Habitat-specific guild structure of forest birds in south-eastern Australia: a regional scale perspective

RALPH MAC NALLY

Department of Ecology and Evolutionary Biology, Monash University, Clayton 3168, Australia

Summary

1. The feeding guild is a useful tool for analysing community structure. Unfortunately, although there has been much work done on guilds of forest and woodland birds, there have been few studies in which differences between habitats have been assayed for consistency of guild structure. This can be done only by surveying replicate sites of each habitat type because this yields an indication of similarity between sites of the same class of habitat. If guild structure differs little between each replicate site, then one has confidence that that structure meaningfully characterizes the habitat type in question.

2. In this study, foraging information is used to produce a guild classification for birds of forests and woodlands of central Victoria, Australia. Four replicate sites of five forest and woodland classes were censused.

3. Guild structures in two habitat classes (open woodlands of the Goulburn River valley, and Gippsland manna gum *Eucalyptus pryoriana* woodlands) were distinct from both each other and also from those of three other habitat types (montane forests, foothill woodlands, and box-ironbark dominated forests). There was little differentiation between the latter three habitat types.

4. Much the same guild structure occurred in replicate sites of each habitat class, indicating that there is a systematic basis for guild structure that can be broadly related to habitat structure. In some habitats, maintenance of guild structure from replicate to replicate is mediated by similar arrays of species, whilst in other habitat types, there are significant differences in the actual species occupying guilds even though numbers of species in each guild are similar. Thus, use of replicate sites provides important additional information on how guilds are composed in different habitats.

Key-words: Australia, avifauna, bird community, foraging, guild, habitat, regions, Victoria.

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Introduction

Breaking down assemblages of species into feeding guilds (Root 1967) or functional groups (Cummins 1973) is one of the main techniques animal ecologists have developed to try to come to grips with community structure and dynamics. Determining guild structure has been beneficial for many reasons (Hawkins & MacMahon 1989; Simberloff & Dayan 1991), not the least of which are that: (i) guilds bring or impose order on systems that may appear to be difficult to interpret otherwise; and (ii) guilds have been viewed as 'natural ecological units' (Hawkins & MacMahon 1989, p. 427), which are recurrent in different communities and are, in a sense, the building blocks of ecological communities.

Guilds have been used extensively in analyses of many taxonomic groups and in many types of biome, but ornithologists have been among the most active in interpreting assemblages of species in these terms (e.g. Salt 1953, 1957; Emlen 1977; Holmes, Bonney & Pacala 1979; Wiens & Rotenberry 1979; Landres & MacMahon 1980; Sabo & Holmes 1983; Recher *et al.* 1985). Most investigations of guild structure concentrate on just one or a few locations (e.g. Herrera 1978; Saether 1982; Landres & MacMahon 1983). These studies often focus on how structure might be determined by interspecific competition, i.e. how are species differentiated in foraging and other characteristics so that they might coexist locally (e.g. Crome 1978; Recher *et al.* 1985; Ford, Noske & Bridges 1986)? Comparatively few studies simultaneously con-

sider many different locations, although studies based on environmental gradients are not uncommon (e.g. Ford & Paton 1977; Wiens & Rotenberry 1981; Woinarski, Tidemann & Kerin 1988; Brooker, Braithwaite & Estbergs 1990). More studies at broader spatial scales are needed if we are to capitalize on some of the insights gained in recent thought on large-scale dynamics (see Bock 1987; Pulliam & Danielson 1991; Rosenzweig 1991; Dunning, Danielson & Pulliam 1992; Holling 1992; Levin 1992; Palmer 1992).

In light of these comments, the purpose of the current study is to give an integrated picture of the representation of avian feeding guilds in a selection of habitats at a regional scale (i.e. over 100s of km). The habitats are forests and woodlands located along a 250 km long, north–south transect running through central Victoria, Australia (see Mac Nally 1989). The main novelty of this study is the sampling design, which consists of replicates of each of several different types of forest and woodland habitats. Although there are a few reports of guild structure in which multiple examples of habitat classes are considered, replicates usually were distributed over vast areas subject to very different climates (e.g. Vale, Parker & Parker 1982), or included seral stages in which the age of the plant community since disturbance was a major factor (e.g. DeGraaf & Chadwick 1984), neither of which applies to the current study.

Replication is important because it permits one to gauge the specificity of patterns evident in a given type of habitat. Without replication, it is not possible to determine whether a site deemed to be representative of a class of habitat is idiosyncratic or actually representative of that habitat type. This argument is a straightforward application of conventional sampling philosophy to a regional analysis of community structure. Thus, the current study should yield a quantitative idea of the distribution of species among guilds in different types of forest and woodland in this region. It also provides information of how similar replicate plots of particular habitats are to one-another in terms of their guild structure, which has implications for the sorts of inferences one can make on the basis of unreplicated habitat plots.

The specific objectives, then, are to: (i) construct a classification of feeding guilds for the region; (ii) allocate each species to the most appropriate guild; (iii) characterize species richness of guilds at each site; and (iv) determine the level of variation in community structure in replicates of each type of habitat.

USE OF FEEDING GUILDS

Some advantages of using guilds to tease apart community structure were touched upon briefly above (see Hawkins & MacMahon 1989; Simberloff & Dayan 1991). It is important to realize, however, that guilds are human constructs that may indeed impose structure that is not necessarily of ecological relevance

(Landres & MacMahon 1980). In particular, many, perhaps most, species of birds display some level of opportunism in feeding (Coward 1985; Dial & Vaughan 1987; Ford, Huddy & Bell 1990). Many putative carnivores regularly eat fruits (O'Donnell & Dilks 1989; French 1990), nectarivores consume invertebrates (Remsen, Stiles & Scott 1986), and some rather unexpected nectarivory occurs (Richardson 1988). Diets reflect the incidence of greater food generalization than is apparent in foraging activities (see Lea & Gray 1935a,b; Hawkins & MacMahon 1989; French 1990). Another problem is that some species show idiosyncratic combinations of foraging activities, which makes them difficult to place in a general guild structure. For example, the yellow-tailed black cockatoo (*Calyptorhynchus funereus* (Shaw); see the Appendix for a complete list of Linnaean names) shows characteristics of both granivores and carnivorous bark probers/tearers (Lea & Gray 1935a; McInnes & Carne 1978), and even include fungi in their diets (Taylor & Mooney 1990). Thus, although powerful, the guild idea does have its limitations (Hawkins & MacMahon 1989). Guilds are used here in the sense of the *routine* manner and location in which individuals of a species gather food (see Holmes *et al.* 1979; Vale *et al.* 1982). Results of the following analyses are predicated on this interpretation.

Methods

STUDY REGION AND SITES

The study region consisted of a longitudinal transect through central Victoria, Australia. The region extended for 250 km from north to south, but was just 40 km at its greatest east–west extent. Twenty sites were selected at locations along the transect running from the most northerly site at Undera in the Goulburn River valley (36°28′S, 145°13′E) to the most southerly site at Cape Schanck, adjacent to Bass Strait (38°28′S, 144°52′E). The transect traversed the Great Dividing Range (GDR), and was chosen so that representative eucalypt-dominated forest and woodlands of central Victoria were included in the survey. The selection of habitats included: (i) woods of the southern lowlands and maritime plains, mostly of Gippsland manna gum (*Eucalyptus pryoriana* L. Johnson), swamp gum (*E. ovata* Labill.), and messmate stringybark (*E. obliqua* L'Hér.); (ii) an assortment of forests and woodlands in the northern and southern foothills of the GDR, consisting of a variety of box, peppermint, and stringybark species; (iii) tall montane forests of the GDR, which include mainly mountain grey gum (*E. cypellocarpa* L. Johnson), candlebark (*E. rubida* Deane & Maiden), messmate stringybark, blackwood (*Acacia melanoxylon* R. Br.), and mountain ash (*E. regnans* F. Muell.); (iv) woodlands dominated by red ironbark (*E. tricarpa* L. Johnson) and grey box (*E. microcarpa* (Maiden) Maiden) on the central uplands

of Victoria; and (v) open woodlands of the Goulburn River valley, consisting mainly of river red gum (*E. camaldulensis* Dehnh.) and grey box. For brevity, these five main forest and woodland types are referred to by using the mnemonics GMG (i.e. Gippsland manna gum), FHNS (foothill woodlands), MGCMA (montane forests), RIGB (red ironbark–grey box), and RGGB (river red gum–grey box).

