DETERMINANTS OF GUILD STRUCTURE IN FOREST BIRD COMMUNITIES: AN INTERCONTINENTAL COMPARISON[1]

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Abstract. We examined the patterns of food resource utilization (guild structure) of 41 species of birds that breed in eucalypt forests and woodlands in south temperate Australia, and compared them to the results of a similar study in a north temperate, broad-leaved forest in North America (Holmes et al. 1979). Both studies used the same field methods and analytical techniques. The Australian community was more complex as inferred from the greater number of guilds (9 vs. 4) and from the results of principal components and factor analyses of the foraging data. These multivariate methods showed that guilds at the Australian site were separated first by differences in foraging height and bird weight, and second by foraging methods and food substrates. Use of specific foraging substrates (e.g., exfoliating bark) and food resources (e.g., nectar and other carbohydrates) were important at finer scales of separation. The results support the hypothesis that vegetation structure and food availability, which vary with plant species and vertical strata, produce particular sets of foraging opportunities for birds. These in turn influence which species can obtain food successfully, and thus can be considered primary determinants of guild structure. This comparison of food utilization patterns of birds in contrasting habitats provides insight into the factors determining bird community organization.

Key words: *Australian forest birds; bird community ecology; bird foraging; community structure; foliage structure; guild structure; resource availability; resource partitioning.*

INTRODUCTION

The major goals of avian community ecology are to identify recurrent patterns of species composition, guild structure, diversity, and other parameters among co-occurring species and to understand the factors promoting those patterns (Wiens and Rotenberry 1980). Guild structure can be defined as the patterns of resource use among co-occurring species, with emphasis on the similarities and differences in how those species exploit resources. For birds in terrestrial habitats, food is usually considered to be the important resource, and measurements of foraging behavior are often used to indicate how, where, and which food resources are obtained.

Although bird species have often been assigned to foraging guilds on the basis of a general knowledge of their feeding behavior (Eckhardt 1979, Alatalo and Alatalo 1979, Airola and Barrett 1985), few studies have identified guild structures objectively or have assessed the relative importance of the factors that define guilds (e.g., Cody 1974, Holmes et al. 1979, Landres and MacMahon 1980, 1983, Sabo 1980, Sabo and Holmes 1983). The latter studies show that guild structure varies from site to site and is correlated with particular features of the habitat and resource base. Holmes et al.

(1979) proposed that bird species composition in forest habitats depends largely on the foraging opportunities afforded by the environment at any particular site. They suggested that these were determined primarily by the physical structure of the vegetation, the kinds and distributions of foraging substrates, and the availability of food resources, each of which varies among plant species. Additional studies have shown that insectivorous birds often forage preferentially on certain tree species (Franzreb 1978, Holmes and Robinson 1981, Airola and Barrett 1985), probably because they differ in their abilities to sight and capture prey on plants with different physical attributes (Robinson and Holmes 1982, 1984) and because of different prey availabilities and abundances (Holmes and Robinson 1981, R. T. Holmes and J. C. Schultz, unpubl. data). These findings lead to the hypothesis that vegetation structure coupled with food resource availability and abundance, provide particular combinations of foraging opportunities for birds that in turn determine which bird species can forage successfully and survive there.

The purpose of this paper is to examine the generality of this hypothesis by comparing the foraging guild structure of birds in a south temperate, broad-leaved forest in southeastern Australia with that reported by Holmes et al. (1979) for birds in a north temperate broad-leaved forest. The avifaunas at these two sites have independent evolutionary histories (Sib-

ley and Ahlquist 1985), and occupy habitats that are broadly similar in structure but which differ in floristics and in some food resources available to birds. Such a comparison of birds in contrasting habitats helps to identify the effects of specific food and habitat characteristics on bird foraging, and thus on bird community structure (see also Cody 1975, Pearson 1977, Stiles 1978, Landres and MacMahon 1983, Sabo and Holmes 1983).

To facilitate the comparison, we used the same field methods and analytical procedures as Holmes et al. (1979). The latter include multivariate statistical techniques that reduce a large number of correlated variables to a smaller number of identifiable factors that indicate which variables are most important in segregating species and guilds (Cooley and Lohnes 1971). Note that we use guild in the sense of Root (1967) to refer to species exploiting a resource in similar ways and that we limit our analyses to the avian component of these communities, acknowledging that other taxa in a more inclusive biological community may also use some of the same resources (see Jaksic 1981).

STUDY AREA

This study was conducted on the Southern Tablelands of New South Wales (N.S.W.) and Victoria in southeastern Australia. The three 10-ha study areas were located approximately 40 km southeast of Bombala, N.S.W. (36°54'S, 149°14'E, elevation = 800 to 850 m) adjacent to Bondi State Forest.

The study areas consisted of forest-woodland ecotone grading from a moist, tall open-forest through drier, open-forest to woodland at the edge of grazed pastures. The dominant trees in the moist forest were narrow-leaved peppermint (*Eucalyptus radiata*), ribbon gum (*E. viminalis*), and mountain gum (*E. dalrympleana*). Brown barrel (*E. fastigata*) and monkey gum (*E. cypellocarpa*) occurred infrequently. Canopy height averaged 22 m, with a few trees emerging to 40 m. Young eucalypts, with scattered blackwood (*Acacia melanoxylon*) and silver wattle (*A. dealbata*), formed a subcanopy to 13 m in height. The shrub layer extended from 1 to 4 m, and was diverse and often dense. It contained mostly Gippsland waratah (*Teleopea oreades*), lomatia (*Lomatia ilicifolia*), blackthorn (*Bursaria spinosa*), and wattles (*Acacia* spp.). Ground cover consisted of ferns (mostly bracken, *Pteridium*), a sedge (*Lomandra longifolia*), occasional forbs, and considerable fallen wood, strips of bark, and leaf litter. There was no evidence of logging or recent burning.

The areas of drier forest were dominated by

the same three eucalypt species on well drained soils, and by swamp gum (*E. ovata*) where drainage was impeded. Trees were more widely scattered and the canopy slightly more open than in the moist forest. Canopy height averaged 16 to 20 m. The understory consisted entirely of small eucalypts, and the shrub layer was more open, due to occasional grazing of domestic stock, and some selective logging of pole-size trees. The dry forest graded into woodland dominated by snow gum (*E. pauciflora*) and black sally (*E. stellulata*), which were shorter (8 to 10 m) than trees in the forest. In this woodland, the ground was sparsely covered with litter, patches of grass (*Poa* spp.), bracken, and sedge. Both dry forest and woodland showed evidence of past burning, but none within several years prior to our study.

