TECHNIQUES FOR MEASURING BIOGEOGRAPHIC ATTRIBUTES OF NATURE RESERVES

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A thesis submitted for the degree of
Master of Arts
in Geography
University of Adelaide
June, 1982

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ABSTRACT

There is speculation that nature reserves may not be able to maintain high levels of species diversity if they are managed as isolated and independent units. This speculation has been prompted by Island Biogeography Theory and its application to nature reserve design. However, Island Biogeography Theory has been strongly criticized in recent years. The present study examines this criticism and concludes that, although some of it is well founded, there is considerable evidence which supports the basic principles of the theory. It is these basic principles which have been incorporated in design specifications for nature reserves.

To date, design specifications for nature reserves have been wholly qualitative and have not included techniques for measuring isolation and compactness. These, together with area, are the most important biogeographic attributes of habitat isolates and their measurement is essential for an analysis of the relative effectiveness of different nature reserve designs.

The primary purpose of the present study was to develop techniques for measuring the isolation and compactness of nature reserves in areas where fragmentation of the original native vegetation cover has created a complex pattern of habitat isolates. The nature reserves and intervening native vegetation patches of the Mt. Lofty Ranges, South Australia, provided a suitable test area for the techniques developed and demonstrated their application to conservation planning and management.

I hereby declare that none of the material contained in this thesis has been accepted for the award of any other degree or diploma in any institution and that, to the best of my knowledge and belief, the thesis contains no material previously published or written by another person, except where due reference has been made in the text of the thesis.

ACKNOWLEDGEMENTS

I wish to thank T. Dendy of the South Australian Department of Environment and Planning for his much valued assistance in the provision of information for this study. Similar thanks must also go to S. Pillman and J.A. Lothian of the Department of Environment and Planning and M. Crowley of the National Parks and Wildlife Service. The Engineering and Water Supply Department, the Lands Department and the State Planning Authority also assisted in the mapping of the Mount Lofty Ranges.

Financial assistance was received from the Department of Geography at the University of Adelaide, and the author held a Postgraduate Scholarship under the University of Adelaide Research Grant.

Further thanks are due to my fellow students for their helpful discussions on the study; M. Foale, D. Oakley, C. Crothers, N. Murray and V. Broughton for their assistance in the preparation of the manuscript, and E. Bamford for his aid and advice in the computational procedures.

Finally, this thesis could not have been possible without the dedication of my supervisors, Mr. T.L.C. Griffin and Dr. S.G. Taylor, whose constructive advice and assistance is gratefully acknowledged.

I. INTRODUCTION

There is speculation that nature reserves may not be able to maintain high levels of species diversity if they are managed as isolated and independent units. This speculation has been prompted by Island Biogeography Theory and its application to nature reserve design. However, Island Biogeography Theory has been strongly criticized in recent years. This chapter examines Island Biogeography Theory, its application to habitat islands and nature reserves, and the criticisms put forward against these applications.

A. Island Biogeography Theory

Islands have long been perceived as natural laboratories for the study of a number of important ecological and evolutionary processes. Some of the earliest examples of such research are Darwin's work on the Galapagos Islands and Wallace's work in the Malay Archipelago. The modern period of island biogeography research began in the mid-1950's when Darlington (1957) published his text, *Zoogeography : The Geographical Distribution of Animals*. This text noted that the number of species on an island tends to increase with increasing island area and to decrease with increasing island isolation, all other factors being equal. Preston (1962), expanding on a concept proposed by earlier natural historians, stated that the number of species in a given taxon on an island is the product of the density of those species and the area of the island. Later, Carlquist (1965, 1966a-d, 1974) published a series of important works on long-distance dispersal to oceanic islands and the evolutionary changes that occur after species colonization.

However, it was the work of MacArthur and Wilson (1963, 1967) which changed island biogeography research from an idiographic discipline with few organizing principles to a nomothetic science with predictive general laws. In their earliest paper MacArthur and Wilson (1963) suggested that a dynamic equilibrium between immigration rates and extinction rates might explain the richness of the flora or fauna of any island. However, MacArthur and Wilson (1967) later expanded this hypothesis in a monograph entitled, *The Theory of Island Biogeography.*

In this monograph they began by extending the *species-area relationship* which had originated in the mid-1950's (e.g., Evans, Clark and Brand, 1955; Hopkins, 1955, etc.) and which was later discussed by Preston (1962). This relationship is commonly expressed by the equation

$$S = C.A^{z} \tag{1.1}$$

where S is the number of species of a particular taxon inhabiting an island of area A; C is the population density which depends on the taxon and the biogeographic region; and z is a constant for a given region. Most values of z cluster in the range 0.20 to 0.35, with 0.263 being the most common value. Higher z values are experienced by oceanic islands whereas comparable mainland habitats have lower z values (i.e., 0.15-0.25). Thus, mainland habitats tend to contain more species than comparable oceanic islands.

MacArthur and Wilson (1967) illustrated this relationship with a number of examples from earlier papers, most notably Darlington's (1957) study of the herpetofauna of the West Indies and the relationship of area to number of ponerine ant species in the faunas of various Moluccan and Melanesian islands (Wilson, 1961). These studies demonstrated a strikingly orderly relation between island area and species diversity.

MacArthur and Wilson then attempted to identify and measure the factors contributing to this relationship. They found, utilizing the relatively limited amount of information available at that time, that area alone tends to account for most of the variation in species numbers on islands. In addition, island area was generally found to be correlated with environmental diversity or heterogeneity which exerts a more direct influence on species numbers (Williams, 1964).

1. The Species Equilibrium

MacArthur and Wilson (1963) and Preston (1962) independently presented the concept of an *equilibrium* between immigration and extinction to explain at least part of the species diversity of islands. The equilibrium model presented in MacArthur and Wilson's monograph attempts to go beyond mere description and give Island Biogeography Theory predictive power. For instance, MacArthur and Wilson (1967, 20-21) state:

> *"A perfect balance between immigration and extinction might never be reached, since it would be approached exponentially; but to the extent that the assumption of a balance has enabled us to make certain valid new predictions, the equilibrium concept is useful as a step beyond the more purely descriptive techniques of multiple regression."*

The equilibrium model assumes that, over ecological time,

$$dS_i/_{dt} = f(S_i, P_{i,j}, \text{ for all } i,j) \qquad (1.2)$$

where the change in species number on an island (dS_i) over time (dt) is a function of the number of species on the island (S_i) and P_{ij}, the measurement of the jth physical parameter for island i ($j = 1,\ldots,n$) (Simberloff, 1972). In other words, the rate of change in species number for any island is determined by the physical parameters of the island. These parameters may include not only the intrinsic characteristics of the island, such as area and maximum elevation, but also characteristics of its relationship with other locations, such as distance between the island and some other location. However, simplifying assumptions need to be made to the function (f) so that approximate solutions may be achieved. These assumptions include : 1) only one source of immigrating species (source region) exists, and 2) internal environmental heterogeneity is minimized as much as possible.

Figure 1 illustrates the essence of the equilibrium model. Both immigration and extinction rates vary with the number of species present. All other factors remaining constant, the immigration curve (Is) should be a decreasing function of the number of species present because the more species already present on an island the fewer are the immigrants that belong to new species. MacArthur and Wilson (1967) explain the exponential nature of the immigration rate as due to the fact that, on average, more rapidly dispersing (tramp) species become established very quickly. This causes a rapid initial drop in the overall immigration rate. The later arrival of slower colonizers subsequently has less of an effect on lowering the immigration rate.

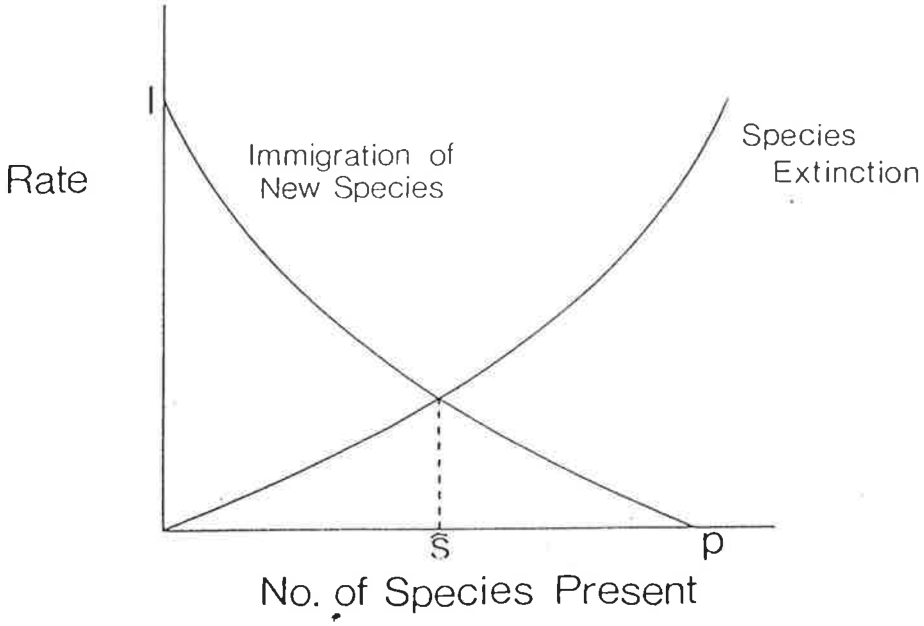
The extinction rate (Es) is an increasing function of the number of species present for two reasons. First, the more species

Figure 1

Equilibrium model of a biota on a single island

Notes: The equilibrium species number ($\hat{s}$) is reached at the intersection point between the curve of rate of immigration of new species, not already on the island, and the curve of extinction of species from the island.

Source: MacArthur and Wilson (1967, 21)


I
Rate
Immigration of New Species
Species Extinction
Ŝ
p
No. of Species Present

present on an island the more species there are to become extinct from purely non-interactive causes such as natural catastrophies. Second, the greater the number of species that are present, the more frequently will competitive interactions cause extinctions. One is then able to study the species equilibrium in two basic forms, the *non-interactive equilibrium* and the *interactive equilibrium*. Wilson (1969) did this in an article entitled simply, *The Species Equilibrium*. He described the non-interactive equilibrium (Fig.2a) as existing when the population densities of the resident species are so low as to minimize the possibility of extinction by interference, such as competitive exclusion and excessive predation. The interactive equilibrium (Fig.2b), on the other hand, does include exclusions of species by other species. Interactive equilibria can be expected to occur in all but the youngest and least stable communities. Wilson (1969) and Simberloff and Wilson (1970) have hypothesized that new islands or other vacant habitats that are rapidly colonized are likely to attain a non-interactive equilibrium first and then quickly shift to an interactive equilibrium as the resident populations of individual species approach their saturation levels. Figure 3 illustrates this concept.

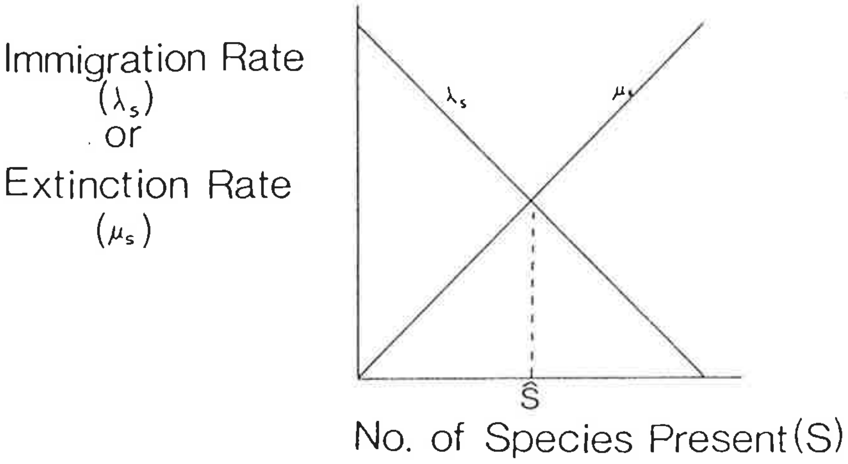
If both immigration and extinction curves are given as straight lines (i.e., non-interactive equilibrium) it is possible to formulate a relation between immigration rates, extinction rates, and the number of species at equilibrium. Examples of such relations are provided by Wilson (1969), Simberloff (1972) and the pioneering attempt by MacArthur and Wilson (1967). The equation formulated by MacArthur and Wilson states:

Figure 2

The two forms of species equilibrium model, specifying the simplest conditions necessary for (A) the non-interactive equilibrium and (B) the interactive equilibrium.

Source: MacArthur and Wilson (1967, 39)

A. Non-Interactive



B. Interactive

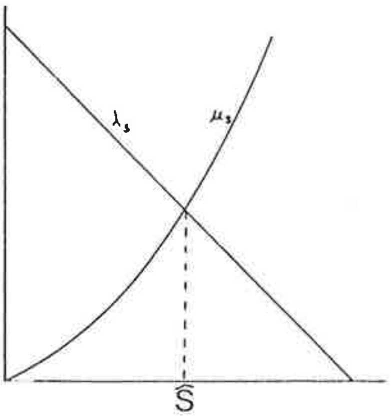
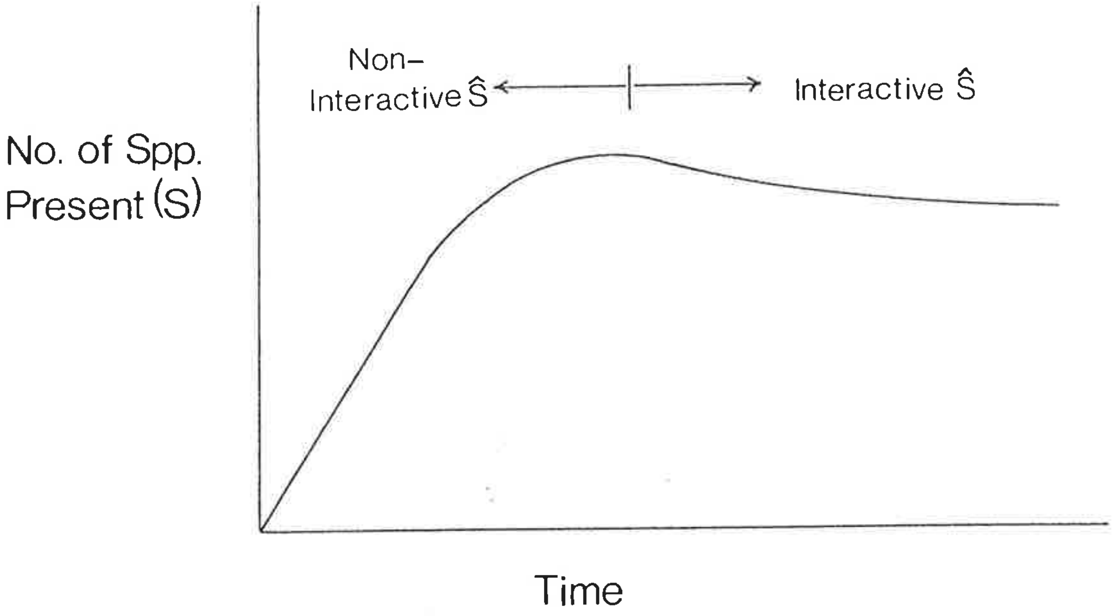


Figure 3

Generalized colonization curve with number of species present over time

Source: Wilson (1969, 42)


Non–
Interactive $\hat{S}$
Interactive $\hat{S}$
No. of Spp.
Present (S)
Time

$$\frac{d \log \hat{s}}{dA} = \frac{-dE/dA}{E+I} \qquad (1.3)$$

where $\hat{s}$ is the equilibrial number of species and E and I are the extinction and immigration rates respectively.

MacArthur and Wilson (1967) used this equation to study the effects of varying the area of an island and its distance from the source region. First, they considered the example of two islands of equal area located at different distances from the source region (Fig.4); that is, $\frac{dE}{dA}$ and A are the same for both islands. However, because the island nearest the source region has a larger immigration rate than the more distant island the denominator in equation (1.3) becomes larger and thus the absolute value of the whole expression becomes smaller. The closer island will have an increased slope for its immigration curve and hence a reduced area effect (Fig.4).

Second, MacArthur and Wilson (1967) standardized the distance from the source region (i.e., the immigration rates are equal) and varied the size of the island (Fig.5). An equation of a form similar to equation (1.3) was used. MacArthur and Wilson found the change in species number with distance to be larger when the extinction rate was larger (i.e., when the area was smaller). Consequently, larger islands should show less distance effect on a logarithmic plot (Fig.5).

MacArthur and Wilson (1967) summarize the equilibrium theory by stating that the basic model postulates immigration rate curves that fall and extinction rate curves that rise with the number of species. In addition, the model leads to the prediction that the logarithm of the number of species should increase with area more rapidly on distant islands than on near islands, and should decrease

Figure 4

Contrast between near and far archipelagos
within which island area varies

Notes: The number of species increases with area more rapidly on the far archipelago. The scale of the abscissa is in absolute number of species. However, the relationship becomes more nearly universal when the scale is made logarithmic.

Source: MacArthur and Wilson (1967, 28)

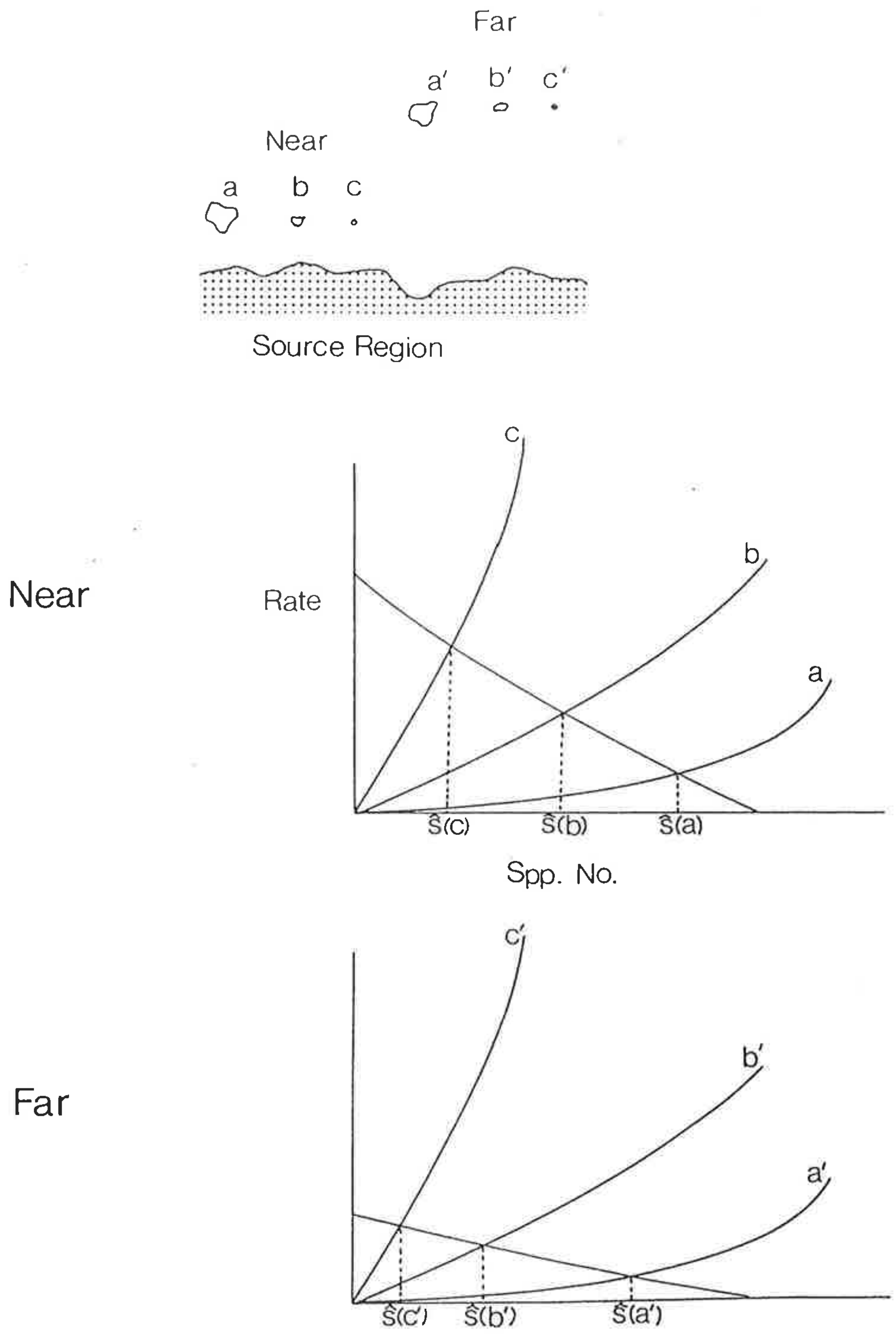
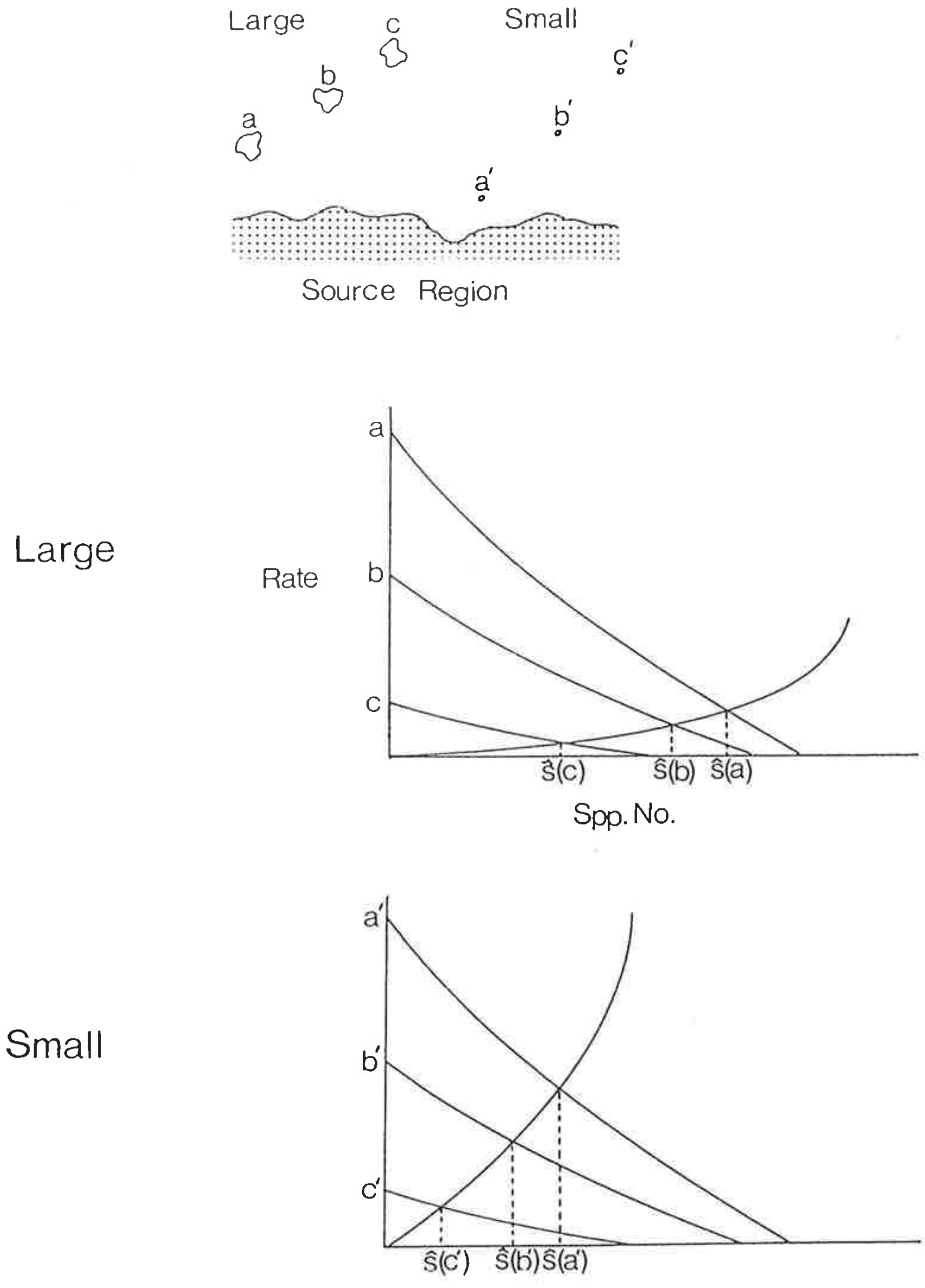

Far
a′ b′ c′
Near
a b c
Source Region
Near
c
b
a
Rate
Ŝ(c)
Ŝ(b)
Ŝ(a)
Spp. No.
Far
c′
b′
a′
Ŝ(c′)
Ŝ(b′)
Ŝ(a′)

Figure 5

Contrast between large and small islands where distance varies but not island area

Notes: The logarithm of the number of species decreases with distance more rapidly in the archipelago with small islands although the absolute number does not.

Source: MacArthur and Wilson (1967, 29)


Large
c
Small
b
c'
a
b'
a'
Source Region
a
Large
Rate
b
c
ŝ(c)
ŝ(b)
ŝ(a)
Spp. No.
a'
Small
b'
c'
ŝ(c')
ŝ(b')
ŝ(a')

more rapidly with distance on small islands than on large islands.

2. Stepping-Stone Islands

One of the major sections of MacArthur and Wilson's monograph is the role of *stepping-stone islands* as an aid to biotic exchange. A stepping-stone island is an island positioned between a source region (which may be an island) and a recipient island. MacArthur and Wilson (1967, 144) state that *"even minute islands can significantly enhance biotic exchange provided they are able to support populations of the species in the first place."* Even though a single stepping-stone island can enhance biotic exchange it should not alter the proportion of species exchanged (Fig.6a). Gilpin (1980) argues that the effect of a single island is relatively small for it chiefly serves to increase the colonization rate of species that would be successful colonists in any case.

The role of stepping-stones in colonization increases very rapidly as the dispersal power of organisms decrease. Both passive and non-passive colonizers are aided by the existence of a stepping-stone island particularly if the stepping-stone island is located nearer to the recipient island (Gilpin, 1980). For instance, a stepping-stone located in such a position effectively captures the passive colonists and relays them in greater numbers to the recipient island. Simberloff (1972) found that, in the case of the non-passive dispersers, the majority of colonists are contributed by the stepping-stone rather than the source. MacArthur and Wilson (1967, 133) even came to the conclusion that *"dispersal across gaps of more than a few kilometers is by stepping-stones whenever habitable stepping-stones of even the smallest size exist."* This

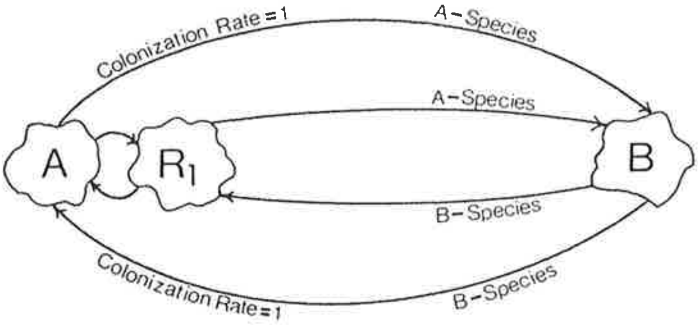
Figure 6

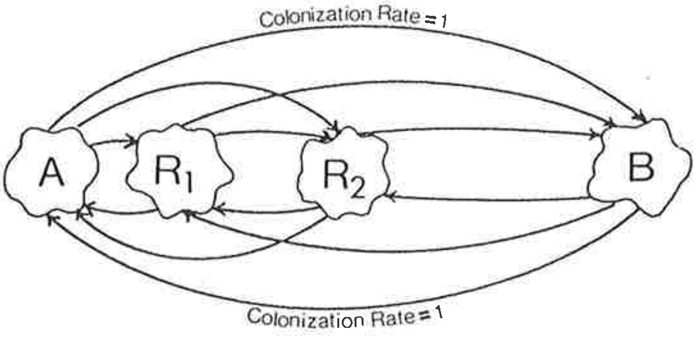
Stepping-stone islands and the fringing archipelago effect

Notes:
Above - Where only one stepping-stone (R1) exists, it contributes equally to the exchange of species between A and B, whatever its position, and neither A nor B gains an advantage.

Below - When a second stepping-stone (R2) arises and is nearer A (i.e., A acquires a fringing archipelago), A gains the advantage.

Source: MacArthur and Wilson (1967, 137)


Colonization Rate = 1
A-Species
A-Species
A
R₁
B
B-Species
Colonization Rate = 1
B-Species


Colonization Rate = 1
A
R₁
R₂
B
Colonization Rate = 1

conclusion has been supported by a study of the Melanesian ant fauna by Wilson and Hunt (1967) who determined that ant species were more likely to have arrived on Samoa from nearby stepping-stone islands than directly from Fiji or other large Melanesian sources. The role of stepping-stone islands becomes exceptionally important when the mean dispersal distance of a species is only a small fraction of the distance between the source region and the recipient island.

MacArthur and Wilson (1967) later consider what they term the *fringing archipelago effect*; that is, the positioning of two or more stepping-stone islands between two source regions. Through the use of a theoretical example they came to the conclusion that such a configuration of islands will increase the relative flow out from the source area closest to them. However, further development of hypotheses on the role of stepping-stone islands requires considerably more and improved data on the dispersal characteristics of a large number of species. Without such data, explanations of the role of stepping-stones in the enhancement of biotic exchange remain largely intuitive.

3. Species-Area Relationship

Since the work of MacArthur and Wilson a number of biogeographers have independently tested Island Biogeography Theory on islands in a wide variety of situations throughout the world. One of the leading exponents of Island Biogeography Theory is Diamond (1973, 1975a,b) who, amongst other studies, has analysed the tropical bird species of New Guinea and its neighbouring satellite islands. In his article, *Assembly of Plant Communities*, Diamond (1975a) examined the ways in which area may affect species numbers in the light of his studies of the New Guinea region. Five possible reasons were given for the effect of area on species diversity.

Diamond first stated that small islands may lack certain habitats and therefore species confined to these habitats (i.e., habitat specialists) will also be missing from such islands. This first reason, termed the *habitat diversity hypothesis*, was developed by Williams (1964) who proposed that, as the amount of area sampled is increased, new habitats with their associated species are encountered and thus species number increases with area. This hypothesis has been consistently supported (Connor and McCoy, 1979) particularly in heterogeneous environments that contain a number of different habitat types.

