

Chapter 5. FORAGING ECOLOGY

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5.1 Introduction

The foraging ecology of bird communities has been investigated in a range of habitats in Australia including lowland tropical rainforest (Crome 1978), upland tropical rainforest (Frith 1984), temperate rainforest (Thomas 1980), eucalypt forest and woodland (Wooller & Calver 1981, Recher *et al.* 1985, Ford *et al.* 1986), forests and woodlands of the wet-dry tropics (Brooker *et al.* 1990), Tasmanian sclerophyll forest (Cale 1994) and Rottnest Island *Melaleuca* woodland (Wheeler & Calver 1996). However, no such studies have been conducted in arid New South Wales, nor in the wider Australian arid zone, despite the fact that it extends over 70% of the Australian continent (Williams & Calaby 1985).

Community studies of foraging ecology lead to an understanding of how birds utilise and partition food resources. They enable description of community structure in terms of feeding guilds and aid interpretation of spatial and temporal trends in bird communities (see Chapter 3). They indicate what food resources are important to the avifauna and hence the potential effects of altering these resources.

Since European settlement in the 1850's to 1870's (Jeans 1972), arid New South Wales has been subject to severe habitat degradation as a result of overgrazing coupled with extended droughts (Anon 1901, Beadle 1948). Since the 1950's the rate of land degradation has slowed. It is debatable whether such improvement is a consequence of improved management by graziers (Palmer 1994), closer settlement (Condon 1986) or a period of better rainfall (Pickard & Norris 1994). Nevertheless, land degradation remains a major problem (Stanley 1983, Soil Conservation Service 1989), especially during dry periods. Of concern for the food resources of birds are the reduction and continued degradation of topsoil and ground layer vegetation and the current lack of effective regeneration of many tree and shrub species (Soil Conservation Service 1989) as a result of overgrazing of their seedlings and saplings by stock, feral herbivores and increased numbers of native herbivores (e.g. Crisp 1978, Lange & Graham 1983, Auld 1990).

In this chapter I present the findings of my investigation of the foraging ecology of the bird community at Peery. I describe quantitatively the foraging behaviour of 44 bird species and describe the structure of the bird community in terms of feeding guilds. I identify

important food resources, including plant species, and describe the manner in which birds utilize these resources. I compare the winter and spring foraging behaviour of 23 species. I compare my findings with those of similar studies from more mesic habitats in eastern New South Wales.

5.2 Study site

The study site is described in detail in Chapter 2. The site was censused in spring 1990, winter and spring 1991 and 1992, autumn, winter and spring 1993 and summer 1993/94 (Chapter 3). The composition of perennial trees and shrubs in census transects is indicated in Table 5.1 (see Chapter 3 for details).

5.3 Methods

5.3.1 Data collection

Periods of data collection coincided with bird censuses (Chapter 3) and data collection was concentrated in census transects. In each period I recorded observations of feeding attempts throughout the day as I moved systematically through the census transects. In order to ensure independence of observations and avoid pseudo-replication (Bell *et al.* 1990, Hejl *et al.* 1990), only the first observation for each individual was recorded. I followed non-feeding individuals until they foraged, so as to reduce bias towards more conspicuous locations and behaviours (Wagner 1981, Franzreb 1984). Observations were not collected at the same location at intervals of less than three days. I sought to spread observations for each species over the study period (1990-94) so that the data would not reflect possible short-term fluctuations in resources and variations in foraging behaviour (Morse 1990). Since most species in the community are sexually monomorphic, I combined data for the sexes of all species. Similarly, I have pooled observations for all age groups.

For each feeding event I recorded the foraging substrate, method and height (recorded to the nearest metre), and the plant species. I recognised six foraging substrates:

Table 5.1. Species composition of perennial trees and shrubs in census transects. Trees are $\geq 4\text{m}$ and shrubs $>0.5\text{m}$ but $<4\text{m}$. Methods used to determine relative abundances are described in Chapter 3.

Plant species	% of SHRUBS	% of TREES
Mulga <i>Acacia aneura</i>	0.60	6.03
Sandhill Wattle <i>Acacia ligulata</i>	0.02	
River Cooba <i>Acacia stenophylla</i>	2.56	15.45
Dead Finish <i>Acacia tetragonophylla</i>	0.35	0.61
Prickly Wattle <i>Acacia victoriae</i>	1.38	1.17
Rosewood <i>Alectryon oleifolius</i>	0.50	2.01
Whitewood <i>Atalaya hemiglauca</i>	0.08	16.76
Wild Orange <i>Capparis mitcheilli</i>		0.06
Belah <i>Casuarina pauper</i>	0.04	
Broad-leaf Hopbush <i>Dodonaea viscosa</i>	0.02	
Canegrass <i>Eragrostis australasica</i>	0.07	
Eurah <i>Eremophila bignoniiflora</i>	0.03	0.08
Harlequin <i>Eremophila duttonii</i>	2.54	
Emubush <i>Eremophila longifolia</i>	0.06	
River Red Gum <i>Eucalyptus camaldulensis</i>	1.12	23.44
Red Box <i>Eucalyptus intertextus</i>		0.12
Black Box <i>Eucalyptus largiflorens</i>	0.57	12.65
Bimble Box <i>Eucalyptus populnea</i>		0.63
Leopardwood <i>Flindersia maculosa</i>		0.11
Beefwood <i>Grevillea striata</i>		1.98
Black Bluebush <i>Maireana pyramidata</i>	0.97	
Pearl Bluebush <i>Maireana sedifolia</i>	0.06	
Lignum <i>Muehlenbeckia florulenta</i>	12.81	
Boobialla <i>Myoporum montanum</i>	49.02	
Weeping Pittosporum <i>Pittosporum phylliraeoides</i>	0.01	0.51
Thorny Saltbush <i>Rhagodia spinescens</i>	0.09	
Santalum <i>Santalum lanceolatum</i>	0.29	0.66
Spiny Fan-flower <i>Scaevola spinescens</i>	0.37	
<i>Senna artemisioides</i> :		
Silver Cassia <i>nothosubsp. artemisioides</i>	2.27	
Dense Cassia <i>nothosubsp. surtii</i>	1.87	
Blunt-leaf Cassia <i>subsp. helmsii</i>	0.60	
Limestone Cassia <i>subsp. oligophylla</i>	0.86	
Woody Cassia <i>subsp. petiolaris</i>	1.01	
<i>subsp. zygophylla</i>	0.52	
Dead plant	19.30	17.74
TOTAL	100	100

foliage (leaves and petioles), bark (trunks, twigs, fallen timber and flood debris), flowers, fruits, air and ground. Fruits were taken directly from plants rather than from the ground and included the small seeds of grasses and ephemeral herbs, hard seeds of shrubs and trees, such as acacias and eucalypts, and fleshy fruits. I noted the health of living substrates and the ripeness of fruits eaten. The ground substrate is a source of both plant and animal food. In the field it was rarely possible to identify food items taken from the ground, so information was sought from published records, including results of stomach content analyses, especially from Barker & Vestjens (1989, 1990). I further defined the ground substrate by assessing ground cover in the immediate vicinity (1m²) of each ground feeding bird. I ranked separately the cover of herbage, litter and stones on a scale of zero to three (0 - no cover, 1 - <10% cover, 2 - 10-50% cover, 3 - >50% cover). The height (1 - <5cm, 2 - 5-20cm, 3 - >20cm) and greenness (1 - mainly dry, 2 - partly green, 3 - mainly green) of any herbage cover was also ranked. The distance of each ground-feeding bird from cover appropriate to the feeding species was estimated.

Living plants that were foraging substrates were identified to species. Dead plants were also identified to species, if possible. They were otherwise classed as standing dead trees or shrubs or fallen timber (includes flood debris in creeklines). Scientific names of plant species mentioned in the text are given in Table 5.1.

The categories of foraging method I used are based on those of earlier workers e.g. Recher *et al.* (1985), Ford *et al.* (1986) and Holmes & Robinson (1988). I defined 10 different prey attack manoeuvres: glean - stationary or walking bird picks food from a substrate surface; probe - bird inserts its bill into a substrate to take food; pounce - perched bird drops to the ground to take prey; flip - bird turns debris on the ground with its bill and takes prey items uncovered; snatch - bird flies or jumps from a perch or the ground and takes a prey item from a substrate, possibly landing momentarily, then returns to the same or a different perch; hover - prey taken from a substrate while bird is hovering in the air; hawk - bird pursues and captures prey in flight; sally - bird leaves a perch, captures prey in flight and returns to perch; chew - bird chews items, such as fruit or leaf galls, which may be held in the foot, extracting food then discarding the item; swallow - bird pecks fruit from plant and swallows it whole. I recorded the size and species composition of feeding flocks.

The relative abundances of birds in the study site were determined from the averaged results of all censuses (Chapter 3). Where possible, weights of birds were derived from banding data collected in the study area. Otherwise, weights were obtained from the literature.

5.3.2 Data Analysis

The four main dimensions of the foraging data: substrate, height, plant species and feeding method, are highly correlated. Therefore I classified species into feeding guilds on the basis of a single dimension, substrate. Similarity between species was derived from their relative use of each of the six substrates using the Bray & Curtis association measure (Belbin 1990). A hierarchical agglomerative clustering strategy, flexible Unweighted Pair Group Arithmetic Averaging (UPGMA) with $\beta = -0.1$ (Belbin 1990), was used to classify species into feeding guilds. A dendrogram was drawn to display the history of this classification. I used an ordination analysis, semi-strong-hybrid multidimensional scaling (Belbin 1990), to further illustrate similarities between species in their use of foraging substrates.

I determined niche breadth for each species for three dimensions, substrate, height and feeding method, using the Shannon-Weiner diversity index, $H^1 = -\sum P_i \log_e P_i$, where P_i is the proportion of all observations that belong to category i .

I used *Chi*-square analysis to test for seasonal differences in substrate use in species for which I obtained at least 30 observations in winter and in spring. *Chi*-square analyses were also used to compare the use of the ground substrate among species for which I obtained at least 30 observations of ground cover condition.

5.4 Results

5.4.1 Species included in quantitative analysis (Table 5.2)

Forty four species were included in the quantitative analysis. For 36 of these I obtained more than 50 feeding observations. This minimum sample size follows Recher *et al.* (1985) and Ford

TABLE 5.2. **Species included in quantitative analysis.** STATUS refers to status of each species at Peery within the study period (**B** breeding, **N** non-breeding, **R** resident, **W** winter migrant, **S** summer migrant, **I** irregular nomad). **FEEDING FLOCK** types are **A** alone, in pairs or small family groups, **S** single species flocks, **M** mixed species flocks. **WEIGHTS** are average weights of birds banded at Peery except for those marked *. Sources of weights for these birds include Rogers *et al.* (1986, 1990) and Forshaw (1981). **ABUNDANCE** is the mean density (number/10ha) of each species in all census transects over the study period (see Chapter 3).

SPECIES	NO.OBS	STATUS	FEEDING FLOCK	WEIGHT (g)	ABUNDANCE (no./10ha)
Ground Feeders					
Apostlebird	645	B,R	S	122	7.31
Diamond Dove	20	B,I	S	33	0.56
Peaceful Dove	20	N,I	S	54	0.05
Rufous Songlark	26	B,I	A	24	0.81
Australian Magpie-lark	123	B,R	A/S	89*	1.54
Australian Magpie	81	B,R	A/S	255	0.44
Crested Pigeon	213	B,R	S	229	2.88
Zebra Finch	361	B,I	S	12	8.18
Pink Cockatoo	112	N,I	S/M	384*	0.06
Richard's Pipit	52	B,R	A	22*	0.27
Red-capped Robin	71	B,W	M	9	0.42
Chestnut-crowned Babbler	208	B,R	S	50	3.72
Southern Whiteface	178	B,R	S/M	12	2.04
White-winged Chough	27	B,R	S	372*	0.32
Blue Bonnet	218	B,R	S	88*	3.09
Mulga Parrot	52	B,R	A	63	0.63
Crimson Chat	162	B,I	S	11	0.83
Yellow-rumped Thornbill	119	B,R	S/M	8	1.18
Ground/Aerial Feeders					
Black-faced Woodswallow	98	B,R	S	34	0.69
Willie Wagtail	275	B,R	A	20	4.64
Bark/Ground Feeders					
Brown Treecreeper	176	B,R	A	27	1.50
Grey Shrike-thrush	51	B,R	A	65	1.05
Ground/Fruit Feeders					
Budgerigar	169	B,I	S	27	7.65
Galah	451	B,R	S/M	318*	1.96
Little Corella	406	B,R	S/M	702*	0.84
Emu	71	B,R	S	40000*	0.16
Mallee Ringneck	149	B,R	A	114	2.09
Foliage Feeders					
Black-faced Cuckoo-shrike	23	B,R	A	107*	0.58
Chestnut-rumped Thornbill	195	B,R	S/M	7	1.59
Variegated Fairy-wren	237	B,R	S/M	8	3.36
White-winged Fairy-wren	88	B,R	S/M	8	1.88
Striated Pardalote	112	B,R	A	10	0.40
White-winged Triller	57	B,S	A	15	0.38
Flower/Foliage Feeders					
Spiny-cheeked Honeyeater	238	B,R	A	45	3.27
White-fronted Honeyeater	33	B,I	A	17	0.44
Singing Honeyeater	78	B,R	A	25	0.83
Yellow-throated Miner	371	B,R	A/S	56	9.20
White-plumed Honeyeater	704	B,R	A	18	25.37
Aerial Feeders					
White-browed Woodswallow	312	B,I	S	35*	0.61
Rainbow Bee-eater	137	B,S	S	28	0.93
Tree Martin	497	B,R	S	15	18.66
White-breasted Woodswallow	77	B,S	A	43*	0.54
White-backed Swallow	38	N,I	S	*	0.07
Grey Fantail	30	N,W	M	8	0.12

et al. (1986) and exceeds the minimum of 30 observations recommended by Morrison (1984). I included a further eight species in the analysis for which I collected between 20 and 50 observations and whose foraging behaviour was relatively invariant. Results for these eight species should be treated with some caution.

Species included in the analysis comprised 30 residents, 9 nomads, seven of which bred at the site, three breeding spring-summer migrants and two winter migrants, one of which bred at the site (classifications are derived from Chapter 3). The 44 species were drawn from 21 families. Families best represented were the parrots (Psittacidae - seven species) and honeyeaters (Meliphagidae - five species). There were seven sets of congeneric species: the Diamond and Peaceful Doves; Variegated and White-winged Fairy-wrens; Grey Fantail and Willie Wagtail; Galah, Little Corella and Pink Cockatoo; White-breasted, White-browed and Black-faced Woodswallows; Singing and White-plumed Honeyeaters; Chestnut-rumped and Yellow-rumped Thornbills.

Species ranged in size from the Thornbills, Fairy-wrens and Grey Fantail (7-8g) to the Emu (~40kg). Fifteen species generally fed alone, in pairs or small family groups; 16 in single species flocks and two in mixed species flocks. A further eight species commonly fed in both single and mixed species flocks. The Australian Magpie-lark, Australian Magpie and Yellow-throated Miner fed alone or in small family groups, as well as in single species flocks in non-breeding periods. An indication of the relative abundance of each species over the study period is included in Table 5.2.

5.4.2 Substrate use and feeding guild classification

One substrate, ground, accounted for almost half of all foraging observations (Table 5.3). The next most important substrates were foliage and air, which each accounted for about 16% of all observations. Of lesser importance overall were the fruit, flower and bark substrates.

Potentially, niche breadth ranges from 0 (species feeds entirely on one substrate) to 1.8 (species makes equal use of each substrate). Most species specialised on one or two substrates and had low niche breadth values (Table 5.3). Only nine species had values over 1.0. The most generalized feeder was the White-winged Triller, with a niche breadth of 1.45.

TABLE 5.3. **Percentage use of substrates and niche breadth (H').**

Ground, ground/fruit, ground/aerial and ground/bark feeders are classified according to diet (S mainly seeds, P other plant material, I invertebrates, A other animal matter) based on Wyndham (1980), Forshaw (1981), Frith (1983), Morton (1985), Barker & Vestjens (1989, 1990), Lepschi (1993).

	GROUND	FRUIT	FLOWER	FOLIAGE	BARK	AIR	H	DIET
Ground Feeders								
Apostlebird	100						0	I,S
Diamond Dove	100						0	S
Peaceful Dove	100						0	S
Rufous Songlark	100						0	I
Australian Magpie-lark	99.2			0.8			0.05	I,S
Australian Magpie	97.5			2.4			0.11	A,I,P,S
Crested Pigeon	93.9	6.1					0.23	S
Zebra Finch	94.2	5.8					0.22	S
Pink Cockatoo	89.3	7.1		2.7	0.9		0.43	P,S
Richard's Pipit	94.2			3.8		1.9	0.26	I
Red-capped Robin	90.1			5.6	2.8	1.4	0.42	I
Chestnut-crowned Babbler	78.8			12.5	8.7		0.66	I
Southern Whiteface	85.4		1.1	7.3	6.2		0.55	I,S
White-winged Chough	85.2	7.4			7.4		0.52	I,P,S
Blue Bonnet	53.6	23.4	22.5	0.5			1.03	S
Mulga Parrot	63.5	23.0	11.5				0.88	S
Crimson Chat	72.8		21.6	1.9	3.1	0.6	0.78	I,S
Yellow-rumped Thornbill	64.7	0.8	5.0	21.0	6.7	1.7	1.05	I
Ground/Aerial Feeders								
Black-faced Woodswallow	39.8			15.3		44.9	1.01	I
Willie Wagtail	47.6		0.4	8.0	2.2	41.8	1.03	I
Bark/Ground Feeders								
Brown Treecreeper	32.4			1.1	66.5		0.69	I
Grey Shrike-thrush	37.3			31.4	31.4		1.10	A,I,P
Ground/Fruit Feeders								
Budgerigar	56.8	43.2					0.68	S
Galah	52.1	47.9					0.69	P,S
Little Corella	31.8	68.2					0.63	P,S
Emu	33.8	62.0	4.2				0.80	I,P,S
Mallee Ringneck	2.0	73.2	14.8	9.4	0.7		0.78	P,S
Foliage Feeders								
Black-faced Cuckoo-shrike	8.7			78.3	8.7	4.3	0.75	
Chestnut-rumped Thornbill	6.2	1.0	2.1	75.4	14.4	1.0	0.82	
Variegated Fairy-wren	14.0		3.0	68.8	13.9	0.4	0.93	
White-winged Fairy-wren	22.7	1.1	2.3	59.0	14.8		1.07	
Striated Pardalote				98.2	1.8		0.05	
White-winged Triller	21.1	3.5	8.8	49.1	5.3	12.3	1.45	
Flower/Foliage Feeders								
Spiny-cheeked Honeyeater	0.4	22.3	57.6	12.2	5.5	2.1	1.17	
White-fronted Honeyeater			93.9		3.0	3.0	0.09	
Singing Honeyeater	2.6	7.7	47.4	37.2	5.1		1.17	
Yellow-throated Miner		2.2	44.5	49.6	3.5	0.3	0.93	
White-plumed Honeyeater	2.6	0.4	25.4	64.5	3.1	4.0	0.98	
Aerial Feeders								
White-browed Woodswallow				0.3		99.7	0.02	
Rainbow Bee-eater				0.7		99.3	0.04	
Tree Martin	0.8					99.2	0.05	
White-breasted Woodswallow				1.3		98.7	0.07	
White-backed Swallow	2.6					97.4	0.12	
Grey Fantail				6.7		93.3	0.25	
% TOTAL SUBSTRATE USE	46.2	9.0	8.2	16.1	4.8	15.7		

Even this species showed a marked preference for certain substrates (49% foliage and 21% ground).

Seven feeding guilds were distinguished in the UPGMA analysis (Figure 5.1). An initial separation was made of species which fed almost entirely in the air. These six species were relatively specialised feeders (as indicated by their low niche breadth values in Table 5.3) and showed low overlap with other species. Next, a division was made between species for which the ground is an important substrate and species for which foliage is an important substrate. The former species were divided into four groups: ground feeders (17 species), ground/air feeders (two species), ground/bark feeders (two species) and ground/fruit feeders (five species). Ground accounted for at least 50% of substrate use of members of the ground feeding group, and 100% for the Apostlebird, Diamond Dove, Peaceful Dove and Rufous Songlark. The Mallee Ringneck was something of an anomaly in the classification. Its heavy use of fruit placed it with the ground/fruit feeders though it rarely fed on the ground. The species for which foliage is an important substrate fell into two closely associated groups, the foliage feeders (six species) and flower/foliage feeders (five species). Apart from the Striated Pardalote, which specialised on foliage, and the White-fronted Honeyeater, which only visited the area sporadically to feed on nectar, species in these two groups were among the least specialised in substrate use.

The ordination (Figure 5.2) further clarified the classification of species into feeding guilds. Central to the ordination is the White-winged Triller, the species most generalized in its use of feeding substrates (niche breadth 1.45). From this central position radiate gradients of specialisation for each substrate. Species at the periphery of the ordination show greatest substrate specialisation, namely the Striated Pardalote (foliage), Brown Treecreeper (bark), Apostlebird, Diamond Dove, Peaceful Dove and Rufous Songlark (ground), Mallee Ringneck (fruit), White-browed Woodswallow (air) and White-fronted Honeyeater (flowers). The relative homogeneity of the aerial and ground feeding groups is apparent. The Grey Fantail is separated from other aerial feeders by its greater use of foliage. The Yellow-rumped Thornbill, Blue Bonnet and Mulga Parrot, which made substantial use of other substrates (fruit, flowers or foliage), as well as the ground substrate, are removed from more specialised ground feeders. The foliage and flower/foliage groups merge into each other.

