

# Foraging Segregation of Australian Warblers (Acanthizidae) in Open Forest near Sydney, New South Wales

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## Summary

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Nine species of Australian warblers (Acanthizidae) occur together in open eucalypt forests near Sydney, New South Wales. The ecological segregation of six of these species, which foraged primarily in shrub and tree vegetation and are similar sized (5-8 g), was studied during 1984. Seasonal data were obtained for five species; Weebill *Smicromis brevirostris*, White-throated Warbler or Gerygone *Gerygone olivacea*, Striated Thornbill *Acanthiza lineata*, Little Thornbill *A. nana* and Buff-rumped Thornbill *A. reguloides*. The sixth species, Brown Thornbill *A. pusilla*, was uncommon and seasonal comparisons were not possible. As has been reported for similar species associations in the northern hemisphere, the species studied differed in prey attack behaviour, foraging heights, use of plant species and selection of foraging substrates. There were significant seasonal differences in the use of foraging resources. For example, bark was more important as a foraging substrate in autumn and winter than in spring and summer. *A. reguloides* foraged more on the ground outside the breeding season than when nesting. The increased abundance of flying insects during summer correlated with an increased use of hawking and snatching as prey attack behaviours by all species. Despite their differences, species broadly overlapped in their use of resources and had similar niche breadths. Overlaps in the use of resources were greatest during spring, when prey resources were probably most abundant, and least in autumn when prey decreased in abundance. The forest in which the study was conducted was dominated by two species of eucalypts. Birds selected between these species but used the same foraging behaviours in each. Despite the selection between eucalypt species, the limited array of plant species had little effect on species richness. Comparison of niche breadths for the same species at other sites where there were different numbers of co-existing species suggests that niche breadth and overlap may be primarily determined by the availability of resources (e.g. substrates, plant species) and not by competitive interactions between the species themselves.

## Introduction

Australian warblers (Acanthizidae) are common, small insectivorous birds in eucalypt forests and woodlands. Two or more species normally occur together and several recent studies have described the ways co-existing species differ in their use of resources (Keast 1975, 1976, 1985; Bell 1985; Recher *et al.* 1985, 1987; Woinarski 1985a,b; Ford *et al.* 1986). These workers reported that species differ in behaviour, use of substrates, foraging height and kinds of plants on which they forage. The pattern is not dissimilar to that reported for comparable guilds in European and North American forests (e.g. Hartley 1953; MacArthur 1958; Lack 1971; Holmes & Robinson 1981; Alatalo 1982).

In this paper, I describe the foraging segregation of Australian warblers during 1984 in open forest on the Cumberland Plain north-west of Sydney, New South Wales. These forests have an exceptionally rich avifauna (60-65 breeding species) (Recher unpubl. data). In contrast, the vegetation is dominated by two species of eucalypts. The understorey and shrub vegetation is also poor in species. This combination of factors simplifies the study of plant species selection by foraging birds. The work des-

cribed was initiated to provide baseline data on the use of resources, including species of eucalypts, by foliage-gleaning acanthizids. Subsequent work has been designed to study the selection of plant species in detail and to investigate the relationships between plant species selection, foliage structure and canopy invertebrate communities — it will be published separately.

## Study site

### Location

A 25 ha plot was selected within a remnant patch (c. 400 ha) of forest at Scheyville 40 km north-west of Sydney. The plot is 20-40 m asl and has a level to gently sloping topography. Soils are derived from the Winnimatta Group of shales. Two creeks drain the area but were dry except during wet weather. The area receives an average of 774 mm of rain annually (c. 930 mm fell during 1984) (Pitt Town Meteorological Station records, 3 km from Scheyville, 42 year mean). Mean maximum temperatures during January (mid-summer) and July (mid-winter) are 30°C and 17°C respectively. Mean minimum temperatures for January and July are 17°C and 3°C respectively (records of Meteorological Station at Hawkesbury Agricultural College near Richmond, 20 km SW of Scheyville, 49 year mean).

The plot was bisected by an electrical transmission corridor and bounded on one side by pasture. The area is now included within

TABLE 1 Species composition of canopy and sub-canopy vegetation at Scheyville.

Tree species	% Individuals			% Foliage
	Canopy (n = 473)	Sub-canopy (n = 987)	All (n = 1460)	
Grey Box	48	37	41	52
Ironbark	40	56	51	41
Red Gum	11	07	08	06
Stringybark	< 01	< 01	< 01	1

the Longneck Lagoon Nature Reserve. The centre of the plot was the intersection of the transmission corridor and Gravel Pits Road. The eastern boundary of the plot was Scheyville Road. At the time of the study, the area was leased for grazing and there was some cutting of trees for posts and firewood. There is no undisturbed forest on the Cumberland Plain and the patch within which this study took place has been extensively cleared and logged at various times during the past 200 years.

#### Vegetation

The forest was open with extensive grassy areas and patches of low shrubs to 2 m. The ground vegetation was dominated by exotic species. Blackthorn *Bursaria spinosa* dominated the shrub vegetation (> 98% of shrub foliage) and Blackthorn thickets covered about 50% of the plot. Wattles *Acacia* spp. were uncommon (< 1% of foliage) and did not exceed 4 m in height.

The sub-canopy and canopy vegetation was dominated by Grey Box *Eucalyptus mollucana* and Narrow-leaved Ironbark *E. crebra*. Two other eucalypts, Forest Red Gum *E. tereticornis* and Thin-leaved Stringybark *E. eugenoides*, were present in smaller numbers (Table 1). Other trees normally encountered in eucalypt forest (e.g. *Casuarina*, *Acacia*, *Banksia*) were absent. Although highly variable with extensive open areas, projected cover values for vegetation above 4 m averaged 40–45% for the plot. Most canopy trees were 14–18 m in height with taller stands to 25 m.

#### Methods

##### Vegetation measurements

Vegetation was measured along seven transects spaced evenly throughout the plot. Each transect was 180 m in length. All canopy and sub-canopy trees within 10 m of either side of the lines were identified and the data combined as a measure of the abundance of each species (Table 1). The proportion of foliage contributed by each species was measured as follows. At one metre intervals along each transect a 400 mm lens was focused vertically through the vegetation. All leaves above 4 m intersected by the centre focus of the lens were identified and their height estimated to the nearest metre using the lens rangefinder which had been previously calibrated. Contacts along a 4 m pole were used to measure vegetation below 4 m. The per cent of points intersecting leaves summed for all transects ( $n = 1260$  points) was used as a measure of projected cover for the canopy and sub-canopy vegetation, while the proportion of leaves of different species intersected indicates the amount of foliage contributed by each species.

