FORAGING OF BIRDS IN EUCALYPT WOODLAND IN NORTH-EASTERN NEW SOUTH WALES

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SUMMARY

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The foraging behaviour of 40 species of birds in eucalypt woodland near Armidale is described. The foraging method, substrate, height and plant were noted for each foraging observation. Six guilds can be recognized on the basis of the substrate on which they forage. (1) Eleven species forage on the ground. This group includes two seed-eaters, and three insectivores that pounce on terrestrial invertebrates from low perches or the air. The remainder are gleaners of invertebrates. (2) Four species are bark-foragers. One is a trunk specialist, while the other three feed on upper branches, exfoliating bark and horizontal boughs respectively. (3) Foliage foragers make up the largest guild, with 13 species. Four species glean from both acacias and eucalypts. Three species mostly snatch insects from leaves whereas the rest glean from eucalypt leaves. This last group of species includes pardalotes and some honeyeaters, which feed on carbohydrate foods such as manna and honeydew as well as on arthropods. (4) There is single frugivore, specializing on mistletoe fruits. (5) The six aerial feeders include species that capture prey by hawking from a perch and others that continuously sweep through the air after insects. (6) Finally five nectarivores visit the flowers of eucalypts (three species) or mistletoe (two species)

Several very similar pairs or groups of species were identified (pardalotes *Pardalotus*, honeyeaters *Melithreptus*, thornbills *Acanthiza*). These merit more detailed study; indeed several have already been investigated.

INTRODUCTION

Studies of comparative foraging behaviour of birds have proliferated since the pioneering studies of Hartley (1953) and MacArthur (1958). Such studies have either examined a whole community in one area (e.g. Holmes *et al.* 1979; Karr 1971) or have chosen particular guilds of closely related, ecologically similar species (Feinsinger 1976; Waugh & Hails 1983). Results were often used to illustrate the role that interspecific competition plays in organizing the structure of communities (e.g. Cody 1974). Differences in foraging behaviour, and hence use of food, between species were assumed to be essential if species were to co-exist. Some workers, however, believe that the importance of competition in structuring bird communities has been overemphasized (Connell 1975; Wiens 1977). Bird populations need not be limited by resources such as food. Indeed food is usually most abundant in the breeding season, when most of the studies comparing foraging behaviour are carried out. Comparative studies of foraging behaviour should therefore be used as a starting point for our understanding of the structure of communities. At the same time, or subsequently, the abundance of food should be measured and detailed studies of individual species carried out.

Our knowledge of the foraging behaviour and community structure of Australasian birds has accumulated rapidly over the last ten years (Keast *et al.* 1985). Studies of the communities have been carried out in lowland rainforest in New Guinea (Bell 1984), rainforest in northern Queensland (Crome 1978; Frith 1984), temperate rainforest in Tasmania (Thomas 1980) and eucalypt forest in Western Australia (Wooller & Calver 1981) and southern New South Wales (Recher *et al.* 1985). Guilds that have received particular attention include honeyeaters (Keast 1968; Ford & Paton 1977; Wykes 1982), pardalotes (Woinarski & Rounsevell 1983), thornbills (Bell 1983), treecreepers (Noske 1979) and fantails (Cameron 1985).

In the present paper we describe and compare the foraging behaviour of forty bird species in eucalypt woodland on the northern tablelands of New South Wales. The behaviour of particular species is compared with that from other studies, and pairs or groups of species with similar ecology are identified.

STUDY AREA AND METHODS

Ninety percent of the observations were made at Eastwood State Forest, 10 km SE of Armidale (30°35'S, 151°44'E), and about 10% at Hillgrove Creek State Forest, 12 km E of Armidale. Both sites were dominated by stringybarks *Eucalyptus caliginosa* with Blakely's Red Gum *E. blakelyi*, Ribbon or Manna Gum *E. viminalis* and Yellow Box *E. melliodora* also common trees. *Eucalyptus melliodora* flowered each year from September to December and *E. blakelyi* flowered well in November and

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December 1982 and 1984. The only other flowers of importance to birds were mistletoes *Amyema pendulum, A. miquelii* and *Muellerina eucalyptoides.* There were *ca* 400 trees per hectare and 160–400 shrubs/ha. The latter were mostly *Acacia* and various fabaceous shrubs. Except in times of drought there was extensive ground cover of grasses and herbs. The canopy averaged 15 m in height with occasional trees up to 20 m (mostly *E. viminalis*). The study sites are described in detail elsewhere (Ford *et al.* 1985).

Armidale has a mean of 792 mm of rain annually, with November to February being the wettest months. The first half of 1981 was dry, following two years of drought, but average rain fell in the second half. Both 1982 and 1984 were wetter than average.

Foraging data were collected throughout 1981, 1982 and 1984 by HAF, from January–August 1981 by SN, and from August 1981 to February 1982 by LB. All data were combined. Observers pursued no fixed routes but followed birds as they were located.

A bird was observed until it made an apparently successful foraging attempt, e.g. captured a flying insect, pecked deliberately at a leaf or probed into a flower. A single foraging record was then taken, a second record being occasionally taken, no less than two minutes later, from the same bird. For each record we noted: the foraging method, substrate, height and plant species. Occasionally the type of food taken was recorded. The seven categories of foraging method were: glean — perched bird taking food from a substrate, probe — perched bird inserting beak at least partly into a substrate, tear — perched bird tearing at substrate to reach concealed prey, snatch — flying bird taking a prey item from a substrate, hover — similar to snatch but the bird remains stationary in the air before or while taking the prey, hawk — flying bird takes a flying insect, pounce — a bird flies or drops down from a perch to take a prey item on the ground. Similar categories were used by Recher *et al.* (1985) except that they combined probe and prise (prise = tear), had an additional method (hang-glean) and regarded nectar and seeds as methods.

The substrates were fruit, flowers, leaves, twigs, branches, trunk, ground (either grassy, bare or leaf litter) and air. The first two substrates relate to food type: fruit was seen to be swallowed, or flowers were probed in a way that suggested nectar was being consumed. Seeds should perhaps have been another category, but it was often hard to see what birds were eating when they were gleaning from the ground.

