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Foraging patterns of breeding birds in eucalypt forest and woodland of southeastern Australia

H. F. RECHER
The Australian Museum, PO Box A285, Sydney South, NSW 2000, Australia

R. T. HOLMES
Department of Biological Sciences, Dartmouth College, Hanover, New Hampshire 03755, USA

M. SCHULZ
Mountain Forest Research Station, Sherbrooke Road, Sherbrooke, Vic. 3789, Australia

J. SHIELDS
R. KAVANAGH
Forestry Commission of NSW, PO Box 100, Beecroft, NSW 2119, Australia

Abstract

The foraging ecology of eucalypt forest and woodland birds was studied on three 10 ha plots in southeastern Australia. Quantitative data were obtained for 41 species of which 31 were insectivorous, eight were nectar-feeders, and two were parrots that fed primarily on eucalypt seeds. Birds-of-prey, large omnivores and frugivores were uncommon. Insectivorous birds differed in foraging behaviour, the substrates on which they found prey, and foraging height. Nectar-feeders exploited a variety of carbohydrates including nectar, honeydew, lerp, manna and sap. Nectarivorous birds were separated by foraging behaviour, substrate, height and by the extent to which they used the different types of carbohydrates. Carbohydrates were also an important food resource for some insectivores. By understanding how birds exploit food resources within forest and woodland environments, the features of the environment which need to be conserved or manipulated to manage forest avifaunas can be identified. For example, in addition to the substrates such as foliage and bark, usually associated with the foraging of forest birds, carbohydrates and loose bark were identified as important resources for birds in eucalypt forests and woodlands. The broad importance of these two resources to the avifauna had not been previously appreciated, yet both may be sensitive to environmental changes associated with logging and other forest management practices which alter the composition or age-class structure of forests.

Introduction

Birds occupying forests often exhibit differences in how they exploit resources. Some species, for instance, are generalists that will search for food at all heights and on a variety of substrates, while others show varying degrees of specialization. These species will therefore differ in their response to changes to their habitat that may result from human activities. Logging, the establishment of plantations, hazard reduction burning or an increased incidence of wildfires are examples of events initiated by people which can change the vegetative structure and plant species composition of forests and thereby affect the survival of forest birds. A knowledge of the ways in which birds exploit resources within a forest will not only increase understanding of how they use their environment, but will help to identify the features of that environment which are necessary for their survival. This information, in turn, is required for the development of sound, scientifically based plans of management for national parks, state forests and other land units as well as for evaluating many topics of current interest in avian ecological and evolutionary biology, such as mechanisms of habitat selection, foraging theory, competitive relations and community structure.

Although general knowledge is available on the foraging behaviour of Australian forest birds, there is little quantified information,

especially for communities of forest birds. Avian community analyses from Australia have been made for rainforests in Queensland and Tasmania (Crome 1978; Frith 1984; Thomas 1980), for the Karri Forest in south-western Australia (Wooller & Calver 1981), and for some taxa of birds such as honeyeaters (Meliphagidae), thornbills (Acanthizidae), pardalotes (Pardalotidae) and fantails (*Rhipidura*) in a variety of shrub and forest habitats (e.g. Ford & Paton 1976, 1977; Pyke 1983; Bell 1985; Woinarski 1985; Cameron 1985). In addition, Croxall (1977) and Bell (1982a, b, 1984) described foraging in forest bird communities in New Guinea which share many genera with Australia. However, no community-wide study has quantified the foraging ecology of birds in the eucalypt forests and woodlands of southeastern Australia despite the fact that this sector has been settled longest, has the most people, and its forests are heavily utilized for timber production and recreation. Moreover, large tracts of forest and woodland in this region continue to be cleared for agriculture and forest plantations which lends importance and urgency to studies concerning the remaining forests and their fauna.

In response to a need to develop guidelines for the management of wildlife in forests extensively managed for pulp (woodchips) and sawlog production, we initiated studies in 1975 of the ecology and behaviour of forest birds in southeastern New South Wales (Recher *et al.* 1980). In the present paper, we provide information on the foraging patterns of birds dwelling in the eucalypt forests and woodlands along the border of New South Wales and Victoria on the Southern Tablelands. Our objective is to describe the ways in which forest birds forage during the breeding season and the kinds of resources which appear to be important for their survival and to relate these to forest management. These are baseline data for subsequent publications which will consider in detail seasonal foraging patterns, community structure and the theoretical and management implications of our findings.

Study areas

During the summer (October–January) of 1980/81, studies of foraging birds were made at three localities near Bombala, New South Wales (36° 54′S, 149° 14′E). Two plots (Woodlot 1 and Woodlot 2) were in New South Wales adjacent to the Bondi State Forest near the Bondi Forest Camp. The third plot (Woodlot 3) was located in Victoria along Coast Range Road adjacent to the border with New South Wales. All were within 5 km of each other at an elevation of 800–860 m a.s.l. and, as best as we could determine, none had burnt within the previous 15–20 years. Each plot was 10 ha (420 m×240 m) and marked as a grid at 30 m intervals. Topography was flat to undulating, with slopes generally less than 10°. The plots and their vegetation are described in Table 1.

On Woodlots 1 and 2 vegetation was measured along two parallel transects 300 m in length, spaced 120 m apart and set back 60 m from the plot boundaries. One transect on each of these plots was located in woodland and the other in forest. At points 30 m apart along the transects, the 20 nearest subcanopy trees and 20 nearest shrubs within 15 m were identified. These data were used to calculate subcanopy and shrub species diversities using the Shannon–Wiener equation: $H' = \Sigma p_i \log_e p_i$ where p_i represents the proportion in the ith category (Table 1). At the same points along the transects, foliage height densities were estimated along four randomly located transects at a series of heights above the ground (0–20 cm, 50 cm, 100 cm, 2 m, 3 m, 4 m, 7 m, 10 m, 15 m, and so on) using the procedures described by MacArthur and MacArthur (1961). The foliage height data were later averaged and grouped into categories corresponding to vegetation layers (ground, shrub, subcanopy and canopy) and the proportion of vegetation in each layer used to calculate foliage height diversities (H′). An index of the amount of foliage on each plot and for each layer of vegetation was obtained from the area described by the foliage height profiles. Similar procedures were used on Woodlot 3 with the difference that vegetation was measured along three transects 420 m in length spaced 60 m apart. At each of 14 points spaced 30 m apart along the transects, the four nearest canopy and subcanopy trees and eight nearest shrubs within 10 m were identified and their heights estimated using a calibrated binocular range finder. On Woodlots 1 and 2 the species composition of the canopy and canopy height was determined by identifying the 10 nearest

TABLE 1. Vegetation and major features of the three study plots at Bondi

	Woodlot 1		Woodlot 2		Woodlot 3
Elevation (m)	800		860		840
History	logged, grazed		logged, grazed		unlogged, ungrazed
Structural formations	woodland	dry, open-forest	woodland	dry, open-forest	moist, open-forest
Area (ha)	5	5	4	6	10
Canopy tree species (*n*)	539	582	350	700	168
Eucalyptus					
subgenus *Monocalyptus*					
radiata	20	60	15	72	88
fastigata	0	0	0	0	+*
stellulata	35	8	11	0	0
subgenus *Symphyomyrtus*					
cypellocarpa	0	0	0	0	+
dalrympleana	4	2	11	27	6
pauciflora	29	7	56	1	0
ovata	8	9	0	0	0
viminalis	1	14	+	0	6
hybrids (*pauciflora*×*radiata*)	2	+	6	0	0
Number of canopy tree species	6	6	6	3	5
Canopy species diversity (H')†	1.50	1.26	1.27	0.64	0.45
Canopy height (m) ($\bar{x} \pm$ s.e.m.)	17±0.2	19±0.3	16±0.1	17±0.2	22±0.5
Number of subcanopy species	7	7	2	2	7
Subcanopy species diversity (H')	1.43	1.45	0.23	0.61	1.03
Number of shrub species	2	7	5	2	11
Shrub species diversity (H')	0.38	1.25	0.87	0.66	1.69
Foliage height profiles (% of total foliage)					
Canopy	69	74	59	72	50
Subcanopy	20	17	27	18	23
Shrub layer	10	5	12	9	17
Ground vegetation	1	4	2	1	10
Total foliage	228	229	221	291	340
Foliage height diversity (H')	0.85	0.80	0.99	0.81	1.22

* + refers to species present on plots, but not recorded along transects.