Second, those species with large *territorial requirements* will find that there is a threshold of island size below which a single breeding pair cannot exist, even if the island is covered with suitable habitat. Species high in the food chain, particularly the large predators, are especially hampered in this respect.

Third, Diamond stressed that, for tropical bird species in particular, available habitat resources are often *patchily distributed* in both time and space. Thus, islands of potentially suitable habitat and territorial size must carry enough food to sustain species throughout the entire twelve months of the year. Fauna on islands in the temperate regions have the problem of seasonality of food supplies, although available resources are often found in concentrated patches which allows the resources to be successfully defended against competitors. On tropical islands such defence is often not possible. A species, therefore, can persist on an island only if the area is of sufficient size to provide a year-round food supply (Diamond, 1975a).

Fourth, a population of any size runs a finite risk of extinction due to *natural population fluctuations* (Leigh, 1975). Such fluctuations may occur for a number of reasons. These include rare climatological or geological events (e.g., droughts, cyclones, volcanoes, etc.), fire, and intensive competition from a temporarily superabundant species. The risk of extinction is increased with smaller population sizes found on islands of small size.

Finally, the availability of resource *hot spots* on an island may be able to prolong a species' survival on that island for many generations past that expected. Figure 7 illustrates the concept of species survival using resource hot spots. Within an area of suitable habitat for a species not all of that area is of equal suitability for the survival of the species, there are sometimes areas of especially high utilizable resource production or hot spots. Increased island size will increase the possibility of larger or more numerous resource hot spots. These hot spots can become refuges during periods of unfavourable climate (Tolmatchev, 1972) or intense competition by another species, and may also act as an establishing point for recent immigrants thus allowing them to survive the hazardous initial phases of colonization.

A number of studies on islands have not found any simple relationship between area and species diversity. Main and Yadav (1971), for instance, discovered that islands of approximately equal size off the Western Australian coast have vastly different species numbers although there is still a general tendency for increased species numbers with increased area. Whitehead and Jones (1969)

Figure 7

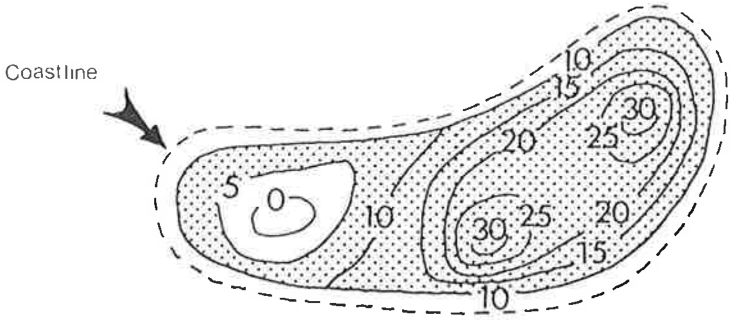
Hypothetical example of the importance of 'hot spots'

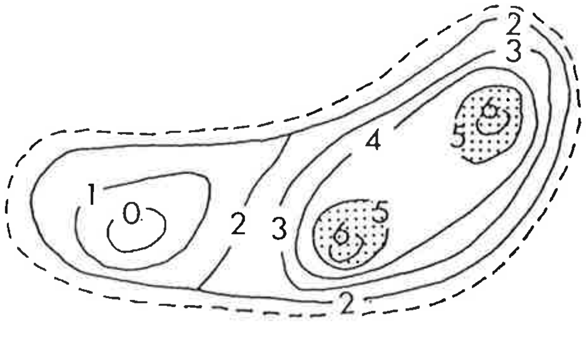
Notes: The example refers to a forest bird species on a forested island, on which the rate of production of resources utilizable by the species (R) varies locally. Contours connect points with equal values of R, in arbitrary units. The species can survive only in areas where R>5 (distinguished by stippling).

Above - situation in the absence of a competitor and during a productive year. The species occupies most of the island except near the west end. An especially productive area in the centre and another at the east end (R>25) function as 'hot spots', where steady-state population density is highest, and where the species could increase most rapidly if it were initially colonizing the island or re-expanding after a population crash.

Below - same, except that R is uniformly reduced by 80 per cent over the whole island, either because of an unproductive year, or because of an abundant competitor that utilizes the given resources in the same proportion. The species now can survive only on the two hot spots.

Source: Diamond (1975a, 369)


Coastline
10
15
30
20
25
5
0
10
30
25
20
15
10


2
3
6
5
4
1
0
2
3
5
6
2

found that for the biota of the Florida Sand Keys there is a marked inflection in the species-area curve at an area of approximately 3.5 acres (2.43ha.). They maintained that the sudden increase in species numbers after this threshold size is due to the inlets now being able to sustain a freshwater reservoir and thus salt-intolerant species, whereas only salt-tolerant species are found on inlets below the threshold size. Heatwole (1975) discovered that the species numbers of reptiles on rocky islands off eastern New Guinea are highly area dependent. However, on sand cays in the same region species number is largely independent of area. Also, studies of avifaunal communities on some islands have demonstrated that the numbers of bird species present is largely accounted for by the numbers of plant species (or habitat diversity), while area alone is a poor predictor of bird species diversity (Lack, 1973; Power, 1972). However, habitat diversity is largely determined by island area (Lack, 1969, 1973). In fact, area generally tends to be the best predictor of plant species numbers (e.g., Linhart, 1980).

Thus, the species-area relationship is not always clear-cut. However, few doubt the validity of the species-area concept, at least in its general form.

4. Species Turnover and Equilibrium

One aspect of equilibrium theory not yet mentioned is the rate of turnover of species once the dynamic equilibrium is reached. The general concensus among those studying island biogeography is that some species turnover occurs under natural conditions on islands, but the magnitude of such turnover is still open to question (Abbott and Black, 1980; Diamond, 1969; Hunt and Hunt, 1974; Jones and

Diamond, 1976; May, 1977; Mayr, 1965; Reed, 1980; Simberloff and Wilson, 1969, 1970; Terborgh and Faaborg, 1973; Vaisanen and Jarvinen, 1977).

Diamond's (1969) article, *Avifaunal Equilibria and Species Turnover Rates on the Channel Islands of California*, is probably the most widely cited paper on species turnover at equilibrium. The papers by Terborgh and Faaborg (1973) and Simberloff and Wilson (1969, 1970) are also frequently referenced. Diamond (1969) compared the number of land and freshwater birds breeding on the nine Channel Islands in 1968 with the results of a similar survey for the years up to 1917. Most of the islands were found to be in equilibrium and some species turnover was discovered. However, Lynch and Johnson (1974) and later Gilbert (1980) have critically examined Diamond's work on the Channel Islands and have cast doubts on its validity. Lynch and Johnson highlight some basic faults not only in Diamond's work on the Channel Islands but also in other works of a similar nature. First, there are problems with the definitions of colonization and extinction in the equilibrium model, particularly with respect to avifauna. Such highly mobile species do not conform well to the definitions of colonization and extinction developed by MacArthur and Wilson (1967).

The second general criticism, levelled particularly at Diamond, is that a large number of his supposed extinctions and immigrations are examples of what Lynch and Johnson term *pseudo-turnover*; that is, they are based on improper evaluation of faulty or incomplete data. Lynch and Johnson, therefore, question the validity of Diamond's claims and, in fact, go further to demonstrate that there is no reliability in supposing that the rates of turnover were significantly different from zero under natural conditions.

Probably the most detailed and thorough experiment on the process of insular colonization and species equilibrium has been provided by Simberloff and Wilson (1969,1970) and Wilson and Simberloff (1969). In order to test some of the predictions of the equilibrium theory they devised an experiment in which all the anthropods were removed from very small islands and the subsequent recolonization of the islands was monitored by frequent censuses for an initial period of one year.

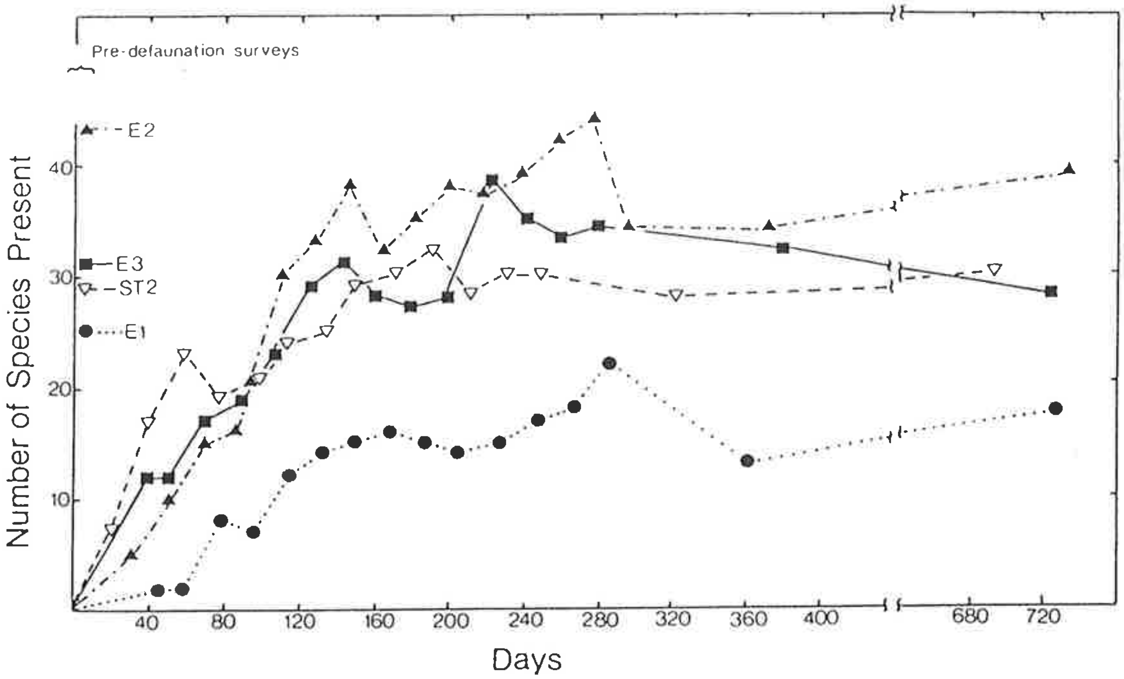
The results from the censuses confirmed the general correctness of the dynamic equilibrium model. For instance, by 300 days after defaunation, the faunas of the experimental islands, except the most distant (E1, 500 metres from nearest source region), had risen to a point slightly above the defaunation number (i.e., the non-interactive equilibrium), then fell and oscillated in the vicinity of this figure (i.e., interactive equilibrium) (Figure 8). The fact that Simberloff and Wilson discovered a dynamic equilibrium was significant for Island Biogeography Theory given the limitations of the previous studies.

Further censuses two years after defaunation found that numbers of species on the islands had changed little from the previous year, which provided further evidence that they were in equilibrium. However, E1 was still in the process of climbing towards equilibrium (Fig.8). It was also observed that the species compositions on three of the four islands appeared to be moving slowing in the direction of the original prefaunation states (Simberloff and Wilson, 1970). Simberloff (1974) summed up by stating that the communities were not just haphazard assemblages but that there is a definite

Figure <u>8</u>

The colonization curves of four small mangrove islands
in the lower Florida Keys whose entire faunas,
consisting almost solely of anthropods, were
exterminated by methyl bromide fumigation

<u>Source</u>: Wilson (1969, 41)


Pre-defaunation surveys
E2
E3
ST2
E1
Number of Species Present
10
20
30
40
40
80
120
160
200
240
280
320
360
400
680
720
Days

sequence of events.

Finally, Simberloff (1976a) conclusively demonstrated that a smaller island will support fewer species than a larger one, all other things being equal. The area effect in the experiment was seen to be a consequence of the dynamic equilibrium on any island between immigration of new species and extinction of those already present. The notion that any species is more likely to become extinct on a smaller island was supported.

5. Land-Bridge Islands and Relaxation

Whilst experimenting with the biota of islands a number of biogeographers discovered that islands could be roughly divided into two categories, namely those that were recently connected to the mainland and whose colonists need not have crossed a water gap (termed land-bridge islands) and those that have never been connected to the mainland and whose species must have colonized across a water gap (termed oceanic islands).

Mainland areas of native vegetation are known to contain larger species numbers than comparable oceanic islands because of the decreased isolation effects of crossing land rather than oceanic waters (i.e., lower z values in the species-area relationship [Equation 1.1]). Since land-bridge islands were once connected to a larger land mass Diamond (1975) and Terborgh (1974) claim that they would therefore have earned the full compliment of species for that given area before separation. This Terborgh (1974) supports with palaeobiogeographical evidence from the Greater Sundra Islands off Indonesia.

With the severing of the islands' connections to the mainland by the rising seas after the last glaciation the islands became supersaturated with species, with a resultant increased extinction rate fostered by the decreased area. The rate of extinction on the land-bridge islands is not constant. Certain species are especially prone to extinction and consistently tend to disappear first. These species are generally those that have already been mentioned with respect to the species-area relationship (e.g., habitat specialists, high trophic level, etc.). As these species disappear the resulting release of the remaining species from competition/predation tends to increase their population densities and to decrease their risk of extinction.

Dimaond (1972) has tried to calculate the *relaxation time* for a land-bridge island after its formation; *relaxation* being defined as *"the process by which islands gradually return to equilibrium as a result of a temporary imbalance between immigration and extinction"* (Diamond, 1973, 763). Diamond (1972) provides some interesting figures from the New Guinea land-bridge islands relating to relaxation rates. Diamond claims that on an island of 3000 square miles (7800 sq.kms.) about 51 per cent of the original bird species have become extinct after 10,000 years, and about 72 per cent of the survivors are widespread characteristic second-growth vegetation species rather than endemic forest species. Diamond then compares these figures with that of an island of only 56 square miles (145 sq. kms.). This island has 92 per cent of its original species extinct, and 89 per cent of the survivors are second-growth species.

Diamond (1972, 1973) and Terborgh's (1973, 1974) relaxation studies have come under heavy criticism by Simberloff and Abele

(1976a,b) and Gilbert (1980). The criticism is directed toward three main elements of their studies. First, Simberloff and Abele question the data bases from which both Diamond and Terborgh calculate their relaxation rates. For instance, Simberloff and Abele (1976b, 1032) state that:

> *". . .with one exception, the 'evidence' from land-bridge islands rests not on observation of which species were originally present, but rather on inference from the present source fauna and the species-area equation. Even were habitat differences well quantified, which they are not, the wide variance in fitting data to the standard species-area curve would make such a deductive step suspect."*

A classic example to illustrate this criticism is supplied by Soule, Wilcox and Holtby (1979) who, in order to find the initial number of species on a land-bridge island in the Malay Archipelago at the time of the island's creation, assume that the island's initial species number is equivalent to the average number of species at present occurring on the Malaysian mainland (Malay Peninsula) within an area of the same size. Not content with this generalization they proceed to state that,

> *"where sample observations are lacking, as is the case with the Malay Peninsula, an alternative method for estimating* S_0 [initial species number] *from area is possible. Since z values for continental faunas range between only 0.12 and 0.17 an approximately median value within that range (i.e., 14* [sic]*) should provide an adequate estimate for the true z-value of any continental fauna"* (Soule, Wilcox and Holtby, 1979, 263).

If one is talking of perhaps a dozen or so extinctions over such a period of relaxation (i.e., 10,000 years or less) then initial estimates established in such a gross, unscientific manner are

are certainly not acceptable. Diamond (1972,1973) and Terborgh's (1973,1974) studies are only slightly more sound.

The second criticism, expounded by Gilbert (1980), concerns the 10,000 years or so of relaxation that the land-bridge islands have undergone since the last glaciation. Gilbert (1980, 224) states that the relaxation times calculated by Diamond in particular *"are so long that by the time that the number of species on a 'supersaturated island' has reached even half way along the path towards the equilibrial number, the latter is likely to have been altered by climatic and geological changes."*

The final criticism, aimed this time specifically at Terborgh's (1974) study of the West Indian avifauna, is that such studies of the relaxation rates of land-bridge islands have tended to ignore the influences of man upon the birds and other biota of these islands. To consider present species numbers of such islands and Bali and Penang in Indonesia (Soule, Wilcox and Holtby, 1979) and the more densely populated islands in the West Indies (Terborgh, 1974), one cannot in any way discount the effects, either beneficial or adverse, of man.

One study that can pass through the above three criticisms unscathed is that of Willis (1974) on Barro Colorado Island, a 15.6 sq.km. hilltop of lowland evergreen forest that was separated from nearby forests in 1910-14 when Gatun Lake rose behind a dam to form the central part of the nearby Panama Canal (Willis, 1974; Wilson and Willis, 1975). Willis was able to study the change in bird species numbers since the formation of the island due to the availability of a number of detailed studies that had taken place in previous years. Thus, the criticism of the unreliable data base for the initial species number was more or less accounted for, although the general criticism of observer bias may still apply. This problem is acknowledged by Willis (1974) but seems to have been forgotten by many of those who have utilized his results (e.g., Diamond and May, 1976; May, 1975; Terborgh, 1974; etc.).

Willis (1974) found that, by 1970, 45 of the 208 original bird species had disappeared. Such species losses were attributed to a number of causes apart from those related to island equilibrium. These included observer error in earlier studies (see above) and the loss of second-growth or forest edge that disappeared due to natural succession on the island. This factor alone accounted for about 32 of the 45 local extinctions. Finally, high densities of monkeys resulting from the lack of predator species on the island, could have led to increased destructive levels of predation on the nests of some birds. Thus, a large number of the local extinctions of bird species on Barro Colorado could be due to other factors than the 'island effect'. However, one must not underrate the fact that some species did become extinct due to area and isolation effects and that no new species had replaced them (Willis, 1974).

6. Competitive Release

The knowledge of the roles of isolation and area in the construction of island biotas has enabled the explanation of a certain peculiarity of such biotas. It has been discovered that islands tend to have depauperate biotas with respect to comparable mainland areas. However, even though species numbers are frequently lower on islands, the densities of the species present have been known to equal or exceed those on the mainland. This, in fact, is usually due to the dominance of one or two species on an island. Yeaton (1972), when comparing bird populations on Santa Cruz Island and the Santa Monica mainland of California, discovered that although the island bird community supported only about two-thirds of the mainland community, the density of breeding pairs was no different between island and mainland. In this study two species made up 44 per cent of the total island bird population compared with 24 per cent on the mainland. Similar results were also found in the studies of Crowell (1962), Grant (1966), MacArthur, Diamond and Karr (1972) and Yeaton and Cody (1974).

This phenomenon may be due to differences between island and mainland habitats in productivity and predictability of food sources as described by MacArthur (1970) and Terborgh (1973). The more popular explanation, however, is the process termed *competitive release* (Yeaton and Cody, 1974). This process occurs on islands that are either isolated from a source region and thus do not allow the complete species source pool to colonize or those islands, such as land-bridge islands, that are undergoing a process of relaxation or species loss. In either case a certain species may find itself freed from the restraints of competition or predation that limit its expansion in other environments. This sometimes results in niche expansions and higher abundances of the island species compensating for the absence of its mainland competitors (MacArthur, Diamond and Karr, 1972). The monkeys on Barro Colorado are such an example.

7. Summary

Like all scientific theories Island Biogeography Theory is necessarily a simplified explanation of reality. This has led to various problems when researchers have attempted to use the theory alone to fully explain real world examples, even though the theory is not yet fully developed and much of its detail needs refinement. However, the broad generalizations of Island Biogeography Theory appear to be feasible explanations for at least part of the biogeographic processes operating on islands. The general acceptance of the broad generalizations has led to the application of Island Biogeography Theory to mainland habitat islands.

B. Habitat Islands

The application of Island Biogeography Theory to mainland habitat islands has been well received. Such studies have differed widely in character; most particularly in the scale of the system investigated. MacArthur (1972) has stated that Island Biogeography Theory should be relevant to small scale, local systems as well as to larger systems. Subsequent studies have proven this assertion to be correct. For instance, Island Biogeography Theory has been used to explain species distributions over whole continents (Glazier, 1980) and along peninsulas (Taylor and Regal, 1978) as well as to compare the species numbers in woodlots of less than one hectare. Larger scale studies have tended to examine the effects of isolation on speciation and endemism (e.g., Beard, 1969; Hopper, 1979; Schmitt, 1978). Smaller scale studies, on the other hand, have tended to examine the species-area relationship and species movements between patches of habitat (e.g., MacClintock, Whitcomb and Whitcomb, 1977; Galli, Leck and Forman, 1976).

Island Biogeography Theory is utilized to describe the processes that occur on and between patches of habitat that resemble islands within the bounds of land masses. Any patch of habitat isolated from similar habitat by terrain relatively inhospitable to organisms within the habitat patch may be considered as an island. These patches have been termed *habitat islands* (Kilburn, 1966; MacArthur and Wilson, 1967). The chief difference between habitat islands and true islands has been stated by MacArthur (1972, 105):

> ". . . *the latter* [true islands] *are separated by a vacuum insofar as land birds or insects are concerned, whereas mainland* [habitat] *islands are separated by other habitats filled with birds and insects. Consequently, provided that the mainland islands are not too different from their surroundings, the birds from the surroundings are able to immigrate 'onto' mainland islands more frequently and with more success than is true of immigration onto* [true] *islands. There is no vacuum to be jumped on the mainland and dispersal over land is less hazardous to a bird species than dispersal over water."*

However, it must be noted that less mobile organisms, such as many mammals, amphibians and reptiles, may not be able to traverse the surroundings of habitat islands quite so capably. To such organisms the analogy between true islands and habitat islands may consequently be more complete.

Although the number of analyses of habitat islands is not yet great, those that have been published cover a very diverse range of habitat types. Such studies include the analysis of aquatic anthropods in caves (Culver, 1970), species diversity in lakes (Barbour and Brown, 1974; Browne, 1981; Maguire, 1963), species diversity in the vascular flora of vernal pools (Holland and Jain, 1981), insect diversity on host plants (Janzen, 1968,1973; Opler, 1974; Strong, 1974) and, the distribution of freshwater mussels in coastal rivers (Sepkoski and Rex, 1973).

Two of the most noticeable habitat island studies have been conducted by Brown (1971) and Vuilleumier (1970). Brown studied the boreal mammals that inhabit montane islands scattered at irregular intervals within the Great Basin of North America. During the Pleistocene, colder climates forced the piñon-juniper woodland down approximately 600 metres below its present distribution, which was sufficient to make woodland continuous across most of the Great Basin as recently as 8,000 years ago (Brown, 1971). Subsequent extinctions, which Brown relates mainly to island size, have reduced the mammalian faunas of each habitat island. However, no colonizations by boreal mammals have occurred on the islands due to the extremely harsh intervening climatic and habitat conditions and the relatively poor colonizing ability of the mammals present (excluding bats). Brown (1971, 477) thus concludes that the mammalian faunas of the montane islands are *"true relics and do not represent equilibria between rates of colonization and extinction"*. Brown's study may alternatively be regarded as true testimony of the length of time required for relaxation of organisms on islands under relatively stable natural conditions and the absence of disturbances by man.

Like Brown, Vuilleumier (1970) also studied the island effects of isolated mountain peaks. Vuilleumier, however, concentrated on species numbers and endemism among the avifauna resident in islands of páramo vegetation in the Andes of Venezuela, Columbia and northern Ecuador (Vuilleumier, 1970). Certain similarities were found between oceanic and continental insular situations, the two most important being: a) propagules have a greater probability of reaching an island, and of colonizing it, the greater the area of that island, and b) the probability that a propagule will reach an island far away from the source area is inversely correlated with the distance from that source. Thus, Vuilleumier discovered that the mountaintops with páramo vegetation which lie near the main high Andes of Peru (source area) are quite rich in species, while the more remote and smaller islands tended to be impoverished.

1. Forest Fragmentation

In the studies examined to this point, the *effects of man* have been either negligible or ignored when analyses of true and habitat islands have been undertaken. However, the influence of man on the world's natural systems is rapidly increasing. Particularly with the advent of modern agricultural techniques and mechanization, many of the once large expanses of natural vegetation have either been totally cleared or fragmented into smaller isolated units. Curtis (1962) was one of the first fully to appreciate the effects of this process in a biogeographical context. Curtis discovered that only 3.6 per cent of the original continuous native vegetation remained in Green County, Wisconsin, after only 120 years of settlement. Those patches that remained were confined to rocky outcrops and thin-soil hilltops, that is, those parts of the landscape with the least productive potential.

It is now obvious that man is creating habitat islands which should, theoretically, have the same biogeographical characteristics as true islands or natural habitat islands. Thus, the study of forest fragments as habitat islands has become an important area of research. MacArthur and Wilson (1967) even stressed the importance of such research in the opening chapter of their monograph.

Moore (1962), in a study similar to the Curtis (1962) study, investigated the fragmentation of the Dorset-Poole Basin heathlands since 1811. Only one-third of the original cover of heathland remained and that which did remain was fragmented into one-hundred pieces of four or more hectares. Subsequent studies in the same region by Rippey (1973) and Webb and Haskins (1980) have verified Moore's initial findings. Webb and Haskins (1980) found 160 heathland sites with an area of four or more hectares, out of a total of 768 patches of heathland in the region. Moore (1962) found preliminary evidence, using a number of indicator species, that increased isolation resulting from fragmentation was already causing slight impoverishment of the fauna.

Many studies involving the analysis of forest fragments as biogeographic islands have tended to concentrate on the species-area relationship, particularly with respect to the avifauna present (e.g., McLaren, 1979). One of the most widely cited works in this field is that of Galli, Leck and Forman (1976). Forest islands ranging from 0.01 to 24.0 hectares in central New Jersey were used. These islands had to have the following characteristics: a) slope less than 10°; b) well-drained silt or clay-loam of the Penn series; c) mature trees over the entire site; d) presence of all vegetational strata; e) not recently burned; f) absence of streams; g) distant from towns, air pollution sources, and other forests; h) minimal internal environmental heterogeneity; i) presence of a mature forest edge; and j) surrounded by fields (Galli, Leck and Forman, 1976). A total of thirty forest islands fulfilled this criteria. Analysis of these islands discovered that forest size had a very significant effect on number of bird species (r=0.92), which is not surprising considering the above constraints on the selection of island sites. Bird species richness was also found to increase over the island size range of 24 hectares. One important finding of the study was that almost half of the bird species found in the larger habitat islands were considered size-dependent, requiring a large area and/or forest interior for survival (Forman, Galli and Leck, 1976).

Howe (in prep.) has recently completed an analysis of the avifauna inhabiting small *Eucalyptus* forest fragments in the Walcha district, northeastern New South Wales. This study displayed a number of well-known features of true islands. Bird species number and area were again strongly correlated and the number of new species was again found to have a logarithmic relationship with the increase in area. However, the fragmentation of the forests had not yet affected the numbers of species occurring on the remnant forest areas. This again was probably due to the choice of the avifauna for analysis. Many species were commonly observed flying between nearby habitat island sites. In a similar study Howe, Howe and Ford (in press) achieved similar results with bird species distributions on small rainforest remnants in New South Wales. Although the significance of area declined marginally, area plus the distance from a large extensive forest, which was generally no greater than four kilometres away, explained over 75 per cent of the variance in bird species numbers. Again, island sizes were very small (0.08-25 hectares) but they were still inhabited by a significant number of bird species. This led to the conclusion that patches of rainforest or rainforest-like vegetation may be inhabited by a variety of species, *at least as long as a large source area is nearby* (Howe, Howe and Ford, in press). The latter point is most important and will be considered later in this chapter.

In a study of the bird species present in 433 woods in Great Britain over a period of 8 years, Moore and Hooper (1975; Moore, 1977) discovered that the number of species present was related to the area of the wood. The form of the relationship suggested a general similarity between habitat and true islands, for it was discovered that, as with many oceanic islands, a tenfold increase in area virtually doubled the species number. Other avifaunal studies to reach similar conclusions include Whitcomb, Whitcomb and Bystrak (1977), Robbins (1979), Gilpin and Diamond (1980) and Gromadzki (1970).

Analyses of the effects of forest area on other biota unfortunately have been less numerous, due no doubt to the comparative ease of censusing bird populations compared with most other animal taxa. Among the non-avifaunal studies that have been conducted are the study of the incidence of anthropods on different sized patches of thistles (Brown and Kodric-Brown, 1977), phytophagous anthropods on juniper patches in Southern England (Ward and Lakhani, 1977) and of mammals in vegetation remnants (including reserves) in Western Australia (Kitchener, Chapman, Muir and Palmer, 1980). All these studies demonstrated a high positive correlation between area and species diversity.

However, Levenson (1976), in his thesis on the island biogeographic characteristics of isolated forested woodlots in urban areas of Milwaukee, discovered that the richness of woody plant species in the woodlots is largely a function of disturbance, whether natural or human induced. The species-area relationship was found to be an inappropriate predictor of woody species diversity. The heavy human usage of the urban lands maintains a continued state of disturbance, resulting in an increased edge effect and a higher species richness from colonization of edge species (Levenson, 1976). Tramer and Suhrweir (1975) also discovered that tree species richness on small woodlots in north-western Ohio was strongly affected by human interference. However both of these studies were on very small habitat islands. Different results may well have been obtained on habitat islands of larger size that are able to 'buffer' most disturbance effects.

2. Edge Effects

One of the major differences between true islands and habitat islands, particularly those of relatively small area, is related to *perimeter* or *edge effects*. The perimeter of true islands generally consists of either rocky headlands or sandy beaches. Both of these environments are species depauperate and are known to act as barriers to the effective colonization of many organisms (Cox, 1973). The perimeters of habitat islands, on the other hand, often contain the greatest concentration of species for a given site. Such edge effects on species diversity is a common occurrence in ecotoral situations (Ghiselin, 1975; Whittaker, 1975). When occurring between a forested woodlot and cleared or modified contiguous areas, such an ecotone is termed a *forest edge* (Ranney, 1978). Ward-Thomas, Maser and Rodiek (1977, 91) define an 'edge' as, *"that area where two or more plant communities or successional stages within plant communities meet"*. Thus edges may occur between successional stages within a woodlot.

The recognition of the importance of edges probably stems from the work of Leopold (1933) who noticed an increase in wildlife where the types of food and shelter which it requires occur in different but adjacent habitats. The theoretical importance of edges has been explored by Ward-Thomas *et al.* (1977) who also attempted to quantify edge characteristics. Detailed studies of the structure and composition of edges have been undertaken by Ranney (1978) and Wales (1972). Both studies found marked structural differences between edge and interior individuals of plant species. Edges were also found to have different plant species compositions than the interiors of the woodlots analysed.

