

CHAPTER 1

INTRODUCTION

1. Darwin (1859) raised the topic of interspecific competition under the title of 'the struggle for existence'. Unfortunately, for many years thereafter competition was generally understood to mean physical conflict between species, a concept which Darwin's writings were not intended to convey, instead of being 'more often reflected in peaceful coexistence or in permanent exclusion than in running warfare' (Diamond 1978). Competition is said to occur: 'when a number of animals (or plants) utilize common resources, the supply of which is short relative to the demand, or when animals seeking a resource nevertheless harm one another in the process' (Birch 1957). It was many years after Darwin's statement until study into competition was undertaken. This should not be surprising. The emphasis in biology then was necessarily on describing new species (taxonomy) rather than finding out what the species did.

2. Various naturalists independently arrived at the conclusion that different species in one locality occupied different microhabitats or foraged in different ways (Steere 1894; Grinnell 1904, 1914; Lack 1944; Elton 1946). Grinnell seems to be the originator of the term 'niche' to describe the place and role of a species in its habitat. Differences in species' niches apparently enabled them to co-exist. Haldane (1924) and Volterra (1926) predicted theoretically that two species whose ecology is identical cannot co-exist. Later laboratory scientists, in experiments with insects and micro-organisms, found that species which thrived when on their own were sometimes unable to survive if cultured with related species (e.g. Gause 1934, Crombie 1946).

3. Gause's Principle, or the Competitive Exclusion Principle (Hardin 1960), which arose from these theoretical, natural and laboratory observations, stated that if the niches of two species are very similar, they cannot co-exist. Attempts have been made to mathematically describe niches (e.g. Hutchinson 1958, Levins 1968, MacArthur 1968). Numerous studies have compared the niches of similar species in one area (Schoener 1974) but their frequent conclusion, that species' niches arose out of

competition with other species, have been arrived at mainly by inference. Several workers have criticized the evidence as unconvincing (e.g. Andrewartha and Birch 1955, Williamson 1972, Connell 1975). There are numerous examples of a species occupying a niche far broader in the absence of a potentially competing species than when they co-occur (e.g. Mayr 1931, Lack 1947, Brown and Wilson 1956, Crowell 1962, Diamond 1975). The critics claim that niche shift may arise because changes (e.g. climatic) unconnected with presence or absence of competitors, have taken place. Nevertheless the wealth of examples is so overwhelming that as Diamond (1978) says 'the objections strain one's credulity'.

4. Where one species denies another species access to a resource by attack or threat this is termed 'interference competition' (e.g. Ripley *et al.* 1959, Miller 1967, Wolf 1978). However, most competition (particularly in theoretical models) is assumed to be 'exploitation competition', where species deplete a common resource. The species that is able to exploit the resource more efficiently survives (e.g. *Parus caeruleus* vs *P. cyanus*, Vaurie 1957; pheasants, Phasianidae vs megapodes, Megapodiidae, Olson 1980). It must not be forgotten that competition may not necessarily be between species in the same Class; competition may take place, for example, between birds and such diverse groups as bats (Fenton and Fleming 1976), lizards (Wright 1979) and spiders (Pearson 1977).

5. Evidence for competition has been obtained by the following methods, which I suggest range from weakest to strongest in their direct evidence for competition:

- a. Measurement of 'niche overlap' i.e. the degree of similarity between two species, either of their diets or of some aspects of their foraging behaviour, demonstrating relationships between overlaps and niche shifts and/or changes in population density (e.g. Schoener 1975, Cody and Walters 1976, Holmes *et al.* 1979).

- b. Documentation of niche expansion in the absence of potential competitors, often demonstrated in depauperate communities on islands and ecological displacement in areas of sympatry (e.g. Keast 1968, Lack 1971, Diamond and Marshall 1977).
- c. Measurement of depletion of resources being used by several species has been carried out mainly on nectarivores (e.g. Ford and Paton 1982) probably because the resource lends itself to quantification.
- d. Laboratory experiments that compare the survival and size of populations of species by themselves and in competition (e.g. Colwell and Fuentes 1975, with mites; Connell 1975, with barnacles; Grant 1972 with rodents).
- e. Field experiments where populations can be manipulated, e.g. Inger and Greenberg (1966) with frogs; Dhondt (1977) on titmice, Paridae; and Högstedt (1980) on magpies *Pica pica*. Such experiments are difficult and hence have not been carried out frequently.

6. Lack (1947) and Svårdson (1949) proposed that, if the interspecific competition determines the partitioning of resources between species, co-existence should result in divergence in diet as food becomes scarce. Each species should specialise in its diet according to its morphological adaptations i.e. towards those foods that each species can exploit most efficiently. Conversely, Svårdson (1949), MacArthur and Pianka (1966) and others have postulated that as intraspecific competition should be stronger than interspecific competition then a species should, in time of scarcity, broaden its diet. Another way of viewing the problem is in terms of optimal foraging theory: as food becomes scarce an individual should then take a wider range of types regardless of what other species are doing (Krebs and Davies 1981).

7. Diets of insectivorous birds are more difficult to determine than those of most other groups, such as granivores or piscivores, because every method of sampling insectivorous diets is subject to bias. Direct observations are biased towards the larger and more easily observed

prey and those that are processed before swallowing. Analysis of stomach contents is biased towards the less easily digested items (Hartley 1948). Inferring overlap between potentially competing species from diet alone is fraught with danger, not only because there are biases, but because even if diets were similar they may have been obtained, by the species being compared, from quite distinct and mutually inaccessible sources. Accordingly, inference of overlaps for insectivorous birds is more often arrived at by comparing the behaviour involved in foraging for insects. Variables measured may include height, substrate foraged upon, plant species foraged upon, foraging technique and time of day.

8. One variable considered to be of great importance as an ecological separating mechanism is that of size. Hutchinson (1959) proposed that two species in the same trophic level can avoid competition and co-exist if the ratio of their sizes or the ratio of their trophic apparatuses (e.g. beaks) is sufficiently large (greater than 1.2). Since then numerous workers have presented examples of such ratios (e.g. Ricklefs 1973, Pianka 1978) but recently Simberloff and Boecklen (1981) have questioned the representativeness of the data. Certainly, proponents have tended, when quoting examples, to ignore other examples where size differences are small. Diamond (1973) provides a well-known example of size-ratios in sympatric fruit-doves, *Ptilinopus* spp. However several groups of insectivorous congeners occur in the same localities (*Rhipidura* spp., *Gerygone* spp., *Sericornis* spp.) where species pairs differed by less than 1.2. From my own studies in New Guinea (Bell 1977) I established that size was of much less importance than the height of foraging in separating insectivores. However with frugivores, whose food was all concentrated at the same height (the jungle canopy) size ratios were indeed the most important factor. Of course, among insectivores, an Australian Raven *Corvus coronoides* weighing 600 g is likely to take different prey from a thornbill of only 7g weight. But many small insectivorous passerines probably eat much the same range of items and may differ only in that they take those things by different methods and in different places. Therefore,

when studying resource-partitioning among small insectivores such variables as foraging techniques, substrate foraged upon and height may be more useful indicators of separation than mere size or even, given sampling bias, of diet itself.

9. Pianka (1978) proposed that the maximum overlap 'tolerable' between co-existing species should be lower when resources are scarce. This has been demonstrated in field studies on lizards (Pianka 1974), rodents (Brown 1975) and birds (Rusterholz 1981).

10. Smith *et al.* (1978) pointed out that, although many studies had been made of resource-partitioning between potentially competing species, only eleven had measured overlap in times of both abundance and scarcity of food. Schluter (1981) and Schoener (1982) later extended the list of known studies to 27. In 25 overlap was less when food was scarce. In only two was overlap greater in times of scarcity but in one of these (Ulfstrand 1977) the situation seems confused by considering insectivores and granivores together. Despite extensive search, I have been unable to find any published study in which both overlap and the abundance of food has been measured on a continuous year-round basis.

11. The social organisation of species has a direct bearing on their foraging behaviour, and should be investigated in any study of resource-partitioning* (e.g. Thompson *et al.* 1974), or to take certain prey (e.g. Hespenheide 1975) or to feed in exposed situations (e.g. Goldman 1980); thus differences in groupings of species under study may be linked to their foraging behaviour. A further extension of grouping is participation in mixed-species feeding flocks, membership of which may enable a species to forage in ways not otherwise possible (e.g. Krebs 1973) or confer the advantages of flocking on a species that does not live in intraspecific flocks (e.g. Thompson *et al.* 1974). The spatial organisation of each species can be linked to their foraging ecology such as in exclusion of intraspecific competitors (e.g. Snow 1956) and in quality of territory (e.g. Brown and Balda 1977).

12. In Australia studies on resource partitioning are in their infancy. Indeed, a more pressing need is for basic life-history studies, few of

*:Changes in size of foraging parties may enable species to feed in otherwise inaccessible locations,

which have been done, even for the commonest species (Rowley 1974). Most studies on resource-partitioning in Australia have been on the honeyeaters, Meliphagidae (e.g. Keast 1968; Recher and Abbott 1970; Recher 1971, 1977; Ford and Paton 1976, 1977; Halse 1978; Thomas 1980a) but some recent studies have been made on obligate insectivores, namely fantails *Rhipidura* spp. (Cameron 1975), scrub-wrens *Sericornis* spp. (Keast 1978), tree-creepers *Climacteris* spp. (Noske 1978), or on whole communities in rainforest (Crome 1978, Thomas 1980b) and eucalypt forest (Wooller and Carver 1981). I decided to study thornbills *Acanthiza* spp. because three or more species can be found together in most areas. Also, though they are common and familiar birds little has been found out about most of them since Gould's (1865) great work of the last century.

13. Thornbills are a genus of small (ca. 7-10g) insectivores, similar in habits to titmice Paridae and kinglets *Regulus* spp. of the Northern Hemisphere. Sibley and Alquist (1982), using DNA hybridisation, have indicated that thornbills, once believed to be sylviids, are part of an old Australian passerine stock which has radiated to fill niches occupied elsewhere by other families. Their close relatives include fairy-wrens *Malurus* spp., scrub-wrens *Sericornis* and, more distantly, the honeyeaters Meliphagidae. *Acanthiza* is predominantly found in the Temperate Zone, major extensions into the tropics being mainly in cool montane forests of Queensland and New Guinea. Although the taxonomy of thornbills has received little modern attention there appear to be three superspecies: the *A. lineata-nana* group of arboreal feeders; the *pusilla* group currently regarded as six species, all shrub-dwelling; and the *reguloides* group of five species which tend towards ground-foraging. One of each group (*A. lineata*, *A. pusilla* and *A. reguloides*) occurred in my study area. What little was known of their habitat, social organisation and ecology is summarized by McGill (1970), Frith (1969, 1976) and MacDonald (1973). The breeding biology of one species *A. chrysorrhoa* has been studied (Ford 1963); otherwise there are no accounts of field studies specifically on thornbills. The best anecdotal account of habits is that of Roberts and Jarvis (1922).

14. The overall aim of the study was to compare the ecology of these three species of thornbills. In particular I quantified their foraging behaviour (foraging substrate, plant species, height, method and speed), social organisation (group size, breeding behaviour and success, mortality and associations with other species), and food. In addition I measured the abundance of arthropods in sites from which thornbills took their food. The major questions asked were:

- a. How do they differ in foraging ecology?
- b. How do they differ in the food they eat?
- c. How are these ecological differences related to morphological differences between the species?
- d. Did the species differ most in their foraging ecology when food was most scarce?
- e. Were breeding and mortality related to relative abundance, and scarcity of food, respectively?
- f. Could differences in foraging ecology explain the differences in social organisation (or vice versa)?

15. This dissertation is divided into four parts. Part I (Chapters 2-4) describes the environment in which the three species of thornbills live: the climate, vegetation, availability of food and the bird community of which thornbills are a part. Part II (Chapters 5 and 6) describes the social organisation of each species and their interactions with each other and with other species in feeding associations. Part III (Chapters 7-12) presents the feeding data on which the account is based. Chapters 7-10 discuss the differences between species in use of substrate, plant species, height and foraging methods. Chapter 11 compares the diet of the three species and Chapter 12 deals with morphological differences between them. Part IV (Chapters 13 and 14) compares, in Chapter 13, foraging overlap by time with abundance of food, changes in social organisation, breeding and mortality. Chapter 14 is a summary.

PART I

ENVIRONMENT, AVAILABILITY OF FOOD, AND THE BIRD COMMUNITY

CHAPTER 2

THE ENVIRONMENT

INTRODUCTION

16. I required study areas that had at least three resident species of thornbills *Acanthiza*, where the vegetation and avifauna were already fairly well-known, and where human activity was unlikely to disturb the area during the period of study. Three sites were selected, Eastwood State Forest, Stringybark Hill (near Armidale) and the Wollomombi Falls Reserve. After three months it became apparent that I could only cope with a single site. Wollomombi was finally selected because the vegetation and avifauna were already under study (Noske 1976), and because the local land-holder was co-operative and also kept local rainfall records. Five species of thornbill occurred at Wollomombi: the Brown *Acanthiza pusilla*, Buff-rumped *A.reguloides*, Striated *A.lineata*, Yellow-rumped *A.chrysoorrhoa* and Yellow *A.nana*. The last was a rare vagrant while the Yellow-rumped, although resident, was not syntopic with the remaining three; it occurred only in grazing land adjacent to the study area and rarely occurred with the others.

Several aspects of the environment at Wollomombi were measured. These were the vegetation on which the thornbills foraged and the climatic conditions affecting food supply.

THE STUDY AREA

17. The site was the Wollomombi Falls Recreation Reserve (30° 32'S, 152° 02'E; altitude 920m), 42 km East by road from the city of Armidale. The actual study area was a relatively flat plateau on a spur running South into the gorges of the Macleay River system. The edges of the plateau fell away sharply in a combination of escarpments and very

steep slopes. Owing to this steepness the study was confined to the plateau with only occasional visits into the gorge. To the North the study area was bounded by 'Rosewood', a grazing property from which most trees had long been removed. To the East the spur joined another, known as Quail Thrush Spur which was included in the study areas of Noske (1978) and Huddy (1979) who were both concurrently studying at Wollomombi. Figure 1 depicts the study area.

