

Differential use of habitat aids local coexistence of three species of wrens (Maluridae) and the White-browed Scrubwren *Sericornis frontalis*: Pardalotidae in Myall Lakes National Park

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ABSTRACT

Four species of small insectivorous birds, the Superb Fairy-wren *Malurus cyaneus*, Variegated Fairy-wren *M. lamberti*, Southern Emu-wren *Stipiturus malachurus* and White-browed Scrubwren *Sericornis frontalis* have similar foraging methods which has often led to them being grouped into the same foraging guild. These four species occur in sympatry at Myall Lakes National Park, 300 km north of Sydney. Discriminant function analysis was used to test for any differential use of habitat between the four species. *Malurus cyaneus* was observed more often in open grassland habitats which is likely to be their preferred habitat. *Stipiturus malachurus* were more common in reedy (*Baumea* sp.) areas where their unique foraging behaviour may increase foraging efficiency. The remaining two species had some differences in habitat use, but foraged at significantly different heights in the vegetation.

Key words: *Malurus cyaneus*, *Malurus lamberti*, *Stipiturus malachurus*, *Sericornis frontalis*, habitat differentiation, coexistence, low-foliage gleaners, Variegated Fairy-wren, Superb Fairy-wren, White-browed Scrubwren, Southern Emu-wren.

Introduction

MacArthur (1958) studied the methods of resource partitioning employed by five species of warblers and explained their differential use of habitat in terms of competition. He suggested that these differences in foraging patterns allow coexistence between otherwise ecologically similar species.

Many studies since MacArthur's have shown that bird communities actually consist of groups or sets of species with similar resource utilisation patterns (Recher *et al.* 1985; Holmes and Recher 1986; Ford *et al.* 1986; Mac Nally 1994). Members of these groups often have similar foraging behaviours and are referred to as guilds (Root 1967) or functional groups (Cummins 1973).

Since members of each guild have similar foraging patterns, it seemed logical that co-members are more likely to share similar resources and hence experience more severe competition than non co-members. This belief led to a flurry of studies into resource partitioning between guild co-members. Many of these studies found that guild members often differ in their horizontal habitat selection and vertical foraging height (Cody 1968; Schoener 1974). For example, in Australia horizontal habitat differentiation was observed in treecreepers (Noske 1985), fantails (Cameron 1985), robins (Robinson 1992) and most often in honeyeaters (Recher 1971; Ford and Paton 1976; Chan 1990). Differences in foraging height were shown in Gerygones and thornbills (Recher 1989), and pardalotes (Woinarski 1985).

Recently, the role of competition in leading to these differences, and the importance of such differences, has been questioned. Australia has extremely dynamic bird communities (Mac Nally and McGoldrick 1997) with many migratory or nomadic bird species (Chan 2001; Griffioen and Clarke 2002). Therefore the likelihood of two species co-occurring for sufficient time to allow co-evolution seems unlikely. Furthermore, effects of immigration from nearby communities may mask any ecological differentiation. For these reasons, the explanation of resource differentiation in terms of facilitating coexistence has generally lost favour.

This change in view point has highlighted the danger in applying results from short-term small scale studies to bird communities on a regional scale. However, such studies do provide important information on resource differentiation, if it occurs (e.g. Mac Nally 2000), at a local scale. Therefore local habitat and resource utilisation studies are still of value.

One particular guild that has received little attention includes birds that forage by gleaning prey in the low vegetation, referred to as the low vegetation gleaners (Holmes and Recher 1986). This guild typically consists of small insectivorous birds from the family of Maluridae. However, studies into the community structure of Australian birds (Recher *et al.* 1985; Holmes and Recher 1986) have also included other species that are not members of the Maluridae family. These

include the White-browed Scrubwren *Sericornis frontalis* (Pardalotidae), and sometimes the Eastern Whipbird *Psophodes olivaceus* (Cinclosomatidae).

This study examines the relationships between vegetation structure, foraging methods, substrates and heights, and the local distributions of four sympatric species of low vegetation gleaners at Smiths Lake in Myall Lakes National Park on the central coast of NSW. These four species are the Variegated Fairy-wren *Malurus lamberti*, Superb Fairy-wren *M. cyaneus*, Southern Emu-wren *Stipiturus malachurus* and White-browed Scrubwren *Se. frontalis*. All four species are similar in size (*M. cyaneus* 9-11 gm, *M. lamberti* 7-10 gm, *St. malachurus* 6-9 gm, *Se. frontalis* 11-13 gm; see Rowley and Russell 1997), and all form highly social territorial groups of several individuals (*M. cyaneus* 6-12, *M. lamberti* 5-10, *St. malachurus* 2-8, *Se. frontalis* 2-4; see Rowley and Russell 1997 and Magrath and Yezerinac 1997). All have been shown to be cooperative breeders (Rowley 1965; Bell 1983; Tidemann 1986; Magrath and Yezerinac 1997) except for *St. malachurus*, which appears to breed only in monogamous pairs (Higgins et al. 2001).

Methods

Study area

This study was conducted on the shores of Smiths Lake near the University of NSW field station in the Myall Lakes National Park (32° 23' S, 152° 31' E), 250 km north of Sydney. Mean monthly temperatures ranged from 18.6 °C to 21.9 °C. The site occupies the area between the lakes edge and about 25 m south of Horse Point Road for approximately 750 m, a total of about 11.25 ha. Fifteen mist net sites were placed in close proximity to the road, no more than 100 m apart (Fig. 1). The area can be divided subjectively into several macrohabitats, based on estimates of the vegetation structure and main botanical components.

