Vegetation and bird community characteristics in an Australian arid mountain range

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Eight habitat types, defined by vegetation associations, were delimited within a central Australian arid mountain range. Floristic and physiognomic vegetation characteristics and four bird community characteristics were measured in each habitat type. The latter were influenced primarily by vegetation physiognomy, particularly life form diversity. This influence was not directly related to the broad diversity of feeding categories within the habitats. Similarity of bird species composition, as indicated by both a discriminant function analysis and a Motyka similarity matrix, was affected primarily by geographic proximity rather than by similarity of plant species composition.

Introduction

Distinctive vegetation patterns occur in arid mountain ranges primarily due to the effects of topography and soil parent material upon moisture availability. These effects have been documented in arid regions throughout the world (e.g. Cloudsley-Thompson, 1968; Hillel & Tadmor, 1962; Kassas, 1952; Tadmor *et al.*, 1962). Other studies have shown that spatial variation in arid vegetation, in turn, affects the distribution of animals, particularly birds (e.g. Austin, 1970; Hensley, 1954; Pianka & Huey, 1971; Raitt & Maze, 1968; Tomoff, 1974). However, few studies have specifically examined the relationship between vegetation and birds in an arid mountain range. It was the objective of the present study to obtain information upon the vegetation pattern within a central Australian arid mountain range and to investigate the effects of this pattern upon the composition and structure of bird communities.

Comparative studies of bird communities most often use vegetation formations, i.e. vegetation with uniform physiognomy and dominated by a given life form (Mueller-Dombois & Ellenberg, 1974), to delimit bird community habitats (e.g. Cody, 1975; Karr, 1971; Salt, 1953). However, formations do not adequately differentiate habitats when working within a restricted geographic area such as an arid mountain range. More detail is obtained by using the vegetation association which, like the formation, has uniform physiognomy but also has a distinctive floristic composition (Mueller-Dombois & Ellenberg, 1974). Small areas such as arid mountain ranges may support few vegetation formations but a greater number of vegetation associations.

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The vegetation association has been chosen as the basic inventory unit by the International Biological Program (Peterken, 1967). It also meets Elton's (1966) requirements that units employed to delimit animal habitats have readily mappable boundaries and be homogeneous with respect to characteristics which are ecologically meaningful to their inhabitants.

The present study delimited bird community habitats by vegetation associations. Each habitat type was inventoried for vegetation parameters, bird species composition and abundance, and other bird community characteristics. Feeding observations were also made as a means of investigating the causal relationship between the vegetation parameters and the bird community characteristics.

Study area

The study was conducted in the Everard Ranges, located approximately 1000 km northwest of Adelaide, South Australia. The Everards extend from latitude 27° 00′ to 27° 10′ S and longitude 132° 10′ to 132° 45′ E. Rainfall records from the nearest meteorological station, Ernabella in the Musgrave Ranges (26° 17′ S, 132° 08′ E, elevation 676 m), show an annual average of 267 ± 147 mm for the period 1935–74 (Australian Bureau of Meteorology). Rainfall is highest in the summer months, December to February (average 33 mm per month), and lowest in the winter months, July to September (average 12 mm per month). Average maximum daily temperatures range from 17·8 °C in July to 38·1 °C in February. Minimum temperatures range from 3·7 °C in July to 20·1 °C in January. Relative humidity is highest in June (0900 h, 66 per cent; 1500 h, 38 per cent) and lowest in November and December (0900 h, 30 per cent; 1500 h, 18 per cent).

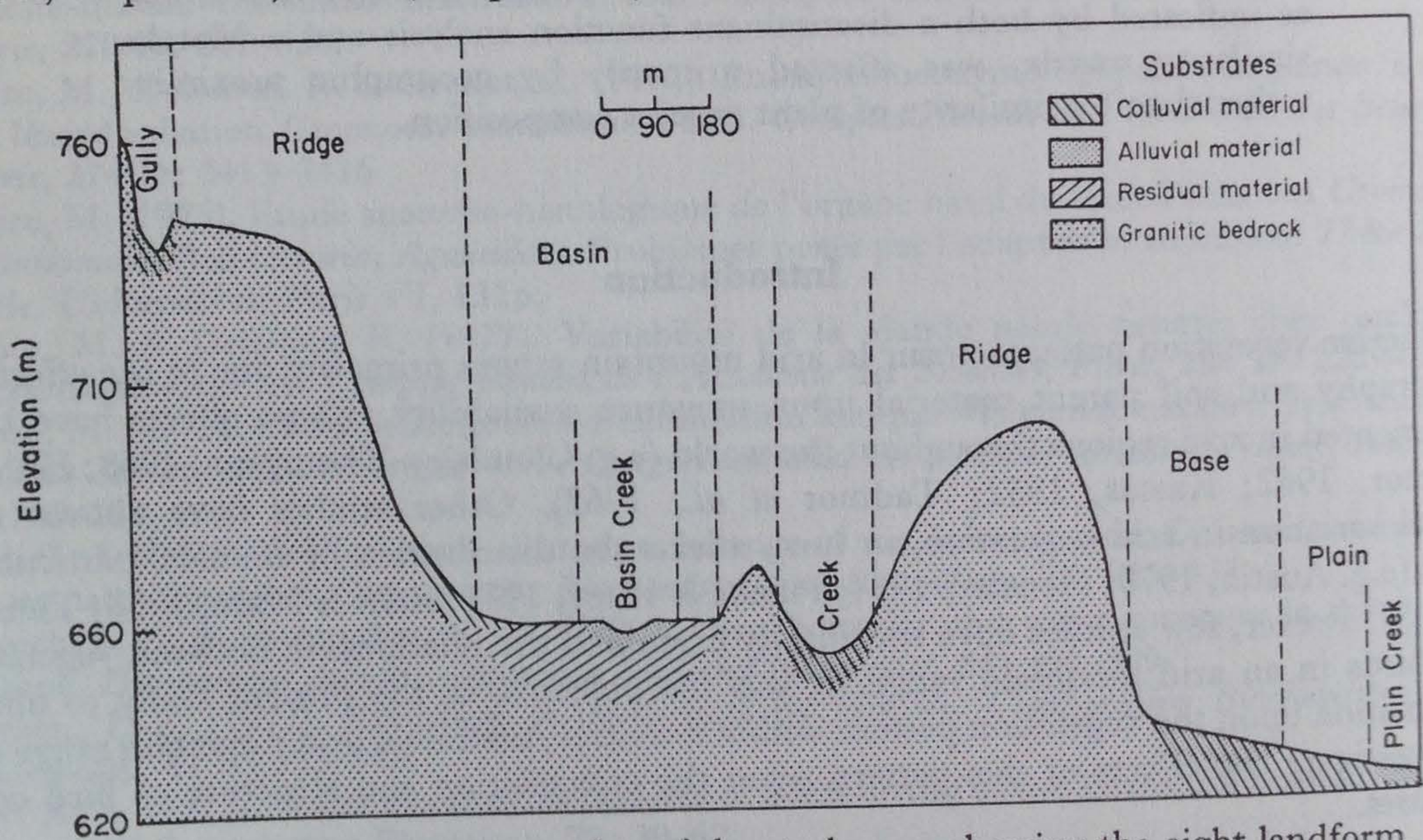

Figure 1. Generalized cross-section of the study area showing the eight landform types and substrates.

The Everard Ranges are a series of granitic outcrops varying in area from a few hectares to several square kilometres. The predominance of sheet structure and massive, tight jointing within the rock has resulted in large domed inselbergs (Twidale, 1964). They rise some 600 m above the surrounding plains and reach a maximum elevation of 917 m at Mt Illbillee.