The climate at Bondi Forest is cool temperate, with mean monthly temperatures of 18°C in January and of −1°C in July (Recher et al. 1983). During October 1980 to January 1981 when this study was conducted, night temperatures were 5 to 10°C, mornings were often foggy, and mid-day temperatures climbed to 20 to 25°C. Rainfall is variable but occurs throughout the year. From 1970 to 1982, it averaged 1,000 mm per year at Bondi Forest, but in 1980, which was the beginning of a drought, the annual total was only 650 mm (Forestry Commission, N.S.W., weather records; H. F. Recher, unpubl. data). These study areas and their characteristics are described in greater detail by Recher et al. (1983, 1985) and Recher and Holmes (1985).

METHODS

BIRD FORAGING PATTERNS

We quantified foraging behavior of birds at Bondi Forest between 15 October 1980 and 15 January 1981, which was the breeding season for all species (Recher and Holmes 1985). Foraging data were gathered throughout the study period, primarily in the morning hours but also at other times of day. Each time a bird under obervation took or attempted to capture a food item, we recorded the foraging method, the substrate from which the food was taken or towards which the attack was directed, the height above ground (to the nearest m), and, whenever possible, the type of food taken. An individual bird was followed until a maximum of five successive foraging attempts was recorded or the bird was lost from sight. This procedure increased the chance that the less conspicuous and/or rarer foraging actions were recorded, and reduced the problem of serial dependency (Morrison 1984). Data were obtained from at least 20 to 30 individuals for

the more common species to at least 6 to 8 for the less common ones (Table 1). The individuals observed were chosen randomly as we moved through the study areas. Some individuals were undoubtedly observed more than once during the study, but never on the same day and rarely in the same week. Sample sizes represent the cumulative number of foraging attempts observed for each species (see Table 1).

Foraging methods were categorized as follows: (1) glean—a stationary food item (e.g., insect, fruit, nectar) is picked from its substrate by a standing or hopping bird; (2) probe or prise—like glean only the bird's beak penetrates or lifts the substrate to locate concealed food; (3) hover—a bird takes flight, hovers in a stationary position, sometimes only momentarily, near a substrate, and picks the food item from the substrate's surface; (4) snatch—like hover but the flying bird does not hover; instead it plucks the food from the substrate as it flies past; (5) pounce—a bird flies from a perch and grabs the food item as it lands on the substrate (usually the ground); and (6) hawk—a bird sallies into the air to catch flying prey. This last category is equivalent to "sally" or "flycatch" as used by Fitzpatrick (1980) and others.

Substrates from which food items were taken were classified as: (1) ground, including debris, litter, and grass; (2) trunks—the main axes of trees; (3) branches—smaller secondary axes of trees, >1 cm in diameter; (4) twigs—small branches <1 cm in diameter to which leaves were attached; (5) leaves, including leaf blades and petioles; (6) loose bark—mainly strips or coils of peeling or exfoliating bark most common on upper trunks and branches of certain species of *Eucalyptus,* but also caught as debris in the foliage of understory plants; (7) flowers; (8) *Eucalyptus* capsules (seeds); and (9) air. Plant species on the study plots were categorized as follows (note eucalypts were grouped by major physiognomic types): (1) rough-barked eucalypts (*E. radiata* and *E. fastigata*) with rough, corrugated, dark-colored, non-deciduous bark; (2) forest gums (*E. dalrympleana, E. ovata, E. viminalis*)—large, tall forest trees with smooth, light-colored bark that often peels in long strips or coils; (3) woodland gums (*E. pauciflora, E. stellulata*), similar to forest gums but of smaller size and shorter stature; (4) small trees and shrubs of the genus *Acacia*; (5) Gippsland waratah, a shrub bearing nectar-rich flowers during the period of this study; (6) other shrubs, mostly *Lomatia* and *Bursaria*; and (7) ground vegetation, mostly monocots and ferns.

From these categories, we recognized 22 for-aging characters for the multivariate analyses. These consisted of 15 foraging method-substrate combinations (see Table 2 and Appendix) and the 7 vegetation categories listed above. We also used mean foraging height, one standard deviation of foraging height (to represent the species' use of vertical strata), and the species' average body weight (Table 1). The latter was included as an index to bird size; it also serves as an approximate indicator of prey size, at least for insectivorous species (cf. Hespenheide 1975). These 25 variables were similar to the 27 characters used by Holmes et al. (1979), except that for the present study: (1) several unique foraging method-substrate categories were recognized (e.g., glean flower, glean loose bark); (2) tree species were grouped by physiognomic or life-form categories (although these were generally taxonomically-affiliated groupings); and (3) foraging in the proximal and distal portions of trees was not distinguished.

MULTIVARIATE ANALYSES

For the multivariate analyses, we followed the procedures described by Holmes et al. (1979). In this case, the data matrix consisted of 41 bird species (rows) by 25 foraging characters (columns). The first 22 characters, representing utilization frequencies of foraging categories, were log-transformed to reduce skewness. The last three columns involving mean and SD of foraging height and body weight were not transformed. All 25 columns were standardized to bring the means to 0 and variances to 1.0, with the result that each measurement was expressed in standard deviation units from its column mean. The effect of this standardization is to weight all categories equally.

The 25 foraging character × 41 bird species matrix was used to calculate Euclidean distances between all 41 species in the hyperspace defined by the 25 foraging characters (Q-technique of Sneath and Sokal 1973). This distance matrix was subjected to a hierarchical clustering analysis (maximum method, Johnson 1967) to produce a dendrogram showing foraging relationships among bird species. Principal components were obtained by multiplying eigen vectors by the transposed 41 × 25 matrix (Harman 1967). Finally, a varimax rotated factor analysis was performed on the 41 × 25 matrix (R-technique, Sneath and Sokal 1973). Eigen roots >1.0 were used to calculate an orthogonally-rotated factor pattern, following the procedures of Cooley and Lohnes (1971). The analyses were run on the Dartmouth Time Sharing System, using programs developed by McGee (1978).

TABLE 1. Characteristics of the 41 common bird species breeding in the eucalypt forests and woodlands near Bondi State Forest, N.S.W.

