BEHAVIORAL MECHANISMS AND HABITAT USE BY BIRDS IN A FRAGMENTED AGRICULTURAL LANDSCAPE

JAMES R. MILLER[1,3] AND PETER CALE[2]

[1]*Department of Biology/Graduate Degree Program in Ecology, Colorado State University, Fort Collins, Colorado 80523 USA, and Commonwealth Scientific and Industrial Research Organization (CSIRO), Division of Wildlife and Ecology, Helena Valley, Western Australia, Australia*
[2]*CSIRO Division of Wildlife and Ecology, Private Bag P.O. Wembley, Western Australia 6014, Australia*

Abstract. Effective conservation and habitat restoration strategies in human-dominated landscapes must be based on an understanding of the ways that habitat loss and fragmentation affect native species. We studied avian foraging behavior and patterns of occurrence in the highly fragmented agricultural landscape of the Kellerberrin district of Western Australia to better understand the factors underlying species declines and losses. We conducted three surveys of 30 wandoo woodland patches that ranged in size from 1.3 to 101.3 ha. Some patches were part of larger remnants of native vegetation, ranging in size from 3.5 to 1204.8 ha and including other habitat types. We examined the extent to which patterns of species richness, the occurrence and composition of foraging guilds, and the occurrence of individual species varied with features of woodland patches, remnants, and the surrounding landscape.

Using multiple regression analyses, the best model for species richness included terms for the log of remnant area, the patch diversity of each remnant, and woodland patch condition. We delineated eight foraging guilds based on similarities in the substrate/method dimension and also using multidimensional scaling analyses. The best model for the number of foraging guilds present in a patch included a single variable representing shrub density. Analyses of nestedness based on guilds and on individual species were both significant; and for the latter, 11 of 13 species made a significant contribution to the overall pattern. We derived separate models for the occurrence of each of eight species and one guild using multiple logistic regression. Significant models included, either separately or in combination, the following variables: the log of remnant area, patch area, the total area of woodland in a remnant, and the distance to other woodland patches. For four species that had sufficient records to examine shifts in foraging behavior, we observed significant differences in both foraging methods and substrates with changes in remnant size and/or the presence of other species or guilds.

Our analyses indicated that remnant area was the best single variable for measures of community structure, in part because it was strongly correlated with other variables, such as total woodland area, patch area, remnant patch diversity, number of corridor connections, and measures of isolation. For foraging guilds and for individual species, variables other than remnant area assumed greater importance. The strong patterns of nestedness for foraging guilds by remnant area may reflect the diminished availability of certain prey items in small, degraded remnants. This notion is reinforced by the relatively high species and guild richness recorded in small patches that were either fenced from grazing or embedded in large remnants. The nested pattern of species within some foraging guilds, however, indicates the importance of additional aspects of their ecology. A focus on richness alone may mask the unique responses of bird species to fragmentation and may divert attention from important considerations in the development of land-use policy and reserve acquisition.

Key words: birds; bird community; foraging guild; fragmentation; habitat relationships; landscape pattern; nestedness; species area; Western Australia.

INTRODUCTION

Habitat loss associated with the expansion of human land use is considered to be a primary force in the decline of species worldwide (Heywood and Watson 1995). As anthropogenic activities such as agriculture, silviculture, or urban development become prevalent in a region, native habitats are reduced in area and exist ultimately as remnants in a highly altered matrix. In many parts of the world, the fate of regional biotas depends entirely on the management of such remnants (Janzen 1986, Saunders et al. 1987, Hobbs and Saunders 1993, McDade et al. 1994, Schwartz 1997). It is therefore imperative that land managers charged with

[3] Present address: Department of Zoology, Birge Hall, 430 Lincoln Drive, University of Wisconsin, Madison, Wisconsin 53706 USA.

developing successful conservation and habitat restoration strategies understand the effects of reduced area, increased isolation, and altered habitat structure on native species.

To understand the consequences of habitat loss and fragmentation, much attention has been focused on the size of individual habitat patches. This emphasis reflects the conceptual foundation of the fragmentation paradigm, which has largely been derived from the theory of island biogeography (MacArthur and Wilson 1967). For wooded fragments in human-dominated landscapes, woodland patch area has been found to explain a high percentage of variation in the number of avian species present (Whitcomb et al. 1981, Kitchener et al. 1982, Opdam et al. 1985 Freemark and Merriam 1986, Blake and Karr 1987, Ford 1987, Loyn 1987, Soulé et al. 1988, Askins et al. 1990, Ford et al. 1995). Some bird species have been termed ''area-sensitive'' because evidence suggests that they do not occupy woodland patches below a given size threshold (Whitcomb et al. 1981, Robbins et al. 1989). This does not, however, necessarily reflect sensitivity to area per se.

There is evidence suggesting that area is in fact a surrogate variable that represents a number of factors affecting species persistence in a given patch, such as insufficient resources, isolation from source habitats, or elevated levels of nest parasitism and predation (Askins 1995, Robinson et al. 1995). The latter have often been grouped under the rubric of edge effects (Paton 1994), although the exact nature of such effects is still a matter of debate (Donovan et al. 1997). Indeed, some patterns of habitat use by birds that in the past have been attributed to avoidance of areas of predation risk near habitat edges, or ''ecological traps'' (Ratti and Reese 1988), now appear to mirror patterns of invertebrate prey abundance (Burke and Nol 1998, Robinson 1998).

If food resources play a large role in determining patterns of habitat occupancy for birds in fragmented systems, a reasonable approach to investigating such patterns might be to focus on avian foraging behavior and foraging guilds. Studies of foraging guilds have usually been conducted in one or a few locations and have examined guild structure from the perspective of interspecific competition (Root 1967, Crome 1978, Recher et al. 1985, Ford et al. 1986, Holmes and Recher 1986). More recently, studies of patch occupancy across habitat types in fragmented landscapes (Cale 1994) and comparisons between continuous and fragmented habitat of a single type (Recher and Davis 1998) have been based on foraging guilds.

We studied patterns of avian foraging behavior and habitat use in the Kellerberrin district of Western Australia. Because pre-settlement vegetation there has been drastically reduced and exists only in scattered remnants, this area represents one extreme of the fragmentation continuum (Wiens 1995, McIntyre and Hobbs 1999). There is both model-based and empirical support for the assertion that fragmentation effects are primarily due to habitat loss in landscapes with >70% suitable habitat remaining, but that patch size and isolation assume greater importance in highly fragmented systems (Andrén 1994). One might therefore expect that patterns of species occurrence in the Kellerberrin district would reflect the importance of all three of these variables.

To better understand the effects of habitat fragmentation, we restricted our attention to species that rely on invertebrate prey and that are associated with woodland patches. Such species have suffered disproportionately great declines in the central wheat belt, attributable to a combination of preferential clearing of these habitats and subsequent modification of remnant vegetation (Saunders and Curry 1990, Cale 1994, Saunders and Ingram 1995).

We examined habitat use and foraging behavior at several levels of resolution. At the community level, we examined species richness across a range of woodland patch sizes. To investigate compositional patterns that underlie variation in species richness, we also investigated the degree to which patterns of patch occupancy for foraging guilds and for individual species were nested. We then asked how the occurrence and composition of foraging guilds vary with differences in features of woodland patches and the remnants in which these patches are embedded, as well as with several measures of overall landscape configuration. At the finest resolution, we investigated patterns of occurrence for individual species, the degree to which these species contribute to overall patterns of nestedness, and the extent to which various species exhibit plasticity in their foraging behavior as local habitat conditions, landscape configurations, and/or species composition changes.