Figure 5.1. **Feeding group classification based on proportional use of substrates.**
The dendrogram illustrates the history of the UPGMA classification.

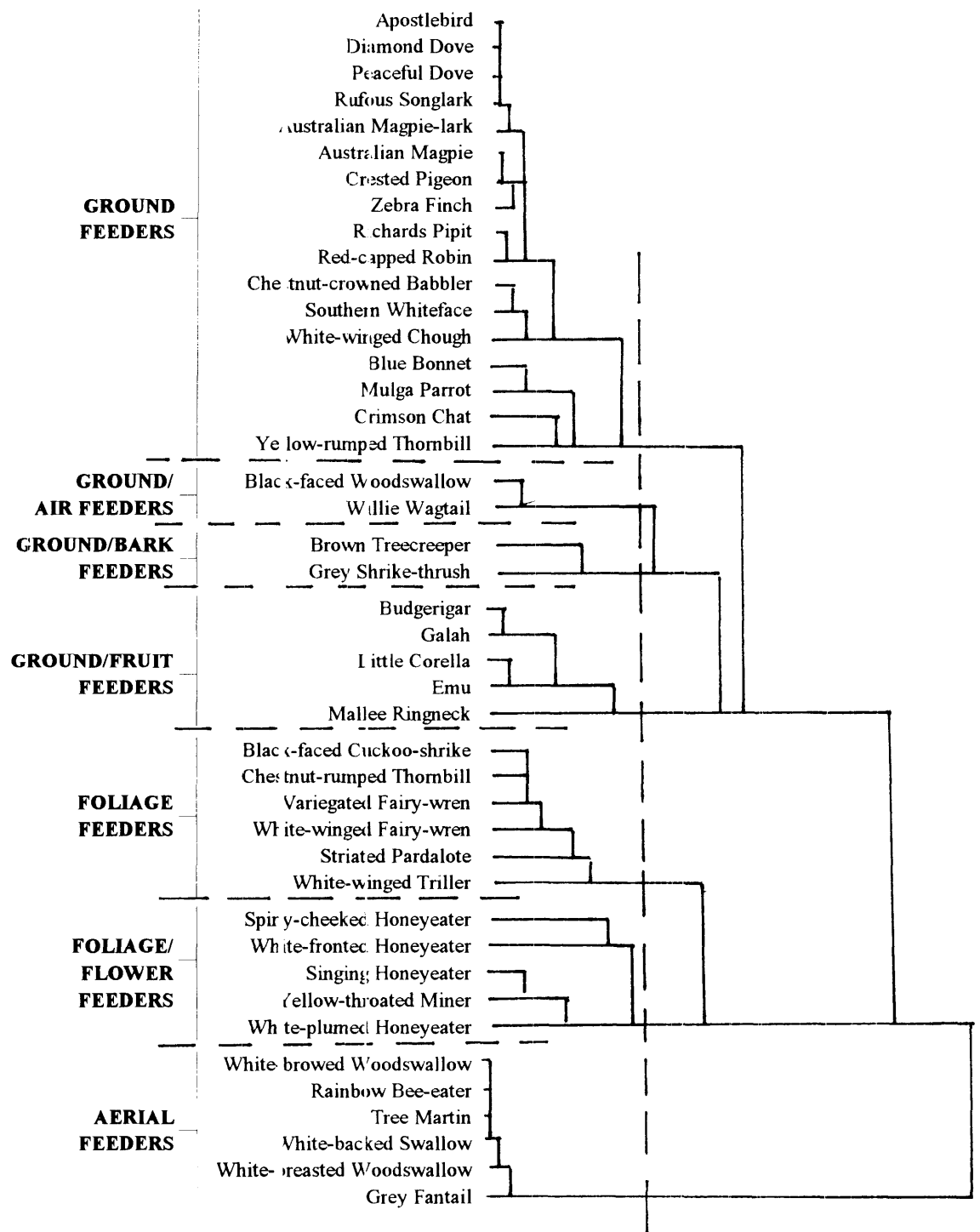
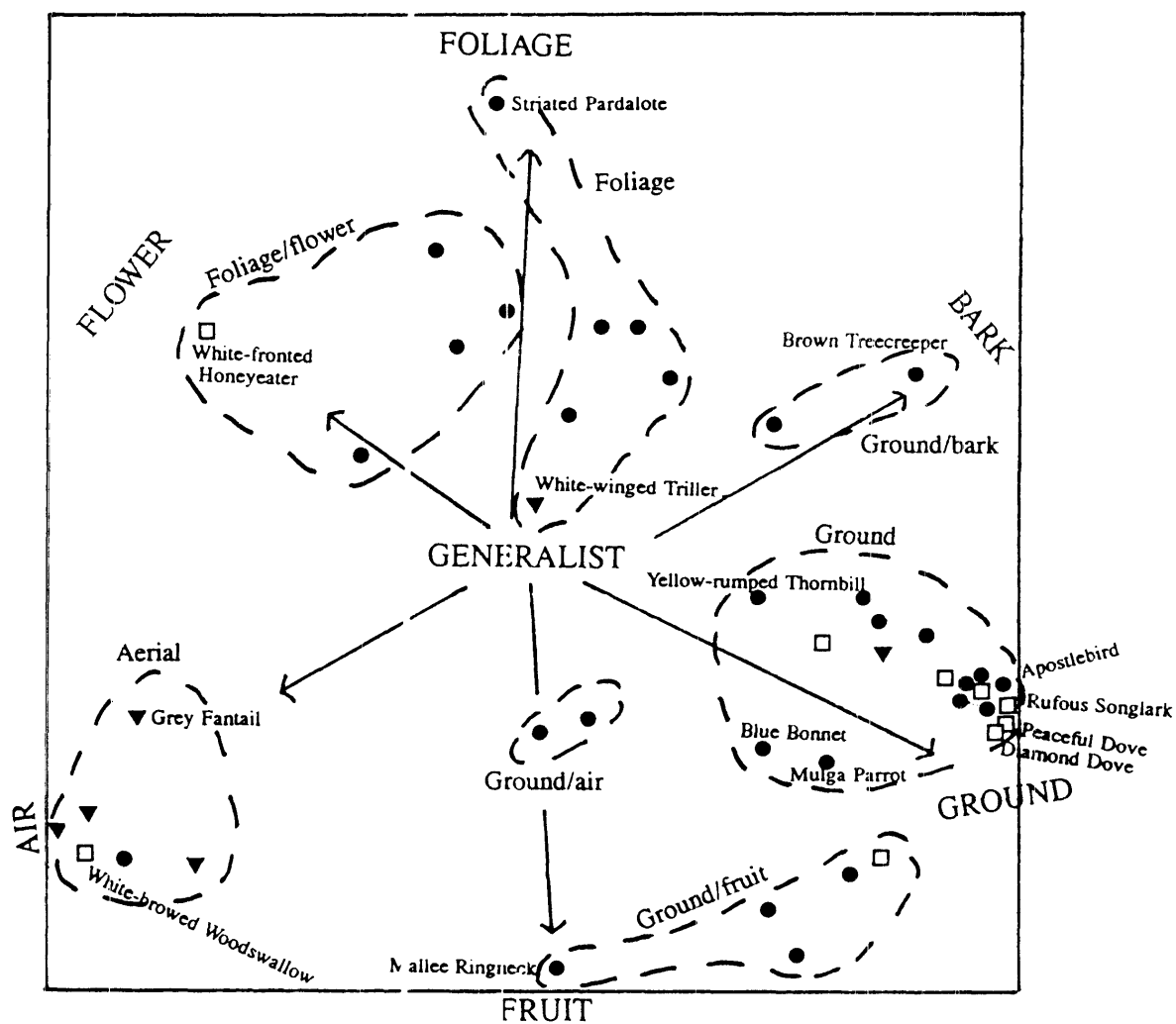


Figure 5.2 **Ordination of bird species based on substrate use.** Axes are dependently scaled. Arrows indicate direction of specialisation on substrates foliage, flowers, fruit, air, ground and bark. Bird species are indicated as residents ●, nomads □, or migrants ▼.



Resident species made substantial use of all substrates and are represented in each feeding guild (Figure 5.2). In contrast, most nomads were ground feeders and most migrants were aerial feeders. Nomads were among the most specialised feeders. Apart from the ground feeders, they included an aerial feeder (White-browed Woodswallow), a flower specialist (White-fronted Honeyeater) and a granivorous ground/fruit feeder (Budgerigar). Nomads made little, if any, use of the foliage and bark substrates.

5.4.3 Plant species as food sources

Plant species available to birds (Appendix 2.1, Chapter 2) included perennials (20 tree, 30 shrub, 22 sub-shrub, 43 forb, 4 mistletoe, 15 grass, 1 sedge and 2 rush species recorded during study), and biennials, annuals and ephemerals (1 shrub, 17 sub-shrub, 84 forb, 17 grass and 1 sedge species). Perennial trees and shrubs, despite the drought in 1991-92, flowered and fruited regularly in the study period. At the height of the drought, many perennial trees and shrubs suffered extensive leaf fall and the above ground portions of most perennial sub-shrubs, forbs and grasses, and virtually all annuals and biennials, died. A diverse and changing array of ephemerals appeared and fruited when conditions were favourable.

5.4.3.1. Foliage Sources (Table 5.4)

Perennial trees and shrubs were the main substrates for foliage feeders. Over 98% of all feeding observations in live foliage were made in perennials. Major foliage sources included Black Box, River Red Gum and Prickly Wattle. Comparison of substrate use with densities of perennial trees and shrubs in census transects (Table 5.1) indicated that in general birds showed a marked preference for Black Box and Prickly Wattle foliage. Eucalypts were the chief foliage substrate of the White-plumed Honeyeater, Striated Pardalote, Mallee Ringneck, Grey Shrike-thrush, Black-faced Cuckoo-shrike and Yellow-throated Miner. Prickly Wattle was used extensively by small birds including the Chestnut-rumped Thornbill, White-winged Triller and Variegated and White-winged Fairy-wrens.

Foliage sources less widely used but of particular importance to one or two birds

Table 5.4. **Plant species with foliage used by birds as a foraging substrate.** Figures in table indicate percentage of total substrate use by birds. Niche breadth (Shannon-Weiner diversity index) potentially ranges from 0 to 3.3. The order of bird species follows the UPGMA classification in Figure 5.1.

	CHESTNUT-CROWNED BABBLER	YELLOW-RUMPED THORNBILL	BLACK-FACED WOODSWALLOW	GREY SHRIKE-THRUSH	BLACK-FACED WOODSWALLOW	CHESTNUT-RUMPED THORNBILL	VARIEGATED FAIRY-WREN	WHITE-WINGED FAIRY-WREN	STRIATED PARDALOTE	WHITE-WINGED TRILLER	SPINY-CHEEKED HONEYEATER	SINGING HONEYEATER	YELLOW-THROATED MINER	WHITE-PLUMED HONEYEATER	TOTAL
NICHE BREADTH (H')	1.2	1.3	.6	0.9	1.2	1.9	0.7	1.6	1.3	1.7	2.2	2.0	1.7	1.1	
PERENNIAL TREES															
<i>Acacia aneura</i>	3.4	4.2				11.8	1.7		2.7	3.5	1.3	5.1	4.6	0.6	38.9
<i>A. stenophylla</i>				2.0		1.0	8.9	2.3		3.5	1.3			1.4	17.4
<i>Alectryon oleifolius</i>						3.6	0.8							0.1	4.5
<i>Atalaya hemiglauc</i>	0.5		.0		13.0	2.6	0.4		3.6	15.8	0.8	5.1	8.4	0.4	37.6
<i>Casuarina pauper</i>		3.4													3.4
<i>Eucalyptus camaldulensis</i>				3.9	13.0	3.1	0.8	1.1	47.3	1.8	0.8		10.2	32.7	102.0
<i>E. largiflorens</i>			14.3	21.6	47.8				38.4	1.8	2.5		17.8	26.6	171.0
<i>E. populnea</i>									3.6				0.3	0.4	4.3
<i>Grevillea striata</i>						0.5				1.8			1.1		3.4
<i>Pittosporum phylliraeoides</i>						2.6						2.6			5.2
<i>Santalum lanceolatum</i>						0.5			0.9		0.4	2.6		0.3	4.7
PERENNIAL SHRUBS															
<i>Acacia tetragonophylla</i>						4.1	0.4					2.6	0.8		7.9
<i>A. victoriae</i>	4.3	7.6	.3			29.8	13.1	11.4	0.9	1.4	1.7	7.7	6.2	1.1	102.1
<i>Eremophila duttonii</i>						0.5	5.9				0.4	9.0			6.8
<i>E. sturtii</i>						1.5		1.1	0.9					0.1	4.0
<i>Muehlenbeckia florulenta</i>						1.5	16.5	28.4						0.1	46.5
<i>Myoporum montanum</i>	2.4	4.2		2.0	4.3	4.1	15.6	5.7			2.1		0.3	0.4	39.1
<i>Rhagodia spinescens</i>							0.4	1.1							1.5
<i>Scaevola spinescens</i>						0.5	0.4					1.3			2.2
<i>Senna artemisioides</i> ssp. <i>helmsii</i>						1.0	0.4			3.5		1.3			5.2
ssp. <i>petiolaris</i>							0.4								0.4
PERENNIAL CLIMBERS															
<i>Jasminum lineare</i>							0.4								0.4
ANNUAL/BIENNIAL SHRUBS															
<i>Atriplex holocarpa</i>														0.1	0.1
<i>Halosarcia pergranulata</i>							0.4	5.7							6.1
<i>Sclerolaena intricata</i>											0.4				0.4
<i>S. longifolia</i>									1.8						1.8
EPHEMERAL HERBS															
<i>Centipeda thespidioides</i>								1.1	1.8						2.9
UNIDENTIFIED DEAD SHRUBS															
Dead standing shrub								0.8							0.8

included Lignum (Variegated and White-winged Fairy-wrens), Whitewood (White-winged Triller), Boobialla (Variegated Fairy-wren) and Mulga (Chestnut-rumped Thornbill).

The Spiny-cheeked and Singing Honeyeaters were the most diverse in their use of plant species for foliage foraging.

5.4.3.2 Fruit Sources (Table 5.5)

Birds at the study site foraged on fruits mostly to obtain seeds. In contrast to foliage, most fruit feeding observations (63%) were made in ephemerals, annuals and biennials. The only perennial to provide a substantial fruit source was the Boobialla shrub *Myoporum montanum*. Boobialla fruited prolifically in each spring of the study and was the single most important fruit source. It was heavily used by the resident Spiny-cheeked Honeyeater, Mallee Ringneck and Emu. The Mallee Ringneck and Emu took both ripe and unripe fruits, the Spiny-cheeked Honeyeater searched shrubs for ripe fruit.

Grasses flowered only when conditions were favourable and provided fruit for the nomadic Zebra Finch and Budgerigar. The major sources of grass seed were introduced annuals, *Cenchrus ciliaris* and *Schizanthus barbatus*. Fruits of annual sub-shrubs, especially *Atriplex* spp., were well used by parrots and cockatoos. Flocks of the Blue-winged Parrot (not included in analysis) were only present in Spring 1992 when they fed on the fruits of Pop Saltbush *A. spongiosa*, which were then abundant. Seeds of introduced ephemeral Camel Melons *Citrullus lanatus* were favoured by Pink Cockatoos and Galahs.

The Mallee Ringneck and Blue Bonnet were the most diverse in their use of fruit sources. The range of fruits eaten was probably underestimated in this study. It was not always possible to identify the plant source of fruit taken from the ground, especially seeds stored in the soil.

5.4.3.3 Flower Sources (Table 5.6)

Ephemerals, annuals and biennials produced shows of flowers which were spectacular but rarely used by birds. Over 99% of all flower feeding observation involved perennials. Almost

Table 5.5. **Plant species with fruit used by birds.** Figures in table are percentage of total substrate use. Niche breadth (Shannon-Weiner diversity index) potentially ranges from 0 to 3.7.
* indicates introduced plant species.

	CRESTED PIGEON	ZEBRA FINCH	PINK COCKATOO	WHITE-WINGED CHOUGH	BLUE BONNET	MULGA PARROT	BUDGERIGAR	GALAH	LITTLE CORELLA	EMU	MALLEE RINGNECK	SPINY-CHEEKED HONEYEATER	SINGING HONEYEATER	TOTAL
NICHE BREADTH (H')	0.4	0.0	0.6	0	2.0	2.0	1.2	1.4	0.9	0.4	2.2	0.7	1.0	
PERENNIAL TREES														
<i>Acacia aneura</i>			3.6		2.8			1.1	8.9		2.0			16.4
<i>Eucalyptus camaldulensis</i>											11.4			11.4
<i>E. largiflorens</i>					0.5						2.0			0.5
<i>E. populnea</i>											1.3			1.3
<i>Pittosporum phylliraeoides</i>											2.7	1.3		4.0
<i>Santalum lanceolatum</i>	5.2				3.7						1.3	2.1		12.3
PERENNIAL SHRUBS														
<i>Acacia tetragonophylla</i>			3.6											3.6
<i>A. victoriae</i>					0.9									0.9
<i>Enchylaena tomentosa</i>				7.4	0.9	3.8						0.4	1.3	13.8
<i>Eremophila duttonii</i>											6.7			6.7
<i>Maireana pyramidata</i>					2.3						0.7			3.0
<i>Myoporum montanum</i>					3.2	5.8				56.3	26.2	17.6	3.8	112.9
<i>Scaevola spinescens</i>												0.4		0.4
PERENNIAL CLIMBERS														
<i>Einadia nutans</i>					0.9							2.6		3.5
MISTLETOES														
<i>Lysiana murrayi</i>											3.6			3.6
ANNUAL/BIENNIAL SHRUBS														
<i>Atriplex holocarpa</i>					4.6	7.7		10.6	58.4		7.4			88.7
<i>A. intermedia</i>								11.1						11.1
<i>A. lindleyi</i>											2.7			2.7
<i>A. nessorhina</i>						3.8								3.8
<i>A. spongiosa</i>					1.8			20.4	25.6					47.8
<i>Salsola kali</i>											1.3			1.3
<i>Solanum quadrilocutum</i>										2.8	1.3			4.1
EPHEMERAL HERBS														
* <i>Asphodelus fistulosus</i>											0.7			0.7
<i>Bulbinopsis semibarbata</i>						1.9				1.4				3.3
<i>Chenopodium cristatum</i>					0.9									0.9
* <i>Citrullus lanatus</i>			30.4					8.9	1.5					40.8
* <i>Cucumis myriocarpus</i>	0.9													0.9
<i>Tetragonia tetragonoides</i>										1.4	1.3			2.7
<i>Trianthema triquetra</i>						1.9								1.9
PERENNIAL GRASSES/SEDGES														
<i>Aristida ramosa</i>		8.7												8.7
<i>Cymbopogon oblectus</i>		0.6												0.6
ANNUAL GRASSES														
<i>Aristida contorta</i>		0.3												0.3
* <i>Cenchrus ciliaris</i>		15.0					16.6							16.6
<i>Digitaria coenicola</i>		0.8												0.8
<i>Enneapogon avenaceus</i>		0.3					8.9							9.2
<i>Paspaladium constrictum</i>							8.9							8.9
* <i>Schismus barbatus</i>		2.8					39.1							41.9

Table 5.6. Plant species with flowers used by birds. Figures in table indicate percentage of total substrate use by birds. Niche breadth (Shannon-Weiner diversity index) potentially ranges from 0 to 3.2.