Plant species were mostly the main tree species mentioned earlier, plus mistletoes and acacias, divided into bipinnate (mostly *A. filicifolia*) and phyllodenous.

Heights of foraging observations were estimated to the nearest metre and then classed into one of six categories (0 m, 1–2 m, 3–5 m, 6–9 m, 10–14 m and 15 m+).

As only single observations were taken for most birds, the individual records should be reasonably independent. Morrison (1984) has shown that a minimum of 30 independent observations are required to provide a reliable picture of a species' foraging behaviour. We have chosen a more conservative figure of 50 because our observations were made over a long period.

For each species and each dimension we calculated niche breadth, using the Shannon-Weiner diversity index

$$H = -\Sigma P_i \log_e P_i,$$

where P_i is the proportion of all observations that belong to category i. For each pair of species for each dimension we calculated the overlap using the formula: $0 = 1 - \Sigma |P_{ij} - P_{ik}|$ where P_{ij} and P_{ik} are the proportions of all observations for species j and k that belong to category i. Average overlaps were calculated for the four dimensions; method, substrate, plant species and height for each pair of species. A dendrogram was then constructed to illustrate guilds of species that resembled each other in foraging behaviour (Cody 1974).

RESULTS

We have 50 or more observations for forty species, which are listed in Table I with weights, sample sizes for foraging observations and average density. Densities were the means from sites 1 to 3 in Ford *et al.* (1985). The best represented families were the Corvidae (*sensu* Sibley & Ahlquist 1985 including the Australian flycatchers, woodswallows, magpies — 15 species), Acanthizidae (8 species) and Meliphagidae (7 species).

Foraging Method (Table II)

Gleaning was the principal foraging method used by twenty-one species. The Chough combined gleaning with probing, among leaf litter, whereas the Red Wattlebird and Noisy Friarbird also probed into flowers. The two very small honeyeaters (Eastern Spinebill and Scarlet Honeyeater) and the Lorikeet mostly probed flowers. The other three honeyeaters also probed flowers but to a lesser extent (10–20% of observations). The Sittella and two treecreepers probed into the bark of rough-barked trees. Four species combined gleaning and snatching; the Gerygone, Cuckoo-shrike and the two whistlers. Although the Gerygone was recorded as gleaning more frequently than snatching, it foraged by moving rapidly among foliage, combining both methods. The Rosella and Shrike-tit were the only species to include tearing frequently in their repertoires. The Shrike-tit typically tore at the peeling bark of eucalypts, whereas the Rosella chewed up eucalypt fruits, presumably in search of seeds, and attacked galls on eucalypt leaves.

The two robins pounced from low perches onto the ground. They appeared to locate their prey before leaving the perch, then land near to it, pick it up and return to the perch. Where they hopped after landing on the ground, this was called gleaning. They also snatched prey from other substrates. The Restless Flycatcher showed a diverse array of foraging methods as well as employing a unique method, which should perhaps be termed a 'hover-pounce'. It frequently hovered 1–2 m above the ground, gave its scissors-grinding call, then dropped to the ground. The remaining six species mostly hunted by hawking, although a distinction could be made between the Grey Fantail and Willie Wagtail, which sallied after insects from a perch, and the hirundines, which sweep through the air. The woodswallows

TABLE I

List of species for which foraging data were presented, with weight, number of foraging records (n) and density in 1981 (from Ford et al. *1985).*

		Weight	*n*	Density no./ha
Little Lorikeet	*Glossopsitta pusilla*	45 g	50	< 0.01
Eastern Rosella	*Platycercus eximius*	110	129	0.56
Welcome Swallow	*Hirundo neoxena*	20	62	0.02
Tree Martin	*Cecropis nigricans*	20	162	< 0.01
Black-faced Cuckoo-shrike	*Coracina novaehollandiae*	130	155	0.08
Scarlet Robin	*Petroica multicolor*	13	53	0.06
Eastern Yellow Robin	*Eopsaltria australis*	20	346	0.22
Crested Shrike-tit	*Falcunculus frontatus*	24	335	0.15
Golden Whistler	*Pachycephala pectoralis*	24	300	0.06
Rufous Whistler	*P. rufiventris*	25	373	0.25
Grey Shrike-thrush	*Colluricincla harmonica*	64	191	0.17
Restless Flycatcher	*Myiagra inquieta*	24	109	0.04
Grey Fantail	*Rhipidura fuliginosa*	8	174	0.09
Willie Wagtail	*R. leucophrys*	22	192	0.10
Superb Fairy-wren	*Malurus cyaneus*	9	634	0.53
Speckled Warbler	*Sericornis sagittatus*	13	278	0.27
White-throated Gerygone	*Gerygone olivacea*	10	113	0.02
Brown Thornbill	*Acanthiza pusilla*	7	60	0.01
Buff-rumped Thornbill	*A. reguloides*	8	334	0.33
Yellow-rumped Thornbill	*A. chrysorrhoa*	10	77	< 0.01
Striated Thornbill	*A. lineata*	7	115	0.09
Varied Sittella	*Daphoenositta chrysoptera*	16	357	0.32
White-throated Treecreeper	*Climacteris leucophaea*	24	539	0.50
Brown Treecreeper	*C. picumnus*	34	285	0.19
Red Wattlebird	*Anthochaera carunculata*	125	155	0.10
Noisy Friarbird	*Philemon corniculatus*	107	123	0.09
Fuscous Honeyeater	*Lichenostomus fuscus*	18	2251	2.52
Brown-headed Honeyeater	*Melithreptus brevirostris*	15	146	0.12
White-naped Honeyeater	*M. lunatus*	15	340	0.51
Eastern Spinebill	*Acanthorhynchus tenuirostris*	12	63	0.04
Scarlet Honeyeater	*Myzomela sanguinolenta*	8	50	0.01
Mistletoebird	*Dicaeum hirundinaceum*	8	85	0.15
Spotted Pardalote	*Pardalotus punctatus*	8	245	0.19
Striated Pardalote	*P. striatus*	12	343	0.69
Silvereye	*Zosterops lateralis*	10	82	0.05
Diamond Firetail	*Emblema guttata*	19	76	0.04
White-winged Chough	*Corcorax melanorhamphos*	330	232	0.13
White-browed Woodswallow	*Artamus superciliosus*	40	51	< 0.01
Dusky Woodswallow	*A. cyanopterus*	40	148	0.10
Australian Magpie	*Gymnorhina tibicen*	380	102	0.18

are intermediate in behaviour but tend to resemble the hirundines more.