STUDY AREA AND METHODS

We studied the foraging behavior of insectivorous birds during the breeding season in a 1680-km² area north of the town of Kellerberrin in the central wheat belt of Western Australia (see Hobbs and Saunders 1993, Saunders et al. 1993; Fig 1). The presettlement flora in this region existed as a complex mosaic of heathlands, shrublands, and woodlands (Beard 1980, McArthur 1993). Typical of the central wheat belt, nearly 93% of the original vegetation in the Kellerberrin district was cleared for crop production and sheep grazing prior to 1980, but there has been little additional clearing since then (Arnold and Weeldenberg 1991). Native vegetation is now restricted to 457 remnants, of which 77% are <20 ha in size, and to narrow verges along the district's 600 km of roads (Saunders et al. 1987, Arnold and Weeldenberg 1991). Eucalypt woodlands were thought to be indicative of better soils and were therefore cleared preferentially (Beard 1980, Main 1993). This has resulted in their
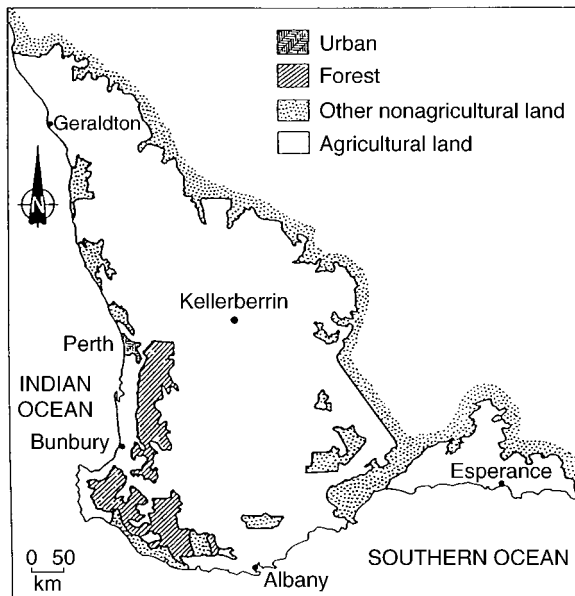
FIG. 1. Southwestern Australia, showing the location of the town of Kellerberrin in the central wheat belt, plus adjacent forest and uncleared areas (from Hobbs 1994).

underrepresentation in the remnant vegetation (Arnold and Weeldenberg 1991).

Some remnants in the Kellerberrin area consist of a single habitat type, or "patch," while others are a mosaic of patches of different habitat types that might include shrubland, York gum (*Eucalyptus loxophleba*; a relatively short eucalypt associated with granitic outcroppings), mallee (a particular growth form of small eucalypts that is multi-stemmed and forms dense stands), and/or open eucalypt woodlands dominated by salmon gum (*Eucalyptus salmonophloia*), gimlet (*Eucalyptus salubris*), or wandoo (*Eucalyptus capillosa*; Fig. 2). We attempted to standardize variation in habitat features as much as possible by focusing exclusively on individual patches of wandoo woodland. Wandoo grows to ~25 m and tends to occur in stands characterized by open canopies (<30% coverage) and understories dominated by *Acacia* spp. We identified wandoo patches in the study area by visiting remnants known to have a woodland component. All available wandoo-dominated patches were used as study sites, for a total of 30 patches in 29 remnants. Patch sizes ranged from 1.3 to 100 ha, while their associated remnants ranged from 3.5 to 1205 ha (Table 1).

Landscape, remnant, and patch variables

For each of the 30 woodland patches, we quantified a number of landscape, remnant, and local habitat features (Table 2). To measure landscape and remnant variables, we used 1:25 000 color aerial photographs (1996) and a classified Landsat TM image (1994; both produced by CSIRO Division of Wildlife and Ecology, Wembley, Western Australia) with 30-m resolution. We

determined the area of each study patch of wandoo woodland (PATCH AREA) using aerial photos. The total area of all woodland patches in the remnant (WOOD AREA), the total area of patches for each of the other habitat types in the remnant, and the total area of the remnant (REM AREA) were quantified using the Geographic Information System GRASS. We used the Shannon-Wiener index to describe habitat diversity (HD) in each remnant using the formula

$$HD = \sum_{i=1}^{k} f_i \log f_i \qquad (1)$$

where f_i is the proportion that habitat i constitutes of the total area of the remnant and k is the number of habitat types in the remnant. In addition to woodland (wandoo, salmon gum, and gimlet), other habitat types included shrubland, mallee, and York Gum.

The degree to which a remnant was isolated from other remnants was determined in three ways. For each remnant that contained a study patch of wandoo, we calculated the mean distance to each of the nearest ten remnants (DIST) and also to each of the nearest ten remnants that contained woodland (DIST-W). As another measure of isolation, we tallied the number of corridors connecting the focal remnant to other remnants (CORR), using only vegetated strips with internal gaps <100 m. This distance is based on the maximum gap that the Blue-breasted Fairy Wren (*Malurus pulcherrimus*), one of the few remnant-dependent species whose movements have been well-studied in the area (Brooker and Brooker 1997), is known to cross (L. Brooker, *personal communication*).

In each patch, we sampled variation in habitat conditions using 100-m transects. Transects were established in representative areas of the patch using a random compass direction and random starting point. We recorded the species and height of any shrubs whose canopy intersected a vertical plane extending the length of the transect, and the species of each tree whose bole was within 2 m of the transect line in any direction. Based on diameter at breast height (dbh), trees were categorized as small (<20 cm), medium (20–50 cm), and large (>50 cm). Logs that intersected a transect line were recorded in these same categories. We established three 1-m^2 quadrats along each transect at 0, 49.5, and 99 m. For each quadrat, we estimated percent cover of bare ground, litter (leaves and twigs), weeds, and other herbaceous vegetation. To avoid large error terms associated with such estimates, we categorized percent cover using the following numbering system (0–5): 0, 1 = <2%, 2 = 3–10%, 3 = 11–30%, 4 = 31–70%, 5 = 71–100%. The number of transects per patch was based on patch area: 1 transect for small patches (<10 ha), 3 transects for medium patches (10–20 ha), and 5 transects for large patches (>20 ha).