#### Foraging behaviour

For each bird located, up to five consecutive attempts at prey capture ('prey attacks') were recorded regardless of whether or not these were successful (see Recher *et al.* 1985, 1987 for details). The substrate and plant species on which prey were located, and the height and foraging manoeuvre of the bird were recorded for each prey attack. Foraging heights were estimated to the nearest metre but in this analysis are grouped into vegetation layers: ground (0–0.1 m); shrubs (> 0.1–2 m); saplings and coppice (2.1–5 m); small trees (5.1–8 m); sub-canopy (8.1–11 m); and canopy (> 11 m). Foraging manoeuvres are those described by Recher *et al.* (1985). The ones relevant to this study are: *glean*, a standing or hopping bird takes prey from nearby substrates; *hang-glean*, a form of glean in which the bird hangs vertically while taking prey; *hover*, a flying bird remains stationary in the air while taking prey from a substrate or from the air; *snatch*, the bird flies or jumps up to take prey from a nearby substrate, usually returning to a different perch; and *hawk*, the bird flies from a perch to capture or pursue a flying insect.

Twelve categories of substrate were recorded. Many substrates (i.e. spider web, hanging debris) were seldom used, and others (e.g. small [ $< 4.5$  cm diameter] and large [ $> 4.5$  cm] branches) were not used significantly differently by birds. For most analyses substrates were therefore grouped into four categories: foliage (including flowers, eucalypt seed capsules and twigs), bark (branches and trunks), ground (including debris) and air. However, niche breadth and overlap values were calculated using the original twelve categories.

Data were collected during 1984 in summer (31 January–16 February), autumn (26 April–8 May), winter (31 July–7 August) and spring (13 September–1 November). During each period I attempted to obtain a minimum of 100 prey attacks per species representing a minimum of 20 different foraging bouts (Table 2). Weather permitting, this was usually achieved in 20–50 h of observation spread over 4–6 mornings in a two-week period. Observations generally began within an hour of sunrise and ceased at 1100–1200 h Eastern Standard Time. In some seasons it was necessary to revisit the plot and concentrate on a single species.

Although it was not possible to avoid recording data on some of the same individuals, the number of foraging bouts is a guide to the relative number of individuals of each species for which data were recorded. Where birds occurred in either single- or mixed-species flocks, data were recorded for as many individuals as possible without repeating observations on the same birds. Generally this meant that fewer than half the birds present in the flock

were recorded. Observations were made on different parts of the study site on successive days to reduce the duplication of observations on the same individuals.

Some species were difficult to locate while they were nesting. For this reason, breeding season data were collected over a six week period from mid-September through October. In some analyses these data are separated into early (13 September-11 October) and late spring (15 October-1 November).

#### Data analysis

Unless shown otherwise, the accepted level of significance was set at  $P < 0.01$ . This was done to allow for small sample sizes in some categories and the possible lack of independence of consecutive prey attacks by the same individual. However, a separate analysis of these data has shown that there were few significant ( $P < 0.05$ ) differences in the proportions of foraging categories recorded on the first versus subsequent (i.e. 2nd to 5th) prey-attacks (Recher & Gebski in press).

#### Niche breadth and overlap

Niche breadth was calculated using the Shannon-Weiner index of diversity:

$$H = -\sum_{i=1}^n (p_i \log p_i)$$

where  $p_i$  is the proportion of prey attacks in the  $i$ th category,  $n$  is the number of categories.

Niche overlaps for each pair of species was calculated using the formula:

$$\alpha_{jk} = 1 - \frac{1}{2} \sum_{i=1}^n |p_{ij} - p_{ik}|$$

where  $p_{ij}$  and  $p_{ik}$  are the frequencies of observations for species  $j$  and  $k$  in the  $i$ th category.

As the foraging dimensions recorded (e.g. substrate and forag-

ing height) were not independent (see below), overlaps for the four foraging dimensions (prey attack behaviour, foraging height, substrate, plant species) were averaged (see Cody 1974 for a justification). Seasonal data were combined. Average overlap values for each species pair were used to construct a dendrogram progressively grouping species on the similarity of their foraging behaviour (Cody 1974).

#### Avifauna

##### Bird species and abundances

Nine species of Australian warblers occurred on the plot. Three of these, White-browed Scrubwren *Sericornis frontalis*, Speckled Warbler *S. sagittatus* and Yellow-rumped Thornbill *Acanthiza chrysorrhoa*, forage mainly on the ground or in low vegetation (Recher et al. 1985; Woinarski 1985a; Ford et al. 1986) and were not considered in this study. The remaining species, Weebill *Smicromys brevirostris*, White-throated Warbler or Gerygone *Gerygone olivacea*, Brown Thornbill *A. pusilla*, Buff-rumped Thornbill *A. reguloides*, Little Thornbill *A. nana* and Striated Thornbill *A. lineata*, are shrub and canopy foragers and were the species studied. All are small (5-8 g), active foragers (Table 2). The thornbills are very similar in appearance.

Of the species studied, *A. pusilla* was uncommon and insufficient data were obtained for seasonal comparisons. *G. olivacea* migrated and was absent from March through August. *A. lineata* and *A. nana* were the most abundant species with seven to nine nesting groups (35-50 individuals) and 20 to 25 pairs (40-50 individuals) respectively. There were four nesting groups of *A. reguloides* (20-25 individuals) and two pairs of *A. pusilla* (four individuals). Between 12 and 20 pairs (24-40 individuals) of *S. brevirostris* nested on the plot. There were ten pairs (20 individuals) of *G. olivacea*. Bell (1985), Bell & Ford (1986) and Woinarski (1985b) discuss the breeding biology of several of these species.

TABLE 2 Number of observations recorded for each season at Scheyville during 1984 and the average weight of acanthizid warblers studied.

Species	Average <sup>2</sup> weight (g)	Observations <sup>1</sup>					Total
		Summer	Autumn	Winter	Early spring	Late spring	
<i>Acanthiza nana</i>	5.9	143 (62)	269 (68)	272 (78)	145 (41)	263 (75)	1092 (324)
<i>A. lineata</i>	6.7	257 (87)	206 (52)	248 (63)	186 (52)	222 (67)	1119 (321)
<i>A. pusilla</i>	6.2	—	—	—	—	—	125 (35)
<i>A. reguloides</i>	7.5	162 (46)	208 (47)	106 (24)	48 (13)	86 (30)	610 (160)
<i>Smicromys brevirostris</i>	5.1	210 (56)	257 (62)	213 (54)	115 (37)	137 (45)	932 (254)
<i>Gerygone olivacea</i>	7.7	115 (30)	n.d.	n.d.	61 (16)	140 (38)	316 (84)

<sup>1</sup> Numbers are shown as number of prey attacks with number of foraging bouts in parenthesis

<sup>2</sup> Measurements are means of 10 or more individuals from the Australian Museum collection.

### Habitat

In south-eastern Australia, *A. pusilla* and *A. lineata* are most abundant in open eucalypt forests (McGill 1970; Reader's Digest 1976; Recher *et al.* 1987). *A. pusilla* is most abundant in forest with a dense shrub layer and also occurs in tall shrub and heath habitats. *A. reguloides* is most common in open forest and woodland with a sparse shrub layer. *G. olivacea* and *S. brevirostris* are dry, open forest and woodland species that are usually absent from the moister eucalypt forests where *A. pusilla* and *A. lineata* are abundant. *A. nana* occupies a wide range of habitats including paperbark *Melaleuca* forest, wattle *Acacia* scrubs and open eucalypt forests (McGill 1970). Although not evenly distributed, all species occurred throughout the study area.