	CRIMSON CHAT	YELLOW-RUMPED THORNBILL	BLUE BONNET	MULGA PARROT	MALLEE RINGNECK	SPINY-CHEEKED HONEYEATER	WHITE-FRONTED HONEYEATER	SINGING HONEYEATER	YELLOW-THROATED MINER	WHITE-PLUMED HONEYEATER	TOTAL
NICHE BREADTH (H^1)	0.7	0	1.5	1.0	1.1	1.6	0	1.2	1.7	1.3	
<u>PERENNIAL TREES</u>											
<i>Acacia aneura</i>						0.4		7.7			8.1
<i>Atalaya hemiglauc</i>						0.8			0.5	0.1	1.4
<i>Eucalyptus camaldulensis</i>						0.4				1.6	2.0
<i>E. largiflorens</i>			1.4	1.9	4.7	3.8			9.2	16.6	37.6
<i>E. populnea</i>						0.4				1.0	0.4
<i>Pittosporum phylliraeoides</i>										0.1	0.1
<i>Santalum lanceolatum</i>								3.8		0.1	3.9
<u>PERENNIAL SHRUBS</u>											
<i>Acacia victoriae</i>	16.7	5.0				2.1			5.7	0.4	24.9
<i>Eremophila bignoniiflora</i>					1.3	5.5			5.1	1.8	13.7
<i>E. duttonii</i>	1.9		8.3	3.8	7.4	32.4	94.0	30.8	10.5	0.9	96.0
<i>E. longifolia</i>	2.9		6.4		1.3	4.2		1.3	0.8		16.9
<i>E. sturtii</i>			3.2	5.8					1.1		10.1
<i>Muehlenbeckia florulenta</i>			2.8								2.8
<i>Myoporum montanum</i>						3.4		1.3		2.0	4.7
<i>Senna artemisioides</i> ssp. <i>helmsii</i>								1.3			1.3
ssp. <i>sturtii</i>						0.4					0.4
<u>PERENNIAL CLIMBERS</u>											
<i>Jasminum lineare</i>						0.8					0.8
<u>MISTLETOES</u>											
<i>Amyema maidenii</i>						2.5		2.6	0.5		5.6
<i>Lysiana subfalcata</i>									0.3		0.3
<u>ANNUAL/BIENNIAL SHRUBS</u>											
<i>Lavatera plebeia</i>										0.3	0.3
* <i>Nicotiana glauca</i>									0.5	0.3	0.8
<u>EPHEMERAL HERBS</u>											
<i>Centipeda thespidioides</i>			0.5								0.5
<u>PERENNIAL GRASSES/SEDGES</u>											
<i>Cyperus gymnocaulos</i>						0.4					0.4
<i>Themeda australis</i>										0.1	0.1

60% of observations were recorded at flowers of the shrub Harlequin Eremophila, though it comprised less than 3% of shrubs in census transects (Table 5.1). It flowered prolifically each winter of the study. Its large, yellow to red, tubular flowers, attracted large numbers of honeyeaters including resident Spinny-cheeked, Yellow-throated and Singing Honeyeaters and nomadic White-fronted, Black and Pied Honeyeaters. The highly specialised diet of the White-fronted Honeyeater is indicated by its niche breadth of 0.09 and the high proportion of substrate use (94%) attributable to flowers. Flowers of Emubush, an uncommon winter-flowering eremophila, were also favoured by these honeyeaters. Blue Bonnets, Mulga Parrots and Mallee Ringnecks chewed the flowers of eremophilas, to obtain immature ovules, nectar or pollen. Black Box flowered between winter and early spring and was an important source of flowers for the White-plumed Honeyeater, Yellow-throated Miner and Mallee Ringneck. The clusters of small globular Prickly Wattle flower heads were favoured by flower feeders in spring. Species involved included the Crimson Chat, Yellow-rumped Thornbill and Yellow-throated Miner. The pecking action of these birds at the flowers suggested they were seeking insects from the flower heads.

5.4.3.4 **Bark Sources** (Table 5.7)

Virtually all bark feeding observations in live plants were made in perennials. The chief substrate source for bark feeders was the rough-barked Black Box. It was favoured over the more abundant River Red Gum (Table 5.1) which has only a stocking of rough bark at the base and occasional ribbons of peeling bark. Fourteen per cent of bark feeding observations were made in dead trees and shrubs. Species utilising dead plants included the Chestnut-crowned Babbler, Chestnut-rumped Thornbill, Brown Treecreeper and White-winged Chough. When feeding in live plants the Southern Whiteface (63% of bark feeding observations in living plants) and Chestnut-rumped Thornbill (88%) used dead branches more often than live.

5.4.4 **Foraging Method** (Table 5.3)

Most species showed low diversity in foraging method. The maximum possible niche breadth

Table 5.7. Plant species with bark used by birds as a foraging substrate. Figures in table indicate percentage of total substrate use by birds. Niche breadth (Shannon-Weiner diversity index) potentially ranges from 0 to 2.9.

	WHITE-WINGED CHOUGH	CHESTNUT-CROWNED BABBLER	SOUTHERN WHITEFACE	YELLOW-RUMPED THORNBILL	BROWN TREECREEPER	GREY SHRIKE-THRUSH	BLACK-FACED WOODSWALLOW	CHESTNUT-RUMPED THORNBILL	VARIEGATED FAIRY-WREN	WHITE-WINGED FAIRY-WREN	WHITE-WINGED TRILLER	SPINY-CHEEKED HONEYEATER	SINGING HONEYEATER	YELLOW-THROATED MINER	TOTAL
NICHE BREADTH (H')	0.7	1.7	1.	1.0	1.3	0.9	0.9	1.5	1.5	1.5	1.0	1.4	1.0	1.7	
PERENNIAL TREES															
<i>Acacia aneura</i>		0.5		1.7		2.0		2.0			1.8	2.1	1.3	0.8	8.2
<i>A. stenophylla</i>			0.1		0.6				0.8	3.4					5.4
<i>Alectryon oleifolius</i>		1.0			0.5			1.5							2.1
<i>Atalaya hemiglauc</i>		0.5			14.8		4.3		0.4		1.8			0.3	22.1
<i>Casuarina pauper</i>					0.5		0.5								1.1
<i>Eucalyptus camaldulensis</i>		0.5			3.4	9.8						0.4		0.8	14.9
<i>E. largiflorens</i>	3.7		0.1		37.5	13.7	4.3					0.8		0.8	61.4
<i>E. populnea</i>					6.8										6.8
<i>Grevillea striata</i>		1.0													1.0
<i>Santalum lanceolatum</i>										1.1					1.1
PERENNIAL SHRUBS															
<i>A. victoriae</i>		1.0		1.6				4.6	1.3		3.6		1.3		12.4
<i>Muehlenbeckia florulenta</i>									8.0	6.8					6.8
<i>Myoporum montanum</i>			3.					0.5	0.4	1.1		1.3		0.3	7.0
<i>Senna artemisioides</i> ssp. <i>sturtii</i>													2.6		2.6
ANNUAL/BIENNIAL SHRUBS															
<i>Halosarcia pergranulata</i>									0.4						0.4
UNIDENTIFIED DEAD MATERIAL															
Dead standing tree	3.7				3.4					1.1		0.4			8.6
Dead standing shrub		4.3	0.	3.4				3.6	1.3	1.1				0.5	14.8
Fallen timber			1.					0.5	1.7						3.3

Table 5.8. **Foraging method.** Figures in table indicate the percentage use of foraging methods and niche breadth (H').

	GLEAN	HAWK	CHEW	PROBE	SALLY	SNATCH	POUNCE	SWALLOW	FLIP	HOVER	H'
<i>Ground Feeders</i>											
Apostlebird	100										0
Diamond Dove	100										0
Peaceful Dove	100										0
Rufous Songlark	22.3			7.7							0.27
Australian Magpie-lark	100										0
Australian Magpie	100										0
Crested Pigeon	33.9		6.1								0.23
Zebra Finch	71.5		28.5								0.6
Pink Cockatoo	52.5		37.5								0.66
Richard's Pipit	100										0
Red-capped Robin	16.9				1.4	5.6	76.1				0.73
Chestnut-crowned Babbler	21.3			6.7					1.9		0.34
Southern Whiteface	91					1.7	2.2		5.1		0.39
White-winged Chough	38.8			3.8				7.4			0.42
Blue Bonnet	54.1		45.9								0.69
Mulga Parrot	53.5		36.5								0.66
Crimson Chat	77.8			21.6	0.6						0.56
Yellow-rumped Thornbill	27.5				1.7	0.8					0.13
<i>Ground/Aerial Feeders</i>											
Black-faced Woodswallow	54.1	42.9			2.0	1.0					0.82
Willie Wagtail	49.8				41.8	7.6	0.4			0.4	1.0
<i>Bark/Ground Feeders</i>											
Brown Treecreeper	100										0
Grey Shrike-thrush	50.8			25.5		13.7					0.92
<i>Ground/Fruit Feeders</i>											
Budgerigar	56.8		43.2								0.68
Galah	52.1		47.9								0.69
Little Corella	31.8		68.2								0.63
Emu	33.8		66.2								0.64
Mallee Ringneck	2.7		97.3								0.12
<i>Foliage Feeders</i>											
Black-faced Cuckoo-shrike	21.7	4.3				65.2	8.7				1.0
Chestnut-rumped Thornbill	95.4				1.0	2.1	1.0			0.5	0.24
Variegated Fairy-wren	93.7				0.4	5.9					0.25
White-winged Fairy-wren	97.7					2.3					0.11
Striated Pardalote	100										0
White-winged Triller	56.1	3.5			8.8	28.1		3.5			1.13
<i>Flower/Foliage Feeders</i>											
Spiny-cheeked Honeyeater	18.9			53.8	2.1	3.4		21.8			1.18
White-fronted Honeyeater	3.0			93.9	3.0						0.27
Singing Honeyeater	53.8			38.5				7.7			0.9
Yellow-throated Miner	58.0		0.3	39.4	0.3	2.2					0.8
White-plumed Honeyeater	70.2			25.4	4.0			0.4			0.75
<i>Aerial Feeders</i>											
White-browed Woodswallow	0.3	99.7									0.02
Rainbow Bee-eater		96.4			2.9	0.7					0.17
Tree Martin	0.8	99.0			0.2						0.06
White-breasted Woodswallow		96.1			2.6	1.3					0.19
White-backed Swallow	2.6	97.4									0.12
Grey Fantail	6.7	3.3			90.0						0.39

is 2.3 but only two species, the White-winged Triller and Spiny-cheeked Honeyeater, had a niche breadth greater than one. Gleaning was the most common foraging method. Six ground feeders and one foliage feeder, the Striated Pardalote, only gleaned. Aerial feeders hawked or sallied almost exclusively. The Mallee Ringneck obtained food largely by chewing, a method used by other parrots and the Emu. The Red-capped Robin was the only species to pounce to any extent. Usually it perched within 2m of the ground, often on fallen timber, before pouncing down. Flipping was used only by Southern Whitefaces and Chestnut-crowned Babblers. Pieces of earth and litter were vigorously flipped aside with the bill and prey then gleaned from the exposed ground.

Several species used their feet to manipulate or expose food items. Mallee Ringnecks chewed eucalypt seed capsules and sprays of flower buds held in the foot. White-breasted Woodswallows took large insects captured in flight to perches where they were held in the foot and devoured. Galahs and Little Corellas often held Camel Melons on the ground with their feet, as they devoured their seeds. Australian Magpie-larks regularly pecked at freshly turned earth exposed by a raking, twisting motion of the feet.

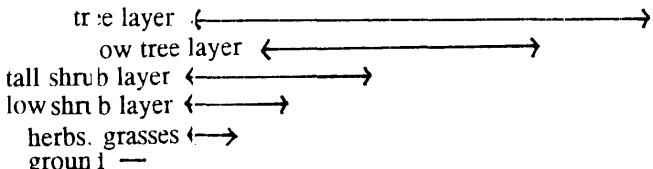
5.4.5 Foraging Height (Table 5.9)

For the purpose of analysis the height of each feeding bout was placed into one of nine height categories. The possible range of niche breadth is from 0 to 2.2.

Apart from ground feeders, most species foraged over a wide range of heights. Niche breadth values are at the upper end of the spectrum, in marked contrast to substrate and method values.

Ground/fruit feeders fed on or near the ground whereas ground/aerial feeders extended up to greater heights within or above the canopy. Ground/bark feeders, the Brown Treecreeper and Grey Shrike-thrush, tended to take prey from the rough bark of trunks and thick lower branches rather than from finer, less furrowed branches of the upper canopy. Fruit and flower feeders, including the Spiny-cheeked Honeyeater, White-fronted Honeyeater and Mallee Ringneck, fed mainly in shrubs as did smaller foliage feeders including the Variegated and White-winged Fairy-wrens and Chestnut-rumped Thornbill. Remaining species

Table 5.9. **Foraging height.** Percentage use of height categories and niche breadth (H').

Height above ground (m)										H'
0	>0-1	>1-2	>2-4	>4-6	>6-8	>8-10	>10-20	>20		
										
Ground Feeders										
Apostlebird	100									0
Diamond Dove	100									0
Peaceful Dove	100									0
Rufous Songlark	100									0
Australian Magpie-lark	99.2	0.8								0.05
Australian Magpie	97.5	2.5								0.12
Crested Pigeon	93.9	0.9		5.2						0.26
Zebra Finch	94.2	5.8								0.22
Pink Cockatoo	89.3	2.7	3.6	3.6	0.9					0.48
Richard's Pipit	94.2	3.8	1.9							0.26
Red-capped Robin	90.1	5.6	2.8		1.4					0.42
Chestnut-crowned Babbler	79.8	5.3	7.2	6.3	1.0	0.5				0.77
Southern Whiteface	86.0	6.2	3.9	3.4	0.6					0.57
White-winged Chough	85.2	7.4		3.7			3.7			0.57
Blue Bonnet	56.0	23	11.9	7.3	0.5	1.4				1.19
Mulga Parrot	63.5	34.6				1.9				0.73
Crimson Chat	72.8	9.3	14.2	3.7						0.85
Yellow-rumped Thornbill	63.9	11.8	10.9	12.6	0.8					1.08
Ground/Aerial Feeders										
Black-faced Woodswallow	39.8	14.3	7.1	3.1	12.2	14.3	1.0	7.1	1.0	1.72
Willie Wagtail	46.2	16.7	13.1	8.7	9.8	4.7	0.4	0.4		1.55
Bark/Ground Feeders										
Brown Treecreeper	32.4	14.2	12.5	22.7	12.5	4.5		1.1		1.69
Grey Shrike-thrush	37.2	11.8	3.9	19.6	17.6	7.8	2.0			1.65
Ground/Fruit Feeders										
Budgerigar	56.8	43.2								0.68
Galah	52.1	46.8		1.1						0.74
Little Corella	31.8	59.4	1.2	7.1	0.5					0.94
Emu	33.8	32.4	33.8							1.1
Mallee Ringneck	4.0	33.6	25.5	12.1	14.1	8.1	2.7			1.57
Foliage Feeders										
Black-faced Cuckoo-shrike	8.7	13.0	8.7	8.7	43.5	17.4				1.57
Chestnut-rumped Thornbill	6.2	25.6	39.0	27.2	2.1					1.32
Variegated Fairy-wren	11.8	57.0	22.8	6.8	1.7					1.16
White-winged Fairy-wren	19.3	52.3	26.1	2.3						1.09
Striated Pardalote			8.0	28.6	36.6	17	8.0	1.8		1.5
White-winged Triller	22.8	21.1	10.5	21.1	14.0	7.0	3.5			1.81
Flower/Foliage Feeders										
Spiny-cheeked Honeyeater	0.8	54.9	38.7	16.0	7.6	1.3	0.4	0.4		1.35
White-fronted Honeyeater		54.2	60.6	15.2						0.93
Singing Honeyeater	1.3	58.5	26.9	28.2	5.1					1.29
Yellow-throated Miner	10.8	10.0	19.9	32	18.6	4.9	3.0	0.8		1.92
White-plumed Honeyeater	4.0	5.8	9.4	25.8	32.2	12.6	5.7	3.4		1.68
Aerial Feeders										
White-browed Woodswallow		3.0	2.3	1.5	6.8	9.0	3.8	35.3	38.3	1.51
Rainbow Bee-eater		0.2	8.8	6.6	13.1	14.6	8.8	21.9	16.0	2.0
Tree Martin	0.8	5.6	2.0	10.5	6.0	5.2	6.6	54.3	8.8	1.5
White-breasted Woodswallow		1.7	2.6	6.5	11.7	9.1	9.1	40.3	9.1	1.8
White-backed Swallow	2.6		5.3	2.6	10.5	2.6		52.6	23.7	1.0
Grey Fantail		20.0	33.3	30.0	13.3	3.3				1.44

showed little height specialisation. Aerial feeders were among the least specialised, though the Grey Fantail was associated, in part with the shrub layer.

5.4.6 Partitioning of the Ground Substrate

5.4.6.1 Feeding Distance from Cover

Ground, ground/fruit, ground/air and ground/bark feeders made substantial (at least 30% of observations) use of the ground substrate except for the Mallee Ringneck. These birds varied in the distances from cover at which they fed on the ground (Figure 5.3). The Grey-shrike Thrush and Rufous Songlark fed entirely under cover, often in dry creekbeds. Eight species fed either under or adjacent to cover. Eight other species also fed partly under cover, but regularly ventured out to around 50 m from cover. This group included many seed-eaters, such as the Mulga Parrot and Blue Bonnet. The cryptic colouration of some made them difficult to detect at a distance on the ground and foraging observations well away from cover may be under represented in the sample. The Australian Magpie-lark fed almost equally at all distances from cover. Finally, five species preferentially fed at least 50 m from cover. While there was considerable overlap, in terms of feeding distance from cover, the different groupings partitioned the ground resource spatially. Species at either end of the continuum did not overlap at all.

5.4.6.2 Condition of Ground Cover

Figure 5.4 summarises records of ground-layer herbage, stone, and litter cover, and herbage greenness and height, in the immediate vicinity of ground-feeding individuals for all species in total and for 16 individual species: 12 ground feeders, two ground/fruit feeders, one ground/air and one ground/bark feeder. For each aspect of ground condition there were considerable differences between species as indicated by the high number of species differing significantly from the summed results of all species (*chi-square* analysis, $p < 0.001$). The Brown Treecreeper and Willie Wagtail, for example, fed on ground with little herbage cover but

Figure 5.3. **Feeding distance from cover.** Bars in figures indicate percentage of ground feeding observations made at increasing distances from cover. Categories and their equivalent distances from cover are: 1 - under cover, 2 - >0-5m, 3 - >5-10m, 4 - >10-25m, 5 - >25-50m, 6 - >50m. Numbers in brackets refer to the total number of ground feeding observations made for each species

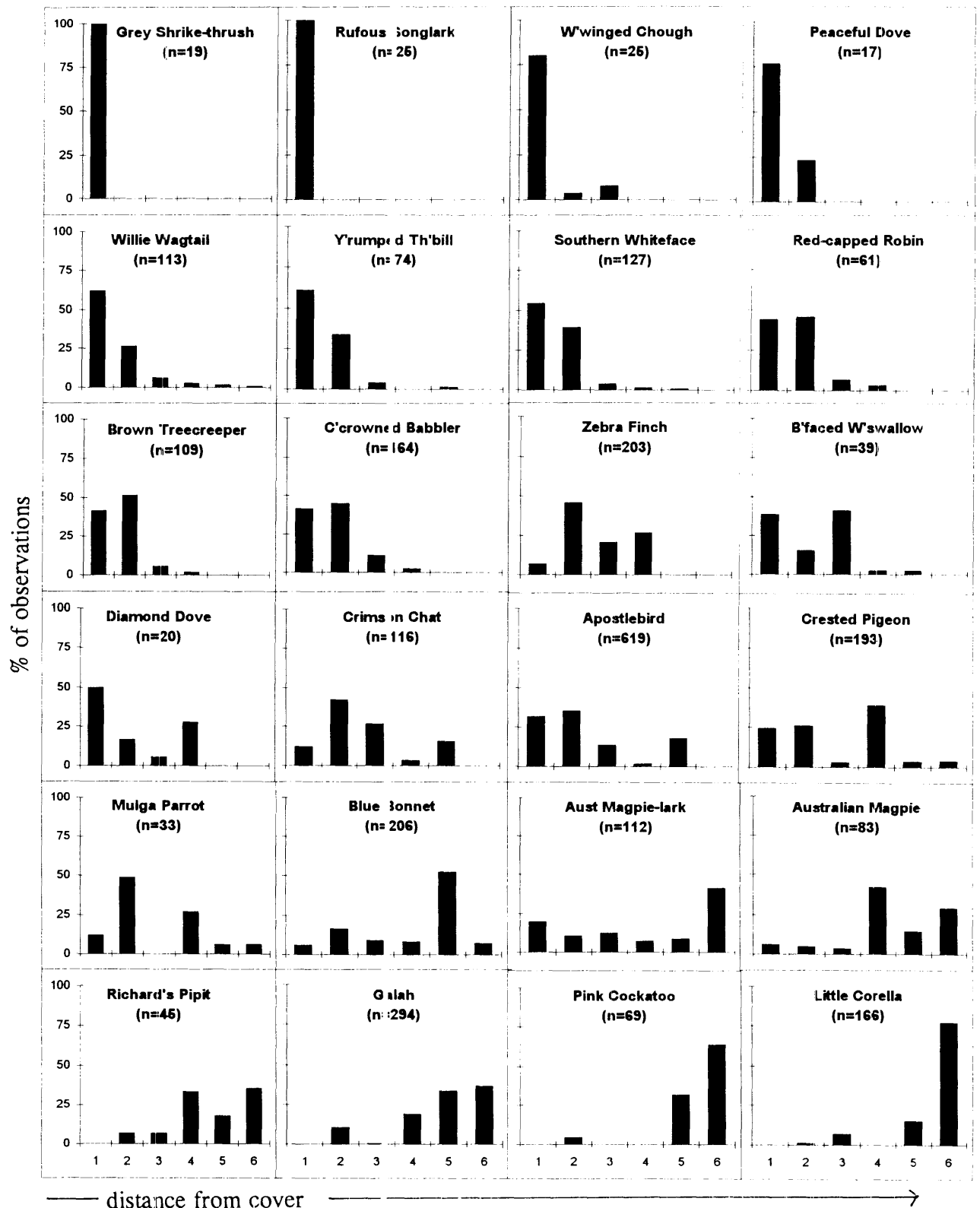


Figure 5.4. Use of the 'ground' substrate. Figures a) - e) summarise observations made for ground feeding individuals of 16 species and for all ground feeding individuals combined. *** indicates that results for a species are significantly different ($\chi^2, p < 0.001$) from the sum of all other ground feeding observations.