For all analyses, we combined logs of all size categories to create the variable LOGS. We did likewise
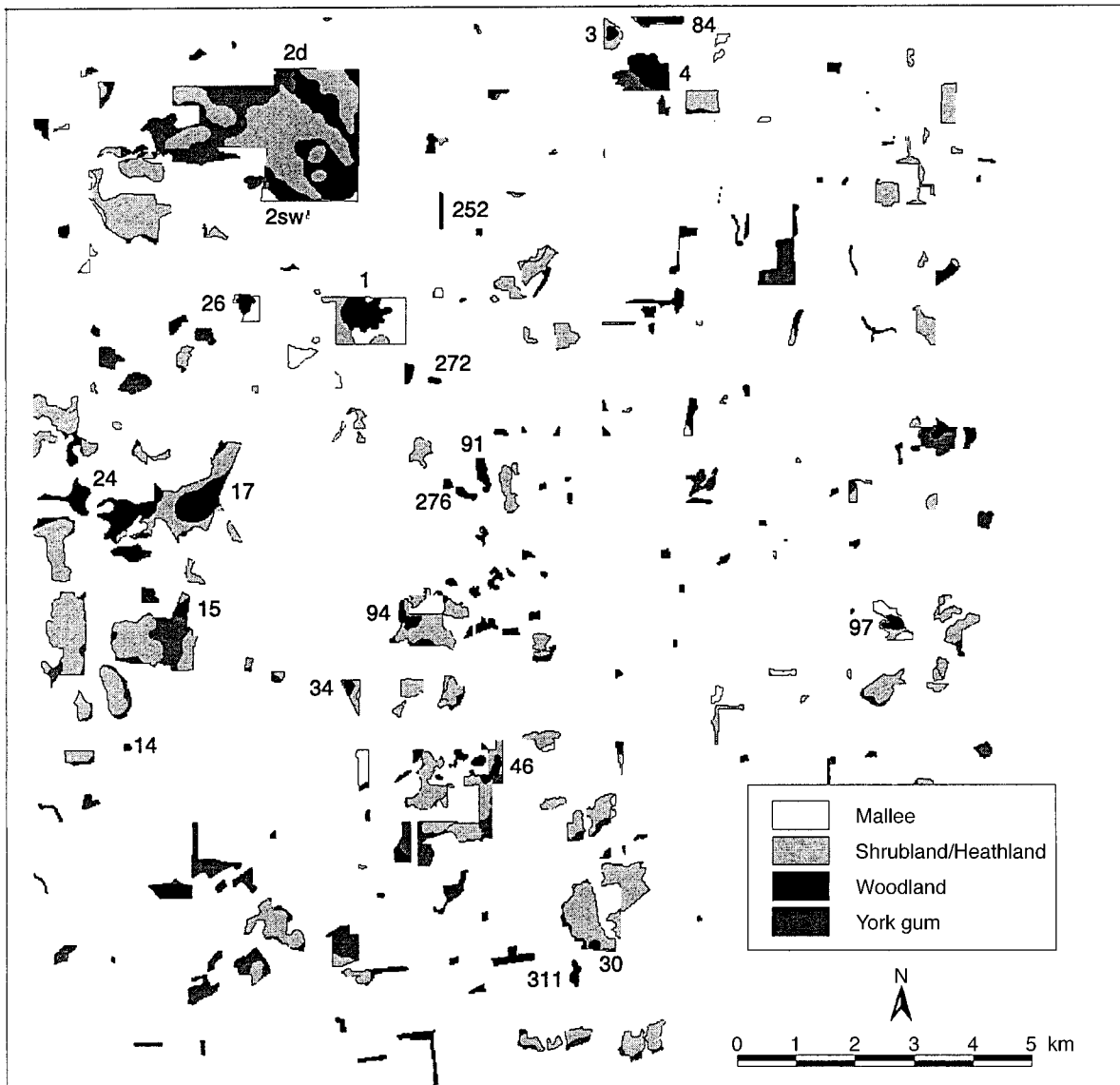
FIG. 2. A representative section of the Kellerberrin district in the central wheat belt of Western Australia, north of the town of Kellerberrin, showing remnants of presettlement vegetation. Some remnants include only one habitat type, or "patch," while others are composed of patches of several habitat types. Remnants containing patches of wandoo woodland used in this study are labeled. For remnants that contain more than one woodland patch, the label is nearest to the study patch.

to create TREE, the total number of trees of all sizes within 2 m of the transect, and also created the variable TREE-LG for trees with dbh >50 cm. We created an index of habitat condition (COND), which equals the sum of the scores for litter and herbaceous vegetation minus the score for weeds.

Data collection

J. R. Miller conducted area searches in all patches during each of three two-week sampling periods between 22 September and 21 November, 1997. All patches were searched once in the early morning (between 0600 and 0900), once in the late morning (between 0900 and 1200), and once in the late afternoon (between 1500 and 1900). The amount of time spent searching each patch on each visit was based on its size: small patches were searched systematically for ≤1 h, medium patches for 2–3 h, and large patches for ≤4 h.

Foraging observations were recorded during and after each census. For each individual encountered, up to five consecutive prey attacks were recorded following the procedures of Recher et al. (1985) as modified by Cale (1994). Recher and Gebski (1990) found no significant differences in foraging behavior between initial and subsequent observations. Moreover, multi-

TABLE 1. Size of 29 vegetation remnants and 30 associated wandoo woodland patches in the Kellerberrin district of the Western Australian wheat belt.

Remnant/ patch	Remnant size (ha)	Study Patch size (ha)
1	230.5	56.9
2d	1204.8	39.5
2sw	1204.8	19.1
3	29.2	12.0
4	119.1	24.0
10	128.2	35.1
13	80.3	10.9
14	3.5	3.5
15	232.7	12.1
17	341.2	100.1
23	10.7	1.3
24	214.8	2.0
26	32.7	15.0
27	24.9	2.4
29	111.0	10.0
30	122.2	8.0
34	30.7	11.3
46	322.0	22.8
56	21.9	17.6
66	100.7	59.5
78	25.9	12.6
84	61.6	12.7
91	19.9	19.9
94	112.5	19.8
97	53.6	22.1
127	10.0	10.0
252	11.2	11.2
272	3.7	3.7
276	10.2	10.2
311	9.4	9.4

ple observations have been shown to increase the chance of recording infrequent or unusual behavior (Recher et al. 1985), and this is important considering that one of our objectives was to quantify changes in

foraging behavior associated with differences in habitat features or in co-occurring species. For these reasons, we considered each prey attack to be an independent sample. Only one series of prey attacks was recorded for any individual encountered during a given visit, but observations on the same individual during different visits could not be avoided. Some patches were visited a fourth time during mid-December for the purpose of obtaining additional foraging records, but no area searches were conducted at this time.

For each prey attack, the height, foraging method, substrate (including plant species if possible, or life-form), and microhabitat were recorded. The foraging methods included pounce, probe, glean, hang-glean, snatch, hover, hawk, and taking nectar (Recher et al. 1985). Substrates included bare ground, litter, debris (sticks and twigs), logs, trunks and branches of trees or shrubs (including subcategories of smooth bark or rough bark, live or dead), foliage, flowers, and air. Life-forms were comprised of tree, mallee, or shrub, and microhabitats included small patches of shrub or mallee embedded in the larger wandoo patch.

Foraging guilds

Using the methods of Cale (1994), we delineated guilds on the basis of a single dimension that combines both foraging method and substrate. For a given pair of species, we calculated foraging overlap by summing the minimum relative frequency of prey attacks for each category of method/substrate (Hurlbert 1978). We defined the criteria for guild membership as a foraging overlap of >50% among species of a guild, and <50% overlap with those species not in the guild. The mean foraging overlap between each pair of guilds was calculated by averaging the foraging overlaps between the

TABLE 2. Definitions and summary statistics for landscape, remnant, and patch characteristics of 30 patches of wandoo woodland in the Kellerberrin district of the Western Australian wheat belt.

Variable code	Definition	Units	Minimum	Maximum	Mean
REM AREA	(log) area of a remnant in which study patch is located	ha	0.54	3.08	1.74
WOOD AREA	(log) area of all woodland patches in a remnant	ha	0.11	2.15	1.22
PATCH AREA	(log) area of wandoo woodland study patch	ha	0.11	2.00	1.11
DIST	distance to nearest remnant	km	0.71	2.58	1.40
DIST–W	distance to nearest remnant with woodland patches	km	0.92	3.20	1.87
CORR	number of corridors that connect a remnant with other remnants	0–6	0.00	6.00	2.20
HD	habitat patch diversity in a remnant based on the Shannon-Wiener index	0–1	0.00	0.47	0.28
COND	habitat condition of a patch, based on percent cover of litter and herbaceous vegetation minus cover for weeds	0–10	0.00	6.00	3.70
SHRUB	mean number of shrubs per 100-m transect in a woodland patch	shrubs/100 m	0.00	23.00	9.22
LOG	mean number of logs per 100-m transect in a woodland patch	logs/100 m	0.00	10.00	4.40
TREE	mean number of trees per 100-m transect in a woodland patch	trees/100 m	1.67	19.80	7.75
TREE-LG	mean number of trees with dbh > 50 cm per 100-m transect in a woodland patch	trees/100 m	0.00	2.00	0.52

TABLE 3. Scientific and common names (Christidis and Boles 1994) and species codes for insectivorous birds observed in wandoo woodland in the Kellerberrin District.