Using aerial photographs and ground measurements, a detailed map of the area showing the subjective habitat types was constructed (Fig. 1). This could then be superimposed with group and species boundaries using information gathered on individuals.

Bird surveys

Individuals were caught by mist nets over a six month period from mid-October of 1999 to late March of 2000. Trapping periods were conducted two weeks apart and each comprised three successive trapping days. Standard measurements (Lowe 1989) were taken from captured individuals of each of the four target species and had both metallic and colour bands placed on their legs. Each individual bird was given a unique combination of two colour bands to allow for later identification in the field. This meant that foraging manoeuvres for individuals could be recorded, as well as group associations being recognised and group boundaries determined.

Foraging and habitat data were collected throughout the trapping period in both morning and afternoon. Groups of birds were located within the study area by call, and then followed until all the colour-banded individuals were observed or the group was lost. Individuals were followed, and up to five sequential foraging manoeuvres recorded where possible. This method is more likely to show rarer foraging manoeuvres than a single point observation method and reduces problems associated with serial dependency (Morrison, 1984). When following a bird, a number of variables were recorded. These were its height above the ground, the substrate of the foraging manoeuvre, the species of plant on which the prey was located and the foraging manoeuvre. Above ground foraging substrates were similar to those defined in Holmes and Recher (1986). These were trunks, branches, twigs, leaves, loose bark, flowers, seeds and air. Foraging manoeuvres defined in Holmes and Recher (1986) were used with the exception of hang-glean, which was excluded and an additional manoeuvre of scratch was included (Table 1). Scratch, in this study, is defined as the movement of litter to extract food beneath the litter surface.

For each sighting of a recognised individual, its position in the study area and type of habitat in which it was observed was also recorded. The range of each species was estimated by pooling the territories of all individual groups. The proportion of habitats within each species range of occurrence was calculated by overlaying the vegetation map and species distribution with a grid. The habitat overlap index ($O_{hi} = O_{ih}$) was calculated from the proportions (P_{ij} and P_{ji}) of each habitat (j), within the

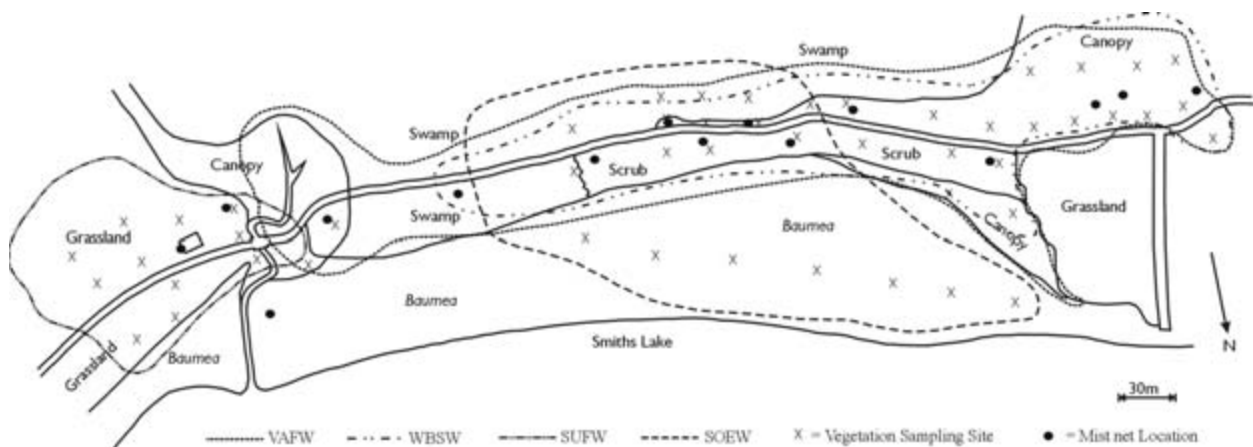


Figure 1. Distributions of habitat types and group boundaries on the study site at Smiths Lake.

Table 1. Definition of foraging manoeuvres used during the study. Foraging manoeuvres follow those defined by Holmes and Recher (1986). However, hang-glean was excluded and scratch has been added.

Manoeuvre	Definition
Glean	A stationary food item is picked from its substrate by standing or hopping bird
Probe/Prise	Like glean only the bird's beak penetrates or lifts the substrate to locate concealed food
Hover	A bird takes flight, hovers in a stationary position, sometimes only momentarily, near a substrate, and picks the food item from the substrates surface
Snatch	Like hover but the flying bird does not hover; instead it plucks the food from the substrate as it flies past
Pounce	A bird flies from a perch and grabs the food item as it lands on the substrate.
Hawk	A bird sallies into the air to catch flying prey
Scratch	The movement of litter to extract food beneath the litter surface

observed range of occurrence of each species (i and h). Overlap is defined (Pianka 1973) by the equation relating species i and species h that share j habitat states:

$$O_{hi} = O_{ih} = \left[\sum_j P_{ij} P_{hj} \right] / \left[\sum_j (P_{ij})^2 \cdot \sum_j (P_{hj})^2 \right]^{1/2}$$

Vegetation surveys

The vegetation of the study area was classified based on subjective estimation of vegetation structure and the dominant species.

