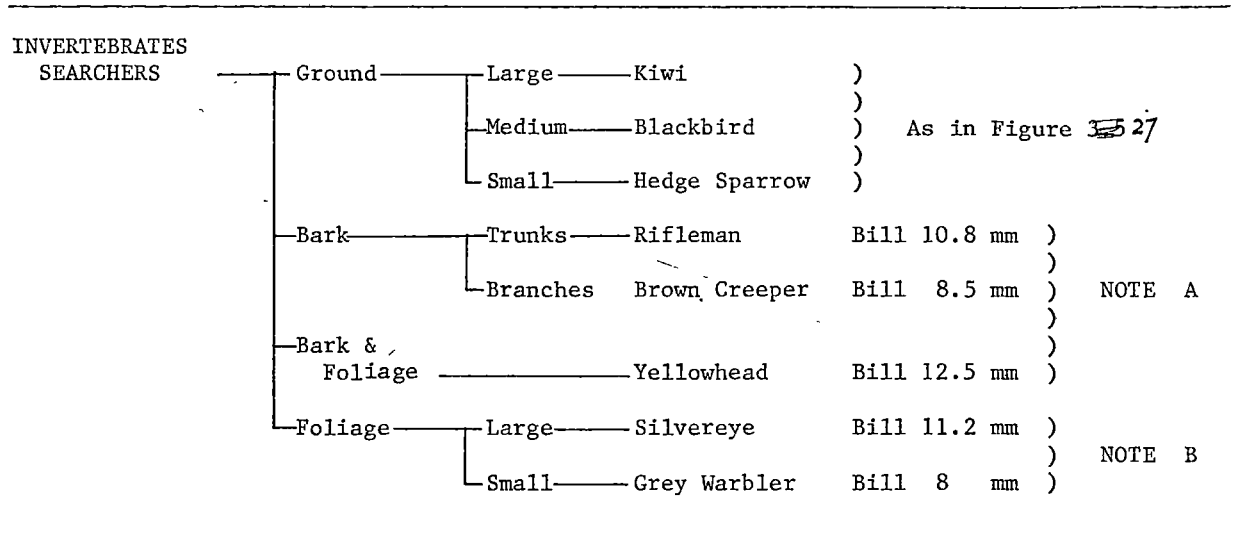
community matrix of Figure 27 will serve the South Island equally with the following amendments :

- 1) A new category 'Omnivore' is added in which the Weka and Kaka belong. The Weka takes invertebrates, vertebrates and seeds on the ground. The Kaka feeds at all levels and also takes carrion.
- 2) The category 'Invertebrates - searchers' becomes as shown in Figure 28.

(The Weka and Kaka may not strictly be birds of temperate rainforest. Possibly they occur on the forest edge or enter temperate rainforest from other habitats).

Some numerical data are given by Gravatt (1971) for forest (including Nothofagus) species on Little Barrier Island, Hauraki Gulf, Northland. These data are presented in Appendix 25 for vertical stratification and feeding behaviour as partial community overlap matrices. They confirm the community structure of Figure 28. The only overlaps in feeding behaviour that exceed 70 per cent in Appendix 25 are for the Tui - Whitehead and Stitchbird - Grey Warbler species pairs. However, the overlaps in vertical stratification for these species pairs are 56 and 34 per cent respectively, neither of which exceeds 70 per cent. This provides additional justification for the sequential approach to determining community structure developed in Chapter 5.5.

FIGURE 28 Community matrix for temperate rainforest, New Zealand
South Island - other categories as far North Island (Figure 3.5).
plus "Omnivores" (see text).



NOTE A. Rifleman and Brown Creeper would not be expected to coexist by size difference (Bill length difference 24%.) Rifleman feeds more on trunks, Brown Creeper on branches. The Yellowhead also feeds on branches where size difference should permit coexistence with Brown Creeper (Bill length difference 35%).

NOTE B The Grey Warbler is significantly smaller than both Silvereye and Yellowhead , the bill length differences being 33% and 44%. The Silvereye and Yellowhead are the same size (bill length difference 11%). The Silvereye is nomadic and an opportunistic breeder and also eats fruits and nectar whereas the Yellowhead is sedentary and also takes invertebrates from bark.

CHAPTER 7

AUSTRALIAN TEMPERATE RAINFOREST COMMUNITIES :
NICHE STRUCTURE AND PARALLEL EVOLUTION IN
BEECH FORESTS

7.1 INTRODUCTION

In the first part of this chapter the avifaunas of the various Australian rainforests are compared. In the second part Cody's (1974) idea of parallel evolution in beech forests is explored.

7.2 AUSTRALIAN TEMPERATE RAINFOREST COMMUNITIES

7.2.1 NUMBERS OF SPECIES

Because temperate rainforest exists in Australia as a number of isolates surrounded by a 'sea' of different habitat, it is tempting to apply the theory of island biogeography developed by MacArthur and Wilson (1967). On this theory, the number of species on each island is determined by island area and distance from the source region.

It is immediately apparent that the familiar number of species - island area relation does not hold. The area of temperate rainforest in Tasmania is considerably greater than areas of this habitat in northern New South Wales and southern Queensland (even if these isolated areas are combined), yet Tasmanian rainforest has significantly fewer species.

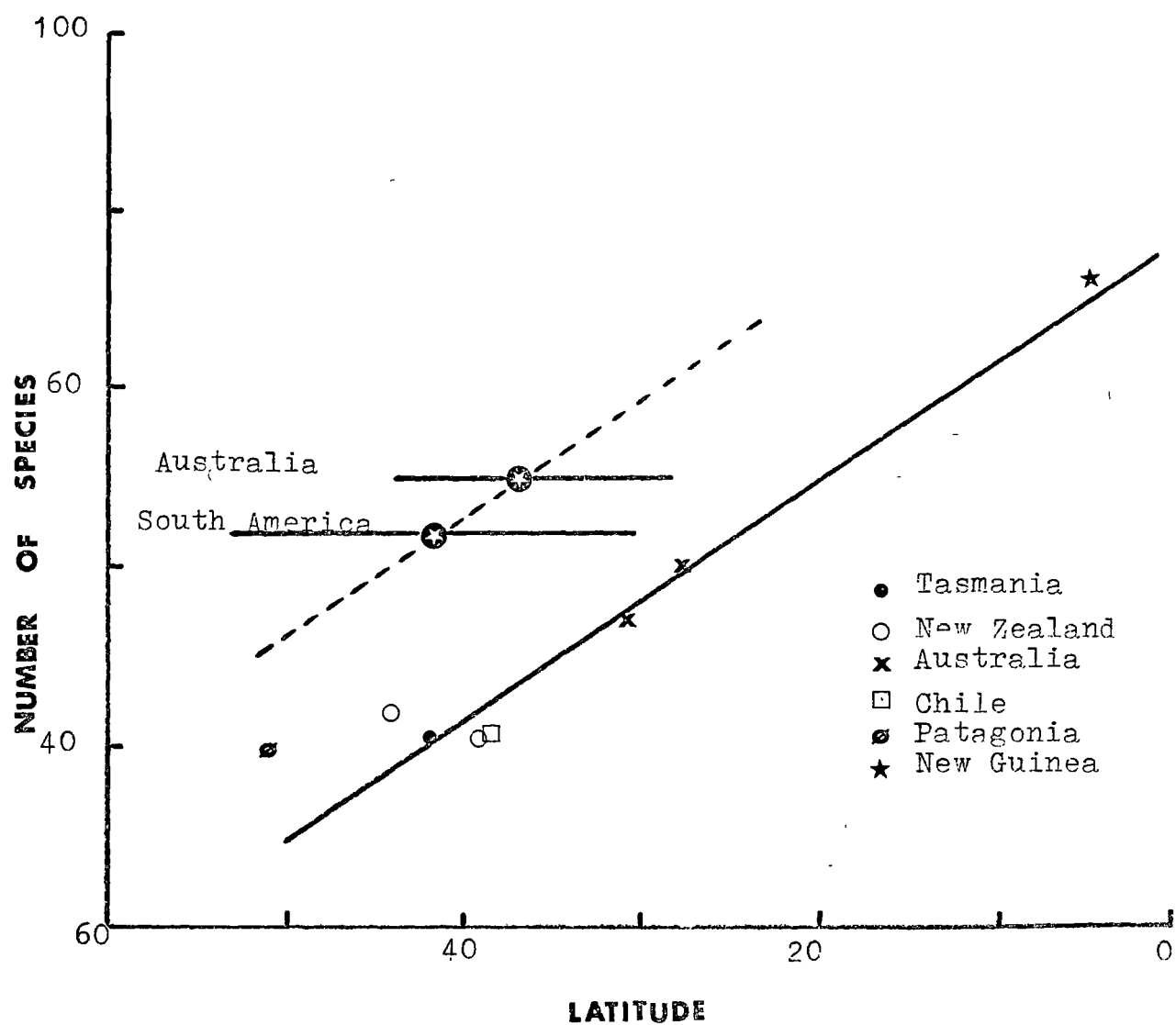
This can be explained easily : temperate rainforest does not have an unique avifauna in Australia and would not be expected to act as a habitat island. How then can the differences in the numbers of bird species inhabiting temperate rainforests in different localities be explained ?

Recher (1971) has illustrated how the number of bird species increases as one moves towards the equator along the better watered eastern part of Australia. Figure 29 is a plot of number of species against latitude for areas of temperate rainforest in Australia and New Zealand. A straight line can be fitted to the points. There is no evidence that island effects have resulted in New Zealand temperate rainforests having fewer species than are found at comparable latitudes in Tasmania. However, island effects may have been swamped by the introduction of exotic species which can be regarded as recent colonists. Further, some endemic species have become extinct, but it is not known to what extent man has been responsible for these extinctions.

We have no information as to the number of species in temperate rainforest in New Guinea. Extrapolation of the number of species - latitude relation predicts that New Guinea temperate rainforest should have about 70 species. Rose (ms.) suggests that 72 species occur in temperate rainforest at Wau. This predicted value will be a minimum total because it does not allow for speciation in isolation in New Guinea, as illustrated by the birds of paradise of the genus Parotia (Schodde and McKean 1973).

The reason why the number of bird species should increase towards the equator, which is a general phenomenon (Fischer 1960), probably is connected with greater productivity and lesser harshness of the environment associated with lesser seasonal change nearer the equator.

FIGURE 29. Variation in number of species with latitude in southern hemisphere temperate rainforests.



7.2.2 COMMUNITY STRUCTURE AND FOOD-HABITS

The food-habit distributions of species inhabiting temperate rainforest in Tasmania, New South Wales, Queensland and the North and South Islands of New Zealand are compared in Tables 43 and 44. In Table 43 species relying on two kinds of food are allocated one half species to each of the kinds of food. In Table 44 such species are allocated one species to each of the kinds of food. In this way, emphasis is placed on the numbers of species that rely, wholly or partly, on each kind of food. It is clear from Table 44 that the main difference between Australian temperate rainforests is the increase in the numbers of fr^ugivor^uous and insectivorous species with decreasing latitude.

The avifaunas of Tasmanian and New Zealand temperate rainforests are essentially similar both in total number of species and food-habit distribution. In the proportional distribution of food-habits (Table 43) the percentage similarities are :

Tasmania - North Island	91.5 %
Tasmania - South Island	95.0 %
North Island - South Island	91.7 %

Within Australia (including Tasmania) the ratio of searchers to pursuers is

Tasmania	2.0
New South Wales	2.1
Queensland	3.0

These values can be interpreted in the following way :

Tasmanian and New South Wales rainforest are cool temperate

TABLE 43. Food-habit distribution of birds in Australian, Tasmanian and New Zealand temperate rainforests. Where a species relies on two kinds of food it has been allocated $\frac{1}{2}$ - species to each of the kinds of food.

<u>FOOD-HABIT</u>	TAS		NSW		Q'd		NZ- NI		NZ- SI	
	S	%	S	%	S	%	S	%	S	%
Frugivore	$\frac{1}{2}$	2.4	3	8.8	$5\frac{1}{2}$	13.8	$1\frac{1}{2}$	7.2	$1\frac{1}{2}$	6.3
Graminivore	$1\frac{1}{2}$	7.2	1	2.9	1	2.5	2	9.5	2	8.3
Nectarivore	1	4.8	$1\frac{1}{2}$	4.4	1	2.5	1	4.8	1	4.2
Insectivore	14	67.6	$24\frac{1}{2}$	72.1	$28\frac{1}{2}$	71.2	$14\frac{1}{2}$	69.0	$15\frac{1}{2}$	64.6
Carnivore	2	9.5	2	5.9	2	5.0	2	9.5	2	8.3
Omnivore	2	9.5	2	5.9	2	5.0	-	-	2	8.3
TOTAL	21		34		40		21		24	

TABLE 44. Proportions of species relying to some extent
on each kind of food.

KIND OF FOOD	TAS	NSW	Q'd	N.Z. N.Is.	N.Z. S.Is.
Fruits	1 →	5 →	7	2	2
Seeds	2	2	2	3	3
Nectar	2	2	2	2	2
Invertebrates	17 →	28 →	32	18	18
Vertebrates	2	2	2	2	2
Omnivores	2	2	2	0	2

and the difference in the number of species is a direct consequence of the difference in latitude. As new species are added, the ratio of searchers to pursuers remains constant. The Queensland formation is warm temperate and this opens up new niches for searchers, particularly those that obtain food on or close to the ground (see below).

7.2.3 NICHE STRUCTURE IN AUSTRALASIAN TEMPERATE RAINFOREST

A comparison is made in Table 45 between the niche structures in temperate rainforest in Tasmania, New South Wales and Queensland. The classification of niches used is that devised by Cody (1974). This particular classification was adopted so that comparisons could be made in a following section (Chapter 7.3) with niche structures in South American Nothofagus forest and northern hemisphere Fagus forests.

Table 45 shows clearly that the main difference is the addition of species with decreasing latitude. It also shows that the Tasmanian species assemblage persists with few changes throughout Australian temperate rainforests.

Other points shown by Table 45 are :

- 1) Three species (Fan-tailed Cuckoo, Red (=Yellow) Wattlebird, Spotted Pardalote) that are included in temperate rainforest assemblages in Queensland and New South Wales occur commonly in Tasmania but not in temperate rainforest. They have been recorded in temperate rainforest (Chapter 3.2). Their absence must be attributed to lack of suitable niches in Tasmanian rainforest.
- 2) The only evidence for possible speciation in temperate rainforest is provided by the species pair Superb Lyrebird/

NICHE	QUEENSLAND	N.S.W.	TASMANIA
1. Sallying flycatchers	Grey Fantail Rufous Fantail Black-faced Monarch	Grey Fantail Rufous Fantail Black-faced Monarch Rose Robin*	Grey Fantail Pink Robin*
3. Foliage insectivores Canopy	Golden Whistler Silvereye Brown Warbler Striated Thornbill Spotted Pardalote Lewin's H'eater	Golden Whistler Silvereye Brown Warbler Striated Thornbill Spotted Pardalote White-eared H'eater	Golden Whistler Silvereye Tasmanian Thornbill*
4. Foliage insectivores Understory	Olive Whistler Brown Thornbill Large-billed S'wren* White-browed S'wren	Olive Whistler Brown Thornbill Large-billed S'wren* White-browed S'wren	Olive Whistler Tasmanian Thornbill* Brown Scrubwren*
5. Insectivores-Branches, twigs	E. Yellow Robin* Paradise Riflebird	E. Yellow Robin* Rose Robin*	} Pink Robin* Yellow-throated H'eater Crescent H'eater*
6. Trunk surface	White-throated Treecreeper Large-billed S'wren*	White-throated Treecreeper Large-billed S'wren*	} Scrubtit Grey Shrike-thrush* Yellow-throated H'eater* Crescent H'eater*
7. Trunks	Yellow-tailed Black Cockatoo		Yellow-tailed Black Cockatoo
8. Ground feeders	Brush Turkey Albert's Lyrebird Scaly Thrush Grey Shrike-thrush Yellow-throated S'wren E. Yellow Robin* Noisy Pitta Spine-tailed Chowchilla Eastern Whipbird Rufous Scrub-bird	Superb Lyrebird Scaly Thrush Grey Shrike-thrush Yellow-throated S'wren E. Yellow Robin* Spine-tailed Chowchilla Eastern Whipbird	Scaly Thrush Grey Shrike-thrush* Brown Scrubwren* Pink Robin*
9. Raptors - diurnal nocturnal	Grey Goshawk Spotted Owl	Grey Goshawk Spotted Owl	Grey Goshawk Spotted Owl
10A Seeds & Fruit	Crimson Rosella King Parrot Satin Bowerbird Green Catbird White-headed Pigeon Brown Pigeon	Crimson Rosella King Parrot Satin Bowerbird Green Catbird	Green Rosella ? Brush Bronzewing
10B Omnivores	Pied Currawong	Pied Currawong	Black Currawong
11. Nectar feeders	Eastern Spinebill Red Wattlebird	Eastern Spinebill Red Wattlebird	Eastern Spinebill
12. Scavengers	Torresian Crow	Corvus sp.	Forest Raven
13. Brood parasites	Fan-tailed Cuckoo Shining Bronze Cuckoo	Fan-tailed Cuckoo Shining Bronze Cuckoo	Shining Bronze Cuckoo

* Split allocation

TABLE 45. Bird species and niches in temperate rainforests in Tasmania, New South Wales and Queensland. Niche classification after Cody (1974)

Albert Lyrebird.

3) There is some evidence that some Tasmanian species occupy broader niches than their mainland counterparts. The Pink Robin appears to occupy the niches of the mainland Rose Robin and Eastern Yellow Robin, as suggested by Keast (1970). The Brown Scrubwren appears to occupy the niches of the White-browed and Yellow-throated Scrubwrens. The Scrubtit appears to occupy the niches of the Large-billed Scrubwren and White-throated Tree-creeper although the situation is complicated by the presence in Tasmania of two honeyeaters with large bark foraging components which appear to have no mainland counterparts. That two species can replace a single species has been shown theoretically by MacArthur and Levins (1967).

7.3 NICHE STRUCTURE AND PARALLEL EVOLUTION IN BEECH FORESTS

Cody (1974) compared the niches of birds in southern hemisphere Nothofagus forests and northern hemisphere Fagus-Acer beech-maple forests. In what follows I have used Cody's data and have added data generated in the present study for temperate rainforest in Queensland and Tasmania. The full data are given in Table 46 which includes both species lists and the results of seven censuses, expressed as proportions of the total census.

It has already been shown (Figure 29) that the number of species decreases with latitude. It follows that the numbers of species included in each niche category would not be the same for each locality. When niches are grouped, as in

TABLE 46. Bird species and niches in north temperate Fagus-Acer in comparison to those of south temperate Nothofagus forests.

	JAPAN	DENMARK	OHIO	NEW ZEALAND	QUEENSLAND	TASMANIA	CHILE
1. Scaly up flycatchers low - medium - high	Muscicapa latirostris 0.07 Muscicapa latirostris 0.01 Muscicapa cyanocephala 0.01	Phoenicurus phoenicurus 0.03 Muscicapa striata 0.01 Muscicapa hypoleuca 0.02	Sayornis phoebe 0.01 Empidonax vireocinus 0.02 Contopus virens 0.05 Myiarchus cinerascens 0.01	Rhipidura fuliginosa 0.04	(Rhipidura rufifrons) Monarcha melanopala (Rhipidura fuliginosa) 0.05	Petroica rodinogaster * 1/3 x 0.05 Rhipidura fuliginosa 0.09	Elaenia albiceps * 1/2 x 0.20
2. Aerial Flycatchers	(Delichon urbica)		(Progne subis)				(Tachycineta leucopygia)
3. Foliage Insectivores - Canopy high - medium - low	Phylloscopus occipitalis 0.09 Phylloscopus collybita 0.03 Aegithalos caedatus 0.05	Phylloscopus sibilatrix 0.02 Phylloscopus collybita 0.03 Phylloscopus trochilus 0.04 Regulus regulus P	Vireo flavifrons 0.03 Dendroica cerulea 0.01 Piranga erythronotus 0.05 Dendroica virens 0.02 Vireo olivaceus 0.21	Mohoua ochrocephala * 1/2 x 0.10 Zosterops lateralis 0.07	Acanthiza lineata (Zosterops lateralis) Pardaliparus punctatus 0.01 Meliphaga lewinii 0.05 Gerygone moulei 0.01 Pachycephala pectoralis	Zosterops lateralis 0.10 Pachycephala pectoralis 0.12 Acanthiza ewingii * 1/2 x 0.09	Spinus barbatus 0.09 Elaenia albiceps * 1/2 x 0.20 Sylvornithops desmursii 0.40
4. Foliage Insectivores - Understory	Urosalpinx squamiceps 0.08 Cettia diphone 0.08	Hippoboscus ictericus 0.01 Sylvia borin 0.07 Sylvia atricapilla 0.03 Sylvia communis 0.01	Setophaga ruticilla 0.11 Wilsonia citrina 0.09	Gerygone igata 0.05	Pachycephala olivacea 0.04 Acanthiza ewingii * 1/2 x 0.08 Sericornis magnirostris * 1/2 x 0.04 Sericornis frontalis 0.13	Pachycephala olivacea 0.13 Acanthiza ewingii * 1/2 x 0.09 Sericornis humilis * 1/2 x 0.05	Aphrastura spinicauda 0.15
5. Insectivores - twigs & branches	Parus ater 0.01 Parus atricapillus 0.06 Parus varius 0.06 Parus major 0.10	Parus caeruleus 0.05 Parus palustris 0.01 Parus major 0.08	Parus atricapillus 0.03 Parus bicolor 0.05	Phylloscopus novaeseelandiae 0.03 Mohoua ochrocephala * 1/2 x 0.10	Eopsaltria australis * Ptilinopus parvirostris 0.03	Petroica rodinogaster * 1/3 x 0.05 Lichenostomus flavicollis * 1/2 x 0.02 Phylidonyris pyrrhoptera * 1/2 x 0.18	Anaethetus parulus 0.06
6. Trunk Surface	Sitta europaea 0.04 Trogodytes troglodytes 0.05	Sitta europaea 0.03 Certhia spp. 0.04 Trogodytes troglodytes 0.05	Sitta carolinensis 0.02	Acanthisitta chloris 0.14	Climacteris leucophaea Sericornis magnirostris * 1/2 x 0.04	Acanthornis magna 0.05 Colluricincla harmonica * 1/2 x 0.04 Lichenostomus flavicollis * 1/2 x 0.02 Phylidonyris pyrrhoptera 0.18	Pygahichas albogularis 0.02 Trogodytes aedon 0.06
7. Trunks	Dendrocopos kizuki 0.05 Dendrocopos major 0.01 Dendrocopos leucotus 0.01 Ficus avokera 0.01	Dendrocopos major 0.01	Dryobates pubescens 0.01 Dryobates villosus 0.02 Centurus carolinus Dryocopus pileatus (Colaptes auratus)	Nestor meridionalis 0.01	Calyptrorhynchus funereus	Calyptrorhynchus funereus	(Dendrocopos lignarius) (Campephilus megalanicus) Colaptes piceus 0.01
8. Ground feeders	Phasianus versicolor 0.02 Turdus dauma 0.01 Turdus sibiricus 0.01 Turdus chrysolaus 0.01 Erithacus cyaneus 0.14 Erithacus rubecula	Phasianus colchicus Turdus merula 0.10 Turdus philomelos 0.05 Fringilla coelebs 0.12 Emberiza citrinella 0.01 Erithacus rubecula 0.07 Pernella modularis 0.02	(Bonasa umbellus) Turdus migratorius 0.01 Hylodichia mustelina 0.13 Pipilo erythrophthalmus 0.01 Seiurus aurocapillus 0.08 Seiurus monticola	(Apteryx australis) Callirallus australianus 0.03 Turdus merula 0.03 Turdus philomelos 0.02 Miro australis 0.05 Fringilla coelebs 0.04 Pernella modularis 0.01 Petroica macrocephala 0.09	Alectura lathami Menura alberti (Zosterops dauma) Colluricincla harmonica (Sericornis citreogularis) Eopsaltria australis * Pitta versicolor (Ornithyx temminckii) Psophodes olivaceus 0.10 Atrichornis rufescens	Zosterops dauma 0.02 Colluricincla harmonica * 1/2 x 0.04 Sericornis humilis * 1/2 x 0.05 Petroica rodinogaster * 1/3 x 0.05	Turdus falklandii 0.04 Pteroptochos tami 0.04 (Sclerorchilus rubecula) Seytalopus magellanicus 0.04
9. Raptors - nocturnal - diurnal	Otus scops Spilargus ripalensis	Strix aluco (Buteo buteo) (Accipiter nisus)	Strix varia (Buteo jamaicensis) 0.01	Ninox novaeseelandiae 0.01 (Falco novaeseelandiae)	Ninox novaeseelandiae Accipiter novaehollandiae	Ninox novaeseelandiae Accipiter novaehollandiae	Bubo virginianus Mylago chinensis 0.02
10. Seeds & Fruits Omnivores	Sphenurus sieboldii 0.01 Garrulus glandarius 0.03	Chloris chloris 0.01 Carduelis cannabina P Coccothraustes coccothraustes P Columba palumbus 0.04 Columba oenas 0.01 Oreolus oriolus 0.04 Garrulus glandarius	Richmondia cardinalis 0.03 Hedymeles ludovicianus (Coccyzus cristatus) (Coccyzus americanus)	Cyanocitta stelleri 0.08 Carduelis flamma 0.04 Hemiphysalis novaeseelandiae 0.02 Prosthemadera novaeseelandiae 0.04	Platycercus elegans 0.15 Alistorus scapularis (Ptilinopus violaceus) Allurorodius crassirostris 0.01 Columba leucomela 0.01 Macropygia arborescens Streptopelia gracillina 0.01	Platycercus caledonicus 0.07 Phaps elegans 0.08 Streptopelia fuliginosa	Micrositta ferruginea 0.02 Columba araucana 0.02 Circus cyaneus 0.10
11. Nectivores				Anthornis melanura 0.08	Acanthorhynchus tenuirostris 0.03 (Anthracoceros carunculata)	Acanthorhynchus tenuirostris 0.07	Sephanoides sephanioides 0.04
12. Scavengers		Corvus corone P	(Cathartes aura)		Corvus corax	Corvus tasmanicus 0.05	Coragyps atratus 0.03
13. Broad Parasites	Cuculus saturatus			Chrysocolaptes lucidus 0.02 Eudynamis taitensis 0.01	(Cuculus pyrrhophanus) (Chrysocolaptes lucidus)	Chrysocolaptes lucidus 0.01	

Table 46, ecologically similar species are lumped. Within these groups the absence of species could well be compensated by an increased density of one or more of the other species within the group. If the forest has the same structure at each locality, it would be expected that each niche group would be occupied by the same proportion of individuals comprising the total census. This is investigated in Table 47. Similarities in niche occupation patterns, calculated from equation (9), are given in Table 48.

Similarities in niche occupation patterns can be summarised as follows :

Within <u>Fagus-Acer</u> forests (3 comparisons)	72 %
Within <u>Nothofagus</u> forests (6 comparisons)	70 %
Within Australian <u>Nothofagus</u> forests (3 comparisons)	67 %
Between <u>Fagus-Acer</u> and <u>Nothofagus</u> forests (12 comparisons)	65 %
Between <u>Fagus-Acer</u> and Australasian <u>Nothofagus</u> forests (9 comparisons)	63 %

To provide a basis for comparison, the niche occupation patterns for three Tasmanian temperate rainforest sites are given in Table 49. These provide a mean similarity between Tasmanian sites of 86 per cent.

All comparisons give similarities less than the within Tasmania similarity. The within forest similarities are broadly similar and are slightly greater than the between forest values. The similarity between the Chilean and Tasmanian Nothofagus forests, 83 per cent, falls within the

NICHE	JAPAN	DENMARK	OHIO	NEW ZEALAND	QUEENS- LAND	TASMANIA	CHILE
1 Sallying flycatchers	11	6	8	4	5	11.2	10
2 Aerial flycatchers	0	0	0	0	0	0	0
3 Foliage insecti- vores - canopy	17	9	31	12	15	17	23
4 Foliage insecti- vores - understory	17	12	20	5	26	15	15
5 Insectivores - trunks & branches	13	14	7	8	3	8.7	6
6 Trunk surface	9	12	2	14	2	16.5	8
7 Trunks	8	1	4	1	1	0	0
8 Ground feeders	20	37	23	27	14	8.2	12
9 Raptors	0	+	+	1	0	0	1
10 Seeds & fruits. Omnivores	4	9	3	17	32	15	14
11 Nectarivores	0	0	0	8	3	7	4
12 Scavengers	0	+	0	0	1	0.5	3
13 Brood parasites	0	0	0	3	0	1	0

TABLE 47. Niche occupancy patterns in beech forests.

TABLE 48. Similarities in niche occupancy patterns in
beech forests.

	Japan	Denmark	Ohio	New Zealand	Queensland	Tasmania	Chile
Japan	100	74	78	63	60	73	73
Denmark		100	63	75	54	65	63
Ohio			100	57	62	60	70
New Zealand				100	60	74	67
Queensland					100	67	70
Tasmania						100	83
Chile							100

TABLE 49. Niche occupancy patterns of three Tasmanian temperate rainforest sites. Niches as in Table 47.

NICHE	GORDON RIVER A	GORDON RIVER B	OLGA CAMP
1	9	2.3	11.2
2	0	0	0
3	24	18	17
4	16.5	16.5	15
5	13	12.8	8.7
6	16.2	15	16.5
7	0	0	0
8	4.7	3.3	8.2
9	0.5	1	0
10	11	21	15
11	6	12	7
12	0.5	0	0.5
13	0.5	0	1

SIMILARITIES :

Gordon River A / Gordon River B	85 %
Gordon River A / Olga Camp	89 %
Gordon River B / Olga Camp	83 %

range for Tasmanian forests. This suggests that the expectation that each niche group would be occupied by the same proportions of the total is broadly true. Cody (1974) recognises that deviations can be attributed to a) chance effects, b) non-correspondence of habitat, c) productivity differences, and d) historical factors (man's influence, island effects, introduced competitors and predators, etc.).

