

Temporal Changes in the Foraging Behaviour of Insectivorous Birds in a Sclerophyll Forest in Tasmania

Peter Cale

Forest Practices Unit, Forestry Commission of Tasmania, 30 Patrick Street, Hobart, Tas. 7000
Present address: 260 Selby Street, Floreat, W.A. 6014

Summary: Seasonal changes in the foraging behaviour of 13 insectivorous bird species were investigated in a sclerophyll forest in north-eastern Tasmania between April 1989 and May 1990. Six guilds (ground gleaners, ground pouncers, foliage gleaners, a foliage snatcher, bark probers and a hawk) were identified in the winter period (April to September). In the summer period (October to March), the same guilds were identified, except that the winter ground pouncing and foliage snatching guilds were replaced by a more diffuse general foraging guild. Three of the four winter ground foraging species expanded their range of foraging substrates and methods during summer. The fourth winter ground foraging species (White-browed Scrubwren) continued to forage predominantly on the ground during summer but expanded the range of methods used when foraging on this substrate.

The two bark foraging species showed changes in the types of bark substrates used throughout the year. The observed seasonal changes in foraging behaviour resulted in an increase in community foraging overlap and in the overlap between guilds during the summer. The seasonal changes in foraging behaviour observed in this study suggest that it is important that those managing the forest, retain a diversity of both foraging substrates and habitat types, to sustain the normal foraging activities of the bird community.

The foraging behaviour of bird assemblages in sclerophyll forests and woodlands of southern Australia has been investigated in two studies, which have demonstrated a common pattern of community structure (Recher *et al.* 1985; Ford *et al.* 1986). These assemblages were broadly divided into guilds, based on the type of food used (i.e. insects, nectar and seeds), with further sub-divisions based on substrate and foraging method.

In the northern hemisphere, studies of forest bird communities have demonstrated seasonal changes in foraging behaviour (Stallcup 1968; Ulfstrand 1977; Alatalo 1980; Wagner 1981; Székely & Moskát 1991). Some of these studies have shown that the foraging overlap between species having similar foraging niches was generally lower during periods of low food abundance than in periods of high food abundance (Alatalo 1980; Wagner 1981; Székely & Moskát 1991).

In Australia, studies on specific groups of species, such as thornbills (Bell 1985), fantails (Cameron 1985), bark foragers (Noske 1986) and robins (Robinson 1992), have also demonstrated seasonal changes in foraging behaviour. Cameron (1985), Noske (1986) and Robinson (1992) attributed these changes to changes in food availability. Recher *et al.* (1983) also demonstrated a relationship between seasonal changes in the availability of food resources and the movement and breeding behaviour of birds. Despite these findings, community-

based studies in southern Australia have, to date, not considered how seasonal changes in foraging behaviour affect guild structure in these communities.

This paper is derived from a long term study of the value of habitat retention strips in logged forest, conducted by the Forestry Commission of Tasmania (Taylor 1992). It describes the foraging behaviour of 13 species of insectivorous birds in a sclerophyll forest in north-eastern Tasmania, with respect to how these species partition the available resources and how this partitioning varies seasonally.

Study area

This study was carried out within an area of 340 ha of mature sclerophyll forest in north-eastern Tasmania, approximately 30 km north-west of the town of St. Helens (41°06'S, 148°03'E). It consisted of a series of south-running gullies and associated slopes and ridges. The gullies contained one of two vegetation communities: *Acacia melanoxylon* (Blackwood) gully forest in the steeper gullies and scrub woodland dominated by *Melaleuca squarrosa* in the shallow gullies.

Blackwood gullies contained a canopy of *A. melanoxylon* (20-30 m) with *E. obliqua* on the slopes of the gullies and a dense mid-storey dominated by *Pomaderris apetala*, *Zieria arborescens*, *Olearia argophylla* and the tree fern *Dicksonia antarctica*. The ground was fre-

quently open within the gully but had a dense cover of *Culcita dubia* and *Blechnum nudum* ferns on associated slopes.

Melaleuca gullies contained an open canopy of *E. obliqua* and *E. amygdalina* (to 30 m), with a dense mid-storey dominated by *M. squarrosa* that was restricted to the gully line. The gully floor had a dense cover of ferns dominated by *B. nudum* and *Gleichenia microphylla*.

The slope and ridge vegetation ranged from *E. amygdalina*–*E. obliqua* dry sclerophyll forest (to 30 m) with little understorey except bracken *Pteridium esculentum* on drier slopes and ridges, to *E. obliqua*–*E. amygdalina* damp sclerophyll forest (>30 m) with a diverse range of shrub layers and a dense ground cover of *P. esculentum* and *C. dubia* on the lower wetter slopes.

The area has mild summers (February mean maximum and minimum 22.9°C and 11.9°C respectively) and cold winters (July mean maximum and minimum 13.6°C and 2.5°C respectively). The mean yearly rainfall is 978 mm (from Pioneer, 10 km from the study area), with April to October being the wettest months. During the period of this study (April 1989 to March 1990) the area had above average rainfall (1340 mm) due mainly to severe storms in November 1989.

Methods

Collection of data

Foraging records were collected at the study site for ten days each month, from April 1989 to May 1990. Most records were collected within the first three hours after sunrise. For rarer species additional observations were made throughout the day. All observations were made by the author from sightings on set routes used to census the study area for birds. Because of this, the effort made in each habitat type each month was the same.

