

SPECIAL FEATURE Interspecific segregation and attraction in forest birds

Comparative foraging ecology of five species of ground-pouncing birds in western Australian woodlands with comments on species decline

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Abstract In this paper, we compare the foraging ecology of five Australian robins (*Petroica multicolor*, *P. goodenovi*, *Eopsaltria griseogularis*, *Microeca fascinans*, and *Melanodryas cucullata*) in woodlands of Western Australia. Australian robins are insectivorous and obtain the greatest proportion of their prey by pouncing from a perch to the ground. Data were collected at three different sites in eucalypt (*Eucalyptus*) woodland and two sites in acacia (*Acacia*) woodland. The species differed in habitat, structure of the ground substrates where prey were taken, proportion of foraging manoeuvres used, height of foraging perches and prey-attack distances, though there were broad overlaps in all foraging dimensions. Within a site, species were more similar to each other in their foraging behaviour and selection of foraging substrates than they were to conspecific individuals occurring elsewhere. This indicates that potential foraging behaviours were very broad, and their expression is determined by the characteristics of the habitat and available prey. At all sites, robins took prey from ground substrates characterised by a mosaic of bare soil, low ground vegetation, and litter. The smallest species, *P. goodenovi*, used lower perches than the other robins and probably searched for small prey which it located at short distances. *P. goodenovi* had the widest distribution and was the most abundant of the species studied. The implications of these findings for the conservation of ground-foraging birds in Australia are discussed.

Key words Foraging ecology, Ground-pouncing birds, Petroicidae, Threatened species conservation, Woodlands

Ground-foraging birds are common in Australian woodlands (Recher et al. 1985; Ford et al. 1986; Recher & Davis 1997, 1998). Among them are species which search for prey from a perch and pounce on ground-dwelling invertebrates and small vertebrates. This pouncing guild is comprised of such different birds as kingfishers (Alcedinidae), cuckoos (Cuculidae), Australian robins (Petroicidae), and butcherbirds (Artamidae), all of which are important components of bird communities in Australian woodlands and forests (Recher et al. 1985; Holmes and Recher 1986).

In this paper, we compare the foraging ecology of

five Australian robins (Scarlet Robin *Petroica multicolor*, Red-capped Robin *P. goodenovi*, Western Yellow Robin *Eopsaltria griseogularis*, Jacky Winter *Microeca fascinans*, and Hooded Robin *Melanodryas cucullata*) in eucalypt (*Eucalyptus*) and acacia (*Acacia*) woodlands of Western Australia. All are insectivorous and only rarely take small vertebrates and seeds (Barker & Vestjens 1990). Our objective is to describe the foraging behaviour of each species and the structure of the ground habitats from which they obtain prey. Previous studies of ground-foraging birds in Australia have considered the ground as a single substrate (e.g., Recher & Davis 1997, 1998), but the ground surface is a mosaic of vegetation, litter, bare ground and coarse woody debris. There is therefore the potential for ground-foraging birds to

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partition different parts of this mosaic and minimize competition for food resources on what is otherwise a single, horizontal plane. Thus, in considering the partitioning of foraging resources among ground-pouncing birds, our emphasis is on micro-habitat selection of ground substrates. Because ground-foraging birds are among the most threatened on the Australian continent (Recher 1999; Garnett & Crowley 2000), we conclude with comments on the reasons for their decline.

METHODS

1) Study Sites

Data were collected in Western Australia from June to October 1997 in Wandoo *Eucalyptus wandoo* and Powderbark Wandoo *E. accedens* woodlands in Dryandra State Forest (centred on 32°45'S, 116°55'E; 400 m asl) near the town of Narrogin; in mallee and Wheatbelt Wandoo/York Gum (*E. capillosa*/*E. loxophleba*) woodlands in Durrakoppin Nature Reserve near Kellerberrin (31°07'S, 117°13'E; 350 m asl); and in Salmon Gum/Gimlet/Morrel (*E. salmonophloia*/*E. salubris*/*E. longicornis*) woodlands at Yellowdine (31°22'S, 119°09'E; 400–450 m asl) east of Southern Cross. During July and August 1999, we collected data on ground-pouncers in woodlands dominated by *Acacia* spp. near Gascoyne Junction (25°03'S, 115°12'E; 150 m asl) and Mt Magnet (28°04'S, 117°20'E; 375–400 m asl). Sites were selected where birds, including ground-pouncers, were abundant.

None of the eucalypt woodlands in which we worked was grazed by domestic stock, nor had any been recently burnt. Winter rainfall in 1997 was average with good herbaceous and shrub growth on all sites. In contrast, the *Acacia* woodlands at Gascoyne Junction and Mt Magnet were grazed heavily by sheep, goats and cattle and had significant soil degradation and loss. This was particularly so for the Mt Magnet area. There was no evidence of recent fires. Both sites had had two seasons of above average rainfall. Where it survived grazing by domestic animals, ground vegetation in the acacia woodlands had an abundance of green foliage, flowers and seed.

2) Birds

Although we sought out as many different pairs and individuals as possible, we inevitably recorded data on the same individuals on more than one occasion. Appendix 1 presents the number of observed foraging manoeuvres for each species at each site and

the estimated minimum number of pairs for which data were obtained. In 1997, only Red-capped (RCR), Scarlet (SR), and Western Yellow Robins (WYR), and Jacky Winter (JW) were present at Dryandra. For comparison of foraging behaviour, we therefore include observations of Hooded Robins (HR) at Dryandra made in 1995 (Recher & Davis 1998; unpubl.), but these were not used in analyses as conditions between the years differed and the ground substrates around perches were not recorded in 1995. Jacky Winter and Red-capped Robin occurred at Durrakoppin and Yellowdine, but only Red-capped Robins were found at Gascoyne Junction. At Mt Magnet, Hooded and Red-capped Robins were present, but despite extensive searching only two pairs of Hooded Robins were found (Appendix 1).

All data were collected during the breeding season (August–October) and individuals were nesting or feeding fledglings at the time of observation. None of the data is from birds in their year of hatching. Morphological data were obtained from Baker et al. (1997; see Appendix 2).