On the basis of morphology and substrate, eight landform types were recognised in the study area. These include the rock slopes and domes, the gullies which form along minor joints, the basins which occur where major joints have been extensively weathered, the bases of the steep rock slopes, the plains immediately surrounding the rock outcrops, and the various types of creeks which occur in the basins, on the plains, and along major joints which extend from the ridges onto the plains. A generalized cross-section illustrating

Plate 1. Aerial photograph of study site showing approximate boundaries of the eight habitat types: B, Base; Bn, Basin; Bc, Basin Creek; C, Creek; G, Gully; P, Plain; Pc, Plain Creek; R, Ridge.

these landform types and their substrates is presented in Fig. 1. This complex of landform types occurs on an otherwise fairly homogeneous plain overlain with Quarternary red sands (Geological Survey of South Australia, 1972) and vegetated predominantly by mulga (*Acacia aneura*) woodland.

Methods

Examination of conventional aerial photographs and a preliminary field survey established that each of the eight landform types supports a unique vegetation association. These vegetation associations were named after the landform type in which they occur: Plain, Plain Creek, Base, Creek, Basin, Basin Creek, Ridge and Gully. A study site, which included representative examples of these eight types, was chosen within the main Illbillee massif. Plate 1 shows this study site with the approximate boundaries of the associations.

Vegetation parameters for each association were obtained by sampling a minimum 0·1 ha area, as recommended by Whittaker & Niering (1965). To ensure adequate representation of an association, this sample area was obtained by locating a set of 100 m^2 circular plots within the boundaries of the associations. As these plots were also used to locate the bird samples (see below), systematic placement was used to reduce the probability of resampling the same bird individuals.

Species, canopy diameters, canopy heights, and phenology were recorded for all plants taller than 2 m. Species name, cover-abundance class, number of individuals, modal height, and phenology were recorded for species 0·5–2·0 m in height. Total ground cover (<0·5 m) was estimated in each of eight equal pie sections of the circular plot. One section (12·5 m^2 area) was then randomly chosen from among those having the modal value for the eight ground cover estimates. All plants within this section were sampled as for the 0·5–2·0 m height interval.

Each vegetation association served as a bird community habitat. The bird communities were sampled by transect counts. Sampling was conducted three times in May, twice in September, and once in December 1976. One-third of the study site was traversed in a 4-hour morning session. The sampled area was covered by a series of transects, located to include each habitat unit which occurred in the area and spaced at intervals of approximately 50 m. Each transect was divided into 5-minute segments, alternate walking and stopping (*after* Bond, 1957). All contacts with individuals were recorded. Additional data on numbers and movements were obtained by mist netting, which was conducted during April–May 1976.

In addition to the data on bird species distributions and abundances, observations on feeding behaviour were made during May and September 1976. These data were employed to determine the pattern of food usage within each habitat unit. Upon contact with a bird in any given unit, its feeding behaviour was recorded until it was lost from sight or it moved into another unit. Information recorded included bird species, plant species, feeding position, feeding height, and time spent feeding.

Both plant species similarity and bird species similarity were calculated by the Motyka index of species abundance similarity,

$$IS = \frac{2\,Mw}{Ma + Mb} \times 100 \text{ per cent}$$

The Motyka index expresses the sum of the smaller of the two abundance values for all species common to two units (*Mw*) as a proportion of the total abundance values in the two units (*Ma*, *Mb*) (Mueller-Dombois & Ellenberg, 1974). Simpson's reciprocal index was used to calculate all diversity measures because of its simplicity and ease of interpretation (MacArthur, 1972; May, 1976). The dominance index developed by McNaughton & Wolf (1970), which expresses the sum of the numbers of individuals of the two most abundant species as a percentage of the total number of individuals of all species in a sample, was used to characterize dominance in the bird communities.

Results

Vegetation

The initial subjective field determination of eight vegetation associations was supported by the results of the plot samples. Table 1 lists growth form cover, formation class, and sub-formation after Fosberg's hierarchical classification system (Fosberg, 1961; Peterken, 1967). These values were derived from the foliage cover data obtained from the plots. Of the eight vegetation units, only three, Plain Creek, Basin and Gully, are in the same formation class. However, they each have different predominant species (as determined by most cover-abundant), thus justifying their separation into different associations.

Further comparisons among the associations are made with the two floristic parameters (a) plant species similarity, (b) plant species diversity, and the physiognomic parameters, (c) life form spectrum and diversity, and (d) foliage height diversity.

Plant species similarity

The Motyka index of species abundance similarity was calculated for all pairs of vegetation units (Table 2). These values were generally very low, indicating considerable variation in plant species composition and abundance among the associations. Only two pairs of associations had index values greater than 50 per cent, Gully–Base (67 per cent) and Basin–Ridge (58 per cent). The high similarity between the Gully and Base appears to be related to the similarities in their physical environments: both are limited in areal extent, are disjunctly distributed (Plate 1), receive run-off from surrounding slopes, are topographically shaded, and have mixed colluvial alluvial substrates (Fig. 1). The lower similarity value between the Basin and Ridge can be attributed to a common dense ground cover of a single species *Triodia irritans*, which is abundant on coarsely weathered substrates.

Total index values for each association, listed in Table 2, indicate that the Plain is very dissimilar from the other associations (a total value of 68 in comparison to other values which range from 117 to 252). The Plain is also an unique formation (see Table 1), having a closed ground layer. The index values among the other units vary according to general vegetation physiognomic similarities, physical environment similarities, and geographic proximity.

Plant species diversity

The diversity of floristic composition within the associations was measured by a plant species diversity index (PSD), which considers both species number and relative abundances. The highest plant species diversity values generally occur in those units with the highest run-on moisture status: Plain Creek, Creek and Base (Table 3). The one exception, Basin Creek, has the lowest value due to very high cover of a single species, *Melaleuca glomerata*.

Life form spectrum and diversity

A life form spectrum for each association was compiled using nine life form categories (*after* Raunkiaer, 1934): mesophanerophyte (>8 m high), microphanerophyte (2–8 m), nano-phanerophyte (0·5–2 m), chamaephyte, hemicryptophyte, geophyte, therophyte, liana and semi-parasite. Phanerophyte categories were further subdivided into broad-leaved and narrow-leaved categories. The percentage cover of each major life form category for the units is presented in Table 4. Most variation among the units occurs in the categories meso-phanerophyte, microphanerophyte, chamaephyte and hemicryptophyte.

To order the units along a simple life form gradient, each was given a value as measured by a life form diversity index (LFD). Simpson's reciprocal index was used with P_i representing the proportion of the ith life form category, as listed above. The values derived from this index are listed in Table 3. LFD is highly correlated with PSD (Spearman's $r_s = 0{\cdot}98$, $N = 8$, $P < 0{\cdot}01$). This high correlation is no doubt due to the overall low number of plant species in the study area (93). Thus, almost every species in each association corresponds to a separate life form category.

Table 1. *Physiognomic classification and characteristics, plus predominant plant species, for each vegetation type*

Vegetation association	*Growth form cover* Tree	Shrub	Dwarf Shrub	Tussock Grass	Hummock Grass	Forb	Bryoid	Formation class	Sub-Formation	Predominant species	Species growth form
Basin Creek	—	C	—	—	—	—	—	Scrub	N	*Melaleuca glomerata*	Sb
Plain	S	S	S	C	—	S	—	Open scrub	N	*Enneapogon avenacerus*	TG
Creek	O	O	O	S	—	O	—	Steppe forest	B	*Eucalyptus camaldulensis*	T
Plain Creek	—	O	O	S	—	S	—	Steppe scrub	N	*Acacia tetragonophylla*	Sb
										Enneapogon avenacerus	TG
Basin	—	O	S	—	O	—	S	Steppe scrub	B	*Triodia irritans*	HG
Gully	—	O	S	—	S	—	—	Steppe scrub	B	*Acacia signata*	Sb
Base	S	O	O	—	O	—	—	Steppe savanna	B	*Acacia signata*	Sb
Ridge	—	S	S	—	O	S	S	Shrub steppe savanna	B	*Triodia irritans*	HG

Key: Cover classes: C, closed; O, open; S, sparse (see Peterken, 1967, for criteria).
Growth forms: Sb, shrub; T, tree; TG, tussock grass; HG, hummock grass; N, narrow-leaved; B, broad-leaved.