Substrate (and food) (Table III)

Nine species were principally ground foragers, though they may differ in the type of ground that they use (Table III). For instance, Choughs and Speckled Warblers favoured bare or litter-strewn ground far more than Magpies or Fairy-wrens did. The Diamond Firetail and Rosella both fed extensively on seeds (Ford unpubl. and Cannon 1981) whereas the others took mostly invertebrates. The Brown Treecreeper and Shrike-thrush combined ground- and bark-feeding, while the Sittella, Shrike-tit and White-throated Treecreeper were primarily bark-feeders. The treecreepers foraged more from trunks than branches, whereas the other species concentrated on branches. Sittellas climbed up and down rough branches at all heights, Shrike-tits specialized on exfoliating bark and Shrike-thrushes fed mostly off horizontal boughs. Noske (1979, 1983) found similar differences among the bark-foraging guild at Wollomombi, 40 km E of Armidale. His data are far more extensive but he did not include the Shrike-thrush.

The Lorikeet, two very small honeyeaters and two large honeyeaters were the main nectar-feeders in the community, though the Wattlebird and Friarbird consumed

TABLE II

Proportion of observations for each species by each foraging method.

Species	Glean	Snatch	Probe	Tear	Hover	Pounce	Hawk	Niche breadth
Yellow-rumped Thornbill	0.987	0.013						0.069
Diamond Firetail	0.987	0.013						0.069
Silvereye	0.963		0.037					0.158
Brown Treecreeper	0.916		0.081			0.004		0.306
Speckled Warbler	0.899	0.097			0.004			0.344
Brown-headed Honeyeater	0.897	0.007	0.096					0.357
Mistletoebird	0.847	0.047			0.094		0.012	0.560
Australian Magpie	0.833		0.167					0.451
White-naped Honeyeater	0.832	0.012	0.135	0.003			0.018	0.566
Grey Shrike-thrush	0.827	0.115	0.037	0.005		0.005	0.010	0.627
Superb Fairy-wren	0.793	0.177	0.002		0.003	0.005	0.021	0.628
Striated Pardalote	0.793	0.198		0.006	0.003			0.553
Brown Thornbill	0.783	0.183			0.033			0.615
Spotted Pardalote	0.776	0.184			0.041			0.639
White-throated Treecreeper	0.753	0.006	0.184	0.043			0.015	0.754
Varied Sittella	0.751		0.205	0.042			0.003	0.691
Striated Thornbill	0.722	0.200			0.070		0.009	0.786
Buff-rumped Thornbill	0.704	0.231			0.045	0.003	0.018	0.816
Fuscous Honeyeater	0.641	0.069	0.202		0.020	0.001	0.068	1.061
White-winged Chough	0.504		0.453	0.043				0.839
Red Wattlebird	0.407	0.097	0.471		0.007		0.019	1.057
Noisy Friarbird	0.285	0.122	0.529				0.065	1.129
Eastern Spinebill	0.064	0.048	0.667		0.048		0.175	1.043
Scarlet Honeyeater	0.020	0.020	0.920				0.040	0.362
Little Lorikeet			1.000					0.000
White-throated Gerygone	0.504	0.416			0.027		0.053	0.866
Golden Whistler	0.403	0.573					0.023	0.772
Rufous Whistler	0.201	0.759	0.003		0.011	0.005	0.022	0.709
Black-faced Cuckoo-Shrike	0.136	0.819			0.013		0.032	0.602
Eastern Rosella	0.643		0.008	0.349				0.690
Crested Shrike-tit	0.332	0.003	0.042	0.617		0.003	0.003	0.849
Yellow Robin	0.127	0.136	0.012	0.003		0.671	0.052	1.025
Scarlet Robin	0.036	0.255			0.036	0.509	0.164	1.228
Restless Flycatcher	0.064	0.413	0.018		0.128	0.073	0.321	1.426
Willie Wagtail	0.198	0.162				0.016	0.625	0.975
Dusky Woodswallow	0.128	0.081	0.020		0.007	0.073	0.689	0.993
White-browed Woodswallow	0.020		0.235				0.745	0.638
Grey Fantail	0.023	0.184			0.017		0.776	0.664
Tree Martin	0.031						0.969	0.138
Welcome Swallow							1.000	0.000

many insects, specially large beetles (Scarabaeidae and Chrysomelidae) from the foliage during summer.

Thirteen species fed mostly on invertebrates from leaves though the honeyeaters and pardalotes included carbohydrate foods such as honeydew and manna in their diets (Paton 1980; Woinarski 1985). We were unable to ascertain the relative importance of carbohydrate versus arthropods for these species. Stomach flushing indicated that a variety of insects and spiders is taken (Ford & Harrington unpubl.). However, manna, honeydew and lerp are not easily picked up in stomach samples. The Whistlers and Cuckoo-shrike, which were mostly snatchers (Table II), appeared to take large items such as larvae and leaf-beetles (Chrysomelidae), whereas the gleaning thornbills take mostly small insects and spiders (Bell 1983).

The Restless Flycatcher was as diverse in its use of substrates as it was in its foraging behaviour. It pounced on terrestrial prey, pursued flying insects and snatched from bark with almost equal frequency. As with the foliage snatchers, it appeared to take large prey, with long intervals between successful captures. Six species took mostly flying prey, with the Willie Wagtail and Dusky Woodswallow taking some prey from the ground, and these two, plus the Grey Fantail, taking arthropods from foliage and bark. The White-browed Woodswallow also visited flowers. This foraging behaviour may have been over-emphasized as an influx of this species coin-

TABLE III

The proportion of observations for each species on each of the ten substrates.