Replicate sites of each habitat type were separated by at least 10 km, and often by much more (up to 120 km for FHNS) depending on the geographic distribution of forest or woodland types. Each study site was an area of forest or woodland between 10 and 20 ha in extent. At each site, a plot of 0·25 ha, which seemed representative of the site as a whole, was chosen for habitat ordination measurements. Use of sample plots of this size within the larger context of the census plot is a common way of characterizing habitat physiognomy (see, for example, Dueser & Shugart 1979). Twenty-three variables were defined to characterize the physiognomy of each ordination plot (see the Appendix of Mac Nally 1989).

CENSUSES

Censuses of avifaunas of each location were undertaken during every season. The seasons were regarded as follows. (i) Summer: 22 December 1985–21 March 1986. (ii) Autumn: 22 March 1986–21 June 1986. (iii) Winter: 22 June 1986–21 September 1986. (iv) Spring: 22 September 1986–21 December 1986.

Censuses consisted of a series of constant-bearing (but not necessarily parallel) transects traversing a given study site. Each census took 4 h, and was conducted in either the morning (commenced within 90 min after sunrise) or the afternoon (completed at least 90 min before sunset). The allocation of sites, and seasons within a site, to morning or afternoon censuses was randomized such that biases associated with time of census were reduced. There was little difference in either numbers of species or numbers of individuals between morning and afternoon censuses ($20·6 \pm 5·7$ [SD] vs. $19·9 \pm 3·8$ [species richness]; $83·3 \pm 20·5$ vs. $87·4 \pm 22·0$ [individuals]; each $n = 40$).

All individuals were identified by sight and/or by songs. The time during a particular census at which an individual specimen was observed was recorded. The temporal distributions of sightings of previously unrecorded species in a census were used to assess whether the 4-h period was effective, or at least unbiased, in determining which species were present at a given site during each season. In only six (7·5%) of the 80 censuses was a previously unrecorded (during that census) species identified in the fourth hour of a census, and of these six, there was no discernible bias with respect to habitat type. These data suggest that the censusing procedures were effective in determining the avifaunas at each site in an unbiased way.

FORAGING ACTIVITIES

The initial set of foraging activities used to quantify foraging activities was comprehensive, such that many more categories were used than were likely to be needed during the final analysis. Activities were not just foraging activities *per se,* but also included location. Thus, gleaning leaves of trees was regarded as distinct from gleaning from the leaves of bushes (see Holmes *et al.* 1979). Although this approach yields a comparatively large number of classes information can be combined at a later time if necessary, but initial lumping may lead to an undesirable loss or resolution (Mac Nally 1994). There were 21 activities (Table 1). In general terms, activities can be regarded as carnivory (aerial, arboreal and ground), floral exploitation, and granivory (arboreal and ground) (Table 1; see also Recher *et al.* 1985).

FORAGING DATA COLLECTION

Foraging information was collected in conjunction with censuses. The type of activity, substrate, and height above ground level of each action were recorded for each individual (one observation per individual). For the purposes of this paper, information for a given species was pooled irrespective of location and season. These aspects will be addressed in a subsequent paper, but some discussion of possible effects of this pooling is provided below.

GUILD DETERMINATION

Partitioning species among guilds may be a difficult problem because workers often set arbitrary fusion levels when undertaking clustering analyses (Jaksic 1981; Simberloff & Dayan 1991). This difficulty cannot be resolved by using predefined guilds (Jaksic 1981), although this approach has been used (e.g. Willson 1974; Vale *et al.* 1982; see also Hawkins & MacMahon 1989, p. 430). The method used here has a statistical basis in that the number of clusters ($\equiv$ guilds) was determined by reference to the ratio of variation within clusters to that between clusters.

Foraging-guild allegiances normally are determined by using a clustering algorithm based on the similarity of species to one another. However, the algorithms and similarity criteria available for use in clustering are so numerous that objective criteria have to be used for clustering (Milligan & Cooper 1985). This involves both finding the most likely number of clusters (Dubes 1987) and also the most robust clustering algorithm (Jain, Indrayan & Goel 1986). Therefore, I followed the recommendation of Jain *et al.* (1986) by using complete-linkage fusion, and the method of Xu, Kamath & Capson (1993) to determine the most likely number of clusters in the foraging data-set.

The data-set was vectors of information for each species. A vector consisted of the proportions of for-

Table 1. Definitions of foraging activities used to assess cluster structure of avifaunas. Activities are ordered generally from aerial to arboreal to ground carnivory, floral exploitation, and granivory

Activity	Description (and characteristic taxon)
Sweep	Airborne insects caught on wing (screen of Emlen 1977) (swallow)
Canopy sally	Sally from perched position to airborne insects in or above the main canopy (bee-eater)
Subcanopy sally	Sally from perched position to airborne insects below main canopy, but above bushes (grey fantail)
Ground/bush sally	Sally to airborne insects from the ground or bushes (willie wagtail)
Hover-snap	Pecking perched prey from substrates whilst hovering (flycatcher)
Ground pounce	Attack on grounded prey from perched position (robin)
Leaf glean	Gleaning of perched prey from leaves of trees by perched birds (pardalote)
Twig glean	Gleaning of perched prey from twigs of trees by perched birds (thornbill)
Wood search	Gleaning of perched prey on branches and trunks by perched birds (shrike-thrush, sittella)
Bark prise	Probing and prising bark (tree-creepers)
Ribbon search	Searching bark ribbons of decorticating trees (shrike-tit)
Bark tear	Searching for prey by tearing bark (currawong, shrike-tit)
Bush glean	Gleaning of perched prey from bushes (silvereye)
Bracken glean	Gleaning of perched prey from bracken (scrubwren)
Litter search	Scratch and search through litter (superb lyrebird)
Log/fallen branch glean	Searching logs (eastern whipbird)
Ground search	Searching ground, often by probing (Australian magpie)
Flower exploitation	Consumption of pollen and nectar, or blossoms (honeyeater/lorikeet)
Arboreal granivory	Consumption of seeds in trees (gang-gang cockatoo)
Understorey granivory	Consumption of seeds in understorey (rosella)
Ground granivory	Consumption of fallen seeds and seeds of grasses (firetail)

aging activities of each type listed in Table 1. The (dis)similarity matrix for clustering was calculated by using the Pearson correlation coefficient (see Wilkinson 1987). This is the basis by which species for which I had at least 20 foraging observations (66 species) were allocated to the most appropriate clusters, where, in this sense, clusters can be identified with foraging guilds (see Simberloff & Dayan 1991). Although 20 observations may seem small, numbers for the majority of the 66 species far exceeded this figure (Appendix). For the remainder, foraging activities generally were stereotyped to such an extent that additional information would largely reflect the existing distributions so that one can have reasonable confidence in guild associations.