### Results

#### Foraging heights

Most species foraged throughout the vegetation profile and broadly overlapped in their use of different layers (Fig. 1). *S. brevirostris* and *A. nana* foraged mainly (> 50% of observations) in the canopy and sub-canopy, *A. lineata* and *G. olivacea* mainly in the sapling, small tree and sub-canopy layers, and *A. reguloides* mainly in the shrub and sapling layers and on the ground. *A. pusilla* foraged almost exclusively in the shrub layer (84% of foraging was between 0.5 and 3 m). Figure 2 shows the mean and standard deviation of foraging heights for each season. It illustrates the extent of overlap in foraging height and shows that for most species there were relatively small differences between seasons in average foraging heights. The important differences between species were in the extent to which they used different layers of vegetation.

Despite considerable overlap, most species differed significantly in their use of vegetation layers. With the exception of *S. brevirostris* and *A. nana* (Chi Square,  $P > 0.1$ ) and *A. lineata* and *G. olivacea* (Chi Square,  $P < 0.025$ ) during the spring, differences between species in their use of different vegetation layers were highly significant (Chi Square,  $P$ 's  $< 0.001$ ) for all seasons. The greatest contributions to Chi Square values were in the extent to which species differed in their use of the highest (canopy and/or sub-canopy) and lowest (shrub and/or sapling) layers, suggesting a major difference in the distribution of resources between the eucalypt canopy and understorey vegetation.

Although the proportional use of vegetation layers differed for all species between seasons (Fig. 1), the differences were not significant (ANOVA, early and late spring grouped,  $P$ 's  $> 0.1$ ). *A. reguloides* had the greatest seasonal shifts in foraging height distribution. *A. reguloides* foraged lower and was recorded on the ground more frequently in autumn and winter than in spring and summer (Figs 1 & 2). This difference was related to the changed behaviour of the species during the breeding season. In autumn and winter *A. reguloides* formed large flocks (8-12 birds) and

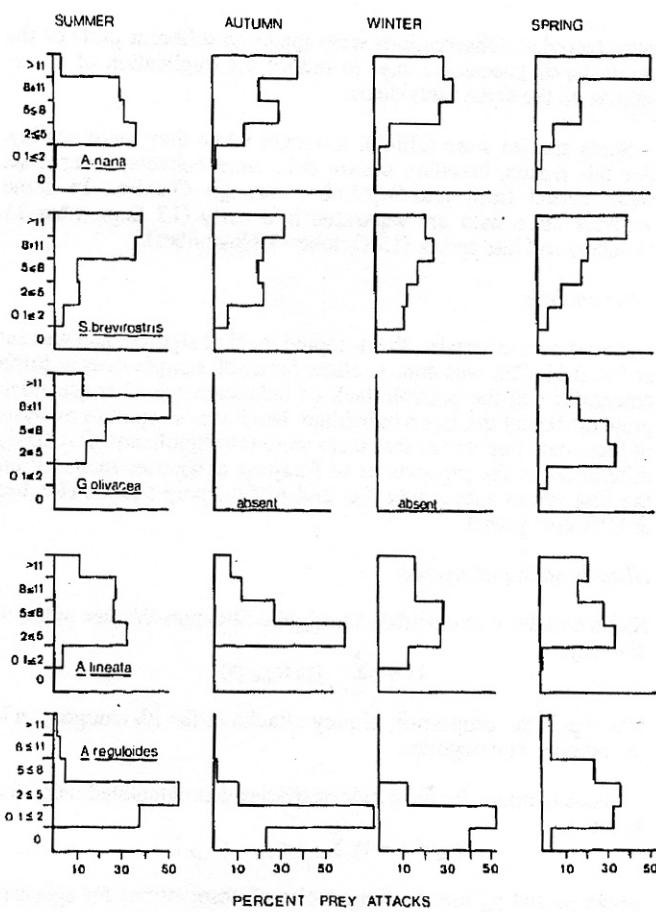


FIGURE 1 Foraging height (prey-attack) distribution by foliage layer for Australian warblers at Scheyville during 1984. Data for early and late spring have been combined.

fed mainly along forest edges. In early spring the flocks dispersed and nesting territories, defended by two to four or more individuals, were established.

Two of the three *A. reguloides* nests located during 1984 were in the forks of trees 6-7 m above ground. The third nest was behind bark on a tree trunk 1.5 m above ground. Most observations during spring were of birds associated with the higher nests. These individuals foraged in trees near and at the height of the nest. This was particularly pronounced while nestlings were being fed and resulted in significantly higher foraging during September (Kolmogorov-Smirnov two sample test,  $P < 0.001$ ) compared to earlier and later in the year (Fig. 2). In September, 35% of foraging was between five and eight metres (small tree layer) with 23% in the sapling layer (2-5 m). After fledging, the young moved to the ground in Blackthorn thickets and the adults ceased feeding in trees. During this period, 76% of foraging observations were of birds in the shrub and sapling layers ( $> 0.1-5$  m).