Species code	Scientific name	Common name
BFCS	*Coracina novaehollandiae*	Black-faced Cuckoo Shrike
BFWO	*Artamus cinerus*	Black-faced Woodswallow
BHHO	*Melithreptus brevirostris*	Brown-headed Honeyeater
CRTH	*Acanthiza uropygialis*	Chestnut-rumped Thornbill
GRFA	*Rhipidura fuliginosa*	Grey Fantail
GRST	*Colluricincia harmonica*	Grey Shrike-thrush
INTH	*Acanthiza apicalis*	Inland (Brown) Thornbill
JAWI	*Microeca fascinans*	Jacky Winter
MAWO	*Artamus personatus*	Masked Woodswallow
RABE	*Merops ornatus*	Rainbow Bee-eater
RCRO	*Petroica goodenovii*	Red-capped Robin
RUWH	*Pachycephala rufiventris*	Rufous Whistler
SIHO	*Lichenostomus virescens*	Singing Honeyeater
STPA	*Pardalotus striatus*	Striated Pardalote
TRMA	*Hirundo nigricans*	Tree Martin
VASI	*Daphoenositta chrysoptera*	Varied (Black-capped) Sittella
WBBA	*Pomatostomus superciliosus*	White-browed Babbler
WEEB	*Smicrornis brevirostris*	Weebill
WEGE	*Gerygone fusca*	Western Gerygone
WEHO	*Lichenostomus leucotis*	White-eared Honeyeater
WIWA	*Rhipidura leucophrys*	Willie Wagtail
WYRO	*Eopsaltria griseogularis*	Western Yellow Robin
YRTH	*Acanthiza chrysorrhoa*	Yellow-rumped Thornbill
YTMI	*Manorina flavigula*	Yellow-throated Miner

species in the two guilds (Cody 1974, Cale 1994). For these analyses, we collapsed the substrate categories of litter, debris, bare-ground, and logs to a single category, "ground;" and the categories for trunk and branch to "bark."

We used monotonic multidimensional scaling (SAS Institute 1996) to summarize foraging guilds and to assist in determining guild boundaries. Multi-dimensional scaling provides a graphical way of depicting species' relative positions in multidimensional space based on their similarity with regard to (in this case) substrate and foraging method. For ease of visual interpretation, we depicted foraging relationships using two dimensions.

Data analysis

We used an interactive method for building multiple regression models (Henderson and Velleman 1981, James and McCulloch 1990) for all possible subsets of the independent variables to examine the relationships between measures of the avian community and various patch, remnant, and landscape variables. The underlying assumption of interactive model building is that variable selection is best accomplished when variables are screened by an analyst who is familiar with the data and subject matter, using graphical and statistical diagnostic procedures (Henderson and Velleman 1981, James and McCulloch 1990, Tabachnick and Fidell 1996).

We calculated species richness and guild richness for each of the 30 patches. We subsequently assessed the normality of these and other variables by examining stem-and-leaf plots and normal probability plots of re-

siduals. Species richness met standard criteria for multiple linear regression, while patch, woodland, and remnant areas were log transformed. Regression models were compared and evaluated on the basis of their adjusted r^2, ability to meet assumptions, and influential cases. We assessed the influence of individual observations on the fitted models by examining leverage plots and Cook's distance (Weisberg 1985, Tabachnick and Fidell 1996). After examining the distribution of guild richness and finding it to be approximately Poisson, we used a generalized linear model with a log link function (McCullagh and Nelder 1983).

If the species composition of smaller patches tend to be subsets of larger patches with higher species richness, the community is said to be nested. To assess the overall degree of nestedness, we compared observed patterns of patch occupancy with a distribution of patterns generated by 1000 Monte Carlo simulations (z value and t test) using the RANDOM1 option in the BASIC program developed by Patterson and Atmar (1986). This option weights the selection of a species for random distribution among patches by the number of patches in which that species was observed. Similarly, we examined the contribution of individual species to the overall nested pattern using the large-sample approximation of the Wilcoxon rank-sum test (Simberloff and Martin 1991, Worthen 1996).

We used multiple logistic regression to identify patch, remnant, and landscape variables associated with the probability of occurrence of individual species. Regression models for all possible subsets of independent variables were evaluated on the basis of the log-likelihood chi-square and percent concordance for

TABLE 4. Percentage of foraging records in observed substrate/method categories for insectivorous birds in wandoo woodland in the Kellerberrin District.

Species	Ground/litter			Bark				Foliage		
	Glean	Probe	Pounce	Glean	Probe	Snatch	Hover	Glean	Snatch	Hover
Rainbow Bee-eater	···	···	···	···	···	···	···	3	···	2
Striated Pardalote	3	···	···	7	···	2	···	82	3	3
Weebill	1	···	···	8	···	···	1	62	8	19
Western Gerygone	···	···	···	7	···	4	···	39	18	17
Yellow-rumped Thornbill	68	···	···	12	···	···	···	11	3	1
Chestnut-rumped Thornbill	17	···	2	31	1	2	4	23	6	8
Inland Thornbill	5	···	2	33	2	4	2	37	5	6
Brown-headed Honeyeater	···	···	···	2	1	1	···	69	3	7
White-eared Honeyeater	···	···	···	33	16	2	···	22	2	···
Singing Honeyeater	···	···	···	27	···	···	3	35	···	···
Jacky Winter	2	···	32	1	···	24	···	···	2	···
Red-capped Robin	24	···	56	···	···	6	1	1	3	1
Western Yellow Robin	4	···	87	1	···	7	···	···	···	···
White-browed Babbler	15	15	···	37	24	···	···	7	···	···
Varied Sitella	4	···	···	90	4	···	···	2	···	···
Rufous Whistler	4	···	2	21	···	34	1	12	18	1
Grey Shrike-thrush	31	5	···	52	7	···	···	2	2	···
Grey Fantail	···	···	···	···	···	···	···	5	7	···
Willy Wagtail	10	···	10	4	···	1	···	3	···	1
Tree Martin	···	···	···	···	···	···	···	···	···	···

the overall model, and the Wald chi-square values for individual variables.

For species that had sufficient records, we examined foraging behavior for evidence of plasticity. We used likelihood ratio chi-square tests to assess differences in the foraging behavior of each species among remnants in different size classes and in relation to the presence/absence of select foraging guilds. To increase sample size, substrate/method categories were collapsed to ground, bark, and foliage.

Our goals were to identify patterns in foraging behavior and patch occupancy and to generate hypotheses regarding the processes determining these patterns. The variability inherent in natural systems over broad scales could result in low power and Type II errors. To compensate for this possibility, we selected an alpha of 0.1 when conducting all statistical tests.

RESULTS

We observed 24 insectivorous species in patches of wandoo woodland (see Table 3 for common and scientific names). Of these, 20 species had sufficient records (>40) for inclusion in our analyses of foraging guild structure (Table 4).

Foraging guilds

Based on foraging overlaps in the substrate/method dimension, we identified eight foraging guilds; six guilds based on a dominant substrate/method combination, and two guilds comprised of species with intermediate values (Table 5). There was a clear separation between species that hawk or sally to catch flying prey and those that pounce or fly from a perch and grab prey as they land, with one exception (Fig. 3). The

Jacky Winter exhibited nearly equal proportions of hawking and pouncing in its prey attacks (Table 4). Its mean overlap values, however, were too low for inclusion in either of those guilds (Table 6), and we concluded that it was biologically more realistic to consider it separately in an intermediate guild (Ground Pouncer-Hawker; Fig. 3). There was also an apparent split between these three groups and those species that glean or snatch prey items from foliage, bark, or the ground (Fig. 3). The remaining guilds are finer subdivisions of this latter group.

