

## Chapter 11

## FOOD AVAILABILITY AND DIET

## 11.1 Introduction

While differences in the foraging behaviour of closely-related syntopic species of birds are often assumed to relate to dietary differences, relatively few studies have attempted to quantify the foods eaten, and even fewer investigate the availability of food at foraging sites. Temporal shifts in foraging behaviour of insectivores are often treated as evidence of changes in the availability of arthropods, despite inadequate documentation of the latter. At high latitudes where winters are harsh and the majority of birds are migratory, this inference is perhaps justified. Prominent among overwintering birds in northern North America are woodpeckers and nuthatches, many species of which have been shown to switch from an insectivorous diet in warm months to a primarily granivorous or frugivorous one in cold months (e.g. Stållcup 1968; Conner 1979; Williams and Batzli 1979a).

Treecreepers are entirely insectivorous during the non-breeding season (Noske 1979). Though there have been no studies of the foods eaten by sittellas, observations of their foraging behaviour and information in Lea and Gray (1936) indicate that they are also largely insectivorous. As shown in the present study, differences in their foraging patterns were largely based on texture and condition of bark; selection of tree-types by each species reflected these differences. The two treecreepers at Wollomombi also showed marked seasonal and diurnal variation in their choice of foraging substrates. With these sources of variation in mind, I asked the following questions relating to food availability:

- (1) Does the abundance of bark-dwelling arthropods differ between tree (or bark) types, and how much does this vary temporally?
- (2) Do the types of arthropods on the bark differ according to the type of tree and time of year?

These questions posed several problems. Due to obvious differences in the structure of their bark (e.g. in thickness and volume), tree-types were not directly comparable; thus, comparisons at this level were not entirely valid. Secondly, owing to the inaccessibility of most branches on eucalypts at the study sites, the present investigation was restricted to the lower trunk. Food availability was therefore, only assessed for a narrow part of the vertical range of the birds studied. This limitation was somewhat counter-balanced by the fact that bark texture was more important than height in separating the species in their foraging behaviour.

In the previous study (Noske 1979), I showed that the diets of the three species of treecreepers were basically similar, and that their major food was ants. However, these findings were based on an examination of a small sample of stomachs of birds taken from widely separated localities and was confined to the non-breeding season. A more detailed account of the foods eaten by these species might detect some dietary differences associated with their differential selection of foraging substrates. Intraspecific variation in diet might also be expected owing to temporal and/or sexual differences in the foraging behaviour of all the study species. Indeed, Williams (1980) discerned sexual differences in the food of Downy Woodpeckers which related to their differentiated foraging substrates and techniques.

## 11.2 Methods

### 11.2.1 Food availability

There does not appear to be any established technique for sampling the invertebrate macrofauna of bark. Calder (1973) and Lawrie (1974) examined the arthropod communities of the lower trunks of eucalypts by collecting small samples of bark with a metal corer or axe, and extracting the arthropods with Tullgren funnels. However, most of the animals they found seemed too small (less than 1 mm) or too deeply buried to be profitable food sources for the birds in this study. Jackson (1979) collected arthropods from the surface of trunks using a paint brush dipped in alcohol. This method seemed inefficient to adequately quantify large numbers of arthropods and apparently ignored those occurring beneath the bark surface.

Treecreepers and sittellas obtained prey from the surface of the bark, as well as underneath it, particularly inside ribbons of peeling bark. They excavated bark to gain access to surface-dwelling arthropods which hid in crevices and possibly, to expose arthropods (and their eggs) which lived permanently beneath the bark surface. In order to sample arthropods from both above and below the surface, I employed two methods: (1) "surface censuses", in which marked areas (on tree trunks) were repeatedly examined and left undisturbed, and (2) "bark collections", in which bark was removed from tree-trunks and collected in plastic bags for subsequent analysis. Although the latter method did not discriminate between surface- and sub-surface-dwelling arthropods, it ensured the inclusion of those that were hidden or inactive during surface censuses.

#### *Surface Censuses*

At Wollomombi, eight mature trees of each of the four major tree-types were selected randomly within an area of 5 hectares in the western half of the study site. Long nails were used to mark the corners of grids measuring  $50 \times 50$  centimetres, or  $25 \times 100$  centimetres on the trunks of each tree between one and two metres from the ground. Thus, ignoring surface irregularities (e.g. corrugation and loose bark), all grids had the same surface area (2,500 sq.cm.). Grids were placed on both north and south faces of each tree-trunk to avoid sampling bias associated with aspect. At Swan Vale, I marked 30 trees, representing all seven tree-types, from four plots in the eastern sector; three plots were in lightly-wooded areas, and the other, just inside the forest.

From March 1978 to March 1980 (January 1980 at Swan Vale), I counted the arthropods on each marked tree at both sites on one day each month. Two censuses were conducted: one during the morning (08:00-11:00 hours) and the other in the afternoon (14:00-17:00). Censuses were conducted only on fine days; air temperature was recorded at the beginning and end of each censusing period. For each census I walked a standard route, visiting each tree (grid) in the same sequence. Each grid was inspected thoroughly for 2.5 to 3 minutes, during which the bark surface was tapped lightly in order to flush any cryptic arthropods and loose bark lifted to expose hidden ones. Care was taken not to damage or alter the bark structure though several gums shed their rough bark through natural means.

During each census, the number, type and length (to nearest mm) of all arthropods observed was recorded directly onto data sheets; only animals within the grid areas were counted. When large numbers of ants were encountered (usually in a narrow vertical band), the number of individuals within the grid was counted three times and the average recorded. Few flying insects alighted on grids during inspection, but many departed; those which flushed too rapidly to permit identification were assigned to an "unknown" category. On the final census, specimens of the more common arthropods were collected for identification.

### *Bark Collections*

This method was essentially opportunistic, as many trees proved unsuitable for sampling: the bark of some stringybarks for instance, was too hard and compacted to enable its collection, and the thin, flaky bark of many boxes too superficial. Consequently, trees with loosely fibrous or crumbly (friable) bark were favoured. Only gums with rough bark near the base were sampled, and ironbarks (at Swan Vale) were excluded owing to their tough persistent bark. The apparent bias of this sampling technique was somewhat compensated by the fact that such situations provide protection and shelter for bark-dwelling arthropods (e.g. Curtis and Morton 1974) as well as sites for excavation by birds.

During the first year of surface censuses, bark-collecting sites were chosen from within the censusing area to make results more comparable. Two trees of each of the four major types were sampled each month during the late afternoon. Dead bark was collected from standing dead trees, or branches of live trees, but this was discontinued after winter owing to sampling difficulties. All other samples were taken from trunks at heights between 0.5 and 2.0 metres. In the second year I collected samples of peeling curled bark from the smooth branches of boxes (*E. sp. aff. cypellocarpa*) on the north-eastern fringe of the Wollomombi study site, where trees were stunted and branches accessible. Samples from nearby stringybarks (trunks) were taken concurrently for comparison.

The bark was torn from the tree by hand or with large forceps, and allowed to drop into a plastic bag pinned below the selected site or

held in position by a second person. After collection, bags were weighed and the wet weight of the bark determined. Cottonwool saturated with chloroform was inserted into the bag, which was then sealed. Samples were collected on the final day of field trips so that they could be examined in the laboratory on the following day. The bark was sorted thoroughly by hand and any arthropods found were stored in 70% alcohol.

Arthropods from each sample were examined in petri dishes under a binocular microscope and identified to family level, where possible, using CSIRO (1973) and Clyne (1969). Representatives of common taxa were sent to entomologists at the Division of Entomology, CSIRO, Canberra, and other institutions, for identification to lower taxonomic levels. The length of each arthropod was measured from the frons to the tip of the abdomen against millimetre graph paper placed under the petri dish. Although generalized regression equations have been developed for estimating the dry weight of insects based on length (e.g. Rogers *et al.* 1976), this relationship varies considerably between different taxa. Zug and Zug (1979) calculated power equations and correlation coefficients for "live" weight-length relationships of 18 different arthropod taxa. Due to inaccuracies in their computations, I recalculated these equations (data supplied by G. Zug), and used them to estimate wet weights of arthropods from their recorded lengths.

The weight of individual bark samples varied with the availability of suitable bark on trees selected, but the total weight of bark from each tree-type was roughly equivalent for each season. To compare individual samples, the number and biomass of arthropods in each was corrected to a standard (100 grams). Because the bark of each tree-type differed in depth and density, it was impractical to collect samples of equivalent weights or surface areas; interspecific comparisons were therefore limited.

#### *Statistical Analysis*

Numbers and biomass (represented by wet weight) of arthropods recorded during surface censuses were subjected to 4-way analyses of variance using NEVA (Burr 1980), with factors: year, month, time of day and tree-type. Results from these tests were interpreted cautiously because of possible serial correlation effects due to repeated sampling of

the same trees. Data from bark collections were analysed similarly, with three factors: bark weight, season and tree-type. Residuals for each test were examined and appropriate transformations applied where necessary. Chi-square tests were used to compare the frequency of occurrence of different taxa on different tree-types and over the four seasons. Taxonomic diversity ( $H'$ ) was calculated using the formula given in Section 9.2.2.

#### 11.2.2 Diet

Data on the diet of each species were collected using three methods: (1) analysis of stomach contents, (2) collection of faeces, and (3) direct observation of prey taken.

##### *Stomach Contents*

Up to three specimens of each species were collected (see Section 2.2.3) each month between March 1978 and March 1979 from areas outside the study sites. "Wollomombi" specimens were taken from two areas, two and eleven kilometres from the study site. The latter locality was characterized by taller trees than typical of the study site, but was composed of similar tree-types, viz. stringybarks (*E. cameroni* and *laevopinea*), gums (*E. saligna* and *amplifolia*), and New England Blackbutt, *E. andrewsii campanulata*, which resembled yellow boxes in having smooth bark extending down to the inner branches. These forests were the nearest areas to Wollomombi Falls containing populations of Red-browed, much of the intervening country being inhabited only by White-throated. These two species were collected only where both were present, often in adjacent trees, to allow direct comparisons of diet.

"Wollomombi" sittellas included several specimens taken from Stringybark Hill. Sittellas collected from the "Northern Rivers" region were separated from the latter because of possible geographical variation in diets, though the two populations did not differ significantly in morphology (see Section 3.2.1). However, "Northern Rivers" specimens were found in sclerophyll forests which were taller and wetter than local forests. White-throated Treecreepers were present at all, and Red-browed at most, of the collection sites in that region. "Swan Vale" treecreepers were

collected from areas between two and four kilometres from the study site. Vegetation at these collection localities was identical to that occurring at the study site. All specimens were collected in the late afternoon to minimize the possibility of diurnal variation in the fullness of the stomach and taxonomic composition of the prey. Additional juvenile treecreepers were taken from within the study sites at the end of the study.

The methods used in obtaining specimens were described in Section 2.2.3. The contents of the stomach and intestines of each specimen were examined under microscope in the laboratory. All items were counted and identified, where possible, to family level. As most insects were disarticulated, I counted head capsules or pairs of wings, or in cases where such parts were absent, legs (divided by six). As chelicerae were often the only remaining parts of spiders, these were counted and divided by two. The total body length of all items was estimated by comparison with entire specimens, or parts thereof collected from bark samples. Biomass was calculated using the formulae referred to in the previous section.

#### *Faeces and Food Sightings*

Faeces were collected opportunistically at the study sites during observations of foraging and while handling captured birds. Faecal sacs of nestlings were also obtained during banding operations, or when adults deposited them in a conspicuous place. All faecal samples were examined by S. Harrington. Unfortunately dietary data derived from examination of either faecal sacs or stomach contents are undoubtedly biased towards the orders Hymenoptera and Coleoptera, since the hard heads of both and elytra of the latter persist longer in the digestive tract of birds than do the remains of soft-bodied insects (e.g. Diptera, Lepidoptera), as Cameron (1975) noted. Occasionally, during observations of foraging, prey items could be identified prior to their ingestion. This method was also strongly biased towards large items (especially larvae) because they required the longest time to be killed and prepared. Smaller items, on the other hand, were usually ingested quickly, and thus rarely identified.

### 11.3 Results

#### 11.3.1 Distribution and abundance of arthropods on and under bark

##### *Surface Censuses*

At both sites there were marked peaks in arthropod numbers on tree-trunks in spring and summer followed by troughs in autumn and winter (e.g. Figure 11.1). As ants were the most numerous and conspicuous arthropods they were separated from all others (non-ants) in the following analyses. Arthropod numbers were significantly correlated with mean air temperature for each census (22 df,  $p < 0.01$ ); correlation coefficients were higher in the morning than in the afternoon for ants at Wollomombi ( $r = 0.83$  and  $0.73$ , respectively) but for non-ants, the reverse occurred ( $r = 0.78$  versus  $0.83$ ). At Swan Vale, however, there was little difference between morning and afternoon correlation coefficients in either ants or non-ants.

Numbers of ants at Wollomombi were significantly lower in the morning than in the afternoon in only two months (August and November), and this diurnal effect was significant only in the first year (Figure 11.1; Table 11.1). Gums hosted more ants than the other tree-types in two months (February and March); numbers of ants on stringybarks were significantly lower than those on gums in most months (except in winter and late autumn). Ants were generally scarcest on stringybarks (Figure 11.2). Biomass of ants did not generally vary significantly between years (Table 11.1). Few consistent differences occurred between tree-types in ant biomass, but again, gums showed significantly higher values than at least two other tree-types in four consecutive warm months (October to January). Afternoon biomass was significantly greater than morning biomass in two months (November and January), but less in September.

Numbers of non-ants at Wollomombi in the second year were significantly greater than in the first year in most months (Figure 11.1). Non-ants, like ants, were generally more abundant in the afternoon than in the morning, but significant differences occurred only in one month. Differences between tree-types were inconsistent over months (Figure 11.2; Table 11.1) but gums had significantly fewer non-ants than at least one other type in

FIGURE 11.1: *Diurnal variation in numbers of arthropods encountered on monthly surface censuses at Wollomombi*

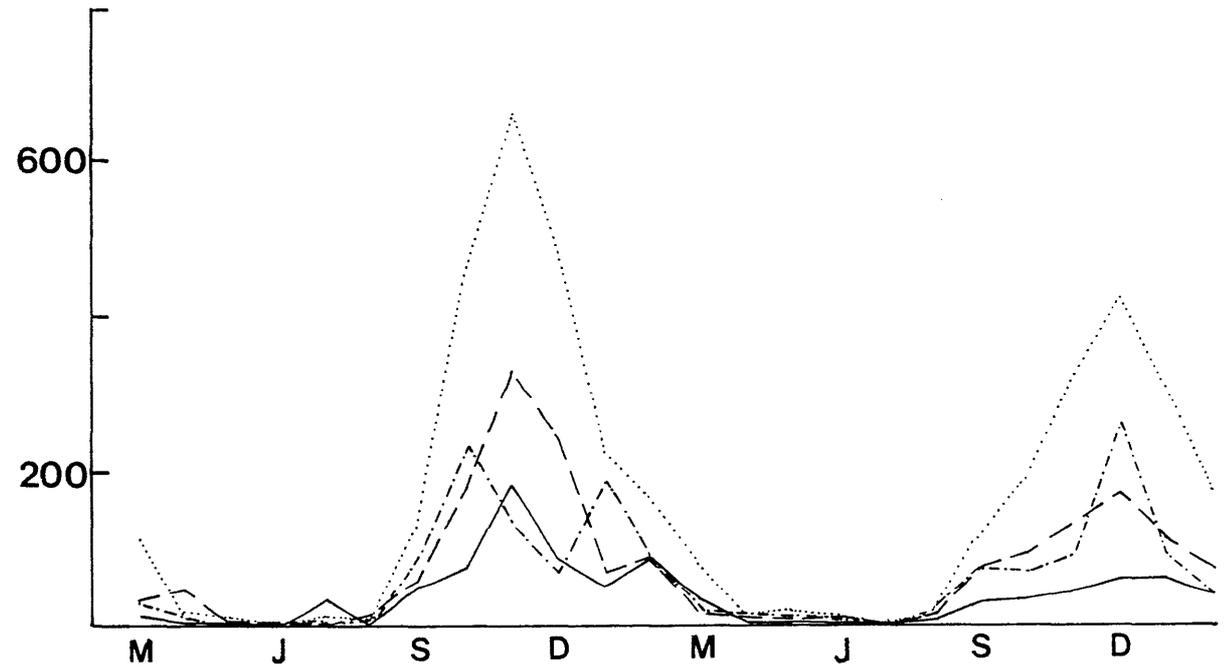


TABLE 11.1: Results of analyses of variance of surface censuses

SOURCE	df	NUMBERS						BIOMASS					
		ANTS			NON-ANTS			ANTS			NON-ANTS		
		MEAN	SQUARE	SIG.	MEAN	SQUARE	SIG.	MEAN	SQUARE	SIG.	MEAN	SQUARE	SIG.
<u>WOLLOMOMBI FALLS</u>													
TREE-TYPE	3	10.70		*	29.69		NS	0.056		[*]	0.031		NS
TIME OF DAY	1	1.85		NS	47.01		NS	0.017		NS	0.007		NS
ERROR (a)	3	0.84			17.66			0.006			0.034		
YEAR	1	0.93		NS	71.30		**	0.006		NS	0.056		NS
MONTH	11	42.27		***	324.19		***	0.089		***	0.635		***
YEAR x MONTH	11	1.39		***	56.68		***	0.011		**	0.036		NS
YEAR x TREE	3	0.39		NS	7.81		NS	0.001		NS	0.002		NS
YEAR x TIME OF DAY	1	2.07		*	3.26		NS	0.004		NS	0.037		NS
MONTH x TREE	33	0.59		*	11.35		NS	0.011		***	0.029		NS
MONTH x TIME OF DAY	11	0.62		*	22.78		**	0.014		**	0.066		*
YEAR x MONTH x TREE	33	0.49		[*]	7.11		NS	0.003		NS	0.021		NS
YEAR x MONTH x TIME OF DAY	11	0.44		NS	6.94		NS	0.008		*	0.010		NS
ERROR (b)	69	0.30			8.19			0.004			0.030		
<u>SWAN VALE</u>													
TREE-TYPE	3	25638.2		**	117.79		NS	0.024		*	0.005		NS
TIME OF DAY	1	943.8		NS	2.67		NS	0.004		NS	0.008		NS
ERROR (a)	3	240.6			22.80			0.001			0.062		
MONTH	11	25640.1		***	140.34		***	0.035		***	0.257		***
MONTH x TREE	33	3658.9		***	24.33		**	0.003		*	0.073		*
MONTH x TIME OF DAY	11	245.7		NS	13.42		NS	0.003		*	0.034		NS
ERROR (b)	33	173.7			10.04			0.002			0.032		

FIGURE 11.2: *Variation in numbers of arthropods encountered on monthly surface censuses at Wollomombi, according to tree-type*

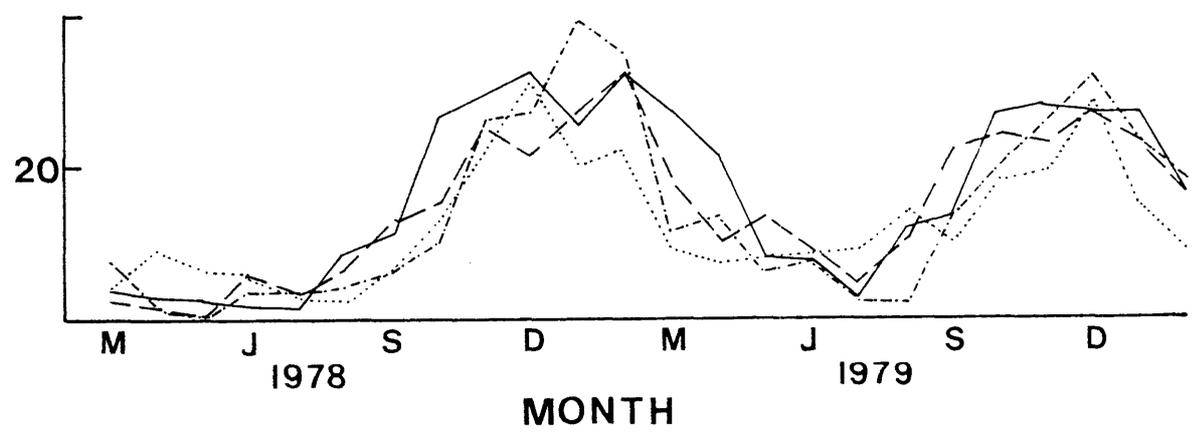
### ANTS



NUMBERS

- stringybark
- - - rough box
- · - yellow box
- · · gum

### NON-ANTS



MONTH

four months during summer and spring. In contrast to ants, non-ants were generally most numerous on stringybarks. Biomass of non-ants did not vary significantly between years, except in one month (Table 11.1). There was no significant variation in biomass between tree-types, and diurnal differences were highly inconsistent over months.