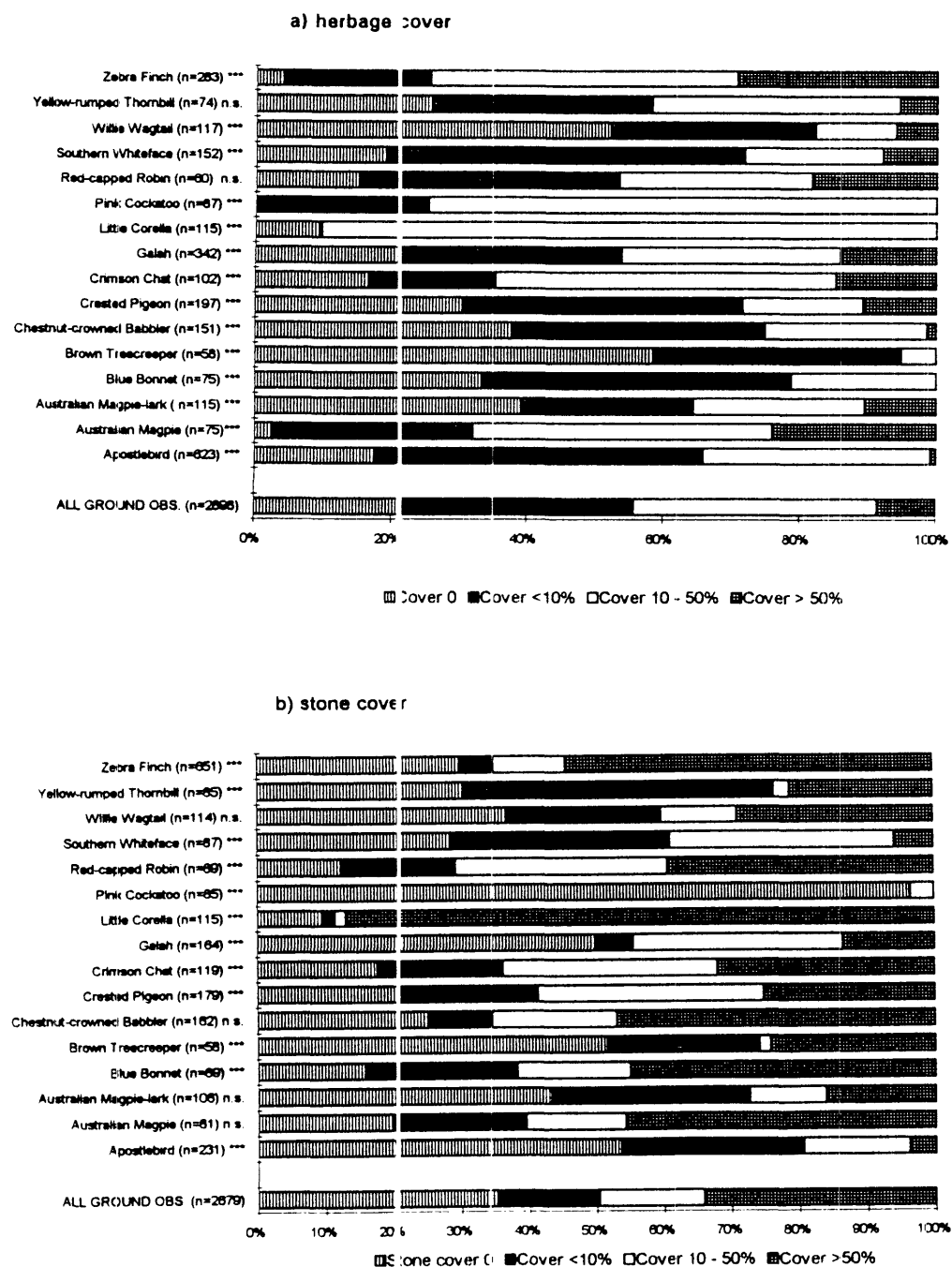
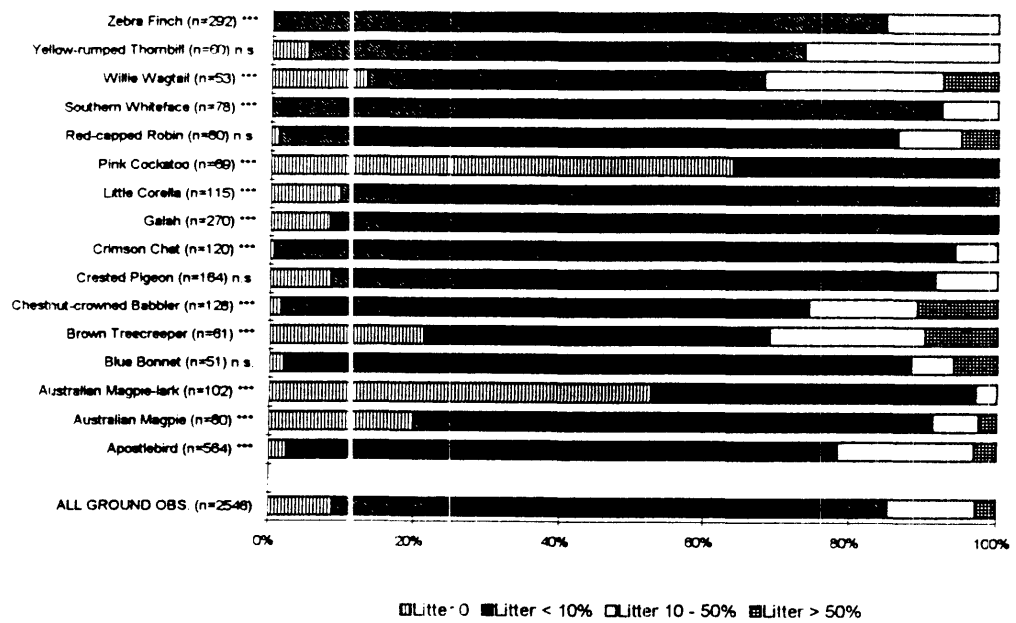
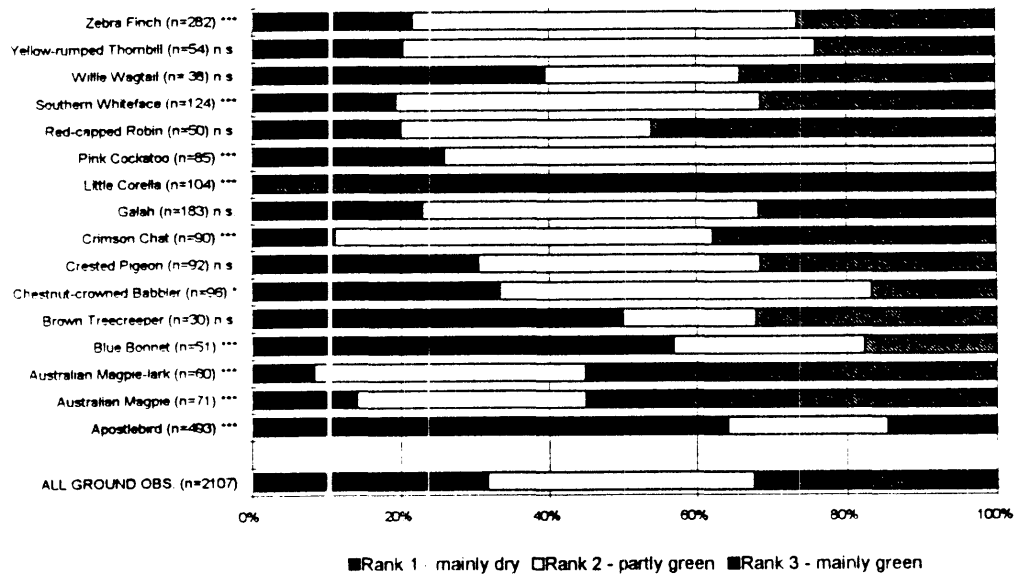


Figure 5.4 ctd.

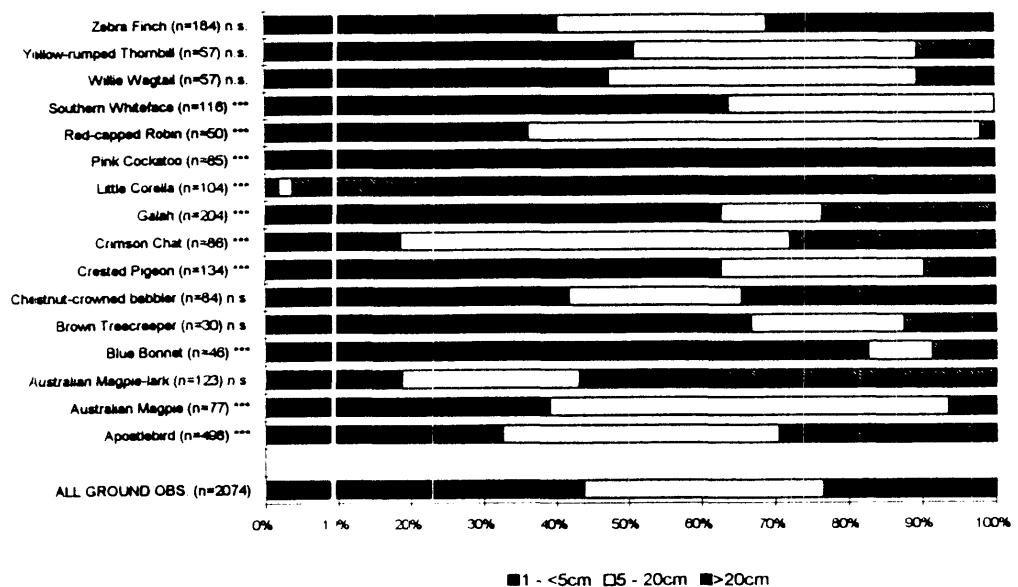
c) litter cover



d) greenness of herbage cover



e) height of herbage cover



plenty of litter. Stony ground was favoured by the Zebra Finch and Little Corella, but avoided by the Apostlebird. The Australian Magpie and Australian Magpie-lark fed mainly in patches of fresh green herbage, while the Apostlebird and Blue Bonnet tended to feed where herbage had dried off. The Blue Bonnet, Pinl. Cockatoo and Southern Whiteface tended to feed where ground-layer herbage was low, while the Australian Magpie-lark and Little Corella were more often seen feeding in taller herbage.

5.4.7 Seasonal Differences in Substrate Use at Peery

Comparison of the relative use of substrates in spring and winter was made for 20 resident and three nomadic species. Ten resident species (Table 5.10) differed significantly (*chi-square* analysis, $p < 0.01$) between winter and spring. These included birds from all feeding groups except aerial feeders. Five insectivorous species: Chestnut-crowned Babbler, Yellow-rumped and Chestnut-rumped Thornbills, Willie Wagtail and Brown Treecreeper, fed significantly more on the ground in winter. The seed-eating Galah tended to take seed directly from plants in spring but in winter took more fallen seed from the ground. Fruit was more important in spring for the Mallee Ringneck and Spiny-cheeked Honeyeater, whereas flowers were more important in winter for the Mallee Ringneck, Yellow-throated Miner, Spiny-cheeked and White-plumed Honeyeaters.

Eight ground, three foliage and two aerial feeders did not differ significantly in substrate use between seasons.

5.5 Discussion

Birds of the Peery bird community must find a continuous supply of food in an environment driven principally by rainfall, which is both variable and unpredictable (Stafford Smith & Morton 1990), or otherwise leave that environment when food is scarce. In such a climatically variable environment generalisation in feeding habits has been predicted (Levins 1968, McNaughton & Wolf 1970) and confirmed by a number of studies, e.g., Wiens & Rotenberry (1979), Rotenberry (1980), Brooker *et al.* (1990).

Table 5.10. Relative use of substrates in winter and spring. 23 species for which >30 foraging observations were obtained in winter and spring were included in the analysis. Only species showing a significant seasonal difference in substrate use (χ^2 analysis, $p < 0.01$) are included in the table. (n) indicates number of observations made in each season.

SPECIES	(n)	Ground	Fruit	Flower	Foliage	Bark	Air
Ground Feeders							
Chestnut-crowned Babbler							
sp.	107	68.2	0	0	19.6	12.1	0
wi.	101	90.1	0	0	5.0	5.0	0
Yellow-rumped Thornbill							
sp.	58	55.2	1.7	10.3	20.7	8.6	3.4
wi.	60	75.0	0	0	20.0	5.0	0
Ground/Aerial Feeders							
Willie Wagtail							
sp.	128	28.1	0	0.8	12.5	3.1	55.5
wi.	147	64.6	0	0	4.1	1.4	29.9
Bark/Ground Feeders							
Brown Treecreeper							
sp.	83	16.9	0	0	0	83.1	0
wi.	147	64.6	0	0	4.1	1.4	29.9
Ground/Fruit Feeders							
Galah							
sp.	256	46.5	53.5	0	0	0	0
wi.	195	59.5	40.5	0	0	0	0
Mallee Ringneck							
sp.	85	1.1	90.8	2.3	4.6	1.1	0
wi.	62	3.2	48.4	32.3	16.1	0	0
Foliage Feeders							
Chestnut-rumped Thornbill							
sp.	104	1.9	1.9	3.8	66.3	24.0	1.9
wi.	92	10.9	0	0	84.8	4.3	0
Flower/Foliage Feeders							
Spiny-cheeked Honeyeater							
sp.	102	0	48.0	25.5	15.7	6.9	3.9
wi.	133	0	2.3	83.5	9.8	3.8	0.8
Yellow-throated Miner							
sp.	191	0	2.1	39.1	52.1	6.3	0.5
wi.	176	0	2.3	51.1	46.6	0	0
White-plumed Honeyeater							
sp.	312	4.5	0.6	23.4	60.9	5.1	5.4
wi.	389	1	0	26.7	67.9	1.5	2.8

1. Species included in analysis but not showing a significant seasonal difference in substrate use: Apostlebird, Australian Magpie-lark, Australian Magpie, Crested Pigeon, Zebra Finch, Crimson Chat, Southern Whiteface, Blue Bonnet, Variegated Fairy-wren, White-winged Fairy-wren, Striated Pardalote, White-browed Woodswallow, Tree Martin.

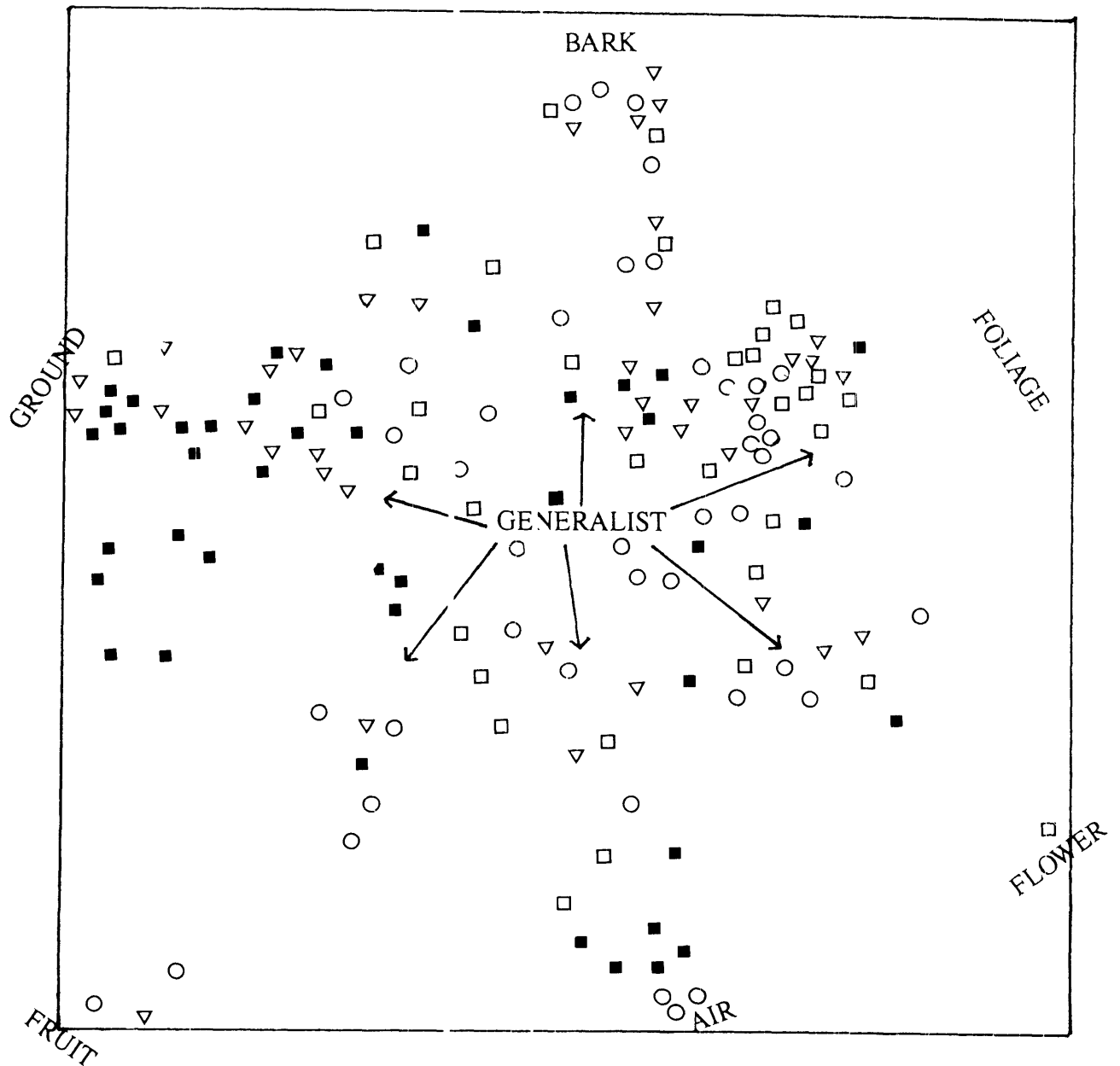
Results of this study suggested that most birds were relatively specialised in terms of foraging substrate and method but, apart from ground feeders, not height. An indication of the degree of specialisation can be obtained by comparing the feeding ecology of birds in this community with those of communities in more mesic eastern New South Wales, namely in eucalypt woodland near Armidale (Ford *et al.* 1986), in eucalypt forest and woodland near Bombala (Recher *et al.* 1985), and in eucalypt forest, rainforest and coastal scrub near Bega (P. Smith & J. Smith unpublished data). Data were collected in a similar way in these three studies and the Peery study, and similar numbers of species were involved (44 at Peery, 40 at Armidale, 41 at Bombala and 46 at Bega). A comparison of birds of these communities, in terms of their relative use of substrates, using multivariate methods similar to those used previously to describe the Peery bird community, is illustrated in Figure 5.5.

The Peery community is well endowed with specialised ground and aerial feeders. However, bark, fruit, flower and foliage feeders, apart from the Striated Pardalote and White-fronted Honeyeater, have a relatively generalised feeding habit. All bark, fruit, flower and foliage feeders, apart from the White-fronted Honeyeater, were residents which must endure the vagaries of the climate. The White-fronted Honeyeater was able to evade climatic fluctuations at the site and to feed entirely at one substrate, flowers, by virtue of its nomadic habits. Its presence at the site coincided with the flowering of Harlequin Eremophila, though it was not present in every flowering period (Chapter 3). The specialised Striated Pardalote gleaned invertebrates, especially psyllids (Woinarski 1988), and was always present at the study site in low numbers. Its numbers fluctuated some sixfold over the study (Chapter 3) and, though classed as a resident, at least part of the population may have wandered to follow psyllid outbreaks elsewhere.

In contrast to the generalised bark, fruit, foliage and flower feeders, the specialised aerial feeders were, apart from the Tree Martin, nomadic or migratory species. Numbers of Tree Martins fluctuated some sixtyfold over the study (Chapter 3) and, like Striated Pardalotes, at least part of the population may have been nomadic or migratory.

The large contingent of Peery birds which fed wholly or largely on the ground included resident and nomadic species. Of these, the smaller granivorous species including the Budgerigar, Zebra Finch, Diamond Dove and Peaceful Dove, were only present when

Figure 5.5. Ordination of bird species included in foraging studies at Peery (■), and near Armidale (□), Bega (○), and Bombala (▽). The association between species is based on their relative use of substrates. Axes are dependently scaled.



conditions were favourable and seed especially grass seed, was plentiful. The Zebra Finch (Immelmann 1965, Davies 1977, Morton & Davies 1983) and Budgerigar (Wyndham 1980) feed predominantly on grass seed. The larger, granivorous Crested Pigeon was resident and persisted at the site possibly by virtue of its size. Morton & Davies (1983) found that larger seed eaters had more diverse diets than smaller species as they are able to include larger and harder seeds of shrubs and trees such as acacias, cassias, casuarinas and eucalypts, as well as grasses, in their diets. Crested Pigeons, thus, may have wider dietary options than the smaller seed-eating species. The Galah and Little Corella were also residents. They are large, range widely to feed, and exploit opportunistically the available seed and herbaceous matter (Forshaw & Cooper 1981, Beeton 1985, Tenby & Emison 1986, Rowley 1990, Smith & Moore 1991). The resident Blue Bonnet and Mulga Parrot made substantial use of flowers and fruit (which they chewed) as well as taking seed from the ground. All other specialized ground feeders were not entirely dependent on plant production, being at least partly insectivorous.

