

Coexistence of a locally undifferentiated foraging guild: avian snatchers in a southeastern Australian forest

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Abstract Three species of sexually dichromatic, insectivorous birds (Golden Whistler, *Pachycephala pectoralis*; Rufous Whistler, *Pa. rufiventris*; Rose Robin, *Petroica rosea*) employ a characteristic foraging manoeuvre (snatching or sally-striking) disproportionately often, leading several studies to group them together in one foraging guild. The three species synchronously co-occupy an extensive eucalypt forest east of Melbourne, Australia (Olinda State Forest). All assemble in relatively high densities in late winter and through spring and early summer to breed. Log-linear modelling of use of foraging techniques, substrate, plant species and heights within the forest indicate that all six species–gender groups virtually do not differ from one another: a situation in which very similar species coexist at high densities. The results are considered in the context of interspecific competition among ecologically similar species and it is suggested how such a situation might arise and be sustained. The absence of gender-specific differentiation within species is also addressed.

Key words: Australia, birds, *Eucalyptus*, foraging, Golden Whistler, log-linear model, Rose Robin, Rufous Whistler.

INTRODUCTION

Foraging behaviour of five species of warblers of the genus *Dendroica*, now known as MacArthur's warblers, and their feeding zones in conifers have been used literally as a textbook example of resource partitioning for a generation. MacArthur's (MacArthur 1958: figs 2–7) were combined, perhaps overly simplified, adapted and reproduced widely (e.g. Hutchinson 1968 [fig. 2]; Collier *et al.* 1973 [fig. 6.13]; Ricklefs 1976 [fig. 14.23]; Pianka 1983 [fig. 6.9]; Krebs 1985 [fig. 13.18]; Real & Brown 1991; Chapman & Reiss 1992: [fig. 10.6]; Colinvaux 1993 [fig. 9.3]). MacArthur's (1958) field methods were open to question (Wiens 1989), and other workers found mixed results for these species in northeastern North America. Yet MacArthur's (1958) study remains as perhaps the most famous example of coexistence by resource (microhabitat) partitioning and one frequently presented to undergraduate students.

However, local coexistence by resource partitioning seems to be at odds with observations that sets of species within communities commonly have similar characteristics, resource utilization patterns and behaviours (Pontin 1982; Wheeler & Carver 1996). These similarities led to the development of the related concepts of the guild (Root 1967) and the functional group (Cummins 1973), which apparently filled a conceptual void (Hawkins & MacMahon 1989). Therefore, rather than the even species packing implicit in many models

of coexistence by resource partitioning (e.g. May 1974), there appear to be certain regions within resource space that are exploitable (Eckhardt 1979; Oksanen *et al.* 1979), leading to the formation of guilds.

Guild membership refers to the routine manner and location of foraging displayed by species because many species utilise resources opportunistically (Martin & Karr 1990; Mac Nally 1994a). This indicates that some level of differentiation may occur among guild co-members and differences such as those reported by MacArthur (1958) need to be assessed statistically.

One of the primary drawbacks with many of the reports on resource partitioning and coexistence is a reliance on overlap metrics, many of which are of doubtful use (Mac Nally 1995a). In interpreting resource use and coexistence, overlap metrics have been considered to be synonymous with competition coefficients (e.g. MacArthur & Levins 1967) so that there has been an expectation that there should be minimal levels of overlap so that mutual impacts on hetero-specific populations will be minimal (Roughgarden 1979). For example, Schoener (1986) suggested that proportional similarity overlap indices greater than 0.6 may be ecologically significant. However, overlap metrics are not statistics and cannot be used to judge the significance of patterns of resource use. Therefore, when addressing questions of the local coexistence and resource use of animals such as forest-dwelling birds, one needs to use appropriate analytical methods rather than overlap indices (e.g. log-linear modelling; see Noon & Block 1990).

The work described here is an analysis and interpretation of a subset of information derived from a more general study of the dynamics and ecological relationships of birds at one study site. The site at Olinda State Forest, about 50 km east of Melbourne, Australia, was established for studying longer-term patterns than those that are normally considered. Several papers describing a variety of outcomes of the general study have been published (Mac Nally 1996; 1997a,b,c).

One evident observation about the foraging behaviour of birds in Olinda State Forest was the similarity of activities undertaken by three particular species, which was seemingly at variance with the differentiation normally assumed to be necessary for coexistence. Two are congeners of the genus *Pachycephala*: the Golden Whistler, *P. pectoralis* (Latham) 1801, and Rufous Whistler, *P. rufiventris* (Latham) 1801. Indeed, their foraging is so similar that Ford *et al.* (1986) suggested: 'Possibly this pair of species is too similar to be able to coexist.' The third is an Australian robin, the Rose Robin, *Petroica rosea* Gould 1839. All frequently employ a particular foraging manoeuvre, snatching, and often co-occur in wetter sclerophyll forests of southeastern Australia. Snatching, which is synonymous with sally strike, is defined as 'the [wing-powered] attack in a fluid movement without gliding, hovering, or landing in fly[ing] from a perch to attack a food item (and then return to a perch)' (Remsen & Robinson 1990). Most typically, the snatchers attack prey located in foliage, twigs or smaller branches. The three species have been previously grouped together as members of the snatching guild (e.g. Recher *et al.* 1985; Ford *et al.* 1986; Mac Nally 1994a). A fourth snatcher, the Black-faced Cuckoo-shrike, *Coracina novaehollandiae* (Gmelin 1879), also co-occurs with these three species but was rare at the site studied here (Mac Nally 1997a) and so is not considered further.

To place this observation of great similarity on a more substantive footing, I present analyses of an extensive data set on foraging behaviour, locations and substrates and heights of the three main snatching species. There is pronounced gender dichromaticity in all three species, so it is possible to extend the analysis to gender also. The occurrence of gender-specific foraging differences in the Golden Whistler is contentious (see Bell 1986 vs. Wheeler & Carver 1996). Therefore, differences among the sexes of the three species in foraging attributes is also considered.

This study therefore provides an analysis of the foraging activities of these three species to ascertain whether the superficial impressions of similarities are backed-up by more critical statistical assessment. Without anticipating the outcomes, there do appear to be only minor differences in foraging activities among the three snatching species, and these differ-

ences have to be interpreted given the more general claims for the need for differentiation for long-term coexistence (e.g. Cole 1960).

