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The Foraging Ecology of Birds of Eucalypt Forest and Woodland. I. Differences Between Males and Females

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Summary: For six of nine species of sexually dichromatic, insectivorous birds of eucalypt forest, there were significant intersexual differences in foraging ecology. The most pronounced differences between sexes were in foraging height distribution (five species). Three species showed differences between the sexes in the behaviour used to capture prey, while males and females of four species differed in their use of foraging substrates. Differences were most pronounced among bark-foragers and least among ground-foragers. Intersexual differences in foraging by eucalypt forest birds appear to be a general phenomenon and one that is not necessarily associated with morphological differences nor with differences in reproductive roles. Among species with little morphological difference between the sexes, divergence between the sexes in foraging is most easily accomplished by foraging at different heights. This exposes each sex to a different array of substrates and leads to the use of different prey-attack behaviours. Ground-foragers do not have these options and therefore show little or no difference between the sexes in foraging ecology. Foraging data were obtained from three plots which differed in vegetation structure and floristics. Often differences in foraging ecology between plots were more pronounced for one sex, and males and females did not always change their foraging behaviour to the same extent or in the same direction. Combining the data from the different plots reduced the differences between the sexes in foraging ecology. Differences in the response of males and females to changes in habitat structure or resource availability may be an attribute of male/female differences in foraging behaviour, but such differences cannot be quantified from studies at a single location or time.

Among birds, males and females often use different foraging substrates, forage at different heights, use different foraging behaviours, or occupy different habitats (Selander 1966, 1972; Myers 1981; Holmes 1986; Shine 1989; Ornat & Greenberg 1990). Consequently they take different prey or exploit different parts of the same prey population. These differences are most pronounced among species that are sexually dimorphic with one sex much larger than the other or having a different sized or shaped bill (Selander 1966,1972; Mueller & Meyer 1985; Shine 1989). There may also be intersexual differences in wing length, wing shape, and/or structure of the leg and foot associated with different kinds of foraging behaviours (Nystrom 1991; Hunt & McLean 1993). However, species with males and females of similar size and without substantial differences in foraging morphology may also exhibit sexual differences in foraging ecology (Morse 1968; Holmes 1986). If there are advantages in males and females using different resources, either to reduce intersexual competition or to broaden the resource base for reproductive units thereby improving reproductive success, differences in the foraging of males and females should be expected.

Among insectivorous birds of eucalypt forests and woodlands in Australia, intersexual foraging differences have been reported for Golden Whistlers *Pachycephala pectoralis* (Bell 1986; Marchant 1992; Wheeler & Calver 1996), Rufous Whistlers *P. rufiventris* (Recher & Davis 1997), Varied Sittellas *Daphoenositta chrysoptera* (Orange-winged Sittella), White-throated *Cormobates leucophaeus* and Red-browed *Climacteris erythrops* Treecreepers (Noske 1986). The treecreepers and sittella are specialised bark-foragers, while the whistlers snatch prey from foliage and bark (Recher et al. 1985; Ford et al. 1986; Recher & Davis 1997; Mac Nally 2000). Northern Hemisphere studies have shown that intersexual foraging differences are common among bark-foragers (Ligon 1968; Morrison & With 1987; Suhonen & Kuitunen 1991a, b) but also occur among foliage gleaners and other insectivores (Morse 1968; Holmes 1986). In contrast, Mac Nally (2000) concluded there was an absence of gender-specific differentiation among foraging male and female Golden and Rufous Whistlers, and Rose Robins *Petroica rosea* in upland eucalypt forest in the Dandenong Ranges, Victoria.

During studies of the foraging ecology of eucalypt forest and woodland bird communities (see Recher et al. 1985), we obtained data for nine species where

plumage differences (sexual dichromatism) separated adult males and females. Apart from plumage, none of these species is obviously sexually dimorphic. That is, neither sex is obviously (visibly) larger than the other, or has an obviously different sized or shaped bill, wing, tail, leg or foot.

The nine species are typical members of four of the eight foraging guilds identified for the forests studied (Recher et al. 1985; Holmes & Recher 1986). As in the study by Holmes (1986), this provides an opportunity to present information on the generality of intersexual foraging differences among an ecologically diverse array of forest bird species. We also compare intersexual and intrasexual differences in foraging behaviour in structurally different, but nearby, habitats.

