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THE SURVEY OF SMALL MAMMAL COMMUNITIES
IN FOREST ENVIRONMENTS OF AUSTRALIA.

A thesis presented to
The Centre for Resource and Environmental Studies

of
The Australian National University

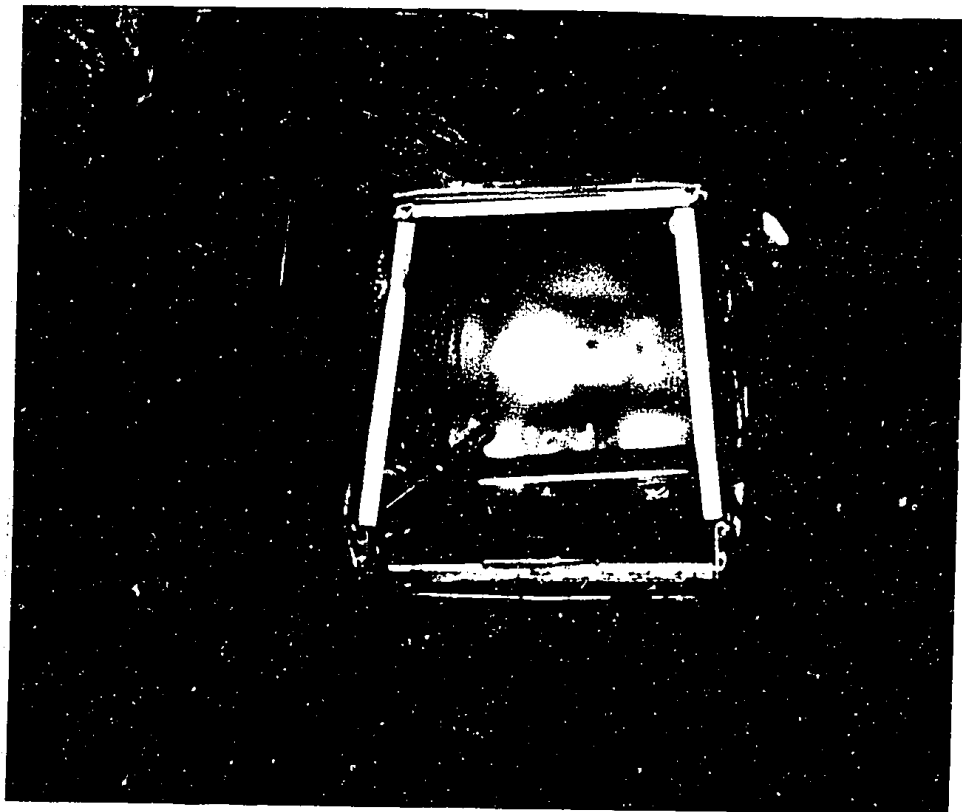
by
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April, 1984

V.T. Read, 1984



THE SURVEY OF SMALL MAMMAL COMMUNITIES
IN FOREST ENVIRONMENTS OF AUSTRALIA.

VIVIAN T. READ

DECLARATION

Except where otherwise indicated, this dissertation
is my own work.

Vivian T. Read.

April, 1984

ABSTRACT

In an analytical review of a sample of past Australian faunal surveys, the survey of small mammal communities was identified as requiring most immediate attention. Variables in survey design were found to be inconsistent and most of the results were not comparable. The most important variables that were used inconsistently were sampling configuration, intensity and size. Almost all surveys were conducted without reference to the relationships between methods and small scale environmental heterogeneity.

Field trials were established in the Brindabella Range (ACT) and Bodalla State Forest (N.S.W.) to evaluate the above key survey variables. The first site (Brindabella Range) consisted of a discrete area of small mammal habitat containing a well studied small mammal community which provided a stable, known situation with which the results of all methods could be compared. Three other sites (Bodalla S.F.) represented a successional gradient following major forestry disturbance, which allowed the methods to be evaluated under a range of environmental conditions.

Capture data were used to compute indices of diversity to provide a basis for evaluating methods in terms of their capability of sampling community structure. Characteristic responses of diversity indices to small number data sets were studied by modelling hypothetical data sets. Analysis of the indices showed that methods used in a grid configuration were sensitive to changes in sampling intensity and frequently misrepresented community structure. In contrast, trapline (index-line) methods were found to be more consistent and accurate in measuring community structure. When consistency under different environmental conditions, field effort and species representation are taken into consideration, trap spacings of 10m are preferred.

Sample sizes for index-line methods were analysed by progressively accumulating capture data. Most sites were adequately sampled by 120m of index-line. Values of indices for the richest site (5 species) were still increasing up to a length of 170m, the full extent of the line at this site. Further extensions to the line may have returned additional information. A supplementary length of 50m is suggested for any index-line to account for variations caused by the end traps. Similar analyses for grid methods revealed that only the 5m spacing method was adequately sampling the community. Other spacings

may have returned additional information with increased frequency of sampling.

Five environmental attributes were found to be significantly correlated with indices of community diversity at the first site. These were used to evaluate the ways in which the different methods responded to environmental patchiness. Neither grid nor index-line methods were found to differ amongst themselves, however there was a significant difference between the two configurations in their ability to sample fern cover, one of the key attributes found to be correlated with species in the community. Index-line methods sampled the dense patches more efficiently than did the grid methods. The potential is recognised for developing a model of environmental complexity and small mammal community diversity against which survey methods may be calibrated to sample a range of environments in a comparable way.

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PREFACE

To many minds, a survey of the vertebrate fauna within a defined area implies elaborate field excursions involving a wide variety of methods to obtain representative specimens of the species inhabiting that area. The planning of such surveys is based on naturalists' intuition, which results in areas rich in species receiving almost undivided attention. In a similar way, rarer species are given disproportionately more time than more abundant and ecologically significant common species.

The initial wave of discovery of vertebrate species is now waning (with the possible exception of bats) permitting the development of a more rational approach to ecological survey. This coincides with the waxing environmental awareness at all levels of society, which now expects both biotic and abiotic components of the environment, once subordinate to the forces of national progress, to be accounted for.

Consequently, a wide range of interested parties, both private and public, are seeking avenues to develop quantitative statements about the faunal component in land resource surveys, whether for the simple purpose of focusing public awareness, or for adequate representation of conservation values in complex land use decision making processes.

With such requirements, research on land evaluation for conservation purposes has commenced in a newly formed group within the Division of Water and Land Resources (CSIRO). Historically, the Division (formerly Land Use Research) developed a system of integrated land classification for large scale resource surveys based on identifiable patterns of vegetation, geology and geomorphology using aerial photographs (Christian and Stewart, 1953). The new research group will test the applicability of this and other methods of land classification for initial horizontal stratification

of the environment into relatively homogeneous subdivisions to allow sampling of fauna, and for subsequent extrapolation based on the repetition of the patterns measured.

The success of environmental mapping from stratified sampling for faunal surveys depends largely upon the animal communities being sampled corresponding with those attributes of the environment that are measured by remote sensing and in related ground truthing. Clearly the problem is a question of scale of mapping relative to the most ecologically relevant scale as interpreted by animal communities. It is to this question that my co-worker, Mr R. Thackway, has addressed his research attention.

A closely related research requirement is the measurement of animal communities in a systematic manner within, or across, the mapped areas of environment. This defines the scope of the research field with which this thesis deals, that is, the quantification of recognizable animal communities within measured landscape boundaries. One of the objectives of such research is to determine optimal methodologies relative to the habitat being sampled that may be used in a standardized way to permit objective comparisons for conservation status. Included in the methodologies are the field tools for observation and capture plus tools for data presentation and analysis.

The research project, and hence this thesis, has been structured to identify some of the more urgent requirements for survey. Analysis of samples of Australian faunal surveys has shown that sampling the small mammal community is a major component of most studies (see text). While much work has been directed towards methods of sampling, no two surveys used the same single method. Measurement of the small mammal community is sensitive to variations in sample design, timing and techniques and was selected as the objective of this study. The need for research into standardized census methods for other faunal taxa remains undiminished, although the limitations of a short term study necessitate their exclusion from this project.

The following thesis records the procedure, results and discussion of a research project to fulfil the requirements for a Masters degree in Resource and Environmental Studies, to be submitted to the Centre for Resource and Environmental Studies, Australian National University.

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Chapter 1

INTRODUCTION

1.1 A Historical Review

Faunal surveys in Australia may be said to have begun with John Gould and his indefatigable collecting companion, John Gilbert, who set the stage with the taxonomic composition and distribution of the main vertebrate faunal groups. These men, and others like them, were collectors in a land of fauna previously unknown to science. The splendor of what he saw and the foresight of his prophetic mind lead Gould to write ".....Australia - a part of the world's surface still in maiden dress, but the charms of which will 'ere long be ruffled and their true character no longer be seen! Those charms will not long survive the intrusion of the stockholders, the farmer and the miner, each vying with the other to obliterate that which is so pleasing to every naturalist; and fortunate do I consider the circumstances which induce me to visit the country while so much of it remained in its primitive state" Gould, J. (1870), "Mammals of Australia".

These predicted conflicts between land use and the well-being of native fauna are today, more than a century after writing, an unsolved and increasing predicament.

Fundamental faunal surveys early in this century were ad hoc observation and collection to provide annotated information on distribution and abundance in specific areas (Chisholm, 1923, 1925; Calaby, 1966).* Marlow (1958) used observations by local naturalists and records of established collections in combination with extensive field work to provide a more comprehensive account on a state-wide (N.S.W.) basis.

* Refer to separate Faunal Survey Bibliography for all surveys included in the review.

Initiative was subsequently taken in Queensland to conduct wider ranging surveys in a systematic way (Kirkpatrick, 1968; Kirkpatrick and Amos, 1977; Kirkpatrick and Searle, 1977; Lavery, 1968, 1969; Lavery and Grimes, 1974(a); Lavery and Johnson, 1968, 1974; Lavery and Seton, 1974; McEvoy *et al.*, 1979; and Vernon and Martin, 1975). Selection of locations were "..... governed by location of available staff, which had been in the first instance deliberately placed in areas of diverse zoological interest and opportunity ..." (Kirkpatrick and Lavery, 1979), which limits their use for extrapolation to less diverse areas. Despite the effort required in these surveys, the results are simple species lists with subjective indices of abundance which are of limited value in quantitative evaluation of land for conservation purposes.

In a similar style, surveys by the Department of Fisheries and Fauna in Western Australia (e.g. Burbidge, 1971; Burbidge and Fuller, 1979; Burbidge and George, 1978; Burbidge and Prince, 1972; and McKenzie *et al.*, 1973) resulted in isolated pockets of non-quantified distribution data.

In Victoria, the Fisheries and Wildlife Division of the Ministry for conservation has undertaken a series of systematic surveys (Callanan and Menkhorst, 1980; Emison and Porter, 1978; Emison *et al.*, 1975(a), 1975(b); Gilmore, 1976; Gilmore *et al.*, 1979; Menkhorst and Gilmore, 1979; Norris *et al.*, 1979; and Thomas and Gilmore, 1976). They were systematic in that observations were recorded into 5 minute grid-cells from a map. Methods of survey, while apparently standardized for each survey, varied between surveys so comparisons of different areas may have been distorted. Some innovations were introduced with attempts to correlate animal communities and vegetation structural formations (Emison *et al.*, 1975(a)), however, their descriptions of communities were as species lists without quantification to express structure and organization.

It is pleasing to note that modern surveys throughout Australia are now seriously addressing the shortcomings of the earlier surveys mentioned above (see Myers *et al.*, 1984).

Two surveys have included method evaluation as a major objective of study. The faunal component of a study of land use on the South Coast of New South Wales (Nix *et al.*, 1978) sought to devise a rapid, economical strategy and a set of techniques for identifying faunal assemblages using predictive indices. While their basic findings were inconclusive, two constructive points of evaluation were made; (i) emphasis should be on sampling the fauna along complete toposequences rather than at single disjunct sites. (ii) methodologies should be flexible to suit a hierarchical range of scales. The second survey studied the impact of the pulp wood industry on wildlife in Tasmania (Pattemore, 1977). A range of techniques were attempted for four taxonomic groups with some critical evaluation of their use. The development of indirect methods (e.g., sound recording, faecal pellet counts etc.) was emphasised for future studies. Both the above surveys introduced species diversity indices into the analysis of data.

Another form of faunal survey has been that included in environmental impact assessments. (Friend, 1979; Pattemore, 1977; Recher *et al.*, 1980; Braithwaite, L.W. *et al.*, 1982). This has developed the importance of relating animal distribution patterns to structural components of the environment.

Similarly, surveys have been conducted to provide a resource base for park management. Frith and Calaby (1974) used opportunistic collection supplemented with historic notes to determine the vertebrate species for this purpose at the Cobourg Peninsular Wildlife Sanctuary and Flora and Fauna Reserve (N.T.). With the Ayers Rock Mt Olga National Park Environmental Study, Hooper *et al.* (1973) listed fauna in taxonomic groups using *a priori* and survey information. These groups were then related to habitats and land units and the study became one of the first in Australia to attempt to use the landscape approach of land classification (Christian and Stewart, 1953) to relate fauna to their environment.

A more recent addition to the objectives of faunal survey has been ecological interpretation of data collected. Broadbent and Clark (1976) attempted to obtain an understanding of the relationships between several faunal taxa and the structure and floristics of different rainforest types. Initial planning included enterprising attempts to standardize survey techniques for a more meaningful interpretation of results. These were later abandoned on the grounds of being inefficient and selective of only a small range of animal groups. In their own criticism of results, Broadbent and Clark found that relationships were difficult to identify due to unequal sampling effort, low numbers of standardized sites studied and inadequate habitat classification. Kikkawa and Monteith (1980) made some conclusions on biogeographical and ecological associations in monsoon forests of the Kakadu region (N.T.) based on data collected by specialists of select taxa without clearly defined methods. Such characteristics of survey render them of little value for repetition and comparison in subsequent seasons.

A more inquiring survey of the fauna at present being conducted in Kakadu National Park (Braithwaite and Dudzinski, 1982) is seeking the physical and biological determinants of vertebrate species diversity in the monsoonal forests for the purposes of ecological interpretation and park management. The methodology being used is directed towards measuring species distribution and abundance in relation to appropriate environmental parameters at sites based on considerations of geography, land-use and accessibility. The methods are comprehensive and standardized making it the most advanced survey to date in Australia, however it lacks suitable environmental stratification for subsequent extrapolation to other ecological associations.

Since the first serious attempts during the 1930s, faunal surveys have evolved from elementary findings on distribution and abundance through stages that have attempted

standardization of methods, association of fauna with the environment and more sophisticated means of analysis to the present day position. The demand to include consideration of ecological values in environmental impact assessment and nature reserve management has developed significantly since the mid 1970s. This calls for methods of survey that are standardized, quantified, repeatable, flexible in scale and capable of extrapolation to areas of similar environmental quality.

There has been much discussion about the need for such objectives of survey, although all surveys so far have failed to address them in their own attempts in one degree or another. There is a dearth of scientifically based information on survey methodology for use in a standardized way across a range of environments.

1.2 Characteristics of Past Faunal Surveys

To permit a more objective perspective of methodological characteristics pertaining to past Australian faunal surveys, 75 reports were obtained representing 71 different surveys. These reports are by no means a complete collection of faunal surveys, but may be considered to be a large and representative sample. The sample is reasonably randomized, resulting from initial inquiries addressed equally to all States and Territories. In selecting suitable surveys for inclusion, preference was for those treating more than one taxa and excluding a large number of single species surveys (essentially population studies). For each stage of the analysis, only those surveys containing information relevant to its requirements have been included.

1.2.1 Time range, scale and distribution of surveys

The surveys range from Chisholm (1923) to present day surveys (Braithwaite, *et al.*, unpublished). Table 1.1(a) shows the distribution of surveys over the years indicating peaks of activity during the mid and late 1970s. Notable is a decline in the early years of the present decade.

TABLE 1.1 TIME RANGE (a), SCALE OF SURVEYS (b) AND DISTRIBUTION AMONG THE STATES (c) OF THE FAUNAL SURVEY SAMPLE

(a)	Before												Up to Aug.
	1971	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982
Number of Surveys	8	1	1	4	5	9	6	5	8	11	6	3	2
(b)													
Area Classes (Km ²)	0 - 50	-100		-200	=500	-1000	-5000	-10,000	-20,000				
Number of Surveys	3	1		2	2	3	7	2	3				
%	13.0	4.4		8.7	8.7	13.0	30.4	8.7	13.0				
	<u>SMALL</u>			<u>MEDIUM</u>				<u>LARGE</u>					
Number of Surveys	4			7				12					
%	17.4			30.4				52.2					
(c)	N.S.W.	VIC.	QLD.	W.A.	S.A.	N.T.	TAS.	A.C.T.					
Number of Surveys	16	18	15	16	0	4	3	1					

Only 23 reports stated the area of their survey. These are listed in 8 frequency classes and subsequently agglomerated into 3 classes of scale (Table 1.1(b)). This shows that larger areas (1000-20,000 km²) have been given more serious attention, especially the 1000-5000 km² area class. Obviously, there is a need for methods to be sufficiently flexible for extrapolation at smaller scales.

The distribution of surveys around Australia (Table 1.1 (c)) shows the major States being approximately equally represented with the obvious exception of South Australia. This possibly reflects the lack of forest cover in that State. When considered by area, the States exhibit disproportionate attention to faunal survey. The Northern Territory is a large tract of land with efforts being concentrated on the more popular parks, neglecting a large proportion of what is in many places, rich but threatened habitat. Tasmania, although small, has great diversity of habitats yet is represented by only 3 surveys.

1.2.2 Importance attributed to six taxonomic classes by the surveys.

Selecting those surveys considering more than one taxonomic class, a sample of 54 was available for analysis. The number of surveys that directed at least some effort towards each taxonomic class is expressed in Table 1.2. While birds are the better known group of animals, mammals quite clearly have received the greatest relative attention. This may in part be due to their popular appeal, although it is more likely a result of their restricted mobility and more specific habitat requirements, which facilitates a more definitive statement on animal/environment associations.

TABLE 1.2 FREQUENCY OF INCLUSION BY SURVEYS OF SIX TAXONOMIC CLASSES

Taxonomic Class	Mammals	Birds	Reptiles	Amphibians	Fish	Invertebrates
Number of Surveys	52	39	30	25	9	9
%	96.3	72.2	55.5	46.3	16.6	16.6

Reptiles and amphibians were reported from about half of the surveys. Reptiles are often treated with apprehension by survey planners, not because of their venomous manners, but rather due to their cryptic behaviour, seasonal activity and difficult taxonomy. Their survey requires a specialist who, for some reason, is infrequently included. Amphibians are most detectable following rain which makes their survey an unpredictable event. If they are considered at all, therefore, it is usually on an opportunistic basis.

Fish, being non-terrestrial, are too frequently ignored by broad spectrum surveys as is evidenced from the analysis. Similarly, invertebrates receive scant attention due either to sampling difficulties or the erroneous assumption of their insignificance.

Table 1.3 indicates the range of techniques considered necessary to survey the six taxonomic classes. That more than one technique for mammals is most frequently used implies the inadequacy of any one technique to sample the full range of species. The reason becomes obvious when considering the composition of the class ranging from small ground mammals and larger ground mammals, to arboreal mammals and bats, thus requiring a diverse range of techniques for their detection. Other taxonomic classes however, have been treated more confidently with a single technique.

1.2.3 Methods used to survey mammals

When considering survey methodology as a research topic, it is debatable whether attention should be directed towards the class most commonly examined and for which there is a richer literature, or alternatively towards those classes often ignored due to inadequate methods. With time limitations on this study, the former approach has been preferred. Research into bird community censusing techniques is well developed, although by no means concluded. Mammals world wide, however, have rarely been censused on a community basis; instead the abundant literature on field techniques refers primarily to single species population studies. With mammals ranking most important (Table 1.2), and with no information on the holistic approach to their survey, they have been chosen for study in this thesis.

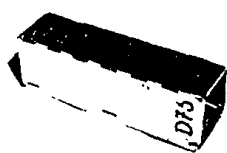
A wide variety of field techniques, both direct and indirect have been used in surveying mammals (Table 1.4). In most reports, the choice of methods has not been quantitatively justified nor critically evaluated. One exception by Pattemore (1977) states generally that Elliott live-capture and wire cage small mammal traps sampled a wider range of species than other methods, that snap traps were "virtually useless" and baited pitfall traps caught no mammals. Otherwise, the choice of techniques has been based on naturalists' intuition concentrating on capturing a wide range of species.

TABLE 1.3 NUMBER OF SURVEYS USING AN INCREASING RANGE OF TECHNIQUES
FOR EACH TAXONOMIC CLASS

TAXONOMIC CLASS	MAMMALS	BIRDS	REPTILES	AMPHIBIANS	FISH	INVERTEBRATES
Total number of techniques used in all surveys recorded	26	10	10	6	4	7
Number of surveys using:						
1 technique	7	29	16	16	7	6
2 techniques	9	5	7	2	2	2
3 techniques	9	4	3	3		
4 techniques	11					1
5 techniques	3					
6 techniques	5					
7 techniques	2					
8 techniques	1					
9 techniques	1					

TABLE 1.4 FREQUENCY OF USE OF DIRECT AND INDIRECT SURVEY TECHNIQUES FOR MAMMALS.

DIRECT TECHNIQUES		INDIRECT TECHNIQUES	
Elliott live-capture trap	28	Literature search	4
Longworth live-capture trap	1	Museum records	5
Sherman live-capture trap	1	Anecdotal information	4
Snap trap	17	Faecal pellets	5
Rabbit trap	1	Predatory bird pellets	2
Pitfall trap	4	Predator scat analysis	1
Pitfall trap with drift-fence	5	Tracks	1
Wire cage trap	26	Diggings	3
*Shooting	7	Homesite location	2
*Mistnetting	4	Carcass remains	2
*Steel wire over water	2	Signs (unspecified)	6
Spotlighting (by walking)	10	Roadkills	2
Spotlighting (by driving)	9		
Spotlighting (not specified)	17		
Opportunistic sightings	10	Methods not stated	3
Elliott	Longworth	Sherman	Mascot Wire Cage



* These methods are used to survey bats (although shooting has also been used to collect other species). No reports mentioned use of Constantine bat traps although they have been shown to be successful (Tidemann and Woodside, 1978) and are now widely used.

Elliott live-capture and wire cage traps have clearly been the most popular techniques (Table 1.4). The Elliott trap is small and easily portable but is restricted to small mammal* capture while in contrast the wire cage trap is large

* Body weight of ≤ 300 gms.

and heavy although it captures a greater range (by body weight) than does the smaller trap.

Spotlighting is used primarily for surveying the arboreal mammal community. While many surveys have quantitative data by time and/or distance, it remains a technique that is little standardized. Similarly, the larger terrestrial mammals (e.g. paramelids, macropodids) have frequently been treated in a non-standard way, usually being listed in opportunistic sightings.

The use of indirect methods has largely been neglected in past surveys, especially the identification of animal tracks. Signs offer potentially quantifiable techniques for the fauna that are difficult to trap or detect.

All forms of field techniques for mammals require further refinement to ensure their suitability in a standardized and quantitative survey. Time limitations force the perspective of this study to be narrowed again, so only techniques applicable to the small mammal community will be considered forthwith. This group has been selected as it is usually the most diverse, most abundant and most frequently sampled community yet the techniques used have been varied in both type and frequency.

1.2.4 Efficiency of six direct techniques for small mammal survey.

Of the techniques for directly sampling a small mammal community, six trap types have been used in various combinations in the surveys under consideration. Table 1.5 lists 27 surveys that included quantitative results relative to the types of traps used, from which the number of species caught and the percentage trap success were calculated. Cautious interpretation of these values is required as it may reflect the abundance of animals in an area more than trap efficiency. However, mean values from a reasonably large number of surveys is meaningful.

TABLE 1.5 RELATIVE EFFICIENCIES OF SIX MAMMAL TRAPPING TECHNIQUES

Source	S	C	TN's	% Success	No. Trap Types	E	W	B	L	P	R
Barnett <i>et al.</i> (1976)	12	651	41,241	1.58	3	*	*	*	*		
Braithwaite & Gullan (1978)	5	506	13,200	3.83	2	*	*				
Braithwaite <i>et al.</i> (1978)	11	530	12,120	4.37	2	*	*				
Callanan & Menkhorst (1980)	6	46	785	5.86	2	*	*				
Cockburn <i>et al.</i> (1979)	4	580	6,480	8.95	1	*					
Friend (1979)	7	500	5,534	9.03	2	*	*				
Gall (1976)	6			19.00	1				*		
Gilmore (1976)	7	121	1,712	7.07	3	*	*	*	*		
Happold (1980)	4	263	1,360	19.30	1	*					
Hopper (1981)	4	28	240	11.67	1					*	
Kingston <i>et al.</i> (1979) (1)	4	425	23,000	1.85	3	*	*	*	*		
(2)	3	30	2,140	1.40	3	*	*	*	*		
Kitchener <i>et al.</i> (1976)	5	139	3,687	3.77	4	*	*	*	*	*	
Loyn <i>et al.</i> (1980)	4	27	375	7.20	2	*	*				
McKenzie <i>et al.</i> (1973)	6	6	2,774	0.22	4	*	*	*	*	*	
Menkhorst & Gilmore (1979)	6	107	4,657	2.30	1	*					
Milledge (1979)	9	845	8,800	9.60	1	*					
N.P.W.S. (Tas.) (1978)	4	4	432	0.90	2	*	*				
Nicol (1978)	10	301	1,618	18.60	1	*					
Osborne & Marsala (1981) (1)	3	91	360	25.28	1	*					
(2)	3	70	260	26.92	1	*					
(3)	4	102	240	42.90	1	*					
Pattemore (1977)	10	31	1,360	2.23	4	*	*	*	*	*	
Recher <i>et al.</i> (1980)	7	29	200	14.50	2	*	*				
Rose (1976)	7	104	691	15.05	2	*	*				
Suckling & Heislars (1978)	4	824	6,634	12.42	1	*					
Thomas & Gilmore (1976)	8	494	10,461	4.72	3	*	*				*
Mean values	6.12	263.62		10.37	2						

<u>Key</u>	S	- Number of species	W	- Wire cage trap
	C	- Number of captures	B	- Shap trap
	TN's	- Number of trap nights (=No. traps x No. nights of trapping)	L	- Longworth live-capture trap
			P	- Pitfall trap
	E	- Elliott live-capture trap	R	- Rabbit leg-hold trap

The average trap success over all 27 surveys using one or more trap types is 10.37%, ranging from 0.22% to 42.9% (Table 1.5) with a standard deviation of 9.95 indicating a wide spread of values about the mean. Analysis following from this seeks to demonstrate the efficiency of using more than one type of trap and to identify which trap type provides the richest and most efficient information.

TABLE 1.6 SPECIES RICHNESS ($\bar{S}$) AND TRAP EFFICIENCY USING INCREASING NUMBERS OF TRAP TYPES

	NUMBER OF SURVEYS	$\bar{S}$	% TRAP SUCCESS
Surveys using 1 trap type only	11	5.18	17.90
Surveys using 2 trap types	8	6.37	7.65
Surveys using 3 trap types	4	7.50	3.69
Surveys using 4 trap types	2	5.50	1.99

Table 1.6 summarises results from surveys using one or more trap types. When a greater variety of traps is used, more species of mammals are caught; this is a general trend, although the efficiency of capture declines sharply indicating that some trap types are significantly less efficient.

Considering the efficiency of trap types and some combinations, Figure 1.1 represents their relative importance. The height of each column represents the mean trap success values for an increasing number of trap types discussed previously while the sub-divisions within each column are proportional to the contribution made to the overall mean value by each trap type or combination of types. It shows Elliott and Longworth live-capture traps to be equally efficient and both are about twice as efficient as pitfall and wire cage traps. The efficiency of Longworth traps is based on a single survey and should not be overemphasized. In contrast, the wire cage trap has more success at catching a wider range of species.

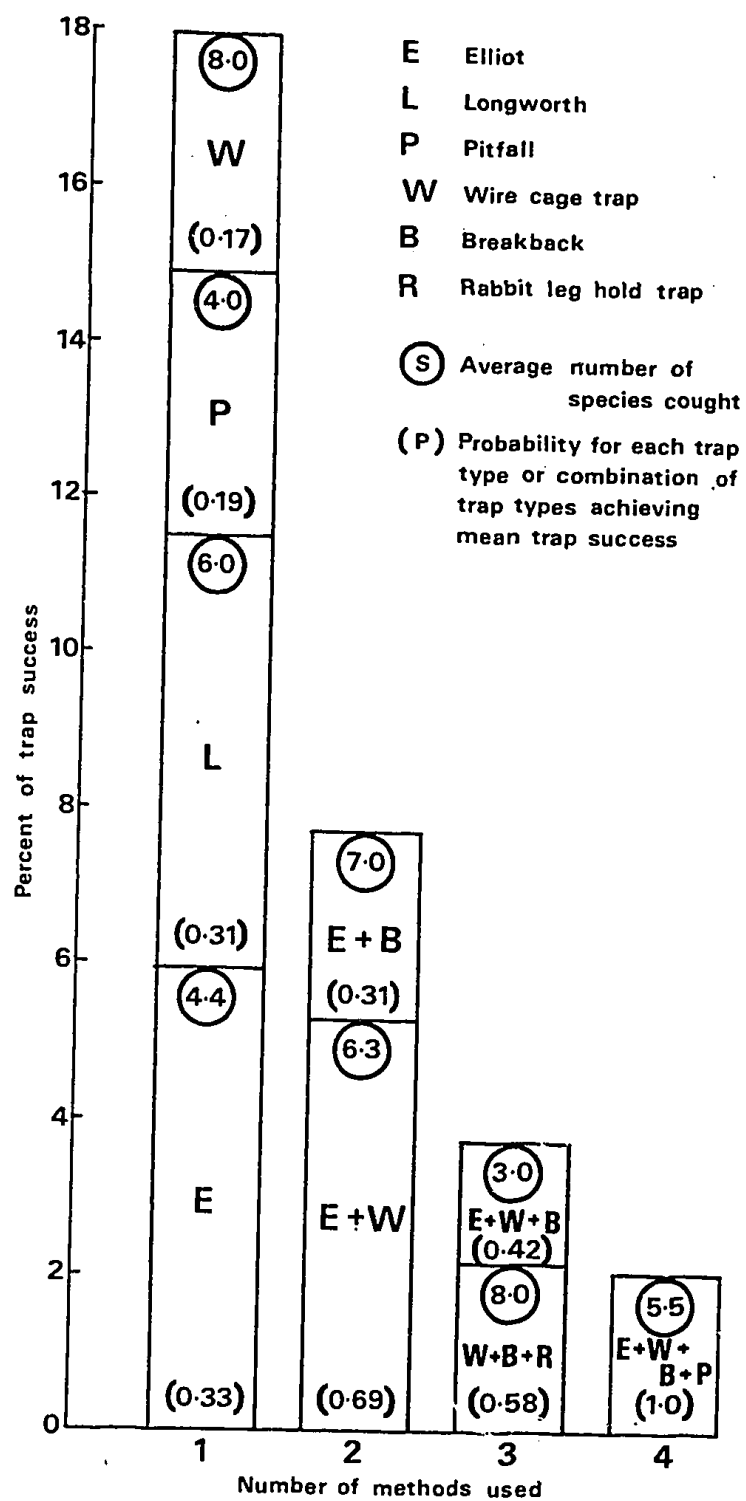


Figure 1.1 Probability of success with each trap type plus some combinations of trap types.

Where more than one trap type has been used, Elliott live-capture and wire cage traps together are outstandingly more efficient than all the other combinations represented in Figure 1.1.

1.2.5 Relative success of capture for mammal species in the surveys.

Having identified the trap types that are capturing most species with greatest efficiency, it becomes pertinent to analyse the response to trapping by the animals. Table 1.7 lists 40 mammal species caught in 22 of the surveys that had quantitative results, with the numbers caught in each of the surveys respectively. Trap success rates (%) were calculated* allowing mean values to be determined for each species. These values are representative of both the animals' abundance and their behavioural attitude towards entering a trap, however this complexity is not important. The use of the trap success values is to provide a crude estimate of the proportions in which the different species may be expected to be caught and the trap effort required.

These values display wide variation, ranging from 0.2/10,000 T.N.'s (*Potorous tridactylus*) to 467/10,000 T.N.'s (*Rattus fuscipes*). Those species with low values are represented in very few surveys which confirms their rarity or difficulty of capture. Similarly, the higher values occur in greater numbers of surveys. While the parameter used is a mean value, the highest have large deviations from the mean (Table 1.7) indicating a wide range of success rates. Cautious use of the values for larger species is necessary as the trapping programs usually include many more small traps than large traps. This indicates the need to analyse species' response to the various trap types.

* Captures calculated as a percentage of total trapnights (T.N.'s). The number of trapnights is the number of traps used multiplied by the number of nights they were set.

1.2.6 Species response to trap type.

From surveys that contained suitable information, Table 1.8 lists 32 species against the types of traps that caught them. Totals from the table show:-

- Elliott live-capture traps caught 16 species (+4 not in survey information), (C. Dickman, *pers. comm.*)
- Longworth live-capture traps caught 6 species
- Wire cage traps caught 16 species
- Snap traps caught 10 species
- Pitfall traps caught 8 species (+1 not in survey information, (*pers. obs.*))

Clearly, the Elliott live-capture and wire cage traps are catching more species.

Table 1.9 lists the species not caught by these two trap types and their respective head - body lengths. The most commonly used Elliott trap size is 300 x 100 x 90 mm so the four species that have H.B. length $\geq$ 300 mm obviously cannot be trapped as adults due to size. Four other species are known to be caught by Elliott traps from information other than the present surveys (C. Dickman, *pers. comm.*) leaving four relatively uncommon species (*Cercatetus concinnus*, *C. lepidus*, *Ningui sp.*, *Tarsipes spencerae*) not represented in Elliott trap captures in the survey information.

All species not caught by wire cage traps are considerably smaller than the traps (560 x 210 x 210 mm or larger). Trap failure with these smaller species is due to unsuitable and insensitive trigger mechanisms.

There are other species and other trap success ratings not included in the surveys which would complement this analysis. However, the surveys used have included the most common species and most frequently used trap types. Rare species require extra survey effort to be caught so they come in a class of survey not relevant to this study.

TABLE 1.8 NUMBER OF SURVEYS IN WHICH MAMMAL SPECIES WERE CAUGHT
BY FIVE TYPES OF TRAP

	Elliott live- capture	Longworth live- capture	Wire cage	Snap trap	Pitfall trap
BURRAMYIDAE					
<i>Acrobates pygmaeus</i>				1	
<i>Burramys parvus</i>		1			
<i>Cercartetus concinnus</i>					1
<i>C. lepidus</i>					1
<i>C. nanus</i>	*	1		1	
DASYURIDAE					
<i>Antechinus flavipes</i>	*		1		*
<i>A. stuartii</i>	4	1	2	1	
<i>A. swainsonii</i>	2	1	1	1	
<i>Dasyurus maculatus</i>	1		1		
<i>Ningau sp.</i>					1
<i>Phascogale calura</i>	1				
<i>P. tapoatafa</i>	1		*		
<i>Smithopsis leucopus</i>	3		1		1
TARSIPEDIDAE					
<i>Tarsipes spencerae</i>					3
MACROPODIDAE					
<i>Bettongia gaimardi</i>			1		
PERAMELIDAE					
<i>Isoodon macrourus</i>			1		
<i>Perameles nasuta</i>	*		1		
PHALANGERIDAE					
<i>Trichosurus caninus</i>			2		
<i>T. vulpecula</i>			3		
MURIDAE					
<i>Hydromys chrysogaster</i>			1		
<i>Mastacomys fuscus</i>	*	1		1	
<i>Melomys cervinipes</i>	3				
<i>Mus musculus</i>	5		1	1	2
<i>Notomys mitchelli</i>	2			1	
<i>Pseudomys apodemoides</i>	1				1
<i>P. gracilicaudatus</i>	1				
<i>P. higginsii</i>	2				
<i>P. occidentalis</i>	2			1	
<i>Rattus fuscipes</i>	4	1	1	1	1 (Juv.)
<i>R. lutreolus</i>	3		1		
<i>R. rattus</i>	2		1	1	
FELIDAE					
<i>Felis catus</i>			1		

* Known to be caught by these methods from information other than the surveys.

TABLE 1.9 MAMMAL SPECIES NOT CAUGHT IN (a) ELLIOTT LIVE-CAPTURE TRAPS AND (b) WIRE CAGE TRAPS FROM SURVEY INFORMATION. (H.B. = Head and body length; * otherwise known to be caught in this trap type).

(a)		(b)	
SPECIES	H.B. (mm)	SPECIES	H.B. (mm)
* <i>Burramys parvus</i>	120	<i>Acrobates pygmaeus</i>	66
* <i>Cercartetus concinnus</i>	80	<i>Burramys parvus</i>	120
* <i>C. lepidus</i>	70	<i>Cercartetus concinnus</i>	80
* <i>C. nanus</i>	125	<i>C. lepidus</i>	70
* <i>Antechinus flavipes</i>	115	<i>C. nanus</i>	125
* <i>Ningui sp.</i>	65	<i>Ningui sp.</i>	65
* <i>Tarsipes spencerae</i>	Small	<i>Phascogale calura</i>	120
<i>Perameles nasuta</i>	410	<i>P. tapoatafa</i>	250
<i>Trichosurus caninus</i>	560	<i>Tarsipes spencerae</i>	Small
<i>T. vulpecula</i>	500	<i>Mastacomys fuscus</i>	165
<i>Hydromys chrysogaster</i>	300	<i>Melomys cervinipes</i>	200
* <i>Mastacomys fuscus</i>	105	<i>Notomys mitchelli</i>	120
		<i>Pseudomys apodemoides</i>	70
		<i>P. gracilicaudatus</i>	100
		<i>P. higginsii</i>	160
		<i>P. occidentalis</i>	115

1.3 Selection of the most suitable technique for small mammal survey.

As discussed previously (1.2.3), this study has been restricted to the survey of small mammal communities. Consistent with earlier decisions, study of the trap type representing the widest range of the common species in its catch will be selected in favour of techniques successful with just a few or the rarer species.

Wire cage traps are unsuitable as they fail to adequately represent the small mammal community and are physically too cumbersome to sample with sufficient numbers in places of difficult access.

Snap traps have been used widely in survey, particularly for museum collection. While they have been shown to be equally effective as live-capture traps in one study of five species (Fox and Posamentier, 1976), they have elsewhere been considered as useless (Pattemore, 1977). Their deficiencies are in their being frequently sprung without capture and the removal of the (dead) animal reduces the potential for quantitative and robust analysis.

Pitfall trapping in combination with a driftfence to increase the chance encounter by the animal with the trap, has been used in more recent surveys (Cockburn *et al.*, 1979; Braithwaite, 1981; Hopper, 1981 and Myers *et al.*, 1982 (unpubl. data)). Cockburn *et al.*, (1979) found *Cercartetus sp.* and *Ningauia sp.* caught in pitfalls though not in Elliott live-capture traps which expands the range of species sampled during a survey. In two surveys of predominantly coastal heath at Evans Head (N.S.W.) (Myers *et al.*, 1982), 100 individuals of 8 species were caught on a trap grid compared with 46 individuals of the same number of species caught along driftfences (Table 1.10). Compared statistically, and compensating for the variation in the number of trap nights, the difference between the methods is significant ($\chi^2 = 11.06$, $df = 1$, $p < .001$).

TABLE 1.10 DRIFTFENCE AND GRID TRAPPING DATA COMPARED FOR SMALL MAMMAL SURVEY OVER TWO PERIODS
(SEPT, 1981; FEB, 1982) AT BUNDJALUNG NATIONAL PARK, N.S.W. (Myers *et al.*, unpub. data)

SURVEY:	Trap Grid		Driftfence	
	<u>1</u>	<u>2</u>	<u>1</u>	<u>2</u>
SPECIES				
<i>Antechinus flavipes</i>	1	0	1	0
<i>A. stuartii</i>	0	0	1	0
<i>Sminthopsis murina</i>	1	0	3	0
<i>Planigale maculatus</i>	0	0	1	0
<i>Isodon macrourus</i>	2*	1*	0	1*
<i>Melomys burtonii</i>	3	0	0	0
<i>Mus musculus</i>	39	35	15	17
<i>Pseudomys novaehollandiae</i>	8	4	2	2
<i>Rattus lutreclus</i>	4	0	0	0
<i>R. rattus</i>	0	2	0	3*
Number of Species	7	4	6	4
Number of Individuals	58	42	23	23
Number of Traps/site	(25E+5M)	(25E+5M)	(11PF,10E,4M)	(11PF,10E,4M)
Time to lay out Trapsite	2 man/hrs.	2 man/hrs.	5 man/hrs.	5 man/hrs.
% Trap Success	4.30	3.11	2.04	2.04

* = Caught in Mascot wire cage traps
M = Mascot wire cage traps

E = Elliott live-capture traps
PF = Pitfall traps

Table 1.10 also shows that digging the pitfall traps and erecting the driftfence took more than twice as long as laying out the trap grid. Considering also that pitfall traps cannot be used in areas with shallow soils, they cannot be given high priority in small mammal survey.

Elliott live-capture traps are clearly the preferred type for small mammal survey. While other types have importance in expanding the range of species caught, particularly in integrated surveys which include other taxonomic classes (reptiles and amphibians), the need to standardize the method in which they are used is less immediate.

1.4 A framework for research

The historical review and past survey analysis have served to elucidate deficiencies of faunal survey, and to identify the small mammal community as requiring most immediate research attention. This is followed by a theoretical expansion of ecological community concepts, environmental heterogeneity, sampling design, methods of estimating numbers and variables of survey leading to the objectives of this survey research.

A program of fieldwork was developed to meet these objectives, sampling at four sites in two different areas. The sites are described geographically and environmentally. The sampling design and field procedures for the collection of data to evaluate methods and the effect of environmental heterogeneity are also described. This is followed by a discussion of methods for analysing the data. Diversity of communities is considered as are indices of their structure and similarity. Then, two approaches are discussed for the analysis of environmental data.

The results of analysis are presented such that method evaluation based on animal capture data precedes investigation of the effect of environmental heterogeneity.

Chapter 2

THE SURVEY OF SMALL MAMMAL COMMUNITIES

To elucidate the deficiencies of surveys described in the previous chapter, theoretical concepts of ecology need to be examined. Such an expansion develops ideas on the quantitative and qualitative requirements for collection of survey data. The methods available to accumulate relevant data in a systematic way and the variables encountered by use of those methods then require discussion in relation to the objectives of survey research. The succeeding subsections follow this approach.

2.1 Requirements of survey.

2.1.1 Limitations to interpretation of previous surveys.

Characteristic of the majority of past Australian faunal surveys has been the simple listing of species in geographic regions or broad habitat classifications. Species lists provide a basis for preliminary assessment of faunally rich or depauperate areas but they allow no formal interpretation of ecological stability and change, as each species is given equal attention. In some more recent examples, discussion of these lists has introduced community concepts. Rarely, however, has this extended beyond description of what should be more correctly termed species associations, or common groupings of species. More penetrating discussion on the significance of relative proportions of each species within these groupings has been neglected.

