

On the Selection of Tree Species by Acanthizidae in Open-forest Near Sydney, New South Wales

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Summary: Selection between tree species as foraging substrates by four species of Acanthizidae was studied in an open eucalypt forest near Sydney, New South Wales. Weebills *Smicrornis brevirostris*, Striated and Little Thornbills *Acanthiza lineata* and *A. nana* foraged more often than expected on the foliage of Narrow-leaved Ironbark *Eucalyptus crebra* than on that of Grey Box *E. moluccana*. By contrast *Gerygone olivacea* used the two trees in about the same proportion as the amount of foliage of each species. Weebills and Striated Thornbills selected Narrow-leaved Ironbark foliage as a foraging substrate more often than Little Thornbills in winter but not in spring. Little Thornbills foraged on Narrow-leaved Ironbark foliage more often in spring than in winter. The selection of eucalypt foliage as a foraging substrate is correlated with the abundances and kinds of invertebrates found on the two tree species. Invertebrates were gen-

erally more abundant on the foliage of Narrow-leaved Ironbark than on that of Grey Box in both winter and spring. Lerp-forming psyllid insects, however, were more abundant per leaf on Grey Box than Narrow-leaved Ironbark in winter, but not in spring. Grey Box leaves are larger than those of Narrow-leaved Ironbark and when the abundances of psyllids were corrected for leaf area (i.e. as numbers/cm²), the difference between Grey Box and Narrow-leaved Ironbark in winter was not significant. However, in spring the numbers of psyllids/cm² on Narrow-leaved Ironbark foliage was greater than on Grey Box foliage. The differences in invertebrate abundances account for some of the differences in the use of the two eucalypts as foraging substrates, but variability in invertebrate abundances between leaves and individual trees, as well as differences in foliage morphology, may also have been important.

Recher (1989) reported that Acanthizidae differentiated between different species of eucalypts as foraging substrates in open-forest near Sydney, New South Wales. He suggested that the differences in the use of eucalypts as foraging substrates was related to differences in foliage morphology and to possible differences in invertebrate communities between tree species. Recher *et al.* (1991) presented data from chemical fogging which showed that the abundance and biomass of invertebrates on eucalypts selected by birds as foraging substrates was greater than on less preferred species. Differences in the abundance of lerp-producing psyllid insects (Hemiptera: Psyllidae) appeared particularly important, with lerp-eating birds differentiating between tree species more strongly than other kinds. Among Acanthizidae in open-forest near Sydney, Weebills *Smicrornis brevirostris*, Striated and Little Thornbills *Acanthiza lineata* and *A. nana* differentiated more strongly between eucalypt species than did *Gerygone olivacea*.

In this paper we present additional information on the selection of tree species by Acanthizidae in open-forest near Sydney and compare this to invertebrate abundances and composition as determined by branch

clipping. Branch clipping provides a more precise measure of invertebrate communities on foliage than chemical fogging which samples canopy invertebrates irrespective of whether they are on leaves or bark (Majer & Recher 1988).

Methods

Study site and vegetation

The study was conducted in 1985 within open-forest at Scheyville 40 km NW of Sydney on the site described previously by Recher (1989). The site was dominated (92% of trees and 93% of canopy and understorey foliage) by two eucalypts, Grey Box *Eucalyptus moluccana* and Narrow-leaved Ironbark *E. crebra* (Recher 1989). Of these two species, 56% of foliage (45% of individuals) was Grey Box and 44% of foliage (55% of individuals) was Narrow-leaved Ironbark. About 8% of trees and 6% of foliage was Forest Red Gum *E. tereticornis*. Fewer than 1% of trees and about 1% of foliage was Thin-leaved Stringybark *E. eugenoides*. The proportion of foliage contributed by each species in the different vegetation layers was determined using a cam-

era fitted with a rangefinder as described by Recher (1989).

Invertebrate samples

Foliage invertebrates were sampled in late winter (17 July to 8 August) and spring (9–24 October) using the branch clip procedure described by Majer & Recher (1988). Briefly, with minimal disturbance, a small leafy branch was inserted into a clear plastic bag and the branch cut. A small amount of insecticide was sprayed into the bag and the bag sealed. The bags and their contents were then frozen until required for analysis.