Objective vegetation samples were taken at regularly spaced intervals throughout the study site in all types of habitat (Fig. 1), but concentrated in those areas frequented by the birds. At each of the 47 sample sites, sets of observations from 1 m were replicated along four perpendicular transects intersecting at the sample site. These four replications for each sample site were used to calculate the mean value for horizontal density (Mean) for each layer, and the coefficient of variation (CV) for each layer, the latter is a measure of understorey patchiness. Horizontal density was assessed using a modification of the method used by MacArthur and MacArthur (1961) which involved observing a 20x50 cm coverboard and estimating the area obscured by the vegetation. Observations were made for the layers 0-20 cm (Mean 0), 20-50 cm (Mean 20), 50-100 cm (Mean 50) and 150-200 cm (Mean 150) (see Fox 1979; Fox and Fox 1984). Few observations above this highest layer showed any vegetation cover and hence were not recorded.

To determine the preferred vegetation profile for a species or group, we needed to collect vegetation variables at each foraging site for every individual belonging to that species or group. This proved impractical and time consuming due to the vigorous foraging behaviour of the four target species. To overcome this, estimates of the vegetation variables at each foraging site were obtained by averaging the four nearest sample sites around the foraging site. If the vegetation of any of these was noticeably different to the foraging site, it was excluded from the average. While this method of estimation saves time, it is conservative and any differences found during the analysis may be greater than indicated.

Data analysis

Discriminant function analyses (SPSS 1995) was used to establish the degree of ecological separation between the four species in discriminant habitat space and identify which variables contributed most to any species separation.

The discriminant analyses involved a stepwise procedure to select the optimal set of functions that best separate groups identified *a priori*. The Wilks Lambda statistic was used as the selection criterion when selecting variables for inclusion in functions. The function loadings were determined from the correlations between the vector for each function and the vector for each variable. Interpretations for the meaning of each function can be obtained from inspection of the function loadings. The functions are used to calculate function scores for each foraging site for each species. Statistical separation between species was evaluated using the variance ratio for between-species and within-species differences for Mahalanobis distance (equivalent to Euclidean distance, but in multidimensional space) derived from a one-way analysis of variance (ANOVA), followed by post-hoc tests using Bonferroni-Dunn corrections (Rosenthal and Rosnow 1985).

Results

Subjective habitats

Based on overall structure and dominant plant species, five types of habitat were identified subjectively (Fig 1). These were canopy, scrub, swamp, grassland and *Baumea*. Mean vegetation layer densities and coefficients of variation (CV) for each of these habitats were calculated from the objective vegetation data (Table 2).

The canopy habitat had a dense understorey dominated by a mixture of sedge and short ferns including *Blechnum indicum* and Bracken Fern *Pteridium esculentum*. However, the most distinguishing feature of this habitat was the presence of a tall (25-30 m) canopy of Swamp Mahogany *Eucalyptus robusta*. The scrub vegetation had a similar understorey structure to the canopy vegetation, but was more open and taller (up to 150 cm). It also lacked a canopy and therefore was easily distinguishable from the canopy habitats.

The thickest vegetation occurred in the swampy areas, which were distinct in that they were wet underfoot and did not have a canopy. The swamp was dominated by dense Coral Fern *Gleichenia dicarpa* to a height of about 1 m. Above this height there was very little vegetation except for the occasional Swamp Banksia *Banksia robur* to a maximum height of about 3 m.

Table 2. The mean vegetation densities and coefficient of variation (CV) of each layer of the five subjectively identified habitats

Measurement	Canopy	Scrub	Swamp	Grassland	Baumea
Mean 0	98.81	95.00	100.00	98.17	93.91
Mean 20	86.88	89.08	99.75	56.92	76.41
Mean 50	57.60	64.17	85.50	12.60	22.63
Mean 100	7.50	19.83	7.75	1.73	0.00
Mean 150	2.40	3.75	1.25	0.00	0.00
CV 0	0.01	0.03	0.00	0.01	0.04
CV 20	0.16	2.24	0.00	0.39	0.18
CV 50	0.29	0.23	0.14	0.94	0.60
CV 100	1.51	0.49	0.99	1.78	0.00
CV 150	2.48	0.96	2.06	0.00	0.00
No. Samples	18	6	11	10	7

The *Baumea* areas were closest to the lake and may or may not have a canopy of Broad-leaved Paperbark *Melaleuca quinquenervia*. The understorey was approximately 1 m in height and dominated by *Baumea juncea*. This understorey vegetation was less dense above 20 cm than all the other habitats except the grasslands. The grassland, which was an old farming area, had a thick, low layer of grass to a height of about 20 cm and may or may not have a tall canopy of *M. quinquenervia*. Between the grass and canopy layers was the occasional *Melaleuca* ranging in height from 2-10 m.

Home ranges and group dynamics

Four groups of *M. lamberti* (VAFW) were identified in the study area, but the territory of one group only marginally extended into the study area. The birds from this last group were observed too few times to be included in the study. Three groups of *Se. frontalis* (WBSW) were recognised, but similar to *M. lamberti*, one group was excluded due to the lack of observations. Two *M. cyaneus* (SUFW) groups were recognised and only one group of *St. malachurus* (SOEW) was observed.

Not all individuals in each group were banded, and hence each group may be larger than indicated in Table 3. However, observations suggested that the majority (~80%) of each group was banded for all species except *St. malachurus*. Individuals of this species in particular were able to slip very easily through the larger nets (3.8 cm) and had a very low catch rate.

Table 3. Groups recognised in each species and the number of banded birds in each group respectively found in the study area (October 99 - March 00) (SUFW = Superb Fairy-wren *M. cyaneus*; SOEW = Southern Emu-wren *St. malachurus*; WBSW = White-browed Scrubwren *Se. frontalis*; VAFW = Variegated Fairy-wren *M. lamberti*).