Similarly, habitat descriptions have been either simply descriptive to distinguish geographical areas, or quantified in varying degrees for the purpose of prediction of species' occurrence in similar habitats elsewhere. The practice of recording structural stratification in the habitat to relate to species diversity, and measuring resources to develop an explanation of community structure have entered survey planning only in more recent attempts. The levels

of competence of these attempts appear rudimentary in terms of the potential posed by theoretical ecology.

It is clear from the analysis of surveys in the previous chapter, there is a lack of standardization of methodologies both within and between surveys. Without this discipline, the usefulness of data for comparison between habitats or between larger regions, through seasonal change and over years, is diminished.

2.1.2 The community concept.

The most general definition of a community is "..... any assemblage of populations living in a prescribed area or physical habitat" (Odum, 1971; Krebs, 1978), which encompasses a range of scales of magnitude. A more pertinent definition is "..... a natural assemblage of organisms which, together with its habitat, has reached a survival level such that it is relatively independent of adjacent assemblages of equal rank; to this extent, given radiant energy, it is self sufficient" (Allee *et al.*, 1949). This implies recognizable, discrete units. While such a definition is theoretically robust, the implication of a discrete community composition containing exclusive species is misleading. Rather, the distribution of species ranges from broad to narrow with residents of the dominant species describing the community characteristics.

Interpretation of community boundaries has long been debated, though predominately in the field of plant ecology. The view that communities are discrete units with sharp boundaries is derived from Clements (1916) who postulated that plant associations were distinguishable and separated by a sharp gradient of overlapping species. Many situations that comply with this concept may occur, particularly in Northern Hemisphere countries where seasonal patterns are stable resulting in relatively homogeneous vegetation associations that are responsive to predictable environmental change.

Alternatively, Gleason (1926) postulated open communities with organization being a fortuitous association of organisms, the adaptations of which enabled them to live together under the particular physical and biological conditions found at a particular location. These associations were separated by zones of rapid replacement of species along a gradient, known as ecotones, which may be defined as broad boundaries between such associations. The more distinctive vegetation types thus represent a higher degree of evolutionary adjustment between associated populations of species which become an indicator directly related to community efficiency and stability.

Parallel conceptual conflicts exist in understanding animal communities, although the distinctiveness of their patterns is not so easily defined. Associations of animal populations differ from those of vegetation primarily as a result of mobility. Whole populations may depart one habitat type in search of alternative food resources or they may migrate from the region following favourable breeding conditions. Such behaviour is characteristic of avian populations, facilitated by flight, which rarely form consistent associations of species.

Populations of small mammals are limited in their dispersal capacity to movements usually less than a few kilometres (with the obvious exception of erupting populations of rodents e.g., *Rattus villosissimus*). Consequently their populations tend to have more stable associations with each other and with particular habitats although each species differs in its general distribution throughout a range of habitats. Coexistence of species with similar resource requirements appears to result in specialization of feeding strategies including vertical stratification (e.g. arboreal behaviour in sympatric species of *Antechinus*, C. Dickman, *pers. comm.*). Communities of small mammals may thus be typified by a core of selective species (i.e. habitat specialists such as *Antechinus swainsonii*, *Rattus lutreolus*) with a fluctuating component

of more generalized species (e.g. *A. stuartii*, *R. fuscipes*). Elton (1927) claims animals form communities as a result of two factors

- (i) no one animal is sufficiently elastic in its organization to withstand a wide range of environmental conditions
- (ii) animals adapt to a narrow range of environmental conditions.

This perceived correlation with environmental conditions coincides with Gleason's (1926) concept of open vegetation communities. In addition to reacting with the physical conditions of the environment, animals also interact with each other, often in a density-dependent manner, and both within and between species. Small mammal communities thus form associations of populations characteristic of the resource base in a particular habitat. Species expected but not found in the community then raise questions about the community's efficiency or stability.

2.1.3 Animal community characteristics.

Quantitative information about the structure of animal communities is most frequently expressed as the number of animals or as their biomass. To measure biomass, the assessment of numbers is a prerequisite. Elton (1947) states that the subject of animal numbers is an extremely important one and that less is known about it than about almost any other biological subject.. Since that time, considerable attention has been devoted to modelling numbers at the community level but it remains in need of some fundamental biological understanding.

Models of this kind may be conveniently separated as statistical or resource-partitioning (Pielou, 1975). Earliest attempts at modelling species-abundance relationships in communities were statistical. Plotting the number of species in a community against increasing levels of abundance, revealed a logarithmic series (Fisher *et al.*, 1943). In a similar way, Preston (1948) observed that common and rare species occurred less frequently than species

with intermediate numbers of individuals. By assigning species to classes of abundance on a logarithmic scale, the abundance classes tend to assume a normal distribution which is the basis of the lognormal distribution model. This second model gives a measure of dispersion (standard deviation (σ) about the mean) which becomes an indicator of community diversity. It also varies according to sample size. Both models theoretically have the ability to predict the number of species from a sample; however, they require large data sets to express this. Both lack a sound biological explanation.

Of the resource partitioning models, the niche preemption model (geometric series model of Whittaker, 1972; May, 1975) supposes the dominant species to preempt its share of the limiting resource, followed by the second strongest species and so on, such that the propositions taken from a diminishing geometric series. It assumes that the degree of dominance in the community is very pronounced (Pielou, 1975). Alternatively, MacArthur (1957) proposed the "broken stick" model by suggesting that the abundance of such species was determined by the random partitioning of resources distributed along a continuum of resource types. It is a model suited to large-bodied and relatively long-lived species, the abundances of which are in a fairly stable equilibrium (MacArthur, 1960).

Cautious application of the models permits some insight into the relationships of species abundance in community organization. They provide a basis for comparing observed against expected distributions which permits comment on community efficiency and stability.

MacArthur's "broken stick" model assumes distributions to be caused by competition for resources. Cohen (1968), however, constructed an equivalent model based on distributions as determined by other environmental variables. An understanding of how environmental influences cause variation in relative abundance of species requires some integration of community patterns and

population processes. This leads to a theoretical consideration of the niche.

The most adequate description of the niche is derived from Hutchinson (1958) who proposed that if the adaptive ability of each species is plotted relative to every attribute of its environment, each plot may be viewed as one dimension in an n-dimensional adaptive space, which defines its niche. The number of species in a community then depends upon the total amount of niche space available and the average size of each species' niche. Objective measurement of niche breadth and overlap assists in the understanding of interactions between species, particularly the way in which resources are shared. The most significant resources determining species abundance are habitat, food and time (Schoener, 1974). Relationships with these represent the key dimensions defining niche.

Measurement of niche for vertebrate faunal communities has received considerable attention (Schoener, 1968; Pianka, 1973; Cody, 1974; Brown, 1975 and Werner, 1977). Cody's study of bird communities showed that niche overlap increased in direct relation to the number of species in the community. These findings were not supported in a similar study of lizards by Pianka (1973), suggesting weaknesses in using the niche concept for describing community organization. One cause of the weakness may have been in the field techniques and analysis, as the dimensions were measured in different types of habitat (Ricklefs, 1979). It is possible that this problem may be avoided by direct morphological analysis of adaptive structures of the animals which are independent of habitat.

Theoretical development of the animal community concept facilitates stratification of faunal taxa into groups of species with significant similarity in their ecological requirements. The importance of such groupings to faunal survey is that they have the best possibility of being adequately represented by a single, or a limited number of

field techniques that may be optimized for use across a range of environments. Rather than surveying each species independently, the optimized technique becomes a measure of all species of similar ecological requirements, interacting in their habitat. These techniques, if correctly calibrated, provide a quantitative index which represents the summation of all interactions between species in that community. Such indices then provide a comparative basis between similar communities in different places or time, and between different communities.

Species-abundance models and related niche theory are not yet directly applicable to generalized faunal surveys. They do, however, provide guidance to the development of surveys in that there is the possibility of incorporating a measure of community stability with an ecological explanation. The foregoing discussion on niche emphasises its limited application at present; however, its potential usefulness remains.

Similarly, the measurement of key adaptive morphological features of animal species within a community may offer an efficient means of determining the stability of community organization and providing a judgement of its sensitivity to environmental change.

2.1.4 The effect of environmental heterogeneity on survey.

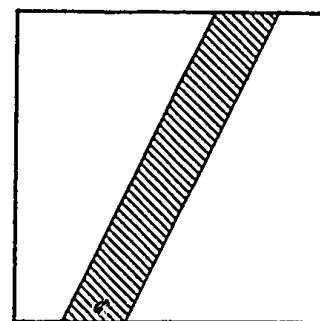
Species of a small mammal community select for and respond to changes of some features of the environment in which they exist. However, such environments rarely contain a uniform spatial distribution of these attributes which is reflected by the distribution pattern of the animal community. Pielou (1975) notes that this spatial heterogeneity is present at a hierarchy of scales and is itself a form of diversity. Environmental patchiness, if significant, acts to reduce competitive interactions within and between species so improving the opportunities for co-existence. When the size of the animals and their home range is small relative to the scale of patchiness, as

appears to be the case with small mammals, then this factor becomes important in their survey.

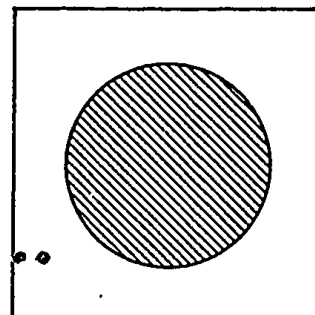
Some measure of spatial heterogeneity becomes necessary in survey for two reasons. Firstly, the overall species diversity of the animal community is composed of two components. Endogenous diversity is that which would occur in a perfectly homogeneous habitat as a result of competition between species for resources available. Exogenous diversity is the diversity caused by environmental patchiness. While measurement of the two is practically inseparable, they emphasize the importance of adequately measuring patchiness to ensure that all combinations of species are represented for the entire habitat.

Exogenous diversity is determined by the number, size, configuration and distribution of the patches, some of which are represented in Fig. 2.1 for variation of a single habitat attribute (e.g. dense fern cover to a height of 100cm for small mammals). Linear patches have more "edge" than the same area in circular configuration, so they disadvantage prey species not well adapted to predator avoidance. Patches close together have diversities more similar than those that are separated, resulting from varying dispersal ranges of different animal species, and small patches close to a larger "source" patch have more chance of species replenishment than those far away. These concepts become more complex as more attributes of habitat are added.

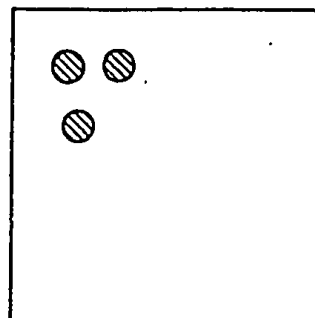
The second reason for measuring spatial heterogeneity is to determine how well the method used has measured variation in the animal community, i.e., are all relevant variations adequately represented? Fig. 2.2 represents three examples of regularly spaced transect sampling. In the first example, dense habitat is sampled with sufficient points to represent all three species in the community resulting in a sampling success of 80%. The sparse habitat contains the same number of species though they are less abundant and more dispersed. The same sampling effort



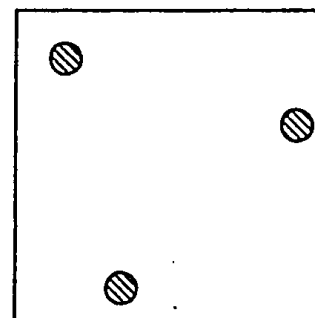
LINEAR



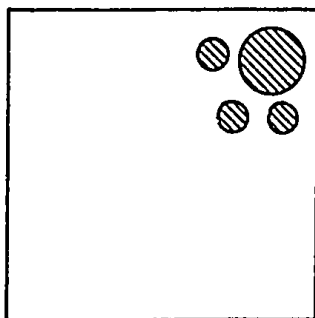
CIRCULAR



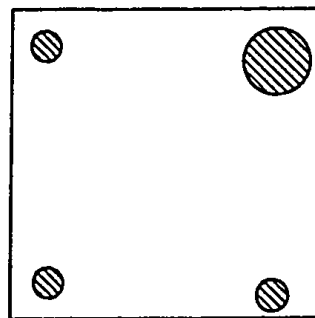
ADJACENT



DISPERSED



CLOSE to a large patch



DISTANT from a large patch

Figure 2.1 Configuration, location and distribution effects of environmental patchiness.

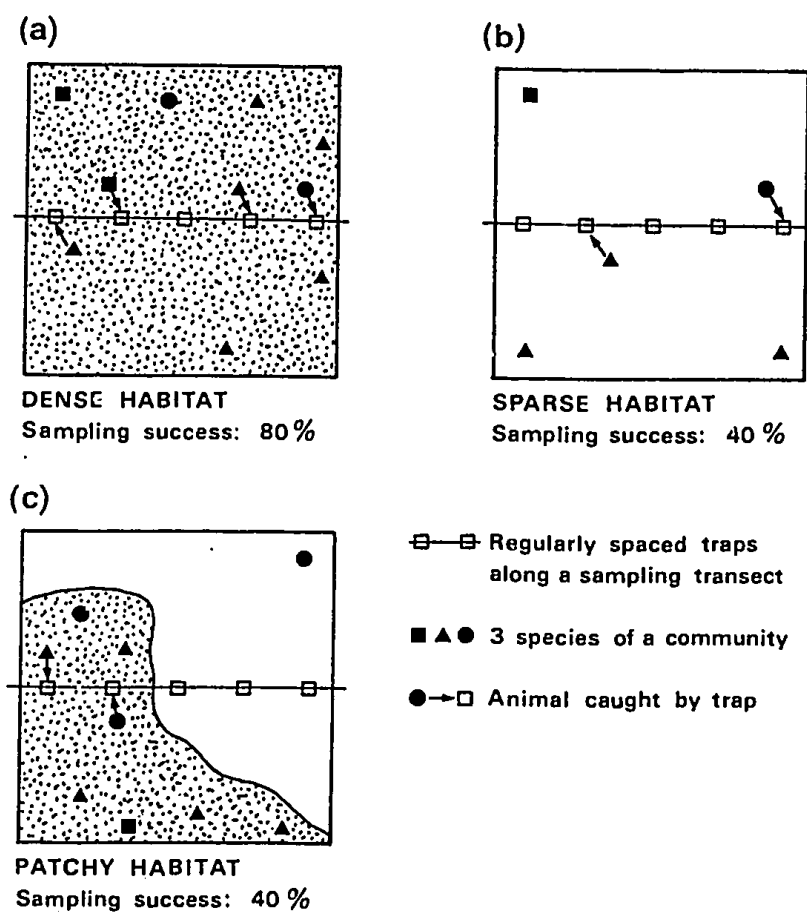


Figure 2.2 Efficiency of sampling in uniform and patchy environments.

results in 40% success which is proportional to that of the dense habitat. The third example contains both dense and sparse habitat with their respective animal distributions and are sampled by the same effort, resulting again in a success of 40%. This last example quite clearly has more abundant fauna although the sampling effort fails to show this. Some measure of habitat patchiness in relation to sampling effort is required to demonstrate these differences.

2.1.5 Measuring heterogeneity of the habitat.

The discussion in the previous section outlined the importance of measuring environmental heterogeneity to enhance and verify results obtained during a faunal survey. It emphasised the recognition of exogenous diversity and attempted to explain its contribution to total diversity, and the need to indicate how well the environmental variability of the area being surveyed has been sampled. Patchiness of environmental variables, be they biological, physical or chemical, may affect distributions of species within an animal community. For example, Pielou (1975) discusses the "nook and cranny" effect by factors of the physical environment that offer protection to prey species. When such resources (e.g., rock outcrops) are not uniformly distributed, the animals concentrate where they are most abundant. The size, shape and quality of such patches are then significant in determining local stability or extinction.

In defining the environment of an animal, Andrewartha (1971) proposes it to be all that determines an animal's chance to survive and multiply, dividing it into five components, i.e.:

- (i) resources;
- (ii) mates;
- (iii) predators, pathogens and aggressors;
- (iv) weather; and
- (v) malentities.

Any animal is thus treated as an individual; all other animals, whether of the same species or not, form part of its

environment. The components of environment in the definition are sufficiently broad to encompass both direct and indirect influences, which contrasts with the "effective environment" approach adopted by Maelzer (1965) and is modified by Niven (1980). For the purposes of this study, the more holistic approach by Andrewartha (1971) is accepted leaving the identification of resources directly influencing the animal to be included as habitat.

Understanding and defining habitat has long been debated by plant and animal ecologists resulting in a general dichotomy of perception (Campbell, 1982). The first interpretation is oriented towards theory of the niche following Hutchinson (1967) who defines habitat as those parts of the environment¹ that must be present for that species to occur. It is assumed then that habitat may be described by a unique set of environmental variables that have a correlation with the distribution and abundance of each species in the animal community. This multivariable approach to habitat depends upon the ecologist's ability to recognize and adequately represent these determining variables.

The other general concept of habitat perceives it to be areas of uniform physical, chemical and biotic factors, the sum of which define natural boundaries to unique animal communities. This view has received considerable support (Andrewartha, 1971; Elton, 1949, 1966) and is clearly useful for relevant landscape stratification although at a scale too small to allow interpretation of localized presence/absence and abundance of small mammal species. Additionally, this approach does not usually account for variations that may occur within an animal community caused by different adjacent habitats at different locations.

¹ The word 'environment' has been used here to replace the original word 'ecosystem' for consistency in terminology.

Considering that the current objective is to measure heterogeneity of the environment at a scale that expresses local diversity and sampling efficiency, the multivariable approach is preferred. Requirements of the heterogeneity measure are that it be flexible in a wide range of environments and that the data are suitable for use in a combinatorial index such as a multi-attribute score of vertical or horizontal structural diversity (e.g., Foliage Height Diversity as used in bird studies by MacArthur and MacArthur, 1961). With such requirements, survey sampling in different environments may be adjusted for valid comparison.

2.1.6 Requirements of the survey of small mammal communities.

The foregoing discussion outlines the basic requirements and possible developments in small mammal survey. A set of criteria may now be compiled to provide most information with the most efficient sampling strategy, within the limitations of present day knowledge of animal community, structure and function. Such a set is as follows:-

- A. The animal community
 - (i) number of species - this value allows preliminary assessment of richness of communities
 - (ii) relative number of individuals of each species - the element of evenness of numbers of individuals between species may be added to richness as an index of diversity
 - (iii) average weight for each age class of each species - as well as being able to separate juveniles from adults on body weight, this measure allows subsequent quantitative statements on biomass
 - (iv) sex of each individual caught - females of some species become prone to capture while pregnant or lactating. This causes a bias in sampling that may be exposed by knowledge of sex ratios

- (v) reproductive condition - some indication of breeding status in relation to the annual cycle for the species allows some assessment to be made of that population's stability at the time of survey.

B. Environmental complexity

- (i) spatial heterogeneity - a measure of patchiness of the environment is required to be incorporated in the sampling design
- (ii) vertical diversity of structural components of the habitat - if quantified (e.g., as percentage cover), habitat diversity may be correlated with faunal diversity to monitor for ecological perturbation
- (iii) resource availability - availability of habitat and food, and time of activity for each species may be scored to give an index of efficiency of utilization of the environment.

Faunal community structure fluctuates seasonally in relation to environmental change (Nix, 1974). To ensure that the range of fluctuations is represented in survey results, sampling should be repeated at times that correspond to maximums and minimums of resource availability.

For meaningful comparisons between seasons and habitats, it is important that the information required is produced by methods that are strictly standardized. Most survey groups procrastinate on attempts to standardize methods assuming that to use a similar sampling intensity in both rich and poor habitats is wasting field effort when the numbers recorded are low. However, it is equally important to compare both types of habitat to facilitate these comparisons. For this reason it becomes necessary to identify methods which allow optimum efficiency in providing relevant data so that standardization in survey is achieved.

2.2 Methods of survey.

Discussion in the previous chapter concluded from analyses of past surveys that the use of Elliott live-capture traps were the most widely accepted technique in Australian small mammal surveys. They were also shown to have the greatest success in capturing a wide range of species with body weights less than 300 gms. In this section, consideration is given to sample designs and methods of enumeration using this technique.

2.2.1 Sample design used in Australian small mammal surveys.

Twenty four recent (1977 and later) Australian small mammal surveys have been listed (Table 2.1) to compare methods of configuration, trap spacing, sample size and period. Not all surveys provided all types of information, so analysis is limited to what was available.

One half (54%) of the surveys trapped used a grid configuration, while one third (33%) set traps in straight lines (hereafter referred to as index-line trapping). Two surveys used both configurations and one survey used an alternative (4 sets of 8 traps in a cluster, 8m between each cluster). On grids, trap spacing ranged from 10m to 50m with most (43%) using 20-25m while with index-line trapping, spacing ranged from 3m to 20m with most (50%) using 5-10m. Grid sizes ranged from 1.0 Ha to 9.0 Ha with an average size of 5.35 Ha while the length of index-lines used range from 200m to 1400m, averaging 554m. The length of time over which traps were used ranged from 2 to 5 consecutive nights with 3 or 4 nights being most commonly used.

This simple analysis clearly highlights the need to further investigate grid and index-line configurations, with their associated variations of design, in relation to their efficiency at sampling and the relative time (cost) efficiency of use.

2.2.2 Grid and index-line trapping configurations.

The choice of grid or index-line configurations has received much attention in literature on methods.

TABLE 2.1 RANGE OF SAMPLE DESIGN VARIABLES USED IN AUSTRALIAN SMALL MAMMAL SURVEYS

SOURCE	CONFIGURATION	SPACING (m)	SIZE (Ha)	LENGTH (m)	NO. NIGHTS
Braithwaite L.W. (in prep.)	grid				3
Braithwaite <i>et al.</i> (1978)	grid		12x10		4
Braithwaite and Gullan (1978)	grid	23	12x10(6.6)		4
Cockburn <i>et al.</i> (1979)	grid	25	12x10(7.5)		4
Dickman (1980)	grid & line				
Friend (1979)	grid	20	6x5(1.2)		3
Fox & McKay (1981)	grid				
Hall & Lee (1982)	grid	25	10x12(7.5)		
Happold (1980)	grid & line				
Kingston <i>et al.</i> (1979)	line	3-5			5
Kitchener <i>et al.</i> (1976)	line				
Loyn <i>et al.</i> (1980)	grid	20	(1.0)		3
Milledge (1979)	line	5-8		420	4
Moritz (1982)	grid	20	10x10(4)		
N.P.W.S. (TAS) (1978)	line	10		200	
Newsome & Catling (1979)	grid				
Osborne & Marsala (1981)	"cluster of 8"	8		800	3
Pattemore (1977)	line	10		500	
Read D. (1982)	grid	10	15x18(2.4)		
Retcher <i>et al.</i> (1980)	line	4-5		250	4
Statham (1982)	grid		(9.0)		
Statham and Harden (1982)	grid	50	(9.0)		
Stewart (1979)	line	5		685	2-5
Suckling & Heislars (1978)	line	20		1400	3

Pelikan *et al.* (1964) have shown 50 x 50 m grids (5 m spacing) to provide reliable estimates of absolute population density over a range of 13 species. Large area grids also give reliable results (Dice, 1938; Southern, 1973). However, as Stickel (1948) notes, they are too laborious and time consuming for extensive studies so are not practical for sampling a large number of habitats in a single season. Her study compares grid and index-line trapping in forest and woodland. It shows that the relationship between trap configurations varies between habitats as index-line trapping overestimates population densities of mice (*Peromyscus leucopus*) when their home range was small. Index-line trapping was concluded to be unreliable for measuring relative abundance.

In a similar study, Petticrew and Sadlier (1970) provide contrasting results from data in three habitats. They state that a 100 m index-line (10 m spacing), gives an excellent indication of population parameters over a 1 Ha area in comparison with a grid which requires eleven times more trapping effort. Brant (1962) claims it is possible to determine absolute density by index-line trapping although others (Fowle and Edwards, 1954; Tanaka, 1960) had previously expressed doubts as to its accuracy. Flowerdew (1976) more cautiously refers to the usefulness of index-line trapping for comparisons between habitat or seasons and shows that the results may be related to actual densities by comparison with a more accurate grid.

The contrasting conclusions by different authors appear to be caused by their varying objectives and sampling intensities. Most literature relates to population studies *per se*, where absolute estimates are preferred and comparisons between habitats with differing combinations of species are not so important. For survey purposes, a relative measure that adequately represents the small mammal community for comparisons of species populations in time and space is sought. Which configuration best provides this information, and the relationships between results of these configurations remain unknown, particularly for Australian conditions.

2.2.3 Methods of estimating numbers

Another important consideration for sample design in survey is to select the most suitable method for establishing the numbers of each species. The range of methods may be categorised as:

- (1) mark/recapture methods
- (2) removal methods
- (3) frequency of capture methods
- (4) enumeration.

(1) Mark/recapture methods have been most commonly used for single species population studies to obtain an estimate of the absolute population. The methods are based on a sample of marked animals being released into the population, which is then resampled after a period of time (1-4 weeks). The ratio of recaptured marked animals to unmarked animals is used to give the population estimate. The simplest form is the Lincoln Index on which more sophisticated models have been built (Caughley, 1977). All mark/recapture estimates are based upon a set of assumptions (Southwood, 1978), which are easily violated and rarely accounted for. The most serious violation is of the assumption that animals have equal probability of capture (Eberhardt, 1969) which leads (usually) to an underestimation of the population.

Caughley (1977) comments that "Mark-recapture is both time consuming and expensive, and the results are often inaccurate because mark-recapture models are seldom more than a vague approximation to reality". Field trials to test these estimates against known populations (Dieterlen, 1967; Smith, 1968) suggest Caughley's statement to be correct.

(2) Removal methods include both actual removal of the animal from the study area (usually by killing) or assumed removal by marking the animals. Theoretically, the number of new animals caught on consecutive days decreases such that when plotted, a line drawn by eye or linear regression, intersects the abscissa, when no new animals are being caught,

thus providing an estimate of the total population (for example, the trap-out method by Hayne, 1949). Difficulties arise when numbers increase rather than decrease over consecutive days of trapping, or if results are erratic such that a straight line is not an efficacious representation of the data. Southern (1973) shows also that unless the numbers of animals caught at each trapping are similar, Hayne's trap-out method may give very misleading results.

Ryszkowski *et al.* (1966) examined results from the release of marked animals and complete removal of animals by regression analysis to find that estimates, while similar, were dependent upon animal mobility and trap-proneness. For community survey purposes, the actual removal of animals would give less than satisfactory results due to this variation in trap-proneness between species.

(3) Frequency-of-capture methods use the frequency with which animals are caught once, twice and so on to determine the number of animals that are never caught by modelling with either a truncated negative binomial distribution (Tanton, 1965), a zero-truncated Poisson distribution (Craig, 1953) or a geometric distribution (Eberhardt, 1969). The methods require traps to be randomized (by moving them during the trapping period) (Eberhardt, 1969) and fail if animals die during the period (Caughley, 1977). As each model suits some populations of species better than others (Caughley, 1977), their use for community studies may be complex.

(4) Simple enumeration may be derived from data based on grid or line sampling. The % trap success from a sampling period provides reasonable indices of abundance for each species although this depends upon variations in proneness to capture (Dice, 1931).

Methods of enumeration should avoid statistical assumptions of random sampling (Krebs *et al.*, 1976). A reliable estimate is the minimum known to be alive (M.K.B.A.) which includes all presently caught animals plus previously

caught animals that are caught again after the present capture (Krebs, 1966). The accuracy has been tested on 5 species of voles (*Microtus*) which gave an underestimation of 10-20% (Hilborn *et al.*, 1976), a result that compares well with other methods of estimation. However, the M.K.B.A. method may require more field time than is available under normal survey conditions.

2.3 Variables of survey.

In small mammal survey, many variables affect the probability of capture. Some variables (e.g. trap type, configuration) are discrete and may to some extent be controlled in the sampling design. Others (e.g., weather) are continuous variables and are uncontrollable.

2.3.1 Trap types and indirect techniques.

Discussion of attributes of traps used in Australian surveys has been included in the previous chapter (description of some trap types 1.2.3; efficiency, 1.2.4; species response, 1.2.6; evaluation, 1.3). While Elliott live-capture traps are clearly the most efficient, a single type is not necessarily to be recommended for application to a range of situations.

Selection of trap type depends largely upon the chosen method for estimating numbers (2.2.3). While snap traps have been shown to be more successful than live-capture traps for some species (Wiener and Smith, 1972; Fox and Posamentier, 1975), they are restricted to estimates by actual removal or simple indices. Live-capture traps allow more sophisticated enumeration and are less likely to distort the community structure. Pitfall traps, while being less efficient (1.3) and limited by soil type, have the advantage of being multiple capture i.e., they may catch more than one species and individual. Trap types less relevant to Australian survey are discussed in detail elsewhere (e.g., Smith *et al.*, 1975; Twigg, 1975; Flowerdew, 1976).

The probability of capture for many species varies yet changes are not readily detected by statistical methods (Roff, 1973). Statham (1982) was able to show variations in probability of capture between habitat, seasons and sex for *Antechinus stuartii* by using tracking techniques. Results showed also that 18% of the population were tracked but not caught in live-capture traps which indicates the need for alternative methods. Tracking has been used successfully for studies of space utilization (Bider, 1968) giving information on 58 vertebrate species. Marten (1972) claims that precise estimates can be made of single species populations by tracking techniques.

Other indirect techniques include hair sampling tubes (Suckling, 1978) and predator scat analysis (Friend, 1978), both of which require additional time for analysis which become valuable when the objectives of survey are to detect the presence of the rarer species.

2.3.2 Bait and prebaiting

The purpose of using bait in traps is to attract more animals towards the traps and provide more uniform capture results. Using bait significantly increases the chance of capturing rodents (Gurnell, 1976) although unbaited traps can still be successful (Kikkawa, 1965). The response to bait is seasonal and appears to be in response to the availability of natural food resources (Fitch, 1954). The choice of bait type in Australia ranges from oily rag to sophisticated combinations, however, by far the most popular is the rolled oats/peanut butter/honey mix.

The practice of prebaiting, or placing bait at the trap site for up to one week prior to trapping, is intended to increase the probability of capture and reduce the variance between days so that regression models provide a better fit to data from removal methods (Smith *et al.*, 1975). However, the response to prebaiting has shown it to be ineffective (Grodzinski *et al.*, 1966). That the response may be variable between species and that other animals might

be attracted to the study area makes the practice an unnecessary variable in survey.

2.3.3 Trapping configuration.

Some discussion of the two main trapping configurations, lines and grids, has been included previously (2.2.2). Smith *et al.* (1975) comment on variations and assessment of accuracy for density calculations. Most authors however, discuss configuration in relation to long term studies of populations and dispersion. For survey purposes, the configuration that most efficiently produces data on community structure in a heterogeneous habitat is required.

2.3.4 Number of traps used at each station.

Sample designs should aim to have no animals prevented from being caught so where more than one species coexist, their overlapping home ranges should be considered. Flowerdew (1976) recommends 2 traps or more while Andrzejewski *et al.* (1966) have shown significant capture increases up to 4 traps per station. However, both are discussing European conditions where trap success may be expected to exceed 50%. The average Australian trap success rate is about 10% (1.2.4) so their recommendations are not necessarily applicable.

Considering the coexistence of several species under Australian conditions, field trials at Lee's Creek, Brindabella Range (A.C.T.) resulted in there being no significant difference ($\chi^2 = 0.94$, $P > 0.1$) between using one or two traps per station (Read, unpub. data). The consequence was more effort required to set twice as many traps.

2.3.5 Trap spacing.

The distance between trap stations, or sampling intensity, should be such that all animals have sufficient opportunity to approach a trap (Flowerdew, 1976). This opportunity decreases as spacing increases so that when it is too great, inbetween animals will be missed altogether.

(Kikkawa, 1964). The chance of an animal encountering a trap then becomes one factor determining its proneness to capture (equals trapability used by some authors).

Several attempts have been made to relate trap spacing to population estimates with the objective of selecting an optimized standard. Gurnell (1967) used a two stage increase in sampling intensity (by reduced spacing) to show that increasing captures but decreasing sampling efficiency resulted. By more than doubling trap spacing (to 43.5m), Kikkawa (1964) found population estimates to be irregular and unreliable. Smith *et al.* (1975) note that 15m is a good compromise for most common species of small mammals. All empirical attempts however, have been outside Australia. As discussed previously (2.2.1), grids and index lines in Australian surveys have used 3m to 50m spacing, the choice of which is intuitively based.

In order to rationalize empirical or intuitive selection of trap spacing, attempts have been made to relate them to the animals' home ranges. Smith *et al.* (1975) discuss a 'recognition distance' as being related to the animals' ability to detect traps at a distance. Such a distance has been considered as the equivalent of 1/6th the average home range diameter of the dominant species (Smith *et al.*, 1969-70). The concept of home range however does not allow such simple objective measurement as it varies with environmental factors (Stickle, 1948), sex, age, season (Burt, 1943) and probably with community composition.

Clearly, the question of trap spacing is unresolved for Australian conditions. The approach to its resolution should be based on relationships with the density of the animal community and their habitat (Flowerdew, 1976) rather than on home range or dominant species population estimates.

2.3.6 Sampling area.

Effects of grid size or length of an index-line have received little attention in literature on sampling design. Population studies have related grid size to animal movement by the proportion of 'edge' the animal is likely to encounter to estimate its home range (e.g. Faust *et al.*, 1971). Small grids detect mostly resident individuals while larger grids with a more extensive edge, sample residents and migrants through the area (Faust *et al.*, 1971). Grid size is also a function of trap spacing (Smith *et al.*, 1975) so they should be considered concurrently when designing a sampling programme.

In Australian faunal surveys, sample size appears to be more related to the extent of relatively homogeneous habitat rather than to the structural complexity or diversity of the animal community contained within. The size of the sample is important for the efficiency of survey design as it is in plant community studies. Similar species-area curves have not been used for mammal communities.

2.3.7 Trapping period.

No Australian study to date has attempted empirically to show the optimum period of trapping to adequately represent small mammal communities. Faunal surveys have trapped over 2-5 days with 3-4 days being most common (2.2.1). While longer periods may be suited to removal methods of estimating numbers, they are not suited to live-captured animals as the incidence of trap losses becomes unacceptably high (A. Newsome, *pers. comm.*).

2.3.8 Seasons and weather.

Trapping the same small mammal community in different seasons can cause vastly different results due to natural population decline, low female activity during breeding or the unusual occurrence of male die-off in some species (e.g. *Antechinus* sp.). Females of the small dasyurid *A. stuartii* have been shown to become much less prone to capture during breeding (Statham, 1982) which, combined

with male die-off, may result in a drop in estimated numbers to just 8% of those in the peak period (C. Dickman, unpub. data). Knowledge of the reproductive timing for a species in one area is not suitable for other geographically separated areas as breeding can be related to such factors as altitude (e.g. Dickman, 1982).

It is important then that trapping should not become just a reflection of probability of capture (Smith *et al.*, 1975). If the local reproductive biology is not known, trapping should be at regular periods through the year. Otherwise it should be at two critical periods, during breeding and at peak density following dispersion of young (Ryszkowski, 1969).

Variation of weather conditions within a climatic season can not be planned. Cloud cover, temperature and rain appear to cause some variation in probability of capture (C. Dickman, *pers. comm.*) so a minimum period of 3 days trapping should be allowed to account for some variation.

2.4 Objectives of survey research.

From the preceding discussion, several issues in survey emerge and form the basic objectives of the research project described here:

- (i) to determine which trap configuration (i.e., square grid or index-line) returns data which are most representative of the small mammal community most efficiently by varying -
 - (a) the spacing between trap stations;
 - (b) the sampling area (grids); and
 - (c) the sampling length (index-lines).
- (ii) to investigate the use of indices of diversity (2.1.6) as a means of representing community variance using small data sets.
- (iii) to determine the ability of each of the eight methods (four grid and four index-line methods; 3.1) used to deal with environmental heterogeneity.

Chapter 3

FIELD SITES AND METHODS

3.1 Introduction

To carry out the previously stated objectives of research (2.4), field studies were established in two different areas. The first area was chosen as a site of clearly delineated habitat with well documented information on the small mammal community. The second area contained three sites which differed in the time since the last major disturbance such that they supported different floristic structure and composition. The former area was sampled first to study configurations and optimize trap spacing and sample size; these were then measured in the range of environmental conditions at the second area. Both areas were part of forest ecosystems.

Consistent with the objectives, the methods used were designed to compare:

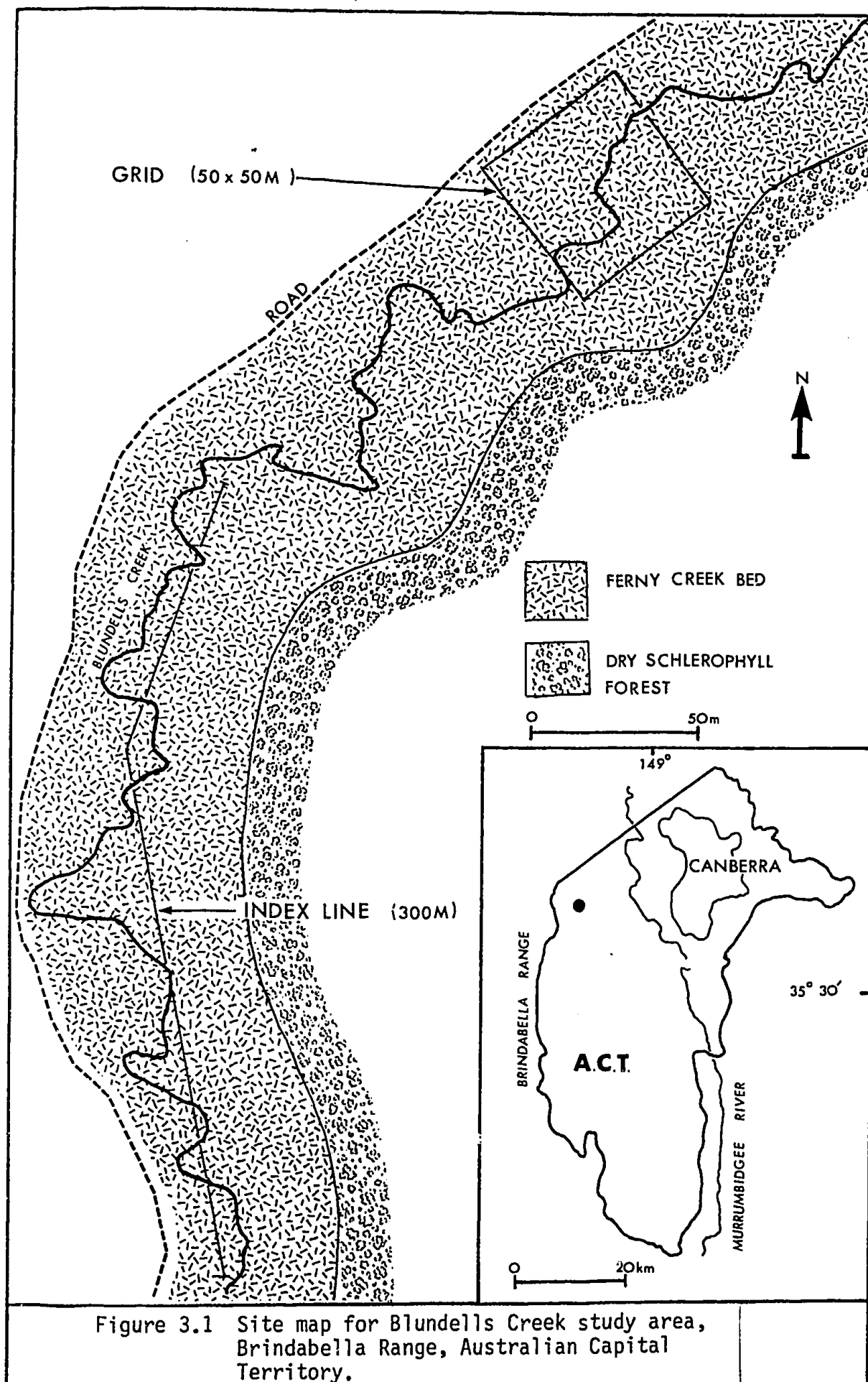
- (i) grid (50m x 50m) and index-line (maximum possible length) configurations, at
- (ii) four intervals of trap spacing (5m, 7.5m, 10m, 20m) and using
- (iii) sample sizes ranging from the minimum to the maximum area (grids) and lengths (index-lines) available.

Measures were taken of habitat structure at all sites to assess the response of each method used to variation in parameters significant to the distribution of small mammals.

3.2 Field Site Description

3.2.1 Blundells Creek - a site of known community characteristics

The Blundells Creek site (B.B.C.) lies 0.25 km upstream of that creek's confluence with Lee's Creek, located in the eastern foothills of the Brindabella Range approximately 25 km west of Canberra, Australian Capital Territory (Figure 3.1 insert). It extends 700 m along Blundells Creek and



varies in width from 60 to 80 m, being bounded on one side by a gravel road and by a steep hill relatively devoid of understorey on the other (Figure 3.1). Each end of the site tapers abruptly which isolates it from adjacent habitats defined in terms of small mammal communities. Ecological studies at the site over 3 years prior to the present study give evidence of its isolation as negligible immigration or emigration of any species was recorded (C. Dickman, unpub. data).

The habitat includes the creek which has a permanent fresh flow. Records from a meteorological station (maintained by the hydrology section, Division of Water and Land Resources, CSIRO) located 100 m from the western end, show the mean monthly rainfall to be relatively uniform with a slight increase in October. However, the year of the study was exceptionally dry with the annual total (491.9 mm) being only 36% of the mean annual average (1337.6 mm) and the two months during which field work was conducted (April, May) being well below their mean. During summer months, mean monthly maximum and minimum temperatures range from 12°C to 25°C while in winter, the period of the study, the range drops from <0°C to 10°C. Extremely cold, bleak days with associated sleet occur frequently, although only once during the trapping period. Snowfalls were not recorded until two months after the study.

Geology and soils of the site typify the Cotter River catchment and are described elsewhere (Florence, 1973).

The natural vegetation is classified as the "lower peppermint zone" by Florence (1973) and is characterised by a tall, open eucalypt canopy, a patchy understorey predominantly of acacias and a very dense ground cover of fishbone waterfern (*Blechnum nudum*). A list of dominant species is included in Table 3.1 and a quantitative structural description given in a later section (Appendix VI).

TABLE 3.1 LIST OF DOMINANT PLANT SPECIES AT EACH SITE.

(Numbers in parenthesis for the two lower strata is the total number of species occurring).