An attempt has been made to allow for productivity differences by using proportional species totals rather than densities. Chance effects must be important and include inaccuracy of censusing (no census technique is 100 per cent accurate) and local effects of both place and time. Historical factors are particularly important in New Zealand where a significant proportion of the avifauna consists of introduced species. Insufficient data are available to assess the importance of habitat differences.

In spite of the above difficulties, correspondence between sites is sufficiently good to make the statement that birds of dissimilar affinities and origins have evolved adaptations that enable them to occupy similar niches. For example, in the absence of woodpeckers, the trunk niche has been occupied by members of the Cacatuidae that have evolved bills that enable them to obtain invertebrates from beneath the surface of trunks and branches. The tit Parus spp. niche of the northern hemisphere is filled in Australasia by species in several genera belonging to several families, including the Muscicapidae and Meliphagidae.

CHAPTER 8

TEMPERATE RAINFOREST AND THE ORIGINS AND
EVOLUTION OF THE TASMANIAN AVIFAUNA.

8.1 INTRODUCTION

Nothofagus undoubtedly is a very old genus and Nothofagus-dominated temperate rainforest a long-established habitat. The fact that no bird species is restricted to temperate rainforest in Australia is odd and has prompted this review of the probable history of temperate rainforest in Tasmania, the origins and the evolution of the present day Tasmanian avifauna and the relevance to theories of speciation in Australia.

8.2 THEORIES OF SPECIATION IN AUSTRALIA

The present day pattern of species distribution in Australia is explicable in terms of humid refuges separated by arid areas. Tasmania is one such refuge although it is now separated from other humid areas by Bass Strait. The main contributions to the theory of speciation in Australia, including those concerned with the origins of the Tasmanian avifauna, are reviewed in chronological order.

Gentilli (1949)

Gentilli was one of the first to introduce the concept of humid refuges which have subsequently formed the basis of theories of speciation in Australia. In reconstructing past climates, Gentilli assumed that glacial periods were wet as well as cold. Under these conditions, temperate rainforest would be the dominant vegetation over much of southern Australia, including those parts of the Tasmanian peninsular not covered with ice or subject to periglacial activity.

At some time after 20,000 B.P., as the climate became warmer, it became drier and forest habitats shrank, eventually breaking up into isolated refuge areas. Gentilli envisaged a great arid period which reached its maximum about 10,000 B.P. Since then there has been some climatic amelioration.

Gentilli recognised that speciation may be rapid for he wrote ".....the species which we now know have spread, or arisen and spread, at a very rapid rate", i.e. in less than 10,000 years.

Keast (1961)

Keast developed the first comprehensive theory of speciation for birds in Australia. Like Gentilli, he assumed that glacial periods were wet. During arid periods relict fragments of humid forest acted as refuges, each isolated from its neighbours by arid zones that reached Australia's eastern coast. Populations isolated in the refuges became species that radiated throughout Australia as climatic conditions changed and the arid areas retreated. Keast's theory, as it applies to Tasmania, is considered when his later papers are discussed.

Brereton and Kikkawa (1963)

These workers modified Keast's hypothesis by suggesting that the refuges were semi-arid areas separated by arid corridors. (In Gentilli's original nomenclature these refuges are more likely to have been sub-humid zones separated by semi-arid and arid corridors. The climax vegetation of Gentilli's

sub-humid zone is open woodland whereas that of the semi-arid zone is grassland). In this way Brereton and Kikkawa accounted for the richness of species in Australian woodland, including many species belonging to genera that do not contain rainforest species. Speciation occurred in the isolated woodland refuges. To account for the small number of rainforest species, Brereton and Kikkawa assume wholesale extinction during arid periods; a very slow rate of recolonisation by rainforest forms from New Guinea when arid conditions no longer prevailed; and the inability of woodland forms to colonise rainforest because they are not pre-adapted to this habitat.

Ridpath and Moreau (1966)

Ridpath and Moreau also assumed that glacial periods in Tasmania were at least as wet as the present day climate. From a consideration of the habitat preferences of the Tasmanian endemic species, as then known, they concluded that only one, the Scrubtit, could with certainty have withstood the full rigours of the last glaciation. They believe that most species entered Tasmania during the warming phase of the last glaciation, i.e. from 20,000 to 12,000 B.P., the latter date being fixed by the disappearance of the Bass Strait land bridge. Ridpath and Moreau recognise that because of low temperatures at the height of the last glaciation many species of birds now present in Tasmania would not have been able to survive.

Keast (1970)

In this paper Keast states: "[the contemporary forest types]

probably existed through the last glaciation [in Tasmania]. This conclusion would indicate that there has been no major evolution of new avian habitats, just shifts in relative extent of each." He further states: "the more distinctive endemic species and races undoubtedly antedate the post-glacial isolation of the island, when sea levels rose, and probably antedate the glaciation itself. The glacial period, when about one thirteenth of the island was covered by ice, and temperatures must have been severe, presumably eliminated many bird species. Temperatures were already warming and habitats expanding, however, prior to the isolation of the island about 12,000 years ago. Many of the major elements probably reached Tasmania at that time, and there has undoubtedly been a dribble of new colonisers ever since."

Horton (1972)

Horton attempted to reconcile the views of Keast and of Brereton and Kikkawa using mathematical modelling. He concludes that, in Australia, the amount of rainforest habitat is small and does not break up sufficiently to isolate populations. It is difficult to reconcile this conclusion with the assertion (p. 106) that Australian rainforest is "fragmented sufficiently to form subspecies and varieties". Horton also concludes that rainforest species definitely do not become extinct. He assumes that glacial periods are wet and are periods of uniformly benign conditions.

Abbott (1973)

Abbott concludes: "when Bass Strait was last flooded, the

islands so formed acted virtually as closed systems, in that many species so isolated have since become extinct and most mainland species have been unable to invade. The pattern of distribution of species is largely relict. Fifty-one species of land birds in southern Victoria apart from three breeding on King Island are accidental or unknown from Tasmania and the Bass Strait islands. These are probably post-glacial intrusives into southern Victoria." Abbott believes that land birds rarely cross water.

Keast (1974)

Again Keast emphasises that each time Tasmania was joined to south-eastern Australia its avifauna would have been re-charged by the entry of species from the mainland and that there ought to have been ample opportunity for increasing the number of species.

Keast (1976)

Keast slightly modifies his earlier statements in respect of time of entry of species into Tasmania in accordance with more recent evidence that the last glaciation was both cold and dry rather than cold and wet. The main elements of the Tasmanian avifauna are now considered to have arrived after 18,000 B.P. and towards the time the Bass Strait land bridge disappeared. This is very little different from his earlier contention (Keast 1970) except that it is implied that some of the more distinctive endemic species and races may not have been able to survive a dry glacial period. Keast (1974) considers that active speciation is occurring today in Tasmania.

In many of the above references it is far from clear whether temperate rainforest and subtropical rainforest are included in the 'rainforest' category. For example, in Figure 3 of Keast (1974) rainforest is shown as occurring in western Tasmania but no rainforest is shown as occurring in Tasmania as a whole in Figure 2 of the same paper. (Most of the area shown as rainforest in Figure 3 appears as 'desertic vegetation' which occupies virtually the southern half of the island in Figure 2). It is also not clear whether the Nothofagus forests of New Guinea are included in 'rainforest' or 'montane vegetation'.

I believe that temperate rainforest is best treated by including it in montane forest rather than lumping it with subtropical and tropical rainforest. Not only does temperate rainforest lack the structural and floristic complexity normally associated with rainforest but, as Kikkawa (1968) has shown from similarity analysis, there is a unique association of bird species within rainforest habitats of northern Queensland, "reflecting comparative richness of the tropical fauna in rainforest". By contrast, temperate rainforest is species poor and has no single bird species uniquely associated with it. The transition from subtropical to temperate rainforest is gradual and occurs along an altitudinal (temperature) gradient. Thus, in northern New South Wales, similarity analysis groups temperate rainforest and subtropical rainforest with wet sclerophyll forest in 'tall wet formations' (Kikkawa 1968, 1974). New England is in the transition zone and some species that are predominantly subtropical rainforest species (Brown Warbler, Yellow-throated Scrubwren, Rufous Fantail, Eastern Whipbird) also

occur in temperate rainforest (Kikkawa et al. 1965). However many of the species occurring in temperate rainforest have a southern distribution in eastern Australia whereas many of the species occurring in subtropical rainforest are northern species (Holmes 1977).

Two conclusions can be drawn from the combined work of the authors discussed above :

- 1) Tasmania and southern Victoria shared the same avifauna when the Bass Strait land bridge existed, and
- 2) most species entered Tasmania across the land bridge, i.e. before 12,000 - 13,000 B.P.

The first point is not disputed, although Tasmania may have had fewer species than expected because of the peninsular effect (MacArthur and Wilson 1967).

The second conclusion is based on the assumption that the last glacial period was one of high rainfall and that all the present day avian habitats were well-developed in Tasmania, at least by 12,000 B.P. There is now considerable evidence that the waning phase of the last glacial was drier than at present and that the cold-dry phase did not end until after the Bass Strait land bridge had disappeared.

8.3 PROBABLE HISTORY OF NOTHOFAGUS IN TASMANIA

Before reviewing the paleobotanical evidence for a cold-dry period that persisted until after 12,000 B.P., a suggestive piece of ornithological evidence will be considered. If the last glacial period had been wet and if, as Gentilli suggests, temperate rainforest had been the dominant vegetation in southern Australia throughout the glacial period, which

lasted for some 50,000 years, it is inconceivable that an avifauna uniquely adapted to this habitat had not evolved. Temperate rainforest would have been expected to persist in Tasmania during the preceding interglacial period and would have been in continuous existence for much longer than 50,000 years. In a subsequent dry period, temperate rainforest would have contracted and eventually become fragmented, much as it is today. A few species of birds that were restricted to temperate rainforest would have been expected to survive although many would have become extinct. However, no species is restricted to temperate rainforest which implies that temperate rainforest, in its present form, virtually disappeared at some time in the past. A cold-dry period would provide conditions that favoured the disappearance of temperate rainforest.

In considering the origins of the Tasmanian avifauna, the crucial question is : What was the vegetation of south-eastern Australia and Tasmania when the land bridge finally disappeared ?

Both Galloway (1967, 1971) and Macphail (1975) have argued strongly against the concept of a glaci-pluvial, a concept that has been extensively incorporated in zoological thought (see above). The evidence implies that, while the waxing phase of the last glacial (i.e. before 20,000 B.P.) may have been wet, the waning phase has been drier. Temperature alone in Tasmania and rainfall/temperature limitations in south-eastern Australia would not have been conducive to large forests of Nothofagus between 20 - 10,000 B.P. There is some evidence for the presence of N. cunninghamii

outside its present limits at c. 30,000 B.P. (Jennings 1959 for Bass Strait islands and Caine and Jennings 1968 for below the Snowy Mountains).

One of the few globally recorded events is the rapid rise in temperature at c. 10,000 B.P., the culmination of a global warming beginning some 4,000 years earlier (see, for example Kershaw 1974). Macphail and Petersen (1975), from pollen analyses, record a marked upslope migration of the timberline in Tasmania at c. 11,500 B.P., i.e. after the cutting of the land bridge. Before this all mesophytes, including N. cunninghamii, were absent or negligible over most of Tasmania. Arboreal species were restricted to c. 200 - 300 m above present day sea level in eastern Tasmania and probably to as low as sea level in northern Tasmania (Chick and Colhoun 1972). The present day timberline, the altitude of which varies locally with latitude and aspect, is formed in Tasmania by either sub-alpine eucalypts, Eucalyptus coccifera for example, or N. cunninghamii. Macphail (1975) has suggested that forest vegetation, probably eucalypts, could have existed only on the now flooded continental shelf off the far south-east and south-west coasts. In western Tasmania ice was still present in the high discrete cirques as late as c. 9,000 B.P. Pollen analysis has shown that N. cunninghamii closed-scrub became established in a small cirque basin at 880 m on Adamson's Peak about this time (Macphail and Petersen 1975). It is likely that stands of rainforest were in existence on the slopes of the discrete mountains in western, central and far south-eastern Tasmania by c. 9,000 B.P., certainly by 8,000 B.P. (Macphail in litt.).

Lowland vegetation in the late Pleistocene is likely to have been sparse grasslands in eastern Tasmania and either grasslands or sclerophyll heath and sedgeland in western Tasmania. The absence of N. cunninghamii, Phyllocladus, Dicksonia and Pomaderris apetala pollen from late-glacial assemblages is good evidence for the absence of temperate rainforest and P. apetala wet scrub across Tasmania in general (Macphail 1975).

The evidence is, then, that forest habitats were poorly represented in Tasmania at the time of its final isolation. The postglacial succession appears to have been Eucalyptus - Pomaderris apetala/Phyllocladus - N. cunninghamii. This suggests that all of Tasmania was drier as well as colder in the late Pleistocene, i.e. until 10,000 B.P., and that what forest that was present was similar to present day sub-alpine forest and was not rainforest.

Moreau (1966) has pointed out that the nuclei of plant species that form a particular habitat can persist almost indefinitely through an inimical climate and long after the associated bird species have been forced to move or become extinct. The absence of bird species uniquely adapted to temperate rainforest suggests that, at the time Tasmania was isolated, these forests were present in such small pockets or, alternatively, were so structurally different (e.g. present as krumholtz shrubs) that most if not all rainforest species of birds had become extinct, which agrees with the ideas of Brereton and Kikkawa (1963) but is opposed to the view of Horton (1972) as far as temperate rainforest birds are concerned. This may not be the case for tropical

rainforest with its unique association of bird species.

Temperate rainforest reached its maximum development in Tasmania c. 8,000 B.P. in response to the warmer wetter climate. Since then increasingly severe climates and fire pressure, the effects of which have been greatest in the east, have caused a steady decrease in the extent of temperate rainforest (Jackson 1965, Macphail in litt.).

Even if all present day forested habitats had come into existence by 12,000 B.P., the extent of most would have been very much less than it is today. As Bosworth et al. (1976) have shown for dry sclerophyll forest, the well-known logarithmic species - area relation would be expected to apply. Consequently, the number of forest species in Tasmania would have been much smaller than it is now.

8.4 ORIGINS AND EVOLUTION OF THE TASMANIAN AVIFAUNA

If, as suggested above, the late Pleistocene was cold and dry, most species of forest and woodland birds must have entered Tasmania after it became an island. Thus, one of the central tenets of Abbott's (1973) theory, namely that passerine land birds rarely cross water, cannot be correct.

It follows that the Tasmanian populations of many species have been isolated for less than 10,000 years. Despite this, the degree of endemism is pronounced (Ridpath and Moreau 1966) and some speciation must have occurred in this time. Although Gentilli (1949) based his argument on the assumption that the last glaciation was wet, he deduced the same

speciation time.

Some of the theories discussed in Chapter 8.2 appear to be based on the supposition that speciation only occurs over very long periods of time by the slow accumulation of micromutations and in geographical isolation. For example, Horton (1972) makes no allowance for speciation after the Wurm glaciation. This view of speciation is contrary to that of Goldschmidt (1940) and is not in accordance with Gentilli's (1949) conclusions regarding speciation time. Keast (1974), while adhering to the view that "....speciation occur[s] when populations of species are isolated from parental stocks for long periods" later recognised that the present patterns of speciation are very well established at 11,000 - 13,000 years (Keast 1976). I agree with Goldschmidt and Gentilli because I believe that the alternative view largely ignores natural selection, the driving force of evolutionary change. While Horton argues that variants separated long enough will develop into species, this begs the question of how long is long enough. Potentially, any isolated population may evolve away from other populations, eventually reaching a level of divergence to be judged a subspecies and, finally, a species (MacArthur and Wilson 1967). However, by no means all isolated populations diverge from other populations.

That evolution can be rapid was recognised by Fisher (1929) when he wrote ".....selection will itself act by increasing the intensity of the preference to which it is due, with the consequence that both the feature preferred and the intensity of the preference will be augmented with ever-increasing velocity, causing a great and rapid evolution of certain

conspicuous characters.....". Gilliard (1969) brilliantly exploited this concept to explain the radiation of the birds of paradise and bowerbirds in New Guinea as the result of a "runaway surge of evolution".

Moreau (1930) inferred that subspeciation in birds could take place in less than 4,000 years. Subsequently, Johnston and Selander (1964) have shown that subspeciation in the House Sparrow can occur in as little as 30 generations. Gentilli (1949), Mayr (1963), Horton (1972) and others have pointed out that results at the subspecific level cannot necessarily be extrapolated to the specific level. However, at the specific level, Hall (1963) has argued that some speciation must have taken place in some African francolins within the last 18,000 years and Fisher and Petersen (1964) believe that five sibling species of gulls arose from a common ancestor between 15,000 and 10,000 years ago.

I agree with Moreau (1966) that, while the evidence is still meagre, there is a very real possibility that in birds speciation can occur within a small fraction of the Pleistocene and Holocene.

It is accepted generally that geographical isolation is a necessary prerequisite for speciation (e.g. Ford 1974), although the comments of Thomson (1969) on differentiation at the subspecific level should not be overlooked if geographical isolation produces the evolutionary sequence
isolation - subspeciation - speciation at the level
of the superspecies - full speciation.

If geographical isolation was the sole cause of speciation, one can envisage evolution occurring through the slow accumulation of micromutations by such processes as the founder effect and genetic drift. However, if a continuous habitat breaks up into a number of isolates, the structure of which remains unchanged, there is no reason to believe that each isolate will produce new bird species even after very long periods of time with no gene flow. Such a situation is more likely to produce clines or some degree of subspeciation (perhaps depending on the taxonomist concerned) as envisaged by Gentilli (1949) and Horton (1972). Some speciation may occur if a species modifies its foraging behaviour because the set of competitors encountered is different in different patches of habitat. These points are amply illustrated by the montane bird faunas of Africa discussed by Moreau (1966). Geographical isolation alone cannot explain the radiation of the Geospiza finches in the Galapagos Islands and the birds of paradise in New Guinea, or the intense speciation achieved by some (but not all) species in montane forests, often within sight of one another, near the Kenya - Tanzania border. Other species inhabiting African montane forests, which are as fragmented as Australian Nothofagus forests, show little or no differentiation although separated by distances as great as 1,900 km.

The Tasmanian population of the Grey Shrike-thrush has evolved a bill that is so much larger than its mainland relative that Macdonald (1968) recognised it as a distinct subspecies. In a more recent revision, Ford and Parker (1974) include the Tasmanian population in one of two mainland races. Although no reasons are given, these can be deduced

from Ford (1974) who believes that ecotypic variation is reversible. Tasmanian Grey Shrike-thrushes show a shift in foraging behaviour, foraging more on bark than their mainland counterparts (Keast 1970, pers. obs.). Presumably, the larger bill of Tasmanian birds is an adaptation resulting from and/or facilitating such a shift. Environmental conditions in Tasmania could change in one of two ways : one favouring the evolution of a still larger bill, the other the evolution of a smaller bill. If the difference in mean bill lengths, expressed as a percentage of the overall mean, exceeds 30 per cent there is reason to believe that the two populations could coexist if they met (Hutchinson 1958, Schoener 1965, MacArthur and Wilson 1967). This difference is already 24 per cent so there is a distinct possibility that the Tasmanian population could diverge sufficiently to become a distinct species. Although Ford claims that taxo-evolutionists would not recognise ecotypic variation, which he appears to equate with clinal variation, the increase in bill size of Tasmanian birds is hardly the result of 'clinal variation'. Failure to recognise the Tasmanian population as subspecifically distinct results in a loss of information about a population that could become specifically distinct given a particular change in its environment. Certainly, the marked change in bill size, granted that the bill is a particularly plastic morphological character, allied to a shift in ecological behaviour seems a more fundamental difference than the slight differences in plumage ("greyer above and in having a buff or cinnamon wash on the linings of the wings and much of under-surface") recognised by Ford and Parker. Such differences could arise from genetic drift if the two populations had once been separated but such

minor variation may represent neutral adaptation of little or no selective value unless, of course, it can be linked with behavioural or ecological differences that could act to prevent interbreeding. In the present case this seems unlikely and the two 'subspecies' freely hybridise in some areas.

The Grey Shrike-thrush has been considered at length because I believe that recent trends in Australian avian taxonomy (Ford 1974, Schodde 1975) have lost sight of the importance of prezygotic isolating mechanisms (Bossert 1963) such as differences in ecology and courtship, including vocalisation, for, as Mechim (1961) has recognised, evolution is most likely to occur through prezygotic mechanisms rather than through postzygotic mechanisms such as decreased hybrid fitness.

Field observations over the last century have shown the remarkably rapid evolution of introduced species, or of species responding to changed environments (Levins 1968). The ancestral stock of the birds of paradise and bowerbirds, on reaching New Guinea from Africa or Asia, probably found many vacant niches in the forests and diverged rapidly in many directions (Gilliard 1969). This produced many distinctive species, some of which also adopted arboreal polygony. Here, radiation can be regarded as the natural introduction of species into a new and, presumably, empty environment. Recher (1974) has pointed out that it is a necessary prerequisite for successful colonisation that a suitable vacant niche exists. Vacant niches are likely to arise during periods of rapid

environmental change, such as occurred in Tasmania after 10,000 B.P.

Probably, the differentiation of Tasmanian endemic species occurred rapidly once the new and expanding habitats had been successfully invaded, as predicted by MacArthur and Wilson (1967).

The importance of changing environments, and the rapidity with which such changes can occur, in producing speciation must not be overlooked. MacArthur and Levins (1967) have shown theoretically how, under certain conditions, two or more specialists can exclude or replace a lesser number of generalist species. Their argument can be extended to explain how a generalist can, under the conditions envisaged in south-eastern Australia in the past 10,000 years, diverge to become two or more less-generalist species.

To sum up : the Tasmanian avifauna is made up of two components - species that survived the last glacial period of the Pleistocene which was cold and dry, and species that have entered Tasmania since 10,000 B.P. On the evidence of present day habitat preferences, most species have entered Tasmania since Bass Strait came into existence. This has provided enough time for a significant degree of endemism to have evolved. There is no evidence for the persistence of an avifauna uniquely adapted to temperate rainforest. Such an avifauna probably existed in the past but became extinct during the closing phase of the Pleistocene (20,000 - 10,000 B.P.).

Temperate rainforest has been colonised from other forest habitats. Its lack of species cannot be attributed to slowness of colonisation from New Guinea or from a lack of species with the necessary pre-adaptations in other habitats. The lack of species in temperate rainforest must be accounted for from a consideration of temperate rainforest itself (Chapters 3 - 5).

8.5 SPECIATION BY DOUBLE INVASION

One way the number of species on an island can increase is by double invasion.

Tasmanian habitats form a continuum along the xeric-mesic gradient and there are no well-defined habitat barriers. There are a few examples of closely related species replacing each other along the xeric-mesic gradient. The few examples that there are are provided by the following species pairs (the species occupying the more mesic habitats listed first) :

Grey Goshawk / Brown Goshawk

Brush Bronzewing / Common Bronzewing

Tasmanian Thornbill / Brown Thornbill

Black Currawong / Clinking (Grey) Currawong

Because ecological separation by habitat is uncommon and because Tasmania lacks geographical internal isolating features, speciation by double invasion should be uncommon. This is so.

Keast (1961, 1970, 1974, 1976) claims that there have been three instances of speciation by double invasion which involve

Tasmanian Thornbill / Brown Thornbill

Scrubtit / Brown Scrubwren

Forty-spotted Pardalote / Spotted Pardalote.

Keast (1976) supports his argument by stating that the two species in each species pair occupy different habitats. This is true only for the thornbills. The pardalotes provide an example of one species replacing another. The older invader, the Forty-spotted Pardalote, has declined markedly during the present century and is now confined to a few localities on the periphery of its former range (D.R. Milledge ms.). Even in these localities both the Spotted and Striated Pardalotes are common (pers. obs.) and the inescapable conclusion is that the Forty-spotted Pardalote is heading for extinction.

It is doubtful if the Scrubtit and Brown Scrubwren are members of the same genus, let alone being derived from a common stock. Keast (1970) thought originally that the Scrubtit was "very rare" and "confined to shrinking areas of rainforest where, apparently, it is steadily being compressed by the later coloniser, S. (frontalis) humilis." This is untrue for both species occur commonly in a range of habitats where they forage in very different ways (Thomas 1974, Chapters 2 and 5). This would be most unusual if a case of speciation by double invasion. The most likely outcome would be that one species would replace the other (as in the pardalotes) or the two species would occupy different habitats with neither penetrating the other's range (as in the thornbills).

Is the Scrubtit a scrubwren ? According to Schodde (1975)

"Acanthornis is like Sericornis in all external characters, foraging behaviour, song and nidification except for its Acanthiza-like eggs. It has the facial pattern of the Sericornis frontalis group and its whitish speculum; apparently a derivative of Sericornis, it may have arisen from early frontalis stock. Following Macdonald (1973), I have included it in Sericornis." Incidentally, Macdonald gave no reasons. Many of the above statements are of doubtful validity. In size and shape Acanthornis resembles Acanthiza rather than Sericornis. To say that the foraging behaviour is like that of Sericornis is meaningless because some Sericornis spp. (e.g. magnirostris) are arboreal whereas others (e.g. frontalis) are terrestrial. No Sericornis sp. has the large trunk foraging component characteristic of Acanthornis. Both Acanthiza pusilla and A. ewingii forage on trunks at times. When foraging, Acanthornis is animated, again resembling Acanthiza more than Sericornis. Although some of its calls resemble those of Sericornis, others resemble those of Acanthiza and Acanthornis has some quite distinctive calls (pers. obs.). It is not clear on what Schodde bases his statement regarding calls for the literature is far less specific. Acanthornis differs from frontalis and its Tasmanian derivative humilis in bill and eye colour, in which respect it resembles magnirostris although not resembling it in other aspects apart from being arboreal and inhabiting dark damp habitats. Species of Sericornis and Acanthiza in Tasmania are almost invariably found in small groups, probably family parties, and have 'helpers at the nest' when breeding. As far as is known, Acanthornis occurs normally in pairs and does not have 'helpers'. Acanthiza spp. lay eggs at 48-hour intervals, Sericornis

at 24-hour intervals. The egg laying interval of Acanthornis is not known.

On present knowledge it seems better to retain Acanthornis as a monotypic genus, just as Oriama (which also has a 48-hour egg laying interval) has been retained^a. Certainly, the grounds for separating Acanthornis and Sericornis are more substantial than those used by Schodde and McKean (1976) for splitting Melanodryas from Petroica.

8.6 HAS THE TASMANIAN AVIFAUNA REACHED EQUILIBRIUM ?

At first sight Tasmania appears to be a first-order land bridge island (Diamond 1976). This implies that when the land bridge was finally broken, Tasmania and southern Victoria shared the same avifauna. Subsequently, the number of species on Tasmania has declined because of species - area effects.

Recent paleobotanical evidence suggests that the above is an inadequate explanation because, while Tasmania and Victoria had a common avifauna, most species must have entered Tasmania after the land bridge disappeared because forested habitats did not develop until after that time. Tasmania has subsequently acted as a 'new' island. On the equilibrium theory of MacArthur and Wilson (1967), the number of species on Tasmania would have increased subsequently to an equilibrium number determined by island area and distance from the source region.

In either case, the important question is : has the number

of species on Tasmania reached equilibrium ? Diamond (1972) has proposed a method of determining the relaxation time t_r , which is the time for an island avifauna to reach equilibrium. Diamond proposed the following formula

$$\left[S(t) - S(eq) \right] / \left[S(0) - S(eq) \right] = e^{-t/t_r} \quad (13)$$

where

$S(t)$ = number of species present at time t

$S(eq)$ = equilibrium number of species

$S(0)$ = number of species present initially, or
in the source region.

$S(t)$ is the instantaneous number of species present t years after the island was formed. $S(eq)$ can be obtained from the species (S) - area (A) relation for the Tasmanian region devised by Rounsevell et al. (1977)

$$\log S = 0.23 \log A + 0.68 \quad (14)$$

and equals 173. $S(0)$ is taken as 285, total number of species breeding in Victoria (Ridpath and Moreau 1966) and $S(t)$ is 108 (Thomas unpub. data).

For $\tau = 12,750$ years, $t_r = 23,500$ years and for $t = 10,000$ years (the close of the last Pleastocene glaciation), $t(r) = 18,380$ years. In either case Tasmania can expect to receive additional species.

This is a surprising result because intuitively the Tasmanian avifauna has reached, or is close to, equilibrium. However, the immigration rate needed to reach equilibrium, with zero extinction rate, of one species in more than 100 years would be difficult to detect. An alternative explanation can be provided, based on Schoener's (1976) contention that the slope of the species area curve decreases with increasing area. Fitting a curve by eye to the points in Figure 1 of Rounsevell et al. (1977) suggests a value for $S(eq)$ of 2128.

Using this value in equation (13) yields relaxation times of 12,166 years for $t = 12,750$ and 9,542 years for $t = 10,000$. In both cases the Tasmanian avifauna has reached equilibrium.

At present it is not possible to decide which of the two possibilities is to be preferred.

SPECIATION IN TEMPERATE RAINFOREST

CHAPTER 9

9.1 INTRODUCTION

Ridpath and Moreau (1966) believe that the temperate rainforests of the southern hemisphere have always been a poor habitat for birds and have never been important in the evolution of the class. The widely scattered Nothofagus forests of the southern hemisphere have somewhat different histories. The importance of these forests as sources of bird species can now be reviewed in terms of what is known of their past histories and present avifaunas.

9.2 AUSTRALIA AND TASMANIA

Undoubtedly temperate rainforests once extended over a far greater area of Australia and Tasmania than they do at present. Gentilli (1949), for example, shows temperate rainforest as extending as far north as c. 20° south during the Riss glaciation. It was thought that these forest were as extensive as this during the closing stages of the final glaciation of the Pleistocene which lasted until 10,000 B.P. It is now thought that the closing stages of the Pleistocene were dry in south-eastern Australia. Temperate rainforest probably only survived this period in stream gullies and other favourable retreats (Kershaw 1974). There is evidence from widely scattered sites consistent with an increase in rainfall starting about 12,000 to 10,000 B.P. (e.g. Kershaw 1974, Bowler et al. 1976, Binder and Kershaw 1978).