In the case of the bark gleaners, although the overlap between the Varied Sittella and White-browed Babbler is only 47%, the latter engages in bark gleaning more than any other combination of substrate/method. Moreover, the White-browed Babbler had a higher overlap with the Grey Shrike-thrush than with any other species (Table 5). For these reasons, we assigned the White-browed Babbler to the Bark Gleaner guild. Each of the general gleaners tended to concentrate its prey attacks in two of the three substrates but did not have a dominant foraging substrate.

For species that foraged on bark and foliage, we conducted a second multidimensional scaling analysis using pairwise foraging overlaps that were based on proportions of foraging observations in the shrub, mallee, and tree substrate categories, standardized to total 100%. Here, the greatest amount of separation was between species that tend to forage on shrubs (Western Gerygone, Chestnut-rumped Thornbill, Inland Thornbill, and White-browed Babbler) and those that forage on the trunks, branches, and foliage of mallee and trees (Fig. 4). Intermediate between these two groups in two-dimensional space were the Singing Honeyeater and

TABLE 4.   Extended.

Air Hawk	Nectar	Total Records
95	···	99
···	···	272
1	···	705
15	···	46
5	···	395
6	···	414
4	···	126
···	17	98
6	19	49
2	33	63
39	···	282
8	···	390
1	···	69
2	···	41
···	···	138
7	···	138
1	···	90
88	···	42
71	···	72
100	···	200

White-eared Honeyeater; both species showed a tendency to use shrubs and trees in roughly equal proportions.

Patterns of occurrence

Our analyses of richness focused on the same species that we included in our delineation of foraging guilds, except that the Yellow-throated Miner was included in our calculation of richness while the Grey Fantail and Western Gerygone were not, for a total of 19 species. The latter two species were excluded because they began to migrate from the Kellerberrin District during the early weeks of the study, which may have biased our surveys in some patches. We also examined richness for a subset of species whose primary habitat was woodland (hereafter, woodland residents; $n = 13$), removing the Willie Wagtail, Yellow-rumped Thornbill, and Yellow-throated Miner because these species also forage on agricultural land (Cale 1994), the Rainbow Bee-eater because it is more closely associated with shrublands than woodlands (Cale 1994), and the Singing Honeyeater and White-eared Honeyeater because their occurrence in woodlands is probably driven primarily by nectar in the spring (Lambeck 1995).

There was substantial correlation among the independent variables (Table 7). This was particularly the case with regard to REM AREA, which had relatively high positive correlations with WOOD AREA, PATCH AREA, CORR, and HD, and negative correlations with DIST and DIST-W. REM AREA was also the best single predictor for overall species richness (adjusted r^2 = 0.654), while the most robust model, based on our performance criteria, included three independent variables: REM AREA, HD, and COND (adjusted r^2 =

0.753). The next best three-variable model replaced the variable COND with the variable TREE (adjusted r^2 = 0.747). The overall best model for species richness using the reduced set of species also included REM AREA, HD, and COND (adjusted r^2 = 0.795).

When examining the number of foraging guilds present in a remnant, the best performing model included the single independent variable SHRUB (chi-square P = 0.045). The addition of other variables did not improve the model. For our analyses of nestedness at the level of guilds and individual species, we focused on woodland residents. Community-level patterns of patch occupancy were highly nested for foraging guilds (P < 0.0001; Table 8) and for individual species (P < 0.0001; Table 9), 11 of which contributed significantly to the nested pattern (P < 0.05; Table 9). A Spearman rank correlation test revealed no relationship between the rank order of patch areas and species richness (P = 0.66, r = 0.083), but this test did indicate that the community is nested by remnant area based on a highly significant association between that variable and richness (P < 0.001, r = 0.907).

Eight individual species and one foraging guild had sufficient numbers of presences and absences for multiple logistic regression. A single-variable logistic model including REM AREA was the most robust for predicting the occurrence of the Grey Shrike-thrush, the Yellow-rumped Thornbill, the Rufous Whistler, and the Bark Gleaner guild (all log-likelihood chi-square tests, P = 0.0001). For the Red-capped Robin the best performing model included REM AREA and TREE (log-likelihood chi-square, P = 0.0001 and 96.9% concordance). A two-variable model including SHRUB
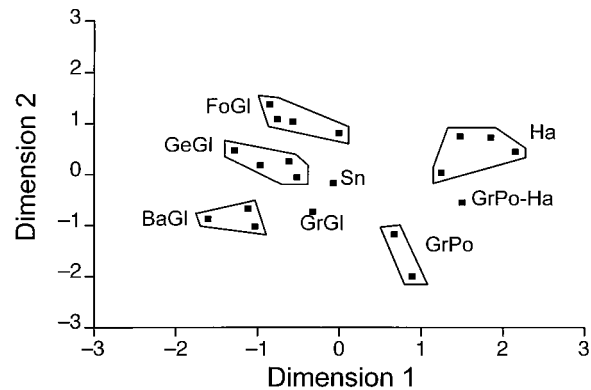
FIG. 3.   The relationship between foraging guilds based on a multidimensional scaling analysis of the combined substrate/method foraging dimension for 20 species of insectivorous birds associated with wandoo woodlands in the Kellerberrin district, Western Australia. Guilds were defined on the basis of foraging overlaps >50% in the substrate/method dimension with all other species in a given guild and include Foliage Gleaners (FoGl), General Gleaners (GeGl), Bark Gleaners (BaGl), a Ground Gleaner (GrGl), a Snatcher (Sn), Ground Pouncers (GrPo), Hawkers (Ha), and a Ground Pouncer–Hawker (GrPo–Ha).

TABLE 5. Pairwise foraging overlaps for 20 species of insectivorous birds associated with wandoo woodlands in the Kellerberrin district, Western Australia.

Guild species	YRTH	RCRO	WYRO	JAWI	RABE	TRMA	WIWA	GRFA	WBBA
GroundG1									
YRTH	1.00								
GrPo									
RCRO	0.34	1.00							
WYRO	0.06	0.67	1.00						
GrPo-Hawk									
JAWI	0.10	0.50	0.43	1.00					
Hawk									
RABE	0.07	0.10	0.01	0.39	1.00				
TRMA	0.05	0.08	0.01	0.39	0.95	1.00			
WIWA	0.23	0.31	0.17	0.53	0.72	0.71	1.00		
GRFA	0.13	0.12	0.01	0.41	0.88	0.88	0.74	1.00	
BaGl									
WBBA	0.36	0.18	0.06	0.05	0.02	0.02	0.19	0.07	1.00
GRST	0.48	0.28	0.06	0.06	0.02	0.01	0.16	0.04	0.65
VASI	0.18	0.05	0.05	0.03	0.00	0.00	0.10	0.02	0.47
FoGl									
WEGE	0.26	0.18	0.06	0.22	0.17	0.15	0.24	0.27	0.16
BHHO	0.17	0.07	0.02	0.04	0.05	0.00	0.07	0.08	0.10
WEEB	0.25	0.19	0.03	0.05	0.06	0.01	0.10	0.13	0.17
STPA	0.25	0.05	0.06	0.07	0.05	0.00	0.12	0.08	0.17
GeGl									
SIHO	0.25	0.04	0.02	0.03	0.04	0.02	0.09	0.07	0.36
WEHO	0.29	0.11	0.04	0.11	0.06	0.06	0.14	0.13	0.58
INTH	0.36	0.23	0.12	0.16	0.07	0.05	0.21	0.16	0.49
CRTH	0.49	0.34	0.10	0.15	0.09	0.06	0.27	0.17	0.56
Snatch									
RUWH	0.36	0.25	0.15	0.37	0.08	0.07	0.22	0.19	0.33

Notes: Guilds were defined on the basis of foraging overlaps >50% in the substrate/method dimension with all other species in a guild and <50% overlap with those species not in the guild (see *Results: Foraging guilds* for exceptions). Guilds include a Ground Gleaner (GrGl), Ground Pouncers (GrPo), a Ground Pouncer-Hawker (GrPo-Hawk), Hawkers (Hawk), Bark Gleaners (BaGl), Foliage Gleaners (FoGl), General Gleaners (GeGl), and a Snatcher (Snatch). See Table 3 for common and scientific names of species.

and PATCH AREA was the best performer (log-likelihood chi-square, $P = 0.0001$ and 90.3% concordance) for Inland Thornbills. For Brown-head Honeyeaters and Varied Sittellas, a single-variable model including DIST-W was the most robust (log-likelihood chi-square, $P < 0.0001$, 92.1% and 90.9% concordance, respectively). The most robust model for the Jacky Winter included DIST-W and either WOOD AREA or PATCH AREA (log-likelihood chi-square $P < 0.0001$, 97.5% concordance), a slight improvement over a single-variable model that included REM AREA (96.3% concordance).