Species	Groups	Group size
VAFW	RR, PB, YY	11, 12, 7
WBSW	WW, UU	2, 2
SUFW	RR, OO	4, 4
SOEW	RR	4+

The positional data collected for each sighting of each individual was used to map the ranges of occurrence for the four species (Fig. 1). This information showed that *M. lamberti* and *Se. frontalis* have the most similar areas of occurrence, with their ranges including high proportions of canopy and scrub habitats (Table 4). The habitat overlap index based on the five habitats shows that 87% of the habitat within the two species ranges was similar (Table 5). *Stipiturus malachurus* range overlapped and extended beyond that of *M. lamberti* and *Se. frontalis* (Fig. 1), extending into the *Baumea* close to the lake and further into the swamp. Consequently, they had less habitat in common with *M. lamberti* and *Se. frontalis* (Table 5).

Table 4. The proportions of each type of subjective habitat within the identified ranges of each species (SUFW = Superb Fairy-wren *M. cyaneus*; SOEW = Southern Emu-wren *St. malachurus*; WBSW = White-browed Scrubwren *Se. frontalis*; VAFW = Variegated Fairy-wren *M. lamberti*).

	Canopy	Scrub	Swamp	Grassland	Baumea
VAFW	0.43	0.46	0.09	0.01	0.01
WBSW	0.76	0.24	0	0	0
SUFW	0.05	0.05	0	0.90	0
SOEW	0.07	0.10	0.18	0	0.65

Table 5. Habitat overlap index calculated from the proportions of habitats within each of the species observed range of occurrence (SUFW = Superb Fairy-wren *M. cyaneus*; SOEW = Southern Emu-wren *St. malachurus*; WBSW = White-browed Scrubwren *Se. frontalis*; VAFW = Variegated Fairy-wren *M. lamberti*).

	VAFW	WBSW	SUFW
WBSW	0.87		
SUFW	0.09	0.07	
SOEW	0.23	0.14	0.01

In comparison to the other three species, *M. cyaneus* was the only species often found in the grassland to the east of the study area, and rarely ventured into thicker cover. This resulted in a disjunction between the range of *M. cyaneus* and the ranges of the other three species (Fig. 1) and very low habitat overlap with the other three species (Table 5).

Foraging characteristics

All four species use similar foraging manoeuvres, spending the majority of their time gleaning their prey (Fig. 2). The remaining time was mostly taken up by snatch attacks. For all four species, dominant foraging behaviours were directed primarily towards leaves and then less often twigs (Fig. 3). In comparison with the other species, *M. cyaneus* spent larger amounts of time on the ground while *Se. frontalis* often foraged in leaf litter, either by gleaning from the leaf litter surface or less often by scratching or probing into the litter. This is reflected not only in their higher percentage of time spent foraging on dead material, but also the percentage of time they spend on the ground (Fig. 3).

Observations of the foraging height for each of the four species suggested that *Se. frontalis* and *M. cyaneus* had their maximum foraging layer at 50 m or below, lower than the other two species (Fig. 4). *Sericornis frontalis* were most often seen at 0.5 m in the thick dense vegetation, while *M. cyaneus* was more often seen at 0.5 m or foraging on the ground. *Stipiturus malachurus* and *M. lamberti* on the other hand ranged into the upper strata of the low vegetation, or foraged above it (Fig. 4). *Sericornis frontalis* foraged at significantly different heights to the other three species (Fig. 5). *Malurus cyaneus* was also shown to forage at significantly different heights from *M. lamberti* and *Se. frontalis*, but not *St. malachurus* (Fig. 5).