Family and species[a]	Code	Body weight[b] (g)	Foraging height (m) $\bar{x} \pm SD$	Minimum number of individuals[c]	Foraging maneuver sample size[d]
Cacatuidae					
Gang-gang Cockatoo					
Callocephalon fimbriatum	GG	219.0	13.1 ± 5.3	8	280
Platycercidae					
Eastern Rosella					
Platycercus elegans	ER	116.3	10.5 ± 5.2	30	1,309
Cuclidae					
Fan-tailed Cuckoo					
Cuculus pyrrhophanus	FTC	46.3	0.5 ± 1.8	12	100
Menuridae					
Superb Lyrebird					
Menura novaehollandiae	LB	746.0	0.0 ± 0.0	8	62
Campephagidae					
Black-faced Cuckoo-shrike					
Coracina novaehollandiae	BFC	109.8	11.4 ± 6.0	12	75
Muscicapidae					
Ground Thrush					
Zoothera dauma	GT	106.2	1.2 ± 3.0	10	225
Rose Robin					
Petroica rosea	RR	8.7	3.9 ± 4.2	10	195
Flame Robin					
Petroica pheonicea	FR	13.3	3.3 ± 3.5	30	830
Scarlet Robin					
Petroica multicolor	SR	13.0	1.1 ± 2.3	8	465
Eastern Yellow Robin					
Eopsaltria australis	YR	20.0	1.0 ± 2.4	40	408
Eastern Shrike-tit					
Falcunculus frontatus	EST	28.6	11.2 ± 6.3	12	518
Rufous Whistler					
Pachycephala rufiventris	RW	25.8	8.7 ± 5.6	45	983
Golden Whistler					
Pachycephala pectoralis	GW	25.3	5.1 ± 4.9	20	551
Grey Shrike-thrush					
Colluricincla harmonica	GST	75.6	4.2 ± 4.2	8	258
Black-faced Flycatcher					
Monarcha melanopsis	BF	23.6	7.0 ± 6.5	8	283
Satin Flycatcher					
Myiagra cyanoleuca	SF	17.5	10.7 ± 4.4	22	429
Grey Fantail					
Rhipidura fuliginosa	GFT	9.3	7.3 ± 6.7	80	2,354
Rufous Fantail					
Rhipidura rufifrons	RFT	10.4	1.4 ± 1.6	15	303
Orthonychidae					
Eastern Whipbird					
Psophodes olivaceus	WB	62.2	1.1 ± 1.6	10	133
Maluridae					
Superb Blue Wren					
Malurus cyaneus	SBW	9.7	0.2 ± 0.8	25	803
Acanthizidae					
White-browed Scrubwren					
Sericornis frontalis	WBS	12.8	0.3 ± 0.8	40	711
Brown Thornbill					
Acanthiza pusilla	BT	6.9	2.5 ± 2.8	50	1,832
Buff-rumped Thornbill					
Acanthiza reguloides	BRT	7.5	1.5 ± 2.6	30	559
Striated Thornbill					
Acanthiza lineata	ST	7.1	10.3 ± 6.4	100	1,331
Yellow-rumped Thornbill					
Acanthiza chrysorrhoa	YRT	8.8	0.3 ± 1.4	12	378

TABLE 1. Continued.

Family and species[a]	Code	Body weight[b] (g)	Foraging height (m) $\bar{x} \pm SD$	Minimum number of individuals[c]	Foraging maneuver sample size[d]
Neosittidae					
Orange-winged Sittella					
Daphoenositta chrysoptera	OWS	11.9	8.8 ± 2.8	18	454
Climacteridae					
Red-browed Treecreeper					
Climacteris erythrops	RBT	23.3	5.9 ± 4.4	16	1,238
White-throated Treecreeper					
Climacteris leucophaea	WTT	21.8	6.1 ± 4.2	25	1,224
Meliphagidae					
Red Wattlebird					
Anthochaera corunculata	RWB	99.2	3.1 ± 4.2	18	254
Yellow-faced Honeyeater					
Meliphaga chrysops	YFH	17.1	7.0 ± 4.8	35	909
White-eared Honeyeater					
Meliphaga leucotis	WEH	24.5	6.8 ± 4.6	15	614
Brown-headed Honeyeater					
Melithreptus brevirostris	BHH	14.6	16.7 ± 5.0	20	235
White-naped Honeyeater					
Melithreptus lunatus	WNH	14.7	11.9 ± 10.3	100	2,805
Crescent Honeyeater					
Phylidonyris pyrrhoptera	CHE	16.4	2.7 ± 0.6	10	177
Eastern Spinebill					
Acanthorhynchus tenuirostris	ESB	10.9	2.2 ± 0.8	10	157
Pardalotidae					
Spotted Pardalote					
Pardalotus punctatus	SP	8.3	9.9 ± 5.4	15	317
Striated Pardalote					
Pardalotus striatus	STP	11.9	13.0 ± 5.0	35	810
Zosteropidae					
Silvereye					
Zosterops lateralis	SE	10.4	7.9 ± 6.7	25	530
Corcoracidae					
White-winged Chough					
Corcorax melanorhamphus	WWC	684.0	0.0 ± 0.0	10	250
Artamidae					
Dusky Woodswallow					
Artamus cyanopterus	DWS	35.7	4.6 ± 2.8	10	145
Cracticidae					
Australian Magpie					
Gymnorhina tibicen	AM	314.0	0.0 ± 0.3	18	622

[a] Nomenclature follows Condon (1975) and Schodde (1975).
[b] Mean body weights from Recher et al. 1985 and H. F. Recher, unpubl. data.
[c] Minimum number of individuals residing in the study areas, based on average numbers seen per four 4-hour censuses (Recher et al. 1985 and H. F. Recher, unpubl. data).
[d] Sample sizes used in multivariate analyses.

RESULTS

At Bondi Forest, there were 41 common breeding bird species for which we were able to obtain relatively large samples of foraging behavior (Table 1). These ranged in weight from the 6- to 8-g thornbills to the 746-g lyrebird. We were not able to obtain data on raptors, nocturnally-active birds (e.g., Tawny Frogmouth, *Podargus strigoides*; Owlet Nightjar, *Aegotheles cristatus*) or several rare species (see Recher and Holmes 1985), which were difficult to observe. Our analyses are therefore of the common, diurnally active, non-raptorial birds breeding in this eucalypt woodland-forest habitat.

