



A BIOGEOGRAPHICAL ANALYSIS OF BIRD COMMUNITIES
IN THE EVERARD RANGES, SOUTH AUSTRALIA

by

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SUMMARY

The relationship between the vegetation and avian components of the biogeocoenoses within a South Australian arid mountain range was investigated. Eight biogeocoenoses, based on landform types and vegetation associations, were delimited in two study areas. Each biogeocoenose was characterized by its plant species composition, foliage cover profile, plant species diversity, plant life form diversity, foliage height diversity, bird species composition, and several bird community characteristics including total number of individuals, number of species, species diversity, and a dominance index. In addition, bird feeding profiles and spectra were constructed for the biogeocoenoses.

Bird species composition was sampled using both mist net captures and transect counts. Since a comparison of the two sets of data indicated that the mist net captures underestimated the total number of individuals and number of species in those biogeocoenoses with a tree layer (>8 m), most analyses were based on the transect data.

Three of the bird community characteristics measured were significantly correlated with life form diversity. However, life form diversity did not accurately predict the total number of individuals for those units in which White-plumed Honeyeaters accounted for over half of the total population sampled. Total number of individuals was predicted by a foliage height diversity index, which is also an index of total foliage cover. These results support those of other arid area bird studies and indicate the difficulties of extending principles developed by extensive work in one vegetation type to other vegetation types.

Although vegetation physiognomy successfully predicted the bird community characteristics, geographic proximity was the main factor affecting the similarity of bird species composition, as indicated by

both a discriminant function analysis and a Motyka similarity matrix. Investigation of the pattern of feeding profiles and spectra indicated that they were not closely related to the foliage cover profiles. Thus, foliage cover does not appear to be a very accurate index of resource availability in the vegetation types sampled. This helps to explain why foliage height diversity is not significantly related to the bird community characteristics. Also, life form diversity was not significantly correlated with feeding spectra diversity. Inadequacies of the procedures used to determine feeding behavior could be largely responsible for these results.

The results of this study indicate that biogeocoenoses, as determined by plant associations, are useful organizing units for detailed investigations of bird communities in a limited geographic area.

I hereby declare that none of the material contained within this thesis has been submitted for a degree at any other university and that, to the best of my knowledge and belief, none of the material has been previously published or written by another person, except where due reference has been made in the text.

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I. INTRODUCTION

'In desert environments water is the limiting factor and even slight changes in environmental conditions affecting moisture available to plants may have a pronounced effect on vegetation' (Tadmor, Orshan and Rawitz 1962, p.148). Distinctive vegetation patterns occur in arid regions where mountain ranges are present due to the effects of the ranges' topography and soil parent material upon moisture availability. These effects have been documented in arid regions throughout the world (Cloudsley-Thompson 1968; Hillel and Tadmor 1962; Kassas 1952, 1966; Messerli 1973; Shreve 1942; Tadmor *et al.* 1962; Whittaker and Niering 1965). Other studies have shown that spatial variation in arid vegetation, in turn, affects the distribution of animals, particularly birds (e.g. Austin 1970; Dixon 1959; Hensley 1954; Pianka and Huey 1971; Raitt and Maze 1968; Tomoff 1974). However, only a single study by Hensley (1954) has included any information on the relationship between vegetation and birds in an arid mountain range. Hensley found marked differences in the species composition of the bird communities of a mountain canyon and the adjoining plain in the Sonoran Desert, but he did not investigate differences among the bird communities of the vegetation types found within the mountain range itself. Thus, little is known about the nature of the bird communities associated with arid mountain range vegetation. It was the objective of the present study to obtain information on the vegetation pattern within an Australian arid mountain range and to investigate the effects of this pattern upon the composition and structure of bird communities.

1. Theoretical Considerations

The habitat concept has proven to be very successful for organizing investigations of bird species distribution. *Habitat* is a general term for the environment in which a species population or community of species lives (Hanson 1962). This environment has both an abiotic and biotic component.

The habitat of a species population can be defined in two ways: as an area of geographic space or as an abstract *hyperspace* of environmental factors. The geographic definition has been the traditional one and has been used by a variety of authors over many years (e.g. Andrewartha and Birch 1954; Beecher 1942; Buse 1974; Diver 1938; Elton 1966; Elton and Miller 1954; Holmes and Black 1973; Lack 1933, 1966; Lack and Venables 1939; Society Promotion Nature Reserves 1969). However, since the pioneering work of Hutchinson (1957), more recent studies have often conceptualized the habitat of a species population as lying within an abstract hyperspace defined by a number of axes which correspond to gradients of environmental factors (Whittaker, Levin and Root 1973).

The environmental factors most commonly employed as hyperspace axes for the habitats of bird species populations are vegetation and substrate parameters (see Wiens 1969). Most of the vegetation parameters are physiognomic (e.g. per cent ground cover or canopy height) rather than floristic (e.g. relative abundance of particular plant species). Multivariate statistical procedures are used to determine which parameters are critical for distinguishing the habitat of one species population from that of another species population (Cody 1968, 1974; Emlen 1956; James 1971; Whitmore 1975, 1977; Wiens 1969).

Both the geographic and the hyperspace definitions of habitat have advantages and limitations. The abstract hyperspace definition is an

attempt to identify those environmental factors which affect the geographic distribution of individual species; whereas the geographic definition is merely descriptive. However, the hyperspace definition has not been successfully applied to the study of bird community habitats.

In theory, a bird community habitat should encompass the habitats of all its members. However, birds, like most animals, are not organised into discrete units with consistent membership (Bond 1957; Kendeigh 1944, 1948; Kikkawa 1968; Terborgh 1971; Whittaker 1962). Thus, bird communities are abstractions which can only be delimited by criteria chosen according to the objectives of a particular study. As MacArthur (1971, p.190) states, an animal community can be defined as 'any set of organisms currently living near each other and about which it is interesting to talk'. Most studies of bird communities define them as those individuals living together within a specified geographic area; that is, they define the community by first delimiting its habitat (e.g. Beecher 1942; Cody 1975; Karr 1971; Lack and Venables 1939; Lovejoy 1974; Pearson 1977; Salt 1953). The distribution of a species population delimits its habitat; whereas the distribution of the community's members cannot be used to delimit its habitat, for the habitat is used to delimit the community. Communities and their habitats are delimited by a geographic definition. The hyperspace concept can then be used to describe the environmental attributes of the community habitat.

The use of the geographic definition to delimit bird community habitats has its theoretical basis in the concept of the *biogeocoenose*. A biogeocoenose is a concrete, bounded ecosystem (Hanson 1962; Sukachev 1960; Walter 1973); that is, a segment of the landscape which is relatively homogeneous with respect to the structural components of the ecosystem it encompasses. These components include a biotic community

(*biocoenose*) and its abiotic environment. A biocoenose can be divided into several components: a plant community (*phytocoenose*), an animal community (*zoocoenose*), and a community of micro-organisms (Sukachev 1960). Each of these can be further subdivided; for example, the zoocoenose consists of bird, mammal, insect, and other communities.

The boundaries of a biogeocoenose correspond to the boundaries of a plant community (Aleksandrova 1973; Carpenter 1939; Mueller-Dombois and Ellenberg 1974). This is because the plant component of a biogeocoenose integrates the abiotic and all other biotic components into a functional system. The nature of a plant community reflects the nature of its abiotic environment (Christian 1952, 1958; Jurdant 1969; Mueller-Dombois 1965; Sochava 1971). Moreover, the plant community is the primary trophic level of animal food webs and supplies other resources, such as shelter and nesting sites, which are essential for sustaining animal populations (Sobolev 1971; Voronov 1970).

The delimitation of plant communities like the delimitation of animal communities, is an arbitrary procedure (Poore 1964; Whittaker 1962, 1973c). There is no single correct set of criteria for delimiting plant communities, and many different ones have been used (see Mueller-Dombois and Ellenberg 1974; Whittaker 1973a). The criteria which seem to correspond most closely to the definition of the biogeocoenose are those embodied in the plant *association* concept (Carpenter 1939). The association is a vegetation unit 'of definite floristic composition, uniform physiognomy and ... occurring in uniform habitat conditions' (1910 *International Botanical Congress* as quoted in Mueller-Dombois and Ellenberg 1974, p.173). An association is a subunit of a vegetation formation (Peterken 1967; Specht 1972; Warming 1909), which is a geographic unit of vegetation with relatively homogeneous physiognomy; that is, relatively homogeneous growth form composition, abundance and

spatial arrangement (Beard 1973; Hanson 1962). The associations of a formation differ in the species composition of their component layers.

The association was chosen as the basic inventory unit for the International Biological Program/Conservation of Terrestrial Biological Communities Section (I.B.P./C.T.) because of its suitability for management purposes (Peterken 1967). The association also meets Elton's (1966) requirements that the units employed to delimit animal habitats have readily mappable boundaries and be homogeneous with respect to features which are ecologically meaningful to their inhabitants. Since associations are usually recognized by the predominant species in different layers (Beard 1973; Mueller-Dombois and Ellenberg 1974; Peterken 1967; Specht 1972), their boundaries can be readily seen in the field and mapped on aerial photographs. Moreover, the physiognomic features of associations are ecologically significant for birds. It has been demonstrated that birds use vegetation physiognomy to recognize areas suitable for habitation and nesting (Cody 1975; Emlen 1956; Hildén 1965; Verner 1975; Wiens 1969). Cody (1975, p.216), speaking on formations, goes so far as to state 'Clearly the bird species are recognizing and selecting habitats on the basis of many of the same criteria that we use to classify these vegetation types'. Also, physiognomic parameters such as foliage height diversity and physiognomic cover diversity have been found to be better predictors of bird species diversity than floristic parameters such as plant species diversity (Cody 1974; MacArthur and MacArthur 1961; MacArthur 1972; Pianka and Huey 1971; Tomoff 1974; Wiens 1974).

Although the concept of the biogeocoenose was formally stated in the 1940's (Aleksandrova 1973; Major 1969; Sukachev 1945) and is related to similar concepts such as that of the land type or phase (Jurdant 1969), land unit (Christian 1958), microlandscape (Whittaker 1973c), and site

(Hills 1959), it has been a neglected theme in biogeographical research. As recently as 1970, Voronov (1970, p.184) asked that more studies deal with the comparative analyses of biogeocoenoses and their components, especially the biocoenoses, within a restricted geographical location:

No work at all has been done on geographical aspects of the microstructure of biocenoses, the extent of their mosaicism, the character of the microcenoses into which the cenoses are broken down in different zones, and so forth. In short, although the geographical aspects of the combinations of biocenoses in various zones and regions of the earth's land areas have been generally established by now; a comparative geographical analysis of the structure of biocenoses is only just beginning.

Several comparative studies of bird communities have been completed, but these most often use vegetation formations rather than associations to delimit the bird communities and their habitats (Cody 1975; Karr 1971; Kikkawa 1968; Pearson 1977; Salt 1953). Formations are appropriate for investigations of the 'geographical aspects of the combinations of biocenoses in various zones and regions of the earth's land areas', but they are not appropriate for work at a local scale. Thus, the present study was conducted within a framework of biogeocoenoses delimited by vegetation associations. Following Whittaker's (1973b) general guidelines for community investigations, each biogeocoenose delimited in the study area was inventoried for its range of physical substrate and vegetation parameters, bird species composition and abundance, and bird community characteristics. Feeding profiles and spectra of each biogeocoenose were also constructed, as a means of investigating the causal relations between the biogeocoenoses and their bird communities composition and characteristics.

2. The Study Area

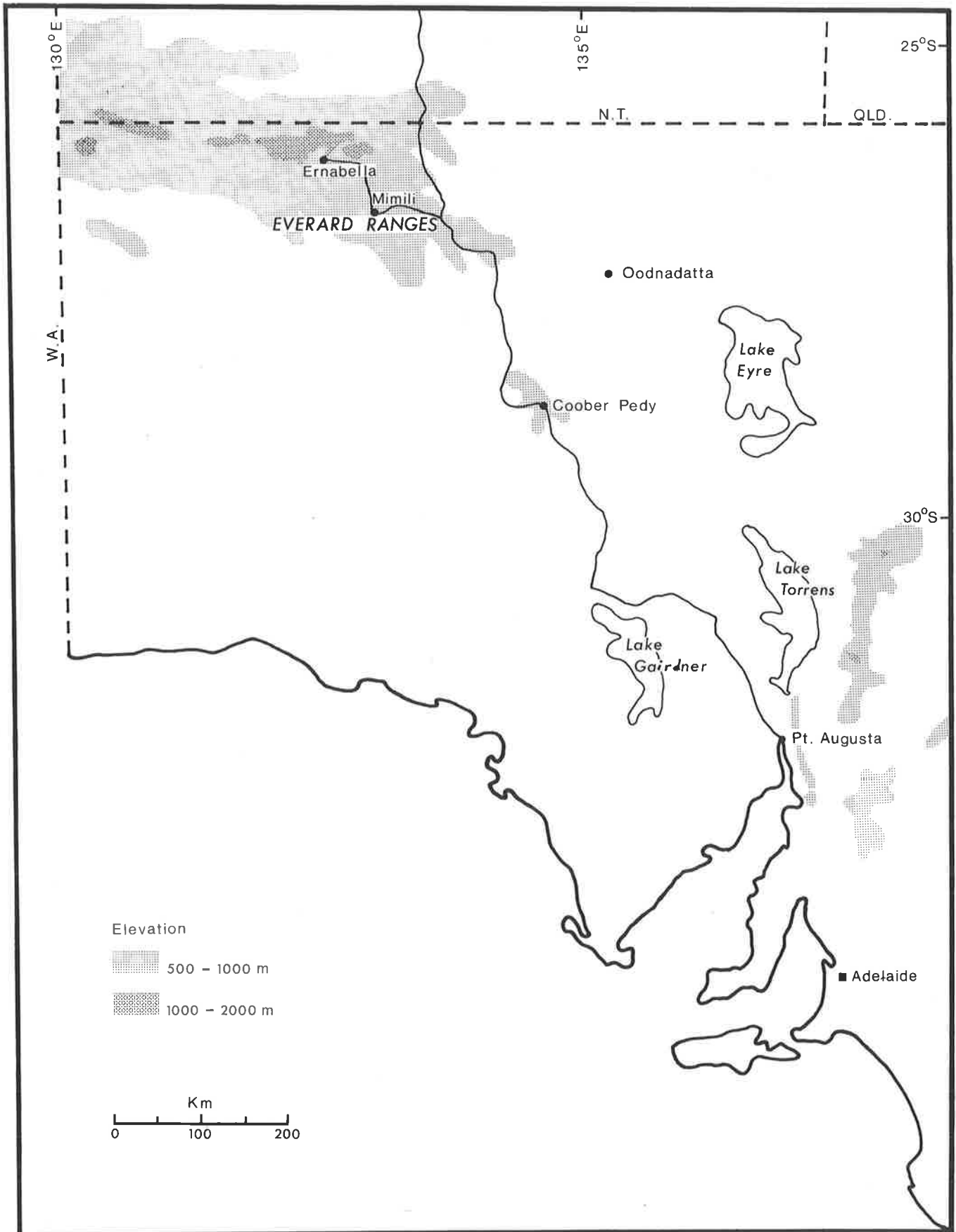
The study was conducted in the Everard Ranges, located approximately 1000 km northwest of Adelaide, South Australia (Fig. 1). The ranges are a series of granitic outcrops varying in area from a few hectares to several square kilometres. They extend from latitude $27^{\circ} 00' S$ to $27^{\circ} 10' S$ and longitude $132^{\circ} 10' E$ to $132^{\circ} 45' E$. They rise some 600 m above the surrounding plains and reach a maximum elevation of 917 m at Mt. Illbillie.

The granitic bedrock of the outcrops is the Illbillie adamellite formation of the Early Adelaidean period (Geol. Survey of S.A. 1972). The dominance of sheet structure and massive, tight jointing within the rock has resulted in a series of large domed inselbergs (Twidale 1964). Several of the largest massifs are intersected by gabbro and microgabbro dykes. Weathering along some of the major joints has proceeded to the extent that basins up to 3 km long and 400 m wide occur within the main Illbillie massif. The slopes of the domes and ridges are interrupted by gullies and a few major creeks which drain onto the surrounding plains. Minor creeks also occur within the basins and on the plains due to runoff from the surrounding slopes. All of these creeks are ephemeral and flow only after heavy rain; however, according to the Mimili Aborigines, some of the rockholes have a permanent water supply. Alluvial deposits are found in the creeks and, to a lesser extent, in the gullies and at the base of steeply sloping domes. Colluvial deposits occur in the gullies, major creeks, at the basin edges, and on the plains at the base of the rock outcrops. On the basis of morphology and substrate, a total of eight landform types were recognised in the study area. These include Gullies; the rock slopes and domes, termed Ridges; the Basins; Basin Creeks; the major creeks which flow from the Ridges onto the plains,

FIGURE 1

Map of South Australia showing location of the Everard Ranges with respect to major physical and cultural features.

Source: Bartholomew (1969), Australia sheet, 1:5 000 000 series.



termed Creeks; the bases of the steep rock slopes where gullies reach the plains, termed Bases; the small Plains Creeks; and the Plains immediately surrounding the rock outcrops. A generalized cross-section illustrating these landform types and their substrates is presented in Figure 2. This complex of landform types occurs in an otherwise fairly homogeneous plain overlain with Quarternary red sands (Geol. Survey of S.A. 1972) and vegetated by mulga (*Acacia aneura*) woodland.