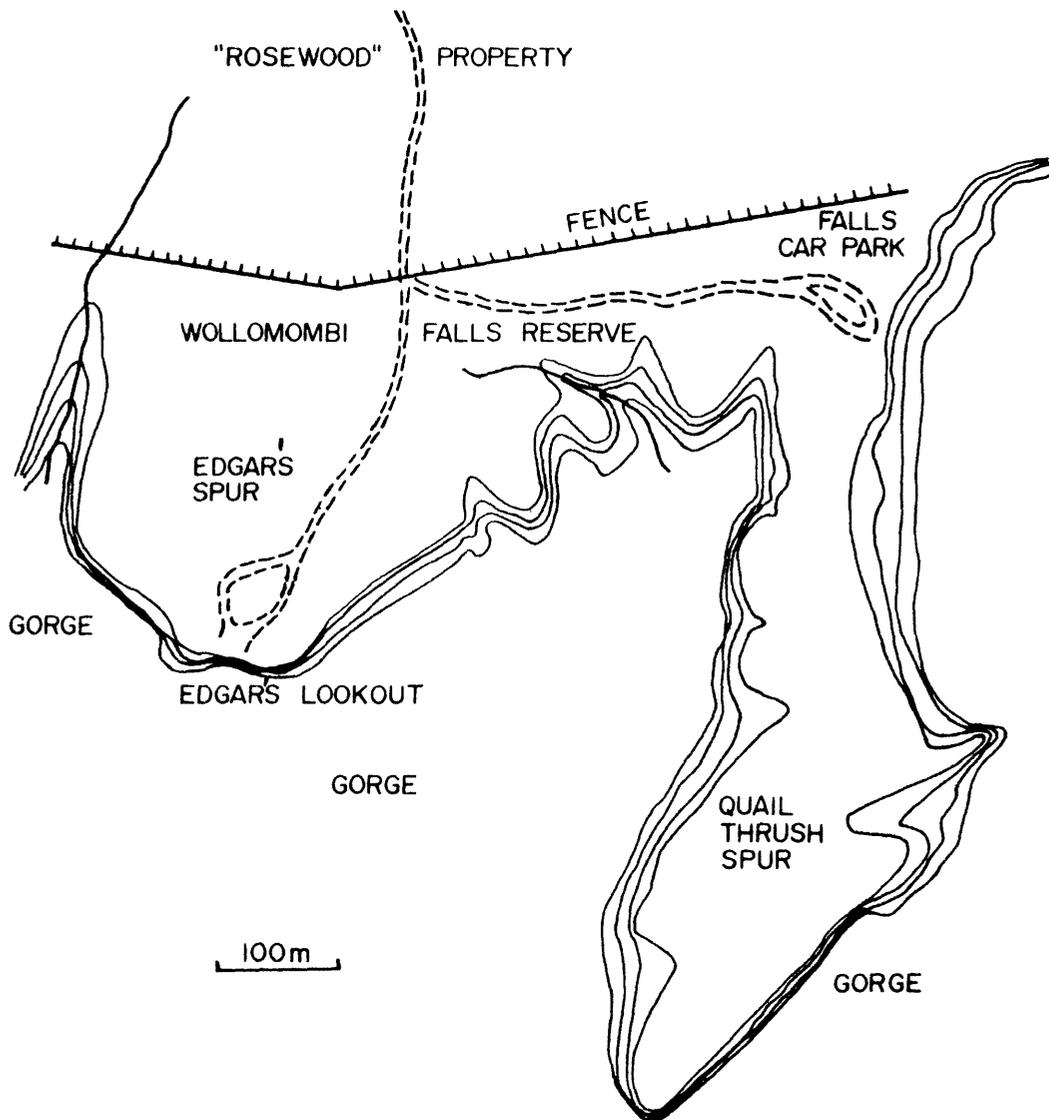
18. The study area was *ca.* 25 ha in extent. The size was intended to encompass the home range of at least one flock of thornbills of each species. The area was mapped from the EBOR 1:100,000 sheet, Australian National Topographic Series, and from aerial photographs obtained from the Lands Department of New South Wales. Detail was mapped by triangulation using prismatic compass and pacing (*vide* Anon 1955). To facilitate later spot-mapping of observations I mapped a series of easily-seen reference points, and all mist-net sites.

19. The soil is Yellow Podzolic on Paleozoic basement rocks (Lea *et al.* 1976). Little surface rock occurs. On the North-west boundary of the study area a shallow gully has a friable soil, presumably because it has accumulated organic debris and top-soil washed from higher grazing land. The area was rough-grazed, fairly heavily, for almost a century until gazetted as a reserve (R.W. Edgar, pers. comm.) and although much regeneration of tree species and some shrubs has occurred, soils appear to be compacted with many patches of bare 'hard-pan'. Thus, water absorption seems to be impeded but, conversely, water retention appears to be high. No permanent surface water exists in the study area. Two streams (see Figure 1) run after heavy rain. The stream on the North-west boundary held some water in pools except at the height of drought.

20. Data on rainfall were taken from the records of Mr R.W. Edgar, of 'Rosewood', Wollomombi, who has kept official records for over forty years. All other climatic data came from readings at the official Armidale weather station. Temperature readings at Wollomombi closely match those at Armidale (R.W. Edgar, pers. comm.) but rainfall may differ in some years. Rainfall data from Wollomombi were supplied to Mr H.A. Nix,

Figure 1

Study areas at Wollomombi Falls Reserve of R.A. Noske and L. Huddy
(Edgar's Spur and Quail Thrush Spur) and H.L. Bell (Edgars Spur)



Principal Research Scientist, CSIRO Division of Water and Land Resources, who, using them, and data on other climatic variables taken at Armidale, constructed a Plant Growth Index (PGI), to cover the study period (September 1978 to August 1981). The CSIRO PGI programme takes into account rainfall, evaporation, temperature, solar radiation and day-length (Fitzpatrick and Nix 1970). I also recorded a Leaf Growth Index (see paragraph 26).

21. Mean monthly rainfall (forty year average) and rainfall during the years of study (1978) to 1981) are given in Figure 2. The rainfall at Wollomombi averages at 822 mm annually. There is usually a peak in summer with higher values for November to February. However much of this summer rainfall depends on cyclonic disturbances which in some years, including all those of my study, do not occur. Rainfall for the study period was seriously deficient in the second and third years (1979/80 and 1980/81). Only eight out of 36 months of the study show above average rainfall.

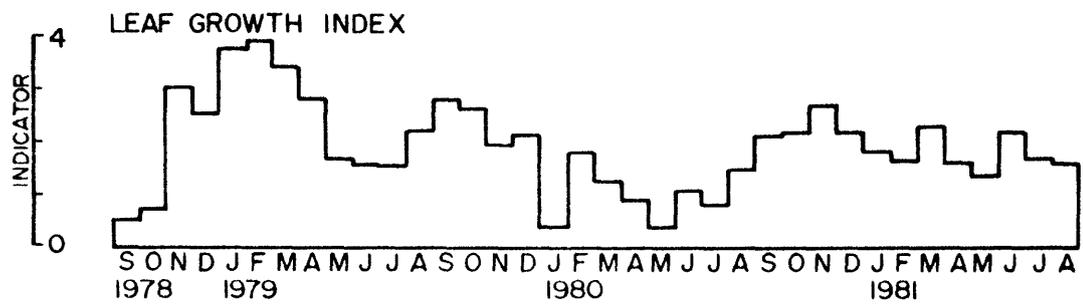
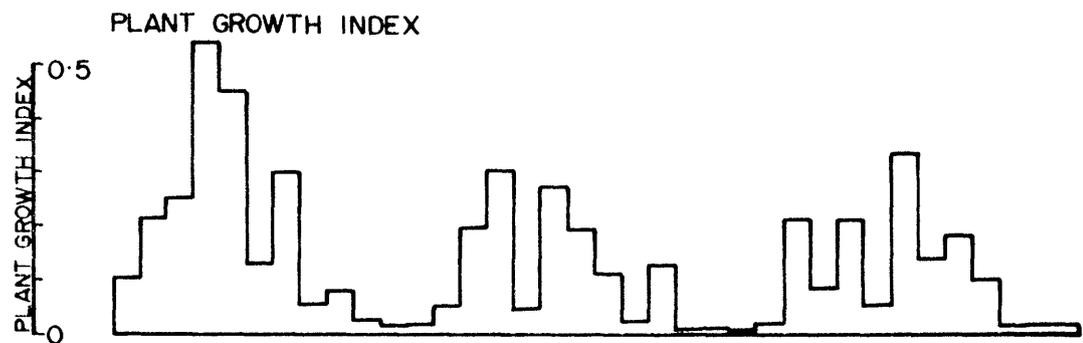
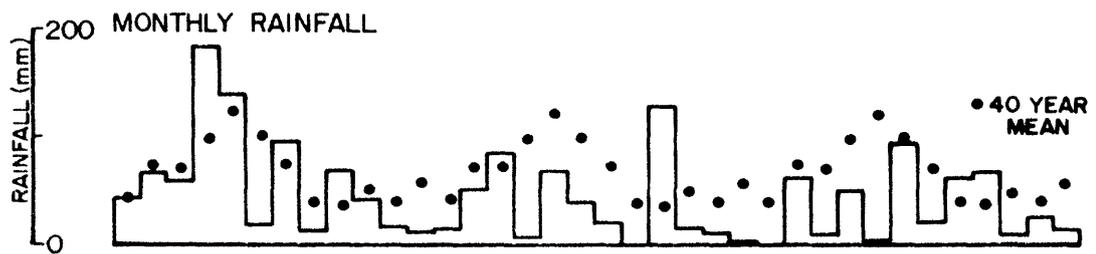
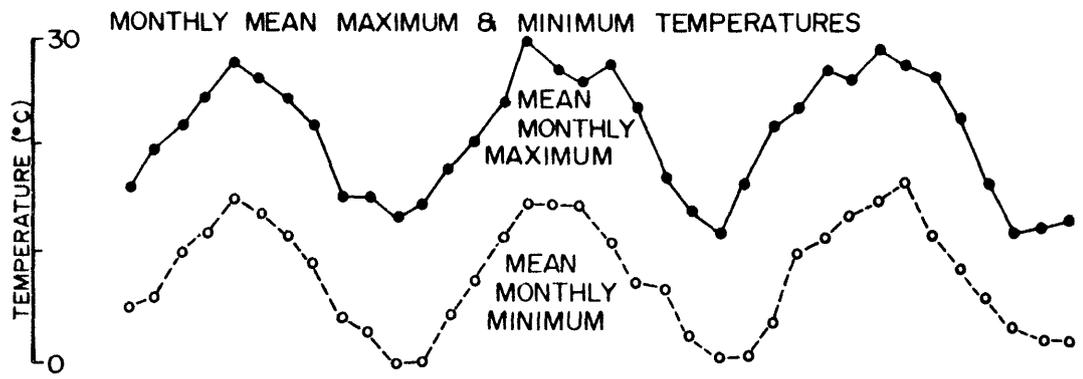
22. Mean temperatures and those for the study period for Armidale are also given in Figure 2 and I believe that these generally reflect the situation at Wollomombi. May to September show average temperatures of 10°C or less and during June, July and August temperatures often fall below freezing each night, and may fall as low as -13°C at grass level (R.W. Edgar pers. comm.). Owing to the absence of cloud, the winters of 1980 and 1981 tended to have warmer days than those of 1978 and 1979, when cold days (i.e. $< 10^{\circ}\text{C}$) combined with strong winds were not infrequent.

23. The Plant Growth Index (PGI) produced by CSIRO Division of Water and Land Resources, is given in Figure 2. The actual print-out is by weeks but because my other data are by months, the weekly data for PGI are converted to an average for each month. The Leaf-growth Index (see paragraph 26) is also given in Figure 2, and consists of all the data from all plant species combined, weighted to the proportion that each plant species contributed to the overall volume of foliage (Table 3). The monthly values for leaf-growth do not correlate with those of the PGI, but do correlate with PGI values for each preceding month (Spearman

Figure 2

Mean monthly maximum and minimum temperatures, monthly and mean monthly rainfall, monthly Plant Growth Index and monthly Leaf Growth Index at Wollomombi Falls Reserve (September 1978 to August 1981)

(PGI see para 20; LGI see para 26)



Rank Correlation, $r: 0.518, P: < 0.01$). As can be seen in Figure 2 plants grew better in the first year than in the second and third years.

VEGETATION

Method

24. My aims, to study the plant species, and substrate used, and tree height frequented by thornbills when foraging, determined how I assessed the vegetation. I measured: the proportion of canopy cover, at each height level, contributed by each plant species; differences in substrate offered by each species to a foraging thornbill; and any variation in the distribution and composition of vegetation between the territories or home ranges of different pairs or groups of thornbills. Because I had observed, in my preliminary observations, that ground-feeding thornbills almost never foraged on grasses or herbs, but usually foraged on bare ground, I placed less emphasis on gathering data from the ground layer. Vegetation was assessed by the following methods:

a. Line transect interception technique (McIntyre 1953, Cox 1967).

I plotted a grid, with lines 10 m apart and running North-South and East-West across the map of the study area, I then selected grid-lines from a table of random numbers and used them as transect lines. Direction was maintained by prismatic compass and distance recorded by pacing (1 pace: 0.75 m). Total transects covered totalled 14720 m. Each intercept of a tree or shrub canopy was recorded. For each intercept data recorded were: species, height of the whole plant and not just that part intercepted (taken by clinometer), depth of the canopy at its deepest point (also taken by clinometer), and for trees the diameter of the trunk at breast height (dbh). From these data I aimed to obtain the relative proportions of tree and shrub canopies that were contributed by each species of plant. The data on size and depth of canopies was used to construct a 'volume of space occupied by foliage'. This assumes all foliage crowns to be cylinders based on their maximum depth and

width. From this a crude estimate can be made of the total foliage of each species of plant available to birds.

b. Point-centred quarter technique (Cottam *et al.* 1953)

Because line transects do not readily give the absolute density of plants as opposed to relative proportions of cover, I carried out the point-centred quarter technique on four 500 m grid-lines, selected at random using a table of random numbers to select both the grid-lines and to select points along each for the measurements. Data taken were: species, diameter of canopy, point to point distance and dbh of trees. The data proved of little importance to the study.

c. Quadrat sampling technique (Greig-Smith 1964)

Quadrat sampling was used only to assess cover in the ground layer. One hundred quadrats of 1 × 1 m, at intervals on the grid-lines used in the Point-centred method, were randomly selected using a table of random numbers. The percentage of ground cover in each quadrat was estimated by quartering the quadrat and then assessing by sight. Grasses, herbs, small (< 0.05 m high) woody plants and seedlings, and fallen logs and branches were recorded as present or absent.

d. Visual estimation of leaf biomass (Carbon *et al.* 1979)

Because sampling of insects was measured as insects per weight of leaves an attempt was made to estimate the relative proportions of leaf biomass present that was contributed by each species of plant. The method of Carbon *et al.* (1979) involves visual estimation of volume of leaves on a plant by using, as a calibration standard, selected branches or clumps of branches, from which leaves are later stripped and weighed. Fifty plants of each species, representing the size ranges indicated in data

from the line transects (24a. above) were measured, and five branches or clumps from each species were used as calibration standards. The resulting data were to be used for comparison with those from 24a. above, which gave 'volume of foliage' by plant species.

- e. From data obtained in the Point-centred Method an estimate of the relative areas of bark surface on each tree species was obtained. Each bole was assumed to be a cylinder with a diameter equal to the dbh, and the surface area was computed accordingly.

25. In 1979/81 a drought, the worst since that of 1902, occurred on the Northern Tablelands and other regions of New South Wales. By December 1980 the effects of the drought upon vegetation were so apparent that I repeated the line transect sample of vegetation (see paragraph 24a) and recorded, in addition to data collected previously, individual plants as (a) Dead: completely defoliated with no sign of life, (b) Half-dead: completely defoliated but showing signs of epicormic shoots or shooting from the base of the plant, (c) Live: retaining some, at least, mature green leaves. Care was taken to distinguish between the newly-dead and those trees dead before my study began. However at this stage of the study I knew the area well enough to recognize individual trees and their history throughout the drought.

26. Each month I sampled arthropods on foliage of seven plant species and on grasses (details in next chapter). At each sampling I recorded a qualitative description of the state of the foliage. This was later converted to a 'Leaf Growth Index' for each species on a scale of 4-1; 4: foliage green, many shoots; 3: foliage green, some shoots; 2: foliage green, no shoots; 1: foliage wilting, or yellowing, no shoots.