METHODS

Study site

Data were collected in an upland forest in the Dandenong Ranges, east of Melbourne. Olinda State Forest (37°55'S, 145°19'E) is a continuous tract of forest of approximately 1000 ha lying between 260 and 550 m in elevation. Olinda State Forest is effectively continuous with other large forest reserves (also exceeding 1000 ha) in its vicinity, such as the Doongalla Estate, Ferntree Gully National Park, Monbulk State Forest and the Sherbrooke Forest Park. The forest had not experienced wildfire from 1962 until after the data were collected.

Three fixed transects were established for censusing the avifauna, namely, the Olinda transect in the north, the Eyrie transect in the middle and the Silvan transect in the southwest area of Olinda State Forest. Three species of *Eucalyptus* dominated these transects, but in different proportions in each. The Olinda transect consisted of narrow-leaved peppermint, *Eucalyptus radiata*, and messmate stringybark, *Eucalyptus obliqua*, at a ratio of almost two-to-one (based on trunk densities of canopy-level trees). Small numbers of individuals of a third species of eucalypt, the mountain grey gum, *Eucalyptus cypellocarpa*, were sprinkled among the other species on this transect. Similar comments apply to the Silvan transect except that messmate outnumbered peppermint by 1.5 : 1.0. There were very few peppermints on the Eyrie transect, with messmate being the dominant species. Mountain grey gums were a conspicuous element of the Eyrie plant community, with higher densities of this species than on the other two transects. Silver wattle, *Acacia dealbata*, was a common understorey (5–15 m) component of the Eyrie transect. The shrub layer (0.3–1.7 m) was dominated by dusty miller, *Spyridium parvifolium*, and rough bush-pea, *Pultenaea scabra*, in both the Olinda and Silvan transects, while ferns (e.g. *Dicksonia antarctica*) and bracken, *Pteridium esculentum*, were the common shrub-layer elements over much of the Eyrie transect.

Censusing methods

Ninety-two censuses were conducted beginning in the winter of 1993 (last week of June) and continuing through to the end of autumn 1996 (third week of May). A census visit consisted of the collection of data for each transect, so that the snatching guild on each

transect was monitored on each occasion. To reduce the potential for systematic biases, the order in which the three transects were visited was rotated. Several months were spent prior to the 1993 winter gaining familiarity with the transects and the birds, which entailed nine visits comparable to the real census visits. Mock censusing was carried out on these occasions so that standard methods could be established. In addition, the author had extensive prior experience in similar forests (e.g. Mac Nally 1989; 1994a,b). Censuses for the study proper were performed on average 10–15 days apart over the 3 years. Times are expressed as days after 21 June 1993.

Censusing was always conducted under the most favourable conditions, namely calm, dry weather. Censuses of each transect were performed by using a standard fixed-width (35 m either side of mid-line) strip method (Recher 1989). Census work started at sunrise and each transect was traversed for 2 h in turn (according to the predetermined order), making a total of 6 h per census visit. A near-constant rate of progress was maintained (0.85 km h^{-1}). All individual birds were identified by sight or by voice. Only individuals in the 90° arc immediately ahead (i.e. $\pm 45^\circ$) were recorded and only individuals on transects were included in the data sets used here.

Density calculations used the method of Mac Nally (1997a) and are expressed as individuals per 50 ha.

Foraging variables

Data on foraging activities were collected during censusing. Analyses are conducted at four levels: (i) foraging manoeuvres; (ii) launch position of foraging act; (iii) target position of prey item; and (iv) plant species upon which foraging occurs.

Manoeuvres

The scheme of Remsen & Robinson (1990) was used for classifying foraging manoeuvres and to underlie analyses of foraging similarities. This scheme recognises the importance of the link between the manoeuvre and the substrate used by the bird and places importance on the position from which the manoeuvre is launched. For example, sally strike (leaf) involves a launch position, which is tallied in the appropriate launch category (e.g. twig) and also a target position, the foliage, which also adds to the tallies for the target position data.

Seventeen classes were used to describe the foraging methods/substrates used by birds in the Olinda State Forest. These are named and defined in Table 1 and are listed in order of frequency of use within the snatching guild. (This ordering helps in the presentation of figures.)

Table 1. Definition of foraging methods (see Remsen & Robinson 1990) used by members of the snatching guild, listed by frequency of use

Method	Definition
Glean (wood)	Searching motion along branch; invertebrate(s) sometimes collected while bird is moving
Sally-strike (leaf)	Bird visually locates prey on leaf (usually >1 m distant) from perched position and attacks by flying and snatching
Glean (twig)	From perched position bird searches and pecks invertebrate from nearby twig
Reach-out/up (leaf)	Bird visually locates prey on nearby leaf from perched position and attacks by craning body/neck and sharply snatching
Reach-out/up (twig)	Bird visually locates prey on nearby twig from perched position and attacks by craning body/neck and sharply snatching
Sally-strike (wood)	Bird visually locates prey on branch, trunk or bark ribbon (usually >1 m distant) from perched position and attacks by flying and snatching
Sally-strike (twig)	Bird visually locates prey on twig (usually >1 m distant) from perched position and attacks by flying and snatching
Glean (foliage)	From perched position bird searches and pecks invertebrate from nearby leaf
Pry/pull (bark)	Prising into bark to locate and extract hidden invertebrates
Sally-strike (air)	From initially perched position, direct aerial sally to capture single airborne prey target
Flutter-chase (air)	From initially perched position, fluttering, extended flight usually in pursuit of a large or mobile prey item
Sally-hover (leaf)	From hovering position, location and snatching of prey from foliage
Sally-hover (twig)	From hovering position, location and snatching of prey from twig
Sally-hover (bark/wood)	From hovering position, location and snatching of prey from branch, trunk or bark ribbon
Glean (bush)	Gleaning prey from any part of bushes <1 m tall
Glean (fern)	Gleaning prey from any part of a fern
Glean (ground)	Pecking prey from the ground or litter

Substrates

Substrates used by birds were divided in two ways: by plant taxonomy and age-class, and by location. For taxonomy, eight classes were used: (i) messmate canopy-level trees; (ii) narrow-leafed peppermint canopy-level trees; (iii) mature silver wattles; (iv) mountain grey gum canopy-level trees; (v) messmate saplings and juveniles; (vi) narrow-leafed peppermint saplings and juveniles; (vii) prickly moses, *Acacia verticillata* (a large understorey shrub or small tree); and (viii) all other understorey plants, which were rarely used.