Foliage height diversity

Foliage height diversity (FHD) (MacArthur & MacArthur, 1961) of each unit was calculated using three layers: ground (0–0·5 m), shrub (0·5–8 m), and tree (>8 m). The values, listed in Table 3, have a limited range, 1·10 to 2·01, indicating that the foliage distributions are very similar among the units. This index is also negatively correlated with the total foliage cover ($r_s = 0{\cdot}64$, $N = 8$, $P < 0{\cdot}05$).

Bird communities

A complete list of the 37 bird species sampled and their abundance values appears in Appendix I. These sampled species represent 65 per cent of the total number of species (56), excluding raptors and nocturnal birds (10), observed by the author in the study area. Observations of banded birds indicated that a high proportion of the resident population was contacted, but no precise estimate of this proportion was obtained.

Community characteristics

Four parameters, species number (S), total number of individuals (N), species diversity (BSD) and dominance index (DI), were used to assess similarities and differences in bird community characteristics among the eight habitat types. The segment of each transect run within a unit was treated as a single sample and all counts were standardized for a 10-stop segment. The mean values for each parameter varied significantly among the vegetation units, as determined by non-parametric Friedman two-way analysis of variance (Table 5(a)). Variation in the parameters from one transect sampling period to the next was also tested. Except for the dominance index, which showed a lower level for the December sampling period, there was no significant difference among the values, indicating that the bird community characteristics within each unit were stable for the duration of the study (Table 5(b)).

Table 2. *Plant species similarity matrix*

	Bn Ck	Plain	Creek	Pl Ck	Basin	Gully	Base	Ridge
Plain	8							
Creek	32	5						
Plain Creek	14	24	23					
Basin	24	8	18	7				
Gully	31	7	36	15	26			
Base	31	7	42	18	30	67		
Ridge	35	9	38	16	58	49	47	
Total	175	68	194	117	171	231	242	252

The strength of relationships between the bird community parameters and the vegetation parameters, life form diversity and foliage height diversity, were tested by Spearman rank correlation coefficients. Life form diversity was significantly correlated with all bird community parameters except total number of individuals, which was the only parameter significantly correlated with foliage height diversity (Table 6). Figure 2 presents each of the four bird community parameters graphed against life form diversity. In the first three graphs (Fig. 2(a)–(c)), the Creek unit, which has the highest life form diversity value, has bird community parameter values which are lower than those which would be expected if a simple linear relationship existed between life form diversity and the community parameters.

Table 3. *Values of PSD (plant species diversity), LFD (life form diversity), FHD (foliage height diversity), and FdD (feeding diversity) for each vegetation type*

	PSD	LFD	FHD	FdD
Basin Creek	2·95	2·68	1·10	4·03
Basin	2·95	2·45	1·70	3·36
Ridge	3·68	2·73	1·68	4·28
Plain	5·06	3·04	2·01	2·56
Gully	4·97	3·00	1·40	2·64
Base	5·68	3·17	1·35	3·92
Plain Creek	11·36	3·69	1·50	3·15
Creek	7·70	5·00	1·59	3·27

It appears that beyond a critical level more diverse life form composition does not effectively increase bird species numbers and bird species diversity, or decrease dominance. The number of bird species found in the Creek unit is substantially lower than might be expected on the basis of the trend established by the other units (Fig. 2(a)). This discrepancy could be related to the Creek's extensive tree cover, which poses difficulties for thorough bird sampling.

The only bird community parameter not significantly correlated with life form diversity is the total number of individuals (N). As illustrated in Fig. 2(d), the Base and Basin Creek have abnormally high numbers of individuals in comparison to the other units. In both these units, the honeyeater *Lichenostomus penicillatus* accounted for over half the total numbers. This species' abundance is positively correlated with the amount of shrub cover (Pearson's $r = 0{\cdot}21$, $N = 93$, $P < 0{\cdot}04$), and these two units have the highest shrub cover of all units (Fig. 4). Total foliage cover is significantly correlated with total number of individuals ($r_s = 0{\cdot}81$, $N = 8$, $P < 0{\cdot}05$) and the negative correlation between total foliage cover and foliage height diversity may explain why the latter measure was significantly correlated to total number of individuals.

Table 4. *Life form spectra of the vegetation units, showing percentage cover of each life form*

Vegetation unit	Phanerophytes			Chamaephyte	Hemicryptophyte	Therophyte	Geophyte	Lianas	Semi-parasites
	Meso-	Micro-	Nano-						
Basin Creek	—	73	9	11	6	—	1	1	0·1
Basin	—	39	6	53	0·1	2	—	1	0·1
Ridge	—	36	5	48	9	3	—	0·1	0·1
Plain	16	16	7	2	53	6	—	0·1	—
Gully	2	52	9	18	15	3	0·1	0·1	0·1
Base	14	48	8	3	26	1	—	0·5	0·1
Plain Creek	—	36	9	15	33	2	—	4	—
Creek	20	21	29	8	19	1	1	1	0·1

Table 5. *Standardized values of the bird community characteristics for each habitat type and over the three sampling periods*

Unit	Community characteristics *N*	*S*	*BSD*	*DI* (%)
(a) *Over habitat units*				
Basin Creek	74	14	3·10	69
Plain	42	17	4·81	53
Creek	68	16	5·31	52
Plain Creek	62	26	4·96	50
Basin	50	9	2·19	81
Gully	55	13	2·78	74
Base	122	22	3·03	68
Ridge	53	11	3·14	66
Probability level*	0·02	0·001	0·001	0·001
(b) *Over the three sampling periods*				
April	43·9	8·6	3·74	66
September	35·0	8·6	3·62	66
December	37·8	7·5	4·39	56
Probability level*	0·53	1·00	0·29	0·03

* Measured by Friedman two-way analysis of variance: $k = 3$, $N = 8$.

Bird species composition

The similarity of the bird species compositions of the units was measured by the Motyka index. Values ranged from 9 per cent (Plain Creek–Basin) to 84 per cent (Gully–Ridge; Table 7). A non-significant Pearson correlation coefficient ($r = 0{\cdot}24$, $N = 26$, $P > 0{\cdot}10$) indicated no simple relationship between bird species similarity and plant species similarity. High bird species similarity values occur between geographically adjacent units (Gully–Ridge 84 per cent, Plain–Plain Creek 71 per cent, Basin Creek–Creek 67 per cent, Basin–Gully/Ridge 55 per cent). The one exception to this general pattern, the Base, has its highest similarity value with the Basin Creek. This high value is due to large relative abundances of *Lichenostomus penicillatus* in both units.

The highest values occur for the two pairs which make up complex geographic mosaics, Ridge–Gully and Plain–Plain Creek. In both pairs, the second unit is completely surrounded by the first (Plate 1). These high similarity values are no doubt largely due to edge effects, such as reported by Dwyer (1972), Kendeigh (1944) and others.

Table 6. *Spearman rank correlation coefficients between bird community characteristics and vegetation physiognomic parameters*

Bird community characteristics	Vegetation parameter *FHD*	*LFD*
S	0·26	0·72*
N	−0·88†	0·36
BSD	0·17	0·74*
DI	0·17	−0·67*

* $P < 0{\cdot}05$; † $P < 0{\cdot}01$.

A test of the uniqueness and consistency of the bird species composition of each unit was performed with discriminant function analysis. Discriminant function analysis is a multivariate statistical technique which is used to differentiate a number of classes from each other on the basis of functions consisting of weighted variable scores. The weighting factors are derived to maximize the separation of the classes' total scores on all variables. Multiple functions are often necessary to differentiate among three or more classes. The functions established with the initial data can be used to reclassify the sets of variable scores. The number of misclassifications between the original and this second classification is a measure of how well the variables and their weighting coefficients actually discriminate among the original classes (Cooley & Lohnes, 1971; Klecka, 1975).