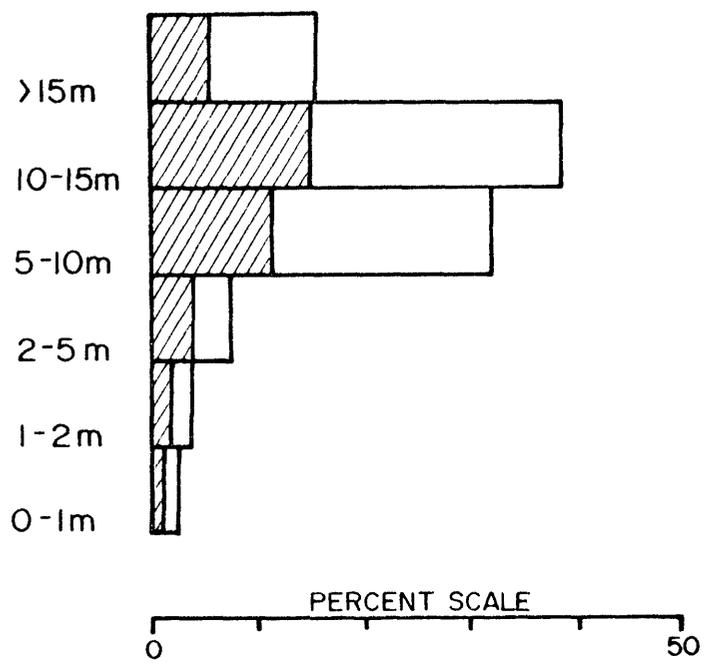
Results

27. Results of the line transects are given in Table 1. Of the transect lines, 36.7% was covered by tree canopy and only 13.6% by shrub canopy. The tree canopy was almost entirely *Eucalyptus*, with Stringybarks (*E.caliginosa*, *E.laevopinea*), Boxes (*E.sp. aff. cypellocarpa*, *E.conica*, *E.melliodora*, *E.bridgesiana*) and Gums (*E.viminalis*, *E.amplifolia*, *E.blakelyi*) and was about 15 m high, with individuals as high as 30 m. The shrub layer consisted mostly of bipinnate *Acacia* (*A.irrorata* with a few *A.filicifolia*) *Cassinia* spp (*C.quinquefaria* and *C.laevis*), *Olearia viscidula* and *Jacksonia scoparia*, and a small number of eucalypt saplings, mainly *E.caliginosa*. Most shrubs were under 2 m high except for the *Acacia* which grew to about 5 m and occasionally higher. Other shrub species made up less than 10% of plants present but important among these was *Exocarpos cypressiformis* which, as will be shown, was frequented by thornbills out of proportion to its low density. Stringybarks predominated in the tree layer and bipinnate *Acacia* in the shrub layer. Table 2 gives the density of species, taken by the Point-centred Method.

28. The 'volume occupied by foliage' is shown in Table 3 and is divided into plant species and the height categories used for observations of thornbills (see Chapter 9). That part of each plant species by height category that was either killed or defoliated by drought is also shown in Table 3. The proportion of volume contributed by each species was within $\pm 10\%$ of those derived by the visual estimate method of Carbon *et al.* (1979) (paragraph 24d.), except for *Exocarpos* which by visual estimate contributed five times more biomass than suggested by the value shown in Table 3. However the values, by both means, for *Exocarpos* are an insignificant part of the total. Because the visual estimate of leaf biomass did not give data by height categories I discarded its data in favour of the 'volume of foliage' estimate. As Table 3 shows, the tree canopy provides the bulk (86%) of the foliage. Bipinnate *Acacia* contributes half of the foliage in the shrub layer at 2-5 m and two thirds at 1-2 m. *Olearia* and *Cassinia* made up the bulk of foliage at 0-1 m. The distribution of foliage by heights is shown in Figure 3, with the proportion of foliage lost during the drought.

Figure 3

Distribution, by height categories, of foliage present at Wollomombi
showing proportions killed or defoliated by drought
as at June 1980.



 PROPORTION DEFOLIATED

Results of Transect Counts of Vegetation at Wollomombi Showing Percentage
of Numbers and Canopy Cover by Plant Species, and the Extent
of Defoliation During Drought

Species	Percentage of:		Individuals (%):		Canopy cover (%):	
	Individuals	Canopy	Died	Defoliated	Died	Defoliated
TREES						
<i>Eucalyptus</i> -Stringybarks	51.5	62.9	5.6	51.3	5.2	45.2
-Boxes	28.2	23.2	0.9	15.4	0.3	24.4
-Gums	18.8	13.8	0.7	11.3	0.5	7.7
<i>Acacia diphylla</i>	0.1	0.2				
Dead trees	<u>1.4</u>					
Total	100.0	100.1	3.4	33.3	3.4	35.1
n	1487	5408m	50	496	184m	1900m
SHRUBS						
Bipinnate <i>Acacia</i>	17.2	44.9	28.6	35.2	29.9	39.7
<i>Cassinia</i> spp.	17.9	18.2	23.6	42.5	20.6	37.1
<i>Olearia viscidula</i>	44.3	20.8	20.5	50.0	23.5	56.2
<i>Jacksonia scoparia</i>	15.8	8.9	15.3	14.2	9.4	7.7
<i>Exocarpos cupressiformis</i>	0.3	1.4				
Others *	<u>4.5</u>	<u>5.8</u>	<u>1.9</u>	<u>30.8</u>	<u>0.9</u>	<u>38.5</u>
Total	100.0	100.0	20.7	39.5	23.1	39.0
n	2316	2003m	480	914	463m	781m
TOTAL ALL PLANTS	3803	7411m	530	1410	647m	2681m

*: *Eucalyptus* spp (saplings), *Acacia implexa*, *Angophora floribunda*, *Bursaria* spp, *Casuarina littoralis*, *Dodonaea* spp, *Hakea eriantha*, *Helichrysum* spp, *Hovea*, *Leucopogon* spp, *Myoporum* sp., *Persoonia cornifolia*, *Pimelea linifolia*, *Prostanthera lasianthos*, *Rubus vulgaris*.

Table 2
Mean Density of Plant Species at Study Area, Wollomombi
(individuals/ha) (data from point-centred quarter
sampling method)

Tree layer

Eucalypts-Stringybarks	46
Boxes	24
Gums	<u>14</u>
	84/ha

Shrub layer

<i>Bipinnate Acacia</i>	47
<i>Cassinia</i>	49
<i>Olearia viscidula</i>	147
<i>Jacksonia scoparia</i>	62
<i>Exocarpos cupressiformis</i>	1
Other species	<u>10</u>
	316/ha

Table 3

Proportions, by Height Categories, of Volume of Foliage of Plant Species at Study Area
 (died or defoliated shown in brackets)

Height	Stringybarks	Boxes	Gums	<i>Acacia diphylla</i>	Bipinnate	<i>Acacia</i>	<i>Cassinia</i>	<i>Olearia</i>	<i>Jacksonia</i>	<i>Exocarpos</i>	Others	Total
>15m	7.82 (3.76)	6.14 (1.57)	1.70	0.03								15.69 (5.33)
10-15m	22.70 (11.69)	11.93 (2.96)	3.58 (0.36)	0.02	0.09 (0.02)							38.32 (15.03)
5-10m	20.97 (8.66)	6.59 (1.62)	3.51 (0.47)		1.41 (0.83)			0.05			0.03 (0.03)	32.56 (11.61)
2-5m	0.81 (0.31)	0.64 (0.30)	0.58 (0.07)		3.52 (2.48)	0.56 (0.33)	0.23 (0.19)	0.64 (0.10)	0.05		0.19 (0.13)	7.22 (3.91)
1-2m	0.02	0.03 (0.01)	0.03		2.28 (0.97)	0.44 (0.31)	0.48 (0.39)	0.41 (0.11)	0.03		0.10 (0.05)	3.82 (1.84)
0-1m	0.02	0.03	0.03		0.37 (0.26)	0.60 (0.37)	0.69 (0.48)	0.48 (0.12)			0.17 (0.06)	2.39 (1.29)
	52.34 (24.42)	25.36 (6.46)	9.43 (0.90)	0.05	7.67 (4.56)	1.60 (1.01)	1.40 (1.06)	1.58 (0.33)	0.08	0.49 (0.27)		100.0 (39.01)

29. Table 4 shows the proportion of bark surface area on trunks and the distribution of trunk-widths among the tree species, contributed by each species. Stringybarks and Boxes were of larger average dbh than Gums. There were many spindly *E.amplifolia* on the western side of the study area. Most of the trees with very big girths (> 1.5 m dbh) were Boxes. Differences in girth between types are represented in the proportions of total bark surface area, of which Gums contributed much less in proportion to their numbers.

30. The one hundred quadrats taken of the ground layer produced a mean percentage cover of $51 \pm$ S.D. 31%. The cover was chiefly grasses, *Poa sieberana*, *Themeda australis* and *Danthonia* sp. Herbs averaged little more than one per quadrat, being mainly *Lomandra* sp, *Dianella revoluta*, *Wahlenbergia* sp. *Ajuga australis* and *Goodenia hederacea*. Small woody plants averaged about one per five quadrats and were mainly *Hibbertia peduncularis*, *H.obtusifolia*, *Melichrus urceolatus* and seedlings of *Eucalyptus* spp, *Acacia irrorata* and *Cassinia* spp, all rarely more than 0.2 m high. From the transect data 0.8% of the ground was covered in dead stumps or fallen logs, limbs and branches. There was very little leaf litter.

31. The eucalypts were separated into three main types on the properties of their bark (Hall *et al.* 1975). Stringybarks have persistent thick spongy fibrous bark, Boxes have thinner persistent flakey or brittle fibrous bark, and Gums have smooth bark which is shed periodically, usually in long peeling strips. Unfortunately I did not separate Yellow Box (*Eucalyptus melliodora*; about 40% of all Boxes present) which has Box-like bark on the trunk and some limbs, but smooth bark on branches and most limbs. Figure 4 and Plate 1 illustrate the different types of bark.

32. The habit of various tree types is difficult to describe, because so many variations occur, caused by age, site conditions and local competition. Generally, at Wollomombi, Stringybarks have slender trunks and limbs in proportion to height, denser foliage and narrower but deeper crowns than other eucalypts. Boxes tend to have thicker trunks and wide but comparatively shallow crowns. Gums tend to have

Table 4

Proportions, by Eucalypt Species, of Trunk Bark Available to Birds;
and of Trunk Sizes by dbh at Wollomombi

Area (m²) of trunk bark

Stringybarks	57.6%
Boxes	32.8%
Gums	9.6%
Total area measured	6692.6m ²

Distribution of trunk sizes by tree types

<u>dbh</u>	<u>Stringybarks</u>	<u>Boxes</u>	<u>Gums</u>	<u>Dead trees</u>	<u>Total</u>
0.1 - 0.3 m	172	92	94	6	364
0.4 - 0.6 m	82	27	8	7	124
0.7 - 1.0 m	59	23	9		91
1.1 - 1.5 m	50	8	4	2	64
1.6 - 2.0 m	2	7	4	3	16
> 2.0 m	3	5		1	9
	<u>368</u>	<u>162</u>	<u>119</u>	<u>19</u>	<u>668</u>

Figure 4

Cross-section of bark on trunks, at breast height, of three

Eucalyptus spp. (life-size)

Representation; E.caliginosa : Stringybarks; E.sp. aff. cypellocarpa : Boxes;
E.amplifolia : Gums.

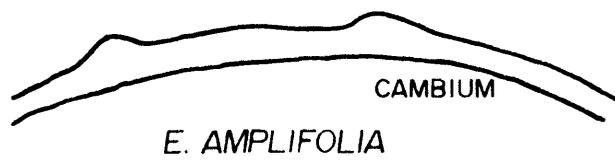
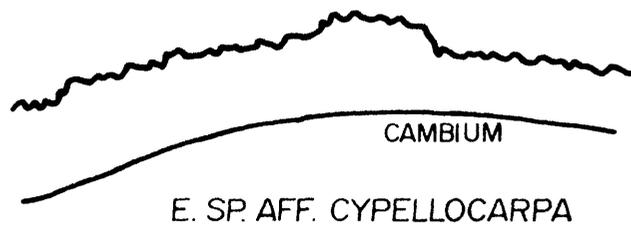
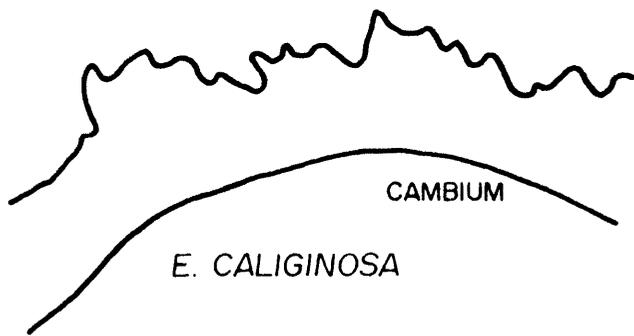


Plate 1

Typical Trunk Bark of (Top) Stringybark, (Centre) Box and (Bottom) Gum



thin trunks, deep boles, small narrow crowns, and limbs that spread more upwards than outwards. Leaves vary according to species but more importantly according to age. Figure 5 shows representative leaves of a Stringybark (*E. caliginosa*), a Box (*E. sp. aff. cypellocarpa*) and a Gum (*E. viminalis*) but other Boxes and Gums can have different leaves. Stringybark leaves tend to be tightly packed, for an eucalypt, and only the most mature leaves hang. The immature leaves of Boxes, which appeared to be in greater proportion than immature leaves of other types, tend to be rounded, but mature leaves are long and hang. The leaves illustrated in Figure 5 are immature. Gums appear to carry far greater proportions of mature leaves than the other types of eucalypts. The mature leaves are usually very long and hanging, and foliage tends to be sparser than in the other types.

