

Plasticity and stereotypy in avian foraging during secondary succession in temperate forests

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ABSTRACT

Some bird species cannot persist during early secondary succession after natural or anthropogenic disturbance of Australian Mountain Ash (*Eucalyptus regnans*) forest, whilst others remain abundant throughout regeneration. To conserve bird species diversity optimally in such forests, we need to know, *inter alia*, exactly why the latter species can persist after disturbance. Using a chronosequence approach, we documented four facets of foraging in a suite of these persistent species effectively covering 100 years of succession in *E. regnans* forest disturbed by wildfire or timber harvesting, namely the foraging strata, locations, substrates and behaviours used. Most species showed plasticity in their use of foraging strata and locations during succession, but four exhibited some limited stereotypy in these facets. In contrast, use of foraging substrates and behaviours was largely invariant within species during secondary succession. We suggest that switching foraging strata and locations was probably critical to persistence of most of these bird species during secondary succession, given the marked variation in structural and floristic variables that characterises this regeneration process. Some plasticity in foraging behaviour repertoire and substrate use was probably possible, but not beneficial. Although some resident bird species' populations were severely reduced by disturbance in these forests, a substantial subset of species was sufficiently flexible in choosing foraging microhabitats to persist throughout secondary succession at pre-disturbance abundances.

Keywords: secondary succession, chronosequence, avian foraging behaviour, plasticity, stereotypy

1. INTRODUCTION

About 30% of earth's land surface is forested, but ~13 million ha of forest annually have been converted to other uses or lost through natural causes in recent years (Forest Resources Assessment, 2010). Naturally occurring and deliberately ignited wildfires and anthropogenic timber harvesting are common disturbances in forests worldwide and cause significant local reductions in biodiversity if they result in extensive, permanent loss of forest habitat (Bowman et al., 2009; Bradshaw, 2012). Even when secondary succession proceeds unhindered, these disturbance phenomena can cause a transient, but nonetheless quite protracted, loss of local animal diversity if some resident animal species cannot thrive in the early successional regrowth. Therefore, from an animal conservation perspective, it is important to determine how forest-dwelling species react to secondary succession. This knowledge should help in applying management strategies that limit permanent or temporary animal diversity loss in forests subject to natural and anthropogenic disturbance.

There have been many investigations of how bird communities react to secondary succession in forests after disturbance (e.g. Loyn, 1985; Smucker et al., 2005; Massimino et al., 2008; Fontaine et al., 2009;

Lindenmayer et al., 2012; Ramachandran and Ganesh, 2012). Patterns of change discernible during succession are: (1) increasing species richness, species diversity and overall bird abundance (Loyn 1985; Williams et al., 2001; Kavanagh and Stanton, 2003); (2) a bimodal increase in species richness and diversity, usually with one peak being greater than the other (Taylor et al., 1997; Keller et al., 2003); and (3) decreasing species richness and bird abundance where climax forest is bird species poor and disturbance creates more niches (Kricher and Davis, 1992; Fisher, 2001). However, as several authors note, despite this quite good documentation of the changes in bird species community composition during forest secondary succession, we have only a very limited understanding of how bird species actually adjust to seral vegetation changes (e.g. VanderWerf, 1994; Ward and Paton, 2004). Disturbance of forests will continue and probably increase worldwide. Therefore, understanding this adjustment process by birds is critical for effectively managing forests in a way that restores local bird species diversity as completely and rapidly as possible after disturbance events.

From about three to six years after disturbance, secondary succession in tall wet temperate Mountain Ash forests in the Victorian Central Highlands, Australia proceeds

in a similar manner in sites disturbed by either wildfire or clearcut logging (Serong and Lill, 2008). At this stage the new vegetation is dense, vertical strata are becoming distinguishable, the canopy is closed and *E. regnans* and Silver Wattle (*Acacia dealbata*) trees are present in the canopy. As secondary succession proceeds, canopy stem density decreases, mean canopy stem diameter increases and there is a huge increase in canopy height and a vertical separation of *E. regnans* in the canopy from *A. dealbata* in the sub-canopy. Sixty to 100 year old mature climax forest has a fairly open *E. regnans* canopy, a sparse sub-canopy, a complex shrub/tree fern stratum and abundant ground litter cover (Loyd, 1985; Ashton and Attiwill, 1994; Serong and Lill, 2008). Bird abundance and species richness vary little during secondary succession in these forests (Serong and Lill, 2012). However, the composition of bird species assemblages alters chronologically during succession, the pattern and rate of change reflecting those of the regenerating vegetation. Unlike the situation in some other forest ecosystems (Dessecker and McCauley, 2001), no bird species is abundant and a specialist only in early successional forest more than three years old. However, some species are consistently abundant only in mid- to late succession, whilst others that are the focus of the present study are common throughout succession (Serong and Lill, 2012).

Our aim was to elucidate how some bird species can remain abundant throughout secondary succession after wildfire or timber harvesting in *E. regnans* forests despite the major floristic and structural changes that occur. In particular, we determined whether such birds

acquired adequate food resources through behavioural plasticity (i.e. adjustment of foraging behaviour to vegetation changes) or through behavioural stereotypy (i.e. specifically targeting particular forest food sources available throughout succession without adjusting foraging behaviour). In view of the major changes in forest structure and floristics occurring during succession, we predicted that the persistent bird species would show flexibility in most aspects of foraging during forest regeneration. We tested this prediction by documenting where (stratum, location and substrate) and how (types and rates of behaviour) several such species foraged at five disparate stages of secondary succession. The foraging behaviour of easily distinguishable immature and adult insectivorous Golden Whistlers (*Pachycephala pectoralis*) (total length 16.5–18.5 cm) was also compared to determine whether relatively inexperienced and experienced conspecifics responded differently to secondary succession.

2. METHODS

2.1 Study area, forest age classes and study sites

The study was conducted in the Victorian Central Highlands, Australia, in an approximately 40×30 km area of forest within the coordinates 37°26' to 37°42' S and 145°25' to 145°53' E (Figure 1). These forests are 200–1250 m above sea level in sheltered areas with a mild climate, high annual precipitation (>1000 mm) and

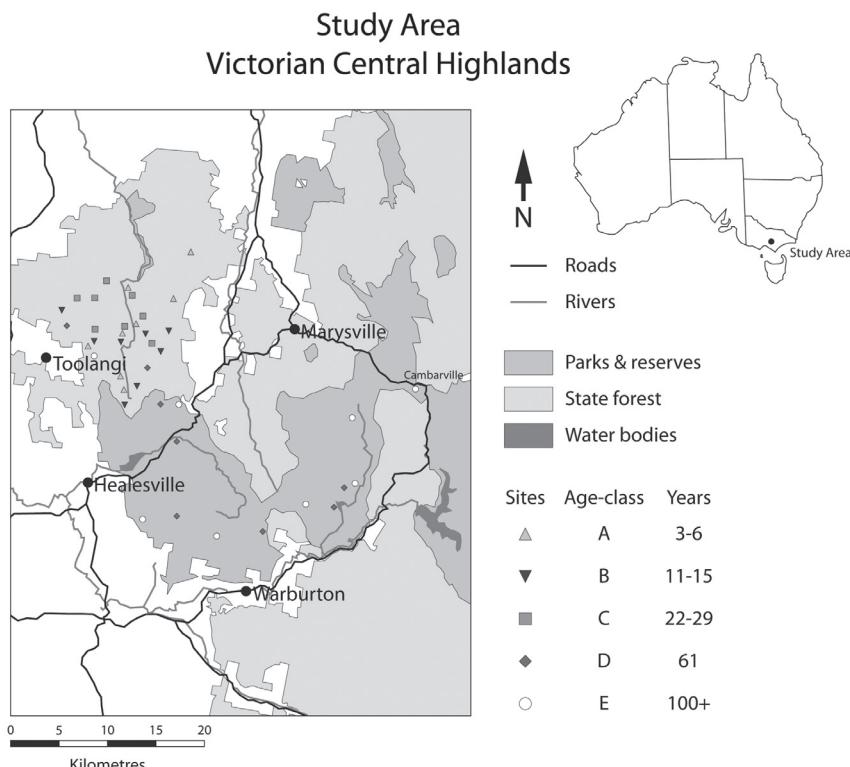


Figure 1 The study area and study sites in the Victorian Central Highlands.

deep soils (Ough and Ross, 1992). They have experienced major disturbance by periodic wildfire and regular timber harvesting, so that at the time of study they comprised a mosaic of even-aged stands at various stages of secondary succession, interspersed with small areas of mixed-age or old forest that had escaped substantial disturbance (Lindenmayer and McCarthy, 2002).

A chronosequence approach (Squire *et al.*, 1992) allowed data collection simultaneously in forests of differing ages since disturbance (*i.e.* at differing stages of secondary succession). We deliberately omitted sites in which disturbance had occurred <3 years previously because Loyn (1985) showed that these sites are very depauperate for birds and are occupied substantially by a different suite of species not typical of tall wet forest, namely open-country and wide-ranging species. The five forest age classes (FACs, labelled A–E youngest to oldest) chosen for study on the basis of their disturbance history and floristic and structural disparities had post-disturbance ages respectively of 3–6, 11–15, 22–29, 61 and >100 years (Figure 2). The three youngest FACs (A–C) resulted from clearcutting, D from fire and salvage logging and E from wildfire (details in Serong and Lill, 2008). Floristic change during secondary succession is chronological in these forests and occurs mostly in the first few decades post-disturbance. The largest floristic disparity was between FACs B and C (Serong and Lill, 2008). However, structural vegetation change occurs throughout succession. We studied eight geographically dispersed, 300×400 m sites in each FAC; the sites in the various FACs were spatially interspersed and each had a central track on its long axis.

