Corella, 2019, 43: 89-105

The potential for food resource partitioning among the predominant species in a Mountain Ash *(Eucalyptus regnans)* forest bird assemblage

Alan Lill

Department of Ecology, Environment and Evolution, School of Life Sciences,
La Trobe University, Bundoora, Victoria, Australia 3086.
Email: A.Lill@latrobe.edu.au

Received: 20 January 2019
Accepted: 10 March 2019

Food exploitation patterns in forest bird assemblages have: (1) management significance, with respect to maintaining the resources required to support these assemblages under various forest usage regimes, and (2) theoretical interest, regarding the roles of interspecific and intersexual competition in shaping such assemblages. The foraging behaviour of the bird assemblage of a vertically stratified Mountain Ash *Eucalyptus regnans* forest was studied over two years. Forty-seven bird species were recorded in the study area and assemblage members mainly consumed invertebrates. The predominant member species foraged disproportionately in the short tree stratum 3–12 m above ground level, and on foliage. The tall tree stratum was also used substantially for foraging, but relatively few of the more common member species foraged in the ground cover and herb strata. Gleaning and sally-snatching were the main foraging macro-behaviours, and 22 micro-variations of these behaviours were exhibited. Hawking and probing/prising were recorded for only a few of the common assemblage member species. Sexually dichromatic Golden Whistlers and White-throated Treecreepers exhibited only limited sex-specific foraging in just vegetation stratum use. There was considerable overlap in foraging variables among species with broadly similar foraging behaviour, which did not appear particularly consistent with a major role of interspecific competition in promoting foraging niche segregation. However, there probably was some food resource partitioning, because probing, hawking and trunk- and ground-gleaning most likely gave their few proponents access to invertebrates largely unexploited by the larger foliage-gleaning and sally-snatching guilds. Maintaining the integrity of the tall and short tree strata is likely to be very important in conserving avian diversity in this cool temperate rainforest habitat.

INTRODUCTION

Several investigations in temperate and tropical areas have greatly helped us to understand how bird species and guilds exploit food resources in Australian forests and woodlands (e.g. Frith 1984; Recher *et al*. 1985; Ford *et al*. 1986; Brooker *et al*. 1990; Cale 1994; Hannah *et al*. 2007; Antos *et al*. 2008). Understanding how birds exploit such resources is critical for designing effective management plans incorporating biodiversity conservation for forests used primarily for recreation or commercial timber production. It is also important from a fundamental, theoretical perspective with respect to the role of interspecific competition in determining the composition of forest bird assemblages.

McArthur's (1958) iconic study of co-habiting insectivorous warbler (Parulidae) species partitioning food resources in conifers by foraging in different microhabitats and in different ways stimulated many similar investigations and wide acceptance of the notion of species coexistence evolving through resource partitioning ('competitive exclusion') (*e.g.* Alatalo and Alatalo 1979; Holmes *et al*. 1979; Lara *et al*. 2015). This competition model has been extended to encompass the concept of coexistence of guilds of species with similar foraging behaviour within assemblages (Recher 2018). The evolution of sex differences in foraging ecology has also been attributed to selection for traits that reduce intersexual resource competition (Mand *et al*. 2013). Such sex differences occur in a diversity of bird species and are manifested in many ways, including foraging in disparate habitats or locations, at differing distances from the nest, at varying heights, on different substrates and using contrasting behaviours (Holmes 1986; Lewis *et al*. 2002; Noske 2003; Falconer *et al*. 2008; Hogstadt 2010; Buij *et al*. 2012; Widman *et al*. 2015). However, the resource partitioning model has been seriously questioned for bird assemblages by some authors, because it has been argued that: (a) the conditions necessary for competitive co-evolution to occur are likely to be rare, and (b) avian mobility is likely to limit opportunities for genetic differentiation driven by the selection pressure of interspecific competition (Mac Nally 1995). The role of resource partitioning through interspecific and intersexual competition in shaping avian assemblages is thus still somewhat contentious and warrants further investigation (Jankowski *et al*. 2012).

Mountain Ash *Eucalyptus regnans*, the dominant canopy tree species in some Victorian and Tasmanian tall wet forests, is the world's tallest flowering plant (Ashton 1975). Mountain Ash forest is valued for water and timber production, recreational and aesthetic attributes and its unique biodiversity (Lindenmayer 2009; Viggers *et al*. 2013). However, as a functioning ecosystem it is classified as critically endangered under the IUCN Ecosystem Assessment protocol, mainly due to the effects of wildfire and commercial logging (Burns *et al*. 2015). Mature Mountain Ash forests often have several distinct vertical vegetation strata, namely ground cover, herb, shrub, intermittent short and tall tree layers, and a canopy stratum. This structure creates a complex array of varying microhabitats that bird species can potentially exploit in diverse ways (Holmes and Recher 1986). There has been a substantial volume of research on the composition of avian assemblages in this habitat (e.g. Loyn 1985; Lindenmayer *et al*. 2015; Serong and Lill 2016), but more detailed work at more sites on the constituent species' foraging ecology and behaviour will help in fully determining the extent to which the potential alluded to by Holmes and Recher (1986) is exploited.

The main aims of this study were therefore to: (a) determine how the stratified vegetation of this forest is exploited for foraging by the various bird assemblage member species, (b) examine whether resource partitioning among species is likely to have been important in structuring the bird assemblage, and (c) investigate whether the sexes forage sufficiently differently to reduce intersexual food competition in two sexually dichromatic member species. To achieve these aims, regular observations were conducted over two successive years, and the vegetation strata, approximate heights, substrates and macro- and micro-behaviours used in foraging by assemblage members were documented and compared.

METHODS

Study area

The study was conducted in an ~200 ha segment of a tract of cool temperate rainforest in the East Victorian Central Highlands. The area's vegetation ranges from fern gullies dominated by tree-ferns and epiphytic ferns to tall open forest (Specht 1970) characterised by a high canopy dominated by Mountain Ash. An intermittent sub-canopy is formed by a mixture of short and tall trees (including the genera *Acacia*, *Bedfordia*, *Leptospermum* and *Pomaderris*), and there is a patchy shrub layer (including *Goodenia*, *Cassinia*, *Coprosma* and *Olearia*) and a ground cover of mesophytic herbs. Mean annual rainfall is over 1,000 mm and monthly mean maximum and minimum ambient temperatures range from 4–9ºC (winter) to 11–22ºC (summer).

Foraging observations

Forty-five observation sessions were conducted over the two-year study period. In Year 1 (Y1), 27 sessions were carried out at a frequency of two to four per month, using three transects approximately equally (transect sessions). Transects were necessarily mostly along established tracks, the longest being ~1.7 km. An additional 18 more opportunistic sessions were conducted over the two years; they were carried out on the same transects, but allowed greater observer flexibility to obtain observations on species encountered less often. The early to mid-morning observation sessions lasted 3.5–4 hours. For the transect sessions, the researcher walked a transect slowly, identifying and documenting the foraging behaviour of all birds seen. In both transect and opportunistic sessions, the observer used 10 × 50 power binoculars. Appendix 1 gives the scientific names of all bird species referred to in this paper. Despite the considerable number of sessions conducted, many uncommon species provided insufficient data for meaningful analysis of foraging behaviour.

Up to five records of foraging stratum, substrate and macro- and micro-behaviours were obtained per focal bird, but usually only one (the initial) estimated foraging height was recorded. The foraging variables recorded were:

(a) Stratum: the vertical vegetation stratum in which the focal bird was foraging, namely ground, herb (grasses, sedges, bracken, false bracken), shrub, short tree, tall tree and canopy tree crown.

(b) Height: the estimated categorical height (m) at which focal bird was foraging; 0 = ground, 1 = 0.1–3.1, 2 = 3.2–12.2, 3 = 12.3–24.4, 4 = 24.5–30.5, and 5 = > 30.5.

(c) Substrate: the surface from which food item was procured: air, leaf (including fronds), twig (up to ~1 cm diameter), branch (> ~1 cm in diameter), trunk, bud, inflorescence, ground (soil, ground litter), bark (including partly shed and detached bark) and 'other' (including cobweb, fungus, lichen, vine and gall).

(d) Macro- behaviour: the broad mode of behaviour employed: [i] glean (GL)- pick item off substrate with bill, [ii] sally-snatch (SS)- fly/jump from perch to take food item from *solid* substrate, such as leaf or twig, and fly/jump to original/ different perch, [iii] hawk (HWK)- fly from perch to capture invertebrate(s) *in air* and fly to original/ different perch to consume it, [iv] probe and prise (PP)- push bill below surface of substrate to acquire food item, sometimes after prising or tearing substrate open (*e.g.* decorticating bark), and [v] turn litter (TL) – performed with bill or feet, the invertebrates exposed underneath being consumed.

(e) Micro-behaviour: variants of basic GL, PP, SS and HWK *e.g.* GL while clinging upside down to vegetation, rather than perching upright; SS in which the food item is snatched from vegetation while hovering close to it (Table 5 footnote contains full list).

Crimson Rosellas' foraging behaviour was not recorded because Magrath and Lill (1983) had earlier documented the species' winter foraging ecology in this habitat in detail.

Data analysis

Foraging behaviour frequencies were pooled across sessions because totals were too small for meaningful analysis at the individual session level. Ideally, variation in the kind of data obtained here is analysed with statistical procedures such as log linear or generalised linear modelling. However, the foraging records were all obtained from the same relatively small area and often comprised several records per focal individual; they therefore included many within- and probably among-session repeat observations on the same, unmarked individuals that are not statistically independent. Consequently, rather than interrogating the data with significance testing of dubious validity, quantitative summaries of foraging behaviour are presented and interpreted conservatively. Pairwise percentage overlap indices between species for the various foraging variables were calculated with a formula commonly used in this context:

$\mathrm{p}_{jk = [\sum (\text{minimum}}\, \mathrm{p}_{ij}\, \mathrm{p}_{ik]100}$ (Krebs 2014)

where p_{ij} is proportion resource *i* is of total resources used by species *j* and p_{ik} is proportion resource *i* is of total resources used by species *k*, modified to examine each foraging variable separately.

RESULTS

All observation sessions combined yielded 3,629 sightings of members of 47 bird species. Transect sessions provided the most rigorous and comprehensive picture of the species composition of the bird assemblage. The relative representation in such sessions of the 16 species that each contributed at least 1% of the total sightings is given in Table 1. Six of all the species observed were recorded in 85–100% of the transect sessions (Crimson Rosella, Golden Whistler, Grey Fantail, White-browed Scrubwren, Silvereye and Brown Thornbill), three in 44–89% (Striated Thornbill, White-naped Honeyeater and Eastern Yellow Robin) and 38 in only 4–59% of transect sessions.

Diet

Foraging information for 19 species providing sufficient data for analysis (hereinafter termed analysable species) translated into the following *likely* dietary breakdown:

1. Exclusively invertebrates: 14 species (n = 20–893 foraging records per species).

2. Predominantly invertebrates, plus small volumes of fruit (0.4% and 7.7%, respectively): two species; Golden (n = 234 records) and Olive (n = 26) Whistlers.