Study area and methods

Bird foraging behaviour was studied during the spring and summer of 1980–81. Three study areas, Plots 1, 2 and 3, were located at Bondi (36°08′S, 149°09′E; 850 m asl) on the Southern Tablelands of New South Wales. Plots were 10 ha in area and within 5 km of each other. The plots are described in Recher et al. (1983, 1985).

Briefly, Plots 1 and 2 were mostly regrowth forest and woodland 20 to 80 years old with a scattering of mature and senescent trees. Both were grazed and timber removed for fencing. Plot 3 was located in an extensive area of mature forest with no evidence of recent logging or grazing. About half of plot 1 was a Snow Gum *Eucalyptus pauciflora* and Black Sallee *E. stellulata* woodland with the remainder being forest dominated by Narrow-leaved Peppermint *E. radiata*, Swamp Gum *E. ovata* and Manna Gum *E. viminalis*. Plot 2 had a Snow Gum/Black Sallee woodland along one side but was otherwise fairly uniform forest dominated by Mountain Gum *E. dalrympleana* and Narrow-leaved Peppermint. Plot 3 was dominated by Mountain Gum, Manna Gum, and Narrow-leaved Peppermint with some Brown Barrel *E. fastigata* and Monkey Gum *E. cypellocarpa*. Canopy height on plot 3 averaged 22 m and on plot 2 it averaged 16-17 m. Emergents reached 25 m on plot 2 and 40 m on plot 3. The woodland canopy on plot 1 averaged 10 m with the forest canopy varying from 15 to 30 m. The shrub layer on plots 1 and 2 was sparse, but on plot 3 it was well developed and rich in species.

The plots were censused monthly using a transect procedure with seasonal trends in avian abundance presented in Recher et al. (1983). Using the December counts, bird abundances for the three plots for December 1980 are presented in Table 1 (see also Recher et al. 1985 and Recher & Holmes 1985). Table 1 also provides a count of the number of nesting males and females on plots 1 and 2 based on colour marking and territory mapping (HFR unpubl. data). Banding and mapping was not done on plot 3. Individuals which foraged on the plots, but did not nest there, are not included in counts based on territory mapping. Abundances are an average of four, four hour transect counts covering the 10 ha area of each plot (for more details see Recher et al. 1983; Recher & Holmes 1985). Males and females were not distinguished during counts as most census observations were based on sound and not visual records. Averages underestimate the total number of birds using the plots. Moreover, as foraging data were collected from October through January, it is likely that many more individuals used the plots to forage than are represented in any of the estimates of abundance. Thus, the number of nesting individuals, together with the monthly census results, are a conservative estimate of the least number of birds for which foraging data were obtained.

Foraging data were collected by a number of observers who spent equal amounts of time on all parts of the plots. For each bird encountered, up to five consecutive foraging behaviours were recorded. A foraging manoeuvre was equated to an attempt to take or capture prey (a prey-attack) whether or not this was successful. Observers moved continuously through the plots and avoided recording data on the same individual on the same day. For each prey-attack, the following data were recorded; height of prey, substrate of prey, foraging manoeuvre, and species and sex of the bird. Terminology for foraging manoeuvres follows Recher et al. (1985). Manoeuvres which were difficult to distinguish in the field have been combined with similar foraging actions; thus, for some species, probe has been combined with glean, and hover combined with hawk. Manoeuvres that were combined occurred infrequently. Species were assigned to foraging guilds following Recher et al. (1985) and Holmes & Recher (1986).

Substrates were recorded in detail (e.g. small branch, < 2 cm diameter; large branch, > 2 cm; dead leaf) but for this paper have been combined into a smaller number of categories; foliage (leaves, twigs and flowers), bark (trunks and stems, branches and loose bark), air and ground. No distinction has been made between live and dead substrates and some substrates with fewer than five observations for a species have been

Table 1 Number of resident, nesting individuals of each sex on study plots 1 and 2 in December 1980 as determined by colour banding and territory mapping (HFR unpubl. data). For plot 3, where banding was not done, the mean number of individuals, males and females combined, recorded during four censuses of four hours duration in December 1980 is given. For comparison, the December census data (M + F) are also presented for plots 1 and 2 (data from Recher & Holmes 1985). Each plot is 10 ha.