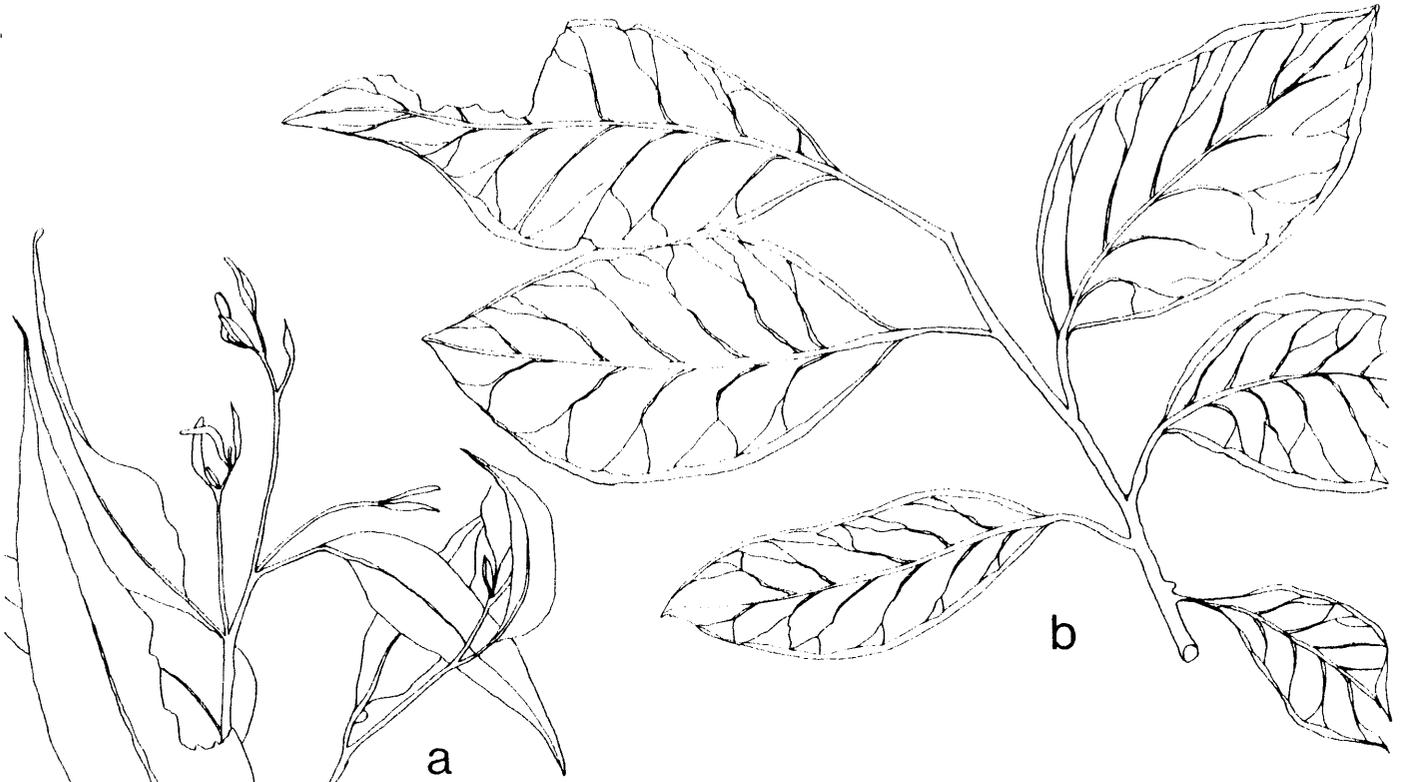
33. Shrub species vary considerably in habit, as depicted in Figures 5 and 6, and Plate 2. Bipinnate *Acacia* have dense foliage on the outer branches but there is often clear space between branches. The tightly-packed foliage has a very great surface area which provides many hiding places for insects. *Cassinia* bushes have very dense, packed foliage (except during the drought) and appeared to be much-favoured as nesting-sites by birds including thornbills. *Olearia viscidula* has fairly dense foliage on canes that extend up from the base of the bush, and even at the height of growth each bush is crowded with dead canes. *Exocarpos* is a small tree, with a dense crown that is hard to see through, the apparently open branchlets as shown in Figure 6 being very tightly packed together to form a somewhat impenetrable mass. *Jacksonia* is a spindly sparse shrub with very few 'leaves' (in fact, cladodes) and affords few hiding places for birds or insects. None of the flowers of these species is important to birds, though sometimes thornbills peck at *Acacia* blossoms, possibly because many small insects shelter in the inflorescences or feed on pollen.

34. Tables 1 and 3 and Figure 3 show the effects of drought, with ca. one third of the tree canopy and two thirds of the shrub layer either killed or totally defoliated. About 14% of all plants died and 37% were defoliated, the latter recovering to varying extents after rain

Figure 5

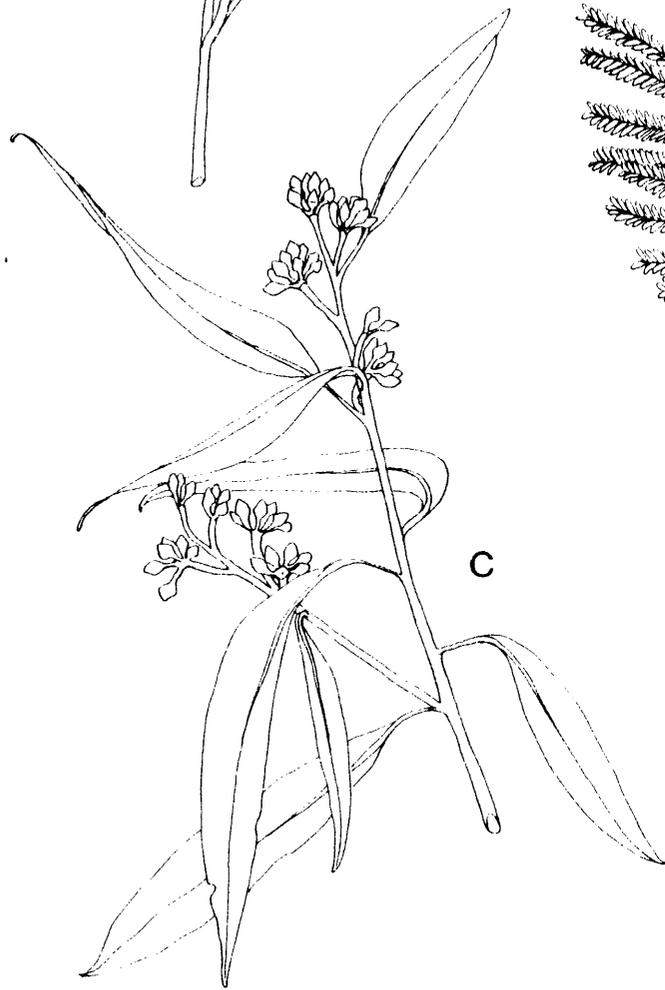
Leaves of (a) Stringybark *Eucalyptus caliginosa*, (b) Box, *E. sp. aff. cypellocarpa*, (c) Gum, *E. viminalis*, (d) bipinnate *Acacia*, *A. irrorata*

(see Fig 4)

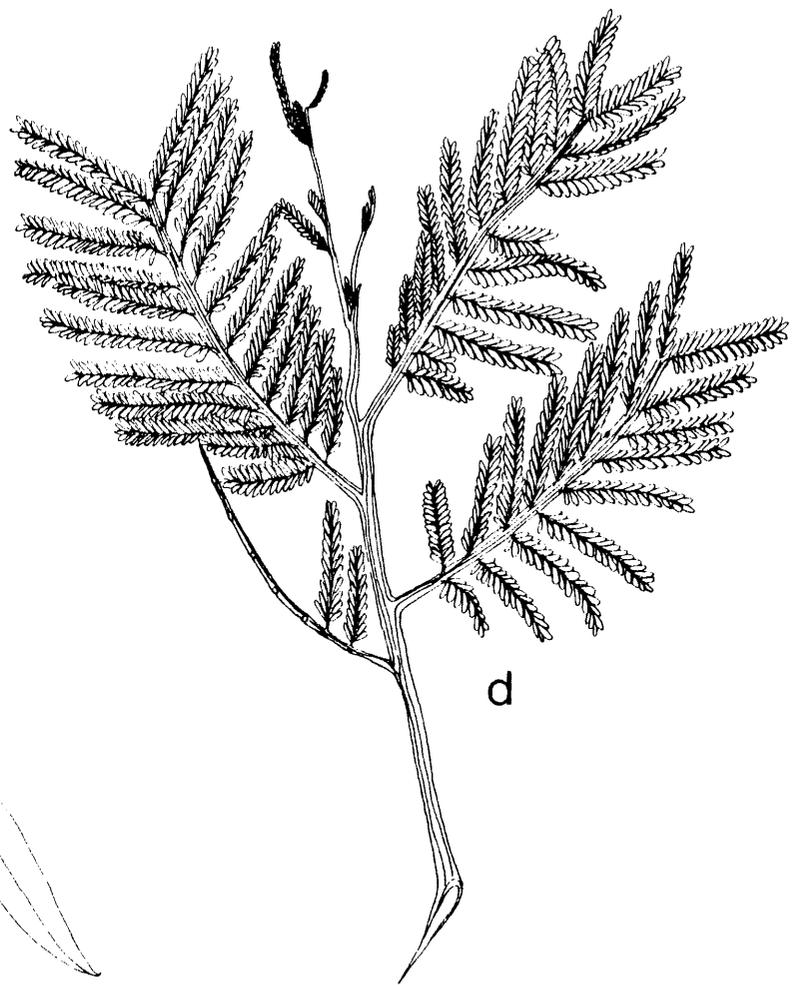


a

b

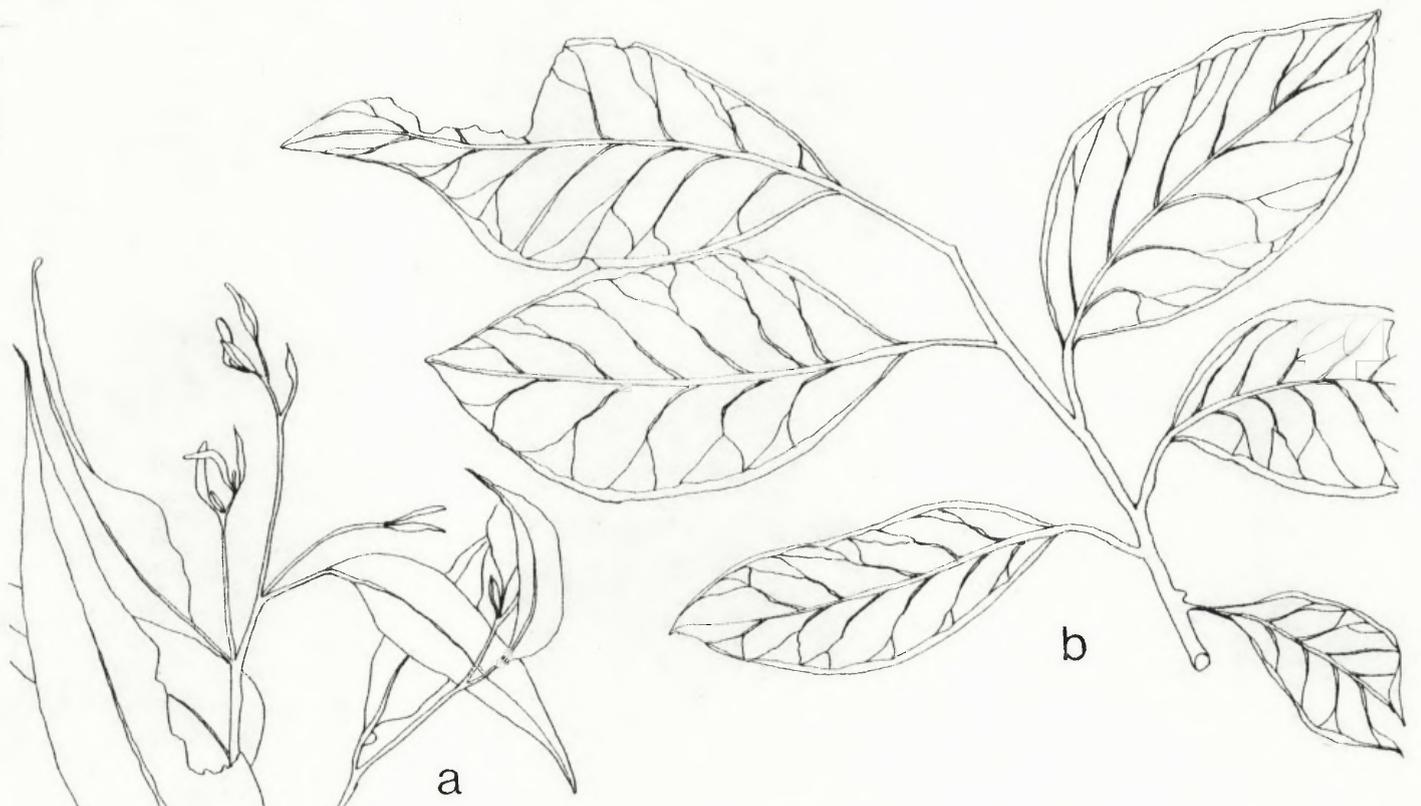


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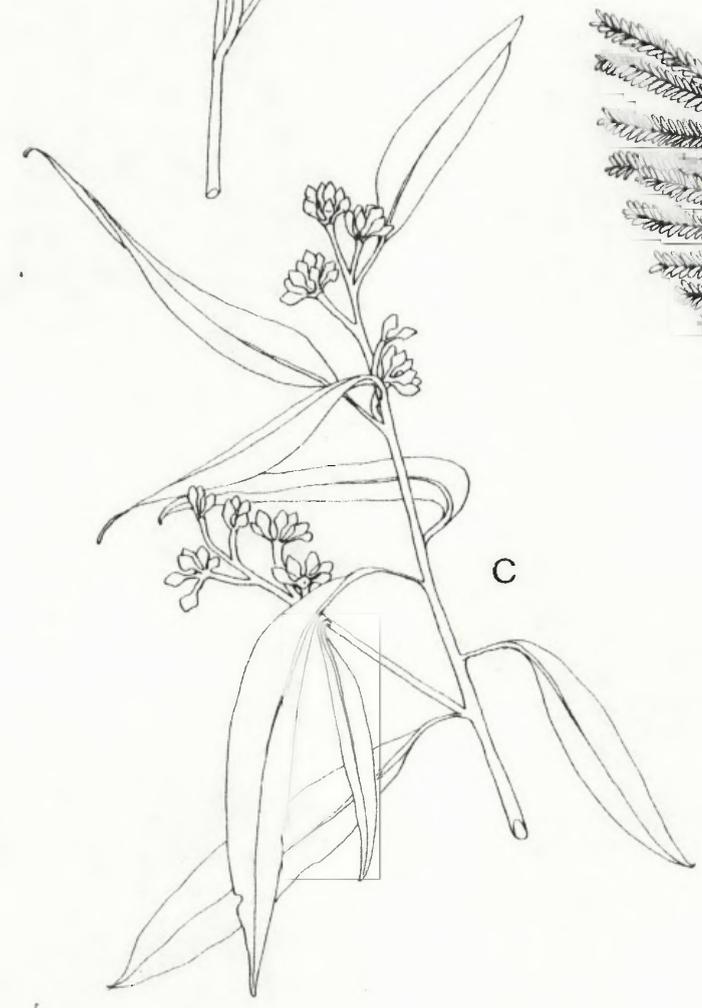
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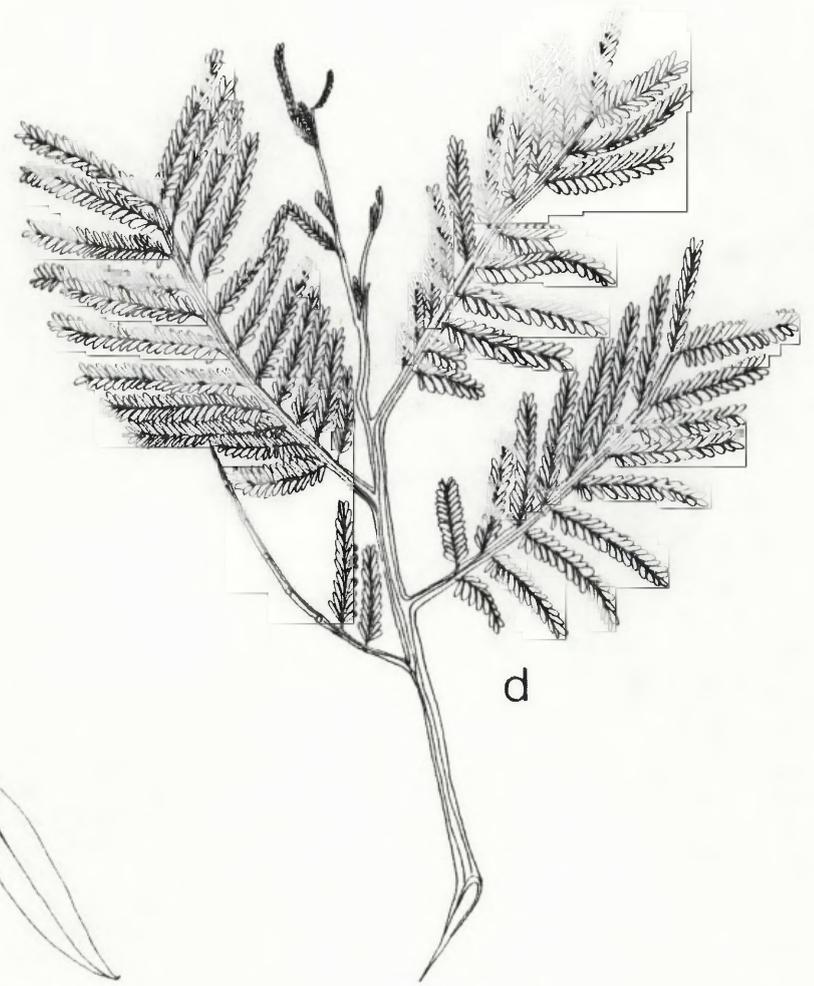