The value of edges for biotic enrichment has become increasingly recognised over the past few decades. The importance of edges for the maintenance of bird species diversity was recognised as early as 1935 (i.e., Carpenter, 1935) and has consequently been expanded on by Johnson (1947), Martin (1960) and Taylor and Taylor (1979) amongst others. Rueger and Giles (1975) have discussed the importance of forest edges for deer populations. Forsyth and Smith (1973) found that edges provided additional food supplies for eastern chipmunks in Ontario.

Ranney (1978) has conducted one of the most comprehensive studies on the effects of edge on habitat island ecology. This study discovered that the basal-area of edge trees was about 50 per cent more than that of trees in the interiors of forested woodlots in Milwaukee. The larger edge trees produce more propagules that invade and affect forest interiors. Also affected is the dispersal of propagules exposed to dispersal vectors. Edges were seen to contribute more propagules to inter-island propagule exchange than would normally be associated with islands if edges were not considered and propagule exchange was based on interior composition (Ranney, 1978). In addition, Levenson (1976) likened a forest edge to a selectively permeable membrane screening propagule establishment, at least with respect to the attempted establishment of woody plant species after immigration. Thus the presence of edges around a forest woodlot tends to 'control' the processes of dispersal and colonization for that island, particularly if the woodlot is small. As island size increases the effect of edge decreases. The effect of edge also decreases when islands become more compact (i.e., less irregular). This point will be discussed further later in this chapter.

3. Biological Corridors and Propagule Exchange

Propagule exchange between habitat islands tends to be of a slightly different form than that experienced between true islands. It has already been noted, from the papers of Vuilleumier (1970), Galli *et al.* (1976) and other avian studies, that the isolation effects of distance on the mainland are not absolute. The degree of isolation of two habitat islands is dependent upon the nature of the intervening environment in addition to the established effect of distance. Thus, the analysis of species dispersal between habitat islands is an important prerequisite before the island nature of habitat patches can be fully comprehended.

Studies of species movements between habitat islands have tended to concentrate on the readily observable species or those that are easily captured. Thus, most of the available data concerns the mammalian and avian components of the biota. Due to sampling difficulties, the dispersal abilities of insects and vegetation between habitat islands has remained basically intuitive (Ranney, 1978).

The dispersal of organisms across suitable environmental conditions on the mainland can be very rapid, particularly when man is involved as a dispersing agent (Elton, 1958). The rapid establishment of many exotic species throughout the world testifies to the colonizing ability of many organisms (Baker and Stebbins, 1965; Anderson, 1977). However, many species, particularly native species with restricting habitat requirements, do not share such colonizing abilities at least within their own native areas. It is for these species that stepping-stone islands and other aids to dispersal become important for the continued interaction between disparate communities.

The role of stepping-stones between habitat islands is basically equivalent to their role between true islands. However, dispersal between habitat islands, particularly if the intervening distance is not too great, can also proceed along the linear stretches of vegetation that commonly occupy road verges, fencerows, gullies, etc. Such linear stretches of vegetation have been termed *biological* or *wildlife corridors* (MacClintock, Whitcomb and Whitcomb, 1977; Robinson, 1978; Sullivan and Shaffer, 1975; Kolata, 1974).

Corridors in forest areas are usually required to have an overstory similar to the remnant woodlots. However, the floristic composition need not always be the same as adjoining habitat islands although for conservation purposes this is preferable. In fact, corridors are often dominated by edge species (MacClintock *et al.*, 1977; Way, 1977; Wegner and Merrian, 1979), although they may also harbour rare or endangered species (Way, 1977). In addition, corridors preferably should be continuous from one habitat island to another. However, they need not necessarily be so and, in fact, they rarely are. A series of stepping-stones can therefore be regarded as a biological corridor for the purposes of most habitat island studies. Nevertheless, gaps of a critical size may severely limit or totally prevent the movement of organisms along stepping-stone corridors. Important variables are: a) the width of the gap; b) the nature of the gap (i.e., bitumen, water, open field, etc.) and c) the species involved. Oxley, Fenton and Carmody (1974) discovered that small forest mammals were reluctant to venture on to road surfaces where the distance between forest margins exceeded 20 metres, and wider roads were crossed almost exclusively by medium-sized mammals. In addition, it was hypothesized that a four-lane highway may be as effective a barrier to the dispersal of small forest mammals as a body of fresh water twice as wide.

A number of other studies have demonstrated the reluctance of many species, including birds, to cross an open field between forest patches, particularly if a corridor is available for movement. Rueger and Giles (1975) state that deer may not venture more than 100 metres into a clearing. Forsyth and Smith (1973) observed that eastern chipmunks avoided the open fields contiguous to a forest patch within which they were numerous. Hooper (1971) has suggested that the critical distance for the constituents of the ground flora of woodland in Monks Wood is something under 800 metres.

Wegner and Merriam (1979), however, have probably undertaken the most comprehensive study of species movements between forested woodlots. The study wood was approximately twelve hectares in size and was located just south of Ottawa, Canada. Tree species composition was dominated by beech (*Fagus grandifolia*) and sugar maple (*Acer saccharum*). The woodlot was surrounded by pasture fields, apart from a number of fencerows which emanated from it. Three other woods of varying sizes were located different distances from the main woodlot. Movements of birds and small mammals were monitored within and between the three habitats (i.e., woodlot, field, fencerow). The small mammals (i.e., mice, chipmunks) seldom moved between the wood and the adjacent fields. Nor were they ever monitored crossing the fields. Instead, the mammals were found to move freely between the wood and connecting fencerows. This led Wegner and Merriam (1979) to suggest that the fencerows provided important corridors in and out of the wood.

Birds, also, were seldom observed flying directly across open fields between woods. As with the small mammals, more species of birds were observed more frequently moving between the wood and fencerows than between any other habitat. Access to the fields was generally via the fencerows rather than directly from the wood. Bird species characteristic of open field situations tended to utilize the fencerows as singing posts and perches. Thus, the fencerows adjoining the study wood were utilized heavily by both small mammals and birds. This led Wegner and Merriam (1979, 349) to the important conclusion that *"fencerows connect the wood to the surrounding agricultural mosaic and concentrate the activity of small mammals and birds into a habitat corridor that may relieve the isolating effect of farmland surrounding the wood."* The importance of this study lies in the fact that it demonstrates empirically that existing corridors are utilized by precisely those species or life forms that are generally the focus of many conservation programmes.

Other studies have also utilized the importance of corridors for the movement of organisms between separate habitats. Prestt (1971), for instance, has stressed the importance of connections between the summer and winter habitats of the viper (*Vipera berus*) which can be separated by a number of kilometres. Robinson (1978) has commented on the significant benefits of corridors in the conservation of mammals ranging from mice to kangaroos in the Illawarra district of New South Wales. Corridors are also important breeding habitats for many species. Way (1977) has discovered that British roadside verges contain 20 of the 50 species of mammal found in the British Isles, all six reptiles, 40 of the 200 species of birds, 25 of the 60 species of butterflies, eight of the 17 species of bumble bees, and five of the six species of amphibians.

However, not all of the effects of corridors are beneficial in a conservation context. Roadside verges, in particular, pose a number of problems for the native biota. Anderson (1979) has described two of the major problems: a) traffic on the road kills relatively large numbers of wildlife (Oxley *et al.*, 1974), though the effect on the overall populations is generally minimal; and b) there is a build-up of lead and other heavy metals in roadside soils and vegetation. High levels of these metals could not only cause death or mutation of genetic stocks of plants but also of animals which are more susceptible than plants. This problem is compounded even further when it is recognised that it is the younger, fertile males which usually migrate from home areas rather than those sections of a population which contribute less to the breeding process (Hawkins, Klimstra and Autry, 1971; Stickel, 1968). Van der Zande, ter Keurs and van der Weijden (1980) have stressed that the disturbance effects of roads for certain bird species may extend for a distance of up to 1.8 kilometres for a busy highway. Therefore, roadside verges may not offer successful breeding grounds for many bird species.

Unmanaged corridors will consist of edge species, the large majority of which are exotics. Therefore, edge species may benefit more from a corridor than native species. Consequently, corridors may become avenues for the invasion of exotic species into habitat islands consisting of mainly native species. This problem is particularly acute with respect to public thoroughfares through nature reserves and the subsequent invasion of exotics via vehicles.

However, if corridors are able to aid the dispersal of native species between habitat islands in any way, the benefits for those species are great. Roff (1974a,b,1975) has demonstrated that dispersal can significantly decrease the probability of extinction, within a given time interval, of a population living in a heterogeneous environment. Roff (1975) formulated a model which demonstrated that dispersal may increase the time to extinction of a population by at least three orders of magnitude and often more.

4. The Peninsula Effect

Even given a large expanse of uniformly suitable environment for native species, species numbers may still vary if the area exhibits what is known as the *peninsula effect* (Taylor and Regal, 1978). This effect is believed to occur along natural peninsulas. Species numbers have been found to decrease along a peninsula towards the tip. For instance, Taylor and Regal (1978) discovered that the species diversity of heteromyid rodents in the Sonoran Desert portion of Baja California decreased from twelve at the base of the peninsula to only two at the tip. The peninsula pattern has been tentatively explained by the *extinction-recolonization model* where increasing distance from the mainland decreases the probability of recolonization by a species after local extinctions. However, Taylor and Regal's (1978) study is the only one presently available (with an accurate data base) that describes the biogeographic effects of peninsulas on species diversity. More evidence is required to validate this effect, particularly along peninsulas of smaller size.

C. Nature Reserves

Undoubtably, the most prominant application of Island Biogeography Theory, particularly since the mid-1970's, has been its application to the evaluation of the conservation potential of nature reserves. Biogeographers have utilized their experience with both true islands and habitat islands to examine the probable implications of varying reserve size, shape and juxtaposition. One of the pioneering papers devoted to this application was that of Diamond (1975b). In this paper Diamond derived six geometric principles for the design of nature reserves (derived from Island Biogeography Theory). Figure 9 summarizes these principles. An attempt will be made to critically analyse each of these principles using the research results discussed in the preceding sections of this chapter.

1. Principle 1

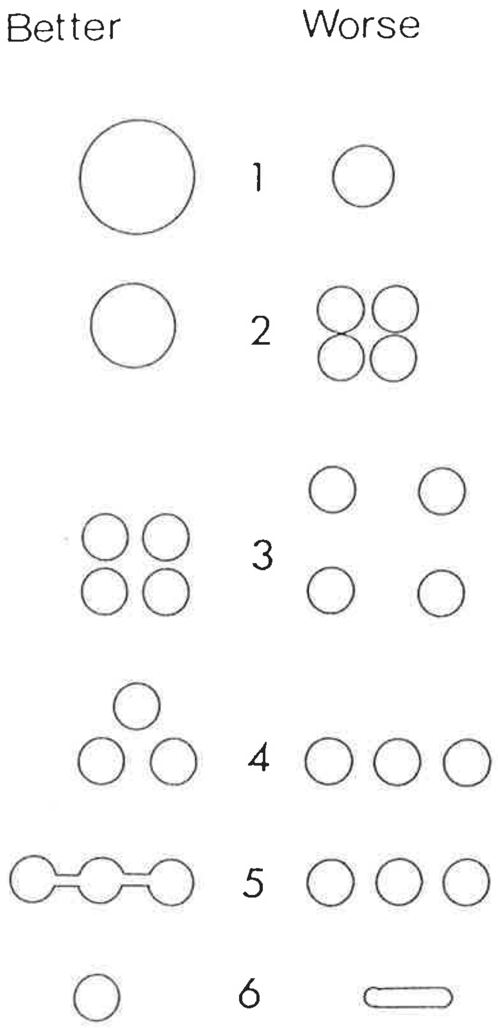
The first principle, that a larger reserve is better than a

Figure 9

Geometric principles for reserve design

Notes: In each case species extinction rates will be lower for the reserve design on the left than for the reserve design on the right.

Source: Diamond (1975b, 143)


Better
Worse
1
2
3
4
5
6

smaller reserve within a homogeneous environment, is almost unanimously acknowledged by biogeographers and ecologists. However, one must justify what the term 'better' implies in the context of conservation. Diamond (1975b, 144) states that the larger reserve is better because it *"can hold more species at equilibrium, and will have lower extinction rates"*. Thus, a better reserve is one which will retain a larger number of species over a long period of time. At the time of their designation, smaller reserves may hold more species. However, subsequent extinction rates related to island size should reduce species numbers below that of larger reserves. Studies which have demonstrated that, in a relatively homogeneous environment, a larger reserve does hold more species than a smaller reserve, include those involving the number of native lizards and mammals in wheatbelt nature reserves in Western Australia (Kitchener, Chapman, Muir and Palmer, 1980; Kitchener, Chapman, Dell, Muir and Palmer, 1980) and species numbers of higher plants in twelve reserves in Yorkshire (Usher, 1973). Examples can also be found where the species-area relationship does not hold (e.g., Miller and Harris, 1977). However, this tends to occur only in non-homogeneous environments or where active management has had some effect on species numbers, overriding the general species-area relationship.

2. Principle 2

It is the second principle, more than any other, that has caused the greatest debate amongst those island biogeographers wishing to apply their theoretical and practical knowledge to reserve design. The second principle, as stated by Diamond (1975b, 144), is that *"given a certain total area available for reserves in a* homogeneous habitat, *the reserve should generally be divided into as few disjunctive pieces as possible*" (emphasis mine). This viewpoint has been supported by the majority of researchers (e.g.; Diamond, 1975b,1976; Diamond and May, 1976; Faaborg, 1979; Nilsson, 1978; Sullivan and Shaffer, 1975; Terborgh, 1975,1976; Whitcomb, Lynch, Opler and Robbins, 1976; Williamson, 1975; Wilson and Willis, 1975; etc.). However, other studies have noted that a number of smaller reserves may be more valuable than a single large reserve (e.g.; Higgs, 1981; Higgs and Usher, 1980; Hooper, 1971; Simberloff and Abele, 1975a,b; etc.). These latter authors have argued that there has been too much reliance upon the *species-area equation* (equation 1.1) which alone does not support either of the two contrasting theories. Higgs and Usher (1980) noticed that, although not formalized, the species-area relationship may favour the setting up of several smaller reserves, depending on the proportion of species that occur on each reserve. That is, in a *heterogeneous environment* two disparate reserves of size (x) may well contain more species than if there was only one reserve present of size ($2x$) (Higgs, 1981). Gilpin and Diamond (1980) also commented that a division in twos produces increased species diversity. However, one may go to extremes and compare two smaller reserves located almost anywhere with a reserve of their combined size just to prove this argument, and to a degree some authors have.

Hooper (1971) was among the first to criticize the already accepted preference for one large reserve. Hooper's (1971) argument was based on the fact that, with an increase in the area of a reserve by a factor of ten, the number of species present will approximately double. Therefore, a series of small reserves, *each of a different* *habitat type*, appear to be better in terms of total number of species conserved.

Other arguments that favour a series of smaller reserves include the fact that many scattered reserves have the advantage over a single large reserve that 'not all of the eggs are in the one basket' (May, 1975). It is argued that *environmental catastrophies* may well cause extinction if all of the land conserved is united in one reserve but would be inconsequential in one of a network of small reserves (Simberloff and Abele, 1976a). In addition, many scattered reserves are less susceptible to epidemiological disasters (Diamond and May, 1976; May, 1975). Numerous smaller reserves may also favour the survival of a set of *vicariant species* by preventing competitive interaction which may otherwise have excluded all but one from a single reserve (Diamond, 1975b; Simberloff and Abele, 1976a). Finally, certain *edge species* will prefer several smaller reserves rather than one single large reserve of equal total area due to the consequent increased perimeter-to-area ratio (Diamond and May, 1976).

However, each of these arguments had already been accepted as valid by those authors proposing the alternative theory. These authors regard the above arguments as important only in the short term and/or of less significance than their own alternative arguments. Probably the major argument with respect to the larger island view is that *species should be weighted not just counted* (Diamond, 1976). That is, maximization of species diversity should not always be the primary aim of nature conservation. Conservation efforts should often be focused on those species with low dispersal abilities, with high incidence functions (i.e., large area requirements) or those that are most threatened by human disturbance. A number of smaller reserves may hold such species at the time of the reserves' designation but will probably lose these species at the expense of more vigorous exotic or edge species after only a relatively short period of time. Numbers of native species may 'relax' toward a lower equilibrium level, as suggested from studies on land-bridge islands. However, species diversity may not decrease and, in fact, may even increase with the invasion and subsequent colonization of exotics. Numerous studies have demonstrated that the species numbers of native species will decrease in relatively small reserves[1], although the rates of the relaxations have varied between studies (e.g., Borner, 1977; Gochfeld and Keith, 1977; Leck, 1979; Miller, 1978; Miller and Harris, 1977; etc.). Those species that have become extinct have been precisely those with the requirements cited above. Thus, Diamond (1976, 1028) has stressed that:

> *". . .as a result of this differential susceptibility of species to extinction in isolated populations, small refuges or islands mainly lose the sedentary species of mature habitats that are most threatened by human activities, and retain the rapidly dispersing successional and edge species that need no protection."*

In addition, particularly in highly developed countries, scattered reserves remain *"the only redoubts for species that are unable to adapt to degraded habitats"* (Terborgh, 1976, 1029). The alternative strategy of smaller reserves generally relies on the existence of a large source region nearby to generate high propagule invasion rates and thus offset the higher rates of extinction (Simberloff and Abele, 1976a). However, in instances where there is no outside source area

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[1] The scale of these reserves will vary with different habitats. In the tropics a small reserve may well be in the order of thousands of hectares, whereas in the temperate zone an area of only tens of hectares would be considered small.

and thus no large influx of propagules to offset extinction, large reserves, if they exist, effectively become the source areas for surrounding woodlots and small reserves. Thus, logic calls for a strategy of minimizing extinctions. This is more effectively achieved through the construction of larger reserves.

Diamond and May (1976) have stressed that even though a single large reserve may be designated, the effective area of the reserve may be halved (if it is bisected by a major road or power line) for those species that are blocked by such dispersal barriers. The construction of such disturbance corridors also decreases the area of reserves that would otherwise be buffered against outside influences (i.e., core areas). The importance of core or 'wilderness' areas is becoming increasingly recognised by park planners as necessary areas for the conservation of many sedentary species (e.g., Crossen, 1979). Large reserves with minimal internal disturbance are therefore necessary to *"minimize the pressures of predation, parasitism and competition exerted by species abundant in the disturbed areas surrounding the reserve"* (Whitcomb *et al.*, 1976, 1031).

The argument against the construction of few large reserves based on the saying 'all your eggs in one basket' does not necessarily have to hold. Pickett and Thompson (1978, 27) for instance, have stated that the design of nature reserves should be based on *minimum dynamic area*, which is *"the smallest area with a natural disturbance regime which maintains internal recolonization sources and hence minimizes extinctions"*. The determination of minimum dynamic area should be based on the knowledge of disturbance generated patch size, frequency, and longevity, and on the mobilities of the species being preserved (Pickett and Thompson, 1978). Thus, a large reserve which fulfills this requirement will not only hold more native species over a longer time span than numerous smaller reserves, but when a catastrophy occurs will allow more native propagules easier access for recolonization of the devastated area.

Even though the designation of several smaller reserves seemingly may be a more logical method for conserving vicariant species, such species have been known to coexist over ecological time periods (Odum, 1971; Pianka, 1975). In fact, Pianka (1975) has stated that niche overlap need not necessarily lead to competition unless resources are in short supply and, with a surplus of resources, niches could presumably overlap completely. Thus, a larger reserve, with increased resource availability could well contain vicariant species for long periods of time.

Whitcomb *et al.* (1976) have stressed that a major argument against fragmentation of our rapidly disappearing large areas of relatively undisturbed habitat is the fact that the process is, for all practical purposes, irreversible. However, Higgs (1981) has replied that if smaller reserves are reasonably far apart and not included in a single large reserve, the destruction of any of these reserves is also irreversible, and criticises Whitcomb *et al.* (1976) along these lines even though they were stressing something entirely different. In fact, this appears to be a common problem within the field of island biogeography. Numerous authors, particularly those arguing for numerous small reserves appear not to have read the alternative arguments with sufficient care.

It can be argued that the construction of large reserves is based on insufficient theoretical knowledge and inaccurate data bases from many of the classical island biogeographical studies (e.g., Diamond, 1969; Terborgh, 1973; Willis, 1974). This argument is valid but the fact that: a) extinctions do occur on nature reserves; b) different birds, mammals and reptiles require different minimum insular areas for survival; and c) population numbers do vary dramatically over short time periods (e.g., Myers, 1972), clearly indicates the need for large reserves. In fact, common sense suggests that we designate large reserves. Small reserves may be necessary to conserve isolated valuable ecosystems (Helliwell, 1976) but their long-term survival depends upon the existence of large 'source' reserves in the same region. In addition, small reserves, unless connected by a network of corridors, do not allow any room for expansion of the rare or important species, thus effectively keeping their levels critically low.

3. Principles 3 and 4

Diamond's (1975b, 144) third principle of reserve design is that *"if the available area must be broken into several disjunctive reserves, then these reserves should be as close to each other as possible, if the habitat is homogeneous."* Increased immigration rates between reserves will occur with the shortening of the intervening distances. This is particularly important for smaller reserves which will probably have the greatest natural extinction rates, and thus are in more need of an influx of native propagules to maintain a relatively stable community structure. This principle leads readily into the next which states that *"if there are several disjunctive reserves, these should ideally be grouped equidistant from each other rather than grouped linearly"* (Diamond, 1975b, 144). Such a grouping minimizes inter-island distances for all of the reserves, allowing recolonization to occur from an increased number of potential source areas. However, in the linear arrangement the terminal reserves are relatively remote from each other, thus effectively limiting their potential source areas for those species with poor colonizing abilities to the one contiguous reserve in the sequence, unless the distances between the reserves are short enough to allow the central reserve to act as a stepping-stone.

4. Principle 5

The fifth principle suggests that *"if there are several disjunctive reserves, connecting them by strips of the protected habitat may significantly improve their conservation function at little further cost in land withdrawn from development"* (Diamond, 1975b, 144). This principle has been generally accepted by island biogeographers as one of the most important principles in the design of a system of nature reserves (e.g., Diamond and May, 1976; Kolata, 1974; Robinson, 1978; Simberloff and Abele, 1976a; Sullivan and Shaffer, 1975; etc.). For instance, May (1975, 177) states that:

> *". . .one way to raise the equilibrium number of species in any one such smaller park is to raise the immigration rate into it. This can be done by judicious juxtaposition of the scattered parks* [Principle 4] *or by providing corridors or stepping-stones of natural habitat between them."*

Evidence has shown that movements of species do take place along corridors and, in addition, if a corridor between two reserves is substantial enough it may well unite the connected reserves into one unit of increased proportions (e.g., Anderson, 1980). If a set of small reserves are designated to conserve a sedentary species with a restricted habitat preference, the existence of corridors between the reserves may significantly increase dispersal rates over what would otherwise be negligible values (Diamond, 1975). However, corridors should be as direct as possible. If too long or indirect the effectiveness of the corridor will diminish due to the peninsula effect and the fact that corridors are generally not favourable for the long-term survival of many native species.

5. Principle 6

The final principle is that *"any given reserve should be as nearly circular in shape as other considerations permit, to minimize dispersal distances within the reserve"* (Diamond, 1975b, 144); that is, one should aim to minimize the area-to-perimeter ratio of a reserve (Diamond and May, 1976). This principle rests on five factors taken from true island and habitat island studies. First, *dispersal distances* within reserves should be minimized as much as possible to allow gene flow between populations within reserves, particularly rare, habitat specializing, or sedentary species. The second factor, closely related to the first, is that reserves should try and avoid *peninsula effects* whereby *"dispersal rates to outlying parts of the reserve from more central parts may be so low as to perpetuate local extinctions, thus diminishing the reserve's effective area"* (Diamond and May, 1976, 185). Unfortunately, this factor has not yet been empirically tested and remains basically intuitive, relying on the evidence collected by Taylor and Regal (1978) and land-bridge studies. Species dynamics on peninsula areas of nature reserves may well be due to factors other than those proposed by the extinction-recolonization model. However, from the information collected by biological corridor and stepping-stone island studies this model may well be applicable.

The third reason why reserves should be as compact as possible is to minimize the *edge effects* of the perimeter areas. The studies of Levenson (1976) and especially Ranney (1978) have demonstrated the significance of edges on forest island dynamics. With edge species usually capable of surviving in alternative habitats (e.g., roadside verges, gardens, refuge dumps, etc.) and in little danger of extinction, efforts should be directed toward the conservation of interior species. A minimization of edge effects will also allow a greater proportion of interior propagules to contribute to colonization of the reserve and dispersal to other reserves. Thus, a minimization of the area-to-perimeter ratio in a reserve of reasonable size[2] and little internal disturbance maximizes the chances of survival of interior species.

The fourth argument follows from the third in that significant *core* or *internal areas* should be created or maintained. The more compact the reserve the more core area is produced for a reserve of a given size. The final consideration is that a compact reserve minimizes the *disturbances* such as herbicide drift (Duffey, 1974), grazing and noise from adjacent modified land for those interior species most threatened by disturbance. Obviously, this principle is of direct importance in the design consideration of nature reserves.

6. Summary

The significance of Diamond's (1975) principles is evident. Nature reserves cannot be considered as isolated entities. Neither

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[2] If a reserve is too small it may only hold edge species.

can a collection or aggregate of nature reserves be considered as a whole without due regard for the intervening environments and the processes involved in species colonization and extinction. Even with intensive reserve management, lack of regard for the contiguous environments may well lead to the collapse of the reserve as a viable conservation unit (e.g., Kushlan, 1979; Myers, 1972). In addition, Miller (1978, 191) has stated that present conservation practice in most instances is almost exclusively based on *"the static view of natural communities, and is directed towards preservation of the structural components without due recognition of underlying dynamic processes"*. The application of Island Biogeography Theory to nature reserve design provides planners with a means of analysing and understanding many of the dynamic processes operating within and between reserves.

However, some authors have expressed concern about seemingly careless applications of general principles from Island Biogeography Theory to actual planning practice without fully understanding the idiosyncracies of a particular area (e.g., Higgs, 1981). For instance, Diamond and May (1976, 185) state that:

> *". . .as for most generalities, such design principles are useful, but must be applied with caution in any one specific instance. There are no substitutes for a painstaking study of extinction and immigration rates, of incidence functions and assembly rules, for each particular conservation unit."*

Also, Kushlan (1979), amongst others, has noted that biogeographic principles derived from true islands are not directly transferable to continental reserves owing to intrinsic differences in the dynamic characteristics of the two types of systems. Especially, it is recognised that area plays less of a role in determining species number on continents than on islands. The hypothesized species equilibrium of nature reserves after isolation also appears to be of a different form than that on true islands and may, in fact, be a higher value than that prior to isolation. Most differences, though, appear to stem from the large number of exotic or edge species that may invade the reserves from adjacent modified sources, a process which does not occur on true islands. However, conservation efforts should be directed toward the native species remaining in the reserves and, if one were to consider only these species, then the analogy between the processes operating on true islands and nature reserves becomes much closer. Finally, although intensive ecological studies are recommended for every area with conservation value, it is often unlikely that such studies will be undertaken, at least in the near future. Thus, other considerations need to be examined that will provide nature reserve planners with a low cost, reasonably accessible, instructive means of adjudging the relative merits of individual nature reserves or a network of such reserves. The application of Island Biogeography Theory to the nature reserves is such a means.

D. Aims

The basic aim of this thesis is to develop techniques for measuring various biogeographic attirbutes of habitat islands that are applicable to established/proposed nature reserves. To assist in the development of these techniques, use has been made of the nature reserves and intervening forest vegetation of the Mount Lofty Ranges, South Australia.

The Mount Lofty Ranges provide an ideal setting for the development of the techniques as they constitute a readily-observable bounded area which contains a variety of environmental conditions from little-modified native forest to urban settlement. The reserves within the Ranges also offer the variety of biogeographic attributes required for effective analysis of the proposed techniques.

II. TECHNIQUES FOR MEASURING BIOGEOGRAPHIC ATTRIBUTES

A. Previous Studies

For both habitat and true islands, two of the most important biogeographic attributes are their degree of isolation and shape. A number of biogeographic studies have formulated measurements for an island's degree of isolation (e.g., Kent and Smart, 1981; Power, 1972; Vuilleumier, 1970; etc.). These measurements tend to rest solely on the absolute distance between a given island and either the nearest other island(s) or a hypothesized source region. Vuilleumier (1970), in fact, developed four measures of isolation for the montane habitat islands in the northern Andes: a) distance from source (i.e., shortest map distance); b) distance to the nearest island; c) distance to the nearest island to the south (i.e., towards source area), and; d) distance to the nearest large island (more than 200 square kilometres). Such measurements are adequate for true islands and even montane habitat islands but have serious faults when applied to the complex pattern of vegetation patches and corridors that occur in a great many areas. The presence of an intervening corridor between two habitat islands can markedly decrease the effect of distance as an isolating agent. Thus, an alternative measurement of isolation is required for situations such as that occurring within the Mount Lofty Ranges.

Human geographers have long been concerned with the measurement of spatial attributes within the human environment. One technique that has been extensively used to measure interactions over a distance is termed *network analysis*. Studies that have utilized network analysis, however, have not directly concerned themselves with isolation; instead, they have analysed accessibility or connectivity. These terms can be regarded as the opposites to isolation and thus, by measuring accessibility, a measure of isolation is inherently contained. For example, increased accessibility is equivalent to decreased isolation. Thus, an avenue is opened for the application of network analysis techniques within island biogeography.

Shape analysis in biogeographic studies has only been examined in a qualitative manner (e.g., Principle 6, Diamond, 1975). There has been no technique devised by biogeographers that adequately measures shape. Shape analysis, however, has been treated in depth within cartographic literature and numerous techniques are available for the comparison and measurement of shape.