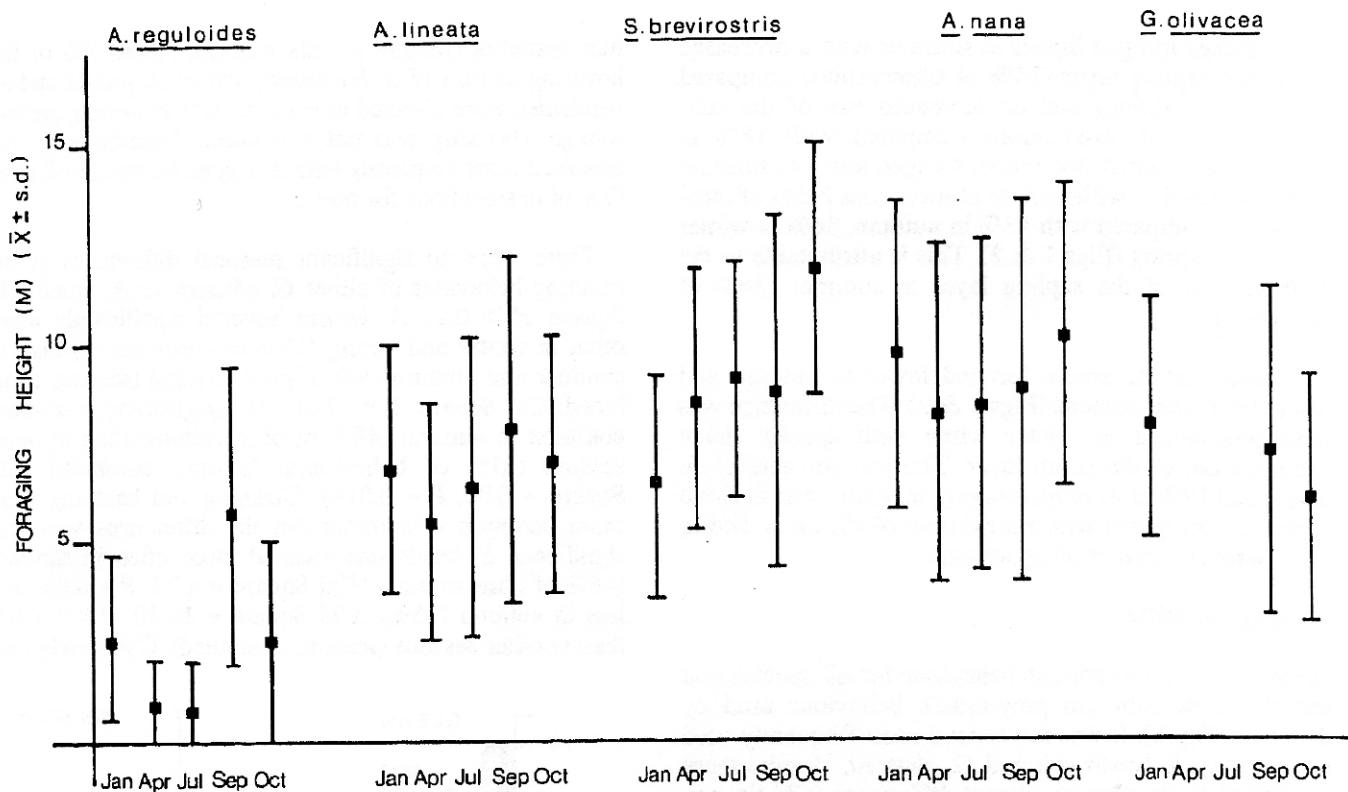


FIGURE 2 Mean (box) and standard deviation (vertical line  $\pm$  s.d.) of foraging heights by season for Australian warblers at Scheyville during 1984.

Shifts in foraging heights between early and late spring were also recorded for *S. brevirostris*, *A. lineata*, *A. nana* and *G. olivacea* (Fig. 2). *S. brevirostris* and *A. nana* foraged significantly higher in October/November than in September (Kolmogorov-Smirnov two sample test,  $P < 0.01$ ). The main nesting period for both species was from late September through November and most nests were located in the canopy. Of 23 *S. brevirostris* nests recorded during 1984 and 1985 at Scheyville, 16 (70%) were in the canopy and the remainder in saplings or shrubs below five metres. Of 25 *A. nana* nests, 17 (68%) were above 11 m and only one was below 8 m in height. In 1984 the average nest height for *S. brevirostris* was  $12 \pm 5$  m ( $n = 10$ ) and for *A. nana* it was  $11.5 \pm 2$  m ( $n = 10$ ). These are near the average foraging heights for both species in late spring (*S. brevirostris*  $12 \pm 3$  m; *A. nana*  $10 \pm 4$  m). Foraging heights at this time may therefore reflect the heights at which the birds were nesting. The converse is also possible and the birds may nest in those vegetation layers where food is most abundant. Data that would resolve this point are not available.

The lower foraging height of *G. olivacea* in late spring (Fig. 2) is also correlated with its breeding and nesting behaviour. Males return to Scheyville in early to mid-September followed by females in late September. On

returning, the males establish territories which they advertise by singing. During territory establishment, they commonly forage in the canopy and sub-canopy where they sing and display. More than 80% of observations during the early spring were of singing males. Twenty-three per cent of these birds were in the canopy. When the females returned, the males followed them closely. Most nests were built in understorey vegetation (mean nest height  $5 \pm 2.5$  m,  $n = 16$  for 1984 and 1985) where both sexes then foraged. Only 8% of observations of *G. olivacea* during late spring were of birds in the canopy.

Although there were differences in the foraging height distribution of *A. lineata* between spring and summer (Figs 1 & 2), these were largely the result of increased canopy foraging in early spring. Thirty per cent of *A. lineata* foraging was above 11 m in early spring compared with 14% in late spring and 11% in summer when birds made greater use of the sub-canopy. There are no differences (Chi Square,  $P > 0.1$ ), if observations above 8 m are grouped. *A. lineata* had finished nesting by mid-September and were feeding fledglings during early spring. The greater use of the canopy by *A. lineata* at this time may be related to the presence of dependent young. *A. nana* also foraged relatively high during summer (mean foraging height,  $9.6 \pm 3.8$  m) when accompanied by young.

*G. olivacea* foraged higher in summer with a decreased use of the sapling layer (14% of observations compared with 34% in spring) and an increased use of the sub-canopy (51% of observations compared with 18% in spring). In contrast, *S. brevirostris* foraged lower in summer than other seasons with 68% of observations being of birds below 8 m compared with 43% in autumn, 36% in winter and 31% in spring (Figs 1 & 2). This is attributable to the increased use of the sapling layer in summer (36% of observations).

*A. nana* and *A. lineata* foraged lower in autumn and winter than other seasons (Figs 1 & 2). The difference was most pronounced in winter when both species made increased use of the shrub layer. Thirteen per cent of *A. lineata* and 12% of *A. nana* foraging in winter was in shrub vegetation compared with a maximum of 4% for *A. lineata* and 6% for *A. nana* at other seasons.

#### Foraging behaviour

Gleaning was an important behaviour for all species and was the most common prey-attack behaviour used by thornbills (Fig. 3). It was the second most frequently used behaviour by *S. brevirostris* and *G. olivacea*. Despite these similarities, there were significant differences (Chi Square,  $P < 0.01$ ) between all species at all seasons in foraging repertoires (i.e. the proportions of different foraging manoeuvres used). Similarly, there were seasonal differences in the use of particular behaviours by some species but these generally related to the less frequently used manoeuvres such as snatching and hawking. In Figure 3, all data for the year are grouped. Differences between species and between seasons are discussed below.

The foraging behaviour of *A. lineata* was distinguished by the frequent use of hang-gleaning (35% of manoeuvres) (Fig. 3), a behaviour rarely used by other species (see also Bell 1985). Most hang-gleaning behaviour was directed at extracting lepidopteran larvae from between leaves tied together by the insect. Such behaviour was commonly preceded by hovering as the bird inspected or searched the foliage. Hanging below the foliage, while probing between the tied leaves (= gleaning in this study), takes advantage of the larvae which have downward facing escape tubes (B. Springett pers. comm.).

*S. brevirostris* and *G. olivacea* used active foraging behaviours (i.e. hover and snatch foraging manoeuvres respectively) more often than the thornbills. Hovering was the most frequent prey-attack behaviour of *S. brevirostris* (43% of manoeuvres) while *G. olivacea* took 51% of their prey by snatching and hawking (Fig. 3). *A. pusilla* and *A. nana* snatched prey more often (14 and 17% of prey attacks respectively) than other thornbills. *A. pusilla* also hovered to take prey (22% of observations). Usually, hovering birds took prey from foliage or from the ends of

thin branches (mainly on Blackthorn). About 2% of the hovering actions of *S. brevirostris*, and of *A. pusilla* and *A. reguloides*, were directed at small insects swarming around foliage. Hawking was not a common behaviour. It was observed most frequently with *A. reguloides* and *G. olivacea* (7% of observations for both).