3) Foraging Data

For each individual encountered, we recorded up to five consecutive foraging manoeuvres (prey-attacks) following the procedures and terminology of Recher et al. (1985). Following Recher and Gebski (1990), the first manoeuvre observed was not recorded; records commenced with the second manoeuvre observed. For each observation, we recorded species, sex (if known), foraging manoeuvre, perch height, height and substrate of prey, and horizontal distance along the ground to prey from perch (distance of attack). For some observations, perch height and/or the distance of attack was not recorded, usually because they were not seen clearly. For this reason, some sample sizes differ between tables.

4) Foraging Habitat

The habitats in which robins occurred were noted, but we did not quantify habitat attributes other than the ground substrates where prey were taken. We measured ground substrates used for foraging in the following way. As we followed foraging robins, perches from which a bird pounced to the ground were flagged with numbered, coloured tape so that they could be located later.

Within a three metre radius of each perch, we estimated percent cover of logs, coarse woody debris (e.g., branches, fallen dead shrubs), litter (e.g., dead

leaves, shed bark), bare ground, ground vegetation (grass, ferns and herbs), trees, and shrubs, and the number of trees and shrubs. The three metre radius was selected following earlier work (Recher and Davis unpubl.) which had shown that the average distance from perch to prey for ground-pouncers was within three metres for all species. In the work reported here, we assumed that the entire three metre circle around a perch was searched equally for prey.

As the measurements made were of superimposed layers of vegetation, debris and litter, total cover can exceed one hundred percent. Birds often moved short distances (<3 m) between perches, or pounced repeatedly from the same perch. We only recorded habitat data for successive pounces if the perches used were at least 6 m apart (i.e., no overlap of the 3 m radius circles around perches). Substrate measurements are therefore fewer than the recorded number of pounces.

5) Analysis

We used all observations in the comparison of differences in foraging behaviour and set the accepted level of significance at $P < 0.01$ to compensate for the lack of independence of some data (see Recher and GebSKI 1989 for a justification of these procedures). Some rare behaviours (<1% of observations) were grouped with more common behaviours: hovering manoeuvres were combined with hawk and probe was combined with glean. Some infrequent behaviours (1–5% of observations) (e.g., pounce bark, glean foliage) were grouped together as others and not included in analyses because of the large number of zero (nil) observations among species and sites.

As we could not always confirm the sex of individuals or for species which are not sexually colour dimorphic, data for males, females and individuals of unknown sex were combined.

All statistical tests were carried out using 'Statistica for Windows (Statsoft Inc. 1999). Loglinear analyses were used to compare foraging manoeuvres between plots and species. Differences between species and site in the use of substrates were not tested as inspection of the data showed a high correlation between foraging manoeuvre and substrate. Correlations were also calculated between perch height and distance of attack. Correlations were calculated separately for species and sites because of differences in the structure, height and floristic composition of the vegetation between sites.

Only the Red-capped Robin was present at all

sites, so the 3-way table showing foraging behaviour for all species at all sites was incomplete. However, it was possible to construct a complete 3-way table (species×site×foraging manoeuvre) for Red-capped Robin and Jacky Winter at Dryandra, Durrakoppin and Yellowdine. For Hooded and Red-capped Robins at Mt Magnet, and for Jacky Winter, Red-capped, Scarlet and Western Yellow Robins at Dryandra, 2-way tables (species×manoeuvre) were constructed.

MANOVA was used to test for differences between species and sites in two foraging attributes (perch height and attack distance) and four habitat attributes (% shrub cover, % bare ground, % ground vegetation and % litter, including coarse woody debris and logs). Prey height was excluded because of the high frequency of 0 height (i.e., the prey were on the ground).

Not every species was present at each site, so we first tested for differences between each species at each site. Jacky Winter and Red-capped Robin occurred at more than one site, so subsequent analyses tested for differences across sites for each of these. Dependent variables in MANOVA were screened for conformity to assumptions and transformed if necessary; perch height and attack distance were log-transformed to meet MANOVA assumptions and all percent data were arcsine transformed (Tabachnik & Fidell 1996). Initial multivariate tests used a significance level of $P < 0.01$, but univariate tests after an initial multivariate test was significant used $P < 0.05$.

The habitat attributes (% shrub cover, % bare ground, % ground plants and % litter) of each individual attack in which the bird pounced on ground-dwelling prey were also assessed using MANOVA (see Table 5 which includes omitted variables for completeness). The pattern of analyses follows that for foraging attributes.

The means of the habitat variables and the means of the foraging variables for each species at each location were standardised before being subjected to cluster analysis based on complete linkage and Euclidean distances. The distance matrix from the clustering exercise was then used in multi-dimensional scaling (MDS) to determine if distinct groups of species or locations could be classified on the basis of habitat and foraging variables. In MDS, the axes do not have a numerical value and are expressed simply as dimensions without units (i.e., a visual picture) and are not proportional to the variances described.

Table 1. Foraging behaviour of ground-pouncing robins at five sites in *Eucalyptus* and *Acacia* woodlands in Western Australia: Red-capped Robin (RCR); Scarlet Robin (SR); Jacky Winter (JW); Western Yellow Robin (WYR); Hooded Robin (HR). Numbers are percent of combined manoeuvre/substrate prey attacks. Sample size is given in parenthesis. See Appendix 1 for the number of pairs for which data were recorded.