Each foraging record consisted of up to three foraging attempts by a single individual. Only one foraging record was taken from any individual or flock encountered, but it was not possible to prevent or quantify observations of the same individuals or flocks on different days. Each foraging attempt was considered an observation for all analyses. For each foraging attempt the height, foraging method, substrate and species of vegetation the prey was on, and the habitat type, were recorded.

Foraging attempts were assigned to one of eight height classes (0 m, <1 m, 1–2 m, 2–5 m, 5–10 m, 10–20

m, 20–30 m and 30+ m) that were chosen, based on the general physiognomy of the vegetation, before the start of the study.

All foraging attempts were assigned to one of seven substrate categories; ground (including litter and small debris), fallen logs (trunks and large branches >50 cm diameter on the ground), trunks of trees and large shrubs, branches (including dead branches), foliage (including twigs), loose bark (including hanging strips of bark) and air. The foraging methods used in this study were those described by Recher *et al.* (1985): glean; hang-glean; snatch; probe/prise; hover; pounce; and hawk.

Foraging attempts were recorded as occurring in one of four habitat types: Blackwood gullies which included the slope associated with it up to approximately 50 m from the gully line; *Melaleuca* gullies; shrub slopes (those having a moderate to dense understorey of shrubs); and open slopes. For analysis these habitat types were combined into two broad divisions: gully habitats; and slope habitats. The plant in which foraging attempts were made was identified to species or genus whenever possible. If this was not possible the life form of the plant (tree, shrub, etc.) was recorded.

Seasonal changes in foraging behaviour

Foraging records for each species were divided into two seasons to ensure sufficient data for statistical analyses of seasonal changes in behaviour. These seasons, referred to as winter (April to September) and summer (October to March), were defined based on temperature and rainfall data for the study area. Chi-squared analyses with Yate's correction for continuity, where appropriate (Zar 1974), were used to determine if the changes in foraging behaviour observed between winter and summer, were greater than expected by chance. Foraging methods or substrates used infrequently by a species were combined into a single category, because they often resulted in cells which had expected values that were too low for the chi-squared test.

Guilds

May (1975) has argued that combining different foraging dimensions by obtaining their products or averages are only rough approximations of a species' multi-dimensional niche, because no two dimensions are completely dependent or independent of each other. To help alleviate this problem in the current study two of the most interdependent dimensions (substrate and for-

aging method) were combined into a single dimension that included all observed combinations of the two dimensions. This combined substrate/method dimension was used to calculate foraging overlap values between species and the influence of the foraging height and habitat dimensions were considered separately.

The foraging overlap between each pair of species was calculated by summing the minimum relative frequency of the two species for each category of a dimension (Hurlbert 1978). The mean foraging overlap for each species was calculated by summing that species' foraging overlaps with all other species (Cody 1974). The community foraging overlap value is the average of the mean foraging overlaps for all species (Cody 1974). It was calculated for both winter and summer, but included only those species that were present throughout both periods. A Wilcoxon paired-sample test (t) was used to test if the difference in the community foraging overlap between summer and winter was greater than expected by chance (Zar 1974).

Of the 13 species analysed in this study (Appendix 1), two were migratory and were absent for most of the winter period. Flame Robins *Petroica phoenicea* were absent between April and July and Welcome Swallows *Hirundo neoxema* were absent between February and August. They are therefore not considered to be present for the determination of winter guilds.

Guilds were defined by foraging behaviour and were delineated by the combined substrate/method dimension only. Guild membership was defined as all species that had a mean foraging overlap with each other of >50% and collectively had a mean foraging overlap with any other species not of the guild of <50%. Guilds were determined separately for winter and summer data.

Monotonic multi-dimensional scaling (MDS) was used to provide a summary graphical display of foraging guilds, and to assist in the determination of guild membership. Multi-dimensional scaling analysis enables the mapping of species in a multi-dimensional space, in such a way that the relative positions in the space reflects the degree of similarity between the species (Dillon & Goldstein 1984). Foraging overlap was used as the measure of the similarity between the species for these analyses. Since a visual display was one aim of using MDS, only 2- and 3-dimensional analyses were considered, with the best chosen by minimising the Kruskal stress value (Dillon & Goldstein 1984).

Results

A total of 25 insectivorous bird species were recorded in the study area. Of these, 13 were considered to have sufficient records of foraging behaviour ($c.$ 50 records) for analysis. These species represent the most common insectivorous species in the area, except the migratory Satin Flycatcher *Myiagra cyanoleuca* and Black-faced Cuckoo-shrike *Coracina novaehollandiae*.

Five honeyeater species (Eastern Spinebill *Acanthorhynchus tenuirostris*, Crescent Honeyeater *Phylidonyris pyrrhoptera*, Yellow-throated Honeyeater *Lichenostomus flavicollis*, Black-headed Honeyeater *Meliphaga affinis* and Yellow Wattlebird *Anthochaera paradoxa*) were also common in the study area. Although these species did forage on insects, most foraging observations from these species were on various forms of nectar. Consequently, they have not been considered in this paper.

