

Birds, resources and time in a tablelands forest

H. F. RECHER¹, G. GOWING¹, R. KAVANAGH², J. SHIELDS² and W. ROHAN-JONES^{2,3}

¹Department of Vertebrate Ecology, The Australian Museum, PO Box A285, Sydney South, Australia 2000

²Forestry Commission of New South Wales, Sydney, Australia 2000

Abstract

Changes in an avian community are predictable. Birds migrate and young are produced according to well-defined seasonal cycles. In forests on the Southern Tablelands of New South Wales seasonal events within the avian community were tied to the annual cycle of cold winters and warm summers. Insect, carbohydrate and seed abundance changed with the seasons and were tracked by the avifauna. Superimposed were events determined on a larger regional scale. Irruptions of birds from the arid interior and drought caused significant, if transitory, changes in the forest avifauna. This has implications for the conservation and management of forest ecosystems which require the close integration of plans of management by regional authorities.

Introduction

Ultimately the abundance of birds, their movements and patterns of reproduction are determined by the abundance and availability of food. Nix (1976) presented an empirical model for Australia which predicted that seasonal movements and the timing of reproduction of birds are coupled to seasonal pulses in plant growth. The timing of plant growth in turn affects the abundance and kinds of food available to birds. In seasonal environments where phenological events are linked to an annual and highly predictable temperature cycle, reproduction and the movements of birds should occur in anticipation of changes in food availability (Lack 1950, 1954; Nix 1976).

The number of bird species, their abundances and the timing of reproduction in forest habitats of south-eastern Australia change in a predictable fashion through the year (Courtney & Marchant 1971; Nix 1976; Bell 1980; Marchant 1981). Num-

bers are lowest in winter and highest in spring and summer. In this paper we investigate the relationship between the abundance of forest birds, their movements and the timing of reproduction with the kinds of food used by birds in forest environments. Do birds in these highly seasonal environments time their activities in anticipation of changes in the abundance of food?

Methods

We used two 10 ha plots gridded at 30 m intervals near the Bondi State Forest on the Southern Tablelands of New South Wales (37°08'S, 149°09'E, elevation 850 m a.s.l.). Each plot consisted of two transects 420 m long and 120 m wide. One transect was based on the C Line and the other on the G Line of the grid. We call the plots 'Woodlot 1' and 'Woodlot 2'.

The woodlots were grazed by domestic stock and small amounts of timber had been removed for fence posts. Neither had been burnt for more than

³Present address: National Parks and Wildlife Service (NSW), Sydney, Australia 2000

25 years. Along three sides the plots were bounded variously by pasture, firebreaks and pine plantations, but connected on the fourth side with a large area of native forest. The woodlots were about 5 km apart and separated by a bog and pasture.

About half of Woodlot 1 was woodland dominated by snow gum *Eucalyptus pauciflora* and black sally *E. stellulata*. The area of woodland corresponded roughly with the C Line. The woodland had a grass ground cover, small amounts of *Lomandra* sp. and bracken, but no shrubs. The G Line was largely moist sclerophyll forest dominated by narrow-leaved peppermint *E. radiata*, ribbon gum *E. viminalis*, and swamp gum *E. ovata*. The sub-canopy layer consisted of young eucalypts and the wattles *Acacia melanoxylon* and *A. dealbata*. There were also extensive areas of shrubs dominated by *Bursaria* sp., *A. dealbata* and *Lomatia* sp. The ground cover was sparse and consisted mostly of patches of bracken and *Lomandra*.

Woodlot 2 was more uniform. The C Line and most of the G Line was dry sclerophyll forest dominated by narrow-leaved peppermint and mountain gum *E. dalrympleana*. Where the G Line bordered pasture the forest included a mixture of snow gum, black sally and ribbon gum. Much of this had regenerated following clearing and tended to be tall (10-15 m) and spindly. During 1978 about one third of the G Line was cleared for pasture. Woodlot 2 lacked ground cover and had few shrubs. In comparison with Woodlot 1, the litter was sparse. Both plots will be described in detail in another paper.

Rainfall on the Bondi State Forest has averaged c. 1000 mm per year since 1970. However, during this study the Southern Tablelands were affected by drought. In the five years since 1976, annual rainfall averaged 820 mm and only 1978 had >1000 mm of rain. Monthly rainfall is variable and there is no seasonal peak (Fig. 1). Characteristic of the tablelands, summers tend to be warm during the day, but cool at night. Winters are cold, but temperatures during the day are seldom below freezing. Snow is infrequent.

Birds were censused each December from 1976 to 1980 and throughout the year during 1978 and from November 1979 to January 1981. In addition to censuses, mist nets were used to capture birds for banding. Birds were netted each month from October through January in 1979/80 and 1980/81, immediately before or after censuses. Eighteen nets, 20 m long, were spaced evenly through each plot and opened at dawn for 6 h on each of two consecutive days.

We used a fixed width transect procedure for counting birds (Emlen 1977; Franzreb 1981). In these habitats, the line transect method gives a reliable estimate of relative densities when compared with estimates of populations as determined by territory mapping, nest searches and mist netting (Recher, Smith & Rohan-Jones unpub. data; Recher unpub. data). Birds were counted separately along the transect using detections based on sight and sound. Counts were of 2 h duration and were repeated on four consecutive days, weather permitting. Each transect was censused twice early in the morning and twice late in the morning. Two observers were normally used and the woodlots censused simultaneously. Each observer censused each woodlot twice. In this paper, our concern is with the relative numbers of birds and not with absolute densities. Therefore, in most instances we have used an index of avian abundance based on the total number of individuals detected during the four counts. Data from the two transects have been combined to provide an index for the woodlot.

The numbers of arthropods used by foraging birds were assessed on the major substrates, viz. ground, bark of trees, foliage of trees and air (i.e. flying insects). In addition, the abundance of nectar and eucalypt seed was scored by counts of flowers and seed capsules ('gum nuts'), but other carbohydrates (e.g. manna, honeydew, grass seed) were not measured. All substrates and flowers were sampled monthly. We were able to run all procedures concurrently only from July 1980 through June 1981. Estimates of food abundance are therefore slightly out of sequence with bird census data.

Ground invertebrates (and reptiles) were sampled by means of 21 plastic pit traps containing a preservative and set flush with the ground surface. Traps were left open and cleared at least once a month. Data from 10 traps on the G Line of Woodlot 1 and the C Line of Woodlot 2 have been analysed. Bark fauna was sampled by removing all loose bark to a height of 2 m on 10 trees of each species on each plot and collecting all invertebrates seen. Trees were selected to give an equal size or diameter class range for each species. Arthropods on foliage were counted by visual inspection of 10 trees of each species per woodlot. The invertebrates (in situ) on 10 samples of 40 leaves on each tree were counted, on foliage up to a height of 2 m.

Small flying insects were sampled with sticky traps which were 10 cm square white boards covered with a sticky substance. The boards were spaced at 1 m intervals along a rope to a height

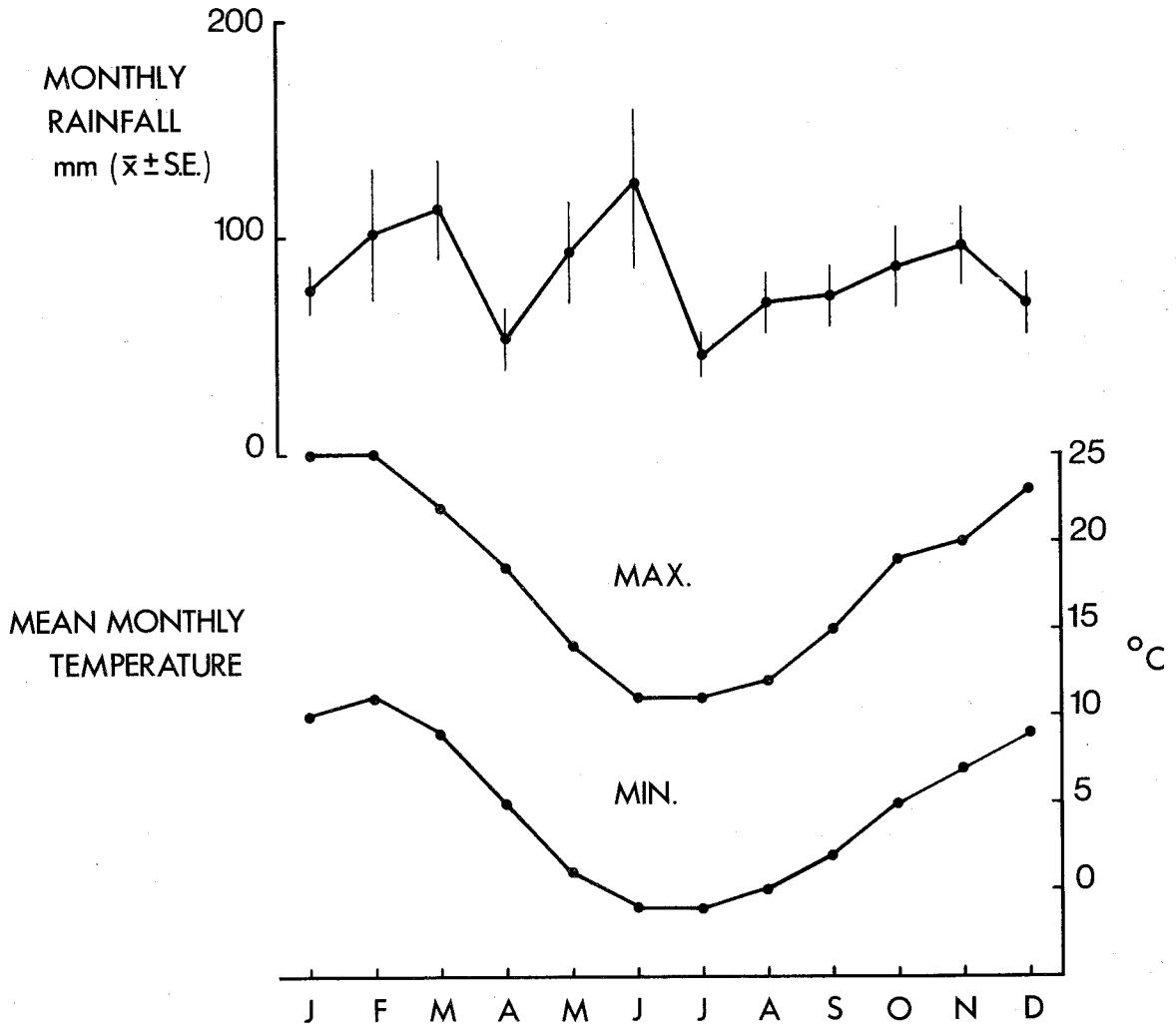


Fig. 1. Mean monthly rainfall (mm) and maximum and minimum temperatures ($^{\circ}\text{C}$) for the Bondi State Forest, New South Wales.

of 10 m, and left in place for four days each month. In this paper the data from all heights have been combined. Large flying insects were sampled with window traps which consisted of 0.5 m square sheets of clear perspex positioned 1.5 m above the ground. Insects flying into the perspex fell into a collecting trough containing a preservative. Window traps were left in place and cleared at least once a month. Three window traps and three sets of sticky traps, positioned to sample the major types of vegetation, were used on each plot.