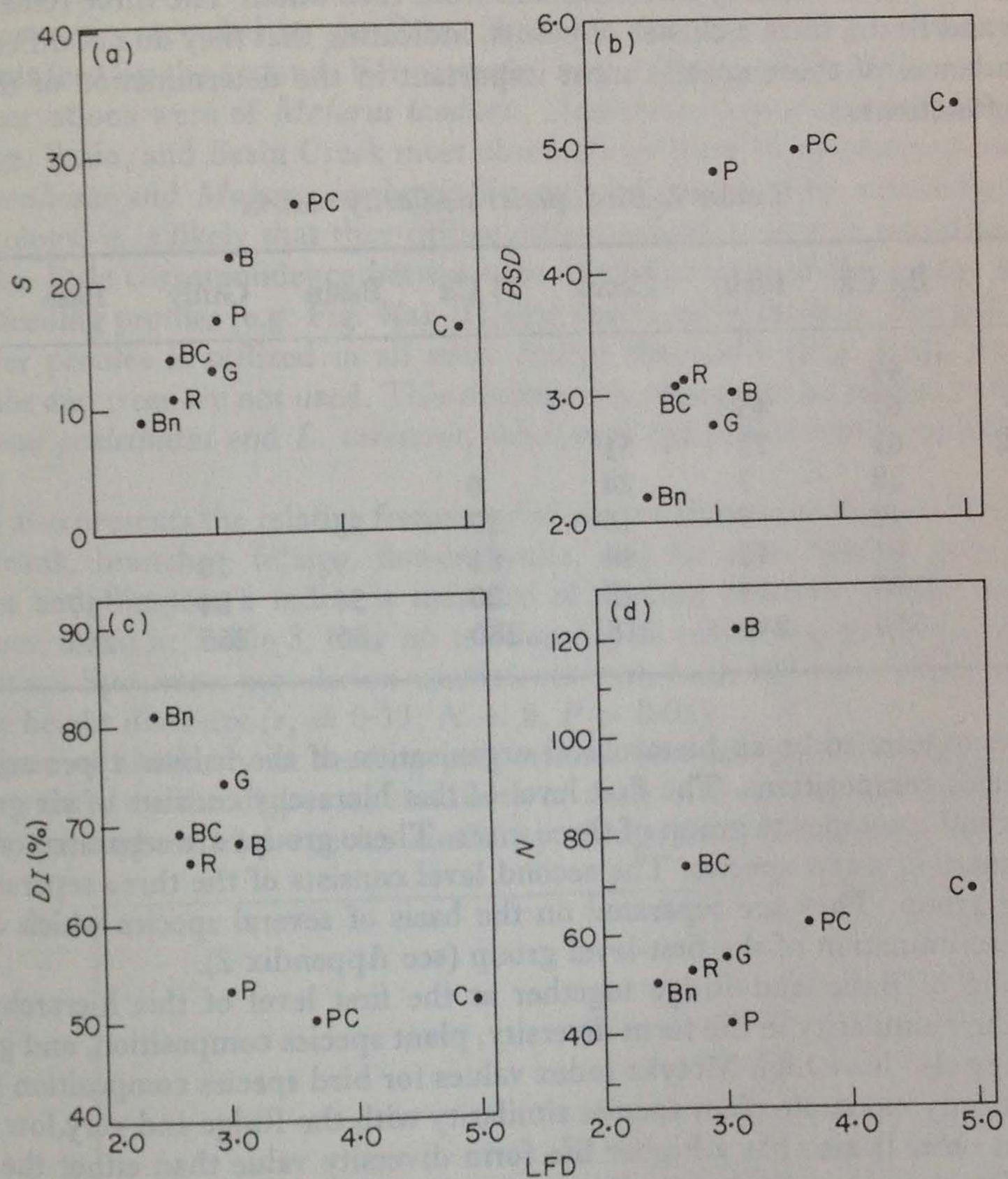

Figure 2. Life form diversity (LFD) graphed against the four bird community characteristics. (a) *S*, number of species; (b) *BSD*, bird species diversity; (c) *DI*, dominance index; (d) *N*, total number of individuals.

A step-wise procedure in discriminant function analysis identifies those variables (or species) which differ most among the classes (or habitat types), having the largest weighting coefficients in the functions. Thus, the habitat types may be differentiated from each other primarily on the basis of a few species. But, unlike the Motyka similarity index, these few species need not be the most abundant ones. An advantage of the discriminant function analysis over the Motyka index is that it permits graphic ordination of the habitat types, showing their positions along axes which represent the discriminant functions. The use of discriminant function analysis is very similar to the differential species approach developed by Braun-Blanquet (1965) for establishing plant communities.

The University of Adelaide Computing Centre's *SPSS* version 7.00, subprogram *Discriminant*, was used for the analysis with variables corresponding to the bird species and the variable scores corresponding to the number of contacts per species for a transect run within a habitat type. Thus, each habitat type was represented by six sets of variable scores with each set representing a sample of the entire bird community of that habitat.

The results of the transect analysis indicate considerable consistency in bird species composition of each habitat type considered as a whole. There are four significant discriminant functions. Using these four functions, only one of the 48 cases was misclassified. Figure 3 is a graph of the positions of these cases with respect to axes representing the two functions with the most discriminating power. In this graph, Plain Creek, Basin Creek, Base, Creek and Plain are clearly discriminated from each other. The three remaining units, Gully, Ridge and Basin, form a cluster of points, indicating that they do not differ noticeably in their abundances of those species most important in the determination of the first two discriminant functions.

Table 7. *Bird species similarity matrix*

	Bn Ck	Plain	Creek	Pl Ck	Basin	Gully	Base	Ridge
Plain	49							
Creek	67	45						
Plain Creek	61	71	51					
Basin	28	7	24	9				
Gully	40	9	45	17	55			
Base	61	45	44	51	9	16		
Ridge	44	14	42	20	54	84	17	
Total	350	240	318	280	186	266	243	275

Thus, there appears to be an hierarchical organisation of the habitat types according to their bird species compositions. The first level of this hierarchy consists of six groups, five separate units and a composite group of three units. These groups are separated on the basis of the abundances of a few species. The second level consists of the three separate units of the composite group. They are separated on the basis of several species which contribute little to the discrimination of the first-level group (see Appendix 2).

The grouping of Basin and Ridge together at the first level of this hierarchy may be explained by their similarity in life form diversity, plant species composition, and geographic proximity. They also have high Motyka index values for bird species composition (Table 7). The Gully has only moderate plant species similarity with the Ridge and very low similarity with the Basin unit. It also has a higher life form diversity value than either the Ridge or Basin unit. However, the previously discussed influence of geographic proximity in the Ridge–Gully complex may explain why the Gully unit falls into the same group as the Basin and Ridge.

There is a general correspondence between the results of the discriminant function analysis, as illustrated by Fig. 3, and the Motyka bird species similarity matrix (Table 7). The nearest neighbor of each unit in Fig. 3 has the highest Motyka similarity value (e.g. Ridge–Gully, Plain–Plain Creek, Creek–Basin Creek, Base–Basin Creek, Basin–Ridge/Gully). Those units most dissimilar from the others on the basis of their Motyka similarity values, Plain, Base and Basin, are positioned at the ends of the two discriminant function axes. The Basin occurs within a cluster which includes the Gully and Ridge, units of moderate similarity to the Basin. This general correspondence between the discriminant function ordination and the Motyka similarity matrix indicates that the critical species of the discriminant functions are good indices of the overall bird species composition of the habitat types.

Feeding observations

The habitat types' feeding profiles, represented as the relative frequency of feeding observations in each 1 m height interval, were graphed against their foliage cover profiles, represented as relative projected foliage cover in each height interval (Fig. 4). There is only general correspondence between them. In most cases, the feeding percentages exceed the foliage cover percentages in the lower height intervals (<3 m). The reverse situation occurs in the upper height intervals. The relative proportion of ground feeding is fairly constant at about 15 per cent in the eight units, despite the variation in amount of ground cover. In the Base, Creek and Basin Creek, feeding at ground level is greater than would be expected from the foliage profiles. Litter quantities have no apparent influence on this result since high amounts were only recorded in the Base. However, there is little consistency in the bird species which feed on the ground. For example, in the Plain and Plain Creek, most ground-feeding observations were of *Malurus lamberti*, *Acanthiza chrysorrhoa* and *Poephila guttata*. In the Ridge, Basin, and Basin Creek most observations were of *Amytornis purnelli*, *Pomatostomus superciliosus* and *Malurus lamberti*. Since these species differ markedly in taxonomy and morphology, it is likely that they utilize different food resources found on the ground. There is also little correspondence between the vertical extent of the foliage cover profiles and of the feeding profiles (e.g. Fig. 4(a), (f), (g)) due to aerial feeders. The full extent of the foliage cover profiles is utilized in all units except the Gully (Fig. 4(h)), where the very tallest shrubs and trees are not used. This discrepancy appears to be related to the absence of *Lichenostomus penicillatus* and *L. verescens*, who were the primary tree feeders in the other units.