Seasonal changes in foraging behaviour

Seasonal changes in the use of substrates and foraging methods were most prevalent in those species that foraged on the ground during the winter period. In winter Scarlet Robins *Petroica multicolor* and Dusky Robins *Melanodryas vittata* foraged predominantly by pouncing on the ground (95% and 100% of records respectively), but this behaviour declined during summer (35% and 23%) ($\chi^2_1 = 33.7$ and 26.5 respectively, $P < 0.001$), when they used a greater range of foraging behaviours. Scarlet Robins foraged mainly by snatching from the foliage and branches of eucalypts and by hawking in the air, while Dusky Robins also moved into the eucalypt canopy, but mainly snatched and probed from the trunks and branches of eucalypts, and also hawked in the air (Fig. 1a,b).

Flame Robins were absent from the study area during the early winter period (April to July) but also showed a decline in ground foraging from 88% of records during August–September to only 20% of records in February–March. When not foraging on the ground Flame Robins foraged predominantly by hawking in the air (Fig. 1c).

During winter Superb Fairy-wrens *Malurus cyaneus* foraged predominantly by gleaning on the ground and on fallen logs (83% of foraging records), but this behaviour declined to only 46% with a corresponding increase in foraging on foliage (45%) during summer ($\chi^2_1 = 15.3$, $P < 0.001$) (Fig 1d).

White-browed Scrubwrens *Sericornis frontalis* were

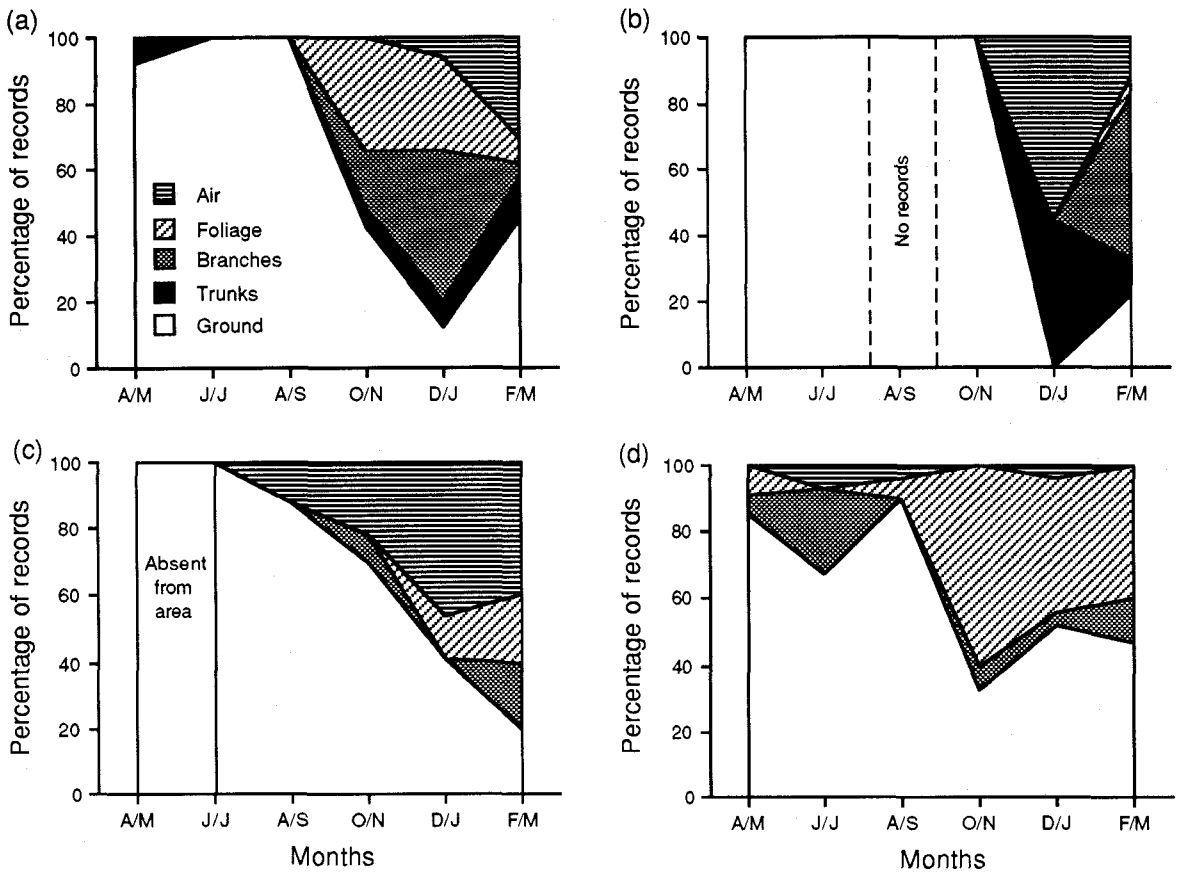


Figure 1 Seasonal changes in the use of substrates by (a) Scarlet Robins, (b) Dusky Robins, (c) Flame Robins and (d) Superb Fairywrens.

the only ground foragers that did not show a major change in their substrate use from winter to summer (Fig. 2a). This species did, however, show a seasonal change in the method of foraging on the ground substrate (Fig. 2b). During winter this species, when foraging on the ground, gleaned 86% of the time but this declined to only 47% in summer with a corresponding increase in probing into the leaf litter ($\chi^2_1 = 15.1$, $P < 0.001$). This probing behaviour involved the movement of litter to reveal invertebrates deeper in the litter layer.