Foraging plasticity

Because remnant area was such a strong independent variable, we inspected the distribution of remnant sizes for discontinuities, and subsequently categorized the remnants as small (<12 ha, $n = 7$), medium (19–81 ha, $n = 10$), and large (>100 ha, $n = 13$). Four bird species had sufficient records across remnant size categories, or in the presence and absence of certain species or foraging guilds, to permit statistical tests to determine the significance of shifts between foraging categories of substrate/method. Striated Pardalotes, a species that foraged on foliage nearly 90% of the time, used other substrates more in large remnants (15%)

when compared with medium (5%) and small (7%) remnants ($P = 0.043$). Weebills, also predominantly a foliage gleaner, showed increases in foraging on bark from 8% to 12% when the Bark Gleaner guild was absent ($P = 0.101$) and from 10% to 18% when the General Gleaner guild was absent ($P = 0.104$). Yellow-rumped Thornbills, the sole member of the ground-foraging guild, foraged nearly twice as much on bark and foliage (54% vs. 28%) when the Bark Gleaner guild was absent ($P < 0.001$).

DISCUSSION

Because we studied avian foraging behavior and species distributions during a single season, some caution should be exercised when interpreting our data. Habitat use and food resources vary seasonally for some species (Cale 1994) and although most birds are resident in this area, there is some annual variability in habitat occupancy, particularly for uncommon species (R. J. Lambeck and P. Cale, *unpublished data*). In spite of the spatial and temporal limitations of our study, however, the foraging behaviors that we observed were in agreement with those described for birds in the Kellerberrin area by Cale (1994), based on data collected across seasons and habitat types. Moreover, our guild designations were generally similar to the foraging pro-

TABLE 5. Extended.

GRST	VASI	WEGE	BHHO	WEEB	STPA	SIHO	WEHO	INTH	CRTH	RUWH
1.00										
0.61	1.00									
0.11	0.09	1.00								
0.04	0.05	0.52	1.00							
0.14	0.11	0.72	0.74	1.00						
0.14	0.12	0.54	0.69	0.72	1.00					
0.30	0.29	0.42	0.54	0.45	0.42	1.00				
0.44	0.39	0.39	0.45	0.33	0.33	0.69	1.00			
0.44	0.39	0.65	0.50	0.60	0.66	0.64	0.66	1.00		
0.54	0.38	0.50	0.36	0.47	0.63	0.54	0.63	0.83	1.00	
0.29	0.26	0.48	0.19	0.32	0.28	0.35	0.42	0.55	0.54	1.00

file of a wandoo woodland avifauna described by Recher and Davis (1998) in another part of the wheat belt region.

Of the landscape, remnant, and patch variables that we examined, remnant area explained the highest percentage of variation in species richness and also the richness of woodland residents. Moreover, patterns of species composition were nested by remnant area and for several of the individual species that we examined, remnant area was the best predictor for occurrence in a woodland patch. We suggest that a suite of charateristics related to remnant size underlies the patterns that we observed. Larger remnants tended to contain more habitat types and a greater amount of woodland, to be closer together, and to have more corridor connections. The size of a remnant, however, showed relatively weak correlations with woodland patch vari-

ables other than patch size and this probably accounts for the additional variation explained by the term describing patch condition in models for species richness.

We tended to observe more species in patches with increased diversity of vegetation structure as has been reported by other investigators (Connor and McCoy 1979, James and Wamer 1982, Kitchener et al. 1982, Lynch and Whigham 1984). A few woodland patches in large remnants had comparatively few shrubs or large trees and lower than expected species richness. Such conditions probably reflect the legacy of past land uses such as logging or grazing (Main 1993) even though these activities may no longer occur there. Most of the woodland patches in remnants <20 ha also had few, if any, shrubs or large trees and relatively low scores for patch condition. Smaller remnants tend to be highly susceptible to negative effects emanating

TABLE 6. Mean foraging overlap between guilds, based on the mean of foraging overlaps of their constituent species.

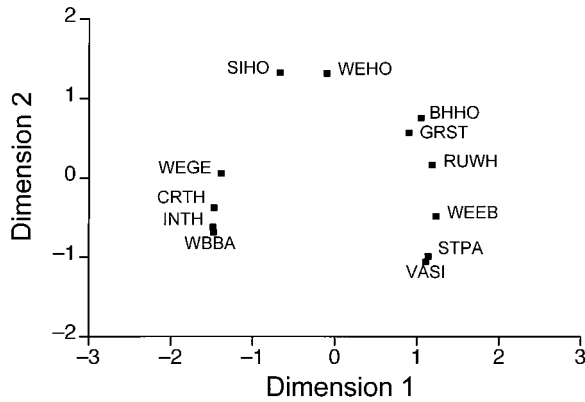|	Ground Gleaner	Ground Pouncer	Ground Pouncer/ Hawker	Hawker	Bark Gleaner	Foliage Gleaner	General Gleaner
Ground Pouncers	0.20						
Ground Pouncer/Hawker	0.10	0.47					
Hawkers	0.12	0.10	0.43				
Bark Gleaners	0.34	0.11	0.05	0.03			
Foliage Gleaners	0.23	0.09	0.10	0.09	0.12		
General Gleaners	0.11	0.12	0.11	0.10	0.43	0.46	
Snatcher	0.35	0.20	0.37	0.14	0.29	0.32	0.47

FIG. 4. The relationship between avian species that forage on vegetation in wandoo woodlands of the Kellerberrin district. Relative positions were derived from a multidimensional scaling analysis of the proportion of prey attacks recorded in the shrub, mallee, and tree substrate categories. See Table 3 for common and scientific names of species.

from the surrounding matrix (Saunders et al. 1991), such as grazing or weed invasion, that reduce the habitat quality of the component patches. Small patches that are embedded in larger remnants may be buffered from such negative impacts. Two woodland patches in large remnants, each less than 2 ha in size but with relatively high scores for condition and numbers of shrubs, had higher species richness than stand-alone patches of similar size. A small patch need not occur in a large remnant, however, to be buffered from adverse impacts emanating from the matrix. Our smallest remnant (3.5 ha) consisted of only one woodland patch, but it was fenced from the surrounding paddocks, thereby minimizing grazing impacts. In this remnant, we observed more than twice the number of species as in the next four largest remnants combined; the latter were all unfenced.

　Patches embedded in larger remnants may also contain more species as a result of proximity to other habitat types, including other woodlands, which may provide additional nesting or foraging opportunities. De-spite a strong correlation with remnant area, the habitat diversity of a remnant still accounted for additional variation in species richness and was included in our models. This was the case not only for overall species richness, but also for the richness of woodland residents, indicating that even birds that nest in woodlands and forage there may benefit from other nearby habitat patches.