At Swan Vale, censuses were conducted for only 17 consecutive months so annual variation was ignored in analyses of variance and data for the twelve months beginning with December 1978 only were used. Similar seasonal patterns of abundance and biomass emerged as those observed at Wollomombi (Figures 11.3 and 11.4). Gums and ironbarks generally had the greatest numbers and biomass of ants but differences between tree-types were highly inconsistent, significant differences occurring in warm months only (Figure 11.4; Table 11.1). Moreover, there was no significant diurnal variation in numbers of ants in any months (Figure 11.3; Table 11.1). In contrast to Wollomombi, morning biomass of ants was significantly greater than afternoon biomass in three out of the four months in which significant differences occurred. Stringybarks generally had more non-ants than the other two tree-types, but differences were again inconsistent over months (Table 11.1).

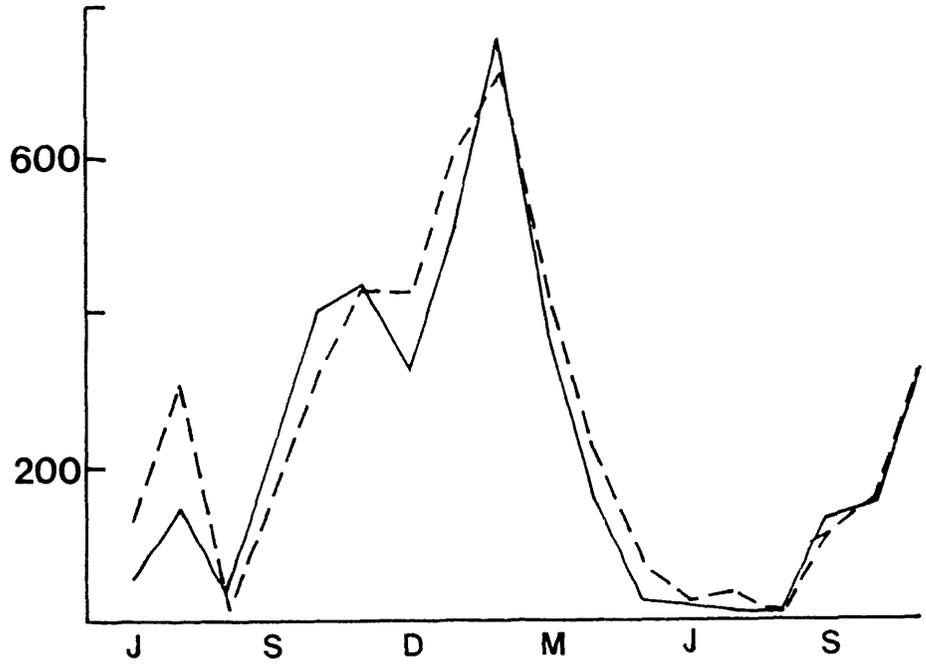
#### *Bark Collections*

Since almost all ants taken while collecting bark were on the surface of the bark at the time of sampling, they were ignored in analyses of bark collections. Data for dead trees were also omitted from these analyses as they were collected in cold months only.

The biomass of arthropods under the bark of stringybark trunks at Wollomombi was significantly greater in autumn than in the other seasons but there was no significant seasonal variation in the abundance of arthropods on this tree-type (Figure 11.5; Table 11.2). On rough boxes, both numbers and biomass of arthropods were significantly greater in winter than in the other seasons. No significant seasonal variation occurred in numbers or biomass of arthropods on yellow boxes or gums. The weight of bark samples had no significant effect on arthropod abundance or biomass on stringybarks or gums but did on the two types of boxes.

FIGURE 11.3: *Diurnal variation in numbers of arthropods encountered on monthly surface censuses at Swan Vale*

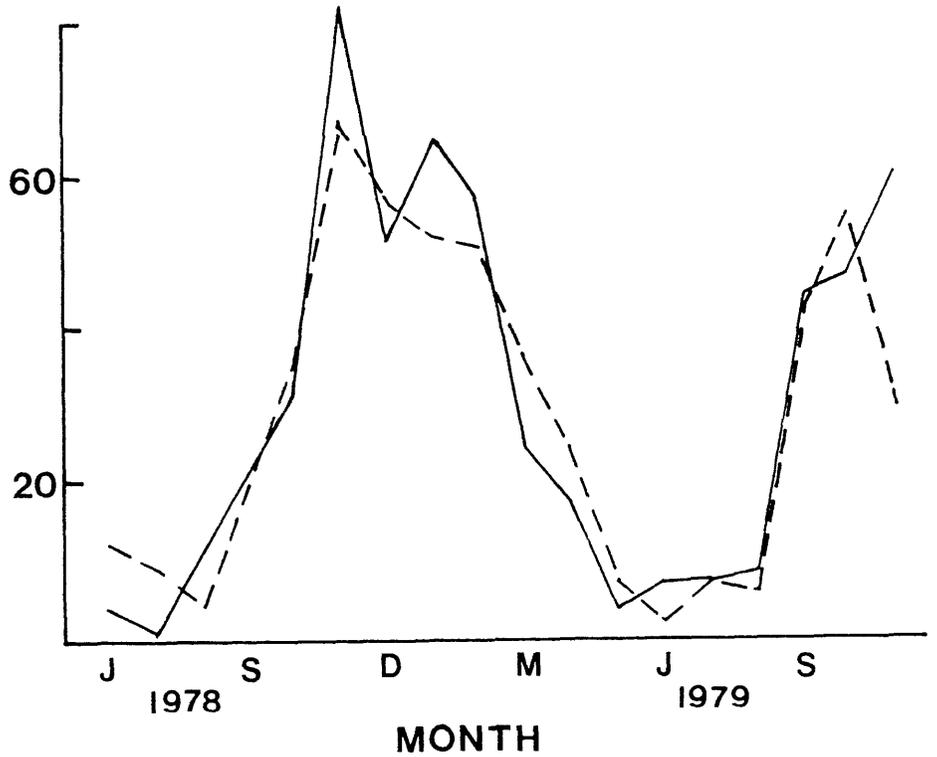
### ANTS



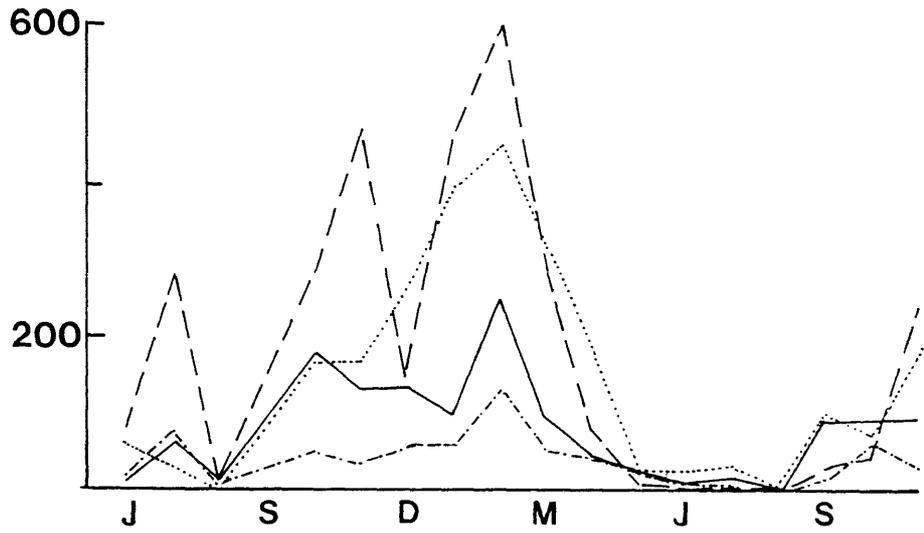
NUMBERS

— morning  
- - - afternoon

### NON-ANTS



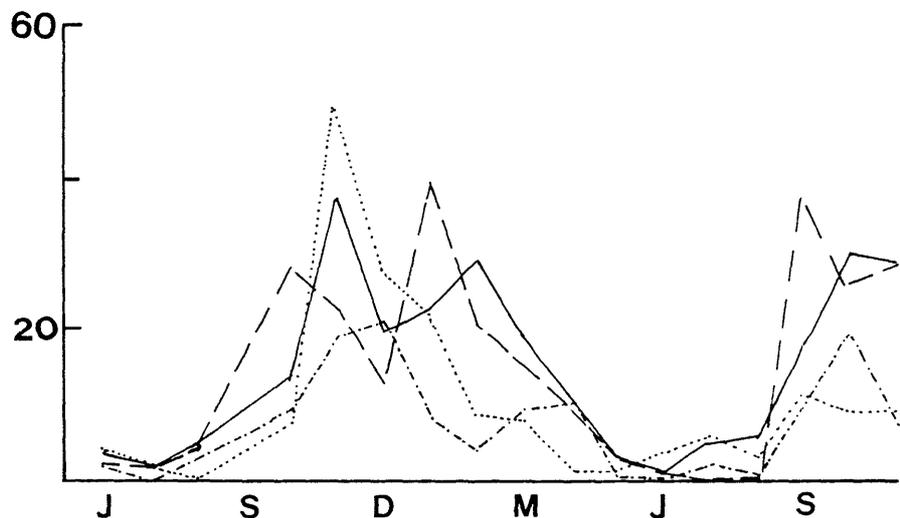
# ANTS



NUMBERS

- stringybark
- - ironbark
- · yellow box
- gum

# NON-ANTS



MONTH

# NUMBERS

# BIOMASS (g)

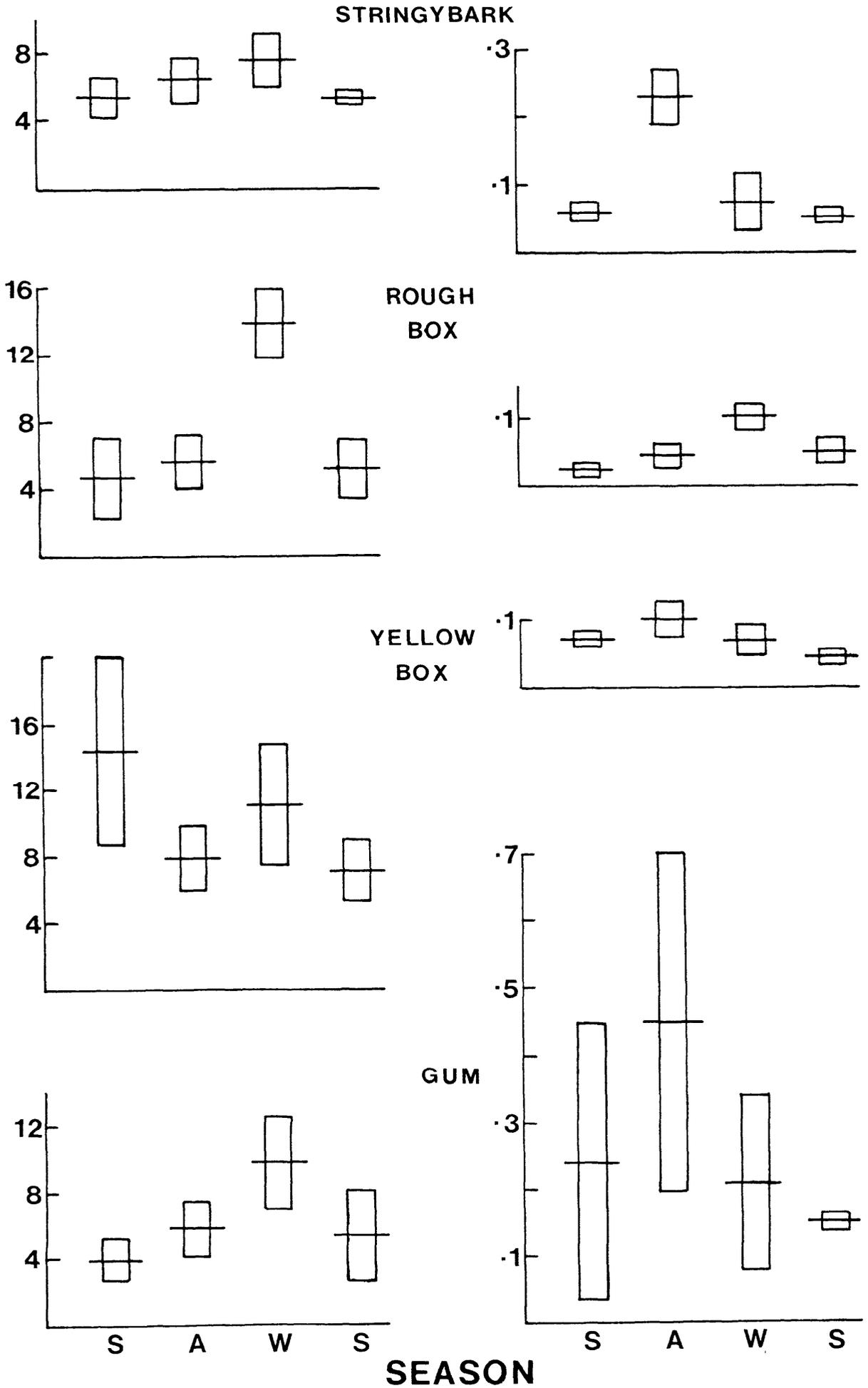


TABLE 11.2: *Results of analyses of variance of arthropod numbers and biomass from bark samples*

		NUMBERS			BIOMASS	
SOURCE	df	MEAN SQUARE	SIG.	MEAN SQUARE	SIG.	
<u>WOLLOMOMBI FALLS</u>						
TREE-TYPE						
STRINGYBARK	WEIGHT	4	2.29	NS	0.002	NS
	SEASON	3	6.22	NS	0.035	**
	ERROR	12	9.213		0.004	
ROUGH BOX	WEIGHT	4	42.1	[NS]	0.004	*
	SEASON	3	94.7	**	0.007	**
	ERROR	12	13.3		0.001	
YELLOW BOX	WEIGHT	4	0.043	*	0.003	NS
	SEASON	3	0.007	NS	0.002	NS
	ERROR	12	0.009		0.003	
GUM	WEIGHT	4	33.0	NS	0.041	NS
	SEASON	3	30.3	NS	0.033	NS
	ERROR	12	20.5		0.081	
<u>SWAN VALE</u>						
STRINGYBARK	WEIGHT	4	25.5	[*]	0.003	NS
	SEASON	3	51.0	**	0.005	NS
	ERROR	12	7.7		0.003	
YELLOW BOX	WEIGHT	4	22.7	NS	14.1	NS
	SEASON	3	26.4	NS	163.6	NS
	ERROR	12	26.8		236.9	
GUM	WEIGHT	4	1.21	*	0.019	NS
	SEASON	3	0.99	NS	0.031	NS
	ERROR	12	0.34		0.040	

At Swan Vale, biomass of arthropods did not vary significantly for any of the three tree-types (Figure 11.6; Table 11.2). However, numbers of arthropods on stringybarks were significantly greater in winter than in other seasons. Sample weights had a significant effect on arthropod numbers in gums only. These results differ somewhat from those at Wollomombi for the same tree-types. Yet both sites shared a tendency for greater arthropod numbers during the winter, except in the case of yellow boxes.