Invertebrates were identified to the lowest taxa

possible (usually order or family) and measured to the nearest 0.1 mm. Lengths were converted to dry weights by appropriate length/weight curves (Gowing & Recher unpub. data).

Flowers and gum nuts were scored by counting the number in a single binocular field at the apex of the tree. The same trees were scored each month and the area of the field standardised by measuring the distance of the observer to the top of the tree. Flowers were counted on up to four trees of each species on each woodlot at 28 points spaced evenly through the plot.

TABLE 1. Foraging guilds and common birds of woodlots

Foraging Guild**	Species	Individuals*			
		WL 1C	WL 1G	WL 2C	WL 2G
Insectivores					
Ground Pouncers	Flame Robin	2.3	4.3	1.0	3.0
	Yellow Robin	2.0	2.3	4.5	2.3
Bark Gleaners	White-throated Treecreeper	3.5	5.0	4.8	6.0
	Red-browed Treecreeper	0.5	0.5	1.5	0.5
Large Ground Foragers	Ground Thrush	0.8	9.0	2.0	0.3
	Grey Shrike Thrush	2.0	2.8	1.5	1.0
Small Ground Foragers	Blue Wren	2.8	10.5	8.5	7.8
	Buff-rumped Thornbill	1.8	1.0	0	0
Rapid Aerial Hawkers	Grey Fantail	12.3	22.0	15.5	12.8
Hawkers and Foliage Snatchers	Golden Whistler	1.3	4.8	0.5	2.0
	Rufous Whistler	4.3	10.5	12.3	6.8
	Satin Flycatcher	3.0	8.3	6.5	3.5
Foliage Gleaners and Hoverers	Striated Pardalote	0.5	1.8	3.8	2.5
	Brown Thornbill	1.0	6.3	1.0	2.3
	Striated Thornbill	14.0	6.3	2.8	6.5
Granivores					
Eucalypt Seed Eater	Crimson Rosella	3.3	1.3	13.5	17.0
Grass/Weed Seed Eater	Red-browed Finch	0.5	0	0	0.3
Nectarivores					
Foliage Gleaners	White-naped Honeyeater	16.5	17.3	18.5	27.3
	Yellow-faced Honeyeater	4.8	2.5	0.5	1.8
Bark Probers	White-eared Honeyeater	3.5	4.3	0	0.5
	Crescent Honeyeater	4.3	2.5	0	0.8
Foliage Snatcher	Red Wattlebird	1.3	1.0	0.8	3.0

* Average number of individuals per 2 h count, December 1979.

** R.T. Holmes (pers. comm.).

Results

Description of the avifauna

The birds of the woodlots were typical of the forest and woodland avifauna of south-eastern New South Wales. Since 1976, 85 species of terrestrial birds were recorded on the plots, 56 of which were common and widely distributed in forest habitats

throughout south-eastern Australia (Recher unpub. data). Forty-seven species nested on one or both woodlots, with 25 species nesting every year. There were differences in the relative abundances of species, but most of the common birds were abundant on both woodlots (Table 1). Colour-banding of more than 2700 individuals over four years revealed no movement of resident birds between plots.

TABLE 2. Number of bird species and individuals per 2 h count during December

A. Species ($\bar{x} \pm S.E.$)					
Transect/Year	1976	1977	1978	1979	1980
Woodlot 1C	20.5 \pm 1.6	22.8 \pm 1.4	26.5 \pm 1.7	22.7 \pm 2.2	23.5 \pm 0.2
Woodlot 1G	n.d.	25.3 \pm 0.7	26.8 \pm 1.0	26.8 \pm 1.1	27.5 \pm 1.9
Woodlot 2C	22.5 \pm 0.5	21.8 \pm 1.9	28.3 \pm 1.5	19.5 \pm 0.8	22.5 \pm 0.9
Woodlot 2G	n.d.	20.0 \pm 1.2	30.5 \pm 1.9	20.5 \pm 2.1	21.0 \pm 1.4
B. Individuals ($\bar{x} \pm S.E.$)					
Woodlot 1C	97 \pm 6	96 \pm 6	100 \pm 6	99 \pm 17	82 \pm 4
Woodlot 1G	n.d.	104 \pm 11	102 \pm 8	138 \pm 8	94 \pm 10
Woodlot 2C	110 \pm 12	113 \pm 9	113 \pm 3	116 \pm 11	103 \pm 5
Woodlot 2G	n.d.	97 \pm 6	108 \pm 10	118 \pm 20	75 \pm 7

From the foraging ecology of the woodlot avifauna (Holmes & Recher unpub. data) seven foraging guilds of insectivorous birds were identified on the basis of prey attack behaviour and the substrates from which the birds obtained their food (Table 1). In addition, there were two groups of seed-eaters (granivores): parrots (Psittacidae) which fed mainly on eucalypt seed, and finches (Fringillidae and Estrildidae) which fed on grass and weed seeds. Honeyeaters (Meliphagidae) and Silvereyes (Zosteropidae) formed a separate foraging group. Honeyeaters commonly take insects, but also exploit a variety of energy-rich carbohydrates including nectar, manna and honeydew (Paton 1980; Pyke 1980). None of the honeyeaters on the woodlots was nectar-dependent. The Brown Goshawk *Accipiter fasciatus* was the only regularly occurring raptor. A pair nested on each woodlot, but foraged over a much larger area, mostly taking rabbits *Oryctolagus cuniculus*. Some of the larger birds, such as the Kookaburra *Dacelo novaeguineae* and Grey Currawong *Strepera versicolor*, commonly fed on small reptiles, but mostly took large insects.

Annual variation in the composition of the avifauna

Although summer bird populations were censused from 1976 to 1980, counts of winter bird populations were obtained only for 1978 and 1980.

Summer avifauna. When the variation in census results which arises from differences between observers and weather is considered, there was relatively little difference in the number of species or the total numbers of individuals on the woodlots

from one summer to the next (Table 2). On three of the four transects there was an increased number of species during 1978. This was due to the presence of a greater number of uncommon birds (e.g. the Cicadabird *Coracina tenuirostris*, Rufous Fantail *Rhipidura rufifrons*) and the more even distribution of common birds. On all transects the number of individuals decreased during 1980.

In contrast to the other years of the study, rainfall in 1978 was above-average. The increased number of species during 1978 may therefore have been related to more favourable conditions for birds, although there was no increase in the estimates of bird numbers. The moister conditions may have facilitated the ability of the observers to detect birds, but it is difficult to explain the high species counts solely on improved detection. Weather during the counts were unexceptional and the large number of species detected (e.g. 44 on the C Line of Woodlot 1) greatly exceeded numbers recorded at other times when the weather during counts was equally good for detecting birds.

In comparison with 1978, conditions in 1980 were poor due to two years of drought. There was little soil moisture and most annual plants and ferns failed to grow. On both woodlots the average number of individuals detected during counts declined from September through December. In the same period in 1978, numbers increased (Fig. 2).

Normally large numbers of young were fledged on the woodlots during November and December (Table 3). The young of the Grey Fantail *R. fuliginosa*, White-naped Honeyeater *Melithreptus lunatus*, Yellow Robin *Eopsaltria australis*, White-throated Treecreeper *Climacteris leucophaea* and Flame Robin *Petroica phoenicea* were particularly abundant. In addition, birds dis-

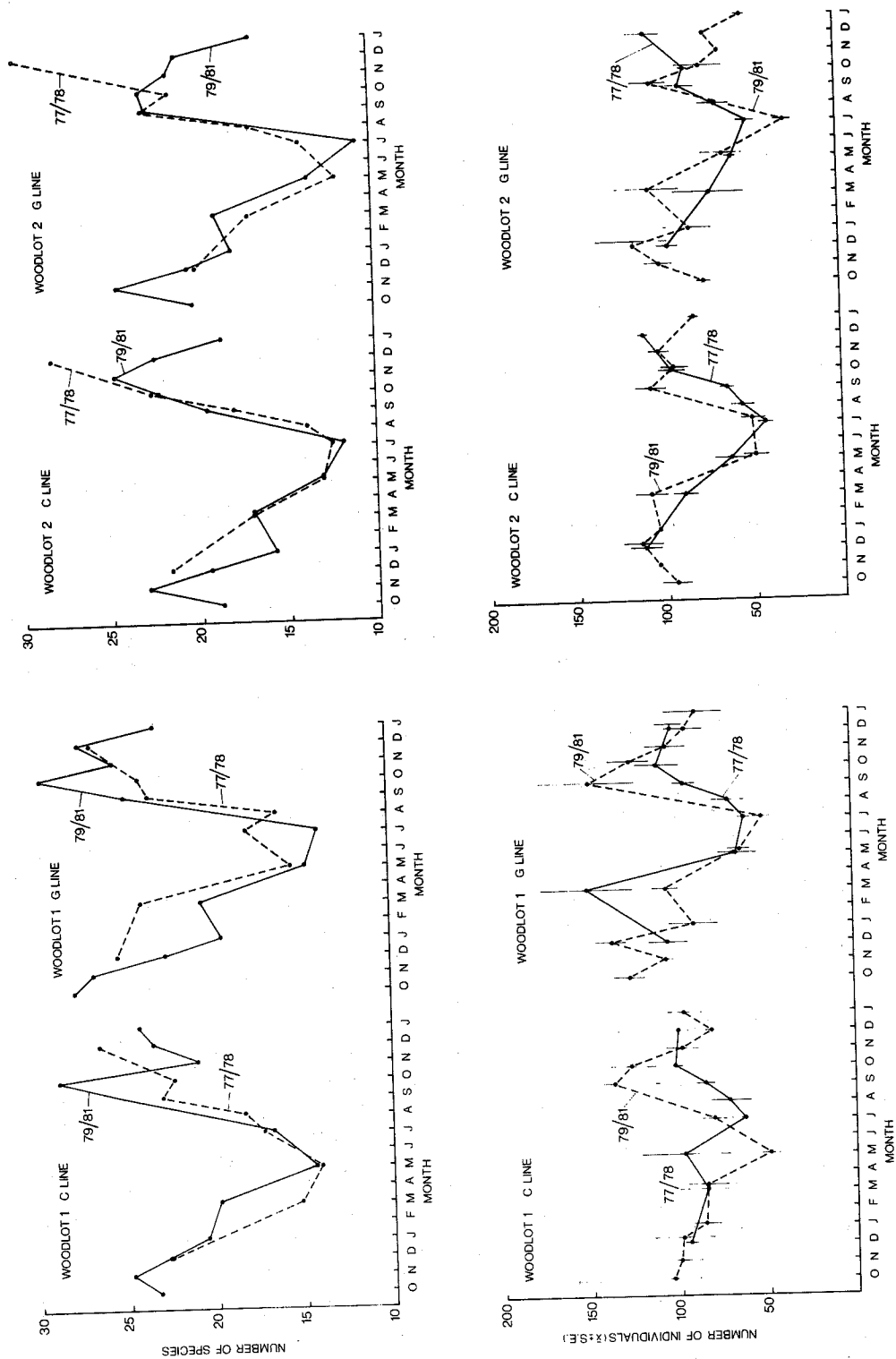


Fig. 2. Average number of species and individuals detected in a 2 h count on each of the woodlot transects during censuses in 1977/78 and 1979/81.