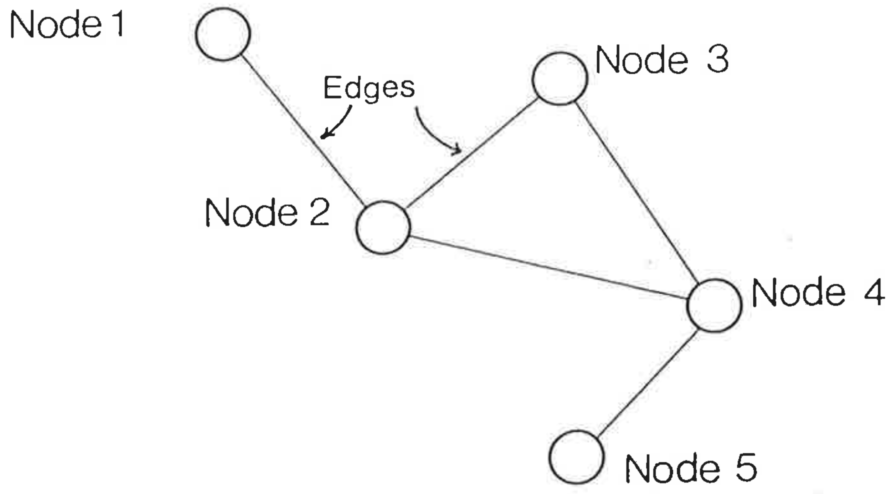
B. Network Analysis

The following is a review of the more widely accepted techniques devised for the analysis of network structure. A network consists of nodes and edges where the nodes, in geographical studies, are generally concentrations of a certain item (e.g., cities, goods yards, information centre, etc.) and the edges are the routeways or means of exchange between the concentrations (e.g., roads, rail links, telephone connections, etc.). Nodes can also be regarded as intersections of edges and this definition is often used in graph theoretic problems. Figure 10 illustrates a typical network. In this form a network is abstract. However, in the geographical applications a network is an illustration of some reality, which is referred to by mathematicians as the embedding of a network in another space (Tinkler, 1977).

The representation of geographical phenomena as a network allows

Figure 10

Typical network showing nodes (5) and edges (5)


Node 1
Edges
Node 3
Node 2
Node 4
Node 5

numerous analyses to be conducted on the phenomena which would otherwise have been impossible. One of the major areas of analysis of network structures concerns the degree of *connectivity* or *accessibility* of a node within a network. Some of the more basic techniques available for describing a node's relationship within a network and the general structure of networks have been provided by Kanksky (1963). These techniques have subsequently been discussed by Alao (1973), James, Cliff, Haggett and Ord (1970), Leinbach (1976) and Tinkler (1977). Kanksky (1963) developed a number of simple indices which are all functions of the number of nodes, edges and subgraphs within a network. These indices, due mainly to their simplicity, often fail to distinguish adequately between networks that have markedly different structures. Therefore, most network studies have moved away from such simplified measures and have utilized techniques with greater discriminatory and operational powers.

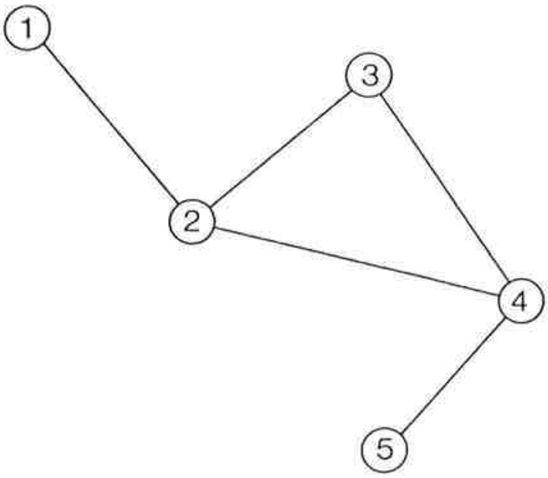
1. Matrix Operational Procedures

One of the most powerful methods available for the analysis of networks is the use of matrix operational procedures. To utilize these procedures a network has to be transformed into an *adjacency* or *connectivity matrix*. For any network of n nodes there is an equivalent $n \times n$ matrix. Relationships (i.e., edges) between the nodes are usually expressed as integers within the matrix. In the most simplified cases the presence of a linkage between two nodes is expressed as a 1 and the absence of a linkage is expressed as a 0. For general networks or graphs $Aij = Aji$ in all cases and the matrix is said to be symmetric. Figure 11 provides a simple example of the above operation. Conventionally the diagonal of the matrix is

Figure 11

Matrix representation of a network

Notes: The degrees of the nodes are shown as a vector



$$\underline{A} \;=\; \begin{array}{r|ccccc} & 1 & 2 & 3 & 4 & 5 \\ \hline \text{Node 1} & 0 & 1 & 0 & 0 & 0 \\ \text{Node 2} & 1 & 0 & 1 & 1 & 0 \\ \text{Node 3} & 0 & 1 & 0 & 1 & 0 \\ \text{Node 4} & 0 & 1 & 1 & 0 & 1 \\ \text{Node 5} & 0 & 0 & 0 & 1 & 0 \end{array} \longrightarrow \begin{pmatrix} 0 & 1 & 0 & 0 & 0 \\ 1 & 0 & 1 & 1 & 0 \\ 0 & 1 & 0 & 1 & 0 \\ 0 & 1 & 1 & 0 & 1 \\ 0 & 0 & 0 & 1 & 0 \end{pmatrix} \begin{array}{l} \Sigma=1 \\ \Sigma=3 \\ \Sigma=2 \\ \Sigma=3 \\ \Sigma=1 \end{array}$$

expressed as 0's. The matrix format is most beneficial for extremely large and complicated networks where visual comprehension is awkward.

Most of the matrix operations that are required for network calculations concern only matrix addition and multiplication. Tinkler (1977) provides an excellent summary of these operations which should be understood in order to fully comprehend the following discussion. This article is also the basic source from which the terminology for the network operations has been taken.

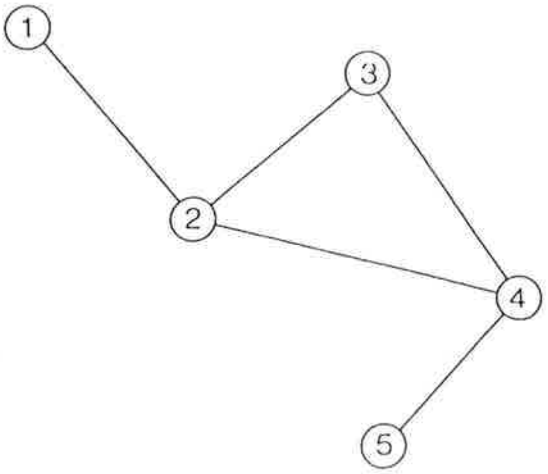
The most basic matrix measure of accessibility is obtained directly from the connectivity matrix. A summation of the individual rows of the matrix produces a vector of values. Each row sum equals the total number of direct linkages from a given node to the set of all other nodes in the network. This sum is defined as the *degree* of a node (Taaffee and Gauthier, 1973). Thus, for example, the degree of node 2 in Figure 11 is equal to 3. However, the degree of a node has serious limitations as a measurement of accessibility, for accessibility within a network usually involves more than just the direct connections between nodal pairs - indirect connections are also of major importance.

The powers of the adjacency matrix $\underline{A}$ provide multiple linkage connections between nodes within a network. The matrix $\underline{A}^n$ (i.e., a matrix $\underline{A}$ to the power n) contains entries showing the number of n-edge paths over which the ith node may be reached from the jth node. Figure 12 illustrates this procedure for the working example in this chapter. Some of the edges will be used more than once from path to path and, with larger values of n, some of the paths may become highly circuitous (Stutz, 1973). To take into account all possible pathways

Figure 12

Powers of the adjacency matrix (A)

Notes: The two most distant nodes, Nodes 1 and 5, are connected after three iterations; thus, the diameter of the network is three.



$$\underline{A} = \begin{pmatrix} 0 & 1 & 0 & 0 & 0 \\ 1 & 0 & 1 & 1 & 0 \\ 0 & 1 & 0 & 1 & 0 \\ 0 & 1 & 1 & 0 & 1 \\ 0 & 0 & 0 & 1 & 0 \end{pmatrix} \qquad \underline{A}^2 = \begin{pmatrix} 1 & 0 & 1 & 1 & 0 \\ 0 & 3 & 1 & 1 & 1 \\ 1 & 1 & 2 & 1 & 1 \\ 1 & 1 & 1 & 3 & 0 \\ 0 & 1 & 1 & 0 & 1 \end{pmatrix}$$

$$\underline{A}^3 = \begin{pmatrix} 0 & 3 & 1 & 1 & 1 \\ 3 & 2 & 4 & 5 & 1 \\ 1 & 4 & 2 & 4 & 1 \\ 1 & 5 & 4 & 2 & 3 \\ 1 & 1 & 1 & 3 & 0 \end{pmatrix} \qquad \underline{A}^4 = \begin{pmatrix} 3 & 2 & 4 & 5 & 1 \\ 2 & 12 & 7 & 7 & 5 \\ 4 & 7 & 8 & 7 & 4 \\ 5 & 7 & 7 & 12 & 2 \\ 1 & 5 & 4 & 2 & 3 \end{pmatrix}$$

in a network, the matrices $\underline{A}$, $\underline{A}^2$, $\underline{A}^3$, $\underline{A}^4$, etc., can be added, as follows:

$$\underline{S} = \underline{A} + \underline{A}^2 + \underline{A}^3 + \underline{A}^4 + \underline{A}^5 + \ldots\ldots \qquad (3.1)$$

where $\underline{S}$ is termed the *accessibility matrix* (Tinkler, 1977). All nodes will have a path connection to all other nodes when the value n is equal to the *diameter* of the network (i.e., the minimal number of links between the two most distant nodes in the network). For example, the two most distant nodes in Figure 12, nodes 1 and 5, are first connected when the matrix $\underline{A}$ is multiplied to the third power since they are three linkages apart. Thus, the diameter of the network is three.

However, the process as it stands has a number of deficiencies. For instance, redundancies occur in the accessibility matrix $\underline{S}$ due to the largely circuitous nature of many of the paths between nodes in the higher matrices. In addition, because the higher matrices contain much larger numbers than the lower matrices they dominate the total sum. The excessive weight of the higher matrix sums in $\underline{S}$ is contrary to our geographical expectations, where we expect a decreasing influence with increasing distance, not an increasing one (Tinkler, 1977, 28).

The latter problem has been solved to a degree by the introduction of a scalar weight into the summation. The most commonly used is of the form

$$\underline{S} = r\underline{A} + r^2\underline{A}^2 + r^3\underline{A}^3 + \ldots\ldots + r^n A^n \qquad (3.2)$$

where r is required to be positive and less than one (Hay, 1973) in order to provide attenuation. Stutz (1973) discusses the implications of varying the scalar weights on the resulting node accessibilities of a network. Optimally the selection of a scalar should reflect the slope of the distance decay function for movement in a network. However, other considerations usually dominate the choice of the weight. For instance, the choice of the principle eigenvalue has been recommended (Tinkler, 1972, 1974, 1977). Also, since the choice of r is made to counteract the ascending tendency of the summation, the chosen weight should be less than the inverse of the largest marginal sum of $\underline{A}$. In Figure 11 the largest marginal sum of the matrix $\underline{A}$ is 3 and thus the weight selected should be less than 1/3 to provide attenuation. It is clear that r^n tends toward zero and thus the summation is, for all practical purposes, finite. The most cited example that utilizes this technique is Garrison's (1968) study of the connectivity of the Interstate Highway System in the Southeastern United States. Garrison transformed the highway system into a network of 45 nodes and 62 linkages. Another example is Pitts' (1965) study of the thirteenth century Russian trade routes.

2. The Shortest Path Technique

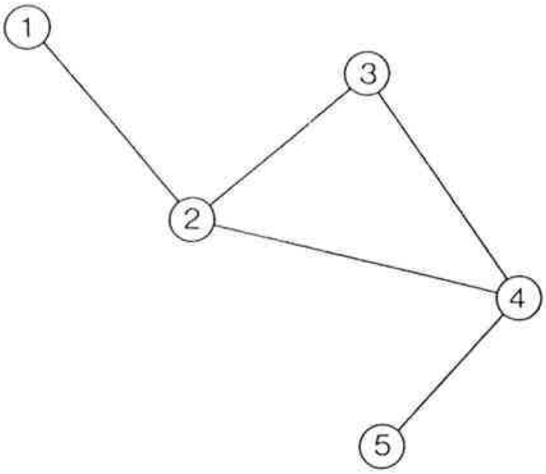
The scalar weight technique, however, still has a number of inherent problems and complexities (Hay, 1973; Taaffee and Gauthier, 1973; Werner, 1968). Therefore, the present study will use a technique devised by Shimbel (1951, 1953) and later modified by Reed (1970) and Taaffee and Gauthier (1973). This technique requires the derivation of the *shortest path matrix*, $\underline{D}$, which is the lowest power of the connectivity matrix for which all entries have positive values. To arrive at the shortest path matrix from the initial connectivity matrix the identical matrix summation in equation (3.1) is employed.

For the techniques previously considered the importance of a connection between two nodes is inversely related to the number of linkages involved in the connecting path. However, the shortest-path technique is concerned with the length of the shortest path between a pair of nodes, thus effectively eliminating the problem of redundancies in the computations. Accessibility is computed in terms of the distance between nodes (Taaffee and Gauthier, 1973). Quite simply, to determine the shortest paths in a network all that is required is to note after each iteration of the adjacency matrix the power at which any new non-zero elements occur. If there are any new non-zero elements the power of that matrix is entered into the appropriate row and column of the new matrix D.

Figure 13 illustrates this procedure for our working example. For instance, in the matrix D2 the value 2 is recorded in the appropriate cells, indicating that these indirect connections occurred for the first time when the adjacency matrix was squared. The procedure is halted when all the cells contain a positive integer, apart from the main daigonal. The final entry in the matrix D is equivalent to the diameter of the network. Thus, in Figure 13, the diameter is 3. Therefore, the matrix D contains the minimum number of steps required to move from any node *i* to any other node *j* in the network with which *i* is connected in finite sequences of direct and indirect steps (Leinbach, 1976; Reed, 1970). Although longer sequences of steps may connect *i* and *j* these sequences are ignored. Summing the matrix D over its rows or columns identifies the total number of steps required for each node to reach or be reached by the other nodes. For each node this value indicates its degree of connectivity within the network (Hay, 1973; Reed, 1970;

Figure 13

Calculation of the shortest-path matrix (D)
and nodal connectivity



$$\underline{A} = \underline{D}^1 = \begin{pmatrix} 0 & 1 & 0 & 0 & 0 \\ 1 & 0 & 1 & 1 & 0 \\ 0 & 1 & 0 & 1 & 0 \\ 0 & 1 & 1 & 0 & 1 \\ 0 & 0 & 0 & 1 & 0 \end{pmatrix}$$

$$\underline{A}^2 = \begin{pmatrix} 1 & 0 & 1 & 1 & 0 \\ 0 & 3 & 1 & 1 & 1 \\ 1 & 1 & 2 & 1 & 1 \\ 1 & 1 & 1 & 3 & 0 \\ 0 & 1 & 1 & 0 & 1 \end{pmatrix} \qquad \underline{D}^2 = \begin{pmatrix} 0 & 1 & 2 & 2 & 0 \\ 1 & 0 & 1 & 1 & 2 \\ 2 & 1 & 0 & 1 & 2 \\ 2 & 1 & 1 & 0 & 1 \\ 0 & 2 & 2 & 1 & 0 \end{pmatrix}$$

$$\underline{A}^3 = \begin{pmatrix} 0 & 3 & 1 & 1 & 1 \\ 3 & 2 & 4 & 5 & 1 \\ 1 & 4 & 2 & 4 & 1 \\ 1 & 5 & 4 & 2 & 3 \\ 1 & 1 & 1 & 3 & 0 \end{pmatrix} \qquad \underline{D}^3 = \underline{D} = \begin{pmatrix} 0 & 1 & 2 & 2 & 3 \\ 1 & 0 & 1 & 1 & 2 \\ 2 & 1 & 0 & 1 & 2 \\ 2 & 1 & 1 & 0 & 1 \\ 3 & 2 & 2 & 1 & 0 \end{pmatrix} \begin{matrix} \Sigma=8 \\ \Sigma=5 \\ \Sigma=6 \\ \Sigma=5 \\ \Sigma=8 \end{matrix}$$

Werner, 1968). This procedure is described by the Shimbel Index (Shimbel, 1953), which is given as:

$$S_i = \Sigma_{j=1}^{n} \; dij \tag{3.3}$$

This operation provides a vector, the individual elements of which are measures of the shortest path connections from each node to all other nodes in a network (Taaffee and Gauthier, 1973). The smaller the resultant numerical value of a node, the greater is the accessibility of that node to the network. Thus, nodes 2 and 4 in Figure 13 are the most accessible with an S value of 5. Nodes 1 and 5, on the other hand, require a total of 8 steps to reach the other nodes in the network and are thus the lease accessible. The mean and variance of the S values of all the nodes in a network can then be used as measures of accessibility of the network as a whole.

The shortest-path procedure not only removes redundancies in the computations as already noted but a *distance-decay relationship* (Taylor, 1975; de Castro Lopo, 1976) is maintained (Taaffee and Gauthier, 1973). Taaffee and Gauthier (1973) have utilized this procedure to re-analyse the Interstate Highway System of the Southeastern United States. Significantly different results were obtained from a similar analysis by scalar weighting, using the data for Garrison's (1968) study due mainly to the removal of redundancies. Reed (1970) also utilized the shortest-path procedure in his analysis of the Indian Airline network.

3. Linkage Weighting Procedure

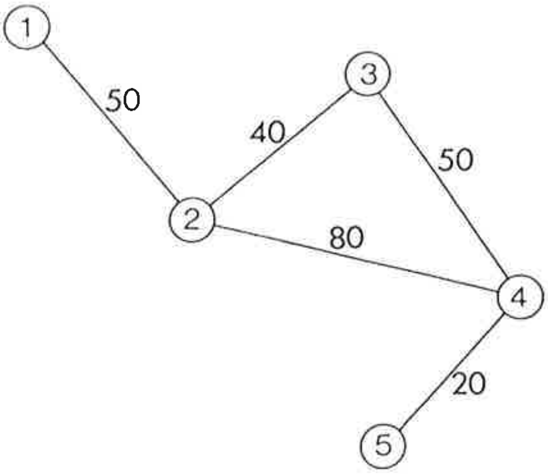
One objection to the matrix procedures described so far is the inflexibility of the binary format. The value of '1' is assigned to a linkage between two nodes regardless of the significance of that linkage. Thus, a major direct linkage is assigned the same value as a minor less direct one. Gauthier (1968), however, rejected the binary assumption and suggested that all connections could be weighted for such characteristics as length, route quality and movement costs. Although such weighting may introduce a subjective element it brings the analysis into closer line with the operating characteristics of the network (Hay, 1973). The binary format is reasonable when analysis is strictly on the structural properties of a network, or when one has only a limited amount of information available about that network (Taaffee and Gauthier, 1973). However, if information is available the weighting procedure is generally preferred (e.g., Gauthier, 1968; Hay, 1973; Taaffee and Gauthier, 1973).

An illustration of the difference that the linkage weighting procedure can produce in a node's degree of accessibility within a network can be illustrated with the working example from Figure 14. For instance, if the linkages between the nodes are now weighted as shown in Figure 14 for linkage distance, node 3 becomes elevated from being the third most accessible node in the previous calculation to the first most accessible node in Figure 14. Node 4 is relegated to third position and node 1 becomes the sole least accessible node.

The procedure required for this computation has been described by Taaffee and Gauthier (1973). The initial connectivity matrix requires a slightly different format than that used in the binary operations. When a direct linkage occurs between two nodes the appropriate weight or value of that linkage is substituted into the corresponding matrix cell. If there is no direct linkage the value

Figure 14

The linkage-weighting procedure and calculation of minimum path lengths



$$L = \begin{pmatrix} 0 & 50 & \infty & \infty & \infty \\ 50 & 0 & 40 & 80 & \infty \\ \infty & 40 & 0 & 50 & \infty \\ \infty & 80 & 50 & 0 & 20 \\ \infty & \infty & \infty & 20 & 0 \end{pmatrix} \qquad L^3 = \begin{pmatrix} 0 & 50 & 90 & 130 & 150 \\ 50 & 0 & 40 & 80 & 100 \\ 90 & 40 & 0 & 50 & 70 \\ 130 & 80 & 50 & 0 & 20 \\ 150 & 100 & 70 & 20 & 0 \end{pmatrix} \begin{matrix} \Sigma=420 \\ \Sigma=270 \\ \Sigma=250 \\ \Sigma=280 \\ \Sigma=340 \end{matrix}$$

Two-step Connection, Node 1→ Node 4

$(N1 \rightarrow N1) + (N1 \rightarrow N4) = 0 + \infty = \infty$

$(N1 \rightarrow N2) + (N2 \rightarrow N4) = 50 + 80 = 130$

$(N1 \rightarrow N3) + (N3 \rightarrow N4) = \infty + 50 = \infty$

$(N1 \rightarrow N4) + (N4 \rightarrow N4) = \infty + 0 = \infty$

$(N1 \rightarrow N5) + (N5 \rightarrow N4) = \infty + 20 = \infty$

Minimum Path is 130

∞ is entered in the appropriate cell (e.g., Figure 14). The resulting matrix provides no more information on network structure than is provided in a strictly topological matrix. However, it does allow measurements of nodal accessibility that are based on a more refined measure of distance (Taaffee and Gauthier, 1973).

The computation differs from the matrix powering procedure in two important ways: a) instead of element-by-element multiplication of row-times-column, element-by-element addition is employed (i.e., $x.y = x+y$), and b) instead of summing the results, the minimum value of $x+y$ is inserted in the appropriate cell of the valued matrix ($\underline{L}$) (Taaffee and Gauthier, 1973). Thus, the new cell value for a two stage linkage is the minimum value of the sums from an origin i to k and then to destination j. A simple illustration of this procedure is provided in Figure 14. Following this procedure successive powers of the valued matrix $\underline{L}$ can be calculated until the matrix of minimum distance has been obtained (i.e., when the value of the diameter is reached).

Gauthier (1968) has utilized the weighting procedure in his analysis of the development of highway transportation and urban growth in the region of São Paulo, Brazil, during the period 1940 to 1960. The procedure was used to investigate the changes in the accessibility of the urban centres during this period of growth in the regional economy and highway network. Taaffee and Gauthier (1973) compared the Shimbel shortest-path procedure to the valued matrix analysis using the Interstate Highway System and 56 of the urban centres in the American Manufacturing Belt. The latter analysis was found to be more sensitive to the multiplicity of short linkages in the eastern portion of the Belt than the shortest-path procedure. However, there were few other notable differences in the results of the two analyses.

C. Shape Analysis

Blair and Biss (1967, 1) have stated that *"shape is a physical characteristic of any unit of area and theoretically and practically may be as important as relief, climate or one of the more traditional physical variables considered in much geographical work"*. Consequently it is not surprising that shape has long played a significant role in geography. For example, shape is implicit in the geomorphologist's concern with the topography and other physical features of the landscape. Urban geographers use shape to classify urban forms. Economic geographers use shape in their analysis of trade areas. A major area in political geography is the analysis of the shape of political units (e.g., Cole, 1971). Christaller's work on central place theory is probably the most noted use of shape in geographical research. Whenever studies are based on data assigned to geographic units, the size and shape of those units have been found to be themselves factors influencing the results (Coulson, 1978). Thus, in the study of any bounded geographical unit, the analysis of its shape may significantly enhance the understanding of a unit's character.

Blair and Biss (1967, 1) define *shape* as *"that quality of an object or form which depends on constant relations of position and distance from all the points composing its outline or its external surface"*. Haggett (1968) has noted that many of geography's basic concepts of shape have come from other disciplines like sedimentary petrology where particle shape has proven to be of vital dynamic significance. However, it is within the field of geography that most of the development on the means of analysing an object's shape has taken place.

A relatively common method for treating shape is the rather vague and arbitrary technique of devising a classification and subjectively assigning shape to it (e.g., circular, rectangular, hexagonal, oxbow, shoestring, etc.) (Bunge, 1966). Another well accepted classification groups shapes as either compact, elongated, indented, punctured or fragmented (e.g., Blair and Biss, 1967; Taylor, 1971; etc.). Many geographers, however, have begun to ask how compact or elongated is a shape. That is, subjective impressions are giving way to quantitative measurements and these measures have been used in the development of theory explaining spatial phenomena (Clark and Gaile, 1973).

A set of early studies that attempted to quantify shape centred around ratios based on some combination of basic measures such as perimeter length, longest axis, radii of enscribing circle, etc. (Gibbs, 1961; Pounds, 1963; Chorley and Haggett, 1965). For instance, Pounds (1963) claimed that the only possible measure of shape is the length of the perimeter in relation to the area. These measures have numerous inherent disadvantages. For example, some tend to be excessively simplistic and fail to capture the essence of shape (Clark and Gaile, 1973). In addition, any measure that relies upon perimeter measurements is extremely sensitive to the difference detailed irregularities of the perimeter itself can make (Blair and Biss, 1967). These measures also fail to incorporate highly complex shapes.

Blair and Biss (1967, 3-4) have developed a list of necessary requirements for any measure of shape. These are:

a) the measure should be given as a 'pure' mathematical ratio and not referred to in any measurable units or quantities;

b) the numerical measure of any property of shape should correspond to the visual impression of the actual property to be measured;

c) the measure should not exaggerate the value of shape out of proportion to its practical meaning;

and d) the measure should not depend solely on one or two extreme points of the shape since in the practical application of this measurement the position of all the points of shape will be important.

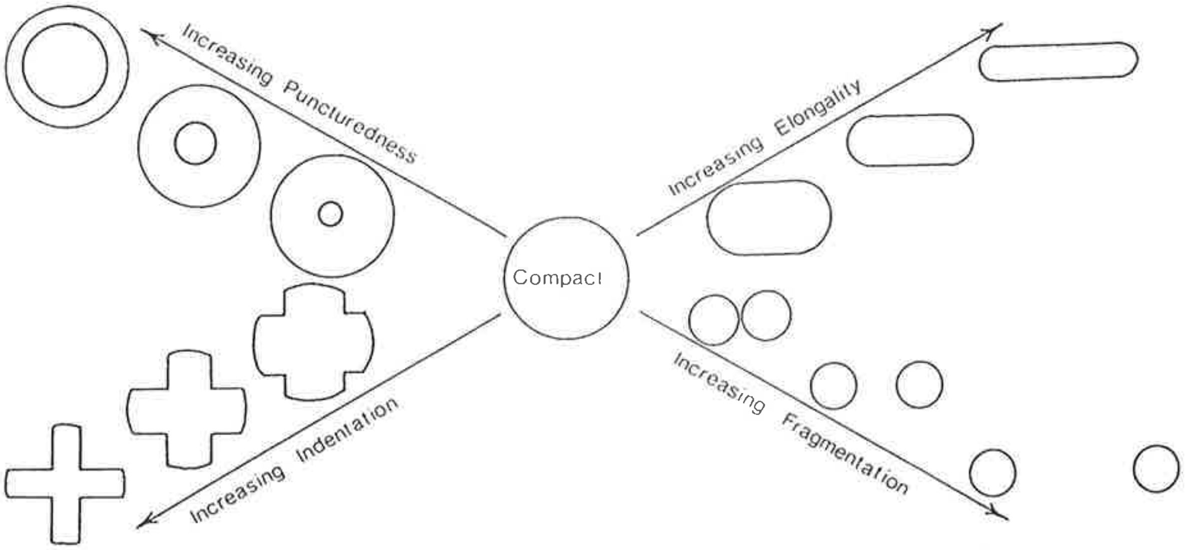
A number of other, more sophisticated, techniques for measuring shape have been devised that, in general, at least satisfy the first three stipulations. Some of the techniques in this category have been developed by Boyce and Clark (1964), Blair and Biss (1967), Bunge (1966), Lee and Sallee (1970) and Taylor (1971).

Taylor (1971) has noted that most quantitative descriptions of shape have a circle, the most compact shape, as the limiting case, with measurements declining or increasing as shapes diverge from this 'ideal' shape. Taylor (1971) noticed four types of divergence from compactness which relate to the qualitative classes of punctuation, elongation, fragmentation and indentation (Figure 15). Thus, any punctured shape becomes less compact as its hole increases in size, an elongated shape becomes less compact as it becomes longer, a fragmented shape consisting of two distinct parts will decline in compactness as the parts are moved further apart, and an indented shape becomes less compact as indentations increase. Taylor (1971) formulated finite frequency distributions related to within-shape distances; each individual shape having its own unique frequency distribution. The frequency distributions of complex shapes, such as political units, can then be compared with those of recognisable forms of divergence from the ideal circular shape.

Figure 15

Types of divergence from compactness

Source: Adapted from Taylor (1971, 43)


Increasing Puncturedness
Increasing Elongality
Compact
Increasing Indentation
Increasing Fragmentation

Bunge (1966) produced a method for measuring shape which was based on two theorems: a) that any singly connected shape can be matched by a polygon of any number of sides, whose sides are of equal but variable length; and b) that if the distances between all vertices of the polygon are summed in a standard manner there exists just one set of sums that uniquely describes the polygon shape (Haggett, 1968). However, Bunge (1966) did not prove that two different shapes can be assigned the same set of numbers; nor is the method able to interpret highly irregular, punctured or fragmented shapes. Another disadvantage with the Bunge method, and which also applies to the previously described method by Taylor (1971), is that it is difficult from the sets of numbers or the frequency distributions to determine how much alike shapes are. Blair and Biss (1967) list numerous other disadvantages with Bunge's technique.

Lee and Sallee (1971) have developed a method for measuring shape which employs the 'symmetric difference metric'. Instead of attempting to assign a unique number to each shape, Lee and Sallee (1971) made comparisons between two shapes, one of which is unknown (e.g., political unit, drainage basin, etc.), and the other easily described and conceptualized in non-technical terms (e.g., circle, square, etc.). Thus, shapes were analysed in terms of their degree of circularity, rectangularity, squareness, etc. However, the information collected is rather simplistic and meaningless for the effort involved in the analysis. For instance, the results from the application of Lee and Sallee's (1971) method on the Sudanese villages produces results of relatively low significance for a meaningful analysis of the villages' attributes.

Boyce and Clark (1964) developed a measure of shape where the distances from the shape's centre of gravity to the shape's perimeter are measured along equally spaced radials. From these measures a simple equation is employed to formulate a shape index. From this index any shape can be ranked relative to others and, in addition, can be classified according to the standard geometric shape it most nearly approximates (Boyce and Clark, 1964). This method, however, also has many disadvantages, most of which were recognised by the authors. For example, different indices will be produced not only by using differing numbers of radials but also by varying the positioning of the radials. Thus, the success of this method depends a great deal on the subjective judgement of the individual (Blair and Biss, 1964). In addition, like Bunge's method, Boyce and Clark's (1964) cannot measure complex, irregular shapes.