As noted above, there are two kinds of locations. Launch-location classes were: (i) tertiary branches; (ii) twigs; (iii) secondary branches; (iv) primary branches; and (v) leaves. Primary branches are those emanating from the trunk. Secondary branches arise from the first bifurcations of the primary branches, while tertiary branches are further divisions of the secondary branches. Twigs are defined as leaf- or phyllode-bearing branches. These locations refer to the points from which the foraging act was initiated.

The positions of the target prey were classed as: (i) wood (including trunks and primary and secondary branches); (ii) leaves; (iii) twigs; (iv) air (aerial foraging acts); (v) bushes; (vi) ground; and (vii) ferns.

The last variable used was foraging height above the ground, which was the average height of the launch and target locations.

Statistical analyses: foraging data

Data were organised as a series of multiway contingency tables. Log-linear modelling was used to determine whether there were differences among species and genders in relation to: (i) foraging method; (ii) foraging-launch location; (iii) foraging-target location and (iv) plants used for foraging. Log-linear models are a subset of general linear models that are designed to analyse 'count' data, such as those considered here. They are also the most appropriate means by which the levels of variability among guild co-members can be assessed statistically to evaluate whether those differences are at least potentially sufficient to permit local coexistence (Noon & Block 1990). Errors are assumed to have a Poisson distribution, and the dependent variable is log-transformed (namely a logarithmic link function, McCullagh & Nelder 1989). Tests of whether distributions differ among species or gender were by analyses of deviance (ANODEV, Manly 1992).

Analyses of deviance involve the fitting of models of differing complexity (various numbers of model terms) in a hierarchy and computing the degree of fit, or deviance, of the model to the data. Unlike analysis of variance (ANOVA), the significance of the main effects

in ANODEV is of little importance because these usually only reflect differences in sample size among treatments or groups. This is similar in logic and rationale to G-tests for association (Crawley 1993). Important differences relate to the significance of interactions among main effects. Thus, significant interactions indicate that there are differences in the relative proportions of activities among species and/or genders.

Several important checks are needed to validate underlying model assumptions. Residuals must be examined for the occurrence of systematic patterns. Also, the analysis should include a test of whether the data conform to the Poisson expectation. Crawley (1993) described a means by which overdispersion can be evaluated for putatively Poisson data, including methods for correction. This involves a test of whether a sufficiently good model can be constructed for the data. A maximal model is used and if the deviance is similar to or less than the model degrees of freedom, then the data are held to be consistent with the Poisson assumption (Crawley 1993). If the data are overdispersed, then the data can be scaled to overcome this deficiency (see Crawley 1993, p. 261).

The GLMStat software package (Beath 1996) was used for log-linear modelling.

RESULTS

Densities

Data are presented in two forms: raw density measures and three-point moving-average, smoothed estimates. The latter are given because much of the sample-to-sample variability evident in the raw data through time represents sampling error due to uncontrolled variation in weather conditions, etc. For the most part, the raw and smoothed data yield similar conclusions concerning changes in density through time.

The Golden Whistler showed pronounced seasonal pulses in density, with large numbers occupying Olinda State Forest from early spring to mid-autumn (Fig. 1a). Although densities fell well below peak values (~50–60 birds per 50 ha) during the 1994 winter, many Golden Whistlers (~10–15 birds per 50 ha) remained at Olinda State Forest throughout (Fig. 1a). However, there were very few present during the subsequent winter (Fig. 1a). In all three years, there appeared to be an autumnal surge in densities, the reasons for which are unclear (MacNally 1997b). Similar surges occurred in several other species, including the Rose Robin (Fig. 1b) and Grey Fantail, *Rhipidura fuliginosa*.

The Rose Robin and Rufous Whistler are warm-season breeding migrants at Olinda State Forest (MacNally 1997b). Both species arrive in late winter or early spring and reach relatively high densities in a

short time (Fig. 1b,c). Residence times vary among years (see Mac Nally 1997b), with Rufous Whistlers