3. Mainly invertebrates, but also small amounts of fruit *and* nectar: two species, White-naped Honeyeater (n = 132 records) – invertebrates (and possibly plant exudates) 95%, fruit and nectar 2% each; Silvereye (n =329) – invertebrates 74.8%, fruit 14.6% and nectar 10.6%.

4. Nectar and invertebrates: one species, Eastern Spinebill – nectar (55.6%) and invertebrates (44.4%), but n was small.

The ensuing sections analyse information on foraging behaviour from the more comprehensive data set obtained from transect sessions for species for which ≥ 50 foraging records were obtained. However, supporting data obtained from the opportunistic sessions are also summarised in the accompanying tables and figures.

Foraging strata and heights

Meaningful analysis (n = ≥ 50 records) was possible for 12 species for foraging strata use (Table 2):

[1] The short tree layer was preferred most by six of these analysable species; no other stratum was preferred most by more than one or two species.

[2] The tall tree layer was the second stratum preference of five bird species, with other strata having this rank for no more than one to three species.

[3] The least-used strata were the ground cover and 'herb' layers, each exploited substantially by only one or two species.

Only White-browed Scrubwrens (herb, shrub and ground) and Eastern Yellow Robins (ground and short trees) foraged predominantly in the lower vegetation strata, and only White-naped Honeyeaters, Satin Flycatchers and Striated Thornbills mainly in the higher strata *i.e.* tall and canopy trees (Table 2). Between these extremes, Large-billed Scrubwrens, Rufous Fantails and Silvereyes foraged mostly in the short tree and shrub layers, whilst White-throated Treecreepers, Golden Whistlers and Grey Fantails mainly used a combination of the short and tall tree strata.

Table 1

Relative abundance of species contributing at least one percent of the sightings of assemblage members over the entire study. Collectively these species accounted for 92.1% of all sightings. Raven sp. indicates either Australian or Little Raven.

Species	Relative abundance (% of sightings)
Crimson Rosella	22.5
Brown Thornbill	17.5
Grey Fantail	9.8
Silvereye	9.0
Golden Whistler	6.5
White-browed Scrubwren	6.0
Striated Thornbill	3.8
White-naped Honeyeater	3.5
Eastern Yellow Robin	3.4
White-throated Treecreeper	2.0
Rufous Fantail	1.7
Eastern Spinebill	1.5
Crested Shrike-tit	1.4
Rose Robin	1.3
Raven sp.	1.2
Grey Shrike-thrush	1.0

Eight pairwise species combinations (12% of all combinations) had overlap indices >80% for foraging strata use (Table 3). White-throated Treecreepers, Brown and Striated Thornbills, Golden Whistlers and Rufous and Grey Fantails overlapped greatly with other assemblage members in foraging strata use (each ≥ 50% overlap with six-eight species), all predominantly using the small and tall tree layers disproportionately. In contrast, three species had low levels of interspecific overlap in foraging strata use. These were the White-browed Scrubwren and Eastern Yellow Robin (≥ 50% overlap with no and one species, respectively), with their extensive use of the lower strata little exploited by other assemblage members, and the Satin Flycatcher (≥ 50% overlap with two species) with its extensive use of the tall and canopy tree strata (Table 2).

With respect to foraging height, nine species were analysable and the six height categories (C) were exploited unevenly by these species (Fig. 1):

C2 (3.2–12.2 m) and C3 (12.3–24.4) were each the preferred height category of three of the analysable species and the second preference of three and four species, respectively.

C1 (0.1–3.1) was the preferred height category of two species and the second preference of one species.

C0, C4 (24.5–30.5 m) and C5 (> 30.5 m) were used relatively infrequently, except that C5 was the preferred category of one species and C0 the second preference of one species.

Table 2

Percentage of foraging conducted in six forest strata by twelve bird species. Only species for which there were ≥ 50 records overall are included. For each species, upper row shows transect data (bold) and lower row shows opportunistic data (smaller font). The two highest values in each row are underlined. Gaps indicate zero values. N is number of records (number of birds contributing). N for all species combined was 2,890 (1,409 birds).

		Foraging strata					
Species	Ground	Herb	Shrub	Small tree	Tall tree	Canopy tree	N (birds)
White-throated Treecreeper		**0.8**	**5.3**	**53.4**	**28.5**	**12**	**133 (50)**
			9.1	39.4	33.3	18.2	33 (9)
White-browed Scrubwren	**21.7**	**42.3**	**31.8**	**4.2**			**189 (121)**
	33.9	55.9	10.2				59 (39)
Large-billed Scrubwren		**5.6**	**12.5**	**75**		**12.5**	**24 (11)**
			36.1	41.7	16.7		36 (18)
Brown Thornbill		**1.8**	**13.7**	**61.2**	**18.8**	**4.5**	**849 (368)**
				62.5	21.9	15.6	32 (18)
Striated Thornbill				**36.6**	**36.6**	**26.8**	**142 (79)**
				17.4	56.5	82.6	23 (20)
White-naped Honeyeater				**13**	**26.9**	**60.1**	**108 (61)**
				15.7	19.6	64.7	51 (36)
Golden Whistler		**1.9**	**6.1**	**43.2**	**32.4**	**16.4**	**213 (118)**
Rufous Fantail		**2.5**	**47.5**	**45**	**2.5**	**2.5**	**40 (34)**
	14.3	14.3	31.4	28.6	11.4		35 (18)
Grey Fantail	**1.2**	**1.0**	**9.2**	**43.5**	**31.6**	**13.5**	**490 (202)**
Satin Flycatcher					**54.6**	**45.4**	**22 (14)**
					40.0	60.0	50 (16)
Eastern Yellow Robin	**48.8**	**11.9**	**10.7**	**23.8**	**4.8**		**84 (55)**
Silvereye		**5.5**	**23.9**	**52.8**	**9.8**	**8.0**	**163 (81)**
		0.9	41.2	55.3	1.7	0.9	114 (41)

Table 3

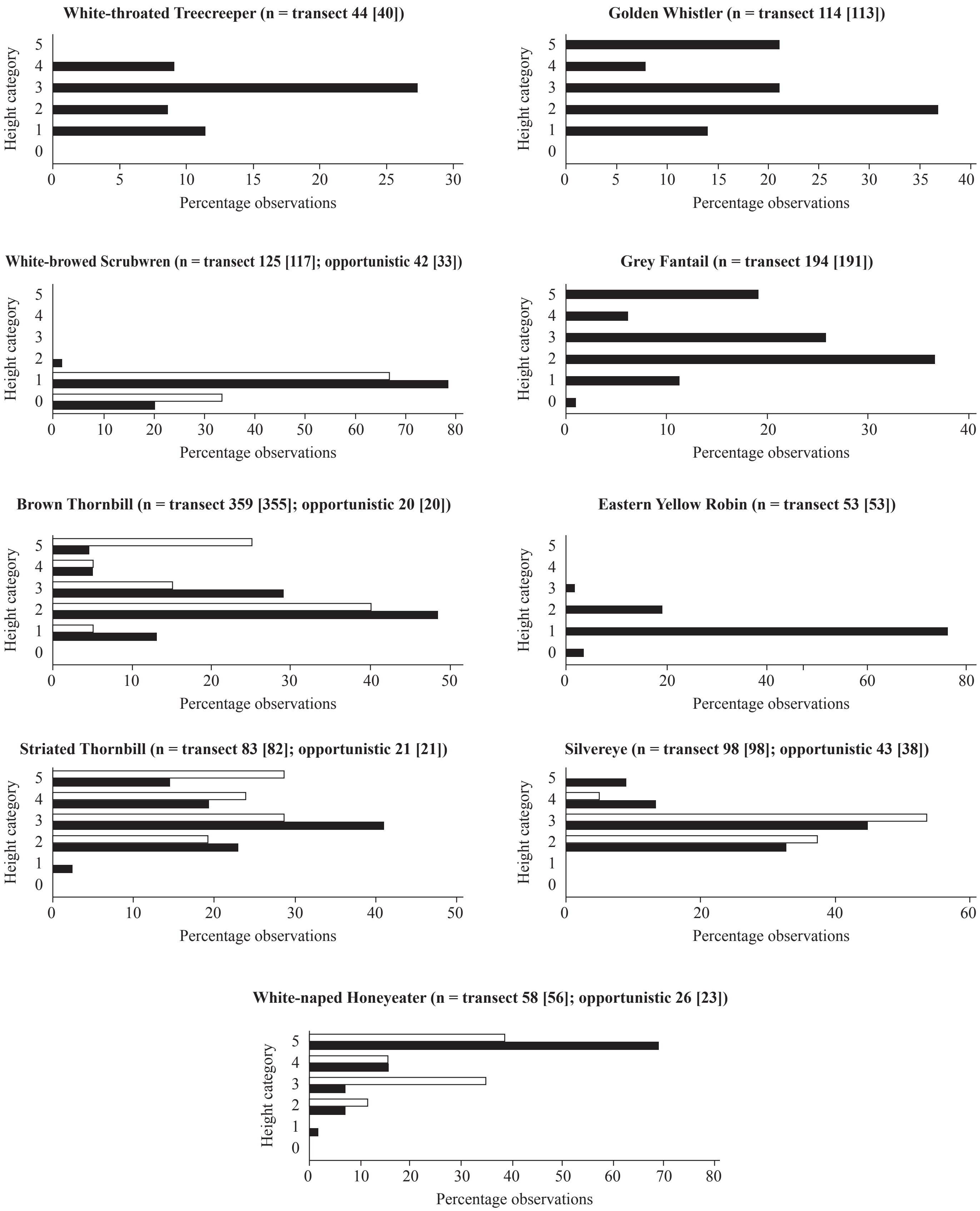
Matrix of percentage overlap indices for foraging stratum use. Values > 50% highlighted in bold font on light blue background. Species' acronyms given in Appendix 1.

	WBSW	**LBSW**	**BTH**	**STH**	**WNH**	**GWH**	**RFAN**	**GFAN**	**SFLY**	**YROB**	**SEYE**
WTTC	10.3	**70.7**	**82.8**	**77.1**	**66.7**	**89.8**	**56.1**	**90.1**	30.5	34.7	**76.7**
	WBSW	16.7	19.7	4.2	4.2	12.2	38.5	14.6	0.0	37.6	33.1
		LBSW	**78.2**	49.1	25.5	**61.8**	**60.0**	**52.7**	12.5	34.5	**66.1**
			BTH	**59.9**	36.3	**74.4**	**65.5**	**77.0**	23.3	**54.3**	**82.6**
				STH	**66.7**	**85.4**	41.6	**81.7**	**55.3**	28.6	**54.4**
					WNH	**56.3**	18.0	**53.4**	**72.3**	17.8	30.8
						GWH	**56.2**	**95.4**	48.8	35.7	**100.0**
							RFAN	**60.2**	5.0	38.0	**76.4**
								GFAN	45.1	39.0	**58.5**
									SFLY	4.8	17.8
										YROB	40.3

Table 4

Matrix of percentage overlap indices among species in use of foraging height categories. Values > 50% highlighted in bold font on light blue background. Species' acronyms given in Appendix 1.