　Thus remnant area correlates strongly enough with a suite of landscape and remnant variables that, together with habitat diversity and patch condition, it accounts for a substantial portion of the variation in species richness. Species richness provides some information on bird distributions, but it is limited. Indeed, one of the main criticisms of island biogeographic theory in conservation applications, aside from its failure to consider the landscape context of habitat islands (Wiens 1997), is the focus on species richness with no attention to community composition (Gilbert 1980, Margules et al. 1982, Wiens 1989a, Soberón 1992, Doak and Mills 1994). By examining presence/absence patterns for foraging guilds, we begin to focus on the underpinnings of richness patterns.

　In contrast to the models for species richness, remnant area was not the most important variable in guild richness models and in fact did not improve the model. Rather, the sole variable in the best model represented the density of shrubs in a patch. General gleaners were most frequently observed foraging in shrubs and the pouncers, particularly Red-capped Robins, often used shrubs for perch sites (J. R. Miller, *unpublished data*). Furthermore, a substantial portion of prey attacks by species in other guilds occurred in shrubs. There was little correlation between remnant size and shrub density (or any other patch-level variables) and shrubs were virtually absent in five of the six smallest remnants. The absence of shrubs is characteristic of disturbed sites, especially those subjected to intense grazing, as is enhanced nutrient enrichment, more acidic soils, fewer tree and shrub species, lower overall productivity, and more non-native annuals (Landsberg et

TABLE 7. The correlation matrix for landscape, remnant, and woodland patch variables considered in the regression analyses.

Variable	REM AREA†	WOOD AREA†	PATCH AREA†	DIST	DISTW	CORR†	HD	COND	SHRUB	TREE†	TREE–LG
WOOD AREA†	0.78										
PATCH AREA†	0.54	0.84									
DIST	−0.51	−0.62	−0.48								
DISTW	−0.58	−0.55	−0.38	0.73							
CORR	0.68	0.52	0.31	−0.40	−0.40						
HD	0.68	0.42	0.29	−0.30	−0.30	0.58					
COND	0.13	0.00	0.00	0.10	0.13	0.42	0.45				
SHRUB	0.20	−0.10	−0.31	0.10	0.13	0.34	0.57	0.61			
TREE	0.01	0.17	0.22	−0.10	−0.20	−0.10	−0.20	−0.40	−0.27		
TREE–LG	0.33	0.36	0.36	−0.30	−0.10	0.17	0.00	−0.20	−0.25	−0.20	
LOG	−0.11	−0.10	0.07	0.00	0.10	−0.20	−0.10	0.00	−0.14	0.00	0.08

† Variable has been log-transformed.

TABLE 8. Community composition patterns of avian foraging guilds associated with wandoo woodlands in the Kellerberrin District, Western Australia.

Remnant	Richness	Foliage Gleaner	General Gleaner	Ground Gleaner	Hawk	Snatch	Bark Gleaner	Pounce	Pouncer/ Hawker
1	8	1	1	1	1	1	1	1	1
15	8	1	1	1	1	1	1	1	1
17	8	1	1	1	1	1	1	1	1
2d	7	1	1	1	x	1	1	1	1
2sw	7	1	1	1	x	1	1	1	1
4	7	1	1	1	1	1	1	1	x
10	7	1	1	1	1	1	1	1	x
24	7	1	1	1	1	1	1	1	x
29	7	1	1	1	1	1	1	1	x
84	7	1	1	1	1	1	1	1	x
13	7	1	1	1	1	1	1	1	x
30	7	1	1	1	1	1	1	1	x
46	7	1	1	1	1	1	x	1	1
97	7	1	1	1	1	1	1	1	x
66	6	1	1	1	x	1	1	...	1
78	6	1	1	1	1	1	x	1	...
34	6	1	1	1	1	x	1	1	...
94	6	1	1	1	1	1	1	...	...
3	4	1	1	1	x	1	x	...	...
23	4	1	x	x	1	1	1	...	...
14	4	1	1	1	1	...	x	...	...
26	4	1	1	1	1	...	x	...	...
27	3	1	1	...	...	...	1	...	...
56	3	1	1	1	...	...	...	...	...
91	3	1	1	...	1	...	...	...	...
127	1	1	...	...	...	...	...	...	...
252	1	1	...	...	...	...	...	...	...
272	1	1	...	...	...	...	...	...	...
276	1	1	...	...	...	...	...	...	...
311	1	1	...	...	...	...	...	...	...
Total		30	24	22	19	19	18	16	7

Notes: Composition patterns: 1 = guild occurrence, x = absence deviating from perfect nestedness. Nestedness score = 20, null score (mean ± 1 SD) = 38.31 ± 4.32, z = 4.24, P < 0.0001.

al. 1990, Scougall et al. 1993). When shrubs are few or missing in a patch, it is often indicative of a relatively poor prey base for some insectivorous birds (Abensperg-Traun et al. 1996, Recher et al. 1996).

Foraging guilds disappeared from woodland patches in a nonrandom fashion as remnant size decreased. Holmes and Recher (1986) have shown that insectivorous birds with different foraging strategies detect and capture different prey. Whereas foliage gleaners such as Weebills and Striated Pardalotes forage on smaller insects and their larvae, for example, pouncers and snatchers tend to focus on larger prey items (Holmes and Recher 1986). Invertebrate species, in turn, respond differently to disturbances resulting from agricultural activities (Landsberg et al. 1990, Gibson et al. 1992, Abensperg-Traun et al. 1996; Abensperg-Traun and Smith, *in press*). Although we did not measure invertebrate abundance, changes in vegetation structure plus the nested pattern of foraging guilds in the Kellerberrin district suggests that some prey items may not be available in sufficient numbers or may be absent entirely as remnants decrease in size.

To what extent can species compensate for changes in prey availability that result from habitat fragmentation and degradation? The nested patterns of community composition in the Kellerberrin area prevented us from examining plasticity in foraging behavior across the spectrum of remnant sizes for any but the most common species. These species did exhibit some plasticity in their use of foraging behaviors and substrates in the smallest remnants. Nour et al. (1997) found little evidence to support the notion that bird species changed their foraging behavior as other species disappeared in small fragments of deciduous forest in northern Belgium. However, they conducted their study over a more restricted range of remnant sizes than we examined in the Kellerberrin area, and based on their description, the smallest fragments were comparable to large woodlots in terms of mature trees and a well-developed understory. The plasticity that we observed may be the result of competitive release, but it is also possible that these species were simply responding to changes in prey availability. We cannot assess the relative importance of these factors within the confines of the current study, although patterns of significant nestedness are unlikely to be compatible with strong interspecific competitive effects (Worthen 1996, but see Cole 1983). Nonetheless, our data suggest that at least some species are able to modify their foraging

TABLE 9. Community composition patterns for 13 species of insectivorous woodland birds observed in wandoo woodlands in the Kellerberrin District, Western Australia.