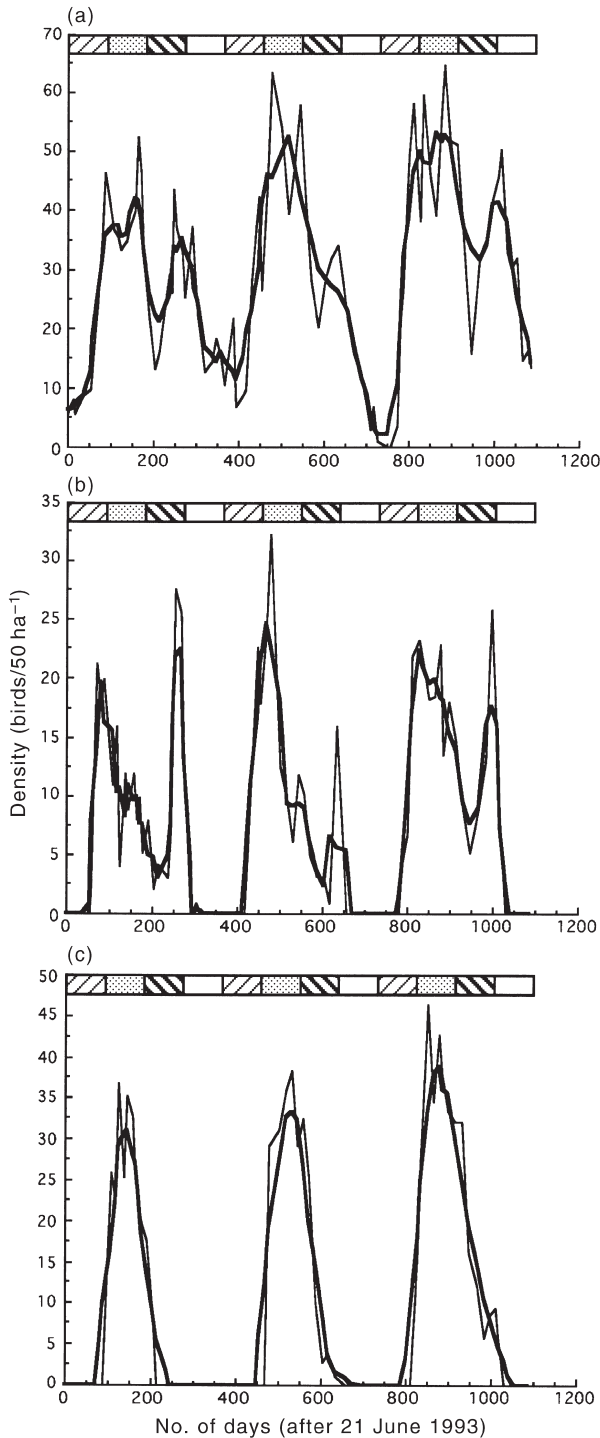


Fig. 1. Density trajectories of the three members of the snatching guild at Olinda State Forest, Victoria: (a) Golden Whistler; (b) Rose Robin; (c) Rufous Whistler. In each panel, the fine line indicates the time-course based on raw data while the heavier line is a smoothed (three-point moving average) trajectory. Horizontal bars indicate seasons: fine hatch, winter; stipple, spring; coarse hatch, summer; clear, autumn.

remaining 90 days fewer in the first year than in the third year (Fig. 1c). Unlike the Rose Robin and Golden Whistler, Rufous Whistlers did not display the late-season surge in densities (Fig. 1c).

Densities of all three species were strongly inter-correlated (Spearman's rank correlation, all $P < 0.001$). Rank correlations using raw data all exceeded 0.54, while correlations based on smoothed data all exceeded 0.65. Thus, there is little differentiation in terms of the occupation of Olinda State Forest, with the three species attaining their respective highest densities simultaneously. The estimated peak guild densities in the three years were 85 (1993–4), 125 (1994–5) and 122 (1995–6) birds per 50 ha.

Foraging

The following analyses are based on 1005 records of Golden Whistler (626 male, 379 female), 269 Rufous Whistler (190 male, 79 female) and 229 Rose Robin (138 male, 91 female) foraging acts. For some projections of the data set there are fewer observations than these because there were missing data, sometimes due to field oversights or when bird activity was intense. For example, there were 66 instances in which heights were inadvertently not recorded in field notes, 50 of which were cases of foraging by Golden Whistlers. Moreover, some elements are irrelevant to certain behaviours, e.g. none of the substrate variables are pertinent to the ground gleaning, foraging class (Table 1).

Foraging methods

In five of the species-gender combinations, glean (wood), sally-snatch (leaf) and glean (twig) were the first, second and third most commonly used foraging methods (Fig. 2a). Rufous Whistler males used glean (twig) a little more frequently than sally-snatch (leaf) (24% vs. 19%), but glean (wood) was still the predominant method (33%) (Fig. 2a). These three methods constituted between 70% (Rufous Whistler males) and 86% (Golden Whistler females) of foraging activities. A simple contingency table calculation of expected values for the three foraging methods partitioned by species and gender produced a good fit (Fig. 2b).

More definitive results emerged from the log-linear analyses (Table 2a). First, a model using all three main effects and the two-way interactions with method produced a model with a deviance of 33.9, yielding a mean deviance of less than unity. Therefore, there is little evidence for overdispersion in this model. Second, the addition of a species \times method interaction to the simpler species + method model could not be justified because of the non-significant decrease in explained

variation ($F_{32,51} = 1.36$, NS). The decrease associated with the interaction was just 2% of the total deviance. Similarly, there was no significant reduction in deviance (1% of total deviance) by appending a method \times gender term onto a method + gender model ($F_{16,68} = 0.24$, NS). Thus, there seems to be little evidence for sexual differentiation in foraging methods in these three species, and distributions of foraging methods did not appear to depend on species or gender.

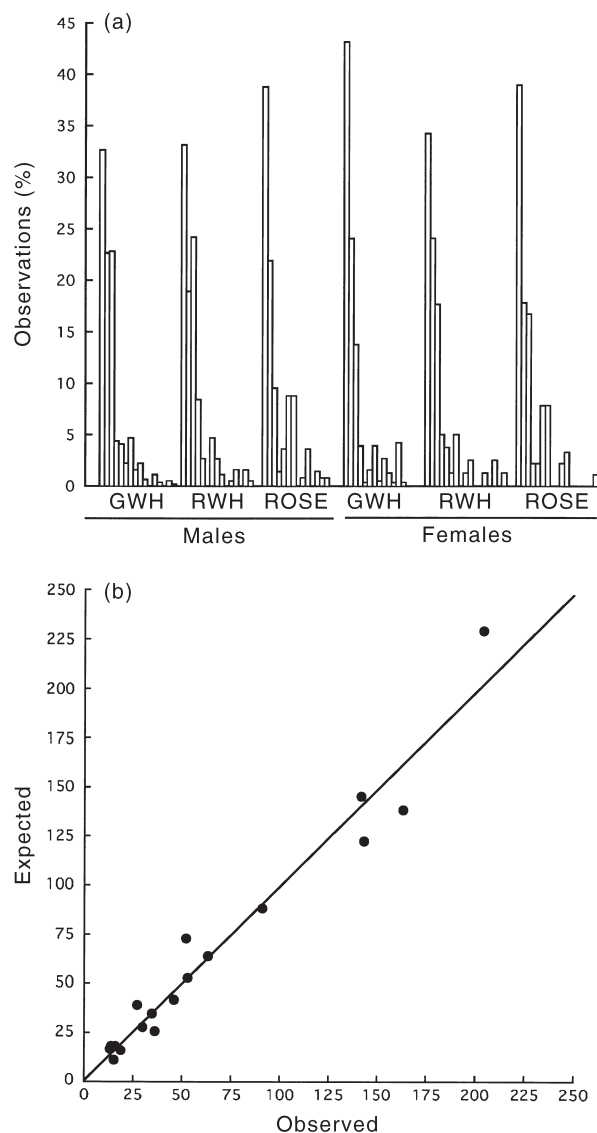


Fig. 2. (a) Percentage distributions of foraging methods for members of the snatching guild. In each case, the histograms are ordered from left to right in accordance with the order in the list of foraging methods in Table 1. (b) Plot of expected numbers of foraging observations for each species/gender combination (derived from simple contingency table calculations) in the three most common methods against the observed values (i.e. 3 species \times 2 genders \times 3 methods = 18 points; slope = 0.984 ± 0.051 , $R^2 = 0.96$).