	WTTC						
WBSW	12.9	**WBSW**					
BTH	**52.3**	14.6	**BTH**				
STH	47.4	3.9	**63.8**	**STH**			
WNH	24.6	18.5	36.4	45.5	**WNH**		
GWH	48.9	15.5	**80.5**	**68.7**	44.4	**GWH**	
YROB	21.6	**80.9**	33.7	23.0	25.5	34.6	**YROB**
GFAN	**53.4**	13.8	**83.2**	**95.4**	40.8	**94.3**	32.9



White-throated Treecreeper (n = transect 44 [40])

Golden Whistler (n = transect 114 [113])

White-browed Scrubwren (n = transect 125 [117]; opportunistic 42 [33])

Grey Fantail (n = transect 194 [191])

Brown Thornbill (n = transect 359 [355]; opportunistic 20 [20])

Eastern Yellow Robin (n = transect 53 [53])

Striated Thornbill (n = transect 83 [82]; opportunistic 21 [21])

Silvereye (n = transect 98 [98]; opportunistic 43 [38])

White-naped Honeyeater (n = transect 58 [56]; opportunistic 26 [23])

Figure 1: *Figure 1. Overall percentage of foraging conducted at various estimated heights by nine bird species. Only bird species for which there were ≥ 50 records are included. For each species, black bars are observations made on transects and (where present) light brown bars are opportunistic records. Height categories (m) are: 0 = ground, 1 = 0.1 – 3.1, 2 = 3.2 – 12.2, 3 = 12.3 – 24.4, 4 = 24.5 – 30.5 and 5 = > 30.5. n is number of observations (focal individuals). Note that focal individuals could contribute > 1 record per sequence, possibly in different height categories.*

Species' use of foraging strata and heights concurred. Thus White-browed Scrubwrens and Eastern Yellow Robins mainly foraged at lower heights (C0-C2), although less predictably Grey Fantails also foraged quite substantially in C0 and C1 (Fig. 1). White-naped Honeyeaters foraged mostly at greater heights (C5), Striated Thornbills and Golden Whistlers mainly in the intermediate to high categories and White-throated Treecreepers, Brown Thornbills and Silvereyes at intermediate heights (C2 and C3) (Fig. 1).

Five pairwise species combinations (18% of combinations) had overlap indices > 80% for foraging height (Table 4). Four species had overlap indices ≥ 50% with three or four other species. Brown Thornbills and Grey Fantails had the highest percentage overlap with other assemblage members (each ≥ 50% overlap with four species); they used a wide range of foraging heights, but especially C2, C3 and C5, which many other species also utilised.

Three species had limited percentage overlap with other assemblage members, exploiting either the comparatively little used lower height categories (C0–C2) or the moderately exploited highest category (C5).

Foraging substrates

Fourteen species were analysable for foraging substrate use. Foliage was the most frequently used substrate by nine of these species, but no other substrate was the most used substrate of more than one species (Table 5a). There was far less variation among species in their second most preferred foraging substrate. Tree branches occupied this rank for three species; all the other nine substrates were the second preference maximally of two species each (Table 5a).

White-browed Scrubwrens, both thornbill species, Rufous Fantails, Golden Whistlers, White-naped Honeyeaters, Rose Robins, Satin Flycatchers and Silvereyes used leaves and buds as their main, or a prominent, foraging substrate (Table 5a). Twigs and branches were used prominently by Golden Whistlers, Crested Shrike-Tits and Large-billed Scrubwrens. The latter two species, plus the White-throated Treecreeper, were the three bark-foraging species in the assemblage for which adequate data were obtained for analysis. The three species that hawked flying insects were the two fantails and the Satin Flycatcher. White-throated Treecreepers were the only common trunk-foraging specialists, and Eastern Yellow Robins and White-browed Scrubwrens the only significant ground-feeders (as alluded to under *Foraging strata*) (Table 5a).

Percentage overlap indices reflected these similarities and disparities in substrate use (Table 5b). A high degree of overlap (indices ≥ 50% with seven to nine other species) occurred among all the predominantly foliage-foraging species; however, only four pairwise species combinations (4% of combinations) had overlap indices > 80% for substrate use. A low degree of overlap (indices ≥ 50% with just one or two other species) characterised the few specialist foraging substrate users that predominantly exploited the air (Grey Fantail), ground cover (Eastern Yellow Robin), tree bark (Crested Shrike-Tit) and tree trunks (White-throated Treecreeper). Large-billed Scrubwrens, which obtained their food mostly from twigs and bark, were intermediate in overlap, having indices ≥ 50% with four species (Table 5b).

Foraging macro-behaviours

Fourteen species were analysable for foraging macro-behaviour use and the five identified macro-behaviours were used unevenly by these species. Gleaning and SS were the most common macro-behaviours of six and five of these species, respectively. The other three macro-behaviours were the most used methods maximally of one species (Table 6). Sally-snatching was also the second most frequently performed foraging behaviour of four species; the other macro-behaviours were the second most commonly employed methods of one to three species, respectively.

Gleaning was the most common foraging behaviour of White-throated Treecreepers, both scrubwren species, White-naped Honeyeaters and Silvereyes. It was also the second most common foraging behaviour of Striated Thornbills, Golden Whistlers, Crested Shrike-Tits and Rose and Eastern Yellow Robins (Table 6). Sally-snatching was the most common foraging behaviour of Golden Whistlers and both robin species, but was also used substantially by Brown Thornbills, White-naped Honeyeaters and Grey Fantails. Hawking was the principal foraging behaviour only of Grey Fantails, and the second most used macro-behaviour only of Rufous Fantails. Probing/prising was the principal foraging behaviour only of the Crested Shrike-Tit, but White-throated Treecreepers and Large-billed Scrubwrens also probed and prised substantially (Table 6).

Sixteen pairwise species combinations (18% of combinations) had overlap indices > 80% for foraging macro-behaviour use. Brown Thornbills exhibited a high degree of overlap (indices ≥ 50%) with nine species, reflecting their behavioural versatility; they employed both of the predominant foraging behaviours used in this assemblage (*i.e.* GL and SS) at high frequencies (Table 7). In contrast, Crested Shrike-Tits and Grey Fantails exhibited low interspecific overlap in foraging macro-behaviour, each specialising in a method infrequently used by most other assemblage members (PP and HWK, respectively). All other species exhibited moderate levels (indices ≥ 50% with five or six species) of macro-behavioural overlap with other assemblage members, because they predominantly used either GL or SS.

Foraging micro-behaviours

Foraging micro-behaviours were analysable for just five species:

[1] Eleven GL variations were recorded among these species (total n = 960). 'Perching upright' was the form used most by three of these species (White-browed Scrubwren, Brown Thornbill and Silvereye) and 'clinging' (White-naped Honeyeater) and 'ambulatory clinging' (White-throated Treecreeper) were used most by one species each (Table 8). This distribution was reflected in the percentage overlap indices (Table 9). Only one pairwise species combination (10% of combinations) had an index > 80% for micro-gleaning. Five (of 10) indices were > 50% and resulted mainly from multiple species using the two most common GL variations, 'perching upright' and 'clinging'.

[2] Three PP (n = 49) variations were observed in the Crested Shrike-Tit, the only analysable species for variants of this macro-behaviour. 'Clinging' was this species' most commonly used PP posture and, with 'perching upright', comprised 98% of the PP events it performed.

Table 5a

Overall percentage use of foraging substrates by fourteen common bird species. A = air, L = leaf, T = twig, Bch = branch, Tk = trunk, B = bud, F = Flower, G = ground, Bk = bark, O = other. *N* = number of records (focal individuals). Focal individuals could potentially use > 1 substrate in a foraging sequence. Upper row for each species contain transect data (*T*) in bold, lower row contain opportunistically (*O*) gathered data (smaller font). Highest two percentages in each data row underlined to facilitate visual assimilation of the patterns. Gaps indicate zero values. Only bird species for which overall ≥ 50 records were obtained are included. Overall N = 2,861 (1,012 birds).

Species		Foraging substrates										
		A	L	T	Bch	Tk	B	F	G	Bk	O	N
White-throated Treecreeper	***T***	**0.7**		**5.3**	**43.3**	**50.0**				**0.7**		**134 (41)**
	O			15.2	51.5	33.3						33 (11)
White-browed Scrubwren	***T***		**46.3**	**8.4**	**4.2**	**9.5**			**26.3**	**2.1**	**3.2**	**95 (57)**
	O		23.7	5.3	2.6	5.3			60.5	2.6		38 (13)
Large-billed Scrubwren	***T***		**7.1**	**28.6**	**16.7**	**14.3**				**26.1**	**7.2**	**42 (13)**
	O		48.5	15.2	3.0	3.0		3.0			12.1	33 (13)
Brown Thornbill	***T***	**2.4**	**74.7**	**9.1**	**2.8**	**2.5**	**0.3**	**4.9**		**2.8**	**0.5**	**889 (265)**
Striated Thornbill	***T***		**63.6**	**5.7**	**2.3**	**1.1**	**26.2**			**1.1**		**88 (33)**
White-naped Honeyeater	***T***	**3.2**	**43.6**	**16.0**	**22.3**	**1.1**	**1.1**			**12.7**		**94 (35)**
	O		20.6	35.3	14.7	2.9				26.5		34 (14)
Crested Shrike-Tit	***T***		**1.5**	**22.4**	**10.4**					**64.2**	**1.5**	**67 (32)**
Golden Whistler	***T***	**5.3**	**68.4**	**12.3**	**4.4**	**2.6**		**3.9**		**2.6**	**0.5**	**228 (91)**
Rufous Fantail	***T***	**29.7**	**51.6**	**4.7**		**1.6**		**7.8**		**2.6**		**64 (24)**
	O	45.5	39.4	9.1		3.0				3.0		33 (13)
Grey Fantail	***T***	**81.3**	**10.8**	**1.5**	**1.1**	**2.5**		**1.5**	**1.3**			**524 (166)**
Satin Flycatcher	***T***	**25.5**	**41.1**	**11.8**	**9.8**	**9.8**				**2.0**		**51 (16)**
Rose Robin	***T***	**11.1**	**37.8**	**15.6**	**20.0**	**11.1**		**4.4**		**8.8**		**45 (18)**
	O		8.8	67.7	2.9	2.9	5.9					34 (17)
Eastern Yellow Robin	***T***	**3.0**	**11.1**	**1.0**	**1.0**	**8.1**			**75.8**			**99 (56)**
Silvereye	***T***	**1.2**	**73.2**	**2.4**	**3.0**		**9.2**	**8.5**		**2.4**		**164 (62)**
	O		62.5				33.3	1.4		2.8		72 (22)

Table 5b

Matrix of percentage overlap indices for foraging substrate use. Indices > 50% highlighted in bold font on light blue background. Species' acronyms given in Appendix 1.).