In summary, in this variable and unpredictable environment, which included a wide range of habitats, two main strategies were adopted by birds. Resident species tended to be generalized or opportunistic feeders and confirm the prediction of more generalised feeding habits compared to birds of more mesic environments. Other species concentrated on a narrower range of resources, but evaded resource fluctuations by adopting a nomadic or migratory lifestyle.

The lack of specialisation in terms of feeding height for above ground feeders was related to the structure of vegetation at the Peery site. Feeding height categories were not strictly comparable with vegetation layers. Trees were low (< 20m), and most, especially eucalypts, exhibited a typical wood and growth form. They branched extensively near the ground and tree foliage and flowers extended from near ground level to the tops of trees. The variety of food sources, including plant species, utilised by individual species also contributed to the wide range of foraging heights used.

The comparison of Peery birds with those of woodland and forest in more mesic environments (Figure 5.5) demonstrates the greater relative importance of the ground as a feeding substrate at Peery. The Budgerigar, Mulga Parrot, Galah, Blue Bonnet, Little Corella and Emu formed a feeding guild that took fruit and seeds both from the ground and direct from

plants. Apart from the Galah, these birds occur only at Peery. The Galah is found in more coastal areas, but feeds in cleared areas outside woodland and forest. The birds studied at Peery included few representatives of the large suite of birds which specialise on the bark, foliage, fruit and flowers of eucalypt, and which dominates the bird communities of eucalypt forest and woodland in more mesic areas. The composition of the Peery community reflects the availability of food resources and supports the contention of Holmes & Recher (1986) that foraging opportunities at a site are the primary determinants of feeding guild structure. At Peery, eucalypts were largely restricted to drainage lines with a supply of subterranean water. The open plains, dominated by short lived plants which produce vast quantities of fruit (Westoby 1980), provided an extensive ground feeding resource. Ground feeders ranged in size from the Yellow-rumped Thornbill (8 g) to the Pink Cockatoo (almost 400 g), and fed at a range of distances from cover in areas with varied herbage, stone and litter cover. Holmes & Robinson (1988) concluded that such differences in microhabitat use and foraging behaviour might allow for significant dietary differences in ground-feeding species.

The seasonal differences in substrate use of a number of resident species at Peery are a consequence of their opportunistic feeding habits. The importance of fruit to the Mallee Ringneck and Spiny-cheeked Honeyeater in spring reflected their concentration on Boobialla fruits which were then abundant. The greater use of flowers in winter by the Mallee Ringneck, Spiny-cheeked and White-plumed Honeyeaters and Yellow-throated Miner was related to the flowering of Harlequin Eremophila and Black Box at this time. Five small to medium sized, resident, insectivorous species (Chestnut-crowned Babbler, Yellow-rumped and Chestnut-rumped Thornbills, Willie Wagtail and Brown Treecreeper) fed markedly more on the ground in winter than spring. Such a switch has also been noted by Bell (1985) for thornbills, Cameron (1985) for Willie Wagtails, Robinson (1992) for Scarlet *Petroica multicolor* and Flame *P. phoenicea* Robins and Cain (1994) for Scarlet, Flame and Dusky *Melanodryas vittata* Robins and Superb Fairy-wrens *Malurus cyaneus* in more mesic areas, and may reflect a relatively greater availability of invertebrates at ground level than in vegetation in winter. Seasonal measures of invertebrate density and microhabitat distribution in arid areas are required to confirm this.

Birds at Peery obtained food from a wide range of plant species. However, certain

species were especially important, e. g. eucalypts, Prickly Wattle and Lignum as sources of arthropods from foliage, Harlequin Eremophila for flowers, and Boobialla, Spongy Saltbush and Pop Saltbush *Atriplex holocarpa* for fruits. Eucalypt foliage provided carbohydrates in the form of lerps and galls, as well as insects. The Striated Pardalote feeds mainly on lerps found in eucalypts (Woinarski 1985, 1988) while White-plumed Honeyeaters take manna, honeydew and lerps as well as insects (Paton 1980). Eucalypt foliage at Peery supported several species of lerp-forming insects (*Cardiaspina* sp., *Creis* sp. and *Glycaspis* sp.), but lerp populations fluctuated greatly. It was not always possible to determine if birds were taking lerps or insects from foliage. In spring 1991 and 1993, lerps were abundant and White-plumed Honeyeaters apparently favoured lerps over eucalypt flowers as a source of carbohydrates. At these times lerps were fed to nestling and fledgling White-plumed Honeyeaters. Yellow-throated Miners congregated at lerp outbreaks and the Mallee Ringneck sought galls in eucalypt foliage. The heavy use of Prickly Wattle and Lignum foliage, especially by small birds, may be related as much to the need for shelter and protection, as for the food it supplies. Dense branching and small phyllodes give Prickly Wattle a brambly appearance and Lignum forms impenetrable thickets. The importance of Eremophilas as a nectar source for honeyeaters has also been noted by Hobbs (1958, 1967). The White plumed Honeyeater, always the most numerous honeyeater at the site (Chapter 3), was notable by its absence at stands of flowering Harlequin Eremophila. It fed at isolated Eremophilas within creeklines, but rarely ventured away from creeklines to Eremophila stands on the open plains. Joseph (1986) noted that fruit-eating birds of arid areas tend to feed on a variety of plant species. His observation has been supported by studies of pigeons and doves (Frith 1982), Budgerigars (Wyndham 1980), Cockatiels (Jones 1987), corellas (Beeton 1985, Temby & Errison 1986, Smith & Moore 1991), Galahs (Rowley 1990), Pink Cockatoos (Rowley & Chapman 1991) and Zebra Finches (Morton & Davies 1983).

This study identified the ground substrate and perennial plant species as the most important sources of food for birds. Almost half the observations of feeding birds were at ground level. Virtually all feeding observations at foliage, flowers and bark, involved perennial plants. Ephemerals, annuals and biennials were important fruit sources and this was further shown by frequent congregations of fruit-eating birds feeding on the ground well away

from perennial plants. Such birds were generally nomadic or wide-ranging species. In contrast, the sources of fruit of more sedentary species, such as the Mallee Ringneck, Spiny-cheeked Honeyeater and Singing Honeyeater, were predominantly perennial species. The management implications of the reliance of birds on these feeding resources are discussed in the concluding chapter.

Chapter 6. ASPECTS OF AVIAN BREEDING: TEMPORAL PATTERNS IN BREEDING EFFORT, CO-OPERATIVE BREEDING AND NESTING RESOURCES.

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6.1 Chapter outline

In this chapter I describe three aspects of breeding behaviour and ecology at the study site: temporal patterns in breeding effort; the incidence of cooperative breeding; and nesting resources, particularly nest sites.

6.2 Temporal patterns in breeding effort

6.2.1 Introduction

Lack (1968) proposed that each species of bird has evolved the timing of its breeding so that it raises most offspring. Young are produced and reared when food availability is greatest. Rainfall in arid Australia is low and extremely erratic, both spatially and temporally (Leeper 1970, Gentilli 1971, Williams & Calaby 1985, Stafford Smith & Morton 1990). Food supplies for breeding birds and their young would consequently be expected to be variable and unpredictable. Food could be scarce during long droughts but temporarily plentiful after rain. Different lags in response to rainfall in different plant life forms (e.g. ephemeral herbs to perennial trees) and food types (e.g. nectar, seeds) could modify these extremes for generalized species, but stagger the potential breeding times for specialists.

After only a limited period in the arid zone, Carter (1889) observed that 'many species of birds here lay whenever a good rain falls, no matter what time of year'. Carter's observations were supported by later anecdotal accounts of breeding following rain, e.g. McGilp (1919, 1923), Carnaby (1954), Robinson (1955) and Immelmann (1963). Breeding in the arid zone appeared to be opportunistic and related to rainfall itself, 'the very sight of rain appears to stimulate various species to courtship, with copulation and nest building beginning within hours after the start of precipitation' (Dawson & Bartholomew 1968), or the improvements in food (Serventy and Marshall 1957, Keast 1959, Ford & Sedgwick 1967, Serventy & Whittell 1967, Immelmann 1963, 1971, 1973, Serventy 1971) and water (Williams 1979) supplies which followed rain.

The breeding opportunity reported in Australian arid zone birds was not matched

by birds in arid regions of Africa (Moreau 1950, Immelmann 1967, Immelmann & Immelmann 1968), North America (Dawson & Bartholomew 1968) and Asia (Marchant 1963), where breeding appeared more regular. Serventy (1971) questioned whether the flexibility reported in the timing of breeding in Australia was characteristic of all Australian arid areas or only those of the west and centre. Breeding in eastern arid areas appeared to occur predominantly in spring and be more in accord with the situation in Africa, Asia and America and with more mesic areas in eastern Australia.

A number of more recent, longer-term studies of breeding in certain Australian arid zone species, including the Emu (Davies 1973b), plumed pigeons *Geophaps plumifera* and *G. ferruginea* (Frith & Barker 1975), Zebra Finch (Davies 1977) and Budgerigar (Wyndham 1982, 1986), have discerned an underlying seasonal pattern to breeding. This suggests that internal gonadal rhythms and/or cues of a more reliable seasonal nature, such as day length and temperature (Breed 1982, Scholde 1982), may influence the timing of breeding and, or at least, any response to rainfall. However, in contrast to Davies' (1977) finding that Zebra Finches were seasonal breeders in arid south-western Australia, Zann *et al.* (1995) found that, in a seven year period in central Australia, Zebra Finches bred in response to significant rain at any time of year.

In this section I describe patterns in the breeding effort of birds at the Peery study site, at the eastern edge of the arid zone. The three and a half year study period encompassed a severe drought followed by a period of above average rainfall. I investigate the extent to which breeding effort was related to regular seasonal patterns and to short or long-term fluctuations in rainfall. The study was undertaken between spring 1990 and summer 1993/94. A detailed description of the study site is given in Chapter 2.

6.2.2 Methods

6.2.2.1 Classification of breeding birds

Breeding birds were classified according to their movement patterns at the study site as residents, nomads, winter migrants or spring-summer migrants (Chapter 3). They were

assigned to five dietary categories: plant, mixed (plant/invertebrates), aerial invertebrates, other invertebrates, and carrion/live vertebrates. Dietary categories were determined from information contained in Chapter 5 and a review of literature pertaining to birds of the Western Division of New South Wales undertaken by Smith & Smith (1994).

6.2.2.2 Determination of breeding effort

On one occasion before the drought (spring 1990), four occasions during the drought (winter and spring 1991 and 1992), and four occasions after the drought (autumn, winter and spring 1993 and summer 1993/94), a comparable effort was made to determine the level of breeding activity at the study site. Dates of survey periods were: 10 October-7 November 1990, 2-23 July 1991, 1-21 October 1991, 29 June-23 July 1992, 22 September-18 October 1992, 9-22 April 1993, 12-29 July 1993, 28 September-20 October 1993 and 18-26 January 1994. Searches for nests and other evidence of breeding were made while censusing and collecting habitat, foraging and drinking data (Chapters 3, 4, 5, 7). The breeding effort of each species was determined as the number of pairs or groups building nests or incubating or feeding nestlings or fledglings.

Analyses based on estimated laying dates were not attempted. Once a bird has started to nest it may re-nest to replace losses or it may be multiple brooded and will continue to nest while conditions are favourable (Marchant 1981). Observations of marked individuals at the site confirmed that Willie Wagtails and White-plumed Honeyeaters re-nested following nest predation. On one occasion a group of Variegated Fairy-wrens commenced nest building while still feeding fledglings. As I was generally unable to determine if birds were producing a first or subsequent clutch, a finer comparison based on laying date was not justified.

In each data collection period a density adjusted index of breeding effort was derived by dividing the total breeding effort by the mean density of birds at the site (individuals/ha) as determined in the corresponding census (Chapter 3).

The Australian Raven and Little Crow both nested at the site. Records for these species were pooled as I was not always able to distinguish them at nests.

6.2.2.3 Rainfall

Rainfall at the study site is presumed intermediate between that recorded for Wilcannia and White Cliffs, the two nearest rainfall stations. Monthly rainfall records for Wilcannia and White Cliffs for the study period and preceding 12 months are highly correlated ($r = 0.780$, d.f. = 50, $p < 0.001$). I therefore calculated the mean of the two sets of rainfall data to provide the best available indication of rainfall at the study site.

6.2.2.4 Data analyses

Multivariate methods were used to compare the breeding effort of birds in different seasons (spring and winter) and years of the study. Data (number of breeding records for each species in each survey period) were transformed with $\log(x + 1)$ so that analyses would not be dominated by a few very common species (Clarke 1993). Similarity between census periods was calculated using the Bray & Curtis association measure, and an ordination procedure, semi-strong-hybrid multidimensional scaling, was used to elucidate patterns in the data (Belbin 1990).

Relationships between rainfall and the absolute and indexed breeding effort were examined using a correlation analysis. Rainfall totals in the previous one to 12 months were considered to allow for a possible time lag in response to rainfall.

6.2.3 Results

6.2.3.1 Breeding records

A total of 684 breeding attempts deriving from 51 of the 95 native landbird species at the study site was recorded (Appendix 6.2.1). Breeding species included 35 residents, 10 nomads, five spring-summer migrants and a single winter migrant, the Red-capped Robin. Twelve breeding species fed chiefly on plant matter, six on invertebrates and plant matter, seven on aerial invertebrates, 21 on ground or foliage invertebrates, and five on carrion and live vertebrates.

The 12 plant feeders included 11 species which ate mainly seed and the Mallee Ringneck whose diet included seeds, fleshy fruits, flowers and foliage. The six species which fed on plant matter and invertebrates included five honeyeaters and the White-winged Triller.

6.2.3.2 Patterns in breeding effort:

Total breeding effort ranged from 11 records in summer 1993/94 to 266 in spring 1993 (Table 6.2.1). The breeding effort was not correlated ($p > 0.05$) with the total abundance of birds at the site as determined in the corresponding censuses (Chapter 3). The number of species present that were breeding ranged from three (4.2% of all species present) in autumn 1993 to 38 (57.6%) in spring 1993 and was not correlated with the total number of species present at the site.

The study can be divided into three periods: pre-drought in 1990, drought in 1991-92, and post-drought in 1993-94 (Chapter 2). In September 1992 an isolated thunderstorm filled creekline waterholes. The drought was broken by heavy rain in December 1992 which produced local flooding.

The ordination (Figure 6.2.1) indicated differences in the species composition and abundance of breeding birds of different survey periods that could be related to the effects of season, drought and the local thunderstorm. The ordination consistently separated the spring survey periods from winter periods. The first three drought survey periods (winter and spring 1991 and winter 1992) were clearly separated from the post-drought surveys in winter and spring 1993 with the other two surveys (spring 1990 and spring 1992) being intermediate. The greatest change in the species composition and abundance of breeding birds occurred before the drought broke, between winter 1992 and spring 1992. The spring 1992 survey was undertaken several weeks after the localised thunderstorm in September 1992. Thus, the ordination axes can be interpreted as a seasonal (horizontal) and a rainfall-related (vertical) axis.

In each of the three full survey years, more species bred in spring than winter (Figure 6.2.2). Residents bred in each survey period, though more species in spring. Only residents bred in winter 1991 and 1992 when the area was gripped by drought. Nomadic

Table 6.2.1. **Breeding effort over survey period.**

	pre-drought	drought				post-drought			
	Sp 90	Wi 91	Sp 91	Wi 92	Sp 92	Au 93	Wi 93	Sp 93	Su 93/94
TOTAL BREEDING RECORDS	124	13	48	17	153	12	41	266	10
NO. SPECIES BREEDING	28	8	14	6	32	3	15	38	5
NO. SPECIES AT SITE	60	58	61	59	63	71	60	66	58
% of SPECIES BREEDING	46.7	22.4	23	28.8	50.8	4.2	25	57.6	8.6

Table 6.2.2. **Density adjusted index of breeding effort over survey period.**

* indicates not present at site in that census period

	pre-drought	drought				post-drought			
	Sp 90	Wi 91	Sp 91	Wi 92	Sp 92	Au 93	Wi 93	Sp 93	Su 93/94
ALL BIRDS	6.36	2.83	4.4	1.72	17.59	0.67	3.7	16.31	1.16
RESIDENTS	4.49	1.41	4.2	1.99	17.67	0.52	4.1	16.53	1.15
NOMADS	63.22	*	0	0	30.61	0.85	0.7	15.17	0
SPRING-SUMMER MIGRANTS	13.87	*	14	*	18.99	*	*	17.65	5.59

Figure 6.2.1. Ordination illustrating variability in overall breeding effort between seasons and years. Axes are dependently scaled.

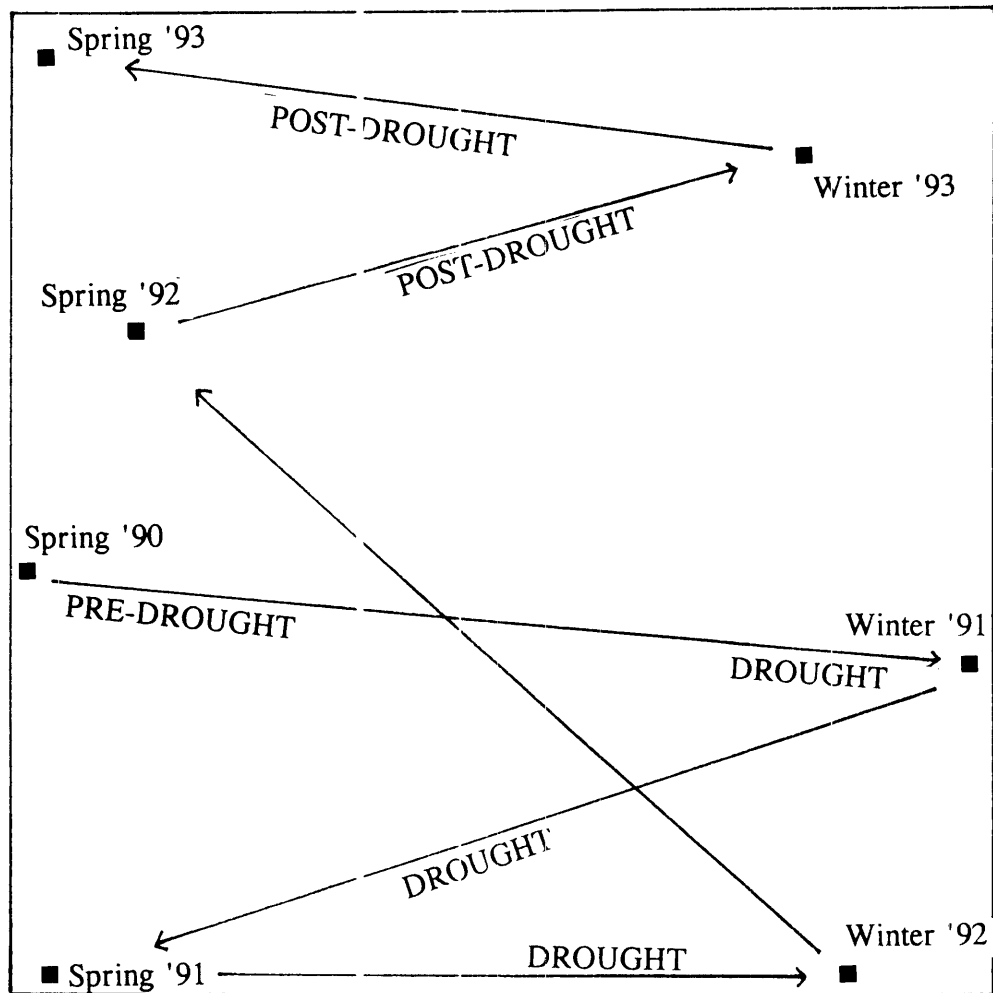
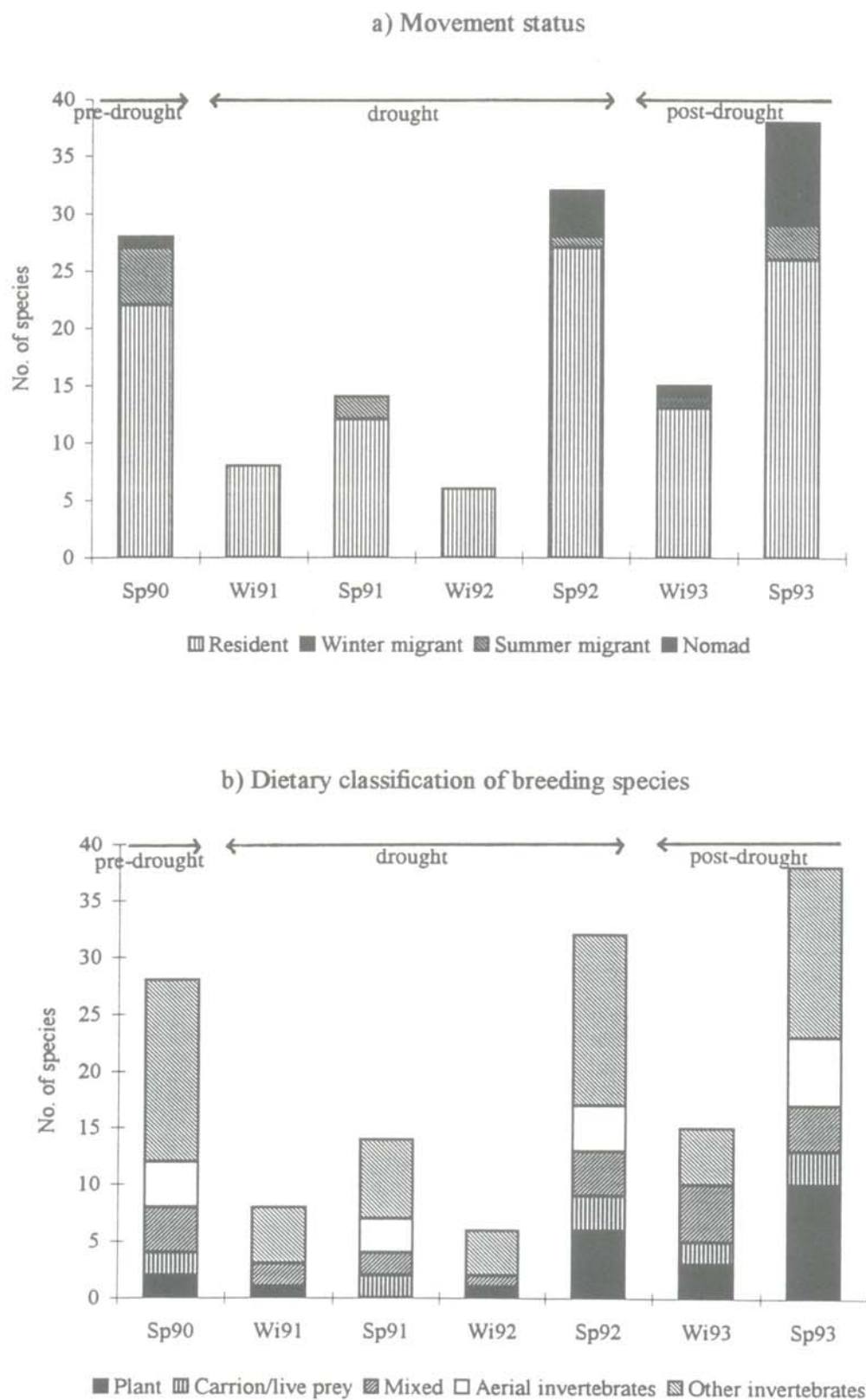


Figure 6.2.2. Species composition of breeding avifauna in each winter and spring survey period.



species nested in autumn, winter and spring, but not, apart from spring 1992, during the drought. Breeding nomads were most numerous in the spring after the drought while breeding summer migrants were most numerous in the spring before the drought. Breeding by particular dietary groups varied between seasons and years. Aerial insectivores bred only in spring. Plant feeders were the only dietary group not to breed in spring 1991 at the height of the drought.