	B.B.C.*	D50 [#]	D68 [#]	D75 [#]
Upper Canopy	<i>Acacia dealbata</i> <i>Eucalyptus fastigata</i> <i>E. radiata</i> <i>E. viminalis</i>	<i>Acacia irrorata</i> <i>A. obtusifolia</i> <i>Eucalyptus bosistoana</i> <i>E. botryoides</i> <i>E. muellerana</i>	<i>Acacia falciformis</i> <i>A. irrorata</i> <i>A. obtusifolia</i> <i>Angophora floribunda</i> <i>Eucalyptus globoidea</i> <i>E. longifolia</i> <i>E. sieberi</i>	<i>Angophora floribunda</i> <i>Eucalyptus globoidea</i> <i>E. muellerana</i> <i>E. sieberi</i>
Lower Canopy	<i>Cassinia aculeata</i> <i>Clematis aristata</i> <i>Coprosma hirtella</i> <i>Pomaderris aspera</i> <i>Rubus fruticosus</i> (10)	<i>Indigofera australis</i> <i>Nolalaea longifolia</i> <i>Persoonia linearis</i> <i>Psychotria esculentum</i> <i>Synowm glandulosum</i> <i>Zieria smithii</i> (8)	<i>Acacia obtusifolia</i> <i>Elaeocarpus reticulatus</i> (11)	<i>Acacia irrorata</i> <i>A. obtusifolia</i> <i>Correa reflexa</i> (8)
Ground Cover	<i>Acaena anseimifolia</i> <i>Blechnum nudum</i> <i>Dicksonia antarctica</i> <i>Geranium sp.</i> <i>Pteridium esculentum</i> (21)	<i>Gahnia sp.</i> <i>Geitonoplesium cynosum</i> <i>Hibbertia dentata</i> <i>Opismenus imbecillis</i> <i>Poa sieberana</i> <i>Pteridium esculentum</i> <i>Smilax australis</i> (29)	<i>Lichen</i> <i>Pandorea pandorana</i> <i>Poa sieberana</i> <i>Pteridium esculentum</i> (18)	<i>Acacia irrorata</i> <i>Entolasia stricta</i> <i>Lomandra filiformis</i> <i>Microsorium diversifolium</i> <i>Moss</i> <i>Pteridium esculentum</i> (25)

* Species with frequency of occurrence $\geq 20\%$ included as dominants (Dept. Forestry, ANU, data)# Species with percentage cover values $\geq 10\%$ included as dominants (Div. W. L.R., CSIRO, data)

3.2.2 Mt. Dromedary - three sites of variable environment.

The three sites (D75, D68 and D50)* are located in an area 16 km WSW of Narooma, a coastal town on the eastern seaboard of N.S.W. (Figure 3.2 insert). The area is within the Bodalla State Forest which has a silvicultural history dating back to the 1920s. Practices over this period have included selective logging, ringbarking (to encourage favoured tree species) and control burns which, with major wildfires in 1952 and 1968, have created a mosaic pattern of growth. The three sites selected from this pattern represent a gradient of successional status following disturbance, with 7, 14 and over 50 years of relatively undisturbed growth which is reflected by differences in floristic structure and composition.

All sites are situated on the same aspect (S.E.) and altitude (150m A.S.L.) in a steeply undulating landscape, and are located between a ridge and a moist gully on similar soils and geology, which have been described elsewhere (Forestry Comm. N.S.W., 1981).

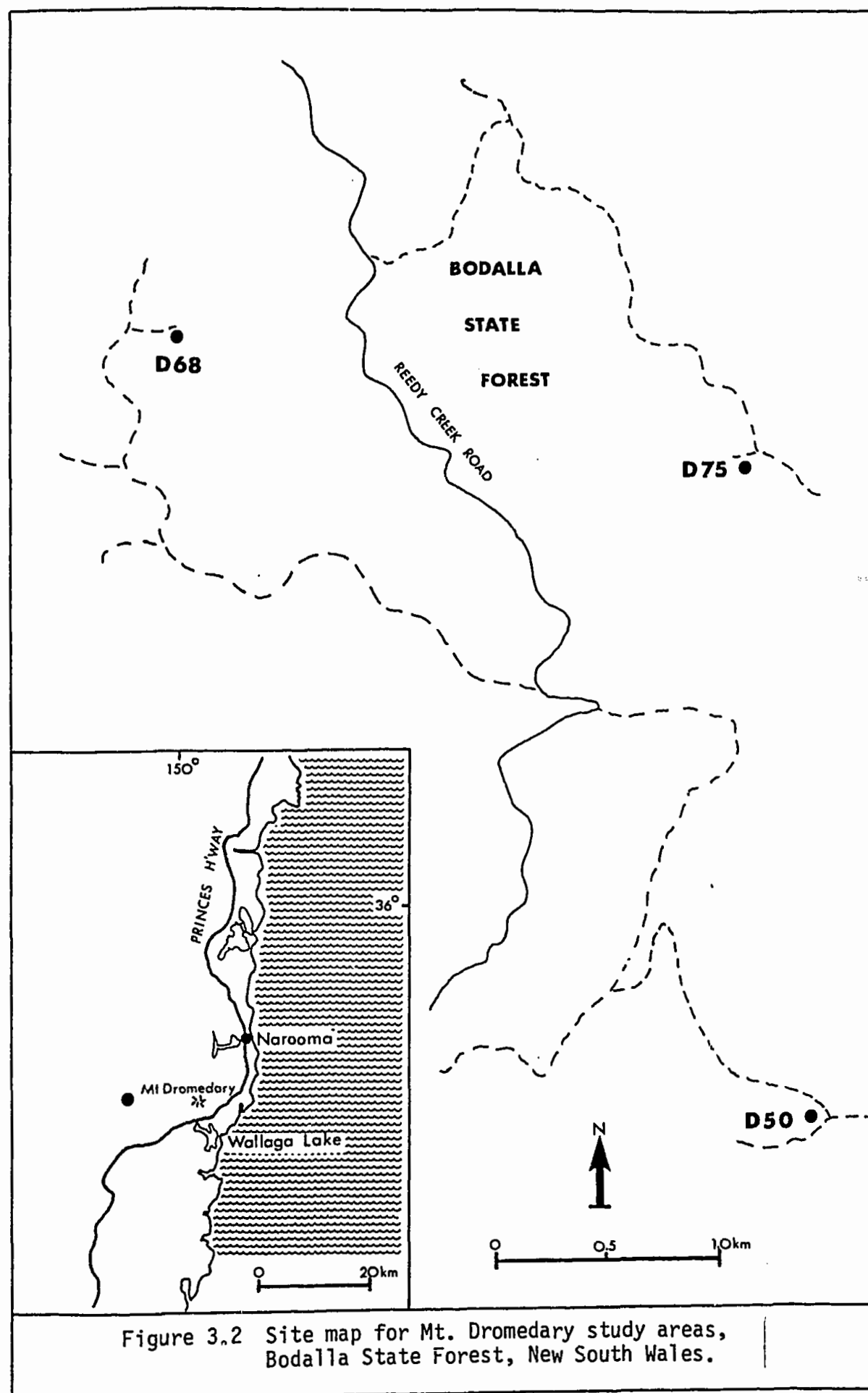
Rainfall for the area is approximately 1100 mm per annum although each site may vary according to its location relative to Mt. Dromedary which has a marked topographical influence on the microclimate (Kalma and McAlpine, 1978). Monthly rainfall values show distinctly dry winter months (June, July, August) while the remaining months are relatively uniform. Winter minimum and maximum temperatures range from 3°C to 16°C while during summer their range increases to 12°C and 23°C.

Vegetation in Bodalla State Forest ranges from dense, pure stands of silver top ash (*Eucalyptus sieberi*) poles to undisturbed wet gullies containing complex pockets of remnant rainforest communities. The sites are representative of environments within this range. D75 has

* D75 was significantly disturbed by logging last in 1975

D68 was significantly disturbed by logging last in 1968

D50 has not been significantly disturbed for more than 50 years.



has an open upper canopy, a poorly developed lower canopy and diverse ground cover, including a significant cover of logs, stones and deep litter. D68 has a well developed upper canopy, poor lower canopy and a species rich ground cover dominated by up to six species of fern. D50, the oldest site, contains some senescing trees dominating the upper canopy but it is the lower canopy that is best developed. Ground cover is diverse though patchy and dependent upon light availability through the sometimes dense lower canopy. Decayed logs and deep litter are a feature of the ground cover. Table 3.1 presents the floristic stratification and diversity for each site and a structural description is given in a later section (Appendix VI).

3.3 Sampling design for survey method assessment.

3.3.1 Site Layout.

At each of the four sites, a 50m x 50m grid was set up with stations marked at 5m intervals. Columns were denoted by letter and rows by number to give an alpha-numeric label for each station. At the B.B.C. site, the grid was set in the broadest section of the habitat with the columns set perpendicular to the long axis of the site. The index-line was set up 120m downstream from the grid again with stations marked 5m apart. The gap of 120m between the two sampling configurations was chosen as being greater than any of the movements by individuals of all species during the initial trapping (Trip 1). This allowed the two configurations to be sampled concurrently. Sampling consecutively by each method would have doubled the time spent in the field causing overlap with breeding, a period of reduced female activity and male die-off in *Antechinus sp.* (Figure 3.3) (after C. Dickman, unpub. data).

The three sites at Mt. Dromedary however, were set up with the index-line overlaying the grid configuration as the area of relatively uniform forest type was not sufficiently extensive to allow their separation. Trapping the configurations at each site was consecutive (i.e. 3 nights

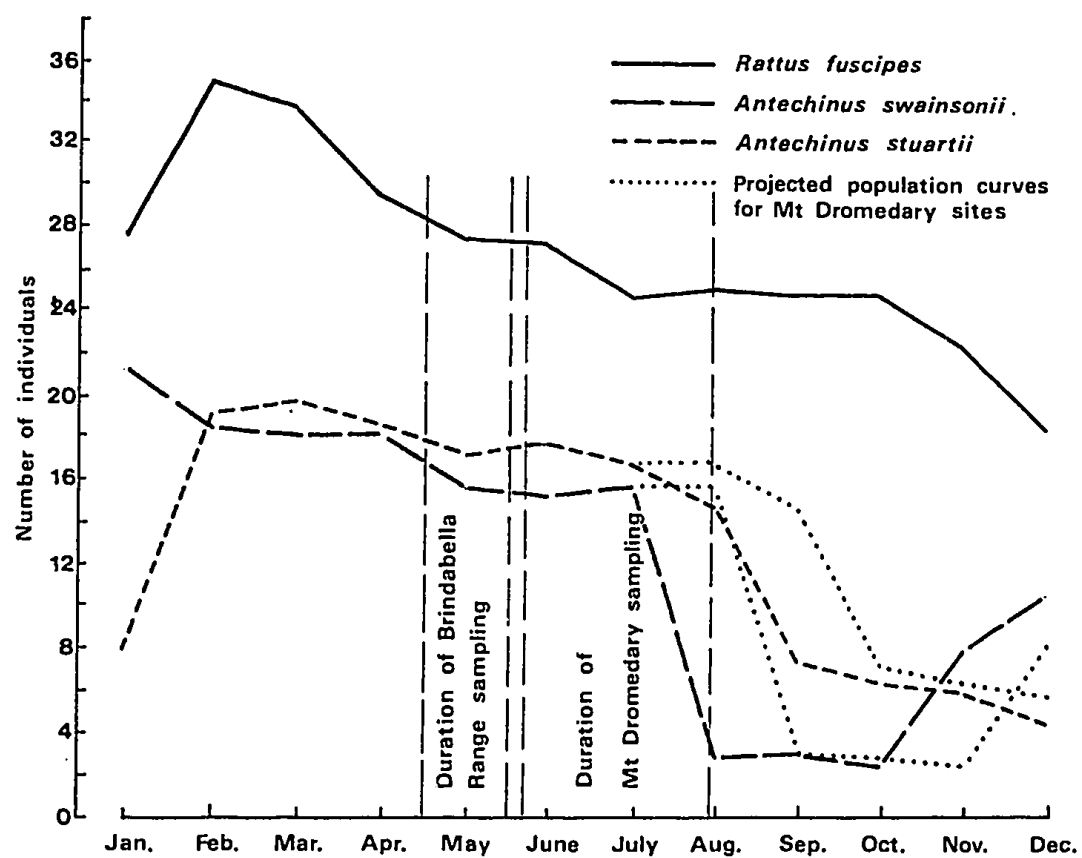


FIGURE 3.3 POPULATION TRENDS FOR THREE DOMINANT SPECIES AT SITE BBC WITH PROJECTED TRENDS FOR THE MT. DROMEDARY SITES (AFTER C. DICKMAN, UNPUB.)

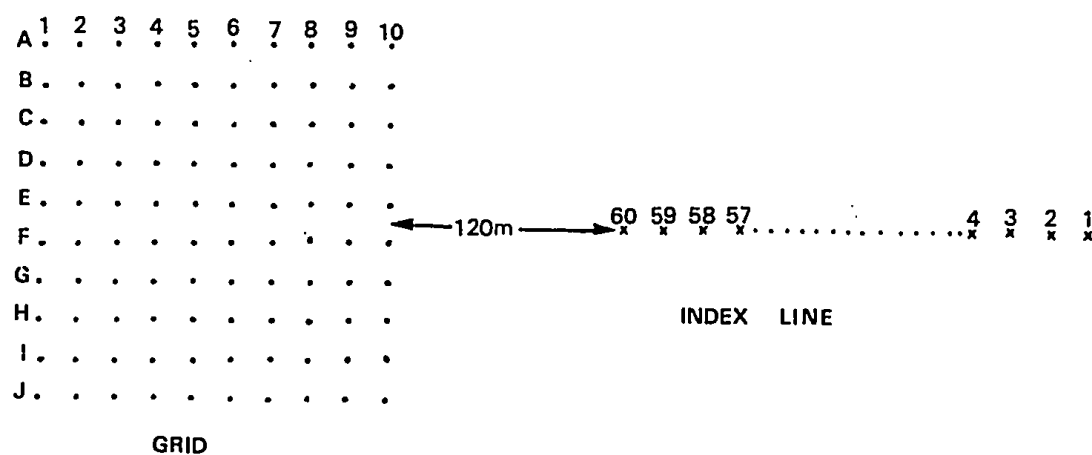
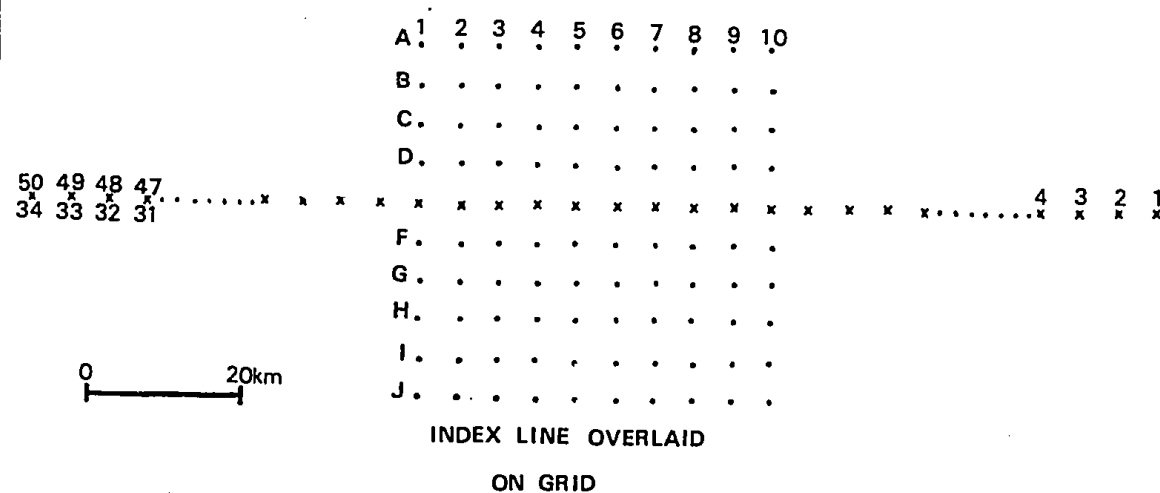
grid trapping followed by 3 nights index-line trapping), which, by working all three sites concurrently, allowed the programme to be completed before the effects of breeding influenced the coastal populations (Figure 3.3). In effect, the configurations at these sites were separated temporally compared to the spatial separation at B.B.C. (Figure 3.4). Grid columns were aligned along the contour to make fieldwork less strenuous as traps were set sequentially along columns. Each grid was centred on previously established plots chosen for a study of vegetation dynamics (Austin and Margules, unpublished).

3.3.2 Sequence of field trips.

With knowledge that breeding of dominant species at the coast occurs at least one month later than populations in the Brindabella Range (C. Dickman, pers. comm.), the B.B.C. site was trapped first. Dates, methods used and cumulative totals of trap-nights are listed for each field trip in Table 3.2.

The first trip to B.B.C. site was used to mark the animals and for site layout. Traps were set at 20m intervals along lines on either side of the watercourse for the full extent of the habitat for three nights. Marking of the grid and index-line occurred on the final day following an estimation of movement by individuals to ascertain the separation distance required between the two configurations. Subsequent trips sampled with grid methods of increasing trap spacing while index methods were treated in the reverse order (Table 3.2) to balance field effort over the trips.

The sequence of methods used at each site at Mt. Dromedary was also arranged to balance field effort. At those sites however, no initial trapping was undertaken. This appeared to cause the first set of results to be lower than expected, probably due to an early behavioural response to the traps. These methods were repeated during a later trip (Table 3.2).

BBC**D75,D68
D50**NUMBER OF TRAPS USED

<u>METHOD</u>	<u>ALL SITES</u>	<u>METHOD</u>	BBC	D75	D68	D50
G(5)	100 traps	I(5)	60 traps	50 traps	50 traps	34 traps
G(7.5)	49 "	I(7.5)	45 "	37 "	37 "	26 "
G(10)	25 "	I(10)	30 "	25 "	25 "	17 "
G(20)	9 "	I(20)	15 "	12 "	12 "	9 "

Figure 3.4 Site layout for trap grid and index-line.

TABLE 3.2 CALENDAR OF TRAPPING PERIODS

TRIP NO.	DATES	SITE + METHODS	SITE + METHODS	SITE + METHODS
1	15-24.4.82	BBC initial trapping + site layout [300]		
2	20-23	BBC G(5) + I(20) [645]		
3	25-29	" G(7.5) + I(10) [882]		
4	4-7.5.82	" G(10) + I(7.5) [1087]		
5	11-14	" G(20) + I(5) [1294]		
6	20-21	D75 site layout	D68 site layout	D50 site layout
7	24-28	" G(7.5) [147]	" G(5) [300]	" G(7.5) [147]
8	1-4.6.82	" G(5) [447]	" G(7.5) [447]	" G(5) [447]
9	9-15	" G(20) + I(7.5) [573]	" G(10) + I(7.5) [621]	" G(20) + I(7.5) [543]
10	17-23	" G(10) + I(5) [798]	" G(20) + I(5) [798]	" G(10) + I(5)* [652]
11	28-1.7.82	" I(10) [873]	" I(10) [873]	" I(10) [703]
12	6-12	" G(7.5) ^R + I(20) [1059]	" G(5) ^R + I(20) [1215]	" G(7.5) ^R + I(20) [877]
13	22-28			" I(7.5) ^R + I(5) ^R [1051]

TOTAL of 4619 Trap Nights

[] cumulative number of trap nights.

* abandoned due to disturbance by dingoes

R repeat

Trips were arranged to have a minimum of three nights between sampling periods as more frequent trapping would have resulted in high mortalities. Exceptions to this were for the Mt. Dromedary sites where the index-line overlaid the grid and trapping periods followed on from each other.

3.3.3 Field procedure.

For each method at all sites, traps were set during the afternoon of the first day and were cleared during early morning on the following three days. Traps on the grid were left closed during the day to prevent re-entry of animals following their release. Immediate re-entry did not occur with index-line trapping as released animals encountered no open traps adjacent to the line, so traps remained set during the day.

Elliott live-capture traps (30 x 10 x 9 cm) were used, each being baited with a peanut butter, rolled oats and honey mixture, lined with cotton wool for insulation and enclosed in a plastic bag to prevent moisture. Each trap was set at the most appropriate location within a 5 x 5m cell centred on the relevant trap station.

All new animals caught were sexed, weighed and toeclipped for subsequent identification and recaptures were recorded for each station. Traps that caught animals were cleaned each day in the field, rebaited and relined. All traps were thoroughly washed at the end of each trip.

3.3.4 Disturbance by predatory animals.

On several occasions, traps were disturbed by either a bandicoot (*Perameles nasuta*) or by dingos (*Caninus familiaris dingo*), probably attracted more by the bait than by the captive animals. Traps were usually only sprung, although at one site (L0) dingos learnt to remove the plastic bag and withdraw the joining wire so dismantling them. The bait was usually, although not always, taken. Frequently, traps containing animals were not disturbed, but one *Antechinus stuartii* was assumed missing following heavy

disturbance at site D50 during Trip 10. That sampling effort was abandoned and repeated on a later trip. The bandicoot was trapped and removed from the site. Dingo disturbance was minimized by frequent visits to the site and by distracting them with fires, radios and scarecrows. The trapping results obtained are considered to have been unaffected by this disturbance.

3.4 Selection of environmental variables.

As discussed previously (2.1.5), the efficacy of using a multivariate approach to habitat analysis depends upon the ecologist's ability to select those environmental variables that are significant in determining an animal's distribution and abundance. They should also be variables that are quick and precise to measure with low intra-seasonal variation and be effective in the immediate vicinity of the capture site (Dueser and Shugart, 1978). While the primary objective of the present study is not to describe habitat requirements for small mammal communities, a similar analytical process is required in order to identify those variables that are significant in causing corresponding heterogeneity of the community.

The first stage in selecting variables was to stratify the habitat. This was necessary to accommodate varying sampling scales (e.g. sample size required for mature trees compared to that for ferns) and to simplify subsequent analysis. The stratification used was

Stratum 1	upper tree canopy	(>4 cm D.B.H.*)
Stratum 2	lower tree canopy	(>4 cm D.B.H.)
Stratum 3	tall shrub layer	(<4 cm D.B.H., >1.5m height)
Stratum 4	low ground cover	(vegetation cover <1.5m height)
Stratum 5	ground cover resources	(litter, stones, logs etc.)
Stratum 6	soils	

* Diameter at Breast Height.

Separation between Strata 1 and 2 was not defined to allow flexibility in the field. These two dominant tree canopies were used if both clearly existed, although Stratum 2 was deleted if not. More tree strata than two and emergent tree species were ignored. The height separation of 1.5m between the tall shrub layer and low ground cover was chosen to ensure that most fern species, shown elsewhere to be important to small mammals, (Woodside, 1983) were included in the lower stratum.

The second stage was to select variables within each stratum that were relevant to the community and were measurable. By considering some related studies, a list of habitat attributes was compiled and those shown to be significantly correlated with the animals were identified (Appendix I). The list clearly shows a preference for measures of floristic richness, some of which were highly correlated with animal distributions (e.g. Fox and Fox, 1978). Most of these studies, however are of heathlands which are floristically rich and relatively simple structurally. The decision was made not to include floristics for several reasons. The objective behind this study is to evaluate survey methodology suitable to a range of environments and the inclusion of floristics would not improve the basis for comparison of life forms and morphological characters varying across the geographical range of some species (Gillison, 1981). In a comparative study of five vegetation classifications ranging from a structural to a systematic floristic survey, structural and floristic variables and classifications based on them were found to be highly correlated and contained much of the same information (Fox and Fox, 1981) which demonstrated that floristics added little to the classification. Considering also that many species of small mammals are wide ranging (e.g. *R. fuscipes*, *A. stuartii*) and are frequently habitat generalists (Robinson, 1975), floristics have little application or predictive power for their distributions (Barnett *et al.*, 1978).

From the structural variables selection was made within each vegetation stratum of those that represented height and estimates of abundance and cover density. Combined, they form a measure of structural complexity and shrub layer density significant to common species of small mammals (Barnett *et al.*, 1978; Braithwaite and Gullan, 1978). Several other variables were added:

bark type - as several common species are partially arboreal (e.g. *A. stuartii*), the type of bark may be significant in their distribution. Arboreality is a form of predator avoidance during breeding and a way of utilizing another food resource (bark-dwelling insects).

presence of acacias - some measure of the abundance of acacias in Stratum 3 was considered important as

- (i) an indicator of ecological succession (significant to *P. novaehollandiae*, Braithwaite and Gullan, 1978)
- (ii) an indication of nitrogenous status of the soil
- (iii) a food supply for *R. fuscipes* (sugary exudates from the bark, Warneke, 1971).

runways - the presence of runways in the components of Stratum 4 has been shown to influence the trapping success of some species (Stewart, 1979).

litter - dense litter provides cover while moist litter encourages an invertebrate food resource.

stoniness - stony soils were avoided by *R. fuscipes* (Taylor, 1961), while rock outcropping provides shelter.

logs and stumps - depending upon size and the state of decay, logs and stumps provide invertebrate food and home sites. Some may serve as runways connecting isolated patches of habitat.

bare soil - considered as an indication of patchiness; included also in other studies (Campbell, 1982; Fox and Fox, 1978).

watercourse - as Blundells Creek (B.B.C.) was flowing during the sampling period, it was considered important as a barrier to movement.

soil type - variations in soil texture and moisture may influence the distribution of fossorial animals (Cockburn, 1978; Newsome and Catling, 1979).

However soil hardness, often recorded, has been shown to have little relevance to small mammal distributions (Posamentier, 1975) so was ignored.

3.4.1 Description and quantification of environmental variables

Lists of variables measured for each stratum are listed in Table 3.3. Those measured as discrete units (numbers of trees, presence/absence of runways, moist/dry soil etc.) are self explanatory. Those measured as continuous units are based on field estimates and are supported by representative photographs in Appendix II.

For Strata 1 and 2, some measure of both the cover and density of each canopy was required. Foliage cover (i.e. the proportion of ground area covered by the vertical projection of foliages and branches) were selected using estimation techniques of Walker and Tunstall (1981). This is the product of two canopy characteristics

- (i) crown ratio (c) - the ratio of gap between the crowns to the diameter of the crowns (most efficiently measured by field estimation)
- (ii) crown type - a measure of canopy density based on a set of comparative photographs (Appendix III).

Crown ratios are converted to crown cover values (tabled in Appendix III) then multiplied by the percentage value of crown type

e.g. if $c = 1$ (i.e. gap between crowns = mean crown diameter) and crown type = 50% (field estimates from photographs), then crown cover values are converted from c (= 20, from table in Appendix III). Foliage cover = $0.5 \times 20 = 10\%$.

TABLE 3.3 ATTRIBUTES MEASURED TO ASSESS HETEROGENEITY OF THE HABITAT

VARIABLE	LIMITATIONS	NOTATION
<u>STRATUM 1 and 2</u>		
(SAMPLE SIZE: 25 m x 25 m)	Number of trees	>4 cm D.B.H.
	Height	mean value
	Diameter at breast height (D.B.H.)	" "
	Canopy ratio	cm
	Crown type	%
	Crown diameter	M
	Bark type - gum	0-3 (0 = absent; 3 = 100% occurrence)
	- fissured	0-3 (" " ; " " ")
	- ribbon	0-3 (" " ; " " ")
	- other	0-3 (" " ; " " ")
<u>STRATUM 3</u>		
(SAMPLE SIZE: 5 m x 5 m)	Number of trees	<4 cm DBH; >1.5 m
	Height	mean value
	Cover	M
	Canopy density	%
	Presence of acacias	0-3 (0 = bare stems; 3 = very dense thicket)
		0-3 (0 = absent; 3 = 100% occurrence)
<u>STRATUM 4</u>		
(SAMPLE SIZE: 5 m x 5 m)	(Height	M
	(Cover	%
Woody plants x	(Cover density	0-3 (0 = bare stems; 3 = very dense thicket)
Ferns	(	
Grasses	(Runways	P/A (present/absent)

TABLE 3.3 (Continued)

VARIABLE	LIMITATIONS	NOTATION
<u>STRATUM 5</u>		
(SAMPLE SIZE: 5 m x 5 m)	Litter - depth - moisture - cover	cm D, M, W (Dry, Moist, Wet) %
	Stoniness - size - cover - rock outcropping - rock ledges	cm % % P/A
	Logs and stumps - diameter) - number) - decay) - number) - decay)	cm 0-3 (0 = green; 3 = extreme decay) 0-3 (" " ; " " ")
	Bare soil	%
	Watercourse	R, S, D (Running, Stagnant, Dry)
<u>STRATUM 6</u>		
(SAMPLE SIZE:	Soil type Soil moisture	S, L, C, G, (Sand, Loam, Clay, Gravel) M, D (Moist, Dry)

3.4.2 Design of sampling

As the environmental variables were to be correlated with animal distributions in the analysis, it was imperative that they be measured correspondingly. This resulted in samples that were non-randomized, however where variations in the environment are distinct and the intensity of sampling is sufficiently large to be not just representing some environmental regularity, this is advantageous (Grieg-Smith, 1957).

The size of sample plots for the lower strata was set at 5m x 5m as this represented the cells about each trap station within which traps were set. A larger size may have resulted in lower variance in the samples, but this would have reduced the number of samples leading to a greater standard error (Kershaw, 1964) and increased field effort. Data were taken at every second trap station for these strata. For the tree strata (Stratum 1 and 2), this sample size was considered too small and was increased to 25m x 25m. Four of these samples included the complete grid while up to nine were required for transects. Clearly, samples on the transects were measuring habitat not directly related to the trap station 'cells'. Samples of this size however were necessary to reduce sampling variance.

All sampling was conducted by one field estimator so that bias in subjective estimates was minimised.

Chapter 4

A REVIEW OF ANALYTICAL METHODS

4.1 Introduction

The objective of comparing methods of sampling small mammals was approached by analysing capture data independently for each site. A subsequent test was carried out for similarity of sites based on the results of the different methods. A further objective was to assess the ability of each method to adequately measure faunal diversity patterns resulting from environmental patchiness. The two data sets have been analysed separately.

Choice of methods of analysis is discussed, along with a review of literature on indices of species diversity. A model using a hypothetical data set demonstrates the response of some of the more robust diversity indices when small numbers are used.

4.2 Analysis of Animal Communities

4.2.1 Selection of an analytical approach

Previous discussion on methods of estimating numbers (2.2.3) outlined weaknesses involved in using estimations based on models or assumptions that are easily violated. A significant weakness of the commonly used mark-recapture estimates is inequality in probability of capture. Causes for this may be due to:

- (i) inherent variation between species and individuals within the community
- (ii) varying abilities to learn about traps by species and individuals (i.e. the development of behaviour that may lead to trap-proneness and trap-avoidance)
- (iii) the relative chance of capture.

While the first two factors will be present regardless of methods, the third factor is dependent upon the density of traps in the sample. Equal chance of capture of different

animals may be possible with close trap spacings but it is likely to vary as the spacing is increased. This is the primary reason why mark-recapture estimates have been avoided in this study in favour of simpler, less biased methods of enumeration. Caughley (1977) states that the former are time consuming, expensive and give results that are often inaccurate.

Other methods of estimating numbers were also avoided because of their incompatibility with the survey design, or their dependence upon unjustified assumptions. The minimum-known-to-be-alive (Krebs, 1966), and simple, cumulated trap captures to represent estimates of the total community and that part of it being sampled by each trapping method respectively, were chosen to avoid statistical assumptions inherent in random sampling (Krebs *et al.*, 1976).

Similarly, analyses to evaluate differences between methods in this study avoided the use of techniques based on mathematical models. Such analyses are usually dependent upon the normal-theory model which assumes that biological distributions fit a Gaussian curve, i.e.:

- (i) the data are continuously distributed
- (ii) the distribution is bell-shaped and symmetrical and
- (iii) the variance of the sample is independent of the mean.

Clearly, small mammal capture data are continuous. A symmetrical bell-shaped distribution of the data is unlikely, as small mammals are not usually randomly distributed and thus not necessarily randomly sampled, and the variance is not independent of the mean (Taylor, 1961).

Parametric methods apply to single species populations. Methods of analysis that apply to a complete community require some inter-population component to quantitatively represent both species numbers and their relative abundances. Indices of diversity provide such a function. Their responses to changes in numbers of species, or individuals in a sample provide a basis for summarising a multivariable situation. This permits their use for analysis of variance in community samples.

An alternative to indices of diversity is the use of similarity indices or coefficients which combine data in such a way as to enable comparison of two or more communities. Such indices may be arranged in matrices for use in multivariate analyses. Diversity indices use capture data in a way that is not sensitive to *a priori* assumptions (i.e. equal probability of capture, and randomized sampling), and is not easily invalidated by changes in sampling design. Such non-parametric methods of analysis are more powerful when these assumptions are not met (Colquhoun, 1971).

4.2.2 Indices of Species Diversity

Indices of species diversity provide a measure of variance within animal communities across a range of scales against which patterns of community stability and organization may be measured. The causes of species diversity remain a well debated although unresolved ecological problem (Krebs, 1978; Ricklefs, 1980). Trends in community organization frequently display wide and unpredictable variation as, for example, that between avian and lacustrine phytoplankton communities (Tramer, 1969). Hurlbert's (1971) criticism of diversity indices as having limited interpretational value for true diversity appears justified. However, as indices of difference between communities their use in analysis of faunal survey data is relevant.

Species diversity has not been clearly defined in the literature. Most attempts consist of a statement of the statistical components of richness and evenness of the individuals in a sample combined to form an index (Margalef, 1969; Pielou, 1969) without a definitive ecological relationship implied. This vagueness of approach is reflected in the large range of indices used to measure diversity, and by the poorly understood relationship between the statistical indices and their ecological interpretation. Such conceptual difficulties do not necessarily negate their use but it does require users to consider the indices analytically before selecting those suited to the animal community being studied and the type of information required.

Whittaker (1972) identified three levels of diversity. Alpha diversity is that which occurs within a pre-defined habitat and is primarily determined by resource availability. Beta diversity occurs between habitats and is dependent upon heterogeneity along environmental gradients. Gamma diversity represents community variation within distinct geographic areas and is composed of both alpha and beta components. This study is restricted to delineated habitats and only alpha diversity is considered.

4.2.2.1 Desirable properties of species diversity indices

It is not possible to measure and describe the total alpha diversity of a given community. Instead, indices are used to give a representative estimate of the diversity based on samples of the populations present. Two important sampling statistics required in the construction of the indices are:

- (i) number of species (S , $S = s_1 + s_2 + \dots + s_i$)
- (ii) number of individuals (N , $N = \sum n_1 + n_2 + \dots + n_i$)

In using these statistics in an index, it is desirable that the index has the following properties (after Pielou, 1975)

- (a) the index has greatest value for a completely even community (i.e. $n_1 = n_2 = \dots + n_i$)
- (b) with two completely even communities, one with s_i species, the other with s_{i+1} species, the latter should have the higher index value
- (c) if the information is classified in two different, independent ways (e.g. species, genus, family or class), the combined information obeys the superposition principle i.e. for two taxa, A and B, $\text{Index (AB)} = \text{Index (A)} + \text{Index (B)}$
- (d) they be relatively independent of sample size.

4.2.2.2 Species richness

Species richness, the number of species (S) in a sample was first quantified by Fisher *et al.* (1943) as a log.

series model of the relationship between the number of species and the relative abundance of each. Preston (1948) later proposed that a lognormal distribution provided a better fit for species abundance data, and that the relationship could be used to calculate the number of species expected in a total sample. Such *a priori* models require the proportionality between the species to be stable. They are also dependent upon sample size. Possibly the most effective measure of richness is provided by direct counts of species numbers in samples (MacArthur, 1965) although sample sizes as effected by time, area or number of individuals must be standardized between communities.

4.2.2.3 Heterogeneity indices

While richness provides a first approximation of diversity within a community, it takes no account of the numbers of individuals in each species (evenness). Dual-concept indices have been developed to combine both richness and evenness of the spread of individuals. Taken from differing theoretical bases, such indices differ to varying degrees in their sensitivity to changes in the number of species, the abundance of common species, the abundance of rare species and to changes in sample size without proportional change between the species. Some of the more robust and commonly accepted indices of community heterogeneity are discussed below.

Simpson (1949) was amongst the first to recognize the dual concept of diversity. He proposed that the probability that two individuals, selected at random from a sample will belong to the same species provides an index of diversity. This may be formulated as:

$$L = \sum_{i=1}^S \left(\frac{n_i}{N} \right)^2 = \sum p_i^2$$

L = Simpson's index of diversity

N = total number of individuals

n_i = number of individuals for the i^{th} species

$$\text{(or, } L = \sum \frac{n_i (n_i - 1)}{N (N - 1)})$$

for incompletely sampled communities (total S is not known)

Simpson's index was recognized by Whittaker (1972) as a measure of dominance, not because of its sensitivity to change in the abundance of common species, but because of its sensitivity to change in the presence and abundance of rare species. The term 'dominance index' has caused it to be misinterpreted as a measure sensitive to commonness (Hill, 1973). Pielou (1969) proposed subtracting L from its maximum value of 1 as it was seen to vary inversely with heterogeneity. She subsequently suggested (Pielou, 1975) a better function to be

$$D = -\log \sum p_i^2$$

A second major approach to the dual concept of diversity was described by Margalef (1957) and later expanded by Pielou (1966). It is based on the application of information theory in that diversity is equated with the amount of uncertainty that exists regarding the species to which an individual selected at random from a population belongs. The information content per individual was quantitatively expressed by Shannon and Weaver (1949) as:

$$H' = -\sum_{i=1}^S p_i \log p_i \quad *H' = \text{Shannon-Wiener index of diversity}$$

S = number of species

i = the i^{th} species

p = percentage importance

(*Wiener developed the concept concurrently with Shannon and Weaver). This approach should only be applied to infinite samples (Peet, 1974).

The Shannon-Wiener function (H') is most frequently used in community studies because of its relative independence of sample size, suitability for significance tests between means (Odum, 1971), independence of sampling efficiency and least inherent variation due to sampling error (Järvinen and Sammalisto, 1973). Such common beliefs usually remain unquestioned yet there is cause for uncertainty. In a critical review of diversity indices, Peet (1974) highlights several weaknesses. The use of $\frac{n_i}{N}$ as an estimate p_i results

in some bias which is usually small for ecological applications although its significance is probably dependent upon sample size. Similarly, sample size determines the significance of additional error in H' if all species of the community are not included in the sample. As H' is supposedly insensitive to the rarer species and as these are the species most likely to be not represented in a sample, this should not be of significant concern. Changes in sample size (number of individuals) without change in the proportion between species are not reflected by H' . Finally, in using H' for calculations of variance (Bowman *et al.*, 1969), the total number of species in the sampled universe should be known. This is less of a problem with communities that have low numbers of species.

The most important difference between the above two indices is that H' gives more weight to the equitability (see below) of the rarer species than does L (or D).

For completely censused communities, the Brillouin formula is favoured as it is not dependent upon estimates of probabilities (as is H') and so is free from statistical error. It is defined as:

$$H = \frac{1}{N} \cdot \text{Log} \frac{N!}{\prod_{i=1} n_i!}$$

N = total number of individuals

n_i = number of individuals in the i^{th} species ($i = 1, \dots, s$)

This may be rewritten as:

$$H = \frac{1}{N} \left[\sum_{K=1}^N \log(K) - \sum_{i=1}^s \sum_{j=1}^{n_i} \log(j) \right]$$

which allows computation with larger values of N and n_i (K. Malafant, pers. comm.). The Brillouin index differs from other indices in that it is sensitive to changes of total abundance (Editors Note in Rosenzweig and Winakur, 1969) which means that changes in sample size without proportional changes between species are reflected by the index. Peet (1974) by example has shown that this change is not necessarily related

to diversity and claims the formula to be an unacceptable index of heterogeneity.

4.2.2.4 Equitability

One component of the dual concept of species diversity is a measure of equitability (J') i.e. the evenness with which importance is distributed among the species. It was first formally discussed by Lloyd and Ghelardi (1964) who emphasised the importance of its separate evaluation, as there may be differing ecological interpretations for each component. In a comparison of nine such indices, Peet (1974) found J' to be at least equal to other indices. J' is based on the frequently used Shannon-Wiener formula so it may well be preferred. It is defined as:

$$J' = \frac{H'}{H'_{\max}} = \frac{H'}{\log(s)} \quad (H'_{\max} = \text{diversity value when all species have equal importance by abundance})$$

when all species in the community are represented in the sample (Pielou, 1975).

A further measure of equitability discussed by Margalef (1957) and Patten (1962) is redundancy, defined as:

$$R = \frac{H'_{\max} - H'}{H'_{\max} - H'_{\min}} \quad (H'_{\min} = \text{diversity value when all but one species are represented by one individual i.e.})$$

$$H'_{\min} = K [\log N! - \log (N-M+1)!]$$

This is identical to the Horn measure of overlap (Horne, 1966) and, unlike J' , is independent of N and S (M. Austin, pers. comm.).

Equitability indices are highly sensitive to species change (Peet, 1974) which casts doubt over their value where a

sample may, or may not include a rare species, or where changing taxonomic status of a species may occur.

4.2.2.5 Correlation between indices

In comparisons of the joint use of diversity indices, correlations between them may be expected, as they measure the same ecological parameters, and the formulae have similar derivations. Biological relationships may thus be confounded with mathematical relationships (De Benedictis, 1973).

In his attempt to separate the two relationships, De Benedictis was able to demonstrate strong positive correlations between richness and H' , between richness and J' , and between H' and J' , concluding that a positive correlation is to be expected independently of any biological phenomena. As may be expected, Simpson's index (L) varies inversely with other indices as it is a measure of similarity, rather than diversity. Pielou's index (D) counters for this difference so it may be anticipated to correlate positively with other indices. Correlation of indices with the Brillouin function has not received much attention.

Although *a priori* correlations may be expected, this in no way justifies the use of a single index to represent community diversity. Instead, it emphasises the importance of investigating fine differences between them which, by understanding the character of each index, may reveal trends. For this reason, indices should be tabled against each other in what may be termed a diversity 'suite'. Such a table supplies considerably more information than point estimates of diversity (Noon *et al.*, 1980).

4.2.2.6 Modelling the diversity index suit.

The use of hypothetical data to model responses in indices of diversity is not untried, although only large data sets have been previously used (Lloyd and Ghelardi, 1964; Peet, 1974). While diversity indices have been used for small communities (Rosenzweig and Winakur, 1969; Brown, 1973;

Fleming, 1973; Posamentier, 1975; Braithwaite and Dudzinski, 1982), none include critical evaluation of index response to small values of N and S.

In an attempt to understand the properties of five indices under conditions of small N and S, sets of hypothetical data representative of the small mammal community were chosen for empirical evaluation. The redundancy index was not included as it was known to respond poorly with small numbers leading to undefined values ($\frac{0}{0}$) for missing data, e.g., when a species in the community was not represented in a sample.