Having done this to determine the number and constitution of each guild, this partition then was used as a basis for a subsequent multiple linear discriminant analysis (LDA) to produce discriminant classification functions (Wilkinson 1987). Again, the data-set consisted of the vectors of proportions of foraging activities used in the previous analysis. The purpose of this part of the analysis was twofold: (i) to check for consistency in the partition such that distinctions between species were sufficient and consistent enough to generate accurate classification of species into nominated clusters; and (ii) to use the classification functions to allocate other species, for which I had between 10 and 20 foraging observations (15 species), to the most appropriate cluster.

Information for the latter was used in conjunction with the discriminant functions to classify these species. The classification was based on a generalization of Fisher's two-class discriminant analysis (Dillon &

Goldstein 1984). Mahalanobis distances of the position in LDA-space of a given species to group centroids for each guild in that space provide a means by which the probable affinities of species can be ascertained. In general, the Mahalanobis distance to one centroid is much less than to any other, leaving little doubt as to the foraging guild to which a species belongs. Infrequently, the location of a particular species did not lie nearer to one guild than any other, so that this species cannot be classified with confidence. Species showing this pattern are labelled 'not classified' in the Appendix.

DIFFERENCES IN GUILD STRUCTURE BETWEEN HABITATS

A major purpose of this paper is to characterize variation in guild structure between the main types of habitat. To do so in a systematic fashion, four sites (replicates) for each of the five main habitat types (i.e. RGGB, RIGB, etc.) were used in an analysis of variance of species richness. Each selected site was representative of the habitat type as judged independently by using habitat ordinations (see Mac Nally 1989). This approach allowed determination of how guilds are distributed among habitats, and also permitted an assessment of how different sites of similar structure and floristics differ from one another in terms of guild structure. The basic information for each site was the distribution of species richness for each guild recorded at the site, irrespective of season. I focus on species richness here rather than analyses of densities because the latter require an additional dimension; namely, seasonal fluctuations. Thus, the

current paper first establishes the grounds for distinguishing guilds, then determines which species are associated with each guild, and finally how guild structure (in terms of species richness) varies between habitats and between replicates of each habitat type. Restriction to patterns of species richness is sufficiently broad in scope to warrant this detailed analysis without the added complications of changes in density, which will be addressed in a subsequent paper.

This systematic sampling design allows straightforward analyses of variance (ANOVA) to be used to characterize the significance of sources of variation. In particular, variance components (see Winer 1971) can be estimated from such designs to quantify the relative contributions of each main effect, interactions, and error terms to variation in guild structure. Thus, the problem can be framed as a repeated measures analysis of variance

$$Y_{ijk} = \mu_{...} + \eta_i + \pi_{j(i)} + \gamma_k + (\eta\gamma)_{ik} + \varepsilon_{(ijk)},$$

where: Y_{ijk} is the species richness in replicate j of habitat i of guild k, $\mu_{...}$ is the model overall mean computed over all replicate sites of all habitats for all guilds, η_i is the mean richness for habitat i (calculated over all guilds), $\pi_{j(i)}$ is a term encompassing the specific effect of a given site (i.e. the object upon which repeated measures are performed), γ_k is the average for guild k (calculated over all habitats), $(\eta\gamma)_{ik}$ is a measure of the interaction between habitat type and guild, and $\varepsilon_{(ijk)}$ is the residual or unexplained variation. Note that $j(i)$ means that information for an individual site was nested within a particular habitat type, and that (ijk) means that there were no true replicate measurements. This model is discussed at length by Neter, Wasserman & Kutner (1990; pp. 1057–1066).

For computing expected mean squares and hence variance components (see Vaughan & Corballis 1969; Dwyer 1974; Susskind & Howland 1980), I regarded habitat as a random factor because the sampled habitats were deemed to be representative of all forest and woodland habitats on the transect (i.e. other aboreal habitat types occur within the region, see DCFL 1984). Guild type is the other main factor, and forms a repeated measurement on individual sites or replicates within habitats (see Neter *et al.* 1990, p. 1057). These 'repeated' measurements were, in effect, performed simultaneously for a given site. Guild type also was treated as a random factor because not all guilds are included in this analysis (e.g. no frugivores, raptors or nocturnal species), nor are the derived guilds necessarily immutable classes. Variance components were calculated by using the techniques described by Neter *et al.* (1990, p. 1015). Residuals were checked for systematic patterns, but none were found so that no transformations were necessary. Distributions of richness for guilds at any one site were assumed to be independent of one another, which seems reasonable given the foraging differentiation involved, and the

types of regional dynamics displayed by species (R. C. Mac Nally, unpublished).

Concurrent measurements on many guilds meant that sample sizes were artificially inflated. Bonferroni correction of type-I error rates was adopted to provide protection against this inflation. In essence, this just means reducing the nominal significance level by a factor commensurate with the number of guilds (10, see next section), from 0·05 to 0·005. Effects and interactions significant at this level can be regarded as meaningful because Bonferroni-type corrections are known to be conservative (Keppel 1982).

Results and Discussion

GUILDS

The number of distinct clusters, or guilds, determined by using the method of Xu *et al.* (1993) was 10. Each guild was given a descriptive name that encapsulated the main foraging activities of members of the guild, which are listed in Table 2. The spreads of activities, or *repertoires,* of guilds are reasonably distinct. The most similar patterns are shown by the bark probers and wood searchers. Ground carnivores and bush carnivores are the next most similar couple of guilds. The distributions of species amongst guilds is shown in Fig. 1. The greater diversity of foliage gleaners is consistent with results of many other studies of guild structure in forest and woodland habitats (e.g. Vale *et al.* 1982; Ford *et al.* 1986).

DISCRIMINANT CLASSIFICATION

Multiple linear discriminant analysis (LDA) of repertoires was performed by using results of the primary clustering above as the means for grouping. The LDA functions were robust enough to be able to clearly differentiate between the defined guilds, and to have each species allocated unambiguously to the nominated guild (i.e. 100% 'correct classification' of the 66 species). Fifteen species for which I had between 10 and 20 observations could be unambiguously assigned to one or other of the 10 guilds (Appendix). Another 19 species either could not be assigned with confidence (e.g. rainbow bee-eater, *Merops ornatus* Latham), or there was insufficient foraging information (Appendix). The small amounts of information for most of these species generally are indicative of low densities, sporadic or seasonal occurrence, or both. On the other hand, some reasonably common species (e.g. fantailed cuckoo, *Cuculus pyrrhophanus* Vieillot) forage infrequently or are stealthy, and this leads to small sample sizes rather than low densities or sporadic occurrence *per se.*

Use of LDA allows an evaluation of the impact of pooling foraging information between seasons. I used the LDA functions to classify the seasonal repertoires displayed by some species for which there were more

Table 2. Predominant foraging activites of members of each guild based on species with $\geqslant 20$ foraging observations (means)

Guild	Major activities (mean %)
Sweeper	Sweep (100)
Hawker	Subcanopy sally (34), ground/bush sally (16), wood search (14)
Pouncer	Ground pounce (74)
Ground carnivore	Ground search (53), litter search (16)
Bush carnivore	Bush glean (35), twig glean (15), ground search (13), wood search (13)
Bark prober	Wood search (46), bark prise (18), bark tear (11)
Wood searcher	Wood search (35), twig glean (30)
Foliage searcher	Leaf glean (40), twig glean (25)
Nectarivore	Flower exploitation (48), leaf glean (10), wood search (10)
Granivore	Arboreal granivory (50), ground granivory (40)

than 20 observations for a season. This amounted to 115 cases (i.e. a case is information for one species in one season, and there may be up to four cases for some species, such as brown and striated thornbills, *Acanthiza pusilla* White and *Acanthiza lineata* Gould, respectively). Of these 115, there were only six cases in which the species was allocated with high probability to a guild different to that nominated in the Appendix. Several of these cases were associated with unusual events, such as mass flowering of one eucalypt species. For example, white-naped honeyeaters (*Melipthreptus lunatus* (Vieillot)) capitalized on an abnormally profuse bloom in one FHNS site during winter, with the effect of greatly boosting the proportion of nectarivory events for that species during that season. Exclusion of these data led to a repertoire during winter resembling closely that of other seasons (i.e. mainly foliage/twig gleaning). As noted in the Introduction, many species are opportunistic and, in a sense, pooling between sites and seasons reduces the perceived impact of comparatively atypical events to provide a better idea of the routine guild associations of individual species.