Samples were taken from two height ranges; canopy (9–13 m) and understorey (1.8–6 m). A cherry-picker was used to sample canopy foliage and ladders for the understorey. Because of the difficulty of moving and positioning the cherry-picker, 10 branch clips (samples) were taken from each canopy tree sampled. These were spaced throughout the tree canopy to give as even a sample as possible. Samples were taken from seven canopy trees of each species in each season. The small size of understorey trees prevented the taking of ten branch clips from individual trees. In order to maintain parity with the canopy samples, we therefore took one sample from each of 10 trees within a monospecific cluster or grove. These were treated as if they had been taken from a single tree. Samples were taken throughout the plot and spaced to give a uniform distribution. Seven of these clusters were sampled for each species in each season.

After freezing and storage, the samples were weighed and the plastic bags inspected for invertebrates dislodged from the branch and foliage. Forty leaves were removed from the branch and the numbers of galls, sessile insects and other invertebrates were counted on each leaf. Leaf area was determined from a random sample of leaves ($n = 160$) collected from each species at each height range. The leaves were measured using a planimeter.

Invertebrates were sorted to major taxa (order, family) and the data from the ten samples from each tree or group of trees pooled for analysis. The numbers of invertebrates were corrected for sample size (wet weight) of the combined foliage and branch material and for leaf area. Branch clips from Grey Box weighed an average of 111 g, while those from Narrow-leaved Ironbark weighed 43 g. Both appeared to have a similar ratio of foliage to bark (twigs and branches) in the samples. There were no significant differences in weight between canopy and understorey samples.

Foraging behaviour

Avian foraging behaviour was recorded during the same period that invertebrates were sampled. For each bird encountered the second attempt at prey capture (prey attack) was recorded regardless of whether or not this was successful. This follows the recommendations of Recher & Gebski (1990) who found a tendency for the first recorded observation to be biased towards conspicuous behaviours. Thus, only one foraging record was taken from each bird encountered. To further increase the independence of foraging data, observations were made throughout the study area with different sections visited on consecutive days. Observations were made on no more than half the individuals of species within a foraging flock. These procedures minimised the chance of recording data from the same individual on a second or third day. A minimum of 70 prey attacks was recorded for each species in each season (Recher & Gebski 1990). Terminology for prey attack behaviour and foraging substrates follows Recher *et al.* (1985). Unless otherwise stated, all means are given \pm standard deviation.

Results

Foliage morphology

The leaves of Grey Box were significantly larger than those of Narrow-leaved Ironbark (Komogorov-Smirnov two-sample test, $P < 0.01$). In the subcanopy Grey Box leaves averaged 17.7 ± 11.5 cm² and in the canopy averaged 16.4 ± 7.3 cm², but the differences were not significant ($P > 0.05$). Narrow-leaved Ironbark leaves averaged 4.9 ± 2.3 cm² in the subcanopy and 3.5 ± 2.2 cm² in the canopy, but the differences were not significant ($P > 0.05$).

In addition to being larger, Grey Box leaves are broadly ovate and the foliage tends to be more open and supported by larger or more robust twigs and small branches than on Narrow-leaved Ironbark. Narrow-leaved Ironbark leaves tend to be narrow (lanceolate) and clustered. The clusters of leaves hang loosely at the ends of branches and offer little support for birds.

Invertebrate abundances

There were no significant differences in the numbers of invertebrates or the proportions of the major taxa (e.g. psyllid insects, spiders) between the canopy and subcanopy samples for either Grey Box or Narrow-leaved

Table 1 Quantity of invertebrates and psyllid insects (mean \pm standard deviation) on the foliage and twigs of Narrow-leaved Ironbark and Grey Box at Scheyville, New South Wales, during winter (W) and spring (S) in 1985.

Invertebrates	Tree species			
	Narrow-leaved Ironbark		Grey Box	
	W	S	W	S
Total invertebrates (excluding psyllids) (nos./g sample) $\times 100$	53 \pm 78	134 \pm 59	10 \pm 8	37 \pm 22
Abundance of psyllids on 400 leaves	9 \pm 9	28 \pm 26	27 \pm 20	37 \pm 22
Density of psyllids (nos./cm ² foliage) $\times 100$	28 \pm 27	89 \pm 94	20 \pm 15	26 \pm 16

Ironbark, Analysis of Variance (ANOVA) $P > 0.1$. High and low samples have therefore been pooled in subsequent analyses. (For details of the taxonomic and species composition of invertebrates on these tree species see Majer *et al.* 1994).

In the comparison of bag contents (corrected for weight), there were significantly more invertebrates on Narrow-leaved Ironbark than Grey Box in both winter (χ^2 , $P < 0.05$) and spring ($P < 0.001$) (Table 1).