	WBSW	**LBSW**	**BTH**	**STH**	**WNH**	**CST**	**GWH**	**RFAN**	**GFAN**	**SFLY**	**RROB**	**YROB**	**SEYE**
WTTC	**70.6**	**62.4**	12.0	9.4	30.1	17.1	13.7	7.7	5.7	26.3	37.8	10.8	6.8
	WBSW	34.5	**62.6**	**56.5**	**59.4**	17.7	**64.1**	**54.7**	16.8	**65.2**	**62.0**	47.5	**53.8**
		LBSW	26.2	17.3	**53.6**	**61.8**	29.5	9.0	12.1	40.2	**59.3**	17.2	14.9
			BTH	**74.1**	**62.1**	16.7	**92.2**	**62.9**	18.2	**59.9**	**70.5**	18.6	**87.4**
				STH	**54.9**	10.6	**76.4**	**56.1**	14.4	**51.3**	48.0	14.2	**78.6**
					WNH	40.6	**67.2**	**55.2**	17.5	**68.9**	**77.6**	17.1	**53.7**
						CST	21.3	8.8	4.1	25.1	35.5	3.5	9.3
							GWH	**69.7**	22.7	**67.2**	**74.9**	18.7	**81.3**
								RFAN	45.1	**74.9**	**62.2**	16.7	**65.4**
									GFAN	41.4	28.5	19.6	16.1
										SFLY	**81.5**	24.2	49.7
											RROB	24.2	**51.2**
												YROB	14.3

Table 6

Percentage use of five macro-foraging behaviours by 14 bird species. For each species, upper row shows transect data (in bold) and bottom row opportunistic data (smaller font). The two highest values in each row are underlined to facilitate assimilation of patterns. Gaps indicate zero values. N is number of records (number of contributing birds). Overall N = 2,628 (1,063 birds).

Species	Foraging macro-behaviours					
	Glean	Sally-snatch	Hawk	Probe	Litter-turn	N (birds)
White-throated Treecreeper	**86.9**	**0.8**		**12.3**		**122 (44)**
	74.3			25.7		35 (11)
White-browed Scrubwren	**86.0**	**2.2**		**12.3**	**11.8**	**93 (40)**
	75.7	2.7		2.7	18.9	37 (13)
Large-billed Scrubwren	**92.9**			**7.1**		**42 (13)**
	81.8	6.1		12.1		33 (14)
Brown Thornbill	**55.9**	**42.0**	**3.9**			**894 (270)**
Striated Thornbill	**28.4**	**70.5**		**1.1**		**88 (33)**
White-naped Honeyeater	**78.1**	**14.6**	**3.1**	**4.2**		**96 (38)**
	55.6	19.4		25.0		36 (17)
Crested Shrike-tit	**22.7**	**3**		**74.3**		**66 (21)**
Golden Whistler	**13.6**	**81.2**	**5.2**			**229 (113)**
Rufous Fantail	**12.5**	**57.8**	**29.7**			**64 (24)**
	15.2	36.4	48.5			33 (14)
Grey Fantail	**3.6**	**14.9**	**81.5**			**524 (166)**
Satin Flycatcher			**74.5**	**25.5**		**51 (17)**
Rose Robin	**6.7**	**82.2**	**11.1**			**45 (18)**
	2.9	88.2	8.8			34 (17)
Eastern Yellow Robin	**23.2**	**65.7**	**3.0**		**8.1**	**99 (48)**
Silvereye	**93.0**	**6.0**	**0.9**			**215 (81)**
	98.2	1.8				113 (41)

Table 7

Matrix of percentage overlap indices for foraging substrate use. Indices > 50% highlighted in bold font on light blue background. Species' acronyms given in Appendix 1.).

	WBSW	LBSW	BTH	STH	WNH	CST	GWH	RFAN	GFAN	SFLY	RROB	YROB	SEYE
WTTC	**90.9**	**94.0**	**63.9**	37.5	**90.3**	38.0	21.6	20.5	11.6	8.0	14.7	31.2	**93.0**
WBSW		**88.7**	**58.1**	31.7	**81.0**	27.5	15.8	14.7	5.8	2.2	8.9	31.2	**88.2**
LBSW			**55.9**	29.5	**82.3**	29.8	13.6	12.5	3.6	0.0	6.7	23.2	**92.9**
BTH				**70.4**	**72.6**	25.7	21.6	**56.6**	20.6	44.1	**50.8**	**67.3**	**62.9**
STH					44.1	26.8	**84.1**	**70.3**	18.5	**70.5**	**77.2**	**88.9**	34.5
WNH						41.5	31.3	30.2	21.3	17.7	24.4	40.8	**85.1**
CST							16.6	15.5	6.6	0.3	9.7	25.7	25.7
GWH								**75.5**	23.7	**79.7**	**93.1**	**82.3**	20.6
RFAN									48.2	**83.3**	**76.3**	**73.3**	19.5
GFAN										40.4	30.3	21.5	10.6
SFLY											**86.3**	**68.7**	7.0
RROB												**75.4**	13.7
YROB													30.2

Table 8

Percentage use of micro-foraging behaviours of ten bird species during transect surveys. Micro-behaviours are described below table. The two highest percentages for each species are underlined to facilitate easy assimilation of the patterns present. Gaps indicate zero values. Species' acronyms given in Appendix 1. Sample size = number of records of the macro-behaviour obtained for a species (number of focal individuals). Number of focal individuals was not recorded in three instances. Only species for which ≥ 49 records for the relevant macro-behaviour were obtained are included. var = variation.

Micro-behaviour	Micro-behaviour	Bird species				
		WTTC	WBSW	BTH	WNH	SEYE
GLEAN:	Perching upright	0.9	81.0	77.0	25.3	73.0
	Ambulation		19.0			1.0
	Cling	30.2		15.2	58.7	18.5
	Cling inverted	4.7		4.4	16.0	7.5
	Ambulatory cling	50.9		1.0		
	Ambulatory cling inverted	13.2				
	Jump up-jump back			1.4		
	Other Jump-up variants			1.0 (Four var)		0.5 (One var)
	Sample size:	**106 (57)**	**79 (38)**	**500 (214)**	**75 (31)**	**200 (80)**
		CST				
PROBE/PRISE:	Perching upright	34.7				
	Cling	63.3				
	Cling inverted	2.0				
	Sample size	**49 (23)**				
		BTH	STH	YROB	GWH	GFAN
SALLY-SNATCH:	Fly out-fly on to new perch	33.7	13.8	14.3	67.2	62.8
	Fly out-cling-fly on	9.1	50.0	1.6	3.3	3.9
	Fly out-hover-fly on	21.9	5.2		5.5	12.8
	Fly out-cling inverted-fly on	1.6	10.3			
	Fly out-flutter-fly on	2.1			0.6	1.3
	Fly out-cling-flutter-fly on	1.9	1.7	1.6	0.6	
	Fly out- hover-cling inverted-fly on	0.8				
	Fly out-hover-cling-fly on	0.8	5.2			
	Four other variants of fly out-move on to new perch	1.2				
	Fly out-fly back to same perch	11.8			14.2	7.7
	Fly out-cling-fly back	5.9	5.2	1.6	1.1	3.9
	Fly out-hover-fly back	7.0	3.5		4.9	5.1
	Fly out-flutter-fly back	1.1			2.7	1.3
	Fly out-cling-flutter-fly back	0.3	3.5			1.3
	Fly out-cling inverted-fly back	0.5	1.7			
	Three other variants of fly out-return to same perch	1.3				
	Fly down-fly up			81.0		
	Sample size	**375 (201)**	**57 (29)**	**60 (36)**	**183 (77)**	**78 (50)**
HAWK:	Fly out-fly on to new perch					37.7
	Fly out-hover-fly on					21.0
	Fly out-fly back to same perch					18.6
	Fly out-hover-fly back					22.6
	Sample size					**424 (105)**

Descriptions of micro-behavioural variants:

GLEANING –

Stationary perching upright: perching in upright standing posture.

Ambulation: gleaning during locomotion (other than flying).

Stationary cling: clinging to the vegetation from which food procured, not in upright posture.

Inverted stationary cling: clinging completely upside down to vegetation from which food procured.

Ambulatory cling: gleaning during locomotion involving clinging to substrate (e.g. WTTC feeding on tree trunk).

Inverted ambulatory cling: as in previous micro-behaviour, but moving downwards head first

Jump up-jump back: jump up to glean from surface above bird and then jump back down.

PROBING –

Three variants same as in gleaning, except that prey item obtained from beneath substrate.

SALLY-SNATCHING –

Fly out-fly on: fly out from perch, seize food item from vegetation and then fly to new perch.

Fly out-flutter-fly on: as in previous behaviour, but wings fluttered briefly while picking food off vegetation.

Fly out-cling-fly on: as in previous micro-behaviour, but clinging to vegetation to procure food item.

Fly out-cling inverted-fly on: as in previous micro-behaviour, but clinging upside down on target substrate.

Fly out-hover-fly on: hovering close to vegetation to pick item off it.

Fly out-cling-flutter-fly on: wings briefly fluttered while clinging to vegetation and picking food off it.

Fly out-hover-cling-fly on: hovering close to target vegetation before removing prey item while clinging to vegetation.

Fly out-hover-cling inverted-fly on: as in previous behaviour, but clinging upside down while removing prey item.

Fly out-fly back to same perch: fly out, snatch food item from vegetation and fly back to original perch.

Fly out-cling-fly back: as in previous behaviour, but clinging to target vegetation while removing prey item.

Fly out-hover-fly back: hovering near vegetation while removing food item from it.

Fly out-flutter-fly back: fluttering wings briefly while picking food item off vegetation.

Fly out-cling-flutter-fly back: clinging to vegetation while removing prey from it.

Fly out-cling inverted-fly back: as in previous behaviour, except clinging upside down while removing prey item.

Fly down-fly up: fly down from perch usually to ground, pounce on prey and fly back to original or a new perch.

HAWKING –

Four variants same as sallying equivalents, except that prey item snatched from the air.

[3] Twenty-four SS variations (n = 753 records) were recorded among the species analysed. The most common variations were ‘fly out-fly on’, ‘fly out-cling-fly on’, ‘fly out-flutter-fly on’, ‘fly out-cling-flutter-fly on’ and ‘fly down-fly up’; the other variations occurred at very low frequencies (Table 8). Brown Thornbills, Golden Whistlers and Grey Fantails used ‘fly out-fly on’ most. Striated Thornbills and Eastern Yellow Robins respectively used ‘fly out-cling-fly on’ and ‘fly down-fly up’ most, whilst ‘fly out-hover-fly on’ was quite prominent in the SS repertoires of Brown Thornbills and Grey Fantails. Golden Whistlers used ‘fly out-fly back’ quite frequently (Table 8).

No pairwise species combinations had an overlap index > 80% for micro-SS. Brown Thornbills, Golden Whistlers and Grey Fantails each had high (≥ 50%) overlap indices with two other SS species, mainly because they frequently used the most common variation, ‘fly out-fly on’. In contrast, neither Striated Thornbills nor Eastern Yellow Robins overlapped in their use of SS variations with any other species to this extent, principally because they mainly employed two less common variations, respectively ‘fly out-cling-fly on’ and ‘fly down-fly up’ (Table 9).