There were no significant seasonal differences in the foraging behaviour of either *G. olivacea* or *A. nana* (Chi Square,  $P > 0.1$ ). *A. lineata* hovered significantly more often in winter and spring (17% of observations) than in summer and autumn (6% of prey attacks) (seasons combined, Chi Square,  $P < 0.01$ ). Hang-gleaning was more common in autumn (48% of observations) than in other seasons (31% of behaviours) (seasons combined, Chi Square = 6.00,  $P = 0.014$ ). Gleaning and hawking were more common in summer but the differences were not significant. *S. brevirostris* gleaned more often in summer (46% of observations) (Chi Square = 4.37,  $P = 0.04$ ) and less in autumn (25%) (Chi Square = 14.49,  $P \ll 0.01$ ) than at other seasons (seasons combined). Conversely they

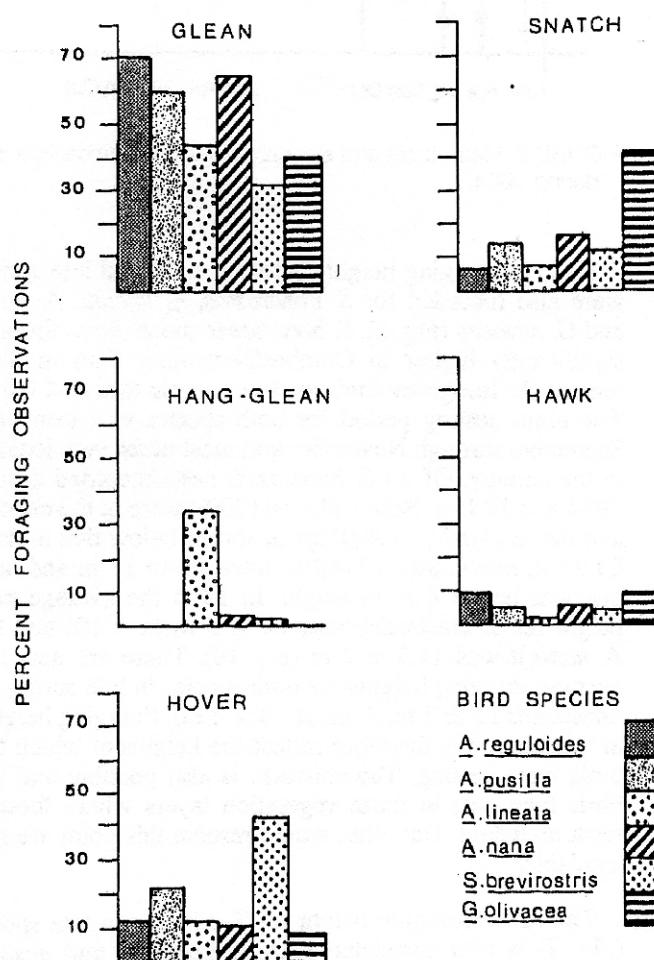


FIGURE 3 Foraging behaviour of Australian warblers at Scheyville during 1984. Seasonal data have been combined.

hovered more in autumn (54%) and less in summer (26%). *A. reguloides* had the greatest seasonal variations in foraging behaviours. *A. reguloides* snatched more in spring (16% of prey attacks), hawked more in summer (20%) and hovered more in winter and early spring (23%) than at other times.

#### Substrate

Apart from *A. reguloides*, which took nearly half (48%) of their prey from the ground or bark, foliage was the most important foraging substrate for these birds (Fig. 4). During the year, *A. lineata*, *S. brevirostris* and *G. olivacea* took significantly more of their prey (> 85%) from foliage than *A. pusilla* (78%), *A. nana* (77%) and *A. reguloides* (45%) (Chi Square,  $P < 0.01$ ). Species also differed in their use of bark with 24% of prey attacks by *A. reguloides*, 16-17% by *A. nana* and *A. pusilla* and 10% by *A. lineata* directed at prey on or in bark. *S. brevirostris* and *G. olivacea* used bark less than 3% of the time. Air (insects in flight) was an important substrate for *G. olivacea* and *A. reguloides* (9-10% of prey attacks).

*A. reguloides* foraged extensively on the lower trunks of trees (< 1 m above ground) (16% of prey attacks) and seldom on branches (5% of prey attacks). *A. pusilla* took 16% of their prey from bark surfaces and used branches (7%) about as often as tree trunks (5%). Hanging bark and other debris accounted for the remaining 4% of prey taken

from bark by *A. pusilla*. *A. reguloides* was the only species to forage on the ground (22% of observations) where 6% of prey were taken from logs, fallen branches and other debris.

There were few seasonal differences in the use of substrates. Excluding *G. olivacea*, which was migratory, and combining the data for all other species, significantly more flying insects (air as a substrate) were taken in summer and autumn when insects were active than winter and spring (seasons combined, Chi Square,  $P < 0.001$ ). More flying insects were taken in summer than autumn (Chi Square,  $P < 0.01$ ) but the difference between winter and spring was not significant (Chi Square,  $P < 0.05$ ). Data were combined because of small sample sizes for individual species but all showed the same pattern of greater use of flying insects in summer and autumn than in winter and spring.

*A. reguloides* took significantly more prey from the ground in autumn and winter than in spring and summer when they made greater use of foliage (seasons combined, Chi Square,  $P < 0.01$ ) (Fig. 4). The advantage of ground foraging at this time is not clear but the birds may have been feeding on seeds as well as insects. *A. lineata* foraged significantly more often on bark in winter than in other seasons (seasons combined, Chi Square,  $P < 0.01$ ) (Fig. 4). The increased use of bark substrates in winter and autumn were probably related to decreases in the numbers of