Figure 4 also presents the relative frequency of observations in each of six feeding positions (ground, trunk, branches, foliage, flowers/fruits, air) for each habitat type. Using these percentages and Simpson's index, a measure of feeding diversity (*FdD*) was calculated. These values, listed in Table 3, bear no relationship to either vegetation parameter, having non-significant Spearman correlation coefficients with both life form diversity ($r_s = 0{\cdot}40$) and foliage height diversity ($r_s = 0{\cdot}33$; $N = 8$, $P > 0{\cdot}05$).

The degree of similarity in feeding proportions between pairs of habitat types is not necessarily related to the degree of similarity of their bird species compositions. The two types with the highest bird species similarity, Ridge and Gully, have different feeding

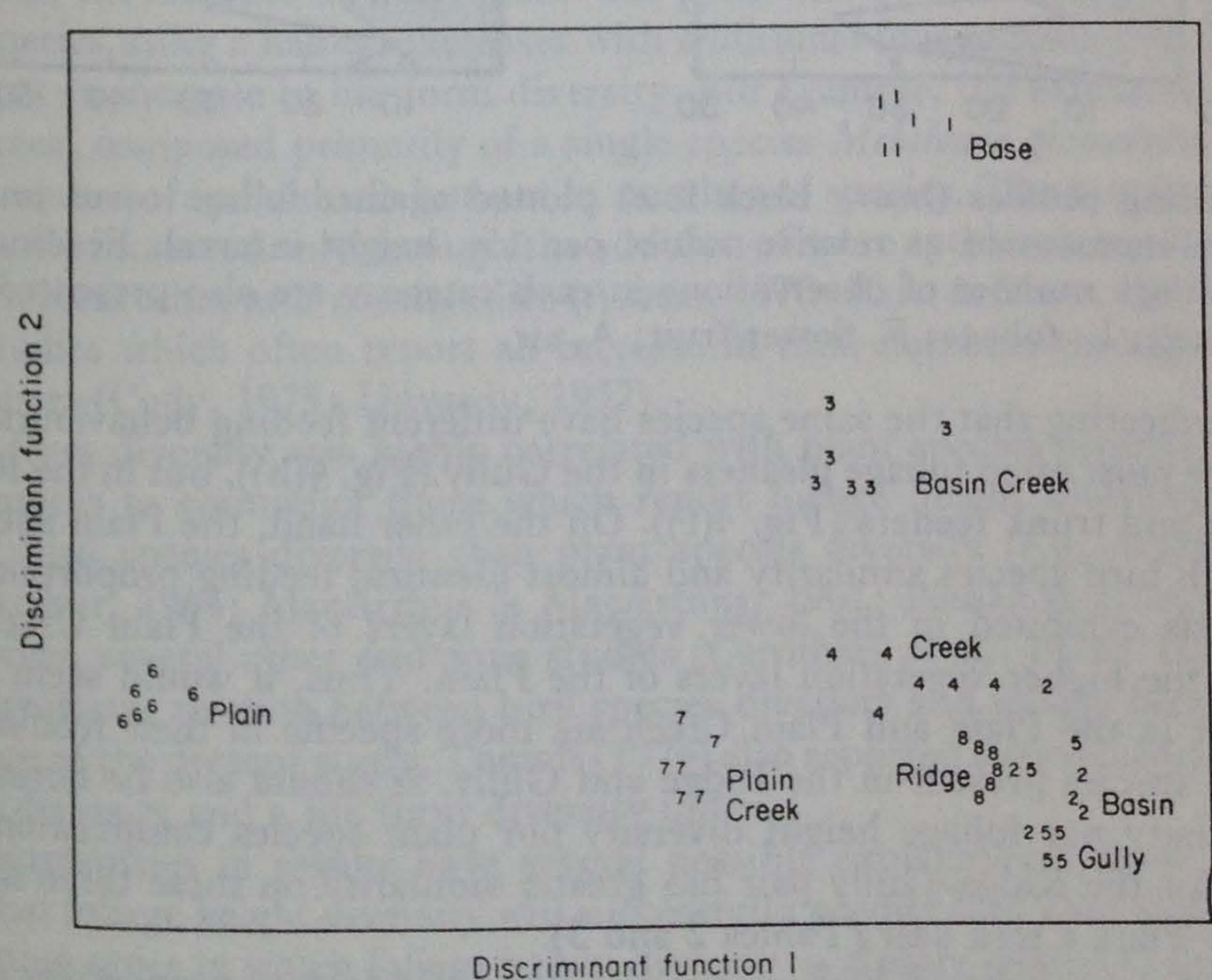

Figure 3. Positions of the 48 transect samples plotted against the first two discriminant functions.