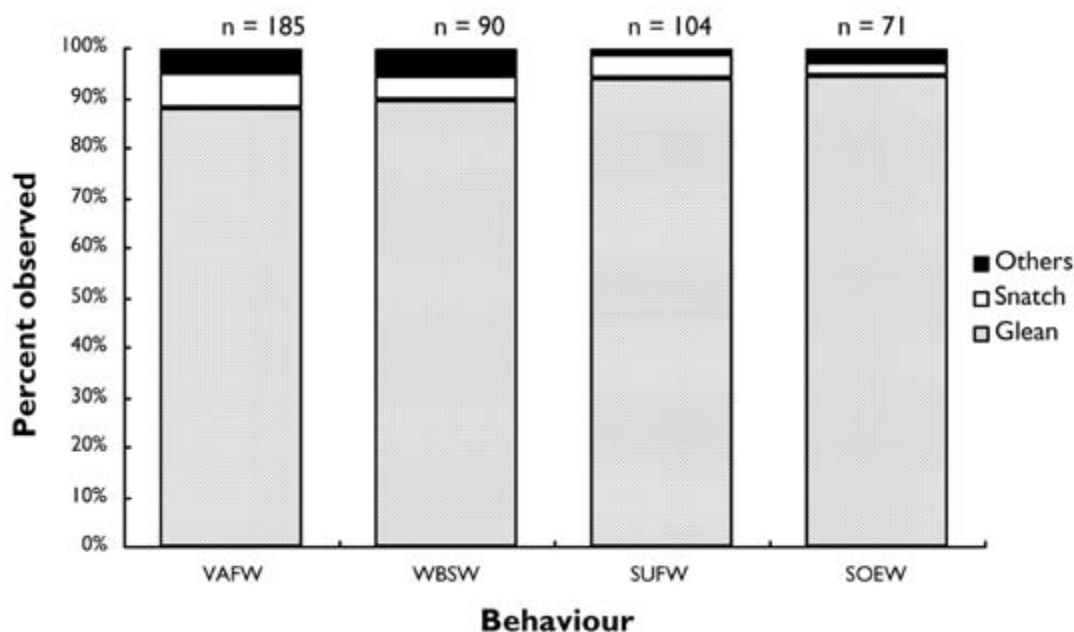


Figure 2. The proportion of observed feeding behaviours for Variegated Fairy-wrens *M. lamberti* (VAFW), White-browed Scrubwrens *Se. frontalis* (WBSW), Superb Fairy-wrens *M. cyaneus* (SUFW) and Southern Emu-wrens (*St. malachurus*) (SOEW) in the study area. Sample size is indicated for each species above their respective columns.

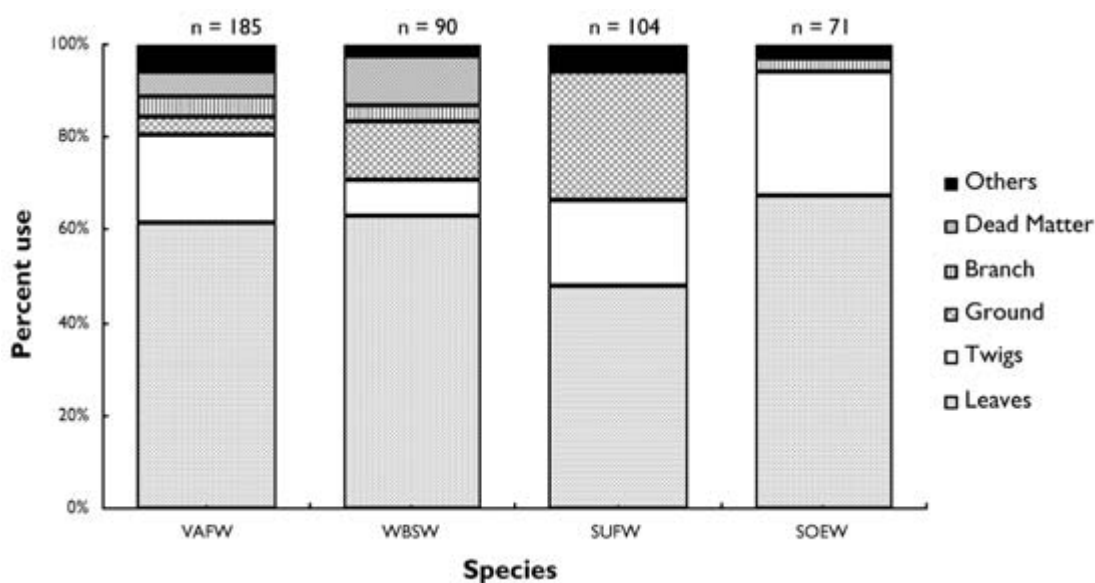


Figure 3. Substrate use of the four low vegetation gleaners at Myall Lakes National Park. bare ground, grass and litter were recombined into the ground category as defined by Holmes and Recher (1986) previously. Sample size is indicated for each species above the respective columns (SUFW = Superb Fairy-wren *M. cyaneus*; SOEW = Southern Emu-wren *St. malachurus*; WBSW = White-browed Scrubwren *Se. frontalis*; VAFW = Variegated Fairy-wren *M. lamberti*).

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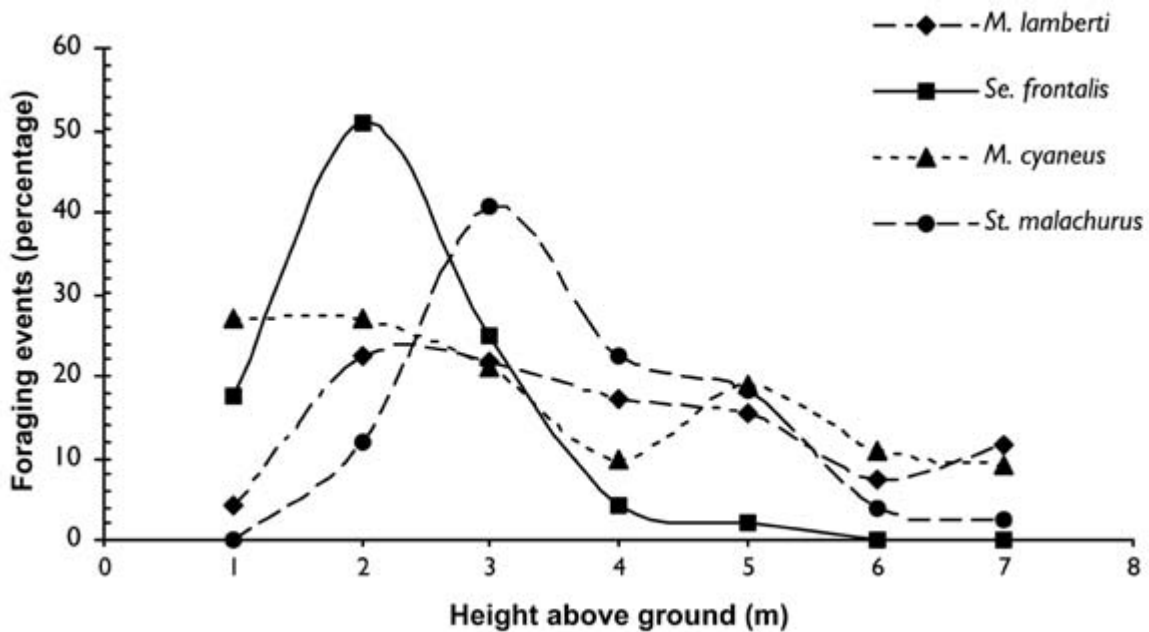