GUILD STRUCTURE AND HABITAT

Guild structure differed between the five different habitat types (Fig. 2). In all habitats except RGGB, the richest guild on average was the foliage searching guild. The number of species of wood searchers was relatively insensitive to habitat type, ranging from mean richness of 3·25 in GMG through to 5·0 in RIGB. Pouncers too showed consistent representation, although richness in FHNS and RIGB was somewhat higher than GMG. The most diverse guilds of bark probers occupied montane forests, with only two species on average occurring in GMG. The hawking guild was most strongly represented in RGGB,
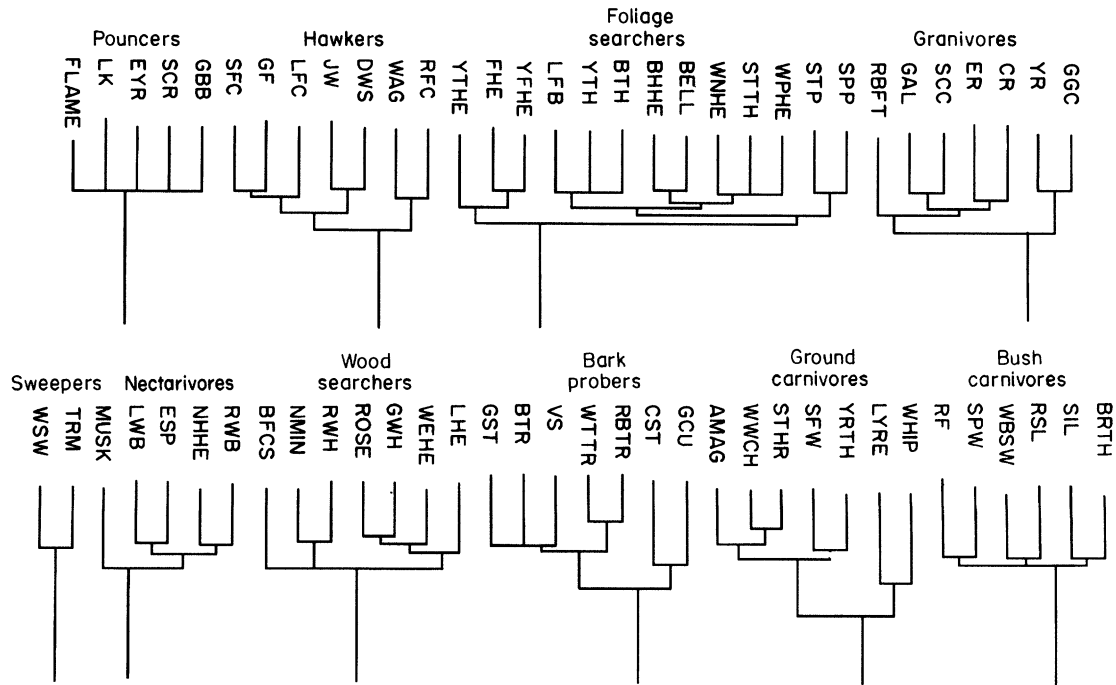
Fig. 1. Dendrogram derived from clustering analysis. See the Appendix for species mnemonics. Fusion levels for different guilds are at similarities much less than the final fusion level for any of the guilds.
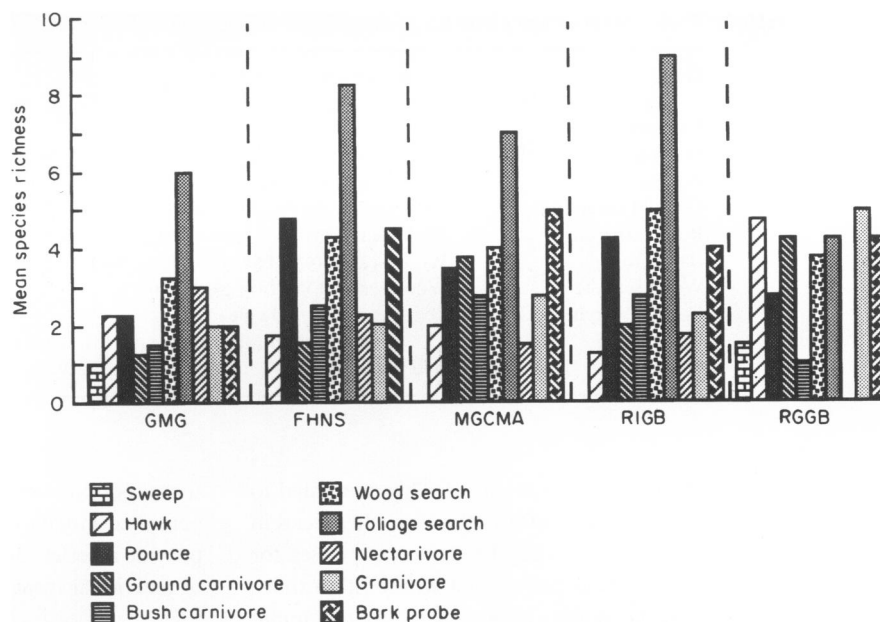
Fig. 2. Mean species richness for each foraging guild calculated over four replicate plots for each habitat type.

but was under-represented in RIGB. Sweepers were recorded only in GMG and RGGB, probably because these are the most open types of habitat (Mac Nally 1990; see below). Ground carnivores were depauperate in GMG and FHNS, but strongly represented in RGGB. Bush carnivores are not a dominant component in any habitat (maximum 2·75), and only one species on average occurred in RGGB. Nectarivores are most rich in GMG, and least in RGGB, whilst the reverse pattern occurs in granivores.

Patterns just related are for habitat types as units, but what variation is there between replicate sites within habitats? A cursory examination of results presented in Fig. 3 shows that guild structures in replicate sites shared many similarities in terms of richness of each guild. However, it is also clear that there were site-specific idiosyncrasies. For example, data for sites at the extreme left of the GMG (Fig. 3a) and MGCMA (Fig. 3c) plots demonstrate that these locations were comparatively depauperate overall, but especially in terms of the foliage searching guild. Differences of this magnitude were not so evident for FHNS (Fig. 3b), RIGB (Fig. 3d) and RGGB (Fig. 3e). Guild structure between RGGB sites seemed quite consistent.

Differences in richness between guilds was a significant source of variation (ANOVA, Table 3). On average, there were many more species of foliage searchers than sweepers or nectarivores. However, differences in total community richness (i.e. richness of the entire avifauna at each site) between habitats were not significant. Together, these results imply that there must be substantial habitat-specific differences in the numbers of species in each guild, or in ANOVA parlance, a significant two-way interaction between the main factors (Table 3). Although significant interactions

lessen inferential power in general (Neter *et al.* 1990), there appears to be little reason to doubt that habitat effects are mediated through differences in guild structure and not through differences in total diversity. Differences between guilds accounted for 47% of variation in species richness within these 20 sites, habitat-specific differences in guild representation another 20% (i.e. the interaction), just 6% was due to variation between replicates within habitats, and 27% was left unexplained (Table 3). The small amount of variation due to replicates within habitat types (6%) indicates only that total species richness differs little between replicates within habitat types.