Data used in the multivariate analyses are given in Table 1 (mean body weights, mean foraging heights, and standard deviations of foraging heights) and in the Appendix (the 22 categories of foraging method-substrate and plant use). The correlation and Euclidean distance matrices from the multivariate analyses are available from the authors upon request. Descriptions of the foraging behavior of these bird species are given by Recher et al. (1985) and Holmes and Recher (1986).

TABLE 2. The rotated factor pattern showing the most heavily weighted factors, either positive or negative, for each of the 25 characters.

	Factors								Row SS
	I	II	III	IV	V	VI	VII	VIII	
Eigen roots	5.68	4.50	2.83	2.14	1.99	1.62	1.42	1.00	
Factor contribution to community variance (%)	22.74	18.01	11.34	8.57	7.96	6.67	5.67	3.98	
Cumulative %	22.74	40.75	52.09	60.65	68.61	75.28	80.95	84.93	
1. Hover leaf		-0.5911							0.7440
2. Glean leaf		-0.8654							0.8641
3. Snatch leaf							0.8883		0.9422
4. Glean flower				0.9391					0.9236
5. Glean twig		-0.8066							0.8041
6. Glean eucalypt capsules						0.8974			0.9150
7. Glean loose bark					0.8112				0.7907
8. Hawk							0.6051		0.7917
9. Glean branch		-0.5487			0.5353				0.7742
10. Snatch branch							0.8918		0.8560
11. Glean trunk					0.8700				0.8068
12. Snatch trunk		0.6414							0.8970
13. Glean ground								-0.9011	0.8711
14. Pounce ground		0.6857							0.8599
15. Probe ground	-0.8933								0.8764
16. Rough-barked eucalypts	0.7958								0.8964
17. Forest gums								0.5839	0.6994
18. Woodland gums	0.7992								0.8483
19. *Acacia*			-0.7846						0.9084
20. Waratah				0.9552					0.9446
21. Other shrubs			-0.9309						0.9059
22. Ground vegetation			-0.5597						0.7038
23. Foraging height $\bar{x}$	0.5236							-0.5822	0.9254
24. Foraging height SD						0.5286		0.4974	0.8938
25. Body weight	-0.7986								0.7889

GUILD STRUCTURE: CLUSTER ANALYSIS OF EUCLIDEAN DISTANCES

The relationships among the 41 bird species, based on the 25 foraging characters, are summarized in the cluster diagram in Figure 1. The species are separated into a number of distinct groups whose members exploit food resources in similar ways, and can thereby be considered guilds (cf. Root 1967). We define guilds operationally as those groups of species that are separated from one another by Euclidean distances greater than the mean distance ($\bar{x}$ = 6.91, in this case) between all species pairs (Holmes et al. 1979). Using this arbitrary criterion, we recognize nine guilds among the 41 bird species at Bondi (Fig. 1).

Starting from the top of Figure 1, and basing interpretations on the Appendix (see also Recher et al. 1985), we characterize the guilds as follows: Guild I contains three honeyeaters that fed extensively on nectar obtained from flowers, primarily of Gippsland waratah. Guild II consists of three species that predominately gleaned prey from ground litter, debris, and low vegetation. The five species in guild III were those that foraged by gleaning prey from foliage and associated twigs and small branches. Within this guild, the Silvereye and Brown Thornbill foraged mostly in the shrub layer, where they took prey from a diverse array of plant species. The other three species — the two pardalotes and the Striated Thornbill — foraged exclusively on eucalypt foliage, mainly in the subcanopy and canopy. Guild IV is a taxonomically diverse group of 11 species, including two thornbills, four honeyeaters, a sittella, two treecreepers, a shrike-thrush, and a shrike-tit, all of which foraged by gleaning but differed in their use of substrates. The sittella and treecreepers were bark foragers, with the sittella foraging mainly on dead branches and the treecreepers on the trunks of trees (Appendix). The shrike-tit and White-eared Honeyeater foraged extensively on hanging and loose or exfoliating bark. Loose hanging bark was also used by Brown-headed and White-naped Honeyeaters, but they and the Yellow-faced Honeyeater were primarily foliage gleaners (Appendix). The Grey Shrike-thrush was a generalist forager. It used a wide range of substrates including bark and foliage, but it foraged extensively on the ground and is grouped with the two smaller ground-foraging thornbills. Guild V contains species that primarily caught flying prey (e.g., Grey Fantail, Satin Flycatcher) or snatched prey from foliage (two whistlers, Black-faced Flycatcher, and Black-faced Cuckoo-shrike) in the subcanopy and canopy. Guild VI consists of the Rose Robin and Rufous Fantail which also pursued aerial
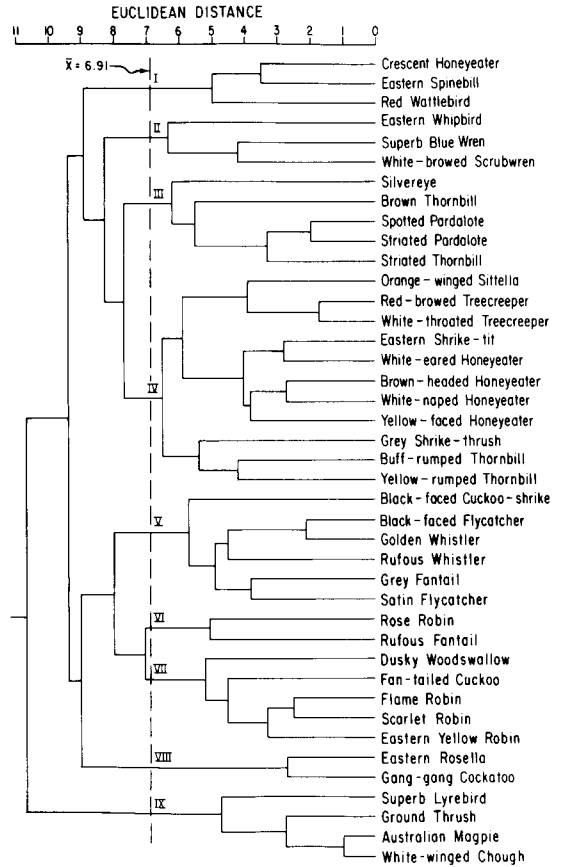

FIGURE 1. Cluster diagram of Euclidean distances between 41 species of birds near Bondi State Forest, N.S.W., Australia, based on their similarities and/or differences in foraging. Dashed line represents the mean Euclidean distance between all combinations of species pairs at Bondi. The roman numerals refer to the guilds described in the text.

prey but are smaller (9 to 10 g) than species in Guild II and foraged among the ground and low shrub vegetation. Guild VII consists of five species that fed by pouncing on ground- and trunk-dwelling invertebrates, although the Dusky Woodswallow frequently took aerial insects (Appendix). Guild VIII comprises the two parrots which fed almost exclusively on the seeds of eucalypts that they extracted from the ripening capsules. Guild IX contains four species of large ground foragers (>100 g body weight), and is thereby distinguished from the much smaller ground-foraging bird in Guilds II and IV. The relative importance of these various differences and characteristics among the nine guilds will be considered below.