Manoeuvre Substrate	Foraging behaviour					Others ²	
	Pounce Ground	Glean Ground·····Bark	Hawk Air	Snatch Foliage·····Bark			
A. EUCALYPTUS Woodlands							
Dryandra							
RCR (158)	74	6	1	6	4	6	3
SR (189)	80	1	3	5	7	3	1
JW (206)	64	0	0	15	10	10	1
WYR (198)	93	0	0	2	2	1	2
HR (41) ¹	80	0	15	0	5	0	0
Durrakoppin							
RCR (75)	83	1	1	7	5	1	2
JW (86)	52	0	7	25	1	15	0
Yellowdine							
RCR (55)	38	5	11	35	0	2	9
JW (73)	29	0	1	55	4	11	0
B. ACACIA Woodlands							
Gascoyne							
RCR (69)	59	0	6	20	10	1	4
Mt Magnet							
RCR (92)	79	3	9	4	1	1	3
HR (66)	89	0	0	2	3	0	6

¹ 1995 data adapted from Recher and Davis (1998); ² includes glean foliage, pounce bark

RESULTS

1) Foraging manoeuvres and substrates

Table 1 combines the substrate of the prey with the foraging manoeuvre of the bird for the most common foraging behaviours. Except at Yellowdine, ground-pouncing was the most frequent foraging behaviour recorded and ground was the most common foraging substrate (Table 1). Hawking insects from the air and snatching prey from foliage and bark were the next most common behaviours and were the most frequent behaviours at Yellowdine. Red-capped Robins often gleaned prey, usually from the ground or bark, as did Hooded Robins at Dryandra in 1995 (Table 1). Red-capped robins sometimes hopped along the ground and gleaned prey from the soil surface, litter and low (<2 cm high) vegetation. At Yellowdine, 5% of prey taken by Red-capped Robins were gleaned from the foliage of ground vegetation. Birds hopping on the ground also snatched prey from low vegetation or hawked it from the air.

Loglinear analysis of the 3-way table (species×

site×foraging manoeuvre) for Red-capped Robins and Jacky Winters fitted a model involving significant 2-way interactions between behaviour and species ($\chi^2_3=49.29$, $P<0.01$) and between behaviour and site ($\chi^2_6=201.16$, $P<0.01$). A higher proportion of Jacky Winter foraging behaviour was spent in hawking insects from the air and less pouncing to the ground than for Red-capped Robin. At Yellowdine, both hawked more frequently and pounced less often than elsewhere (Table 1).

At Dryandra, there was a significant difference in foraging manoeuvres between bird species ($\chi^2_4=18.05$, $P<0.01$). Western Yellow Robins differed from other robins by taking almost all prey by pouncing (93%) and rarely snatching, hawking or gleaning (Table 1). Jacky Winters hawked and snatched prey more frequently than Scarlet and Red-capped Robins. In a 2-way comparison, there was no difference between Red-capped and Scarlet Robins ($\chi^2_3=3.52$, $P>0.25$).

At Mt Magnet, there was no significant difference in foraging manoeuvres between species ($\chi^2_6=3.94$,

Table 2. Mean perch height and attack distance in meters for five species of ground-pouncing robins at five sites in Western Australian woodlands: Red-capped Robin (RCR), Scarlet Robin (SR), Jacky Winter (JW) and Western Yellow Robin (WYR). Standard deviation shown in parenthesis. Hooded Robin (HR) data for Dryandra were obtained in 1995 (Recher and Davis unpubl.). Heights and distances are for ground-pouncing foraging manoeuvres only. Perch height and/or attack distance were not always recorded, while dashes indicate the species was absent from that site.

Species	Site				
	Dryandra	Durrakoppin	Yellowdine	Gascoyne Junction	Mt Magnet
RCR					
No. observations	117	62	22	36	34
Perch height	1.2 (1.0)	1.3 (0.8)	1.5 (1.3)	1.3 (1.1)	0.8 (0.5)
Attack distance	1.9 (1.7)	1.5 (1.3)	3.6 (3.0)	1.8 (1.9)	1.5 (1.3)
SR					
No. observations	53	–	–	–	–
Perch height	1.5 (1.0)	–	–	–	–
Attack distance	2.6 (2.1)	–	–	–	–
JW					
No. observations	129	45	22	–	–
Perch height	1.5 (1.0)	2.1 (1.1)	1.9 (1.6)	–	–
Attack distance	2.3 (1.8)	2.8 (1.8)	3.6 (3.7)	–	–
WYR					
No. observations	83	–	–	–	–
Perch height	1.5 (0.9)	–	–	–	–
Attack distance	2.5 (2.2)	–	–	–	–
HR					
No. observations	15	–	–	–	52
Perch height	2.1 (1.1)	–	–	–	1.1 (0.8)
Attack distance	3.7 (1.7)	–	–	–	2.3 (2.5)

$p=0.03$). However, gleaning comprised 12% of foraging manoeuvres for the Red-capped Robin, but the Hooded Robin did not glean (Table 1).

Red-capped Robins used similar proportions of foraging manoeuvres and substrates at Dryandra and Durrakoppin ($\chi^2_3=1.68$, $P>0.5$), but they pounced less, and hawked and gleaned more at Yellowdine than at Dryandra and Durrakoppin ($\chi^2_3=46.37$, $P<0.01$) (Table 1). Red-capped Robins at Gascoyne Junction pounced less and hawked and snatched more than at Mt Magnet ($\chi^2_1=7.49$, $P<0.01$) (pounce vs all other behaviours combined).

There was no difference in the behaviour of Jacky Winters between Dryandra and Durrakoppin ($\chi^2_1=3.37$, $P>0.1$) (pounce vs all other behaviours combined), but birds at Yellowdine pounced less and hawked more than at the other sites ($\chi^2_4=42.47$, $P<0.01$) (glean and other' categories deleted) (Table 1).

The behaviour of Hooded Robins at Dryandra in 1995 was similar to that of Hooded Robins at Mt

Magnet in 1999, but the Dryandra birds took 15% of their prey by gleaning bark. At Mt Magnet, Hooded Robins took 6% of prey by gleaning foliage (Table 1).

2) Perch height and distance of attack

Although robins occasionally took prey at distances exceeding six metres, most prey were taken within three metres of the perch from which it was sighted (Table 2). Except for Red-capped Robin at Yellowdine, 10 of the 11 species/site comparisons of perch height and attack distance were significantly correlated: the higher the perch, the greater the distance at which prey were attacked (Table 3). For six of the seven comparisons possible, robins used higher perches when hawking than for ground pouncing (Table 4). However, sample sizes were small and the differences were not always significant (Table 4).