Foraging in two sexually dichromatic species

Sexual variation in foraging stratum use occurred in adult White-throated Treecreepers and Golden Whistlers. Male treecreepers appeared to use the tall tree stratum more, and shrub and canopy tree strata less, than females; male whistlers seemed to use the canopy tree stratum more and shrub layer less than females (Fig. 2). However, for all other foraging variables, adult males and females of each of these species seemed to forage very similarly.

SYNTHESIS AND DISCUSSION

Diet

Invertebrates (mainly insects) appeared to dominate the diet of the 18 analysable bird species, although small proportions of the diet of four of these species comprised fruit and nectar. A further 22 species in the study area provided insufficient records for meaningful, quantitative analysis. However, 13 of them are entirely or predominantly invertebrate consumers elsewhere, seven predominantly consume plant components supplemented with some insects, and one is largely granivorous (Higgins *et al.* 2006) (Table 10). Thus, overall the bird assemblage was quite strongly insectivorous; only six or seven constituent species consume more plant than invertebrate material and (adult) Red-browed Finches consume seeds and a very limited amount of invertebrate material. Recher *et al.* (1985) also found that in a bird assemblage in moist eucalypt forest in northern Victoria/southern New South Wales (NSW) insectivory predominated, nectarivory was exhibited by ~20% of species and granivory was rare.

Behaviour and forest attributes used in exploiting food resources

Only 9–14 bird species were analysable for the use of the various foraging variables, but the present synthesis also draws on qualitative information for other species in the study area obtained during this investigation and from the literature (Table 10).

Table 9

Matrices of percentage overlap indices in gleaning and sally-snatching micro-foraging behaviours. Indices ≥ 50% highlighted in bold and on light green background. Species’ acronyms in Appendix 1.

GLEANING MICRO-VARIATIONS:

	WBSW	**BTH**	**WNH**	**SEYE**
WTTC	19.9	21.1	**64.3**	24.1
WBSW		**77.0**	25.3	**74.0**
BTH			44.5	**92.7**
WNH				**51.3**

SALLY-SNATCHING MICRO-VARIATIONS:

	STH	**YROB**	**GWH**	**GFAN**
BTH	41.7	18.6	**52.0**	**68.4**
STH		18.6	31.9	32.9
YROB			18.1	17.5
GWH				**79.2**

(1) Use of vegetation strata and foraging heights

The short and tall tree layers were the strata used most for foraging. These strata were exploited substantially by eight and six of the twelve analysable species, respectively. In marked contrast, the canopy and shrub strata were each used extensively by just three species, whilst only one or two species foraged substantially on the ground and in the ‘herb’ layer (Table 2). Qualitative information for the other 22 species at the site revealed a very similar pattern, except that the ground surface and cover were used by as many species as the intermittent tall and short tree strata (Table 10). In Recher *et al.*’s (1985) study, ~66% of foraging occurred equally in the shrub (0.2–≤ 4 m) and sub-canopy (4.1–10 m) layers, the remainder being split evenly between the ground and canopy (>10 m) strata. Serong and Lill (2016) noted that most foraging occurred in the shrub stratum in the oldest age-classes (60+ years) of wet temperate forest in the Victorian Central Highlands. Bell *et al*. (2010) demonstrated that 74% of species in eucalypt-dominated sites along an aridity gradient in south-western Australia favoured arboreal foraging. More broadly, Loyn (2002) showed that ecological segregation among co-habiting bird species in SE Australian forests and woodland often involves using different foraging strata.

(2) Use of substrates

Foliage, twigs, shed and attached bark and the air were the foraging substrates used by the most bird species (variously 4 to 11 of 12 analysable species); no other substrate was exploited by more than three analysable species (Table 5). Foliage and twigs were used for insectivory by a broad range of generalist insectivore and partial insectivore species, whereas bark and the air were mainly exploited by a few specialist foragers. Qualitative information indicates that foliage and the ground (including soil and leaf litter) are the foraging substrates most used by 22 other species recorded in the study site, but inflorescences, racemes and tree trunks and branches are also exploited substantially (Table 10).

Recher *et al.* (1985) similarly found that foliage was the main foraging substrate of birds inhabiting woodlots in moist *Eucalyptus* forest in NSW and Victoria. The ground acted as a food substrate only about half as often and ~ 11% of prey

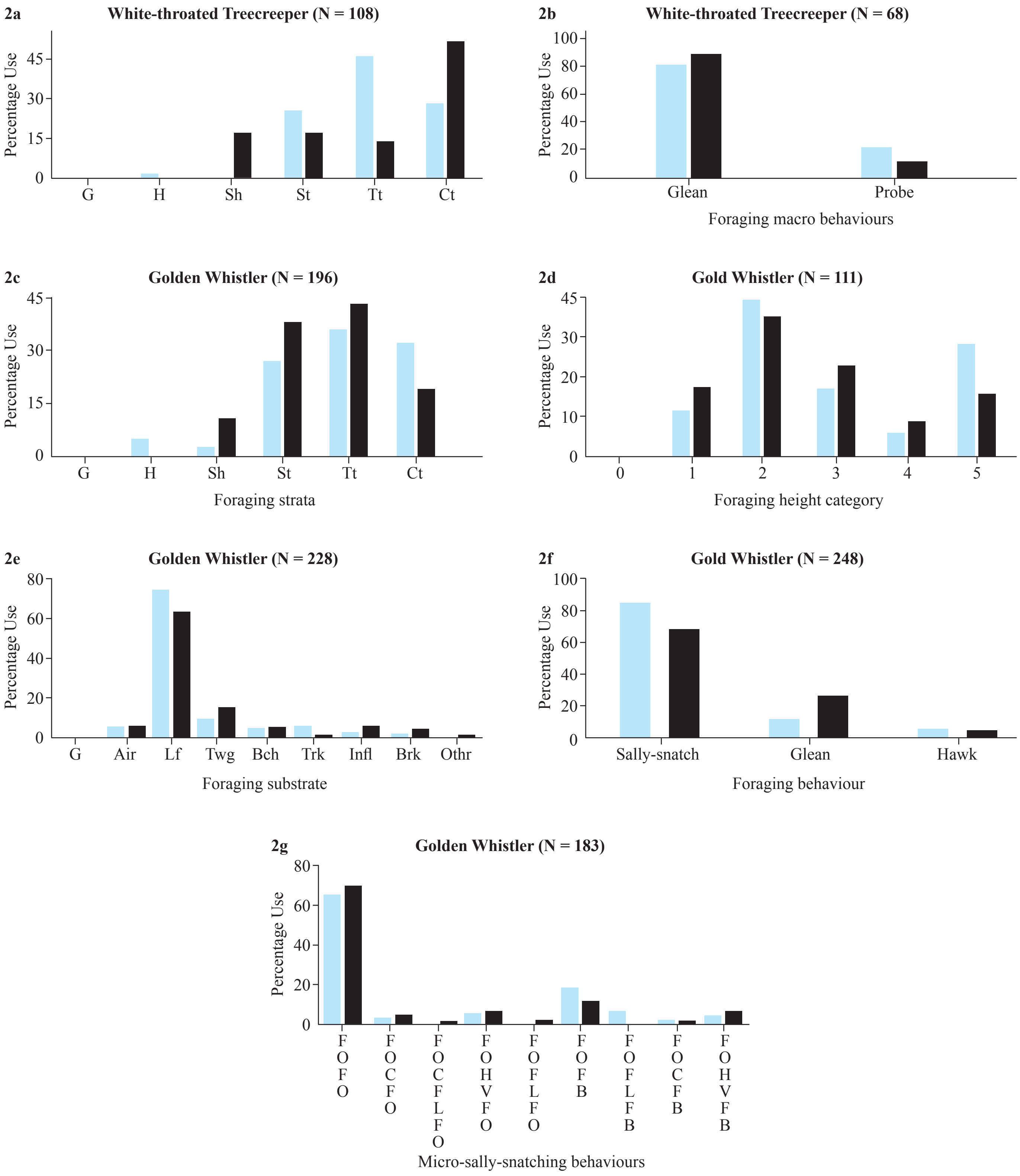


Figure 2: *Overall percentage use of various foraging variables by adult male and female-plumaged White-throated Treecreepers and Golden Whistlers. In all charts, black columns are males and light blue columns are female-plumaged birds. Strata are: G = ground, H = herb layer, Sh = shrub, St = small tree, Tt = tall tree and Ct = canopy tree. Foraging heights (m) are: 0 = ground, 1 = 0.1 – 3.1, 2 = 3.2 – 12.2, 3 = 12.3 – 24.4, 4 = 24.5 – 30.5 and 5 = > 30.5. Substrates are: G = ground, Air, Lf = leaf, Twg = twig, Bch = branch, Trk = trunk, Infl = inflorescence, Brk = bark and Other. Micro-sally-snatching behaviours are: FOFO fly out-fly on, FOCFO fly out-cling-fly on, FOCFLFO fly out-cling-flutter-fly on, FOHVFO fly out-hover-fly on, FOFLFO fly out-flutter-fly on, FOFB fly out-fly back to same parch, FOFLFB fly out-flutter-fly back, FOCFB fly out-cling-fly back and FOHVFB fly out-hover-fly back.*

captures were of flying insects. In contrast, Serong and Lill (2016) recorded that tree branches were the most used foraging substrate in wet temperate forest at various stages of secondary succession in the Victorian Central Highlands; foliage and inflorescences were exploited relatively infrequently. However, foliage was also the predominant foraging substrate in Indian mixed deciduous forest (Thivyanathan 2016), North American montane hardwood and subalpine forest (Sabo and Holmes 1983) and Malaysian mixed dipterocarp forest (Mansor and Sah 2012). Its prevalence as a food substrate for insectivorous forest birds probably reflects the fact that it attracts more insects than do other plant components because of its high content of photosynthetic products and nutrients (Kwok 2009).

(3) Use of macro- and micro-behaviours

Gleaning and SS were by far the most extensively used foraging macro-behaviours, each being the predominant foraging behaviour of six of the 14 analysable species. In contrast, HWK and PP were the predominant foraging behaviours of just one analysable species each. Qualitative information also indicated that GL is the major foraging behaviour of 15 of 22 other species recorded at the site, but SS and PP are also exhibited by four and five of these species, respectively (Table 10).

Serong and Lill (2016) also found that GL was by far the most common prey capture method in wet temperate forest in the Victorian Central Highlands. SS was also moderately common but, as in my investigation, PP and HWK were restricted to a few species. Recher *et al*. (1985) report a similar distribution of foraging behaviours in woodlots in eucalypt forest and woodland in NSW, except that HWK was slightly more common than in the present investigation and that of Serong and Lill (2016). Bell *et al*. (2010) reported that GL comprised 69% of foraging behaviour in bird assemblages in eight *Eucalyptus*-dominated sites in south-western Australia. It was also the most common foraging behaviour in bird assemblages in Indian tropical mixed dry deciduous forest (Thivyanathan 2016) and in North American montane hardwood and subalpine forests (Sabo and Holmes 1983). However, in marked contrast, sallying and hawking were the predominant foraging macro-behaviours in Malaysian mixed lowland dipterocarp forest (Mansor and Sah 2012) and southern Indian thorn forest (Golka 2001), respectively.