Species	Number of individuals		
	Plot		
	1	2	3
Flame Robin			
M	3	8	no data
F	3	8	no data
M + F	7.6	13.1	3.6
Scarlet Robin			
M	4	2	no data
F	4	2	no data
M + F	4.3	1.3	0
Superb Fairy-wren			
M	3	2	no data
F	2	1	no data
M + F	5.0	4.8	0
Golden Whistler			
M	1	2	no data
F	1	2	no data
M + F	3.3	1.8	9.5
Rufous Whistler			
M	6	10	no data
F	6	10	no data
M + F	15.5	15.8	6.3
Satin Flycatcher			
M	3	7	no data
F	3	7	no data
M + F	6.6	4.3	4.8
Crested Shrike-tit			
M	1	1	no data
F	1	1	no data
M + F	1.8	0.5	5.6
White-throated Treecreeper			
M	2	2	no data
F	2	2	no data
M + F	6.3	6.6	8.3
Red-browed Treecreeper			
M	1	1	no data
F	1	1	no data
M + F	1.5	2.5	5.0

deleted. Foraging heights were estimated to the nearest metre, but were combined in categories representing average heights of vegetative layers across the three plots; ground and low shrubs (0-1 m), shrubs and the lower part of the understorey (1-6 m), understorey or subcanopy (6-10 m), canopy and emergents (> 10 m) (see Recher et al. 1985). In this paper, foraging height data are combined into heights less than and greater than 6 m (i.e. ground and shrub vegetation *v.* subcanopy and canopy vegetation).

Although consecutive foraging observations on the same individual are not independent, comparisons of the first or second recorded observation against all observations showed no significant differences (Recher & Gebski 1989). As in Recher et al. (1985), we have therefore used all observations in the comparison of differences in foraging behaviour. Chi-squared analysis was used to compare intrasexual foraging behaviour between plots, and to test for intersexual differences within plots.

Scientific nomenclature follows Christidis & Boles (1994), while vernacular names are kept consistent with previous publications.

Results

Table 2 combines the data from the three plots and compares the foraging behaviour of males and females for each of the species studied. Table 3 presents foraging height data and the number of foraging observations recorded for each sex on each plot.

Flame Robins *Petroica phoenicea*, Scarlet Robins *P. multicolor* and Superb Fairy-wrens *Malurus cyaneus* (Superb Blue Wren) were primarily ground-foragers which took their prey either by pouncing from a perch (Flame and Scarlet Robins) or by gleaning (Superb Blue Wren) (Table 2). Rufous Whistlers and Golden Whistlers foraged by snatching and gleaning prey from foliage and bark, while Satin Flycatchers *Myiagra cyanoleuca* took the majority of their prey by hawking. Crested Shrike-tits *Falcunculus frontatus* (hereafter Shrike-tit), White-throated Treecreepers and Red-browed Treecreepers foraged on bark invertebrates; the treecreepers by gleaning and probing, and the Shrike-tit by probing and tearing loose bark.

Using the combined data, there are few significant differences between males and females (Table 4). Male and female Rufous Whistlers differed in their use of substrates; males took more prey from foliage, while females took more prey from bark (Table 2). Males also

gleaned less often and snatched prey more often than females. In contrast, male Golden Whistlers hawked more often and gleaned less often than conspecific females. Female Red-browed Treecreepers gleaned more often and probed less often than males. Male Shrike-tits, Rufous Whistlers, and White-throated and Red-browed Treecreepers, foraged higher than conspecific females, while female Satin Flycatchers foraged higher than males (Tables 3 and 4).

Intrasexual differences between plots

Ground pouncers and gleaners There was a significant difference between plots for male and female Flame Robins in the use of foraging substrates and manoeuvres (Table 5). Both sexes took more prey from the ground on plot 1 than on plots 2 or 3. Comparing plot 1 to plot 2, males took more prey by hawking, while females hawked and snatched more often. On plot 3, males and females hawked and snatched prey more often and pounced less often than on plot 1, while taking more prey by snatching and less by pouncing than on plot 2. There was no difference in the foraging heights of males between plots (Table 5), but females foraged higher on plots 2 and 3 than on plot 1.

Table 2 Foraging behaviour of dichromatic bird species on the Southern Tablelands of New South Wales. Data are expressed as percent of prey-attacks for combined foraging manoeuvre and substrate for the three plots studied. The combined number of prey-attacks recorded for each sex for the three plots is given in parenthesis with the number of individuals given in Table 1.