The Everards are located within the Thornthwaite general climatic region described as arid, mesothermic and with deficient rainfall throughout the year (Keast 1959a). The nearest meteorological station which has records for any extended period of time is Ernabella in the Musgrave Ranges, 100 km northwest of the Everards, at latitude $26^{\circ} 17' S$, longitude $132^{\circ} 08' E$, and elevation 676 m (Fig. 1). A summary of the monthly averages for the period 1938-73 are presented in Table 1. Annual temperatures are lowest in July and highest in February. The average daily temperature range is $14.4^{\circ} C$. The average annual rainfall is approximately 255 mm; but the yearly total is highly variable, ranging from 53 mm in 1961 to 740 mm in 1974. Rainfall is highest in the summer months and peaks in February. It is lowest in July, August, and September. The number of raindays per month is fairly stable as the increased rainfall in the summer is due primarily to large rainfalls from thunderstorms. This general climatic pattern is confirmed by the limited data available from other neighboring meteorological stations: Kenmore Park, Granite Downs, Wallatina, and Amata.

Since the early part of this century several scientific expeditions (e.g. Black 1936; White 1915; White, Black, Waite, Lea, Zieta, Riddle, Rainbow, Turner and Wheeler 1915) have collected and recorded the flora and fauna of the Everard Ranges. The general geographical distributions of most bird species are known for this section of the continent

FIGURE 2

Generalized cross-section of the study area, showing the eight landform types and their substrates.

Source: South Australia Department of Lands aerial photographs and field observations by author.

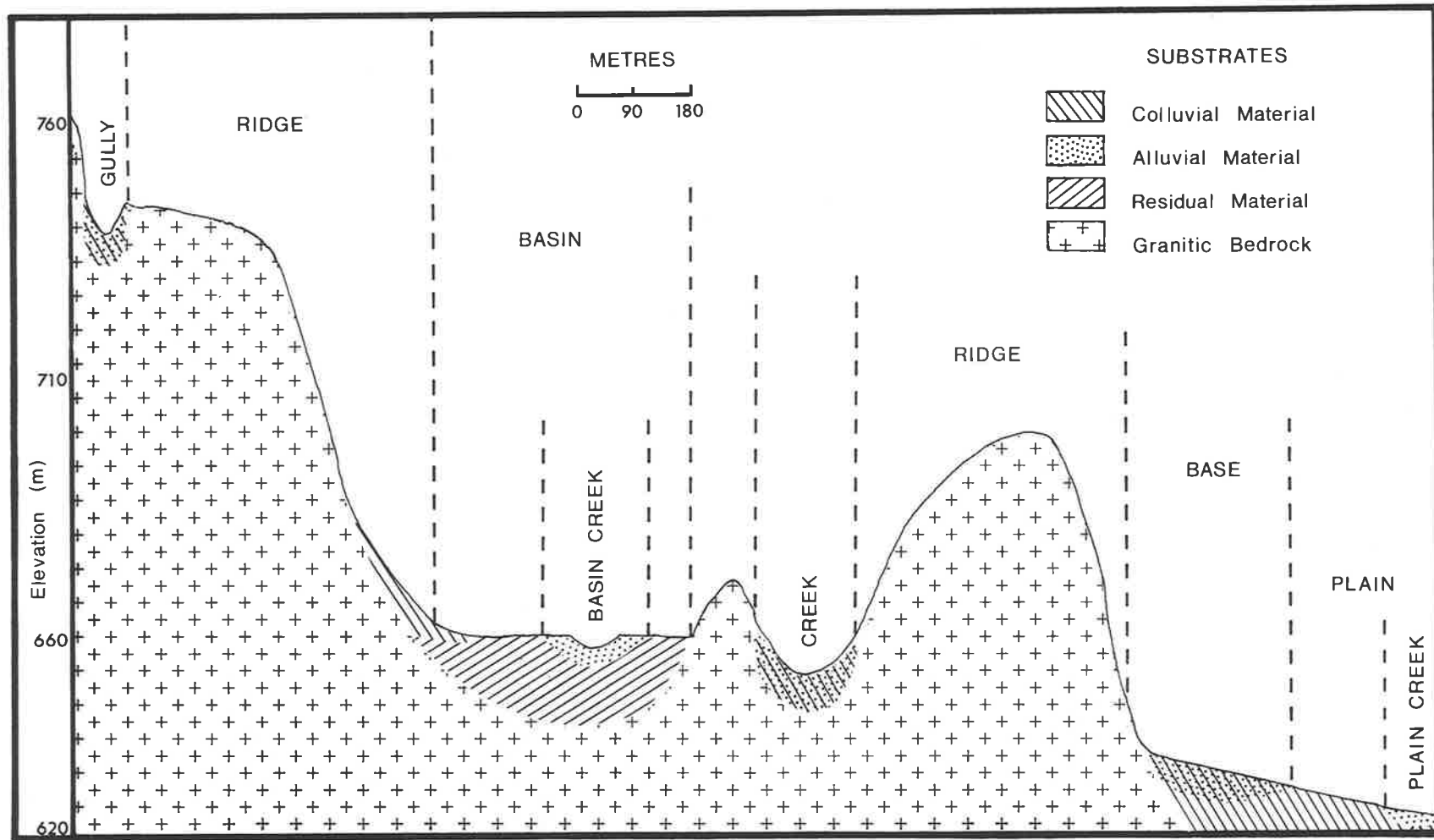


TABLE 1

Monthly averages for meteorological data from Ernabella, 1938-73

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Annual
Temperature ($^{\circ}\text{C}$)													
Maximum	34.4	38.1	31.2	26.4	21.2	18.7	17.8	20.1	24.7	28.4	31.2	33.7	26.7
Minimum	20.1	19.2	16.7	12.2	7.4	4.8	3.7	4.8	9.1	13.3	16.5	19.2	12.3
Relative Humidity (%)													
9 a.m.	35	35	43	47	59	66	57	47	41	35	30	31	44
3 p.m.	22	21	24	28	34	38	31	30	23	21	18	18	26
Rainfall (mm) *	33	35	21	18	18	18	13	13	9	25	19	30	256
Raindays	3	3	3	2	3	4	2	2	2	3	4	4	35

* Averages are for the period 1935-76 inclusive.

Source: Australian Bureau of Meteorology, South Australian Branch

(e.g. Ford 1971, 1974; Ford and Sedgwick 1967; McGilp 1935; Pianka and Pianka 1970; Slater 1970, 1974), although distributions within the Everards are largely unknown. Only a few vegetation or soil studies have been completed in this area (e.g. Bennett 1935; Jessup 1951; Lange 1966; Specht 1972).

Since the 1930's the Everard Ranges have been part of the pastoral lease known as Everard Park. This name was changed to Mimili in 1972 when the Australian government purchased the lease for the local Aboriginal community. The property is still being used for cattle grazing today and a number of wells and storage tanks are maintained for this purpose. The effects of cattle grazing are noticeable but restricted to areas around the granitic outcrop bases and are greatest in the immediate vicinity of the storage tanks. Steep slopes and boulder-strewn creeks prevent cattle from penetrating into the ranges proper. Populations of euros (*Macropus robustus*), dingoes (*Canis familiaris dingo*), European foxes (*Vulpes vulpes*), rabbits (*Oryctolagus cuniculus*) and feral cats (*Felis catus*) live throughout the ranges.

II. THE BIOGEOCOENOSES

A preliminary study site was established in Bloodwood Valley, located within the main Illbillee massif, approximately 25 km west of Mimili homestead (Plate 1). This site was chosen after an initial reconnaissance because it included representative examples of each of the eight different landform types found within the ranges (Fig. 2). An area of approximately 55 ha was sampled during August and September of 1975. It was intended to continue work at this site throughout the year. However, the Mimili Aboriginal community requested that the study site be relocated. A suitable alternative was found at Victory Creek, approximately 3 km south of Bloodwood Valley (Plate 1). Work continued at this site until December 1976.

Examination of aerial photographs and a preliminary field survey established that each of the eight landform types found within the two study sites supports a unique vegetation association. Thus, each landform type with its vegetation association delimits a biogeocoenose. The eight biogeocoenoses were named after their associated landform type: Plain, Plain Creek (Pl Ck), Base, Creek, Basin, Basin Creek (Bn Ck), Ridge, and Gully. The boundaries of the Creek, Basin, Basin Creek, and Gully biogeocoenoses are well defined by physical features such as water courses or steep rock walls. The boundaries of the other biogeocoenoses are defined only by the distribution of the predominant plant species of the associations. The Base, Gully, and Plain Creek biogeocoenoses are broken into small, disjunctly distributed units; whereas each of the other biogeocoenoses are one contiguous unit. Plate 2 (inside back cover) shows the biogeocoenoses and their approximate boundaries at Victory Creek.

PLATE 1

Aerial photograph showing the location of the two study sites within the Illbillee massif: Bloodwood Valley and Victory Creek.

Source: South Australia Department of Lands aerial survey photographs.



1. Vegetation and Substrate Sampling

To objectively describe the vegetation parameters of each biogeocoenose so that they could be related to the bird community characteristics, the biogeocoenoses were inventoried for the following items: physical substrate characteristics and plant species composition, abundance, and phenology.

Circular plots, 100 square metres in area (radius 5.6 m), were used to sample plants taller than 0.5 m; a one-eighth section of each plot (area 12.5 square metres) was used to sample plants shorter than 0.5 m. These areas are those suggested for sampling non-tree vegetation (Mueller-Dombois and Ellenberg 1974). Table 2 lists the area of each biogeocoenose and the number of plots established within it. Examples of the field data sheets used for sampling are given in Appendix 1.

The physical substrate features measured for each plot were slope aspect; slope gradient; slope shape; the cover class (using the Daubenmire cover class scale presented in Appendix 2) of exposed bedrock, bare soil and litter; the cover class and predominant size class (using categories of U.S. Dept. Agric. 1951; Appendix 2) of surface stoniness; and the depth and composition of O_1 and O_2 litter horizons. Nearby water bodies, water courses and extent of erosion were recorded. General notes on the soil profile morphology were also taken. Absolute elevations were obtained from a topographic map which had been constructed by the author from aerial photographs with a Zeiss-Jena stereometrograph precise plotter. Ground control for this map was established by altimeter readings.

The following data were recorded for each individual plant taller than 2 m within a plot: species name, two perpendicular canopy diameters, upper and lower canopy heights, and phenology (categories are listed in Appendix 2). Trunk diameters at 1.5 m and at ground level were also

TABLE 2

Areas and sample plot numbers for the eight biogeocoenoses in the two study sites

	Victory Creek		Bloodwood Valley		Total	
	Area (ha)	No. Plots	Area (ha)	No. Plots	Area (ha)	No. Plots
Basin Creek	4	10	-	-	4	10
Plain	35	8	18	4	53	12
Creek	8	12	1	3	9	15
Plain Creek	*	5	*	1	*	6
Basin	18	12	-	-	18	12
Gully	**	4	**	7	**	11
Base	10	8	9	5	19	13
Ridge	24	10	20	4	44	14
Totals	99	70	48	24	147	93

* Area estimate included in figure for Plains

** Area estimate included in figure for Ridge

measured for plants taller than 8 m. The height, canopy extent, and phenology were recorded for epiphytes. The species name, Braun-Blanquet cover-abundance class (Appendix 2), number of individuals, modal height, and phenology were noted for species shorter than 2m.

2. The Biogeocoenose Associations: Physiognomic Classification

As a means of systematically describing the physiognomy of the biogeocoenose associations and establishing their similarities and differences, the associations were classified according to the physiognomic system developed by Fosberg (1961) and revised for the I.B.P./C.T. (Peterken 1967). The purpose of this system is to standardize the description and classification of vegetation throughout the world. Its open-ended, hierarchical structure permits its ready adaption for use at any scale.

There are five levels in Fosberg's system. The first level, the primary structural group, is determined by the coverage of the densest vegetation layer. The second level, the formation class, is determined by growth form coverage. A summary table of these two levels with their respective categories is presented in Figure 3. The next three levels, formation group, formation, and subformation, are based upon growth form function and morphology. Formation groups are either evergreen, deciduous or seasonally dormant. Formation and subformation categories are based upon leaf size and texture and other distinctive morphological features such as gnarled habit, thorns, etc.

Vegetation foliage cover profiles (Fig. 4), constructed from the average canopy diameters, canopy heights, and cover class estimates for all plots in each biogeocoenose, were used to classify the associations into primary structural groups and formation classes. As shown in Table 3, two associations are in the closed primary structural group, as

FIGURE 3

Summary table of the first two levels, primary structural group and formation class, in Fosberg's physiognomic classification system.

Source: Peterken 1967.

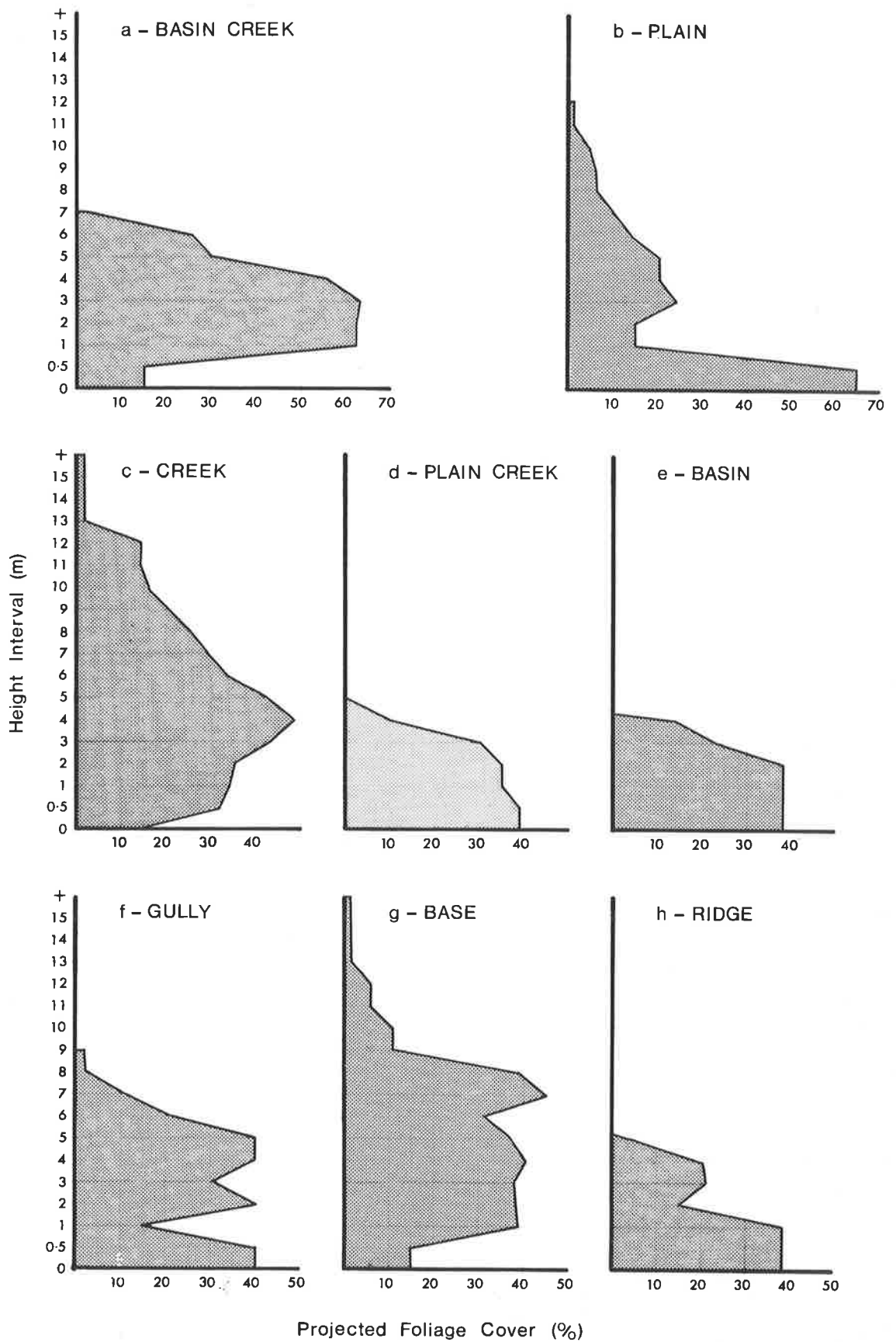
TABLE 3

The eight biogeocoenose associations classified according to Fosberg's physiognomic system.

Biogeocoenose	Primary Structural Group	Formation Class	Formation Group	Formation	Subformation
Basin Creek	Closed	Scrub	Evergreen	Sclerophyllous	Narrow-leaved
Plain	Closed	Low savanna	Evergreen	Sclerophyllous	Narrow-leaved
Creek	Open	Steppe forest	Evergreen	Sclerophyllous	Broad-leaved
Plain Creek	Open	Steppe scrub	Evergreen	Sclerophyllous	Narrow-leaved
Basin	Open	Steppe scrub	Evergreen	Sclerophyllous	Broad-leaved
Gully	Open	Steppe scrub	Evergreen	Sclerophyllous	Broad-leaved
Base	Open	Steppe savanna	Evergreen	Sclerophyllous	Broad-leaved
Ridge	Open	Shrub steppe savanna	Evergreen	Sclerophyllous	Broad-leaved

FIGURE 4

Average foliage cover profiles of each biogeocoenose association.



determined by foliage cover values greater than 60%. These are Basin Creek (Fig. 4a) with a closed shrub layer and Plain (Fig. 4b) with a closed short tussock grass layer. All other units are in the open primary structural group, with shrubs forming the densest vegetation layer. There are only six different formation classes since three units (Plain Creek, Basin, and Gully) have very similar foliage cover profiles (Fig. 4c-4e) and are all classified as Steppe Scrub. The Base (Fig. 4f) and Creek (Fig. 4g) differ in the extent of tree cover (>8 m tall) and are classified as Steppe Savanna and Steppe Forest respectively. The Ridge (Fig. 4h), with its relatively low shrub cover, is placed into Shrub Steppe Savanna. Basin Creek fits into the formation class Scrub, and Plain into Low Savanna.