Figure 4. Foraging height patterns for each species, Variegated Fairy-wrens *M. lamberti* (VAFW), White-browed Scrubwrens *Se. frontalis* (WBSW), Superb Fairy-wrens *M. cyaneus* (SUFW) and Southern Emu-wrens *St. malachurus* (SOEW)

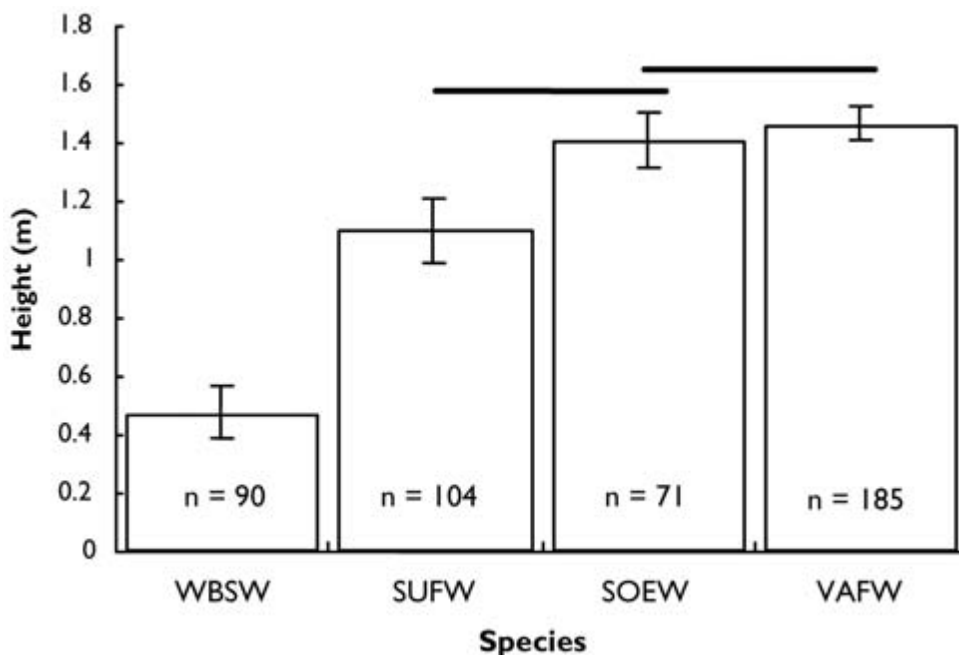


Figure 5. Foraging height (\pm s.e.) comparisons for each of the four species. Bold lines above pairs of columns indicate those species that forage at similar heights (not significantly different, ANOVA). Sample size for each species is indicated (SUFW = Superb Fairy-wren *M. cyaneus*; SOEW = Southern Emu-wren *St. malachurus*; WBSW = White-browed Scrubwren *Se. frontalis*; VAFW = Variegated Fairy-wren *M. lamberti*).

Discriminant function analysis

Using a stepwise discriminant function analysis, we separated each of the identified territorial groups in a multidimensional space based on the vegetation in which each of the eight groups were observed feeding. Differences between the species along single functions can then be obtained by pooling the discriminant function scores for each group within a species and testing for significant variance using ANOVA. The resulting eight group analysis identified seven functions which explained 71.3%, 15.13%, 7.51%, 4.11%, 1.25%, 0.64% and 0.05% of the variance respectively.

The first discriminant function was interpreted as dense, even vegetation between 20 cm and 100 cm (Table 6). The second function was interpreted as dense even vegetation between 50 cm and 150 cm. Function 3 was interpreted as a lack of vegetation from 150 cm to 200 cm while function 4 was interpreted as sparse, patchy vegetation below 50 cm, but denser vegetation above 50 cm. Differences in habitat selection were best explained by function 1 and foraging heights. The position of each species along function 1 is presented in Fig 6, where 95% confidence ellipses (Sokal and Rohlf 1969) are plotted around each groups centroid. *M. cyaneus* has the only

Table 6. The four most important functions identified by the discriminant function analysis

Variable	Function 1	Function 2	Function 3	Function 4
Eigenvalue	3.5714	0.7577	0.3760	0.2057
% of Variance	71.31	15.13	7.51	4.11
Cumulative %	71.31	86.44	93.95	98.06
Mean 20	0.648			-0.381
Mean 50	0.628	0.439		0.370
CV 20	-0.383		0.311	0.302
CV 50	-0.322			
Mean 100		0.449		0.368
Mean 150			-0.545	
Mean 0				-0.471
CV 0		-0.314		0.450
Interpretation	+ve Dense even vegetation 20-100 cm	+ve Dense vegetation from 50 - 150 cm	+ve Sparse vegetation above 150 cm	+ve Sparse, patchy vegetation below 50 cm, dense above
	-ve Sparse patchy vegetation 20-100 cm	-ve Sparse vegetation from 50 - 150 cm	-ve Dense vegetation above 150 cm	-ve Dense vegetation below 50 cm, sparse above 50 cm

Correlation coefficients for variables making major contributions to a function are shown in bold-face type, while minor contributions above 0.3 are also shown, but correlations below 0.3 are omitted to simplify the table.

negative mean association (-3.67) with function 1 and the pooled discriminant function scores for this species were statistically different from all other species (Table 7). Function 1 is also useful in identifying a difference between the mean position for *St. malachurus* (0.229) from the more positive association of *M. lamberti* (0.992) and *Se. frontalis* (0.883).