If temperate rainforest existed over a large area it is likely that an avifauna uniquely adapted to this habitat existed. The virtual elimination of temperate

rainforest at the close of the Pleistocene would bring about the almost complete extinction of the avifauna. Robinson (1977) has drawn attention to the possibility that the Menurae originated in temperate rainforest. However, just as the vegetation responds to the xeric-mesic gradient, so does the avifauna and no bird species is restricted to temperate rainforest. While Robinson may be right, on the available evidence it would be more correct to say that the Menurae originated in cool wet forests which includes wet sclerophyll forest, presently the main habitat of the Superb Lyrebird and Noisy Scrub-bird. Wet sclerophyll forest is also inhabited by the Rufous Scrub-bird. Two refuge areas must have existed at one period to give rise to the two species of Lyrebird.

Today no species of bird is restricted to temperate rainforest. On a purely local scale, the Olive Whistler is restricted to temperate rainforest in northern New South Wales (Kikkawa 1968) and southern Queensland (Marshall 1935) although I recorded it in subtropical rainforest at Binna-Burra in the Macpherson Ranges. According to Marshall the population of the Olive Whistler in the Macpherson Ranges is so distinctive that it can be regarded as a distinct subspecies. This is the only example known of speciation within Australian temperate rainforest.

9.3 NEW ZEALAND

The New Zealand avifauna is the result of a continuous and continuing process of immigration, mainly from Australia (Falla 1953). It is hardly surprising that a significant

proportion of the New Zealand avifauna consists of distinctive species. There has been some differentiation between forms on the two main islands and on some of the off-shore islands. However, there is little or no evidence for speciation within temperate rainforest. Most species appear to occupy a range of forest habitats (Kikkawa 1966) although the picture is complicated by recent introductions and extinctions as well as by extensive habitat modification. However, the conclusion that New Zealand Nothofagus forest has been an insignificant source of species is inescapable.

9.4 NEW GUINEA

As far as I am aware there have been no studies relating specifically to Nothofagus forests in New Guinea. The distribution of these forests is broadly correlated with altitude. Bird distribution on New Guinea can also be correlated with altitude even though the line which sharply divides the ranges of two species may appear to be unrelated to habitat turnover (Diamond 1972). Cody (1974) has pointed out that "there must be a feedback mechanism from the character of the vegetation into the mechanisms of competition, even though the vegetation varies clinally with few if any abrupt changes along the altitudinal transects".

In view of the above it is by no means clear to what extent bird species are restricted to Nothofagus forest. Cody (1974) has suggested that altitudinal ranges may be determined largely by physiological tolerances. Support for this view is provided by Schodde and Hitchcock (1968) : Nothofagus forest occurs uncharacteristically at 800 m at

Lake Kutuba and supports a predominantly lowland avifauna and at least 14 species that are characteristic of the nearby montane beech forests are absent.

During the Pleistocene, the extent and altitudinal range of the beech forests would vary. At present they occur at altitudes up to 3,000 m and patches are isolated on individual mountains. Species characteristic of lower montane forests (800 - 1,100 m, below the normal range of Nothofagus forests) have distributional patterns similar to the fundamental species - area relation of island biogeography. Diamond (1972) considers that the dispersal rates of birds between New Guinea mountains separated by valleys a few kilometers wide are so low that the peaks behave as islands. Presumably, this applies also to the birds of Nothofagus forest. Such a situation should be conducive to phyletic evolution. It is not known to what, if any extent this has occurred.

In view of the situation in Australia (above) and South America (below) one would predict that the New Guinea Nothofagus forests have generally been a poor source of species and, apart from spectacular bursts of adaptive radiation, that speciation has been by phyletic change. This involves processes such as genetic drift over long periods of time in isolation. Much new data are needed to establish the correctness (or otherwise) of this prediction.

New Guinea has witnessed the spectacular radiation of the birds of paradise and bowerbirds (Gilliard 1969) but this may have been in response to an empty environment or to one undergoing rapid and drastic ecological change. Couper (1960)

believes that Nothofagus, Dacrydium, Phyllocladus and Podocarpus invaded New Guinea from Australia in late-Pliocene or Pleistocene times. If this invasion coincided with the invasion of New Guinea by the ancestral stock of the birds of paradise and bowerbirds, adaptive radiation could have occurred at about this time.

9.5 SOUTH AMERICA

A difficulty immediately arises because of conflicting statements as to the extent to which bird species are restricted to Nothofagus forests. Vuilleumier (1967) claims that 50 per cent of species are endemic to "the Nothofagus forest region". Cody (1970), on the other hand, states : "Bird species occupy most habitats in limited areas, and are replaced by others only by major shifts in vegetation type or latitude" and "Most species occupy an unusually wide range of habitats....". Cody (1970 Appendix) lists 18 species as occurring in Nothofagus forest of which 13, 72 per cent, are listed as occurring in other habitats. Of 20 species listed by Vuilleumier (1970), six also occur in steppe habitats (3 in Festuca - Mulinum steppe and 3 in Nothofagus steppe) and 18 also occur in Nothofagus - Araucaria montane forest. The two areas considered by Cody in Chile and Vuilleumier in Patagonia were small. A total of 27 species was recorded, 15 being common to both sites, 7 were recorded only in Chile and 5 only in Patagonia (Appendix 26). This illustrates the paucity of species in South American Nothofagus forests which extend over 2,000 km along the Andes from south-central Chile to Tierra del Fuego and contain 44 species in 40 genera (Vuilleumier 1967). In contrast, 50 species occur in Australian and Tasmanian temperate

rainforests. These points have been plotted against the mid-points of the latitudinal range occupied by temperate rainforest in Figure 29. A line drawn through the two points is roughly parallel to that deduced for Australasian forests.

Vuilleumier (1967) believes that evolution in the South American Nothofagus forests has been by phyletic change rather than by splitting (speciation). This is not entirely consistent with his contention that there is no active speciation within the forest region because of its ecological uniformity, a conclusion reached earlier (Chapter 8) for Tasmanian Nothofagus forests. It is possible that evolution was not uniform and occurred in bursts either on colonisation or during periods of environmental change associated with ice ages.

9.5 TEMPERATE RAINFOREST AS A SOURCE OF SPECIES

It can only be concluded that the southern hemisphere temperate rainforests are a species-poor, but saturated, habitat that have been of little importance in the evolution of birds. With the possible (but doubtful) exception of New Guinea, the uniformity of temperate rainforest acts as a barrier to speciation. What little speciation that has occurred is probably the result of phyletic change in forests that have remained unchanged structurally, although not in extent, for a very long time.

CHAPTER 10

CONCLUSIONS

10.1 TASMANIA

The distributions of both habitats and birds are determined by the xeric-mesic gradient. No species of bird is restricted to temperate rainforest. The number of bird species decreases along the xeric-mesic gradient, the more-mesic habitats having the fewest species.

On average, temperate rainforest has lower species diversity, as measured by the Shannon-Wiener information statistic, than the more-mesic habitats. Locally some rainforest sites may have high species diversity.

The equitability component of bird species diversity rises initially as the xeric-mesic gradient is traversed, reaches a maximum in wet sclerophyll and mixed forests and then falls. In contrast, dominance index increases steadily along the xeric-mesic gradient. This suggests that temperate rainforest is a harsher environment than the less-mesic habitats. The adaptations for breeding of temperate rainforest birds suggest that harshness should be equated to low productivity. Species number decreases along the xeric-mesic gradient because the number of available niches decreases. This is most marked for insectivorous species that pursue their prey.

Bird density tends to increase initially along the xeric-mesic gradient and then decline. Density is correlated to some extent with foliage height diversity.

There is some evidence that some Tasmanian temperate

rainforest and other of the more mesic sites conform to the MacArthur et al. regression of bird species diversity on foliage height diversity only if the vegetation is treated as consisting of two layers. The more-xeric sites conform to the MacArthur et al. relation.

The Shannon-Wiener information statistic is suitable for comparing bird species diversity of sites with similar equitability components. Bird species diversity is better expressed by the Shannon-Wiener function and the number of species than by either alone. Bird species diversity is more closely related to the per cent vegetation cover than is number of species, particularly where the vegetation cover exceeds 200 per cent.

In determining the limiting similarity between coexisting species it may be necessary to take more than three niche dimensions into account. The suggestion that species pairs achieve a minimum difference of 30 per cent along a single niche dimension has merit and suggests a sequential method of determining niche structure that is not limited to any given number of niche dimensions.

10.2 AUSTRALIA

The number of species in temperate rainforest decreases with increasing latitude, presumably because of productivity effects. There is some evidence that on an island, Tasmania, the niches of two or more species on the mainland may be filled by a lesser number of species. However, the major part of the decrease in number of species appears to be

caused by decreasing niche availability.

Bird species diversities are similar for Tasmanian and Queensland temperate rainforest sites even though the mainland forest has more species. Recher et al. (1971) obtained a similar result for dry sclerophyll forest in Tasmania and New South Wales.

Current theories of speciation in Australia rely on the concept of forested or woodland refuge areas. It has been shown that these could not have consisted of Nothofagus forest.

Australian subtropical rainforest avifaunas have stronger affinities with temperate rainforest avifaunas than they do with the avifauna of tropical rainforest. A south-eastern Australian origin is suggested for most species found in temperate rainforest. This origin (=refuge) could not have been Tasmania because forest habitats did not become extensive until after the Bass Strait land-bridge had disappeared. Most species entered Tasmania after this date, c. 12,755 B.P., and probably after 10,000 B.P. Some evolution has taken place since then in which temperate rainforest has been unimportant.

10.3 BEECH FORESTS

Temperate rainforests in Chile, Tasmania and New Zealand have comparable bird species diversities, equitabilities and dominance indices. The one Patagonian site for which data are available appears to be atypical.

The similarity in niche occupation, based on censuses of small unequal areas, in northern hemisphere Fagus-Acer and southern hemisphere Nothofagus forests is high (parallel evolution) with some niches being occupied by unrelated groups of species.

The evidence strongly supports the contention that Nothofagus forests have never been important as a source of bird species and have been unimportant in the evolution of the class.

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APPENDICES

- Appendix 1. Scientific names of species mentioned in text.
- Appendix 2. Location, habitat and effective rainfall of sites included in similarity analysis.
- Appendix 3. Habitat preferneces of Tasmanian birds.
- Appendix 4. Species lists for 15 sites in Tasmanian temperate rainfort.
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- Appendix 14. Comparison of vertical stratification in wet sclerophyll, mixed and temperate rainforest.
- Appendix 15. Comparison of feeding behaviour in wet sclerophyll, mixed and temperate rainforest.
- Appendix 16. Overlaps in patch preference, α_H
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- Appendix 19. Community matrix for Tasmanian temperate rainforest.
- Appendix 20. Feeding behaviour in dry sclerophyll and temperate rainforest.
- Appendix 21. Food and foraging behaviour of birds in temperate rainforest in northern New South Wales.
- Appendix 22. Species recorded in temperate rainforest, Macpherson Range, Queensland.
- Appendix 23. Species occurring in wet sclerophyll forest in the Otways, and temperate and subtropical rainforest in New South Wales and Queensland.
- Appendix 24. Food and foraging behaviour of birds in temperate rainforest in southern Queensland not occurring in northern New South Wales.
- Appendix 25. Overlaps in vertical stratification and feeding behaviour in forests on Little Barrier Island, New Zealand.
- Appendix 26. Comparison of species recorded in censuses of small areas in Chile and Patagonia.

APPENDIX 1

Scientific names of species referred to in the text.

1. AUSTRALIA

Brown Goshawk	<u>Accipiter fasciatus</u>
Collared Sparrowhawk	<u>A. cirrhocephalus</u>
Grey Goshawk	<u>A. novaehollandiae</u>
Wedge-tailed Eagle	<u>Aquila audax</u>
Swamp Harrier	<u>Circus aeruginosus</u>
Brown Falcon	<u>Falco berigora</u>
Nankeen Kestrel	<u>F. cenchroides</u>
Brush-turkey	<u>Alectura lathami</u>
Brown Quail	<u>Coturnix ypsilophorus</u>
Masked Plover	<u>Vanellus miles</u>
Banded Plover	<u>V. tricolor</u>
White-headed Pigeon	<u>Columba leucomela</u>
Brown Pigeon	<u>Macropygia amboinensis</u>
Common Bronzewing	<u>Phaps chalcoptera</u>
Brush Bronzewing	<u>P. elegans</u>
Yellow-tailed Black Cockatoo	<u>Calyptorhynchus funereus</u>
Sulphur-crested Cockatoo	<u>Cacatua galerita</u>
Musk Lorikeet	<u>Glossopsitta concinna</u>
Swamp Parrot	<u>Pezoporus wallicus</u>
Swift Parrot	<u>Lathamus discolor</u>
Green Rosella	<u>Platycercus caledonicus</u>
Crimson Rosella	<u>P. elegans</u>
Eastern Rosella	<u>P. eximius</u>
King Parrot	<u>Alisterus scapularis</u>
Blue-winged Parrot	<u>Neophema chrysostoma</u>

Orange-bellied Parrot.	<u>N. chrysogaster</u>
Pallid Cuckoo	<u>Cuculus pallidus</u>
Fan-tailed Cuckoo	<u>C. pyrrhophanus</u>
Rufous-tailed Bronze Cuckoo	<u>Chrysococcyx basalis</u>
Shining Bronze Cuckoo	<u>C. lucidus</u>
Spotted Owl	<u>Ninox novaeseelandiae</u>
Masked Owl	<u>Tyto novaehollandiae</u>
Tawny Frogmouth	<u>Podargus strigoides</u>
Owlet-nightjar	<u>Aegotheles cristatus</u>
Kookaburra	<u>Dacelo novaeguineae</u>
Noisy Pitta	<u>Pitta versicolor</u>
Albert's Lyrebird	<u>Menura alberti</u>
Superb Lyrebird	<u>M. novaehollandiae</u>
Rufous Scrub-bird	<u>Atrichornis rufescens</u>
Noisy Scrub-bird	<u>A. clamosus</u>
Welcome Swallow	<u>Hirundo neoxena</u>
Tree Martin	<u>Cecropsis nigricans</u>
Richard's Pipit	<u>Anthus novaeseelandiae</u>
Black-faced Cuckoo- shrike	<u>Coracina novaehollandiae</u>
Scaly Thrush	<u>Zoothera dauma</u>
Common Blackbird	<u>Turdus merula</u>
Rose Robin	<u>Petroica rosea</u>
Pink Robin	<u>P. rodinogaster</u>
Flame Robin	<u>P. phoenicea</u>
Scarlet Robin	<u>P. multicolor</u>
Dusky Robin	<u>Melanodryas vittata</u>
Eastern Yellow Robin	<u>Eopsaltria australia</u>
Pale Yellow Robin	<u>Tregellasia capito</u>
Olive Whistler	<u>Pachycephala olivacea</u>
Golden Whistler	<u>P. pectoralis</u>

Grey Shrike-thrush	<u>Colluricincla harmonica</u>
Black-faced Monarch	<u>Monarcha melanopsis</u>
Satin Flycatcher	<u>Myiagra rubecula</u>
Rufous Fantail	<u>Rhipidura rufifrons</u>
Grey Fantail	<u>R. fuliginosa</u>
Spine-tailed Chowchilla	<u>Orthonyx temminckii</u>
Eastern Whipbird	<u>Psophodes olivaceus</u>
Spotted Quail-thrush	<u>Cinclosoma punctatum</u>
Little Grassbird	<u>Megalurus gramineus</u>
Superb Blue Wren	<u>Malurus cyaneus</u>
Southern Emu-wren	<u>Stipiturus malachurus</u>
Large-billed Scrubwren	<u>Sericornis magnirostris</u>
Yellow-throated Scrub- wren	<u>S. citreogularis</u>
White-browed Scrubwren	<u>S. frontalis</u>
Brown Scrubwren	<u>S. humilis</u>
Fieldwren	<u>S. fuliginosus</u>
Scrubtit	<u>Acanthornis magnus</u>
Brown Warbler	<u>Gerygone mouki</u>
Brown Thornbill	<u>Acanthiza pusilla</u>
Tasmanian Thornbill	<u>A. ewingii</u>
Yellow-rumped Thornbill	<u>A. chrysorrhoa</u>
Yellow (Little) Thorn- bill	<u>A. nana</u>
Striated Thornbill	<u>A. lineata</u>
White-throated Tree- creeper	<u>Climacteris leucophaea</u>
Red Wattlebird	<u>Anthochaera carunculata</u>
Yellow Wattlebird	<u>A. paradoxa</u>
Little Wattlebird	<u>A. chrysoptera</u>
Noisy Miner	<u>Manorina melanocephala</u>
Lewin's Honeyeater	<u>Meliphaga lewinii</u>

White-eared Honeyeater	<u>Lichenostomus leucotis</u>
Yellow-throated Honey-eater	<u>L. flavicollis</u>
Strong-billed Honeyeater	<u>Melithreptus validirostris</u>
Black-headed Honeyeater	<u>M. affinis</u>
Crescent Honeyeater	<u>Phylidonyris pyrrhoptera</u>
New Holland Honeyeater	<u>P. novaehollandiae</u>
Tawny-crowned Honeyeater	<u>P. melanops</u>
Eastern Spinebill	<u>Acanthorhynchus tenuirostris</u>
White-fronted Chat	<u>Epthianura albifrons</u>
Spotted Pardalote	<u>Pardalotus punctatus</u>
Forty-spotted Pardalote	<u>P. quadragintus</u>
Striated Pardalote	<u>P. striatus</u>
Silvereye	<u>Zosterops lateralis</u>
Beautiful Firetail	<u>Emblema bella</u>
House Sparrow	<u>Passer domesticus</u>
Satin Bowerbird	<u>Ptilonorhynchus violaceus</u>
Green Catbird	<u>Ailuroedus crassirostris</u>
Paradise Riflebird	<u>Ptiloris paradiseus</u>
Dusky Woodswallow	<u>Artamus cyanopterus</u>
Grey Butcherbird	<u>Cracticus torquatus</u>
Australian Magpie	<u>Gymnorhina tibicen</u>
Pied Currawong	<u>Strepera graculina</u>
Black Currawong	<u>S. fuliginosa</u>
Grey Currawong	<u>S. versicolor</u>
Forest Raven	<u>Corvus tasmanicus</u>
Torresian Crow	<u>C. orru</u>

2. NEW ZEALAND

Kiwi	<u>Apteryx australis</u>
Australasian Harrier	<u>Circus aeruginosus</u>

New Zealand Falcon	<u>Falco novaeseelandiae</u>
Weka	<u>Gallirallus australis</u>
New Zealand Pigeon	<u>Hemiphaga novaeseelandiae</u>
Kaka	<u>Nestor meridionalis</u>
Red-crowned Parakeet	<u>Cyanoramphus novaezelandiae</u>
Yellow-crowned Parakeet	<u>C. auriceps</u>
Shining Cuckoo	<u>Chrysococcyx lucidus</u>
Long-tailed Cuckoo	<u>Eudynamis taitensis</u>
Morepork	<u>Ninox novaeseelandiae</u>
Rifleman	<u>Acanthisitta chloris</u>
Fantail	<u>Rhipidura fuliginosa</u>
Pied Tit	<u>Petroica macrocephala</u>
Robin	<u>P. australis</u>
Brown Creeper	<u>Finschia novaeseelandiae</u>
Whitehead)	<u>Mohua ochrocephala</u>
Yellowhead)	
Grey Warbler	<u>Gerygone igata</u>
Song Thrush	<u>Turdus philomelas</u>
Hedge Sparrow	<u>Prunella modularis</u>
Bellbird	<u>Anthornis melanura</u>
Stitchbird	<u>Notiomystis cincta</u>
Tui	<u>Prosthemadera novaeseelandiae</u>
Silvereye	<u>Zosterops lateralis</u>

3. OTHER

Black and White Mannikin Manacus manacus

APPENDIX 2

Location, habitat and effective rainfall of sites included in similarity analysis. The reference numbers correspond to those in Figure 5.

REF NO.	LOCALITY	HABITAT	EFF. RAINFALL
1	Bond Tier	Mixed forest	H
2	Arthur River	Coastal heath	H
3	Loongana	Sedgeland	H
4	Weindorfer's Forest	Temperate rainforest	P
5	Renison	Temperate rainforest	P
6	Cape Portland	Coastal heath/pasture	S
7	The Gardens	Coastal heath	S
8	Diana's Basin	Coastal heath	S
9	Storey's Creek	Dry sclerophyll forest	H
10	Henty River	Coastal heath	P
11	Ocean Beach, Strahan	Coastal heath	P
12	Cardigan Plains	Sedgeland	P
13	Crotty	Sedgeland	P
14	Kelly Basin Track	Temperate rainforest	P
15	Mount Rufus	Dwarf coniferous forest	P
16	Central Plateau	Moorland	H
17	Scamander	Dry sclerophyll forest	S
18	Campbell Town	Dry sclerophyll forest	S
19	Ross	Savannah woodland	S
20	Kelvedon	Savannah woodland	S
21	Tooms Lake	Dry sclerophyll forest	S
22	Lake St Clair	Temperate rainforest	P
23	Lake St Clair	Sub-alpine forest	P
24	Lake St Clair	Sedgeland	P

25	Mount Field N.P.	Sub-alpine forest	H
26	Tarn Shelf	Dwarf coniferous forest	H
27	Mount Field N.P.	Mixed forest	H
28	Gatehouse Marsh	Savannah woodland	S
29	Tim's Track	Mixed forest	P
30	Tim's Track	Wet scrub	P
31	The Sentinels	Sedgeland	P
32	Frodsham's Pass	Wet scrub	P
33	Forest Walk	Temperate rainforest	P
34	Mount Bowes	Mixed forest	P
35	Condominium Creek	Wet scrub	P
36	Mount Lloyd	Wet sclerophyll forest	H
37	Mount Arthur	Sub-alpine forest	H
38	Pottery Road	Dry sclerophyll forest	S
39	Mount Wellington	Wet sclerophyll forest	H
40	Queen's Domain	Savannah woodland	S
41	Pine Creek	Dry sclerophyll forest	S
42	Tahune	Wet sclerophyll forest	H
43	Tahune	Mixed forest	H
44	Tahune	Sedgeland	H
45	Tinderbox	Dry sclerophyll forest	S
46	Eaglehawk Neck	Coastal heath	S
47	Waterfall Bay	Wet sclerophyll forest	H
48	Hartz Mountains N.P.	Dwarf coniferous forest	P
49	Adamson's Peak	Dwarf coniferous forest	H
50	Hastings	Wet sclerophyll forest	H
51	Hastings Caves	Mixed forest	H

APPENDIX 3

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Habitat preferences of Tasmanian birds. "1" - present at 50 % of sites; "2" - present at \leq 50 % of sites.

	Coastal Heath	Savannah Woodland	Dry Sclerophyll	Wet Sclerophyll	Mixed Forest	Rain Forest	Sub-Alpine Forest	Dwarf Coniferous Forest	Wet Mallee	Sedgeland	Moorland
NO. OF SITES (52)	7	4	7	5	6	5	3	4	3	6	2
Grey Goshawk				1	1						
Australian Goshawk			2		1		1	1			
Collared Sparrowhawk			2								
Wedge-tailed Eagle	1	1	1			1	1	1		1	2
Swamp Harrier	2	2	1							1	1
Peregrine Falcon											1
Nankeen Kestrel	1	1									
Brown Hawk	2	2	2				1			2	1
Brown Quail	2	1	1							1	
Spurwinged Plover	2	2									1
Banded Plover	1	1									
Common Bronzewing	1	1	2								1
Brush Bronzewing				2	2	1				1	
Musk Lorikeet			1								
Swift Parrot	1	1	2	1							
Yellow-tailed Black Cockatoo	2	1	1	2	2	2	2	1		1	
Sulphur-crested Cockatoo										1	
Green Rosella	2	2	2	2	2	2	1	1	2	2	1
Eastern Rosella		2	1								
Blue-winged Parrot	1	1	1							2	2
Ground Parrot	1									2	
Pallid Cuckoo	2	1	2							1	
Fan-tailed Cuckoo	2	1	2	2	2		2		2	1	1
Horsfield Bronze Cuckoo	1		2								
Golden Bronze Cuckoo	1	1	2	2	2	1	1		1	1	
Boobook Owl			1			1	1			1	
Masked Owl			1								
Tawny Frogmouth			1						1		
Owlet Nightjar			1								
Welcome Swallow	2	2			1				2	1	1
Tree-Martin	1		2	1	1					1	2
Australian Pipit	2	1	1					1		1	2
Black-faced Cuckoo-Shrike	1	2	2	1	1		1		1	1	1
Ground Thrush				2	2	2				1	

	Coastal Heath	Savannah Woodland	Dry Sclerophyll	Wet Sclerophyll	Mixed Forest	Rain Forest	Sub-Alpine Forest	Dwarf Coniferous Forest	Wet Mallee	Sedgeland	Moorland
Spotted Quail-Thrush			2								
Superb Blue Wren	2	2	2	2	2		1		2	2	2
Southern Emu-Wren	1								2	2	
Tasmanian Thornbill	2			2	2	2	2	2	2	2	2
Brown Thornbill	2	2	2								
Yellow-rumped Thornbill	1	2	1								
Scrub-Tit				2	2	2	2	1			
Brown Scrub-Wren	2		2	2	2	2	2	1	2	1	1
Field-Wren	2						1	2	2	2	1
White-fronted Chat	2	1									
Scarlet Robin	1	2	2							1	
Flame Robin	2	2	2	2	1	1	2	1	1	2	2
Pink Robin				2	2	2	1				
Dusky Robin	2		2	2			2			2	
Grey Fantail	2	1	2	2	2	2			1	1	
Satin Flycatcher	1	1	2	1	2						
Golden Whistler	1		2	2	2	1	1		1	1	
Olive Whistler	1			2	2	2	2	1	2	2	
Grey Shrike-Thrush	2	2	2	2	2	2	2		2	2	2
Spotted Pardalote	2	1	2	2	2		2		2		1
Yellow-tipped Pardalote	2	2	2	2	2	1	2				1
Grey-breasted Silveryeye	2	1	2	2	2	2	2		2	2	1
Yellow-throated Honeyeater	2	2	2	2	2	1	2		2	2	1
Black-headed Honeyeater	1	1	2	1	1		1		1		1
Strong-billed Honeyeater	1		2	2	2	1	1		2	1	1
Crescent Honeyeater	2		2	2	2	2	2	2	2	2	2
New Holland Honeyeater	2	1	1	1					2	1	
Tawny-crowned Honeyeater	2										
Eastern Spinebill	1		2	2	2	1	1		2	1	
Noisy Miner		2									
Little Wattlebird	2	1	1								
Yellow Wattlebird		1	2	1	1	1	2			1	1
Beautiful Firetail	1		1	2	1		2		2	2	
Dusky Wood-Swallow	2	2	2							1	
Black Currawong	1		1	2	2	2	2	2	2	2	2
Clinking Currawong	1		2								
Grey Butcherbird	1	2	2								
White-backed Magpie		2									
Forest Raven	2	2	2	2	2	2	2	1	2	2	2
No. of Species											
Common	28	20	35	25	25	14	18	4	20	18	11
Total	54	41	53	35	34	25	32	14	27	42	29

APPENDIX 4

Species lists for 15 sites in Tasmanian temperate rainforest

	LAKE ST. CLAIR	RENISON	WEINDORFER'S FOREST	KELLY BASIN TRACK	FOREST WALK	SIR JOHN FALLS CAMP	GORDON RIVER LINE 10L	GORDON RIVER LINE 10R	GORDON RIVER LINE 11L	GORDON-FRANKLIN RIVER JUNCTION	MCINTOSH MANGANA	OLGA CAMP	HARDWOOD RIVER	DENISON RIVER	DOHERTY'S RANGE
Grey Goshawk						✓	✓			✓				✓	
Wedge-tailed Eagle		✓				✓									
Brush Bronzewing		✓		✓		✓				✓					
Yellow-tailed B. Cuckatoo	✓		✓	✓	✓	✓	✓		✓	✓		✓			
Sulphur-crested Cockatoo												✓			
Green Rosella	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
Fan-tailed Cuckoo						✓									
Shining Bronze Cuckoo		✓		✓		✓			✓	✓		✓		✓	✓
Spotted Owl				✓		✓						✓			
Scaly Thrush	✓	✓	✓	✓		✓			✓	✓		✓	✓	✓	✓
Pink Robin	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
Flame Robin	✓					✓				✓					
Olive Whistler		✓	✓	✓		✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
Golden Whistler		✓		✓		✓	✓	✓	✓	✓		✓	✓		✓
Grey Shrike-thrush		✓	✓	✓	✓	✓	✓	✓	✓	✓		✓		✓	✓
Grey Fantail	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
Brown Scrubwren	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
Scrubtit	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
Tasmanian Thornbill	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
Yellow Wattlebird			✓												
Yellow-throated Honeyeater			✓	✓		✓	✓	✓		✓		✓	✓	✓	✓
Strong-billed Honeyeater				✓											
Crescent Honeyeater	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
Eastern Spinebill		✓		✓		✓	✓	✓	✓	✓		✓	✓	✓	✓
Spotted Pardalote											✓				
Striated Pardalote	✓		✓												
Silvereye	✓	✓		✓		✓	✓	✓	✓	✓	✓	✓		✓	✓
Black Currawong	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓		✓	
Forest Raven		✓	✓	✓		✓				✓	✓	✓			

APPENDIX 5

In what follows, the major references are abbreviated as follows : C = Cayley (1959), F = Frith (1969), G = Green (1966), G & M = Green and McGarvie (1971), L = Leach (1958), R = Rose (1973), R & M = Ridpath and Moreau (1966).

Grey Goshawk

C - birds, insects. L - reptiles, mice, birds. F - birds, small mammals, large insects. R & M - vertebrates.

(VERTEBRATES)

Brush Bronzewing

C - seeds, native fruits, berries. L - seeds. F - feeds on the ground on seeds and berries. R & M - vegetable matter.

G & M - (2 birds) : seeds - Acacia sp., Trifolium subterraneum, Beyeria sp., Cyperaceae.

(SEEDS)

Yellow-tailed Black Cockatoo

L - wood-boring larvae, seeds. F - feeds largely on the larvae of cossid moths. Also eats seeds of eucalypts, Banksia, Acacia, introduced pines. R & M - vegetable matter and invertebrates.

Forshaw (1969) suggests that wood-boring insect larvae are the staple diet although it also takes seeds, fruit and berries, nectar and blossoms.