GUILD STRUCTURE: PRINCIPAL COMPONENTS ANALYSIS

Another approach to identifying guild structure is to examine patterns revealed by principal components analysis (PCA). The first two PC axes in the analysis of the Bondi data ac-

counted for 22.7 and 18.0% of the community variance, respectively, and provide relatively interpretable divisions among the species (Fig. 2). Axis 1 segregates species that forage mostly in subcanopy and canopy layers (positive values) from those that forage on the ground or in low vegetation (negative values). Axis II separates species that hawk, snatch, and pounce (positive values) from those that glean, and/or probe, and prise. Thus, differences in use of forest strata followed by differences in foraging methods are the primary factors segregating species in how they exploit food resources in this habitat. The species in the PCA (Fig. 2) are positioned in ways that closely reflect the guilds distinguished in the cluster analyses (Fig. 1). The heterogeneity of guild IV, which contained 11 species according to the cluster analysis (Fig. 1), is upheld by the spread of these species along the two PC axes (Fig. 2).

The third and subsequent PC axes were not easily or clearly interpretable, probably because each accounted for so little (<11.5%) of the community variance (R. T. Holmes and H. F. Recher, unpubl. data; see Table 2).

DETERMINANTS OF GUILD STRUCTURE: VARIMAX FACTOR ROTATION

The Varimax rotated factor analysis determines more explicitly which variables or groups of variables were important in segregating these bird species and guilds (Table 2). The first eight eigen vectors extracted from the correlation matrix had values ≥ 1.0, and accounted for 85% of the community variance (Table 2). Following Aspey and Blankenship (1977), we only list factor loadings in Table 2 that are >0.45, because lower values share <20% of the variance with a particular factor.

Factor I has positive loadings for "rough-barked eucalypts," "woodland gums" and "standard deviation of foraging height" and negative values for "probe ground" and "body weight" (Table 2). Thus, birds that foraged on these trees had broad foraging height ranges and differed from those large (heavy) species that probed on the ground. This separation of birds that forage at many heights above the ground from ground foragers confirms the above interpretation of the first PCA axis, i.e., guilds are first segregated by height. These findings also suggest that differences in body size may be involved in segregating species.

Factor II has positive loadings for "pounce ground" and "snatch trunk," and negative loadings for "hover leaf" and "glean leaf, twig and branch." This separates the species that pounce on their food from those that primarily glean, and supports the interpretation of Axis 2 of the PCA (Fig. 2) that foraging methods are the second major set of characteristics that segregate guilds.

Factor III has negative loadings for "*Acacia*," "other shrubs," and "ground vegetation." This separates shrub-foraging insectivorous species (e.g., Brown Thornbill, Golden Whistler) from the shrub-foraging nectarivores (e.g., Crescent Honeyeater, Eastern Spinebill). Nectar-feeders are further segregated on Factor IV, which has positive loadings for "glean flower" and the plant species, "waratah."

Although factors V and VIII each account for <8% of the variance in community patterns (Table 2), they help to explain smaller groupings within the community. Factor V has positive loading for "glean loose bark," "glean branch," and "glean trunk," separating the bark foragers (e.g., Eastern Shrike-tit, treecreepers) from other species (see Appendix). Factor VI has positive loadings for "glean *Eucalyptus* capsules" and "mean foraging height," which segregates the two canopy-foraging parrots from the rest of the community (Table 1 and Appendix). Factor VII has positive loadings for "snatch leaf," "snatch branch," and "hawk" which distinguishes the active foragers such as fantails, flycatchers, and whistlers. Factor VIII has positive loadings for "forest gums" and "mean foraging height," and negative for "glean ground" and "ground vegetation." This reinforces the distinction between foraging higher in the forest, and foraging on the ground, or in low vegetation as found with Factor I.

COMPARISONS AND DISCUSSION

Since it is difficult to compare guild structures without objective or standardized techniques, we focus this discussion on the patterns of bird guild structure at Bondi and in the northern hardwoods forests at Hubbard Brook in New Hampshire (Holmes et al. 1979), which were studied with the same field methods and analytical techniques. These two studies also considered the same range of species, i.e., all of the common, diurnally-active, nonraptorial breeding bird species occupying the study areas. Although other studies of bird foraging relations in forested habitats have been made, for example, by Cody (1974), Landres and MacMahon (1980, 1983), Sabo (1980), Alatalo (1982), and Airola and Barrett (1985), these have either used different techniques (Cody, Landres and MacMahon, Sabo) or have considered only some components of the avian assemblage (Alatalo, Airola and Barrett). The only studies quantifying bird foraging behavior in Australian habitats are those of Crome (1978) and Frith (1984) in Queensland rain-
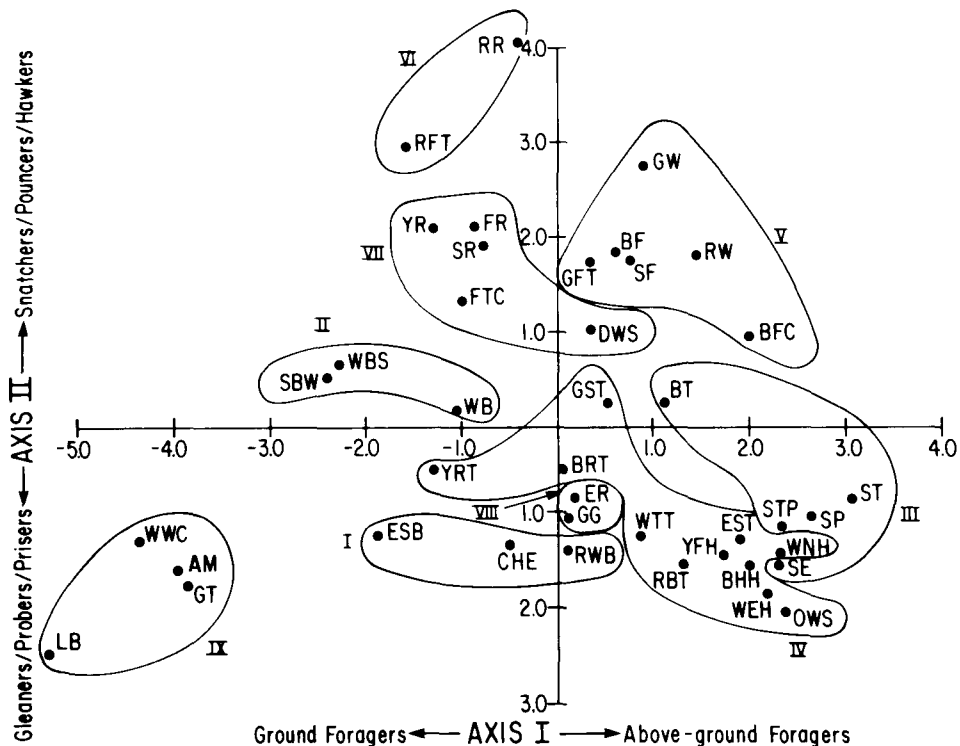
FIGURE 2. Projection of 41 bird species along the first two principal component axes, based on foraging data. Axes I and II account for 23% and 18% of total variance, respectively. Encircled species groups are those identified as guilds I–IX in the cluster analyses (Fig. 1). See Table 1 for species symbols.