At Wollomombi, ribbons (peeling bark from box branches) were apparently more productive than the stringybark samples collected concurrently, in terms of both numbers and biomass of arthropods (Figure 11.7). Variance ratios indicated that there was no significant difference between autumn and spring variance in arthropod numbers in either stringybark or ribbon samples ( $F = 1.6$  and  $1.68$ , respectively,  $9$  df,  $p > 0.05$ ). However, in terms of biomass, the variance of ribbon samples was significantly greater in autumn than in winter ( $F = 7.85$ ,  $9$  df,  $p < 0.01$ ); this seasonal difference was less significant in the stringybark samples ( $F = 4.00$ ,  $9$  df,  $p > 0.05$ ). Winter productivity of ribbons was similar to that in autumn (Figure 11.7); no stringybark samples were taken in winter. Overall, the variance of the ribbon samples was significantly higher than that of the stringybark samples in terms of both numbers ( $F = 6.14$ ,  $19$  df,  $p < 0.01$ ) and biomass ( $F = 3.19$ ,  $19$  df,  $p < 0.01$ ).

Thus, although box ribbons were potentially more productive than stringybark trunks as a source of arthropods, they were apparently much more variable. This disparity was also evident in the previous year: arthropod numbers on the trunks of rough and yellow boxes were relatively high, and biomass (but curiously not numbers) was exceedingly variable on the trunks of gums (Figure 11.5). The latter samples were in fact mostly ribbons, very similar to those collected from the branches of boxes. Similarly, at Swan Vale, biomass of arthropods in yellow boxes and gums was apparently more variable than that in stringybarks (Figure 11.6).

### 11.3.2 Taxonomic composition of arthropods on and under bark

#### *Surface Censuses*

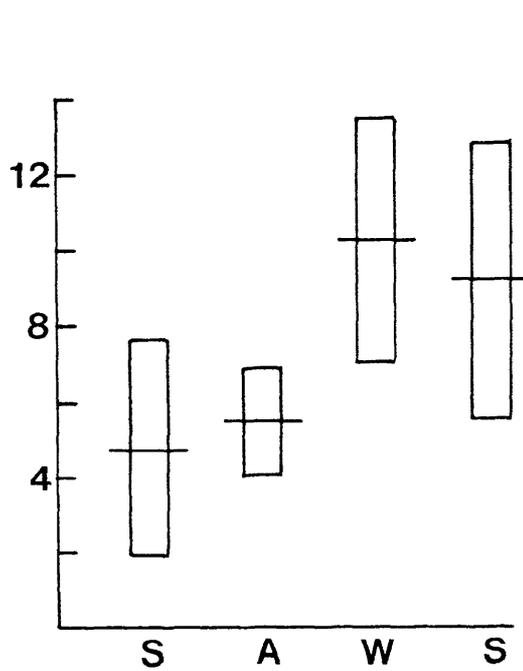
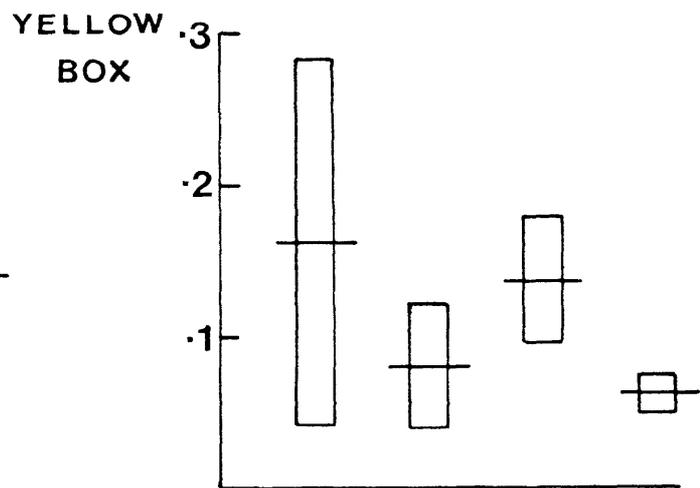
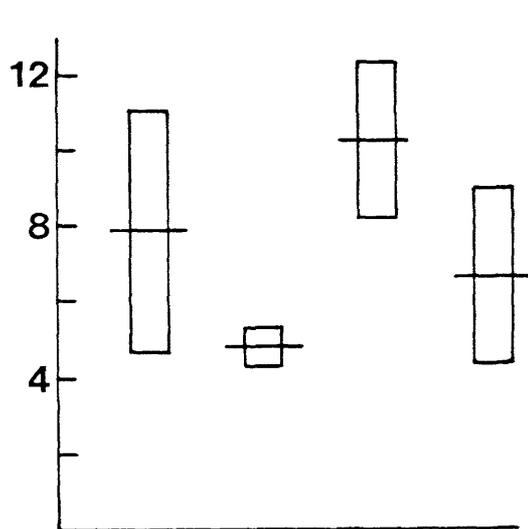
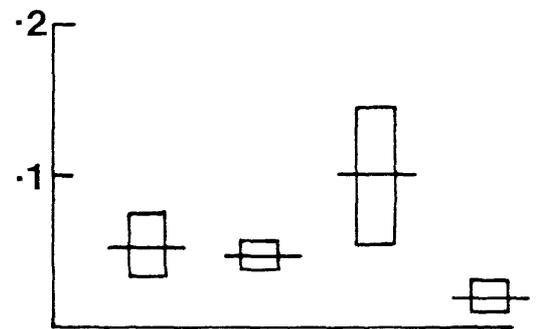
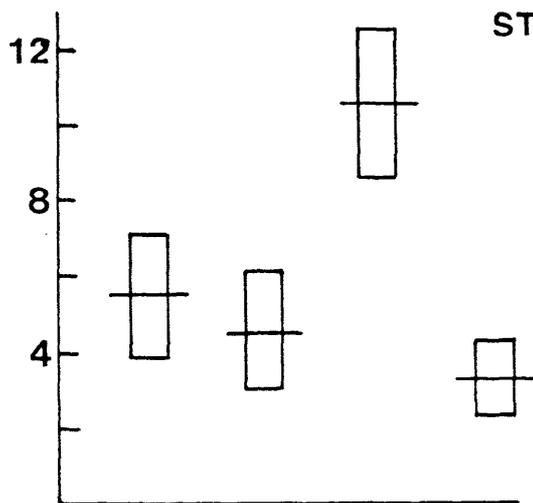
Over 75% of the ants recorded during surface censuses at Wollomombi were *Iridomyrmex* 'A' sp., about 3-4 millimetres in length. The slightly

FIGURE 11.6: *Seasonal variation in numbers and biomass of arthropods per 100 grams of bark collected at Swan Vale*

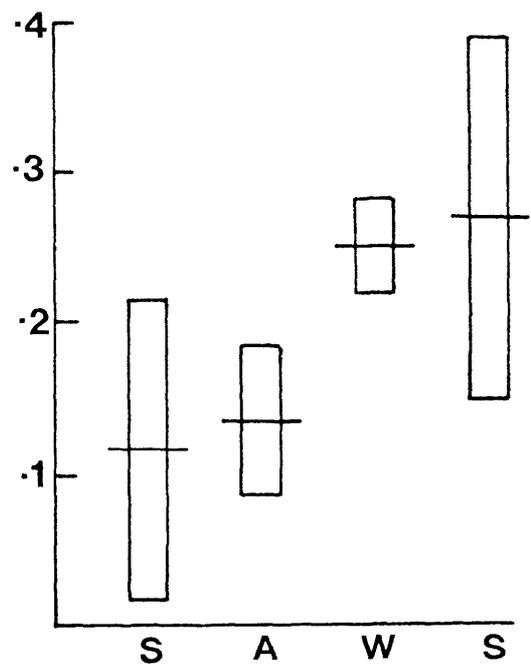
Rectangles, one standard error either side of mean (horizontal line) for five samples

### NUMBERS

### BIOMASS (g)



### GUM



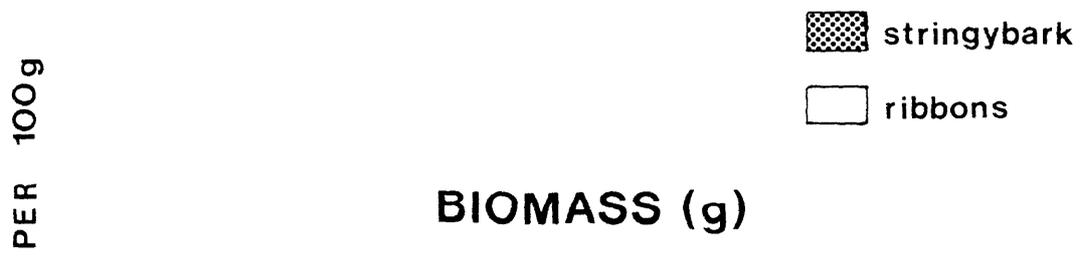
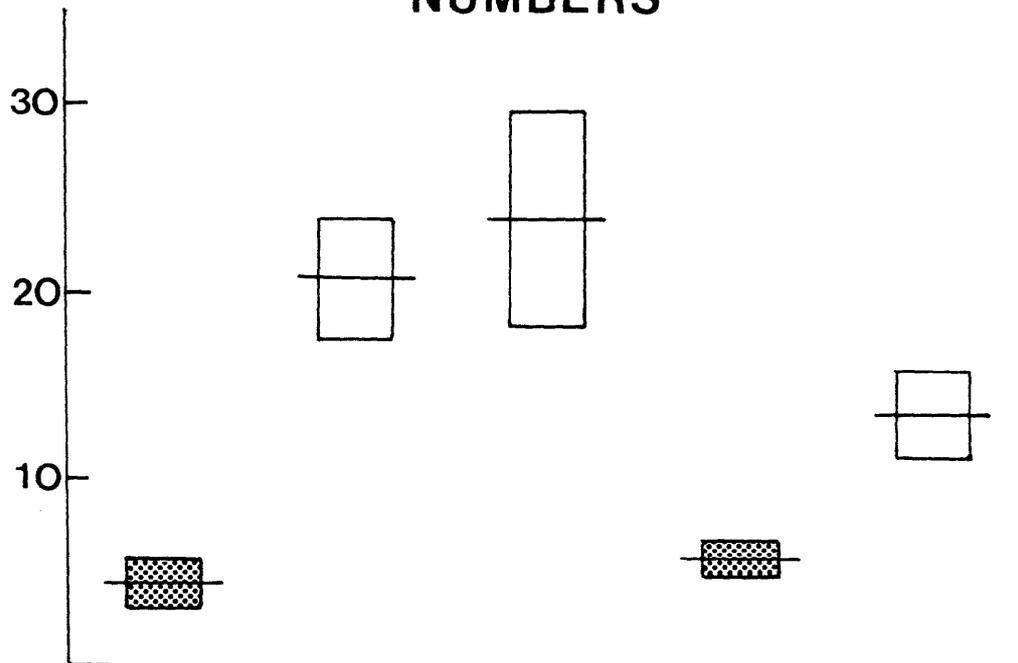
SEASON

FIGURE 11.7: *Numbers and biomass of arthropods from bark collections at Wollomombi during second year*

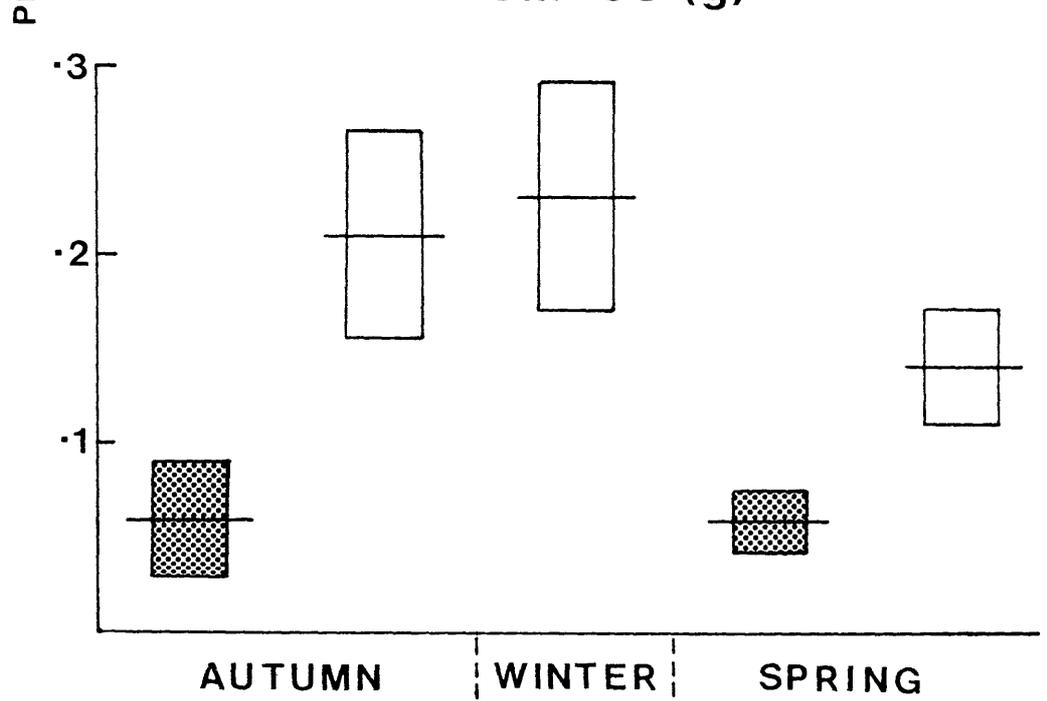
Rectangles, one standard error either side of mean (horizontal line) for ten samples

Stringybark samples taken from trunk, ribbons (cylinders of peeling bark) from branches of boxes; no stringybark samples taken in winter

### NUMBERS



### BIOMASS (g)



more robust *Crematogaster* (3-5 mm) comprised another 10% of the total number of ants. The remainder included (in order of decreasing frequency): *Iridomyrmex* 'B' (1-2 mm), *Pheidole* (6-7 mm), *Camponotus* (4-9 mm), *Polyrhachis* (6-10 mm) and *Rhytidoponera* (5-8 mm). At Swan Vale, about 92% of ants were less than 4 millimetres in length (mostly *Iridomyrmex*). *Polyrhachis* (6-12 mm) and *Crematogaster* (4-5 mm) composed a further 6%. The latter were more common in the "forest" plot than in the open areas. As the distribution (according to tree-type) and seasonal pattern of abundance of ants has already been described (above), the following results and analyses are confined to other taxa.

The frequency of occurrence of non-ant taxa varied significantly according to both seasons and tree-types. All seasons were significantly different from each other in taxonomic composition, except autumn and winter at both Wollomombi and Swan Vale ( $\chi^2 = 6.8$  and  $7.5$  respectively, 6 df,  $p > 0.2$ ) (Figure 11.8). Similarly, arthropods on all four tree-types at both sites showed significant taxonomic differences, except between stringybarks and rough boxes at Wollomombi ( $\chi^2 = 10.5$ , 6 df,  $p > 0.1$ ) (Figure 11.8). Spiders (Arachnida: Araneidae) and flies (Insecta: Diptera) were the two most abundant types of non-ant arthropods encountered during surface censuses overall. Though recorded more frequently during the warm months, spiders formed a greater proportion of total arthropod numbers during the cold seasons at both sites (Figure 11.8), and were apparently the major cause of seasonal variation of taxa. Spiders were generally less common on the trunks of ironbarks, yellow boxes and gums than on those of stringybarks or rough boxes (Figure 11.8).

At least a half of the spiders observed during censuses belonged to the family Salticidae (jumping spiders), but during winter they were outnumbered by *Tama* sp. (Hersiliidae), a cryptic species which occurred almost exclusively on rough boxes. The regular occurrence of the latter species, as well as others belonging to the families Thomisidae and Nicodamidae, on certain trees suggested that these spiders were sedentary. In contrast, flies (mainly of the superfamily Muscoidea), often perched only briefly on the tree-trunks and could thus be considered as "transients" there. "Gnats" (mostly Sciarids) were present in large numbers at most times of the year but because they were so small (mostly 2 mm or less) and

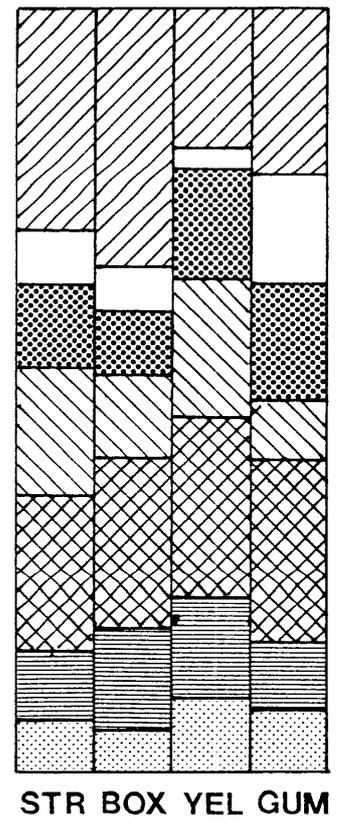
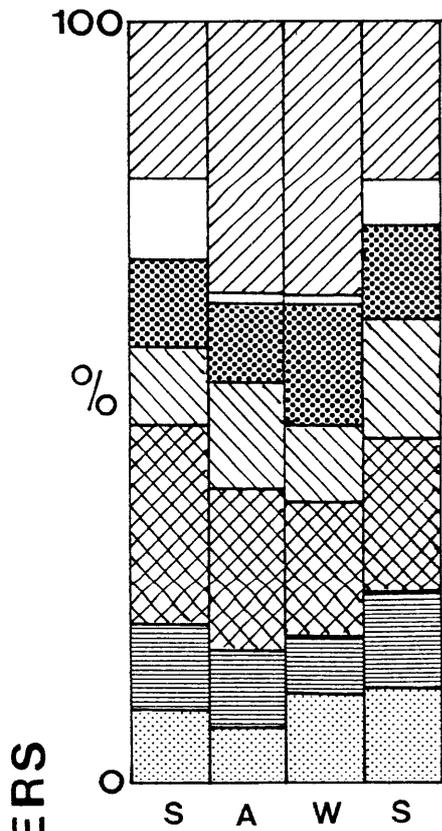
FIGURE 11.8: *Taxonomic composition of arthropods (ants excluded) encountered during surface censuses at both study sites, according to season and tree-type (years combined)*

NUMBER OF ARTHROPODS:		
	WOLLOMOMBI	SWAN VALE
<u>SEASON</u>		
SUMMER	525	312
AUTUMN	168	112
WINTER	109	38
SPRING	424	274
<u>TREE-TYPE</u>		
STRINGYBARK	349	242
ROUGH BOX/IRONBARK	324	223
YELLOW BOX	288	110
GUM	265	161
TOTAL	1226	736

## KEY

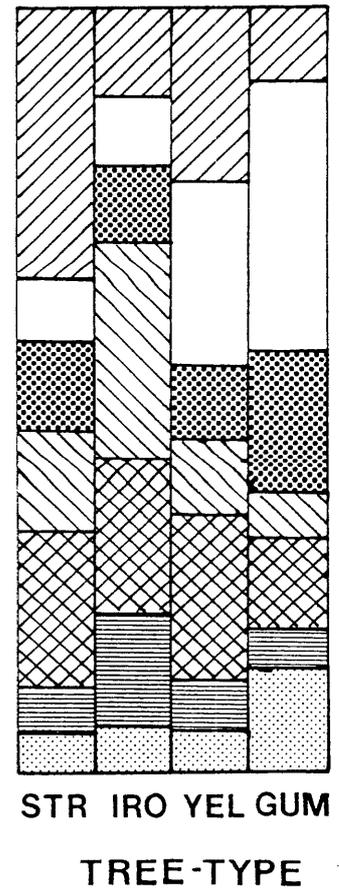
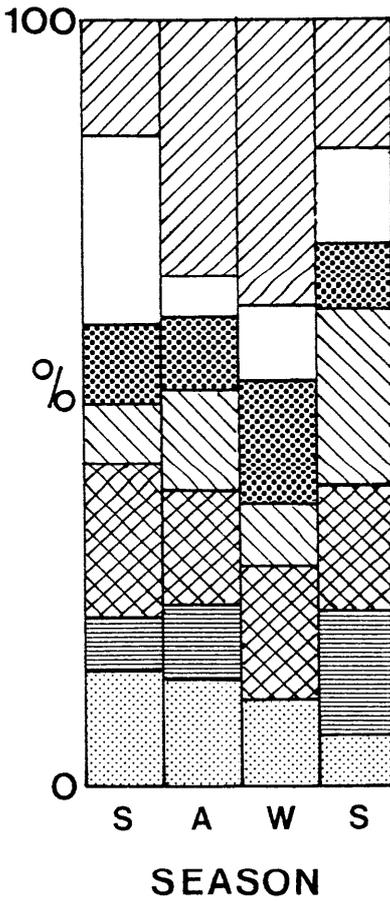
	SPIDERS
	BETTERLES (COLEOPTERA)
	BUGS (HEMIPTERA)
	MOTHS (LEPIDOPTERA)
	FLIES (DIPTERA)
	WASPS (HYMENOPTERA)
	OTHER

# WOLLOMOMBI



NUMBERS

# SWAN VALE



SEASON

TREE-TYPE

usually in the air above the surface of the bark rather than resting on it, they were excluded from censuses.