† $H' = \sum_{i=1} p_i \log_e p_i$, where p_i is the proportion of the ith species.

canopy trees within 10 m of each grid intersection and estimating their heights using binoculars.

Woodlots 1 and 2 were mostly regrowth forest and woodland, 20–80 years old. Mature and senescent trees with numerous hollows for hole-nesting birds were abundant on Woodlot 2, but not on Woodlot 1. During the study, both plots were grazed by sheep and cattle and small amounts of timber removed for fencing. Woodlots 1 and 2 were bounded on three sides variously by pine plantations, pasture, and firebreaks, but one side was continuous with extensive areas of native eucalypt forest and woodland.

Half (5 ha) of Woodlot 1 was woodland dominated by Snow Gum (*Eucalyptus pauciflora*) and Black Sally (*E. stellulata*; Table 1). The woodland graded into pasture with a closely cropped grass ground cover and small patches of Matt Rush (*Lomandra longifolia*) and Bracken Fern (*Pteridium esculentum*). This half had few shrubs and most of the foliage within the shrub layer was of sapling eucalypts. The forested half of Woodlot 1 was dominated by Narrow-leaved Peppermint (*E. radiata*) and Manna or Ribbon Gum (*E. viminalis*) on well drained soils and by Swamp Gum (*E. ovata*) where drainage was impeded. Canopy heights in the woodland ranged from 10 to 20 m with

an average height of 17 m and in the forest from 15 to 30 m with an average height of 19 m. The woodland lacked a subcanopy but in the forest the subcanopy was dominated by young eucalypts with occasional older Blackwood (*Acacia melanoxylon*) and Silver Wattle (*A. dealbata*). The forest also had extensive areas of shrubs dominated by Blackthorn (*Bursaria spinosa*), Silver Wattle and Holly-leaved Lomatia (*Lomatia ilicifolia*). The ground cover in the forest was sparse and consisted mostly of patches of Snow Grass (*Poa* sp.), Bracken Fern and Matt Rush. There was a continuous layer of litter.

Woodlot 2 was more uniform. It had a woodland fringe of Snow Gum and Black Sally bordering pasture along one side, but was mostly dry open-forest dominated by Narrow-leaved Peppermint and Mountain Gum (*E. dalrympleana*; Table 1). Much of the woodland consisted of a dense regrowth of Snow Gum interspersed with Mountain Gum. The canopy averaged 16–17 m throughout the plot with individual trees in the open forest to 25 m and in the woodland to 20 m. The subcanopy consisted entirely of small eucalypts. Woodlot 2 essentially lacked low growing vegetation and shrubs were patchy in occurrence. Again, the shrub layer consisted mainly of sapling eucalypts with scattered, low (<1 m) patches of Blackthorn, Matt Rush, *Bossiaea foliosa*, *Hibbertia obtusifolia*, and the prostrate *Oxylobium procumbens*. The litter layer tended to be sparse with considerable bare ground.

In contrast to Woodlots 1 and 2, there was no evidence of logging on Woodlot 3 nor had it been grazed by domestic animals. Narrow-leaved Peppermint dominated the canopy with Ribbon Gum, Mountain Gum, Brown Barrel (*E. fastigata*) and Monkey Gum (*E. cypellocarpa*) present in small numbers (Table 1). The canopy averaged 22 m in height with emergents to 40 m. Subcanopy, shrub and ground vegetation was well developed. Small eucalypts and Silver Wattle formed a subcanopy to 13 m in height. The shrub layer varied from 1 to 4 m in height and was diverse, with Gippsland Waratah (*Telopea oreades*), Geebung (*Persoonia confertiflora*), *Oxylobium arborescens*, Holly-leaved Lomatia, Blackthorn, and wattles (*Acacia dealbata*, *A. mucronata* and *A. melanoxylon*) contributing most of the foliage. Ground vegetation was moderately dense and consisted of ferns, sedges, Matt Rush and various forbs. There was a deep layer of litter and large amounts of debris in the form of fallen branches and trees. Foliage height diversity, total foliage, and shrub species diversity was greater on Woodlot 3 than on Woodlots 1 and 2 (Table 1). However, canopy species diversity was lower on Woodlot 3 and in the forested portions of Woodlots 1 and 2 than in the woodlands due primarily to the abundance of Narrow-leaved Peppermint. The relatively low index of subcanopy species diversity (H′) on Woodlot 3 was also a result of the abundance of this eucalypt.

The climate at Bondi is seasonal with mild summers (January mean maximum and minimum 24.2°C and 6.1°C respectively) and cold winters (July mean maximum and minimum 10.3°C and −3.7°C respectively). At a weather station near Woodlot 1, rainfall averaged 1000 mm per year between 1970 and 1982 (Forestry Commission of NSW, weather records). However, between 1976 and 1981 the rainfall averaged 820 mm annually and 1978 was the only year with more than 1000 mm of rain. Rainfall in 1980 was 655 mm. This study, therefore, was conducted in a relatively dry year occurring just prior to a period of drought. Weather on the three plots in 1980/81 was similar, but Woodlot 3 was cooler and wetter than the other sites and had frequent morning fogs.

Methods

Birds' foraging behaviour was observed almost daily from 14 October to 15 December 1980 and again during the first week of January 1981 which covered the main breeding period on our plots (Recher *et al.* 1983a). Foraging data were collected at all times of day, but primarily between 0600 and 1300 (EST). Observers worked independently and generally visited a different plot each day. Approximately equal amounts of time were spent on each woodlot. At the start of each two-week period, data were recorded for each foraging bird as it was encountered. However, once 100 or more foraging acts had been recorded (see below) for a species on a woodlot, observations on that species ceased and were concentrated on others in the community for the remainder of that

two-week period. The foraging data were therefore relatively evenly spread throughout the summer.

For each individual encountered, up to five, usually sequential foraging acts were recorded in which food items (e.g. arthropods, nectar, seeds, etc) were taken or attempts to capture prey were made. Although some investigators recommend taking only the first foraging manoeuver observed (Morrison 1984), we selected five to ensure recording inconspicuous foraging methods and to reduce biases towards the more conspicuous behaviours. Each attempt at capturing prey (prey attack) was recorded whether or not it was successful. For each foraging act the behaviour used by the bird, the height of the food item and where it was located was recorded. Heights were estimated to the nearest metre, but in the analysis, these have been grouped according to vegetation layers: ground and debris (0–20 cm), forbs and shrubs (0.2–4.0 m), subcanopy and small trees (4.1–10.0 m) and canopy (>10.0 m).

The substrates from which food items were taken were also recorded. For analysis these have been divided into six categories: ground (including debris, litter and vegetation <20 cm), tree trunks, loose bark (on trunks and branches, or hanging), branches (large and small), foliage (leaves, petioles and twigs), and air. Additionally, two kinds of food are equated with substrates: nectar (flowers) and seeds (including eucalypt capsules, wattle seed pods, grass seeds, etc).

Nine types of foraging or prey attack behaviour were recognized. These encompass the behaviours used by Crome (1978) and expand the categories used by Holmes *et al.* (1979) and Robinson and Holmes (1982). These are:

(1) *Probe or prize.* In probing, a bird extracts prey from within a substrate such as soil, litter, crevices or soft wood. This is the same as Crome's (1978) 'probing' and includes his 'scratching' category. Prizing differs from probing in that the bird lifts up or flakes off part of the substrate. Several species prized up bark to obtain insects, but we could not always distinguish prizing from probing and thus consider them together in this analysis.

(2) *Pounce.* The bird flies down from a perch to take a prey organism from the ground or low vegetation. The bird lands and almost simultaneously takes the prey, and then returns to a perch. Pouncing is included in Crome's category of 'sallying' (1978).