2.2 Occurrence of plant species

To examine the relationship between plant species' occurrence and their use by foraging birds, the occurrence of all plant species in two 50×50 m quadrats, each divided into 50 1×15 m subdivisions, was determined in each study site in parallel with observations of avian foraging. The quadrats abutted opposite sides of the central track and were ≥50 m apart, but otherwise randomly positioned along the track. A plant species' frequency of occurrence (maximum score 100) in a quadrat was determined as the number of subdivisions in which it grew or which it overhung (Serong and Lill, 2008).

2.3 Foraging behaviour

Five 100 min observation sessions were conducted by the same observer at each study site over seven months from October to April (*i.e.* spring, summer and autumn). Sessions were not conducted on very hot days, but they were distributed evenly among FACs throughout daylight hours and over the entire study period. The observer walked the central track and, using 8×32 binoculars,

recorded one foraging behaviour per bird encountered and foraging records from ≤3 birds per flock in order to increase data independence. The following data were recorded for each focal foraging bird.

(1) Species' identity – total adult length (Pizzey and Knight, 2012) given at first mention of each study species in text.

(2) Foraging stratum – vertical forest layer in which bird commenced a prey capture attempt or in which it was searching for food; categorised as: (a) canopy of tall trees; (b) sub-canopy of small trees; (c) shrub/tree fern layer; and (d) ground layer (*i.e.* forest floor and all vegetation <1 m tall). This categorisation followed that of Ough and Ross (1992) and Ashton and Attiwill (1994).

(3) Foraging height – bird's vertical position in the plant expressed as an estimated percentage of the plant's height. A bird's vertical location in the vegetation has been documented in this manner as an important aspect of foraging behaviour in numerous studies of avian foraging (*e.g.* Laiolo *et al.*, 2003). Two to four equal-sized percentage categories were used per species, depending on the sample size obtained. The actual categorisations were: low and high (0–50 and 51–100%), low, mid and high (0–33, 34–66 and 67–100%) or low, lower mid, upper mid and high (0–25, 26–50, 51–75 and 76–100%).

(4) Foraging location – location of focal bird when food item was detected (*i.e.* capture manoeuvre commenced) or on which searching for, or handling of, item occurred (*e.g.* plant species, fallen branch, ground cover or 'other'). This is a key element of avian foraging behaviour during succession, given the marked floristic changes that occur.

(5) Foraging substrate – substrate on which food item was captured or handled or on which bird was searching for item (*e.g.* particular plant species, branch, bare vegetation, bark).

(6) Foraging mode - based on Remsen and Robinson (1990), foraging behaviour was categorised as: (a) food item handling – hold item in bill, beat it on hard surface, shake or eat it; (b) near-perch manoeuvres – glean (pick off surface with bill), hang (cling inverted from support), probe (insert bill into substrate), peck (forceful pecking at item or substrate), pull, reach (stretch to obtain food item), lunge (precipitous movement towards item) and drink; (c) aerial manoeuvres – leap, sally (fly to capture prey and return to consume it on original or new perch), sally-pounce, hover and pursue; (d) searching for food item; and (e) clasping food item – clasp substrate or food item in foot.

This approach was extended to examine possible age/sex differences in Golden Whistlers' foraging during secondary succession, but in a different year. This was the only one of the bird species abundant throughout secondary succession in which first-year individuals, adult males and adult females could be readily visually distinguished. Brightly multi-coloured adult males are easily distinguished from predominantly grey females, and first-year immatures differ from adult females in having rufous wing coverts (Pizzey and Knight, 2012).



A is 2–6 years after clearcutting, **B** is 10–15 years after logging, **C** is 21–30 years after clearcutting, **D** is approximately 60 years after wildfire and **E** is relatively undisturbed for >100 years.

Figure 2 Representative images of the study sites in each of the forest age classes.

2.4 Foraging rates

Foraging rates were determined for Brown Thornbills (*Acanthiza pusilla*) (10 cm), Golden Whistlers and Grey Fantails (*Rhipidura fuliginosa*) (14–17 cm) in FACs A, C and E. These species were chosen because they were common throughout secondary succession, but typically forage in rather contrasting ways. The three FACs varied sufficiently in floristics and vegetation structure to reflect the differences in these characteristics apparent during secondary succession. Observations were made similarly to those for foraging behaviour. Each foraging bird encountered was observed for up to 1 min (minimum 19 sec) and the following behaviours were counted using the program Count It v. 2.7 (Kim Molgaard, 1999) on a Palm m505 hand-held, electronic device: search hops (hops between two perching sites); (2) search flights (flying between two perches); (3) near-perch prey capture attempts (prey attacks made on foot); and (4) aerial prey capture attempts (prey attacks made in flight). When median search hop and search flight rates varied inversely amongst FACs, the two rates were summed to generate a composite variable, 'total search-movement rate'.

2.5 Data analysis

Data analyses were conducted with Systat (Systat Inc, CA). To examine relative occurrence, we used the ratio of each plant species among FACs for each bird species. Frequencies of occurrence and use were summed for all sites in each FAC, converted to proportions of total occurrence and use for that FAC, and differences between the occurrence and use totals calculated. Spearman rank correlation coefficients (r) were calculated between all pairs of FACs for each bird species for which data were sufficient using these difference scores. Significant positive correlations between chronologically sequential FACs were considered to provide evidence of 'tracking' of floristic changes during secondary succession by a particular bird species.

Serong and Lill (2008) showed that replicate sites within each of the FACs were statistically indistinguishable in structure and floristics. Thus there was no rationale for expecting bird species' foraging to vary among sites within FACs in a manner that would invalidate comparing a species' foraging among forest age classes using total scores for each foraging variable. Accordingly, foraging records (frequencies) for each bird species were pooled for all sites in a FAC and arranged in contingency tables that cross-classified the variables. Sparseness (too many zeros) was reduced by omitting some categories with too few data, meaningful category pooling, splitting of tables and addition of the smallest possible constant (0.01–0.3) to all cells (Hejl and Verner, 1990). Data were analysed with log-linear modelling (LLM) (Agresti, 2002). The composition and fit of the most parsimonious model provided a description of the significant associations

and interactions among the variables. The fit of simpler models was tested with Pearson chi square and likelihood-ratio (LR or G₂) goodness-of-fit tests ($\alpha=0.05$). We analysed stratum use plus foraging height (where the bird was foraging) separately from specific foraging location, substrate and mode (how the bird was foraging) because it is often difficult to use LLM satisfactorily with large numbers of variables. Models for foraging location, substrate and mode fitted the data for all species without including three- or four-way interaction terms, and the most parsimonious model for each bird species also excluded at least one second-order interaction term.

The ratios of parameter estimates to their standard errors ($\lambda/\text{SE}_\lambda$) in the most parsimonious LLM can be interpreted as standard normal deviates for large sample sizes and were used to indicate: (a) the strength and direction of associations between categories within interacting pairs of variables; (b) and the effects of each category of a variable that did not interact with other variables but had an independent main effect. Values ≤ -1.96 or $\geq +1.96$ were judged to indicate strong, significant associations and those more extreme than ± 2.58 to indicate very strong, significant associations between categories (Ferguson and Takane, 1989).

Variation in species' foraging rates amongst FACs was analysed with Kruskal–Wallis single-factor ANOVA. Where variation was significant, post hoc pair-wise comparisons between FACs were conducted.

3. RESULTS

3.1 Overall foraging patterns

Sufficient data (≥ 50 foraging records) for meaningful analysis were obtained for only 11 of the 55 bird species recorded in the study sites, for each of which ≥ 5 foraging records were acquired for each of at least four FACs. Foraging diversity was sufficient in all these species for it to potentially exhibit succession-related variation in the measured foraging variables. These species comprised eight insectivores, one nectarivore–insectivore (Eastern Spinebill *Acanthorhynchus tenuirostris*) (15–16.5 cm), one that consumes a variety of plant components (Crimson Rosella *Platycercus elegans*) (30–37 cm), and one insectivore–frugivore (Grey-breasted White-eye *Zosterops lateralis*) (hereinafter White-eye) (10–12.5 cm).

Ten of these species exhibited succession-related variation in both foraging stratum and location, but only four in foraging height (Table 1 and 2). The most parsimonious LLMs were identical for some parameters among phylogenetically diverse species (e.g. Eastern Yellow Robin *Eopsaltria australis* [15–16 cm] and Golden Whistler for foraging stratum and height). However, the most parsimonious models for several species were unique (Table 1 and 2). For example: (1) the Eastern Spinebill was the only species in which both foraging stratum use and

Table 1 Factors and interactions in log-linear models of foraging of eleven bird species, foraging stratum and height. The ticks indicate the presence of a factor or interaction in the most parsimonious log-linear mode

Bird species	n ^a	N ^b	Factors and interactions in model				
			A ^c	St ^d	H ^e	A×S	A×H
Crimson Rosella	86	45	✓	✓	✓	✓	
White-browed Scrubwren	195	60	✓	✓	✓	✓	✓
Brown Thornbill	641	60	✓	✓	✓	✓	✓
Striated Thornbill	70	45	✓	✓	✓ ^f	✓	
Eastern Spinebill	98	45	✓ ^f	✓ ^f	✓ ^f		
Eastern Yellow Robin	98	5	✓	✓	✓	✓	✓
Golden Whistler	27	60	✓	✓	✓	✓	✓
Grey Shrike-Thrush	45	30	✓	✓	✓	✓	✓
Rufous Fantail	97	45	✓	✓	✓ ^f	✓	
Grey Fantail	331	60	✓	✓	✓ ^f	✓	
Grey-breasted White-eye	139	45	✓	✓	✓	✓	✓

^an = number of foraging records.