Initial MANOVA at Dryandra found that species differed significantly (Wilks lambda_(21,1404)=0.97, $P<0.001$). Univariate tests revealed that these differ-

Table 3. Correlation coefficients between perch height and distance of attack for Red-capped Robin (RCR), Scarlet Robin (SR), Jacky Winter (JW), Western Yellow Robin (WYR), and Hooded Robin (HR) at five sites in eucalypt and acacia woodlands in Western Australia during 1997 and 1999. Data includes all available foraging behaviours including ground-pouncing and hawking (sally). Sample size is in parenthesis. (**P<0.001, *P<0.01, NS – not significant, P>0.01). Dashes indicate species was absent from that site in 1997.

Species	Site				
	Dryandra	Durrakoppin	Yellowdine	Gascoyne Junction	Mt Magnet
RCR	0.39**(130)	0.62**(62)	0.32 (NS)(41)	0.71**(41)	0.46**(56)
SR	0.30**(165)	–	–	–	–
JW	0.31**(163)	0.66**(45)	0.82**(21)	–	–
WYR	0.45**(188)	–	–	–	–
HR	–	–	–	–	0.70**(53)

Table 4. Mean perch heights of ground pouncing robins compared to the perch heights of robins hawking and snatching. Species and sites without perch height data for hawking and snatching robins have been deleted. All P-values are significant using P=0.0014, after Bonferroni correction from an initial P of 0.01.

Site	Species	GP Ht	Hawk Ht	t	P
Dryandra	RCR	1.15 (106)	1.08 (4)	$t_{(88)}=0.13$	0.89
	SR	1.63 (137)	2.52 (4)	$t_{(139)}=1.62$	0.11
	JW	1.51 (134)	3.26 (34)	$t_{(166)}=4.92$	<0.0001
Durrakoppin	JW	2.10 (45)	3.18 (20)	$t_{(63)}=3.32$	0.001
Yellowdine	RCR	1.47 (290)	5.13 (18)	$t_{(35)}=7.34$	<0.0001
	JW	1.90 (22)	4.82 (41)	$t_{(61)}=3.04$	0.003
Gascoyne	RCR	1.26 (36)	2.61 (7)	$t_{(41)}=3.19$	<0.003

ences were related to differences in perch height ($F_{3,642}=4.53$, $P<0.01$) and attack distance ($F_{3,642}=3.23$, $P=0.02$). Red-capped Robins used lower perches and attacked prey closer to the perch than co-occurring robins (Table 2). Scarlet Robins, Jacky Winters and Western Yellow Robins used the same height perches and attacked prey at similar distances (Table 2). At 2.1 m, the perch height of Hooded Robins at Dryandra in 1995 was greater than for other robins at Dryandra in 1997 (Table 2).

Initial MANOVA at Durrakoppin found strong differences between the species (Wilks lambda $_{2,104}=0.82$, $P<0.001$), while univariate tests revealed that these were caused by variation in perch height ($F_{1,105}=15.19$, $P<0.001$) and distance of attack ($F_{1,105}=21.24$, $P<0.001$). Red-capped Robins perched lower and attacked prey at closer distances than Jacky Winters (Table 2).

No significant interspecific differences in foraging attributes occurred at either Yellowdine or Mt Magnet at the 0.01 level (Wilks lambda $_{2,59}=0.90$, $P=0.045$;

Wilks lambda $_{2,119}=0.98$, $P=0.39$, respectively).

Initial MANOVA found significant differences between locations for Red-capped Robin (Wilks lambda $_{8,686}=0.81$, $P<0.001$), which univariate tests attributed to perch height ($F_{4,325}=15.48$, $P<0.001$) and distance of attack ($F_{4,325}=3.77$, $P=0.005$). Perch height at Yellowdine was markedly higher than other sites (Table 2). Attack distances varied considerably, with the greatest values at Yellowdine (Table 2). There were significant differences in the foraging attributes of Jacky Winter between Durrakoppin, Dryandra and Yellowdine (Wilks lambda $_{4,450}=0.94$, $P=0.005$), which univariate tests attributed to differences in perch heights ($F_{2,226}=7.26$, $P<0.001$). Perch heights at Durrakoppin and Yellowdine were similar, but higher than those at Dryandra (Table 2).

3) Characteristics of foraging habitat

Initial MANOVA at Dryandra found that species differed significantly (Wilks lambda $_{12,1307}=8.60$, $P<0.001$). Univariate tests revealed that these differ-

Table 5. Habitat characteristics of ground substrates of Western Australia eucalypt and acacia woodlands on which Red-capped Robin (RCR), Scarlet Robin (SR), Jacky Winter (JW), Western Yellow Robin (WYR), and Hooded Robin (HR) hunted for prey. Sample size (N) is shown in parentheses. Measurements are based on a three metre radius around the perch from which the bird attacked prey. Values are means \pm standard deviation.

Location	% Cover						
	Trees	Shrubs	Ground vegetation	Logs	Coarse woody debris	Litter	Bare ground
Dryandra							
RCR (122)	13 \pm 17	9 \pm 12	24 \pm 25	1 \pm 3	5 \pm 7	42 \pm 27	30 \pm 29
SR (140)	14 \pm 12	8 \pm 12	31 \pm 26	3 \pm 4	5 \pm 6	46 \pm 26	18 \pm 19
JW (111)	16 \pm 10	4 \pm 7	22 \pm 23	3 \pm 5	4 \pm 3	44 \pm 25	29 \pm 26
WYR (156)	17 \pm 16	10 \pm 14	21 \pm 22	4 \pm 5	3 \pm 5	57 \pm 28	17 \pm 19
Durrakoppin							
RCR (63)	15–20 ¹	8 \pm 13	47 \pm 24	3 \pm 6	no data ²	34 \pm 24	16 \pm 16
JW (48)	15–20 ¹	10 \pm 13	30 \pm 19	4 \pm 6	no data ²	41 \pm 21	25 \pm 23
Yellowdine							
RCR (20)	12 \pm 14	17 \pm 16	1 \pm 2	2 \pm 3	8 \pm 6	35 \pm 29	44 \pm 22
JW (27)	12 \pm 13	6 \pm 10	2 \pm 2	4 \pm 4	5 \pm 5	48 \pm 26	43 \pm 25
Gascoyne junction							
RCR (21)	10 \pm 20	15 \pm 13	13 \pm 11	1 \pm 2	6 \pm 5	21 \pm 19	59 \pm 21
Mt Magnet							
RCR (55)	15 \pm 20	14 \pm 14	14 \pm 16	0	2 \pm 3	23 \pm 16	59 \pm 19
HR (43)	21 \pm 22	5 \pm 6	16 \pm 12	0	3 \pm 4	18 \pm 16	62 \pm 19

¹ Range of projected canopy cover for study site as measured by HFR in 1986.