TABLE 3. Numbers of birds banded in 1979/80 and 1980/81 (432 net hours/month)*

Month/Year	1979/80				1980/81			
	Oct	Nov	Dec	Jan	Oct	Nov	Dec	Jan
A. All Species								
Number of Species	26	28	28	27	29	22	23	12
Individuals								
Adults	59	99	103	80	84	60	20	27
Young	1	16	47	100	4	10	11	37
Per Cent Young	2	14	31	56	5	14	35	58
B. Selected Species								
White-throated Treecreeper								
Adults	3	3	12	8	1	4	3	3
Young	0	0	5	2	0	0	7	4
Red-browed Treecreeper								
Adults	6	7	8	1	1	4	3	3
Young	0	2	5	1	0	0	1	0
Flame Robin								
Adults	9	4	7	18	5	6	3	2
Young	0	0	5	65	1	7	6	25
Yellow Robin								
Adults	6	3	6	4	6	1	0	0
Young	0	3	12	5	1	0	1	3

* Data from both woodlots have been combined and only birds identified as adults or juveniles have been used in the tabulations. Numbers include both resident and non-resident birds.

persed from other areas and passed through the study plots. The most obvious were the Flame Robin, White-throated Treecreeper, Golden Whistler *Pachycephala pectoralis* and the Ground Thrush *Zoothera dauma*. It is likely that the Flame Robins and White-throated Treecreepers dispersed from woodlands west of the study plots, and the Golden Whistler and Ground Thrush moved from pine plantations and moist forest south-east of the woodlots.

Mist net captures for the summers of 1979/80 and 1980/81 (Table 3) indicated that about the same number of species were caught each year, but a total of 646 individuals were trapped in 1979/80 and only 273 in 1980/81. The overall proportions of adult birds to those identified as juveniles remained the same. However, for several species, including the Grey Fantail, Golden Whistler and Red-browed Treecreeper *Climacteris erythrops*, the proportion of young birds was lower in 1980 than in 1979.

There are several reasons which might explain the smaller number of birds caught in 1980/81. In contrast to the breeding season of 1979/80, when reproductive success on the woodlots was high, it

was poor for some species during the summer of 1980/81, probably due to drought. The Grey Fantail, Yellow Robin, Flame Robin and Satin Flycatcher *Myiagra cyanoleuca* failed to raise young on the woodlots, and the young birds netted in 1980/81 were individuals dispersing from other places. There was also a decrease in the numbers of resident adults of many breeding species during the summer, suggesting either that birds were moving from the woodlots or that there was increased mortality. The small numbers of Flame Robin, Golden Whistler and Ground Thrush in the summer of 1980/81 would also result if the birds which normally moved through the woodlots dispersed in other directions or moved through more rapidly due perhaps to a shortage of food.

Although the numbers of Red-browed and White-throated Treecreepers caught in nets was lower in 1980/81 than in 1979/80 (Table 3), this was not shown in census results, where the numbers were similar in both years. Since mist net captures can be affected by weather, the dry, warm conditions which prevailed during the summer of 1980/81 may have affected the results. For example, observations in December 1980 suggested that

birds were not foraging as close to the ground as normal, but were moving above the height of the nets (2.5 m) and avoiding capture.

Another possible effect of drought is illustrated by the invasion of Woodlot 2 during 1980 by White-browed Wood-swallows *Artamus superciliosus* (Recher & Schulz unpub. data). These birds normally nest in woodland and shrub habitats west of the tablelands (Reader's Digest 1976), but during drought disperse to the coast where they then nest (Keast 1958). Two colonies totalling 60 pairs established along the G Line where they nested and fledged young. We had not previously recorded this species in the area, and we consider their presence was almost certainly the result of extreme drought conditions further west.

Winter avifauna. There were few differences between winter bird communities in 1978 and 1980 (Fig. 2). Transects differed in species number and the total number of individuals between years in both May and July counts, but the differences were not consistent. Many of the individuals which foraged on the ground (e.g. Flame Robin) or took flying insects (e.g. Grey Fantail) were absent during the winter. As these birds were most affected by drought, fewer differences would be expected between winter avifaunas.

Common species. Despite the effects of the drought, population sizes of the most abundant species were generally similar in 1978 and 1980 (Fig. 3,4), although there were differences in the relative abundances of species between years. These differences may be caused by many factors. In some instances the time of censuses may be important. For example, White-naped Honeyeaters were more numerous in the March 1980 census than in the March 1978 census (Fig. 3). However, this species migrates in the autumn, and the difference between counts may simply mean that the 1980 census coincided with the movement of birds through the woodlots and the 1978 census did not. Variations in the numbers of other honeyeaters can also be explained in this manner. For other birds, the differences in numbers may reflect better conditions and more abundant food resources in one year than another. This is probably the case with the Yellow Robin and White-throated and Red-browed Treecreepers, where mapping of territories confirmed larger populations in 1978 and 1979 than in 1980 (Recher unpub. data). Unfortunately we lack comparative data on food abundances between years, but the moist conditions extending through

1979 following above-average rainfall in 1978 should have favoured more abundant insect populations than were available in the summer of 1980 after two years of drought.

The relative lack of rain in 1980 may have favoured higher winter and breeding populations of Striated Thornbills (Fig. 4). It appears that these birds use a variety of carbohydrates including nectar, manna and honeydew as a source of energy (Recher & Davis unpub. data). Heavy rain in 1978 would have reduced the abundance of these foods on the leaves and twigs where the thornbills forage. The decline from May to July in the numbers of Striated Thornbills on both woodlots was associated with heavy rain (396 mm) and cold conditions in June. The decline could also reflect increased mortality as a result of severe weather which interfered with feeding and increased the thornbills' energy requirements.

Seasonal events

The greatest variation in the numbers of individuals or species between years was small when compared with the changes which occurred between summer and winter. Species richness and the number of individuals on the woodlots was greatest during spring and summer and lowest in winter (Fig. 2).

The abundance of invertebrates and the number of taxa which were sampled were also highest in the summer and lowest in winter (Fig. 5,6,7). Because invertebrates are more active in warm weather, this affects the numbers sampled. The activity and hence the sampled abundance of reptiles also change in this way through the year (G. Webb unpub. data). Hence our ability to sample the kinds of prey which birds are most likely to feed upon is probably an accurate index of their availability to birds. Thus we can conclude that in winter, when energy requirements of birds for individual maintenance were highest because of low temperatures and the short time available for feeding, the invertebrate and reptile prey of birds on the woodlots were less abundant or less available than in summer. These food resources should also decline in agreement with Nix's (1976) growth indices for plants as conditions become hotter or drier in late summer and early autumn.

The pattern of abundance for energy-rich carbohydrates differed from that of the invertebrates. On the woodlots the only source of nectar was from the eucalypt flowers. Nectar was

WHITE-NAPED HONEYEATER

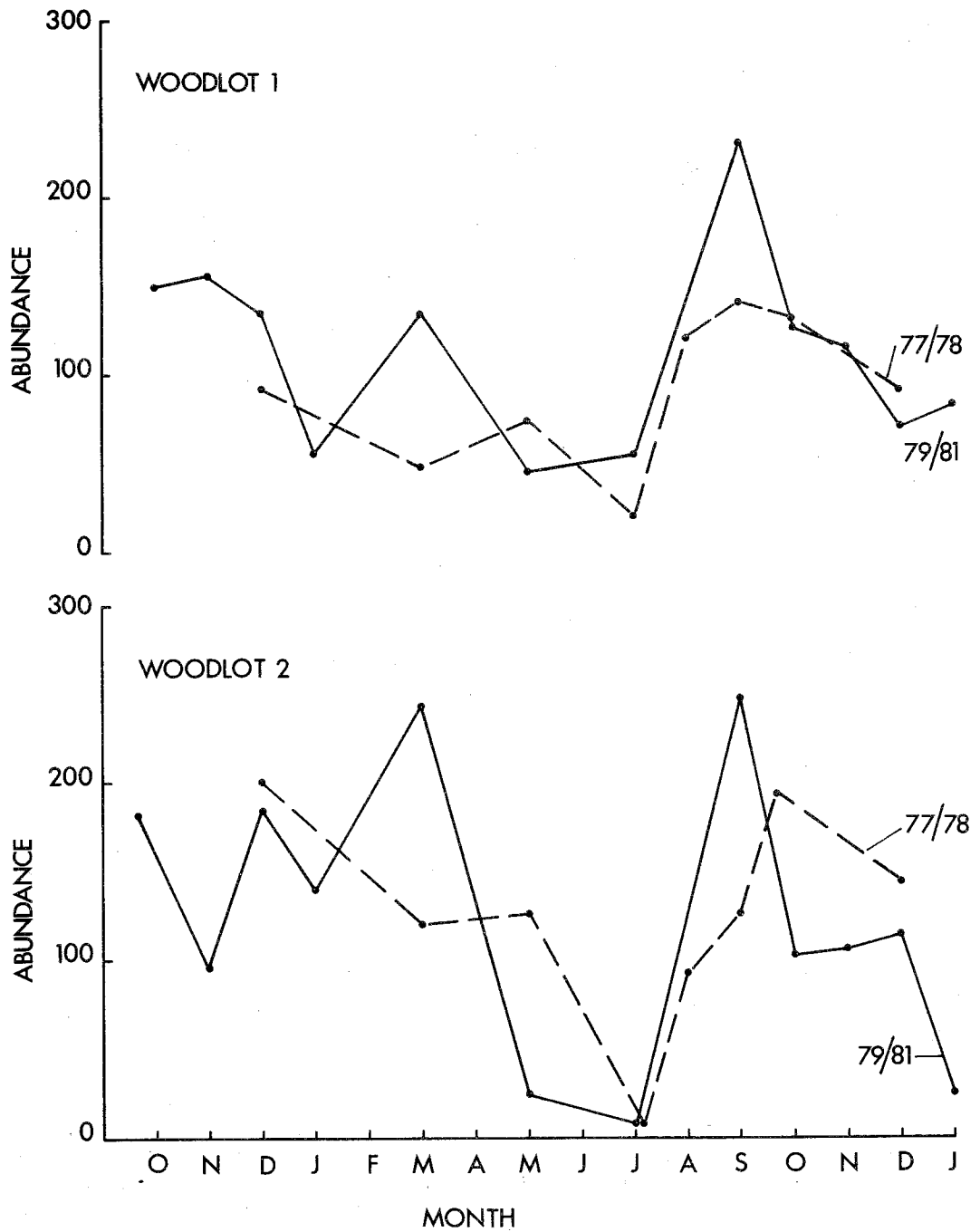


Fig. 3. Abundance of White-naped Honeyeaters based on total detections on woodlots during censuses in 1977/78 and 1979/81. The White-naped Honeyeater was the most abundant nectar-feeding bird on the woodlots and its movements greatly affected the total numbers of nectarivorous birds detected in a census.