Species	Bare	Ground litter	Grass	Leaves	Twigs	Branch	Trunk	Flowers	Air	Fruit	Niche breadth
White-winged Chough	0.040	0.366	0.589				0.005				0.835
Speckled Warbler	0.068	0.345	0.399	0.130	0.011	0.040	0.007				1.395
Yellow Robin	0.023	0.292	0.420	0.029	0.003	0.090	0.090		0.053		1.520
Scarlet Robin	0.019	0.264	0.245	0.170	0.019	0.113			0.170		1.696
Australian Magpie	0.029	0.108	0.863								0.470
Diamond Firetail	0.041	0.055	0.890			0.014					0.454
Yellow-rumped Thornbill	0.054	0.095	0.608	0.095	0.095	0.054					1.289
Superb Fairy-wren	0.013	0.097	0.451	0.242	0.038	0.113	0.024		0.021		1.527
Eastern Rosella		0.017	0.538	0.219	0.025	0.050	0.008	0.143			1.294
Brown Treecreeper	0.050	0.239	0.168			0.129	0.414				1.421
White-throated Treecreeper		0.006	0.002	0.002		0.271	0.720				0.646
Grey Shrike-thrush		0.141	0.084	0.141	0.031	0.518	0.072		0.011		1.448
Crested Shrike-tit			0.003	0.318	0.049	0.541	0.085	0.003	0.003		1.106
Varied Sittella					0.003		0.907	0.087	0.003		0.336
Little Lorikeet								1.000			0.000
Scarlet Honeyeater				0.040	0.020			0.900	0.040		0.246
Eastern Spinebill				0.143	0.016	0.016		0.651	0.175		0.995
Noisy Friarbird			0.008	0.336		0.049	0.008	0.533	0.066		1.106
Red Wattlebird				0.374	0.032	0.123	0.013	0.439	0.019		1.229
Fuscous Honeyeater		0.006	0.010	0.585	0.030	0.102	0.022	0.177	0.067		1.300
Silvereye			0.084	0.639		0.012	0.012	0.157		0.096	1.116
White-naped Honeyeater				0.788	0.015	0.065	0.012	0.103	0.018		0.790
Brown-headed Honeyeater				0.897		0.014	0.007	0.082			0.397
Buff-rumped Thornbill	0.006	0.107	0.086	0.521	0.066	0.143	0.054		0.018		1.508
Brown Thornbill				0.746	0.182	0.073					0.720
Golden Whistler		0.003	0.020	0.811	0.030	0.094	0.017		0.024		0.752
Rufous Whistler	0.008	0.019	0.814	0.019	0.103	0.016			0.022		0.741
Black-faced Cuckoo-shrike				0.897		0.065	0.007		0.032		0.490
Striated Thornbill		0.009		0.901	0.027	0.054			0.009		0.434
White-throated Gerygone				0.914		0.035			0.052		0.353
Striated Pardalote			0.003	0.924	0.062	0.009	0.003				0.328
Spotted Pardalote		0.004	0.004	0.951	0.033	0.008					0.243
Restless Flycatcher	0.018	0.036	0.207	0.135	0.054	0.171	0.063		0.315		1.786
Willie Wagtail	0.032	0.005	0.182	0.075		0.054	0.011		0.642		1.133
Grey Fantail			0.006	0.145	0.006	0.046	0.017		0.780		0.746
Dusky Woodswallow	0.020	0.027	0.095	0.034	0.007	0.047	0.068	0.007	0.694		1.164
White-browed Woodswallow	0.020							0.235	0.745		0.638
Tree Martin	0.031								0.969		0.138
Welcome Swallow									1.000		0.000
Mistletoebird				0.259	0.061	0.024		0.012		0.642	0.948

cided with heavy flowering of *E. blakelyi* in spring 1982.

The Mistletoebird was the sole specialist frugivore, taking mistletoe fruits. It also took insects, chiefly from foliage. Silvereyes, and probably Speckled Warblers, took fruit of *Chenopodium trigonum*, and Pied Currawongs *Strepera graculina* and Yellow-faced Honeyeaters *Lichenostomus chrysops* occasionally took blackberries, *Rubus* sp.

Plant species (Table IV)

The non-vegetation sites, such as air and bare ground or litter, are pooled into one category and included within Table IV so that appropriate overlap values can be calculated between species.

Seventeen species foraged mostly upon eucalypts and sixteen species from air or ground. Among the eucalypt feeders some appeared to show preferences for particular species. However, these should be interpreted cautiously as there are local differences in the relative abundance of both the different tree and bird species. For instance, at Eastwood State Forest some areas have almost 100% *E. caliginosa*, others have almost all *E. viminalis*. If a bird species occurs in an area, for some reason other than the presence of the predominant tree species, such as *E. viminalis*, then in the latter areas its foraging may indicate a preference for feeding on *E. viminalis*. This bias notwithstanding, some apparent preferences can be

TABLE IV

Proportion of observations for each species on each plant species or type, including non-vegetable material (air, bare ground or litter).