² At this site, coarse woody debris was included with litter as a single measure.

ences were caused by differences in % shrub cover ($F_{3,497}=6.75$, $P<0.001$), % bare ground ($F_{3,497}=13.45$, $P<0.001$), % cover of ground plants ($F_{3,497}=5.99$, $P<0.001$), and % litter cover ($F_{3,497}=7.75$, $P<0.001$). Jacky Winters used ground substrates with less shrub cover than other species (Table 5). Red-capped Robins and Jacky Winters selected substrates with more bare soil than either Scarlet or Western Yellow Robins (Table 5). The cover of ground vegetation was higher on the substrates used by Scarlet Robins, while Western Yellow Robins selected sites with a high proportion of litter (Table 5).

Initial MANOVA at Durrakoppin found strong differences between the species (Wilks $\lambda_{4,101}=0.86$, $P=0.003$). Univariate tests revealed that these were caused by variation in % cover of ground vegetation ($F_{1,104}=14.65$, $P<0.001$) and % of bare ground $F_{1,104}=7.03$, $P<0.001$). Red-capped Robins foraged on substrates with more ground vegetation than those used by Jacky Winters (Table 5). Jacky Winter substrates had proportionately more litter and bare soil.

Initial MANOVA at Yellowdine found no sig-

nificant differences between the species (Wilks $\lambda_{4,32}=0.75$, $P=0.054$), but the foraging sites frequented by Red-capped Robins had more shrubs and less litter than where Jacky Winters foraged (Table 5).

Initial MANOVA at Mt Magnet found strong differences between the species (Wilks $\lambda_{4,91}=0.78$, $P<0.001$). This was the result of higher shrub cover at the foraging locations used by Red-capped Robins compared with those used by Hooded Robins ($F_{1,94}=20.78$, $P<0.001$) (Table 5).

4) Intraspecific differences between sites

Initial MANOVA found significant differences between locations for Red-capped Robin (Wilks $\lambda_{16,837}=0.42$, $P<0.001$). Percentage shrub cover ($F_{4,227}=5.96$, $P<0.001$), % bare ground ($F_{4,227}=34.10$, $P<0.001$), % litter cover ($F_{4,227}=33.17$, $P<0.001$), and % ground vegetation ($F_{2,227}=10.05$, $P<0.001$) were significant univariate variables.

Ground foraging substrates used by Red-capped Robins at Durrakoppin had more ground vegetation than all other sites, and there was more ground vege-

tation at Dryandra than Yellowdine (Table 5). The differences in ground vegetation were not significant between Dryandra and the *Acacia* woodland sites, but Yellowdine had less ground vegetation than Gascoyne Junction and Mt Magnet. Shrub cover and the amount of bare soil were greater at Gascoyne Junction and Mt Magnet than at Dryandra and Durrakoppin (Table 5).

An initial MANOVA found significant differences in the attack characteristics of Jacky Winter between Durrakoppin, Dryandra and Yellowdine (Wilks $\lambda_{8,324}=0.70$, $P<0.001$). Percentage shrub cover ($F_{2,165}=9.02$, $P<0.001$) and % ground vegetation ($F_{2,165}=23.14$, $P<0.001$) differed across sites.

The ground foraging substrates used by Jacky Winters at Durrakoppin had greater shrub cover than those at Dryandra and Yellowdine (Table 5). For Jacky Winter foraging sites, ground cover was greater at Durrakoppin and less at Yellowdine than other sites. Correspondingly, the cover of litter and area of bare of soil was greater at Yellowdine (Table 5).

5) Foraging and Habitat Profiles

With the Red-capped Robin at Durrakoppin forming an outlier, there are three distinct groups of woodlands and species; Mt Magnet and Gascoyne Junction (*Acacia* woodlands), Yellowdine (Salmon Gum/Gimlet/Morrel eucalypt woodlands), and Dryandra/Durrakoppin (wandoo eucalypt woodlands) (Fig. 1). Individual species fit more neatly into location groupings than species groupings. That is, different species were more similar in their foraging and habitat pro-

files at the same location than to conspecifics at other locations. Thus, woodland type is more important than species in describing the foraging behaviour of ground-pouncing robins.

DISCUSSION

As with all studies which compare co-existing species within a foraging guild, there were broad overlaps between species in the frequency of foraging manoeuvres, perch heights and foraging substrates (e.g., MacArthur 1958; Recher 1989). However, as shown by Calver and Wooller (1981) and Wooller and Calver (1981a), overlap can be high in some resource dimensions, but when taken together the overlap falls. For this reason, Cody (1974) emphasised the need to consider all resource dimensions together when investigating the competitive relationships among co-existing species. The results presented here considered only resource use during the breeding season and at times when food was likely to be most abundant. Under these conditions, co-existing species may have very similar foraging ecology without necessarily competing for resources (Recher 1989; Wiens 1989). As food becomes less abundant, species become increasingly different in their use of resources (e.g., Recher 1989), a factor not considered in this study.