1. The Compactness Index

Blair and Biss (1967) have expressed their concern over the attempts at developing a unique measure of shape. They stress that one can only define certain properties of shape, not shape itself. Consequently, the authors developed an index that measures a certain property of shape, namely *compactness*. 'Compactness' as defined by Blair and Biss (1967, 3) is *"the extent to which area is grouped or packed around its central point"*. Blair and Biss (1967) also developed indices of elongation, orientation, and centrality from their compactness index.

The development of the compactness index necessitated that the area of a shape be divided into an infinite number of infinitesimal elements of area. The index was based on the position of all of these elements, using infinitesimal calculus. Blair and Biss (1967) describe the mathematical operations involved in the development of the compactness index

$$C = \frac{D}{\sqrt{2\pi S_A r^2 \ dA}} \tag{3.4}$$

where A is the shape being measured, D is the area of A, dA is an infinitesimal element of area of A and r is the radial distance from the centroid to the elements of the area A. Blair and Biss (1967) subsequently proved that the compactness index derived for a shape is invariant with its scale and position and that a circle obtains the highest possible compactness of 1.00. One fault of the compactness index is that the calculations involved in obtaining the compactness index of a particular shape are quite complex and almost impossible without the aid of a computer.

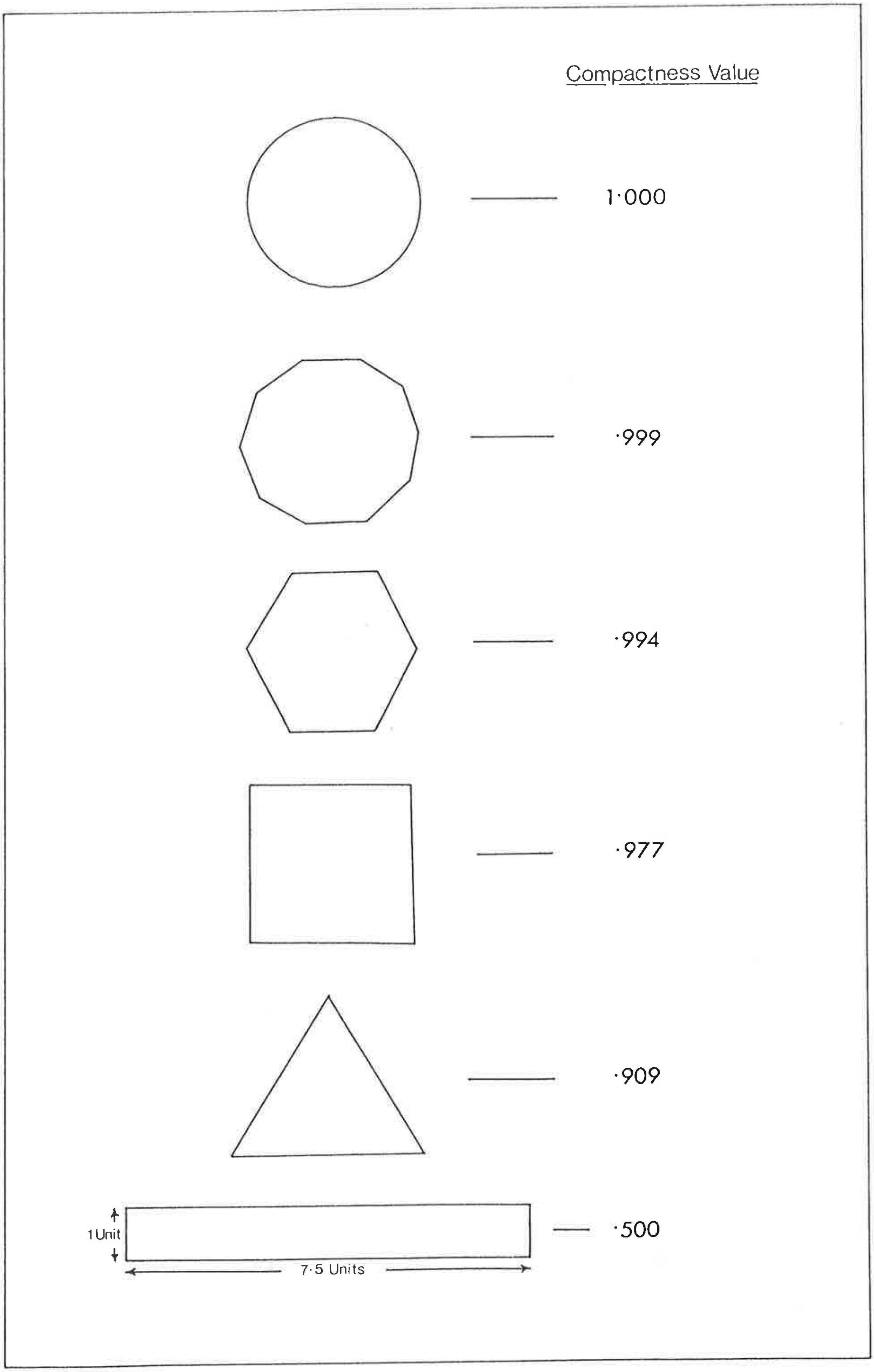
The compactness index was designed by Blair and Biss (1967) to incorporate their desirable features for a measure of shape which were listed earlier in this section. Nevertheless, Taylor (1971) has noted that, in the measure of shape by Blair and Biss, no account is taken of the type of divergence from compactness and that, for example, an elongated and a fragmented unit can have identical indices. Thus, the compactness index does not produce a unique number for each individual shape. However, this may be of more benefit than hinderance in shape analysis for it enables comparisons to be made between different types of divergence from the ideal circular shape.

As an illustration of the behaviour of the compactness index Blair and Biss (1967) first analysed a number of regular geometric shapes (Fig.21). It was noted that the gradient from compact to less compact shapes was relatively low and intuitively appealed to

Figure 16

A comparison of compactness values of regular shapes

Source: Blair and Biss (1967, 13)


Compactness Value
1·000
·999
·994
·977
·909
1 Unit
7·5 Units
·500

the visual impression of a shape's relative compactness. Secondly, Blair and Biss used political units ranging in size and status from parishes to sovereign states as examples of 'real world' shapes. Countries such as Chile and Norway (elongated), Pakistan and the Philippines (fragmented) ranked lowest in compactness index, whereas Rhodesia, Rumania, Uruguay and Kenya ranked highest.

Blair and Biss (1967) extended the principles developed for compactness to the properties of elongation and orientation. *Orientation* was defined as the direction of the longest axis of a shape and *elongation* as the eccentricity of any of a shape's momental ellipses. Both elongation and orientation are properties that are closely related to compactness and, in fact, techniques prior to that developed by Blair and Biss were unable to isolate these properties from their measure of shape (Bunge, 1966; Blair and Biss, 1967). Blair and Biss (1967) provide the necessary mathematical operations and proofs for the extension of the compactness index to incorporate both elongation and orientation. The authors conclude by stating that it is possible to regard a shape's lack of compactness as resulting partly from its elongation and partly from general dispersal. This observation enables either source of incompactness to be isolated if desired (Blair and Biss, 1967).

III. THE STUDY AREA

A. Physical

The Mount Lofty Ranges are a series of fault blocks of great antiquity (Twidale, 1976) with Precambrian rocks dominating their geological character (Daily, Firman, Forbes and Lindsay, 1976). Subsequent stripping of the mantle from the old land surface has left a series of relatively low, rolling hills rather than the steep, rugged mountains characteristic of geologically recent ranges. Isolated peaks occur where the ancient laterite capping remains and include Mount Torrens (584m), Mt. Gawler (543m) and Mount Barker (517m). The highest peak in the Ranges is Mt. Lofty at 727m (Twidale, 1976).

The Ranges have a readily definable boundary in all directions except the north where they merge into the Southern Flinders Ranges (Figure 17). The Ranges are divided from the plains to the east and west by a marked break of slope and adjoin the coast in their southern portions. The abrupt break of slope between the Ranges and the plains has the effect of accentuating their relief (Corbett, 1977).

The topographic contrast of the Ranges with the rest of the southern and coastal portions of South Australia creates a marked regional climatic anomaly. The significant effect of the Ranges on the mean seasonal rainfall pattern of the region is illustrated in Figure 18. Mean annual rainfall varies from only 400mm in the north and east of the Ranges to 1100mm at Mount Lofty. Temperatures vary from cool to cold in winter and from cool to hot in summer with relatively low diurnal variation (Laut, Heyligers, Keig, Löffler, Margules, Scott and Sullivan, 1977).

The soil regime of the Ranges is very complex. For instance,

Figure 17

The Mount Lofty Ranges Study Area

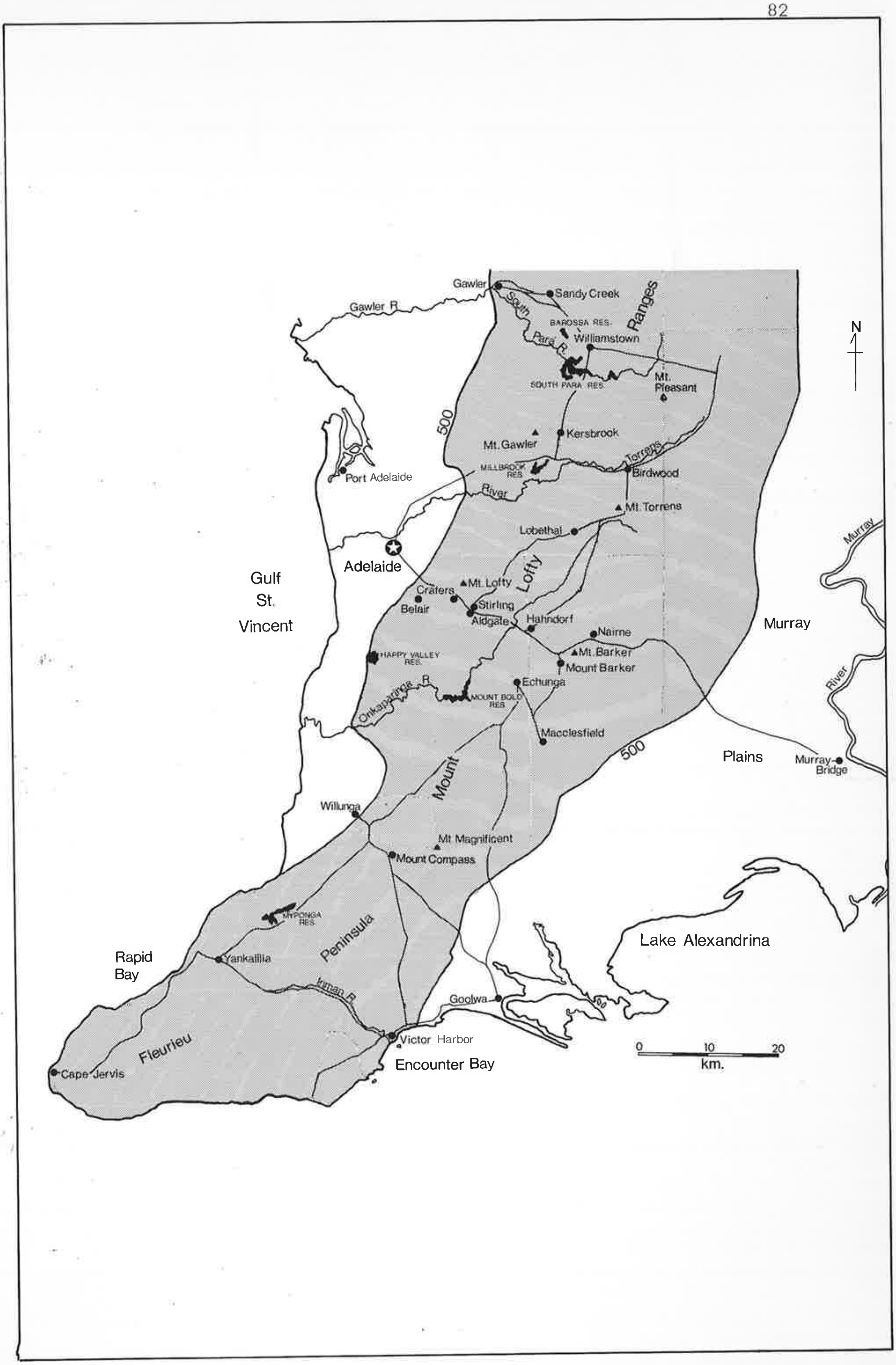
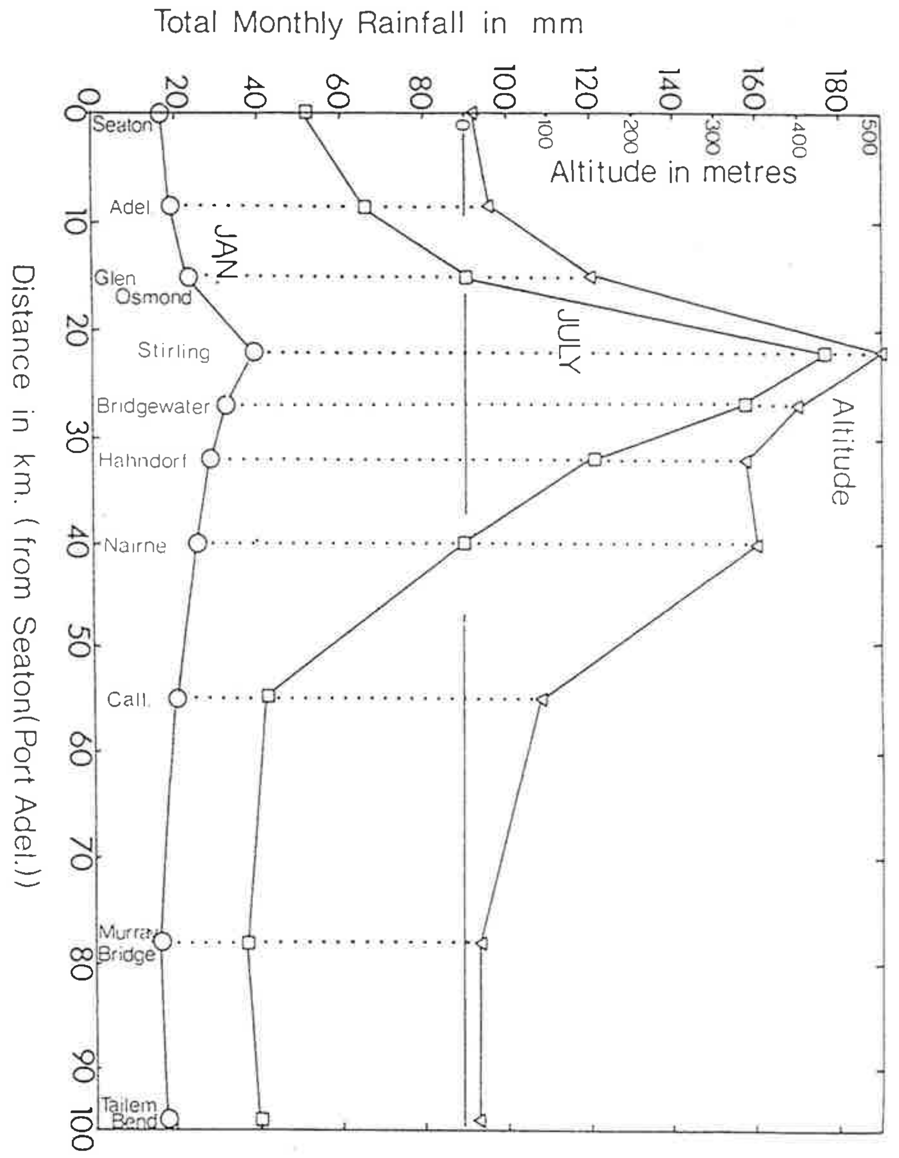

Gawler
Sandy Creek
Gawler R.
South
Ranges
BAROSSA RES.
Para R.
Williamstown
N
SOUTH PARA RES.
Mt. Pleasant
500
Mt. Gawler
Kersbrook
Torrens
MILLBROOK RES.
Birdwood
Port Adelaide
River
Mt. Torrens
Lobethal
Murray
Adelaide
Gulf St. Vincent
Mt. Lofty
Lofty
Crafers
Belair
Stirling
Aidgate
Hahndorf
Nairne
Murray
Mt. Barker
Mount Barker
HAPPY VALLEY RES.
River
Echunga
Onkaparinga R.
MOUNT BOLD RES.
Macclesfield
500
Plains
Murray Bridge
Mount
Willunga
Mt Magnificent
Mount Compass
MYPONGA RES.
Peninsula
Lake Alexandrina
Rapid Bay
Yankalilla
Inman R.
Goolwa
Victor Harbor
0
10
20
km.
Fleurieu
Encounter Bay
Cape Jervis

Figure 18

Mean total rainfall for January (summer) and July (winter) for stations on a path between Seaton (near Port Adelaide) and Tailem Bend, plus the attitudinal cross-section through the Mount Lofty Ranges

Source: Schwerdtfeger (1976, 77)


Total Monthly Rainfall in mm
0
20
40
60
80
100
120
140
160
180
Altitude in metres
0
100
200
300
400
500
Seaton
Adel.
Glen Osmond
Stirling
Bridgewater
Hahndorf
Nairne
Call.
Murray Bridge
Tailem Bend
JAN.
JULY
Altitude
0
10
20
30
40
50
60
70
80
90
100
Distance in km. (from Seaton(Port Adel.))

Northcote (1977, 71) states that:

> *". . .within the Adelaide region soil distribution is complex and there is a wide range and variability in soil properties. It is generally appreciated that the basis for this situation resides in the great mineralogical variations of the basement rocks, and the superimposed geological and geomorphological events: particularly Permian glaciation, Mesozoic peneplanation, Tertiary deep weathering with laterite formation and marine incursions followed by upward block faulting in the Ranges, marine sedimentation and changes in sea level together with the possible incorporation of aeolian material in the coastal strip. All these events have contributed to the diversity of soil parent materials from which the present day soils and their subsolum materials. . .have been developed."*

Regional studies of soil characteristics have also exemplified this situation with discoveries of acute changes in soil types over short distances (e.g., Jackson, 1957; Taylor and O'Donnell, 1931). Basically, however, the soils within the Ranges can be divided into two broad categories; 1) Lateritic podsolic soils in the southern dissected tableland area, and; 2) Podsolic soils in the remainder of the Ranges (Northcote, 1976).

The steep climatic gradient across the Ranges and the complex diversity of soil types have aided the development of a highly variable vegetative pattern. The dominant species (i.e., *Eucalyptus* spp.) are distributed according to the variations in the physical characteristics within the Ranges. Numerous studies have been undertaken that describe the relationships between the vegetation and the physical features of the Ranges, on both a large and small scale (e.g., Adamson and Osborn, 1924; Boomsma, 1946, 1948a; Martin, 1961; Specht, 1972; Specht, Brownell and Hewitt, 1961; Specht and Perry, 1948; West, 1977; Wood, 1930, 1937; etc.). A concise summary of the relationships between the physical environment and the numerous

Eucalypt species has been provided by Laut *et al.* (1977, 44) who state that:

> *. . .the various types of open forest and woodland which originally covered most of the region exist as scattered remnants in native reserves and small, isolated, rather inaccessible areas as yet uncleared. Open forest and low-open forest, commonly dominated by messmate (*E. obliqua*) and brown stringybark (*E. baxteri*) are found in areas of higher rainfall on deep lateritic soils. Where soils are shallower or sandy, pink gum (*E. fasciculosa*), cup gum (*E. cosmophylla*) and, in the northern part of the region, longleaved box (*E. goniocalyx*) are characteristic species. Blue gum (*E. leucoxylon*) is the dominant species of the woodlands, which usually occur in the lower rainfall areas and on podsolized soils. Manna gum (*E. huberana* and *E. viminalis*) occurs in the wetter and cooler woodlands, while peppermint box (*E. odorata*) characterizes drier sites. In the most arid parts of the woodland formation eucalypts give way to drooping sheoak (*Casuarina stricta*).*

In addition, the river red gum (*E. camaldulensis*) is found along watercourses in the drier parts of the Ranges and is also dominant along the Torrens, Sturt and Onkaparinga Rivers. Finally, the Ranges now support only a small number of candlebark gums (*E. rubida*) which occur sporadically in swamps and along gully heads on leached, grey-brown podsols in the areas of highest rainfall (West, 1977); in other words, mainly in the environs of Mount Lofty.

In addition to the geomorphological boundary between the Ranges and the plains, increased vegetation clearance north of Gawler and in the eastern portions of the Ranges has also created a marked biogeographical boundary between the woodland vegetation of the Ranges and the mallee vegetation of the plains. The clearing of these lands has minimized any interaction between the biota of the two regions.

The history of the Mount Lofty Ranges flora as a remnant of a once continuous band of forest extending across southern Australia has been comprehensively described by Crocker and Wood (1947) and Specht (1972). Thus, there is a reasonably large amount of information available concerning what plant species are present within the Ranges. However, their precise distributions are generally not fully known, although a few simplified, local maps have been attempted (e.g., Boomsma, 1948b; Specht, 1972; Specht, Brownell and Hewitt, 1961; etc.).

The status and/or occurrence of native plant species and alliances has been explored by Black (1943-1957), Bonython (1974), Eichler (1965), Jessop (1977), Kraehenbuehl (1970), Margules (1978), and Specht and Cleland (1961). These works clearly illustrate the botanical importance of the Mount Lofty Ranges as a haven for a large number of plant species.

The information available on the avifauna within the Ranges is less extensive. A description of the broad scale distributions of individual bird species in the Ranges has been undertaken by the South Australian Ornithological Association (S.A.O.A., 1977). Condon (1968) has produced a handbook of the avifauna in South Australia, including the Mt. Lofty Ranges, which provides useful information on the characteristics of individual bird species. Specific studies available on the avifauna of the Ranges include Chapman and Schodde (1969), Baxter (1980), Ford and Paton (1976), and Ford and Howe (1980). It is not positively known if any of the endemic bird species present in the Ranges at the time of settlement have become extinct.

For the mammals recorded in the Ranges, of the 30 species present at the time of settlement, nine are thought to have become extinct and several others have been greatly reduced in number (S.A. State Planning Authority, 1974). Lothian (1971) has provided a listing of the status of the mammals recorded in the Ranges. Only 12 of the 30 species were regarded as common or abundant, although the list includes those that have become extinct. Four species are regarded as rare and in need of immediate protection (i.e., Platypus [*Ornithorhynchus anatinus*], Mouse Sminthopsis [*Sminthopsis murina*], Yellow-bellied Free-tailed Bat [*Taphozous flaviventris*], Little Broad-nosed Bat [*Nycticeius greyi*]). Watts (1973) has published a handbook equivalent to that of Condon (1968) for the rodents and small marsupials of South Australia. However, detailed information is lacking on the distributions of species throughout the Ranges.

The Mount Lofty Ranges are a region of great ecological importance. Because the Ranges are separated widely from similar environments they have, to a degree, tended to develop an island ecology. Some of the native bird species, for instance, have developed different sub-species than elsewhere in Australia. The fauna is generally regarded as similar to the coastal fauna of southeastern Australia. Due to the isolated nature of the Ranges the populations of endemic species are finite; they are not replenished from elsewhere as they die out (Cornwall, 1969; Lothian, 1971). Many of the species in greatest danger of extinction require large areas of undisturbed native scrub or woodland in order to survive. Other species in danger of extinction require specialized habitats (i.e., swamps, marshes, etc.) which are now threatened by increased agricultural and urban land demands.

B. History and Land Use

The present landscape pattern can best be understood within the context of its historical development. The attitudes of the early settlers during the 1830's and 40's had a marked effect upon the way in which the Ranges were to be utilized over the next century or so. Williams (1974, 1977) has written an excellent account of the early years of exploitation and settlement in the Adelaide Hills. Williams (1974, 15) sums up the attitudes of the early settlers toward the Ranges as:

> *" 'Rescued from a state of nature!' Like the aborigines the land had to be saved from being raw, untamed and natural; it had to be civilized, subdued and made. This attitude is not altogether surprising - the environment was unfamiliar, uncomfortable, stark in its largeness, and not a little frightening - it was a hard land to love. There are many disparaging references to the Mount Lofty Ranges where the forests were 'dreary', 'sombre', 'gloomy', and 'by no means cheering'. . .".*

The first real exploitation of the Ranges was by professional woodcutters who concentrated on the abundant supplies of stringybark (*E. obliqua* and *E. baxteri*) that the Adelaide Hills region, in particular, contained. The demand for stringybark timber arose mainly from the dearth of timber on the Adelaide Plains and the fact that the grain of the stringybark was straight and free from knots, unlike some of the other available species of eucalypt. The supply of stringybark was thought to be limitless; there was *"plenty of it within seven or eight miles of the town, and if we had 20,000 Emigrants every year for the next century, there would be enough for them all"* (Williams, 1974, 129). Woodcutting was generally by individual concerns and as the Ranges became settled, mainly on the eastern side between Mount Barker and Strathalbyn, by the individual farmer as he cleared his block of land. Clearing of the native vegetation was regarded as part of the normal farm operations that all new settlers faced when colonizing the land. The timber was used mainly for fuel, fencing and construction purposes (e.g., dwellings, barns, etc.).

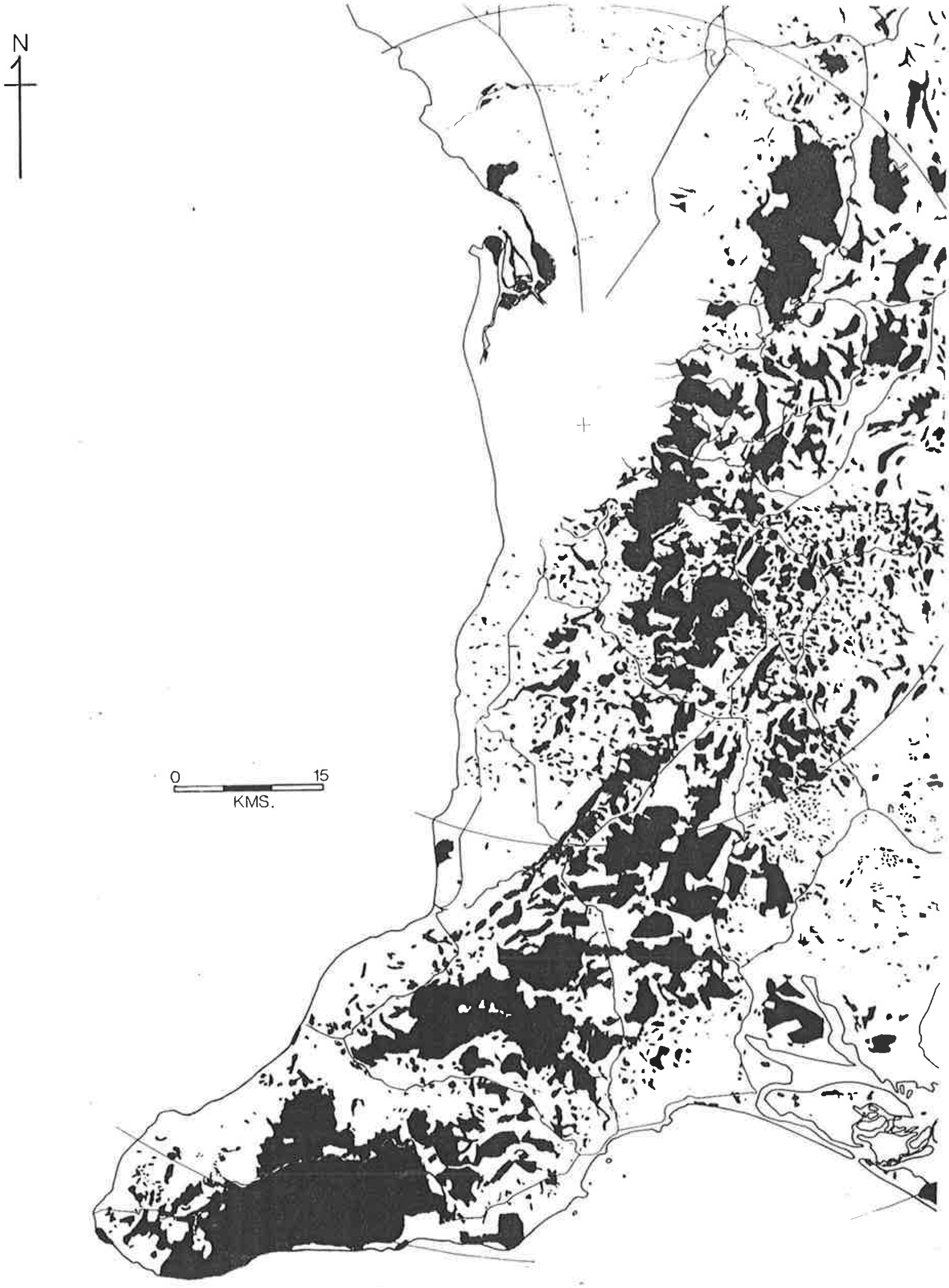
There were three main concentrations of clearing within the Mount Lofty Ranges; on Fleurieu Peninsula between Rapid Bay and Encounter Bay, on the eastern side of the Ranges in the Echunga-Macclesfield area, and particularly north of Gawler in the foothills between the mallee scrub and the *E. odorata* woodland. The central Mount Lofty Ranges were avoided by the settlers because of steep slopes, podsolized soils and the relatively dense cover of the stringybark forests. Unfortunately, detailed information on the clearing of the woodland in the Mount Lofty Ranges is very slight, the main reason being that its end result is negative; nothing of it remains (Williams, 1974). Even in the remaining areas of native vegetation very few of the original stringybark eucalypts, which often had diameters in excess of 80 centimeters (Schwerdtfeger, 1979), remain today.

During the search for land by the early settlers it was the general consensus that the presence of trees on a particular site was regarded as an index of good soil and fresh water as well as providing a good supply of timber. Thus, those areas covered in native forest were eagerly settled and cleared by the farmers. However, even by the end of the Second World War large tracts of uncleared land still remained in the Ranges (Fig. 19). From Williamstown in the north to Cape Jervis in the south there was still an almost continuous band of native vegetation, with the Inman Valley providing the only break of any significance. The area south of the Inman Valley contained the largest single stand, totalling almost 40,000 hectares. Slightly

Figure 19

1945 Native Vegetation Plan of
the Mount Lofty Ranges

Notes: Drawn from military ordnance maps and thus accuracy is questionable. However, the map does clearly illustrate the extent of the native vegetation at that time.
Reproduced with permission from Mr. J.A. Lothian, S.A. Department of Environment and Planning.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(Lothian, 1971). Figure 20 illustrates the native vegetation that remained in 1968. The map clearly shows that there has been a concerted effort of forest clearance over this period. This process, in fact, has also been noticed in other relatively developed areas within Australia during the post-war years up to the late 1960's (e.g., Western Port Regional Planning Authority, 1976).