Psyllids were significantly more abundant on the leaves of Grey Box than Narrow-leaved Ironbark in winter (ANOVA, $P < 0.01$) (Table 1). Differences in the abundance of psyllids on Grey Box and Narrow-leaved Ironbark foliage in spring (Table 1) were not significant ($P > 0.05$). When corrected for leaf area, there was no significant difference in the density (number/cm²) of psyllids on Grey Box and Narrow-leaved Ironbark in

winter ($P > 0.05$) (Table 1). However, the density of psyllids was significantly greater on Narrow-leaved Ironbark than Grey Box in spring ($P < 0.05$). There was no significant difference in the abundance of psyllids on Grey Box in winter versus spring ($P > 0.05$), but psyllids were significantly more abundant on Narrow-leaved Ironbark foliage in spring than in winter ($P < 0.05$).

The kinds of psyllids and the type of lerp produced appeared to be the same on both Grey Box and Narrow-leaved Ironbark. However, the dispersion of psyllids was significantly more variable on Narrow-leaved Ironbark than Grey Box in winter and spring (F -test, $P < 0.01$) (Table 1).

Foraging behaviour

Data on foraging behaviour were obtained for Weebills, Striated and Little Thornbills in winter and spring and for *Gerygone olivacea* in spring.

There was no significant difference in the use of Narrow-leaved Ironbark and Grey Box foliage by Weebills, Striated and Little Thornbills between winter and spring (χ^2 , $P > 0.05$). In both seasons, Weebills, Striated and Little Thornbills foraged significantly more often on Narrow-leaved Ironbark than on Grey Box foliage than expected by chance ($P < 0.001$) (Table 2). Weebills also foraged more often than expected on Forest Red Gum in winter and spring ($P < 0.05$). Little Thornbills used Forest Red Gum foliage in winter in about the same proportion as its availability (7% of observations), but foraged on Forest Red Gum significantly more often (16%) than expected in spring ($P < 0.01$). There was no significant difference between seasons in the use of Forest Red Gum by Striated Thornbills ($P > 0.05$). In comparison with other eucalypts on the site,

Table 2 Per cent use by Acanthizidae of different eucalypt foliage as a foraging substrate during winter (W) and spring (S) at Scheyville, New South Wales, in 1985.

Bird species	Tree species (% eucalypt foliage)									
	Grey Box (52)		Narrow-leaved Ironbark (41)		Red Gum (6)		Stringybark (< 1)		No. observations	
	W	S	W	S	W	S	W	S	W	S
Little Thornbill	17.3	14.2	73.5	63.3	7.1	15.8	2.0	6.7	98	120
Striated Thornbill	19.7	15.6	72.7	71.9	3.8	10.4	3.8	2.2	132	135
<i>Gerygone olivacea</i>	*	35.3	*	38.8	*	23.5	*	2.4	*	85
Weebill	6.8	9.4	75.3	70.1	17.8	16.2	0.0	4.2	73	117

* absent from area in winter.

Gerygone olivacea used Forest Red Gum significantly more often (24%) ($P < 0.001$) and Grey Box less often (35%) than expected ($P < 0.05$) (Table 2). They took prey from Narrow-leaved Ironbark foliage in about the same proportion (39% of observations) that Narrow-leaved Ironbark foliage occurred on the site (41% of eucalypt foliage). There was no significant difference in the use of Narrow-leaved Ironbark and Grey Box foliage as foraging substrates by *Gerygone olivacea* from that expected by chance ($P > 0.1$).

Gleaning was the most frequently observed foraging behaviour used by Striated and Little Thornbills (Table 3). Striated Thornbills often used hang-gleaning to take prey from foliage. Weebills took prey while hovering more than twice as often as any other species. They used hovering and gleaning in nearly equal proportions, but frequently hovered at the outer foliage before landing to glean. Apart from when taking prey, it appeared that Weebills hovered to search the outer foliage for prey. To a lesser extent this was done also by Striated Thornbills, but the frequency with which birds hovered other than to take prey was not recorded. Hovering by Striated Thornbills commonly precedes hang-gleaning behaviour (HR pers. obs.). Little Thornbills and *Gerygone olivacea* were observed to hover only when taking prey. The latter took most of their prey by snatching (53% of observations). Weebills, Striated and Little Thornbills snatched more frequently in spring than winter.

Little Thornbills and Weebills foraged higher (mean foraging height > 8 m) than Striated Thornbills and *Gerygone olivacea* (< 8 m). This difference was consistent in all sizes of trees (i.e. sapling, understorey and canopy trees) with Little Thornbills and Weebills foraging in the higher vegetation and Striated Thornbills and *Gerygone olivacea* foraging in the lower vegetation (HR unpubl. data). There was a tendency for Little

Thornbills and Weebills to forage higher in the spring than winter but differences were not significant (t -test, $P > 0.05$).