Foraging modes *inter alia* presumably maximize the net rate of energy gain per unit foraging time (Bautista *et al*. 2000). The main foraging macro-behaviours observed in the present study can realistically be ranked in terms of estimated energy expenditure (from greatest to least): HWK, SS, PP and GL. Gleaners tend to be small and hence have relatively high mass-specific energy requirements. However, they may be able to subsist on prey yielding a comparatively small individual energy reward provided that such items are abundant, precisely because GL is energetically a relatively low-cost behaviour. The co-existence of several foliage-gleaning species in the study assemblage suggested that insects were indeed abundant on this substrate. Bark PP, as displayed by Crested Shrike-Tits, is probably costlier than GL because it requires: (a) considerable force and (b) a substantial time expenditure per item acquired because many of the prey are concealed. Unlike GL and SS, it was the predominant foraging mode of only one species and so interspecific competition for bark insect prey was probably limited among the predominant species in this assemblage. Sally-snatching is likely to be more energetically costly than PP because it usually involves flight. However, its main benefit presumably lies in providing access to prey that are otherwise impossible or difficult to acquire, particularly by relatively heavy birds lacking agility. Hawking (especially hover-hawking) is presumably costlier energetically than SS because it consists entirely of flying (Dial *et al*. 1997), so one would predict that the individual prey of hawkers must provide a relatively high energy reward. However, this logic requires some qualification for the principal hawker in my study, the Grey Fantail, because many of its hawking manoeuvres involved apparent capture of multiple prey items, which was facilitated by its wide gape, a common trait in hawking flycatchers.

'Perching upright' was the predominant micro-behavioural GL posture. This is not surprising, as it is probably the least energetically expensive GL variation observed. 'Clinging' is limited by body size and was restricted to relatively small species (*e.g.* thornbills, treecreepers and small honeyeaters). 'Fly out-fly on' was the predominant SS variation (occurring in three of five species), with 'fly out-cling-fly on' and 'fly down-fly up' predominating in just Striated Thornbills and Eastern Yellow Robins, respectively. The main PP species, the Crested Shrike-Tit, commonly exploited insects found in hanging, decorticating bark, and so it probed while 'clinging' about twice as often as it probed while 'perching upright'.

Presumably the GL and SS variations observed are adaptive. Theoretically, for example, 'fly out-hover-fly on or back' could enable some SSs to obtain prey from foliage insufficiently robust and/or too flexible to snatch prey from in normal flight, or cling to or perch on. However, this cannot entirely explain hovering, because there were variations in which it was preceded or succeeded by clinging to the target foliage (Table 6). Conceivably it could sometimes allow a foraging bird to make a closer, more accurate assessment of the likely rewards and risks of landing on the target substrate to attack a prey item. Whatever the explanation for the hovering variant 'fly out-fly on or back', the benefits of using it must be substantial, because hovering is energetically costly. It requires the generation of much force and is therefore confined to small birds, because available power does not increase as a function of body size as rapidly as does the power required for flight. Species using hovering are also likely to be slow flyers, because it requires wings with a high aspect ratio (Dial *et al*. 1997). Relatively few studies have examined avian foraging micro-behaviours quantitatively, although Serong (2007) lists the bird species in a Victorian tall wet temperate forest that exhibited some of the GL and SS variations discussed here.

Sex-specific foraging

Major theories concerning the evolution of sex differences in avian foraging contend variously that they: (1) result from, and reduce, intersexual resource competition, (2) are the consequence of foraging constraints associated with reproductive or other sex-related activities, such as nest and song post locations, or (3) are a secondary consequence of sexual selection that results in sexual size dimorphism and hence differing nutritional requirements in males and females (Mand *et al*. 2013).

Table 10

Qualitative summary of foraging behaviour of twenty-two bird species recorded in the study site, for each of which < 50 foraging records were obtained. Not all descriptions are from studies conducted in temperate wet forests. beh = behaviour.

Species	Diet	Site(s)	Principal substrate(s)	Main beh (s)	Sources
Yellow-tailed Black-Cockatoo	seeds, insect larvae	tall and canopy trees	trunk, branch, cones, growing tips	excavate, manipulate, probe	1, 4, 22
Sulphur-crested Cockatoo	seeds, fruit, inflorescences, roots, insect larvae	ground, herb, short, tall and canopy tree	raceme, soil	glean, manipulate, dig	9, 10
Gang-Gang Cockatoo	seeds, fruit, nuts, insect larvae	tall and canopy tree	raceme, seed capsule	glean, manipulate, tear	11, 12
Crimson Rosella	seeds, buds, pith, sori, inverts	ground, shrubs, short, tall and canopy trees	ground, foliage, bark, branch	glean, manipulate	3, 23
Superb Lyrebird	inverts	ground	soil	dig	2
Fan-tailed Cuckoo	inverts, verts, fruit	ground,	ground, bark	sally-snatch, glean, hawk, pounce	21
Shining Bronze-Cuckoo	inverts	short and tall trees, shrubs	Foliage, bark, trunk	glean	22
Red-browed Treecreeper	insects, spiders	tall trees, shrub	bark on trunks and branches, ground	glean, probe, prise	1, 13, 14, 21, 23
Spotted Pardalote	inverts, exudates	tall trees	foliage	glean	5, 28
Crescent Honeyeater	nectar, fruit, insects, exudates	tall and canopy trees, shrubs	inflorescence, foliage, trunk, twig, branch	probe, glean, sally-snatch	6,18, 19, 22
Eastern Spinebill	nectar, inverts	herb, shrub, short tree	flower, foliage	probe, glean	1, 7, 22
Yellow-faced Honeyeater	nectar, pollen, fruit, seeds, exudates, inverts	shrub, short tree	flower, foliage, bark	glean, probe, sally-snatch	17, 21
White-eared Honeyeater	insects, nectar, fruit, exudates,	tall and canopy tree	bark on trunks and branches, foliage, inflorescences	probe, glean	14, 15, 16
Eastern Whipbird	inverts, verts	ground	leaf litter, fallen bark	litter turn, probe	8, 21, 28
Olive Whistler	inverts, fruit	shrub, herb		glean	1, 22, 28
Rufous Whistler	inverts, seeds, fruit	shrub, short and tall tree	Foliage, bark, air	sally-snatch, glean, hawk	1, 17, 21
Grey Shrike-Thrush	inverts, verts, eggs, carrion, fruit, seed	ground short and tall tree	ground, branch, trunk, foliage	glean	1, 17, 23
Raven sp.	inverts, verts, carrion, refuse, fruit, seeds, nectar	ground, short and tall tree	ground, foliage	glean, probe, manipulate, sweep	20, 26
Pink Robin	inverts	ground, shrub	ground, foliage	glean, sally-snatch	17, 22, 28
Common Blackbird	inverts, fruit, seeds	ground, short tree	ground, leaf litter	litter turn, glean	17
Bassian Thrush	inverts, fruit	herb, ground	ground, shrub	litter turn, probe	22, 23, 27
Red-browed Finch	seed, inverts	ground, herb	raceme, ground	glean	1, 24, 25

References: 1 this study, 2 Lill (1996), 3 Magrath and Lill (1983), 4 Mcinnes *et al*. (1978), 5 Woinarski (2008), 6 Thomas (1980), 7 Ford and Pursey (1991), 8 Rogers and Mulder (2004), 9 Emison and Nicholls (1992), 10 Noske (1980), 11 Osborne and Green (1992), 12 Recher and Holmes (1985), 13 Noske (1979), 14 Wykes (1985), 15 Paton (1980), 16 Loyn (1980), 17 Recher *et al.* (1985), 18 Routley (1980), 19 Paton and Ford (1977), 20 Lill and Hales (2015), 21 Holmes and Recher (1986), 22 Thomas (1980b), 23 Recher (2016), 24 Todd (1996), 25 Read (1994), 26 Stewart (1997), 27 Edlington (1983), 28 Thomas (1978).

Adult male and female Golden Whistlers are similarly-sized (Bell 1986) and generally foraged very similarly, as noted in other studies in mature wet temperate forest (Recher and Holmes 2000; Mac Nally 2000; Serong and Lill 2016). However, males appeared to forage in the canopy more, and possibly the shrub and short tree strata less, than females. This seemed to result, on average, in males foraging at greater heights than females, as recorded in several other temperate forest habitats (Bridges 1980; Paton 1981; Bell 1986; Wheeler and Culver 1996). This height disparity cannot be a product of sexual size dimorphism nor, as it was not restricted to the breeding season, of constraints imposed by reproduction, but it could potentially reduce intersexual food competition. However, it should be noted that Recher and Holmes (2000), Mac Nally (2000) and Serong and Lill (2016) found no sex difference in foraging heights in this species.

Male White-throated Treecreepers are slightly larger than females (Noske 1986) and appeared to forage in the tall tree layer more, and the canopy and shrub strata less, than did females. There was no sex-specificity in other foraging variables (Bell 1986; Recher and Holmes 2000). Noske (1986) documented sex differences in foraging substrates, but not heights, in this species in dry sclerophyll eucalypt forest, whereas Recher and Holmes (2000) reported sex differences in foraging height, substrate and behaviour in populations in regrowth and mature temperate eucalypt forest. The sex differences in foraging in the size-dimorphic treecreepers in the present investigation could potentially be an adaptive consequence of either sexual selection or intersexual competition. However, the disparity in foraging strata use was more complex than that in Golden Whistlers and it is less clear theoretically whether it could limit intersexual competition.

Species-specific foraging viewed from three perspectives:

(1) Overlap indices

Considering all five foraging variables *in toto*, 60% of the 306 pairwise species overlap indices calculated were ≥ 50%. However, no pairwise species combinations had overlap indices > 70% for all five, or even four, of the foraging variables, and only four species combinations had them for three foraging variables (Golden Whistler × Brown Thornbill, Striated Thornbill and Grey Fantail; Silvereye × Brown Thornbill). Only one species combination (White-browed Scrubwren × Grey Fantail) had very low overlap indices (< 30%) for four foraging variables, and three species combinations (White-browed Scrubwren × White-throated Treecreeper, White-naped Honeyeater and Golden Whistler) had them for three variables. Thus overall, the overlap indices indicated some interspecific overlap in foraging behaviour, particularly for the Golden Whistler, but the White-browed Scrubwren appeared to occupy a relatively exclusive foraging niche.

(2) Individual foraging variables

At the individual foraging variable level, stratum use and type of micro-GL behaviour employed varied *least* among analysable assemblage member species, both having overlap indices ≥ 50% among half of the member species. In contrast, foraging height and type of micro-SS behaviour used varied *most* among analysable assemblage member species, both having overlap indices of < 50% in ~70% of pairwise species comparisons. Foraging substrate use and macro-behaviours were intermediate in overlap among species, having indices < 50% in 57% and 63%, respectively, of species interactions. Thus, at this level of resolution, there were indications of both niche segregation and overlap.