No further divisions are necessary at the formation group or formation levels, as all the associations have predominantly evergreen and sclerophyllous foliage. However, seven subformations, based on the leaf shape categories of broad and narrow, are present. The Steppe Scrub formation class divides into a narrow-leaved subformation with one member, Plain Creek, and a broad-leaved subformation with two members, Basin and Gully.

Thus, of the eight biogeocoenose associations, only two, Basin and Gully, are similar enough at the subformation level to be placed within the same category. However, these two have different predominant species. As shown in Table 4, the predominant species in the shrub layer of the Basin are two species of mallees, *Eucalyptus intertexta* and *E. oxymitra*, and the predominant species in the ground layer is the hummock grass *Triodia irritans*. *Triodia irritans* is also the ground layer predominant in the Gully, but *Acacia signata* is its shrub layer predominant.

Triodia irritans is the ground layer predominant in all units except the two on the plains. The shrub and tree layer dominants are different

TABLE 4

Cover predominant Species of Each Biogeocoenose association.

Species	Growth form	Total Cover (m ² /1000 m ²)								
		P1	PC	B	C	BC	Bn	R	G	Total
<i>Enneapogon avenacerus</i>	SG	300	135	1	11	15	1	-	-	338
<i>Acacia estrophiolata</i>	T	138	12	-	-	-	-	-	-	150
<i>Hakea suberea</i>	T	88	15	-	-	-	-	-	-	103
<i>Acacia tetragonophylla</i>	S	4	117	5	18	5	-	-	-	149
<i>Cassia nemophila</i>	S	10	90	-	-	-	-	-	-	100
<i>Acacia signata</i>	S	-	-	395	146	77	-	143	390	1151
<i>Eucalyptus intertexta</i>	S	47	-	187	13	60	124	58	76	565
<i>Triodia irritans</i>	HG	6	35	119	86	93	327	293	109	1068
<i>Eucalyptus camaldulensis</i>	T	-	-	83	250	-	-	-	-	333
<i>Dodonea viscosa</i>	S	0.1	80	22	128	22	8	2	23	285
<i>Melaleuca glomerata</i>	S	-	-	-	15	562	28	-	-	605
<i>Eucalyptus oxymitra</i>	S	-	-	-	-	-	86	-	-	86

Notes: SG - short grass, T - tree, S - shrub, HG - hummock grass

Nomenclature follows Black (1960) and Eichler (1965)

in all units except the Gully and Ridge, in which *Acacia signata* is dominant. However, these units represent two associations because of differences in their physiognomic and landform characteristics, as discussed previously. Representative photographs of each biogeocoenose association are presented in Plates 3-6.

3. The Biogeocoenose Associations: Vegetation Parameters

In addition to being systematically described by their physiognomic classification, the biogeocoenose associations were characterized and ordered by a number of vegetation parameters. These parameters are measures of floristic composition and physiognomy. The particular parameters used in this study were chosen for their previously reported success in investigations of relationships between vegetation characteristics and bird community characteristics, particularly bird species diversity.

(i). Floristic composition parameters

The delimitation of the biogeocoenose associations was based upon only the predominant plant species in each layer. To investigate the relationships among the associations with respect to their total species composition, an index of species abundance similarity was calculated. This was the Motyka index, which is

$$IS = \frac{2 M_w}{M_a + M_b} \times 100\%.$$

The Motyka index expresses the sum of the smaller of the two abundance values for all plant species common to two associations (M_w) as a proportion of the total abundance values in the two units (M_a , M_b) (Mueller-Dombois and Ellenberg 1974). Weighting species composition with abundance values reduces any effects due to unequal total sampling areas. Comparisons

PLATE 3a

Example of the Plain biogeocoenose, showing scattered trees of *Hakea suberea* and ground cover of the tussock grass *Enneapogon avenacerus*.

PLATE 3b

Example of Plain Creek biogeocoenose, showing *Acacia* sp. and *Cassia* sp. shrubs and tussock grass *Enneapogon avenacerus*.



PLATE 4a

Example of Basin Creek biogeocoenose, indicated by the dense coverage of *Melaleuca glomerata* shrubs along the gravel creek bed.

PLATE 4b

Example of Basin biogeocoenose, showing *Eucalyptus* mallee shrubs and ground cover of the hummock grass *Triodia irritans*.

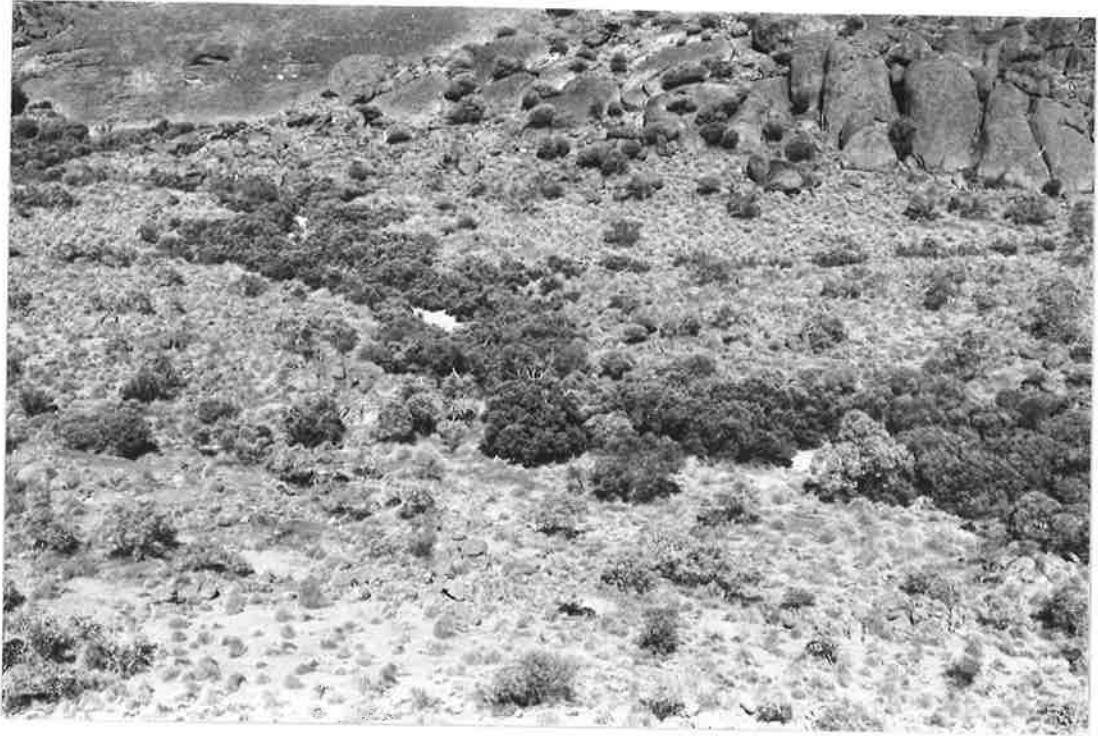


PLATE 5a

Example of Base biogeocoenose, showing shrub cover of *Acacia signata*
and scattered trees of *Eucalyptus camaldulensis*.

PLATE 5b

Example of Creek biogeocoenose, with *Eucalyptus camaldulensis*
trees and *Acacia* and *Dodonea* shrubs.

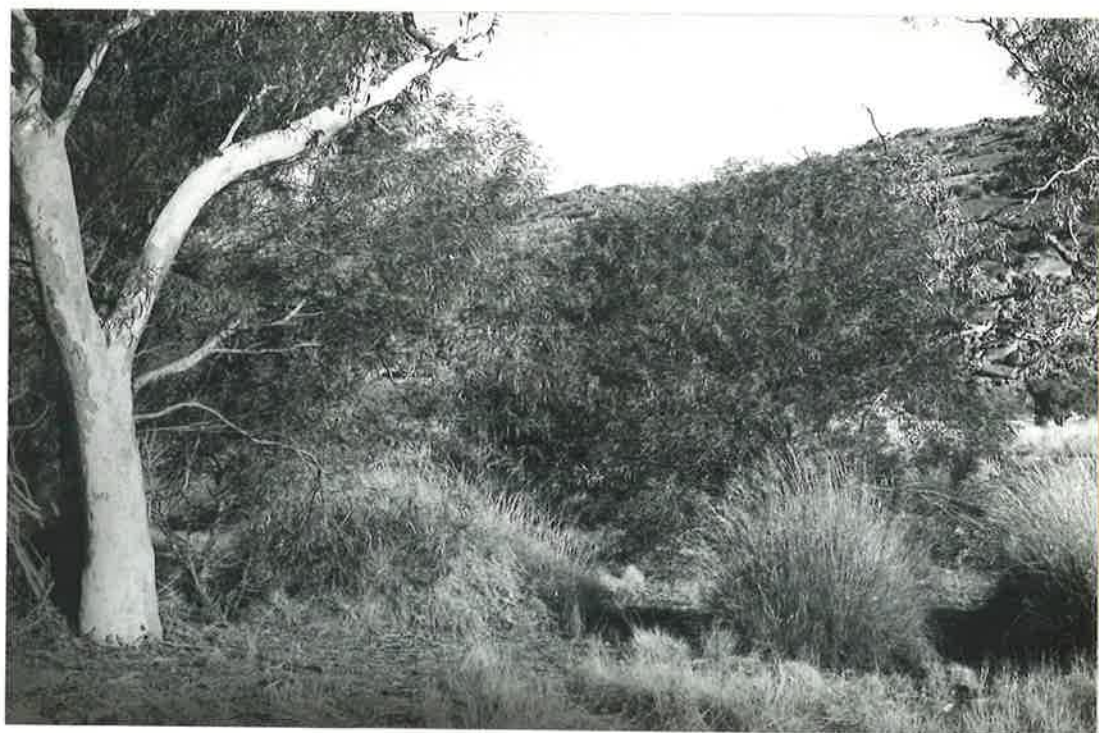


PLATE 6a

Example of Ridge biogeocoenose, with scattered *Acacia signata*
low shrubs and *Triodia irritans*.

PLATE 6b

Example of Gully biogeocoenose, with *Acacia signata* shrubs.



were made between all pairs of associations to produce the symmetrical similarity matrix shown in Table 5.

As shown in Table 5, the Motyka index values are generally very low, indicating considerable dissimilarity in the abundance of plant species among the associations. This is to be expected since the associations are partly delimited by predominant species and these have the most influence upon the Motyka index values. Only two pairs of associations have index values greater than 50%: Gully-Base (67%) and Basin-Ridge (58%).

The Gully and Base have similar predominant species in most vegetation layers (Table 4, p.26), except for *Eucalyptus camaldulensis* which forms a tree layer in the Base but is absent in the Gully. This difference, as well as the basic similarities between these two associations, is also reflected in their respective subformation classifications: broad-leaved Steppe Scrub (Gully) and broad-leaved Steppe Savanna (Base) (Table 3, p.22). The vegetation of the Base appears to be essentially the same as the Gully but with the addition of trees (compare Plates 5a and 6b). These vegetation similarities reflect the similarities of the Base and Gully physical environments. Both are limited in areal extent, are disjunctly distributed (Plate 2), receive run-off from surrounding slopes, are topographically shaded, and have mixed colluvial-alluvial substrates (Fig. 2, p.12). However, the presence of trees in the Base unit suggests that its physical environment is more favorable for plant growth. The Base has lower slope gradients, deeper substrate deposits, and the surrounding water-shedding slopes are more extensive. These factors probably mean that a greater amount of water is supplied to and stored in the Base's substrate than is the case with the Gully.

The relatively high similarity value between the Basin and Ridge

is due to the fact that both have a dense ground cover of *Triodia irritans* and both have *Eucalyptus intertexta* as an abundant shrub species. In addition, they have similar foliage profiles but slightly different subformation classifications since the Ridge has less shrub cover than the Basin (Fig. 4, p.24).

Motyka index values indicate that the Plain is very dissimilar from the other biogeocoenose associations. The Plain is an unique subformation, having a closed ground layer. The highest similarity is with the Plain Creek, which is a geographic subunit of the Plains (Plate 2). The index values among the other units vary according to general physiognomic similarities, geographic proximity, and physical environment similarities.

The diversity of the floristic composition within the associations was measured by the number of plant species present on each of their sample plots, and by plant species diversity which considers both species number and relative abundance for all sample plots within an association. Simpson's reciprocal index was used to calculate plant species diversity because of its simplicity and ease of interpretation (MacArthur 1972; May 1976). The index is

$$D = \frac{1}{\sum_i P_i^2}$$

where P_i is the number of individuals for the i th species divided by the total number of individuals of all species in an association.

The sample plot means and 95% confidence intervals for the number of plant species are presented in Table 6. A non-parametric Kruskal-Wallis analysis of variance (Siegel 1956) indicated significant differences among the biogeocoenose values. Those associations with the highest number of plant species per plot are the three creek units: Basin Creek, Plain Creek, and Creek. Two of these units, Plain Creek and Creek, also have

TABLE 6

Number of plant species and plant species diversity for the biogeocoenose associations.

	Bn Ck	Plain	Creek	P1 Ck	Basin	Gully	Base	Ridge	
<u>Plant Species Number</u>									
Mean	11.0	5.7	10.1	10.8	5.8	9.2	8.9	6.6	
95% Confidence Intervals	9.9-12.1	4.7-6.6	8.5-11.7	6.7-15.0	4.4-7.1	7.7-10.6	7.6-10.1	5.5-7.8	$\chi^2 = 18.3^*$
<u>Plant Species Diversity</u>									
	2.95	5.06	7.70	11.36	2.95	4.97	5.68	3.68	

* as approximated by Kruskal-Wallis one-way analysis of variance by ranks; significant at $p < 0.01$.

high plant species diversity values (Table 6). The Basin Creek has a low value because it has a very high relative coverage of a single species, *Melaleuca glomerata* (Table 4, p.26). The Basin has both the lowest number of species and lowest plant species diversity value.

(ii) *Physiognomic parameters*

As a means of quantifying the physiognomic characteristics implicit in the Fosberg classification of the biogeocoenose associations, each association was described according to its life form spectrum, an index of life form diversity, and an index of foliage height diversity.

To describe the general growth form composition of the associations, life form spectra, based upon Raunkiaer's (1934) classification system, as modified by Mueller-Dombois and Ellenberg (1974), were constructed. It should be noted that, in this study, *life form* is a specific term which refers only to the Raunkiaer system of classifying plant growth forms (after Beard 1973). Nine life form categories were used: mesophanerophyte (woody plant >8 m), microphanerophyte (woody plant 2-8 m), nanophanerophyte (woody plant 0.5-2 m), chamaephyte (perennial plant <0.5 m), hemicryptophyte (perennial herbaceous plant which dies back to or near ground level), geophyte (perennial herbaceous plant which dies back to storage organ within ground), therophyte (annual plant), liana (rooted plant supported by another plant), and semi-parasite (semi-autotrophic vascular plant).

The percentage cover of each life form category for the associations is presented in Table 7. Most variation among the associations occurs in the categories mesophanerophyte, microphanerophyte, chamaephyte, and hemicryptophyte. There appears to be a general relation between life form spectrum and foliage cover profile (Fig. 4, p.24). The three units, Basin, Ridge, and Plain Creek, with similar foliage cover profiles

TABLE 7

Life form spectra and life form diversity (L.F.D.) for the biogeocoenose associations.

Biogeocoenose	Phanerophytes			Chamae- phyte	Hemi- cryptophyte	Thero- phyte	Geo- phyte	Lianas	Semi- parasites	L.F.D.
	Meso-	Micro-	Nano-							
Basin Creek	-	73	9	11	6	-	1	1	0.1	2.68
Basin	-	39	6	53	0.1	2	-	1	0.1	2.45
Ridge	-	36	5	48	9	3	-	0.1	0.1	2.73
Plain	16	16	7	2	53	6	-	0.1	-	3.04
Gully	2	52	9	18	15	3	0.1	0.1	0.1	3.00
Base	14	48	8	3	26	1	-	0.5	0.1	3.17
Plain Creek	-	36	9	15	33	2	-	4	-	3.69
Creek	20	21	29	8	19	1	1	1	0.1	5.00

have similar life form spectra. However, the relationship is not exact, since Basin and Ridge have more similar spectra than Basin and Plain Creek, but Basin and Plain Creek have the more similar foliage cover profiles. The Plain Creek differs from the other two units in its relative proportions of chamaephytes and hemicryptophytes. The Basin Creek has an unique life form spectrum, as well as an unique foliage profile.