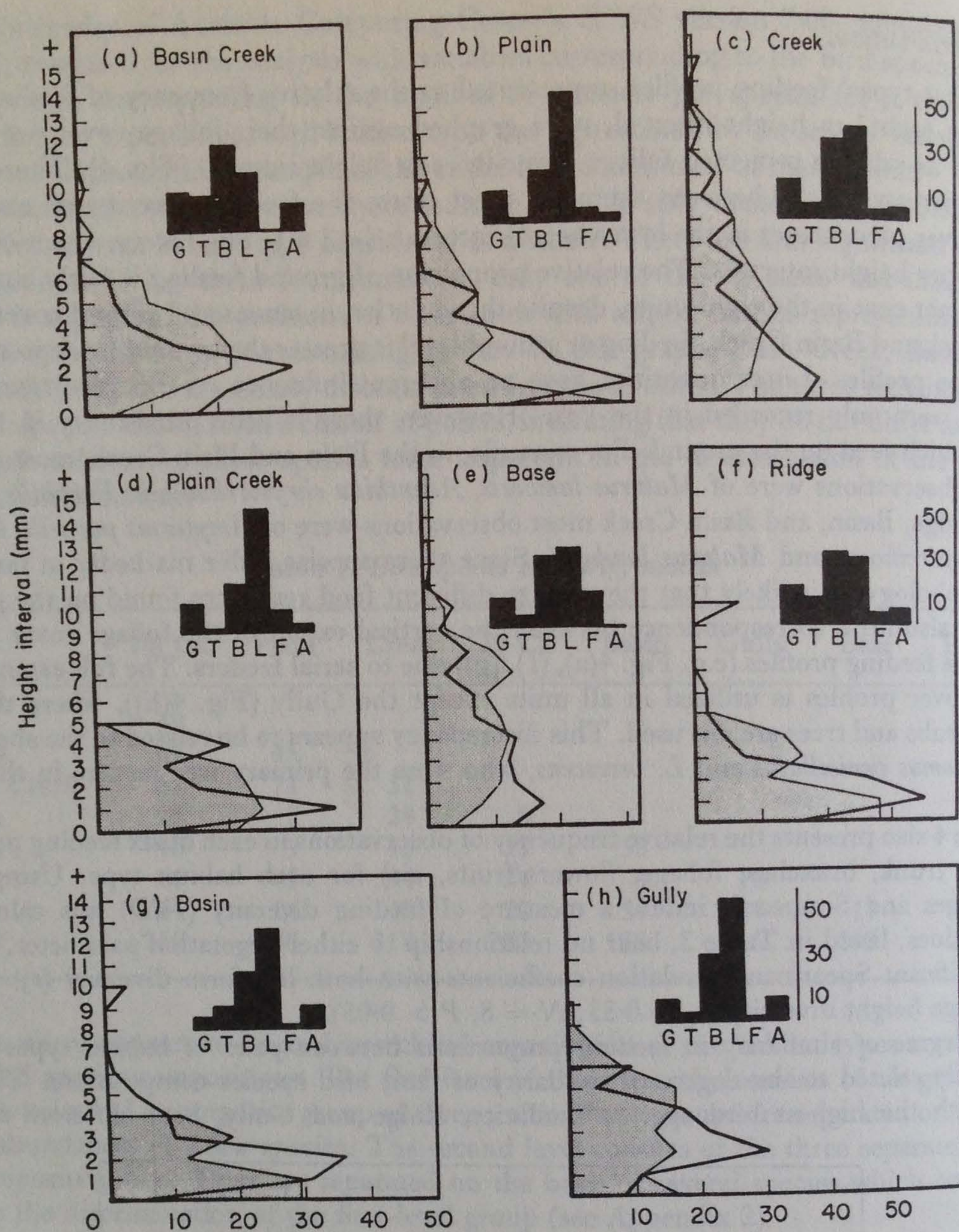

Figure 4. Feeding profiles (heavy black line) plotted against foliage cover profiles (shaded area). Both are represented as relative values per 1 m height interval. Feeding proportions given as percentage number of observations in each category are also presented. G, ground; T, trunk; B, bark; L, foliage; F, flower/fruit; A, air.

proportions, indicating that the same species have different feeding behaviours in these two types. Birds are most often foliage gleaners in the Gully (Fig. 4(h)), but in the Ridge they are mostly branch and trunk feeders (Fig. 4(f)). On the other hand, the Plain and Plain Creek types have high bird species similarity and almost identical feeding proportions. The same feeding patterns exhibited in the lower vegetation layers of the Plain Creek are merely extended into the higher vegetation layers of the Plain. Thus, it would seem that the bird species present in the Plain and Plain Creek are more specific in their feeding behaviours than are those species present in the Ridge and Gully. It should also be noted that neither life form diversity nor foliage height diversity nor plant species composition can explain these results, for the Ridge–Gully pair has greater similarity on these three measures than does the Plain–Plain Creek pair (Tables 2 and 3).

The inconsistencies between bird species similarity and feeding proportions similarity can be partly explained by the distribution and feeding patterns of the two most abundant species, *Lichenostomus keartlandi* and *L. penicillatus*. These two species together account for

over 50 per cent of the total transect counts and for 40 per cent of the total feeding observations. Thus, they greatly affect both bird species similarity and feeding proportions. The two species have complimentary abundance distributions. Only one habitat, Basin Creek, has a moderate number of both species. This co-occurrence helps to explain why the Basin Creek has moderate to high bird species similarity values with all other units (Table 7). The two species are congeneric and are similar in morphology and apparent social organization, as indicated by field observations made during this study. They also have similar feeding proportions (Shurcliff, 1978). They are both predominantly foliage and branch gleaners, although their actual food appears to be different. *L. keartlandi* eats predominantly small ants which are found on the trunks, branches and foliage of shrubs. *L. penicillatus* also eats ants found on *Melaleuca glomerata* shrubs in the Basin Creek and leaf scale insects (Coccina, Homoptera) found on eucalyptus. This species eats more nectar and fruits than *L. keartlandi*, which reflects differences in the availability of these foods within the different habitat types. It is possible for two habitat types, one with a high proportion of *L. penicillatus* (e.g. Plain Creek) and the other with a high proportion of *L. keartlandi* (e.g. Gully), to have low bird species similarity (17 per cent) but similar feeding proportions (Fig. 4(d), (h)). Thus, feeding profiles and feeding proportions have only a limited relation to foliage cover profiles, vegetation parameters, or bird species compositions.

Discussion

Each of the eight landform types within the Everard Ranges supports a distinctive vegetation association with its own physiognomic characteristics and plant species composition. Five of these associations (Creek, Plain Creek, Basin Creek, Gully and Base) are riparian, being situated along drainage courses or receiving extensive run-on moisture (Fig. 1 and Plate 1). These riparian units generally have the highest plant species diversity, life form diversity (Table 3), and total foliage cover. However, unlike the desert-riparian communities in the North American Southwest (Raitt & Maze, 1968), they are not always characterized by the presence of trees or arborescent shrubs.

Each of the eight vegetation associations supports a bird community with distinctive composition and community characteristics. The vegetation physiognomic index, life form diversity, successfully predicted species number, bird species diversity, and the dominance value; whereas, the number of individuals was predicted by total foliage cover. Thus, the number of species using a habitat increases with additional foliage cover only if this addition also represents an increase in life form diversity. For example, the extensive shrub cover in the Basin Creek, composed primarily of a single species *Melaleuca glomerata*, resulted in an increase in number of individuals but not in number of species. The number of individuals is not necessarily increased only through the addition of more species; a result which has been reported by several other arid zone studies (Austin, 1970; Raitt & Maze, 1968), in contrast to temperate studies which often report an increase in total numbers through an increase in species numbers (Cody, 1975; Udvardy, 1957).

Since life form diversity was highly correlated with plant species diversity, the results of this study appear to contradict those which report foliage height diversity to be a better predictor of bird species diversity than plant species diversity (e.g. Austin, 1970; Karr, 1968; MacArthur, 1964; MacArthur & MacArthur, 1961; Pianka & Huey, 1971; Recher, 1971). However, several other arid zone studies (Carothers *et al.*, 1974; Tomoff, 1974) did not find a significant relation between bird species diversity and foliage height diversity. As in the findings of the present study, Tomoff (1974) also reported a strong correlation between bird species diversity and a life form diversity index.

These discrepancies in results have several possible explanations. First, Tomoff (1974) concluded that foliage height diversity will successfully predict bird species diversity for only those vegetation types in which foliage height diversity is closely related to life form diversity and that this is the case for temperate deciduous forests. Thus, both indices measure vegetation factors which are critical in affecting bird species diversity and other bird community

characteristics. These indices are measures of vegetation physiognomy. Foliage height diversity is a function of only two physiognomic characteristics, vertical spacing and foliage cover spacing. Because life form categories are partly based upon height criteria, particularly the phanerophyte categories, and because the diversity index used in this study employed foliage cover as a measure of life form abundance, life form diversity is a function not only of life form composition but also foliage cover and vertical spacing. Thus, life form diversity is a composite measure, utilizing more physiognomic characteristics than does foliage height diversity. In some vegetation types, such as temperate deciduous forests, the foliage spacing index, foliage height diversity, may be a close approximation of the more general physiognomic index life form diversity. In other vegetation types, such as arid woodland and scrub, the two indices may not be closely related. In these cases, it appears that the more general life form diversity index is the better predictor of bird community characteristics.

Since few studies have actually investigated the relationship between life form diversity and foliage height diversity or the influence of life form diversity upon bird species diversity, it remains to be determined whether this index is the best in all vegetation types or only in some. Karr (1968), working in regenerating deciduous forests, found that his physiognomic and physiographic diversity index, which is very similar to life form diversity in the present study, was not significantly correlated with bird species diversity. However, he used a limited sample of four vegetation types, and also recognised that at least one of his vegetation types was very heterogeneous. Willson (1974), working in temperate forests, suggested that the inclusion of life forms would have given higher correlations with bird species diversity than just foliage spacing, and Ulfstrand (1975), working in boreal tree plantations, found that tree size and morphology influenced the number of bird species. Several other studies (MacArthur & MacArthur, 1961; Pianka & Huey, 1971) have investigated the relationship between plant species diversity and bird species diversity. Unfortunately, it is not known what the relationship between plant species diversity and life form diversity was in these studies. There are enough data reported for a variety of vegetation types to indicate that physiognomic features are generally the most important in predicting bird species diversity, but that foliage height diversity may be an adequate index of these in only a limited range of vegetation types.