Discussion

Strong differentiation between tree species as foraging substrates is shown by Acanthizidae in open-forest near Sydney (Recher 1989; this study). Weebills, Little and Striated Thornbills and *Gerygone olivacea* took prey from Narrow-leaved Ironbark foliage more often than expected in winter and spring. Grey Box foliage was used less often than expected. In spring Weebills, Little Thornbills and *Gerygone olivacea* also foraged more often on Forest Red Gum than expected from the amount of Forest Red Gum foliage available. Weebills also selected Forest Red Gum in winter as a preferred foraging substrate. Forest Red Gum is an uncommon tree at Scheyville (6% of eucalypt canopy foliage and 8% of trees). Because of the difficulty of finding enough gum trees for sampling and the large amount of work required to sample the more abundant eucalypts, invertebrate populations were not measured on Forest Red Gum and it is not possible to associate the use of this species with food type or abundance. However, the frequent use of this tree as a foraging substrate by Weebills and other species suggests that lerp-producing psyllids (see below) and other invertebrates were abundant on Forest Red Gum foliage.

Weebills and Striated Thornbills are eucalypt specialists and may be dependent on lerp-producing psyllid insects as an energy source (Woinarski 1985a,b; Recher *et al.* 1987; Recher 1989). Psyllids were generally more abundant on Grey Box than Narrow-leaved Ironbark foliage, but densities (numbers/cm²) were generally greater on Narrow-leaved Ironbark (Table 1). In addition the dispersion of psyllids and other insects was

Table 3 Foraging behaviour of Acanthizidae at Scheyville, New South Wales, during winter (W) and spring (S) in 1985.

Bird species	Prey attack behaviour (%)											
	Glean		Hang-glean		Snatch		Hover		Hawk		No. obs.	
	W	S	W	S	W	S	W	S	W	S	W	S
Little Thornbill	71	64	3	0	12	21	11	11	4	4	130	145
Striated Thornbill	49	52	38	16	4	14	7	17	2	1	141	151
<i>Gerygone olivacea</i>	*	29	*	0	*	53	*	13	*	5	*	95
Weebill	32	34	5	3	16	22	47	38	0	3	75	125

* absent from area in winter.

more variable (i.e. more clumped or patchy) on Narrow-leaved Ironbark than Grey Box (Table 1; also see Majer *et al.* 1989).

The more frequent use of Narrow-leaved Ironbark than Grey Box foliage as foraging substrates by Weebills and Striated Thornbills may therefore be related to the densities and dispersion of psyllids (Recher *et al.* 1991). Although an individual Grey Box leaf is more likely to have lerp, there may be significant advantages in searching for lerp on Narrow-leaved Ironbark, where their clumped distribution on branches may allow large numbers of leaves to be scanned rapidly. Psyllid insects commonly occur in small colonies (HR pers. obs.). Thus, when lerp is located on Ironbark with its clumped foliage, it is more likely to be a larger patch than on Grey Box. If a species is capable of rapidly locating these patches, it pays to specialise on the resource because it has the effect of minimising search times and maximising rewards (MacArthur & Pianka 1966). As a behaviour, hovering at the outer foliage of a tree may be an effective way to search large numbers of leaves and rapidly locate prey.

However, hovering is energetically expensive and for this reason is primarily associated with small birds (e.g. hummingbirds) that exploit abundant, energy-rich foods, such as nectar (see Collins & Paton 1989 for a review). The energetic cost of hovering increases almost linearly with size (Tucker 1974 in Collins & Paton 1989). The small size of Weebills (mean weight of 5.1 g) and their frequent use of hovering to search for and take prey from the terminal foliage of eucalypts may be an adaptive strategy for the exploitation of energy-rich patches of lerp that are unavailable to larger birds because of the absence of suitable perches. Collins & Paton (1989) point out that one reason hummingbirds may hover at flowers is the absence of suitable perches from which to probe the flowers. A second reason is that hovering allows rapid movement between flowers (Collins & Paton 1989). Evidence for each of these explanations of hovering among nectarivores is equivocal.