(3) *Glean.* A standing or hopping bird takes prey from nearby substrates. The bird normally moves along searching for, and taking, prey from substrates at relatively close distances. Crome described this behaviour as 'searching' and included short flights or sallies.

(4) *Hang-glean.* A form of glean, in which the bird hangs upside down in a stationary posture while taking prey from the substrate (e.g. the underside of a leaf). It could be described as 'hang-probe' and would fall within Crome's categories of 'searching' and 'probing'.

(5) *Hover.* A flying bird hovers in the air for a brief period while picking a food item from a substrate. This is identical to Crome's category of 'hovering'.

(6) *Snatch.* The bird flies or jumps up to take a prey from a nearby substrate. The bird does not land and normally returns to a different perch from where it started. Most often prey were snatched from surfaces a short distance above the bird. Snatching is included in Crome's category of 'sallying'.

(7) *Hawk.* The bird flies from a perch to capture a flying insect. Most of the prey attacks recorded as hawking fit Crome's description of this behaviour, but also included two other of Crome's foraging behaviours, 'flitting' and 'spiralling'. These, which are also equivalent to the 'flush-chase' described for the American Redstart (*Setophaga ruticilla*) by Robinson and Holmes (1982), refer to rapid flying movements, usually among vegetation, in which prey is disturbed and then pursued by the flying bird. On our plots, only fantails (*Rhipidura* spp.) foraged in this way, and since we did not always distinguish such behaviours from hawking, they have been grouped.

(8) *Nectar.* The bird visits flowers to feed on nectar, essentially a gleaning or probing action.

(9) *Seeds.* The bird visits mature seed heads (as on grass) or capsules (as on eucalypts) to feed on seeds, essentially a gleaning action.

Although vegetation was identified to species, we have used broader categories in analysing the foraging patterns of birds for this paper. Species of ground and shrub plants have been grouped into genera. The two species of

understorey wattles, Blackwood and Silver Wattle, have been kept separate, but the eight species of eucalypts have been grouped into two categories according to the characteristics of their bark. The first group consists of the predominantly smooth-barked gums, *E. dalrympleana*, *E. viminalis*, *E. ovata*, *E. pauciflora*, *E. pauciflora*×*E. radiata* hybrids, and *E. cypellocarpa*, which shed most of the bark from their branches and trunks. These trees were characterized by an abundance of loose and hanging bark strips, particularly when bark was being shed. All of these gums belong to the subgenus *Symphyomyrtus* (Pryor & Johnson 1971). The second group consists of the predominantly rough-barked eucalypts, *E. radiata*, *E. fastigata* and *E. stellulata* within the subgenus Monocalyptus. These trees shed bark only from the smaller branches and upper portions of the trunk.

To determine the average number of birds on each plot, two census transects (420 m×120 m, 5 ha) were located on each woodlot. Birds were counted along each transect for 2 h on each of four consecutive mornings (weather permitting) during December 1980 (see Recher *et al.* 1983b for details of the census procedure). The average numbers of each species recorded on both transects during the four counts were added together to provide an index of abundance for each woodlot of the species for which there were foraging data.

Results

In this paper the woodlots are considered as a single unit grading from a Snow Gum–Black Sally woodland through dry, open-forest on Woodlots 1 and 2 to the complex moist, tall open-forest on Woodlot 3. Although the plots differed in vegetation and the degree of disturbance, they shared many of the same species of birds; of the 41 species for which foraging data were obtained, 30 occurred on all three woodlots (Table 2). The same species on each of the three plots showed the same basic foraging patterns. Such differences as did occur will be discussed in a subsequent paper (H. F. Recher and R. T. Holmes), but are primarily related to the differences between the plots in the type (e.g. trees vs shrubs) and density of vegetation (e.g. woodland vs forest) available to the birds as foraging substrates.

Bird species composition and abundance

Table 2 presents census data from December 1980, comparing the relative abundances of birds on the woodlots during the summer. Scientific names are given in Table 2 and to conform with other papers published from our research in New South Wales, terminology follows CSIRO (1969). Although species composition and the numbers of individuals change seasonally and differ from year to year (Recher *et al.* 1983a), December is a time of peak abundance, when most species are occupied with rearing young and before the post-breeding dispersal of juveniles.

The avifauna of the woodlots is typical of forest and woodland bird communities throughout southeastern Australia (Recher *et al.* 1980; Loyn 1980; Milledge & Recher 1985; Smith 1984). Between 1975/76 and 1981/82, 90 species of terrestrial birds were recorded on the plots. Fifty-six of these are common and widely distributed in forest habitats throughout southeastern New South Wales from sea level to 1000 m a.s.l. (H. F. Recher, unpublished data). Between 1975/76 and 1981/82, 50 species were recorded nesting on one or the other of the woodlots with an average of 38 species nesting each year on the three plots combined (Table 2; Recher *et al.* 1983a).

Woodlot 3 had the richest avifauna with a total of 46 species recorded during censuses and an average of 37 species and 334 individuals per count (on 10 ha). Forty-six species were also recorded on Woodlot 1 and 41 on Woodlot 2, but average counts were lower than on Woodlot 3. Woodlot 1 averaged 34 species and 176 individuals and Woodlot 2 averaged 26 species and 188 individuals per count. The woodland areas of Woodlots 1 and 2 had fewer species and supported fewer individuals than the forested portions of the plots. On Woodlot 1, the woodland transect averaged 24 species and 82 individuals per count while the forest averaged 28 species and 94 individuals. On Woodlot 2, the woodland averaged 21 species and 75 individuals compared with 23 species and 103 individuals along the forested transect. It must be stressed that these numbers are indices of diversity and abundance and do not allow for the movement of birds between transects during censuses.

The denser and more diverse ground, shrub and subcanopy vegetation on Woodlot 3 and

the greater amount of litter and debris on the ground compared to Woodlots 1 and 2, account for many of the differences in species composition and abundances between woodlots. Birds which foraged among litter and in the lower layers of vegetation were more abundant on Woodlot 3 than on the other plots. Eastern Yellow Robin, Eastern Whipbird, Brown Thornbill, Golden Whistler and White-browed Scrubwren are typical of this group. Species such as White-naped Honeyeater and Striated Thornbill which foraged mainly in the subcanopy and canopy were also more abundant on Woodlot 3 (Table 2). In contrast, species which normally frequented pastures were more abundant on Woodlots 1 and 2. Yellow-rumped Thornbill and Australian Magpie were typical of these species and were restricted to woodlands. Buff-rumped Thornbill, Flame and Scarlet Robin, Rufous Whistler and Yellow-faced Honeyeater are examples of woodland and open-forest birds which were also more abundant on Woodlots 1 and 2 than on Woodlot 3 (Table 2). Recher *et al.* (1983a) describe the pattern of seasonal events and give further details of abundance for the avifauna on Woodlots 1 and 2.

Foraging patterns

Quantitative analyses of foraging patterns were restricted to the 41 species for which we recorded 50 or more prey attacks (Table 2). In addition, we have some data for another 14 species which permit us to comment on their foraging behaviour.

Foraging substrates and diet. In Table 3 the substrates from which food was taken by forest and woodland birds are grouped into eight categories. Two of these, flowers (nectar) and eucalypt capsules (seeds), represent the food actually sought by birds. The others are substrates from which birds primarily took invertebrates (e.g. insects, spiders). However, carbohydrates (manna, honeydew, lerp and sap) were also taken from foliage and bark surfaces and it was not always possible to distinguish between a bird foraging for insects and one taking carbohydrates.

Of the 41 species for which there were quantitative data, 31 were primarily insectivorous (Table 2). The two parrots, Gang-gang Cockatoo and Crimson Rosella, fed mainly on seeds taken from eucalypts. Seeds were also the principal food of the two finches which visited the woodlots. The European Goldfinch (*Carduelis carduelis*) fed mainly on the seeds of exotic weeds (e.g. Spear Thistle *Cirsium vulgare*) while the Red-browed Finch (*Emblema temporalis*) fed mainly on seeds of native and introduced grasses.