At Wollomombi, bugs (Hemiptera) and moths (Lepidoptera) were the next most frequently recorded orders of insects during censuses. The majority of bugs observed were Cicadellids - some of which appeared to be sedentary. Pentatomids were encountered frequently at Swan Vale but rarely at Wollomombi. Moths, mostly cryptic, comprised about 13% of identified taxa at both sites, and at Swan Vale, appeared to favour ironbarks. Beetles (Coleoptera) were more important at Swan Vale (16%) than at Wollomombi (7%), but at both sites, they were most prevalent on gums, owing to concentrations of large Chrysomelids (subfamily Chrysomelinae) half-hidden beneath loose strips of peeling bark. At both sites the diversity ( $H'$ ) of non-ant taxa was least on stringybarks (Figure 11.8), shared with gums at Swan Vale, but there were great discrepancies between sites in the taxonomic composition on yellow boxes and gums.

#### *Bark Collections*

Arthropods beneath the bark also showed significant taxonomic differences between seasons and between tree-types, with the following exceptions: autumn and spring at Wollomombi ( $\chi^2 = 11.4$ , 7 df,  $p > 0.1$ ), autumn and winter at Swan Vale ( $\chi^2 = 12.7$ , 7 df,  $p > 0.05$ ), and rough box and yellow box at Wollomombi ( $\chi^2 = 8.3$ , 7 df,  $p > 0.3$ ).

Spiders constituted 31% of total numbers and 57% of total biomass of arthropods beneath bark at Wollomombi, but their contribution was smaller at Swan Vale. Though the number of spiders collected from beneath the bark was greatest in winter at both sites, they comprised less of the total number of arthropods in winter than in spring (at Wollomombi) or summer (at Swan Vale) (Figure 11.9). Gums and dead trees yielded more spiders than the other tree-types in terms of both numbers and biomass at Wollomombi, but not at Swan Vale (Figures 11.9 and 11.10). Spiders from "ribbons" comprised a greater proportion of total arthropod biomass than they did in stringybark samples taken concurrently, but a similar proportion, numerically (Figure 11.11).

Clubionids represented a third to a half of the total number of spiders collected from tree-trunks at both sites. Salticids, commonly en-

FIGURE 11.9: *Taxonomic composition of arthropods from bark collections, according to numbers*

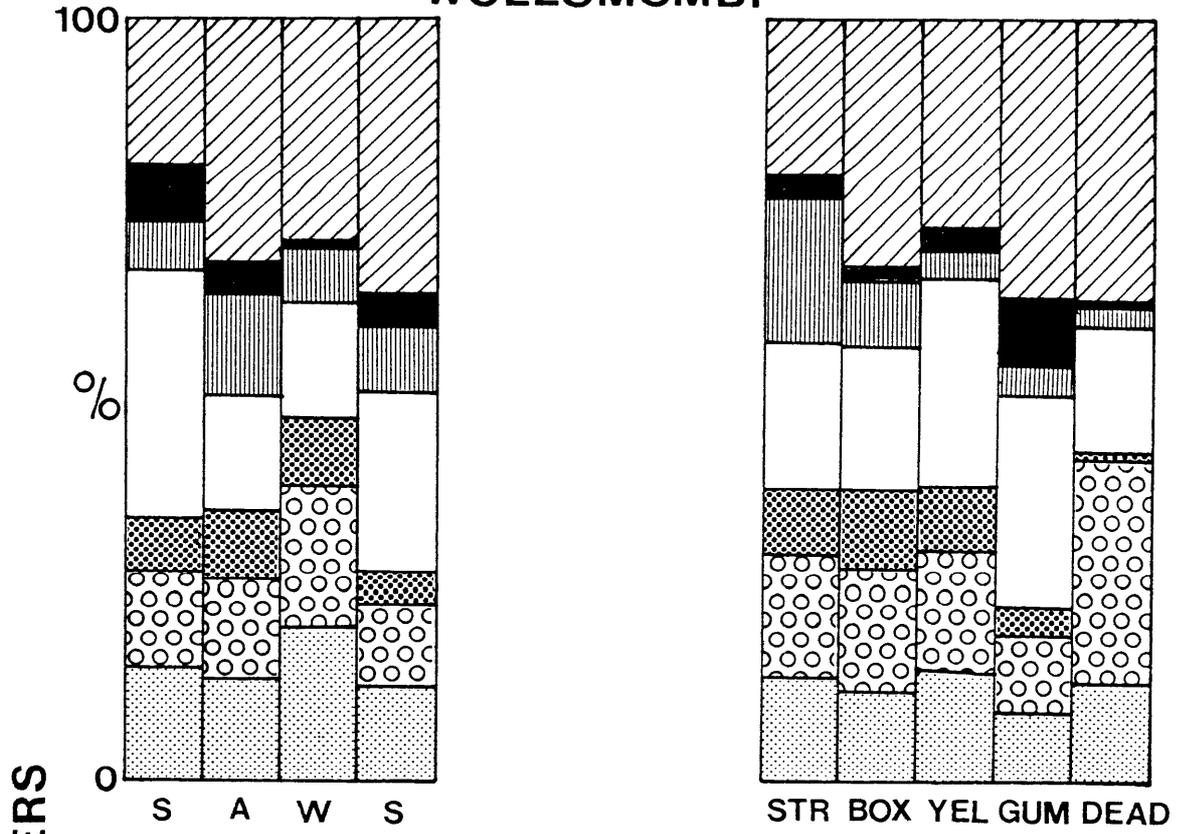
<u>SEASON*</u>	NUMBER OF ARTHROPODS:	
	WOLLOMOMBI	SWAN VALE
SUMMER	220	147
AUTUMN	216	152
WINTER	317	275
SPRING	182	236
 <u>TREE-TYPE</u>		
STRINGYBARK	261	166
ROUGH BOX	226	-
YELLOW BOX	213	300
GUM	235	344
DEAD	236	128

\* excluding arthropods from dead trees

KEY

	SPIDERS	
	PSEUDOSCORPIONS	
	COCKROACHES	(BLATTODEA)
	BEETLES	(COLEOPTERA)
	BUGS	(HEMIPTERA)
	LARVAE	
	OTHER	

### WOLLOMOMBI



### SWAN VALE

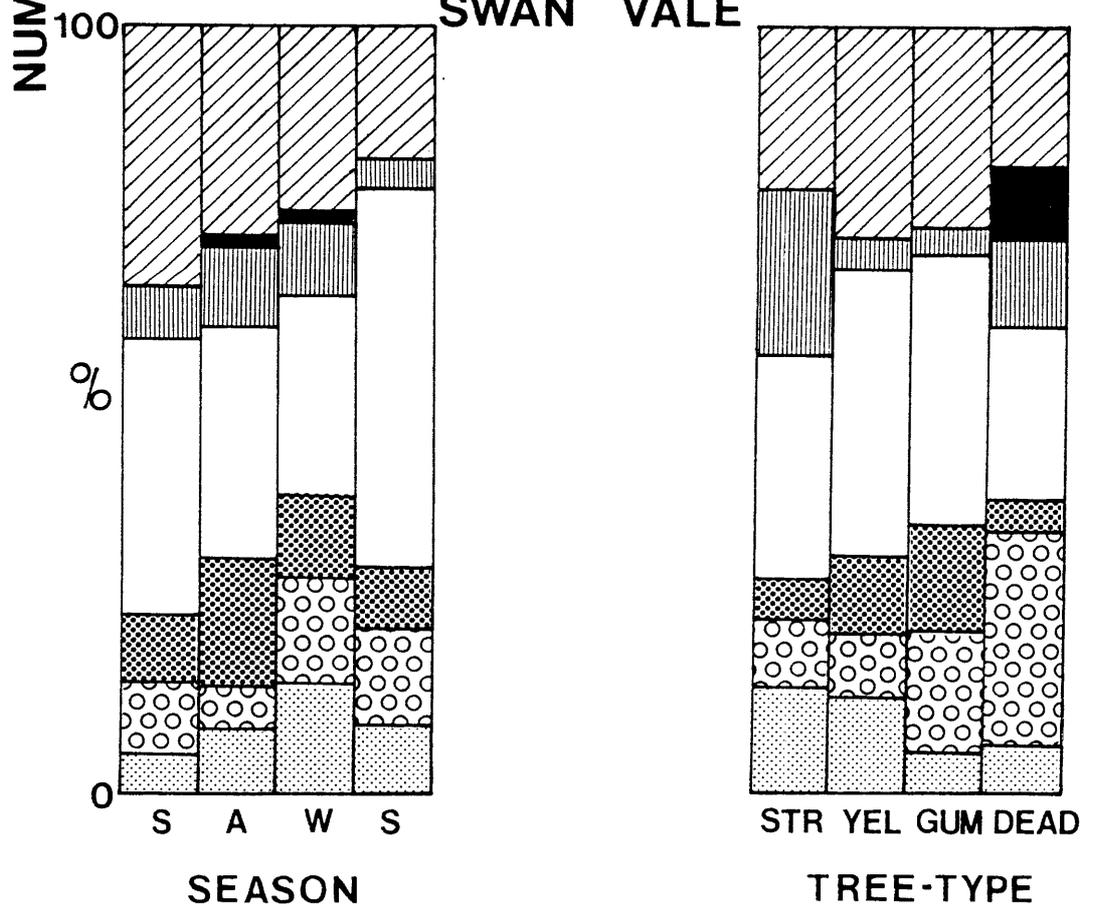


FIGURE 11.10: *Taxonomic composition of arthropods from bark collections, according to biomass (wet weight)*

	BIOMASS OF ARTHROPODS (GRAMS)	
	WOLLOMOMBI	SWAN VALE
STRINGYBARK	4.6	1.8
ROUGH BOX	1.7	-
YELLOW BOX	1.9	4.5
GUM	13.1	8.8
DEAD	5.2	2.6

## KEY

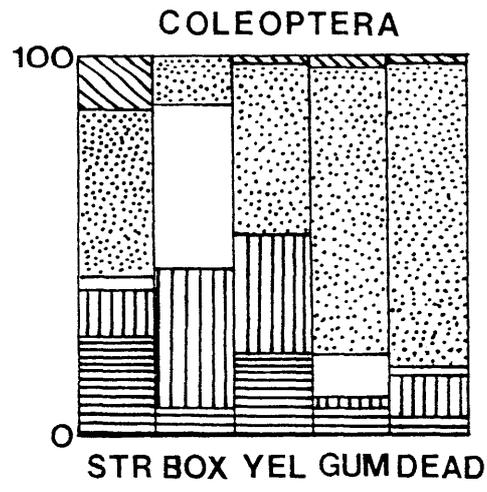
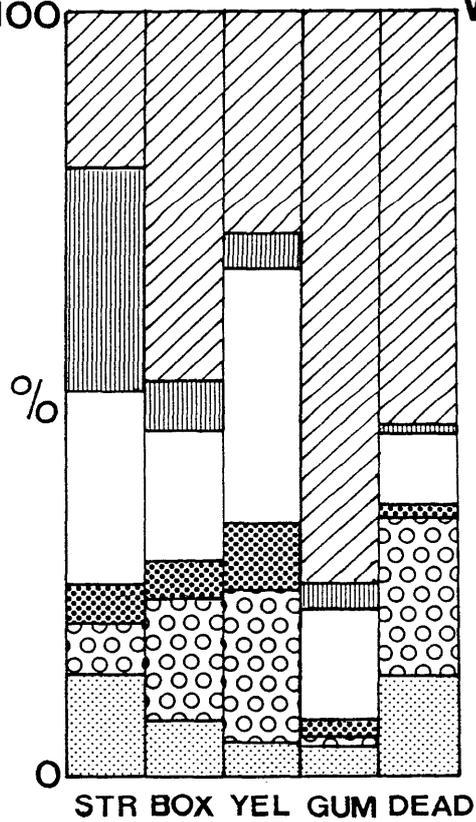
Left, as in FIGURE 11.9

Right, as below

## COLEOPTERA (families)

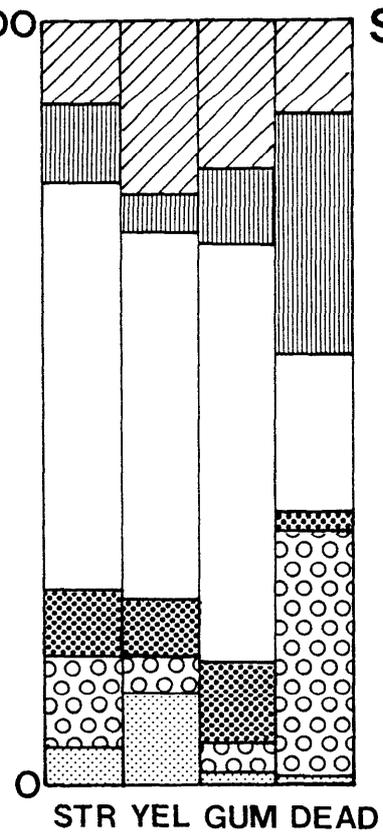
	Curculionidae
	Chrysomelidae
	Elateridae
	Carabidae/Tenebrionidae
	Other

100 WOLLOMOMBI



BIOMASS

100 SWAN VALE



TREE - TYPE

FIGURE 11.11: *Taxonomic composition of arthropods from bark collections at Wollomombi in second year (stringybark vs. ribbons)*

RIB, ribbons

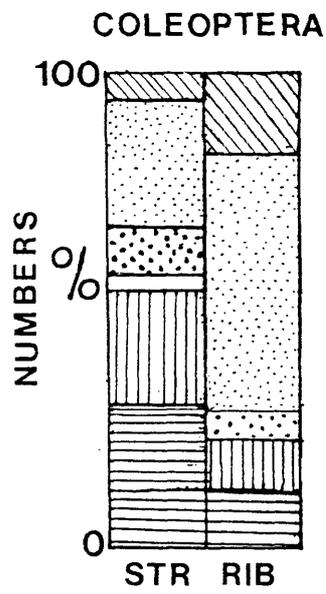
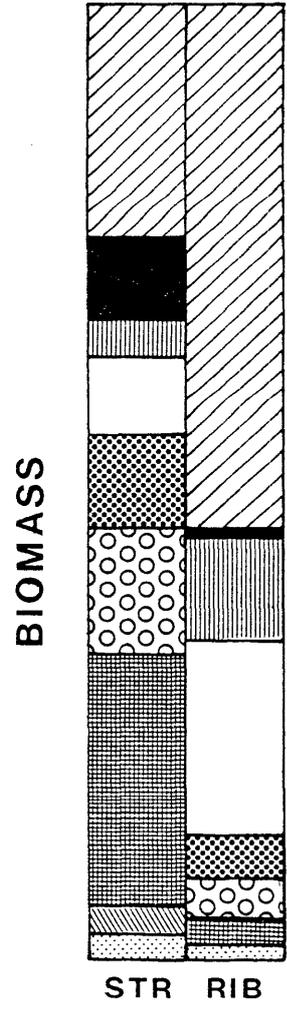
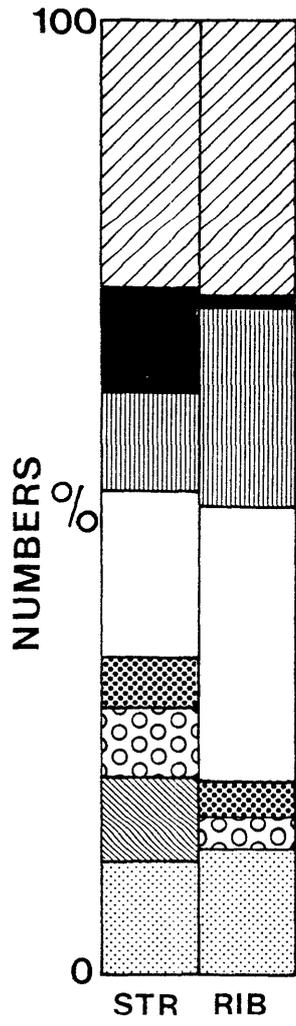
KEYS

UPPER

-  CRICKETS (ORTHOPTERA)  
 SILVERFISH (THYSANURA)  
 Other taxa as in FIGURE 11.9

LOWER

-  Curculionidae  
 Chrysomelidae (mostly Eumolpinae)  
 Chrysomelidae (Chrysomelinae)  
 Elateridae  
 Carabidae/Tenebrionidae  
 Other



countered during surface censuses, formed less than 20% of all spiders collected from each of the tree-types at Wollomombi and Swan Vale. The disproportionately high biomass of spiders on gums at Wollomombi resulted principally from the occurrence of many large Huntsman Spiders (Heteropodidae). Clubionids and Thomisids predominated in ribbons.