forests, Thomas (1980) in a temperate rainforest in Tasmania, and Ford et al. (in press) in a eucalypt woodland near Armidale in northeastern N.S.W. None, however, used multivariate statistical techniques to identify factors underlying guild structure.

The habitats and avifaunas at Bondi Forest and Hubbard Brook are broadly similar in a number of ways, yet differ in important details. Bondi Forest is characterized by a relatively mild climate, the vegetation is composed of sclerophyllous, mostly evergreen, broad-leaved trees, dominated by 3 to 4 species of *Eucalyptus*, and there are 41 common bird species that breed in this forest-woodland ecotone. At Hubbard Brook, the climate is more strongly seasonal, with long, cold, snowy winters and warm, moist summers, the vegetation is dominated by 3 species of broad-leaved deciduous trees, and there are 22 common breeding bird species. The avifaunas at the two sites are phylogenetically distinct (Sibley and Ahlquist 1985). The forest structure at both sites is roughly comparable, with canopy heights averaging 20 to 30 m, although physical characteristics of the vegetation (e.g., leaf shapes and sizes, branching patterns) differ considerably (see below).

In spite of these differences in climate, plant structure, bird species richness, and the historical factors which have influenced all of these features, the avian guild structures at Bondi Forest and Hubbard Brook are basically similar. The guilds at both sites are separated into foliage-, bark-, and ground-foraging groups, and these are further subdivided by differences among species in their use of foraging substrates and methods, and in body size. The Australian community, however, is more complex as evidenced by (1) the greater number of species (41 vs. 22) and guilds (9 vs. 4), (2) the emergence in the factor analysis of more eigen roots with values > 1 (8 vs 5), (3) more equitable distribution of variance among the different factors (the first two factors combined accounted for only 40.8% of the variance in the Australian community compared to 60.9% for Hubbard Brook), and (4) by the less easily interpreted multivariate axes, especially in the PCA. In the Hubbard Brook analysis, the factor analysis produced fewer, more heavily weighted and more clearly interpretable factors (Holmes et al. 1979). Also, species in the Australian community are generally more specialized in their foraging, using one or at most two of the major foraging method-substrate combinations (Appendix). At Hubbard Brook, most species have broader foraging repertoires

(Holmes et al. 1979, Robinson and Holmes 1982, R. T. Holmes and H. F. Recher, unpubl. data).

Some of these differences, especially the number of species and guilds, are related to the ecotonal forest and woodland habitat considered at Bondi Forest. However, analyses of data from only the moist forest at Bondi Forest, which is more directly comparable to Hubbard Brook (26 vs. 22 bird species, similar canopy heights, etc.) but for which we had relatively small sample sizes of bird foraging behavior, show the same differences in complexity as enumerated above (R. T. Holmes and H. F. Recher, unpubl. data). It therefore seems that more diverse factors must be influencing the foraging patterns and guild structure of birds in the Australian forest. Comparisons of the two communities help to elucidate the factors underlying these differences and to identify what aspects of the environment determine guild structure at each site.

The initial separation of guilds in the Australian community was related to birds' differential use of vertical strata, particularly ground versus above-ground foraging. The occurrence of body size on the first factor can be attributed to the influence of three large species (Superb Lyrebird, White-winged Chough, and Australian Magpie), which foraged exclusively on the ground, thus accentuating the body size-low stratum relationship. Since the first factor separating guilds at Hubbard Brook was also height-related (Holmes et al. 1979, see also Sabo and Holmes 1983), forest stratification seems to be a major factor segregating species, suggesting that foraging opportunities for birds in these forests differ with height.

The second major factor separating guilds at Bondi Forest was related to differences in foraging methods, especially how birds obtained their food (foraging method) and the substrates from which prey were taken. This contrasts with Hubbard Brook where foraging zones (tree boles versus more distal foliage) were the major categories on the second axis. This latter dichotomy may be more distinct in the north temperate forest because of the presence of bark-burrowing insects and of birds (woodpeckers: Picidae) that excavate these prey. At the Australian site, such prey were lacking or at least unavailable in the dense eucalypt wood (G. Gowing and H. F. Recher, unpubl. data), and no birds at Bondi Forest fed by probing or drilling into eucalypt trunks or branches.

Finer divisions of guilds at Bondi Forest were related to the effects of different plant species, or physiognomies, and bird foraging methods, coinciding with the interpretations of the third

and succeeding factors in the Hubbard Brook analysis. As at Hubbard Brook, plant species in the south temperate eucalypt forests in Australia support different food resources for birds (Ohmart et al. 1983, Recher et al. 1983, Woinarski and Cullen 1984) and have different foliage arrangements and substrates on which prey may sit or within in which they may hide (see below). These characteristics, which also vary over the vertical profile of a forest, produce particular sets of foraging opportunities for birds, which, as shown by the results of the multivariate analyses here, are important as segregators of guilds. If such foraging opportunities are correlated with increased vegetational complexity, this would help to explain the findings of MacArthur and MacArthur (1961), Recher (1969) and others that bird species diversity is related to vegetational diversity, but in this case, the importance of plant species and their different physiognomies, and associated food resources is emphasized. Plant species and their differing structures may also be important in the latter regard by providing suitable nest sites, especially for cavity nesters (Recher and Holmes 1985).