Weebills are smaller than any other birds with which they co-exist and which might also forage on lerp. Among the acanthizids, Little Thornbills weigh an average of 5.9 g, Striated Thornbills 6.7 g and *Gerygone olivacea* 7.7 g (data from Recher 1989). Each of these species hovers less often than Weebills, although the larger Striated Thornbill hovers more often than the Little Thornbill (HR unpubl. data; Table 3). The large (8-10 g, Recher *et al.* 1985) Striated and Spotted Pardalotes *Pardalotus striatus* and *P. punctatus* that

Woinarski (1985) described as lerp specialists, also occur with Weebills. Pardalotes rarely hover (< 5% of observations) and take prey from foliage primarily by gleaning (> 75% of observations) (Ford *et al.* 1986, Recher *et al.* 1985, Woinarski 1985a). Silvereyes *Zosterops lateralis* (10 g) and *Melithreptus* honeyeaters (15 g) are the next largest foliage gleaners commonly occurring with Weebills. *Zosterops* and *Melithreptus* spp. take lerp (HR pers. obs.), but rarely hover (< 1% of observations) (Recher *et al.* 1985; Ford *et al.* 1986). While several species use lerp as an energy source, only Weebills, and to a lesser extent Striated Thornbills, specialise on the outer foliage of eucalypts where foraging perches are absent.

The strong selection of Narrow-leaved Ironbark foliage as a foraging substrate by Weebills at Scheyville can therefore be explained in the following way. Invertebrates, and in particular lerp-forming psyllids, are abundant, but patchily distributed, on Narrow-leaved Ironbark foliage. The absence of suitable perches precludes all but the smallest birds from foraging on the outermost foliage of Narrow-leaved Ironbark. Because of their small size, Weebills can rapidly explore the outer foliage by hovering and either landing to glean lerp from the leaves or removing it while in flight. Rapid exploration of large numbers of leaves is probably necessary for the efficient utilisation of a patchily distributed resource such as lerp on Narrow-leaved Ironbark foliage. Invertebrates and lerp-forming psyllids are less abundant per unit leaf area (i.e. the density of invertebrates is less) and invertebrates are more evenly distributed on Grey Box (Table 1; Majer *et al.* 1989, 1994). This means that hovering as a searching and prey-attack strategy becomes too costly in terms of energy expenditure relative to energy gain and explains the limited use of Grey Box foliage by Weebills.

The absence of perches on the outer foliage of Narrow-leaved Ironbark may pose less of a problem to Striated Thornbills than to similar sized species. Striated Thornbills have stronger grasping abilities with their feet than other acanthizids that, combined with shorter legs, a wide foot-span and deeply curved claws, enables them to forage by hang-gleaning from leaves and small twigs (Bell 1985). Striated Thornbills mainly hover to search for prey on the outer foliage and land to glean or hang-glean (HR pers. obs.). Such behaviour minimises energy costs while allowing the birds to exploit the same energy-rich patches of lerp which are available to the smaller Weebills. Competition between these two species for this resource is minimised by their spatial

segregation within the forest profile. Throughout most of the year Weebills forage higher than Striated Thornbills (Recher 1989; this study). Perhaps more importantly, Striated Thornbills rarely forage at exposed canopy vegetation and remain within the canopy or understorey. Foraging Weebills, by contrast, most commonly forage at the outer foliage of the canopy where they are in the open (HR pers. obs.).

Little Thornbills and *Gerygone olivacea* are not eucalypt specialists nor are they dependent on lerp in the same sense as Weebills and Striated Thornbills (Recher 1989). Thus, the differentiation between Narrow-leaved Ironbark and Grey Box foliage by Little Thornbills and *Gerygone olivacea* while foraging (Table 2) is probably related to the greater densities of invertebrates on Narrow-leaved Ironbark than Grey Box (Table 1) rather than any differences in the abundances or dispersion of psyllids. The selection of plant species by this group of foliage-gleaning birds therefore appears to be a function of both invertebrate abundances and dispersion as well as foliage morphology and vegetative structure (see Holmes & Robinson 1981; Robinson & Holmes 1984). Changes in the proportions of less active (e.g. gleaning) and more active (e.g. snatching) foraging behaviours from winter to spring are probably associated with increases in the abundances of invertebrates, particularly large insects (Recher *et al.* 1983; Recher & Majer unpubl. data).

Acknowledgments

This research was conducted while the senior author was employed at the Australian Museum, Sydney. Lyn Albertson, Nick Carlisle, Greg Gowing, Stuart Little and Paul O'Connor assisted with fieldwork and sorting invertebrates. Greg Gowing was responsible for coordinating the collection and sorting of invertebrate material. We are particularly grateful for his contribution to our research. Hugh Ford and Adrian Stokes reviewed the manuscript for us and made many helpful suggestions, as did Mike Brooker, Peter Cale and Peter Woodall in their capacity as referees. Research on the ecology of eucalypt canopy invertebrates has been supported by grants from the Australian Research Council to J.D. Majer and H.F. Recher.

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