Table 7. Statistical separation of species based on their discriminant functions scores for function 1. * indicates those species that are significantly different at the 5% level (SUFW = Superb Fairy-wren *M. cyaneus*; SOEW = Southern Emu-wren *St. malachurus*; WBSW = White-browed Scrubwren *Se. frontalis*; VAFW = Variegated Fairy-wren *M. lamberti*).

	WBSW	SUFW	SOEW
SUFW	< 0.001*		
SOEW	0.014*	< 0.001*	
VAFW	0.536	< 0.001*	0.001*

Using the interpretation provided in Table 6, we can see that the negative scores of *M. cyaneus* (-3.67) indicate that they were observed in open areas with open vegetation above 20 cm (ie grasslands; see Table 2). The observed occurrence of *M. cyaneus* in the grassland

areas (Fig. 1) supports this interpretation. In contrast to *M. cyaneus*, positive centroids of *M. lamberti* and *Se. frontalis* (0.992 and 0.883 respectively) represents dense, even vegetation between 20 cm and 100 cm. This vegetation structure is typical of canopy, scrub and swamp habitats (Table 2). Examination of Fig. 1 shows that their observed ranges were strongly associated with these habitats.

Finally, *St. malachurus* has scores lower than *M. lamberti* and *Se. frontalis*, placing their group centroid closer to zero (0.229). Consequently, *St. malachurus* were observed in vegetation that was less dense and more patchy than habitat inhabited by *M. lamberti*, but more dense and even than that where *M. cyaneus* occurred. Such a vegetation structure is typical of the *Baumea* habitat in which they were the only species regularly observed (Table 2).

While *Se. frontalis* and *M. lamberti* were separated in the discriminant function analysis, greater separation was obvious in their foraging height (<0.0001; see Fig. 5). Consequently, these results suggests that the most habitat differentiation between the four species occurs along function 1, which relates to the density of vegetation between 20 cm and 100 cm, and their foraging heights (Fig 6).

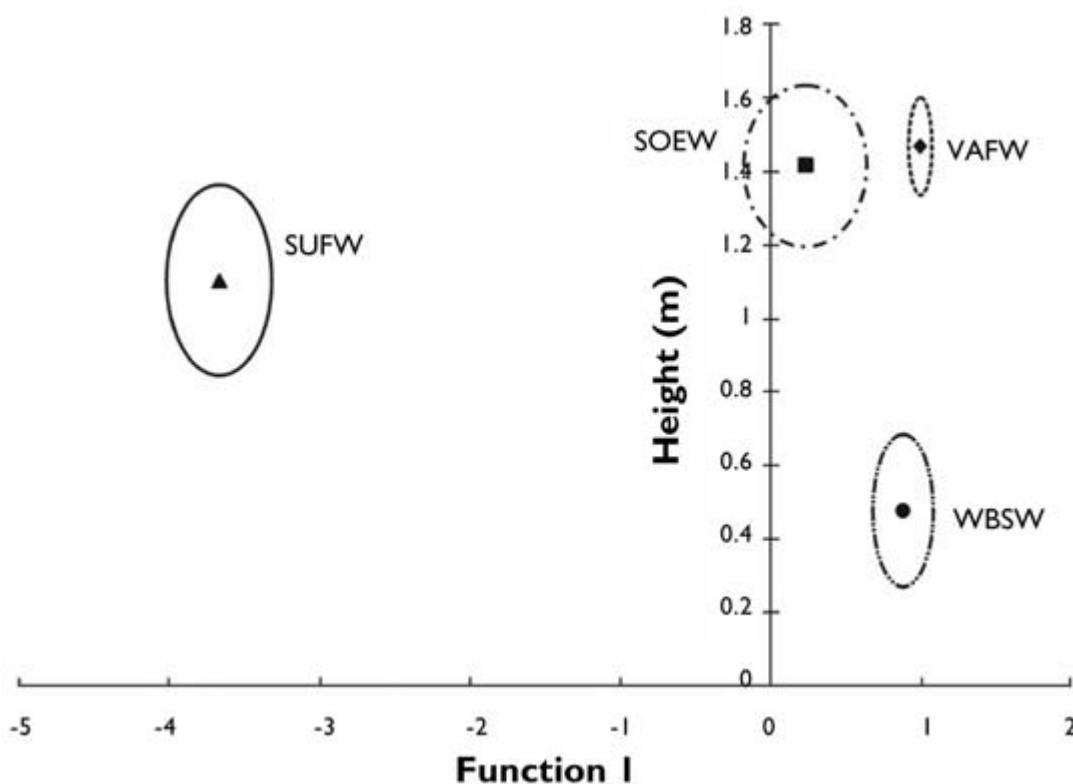


Figure 6. Species separation (mean values and 95% confidence intervals) using function 1 and the foraging height. This more clearly separates Variegated Fairy-wrens *M. lamberti* (VAFW) and White-browed Scrubwrens *Se. frontalis* (WBSW) than any of the vegetation functions identified by the discriminant function analysis (SUFW = Superb Fairy-wren *M. cyaneus*; SOEW = Southern Emu-wren *St. malachurus*).