After some hesitation I have classed it as an insectivore.

(INVERTEBRATES)

Green Rosella

C - seeds. R & M - vegetable matter.

Forshaw (1969) gives the food as the seeds of grasses, shrubs and trees, especially eucalypts, and on blossoms, berries,

nuts and fruits and insects and their larvae. Lea and Gray (1935-6) found insect larvae in the crops of two birds from Flinders Island and Green and Swift (1965) report birds feeding on psyllids (Hemiptera, sub-order Homoptera). Holyoak (1973) regards the food of Platycercus spp. as seeds (fruit).

G & M - (4 birds) : seeds - Euphorbiaceae, Rumex sp., Solanum sp., Pimelia sp., Senecio (?) sp.

Although a wide variety of food is eaten, I regard the Green Rosella as primarily a graminivore.

(SEEDS)

Shining Bronze Cuckoo

C, L - insects, mainly caterpillars. F - caterpillars favoured but a variety of other insects taken. R & M - invertebrates.

G, G & M - (2 birds) : moth larvae (Lepidoptera)

(INVERTEBRATES)

Spotted Owl

L - insects, birds. F - insects and other invertebrates, also small mammals and birds. R & M - invertebrates and vertebrates. R - (5 birds) : mammals (rodents); spiders Araneida (Arachnida), cockroaches (Blattodea), beetles (Coleoptera), moths (Lepidoptera).

G - (1 bird) : spiders Araneida (Arachnida), cockroaches (Blattodea), long-horned grasshoppers Tettigonidae (Orthoptera), beetles (Coleoptera), moths (Lepidoptera).

Green (1969) - (1 bird) : huntsman spider (Arachnida), beetles (Coleoptera).

(INVERTEBRATES AND VERTEBRATES)

Scaly Thrush

C - insects, crustaceans. L - snails, insects, worms. F - chiefly insects and worms. R & M - invertebrates.

G & M - (3 birds) : leaves - Epacridaceae; earthworms Annelida (Oligochaeta), centipedes Chilopoda (Myriapoda), ground beetles Carabaeidae, dung beetles Coprinae, click beetle larvae Elateridae, tenebrio beetles Tenebrionidae, chafers Dynastinae and weevils Curculionidae (Coleoptera), fly larvae (Diptera), moth larvae (Lepidoptera).

Green (1969) - (1 bird) : wireworms, wood-boring larvae.

R - (2 birds) : spiders Araneida (Arachnida), beetles (Coleoptera).

(INVERTEBRATES)

Pink Robin

C, L - insects. F - insects. R & M - invertebrates.

(INVERTEBRATES)

Olive Whistler

C, L - insects. F - mainly insects and their larvae. R & M - invertebrates.

G & M - (5 birds) : seeds - Epacridaceae, Leguminosae; leaf fragments; cockroach ootheca (Blattodea), longicorn beetles Cerambycidae and weevils Curculionidae (Coleoptera), hoverflies Syrphidae.

(INVERTEBRATES)

Golden Whistler

C - insects. L - insects, mainly caterpillars. F - insects and some berries. R & M - invertebrates.

Matthiessen (1973) - (5 birds) : spiders (Arachnida), grasshoppers (Orthoptera), bugs (Hemiptera), beetles (Coleoptera), wasps and ants (Hymenoptera).

(INVERTEBRATES)

Grey Shrike-thrush

L - insects. F - the main foods are insects, spiders and worms, but it has been reported to take eggs and nestlings of smaller birds, small marsupials and frogs. R & M - invertebrates.

R - (6 birds) ; centipedes Chilopoda and millipedes Diplopoda (Myriapoda), spiders Araneida (Arachnida), cockroaches (Blattodea), praying mantids (Mantodea), grasshoppers (Orthoptera), cicadas Cicadidae (Hemiptera sub-order Homoptera), beetles (Coleoptera), moth larvae (Lepidoptera).

G, G & M - (7 birds) : bird remains; reptiles (skink lizard); amphibia (Brown Treefrog Hyla ewingii); earwigs (Dermaptera), long-horned grasshoppers Tettigonidae (Orthoptera), shield-bugs Pentatomidae (Hemiptera sub-order Heteroptera), dung beetles Coprinae, water tiger-beetles Dytiscidae, water beetles Hydrophilidae, weevils Curculionidae and ground weevils Phaladurinae (Coleoptera), moths (Lepidoptera), parasitic wasps Ichneumanidae and ants Formicidae (Hymenoptera).

(INVERTEBRATES)

Grey Fantail

C, L - insects. F - insects, taken on the wing, appear to be the only food. R & M - invertebrates.

Matthiessen (1973) - (6 birds) : bugs (Hemiptera), beetles (coleoptera), flies (Diptera), moths (Lepidoptera), wasps/ants (Hymenoptera).

G, G & M - (2 birds) : shield-bugs Pentatomidae (Hemiptera sub-order Heteroptera), leaf beetles Chrysomelidae (Coleoptera), flies Muscoida and Staphylinidae (Diptera)

(INVERTEBRATES)

Brown Scrubwren

C - insects. R & M - invertebrates.

G & M - (3 birds) : seeds - Myosotis sp., Euphorbiaceae, Leguminosae; leaves - Epacris sp.; cockroach ootheca (Blattodea), termites (Isoptera), longicorn beetles Cerambycidae (Coleoptera), fly larvae (Diptera), moths (Lepidoptera), ants Formicidae (Hymenoptera).

Thomas (1974) - (4 birds) : craneflies, spiders, beetles, weevils; small seeds (3 stomachs), plant remains (2 stomachs); small quartz particles (2 stomachs).

(INVERTEBRATES)

Scrubtit

C - insects. R & M - invertebrates.

Thomas (1974) - (1 bird) : entirely insect remains - legs of spiders, beetles, etc.

(INVERTEBRATES)

Tasmanian Thornbill

C - insects. R & M - invertebrates.

(INVERTEBRATES)

Yellow-throated Honeyeater

C - insects and nectar. R & M - vegetable matter and invertebrates. Keast (1970) regards the Meliphaga (which includes Lichenostomus) honeyeaters as predominantly insectivorous.

G & M - (3 birds) : spiders Araneida (Arachnida), soldier beetles Telephoridae, leaf beetles Chrysomelidae, weevils Curculionidae and jewelbeetles Buprestidae (Coleoptera), moths (Lepidoptera).

In my experience Yellow-throated Honeyeaters rarely take nectar.

(INVERTEBRATES)

Crescent Honeyeater

C - insects, nectar. F - insects appear to be the staple diet though its nomadic winter movements seem to relate to search for nectar. R & M - vegetable matter and invertebrates. Keast (1970) regards Phylidonyris honeyeaters as largely nectarivorous.

G & M - (1 Bird) : flies (Diptera), moths (Lepidoptera). Although the importance of nectar to this species when breeding is questionable, it seems best to regard its food as

(INVERTEBRATES AND NECTAR)

Eastern Spinebill

C, L - insects. F - a nectar feeder taking small insects in the absence of nectar. R & M - vegetable matter and invertebrates. Keast (1970) regards Acanthorhynchus honeyeaters as largely nectarivorous.

Although the importance of invertebrates is questionable they provide protein of which nectar is a poor source (Recher and Abbott 1971). The food of the Eastern Spinebill is best regarded as

(NECTAR AND INVERTEBRATES)

Silvereye

C, L - insects, fruits and berries. F - insects, fruit, berries. R & M - vegetable matter and invertebrates.

R - (1 bird) : berries; spiders Araneida (Arachnida), leopards Psyllidae (Hemiptera sub-order Homoptera), moth larvae (Lepidoptera);

G, G & M - (2 birds) : seeds - Rhagodia baccata, Solanum sp.; moth larvae (Lepidoptera).

(FRUITS AND INVERTEBRATES)

Black Currawong

L - insects, fruits. R & M - vegetable matter and invertebrates.

G & M - (2 birds) : seeds - Epacridaceae; click beetles Elateridae, leaf beetle adults and larvae Chrysomelidae and weevils Curculionidae (Coleoptera), moths (Lepidoptera), ants Formicidae (Hymenoptera). Rose (1973) analysed 152 pellets of the closely-related Pied Currawong in New South Wales and confirmed that this species takes a very wide range of foods.

Seems best regarded as being an omnivore.

(OMNIVOROUS)

Forest Raven

C, L - omnivorous. R & M - vertebrates and invertebrates.

G - (1 bird) : grasshoppers Acrididae (Orthoptera), ground beetles Scarabaeidae and weevils Curculionidae (Coleoptera). Rowley and Vestjens (1973) analysed the food in the stomachs of 53 birds of the race tasmanicus, mostly obtained in Tasmania, and found a very wide range of food items. Although an omnivore, the Forest Raven probably occupies the scavenging niche.

(OMNIVOROUS)

Breeding adaptations of birds in Tasmanian temperate rainforest. M = monogamous. S = solitary. O = open. D = domed. H = hole.

SPECIES	PAIR BOND	NESTING DISPERSAL	NEST TYPE	NEST SITE ⁽¹⁾	CLUTCH (2)	OTHER
Grey Goshawk	M	S	O	Tree (3)	2 - 3	Sexual size dimorphism
Brush Bronzewing	M	S	O	Low shrub (1)	2	
Yellow-tailed Black Cockatoo	M	S	H	Hole	2	
Green Rosella	M	S	H	Hole	4 - 9	
Shining Bronze Cuckoo	M	S	-	-	?	Parasitic
Spotted Owl	M	S	H	Hole	2	
Scaly Thrush	M	S	O	Shrub (2)	2 - 3	
Pink Robin	M	S	O	Shrub (2)	3 - 4	
Olive Whistler	M	S	O	Shrub (2)	3 - 4	
Golden Whistler	M	S	O	Shrub (2)	2 - 3	
Grey Shrike- thrush	M	S	O	Tree (3)	2 - 4	
Grey Fantail	M	S	O	Shrub (2)	3 - 4	
Brown Scrub- wren	M	S	D	Low shrub (1)	3 - 4	'Helpers'
Scrubtit	M	S	D	Low shrub (1)	3 - 4	
Tasmanian Thornbill	M	S	D	Shrub (2)	3 - 4	'Helpers'
Yellow-throated Honeyeater	M	S	O	Low shrub (1)	2 - 3	
Crescent Honeyeater	M	S(?)	O	Low shrub (1)	3 - 4	
Eastern Spinebill	M	S	O	Shrub (2)	2 - 3	
Silvereye	M	S	O	Low (1) shrub/ Shrub (2)	3 - 4	
Black Currawong	M	S	O	Tree (3)	2 - 4	
Forest Raven	M	S	O	Tree (3)	4 - 5	

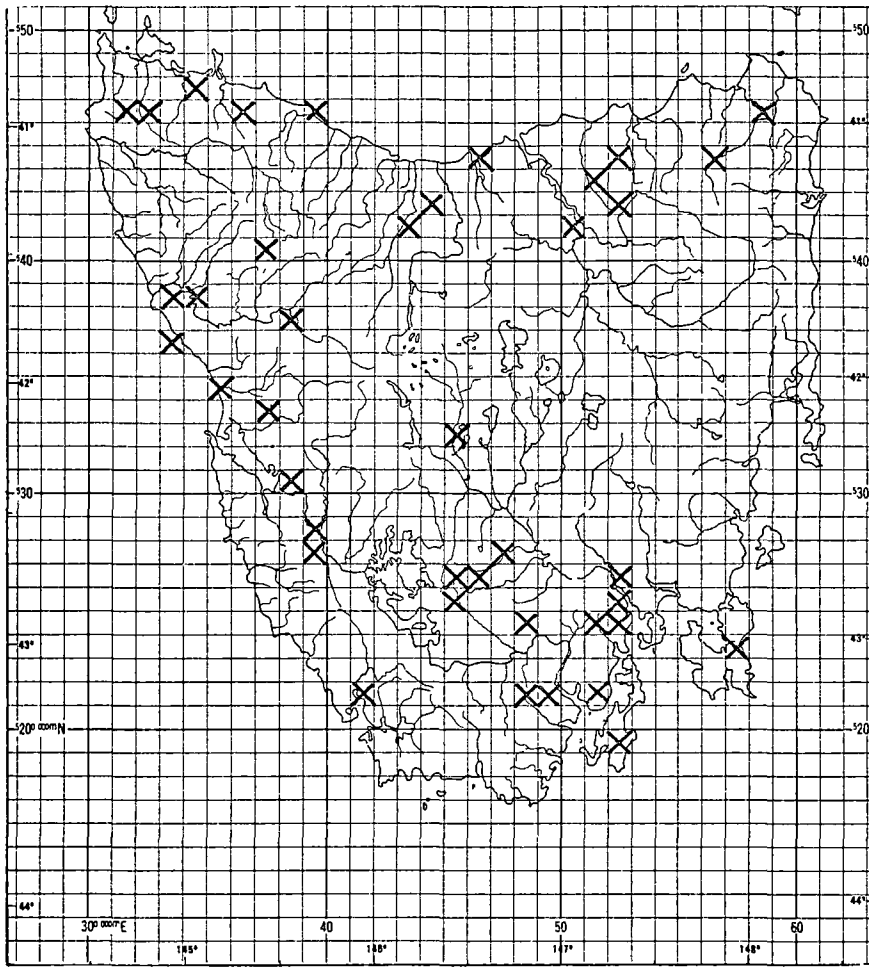
(1) Figures in brackets refer to the vegetation layer : (1) - herb/low shrub, (2) - shrub, (3) - tree.

(2) Based on Sharland 1958.

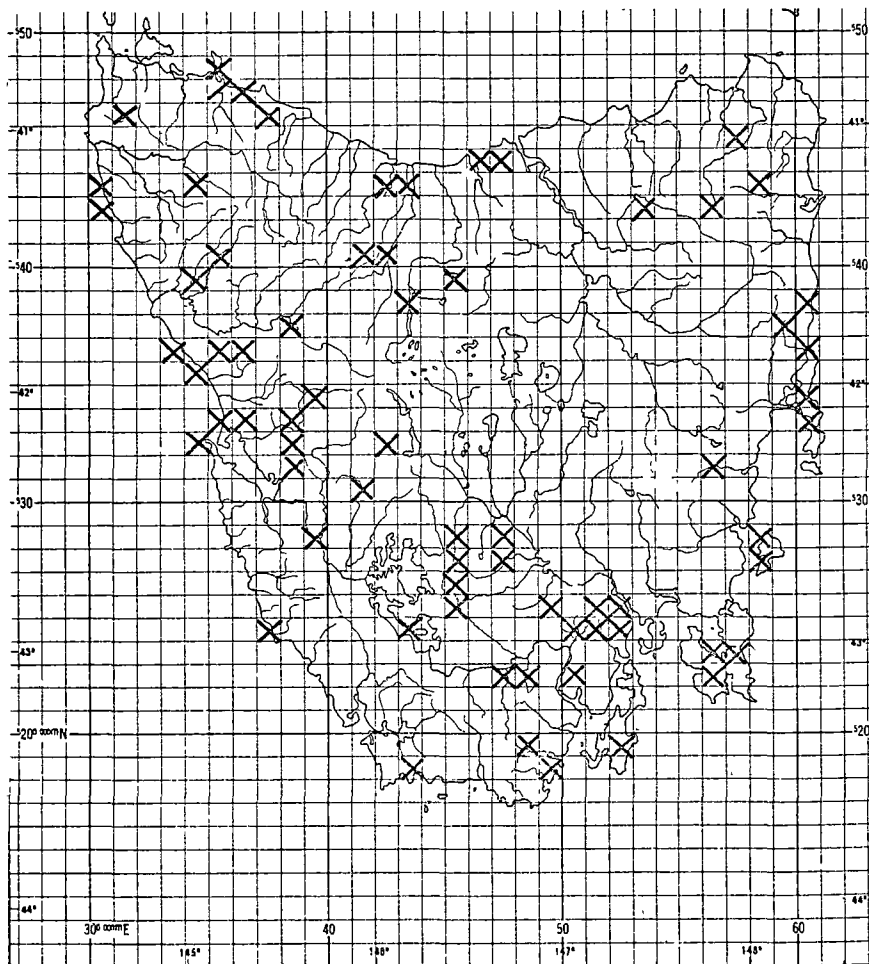
Tasmanian distribution of species breeding in temperate

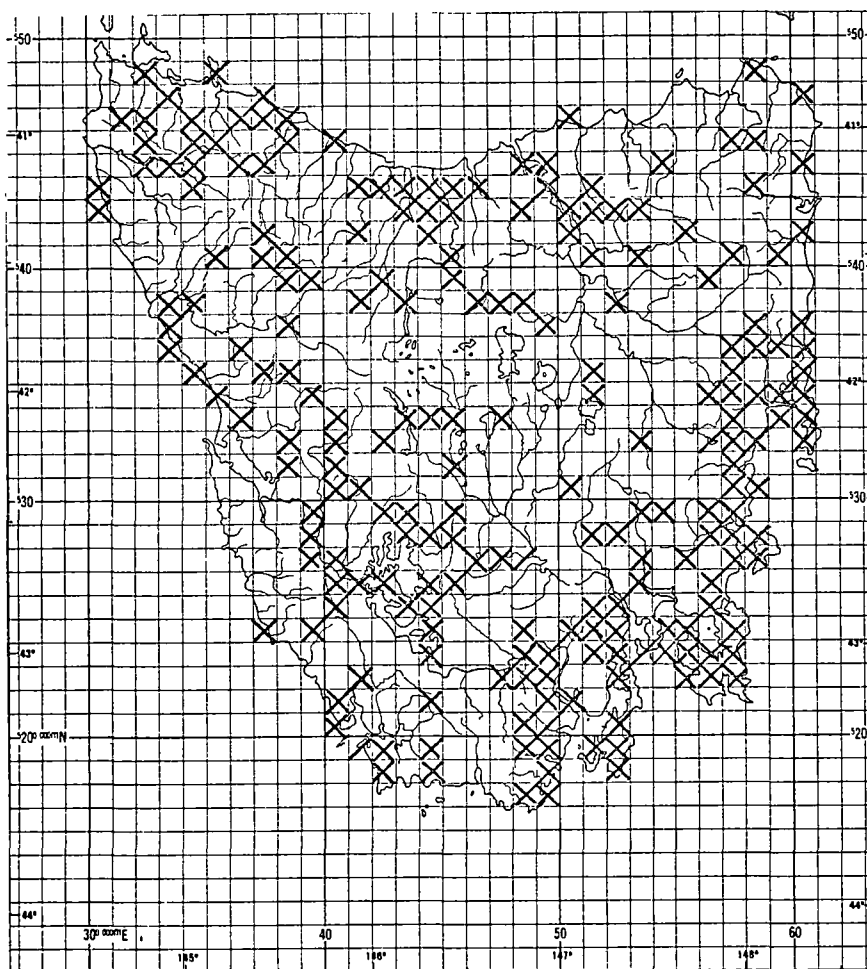
rainforest.