Honeyeaters and the Silvereye took insects as a source of protein, but also relied on sugar-rich carbohydrates (i.e. nectar, manna, honeydew, lerp and sap) as a source of energy. Honeydew and lerp are sugary exudates of sap-sucking insects while manna and sap are exuded by plants (especially eucalypts) usually following damage by insects (Paton 1980). On the woodlots, only the Crescent Honeyeater, Red Wattlebird and Eastern Spinebill fed extensively on nectar (Table 3). White-eared Honeyeaters foraged mainly under loose bark while Yellow-faced and White-naped Honeyeaters fed mostly in foliage. The Brown-headed Honeyeater fed, almost equally, from loose bark and foliage. Visual inspection showed that sugar-rich carbohydrates were abundant under the bark of eucalypts as it was first being loosened and shed. Peeling bark was therefore attractive to honeyeaters. For example, large numbers of White-eared and Crescent Honeyeaters aggregated on Woodlot 1 during the winter when Swamp Gum shed its bark. At this time, these birds foraged by probing under the bark just at the point where it was loosening from the tree (H. F. Recher and J. Shields, unpublished data).

Psyllid insects were abundant on eucalypt foliage throughout the plots (G. Gowing and H. F. Recher, in prep.). Manna and the sugary secretions (lerp) of these insects were probably the carbohydrates sought by honeyeaters which foraged among the foliage. Other foliage gleaners, such as the Striated Thornbill and Striated and Spotted Pardalotes, also fed on manna and lerp and such carbohydrates may be an important source of energy for these birds (Woinarski 1984; Recher *et al.* 1986). Few fruits were available on the woodlots, but the Silvereye fed on Blackberries (*Rubus* sp.) along the edges of nearby pine plantations. Bark as a substrate occurred on tree trunks and branches and food taken from bark accounted for 25% of foraging manoeuvers (Table 3). Although loose

TABLE 2. Size and relative abundance of the most common bird species using the woodlots during summer 1980/81

	Species and main food		Average weight‡ (g)	Abundance* Woodlot 1	2	3	Number of foraging§ acts recorded
Seed-eaters	Gang-gang Cockatoo	*Callocephalon fimbriatum*	219	0.5†	0.3	4.3†	280
	Crimson Rosella	*Platycercus elegans*	116	5.5	8.5†	14.5†	1309
Insect-eaters	Fan-tailed Cuckoo	*Cuculus pyrrhophanus*	46	4.3†	0.6†	0.6†	100
	Superb Lyrebird	*Menura novaehollandiae*	746	1.0†	+	2.6	62
	Black-faced Cuckoo-shrike	*Coracina novaehollandiae*	110	1.5†	3.3†	1.3	75
	Ground Thrush	*Zoothera dauma*	106	+†	0.3	4.3†	225
	Rose Robin	*Petroica rosea*	9	0.3†	0	6.0†	195
	Flame Robin	*P. phoenicea*	13	7.6†	13.1†	3.6†	830
	Scarlet Robin	*P. multicolor*	13	4.3†	1.3†	0	465
	Eastern Yellow Robin	*Eopsaltria australis*	20	5.5†	4.0†	16.6†	408
	Shrike-tit	*Falcunculus frontatus*	29	1.8†	0.5	5.6	518
	Golden Whistler	*Pachycephala pectoralis*	25	3.3	1.8	9.5†	551
	Rufous Whistler	*P. rufiventris*	26	15.5†	15.8†	6.3†	983
	Grey Shrike-thrush	*Colluricincla harmonica*	76	5.6†	3.0†	5.3†	258
	Black-faced Flycatcher	*Monarcha melanopsis*	24	2.0†	1.0	1.3	283
	Satin Flycatcher	*Myiagra cyanoleuca*	18	6.6†	4.3†	4.8†	429
	Rufous Fantail	*Rhipidura rufifrons*	10	0.5†	0.3	3.3†	303
	Grey Fantail	*R. fuliginosa*	9	19.3†	19.0†	20.3†	2354
	Eastern Whipbird	*Psophodes olivaceus*	62	0	0	4.5†	133
	Superb Blue Wren	*Malurus cyaneus*	10	5.0†	4.8†	0	803

	White-browed Scrubwren	*Sericornis frontalis*	13	0.5†	0.3	30.3	711
	Brown Thornbill	*Acanthiza pusilla*	7	6.8†	7.1†	26.6†	1832
	Buff-rumped Thornbill	*A. reguloides*	8	3.8†	0	0	559
	Yellow-rumped Thornbill	*A. chrysorrhoa*	9	+†	0	0	378
	Striated Thornbill	*A. lineata*	7	8.8†	22.8†	55.1†	2331
	Orange-winged Sittella	*Neositta chrysoptera*	12	+†	+†	1.3	454
	White-throated Treecreeper	*Climacteris leucophaea*	22	6.3†	6.6†	8.3	1224
	Red-browed Treecreeper	*C. erythrops*	23	1.5†	2.5†	5.0	1238
	Spotted Pardalote	*Pardalotus punctatus*	8	1.3	0.6	3.3	317
	Striated Pardalote	*P. striatus*	12	4.6†	11.5†	10.5†	810
	White-winged Chough	*Corcorax melanorhamphos*	379	0	2.8†	0	250
	Dusky Woodswallow	*Artamus cyanopterus*	36	0	0.8†	0	145
	Australian Magpie	*Gymnorhina tibicen*	314	0.3	2.0	0	622
Nectar-feeders	Red Wattlebird	*Anthochaera carunculata*	98	4.3	+†	4.0	254
	Yellow-faced Honeyeater	*Meliphaga chrysops*	17	14.1†	4.5†	7.6†	909
	White-eared Honeyeater	*M. leucotis*	25	2.8	0.3	0	614
	Brown-headed Honeyeater	*Melithreptus brevirostris*	15	2.5	3.1	9.1	235
	White-naped Honeyeater	*M. lunatus*	15	17.8†	23.3†	52.3†	2805
	Crescent Honeyeater	*Phylidonyris pyrrhoptera*	16	0.3	0	1.8	177
	Eastern Spinebill	*Acanthorhynchus tenuirostris*	11	1.0†	0.8	2.5	157
	Silvereye	*Zosterops lateralis*	10	0.8	0	7.5	530
Total							27 116

*Abundance is based on the average number of individuals recorded during counts of 4 h each on four mornings during December 1980. Each count covered the 10 ha plot. + indicates present on plot, but not recorded during censuses. †Breeding on the woodlot was confirmed on at least one occasion between 1976 and 1981. ‡Size measurements obtained from mist-netted birds on Woodlots 1 and 2. §Only species where 50 or more prey attacks were recorded are considered.

and hanging bark was associated with tree trunks and branches, it formed a distinctive and important substrate accounting for 8% of all foraging acts. It was the most important substrate for two species (Shrike-tit and White-eared Honeyeater; Table 3). Loose bark was the second most important substrate for six other species (Grey Shrike-thrush, Red-browed Treecreeper, Orange-winged Sittella, White-naped, Brown-headed and Yellow-faced Honeyeater; Table 3). Shrike-tits took mainly insects and spiders from under loose bark or from within coiled strips of hanging bark, but bark-foraging honeyeaters took carbohydrates in addition to arthropods. Other bark foragers took mainly insects from the bark surface with the White-throated and Red-browed Treecreepers taking mainly ants (Formicidae, Hymenoptera; see also Noske 1979).

Insects in flight were the most important category of prey for four species of birds (Grey and Rufous Fantail, Dusky Woodswallow and Satin Flycatcher) and the second most important for four other species (Black-faced Flycatcher, Flame, Scarlet and Rose Robins; Table 3). Air as a substrate, accounted for 11% of the prey attacks recorded. In addition, Tree Martins (*Cecropis ariel*), Welcome Swallows (*Hirundo neoxena*), White-browed Woodswallows (*Artamus superciliosus*) and Spine-tailed Swifts (*Hirundapus caudacutus*), for which quantitative data are lacking, foraged extensively on airborne insects.