STRIATED THORNBILL

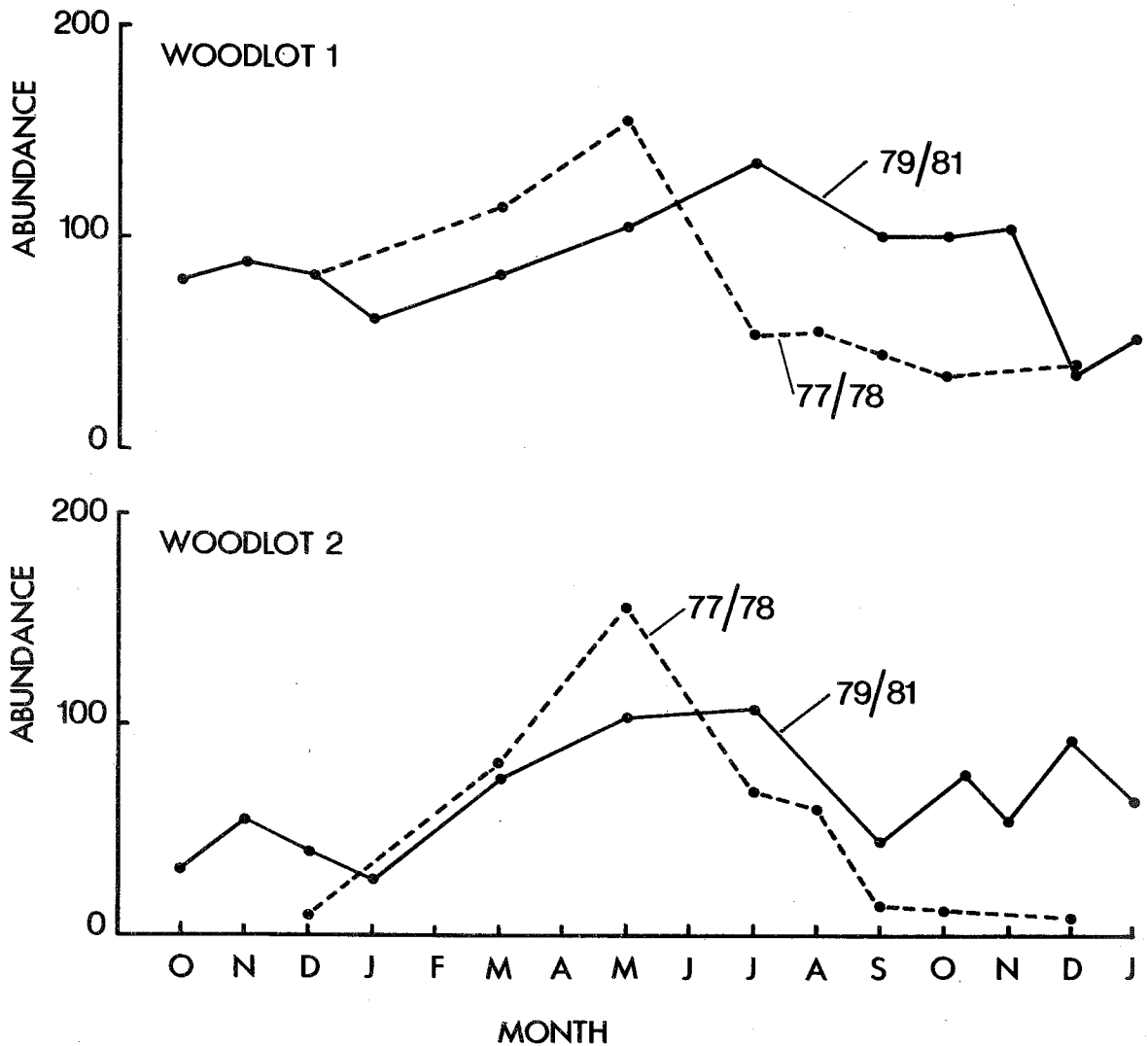


Fig. 4. Abundance of Striated Thornbills based on total detections on woodlots during censuses in 1977/78 and 1979/81.

available at intervals through the year, but was never abundant for much more than a few weeks at a time (Fig. 8). The abundance of flowers also differed from year to year, which in turn affected the abundance of seeds available to parrots which fed on the ripening capsules. Other carbohydrates were associated with loose or peeling bark, and, judging by use by honeyeaters, were most easily obtained in autumn and winter when trees were shedding bark. Birds also obtained honeydew and

manna from insects on the leaves and small branches of eucalypts. These carbohydrates may be used by birds other than honeyeaters and are available throughout the year. However, they are probably most abundant in spring and summer when insects producing them are most likely to be active. For example, the greatest numbers of psyllids were counted on eucalypt leaves from late winter (July) to early summer (November) (Gowing & Recher unpub. data).

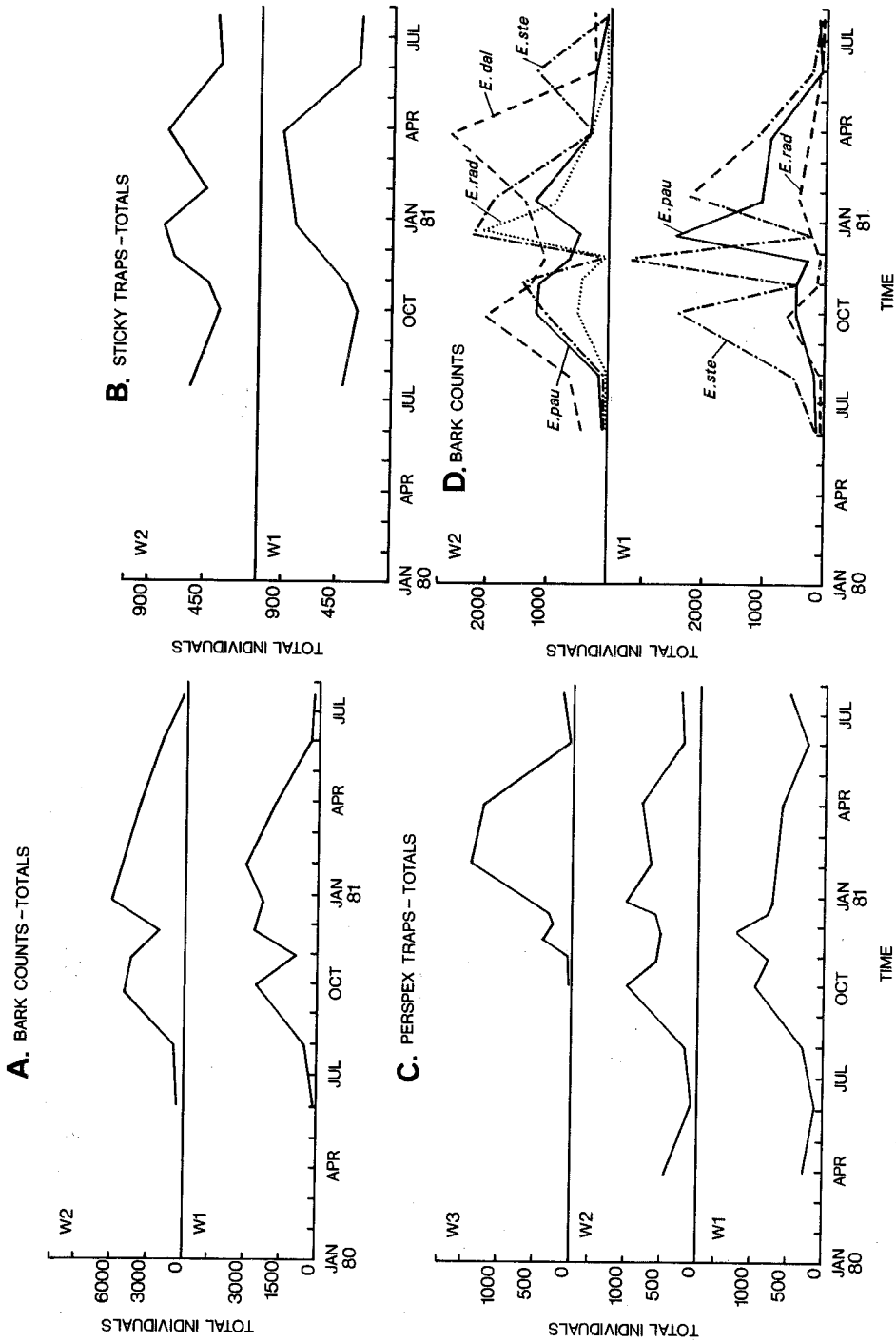


Fig. 5. Number of invertebrates collected on bark (A,D) or trapped with sticky traps (B) and window traps (C), July 1980 — July 1981. Note difference in numbers of invertebrates on bark of different tree species. E. ste = *Eucalyptus stellulata*, E. dal = *E. dalrympleana*, E. rad = *E. radiata*, E. pau = *E. pauciflora*.