Nine differing data sets were used in the model of a diversity index suite (Appendix IV), each representing changes in abundance of common and rare species, changes in abundance without proportional change in species, or changes in the number of species. Rows of numbers within each data set are representative of sampling results during a period in which the survey is repeated. Characteristics of these data sets are:-

- (i) one species in the community becoming rare
- (ii) two species in the community becoming rare
- (iii) three species in the community becoming rare
- (iv) one species in the community is rare and one species becomes rare during subsequent surveys
- (v) two species not subsequently recaptured in the sampling period and one species becomes rare
- (vi) one common species becoming less abundant
- (vii) two common species becoming less abundant
- (viii) proportional decrease in abundance for all species in the community
- (ix) new but rare species captured in subsequent surveys.

The five indices were calculated for each of the hypothetical survey results in the data sets and the differences

between these values were then taken (Appendix IV). Table 4.1 shows the magnitude of change between the first and final survey in each set for the five indices. The differences between values were also calculated as proportions of the original communities (i.e. the first row in each data set) (Appendix IV) and are shown graphically (Figure 4.1).

TABLE 4.1 MAGNITUDE OF CHANGE OF FIVE INDICES IN RESPONSE TO HYPOTHETICAL DATA EXPRESSING CHANGES IN PROPORTIONS AND NUMBERS OF DOMINANT AND RARE SPECIES IN A COMMUNITY

DATA SET	DIVERSITY INDICES				
	SIMPSON	PIELOU	SHANNON-WIENER	BRILLOUIN	EQUITABILITY
1 (One species becoming rare)	-0.0695	0.2452	0.2068	0.2131	0.1492
2 (Two species becoming rare)	-0.1914	0.5685	0.4594	0.4789	0.3314
3 (Three species becoming rare)	-0.4537	1.0349	0.7526	0.2658	0.1822
4 (One species rare, one species becoming rare)	-0.1219	0.3233	0.2526	0.2658	0.1822
5 (Two species not subsequently recaptured, one species becoming rare)	-0.2500	0.9163	0.8240	0.8015	0.5944
6 (One common species becoming less abundant)	-0.0009	0.0028	0.0055	0.0072	-0.0040
7 (Two common species becoming less abundant)	-0.0146	-0.0455	-0.0352	-0.0054	-0.0254
8 (Proportional decrease in abundance for all species)	0.0000	0.0000	0.0000	0.0775	0.0000
9 (New but rare species captured in subsequent surveys)	0.0537	-0.1790	-0.3191	-0.2418	-0.1535

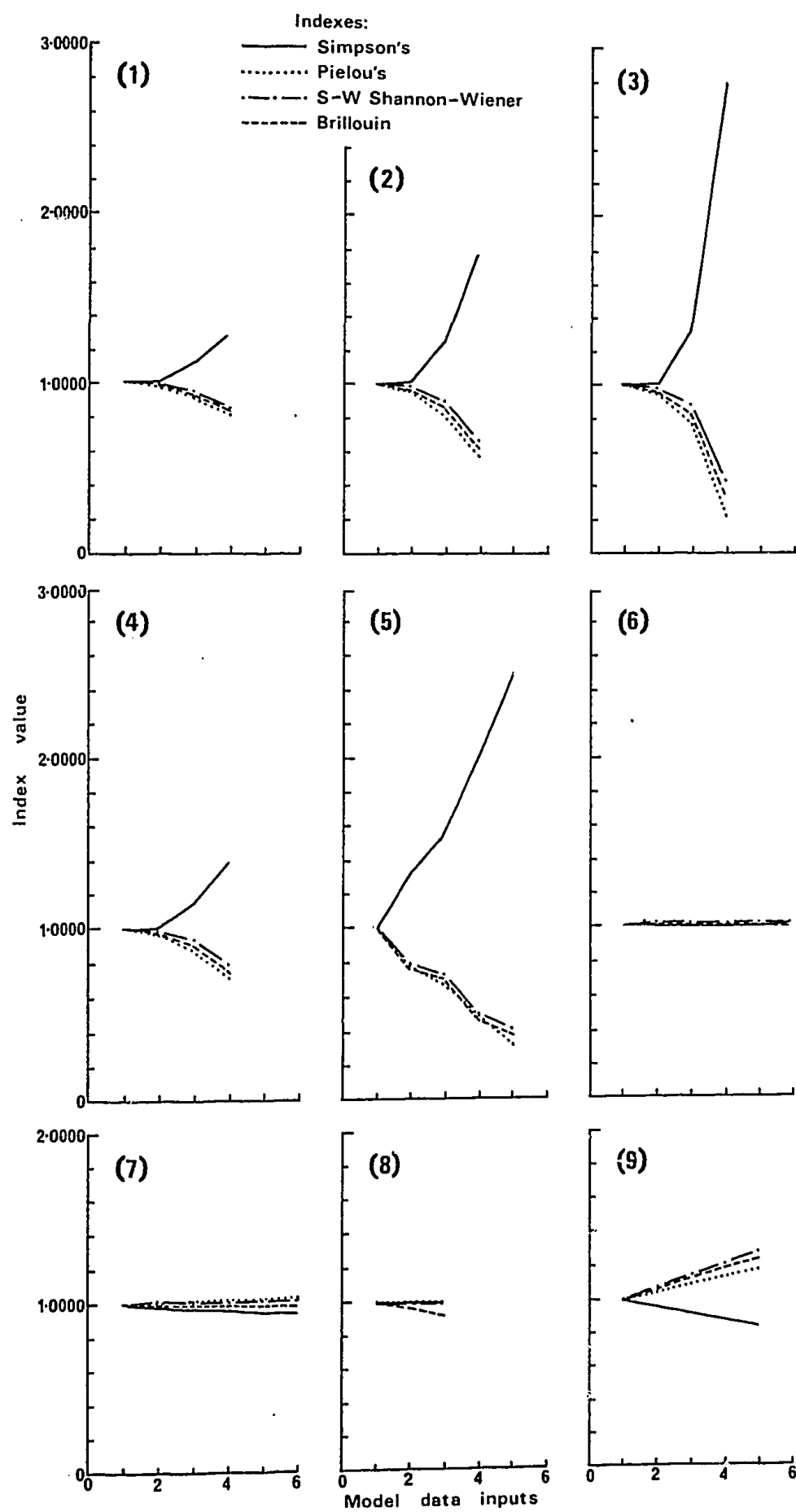


FIGURE 4.1 PROPORTIONAL CHANGES IN FOUR DIVERSITY INDICES CALCULATED FROM HYPOTHETICAL SURVEY DATA FOR COMMUNITIES.
(SEE APPENDIX IV AND TABLE 4.1)

Two approaches may be adopted in analysis of the first three modelled sets of data.

(a) Firstly, the responses of diversity indices to change within the community may be considered, e.g. one, two or three species may become successively rare over a series of sampling periods. Table 4.1 (1-3) shows the magnitude of differences within each of these communities for all indices. Clearly, the Simpson index (L), noted for its sensitivity to rare species, is almost consistently the poorest indicator, while the Pielou index (D), itself a function of L, is consistently the best and is improving as more rare species become involved. The failure of L here is caused by the relatively small figures involved. If, however, proportional differences are calculated then L is notably the more responsive (Figure 4.1; (1), (2) and (3)) while D remains the most responsive of all other indices. In this way, when emphasis is on the proportional change rather than the difference between the computed numbers, then L appears to be the more robust indicator of rarity.

(b) The second approach considers the use of the indices for comparison between communities. Three communities with one, two and three rare species respectively may be compared, e.g.,

	Numbers of Individuals			
	S1	S2	S3	S4
Final survey of Data Set (1)	15	15	15	1
Final survey of Data Set (2)	15	15	1	1
Final survey of Data Set (3)	15	1	1	1

Table 4.2 shows that the properties of L behave similarly to those of L in the first approach. When the differences of index values are considered, L is weakest but when considered by proportion of change in index value, it is the most responsive. D is responsive in both situations.

Comparing a community in which one species is always rare, with a second species becoming rare (data set 4, Table 4.1), similar trends occur for each of the indices as in the previous examples. D and L remain the strongest of the suite. They are shown here not to over emphasise rarity in that results of data set 4 are intermediate to those for data sets 1 and 2.

TABLE 4.2 USE OF DIVERSITY INDICES TO COMPARE THREE COMMUNITIES WITH INCREASING NUMBERS OF RARE SPECIES.

N.B. Central values are the index values; right side values are the differences between index values; left side values are the proportional changes between index values.

	DIVERSITY INDEX				
	Simpson (L)	Pielou (D)	Shannon-Weiner (H')	Brillouin (H)	Equitability (J')
Community (1)	0.3195	1.1411	1.1795	1.0708	0.8508
	-0.1219	0.3233	0.2526	0.2658	0.1822
	1.3815	0.7167	0.7858	0.7518	0.7858
Community (2)	0.4414	0.8178	0.9269	0.8050	0.6686
	-0.2623	0.4664	0.2932	0.3330	0.2115
	2.2025	0.3079	0.5373	0.4408	0.5373
Community (3)	0.7037	0.3514	0.6337	0.4720	0.4571

The fifth situation involves the complete loss of two species from a community, as may exist during an extended sampling program. Figure 4.1 (5) shows all indices to be sensitive to the change although it does not distinguish between a species becoming rare and one being lost to the community. By selecting figures from data sets 4 and 5, this difference may be demonstrated (Table 4.3). The Shannon-Wiener index (H') gives the largest drop in value when the species becomes absent (i.e. $\Delta H' = 0.0809$) and the proportion of this change compared with that for one species being rare is greatest for this index. However, the indices are deceptive for comparison between communities as all indices, with the exception of Equitability (J'), ignore the absence of a species, i.e. a community that has lost one species during the sampling program now gives index values that are similar to a community in which that species never existed. This may be shown by comparing maximum community values for each index (Figures 4.2 and 4.3). From data set 5, the loss of the first species results in L , D , H' and Brillouin index (H) having maximum values which are equal to those of an even 3 species community (Figures 4.2 and 4.3). Similarly, for the loss of the second species, the four indices give values equal to an even two species community. J' has a maximum value of 1.000 for an even community and when a species becomes absent, J' includes this as zero abundance rather than ignoring the value, so this index takes importance as an indicator of absence.

Data sets 6 and 7 represent situations of one and two declining common species in a community respectively. For this particular community, all indices respond weakly to a 30% decrease of one common species as this initially causes an increase in evenness, followed by a decrease as is shown by changes in J' (Appendix IV). With the abundance of two common species declining by 30%, maximum evenness is not reached, D , H' and J' show continuous increase and L shows a continuous decrease. H , however, shows a slight downturn.

TABLE 4.3 DIFFERENCES IN INDEX RESPONSE TO RARITY AND ABSENCE OF SPECIES IN COMMUNITIES
(N.B. Differences between index values are offset to the right).

Community	Numbers of Individuals			
	S1	S2	S3	S4
1 (Even community)	15	15	15	15
2 (One species rare)	15	15	15	1
3 (One species absent)	15	15	15	0

Community	Index Values				
	Simpson (L)	Pielou (D)	Shannon-Wiener (H')	Brillouin (H)	Equitability (J')
1	0.2500	1.3863	1.3863	1.2839	1.0000
	-0.0695	0.2452	0.2068	0.2131	0.1492
2	0.3195	1.1411	1.1795	1.0708	0.8508
	-0.0138	0.0425	0.0809	0.0613	0.0583
3	0.3333	1.0986	1.0986	1.0095	0.7925

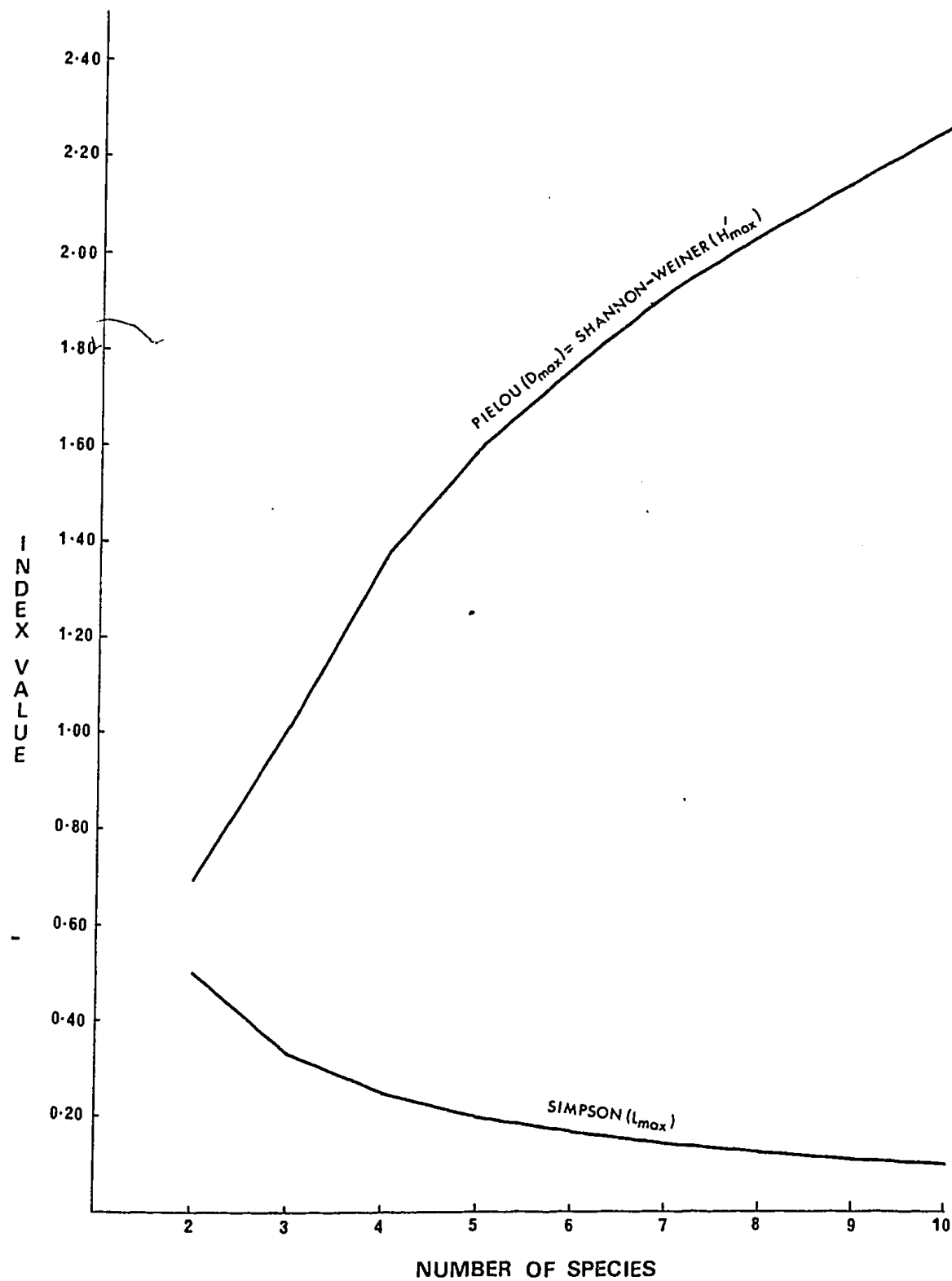


FIGURE 4.2 MAXIMUM VALUES FOR SIMPSONS ($L_{\max}$), Pielous ($D_{\max}$) AND SHANNON-WIENER ($H'_{\max}$) DIVERSITY INDICES WITH INCREASING SPECIES RICHNESS.

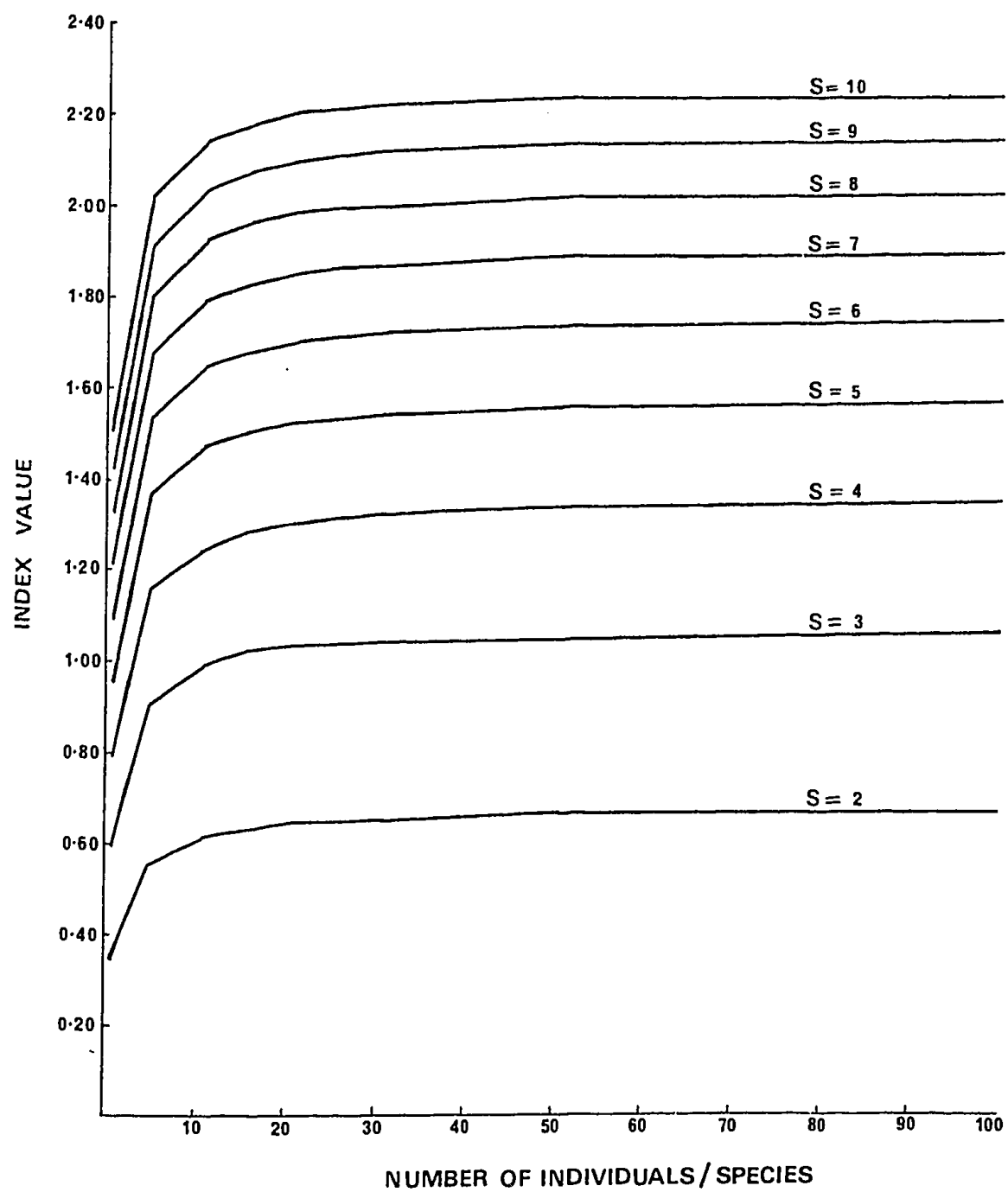


FIGURE 4.3 MAXIMUM VALUES FOR BRILLOUIN'S ($H_{\max}$) DIVERSITY INDEX WITH INCREASING SPECIES RICHNESS (S) AND SAMPLE SIZE (N)

While none of the indices are strong indicators of change, L and D give slightly better values (Figure 4.1 (7)) although the ranking may well alter for other community structures.

Considering 4-species communities that are proportionally equal, although varying in the abundance of each species, as represented by data set 8, the only index to indicate the difference is H. All other indices are calculated by probability of capture relative to other species in the community and ignore proportional change. H gives decreasing values corresponding to the declining community abundance (Figure 4.1).

The final data set investigates the effect of adding new species to the community on index response. All indices respond variously to show increased diversity with H' clearly being the more robust (Table 4.1; Figure 4.1 (9)).

Modelling the hypothetical data rationalizes the use of all five diversity indices to assess changes within and between small-number communities. L and D best represent changes of abundance with less common species while J' is the only sound indicator of a community with a species absent from the sample. H is the only index responding to proportional changes in abundance in a community with a fixed number of species and H' responds strongly to the addition of new species. No index is reliably representative of changes in the abundance of common species.

4.2.2.7 The use of maximum diversity values for community comparison.

When analysing differences within or between communities using indices, a stronger comparison exists if they can be related to a fixed value as well as between themselves. One possibility for a comparative fixed value is the maximum possible value for each index, i.e., if all species that occur in the community are equally abundant.

By including a series of maximum possible index values in the model, graphs have been produced for four of the

indices. J' , by definition, has a value of 1.000 for all even communities. Figure 4.2 shows the resulting curves for $L_{\max}$, $D_{\max}$ and $H'_{\max}$. Maximum values for each of the three indices are independent of sample size (i.e. the abundance of each species) and respond only to increasing richness. $D_{\max}$ always equals $H'_{\max}$ as a consequence of their formulation (K. Malafant, pers. comm.) so only one need be considered. $L_{\max}$ declines in response to increasing richness with the rate of decline approaching a plateau for communities of eight or more species. Australian small mammal communities contain 6 species on average (Table 1.5) which vary considerably between communities. Maximum possible index values are of little use for comparative purposes across such an array of communities. However, for communities of equal richness, or for comparison of repeated samples within a community, the fixed maximum values can be of use.

Maximum values for the Brillouin index ($H_{\max}$) are not independent of sample size. Figure 4.3 represents changes in $H_{\max}$ for increasing abundance and richness. Clearly, $H_{\max}$ values stabilize for any community with approximately 25 or more individuals in each species. Used comparatively, a community with the most common species having 25 or more individuals may be related to the index value assuming all species have 25 individuals, i.e. $H_{\max}$. Again, $H_{\max}$ varies according to richness so it is likely to be of most use comparing fixed species communities.

4.2.3 Similarity Indices

The use of indices of similarity provide a limited function, similar to that of diversity indices. The index used in this work, the Morisita Similarity Index is recommended by Wolda (1981) following detailed analysis of 22 indices using 4 hypothetical faunas. It is virtually independent of sample size and independent of species diversity (Morisita, 1959). The index, based on Simpson's index of dominance, is calculated as:

$$I_m = \frac{2 \sum n_{1i} \cdot n_{2i}}{(\lambda_1 + \lambda_2) N_1 N_2}$$

n = number of individuals
in the i^{th} species by
that method

N = total number of individuals
sampled by that method

i = species

j = methods

where $\lambda_i = \frac{\sum n_{ji}^2}{N_j^2}$

Values of the index lie between zero and approximately one (Brower and Zar, 1977). Uncertainty of the upper limit results when combinations of different sample sizes are used (Wolda, 1981).

The use of the Morisita Index here is not to compare small mammal communities *per se*, but to measure the similarity between representative samples of these communities made by the different methods.

4.2.4 Analysis of Indices

With the capture data expressed as diversity indices or similarity matrices a comparative evaluation of methods and sites can be done.

There are three factors which can be considered in comparing the methods for any single diversity measure. These are:

- (i) the 8 methods of trap configuration
- (ii) the 4 sites
- (iii) the 3 trapping days

This provides 96 observations and may be analysed using standard analysis of variance methods. However, since no replication of the design exists it is first necessary to check the existence of high order interactions between the three factors using techniques such as the Tukey test of non-additivity (Tukey, 1949). Once it is established that the design is additive then the standard analysis of variance can proceed.

To assess the constancy of performance by sampling methods between the four sites the Morisita Index of similarity between the 8 methods were obtained. By applying Principal Coordinate Analysis (Gower, 1966), four new reduced sets of coordinates are obtained for each site/methods. Then using a Generalized Procrustes Analysis (Gower, 1975), which provides a rotation and scaling of the new coordinates to minimize a "distance" measure between the four sets of coordinates, a centroid (mean) or consensus configuration can be produced. Comparison of the individual site configurations with this consensus gives measures of differences between sites and methods.

The reduced set of coordinates may also be plotted to illustrate any clustering of methods in the reduced space. This is justifiable if the reduced set of configurations provides a good representation of the original multidimensional configurations.

4.3 Methods of Analysis of the Effect on Survey of Environmental Heterogeneity

4.3.1 Introduction

The intention of this analysis is to show whether differences exist between the eight methods used when sampling in heterogeneous environments. Not all attributes measured exert an influence on the species caught or the community measured, nor is the influence likely to be equal between attributes, so the first requirement of the analysis is to reduce the field data set to a more concise and relevant subset of attributes.

This reduction was attempted in two ways. The first was by multivariate methods without *a priori* correlation with the animal capture data, and the second was by multiple regression analysis.

4.3.2 Multivariate analysis

Methods of multivariate analysis assume the variables of the complete data set to be interdependent and of equal

significance. The intent of this approach is to identify similarity within the data set and group attributes on this basis. Using a model to account for standardized variation within the data set (i.e. $\frac{x-\mu}{\sigma}$; μ = mean value, σ = standard deviation) (Pimentel, 1979) a correlation matrix of the attributes measured at sites was established. A Principal Components Analysis (PCA) of this matrix restructured the set producing new axes (eigenvectors) with variance represented by eigenvalues. Eigenvalues of the principal axes were maximized so that the selection of them successively (i.e. highest value first, followed by lesser values) allowed an optimal account of variation within the data set.

In theory, the use of PCA should identify linear combinations of the original variables that could be used to delineate environmental patchiness. These components are a combination of the original variables in the data set, but unless the latter are sampled randomly and are linearly related, the components are likely to be biologically meaningless (Pimentel, 1979). In addition, PCA is not always useful in discovering the underlying structure of variables, nor are the components necessarily related to the species' or the community needs (Johnson, 1981). The major purpose of PCA is to reduce the complexity of the data, but it includes no test of significance of the adjustment (Karr and Martin, 1981).

4.3.3 Multiple regression analysis

Multiple regression analyses differ from the former methods in that a set of independent variables are regressed on a single dependent variable. For the purposes of this research, the dependent variable is either one of the species or an index of community diversity, while the independent variables are the set of measured environmental attributes. As not all sampling stations were equally trapped during the field program, animal captures for each trapping station were tallied then adjusted to account for this discrepancy. Adjusted totals were then used for each species independently, or were combined using two of the indices of diversity, the Shannon-Wiener (H') and Simpsons (L) indices, to provide

community measures at each station. Regressions using species independently were not required but were carried out for comparison with regressions using community indices of diversity.

The original sets of measured variables were culled to eliminate those of completely zero values or with no variation within a site. From the reduced number of variables, an optimized subset was chosen using the leaps and bounds algorithm of Furnival and Wilson (1974) which accounted for most variation. Both the Mallows statistic, C_p , (Mallows, 1973) and the adjusted coefficient of determination, R_a^2 , statistic were used.

The algorithm is based on the linear multiple regression model, i.e.

$$Y_i = \beta_i + \sum_{j=1}^K \beta_j X_{ij} + \epsilon_i$$

where β_i is a coefficient,

ϵ_i is an error term, assumed to be normally distributed,

$(\epsilon_i \sim N(0, \sigma^2))$; N - number of observations

σ^2 - variance

and K is the number of variables (X_i).

The model may be rewritten as

$$\hat{Y}_i = \beta_i + \sum_{j=1}^P \beta_j X_{ij} \quad \text{for a subset } P \text{ of the total number of variables } (K)$$

such that the resulting residual sums of squares (RSS_P)

$$(RSS_P) = \sum_{i=1}^P (Y_i - \hat{Y}_i)^2$$

In selecting the optimized subset P , the C_p statistic was calculated for each combination of variables. This statistic is defined to be:

$$C_p = \frac{1}{\sigma^2} RSS_P - N + 2p$$

The minimum C_p value identifies a subset of the original number of variables that accounts for most variance in the data.

Similarly the R^2 statistic was used to select a subset P. It was defined as:

$$R_p^2 = 1 - \frac{RSS_p}{TSS}$$

where total sums of squares (TSS) = $\sum (\frac{y}{y-\bar{y}})^2$; $\bar{y}$ is the mean value. This statistic was used in the adjusted form, i.e.

$$R_a^2 = 1 - \frac{N-p}{N-p-1} (1-R_p^2)$$

which allows it to decrease for variables that are added but are of little importance so rendering it more sensitive. The R_a^2 value for the optimal subset P has a maximum value.

In brief, the leaps and bounds algorithm identifies a subset of variables (P) that accounts for most variation ($\hat{y}_i$). The method of identifying this subset was by analysis of Residual Sums of Squares (RSS_p) using the Cp statistic, or by analysis of the Total Sums of Squares using the adjusted R^2 statistic. The choice between the two statistics depends upon consistency of results.

For each variable of the optimum subset, a Beta (β') coefficient was calculated. This is a ratio of the additional variance accounted for by that variable against the total variance, i.e.

$$\beta' = \frac{\beta_i \sigma_i}{\sigma_y}$$

In general, the most important variables in the subset have the greatest $|\beta'|$ values, the significance of which may be tested using a t-test while the sum effect of all variables may also be tested using an F test (Snedecor and Cochran, 1967).

A supplementary approach is to use stepwise regression (Pimentel, 1979) which combines the attributes from within the subset one at a time so the importance of each may be determined.

Regression methods are considered to be a powerful and statistically robust analytical tool, particularly when more than a single species is involved (Johnson, 1981).

4.3.4 Method evaluation

Following the identification of those attributes of the environment most significantly correlated with diversity of the animal community, the trapping methods were evaluated in terms of their respective responses to variation of the attributes. A computer program was used to plot contour lines for grid methods linking trap stations of equal value for each of the significant environmental variables and to draw histograms for index-line methods. These provided a graphical representation of environmental patchiness for comparison with trap data. With the patches delineated, capture data were divided into sites that were inside and sites that were outside each patch. The results were analysed in relation to diversity indices to determine the additional affect caused by environmental heterogeneity.

4.4 Computer Hard and Soft-ware Used in Analyses

Field data for both animal captures and environmental variables were coded onto cards and subsequently stored on disc drive files. All computing was conducted on a VAX 11/750 using the UNIX operating system, located in the C.S.I.R.O., Division of Mathematics and Statistics, Canberra.

Programs used came from three sources. The "GENSTAT" package (Alvey *et al.*, 1977) provided programs used for the principal coordinates analysis, the generalized Procrustes analysis and for the analysis of variance. These had application to the analysis of animal capture data. Analysis of environmental variables used programs drawn from the more recent 'S' package (Becker and Chambers, 1981) to conduct multiple regressions, principal components analysis and the contour plotting. All remaining analyses were run using impromptu programs, written to calculate diversity indices, similarity matrices and the station accumulation techniques used to optimize sample size for both grid and index methods.

Chapter 5

RESULTS

5.1 Introduction

Following the pattern of field data collection, analysis of the capture data will be treated first. This will be followed by analysis of the effects of environmental heterogeneity on trap performance. The analytical techniques discussed in the previous chapter are used here initially to construct sample indices of diversity as measured by each of the eight methods at the four sites. These indices are then compared with indices of the total small mammal community (maximum possible) to determine the success of each method. The analysis then considers how three factors (methods, days and sites) affect variation and independence between sites, using analysis of variance and similarity indices. Then, using a computer-based technique for constructing grids and index lines, sample areas (for grids) and lengths (for trap lines) are examined for each method to investigate the possibility of there being optimal areas from grid trapping and optimal lengths of lines for line trapping.

Environmental data are analysed separately for each of the six vertical strata at each site in accordance with their variations in sampling scale. Both analytical approaches discussed (4.3.2, 4.3.3) were attempted but the multivariable analysis was abandoned due to difficulty of interpretation. Multiple regression was preferred as the resulting patterns of environmental heterogeneity were derived directly from measured field attributes with which small mammals have been shown to be significantly correlated (Appendix I).

5.2 Analysis of Trapping Methods

5.2.1 Species data at each site

Information on the number of species caught at each site, the calculated indices of diversity, and details of trapping effort are tabulated in Table 5.1.

5.2.1.1 Species richness

The numbers of species of small mammals caught (Column 1, Table 5.1) ranged from 2 (D68) to 5 (D50). No single method consistently sampled all species at a site. This may have been partly due to rarer species (e.g. *Rattus rattus*, *Peromyscus nasuta*) being caught once only during the sampling period, a reflection of their transient character rather than variation in method efficiency. While there were no large differences between the methods in their ability to sample all species at a site (Table 5.2), it is clear that the 20 metre trap spacing for both grids and index-lines were consistently the worst. The larger spacing also generally failed to sample total species at a site as the number of species in the community increased (Figure 5.1).

TABLE 5.2 MEAN NUMBER OF SPECIES CAUGHT BY EACH METHOD AS A PERCENTAGE OF TOTAL SPECIES

	Grid				Index-line			
Method	G(5)	G(7.5)	G(10)	G(20)	I(5)	I(7.5)	I(10)	I(20)
% Species Caught	81.50	88.75	80.25	78.75	88.75	80.25	88.75	75.25

5.2.1.2 Number of individuals

The number of individuals of each species caught by each method (column 1, Table 5.1) represents cumulative captures over the three day trapping period (i.e. Day 1 captures + Day 2 new captures + Day 3 new captures). Numbers at the Brindabella site (BBC) were much greater than those at the Mt Dromedary site, and are shown by all methods. It is obvious that as the number of traps decreased, there was a general, although not consistent, decline in the numbers caught.

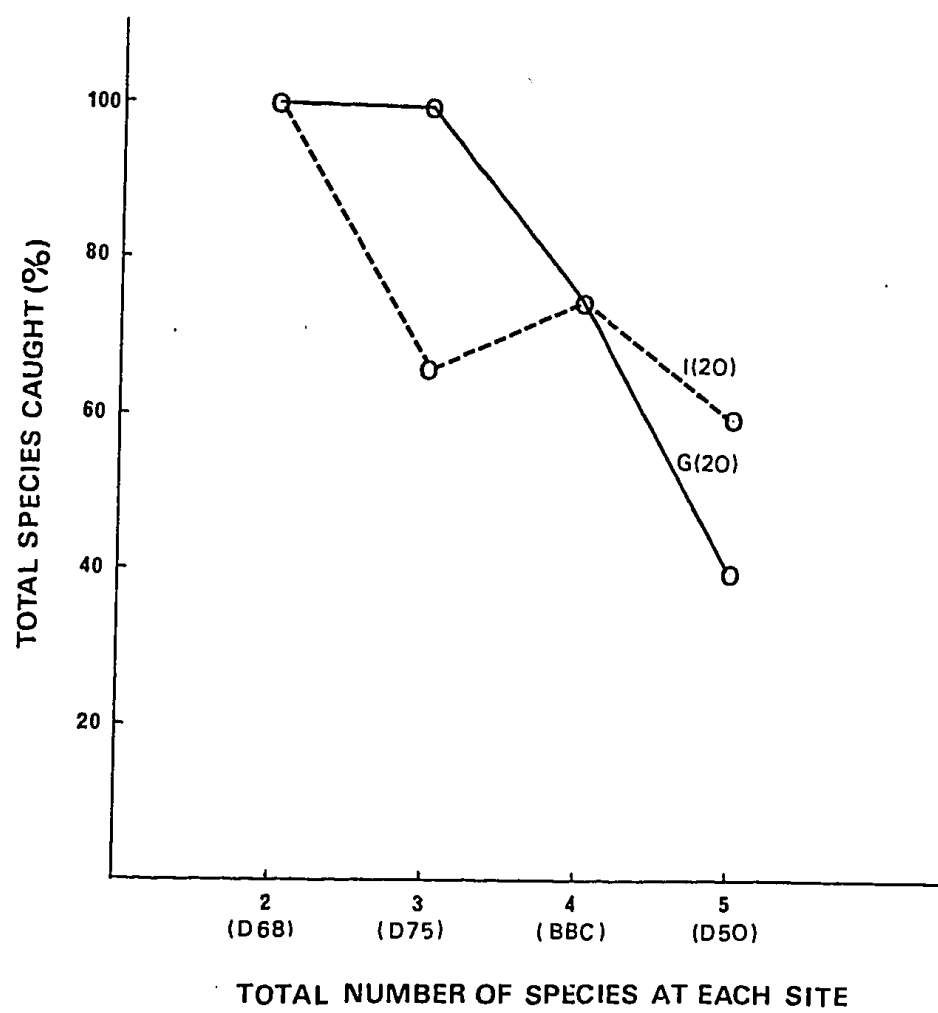


Figure 5.1 Percentage of total species represented by 20 metre trap spacing methods.

NOTES FOR TABLE 5.1 (a), (b), (c) and (d)

COLUMN 1 1 = *Antechinus stuartii* 5 = *R. rattus*
 2 = *A. swainsonii* 6 = *Pseudomys novaehollandiae*
 3 = *Sminthopsis leucopus* 7 = *Mus musculus*
 4 = *Rattus fuscipes* 8 = *Peromyscus nasuta*

COLUMN 2 Minimum-known-to-be-alive (Krebs, 1966) was calculated for each day of each method. The highest value over the 3 day period is used here.

COLUMN 3-7 Indices of diversity calculated using number of individuals over the 3 day period.
 S-W = Shannon-Weiner index.

COLUMN 8 Biomass calculated as the sum of mean body weights for each individual caught for each method.
 Values used are:

A. stuartii = 20 gms *R. rattus* = 125 gms
A. swainsonii = 56 gms *P. novaehollandiae* = 10 gms
S. leucopus = 15 gms *M. musculus* = 15 gms
R. fuscipes = 100 gms *P. nasuta* = 300 gms

COLUMN 10 Mean values over 3 days trapping.

COLUMN 11 Time (minutes) for each method includes layout, clearing and collecting over the 3 day period. Where two people were involved in field work, actual field time was multiplied by 1.25.

TABLE 5.1(a) SMALL MAMMAL COMMUNITY CHARACTERISTICS REPRESENTED BY EACH METHOD

SITE BBC

METHOD USED	1	2	3	4	5	6	7	8	9	10	11
	SPECIES NUMBER AND NUMBER OF INDIVIDUALS (BRACKETS)	MKTBA	INDICES OF DIVERSITY					BIOMASS (gms)	NO. OF TRAPS USED	TRAP SUCCESS (%)	EFFORT (mins)
			SIMPSON (L)	PIELOU (D)	S-W (H')	BRILLOUIN (H)	EQUIT- ABILITY (J')				
GRID											
G(5)	1(13), 2(5) 4(13), 5(1)	1(23), 2(6) 4(36), 5(1)	-0.0343	1.0343	1.1302	0.9896	0.8153	1965	100	20.33	560
G(7.5)	1(7), 2(4) 4(16)	1(21), 2(6) 4(35), 5(0)	0.1798	0.8202	0.9429	0.8216	0.6802	1964	49	36.70	450
G(10)	1(6), 2(2) 4(18)	1(25), 2(5) 4(33), 5(0)	0.3810	0.6190	0.7903	0.6767	0.5701	2032	25	48.00	215
G(20)	1(3), 2(1) 4(11)	1(18), 2(5) 4(25), 5(0)	0.4591	0.5409	0.7299	0.5737	0.5265	1216	9	88.83	90
INDEX-LINE											
I(5)	1(16), 2(5) 4(20)	1(18), 2(6) 4(29), 5(0)	0.0964	0.9036	0.9740	0.8839	0.7026	2600	60	48.30	404
I(7.5)	1(16), 2(4) 4(16)	1(25), 2(5) 4(33), 5(0)	0.1021	0.8979	0.9650	0.8666	0.6961	2144	40	65.83	380
I(10)	1(12), 2(3) 4(14)	1(21), 2(6) 4(35), 5(0)	0.1205	0.8795	0.9514	0.8375	0.6863	1808	30	58.90	356
I(20)	1(8), 2(2) 4(12)	1(23), 2(6) 4(36), 5(1)	0.1745	0.8255	0.9165	0.7812	0.6611	1472	15	66.63	220

TABLE 5.1(b) SMALL MAMMAL COMMUNITY CHARACTERISTICS REPRESENTED BY EACH METHOD

SITE D75

METHOD USED	1	2	3	4	5	6	7	8	9	10	11
	SPECIES NUMBER AND NUMBER OF INDIVIDUALS (BRACKETS)	MKTBA	INDICES OF DIVERSITY				EQUIT- ABILITY (J')	BIOMASS (gms)	NO. OF TRAPS USED	TRAP SUCCESS (%)	EFFORT (mins)
			SIMPSON (L)	PIELOU (D)	S-W (H')	BRILLOUIN (H)					
<u>GRID</u>											
G(5)	1(4), 4(1)	1(4), 3(0) 4(1)	0.6143	0.3857	0.5004	0.3219	0.4555	180	100	4.00	312
G(7.5)	1(2), 4(2)	1(3), 3(1) 4(2)	0.3069	0.6931	0.6931	0.4479	0.6309	240	49	5.30	225
G(10)	1(2), 4(1)	1(4), 3(0) 4(2)	0.4122	0.5878	0.6365	0.3652	0.5794	140	25	6.60	169
G(20)	1(2), 3(1) 4(1)	1(3), 3(1) 4(1)	0.0192	0.9808	1.0397	0.6212	0.9464	155	9	22.20	106
<u>INDEX-LINE</u>											
I(5)	1(4), 3(1) 4(2)	1(4), 3(2) 4(2)	0.1527	0.8473	0.9557	0.6649	0.8699	295	50	8.66	212
I(7.5)	1(4), 4(3)	1(4), 3(0) 4(3)	0.3271	0.6729	0.6829	0.5079	0.6216	380	33	12.10	225
I(10)	1(3), 3(2) 4(2)	1(3), 3(2) 4(2)	0.0586	1.0586	1.0790	0.7639	0.9821	290	25	14.66	125
I(20)	1(3), 4(2)	1(3), 3(0) 4(2)	0.3461	0.6539	0.6730	0.4605	0.6126	260	13	23.10	116

TABLE 5.1(c) SMALL MAMMAL COMMUNITY CHARACTERISTICS REPRESENTED BY EACH METHOD

SITE D68

	1	2	3	4	5	6	7	8	9	10	11
METHOD USED	SPECIES NUMBER AND NUMBER OF INDIVIDUALS (BRACKETS)	MKTBA	INDICES OF DIVERSITY					BIOMASS (gms)	NO. OF TRAPS USED	TRAP SUCCESS (%)	EFFORT (mins)
			SIMPSON (L)	PIELOU (D)	S-W (H')	BRILLOUIN (H)	EQUIT- ABILITY (H')				
GRID											
G(5)	1(4), 4(7)	1(5), 4(11)	0.3786	0.6214	0.6555	0.5272	0.5966	780	100	7.00	385
G(7.5)	1(4), 4(6)	1(4), 4(7)	0.3461	0.6539	0.6730	0.5347	0.6126	680	49	14.29	219
G(10)	1(4), 4(3)	1(6), 4(7)	0.3271	0.6729	0.6829	0.5079	0.6216	380	25	16.00	180
G(20)	1(1), 4(3)	1(7), 4(13)	0.5300	0.4700	0.5623	0.3466	0.5116	320	9	25.90	119
INDEX-LINE											
I(5)	1(6), 4(12)	1(7), 4(13)	0.4122	0.5878	0.6365	0.5461	0.5794	1320	50	24.66	306
I(7.5)	1(5), 4(9)	1(7), 4(10)	0.3853	0.6147	0.6518	0.5430	0.5933	1000	33	29.30	310
I(10)	1(5), 4(10)	1(6), 4(13)	0.4122	0.5878	0.6365	0.5338	0.5794	1100	25	42.66	230
I(20)	1(4), 4(8)	1(4), 4(8)	0.4122	0.5878	0.6365	0.5170	0.5794	880	13	66.63	145

TABLE 5.1(d) SMALL MAMMAL COMMUNITY CHARACTERISTICS REPRESENTED BY EACH METHOD

SITE D50

METHOD USED	1 SPECIES NUMBER AND NUMBER OF INDIVIDUALS (BRACKETS)	2 MKTBA	3 4 5 6 7 8 9 10 11					10 TRAP SUCCESS (%)	11 EFFORT (Mins)		
			INDICES OF DIVERSITY								
			SIMPSON (L)	PIELOU (D)	S-W (H')	BRILLOUIN (H)	EQUIT- ABILITY (H')			BIOMASS (gms)	NO. OF TRAPS USED
GRID											
G(5)	1(4), 4(3) 6(1)	1(3), 4(3) 6(1), 7(0) 8(0)	0.0992	0.9008	0.9743	0.7043	0.6054	390	100	4.66	331
G(7.5)	1(2), 4(3) 6(1), 7(2)	1(3), 4(3) 6(1), 7(3) 8(0)	-0.2685	1.2685	1.3209	0.9283	0.8207	380	49	6.80	256
G(10)	1(1), 4(2) 6(1), 7(1)	1(3), 4(3) 6(1), 7(1) 8(0)	-0.2730	1.2730	1.3322	0.8189	0.8277	245	25	8.00	156
G(20)	1(1), 4(3)	1(3), 4(3) 6(1), 7(0) 8(0)	0.5300	0.4700	0.5623	0.3466	0.3494	320	9	22.22	108
INDEX-LINE											
I(5)	1(6), 8(1) 7(1)	1(6), 4(3) 6(1), 7(1) 8(1)	0.0544	0.9456	1.1210	0.8301	0.6965	735	35	19.09	217
I(7.5)	1(4), 4(3) 7(1)	1(4), 4(3) 6(0), 7(1) 8(0)	0.0992	0.9008	0.9743	0.7043	0.6054	395	23	26.05	145
I(10)	1(4), 7(2) 6(1)	1(4), 4(4) 6(1), 7(3) 8(0)	-0.1412	1.1412	1.2367	0.9440	0.7684	620	17	39.20	160
I(20)	1(3), 4(3) 7(1)	1(3), 4(3) 6(0), 7(2) 8(0)	0.0526	0.9474	1.0042	0.7059	0.6240	375	9	44.40	100

5.2.1.3 Minimum Number Known To Be Alive

As a basis for comparison of relative abundance, conservative estimates of the total number of individuals of each species were made by calculating the minimum known to be alive (MKTBA; Krebs, 1966) during each trip, for all sites (column 2 Table 5.1). These values are the sum of individuals caught during a given period plus those caught in earlier periods that were subsequently caught again. As well as being comparative, they demonstrate the stability in community structure within each site between sampling trips and provide sound basis for evaluation of sampling methods.