A second consideration is the size of the area covered. The present study was conducted within a very localized area and the habitat types were determined by associations rather than formations. In contrast, other studies have been conducted at a much larger scale, covering entire regions (MacArthur, 1964), continents (MacArthur & MacArthur, 1961), or even hemispheres (Pianka & Huey, 1971). An index of foliage cover spacing may produce accurate predictions of bird species diversity when working with such large areas and with vegetation formations. Under these circumstances, foliage height diversity may again be a fairly accurate index of more general physiognomic characteristics. The results of the present study indicate that differences do exist among the bird communities of vegetation associations within a limited geographic area, and that parameters such as life form diversity are needed to predict these differences.

The non-linear relationship between life form diversity and bird species diversity in this study has been reported for other vegetation measures, especially the total percent foliage cover (Cody, 1975; Karr, 1968; Karr & Roth, 1971; Willson, 1974). Willson (1974) found that the amount of canopy cover in the tree layer did not influence the number of species, but that only the presence of a tree layer was important. Thus, in the present study the Creek unit would not necessarily have higher community characteristic values than the other units with a tree layer (Base, Plain, Gully). The plateauing of characteristic values also indicate that a saturation level of bird species has been reached, due to the generally impoverished species pool available in the Australian arid zone. Keast (1959) lists 24, 17 and 54 species for desert mulga (*Acacia* spp.), desert spinifex (*Triodia* spp.) and savanna-grassland vegetation respectively. Thus, beyond a critical level, increases in physiognomic complexity result only in increases in the total number of individuals and not in the number of species.

Although vegetation physiognomy successfully predicted the bird community character-

istics, geographic proximity appeared to be the main factor affecting the similarity of bird species compositions among the habitat types, as indicated by both the discriminant function analysis and the Motyka similarity matrix. The influence of geographic proximity is especially marked if one unit is small in aerial extent and forms a complex mosaic with another unit (Ridge–Gully and Plain–Plain Creek units). In some studies (e.g. Raitt & Maze, 1968), such mosaics are treated as a single sampling unit or are completely avoided. If a mosaic is treated as a single unit, BSD is often higher than expected from general vegetation characteristics (Dwyer, 1972; Karr, 1968). This study has illustrated that each component unit of such mosaics has distinctive bird community composition and characteristics. The smaller, but physiognomically more diverse units (Gully and Plain Creek), have larger numbers of individuals and species, higher bird species diversity, and lower dominance values than their associated units (Ridge and Plain). Different feeding proportions in the Ridge and Gully indicate marked changes in feeding behaviors of the same bird species. Therefore, steps should be taken to either explicitly include or exclude small but physiognomically distinct vegetation units from a sample.

The influence of plant life form diversity upon bird community characteristics cannot be simply attributed to its influence upon the diversity of feeding strategies, since there was no significant correlation between life form diversity and feeding diversity. The broad feeding categories used in this study give no indication of the actual variety and abundance of the food resources being utilized by the birds within each category. The unit with the highest feeding diversity, the Ridge, has a general paucity of food supplies, forcing birds to be generalists, taking food wherever it can be found. These same bird species have different feeding strategies in the Gully. Insufficient data exist to determine if number of bird species is related to the variety of food sources within the broad feeding categories, and if this variety is directly related to life form diversity.

Summary

The eight habitat types recognised within the Everard Ranges represent a more complex pattern than has been investigated in other arid zone bird studies, conducted in topographically simple areas. The present results indicate that topographically complex areas support a variety of vegetation associations, which are habitats for distinctive bird communities. The bird community characteristics are influenced primarily by vegetation physiognomy, in particular life form diversity. This influence does not appear to be directly related to the variety of broad feeding categories supported within a habitat. The bird species composition of each habitat is a function not only of the community characteristics but also the bird species composition of adjacent habitats as well as the total bird species pool available to the localized geographic area within the arid zone. The primary influence of neighboring habitats in determining bird species composition is to be expected because of the lack of sharp boundaries between the units and the fact that the habitat areas are not large enough to exclusively support many of the bird individuals. The importance of small physiognomically distinct vegetation associations in maintaining bird community diversity should be recognised in investigations of arid regions.

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References

Austin, G. T. (1970). Breeding birds of desert riparian habitat in southern Nevada. *Condor*, **72**: 431–436.

Bond, R. R. (1957). Ecological distribution of breeding birds in the upland forests of southern Wisconsin. *Ecological Monographs*, **27**: 351–384.

Braun-Blanquet, J. (1965). *Plant Sociology: the Study of Plant Communities*. London: Hafner. 439 pp.

Carothers, S. W., Johnson, R. R. & Aitchison, S. W. (1974). Population structure and social organization of south western riparian birds. *American Zoologist*, **14**: 97–108.

Cloudsley-Thompson, J. L. (1968). The Merkhiyat Jebels: a desert community. In Brown, G. W. (Ed.). *Desert Biology*, Vol. 1, pp. 1–20. New York: Academic Press.

Cody, M. L. (1975). Towards a theory of continental species diversities: bird distributions over Mediterranean habitat gradients. In Cody, M. L. & Diamond, J. M. (Eds). *Ecology and Evolution of Communities*, pp. 214–257. Cambridge, Massachusetts: Belknap.

Condon, H. T. (1975). *Checklist of the Birds of Australia I. Non-passerines*. Melbourne: Royal Australasian Ornithologists Union. 311 pp.

Cooley, W. W. & Lohnes, P. R. (1971). *Multivariate Data Analysis*. New York: Wiley. 364 pp.

Dwyer, P. D. (1972). Feature, patch and refuge area: some influences on diversity of bird species. *Emu*, **72**: 149–156.

Elton, C. S. (1966). *The Pattern of Animal Communities*. London: Methuen. 432 pp.

Fosberg, F. R. (1961). A classification of vegetation for general purposes. *Tropical Ecology*, **2**: 1–28.

Geological Survey of South Australia. (1972). Geological Atlas Series, sheet SG53-13, Zone 4, 1:250 000. Adelaide: Government Printer.

Hensley, M. M. (1954). Ecological relations of breeding birds of the desert biome in Arizona. *Ecological Monographs*, **24**: 185–207.

Hillel, D. & Tadmor, N. H. (1962). Water regime and vegetation in the Central Negev highlands of Israel. *Ecology*, **43**: 33–41.

Karr, J. R. (1968). Habitat and avian diversity on strip-mined land in east-central Illinois. *Condor*, **70**: 348–357.

Karr, J. R. (1971). Structure of avian communities in selected Panama and Illinois habitats. *Ecological Monographs*, **41**: 207–233.

Karr, J. R. & Roth, R. R. (1971). Vegetation structure and avian diversity in several New World areas. *American Naturalist*, **105**: 423–435.

Kassas, M. (1952). Habitat and plant communities in the Egyptian desert. I. Introduction. *Journal of Ecology*, **40**: 342–351.

Keast, A. (1959). Australian birds: their zoogeography and adaptations to an arid continent. In Keast, A., Crocker, R. L. & Christian, C. S. (Eds) *Biogeography and Ecology in Australia*, pp. 89–114. *Monographiae Biologicae*, Vol. 8. The Hague: Junk.

Kendeigh, S. C. (1944). Discriminant analysis. In Nie, N. H., Hull, C. H., Jenkins, J. G., Steinbrenner, K. & Bent, D. H. (Eds) *Statistical Package for the Social Sciences*, pp. 434–467. New York: McGraw-Hill.

Klecka, W. R. (1975). Discriminant analysis. In Nie, N. H., Hull, C. H., Jenkins, J. G., Steinbrenner, K. & Brent, D. H. (Eds) *Statistical Package for the Social Sciences*, 2nd edition, pp. 434–467. New York: McGraw-Hill.

MacArthur, R. H. (1964). Environmental factors affecting bird species diversity. *American Naturalist*, **98**: 387–397.

MacArthur, R. H. (1972). *Geographical Ecology: Patterns in the Distribution of Species*. New York: Harper & Row. 269 pp.

MacArthur, R. H. & MacArthur, J. W. (1961). On bird species diversity. *Ecology*, **42**: 594–598.

May, R. M. (1976). Patterns in multi-species communities. In May, R. M. (Ed.) *Theoretical Ecology: Principles and Applications*. Oxford: Blackwell Scientific. 371 pp.