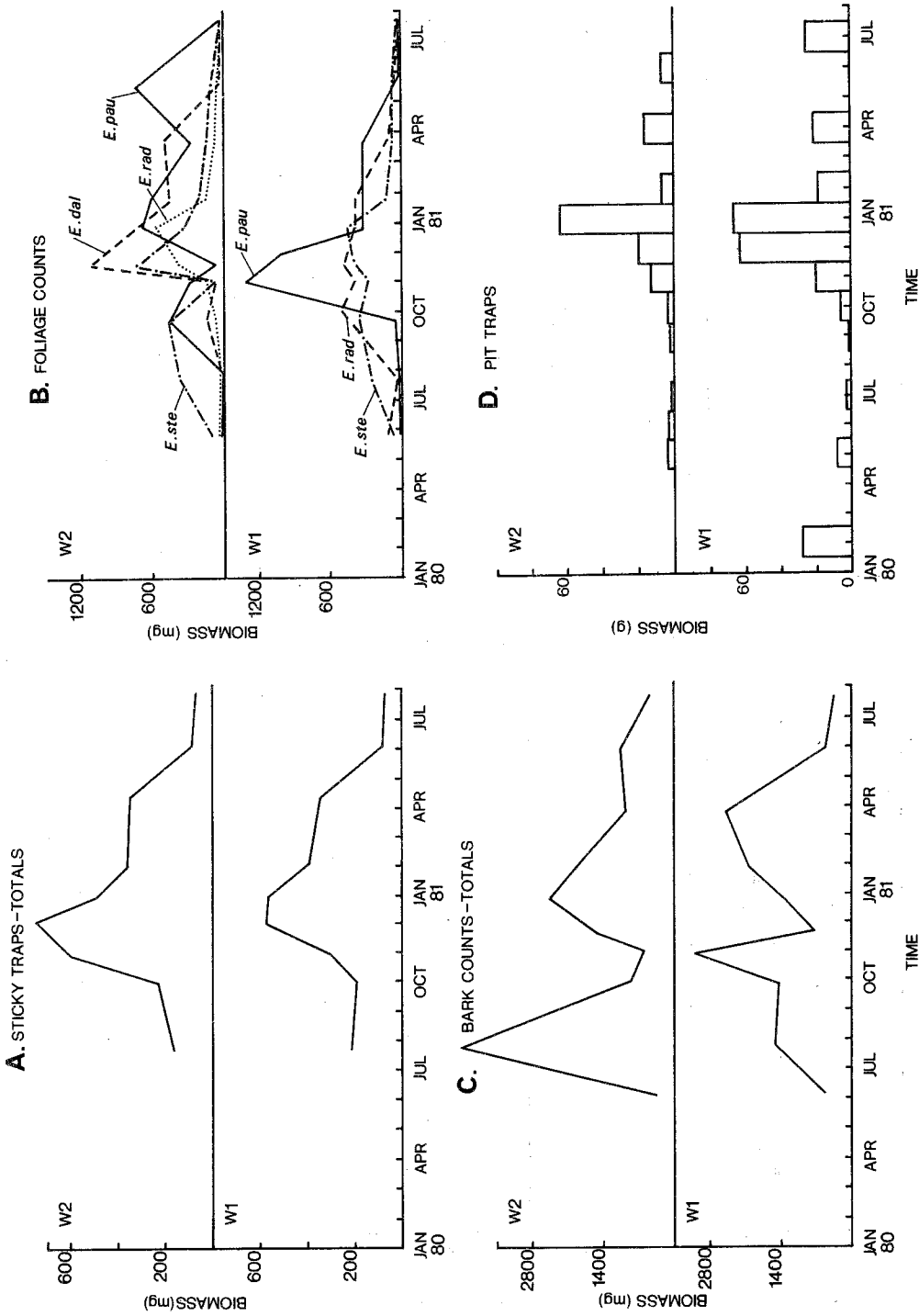
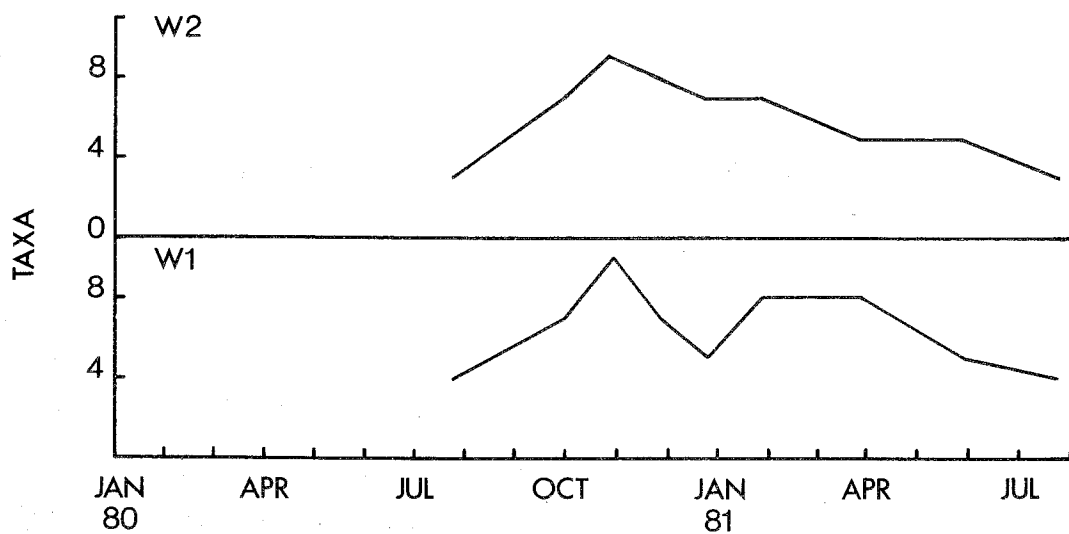


Fig. 6. Biomass of invertebrates collected on sticky traps (A), foliage (B) and bark (C), July 1980 - July 1981, and caught in pit traps (D), January 1980 - July 1981. Note difference in insect biomass on foliage of different tree species and variation between woodlots. Codes as for Fig. 5.

A. STICKY TRAPS - TOTALS



B. PERSPEX TRAPS - TOTALS

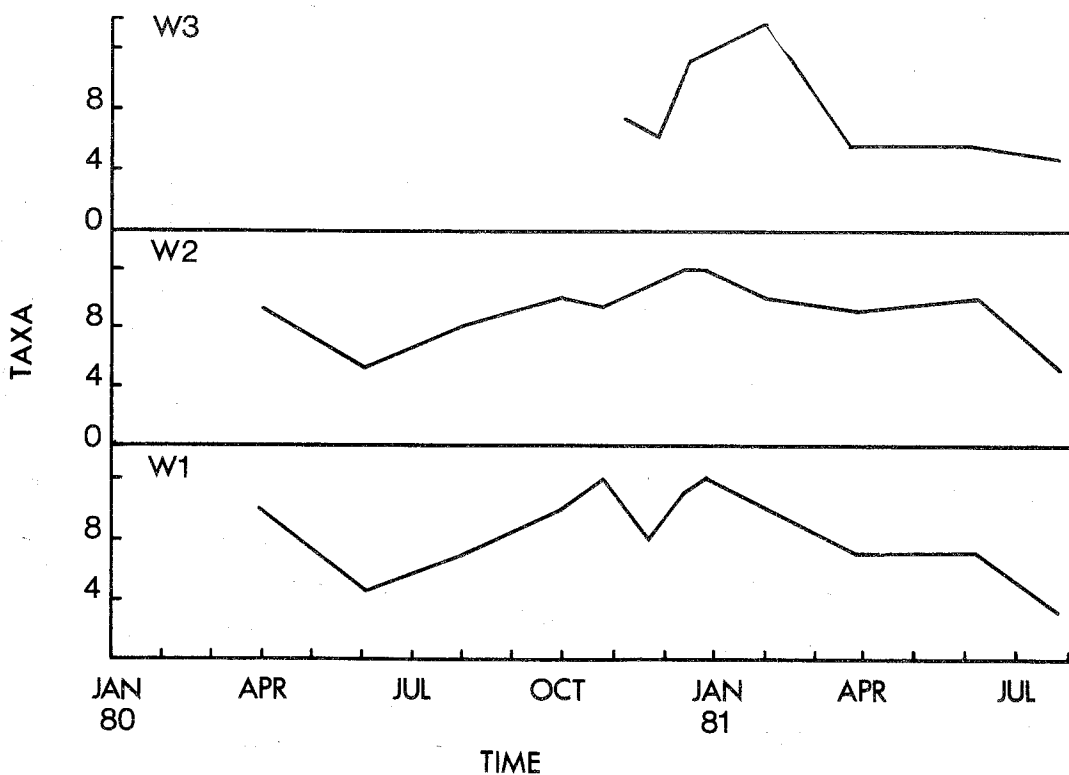


Fig. 7. Number of different invertebrate taxa sampled by sticky traps (A) and window traps (B), July 1980 - July 1981.

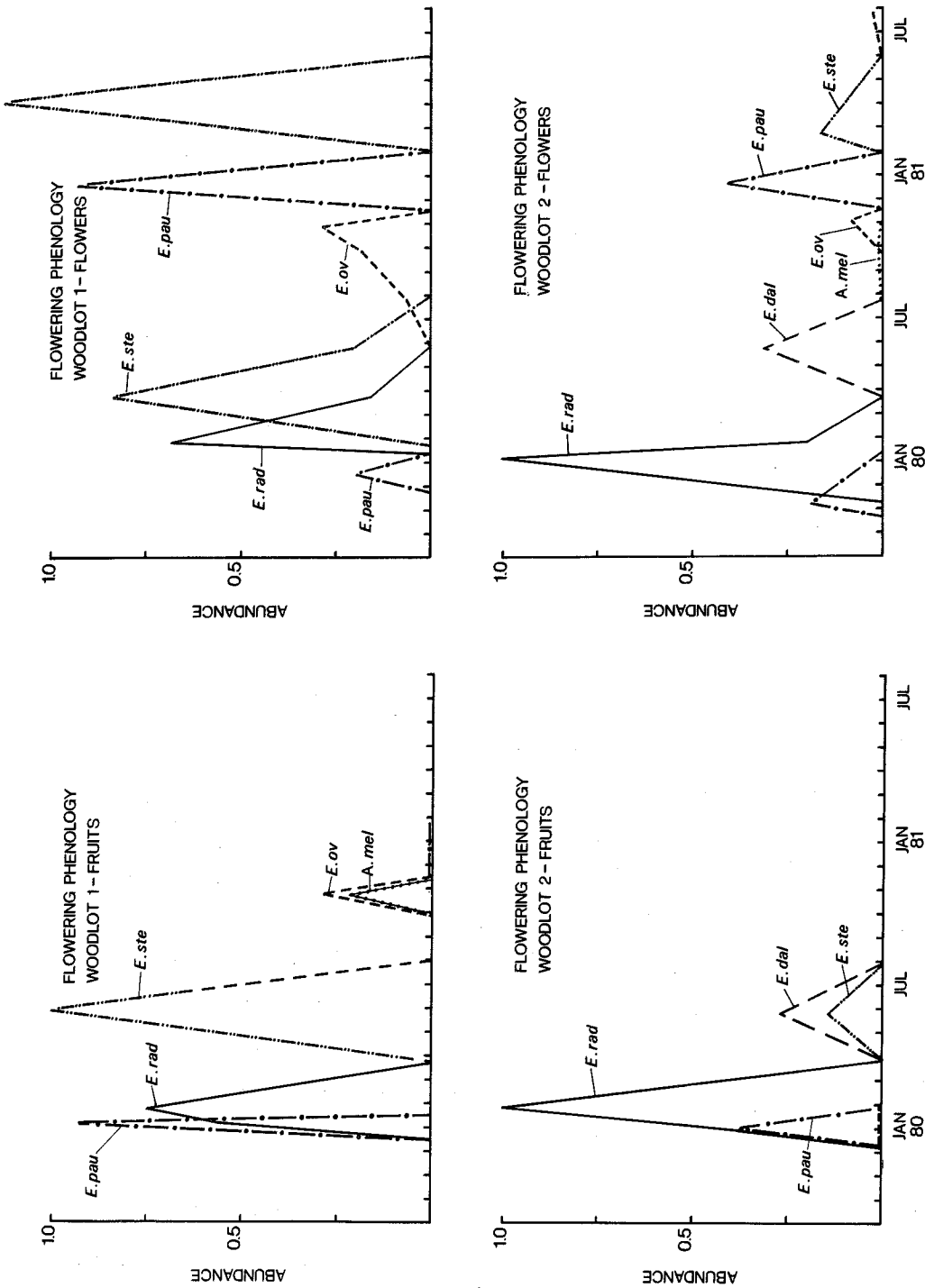


Fig. 8. Abundance of eucalypt flowers and fruits (seed capsules) on woodlots, December 1979 — July 1981. Abundance is simply an index, where the maximum value is taken as unity. *E. ste* = *Eucalyptus stellulata*, *E. dal* = *E. dalrympleana*, *E. rad* = *E. radiata*, *E. ov* = *E. ovata*, *A. mel* = *Acacia melanoxylon*.