^bN = number of cells in 5 × 3 × 4, 5 × 4 × 3 or 5 × 3 × 2 contingency tables.

^cFactors in contingency tables are forest age class.

^dForest stratum.

^eForaging height.

^fIndependent effect of a factor in the absence of interactions.

foraging height were invariant among FACs; (2) the Grey Shrike-thrush (*Colluricinclla harmonica*) (22–26 cm) was the only species whose foraging location was invariant among FACs; and (3) the Brown Thornbill was the sole species whose foraging mode varied among FACs.

3.2 Foraging stratum and height

Four profiles of foraging stratum use were identified among the 11 species.

(1) Predominantly canopy foraging in the youngest FACs (A and/or B), but shrub stratum foraging in the older FACs (C, D, and/or E) (Tables 3 and 4). Five species (Brown Thornbill, Striated Thornbill *Acanthiza lineata* 10 cm, Eastern Yellow Robin, Golden Whistler and Grey Fantail) clearly exhibited this profile; three others (White-browed Scrubwren *Sericornis frontalis* 11–13 cm, Rufous Fantail *Rhipidura rufifrons* 15–16.5 cm and White-eye) had similar, but less pronounced, profiles (Table 4).

(2) Variation in sub-canopy use for foraging during secondary succession observed only in Brown Thornbills, although the pattern was not unidirectional (Table 4).

(3) Ground foraging less in the youngest FAC (A) than in the older ones (Table 4); observed in the White-browed Scrubwren, but this was the sole species in which ground foraging in the various FACs could be examined satisfactorily.

(4) No succession-related variation in foraging stratum use; Crimson Rosellas (omitted from Table 3 as there were no $\lambda/(SE_\lambda)$ values $> \pm 1.65$) and Grey Shrike-thrushes displayed this profile.

Only three species exhibited serial variation in foraging height: (1) Brown Thornbills foraged proportionately

more frequently in the lower- and upper-mid height ranges and less in the low range in FAC A (and to some extent FAC B) than they did in the older FACs, particularly FAC E (Tables 3 and 4); (2) Grey Shrike-thrushes foraged mainly at lower heights in FACs B–D, but at greater heights in the oldest FAC E; and (3) White-eyes foraged low down in plants in FAC C, deviating from their usual pattern in the other FACs of foraging high up in the vegetation.

LLM summaries (Table 1) indicate that foraging height of four species varied as a function of foraging stratum. However, this was clearly not a response to secondary succession; the independent effects for foraging height in five species (Table 1) indicated that they showed strong biases for foraging at particular heights irrespective of forest succession stage.

3.3 Foraging location

Trends evident amongst the ten bird species that exhibited serial variation in foraging location (Table 5) were: (1) more frequent use of *A. dealbata* and/or eucalypts in one or both of the two youngest FACs (A and B) than in the two oldest ones (D and E). For example, in FAC A, 42% of White-browed Scrubwrens' foraging was on *A. dealbata*, 20% on eucalypts and 3% on other plant species or the ground; in contrast, they did not forage on *A. dealbata* or significantly on eucalypts in the two oldest FACs (D and E), where about 25% of their foraging was on other plant species. Mountain Correa (*Correa lawrenciana*) was a particularly common foraging location for Scrubwrens in FACs C and D and tree fern species in FACs D and E (Table 5); and (2) using a broader range of foraging

Table 2 Factors and interactions in log-linear models of foraging of eleven bird species, foraging location, substrate and mode. The lower panel is for the Golden Whistler split into age-sex classes. The blank spaces indicate that there was no significant interaction between the factors or an independent effect of the factor in the absence of interactions. A dash (–) indicates that a term could not occur in a particular model

Bird species	n ^a	Factors	Cells ^b	Terms and interactions in model									
				A ^c	L ^d	S ^e	M ^f	A×L	A×S	A×M	L×S	L×M	S×M
Crimson Rosella	97	A, L, S	5×4×4	✓	✓	✓	–	✓	–	✓	✓	–	–
		A, L, M	5×4×3	✓	✓	–	✓ ^g	✓	–	–	–	–	–
White-browed Scrubwren	288	A, L, S, M	5×9×3×2	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
Brown Thornbill	652	A, L, S, M	5×12×3×3	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
Striated Thornbill	71	A, L, S	5×5×2	✓	✓	✓ ^g	–	✓	–	–	–	–	–
		A, L, M	5×5×3	✓	✓	–	✓ ^g	✓	–	–	–	–	–
Eastern Spinebill	59	A, L, S	5×4×3	✓	✓	✓	–	✓	–	✓	✓	–	–
		A, L, M	5×7×3	✓	✓	–	✓	–	–	–	–	✓	–
Golden Whistler (all)	230	A, L, S, M	5×6×2×3	✓	✓	✓	✓	✓	✓	✓	–	✓	✓
Grey Shrike-thrush	51	A, L, S	5×3×3	✓	✓	–	–	–	–	–	✓	–	–
		A, L, M	5×3×3	✓	–	✓	–	–	–	–	–	✓	–
Rufous Fantail	113	A, L, S	5×6×3	✓	✓	✓	–	✓	✓	✓	–	✓	–
		5×6×3	✓	✓	–	✓ ^g	✓	✓	–	–	–	–	–
Grey Fantail	353	A, L, S, M	5×8×3×3	✓	✓	✓	✓	✓	✓	✓	–	✓	–
Grey-breasted White-eye	146	A, L, S	5×7×4	✓	✓	–	✓	✓	–	✓	–	✓	–
		A, L, M	5×7×2	✓	✓	–	✓ ^g	✓	–	–	–	–	–

Golden Whistler			Factors and interactions (age-sex classes)															
n	Factors	Cells	Z ^h	A	L	M	St	H	S	Z×A	Z×L	A×L	Z×S	Z×M	A×S	A×M	Z×St	A×St
45	Z×A×L	3×5×3	✓	✓	✓	–	–	–	–	✓	✓	✓	–	–	–	–	–	
30	Z×A×S	3×5×2	✓ ^g	–	–	–	–	–	–	–	–	–	–	–	–	–	–	
45	Z×A×M	3×5×3	✓	–	✓ ^g	–	–	–	–	–	–	–	–	–	–	–	–	
135	Z×A×St×H	3×5×3×3	✓	✓	–	✓	✓ ^g	✓	–	–	–	–	–	–	✓	✓	✓	

^an = number of records.

^bNumber of cells in the log-linear model contingency table.

Factors in the contingency tables are:

^cForest age class.

^dForaging location.

^eForaging substrate.

^fForaging mode.

^gIndependent effect of a factor in the absence of interactions.

locations in the two oldest FACs (D and E) than in the younger ones (Table 5). This use of particular foraging locations in particular FACs was reflected directly in large, significant, positive $\lambda/(SE_\lambda)$ values and indirectly in large, significant, negative $\lambda/(SE_\lambda)$ values where such association was lacking (Table 6). This trend was apparent in White-eyes, which particularly foraged in Elderberry Panax (*Polyscias sambucifolia*) in FAC D, Victorian Christmas Bush (*Prostanthera lasianthos*) in FAC C, A. *dealbata* in FACs B and D and eucalypts in FAC A. Brown Thornbills also used predominantly different plant species as foraging locations in FACs B to

D, and Crimson Rosellas foraged on the ground more in FAC D than in other FACs.