There may be some concern that guild-specific differences in richness do not accurately reflect the composition of the avifaunas in these habitats because 19 species were not classified owing to a paucity of foraging information (see Appendix). Therefore, on the basis of the limited information that I collected, and reported foraging activities and diets in the literature, I provisionally assigned where possible the unclassified species to the most probable guilds. This analysis produced much the same picture as above. Again, most of the attributable variance was due to differences between guilds (50%), and to differences in guild representations in the various habitat classes (27%). The main difference was a redistribution of variance from the residual (27% to 4%) to replicates within habitats components (6% to 19%). In short, these results indicate that interpretations provided here are generally valid, and are unlikely to change much as more information for the species listed as not classified in the Appendix accumulates. However, guild structure within replicates of habitat types may become more dissimilar as currently doubtful species are classified with greater surety. This reflects the
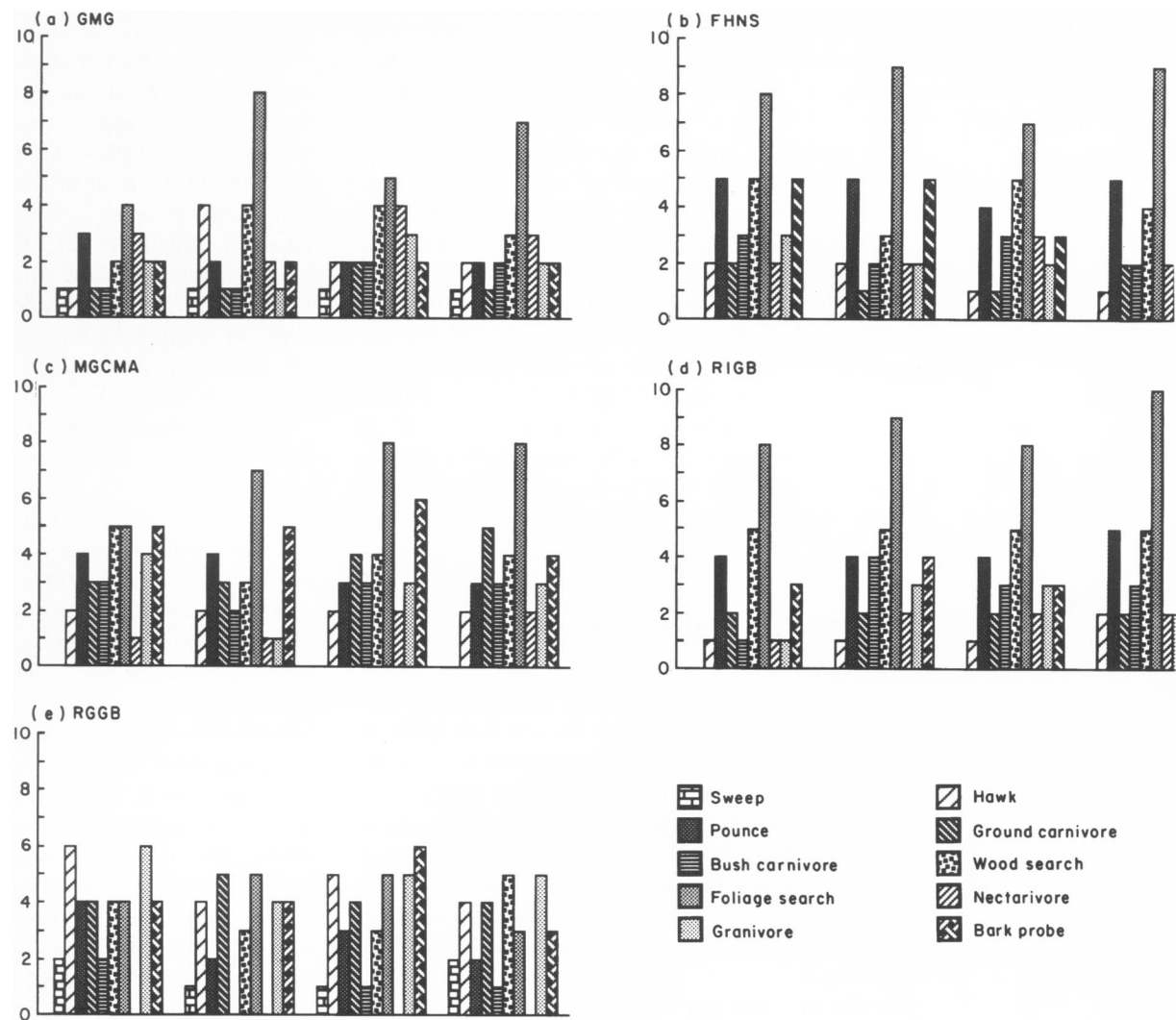
Fig. 3. Data upon which Fig. 1 and Table 3 are based: species richness of guilds in replicate plots of each type of habitat.

Table 3. ANOVA of species richness. The main effects are regarded as being random factors for purposes of computing expected mean squares (E(MS)—see Winer 1971). The design requires a quasi-F-ratio and test degrees of freedom for the forest type factor (see Winer 1971, p. 375). For expected mean square formulae, $p = 5$, $q = 10$ and $n = 4$

Factor	df	MS	F-ratio	df test	VC (%)	E(MS)
Forest type (η)	4	4·420	0·77	5, 48	0	$qn\sigma_\eta^2 + n\sigma_\pi^2 + q\sigma_{\gamma\eta}^2 + \sigma_\varepsilon^2$
Plot within forest type (π)	15	1.252	1.98	15, 135	6	$n\sigma_\pi^2 + \sigma_\varepsilon^2$
Guilds (γ)	9	60·056	11.24*	9, 36	47	$pq\sigma_\gamma^2 + q\sigma_{\gamma\eta}^2 + \sigma_\varepsilon^2$
Interaction ($\gamma\eta$)	36	5.342	8.44*	36, 136	20	$q\sigma_{\gamma\eta}^2 + \sigma_\varepsilon^2$
Residual (ε)	135	0.633	—	—	27	σ_ε^2

* $P \leqslant 0·005$.
MS, mean square.
VC, variance component.

patchy and sporadic occurrence of most of these species (hence comparatively little foraging information).

GUILD STRUCTURE AND PHYSIOGNOMY

Another way of looking at the relationship between guild stucture and habitat structure or physiognomy

is to calculate all pairwise dissimilarities between the 20 sites for both variables. This is a rather direct titration of the relationship not requiring allocation of individual sites to nominal groups, like GMG, RGGB, etc. Physiognomic dissimilarities were computed by using the structural variables described by Mac Nally (1989). The Canberra dissimilarity measure was used (Lance & Williams 1967).

There was a significant positive correlation between dissimilarities of guild structure and habitat structure (Fig. 4). That is, structural similarity appears to be related directly to similarity in guild structure. I used a Bonferroni approach in asserting that there were only 18 (i.e. 20 − 2) degrees of freedom for the test of the correlation coefficient because there were really just 20 independent sites. Even so, the correlation computed over all 190 pairs of sites (0·672) was highly significant. This result indicates that there is a sub-stantial linkage between how similar sites are in purely structural terms and the associated distribution of bird species among guilds. The function provides little predictive power because it accounts for less than half of the variance (48.9%). Nevertheless, this result is consistent with those of Vale *et al.* (1982) who found that habitat structure strongly influences guild structure.

CONSISTENCY WITHIN HABITATS

It is clear that the respective richnesses of guilds differ significantly, e.g. there are many more species of foli-age searchers than sweepers. But the main question posed in this study involves the consistency of guild structure between replicate sites of the same general forest or woodland type, and whether there are mani-festly different distributions among guilds in different habitat classes. Results presented in Fig. 3 illustrate variation in guild structure within classes, whilst differences between habitats are shown in broad terms in Fig. 2.