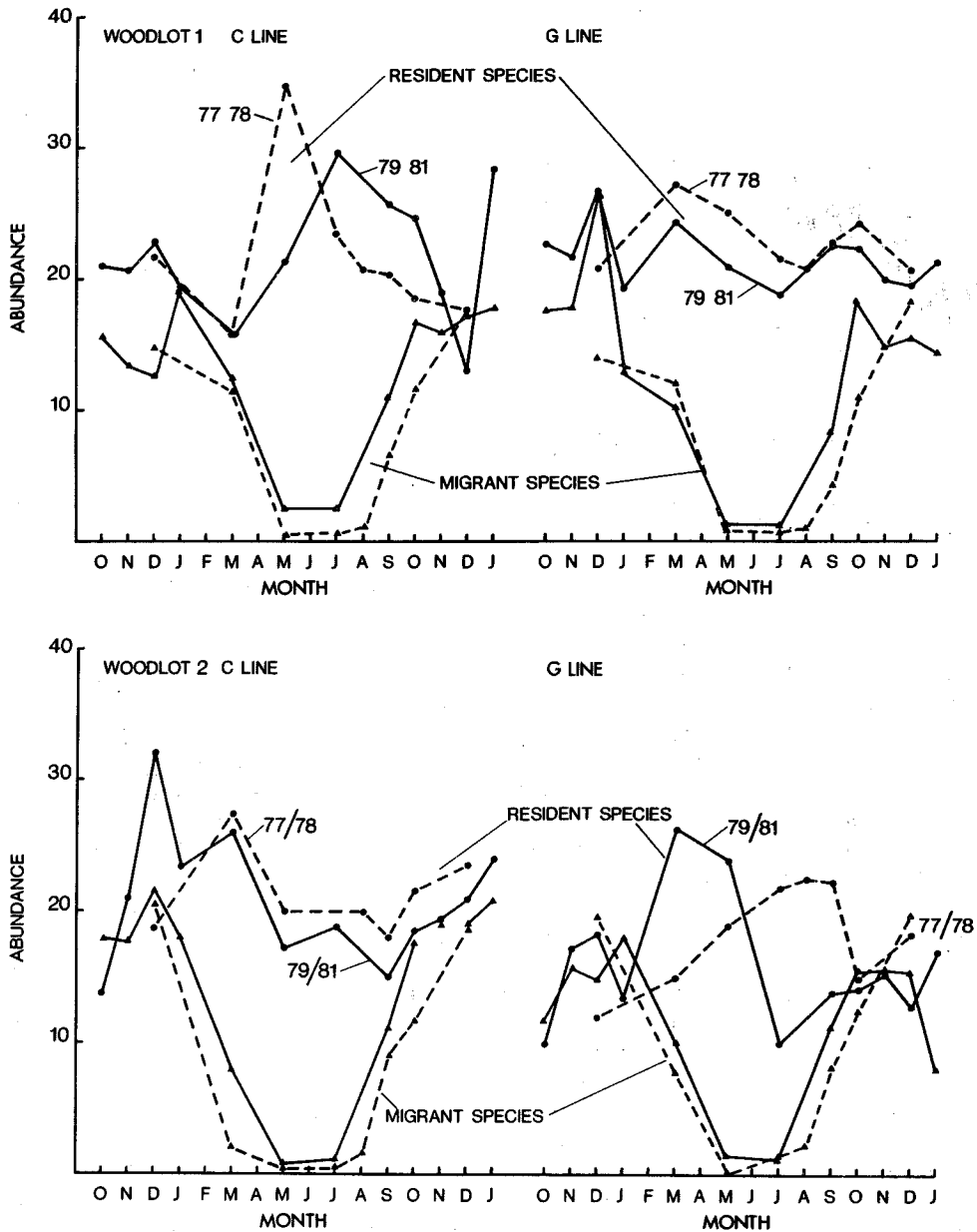


Fig. 9. Relative abundance of migrant and resident insectivorous birds on woodlots, 1977/78 and 1979/81. Abundance is based on the average number of detections of all species during each 2 h count.

Movements of birds

About half the species which nested on the woodlots migrated, i.e. they were absent during the winter or present in very low numbers relative to the size of breeding populations (Fig. 9). Migration

is more common among Australian birds than was thought (Keast 1959; Nix 1976). However, it is not as obvious as in the Northern Hemisphere and relatively few species migrate to the tropics (Purchase 1975). Only nine of the species which nested on the woodlots migrate to the tropics for

the winter; all are insectivorous. Three honeyeaters and the Silvereye *Zosterops lateralis* also migrated, but these species do not reach the tropics and large numbers winter in northern New South Wales. Many of the other birds on the woodlots left during the winter (Fig. 2), but their movements are hard to describe. Perhaps they could be called 'diffuse migrants'. Many probably 'drifted' northwards, but large numbers are present in coastal forests at the same latitude as the study plots. Our view is that altitudinal migration is an important part of their post-breeding dispersal.

Regardless of the nature of the movements, they were not synchronous: species departed and returned at different times. Migrants began to return in August (e.g. Flame Robin, Striated Pardalote *Pardalotus substriatus*), but some, like the Satin Flycatcher and Rufous Whistler, often did not return until late October or November (Fig. 10, 11). Species which returned late were among the first to depart; individuals of these species may winter as far north as New Guinea. Migration or dispersal from the plots began in January and few migrants remained through March (Fig. 2, 10).

Many insect-eaters passed through the woodlots on migration. With the exception of species which were not resident during the summer (e.g. Leaden Flycatcher *Myiagra rubecula*), it was difficult to distinguish these birds unless most residents were colour-banded (e.g. Rufous Whistler). However, except for the Striated Thornbill and pardalotes (Pardalotidae), transient insectivores appeared to migrate in small numbers and individuals spent little time on the woodlots. In effect, migrants were constantly on the move and did not seem to intersperse rapid long-distance movements with bouts of resting and foraging. Migrating birds caught for banding were not fatty (nor were they emaciated), nor did summer visitors accumulate fat before departing. This was true for all species caught, including honeyeaters, and contrasts strongly with the situation in the Northern Hemisphere where migrants accumulate large reserves of fat before migrating and moving long distances in short periods of time (Dorst 1962).

Migrating honeyeaters and silvereyes behaved differently. These birds moved in large flocks and their passage through the woodlots, though transitory, was obvious. The most conspicuous were the Silvereye and the three honeyeaters Red Wattlebird *Anthochaera carunculata*, Yellow-faced Honeyeater *Lichenostomus (Meliphaga) chrysops*, and White-naped Honeyeater. The honeyeaters also nested on the woodlots and the White-naped Honey-

eater was one of the most abundant breeding birds (Fig. 3). Honeyeaters and silvereyes moved north in late summer or autumn and returned south in spring. Generally Red Wattlebirds and White-naped Honeyeaters moved south in September and Yellow-faced Honeyeaters and Silvereyes in October. In other respects the movements of these birds are difficult to describe.

There was often considerable weekly variation in the numbers of White-naped and Brown-headed (*M. brevirostris*) Honeyeaters on the woodlots during summer. Non-breeding birds were abundant and flocks appeared to move over large areas, spending little time at any one place. Pyke & Recher (unpub. data) have made similar observations on heathland honeyeaters north of Sydney. The number of honeyeaters on the heaths is not necessarily related to the abundance of nectar (Pyke unpub. data), but instead seems to be determined by patterns of food abundance on a regional scale (Recher 1981).

When eucalypts were in bloom, honeyeaters visited the flowers and there was an increase in the number of individuals and species on the plots. We did not record massive aggregations of nectar-feeders, and the aggregations that occurred did not always coincide with censuses. There appeared to be a shift of small numbers of Yellow-faced Honeyeaters, Brown-headed Honeyeaters, Crescent Honeyeaters *Phylidonyris pyrrhoptera* and White-eared Honeyeaters *Lichenostomus (Meliphaga) leucotis* from nearby pine plantations and eucalypt forest, where nectar was less abundant, to the woodlots when trees were in full bloom. White-eared and Crescent Honeyeaters also increased their use of the woodlots during autumn and winter when trees shed bark and exposed other carbohydrates.

A detailed analysis of the relation between numbers of honeyeaters and food resources will require the measurement of abundance of all energy-rich carbohydrates, more frequent censuses and a regional assessment of the distribution and abundance of nectar-rich flowers.

Birds other than honeyeaters responded to increased food availability on the woodlots. In autumn, the Crimson Rosella *Platycercus elegans* and Gang-gang Cockatoo *Callocephalon fimbriatum* congregated on narrow-leaved peppermint trees and fed on ripening capsules (Fig. 11). Gang-gangs also responded to the ripening capsules of snow gums. Flocks of Crimson Rosellas moved onto the plots in June (and, hence, were not censused) to feed on carbohydrates exposed on the terminal

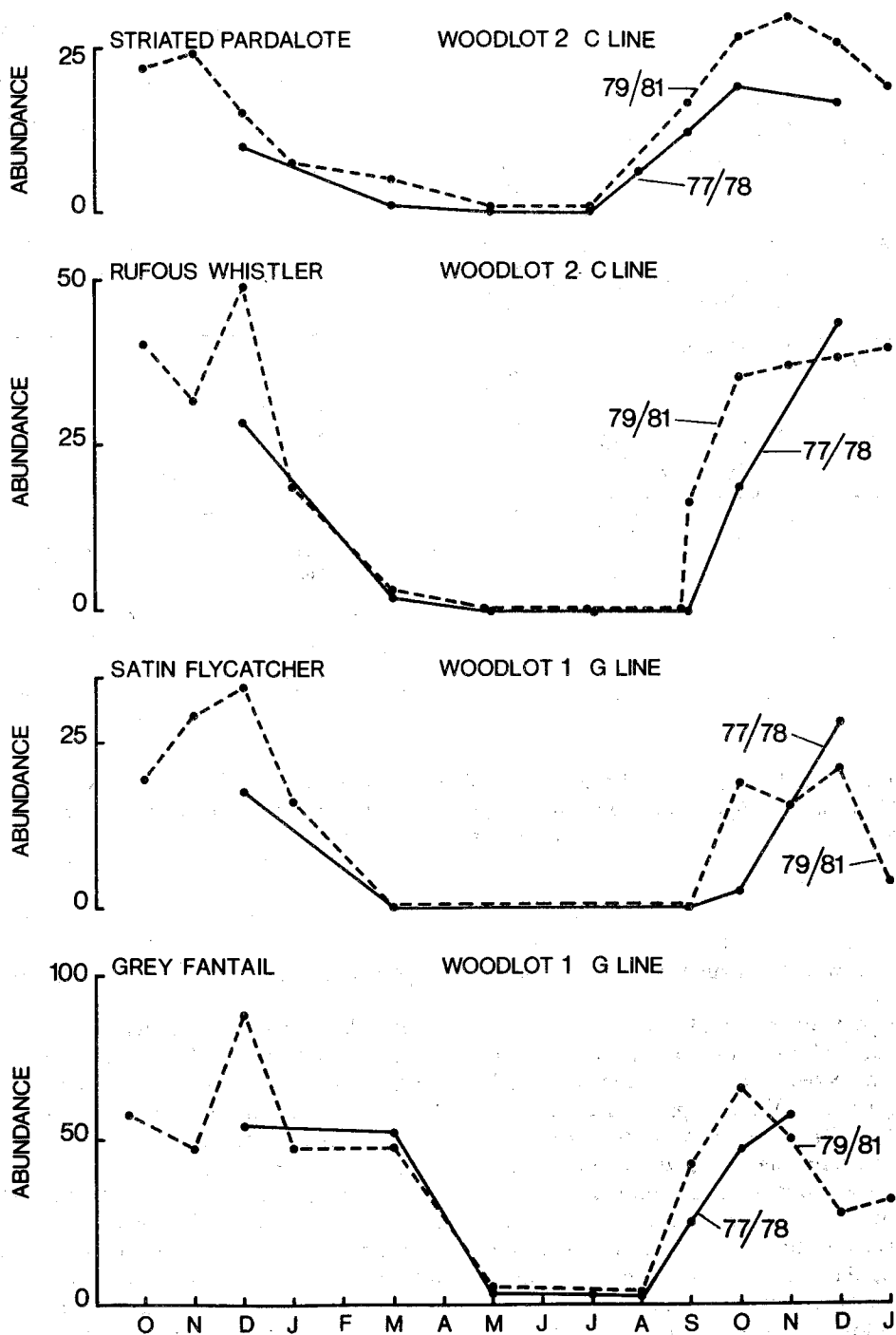


Fig. 10. Relative abundance of Striated Pardalote, Rufous Whistler, Satin Flycatcher and Grey Fantail, 1977/78 and 1979/81. The species are migrants absent during the winter, but migrating at different times. Abundance is based on total detections during a census, but only the transect on which the species was most abundant is illustrated. Patterns of change were the same for all transects.