3.4 Foraging mode

Seral variation in foraging mode occurred only in Brown Thornbills (Table 2). This behaviourally-versatile species (Recher et al., 1987) exhibited 12 modes, gleaning, reaching, hanging, hovering, sallying and searching being most common. ‘Searching’ was particularly common in the youngest FAC (A) and very uncommon in the oldest

Table 3 Percentages (rounded) of foraging records in five strata and 2–4 height categories across five forest age classes for eleven bird species. The forest age classes are labelled A–E in order of increasing age since last major disturbance. Foraging height was estimated as percentage of plant height in 2–4 equal-sized categories. Height categories and strata are omitted for a bird species where no score for any forest age class was $\geq 10\%$. The sample size is given in parentheses for each species

Foraging stratum (no. records)	Height in plant	Forest age class					Foraging stratum (no. records)	Height in plant	Forest age class					
		A	B	C	D	E			A	B	C	D	E	
<i>Crimson Rosella</i> (97):														
Canopy	High	50	61	32	22	13	34	Canopy	High	7	15	8	4	7
	Mid		14	20	6	29	18		Upper mid	24	25	10	2	5
Sub-canopy	High		7	8	6	33	13		Lower mid	41	25	12	8	18
Shrub	High			24	11	21	13		Low	17	7	4		6
	Mid			8	17	4	6	Sub-canopy	High	3	10	12	13	7
Ground ^a	Low	50	14		33		11		Upper mid	2	3	10	4	5
<i>White-browed Scrubwren</i> (288):														
Shrub	High	15	17	18	15	13	16	Shrub	High	3	10	12	13	7
	Mid	8	26	24	28	36	23		Upper mid	2	3	10	4	5
	Low	5	13	19	23	4	13		Lower mid	5	8	20	10	13
Ground	High	3	11	11	3	4	7		High	3	10	12	13	7
	Low	12	22	23	28	36	23		Upper mid	2	3	10	4	5
<i>Brown Thornbill</i> (651):														
Canopy	High	8	12	0	1	1	4	Shrub	Mid	23	14	3		8
	Upper mid	17	11	3	2	1	6		Low	10				2
	Lower mid	36	14	4	6	2	11	Sub-canopy	Mid			3	4	14
Sub-canopy	High	3	10	11	4	14	9		Golden Whistler (male) (71):					
	Upper mid	3	10	7	1	9	6	Canopy	High		10	6	2	4
	Lower mid	7	6	13	6	11	8		Mid	13	12	3	7	5
Shrub	High	5	9	23	30	22	18		Low	10	4	4		8
	Upper mid	7	15	13	19	17	15	Sub-canopy	High	2	6	11	18	7
	Lower mid	8	7	19	23	12	14	Golden whistler (female) (58):						
<i>Striated Thornbill</i> (71):														
Canopy	Mid	31	26	25			20	Canopy	High	7	14	3	2	6
	Low	6	5		15		6		Mid	16	6			4
Sub-canopy	High		11	13		43	10	Sub-canopy	High	2	9	11	11	6
	Mid	6	21	13			10		Mid	2	12	7	7	5
Shrub	High		5	19	77	14	21	Grey Shrike-thrush (51):						
	Mid		5	6	8	43	9	Emergent ^a	High	17				2
<i>Eastern Spinebill</i> (59):									Low	33	11			6
Emergent ^a	High		40				3	Canopy	High	17	11	36	7	20
Canopy	High	100		5	18		7		Low	17	67	27	33	18
	Low		20			9	Sub-canopy	High		11		20	50	18
Sub-canopy	High			11		13	9		Low		27	20	10	14
	Low				4		Shrub	High			7	20	6	
Shrub	High		20	63	64	52	54		Low			13		4
	Mid		20	11	18	13	14	Ground ^a	Low	17	9			4
<i>Eastern Yellow Robin</i> (110):								<i>Rufous Fantail</i> (110):						
Canopy	Mid	31	9				6	Canopy	High	3	15	4	5	6
	Low	38	36	4	7	16	18		Mid	20	10			7
Sub-canopy	Mid		9	8	10		6		Low	7	15	4		6
	Low			17	7	16	8	Sub-canopy	High	7		8	15	6
Shrub	High	6	18	38	7	21	18		Mid	10	5	8	6	7
	Mid		5	17	21	26	15		Low	10		4	10	6
	Low		9	13	35	11	16	Shrub	High	10	10	25	19	30
Ground ^a	Low	19	9	4	14	11	11		Mid	17	35	25	56	28
									Low	7		6	10	5
							Ground ^a	High			13		2	
								Low	3	10	21		5	8

Table 3 Contd.

Foraging stratum (no. records)	Height in plant	Forest age class					Total
		A	B	C	D	E	
<i>Grey Fantail</i> (342):							
Canopy	High	21	23	17	6	9	17
	Upper mid	18	19	4	8	7	13
	Lower mid	25	19	17	13	11	18
Sub-canopy	High	2	8	13	2	13	7
	Upper mid	6	6	6	6	11	7
Shrub	High	4	3	6	19	11	7
	Upper mid	5	3	10	27	11	9
	Lower mid	3	2	8	10	7	5
<i>Grey-breasted White-eye</i> (144):							
Canopy	High	41	39				15
	Mid	13	9	8	3		6
Sub-canopy	High	3	13	19		15	10
	Mid	9	9	8	15		8
Shrub	High	13	26	15	62	44	33
	Mid	3	4	19	21	24	15
	Low	3		15	7		5
Ground ^a	Low	3		4	10		4

^aIndicates data not included in statistical analysis due to small sample size.

(E), whilst near-perch manoeuvres involving food item handling were very rare in FAC A (Table 2).

3.5 Foraging substrate

No species varied in foraging substrate use amongst FACs. Thus Brown Thornbills used three main foraging substrates, but they exhibited no more than a two-fold variation in percentage substrate use amongst FACs (Figure 4). This contrasted dramatically with their seven-fold seral variation in percentage use of some foraging locations (e.g. *A. dealbata*). Similarly, Golden Whistlers varied two-fold or less amongst the FACs in percentage use of the foraging substrates wood, foliage, cobwebs and the air, but three- to five-fold in percentage use of certain foraging locations (Figure 4 and Table 5).

3.6 Age and sex variation in Golden Whistlers' foraging during secondary succession

Thirty two percent of 189 Golden Whistler foraging records were for immature individuals, 30% for adult females and 38% for adult males. The factors and interactions in the most parsimonious LLMs constructed indicated that use of FACs for foraging, foraging locations and strata all varied significantly among Golden Whistlers of different ages, but not between adult males and females (Tables 1, 2, 3, 7 and 8). Principal patterns evident were that: (1) immatures mostly foraged in the younger FACs

Table 4 The strength and direction of associations expressed as $\lambda/(SE_{\lambda})$ between forest age class (A-E, youngest to oldest) and forest stratum and vertical position (height) of foraging birds in plants. Bird species are those that exhibited an interaction between stratum or vertical position and forest age class in their most parsimonious log-linear model. Vertical foraging heights were categorised as low and high (0–50 and 51–100%), low, mid and high (0–33, 34–66 and 67–100%) or low, lower mid, upper mid and high (0–25, 26–50, 51–75 and 76–100%). A stratum or foraging height category is excluded for a particular species when no foraging occurred there or there were no $\lambda/(SE_{\lambda})$ values more extreme than ± 1.65 ($P \leq 0.1$)

Bird species	Forest stratum	Forest age class				
		A	B	C	D	E
White-browed Scrubwren:	Shrub	-3.05 ^a				
Brown Thornbill:	Ground	-2.82 ^a				
Striated Thornbill:	Canopy	+8.97 ^a	+5.19 ^a	-3.61 ^a	-1.78	-5.15 ^a
Eastern Yellow Robin:	Sub-canopy	-3.0 ^a		+2.65 ^a	-2.93 ^a	5.12 ^a
Golden Whistler:	Shrub	-4.91 ^a	-5.2 ^a	+2.27 ^a	+6.11 ^a	+2.49 ^a
Grey Shrike-thrush:	Canopy	+3.36 ^a				-2.1 ^a
Rufous Fantail:	shrub	-1.96	-1.82		+3.26 ^a	
Grey Fantail:	Canopy	+3.89 ^a	+2.1 ^a	-2.34 ^a	-1.93	
Grey-breasted White-eye:	Shrub	-2.16 ^a		+1.96 ^a	+1.97 ^a	
Brown Thornbill:	Canopy	+5.03 ^a	+4.2 ^a	-3.25 ^a	-2.82 ^a	-3.92 ^a
Striated Thornbill:	Sub-canopy					+1.75
Golden Whistler:	Shrub	-2.09 ^a	-2.16 ^a	+1.96 ^a	+2.80 ^a	+2.78 ^a
Grey Shrike-thrush:	Canopy					-1.83
Rufous Fantail:	Canopy		+1.88			
Brown Thornbill:	Sub-canopy		-1.80			
Striated Thornbill:	Shrub	-2.20 ^a				
Grey Fantail:	Canopy	+3.88 ^a	+3.27 ^a		-2.36 ^a	-2.33 ^a
Grey Fantail:	Shrub	-2.05 ^a	-3.22 ^a		+4.94 ^a	
Grey-breasted White-eye:	Canopy	+1.71 ^a				
Grey-breasted White-eye:	Shrub	-2.82 ^a				

Bird species	Height	Forest age class				
		A	B	C	D	E
Brown Thornbill:	High		+1.76			
Brown Thornbill:	Upper mid	+2.07a	+3.38a		-2.74a	
Brown Thornbill:	Lower mid		+3.18a			-3.0a
Brown Thornbill:	Low	-2.52a	-2.14a		+1.90	+3.80a
Grey Shrike-thrush:	High					+2.39a
Grey Shrike-thrush:	Low					-2.39a
Grey-breasted White-eye:	High					-2.11a

^aSignificant positive and negative associations ($P < 0.05$).