5.2.1.4 Diversity indices

The earlier modelling (4.2.2.6) of hypothetical data sets for five diversity indices using small numbers permitted an understanding of their characteristics. Index values, calculated for each method at the four sites are shown in column 3-7, Table 5.1. These indices receive only initial examination in this section, and are more fully dealt with in section 5.2.2.

As shown earlier, the Simpson (L) and Pielou (D) indices are inversely related and, respond with a similar magnitude of change. Large changes of index value, as shown in the grid methods, at Site BCC are caused by changes in numbers of species present and changes in evenness of individuals but the two components are difficult to separate. When compared with the equitability index (J'), a direct measure of evenness, the effects of the two components are obvious. However, J' is the only index which provides measurement of a species that occurs in the community although not represented in all samples. Thus J' responds to changes in S when total S is known. This is demonstrated at Site D75 with the index-line methods, where *Sminthopsis leucopus* (species 3) was caught by only two of the four methods. The values for J' are high when *S. leucopus* is present and low when absent, indicating that the index treats species' absence as a deviation from evenness.

The Brillouin index (H) is the only index that responds to change in sample size without a change in proportionality between the species. This situation occurred at Site D68 for methods I(5), I(10) and I(20). All indices other than H show the same values between methods.

Interpretation of indices of diversity is difficult. With the knowledge of the number of species in each sample and in the fully censused community, the use of J' is of most value. It is a direct measure of evenness of the species with a simple account of those species not represented in the sample.

An index value on its own is of limited value. Its importance becomes apparent when used comparatively across a series of samples repeated in an area, or over time. Differences between the indices are not always evident, but the continued use of all five indices is justified as they have been shown to possess the potential to represent distinctly different characteristics in sets of data.

5.2.1.5 Biomass

A measure of biomass of an animal community (column 8, Table 5.1) gives an indication of the level of its productivity. This is a time-dependent measure and the data presented should not be assumed to represent the contribution to productivity by small mammals in the ecosystem. Biomass, or the accumulated weights (mean values) of individuals trapped, do not necessarily decline as a result of less traps being used. Elliott traps, being a single-capture mechanism, are in effect 'removed' from the sample following the capture of an animal, which renders them susceptible to behavioural differences in species. The two *Antechinus* species are frequently active in the late afternoon so that their early capture may exclude other species, which can become significant when trap numbers are low. These two species however, have relatively small body weights so a different species of much greater body weight (e.g. *Peromyscus nasuta*) displaying similar behaviour with low numbers of traps could be over-represented if taken on biomass alone.

At the most abundant site (BBC), all methods on average caught only 15-28% of the total small mammal biomass known to occur, compared with 42% averaged over the three less abundant sites. This difference suggests that biomass is not a reliable measure of community diversity.

5.2.1.6 Trap success

Trap success (proportion of traps catching animals) is a frequently used index of relative abundance in small mammal survey. The results of this study (column 10, Table 5.1) show that trap success varied according to trap spacing, and was inversely related to diversity. Index-lines at each site measured large increases in percentage trap success from 5 m to 20 m trap spacing yet the corresponding indices of diversity display no such trend. What this measure does suggest is the inefficiency of methods using 5 m spacing, particularly with grid configurations, when expressed in terms of effort.

Considering the amount of field effort required for each method, the time spent laying out, clearing, and collecting traps over each three day trapping period were recorded, with adjustments for more than one person operating in the field (column 11, Table 5.1). Field effort is a function not only of the number of traps set, but also of the relative trap success. Thus the steep decline in effort does not parallel the decline in trap numbers used. With grid configurations, G(5) on average took four times longer than G(20). The index-line methods were generally much less time consuming.

5.2.2 Efficiency of methods in sampling diversity of a known small mammal community.

5.2.2.1 Index values of cumulative captures for each trapping method compared with those of MKTBA and total diversity.

An important aspect of the survey of small mammal communities is accurate estimation of diversity by sampling.

Methods using different configurations or trap spacing need to be carried out in a community with known diversity to evaluate their capability for that purpose. Site BBC, being a discrete habitat with negligible movement of animals into or out of it (C. Dickman, *pers. comm.*) provided a suitable situation for such a study.

An evaluation of methods may be made in two ways. Firstly diversity indices based on the cumulated captures of small mammals over a three day trapping period for each method may be compared with those for the minimum number of animals known to be alive at the time of sampling. In a similar way, indices from cumulated captures may be compared with the total diversity at the site calculated from the numbers caught and marked during the total time in the field. Figure 5.2 shows the rates of capture of new animals of the three dominant species at Site BBC which indicates that marking the community was almost complete by the end of the trapping period. The final values for each curve plus the single *Rattus rattus* caught were then used to compute indices of total diversity (Table 5.3). Comparison of total numbers and index values for the same period during the previous two years shows two species to be more abundant in this study, with distribution between the species less even, and diversity values lower.

TABLE 5.3 ESTIMATED TOTAL NUMBERS OF ANIMALS AT SITE BBC DURING APRIL FOR THREE SUCCESSIVE YEARS, AND THEIR RESPECTIVE DIVERSITY INDEX VALUES.

SPECIES	TOTAL NUMBERS				DIVERSITY INDICES		
	1980*	1981*	1982		1980	1981	1982
<i>Antechinus stuartii</i>	22	15	41	L	0.3335	0.3878	0.4156
<i>A. swainsonii</i>	21	15	12	D	1.0981	0.9474	0.8780
<i>Rattus fuscipes</i>	21	33	59	H'	1.0984	1.0221	0.9871
<i>R. rattus</i>	0	0	1	H	1.0303	0.9549	0.9374
				J'	0.7923	0.7373	0.7121

* C.R. Dickman, Unpub. Data

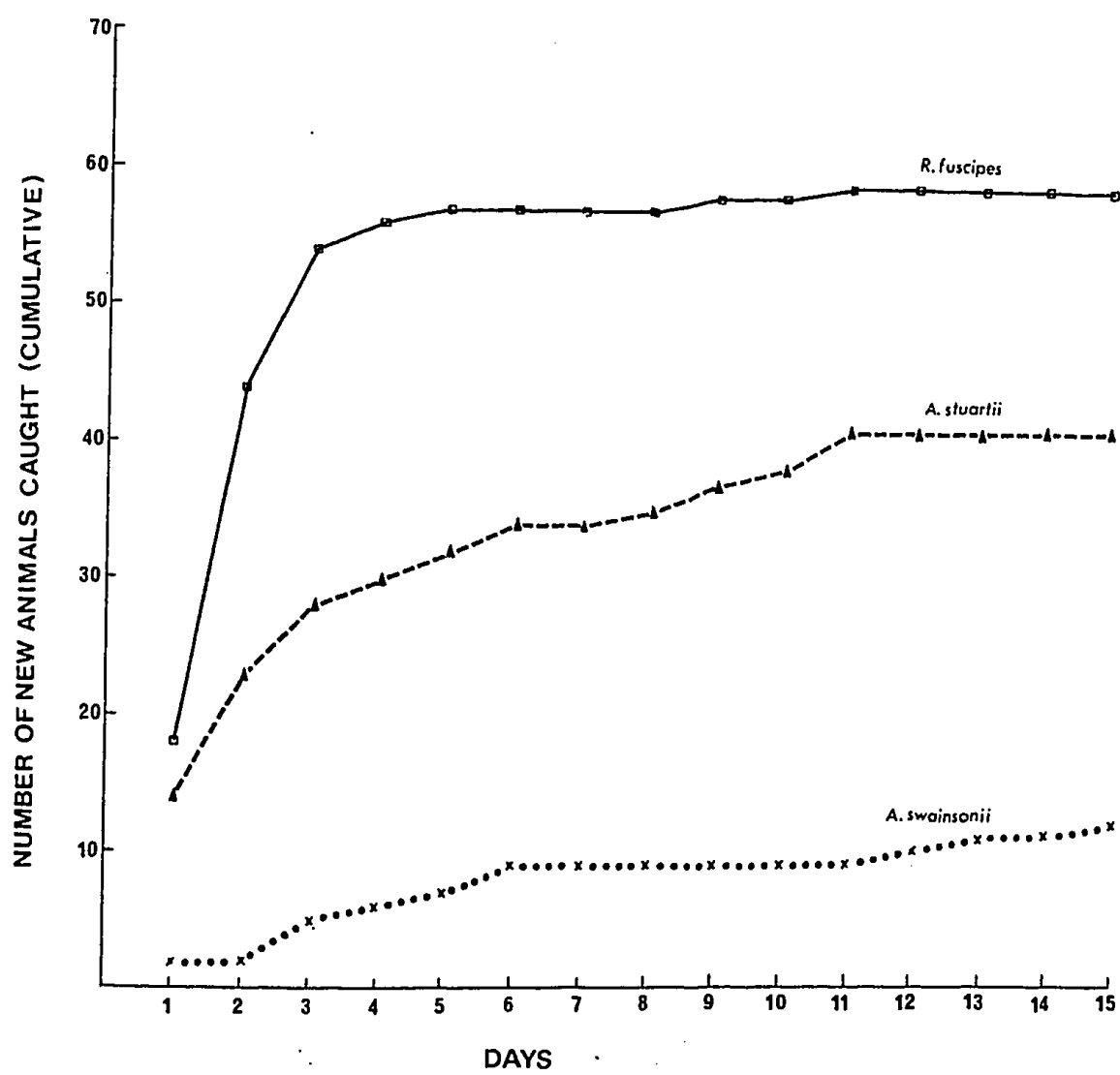


Figure 5.2 Rate of capturing new animals at Site BBC.

When index values of cumulative captures are plotted with those for MKTBA (Figure 5.3), the grid methods exhibit a steep decline in all indices as trap spacing increases. Only one method (G(7.5)) yields a good estimate of diversity. Closer spacing results in an overestimation and wider spacings and underestimation of the known diversity as represented by MKTBA. Similarly, when the known diversity is represented by total diversity, G (7.5) gives the closest estimate by the grid methods of three indices, although G(5) is marginally better when using H (Figure 5.4).

In contrast, the index-line methods are more uniform in their estimation of diversity using both MKTBA and total diversity as controls. Method I(20) is weakest when compared with total diversity although it results in a close estimate using D, H' and J' for MKTBA. The closer-spaced index-line methods generally yield better estimates of both measurements of the known diversity. All give values comparable with G(7.5) and all are more accurate than G(5), G(10) and G(20).

The trends of declining values of diversity indices in grid methods and their similarity in index-line methods may have any of three causes:

- i. Different methods may be sampling more or fewer species.
- ii. Different methods may be sampling more or lower numbers of animals.
- iii. Different methods may be sampling changing proportions of each species.

5.2.2.2 Species number as a cause of difference between methods

All methods with the exception of G(5) caught the same number of species. On one occasion only, G(5) caught a fourth species, *R. rattus*. To ascertain what impact the species had on the indices values were recalculated for G(5) and for the MKTBA during that period of sampling, assuming that *R. rattus* had not been caught. For D and H', both method and MKTBA values declined slightly and proportionally

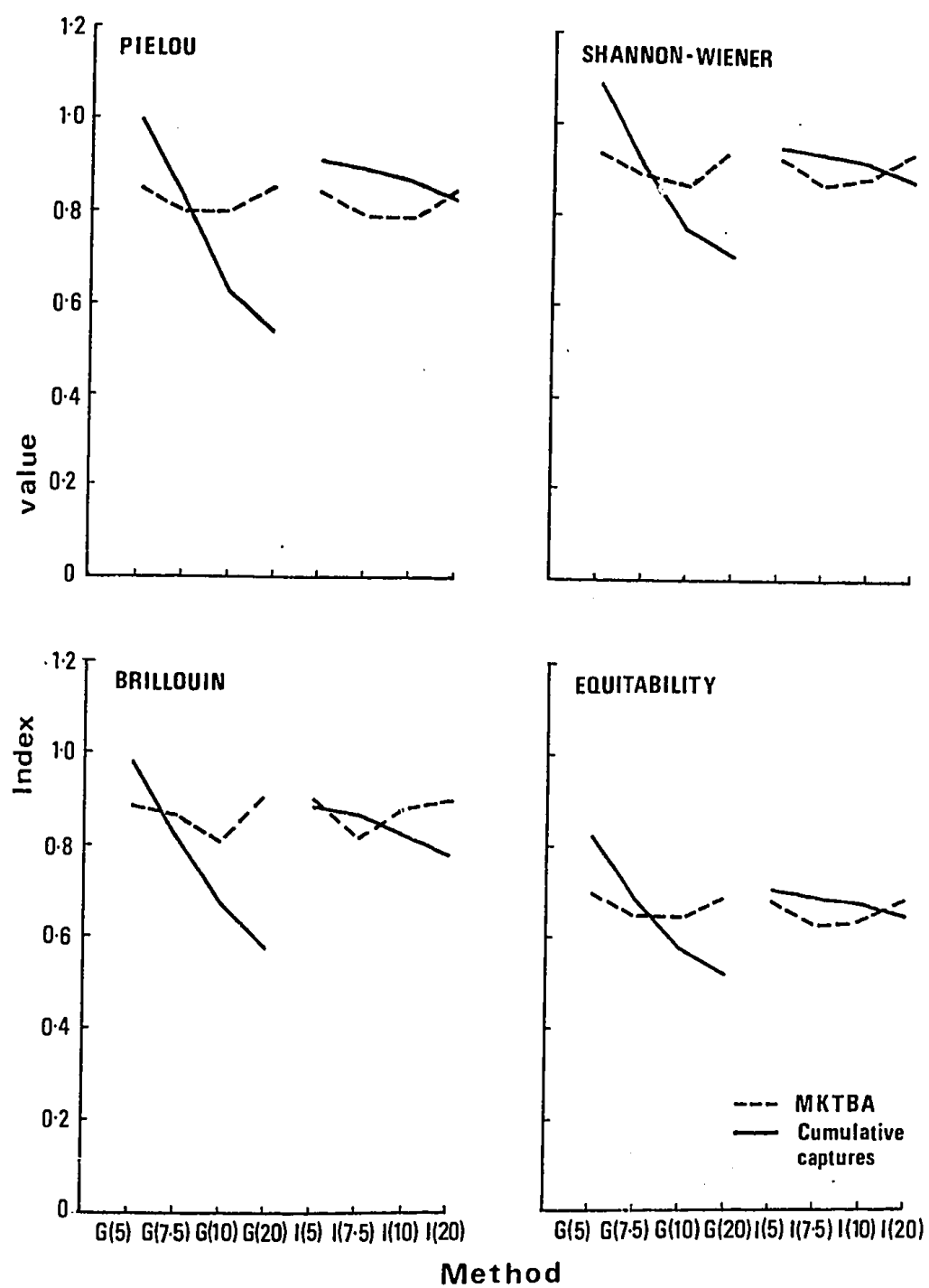


Figure 5.3 Diversity indices based on minimum known to be alive (MKTBA) and cumulated captures for all methods at Site BBC.

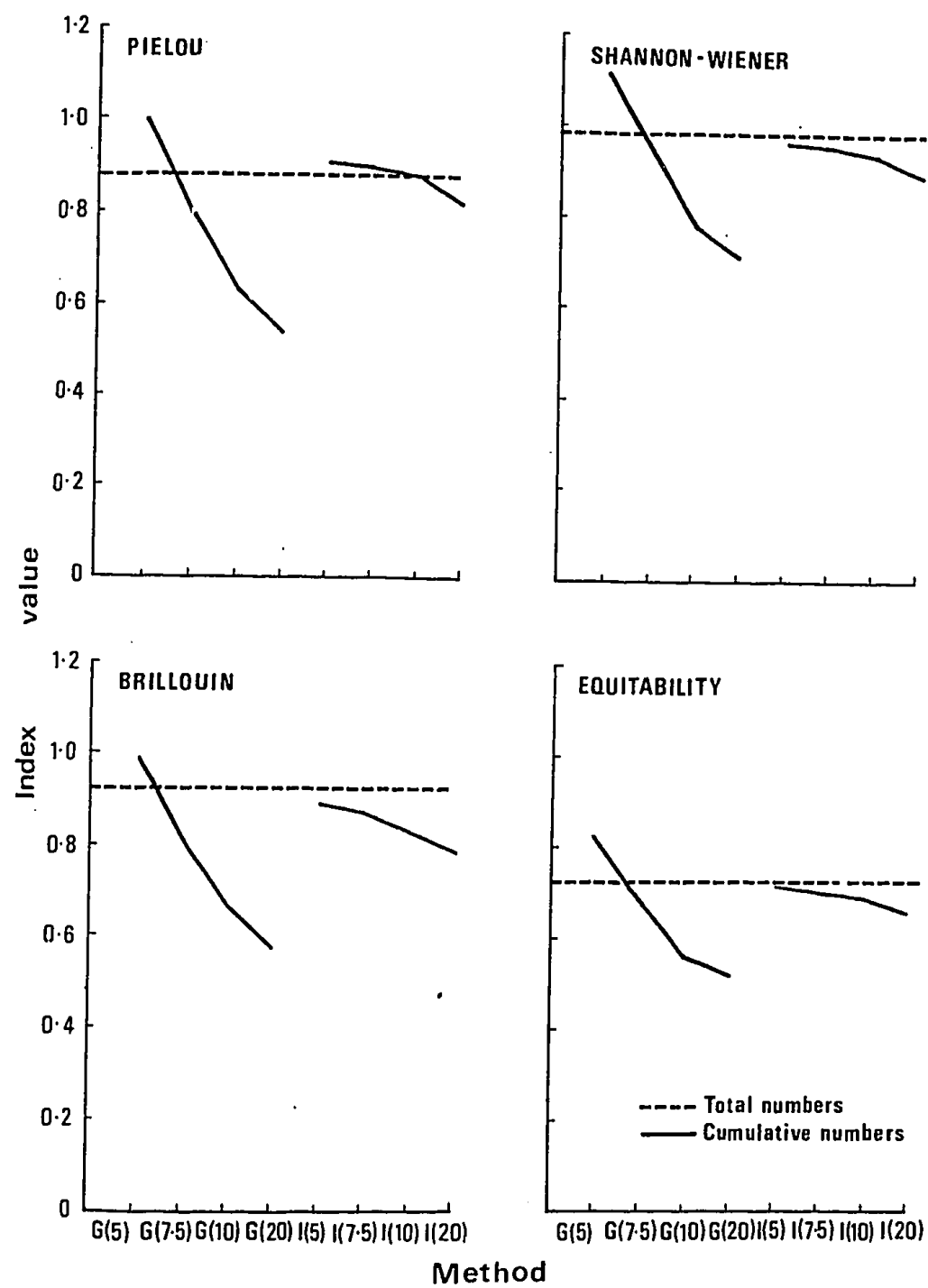


Figure 5.4 Diversity indices based on total numbers at the site and cumulated captures for all methods at Site BBC.

causing little change to the trend measured by different methods. The proportional change for H was greater resulting in G(5) being a closer approximation to MKTBA although still inferior to G(7.5). Both values increased for J' due to improved evenness, although again, G(5) is inferior to the representation by G(7.5). From modelled hypothetical data (4.2.2.6), H' was shown to be most sensitive to change of species number. In the current situation, H' displays minimal change in response to deleting the rare species which substantiates the conclusion that the number of species caught is not a significant cause of the trends measured by methods at Site BBC.

5.2.2.3 Numbers of animals caught as a cause of difference between methods

As may be expected, the numbers of animals caught declined as the spacing between traps was increased, due to fewer trapping stations being present (Table 5.4). When these data are compared proportionally for each configuration (Figure 5.5), there is clearly little difference between the trends measured. Similar changes between trap spacing for each configuration results in a corresponding proportional change in numbers of animals caught. Clearly, this alone is not the cause of the differences observed.

TABLE 5.4 CUMULATED NUMBERS OF ANIMALS CAUGHT BY EACH METHOD AT SITE BBC

GRID METHOD	NO. OF TRAPS	NO. ANIMALS CAUGHT	GRID METHOD	NO. OF TRAPS	NO. ANIMALS CAUGHT
G(5)	100	32	I(5)	60	41
G(7.5)	49	27	I(7.5)	40	36
G(10)	25	26	I(10)	30	29
G(20)	9	15	I(20)	15	22
TOTAL :	183	100		145	128

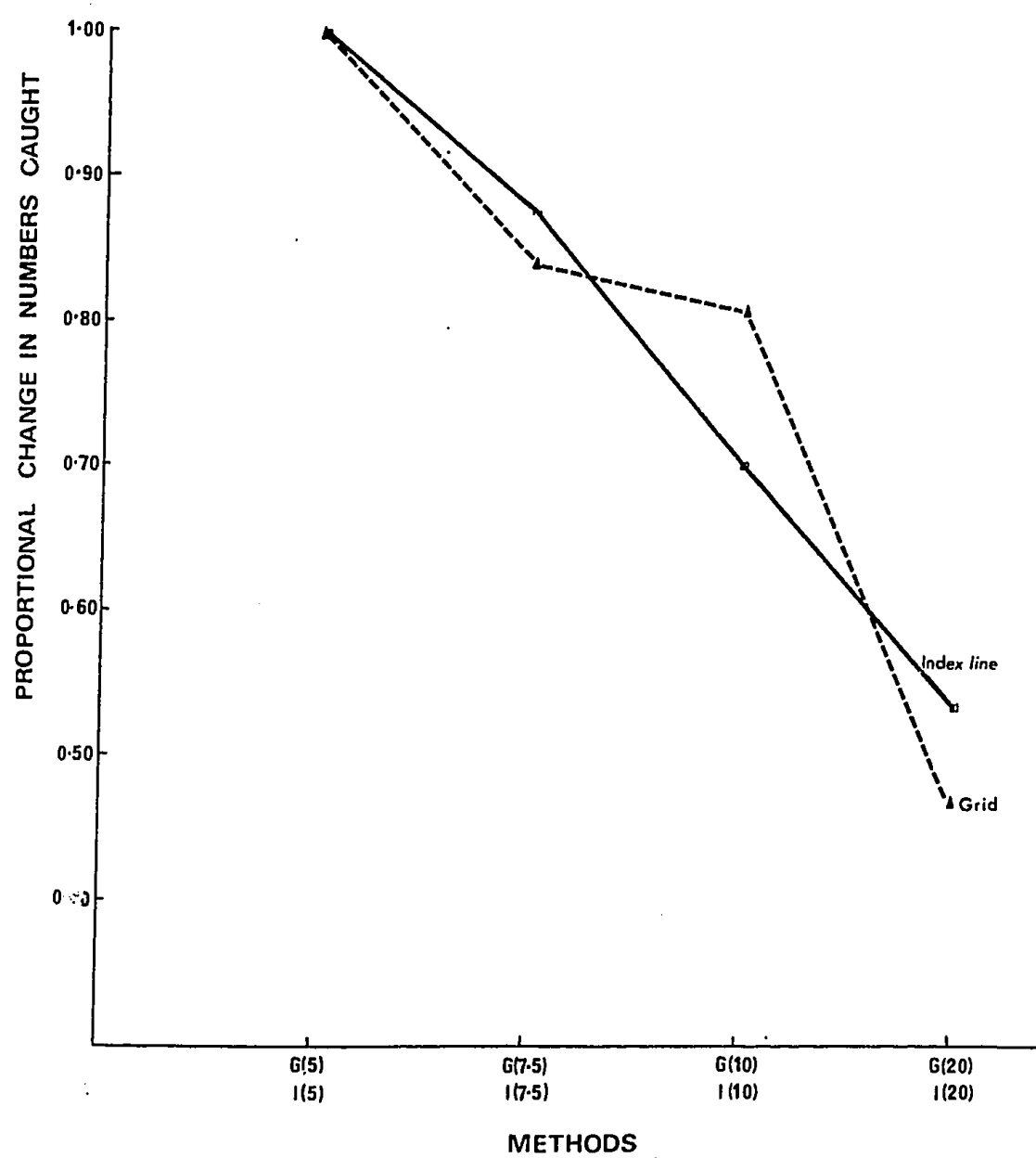


Figure 5.5 Proportional decline in the number of animals caught as trap spacing is increased for grid and index line methods at Site BBC.

5.2.2.4 Changing proportions between each species as a cause of difference between methods

The third possible cause of differences between methods is if they sampled species in different proportions to that which actually existed in the community. Table 5.5 lists for each method, the relative proportions in which each species was caught. If these values are compared with those for the total community deviations may be calculated.

Clear trends occur in the results of the grid trapping methods. *A. stuartii* was caught in proportions equal to *R. fuscipes* by method G(5), each representing 40.6% of the total animals caught. At this spacing, *A. stuartii* was over-represented by 4.3%. However, as the spacings were increased, the proportions of this species declined to be under-represented by 16.3% for method G(20). Contrary to this, *R. fuscipes* was initially under-represented by 11.6% for G(5) but increased its proportion in the catch as the spacings were increased to be over represented by 21.1%. Proportional changes in *A. swainsonii* were less exaggerated with a trend from over-representation of 5.0% to under-representation by 3.9% as spacings were increased. *R. rattus* was caught once only and is of no significance. Of the grid methods, G(7.5) has least sum deviation from the total community proportions for all species while G(20) has greatest. These trends are summarized graphically in Figure 5.6.

In contrast, results of the index-line methods display little consistency. *A. swainsonii* declined slightly in proportions, but with a range of deviation of +1.6% to -1.5%, this species was adequately sampled by all index-line methods. The two more abundant species have inverse responses. *A. stuartii* was over-represented by each method, ranging from 8.1% to 0.1%, while *R. fuscipes* was variably under-represented by the closer spacings, and minimally (1.5%) over-represented by I(20). With the deviations summed for each species, I(20) has the least value indicating that this method caught species in proportions most similar to those of the total community.

TABLE 5.5 RELATIVE PROPORTIONS OF SPECIES CAUGHT BY EACH METHOD AT SITE BBC

METHOD	PROPORTIONS OF SPECIES AND DEVIATIONS (BRACKETS)				Σ DEVIATIONS
	<i>A. stuartii</i>	<i>A. swainsonii</i>	<i>R. fuscipes</i>	<i>R. rattus</i>	
G(5)	0.406 (+0.043)	0.156(+0.050)	0.406 (-0.116)	0.032 (+0.023)	0.232
G(7.5)	0.259 (-0.104)	0.148 (+0.042)	0.593 (+0.071)	0.000 (-0.009)	0.226
G(10)	0.231 (-0.132)	0.077 (-0.029)	0.692 (+0.170)	0.000 (-0.009)	0.340
G(20)	0.200 (-0.163)	0.067 (-0.039)	0.733 (+0.211)	0.000 (-0.009)	0.422
I(5)	0.390 (+0.027)	0.122 (+0.016)	0.488 (-0.034)	0.000 (-0.009)	0.086
I(7.5)	0.444 (+0.081)	0.112 (+0.006)	0.444 (-0.072)	0.000 (-0.009)	0.168
I(10)	0.414 (+0.051)	0.103 (-0.003)	0.483 (-0.039)	0.000 (-0.009)	0.102
I(20)	0.364 (+0.001)	0.091 (-0.015)	0.545 (+0.023)	0.000 (-0.009)	0.048
Total Community	0.363	0.106	0.522	0.009	

N.B. Values for each species are the relative proportions of the total number of animals caught by each of the methods. Deviations from values for the total community are included in parentheses.

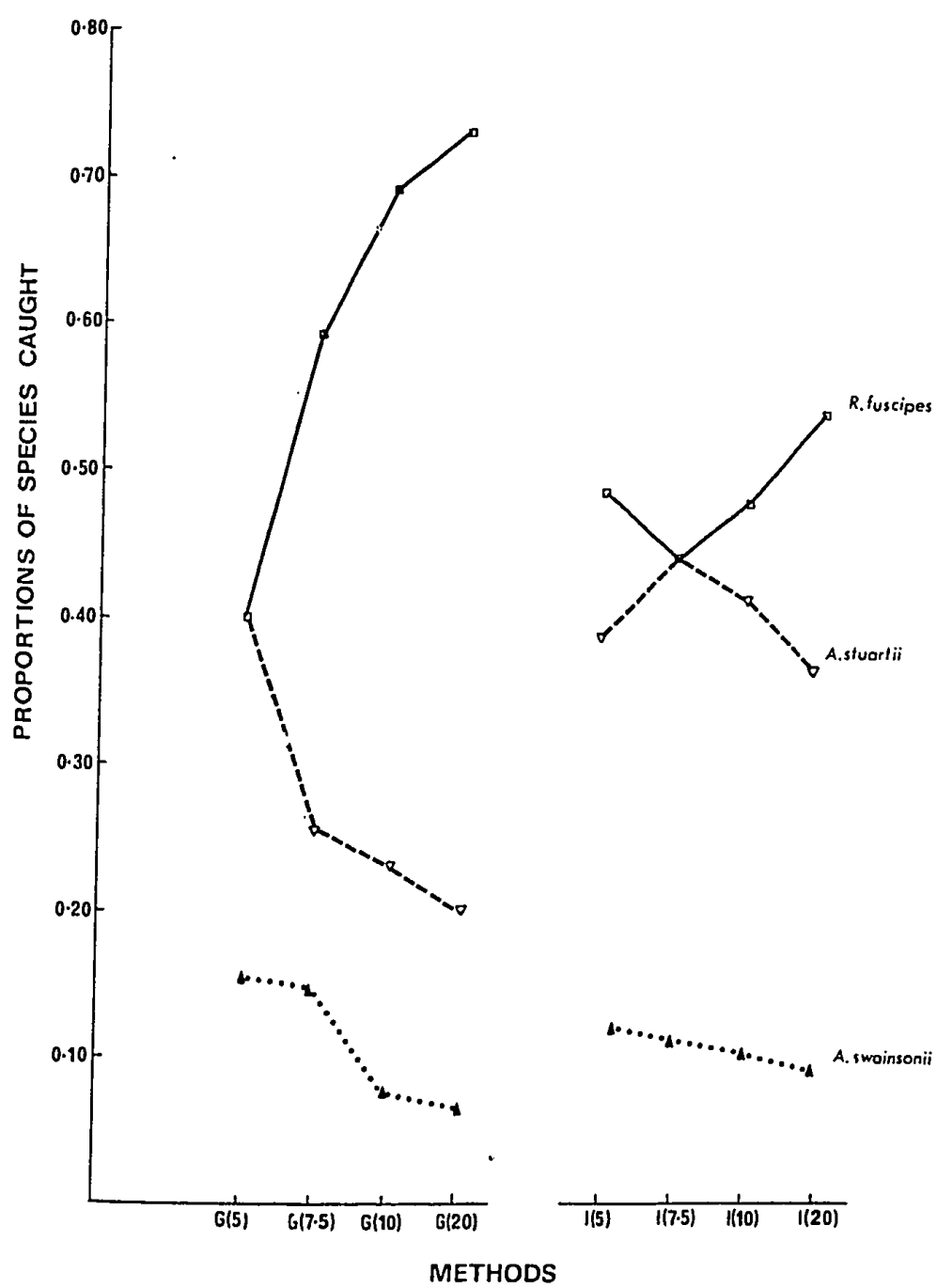


Figure 5.6 Relative proportion of each species caught by methods at Site BBC.

The descending rank for other index-line methods is I(5), I(10) and I(7.5) with all index-line methods proving to have greater accuracy than all grid methods.

This analysis shows that methods with traps placed in a grid configuration are very sensitive to the dominance characteristics of each small mammal species while those with traps along an index-line give results which more accurately represent actual proportions of species present. Understanding the intricacies of dominance behaviour between interacting species as represented by field trapping is beyond the requirements of this study. It is clear, however, that such differences do occur and they affect sampling methods. More significant is the close correspondence of these findings with diversity index values for both grid and index-line methods (5.2.2.1). Clearly, as *R. fuscipes* increases in dominance, the evenness component of diversity deteriorates; this is expressed directly by J' , and indirectly by other indices for grid methods as a trend with increasing trap spacing. This factor alone, rather than numbers of species or total numbers of animals caught, provides adequate explanation for diversity values which vary markedly from those of the total community.

5.2.3 Consistency of methods in differing sites

Analysis of capture data from the known site, BBC, clearly showed that grid and index-line configurations sampled the small mammal community in different ways. There is a need to examine these differences across a range of environments in forest ecosystems. Data sets from all four sites have thus been included in this analysis, for which the diversity indices were recalculated, treating each of the three days independently rather than cumulatively. The analysis involves two stages, the first being a 3-factor analysis of variance to ascertain similarities and variations between sites, methods and days. The second stage is to rank method similarity to determine which of them varied least between the sites.

5.2.3.1 3-factor analysis of variance of diversity

Factors that may have caused variation in diversity between methods were the sites and the day of sampling. With methods, these factors were combined to provide a basis for analysis of variance of each of the diversity indices. In general, each measure, a combination of 4 sites x 8 methods x 3 days, had 96 observations in a 4 x 8 x 3 factorial design. Using a Tukey test of non-additivity (Sokal and Rohlf, 1969) on the 4 x 8 tables of values over 3 days, no significant interactions were detected between factors, which supported the assumption that the three factor interaction did not exist. The three factor interaction was then used as an estimate of error in the measure. It was then possible to judge the effects of each of the factors on the measure.

In this analysis, mean values of indices of diversity for sites, days and methods were compared and variations between them evaluated.

For each diversity index, variance ratios were computed for all combinations of the three factors and tested for levels of significance (Table 5.6). Only the Simpson index revealed a significant interaction between factors, that being between methods used and the day of sampling at the 5% level of significance. This contrasts with the Tukey test of non additivity between factors, but the significance of the interaction is weak and apparently only applicable to method G(20) (Figure 5.7). As this index is sensitive to the less abundant species, it is probably reflecting an almost uniform distribution of species present at sites, caused by the low number of traps being used and relatively low captures of the more abundant species on the first day. Otherwise, there is no significant factor interaction, indicating that methods behave similarly across sites and between days.

All indices reveal strongly significant differences between methods (Table 5.6). Examination of standard errors for each index of diversity (Table 5.7) show consistent groupings of five methods, G(5), I(5), I(7.5), I(10) and I(20), which are

TABLE 5.6 COMPARATIVE ANALYSIS OF VARIANCE (VARIANCE RATIO) FOR EACH INDEX OF DIVERSITY CONSIDERING SITES, METHODS, DAYS AND THEIR COMBINATIONS AS FACTORS.

FACTOR	df	SIMPSON		PIELOU		S-W		BRILLOUIN		EQUITABILITY	
Site	3	4.544	**	9.060	***	11.656	***	31.427	***	2.350	NS
Method	7	3.270	**	5.279	***	6.148	***	10.891	***	5.516	***
Day	2	2.620	NS	3.194	NS	4.424	*	8.033	**	4.806	*
Site x Method	21	1.634	NS	1.430	NS	1.088	NS	0.852	NS	0.986	NS
Site x Day	6	0.482	NS	0.788	NS	1.295	NS	1.034	NS	1.647	NS
Day x Method	14	2.052	*	1.596	NS	1.269	NS	1.296	NS	1.301	NS
Residual	42										

N.B. *** = 0.001 significance level

** = 0.005 significance level

* = 0.05 significance level

NS = not significant.

not significantly different. The remaining three methods, G(7.5), G(10) and G(20), are significantly different from the first grouping, and between themselves. Simply, this means that the closely spaced grid method (G5) and all the index-line methods returned similar results for the site at which they were used. This association holds for all four sites sampled, as shown in Figure 5.8.

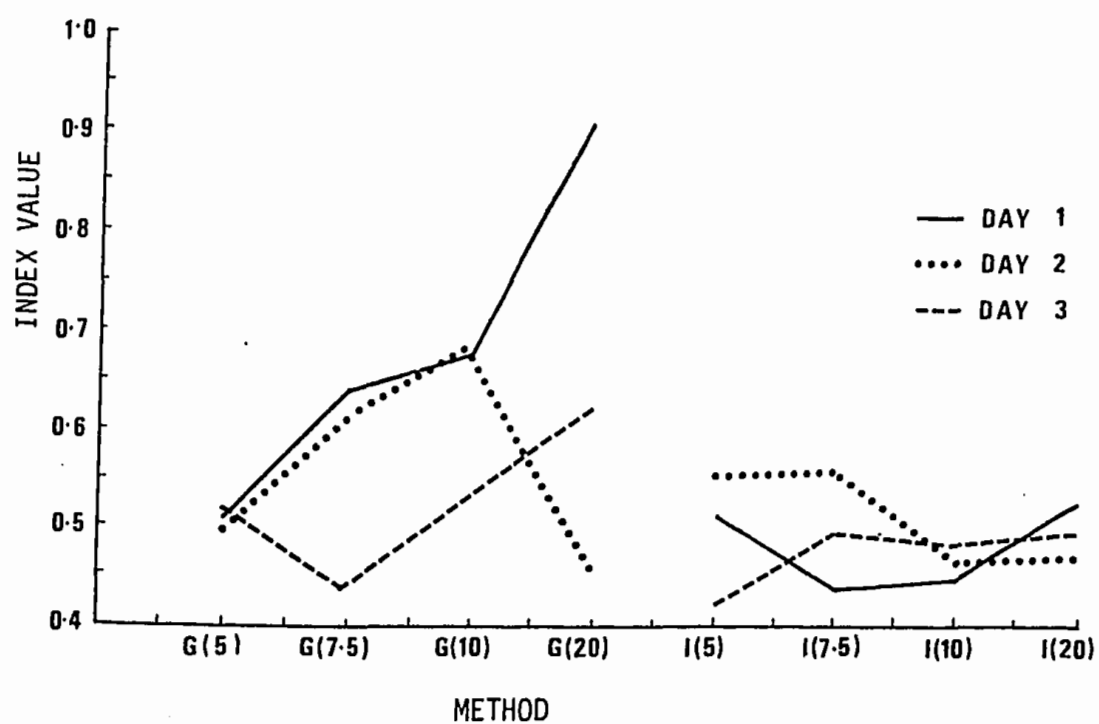


FIGURE 5.7 METHOD AND DAY INTERACTION FOR SIMPSON'S DIVERSITY INDEX.

TABLE 5.7 MULTIPLE COMPARISONS FOR EACH INDEX OF DIVERSITY SHOWING SIGNIFICANT DIFFERENCES BETWEEN METHODS.

METHOD	PIELOU	S-W	BRILLOUIN	EQUITABILITY
G(5)	0.715 a	0.779 ab	0.555 ab	0.597 ab
G(7.5)	0.637 ab	0.667 bc	0.463 bc	0.500 bc
G(10)	0.498 bc	0.556 cd	0.354 cd	0.423 cd
G(20)	0.394 c	0.395 d	0.243 d	0.317 d
I(5)	0.724 a	0.790 ab	0.596 a	0.612 ab
I(7.5)	0.732 a	0.780 ab	0.579 a	0.599 ab
I(10)	0.781 a	0.848 a	0.608 a	0.659 a
I(20)	0.721 a	0.767 ab	0.516 ab	0.591 ab
SED	0.0830	0.0867	0.0557	0.0697

N.B. i. Index values with the same letter are not significantly different.
 ii. SED = Standard Error Difference.

With the exception of the equitability diversity index, all indices show significant differences between sites (Table 5.6). Equitability is essentially a measure of the spread, or relative proportions of individuals amongst the species at a site whereas the other indices are also sensitive to the number of species and the numbers of animals belonging to each (Table 5.1). The Simpson index groups sites inversely to the Pielou index, which is to be expected as their formulations are inversely associated. The Shannon-Wiener index is however consistent with the grouping of Pielou's. Grouping by the Brillouin index differs only in that Site D50 is dissociated from Site BBC (Table 5.8). Otherwise, strong associations occur between Sites BBC and D50 (the sites with most species and numbers of individuals), and between Sites D75 and D68 (sites with least species and numbers) with significant differences between the groups. Although the sites have been shown to be significantly different, the trapping methods used are behaving similarly between sites. Associations of this similarity is shown graphically in Figure 5.9.