These results can be presented in a more compact way to emphasize patterns of guild structure by using measures of similarities or dissimilarities between pairs of sites. Vale *et al.* (1982) and DeGraaf & Chad-wick (1984) used p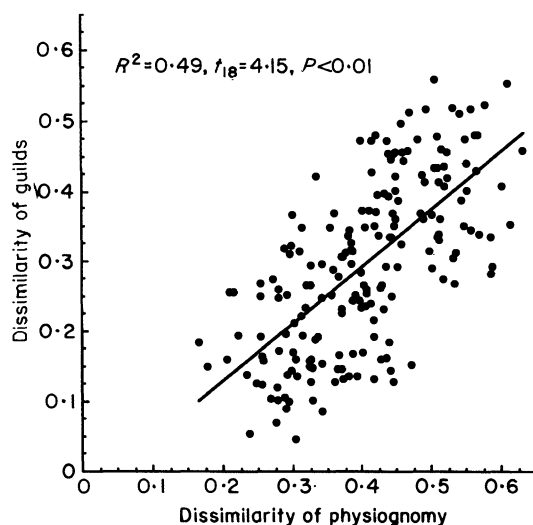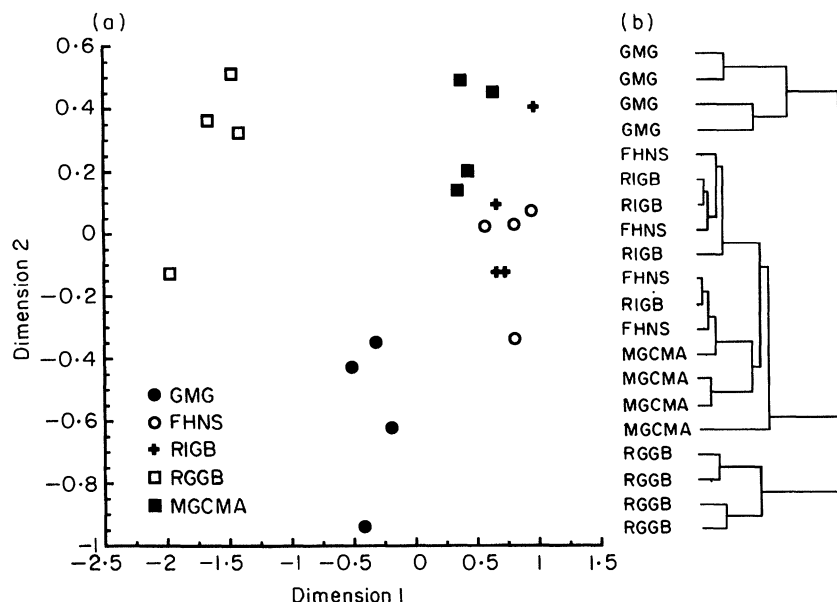olar ordinations to do this, but a more powerful way is to use multidimensional scaling (MDS). This method involves iteratively computing a distribution of points in an abstract space in such a way that the distances between points, representing sites, is matched to dissimilarities in site characteristics (Kruskal 1964). If distributions of species among guilds are used to compute these dissimilarity measures, then the derived MDS-space yields a picture of dissimilarities of guild structure between sites. In the current example, a two-dimensional space was sufficient to provide a satisfactory representation for the guild data (stress = 0·08, Wilkinson 1987; Can-berra dissimilarity measure).

Guild structures of replicates of all types of wood-land and forest habitat were reasonably consistent with one another (Fig. 5a). This means that within a given class of habitat, similar guild structures were recorded in replicates. However, guild structure in two habitat types consistently differed from each other and also from the other three habitat classes. In other words, knowing the distribution of species among guilds would allow one to differentiate between sites consisting of RGGB, GMG and all others, but not between RIGB, MGCMA and FHNS. The latter are not particularly distinct from one another in guild structure (Figs 2, 5a, b). An alternative approach, using clustering methods, confirmed these interpret-ations—the GMG sites clustered first among each other, as did the RGGB sites among themselves, whilst guild structure in the other three habitat types was sufficiently similar among replicates to prevent clear separation (Fig. 5b). Similar results to these were reported by Vale *et al.* (1982), who found that guild structures in closed forest habitats were similar to one another yet substantially different from those in shrublands, open woodlands, and grasslands. They suggested that the common guild structure in forests is mainly due to the physiognomy of forests, which dictates substrate availability. Some of the differences they noticed between forest types could be related to particular properties of some forest types, particularly needle-leaf evergreen forest (e.g. dominated by few species of trees, bark texture, aromatic compounds; see below).

The main reason for the separation of RGGB and GMG from the other habitat types was the occurrence of the sweeping guild in the former two habitat classes. RGGB and GMG differed from one another in several respects. Hawkers, granivores, ground carnivores, and bark probers were better represented in RGGB than GMG, whilst foliage-searching species were dis-proportionately more diverse in GMG than RGGB. No primary nectarivores were recorded in the four representative plots of RGGB (Fig. 2). There was some variation in guild structure between replicate sites in RGGB and GMG but, at least in this sample of sites, replicate plots of FHNS, RIGB and MGCMA were remarkably consistent with one another (Fig. 5a). Thus, consistency of guild structure was habitat-

Fig. 4. Relationship between dissimilarities of guild structure and dissimilarities of physiognomic or structural similarity in all pair-wise combinations of 20 sites. (Canberra dissimilarity measure; Lance & Williams 1967).

Fig. 5. (a) Positions of sites in a canonical space based on proportions of each guild (two-dimensional multidimensional scaling [MDS]; Canberra dissimilarity measure). (b) Dendrogram of similarities of guild structure among all 20 sites (complete-linkage, Pearson correlation similarity measure).

specific, with little variation in some habitats (e.g. FHNS) but substantial differences in others (e.g. RGGB).

These results show that each forest or woodland class has a particular guild structure, but that this structure is similar in three of the habitat types considered here. Does this consistency within habitat types merely reflect similarity of avifaunas at replicate sites, species by species? Or is there turnover of species yet maintenance of guild structure in spite of specific differences (see Evans & Murdoch 1968)? One could, of course, provide a detailed listing of all replicate sites and judge whether there is repetition of the same sets of species in each guild or not. An alternative is to compare guild dissimilarities with specific dissimilarities of all pairs of sites within habitat types. If there is substantial specific differentiation, then specific dissimilarities should be significantly higher than guild dissimilarities. If similar sets of species constitute guilds at each replicate site, then specific and guild dissimilarities should not differ greatly.

Of the 30 combinations of replicates of the same habitat type (i.e. five habitats with six combinations of four sites in each type), there were substantial specific differences in almost two-thirds of combinations (i.e. the left cluster, circled, in Fig. 6). This means that guild structure was largely maintained despite differences in the actual species constituting guilds in these cases (i.e. dissimilarities based on species composition were higher than disimilarities based on guild structure). The habitats in which this pattern was most evident were MGCMA (six of six combinations), and RGGB and FHNS (both five of six). Guild structure reflected an underlying conservative list of species in all combinations of RIGB, and in three combinations

of GMG. In short, these results indicate that habitats differ in terms of the homogeneity of guild composition—guild structure is maintained in some habitats by virtue of similar sets of species in each guild, whilst in other habitats, guild structure is maintained in face of different species occurring in guilds.