Bark foragers, Grey Shrike-thrushes *Colluricincla harmonica* and Strong-billed Honeyeaters *Melithreptus validirostris*, were the only other group of species that showed seasonal changes in substrate use and foraging method. Grey Shrike-thrushes showed significant seasonal variation in substrate use, most of which did not

correspond to the winter/summer periods defined in this paper (Fig. 3a). This species showed a shift from prising the bark of eucalypt trunks (52% of foraging records) during February to July, to foraging on eucalypt branches (60% of records) during August to January ($\chi^2_2 = 32.5$, $P < 0.001$). Grey Shrike-thrushes also showed changes in the frequency of ground foraging throughout the year but these changes showed no obvious seasonal pattern.

Strong-billed Honeyeaters showed only minor changes in foraging behaviour with an increase in gleaning and hang-gleaning from hanging bark and trunks ($\chi^2_2 = 11.4$, $P < 0.005$) during summer (Fig. 3b).

No species showed any foraging height specialisation. All generally foraged over the whole range of heights where their preferred substrates were found.

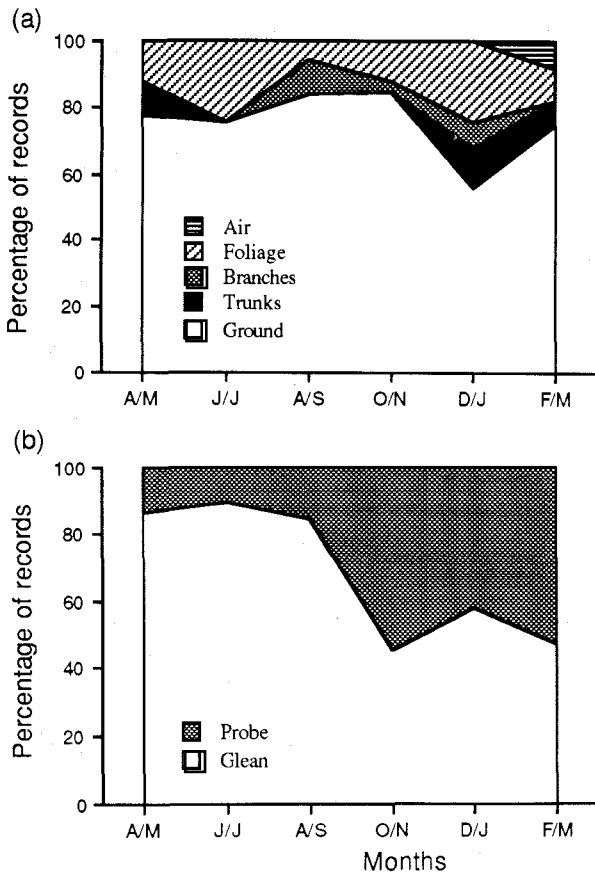


Figure 2 Seasonal changes in the (a) use of substrates and (b) foraging method used in ground foraging by White-browed Scrubwrens.

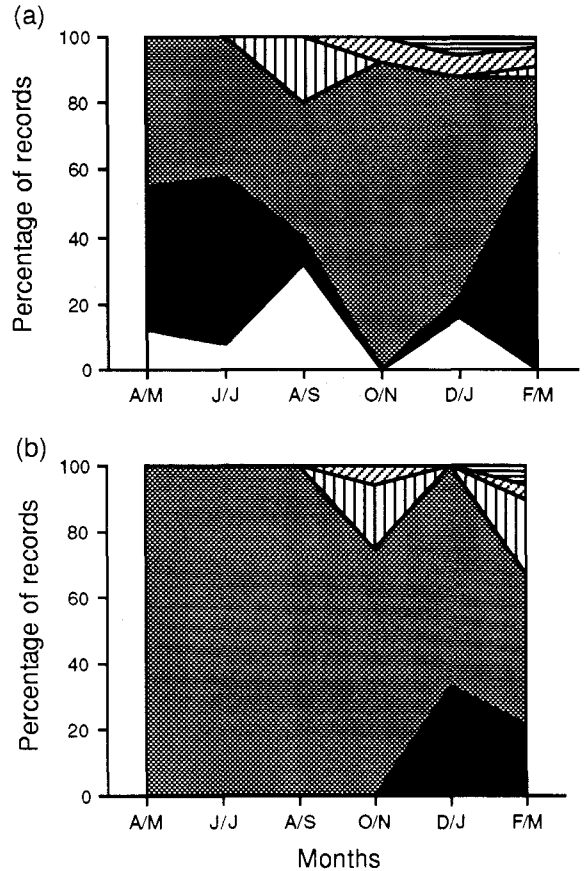


Figure 3 Seasonal changes in the use of substrates by (a) Grey Shrike-thrushes and (b) Strong-billed Honeyeaters. Legend as for Figure 1. Vertical hatching represents use of loose bark.

Seasonal changes in foraging height were found in those species that foraged on the ground during winter, and reflected the observed changes in substrate use by these species.

Only Tasmanian Thornbills *Acanthiza ewingii* showed seasonal changes in foraging height that did not reflect changes in substrate use. In winter this species foraged between 1 and 20 m but this declined to a more restricted range of heights during summer (1 to 5 m: $\chi^2_4 = 37.6$, $P < 0.001$). This corresponded to an increased use of gullies (the habitat used most frequently by Tasmanian Thornbills) by Brown Thornbills *Acanthiza pusilla*. During winter these two species show no difference in their foraging height range in gullies ($\chi^2_4 = 9.2$, $P > 0.05$), but in summer they diverged in the range of

heights used in gully habitats, due to the reduced foraging height range of Tasmanian Thornbills ($\chi^2_4 = 64.3$, $P < 0.001$).