Launch position

Launch positions are the locations from which the birds commenced a foraging act. Tertiary branches and twigs were the main launch locations for all species-gender combinations, ranging from 66% for Rufous Whistler females to 85% for Rose Robin females (Fig. 3a). Rose Robins were not observed gleaning on foliage (Fig. 3), although they fly to and snatch from foliage commencing from a perch on branches or twigs (see below).

In log-linear modelling, a model including the three main effects (species, gender, launch position) and the two-way interactions involving location yielded a mean deviance of 1.67, which indicates mild overdispersion. The data were scaled producing a mean

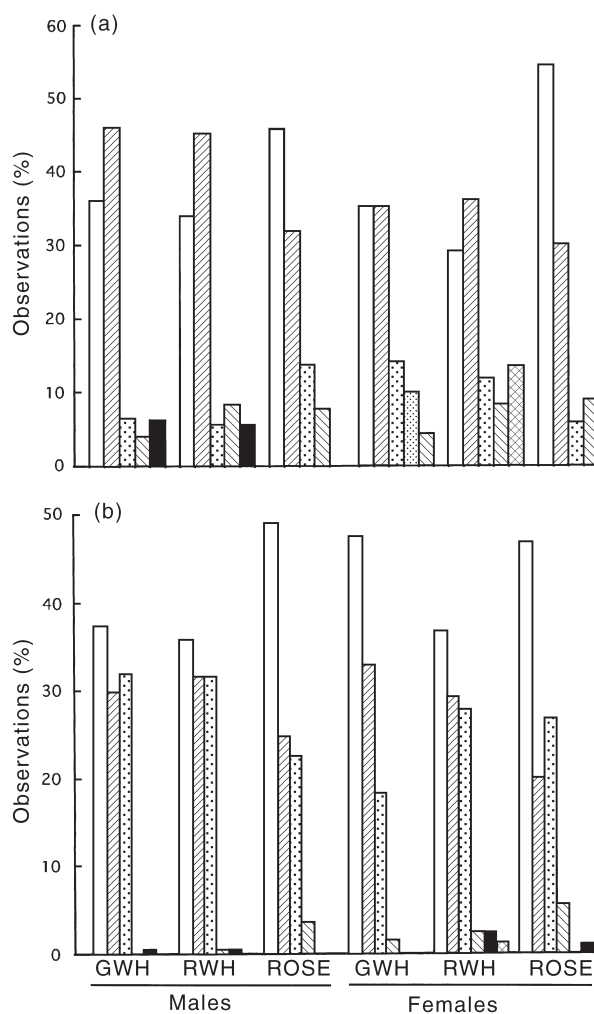


Fig. 3. Percentage distributions of foraging locations for members of the snatching guild: (a) launch, and (b) target. In (a), the histograms are ordered from left to right: tertiary branches (clear), twigs (fine hatch), secondary branches (stipple), primary branches (coarse hatch) and foliage (solid). In (b), the histograms are ordered from left to right: wood (□), leaves (▤), twig (▥), air (▦), bush (■) and ground (▧).

deviance of unity (Table 2). There was little evidence of significant differences in foraging location among species ($F_{8,15} = 0.43$, NS; Table 2b). The decrease associated with the location \times species interaction was just

2.5% of the total deviance. There also was no significant reduction in deviance (1.1% of total deviance) by appending a location \times gender term to a location + gender model ($F_{4,20} = 0.16$, NS). Thus,

Table 2. Analyses of deviance for foraging method, launch and target positions and plant species for three species of snatchers at Olinda State Forest

Model	d.f.	Deviance	Mean	<i>F</i> -ratio [‡]
(a) Foraging method				
<i>Method, species, gender*</i>				
Method \times species				
Method \times gender	34	33.9	0.99	
<i>Species by method</i>				
Species + method	83	314.3		
Species + method + interaction	51	214.9	4.21	
Difference due to interaction	32	99.3	3.10	1.36
<i>Gender by method</i>				
Gender + method	84	909.9		
Gender + method + interaction	68	861.7	12.67	
Difference due to interaction	16	48.2	3.01	0.24
(b) Launch position				
<i>Launch, species, gender*†</i>				
Launch \times species				
Launch \times gender	10	10.01	1.0	
<i>Species by launch</i>				
Species + launch	23	120.6		
Species + launch + interaction	15	97.9	6.53	
Difference due to interaction	8	22.6	2.83	0.43
<i>Gender by launch</i>				
Gender + launch	24	318.5		
Gender + launch + interaction	20	308.6	15.43	
Difference due to interaction	4	10.0	2.49	0.16
(c) Target position				
<i>Target, species, gender*†</i>				
Target \times species				
Target \times gender	14	14.00	1.0	
<i>Species by target</i>				
Species + target	33	99.7		
Species + target + interaction	21	82.5	3.93	
Difference due to interaction	12	17.2	1.43	0.36
<i>Gender by target</i>				
Gender + target	34	392.3		
Gender + target + interaction	28	377.9	13.50	
Difference due to interaction	6	14.5	1.47	0.11
(d) Plant species				
<i>Plant, species, gender†‡</i>				
Plant \times species				
Plant \times gender	18	18.0	1.0	
<i>Species by plant species</i>				
Species + plant	43	238.1		
Species + plant + interaction	27	120.4	4.46	
Difference due to interaction	16	117.7	7.36	1.65
<i>Gender by plant species</i>				
Gender + plant	44	597.2		
Gender + plant + interaction	36	569.2	15.81	
Difference due to interaction	8	27.9	7.36	0.22

*Tests for overdispersion in data; †data scaled to overcome overdispersion; ‡none of the *F*-ratios was statistically significant.

foraging launch positions did not appear to differ among species or genders.