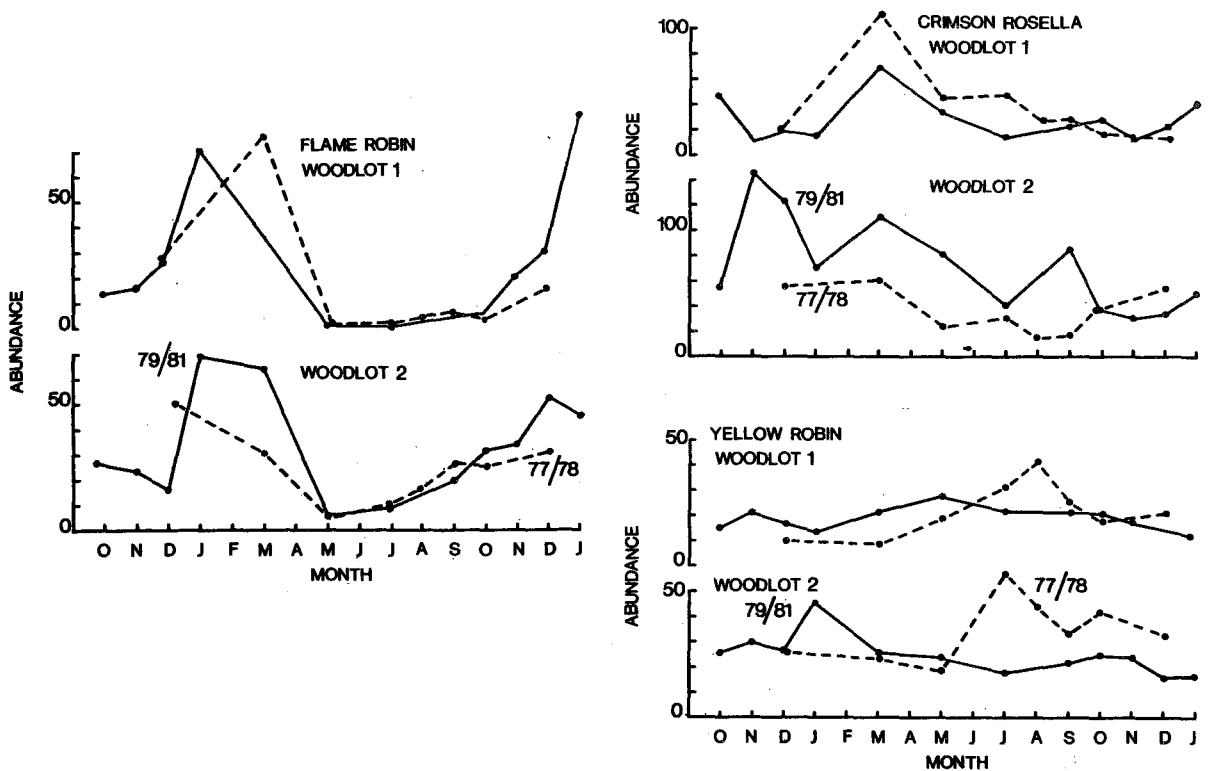


Fig. 11. Relative abundance of Flame Robin, Crimson Rosella and Yellow Robin on woodlots, 1977/78 and 1979/81. Abundance is based on total detections during a census with counts from both transects combined.

branches of narrow-leaved peppermints as bark was shed.

Although part of a post-breeding dispersal, flocks of Flame Robins remained on the woodlots through autumn when they fed mainly on small insects emerging from the droppings of cattle and sheep (Fig. 11). Within the woodlots, Yellow Robins shifted from the forest habitats, where they mostly nested, to the woodland. This contributed to higher numbers of detections during winter, but from colour-band records there was no evidence of an increase in population. The shift to the woodlands was probably related to the warming effect of more sunlight reaching the ground and a consequent increase in the activity of ground invertebrates in the woodland habitats relative to the forest. An opposite shift occurred in late summer when a number of species (e.g. Grey Fantail) which nested in the woodland shifted to the forest as the woodland dried out with the summer heat.

Reproduction and post-breeding dispersal

Resident species commenced nesting on the woodlots in winter. Lyrebirds *Menura novae-hollandiae* had eggs by July and Striated Thornbills began nest building in early August. By October all resident species had eggs or young. Migrants began to nest as soon as they returned. The greatest number of species and individuals nested from late September to early December. The number of active nests on the woodlots had declined rapidly by January when few birds were nesting (Fig. 12). Late nests were almost always attempts at re-nesting by birds which had failed in their earlier efforts. Although these nests were completed and in some cases eggs laid, we have no records of any such nests started after December 25th being successful. However, the Red-browed Finch *Emblema temporalis*, which sometimes initiated nesting at this time in response to the availability

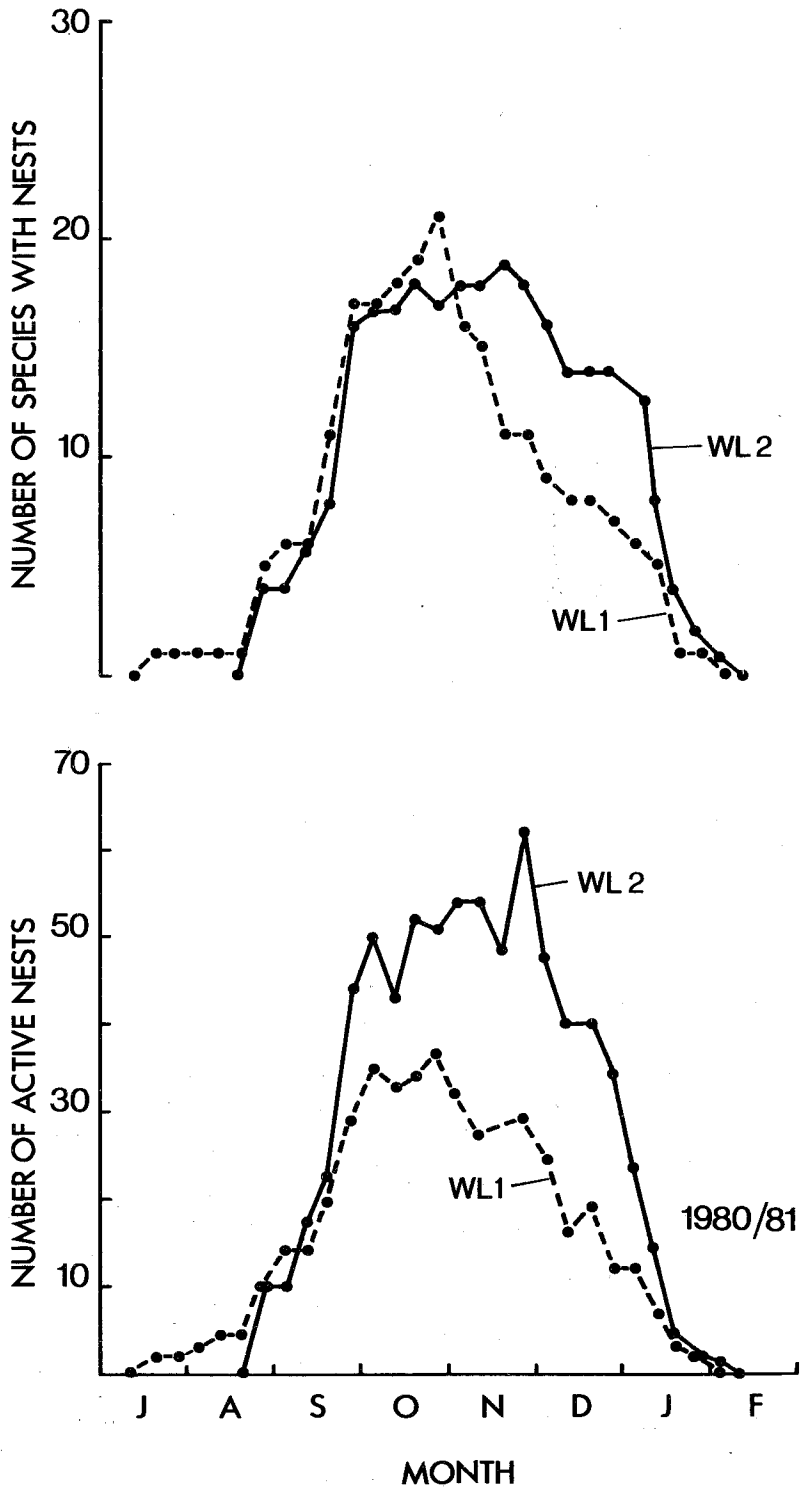


Fig. 12. Numbers of breeding species and active nests on woodlots during each fortnight, 1980/81 breeding season.

of grass and weed seeds, did successfully raise young.

In the strict meaning of the word, we did not monitor the success of individual nests. In most years young birds were abundant during December and January (Table 3) and many could be associated with colour-banded adults. Thus, there were individuals fledged from nests on the woodlots, as well as young birds dispersing from other areas. As mentioned earlier, nest success for some species on the woodlots was poor in 1980 due to drought.

Nesting by birds on the woodlots coincided with conditions most favourable for plant growth (Fig. 1) and was initiated when invertebrate food resources were increasing (Fig. 5, 6). At the time when most species were feeding young, insects from all substrates were abundant. Hence young were fledged and became independent during the period when food was probably at its maximal abundance.

Although the drought affected the amount of food available for birds, we consider the pattern of abundance through the summer of 1980 to be an accurate portrayal of conditions when rainfall is normal. Insect abundance on a third plot, located in moist forest where drought effects were less severe, changed through the summer in the same ways as on the woodlots. Peak abundances were recorded later in the summer than on the woodlots, but this was consistent with differences on the woodlots themselves. Numbers of invertebrates tended to increase earlier in the summer in the woodland areas of the study plots than in the forest. As conditions became hot and dry in mid-summer, insect abundance in the woodland fell, but remained high in the moister and cooler forest. The third plot was an extension of this sequence.