Species	*Eucalyptus* *calig.*	*mell.*	*vim.*	*blak.*	bip. *Ac.*	*Amy.*	Other tree	Other shrub	Grass	Non-veg.	Niche breadth
Varied Sittella	0.885	0.045	0.017	0.036	0.011	0.003				0.003	0.521
White-throated Treecreeper	0.724	0.122	0.028	0.024	0.062		0.017		0.002	0.021	1.015
Brown-headed Honeyeater	0.669	0.194	0.036	0.043		0.058					1.007
Rufous Whistler	0.621	0.093	0.049	0.106	0.071		0.011		0.019	0.030	1.320
White-naped Honeyeater	0.602	0.083	0.156	0.062		0.065	0.015			0.018	1.287
Grey Shrike-thrush	0.576	0.044	0.044	0.061	0.048	0.018	0.013		0.070	0.127	1.321
Crested Shrike-tit	0.550	0.049	0.179	0.100	0.103	0.009	0.003		0.003	0.003	1.344
Black-faced Cuckoo-shrike	0.520	0.136	0.078	0.091	0.130	0.013				0.033	1.463
Striated Pardalote	0.488	0.183	0.243	0.077			0.006		0.003		1.250
Spotted Pardalote	0.422	0.160	0.225	0.184					0.004	0.004	1.349
White-throated Gerygone	0.412	0.211	0.070	0.211	0.018		0.026			0.053	1.531
Fuscous Honeyeater	0.360	0.148	0.124	0.114	0.039	0.125	0.005		0.011	0.076	1.815
Red Wattlebird	0.147	0.346	0.128	0.186	0.019	0.128	0.026			0.019	1.734
Noisy Friarbird	0.133	0.292	0.075	0.175	0.067	0.167	0.017		0.008	0.067	2.078
Little Lorikeet		0.360		0.640							0.653
Eastern Spinebill	0.111	0.048		0.016	0.016	0.587		0.048		0.175	1.286
Scarlet Honeyeater	0.100	0.140		0.080		0.640				0.040	1.122
Mistletoebird	0.118	0.012	0.012	0.012	0.024	0.765	0.047			0.012	0.903
Golden Whistler	0.438	0.081	0.044	0.104	0.269		0.017		0.020	0.027	1.540
Striated Thornbill	0.439	0.094	0.019	0.094	0.271		0.065			0.019	1.488
Buff-rumped Thornbill	0.266	0.070	0.024	0.073	0.323		0.024		0.088	0.133	1.756
Silvereye	0.187	0.027			0.507	0.080		0.107	0.093		1.418
Brown Thornbill	0.278		0.019		0.685		0.019				0.766
Diamond Firetail	0.014								0.890	0.096	0.388
Australian Magpie									0.870	0.130	0.386
Yellow-rumped Thornbill	0.111		0.014	0.014	0.083				0.625	0.153	1.151
Eastern Rosella	0.191	0.040	0.048	0.016	0.135	0.032	0.016		0.508	0.016	1.514
Superb Fairy-wren	0.227	0.028	0.027	0.020	0.084	0.002	0.008		0.469	0.136	1.576
Yellow Robin	0.156		0.015	0.024	0.015				0.422	0.370	1.237
Speckled Warbler	0.083	0.018			0.073	0.007			0.402	0.417	1.236
Scarlet Robin	0.113	0.019		0.038	0.113	0.019			0.245	0.453	1.471
Restless Flycatcher	0.238	0.028	0.019	0.067	0.028			0.010	0.219	0.391	1.544
White-winged Chough	0.005								0.589	0.406	0.704
Brown Treecreeper	0.357	0.074	0.011	0.011	0.055		0.022		0.173	0.298	1.567
Willie Wagtail	0.075		0.011	0.016	0.032				0.183	0.683	0.991
Dusky Woodswallow	0.076	0.022	0.022	0.014	0.014	0.007			0.097	0.752	0.959
White-browed Woodswallow				0.235						0.765	0.545
Grey Fantail	0.176	0.017		0.011	0.023				0.006	0.767	0.746
Tree Martin										1.000	0.000
Welcome Swallow										1.000	0.000

calig. = *caliginosa, mell.* = *melliodora, vim.* = *viminalis, blak.* = *blakelyi,* bip. *Ac.* = bipinnate *Acacia, Amy.* = *Amyema.*

noted. Sittellas, and to a lesser extent White-throated Treecreepers, preferred stringybarks as noted by Noske (1985). Shrike-tits visited *E. viminalis* proportionally more than the other bark-feeders did, probably because this tree loses its bark in long ribbons. The pardalotes and perhaps the White-naped Honeyeater also tended to feed more on *E. viminalis* than expected, possibly because they take much manna, which is produced by this tree. The Red Wattlebird, Noisy Friarbird and Little Lorikeet fed most from *E. melliodora* and *E. blakelyi* because these trees flowered extensively.

The three arboreal thornbills, the Silvereye and the Golden Whistler, fed often from bipinnate *Acacia* as well as from eucalypts. Mistletoes were visited by Mistletoebirds (for fruit) and by the honeyeaters for nectar. The Scarlet Honeyeater and Spinebill fed most on mistletoe flowers, in contrast to the larger Wattlebird and Friarbird, which were eucalypt specialists. Unlike other honeyeaters the Scarlet Honeyeater also fed on the small flowers of *E. caliginosa*. Other trees included *E. bridgesiana, Angophora floribunda* and *Casuarina torulosa*, which were all uncommon and only occasionally visited by birds. Other shrubs included *Melichrus urceolatus*, visited by Spinebills for nectar, and *Chenopodium trigonum* visited by Silvereyes for fruit.

TABLE V

Proportion of observations of foraging for each species at each of six heights (in metres).

Species	0	1–2	3–5	6–9	10–14	15+	Niche breadth
Australian Magpie	1.000						0.000
White-winged Chough	0.996	0.004					0.026
Diamond Firetail	0.921	0.079					0.276
Yellow-rumped Thornbill	0.851	0.030	0.060	0.045		0.015	0.614
Speckled Warbler	0.817	0.083	0.072	0.022	0.007		0.680
Yellow Robin	0.730	0.073	0.061	0.111	0.026		0.930
Scarlet Robin	0.556	0.037	0.148	0.185	0.074		1.236
Superb Fairy-wren	0.554	0.335	0.070	0.036	0.002	0.002	1.024
Eastern Rosella	0.496	0.054	0.070	0.155	0.186	0.039	1.420
Brown Treecreeper	0.455	0.250	0.156	0.094	0.045		1.357
Restless Flycatcher	0.250	0.233	0.086	0.181	0.207	0.043	1.668
Willie Wagtail	0.228	0.508	0.130	0.109	0.021	0.005	1.296
Grey Fantail	0.006	0.345	0.172	0.224	0.236	0.017	1.446
Silvereye	0.169	0.277	0.337	0.133	0.036	0.048	1.556
Buff-rumped Thornbill	0.194	0.280	0.268	0.188	0.071		1.530
Striated Thornbill	0.026	0.224	0.302	0.181	0.216		1.432
Brown Thornbill	0.056	0.333	0.370	0.241			1.238
White-throated Treecreeper	0.007	0.191	0.206	0.366	0.225	0.006	1.411
Golden Whistler	0.028	0.120	0.127	0.381	0.275	0.069	1.524
Eastern Spinebill		0.079	0.175	0.381	0.333	0.032	1.350
Crested Shrike-tit	0.006	0.063	0.147	0.353	0.398	0.033	1.334
Varied Sittella		0.025	0.058	0.339	0.519	0.058	1.130
Mistletoebird		0.082	0.153	0.294	0.353	0.118	1.472
White-throated Gerygone		0.064	0.101	0.284	0.404	0.147	1.413
Noisy Friarbird	0.008	0.050	0.142	0.275	0.367	0.158	1.480
Fuscous Honeyeater	0.020	0.082	0.131	0.273	0.385	0.109	1.513
Spotted Pardalote	0.008	0.179	0.136	0.271	0.311	0.096	1.560
Rufous Whistler	0.030	0.121	0.096	0.251	0.401	0.101	1.531
Grey Shrike-thrush	0.223	0.073	0.067	0.249	0.352	0.036	1.540
Striated Pardalote	0.003	0.041	0.085	0.226	0.510	0.135	1.308
Little Lorikeet				0.120	0.780	0.100	0.679
White-naped Honeyeater		0.029	0.067	0.199	0.605	0.099	1.138
Brown-headed Honeyeater		0.021	0.048	0.193	0.621	0.117	1.091
Red Wattlebird		0.026	0.052	0.162	0.481	0.279	1.252
Black-faced Cuckoo-shrike		0.013	0.059	0.170	0.471	0.288	1.237
Scarlet Honeyeater			0.080	0.060	0.400	0.460	1.095
Dusky Woodswallow	0.149	0.081	0.088	0.101	0.155	0.426	1.585
Welcome Swallow		0.213	0.115	0.131	0.049	0.492	1.341
Tree Martin	0.032	0.096			0.122	0.750	0.808
White-browed Woodswallow	0.019			0.059	0.173	0.750	0.762