Target locations

Target positions are the substrates at which the attacks are directed, and thus where the prey are located. A model including the three main effects (species, gender, target location) and the two-way interactions involving target location yielded a mean deviance of 1.53, which indicates mild overdispersion. Data were scaled leading to a mean deviance of unity. Again, there was little evidence of differences among species ($F_{12,21} = 0.36$, NS, 0.9% of total deviance; Table 2c) or genders ($F_{6,34} = 0.11$, NS, 0.9% of total deviance; Table 2c) in the target locations of foraging attacks.

Plant species used

Each of the species is primarily arboreal, mainly using the major canopy-level species of trees (Fig. 4). Adults of messmate stringybarks are used most commonly, with 33% of all records, while mature narrow-leaved peppermints (22%) and silver wattles (20%) are also prominent. It is among these species of trees that the only differences occur among members of the snatching guild. Rufous Whistlers (Fig. 4) were not recorded using silver wattles, while Rose Robins (Fig. 4) used the wattles more frequently than messmate stringybarks.

However, the qualitative differences just described are not supported by quantitative analyses using log-linear models. Only three individual foraging acts

(of 1503) had different launch and target plant species; these were excluded from the following analysis. The mean deviance of a model including the three main factors and the two-way interactions involving plant species was 1.66, so that this figure was used as a scaling factor in subsequent analyses. The bird species \times plant species interaction was not significant ($F_{16,27} = 1.65$, $P > 0.12$; Table 2d), which indicates that the three species do not differ greatly in their use of foraging plants. The reduction in deviance due to this interaction was 9.4% of the total deviance, which is the largest percentage of any of the interactions considered in these foraging analyses. The gender \times plant species interaction also was non-significant ($F_{8,36} = 0.19$, NS; Table 2d), contributing just 1.9% of the total deviance.

Height distributions

Mean foraging heights ranged from 9.0 m for Rose Robin females through to 11.6 m for male Rufous Whistlers (Fig. 5). However, in all species-gender combinations there was a wide range in heights used. The smallest standard deviation was 3.9 m for female Rufous Whistlers. Mean foraging heights of males exceeded those of conspecific females in each species: by 1.9 m in the Golden Whistler, by 1.4 m in the Rufous Whistler and by 0.5 m in the Rose Robin (Fig. 5).

A one-way ANOVA was conducted on the foraging height distributions, treating each of the six species-gender combinations as single groups. There were significant differences among the groups ($F_{5,1431} = 11.23$,

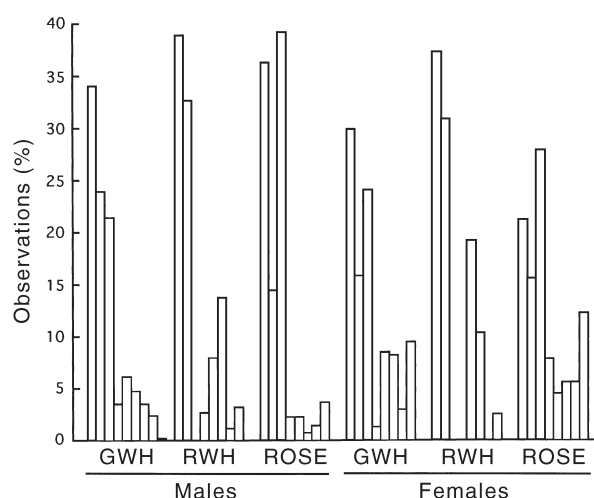


Fig. 4. Percentage distributions of plant species used by members of the snatching guild. In each case, the histograms are ordered from left to right: messmate, narrow-leaved peppermint, silver wattle, mountain grey gum, messmate saplings, narrow-leaved peppermint saplings, spiny moses, understorey, ferns.

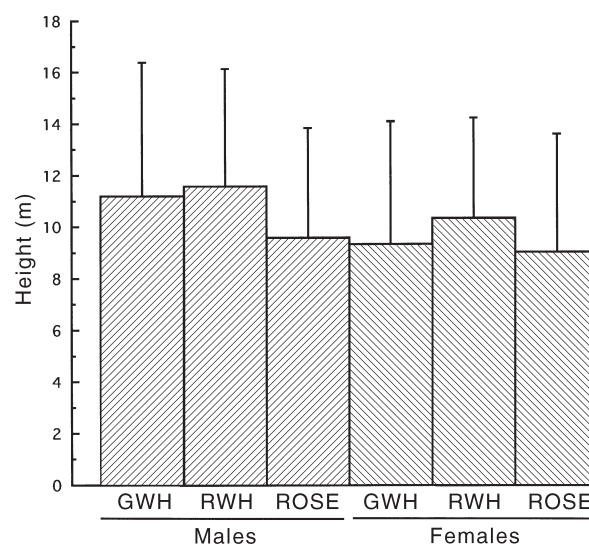


Fig. 5. Means and standard deviations of heights above ground for foraging records of three species of the snatching guild: Golden Whistlers (GWH), Rufous Whistlers (RWH), and Rose Robins (ROSE).

$P < 0.001$). However, this highly significant result is largely a function of the high power associated with the large error mean square degrees of freedom (1431). ANOVA components showed that little of the overall variation was explained by the differences among groups. The estimated variance component for the among-groups term was 1.13, while the estimate for the residual was 23.38. Thus, just 4.6% (4.3–4.9%, 95% confidence range) of the variation is attributable to differences among species-gender groups. Thus, while the means differed significantly, there are unlikely to be substantial ecological differences in foraging heights among the species and sexes of the snatching guild.

DISCUSSION

The question of coexistence of apparently ecologically similar species has been an important and dominant theme in community ecology throughout its history (MacArthur 1972; Cornell & Lawton 1992). The intuitively obvious contention that species too similar to one another ought not to coexist for long (Cole 1960) sent many workers to look for corroborative evidence of ecological segregation. Coexistence was thought to be facilitated by different morphology (e.g. character or size displacement, Hutchinson 1959; Grant 1975; Lundberg & Stenseth 1985; Schluter 1988); spatial isolation (e.g. parapatry, Bull 1991); interspecific territoriality (Robinson 1990); altitudinal segregation (Diamond 1986) or through local resource partitioning (Schoener 1974; Pacala & Roughgarden 1982; Toft 1985).