Table 5 Foraging locations of eleven bird species in five forest age classes (A–E, from youngest to oldest). Data are percentage (rounded) use of broad foraging location categories. The numbers accompanying some structural location categories (e.g. '5 fallen timber') indicate that there were multiple sub-categories used. The location categories and category details omitted for a bird species where no score for any forest age class was $\geq 10\%$. Sample sizes are as in Table 3. The fine details of broad location categories used are available from the authors

Foraging location category	(Broad location category detail)	Forest age classes					Total
		A	B	C	D	E	
Crimson Rosella:							
<i>Eucalyptus</i> sp.	(2 <i>Eucalyptus</i> sp.)	50	32	52	33	38	39
<i>Acacia dealbata</i>			54	16	17	13	26
Other	(8 plant sp.; bare tree)			32	17	50	24
Ground	(Cover; soil surface)	50	14		33		11
White-browed Scrubwren:							
Ground	(5 fallen timber; forbs; rock and soil surfaces)	15	33	21	27	38	26
Other	(15 plant sp.)	3	7	15	25	27	15
Tree-ferns	(<i>Cyathea australis</i> or <i>Dicksonia antarctica</i>)		2	3	13	18	7
<i>Eucalyptus</i> sp.	(3+ <i>Eucalyptus</i> sp.)	21	4			4	6
Brown Thornbill:							
<i>A. dealbata</i>		46	56	31	8	32	34
Other	(23–24 plant sp.; 2 fallen timber; soil surface)	6	9	17	21	25	16
<i>Eucalyptus</i> sp.	(3+ <i>Eucalyptus</i> sp.)	33	11	12	16	8	15
<i>Pomaderris aspera</i>		3	2	10	21	12	10
<i>Prostanthera lasianthos</i>		4	5	12	1		4
<i>Acacia obliquinervia</i>		7	2	11	1		4
<i>Cassinia trinerva</i>					16	1	4
<i>Nothofagus cunninghamii</i>					1	15	4
Striped Thornbill:							
<i>Eucalyptus</i> sp.	(4+ <i>Eucalyptus</i> sp.)	81	32	31	15	43	41
<i>A. dealbata</i>		13	37	44			23
Other	(6–7 plant sp.)		26	6	46	43	21
<i>P. aspera</i>					39	14	9
<i>A. obliquinervia</i>		6	5	19			7
Eastern Spinebill:							
<i>C. lawrenciana</i>				63	27	44	42
Other	(10+ plant sp.)		80	16	46	3	32
<i>P. aspera</i>				5	27	17	14
<i>A. dealbata</i>		100	20	16		9	7
Eastern Yellow Robin:							
<i>A. dealbata</i>		69	59	25	7	21	32
Other	(15+ plant sp.)	6	5	25	40	37	2
Material tangled in vegetation	(Branch; bark)	6	9	21	17	21	15
<i>Eucalyptus</i> sp.	(2 <i>Eucalyptus</i> sp.)		5	4	17	11	8
Ground	(Fallen tree and branch; cover; soil surface)	13	5	4	17	5	9
<i>P. lasianthos</i>		6	5	17			5
Bare vegetation			14	4	3	5	5
Golden Whistler:							
<i>A. dealbata</i>		55	80	50	33	46	54
<i>Eucalyptus</i> sp.	(3+ <i>Eucalyptus</i> sp.)	41	13	25	25	13	23
Other	(9 plant sp.; bare tree; fallen branch; soil surface)	2	2	15	20	23	12
<i>P. aspera</i>				3	14	10	5
Grey Shrike-thrush:							
<i>Eucalyptus</i> sp.	(2 <i>Eucalyptus</i> sp.)	33	67	64	40	20	45
Other	(7–8 plant sp.; bare tree; soil surface)	50		9	40	50	29
<i>A. dealbata</i>		17	33	27	20	30	26

Table 5 Contd.

Foraging location category	(Broad location category detail)	Forest age classes					Total
		A	B	C	D	E	
Rufous Fantail:							
Other	(14–15 plant sp.; bare branch; bare tree; air)	25	43	29	63	50	39
<i>A. dealbata</i>		41	29	21	6	25	27
Ground	(Bark; fallen branch; soil surface)		10	21		5	7
<i>E. regnans</i>		28	19	8		5	14
<i>O. argophylla</i>		3			31	10	7
<i>P. aspera</i>		3		21		5	6
Grey Fantail:							
<i>A. dealbata</i>		47	64	26	16	25	41
<i>Eucalyptus</i> sp.	(3 + <i>Eucalyptus</i> sp.)	28	24	40	25	32	29
Other	(19 plant sp.; fallen tree; fallen branch; air)	8	6	6	27	29	13
<i>P. aspera</i>		1		10	12	5	4
Grey-breasted White-eye:							
<i>A. dealbata</i>		58	63	35	10	38	40
Other	(14–16 plant sp.; fallen branch; ground; air)	12	13	8	55	38	26
<i>P. sambucifolia</i>		12			21	6	8
<i>Eucalyptus</i> sp.	(2 + <i>Eucalyptus</i> sp.)	6	17	15		3	8
<i>O. phlogopappa</i>		6	4	12	3	6	6
<i>P. aspera</i>		3		12	7	9	6
<i>P. lasianthos</i>		3	4	19	3		6

(high, significant, positive $\lambda/(SE_\lambda)$ values for FACs A and B) and avoided the older ones (large, significant, negative $\lambda/(SE_\lambda)$ value for FAC D). In contrast, adult males rarely foraged in the youngest FAC (large, significant, negative $\lambda/(s.e.\lambda)$ value for FAC A), but commonly did so in the older FAC D (high, significant, positive $\lambda/(s.e.\lambda)$ value for FAC D) (Tables 1, 2 and 3); (2) throughout succession, immatures mostly avoided *Acacia* and *Eucalyptus* trees and mainly foraged in 'other' locations (high, significant, positive $\lambda/(SE_\lambda)$ value), whereas adult males mainly avoided 'other' locations (large, significant negative $\lambda/(SE_\lambda)$ value) and foraged extensively in eucalypts (Table 7); and (3) immatures mostly avoided the canopy and foraged in the shrub stratum (high, significant negative and positive $\lambda/(SE_\lambda)$ values, respectively), whereas adults mainly avoided the shrub layer, males particularly having a strong propensity for canopy foraging (high, significant $\lambda/(SE_\lambda)$ value) (Tables 7 and 8).

3.7 Foraging rate

There were few disparities amongst FACs in foraging rates of any of the three bird species in which this parameter was studied. However, Brown Thornbills had higher rates of: (1) search hops in the oldest (E) than in the youngest FAC (A) ($KW=10.92$, $P=0.004$); (2) search flights in FAC A than in C and E ($KW=10.95$, $P=0.004$); and (3) near-perch prey attacks in FAC C than in A ($KW=7.2$, $P=0.027$) (Figure 3). Their median total search-movement rate, however, was similar amongst FACs (31, 30 and 31

movements min⁻¹, respectively; $KW=3.05$, $P=0.223$). Grey Fantails had higher search flight rates in FAC C than in the oldest FAC (E) ($KW=8.5$, $P=0.01$).

3.8 Relationship between occurrence of plant species and their use by foraging birds

In the four species that could be satisfactorily examined in this context (Golden Whistler, Brown Thornbill, Grey Fantail and White-browed Scrubwren), proportional use of a particular plant species for foraging usually exceeded the plant species' proportional occurrence in the FAC, although by <10% (Table 9). The two exceptions to this <10% 'overexploitation' trend were: (1) that all four bird species used *A. dealbata* disproportionately to its percentage occurrence in all or most FACs by >10% (Table 9); and (2) *E. regnans* was used disproportionately to its occurrence by >10% by some bird species in some FACs (Table 9). These two plant species accounted for over half of the instances where relative occurrence and use of a plant species by a bird species differed by >10%. The Brown Thornbill, for which we obtained most foraging records, used particular plant species for foraging either proportionately to their occurrence in a FAC or disproportionately more, but never disproportionately less.

The four bird species all varied amongst FACs in their use of plant species for foraging. Positive correlations between chronologically sequential FACs for ratios of occurrence; use of all plant species (Table 10) indicated

Table 6 The strength and direction of associations expressed as $\lambda/(SE_\lambda)$ between forest age class (A–E, youngest to oldest) and foraging location for eight bird species. Bird species are those that exhibited a significant interaction in the most parsimonious log-linear model between forest age class and foraging location. Only values exceeding ± 1.65 ($P \leq 0.1$) are shown. The locations and bird species (*Striated Thornbill* and *Eastern Spinebill*) for which there were no $\lambda/(SE_\lambda)$ values exceeding this level for any forest age class were omitted from the table