More individuals, as well as species, bred in spring than winter (Figure 6.2.3). The breeding effort of residents and nomads declined with the onset of drought. In spring 1992, several weeks after a local thunderstorm, the number of breeding records for residents, especially the White-plumed Honeyeater, Willie Wagtail, Tree Martin and Southern Whiteface, increased. At this time there was also an influx of nomadic White-browed Woodswallows which commenced nesting on arrival. The spectacular total breeding effort in spring 1993 was largely due to the increased effort of nomads, especially Budgerigars, Crimson Chats, Rufous Songlarks and Zebra Finches. The breeding effort of migrants was relatively consistent and low over the study period. Carrion/live vertebrate and invertebrate feeders bred mainly in spring. In the very dry year 1991, more plant and mixed plant/invertebrate feeders bred in winter than spring. The numbers of breeding records for plant feeders varied most between years, ranging from zero in spring 1991 to 90 in spring 1993.

6.2.3.3 Comparison of absolute and density-indexed breeding effort

The numbers of breeding records for all birds, residents and nomads peaked in spring 1993 and for spring-summer migrants in spring 1990. In contrast, the breeding effort per bird was greatest in spring 1992 for all birds, residents and spring-summer migrants, and in spring 1990 for nomads (Table 6.2.2).

6.2.3.4 Relationship of breeding effort to rainfall

Over the entire study period the absolute and density-indexed breeding efforts of all birds, residents, nomads and spring-summer migrants were not significantly correlated with rainfall in the previous month or cumulative 2-12 months (Figure 6.2.4). When results of the spring

Figure 6.2.3. Numbers of nest records in each winter and spring survey period.

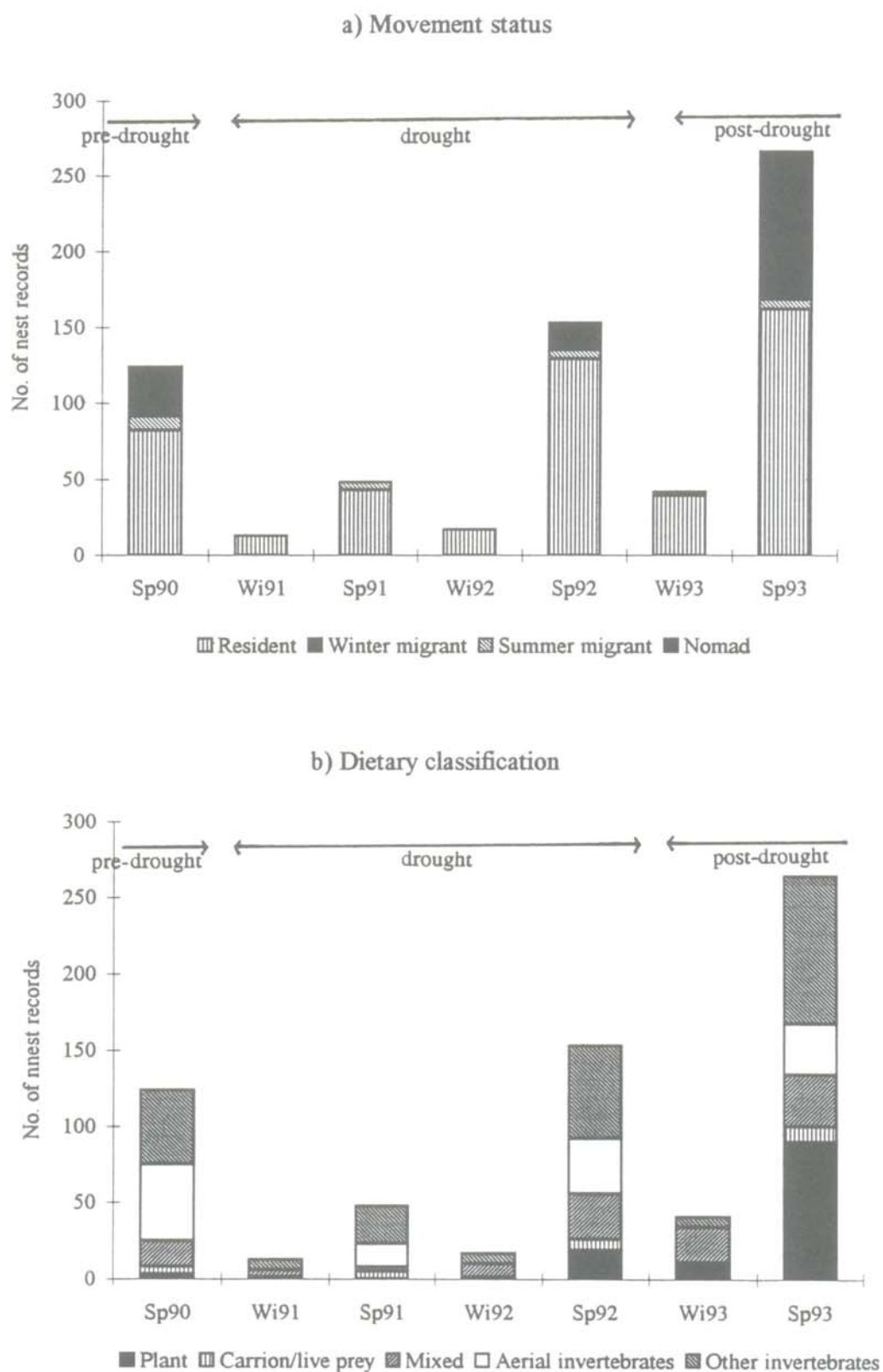
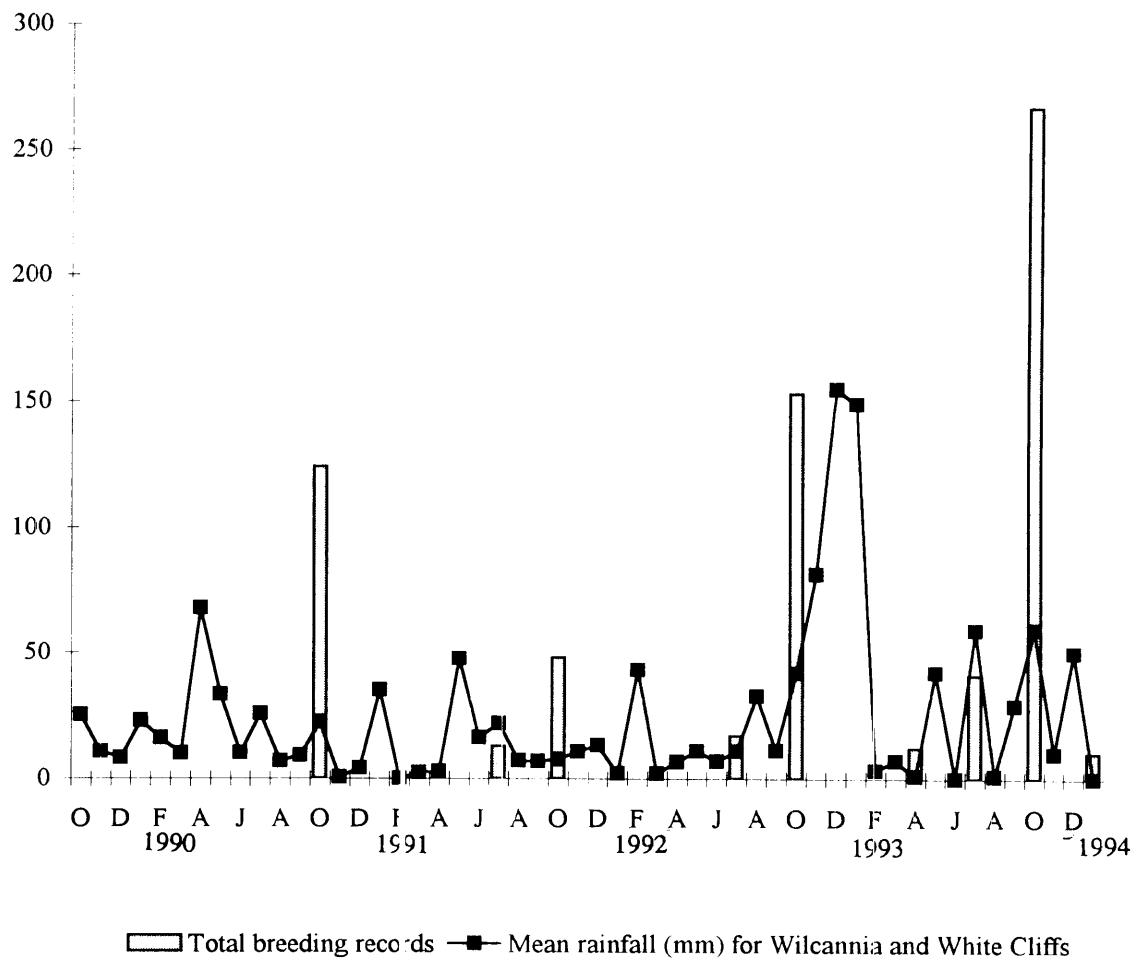


Figure 6.2.4 Relationship of total breeding effort to rainfall



surveys were considered in isolation, only the absolute breeding effort of nomads was correlated with rainfall in the previous one ($r = 0.997$, d.f. = 2, $p < 0.01$) and four ($r = 0.996$, d.f. = 2, $p < 0.01$) months.

6.2.4 Discussion

In the period of this study the overall breeding effort was influenced primarily by season and secondarily by local conditions. More individuals and more species nested in spring than winter in both wet and dry years. A predominance of spring breeding was also reported by Schmidt (1978) at Cobar to the east and Denny *et al.* (1977) in the Cooper Creek basin to the north-west of the study area. Henle (1989) recorded breeding in Kinchega National Park to the west between late autumn and spring; in a two year period in which the late summer/autumn period was very dry and the winter/spring period received above average rainfall in each year, breeding peaked in July. At Peery, the breeding effort in each year was modified by prevailing site conditions. The numbers of individuals and species breeding were greatly reduced during drought. In a long-term study of breeding activity at Moruya in south-eastern New South Wales, Marchant (1992) reported a predominance of spring-summer breeding. In this more mesic environment drought was similarly associated with a reduction in levels of breeding activity.

However, as Davies (1979) found, there was no simple relationship between rainfall and breeding response. The different movement status and dietary groups varied in their breeding responses. When conditions at the site deteriorated, the numbers (Chapter 3) and breeding effort of residents declined. After two dry years a localised thunderstorm was apparently sufficient stimulus to promote breeding in residents in spring 1992. The storm filled waterholes in creeklines and promoted germination of ground-layer vegetation. At this time residents achieved their greatest breeding effort on a per individual basis. Carnaby (1954), in north-west Western Australia, noted a similar effect when local thunderstorms after a period of dry conditions promoted breeding in a circumscribed area. In 1993, after good rain in November-December 1992 and January 1993, the breeding effort of residents was low in autumn and winter. The 1993 spring breeding effort of residents was much increased compared

to their breeding efforts in the springs before (1990) and at the height of the drought (1991). It thus appears that resident species are not capable of a prolonged major aseasonal breeding effort as soon as conditions improve.

In contrast to residents, nomads were generally absent and did not nest at all at the site when conditions were poor. The magnitude of the breeding effort of nomads in the one pre-drought survey in spring 1990, when conditions were about average, is misleading as all nomad breeding records at this time derived from two Fairy Martin colonies. This was the only time that Fairy Martins were recorded breeding at the site. Following the thunderstorm in spring 1992 the only nomad to show a concerted nesting effort was the White-browed Woodswallow, an aerial insectivore. Other aerial insectivores, including the resident Tree Martin and Black-faced Woodswallow, and spring-summer migratory White-breasted Woodswallow, also had an increased nesting effort at this time. Small numbers of seed-eating Cockatiel, Budgerigar and Zebra Finch were the only other nomads to breed in spring 1992. Numbers of nomads peaked after the drought in autumn and spring (Chapter 3), but the breeding effort per nomad was far greater in spring than autumn.

The breeding effort of migratory species, whose populations are determined by conditions away from the site as well as at the site, was relatively constant between years. The Red-backed and Sacred Kingfishers were only recorded nesting in spring 1990. However, pairs of these species, as well as other spring-summer migrants, were courting, but not yet nesting, in all spring surveys. Spring-summer migrants appeared to nest later than residents and, by conducting spring surveys in October each year, it is likely that I consistently under-estimated their breeding efforts. In southern Victoria the Rainbow Bee-eater does not commence egg-laying until November and fledging peaks in January (Lill 1993). The earlier breeding in spring 1990 may have been induced by the flooding of the adjacent Peery Lake. Possibly the migrants arrived earlier in 1990 (and hence nested earlier) because of climatic factors.

The 51 breeding species showed considerable individual variation in the timing and magnitude of their breeding effort. Though spring breeding predominated, a number of species, such as the Yellow-throated Miner, White-plumed Honeyeater, and Southern Whiteface, also nested in winter, though to a lesser extent. The Emu, Black Honeyeater and Red-capped Robin, were only recorded nesting in winter. The breeding effort of most species

increased or remained steady after the drought, but the resident Chestnut-rumped Thornbill and Striated Pardalote, which had nested in each winter and spring of the drought, were not found nesting at all during post-drought surveys.

Davies (1979) related the timing of breeding in the arid zone to the availability of food for parents rather than potential food for young. Differences in the types of foods eaten and dietary breadth of individual species (Chapter 5) could be expected to lead to differences in the timing and magnitude of species' breeding efforts and responses to rainfall. Nix (1976) suggested that breeding seasons of insectivores, nectarivores, frugivores and granivores would succeed each other, just as the stages of growth of the plants succeeded each other. In arid areas the availability of food is influenced by the amount and timing of rainfall. It is complicated by localised spatial heterogeneity, as run-on areas allow for far greater regularity of plant growth than occurs in run-off areas (Ludwig 1987). In perennial plants the timing, if not the level, of foliage, fruit and flower production, is relatively regular (Davies 1976). Short-lived plants produce vast quantities of seeds and fruit (Westoby 1980), but in contrast to perennials, the timing and level of their production is more directly tied to short-term rainfall fluctuations.

At Peery, patterns in overall breeding effort supported Schodde's (1982) suggestion that most arid zone species are spring breeders, but the breeding effort and probably productivity are modified by local conditions. Spring breeding probably predominated at Peery because, in the study area, this was the period of maximum food availability for most species. For resident species that fed in perennial plants in relatively mesic areas, the timing of food production was fairly regular. Birds with generalised feeding habits, such as the White-plumed Honeyeater (Chapter 5), were able to nest in winter and spring. For nomads however, breeding followed rainfall more closely as nomads tend to move out of areas of drought and congregate in areas with more favorable conditions. At Peery, the greater nesting effort by nomads in spring than autumn after the drought may simply have reflected the greater availability in spring of food suitable for the nomadic species present at the site.

Within this local study, the varied breeding patterns of individual species with different dietary requirements supported Nix's (1976) conclusion that reproduction is ultimately determined by the timing and availability of food. Given the varied diets and

movement patterns of different species, and the variability in the timing and regularity of plant production that occurs between different plant life forms within regions and between regions within the arid zone (Zann *et al.* 1995), it is probably not surprising that generalisations made about the breeding of arid zone birds have appeared contradictory.

6.3 Incidence of cooperative breeding at the Peery site

6.3.1 Introduction

Cooperative breeding occurs when individuals other than the breeding pair contribute to the care of nestlings or fledglings or both (Clarke 1984, Ford *et al.* 1988). Brown's (1987) list of known cooperative breeders included only 222 of the approximately 9000 bird species of the world. Recent studies, e.g., Aston (1988), Rowley & Russell (1993), Sandbrink & Robinson (1994), have revealed only a few additional cooperative species. Currently eighty cooperatively breeding species are known to occur in Australia (Clarke 1995) and by world standards the incidence of cooperative breeding is high, particularly among birds of eucalypt and semi-arid woodlands (Ford *et al.* 1988) and passerines of old endemic families (Russell 1989).

A number of ecological factors have been implicated to explain this high incidence: the generally equable conditions and consequently low fluctuations in resource levels (Thomas 1974, Dow 1980, Ford *et al.* 1988) the arid climate (Harrison 1969) and harsh conditions which require rapid population increases in limited periods of favourable conditions (Rowley 1968, 1976), and vulnerability to predation (Ford *et al.* 1988). Recent advances in phylogenetic taxonomy (Sibley & Ahlquist 1985, Christidis & Schodde 1991) have prompted investigation of cooperative breeding in a phylogenetic context. Russell (1989) and Edwards & Naeem (1993) found that cooperative breeding is not randomly distributed among genera and may be ancient in some lineages. Russell (1989) concluded that cooperative breeding is an ancient trait that has persisted in Australian birds. She noted the high level (22%) of cooperative breeding in Australian passerines of old endemic families (parvorder Corvi). None of the more recent passerine arrivals (parvorder Muscicapae) breed cooperatively and the overall incidence world-wide for passerines is 3%. Cooperative breeding may thus be a

consequence of past, rather than present, ecological factors and may not necessarily be as advantageous to birds today as it was to their ancestors (Dow 1980).

In this section I consider the incidence of cooperative breeding overall and among breeding birds in an arid environment that is variable from year to year, generally unpredictable, but also to some extent seasonal. I compare this incidence with that reported from communities in other arid and more mesic Australian environments. I compare the frequency of cooperative breeding in different movement, foraging and dietary groups and compare my findings with those of Ford *et al.* (1988) from more mesic north-eastern New South Wales. Finally, I compare the population trends during the study of resident species that have been identified as cooperative breeders with those of residents that are non-cooperative breeders.

6.3.2 Methods

The study site is described in Chapter 2. Classification of species as cooperative or non-cooperative breeders was based on records summarised in Clarke (1995) and opportunistic observations made at nests within the study site. A species was considered to be cooperative if more than two adults were confirmed feeding a group of nestlings or fledglings. Breeding birds were classified according to their movement status at the study site (Chapter 3), foraging substrate and method (Chapter 5), and diet (Section 6.2.3.1, this chapter). *Chi*-square analysis was used to test the significance of differences between cooperative and non-cooperative breeders in each of these factors.

6.3.3 Results

6.3.3.1 Incidence of cooperative breeding among breeding birds and all birds

Eighteen of the 51 breeding species (35.3%) at the study site were classified as cooperative breeders (Table 6.3.1). Cooperative breeding at the site was confirmed in four species: Chestnut-crowned Babbler, White-winged and Variegated Fairy-wrens, and Apostlebird, and

Table 6.3.1. Incidence of cooperative breeding among breeding birds.