a

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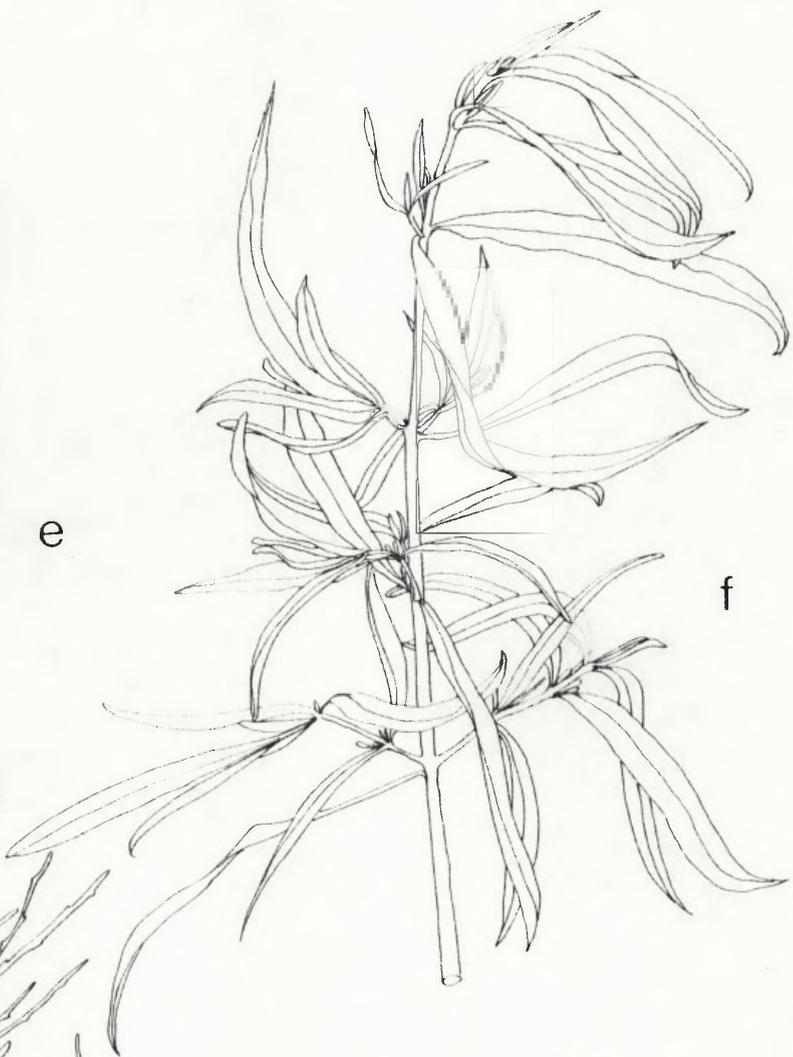


Figure 6

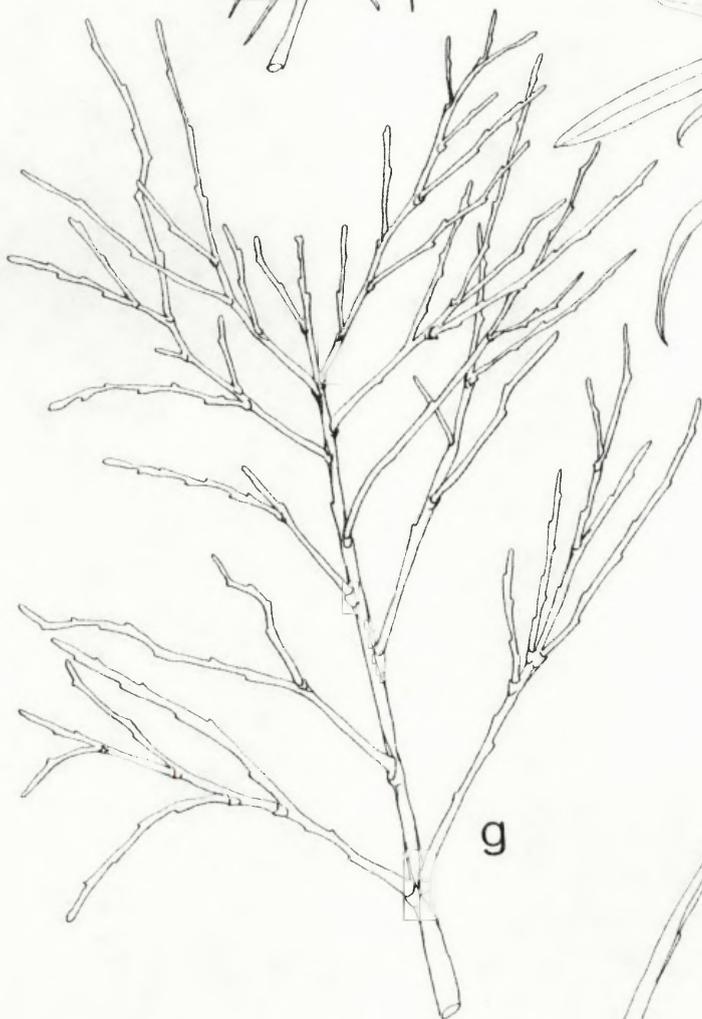
Leaves of (e) *Cassinia quinquefaria*, (f) *Olearia viscidula*,
(g) *Jacksonia scoparia*, and (h) *Exocarpos cupressiformis*



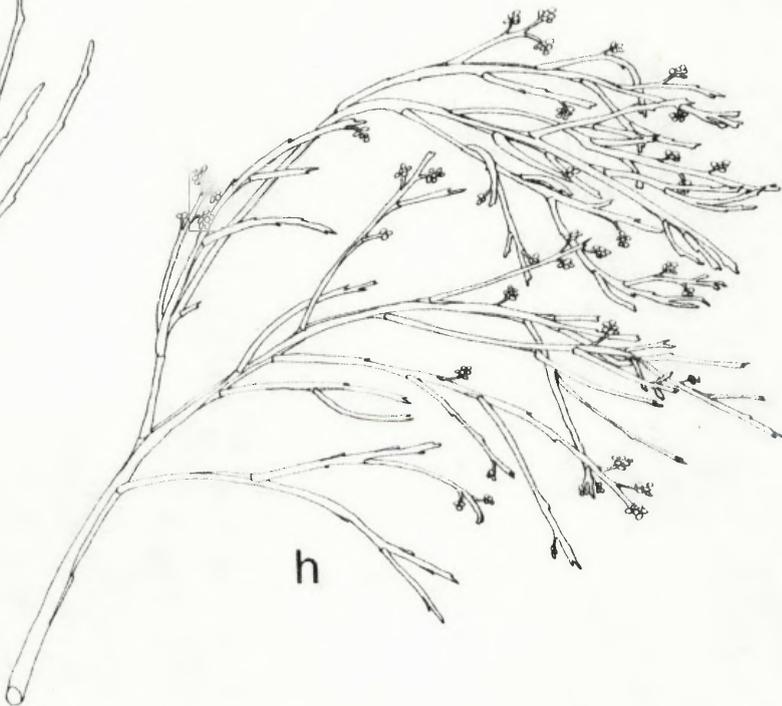
e



f



g



h



Plate 2

(Top left) *Acacia irrorata*, (Top Right) *Cassinia* sp., (Bottom Left)
Exocarpos cupressiformis, (Bottom Right) *Olearia viscidula*



fell in significant amounts in early 1981. The pattern, however, varied between types. Virtually no Boxes or Gums died and comparatively few were defoliated; in contrast 57% of Stringybarks lost all leaves and almost 6% died. Many Stringybarks had lost all leaves by November 1979 but in January sprouted epicormic shoots that withered and died by February 1980. After rain, more shoots sprouted in April only to be killed by frost in June. Yet more shoots sprouted in October but died in January 1981. Finally in April 1981, after significant rain, the Stringybarks, other than those that had died, sprouted more shoots which continued to grow without interruption. By contrast Boxes and Gums showed little stress until the winter of 1980 and then mainly in areas of presumably shallow soils, near the escarpment. Numbers of trees defoliated do not accurately depict the overall situation. Trees which retained some foliage lost much of it and had some branches bare.

35. Among the shrub species bipinnate *Acacia* were hardest hit, two thirds being defoliated and many died. *Acacia irrorata*, which flowers in both late winter and mid-summer, failed to set seed in the summer of 1979/80 and aborted flowering in winter and summer of 1980. Two thirds of *Olearia* and *Cassinia* also were defoliated but a much higher proportion (compared to *Acacia*) recovered after the drought. *Olearia* flowered each year but *Cassinia* failed to flower in 1980. *Jacksonia* suffered least but failed to flower in 1979/80 and aborted seeding in 1980/81. *Exocarpos* was unaffected, possibly because it is a root parasite of other plant species (Beadle *et al.* 1963).

36. The grass, which was 0.5 m high and seeding during the Autumn of 1979, was only 0.2 m high in Autumn 1980 and failed to set seed. By early 1981, the ground was virtually bare, and such grass as was still present was about 0.05 m high. Following rain in Autumn 1981 the remaining grass set some seed. During the drought most of the herbs disappeared and most small woody plants, particularly those near large trees, died.

37. Table 3 shows that leaves were lost entirely from about 40% of all 'space occupied by foliage'. However, as previously mentioned, the foliage that remained was greatly thinned. I have no quantitative data for this but some anecdotal descriptions may give an idea of the overall defoliation. At Edgars Lookout, in July 1978, a 44 gallon oil drum, painted bright yellow and on the ground, was completely obscured from view from the road junction at the Lookout roundabout 50 m distant. By December 1980, from the same viewing point, the writing on the drum could be easily read. At the territory of Brown Thornbill LIGHT GREEN/LIGHT GREEN, ca. 50 m in diameter, a human standing at any part of the boundary was, in 1978, invisible from the opposite side. By mid 1980 it was possible to easily see a notebook left at the opposite side. In the summer of 1980/81, on most days, I could not find sufficient shade under which to eat my midday meal.

DISCUSSION

38. The plant community at the study site fits Beadle and Costin's (1952) classification of savanna woodland and not forest, inasmuch as the average gaps between tree canopies exceeded the average width of the canopies. However the density of trees was patchy and many sites within the study area would fit the criteria for forest (i.e. with the canopy widths greater than the gaps between canopies). Numbers, and composition of both tree and shrub layers differ from those of Huddy (1979) who also worked in my area during 1979. Huddy recorded 133 trees and 271 shrubs per hectare, compared to my 84 trees and 316 shrubs. The discrepancy is because Huddy's area included Quail Thrush Spur (see Figure 1), larger than my whole area. From personal observation and from data of R.A. Noske (pers. comm.) Quail Thrush Spur has a denser tree layer and a sparser shrub layer than does my area. Huddy also recorded as many Boxes as Stringybarks but again, this is influenced by her data from Quail Thrush Spur, where Boxes are dominant, probably because aspect determines the density of Stringybarks (e.g. as at Canberra, Elliott and Douglas 1972).

39. The shrub layer, although sparse, was unevenly distributed, with clumps of dense understorey separated by much greater expanses of ground bare of any shrubs (see Plate 3, Chapter 2). In my opinion the sparse shrub layer is the outcome of long-term grazing by domestic livestock. For example, Papilionaceae, possibly the most abundant plants found in the New England area where no grazing has occurred, are, except *Jacksonia*, absent at Wollomombi Falls Reserve. Frith (1962) stated that small legumes are the first plants to be exterminated by livestock. Moreover, the impaction of soil by stock and subsequent formation of 'hard-pan' on the surface, along with the scarcity of seed-sources, probably inhibited regeneration when livestock were removed about fifteen years ago. Also trees have inhibited regeneration of shrubs. This was illustrated in 1980, when at the height of the drought Mr R.W. Edgar poisoned a grove of Stringybarks on his land. An almost immediate flush of growth of *Cassinia* and *Olearia* took place, at a time when both species were dying of water stress in the nearby Reserve. Thus, the understorey vegetation of the study area may have borne little resemblance to pre-European conditions.

40. From Table 3, the tree layer provided 85% of the foliage, and potential habitat for foliage-foraging birds. The shrub layer made up only 15%, half of it bipinnate *Acacia*. However, as indicated in paragraph 33, the structure of each species' foliage differs greatly in its density, in its surface area of leaf and in its potential as a feeding and hiding place for arthropods. Thus the 15% shrub layer may have proportionately more arthropods present than the more simple and sparse foliage of eucalypts. This will be shown in the next chapter. The potentiality of bark, too, as a source of insect food, varies between species. As shown in Table 4 Stringybarks and Boxes contribute a disproportionately greater surface area of bark than do Gums. Furthermore, the structure of bark differs (Figure 4) so Stringybarks may be even more important for insects than surface area alone suggests.

41. The ground layer, with a fairly sparse cover of grass, possibly represents good habitat for ground-feeding birds that are not obligate inhabitants of dense grass (e.g. button-quail). The relative sparseness of the grass leaves sufficient open space in which birds can forage but also sufficient cover to harbour arthropods and seeds at ground level.

Plate 3

Typical Views of Wollomombi Reserve. Top: Territory of Brown Thornbill

YELLOW/YELLOW, Bottom: Territory of Brown Thornbill

LIGHT GREEN/LIGHT GREEN



The presence of dead wood, although covering only 0.8% of the ground, provides a refuge for arthropods and is a significant substrate available for birds to forage upon (N.B. 0.8% of the study area covers 2000 m² of ground).

42. The effects of the drought on the vegetation were so great that in later chapters I shall discuss how the drought appears to have changed the foraging and social organisation of the thornbills. The deaths and defoliation of so many Stringybarks, in relation to other trees agrees with other studies that found them susceptible to drought (e.g. Pook and Moore 1966). The drop, in both 1979/80 and 1980/81, in the Plant Growth Index, to less than that of the previous year 1978/79, matched massive defoliation but even the value of 39%, shown in Table 3, greatly understates the true situation. For reasons given in paragraph 34 I believe that, at the height of the drought, less than one fifth the volume of foliage present at the commencement of the study remained as habitat and foraging sites for insectivorous birds.

CHAPTER 3

AVAILABILITY OF ARTHROPODS

INTRODUCTION

43. A necessary part of any study on resource-partitioning is an assessment of the food that the species are consuming, in this case arthropods. The abundance of arthropods is measured rarely in such studies (e.g. MacArthur 1958, Williamson 1971, Verbeek 1975) perhaps because it is difficult. A major reason for failure to measure the availability of arthropods is that, at the outset of a study, the feeding stations used by birds, and therefore the places in which their prey should be measured, may not be known. Often the best that can be achieved is a crude measure of the general abundance of food in the study area, in the hope that abundance in the various feeding stations will correspond to general abundance.

44. Some studies of the seasonal abundance of prey are mainly qualitative (e.g. Fogden 1972). But even wholly quantitative methods are biased towards particular types of prey whose abundance may not necessarily reflect the overall abundance of arthropods (Southwood 1966, Clark *et al.* 1967). For instance Cameron (1975) found that flying insects were most abundant in autumn, whereas phytophagous forms were most abundant in summer, thus showing the risks of relying on one method, such as trapping of aerial insects, as a guide to general abundance of all forms.