To order the associations along a simple life form gradient, each unit was given a value as measured by an index named life form diversity (L.F.D.). Simpson's reciprocal index (p.34) was used with P_i representing the proportion of the i th life form category. In order to make this index correspond more closely to Tomoff's (1974) physiognomic cover diversity index, which successfully predicted bird species diversity in the Sonoran Desert, the phanerophyte categories were subdivided into broad-leaved and narrow-leaved categories. The values derived from this index are listed in Table 7. Again, there is a very general relation between life form diversity and foliage cover profile. However, the Plain Creek has a higher life form diversity value than would be expected on the basis of its foliage cover profile. Life form diversity is highly correlated with plant species diversity (Spearman's r , $r_s = 0.98$, $N = 8$, $p < 0.01$). This high correlation is no doubt due to the overall low number of plant species in the study area. Thus, almost every species in each association corresponds to a separate life form category.

Foliage height diversity (F.H.D.) is a parameter developed by MacArthur and MacArthur (1961) to quantify foliage profile characteristics as a means of predicting bird species diversity. It is calculated by a diversity index, such as Simpson's reciprocal index, which is based upon the relative proportion of foliage in each of several vegetation layers. MacArthur and MacArthur (1961) used three vegetation layers in their

investigations (0-0.5 m, 0.5-8 m, >8 m). Austin (1970), working with arid vegetation, found breaks in the foliage layering at 1 m and 2 m. The foliage height diversity measures based upon his three layers (0-1 m, 1-2 m, >2 m) were better predictors of bird species diversity than those based upon the MacArthur's'.

In the present study, both layering systems were used to describe the foliage height diversity of the eight biogeocoenose associations. The proportion of foliage cover in each vegetation layer, as defined by Austin and the MacArthur's, was obtained for the associations from the foliage cover profiles in Figure 4 (p.24). Simpson's reciprocal index was then used to calculate foliage height diversities from these cover values. The results for both layering systems are presented in Table 8. There is a general correspondence between the foliage cover profiles and Austin's foliage height diversity values. For instance, the four biogeocoenoses with trees, Base, Creek, Gully, and Basin, have the lowest Austin foliage height diversities. The highest values are those for biogeocoenoses with no tree layer. This general correspondence does not exist with the values obtained from the MacArthur's' foliage height diversity index. Instead, the MacArthur's' index corresponds to the total foliage cover. Those biogeocoenoses with the lowest index values have the highest areas under the foliage cover profiles of Figure 4 ($r_s = -0.64$, $N = 8$, $p < 0.05$). Both Austin's and the MacArthur's' indices were used in the analysis of bird community characteristics.

TABLE 8

Foliage height diversity values for the MacArthurs' and Austin's
vegetation layers.

Base	Creek	Gully	Plain	Bn Ck	Ridge	Basin	P1 Ck
<u>Austin's Values</u>							
1.58	1.61	2.24	2.27	2.27	2.30	2.33	2.59
<u>MacArthurs' Values</u>							
1.35	1.59	1.40	2.01	1.10	1.68	1.70	1.50

III. THE BIRD COMMUNITIES

1. Sampling Procedures

Ideally the composition of a bird community should be determined by a complete census of all birds living within the community. However, censusing techniques, many of which have been developed in temperate forests, require information which is time consuming to obtain or conditions which are not existent in arid environments. For example, the widely used spot-map technique is based upon defended territories (International Bird Censusing Committee 1969), but many Australian arid bird species are non-territorial or territorial only when breeding (Keast 1959b; Rowley 1974). This technique has also been criticized on the grounds of inconsistency and inaccurate counts (Berthold 1976; Best 1975; Enemar 1959; Enemar and Sjöstrand 1970; Erskine 1974; Järvinen and Sammalisto 1973; Simms 1971). It produces varying results depending upon how territories are determined. It can only effectively inventory the breeding members and territory-holders of a species population, and thus may underestimate the total species population by as much as 50% (Berthold 1976). Therefore, in arid environments, the spot-map technique has been restricted to studies of breeding populations (e.g. Austin 1970; Hensley 1954; Raitt and Maze 1968; Tomoff 1974). Other techniques derive population estimates from sample counts, primarily transect counts. These techniques attempt to compensate for differences in species visibility and rate of movement, as well as the rate of movement of the observer, to derive accurate absolute density estimates (Brewer 1972; Emlen 1971; Nilsson 1974). After reviewing several of these techniques and their respective sources of error, Emlen (1971, p.327) concluded that a complete population estimate 'is at best an elusive target'.

No attempt at complete population estimates was made in this study. Instead, transect counts and mist netting were used to determine the relative abundances of bird species in each biogeocoenose. Relative abundances are appropriate for comparative studies of bird communities (e.g. Beals 1960; Bond 1957; Karr 1971; Lovejoy 1974; Terborgh 1971), but transect counts and mist netting can produce biased results. Visual transect counts are influenced by a bird's conspicuousness (Colquhoun 1940; Emlen 1971; Kendeigh 1944), while mist nets limit the effective sampling space to that of the net itself. Moreover, some species are more prone to capture than others (Low 1957; MacArthur and MacArthur 1974; Stamm, Davis and Robbins 1960). For example, if a member of a gregarious species is netted, its distress calls often attract other members of the species, thus producing abnormally high capture rates for that species. By using both transect counts and mist netting in the present study, two independent measures of relative abundances were obtained.

A total of 93 mist nets were placed in the eight biogeocoenoses at the locations of the vegetation sample plots. Each net measured 12 m long and 2 m high. Nets were operated in groups of ten for six hours from sunrise on each of three days. Birds caught were banded with an aluminum-alloy numbered band (supplied by Australian C.S.I.R.O.) and two or three plastic color bands. The color bands were used to identify individual birds so that their movements could be traced in an effort to determine home ranges and territory sizes. Mist netting was conducted in Bloodwood Valley during September 1975 and in Victory Creek during April-May 1976.

Because transect counts require relatively little time and effort to complete in comparison to mist netting, they were used to sample bird species populations throughout the year. Victory Creek was sampled three

times in May 1976, twice in September 1976, and once in December 1976. One-third of the study site was traversed in a four-hour morning session. The sample area was covered by a series of transects, placed to include each biogeocoenose which occurred in the area and spaced at intervals of approximately 50 m. Each transect was divided into five-minute segments, which alternated between walking and stopping (after Bond 1957). All contacts with individuals were recorded.

A total of 870 captures, representing 26 species, were made during 1692 mist-net hours. Transect counts added another 11 species. A complete list of these species, with both scientific and vernacular names, and their abundances appears in Appendix 3. The 37 species sampled represent 65% of the total number of species (56), excluding raptors and nocturnal birds (10), observed by the author in the study sites. Observations of banded birds indicated that a high proportion of the resident population was caught, but no precise estimate of this proportion was obtained.

In addition to the data on bird species distributions and abundances, observations on feeding behavior were made in Victory Creek during May and September 1976. These data were employed to determine the pattern of food usage within each biogeocoenose. Upon contact with a bird in any given biogeocoenose, its feeding behavior was recorded until it was lost from sight or it moved into another biogeocoenose. No attempt was made to control the amount of time spent observing a particular bird species, thus the number of contacts with a given species reflects its relative abundance. Information recorded included bird species, plant species, feeding position, feeding height, and time spent feeding.

2. Bird Community Characteristics

A number of parameters were used to assess similarities and differences

in bird community characteristics among the eight biogeocoenoses. These parameters were the number of bird species, the total number of individuals, species diversity, and species dominance. Separate values for these parameters were obtained for mist net and transect data. Bird species diversity was measured by Simpson's reciprocal index (see section II.3 [2], p.34). Dominance was measured using the index suggested by McNaughton and Wolf (1970) and Karr (1971). This index 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.

All the individual mist net results for a biogeocoenose were combined to give a single value for each parameter calculated on the basis of a ten mist net standard. The results of these calculations are presented in Table 9. Six transect runs were made in Victory Creek over a period of nine months. The segment of each transect run within a biogeocoenose was treated as a single sample and all counts were standardized for a ten stop segment. The mean values for the parameters of the six segments in each biogeocoenose are presented in Table 9. The values for each parameter varied significantly among the biogeocoenoses, as determined by the nonparametric Friedman two-way analysis of variance (Siegel 1956). Variation in the parameters from one transect sampling period to the next was also tested. As shown in Table 10, except for the dominance index, there was no significant difference among the parameter values, indicating that the bird community characteristics were fairly stable for the duration of the study.

The pattern of results for the transects and mist nets are similar but not identical (Table 9). The total number of individuals captured per six-hour mist netting period and the number contacted per four-hour transect period are very similar in three biogeocoenoses, Basin Creek,

TABLE 9

Value of bird community characteristics for standardized net data and transect data

Biogeocoenoses	Bn Ck	Plain	Creek	Pl Ck	Basin	Gully	Base	Ridge	Prob.* level
<u>Number of individuals</u>									
Mist Net	63	17	22	72	58	14	34	11	
Transect	74	42	68	62	50	55	122	53	0.02
<u>Number of Species</u>									
Mist Net	13.0	9.2	12.0	20.0	10.0	8.2	10.0	7.9	
Transect	14.0	17.0	16.0	26.0	9.0	13.0	22.0	11.0	0.001
<u>Bird Species Diversity</u>									
Mist Net	3.04	3.32	4.67	4.30	1.96	3.41	2.58	4.14	
Transect	3.10	4.81	5.31	4.96	2.19	2.78	3.03	3.14	0.001
<u>Dominance Index</u>									
Mist Net	76.9	66.2	60.0	59.8	88.1	64.5	70.2	64.2	
Transect	68.6	53.2	51.7	49.6	81.0	73.7	68.2	66.0	0.001

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

TABLE 10

Variation in transect bird community characteristics
over a nine-month period

	April	Sept.	Dec.	P level*
Number of Contacts/Unit	43.9	35.0	37.8	0.53
Number of Species/Unit	8.6	8.6	7.5	1.00
Alpha Diversity/Unit	3.74	3.62	4.39	0.29
Dominance Index/Unit	66.2	66.4	56.3	0.03

* measured by Friedman two-way analysis of variance; k=3, N=8.

Plain Creek, and Basin. These units have no tree layer (>8 m) in the vegetation (Fig. 4, p.24). For the five units in which mist net captures are lower than transect counts, all but the Ridge unit has a tree layer. However, the shrub cover in the Ridge unit is generally much lower than in the other units. From these observations, it appears that mist net sampling, with 2 m high nets, underestimates the number of individuals in vegetation with a tree layer or with sparse (<20%) shrub cover.

The largest discrepancies between mist net and transect numbers of individuals occur in the biogeocoenoses with the greatest cover of trees; i.e. the Base and Creek. These discrepancies appear to be affected by the bird species composition of the biogeocoenoses. There is a greater difference between the mist net and transect counts in the Base unit than in the Creek unit. Over half of the individuals either caught or contacted in the Base unit are White-plumed Honeyeaters, a species which spends much of its time in tree foliage. The Creek has fewer individuals of this species and a lower total transect count. Thus, the high Base transect count could be due to the abundance of this species. The high Base transect count could also be due to sampling bias. Transect contacts could overestimate the actual abundance of a conspicuous species such as the White-plumed Honeyeater. However, this species was also very abundant in the Basin Creek, where transect and mist net counts are very similar. A more precise estimate of the number of individuals in the Base may be obtained by reducing the transect count by 25%, which is the rate of recapture of White-plumed Honeyeaters in this unit. However, the new value 92 is still considerably higher than those of the other biogeocoenoses. Thus, it seems that the high transect value for the Base unit is an accurate reflection of the actual situation and not a result of sampling bias.

In Table 9, the number of transect species is slightly higher than the number of mist net species in all cases but the Basin unit. As with the number of individuals, the largest discrepancies occur in those biogeocoenoses with a tree layer. Since there was no significant change in the actual numbers of species during the transect sampling period, the disparity between mist net and transect results cannot be accounted for by the simple addition of species during a new sampling period. These results support the conclusion that the mist nets did not adequately sample the tree layers of the biogeocoenoses.

Both bird species diversity and dominance are measures of the dispersion of the relative numbers of individuals among the species of a sample. The dominance index used considers the relative abundance of only the two most abundant species; whereas, the diversity index considers the relative abundance of all species. In the present study, the values of these two indices are negatively correlated for both the mist net data ($r_s = 0.95$, $N = 8$, $p < 0.01$) and the transect data ($r_s = 0.74$, $N = 8$, $p < 0.05$). The rank ordering of the biogeocoenose values on these parameters are consistent between the mist net and transect data ($r_s = 0.80$, $N = 8$, $p < 0.05$), indicating that species were both caught and contacted in proportion to their actual populations.

Relationships between the bird community characteristics and the vegetation parameters, life form diversity and the two foliage height diversity indices, were tested for significance by Spearman rank correlation coefficients. As shown in Table 11, the Austin foliage height diversity index is not significantly correlated with any bird community characteristic. The MacArthur's index is only significantly correlated with the number of transect individuals. Life form diversity is significantly correlated with three of the four transect parameters and two of the four mist net parameters. Since, as previously discussed, the

TABLE 11

Spearman correlation coefficient matrix between bird
community characteristics and vegetation parameters

Bird Community Characteristics	Vegetation Parameter		
	Austin F.H.D.	MacArthur F.H.D.	L.F.D.
Mist Net Number of Species	0.220	0.399	0.313
Transection Number of Species	-0.214	0.262	0.719*
Mist Net Total Individuals	0.381	0.357	0.048
Transect Total Individuals	-0.452	-0.881**	0.357
Mist Net B.S.D.	0.024	0.071	0.667*
Transect B.S.D.	0.00	0.167	0.738*
Mist Net Dominance	0.071	0.071	-0.755*
Transect Dominance	0.048	0.167	-0.667*

* $p < 0.05$

** $p < 0.01$

transect counts seem more reliable than the mist net counts, only the former are used in the following discussion.

Figure 5 presents life form diversity graphed against the four transect bird community characteristics. In the first three graphs (Fig. 5a-c), the Creek unit, which has the highest life form diversity value, has community characteristic values which do not fit the trend lines established by the other biogeocoenoses. It has a lower number of species (Fig. 5a), lower bird species diversity (Fig. 5b), and higher dominance index (Fig. 5c) than would be expected. In the last two cases the Creek community characteristic values are still the highest and next to lowest respectively, but they indicate that the relationship between life form diversity and these two parameters is non-linear. Beyond a critical level, more complex life form composition does not effectively increase bird species diversity or decrease dominance. The critical level of life form diversity is somewhere between that of the Plain Creek and Creek units.

The number of species in the Creek unit cannot be as easily explained. It is substantially lower than that expected on the basis of the trend line in Figure 5a. This discrepancy could be related to the high cover of tree vegetation that occurs in the Creek. The unexpected bird community characteristic values may thus be due to difficulties inherent in sampling very tall vegetation. However, the Base unit, which has a similar foliage cover profile (Fig. 4c, 4g), does not have unexpected values for these bird community characteristics (Fig. 5a-c). It is not known whether the difference in tree cover between these two units could be responsible for these different patterns.

The only transect parameter not significantly correlated with life form diversity is the total number of individuals. As illustrated in Figure 5d, Base and Basin Creek have abnormally high numbers of individuals