Guilds

The 11 species present during the winter period that were analysed can be divided into six guilds based on the combined substrate/method dimensions (Fig. 4a). Two ground foraging guilds can be distinguished by differing foraging methods, the ground gleaners (Superb Fairy-wren and White-browed Scrubwren) and ground pouncers (Scarlet Robin and Dusky Robin). Two foliage foraging guilds can also be distinguished, the foliage gleaners (Brown Thornbill, Tasmanian Thornbill and Striated Pardalote *Pardalotus striatus*)

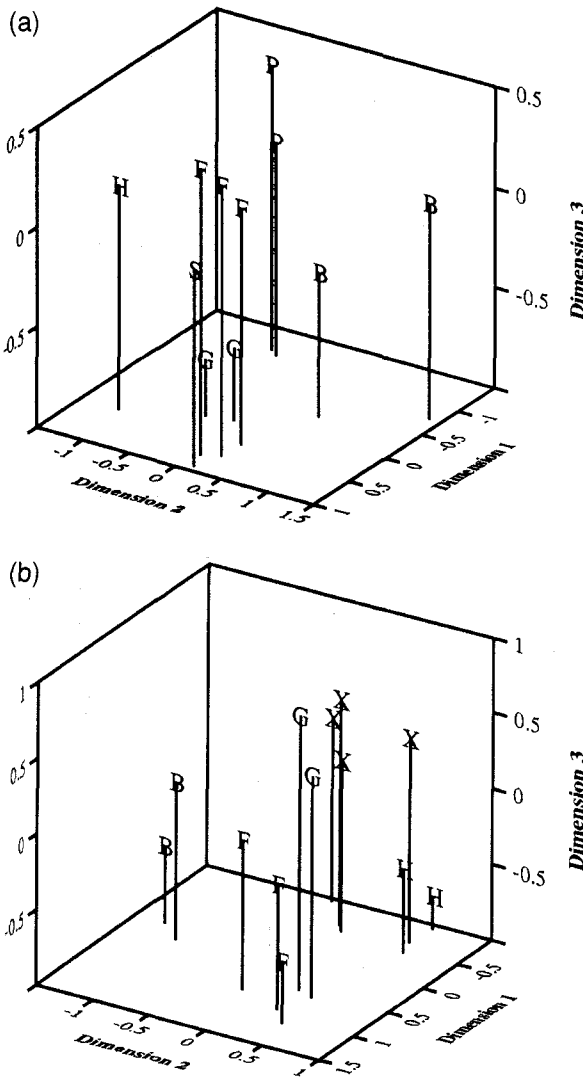


Figure 4 A multi-dimensional scaling analysis of foraging overlap in the substrate/method dimension, showing the guilds: G – ground gleaners; P – ground pouncers; B – bark foragers; F – foliage gleaners; S – foliage snatcher; H – hawkers; and X – general foragers, for (a) winter and (b) summer. The distance between species in the 3-dimensional space represents the degree of foraging overlap between them.

and a foliage snatcher (Golden Whistler *Pachycephala pectoralis*). The Grey Fantail *Rhipidura fuliginosa* was the single representative of the hawking guild. Grey Shrike-thrushes and Strong-billed Honeyeaters foraged predominantly on bark, though they differed consider-

Table 1 Changes in the mean foraging overlap of species between winter (April to September) and summer (October to March). Flame Robins and Welcome Swallows were not included as they were absent for the majority of the winter period.

Species	Mean foraging overlap		Difference
	Winter	Summer	
Superb Fairy-wren	0.181	0.278	-0.097
White-browed Scrubwren	0.208	0.220	-0.012
Scarlet Robin	0.099	0.255	-0.156
Dusky Robin	0.132	0.213	-0.081
Tasmanian Thornbill	0.231	0.292	-0.061
Brown Thornbill	0.253	0.315	-0.062
Striated Pardalote	0.191	0.185	+0.006
Golden Whistler	0.169	0.269	-0.100
Grey Shrike-thrush	0.148	0.220	-0.072
Strong-billed Honeyeater	0.033	0.138	-0.105
Grey Fantail	0.085	0.219	-0.134
Community overlap	0.157 ± 0.02	0.237 ± 0.02	

ably in the types of bark substrates used (Appendix 2). For this reason they met the definition of a guild used in this paper only if all bark substrates were considered collectively.

The seasonal changes in foraging behaviour resulted in an increase in the community foraging overlap from winter to summer ($t = 1$, $P < 0.005$). All species except the White-browed Scrubwren showed an increase in mean foraging overlap (Table 1). These changes also resulted in some differences in the guilds observed in these two periods (Fig. 4). The members of the winter ground pouncing guild (Scarlet Robin and Dusky Robin) became more general in their foraging behaviour, as did the Golden Whistler (Appendix 2), and these three species formed a diffuse general foraging guild with the migratory Flame Robin (Fig. 4b). The ground gleaning and foliage gleaning guilds showed no changes in membership from winter to summer, but both showed decreased within-guild foraging overlap and increased foraging overlap with other guilds (Table 2). The hawking guild was enlarged by the addition of the migratory Welcome Swallow and this guild's foraging overlap with other guilds increased (Table 2). Only the bark probing guild showed an increase in within-guild foraging overlap during summer but, like the other guilds, this guild showed increased between-guild foraging overlap during this period (Table 2).