Foraging height (Table V)

As shown in Table III, ten species spent most of their time foraging on the ground (0 m). Fifteen species foraged more in the canopy (> 10 m) than at other heights. To a major extent differences in foraging height reflect differences in substrate. Foliage and flower foragers tended to feed high, ground foragers obviously low and bark and aerial foragers tended to be intermediate. We shall therefore limit comparisons of foraging height to species that use similar substrates. The bark-foraging Sittella fed higher than the White-throated Treecreeper, which foraged higher than the Brown Treecreeper when the latter was off the ground. The Shrike-tit and Shrike-thrush fed above the treecreepers but below the Sittella. Of the leaf foragers the three thornbills and Silvereye frequently foraged low (< 5 m), which agrees with their preference for wattles. Among the aerial insectivores the Grey Fantail on average foraged above the Willie Wagtail, whereas the hirundines and woodswallows fed at canopy level or above it. Tree Martins fed higher than Welcome Swallows, and were sometimes very high (> 30 m), as were woodswallows. Red Wattlebirds and Scarlet Honeyeaters tended to forage on higher flowers than Noisy Friarbirds and Spinebills did, but the reason for this is not clear.

Foraging guilds

When species are compared for all four foraging dimen-

sions combined, the dendrogram displays six separate major guilds, based primarily on substrate (Fig. 1). These guilds can be subdivided by foraging method and to a lesser extent by plant species. Most of the ground-feeders glean their food from the surface, though the Eastern Rosella and Brown Treecreeper may be considered outliers, as they fed frequently from foliage and bark respectively. The robins and Restless Flycatcher form a group that pounced on terrestrial prey, from a perch or from the air. The four bark foragers varied in the degree to which they use other substrates, and in the relative importance of tree-trunks and branches.

The foliage foragers are the biggest and most complex guild. Six species were principally leaf gleaners in eucalypts, though the White-throated Gerygone frequently snatched. It is interesting that this group (excepting the White-throated Gerygone) includes the species that take much carbohydrate food such as manna, honeydew and lerp. The three leaf-snatchers in eucalypts are larger birds than the members of the former group and took larger prey. The three thornbills and Silvereye fed frequently from *Acacia*, as well as from eucalypts, and are well separated from the other leaf-gleaners.

The aerial feeders tend to be separated by height and by the extent to which they use other substrates. The Little Lorikeet is separated from the four nectarivorous honeyeaters as these last include many insects in their diet. The two large honeyeaters preferred eucalypt flowers, whereas the two small species preferred mistletoes.

Two other dimensions could have been considered in determining the structure of this bird community: food and size of the bird. Seed-eating species could have been separated from insectivores, though this would merely have separated the Diamond Firetail and Eastern Rosella from the large ground-gleaning guild. As regards differences in arthropod prey, this is determined to a large extent by the size of the bird, and its foraging method and substrate. Generally species that are grouped together in Figure 1 are similar in size. The only major exceptions are the Australian Magpie grouped with the small ground gleaners, and the Black-faced Cuckoo-shrike with the whistlers. The Australian Magpie takes far larger prey than the other small ground feeders (Vestjens & Carrick 1974), but the Black-faced Cuckoo-shrike could take similar-sized prey to the whistlers (Harrington & Ford, unpubl.).

Several additional species, mostly seasonal visitors, occur in eucalypt woodland and we have some foraging data for these. We shall discuss some of the more common ones briefly. Sacred Kingfishers *Halcyon sancta* (11 observations) pounced on large arthropods and small reptiles on the ground. White-winged Trillers *Lalage sueurii* occurred in variable numbers in summer and mostly snatched insects from leaves (42 observations). Satin and Leaden Flycatchers *Myiagra cyanoleuca* and *M. rubecula* were summer visitors that hawked or snatched from leaves or branches (48 observations). Rose Robins *Petroica rosea* also hawked and snatched insects from plants but were winter visitors (30 observations). Shining Bronze-cuckoos *Chrysococcyx lucidus* were leaf gleaners (31 observations), which specialized on hairy caterpillars. Pied Currawongs gleaned from leaves or the ground (25 observations) and Crimson Rosellas *Platycerus elegans* foraged in the canopy (29 observations) for eucalypt seeds and insects, specially those in galls.

DISCUSSION

Recher *et al.* (1985) compared the foraging behaviour of 41 species of birds in eucalypt forest and woodland in south-eastern NSW. Twenty-five species were included in both studies and our results are very similar for these species. Some differences may result from our observations being made throughout the year, whereas those of Recher *et al.* (1985) were made only during summer.