Grey Goshawk

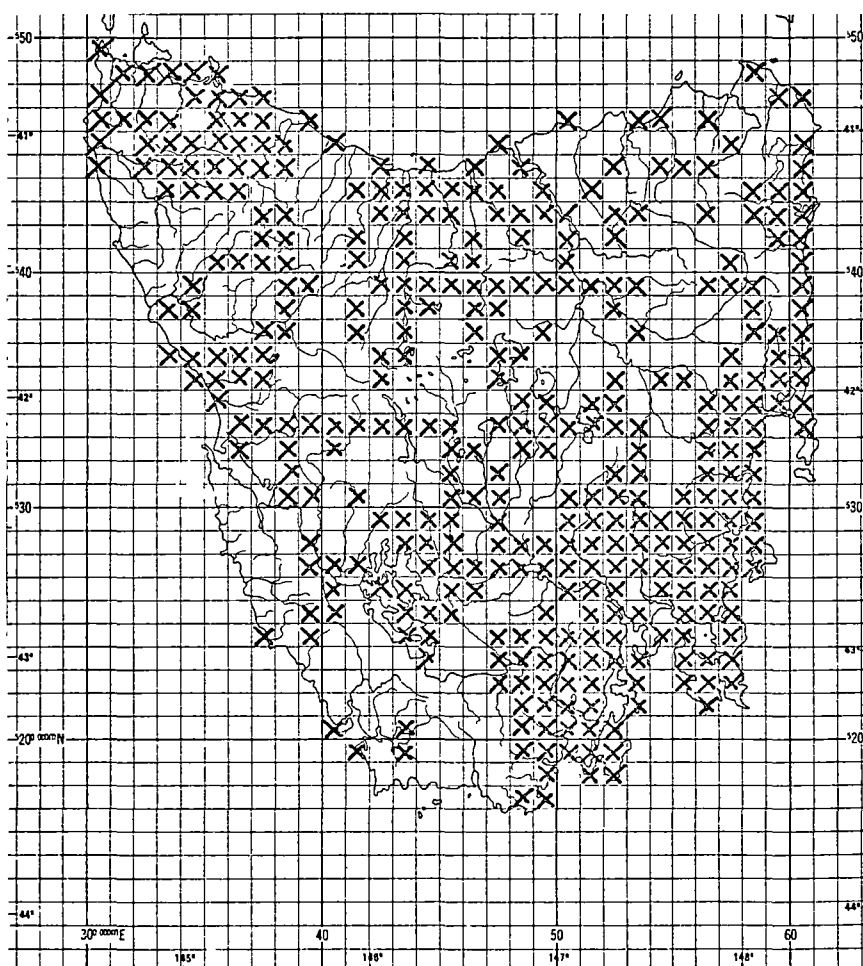


Brush Bronzewing

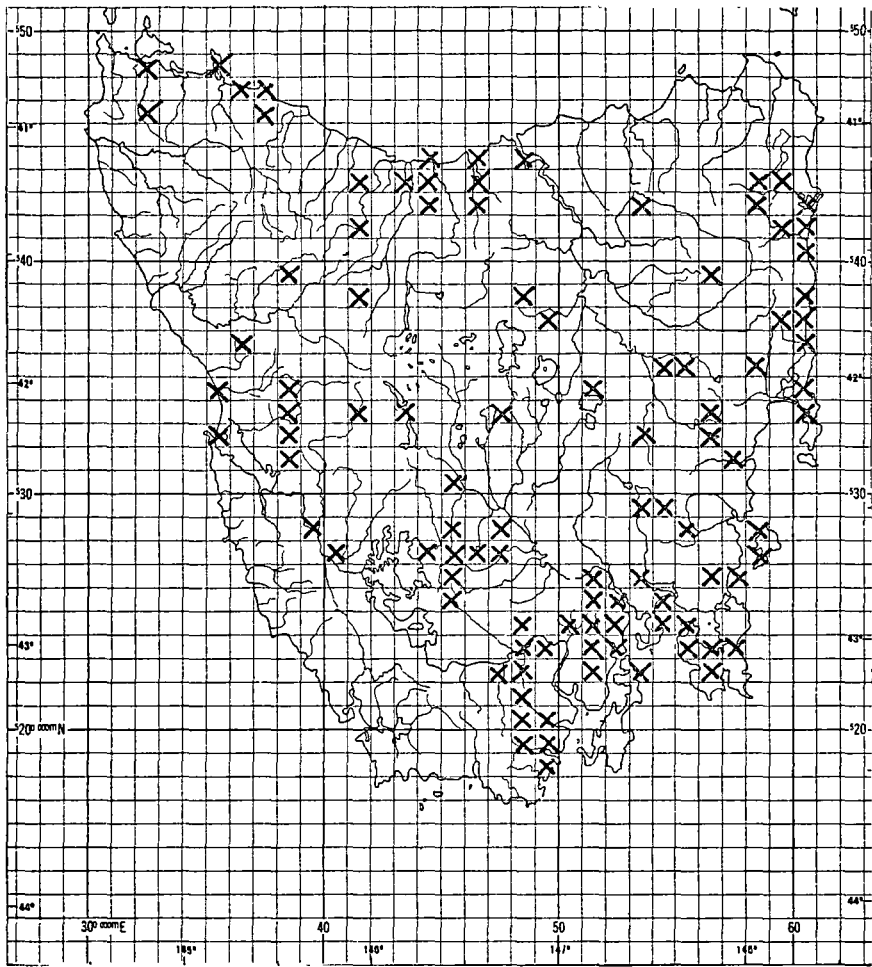




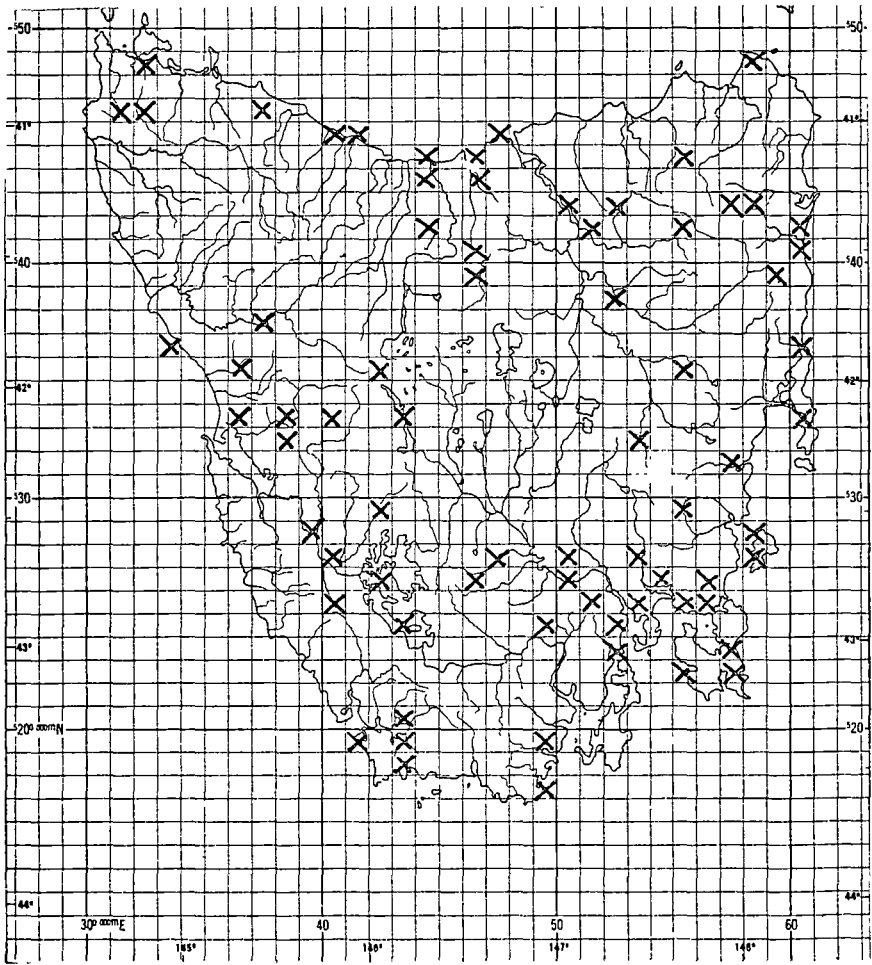
Yellow-tailed
Black Cockatoo



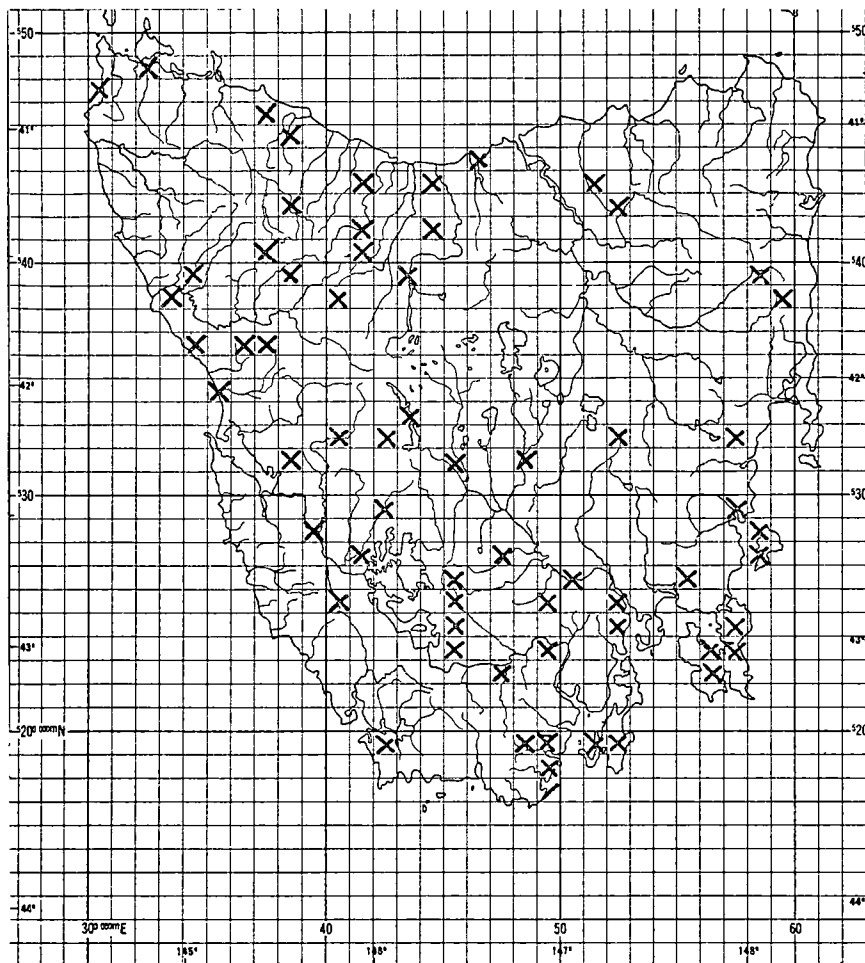
Green Rosella



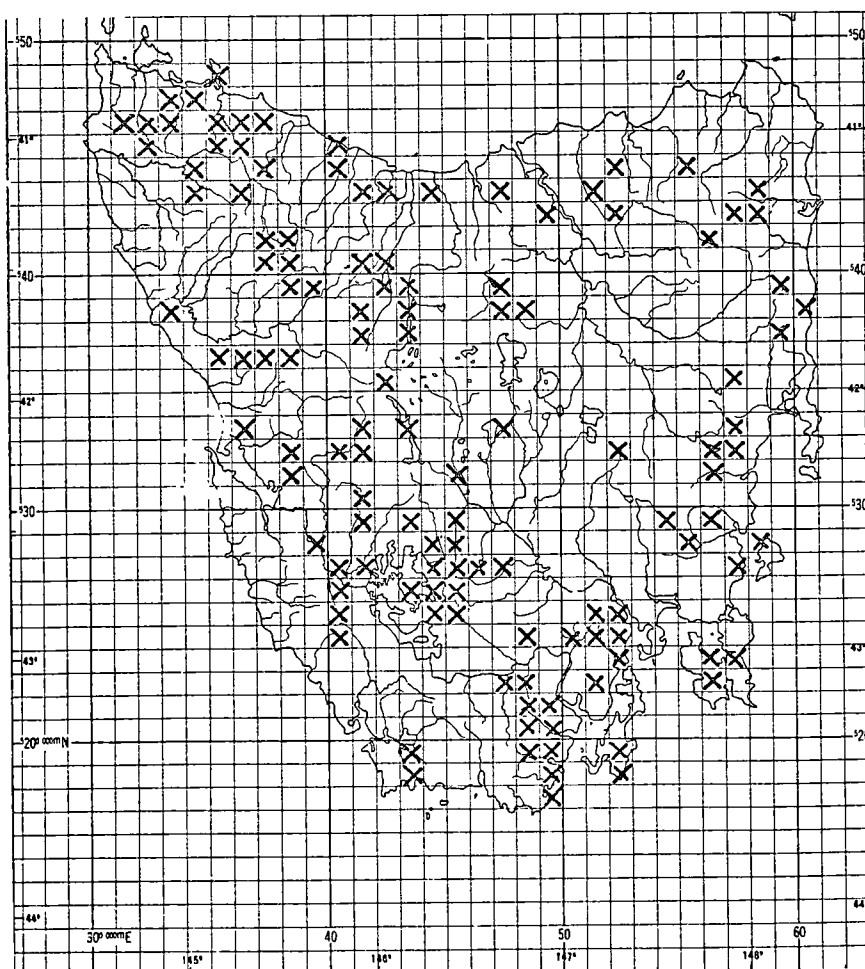
Shining Bronze
Cuckoo



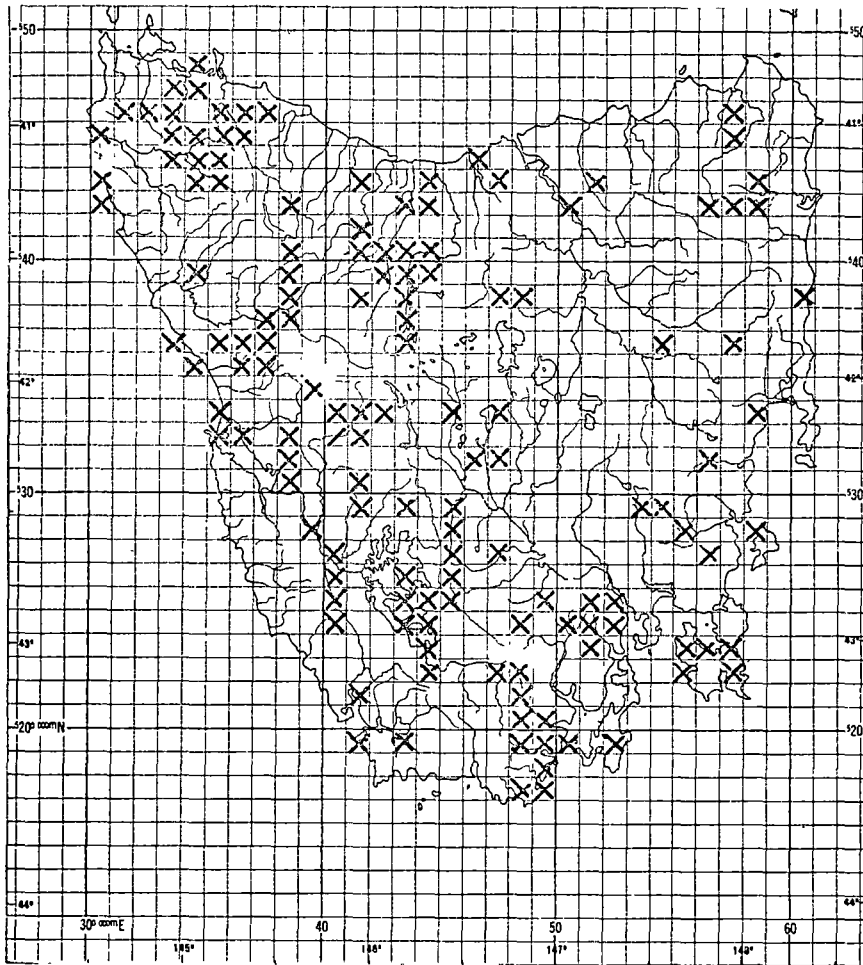
Spotted Owl



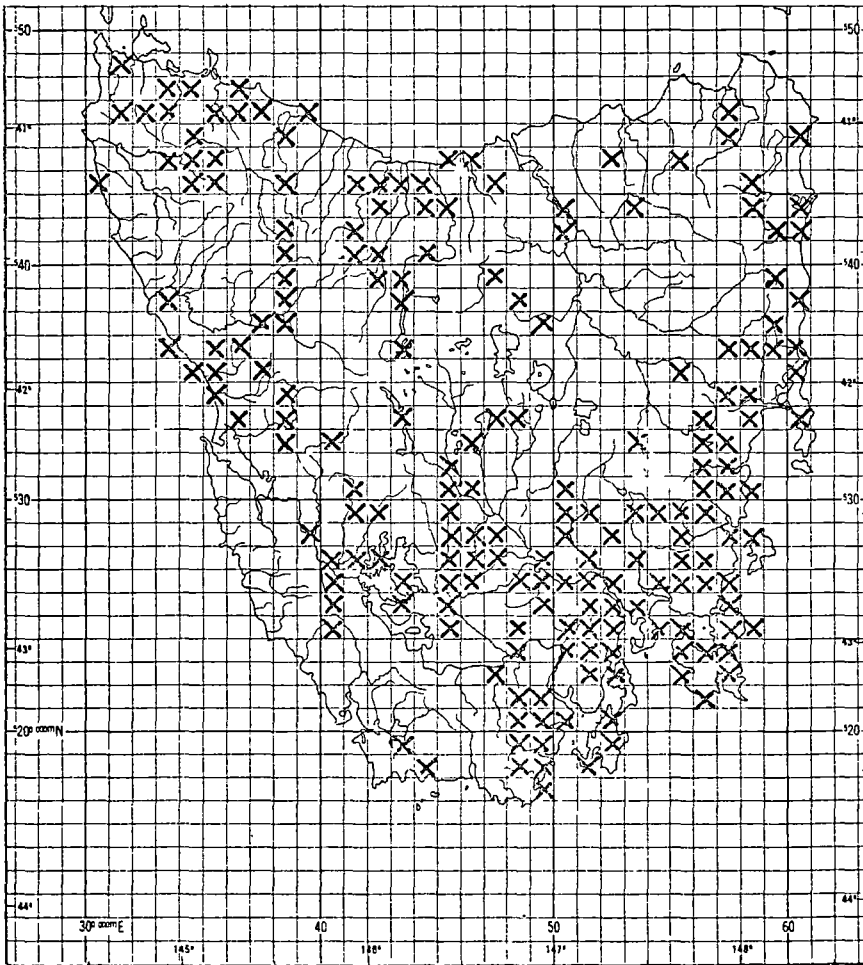
Scaly Thrush



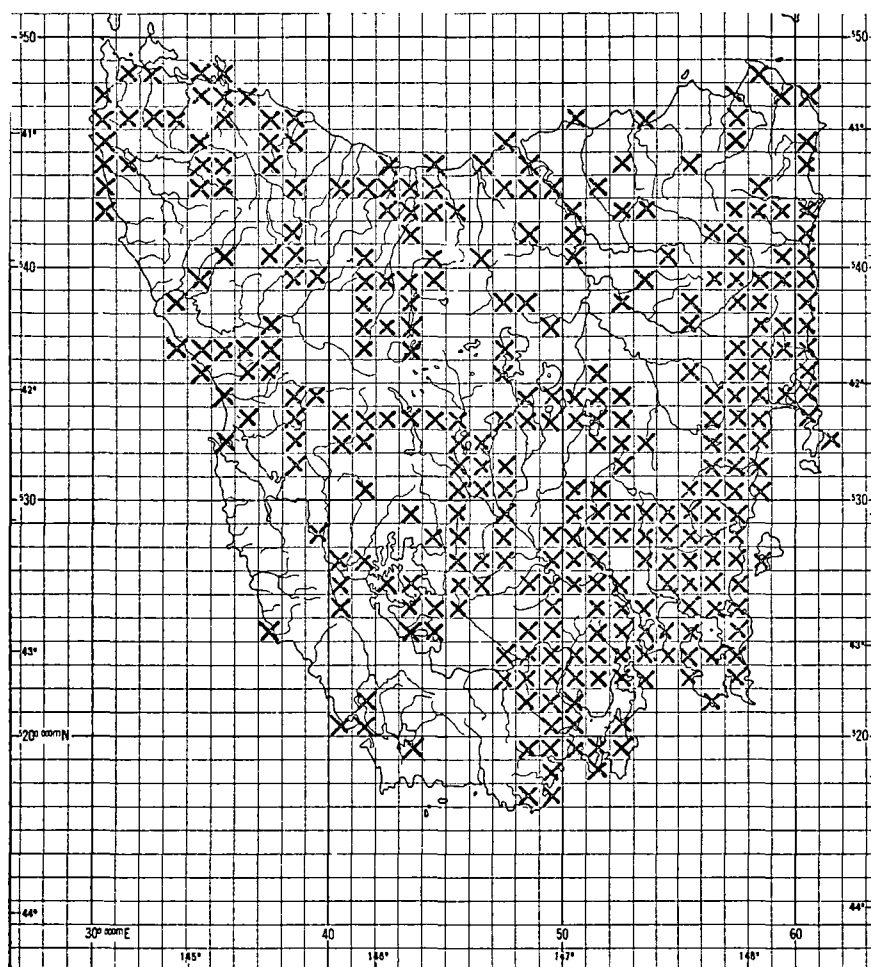
Pink Robin



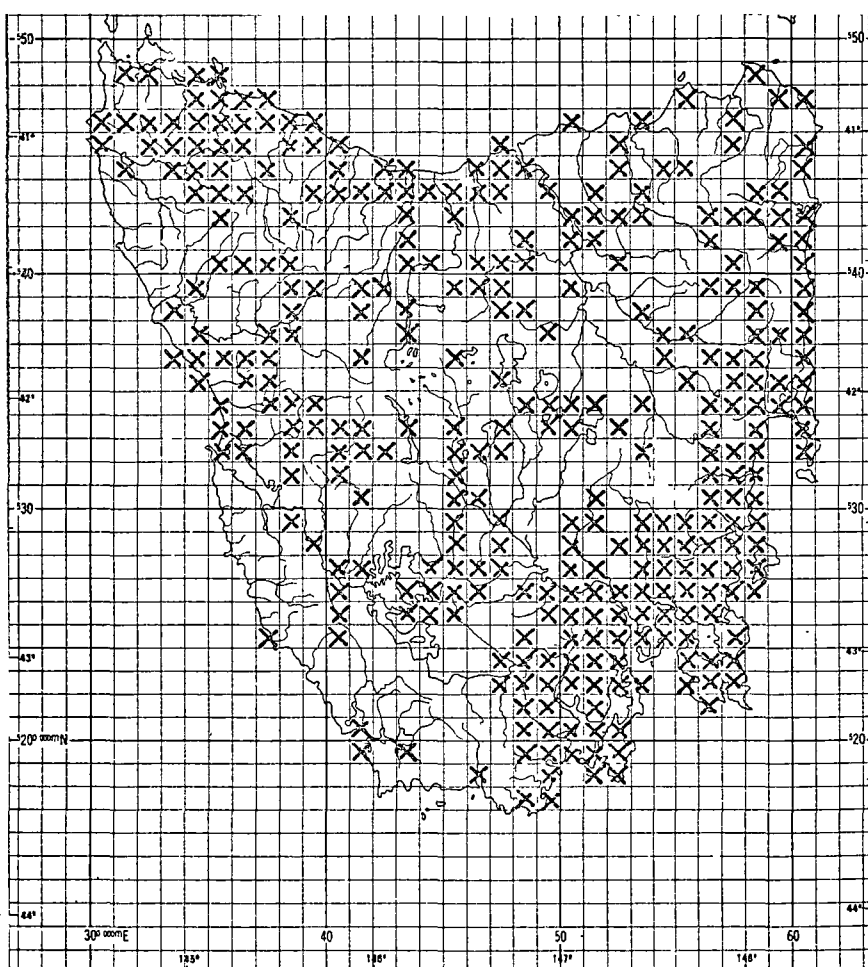
Olive Whistler



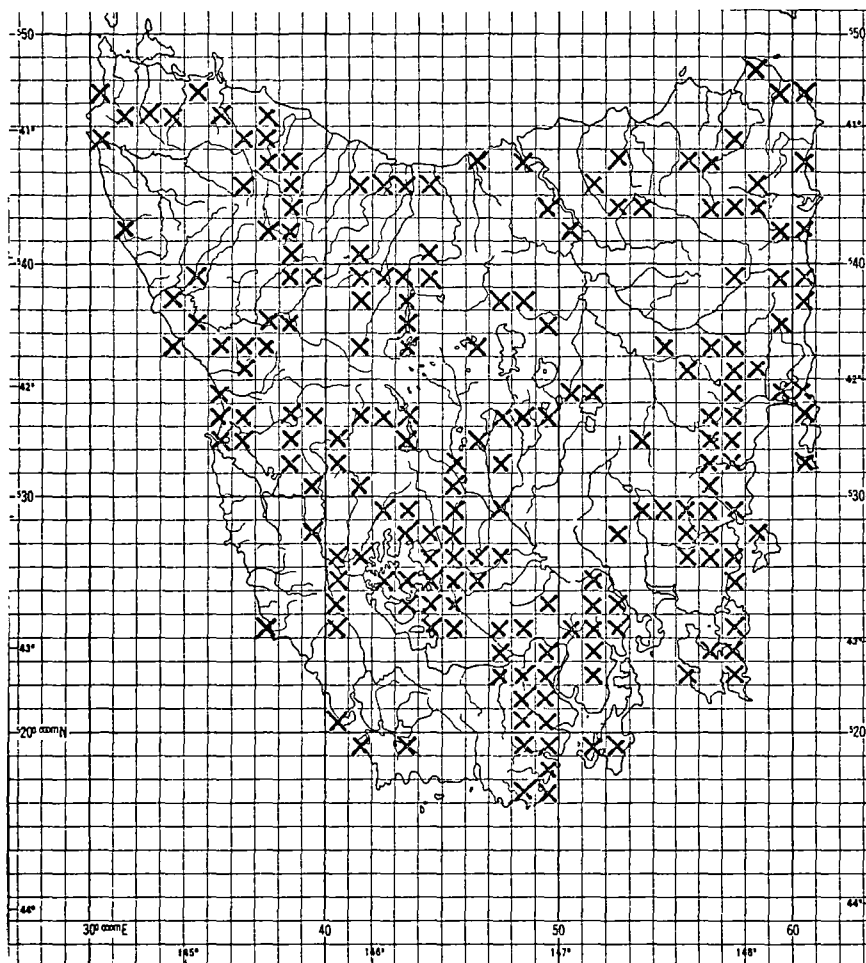
Golden Whistler



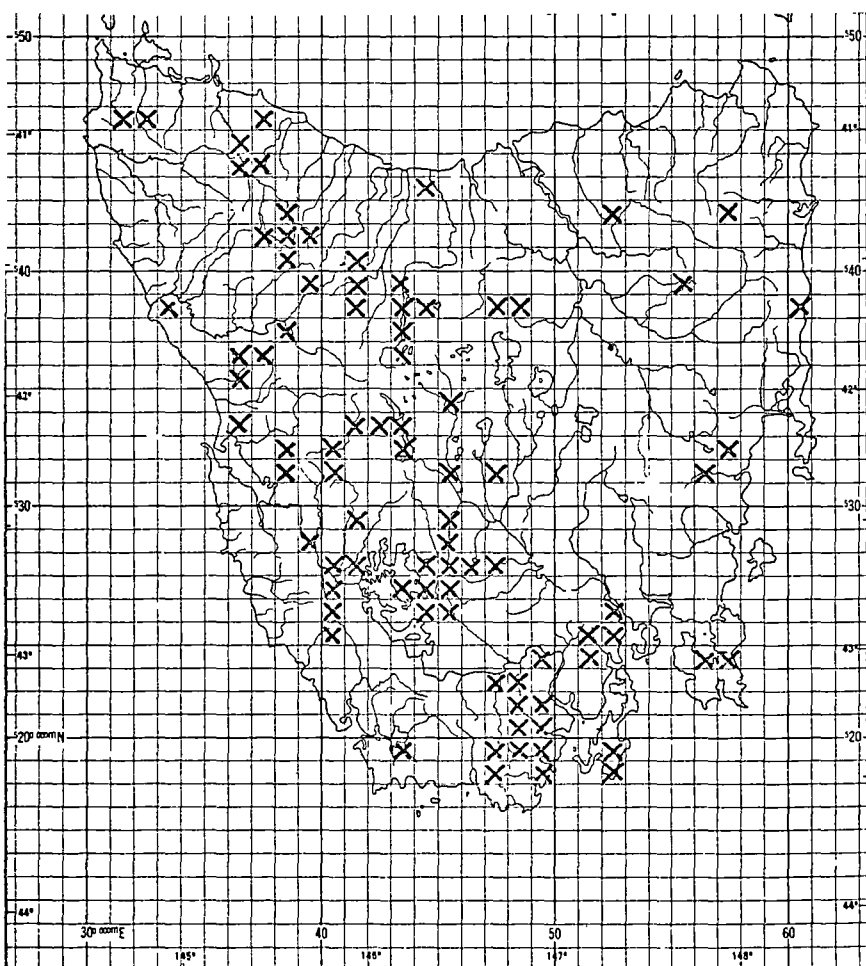
Grey Shrike-thrush



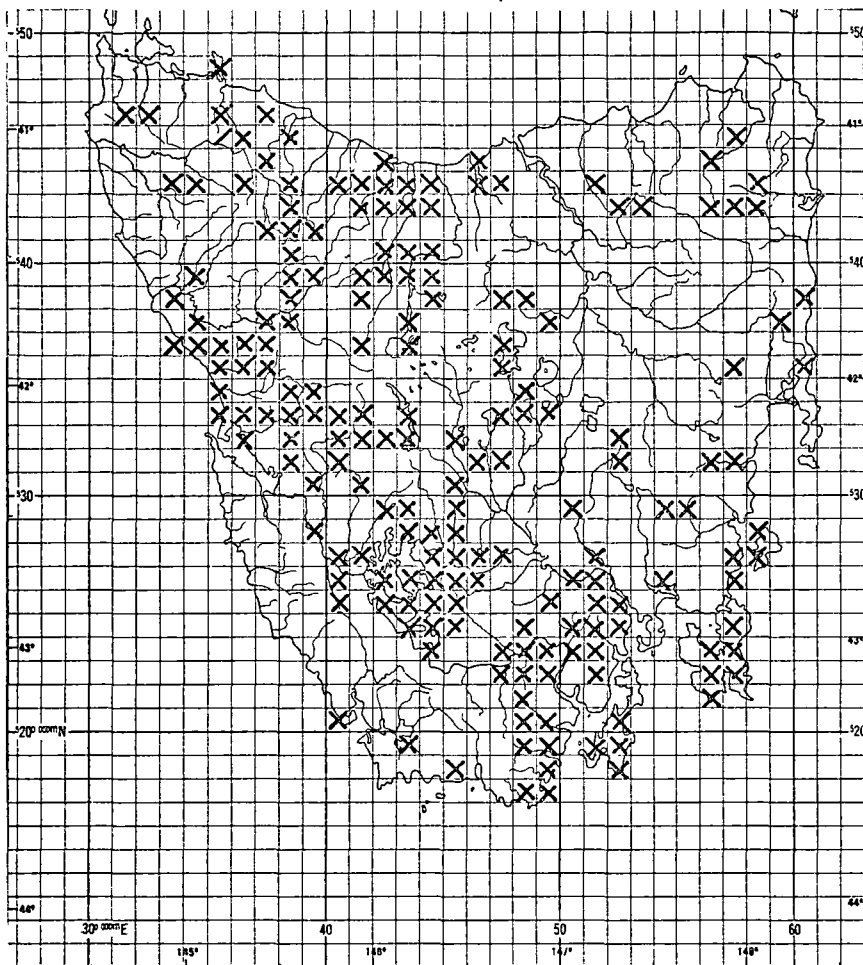
Grey Fantail



Brown Scrubwren

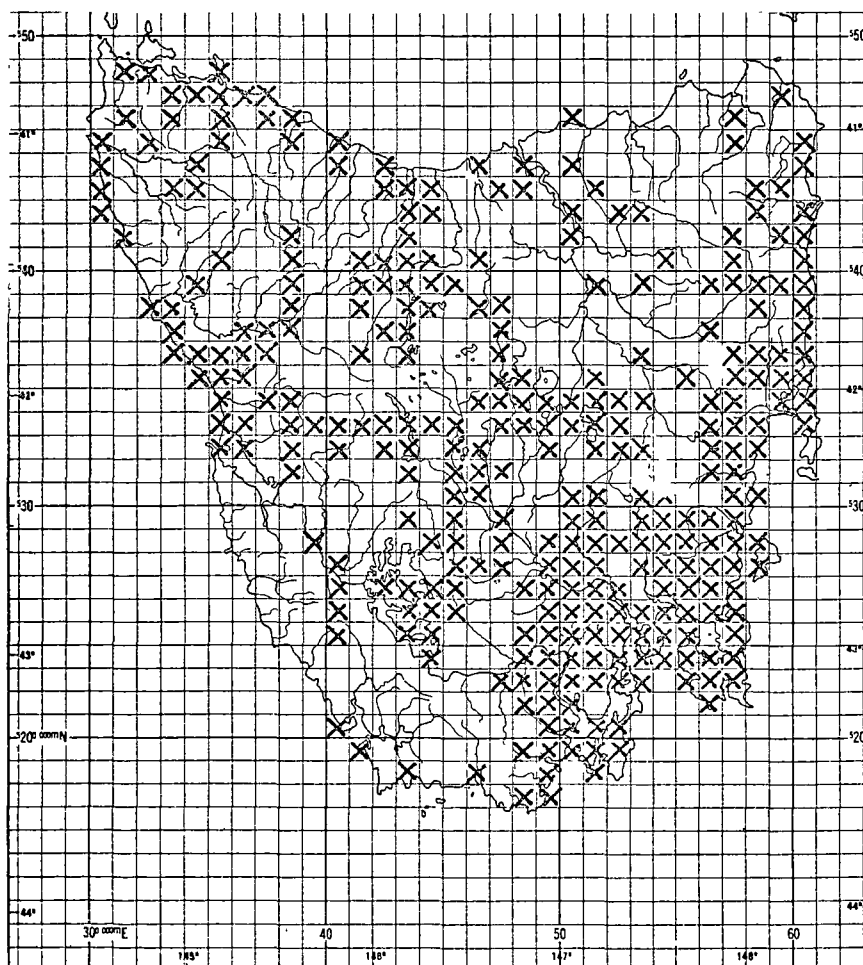


Scrubtit



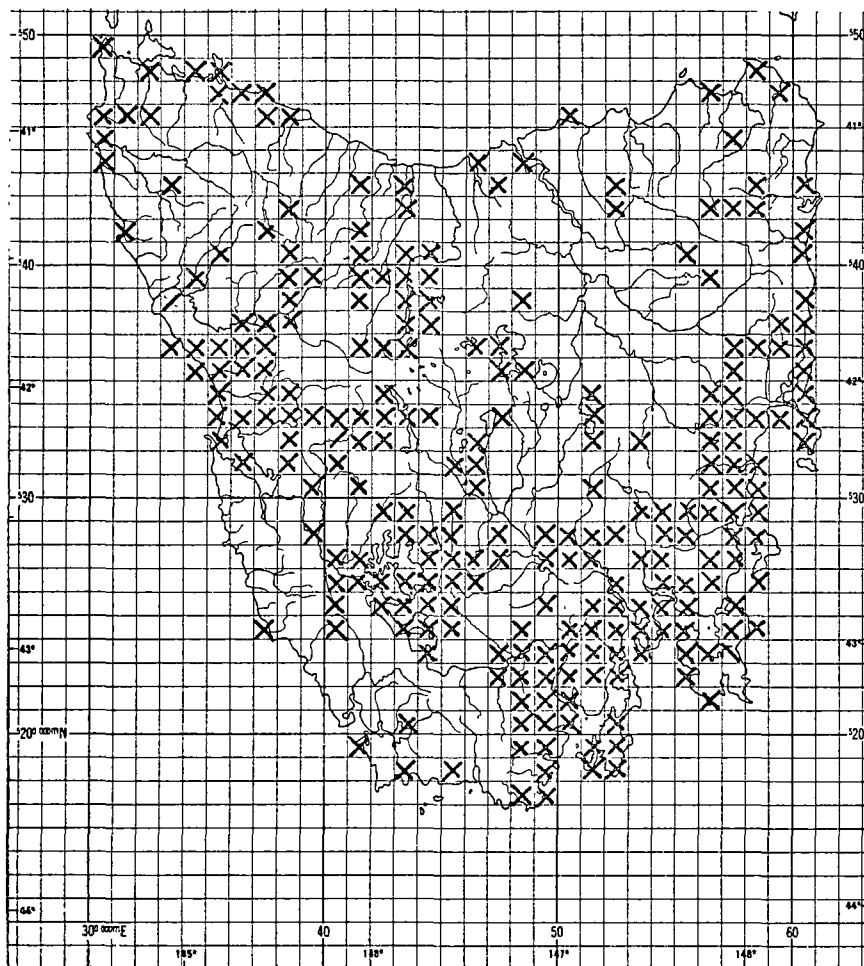
Tasmanian

Thornbill

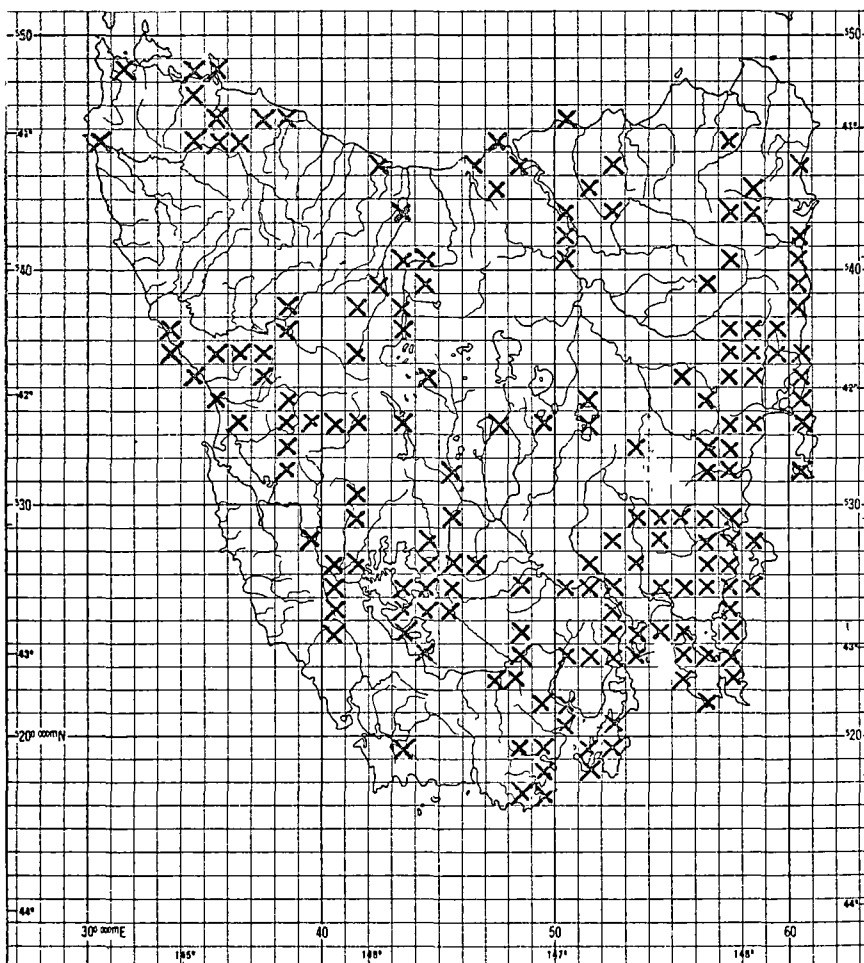


Yellow-throated

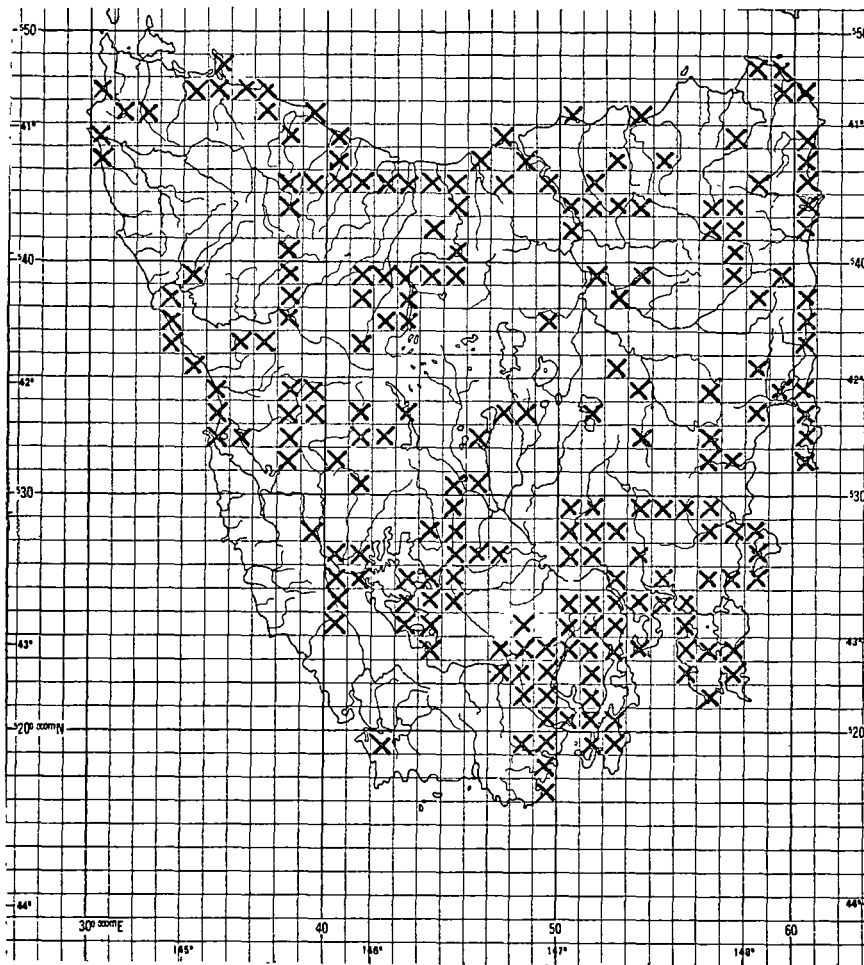
Honeyeater



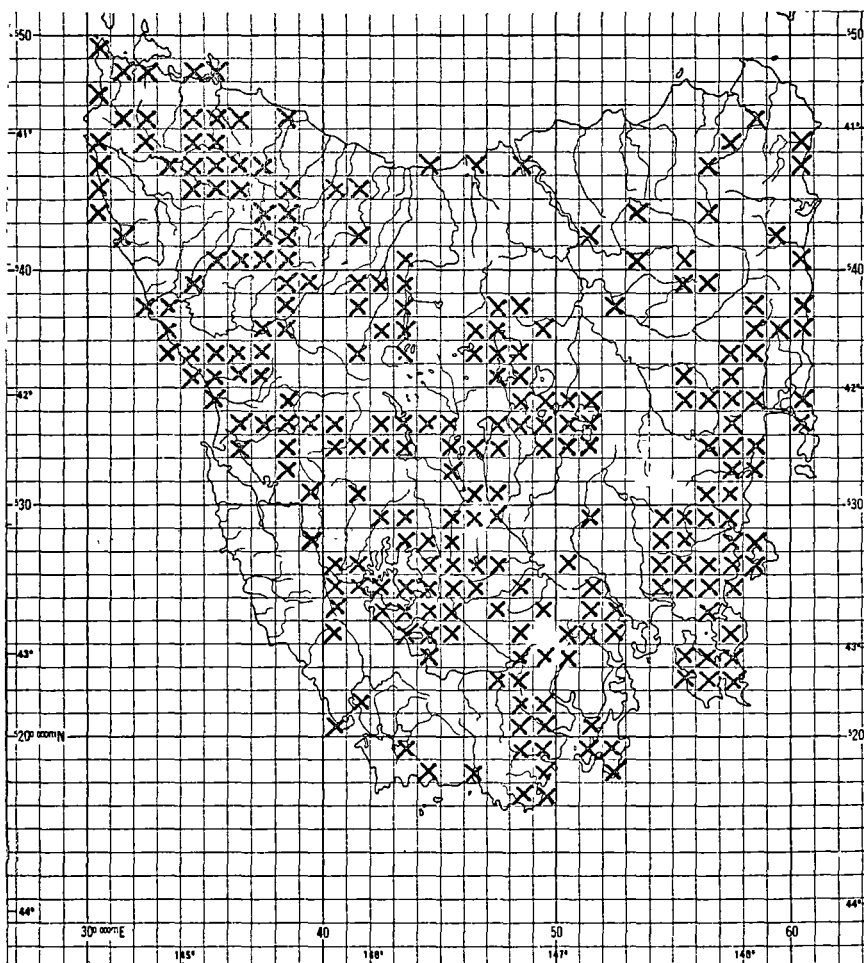
Crescent
Honeyeater



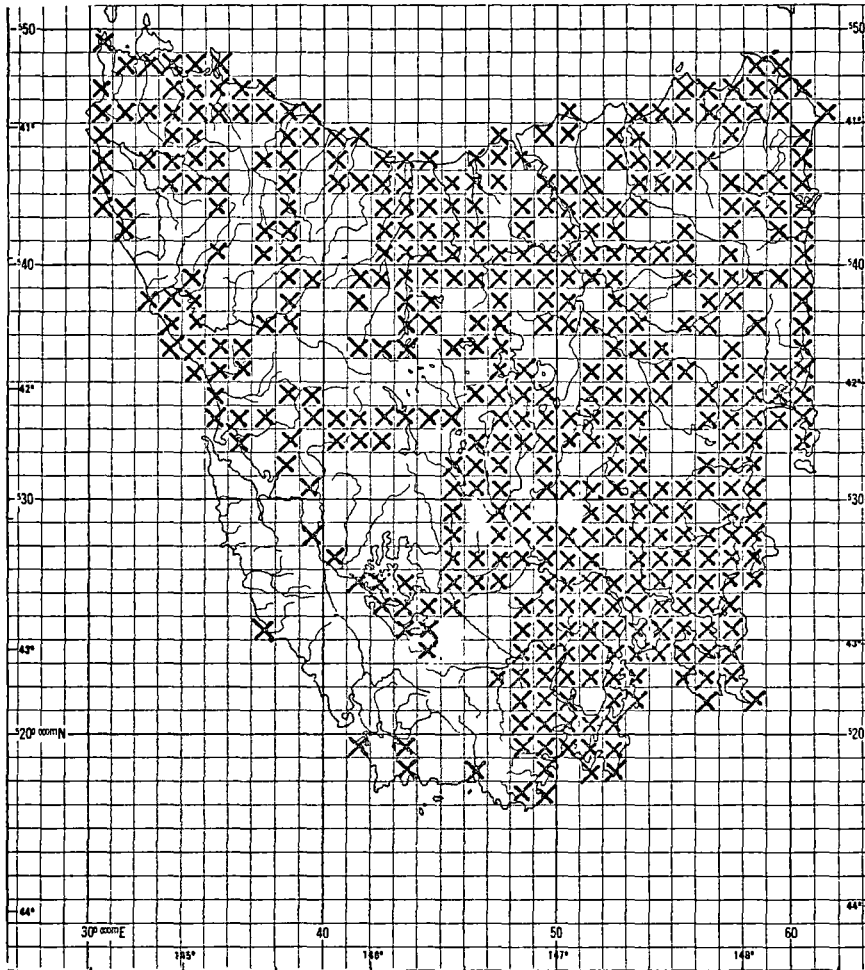
Eastern
Spinebill



Silvereye



Black Currawong



Forest Raven

APPENDIX 8

Abundance of species in the '100 km' squares of Figure 9. The numbers are

$$\frac{\text{no. of 10km squares in which the species was recorded}}{\text{no. of 10km squares in which the Forest Raven was recorded}} \times 100$$
[illegible]

APPENDIX 9

256

Occurrence of species breeding in Tasmanian temperate
rainforest on six of the larger off-shore islands.

	ISLAND					
	KING	HUNTER	FLINDERS	CAPE BARREN	MARIA	BRUNY
Grey Goshawk						+
Brush Bronzewing	+		+		+	+
Yellow-tailed Black Cockatoo	+	+	+	+	+	+
Green Rosella	+	+	+	+	+	+
Shining Bronze Cuckoo	+	+	+		+	
Spotted Owl	+	+	+	+	+	
Scaly Thrush	+		+	+	+	+
Pink Robin	+		+	+	+	+
Olive Whistler	+		+		+	+
Golden Whistler	+	+	+	+	+	+
Grey Shrike-thrush	+	+	+	+		+
Grey Fantail	+	+	+	+	+	+
Brown Scrubwren	+	+	+	+	+	+
Scrubtit	+					+
Tasmanian Thornbill	+	+	+	+	+	+
Yellow-throated Honeyeater	+		+	+	+	+
Crescent Honeyeater	+	+	+	+	+	+
Eastern Spinebill			+	+	+	+
Silvereye	+	+	+	+	+	+
Black Currawong	+	+	+	+	+	+
Forest Raven		+	+	+	+	+

Australian distribution of species breeding in Tasmanian
temperate rainforest.

GREY GOSHAWK



BRUSH BRONZEWING

YELLOW-TAILED BLACK
COCKATOO

CRIMSON ROSELLA



SHINING BRONZE CUCKOO



SPOTTED OWL



SCALY THRUSH



PINK ROBIN



OLIVE WHISTLER



GOLDEN WHISTLER



GREY SHRIKE-THRUSH



GREY FANTAIL



LARGE-BILLED SCRUBWREN



WHITE-BROWED SCRUBWREN



BROWN THORNBILL



WHITE-EARED HONEYEATER



CRESCENT HONEYEATER



EASTERN SPINEBILL



SILVEREYE



PIED CURRAWONG



FOREST RAVEN



APPENDIX 11

Bird census results.

1. POTTERY ROAD D Dry sclerophyll woodland.

10 x 350 m transects.

Collared Sparrowhawk	1	0.7	%	
Brown Falcon	1	0.7		
Swift Parrot	1	0.7		
Green Rosella	3	2.2		
Fan-tailed Cuckoo	7	5.2		S = 25
Rufous-tailed Bronze Cuckoo	2	1.5		H = 2.6244
Black-faced Cuckoo-shrike	8	5.9		H/log _e S = 0.81
Common Blackbird	3	2.2		Density = 1.929
Scarlet Robin	1	0.7		
Dusky Robin	2	1.5		
Golden Whistler	2	1.5		
Grey Shrike-thrush	7	5.2		
Satin Flycatcher	2	1.5		
Superb Blue Wren	1	0.7		
Brown Thornbill	14	10.4		
Yellow-throated Honeyeater	15	11.1		
Black-headed Honeyeater	3	2.2		
New Holland Honeyeater	1	0.7		
Spotted Pardalote	14	10.4		
Striated Pardalote	13	9.6		
European Goldfinch	8	5.9		
European Greenfinch	1	0.7		
Dusky Woodswallow	11	8.1		
Grey Currawong	1	0.7		
Forest Raven	13	9.6		

2. POTTERY ROAD A Dry sclerophyll forest.

10 x 450 m transects

Brown Falcon	1	0.3	%	
Green Rosella	1	0.3		
Pallid Cuckoo	2	0.5		
Fan-tailed Cuckoo	57	15.2		
Shining Bronze Cuckoo	22	5.9		S = 21
Black-faced Cuckoo-shrike	3	0.8		H = 2.5080
Common Blackbird	6	1.6		H/log _e S = 0.81
Scarlet Robin	4	1.1		Density = 4.178
Golden Whistler	14	3.7		
Grey Shrike-thrush	52	13.8		
Satin Flycatcher	21	5.6		
Grey Fantail	1	0.3		
Brown Thornbill	31	8.2		
Yellow-throated Honeyeater	60	16.0		
Black-headed Honeyeater	4	2.7		
Spotted Pardalote	42	11.2		
Striated Pardalote	28	7.4		
Silvereye	5	1.3		
European Goldfinch	3	0.8		
Grey Currawong	3	0.8		
Forest Raven	10	2.7		

3. POTTERY ROAD C Dry sclerophyll forest.

10 x 600 m transects

Grey Goshawk	1	0.2 %	
Brown Falcon	1	0.2	
Swift Parrot	2	0.4	
Green Rosella	2	0.4	
Pallid Cuckoo	12	2.4	S = 25
Fan-tailed Cuckoo	33	6.7	H = 2.7223
Shining Bronze Cuckoo	25	5.1	H/log _e s = 0.85
Black-faced Cuckoo-shrike	3	0.6	Density = 4.083
Common Blackbird	3	0.6	
Flame Robin	2	0.4	
Scarlet Robin	12	2.4	
Dusky Robin	7	1.4	
Golden Whistler	32	6.5	
Grey Shrike-thrush	51	10.4	
Satin Flycatcher	52	10.6	
Spotted Quail-thrush	1	0.2	
Superb Blue Wren	22	4.5	
Brown Thornbill	41	8.4	
Yellow-throated H' eater	15	3.1	
Black-headed Honeyeater	24	4.9	
Spotted Pardalote	85	17.3	
Striated Pardalote	29	5.9	
Silvereye	10	2.0	
Dusky Woodswallow	7	1.4	
Forest Raven	18	3.7	

4. POTTERY ROAD E Wet sclerophyll gully.

10 x 250 m transects.

Brown Goshawk	6	2.3 %	
Swift Parrot	1	0.4	
Green Rosella	1	0.4	
Pallid Cuckoo	1	0.4	
Fan-tailed Cuckoo	2	0.8	S = 22
Shining Bronze Cuckoo	7	2.7	H = 2.7314
Black-faced Cuckoo-shrike	2	0.8	H/log _e S = 0.88
Common Blackbird	24	9.3	Density = 5.180
Golden Whistler	4	1.5	
Grey Shrike-thrush	16	6.2	
Satin Flycatcher	34	13.1	
Grey Fantail	32	12.4	
Superb Blue Wren	17	6.6	
Brown Scrubwren	1	0.4	
Brown Thornbill	31	12.0	
Yellow-throated Honeyeater	8	3.1	
Strong-billed Honeyeater	11	4.2	
Black-headed Honeyeater	1	0.4	
Spotted Pardalote	11	4.2	
Striated Pardalote	22	8.5	
Silvereye	21	8.1	
Forest Raven	6	2.3	

5. POTTERY ROAD B Dry/wet sclerophyll ecotone.

10 x 250 m transects.

Swift Parrot	1	0.4 %	
Green Rosella	1	0.4	
Fan-tailed Cuckoo	30	13.0	
Shining Bronze Cuckoo	5	2.2	
Black-faced Cuckoo-shrike	1	0.4	s = 24
Common Blackbird	3	1.3	H = 2.6267
Flame Robin	6	2.6	H/log _e S = 0.83
Scarlet Robin	6	2.6	Density = 4.620
Dusky Robin	3	1.3	
Golden Whistler	16	6.9	
Grey Shrike-thrush	30	13.0	
Satin Flycatcher	3	1.3	
Grey Fantail	6	2.6	
Superb Blue Wren	4	1.7	
Brown Thornbill	14	6.1	
Yellow-throated Honeyeater	28	12.1	
Strong-billed Honeyeater	6	2.6	
Black-headed Honeyeater	8	3.5	
Crescent Honeyeater	7	3.0	
Spotted Pardalote	28	12.1	
Striated Pardalote	12	5.2	
Silvereye	1	0.4	
Grey Currawong	1	0.4	
Forest Raven	11	4.8	

6. MYRTLE GULLY Wet sclerophyll forest.

8 x 550 m transects.

Brown Falcon	1	0.2 %	
Swift Parrot	1	0.2	
Green Rosella	19	3.4	
Fan-tailed Cuckoo	43	7.6	
Shining Bronze Cuckoo	20	3.5	S = 26
Common Blackbird	14	2.5	H = 2.7812
Pink Robin	6	1.1	H/log _e S = 0.85
Olive Whistler	10	1.8	Density = 6.410
Golden whistler	23	4.1	
Grey Shrike-thrush	46	8.2	
Satin Flycatcher	1	0.2	
Grey Fantail	79	14.0	
Superb Blue Wren	8	1.5	
Brown Scrubwren	50	8.9	
Scrubtit	2	0.4	
Tasmanian Thornbill	40	7.1	
Yellow-throated Honeyeater	17	3.0	
Strong-billed Honeyeater	6	1.1	