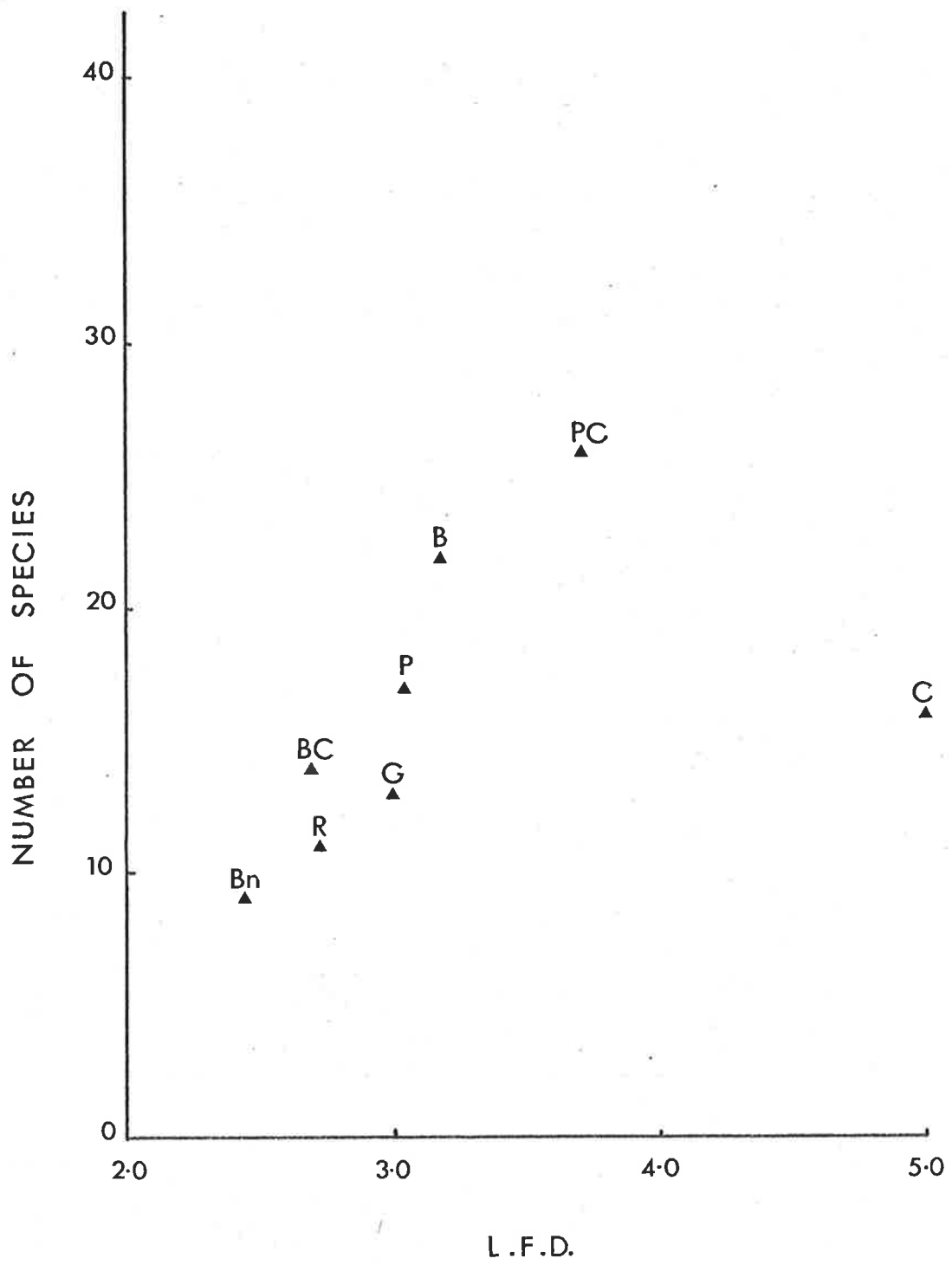
FIGURE 5

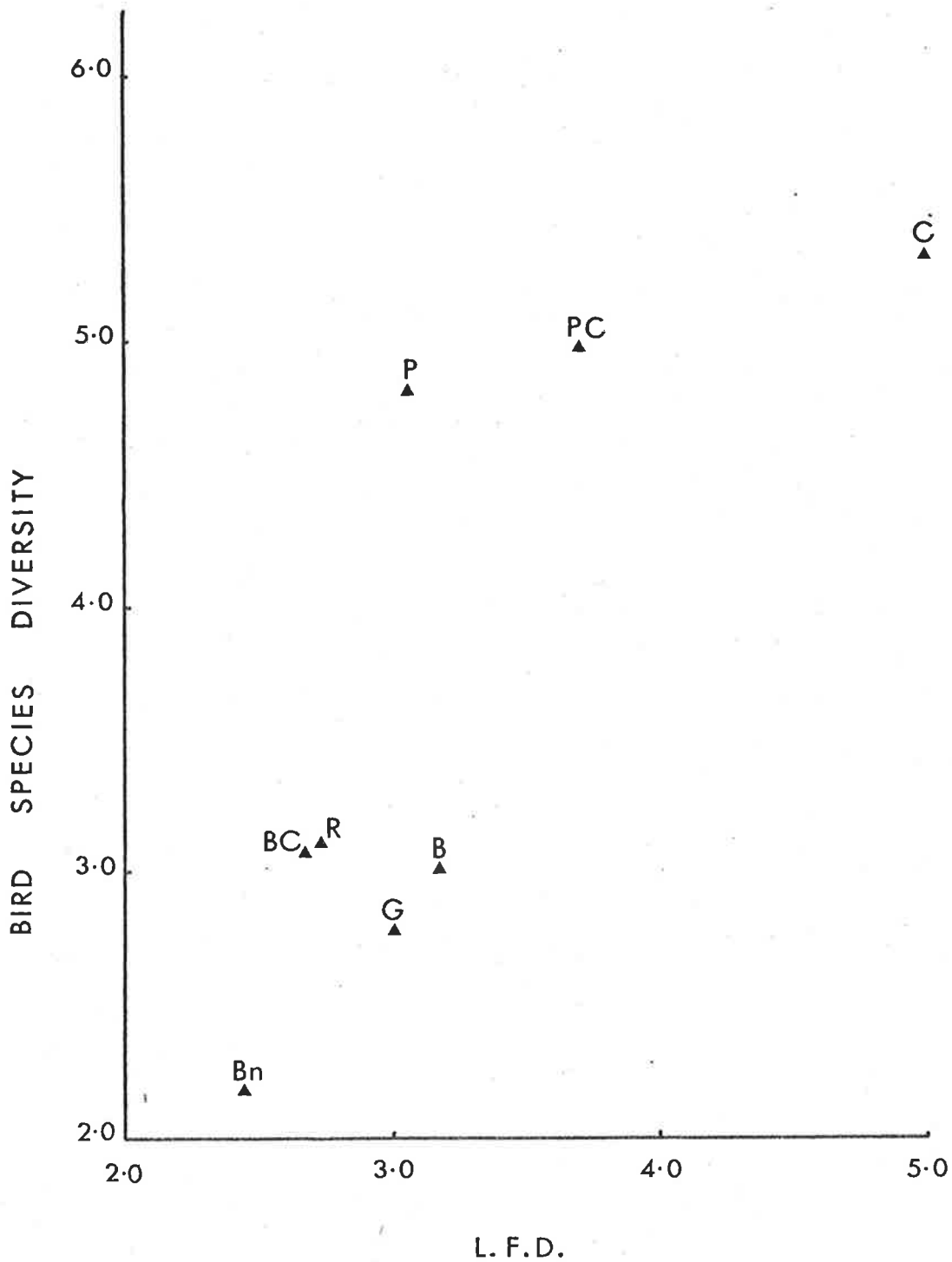
Life form diversity (L.F.D.) graphed against the four transect
bird community characteristics:

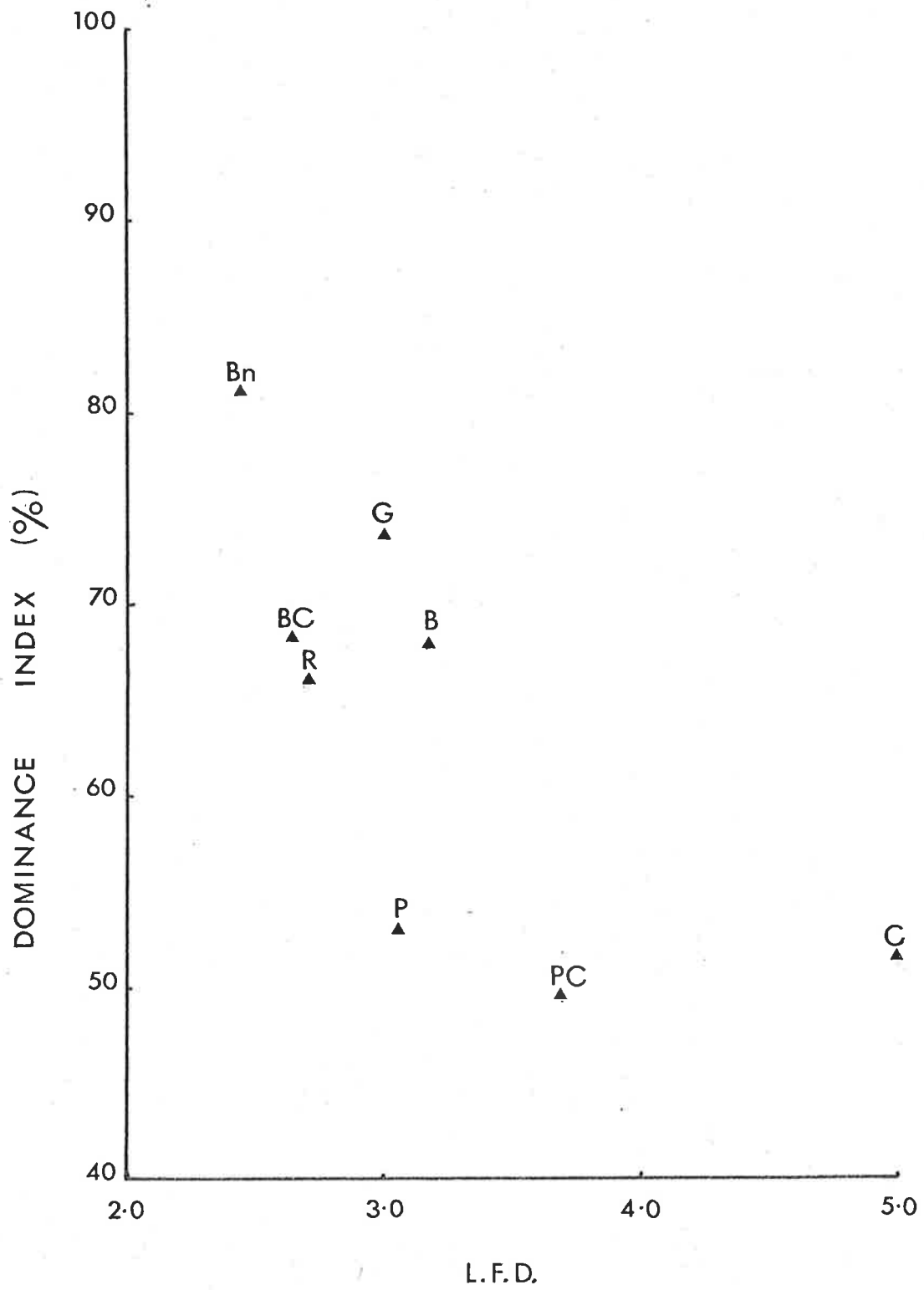
- a - Number of species
- b - Bird species diversity
- c - Dominance index
- d - Number of individuals

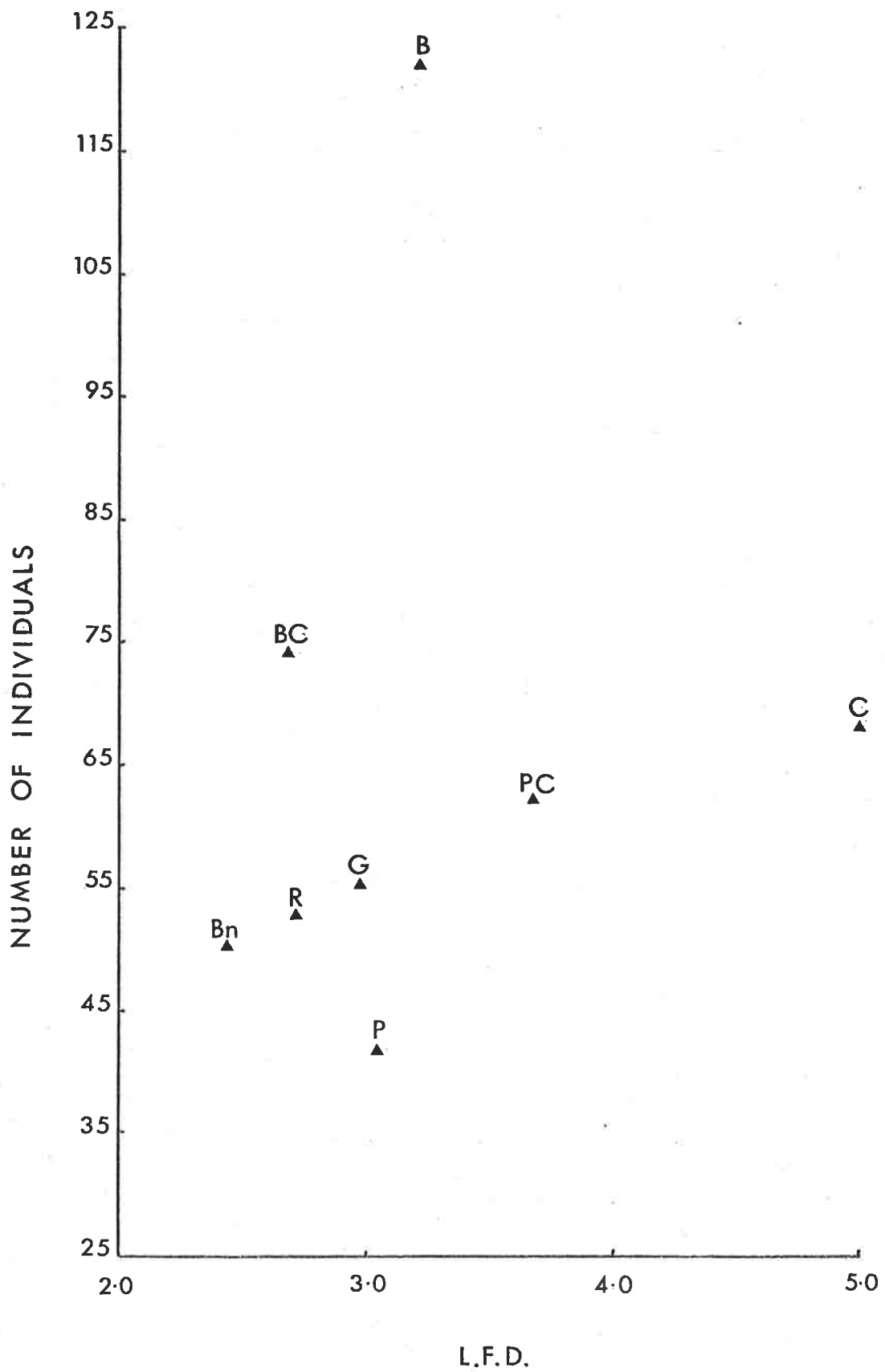
KEY

B	-	Base	G	-	Gully
Bn	-	Basin	P	-	Plain
BC	-	Basin Creek	PC	-	Plain Creek
C	-	Creek	R	-	Ridge









in comparison to the other biogeocoenoses. Both of these units have large numbers of White-plumed Honeyeaters (66 in Base, 41 in Basin Creek, in comparison to 25 in Plain Creek with the next highest number; Appendix 3). Thus, it would appear that life form diversity cannot adequately predict the total number of individuals if over half of the individuals are White-plumed Honeyeaters. It should be noted that this effect is restricted only to White-plumed Honeyeaters, since other biogeocoenoses also have high proportions of their total abundances accounted for by a single species. For instance, 62% of the Basin's total individual count is Grey-headed Honeyeaters.

There is a significant negative correlation between the total number of individuals in a biogeocoenose and the MacArthur's foliage height diversity index (Table 11). As mentioned in the previous chapter (section II. 3 [ii], p.39), those biogeocoenoses with the highest total foliage cover have the lowest foliage height diversity values. Therefore, it is not surprising that the total number of individuals is also highly correlated with the total foliage cover ($r_s = 0.81$, $N = 8$, $p < 0.05$). Since foliage height diversity is not significantly correlated with the other bird community characteristics, its significant correlation with the total number of individuals could be due to the fact that it is an indirect measure of total foliage cover.

3. Bird Species Composition

The similarity of the biogeocoenoses with respect to bird species composition was measured by the Motyka index of similarity (see section II.3 [i], p.31). Similarity matrices for both the mist net and transect data were constructed and these are presented in Tables 12 and 13. The mist net index values have a much lower range (21% to 67%) than do the transect values (9% to 84%). As demonstrated in the previous section of

this chapter, the total numbers of bird species and individuals captured were lower than those contacted, thereby restricting the range of variation in the mist net index values.

There are some consistencies in both matrices. The biogeocoenose most similar to the other units, as demonstrated by the largest sum of the index values (Tables 12, 13), is Basin Creek. The Basin is clearly the most dissimilar from the other units on the basis of the transect data, but is one of three units with low sum values on the basis of the mist net data. The Gully-Ridge comparison has high index values, while the Plain Creek-Basin comparison has low index values for both data sets. Because the mist net data suffers from obvious sampling deficiencies, as previously noted, only the transect matrix is discussed in further detail.

A list of each biogeocoenose and the biogeocoenose with which it has the highest similarity value appears as part of Table 13. These pairs of biogeocoenoses indicate that each unit, except for the Base unit, has its highest index value in comparison with a biogeocoenose which is geographically adjacent. The highest index values occur for the two pairs which make up a complex geographic mosaic, Ridge-Gully and Plain-Plain Creek. In each of these two pairs, the second biogeocoenose is completely surrounded by the first (see Plate 2). Thus, these high similarity values are no doubt due to edge effects, as reported by Beecher (1942), Dwyer (1972), Kendeigh (1944), and others. The next highest value occurs for the two units that are connected by the same drainage course, Basin Creek-Creek. Of the Basin, Ridge, and Gully units, the Basin unit is not only completely surrounded by the Ridge/Gully complex, but the Basin and Ridge units are similar in vegetation physiognomy (see section II. 3 [ii] and plant species composition (Table 5, p.33). The one exception to this general pattern, the Base unit, has its highest similarity value with the Basin Creek. This high value is due to the fact that both units have large

TABLE 13

Bird species similarity matrix based on transect data

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

Highest value for each biogeocoenose

Gully - Ridge	84	Plain - Plain Creek	71
Ridge - Gully	84	Plain Creek - Plain	71
Basin Creek - Creek	67	Base - Basin Creek	61
Creek - Basin Creek	67	Basin - Gully Ridge	55

relative abundances of White-plumed Honeyeaters (see Appendix 3).

A test of the uniqueness and consistency of the bird species composition of each biogeocoenose 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 weighted scores on a series of variables. The technique establishes a set of linear equations, termed functions, of the general form

$$D = d_1 Z_1 + d_2 Z_2 + \dots + d_n Z_n ,$$

where Z_1 to Z_n are standardized scores on n variables and d_1 to d_n are their respective weighting coefficients (Klecka 1975). The coefficients are derived to maximize the separation of the classes' respective D values. The differences among the D values of members of the classes can be subjected to tests of significance (Cooley and Lohnes 1971; Sokal and Rohlf 1969). If there are three or more classes, multiple functions are often needed to differentiate all the classes from each other. The functions established with the initial data can be used to predict the class membership of an unclassified set of variable scores. Each initial set of scores can also be reclassified, being assigned to that class whose predicted D values most clearly match its own. The number of misclassifications between the original and this second classification is a good index of how well the variables and their weighting coefficients actually discriminate among the classes (Cooley and Lohnes 1971; Klecka 1975).