Ground, which included low vegetation and debris as well as litter and soil, accounted for 18% of the foraging acts recorded (Table 3). It was the principal foraging substrate for 14 species, but was little used by other birds. Birds foraging on the ground took mainly insects and spiders, but were also seen to take earthworms, centipedes and small lizards.

Leaves, petioles and twigs were grouped together as foliage and these substrates accounted for 37% of the prey attacks observed. Foliage was the most important foraging substrate for 13 species and the second most important for seven others. Birds foraging in the foliage took mainly insects (spiders were not abundant on eucalypt foliage; G. Gowing and H. F. Recher, in prep.), but some species also took manna, lerp and honeydew as described above.

We were unable to quantify the feeding of several larger birds which frequented the woodlots in small numbers. Pied and Grey Currawong (*Strepera graculina* and *S. versicolor*) were omnivorous. Currawongs were seen to feed mostly on large insects, but also took nestlings, eggs, lizards, and carrion. Grey Currawongs spent considerable time gleaning, probing and prying bark in the canopy. Pied Currawongs seldom foraged in this manner but seemed instead to take most of their prey from foliage. Laughing Kookaburra (*Dacelo novaeguineae*) and Sacred Kingfisher (*Halcyon sancta*) fed mainly on large ground-dwelling insects, but also took small vertebrates such as lizards. The Brown Goshawk (*Accipiter fasciatus*) mostly took rabbits, but also hunted birds. Three nocturnal birds occurred on the woodlots: Boobook Owl (*Ninox novaeseelandiae*), Tawny Frogmouth (*Podargus strigoides*), and Owlet-nightjar (*Aegotheles cristatus*). They probably fed mostly on insects.

Use of plant species Measures of plant species composition were made by counts of individuals and did not allow for differences in foliage densities or volumes between species. However, for the bird community as a whole it appears that, with the exception of Ribbon Gum, subcanopy and canopy trees were used in about the proportions that they occurred. For example, Narrow-leaved Peppermint accounted for about 60% of all trees and 66% of foraging observations recorded in eucalypts were in this species. Ribbon Gum accounted for approximately 5% of trees, but only 1% of the foraging behaviour recorded was in this species. There were differences in the use of tree species by some birds, but these are affected by the different abundances of tree and bird species between plots and in woodland and forest. For example, the Striated Pardalote was most abundant in forest habitats on Woodlots 2 and 3 where it nested in hollows in Mountain Gums. On Woodlot 1 it was only common in the woodland where it nested in Snow Gums and Mountain Gums. On Woodlot 2 it foraged slightly more often in Narrow-leaved Peppermint and Mountain Gum (58% and 31% of prey attacks respectively) and less often in Snow Gum (9% of prey attacks) than expected by the

TABLE 3. Substrate of prey taken by bird species (percentage of prey attacks)

	Substrate							
	Ground	Bark			Foliage	Air	Flowers (nectar)	Eucalyptus capsules (seed)
		Tree trunks	Branches	Loose bark				
Ground foragers								
Superb Lyrebird	100							
White-winged Chough	100							
Australian Magpie	98				1	1		
Ground Thrush	98		2					
Yellow-rumped Thornbill	93		1	2	3	1		
Superb Blue Wren	85		2		9	4		
Fan-tailed Cuckoo	84	10	4		1	1		
White-browed Scrubwren	82	1	5	1	11			
Eastern Yellow Robin	77	8	2	1	5	7		
Scarlet Robin	68	9	3	1	3	16		
Flame Robin	64	9	2		6	19		
Buff-rumped Thornbill	58	3	16	6	16	1		
Eastern Whipbird	53	6	32	6	3			
Grey Shrike-thrush	41	8	17	22	12			
Bark foragers								
Tree trunks								
White-throated Treecreeper	2	80	11	6	1			
Red-browed Treecreeper		56	14	28	2			
Branches								
Orange-winged Sittella		4	80	16				
Loose bark								
Shrike-tit		2	4	90	4			
White-eared Honeyeater		6	13	58	19	3	1	
Foliage foragers								
Striated Pardalote			5	1	92	2		
Spotted Pardalote			10		90			
Striated Thornbill		1	12	5	81	1		
White-naped Honeyeater		1	7	11	77		4	
Black-faced Flycatcher	1	2	10	1	65	21		
Yellow-faced Honeyeater	1	1	9	10	66	2	11	
Golden Whistler	2	5	13	3	67	10		
Brown Thornbill	7	4	14	5	65	5		
Rufous Whistler	2	6	16	3	59	14		
Black-faced Cuckoo-shrike	8	1	25		59	7		
Brown-headed Honeyeater	2		16	33	48		1	
Silvereye	5		27	2	41		25	
Rose Robin	11	14	2	9	38	26		
Aerial foragers								
Grey Fantail	4	2	2		14	78		
Dusky Woodswallow	11	13	4		4	68		
Satin Flycatcher	1	3	3		32	61		
Rufous Fantail	15	3			28	54		
Nectar feeders								
Crescent Honeyeater		2	2	6	5	1	84	
Eastern Spinebill	1	1	1	9	3	2	83	
Red Wattlebird	2		7		24	2	65	
Seed eaters								
Gang-gang Cockatoo								100
Crimson Rosella	1		2	1	6			90
Per cent of total foraging acts	18	8	8	9	37	11	3	6

abundances of the trees (53%, 22% and 19% respectively). This was possibly due to the pardalotes nesting in the Mountain Gums away from the woodland fringe where Snow Gum was most abundant. On Woodlot 3 it foraged less in Peppermint (64% of prey attacks) and more in Mountain Gum (31% of prey attacks) than expected by the abundance of the trees (88% and 6% respectively). On Woodlot 1 Striated Pardalotes foraged preferentially in Snow Gum (52% of prey attacks) and less in Black Sally (5% of prey attacks) than expected by the abundance of these trees in the woodland (29% and 35% respectively). It used other tree species in about the proportions they occurred. Other species showed similar variations in their use of tree species and these differences will be considered in detail in another paper and compared with the differences between trees in the composition and abundance of their insect faunas (G. Gowing and H. T. Recher, in prep.).

Gippsland Waratah was the only nectar-rich shrub in bloom during our study and nectar-feeding was restricted to this species. Shrubs such as *Oxylobium*, Blackthorn, Geebung, Silver Wattle and Blackwood each accounted for 1–2% of foraging actions. Relative to other shrubs, Geebung and Blackwood were not abundant (<1% of shrubs recorded) and may therefore have been preferred foraging sites. Other shrub species appear to have been used in proportion to their abundance.

Foraging height distribution Although most species foraged over a broad range of heights, they were grouped according to the layer of vegetation in which the majority of their foraging was recorded (Table 4). Foliage was apportioned between four layers or strata: ground (0–20 cm), shrub (0.2–4.0 m), subcanopy (4.1–10 m), and canopy (<10 m). The division of foliage into these height layers was a compromise between the actual height distributions of foliage throughout the three plots. For example, Woodlots 1 and 2 had few shrubs greater than 2 m and the height range to 4 m for the shrub layer, which was necessary for Woodlot 3, inevitably includes some subcanopy vegetation. Similarly, in some sections of the woodlands on Woodlots 1 and 2, the 'canopy' was less than 10 m in height and therefore by our definition fell into the subcanopy category.

The distribution of foliage on each woodlot is presented in Table 1. When the foliage profiles for the three sites are combined, 61% of the foliage is in the canopy, 22% in the subcanopy, 12% in the shrub layer and 5% is ground vegetation. We did not measure the area of bark, but probably the major portion of the surface area of bark on tree trunks and large branches occurred within the shrub and subcanopy layers. For the avian community as a whole, a higher percentage of foraging manoeuvers were recorded in the shrub and subcanopy layers than at ground level or in the canopy (Table 4). The foraging heights of bark-foraging species (e.g. treecreepers) corresponds well with the height distributions of tree trunks and large branches, but fewer birds foraged in the canopy than might have been expected from the distribution of foliage. Probably this is because birds respond to a wider range of substrates and food resources (e.g. bark, nectar, seeds) than is included in a measure of foliage alone. Foliage is a better predictor of the height distribution of birds when species which took most of their food from leaves, petioles and twigs are considered separately. Of the 13 species grouped as foliage foragers (Table 3), eight (e.g. pardalotes, Striated Thornbill) foraged mainly in the subcanopy and canopy (73–99% of prey attacks) while five (e.g. Brown Thornbill, Rose Robin) foraged primarily in the subcanopy and shrub strata (72–88% of prey attacks). The latter species tended to take more insects from air, from tree trunks and the ground, or to use nectar, than those birds foraging higher above the ground.