Foraging substrates, heights and behaviours varied among species in insectivorous bird assemblages inhabiting *Eucalyptus* forest and woodland in NSW (Recher *et al*. 1985) and among honeyeaters in Western Australian *Eucalyptus* woodlands (Recher *et al*. 2016). Loyn (2002) concluded more generally that using different foraging strata and substrates was important in ecological segregation of co-habiting bird species in SE Australian temperate forests and woodlands. These variables are also important to varying degrees in niche segregation in bird assemblages in forest habitats elsewhere, including North America, South India, Europe, Malaysia and the West Indies (Sabo and Holmes 1983; Latta and Wunderle 1998; Styring and Zakaria 2004; Somasudaram and Vijayan 2008; Kornan *et al*. 2013).

(3) Foraging 'guilds'

Using a categorization based simply on type of foraging behaviour, two main 'guilds' were recognisable among the analysable species:

(a) the six primarily GL species showed substantial overlap in substrate use. Four of them were principally foliage gleaners (White-browed Scrubwren, White-naped Honeyeater, Silvereye and Brown Thornbill), but of these the scrubwren mostly exploited 'herb' and shrub foliage, whereas the other three species mainly exploited tree foliage. The White-naped Honeyeater was further distinguished by its tendency to exploit the highest tree layer (canopy) and to predominantly use the 'clinging' variation of GL, whereas Brown Thornbills and Silvereyes mostly used the lower tree layers and the 'perching upright' variation. The two GL species that did not significantly exploit foliage mainly used tree trunks and branches (White-throated Treecreeper) and bark and twigs (Large-billed Scrubwren), respectively, as their main foraging substrates. Thus, among GL 'guild' member species there was some foraging behaviour diversity that would probably translate into dietary differences.

(b) Five of the six primarily SS analysable species overlapped strongly because they foraged mainly in foliage. However, there was some variation among them in foraging strata use, because Rufous Fantails and Satin Flycatchers exhibited biases for the shrub and tall tree layers, respectively, whereas Striated Thornbills and Golden Whistlers both favoured the short tree layer, but predominantly used different SS variations ('fly out-fly on' and 'fly out-cling-fly on', respectively). The Grey Fantail was secondarily an SS species; its SS profile closely resembled that of Golden Whistlers, but it used the 'fly out-hover-fly on' variation more.

Additionally, two analysable species hawked insects in the air to a substantial extent; the Grey Fantail was primarily a hawker, whereas the Rufous Fantail was only secondarily a hawker. The latter species foraged mainly in the shrub and small tree layers, whereas the former only exploited the tree strata prominently. As observed elsewhere (Noske 2003), the Crested Shrike-Tit was a specialist bark forager, employing tearing and probing to access insects beneath attached and decorticating bark. No other analysable species exploited this niche substantially, but Eastern Whipbirds and Red-browed Treecreepers, which both occurred at the study site, are also bark foragers (Table 8).

Even if the insect fauna varied among foraging strata and substrates, there was probably considerable overlap in foraging ecology within and between the SS and GL 'guilds'. However, there was some very clear resource partitioning in the assemblage too, because probing, hawking and trunk-gleaning presumably gave their few proponents access to food resources largely unexploited by most GL and SS species.

Caveats

A limitation of the investigation was that the focus on one relatively small area of forest precluded valid statistical analysis of results. Some researchers reporting similar studies have simply ignored this problem, although admittedly it would be difficult to eliminate it. Further, although considerable effort was expended on observation over two years, insufficient data were obtained to quantitatively characterise the foraging behaviour of many less common species. Notwithstanding these limitations, the study provides some useful insights into the likely role of foraging niche segregation in shaping a Mountain Ash forest bird assemblage. From a management perspective, it highlights the importance of the short and tall tree strata in the food acquisition of assemblage member species.

ACKNOWLEDGEMENTS

I thank Graham Fry and another reviewer for valuable comments on the manuscript.

REFERENCES

Alatalo, R.V. and Alatalo, R.H. (1979) Resource partitioning among a flycatcher guild in Finland. *Oikos* **33**: 46–54.

Antos, M.J., Bennett, A.F. and White, J.G. (2008). Where exactly do ground-foraging woodland birds forage? Foraging sites and microhabitat selection in temperate woodlands of southern Australia. *Emu* **108**: 201–211.

Ashton, D. (1975). The seasonal growth of *Eucalyptus regnans* F. Muell. *Australian Journal of Botany* **23**: 239–52.

Bautista, L.M., Tinbergen, J. and Kacelnik, A. (2000). To walk or to fly? How birds choose among foraging modes. *Proceedings of National Academy of Sciences* **98**: 1089-1094.

Bell, H.T. (1986). Sexual differences in the behaviour of wintering golden whistlers *Pachycephala pectoralis* at Wollomombi, N.S.W. *Emu* **86**: 2-11.

Bell, D.T., Bell, R.C. and Cousin, J.A. (2010). Winter foraging patterns in the avifauna from south-western Australia with special reference to the Acanthizidae and Meliphagidae. *Amytornis* **2**: 1-13.

Bridges, L. (1980). *Some examples of the behaviour and feeding ecology of the Rufous (Pachycephala rufiventris) and Golden (Pachycephala pectoralis) Whistler*. B.Sc. (Hons) thesis, University of New England, Armidale, N.S.W.

Brooker, M.G., Braithwaite, R.W. and Estbergs, J.A. (1990). Foraging ecology of some insectivorous and nectarivorous species of birds in forests and woodlands of the wet-dry tropics of Australia. *Emu* **90**: 215-230.

Buij, R., Van der Goes, D., De Iongh, H.H, Gagare, S., Haccou, P., Komdeur, J. and De Snoo, G. (2012). Interspecific and intraspecific differences in habitat use and their conservation implications for Palaearctic harriers on Sahelian wintering grounds. *Ibis* **154**: 96–110.

Burns, E.L., Lindenmayer, D.B., Stein, J., Blanchard, W., McBurney, L., Blair, D. and Banks, S.C. (2015). Ecosystem assessment of mountain ash forest in the Central Highlands of Victoria, south-eastern Australia. *Austral Ecology* **40**: 386-399.

Cale, P. (1994). Temporal changes in the foraging behaviour of insectivorous birds in a sclerophyll forest in Tasmania. *Emu* **94**: 116-126.

Dial, K.P., Biewener, A.A., Tobalske, B.W. and Warrick, D.R. (1997). Mechanical power output of bird flight. *Nature* **390**: 67-70.

Edlington, J.S.L. (1983). White's Thrush: some observations on its ecology and feeding behaviour. *South Australian Ornithologist* **22**: 57-59.

Emison, W. B. and Nicholls, D. G. (1992). Notes on the feeding patterns of the Long-billed Corella, Sulphur-crested Cockatoo and Galah in southeastern Australia. *South Australian Ornithologist* **31:** 117 121.

Falconer, C.M., Mallory, M.L. and Nol E. (2008). Breeding biology and provisioning of nestling snow buntings in the Canadian High Arctic. *Polar Biology* **31**: 483–489.

Ford, H.A., Noske, S. and Bridges, L. (1986). Foraging of birds in eucalypt woodland in north-eastern New South Wales. *Emu* **86**: 168-179.

Ford, H.A. and Pursey (1991). Status and feeding of the Eastern Spinebill *Acanthorhynchus tenuirostris* at the New England National Park, North-eastern NSW. *Emu* **82**: 203–211.

Frith, D.W. (1984). Foraging ecology of birds in an upland tropical rainforest in North Queensland. *Australian Wildlife Research* **11**: 325 – 347.

Golka, V. (2001). Foraging patterns of birds in thorn forest of Mudumalai Wildlife Sanctuary, south India. *Journal of South Asian Natural History* **5**: 143-152.

Hannah D., Woinarski J. C. Z., Catterall C. P., McCosker J. C., Thurgate N.Y. and Fensham R. J. (2007) Impacts of clearing, fragmentation and disturbance on the bird fauna of Eucalypt savanna woodlands in central Queensland, Australia. *Austral Ecology* **32:** 261–76.

Higgins, P.J., Peter, J.M. and Cowling, S.J. (Eds.) (2006). *Handbook of Australian, New Zealand and Antarctic Birds. Volume 7: Boatbill to Starlings.* Oxford University Press, Melbourne.

Hogstadt, O. (2010). Sex differences in foraging behaviour in the Lesser Spotted Woodpecker. *Ornis Norvegica* **33**: 135-146.

Holmes, R.T. (1986). Foraging patterns of forest birds: male–female differences. *Wilson Bulletin* **98**: 196-213.

Holmes, R.T., Bonney, R.E. and Pacala, S.W. (1979) Guild structure of the Hubbard Brook bird community: a multivariate approach. *Ecology* **60**: 512–520.

Holmes, R.T. and Recher, H.F. (1986). Determinants of guild structure in forest bird communities: an intercontinental comparison. *Condor* **88**: 427-439.

Jankowski, J.E., Graham, C.H., Parra, J.L., Robinson, S.K., Seddon, N., Touchton, J.M. and Tobias, J.A. (2012). The role of competition in structuring tropical bird communities. *Ornitologia Neotropical* **23**: 115-124.

Korňan, M., Holmes, R. T., Recher, H.F., Adamík, P. and Kropil, R. (2013). Convergence in foraging guild structure of forest breeding bird assemblages across three continents is related to habitat structure and foraging opportunities. *Community Ecology* **14**: 89-100.

Krebs, C.J. (2014). *Ecological methodology 3rd edn*. Addison-Wesley Educational Publications Inc.

Kwok, H.K. (2009). Foraging ecology of insectivorous birds in a mixed forest of Hong Kong. *Acta Ecologica Sinica* **29**: 341-346.

Lara, C., Pérez, B., Castillo-Guevara, C. and Serrano-Meneses, M.A. (2015). Niche partitioning among three tree-climbing bird species in subtropical mountain forest sites with different human disturbance. *Zoological Studies* **54**: 28.

Latta, S.C. and Wunderle, J.M. (1998). The assemblage of birds foraging in native West Indian Pine (*Pinus occidentalis*) forests of the Dominican Republic during the nonbreeding season. *Biotropica* **30**: 645-656.

Lewis, S., Benvenuti, S., Dall'Antonia, L., Griffiths, R., Money L., Sherratt, T.N., Wanless, S. and Hamer, K.C. (2002). Sex-specific foraging behaviour in a monomorphic seabird. *Proceedings of Royal Society of London*. B **269**: 1687–1693.

Lill, A. (1996). Foraging behavioural ecology of the superb lyrebird. *Corella* **20**: 77–87.

Lindenmayer, D. B. (2009). *Forest pattern and ecological process: A synthesis of 25 years of research*. CSIRO Publishing, Melbourne.

Lindenmayer, D., Blair, D., McBurney, L. and Banks, S. (2015). *Mountain Ash: fire, logging and the future of Victoria's giant forests*. CSIRO Publishing, Melbourne.

Loyn, R.H. (1980). Bird populations in a mixed eucalypt forest used for production of wood in Gippsland, Victoria. *Emu* **80**: 145-156.

Loyn, R.H. (1985). Bird populations in successional forests of mountain ash *Eucalyptus regnans*. *Emu* **85**: 213–230.