The impact of this massive reduction of the native vegetation has been summarized by Lothian (1971, 15) who states that:

> *". . .two of the most noticeable changes which have occurred between 1945 and 1968 are the shrinking of the former extensive tracts of vegetation, and their separation into isolated clumps. Where formerly the large areas were measured in terms of tens of thousands of acres they are in mere thousands. Where formerly the Inman Valley was the only break of any consequence in an otherwise continuous band of vegetation down the ranges, now it itself is wider and only one of many such breaks. Where formerly all environments existed, including the river, swamp, valley, plains, hillslopes, ridge-tops or hilltops, now only the slopes and tops of hills are adequately represented."*

Since the 1971 report by Lothian, Caldicott (1977, 1980) has undertaken a study to further assess the rate of clearing and extent of the indigenous vegetation. Caldicott discovered that, apart from the area south of the Inman River on Fleurieu Peninsula, the rate of vegetation clearance between 1968 and 1974 was less than that between 1945 and 1968. However, part of the reason for this decrease is that in some areas very little of the vegetation that existed in 1945 remained and that which did remain was on the least productive land, thus rendering clearing uneconomical.

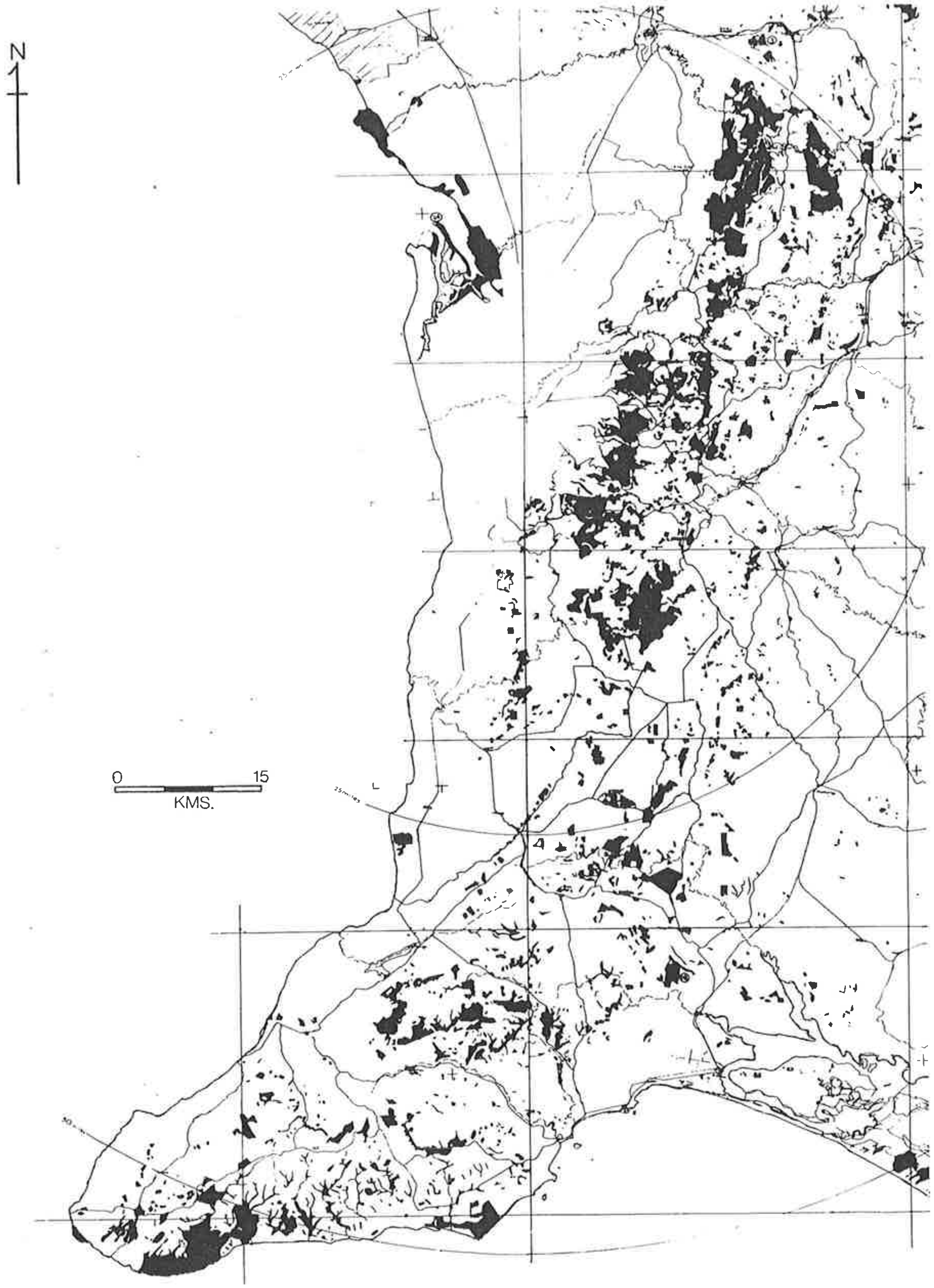
Since the 1960's a slightly different threat to the remaining vegetation units has occurred. The growing trend within the western world toward rural retreats has begun a programme of large scale subdivision of once large holdings of land to accommodate these less contiguous but large stands occurred north of the Inman Valley. The environs of Mount Magnificent contained 14,000 hectares of native forest. Further north there were stands of 8,700 hectares at Mount Bold, 4,900 hectares around Belair, 6,250 hectares along the hills face and over 14,000 hectares from Milbrook Reservoir to the South Para River (Lothian, 1971). In all, some 240,000 hectares of bushland remained in 1945.

The greatest onslaught on the native vegetation in the Ranges has occurred during the post-war years following 1946. In many instances the destruction of the vegetation was the result of *"impulsive and uninformed land-use decisions which subsequently led to uneconomic practices and unstable land surfaces"* (Schwerdtfeger, 1979, 6). For example, there was a concerted attempt at the cultivation of tobacco within the Ranges which failed, as did the attempt at growing grape vines near Mount Lofty Summit in the 1860's. In areas of wheat growing within the Ranges, heavy bullocks were sometimes used to plough up and down the slopes, which consequently caused mass wasting and gullying along many of the furrows. One of the most damaged areas is that around Yankalilla in the mid-south of the Ranges where wholesale clearing of eucalypts on relatively unstable valley slopes compounded the effects (Pridham, 1955). Other farming practices became increasingly common as settlement within the Ranges began to expand. Dairying, orchards (e.g., apples, pears, cherries, etc.) and timber production, particularly using *Pinus radiata*, have become increasingly accepted sights since World War Two. All of these activities have grown at the expense of the native forests and woodland. By 1968, only 96,000 ha. of native vegetation remained, a reduction of 60 per cent since World War Two

Figure 20

1968 Native Vegetation Plan of
the Mount Lofty Ranges

Notes: Drawn from aerial photographs up to 1965. The information shown is judged to be at least 95 per cent accurate.
Reproduced with permission from Mr. J.A. Lothian, S.A. Department of Environment and Planning.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so-called 'hobby farmers'. Many towns within the Ranges, particularly those within easy commuting distance of the Adelaide CBD (e.g., Crafers, Stirling, Mount Barker, etc.), have begun to expand dramatically over the last decade or so. The threat of this growing trend has been recognised by Caldicott (1974) who regards the continued subdivision as the greatest threat to responsible land use and recommends a freezing of all subdivision within the Ranges. The State Planning Authority (1974) report also reached similar conclusions.

By 1980, only three main stands of vegetation remained within the Ranges and even these, by 1945 standards, are rather small. These stands are found in the Kersbrook-Williamstown district, the central Ranges, and the pockets of vegetation in the southern Ranges. The survival of these stands has owed a great deal to their large percentage of public ownership.

Much of the reason for this public ownership of land is due to the reasonably large number of nature reserves, in the form of Conservation Parks and Recreation Parks, scattered throughout the Ranges. The history of the reserve movement has been adequately covered by Bonython (1972) and Harris (1974) and thus will not be discussed here. In 1974, for South Australia as a whole, 3.7 per cent of the State was reserved for conservation purposes in one form or another, which was approximately twice the national average. Only Tasmania and the territories had a larger percentage of total land reserved (South Pacific Conf. on National Parks and Reserves, 1975). Since 1974, new additions have been made to the reserve system. In addition, various reports and publications have been written which provide at least foundations for further reserve acquisition and management particularly with respect to the plant associations or alliances that are in need of preservation (e.g., Specht and Cleland, 1961, 1963; Cornwall, 1966; South Australian National Parks and Wildlife Service, 1973; etc.).

Other public organizations that have aided in the retention of the native vegetation within the Ranges include the Engineering and Water Supply Department which owns large areas of native vegetation within reservoir catchment areas (e.g., Mt. Bold, South Para-Warren, Milbrook, etc.) and the Woods and Forestry Department whose State Forest land contains significant stands of native forest and scrub. Other public departments which have minor areas of native vegetation under their administration are the Highways Department, Electricity Trust and the Mines Department, although these departments are more known for their activities in the clearing or disturbance of the remaining native vegetation. However, only about 40 per cent of the remaining vegetation is publically owned, leaving 60 per cent in private hands and thus at greater risk of being cleared (Caldicott, 1977). Caldicott also discovered that the amount of native vegetation publically owned at the Hundred level varies from a high of 84 per cent in Barossa to a low in Encounter which contains only two hectares of publically owned vegetation. This illustrates the patchy nature of past public acquisition of land, particularly for conservation purposes.

This situation is gradually improving, particularly with the advent of five reports which have analysed the conservation potential, with respect to species present and degree of disturbance, of many of the remaining tracts of native vegetation in private hands (i.e., Lamprey and Mitchell, 1979; Mitchell, Prizibilla and Dendy, 1981; Pillman, 1972; Society for Growing Australian Plants, 1975; Wells, 1976). The purpose of these reports was to rank the remaining large tracts of native vegetation with respect to their botanical importance as an aid to any future policy of land acquisition for conservation. These patches of vegetation generally occur on rather inaccessible sites (e.g., ridge-tops, steep slopes, etc.) or in areas of very poor agricultural productivity (e.g., boulder strewn or very sandy soils, etc.). This feature has already been recognised by Laut *et al.* (1977) and demonstrates a striking similarity to the results from the study by Curtis (1962) on the remaining patches of forest in Wisconsin.

C. Mapping of Remnant Patches

Mapping of the remnant vegetation patches in the Mount Lofty Ranges as of 1980 was undertaken with the use of 1:5,000 (1975) and 1:16,000 (1977) coloured aerial photographs. In addition, 1:10,000 black and white Orthophotomaps and information obtained from recent publications (i.e., Lamprey and Mitchell, 1979; Mitchell, Prizibilla and Dendy, 1981; Pillman, 1972; Wells, 1976; etc.) were used to supplement and check the initial mapping results. Field checking was undertaken in areas of contradiction between the above sources. The presence of roadside vegetation and *Pinus radiata* plantations were also noted during the mapping process. Mapping of the native vegetation remnants was done with as much detail as possible and includes units as small as two hectares. The final results were transferred onto 1:50,000 Cadastral maps for the purpose of clarity and for future analysis.

Native vegetation within the Ranges was recognised not just by the presence of a native overstory but also by the presence of a shrub layer, either open or closed. The presence of this layer indicates that natural regrowth of the overstory vegetation is occurring and that the unit is thus self-maintaining. Also the shrub layer generally typifies Mount Lofty Ranges forest vegetation. In contrast, many areas within the Ranges are of a 'parkland' nature with a uniform height of overstory vegetation and a ground cover of exotic grasses upon which grazing occurs. The density of the overstory vegetation is generally less than that in forest patches due to the degree of clearing that is usually associated with these areas and the prevention of regrowth by grazing. In addition, the absence of a shrub layer has the unfortunate effects of eliminating the shelter required for many endangered native plant and animal species. Also, it increases the disturbance effects, such as noise, herbicide drift, pest species and erosion, for an area. Thus, these areas, in their present condition, cannot be considered as units of native vegetation.

Information on public holdings within the Ranges was obtained from the South Australian Department of Lands and the relevant government departments (e.g., National Parks and Wildlife Service, Engineering and Water Supply Department, etc.). These holdings were also displayed on the resultant Cadastral maps, with the remainder of the study area being in private hands.

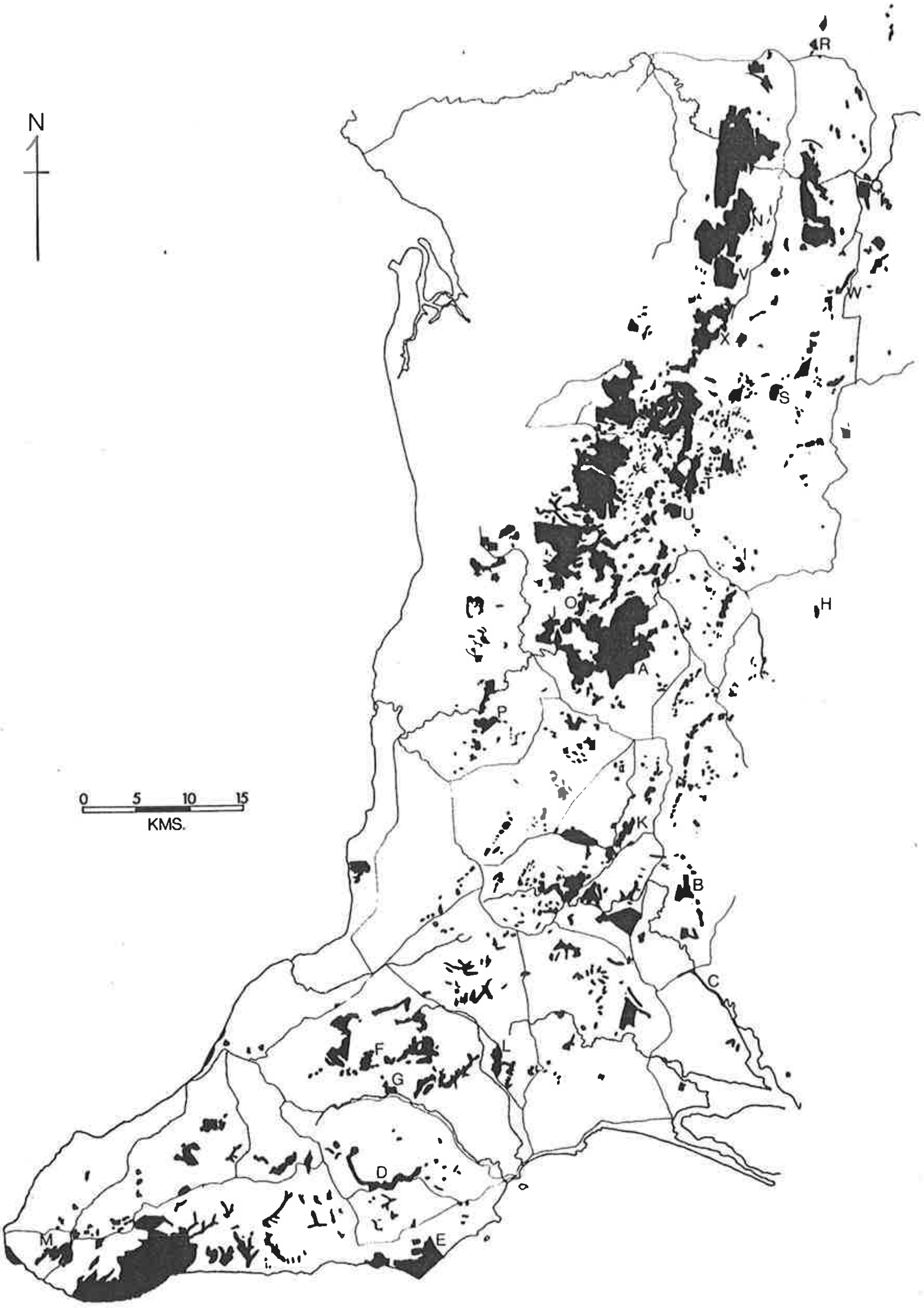
For the purposes of this study, *nature reserves* within the Mount Lofty Ranges are considered as those holdings administered by the National Parks and Wildlife Service (i.e., Recreation Parks and Conservation Parks). These holdings are managed, at least in part, for the conservation of their native biota.

The final map produced (Figure 14) illustrates the complexity of the present biogeographical situation within the Mount Lofty Ranges. The remaining patches of native vegetation vary considerably in both

Figure 21

1980 Native Vegetation Plan of
the Mount Lofty Ranges

Notes: Plan drawn by author (see text for details)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size and degree of protection, with the greatest protection being offered by the nature reserves and, to a lesser extent, reservoir catchment areas. The map also clearly illustrates Caldicott's (1977, 1980) findings that the rate of vegetation clearance has slowed over the past several years.

IV. APPLICATION OF NETWORK AND SHAPE ANALYSIS TO NATURE RESERVES

A. Application of Network Analysis

1. Binary Format

The vegetation map produced for the Mount Lofty Ranges (Fig. 21) illustrates a situation where network analysis techniques may be employed to measure isolation. However, in order to utilize these techniques, the vegetation pattern must be transformed into a network consisting of nodes and edges. For the purposes of this study, the nodes are the nature reserves within the Ranges (unless otherwise stated), for it is the design of nature reserves that is under consideration.

Biological corridors and stepping-stone islands have been shown to act, at least theoretically, as routeways for the movement of biota between habitat islands. Thus, there is an obvious analogy between these natural avenues of movement and the man-induced avenues of movement that have been regarded as edges in networks within Human Geography (e.g., Dicks, 1972; Gauthier, 1968a,1968b; Wood, 1975; etc.). However, unlike most of the Human Geographer's routeways, biological corridors and stepping-stone island linkages between nature reserves are often not continuous; numerous gaps or breaks usually occur along their lengths. Thus, some threshold size of gap is required above which a potential corridor between two nature reserves no longer exists and the reserves become disconnected. For the purposes of this study the threshold size for a gap between vegetation patches was chosen to be one kilometre.

This size was chosen for two main reasons: a) it is in accordance with the findings of biogeographical studies concerning the isolation effects of distance between habitat islands (e.g., Hooper, 1971) and, just as importantly, b) it creates a network structure that is neither too complex (i.e., larger gap size) nor too disconnected (i.e., smaller gap size) for the analysis of nature reserves within the Ranges. The significance of gap size is something which should be recognised when considering species movement along biological corridors. However, information concerning critical gap sizes is still relatively scarce and since this study is primarily concerned with the development of suitable techniques for measuring biogeographic attributes of nature reserves, a gap size has to be chosen which will enable initial analysis to proceed.

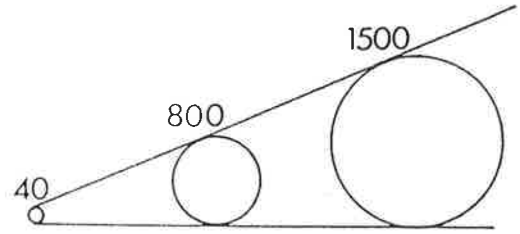
Figure 22 illustrates the network created for the Mount Lofty Ranges vegetation using the one-kilometre threshold gap size. The pattern resulting from the construction of this network allows the measurement of various biogeographic attributes by the network analysis technique described in an earlier chapter.

Other gap sizes were experimented with and their resultant networks constructed. Figure 23 shows the Mount Lofty Ranges reserve network with a 0.5 kilometre gap size. The network now becomes noticeably disconnected and illustrates the partial archipelago nature of the reserve clusters within the total network; a feature which will be discussed in depth later.

The one kilometre gap network created for the Mount Lofty Ranges contains 37 nodes of which 33 are contained in the network proper (Fig. 22). Sandy Creek Conservation Park (C.P.) (Reserve 1), Waitpinga C.P. (Reserve 35), Eric Bonython C.P. (Reserve 36) and Deep Creek C.P. (Reserve 37) are isolated from the main network and thus will be discussed separately. The 33 nodes in the main network are joined by a total of 83 edges. The edges within the network have been

Figure 22

Network created for Mount Lofty Ranges:
one kilometre gap size



Size of Nature Reserves
(ha.)

——— Corridors

— — — — Corridors requiring roadside vegetation

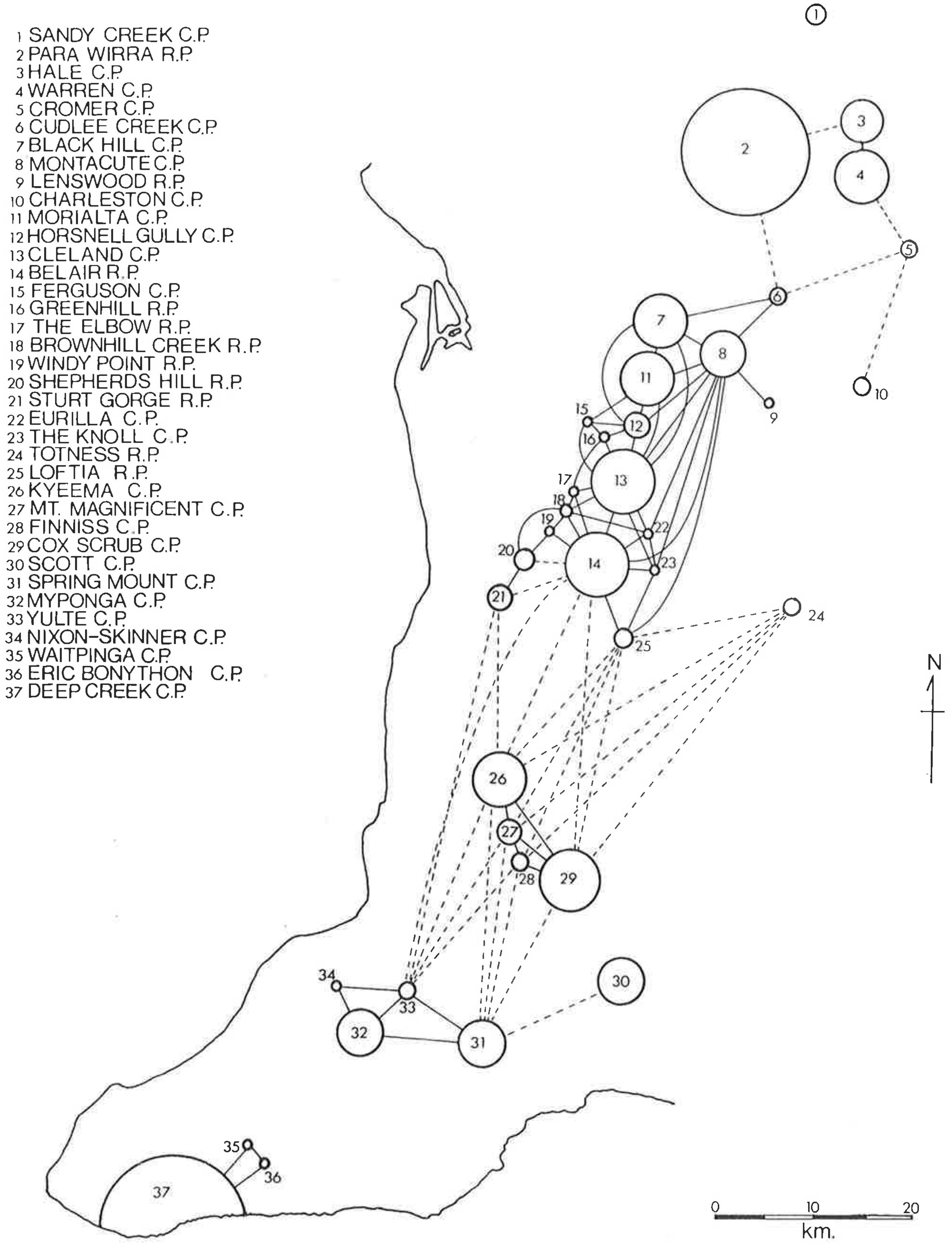
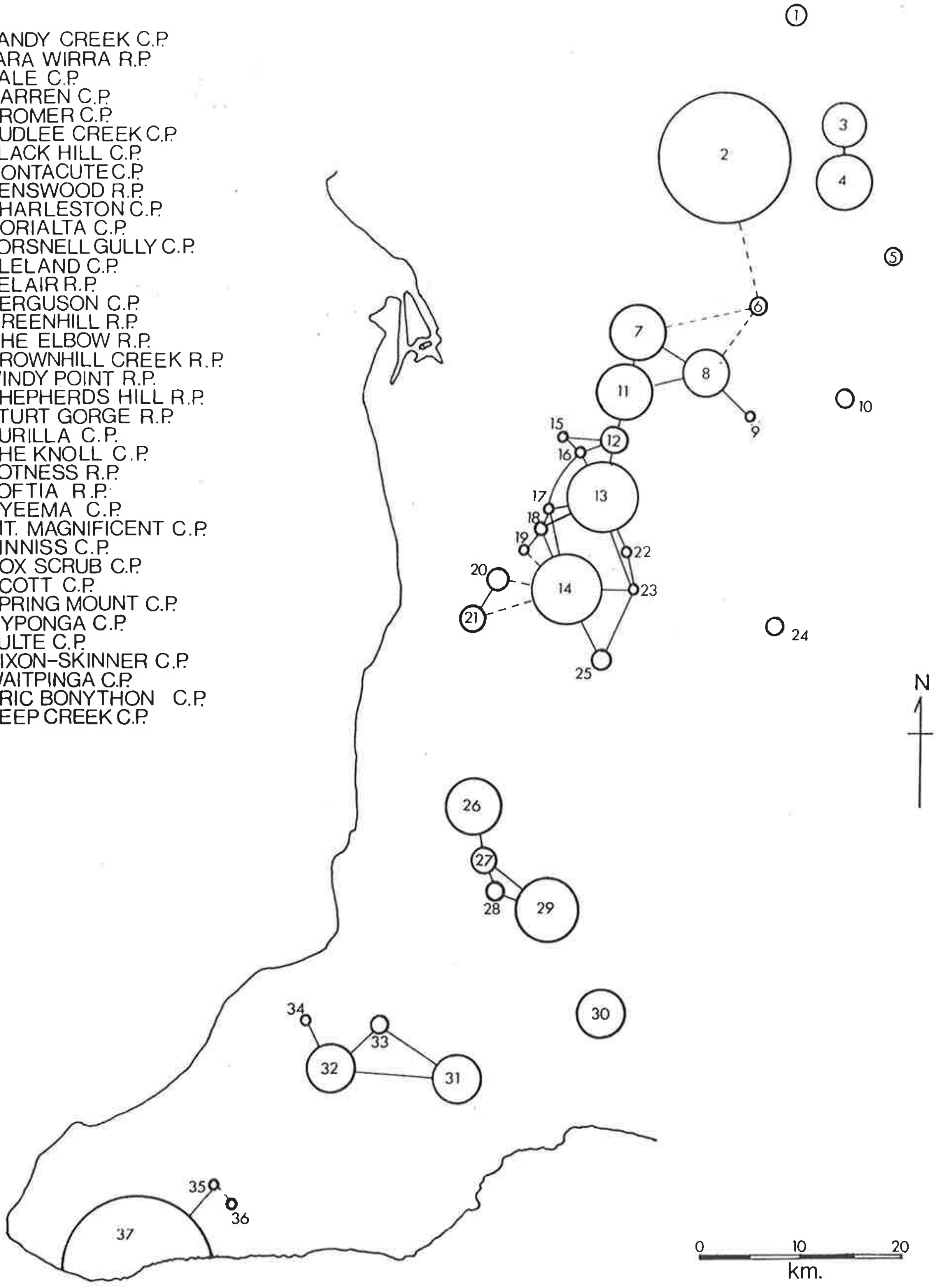

1 SANDY CREEK C.P.
2 PARA WIRRA R.P.
3 HALE C.P.
4 WARREN C.P.
5 CROMER C.P.
6 CUDLEE CREEK C.P.
7 BLACK HILL C.P.
8 MONTACUTE C.P.
9 LENSWOOD R.P.
10 CHARLESTON C.P.
11 MORIALTA C.P.
12 HORSNELL GULLY C.P.
13 CLELAND C.P.
14 BELAIR R.P.
15 FERGUSON C.P.
16 GREENHILL R.P.
17 THE ELBOW R.P.
18 BROWNHILL CREEK R.P.
19 WINDY POINT R.P.
20 SHEPHERDS HILL R.P.
21 STURT GORGE R.P.
22 EURILLA C.P.
23 THE KNOLL C.P.
24 TOTNESS R.P.
25 LOFTIA R.P.
26 KYEEMA C.P.
27 MT. MAGNIFICENT C.P.
28 FINNISS C.P.
29 COX SCRUB C.P.
30 SCOTT C.P.
31 SPRING MOUNT C.P.
32 MYPONGA C.P.
33 YULTE C.P.
34 NIXON-SKINNER C.P.
35 WAITPINGA C.P.
36 ERIC BONYTHON C.P.
37 DEEP CREEK C.P.
N
0
10
20
km.

Figure 23

Network created for Mount Lofty Ranges:
0.5 kilometre gap size

1 SANDY CREEK C.P
2 PARA WIRRA R.P
3 HALE C.P
4 WARREN C.P
5 CROMER C.P
6 CUDLEE CREEK C.P
7 BLACK HILL C.P
8 MONTACUTE C.P
9 LENSWOOD R.P
10 CHARLESTON C.P
11 MORIALTA C.P
12 HORSNELL GULLY C.P
13 CLELAND C.P
14 BELAIR R.P
15 FERGUSON C.P
16 GREENHILL R.P
17 THE ELBOW R.P
18 BROWNHILL CREEK R.P
19 WINDY POINT R.P.
20 SHEPHERDS HILL R.P
21 STURT GORGE R.P
22 EURILLA C.P.
23 THE KNOLL C.P
24 TOTNESS R.P
25 LOFTIA R.P
26 KYEEMA C.P
27 MT. MAGNIFICENT C.P
28 FINNISS C.P
29 COX SCRUB C.P
30 SCOTT C.P
31 SPRING MOUNT C.P
32 MYPONGA C.P
33 YULTE C.P
34 NIXON-SKINNER C.P
35 WAITPINGA C.P
36 ERIC BONYTHON C.P
37 DEEP CREEK C.P



classified into two types, those that require roadside vegetation (in addition to intervening vegetation patches) in order to complete a linkage and those that do not, relying entirely on intervening vegetation patches. Also, for conservation purposes, the latter form of linkage is preferable because of problems involved in native species movement along roadside verges.