Despite this limitation, there were significant differences in foraging behaviour between co-occurring species at all sites. Jacky Winters tended to take more aerial prey than other robins, while Western Yellow

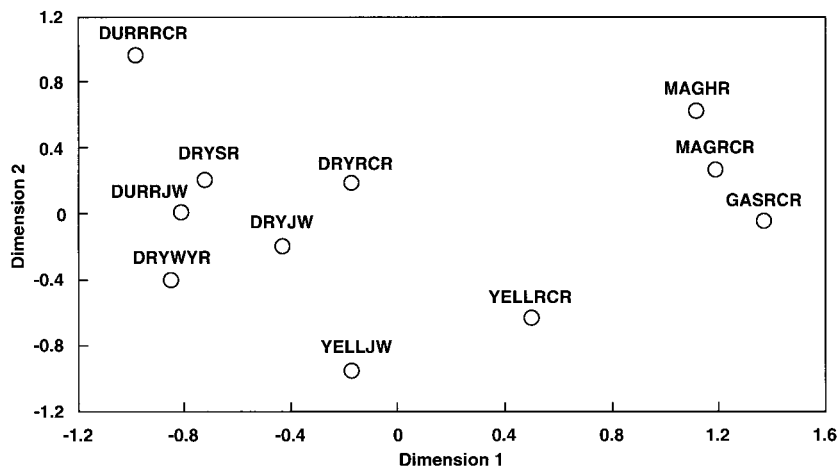


Fig. 1. Multi-dimensional scaling of foraging and habitat attributes for robins at six sites (four in eucalypt woodland and two in acacia woodland). The points are labelled with site and robin species. Sites: YELL (Yellowdine), GAS (Gascoyne Junction), MAG (Mt Magnet), DRY (Dryandra), DURR (Durrakoppin); Species: RCR (Red-capped Robin), SR (Scarlet Robin), JW (Jacky Winter), WYR (Western Yellow Robin), HR (Hooded Robin).

Robins pounced to the ground more frequently than others. Significantly, there was no difference in foraging behaviours between Red-capped and Scarlet Robins at Dryandra, which was the only site where these two species co-occurred. Of the species studied, Red-capped and Scarlet Robins are the most similar in appearance (both are red, black and white), although the Scarlet Robin is half again as large as the Red-capped Robin (Appendix 2).

Despite differences in foraging behaviour, the species studied relied primarily on prey taken from the ground or ground vegetation either by pouncing or snatching. It is therefore necessary to consider other aspects of their foraging ecology to fully appreciate how resources are allocated within this guild.

1) Habitat

While present at the same sites, there were broad habitat differences among the species studied. At Dryandra, Jacky Winters were most common in open Wandoo woodlands with widely spaced large trees and few shrubs. Western Yellow Robins were most often associated with Wandoo and Powderbark Wandoo woodlands on lateritic slopes with a patchy shrub layer to 1.5 m, although they also foraged in open Wandoo woodlands and Mallet *E. astringens* plantations. Red-capped Robins were most common in habitats dominated by sheoak *Allocasuarina* spp. and Jam Wattle *Acacia acuminata*, but also occurred in eucalypt woodlands. Scarlet Robins used Powderbark Wandoo and Wandoo woodlands and frequently occurred in association with Jarrah *E. marginata* and Marri *E. calophylla* which the other species avoided. Most Scarlet Robins were found in habitats with a moderate to dense shrub layer, but they also used Mallet plantations where there is no shrub layer.

The two most similar species at Dryandra, in terms of size, appearance and foraging behaviour, Red-capped and Scarlet Robins, have substantially different geographical distributions. Dryandra is one of the few places where they come into contact (Blakers et al. 1984; Saunders & Ingram 1995; Serventy & Whittell 1951). However, where they came into contact at Dryandra, Scarlet and Red-capped Robins were interspecifically territorial with Scarlet Robins being dominant (H. Recher unpubl. obs.).

At Durrakoppin, Red-capped Robins were most frequent in mallee (woodlands dominated by multi-stemmed eucalypts) and along the edges of Kwongan shrublands (floristically rich, sandy heathlands). Jacky Winters were restricted to Wheatbelt Wan-

doo/York Gum woodland with a patchy shrub layer. At Yellowdine, Jacky Winters were only found in tall Salmon Gum woodland with an extensive, low (to 1 m) shrub layer and broad open areas. Red-capped Robins were most abundant in Salmon Gum/Gimlet/Morrel woodlands with a shrub layer dominated by *Melaleuca* and *Acacia* species. At Mt Magnet, Red-capped Robins were restricted to dense Acacia shrublands, while Hooded Robins occurred in open woodland with widely spaced trees, shrubs and small patches of shrubby woodland. Red-capped Robins were restricted to dense Acacia shrublands at Gascoyne Junction, avoiding more open habitats and edges.

Although the three meter radius around foraging perches was too small to fully describe the habitats used by robins, at Dryandra where all species were present, there were significant differences between species in the percent cover of shrubs, ground vegetation, bare ground and litter. These differences largely reflected the different habitat types each species selected. Although less pronounced, similar differences occurred between Red-capped Robin and Jacky Winter at Durrakoppin and between Red-capped and Hooded Robins at Mt Magnet. In each instance, Jacky Winters and Hooded Robins frequented more open habitats than Red-capped Robins. This was also the case at Yellowdine where Jacky Winters and Red-capped Robins co-occurred, but the differences were not significant, possibly because of small sample sizes and the more uniform abundance of shrubs between habitat types.

2) Resource sharing of ground substrates

Within a site, species were more similar to each other in foraging attributes and the foraging substrates selected than they were to conspecifics at other sites. This indicates that potential foraging behaviours were very broad, but their expression was largely determined by the characteristics of the resource, which in this case are the attributes (structure) of the ground surface.

We conclude that co-existence by apportioning ground substrates is not possible within this group of birds. None of the species studied specialised in taking prey from ground vegetation, litter or bare ground. Instead, as described above, species are primarily segregated by habitat and secondarily by foraging behaviour and substrates.