Several contrasting features of the habitats at Bondi Forest and Hubbard Brook illustrate how forest structure and available food resources influence bird foraging and thus guild structure. For instance, at Bondi, the canopy is relatively open and the foliage is evenly spaced with leaves that are long, narrow, and hang vertically. This means that branches and other perch sites for birds are typically separated from the foliage by relatively long distances, which in turn requires those species that search foliage to scan for prey over long distances. This may explain the greater frequency of species at Bondi Forest that hover, snatch or hawk their prey and that have correspondingly longer prey-attack distances, compared to those at Hubbard Brook (Holmes and Recher 1986). At the latter site, the foliage is denser and more clumped along branches, which makes gleaning close to perches more feasible, and perhaps more productive.

A second example concerns the effects of foliage density in the shrub and litter layer, and the availability of food resources there. At Bondi Forest, the relatively open shrub layer, especially in the drier forest and woodland, coupled with the presence of low exposed perches with views to the ground and the availability of large surface-active prey such as beetles and small lizards (G. Gowing and H. F. Recher, unpubl. data), provide foraging opportunities for bird species, such as the muscicapid robins and the Fan-tailed Cuckoo, that pounce on ground-dwelling prey. In the Hub-

bard Brook forest, the vegetation in the shrub and ground layers is dense, litter is thick, there are few large prey active on the forest floor, at least during the day, and the pouncing foraging method is used only rarely (R. T. Holmes and S. K. Robinson, unpubl. data).

At Bondi Forest, particular plant species provide food resources for birds that are not available in the north temperate forest. The eucalypts have seeds in large, hard capsules, which are fed upon almost exclusively by the two species of parrot. No equivalent resource is available to breeding birds at Hubbard Brook and no seed-eating guild is present there during the breeding season. Also, many of the plants at Bondi Forest, such as waratah and the eucalypts, provide nectar resources that are fed upon extensively by birds such as honeyeaters and silvereyes. Furthermore, such nectar production is not synchronous (Recher et al. 1983), resulting in the need for nectar-feeding birds to shift their use of plant species seasonally. Plants at Bondi Forest also produce, either directly or indirectly, other types of carbohydrate materials, such as manna (bark exudates), honeydew (insect secretions) and lerp (sugary coating of jumping plantlice, Psyllidae:Homoptera), that are used as food by honeyeaters, silvereyes, pardalotes, thornbills, and others (Paton 1980, Woinarski 1985, Ford et al., in press). The relative abundance of these also varies among plant species (Paton 1980, Woinarski and Cullen 1984). The only similar resource at Hubbard Brook is tree sap utilized by the Yellow-bellied Sapsucker (*Sphyrapicus varius*) and its commensal, the Ruby-throated Hummingbird, *Archilochus colubris* (Miller and Nero 1983).

As a final example, the exfoliating bark of forest and woodland gums at Bondi Forest provides specialized foraging opportunities for birds. These strips of peeling bark harbor various insects and spiders, which were exploited specifically by White-eared and Brown-headed Honeyeaters, Eastern Shrike-tits, and Whipbirds. The first three species searched for prey on this foraging substrate high in the canopy, while the Whipbird foraged most commonly among piles of fallen bark on the ground. No comparable foraging substrate/resource is available to birds at Hubbard Brook, although Winter Wrens (*Troglodytes troglodytes*) often searched for food on the bark of fallen branches and boles (Holmes et al. 1979), and thus show some similarity to the Whipbird.

In conclusion, this analysis of foraging guild structure among birds in a eucalypt forest-woodland, when contrasted with the results from a similar study in a north temperate forest, supports the hypothesis that vegetation structure (e.g., foliar arrangements, positioning and accessibility of available substrates) and the types and availabilities of food resources strongly influence how birds forage. Since foliage structure and resource availability change over the vertical profile of forests and vary with plant species, they act in conjunction with forest stratification to shape the kinds of foraging opportunities that can be exploited by birds. These characteristics in turn influence which species can successfully exploit food there, and therefore can be considered primary determinants of guild structure. Other processes, such as historical factors that determine the available species pool and competition among species for available resources, will also affect which particular species are present, the numbers of species per guild, and more subtle relationships among species (Sabo and Holmes 1983).

Further comparisons of guild structures of birds in both similar and contrasting habitats are needed to clarify the importance of vegetation structure and food resources in determining bird community structure. Like the present study, however, the results of such comparisons are correlational and can only suggest what may be the underlying causal agents. Thus, more direct investigations designed to test how foliage structure and food availability affect the foraging success, habitat selection, and ideally the survival of individual birds and species are also urgently needed.

ACKNOWLEDGMENTS

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APPENDIX: Percent utilization of foraging categories by 41 bird species breeding in the forests and woodlands near Bondi State Forest, N.S.W. Values for the 15 foraging method/substrates sum to 100%, as do those for the 7 plant-use categories. See Table 1 for keys to species abbreviations.