Probably because of the pioneering lead set by MacArthur's (1958) work, studies of avian foraging differentiation became a prominent area in which to test ideas relating to local coexistence by means of resource segregation (e.g. Fretwell 1972; Ricklefs 1972; Cody 1974; Rabenold 1978; Rice *et al.* 1980; Emlen & DeJong 1981; Landres & MacMahon 1983). However, the link between foraging and feeding has been questioned: similar foraging can lead to different dietary outcomes and vice versa (Wiens 1989; Maurer 1990; Sherry 1990; Mac Nally 1994b). Diet rather than foraging methods/microhabitats presumably has greater importance in both ecological and evolutionary terms. Thus, observational tests of the hypothesis of resource partitioning as a consequence of competitive co-evolution were never strong and have generally lost favour.

In this study, there is little evidence that the three species of snatchers, nor their genders, are much differentiated in foraging. With almost complete overlap on all dimensions, there is little scope for the complementarity envisioned by Schoener (1974). They use similar repertoires of foraging manoeuvres, similar proportions of major plant species and similar distribu-

tions of foraging substrates. The only axis upon which there is a statistical difference is foraging height. While some might regard such a difference to be the solution to the coexistence puzzle (e.g. Latta & Wunderle 1996; Yamagishi & Eguchi 1996), the substantial overlap among the six species-gender classes (Fig. 5) and small variance component ($4.6 \pm 0.3\%$) appears to be more ecologically important than are the marginal differences among mean foraging heights. At Olinda State Forest, these species forage in very similar ways. Moreover, they congregate in the highest densities synchronously so that the conditions for differentiation under the pressure of interspecific competition, if necessary, are fulfilled.

Foraging need not equate to diet *per se* because of the lack of identity between a foraging manoeuvre and the food obtained (Maurer 1990). Thus, it is possible that the foraging similarities reported here do not apply to equivalent dietary similarities. This relationship needs to be explored in detail. Existing information, although limited, suggests a common taxonomy in the diets of the three species, with spiders, weevils, leaf-eating beetles, bugs, ants, wasps, dipterans and caterpillars being predominant (Lea & Gray 1935). Descriptions of prey sizes also do not differ greatly (Lea & Gray 1935). Thus, neither foraging nor diet (based on existing information) appear to be substantially different.

Gender-specific foraging

Foraging differentiation between the sexes has been widely reported for forest and woodland birds, especially in northern-hemisphere species (Rand 1952). Two main hypotheses have been put forward to account for such differences (see Holmes 1986): (i) alleviation of intraspecific competition for resources (Selander 1966); and (ii) a reflection of differences in locations of advertisement stations (males) and nesting sites (females) (Morse 1968; Franzreb 1983; Morimoto & Wasserman 1991; Suhonen & Kuitunen 1991). In some cases, differences in foraging location and hence activity may reflect behavioural dominance of males over females, forcing the latter to use lower-quality substrates (Grubb & Woodrey 1990). Experimental removal of males has sometimes led to females foraging more like conspecific males (e.g. Peters & Grubb 1983). However, three of six species of woodpecker listed by Grubb & Woodrey (1990) exhibited few differences between males and females.

The set of studies considered by Holmes (1986) provided little compelling evidence that there are consistent differences or patterns between the sexes in many forest-dwelling species. He suggested that most of the cases in which males foraged higher than females involved coniferous forests (e.g. Morse 1968; Morrison

1982; Franzreb 1983) where advertisement stations were positioned in the upper branches of the heavily foliated, cone-shaped trees, while nests were located in understorey thickets at lower heights. In the mixed broad-leaved woodland of Hubbard Brook, New Hampshire, USA, the distribution of foliage and branches was more even as a function of height above ground, and foraging-height differences between males and females were not pronounced (Holmes 1986).

What of the three species considered here? Several workers, especially those in New South Wales, have observed that male Golden Whistlers forage higher in trees than do females (Bell 1986; Marchant 1992). Unfortunately, there are few published reports on gender-specific foraging characteristics of Rufous Whistlers and Rose Robins for comparison, although many such data must have been collected. For example, Recher *et al.* (1985) based analyses of foraging activities of these species on 983 and 195 observations, respectively, while Ford *et al.* (1986) obtained 373 records for Rufous Whistlers.

While some observations suggest that there are gender-specific foraging differences in Golden Whistlers, Wheeler and Carver (1996) found no such differences on Rottneest Island off the coast of Western Australia, and suggested that there may be few consistent patterns in the one species at different locations. The current analyses support the Rottneest Island observations and indicate that results from studies from one or a few locations do not lead to a general representation of a species' characteristics. Other factors operating locally must be influential, including the community in which a species occurs (Bell 1986) and habitat-structural characteristics (Holmes 1986).

Large-scale dynamics and niche co-evolution

Some avian ecologists have questioned whether foraging-niche differentiation is necessary to permit coexistence in bird communities, especially those on large landmasses (see Mac Nally 1995b). There are two main problems with the older, MacArthur–Cole viewpoint. First, the conditions necessary for competitive co-evolution seem rather unlikely in the majority of cases involving birds. These conditions include relatively closed communities, largely local recruitment and a predominance of interspecific competition as the main process influencing the populations (Mac Nally 1995b). Second, given the extreme mobility of birds, the opportunities for genetic differentiation under the pressures of interspecific competition seem limited.

Several workers investigating avian communities in western North America concluded that selective pressures for ecological divergence among putative competitors are likely to vary greatly in intensity and direction in space and time (e.g. Wiens 1974, 1977;

Maurer 1984; Bock 1987). If this is so, then coherent patterns of resource differentiation should not be expected. Maurer (1990) commented that 'sets of insectivorous birds are not assemblages of co-evolved species but rather are collections of species that have the right sets of [general] adaptations that allow them to live together.' Even this view may be overly deterministic. In the extremely dynamic communities found over much of Australia (e.g. Mac Nally 1995b; Mac Nally & McGoldrick 1997), it seems difficult to picture species co-occurring for long enough for competitive interactions to have a pronounced proximal or ultimate effect in most circumstances (see also Marchant 1992). In addition, the majority of individuals are either nomadic or migratory, so that they are unlikely to experience the selective pressures at the one location through time. The competitive asymmetries would have to be very exaggerated for individuals of a resident population of one species to exclude those of an immigrant population of another species. Only in a deterministic view such as that of Cole (1960) could marginal differences in competitiveness lead to ecological differentiation within dynamic communities. A simpler solution seems to be for segments of entire populations to depart from areas where resources are depleted in search of richer areas, which would diminish the pressures of selection (Mac Nally & McGoldrick 1997).