Discussion

Studies into the community structure of birds in Australia have identified a guild of low vegetation gleaners (Holmes and Recher 1986) that typically consist of at least one member of the Maluridae. Members of this guild spend the majority of the foraging activities on or close to the ground, collecting prey items by gleaning; we found that for all four species, 90% or more of foraging is by gleaning. Similar results have been found in previous studies of *M. lamberti*, *Se. frontalis* and *M. cyaneus* (Recher et al. 1985; Ford et al. 1986; Tibbetts and Pruett-Jones 1999). Furthermore, both this study (see Fig. 2 and 6) and previous studies (Recher et al. 1985; Ford et al. 1986; Tibbetts and Pruett-Jones 1999) have shown that *M. lamberti*, *Se. frontalis* and *M. cyaneus* gleaned on or in vegetation close to the ground.

Previous studies have not included *St. malachurus*, however results from this study indicate that this species is also a low vegetation gleaner.

Similar foraging methods in bird species such as those demonstrated above are assumed to indicate that these species have similar diets (Ford et al. 1986; Holmes and Recher 1986) and subsequently may experience competition for dietary resources. However, in recent years the assumption of a link between the foraging method and the food obtained has been questioned (Wiens 1989; Maurer 1990; Mac Nally 1994). Diet, rather than foraging method, would have a greater effect on competition if food were the limiting resource (Mac Nally 2000).

Specific dietary data were not collected in this study and hence only general conclusions may be drawn. However the examination of gut contents by other authors (Lea and Gray 1935; Barker and Vestjens 1990; Rose 1999) indicates that *M. lamberti*, *St. malachurus* and *M. cyaneus* all have similar dietary intakes (to the family level), eating predominantly beetles, bugs, flies, wasps, weevils and small spiders and their eggs.

Competition within guilds has also been questioned by some authors, who argue that many of Australia's birds are nomadic or migratory and hence these individuals are unlikely to experience the same selective pressures for any length of time (Mac Nally 2000). This indeed may be the case for many nomadic inland birds or migratory species. However, previous banding records of the target species in this study show that some individuals studied at this site have remained at the study site for over seven years (L. Win Filewood unpublished data). In addition, the sedentary nature of *M. lamberti*, *Se. frontalis* and *M. cyaneus* is well known (Ambrose and Davies 1989; Rowley and Russell 1997) while it is generally accepted that *St. malachurus* is also sedentary (Higgins et al. 2001).

In light of this evidence, it is possible that the four low-foliage gleaning bird species at Smiths Lake could experience some level of competition in periods when food resources are limited. At Smiths Lake all low-foliage gleaning species have largely overlapping ranges, except *M. cyaneus* which was generally restricted to the grassland habitats. The remaining three species tended to avoid such

areas, instead occurring in areas that have comparatively denser cover. This horizontal differentiation in habitat use may assist in reducing resource depletion and even competition on *M. cyaneus* from one of the other species, or by the combined effect of all the other three species (diffuse competition; MacArthur 1972).

Rowley (1965), in a detailed study of *M. cyaneus*, often observed the birds on the ground foraging as a group in an activity that he termed 'hop-search'. While this behaviour was not observed in this study as often as Rowley's, it was still identified as an important component of *M. cyaneus* feeding behaviour. Such a foraging behaviour that involves movement along the ground would be best suited for open spaces. Appropriate territory therefore needs to have open spaces in order to fulfil the needs of this species.

Sericornis frontalis, *M. lamberti* and *St. malachurus* in comparison to *M. cyaneus* have very similar, overlapping territories (Fig. 2). While some habitat differentiation between *Se. frontalis* from *M. lamberti* and *St. malachurus* was identified in the discriminant function analysis, the distance between *Se. frontalis* and *M. lamberti* was not great (Table 7). Furthermore, these two species also had very similar areas of occurrence (Fig. 2) and similar habitats within their territories (Table 5).

The greatest difference in habitat use of *Se. frontalis* from *St. malachurus* and *M. lamberti* was in foraging height. *Sericornis frontalis* commonly used the lower layers of the vegetation while *M. lamberti* and *St. malachurus* used the upper levels of the vegetation (vertical habitat selection:

Cody 1968). This may explain why *Se. frontalis* consume slightly higher proportions of ground inhabiting insects (Barker and Vestjens 1990).

Our results show that the foraging heights of *M. lamberti* and *St. malachurus* were not significantly different. The most notable difference in habitat use of *St. malachurus* was the use of *Baumea* vegetation. *Stipiturus malachurus* was regularly observed in this vegetation, often in locations well away from other habitats. The other three species were rarely observed in areas dominated by *Baumea*, and when they were they were never far from other identified habitats. The *Baumea* habitat at Smiths Lake is distinctly different from the other identified habitats in that *Baumea* plants have little leaf-surface on which low-foliage gleaners can feed. Fletcher (1915) observed *St. malachurus* splitting stems of reeds (*Juncus* sp.) in order to remove insects, a behaviour not recorded in any other studies of the remaining three species. This behaviour may allow *St. malachurus* to effectively utilise habitats that are otherwise not energy efficient for low-foliage gleaners.

While our results can find clear differences in habitat utilisation between the four species, these results should not be taken out of context. This study was conducted during the warmer months of the year (October to December) and such difference may not be representative for the whole year. Furthermore, observations of *St. malachurus* were extremely difficult in the lower vegetation due to their reclusive and secretive habits. Our results should be considered within these constraints.

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