Table 2 Mean foraging overlap within guilds and between guilds for the winter and summer periods.

WINTER: Guilds	Mean foraging overlap	
	Within guild	Between guilds
Ground gleaners	0.780	0.130
Ground pouncers	0.880	0.030
Foliage gleaners	0.613	0.150
Bark probers	0.250	0.064
Snatcher	*	0.145
Hawker	*	0.089

SUMMER: Guilds	Mean foraging overlap	
	Within guild	Between guilds
Ground gleaners	0.550	0.196
General foragers	0.512	0.194
Foliage gleaners	0.560	0.172
Bark probers	0.430	0.124
Hawkers	0.770	0.146

* The snatcher and hawkler guilds in winter were represented by a single species.

Habitat utilisation

In the ground gleaning and foliage gleaning guilds there was a high degree of separation in the habitats used by guild members during winter, when overlap in the substrate/method dimension was highest between these species (Fig. 5). In the bark probing guild the same pattern was observed but was reversed with high overlap in the substrate/method dimension during summer corresponding to increased separation in habitat use during this period (Fig. 5, Appendix 1).

The only guild not to show this complementarity between foraging overlap and habitat use was the winter ground pouncing guild where both Scarlet Robins and Dusky Robins foraged on the same substrate, in the same way and in the same habitat (Fig. 5a).

Discussion

The structure of the insectivorous foraging guilds observed in this paper was broadly comparable with those found in sclerophyll forest and woodland communities in southern mainland Australia, despite the considerably lower species richness of the Tasmanian community (Recher *et al.* 1985; Ford *et al.* 1986). This was not

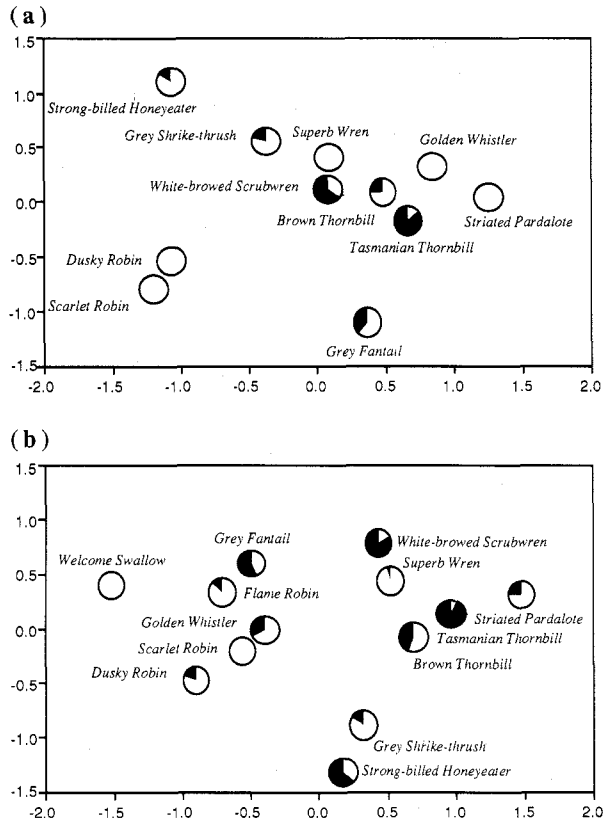


Figure 5 The relationship between the substrate/method dimension of foraging behaviour and habitat utilisation for (a) winter and (b) summer. Species are spaced within the graph by 2-dimensional multi-dimensional scaling using the substrate/method dimension. The pie graphs for each species represent the use of gully (solid) and slope (open) habitats.

surprising considering that ten of the 13 species observed in the current paper also occurred in the community studied by Recher *et al.* (1985) and eight occurred in the community studied by Ford *et al.* (1986). In effect this Tasmanian community is a subset of those from the mainland studied by these authors.

Only Grey Shrike-thrushes and Brown Thornbills differed significantly in their foraging behaviour between this study and those on the mainland; both foraged more extensively on bark substrates. This was also observed by Keast (1968) who attributed it to the absence of the specialist bark foragers, tree-creepers (*Climacteris* spp.) and *Sittella Daphoenositta chrysoptera*, from Tasmania.

The most obvious seasonal change in foraging behaviour observed in this study was the shift by all but one (White-browed Scrubwren) of the winter ground-foraging species to the foliage, bark and air substrates during summer (Figs 1 & 2). The seasonal changes in foraging behaviour observed in this study for Scarlet and Flame Robins have been previously recorded by Ford *et al.* (1990) and Robinson (1992) on the mainland. These authors argued that the shift to ground-foraging during winter was at least in part due to invertebrates being relatively more common on ground substrates than on other substrates during this season. This argument was supported by the observed shift by White-browed Scrubwrens, from probing into the litter during summer to gleaning invertebrates from the surface of the litter layer in winter, suggesting that an increase in the availability of invertebrates may have occurred during winter in this habitat. However, the studies by Ford *et al.* (1990) and others (Recher *et al.* 1983; Woinarski & Cullen 1984) also indicate that the availability of invertebrates in the foliage and the air increased considerably during spring and summer when they may be more readily available than ground invertebrates. It is possible that this increase attracts these winter ground foragers into the canopy.