Status: **R** resident, **N** nomad, **S** spring-summer migrant, **W** winter migrant.

Bird Species	Breeding System	Status at site	Diet Type	Foraging Substrate	Foraging Method
Emu	non	R	Seed	Ground	Glean
Collared Sparrowhawk	non	R	Carnion/prey	Carrion/prey	Hunt
Australian Kestrel	non	R	Carnion/prey	Carrion/prey	Pounce
Little Button-quail	non	N	Seed	Ground	Glean
Diamond Dove	non	N	Seed	Ground	Glean
Crested Pigeon	non	R	Seed	Ground	Glean
Galah	non	R	Seed	Ground/fruit	Glean
Little Corella	non	R	Seed	Ground/fruit	Glean
Cockatiel	non	N	Seed	Ground	Glean
Budgerigah	non	N	Seed	Ground/fruit	Glean
Mallee Ringneck	non	R	Seed	Ground/fruit	Glean
Mulga Parrot	non	R	Seed	Ground	Glean
Blue Bonnet	non	R	Seed	Ground	Glean
Spotted Nightjar	non	R	Insect	Air	Hawk
Red-backed Kingfisher	non	S	Insect	Ground	Pounce
Sacred Kingfisher	non	S	Insect	Ground	Pounce
Rainbow Bee-eater	coop	S	Insect	Air	Hawk
Brown Treecreeper	coop	R	Insect	Ground/bark	Glean
Variegated Fairy-wren	coop	R	Insect	Foliage	Glean
White-winged Fairy-wren	coop	R	Insect	Foliage	Glean
Spiny-cheeked Honeyeater	non	R	Mixed	Flower/foilage	Glean
Yellow-throated Miner	coop	R	Mixed	Flower/foilage	Glean
Singing Honeyeater	non	R	Mixed	Flower/foilage	Glean
White-plumed Honeyeater	coop	R	Mixed	Flower/foilage	Glean
Black Honeyeater	non	N	Mixed	Flower/foilage	Glean
Crimson Chat	non	N	Insect	Ground	Glean
Orange Chat	non	N	Insect	Ground	Glean
Striated Pardalote	coop	R	Insect	Foliage	Glean
Chestnut-rumped Thornbill	coop	R	Insect	Foliage	Glean
Yellow-rumped Thornbill	coop	R	Insect	Ground	Glean
Southern Whiteface	coop	R	Insect	Ground	Glean
Red-capped Robin	non	W	Insect	Ground	Pounce
Chestnut-crowned Babbler	coop	R	Insect	Ground	Glean
Grey Shrike-thrush	non	R	Insect	Ground/bark	Glean
Australian Magpie-lark	coop	R	Insect	Ground	Glean
Willie Wagtail	non	R	Insect	Ground/air	Snatch
Black-faced Cuckoo-shrike	non	R	Insect	Foliage	Snatch
White-winged Triller	non	S	Insect	Foliage	Snatch
White-breasted Woodswallow	coop	S	Insect	Air	Hawk
White-browed Woodswallow	non	N	Insect	Air	Hawk
Black-faced Woodswallow	coop	R	Insect	Ground/air	Hawk
Pied Butcherbird	coop	R	Carnion/prey	Carrion/prey	Hunt
Australian Magpie	coop	R	Insect	Ground	Glean
Australian Raven	non	R	Carnion/prey	Carrion/prey	Glean
Little Crow	non	R	Carnion/prey	Carrion/prey	Glean
White-winged Chough	coop	R	Insect	Ground	Glean
Apostlebird	coop	R	Insect	Ground	Glean
Tree Martin	non	R	Insect	Air	Hawk
Fairy Martin	non	N	Insect	Air	Hawk
Rufous Songlark	non	N	Insect	Ground	Glean
Zebra Finch	non	N	Seed	Ground	Glean

suspected in a number of others. Four species, Little Friarbird, Weebill, Ground Cuckoo-shrike and Grey Butcherbird, which occurred infrequently and in low numbers (Chapter 3), but did not breed at the site, are known cooperative breeders (Clarke 1995). Overall, 23.2% (22/95) of all birds recorded at the site were known to be cooperative breeders.

6.3.3.2 Comparison of cooperatively and non-cooperatively breeding species within the breeding avifauna (Table 6.3.2)

6.3.3.2.1 Movement status

Cooperatively breeding species tended to be residents (*chi-squared* = 8.07, d.f. = 2, $p < 0.05$) rather than nomads or migrants. The only non-residents to breed cooperatively were two spring-summer migrants, the Rainbow Bee-eater and White-breasted Woodswallow.

6.3.3.2.2 Diet

Cooperative breeders tended to feed on insects and other arthropods (*chi-squared* = 10.53, d.f. = 3, $p < 0.05$). None of the seed-eaters, which included all parrots, pigeons and the Zebra Finch and Little Button-quail, breed cooperatively.

6.3.3.2.3 Foraging substrate

Data were insufficient to allow for comparison between each of the eight foraging substrate types. However, species which fed predominantly on the ground could be compared with above ground feeders. Initially, species were classified as ground feeders if ground comprised at least 30% of total substrate use (Chapter 5). A second comparison was made in which the criterion for ground feeding was at least 50% use of ground. Comparisons, using both criteria, were not significant ($p > 0.05$), either for all species or only for insectivorous species.

Table 6.3.2. **Comparison of cooperative and non-cooperative species.**

Numbers in table are number of breeding species.

	MOVEMENT STATUS:							
	Resident	Nomadic	Summer	Winter				
Cooperative	16	0	2	0				
Non-cooperative	18	11	3	1				
	DIET:							
	Insect	Plant	Mixed	Carrion/prey				
Cooperative	15	0	2	1				
Non-cooperative	14	12	3	4				
	FORAGING SUBSTRATE:							
	Ground	Ground/ fruit	Ground/ bark	Ground/ air	Foliage	Foliage/ flower	Air	Carrion/ prey
Cooperative	7	0	1	1	4	2	2	1
Non-cooperative	14	4	1	1	2	3	4	4
	FORAGING METHOD:							
	Glean	Hunt	Hawk	Snatch	Pounce			
Cooperative	14		3	0	0			
Non-cooperative	20		4	3	5			

6.3.3.2.4 Foraging method

Comparison of species which actively pursued prey (glean, hunt or hawk) with those that fed more passively by sitting and waiting until prey was sighted (snatch, pounce) indicated a significant ($\chi^2 = 5.18$, d.f. = 1, $p < 0.05$) tendency for cooperative breeders to be active feeders. In fact, all cooperative breeders were active feeders.

6.3.4 Discussion

Cooperative breeding was confirmed in only four of the 18 known cooperative breeders which nested at the study site. Confirmation of cooperative breeding was hampered by an inability to recognise individuals, apart from a small number of colour-banded birds, and a lack of detailed observation at most nests. However the nests of a number of species classified as cooperative breeders were watched closely, but evidence of cooperative breeding was not found. Du Plessis *et al.* (1995) found differences in the ecological characteristics of obligate and facultative cooperative breeding species in South African birds. They found that obligate cooperative breeders occur mainly in habitats with predictable seasonal peaks in food supply while facultative cooperative breeders live mainly in unpredictable habitats with the greatest variability in both the timing and amount of rainfall. Many of the species classified as cooperative breeders at Peery appear to be facultative rather than obligate cooperative breeders and this fits the pattern found in South Africa.

Confirmed cooperative breeders included the Chestnut-crowned Babbler.

Cooperative breeding had previously been suspected in the Chestnut-crowned Babbler because the other babblers breed cooperatively (Dow 1980), but had not been confirmed before this study. More than two adult Chestnut-crowned Babblers fed young in a nest on four occasions, in spring and winter 1991 (Smith 1992, Appendix 6.3.1) and in spring 1992 and 1993.

Ford *et al.* (1988) found that cooperative breeding in Australian birds was most frequent in habitats of intermediate aridity, namely eucalypt forest (26.7% of all birds recorded for the habitat type) and eucalypt (21.4%) and semi-arid woodland (33.0%), and less frequent in desert (15.3%) and rainforest (7.3%). Their findings agreed with earlier studies in Africa

(Grimes 1976) and India (Gaston 1978).

Results of this study (23.2% of all birds were cooperative breeders) are in keeping with the study area being intermediate between semi-arid woodland and desert. Half the breeding birds at the site that are known cooperative breeders: Rainbow Bee-eater, Brown Treecreeper, Yellow-throated Miner, White-plumed Honeyeater, Striated Pardalote, White-breasted Woodswallow, Variegated Fairy-wren and Chestnut-rumped Thornbill, were closely associated with, and fed in, the relatively mesic run-on areas of the study site (Chapter 4). The remainder fed in both run-on and run-off areas.

Cooperative breeding at Peery was confined to residents and regular migrants. Three woodswallows (genus *Artamus*) bred at the site. The resident Black-faced Woodswallow and migratory White-breasted Woodswallow are both cooperative breeders but the nomadic White-browed Woodswallow is not. The association of cooperative breeding with insectivory and active feeding methods lends support to the findings of Ford *et al.* (1988) in more mesic eucalypt forest and woodland. It should, however, be noted that about one third of the species included in the Peery study were common to both studies. Five honeyeaters bred in the study area and included the congeneric Singing and White-plumed Honeyeaters as well as the Spiny-cheeked and Black Honeyeaters and Yellow-throated Miner. Of these, only the two most insectivorous species, the White-plumed Honeyeater and Yellow-throated Miner, are cooperative breeders. Approximately two thirds of feeding observations made for the White-plumed Honeyeater and half of those for the Yellow-throated Miner involved foliage rather than flowers or fruit (Chapter 5). In contrast to the findings of Ford *et al.* (1988), however, cooperative breeding at Peery was not associated with a ground-feeding habit. Almost one quarter of the breeding species were ground-feeding seed-eaters, none of which bred cooperatively. Most breeding insectivorous species, whether cooperative or non-cooperative, fed on the ground. This predominance of ground feeders among the breeding avifauna reflects the diversity and extent of feeding opportunities offered by the ground substrate in this arid and open environment and, compared to more mesic environments, the rather poor above-ground resources (Chapter 5).

The association between cooperative breeding and sedentariness suggests that cooperative breeding might be advantageous to birds which must endure periodic harsh

conditions. Cooperative breeding would allow families to stay together when resources were scarce. Of 20 breeding resident insectivores, 15 were cooperative and five non-cooperative. These birds endured a severe drought between 1991 and 1992 and populations of all but the White-plumed Honeyeater, Spotted Nightjar and Grey Shrike-thrush decreased (Table 6.3.3). A comparison of the magnitude of population declines between cooperative and non-cooperative insectivores revealed that neither group fared better than the other (Kruskal-Wallis, $H = 0.81$, d.f. = 1, $p = 0.37$). Moreover, cooperative and non-cooperative breeders did not differ in the number of survey periods in which they bred (Kruskal-Wallis, $H = 1.10$, d.f. = 1, $p = 0.29$). In the time frame of this study, the benefits of cooperative breeding, or at least the potential to breed cooperatively, were not apparent at the population level.

Presumably cooperative breeding has evolved either because individuals that delay breeding and dispersal and help their parents (or occasionally others) have a higher fitness in their lifetime than those that disperse and attempt to breed in their first year or because dispersing and breeding is not an option, due to a lack of breeding habitat. A phylogenetic explanation and assumption that cooperative breeding may be a consequence of past, rather than present, ecological factors does not fully account for the distribution of cooperative breeding. Members of the same genus, for example the woodswallow genus *Artamus* and honeyeater genus *Lichenostomus*, differ. Australia-wide, most old endemic passerines are not cooperative breeders. At Peery, the incidence of cooperative breeding among breeding passerines of old endemic families is 52% (17/33) compared with 22% Australia-wide (Russell 1989). This high incidence supports Ford *et al.*'s (1988) proposal that aseasonal but unpredictable environments favour a cooperative breeding strategy. Clarke (1995) reviewed the range of hypotheses relating to why birds breed cooperatively, many of which have yet to be rigorously tested. Hypotheses need to explain why the incidence of cooperative breeding is so high among birds, particularly sedentary insectivores, of aseasonal but unpredictable environments.

Table 6.3.3 Comparison of cooperative and non-cooperative breeding resident insectivores.
Densities are mean densities in study area as determined in censuses (Chapter 3). Numbers of breeding records are given for each species in each survey period.

	Density (no./10ha)		% change	Nests recorded in each survey period							
	Sp 90	Sp 93		Sp 90	Wi 91	Sp 91	Wi 92	Sp 92	Au 93	Wi 93	Sp 93
COOPERATIVE BREEDERS											
Brown Treecreeper	3.5	1.3	-62.9	3		3		2			4
Variegated Fairy-wren	5.0	2.9	-42.0	3		3		2			6
White-winged Fairy-wren	3.4	1.8	-47.1	3		1		1			3
Striated Pardalote	0.4	0.1	-75.0	2		3	3	2			
Chestnut-rumped Thornbill	4.4	0.3	-93.2	3	2	3	1	3			
Yellow-rumped Thornbill	4.5	0.5	-88.9	2	1		1	3		2	3
Chestnut-crowned Babbler	5.3	3.4	-35.9	1	1	1		2		1	4
Black-faced Woodswallow	0.9	0.3	-66.7					3			2
Australian Magpie	0.9	0.6	-33.3	3				3			7
White-winged Chough	0.8	0.4	-50.0	1				1			1
Apostlebird	11.2	5.1	-54.5	3	1			1			8
White-plumed Honeyeater	22.4	33.6	50.9	5	4	2	9	19	5	12	23
Yellow-throated Miner	9.1	7.7	-15.4	2	1			5		6	8
Southern Whiteface	4.4	0.8	-81.8	2	2		2	7		2	4
Australian Magpie-lark	5.2	1.7	-67.3	5				7			9
NON-COOPERATIVE BREEDERS											
Spotted Nightjar	0	0.04									1
Grey Shrike-thrush	1.0	1.2	20.0					2	1		
Willie Wagtail	10.4	4.9	-52.9	12		11		21		1	22
Black-faced Cuckoo-shrike	1.3	1.0	-30.0	4				4			2
Tree Martin	57.3	18.2	-68.2	14		10		16			22

6.4 Nesting resources - nest sites

6.4.1 Introduction

Successful nesting is dependent on the availability of suitable nest sites and building materials (Recher 1991). Though some species, for example, the White-browed Woodswallow (Recher & Schulz 1985), are flexible in their choice of nest sites, others, including both hole (Saunders *et al.* 1982, Noske 1985) and open (Martin & Roper 1988) nesting species, have more specific needs. Factors which determine suitability of nest sites include nest plant species (Middleton 1979), nest height and concealment (Best & Stauffer 1980, Nias 1986) and nest cavity characteristics (Korol & Hutto 1984, Rendell & Robertson 1989).

Knowledge of the resources used by nesting birds is necessary for their effective management and conservation. In this section I describe the nest sites of birds breeding in the study area and identify important nesting habitats and plant species.

6.4.3 Methods

The study site is described in Chapter 2. I searched for nests while censusing (Chapter 3) and collecting habitat, foraging and drinking data (Chapter 4, 5, 7) in spring 1990, winter and spring 1991, 1992 and 1993, autumn 1993 and summer 1993/94. For each active nest located I recorded the species of nesting bird, broad habitat type, type of nest, nest plant species, plant height (to the nearest metre), and plant health, and nest height. Nest types included open (nest of vegetative matter attached to foliage or branch of tree or shrub), natural hollow, ground (in open, under cover or in tunnel) and mud nests, as well as vacant nests of other species.

6.4.3 Results

6.4.3.1 Nest records

A total of 504 active nests deriving from 48 of the 51 breeding species at the study site was

recorded (Table 6.4.1). Nests were located for 32 residents, 10 nomads, five spring-summer migrants and one winter migrant. The three species known to be breeding at the site, but for which nests were not located, were the Mallee Ringneck, Mulga Parrot and Orange Chat.

6.4.3.2 Use of habitats for nesting

Most individuals and species nested in run-on habitats (Table 6.4.1). Sixty-one per cent of nests were located in the narrow strips of eucalypt woodland which fringed major creeklines and 28% of nests were associated with minor creeklines. Forty-two species nested in run-on areas and 23 of these nested only in run-on areas. In comparison, 22 species nested in run-off areas and nests of only seven species were restricted to run-off areas. Most generalized in their use of habitats for nesting were the Crested Pigeon, Spiny-cheeked Honeyeater and Australian Magpie, which nested in each habitat type. Even these species nested more in run-on than run-off areas.

6.4.3.3 Nest types

Most birds constructed open nests (45% of breeding species) or were obligate hollow (28%) nesters (Table 6.4.2). A smaller number built mud nests in trees (8%) or nested at ground level (12%). Ground nesting species included the Emu and Spotted Nightjar which laid on bare ground or rudimentary mats of vegetation, the Little Button-quail and Rufous Songlark which concealed grassy nests in dense ground-layer vegetation, and the Red-backed Kingfisher and Rainbow Bee-eater which nested at the end of tunnels a metre or more in length (Beruldsen 1980). All nest tunnels located for the Red-backed Kingfisher and Rainbow Bee-eater were within 25m of trees or shrubs in which they frequently perched. Most varied in the siting of their nests were the woodswallows and Zebra Finch. The Zebra Finch and Black-faced Woodswallow built grassy nests in dense foliage and in hollows, while the White-browed and White-breasted Woodswallows built in tree forks, dense foliage, hollows and vacant mud nests.

Table 6.4.1. **Occurrence of nests in broad habitat types.** * indicates likely location of nests of the Mallee Ringneck, Mulga Parrot and Orange Chat, which bred at the site, but for which no nests were located.

NESTING SPECIES	HABITAT TYPE				TOTAL
	run-off	run-on			
	open plains	with trees/ shrubs	minor creek	major creek	
Emu	2			2	4
Collared Sparrowhawk				2	2
Australian Kestrel			3		3
Little Button-quail	1				
Diamond Dove			1	3	4
Crested Pigeon	2	1	5	2	10
Galah			1	10	11
Little Corella				7	7
Cockatiel				5	5
Budgerigah			13	45	58
Blue Bonnet		1			1
Spotted Nightjar			1		1
Red-backed Kingfisher			1		1
Sacred Kingfisher				1	1
Rainbow Bee-eater				4	4
Brown Treecreeper				8	8
Variegated Fairy-wren			4	3	7
White-winged Fairy-wren	1		3		4
Spiny-cheeked Honeyeater	1	1	5	1	8
Yellow-throated miner		6	9	1	16
Singing Honeyeater		2			2
White-plumed Honeyeater			12	25	37
Black Honeyeater		1			1
Crimson Chat	6	2			8
Striated Pardalote			3	1	4
Chestnut-rumped Thornbill		2	3		5
Yellow-rumped Thornbill	2		1		3
Southern Whiteface	8		8		16
Red-capped Robin		1			1
Chestnut-crowned Babbler		1	8		9
Grey Shrike-thrush				2	2
Australian Magpie-lark		1	7	11	19
Willie Wagtail		1	17	34	52
Black-faced Cuckoo-shrike			4	1	5
White-winged Triller			4		4
White-breasted Woodswallow		1	1	7	9
White-browed Woodswallow				7	7
Black-faced Woodswallow			2	1	3
Pied Butcherbird		1	1	1	3
Australian Magpie	1	2	5	2	10
Little Crow/Australian Raven			3	3	6
White-winged Chough				1	1
Apostlebird		3	7	14	24
Tree Martin				66	66
Fairy Martin				33	33
Rufous Songlark		1	1	3	5
Zebra Finch	1		10	2	13
Mallee Ringneck				*	
Mulga Parrot			*	*	
Orange Chat	*				
TOTAL RECORDS	25	28	143	308	504
TOTAL SPECIES	10	17	29	32	51

Table 6.4.2 **Nest types of breeding species.** Nest site type classifications were derived from observations within the study area and its surrounds.

NEST TYPE	NO. SPECIES	SPECIES
GROUND:		
In open	2	Emu, Spotted Nightjar
Under cover	2	Little Button-quail, Rufous Songlark
Tunnel	2	Red-backed Kingfisher, Rainbow Bee-eater
HOLLOW:		
Tree	4	Galah, Little Corella, Cockatiel, Budgerigar, Blue Bonnet, Sacred Kingfisher, Brown Treecreeper, Striated Pardalote, Chestnut-rumped Thornbill, Southern Whiteface, Grey Shrike-thrush, Tree Martin, Mallee Ringneck, Mulga Parrot
OPEN:		
Trees/low trees	4	Collared Sparrowhawk, Australian Kestrel, Crested Pigeon, Yellow-throated Miner, Yellow-tailed Thornbill, Red-capped Robin, Chestnut-crowned Babbler, Black-faced Cuckoo-shrike, Black-faced Woodswallow, Pied Butcherbird, Australian Magpie, Little Crow, Australian Raven
Shrubs	4	White-winged Fairy-wren, Singing Honeyeater, Crimson Chat, Orange Chat
Trees /low trees/shrubs	5	Diamond Dove, Variegated Fairy-wren, Spiny-cheeked Honeyeater, White-plumed Honeyeater, Willie Wagtail
MUD NESTS:	4	Australian Magpie-lark, White-winged Chough, Apostlebird, Fairy Martin
VARIED NESTS:		
Hollow /open	2	Black-faced Woodswallow, Zebra Finch
Hollow/ open /old mud nests	2	White-breasted Woodswallow, White-browed Woodswallow
TOTAL	51	

6.4.3.4 Plant species as nest sites

All birds nested in trees and/or shrubs, apart from the Fairy Martin, which nested in mudnests attached to creekbanks, and six ground-nesting species. Nest plants comprised one mistletoe, eight tree, six low tree and 10 shrub species (Appendix 6.4.1). All nest plants, apart from *Haloragis pergranulata*, *Sclerolaena divaricata* and *S. intricata*, were perennials. These three are annual sub-shrubs and were most abundant in spring 1993 after the drought, when they provided nest sites for the Crimson Chat and Variegated and White-winged Fairy-wrens.