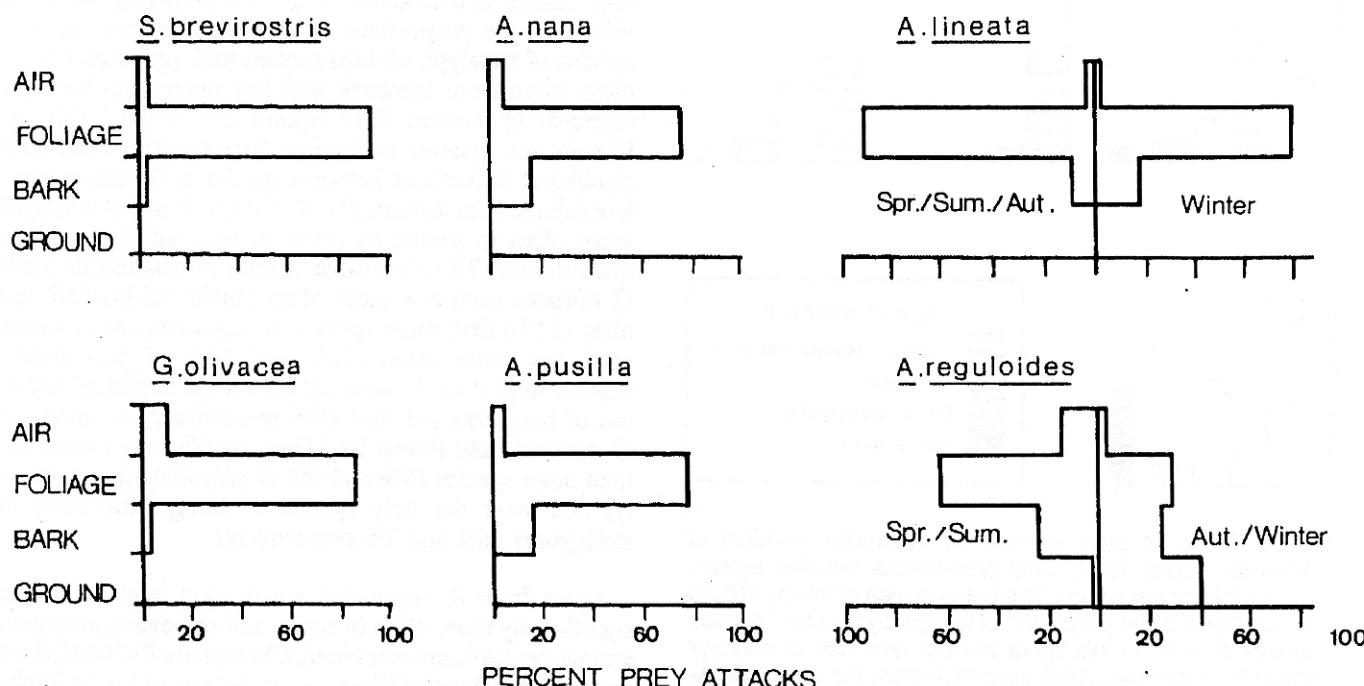


FIGURE 4 Substrates used by Australian warblers at Scheyville during 1984. Except for *A. reguloides* and *A. lineata* where there were significant seasonal differences in substrates used, seasonal data have been grouped.

foliage insects and the availability of insects over-wintering within or under bark (Recher *et al.* 1983; Noske 1985; Recher, Majer & Gowing unpubl.). There were no significant seasonal differences in the use of substrates by *S. brevirostris*, *G. olivacea* and *A. nana* (Fig. 4).

*G. olivacea* appeared to take the largest prey and consistently took large insect larvae, flies, wasps and beetles (pers. obs.) but the majority of their prey was too small for identification. *S. brevirostris*, *A. lineata* and *A. nana* often took prey directly from leaf surfaces and appeared to be feeding on psyllids and/or lerp. About 45% of Woinarski's (1985a) observations of *S. brevirostris*, 10% of *A. nana* observations and 13% of *A. pusilla* observations were of birds feeding on psyllids. In addition, *S. brevirostris* and thornbills took spiders, beetles, flies, ants, wasps, moths, caterpillars and other insect larvae (Woinarski 1985a; pers.

obs.). Bell (1985) reported that 40% of insects seen to be taken by thornbills were caterpillars. Beetles and ants recorded by Bell (1985) from thornbill stomachs were significantly larger than the average size of those found on foliage.

#### Use of plant species

Grey Box dominated the forest canopy (48% of trees). Ironbark dominated the sub-canopy, small tree and sapling layers (56% of trees) (Table 1). Overall, 51% of trees were ironbarks, 41% box and 8% Forest Red Gum. Less than 1% of trees were stringybarks. Despite their greater abundance, only 41% of eucalypt foliage was that of ironbarks. Fifty-two per cent of eucalypt foliage was Grey Box foliage and 7% that of gums and stringybarks combined. Eucalypts comprised 54% and Blackthorn 46% of the above ground foliage available to birds.

There were substantial differences in the use of plant species by birds. Thirty-four per cent of *A. reguloides* and 44% of *A. pusilla* foraging was in Blackthorn. This contrasts with the other species where more than 90% of observations were of birds taking prey from the foliage or bark of eucalypts. Considering only eucalypts (bark and foliage combined), there was no significant difference in the use of species by *A. reguloides* and *G. olivacea*. All other species foraged significantly more often in ironbark.

This disparity in the use of eucalypts is increased when only foliage is considered (Fig. 5). Comparing the use of foliage to the proportions of foliage represented by each species of eucalypt, all bird species took prey significantly more often from ironbark and less often from box than expected by chance (Chi Square,  $P < 0.01$ ) (Fig. 5). Despite the general preference for ironbark, there were significant differences between species in the use of eucalypt foliage (Chi Square,  $P < 0.01$ ). *S. brevirostris* foraged more often in ironbarks (90% of prey attacks) and less often in box (7%) than other species of acanthizids, while *G. olivacea* used box more often (38%) and ironbark less often (51%) than other species. *A. reguloides* and *A. lineata* used box more often (31% and 29% of prey attacks respectively) than *A. nana* (21%) but did not differ in their use of ironbarks (65 and 69% respectively). *A. nana* and *G. olivacea* used Forest Red Gum significantly more often than other species (5% and 9% of prey attacks respectively) and were the only species to forage extensively in stringybark (6% and 2% respectively).

Apart from *A. reguloides*, which used ironbark foliage significantly more often in spring and summer than autumn and winter (seasons combined, Chi Square,  $P < 0.01$ ), there were no significant differences in the use of ironbark foliage between seasons. In contrast, *A. lineata* and *A. nana* foraged in Grey Box significantly more in summer and autumn than in winter and spring. *S. brevirostris* reversed

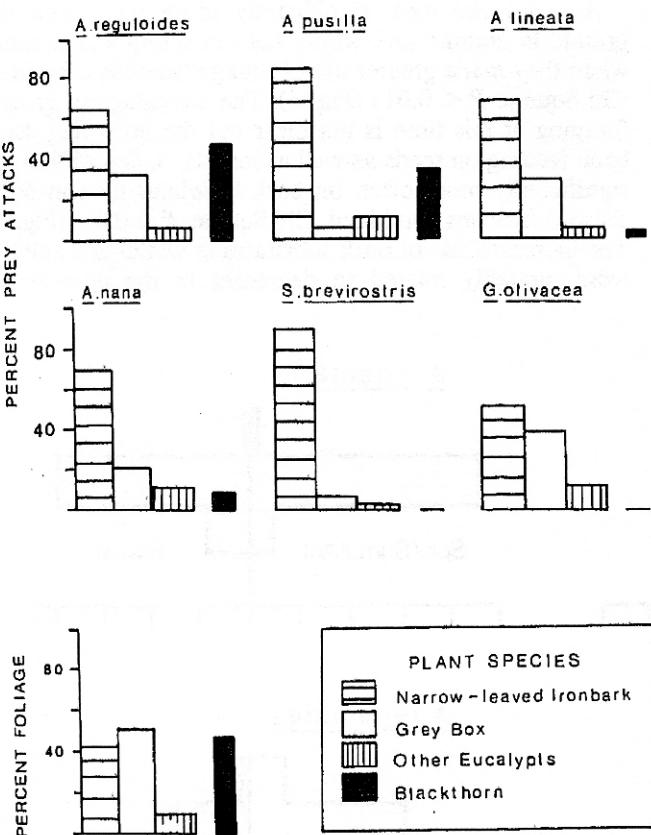


FIGURE 5 Use of plant species by Australian warblers at Scheyville during 1984. Only prey-attacks directed against prey on foliage are shown. The per cent use of foliage should be compared to the proportion of foliage contributed by each species of plant. In this figure the per cent use of eucalypt foliage has been calculated separately from the use of Blackthorn *Bursaria spinosa*. Similarly in showing the per cent foliage for each plant species, Blackthorn is shown as per cent of total foliage and each species of eucalypt is shown as per cent of total eucalypt foliage.

this pattern and used box more in spring than in summer, autumn or winter. *G. olivacea* foraged more in box during summer than late spring when they made greater use of Forest Red Gum. There was a difference in the use of box as a foraging substrate by *A. reguloides* through the year with significantly greater use from late spring through autumn than in winter and early spring (seasons combined, Chi Square,  $P < 0.01$ ). The seasonal differences in the use of box by *A. reguloides* was the same for foliage and bark.