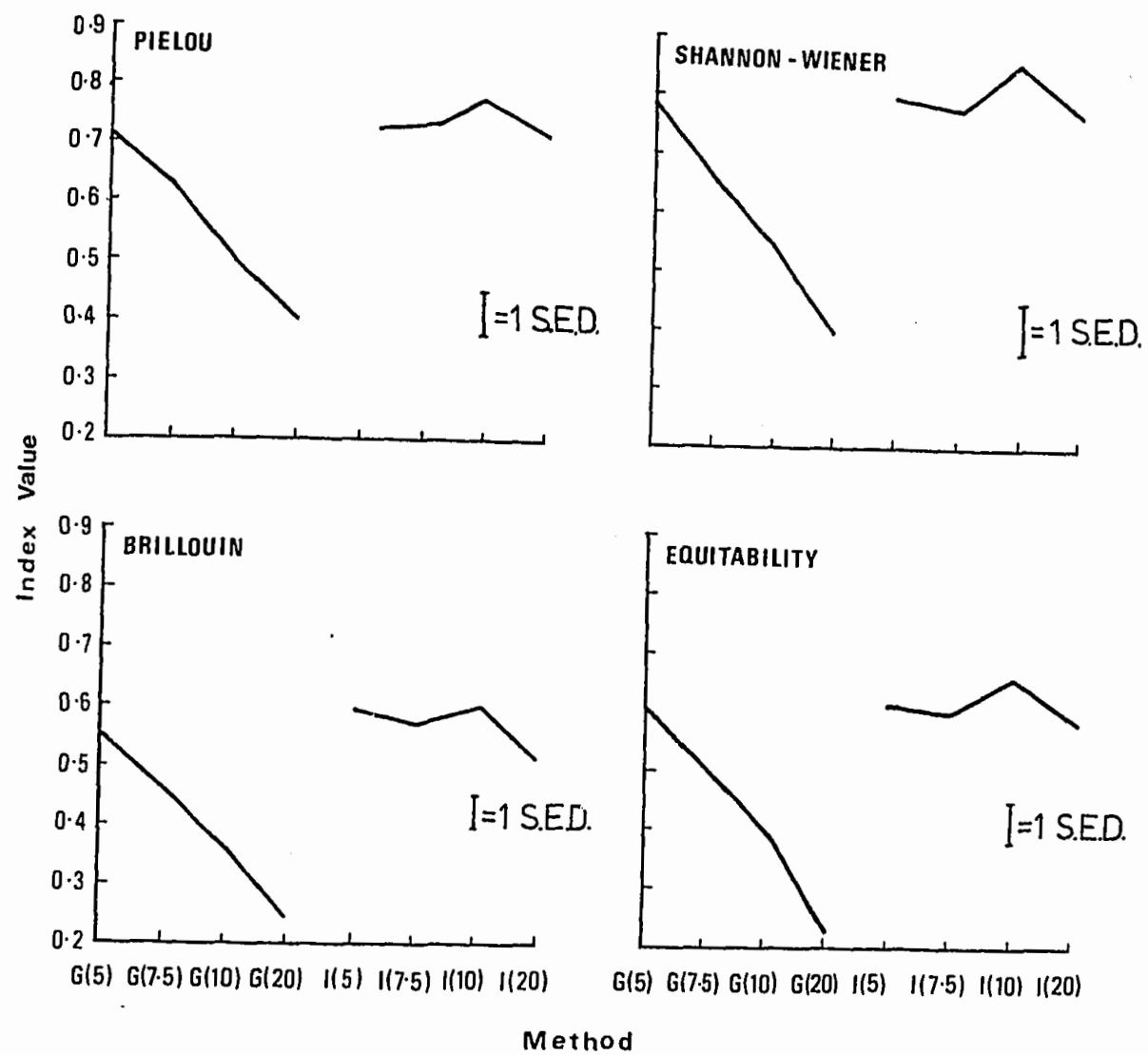


FIGURE 5.8 MEAN DIVERSITY INDEX VALUES FOR GRID AND INDEX-LINE METHODS TAKEN FROM DATA AT FOUR SITES (BBC, D75, D68, D50) OVER THREE DAYS.

TABLE 5.8 MULTIPLE COMPARISONS FOR EACH INDEX OF DIVERSITY SHOWING SIGNIFICANT DIFFERENCES BETWEEN SITES.

SITE	SIMPSON	PIELOU	S-W	BRILLOUIN
BBC	0.478 b	0.757 a	0.852 a	0.702 a
D75	0.582 a	0.547 b	0.563 b	0.495 b
D68	0.595 a	0.538 b	0.580 b	0.424 b
D50	0.491 b	0.760 a	0.796 a	0.336 c
SED	0.0401	0.0587	0.0613	0.0394

- N.B. i. Index values with the same letter are not significantly different.
 ii. SED = Standard Error Difference.

Three of the indices, Shannon-Wiener, Brillouin and equitability show significant differences between the three successive days of capture (Table 5.6). From field notebooks, it was obvious that the numbers of each species increased noticeably each successive day so it is reasonable to accept that the indices most responsive to additions of new species and least responsive to abundance (Simpson and Pielou) are not significantly different. Table 5.9 demonstrates that Day 3 is grouped separately from the first two days, which are themselves not significantly different (Figure 5.10). The methods giving different results on the third day reflecting the increase in numbers caught of each species.

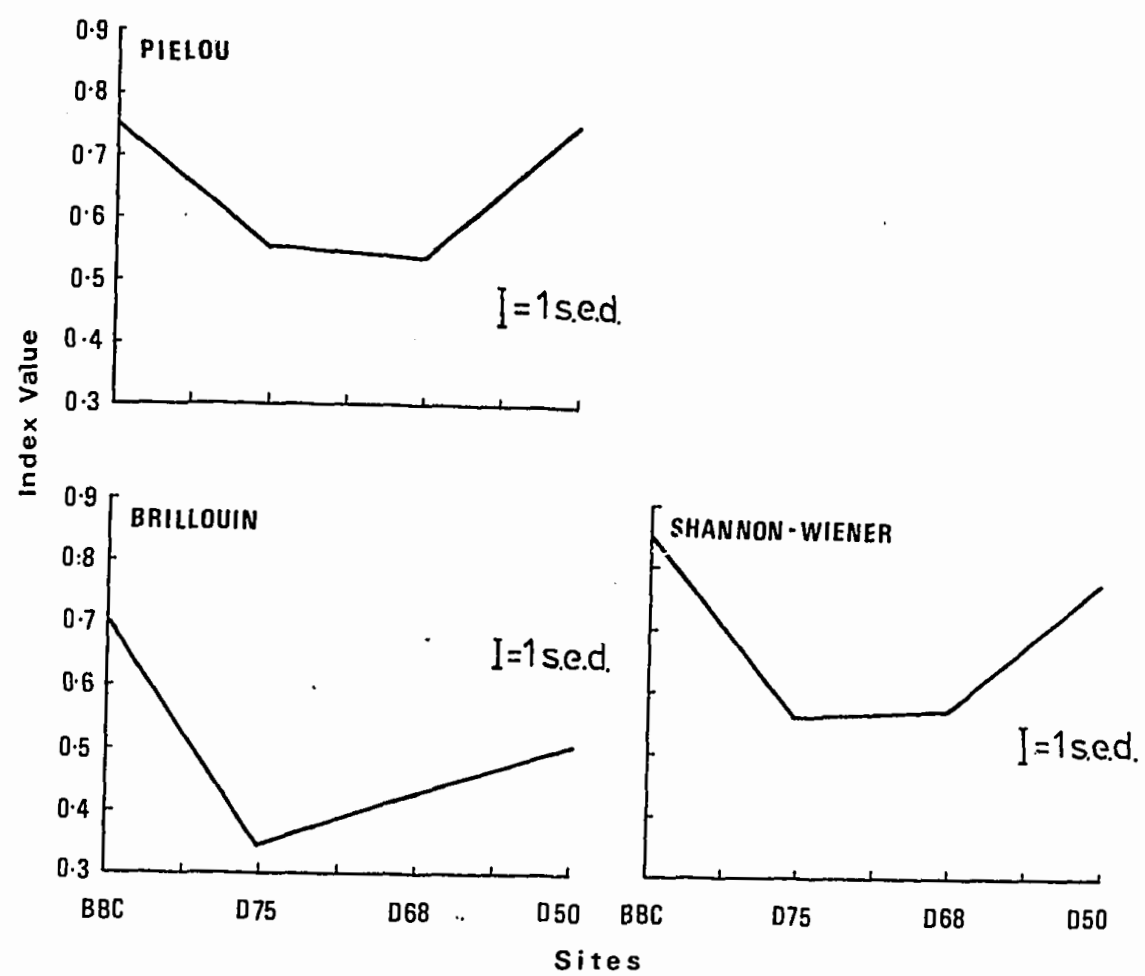


FIGURE 5.9 MEAN DIVERSITY INDEX VALUES FOR FOUR SITES TAKEN FROM EIGHT GRID AND INDEX-LINE METHODS OVER THREE DAYS.

TABLE 5.9 MULTIPLE COMPARISONS FOR EACH INDEX OF DIVERSITY SHOWING SIGNIFICANT DIFFERENCES BETWEEN DAYS.

DAY	S-W	BRILLOUIN	EQUITABILITY
1	0.6355 b	0.432 b	0.487 b
2	0.672 b	0.470 b	0.513 b
3	0.786 a	0.565 a	0.612 a
SED	0.0531	0.0341	0.0427

- N.B. i. Index values with the same letter are not significantly different.
 ii. SED = Standard Error Difference.

5.2.3.2 Similarity of methods

In this, the second stage of the analysis of capture data the preceding discussion is reinforced by establishing a consensus diversity configuration as the best fit for all site/method combinations, with which the differences in diversity between methods and sites can be compared.

The consensus diversity configuration was formed by first applying the Morisita Index of similarity, discussed in Section 4.2.3, to the diversities measured by all combinations of methods for each site and arranged in matrices of similarity of diversity (Appendix VI). The four 8 x 8 matrices were analysed by Principle Co-ordinates Analysis (Gower, 1966) to reduce the number of dimensions to provide a simpler representation of variability in the data. This analysis yielded four new sets of co-ordinates of the eight methods, which were analysed by generalized procrustes rotation (Gower, 1975) to "optimize" the fit of the four reduced sets of co-ordinates to give a single consensus configuration.

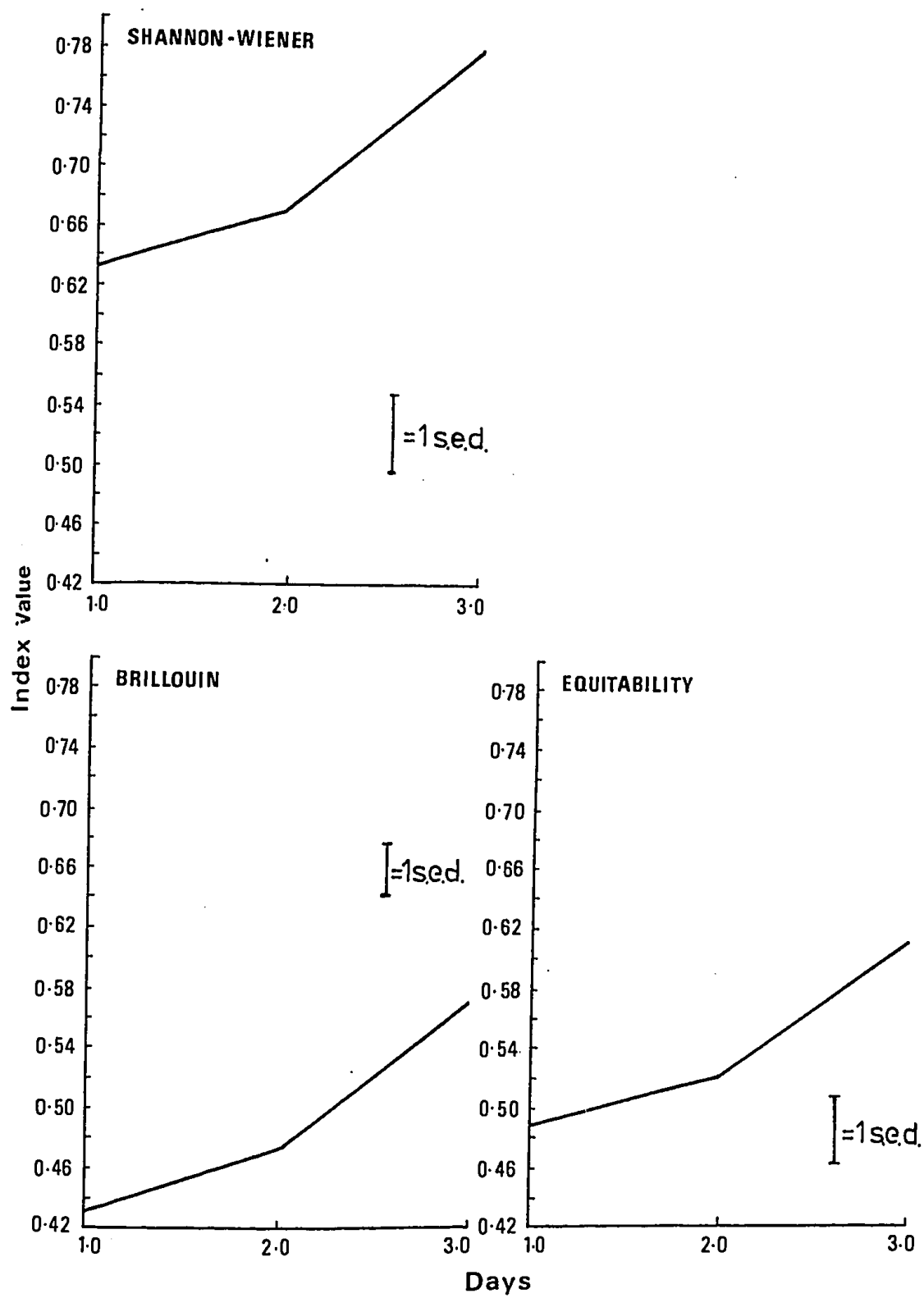


FIGURE 5.10 MEAN DIVERSITY INDEX VALUES FOR THREE DAYS TAKEN FROM EIGHT GRID AND INDEX-LINE METHODS AT FOUR SITES.

Results of the Principle Co-ordinates Analysis are shown in Table 5.10 which clearly demonstrate that the first four dimensions contain almost all the variation in the data, the majority of which is accounted for in the first two. This suggests the decision to use fewer dimensions as a reasonable approximation to the data.

To illustrate now how the methods vary relative to the consensus configuration, their residual variances are displayed in Table 5.11. These indicate that the sites agree least about method G(20) than any of the other methods. The index-line methods in general show more agreement between sites than do the grid methods. Figure 5.11 shows that for most of the sites, method G(20) groups with methods G(7.5) and G(10) but for Site D68, method G(20) is grouped with I(5), I(7.5), I(10) and with G(7.5). The discrepancy with Site D68 and method G(20) is possibly caused by a low number of traps capturing equal proportions of individuals in a species poor (2 species) community.

TABLE 5.10 PERCENTAGE VARIANCE ACCOUNTED FOR BY THE FIRST FOUR CO-ORDINATES IN THE PRINCIPAL CO-ORDINATES ANALYSIS FOR EACH SITE.

Site	PERCENT VARIANCE ACCOUNTED FOR				Total Variance
	Co-ordinate 1	Co-ordinate 2	Co-ordinate 3	Co-ordinate 4	
BBC	94.99	4.05	0.80	0.15	99.99
D75	64.47	33.68	1.65	0.16	99.96
D68	98.04	1.95	0.03	0.01	100.00
D50	55.40	32.93	9.09	1.86	99.28

TABLE 5.11 ANALYSIS OF VARIATION OF METHODS FROM THE CONFIGURATION CONSENSUS PRODUCED BY A GENERALIZED PROCRUSTES ROTATION.

Method	Residual Variance	Total Variance	Residual/ Total (Per cent)
G(5)	0.233	0.367	63.49
G(7.5)	0.213	0.289	73.70
G(10)	0.169	1.091	15.49
G(20)	0.397	0.868	45.74
I(5)	0.108	0.406	26.60
I(7.5)	0.126	0.261	48.28
I(10)	0.244	0.467	52.25
I(20)	0.126	0.252	50.00

Generally, methods G(7.5), G(10) and G(20) group separately from the rest. All methods can be grouped into four categories of effectiveness;

1. I(5), I(10) - best
2. G(5), I(7.5), I(20) - good
3. G(7.5), G(20) - poor
4. G(10) - worst.

TABLE 5.12 ANALYSIS OF SITE VARIATION FROM THE CONFIGURATION CONSENSUS PRODUCED BY A GENERALIZED PROCRUSTES ROTATION

Site	Residual Variance	Total Variance	Residual/Total (Per cent)
BBC	0.400	1.003	39.88
D75	0.396	1.018	38.90
D68	0.439	0.810	54.20
D50	0.381	1.169	32.59

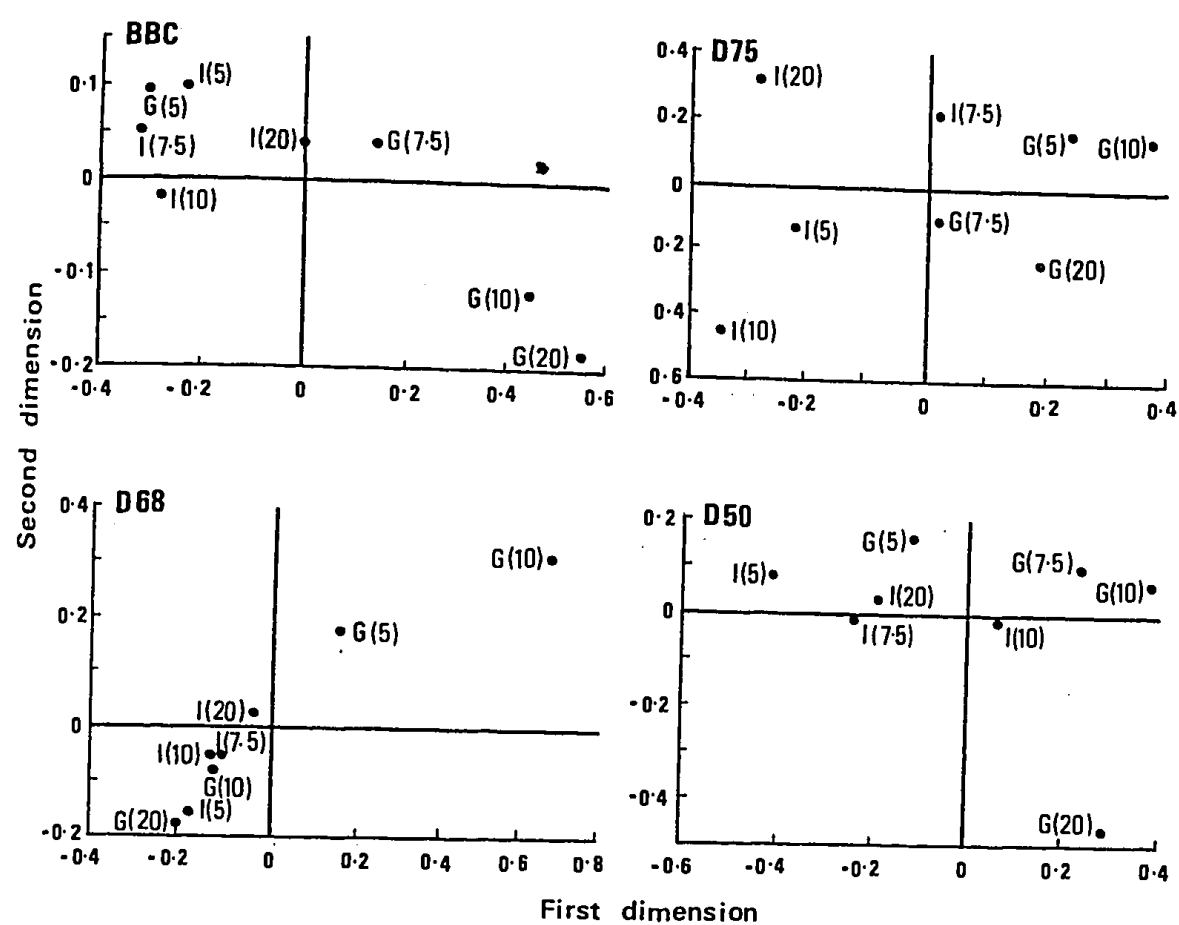


FIGURE 5.11 CLUSTERING OF METHODS FOR EACH SITE USING THE FIRST TWO DIMENSIONS OF THE PRINCIPAL CO-ORDINATE ANALYSIS.

The residuals of variation of sites relative to the consensus configuration (Table 5.12) also shows Site D68 to differ most, although all four sites differ by relatively large amounts. Other than for method G(20), these differences are not reflected in the methods.

5.2.4 Minimum sample size required by each method for community representation

Having identified differences between methods resulting from configuration and distance between traps, in this section an attempt is made to determine the minimum sample size for each method that would return the same results. The approach to this has been to calculate diversity indices cumulatively by subsequentially increasing sample size with the addition of more stations, which are then plotted to show at what sample size total diversity of the community is best measured.

5.2.4.1 Minimum sample size for grid methods

The cumulative approach to analysis in the determination of minimum sample size has been used for grid methods by taking each corner station separately and sequentially adding neighbouring stations (Figure 5.12) to the stage where the complete grid is included from all corners. For methods G(5) and G(7.5) there are 10 stages while for methods G(10) and G(20) there are nine. The cumulated values of capture data at each stage were used to calculate the suite of diversity indices for each corner independently of which mean values were subsequently calculated. Two indices were selected to represent diversity and evenness, the Shannon-Wiener index (H'_c) and Equitability (J'_c), for which their computations, based on cumulated captures, are represented graphically (Figures 5.13 and 5.14).

Asymptotic values were identified and compared with community values for each Site (Tables 5.13 and 5.14). An

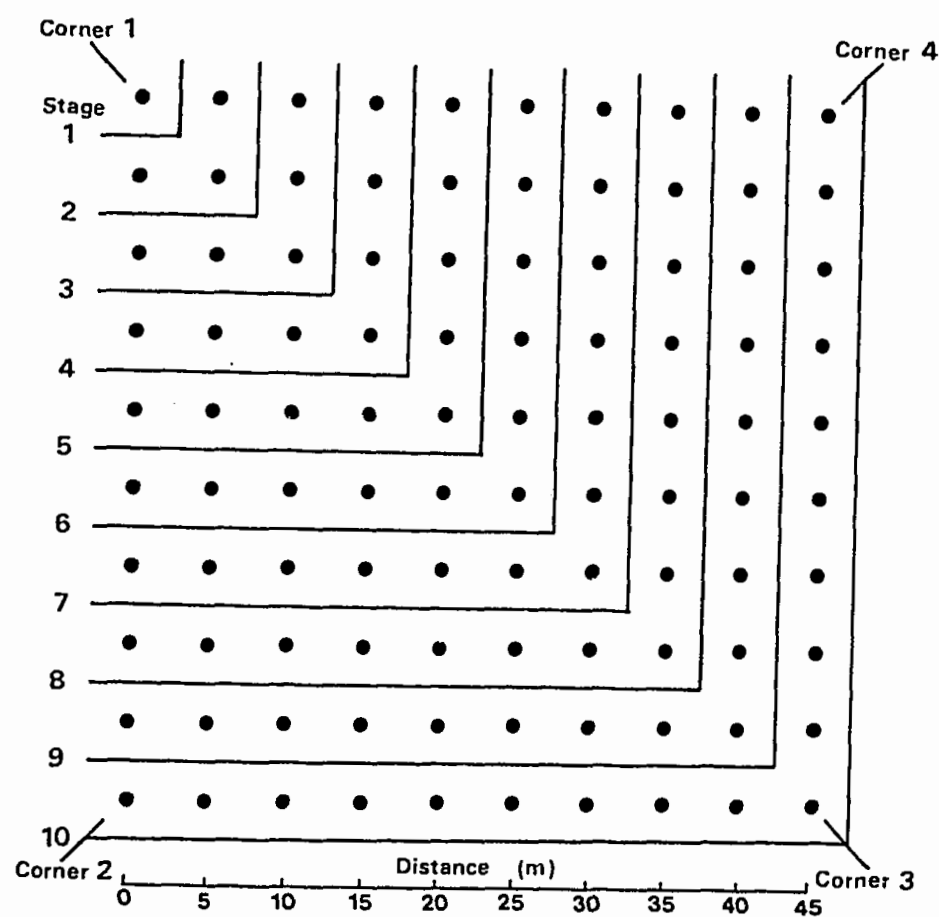


FIGURE 5.12 DESIGN OF ANALYSIS USED FOR ONE OF FOUR CORNERS TO DETERMINE MINIMUM SAMPLE SIZE FOR GRID METHODS

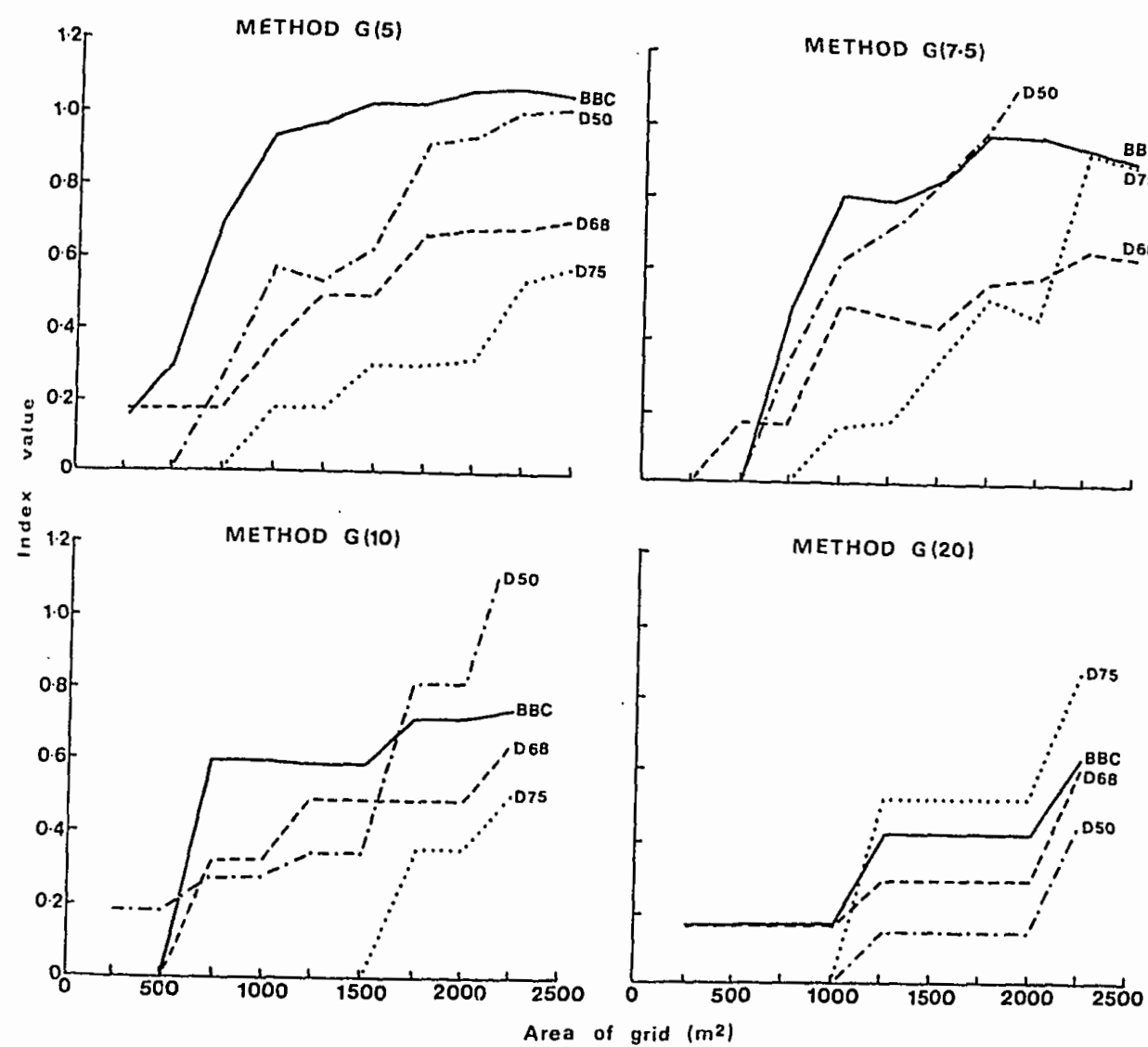


Figure 5.13 The effect of increasing sample area for grid methods on the Shannon-Wiener index of diversity.

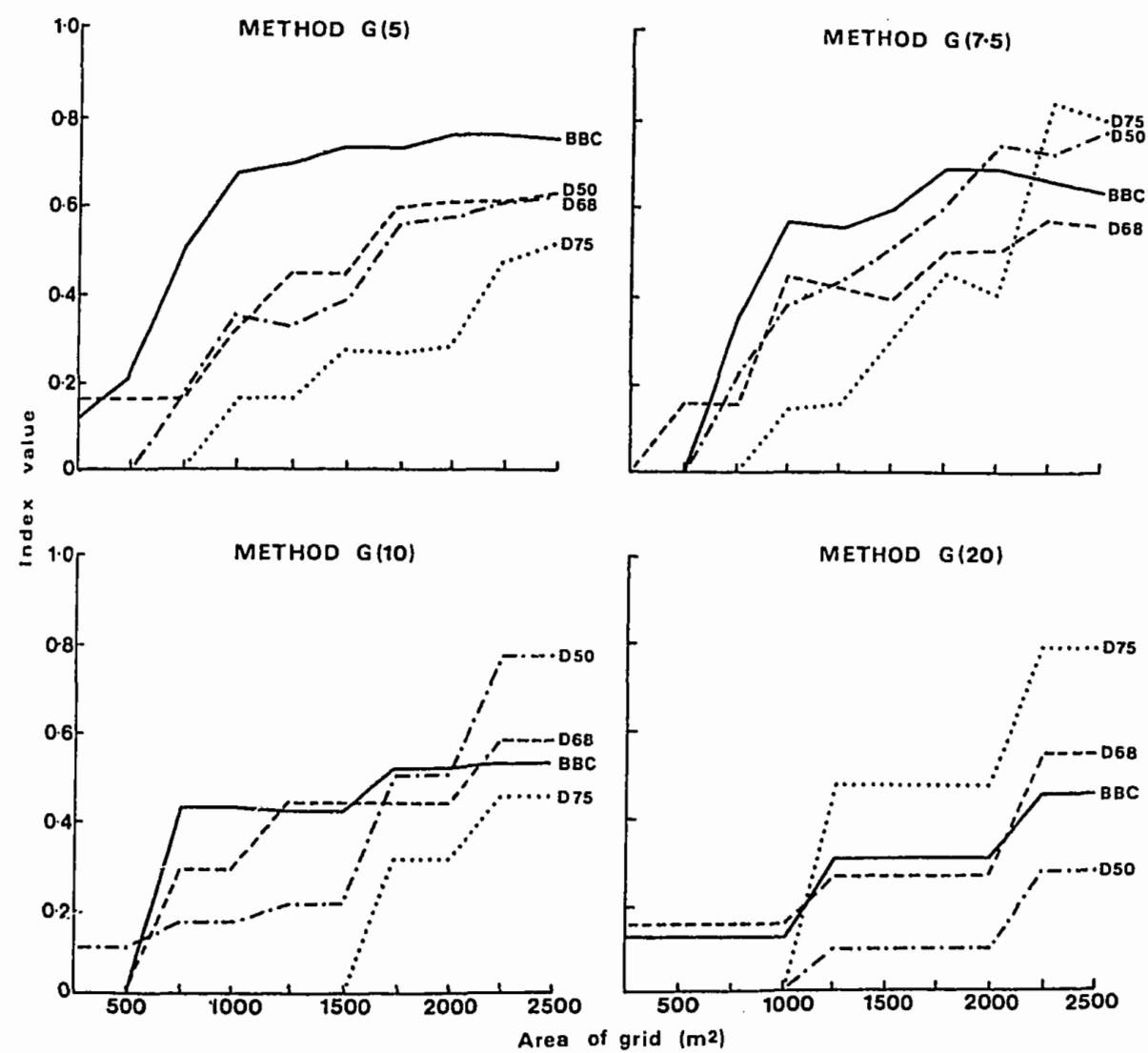


Figure 5.14 The effect of increasing sample area for grid methods on the equitability index.

asymptote is defined for these purposes as having uniform index value (± 0.0500) for a minimum of four consecutive sampling stations. Maximum values are used where an asymptote does not exist. It is recognized that the values may increase for sample areas greater than those measured.

At site BBC method G(5) alone resulted in a plateau from the cumulation analysis (Figure 5.13 and 5.14). The relatively stable value for J'_c underestimates the index of total equitability in the community (J'_{tot}) by 1.97% and the index of equitability using that method calculated on Day 3 data (J'_3) was overestimated by 3.17%. Diversity is not accurately represented with H'_{tot} being underestimated by 16.88% and H'_3 by 12.52%. For J'_c , the stable index value was achieved by Stage 4 of the cumulation (i.e. a grid size of 4 x 4 stations at 5 m intervals) while for H'_c , the stable value was reached by Stage 5 (i.e. a grid size of 5 x 5 stations at 5 m intervals). Other grid methods at this site failed to stabilize suggesting insufficient sample size. The maximum value in each case, however is an overestimate of the total diversity and evenness in the community. This overestimate increases disproportionately with methods of increased trap spacing.

Site D68 is the next most abundant and is the only other site to have index values that plateau, although again only for method G(5). H'_{tot} is well represented by the method with a minor underestimation of 2.4%, while in contrast, J'_{tot} is very poorly represented with an overestimation by 54.67%. Again, other methods at this site did not give results with a plateau and their maximum values are all overestimates of total diversity and evenness. The inaccuracy is greatest for the index of evenness and deteriorates with methods of increased trap spacing.

Sites D75 and D50 with lowest animal numbers give variable index values, the maximum of which always overestimates total diversity and evenness, ranging in inaccuracy from 9.43% (method G(7.5), Site D50) to 210.82% (method G(20), Site D50).

TABLE 5.13 GRID SIZE REQUIRED FOR EACH METHOD BEFORE ASYMPTOTE VALUES ARE REACHED FOLLOWING CUMULATIVE ANALYSIS USING THE SHANNON-WIENER DIVERSITY INDEX FOR CUMULATED CAPTURES (H'_c). COMPARISON IS MADE WITH THE DIFFERENCES BETWEEN THESE VALUES AND THE CORRESPONDING VALUES FOR THE GRID METHOD USED (H'_3 , I.E. CAPTURES ON DAY 3) AND THE TOTAL DIVERSITY AT EACH SITE (H'_{tot}).

	Site			
	BBC	D75	D68	D50
METHOD G(5)				
H'_c	1.1875	0.5620	0.6695	1.0040
$H'_3 - H'_c$	-0.1487	0.0003	0.0225	0.0002
$H'_{tot} - H'_c$	-0.2004	0.4742	-0.0161	0.3967
Grid size to H'_c plateau	25-100		49-100	
	(25-100)		(49-100)	
Grid size to H'_c max. value		100		100
		(100)		(100)
METHOD G(7.5)				
H'_c	0.9780	0.9000	0.6570	1.2800
$H'_3 - H'_c$	-0.0695	0.0003	-0.0205	-0.0001
$H'_{tot} - H'_c$	0.0091	0.1362	0.0350	0.1207
Grid size to H'_c plateau				
Grid size to H'_c max. value	49	81	81	100
	(25)	(36)	(36)	(49)
METHOD G(10)				
H'_c	0.7209	0.5000	0.6370	1.2420
$H'_3 - H'_c$	0.0095	0.0004	-0.0005	0.0005
$H'_{tot} - H'_c$	0.2662	0.5352	0.0164	0.1587
Grid size to H'_c plateau				
Grid size to H'_c max. value	49	81	81	81
	(16)	(25)	(25)	(25)
METHOD G(20)				
H'_c	0.6320	0.8680	0.5980	0.4510
$H'_3 - H'_c$	0.0004	-0.0004	0.0003	-0.0004
$H'_{tot} - H'_c$	0.3551	0.1682	0.0554	0.9497
Grid size to H'_c plateau				
Grid size to H'_c max. value	81	81	81	81
	(9)	(9)	(9)	(9)

N.B. continued over.

Note to TABLE 5.13

N.B. Grid size is measured as the number of trap stations, spaced at 5m intervals. For method G(5) there was a trap placed at each station. Other methods did not have a trap at each station on the grid because of greater trap spacing. The number of traps used by each method is included in parentheses.

Such variations make grid methods at sites of low animal abundance very sensitive to changes within the community.

Comparing maximum index values with H'_3 or J'_3 appears to give exceptionally accurate results, particularly for the wider spacing methods. This, however, is an artefact of the data in that when the cumulation analysis is required to proceed to the final stage in order to produce the maximum value, then the mean value used is calculated for the same data set used in the field trial for that method. Such a comparison is only relevant if a plateau in the index values is produced.

For grid methods, G(5) alone gave diversity index values that plateaued indicating sufficient sample size at the two most abundant sites. These index values were not consistently accurate in their representation of community diversity. At less abundant sites and with all other methods, a grid larger than 50 x 50 m is required for optimum sampling to be achieved, i.e., a larger grid may give more information using these methods.

5.2.4.2 Minimum sample size for index-line methods

Similar to the analysis of sample size for grid methods, the Shannon-Wiener (H') and Equitability (J') indices were calculated for each index-line method and each site independently using sets of capture data taken from the mean values for each sample size. These mean values were taken by starting from both ends of the index-line to minimize environmentally related variance in the capture data.

TABLE 5.14 GRID SIZE REQUIRED FOR EACH METHOD BEFORE ASYMPTOTE VALUES ARE REACHED FOLLOWING CUMULATIVE ANALYSIS USING THE EQUITABILITY INDEX OF EVENNESS FOR CUMULATED CAPTURES (J'_c). COMPARISON IS MADE WITH THE DIFFERENCES BETWEEN THESE VALUES AND THE CORRESPONDING VALUES FOR THE GRID METHOD USED (J'_3 , I.E. CAPTURES ON DAY 3) AND THE TOTAL DIVERSITY AT EACH SITE (J'_{tot}).

	Site			
	BBC	D75	D68	D50
METHOD G(5)				
J'_c	0.7264	0.5120	0.6095	0.5920
$J'_3 - J'_c$	0.0230	-0.0001	0.0204	0.0320
$J'_{tot} - J'_c$	-0.0143	0.4312	0.3332	0.2783
Grid size to J'_c plateau	16-100		49-100	49-100
	(16-100)		(49-100)	(49-100)
Grid size to J'_c max. value		100		
		(100)		
METHOD G(7.5)				
J'_c	0.7060	0.8550	0.5980	0.7950
$J'_3 - J'_c$	-0.0507	-0.0356	-0.0186	0.0002
$J'_{tot} - J'_c$	0.0061	0.0882	0.3447	0.0753
Grid size to J'_c plateau				
Grid size to J'_c max. value	64	64	64	100
	(36)	(36)	(36)	(49)
METHOD G(10)				
J'_c	0.5270	0.4560	0.5790	0.7720
$J'_3 - J'_c$	-0.0001	-0.0010	0.0004	0.0000
$J'_{tot} - J'_c$	0.1851	0.4872	0.3637	0.0983
Grid size to J'_c plateau				
Grid size to J'_c max. value	81	81	81	81
	(25)	(25)	(25)	(25)
METHOD G(20)				
J'_c	0.4560	0.7900	0.5450	0.2800
$J'_3 - J'_c$	0.0002	-0.0003	-0.0004	-0.0001
$J'_{tot} - J'_c$	0.2561	0.1532	0.3977	0.5903
Grid size to J'_c plateau				
Grid size to J'_c max. value	81	81	81	81
	(9)	(9)	(9)	(9)

N.B. continued over.

Note to Table 5.14

N.B. Grid size is measured as the number of trap stations, spaced at 5 m intervals. For method G(5) there was a trap placed at each station. Other methods did not have a trap at each station on the grid because of greater trap spacing. The number of traps used by each method is included in parentheses.

The effects of increasing sample size are most clearly illustrated graphically to demonstrate how changes in index values occur with cumulative addition of more sampling stations. An asymptote is defined for these purposes as having a uniform index value (± 0.0500) for a minimum of four consecutive sampling stations. If the length of index-line represented by the plateau is greater than 150 m, then the method is considered stable for those site characteristics. Plateaus of shorter distance indicate the method to be less stable in response to factors of variance within the animal community or the environment. Some methods were not characterized by plateaus in the data. For these, the maximum value is tabled (Tables 5.15 and 5.16) with the respective length of index line required to achieve that value.

At Site BBC, the most abundant of all sites, all methods result in clearly defined plateaus using H' (Figure 5.15), the shape of which is almost identical to that for J' (Figure 5.16). The plateau values of H' for all methods represent $\geq 98.31\%$ ($J' \geq 98.31\%$) of the value obtained from field use of the full length of index-line (i.e. 60 stations = 300 m), and all represent $\geq 89.82\%$ ($J' \geq 89.80\%$) of the total diversity at the site. Only two of the methods (I (7.5) and I(10)) have a plateau character considered stable. Inferred from this is that both methods require a minimum line length of 60 m and no additional information is gained up to a line length of 250 m. Method I(7.5) gives more accurate results while method I(10) requires less traps (Tables 5.15 and 5.16).