Ford *et al.* (1990) have also observed that ground-foraging declines with increasing temperature, both seasonally and daily. This was supported in the current study where the three species (Scarlet Robin, Dusky Robin and Superb Fairy-wren) that show a decline in ground foraging during summer all forage on slope habitats. These habitats would show a greater increase in ground temperatures during summer than would gullies, where the one species (White-browed Scrubwren) that remained a ground forager during summer foraged.

Recher *et al.* (1985) and Recher (1992) have indicated the importance of bark as a foraging substrate in eucalypt communities. This was also evident in the current study where all species except the Welcome Swallow used bark substrates to some extent, and it was a major substrate for four species (Grey Shrike-thrush, Strong-billed Honeyeater, Brown Thornbill and Dusky Robin) at some period of the year (Appendix 2). The seasonal changes in foraging behaviour of Grey Shrike-thrushes, however, demonstrate the importance of the diversity of bark substrates. During February to July Grey Shrike-thrushes foraged extensively by prising bark from eucalypt trunks. This behaviour occurred predominantly on the thick friable bark of *Eucalyptus obliqua* instead of the equally common *E. amygdalina*,

suggesting that bark structure may have influenced the availability of invertebrates within this substrate. This is supported by the data of Noske (1983 cited in Bell 1985) who found that arthropod numbers in the deeply fissured bark of stringy-bark eucalypts were high, especially during winter. During August to January Grey Shrike-thrushes shifted to foraging on bark mainly associated with the branches of *E. amygdalina*. These changes suggest that for Grey Shrike-thrushes the presence of both *E. obliqua* and *E. amygdalina*, with their different bark structures, is important for the maintenance of their normal foraging behaviour.

The changes in foraging behaviour observed in this study were generally a result of a concentration by each species on a particular foraging strategy during winter, and an expansion of the range of foraging behaviour during the summer period. The results of this concentration of foraging behaviour during winter was the formation of discrete foraging guilds and an overall decline in the foraging overlap within the community (Tables 1 & 2). The declining foraging overlap between species in winter corresponded to the expected period of lowest invertebrate availability, based on studies in other forest communities in Australia (Recher *et al.* 1983; Woinarski & Cullen 1984). This was consistent with the findings of studies in the northern hemisphere for individual guilds, where it has been found that foraging overlap was lowest during periods of lowest food availability (Stallcup 1968; Alatalo 1980; Wagner 1981; Székely & Moskát 1991).

Within all but one guild (bark probing guild), foraging overlap in the substrate/method dimension increased during winter (Table 2). This was contrary to the findings in the northern hemisphere, but in most of my guilds other foraging dimensions maintain a strong separation between guild members during this period. For instance in the ground gleaning guild Superb Fairy-wrens and White-browed Scrubwrens foraged in an almost identical manner during winter, but Superb Fairy-wrens foraged on slopes while White-browed Scrubwrens foraged predominantly in gullies (Fig. 5).

In the foliage gleaning guild, Brown and Tasmanian Thornbills had very high levels of foraging overlap throughout the year. During winter these two species were separated by their differing habitat use. However, during summer Brown Thornbills increased their use of gully habitats (the habitat used most frequently by Tasmanian Thornbills) (Fig. 5). Corresponding to this overall increase in foraging overlap was a decline in the

foraging height overlap between these two species, so maintaining a degree of separation between them.

The two bark foraging species showed the same pattern of complementarity in overlap between the substrate/method and habitat dimensions, but in the reverse seasons. They used different bark substrates during winter and so had low levels of foraging overlap (Table 2); during this period they foraged in similar habitats. In summer these two species converged in their foraging behaviour but diverged with respect to the habitats they used (Fig. 5).

These seasonal changes in foraging behaviour and habitat use, which maintained a degree of separation in foraging overlap between ecologically similar species, suggest the importance of maintaining a diversity of habitats within an area. For instance, the loss through degradation or clearing of either gully or slope vegetation in the study area would dramatically increase the overall foraging overlap between many ecologically similar species at certain periods of the year, if all species remained in the area. This might be sufficient to result in the loss of some of these species. This has important management implications for activities that selectively remove or retain vegetation types, such as forestry activities that preferentially retain gully vegetation in streamside reserves (Recher *et al.* 1980). It indicates that the retention of slope habitats may be important for the maintenance of some species, an observation also made by Recher *et al.* (1987) for forests in south-eastern New South Wales.

Acknowledgements

This research was funded by the Tasmanian Forest Research Council as part of a research program conducted by the Tasmanian Forestry Commission, investigating the value of habitat retention strips. I thank M. Brooker, M. Brown, H.A. Ford, R. Lambeck, H.F. Recher, D. Roberts and R. Taylor for providing valuable comments on an earlier draft of this manuscript; L. Lebel for performing the multi-dimensional scaling analyses; and Forestry staff of the Fingal District, Tasmania, for providing assistance during the field work.