Bird species	Hover leaf	Glean leaf	Snatch leaf	Glean flower	Glean twig	Glean eucalypt capsules	Glean loose bark	Hawk	Glean branch	Snatch branch	Glean trunk	Snatch trunk	Glean ground	Pounce ground	Probe ground	Rough-barked eucalypt	Forest gum	Wood-land gum	Acacia	Wara-tah	Other shrub	Ground vege-tation
CHE	—	2.0	3.0	83.0	—	—	6.0	1.0	2.0	1.0	1.0	1.0	—	—	—	—	23.0	5.0	1.0	70.0	1.0	—
ESB	—	2.0	1.0	81.0	—	—	10.0	2.0	1.0	—	—	2.0	1.0	—	—	2.0	—	3.0	1.0	91.0	3.0	—
RWB	—	17.0	8.0	64.0	—	—	—	2.0	7.0	—	—	—	2.0	—	—	24.0	8.0	19.0	—	49.0	—	—
WB	—	2.0	2.0	—	1.0	—	31.0	—	6.0	—	5.0	1.0	32.0	—	20.0	30.0	20.0	—	33.0	—	15.0	2.0
SBW	—	7.0	2.0	—	—	—	—	4.0	2.0	—	—	—	85.0	—	—	41.0	2.0	11.0	3.0	—	2.0	41.0
WBS	—	9.0	1.0	—	1.0	—	1.0	—	5.0	—	1.0	—	81.0	—	1.0	32.0	—	—	7.0	10.0	38.0	13.0
SE	—	40.0	—	13.0	13.0	—	2.0	—	27.0	—	—	—	2.0	—	3.0	43.0	3.0	24.0	5.0	14.0	5.0	6.0
BT	4.0	44.0	10.0	—	7.0	—	5.0	5.0	14.0	1.0	3.0	—	7.0	—	—	43.0	2.0	10.0	14.0	1.0	27.0	3.0
SP	4.0	76.0	7.0	—	2.0	—	—	—	11.0	—	—	—	—	—	—	42.0	25.0	31.0	2.0	—	—	—
STP	2.0	81.0	7.0	—	3.0	—	1.0	1.0	4.0	—	1.0	—	—	—	—	53.0	28.0	19.0	—	—	—	—
ST	8.0	61.0	5.0	—	7.0	—	4.0	1.0	14.0	—	—	—	—	—	—	71.0	9.0	14.0	2.0	—	4.0	—
OWS	—	—	—	—	—	—	15.0	—	81.0	—	4.0	—	—	—	—	44.0	19.0	37.0	—	—	—	—
RBT	—	—	—	—	—	—	29.0	—	14.0	—	56.0	—	1.0	—	—	72.0	16.0	12.0	—	—	—	—
WTT	—	—	—	—	—	—	7.0	—	11.0	—	81.0	—	1.0	—	—	85.0	6.0	7.0	—	—	—	—
EST	—	1.0	1.0	—	2.0	—	90.0	—	3.0	—	—	—	—	1.0	—	50.0	23.0	20.0	2.0	1.0	4.0	—
WEH	—	13.0	2.0	1.0	3.0	—	59.0	3.0	13.0	—	6.0	—	—	—	—	11.0	38.0	48.0	1.0	—	2.0	—
BHH	—	48.0	—	—	1.0	—	33.0	—	16.0	—	—	—	2.0	—	—	68.0	2.0	30.0	—	—	—	—
WNH	—	77.0	—	1.0	3.0	—	11.0	—	7.0	—	1.0	—	—	—	—	69.0	21.0	10.0	—	—	—	—
YFH	—	63.0	3.0	7.0	4.0	—	10.0	2.0	9.0	—	1.0	—	1.0	—	—	47.0	19.0	26.0	1.0	7.0	—	—
GST	—	4.0	8.0	—	—	—	22.0	—	6.0	10.0	7.0	1.0	38.0	1.0	3.0	66.0	3.0	29.0	2.0	—	—	—
BRT	1.0	8.0	1.0	2.0	3.0	—	6.0	1.0	15.0	1.0	3.0	—	59.0	—	—	44.0	—	48.0	5.0	—	3.0	—
YRT	—	3.0	—	—	—	—	2.0	1.0	1.0	1.0	3.0	—	93.0	—	—	48.0	—	52.0	—	—	—	—
BFC	1.0	—	—	—	—	—	—	7.0	12.0	13.0	—	1.0	—	7.0	1.0	31.0	38.0	31.0	—	—	—	3.0
BF	1.0	5.0	60.0	—	—	—	—	21.0	3.0	7.0	—	2.0	1.0	10.0	—	43.0	5.0	11.0	28.0	—	13.0	—
GW	1.0	6.0	59.0	—	2.0	—	3.0	10.0	4.0	9.0	1.0	3.0	2.0	3.0	—	52.0	4.0	4.0	24.0	1.0	15.0	—
RW	1.0	9.0	49.0	—	2.0	—	3.0	14.0	6.0	9.0	1.0	4.0	1.0	15.0	1.0	66.0	8.0	23.0	2.0	—	1.0	—
GFT	1.0	2.0	10.0	—	1.0	—	—	80.0	1.0	1.0	1.0	1.0	3.0	—	—	58.0	7.0	16.0	10.0	1.0	5.0	3.0
SF	1.0	—	31.0	—	—	—	—	62.0	3.0	3.0	—	2.0	—	1.0	—	73.0	7.0	17.0	1.0	2.0	—	—
RR	—	1.0	35.0	—	—	—	2.0	27.0	1.0	9.0	—	11.0	2.0	10.0	—	46.0	—	—	22.0	6.0	24.0	2.0
RFT	1.0	2.0	26.0	—	—	—	—	55.0	—	—	—	3.0	10.0	3.0	—	18.0	2.0	7.0	9.0	3.0	45.0	16.0
DWS	1.0	—	4.0	—	—	—	—	68.0	3.0	—	—	8.0	2.0	15.0	—	61.0	—	39.0	—	—	—	—
FTC	—	—	—	—	—	—	—	1.0	—	—	1.0	10.0	1.0	85.0	—	12.0	19.0	50.0	—	—	19.0	—
FR	—	—	6.0	—	—	—	—	19.0	1.0	1.0	1.0	7.0	13.0	53.0	—	60.0	4.0	26.0	7.0	—	1.0	2.0
SR	—	—	3.0	—	—	—	1.0	16.0	1.0	2.0	1.0	7.0	2.0	67.0	—	60.0	11.0	27.0	1.0	—	1.0	—
YR	—	—	5.0	—	—	—	—	8.0	1.0	1.0	—	6.0	1.0	76.0	2.0	73.0	8.0	1.0	3.0	—	14.0	1.0
ER	—	5.0	—	3.0	—	88.0	1.0	—	2.0	—	—	—	1.0	—	—	82.0	1.0	6.0	7.0	—	4.0	—
GG	—	—	—	—	—	100.0	—	—	—	—	—	—	—	—	—	91.0	—	2.0	7.0	—	—	—
LB	—	—	—	—	—	—	—	—	—	—	—	—	—	—	100.0	—	—	—	—	—	—	—
GT	—	—	—	—	—	—	—	—	—	—	—	—	—	—	100.0	—	—	—	—	—	—	—
AM	—	1.0	—	—	—	—	—	1.0	—	—	—	—	54.0	—	44.0	—	—	—	—	—	—	—
WWC	—	—	—	—	—	—	—	—	—	—	—	—	30.0	—	70.0	—	—	—	—	—	—	—