By using a step-wise procedure in the discriminant function analysis, those variables (or species) which differ most among the classes (or biogeocoenoses) are identified. These species have the most discriminating power and are given the largest weighting coefficients in the discriminant functions. Thus, the biogeocoenoses may be discriminated 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 biogeocoenoses to show their positions with respect to axes which represent the discriminant functions. This use of discriminant function analysis is very similar to the differential species approach developed by Braun-Blanquet (1965) for establishing plant communities.

In the present study, two discriminant function analyses were performed, one for the mist net data and one for the transect data. The University of Adelaide Computing Centre's *S.P.S.S.* version 7.00, subprogram *Discriminant*, was used for the analyses with variables corresponding to the bird species caught or contacted and the score on each variable being the number of captures or contacts for a particular species. The classes corresponded to the eight biogeocoenoses.

For the mist net data analysis, each set of variable scores was the captures from an individual mist net site. The variables could not discriminate among the eight biogeocoenoses, for only 53% of the original mist net sites were accurately reclassified. (A summary table of the results of this analysis is presented in Appendix 4). These results indicate that there is considerable variation in the composition of captures from one mist net site to another within a given biogeocoenose.

For the transect data analysis, the variable scores for a biogeocoenose were the number of contacts per species over the entire transect segment in a given transect sampling period. Thus, each biogeocoenose was represented by six sets of variable scores with each set representing a sample of the entire bird community of a biogeocoenose. The results of this analysis indicate considerable consistency in the bird species

composition of the biogeocoenoses. As shown in Table 14, there were four significant discriminant functions. Using these four functions, only one of the 48 cases was misclassified. Figure 6 is a graph of the positions of these cases with respect to axes representing the two discriminant functions with the most discriminating power. In this figure, Plain Creek, Basin Creek, Base, Creek, and Plain, are clearly discriminated from each other. The three remaining biogeocoenoses, 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. The results of the step-wise procedure, shown in Table 15, indicate which species have overall discriminating power. These species do not show any marked variation in abundance among the Gully, Ridge, and Basin units (see Appendix 3).

These results indicate that there is an hierarchical organization of the biogeocoenoses according to their bird species composition. The first level of this hierarchy consists of six groups, five separate biogeocoenoses and a composite group of three biogeocoenoses. These groups are differentiated on the basis of the abundances of a few species. The second level consists of the three separate biogeocoenoses of the composite group. They are differentiated on the basis of several species (e.g. White-browed Babbler, Mistletoebird, Port Lincoln Parrot) which contribute very little to the discrimination of the first-level groups (see Appendix 5).

The grouping of Basin and Ridge together at the first level of this hierarchy may be explained by their similarity in life form diversity (Table 7, p.37) and plant species composition (Table 5, p.33). They also have high Motyka index values for bird species composition (Table 13, p.59). The Gully has only moderate plant species similarity with the Ridge

TABLE 14

Discriminating power of the functions for the transect data discriminant function analysis.

Function removed	Eigenvalue	Canonical Correlation	Wilks Lambda	Significance χ^2
0	96.69	0.995	0.000	0.000
1	58.89	0.992	0.000	0.000
2	11.78	0.960	0.001	0.000
3	7.05	0.936	0.007	0.035
4	3.62	0.885	0.059	0.492

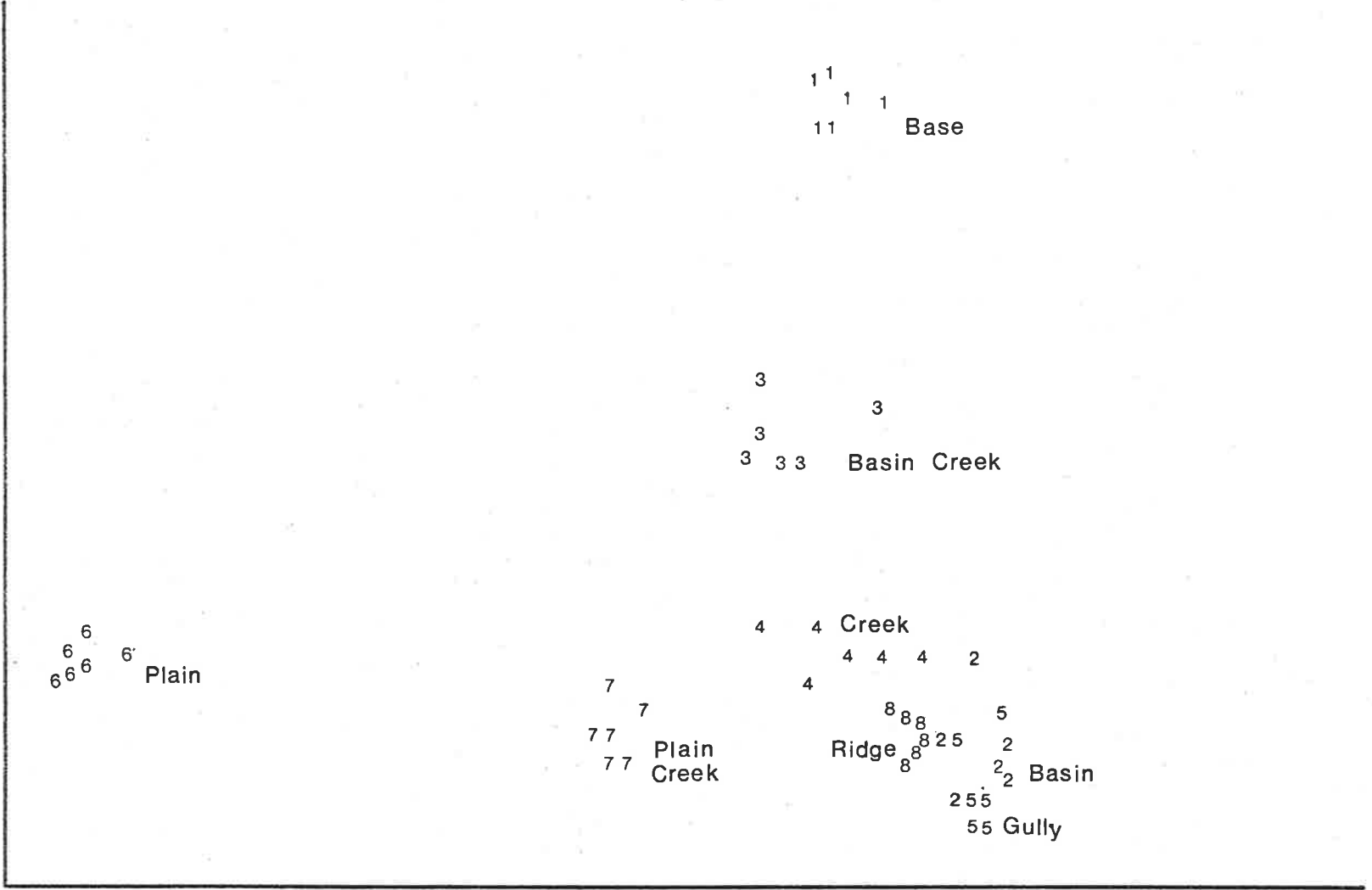
FIGURE 6

Plot of the positions of the 48 transect cases against the first two discriminant functions.

KEY

- | | |
|-----------------|-----------------|
| 1 - Base | 5 - Gully |
| 2 - Basin | 6 - Plain |
| 3 - Basin Creek | 7 - Plain Creek |
| 4 - Creek | 8 - Ridge |

DISCRIMINANT FUNCTION 2



DISCRIMINANT FUNCTION 1

TABLE 15

List of bird species
as entered on the step-wise discriminant function analysis

Bird Species	F value
* White-plumed Honeyeater	29.02
* Australian Magpie	11.41
* Yellow-rumped Thornbill	5.31
* Zebra Finch	5.51
Chestnut-rumped Thornbill	4.70
Crested Pigeon	3.91
Mistletoebird	2.77
Port Lincoln Parrot	2.66
Western Bowerbird	4.03
Red-capped Robin	3.07
* Red-backed Kingfisher	2.35
Welcome Swallow	2.99

* Species most important in the first two discriminant functions as determined by their standardized coefficients presented in Appendix 6.

(Table 5) and very low similarity with the Basin unit. It also has a higher life form diversity than either the Ridge or Basin unit. However, the previously discussed influence of edge effects 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 Figure 6, and the Motyka bird species similarity matrix (Table 13). The nearest neighbor of each unit in Figure 6 corresponds to that unit with the highest Motyka similarity value (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 discriminating species of the discriminant functions are good indices of the overall bird species composition of the biogeocoenoses.

4. Feeding Profiles and Spectra

Following and modifying the work of Balda (1969, 1975), Cody (1974, 1975), Dow (1977), Pearson (1977), Salt (1953), Tomoff (1974), and Willson (1974), among others; an investigation of feeding behavior was made in each biogeocoenose. Feeding profiles, represented as the relative frequency of feeding observations in each 1 m height interval, and feeding spectra, represented as the relative frequency of observations in each of several feeding positions, were constructed for each biogeocoenose. Feeding positions were either ground, trunk, branches, foliage, flowers/fruits, or air. Figure 7 is a graph of the feeding profiles and spectra plotted against

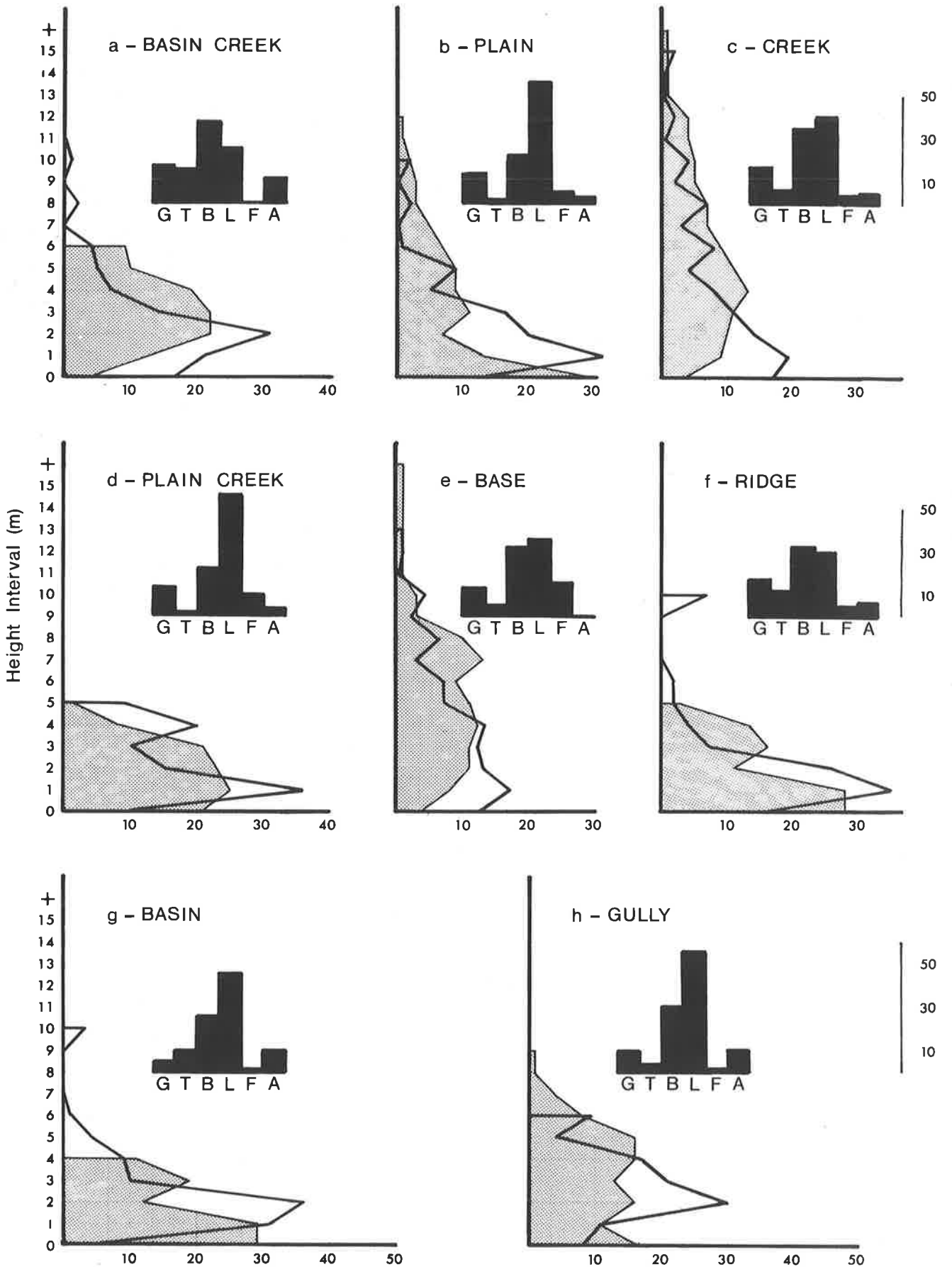
FIGURE 7

Feeding profiles and spectra represented by relative frequencies per height interval/feeding position category, as plotted against relative foliage cover per height interval.

Feeding Categories

G	-	ground
T	-	trunk
B	-	branches
L	-	foliage
F	-	flower/fruit
A	-	air

Note: Shaded area represents foliage cover profile; heavy line represents feeding profile.



the biogeocoenose foliage cover profiles, represented as relative foliage cover in each height interval.

There is only general correspondence between the feeding profiles and foliage cover profiles. In most cases the feeding proportion in the lower height intervals exceeds the foliage cover proportions. In the upper height intervals, the reverse is true. In three biogeocoenoses, Base, Creek, and Basin Creek, the feeding proportion at ground level is greater than would be expected on the basis of foliage cover. The amount of litter cover apparently has no influence on this result because litter cover was observed to be high only in the Base unit. The relative percentage of ground feeding is fairly constant in the eight biogeocoenoses at around 15%, despite the variation in amount of ground cover. However, the species which most often feed on the ground vary among the biogeocoenoses. For instance, in the Plain and Plain Creek most ground-feeding observations were of Variegated Wrens, Yellow-rumped Thornbills, and Zebra Finches. In the Ridge, Basin, and Basin Creek most observations were of Dusky Grasswrens, White-browed Babblers, and Variegated Wrens. Since these species have marked taxonomic and morphologic differences, it is likely that they utilize different food resources found on the ground (e.g. Hespenheide 1971, 1975). Zebra Finches are predominantly seed eaters (Frauca, 1971; Cayley 1968), whereas the thornbills, wrens, and babblers eat various kinds of insects (see Matthiessen 1973; McGill 1970; Rose 1973).

There is also little correspondence between the vertical extent of the foliage cover profile and the feeding profile. In several cases, Basin Creek (Fig. 7a), Ridge (Fig. 7f), and Basin (Fig. 7g), the feeding profile extends beyond the height of the foliage cover profile due to aerial feeders which feed above the shrub layers in these biogeocoenoses. As shown by the feeding spectra, the proportion of aerial feeders tends

to be highest in those units without a tree layer. The full extent of the foliage cover profile is utilized in all units except the Gully, where the very tallest shrubs and trees are not used. This discrepancy can be related to the distribution of White-plumed Honeyeaters. This species accounted for nearly all observations in the tree layers of the Base and Creek, while it and the Singing Honeyeater accounted for nearly all observations in the tree layer of the Plain. Both these species were rare in the Gully (see Appendix 4).

There is little consistency between the feeding spectra and either the vegetation parameters or bird species composition of the biogeocoenoses. The feeding spectra were characterized by Simpson's reciprocal diversity index (section II.3 [i], p.34) on the basis of the relative frequency of each feeding position category. The index values, listed in Table 16, are not significantly correlated with either life form diversity ($r_s = 0.40$, $N = 8$, $p > 0.05$) or the MacArthur's foliage height diversity ($r_s = 0.33$, $N = 8$, $p > 0.05$).

The degree of similarity of feeding spectra between pairs of biogeocoenoses is not related to the degree of similarity of their bird species compositions. The two units with the highest bird species similarity, Ridge and Gully, do not have similar feeding spectra, indicating that the same species have different feeding behaviors in these two units. Birds are most often foliage gleaners in the Gully, but in the Ridge they are mostly branch and trunk feeders. On the other hand, the Plain and Plain Creek units have high bird species similarity and almost identical feeding spectra. 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. It should also be noted that neither life form diversity nor plant species composition can explain these results, for the Ridge-Gully pair has greater similarity on these two

TABLE 16

Feeding spectra diversity values for the biogeocoenoses

Plain	Gully	P1 Ck	Creek	Basin	Base	Bn Ck	Ridge
2.56	2.64	3.15	3.27	3.36	3.92	4.03	4.28

measures than does the Plain-Plain Creek pair. Thus, it would seem that the bird species present in the Plain and Plain Creek are more specific in their feeding behaviors, than are those species present in the Ridge and Gully.