Manoeuvre	Glean/probe			Snatch		Hawk/hover	Pounce	
Substrate	Foliage/twigs	Bark	Ground	Foliage/twigs	Bark	Air	Ground	Bark
Species and Guild (prey-attacks)								
Ground pouncers and gleaners								
Flame Robin								
M (434)	0	1	9	6	0	20	53	11
F (314)	0	1	11	6	0	19	53	11
Scarlet Robin								
M (305)	0	1	1	2	11	18	64	3
F (145)	0	2	1	3	7	11	73	1
Superb Fairy-wren								
M (484)	6	2	85	3	+	4		
F (299)	8	2	82	2	1	5	0	0
Foliage and bark snatchers								
Golden Whistler								
M (249)	4	9	2	59	11	14	0	1
F (276)	10	8	2	59	10	10	0	0
Rufous Whistler								
M (631)	10	7	0	53	17	15	0	0
F (315)	10	14	3	39	16	13	1	4
Hawkers								
Satin Flycatcher								
M (276)	0	1	0	29	6	63	0	0
F (132)	0	0	0	32	7	59	2	0
Bark gleaners and probers								
Crested Shrike-tit								
M (241)	2	98	0	0	0	0	0	0
F (113)	3	96	0	0	1	0	0	0
White-throated Treecreeper								
M (587)	1	97	2	0	0	0	0	0
F (274)	0	100	0	0	0	0	0	0
Red-browed Treecreeper								
M (295)	2	98	0	0	0	0	0	0
F (160)	0	94	3	0	3	0	0	0

Table 3 Foraging height distribution of sexually dichromatic birds on three study plots on the Southern Tablelands of New South Wales. Height distribution is shown as percent of prey attacks above and below 6 m. Sample size of each study plot and each sex shown in parenthesis (*n*). An estimate of the number of individuals on the plots in December 1980 is given in Table 1.

	Female			Male		
Plot	1	2	3	1	2	3
Ground pouncers and gleaners						
Flame Robin						
> 6 m	2	16	20	3	10	14
< 6 m	98	84	80	97	90	86
n	(137)	(138)	(44)	(71)	(286)	(81)
Scarlet Robin						
> 6 m	1	2	no birds	5	8	no birds
< 6 m	99	98	95	92		
n	(60)	(86)	(189)	(115)		
Superb Fairy-wren						
> 6 m	0	0	no birds	0	0	no birds
< 6 m	100	100	100	100		
n	(119)	(330)	(154)	(180)		
Foliage and bark snatchers						
Golden Whistler						
> 6 m	55	19	21	6	66	27
< 6 m	45	81	79	94	34	73
n	(82)	(27)	(161)	(34)	(58)	(155)
Rufous Whistler						
> 6 m	31	52	57	53	67	59
< 6 m	69	48	43	47	33	41
n	(81)	(231)	(14)	(184)	(378)	(69)
Hawkers						
Satin Flycatcher						
> 6 m	74	100	90	69	73	84
< 6 m	26	0	10	31	27	16
n	(63)	(16)	(52)	(131)	(60)	(84)
Bark gleaners and probers						
Crested Shrike-tit						
> 6 m	50	41	56	30	70	82
< 6 m	50	59	44	70	30	18
n	(10)	(27)	(71)	(50)	(125)	(56)
White-throated Treecreeper						
> 6 m	23	16	29	41	37	19
< 6 m	77	84	71	59	63	81
n	(66)	(119)	(90)	(75)	(275)	(242)
Red-browed Treecreeper						
> 6 m	32	42	50	24	36	10
< 6 m	68	58	50	76	64	90
n	(40)	(80)	(40)	(75)	(77)	(143)

Male and female Scarlet Robins used significantly different foraging manoeuvres on plot 1 compared to plot 2 (Table 5). Both sexes hawked and snatched prey more often and pounced less often on plot 2 than on plot 1. Consequently, both sexes took prey more often from the ground on plot 1 than on plot 2, but the differences in foraging heights were not significant. There are insufficient data from plot 3 for analysis.

Male and female Superb Blue Wrens took significantly more prey from foliage, bark and the air on plot 1 than on plot 2 where more than 90 % of prey were taken from the ground (Table 5). There were no differences in foraging manoeuvres or foraging heights between plots. There are insufficient data from plot 3 for analysis.

Foliage and bark snatchers Golden Whistlers used the same substrates and foraging manoeuvres, but foraged at different heights on the three plots (Table 5). Males foraged lower on plots 1 and 3 and higher on plot 2, while females foraged higher on plot 1 and lower on plots 2 and 3 than expected.

Male Rufous Whistlers differed in their use of substrates and foraging heights between plots, but not foraging manoeuvres (Table 5). They took fewer prey from foliage and more from bark on plot 1 than on plots 2 or 3. There was no difference in the use of substrates or foraging manoeuvres between plots by females. Both sexes foraged lower on plot 1 and higher on plot 2 than expected. There were too few observations of females on plot 3 for analysis.