45. Nix (1976) demonstrated that the movements and breeding of birds in Australia and New Guinea were correlated with plant-growth, insectivorous birds being the quickest group to respond to fluctuations in such growth. Therefore I decided to count arthropods on green foliage, the main source of primary production, as an index of overall abundance. I rejected use of aerial sweeps, Malaise Traps, sticky traps, etc which sample flying insects, because I believed that thornbills took few flying insects. Light traps were similarly rejected. Net-sweeps of vegetation were rejected because it could be difficult to standardize sweeps on plant

species of different structure. Because Buff-rumped Thornbills were not seen to turn over ground-litter, no litter samples were taken. Later in the study (March 1979), I included sweeps at ground level because L. Huddy (Huddy 1979) worked in the same area and advised me that insect abundance at ground level seemed not to correspond seasonally with that in foliage.

MATERIALS AND METHODS

46. I took monthly samples of arthropods, from September 1978 to August 1981, on five types of plant in the study area. *Eucalyptus* spp, bipinnate *Acacia* spp, *Olearia viscidula*, *Jacksonia scoparia* and *Exocarpos cupressiformis*. In 1980/81 I also took samples from *Cassinia* spp; Eucalypts were sampled in the proportions of Stringybarks: 6, Boxes: 4, Gums: 1, and bipinnate *Acacia* were sampled in the proportions *A. irrorata*: 9, *A. filicifolia*: 1; their approximate frequency in the study area. No attempt was made to distinguish between *Cassinia* spp. as they were of similar structure and hard to tell apart. Thus plant species comprising more than 98% of the vegetation were sampled. The method used was;

- a. Monthly samples were taken around the 15th of the month, on days that were fine and calm, commencing at 0900.
- b. At least 2000g of green matter, from each plant type, were taken monthly. The sample for each type of plant was taken from at least 20 individual plants and were taken equally from slopes facing North, East, West and South. Samples were taken from the north-eastern side of each plant, merely for uniformity.
- c. Individual samples were collected in clear plastic bags 1 × 1 m. The bag was quickly placed over a leafy branchlet, which was then broken off and left to fall inside the bag. The branchlet was then squirted with Baygon household insecticide and the bag sealed until the next sample was taken. When about 500 g of matter was collected the contents of the bag were sprayed again, and the bag was then sealed, weighed, and left for two hours.

- d. After two hours the bag was opened, each branchlet was vigorously shaken 15 times against the side of the bag and then thrown away. When all branchlets were thus removed the bag was sealed again for removal to the laboratory.
- e. In the laboratory the contents of each bag were placed on metric graph paper under an Olympic binocular microscope. Every animal seen, down to 0.1 mm in length, was identified, if possible, to order. Those unidentified were recorded as such. Certain groups e.g. ants, psyllids, were recorded to family. The length and average width of each animal was also recorded, the measurements being estimated by comparison with the metric graph-paper.
- f. Biomass (wet weight) of each monthly sample was calculated by the weight/length relationship arrived at by Zug and Zug (1979), except for larvae, which were calculated by the weight/length relationship computed by Paton (1979).

47. From March 1979 I took monthly sweep samples at ground level, of 100 x 2 m sweeps with a butterfly net of 40 cm diameter and 1 mm mesh. On each sweep the edge of the net-ring touched the ground. After five sweeps the net was closed, the contents were sprayed with Baygon and then emptied into a plastic bag 1 x 1 m. The samples were treated in the laboratory as for the foliage samples.

48. R.A. Noske was concurrently studying bark-foraging birds in the same study area. By mutual consent he made available his data on arthropods sampled monthly on and inside bark, in exchange for mine on arthropods of the foliage.

RESULTS

49. Sampling bias undoubtedly occurred with the foliage samples. Large flying insects tended to fly away before I could trap them in the plastic bag and other insects, usually large beetles, would drop off the foliage as I approached. Thus insects of the larger size-categories were probably under-represented in my data, although it does seem that

NB 46d above. All leaves were taken to the laboratory for the first two samples. Values of arthropods were very low.

thornbills do not eat large hard-bodied insects. Arthropods that in death cling on to a substrate may not have been dislodged when the bags were opened and foliage shaken. However, as will be shown later, the types of arthropods in the foliage samples, except possibly for psyllids, were roughly similar to those found in the stomachs of thornbills, but not in the same proportions.

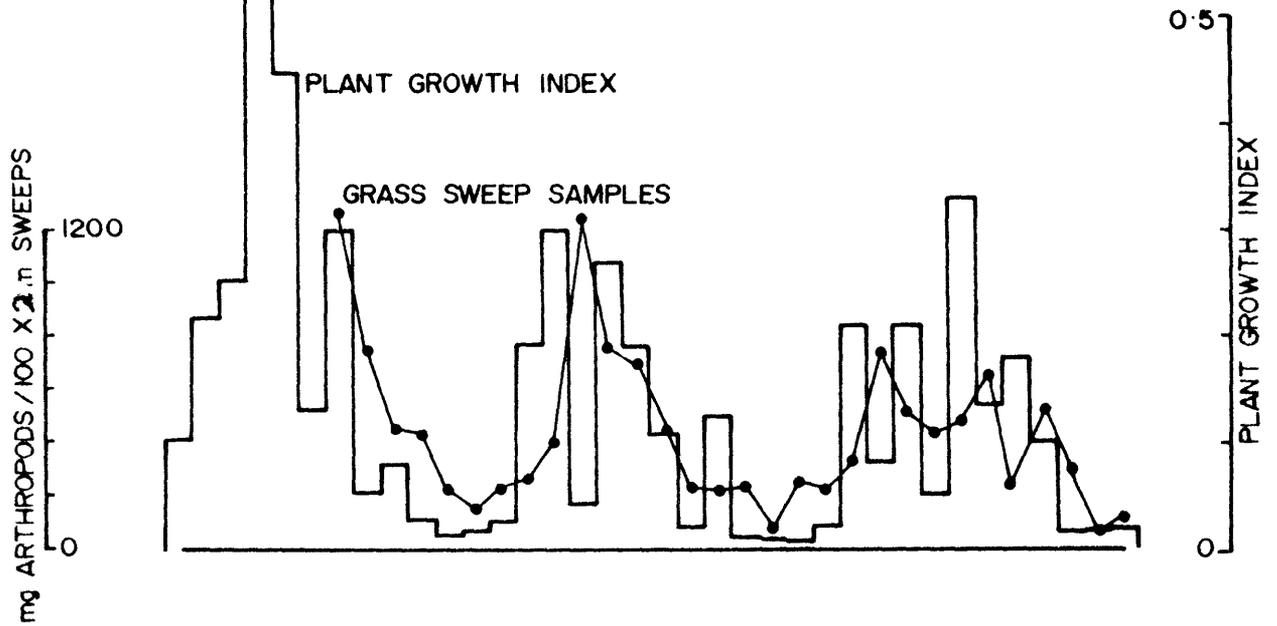
50. Figure 7 shows the biomass (wet weight) of arthropods taken in foliage samples and grass sweeps. The values shown are for all plant species combined, weighted according to each species' proportion of the total foliage present (see Chapter 2). Thus the values strongly reflect those for eucalypts, which made up the bulk (*ca.* 85%) of all foliage present. Abundance of arthropods was clearly lower in the second and third years, with peak values for the first summer (1978/79) being several times greater than for the two succeeding summers when rainfall was much lower (see Figure 2). Monthly values for grass sweep samples are correlated with the PGI (Spearman Rank Correlation, $r: 0.630$, $P < 0.01$). However those for foliage samples are not so correlated, either with the corresponding or the preceding month's values of PGI ($P > 0.1$). Monthly values for foliage samples are strongly correlated with the Leaf Growth Index (Figure 2) (Spearman Rank Correlation, $r: 0.740$, $P < 0.002$). Figure 7 shows that larvae made up the greater part of the biomass in many months, and particularly so in months when values were high. Half of the biomass in the summer of 1978/79 was of the larvae of saw-flies, Pergidae, which appear to be eaten by few birds other than cuckoos Cuculidae, cuckoo-shrikes Campephagidae (Cleland 1911) and parrots (*pers. obs.*). The biomass taken in grass sweeps, which showed less difference between years than the foliage samples, displayed a regular summer peak and winter trough. The biomass appeared lower in the third summer perhaps because there were few large locusts.

51. Figure 8 gives monthly values for samples off the foliage of the various plant types. The general trend was for a spring flush of arthropods followed by a summer peak and a decline in autumn and winter. However eucalypts, bipinnate *Acacia* and *Jacksonia* showed much higher values in the first year (1978/79) than subsequently, possibly reflecting

Figure 7

Monthly biomass (mg wet weight/ 1000g foliage) of arthropods taken
from grass sweeps and foliage sampling at Wollomombi,
September 1978-August 1981
Plant Growth Index (para 20) also shown.

GRASS SWEEPS



FOLIAGE SAMPLES

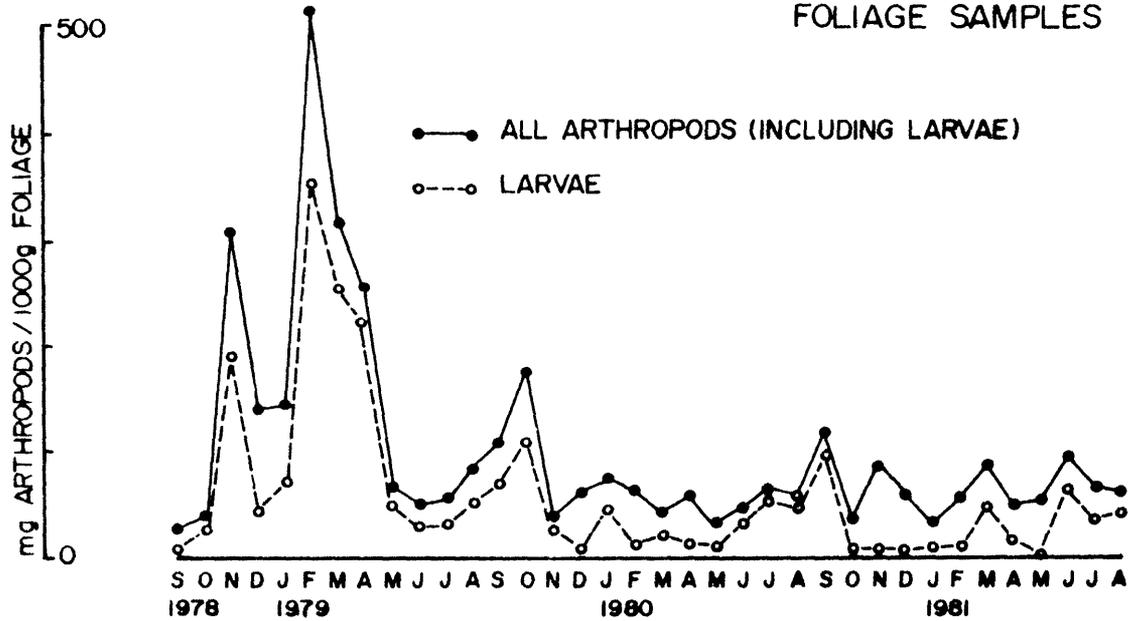
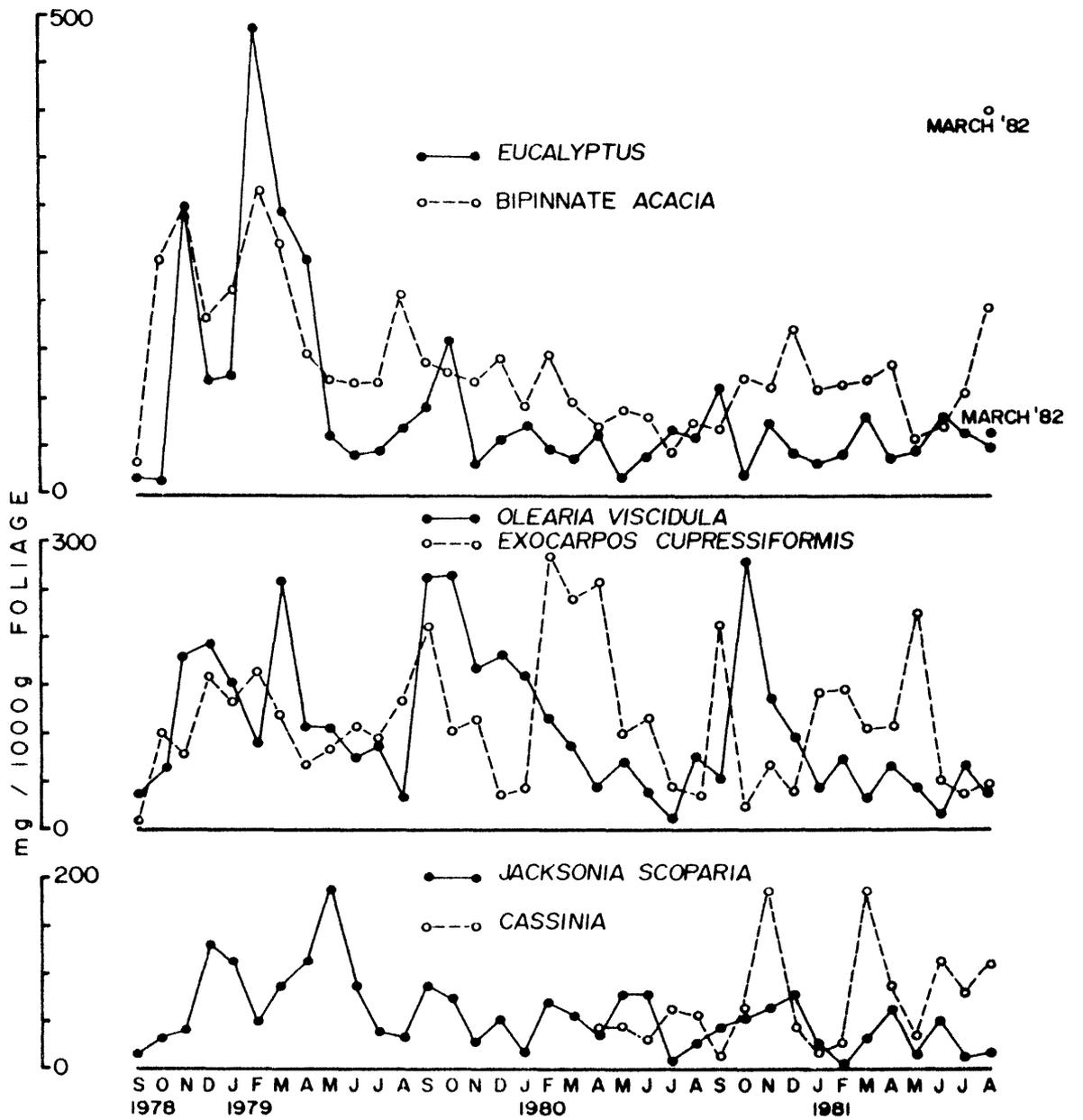


Figure 8

Monthly biomass (mg wet weight, 1000g of foliage) of arthropod samples taken from eucalypts, bipinnate *Acacia*, *Olearia*, *Exocarpos*, *Jacksonia* and *Cassinia* at Wollomombi, (September 1978-August 1981)



the lack of fresh foliage as the drought progressed (see Figure 2). The pattern for *Exocarpos* is at variance with other plant species, possibly because it is a root parasite (Beadle et al. 1963) and is able to maintain fresh young growth in time of drought. *Jacksonia* harboured a lower biomass than any other species and, as will be later shown, only one species of thornbill foraged upon it to any marked degree. Spearman Rank Correlations between monthly values for arthropods on each plant species and the PGI were: eucalypts, no correlation; (but $r: 0.717$, $P < 0.01$ when correlated to the PGI of preceding month); *Acacia*, $r: 0.491$, $P: < 0.01$; *Exocarpos* $r: 0.670$, $P < 0.01$; *Olearia*, *Cassinia* and *Jacksonia*, no correlation for same or previous month. Correlations with the Leaf Growth Index (Figure 2) were: eucalypts, $r: 0.698$, $P < 0.002$; *Acacia*, $r: 0.604$, $P < 0.01$; *Olearia*, $r: 0.504$, $P < 0.01$; *Jacksonia*, $r: 0.476$, $P < 0.01$; *Exocarpos* no correlation.