The inconsistencies between bird species similarity and feeding spectra similarity can be partly explained by the distribution and feeding patterns of the two most abundant species, Grey-headed and White-plumed Honeyeaters. These two species together account for over 50% of the total transect counts (see Appendix 3) and for 40% of the total feeding observations. Thus, these two species greatly affect both bird species similarity and feeding spectra. As illustrated in Figure 8, the two species have complimentary abundance distributions. Only one unit, 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 biogeocoenses (Table 13, p.59). The two species are congeneric (*Lichenostomus*) and are similar in morphology and apparent social organizations, as indicated by field observations made during this study. As shown in Table 17, the two species have similar feeding spectra. They are both predominantly foliage and branch gleaners, although their actual food appears to be very different. Grey-headed Honeyeaters eat predominantly small ants which are found on the trunks, branches, and foliage of the shrubs in the Basin Creek, Basin, Ridge, and Gully units. White-plumed Honeyeaters eat the same ant species found on *Melaleuca glomerata* shrubs in the Basin Creek but they also eat leaf scale insects (Coccina, Homoptera) found on the eucalypts of the Basin Creek, Creek, and Base units. White-plumed Honeyeaters eat more nectar and fruits than Grey-headed Honeyeaters, which reflects differences in the availability of these foods within the different biogeocoenoses. It should be noted that the proportion of flower-feeding to insect-feeding and the proportions of the various

FIGURE 8

Transect abundance distributions of Grey-headed and White-plumed
Honeyeaters.

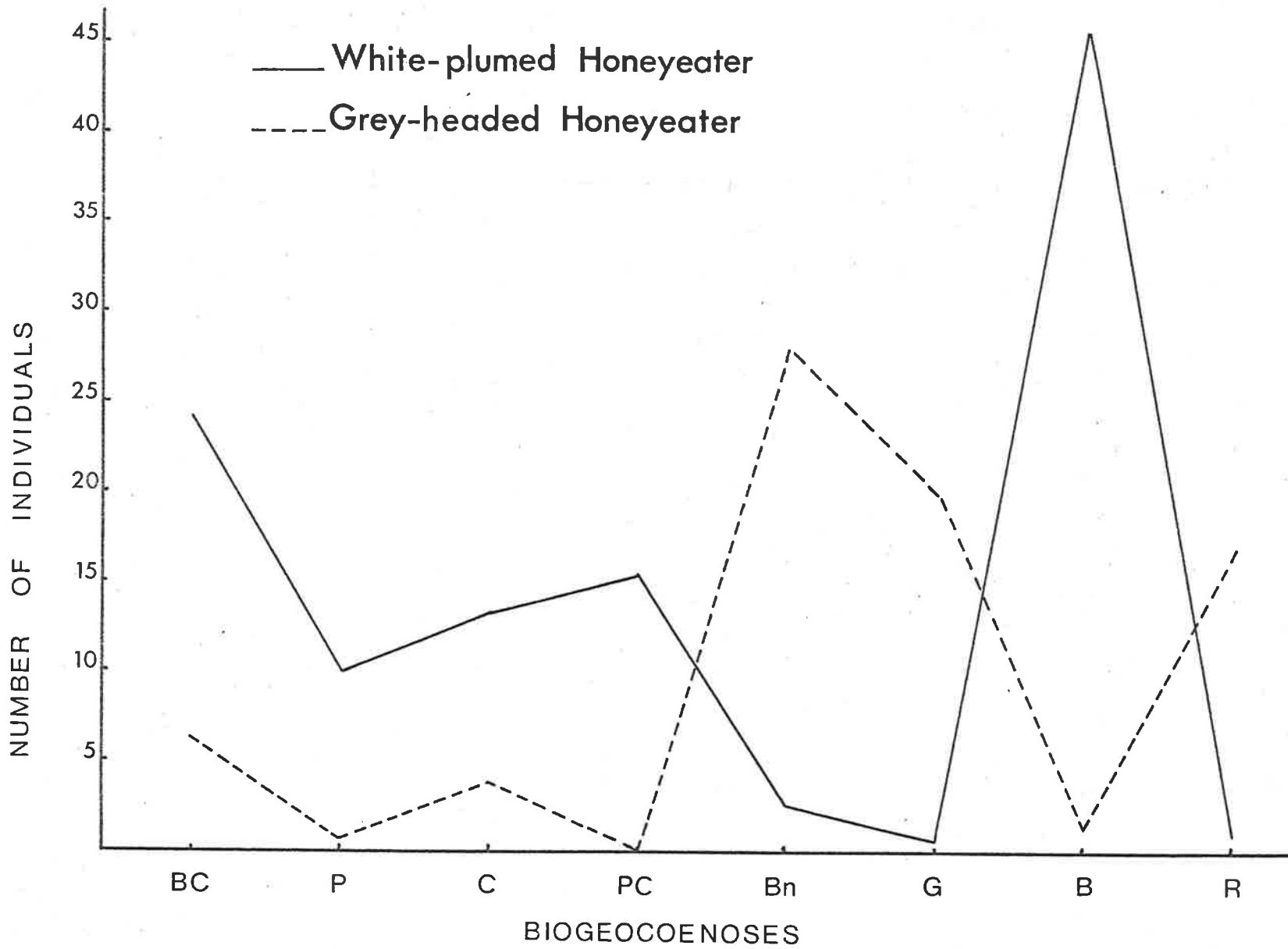


TABLE 17

Feeding spectra of Grey-headed Honeyeater and
White-plumed Honeyeater

Percentage Observations							
	Ground	Trunk	Branch	Foliage	Flower/ Fruit	Air	Total Number
Grey-headed Honeyeater	-	17	25	46	-	12	126
White-plumed Honeyeater	-	3	14	52	23	8	289

feeding positions found for White-plumed Honeyeaters in this study are very similar to those reported by Ford and Paton (1977). It is possible that two biogeocoenoses, one with a high proportion of White-plumed Honeyeaters (e.g. Plain Creek) and the other with a high proportion of Grey-headed Honeyeaters (e.g. Gully), can have low bird species similarity (17%; Table 13, p.59) but similar feeding spectra (Fig. 7d, 7h). Thus, there appears to be only a limited relation between both feeding profiles and spectra and the biogeocoenose foliage cover profiles, vegetation parameters, or bird species compositions.

IV. DISCUSSION AND CONCLUSIONS

Raitt and Maze (1968) recognized the unique vegetation and avian characteristics of mountain canyons in the North American southwest deserts by referring to them as 'desert-riparian communities'. One of the distinctive features of these communities is the presence of trees or arborescent shrubs. Of the eight biogeocoenoses included in the present study, five are situated along drainage courses or have extensive run-on moisture, but only three of these, Gully, Creek, and Base, have a tree layer. Of the biogeocoenoses not situated along drainage courses or not having extensive run-on moisture, the Plain has a tree layer. Thus, in the present study, there is no clear relationship between riparian landform type and the presence of a tree layer. However, there does appear to be a relationship between riparian landform type and the diversity of plant life forms. Those biogeocoenoses with the highest life form diversity values are the riparian types, Creek, Plain Creek, Base, and Gully. An exception is the Basin Creek, a riparian type with low life form diversity due to a very dense cover of the shrub *Melaleuca glomerata*. The Creek, Base, Basin Creek, and Gully also have the highest total foliage cover of the eight biogeocoenoses. Thus, it seems more appropriate to characterize the riparian biogeocoenoses in this study by their high life form diversity and total foliage cover rather than by the presence of trees.

The study has demonstrated that each of the eight biogeocoenoses supports a bird community with distinctive characteristics, which are related to vegetation physiognomy, particularly life form diversity. Life form diversity successfully predicted the total number of individuals, species number, bird species diversity, and dominance index in almost all cases. It failed to predict the total number of individuals for those

biogeocoenoses, Base and Basin Creek, in which White-plumed Honeyeaters accounted for over half the total number. The abundance of this species appears to be influenced by the amount of shrub cover, for these two units have the highest shrub cover of all the units (Fig. 4, p.24). Other factors which may influence the abundance of White-plumed Honeyeaters is the ready supply of food in these two units, ants in the Basin Creek and flowering mistletoes (*Amyema maideni*) and leaf scale insects in the Base.

In contrast to the success of the life form diversity index for predicting bird community characteristics, the MacArthur's foliage height diversity index was significantly correlated with only the total number of individuals. As life form diversity was highly correlated with plant species diversity, these results appear to contradict those studies 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 and MacArthur 1961; Pianka and Huey 1971; Recher 1969, 1971). However, at least two other arid area studies (Carothers, Johnson and Aitchison 1974; Tomoff 1974) did not find a significant relation between bird species diversity and foliage height diversity. In addition, foliage height diversity apparently underestimates bird species diversity in tropical forests (Karr 1971; Karr and Roth 1971). Similar to the findings of the present study, Tomoff (1974) also reported a strong correlation between breeding 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 determining bird species diversity and other bird community characteristics. These indices are measures of vegetation physiognomic characteristics. Foliage height diversity is a function exclusively of the vertical spacing and abundance of foliage cover. 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 spacing. Thus, life form diversity is a composite measure of the characteristics which together determine vegetation physiognomy (see section I.1, pp.4-5). 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 woodlands 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 the life form diversity index used in the present study, was not significantly correlated with bird species diversity. However, he used a limited sample of four vegetation types, and also recognized 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. A few other studies (Krebs 1972; MacArthur and MacArthur 1961; Pianka and Huey 1971) have investigated the relationship between plant species diversity and bird species diversity. They found significant correlations between these two measures but not as strong as between foliage height diversity and bird species diversity. Unfortunately, it is not known what the relation between plant species diversity and life form diversity was in these studies. Thus, there is enough data reported for a variety of vegetation types to indicate that physiognomic features are generally the most important in explaining 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 in discussing its results is the size of the area covered by the present study. This study was conducted within a very localized area and the vegetation units were determined by associations. In contrast, many other studies have been conducted at a much larger scale, covering entire states (MacArthur 1964), continents (MacArthur and MacArthur 1961), or hemispheres (Pianka and Huey 1971). An index of foliage cover spacing may produce accurate predictions of bird species diversity when working with regions. However, the results of the present study indicate that differences exist among the bird communities of biogeocoenose associations within a limited geographic area, and that vegetation parameters such as life form diversity are needed to predict these differences.

Finally, Carothers *et al.* (1974) have suggested that foliage height diversity can predict bird species diversity only when the birds feed exclusively within the sampled area. As most studies previously cited used the spot-map technique to sample birds, only the territory-holders of the

bird community were included in the analyses. The usual assumption made about territories is that their holders feed exclusively within them (see Welty 1962). In the present study and in Carothers *et al.* (1974), the birds were not limited exclusively to any particular sample unit. Several of the banded birds in the present study were found to travel the entire length of the Victory Creek study site, but most were restricted to one biogeocoenose or its neighbor. Foliage height diversity is possibly a good indicator of the bird species diversity that can be maintained exclusively within a sample site. However, as noted previously (section III.1, p.41), many arid area bird species do not hold exclusive territories and thus it is difficult to determine what size area is necessary to support an individual bird. Also, Tomoff's (1974) study, which sampled breeding birds and territory-holders within 10 ha plots, suggests that foliage height diversity may not accurately predict bird species diversity even when applied only to territory-holders.

The results of the present study indicate that the number of equally important vegetation layers, as defined by either MacArthur's or Austin's layers, does not influence the number of bird species, bird species diversity, or the dominance characteristic of the bird community which utilizes a biogeocoenose vegetation association. For example, an association with three vegetation layers (Base) did not support more bird species than one with two layers (Plain Creek). But as the addition of vegetation layers often means an increase in foliage cover (see also Karr 1968; Karr and Roth 1971; Willson 1974), the biogeocoenoses with the larger number of equally important vegetation layers (i.e. the lowest foliage height diversity values) have the larger number of bird individuals. In contrast, the number of bird species using a biogeocoenose increases only if the additional foliage cover represents an addition in life form diversity. Therefore, the number of individuals is not necessarily increased

through the addition of more bird species, as has been reported in several studies (e.g. Cody 1975; Udvardy 1957). This lack of correspondence between total number of individuals and number of species has also been reported in several arid studies (Austin 1971; Raitt and Maze 1968). Karr's data (1971; Table 2) on tropical and temperate vegetation types indicates that there is a relation only if resident and regular species are included. These considerations again emphasize that principles arising from extensive work in one vegetation type, e.g. temperate deciduous forests, do not necessarily apply to other vegetation types, e.g. arid woodland or scrub.

The non-linear relationship between life form diversity and bird species diversity found in this study has been reported for other vegetation measures, especially the total percent foliage cover (Cody 1975; Karr 1968; Karr and Roth 1971; Willson 1974). Willson (1974) found that the amount of canopy cover in the tree layer did not necessarily influence the number of species. Only the presence of a tree layer was important. Thus, the Creek unit of the present study would not necessarily have higher community characteristic values than the other units with a tree layer. The Creek's community characteristic values also indicate that a saturation level of bird species has been reached. This could be due to the generally impoverished species pool available in the Australian arid zone. Keast (1959b) 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 (Fig. 5a, d; pp.52,55).

Although vegetation physiognomy successfully predicted the bird community characteristics, geographic proximity appeared to be the main factor affecting the similarity of bird species composition in the

biogeocoenoses, 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, such as the Ridge-Gully and Plain-Plain Creek units. Usually, such mosaics are treated as a single sampling unit or are avoided (e.g. Raitt and Maze 1968). If a mosaic is treated as a single unit, the bird species diversity is often higher than expected from general vegetation characteristics (Dwyer 1972; Karr 1968). However, this study has shown that each component unit of the mosaics sampled has distinctive bird community characteristics. The smaller, but physiognomically more diverse units (i.e. Gully and Plain Creek), have larger numbers of individuals and species, higher bird species diversities, and lower dominance values than their associated units (i.e. Ridge and Plain). The Ridge and Gully units also have very different feeding spectra, indicating a marked change in the feeding behavior of the same bird species. Therefore steps should be taken to either explicitly include or exclude small but physiognomically diverse vegetation units from a sample (see also Dwyer 1972).

Similarity in bird species composition is only secondarily affected by similarity in vegetation physiognomy. The Basin, Ridge, and Gully form one composite group, as indicated by the transect discriminant function analysis. They constitute a distinct geographic entity with similar vegetation physiognomy. Other biogeocoenoses with similar vegetation characteristics are geographically separate and their bird species similarity is relatively low (e.g. Base and Creek). Geographic proximity was very important in this study because the biogeocoenose areas were often not large enough to support a given bird individual. Sightings of banded birds and recaptures indicated that individuals often flew into adjacent biogeocoenoses. However, other studies conducted at a much larger scale have also

failed to find any relationship between similarity of vegetation physiognomy and similarity of bird species composition (Carothers *et al.* 1974; MacArthur, MacArthur and Preer 1962; Willson 1974).

The non-correspondence between the foliage and feeding profiles found in this study is supported by other arid area bird studies which show that the utilization of some dominant plant species is not in proportion to their abundances (e.g. Austin 1970; Balda 1975; Tomoff 1974). Clearly, not all plant species offer food resources in proportion to their foliage cover. However, there appears to be a contradiction between this conclusion and the finding that the amount of total foliage cover is significantly correlated with the total number of individuals. This apparent contradiction is resolved when it is recalled that food is not the only important resource which the vegetation offers, and indeed in arid environments food resources may actually be a secondary consideration in comparison to other resources such as shelter from predators and climatic conditions (see Noy-Meir 1974). Predation pressures on arid bird populations may be very high. During the course of this study six bird species (*Accipiter cirrhocephalus*, *A. fasciatus*, *Falco berigora*, *F. longipennis*, *Corvus bennetti*, *Cracticus nigrogularis*) and one mammal (*Felis catus*) were observed to prey upon other birds, particularly honey-eaters. Thus, although foliage cover is an indirect and sometimes a poor index of the food resources available to birds, it is a direct index of shelter. The significant correspondence between number of bird individuals and foliage cover may thus be a function of availability of shelter rather than food resources.

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 spectra diversity. The very general

feeding categories used in this study give no indication of the actual variety and abundance of the food resources being used in each category. In the present study the unit with the highest feeding spectra diversity, the Ridge, has a general paucity of food supplies, forcing birds to be generalists, taking food wherever it can be found. The same bird species which occur in the Ridge have very different feeding strategies in the Gully unit. Insufficient data exists to determine if number of bird species is related to the variety of food sources within the general feeding categories, and if this variety is directly related to life form diversity.

The eight biogeocoenoses recognized within the Everard Ranges represent a more complex pattern than has been investigated in other arid area bird studies because these studies have been conducted in topographically simple areas. The results of the present study, plus those presented by Hensley (1954), indicate that topographically complex areas, such as occur in arid mountain ranges, support a variety of biogeocoenoses, each with a distinctive bird community. The bird community characteristics are influenced primarily by vegetation physiognomy, in particular life form diversity. This influence does not appear to be directly linked to the variety of feeding strategies supported by a biogeocoenose. The bird species composition of each biogeocoenose is a function not only of the community characteristics but also the bird species composition of adjacent biogeocoenoses as well as the total bird species pool available to the localized geographic area within the Australian arid zone. The primary influence of neighboring biogeocoenoses in determining bird species composition is to be expected because of the lack of sharp boundaries between the biogeocoenoses and the fact that the biogeocoenose areas are not large enough to exclusively support many of the bird individuals.