Hawkers There were significant differences between plots in the use of substrates, foraging manoeuvres and heights by male Satin Flycatchers (Table 5). Males took more flying prey and less from foliage on plots 1 and 2 than on plot 3. They foraged higher, and hawked less often and snatched more often on plot 3 than plot 1. There were no differences in height distribution between plots 1 and 2 or plots 2 and 3. Foraging manoeuvres and heights of females did not differ between plots, but they took more prey in flight and less from foliage on plot 1 than on plot 3.

Bark gleaners and probers There were no significant differences in the use of substrates or foraging manoeuvres between plots by male Shrike-tits; there are insufficient data on females for analysis of substrates and foraging behaviours (Table 5). Males foraged higher on plots 2 and 3 than on plot 1, but not between plots 2 and 3. There was no difference in the foraging heights of females between plots (Tables 3, 5)

There were no significant differences in the use of

substrates by male White-throated Treecreepers between plots (Table 5). Females foraged more often on branches and loose bark on plot 1 than on plots 2 and 3. Both sexes differed in their foraging manoeuvres between plots (Table 5). Males gleaned more often and probed less often on plot 3 than plots 1 and 2, while females probed more often on plot 1 than on plots 2 and 3. Males foraged lower than expected on plot 3 and higher on plots 1 and 2. There was no difference in the foraging height distribution of females between plots.

There were significant differences between plots by male Red-browed Treecreepers in the use of substrates, foraging manoeuvres and heights (Table 5). Males foraged more often on branches and loose bark and less often on tree trunks on plots 2 and 3 than on plot 1, and more often on branches and less often on tree trunks on

Table 4 Differences between males and females of colour dimorphic bird species on the Southern Tablelands of New South Wales in the use of substrates, foraging manoeuvres, and foraging height. Data from the three plots have been combined and only significant chi squared values are presented.[1] The number of individuals for each plot is presented in Table 1, while the number of observations for each sex is presented in Table 3.

Guild	Ground pouncers and gleaners			Foliage and bark snatchers		Hawkers	Bark gleaners and probers		
Species	Flame Robin	Scarlet Robin	Superb Fairy-wren	Golden Whistler	Rufous Whistler	Satin Flycatcher	Crested Shrike-tit	White-throated Treecreeper	Red-browed Treecreeper
Substrate[2]	NS	NS	NS	NS	14.9***	NS	NS	NS	NS
Foraging manoeuvre[2]	NS	NS	NS	8.4*	7.5*	NS	NS	NS	9.4**
Foraging height[3]	NS	NS	NS	NS	22.3***	4.9*	4.1*	4.0*	22.5***

[1] NS (not significant), $P < 0.05$; significant, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$; [2] *d.f.* = 2; [3] *d.f.* = 1.

Table 5 Intrasexual differences of colour dimorphic bird species in the use of substrates, foraging manoeuvres, and foraging height between three plots on the Southern Tablelands of New South Wales using the chi-square test for heterogeneity.[1] The number of individuals on each plot is presented in Table 1, while the number of observations for each sex is given in Table 3. Only significant chi square values are given.

Species	Flame Robin	Scarlet Robin	Superb Fairy-wren	Golden Whistler	Rufous Whistler	Satin Flycatcher	Crested Shrike-tit	White-throated Treecreeper	Red-browed Treecreeper
Substrate									
Male	59.2*** *d.f.* = 6	30.7*** *d.f.* = 3	25.9*** *d.f.* = 3	NS	39.0*** *d.f.* = 4	16.5** *d.f.* = 4	NS	NS	66.4*** *d.f.* = 4
Female	40.2*** *d.f.* = 6	8.5** *d.f.* = 3	37.4*** *d.f.* = 3	NS	NS	8.6* *d.f.* = 3	ID	9.9* *d.f.* = 4	28.4***, *d.f.* = 4
Foraging manoeuvre									
Male	50.2*** *d.f.* = 6	19.8*** *d.f.* = 3	NS	NS	NS	14.2***, *d.f.* = 2	NS	18.8*** *d.f.* = 4	68.5*** *d.f.* = 4
Female	38.4*** *d.f.* = 6	10.8** *d.f.* = 3	NS	NS	NS	NS	ID	61.8*** *d.f.* = 4	NS
Foraging height									
Male	NS	NS	NS	41.4*** *d.f.* = 2	10.1** *d.f.* = 2	6.8* *d.f.* = 2	34.8*** *d.f.* = 2	24.9*** *d.f.* = 2	22.7*** *d.f.* = 2
Female	18.8*** *d.f.* = 2	NS	NS	31.1*** *d.f.* = 2	11.3** *d.f.* = 2	8.8* *d.f.* = 2	NS	NS	NS