McNaughton, S. G. & Wolf, L. L. (1970). Dominance and the niche in ecological systems. *Science*, **167**: 131–139.

Mueller-Dombois, D. & Ellenberg, H. (1974). *Aims and Methods of Vegetation Ecology*. New York: Wiley. 547 pp.

Peterken, G. F. (1967). Guide to the check sheet for I.B.P. areas. *International Biological Program Handbook*, No. 4. Oxford: Blackwell Scientific. 133 pp.

Pianka, E. R. & Huey, R. B. (1971). Bird species density in the Kalahari and the Australian deserts. *Koedoe*, **14**: 123–130.
Raitt, R. J. & Maze, R. L. (1968). Densities and species composition of breeding birds in a creosotebush community in southern New Mexico. *Condor*, **70**: 193–205.
Raunkiaer, C. (1934). *The Life Forms of Plants and Statistical Plant Geography*. Oxford: Clarendon. 632 pp.
Recher, H. F. (1971). Bird species diversity: a review of the relation between species number and environment. *Proceedings of Ecological Society of Australia*, **6**: 135–152.
Salt, G. W. (1953). An ecologic analysis of three California avifaunas. *Condor*, **55**: 258–273.
Schodde, R. (1975). *Interim List of Australian Songbirds: Passerines*. Melbourne: Royal Australasian Ornithologists Union. 46 pp.
Shurcliff, K. S. (1978). A biogeographical analysis of bird communities in the Everard Ranges, South Australia. Unpublished M.A. Thesis, University of Adelaide.
Siegel, S. (1956). *Nonparametric Statistics for the Behavioral Sciences*. New York: McGraw-Hill. 312 pp.
Tadmor, N. H., Orshan, G. & Rawitz, E. (1962). Habitat analysis in the Negev desert of Israel. *Bulletin Research Council of Israel D*, **11**: 148–173.
Tomoff, C. S. (1974). Avian species diversity in desert scrub. *Ecology*, **55**: 396–403.
Twidale, C. R. (1964). A contribution to the general theory of domed inselbergs: conclusions derived from observations in South Australia. *Transactions Institute of British Geographers*, **34**: 91–113.
Udvardy, M. D. F. (1957). An evaluation of quantitative studies in birds. *Cold Spring Harbor Symposia on Quantitative Biology*, **22**: 301–311.
Ulfstrand, S. (1975). Bird flocks in relation to vegetation diversification in a south Swedish coniferous plantation during winter. *Oikos*, **26**: 65–73.
Whittaker, R. H. & Niering, W. A. (1965). Vegetation of the Santa Catalina Mountains, Arizona. II. A gradient analysis of the south slope. *Ecology*, **46**: 429–452.
Willson, M. F. (1974). Avian community organization and habitat structure. *Ecology*, **55**: 1017–1029.

Appendix 1

A complete bird species list with transect abundance values per 10 transect stops for each habitat type. Nomenclature follows Condon (1975) and Schodde (1975)

Species name	Bn Ck Plain	Creek Pl Ck	Basin	Gully	Base	Ridge
Lichenostomus penicillatus	39·8	16·3	21·7	25·6	3·6	0·3	65·0	1·5
Lichenostomus keartlandi	10·0	0·7	5·4	0	45·8	29·7	1·0	27·6
Lichenostomus virescens	0	5·4	0·2	5·6	0	0	1·0	0
Poephila guttata	3·6	5·0	1·3	7·8	0·3	0·7	4·7	1·9
Colluricincla harmonica	2·9	0·7	5·4	0·6	1·7	4·3	3·3	4·8
Acanthagenys rufogularis	2·1	4·0	1·9	5·6	0·8	2·3	11·3	1·9
Pomatostomus superciliosus	4·8	0	3·3	0	0·8	2·7	3·0	0·9
Acanthiza chrysorrhoa	0	3·7	0·4	2·8	0	0	0	0
Malurus lamberti	2·9	2·3	4·6	4·4	1·4	4·0	1·0	2·0
Pachycephala rufiventris	2·4	0·3	0·4	1·1	0	0·7	0·3	0·7
Barnardius zonarius	0	1·3	5·4	5·0	0	0·3	4·0	0·2
Amytornis purnelli	0·5	0	0·6	0	2·2	2·0	1·0	2·2
Oreoica gutturalis	0	0	0	0	1·1	1·3	0·3	2·0
Chlamydera maculata	1·0	0·3	1·0	1·1	0	0·3	4·3	0·2
Melopsittacus undulatus	0	0	0·2	0	0	0	2·0	0
Melanodryas cucullata	0	0	0·2	0	0	0	0	0
Manorina flavigula	0	0·3	0	0·6	0	0	0·3	0
Rhipidura leucophrys	2·6	1·3	1·5	1·7	2·2	0	4·0	0·7
Dicaeum hirundinaceum	1·4	1·7	4·0	2·8	0·8	3·7	12·3	2·8
Phylidonyris albifrons	0	0	0	0·6	0	0	0	0
Cracticus nigrogularis	0	0·3	0	0	0	0	0	0

Petroica goodenovii	0	0·3	0	0	0	0	0	0
Geopelia cuneata	0·2	0	0	0	0·3	0	0	0·2
Halcyon pyrrhopygia	0	0·7	1·0	0	0	0	0	0
Phaps chalcoptera	0·2	0	0·2	0	0	0	0	0
Acanthiza apicalis	0·7	0	0·4	0	0	0	0	0
Acanthiza uropygialis	0	0·3	0	3·9	0	0	0	0
Ocyphaps lophotes	0	1·0	0	0	0	0	0	0
Cheramoeca leucosternum	0	0·7	0	0	0	0	0	0
Hirundo neoxena	0	1·0	0	0	0	0	0	0
Gymnorhina tibicen	0	3·7	0	0·6	0	0	0	0
Coracina novaehollandiae	0	0·7	0·4	0	0	0	0·7	0
Artamus minor	0	0	0	0	0	1·0	0	2·6

Appendix 2

List of transect species and their standardized coefficients for all discriminant functions

Bird species	Functions 1	2	3	4
BS1	0·88621	−0·50602	−0·41108	−0·34508
BS2	1·83341	2·50234	0·58372	0·58316
BS3	−3·89235	0·76074	−1·40747	0·21473
BS4	−1·01174	−0·30689	−0·62309	0·69426
BS5	−1·44895	−1·09895	0·43894	0·50334
BS6	−0·69272	0·75845	−0·69359	−0·12542
BS7	0·30105	−0·31695	0·35119	0·07873
BS8	2·68037	−1·09437	−1·59957	−1·55453
BS10	−0·19753	−2·87855	−1·72987	−1·28100
BS11	0·74133	−0·27125	−0·28160	−0·21325
BS12	1·46534	−0·20580	−0·19374	0·18345
BS13	1·01444	1·21425	0·42222	−3·33370
BS15	2·47793	1·75700	0·89128	−0·60293
BS16	−1·08915	0·15819	−1·39332	−0·16832
BS17	−1·61604	−0·67106	0·14746	0·02448
BS18	−2·89449	0·26249	−1·73632	0·71551
BS19	−2·69677	6·93610	2·61645	−1·05419
BS20	−2·72748	−2·16451	−1·46188	1·07799
BS21	0·19677	2·02225	1·88181	0·02692
BS22	−3·89181	0·37670	1·55261	2·71469
BS23	1·38124	−1·91108	−2·98694	1·17319
BS26	−0·30494	−1·95336	−3·23450	1·40812
BS27	0·57114	−0·76668	−1·20338	2·08526
BS28	−2·49998	0·88211	1·18703	1·18464
BS29	−1·27763	0·30530	0·13738	0·74926
BS30	1·51362	−0·26862	−5·01821	0·64837
BS32	−4·53023	0·12887	5·11474	−2·86649
BS33	−1·00456	0·98381	−1·86921	0·76775
BS34	−0·72683	−2·10525	1·16474	0·66709
BS35	−1·00552	−0·34798	−0·45252	0·16318
BS36	−0·29536	0·05841	−0·05560	−0·00506