This study has demonstrated that biogeocoenoses, as determined by vegetation associations, can be successfully used as a framework for investigating the biological complexity of an arid mountain range. The vegetation formation, which has been widely employed in bird studies, would not have adequately differentiated this complex area. Due to the critical importance of moisture availability, changes in topography may have more accentuated effects upon the vegetation pattern in arid mountain ranges than in temperate ranges (Tadmor *et al.* 1962). Changes in topography, and hence moisture availability, affect vegetation physiognomy. Changes in vegetation physiognomy, particularly life form diversity, affect the community characteristics of the birds which utilize the vegetation for both food and shelter.

The complex pattern of biogeocoenoses in the Everard Ranges indicates the importance of mountain ranges in maintaining the biological diversity of arid areas. This function of arid mountain ranges has long been recognized, together with their importance as refuges during climatic fluctuations (see Ford 1974; Keast 1959b, 1961). More detailed studies of these biologically complex and intriguing features of arid areas are needed to understand the nature of the interactions among the landform, vegetation, and animal components of their biogeocoenoses.

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APPENDIX 1

A. PHYSICAL FEATURES

QUADRAT NO.:

DATE:

LOCATION:

S.T.:

SHAPE:

BY:

SLOPE: Up:

ASPECT: (dwn.)

Down:

ELEVATION:

Mean:

SOIL

Grd. C. BRock:

Bare Soil:

Surface Stoniness:

Cover:

Litter Cover:

Depth 0₁ :

Composition:

0₂ :

Animal Evidence:

Parent Material:

WATER BODIES: size & depth

WATER WAYS & EROSION:

DESCRIPTION & SKETCH:

B. GENERAL VEGETATION

QUADRAT NO.:

DATE:

LOCATION:

S.T.:

SHAPE:

BY:

FORMATION CATEGORY:

Tallest Stratum:

Dominant spp.:

Cover density:

PER CENT COVER PER HEIGHT:

1m:

5m:

2m:

6m:

3m:

7m:

4m:

8m:

TOTAL GROUND (0-50 cm) COVER:

seg.	CC	Dsp.	Seg.	CC	Dsp.
1			5		
2			6		
3			7		
4			8		

GENERAL REMARKS:

C. INDIVIDUAL PLANTS

LOCATION:

DATE:

QUADRAT NO.:

SITE TYPE:

Size, shape:

TREES (>8m)

Seg.	Species	DBH	BD	CD1	CD2	U<	C<	P<	PD	Dat	Phen.	Remarks

SHRUBS (2 - 5m)

Seg #	Species	CD1	CD2	Hgt.	LCn.	CnH.	Phen.	Remarks

HERBS (<2m)

Seg #	Species	# Ind.	Cover	Hgt.	Phen.	Remarks

APPENDIX 2

A. Daubenmire cover-class scale

6	95 - 100%
5	75 - 95
4	50 - 75
3	25 - 50
2	5 - 25
1	0 - 5

B. Braun-Blanquet cover-abundance scale

5	>75%
4	50 - 75
3	25 - 50
2	5 - 25
1	numerous, <5
+	few, <5
r	solitary

C. Phenology categories (after Mueller-Dombois and Ellenberg 1974)

s	seedling	fr	fruiting
st	sterile	sp	sprouting
b	budding	w	withering
fl	flowering	d	dead, aerial shoots dried

D. Stoniness categories (U.S.D.A. 1951)

Gravel		Cover	
Fine	<5 mm	Slightly	<7%
Medium	5 - 10 mm	Stony	7 - 30
Coarse	10 - 20 mm	Very	>30
Stones			
small	2 - 5 cm		
medium	5 - 10 cm		
large	10 - 20 cm		
Boulders	>20 cm		

APPENDIX 3

A complete bird species list with mist net and transect abundance values for each biogeocoenose.

Nomenclature follows Condon (1975) and Schodde (1975).

Species Name		Bn Ck	Plain	Creek	P1 Ck	Basin	Gully	Base	Ridge	Total
White-plumed Honeyeater	*	58.0	25.8	32.0	86.7	32.5	3.6	62.3	7.9	357
<i>Lichenostomus penicillatus</i>	**	39.8	16.3	21.7	25.6	3.6	0.3	65.0	1.5	
Grey-headed Honeyeater		32.0	6.7	2.0	3.3	115.0	20.0	0	13.6	226
<i>Lichenostomus keartlandi</i>		10.0	0.7	5.4	0	45.8	29.7	1.0	27.6	
Singing Honeyeater		0	2.5	3.3	41.7	2.5	6.4	2.3	1.4	46
<i>Lichenostomus virescens</i>		0	5.3	0.2	5.6	0	0	1.0	0	
Zebra Finch		2.0	2.5	13.3	31.2	0.8	0	0	0.7	46
<i>Poephila guttata</i>		3.6	5.0	1.3	7.8	0.3	0.7	4.7	1.9	
Grey Shrike-thrush		4.0	0	4.0	8.3	0.8	5.5	7.7	2.1	35
<i>Colluricincla harmonica</i>		2.9	0.7	5.4	0.6	1.7	4.3	3.3	4.8	
Spiny-cheeked Honeyeater		2.0	0.8	1.3	6.7	4.2	1.8	10.0	0.7	30
<i>Acanthagenys rufogularis</i>		2.1	4.0	1.9	5.6	0.8	2.3	11.3	1.9	
White-browed Babbler		9.0	0	1.3	6.7	0	0	5.4	0.7	25
<i>Pomatostomus superciliosus</i>		4.8	0	3.3	0	0.8	2.7	3.0	0.9	
Yellow-rumped Thornbill		0	8.3	1.3	15.0	0	0	0	0	21
<i>Acanthiza chrysorrhoa</i>		0	3.7	0.4	2.8	0	0	0	0	
Variegated Wren		3.0	0	0.7	0	4.2	0.9	0.8	3.6	16
<i>Malurus lamberti</i>		2.9	2.3	4.6	4.4	1.4	4.0	1.0	2.0	
Rufous Whistler		0	0.8	0.7	3.3	0.8	0	2.3	1.4	10
<i>Pachycephala rufiventris</i>		2.4	0.3	0.4	1.1	0	0.7	0.3	0.7	

* First line of each entry is the number of captures per 10 mist nets.

** Second line of each entry is the number of contacts per 10 transect stops.

Species Name	Bn Ck	Plain	Creek	Pl Ck	Basin	Gully	Base	Ridge	Total
Port Lincoln Parrot <i>Barnardius zonarius</i>	2.0 0	1.7 1.3	1.3 5.4	0 5.0	0 0	0.9 0.3	2.3 4.0	0 0.2	10
Dusky Grasswren <i>Amytornis purnelli</i>	0 0.5	0 0	0.7 0.6	0 0	2.5 2.2	0.9 2.0	0 1.0	0.7 2.2	6
Crested Bellbird <i>Oreoica gutturalis</i>	1.0 0	0 0	1.3 0	0 0	0.8 1.1	0 1.3	2.3 0.3	0 2.0	5
Spotted Bowerbird <i>Chlamydera maculata</i>	0 1.0	0 0.3	0 1.0	1.7 1.1	0 0	0 0.3	3.1 4.3	0 0.2	5
Budgerygah <i>Melopsittacus undulatus</i>	0 0	0 0	0 0.2	8.3 0	0 0	0 0	0 2.0	0 0	5
Hooded Robin <i>Melanodryas cucullata</i>	1.0 0	0.8 0	0.7 0.2	0 0	0 0	0 0	0 0	0.7 0	4
Yellow-throated Miner <i>Manorina flavigula</i>	0 0	0 0.3	2.7 0	0 0.6	0 0	0 0	0 0.3	0 0	4
Willie Wagtail <i>Rhipidura leucophrys</i>	1.0 2.6	0 1.3	0 1.5	0 1.7	0 2.2	0 0	1.5 4.0	0 0.7	3
Mistletoebird <i>Dicaeum hirundinaceum</i>	1.0 1.4	0 1.7	0 4.0	0 2.8	0 0.8	0 3.7	1.5 12.3	0 2.8	3
White-fronted Honeyeater <i>Phylidomyris albifrons</i>	0 0	0 0	0 0	1.7 0.6	1.7 0	0 0	0 0	0 0	3
Pied Butcherbird <i>Cracticus nigrogularis</i>	0 0	0.8 0.3	0 0	0 0	0 0	0 0	1.5 0	0 0	3
Red-browed Pardalote <i>Pardalotus rubricatus</i>	0 -	0 -	0 -	0 -	1.7 -	0 -	0 -	0 -	2

Species Name	Bn Ck	Plain	Creek	Pl Ck	Basin	Gully	Base	Ridge	Total
Weebill	0	0.8	0	0	0	0	0	0	1
<i>Smicrorornis brevirostris</i>	-	-	-	-	-	-	-	-	-
Red-capped Robin	0	0	0	0	0	0.9	0	0	1
<i>Petroica goodenovii</i>	0	0.3	0	0	0	0	0	0	-
Grey-fronted Honeyeater	1.0	0	0	0	0	0	0	0	1
<i>Lichenostomus plumulus</i>	-	-	-	-	-	-	-	-	-
Grey Butcherbird	0	0	0.7	0	0	0	0	0	1
<i>Cracticus torquatus</i>	-	-	-	-	-	-	-	-	-
Owlet-nightjar	0	0	0.7	0	0	0	0	0	1
<i>Aegotheles cristatus</i>	-	-	-	-	-	-	-	-	-
Diamond Dove	-	-	-	-	-	-	-	-	-
<i>Geopelia cuneata</i>	0.2	0	0	0	0.3	0	0	0.2	-
Red-backed Kingfisher	-	-	-	-	-	-	-	-	-
<i>Halcyon pyrrhopygia</i>	0	0.7	1.0	0	0	0	0	0	-
Common Bronzewing	-	-	-	-	-	-	-	-	-
<i>Phaps chalcoptera</i>	0.2	0	0.2	0	0	0	0	0	-
Broad-tailed Thornbill	-	-	-	-	-	-	-	-	-
<i>Acanthiza apicalis</i>	0.7	0	0.4	0	0	0	0	0	-
Chestnut-rumped Thornbill	-	-	-	-	-	-	-	-	-
<i>Acanthiza uropygialis</i>	0	0.3	0	3.9	0	0	0	0	-
Crested Pigeon	-	-	-	-	-	-	-	-	-
<i>Ocyphaps lophotes</i>	0	1.0	0	0	0	0	0	0	-
White-backed Swallow	-	-	-	-	-	-	-	-	-
<i>Cheramoeca leucosternum</i>	0	0.7	0	0	0	0	0	0	-

Species Name	Bn Ck	Plain	Creek	Pl Ck	Basin	Gully	Base	Ridge	Total
Welcome Swallow <i>Hirundo neoxena</i>	- 0	- 1.0	- 0	- 0	- 0	- 0	- 0	- 0	- 0
Australian Magpie <i>Gymnorhina tibicen</i>	- 0	- 3.7	- 0	- 0.6	- 0	- 0	- 0	- 0	- 0
Black-faced Cuckoo-shrike <i>Coracina novaehollandiae</i>	- 0	- 0.7	- 0.4	- 0	- 0	- 0	- 0.7	- 0	- 0
Little Woodswallow <i>Artamus minor</i>	- 0	- 0	- 0	- 0	- 0	- 1.0	- 0	- 2.6	- 0

APPENDIX 4

Summary table of results of discriminant function analysis for the mist net data.

Function Removed	Eigenvalue	Canonical Correlation	Wilks Lambda	Significance χ^2
0	2.655	0.85	0.033	0.000
1	0.959	0.70	0.120	0.067
2	0.791	0.66	0.235	0.443

APPENDIX 5

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

BIRD SPECIES	1	2	3	4	FUNCTIONS
BS1	.88621	-.50602	-.41108	-.34508	
BS2	1.83341	2.50234	.58372	.58316	
BS3	-3.89235	.76074	-1.40747	.21473	
BS4	-1.01174	-.30689	-.62309	.69426	
BS5	-1.44895	-1.09895	.43894	.50334	
BS6	-.69272	.75845	-.69359	-.12542	
BS7	.30105	-.31695	.35119	.07873	
BS8	2.68037	-1.09437	-1.59957	-1.55453	
BS10	-.19753	-2.87855	-1.72987	-1.28100	
BS11	.74133	-.27125	-.28160	-.21325	
BS12	1.46534	-.20580	-.19374	.18345	
BS13	1.01444	1.21425	.42222	-3.33370	
BS15	2.47793	1.75700	.89128	-.60293	
BS16	-1.08915	.15819	-1.39332	-.16832	
BS17	-1.61604	-.67106	.14746	.02448	
BS18	-2.89449	.26249	-1.73632	.71551	
BS19	-2.69677	6.93610	2.61645	-1.05419	
BS20	-2.72748	-2.16451	-1.46188	1.07799	
BS21	.19677	2.02225	1.88181	.02692	
BS22	-3.89181	.37670	1.55261	2.71469	
BS23	1.38124	-1.91108	-2.98694	1.17319	
BS26	-.30494	-1.95336	-3.23450	1.40812	
BS27	.57114	-.76668	-1.20338	2.08526	
BS28	-2.49998	.88211	1.18703	1.18464	
BS29	-1.27703	.30530	.13738	.74926	
BS30	1.51362	-.26862	-5.01821	.64837	
BS32	-4.53023	.12887	5.11474	-2.86649	
BS33	-1.00456	.98381	-1.86921	.76775	
BS34	-.72683	-2.10525	1.16474	.66709	
BS35	-1.00552	-.34798	-.45252	.16318	
BS36	-.29536	.05841	-.05560	-.00506	

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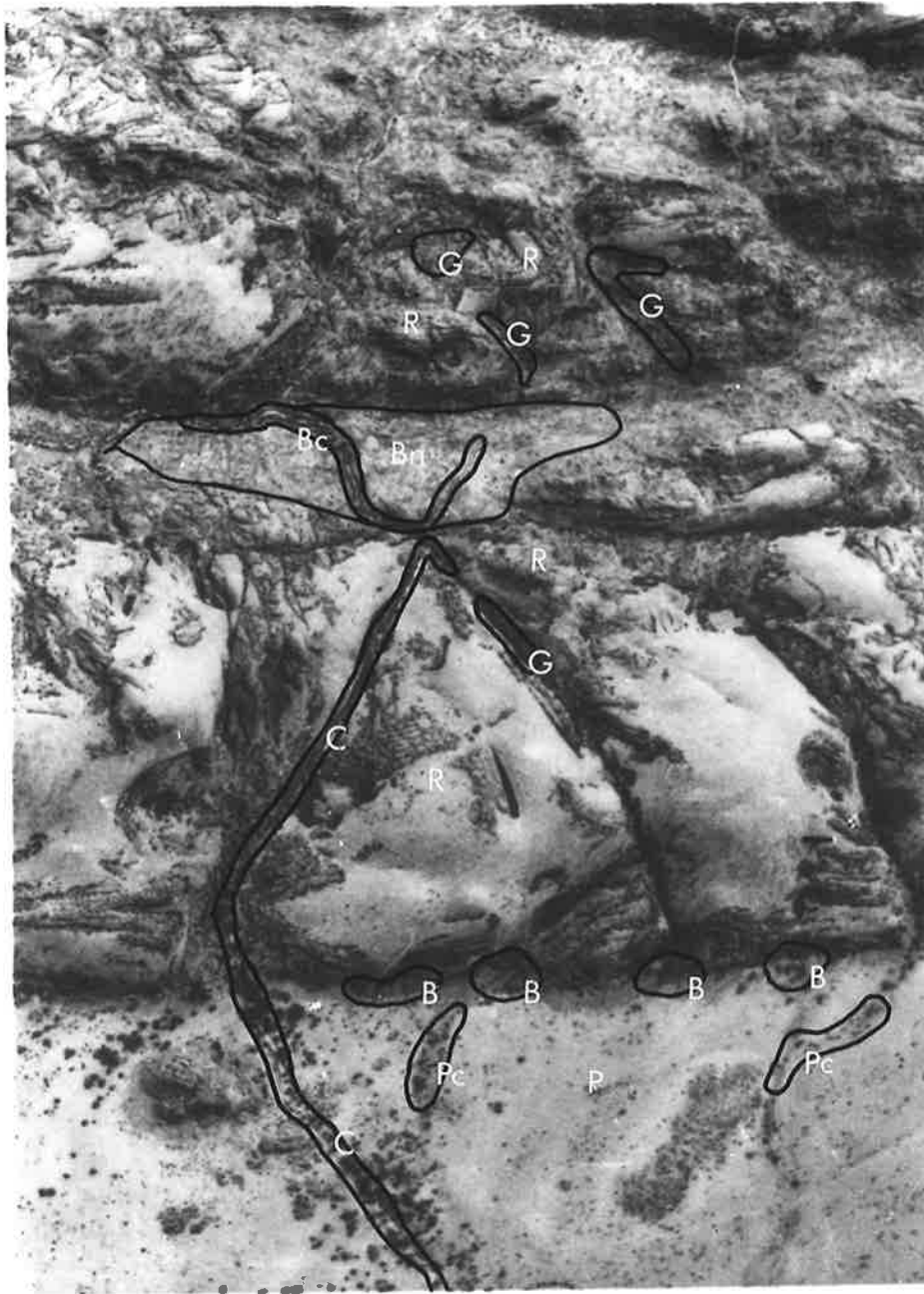
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Left



Right

PLATE 2

Stereo pair of aerial photographs showing
the biogeocoenoses sampled and their
boundaries at Victory Creek.

KEY

B - Base	G - Gully
Bn - Basin	P - Plain
Bc - Basin Creek	Pc - Plain Creek
C - Creek	R - Ridge

Approximate scale 1:16 000