52. Abundance of the more important arthropod groups is shown in Figures 9 and 10. Figure 9 gives the abundance of Coleoptera, Hemiptera, Formicoidea and Araneidea for foliage samples; the values were totals for all plant types weighted according to relative abundance. Despite the drought Coleoptera showed regular summer peaks and winter troughs. Hemipterans may have followed this trend but after an early spring flush in 1979 there followed a reduction in numbers from which they appeared not to recover. In fact, an increase in numbers of large bugs in the two later years (1979/80 and 1980/81) masks what was a general collapse in the population of psyllids, which were the bulk of the hemipteran biomass in the first year. Psyllids in the first year numbered up to 1000 individuals per 1000 g of leaves but after a flush in September 1979 virtually disappeared, only returning in numbers in the last month of the study. Ants showed summer peaks and winter troughs but declined by the third year. This may not have been a decline in numbers but a change in habits because psyllids whose honeydew ants feed on, were scarce or absent in the foliage. Spiders and ticks fluctuated less than the other groups but showed a decline as the drought progressed. In the samples from grass sweeps (Figure 10) flying insects dipterans and hymenopterans tended to be at least as numerous in autumn as in the warmer seasons but spiders and lepidopterans conformed to the overall pattern shown in foliage samples.

Figure 9

Monthly biomass (mg wet weight, 1000g of foliage) of Coleoptera,
Hemiptera, Formicoidea and Araneidea taken in foliage samples
at Wollomombi, September 1978-August 1981

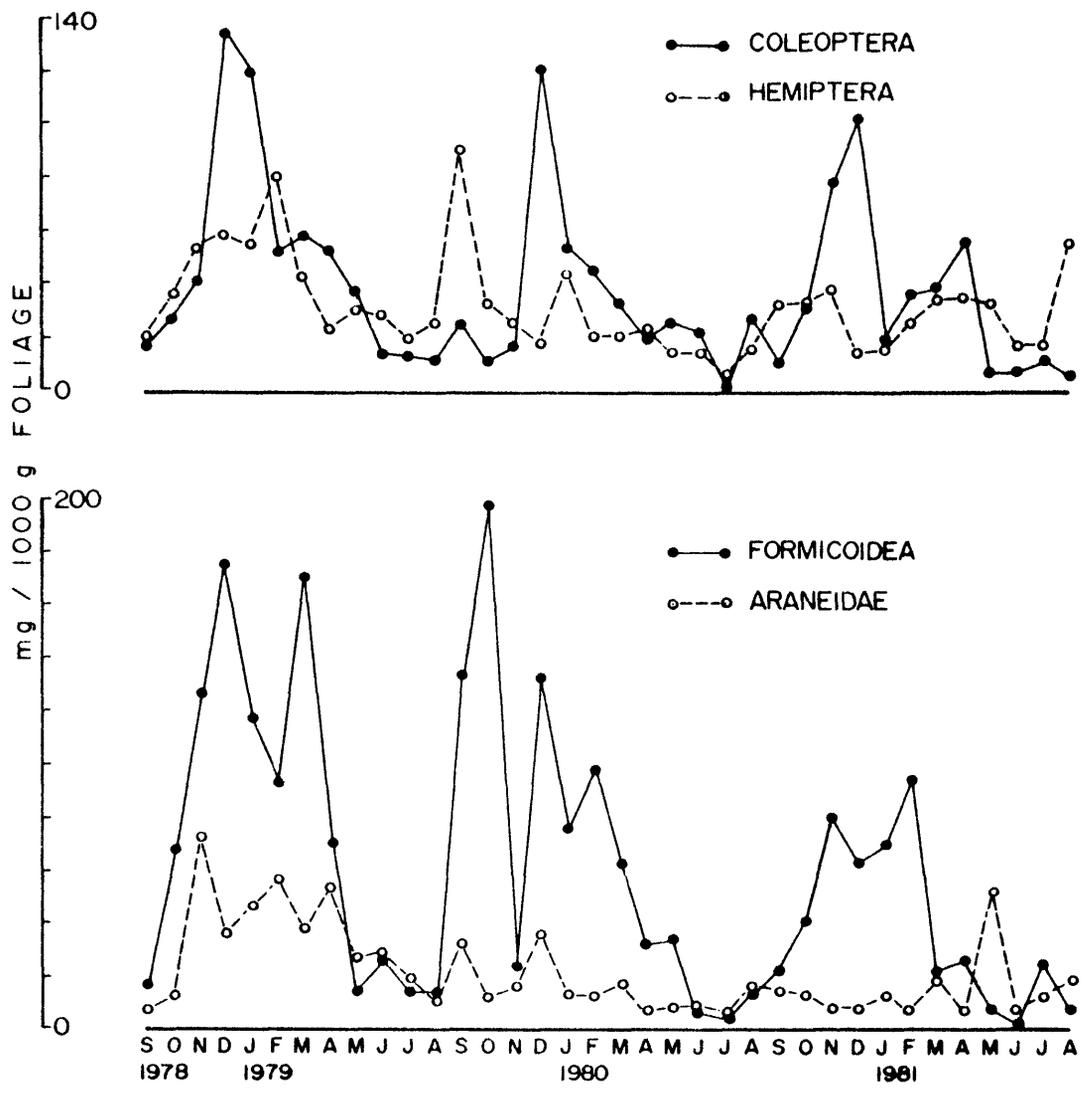
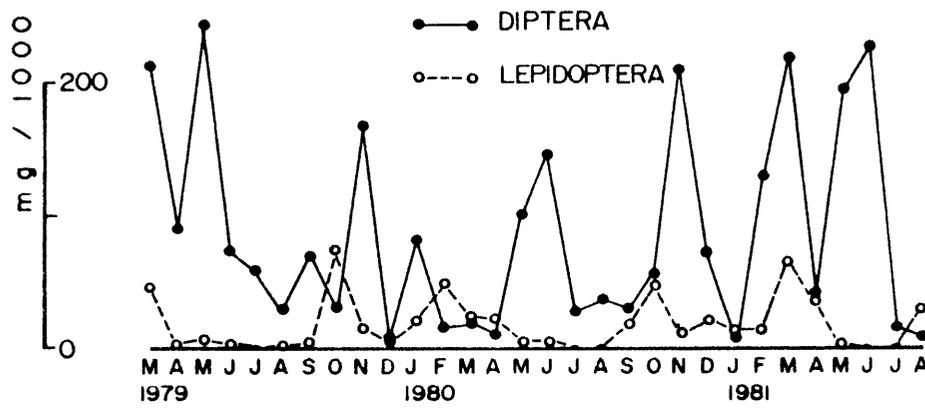
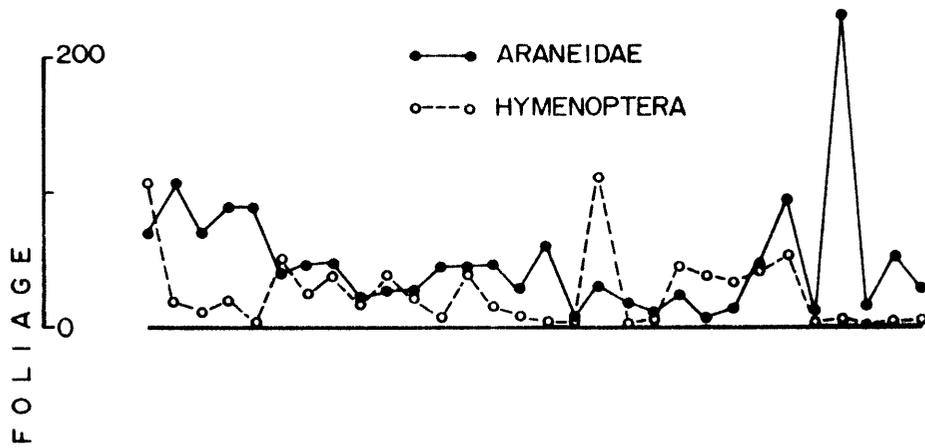


Figure 10
Monthly biomass (mg wet weight/100 X 20 grass sweeps) of Araneidea,
Hymenoptera, Diptera and Lepidoptera taken in grass sweeps at
Wollomombi, September 1978-August 1981



53. The size range of arthropods taken in foliage and grass sweep samples are given in Figure 11. Arthropods in the foliage samples were much smaller on average than those from the sweeps. This was because mites and psyllids, the bulk of individuals taken on foliage, were rarely taken in grass sweeps. Variation in mean size by months is illustrated in Figure 12. Comparing winter with summer means, arthropods were significantly smaller in winter than summer on eucalypts ($P < 0.05$), *Exocarpos* ($P < 0.002$), *Olearia* ($P < 0.002$) and grass sweeps ($P < 0.05$) and, though not significantly different for *Acacia* and *Jacksonia*, were smaller on average (Wilcoxon's Sum of Ranks Test).

54. R.A. Noske's data on bark samples are presented in detail elsewhere (Noske 1982b) but are summarized in Table 5. Values are given for the median month of each of the four seasons and represent the mean of 1978/79 and 1979/80 combined. Insects on the surface of bark followed the trend of summer peaks and winter troughs, the differences being greater than for the foliage samples. Gums showed a greater abundance of arthropods, possibly because insects are concentrated on hanging strips of peeling bark. The abundance inside the bark was quite different from that on the surface. Stringybarks showed a much greater abundance than the other eucalypt types possibly because their thick fibrous bark (see Figure 4) affords accessible and well-insulated habitat for arthropods. Abundance of arthropods inside bark was, in contrast to those on the surface, greatest in winter and spring, suggesting that the majority are dormant forms, which become active and leave the bark on the approach of warm weather.

DISCUSSION

55. Figure 8 shows that arthropods on shrubs differed less in abundance, between winter and summer, than did those on eucalypts. It is interesting that the common small insectivorous birds of the understorey at Wollomombi are breeding residents whereas those of the presumably less-stable (in terms of food availability) eucalypt canopy include all the summer migrants.

Figure 11
Proportions of arthropods, by length classes taken in foliage samples
and grass sweeps at Wollomombi

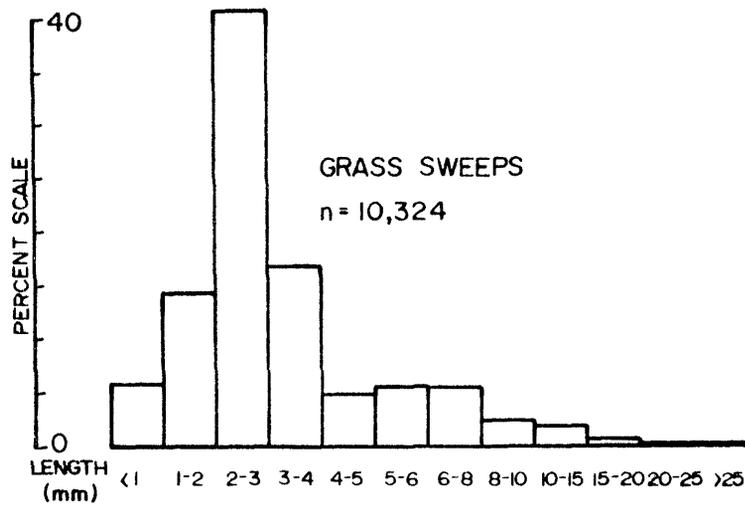
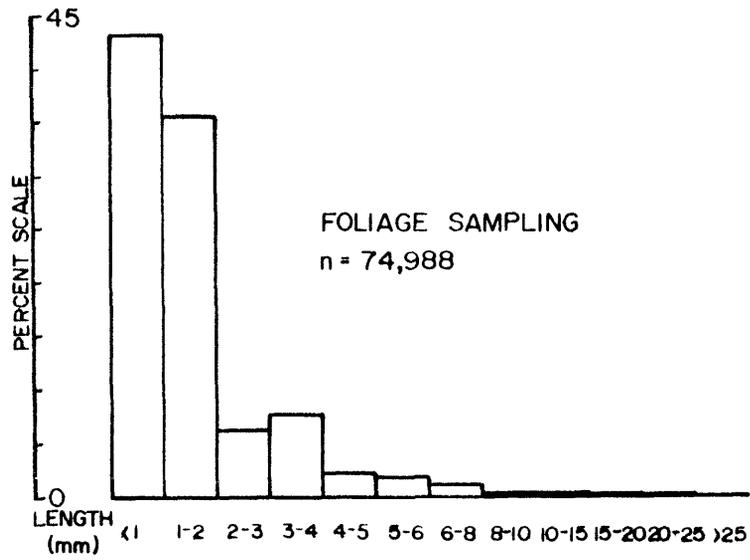


Figure 12

Monthly mean lengths of arthropods taken on grass sweeps and on foliage samples of eucalypts, bipinnate *Acacia*, *Olearia* and *Jacksonia* at Wollomombi, September 1978-August 1981)

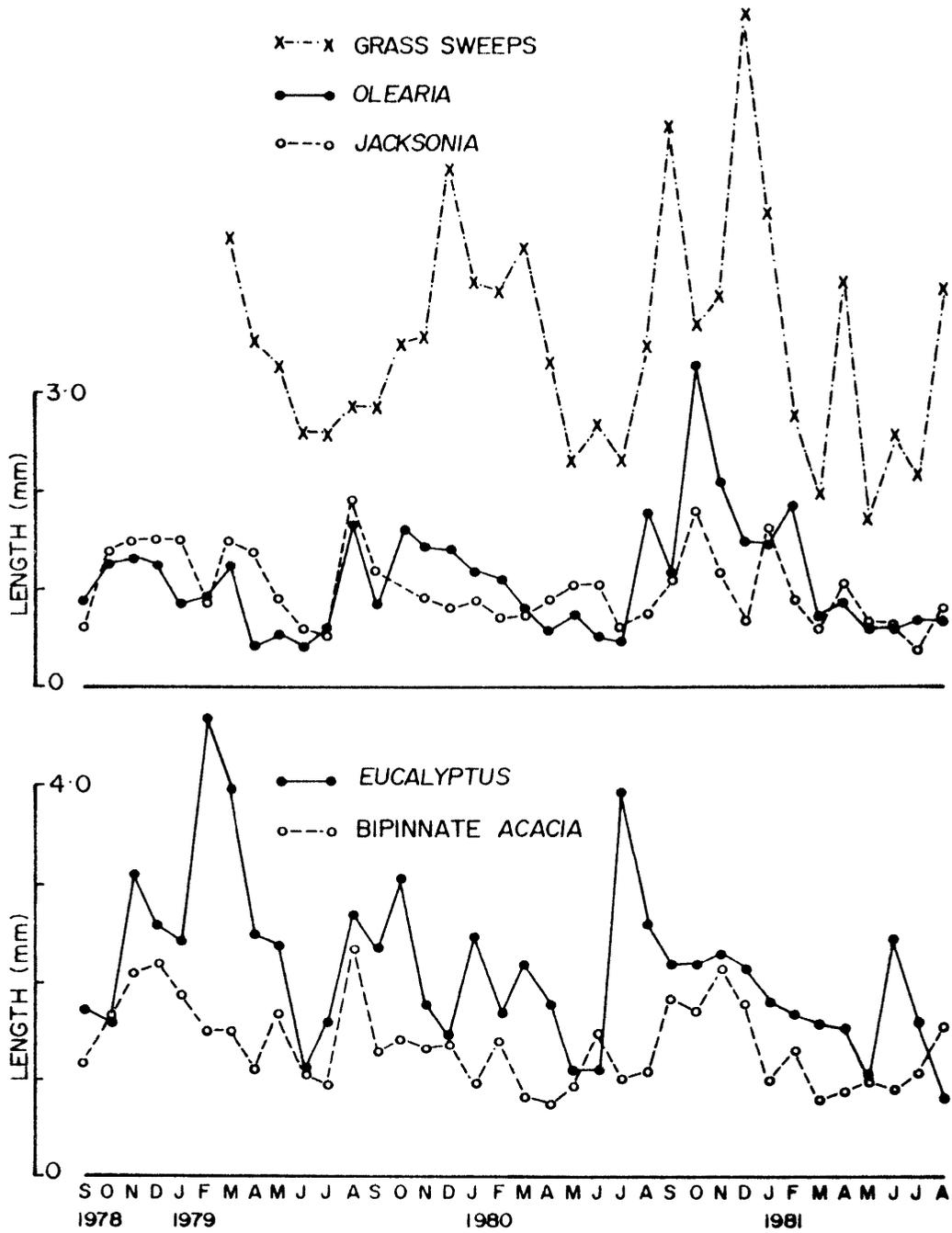


Table 5

Seasonal Abundance of Arthropods Inside and on the Surface of
Bark of Eucalypts at Wollomombi, 1978/79