A major difference in our results is that Recher *et al.* (1985) decided to separate the *Melithreptus* and *Lichenostomus* honeyeaters *a priori* from the insectivores. Our study shows that these honeyeaters form a significant part of the leaf-gleaning guild. Another difference is that in our study the Brown, Striated and Buff-rumped Thornbills are clustered together as eucalypt and *Acacia* leaf-gleaners. Recher *et al.* (1985) and Bell (1983), showed that Striated Thornbills forage high in eucalypts whereas Brown Thornbills feed mostly below 4 m. Buff-rumped Thornbills were ground and bark gleaners in the latter two studies. In addition, Striated Thornbills employ a method 'hang-gleaning' that we did not separate from gleaning. The disparity in our results may indicate biases; for instance we may have overlooked Striated Thornbills in the canopy. On the other hand it may represent true differences in the foraging behaviour of thornbills in different areas.

Several pairs of species in out study are very similar in most aspects of their foraging behaviour. The Brown-headed and White-naped Honeyeaters overlap on average by 90%. They were most different in their choice of tree species, Brown-headed Honeyeaters tending to prefer stringybarks and Yellow Box while White-naped prefer Manna Gums. In this study the latter species fed rather more on bark, in particular on the ribbons of bark from Manna Gums. Ford & Paton (1977) also found that the White-naped Honeyeater was more of a bark feeder in the Mount Lofty Ranges of South Australia. Interestingly the site in South Australia where White-naped Honeyeaters were most abundant also had many Manna Gums. In contrast Recher *et al.* (1985) and Keast (1968) found that the Brown-headed Honeyeater fed far more from

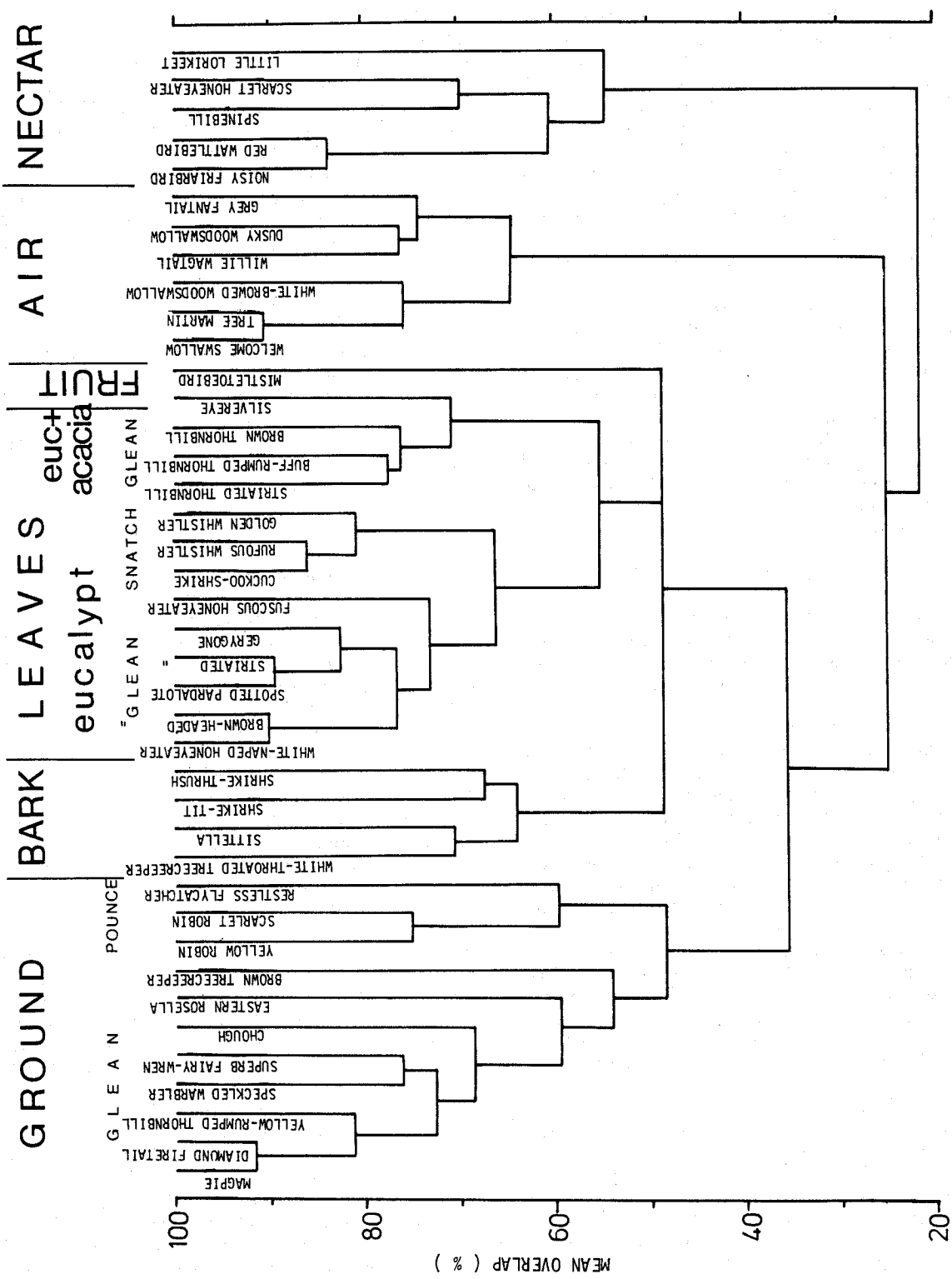

Figure 1. Dendrogram displaying separation of forty species in their foraging ecology, on the basis of mean overlap (%) in foraging method, substrate, plant species and height.

bark than did the White-naped Honeyeater. Cullen (unpubl.) has looked closely at the foraging behaviour of these two species and found that the Brown-headed Honeyeater is more adept at extracting prey from a bark-like substrate, whereas White-naped Honeyeaters seem to be better at stretching for prey on leaf tips. These different results indicate that these honeyeaters modify their behaviour and foraging substrate for different tree species or in different areas.