[1] NS (not significant), $P > 0.05$; significant, * $P > 0.05$, ** $P > 0.01$, *** $P > 0.001$; ID, insufficient data for analysis. [2] Data are available from plots 1 and 2 only.

plot 2 than 3. Males probed more often and gleaned less often on plot 1 than plots 2 and 3, and probed more often on plot 2 than plot 3. They foraged higher on plot 3 and lower on plot 2 than expected. Female Red-browed Treecreepers differed between plots only in their use of substrates (Table 5). They foraged more often on tree trunks and less often on branches and loose bark on plot 2 than on plots 1 and 3.

Intersexual differences within plots

Ground pouncers and gleaners There were no significant differences in foraging behaviour between male and female Flame Robin or male and female Superb Blue Wrens on any plots (Table 6). Male Scarlet Robins used the same foraging manoeuvres and foraged at the same heights as females, but took more prey on plot 2 from air and bark, and less from the ground than females.

Foliage and bark snatchers There were no significant differences between male and female Golden Whistlers in the use of foraging substrates or foraging manoeuvres on any of the plots. However, females foraged higher on plot 1, and lower on plot 2 than males. There was no difference in foraging heights on plot 3.

There were no significant intersexual differences in the use of substrates or foraging behaviours by Rufous Whistlers on plot 1 (Table 6), but males took more prey from foliage and less from bark than females on plot 2. Males snatched more often and gleaned less often than females on plot 2, and foraged higher than females on plots 1 and 2 (Table 3). There were too few data for female Rufous Whistler on plot 3 for analysis.

Hawkers There were no significant differences in the use of substrates, foraging behaviours, or foraging heights between male and female Satin Flycatchers on any plots (Table 6).

Bark gleaners and probers Male Shrike-tits foraged significantly higher than females on plots 2 and 3, but both sexes used the same foraging substrates and foraging behaviours (Tables 3, 6).

Female White-throated Treecreepers foraged more often on branches and less on trunks than males on all plots. The differences were significant on plots 1 and 3, but not on plot 2 (Table 6). Males probed more often and gleaned less often than females on plots 2 and 3, and foraged higher than females on plots 1 and 2. Females foraged higher on plot 3, but the difference was not significant (χ^2 = 3.212, *d.f.* = 1, P = 0.07) (Tables 3, 6).

Female Red-browed Treecreepers foraged more often on trunks and less often on branches and loose bark than males on plot 2, but used branches more often

Table 6 Intersexual differences of colour dimorphic bird species in the use of substrates, foraging manoeuvres, and foraging height on three plots at Bondi on the Southern Tablelands of New South Wales. Males tested against females for each plot using chi squared with Yates correction; only signficant chi square values are given.[1] The number of individuals on each plot is presented in Table 1, while the number of observations for each sex is given in Table 3.

Species	Flame Robin	Scarlet Robin	Superb Fairy-wren	Golden Whistler	Rufous Whistler	Satin Flycatcher	Crested Shrike-tit	White-throated Treecreeper	Red-browed Treecreeper
Substrate[2]									
Plot 1	NS	NS	NS	NS	NS	NS	NS	12.6**	NS
Plot 2	NS	9.9**	NS	NS	44.8***	ID	NS	NS	7.3*
Plot 3	NS	ID	ID	NS	ID	NS	NS	14.3***	19.5***
Manoeuve[2]									
Plot 1	NS	NS	NS	NS	NS	NS	NS	NS	13.5*
Plot 2	NS	NS	NS	NS	12.9**	ID	NS	27.9***	8.7***
Plot 3	NS	ID	ID	NS	ID	NS	NS	5.5*	NS
Height[3]									
Plot 1	NS	NS	NS	21.9***	11.1***	NS	NS	4.7*	NS
Plot 2	NS	NS	NS	14.5***	12.9***	ID	12.1***	16.4***	NS
Plot 3	NS	ID	ID	NS	ID	NS	8.4**	NS	30.8***

[1] NS (not significant), $P < 0.05$; significant, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$; ID, insufficient data for analysis. [2] *d.f.* = 2. [3] *d.f.* = 1.

than males on plot 3 (Table 6). There was no difference in foraging manoeuvres of males and females on plot 3, but males probed more often and gleaned less often than females on plots 1 and 2. Females foraged higher than males on all plots, but the difference was only significant on plot 3 (Tables 3, 6).