This suggests that the availability (but not necessarily the abundance) of ground-dwelling prey within

the size range taken by these species is limited and likely to be easily depleted in the short-term. For this reason alone, ground-pouncing birds should segregate by habitat, use different foraging behaviours or differ in the size and type of prey when co-habiting. The interspecific territoriality between the Red-capped and Scarlet Robins at Dryandra, and between Scarlet and Flame Robins *P. phoenica* in southeastern Australia (Loyn 1980) is confirmation that very marked differences in size are required between ground-pouncing birds before they can co-exist. Other ground-pouncers, such as butcherbirds and kingfishers, which co-exist with the species studied, tend to be much larger and take many large prey including small vertebrates, use very different foraging behaviours (e.g., sweeping by woodswallows), or are prey specialists (i.e., cuckoos) (Baker & Vestjens 1990; Serventy & Whittell 1951; pers. obs.).

3) Sit and Search

Robins are sit and search predators, but move continually between perches often over long distances. Prey are visually located by a perched bird which then flies or drops to where the prey was seen. The area around a perch in which prey are located is a function of the height of the perch, the openness of the immediate habitat, and the behaviour of the bird. Some of the highest perches and attack distances were at Yellowdine where Jacky Winters and Red-capped Robins obtained a large proportion of their prey by hawking. The greater frequency of hawking also explains the higher perches and longer attack distances for Jacky Winters at Durrakoppin. At Dryandra, where most prey were taken by pouncing to the ground or by snatching prey from ground vegetation or the lower part of tree trunks, perch heights were lower and attack distances for Jacky Winter were smaller. The correlation between perch height and attack distance suggests that high perching birds may search for prey at longer distances, while low perching birds search close to the perch.

The frequent changing of perches, even when prey was taken, supports the suggestion that the availability of ground-dwelling prey is limited and that local resources (those around a perch or set of perches) are quickly depleted.

4) Perch height and prey size

There were differences in the height of perches selected by ground-pouncing robins and the distances at which they located and attacked prey. In particular,

the Red-capped Robin used lower perches and took prey at closer distances than the other robins. Presumably, as the smallest of the species studied, the Red-capped Robin takes the smallest sized prey (for examples of prey size choice, see Calver & Wooller 1981; Hespeneide 1971; Wooller & Calver 1981b) and so must be close to the ground to see them. Furthermore, they do not need to scan a large distance because small arthropods are proportionately more abundant than large ones (e.g., Janzen 1973; Majer & Recher unpubl. data). Larger robins presumably take larger prey and hence need to perch higher and scan larger distances to locate them.

By selecting small prey, Red-capped Robins may be able to exploit closed, shrub habitats more efficiently than the larger species. In turn, this may explain their relative abundance and wide distribution throughout Australia (Blakers et al. 1984). Robins using high perches in the denser habitats where Red-capped Robins are most frequent would have limited lines of sight and thereby be restricted in the area of substrate that could be searched for large prey either on the ground or in the air.

5) Implications for conservation

Many studies in Australia and overseas indicate that bird species assemblages co-exist by partitioning the food resource on the basis of one or more of prey type, foraging height, foraging substrate, or foraging behaviour (e.g., Cody 1974; Ford et al. 1986; MacArthur 1958; Recher 1989; Recher & Davis 1998; Wheeler & Calver 1996; Wiens 1989). If the basis of this partitioning is disrupted (e.g., by changes in available foraging substrates) then the pattern of partitioning could be expected to change, with possible loss of one or more species from the assemblage. Australian studies suggest that such changes have occurred and continue to occur, with past (Burbidge & McKenzie 1989; Recher & Lim 1990) and on-going implications for conservation (Recher 1999; Ford et al. 2001).

Although there were differences in the structure of ground substrates on which different species of ground-pouncers foraged, within a site all species selected foraging sites best described as a mosaic of bare ground, litter and ground vegetation. Disturbances, such as nutrient enrichment, which increase the extent and density of ground and shrub vegetation; frequent burning, which creates an open habitat with increased areas of bare ground and reduced amounts of litter; and, grazing by domestic animals,

which reduces the amount of ground and shrub vegetation (Arnold & Weeldenburg 1998), compacts the soil and increases the amount of bare ground (Abensperg-Traun et al. 2000) will disadvantage ground-pouncers. Among the consequences of these disturbances are decreased abundances and possible changes in the size distribution of terrestrial arthropods favouring smaller species (see Abensperg-Traun et al. 2000; Wooller & Calver 1988).

Such environmental changes appear to be responsible for the decline of ground-foraging birds throughout Australia (Garnett & Crowley 2000; Recher 1999). *Post hoc*, we predict that the impact should be greatest on the largest species of robins; those requiring large prey and relatively large areas of suitable substrate around each perch. This appears to be the case with Jacky Winter and Scarlet and Hooded Robins declining significantly in abundance and distribution throughout their range, while Red-capped Robins persist in relative abundance. Ultimately, however, as degradation of ground substrates in Australia intensifies with continued land clearing, weed invasion and over grazing, all species will be adversely affected. Conservation of this group of birds in Australia requires landscape scale changes in grazing and fire management practices to preserve the foraging resources and ground substrates which this study demonstrates are required by each species.