Foraging location		Forest age class			
	A	B	C	D	E
<u>Crimson Rosella:</u>					
Acacia dealbata		+2.88 ^a			
Other plant sp. and bare trees		-2.30 ^a	+1.90		+2.98 ^a
Ground and ground cover			-1.65	+2.08 ^a	
<u>White-browed Scrubwren:</u>					
Tree-ferns	-1.79			+2.55 ^a	+3.20 ^a
<i>Acacia dealbata</i>	+5.62 ^a	+2.66 ^a	-1.66	-1.67	
<i>Eucalyptus</i> sp.	+4.15 ^a				
<i>Correa lawrenciana</i>	-1.76		+3.22 ^a	+2.51 ^a	
Ground cover					+1.87
Other live plant sp.	-2.71 ^a	-1.92		+2.96 ^a	+2.49 ^a
<u>Brown Thornbill:</u>					
<i>Cassinia trinerva</i>				+5.00 ^a	
<i>Nothofagus cunninghamii</i>					+5.64 ^a
<i>P. lasianthos</i>			+3.53 ^a		-1.97 ^a
<i>A. dealbata</i>	+3.41 ^a	+3.54 ^a		-6.22 ^a	
<i>Acacia frigescens</i> or <i>A. melanoxylon</i>				+1.71	
<i>Acacia obliquinervia</i>	+3.08 ^a		+3.73 ^a	-1.73	-1.70
<i>Eucalyptus</i> sp.	+4.33				
<i>Pomaderris aspera</i>		-2.43 ^a		+2.97 ^a	+2.11 ^a
<i>C. lawrenciana</i>			+1.68	+1.69	
Bare plant		+3.31 ^a			
Other live plant sp.; fallen timber; ground)					+3.25 ^a
<u>Eastern Yellow Robin:</u>					
Other live plants		-1.80			
<u>Golden Whistler:</u>					
<i>A. dealbata</i>				-3.14 ^a	
<i>A. frigescens</i> or <i>A. melanoxylon</i>		+1.77			
<i>Eucalyptus</i> sp.				-1.68	
<u>Rufous Fantail:</u>					
<i>Olearia argophylla</i>				+1.93	
<u>Grey Fantail:</u>					
Tree-ferns				+2.23 ^a	
<i>A. dealbata</i>	+1.89	+3.70 ^a		-3.56 ^a	
<i>A. obliquinervia</i>	+1.87				
<i>Eucalyptus</i> sp.				-2.32 ^a	
<i>P. aspera</i>			+1.79	+1.76	
Bare tree		+1.68			
Other live plant sp.; air; ground; ground; Litter					+1.96 ^a
<u>Grey-breasted White-eye:</u>					
<i>Polyscias sambucifolia</i>				+2.58 ^a	
<i>O. phlogopappa</i>					
<i>P. lasianthos</i>			+2.25 ^a		
<i>A. dealbata</i>	+1.96 ^a			-2.27 ^a	
<i>Eucalyptus</i> sp.	+2.13 ^a				

^aSignificant $\lambda/(SE_\lambda)$ values.

Table 7 The percentage (rounded) of Golden Whistlers in five forest age classes (A–E, youngest to oldest) foraging in three locations, on two substrates and using three modes. The modes for which there were no data are omitted

Age/sex	Location	Substrate	Mode	Forest age class					Total
				A	B	C	D	E	
Immature:	Acacia	Foliage/Other ^c	aerial	13 ^b	8		2	4	5
			near	7	8		2	4	4
		Wood	aerial		2				1
			near	3	2				1
			search	7	10 ^b	9		4	6
	Eucalyptus	Foliage/Other ^c	aerial	3	2				1
			near	3	2	3			2
		Wood	near	10 ^b					2
			search	3	2	3	2		2
			aerial			6		4	2
Female:	Acacia	Foliage/Other ^c	near				4		1
			Wood	aerial		3	2		1
		Wood	aerial		3		9	14 ^b	5
			near			3			
			search		2	3	4	11 ^b	4
	Eucalyptus	Foliage/Other ^c	aerial		4		2	4	2
			near			3			1
		Wood	near			6			1
			search		2	3	4	11 ^b	4
			aerial				2		2
Male:	Acacia	Foliage/Other ^c	near			3			1
			Wood	aerial			2		1
		Wood	aerial				11 ^b	4	3
			near				2		1
			search		14 ^b	12 ^b	13 ^b	11 ^b	11 ^b
	Eucalyptus	Foliage/Other ^c	near	3				4	1
			Wood	aerial			2		1
		Wood	aerial				4		1
			near		4		2	4	2
			search	10 ^b	12 ^b	9	4	11 ^b	9
Other ^d	Acacia	Foliage/Other ^c	aerial			3	2		2
			near			3	4		2
		Wood	near			3	4	4	3
			search		3	4	2	4	3
			aerial				2		1
	Eucalyptus	Foliage/Other ^c	near			2			1
			Wood	aerial			2		1
		Wood	aerial				4		1
			near			3	4	4	2
			search	3	4	3	2		1
	Other ^d	Foliage/Other ^c	near				3		1
			Wood	aerial			3		1
		Wood	aerial				4		2
			near			3	4	4	2
			search		3	4	4		2

^aForaging modes were: aerial, prey attack in flight; near, near-perch prey attack; search, looking for food items.^bPercentages ≥ 10%.^c All substrates except foliage and wood.^d All locations except eucalypts and acacias.

that three bird species, the Brown Thornbill, Golden Whistler and Grey Fantail, ‘tracked’ floristic changes among FACs (i.e. their use of a plant species for foraging relative to its occurrence remained constant) over at least

part of secondary succession. ‘Tracking’ was particularly evident in Golden Whistlers, occurring across all stages of the secondary succession, and in Grey Fantails, where it occurred across three of the four FAC transitions (Table 10).

Table 8 $\lambda/(SE_\lambda)$ values derived from log-linear models showing strength and direction of associations of age/sex classes of Golden Whistlers with forest age classes, foraging strata and foraging locations (presentation conventions are as in Table 6)

Age/Sex	Forest age class				
	A	B	C	D	E
Immature	+3.64 ^a	+2.41 ^a	-1.81	-3.03 ^a	
Adult female				+1.77	
Adult male	-2.47 ^a	-1.71		+2.10 ^a	
Age/Sex	Foraging stratum				
	Canopy		Shrub		
Immature	-2.99 ^a		+4.12 ^a		
Adult female			-2.17 ^a		
Adult male	+2.15 ^a		-2.38 ^a		
Age/Sex	Foraging location				
	Acacia	Eucalyptus	All other		
Immature	-2.37 ^a	-2.0 ^a	+3.53 ^a		
Adult male		+1.99 ^a	-2.71 ^a		

^aSignificant $\lambda/(SE_\lambda)$ values.

4. DISCUSSION

With a few exceptions, bird species occurring at relatively high abundances throughout secondary succession exhibited plasticity in their use of foraging strata and locations. However, our initial prediction was only partly fulfilled, because during succession all species displayed stereotypy in their use of foraging substrates, only one varied in its foraging behaviour repertoire and only two varied in rates of searching for, and attacking, prey. Thus behavioural plasticity was marked with respect to where species foraged, but limited with regard to how they foraged.

4.1 Foraging stratum and height

Most bird species were flexible in their use of forest strata during secondary succession, foraging predominantly in the canopy in the 20 years immediately after disturbance, but mainly in the shrub stratum thereafter. A likely reason

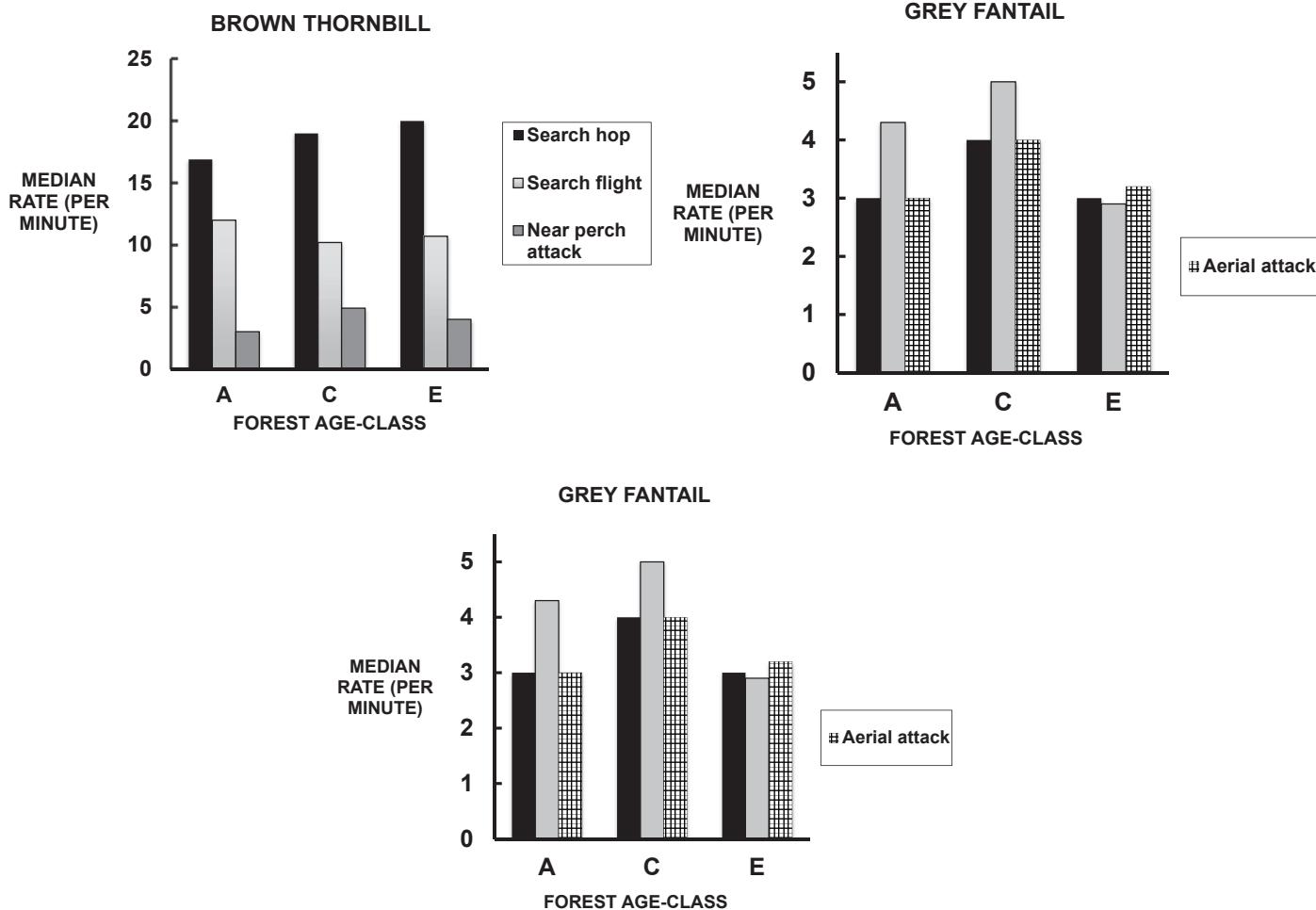


Figure 3 The median foraging rates (behaviours per minute) of three bird species in three forest age classes (A, C and E, youngest to oldest). The legend is the same throughout, except for addition of aerial attack for Grey Fantail. Sample sizes were:

Brown Thornbill – A 99, C 209 and E 234; Golden Whistler – A 76, C 91 and E 88; Grey Fantail – A 173, C 146 and E 94.