DeGraaf & Chadwick (1984) expressly compared the information content of species constitution versus guild structure in bird assemblages of forests consisting of northern hardwoods, softwoods, and mixtures in New England, USA. They believed that habitats were better characterized by particular species
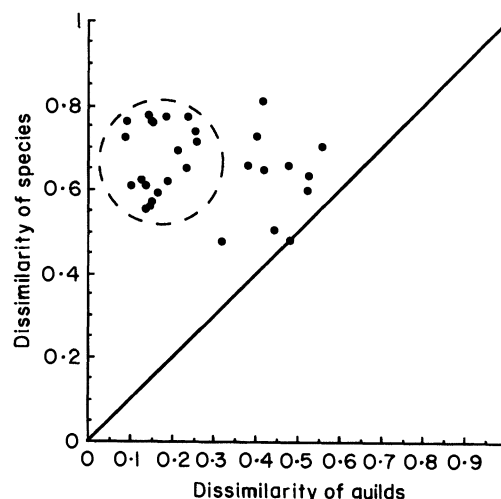
Fig. 6. Relationship between dissimilarities of communities based on individual species and on guild structure in all pairwise combinations of 20 sites. Enclosed points represent pairs of sites in which community dissimilarity based on individual species of birds was much greater than dissimilarity based on species richness of guilds (Canberra dissimilarity measure).

than by guild structure. This means that a similar distribution of species among guilds occurred, but that species replaced one another in particular niches in different habitat types. In this way, patterns in these forests were similar to those of MGCMA, RGGB, and FHNS. DeGraaf & Chadwick (1984) also commented that guild structure was similar across habitats, and that limited differentiation was due largely to the presence or absence of rare or monotypic guilds. This was found to some extent in the current study, in which the presence or absence of sweepers was a key distinction between RGGB and GMG and the other habitats.

Why might guild structure be relatively similar between replicates of the same type of habitat, particularly when species turnover sometimes is pronounced? Several factors probably contribute to this effect. First, as referred to briefly above, the physical structure or architecture of a forest or woodland can permit or exclude certain types of foraging activity (Aldridge & Rautenbach 1987). For example, we have seen that sweepers occupied only RGGB and GMG woodlands, which presumably reflects the openness of these habitats (Mac Nally 1989) allowing comparatively unimpeded sweeping. The other forest types would not be as suitable in this regard. Ground carnivores represent a more significant component of RGGB avifaunas than of GMG, perhaps because of the dense cover of bracken and bushes found in the latter. A second factor that might lead to consistency between replicates is food availability, although this often is a very difficult proposition to test (Ford *et al.* 1990). Nevertheless, the occurrence of a large, abundant, and diverse granivore guild in RGGB woodlands suggests high production of eucalypt and grass seeds compared with other habitat types. Testing the coupling between variation in resource availability and guild structure would be an important extension of the current work. A third factor is geographic position, which might constrain or filter the types of species that can reach habitats. This effect must be of limited impact though, because RGGB woodlands are the most distinct in terms of guild structure, yet are geographically close to RIGB woodlands. The most isolated of these habitats are the GMG woodlands south of the Great Dividing Range, yet these have guild structures more similar to the RIGB, FHNS, and MGCMA sites than do the RGGB sites. Thus, I suspect that, like most phenomena in community ecology, the reasons for a given observation (here similarity of guild structure in habitat replicates) are likely to be multifactorial, and that no single explanation will suffice.

Conclusions

Use of replicate examples of several types of habitat in the present study showed that guild structures differ in a consistent manner from habitat to habitat. Guild structure generally is more similar between replicate sites of one type of habitat than between sites of different habitats. However, three types of habitat, RIGB, FHNS and MGCMA, shared similar guild structure so that differences between replicates of these habitats were of the same order as differences between any two examples of these habitat types. Maintenance of guild structure despite turnover in species composition has been reported in communities changing through time (Evans & Murdoch 1968), but the current study documents a similar phenomenon in different replicates of some types of habitat (see also DeGraaf & Chadwick 1984). On the basis of all of the evidence presented in this paper, I am inclined to contest Hawkins & MacMahon (1989, p. 444), who argued that although the guild concept is useful, it nevertheless is an artificial construct in the minds of ecologists. Many of the inconsistent results leading Hawkins & MacMahon to this conclusion are probably due to technical deficiencies in the way studies were conducted or analysed, and semantic problems, many of which have been discussed by Simberloff & Dayan (1991). Much more work needs to be done on replicated systems to evaluate the generality of the patterns described in this paper. Such work needs to be conducted with a view to elaborating the significance of the factors mentioned in the previous section (e.g. physiognomy and substrates, resource availability) as determinants of local guild structure.

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Appendix

List of species and affiliations to foraging guilds. The first column is the species mnemonic used in Fig. 1. Column 2 indicates numbers of foraging observations for each species.

		Species		
Mnem.	Obs.	Vernacular name	Linnaean name & authority	Guild
TRM	39	Tree martin	*Cecropis nigricans* (Vieillot) 1817	Sweeper
WSW	124	Welcome swallow	*Hirundo neoxena* Gould 1843	Sweeper
DWS	67	Dusky woodswallow	*Artamus cyanopterus* (Latham) 1801	Hawker
DB	10	Dollarbird	*Eurystomus orientalis* (Linnaeus) 1766	Hawker*
JW	42	Jacky winter	*Microeca leucophaea* (Latham) 1801	Hawker
SFC	27	Satin flycatcher	*Myiagra cyanoleuca* (Vieillot) 1818	Hawker
RFC	75	Restless flycatcher	*Myiagra inquieta* (Latham) 1801	Hawker
LFC	27	Leaden flycatcher	*Myiagra rubecula* (Latham) 1801	Hawker
GF	565	Grey fantail	*Rhipidura fuliginosa* (Sparrman) 1787	Hawker
WAG	109	Willie wagtail	*Rhipidura leucophrys* (Latham) 1801	Hawker
GBB	23	Grey butcherbird	*Cracticus torquatus* (Latham) 1801	Pouncer
FTC	10	Fan-tailed cuckoo	*Cuculus pyrrhophanus* Vieillot 1817	Pouncer*
LK	65	Laughing kookaburra	*Dacelo novaeguineae* (Hermann) 1783	Pouncer
EYR	344	Eastern yellow robin	*Eopsaltria australis* (White) 1790	Pouncer
SKF	13	Sacred kingfisher	*Halcyon sancta* Vig. & Horsf. 1827	Pouncer*
RCR	13	Red-capped robin	*Petroica goodenovii* (Vig. & Horsf.) 1827	Pouncer*
SCR	68	Scarlet robin	*Petroica multicolor* (Gmelin) 1789	Pouncer
FLAME	45	Flame robin	*Petroica phoenicea* Gould 1837	Pouncer
YRTH	31	Yellow-rumped thornbill	*Acanthiza chrysorrhoa* (Quoy & Gaim.) 1870	Ground carnivore
WWCH	244	White-winged chough	*Corcorax melanorhamphos* (Vieillot) 1817	Ground carnivore
MGLK	12	Magpie lark	*Grallina cyanoleuca* (Latham) 1801	Ground carnivore*
AMAG	90	Australian magpie	*Gymnorhina tibicen* (Latham) 1801	Ground carnivore
SFW	437	Superb fairy-wren	*Malurus cyaneus* (Latham) 1783	Ground carnivore
LYRE	26	Superb lyrebird	*Menura novaehollandiae* Latham 1801	Ground carnivore
OWH	12	Olive whistler	*Pachycephala olivacea* Vig. & Horsf. 1827	Ground carnivore*
WHIP	56	Eastern whipbird	*Psophodes olivaceus* Latham 1801	Ground carnivore
STHR	53	Scaly thrush	*Zoothera dauma* (Latham) 1790	Ground carnivore
BRTH	509	Buff-rumped thornbill	*Acanthiza reguloides* Vig. & Horsf. 1827	Bush carnivore
SPW	25	Speckled warbler	*Chthonicola sagittatus* (Latham) 1801	Bush carnivore
RSL	26	Rufous songlark	*Cinclorhamphus mathewsi* Iredale 1911	Bush carnivore
RF	118	Rufous fantail	*Rhipidura rufifrons* (Latham) 1801	Bush carnivore
WBSW	187	White-browed scrubwren	*Sericornis frontalis* (Vig. & Horsf.) 1827	Bush carnivore
SIL	152	Silvereye	*Zosterops lateralis* (Latham) 1801	Bush carnivore
WTTR	259	White-throated treecreeper	*Climacteris leucophaea* (Latham) 1801	Bark prober
BTR	230	Brown treecreeper	*Climacteris picumnus* Temm. & Laug. 1824	Bark prober
RBTR	36	Red-browed treecreeper	*Climacteris erythrops* Gould 1841	Bark prober
GST	169	Grey shrike-thrush	*Colluricincla harmonica* Latham 1801	Bark prober
VS	182	Varied sittella	*Daphoenositta chrysoptera* (Latham) 1801	Bark prober
CST	161	Crested shrike-tit	*Falcunculus frontatus* (Latham) 1801	Bark prober
PCU	13	Pied currawong	*Strepera graculina* (White) 1790	Bark prober*
GCU	37	Grey currawong	*Strepera versicolor* (Latham) 1801	Bark prober
BFCS	36	Black-faced cuckoo-shrike	*Coracina novaehollandiae* (Gmelin) 1789	Wood searcher
WWT	14	White-winged triller	*Lalage sueurii* (Vieillot) 1818	Wood searcher*
CHE	15	Crescent honeyeater	*Phylidonyris pyrrhoptera* (Latham) 1801	Wood searcher*
WEHE	170	White-eared honeyeater	*Lichenostomus leucotis* (Latham) 1801	Wood searcher
NMIN	59	Noisy miner	*Manorina melanocephala* (Latham) 1801	Wood searcher
LHE	20	Lewin's honeyeater	*Meliphaga lewinii* (Swainson) 1808	Wood searcher
OBO	10	Olive-backed oriole	*Oriolus sagittatus* (Latham) 1801	Wood searcher*
GWH	151	Golden whistler	*Pachycephala pectoralis* (Latham) 1801	Wood searcher