Philopatry is a necessary condition for local co-evolution. Fledgling philopatry (i.e. local recruitment) is more critical for accumulation of genetic differences than is adult philopatry (i.e. community closure). Strong philopatry appears to be relatively rare in passerines (Weatherhead & Forbes 1994; Koenig *et al.* 1996), although there are exceptions (e.g. Peterson 1992; Murphy 1996). Migratory species generally exhibit lower natal philopatry than resident species (Weatherhead & Forbes 1994). Moreover, males and females often differ substantially in natal allegiance (e.g. Weatherhead & Boak 1986; Nagata 1993; Part 1995; Plissner & Gowaty 1996), while the young typically are rarely recovered at the fledging sites (e.g. Weatherhead & Boak 1986; Morton *et al.* 1991; Noske 1991; Bridges 1994; Todte 1994; Part 1995). Even apparently strict adult philopatry need not necessarily produce sharp genetic differences (Austin *et al.* 1994). Together, these ideas and observations suggest that the potential for ecological differentiation, at least at the local scale, through co-evolutionary means involving passerines (and many non-passerines) is limited.

Each of the three species considered here has a very different large-scale spatial dynamic from the others (see Mac Nally 1995c). Both whistlers are general in their habitat use, while Rose Robins typically occupy the wetter sclerophyll forests of the southeastern ranges. Rufous Whistlers and Rose Robins are seasonally migratory in southern Victoria, arriving in late

winter and departing in autumn. Golden Whistlers appear to be itinerant or altitudinal migrants, dispersing in the colder months into most woodland and forest habitats but congregating during the spring and summer in montane forests. Rufous Whistlers breed in many woodland and forest habitats throughout Victoria, while the other two breed mainly in montane forests. All of these disparities mean that selective pressures arise from different relative sources for any of the individuals that happen to occur in Olinda State Forest during the periods of co-occurrence (see also Martin & Karr 1990).

Little is known about adult or natal fidelity in these snatching species. Bridges (1994) reported that territorial fidelity of adult Rufous Whistlers was high (82–96%) at an isolated forest block in northern New South Wales. However, few fledged birds returned (18%). There is little or no comparable information for Golden Whistlers and Rose Robins. Thus, the question of community closure and local recruitment remains relatively unexplored so that this is a priority for future work.

Intra- and interspecific territoriality

Numerous workers have pointed out that local interspecific coexistence of ecologically similar species may be enhanced if each population is self-limiting (e.g. Chesson 1991). Thus, if intraspecific competition exceeds interspecific competition in each species, then, in principle, arbitrarily similar species can co-occur. At Olinda State Forest, there was very little interspecific aggression among the snatchers but the whistlers, in particular, exhibited intense intraspecific aggression. Male Golden and Rufous Whistlers often sang apparently oblivious to each other within the same tree. Conspecific males never did this; they often gathered at territorial borders and engaged in animated bouts of counter-singing and sometimes chased one another. During early territorial establishment, three to five male Rufous Whistlers often engaged in this form of aggression. It is possible that local population densities are controlled most strongly by intraspecific territoriality, and this may prevent the density of any one species increasing to a point at which it might impinge significantly on that of the other species. Whether intraspecific territoriality results from food limitation or paternity protection, which is likely, the effect is to limit local population densities of conspecific individuals.

Birds as exemplars of community organisation

More than most organisms, the mobility of birds means that local selective pressures necessary to produce ecological divergence (Mac Nally 1995b) are smoothed out

by migration, nomadism and dispersal (Austin *et al.* 1994; Avise 1996). Therefore, one would not *expect* that ecological differentiation should necessarily be widespread in avian communities, especially on continents and large land-masses. There might be some conditions under which divergences may occur, mostly involving the spatial confinement of populations (Mac Nally 1995b). For example, it is not surprising that closely related, relatively sedentary species on small islands might diverge under pressures arising from interspecific competition (e.g. Taper & Case 1992). The populations are hemmed in: mortality rather than emigration accounts for population declines and so selective pressures may be intense and linked to differential resource use; and recruitment is site-specific and presumably reflects selection. Generally speaking, however, the pronounced mobility of birds place their communities at the open end of the community spectrum (see Wiens 1984) at which few manifestations of evolutionary or proximate effects of interspecific competition should be expected. We might anticipate that pelagic, oceanic vertebrates and invertebrates will be similar to birds in this way. Sedentary species with widely dispersing larvae with unpredictable settlement patterns (e.g. many rocky-shore invertebrates; Connell 1985; Gaines & Roughgarden 1985) also fail to satisfy the necessary conditions for local co-evolution through interspecific competition.

Local ecological differentiation, such as that suggested by MacArthur (1958), therefore should not be regarded as being a necessary condition for local coexistence, especially of highly mobile organisms such as migratory and itinerant birds. MacArthur's warblers are usually held up as an exemplary system for the occurrence of resource partitioning but the more important issues probably are as follows: (i) what is the statistical distribution of such differentiation (i.e. is resource partitioning of this form predominant); and (ii) how do local factors, such as the composition of the local assemblage of species, resource availability and predictability etc. interact with biogeographic patterns and large-scale dynamics to influence the *necessity* for resource partitioning?

To conclude, then, although these three co-members of the snatching guild differ little in their foraging when together at Olinda State Forest during the spring–early summer breeding period, they do exhibit gross differences in large-scale dynamics and habitat usage. These gross differences have two related consequences: (i) a probable dilution of selective pressures that may in other circumstances lead to local differentiation; and (ii) individuals of each of the species will be exposed to a vast array of different avian assemblages during migration and itinerancy. While an individual Rufous Whistler, for example, may be exposed more or less constantly to Golden Whistlers during migration, the latter will be different individuals and in different

circumstances *vis-à-vis* habitat structure and resource availability. Thus, the interaction between the two species of whistlers is enacted and integrated over continental spatial scales. For highly vagile organisms, the arena of interactions may be immense, and a myopic concentration on tens-of-hectares plots and on local phenomena is probably misplaced.

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