References

- Alatalo, R.V. 1980. Seasonal dynamics of resource partitioning among foliage-gleaning passerines in northern Finland. *Oecologia* 45, 190-196.
- Bell, H.L. 1985. The social organization and foraging behaviour of three syntopic thornbills *Acanthiza* spp. Pp. 151-163 in *Birds of Eucalypt Forests and Woodlands: Ecology, Conservation, Management*. Eds A. Keast, H.F. Recher, H. Ford & D. Saunders. RAOU and Surrey Beatty, Sydney.
- Cameron, E. 1985. Habitat usage and foraging behaviour of three fantails (*Rhipidura*: Pachycephalidae). Pp. 177-191 in *Birds of Eucalypt Forests and Woodlands: Ecology, Conservation, Management*. Eds A. Keast, H.F. Recher, H. Ford & D. Saunders. RAOU and Surrey Beatty, Sydney.
- Cody, M.L. 1974. *Competition and the Structure of Bird Communities*. Princeton University Press, Princeton.
- Dillon, W.R. & Goldstein, M. 1984. *Multivariate Analysis: Methods and Applications*. John Wiley, New York.
- Ford, H.A., Huddy, L. & Bell, H. 1990. Seasonal changes in foraging behaviour of three passerines in Australian Eucalyptus woodland. Pp. 245-253 in *Studies in Avian Biology* No. 13. Cooper Ornithological Society, California.
- Ford, H.A., Noske, S. & Bridges, L. 1986. Foraging of birds in eucalypt woodland in north-eastern New South Wales. *Emu* 86, 168-179.
- Hurlbert, S.H. 1978. The measurement of niche overlap and some relatives. *Ecology* 59, 67-77.
- Keast, A. 1968. Competitive interactions and the evolution of ecological niches as illustrated by the Australian honeyeater genus *Melithreptus* (Meliphagidae). *Evolution* 22, 762-84.
- May, R.M. 1975. Some notes on estimating the competition matrix α . *Ecology* 56, 737-741.
- Noske, R.A. 1983. Comparative behaviour and ecology of some Australian bark-foraging birds. Ph.D. Thesis, University of New England, Armidale, N.S.W. (Original not read.)
- Noske, R.A. 1986. Intersexual niche segregation among three bark-foraging birds of eucalypt forests. *Australian Journal of Ecology* 11, 255-267.
- Recher, H.F. 1992. The conservation and management of eucalypt forest birds: resource requirements for nesting and foraging. Pp. 25-34 in *Conservation of Australia's Forest Fauna*. Ed. D. Lunney. Royal Zoological Society of NSW, Sydney.
- Recher, H.F., Davies, W.E. & Holmes, R.T. 1987. Ecology of Brown and Striated Thornbills in forests of south-eastern New South Wales, with comments on forest management. *Emu* 87, 1-13.
- Recher, H.F., Rohan-Jones, W. & Smith, P. 1980. Effects of the Eden woodchip industry on terrestrial vertebrates with recommendations for management. Research Note 42. Forestry Commission of N.S.W.
- Recher, H.F., Gowing, G., Kavanagh, R., Shields, J. & Rohan-Jones, W. 1983. Birds, resources and time in a tablelands forest. *Proceedings of the Ecological Society of Australia* 12, 101-123.
- Recher, H.F., Holmes, R.T., Schulz, M., Shields, J. & Kavanagh, R. 1985. Foraging patterns of breeding birds in

- eucalypt forest and woodland of southeastern Australia. *Australian Journal of Ecology* 10, 399-419.
- Robinson, D. 1992. Habitat use and foraging behaviour of the Scarlet and the Flame Robin at a site of breeding-season sympatry. *Wildlife Research* 19, 377-395.
- Stallcup, P.L. 1968. Spatio-temporal relationships of nuthatches and woodpeckers in Ponderosa Pine forests of Colorado. *Ecology* 49, 831-843.
- Székely, T. & Moskát, C. 1991. Guild structure and seasonal changes in foraging behaviour of birds in a Central-European oak forest. *Ornis Hungarica* 1, 10-28.
- Taylor, R.J. 1992. The role of retained strips for fauna conservation in production forests in Tasmania. Pp. 265-270 in *Conservation of Australia's Forest Fauna*. Ed. D. Lunney. Royal Zoological Society of NSW, Sydney.
- Ulfstrand S. 1977. Foraging niche dynamics and overlap in a guild of passerine birds in a south Swedish coniferous woodland. *Oecologia* 27, 23-45.
- Wagner, J.L. 1981. Seasonal change in guild structure: oak woodland insectivorous birds. *Ecology* 62, 973-981.
- Woinarski, J.C.Z. & Cullen, J.M. 1984. Distribution of invertebrates on foliage in forests of south-eastern Australia. *Australian Journal of Ecology* 9, 207-232.
- Zar, J.H. 1974. *Biostatistical Analysis*. Prentice-Hall, Englewood Cliffs, New Jersey.

Appendix 1 Percentage of foraging records in two habitat types for the Winter (April to September) and Summer (October to March) periods.

Species	Winter			Summer		
	Gullies	Slopes	<i>n</i>	Gullies	Slopes	<i>n</i>
Superb Fairy-wren	0	100	54	5	95	60
White-browed Scrubwren	65	35	69	83	17	99
Scarlet Robin	0	100	42	0	100	51
Dusky Robin	0	100	21	20	80	30
Flame Robin	*	*	*	14	86	63
Grey Shrike-thrush	21	79	69	17	83	69
Strong-billed Honeyeater	16	84	57	63	37	81
Striated Pardalote	0	100	21	25	75	24
Tasmanian Thornbill	86	14	147	94	6	141
Brown Thornbill	25	75	240	45	55	216
Golden Whistler	0	100	18	33	67	33
Grey Fantail	39	61	162	56	44	165
Welcome Swallow	*	*	*	0	100	21

* Flame Robins and Welcome Swallows were absent from the study area for the majority of the winter period. *n* = number of records.