As an index of the extent to which species specialized in foraging within a single stratum, foraging height diversities (FHD) were calculated. A species which made an equal number of prey attacks in each layer of vegetation would have a FHD of 1.4 and would be considered a height generalist. A species which specialized and foraged in a single stratum only would have a FHD of 0. The average FHD for all species was 0.8. Sixty-six per cent of species had a FHD greater than 0.8 and are considered height generalists. Birds which foraged mainly on or near the ground had the narrowest foraging height range

TABLE 4. Height distribution of birds in eucalypt forest and woodland at Bondi (% of prey attacks)

	Vegetation layer				Foraging height		Foraging height diversity (H')
	Ground (≤0.2 m)	Shrub (0.2≤4.0 m)	Subcanopy (4.1–10.0 m)	Canopy (>10.0 m)	mean	s.d.	
Canopy							
Gang-gang Cockatoo		7	21	72	13.1	5.3	0.75
Black-faced Cuckoo Shrike	7	4	38	51	11.4	6.0	1.03
Brown-headed Honeyeater		6	46	48	11.4	5.3	0.88
Crimson Rosella	1	9	44	46	10.5	5.2	0.94
Striated Pardalote		21	39	40	9.3	5.3	1.06
Mean							0.93
Subcanopy							
Satin Flycatcher	1	13	49	37	9.5	4.5	1.03
Shrike-tit		17	47	36	9.3	5.0	1.02
Spotted Pardalote		21	43	36	9.9	5.4	1.06
Orange-winged Sittella		5	63	32	8.3	3.7	0.80
White-naped Honeyeater		21	47	32	9.6	7.0	1.05
Rufous Whistler	3	20	47	30	8.4	5.1	1.14
Striated Thornbill		27	45	28	8.5	5.7	1.07
Yellow-faced Honeyeater	2	25	51	23	7.4	4.4	1.10
White-eared Honeyeater	1	33	48	18	6.8	4.6	1.07
White-throated Treecreeper	3	44	40	13	5.6	4.2	1.10
Grey Fantail	9	43	36	12	5.8	5.5	1.20
Red-browed Treecreeper	1	43	44	12	6.3	4.7	1.03
Black-faced Flycatcher	1	40	48	11	6.6	5.0	1.01
Dusky Woodswallow	18	35	47		4.6	2.8	1.03
Mean							1.05
Shrub							
Silvereye	5	43	28	24	6.8	5.7	1.21
Red Wattlebird	2	65	16	17	5.9	5.8	0.95
Golden Whistler	3	52	30	15	5.9	5.5	1.09
Rose Robin	10	55	23	12	4.2	4.5	1.15
Crescent Honeyeater		74	20	6	4.7	3.8	0.71
Brown Thornbill	9	69	18	4	3.1	3.4	0.91
Eastern Spinebill		99	1		2.2	0.8	0.06
Rufous Fantail	21	74	5		1.3	1.5	0.70
Eastern Whipbird	38	58	4		1.1	1.6	0.81
Mean							0.84
Ground							
Grey Shrike-thrush	38	23	28	11	4.6	5.7	1.31
Buff-rumped Thornbill	58	29	12	1	1.5	2.6	0.98
Flame Robin	64	22	13	1	1.6	2.9	0.91
Scarlet Robin	68	25	7		1.1	2.3	0.80
Eastern Yellow Robin	77	17	5	1	1.0	2.4	0.75
White-browed Scrubwren	75	25			0.3	0.8	0.57
Superb Blue Wren	80	20			0.2	0.8	0.50
Fan-tailed Cuckoo	86	12	1	1	0.5	1.8	0.48
Yellow-rumped Thornbill	93	4	3		0.3	1.4	0.30
Ground Thrush	97	3			0.2	0.3	0.14
Australian Magpie	98	2			0.0	0.3	0.10
White-winged Chough	100				0.0	0.0	0.00
Superb Lyrebird	100				0.0	0.0	0.00
Mean							0.53
Per cent of all prey attacks	18	32	33	17			
Total mean							0.83

(Table 4). Thirteen species took more than 50% of their prey from the ground (Table 3). Five of these (Lyrebird, Chough, Magpie, Ground Thrush, Yellow-rumped Thornbill) moved about and foraged exclusively on the ground. Four others (Buff-rumped Thornbill, White-browed Scrubwren, Superb Blue Wren and Eastern Whipbird) foraged on the ground and in low vegetation. The remainder (Flame, Scarlet and Eastern Yellow Robins, and Fan-tailed Cuckoo) fed mostly on ground-dwelling invertebrates, but hunted from low perches (<2.0 m) from which they pounced on prey as did the Brush Cuckoo (*Cuculus variolosus*). The Laughing Kookaburra, Sacred Kingfisher, and Tawny Frogmouth also hunted this way, but used higher perches (>2.0 m). The Grey Shrike-thrush foraged extensively on the ground, but also hunted higher in the vegetation wherever there were large branches on which it could hop.

Nine species foraged mainly in the shrub layer (Table 4). The Eastern Whipbird also foraged on the ground while the Rufous Fantail took flying insects from just above the ground surface (20–100 cm). One species, the Eastern Spinebill, was restricted to the shrub layer. During this study, honeyeaters and Silvereye were attracted to the shrub layer by the abundance of nectar-rich flowers on Gippsland Waratah which accounts for their relatively low average foraging heights. The Silvereye and honeyeaters also foraged extensively in higher vegetation whenever trees were in flower or when searching for other carbohydrates (e.g. manna and lerp on foliage).

A number of birds foraged about equally in shrub and subcanopy vegetation. White throated and Red-browed Treecreepers and the White-eared Honeyeater foraged on tree trunks and large branches from ground level to the canopy. Grey Fantails took small flying insects at all heights and showed a strong diurnal variation in foraging height. Early in the morning they foraged high in (or just above) the canopy moving lower as temperatures rose (H. F. Recher, pers. obs.; Frith 1984). No species was restricted to foraging in the subcanopy or in the canopy and most were foraging height generalists with diversity indices (H′) greater than 0.8 (Table 4).

Only two species, the Gang-gang Cockatoo and Black-faced Cuckoo-shrike, foraged more often in the canopy than in lower vegetation (Table 4). The Gang-gang Cockatoo fed almost exclusively on eucalypt seeds while the Cuckoo-shrike snatched large insects from the canopy foliage. Four species for which quantified foraging data are lacking, Tree Martin, Welcome Swallow, Spine-tailed Swifts and White-browed Woodswallow, often foraged above the canopy on flying insects. These species also foraged over nearby pastures as did the Dusky Woodswallow. It should be noted, however, that our quantified observations of the Dusky Woodswallow were restricted to birds foraging within the forest and woodland.

Foraging method We distinguished nine behaviours used by birds to uncover, attack or take various kinds of food. Eight were used by species that fed mainly on insects and other arthropods although pardalotes and Striated Thornbill also took lerp and manna (Table 5). Parrots and finches fed by 'gleaning' seeds while much of the foraging behaviour of honeyeaters and Silvereyes was related to taking nectar or other carbohydrates (Table 6).

In general, insectivorous birds searched for prey by moving steadily through the vegetation or over the ground gleaning insects and spiders from the substrate (Table 5). Gleaning accounted for 54% of prey attacks by insectivorous birds and was the principal foraging manoeuvre used by 14 species. Hang-gleaning was separated from gleaning on the basis of posture but accounted for only 4% of all prey attacks. However, it was an important behaviour for the Striated Thornbill and distinguished the foraging behaviour of this bird from other gleaners.