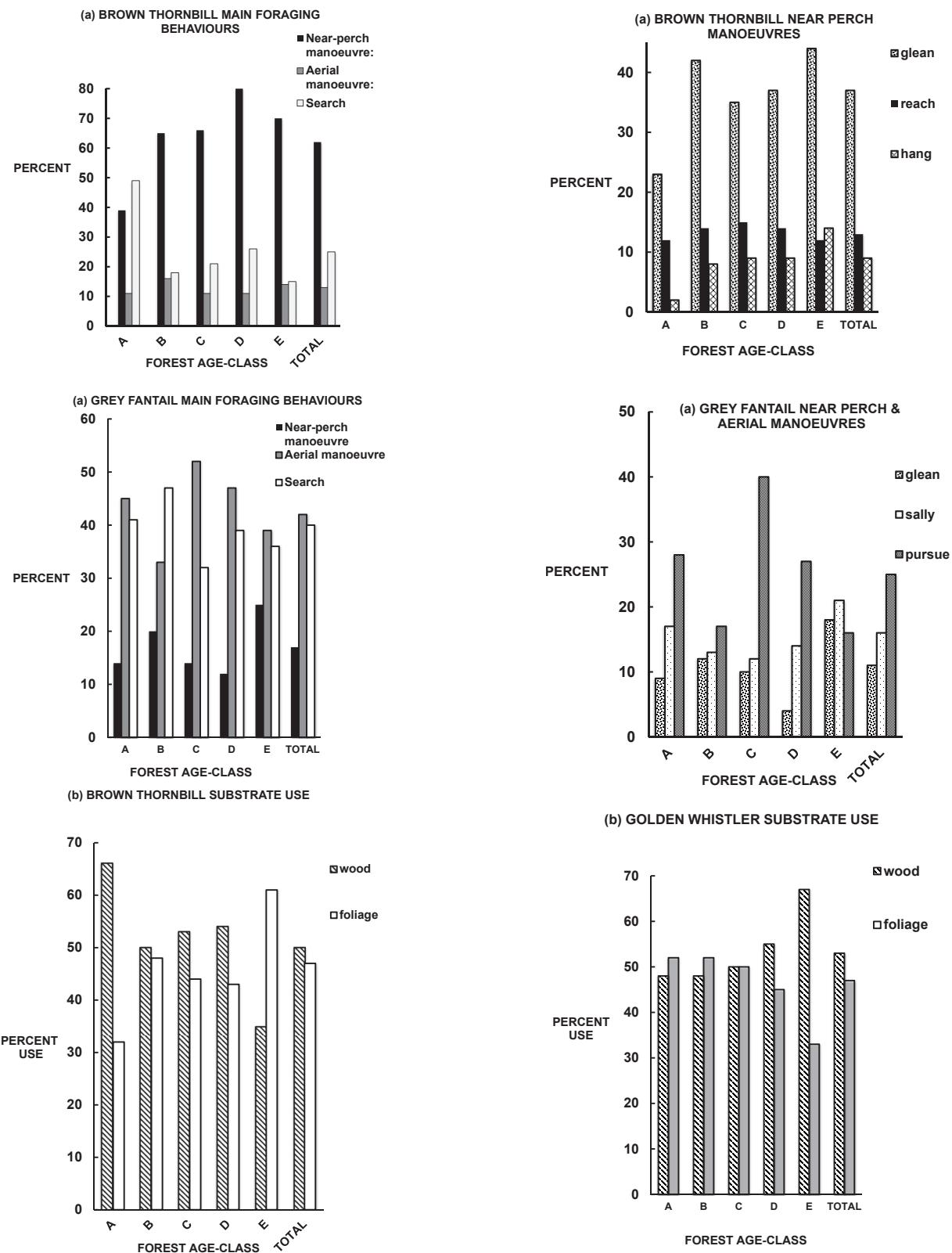


Figure 4 (a) Brown Thornbills and Grey Fantails as examples of percentage use of foraging modes and specific foraging behaviours, and (b) Brown Thornbills and Golden Whistlers as examples of percentage foraging substrate use in five forest age classes (A-E, youngest to oldest). Data are not presented for a species where no score for any forest age class $\geq 10\%$. $\lambda/(SE_\lambda)$ values (exceeding ± 1.65) for Brown Thornbill's foraging mode use were: FAC A Near perch manoeuvre + handling food -3.75 , Search $+4.56$; FAC B Search -1.77 ; FAC E Near perch manoeuvre + handling food $+1.88$, Search -2.19 . Sample sizes are as in Table 3. The wood substrate category for Brown Thornbill comprised stems, trunks, branches, galls and bark and for Golden Whistler the first four of these specific substrates. The foliage substrate category for Brown Thornbills comprised the specific substrates leaves and fronds. The foliage substrate category for Golden Whistler included cobwebs and air.

woodland (Recher et al., 1985) and the species' low relative abundance in the early successional stages in our study was probably due to the limited availability during early regrowth of suitable flowering shrubs, such as Mountain Correa. However, even this bird species exhibits flexibility in foraging stratum use on a broad geographical scale, because in mature, undisturbed *Eucalyptus* forest in New South Wales, it fed mainly at canopy flowers (Smith, 1985).

Some bird species that varied amongst FACs in their forest stratum use also exhibited considerable seral variation in proportional foraging height, but others did not. For example, Brown Thornbills feed substantially in the shrub layer in mature eucalypt forest and woodland (Recher et al., 1987; Bell and Ford, 1990) and foraged mainly in the mid- to high shrub layer in FACs C, D and E in our study, but they foraged substantially in the mid- to high canopy in the youngest FACs, A and B. In contrast, White-browed Scrubwrens foraged mainly in the shrub layer and on the ground in FACs B–E, but in the low canopy in FAC A. However, because mean canopy height was nearly seven times lower in the youngest than in the oldest FAC (Serong and Lill, 2008), their proportionate foraging height was similar throughout succession.

From a comparative perspective, many authors have documented ecological segregation of co-existing bird species and foraging guilds in disturbed and undisturbed forest through exploitation of different vertical foraging strata (e.g. Recher et al., 1987; Mansor and Mohd Sah, 2012; Kornan et al., 2013). However, very few have examined intraspecific variation in foraging stratum and height during forest regeneration; those that have, collectively documented both plasticity and stereotypy in strata use, as observed in our investigation. Some examples of intraspecific plasticity in foraging strata use after disturbance are: (1) Western Slaty Ant-shrikes (*Thamnophilus atrinucha*) foraging in lower strata in regenerating than mature Panamanian moist rainforest (de Zwaan and Roitberg, 2014). This apparently enabled them to maintain prey attack and capture rates comparable to those in mature forest because of the greater insect abundance in the lower than the upper vegetation strata in regrowing stands; (2) four of five passerine species in mixed-coniferous forest in Arizona differing in their foraging heights between logged and unlogged sites (Franzeb, 1983); and (3) Western Yellow Robins (*Eopsaltria griseogularis*) and Rufous Treecreepers (*Climacteris rufa*) foraging at lower heights in West Australian Jarrah forests pre- than post-logging (Craig, 2002). Some examples of intraspecific stereotypy in strata use in disturbed forest are: (1) three of five passerine species inhabiting forest in West Virginia, USA not responding to logging by altering their foraging strata (Maurer and Whitmore, 1981); and (2) Golden Whistlers and White-naped Honeyeaters (*Melithreptus lunatus*) using similar foraging strata in mature and logged Western Australian Jarrah (*Eucalyptus marginata*) forests (Craig, 2002).

4.2 Foraging location

Foraging locations recorded were: living plants, dead structural vegetation items (e.g. fallen branches or shed bark), the ground and the air. As considerable floristic and structural change typically occurs during secondary succession (Guariguata and Osterag, 2001), bird species using the first two of these locations are the ones most likely to exhibit foraging location variation during forest regrowth. Several species showed such variation in our study. Some used *A. dealbata* and/or eucalypts more in the youngest FACs than in the oldest ones, which again may have reflected the structural similarity of these trees in early successional stands to the shrub layer of mature forest. However, a further reason for this trend could be that in early succession after wildfire or slash burning, foliage of young eucalypts and acacias is nutrient-rich, has a low chemical defence capacity and is therefore particularly vulnerable to insect attack (Peet, 1992; Ashton and Attiwill, 1994). The resultant high insect abundance is likely to attract foraging insectivores, such as White-browed Scrubwrens. Other bird species used a wider range of foraging locations in the oldest than in the youngest FACs. This was facilitated by the increases in floristic and structural diversity during succession (Serong and Lill, 2008) which created an opportunity for versatile foragers, such as Brown Thornbills, to exploit a broader range of foraging locations in more mature forest.