Crescent Honeyeater	34	6.0	
Eastern Spinebill	3	0.5	
Spotted Pardalote	52	9.2	
Striated Pardalote	25	4.4	
Silvereye	58	10.3	
Beautiful Firetail	2	0.4	
Grey Currawong	1	0.2	
Forest Raven	3	0.5	

λ VALUES OBTAINED AT MYRTLE GULLY

SPECIES	λ	
	CENSUS 1 ⁽¹⁾	CENSUS 2 ⁽²⁾
Yellow-tailed Black Cockatoo	0.023	
Green Rosella	0.033	0.071
Superb Blue Wren	0.100	
Tasmanian Thornbill	0.105	0.050
Brown Scrubwren	0.121	0.043
Grey Fantail	0.057	0.050
Olive Whistler	0.017	
Grey Shrike-thrush	0.033	
Spotted Pardalote	0.030	0.150
Striated Pardalote	0.036	0.083
Silvereye	0.033	
Yellow-throated Honeyeater	0.025	
Black-headed Honeyeater	0.033	0.118
Strong-billed Honeyeater	0.058	0.025
Crescent Honeyeater	0.023	
Grey Currawong	0.050	
Forest Raven	0.017	

(1) Sight and sound records.

(2) Sight records only.

7. MOUNT FIELD Wet sclerophyll forest.

8 x 500 m transects.

Yellow-tailed Black Cockatoo	6	1.3 %	
Green Rosella	19	4.0	
Fan-tailed Cuckoo	26	5.4	
Shining Bronze Cuckoo	27	5.7	
Pink Robin	24	5.0	S = 17
Olive Whistler	10	2.1	H = 2.5514
Golden Whistler	33	6.9	H/log _e S = 0.90
Grey Shrike-thrush	65	13.6	Density = 5.962
Grey Fantail	76	15.9	
Brown Scrubwren	39	8.2	
Scrubtit	18	3.8	
Tasmanian Thornbill	44	9.2	
Yellow-throated Honeyeater	1	0.2	
Eastern Spinebill	1	0.2	
Striated Pardalote	27	5.7	
Silvereye	48	10.1	
Black Currawong	13	2.7	

8. CLEMES PEAK Wet sclerophyll forest.

8 x 300 m transects.

Grey Goshawk	2	1.2 %	
Brush Bronzewing	1	0.6	
Yellow-tailed Black Cockatoo	1	0.6	
Green Rosella	8	4.7	
Fan-tailed Cuckoo	5	2.9	S = 22
Shining Bronze Cuckoo	7	4.1	H = 2.6987
Pink Robin	5	2.9	H/log _e S = 0.89
Olive Whistler	3	1.7	Density = 3.583
Golden Whistler	1	0.6	
Grey Shrike-thrush	27	15.7	
Grey Fantail	18	10.8	
Brown Scrubwren	10	5.9	
Scrubtit	2	1.2	
Tasmanian Thornbill	24	14.0	
Yellow-throated Honeyeater	3	1.7	
Strong-billed Honeyeater	2	1.2	
Eastern Spinebill	18	10.5	
Spotted Pardalote	4	2.3	
Striated Pardalote	12	7.0	
Silvereye	4	2.3	
Black Currawong	11	6.4	

9. TAHUNE Mixed Forest.

8 x 500 m transects.

Yellow-tailed Black Cockatoo	1	0.3 %	
Green Rosella	36	11.4	
Shining Bronze Cuckoo	14	4.4	
Pink Robin	4	1.3	
Olive Whistler	13	4.1	S = 19
Golden Whistler	14	4.4	H = 2.6843
Grey Shrike-thrush	9	2.9	H/log _e S = 0.91
Satin Flycatcher	5	1.6	Density = 3.938
Grey Fantail	24	7.6	
Brown Scrubwren	27	8.6	
Scrubtit	23	7.3	
Tasmanian Thornbill	21	6.7	
Yellow-throated Honeyeater	12	3.8	
Strong-billed Honeyeater	2	0.6	
Crescent Honeyeater	50	15.9	
Eastern Spinebill	21	6.7	
Striated Pardalote	13	4.1	
Silvereye	20	6.3	
Black Currawong	6	1.9	

10. TIM'S TRACK Mixed forest.

8 x 500 m transects.

Grey Goshawk	2	0.7 %	
Brush Bronzewing	1	0.3	
Yellow-tailed Black Cockatoo	2	0.7	
Green Rosella	18	6.1	
Shining Bronze Cuckoo	17	5.7	S = 20
Black-faced Cuckoo-shrike	5	1.6	H = 2.6059
Pink Robin	16	5.4	H/log _e S = 0.87
Olive Whistler	3	1.0	Density = 3.700
Grey Shrike-thrush	14	4.7	
Grey Fantail	8	2.7	
Brown Scrubwren	34	11.5	
Scrubtit	19	6.4	
Tasmanian Thornbill	62	20.9	
Yellow-throated Honeyeater	11	3.7	
Strong-billed Honeyeater	2	0.7	
Crescent Honeyeater	22	7.4	
Eastern Spinebill	5	1.6	
Striated Pardalote	23	7.8	
Silvereye	10	3.4	
Black Currawong	22	7.4	

11. GORDON RIVER A Temperate rainforest.

10 x 250 m transects.

Grey Goshawk	1	0.5 %	
Green Rosella	16	8.0	
Shining Bronze Cuckoo	1	0.5	
Scaly Thrush	2	0.1	
Pink Robin	11	5.0	S = 17
Olive Whistler	31	15.0	H = 2.362
Golden Whistler	2	1.0	H/log _e S = 0.83
Grey Shrike-thrush	1	0.5	Density = 4.100
Grey Fantail	14	7.0	
Brown Scrubwren	7	3.0	
Scrubtit	10	5.0	
Tasmanian Thornbill	15	7.0	
Crescent Honeyeater	46	22.0	
Eastern Spinebill	12	6.0	
Silvereye	33	16.0	
Black Currawong	7	3.0	
Forest Raven	1	0.5	

12. GORDON RIVER B Temperate rainforest.

10 x 250 m transects.

Grey Goshawk	1	1.0	%	
Brush Bronzewing	1	1.0		
Green Rosella	22	19.0		
Pink Robin	1	1.0		
Olive Whistler	17	15.0		S = 16
Golden Whistler	1	1.0		H = 2.239
Grey Shrike-thrush	1	1.0		H/log _e S = 0.81
Grey Fantail	2	2.0		Density = 3.900
Brown Scrubwren	4	3.0		
Scrubtit	1	1.0		
Tasmanian Thornbill	7	6.0		
Strong-billed Honeyeater	1	1.0		
Crescent Honeyeater	29	25.0		
Eastern Spinebill	14	12.0		
Silvereye	13	11.0		
Black Currawong	2	2.0		

13. NEIKA Sub-alpine forest.

8 x 400 m transects.

Grey Goshawk	1	0.4 %	
Green Rosella	12	4.8	
Fan-tailed Cuckoo	23	9.2	
Shining Bronze Cuckoo	1	0.4	
Pink Robin	2	0.8	S = 17
Olive Whistler	10	4.0	H = 2.3276
Golden Whistler	3	1.2	H/log _e S = 0.82
Grey Shrike-thrush	28	11.2	Density = 3.922
Grey Fantail	26	10.4	
Brown Scrubwren	35	13.9	
Tasmanian Thornbill	18	7.2	
Yellow-throated Honeyeater	2	0.8	
Crescent Honeyeater	63	25.1	
Spotted Pardalote	3	1.2	
Silvereye	3	1.2	
Black Currawong	16	5.6	
Forest Raven	7	2.8	

14. BEATTIE'S TARN Sub-alpine forest.

8 x 300 m transects.

Green Rosella	13	5.4	%	
Fan-tailed Cuckoo	4	1.7		
Shining Bronze Cuckoo	12	5.0		
Black-faced Cuckoo-shrike	1	0.4		
Olive Whistler	12	5.0		S = 19
Golden Whistler	30	12.5		H = 2.3876
Grey Shrike-thrush	10	4.2		H/log _e S = 0.81
Grey Fantail	1	0.4		Density = 5.000
Brown Scrubwren	24	10.0		
Scrubtit	5	2.1		
Tasmanian Thornbill	2	0.8		
Yellow-throated Honeyeater	22	9.2		
Strong-billed Honeyeater	1	0.4		
Crescent Honeyeater	48	20.0		
Eastern Spinebill	2	0.8		
Spotted Pardalote	2	0.8		
Striated Pardalote	6	2.5		
Silvereye	5	2.1		
Black Currawong	30	12.5		

15. LAKE DOBSON Sub-alpine forest.

8 x 350 m transects.

Yellow-tailed Black Cockatoo	3	1.4	%	
Green Rosella	13	6.0		
Fan-tailed Cuckoo	16	7.4		
Shining Bronze Cuckoo	2	0.9		
Pink Robin	1	0.5		S = 18
Olive Whistler	3	1.4		H = 2.3323
Golden Whistler	5	2.3		H/log _e S = 0.81
Grey Shrike-thrush	1	0.5		Density = 3.857
Brown Scrubwren	8	3.7		
Scrubtit	13	6.0		
Tasmanian Thornbill	10	4.6		
Yellow-throated Honeyeater	45	20.8		
Crescent Honeyeater	56	25.9		
Spotted Pardalote	4	1.9		
Striated Pardalote	10	4.6		
Silvereye	7	3.2		
Black Currawong	18	8.3		
Forest Raven	1	0.5		

16. PANDANNI GROVE Dwarf coniferous forest.

8 x 50 m transects.

Pink Robin	2	10.0 %	
Brown Scrubwren	1	5.0	
Scrubtit	3	15.0	$S = 6$
Yellow-throated Honeyeater	3	15.0	$H = 1.6004$
Crescent Honeyeater	8	40.0	$H/\log_e S = 0.89$
Black Currawong	3	15.0	Density = 2.500

17. OLGA CAMP Temperate rainforest.

8 x 200 m transects.

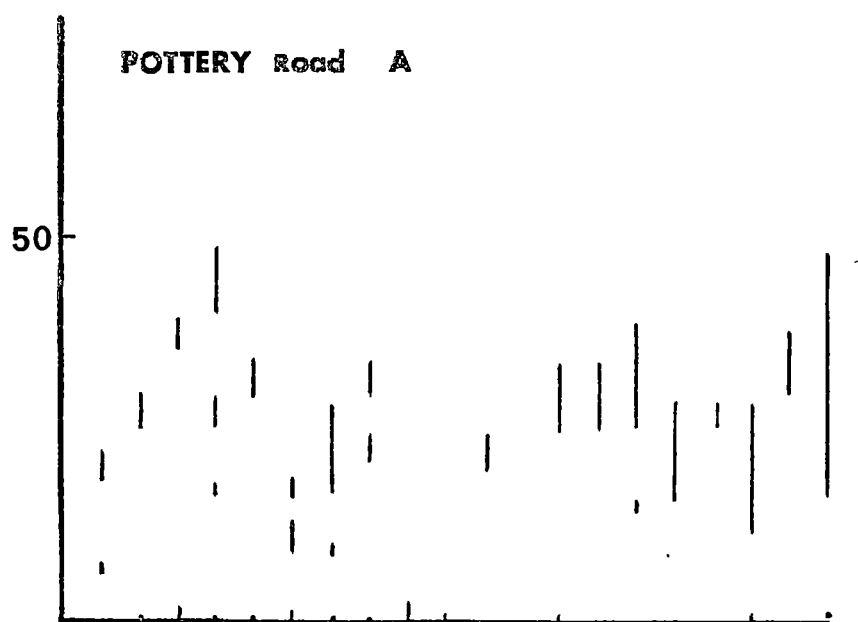
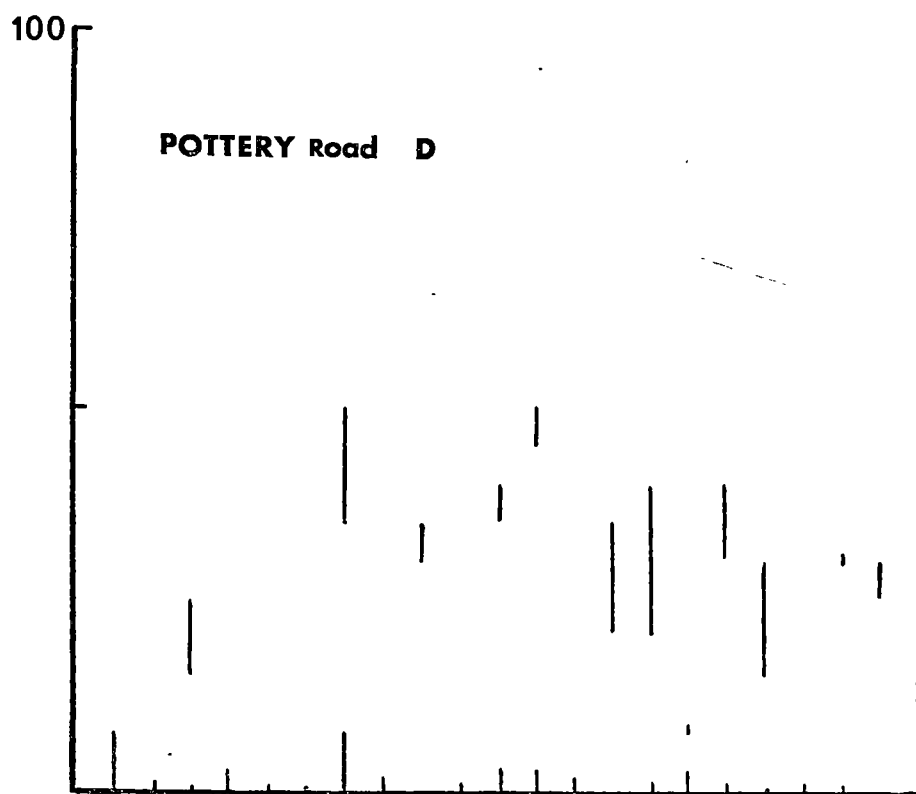
Sulphur-crested Cockatoo	1	0.5 %	
Green Rosella	5	2.3	
Shining Bronze Cuckoo	3	1.4	
Scaly Thrush	5	2.3	
Pink Robin	10	4.6	S = 18
Olive Whistler	25	11.5	H = 2.6398
Golden Whistler	5	2.3	H/log _e S = 0.91
Grey Shrike-thrush	14	6.5	Density = 6.781
Grey Fantail	23	10.6	
Brown Scrubwren	13	6.0	
Scrubtit	11	5.1	
Tasmanian Thornbill	22	10.1	
Yellow-throated Honeyeater	7	3.2	
Crescent Honeyeater	30	13.8	
Eastern Spinebill	15	6.9	
Silvereye	10	4.6	
Black Currawong	17	7.8	
Forest Raven	1	0.5	