The main network is displayed as a connectivity matrix in Figure 24. The two forms of linkages are also differentiated in this matrix. Addition of the rows or columns in the matrix provides the degree of nodes within the network. Reserves 8 (Montacute C.P., Degree = 10), 13 (Cleland C.P., Degree = 11) and 14 (Belair Recreation Park [R.P.], Degree = 14) obtain the highest degrees. In biogeographical terms, this indicates that these reserves are contiguous with other remnants of native vegetation which provide connectivity with adjacent reserves. Reserves with a low degree, such as Lenswood R.P. (Reserve 9, Degree = 1), Charleston C.P. (Reserve 10, Degree = 1) and Scott C.P. (Reserve 30, Degree = 1), are either spatially isolated from the central concentration of the network or have their adjoining areas substantially cleared of native vegetation.

Using this binary form of the connectivity matrix, the accessibility matrix for the network can be computed by the shortest-path technique (Appendix A). The shortest-path matrix is obtained after seven iterations and thus the diameter of the network is seven. That is, a species would have to migrate along a minimum of seven linkages in order to move between the two most isolated reserves within the nature reserve network (i.e., Hale C.P. [Reserve 3] and Scott C.P.).

Addition of the rows or columns of the accessibility matrix now

Figure 24

Connectivity Matrix for Mount Lofty Ranges
Nature Reserve Network

Notes: Linkages not requiring roadside vegetation are given in bold print.

DC	EB	W	NS	Y	M	SM	S	CS	Fi	MM	K	Lo	T	TK	E	SG	SH	WP	BC	TE	G	Fe	B	Cl	HG	Mor	Ch	Le	Mon	BH	CC	Cr	W	H	PW	SC	
																																					SC
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																																			0	1	H
																																		0	1	0	W
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																												0	0	0	0	0	1	0	0	0	Ch
																											0	0	0	1	1	0	0	0	0	0	Mor
																										0	1	0	0	1	1	0	0	0	0	0	HG
																									0	1	1	0	0	1	1	0	0	0	0	0	Cl
																								0	1	0	0	0	0	1	0	0	0	0	0	0	B
																							0	0	1	1	1	0	0	0	0	0	0	0	0	0	Fe
																						0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	G
																					0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	TE
																				0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	BC
																			0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	WP
																		0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	SH
																	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	SG
																0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	0	E
															0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	0	TK
														0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	T
													0	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	Lo
												0	1	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	K
											0	1	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	MM
										0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Fi
									0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	CS
								0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	S
							0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	SM
						0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	M
					0	1	1	0	0	1	1	1	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	Y
				0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	NS
																																					W
																																					EB
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gives the accessibility value (AV) of each node within the network and hence each reserve's degree of isolation can be measured (Table 1). The three most accessible reserves within the network are again Montacute C.P. (AV = 57), Cleland C.P. (AV = 68) and Belair R.P. (AV = 60).[1] However, unlike the situation for the degrees of the nodes, where Belair R.P. had the greatest number of direct linkages, Montacute C.P. now becomes the most accessible reserve within the Mount Lofty Ranges. The three least accessible or isolated reserves in the network are Hale C.P. (AV = 137), Warren C.P. (Reserve 4, AV = 136) and Charleston C.P. (AV = 139) (Table 1).

Additional information on isolation can be obtained with the shortest-path technique by adding or subtracting nodes and their linkages and examining the effects of this operation on the remainder of the network. This approach has been used by both Wood (1975) and Reed (1970). These authors started by subtracting the most accessible node from their networks and then subtracting progressively less accessible nodes in order to test the 'structural integrity' (Tinkler, 1977) of the networks. Reed (1970, 366) noticed that by experimentally including or excluding nodes it is possible to identify those nodes or linkages that have *"the greatest effect on the connectivity for a given activity or the system as a whole"*.

Nature reserves within the Mount Lofty Ranges can be lost through a number of causes ranging from natural disasters, such as fire or disease, to legislation or mining. Therefore, it is important to

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[1] Accessibility values are inversely proportional to the degree of accessibility and directly proportional to the degree of isolation. Thus, an increase in a node's accessibility value is equivalent to a decrease in the node's accessibility or an increase in the node's isolation.

TABLE 1

Accessibility Values of Nature Reserves within the Networks created for the Mount Lofty Ranges

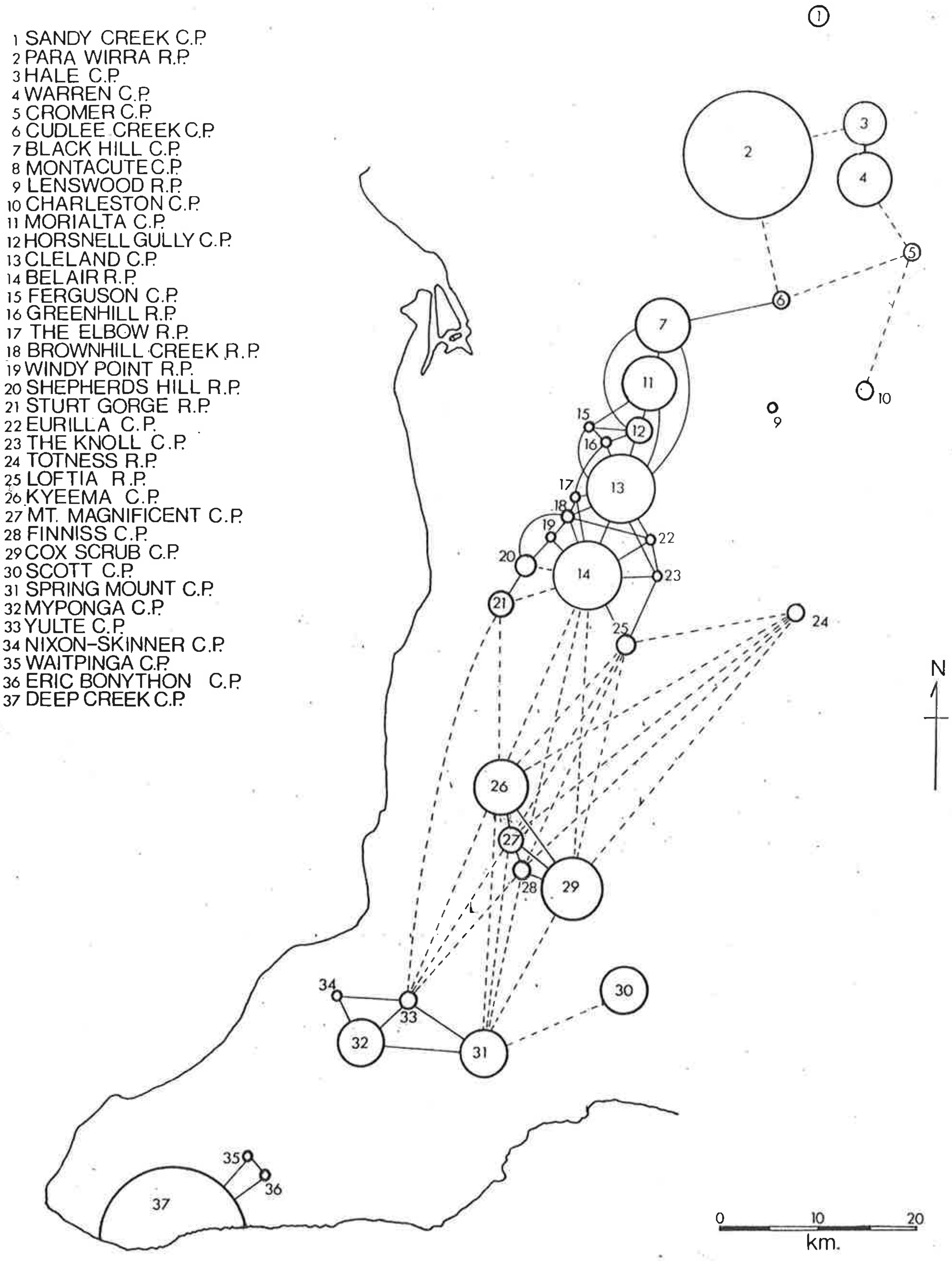
		Full Network	Minus Mon.	Minus Mon,B	Minus Cl Mon,B	Minus Cl, Mon,B,Lo	Minus Le Ch,S	Minus Cl, M,B,link	Plus P.radiata	Plus Mt.Bold	Plus Reserves	Plus Links
	NO. OF RESERVES	33	31	30	29	28	30	29	33	33	37	37
1	SANDY CREEK CP	-	-	-	-	-	-	-	-	-	165	163
2	PARA WIRRA RP	110	125	133	181	172	98	190	81	118	130	128
3	HALE CP	137	150	157	204	194	123	215	108	146	161	160
4	WARREN CP	136	149	156	203	193	123	214	108	145	161	149
5	CROMER CP	108	123	131	179	169	98	188	106	116	130	119
6	CUDLEE CK. CP	82	99	108	157	148	73	166	79	89	100	98
7	BLACK HILL CP	80	80	90	140	132	70	159	75	87	99	97
8	MONTACUTE CP	57	-	-	-	-	55	-	56	68	78	77
9	LENSWOOD RP	93	-	-	-	-	-	-	76	100	113	111
10	CHARLESTON CP	139	152	159	206	196	-	217	81	148	167	109
11	MORIALTA CP	85	85	95	145	138	74	154	78	92	105	104
12	HORSNELL G. CP	84	84	91	126	120	69	135	77	89	106	99
13	CLELAND CP	68	65	76	-	-	60	-	61	73	84	84
14	BELAIR RP	60	62	-	-	-	50	-	53	63	73	72
15	FERGUSON CP	96	91	102	133	127	83	142	89	102	117	116
16	GREENHILL RP	96	91	102	116	111	83	125	89	102	117	116
17	THE ELBOW RP	82	77	96	109	105	70	127	75	87	100	99
18	BROWNHILL CK RP	81	76	84	104	101	68	114	74	86	98	97
19	WINDY PT. RP	87	88	103	129	115	75	125	82	90	105	104
20	SHEPHERDS H. RP	86	87	92	117	104	74	112	81	88	104	103
21	STURT G'RGE RP	80	81	98	121	110	69	112	75	80	95	93
22	EURILLA CP	75	78	91	126	125	65	189	69	78	91	90
23	THE KNOLL CP	72	75	79	130	154	63	162	66	78	89	88
24	TOTNESS RP	90	99	101	139	144	79	139	84	91	108	93
25	LOFTIA RP	70	80	84	124	-	60	137	63	76	84	82
26	KYEEMA CP	75	76	95	119	122	65	119	69	97	87	82
27	MT. MAG'ENT CP	75	76	96	134	139	65	134	69	98	88	83
28	FINNISS CP	86	95	97	135	140	74	135	80	99	98	93
29	COX SCRUB CP	76	77	98	136	141	65	135	70	105	90	85
30	SCOTT CP	127	125	139	163	164	-	163	120	131	142	136
31	SPRING MT. CP	96	95	111	136	138	85	135	92	99	107	102
32	MYPONGA CP	102	101	131	144	143	90	143	97	105	113	109
33	YULTE CP	75	76	107	121	121	65	121	70	77	87	85
34	NIXON-SK'ER CP	105	104	134	147	146	92	146	100	108	119	115
35	WAITPINGA CP	-	-	-	-	-	-	-	-	-	144	140
36	ERIC·BONYTON CP	-	-	-	-	-	-	-	-	-	137	134
37	DEEP CK. CP	-	-	-	-	-	-	-	-	-	170	166
	Network Diameter	7	8	9	12	12	6	13	6	7	8	8
	Aver. Access.Value	90·0	94·3	98·0	142·2	139·7	76·1	50·1	80·4	96·8	112·5	107·6

discover the effects of reserve omission on the overall conservation viability of the Mount Lofty Ranges nature reserve system.

Figure 25 illustrates the Mount Lofty Ranges nature reserve network minus Montacute C.P., the most accessible nature reserve (the resultant matrix is given in Appendix B). With the omission of Montacute C.P. significant changes in the network values are already apparent. For instance, the network diameter has increased from seven to eight, even though the number of reserves within the network has been reduced from 33 to 31 (Lenswood R.P. is disconnected from the network with the removal of Montacute C.P.) (Table 1). Biogeographically, this means that the two most isolated reserves within the network have now become even more isolated; a minimum of eight linkages need to be traversed for interaction between these two reserves to occur. In addition, the average accessibility value (AAV) of the newly created network (Fig. 25) is greater than that for the original network (Fig. 24), the values being 94.8 and 90.0 respectively (Table 1). The greatest increases in accessibility values are felt by the outlying nature reserves within the network, particularly those to the north (e.g., Para Wirra R.P. [Reserve 2], Cromer C.P. [Reserve 5], etc.)(Table 1). Montacute C.P. acts as a stepping-stone reserve between the northern and central reserve concentrations. With its removal the northern reserves are forced to rely solely on the linkage between Cudlee Creek C.P. (Reserve 6) and Black Hill C.P. (Reserve 7) and then the linkages along the western ridge of the Ranges for their connection to the most accessible nature reserves (Fig. 25). This has led to the increased isolation of the northern nature reserves compared with the remainder of the network,

Figure 25

Mount Lofty Ranges nature reserve network minus
1. Montacute C.P.


1 SANDY CREEK C.P.
2 PARA WIRRA R.P.
3 HALE C.P.
4 WARREN C.P.
5 CROMER C.P.
6 CUDLEE CREEK C.P.
7 BLACK HILL C.P.
8 MONTACUTE C.P.
9 LENSWOOD R.P.
10 CHARLESTON C.P.
11 MORIALTA C.P.
12 HORSNELL GULLY C.P.
13 CLELAND C.P.
14 BELAIR R.P.
15 FERGUSON C.P.
16 GREENHILL R.P.
17 THE ELBOW R.P.
18 BROWNHILL CREEK R.P.
19 WINDY POINT R.P.
20 SHEPHERDS HILL R.P.
21 STURT GORGE R.P.
22 EURILLA C.P.
23 THE KNOLL C.P.
24 TOTNESS R.P.
25 LOFTIA R.P.
26 KYEEMA C.P.
27 MT. MAGNIFICENT C.P.
28 FINNISS C.P.
29 COX SCRUB C.P.
30 SCOTT C.P.
31 SPRING MOUNT C.P.
32 MYPONGA C.P.
33 YULTE C.P.
34 NIXON-SKINNER C.P.
35 WAITPINGA C.P.
36 ERIC BONYTHON C.P.
37 DEEP CREEK C.P.
1
2
3
4
5
6
7
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
N
0
10
20
km.

When the second most accessible nature reserve (i.e., Belair R.P.) is also removed from the nature reserve network (Figure 26, Appendix C) a similar pattern emerges. The reserve diameter again increases to nine and the AAV increases to 98.0 (Table 1). However, this time the southern nature reserves receive the greatest increases in accessibility values (e.g., Cox Scrub C.P. [Reserve 29], Nixon-Skinner C.P. [Reserve 34], etc.) (Table 1).

The removal of the third most accessible nature reserve, Cleland C.P., in conjunction with Montacute C.P. and Belair R.P., produces dramatic changes in the network's accessibility values (Figure 27, Appendix D). For instance, the network diameter increases to 12, even though only 29 nature reserves remain within the network (Table 1). This immediately suggests that accessibility *through* the network is poor, although a few concentrations of nature reserves still retain their internal connectivity (Figure 27). Low accessibility through a network generally implies the existence of cutpoints or bridges.[2] In Figure 27 there are five cutpoints, two of which (Black Hill C.P. and Cudlee Creek C.P.) existed in previous networks. The newly created cutpoints are Greenhill R.P. (Reserve 16), The Elbow R.P. (Reserve 17) and Brownhill Creek R.P. (Reserve 18). The largest of these, Brownhill Creek R.P., is only 52 hectares in size. Thus, with the omission of the three most accessible nature reserves, the resultant network is forced to rely on five small reserves in order to maintain its structural integrity.

---

[2] A *cutpoint* is a node whose removal together with the incident links will result in a graph becoming disconnected.

A *bridge* is a single link whose removal disconnects the graph (the nodes at either end are not removed) (Tinkler, 1977).

Figure <u>26</u>

Moung Lofty Ranges Nature Reserve Network minus
1. Belair R.P.
and 2. Montacute C.P.

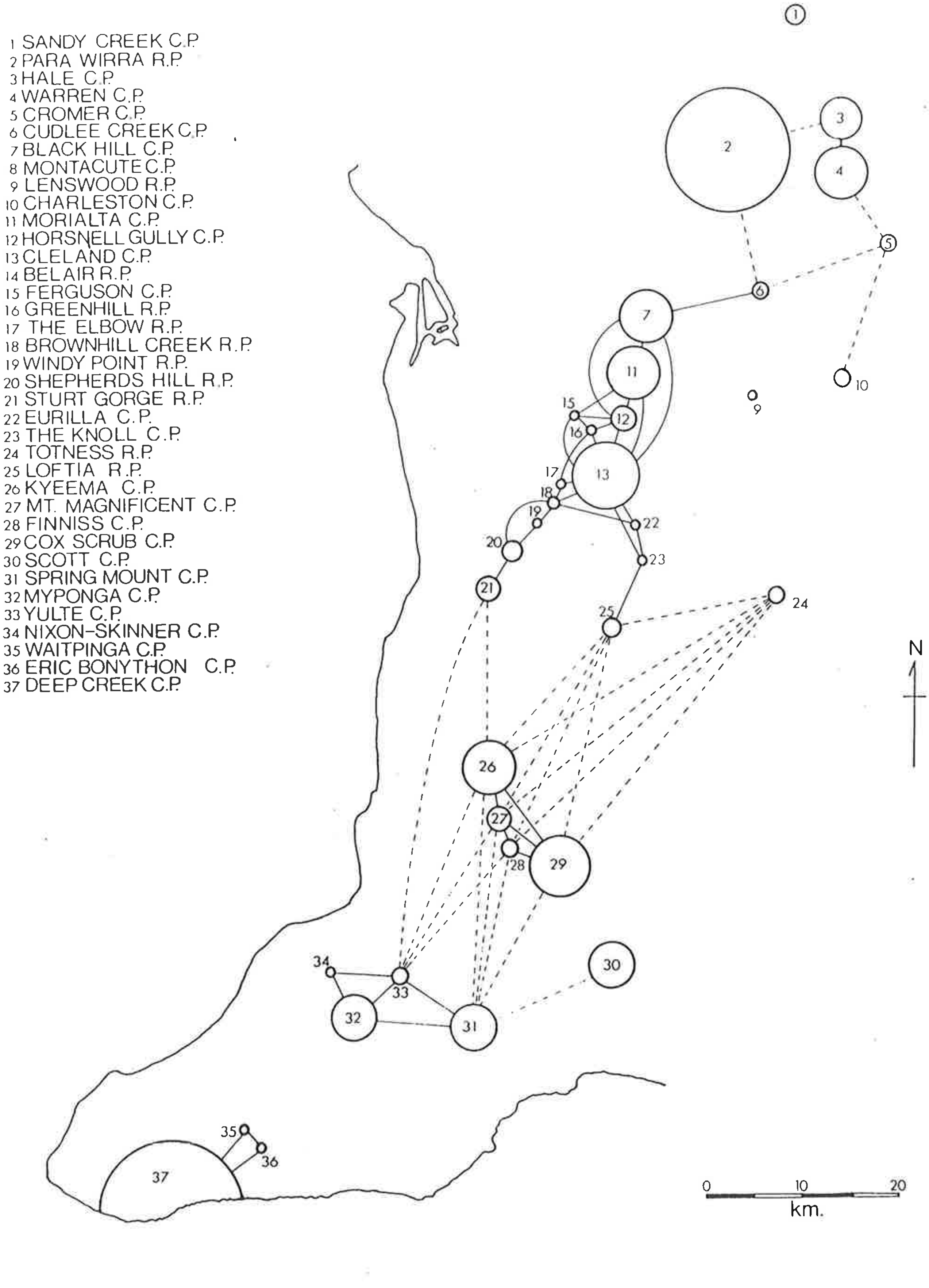
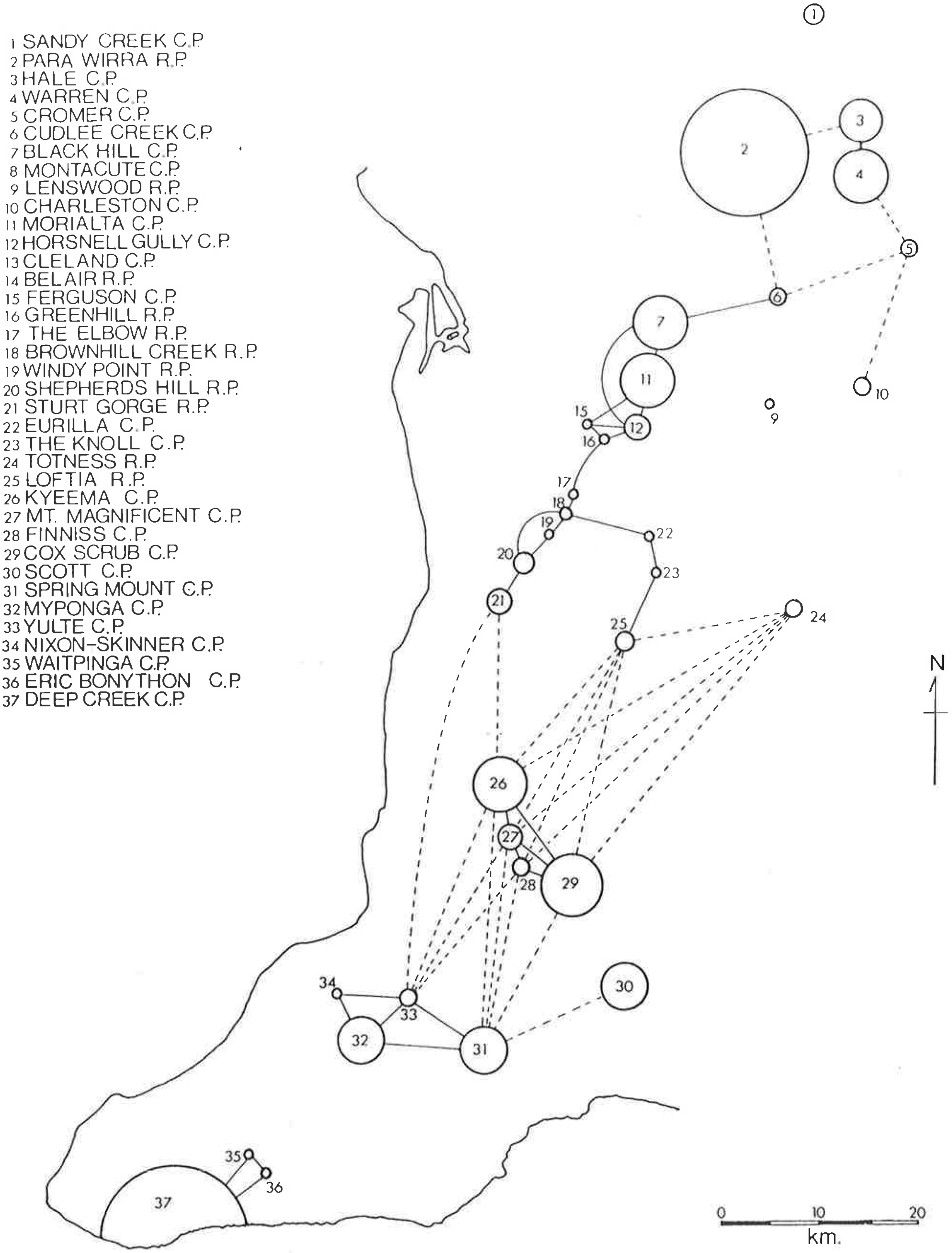

1 SANDY CREEK C.P.
2 PARA WIRRA R.P.
3 HALE C.P.
4 WARREN C.P.
5 CROMER C.P.
6 CUDLEE CREEK C.P.
7 BLACK HILL C.P.
8 MONTACUTE C.P.
9 LENSWOOD R.P.
10 CHARLESTON C.P.
11 MORIALTA C.P.
12 HORSNELL GULLY C.P.
13 CLELAND C.P.
14 BELAIR R.P.
15 FERGUSON C.P.
16 GREENHILL R.P.
17 THE ELBOW R.P.
18 BROWNHILL CREEK R.P.
19 WINDY POINT R.P.
20 SHEPHERDS HILL R.P.
21 STURT GORGE R.P.
22 EURILLA C.P.
23 THE KNOLL C.P.
24 TOTNESS R.P.
25 LOFTIA R.P.
26 KYEEMA C.P.
27 MT. MAGNIFICENT C.P.
28 FINNISS C.P.
29 COX SCRUB C.P.
30 SCOTT C.P.
31 SPRING MOUNT C.P.
32 MYPONGA C.P.
33 YULTE C.P.
34 NIXON-SKINNER C.P.
35 WAITPINGA C.P.
36 ERIC BONYTHON C.P.
37 DEEP CREEK C.P.
N
0
10
20
km.

Figure 27

Mount Lofty Ranges Nature Reserve Network minus
1. Belair R.P.
2. Montacute C.P.
and 3. Cleland C.P.


1 SANDY CREEK C.P.
2 PARA WIRRA R.P.
3 HALE C.P.
4 WARREN C.P.
5 CROMER C.P.
6 CUDLEE CREEK C.P.
7 BLACK HILL C.P.
8 MONTACUTE C.P.
9 LENSWOOD R.P.
10 CHARLESTON C.P.
11 MORIALTA C.P.
12 HORSNELL GULLY C.P.
13 CLELAND C.P.
14 BELAIR R.P.
15 FERGUSON C.P.
16 GREENHILL R.P.
17 THE ELBOW R.P.
18 BROWNHILL CREEK R.P.
19 WINDY POINT R.P.
20 SHEPHERDS HILL R.P.
21 STURT GORGE R.P.
22 EURILLA C.P.
23 THE KNOLL C.P.
24 TOTNESS R.P.
25 LOFTIA R.P.
26 KYEEMA C.P.
27 MT. MAGNIFICENT C.P.
28 FINNISS C.P.
29 COX SCRUB C.P.
30 SCOTT C.P.
31 SPRING MOUNT C.P.
32 MYPONGA C.P.
33 YULTE C.P.
34 NIXON-SKINNER C.P.
35 WAITPINGA C.P.
36 ERIC BONYTHON C.P.
37 DEEP CREEK C.P.
N
0
10
20
km.

The AAV for Figure 27 is 142.2 (Table 1), an increase of 52.2 over the original network (Fig. 22). Figure 28 clearly illustrates the impact of the additional removal of Cleland C.P. on the AAV of the nature reserve network. Again the increase is felt more in the outlying reserves, particularly the northern reserves (Table 1). Thus, the outlying reserves are becoming increasingly isolated with respect to the network as a whole as those reserves with the greatest accessibility are removed.

To aid in the appreciation of the detrimental effects on the network's integrity by the removal of the three most accessible nature reserves, a comparison can be made by removing the three most isolated reserves (i.e., Lenswood R.P., Charleston C.P., Scott C.P.) (Fig. 29, Appendix E). The removal of these reserves leaves a total of 30 nature reserves remaining in the network (Table 1), one more than Figure 27. However, the diameter of Figure 29 is only six, half that of Figure 27, and the AAV is significantly reduced to 76.1, compared with 142.2 for Figure 27 and 90.0 for Figure 22 (original network)(Table 1). Thus, the removal of the three least accessible nodes within the network has produced the opposite effect on network integrity to the removal of the three most accessible nodes.

The removal of additional nodes after Belair R.P., Montacute C.P. and Cleland C.P. produces little change in the diameter and accessibility values, as long as the network remains connected. For instance, the omission of the fourth most accessible nature reserve (Loftia R.P. Reserve 25) together with the three most accessible nature reserves (Fig. 30, Appendix F), produces results similar to those for Figure 27 (Table 1). The levelling-off of values is clearly illustrated in Figure 28. However, with the removal of Loftia R.P. increased

Figure 28

Change in Network AAV and Diameter with removal of successive reserves with greatest accessibility

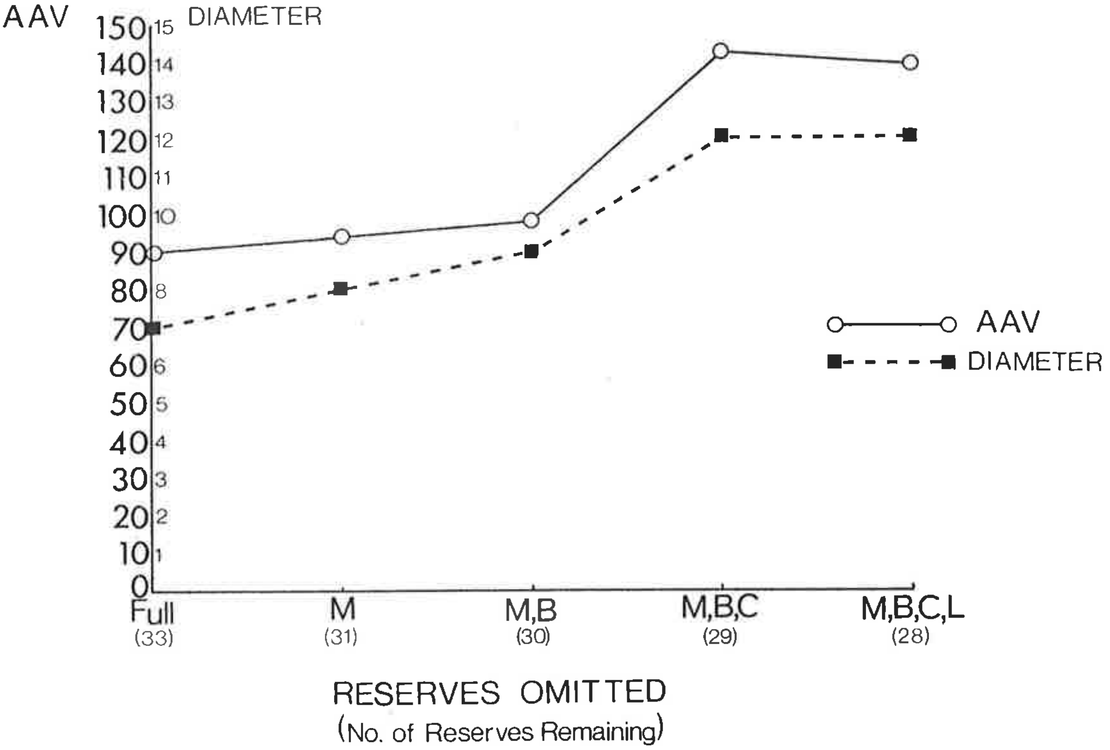

AAV
DIAMETER
150 15
140 14
130 13
120 12
110 11
100 10
90 9
80 8
70 7
60 6
50 5
40 4
30 3
20 2
10 1
0
Full (33)
M (31)
M,B (30)
M,B,C (29)
M,B,C,L (28)
RESERVES OMITTED
(No. of Reserves Remaining)
○——○ AAV
■- - - -■ DIAMETER

Figure 29

Mount Lofty Ranges Nature Reserve Network minus
1. Lenswood R.P.
2. Charleston C.P.
and 3. Scott C.P.