Though rarely encountered during surface censuses, beetles represented the second most important taxonomic group in bark collections, comprising 20% and 34% of total arthropod numbers at Wollomombi and Swan Vale, respectively. The largest numbers of beetles were obtained from yellow boxes and gums at both sites (Figure 11.9). They were slightly more prevalent in ribbons than in stringybark samples (Figure 11.11). Seasonal changes in the relative proportion of beetles were not consistent between the two sites (Figure 11.9). Chrysomelids contributed the greatest amount to biomass of beetles on all trees at Wollomombi, except rough boxes, where Elaterids were significant (Figure 11.10). The majority of Chrysomelids in ribbons belonged to the subfamilies Eumolpinae and Alticinae, most of which were 2-4 millimetres in length. This contrasted with the larger Chrysomelinae typical of tree-trunks, averaging 10 millimetres long.

Larvae were the third most important group, representing 18% and 14% of total arthropod numbers at Wollomombi and Swan Vale respectively, despite their almost complete absence from surface censuses. The largest numbers of larvae occurred in winter at both sites (Figure 11.9). They were most numerous in the decayed bark of dead trees. At Wollomombi, 77% of the larvae were Coleopteran, another 16% Lepidopteran, and the remainder belonged mainly to Dipteran and Neuropteran (lacewing) families. Of the 141 identified beetle larvae, 44% were Melyrids (thin larvae less than 5 mm long). However, Tenebrionid larvae predominated in dead bark, while Elaterid larvae (like adults) were commonest on rough boxes, and Chrysomelid larvae on gums. Over half of the larvae in ribbons were Lepidopteran, mostly Oecophorids and Arctiids.

Cockroaches (Blattodea) constituted about 8% of the total number of arthropods from bark collections at both sites. They were most abundant on stringybarks at both sites (Figure 11.9), though their contribution to total biomass at Swan Vale was greatest on dead trees (Figure 11.10). How-

ever, ribbon samples contained proportionately more cockroaches than the stringybark samples in the second year (Figure 11.11). The majority of specimens belonged to Blattellidae. Bugs comprised less than 10% of total numbers of arthropods at both sites, and contributed even less to total biomass. Very few were collected from the bark of gums or dead trees. Representatives of the suborder Heteroptera outnumbered those of Homoptera, the commonest family of the former being Aradidae.

Other taxa collected from bark were (in approximate order of decreasing abundance): Pseudoscorpions (Pseudoscorpiones), mites (Acarina), wasps (Hymenoptera), psocids (Psocoptera), crickets (Orthoptera), silverfish (Thysanura), flies and moths. Most of these groups were distributed fairly evenly among the different tree-types, though silverfish occurred almost exclusively on stringybarks, while psocids were absent from this tree-type at both sites. Almost half of the pseudoscorpions collected at Wollomombi were from gums, but at Swan Vale, most were in dead wood. Eggs of spiders and insects were excluded from analyses, though sacs containing up to 80 eggs (mostly less than 1 mm in diameter) were found in about 10% of all bark samples from live trees at both sites and in 25% of dead tree samples.

There were considerable discrepancies in the taxonomic composition of stringybark samples from the two years (Figures 11.9, 11.10 and 11.11), which were possibly partly attributable to local differences. In the second year, fewer cockroaches were present and large crickets (Gryllacrididae) contributed significantly to total biomass of arthropods. However, biomass of arthropods in "ribbons" resembled that on gums from the previous year in the prevalence of spiders. In contrast to the situation in surface censuses, the numerical diversity of taxa under the bark was greatest in stringybarks at both sites.

### 11.3.3 Comparison of diets of the study species

#### *Wollomombi Treecreepers*

Overall (all specimens lumped) White-throated and Red-browed differed significantly in the frequency of occurrence of the twelve major taxa found in their stomachs ( $\chi^2 = 118.4$ , 11 df,  $p < 0.001$ ). As expected, ants were the most important food source for these species, occurring in

every stomach and adult faecal sample examined. They comprised 92% and 89% of the arthropods found in the White-throated and Red-browed, a difference which was significant ( $\chi^2 = 23.1$ , 1 df,  $p < 0.001$ ). However, in terms of the numbers of ants per stomach, there was no significant interspecific difference ( $t = 1.34$ , 54 df,  $p > 0.1$ ). Indeed, in both species, the number of ants per stomach ranged from 5 or 6 to 396 or 397. Juveniles of both species contained fewer ants per stomach, on average, than adults collected during the breeding season, but the difference was not significant in either case (for White-throated:  $t = 0.43$ , 14 df,  $p > 0.2$ ; for Red-browed:  $t = 1.76$ , 17 df,  $p > 0.05$ ). Although both species appeared to take fewer ants during the warm seasons than in the cold seasons (Figure 11.12), this difference was not significant (for White-throated:  $t = 0.57$ , 24 df,  $p > 0.2$ ; for Red-browed:  $t = 1.40$ , 28 df,  $p > 0.1$ ). By contrast, the number of non-ants per stomach was greatest, on average, in summer (Figure 11.12), though again seasonal differences were not significant ( $t = 0.88$  and  $1.16$  for White-throated and Red-browed, respectively).

The stomachs of Red-browed contained significantly more large ants (over 4 mm in length) than those of White-throated (Kolmogorov-Smirnov test,  $D = 9.9$ ,  $p < 0.001$ ) and faeces from Wollomombi provided additional evidence of this differential size selection by the two species ( $D = 31.2$ ,  $p < 0.001$ ) (Figure 11.13). Red-browed took relatively more ants of the genera *Camponotus* and *Polyrhachis* plus a large unidentified species (*Iridomyrmex*?) than White-throated. Small *Iridomyrmex* and *Crematogaster* species composed 92% and 81% of the ants in White-throated and Red-browed stomachs, respectively, but the contribution of *Crematogaster* in both species was more than twice that expected from their relative frequencies in surface censuses. Ant remains were found in one of the two faecal sacs from two nestling Red-browed, but only one of the twelve faecal sacs from White-throated nestlings.

I observed both species eating ants on many occasions, but the small size of most ants precluded quantification. Birds often pecked at the bark surface while climbing, presumably gleaning ants at times. At midday on 25 June 1978, I watched three Red-browed and one White-throated feeding on flying (winged) ants, which were emerging from their ground nest. The birds used nearby tree-trunks as perches from which they sallied

FIGURE 11.12: *Seasonal variation in the numbers of ants (upper) and non-ants (lower) found in stomachs of the two Wollomombi treecreepers*

Rectangles, one standard error either side of mean (horizontal line)

	NUMBER OF STOMACHS	
	White-throated	Red-browed
SUMMER	8	11
AUTUMN	5	6
WINTER	5	5
SPRING	8	8

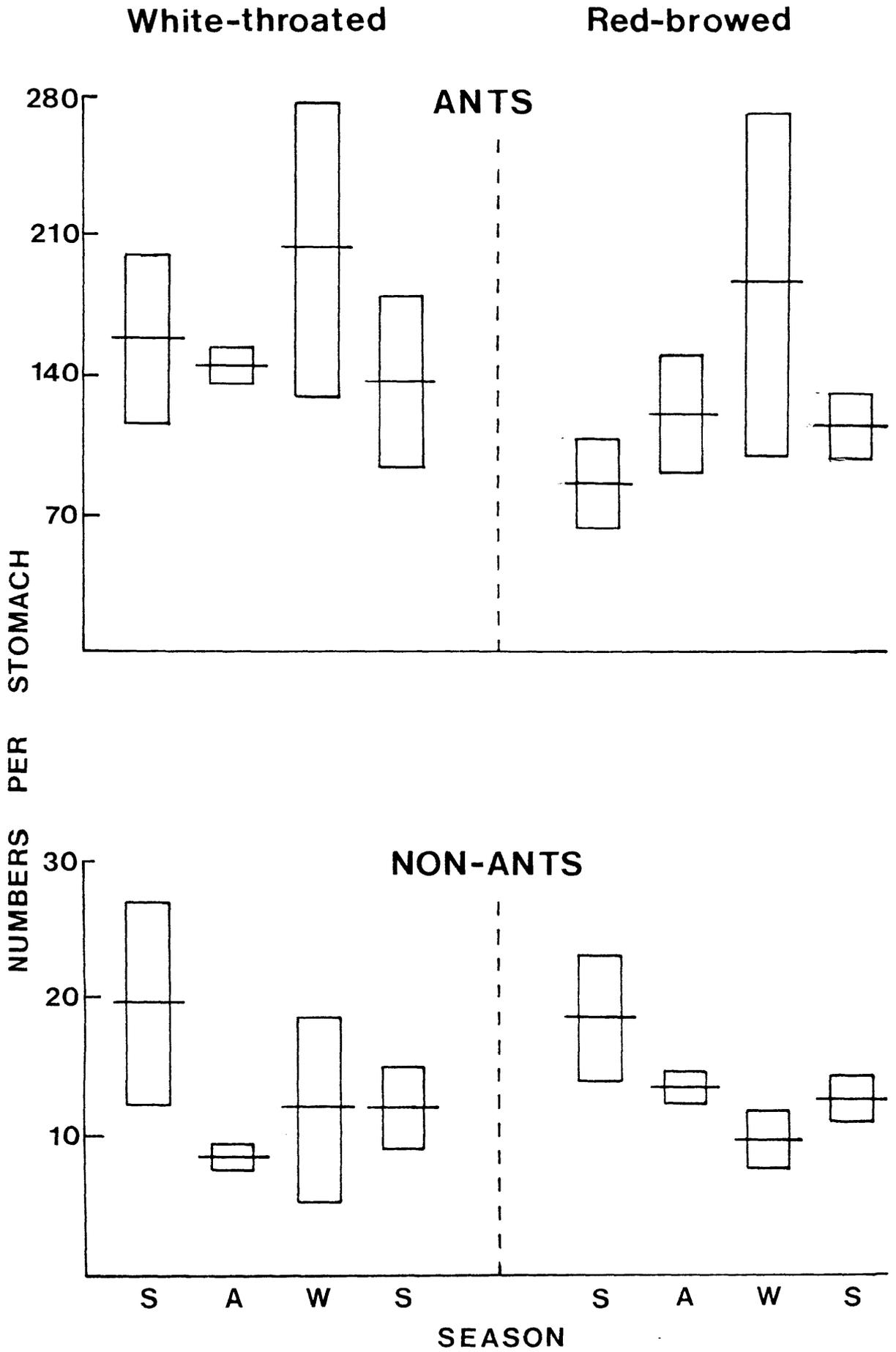


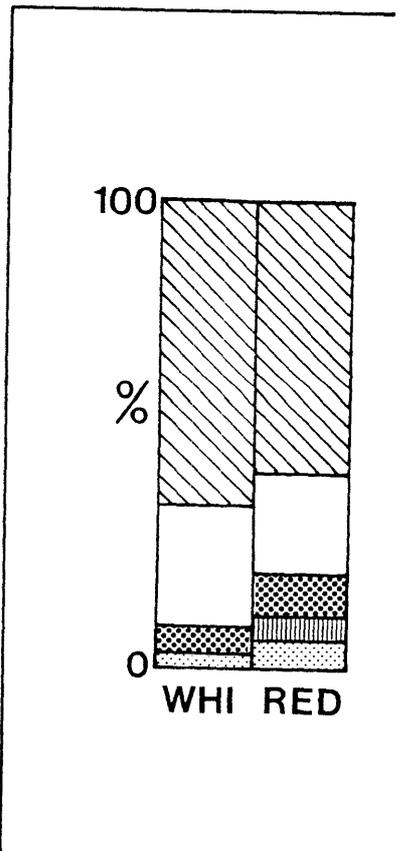
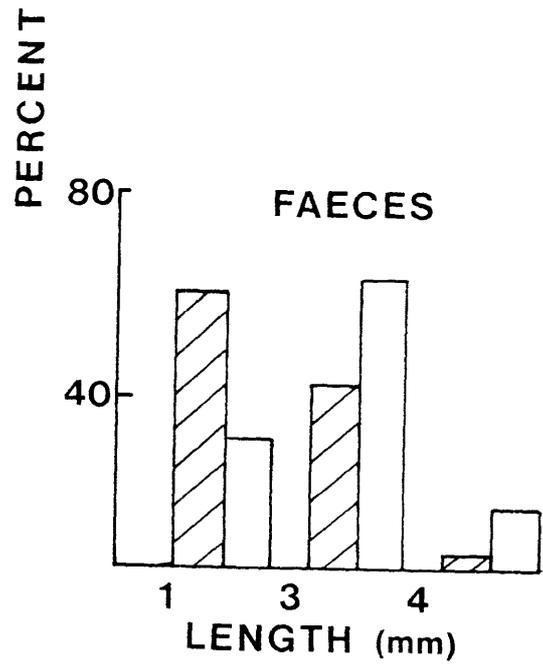
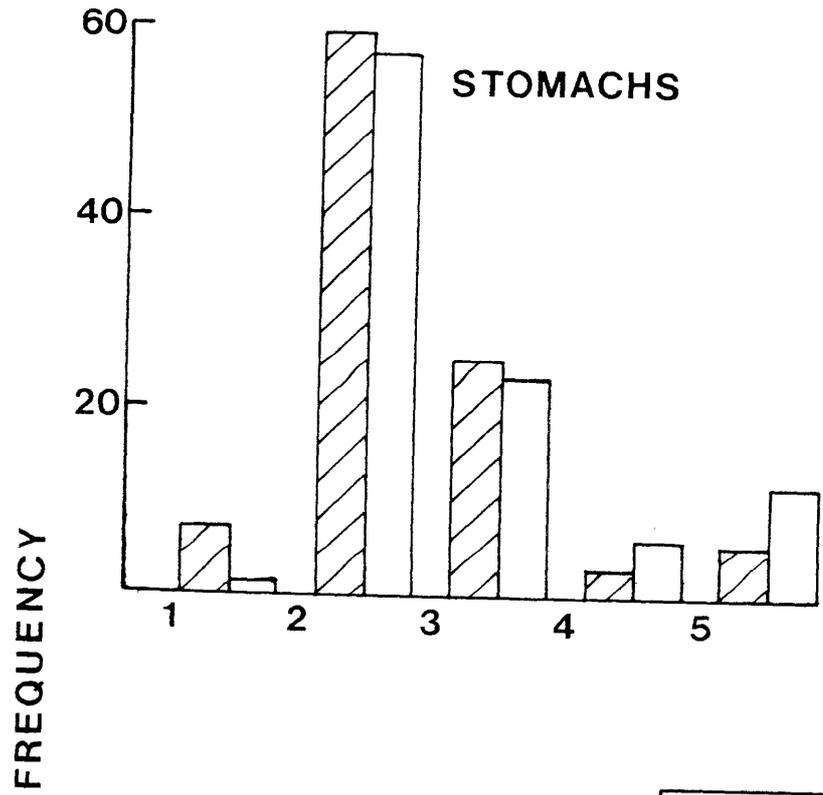
FIGURE 11.13: *Size distribution of ants found in stomachs and faeces of the two Wollomombi treecreepers; and taxonomic composition of ants in former (inset)*

	NUMBER OF ANTS:	
	STOMACHS	FAECES
White-throated	4104	752
Red-browed	3606	405

KEY TO ANT TAXA (inset)

	<i>Iridomyrmex</i> (small)
	<i>Crematogaster</i>
	<i>Campanotus</i>
	<i>Iridomyrmex</i> (large)
	Other

 White-throated  
 Red-browed



at 1-5 metres from the ground. This procedure was repeated continuously for over 30 minutes, each bird making about 50 flights during that time.

Beetles were the next most frequent item in the stomachs and faeces of both treecreepers, occurring in all stomachs examined (Figure 11.14). Like ants, however, the relative importance of these insects may be exaggerated owing to the persistence of their tough exoskeletons. Beetles were relatively more numerous in Red-browed stomachs than White-throated stomachs ( $\chi^2 = 20.4$ , 1 df,  $p < 0.001$ ). Similarly, the mean number of beetles in 19 Red-browed faecal samples was greater than that in 23 White-throated samples (1.05 versus 0.87). Though not significantly different ( $t = 0.17$ , 351 df,  $p > 0.5$ ), the average (estimated) length of beetles in White-throated stomachs was greater than that in Red-browed stomachs (7.0 versus 5.7 mm, respectively). This was partly due to the greater number of large Chrysomelids of the subfamily Chrysomelinae in the former, contrasting with the numerous small Chrysomelids (mostly Eumolpinae) in the latter. The large contribution of beetles to total biomass of arthropods in White-throated (Figure 11.14) reflects this difference. Overall, however, there were no significant differences between the two species in lengths of non-ants in either cold or warm seasons ( $t = 0.47$ , 229 df, and  $t = 0.18$ , 520 df;  $p > 0.5$  for both).

Red-browed stomachs contained relatively more spiders than White-throated ( $\chi^2 = 35.6$ , 1 df,  $p < 0.001$ ) (Figure 11.14), but few spiders were evident in the faeces of either species. Red-browed were observed handling spiders at Wollomombi more often than White-throated ( $\chi^2 = 4.35$ , 1 df,  $p < 0.05$ ) (Figure 11.15). Nine of the 16 identifiable spiders from Red-browed stomachs were Clubionids. The inflated biomass of bugs in the White-throated was chiefly due to the presence of three large (22-25 mm) Cicadids in the stomachs of two fledglings. Cicadellids were the most frequently represented family of bugs in stomachs of both species.