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REFERENCES

- Abensperg-Traun M, Smith GT & Main BY (2000) Terrestrial arthropods in a fragmented landscape: a review of ecological research in the Western Australian central wheatbelt. *Pac Conserv Biol* 6: 102–119.
- Arnold G & Weeldenburg J (1998) The effects of isolation, habitat fragmentation and degradation by livestock grazing on the use by birds of patches of gimlet *Eucalyptus salubris* woodland in the wheatbelt of Western Australia. *Pac Conserv Biol* 4: 155–63.
- Baker G, Dettmann E, Scutney B, Hardy L & Drynan D (1997) *Report on the Australian bird and bat banding scheme, 1995–96*. Environment Australia, Canberra.
- Barker RD & Vestjens WJM (1990) *The food of Australian birds. Vol 2. Passerines*. CSIRO Publ, Melbourne.
- Blakers M, Davies SJJF & Reilly PN (1984) *The atlas of Australian birds*. Melbourne University Press, Melbourne.
- Burbidge AA & McKenzie NL (1989) Patterns in the modern decline of Western Australia's vertebrate fauna: causes and conservation implications. *Biol Cons* 50: 143–198.
- Calver MC & Wooller RD (1981) Seasonal differences in the diets of small birds in the Karri forest understory. *Aust Wildl Res* 8: 653–657.
- Cody, ML (1974) *Competition and the structure of bird communities*. Princeton University Press, Princeton.
- Ford HA, Noske S & Bridges L (1986) Foraging of birds in eucalypt woodland in north-eastern New South Wales. *Emu* 86: 168–79.
- Ford HA, Barrett G, Saunders DA & Recher HF (2001) Why have birds in the woodlands of southern Australia declined? *Biol Conserv* 97: 71–88.
- Garnett S & Crowley G (2000) *The Action Plan for Australian Birds*. Environment Australia, Canberra.
- Hespenheide HA (1971) Food preference and the extent of overlap in some insectivorous birds, with special reference to the Tyrannidae. *Ibis* 113: 59–72.
- Holmes RT & Recher HF (1986) Search tactics of insectivorous birds foraging in an Australian eucalypt forest. *Auk* 103: 515–30.
- Janzen DH (1973) Sweep samples of tropical foliage insects: effects of seasons, vegetation types, elevation, time of day, and insularity. *Ecology* 54: 677–708.
- Loyn RH (1980) Bird populations in a mixed eucalypt forest used for production of wood in Gippsland, Victoria. *Emu* 80: 145–156.
- MacArthur RH (1958) Population ecology of some warblers in northeastern coniferous forests. *Ecology* 39: 599–619.
- Recher HF (1989) Foraging segregation of Australian warblers (Acanthizidae) in open-forest near Sydney, New South Wales. *Emu* 89: 204–215.
- Recher HF (1999) The state of Australia's avifauna: a personal opinion and prediction for the new millennium. *Aust Zool* 31: 11–27.
- Recher HF & Davis WE (1997) Observations on the foraging ecology of a mulga bird community. *Wildl Res* 24: 27–43.
- Recher HF & Davis WE (1998) Foraging profile of a wandoo woodland avifauna during spring. *Aust J Ecol* 23: 514–28.
- Recher HF & Gebski V (1990) Analysis of the foraging ecology of eucalypt forest birds: sequential versus

- single-point observations. In: Morrison ML, Ralph CJ, Verner J & Jehl JR Jr (eds) *Avian Foraging: theory, morphology, and applications*. pp 174–180. Allen Press, Lawrence.
- Recher HF & Lim L (1990) A review of the status of Australia's terrestrial vertebrate fauna. *Proc Ecol Soc Aust* 16: 287–301.
- Recher HF, Holmes RT, Schulz M, Shields J & Kavanagh R (1985) Foraging patterns of breeding birds in eucalypt forest and woodland of south-eastern Australia. *Aust J Ecol* 10: 399–420.
- Saunders D & Ingram J (1995) *Birds of Southwestern Australia. An atlas of changes in the distribution and abundance of the Wheatbelt Avifauna*. Surrey Beatty & Sons, Chipping Norton, NSW.
- Serventy DL & Whittell HM (1951) *A handbook of the birds of Western Australia*. Paterson Brokensha, Perth, WA.
- Statsoft Inc (1999) *STATISTICA for Windows*. Statsoft Inc, Tulsa, Oklahoma.
- Tabachnik B & Fidell L (1996) *Using multivariate statistics*. Harper Collins Publ, New York, NY.
- Wheeler AG & Calver MC (1996) Resource partitioning in a island community of insectivorous birds during winter. *Emu* 96: 23–31.
- Wiens JA (1989) *The ecology of bird communities*. Vol 1. Cambridge University Press, Cambridge.
- Wooller RD & Calver MC (1981a) Feeding segregation within an assemblage of small birds in the Karri forest understorey. *Aust Wildl Res* 8: 401–410.
- Wooller RD & Calver MC (1981b) The diet of three insectivorous birds on Barrow Island, Western Australia. *Emu* 81: 48–50.
- Wooller RD & Calver MC (1988) Changes in an assemblage of small birds in the understorey of dry sclerophyll forest in south-western Australia after fire. *Aust Wildl Res* 15: 331–338.

Appendix 1. Number of observations of ground-pouncing birds at Dryandra, Durrakoppin and Yellowdine during 1997 and at Gascoyne and Mt Magnet during 1999. Data for Hooded Robin at Dryandra were collected in 1995. The estimated number of different pairs for which we obtained data at each site is shown in parenthesis. Dashes indicate the species was absent from that site.

Location	Bird species				
	RCR	SR	JW	WYR	HR
Dryandra	158 (10)	189 (8)	206 (6)	198 (10)	41 (2) ¹
Durrakoppin	75 (3)	–	86 (3)	–	–
Yellowdine	55 (8)	–	75 (2)	–	–
Gascoyne	69 (12)	–	–	–	–
Mt Magnet	92 (15)	–	–	–	66 (2)

¹ From Recher and Davis (1998).

Appendix 2. Comparative size of Red-capped Robin, Scarlet Robin, Western Yellow Robin, Jacky Winter, and Hooded Robin. Males and females are shown separately for sexually colour dimorphic species. Data are from the Australian Bird and Bat Banding Scheme (Appendix H in Baker et al. 1997). Data are means and standard deviation with sample size in parenthesis.

SPECIES	Measurement		
	Weight (g)	Wing chord (mm)	Tail length (mm)
RCR			
Male	8.6–0.7 (62)	62.9–2.1 (67)	47.7–3.3 (35)
Female	8.7–0.6 (65)	61.5–2.5 (67)	46.5–2.2 (38)
SR			
Male	13.1–1.1 (185)	75–2.2 (108)	55.3–3.3 (31)
Female	13.6–1.5 (99)	73.6–2.2 (78)	55.2–5.2 (19)
JW	15.1–2.5 (30)	86.8–7.2 (29)	60.6–8.5 (19)
WYR	19.0–1.9 (21)	89.3–3.7 (19)	60.6–8.5 (19)
HR			
Male	23.6–2.3 (23)	96.4–3.7 (14)	71.2–1.8 (6)
Female	22.5–1.6 (18)	89.8–2.2 (19)	67.7–2.9 (6)