Loyn, R.H. (2002). Patterns of ecological segregation among forest and woodland birds in south-eastern Australia. *Ornithological Science* **1**: 7-27.

Mac Nally, R. (1995). On large scale dynamics and community structure in forest birds: lessons from some eucalypt forests in southeastern Australia. *Philosophical Transactions of Royal Society, London (B)* **350**: 369-379.

Mac Nally, R. (2000). Coexistence of a locally undifferentiated foraging guild: avian snatchers in a southeast Australian forest. *Austral Ecology* **25**: 69-82.

Magrath, R. and Lill, A. (1983). The use of time and energy in the Crimson Rosella in a temperate wet forest in winter. *Australian Journal of Zoology* **31**: 903-912.

Mand, R., Rasmann, E. and Magi, M. (2013). When a male changes his ways: sex differences in feeding behavior in the pied flycatcher. *Behavioral Ecology* **24**: 853-858.

Mansor, M.S. and Modh Sah, S.A. (2012). Foraging patterns reveal niche separation in tropical insectivorous birds. *Acta Ornithologica* **47**: 27-36.

McArthur, R.H. (1958). Population ecology of some warblers of northeastern coniferous forests. *Ecology* **39**: 599-619.

McInnes, R. S., Carne, P.B. and Carne, P.B. (1978). Predation of cossid moth larvae by Yellow-tailed Black Cockatoos causing losses in plantations of *Eucalyptus grandis* in north coastal New South Wales. *Australian Wildlife Research* **5**: 101–21.

Noske, R.A. (1979). Co-existence of three species of treecreepers in north-eastern New South Wales. *Emu* **79**: 120-128.

Noske, R. (1980). Cooperative breeding by treecreepers. *Emu* **80**: 35-36.

Noske, R. (1986). Intersexual niche segregation among three bark-foraging birds of eucalypt forest. *Australian Journal of Ecology* **11**: 255-267.

Noske, R. (2003). Sexual differences in the foraging behaviour of Crested Shrike-tits *Falcunculus frontatus* in winter. *Emu* **103**: 271-277.

Osborne W.S. and Green, K. (1992). Seasonal changes in composition, abundance and foraging behaviour of birds in the Snowy Mountains. *Emu* **92**: 93-105.

Paton, D. C. (1980). The importance of manna, honeydew and lerp in the diets of honeyeaters. *Emu* **80**: 213-226.

Paton, D. C. (1981). Do-it-yourself bird research in one easy lesson. *RAOU Newsletter* **49**: 10-11.

Paton, D. C. and Ford, H.F. (1977). Pollination by birds of native plants in South Australia. *Emu* **77**: 73-85.

Read, J.L. (1994). The diet of three species of Firetail Finches in temperate South Australia. *Emu* **94**: 1-8.

Recher, H. F. (2018). Foraging behaviour of mulga birds in Western Australia. II. Community structure and conservation. *Pacific Conservation Biology* **24**: 87-97.

Recher, H.F. (2016). The winter foraging behaviour of birds in a mixed eucalypt forest and woodland in the Southern Tablelands of New South Wales. *Australian Zoologist* **38**: 1-15.

Recher, H. F. and Holmes, R.T. (1985). Foraging ecology and seasonal patterns of abundance in a forest avifauna. In A. Keast, H. F. Recher, H. A. Ford and D. Saunders [Eds.] *Birds of eucalypt forests and woodlands: ecology, conservation and management*. Pp. 79-96. Surrey-Beatty, Sydney.

Recher, H.F. and Holmes, R.T. (2000). The foraging ecology of birds of eucalypt forest and woodland. I. differences between males and females. *Emu* **100**: 205-215.

Recher, H.F., Holmes, R.T., Schulz, M., Shields, J. and Kavanagh, R. (1985). Foraging patterns of breeding birds in eucalypt forest and woodland of southeastern Australia. *Australian Journal of Ecology* **10**: 399-419.

Recher, H.F., Calver, M.C. and Davis, W.E. (2016). Ecology of honeyeaters (Meliphagidae) in western Australian eucalypt woodlands: I. Resource allocation among species in the Great Western Woodland during spring. *Australian Zoologist* **38**: 130-146.

Rogers, A.C. and Mulder, R.A. (2004). Breeding ecology and social behaviour of an antiphonal duetter, the eastern whipbird *Psophodes olivaceus*. *Australian Journal of Zoology* **52**: 417-435.

Routley, V. (1980). Some birds of the Budawang Ranges. *Canberra Bird Notes* **5**: 24-36.

Sabo, S.R. and Holmes, R.T. (1983). Foraging niches and the structure of forest bird communities in contrasting montane habitats. *Condor* **85**: 121-138.

Serong, M. (2007). *Secondary succession and its effect on avian community composition and foraging behaviour in wet forests in the Victorian Central Highlands*. PhD. thesis, Monash University.

Serong, M. and Lill A. (2012) Changes in bird assemblages during succession following disturbance in secondary wet forests in south-eastern Australia. *Emu* **112:** 117–128.

Serong, M. and Lill, A. (2016). Plasticity and stereotypy in avian foraging during secondary succession in temperate forests. *Avian Biology Research* **9**(3): 1-21.

Somasundaram, S. and Vijayan, L. (2008). Foraging behaviour and guild structure of birds in the montane wet temperate forest of the Palni Hills, South India. *Podoces* **3**: 79–91.

Specht, R.L. (1970). Vegetation. In: *The Australian environment* (Ed. G.W. Leeper) Pp. 44-67. CSIRO and Melbourne University Press, Melbourne.

Stewart, P.J. (1997). *Some aspects of the ecology of an urban Corvid: the Australian Raven (Corvus coronoides) in metropolitan Perth*. Honours thesis, Edith Cowan University, Perth.

Styring, A.R. and Zakaria bin Hussin, M. (2004). Foraging ecology of woodpeckers in lowland Malaysian rain forests. *Journal of Tropical Ecology* **20**: 487-494.

Todd, M. (1996). Diet and foraging behaviour of the Red-browed Finch *Neochmia temporalis* near Newcastle, New South Wales. *Emu* **96**: 245-249.

Thivyanathan, N. (2016). Foraging patterns of birds in resource partitioning in tropical mixed dry deciduous forest, India. *Journal of Energy and Natural Resources* **5**: 16-29.

Thomas, D.G. (1978). *Bird ecology in temperate rainforests*. MSc. Thesis, University of Tasmania.

Thomas, D.G. (1980a). Foraging of honeyeaters in an area of Tasmanian sclerophyll forest. *Emu* **80**: 55-58.

Thomas, D.G. (1980b). The bird community of Tasmanian temperate rainforest. *Ibis* **122**: 298-306.

Viggers, J. I., Weaver, H. J. and Lindenmayer, D. B. (2013). *Melbourne's water catchments: perspectives on a* world *class water supply*. CSIRO Publishing, Melbourne.

Wheeler, A. and Calver, M. (1996). Resource partitioning in an island community of insectivorous birds during winter. *Emu* **96**: 23-31.

Whelan, C. (2001). Foliage structure influences foraging of insectivorous forest birds: an experimental study. *Ecology* **81**: 219-231.

Widman, M., Kato, A., Raymond, B., Angelier, F., Arthur, B., Chastel, O., Pelle, M., Raclot, T. and Ropert-Coudert, Y. (2015). Habitat use and sex-specific foraging behaviour of Adélie penguins throughout the breeding season in Adélie Land, East Antarctica. *Movement Ecology* **3**: 30.

Woinarski, J. (2008). Family Pardalotidae (Pardalotes). In: Eds. J. del Hoyo, E. Elliott and D. Christie. *Handbook of the Birds of the World. Volume 13, Penduline-tits to Shrike*s. Pp. 390–401. Lynx Edicions, Barcelona.

Wykes, B. J. (1985). The Helmeted Honeyeater and related honeyeaters of Victorian woodlands. In: *Birds of Eucalypt forests and woodlands: ecology, conservation, management*. Eds. J.A. Keast, H.F. Recher, H.A. Ford and D. Saunders. Pp. 205-217. Surrey Beatty, Sydney.

Appendix 1

Common and scientific names of the bird species recorded in the study. Acronyms are given for species occurring in Tables 1−10.

Brush Bronzewing *Phaps elegans*
Wedge-tailed Eagle *Aquila audax*
Yellow-tailed Black-Cockatoo *Calyptorhyncus funereus* (YTBC)
Gang-gang Cockatoo *Callocephalon fimbriatum*
Sulphur-crested Cockatoo *Cacatua galerita*
Australian King-Parrot *Alisterus capularis*
Crimson Rosella *Platycercus elegans* (CROS)
Eastern Rosella *P. eximius*
Fan-tailed Cuckoo *Cacomantis flabelliformis*
Shining Bronze-Cuckoo *Chalcites lucidus*
Southern Boobook *Ninox novaeseelandiae*
Laughing Kookaburra *Dacelo novaeguineae* (LK)
Superb Lyrebird *Menura novaehollandiae*
White-throated Treecreeper *Cormobates leucophaea* (WTTC)
Red-browed Treecreeper *Climacteris erythrops*
Superb Fairy-Wren *Malurus cyaneus*
White-browed Scrubwren *Sericornis frontalis* (WBSW)
Large-billed Scrubwren *S. magnirostra* (LBSW)
Brown Thornbill *Acanthiza pusilla* (BTH)
Striated Thornbill *A. lineata* (STH)
Spotted Pardalote *Pardalotus punctatus*
Crescent Honeyeater *Phylidonyris pyrrhopterus*
Eastern Spinebill *Acanthorynchus tenuirostris* (ESPB)
Yellow-faced Honeyeater *Lichenostomus chrysops*
White-eared Honeyeater *L. leucotis*
New Holland Honeyeater *Phylidonyris novaehollandiae*
White-naped Honeyeater *Melithreptus lunatus* (WNH)
Red Wattlebird *Anthochaera carunculata*
Eastern Whipbird *Psophodes olivaceus*
Varied Sitella *Daphoenositta chrysoptera*
Crested Shrike-Tit *Falcunculus frontalis* (CST)
Olive Whistler *Pachycephala olivacea*
Golden Whistler *P. pectoralis* (GWH)
Rufous Whistler *P. rufiventris*
Grey Shrike-Thrush *Colluricincla harmonica* (GST)
Olive-backed Oriole *Oriolus sagittatus*
Australian Raven *Corvus coronoides* (RSP)
Little Raven *C. mellori* (RSP)
Rufous Fantail *Rhipidura rufifrons* (RFAN)
Grey Fantail *R. albiscapa* (GFAN)
Satin Flycatcher *Myiagra cyanoleuca* (SFLY)
Rose Robin *Petroica rosea* (RROB)
Pink Robin *P. rodinogaster*
Eastern Yellow Robin *Eopsaltria australis* (YROB)
Silvereye *Zosterops lateralis* (SEYE)
Common Blackbird *Turdus merula*
Bassian Thrush *Zoothera lunulata*
Mistletoebird *Dicaeum hirundinaceum*
Red-browed Finch *Neochmia temporalis*