Larvae were slightly, but not significantly ( $\chi^2 = 3.5$ , 1 df,  $p > 0.05$ ), more frequent in Red-browed stomachs than White-throated. Coleopteran larvae were more numerous than Lepidopteran larvae in both species, including Melyrids (especially in White-throated stomachs) and Elaterids (Red-browed only). By contrast, most of the larvae recorded during feeding observations were Lepidopteran, presumably because they were generally larger than those of Coleoptera. Over a half of the food items

FIGURE 11.14: *Taxonomic composition of all arthropods (upper) and beetles (lower) in stomachs of the two Wollomombi treecreepers*

NUMBER OF ARTHROPODS:

White-throated 4446  
Red-browed 4038

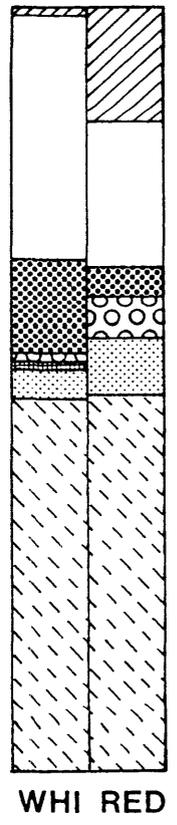
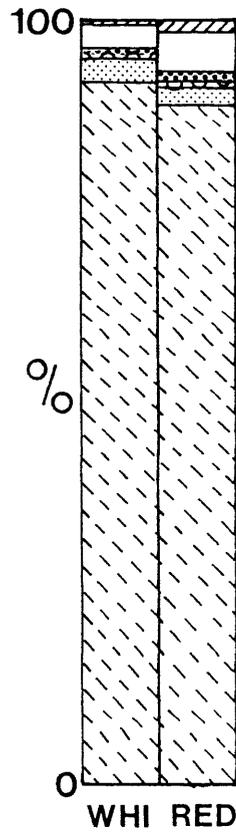
KEYS

UPPER

	SPIDERS
	BETLES (COLEOPTERA)
	BUGS (HEMIPTERA)
	LARVAE
	CRICKETS (ORTHOPTERA)
	OTHER
	ANTS (HYMENOPTERA: Formicidae)

LOWER (COLEOPTERA)

	Curculionidae
	Chrysomelidae: Eumolpinae and other subfamilies
	Chrysomelidae: Chrysomelinae
	Elateridae
	Carabidae/Tenebrionidae
	Other



NUMBERS

BIOMASS

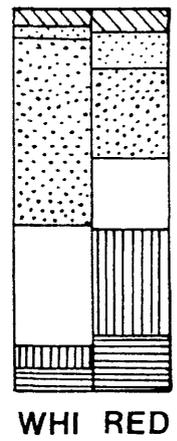
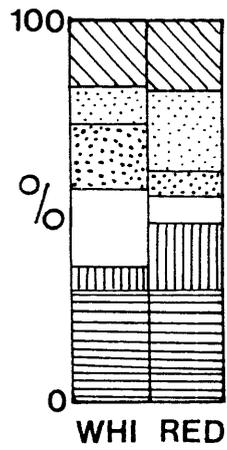


FIGURE 11.15: *Taxonomic composition of items observed being eaten (upper) and intersexual comparison of taxa found in stomachs (lower) of the two Wollomombi treecreepers*

Lower diagram shows biomass only, as ants predominated numerically

UPPER

Number of items:

White-throated	47
Red-browed	69

LOWER

Number of arthropods in stomachs  
(number of stomachs<sup>+</sup> in brackets):

	♂	♀
White-throated	2204 (12)	2200 (12)
Red-browed	2331 (16)	1654 (13)

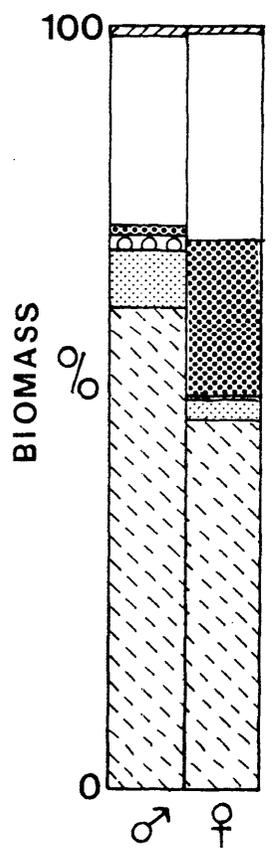
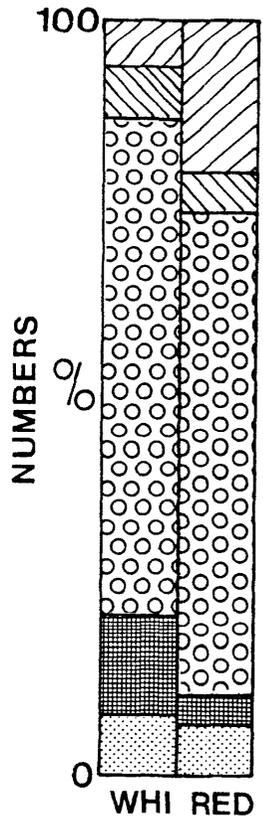
<sup>+</sup> excludes newly-fledged (dependent) birds:  
two White-throated and one Red-browed

KEYS

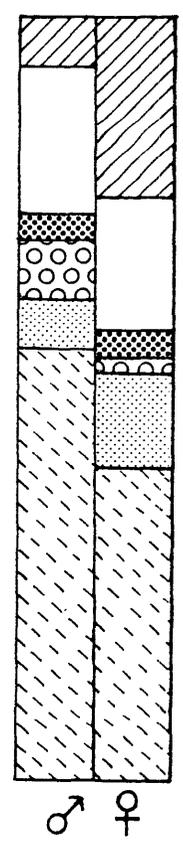
Lower as in FIGURE 11.14

UPPER

	SPIDERS
	MOTHS (LEPIDOPTERA)
	LARVAE
	CRICKETS (ORTHOPTERA)
	OTHER



WHITE-THROATED



RED-BROWED

observed to be taken in both species were larvae (Figure 11.15). Red-browed stomachs contained more cockroaches than White-throated (twelve versus one, respectively) as well as psocids (28 versus six). White-throated, on the other hand, took more flies and wasps than Red-browed (105 versus 40, respectively), and all three lacewings (Neuroptera) occurred in the former. Though crickets (Orthoptera) were scarce in stomachs, I observed the capture of six large (up to 30 mm) Gryllacridids by White-throated at Wollomombi, and three by Red-browed (Figure 11.15). Of 22 identified items brought to nestlings by a pair of White-throated at Stringybark Hill, seven were Gryllacridids.

Dietary overlap (based on the total numbers of arthropods in each taxon) between the two treecreepers in the present study exceeded that found previously ( $\theta = 95.4$  versus  $90.3$ , respectively), despite the smaller sample size in the latter. Diversity of food items was greater in Red-browed than in White-throated (Table 11.3), although this disparity was less evident in the cold seasons, when interspecific overlap was greatest. This indicated that the two species differed most in their food habits in the warm seasons, when White-throated were most specialized, and Red-browed most generalized. Red-browed sexes overlapped slightly more in diet than White-throated sexes. The greatest discrepancy between White-throated sexes in terms of arthropod biomass occurred in the bugs. This was partly due to the one female stomach which contained ten *Catasphaetes* (Reduviidae), each measuring about 9 millimetres in length.

Male White-throated took significantly more ants than females ( $\chi^2 = 16.6$ , 1 df,  $p < 0.001$ ). There were no significant differences between the Red-browed sexes in the proportion of ants in their stomachs ( $\chi^2 = 0.8$ , 1 df,  $p > 0.3$ ). However, female Red-browed took significantly more spiders than males ( $\chi^2 = 5.7$ , 1 df,  $p > 0.02$ ), and this was reflected in the relative contribution of spiders to the total arthropod biomass of each sex (Figure 11.15). Though male stomachs had proportionally more larvae than females in terms of both frequency and biomass, this difference was not significant ( $\chi^2 = 2.0$ , 1 df,  $p > 0.1$ ).

### *Sittellas*

Although overwhelmingly important in the diets of treecreepers, ants formed only a minor proportion (7%) of the arthropods found in the stomachs of sittellas (Figure 11.16). Only a third of the 61 stomachs and one of the ten faecal samples of this species contained ants. Compared to

TABLE 11.3: *Indices of overlap and diversity of food items*

		OVERLAP <sup>†</sup>				SEX	SEASON
		WHI	RED				
WOLLOMOMBI	RED	SUM	91.8	-	WHI	95.7	98.0
		WIN	98.6	-	RED	97.5	93.1
	SIT	14.6	17.4	SIT	86.2	82.1	
SWAN VALE	BRO	SUM	90.6	-	WHI	92.6	94.0
		WIN	91.2	-	BRO	98.4	95.6

		DIVERSITY (H')				
		SEX		SEASON <sup>#</sup>		
		♂	♀	SUM	WIN	TOTAL
WOLLOMOMBI	WHI	.32	.45	.28	.31	.41
	RED	.51	.53	.65	.37	.52
	SIT	1.96	1.68	1.81	1.82	1.86
SWAN VALE	WHI	.72	.51	.54	.69	.47
	BRO	.23	.29	.20	.37	.28

<sup>†</sup> overlap in percentages

<sup>#</sup> SUM = spring and summer; WIN = autumn and winter

FIGURE 11.16: *Intersexual comparison of taxonomic composition of arthropods found in stomachs of Varied Sittellas from Wollomombi (upper) and Northern Rivers (lower) regions. Upper right, taxonomic composition of beetles in terms of numbers (upper; N = 176) and biomass (lower); inset, items observed being eaten in the Wollomombi region (N = 70)*

Number of arthropods in stomachs  
(number of stomachs in brackets):

	♂	♀
Wollomombi	265 (17)	191 (11)
Northern Rivers	346 (23)	190 (8)

#### KEYS

As in FIGURES 11.14, 11.15



treecreepers, the number of items in sittella stomachs was small, but the average number of "non-ants" per sittella stomach (15.8) was greater than in the two treecreepers (13.3 and 14.4 for White-throated and Red-browed, respectively).

Beetles were the most frequently represented taxon in stomachs. Of the many families represented, Curculionidae, Chrysomelidae (mostly Eumolpinae) and Coccinellidae were most important. Beetles in stomachs from the Wollomombi area were significantly longer than those from the Northern Rivers region ( $t = 6.21$ , 388 df,  $p < 0.001$ ). This geographic difference in prey size was also true for spiders ( $t = 2.73$ , 129 df,  $p < 0.01$ ) and bugs ( $t = 2.30$ , 136 df,  $p < 0.05$ ), but not for larvae ( $t = 1.97$ , 161 df,  $p > 0.05$ ). Seven of the eleven faecal samples of sittellas contained beetle remains, but little else.

Sittellas from the Wollomombi area took significantly smaller beetles and spiders than Red-browed Treecreepers ( $t = 4.79$ , 380 df,  $p < 0.001$  and  $t = 2.74$ , 87 df,  $p < 0.01$ , respectively), but there were no significant differences between these species in lengths of bugs or larvae ( $t = 0.0$ , 104 df and  $t = 1.11$ , 131 df, respectively,  $p > 0.2$ ). As with treecreepers, larvae were the most frequently observed food item of sittellas at Wollomombi but they comprised a greater proportion of the total number of observations than in treecreepers (Figure 11.16). The majority of larvae found in stomachs were Coleopteran; the chief identified families being Cleridae and Melyridae. Lepidopteran larvae, however, provided the bulk of the biomass of larvae. Lea and Gray (1936) identified Lepidopteran larvae in two of the five specimens of sittellas they examined. The large contribution of crickets to total biomass of stomachs from the Wollomombi area was mainly because of four Gryllacridids, ranging in length from 20 to 30 millimetres.

Despite the sexual dimorphism of bill-length in sittellas, sexes did not differ significantly in prey size selection (in the Wollomombi area,  $t = 0.84$ , 400 df,  $p > 0.05$ ). No significant differences occurred in the taxonomic composition of stomachs at either Wollomombi ( $\chi^2 = 12.7$ , 7 df,  $p > 0.05$ ) or the Northern Rivers region ( $\chi^2 = 8.7$ , 8 df,  $p > 0.3$ ). However, spiders appeared to contribute more to the total biomass of food items of

females than they did in males in both regions (Figure 11.16). Taxonomic overlap between male and female sittellas was less than the overlap between the two species of treecreepers or their sexes (Table 11.3), though these results are probably chiefly due to the large number of ants in the latter. Undoubtedly, the relative scarcity of ants in sittellas also contributed to the high taxonomic diversity of their diet compared to treecreepers (Table 11.3). Overlap indices indicated that Red-browed were slightly closer to sittellas in diet than were White-throated, probably because of the lesser importance of ants in the former.

#### *Swan Vale Treecreepers*

At Swan Vale, Brown stomachs contained significantly more ants than those of the White-throated overall ( $\chi^2 = 110.7$ , 1 df,  $p < 0.001$ ) (Figure 11.17). The number of ants per Brown stomach was significantly higher than in the White-throated ( $t = 3.05$ , 37 df,  $p < 0.01$ ), while the number of non-ants was significantly lower ( $t = 2.21$ , 37 df,  $p < 0.05$ ). There was no significant difference between warm and cold seasons in the number of ants in White-throated stomachs ( $t = 0.73$ , 14 df,  $p > 0.2$ ), but Brown had significantly more ants in summer than in the other seasons ( $t = 4.24$ , 21 df,  $p < 0.001$ ) (Figure 11.17). Like Red-browed, Brown stomachs contained significantly more large ants (over 4 mm in length) than White-throated at Swan Vale (Kolmogorov-Smirnov test,  $D = 19.9$ ,  $p < 0.001$ ) (Figure 11.18). This was partly because Brown took relatively more large ants, such as *Campanotus* and *Iridomyrmex purpureus*. The latter species, which is carnivorous and mainly terrestrial, did not occur in the area where food availability was measured but was abundant in other parts of the study site. Occasionally Brown were seen hopping over their large nest mounds, gleaning ants.

In the White-throated stomachs, *Crematogaster* ants were slightly more numerous than *Iridomyrmex* of equal size; this contrasted with Wollomombi White-throated, in which *Iridomyrmex* were twice as common as *Crematogaster*. *Crematogaster* were relatively less common at Swan Vale than Wollomombi on surface censuses, but were mainly confined to the forest where there was only one plot at the former site. Accordingly, this genus was poorly represented in the Brown stomachs, although some specimens were collected from forested areas.

FIGURE 11.17: *Seasonal variation in the numbers of ants (upper) and non-ants (lower) in stomachs of the two Swan Vale treecreepers*

Rectangles, one standard error either side of mean (horizontal line)

	NUMBER OF STOMACHS	
	White-throated	Brown
SUMMER	5	6
AUTUMN	4	5
WINTER	5	7
SPRING	2	5

White-throated

Brown

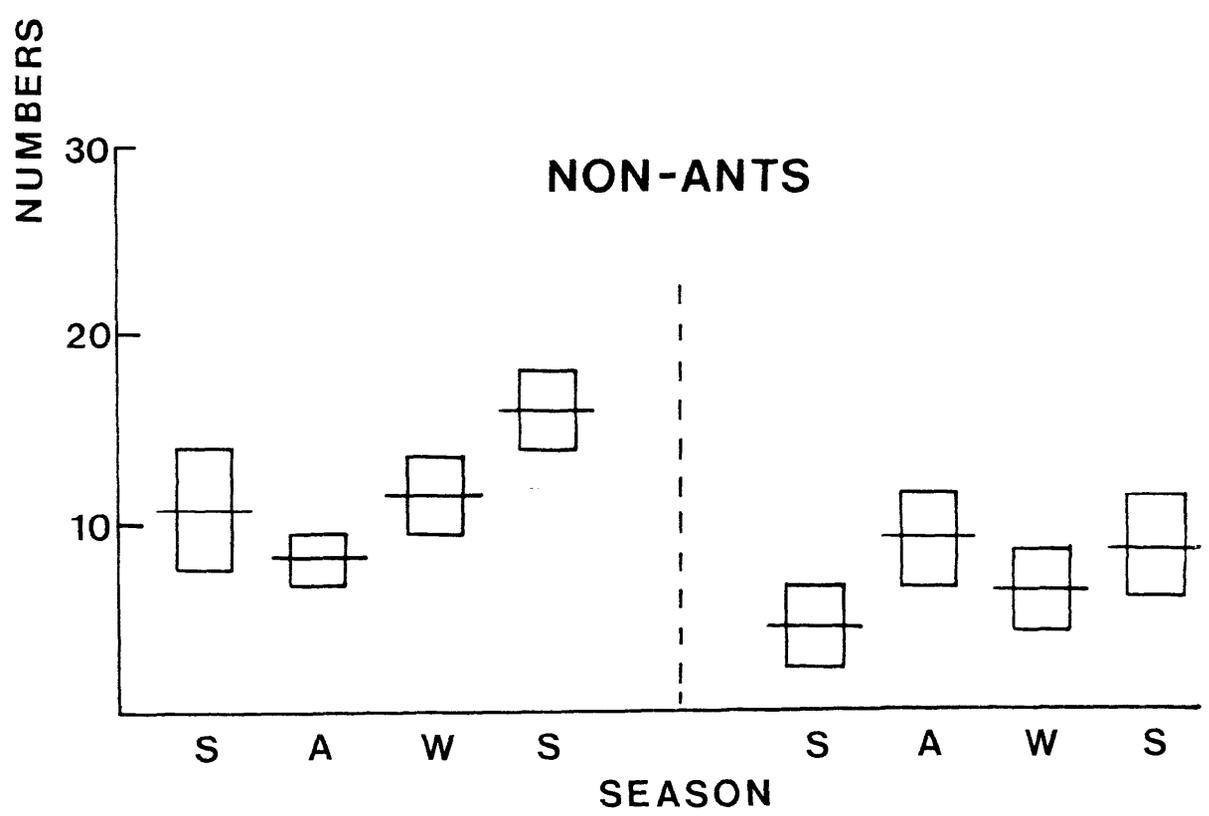
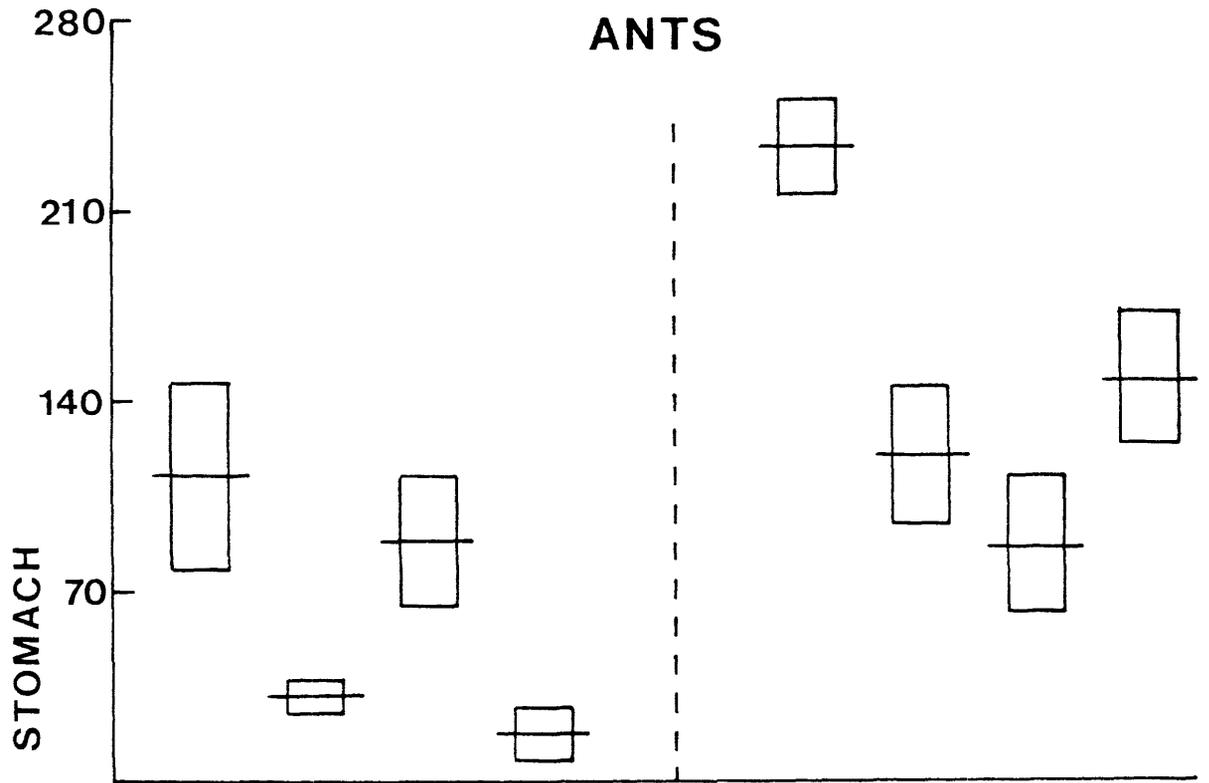