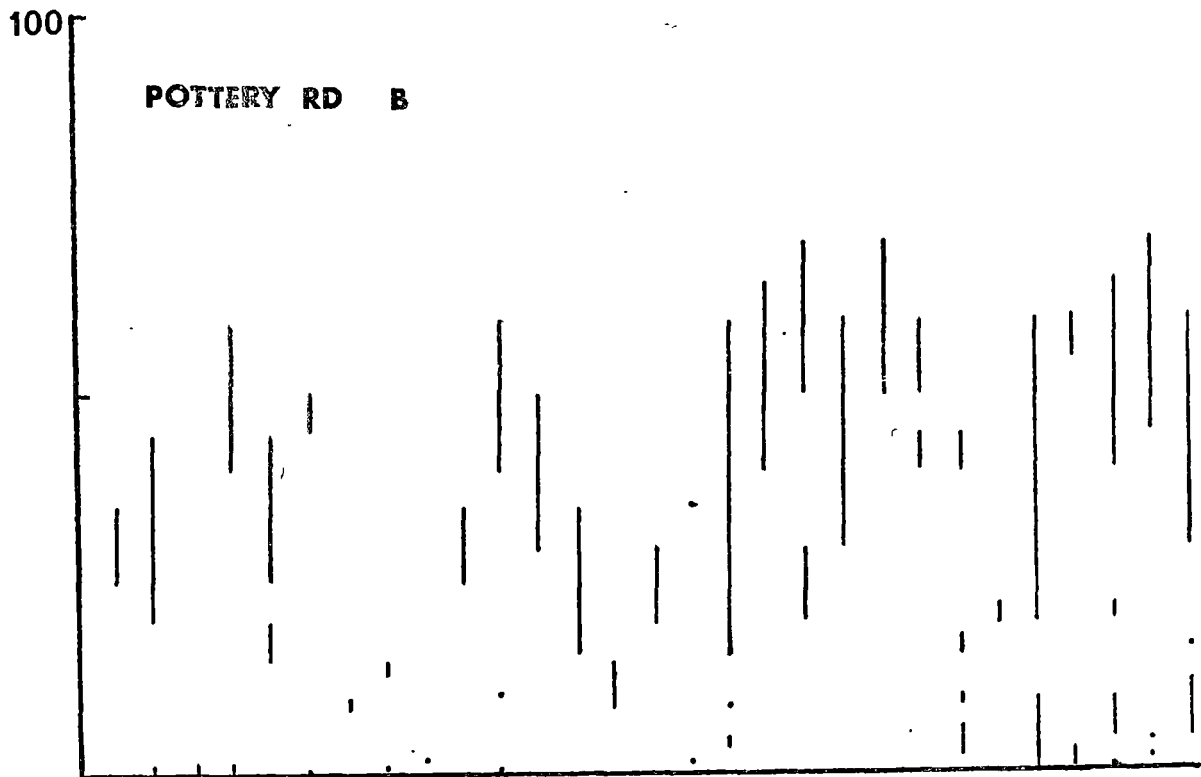
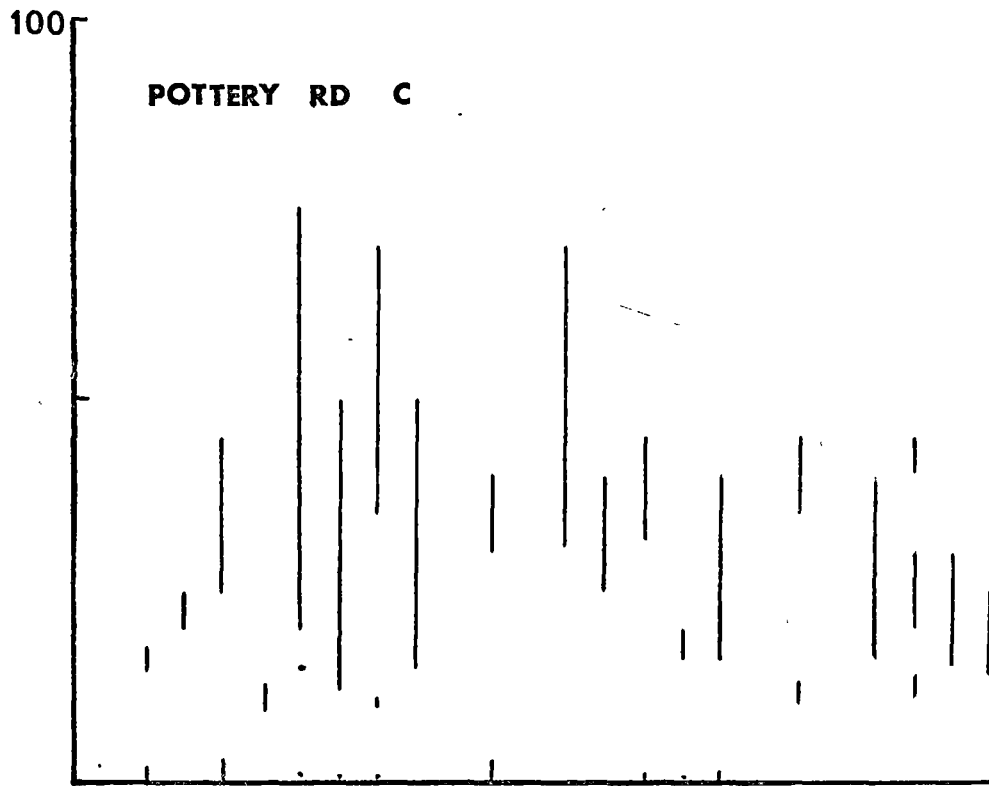
TULLAWALLAL, Queensland. Subtropical (0 - 300 m) and
temperate (400 - 500 m) rainforest.

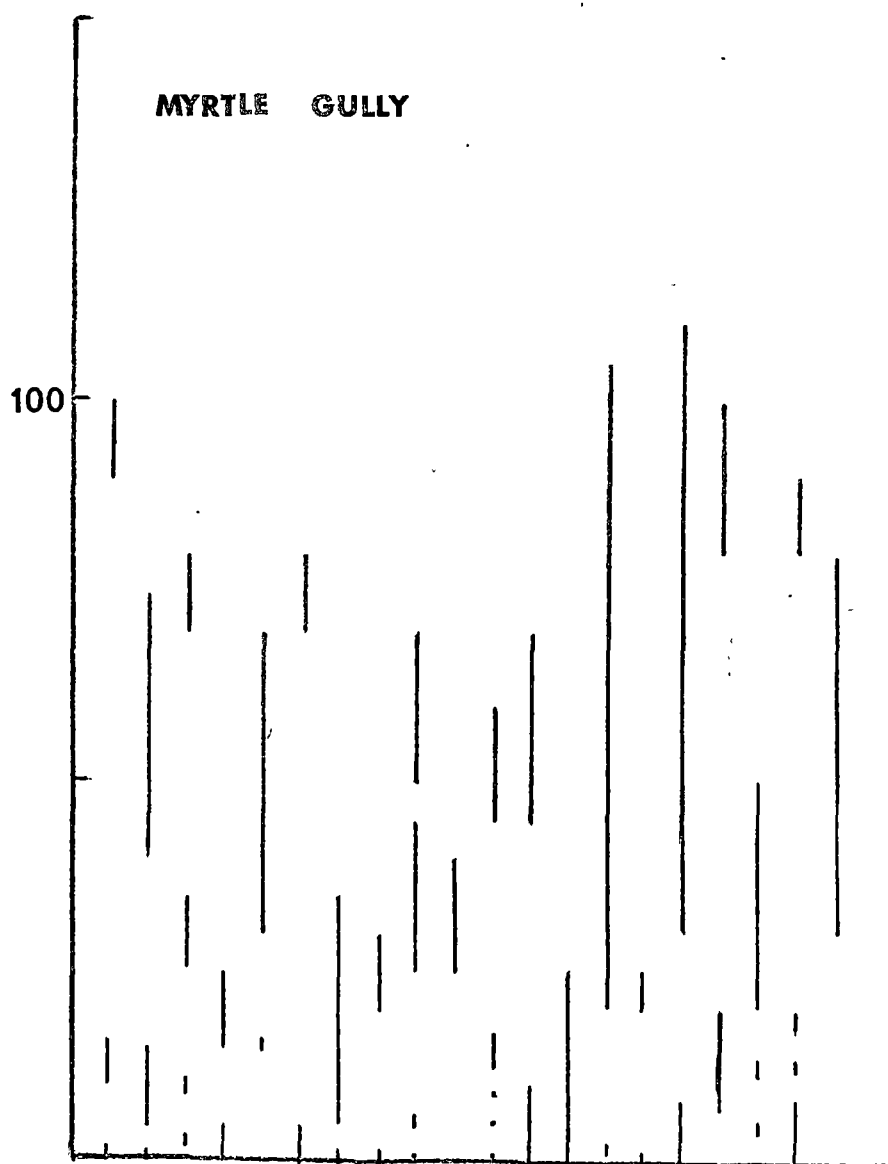
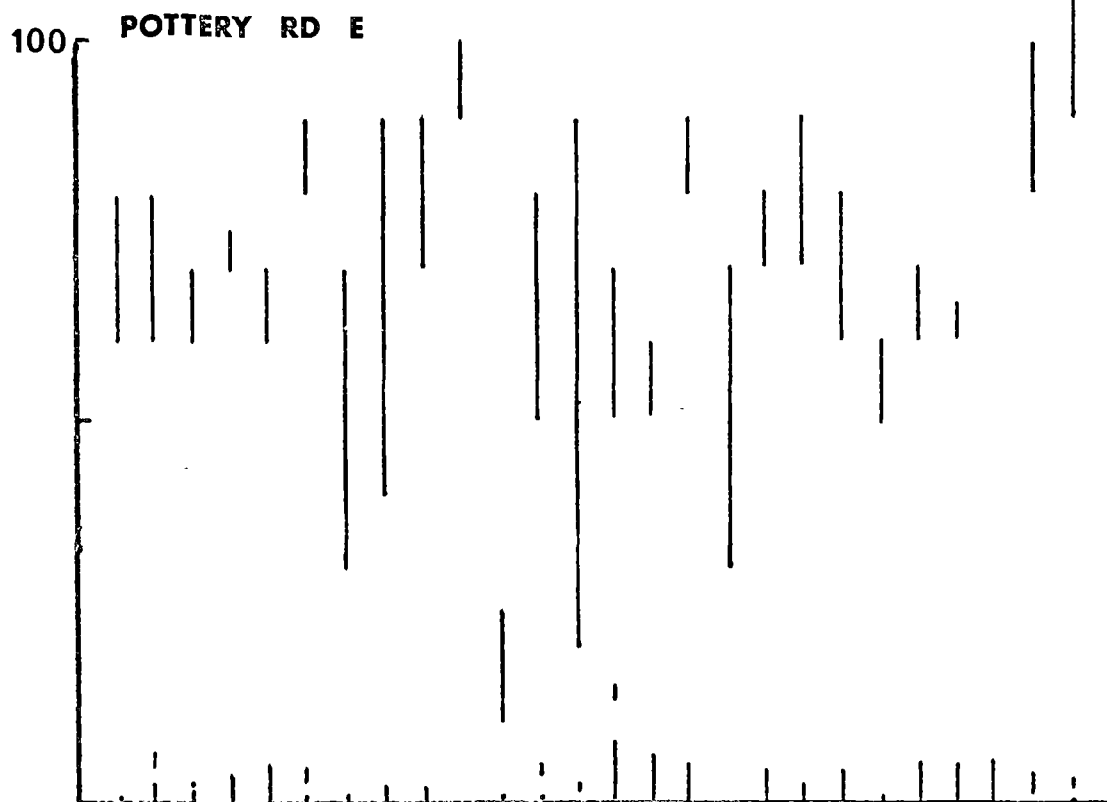
8 x 500 m transects.

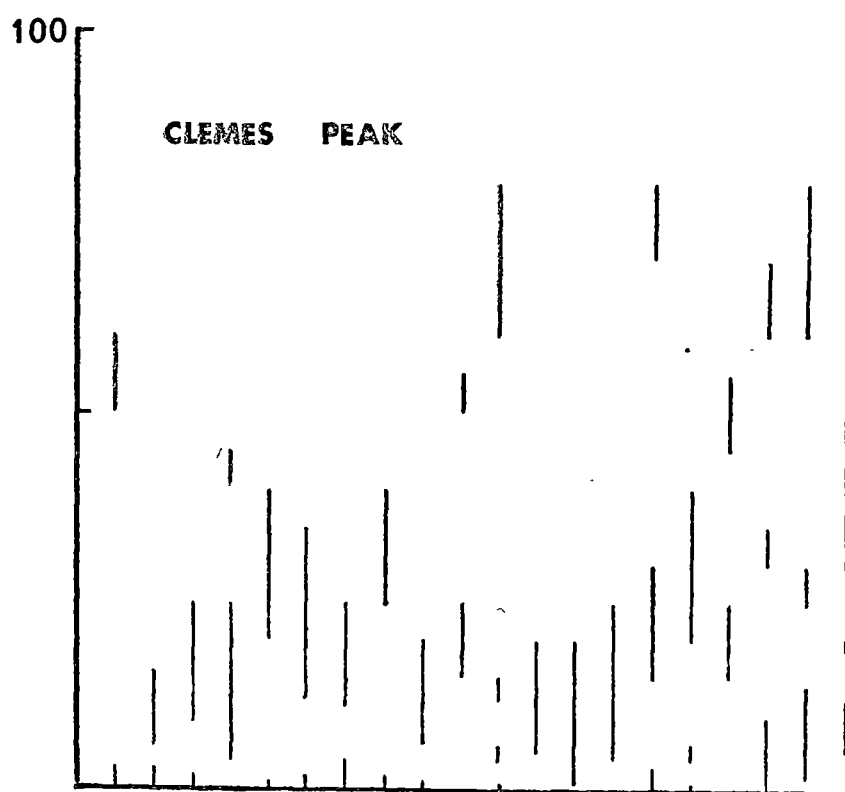
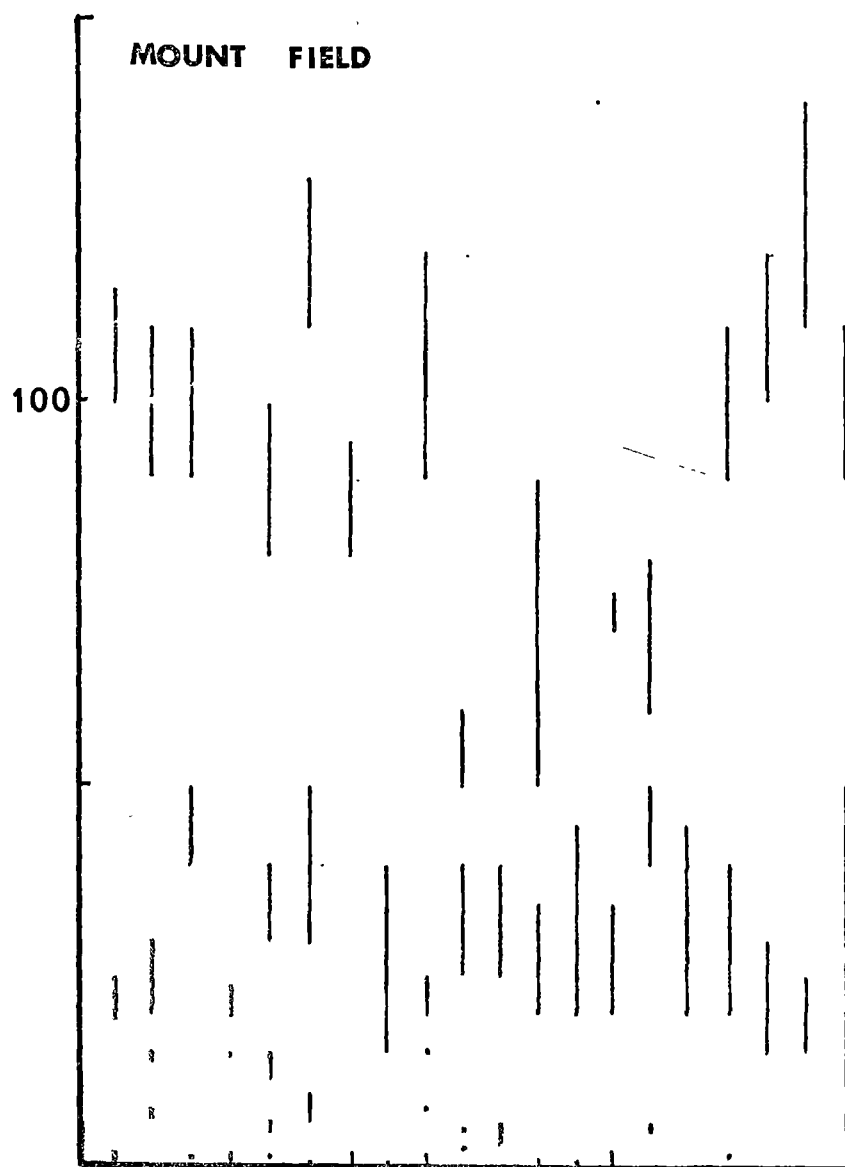
SPECIES	FREQUENCY					
	0-100m	100-200m	200-300m	300-400m	400-500m	
Brown Pigeon	1	3	1		1	6
Crimson Rosella	8	10	8	4	12	42
Fan-tailed Cuckoo			1			1
Shining Bronze Cuckoo				2		2
Brown Warbler	1	1	1	2	1	6
Eastern Yellow Robin		1				1
Olive Whistler		1	1	2	3	7
Golden Whistler	9	10	13	4	6	42
Grey Shrike-thrush	12	13	6	4	3	38
Black-faced Monarch	1	1	2		4	8
Rufous Fantail	4	8	2			14
Grey Fantail	1					1
Eastern Whipbird	11	13	9	7	8	48
Large-billed Scrubwren	7	2	2	3	3	17
Yellow-throated Scrubwren		5	3			8
White-browed Scrubwren	12	14	12	10	10	58
Brown Thornbill	8	8	4	6	6	32
Striated Thornbill			1			1
White-throated Treecreeper	1					1
Red Wattlebird			1			1
Lewin's Honeyeater	8	11	10	7	4	40
Eastern Spinebill	3	1	7	1	2	14
Spotted Pardalote					1	1
Silvereye			1			1
Satin Bowerbird	2					2
Green Catbird	1	2		1	1	5
Paradise Riflebird				1	2	3
Pied Currawong	3	3	3	8	11	28
Torresian Crow					1	1
TOTAL SPECIES	19	18	20	15	18	29

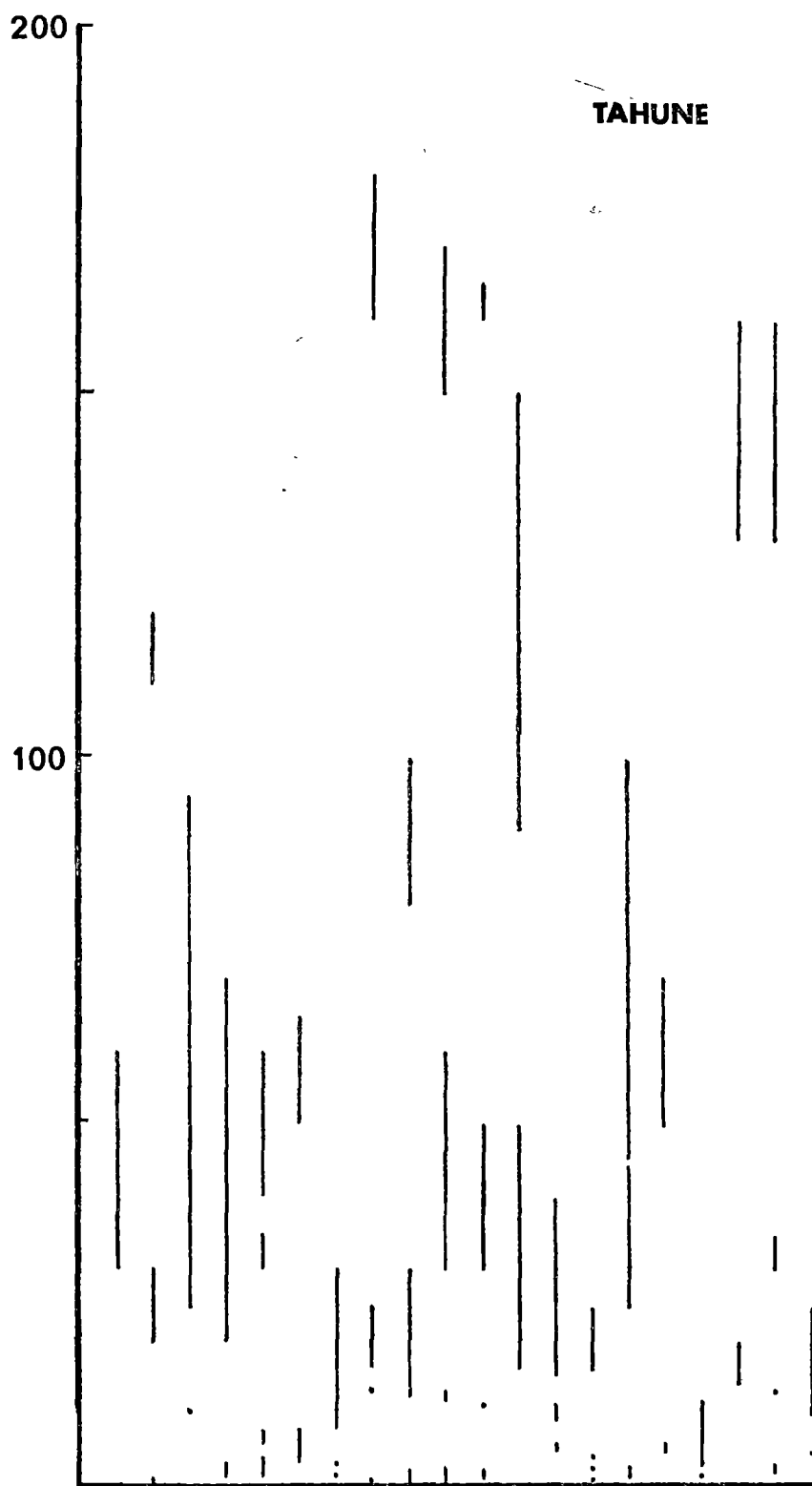
Foliage profiles of census sites

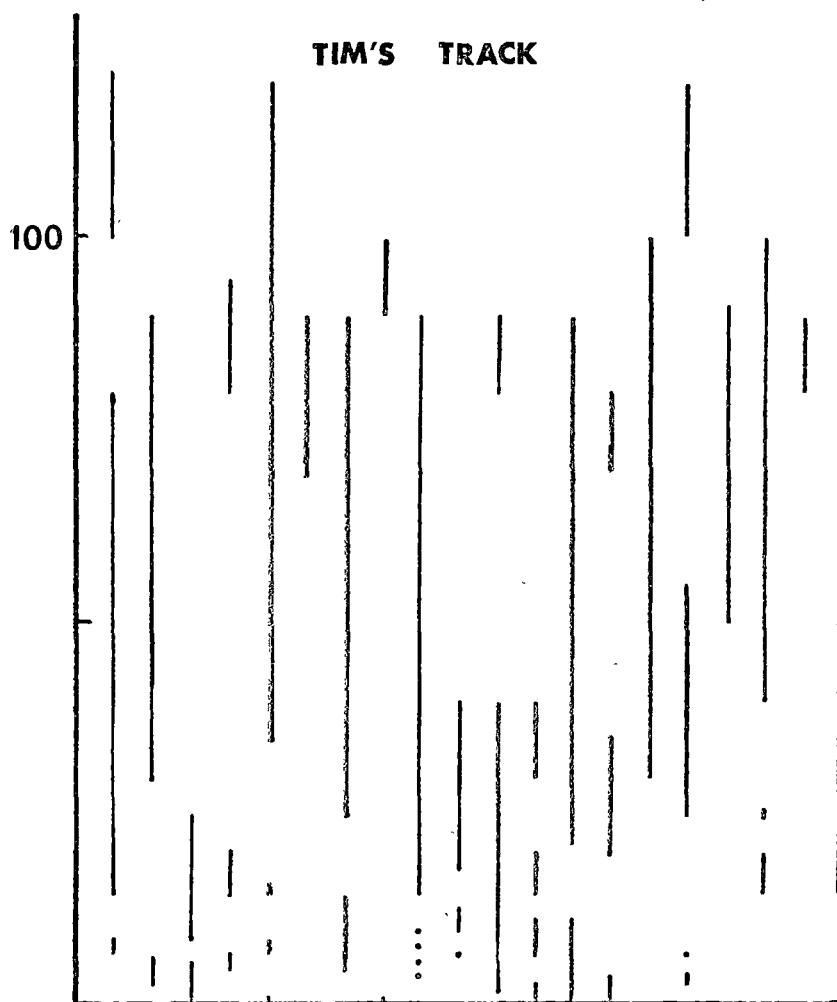


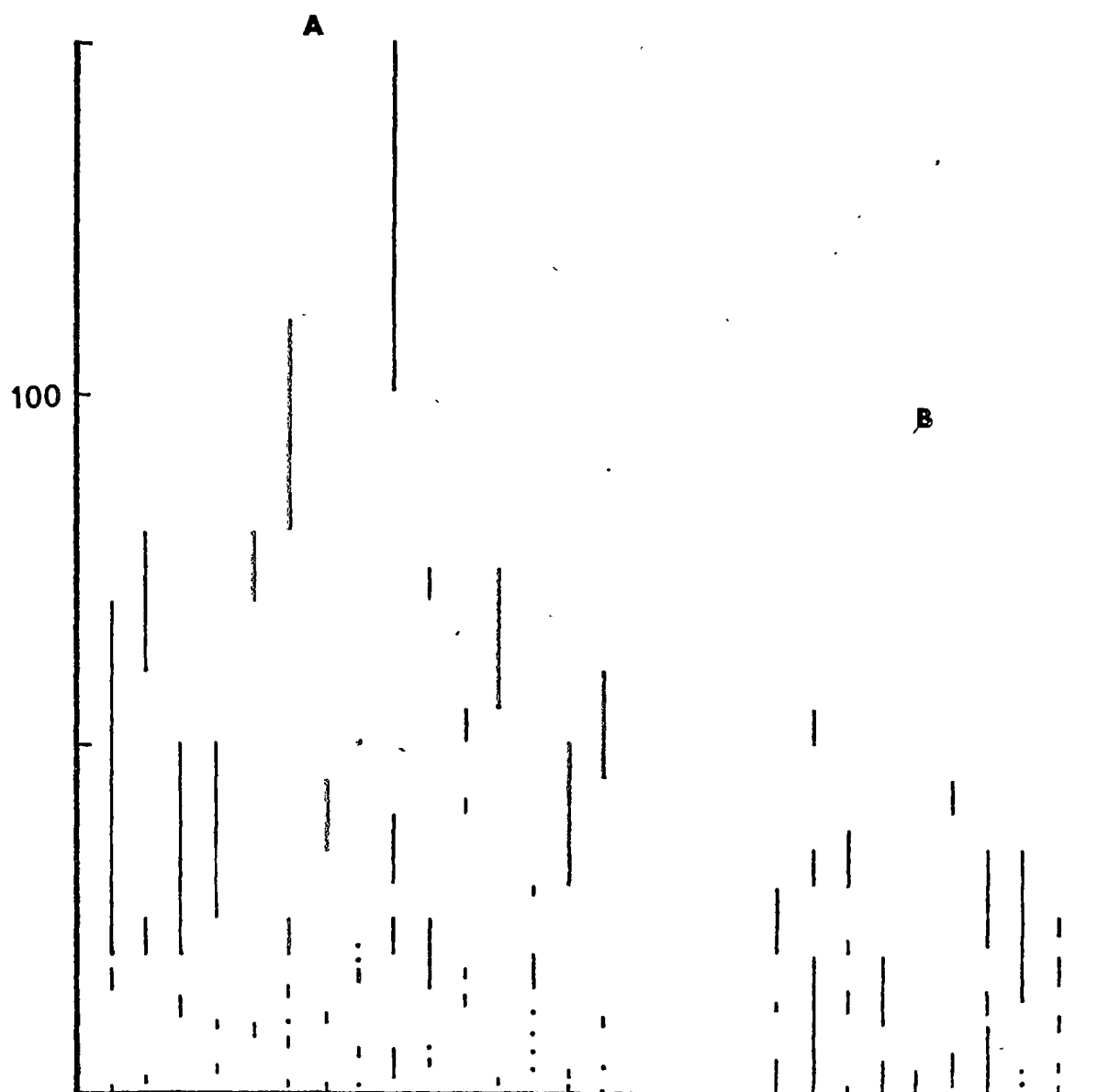


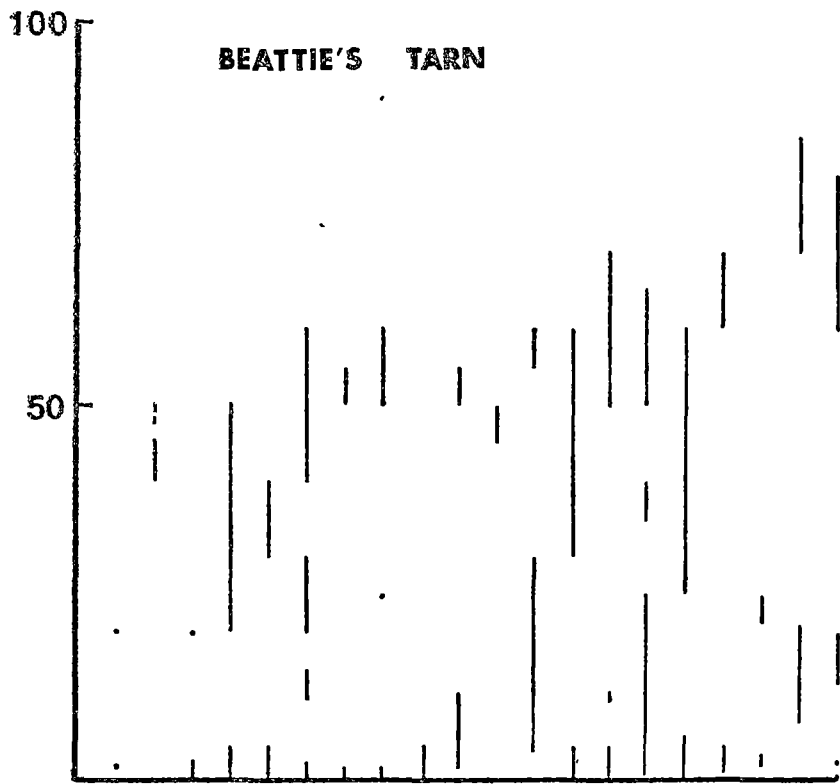
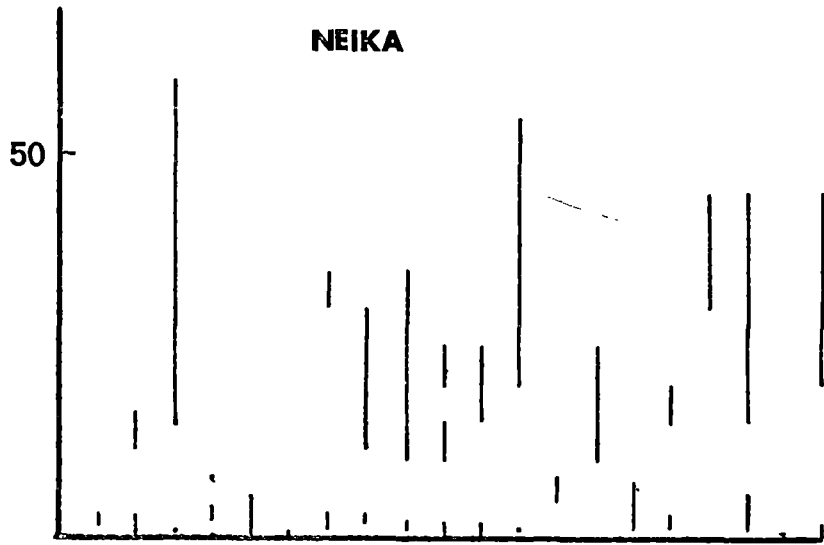