Discussion

There is no single explanation for intersexual differences in foraging ecology (Selander 1966, 1972; Shine 1989). Males and females may forage differently to reduce competition between the sexes for limited food resources, to avoid or reduce aggressive interactions, to expand the range of resources available to a breeding unit, or because of differences unrelated to foraging (e.g. height of song perches for males, location of nests for females). For six of the nine species of birds analysed, males and females differed in some aspect of their foraging behaviour on at least one of the three study plots. Differences were most pronounced among bark-foragers and least among ground-foragers. Snatchers and hawkers showed intermediate levels of difference between the sexes. The most frequent differences between males and females were in foraging height (five species) and least in the foraging manoeuvres used to capture prey (three species). Males and females of four species differed in their use of substrates.

Combining the data from all plots reduced the number of significant differences between sexes, but males and females of five species differed in the heights at which they foraged. With the combined data, only male and female Rufous Whistler differed in their use of substrates. For Golden and Rufous Whistlers, and Red-browed Treecreeper there were also significant intersexual differences in the foraging manoeuvres used to take prey. Conversely, male and female Golden Whistlers used the same foraging manoeuvres on the different plots, but differed when the data were combined.

Intersexual differences within foraging guilds

Intersexual differences in foraging appears to be a general phenomenon and one that is not necessarily associated with obvious morphological or size differences, nor with differences in reproductive roles. Divergence between the sexes is easiest by height among species with little or no morphological divergence. This exposes each sex to a different array of substrates (e.g. bark *v.* foliage, large branches vs small) and leads to the use of different foraging manoeuvres. Ground-foragers are restricted to a single plane with few options for males and females to differ in substrate choice or foraging manoeuvre. Also, the horizontal patchiness of ground substrates and invertebrates probably occurs on too fine a spatial scale for species or sexes to specialise.

Intersexual differences among bark-foragers have been demonstrated for a range of taxonomically unrelated groups (e.g. Ligon 1968; Noske 1986; Morrison & With 1987; Suhonen & Kuitunen 1991a, b). Among bark-foragers, sexes segregate by height above the ground, type of substrate, and foraging manoeuvre. However, differences in height, substrate, and manoeuvre cannot be separated, as substrates (e.g. trunk *v.* branches, large trunk diameter vs small, bark type) and probably type of prey change with height. It is likely that differences in the foraging ecology of treecreepers is a response to structural differences in the vegetation (e.g. plant species, tree height, branching patterns) and bark morphology between different forest types.

Male White-throated Treecreepers foraged more on the trunks of trees, while females used branches more often. Males also tended to forage higher than females, possibly because they tended to stay on the trunk as they climbed up, while females moved out on to branches. Probably, because of thicker layers of bark and deeper crevices on trunks than on branches, males probed more often and gleaned less often than females, while females tended to exploit loose and flaking bark more often than the males. All the eucalypts on the plots decorticated bark from at least the distal sections of branches, but not necessarily from the trunk. Therefore, females foraging on branches may have encountered loose bark more frequently than males, which foraged mainly on trunks.

In contrast to White-throated Treecreepers, female Red-browed Treecreepers tended to forage higher than males. Noske (1986) who studied the foraging ecology of treecreepers on the Northern Tablelands of New South Wales also found that female Red-browed Treecreepers foraged higher than males while female White-throated Treecreepers foraged lower than males on one of his sites, but not the second. Male treecreepers used thicker branches than females and more often exploited dead substrates (Noske 1986). Noske explained these differences by suggesting that the longer bill and/or tongue of the males allowed them to exploit thicker bark substrates than the females. Males also dominate females, possibly forcing them to the

extremities of the trees in which they foraged (Noske 1986).

There is no simple explanation for the differences between the two species of treecreepers. However, on our plots, Red-browed Treecreepers foraged preferentially on eucalypts which decorticated bark along the length of the trunk, while White-throated Treecreepers used eucalypts with other bark types more frequently (Recher et al. 1985). Decorticating species of eucalypts (e.g. Monkey Gum, Ribbon Gum) were large, with long boles to the first branch. Possibly, male Red-browed Treecreepers dominated the best foraging sites on all plots by excluding females from the larger, lower branches on plots 1 and 2, and from the large, clear bole of trunks on plot 3. By doing this, males could forage longer on each tree relative to females. This would explain why females foraged higher than males and why the use of substrates changed between plots. The greater height to branches on plot 3 may also explain why male and female White-throated Treecreepers had a similar height range on plot 3 compared with plots 1 and 2.