Both our study and that of Recher *et al.* (1985) suggested that Spotted and Striated Pardalotes are very similar in many aspects of their foraging behaviour. They have been intensively studied in Victoria and Tasmania (Woinarski 1985; Woinarski & Bulman 1985). In Victoria they were very similar in foraging behaviour (a combination of method and substrate — 96% overlap), but displayed marked differences in tree species (27–75% overlap in four regions). In contrast, in Tasmania they showed little difference in their preferences for tree species. As in our study they showed a preference for *E. viminalis*, which provided the best source of manna. Woinarski & Bulman (1985) also found that Striated Pardalotes ate a wider range of foods than did the Spotted Pardalote, which was a manna specialist. Both species are highly mobile and may tend to concentrate on local abundances of food.

The White-throated Gerygone is also similar to the pardalotes in foraging behaviour, differing in its more rapid movement and frequent hawking and snatching of insects from foliage. We suspect that it takes different foods from the pardalotes, in particular more flies.

The Golden and Rufous Whistlers and Black-faced Cuckoo-shrike are all similar in their foraging behaviour. As mentioned earlier the Cuckoo-shrike is larger, while the two whistlers are almost identical in size. Recher *et al.* (1985) separated the whistlers on the basis of habitat, the Rufous Whistler occurring in woodland whereas the Golden Whistler is a forest-dweller. In our area they differ in season, the Rufous Whistler occurring in summer (September–March) and the Golden Whistler mostly in winter (April–September). In the breeding season the difference here is one of habitat too, as Golden Whistlers are common in summer in eucalypt forests and rainforests east of Armidale. Possibly this pair of species is too similar to be able to coexist. The whistlers are also interesting in that both species exhibit marked sexual differences in foraging (Bridges 1980; Bell 1986).

The Welcome Swallow and Tree Martin are another similar pair of species, exhibiting almost identical foraging behaviour, but differing somewhat in height. They differ slightly in size and, as found in hirundines elsewhere (Waugh & Hails 1983), could well differ in their main foods. Such differences could be tested by examining faecal samples.

The two large honeyeaters are both breeding visitors that feed on large insects from foliage and from eucalypt flowers. Other studies (Recher *et al.* 1985; Ford & Paton 1977) have shown the Red Wattlebird to be eucalypt flower specialist, though it will visit other flowers and spends 30–40% of its time taking insects. These are the first data for the Noisy Friarbird. It is possible that both species exploit abundant sources, as their breeding season (September to December) coincides with the flowering of *E. melliodora* and (in some years) *E. blakelyi*, and the peak of leaf-eating beetles tends to occur in December. On the other hand there are frequent aggressive encounters between the two, in which neither species is a consistent winner. Further research should be carried out on the Red Wattlebird and Noisy Friarbird to determine to what extent they may compete with each other.

There are two main reasons why comparative studies of the foraging behaviour of bird communities are of value. First, they provide basic information that can be used as a starting point to tackle general questions in ecology: how are communities constructed, what differences are there between different communities on the same continent or on different continents? Also, what mechanisms influence community structure, in particular what role does interspecific competition play?

Both our study and that of Recher *et al.* (1985) found that about three quarters of the species were insectivores (29 out of 40, 31 out of 41). There were eight nectar-feeders in each study, though several of these fed extensively on insects, and two seed-eaters. Our study had a single frugivore. In addition both studies found that the bird community was primarily subdivided by food and substrate, with foraging method being the main secondary separator. Wooller & Calver (1981) considered only the understorey species, of Karri forest in Western Australia. Again most species (7 out of 9) were insectivores, the other two were honeyeaters. Both height and substrate separated species, as did food. These studies indicated some predictable structure of the bird community of eucalypt forest and woodland.

Australian rainforests however have markedly different bird communities. Crome (1978) and Frith (1984), working in tropical rainforests, found that only about half of their species were almost totally insectivorous (12 out 27, 13 out 23). They had eight and three frugivores respectively, as well as six and seven species that included fruit and insects in their diets. This last group included three honeyeaters in both studies. Although both authors indicated that height was the best separator of species, their dendrograms show that ground and above-ground species are separated first, with the latter group subdivided into fruit-eaters and insectivores. Thus although

eucalypt and rainforest communities are apparently separated in different ways, this results partly from treating the ground as both a substrate and a height. Temperate rainforest in Tasmania has a bird community more like that of eucalypt than of tropical rainforest. Thomas (1980) found that 13 out of 19 species were insectivorous (including two honeyeaters). One other honeyeater largely took nectar, and there were two seed-eaters, one tree-feeder and one ground-feeder. The remaining two species were omnivores. Only the Silvereye ate fruit, but was almost entirely a leaf gleaner. Thomas separated the community into guilds on the basis of food and substrate.

The habitat on other continents that most resembles eucalypt woodland is evergreen oak woodland. The bird communities of such habitats have been studied in south-western North America (Landres & MacMahon 1983) and southern Spain (Zamora & Camacho 1984). Landres & MacMahon (1983) considered only arboreal species and worked only during the breeding season. All species were insectivores though some would feed on fruit or seeds at other seasons. Five guilds, separated by substrate and method, were recognized in their north-western Mexican site. Their Californian site was more depauperate with only four guilds (on leaves, bark, air and ground). The bird community in evergreen oak in southern Spain (Zamora & Camacho 1984) is characterized by a large number of omnivores, which eat insects and fruit or seeds. Thirteen out of 29 species of passerine fall into this category with 12 species being classed as insectivorous. Four species are graminivores, though three non-passerines could be added to this group. There are no nectarivores. Australian eucalypt forests virtually lack counterparts to the northern hemisphere thrushes, warblers and flycatchers (Muscicapidae), which switch from feeding on invertebrates in the breeding season to fruit at other times of the year (Herrera 1984).

There have been several excellent detailed studies on congeneric species over the last decade in Australia, e.g. on *Lichenostomus* honeyeaters (Wykes 1982), pardalotes (Woinarski 1985), thornbills (Bell 1983), treecreepers (Noske 1985) and fantails (Cameron 1985). Sometimes ecologically similar species are not congeneric and we identified several cases above, where more detailed study would be fruitful.

The second reason for studies on foraging behaviour is to provide basic information on the requirements of bird species. These should help forest managers to maintain habitats for a diverse avifauna. Recher *et al.* (1985) have extensively developed this argument.

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