(Data supplied by R.A. Noske)

Ants on bark surfaces (n/m^2 of surface)	Autumn	Winter	Spring	Summer
Stringybarks	35	15	175	175
Boxes	55	20	435	370
Gums	125	20	900	880
Non-ants on bark surfaces (n/m^2 of surface)	Autumn	Winter	Spring	Summer
Stringybarks	32	14	64	82
Boxes	20	18	57	73
Gums	18	17	43	63
Arthropods inside bark (mg wet weight/100g bark)	Autumn	Winter	Spring	Summer
Stringybarks	0.20	0.60	0.26	0.18
Boxes	0.02	0.04	0.10	0.06
Gums	0.07	0.09	0.06	0.05

56. Seasonal differences in the more prominent groups of arthropods (Figures 9 and 10) roughly follow a pattern of summer peaks and winter troughs except that in the grass sweeps dipterans showed strong autumn peaks. As will be shown later, dipterans were commonly found in the stomachs of thornbills during the cooler months.

57. The size ranges of arthropods sampled differ greatly between the foliage samples and the grass sweeps. This is because the grass sweeps produced very few mites (< 0.4 mm) which made up a great proportion of the numbers of arthropods in the foliage samples. Very small arthropods may still be very important to thornbills as food for larger, predatory arthropods such as ants and spiders, which in turn provide food for the birds. The smaller sizes of arthropods available in winter and the relative scarcity of arthropods at that time suggests that thornbills may need to forage more continuously and/or more efficiently during winter.

58. Noske's samples of bark-dwelling arthropods (Table 5) show that those frequenting the surface conform to the seasonal pattern of abundance shown by arthropods on foliage and grass. However the biomass of arthropods inside the bark is highest during the cooler months, possibly being made up mostly of pupae and other inactive forms. The high biomass inside the bark of Stringybarks, as compared with other types of eucalypts, is probably because the fibrous bark (see Chapter 2) provides good hiding places and insulation for invertebrates.

59. These data on the abundance of arthropods will have a bearing on subsequent chapters. They can be used to indicate the relative value of feeding on different plant species at any time. Changes in feeding behaviour of the thornbills could be linked to this. Also they indicate when food is likely to become scarce and hence when competition is likely to be most severe. Again, changes in behaviour, and especially in overlap of foraging, can be related to relative scarcity and abundance of food.

CHAPTER 4

THE BIRD COMMUNITY

INTRODUCTION

60. The three species of thornbills did not occur in isolation but were part of a fairly rich bird community of some eighty breeding species. It was therefore necessary to obtain some measure of the total population of insectivorous birds of which the thornbills were an integral component. Such a measure could then be compared with the availability of the food supply and perhaps explain the annual cycles of the thornbills and seasonal changes in their foraging behaviour.

METHODS

61. The biomass of all insectivorous birds present including the predominantly insectivorous honeyeaters Meliphagidae was obtained from census results. An average of six transect counts (Emlen 1971) were made each month throughout the study. Yapp (1956) and Royama (1960) give the statistical basis for such counts. Transects followed a 600 m path, covered in 30 minutes, from 08:00 to 08:30 h, and were only conducted in calm weather. I walked slowly along the path, stopping each 20 m to observe. I recorded all birds seen or heard other than those flying overhead, in front of my position, and the estimated distance each was at right angles from the centre-line. I was already familiar with all species encountered. Emlen (1977) considered that it was possible, using the lateral distances estimated, to vary the transect width according to species, to overcome the problem of varying detectability. The method of Balph *et al.* (1977) was used to compute density. They collated all observations of each species by occurrence in belts 20 m wide parallel with and radiating out from the centre-line, and took as the outer limit that belt in which were the greatest number of occurrences, ignoring those beyond the limit. The mean monthly density for each species per ten hectares was calculated as follows:

$$\text{mean density per 10 ha} = \frac{100,000 \text{ (m per 10 ha)}}{\text{length of transect} \times 2 \text{ (distance to outer limit)}} \times \frac{\text{no. of observations}}{\text{no. of censuses}}$$

62. Weights for each species were taken from my own banding data or from Ford and Bell (1981). Daily energy requirement of a species was calculated by the formula of King (1974): $\log_{10} 317.7 + 0.7052 \log_{10} W$ in kcal/day (W is weight in kg), converted to kjoules (1 kcal: 4 kjoules). Values were subjectively weighted for each season; spring by 1.5 to account for cool weather and breeding, winter by 1.5 for cold weather; summer by 1.1 for moult and autumn by 1.1 for cool weather. * 'Resource Demand', as an index of pressure by birds on the food resource, was calculated by dividing energy demand by the unit of measurement of food (mg wet weight/1000 g of foliage- see Chapter 3).

63. Breeding data, on all insectivorous species present, were obtained incidentally in the course of gathering foraging data. In addition, R.A. Noske notified me of all nests found by him and our data were pooled. The date of a nest is that month in which the first egg was laid or estimated to be laid. Only those nests for which the contents were known are included.

RESULTS

*

64. The mean monthly biomass of all insectivorous birds in the study area is shown in Figure 13a. There was a considerable variation in biomass, from ca. 1500 to 4000 g/10ha. There was no correlation between the biomass and monthly values for either abundance of arthropods or Plant Growth Index (PGI), (Spearman Rank Correlation P: > 0.1). As can be seen breeding migrants contribute substantially to spring and summer values, which wintering migrants do not match in autumn and winter. The values for resident species seem remarkably constant (ca. 2000 g/10 ha). The suggestion of increasing values as the study progressed is possibly the outcome of my own improved efficiency in detecting birds. The biomass for thornbills averaged at about 150 g/10 ha, below 10% of the total.

suggested

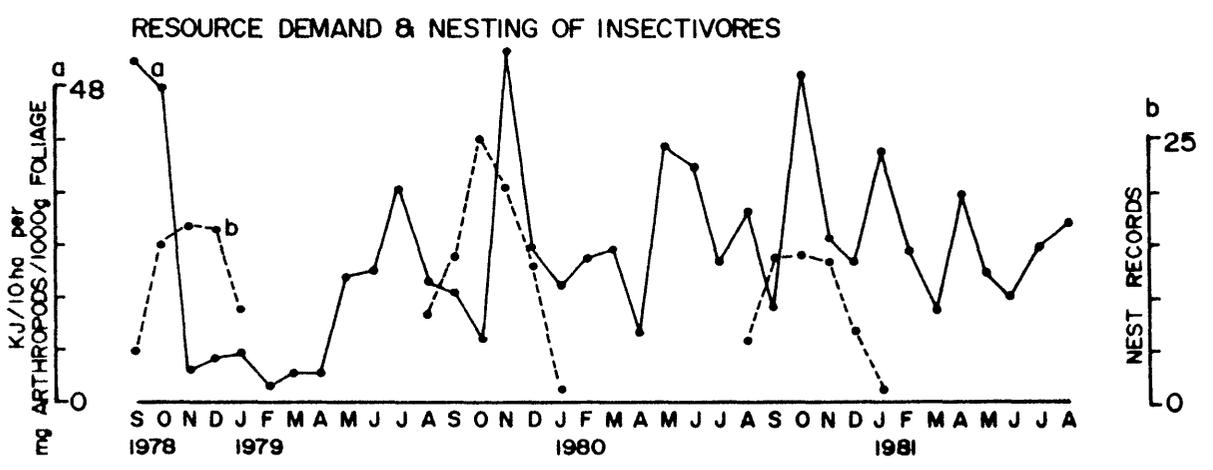
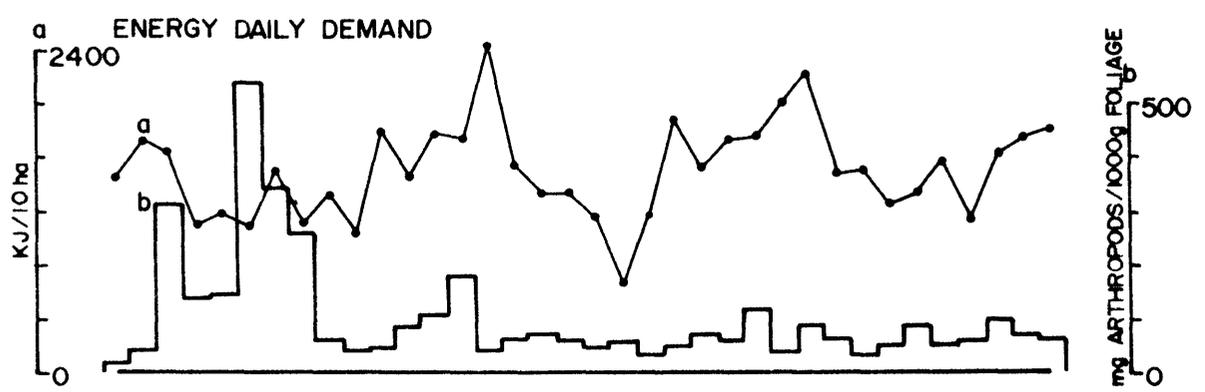
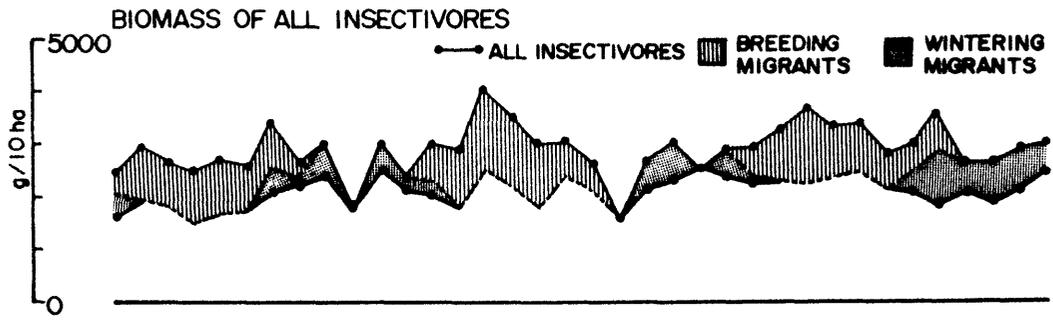
65. The energy demand of the insectivorous bird population is shown in Figure 13b along with monthly values for abundance of arthropods in the foliage. Honeyeaters, Meliphagidae, and the Silvereye *Zosterops lateralis* were included as insectivores because they are substantially,

*Weightings used from H.A. Ford in current study of which this data is a part.

*To be published. Data held Dept. of Zoology, Univ. of New England.

Figure 13

Mean monthly biomass of all insectivores at Wollomombi (13a); mean daily energy demand of insectivores compared with arthropod samples (13b); Resource demand (Kjoules/10 ha per mg arthropods/1000 g of foliage) and distribution of breeding records of insectivores at Wollomombi (13c)



and in most cases predominantly insectivorous, and because there was very little nectar available at Wollomombi on which they could have fed. There was no correlation between energy demand or biomass of birds with the abundance of arthropods (Spearman Rank Correlation, $P > 0.1$). Overall, biomass and energy demand were highest in the two years (1979/80 and 1980/81) of low abundance of arthropods. 'Resource Demand', an index of pressure by the bird community on the food resource (see paragraph 62) is shown in Figure 13c. Resource demand did not correlate with the biomass of insectivores (Spearman Rank Correlation $P > 0.1$). Breeding records for insectivores at Wollomombi are shown, for convenience, in Figure 13c. Breeding records are for the month in which the first egg is laid so maximum demand, by breeding birds, for insects would be about a month later, when young are about to or have just fledged. These peaks in demand by breeding birds coincide approximately with peaks in abundance of arthropods.

DISCUSSION

66. The population of insectivorous birds in the study area averaged at 142 birds/10 ha (monthly range 94-192), compared to 195/10 ha at Eastwood State Forest (Ford and Bell 1981), 75-175/10 ha in Victoria (Loyn 1980) and 98-199/10 ha in Tasmania (Recher *et al.* 1971), all in habitats reasonably similar to that at Wollomombi. Potential competitors of thornbills (insectivores < 14 g) and thornbills themselves showed a pattern similar to that in Figure 13a, of summer peaks and low values for late autumn and early winter. These fluctuations appear caused by the addition of young in late spring, and the departure of breeding migrants before the arrival of wintering migrants. There seems little relation, in this study, between total bird biomass and the availability of food, the peaks and troughs appearing to be regular yearly cycles unconnected with either plant growth or the abundance of arthropods. Overall winter numbers are not much below summer ones, with wintering migrants replacing breeding migrants, unlike many parts of the Northern Hemisphere (e.g. Britain) where there is great disparity in numbers of birds between winter and summer (e.g. Moreau 1972). Indeed

my banding records suggest that many migrants, wintering as well as breeding, hold, and return to the same territory at Wollomombi year after year so perhaps the numbers of migrants which arrive each year are similar regardless of local conditions. Of course it may well be that presumption of competition for food between all insectivores is falsely based. For instance there is a strong likelihood that pardalotes *Pardalotus* feed mainly on scale insects (Frith 1976) and may not compete much with thornbills, and other groups may have dietary specialisations not revealed by studies, like mine, that only identify prey down to the level of Order.

67. The breeding records generally reflect the views of Nix (1976), that insectivores breed with the spring flush of plant growth and consequent increase in insects. However both plant growth and arthropod abundance were very low in the 'drought' springs of 1979 and 1980, which suggests that the proximate factor in initiation of breeding was increasing day-length (Murton and Westwood 1977) which operated whether or not local conditions were propitious for successful reproduction. Unfortunately no conclusion can be drawn for the data for nest success, which was always low. Nest failure at Wollomombi was primarily the result of predation, and rarely due to starvation. However, the defoliation caused by drought must have made detection of nests easier for predators. It is noteworthy that in the spring of 1981, after the vegetation had recovered, thornbills, in most cases reduced to simple pairs rather than groups, were very successful in breeding.