*A. nana* used Blackthorn significantly more often in winter and early spring and less often in late spring, summer and autumn (seasons combined, Chi Square,  $P < 0.01$ ). There were also significant seasonal differences in the use of Blackthorn by *A. reguloides*, which used Blackthorn more often in autumn and winter than spring and summer (seasons combined, Chi Square,  $P < 0.01$ ). Birds foraging in Blackthorn during winter may have been feeding on seeds, as Blackthorn flowers during summer.

#### Niche breadth and overlap

Measures of niche breadth and overlap are convenient to summarise and compare the foraging ecology of co-existing species. Niche breadths for each foraging dimension are given in Table 3. *A. reguloides* had the greatest average niche breadth and used the greatest array of substrates and plant species. Although it had the most diverse foraging repertoire and foraged over a broad height range, *S. brevirostris* used a restricted array of substrates and plant species and had the narrowest average niche breadth. The remaining species had similar overall niche breadths but differed in their use of specific foraging dimensions. After *A. reguloides*, *A. pusilla* used the greatest array of substrates but had a narrow foraging height range. Primarily because of its frequent hang-gleaning behaviour, *A. lineata* had a diverse foraging repertoire but used few different substrates or plant species. *A. nana* had the most diverse foraging height range and, after *A. reguloides*, had the greatest average niche breadth. *G. olivacea* had a diverse foraging repertoire but took prey primarily from foliage.

Resource overlaps were calculated separately for each species pair for each season. These values were then averaged as an index of the degree of overlap with all other species studied (Table 4). With the exception of prey-attack behaviour, average overlaps in the use of foraging resources were highest during spring (76%) and least in autumn (51%). The increased levels of overlap during spring reflected the increased use of eucalypt foliage as a foraging substrate. During spring, birds of all species therefore tended to forage in the same vegetation layers and take prey from the same substrates. Decreased overlaps resulted from an increased use of bark and ground as substrates by some species and the increased use of Blackthorn by thornbills from summer through autumn and winter. Increased use of ground and Blackthorn decreased the foraging height overlap between species. Overlaps for each foraging dimension are therefore not independent.

Relationships between species are illustrated by the dendrogram in Figure 6, which groups species by their average similarity in the use of resources through the year. Species were first separated by foraging height (average annual overlap of 53% for the community as a whole). The canopy and sub-canopy foragers, *A. lineata* and *A. nana*, *S. brevirostris* and *G. olivacea*, were separated from *A. reguloides* and *A. pusilla*. The latter species foraged primarily in lower vegetation and, in the case of *A. reguloides*, on the ground. Canopy and sub-canopy foragers were also similar in their use of eucalypt foliage as their principal foraging substrate. During spring and summer when *G. olivacea* was resident, canopy foragers overlapped least in prey-attack behaviour (average overlap 62%) and foraging height (72%), and overlapped most in their use of substrates (88%) and plant species (78%).

*S. brevirostris* separated from the other canopy foragers by its preference for ironbark and frequent use of hovering as a prey-attack behaviour. *G. olivacea* differed from *A. lineata* and *A. nana*, mainly in their more active foraging, snatching and hawking while the others gleaned prey. *A. lineata* and *A. nana* differed in foraging behaviour with the

TABLE 3 Niche Breadth ( $H'$ ) of Australian Warblers at Scheyville during 1984.<sup>1</sup>

Foraging resource	Bird Species					
	<i>Acanthiza reguloides</i>	<i>A. pusilla</i>	<i>A. lineata</i>	<i>A. nana</i>	<i>Smicromys brevirostris</i>	<i>Gerygone olivacea</i>
Substrate	1.875	1.294	0.650	1.099	0.339	0.682
Prey-attack behaviour	1.024	1.093	1.242	1.063	1.324	1.175
Foraging height distribution	1.141	0.690	1.002	1.188	1.115	1.049
Plant species	1.228	1.031	0.876	1.039	0.449	1.004
$\bar{X}$ Niche breadth	1.317	1.027	0.943	1.097	0.807	0.978

<sup>1</sup> Data for all seasons combined.

greater use of the sub-canopy and hang-gleaning behaviour distinguishing *A. lineata* from *A. nana*.

## Discussion

Woinarski (1985a,b) described *S. brevirostris* and *A. lineata* as 'eucalypt specialists'; neither species in Victoria used other plant genera to a significant extent. Bell (1985) working in north-eastern New South Wales and Recher *et al.* (1987) in south-eastern New South Wales also found that *A. lineata* foraged preferentially on eucalypts. Only 11% of Bell's (1985) observations and less than 4% of the observations of Recher *et al.* (1987) were of *A. lineata* on non-eucalypts. In contrast, *A. pusilla* foraged on a wide range of plant genera including eucalypts (Bell 1985; Woinarski 1985a; Recher *et al.* 1987).

At Scheyville, the limited array of plant species restricted foraging opportunities for foliage-gleaning birds. Only the ground and shrub foraging *A. reguloides* and *A. pusilla* used non-eucalypt vegetation to a significant extent. Foraging segregation of species was therefore achieved by differences in foraging heights, use of bark as a foraging substrate, prey-attack behaviour and selection between species of eucalypts. *S. brevirostris* was the most specialised forager (narrowest niche breadth, Table 3), taking prey primarily by gleaning and hovering at foliage on the outer branches of eucalypts. This is in agreement with Woinarski (1985a) who also found that *S. brevirostris* foraged preferentially on eucalypt foliage insects by gleaning and hovering. Hovering was used by all species as a prey-attack behaviour and to explore large areas of terminal foliage rapidly. I could not always distinguish between these two functions.