Open nesting species were most diverse in their use of nest plants (Table 6.4.3), though they made heavy use of certain trees and shrubs relative to their abundance at the site. Trees favoured by open nesters were Whitewood and Black Box and favoured shrubs included Harlequin Eremophila, Broad-leaf Hopbush, and Black Bluebush. Open nesters avoided dead trees but dead shrubs were well used.

Six species of live trees and dead trees provided nest hollows. River Red Gum provided most hollows and its importance was disproportionate to its abundance at the site. Species ranging in size from the Southern Whiteface (~12 g) to the Little Corella (~700g) nested in River Red Gum hollows. Hollows in dead trees were less widely used, but were important to the Budgerigar, Southern Whiteface and Tree Martin. Dead spouts in live trees provided almost half the nest sites of Budgerigars (21/47) and all sites of Cockatiels (4). Eucalypts were not the only source of nest hollows. Hollows in Whitewood were used by the Budgerigar, Galah and Southern Whiteface. On one occasion a pair of Southern Whiteface nested in a Beefwood hollow.

The Australian Magpie-lark, Apostlebird and White-winged Chough built their mud nests only in trees and, like open nesters, favoured Whitewood and Black Box. The low number of nests found for the varied hollow/open/mud nesters made it difficult to discern any plant species preferences for them. All hollow nests located for these birds were in River Red Gums.

Table 6.4.3 Relative use of plant species as nest sites by the four main nesting types of birds.
 Figures in the table are percentages. % occurrence of trees/shrubs refers to their relative abundance in census transects (Chapter 3).

<u>PLANT SPECIES</u>	<u>% OCCURRENCE OF TREES SHRUBS</u>	<u>NESTING TYPE</u>			
		<u>Hollow</u> (n=180)	<u>Open</u> (n=119)	<u>Mud</u> (n=44)	<u>Hollow/open & Hollow/open/mud</u> (n=29)
TREES					
Mulga <i>Acacia aneura</i>	6.0		2.5		
River Cooba <i>Acacia stenophylla</i>	15.5		12.6	2.3	6.9
Prickly Wattle <i>Acacia victoriae</i>	1.2		3.4		10.3
Rosewood <i>Alectryon oleifolius</i>	2.0		4.2		
Whitewood <i>Atalaya hemiglauca</i>	16.8	2.8	40.3	34.1	6.9
Belah <i>Casuarina pauper</i>	<0.1		1.7	4.5	
River Red Gum <i>Eucalyptus camaldulensis</i>	23.4	60.6	29.4	29.6	48.3
Red Box <i>Eucalyptus intertexta</i>	0.1	0.6			10.3
Black Box <i>Eucalyptus largiflorens</i>	12.7	13.9	28.6	22.7	
Bimble Box <i>Eucalyptus populnea</i>	0.6	5.0	1.7		
Leopardwood <i>Flindersia maculosa</i>	0.1		0.8		
Beefwood <i>Grevillea striata</i>	2.0	0.6	0.8	6.8	
Weeping Pittosporum <i>Pittosporum phylliraeoides</i>	0.5		0.8		
Santalum <i>Santalum lanceolatum</i>	0.7		0.8		
Dead tree	17.7	16.7	0.8		20.7
SHRUBS					
			(n=27)		
Broad-leaf Hopbush <i>Dodonaea viscosa</i>	<0.1		7.4		
Harlequin Eremophila <i>Eremophila dumosa</i>	2.5		11.1		
Black Bluebush <i>Maireana pyramidata</i>	1.0		7.4		
Lignum <i>Muehlenbeckia florulenta</i>	12.8		11.1		
Boobialla <i>Myoporum montanum</i>	49.0		29.6		
Spiny Fan-flower <i>Scaevola spinescens</i>	0.4		3.7		
Dead shrub	19.3		29.6		

6.4.3.5 Nest height

Data on nest heights indicated the vegetation layers in which species nested (Table 6.4.2), but did not indicate any height preferences within these layers.

6.4.3.6 Repeated use of nest sites

Several birds nested in existing, used nests rather than building new ones. Birds which re-used nests of their own species were the Chestnut-crowned Babbler (same nest used in spring 1991, 1992, 1993), Yellow-rumped Thornbill (spring 1990, 1992, winter and spring 1993) and White-winged Chough (spring 1990 and 1992). Hollows were re-used by the Southern Whiteface (same hollow used in spring 1990, winter and spring 1992, spring 1993), Chestnut-rumped Thornbill (winter and spring 1991) and Tree Martin (spring 1992, 1993). Of the birds re-using nests, only one pair of Tree Martins was individually marked. This pair fledged young from the same hollow in a Black Box in spring 1992 and 1993.

Vacant nests of other species were used by the White-browed Woodswallow (Australian Magpie-lark and Apostlebird nests), the White-breasted Woodswallow (Australian Magpie-lark nest), Chestnut-rumped Thornbill (the same Fairy Martin nest in winter and spring 1991) and Australian Kestrel (same corvid nest used in spring 1990, 1992). In spring 1992 Yellow-rumped Thornbills built a nest within the base of the corvid nest occupied simultaneously by Australian Kestrels.

6.4.4 Discussion

Forty-four of the 51 breeding birds in this study built their nests in the foliage, branches or hollows of trees or shrubs. On the open plains 22 of the 25 nests located were in the isolated trees and shrubs which dot these areas. The reliance of these birds on trees and shrubs for nest sites stands in contrast to their feeding habits. More than half the breeding birds were ground feeders (Chapter 5) and the trees and shrubs in which ground feeders nested supplied little, if any, of their foraging sites.

The concentration of nests in the relatively small strips of creekline habitat within the study area emphasised the importance of creeklines as nesting sites in arid areas. Creekline habitats provide a greater variety and number of nest sites than do run-off areas. Trees and shrubs are denser and structurally and floristically more diverse in creekline habitat than in run-off areas (Chapter 3). Several favoured nest plant species, including River Red Gum and Black Box, are associated with creeklines and their supplies of subterranean water. Physical features of creeklines provide nesting opportunities lacking in run-off habitats. Creek banks, for example, provided building sites for the Fairy Martin, Red-backed Kingfisher and Rainbow Bee-eater. Holes scoured in creekbeds often hold water for several weeks after rain and their muddy rims supply building material for the Fairy Martin, Apostlebird, Australian Magpie-lark and White-winged Chough.

Birds nested in a range of plant species but certain plants were especially important, e.g. River Red Gums for hollow nesters, and Whitewood and Black Box for open and mud nesters. Mature River Red Gum hollows had varied capacities and entrance sizes and were thus suitable for birds of varied size (Recher 1991). Tree Martins increased the number of hollows available to them by partially plugging hollow entrances with mud to achieve a preferred entrance size. Reducing the entrance size presumably has the effect of excluding larger hollow-nesting birds. Whitewood and Black Box may have been preferred by Apostlebirds and Australian Magpie-larks because their branches provided suitable attachment points for mud nests. Their rough bark is probably better than smooth bark (as found on the River Red Gum) for attachment. Open nesting species may have selected nest plants on the basis of their height and foliage density and arrangement. The preference of open nesters for Harlequin Eremophila, Broad-leaf Hopbush and Black Bluebush may be related to a need for shelter and protection. These shrubs have dense foliage and a compact habit. Characteristics of nest hollows of a number of arid zone birds have been described by Saunders *et al.* (1982), Rowley (1990) and Rowley & Chapman (1991). Characteristics of trees and shrubs which make them suitable for open and mud nesters warrant similar study.

In arid areas fidelity to a nest site would assist birds to respond quickly to irregular and limited periods in which conditions were favourable for nesting. An attachment of individuals to a specific nest site was demonstrated for Tree Martins and has been shown

elsewhere for a number of species, including the Yellow-rumped Thornbill (Ford 1963), Wedge-tailed Eagle (Hughes & Hughes 1984), Galah (Rowley 1990), Pink Cockatoo (Rowley & Chapman 1991) and Rainbow Bee-eater (Lill 1993). Further banding studies are needed to determine if individual attachments were formed by other species re-using nests in the study area.

6.5 General discussion

In this study, breeding occurred pre dominantly in spring rather than winter, but there was considerable variation in the magnitude and timing of the breeding effort of individual species. The breeding effort in each year was modified by prevailing site conditions and drought greatly reduced the numbers of individuals and species breeding.

Residents tended to be predictable spring breeders and small numbers attempted to breed even during the drought. Several residents, including the White-plumed Honeyeater and Yellow-throated Miner, nested in winter as well as spring. The tendency to breed regularly could be related to the generalized or opportunistic feeding habits of residents (Chapter 5). Residents use a wide range of foods that are supplied largely by perennial trees and shrubs. In perennials the timing, if not the level, of production of flowers, fruits and foliage, and possibly invertebrate populations, is relatively regular. Davies (1973) pointed out that the regular occurrence of food resources would lead to the evolution of regular breeding seasons. A further factor promoting regular breeding in residents, especially those that are insectivorous, could be their tendency to breed cooperatively. Cooperative breeding behaviour would enable them to receive help and thus make it feasible to attempt nesting even if food was scarce.

The breeding season of nomads was less predictable than that of residents. Their greater mobility allows them to capitalise on good nesting opportunities over a wide geographic area. Nomads bred in the study area only when conditions were good and presumably there was an abundance of available food. Nomads tend to be more specialised feeders than residents and, especially for the many which concentrate on the seeds of short-lived plants, their food supplies fluctuate more widely. For nomads, the availability of food is dependent on the amount and timing of rainfall and the lag period between when rain falls and when foods, such

as seeds, are produced. None of the nomads in this study breed cooperatively. It would not be worthwhile for them to attempt breeding unless food was sufficiently abundant that the parents alone could rear young. Suitable nest sites for several nomadic species were only available when site conditions were good. The Little Button-quail, Rufous Songlark and Crimson Chat, for example, nested in the dense, ground-layer vegetation or low, short-lived shrubs that only occurred after the good rains of summer 1993/94.

Like nomads, the breeding effort of migrants is influenced by conditions beyond the study area. The breeding effort appeared to be relatively consistent over the study period, but was too low to discern definite patterns other than perhaps the general unsuitability of this environment for migratory as opposed to resident or nomadic life styles.

Appendix 6.2.1. BREEDING RECORDS. Numbers in table are number of breeding records for each species in each survey period. Status of birds: **R** resident, **N** nomad, **S** spring-summer migrant, **W** winter migrant. Diet: **P** plant, **C** carrion/live vertebrates, **A** aerial invertebrates, **O** other invertebrates, **M** mixed (plant and invertebrates).

Species	Status/ Diet	Sp. 90	Wi. 91	Sp. 91	Wi. 92	Sp. 92	Au. 93	Wi. 93	Sp. 93	Su. 93/94	TOTAL
Emu	R;P				1			3			4
Collared Sparrowhawk	R;C			1					1		2
Australian Kestrel	R;C	2				2					4
Little Button-quail	V;P								1		1
Diamond Dove	V;P								4		4
Crested Pigeon	R;P	1				3			6	2	12
Galah	R;P	2				7		3	3		15
Little Corella	R;P							3	4		7
Cockatiel	V;P					1			5		6
Budgerigah	V;P					5			53		58
Mallee Ringneck	R;P		1						3		4
Mulga Parrot	R;P					2					2
Blue Bonnet	R;P								4		4
Spotted Nightjar	R;A								1		1
Red-backed Kingfisher	S;O	1									1
Sacred Kingfisher	S;O	1									1
Rainbow Bee-eater	S;A	1		3					1		5
Brown Treecreeper	R;O	3		3		2			4		12
Variegated Fairy-wren	R;O	3		3		2			6		14
White-winged Fairy-wren	R;O	3		1		1			3		8
Spiny-cheeked Honeyeater	R;M	6				5		1	3		15
Yellow-throated Miner	R;M	2	1			5		6	8		22
Singing Honeyeater	R;M			1		1		3			5
White-plumed Honeyeater	R;M	5	4	2	9	19	5	12	23		79
Black Honeyeater	V;M							1			1
Crimson Chat	V;O								14		14
Orange Chat	V;O								1		1
Striated Pardalote	R;O	2		3	3	2					10
Chestnut-rumped Thornbill	R;O	3	2	3	1	3					12
Yellow-rumped Thornbill	R;O	2	1		1	3		2	3		12
Southern Whiteface	R;O	2	2		2	7		2	4		19
Red-capped Robin	W;O							1			1
Chestnut-crowned Babbler	R;O	1	1	1		2		1	4		10
Grey Shrike-thrush	R;O					2	1				3
Australian Magpie-lark	R;O	5				7			9		21
Willie Wagtail	R;O	12		11		21		1	22	4	71
Black-faced Cuckoo-shrike	R;O	4				4			2	2	12
White-winged Triller	S;M	4							2		6
White-breasted Woodswallow	S;A	2		2		6			3	1	14
White-browed Woodswallow	V;A					11			4		15
Black-faced Woodswallow	R;A					3			2		5
Pied Butcherbird	R;C	3				1		1	1	1	7
Australian Magpie	R;O	3				3			7		13
Australian Raven/Little Crow	R;C			4		4		1	8		17
White-winged Chough	R;O	1				1			1		3
Apostlebird	R;O	3	1			1			8		13
Tree Martin	R;A	14		10		16			22		62
Fairy Martin	R;A	33									33
Rufous Songlark	N;O								9		9
Zebra Finch	N;P					1	6		7		14

Appendix 6.3.1 Smith, J. **COOPERATIVE BREEDING IN THE CHESTNUT-CROWNED BABBLER** *Pomatostomus ruficeps*. *Australian Birds* 25:64-66.

Cooperative breeding occurs where individuals other than parents contribute to the care of nestlings or fledglings or both (Ford *et al.* 1988). It has been recorded in only some 222 of the approximately 9000 bird species of the world (Brown 1987). By world standards the incidence of cooperative breeding in Australian birds is high, particularly in eucalypt and semi-arid woodlands (Ford *et al.* 1988).

The Chestnut-crowned Babbler *Pomatostomus ruficeps* occurs in the arid and semi-arid regions of south-eastern Australia (Blakers *et al.* 1984). It lives in flocks throughout the year. The closely related Grey-crowned Babbler *P. temporalis*, White-browed Babbler *P. superciliosus* and Hall's Babbler *P. halli* are all known to breed cooperatively (Brown 1987). Hence cooperative breeding has been considered likely in the Chestnut-crowned Babbler (Dow 1980), but has not been confirmed.

During July and October 1991 I observed Chestnut-crowned Babblers about the north-western end of Peery Lake (30° 43' S, 143° 34' E) approximately 50 km east of White Cliffs. The area was severely drought-stricken at these times. Chestnut-crowned Babblers were common in the area and were the only babblers present.

On 17 July 1991 at 08:00 hrs I observed a Chestnut-crowned Babbler nest at a height of 6 m in an 8 m tall River Red Gum *Eucalyptus camaldulensis*. The nest-tree was located in a sparse single line of River Red Gums adjacent to a dry creekbed. Four adults were feeding on sandy ground within 30 m of the nest-tree. The birds were digging into the topsoil with their beaks and extracting worms or grubs up to 5 cm long. The birds were not individually marked but I was able to note at least three individuals carrying food up and into the nest. As I watched the birds made two or three successive trips up to the nest with food. The group then appeared to switch their activity. All four birds started to collect beakfuls of short dry grassy litter from the ground. This material was carried to a second nest at a height of 7 m in a 9 m River Red Gum about 30 m farther along the same creek. I watched the birds for a further 15 minutes but they did not again carry food to the first nest.

On 13 October 1991 I observed another Chestnut-crowned Babbler nest about 3 km from the above nests. This nest was built at a height of 8 m in a 9 m Whitewood *Atalaya hemiglauc*a beside a shallow, dry drainage line. At 09:30 hrs six adult babblers were either in the nest-tree or foraging on the ground within 25 m of the nest-tree. The babblers were not individually marked. However, I was able to distinguish at least four individuals carrying food up through the tree and into the nest. On one occasion four birds were waiting about 1 m below the nest before taking food into the nest. I could clearly hear repeated begging calls of young birds in the nest when an adult approached. I watched the nest for some 15 minutes during which time the birds continued to forage nearby and carry food to the nest. I returned to the nest later in the same morning at 10:45 hrs. Six adults were feeding on the ground in a loose group within 40 m of the nest. On several occasions one or two birds moved up through the nest-tree to the nest. One bird would hop about on top of the nest and then go in and out of the nest. On one occasion four adults went up to the nest for several minutes and went in and out of the nest in turn. Begging calls of young birds within the nest could again be heard at the approach of an adult but this time the babblers did not seem to carry any food to the nest. I left the nest at 11:10 hrs.

On 17 October at 10:10 hrs I returned to the nest for some 15 minutes. No babblers approached the nest and no begging calls were heard. During the late afternoon of the same day Peter Smith watched the nest sporadically. On two occasions he noted a single bird carrying food into the nest.

These observations indicate that birds in addition to the parents help feed young in the nest and that Chestnut-crowned Babblers do at least on occasions breed co-operatively.

Appendix 6.4.1 Plant species providing nest sites for hollow, hollow/open, mud, and open nesting species. Numbers indicate numbers of nests located over study period.

NEST TYPE: HOLLOW													HOLLOW/OPEN			MUD-NEST			
NEST PLANT	Blue Bonnet	Brown Treecreeper	Budgerigar	Cockatiel	Little Corella	Chestnut-rumped T'bill	Galah	Grey Shrike-thrush	Sacred Kingfisher	Striated Pardalote	Southern Whiteface	Tree Martin	Black-faced W'swallow	White-browed W'swallow	Zebra Finch	White-breasted W'swallow	Apostlebird	Australian Magpie-lark	White-winged Chough
MISTLETOE :																			
<i>Lysiana murrayi</i>													1						
LOW TREE:																			
<i>Acacia aneura</i> (dead)	1					3													
<i>Acacia stenophylla</i>															1	1	1		
<i>Acacia victoriae</i>															3				
<i>Casuarina pauper</i>																	2		
TREE:																			
<i>Atalaya hemiglauca</i>			2			1					2		1		1		9	6	
<i>Eucalyptus camaldulensis</i>		3	34	4	7		9	2		1	1	48		2	4	8	3	10	
<i>Eucalyptus imertexta</i>			1																
<i>Eucalyptus largiflorens</i>		2	7			1		1	1	7	6		2	1			6	3	1
<i>Eucalyptus populnea</i>		2	3									4							
<i>Grevillea striata</i>											1						3		
Dead stump		1											1						
Dead tree			11	1						1	5	8		3	3				

NEST TYPE: OPEN																					
	Australian Magpie	Black-faced Cuckoo-shrike	Black Honeyeater	Crimson Chat	Chestnut-crowned Babbler	Crested Pigeon	Little Crow/Aust. Raven	Collared Sparrowhawk	Diamond Dove	Australian Kestrel	Pied Butcherbird	Red-capped Robin	Spiny-cheeked Honeyeater	Singing Honeyeater	Variegated Fairy-wren	White-plumed Honeyeater	Willie Wagtail	White-winged Triller	White-winged Fairy-wren	Yellow-throated Miner	Yellow-rumped Thornbill
NEST PLANT																					
SHRUBS :																					
Dead shrub																	7				
<i>Dodonaea viscosa</i>									2												
<i>Eremophila bignoniiflora</i> (dead)																1					
<i>Eremophila duttonii</i>													1	2							
<i>Haloragis pergranulata</i>				1											2						
<i>Maireana pyramidata</i>																			2		
<i>Muehlenbeckia florulenta</i>															1	1			1		
<i>Myoporum montanum</i>													1			7					
<i>Paspalidium constrictum</i>															1						
<i>Sclerolaena divaricata</i>				1															1		
<i>Sclerolaena intricata</i>				6											1						
LOW TREE:																					
<i>Acacia aneura</i>			1								1	1									
<i>Acacia stenophylla</i>						2			1				2			2	8				
<i>Acacia victoriae</i>						2									1		1				
<i>Acacia victoriae</i> (dead)						1															
<i>Casuarina pauper</i>						1															1
<i>Pittosporum phylliraeoides</i>						1															
<i>Santalum lanceolatum</i>																					1
TREES :																					
<i>Alectryon oleifolius</i>									1								3	1			
<i>Atalaya hemiglauca</i>	7	2			5	2	3				1		2			1	6	3		15	
<i>Eucalyptus camaldulensis</i>	3				2	1	2	2		3						6	14			1	1
<i>Eucalyptus largiflorens</i>		3									1		2			16	12				
<i>Eucalyptus populnea</i>																2					
<i>Flindersia maculosa</i>					1																
<i>Grevillea striata</i>							1														