The data from all methods except I(7.5) at the next most abundant site, D68, exhibit asymptotes in the data. The highest H' values for all methods are $\geq 75.82\%$ ($J' = 78.07\%$) of the value obtained from use of the full index-line

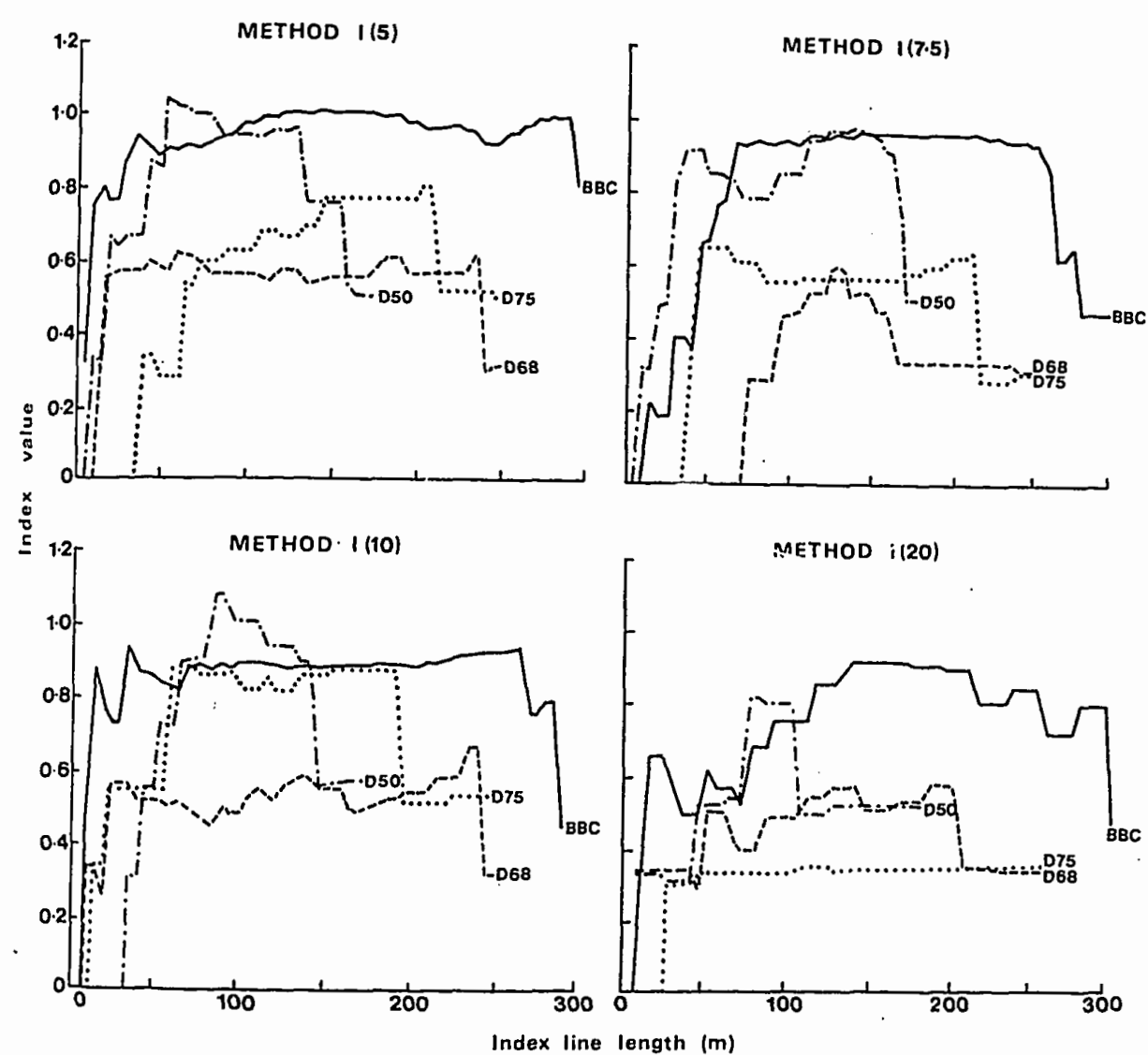


Figure 5.15 The effect of increasing sample length for index-line methods on the Shannon-Wiener index of diversity.

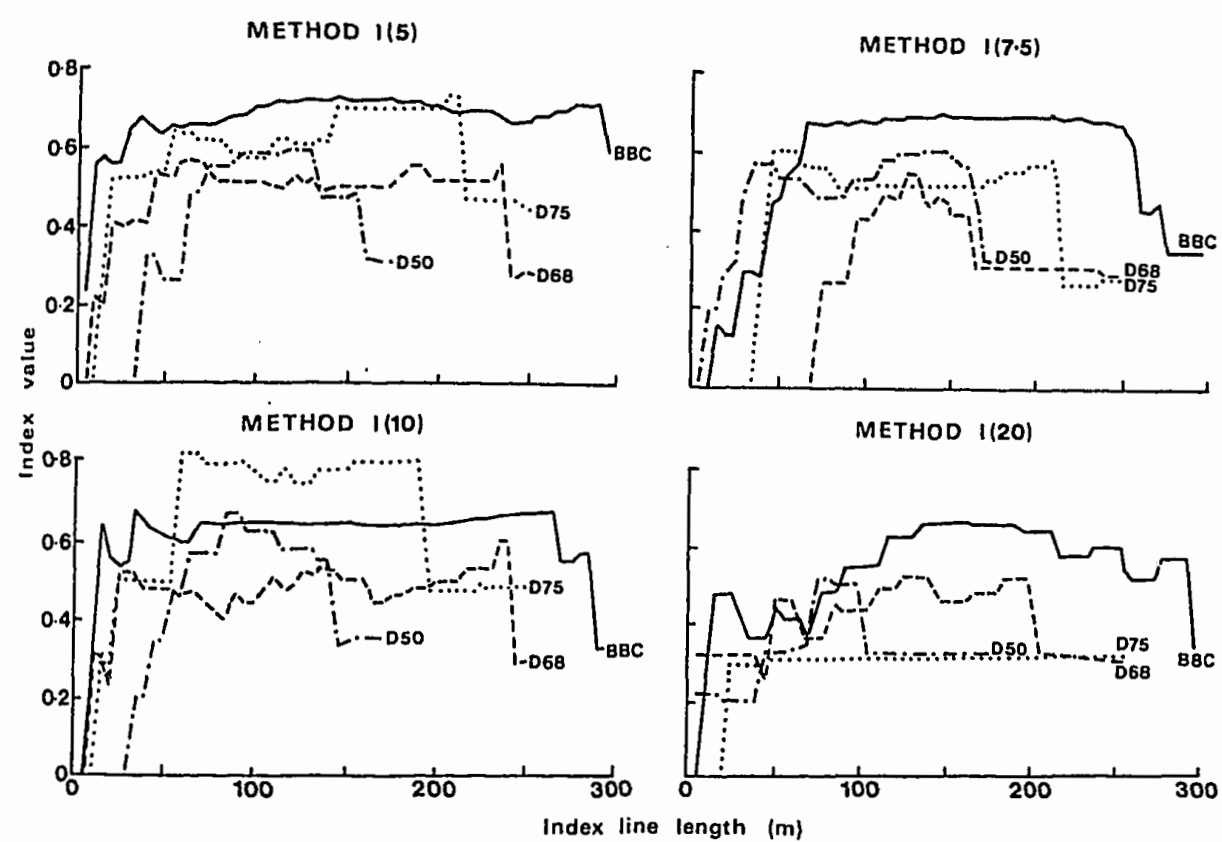


Figure 5.16 The effect of increasing sample length for index-line methods on the equitability index.

TABLE 5.15 LENGTH OF INDEX-LINE REQUIRED FOR EACH METHOD BEFORE ASYMPTOTE VALUES ARE REACHED FOLLOWING CUMULATIVE ANALYSIS USING THE SHANNON-WIENER DIVERSITY INDEX FOR CUMULATED CAPTURES (H'_c). COMPARISON IS MADE AGAINST THE DIFFERENCES BETWEEN THESE VALUES AND THE CORRESPONDING VALUES FOR THE INDEX METHOD USED (H'_3 , I.E. CAPTURES ON DAY 3) AND THE TOTAL DIVERSITY AT EACH SITE H'_{tot} .

		Site			
		BBC	D75	D68	D50
METHOD I(5)					
	H'_c	0.9930	0.8048	0.5455	1.0332
	$H'_3 - H'_c$	0.0028	0.1792	0.0631	-0.0374
	$H'_{tot} - H'_c$	-0.0059	0.2312	0.1045	0.3675
Line length to H'_c plateau		100-235		20-235	
(m)		(21-48)		(5-48)	
Line length to H'_{max} value			205		55
(m)			(42)		(12)
METHOD I(7.5)					
	H'_c	0.9725	0.5719	0.6094	0.9830
	$H'_3 - H'_c$	0.0014	0.0646	0.0348	0.0590
	$H'_{tot} - H'_c$	0.0146	0.4643	0.0440	0.4177
Line length to H'_c plateau		65-250	45-210		
(m)		(10-34)	(17-29)		
Line length to H'_c max value				125	135
(m)				(18)	(19)
METHOD I(10)					
	H'_c	0.8866	0.8770	0.5516	0.0719
	$H'_3 - H'_c$	0.0152	0.1901	0.0919	0.0702
	$H'_{tot} - H'_c$	0.1005	0.1592	0.1018	0.3288
Line length to H'_c plateau		70-265	60-190	90-235	
(m)		(8-27)	(7-20)	(10-25)	
Line length to H'_c max value					85
(m)					(9)
METHOD I(20)					
	H'_c	0.9114	0.3435	0.5052	0.8207
	$H'_3 - H'_c$	0.0069	0.3435	0.1611	0.2075
	$H'_{tot} - H'_c$	0.0757	0.6927	0.1482	0.5800
Line length to H'_c plateau		115-215	25-250	85-200	
(m)		(7-12)	(2-14)	(5-11)	
Line length to H'_c max value					75
(m)					(5)

N.B. continued over

Note to Table 5.15

N.B. The number of traps required by each method to achieve the asymptotic or maximum value are shown in parentheses.

(50 stations along 250 m), while that for all methods is $\geq 77.32\%$ ($J' = 50.23\%$) of the total diversity at the site. Method I(5) alone displays a stable asymptote in that the index value does not vary significantly from 20 m to 235 m. Such stability may be explained by the existence of only two relatively common species. However, this explanation is inadequate in explaining the instability of methods I(10) and I(20), and the failure of method I(7.5) to return consistent values.

Site D50 was rich with species which were not abundant. Indices sensitive to change in species numbers and the numbers of individuals in each species, gave no values that could be defined as plateaus. The highest H' values for all methods are $\geq 79.82\%$ ($J' \geq 79.82\%$) of the values obtained from use of the full index line (34 stations along 170 m), while that for all methods is $\geq 58.59\%$ ($J' \geq 79.82\%$) of total diversity at the site.

With such an erratic index response, nothing definitive may be stated about sample size. It does suggest that index-line methods should be a minimum of 135 m at sites with these environmental characteristics, to reduce the chance of a variable response.

Data from the poorest site, D75, resulted in methods generally being least accurate although there were stable asymptotes for methods I(7.5) and I(20). Highest values for all methods represent only $\geq 50\%$ of both index values from the use of the full length of index line (50 stations along 250 m) and all represent $\geq 33.15\%$ ($J' \geq 33.15\%$) of total diversity at the site. The large discrepancies here are due to the occasional occurrence of *S. leucopus* which was sampled only by methods I(7.5) and I(20), these also being the only methods with stable asymptotes.

TABLE 5.16 LENGTH OF INDEX LINE REQUIRED FOR EACH METHOD BEFORE ASYMPTOTE VALUES ARE REACHED FOLLOWING CUMULATIVE ANALYSIS USING THE EQUITABILITY INDEX OF EVENNESS FOR CUMULATED CAPTURES (J'_c). COMPARISON IS MADE AGAINST THE DIFFERENCES BETWEEN THESE VALUES AND THE CORRESPONDING VALUES FOR THE INDEX METHOD USED (J'_3 , I.E. CAPTURES ON DAY 3) AND THE TOTAL DIVERSITY AT EACH SITE J'_{tot} .

		Site			
		BBC	D75	D68	D50
METHOD I(5)					
	J'_c	0.7160	0.7325	0.5104	0.6420
	$J'_3 - J'_c$	0.0023	0.1630	0.0435	-0.233
	$J'_{tot} - J'_c$	-0.0039	0.2106	0.4323	0.2283
Index length to J'_c plateau	(m)	51-58 (11-12)		20-235 (5-48)	
Index length to J'_c max value	(m)		205 (42)		55 (12)
METHOD I(7.5)					
	J'_c	0.7016	0.5205	0.5547	0.6108
	$J'_3 - J'_c$	0.0167	0.0589	0.0317	0.0366
	$J'_{tot} - J'_c$	0.0105	0.4227	0.3880	0.2595
Index length to J'_c plateau	(m)	65-250 (10-34)	45-210 (9-29)		
Index length to J'_c max value	(m)			125 (18)	135 (19)
METHOD I(10)					
	J'_c	0.6395	0.7983	0.5021	0.6600
	$J'_3 - J'_c$	0.0110	0.1730	0.0836	0.0436
	$J'_{tot} - J'_c$	0.0726	0.1449	0.4406	0.2043
Index length to J'_c plateau	(m)	35-265 (4-27)	60-190 (7-20)	105-235 (11-25)	
Index length to J'_c max value	(m)				85 (9)
METHOD I(20)					
	J'_c	0.6575	0.3126	0.4735	0.5099
	$J'_3 - J'_c$	0.0049	0.3127	0.1330	0.1289
	$J'_{tot} - J'_c$	0.0546	0.6306	0.4692	0.3604
Index length to J'_c plateau	(m)	115-215 (7-12)	25-250 (2-13)	85-200 (5-11)	
Index length to J'_c max value	(m)				75 (5)

N.B. continued over.

Note to Table 5.16

N.B. The number of traps required by each method to achieve the asymptotic or maximum value are shown in parenthesis.

While sample size may be clearly defined at sites of high abundance, this becomes difficult for sites with decreasing abundance, particularly for those with more uncommon species.

5.3 Analysis of Response of Methods to Environmental Heterogeneity

5.3.1 Introduction

Data files containing the environmental attributes measured at each site were rationalized by eliminating those with no record, or without variation between sample stations at a site. Attributes were then regressed against the weighted animal capture data using the leaps and bounds algorithm (Furnival and Wilson, 1974) to obtain an optimized subset of variables that accounted for most variation. A multiple regression was performed for each species independently, then for indices of diversity (H' and L) calculated for each station from the weighted capture data. Environmental attributes accounting for most variation within each subset were identified using the Beta-coefficient (4.3.3) then compared by cross correlation to ascertain how similar the requirements of the community were for the species populations when considered separately. Those attributes correlating significantly with H' and L were then plotted to provide contour maps of equal values, representing environmental heterogeneity. The location of trap stations for each method were then overlaid on the maps and the number of traps within each environmental 'patch' were counted.

Effects of environmental heterogeneity were only detected for strata 3, 4, 5 and 6 at Site BBC. Strata 1 and 2 were recorded on a larger scale so the number of observations were too few for regression. Similarly, the number of captures for some species were insufficient for analysis at Sites D75, D68 and D50.

5.3.2 Optimum attribute subsets for populations of animal species

Subsets of environmental variables for the three dominant species at Site BBC are included in Table 5.17. Both the C_p and the R_a^2 statistic were used in the multiple regression algorithm. The subset selected by R_a^2 accounted for a greater percentage of variance for each species, but it required more attributes to do so. A test of the change in residual sums of squares from the C_p selected subset to the larger R_a^2 subset did not indicate any significant gains of the R_a^2 subset (F-test (Snedecor and Cochran, 1967)) for any of the species (Table 5.18) so the subsets selected by the C_p statistic were used.

A t-test (Snedecor and Cochran, 1967) for each attribute in all three subsets resulted in absolute values ≥ 2.00 (Table 5.17) indicating that all estimates of the linear regression model vary significantly from zero. The results show *A. stuartii* to be positively correlated with the height of woody plants, runways in the fern cover and with the height of grasses, and negatively correlated with the density of woody plants, the density of ferns and the density of grass cover. Two other attributes (size and cover of stones) have larger β' values indicating strong correlations with *A. stuartii*, however these attributes were recorded at only two stations (Appendix VI) so have been excluded from consideration. *A. swainsonii* has a weak negative correlation with grass cover and appears to be relatively unaffected by other attributes. Positive correlations exist with fern density and the number of large logs for *R. fuscipes* while the state of decay of these large logs and runways in areas of fern cover form negative correlations.

5.3.3 Optimum attribute subset for the community

When the community is represented by both L and H' indices of diversity, the C_p statistic again provides the more concise subsets (Table 5.19). For L , the subset is composed of 9 attributes accounting for 50.64% of variance in the total data set. When these attributes are added sequentially to a

stepwise regression analysis, the relative contribution by each may be ordered. Litter cover, fern cover and the number of large logs account for 42.99% of variance so they are assumed to be the main attributes likely to affect the sampling design for small mammal communities.

Similarly for H' , the best subset contains 8 attributes accounting for 56.73% of the variance. Of these, the density and height of grasses account for 41% of variance in the stepwise regression so are pertinent to method evaluation.

5.3.4 Cross correlation between environmental attributes

As the environmental attributes that were significantly correlated with the two diversity indices (L and H') were not the same as those for the dominant species considered independently, cross-correlation between attributes was examined. Significant cross-correlations ($r > 0.4$, $p < 0.001$) for the species and the diversity indices have been listed in Table 5.20. Simpson's index (L) is itself inversely related to community diversity hence its strong negative correlation with fern cover ($R = 10.59\%$, Table 5.19) represents a strong positive correlation between that attribute and community diversity. Percentage fern cover correlates positively with the density of ferns ($r = 0.7050$), and the presence of runways within ferns ($r = 0.6590$) and soil moisture ($r = 0.4525$) each of which are attributes important to the most abundant species, *Rattus fuscipes*. Two of these attributes, density of ferns and runways, are also strongly correlated with *Antechinus stuartii*, the next most abundant species, although the sign of the correlations are opposite to those for *R. fuscipes*. This indicates a distinct separation in the use of these environmental attributes by the two most dominant species, detected by the use of L .

The strong positive correlation between fern cover and litter depth ($r = 0.7664$) identifies a negative relationship with *A. stuartii* and with other index, H' . However, the absence of a species may be just as important as its presence

when using diversity indices. A similar but negative correlation between fern cover and the density of grasses ($r = -0.4715$) emphasises the correlation between L and *A. stuartii*, and establishes a common attribute with H' .

The percentage cover of litter accounts for 22.40% of the variance in L (Table 5.19) but it correlates with only two other attributes (percentage of bare soil and presence of clay soils), both negative and neither of which are strongly related to the individual species.

Increasing diversity (i.e. a decrease in L) correlates significantly with an increase in the number of large logs ($R = 10.00\%$, Table 5.19). This is a trend shared by the H' index ($R = 11.00\%$, Table 5.19). The number of large logs have a strong correlation with increasing decay in logs ($r = 0.7898$), a factor which has a significant (though negative) relationship with the distribution of *R. fuscipes* (Table 5.17).

The density of grasses is the attribute most significantly associated with diversity as measured by H' ($R = 30.00\%$, Table 5.19). The negative association reflects a similar correlation of this attribute with *A. stuartii*. Grass density is positively correlated with grass cover ($r = 0.5262$) which provides an indirect, although again positive association between H' and *A. swainsonii*. Similarly, the height of grasses and the number of large logs are positively correlated with both H' and *A. stuartii*. The second of these attributes also establishes a positive relationship between H' and *R. fuscipes*.

The environmental relationship between diversity indices and species populations is not a clear one although sufficient correlation between them does exist to verify the choice of attributes used to assess the performance of survey methods.

5.3.5 The effect of heterogeneity of some environmental attributes on methods

Five of the environmental attributes measured in the field are significantly correlated with measures of community diversity (5.3.3). Classes of those five attributes were defined and contour plots of their distribution drawn. The numbers of trapping stations within each class of the attributes for both grid and index-line methods were counted and are included in Table 5.21. Contingency table analyses (Snedecor and Cochran, 1967) were performed to investigate possible differences between the four grid methods, and the four index-line methods. A combined contingency table provided a basis to test between grid and index-line methods.

Results of the Chi-squared tests for each contingency table are included in Table 5.21. There are no significant differences between any of the grid methods or between any of the index-line methods in their proportional representation of each attribute. Most of the attributes are sampled similarly by both grid and index-line methods. There is, however, a very significant difference between them for fern cover ($P < 0.005$). The grid methods are oversampling the areas of sparse fern cover (0-60%) and are undersampling the well covered fern patches (81-100%). In contrast, the index-line methods have more stations in the well covered patches relative to sparse patches. While this difference exists for only one of the five attributes, it is important because of related implications. Fern correlates significantly ($P < 0.001$) with ten other measured environmental attributes (Table 5.20), five of which have been shown to be significant in determining the distribution of the communities' composite species (Table 5.17).

TABLE 5.17 OPTIMISED SUBSETS OF ENVIRONMENTAL VARIABLES SELECTED BY THE C_p STATISTIC IN THE MULTIPLE LINEAR REGRESSION MODEL FOR (a) *Antechinus stuartii*, (b) *A. swainsonii* AND (c) *Rattus fuscipes* AT SITE BBC.

(a) *A. stuartii*

<u>Attribute</u>	<u>model estimate</u>	<u>standard error</u>	<u>t</u>	<u>β'</u>
STRATUM 3				
Canopy density	-0.6197	0.1149	-5.39	-0.44
STRATUM 4				
Height, woody plants	0.0213	0.0046	4.63	0.84
Density, woody plants	-1.4107	0.2808	-5.02	-0.94
Density, ferns	-1.2176	0.3425	-3.56	-0.55
Fern runways	2.9295	0.6041	4.85	0.79
Height, grasses	0.0259	0.0055	4.71	0.43
Density, grasses	-0.8480	0.1536	-5.52	-0.52
STRATUM 5				
Litter depth	-0.0466	0.0158	-2.95	-0.31
Size, stones	-0.2740	0.3862	-3.30	-1.16
% cover, stones	1.4993	0.3659	4.10	1.55
Number, small logs	0.1061	0.0393	2.70	0.19
Number, large logs	0.4488	0.1146	3.92	0.34
Water course presence	-0.6291	0.2460	-2.56	-0.21
Constant	1.7518	0.7284	2.40	

$n = 55$
multiple $R^2 = 72.7\%$
 $F_{13,41} = 8.41$ ($P < 0.001$)
R M S = 1.2068

(b) *A. swainsonii*

<u>Attribute</u>	<u>model estimate</u>	<u>standard error</u>	<u>t</u>	<u>β'</u>
STRATUM 3				
% cover, shrubs	0.0181	0.0053	3.42	0.31
STRATUM 4				
Height, wood plants	-0.0071	0.0019	-3.74	-0.35
% cover, grasses	-0.0158	0.0034	-4.65	-0.40
Constant	-1.1598	0.1429	-8.12	

$n = 55$
multiple $R^2 = 44.9\%$
 $F_{3,51} = 13.85$ ($P < 0.001$)
R M S = 1.0434

TABLE 5.17 continued

153.

(c) <i>R. fuscipes</i>				
<u>Attribute</u>	<u>model estimate</u>	<u>standard error</u>	<u>t</u>	<u>β'</u>
STRATUM 3				
Acacia rank	0.5520	0.1840	3.00	0.25
STRATUM 4				
Density, ferns	1.2421	0.2942	4.22	0.64
Fern runways	-1.3662	0.4923	-2.78	-0.42
STRATUM 5				
% litter cover	-0.0196	0.0065	-3.02	-0.25
Number, large logs	0.5764	0.1672	3.45	0.50
Decay, large logs	-0.6407	0.1205	-5.32	-0.73
STRATUM 6				
Soil moisture	0.9152	0.2287	4.00	0.37
Constant	-1.3562	0.8347	-1.62	
n = 55				

multiple $R^2 = 59.7\%$ $F_{7,47} = 9.94$ ($P < 0.001$)

R M S = 1.2139

N.B. n = number of stations included in the analysis

multiple R^2 = multiple regression coefficient of variation

R M S = residual mean square.

TABLE 5.18 DIFFERENCES BETWEEN SUBSETS OF ENVIRONMENTAL ATTRIBUTES
SELECTED BY THE C_p AND R_a^2 STATISTICS FOR DOMINANT SMALL
MAMMAL SPECIES AT SITE BBC.

	R^2	Number attributes	R M S	R S S	d f
<i>A. stuartii</i>					
C_p	72.70%	13	1.2068	49.4788	41
R_a^2	79.50%	19	1.1324	39.6340	35
$F_{6,35} = 1.45$ (N S)					
<i>A. swainsonii</i>					
C_p	44.90%	3	1.0434	53.2134	51
R_a^2	57.20%	8	0.9706	44.6476	46
$F_{5,46} = 1.77$ (N S)					
<i>R. fuscipes</i>					
C_p	59.70%	7	1.2139	57.0533	47
R_a^2	71.20	16	1.2182	46.2916	38
$F_{9,38} = 0.98$ (N S)					

N.B. R^2 = multiple regression coefficient of variation
 R M S = residual mean squared
 R S S = residual sums of squares
 d f = degrees of freedom
 N S = not significant

TABLE 5.19 OPTIMISED SUBSETS OF ENVIRONMENTAL VARIABLES SELECTED BY THE C_p STATISTIC IN THE MULTIPLE LINEAR REGRESSION MODEL FOR THE SMALL MAMMAL COMMUNITY AS MEASURED BY (a) SIMPSON'S (L), (b) SHANNON-WIENER (H') INDICES OF DIVERSITY AT SITE BBC

(a) Simpsons index (L)

Attribute	Model estimate	Standard error	t	β'	R(%)
STRATUM 3					
Acacia rank	0.1239	0.0566	2.19	0.25	7.00
STRATUM 4					
% cover, woody plants	0.0114	0.0047	2.43	0.38	1.00
Height, ferns	-0.0037	0.0018	-2.02	-0.03	6.00
% cover, ferns	-0.0060	0.0018	-3.28	-0.63	10.59
Height, grasses	-0.0026	0.0013	-1.93	-0.22	4.00
STRATUM 5					
Litter depth	0.0201	0.0060	3.35	0.69	2.80
% cover, litter	0.0078	0.0022	-3.53	-0.45	22.40
No. large logs	-0.1019	0.0280	-3.64	-0.40	10.00
STRATUM 6					
Clay	-0.2048	0.0654	-3.13	-0.50	5.31
Constant	1.5103	0.2300	6.57		

n = 55

multiple $R^2 = 50.64\%$ $F_{9,45} = 5.1298$ ($P < 0.001$)

R M S = 0.0464

(b) Shannon-Wiener index (H')

STRATUM 4					
Density, woody plants	-0.0872	0.0043	-1.97	-0.22	3.00
% cover, ferns	0.0078	0.0024	3.27	0.60	4.00
Height, grasses	0.0074	0.0020	3.88	0.46	11.00
Density, grasses	-0.2249	0.0515	-4.37	-0.53	30.00
Litter depth	-0.0154	0.0067	-2.29	-0.39	3.00
STRATUM 5					
% cover, stones	0.0789	0.0264	2.99	0.31	6.00
No. large logs	0.1141	0.0350	3.26	0.32	11.00
Watercourse presence	-0.1891	0.0880	-2.15	-0.24	3.00
Constant	0.3706	0.1699	2.18		

n = 55

multiple $R^2 = 56.73\%$ $F_{8,46} = 7.5390$ ($P < 0.001$)

R M S = 0.0745

N.B.

n = numbered stations included in the analysis

multiple R^2 = multiple regression coefficient of variation

R(%) = percentage of variance accounted for by each attribute use a step-wise regression analysis.

TABLE 5.20 CORRELATION MATRICES FOR THREE DOMINANT SPECIES AND COMMUNITY INDICES AT SITE BBC

(a) *A. stuartii*

	Height, Woody plants	Density, Woody plants	Density, ferns	Runways, ferns	Height, grasses	Density grasses
% cover, shrubs	0.5012	0.4158				
Canopy density, shrubs	0.4751	0.4017				
Height, woody plants	0.8341					
% cover, woody plants	0.5782	0.6566	-0.4944	-0.4152		
Density, woody plants	0.8341					
Height, ferns			0.4051			-0.4157
% cover, ferns		-0.4440	0.7050	0.6590		-0.4715
Density, ferns				0.8154		
Runways, ferns			0.8154			
% cover, grasses			-0.6291	-0.5842		0.5262
Litter depth	-0.4188	-0.4251	0.4939	0.4814		
Litter moisture			0.7614	0.7048		
% bare soil			-0.4415	-0.4774		
Clay soil			-0.4774	-0.5095		
Soil moisture	-0.4671	-0.4379	0.4827	0.4303		

(b) *A. swainsonii*

	% cover, grasses
Height, ferns	-0.5407
% cover, ferns	-0.8047
Density, ferns	-0.6291
Runways, ferns	-0.5842
Density, grasses	0.5262
Litter depth	-0.6201
Litter moisture	-0.7312
Water course presence	0.4263

(c) *R. fuscipes*

	Density, ferns	Runways, ferns	No. large logs	Decay large logs
% cover, woody plants	-0.4944	-0.4152		
Height, ferns	0.4051			
% cover, ferns	0.7050	0.6590		
% cover, ferns		0.8154		
Runways, ferns	0.8154			
% cover, grasses	-0.6291	-0.5842		
Litter depth	0.4939	0.4814		
Litter moisture	0.7614	0.7048		
Diameter, large logs			0.6242	0.8060
No. large logs				0.7898
Decay, large logs			0.7898	
% bare soil	-0.4415	-0.4774		
Clay soil	-0.4774	-0.5095		
Soil moisture	0.4827	0.4303		

TABLE 5.21 CONTINGENCY TABLE ANALYSIS FOR GRID AND INDEX-LINE METHODS INDEPENDENTLY AND COMBINED USING FOUR ENVIRONMENTAL ATTRIBUTES THAT ARE MOST SIGNIFICANTLY CORRELATED WITH INDICES OF THE SMALL MAMMAL COMMUNITY AT SITE BBC. THE FIRST THREE ATTRIBUTES, LITTER COVER (a), FERN COVER (b) AND THE NUMBER OF LARGE LOGS, (c) WERE DETERMINED USING SIMPSON'S INDEX OF DIVERSITY (L) WHILE THE DENSITY OF GRASSES (d) AND THE HEIGHT OF GRASSES (e) WERE DETERMINED BY THE SHANNON-WIENER INDEX (H')

(a)

% cover, litter	<u>No. Traps Occuring in Each Class</u>							
	GRID METHODS				INDEX-LINE METHODS			
	Class	G(5)	G(7.5)	G(10)	G(20)	I(5)	I(7.5)	I(10)
0 - 60	14	7	6	2	3	3	2	1
- 80	33	19	6	3	20	15	9	7
- 100	53	23	13	4	38	22	20	8

$\chi^2 = 3.0653$, df = 6, n.s. $\chi^2 = 1.6921$, df = 6, n.s.

Combined contingency table: $\chi^2 = 13.1240$, df = 14, n.s.

(b)

	<u>No. Traps Occuring in Each Class</u>							
% cover, ferns	GRID METHODS				INDEX-LINE METHODS			
Class	G(5)	G(7.5)	G(10)	G(20)	I(5)	I(7.5)	I(10)	I(20)
0 - 60	65	33	16	7	11	8	7	5
- 80	21	9	5	2	13	8	3	3
- 100	14	7	4	0	37	25	22	8

$\chi^2 = 0.4854, df = 6, n.s.$

$\chi^2 = 3.3038, df = 6, n.s.$

Combined contingency table: $\chi^2 = 95.0989, d.f. = 14, P < 0.001$

N.B. n.s. = not significant

TABLE 5.21 (continued)

(c)

		<u>No. Traps Occuring in Each Class</u>							
No. large logs		GRID METHODS				INDEX-LINE METHODS			
Class		G(5)	G(7.5)	G(10)	G(20)	I(5)	I(7.5)	I(10)	I(20)
0		46	21	15	6	28	22	15	6
1		31	15	6	2	25	15	9	5
2		23	13	4	1	8	4	7	5

$\chi^2 = 3.6289, df = 6, n.s.$

$\chi^2 = 6.0737, df = 6, n.s.$

Combined contingency table: $\chi^2 = 11.9834, df = 14, n.s.$

(d)

		<u>No. Traps Occuring in Each Class</u>							
Grass density		GRID METHODS				INDEX-LINE METHODS			
Class		G(5)	G(7.5)	G(10)	G(20)	I(5)	I(7.5)	I(10)	I(20)
0		22	9	5	2	18	8	13	4
1		43	22	8	4	29	22	9	6
2		35	18	12	3	14	11	9	6

$\chi^2 = 1.9055$, df = 6, n.s.

$\chi^2 = 6.9927$, df = 6, n.s.

Combined contingency table: $\chi^2 = 14.4800$, df = 14, n.s.

(e)

	<u>No. Traps Occuring in Each Class</u>							
Grass height	GRID METHODS				INDEX-LINE METHODS			
Class (cm)	G(5)	G(7.5)	G(10)	G(20)	I(5)	I(7.5)	I(10)	I(20)
0 - 20	72	35	20	7	40	24	22	11
- 40	22	11	4	2	13	11	4	2
> 40	6	3	1	0	9	5	5	3

$\chi^2 = 1.5244$, df = 6, n.s.

$\chi^2 = 3.0834$, df = 6, n.s.

Combined contingency table: $\chi^2 = 12.3876$, df = 14, n.s.

Chapter 6

CONCLUSIONS

6.1 Introduction

The broad objectives at the outset of this research project included a consideration of developing an optimized set of methodologies for faunal survey suited to evaluate the conservational value of areas with a uniform environment, relative to the scale of mapping. By review and analysis of some past Australian faunal surveys, it has been demonstrated that the recent upsurge in survey activity has been predominantly in areas that are large ($>5,000 \text{ km}^2$). For large areas survey methodologies need to be capable of extrapolation to areas of similar environments, quantitative, repeatable, comparable and flexible over a range of geographic scales.

Further analysis of a sample of past surveys established that mammals were the most frequently studied taxonomic class so were given priority for research into survey methodology. Of this class, the small mammal community is usually most diverse in forest environments (4 species on average (Posamentier, 1975)) and has been surveyed using a range of methods that are far from standardized; they were therefore selected for research. The community was defined as those mammal species capable of being caught by Elliott live-capture traps (30 x 9 x 9 cm) as these were shown to be the most efficient single technique for their survey. Such a pragmatic definition is convenient for survey purposes and it is reasonably synonymous with accepted theoretical definitions of ecological communities (2.1.2, after Allee *et al.* (1949), Odum (1971) and Krebs (1978)) and with animal guilds (Root, 1967).

A review of the relevant literature (2.3) identified the key variables capable of being controlled in field sampling design for small mammal surveys as the configuration of trap layout, spacing between traps, the size of the sample taken and the amount of replication. Analysis of the more quantitative Australian surveys (Table 2.1) demonstrates

inconsistent treatment of these variables in the design of sampling. Table 2.1 shows also that the grid and index-line trap configurations predominate, almost to the exclusion of others. Non-Australian literature supports the use of these configurations, however there is considerable dissention as to which is preferred. Grid trapping configurations were strongly defended for estimates of population densities (Stickle, 1948; Fowle and Edwards, 1954; Tanaka, 1960 and Pelikan *et al.*, 1964) while more recent studies have supported the use of index-lines (Dice, 1931; Brant, 1962; Hansson, 1967; Petticrew and Sadlier, 1970 and Flowerdew, 1976). No previous study has investigated the effect on survey of these two configurations in Australian environments.

Similarly, sampling intensity has escaped attention in Australian surveys. Studies elsewhere have suggested that sampling intensity needed to be varied according to size of home range (Stickle, 1948; Smith *et al.*, 1975 and Flowerdew, 1976) or to the susceptibility of species to capture (Burt, 1943; Kikkawa, 1964 and Andrzejewski *et al.*, 1966). Sampling intensity has also been shown to be importantly related to the rate of capture (Gurnell, 1967).

As well as trap spacing, the sample size has varied considerably. Faust *et al.* (1971) suggested the required size should be related to range of movement of the species being surveyed. Movement is primarily a function of resource availability within the habitat which emphasises the need to calibrate survey methodology in relation to environmental heterogeneity, as was discussed by Dice (1931).

Small mammal communities have rarely been surveyed and analysed in an integrated way. Most previous attempts have considered populations of species separately, which ignores interspecific interactions that occur within a community to modify the system as measured by its parts. Diversity indices for analysis of small mammal communities have been used (Rosenzweig and Winakur, 1969; Brown, 1973; Fleming, 1973; Braithwaite and Dudzinski, 1982) although

consideration has not been directed towards the response of these indices when small numbers are used.

The more specific objectives of this research project were then able to be stated (2.4). The primary objectives were optimization of key trapping variables (configuration, spacing and sample size) and the effects of heterogeneity in the environment on sampling methods at scales appropriate to small mammals. The requirement to understand the characteristics of a range of indices of diversity for use in the analysis was recognised as a secondary objective.

6.2 The use of indices of diversity to analyse small number communities

Species diversity is the most representative attribute of community structure. Indices of diversity quantitatively combine species richness of the community and the relative abundance of each species and provide measures of endogenous and exogenous components of diversity (2.1.4., after Pielou, 1975). Some studies suggest these indices are highly correlated with the simplest community attribute, richness (Brown, 1973; De Benedictis, 1973), and this is supported in this work (Table 6.1). However, increasing values of the indices (decreasing for L) are not necessarily comparable due to differences in abundance of the species at a site of species evenness, which is represented by J' . The sites with more species generally have less even species abundances, so S alone is an insufficient representation of the community. The abundance of each species taken without reference to other species is also inadequate, as there is no expression of their dominance relative to the community.

The use of diversity indices is limited by numerical constraints. It is necessary that S be known *a priori*, otherwise the bivariate distribution of S and H' becomes intractable (Bowman *et al.*, 1971). Pielou (1975) discusses similar limitations on H and J' . While this may limit their use in unknown communities (i.e. where the number of species is relatively large, and where species may not be permanently

resident in the community), the problem is alleviated for Australian small mammal communities as the number of species is small (usually less than 6) and they are relatively sedentary. The total number of species in the community, if not predicated *a priori*, will almost certainly be known after the sampling period.

TABLE 6.1 THE RELATIONSHIP OF FIVE INDICES OF TOTAL DIVERSITY (L, D, H', H AND J') WITH SPECIES RICHNESS (S) AT THE FOUR SITES USED IN THE STUDY.

Site	S	L	D	H'	H	J'
D68	2	0.5392	0.6177	0.6534	0.5812	0.9427
D75	3	0.3719	0.9891	1.0362	0.8040	0.9432
BBC	4	0.4156	0.8780	0.9871	0.9374	0.7121
D50	5	0.2769	1.2842	1.4007	1.1577	0.8703

Other maximum/minimum constraints on the values of H' and L (hence D also) for small, unknown values of N (abundance) and S place limits on their usefulness for biological interpretation of diversity (M.P. Austin, *pers. comm.*). Diversity indices in this study are used for comparative and not for analytical purposes. With S known and the sample size standardized between sites, the indices then provide a valid comparative measure.

Modelling hypothetical sets of small mammal community data has provided some insight into characteristics of the indices (4.2.2.6). Both L and D were shown to give the best response to changes in the less abundant species and the more common species, which is supported by the dominance concept discussed by Whittaker (1972). J' was the only index to respond to the temporary absence of a rare species from the community and only H responded to changes in N where there was no change in the proportions of species present. The redundancy index (R), suggested for use by

patten (1962) because of its independence of N and S, was found to give meaningless values when a species was temporarily absent from the community.

The use of indices of diversity for analysis of variance in previous studies has been discussed (4.2.2.3). Their use in this study is valid, as the factorial design used for comparison of methods (5.2.3.1) provided observations of combined variables (methods, sites or days) for each computation which were sufficiently large for robust analysis (K. Malafant, *pers. comm.*).

6.3 Configuration and trap spacing differences between methods

Field studies repeated at four sites in two areas (3.2) provided capture data for comparison between eight different survey methods. The eight methods represented grid and index-line configurations at four trap spacing intervals (3.3).

None of the methods consistently sampled all species at a site. The ability of methods, whether grid or index-line configuration, to sample all species was least for the 20m trap spacing. The work showed that the species least likely to be sampled are the less abundant species, but their capture at least once, if present in the community at the time of sampling, is important for a balanced representation by the diversity indices. The methods displayed general differences in their representation of community biomass (Table 5.1) but these were too inconsistent for biomass to be considered as a community parameter or for the methods to be differentiated. Inconsistencies were caused by some species being up to 30 times heavier than others so the measure of biomass is biased toward size rather than equitably representing abundance.

The measure of trap success rate is frequently used in survey as an index of relative abundance. In this study, it has been shown that percentage success is a function of sampling intensity, and is a poor measure of abundance

between areas in which different sampling intensities are used in relation to the environment. When trap spacing is wide, trap success may exceed 80% which is unacceptable, as less dominant species may be excluded (Flowerdew, 1976). As was demonstrated by the grid methods, an increase in trap success with wider trap spacing resulted in a corresponding decrease in the measures of diversity, and so is inapplicable for evaluation of methods.

From data obtained by each sampling method used at Site BBC, with its discrete and relatively uniform environment and well documented community attributes, four indices of diversity (D , H' , H and J') were calculated. These were then compared with index values of the total known community (Figure 5.4). This clearly demonstrated the grid methods to be very sensitive to trap spacing. Only method G(7.5) provided results similar to the true diversity values while the other grid methods were seriously inaccurate. In contrast, the index-line methods were relatively insensitive to trap spacing and, with the exception of I(20), were well representative of true diversity. When a similar comparison was made with the more conservative estimate of total diversity at the time of sampling for each method (M.K.T.B.A.), the same trends were shown to exist. The methods were subsequently analysed for all four sites to investigate these differences across a range of forest environments (5.2.3).

Analysis of variance demonstrated initially that there were significant differences between the sites (Table 5.6) so the comparison was meaningful. It also showed there were significant differences between the methods at all sites on all days (i.e. the differences between methods were not caused by interactions with differences between sites or between days of capture). As may be seen in Table 5.7, the differences exist primarily between the grid methods. There are no significant differences between the index-line methods, nor do they differ from the closely spaced grid method (G(5)). When the methods were again analysed for their similarity by a Procrustes rotation of principal coordinate axes (based on

the Morisita index of similarity; 5.2.3.2), the same trends again prevailed. Figure 5.11 demonstrates a common grouping of the index-line methods with G(5). Of these methods I(5) and I(10) gave the most consistent results, while G(5), I(7.5) and I(20) were less consistent although equal between each other. The remaining grid methods had poor consistency with G(10) being worst (Table 5.11).

The cause of these distinct configuration and spacing trends was investigated at Site BBC and found to be due to changing proportions of abundance of each species in the samples (5.2.2.4). As the spacing increased for grid methods, capture opportunities became limited so the more dominant species (*R. fuscipes*) was over represented to the detriment of *A. stuartii* and *A. swainsonii*. The least abundant species (*R. rattus*) also had reduced opportunity of capture as trap spacing was increased. Proportions of species captured by index-line methods were more consistent as the spacing increased.

Previous studies of configuration and trap spacing have evaluated capture results for estimates of absolute or relative density, rather than species diversity. Density estimates require consideration of the area being sampled while indices of diversity reflect characteristics of the environment that need not be related to sampling area. However, density estimates for single species populations are calculated from capture data collected from within multi-species communities so some comparison with the present study is relevant.

The accuracy of the index-line configuration in representing community organization is supported by statements of reliable measurement of absolute density (Brant, 1962) and other population parameters across a range of environments (Petticrew and Sadlier, 1970). Stickel (1948) concludes that a 200m index-line with traps spaced at 5m intervals over-estimates densities of *Peromyscus leucopus* when compared with a 3.4 Ha grid, trapped at 15.3m intervals in wood and

forest environments. The basis for comparison was not verified beyond reference to Dice (1938), and other species caught concurrently at each site were not considered. As the grid methods in this study have been shown to be sensitive to sampling intensity as a result of changing proportions of capture of species, this comparative basis may be invalid.