Snatchers and hawkers have the widest range of opportunities to specialise with the possibility of males and females segregating by height, substrate, and foraging manoeuvre. In contrast to bark-foragers, snatchers and hawkers use a wide range of substrates including bark, foliage and aerial prey, and may forage on the ground. However, on the Southern Tablelands, intersexual differences among foliage snatchers and hawkers were primarily height related. As with bark-foragers, intersexual differences among snatchers and hawkers are not consistent between species or habitats.

Rufous Whistlers showed the greatest differences between sexes. Males foraged higher, snatched prey more often, and took more prey from foliage and less from bark than females on all plots; this probably reflects the distribution of these substrates with height. There were no significant differences between male and female Satin Flycatchers, while differences between male and female Golden Whistlers were inconsistent among plots. This contrasts with Bell (1986) who reported significant differences between wintering male and female Golden Whistlers in northern New South Wales.

Bell (1986) found that male Golden Whistlers foraged higher, took prey from foliage more often, and gleaned less often than females. Females took more prey from bark and snatched less often than males. That is, they were similar to Rufous Whistlers on the Southern Tablelands. Wheeler & Calver (1996) reported that male Golden Whistlers on Rottnest Island, Western Australia, foraged more often above 3 m than females. There were also differences in the proportion of foraging manoeuvres used by each sex. We found that male Golden Whistlers hawked more often, and gleaned and snatched prey less often than females, but this was not consistent. There was also a lack of consistency in foraging height differences; males foraging lower than females on plot 1 and higher on plot 2. Two reasons occur to us as to why the foraging height distribution of male and female Golden Whistler varied between plots. First, plots differed in the structure and composition of the vegetation and birds almost certainly responded to these differences by foraging differently (see Holmes 1986). Plot 2 lacked a shrub layer, whereas shrubs and subcanopy foliage were abundant on plot 3 and to a lesser extent on plot 1. Golden Whistlers commonly forage in the lower canopy and shrub layer (HFR pers. obs.) and may prefer these denser layers of vegetation to the more open canopy. If correct, this would explain the tendency for Golden Whistlers to forage lower on plots 1 and 3, and higher on 2. Second, some of the differences may be due to confusion between immature males in female plumage and adult females during data collection. This is particularly likely with Golden Whistlers where the identification of males which are still in a female-like plumage can be difficult.

Referring to Holmes (1986), Mac Nally (2000) points out that there is little evidence of consistent intersexual foraging differences among forest birds. As illustrated by the differences in foraging behaviour between plots reported here and the different results obtained for treecreepers and whistlers by Bell (1986), Noske (1986), Marchant (1992), Wheeler & Calver (1996), Recher & Davis (1997), Mac Nally (2000), and the present study, patterns of intra- and intersexual foraging behaviour are complex, and there is an element of inconsistency. They are also subject to differences in interpretation. For example, Mac Nally (2000) found that male Golden and Rufous Whistlers foraged higher than females, a result similar to that reported by others. However, he concluded that the magnitude of the differences was unlikely to be ecologically significant, whereas others would accept a statistical difference, albeit with broad overlap, as indicative of an ecological difference. This is particularly likely when the differences observed are consistent with theory as to why males and females of the same species should differ in their foraging ecology. While more information is needed on intersexual foraging

differences among eucalypt forest birds, there is no compelling reason to expect consistency when dealing with ecological attributes.

Almost certainly the behaviour of both sexes changes in response to resource availability and the changing structure and composition of the vegetation between habitats. There may also be a response to the presence or absence of conspecific individuals or other species; behaviour may change over time with changes in community composition, or with changes in the distribution and abundance of available prey. What is evident from our work and that of Mac Nally (2000) is the necessity to quantify male/female foraging behaviour in a range of habitats with different resources. We found that differences in foraging ecology between plots were often more pronounced for one sex, and males and females did not always change their foraging behaviour to the same extent or in the same direction; combining the data from the different plots reduced the differences between the sexes. Possibly, differences in the response of males and females to changes in habitat structure or resource availability are an attribute of male/female differences in foraging behaviour and need to be considered when attributing ecological importance. In any event, we can conclude that intersexual foraging differences cannot be quantified from studies at a single location or time.

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