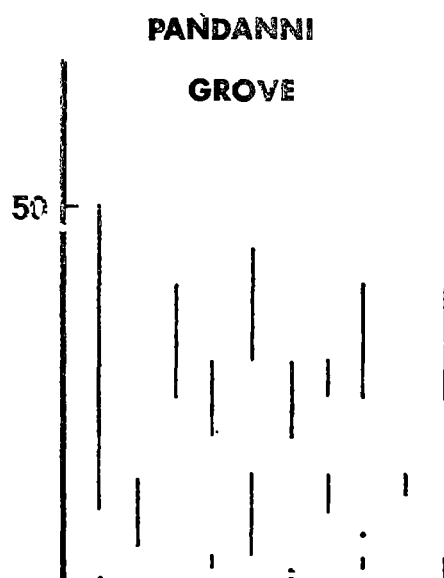
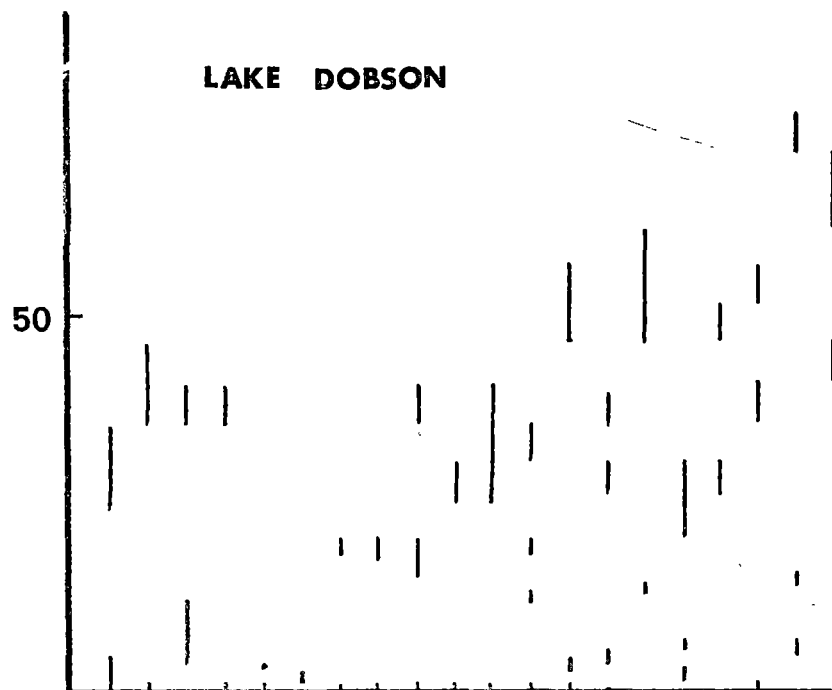


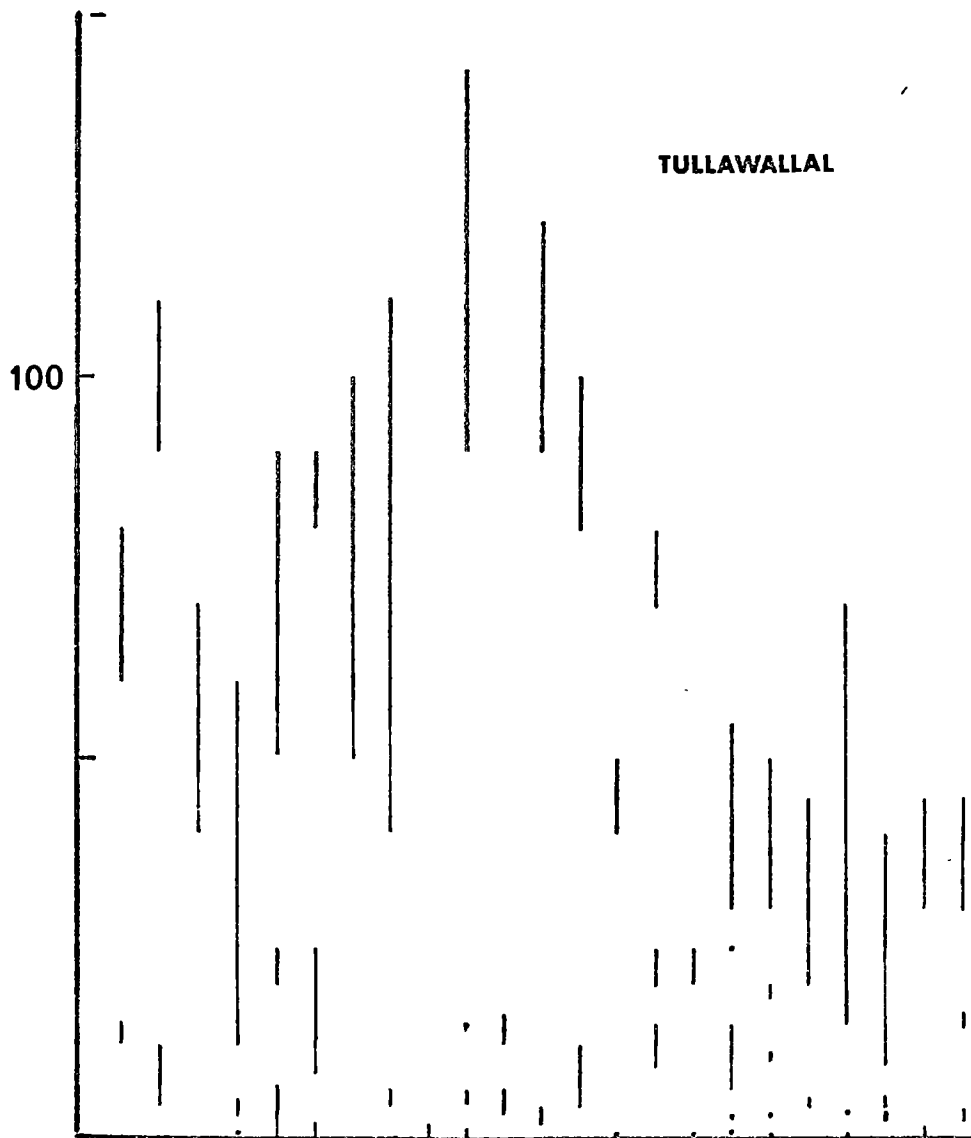
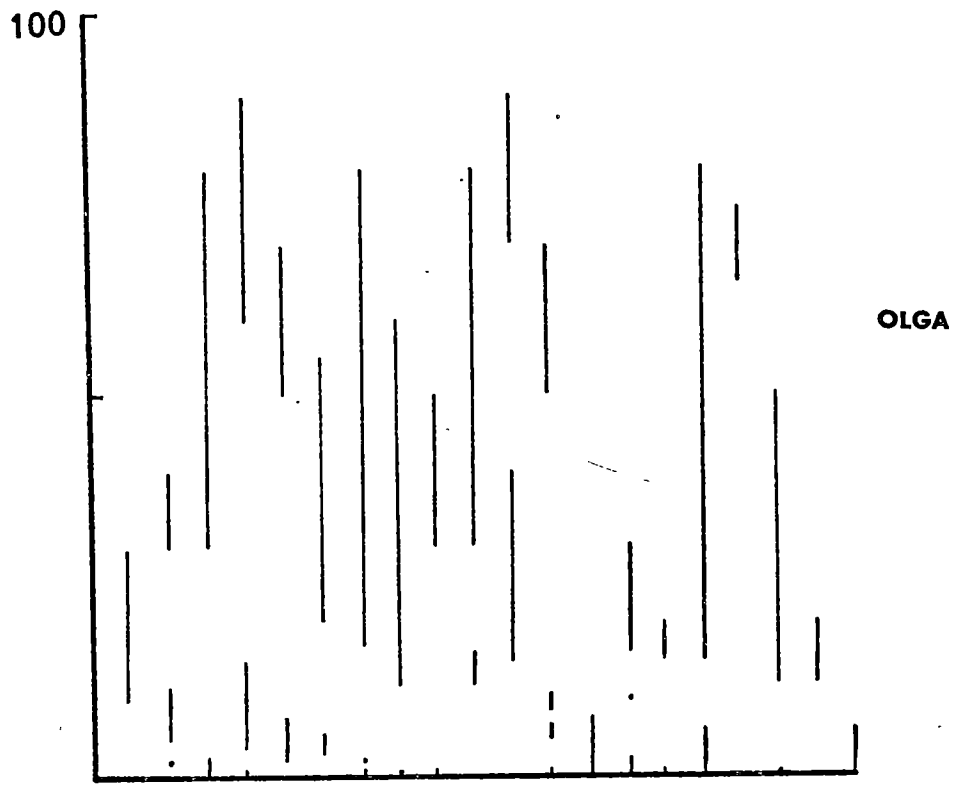




GORDON RIVER







APPENDIX 13

Species distribution along the Tasmanian xeric-mesic gradient.

APPENDIX 13

Species distribution along the Tasmanian xeric-mesic gradient

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SPECIES	D S			DS/WS	W S				M F		T R F			S A F			D C F
	1	2	3	5	4	6	7	8	9	10	11	12	17	13	14	15	16
Brown Goshawk		(✓)	(✓)		✓												
Collared Sparrowhawk	✓																
Grey Goshawk			✓					✓		✓	✓	✓		✓			
Brown Falcon	✓	✓	✓	(✓)		✓								(✓)			
Common Bronzewing	(✓)	(✓)	(✓)														
Brush Bronzewing							(✓)	✓	(✓)	✓		✓		(✓)			
Yellow-tailed Black Cockatoo							✓	✓	✓	✓						✓	
Swift Parrot	✓		✓	✓	✓	✓			(✓)								
Green Rosella	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	(✓)
Pallid Cuckoo		✓	✓	(✓)	✓												
Fantailed Cuckoo	✓	✓	✓	✓	✓	✓	✓	✓						✓	✓	✓	
Rufous-tailed Bronze Cuckoo	✓																
Shining Bronze Cuckoo		✓	✓	✓	✓	✓	✓	✓	✓	✓	✓			✓	✓	✓	
Black-faced Cuckoo-Shrike	✓	✓	✓	✓	✓					✓					✓		
Scaly Thrush						(✓)	(✓)		(✓)	(✓)	✓						
Common Blackbird	✓	✓	✓	✓	✓	✓											
Pink Robin						✓	✓	✓	✓	✓	✓	✓		✓		✓	✓

APPENDIX 13 - cont'd.

SPECIES	D S			DS/WS	W S				M F		T R F			S A F			DC F
	1	2	3	5	4	6	7	8	9	10	11	12	17	13	14	15	16
Flame Robin			✓	✓										(✓)			
Scarlet Robin	✓	✓	✓	✓													
Dusky Robin	✓		✓	✓										(✓)			
Olive Whistler						✓	✓	✓	✓	✓	✓	✓		✓	✓	✓	
Golden Whistler	✓	✓	✓	✓	✓	✓	✓	✓	✓	(✓)	✓	✓		✓	✓	✓	
Grey Shrike-thrush	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓		✓	✓	✓	
Satin Flycatcher	✓	✓	✓	✓	✓	✓			(✓)								
Grey Fantail		✓	(✓)	✓	✓	✓	✓	✓	✓	✓	✓	✓		✓	✓		
Spotted Quail-thrush	(✓)	(✓)	✓														
Superb Blue Wren	✓		✓	✓	✓	✓											
Brown Scrubwren					✓	✓	✓	✓	✓	✓	✓	✓		✓	✓	✓	✓
Scrubtit						✓	✓	✓	✓	✓	✓	✓		(✓)	✓	✓	✓
Brown Thornbill	✓	✓	✓	✓	✓												
Tasmanian Thornbill						✓	✓	✓	✓	✓	✓	✓		✓	✓	✓	✓
Yellow-throated Honeyeater	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓				✓	✓	✓	✓
Strong-billed Honeyeater				✓	✓	✓		✓	✓	✓		✓		(✓)	✓		
Black-headed Honeyeater	✓	✓	✓	✓	✓	(✓)				(✓)							

APPENDIX 13 - cont'd.

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SPECIES	D S			DS/ WS	W S				M F		T R F			S A F			D C F
	1	2	3	5	4	6	7	8	9	10	11	12	17	13	14	15	16
Crescent Honeyeater				✓		✓	(✓)	✓	✓	✓	✓	✓		✓	✓	✓	✓
New Holland Honeyeater	✓																
Eastern Spinebill						✓	✓	✓	✓	✓	✓	✓			✓		
Spotted Pardalote	✓	✓	✓	✓	✓	✓		✓						✓	✓	✓	
Striated Pardalote	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓					✓	✓	
Silvereye		✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓		✓	✓	✓	
European Goldfinch	✓	✓															
European Greenfinch	✓				(✓)												
Beautiful Firetail	(✓)		(✓)		(✓)	✓										(✓)	
Dusky Wood-swallow	✓		✓														
Black Currawong							✓	✓	✓	✓	✓	✓		✓	✓	✓	✓
Grey Currawong	✓	✓	(✓)	✓		✓											
Forest Raven	✓	✓	✓	✓	✓	✓			(✓)		✓			✓		✓	

Comparison of vertical stratification in wet sclerophyll,
mixed and temperate rainforest.

SPECIES	FORMATION	N	OCCURRENCE %		
			HERB	SHRUB	TREE
Brown Scrubwren	Wet sclerophyll	250	87	13	0
	Mixed	56	89	11	0
	Rainforest	30	77	23	0
Scrubtit	Wet sclerophyll	37	22	75	3
	Mixed	36	19	81	0
	Rainforest	28	29	71	0
Tasmanian Thornbill	Wet sclerophyll	234	14	74	12
	Mixed	83	8	61	31
	Rainforest	59	3	78	19
Grey Fantail	Wet sclerophyll	287	13	60	27
	Mixed	38	8	66	26
	Rainforest	24	12	59	29
Crescent Honeyeater	Wet sclerophyll	319	9	48	43
	Mixed	36	6	42	52
	Rainforest	30	0	80	20
Green Rosella	Wet sclerophyll	89	12	25	63
	Mixed	29	7	10	83
Pink Robin	Wet sclerophyll	74	19	80	1
	Mixed	17	0	94	6
Olive Whistler	Wet sclerophyll	66	20	78	2
	Mixed	10	0	90	10
Striated Pardalote	Wet sclerophyll	113	0	1	99
	Mixed	38	0	0	100

A = air, G = ground, H = herb, Li = litter, Tr = trunk
B = branch, Tw = twig, L = leaf, F = flower.

[illegible]

APPENDIX 16

Overlaps in patch preference, α'_H .

APPENDIX 16

Overlaps in patch preference, α_n .

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[illegible]

Overlaps in vertical stratification, α_v .

[REDACTED]

Overlaps in feeding behaviour, α'_F .

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Overlaps in feeding behaviour, α_F .

[illegible]

APPENDIX 19 .

Community matrix for Tasmanian temperate rainforest.

APPENDIX 19

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Community matrix, based on summation alpha, for Tasmanian temperate rainforest

[illegible]

Community Matrix, based on α , for temperate rainforest

[illegible]

Feeding behaviour in dry sclerophyll (DS) and temperate rainforest. The data for rainforest were obtained from all wet formations.

A = air, G = ground, H = herb, Lt = litter, Tr = trunk,
B = branch, Tw = twig, L = leaf, F = flower.

SPECIES	FORMATION	N	OCCURRENCE %								
			A	G	H	Lt	Tr	B	Tw	L	F
Brown Scrubwren	DS (summer)	173		18	28	33	14	4	2		
	DS (winter)	14		29	21	50					
	Wet forms.	783	+	27	14	49	4	3	1	2	
Green Rosella	DS (summer)	20		5			10		35	50	
	Wet forms	81		9			7	6	33	23	21
Shining Bronze Cuckoo	DS (summer)	19					11	84	5		
	Wet forms	62			2	3	15	68	5	8	
Golden Whistler	DS (summer)	155	3	+			+	9	11	76	
	DS (winter)	277	3	+	+		2	13	21	60	
	Wet forms	62	2				2		8	88	
Grey Shrike-thrush	DS (summer)	175		2			35	55	6	2	
	DS (winter)	141		11		6	45	32	1	4	
	Wet forms	94		12		3	49	34	1	1	
Grey Fantail	DS (summer)	623	47	3	13	+	3	3	4	27	
	DS (winter)	251	73				1	+	3	21	+
	Wet forms	850	47	4	1	4	4	3	12	25	+
Yellow-throated Honeyeater	DS (summer)	934	8	1	2	+	20	38	11	12	7
	DS (winter)	824	8	1	+	+	28	45	10	5	+
	Wet forms	584	9	4		1	37	26	11	9	4
Crescent Honeyeater	DS (summer)	565	8	+	6	+	11	25	36	9	3
	DS (winter)	373	4	+			6	35	18	14	23
	Wet forms	465	8	2	1	1	35	15	16	9	14
Eastern Spinebill	DS (winter)	763	7	+	2	1	+	+	3	10	75
	Wet forms	1040	8	+	2	1	1	+	3	12	73
Silvereye	DS (summer)	341	1		29		6		10	52	1
	DS (winter)	29								66	34
	Wet forms	224			+	2				94	4

APPENDIX 21

Food and foraging behaviour of birds in temperate rainforest in northern New South Wales. Based on data in Goodwin (1967), Frith (1969), Gilliard (1969), Officer (1969) and McGill (1970).

<u>SPECIES</u>	<u>FOOD</u>	<u>FORAGING</u>
Grey Goshawk	V & I	Active pursuer. Diurnal.
King Parrot	S & F	Mainly in the canopy.
Crimson Rosella	S & F	At all levels.
Fan-tailed Cuckoo	I	Pursuer.
Shining Bronze Cuckoo	I	Pursuer.
Spotted Owl	I & V	Nocturnal. Pursuer.
Superb Lyrebird	I	Scratches in litter.
Scaly Thrush	I	On ground.
Brown Warbler	I	Foliage & hover gleaner.
Rose Robin	I	Pursuer. Lower strata & ground.
Eastern Yellow Robin	I	Pursuer. Mainly on ground.
Olive Whistler	I	Pursuer. Lower strata.
Golden Whistler	I	Pursuer. Upper strata.
Grey Shrike-thrush	I	? . Mainly on ground.
Black-faced Monarch	I	Pursuer. Hover gleaner.
Rufous Fantail	I	Pursuer. Hover gleaner.
Grey Fantail	I	Pursuer. Aerial hawk.
Spine-tailed Chowchilla	I	Scratches in litter.
Eastern Whipbird	I	On ground and in herb layer.
Large-billed Scrubwren	I	Low trees and undergrowth.
Yellow-throated Scrubwren	I	Ground feeder.
White-browed Scrubwren	I	Ground and low shrubs.
Brown Thornbill	I	Foliage gleaner. Shrubs.
Striated Thornbill	I	High in foliage.

White-throated Treecreeper	I	Bark.
Red Wattlebird	I & N	Canopy.
White-eared Honeyeater	I & F	Canopy.
Eastern Spinebill	N & I	Lower strata.
Spotted Pardalote	I	Outer foliage of trees.
Silvereye	I	From twigs & leaves at all heights. Also eats fruits.
Satin Bowerbird	F	On or near ground.
Green Catbird	F	Shrubs & trees.
Pied Currawong	O	All levels.
<u>Corvus</u> sp.	O	Ground.

FOODS : F - fruits
I - invertebrates
N - nectar
O - omnivorous
S - seeds
V - vertebrates

Species recorded in temperate rainforest in the Macpherson Ranges, Queensland.

	<u>GREEN MOUNTAIN</u>	<u>TULLAWALLAL</u>
	(Apr. 1977)	(Nov. 1977)
Brush Turkey	x	
White-headed Pigeon		x
Brown Pigeon		x
Yellow-tailed Black Cockatoo	x	
King Parrot	x	
Crimson Rosella	x	x
Fan-tailed Cuckoo		x
Shining Bronze Cuckoo	x	x
Noisy Pitta	x	
Albert's Lyrebird	x	
Rufous Scrub-bird	x	
Scaly Thrush	x	x
Brown Warbler	x	x
Eastern Yellow Robin	x	x
Olive Whistler		x
Golden Whistler	x	x
Grey Shrike-thrush	x	x
Black-faced Monarch		x
Rufous Fantail		x
Grey Fantail		x
Spine-tailed Chowchilla	x	x
Eastern Whipbird	x	x
Large-billed Scrubwren		x
Yellow-throated Scrubwren	x	x
White-browed Scrubwren	x	x
Brown Thornbill	x	x

	<u>GREEN MOUNTAIN</u>	<u>TULLAWALLAL</u>
Striated Thornbill	x	x
White-throated Treecreeper		x
Red Wattlebird		x
Lewin's Honeyeater	x	x
Eastern Spinebill	x	x
Spotted Pardalote		x
Silvereye	x	x
Satin Bowerbird		x
Green Catbird	x	x
Paradise Riflebird		x
Pied Currawong	x	x
Torresian Crow		x
TOTALS	24	32

Total species : 38

Species occurring in wet sclerophyll forest in the Otways and temperate and subtropical rainforest in New South Wales and Queensland. * - species occurring in Tasmania.

	VIC	NSW		Q'd	
	WS	TRF	STRF	TRF	STRF
Crested Hawk					X
Grey Goshawk	*				*
Brown Goshawk	*				*
Collared Sparrowhawk	*				
Wedge-tailed Eagle					*
Peregrine Falcon	*				
Brush Turkey			X	X	X
Red-crowned Pigeon					X
Purple-crowned Pigeon					X
Wompoo Pigeon					X
Topknot Pigeon			X		X
White-headed Pigeon			X	X	X
Brown Pigeon			X	X	X
Green-winged Pigeon					X
Wonga Pigeon					X
Yellow-tailed Black Cockatoo	*		*	*	*
Gang-gang Cockatoo	X				
Sulphur-crested Cockatoo	*	*	*		*
King Parrot		X	X	X	X
Crimson Rosella	*	*	*	*	*
Brush Cuckoo					X
Fan-tailed Cuckoo		*	*	*	*
Shining Bronze Cuckoo		*	*	*	*
Spotted Owl	*	*	*		*
Barking Owl					X
Powerful Owl					X
Tawny Frogmouth	*				*
Owlet-nightjar					*
Kookaburra	X	X	X		X
Noisy Pitta				X	X
Albert's Lyrebird				X	X
Superb Lyrebird		X	X		
Rufous Scrub-bird				X	X
Black-faced Cuckoo-shrike	*				
Yellow-eyed Cuckoo-shrike					X
Cicada-bird					X
Varied Triller					X
Scaly Thrush	*	*	*	*	*
Rose Robin	X	X	X		X
Pink Robin	*				
Flame Robin		*			
Eastern Yellow Robin	X	X	X	X	X
Pale Yellow Robin			X		X
Crested Shrike-tit	X				X
Olive Whistler	*	*		*	*
Golden Whistler	*	*	*	*	*
Rufous Whistler		X			
Rufous Shrike-thrush					X
Grey Shrike-thrush	*	*	*	*	*

	VIC	NSW		Q'd	
	WS	TRF	STRF	TRF	STRF
Black-faced Monarch		X	X	X	X
Spectacled Monarch			X		
White-eared Monarch					X
Leaden Flycatcher					X
Satin Flycatcher	*				
Rufous Fantail	X	X	X	X	X
Grey Fantail	*	*	*	*	*
Spine-tailed Chowchilla		X	X	X	X
Eastern Whipbird		X	X	X	X
Superb Blue Wren	*				
Large-billed Scrubwren		X	X	X	X
Yellow-throated Scrubwren		X	X	X	X
White-browed Scrubwren	*	*	*	*	*
Weebill			X		
Brown Warbler		X	X	X	X
Brown Thornbill	*	*	*	*	*
Striated Thornbill	X	X	X	X	
White-throated Treecreeper	X	X	X	X	X
Red-browed Treecreeper		X			
Red Wattlebird		*		*	
Bell Miner					X
Lewin's Honeyeater			X	X	X
Yellow-faced Honeyeater		X			
Brown Honeyeater	X				
White-naped Honeyeater	*				
Crescent Honeyeater	*				
Eastern Spinebill	*	*	*	*	*
Scarlet Honeyeater					X
Mistletoe-bird					X
Spotted Pardalote		*		*	*
Silvereye		*	*	*	*
Red-browed Finch	X				X
Olive-backed Oriole	X				
Spangled Drongo					X
Satin Bowerbird	X	X	X	X	X
Australian Regentbird					X
Green Catbird		X	X	X	X
Paradise Riflebird				X	X
Pied Currawong	*	*	*	*	*
Grey Currawong	*				
Torresian Crow		X		X	X
Forest Raven	*				

Food and feeding behaviour of birds in temperate rainforest in southern Queensland not occurring in northern New South Wales. Sources as for Appendix 21.

SPECIES	MAIN FOOD	FEEDING BEHAVIOUR
Brush Turkey	Invertebrates	Feeds on ground
White-headed Pigeon	Fruits	In trees or on ground
Brown Pigeon	Fruits	At all levels
Yellow-tailed Black Cockatoo	Invertebrates	Obtains much food from bark
Noisy Pitta	Invertebrates	Feeds on ground
Albert's Lyrebird	Invertebrates	Feeds on ground
Rufous Scrub-bird	Invertebrates	Feeds on ground
Lewin's Honeyeater	Invertebrates & Fruits	Feeds mainly in the canopy
Paradise Riflebird	Invertebrates	Obtained from under loose bark

Overlaps in vertical stratification and feeding behaviour
in forests on Little Barrier Island, New Zealand.

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APPENDIX 25

Overlaps in vertical stratification in forests on Little Barrier Island
Calculated from data in Gravatt (1971)

	Tui	Bellbird	Stitchbird	Grey Warbler	Whitehead	Fantail	Pied Tit	Rifleman	Robin	Kaka	Red-crowned Parrakeet	Yellow-crowned Parrakeet
	1	2	3	4	5	6	7	8	9	10	11	12
1 Tui	1.00	0.51	0.59	0.52	0.56	0.11	0.20	0.22	0.07	0.63	0.70	0.73
2 Bellbird		1.00	0.72	0.49	0.78	0.59	0.47	0.46	0.14	0.51	0.71	0.46
3 Stitchbird			1.00	0.72	0.72	0.39	0.34	0.32	0.12	0.35	0.80	0.66
4 Grey Warbler				1.00	0.60	0.16	0.25	0.27	0.09	0.32	0.71	0.65
5 Whitehead					1.00	0.43	0.43	0.53	0.13	0.45	0.81	0.61
6 Fantail						1.00	0.36	0.70	0.12	0.28	0.29	0.04
7 Pied Tit							1.00	0.37	0.70	0.27	0.40	0.23
8 Rifleman								1.00	0.12	0.31	0.40	0.15
9 Robin									1.00	0.07	0.14	0.10
10 Kaka										1.00	0.53	0.41
11 Red-crowned Parrakeet											1.00	0.76
12 Yellow-crowned Parrakeet												1.00

Overlaps in feeding behaviour in forests on Little Barrier Island. Calculated from data in Gravatt (1971)

	Tui	Bellbird	Stitchbird	Whitehead	Pied Tit	Grey Warbler
Tui	1.00	0.31	0.45	0.89	0.42	0.49
Bellbird		1.00	0.07	0.43	0.30	0.09
Stitchbird			1.00	0.44	0.23	0.84
Whitehead				1.00	0.43	0.48
Pied Tit					1.00	0.25
Grey Warbler						1.00

APPENDIX 26

Comparison of species recorded in censuses of small areas in Chile (Cody 1970) and Patagonia (Vuilleumier 1972).

SPECIES RECORDED IN CHILE AND PATAGONIA (15)

Sephanoides sephanoides
Colaptes pitius
Dendrocopus lignarius
Campephilus magellanicus
Aphrastura spinicauda
Pygarrhichas albogularis
Pteroptochus tarnii
Scelorchilus rubecula
Scytalopus magellanicus
Elaenia albiceps
Tachycineta leucopyga
Troglodytes aedon
Turdus falcklandii
Curaeus curaeus
Spinus barbatus

SPECIES ABSENT FROM PATAGONIA (7)

Milvago chimango
Sylviornithorhynchus desmursii
Anaeretes paralus
Bubo virginianus
Microsittace ferruginea
Coragyps atratus
Columba araucana

SPECIES ABSENT FROM CHILE (5)

Geranoaetus melanoleucus
Buteo polysoma
Enicognathus ferrugineus
Pyrope pyrope
Phyrgilus patagonicus