Remnant	Richness	STPA	WEEB†	CRTH†	YRTH†	RUWH†	TRMA†
17	13	1	1	1	1	1	1
1	12	1	1	1	1	1	1
4	12	1	1	1	1	1	1
2d	12	1	1	1	1	1	x
15	11	1	1	1	1	1	1
84	11	1	1	1	1	1	1
2sw	11	1	1	1	1	1	x
10	11	1	1	1	1	1	1
29	10	1	1	1	1	1	1
30	10	1	1	1	1	1	1
24	10	1	1	1	1	1	1
94	9	1	1	1	1	1	1
13	9	1	1	1	1	1	1
46	9	1	1	1	1	1	1
66	9	1	1	1	1	1	x
97	8	1	1	1	1	1	1
78	8	1	1	1	1	1	1
34	8	1	1	1	1	x	1
3	6	1	1	1	1	1	x
26	6	1	1	1	1	x	1
14	5	1	1	1	1	…	1
23	5	1	1	x	…	1	1
56	5	1	1	1	1	…	x
91	4	1	1	1	…	…	1
27	3	x	1	1	…	…	…
276	2	1	1	…	…	…	…
311	2	1	1	…	…	…	…
127	1	1	…	…	…	…	…
252	1	1	…	…	…	…	…
272	1	1	…	…	…	…	…
Total		29	27	24	22	19	19

Notes: Composition patterns: 1 = guild occurrence, x = absence deviating from perfect nestedness. Nestedness score = 30, null score (mean ± 1 SD) = 88.34 ± 7.65, z = 7.63, P < 0.0001. See Table 3 for common and scientific names of species.

† Species that contributed significantly to the nested pattern (P < 0.05) based on the large-sample approximation of the Wilcoxon rank sum test.

behavior as available substrates (and presumably prey availability) change.

It is interesting to note that in addition to nestedness being evident for foraging guilds, species within foraging guilds also exhibited a nested pattern of occurrence. Brown-headed Honeyeaters, for example, were observed in approximately one-third of the patches that other foliage gleaners occupied, and the Western Yellow Robin occurred in only five patches, while the Red-capped Robin was present in 16 patches. Similar patterns were observed for the Grey Shrike-thrush and Varied Sittella in the bark-gleaning guild. These observations imply that factors other than those related to foraging behavior influence species distributions in these remnants.

At the level of individual species, several models included variables representing remnant and patch isolation. Logistic models for the Jacky Winter, Brown-headed Honeyeater, and Varied Sittella all included a term for the shortest distance to another remnant with woodland patches; for the latter two species, the best model included only this term. None of the isolation variables, however, were included in the best species richness model, despite Andrén's (1994) assertion that isolation assumes greater importance at higher levels of habitat loss. This demonstrates a major weakness of models based solely on species richness. Such models identify variables that either affect most, but perhaps not all, species in a similar way or that represent a suite of other variables that collectively produce a pattern at the community level, but individually affect different species in different ways. In either case, the unique responses of species are masked and attention may be diverted from the actual mechanisms underlying richness patterns.

There are two possible explanations why isolation appears to have little importance for most species occupying woodland patches in the Kellerberrin area. It may be that remnant area already accounts for the influence of isolation as a consequence of the correlation between the two variables, rendering additional terms for isolation superfluous once remnant area is in the model. We believe, however, that a more likely explanation is that the species most sensitive to current levels of isolation in this landscape have already disappeared. Fourteen species have become locally extinct in the Kellerberrin district since settlement and many of these are woodland specialists (Saunders and Curry 1990).

TABLE 9. Extended.

GRST†	INTH†	RCRO†	VASI†	BHHO†	JAWI†	WYRO†
1	1	1	1	1	1	1
1	1	1	x	1	1	1
1	1	1	1	1	x	1
1	1	1	1	1	1	1
1	x	1	1	1	1	...
1	1	1	1	1	x	...
1	1	1	1	x	1	1
1	1	1	1	1	x	...
1	x	1	1	1	x	...
1	1	1	1	...	x	...
1	1	1	x	1	x	...
1	1	x	1	...	...	...
1	1	1	...	...	...	...
x	1	1	...	...	1	...
1	1	x	1	...	1	...
1	x	1	...	...	...	...
x	1	1	...	...	...	...
1	1	1	...	...	...	...
x	1	...	...	...	...	...
x	1	...	...	...	...	...
x	...	...	...	...	...	...
1	...	...	...	...	...	...
x	1	...	...	...	...	...
x	...	...	...	...	...	...
1	...	...	...	...	...	...
...	...	...	...	...	...	...
...	...	...	...	...	...	...
...	...	...	...	...	...	...
...	...	...	...	...	...	...
...	...	...	...	...	...	...
18	18	16	11	9	7	5

The Jacky Winter may be one of the last remaining species that is sensitive to existing levels of isolation in this area; it is currently restricted to woodland patches in larger remnants. Because it is rare in the central wheat belt, the ecology of this species is not well studied and its ability to disperse across a highly-altered matrix is virtually unknown.

Our models suggest that the Brown-headed Honeyeater and the Varied Sittella may also be sensitive to isolation. Both of these woodland residents occupy large home ranges (P. Cale, *personal observation*) and in the Kellerberrin landscape this is only achievable by using a cluster of woodland patches. We therefore believe that the isolation term in models for these two species reflect the requirements of individual birds, whereas it reflects population-scale processes for the Jacky Winter. These examples demonstrate that because ecological processes operate across multiple scales while the quantitative aspects of scale (i.e., absolute spatial scales) are species specific (Wiens 1989*b,* Wiens et al. 1993, Ims 1995), accurate interpretations of community patterns are predicated on some understanding of the ecology of individual species.

CONCLUSIONS

In recent years, a ''bigger is better'' attitude toward reserve acquisition has held sway in the conservation community (Schwartz and van Mantgem 1997). One reason for this attitude is that the majority of assessments for purposes of conservation still rely on estimates of species richness (Magurran 1988) and, as our data reflect, larger reserves are likely to support more species than smaller reserves. If the goal is to maximize the number of native species in a fragmented area, or if little is known about the ecology of the individual species found there, large habitat remnants are the logical starting point for avian conservation efforts.

The largest remnants in our study were associated with a number of habitat features that together probably accounted for high bird species richness there. One can safely predict that most native species occurring in the area will be present in such remnants without knowing detailed information about individual patches or about spatial position relative to other remnants. In the Kellerberrin area, however, large remnants are few in number and measured in hundreds, not thousands, of hectares. As a result, at least some species appear to require groups of remnants to satisfy their habitat needs or to ensure population-level persistence. A landscape perspective for managers is especially important in this context, with an emphasis on conservation reserve networks and careful consideration given to the spatial arrangement and complementarity of habitat fragments (Pressey et al. 1993). Larger remnants might represent core areas, but smaller remnants also have a key role to play and may be especially important in this context

(Shafer 1995, Schwartz and van Mantgem 1997, Villard 1998).

As remnant size decreases, details assume greater importance. To prioritize smaller remnants for protection, one must know something about the quality and diversity of patches that are present, proximity to other remnants, and the mechanisms driving the response of different species to variation in these features. There are clear linkages between certain types of habitat degradation, especially by grazing, and a depressed prey base for insectivorous birds. Most of the small remnants in our study appeared to suffer negative impacts associated with grazing, but even the smallest wandoo patches supported relatively high numbers of species if they were buffered from the surrounding croplands. Small patches in large remnants are naturally protected to some extent, but for stand-alone patches, fencing is probably a good first step in maintaining habitat quality.

For vegetation patches that are already degraded, fencing will obviously accomplish little. At this point, habitat restoration may be necessary and must also be guided by an understanding of the factors causing species decline and loss. Clearly, habitat restoration in the Kellerberrin area must include more than the planting of trees. Our data suggest that a shrub understory is an especially important habitat feature for a number of woodland birds and merits careful consideration in revegetation plans. The high levels of heterogeneity present in the wheat belt prior to settlement suggest that restoration efforts pay special attention to structural and floristic diversity both within patches and within remnants.

Over 80% of remnant vegetation in the Kellerberrin district is on private land. Most of these remnants are relatively small and it is not likely that large blocks will be set aside as nature reserves. It follows that the future of avian diversity in this area depends not only on our ability to establish and manage a network of remnants, but also on the cooperation of private landowners. Ultimately, for conservation to succeed, there must be incentives for landowners to maintain or increase the habitat value of remnant vegetation on their properties.

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