From a comparative standpoint, it is not surprising that other authors have also documented flexibility in choice of foraging locations during secondary succession. For example, in South Australian heath vegetation, Slender-billed Thornbills (*Acanthiza iredalei*) foraged more on living *Leptospermum* and *Allocasuarina* plants in regenerating and mature than in recently burnt sites, despite *Leptospermum* being dominant in the latter sites. However, the thornbills showed the opposite trend for many other plant species (Ward and Paton, 2004). In mixed coniferous forest in the United States, five passerine species all differed in their foraging locations (mainly particular tree species) between logged and unlogged sites, most being more generalised in their choices in the disturbed sites (Franzeb, 1983). In contrast, in West Australian eucalypt forest four passerine species used the same foraging locations (tree species) before and after selective canopy-tree removal, although this example may have been unusual in that the disturbance affected only forest structure, not floristics (Craig, 2002).

4.3 Foraging substrate and mode

Intraspecific disparities in birds' foraging substrate use and behaviour between anthropogenically-disturbed and relatively undisturbed vegetation have been documented in a few species, e.g. insectivorous Elepaio (*Chasiempis sandwichensis*) in Hawaiian forests (VanderWerf, 1994), Slender-billed Thornbills in South Australian heath (Ward and Paton, 2004) and five passerine species in mixed-coniferous forest in Arizona (Franzeb, 1983).

In contrast, in the present investigation no species varied significantly amongst FACs in its use of foraging substrates, and only Brown Thornbills varied in foraging behaviour during succession. This species had a broad foraging behaviour repertoire, ranging from gleaning to hovering, a versatility that has also been recorded for the species in other types of forest and woodland (Recher et al., 1987). It was observed searching for food more frequently in the younger than older FACs and was rarely seen actually handling food items in the youngest FAC. This suggests that it may have found food harder to obtain in the younger FACs; its greater rate of performing search flights and lower rates of performing search hops and near-perch prey attacks in the younger than in the older successional stages is consistent with this interpretation.

The study species were probably capable of changing their foraging substrates and behaviour repertoire breadth in response to seral vegetation change. Seasonal changes in foraging substrate use and foraging behaviour have been recorded in Tasmanian sclerophyll forest in two of the present study species, the Grey Shrike-thrush and White-browed Scrubwren, respectively (Cale, 1994), as well as in other small insectivores in other forest habitats (Sakai and Noon, 1990; Craig, 2002; Powell et al., 2015). Such variation indicates that a capacity to adjust foraging substrates and behaviours may be fairly common among small, insectivorous birds. Therefore, the limited seral variation in foraging substrate use and behaviour that we recorded suggests that for the species that were abundant in several FACs such change would not have conferred significant benefit. However, we should bear in mind that plasticity in foraging substrate use and behaviour has not proved to be universal in other investigations. For example, the substrates and foraging behaviours used by most species comprising winter bird assemblages in oak forest in north-west Italy were similar in disturbed and mature forest (Laiolo et al., 2003) and, despite declining in abundance after logging of Western Australian *Eucalyptus–Corymbia* forest, White-naped Honeyeaters and Golden Whistlers also exhibited little change in foraging substrates and behaviours (Craig, 2002). The few documented examples of intraspecific variation in avian foraging behaviour during secondary succession, not surprisingly, rarely involve fundamental change in the motor patterns employed, but rather changes in the relative frequencies at which various foraging behaviours are used and contraction/expansion in inherent repertoire size (VanderWerf, 1994; Craig, 2002).

4.4 Age-related variation in foraging of Golden Whistlers during secondary succession

First-year Golden Whistlers foraged: (1) more in early than late successional stages; (2) little in acacias and eucalypts; and (3) mainly in the shrub rather than the canopy layer. Adults, particularly males, showed the opposite tendencies.

The disparate distributions of first-year individuals and adult males amongst FACs reflects a change in either age structure of the population during succession or, more probably, in the degree of age-class segregation across the spatial mosaic of different FACs in the study area. Theoretically, this segregation could be due to: (1) social dominance of the better quality (older) FACs by adults; (2) age differences in foraging skills or degree of foraging specialisation; or (3) age disparities in spatially fixed activities other than foraging. Displacement of immature conspecifics from prime habitat through aggressive interference competition by dominant adults occurs in several bird species, including Cape May Warblers (*Dendroica tigrina*) (Latta and Faaborg, 2002), and American Redstarts (*Setophaga ruticilla*) and Black-throated Blue Warblers (*Dendroica caerulea*) wintering in Jamaica (Holmes et al., 1989). However, aggression between adult and immature whistlers was negligible in our investigation, making this segregation mechanism unlikely.

Age differences in avian foraging skills and efficiency are common (e.g. Marchetti and Price, 1989; VanderWerf, 1994; Rutz et al., 2006) and apparently lead to considerable habitat segregation of age classes in some species e.g. Crimson Rosellas (Magrath and Lill, 1985) and Rusty Blackbirds (*Euphagus carolinus*) (Mettke-Hofmann et al., 2015). Immature and adult Golden Whistlers differed in foraging stratum and location use, but not in foraging substrate choice or types of foraging behaviour employed. Immatures did have a faster food-searching rate than adult males (means: 7.5 ± 0.9 SE versus 4.8 ± 0.4 search hops min^{-1}), which could indicate less efficient foraging, but the disparity could also be due to the different foraging locations and strata used by the two age classes.

Age-class habitat occupancy differences related to non-foraging activities have been postulated for several bird species. A possible example is the segregation in Portugal of wintering adult male European Robins (*Erithacus rubecula*) in woodland from females and immatures in habitats with more shrub cover that provides anti-predation benefits (Catry et al., 2004). Differences in non-foraging activity might also have been involved in Golden Whistler age-class FAC segregation. Brightly-coloured adult males presumably need to display in relatively open vegetation to be conspicuous to potential mates and sexual competitors in the breeding season, but non-breeding immatures should obtain beneficial concealment from predators by foraging in dense, shrub vegetation rather than the sparser canopies of eucalypt trees.

We found no sex differences in foraging in adult Golden Whistlers during secondary succession. However, they do occur in this genus in relatively undisturbed New Guinean tropical forest, where Freeman (2014) found that adult males of two congeneric species foraged in higher vegetation strata than did adult females.

4.5 Conclusions

Sample sizes varied up to 12.8-fold (for relative foraging height) among the study species. Whilst we feel that even most of the smaller samples provided a representative picture of foraging for the species concerned, clearly the inferences drawn about species for which we obtained the largest sample sizes are the most compelling.

The subset of bird species that remained common throughout post-disturbance secondary succession in Mountain Ash forests mostly adjusted their foraging strata and locations. As succession involved marked structural and floristic change, it would presumably have been difficult for most of these species to persist through early succession without such flexibility. This sort of plasticity has been recorded in birds in other forest ecosystems and may be widespread. However, two species exhibited stereotyped foraging stratum use and one stereotyped foraging location use during succession, suggesting that the strata and locations that they exploited provided the same or suitable alternative food resources throughout succession. Presumably bird species that were abundant only during a limited stage of secondary succession (Serong and Lill, 2012) lacked the plasticity in foraging stratum and location use exhibited by many persistent species or did not have suitable food resources available to them that could be acquired in the same stereotyped manner throughout succession. The White-throated Treecreeper (*Climacteris leucophaea*) (16–17.5 cm) could be an example. This species is a highly specialised forager, mainly capturing insects by stereotyped climbing up the trunks of mature trees with well developed bark and gleaning, probing and drilling the bark (Lindenmayer et al., 2007). It was only common in the later FACs when such mature trees became a prominent feature of the regenerating forest (Serong and Lill, 2008). Similarly, Striated Pardalotes (*Pardalotus striatus*) typically obtain their insect prey mainly by gleaning from canopy foliage in tall trees (Woinarski, 1985) and were only common in FACs D and E when this foraging stratum became available (Serong and Lill, 2012).

There were few adjustments of the persistent species' substrate use or actual foraging behaviour during succession. We would not expect novel foraging motor patterns to appear during succession, but adjustment of foraging substrates, behaviour repertoire breadth and relative frequency of performing particular foraging behaviours have been reported for bird species in other types of regenerating forests. They were only apparent in the Brown Thornbill, a highly versatile species, in our study. It seems likely that some adjustment of foraging behaviour and substrate choice was possible in most study species. After all, some of these species also occur in other structurally and floristically different types of forest and woodland and some members of some species apparently change forest habitats seasonally (Ford, 1989). Therefore, it seems likely that adjusting foraging behaviour

and substrate use was feasible in some study species but not required or advantageous in Mountain Ash regrowth.

The findings of the present investigation expand our understanding of exactly how some bird species can persist in regenerating forest, and should inform management strategies that aim to limit the negative impact of forest resource extraction on bird diversity.

5. ACKNOWLEDGEMENTS

We acknowledge the original custodians of the study area, the Wurundjeri and Taungurong people. We thank scientists, managers and field staff of the then Department of Environment and Primary Industry, Parks Victoria and Melbourne Water collectively for various kinds of assistance.

Published online: 22 July 2016

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