FIGURE 11.18: *Size distribution of ants found in stomachs and faeces of the two Swan Vale treecreepers; and taxonomic composition of ants in former (inset)*

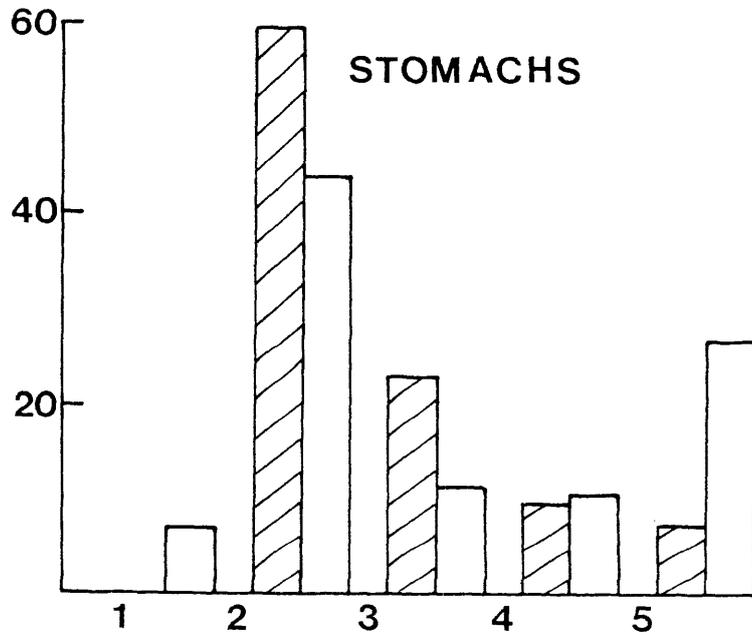
NUMBER OF ANTS:

	STOMACHS	FAECES
White-throated	1135	153
Brown	3303	1333

KEY TO ANT TAXA (inset)

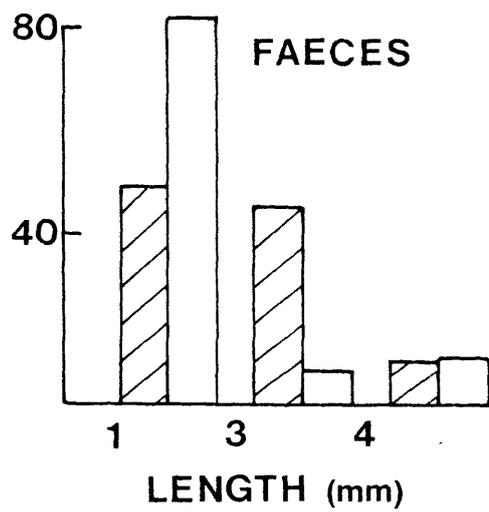
	<i>Iridomyrmex</i> (small)
	<i>Crematogaster</i>
	<i>Campanotus</i>
	<i>Iridomyrmex purpureus</i>
	<i>Rhytidoponera</i>
	Other

 White-throated  
 Brown

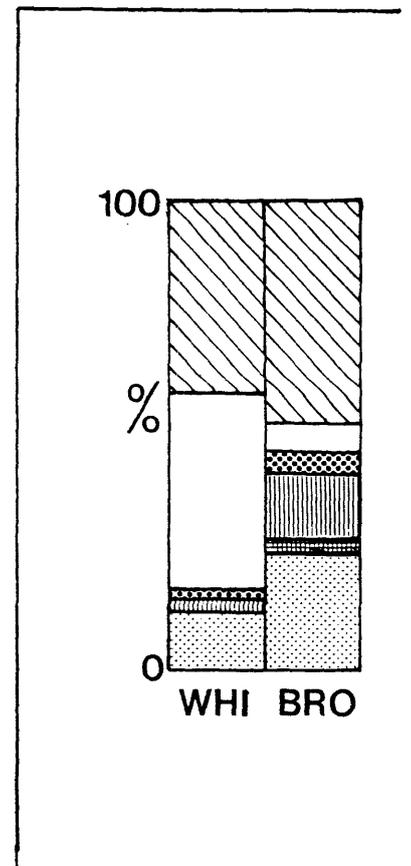


FREQUENCY

PERCENT



LENGTH (mm)



WHI BRO

Diet overlap between the two Swan Vale treecreepers was less than that for the two Wollomombi treecreepers, particularly for the cold half of the year (Table 11.3). Despite its generalized foraging behaviour, the Brown had a lower diversity of taxa in its diet than any of the other study species. During both warm and cold seasons, Brown took significantly larger non-ant prey than White-throated ( $t = 3.72$ , 157 df, and  $t=7.26$ , 179 df, respectively;  $p < 0.001$ ). This differential size selection was evident in the beetles eaten ( $t = 4.48$ , 161 df,  $p < 0.001$ ). Chrysomelidae (Chrysomelinae) was the most important beetle family for both species, but several stomachs of Brown contained up to nine large ground-dwelling dung beetles (*Onthophagus granulatus*, Scarabidae). In common with the other study species, the majority of food items observed for the Brown were larvae (Figure 11.19), although most of these were procured from the ground. During one hour of observations at a Brown nest, almost a half of the items brought to the nestlings were larvae. All but one of fourteen faecal sacs of Brown nestlings contained ants, and eleven contained beetles, including Scarabs.

There was no significant sexual difference in the diet of Brown ( $\chi^2 = 8.8$ , 4 df,  $p > 0.05$ ). However, female White-throated at Swan Vale had significantly more ants than males ( $\chi^2 = 9.2$ , 1 df,  $p < 0.01$ ), a difference which was reflected in estimates of ant biomass for the sexes (Figure 11.19). This was the reverse of the intersexual differences in both White-throated and Red-browed at Wollomombi. Though it is tempting to conclude that this disparity was related to the low foraging levels of female White-throated at Swan Vale, in contrast to high foraging levels of females of the other species (and Wollomombi White-throated), the evidence is circumstantial and assumes the specimens collected showed similar foraging patterns to those at the study side.

#### 11.4 Conclusions

The seasonal pattern of arthropod abundance and biomass on the surface of tree-trunks parallels that observed for aerial insects by Cameron (1975) at Five Day Creek (about 40 km SE of Wollomombi) and Bell (pers. comm.) at Wollomombi Falls. In general, there were more arthropods

FIGURE 11.19: *Taxonomic composition of items observed being eaten (upper) and intersexual comparison of taxa found in stomachs (lower) of the two Swan Vale treecreepers*

Lower diagram shows biomass only, as ants predominated numerically

UPPER

Number of items:

White-throated	26
Red-browed	51

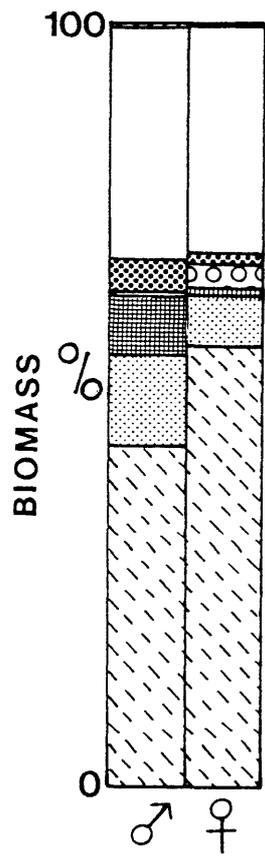
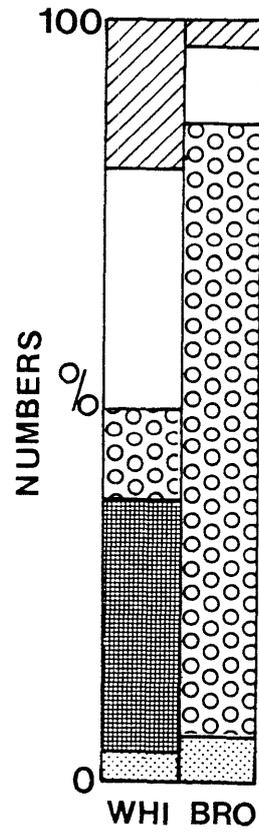
LOWER

Number of arthropods in stomachs  
(number of stomachs in brackets):

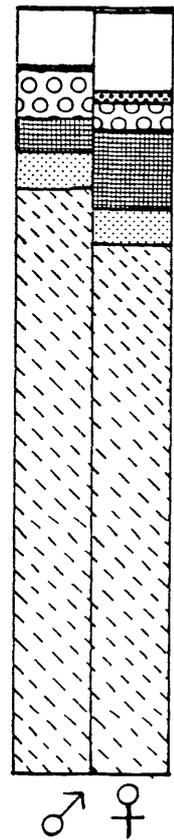
	♂	♀
White-throated	644 (9)	680 (7)
Brown	1836 (11)	1503 (11)

KEYS

As in FIGURES 11.14, 11.15



WHITE-THROATED



BROWN

on the trunks during the afternoon than during the morning at Wollomombi, though this difference was rarely significant according to the analyses of variance. Nevertheless, this diurnal trend provides a possible explanation for the increasing use of trunks and decreasing landing-levels of the two Wollomombi treecreepers on stringybarks as the day progressed. The greater use of branches at higher levels by birds in these trees may, therefore, be a response to greater activity of arthropods thereon during the early part of the day.

Several aerial feeding species of birds have been shown to hawk more during the middle of the day when temperatures were highest and aerial insects were most active (Davies 1977; Greenwood and Harvey 1978; Holmes *et al.* 1978; Huddy 1979). Perhaps subsurface-dwelling arthropods (including many non-flying forms) become active later than aerial or foliage insects because they are less tolerant of extreme temperatures. Many Blattelids (cockroaches), for instance, are mainly active at night (J. Balderson, pers. comm.). The low numbers of arthropods on the surface of trunks during the autumn and winter are also consistent with the reduced utilization of stringybark trunks by birds during these cold seasons, but arthropods at higher levels probably suffered a similar decline.

In contrast to the arthropods observed during the surface censuses, those collected from beneath bark were most abundant during the colder half of the year. Lawrie (1974) also found an increase in the number of invertebrates under the bark of New England Blackbutts, *E. andrewsii*, between March and July. The number of arthropods in the leaf litter at Wollomombi was higher during autumn and winter than during late summer (Huddy 1979) and litter has a very similar fauna to bark (Lawrie 1974). The relative abundance of different taxa I collected under the bark differed quite markedly from that observed on the surface. The bulk of arthropods on the surface were transitory, including ants and flying insects such as flies, moths and wasps. In contrast, bark collections emphasized sedentary groups, such as beetles, larvae and cockroaches, which apparently rested during the day beneath the surface. Similarly, Jackson (1979) concluded that the arthropod communities on the trunks of trees in Mississippi were dominated in terms of numbers of indi-

viduals, by transients such as ants and chance volant insects landing on the bark, but in terms of resident biomass, by spiders. Even among the spiders at Wollomombi, however, this division seemed to hold: the active, hunting Salticids were prevalent on the surface, while under the bark (particularly in ribbons), Clubionids rested within their silken retreats.

On the surface of tree-trunks at both Wollomombi and Swan Vale, ants were generally most abundant on gums, and non-ants, on stringybarks. However, this does not necessarily reflect the availability of these arthropods to the birds. Many of the trunks of gums, where ants were common, were almost entirely smooth and were thus not exploited by treecreepers as these birds require rough or peeling bark on vertical surfaces to maintain a foothold. In addition, many of the arthropods collected from the subsurface of stringybarks were probably inaccessible to treecreepers, because these birds lack the morphological adaptations to enable deep penetration of the bill into the bark. If treecreepers were more specialized in this regard, one might have expected more drilling, particularly by White-throated, during the cold seasons, when surface-dwelling arthropods were scarcest and subsurface-dwellers, most abundant. On the contrary, both species of treecreepers tended to take more ants, which are predominantly surface-dwellers, during this time of year.

The ribbons on the trunks and/or branches of gums and boxes were heavily exploited by the Red-browed. Orenstein (1977) suggested that these birds concentrated on such sites because they provided discrete patches (separated by smooth bark) containing insects, while food on rough-barked trees was probably more evenly distributed. My comparison of ribbons and stringybarks indicated that, not only are the former patchy in distribution, but the arthropods they shelter are patchily distributed in space and time as samples exhibited great variation in arthropod quantities, especially during the cold seasons.

Some correlations occurred between the relative contributions of non-ant taxa in the diets of the two Wollomombi treecreepers, and the availability of those taxa on the preferred tree-types of these birds. Spiders were apparently eaten by Red-browed more than White-throated, and in bark collections, at least, they were most prevalent on boxes and gums.

Though the relative quantity of spiders on stringybark samples in the second year was similar to that on ribbons, the quality of this group was higher in the latter case. Clubionids and Thomisids were the two most important families of spiders in ribbons, as well as in the Red-browed stomachs. Among Chrysomelid beetles, the smaller Eumolpinae predominated in both ribbons and Red-browed stomachs, while the larger Chrysomelinae were dominant in stringybark samples and White-throated stomachs. Of the Coleopteran larvae identified from the stomachs, Melyrids and Elaterids predominated in the White-throated and Red-browed respectively, and were commonest on stringybarks and rough boxes, respectively. Psocids were collected from all tree-types except stringybarks (at both sites), and Red-browed took more of these insects than White-throated.

The numerical proportion of ants in the stomachs of the two treecreepers corresponded with the relative availability of these insects on tree-trunks, as determined by surface censuses, at least during the warm seasons (89% and 86% of total arthropod numbers in spring and summer, respectively). Yet the contribution of ants to the diets of these birds is probably overestimated from analyses of stomach contents and faeces (as mentioned previously), owing to the persistence of their tough exoskeletons long after the decomposition of other, softer-bodied items. Indeed, many ants in the stomach and intestines were intact, giving the impression that treecreepers obtained little nourishment from them. However, the vast majority of ants found on tree-trunks and eaten by treecreepers are nectarivorous, collecting a sugar solution from various sources (for example, honeydew-forming Homopterans) on the tree to feed to their larvae (R.W. Taylor, pers. comm.). Thus, ants could provide a source of carbohydrates for birds. Most of the ants concerned nest in the ground, so that those descending the tree-trunk *en route* to the nest would have fuller crops than those ascending *en route* to their food sources. Unfortunately, it is not known whether treecreepers discriminate between these two "types" of ants.

While ants are presumably an important and reliable food source for treecreepers, it is doubtful that they are their favourite items or that they provide all their energy requirements. Otherwise, one might expect these birds would feed most efficiently by perching beside an ant

trail for long periods, picking off ants as they passed. Instead, tree-creepers seem to forage actively throughout the day, visiting hundreds of trees. On the other hand, little energy is expended in gleaning ants while climbing (perhaps) in pursuit of other food.

Orenstein (1977: 80) noted that none of the prey items brought to a nest of Brown Treecreepers appeared to be ants, and concluded that ants were not fed to young birds. This is refuted by the evidence of ants in almost all of the faecal sacs of this species I examined. Moreover, Brown at Swan Vale were occasionally seen gleaning small ant-like items immediately before flying to their nest to feed the young a larger item. Juvenile treecreepers generally had fewer ants in their stomachs than adults but this difference was not significant. It is not known whether the almost total absence of ants in the faecal sacs of White-throated represents a real difference between this species and the Brown, or merely an artefact of sampling.