After gleaning, snatching and hawking were the most frequently used prey attack behaviours, each accounting for 14% of the manoeuvres recorded (Table 5). Snatching distinguished the foraging behaviour of five species (Rufous and Golden Whistler, Black-faced Flycatcher, Rose Robin and Black-faced Cuckoo-shrike) while four species (Rufous and Grey Fantails, Satin Flycatcher and Dusky Woodswallow) hunted mainly by hawking. Snatchers tended to search for prey like gleaners. Most prey taken was relatively large and located on substrates above the foraging bird.

TABLE 5. Per cent of prey attack manoeuvres by insectivorous birds on the woodlots during the summer of 1980/81

Species	Manoeuvre						
	Pounce	Probe/Prize	Glean	Hang-glean	Hover	Snatch	Hawk
Pouncers							
Fan-tailed Cuckoo	86		2		1	10	1
Eastern Yellow Robin	75	2	3		13	7	
Scarlet Robin	68		3		1	12	16
Flame Robin	52	1	13			15	19
Probers/prizers							
Superb Lyrebird		100					
Shrike-tit		90	8	1		1	
Ground Thrush	1	76	23				
White-winged Chough		70	30				
Gleaners							
Orange-winged Sittella			99	1			
Yellow-rumped Thornbill			98			1	1
White-browed Scrubwren		1	97			2	
Superb Blue Wren			92			4	4
Buff-rumped Thornbill		3	91	1	1	3	1
White-throated Treecreeper		11	88	1			
Striated Pardalote			86	3	3	7	1
Spotted Pardalote			85	3	4	7	1
Red-browed Treecreeper		19	80	1			
Brown Thornbill		1	75	5	4	11	4
Eastern Whipbird		34	64			2	
Striated Thornbill		1	62	23	7	6	1
Grey Shrike-thrush	1	18	61			20	
Australian Magpie		43	56				1
Snatchers							
Black-faced Cuckoo Shrike	7	1	12			74	6
Golden Whistler	1	1	16		1	71	10
Black-faced Flycatcher			8		3	68	21
Rufous Whistler	2	1	19		1	61	16
Rose Robin	10		5			59	26
Hawkers							
Grey Fantail			8		1	13	78
Dusky Woodswallow	15		4			12	69
Satin Flycatcher	1		1		2	36	60
Rufous Fantail	3		12		1	30	54
Per cent of all foraging acts	5	8	54	4	1	14	14

TABLE 6. Foraging behaviour of Honeyeaters and Silvereyes on the woodlots during summer 1980/81. Numbers are per cent of 'prey-attacks' for each species

	Behaviour					
	Glean/Hang-glean		Probe	Snatch	Hawk	Visit flowers
Food	Manna, lerp and honeydew, insects		Sap, manna and honeydew, insects	Insects	Insects	Nectar
Substrate	Foliage	Branches, loose bark	Loose and hanging bark, trunks	Foliage, twigs	Air	Flowers
White-eared Honeyeater	17	19	58	2	3	1
Brown-headed Honeyeater	48	34	17			1
Silvereye	46	29				25
Red Wattlebird	18	7		8	2	65
Crescent Honeyeater	1	2	8	4	1	84
Eastern Spinebill	2	11		2	2	83
Yellow-faced Honeyeater	63	9	11	4	2	11
White-naped Honeyeater	76	14	5	1		4

Three types of behaviour distinguished birds which hawked insects from the air. Swallows, swifts and woodswallows foraged for flying insects above the canopy or in the open above pastures. Grey and Rufous Fantails moved rapidly through and over the vegetation, rapidly changing perches and foraging heights. They fed mainly on very small insects and sometimes hovered in swarms of midges taking prey in quick succession. Often the insects taken were ones disturbed as the birds moved rapidly through the foliage or up and down tree trunks. Probably their behaviour is best described by Crome's (1978) term of 'flitting' which he defines as ". . . moving rapidly, often tumbling, over and through the substrate, which appears to be only briefly examined . . .". Dusky Woodswallow and Satin Flycatcher hawked in the more conventional manner of flying from a perch and taking a flying insect. Apart from Eastern Yellow Robin and Striated Thornbill, few birds hovered and hovering accounted for only 1% of prey attack behaviour.

Four species hunted predominantly by pouncing (Eastern Yellow, Scarlet and Flame Robins, and the Fan-tailed Cuckoo). In addition, four other species for which there were few quantitative observations hunted mainly by pouncing. These are the Laughing Kookaburra, Sacred Kingfisher, Tawny Frogmouth and Brush Cuckoo. As described in the section on foraging heights, pouncers hunted from perches and took most of their prey from the ground or low on tree trunks (Tables 3, 4). Perch changes were frequent (Holmes & Recher, in prep).

Four species (Superb Lyrebird, Ground Thrush, Shrike-tit and White-winged Chough) were considered to forage mainly by probing or prizing. In addition, probing/prizing was an important behaviour for White-throated and Red-browed Treecreepers, Eastern Whipbird, Grey Shrike-thrush and Australian Magpie (Table 5). The Lyrebird, Ground Thrush, Chough, Magpie, Whipbird and Shrike-thrush fed on litter and soil animals which they exposed by moving aside or disturbing the litter. Litter was disturbed by scuffling or raking motions of the feet or by sideways movements of the head and bill. The Lyrebird also raked or scratched deeply into the soil.

White-throated and Red-browed Treecreepers took most of their prey (i.e. ants) from the surface of the bark. However, they also probed into bark crevices and hollows, probed under loose bark and occasionally prized or flaked off small pieces of bark to expose insects and spiders. The Shrike-tit foraged mainly by probing for insects and spiders under loose strips of bark and in coils of hanging bark. Long coils were torn apart so the bird could search the entire length of the strip. The Grey Shrike-thrush also probed for invertebrates under loose bark or within coils of hanging bark, but did not prize, flake or tear apart bark.

Foraging behaviour of honeyeaters and the Silvereye Honeyeaters depend on carbohydrate as an energy source and this distinguishes them from most other forest and woodland birds. For this reason, their behaviour was treated separately. The Silvereye was included with the honeyeaters because it is also abundant and similarly uses carbohydrates. Pardalotes which feed extensively on lerp (Woinarski 1984) may also fit into this category.

Only the Red Wattlebird, Crescent Honeyeater, Eastern Spinebill and Silvereye used nectar to a significant extent (Table 6). The first three species have relatively long, decurved bills and are among the honeyeaters commonly considered to be nectar-dependent (Pyke 1980). White-naped and Yellow-faced Honeyeaters sought most of their food on foliage where they probably took insects, lerp and manna. In the summer of 1979/80, both of these honeyeaters fed extensively on small leaf galls of hymenopterans which were abundant in that summer, but not during 1980/81 (Gowing & Recher, in prep.). The galls were eaten whole and also fed to nestlings. Bark was the major substrate exploited by White-eared and Brown-headed Honeyeaters. The White-eared Honeyeater foraged principally by probing for invertebrates and carbohydrates under loose and hanging bark on tree trunks while the Brown-headed Honeyeater probed and gleaned loose and flaking bark on small branches. The Silvereye gleaned foliage and small branches equally and also took nectar (Table 6). Away from the woodlots it fed on blackberries (*Rubus* spp.).

Discussion

Previous recommendations for the conservation and management of forest birds in southeastern Australia depended on a knowledge of the types of forest in which birds occurred and which forest types had the most diverse avifauna. Recommendations for wildlife management were basically directed at maximizing diversity by conserving particular types of forest (Recher *et al.* 1980). Emphasis was placed on the moister forests (e.g. along creeks or in gullies) which had the richest avifaunas and were used by the largest number of the less common birds (e.g. Sooty Owl *Tyto tenebricosa*). Except in the most general way, information which explained why particular species occurred in one type of forest and not another was not available. Differences in species diversity were correlated with forest structure and floristics, but without relating these environmental parameters to the biology of individual species.