Despite the large number of co-existing and potentially competing species at Scheyville, the pattern of resource use and foraging behaviour for each of the species is similar to that reported for communities with fewer species. *A.*

*reguloides*, *A. pusilla* and *A. lineata* occurred in forest and woodland near Bombala on the Southern Tablelands of New South Wales studied by Recher *et al.* (1983, 1985, 1987). *A. pusilla* and *A. lineata* were most abundant in open

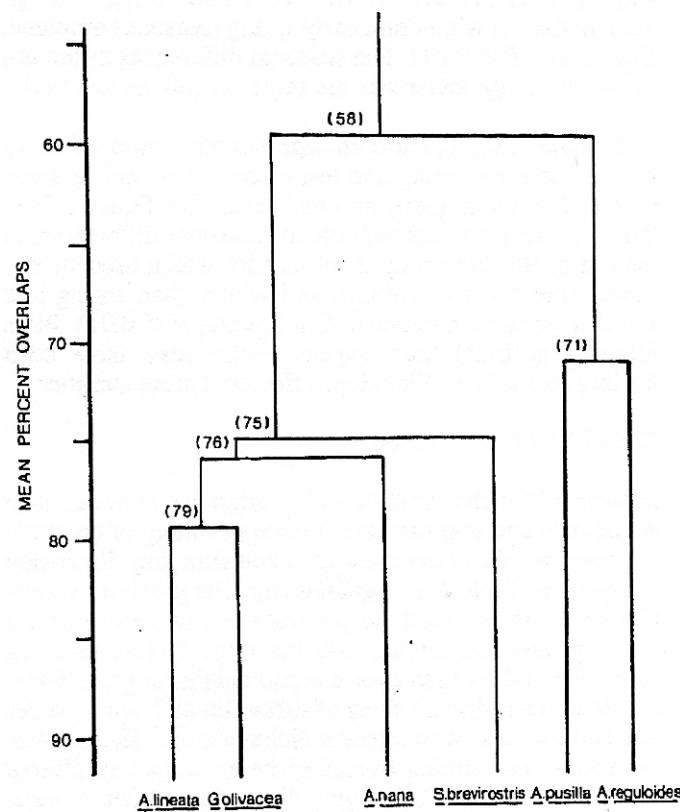


FIGURE 6 In this dendrogram species are grouped according to their similarity in their use of foraging resources (i.e. foraging behaviour, substrate, foraging height distribution, use of plant species foliage) as measured by their mean overlaps.

TABLE 4 Mean percent foraging resource overlaps for species of Australian warblers at Scheyville during 1984.

Species	Season				Mean overlap/ year**
	Summer	Autumn	Winter	Spring	
<i>Acanthiza reguloides</i>	53	36	38	72	57
<i>A. pusilla</i>	*	*	*	*	63
<i>A. lineata</i>	70	56	65	79	70
<i>A. nana</i>	69	60	65	79	71
<i>Smicromys brevirostris</i>	66	53	57	75	65
<i>Gerygone olivacea</i>	68	absent	absent	77	69
' $\bar{X}$ seasonal overlaps***	65	51	56	76	

\* insufficient data \*\* includes overlaps with Brown Thornbill

\*\*\* excludes Brown Thornbill

and tall open forest with a well-developed shrub layer, while *A. reguloides* was restricted to Snow Gum *E. pauciflora*-Black Sallee *E. stellulata* woodland. In this situation *A. reguloides* and *A. pusilla* were separated by habitat (Recher unpubl.). As at Scheyville, *A. pusilla* and *A. lineata* used different vegetation layers with *A. lineata* foraging almost exclusively on eucalypt foliage in the canopy and sub-canopy. *A. pusilla* foraged primarily in the shrub layer, rarely foraged on the ground and used a wide array of plant species as foraging substrates. *A. reguloides* foraged more on the ground than at Scheyville (58% of observations vs 4% at Scheyville for the same season) and took less prey from foliage (16% vs 55%) and bark (14% vs 24%). Niche breadths for *A. pusilla* and *A. lineata* were similar to those at Scheyville but were narrower for *A. reguloides* (Table 5). The reduced niche breadth for *A. reguloides* at Bombala is the result of the high incidence of ground-foraging and gleaning (91% of observations) relative to Scheyville.

The same species, plus *G. olivacea*, occurred in eucalypt woodlands near Armidale on the Northern Tablelands of New South Wales studied by Ford and his colleagues (Ford *et al.* 1986). Niche breadths (corrected for different numbers of categories in foraging dimensions) of *G. olivacea* and *A. reguloides* appear similar to those of the same species at Scheyville (Table 5). *A. pusilla* had a narrower niche breadth while that of *A. lineata* was broader near Armidale than at Bombala and Scheyville. Given differences in methodology and site characteristics (i.e. the number of different foraging dimensions available to birds in terms of plant species and vegetation structure), it would be unwise to make too much of either the differences or the similarities in niche breadths between localities. However, the data do suggest that niche breadth was little affected by the numbers of co-existing species (Table 5).

Niche breadth is probably affected more by the presence or absence of foraging opportunities than the presence or

absence of potential competitors. The narrower niche breadths of *A. reguloides* at Bombala relative to Scheyville and Armidale may also be explained by the narrower time interval during which data were collected. Studies of foraging birds at Bombala were restricted to spring and early summer whereas those at Scheyville and Armidale were carried out through the year.

All of the species studied took most of their prey from foliage and, apart from the *G. olivacea*, strongly selected between the different species of eucalypts. Box and ironbark have different foliage characteristics. The adult leaves of box are lanceolate to broad-lanceolate (8-14 x 2-3 cm) (Boland 1984). Those of ironbark tend to be long and narrow (6-16 x 0.7-1.3 cm) (Boland 1984). Ironbark foliage is also more tightly clustered than that of box and terminal branches or twigs are thinner. These structural differences may affect the ability of birds to locate prey on the foliage. Different kinds of behaviour may be needed to remove insects once seen. As a way to inspect foliage rapidly, hovering may be particularly suited to the foliage characteristics of ironbark and may partially explain the preference of *S. brevirostris* for this species. Selection between the two co-dominants may also reflect differences in abundances and/or types of insects on ironbark and box. Preliminary results show that psyllids (lerp-forming insects) are more abundant on ironbark than box (Recher, Majer & Gowing unpubl. data). Although additional studies are required to resolve these questions, the selection of plant species by acanthizids at Scheyville reinforces the conclusions of North American workers (e.g. Robinson & Holmes 1982, 1984) that the organisation and structure of avian communities is strongly affected by the structural features of individual plant species.

#### Acknowledgements

The paper is dedicated to the memory of Julian Ford whose

TABLE 5 Average niche breadth ( $H'/H'_{\text{Max}}$ ) in the use of foraging resources (substrate, prey-attack behaviour, prey height, and plant species) for Australian warblers at three locations in New South Wales.

Species	Locality		
	Bombala	Scheyville	Armidale**
<i>Acanthiza reguloides</i>	0.52	0.71	0.76
<i>A. pusilla</i>	0.61	0.57	0.50
<i>A. lineata</i>	0.54	0.54	0.62
<i>A. nana</i>	—	0.61	—
<i>Gerygone olivacea</i>	—	0.56	0.61
<i>Smicromys brevirostris</i>	—	0.47	—
Number of co-occurring Acanthizidae	5	9	6

\* Recher *et al.* 1985 \*\* Ford *et al.* 1986

research contributed much to our knowledge of the evolutionary ecology of Australian warblers. His untimely death should remind us that few people understand the procedures of science or appreciate the importance of knowledge for the conservation and management of natural resources. Lyn Albertson, Greg Gowing and Paul O'Connor assisted with vegetation measurements. Brian Collins, Hugh Ford, Dick Holmes, Richard Noske and Denis Saunders commented critically on early drafts of the manuscript.

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