Appendix (cont'd)

Mnem.	Obs.	Species Vernacular name	Linnaean name & authority	Guild
RWH	110	Rufous whistler	*Pachycephala rufiventris* (Latham) 1801	Wood searcher
ROSE	57	Rose robin	*Petroica rosea* Gould 1839	Wood searcher
STTH	1252	Striated thornbill	*Acanthiza lineata* Gould 1838	Foliage searcher
YTH	472	Yellow thornbill	*Acanthiza nana* Vig. & Horsf. 1827	Foliage searcher
BTH	1570	Brown thornbill	*Acanthiza pusilla* White 1790	Foliage searcher
SHBC	12	Shining bronze-cuckoo	*Chrysococcyx lucidus* (Gmelin) 1788	Foliage searcher*
YFHE	222	Yellow-faced honeyeater	*Lichenostomus chrysops* (Latham) 1801	Foliage searcher
FHE	333	Fuscous honeyeater	*Lichenostomus fuscus* (Gould) 1837	Foliage searcher
YTHE	74	Yellow-tufted honeyeater	*Lichenostomus melanops* (Latham) 1801	Foliage searcher
WPHE	518	White-plumed honeyeater	*Lichenostomus penicillatus* (Gould) 1837	Foliage searcher
BELL	20	Bell miner	*Manorina melanophrys* (Latham) 1801	Foliage searcher
BHHE	421	Brown-headed honeyeater	*Melipthreptus brevirostris* (Vig. & Horsf.) 1827	Foliage searcher
WNHE	604	White-naped honeyeater	*Melipthreptus lunatus* (Vieillot) 1802	Foliage searcher
SPP	53	Spotted pardalote	*Pardalotus punctatus* (Shaw & Nodder) 1792	Foliage searcher
STP	91	Striated pardalote	*Pardalotus striatus* (Gmelin) 1789	Foliage searcher
LFB	28	Little friarbird	*Philemon citreogularis* (Gould) 1837	Foliage searcher
ESP	147	Eastern spinebill	*Acanthorhynchus tenuirostris* (Latham) 1801	Nectarivore
LWB	41	Little wattlebird	*Anthochaera chrysoptera* (Latham) 1801	Nectarivore
RWB	230	Red wattlebird	*Anthochaera curunculata* (White) 1790	Nectarivore
MUSK	95	Musk Lorikeet	*Glossopsitta concinna* (Shaw) 1791	Nectarivore
LLOR	11	Little Lorikeet	*Glossopsitta pusilla* (Shaw) 1790	Nectarivore*
NHHE	173	New Holland honeyeater	*Phylidonyris novaehollandiae* (Latham) 1790	Nectarivore
SCC	24	Sulphur-crested cockatoo	*Cacutua galerita* (Latham) 1790	Granivore
GAL	49	Galah	*Cacutua roseicapilla* Vieillot 1817	Granivore
GGC	28	Gang gang cockatoo	*Callocephalon fimbriatum* (Grant) 1803	Granivore
RBFT	110	Red-browed firetail	*Emblema temporalis* (Latham) 1801	Granivore
PDOV	10	Peaceful dove	*Geopelia striata* (Linnaeus) 1766	Granivore*
CBW	16	Common bronzewing	*Phaps chalcoptera* (Latham) 1790	Granivore*
CR	175	Crimson rosella	*Platycercus elegans* (Gmelin) 1788	Granivore
ER	53	Eastern rosella	*Platycercus eximius* (Shaw) 1792	Granivore
YR	23	Yellow rosella	*Platycercus flaveolus* Gould 1837	Granivore
RRP	19	Red-rumped parrot	*Psephotus haematonotus* (Gould) 1837	Granivore*
KING	8	King parrot	*Alisterus scapularis* (Lichtenstein) 1818	Not classified
WBWS	—	White-browed woodswallow	*Artamus superciliosus* (Gould) 1837	Not classified
LCOR	—	Little corella	*Cacatua sanguinea* Gould 1842	Not classified
YTBC	9	Yellow-tailed black cockatoo	*Calyptorhynchus funereus* (Shaw) 1794	Not classified
AKF	—	Azure kingfisher	*Ceyx azureus* (Latham) 1801	Not classified
HBC	3	Horsfield's bronze-cuckoo	*Chrysococcyx basalis* (Horsfield) 1821	Not classified
PCOO	—	Pallid cuckoo	*Cuculus pallidus* (Latham) 1801	Not classified
BCOO	—	Brush cuckoo	*Cuculus variolosus* (Vig. & Horsf.) 1826	Not classified
MB	9	Mistletoebird	*Dicaeum hirundinaceum* (Shaw) 1792	Not classified
DF	—	Diamond firetail	*Emblema guttata* (Shaw) 1796	Not classified
WG	—	Western gerygone	*Gerygone fusca* (Gould) 1838	Not classified
WTG	4	White-throated gerygone	*Gerygone olivacea* (Gould) 1838	Not classified
PCL	—	Purple-crowned Lorikeet	*Glossopsitta porphyrocephala* (Dietrichsen) 1837	Not classified
BCHE	—	Black-chinned honeyeater	*Melithreptus gularis* (Gould) 1837	Not classified
RBEE	9	Rainbow bee-eater	*Merops ornatus* Latham 1801	Not classified
CRP	—	Crested pigeon	*Ocyphaps lophotes* (Temminck) 1822	Not classified
PINK	8	Pink robin	*Petroica rodinogaster* (Drapiez) 1819	Not classified
NFB	5	Noisy friarbird	*Philemon corniculatus* (Latham) 1790	Not classified
PIL	—	Pilotbird	*Pycnoptilus floccosus* Gould 1850	Not classified

* Species not included in initial clustering procedure (i.e. membership based on linear discriminant classification of guilds determined by clustering phase).