By explaining how birds exploit food resources associated with the major structural and vegetative features of forests and woodlands, understanding of the distribution and abundance of forest birds and their probable response to changes in their habitat is extended. Although species broadly overlapped in their use of resources on the woodlots, birds which foraged in similar ways or exploited the same resources for food can be grouped in a schematic way (Fig. 1). The groupings in Fig. 1 are hierarchical and subjective, but are useful in summarizing the differences between species and in highlighting those features of the environment which need to be conserved or manipulated in managing forest avifaunas. Holmes and Recher (1986) and Ford *et al.* (1986) using quantitative procedures for the analysis of community structure in eucalypt

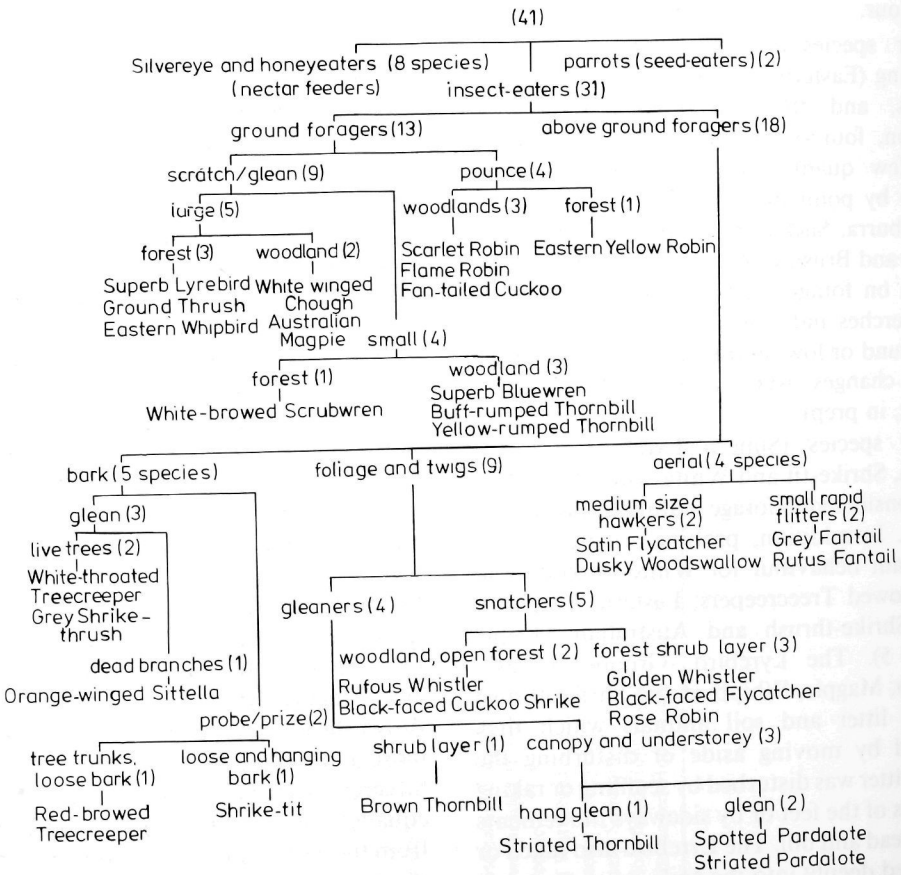

FIG. 1. Schematic diagram of foraging in birds. Numbers in parentheses indicate the number of species.

forest and woodland avifaunas obtained similar guild patterns.

Among the birds on the woodlots there were three major groupings, nectar-feeders (Silvereye and honeyeaters), seed-eaters (parrots and finches), and insect-eaters (all other species; Fig. 1). Frugivores (e.g. Satin Bowerbird *Ptilonorhynchus violaceus*, King Parrot *Alisterus scapularis*) and predators of vertebrates (e.g. Brown Goshawk, Sooty Owl) were rare. Birds, such as kingfishers and currawongs, which took some vertebrates, fed mainly on insects. The schematic portrayal of the groupings in Fig. 1 relies on size, foraging behaviour, substrates and foraging height differences to associate species. The figure illustrates that apart from the parrots which fed on eucalypt seeds in the canopy, the largest birds are insectivorous ground foragers and were mainly separated by habitat. The smaller ground foragers are also insectivorous and differed in foraging behaviour and habitat. Among birds which forage in shrubs and trees, major divisions are by foraging substrate and behaviour. Further subdivisions of species are by habitat, foraging substrate and foraging height. Use of different vegetative layers seems important in separating two pairs of congeners: Brown and Striated Thornbills, and Rufous and Grey Fantails (Table 4). The thornbills also differed in foraging behaviour and their use of substrates as reported by Bell (1985). The Rufous Fantail occupied only a narrow range of habitats compared with the Grey Fantail's ubiquitous distribution (see also Cameron 1985). The congeneric White-throated and Red-browed Treecreepers foraged over the same height range, but the Red-browed Treecreeper probed loose bark and occurred on gums more often than the White-throated Treecreeper.

The emphasis in Fig. 1 on the substrates of prey and foraging behaviour in separating species of insectivorous birds differs from that of Crome (1978) and Frith (1984) who concluded that foraging height was more important than substrate or behaviour in separating species of birds in Queensland rainforests. However, they also reported that most species foraged over a wide vertical range and the differences in emphasis are probably a matter of interpretation. Apart from ground foragers there appears to be little foraging height specialization among eucalypt forest and woodland birds. Management of forest avifaunas is therefore probably best directed at conserving or manipulating substrates (treating shrubs or canopy vegetation as a substrate rather than a vegetative layer) and the kinds of food used by birds.

The avifauna of eucalypt forests and woodlands is distinguished by the abundnace and diversity of birds which feed on carbohydrates such as nectar, manna, lerp, honeydew and sap which are sources of energy for these birds. Honeyeaters, Silvereyes and lorikeets (Psittacidae) are the most conspicuous and widely recognized users of these carbohydrates. Other birds, including pardalotes, treecreepers and some thornbills, also use and may depend on those carbohydrates found on foliage, twigs and under peeling bark. During winter, Crimson Rosellas foraged extensively on the bark peeling from the terminal branches of Narrow-leaved Peppermint where the only detectable food resource was small amounts of carbohydrate (H. F. Recher and J. Shields, unpubl. data). The extent of use of these carbohydrates as a source of energy probably changes seasonally. Striated Thornbills, for example, may only use carbohydrates during the winter (Recher *et al.* 1986). The extent of dependence undoubtedly differs between species, but for at least 14 of the 41 species on which we obtained foraging data, nectar and/or other carbohydrates are an important food resource for forest birds. Paton (1980) suggested that the success and dominance of honeyeaters (Meliphagidae) was related to the abundance of manna, lerp and honeydew on eucalypts and that honeyeaters co-evolved with eucalypts and eucalypt-eating insects .Woinarski (1984) made similar suggestions concerning the evolution of pardalotes and some warblers (Acanthizidae).

Eucalypt communities are also distinguished by the importance of bark as a foraging substrate for birds. Five species are grouped as 'bark foraging specialists' in Fig. 1, but apart from the Rufous Fantail, the Gang-gang Cockatoo and the three largest ground foragers, all species used bark to some extent. Loose and hanging bark and the piles of shed bark at the base of large trees are unique substrates in eucalypt environments. Apart from providing a source of carbohydrates, invertebrates and lizards are also abundant within and under bark

surfaces (G. Gowing and H. F. Recher, unpubl. data). As in the case of carbohydrates, the importance of bark, especially loose bark, as a foraging substrate for birds has not been previously recognized.

It is, of course, potentially misleading to single out carbohydrates and loose bark as important substrates and we do not intend to imply that other foods and substrates are not equally important. The distribution and abundance of several species, for example, depend upon the presence of a well developed shrub layer. Other birds obtain a significant proportion of their food from the ground and litter. These are well recognized substrates for forest and woodland birds. The quantification of the numbers and kinds of birds which obtain their food from particular substrates and of the ways in which they forage allows more accurate prediction of the consequences of management practices. With such information, the forest manager can more easily adjust or compensate for effects which disadvantage particular components of the avifauna. The option is now available to choose between passive and active management of forest and woodland birds.

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