Some of the variation in numbers of birds on the woodlots during late spring and early summer was the result of bird behaviour during the breeding season. When birds were actively engaged in territorial interactions, detection of individuals was facilitated and resulted in high counts during censuses. This was particularly true when migrants first returned. After laying eggs, birds were less conspicuous and counts may have been correspondingly lower. Our view is that, except during the very dry periods, there was relatively little change in the numbers of birds during late spring and summer until young were fledged and post-breeding dispersals were initiated.

After fledging young, many birds dispersed from the woodlots. Among the first to leave were long-distance migrants such as cuckoos, flycatchers, the Rufous Fantail, Satin Flycatcher and Rufous

Whistler. Except for the fantail, these birds mostly fed on large insects and were probably dependent upon peak flushes or emergences of insects such as cicadas, beetles and various foliage eating larvae. The time when food was abundant for these birds was therefore restricted. The fantail is a foraging specialist which exploits insects within 1 m of the ground (Recher & Holmes unpub. data). At Bondi, it probably obtained enough food only when insects were maximally abundant.

At the same time as this dispersal from the woodlots, species dispersing from other habitats appeared on the plots. During December and January there were substantial increases in the numbers of White-throated and Red-browed Treecreepers (Fig. 13), Flame Robin, Golden Whistler and Ground Thrush. Mostly these were juveniles, but often they were accompanied by adults (Table 3). Since the resident adults of these species on the woodlots did not disperse, we conclude that transients moved from places or habitats with declining food resources. The numbers of invertebrates remained high on the woodlots through January and February, decreasing only in the hotter and drier parts of the woodland.

Discussion

Reproduction, the dispersal of young and migration are seasonal events which resulted in substantial changes in the abundance and composition of the avifauna. However, species richness, the number of individuals and their distribution on the woodlots were strongly linked to the abundance and distribution of prey organisms. Reproduction and migration in particular were tied to the seasonal changes in invertebrate numbers. This is the same pattern that Marchant (1981) reported for forest birds at Moruya and that Nix (1976) reported for all groups of terrestrial birds at Canberra and predicted for south-eastern avifaunas in general. Apart from this basic pattern of change, which is linked to temperature mediated pulses in plant growth and avian reproductive cycles, there are other changes which occur in the distribution and abundance of forest birds.

Foremost among the less predictable events at Bondi were the changes in the avifauna caused by drought. Its impact on reproductive success and changed patterns of movement may have long-term consequences for the avifauna, but indicated the

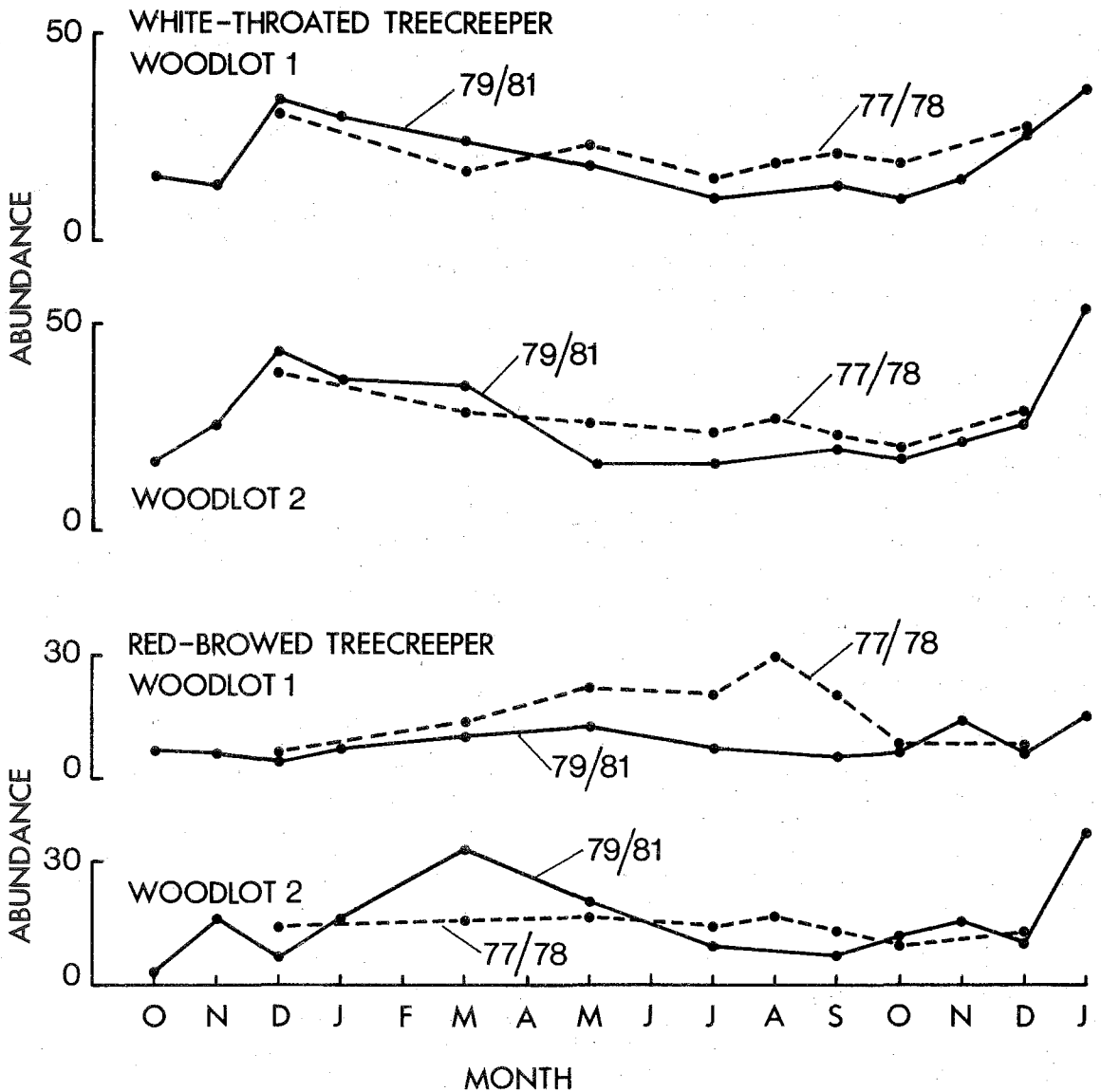


Fig. 13. Relative abundance of treecreepers on woodlots, 1977/78 and 1979/81. Abundance is based on total detections during a census with counts from both transects combined.

importance of alternative habitats as refuges during periods of climatic instability. Other seasonal events have been largely overlooked in the literature, but are probably linked to annual cycles of plant growth. Changes in the kinds of prey and the abundance of alternative carbohydrates when eucalypts shed their bark may be the most significant. For example, it appears that alternative carbohydrates may be the critical resource permitting small passerines (among others) to over-

winter in cold climates (Recher & Davis unpub. data).

The amount of nectar-rich blossom and shed-bark are probably related to the age of trees, older and larger trees producing more resources than young ones. This may be difficult to recognise or monitor, but suggests another impact on the forest fauna that could eventuate from reducing the average age of trees by timber harvesting or from wildfire.

Much of the seasonal change in the forest avifauna was diffuse. Climates in south-eastern Australia are generally mild, the vegetation is evergreen and invertebrate prey are active throughout the year. Although the breeding season and the movements of long-distance migrants may be 'short and sharp' (Marchant 1981), almost all changes and movements at Bondi were protracted and sometimes difficult to detect. Nonetheless our data indicate that the forest avifauna of south-eastern Australia is exceedingly dynamic and this requires consideration in the management of forest environments.

Perhaps easiest and most important to recognise is the need of birds for alternative forest habitats. These are the places used in drought, as way stations during migration and as alternative feeding areas when different plants blossom or trees shed bark. The long distance that birds move during migration and in post-breeding dispersal requires regional management. It achieves little to reserve breeding habitat, if the avifauna which nests there is deprived of a place to winter. Nix (1976) observed that the predicted wintering areas for south-eastern bird populations have been massively disturbed by agricultural development. The intensification of forest management in the last 15 years, with the introduction of extensive hardwood pulp industries and the clearing of large areas of native forest for plantations of exotic pines, has expanded the nature of this disturbance. Birds must have not only alternate areas for breeding and wintering but also areas for loafing and refuelling along migration routes.

It is evident from our observations that Australian forest birds rely on a regular supply of food along whichever paths are followed in their movements. This is a consequence of the year-round availability of food in coastal habitats. However, it does mean that they may not be able to move long distances between widely separated and isolated habitats. Forest managers therefore need to ensure continuity of habitats along the length of the continent. It is especially important that major reserves be linked by corridors of relatively undisturbed vegetation.

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References

- Bell H. (1980) The effects of a power-line clearing on birds of dry sclerophyll Forest at Black Mountain Reserve, Australian Capital Territory. *Corella* 4, 8-19.
- Courtney J. & Marchant S. (1971) Breeding details of some common birds in south-eastern Australia. *Emu* 71, 121-33.
- Dorst J. (1962) *The migrations of birds*. H. Mifflin Co., Boston.
- Emlen J.T. (1977) Estimating breeding season bird densities from transect counts. *Auk* 94, 455-68.
- Franzreb K.E. (1981) The determination of avian densities using the variable-strip and fixed width transect surveying methods. In: *Estimating numbers of terrestrial birds* (eds C.J. Ralph and J.M. Scott), pp. 139-45. Cooper Ornithological Society Studies in Avian Biology No. 6.
- Keast A. (1958) Seasonal movements and geographic variations in the Australian wood-swallows (Artamidae). *Emu* 58, 207-18.
- Keast A. (1959) Australian birds: their zoogeography and adaptations to an arid continent. In: *Biogeography and ecology in Australia* (eds A. Keast, R. L. Crocker and C. S. Christian), pp. 115-35. Dr. W. Junk, The Hague.
- Lack D. (1950) The breeding seasons of European birds. *Ibis* 92, 228-316.
- Lack D. (1954) *The natural regulation of animal numbers*. Oxford University Press, London.
- Marchant S. (1981) The breeding season at Moruya, New South Wales. *Corella* 5, 19-25.
- Nix H.A. (1976) Environmental control of breeding, post-breeding dispersal and migration of birds in the Australian region. In: *Proceedings of the 16th International Ornithological Congress* (eds H.J. Frith and J.H. Calaby), pp. 272-306. Australian Academy of Science, Canberra.
- Paton D.C. (1980) The importance of manna, honeydew and lerp in the diet of honeyeaters. *Emu* 80, 213-26.

Purchase D. (1975) Bird movements in Australia. *Emu* 74 Suppl., 317-18.

Pyke G.H. (1980) The foraging behaviour of Australian honeyeaters: a review and some comparisons with hummingbirds. *Aust. J. Ecol.* 5, 343-70.

Reader's Digest (1976) *Complete book of Australian birds*. Reader's Digest Services Pty Ltd, Sydney.

Recher H.F. (1981) Nectar-feeding and its evolution among Australian vertebrates. In: *Ecological biogeography of Australia* (ed. A. Keast), pp. 1637-48. Dr. W. Junk, The Hague.