It is not clear why Red-browed took more large ants than White-throated, especially since no significant differences occurred between these species in the size of other prey taken. Although there was no significant interspecific difference in bill-length, Red-browed had a significantly deeper slit at the tip of the tongue than White-throated (see Section 3.1.1). Orenstein (1977: 196) suggested that the fimbriations to the tongue-tip of treecreepers were useful in sweeping small insects from deep crevices. Similarly, it could be argued that the greater degree of bifurcation (and possibly greater number of fimbriations) shown by the Red-browed might permit more efficient handling of large ants. Interestingly, the tip of the tongue in sittellas is not fimbriated, a feature which Orenstein (*op.cit.*) related to their greater use of excavating and gleaning as opposed to probing techniques when foraging. Yet, as this study shows, sittellas differ markedly from treecreepers in their avoidance of ants. Ants, unlike many other arthropods, rarely hide in fissures and crannies, and are more likely gleaned from the surface. Indeed, my observations suggest that sittellas glean less often than treecreepers. The fimbriations on the tongue-tip of the latter may, therefore, be more directly related to feeding on ants.

The lack of differences between male and female sittellas in their diets, in terms of both prey size and taxonomic composition does not accord with differences observed in their foraging behaviour and sexual dimorphism in bill length. The specialization of this species on stringybarks, and their more generalized substrate use, including much use of dead branches (by both sexes), in these trees may be partly responsible for the similarities in the taxa taken by the two sexes. The bulk of Coleopteran larvae identified from the stomachs of sittellas was formed by Cleridae, Melyridae and Tenebrionidae, families which were best or solely represented on stringybarks and/or dead trees.

The ground foraging habit of the Brown Treecreeper was reflected by the presence of the terrestrial ant, *Iridomyrmex purpureus*, and dung beetles. The amount of ground foraging by this species at Swan Vale reached its highest levels during the breeding season (late winter-spring). By contrast, ground feeding by Scarlet Robins, *Petroica multicolor* (Huddy 1979) and Buff-tailed Thornbills, *Acanthiza reguloides* (H.L. Bell, pers. comm.) at Wollomombi Falls increased significantly during the autumn and winter. However, these species feed primarily by hawking and foliage gleaning (respectively) at other times of the year. Perhaps foraging on the ground is less energy-consuming than climbing trees for the large Brown Treecreeper during the cold months at the beginning of its breeding season. In addition, insects sheltering in the litter during winter may be more accessible than those under bark, particularly for this relatively short-billed species. Indeed, more time was spent drilling while on the ground during winter than during spring, despite the similar proportion of time devoted to ground foraging in these two seasons.

## Chapter 12

## GENERAL CONCLUSIONS

The two main recognized advantages of living in groups are increased ability to (1) locate food (Crook 1964, 1965; Ward and Zahavi 1973) and (2) detect and deter predators (see Bertram 1978). If food is patchy, unsuccessful foragers in a group may benefit from observing and copying more successful foragers, but if food is evenly distributed and individuals have an equal chance of finding food, there is little advantage to be gained from following conspecifics. As Red-browed Treecreepers occurred in groups, while White-throated Treecreepers were mainly solitary, I (Noske 1979) previously proposed that the food sources of the former were more patchily distributed than those of the latter. Orenstein (1977) realized that the peeling bark used by Red-browed was patchy in distribution, and results in the previous chapter indicated that such sites were potentially more productive than the bark of stringybarks. By contrast, the latter trees provided a poorer but more reliable source of food for the White-throated.

Despite this relationship, there was no evidence that individual Red-browed benefited from watching other group members. On the contrary, individuals were spaced even when in the same tree, through sexual differences in foraging behaviour. It is conceivable that intersexual differences in foraging behaviour evolved only recently, as indicated by lack of sexual dimorphism in the bill, and that social facilitation operated in this species in the past. Yet intersexual niche segregation was even more pronounced in the *sittella*, which exhibited far greater social tendencies than the Red-browed (e.g. huddling and allopreening). Indeed, sociality appears to be directly related to foraging divergence of the sexes in the three Wollomombi species, suggesting that the most efficient means of exploiting resources (for bark foragers at least) may be avoiding, rather than following conspecifics. McEllin's (1979) study of two sympatric nuthatches, however, showed the reverse pattern. The pair-territorial White-breasted Nuthatch showed sexual differences in its foraging behaviour, while the gregarious Pygmy Nuthatch did not.

The specialized feeding sites and localized distribution of the communal Red-browed Treecreeper, conform to the food localization and habitat saturation explanations for the evolution of communal breeding. However, resource localization is unlikely to be significant for the more communal sittella and Brown Treecreeper. Of the bark foragers at Wollomombi, the sittella was the most specialized in its selection of trees, but it was the most generalized in its choice of substrates and perhaps food. Its habitat requirements are very broad, since it occurs throughout the Australian mainland. The Brown was undoubtedly the most generalized of all the species studied in its foraging niche, by virtue of its ground-dwelling habits. Additionally, it is the most widely-distributed of the three treecreepers. Though habitat saturation may well be an important factor underlying reduced dispersal and communal behaviour in the Red-browed, it does not really help to explain why the White-throated, so similar in size, general morphology and diet to the Red-browed, has adopted a totally different way of life.

The many differences between the White-throated and the other two treecreepers in their life history characteristics presumably derive from their different histories. Table 12.1 contrasts these two groups, summarizing much of the information presented in Part B and corroborating the dichotomy in plumage and morphology noted in Part A. As reasoned in Section 3.1.4, the White-throated probably originated in rainforests, whereas the avoidance of this habitat by the other species of treecreepers argues for a sclerophyll history.

The diverse vocal repertoire and strongly territorial nature of the White-throated are consistent with its proposed rainforest origin. Spacing of individuals in dense vegetation, where visual contact is much reduced, could be achieved largely by vocal cues (Buskirk 1976) and other auditory signals such as "clicking", which continually provide locational information. In a society where there is no obvious dominance hierarchy, sexual differences in calls might be helpful in distinguishing trespassers (of the same sex) from mates. The distinctive incubating call of the female White-throated stimulates the male to feed her, and helps him to locate her in the dark rainforest conditions. By contrast, the apparently rigid social structure of the communal Red-browed and Brown makes sexual

TABLE 12.1: *Differences between the White-throated Treecreeper and its congeners in social organization and life-history characteristics*

	WHITE-THROATED	RED-BROWED/BROWN
HABITAT	Rainforest, sclerophyll	Sclerophyll
SOCIALITY	Antisocial	Communal
TERRITORY	Small (5 - 6 ha) Regularly/strongly defended Unstable boundaries	Larger (7 - 20 ha) Irregularly/weakly defended Constant boundaries
APOSEMATIC DISPLAY	Yes (clicking)	No
AGGRESSION	Frequent	Infrequent; appeasement display used
SEX RATIO	Even	More ♂♂
DOMINANCE HIERARCHY	No	Yes ( ♂ ♂ dominant)
NUMBER OF CALLS	8 - 9	4 - 5
SEXUALLY-DIAGNOSTIC CALLS	Yes	No
ROOST-SITE	External	Inside hollow spouts
PRE-COPULATION DISPLAY	'Semaphore' by ♂ ♂ ( ♀ ♀ inactive)	Both sexes active
PREFERRED NEST-SITE	Holes	Hollow dead spouts
BUILDING	Exclusively ♀ ♀	Both sexes
EGG LAYING	Alternate days	Daily (?)
INCUBATION PERIOD	22 - 23 days	16 - 18 days
INDUBATION CALL ( ♀ )	Yes	No
NESTLING CALL	Very distinctive	Similar to adult *
SEXUAL DIMORPHISM	From 8 days	From c.16 days
JUVENILE PLUMAGE	♀ ♀ different from adult	both sexes different from adults
FLEDGLING BEHAVIOUR	Perch/climb in open	Sometimes stay in hollow spouts
NO. OF BROODS	One	One or two
TREATMENT OF PROGENY	Young harassed by parents about 3 weeks after fledging; all expelled after 30-45 days	Majority (?) of young tolerated within natal territory

\* less so in Red-browed

differentiation of calls unnecessary and close visual contact between group members is facilitated by the more open nature of their habitats.

Differences in the nesting and roosting sites of the two groups of treecreepers may also be a result of the opportunities available to them in their original habitats. The White-throated preferred to nest in holes in live trunks and roosted mostly on the surface of trunks. This may reflect the paucity of hollow branches on the softwoods characteristic of rainforests, where wood decomposes rapidly. By contrast, the Red-browed and Brown chose hollow dead eucalypts or dead branches of live eucalypts for both nesting and roosting. Such sites are (and presumably always have been) abundant in sclerophyll forests and woodlands, owing to the slow decomposition of these hardwoods (J.B. Williams, B. Richards, pers. comm.).

Hyem (1936) noted that the White-throated was more flexible in its choice of nest-sites than the other two species: "any sort of hollow seems to suit...in large hollows in the trunks of dead trees, behind loose pieces of bark and in crevices in old, rotting stumps". Red-browed and Brown, on the other hand, usually chose "upright hollow branches" for their nests. Generalized nest-site requirements in the White-throated are consistent with the idea of a lack of suitable holes in its original habitat. The exposed roost-sites of the White-throated also suggest that this species was less subject to predation than the other species during its evolution, or required no thermal insulation overnight (Kendeigh 1961).

The four-day difference between the White-throated and the Red-browed in their incubation periods is rather striking in view of their close size and presumed relationship. The eggs of these two species are not significantly different in size (unpubl. data). Skutch (1945) found little correlation between size of eggs and length of incubation periods among Central American birds, but noted that the incubation period was shortest in species that incubated continuously. However, the White-throated Tree-creeper apparently spends more time on the nest than the Brown, which has an even shorter period than the Red-browed.

It has been shown that tropical passerines generally have longer incubation and nestling periods and grow more slowly than those in temperate

regions (Skutch 1966; Ricklefs 1969a, 1976). Yet the high rate of nest predation in the tropics compared to temperate regions (Skutch 1949, 1966; Ricklefs 1969b) might be expected to favour short nesting cycles to reduce exposure to predators (Ricklefs 1969a, 1979). Oniki (1979), however, questioned the influence of predation and contended that tropical birds had longer nesting periods than temperate birds because of a longer nesting season, or lower average food abundance. Moreau and Moreau (1940) also considered that the brevity of the warm season at high latitudes placed a high premium on shorter nesting cycles. In any case, as Skutch (1966) argued, shorter nesting cycles would not necessarily decrease nest predation. Accelerated development (especially of the young) would require more frequent feeding visits and the resultant increased activity at the nest could attract predators.

It is unlikely that the White-throated and Red-browed Treecreepers experience differential nest predation where they coexist at present, but these two species might have experienced different predation pressures in the past. The shorter incubation periods of the sclerophyll-adapted Red-browed and Brown indicate that predation of eggs was higher in drier, more open habitats than in the moist, closed forests inhabited by the White-throated. This is contrary to the findings of Snow and Snow (1964) and Skutch (1966) for the neotropical region, but as Oniki (1979) rightly pointed out, predators should find nests more easily in open areas than in forests, where there are many more inconspicuous hiding places. The long incubation period of the White-throated may also have evolved due to lower food abundance in rainforests during the breeding season. Many arthropods become inactive or seek shelter during heavy rain (Foster 1974; pers. obs.), so that food may be difficult to locate for long periods in rainforests. Yet this should favour longer spells off the nest, contradicting the evidence available on this species (compared to the Brown).

Long incubation periods may be characteristic of Australian rainforest-adapted passerines. The incubation periods of species which occur in rainforests (as well as sclerophyll) are consistently one to two days longer than those of their more strictly sclerophyll counterparts (Table 12.2). Courtney and Marchant (1971) noted that the Dusky Woodswallow,

TABLE 12.2: Nesting information for four pairs of congeners, contrasting 'dry' and 'wet' adapted species\* (upper and lower pair members respectively)

COMMON NAME	SCIENTIFIC NAME	AVERAGE <sup>†</sup>		CLUTCH SIZE	STATUS <sup>‡</sup>
		INCUBATION PERIOD (N)	NESTLING PERIOD (N)		
Grey Fantail	<i>Rhipidura fuliginosa</i>	13.8 (4)	?	2-3	PM
Rufous Fantail	<i>R. rufifrons</i>	14.9 (1)	?	2	M
Rufous Whistler	<i>Pachycephala rufiventris</i>	14.1 (4)	10.5 (1)	2-3	M
Golden Whistler	<i>P. pectoralis</i>	16.0 (4)	10.4 (1)	2	PM
Striated Thornbill	<i>Acanthiza lineata</i>	16.1 (2)	?	3	S
Brown Thornbill	<i>A. pusilla</i>	18.8 (7)	15.3 (2)	3	S
White-throated Warbler	<i>Gerygone olivacea</i>	16.8 (5)	?	2-3	M
Brown Warbler	<i>G. mouki</i>	18.5 (3)	15.7 (1)	2-3	S

\* 'wet' adapted species breed mainly in rainforests or wet sclerophyll forests (occasionally nest among dense vegetation in dry sclerophyll); 'dry' adapted species, with possible exception of Grey Fantail, never breed in subtropical rainforests; species in each pair similar in size and nest-type

† data taken from Marchant (1980), except for White-throated Warbler, (extrapolated from NRS); averages based on midpoints of the range for each nest (see Courtney and Marchant 1971); data expressed in days to nearest decimal point; N = number of nests

‡ M = migrant between north-eastern and south-eastern Australia;

PM = partial migrant within south-eastern Australia;

S = sedentary

*Artamus cyanopterus*, had a longer incubation period than its xeric inland relative, the White-browed, *A. superciliosus*, a discrepancy they related to the nomadic and opportunistic breeding habits of the latter. The difference between congeners in each of the species "pairs" in Table 12.2, however, does not appear to be attributable to relative mobility, as migratory forms occur in both the 'wet' and 'dry' categories. Unfortunately, while incubation periods may well be correlated with habitat types, we are still ignorant of the ultimate causal factors.

Compared to the White-throated, the Red-browed and Brown have a relatively simple pre-mating ceremony, shorter laying and incubation periods, and probably shorter building periods owing to the participation of males in this activity. In addition, auxiliaries may do most of the caring for the young, leaving the parents free to re-nest. These features are time savings, which undoubtedly facilitate second broods; the White-throated by contrast, is typically single-brooded. The reproductive potential per season of each Red-browed and Brown pair is therefore greater than that of each White-throated pair, despite the small clutch of the Red-browed. Rowley (1965, 1976) believed that auxiliaries permitted the population to increase rapidly during favourable years and buffered the population from rapid decline during harsh periods. Emlen (1982) demonstrated that this group selection interpretation need not be invoked if one considers that an auxiliary has little chance of breeding successfully in harsh years. He found an inverse correlation between the incidence of auxiliaries in the White-fronted Bee-eater and rainfall (as well as insect availability), suggesting that bee-eaters were more likely to remain with groups as auxiliaries when conditions were harsh.

Emlen (*op.cit.*) provided an explanation for communal breeding in both stable, predictable environments and erratic, unpredictable environments *via* ecological constraints. Yet few workers have seriously considered the role of predation in the evolution of group-living and communal breeding. Collias and Collias (1978) suggested that an important advantage of communal breeding in the ground-feeding White-browed Sparrow Weaver, *Plocepasser mahali*, was related to predation. These birds lost a substantial proportion of their foraging time through harassment from predators.

When predators departed, several adults fed the young in rapid succession, thus compensating for the delay. A similar advantage may accrue to the Brown Treecreeper, which is vulnerable to terrestrial predators. The evolution of a distinct alarm-call and "tail-bobbing" (see Section 6.16) are presumably associated with this increased risk of predation. Another advantage of groups in this species is the improved ability to defend young from predators.

It is noteworthy that many, but by no means all, of the species for which communal breeding is well-documented, inhabit open, semi-arid woodlands (e.g. the Florida Scrub Jay, Green Woodhoopoe, Grey-crowned Babbler and White-winged Chough). Gaston (1978), in fact, suggested that such habitats provided the optimal conditions for the evolution of group territorial behaviour, few such species occurring in moist forests (see also Grimes 1976). Indeed, while Dow (1980a) failed to find any relationship between the incidence of communally breeding species and environmental conditions in Australia, it is apparent that the vast majority of species known to breed communally live in sclerophyll communities and few are rainforest species. Hardy (1976) noted that the communal species of New World Jays are characteristic not of climax forests, but of edges and disturbed forests. The Brown and Red-browed Treecreepers conform to this pattern, the former, more widespread species inhabiting the edge of sclerophyll forests (and woodlands), while the latter occurs commonly in the ecotone between sclerophyll and rainforest (as well as in sclerophyll forests). Interestingly, Brereton (1971a,b) found that the social organization of Australian parrots was most complex in semi-arid regions, and least complex on the mesic coast and in the arid inland. The communal Red-browed and Brown are more arid-adapted than the White-throated and less so than the White-browed, which appears to have a social organization more like the White-throated (Noske 1980, unpubl. data).

In conclusion, I propose that the major differences between the White-throated and the other two species of treecreepers are due to historical factors, particularly in relation to predation. Until recently, the White-throated inhabited dense and relatively equable rainforest, where the best strategy for individuals was to disperse and remain well-spaced

and inconspicuous. Nest predation was best avoided by having a long breeding cycle, which reduced activity at the nest. For the Red-browed and Brown, on the other hand, the risk of predation in the more open, sclerophyll habitats placed a high cost on dispersal, but a high premium on group-living and an accelerated breeding cycle. Food localization probably played a more important role in the evolution of communal behaviour in the specialized Red-browed than in the more generalized Brown.

It is conceivable that the bark fauna on the moss and lichen covered trunks of rainforest trees is relatively evenly distributed and that this pre-adapted the White-throated for foraging on those eucalypts with the most homogeneous bark (*viz.* stringybarks and ironbarks), as well as other rough-barked trees, such as *Acacia*, *Callitris* and *Casuarina* species. This may also be the case in the sittella, which presumably also evolved in rainforests, since both New Guinea species are confined to this habitat. An explanation for why the White-throated Treecreeper and sittella represent two extremities along the social continuum found in Australian bark foragers might require an investigation of their behavioural ecology in rainforests.

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