Some explanations of species response to sampling intensity have been discussed. The relationship between trap spacings and the home range of individual species (Burt, 1943; Stickle, 1948; Hansson, 1967 and Smith *et al.*, 1975) becomes obscure when communities are considered in terms of the boundaries of the home ranges between and within species. The home range concept is complicated further as range fluctuates seasonally (Burt, 1943) and with environmental factors (Stickle, 1948). Smith *et al.* (1975) appreciated home range interactions and considered them for the dominant species only in estimating trap spacing as a function of the animals' ability to detect traps. The mobility of animals is implied when trapping intensity is related to the individual's chance encounter with a trap (Kikkawa, 1964; Flowerdew, 1976). Animal movement is intersected better by an index-line than by a grid as it transgresses the space of many more individuals in a way that is not complicated by two dimensional, multiple choice of trap entries. For equitable representation of species abundance within a community, the sampling configuration and intensity should not introduce disturbance to the natural community organization. From this study, empirical evidence suggests that the index-line methods are least disruptive.

While it has been shown that there are no significant differences in results obtained from the four index-line methods (Table 5.7), the choice of trap spacing may be determined in other ways. Figure 6.1 shows differences in the amount of field time required for each of the methods. The wider spacings clearly are more time efficient. However the probability of the widest spacing (I(20)) catching the less abundant species is low so methods I(7.5) and I(10) are preferable.

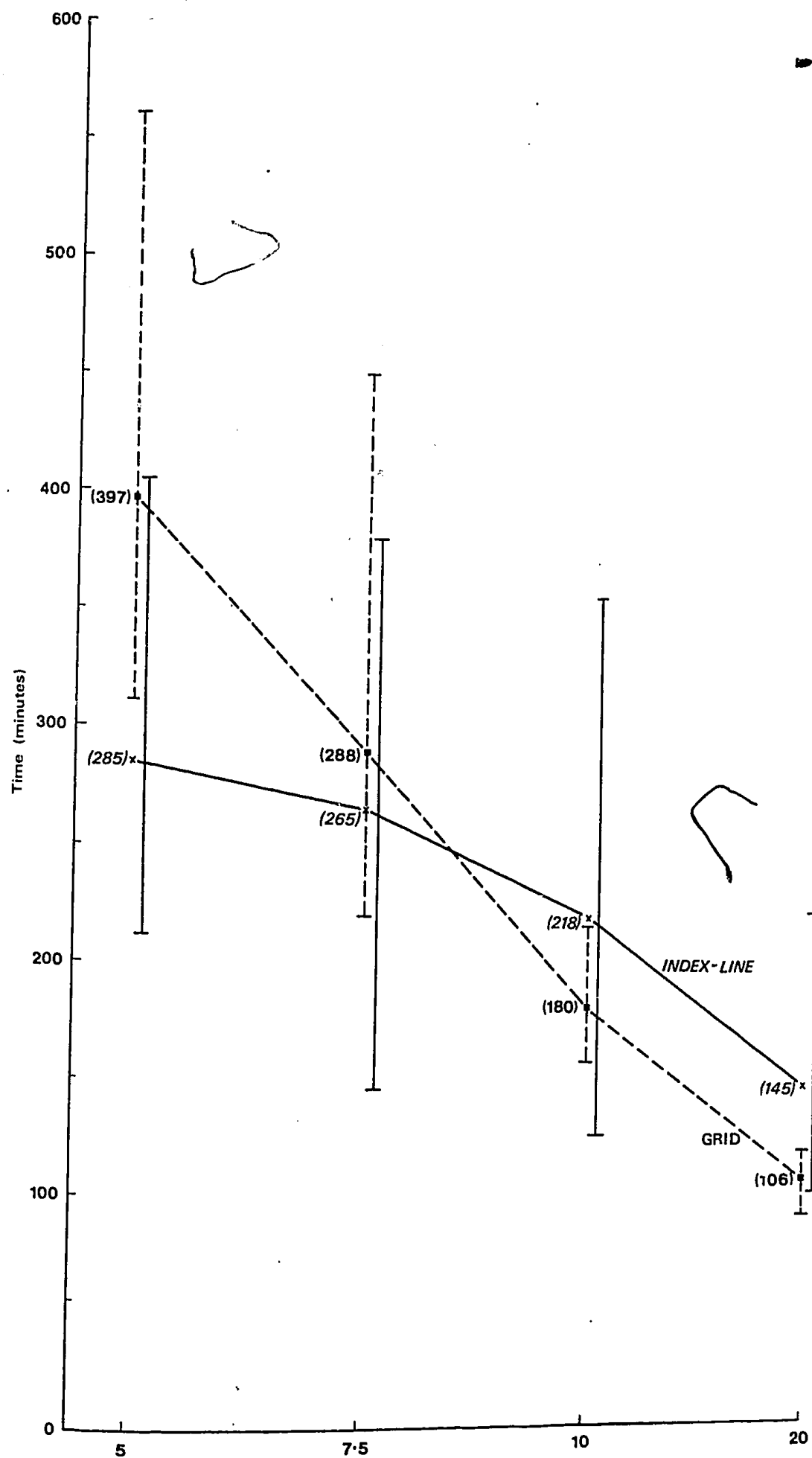


Figure 6.1 Average and range of time required for each method over four sites.

6.4 Optimum Sample size

Accumulation analysis for minimum sample size using index-line methods (5.2.4.2) has shown that at the more abundant sites (BBC and D68), both indices sampling community diversity (H' and J') produced values that plateaued with increasing line length for the four trap spacings (Figures 5.15, 5.16) with the exception of I(7.5) at Site D68 where an irregularity occurred. Additional trapping effort beyond the beginning of the plateau returned no further information about the diversity of the community. Also at these sites, the total diversities were closely represented by the asymptote (Tables 5.15, 5.16) verifying their accuracy. The minimum index-line length required varied between methods although was less than 120m. Minimum length for the preferred method (I(10)) is less than 100m for three of the sites, including the least abundant site (D75). This was the same length suggested by Petticrew and Sadlier (1970) for estimating population parameters. The richest site (D50) had no index-line methods that achieved asymptotic values implying that longer lines (i.e. > 170m) would add more information.

Figures 5.15 and 5.16 show that index values deteriorate if the full extent of all index-lines is used. This effect does not necessarily invalidate the plateau values and is probably caused by the end traps having a larger effective trapping area, thus lowering efficiency (Hansson, 1967). This decline in index value occurs in the last 50m, so this length should be added to the minimum length to compensate.

A similar accumulation analysis for the grid methods (5.2.4.1) resulted in plateau values for method G(5) at three sites (BBC, D68 and D50). At Site BBC, total diversity was well sampled using 16 traps in a 4 x 4 grid while at the other two sites, 49 traps were required (i.e. 7 x 7 grids). All other grids were not sufficiently large to represent diversity at the abundant nor the sparse sites. Faust *et al.* (1971) suggested that the grid size required is related to animal

movements, as the edge of the grid needs to be sufficiently extensive to intercept them. They also discussed a possible advantage with larger grids in that they sample greater environmental heterogeneity. This possibility is limited in most Australian forest environments as the scale of heterogeneity is such that a large grid may sample more than one environmental community and become complicated by an ecotonal, or edge effect.

6.5 The effect of environmental heterogeneity on survey methods.

The sensitivity of survey design for small mammals to environmental heterogeneity has previously been considered important (Stickel, 1948; Hansson, 1967; Faust *et al.*, 1971; Flowerdew, 1976; Stewart, 1979) and was also used to evaluate methods in this study. The basis for evaluation was to determine whether each method was sampling patchiness within the environment equitably and whether the additional component of community diversity due to environmental complexity was being represented (2.1.4). It was not intended to undertake a definitive study of habitat requirements for each species. Rather, environmental variables that correlated well with numbers of individual species at Site BBC were used to identify those variables that were highly correlated with two indices of community diversity. The latter variables were accepted as the major components of environmental heterogeneity most likely to influence the distribution of small mammals and so required adequate sampling.

The most abundant species at Site BBC, *R. fuscipes*, was found to be positively correlated with an index of fern density and with the number of large logs. In a study of a similar small mammal community adjacent to Site BBC, Stewart (1979) found this species to be similarly correlated with fern cover but was unable to detect a significant affect by logs. Another study does confirm the association between *R. fuscipes* and log distribution (Barnett *et al.*, 1978). The present study also found *R. fuscipes* to have strong negative

correlation with runways in the ferns and with an index of decay in large logs, which is in contrast to observations by Stewart (1979).

The most abundant species, *A. stuartii*, was shown to be influenced by the height of woody plants, runways in ferns and the height of grasses. This again differs from the study by Stewart (1979) where *A. stuartii* was not affected by ground cover, logs or runways in ferns; however, the present findings are supported in other studies (Barnett *et al.*, 1978; Milledge, 1979). *A. swainsonii* was negatively correlated with only one variable, grass cover. Stewart (1979) has shown that species to prefer areas of good cover in ferns where runways are present, which supports the correlation between other variables and grass cover in the present study (Table 5.20).

In conjunction with the correlation analysis, those variables that were significant for the individual species were correlated with those that affected L and H' (5.3.4). Values of L correlated strongly with litter cover, fern cover and the number of large logs while H' correlated with the density and height of grasses. While the correlations between species and community attributes were not always significant, they substantiated the choice of the major attributes used to measure environmental heterogeneity.

Contingency table analyses showed no significant differences within grid methods and index-line methods for variations in the five environmental variables (Table 5.21). There were also no differences between grid and index-line methods for four of the attributes; however, there was a very significant difference between them for patches of fern cover. As fern cover is significantly correlated with five other variables that affect the distribution of individual species, this single result is important.

Although it is clear that the two configurations were sampling at least one major attribute differently, it

has yet to be established whether or not this difference caused the capture results to vary correspondingly. It also suggests the basis for a potential model of an environmental heterogeneity index that correlates with community diversity to enable the survey design to be planned prior to the field survey. The concept of such a model has previously been discussed for avian communities (MacArthur and MacArthur, 1961) and for desert rodents (Rosenweig and Winakur, 1969) although the possibility of calibrating field methods against a model remains untried. If developed successfully, it would allow comparable studies between environments of distinctively different complexity using variations in sampling intensity or sample size with a standardized technique. The index-line trapping method is well suited to environmental calibration as it is relatively insensitive to variations in sampling intensity and the minimum sample size does not vary seriously across changes within the one environmental type. Similar field trials in alternative environments would provide a sound structure for an environmental complexity-community diversity model with practical application in calibration of sampling methods.

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APPENDIX I. RANGE OF HABITAT ATTRIBUTES MEASURED BY SOME RELEVANT SMALL MAMMAL STUDIES

Author(s)	Location	Habitat	Community	Attributes measured
Barnett, How & Humphreys (1978)	Clouds Creek, NE N.S.W.	(1) Pine plantation (2) Wet sclerophyll forest	* <i>Rattus fuscipes</i> * <i>R. rattus</i> * <i>Antechinus stuartii</i> <i>Melomys cervinipes</i> <i>R. lutreolus</i> * <i>Mus musculus</i>	Vegetation <1 m + Vegetation 1-2 m logs + litter
Braithwaite and Gullan (1978)	Cranbourne, Vic.	Heath	<i>R. lutreolus</i> * <i>Pseudomys novaehollandiae</i> * <i>M. musculus</i> <i>Isodon obesulus</i> * <i>R. rattus</i>	Floristic richness Sedge-food index Seasonal seed indicator Perennial seed index Structure - P/A at 20 height intervals
Braithwaite, Cockburn and Lee (1978)	Grampians, Vic.	Heath	* <i>A. stuartii</i> <i>A. flavipes</i> <i>A. minimus</i> * <i>M. musculus</i> <i>P. shortridgei</i> * <i>R. fuscipes</i> <i>R. lutreolus</i>	Floristic richness + Structure - P/A at 30cm + intervals soil resistance sedge-food index other monocotyledon-food index
Campbell (1981)	Fraser Is. Qld.	Heath	* <i>R. fuscipes</i> <i>R. tunneyi</i> <i>M. burtoni</i> <i>R. lutreolus</i> <i>M. cervinipes</i> <i>A. flavipes</i> <i>Sminthopsis murina</i> <i>I. macrourus</i>	Floristic richness Height <0.2 m >0.2-1.5 m 1.5-4 m >4.0 m Horizontal density Vertical density Life form Bare ground patches

A 1-2

Author(s)	Location	Habitat	Community	Attributes measured
Cockburn (1978)	Grampians Vic.	Heath	<i>P. shortridgei</i>	Floristic richness + Cover/abundance score Vertical cover Soil type + Litter type Proximity to physiognomic features Disturbance Fire history +
(N.B. Habitat requirements of <i>P. novaehollandiae</i> stated to be similar to <i>P. shortridgei</i>)				
Fox (1979)		Heath	* <i>P. novaehollandiae</i>	Vegetation index (20-50 cm layer) +
Fox and Fox (1978)	Hawks Nest, N.S.W.	Coastal heath	* <i>P. novaehollandiae</i>	Plant species diversity + (Species % cover values (P/A of bare sand (Vegetation height Soil hardness Vegetation index (incident light readings) Ratio of endemic heath species+ to total native species present.
Fox and Fox (1981)	Myall Lakes, N.S.W.	Coastal heath	* <i>A. stuartii</i> <i>S. murina</i> * <i>M. musculus</i> * <i>P. novaehollandiae</i> <i>P. gracilicaudatus</i> * <i>R. fuscipes</i>	Floristic factors + structural factors (esp. 0.5-1.0 m) +

A I-3

Author(s)	Location	Habitat	Community	Attributes measured
Gullan and Norris (1981)	Gippsland Lakes, Vic.	Open forest	* <i>R. fuscipes</i>	Floristic richness Potential food resources
Milledge (1979)	Camden Haven N.S.W.	Forest	* <i>A. stuartii</i> <i>S. murina</i> * <i>R. fuscipes</i> <i>R. lutreolus</i> * <i>R. rattus</i> * <i>M. musculus</i> <i>M. cervinipes</i> <i>P. gracilicaudatus</i>	Vegetation dsy 0-30cm 30-100cm 100-200cm Logcount Canopy (20cm) understorey single limb stump Scale 0 - 3 0 - 3 0 - 3 Source of logs
Newsome and Catling (1979)	Nadgee Nature Reserve, N.S.W.	Forest	* <i>A. stuartii</i> * <i>A. swainsonii</i> * <i>R. fuscipes</i> <i>R. lutreolus</i> * <i>R. rattus</i> * <i>M. musculus</i>	Tree canopy (%) Shrub canopy (%) Ground herbage Logs, rocks, debris etc. Moisture in soil
Pattemore, (1977)	Pulpwood industry areas, Tas.	Forest	<i>A. minimus</i> * <i>A. swainsonii</i> * <i>S. leucopus</i> <i>R. lutreolus</i> * <i>R. rattus</i> <i>Hydromys chrysogaster</i>	Canopy cover Ground cover Density of mature trees Floristic richness

A I-4

Author(s)	Location	Habitat	Community	Attributes measured
Posamentier (1975)	N.S.W.	Coastal heath	<i>R. lutreolus</i> * <i>P. novaehollandiae</i> * <i>M. musculus</i>	Plant species composition Floristic richness Total vegetation + Vegetation density (10, 20, 50 + 100 cm) Bare ground + Leaf litter Soil penetrability Percentage cover 10, 20 cm + 20 cm 50 cm +
Stewart (1979)	Brindabella Range, A.C.T.	Forest	* <i>R. fuscipes</i> * <i>A. stuartii</i> * <i>A. swainsoni</i>	Cover (lightmeter reading) Runways Logs Main ground cover
Dueser and Shugart (1979)	Tennessee, U.S.A.	Forest	<i>Blarina brevicaudata</i> <i>Peromyscus leucopus</i> <i>Ochrotomys nuttalli</i> <i>Tamias striatus</i>	Understorey tree dispersion Evergreenness of overstorey Vertical herbaceous foliage density Litter-soil compactability Tree stump size Index of shrub-level vegetation density Vertical woody foliage density.

* Similar species also caught during the present study.

+ Attributes that were shown significant in the referred study,
to species used in the present study.

APPENDIX II. PHOTOGRAPHIC REPRESENTATION OF STRUCTURAL VARIABLES
USED IN TABLE 3.3 FOR HABITAT HETEROGENIETY ASSESSMENT.

STRATA 1 and 2
BARK TYPE



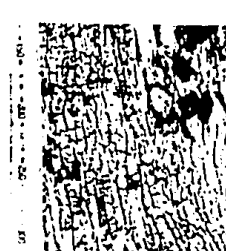
Gum



Fissured



Ribbon



Other

STRATUM 3
CANOPY DENSITY



Rank = 1



Rank = 2



Rank = 3

ACACIA ABUNDANCE



Rank = 1

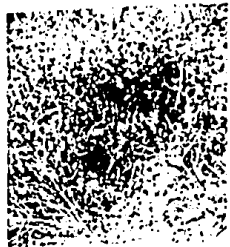


Rank = 2



Rank = 3

APPENDIX II. (continued)

STRATUM 4
WOODY PLANTS

Cover = 100%

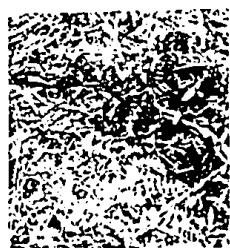


Cover density = 1



Cover density = 2

FERNS



Cover density = 1



Cover density = 2



Cover density = 3

GRASSES



Cover density = 1

Cover density = 2
Cover = 80%

Cover density = 3

APPENDIX II. (continued)

STRATUM 5
LITTERDepth = 5 cm
Cover = 100%

Depth = 10 cm



Depth = 50 cm

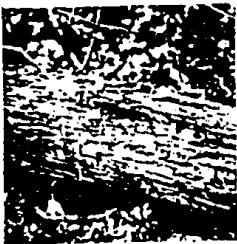
STONINESS

Diameter = 7 cm
Cover = 90%Diameter = 25 cm
Cover = 80%Diameter = 40 cm
Cover = 60%

LOG >10 cm diameter



Decay = 0



Decay = 1



Decay = 2



Decay = 3

APPENDIX III CROWN COVER CONVERSIONS AND CROWN TYPES USED TO CALCULATE FOLIAGE COVER VALUES

Crown cover values calculated from crown ratios assuming square and triangular packing formations

	Overlap															Separation											
C	$\frac{1}{4}$	$\frac{3}{16}$	$\frac{1}{8}$	$\frac{1}{16}$	0	.05	.1	.15	.2	.25	.3	.4	.5	.75	1.0	1.25	1.5	2.0	3.0	4.0	8.0	10	15	20			
Crown cover value	100	95	89	84	78	72	65	58	55	51	47	40	34	26	20	16	13	9	5	3	1	.6	.3	.2			

(From Walker and Tunstall, 1981)

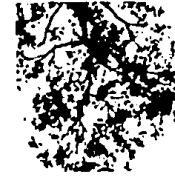
40%



45%



50%



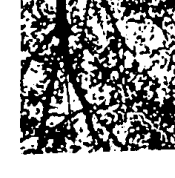
55%



60%



65%



70%



Crown types: the openness of individual tree or shrub crowns is estimated by matching the crown with a photograph. The rows show similar crown types for different leaf sizes (large to small left to right); Acacia phyllodes are in the right hand row. Most Australian woody plants are in the range 40-70%. (Walker and Tunstall, 1981)

APPENDIX IV

DIVERSITY INDEX SUITE MODEL

DATA INPUT									
Data Set	Species Abundance								Comments
	<u>1</u>	<u>2</u>	<u>3</u>	<u>4</u>					
1	15	15	15	15	One species becoming rare.				
	15	15	15	10					
	15	15	15	5					
	15	15	15	1					
2	15	15	15	15	Two species becoming rare.				
	15	15	10	10					
	15	15	5	5					
	15	15	1	1					
3	15	15	15	15	Three species becoming rare.				
	15	10	10	10					
	15	5	5	5					
	15	1	1	1					
4	15	15	15	1	One species rare. One species becoming rare.				
	15	15	10	1					
	15	15	5	1					
	15	15	1	1					
5	15	15	15	15	One disappears early. One disappears late. One becomes rare late.				
	15	15	15	0					
	15	15	5	0					
	15	15	0	0					
	15	5	0	0					
6	15	15	10	1	Decline of one common species.				
	14	15	10	1					
	13	15	10	1					
	12	15	10	1					
	11	15	10	1					
	10	15	10	1					
7	15	15	10	1	Decline of two common species.				
	14	14	10	1					
	13	13	10	1					
	12	12	10	1					
	11	11	10	1					
	10	10	10	1					
8	16	16	8	4	Proportional decrease by two steps of 25%.				
	12	12	6	3					
	8	8	4	2					
9	<u>1</u>	<u>2</u>	<u>3</u>	<u>4</u>	<u>5</u>	<u>6</u>	<u>7</u>	<u>8</u> ...	Adding four new rare species.
	15	15	10	1	0	0	0	0	
	15	15	10	1	1	0	0	0	
	15	15	10	1	1	1	0	0	
	15	15	10	1	1	1	1	0	
	15	15	10	1	1	1	1	1	

APPENDIX IV (continued)

INDEX COMPUTATIONS, DIFFERENCES AND PROPORTIONAL CHANGES

SIMPSON	PIELOU	S-W	BRILLOUIN	EQUITABILITY
1.				
0.2500	1.3863	1.3863	1.2839	1.0000
-0.0062	0.0245	0.0133	0.0198	0.0096
0.2562	1.3618	1.3730	1.2641	0.9904
1.0248	0.9823	0.9904	0.9846	
-0.0238	0.0888	0.0592	0.0643	0.0427
0.2800	1.2730	1.3138	1.1998	0.9477
1.1200	0.9183	0.9477	0.9345	
-0.0395	0.1319	0.1343	0.1290	0.0969
0.3195	1.1411	1.1795	1.0708	0.8508
1.2780	0.8231	0.8508	0.8340	
2.				
0.2500	1.3863	1.3862	1.2839	1.0000
-0.0100	0.0392	0.0201	0.0345	0.0145
0.0.2600	1.3471	1.3662	1.2494	0.9855
1.0400	0.9717	0.9855	0.9731	
-0.0525	0.1839	0.1107	0.1257	0.0799
0.3125	1.1632	1.2555	1.1237	0.9056
1.2500	0.8391	0.9056	0.8752	
-0.1289	0.3454	0.3286	0.3187	0.2370
0.4414	0.8178	0.9269	0.8050	0.6686
1.756	0.5899	0.6686	0.6270	
3.				
0.2500	1.3863	1.3863	1.2839	1.0000
-0.0093	0.0364	0.0174	0.0414	0.0143
0.2593	1.3499	1.3689	1.2425	0.9875
1.0372	0.9737	0.9878	0.9678	
-0.0740	0.2513	0.1264	0.1626	0.0913
0.3333	1.0986	1.2425	1.0799	0.8962
1.3332	0.7925	0.8963	0.8411	
-0.3704	0.7472	0.6088	0.6075	0.4391
0.7037	0.3514	0.6337	0.4720	0.4571
1.8148	0.2535	0.4571	0.3676	
4.				
0.3195	1.1411	1.1795	1.0708	0.8508
-0.0083	0.0257	0.0090	0.0188	0.0065
0.3278	1.1154	1.1705	1.0520	0.8443
1.0260	0.9775	0.9924	0.9824	0.9924
-0.0395	0.1138	0.0672	0.0761	0.0485
0.3673	1.0016	1.1033	0.9759	0.7958
1.1496	0.8777	0.9354	0.9114	0.9354
-0.0741	0.1838	0.1764	0.1709	0.1272
0.4414	0.8178	0.9269	0.8050	0.6686
1.3815	0.7167	0.7858	0.7518	0.7858

APPENDIX IV (continued)

INDEX COMPUTATIONS, DIFFERENCES AND PROPORTIONAL CHANGES

SIMPSON	PIELOU	S-W	BRILLOUIN	EQUITABILITY
5.				
0.2500	1.3863	1.3863	1.2839	1.0000
-0.0833	0.2877	0.2877	0.2744	0.2075
0.3333	1.0986	1.0986	1.0095	0.7925
1.3332	0.7925	0.7925	0.7863	
-0.0545	0.1512	0.0944	0.1081	0.0681
0.3878	0.9474	1.0042	0.9014	0.7244
1.5512	0.6834	0.7244	0.7021	
-0.1122	0.2543	0.3111	0.2727	0.2244
0.5000	0.6931	0.6931	0.6287	0.5000
2.000	0.5000	0.5000	0.4897	
-0.1250	0.2231	0.1308	0.1463	0.0944
0.6250	0.4700	0.5623	0.4824	0.4056
2.5000	0.3390	0.4056	0.3757	
6.				
0.3278	1.1154	1.1705	1.0520	0.8443
0.0015	-0.0047	-0.0035	-0.0011	-0.0026
0.3263	1.1201	1.1740	1.0531	0.8469
0.9954	1.0042	1.0030	1.0010	1.0031
0.0009	-0.0025	-0.0026	-0.0001	-0.0018
0.3254	1.1226	1.1766	1.0532	0.8487
0.9927	1.0065	1.0052	1.0011	1.0052
-0.0001	0.0002	-0.0014	0.0012	-0.0010
0.3255	1.1224	1.1780	1.0520	0.8497
0.9930	1.0063	1.0064	1.0000	1.0064
-0.0010	0.0031	0.0001	0.0027	0.0001
0.3265	1.1193	1.1779	1.0493	0.8496
0.9960	1.0035	1.0063	0.9974	1.0063
-0.0022	0.0067	0.0019	0.0047	0.0013
0.3287	1.1126	1.1760	1.0448	0.8483
1.0027	0.9975	1.0047	0.9932	1.0047
7.				
0.3278	1.1154	1.1705	1.0520	0.8443
0.0037	-0.0112	-0.0075	-0.0030	-0.0058
0.3241	1.1266	1.1784	1.0550	0.8501
0.9887	1.0100	1.0067	1.0029	1.0069
0.0034	-0.0107	-0.0078	-0.0023	-0.0056
0.3207	1.1373	1.1862	1.0573	0.8557
0.9783	1.0196	1.0134	1.0050	1.0135
0.0031	-0.0098	-0.0073	-0.0015	-0.0053
0.3176	1.1471	1.1935	1.0588	0.8610
0.9689	1.0284	1.0196	1.0065	1.0198
0.0026	-0.0082	-0.0067	-0.0002	-0.0047
0.3150	1.1553	1.2002	1.0590	0.8657
0.9610	1.0358	1.0254	1.0067	1.0253
0.0018	-0.0056	-0.0055	0.0016	-0.0040
0.3132	1.1609	1.2057	1.0574	0.8697
0.9555	1.0408	1.0301	1.0051	1.0301

APPENDIX IV (continued)

INDEX COMPUTATIONS, DIFFERENCES AND PROPORTIONAL CHANGES

8.				
0.3058	1.1849	1.2637	1.1407	0.9115
0.0000	0.0000	0.0000	0.0283	0.0000
0.3058	1.1849	1.2637	1.1124	0.9115
			0.9752	
0.0000	0.0000	0.0000	0.0492	0.0000
0.3058	1.1849	1.2637	1.0632	0.9115
			0.9321	
9.				
0.3278	1.1154	1.1705	1.0520	0.5629
0.0149	-0.0464	-0.0846	-0.0639	-0.0407
0.3129	1.1618	1.2551	1.1159	0.6036
0.9545	1.0416	1.0723	1.0607	1.0723
0.0138	-0.0452	-0.0813	-0.0615	-0.0391
0.2991	1.2070	1.3364	1.1774	0.6427
0.9124	1.0821	1.1417	1.1192	1.1418
0.0129	-0.0442	-0.0781	-0.0593	-0.0375
0.2862	1.2512	1.4145	1.2367	0.6802
0.8731	1.1218	1.2085	1.1756	1.2084
0.0121	-0.0432	-0.0751	-0.0571	-0.0362
0.2741	1.2944	1.4896	1.2938	0.7164
0.8362	1.1605	1.2726	1.2298	1.2727

N.B. Centre values are the index computations.
 Lower right side values are the differences between computations.
 Lower left side values are the proportional changes in relation
 to the first computation of the data set for each index.

APPENDIX V

Matrices of Morisita similarity indices between methods
for each site

BBC

G(5)	1.0000							
G(7.5)	0.9561	1.0000						
G(10)	0.8799	0.9770	1.0000					
G(20)	0.8401	0.9558	0.9964	1.0000				
I(5)	0.9967	0.9715	0.9020	0.8645	1.0000			
I(7.5)	0.9995	0.9540	0.8773	0.8374	0.9963	1.0000		
I(10)	0.9955	0.9576	0.8928	0.8568	0.9900	0.9961	1.0000	
I(20)	0.9785	0.9955	0.9575	0.9308	0.9873	0.9772	0.9805	1.0000
	G(5)	G(7.5)	G(10)	G(20)	I(5)	I(7.5)	I(10)	I(20)

D75

G(5)	1.0000							
G(7.5)	0.9714	1.0000						
G(10)	0.9962	0.9576	1.0000					
G(20)	0.9630	0.9892	0.9605	1.0000				
I(5)	0.9306	0.9867	0.9047	0.9598	1.0000			
I(7.5)	0.9882	0.9763	0.9712	0.9474	0.9577	1.0000		
I(10)	0.8346	0.9376	0.8078	0.9211	0.9707	0.8649	1.0000	
I(20)	0.9332	0.9402	0.8993	0.8834	0.9533	0.9767	0.8676	1.0000
	G(5)	G(7.5)	G(10)	G(20)	I(5)	I(7.5)	I(10)	I(20)

D68

G(5)	1.0000							
G(7.5)	0.9614	1.0000						
G(10)	0.9313	0.8000	1.0000					
G(20)	0.9336	0.9960	0.7470	1.0000				
I(5)	0.9409	0.9977	0.7602	0.9998	1.0000			
I(7.5)	0.9671	0.9998	0.8123	0.9939	0.9960	1.0000		
I(10)	0.9666	0.9998	0.8112	0.9941	0.9962	1.0000	1.0000	
I(20)	0.9837	0.9951	0.8530	0.9825	0.9862	0.9971	0.9969	1.0000
	G(5)	G(7.5)	G(10)	G(20)	I(5)	I(7.5)	I(10)	I(20)

D50

G(5)	1.0000							
G(7.5)	0.7893	1.0000						
G(10)	0.8585	0.9474	1.0000					
G(20)	0.7722	0.7174	0.8421	1.0000				
I(5)	0.9433	0.7260	0.7205	0.6654	1.0000			
I(7.5)	0.9657	0.8081	0.8319	0.7912	0.9758	1.0000		
I(10)	0.9299	0.9323	0.9547	0.8585	0.8742	0.9498	1.0000	
I(20)	0.9365	0.8889	0.8627	0.7595	0.9524	0.9781	0.9685	1.0000
	G(5)	G(7.5)	G(10)	G(20)	I(5)	I(7.5)	I(10)	I(20)

APPENDIX VI

Mean values ($\bar{x}$), variance (σ^2) and range (r) of environmental attributes measured at each site.

(a) Site B.B.C.

Attribute	Units	$\bar{x}$	σ^2	r	n
<u>Stratum 1</u>					
No. trees		5.13	14.41	1.0-13.0	15
Height	m	24.40	18.69	18.0-30.0	15
D.B.H.	cm	54.00	240.00	30.0-80.0	15
Crown cover	%	21.80	151.61	4.0-35.8	15
Crown diameter	m	7.93	8.07	4.0-16.0	15
Gum bark	0-3	0.06	0.06	0.0-1.0	16
Fissured bark	0-3	0.12	0.12	0.0-1.0	16
Ribbon bark	0-3	1.75	1.13	0.0-3.0	16
Other bark types	0-3	0.50	0.40	0.0-2.0	16
<u>Stratum 2</u>					
No. trees		26.12	371.18	8.0-90.0	16
Height	m	12.12	5.98	8.0-15.0	16
D.B.H.	cm	12.62	13.45	8.0-20.0	16
Crown cover	%	32.89	169.18	9.4-50.7	16
Crown diameter	m	4.25	1.13	3.0-6.0	16
Ribbon bark	0-3	0.25	0.20	0.0-1.0	16
Other bark types	0-3	2.19	0.30	1.0-3.0	16
<u>Stratum 3</u>					
No. shrubs		10.44	304.54	1.0-99.0	36
Height	m	3.36	0.86	2.0-5.0	36
Cover	%	21.94	451.83	5.0-80.0	36
Canopy density	0-3	1.14	1.03	0.0-3.0	33
Acacia rank	0-3	1.50	0.32	0.0-2.0	33
<u>Stratum 4</u>					
Woody plants					
Height	cm	101.92	1360.15	30.0-150.0	26
Cover	%	11.35	117.12	5.0-45.0	26
Density	0-3	0.80	0.92	0-3	33
Ferns					
Height	cm	88.75	600.23	40.0-130.0	56
Cover	%	65.73	862.16	5.0-99.0	56
Density	0-3	2.62	0.42	1-3	33
Runways	P/A(0/1)	0.82	0.15	0-1	33
Grasses					
Height	cm	27.18	576.05	10.0-100.0	39
Cover	%	35.51	832.62	5.0-90.0	39
Density	0-3	1.12	0.80	0-3	33
<u>Stratum 5</u>					
Litter					
Depth	cm	22.86	91.69	5.0-40.0	56
Moisture	M/D(0/1)	0.30	0.22	0-1	33
Cover	%	80.30	260.51	30.0-99.0	56
Stones					
Diameter	cm	7.00	0.00	7.0-7.0	2
Cover	%	7.50	12.50	5.0-10.0	2

Attribute	Units	$\bar{x}$	σ^2	r	n
<u>Stratum 5 cont.</u>					
<u>Small logs</u>					
No.		2.95	7.10	1-15	41
Decay rank	0-3	1.68	1.35	0-3	33
<u>Large logs</u>					
Diameter	cm	44.55	720.83	12.0-100.0	29
Number		1.72	0.85	1-4	29
Decay rank	0-3	1.39	2.06	0-3	33
Bare soil	%	23.33	376.66	5.0-50.0	6
Water course	R/D(0/1)	0.38	0.24	0-1	33
<u>Stratum 6</u>					
Soil moisture	M/D(0/1)	0.54	0.25	0-1	33
<u>(b) Site D75</u>					
<u>Stratum 1</u>					
No. trees		21.07	48.07	8-32	14
Height	m	24.50	4.88	20.0-28.0	14
D.B.H.	cm	33.21	52.34	20.0-50.0	14
Crown cover	%	27.86	43.21	15.6-35.8	12
Crown diameter	m	7.00	2.92	4.0-10.0	14
<u>Stratum 2</u>					
No. trees		24.14	119.21	12-51	14
Height	m	16.14	4.59	14.0-20.0	14
D.B.H.	cm	12.64	20.71	8.0-20.0	14
Crown cover	%	5.88	10.30	1.5-12.0	14
Crown diameter	m	3.14	0.44	2.0-4.0	14
<u>Stratum 3</u>					
No. shrubs		6.46	23.40	1-25	43
Height	m	3.35	1.14	2.0-6.0	43
Cover	%	14.53	65.25	5.0-40.0	43
Canopy density	0-3	0.90	0.78	0-2	31
Acacia rank	0-3	1.04	0.32	0-2	31
<u>Stratum 4</u>					
<u>Woody plants</u>					
Height	cm	91.45	2008.47	20.0-180.0	48
Cover	%	14.27	122.33	5.0-50.0	48
Density	0-3	1.68	0.30	0-2	31
<u>Ferns</u>					
Height	cm	70.30	390.21	15.0-120.0	50
Cover	%	30.80	349.35	5.0-75.0	50
Density	0-3	1.96	0.04	1-2	31
<u>Grasses</u>					
Height	cm	27.43	234.37	10.0-60.0	35
Cover	%	13.57	230.25	5.0-80.0	35
Density	0-3	1.42	0.25	1-2	24
<u>Stratum 5</u>					
<u>Litter</u>					
Depth	cm	14.40	70.04	5.0-50.0	50
Cover	%	69.60	244.73	30.0-90.0	50
<u>Stones</u>					
Diameter	cm	10.80	32.00	7.0-30.0	50
Cover	%	76.58	405.23	9.0-90.0	50

APPENDIX VI (continued) - 3 -

Attribute	Units	$\bar{x}$	σ^2	r	n
<u>Stratum 5 cont.</u>					
<u>Small logs</u>					
No.		10.26	18.48	2-19	50
Decay rank	0-3	1.9	0.17	1-3	31
<u>Large logs</u>					
Diameter	cm	30.04	404.82	10.0-80.0	45
No.		3.09	6.31	1-16	45
Decay rank	0-3	1.84	0.79	0-3	31
Bare soil	%	21.20	249.55	5.0-60.0	50
<u>Stratum 6</u>					
Soil moisture	M/D(0/1)	0.98	0.02	0-1	31
<u>(c) Site D68</u>					
<u>Stratum 1</u>					
No. trees		1.25	0.25	1-2	4
Height	m	25.00	0.00	25.0-25.0	4
D.B.H.	cm	87.50	91.66	80.0-100.0	4
Crown cover	%	4.97	29.12	1.8-13.0	4
Crown diameter	m	11.00	1.33	10.0-12.0	4
Gum bark	0-3	0.14	0.28	0-2	15
Fissured bark	0-3	0.21	0.64	0-3	15
Other bark type	0-3	0.71	1.60	0-3	15
<u>Stratum 2</u>					
No. trees		106.50	1544.42	60-185	14
Height	m	16.42	4.42	13.0-20.0	14
D.B.H.	cm	14.78	16.64	8.0-20.0	14
Crown cover	%	47.58	181.14	13.0-57.8	11
Crown diameter	m	2.71	0.53	2.0-4.0	14
Gum bark	0-3	1.71	0.68	0-3	15
Other bark type	0-3	1.43	0.72	0-3	15
<u>Stratum 3</u>					
No. shrubs		11.33	150.82	1-69	42
Height	m	4.81	2.30	2.0-8.0	42
Cover	%	27.74	667.32	5.0-90.0	42
Canopy density	0-3	1.14	0.49	0-3	30
Acacia rank	0-3	1.68	0.55	0-3	30
<u>Stratum 4</u>					
<u>Woody plants</u>					
Height	cm	110.36	1586.55	17.0-150.0	33
Cover	%	7.27	45.45	5.0-40.0	33
Density	0-3	0.80	0.49	0-3	30
<u>Ferns</u>					
Height	cm	76.60	1033.81	20.0-140.0	47
Cover	%	30.11	716.84	5.0-90.0	47
Density	0-3	1.80	0.78	0-3	30
Runways	P/A(0/1)	0.20	0.16	0-1	30
<u>Grasses</u>					
Height	cm	13.43	32.02	5.0-30.0	35
Cover	%	20.43	253.49	5.0-60.0	35
Density	0-3	1.00	0.61	0-2	30

APPENDIX VI (continued) - 4 -

Attribute	Units	$\bar{X}$	σ^2	r	n
<u>Stratum 5</u>					
Litter	cm	11.90	56.01	5.0-40.0	50
Depth	M/D(0/1)	0.80	0.16	0-1	30
Moisture	%	74.24	373.45	30.0-99.0	50
Cover					
Stones	cm	14.02	45.77	4.0-40.0	48
Diameter	%	25.81	675.94	5.0-99.0	48
Cover					
Small logs					
No.		6.91	27.51	1-27	47
Decay rank	0-3	1.98	0.47	0-3	30
Large logs	cm	30.03	310.33	1.0-80.0	34
Diameter		2.21	2.58	1-7	33
No.	0-3	1.44	1.27	0-3	30
Decay rank	%	14.02	149.54	4.0-60.0	42
Bare soil					
<u>Stratum 6</u>					
Soil moisture	M/D(0/1)	0.72	0.20	0-1	30
(d) <u>Site D50</u>					
<u>Stratum 1</u>					
No. trees		5.60	3.16	3-8	10
Height	m	28.40	4.93	25.0-30.0	10
D.B.H.	cm	61.00	543.33	30.0-100.0	10
Crown cover	%	32.76	110.70	13.0-42.9	10
Crown diameter	m	9.40	3.60	6.0-12.0	10
Gum bark	0-3	0.80	1.29	0-3	16
Fissured bark	0-3	1.80	1.29	0-3	16
Other bark types	0-3	0.40	0.27	0-1	16
<u>Stratum 2</u>					
No. trees		37.70	1757.57	7-144	10
Height	m	8.7	3.79	5.0-11.0	10
D.B.H.	cm	8.6	2.71	6.0-12.0	10
Crown cover	%	23.31	477.03	1.4-62.3	8
Crown diameter	m	3.30	0.45	2.0-4.0	16
Gum bark	0-3	2.00	0.89	0-3	16
Ribbon bark	0-3	0.10	0.10	0-1	16
Other bark types	0-3	0.50	0.50	0-2	16
<u>Stratum 3</u>					
No. shrubs		3.75	13.56	1-15	36
Height	m	3.08	1.05	2.0-6.0	36
Cover	%	19.17	329.29	5.0-90.0	36
Canopy density	0-3	1.29	0.50	0-2	31
Acacia rank	0-3	0.40	0.30	0-2	31
<u>Stratum 4</u>					
Woody plants					
Height	cm	86.89	1401.88	30.0-150.0	37
Cover	%	10.94	44.22	5.0-30.0	37
Density	0-3	1.17	0.43	0-2	31

APPENDIX VI (continued) - 5 -

Attribute	Units	$\bar{X}$	σ^2	r	n
<u>Stratum 4 cont.</u>					
Ferns					
Height	cm	75.94	1515.22	20.0-150.0	32
Cover	%	14.38	272.18	5.0-90.0	32
Density	0-3	1.31	1.05	0-3	31
Runways	P/A(0/1)	0.02	0.02	0-1	31
Grasses					
Height	cm	10.38	5.85	5.0-15.0	26
Cover	%	12.31	84.46	5.0-40.0	26
Density	0-3	0.78	0.51	0-2	31
<u>Stratum 5</u>					
Litter					
Depth	cm	10.74	96.54	1.0-70.0	42
Cover	%	83.31	126.85	60.0-99.0	42
Stones					
Diameter	cm	12.62	23.06	5.0-30.0	40
Cover	%	34.12	822.93	5.0-90.0	40
Small logs					
No.		14.10	54.14	2-34	42
Decay rank	0-3	2.88	0.11	2-3	31
Large logs					
Diameter	cm	20.20	92.83	3.0-40.0	25
No.		1.72	1.21	1-5	25
Decay rank	0-3	1.50	1.86	0-3	31
Bare soil	%	10.40	32.47	5.0-35.0	37
<u>Stratum 6</u>					
Soil moisture	M/D(0/1)	0.86	0.12	0-1	31

NB $\bar{X}$ = mean values
 σ^2 = variance
 r = range (min.-max.)
 n = number of samples