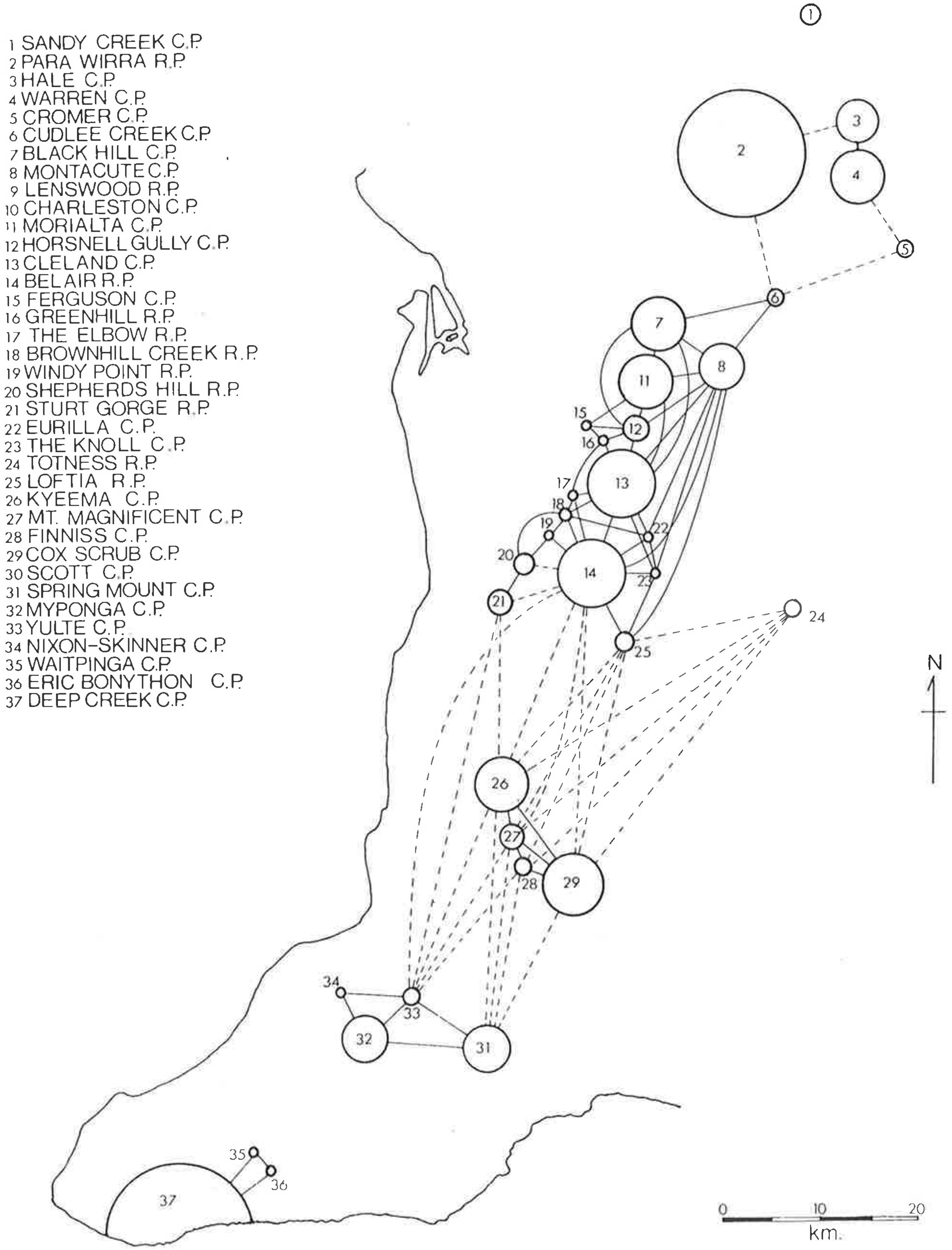
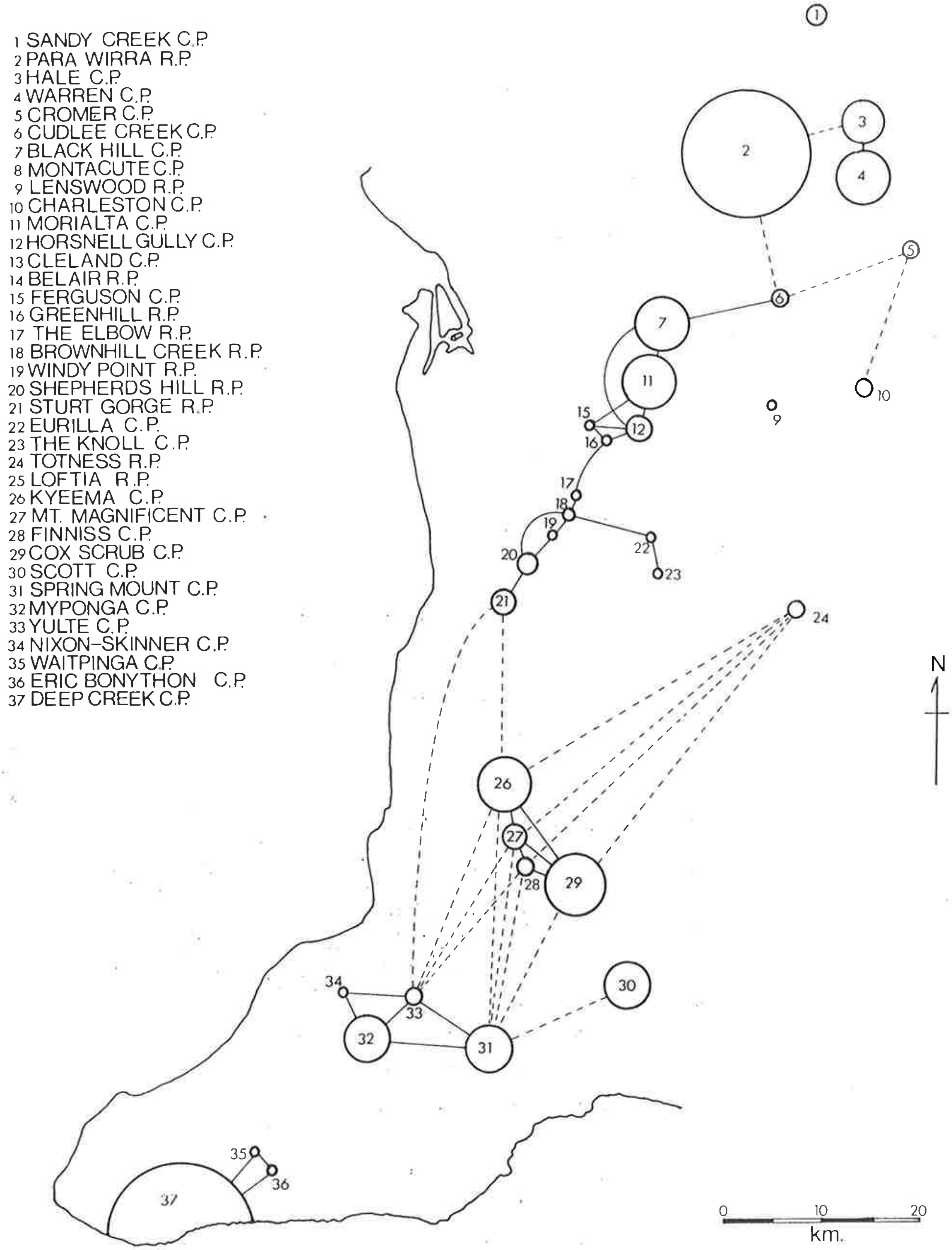

1 SANDY CREEK C.P.
2 PARA WIRRA R.P.
3 HALE C.P.
4 WARREN C.P.
5 CROMER C.P.
6 CUDLEE CREEK C.P.
7 BLACK HILL C.P.
8 MONTACUTE C.P.
9 LENSWOOD R.P.
10 CHARLESTON C.P.
11 MORIALTA C.P.
12 HORSNELL GULLY C.P.
13 CLELAND C.P.
14 BELAIR R.P.
15 FERGUSON C.P.
16 GREENHILL R.P.
17 THE ELBOW R.P.
18 BROWNHILL CREEK R.P.
19 WINDY POINT R.P.
20 SHEPHERDS HILL R.P.
21 STURT GORGE R.P.
22 EURILLA C.P.
23 THE KNOLL C.P.
24 TOTNESS R.P.
25 LOFTIA R.P.
26 KYEEMA C.P.
27 MT. MAGNIFICENT C.P.
28 FINNISS C.P.
29 COX SCRUB C.P.
30 SCOTT C.P.
31 SPRING MOUNT C.P.
32 MYPONGA C.P.
33 YULTE C.P.
34 NIXON-SKINNER C.P.
35 WAITPINGA C.P.
36 ERIC BONYTHON C.P.
37 DEEP CREEK C.P.
N
0
10
20
km.

Figure 30

Mount Lofty Ranges Nature Reserve Network minus
1. Belair R.P.
2. Montacute C.P.
3. Cleland C.P.
and 4. Loftia R.P.


1 SANDY CREEK C.P
2 PARA WIRRA R.P
3 HALE C.P
4 WARREN C.P
5 CROMER C.P
6 CUDLEE CREEK C.P
7 BLACK HILL C.P
8 MONTACUTE C.P
9 LENSWOOD R.P
10 CHARLESTON C.P
11 MORIALTA C.P
12 HORSNELL GULLY C.P
13 CLELAND C.P
14 BELAIR R.P
15 FERGUSON C.P
16 GREENHILL R.P
17 THE ELBOW R.P
18 BROWNHILL CREEK R.P
19 WINDY POINT R.P.
20 SHEPHERDS HILL R.P
21 STURT GORGE R.P
22 EURILLA C.P.
23 THE KNOLL C.P
24 TOTNESS R.P
25 LOFTIA R.P.
26 KYEEMA C.P
27 MT. MAGNIFICENT C.P
28 FINNISS C.P
29 COX SCRUB C.P
30 SCOTT C.P
31 SPRING MOUNT C.P
32 MYPONGA C.P
33 YULTE C.P
34 NIXON-SKINNER C.P
35 WAITPINGA C.P
36 ERIC BONYTHON C.P
37 DEEP CREEK C.P
1
2
3
4
5
6
7
11
9
10
15
12
16
17
18
19
22
20
23
21
24
N
26
27
28
29
34
33
30
32
31
35
36
37
0
10
20
km.

importance is placed on Sturt Gorge R.P. which becomes a cutpoint between the northern and southern sectors of the network (Fig. 30).

The removal of links rather than nodes from a network can equally lessen its structural integrity. For example, Figure 31 and Appendix G portray the network minus the nature reserves Belair R.P., Montacute C.P. and Cleland C.P. and also minus the Brownhill Creek R.P.-Eurilla C.P. (Reserve 22) link (an important bridge). The consequent network has values of 13 for its diameter and 150.1 for its AAV (Table 1), both of which are larger than those obtained for Figure 30. Thus, the removal of a critical linkage may have a greater effect on a network than the omission of a reasonably accessible node plus its incident linkages. This is an important point when considering the overall conservation viability of the Mount Lofty Ranges nature reserve network.

The analysis of node or linkage additions to a network can be as important as the analysis of node or linkage subtractions. For example, within the Mount Lofty Ranges *Pinus radiata* plantations may be important corridors of movement for many native species as well as native species habitats in their own right. Numerous studies have demonstrated the ability of exotic plantations to support populations of native birds and mammals (e.g., Barnett, How and Humphreys, 1977; Gepp, 1976; Gepp and Fife, 1975; Shurcliff, 1974; Suckling and Heislers, 1978; etc.).

Figure 32 and Appendix H represent the original reserve network (Fig. 22) with exotic pine plantations included as linkages between the nature reserves. From Figure 32 it is obvious that Mount Crawford Forest has a significant impact upon the connectivity of the northern nature reserves (e.g., Lenswood R.P., Para Wirra R.P., etc.).

Figure 31

Mount Lofty Ranges Nature Reserve Network minus
1. Belair R.P.
2. Montacute C.P.
3. Cleland C.P.
and 4. Brownhill Creek R.P.-Eurilla C.P. linkage

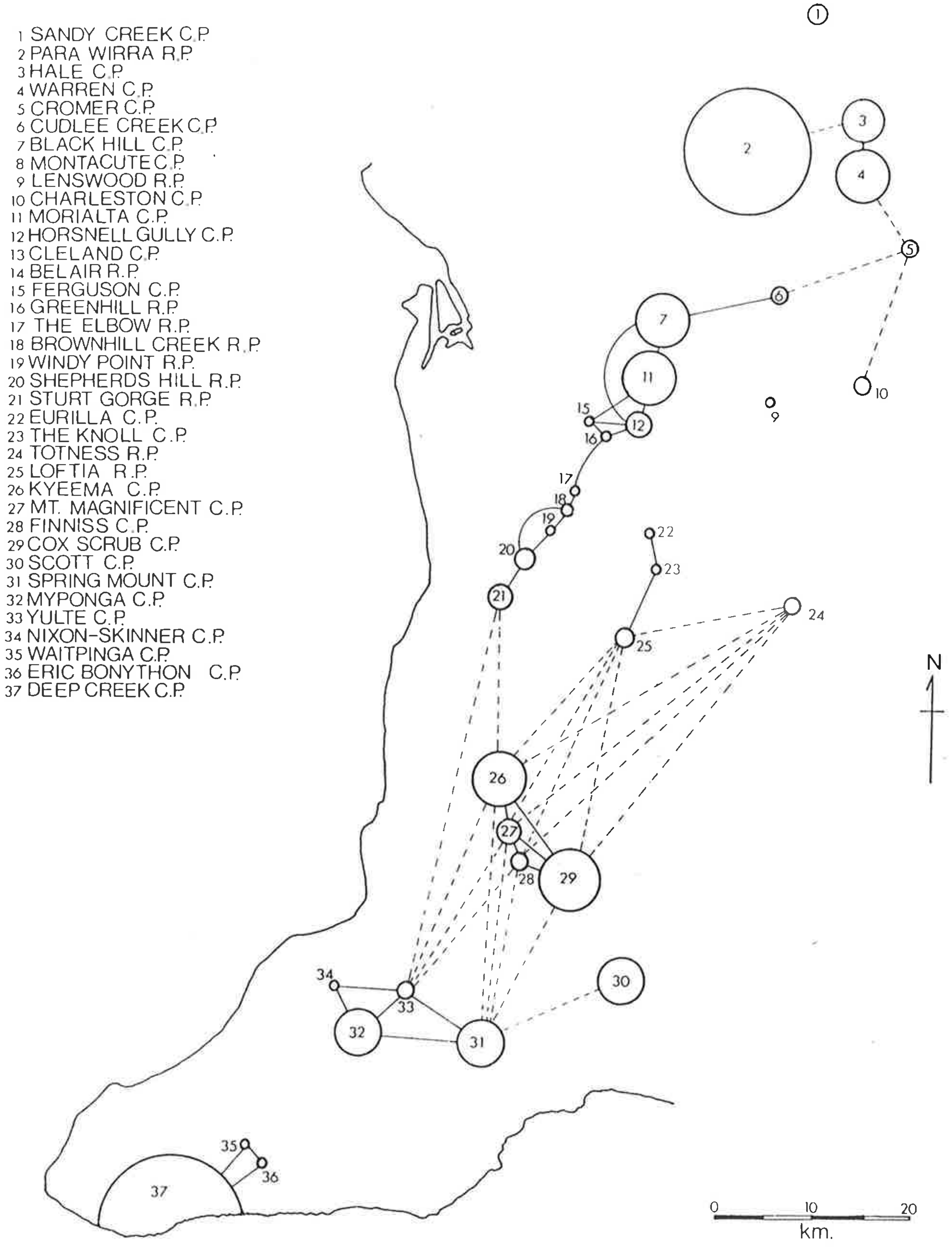
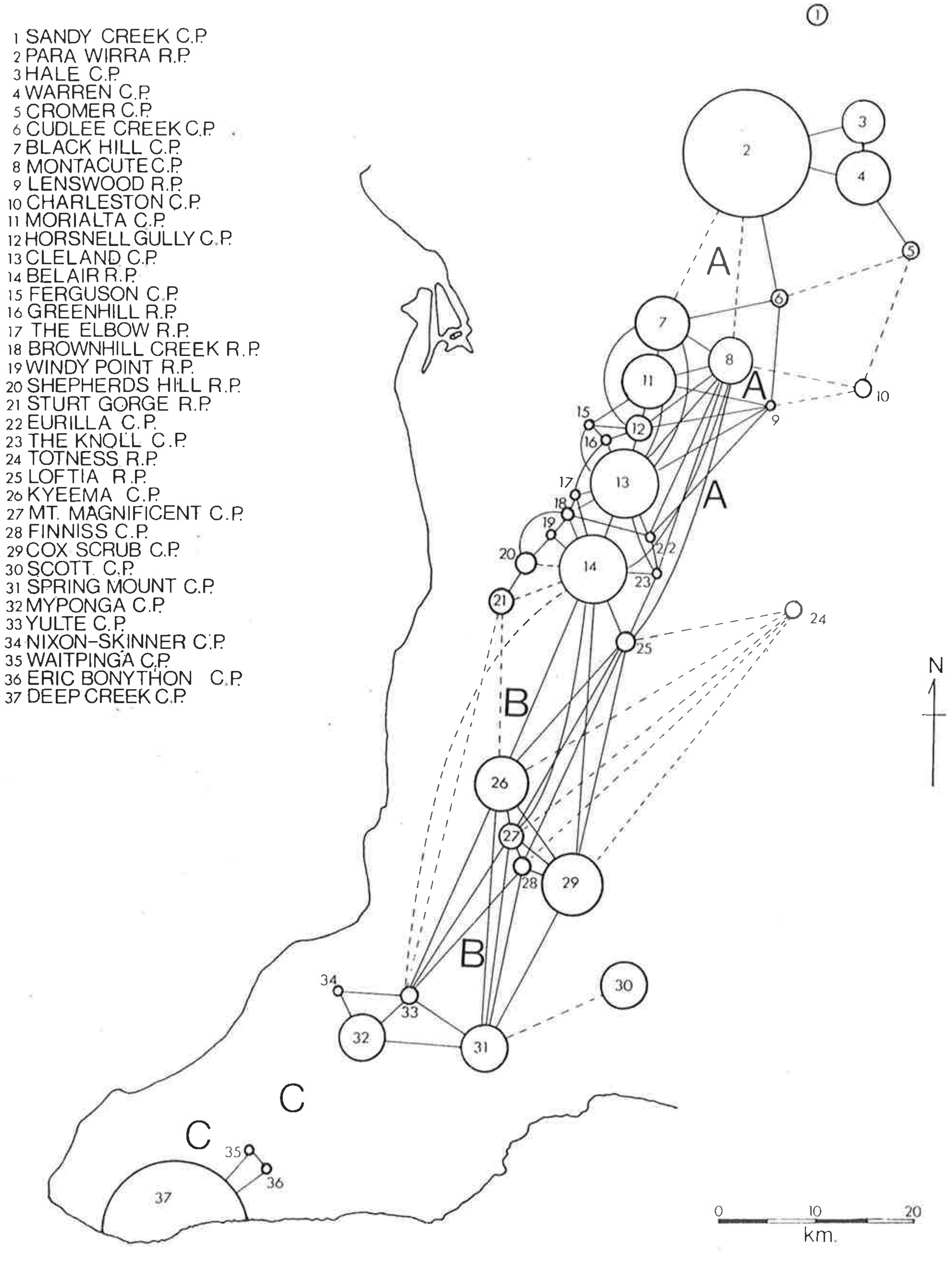

1 SANDY CREEK C.P.
2 PARA WIRRA R.P.
3 HALE C.P.
4 WARREN C.P.
5 CROMER C.P.
6 CUDLEE CREEK C.P.
7 BLACK HILL C.P.
8 MONTACUTE C.P.
9 LENSWOOD R.P.
10 CHARLESTON C.P.
11 MORIALTA C.P.
12 HORSNELL GULLY C.P.
13 CLELAND C.P.
14 BELAIR R.P.
15 FERGUSON C.P.
16 GREENHILL R.P.
17 THE ELBOW R.P.
18 BROWNHILL CREEK R.P.
19 WINDY POINT R.P.
20 SHEPHERDS HILL R.P.
21 STURT GORGE R.P.
22 EURILLA C.P.
23 THE KNOLL C.P.
24 TOTNESS R.P.
25 LOFTIA R.P.
26 KYEEMA C.P.
27 MT. MAGNIFICENT C.P.
28 FINNISS C.P.
29 COX SCRUB C.P.
30 SCOTT C.P.
31 SPRING MOUNT C.P.
32 MYPONGA C.P.
33 YULTE C.P.
34 NIXON-SKINNER C.P.
35 WAITPINGA C.P.
36 ERIC BONYTHON C.P.
37 DEEP CREEK C.P.
N
0
10
20
km.

Figure 32

Mount Lofty Ranges Nature Reserve Network plus Woods and Forests *Pinus radiata* plantations

A. Mount Crawford Forest District
B. Kuitpo Forest District
C. Second Valley Forest District


1 SANDY CREEK C.P.
2 PARA WIRRA R.P.
3 HALE C.P.
4 WARREN C.P.
5 CROMER C.P.
6 CUDLEE CREEK C.P.
7 BLACK HILL C.P.
8 MONTACUTE C.P.
9 LENSWOOD R.P.
10 CHARLESTON C.P.
11 MORIALTA C.P.
12 HORSNELL GULLY C.P.
13 CLELAND C.P.
14 BELAIR R.P.
15 FERGUSON C.P.
16 GREENHILL R.P.
17 THE ELBOW R.P.
18 BROWNHILL CREEK R.P.
19 WINDY POINT R.P.
20 SHEPHERDS HILL R.P.
21 STURT GORGE R.P.
22 EURILLA C.P.
23 THE KNOLL C.P.
24 TOTNESS R.P.
25 LOFTIA R.P.
26 KYEEMA C.P.
27 MT. MAGNIFICENT C.P.
28 FINNISS C.P.
29 COX SCRUB C.P.
30 SCOTT C.P.
31 SPRING MOUNT C.P.
32 MYPONGA C.P.
33 YULTE C.P.
34 NIXON-SKINNER C.P.
35 WAITPINGA C.P.
36 ERIC BONYTHON C.P.
37 DEEP CREEK C.P.
A
A
A
B
B
C
C
N
0
10
20
km.

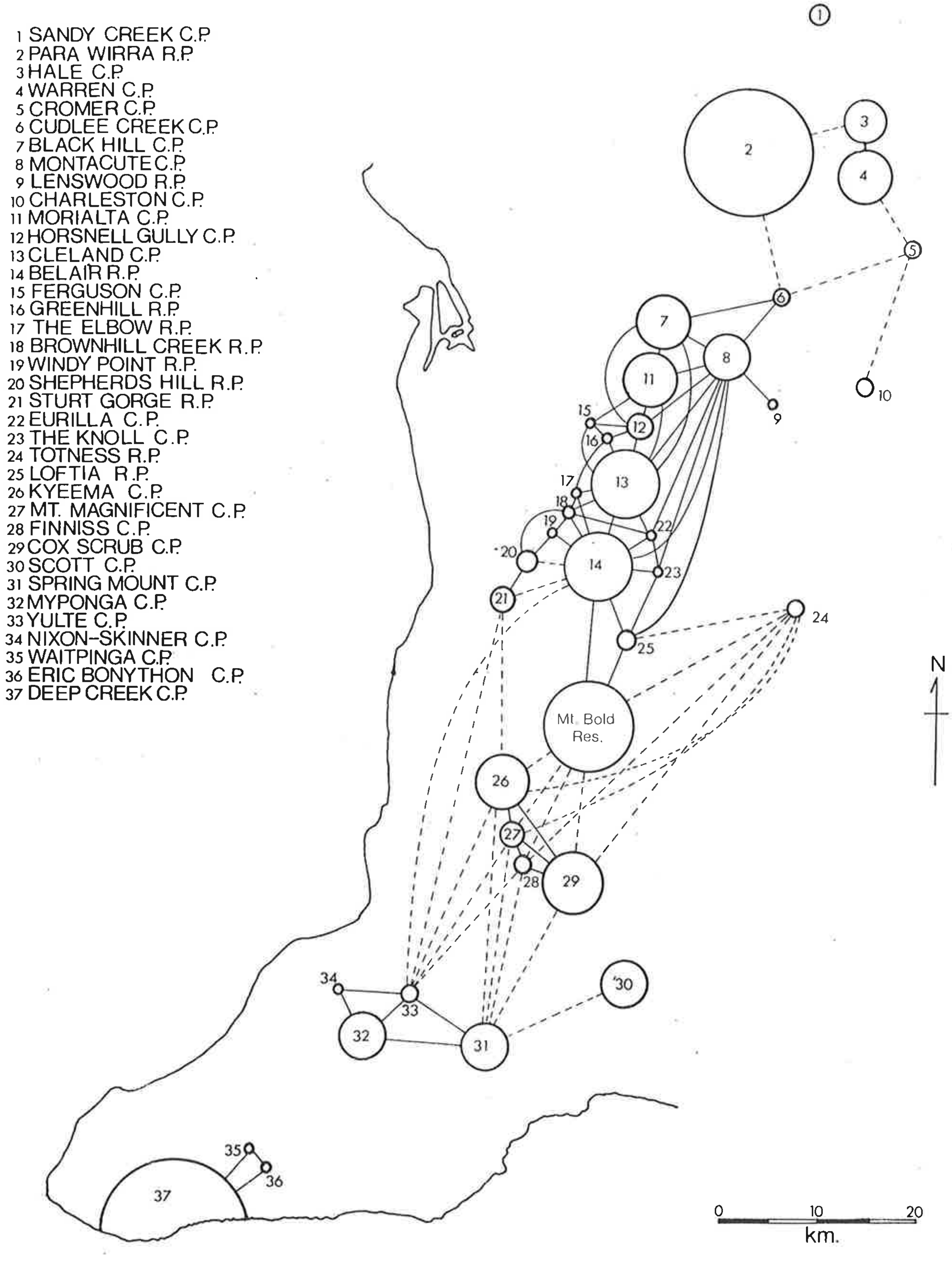
The inclusion of Second Valley Forest, on the other hand, has no effect on the accessibilities of the southern reserves. The inclusion of the *P. radiata* plantations reduces the diameter of the nature reserve network to six and decreases the AAV from 90.0 to 80.4 (Table 1). Most of this reduction in the AAV is experienced by the northern reserves and this makes Belair R.P. the most accessible nature reserve with an AV of 53 (Table 1).

The addition of a node to a network can significantly effect the network's structural values. Thus, the designation of a patch of native vegetation as a nature reserve within the Mount Lofty Ranges would produce a different network structure and hence difference structural values. For example, the addition of the Mount Bold Reservoir Catchment Area to the reserve network as a newly designated reserve (Figure 33, Appendix I) would have the following effects. There would be no effect on the network diameter, which remains at seven, but the AAV would be increased to 96.8 due to the extra linkages now provided between many of the southern and central nature reserves (Table 1, Figure 33). Again, Belair R.P. becomes the most accessible reserve, ahead of Montacute C.P. Different placement of additional nature reserves would produce different structural values for the network and this is an important consideration in optimizing network design.

To this point, reserves disconnected from the main reserve network (i.e., Sandy Creek C.P., Eric Bonython C.P., Waitpinga C.P., Deep Creek C.P.) have been excluded from the analyses. However, to assist in maintaining the viability of these reserves, particularly the smaller ones, attempts should be made to connect these reserves to the Mount Lofty Ranges network. Although the addition of these

Figure 33

Mount Lofty Ranges Nature Reserve Network plus
Mount Bold Reservoir Catchment Area


1 SANDY CREEK C.P.
2 PARA WIRRA R.P.
3 HALE C.P.
4 WARREN C.P.
5 CROMER C.P.
6 CUDLEE CREEK C.P.
7 BLACK HILL C.P.
8 MONTACUTE C.P.
9 LENSWOOD R.P.
10 CHARLESTON C.P.
11 MORIALTA C.P.
12 HORSNELL GULLY C.P.
13 CLELAND C.P.
14 BELAIR R.P.
15 FERGUSON C.P.
16 GREENHILL R.P.
17 THE ELBOW R.P.
18 BROWNHILL CREEK R.P.
19 WINDY POINT R.P.
20 SHEPHERDS HILL R.P.
21 STURT GORGE R.P.
22 EURILLA C.P.
23 THE KNOLL C.P.
24 TOTNESS R.P.
25 LOFTIA R.P.
26 KYEEMA C.P.
27 MT. MAGNIFICENT C.P.
28 FINNISS C.P.
29 COX SCRUB C.P.
30 SCOTT C.P.
31 SPRING MOUNT C.P.
32 MYPONGA C.P.
33 YULTE C.P.
34 NIXON-SKINNER C.P.
35 WAITPINGA C.P.
36 ERIC BONYTHON C.P.
37 DEEP CREEK C.P.
①
2
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Mt. Bold Res.
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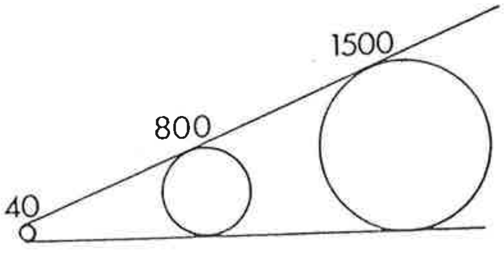
30
31
32
33
34
35
36
37
N
0
10
20
km.

Figure 34

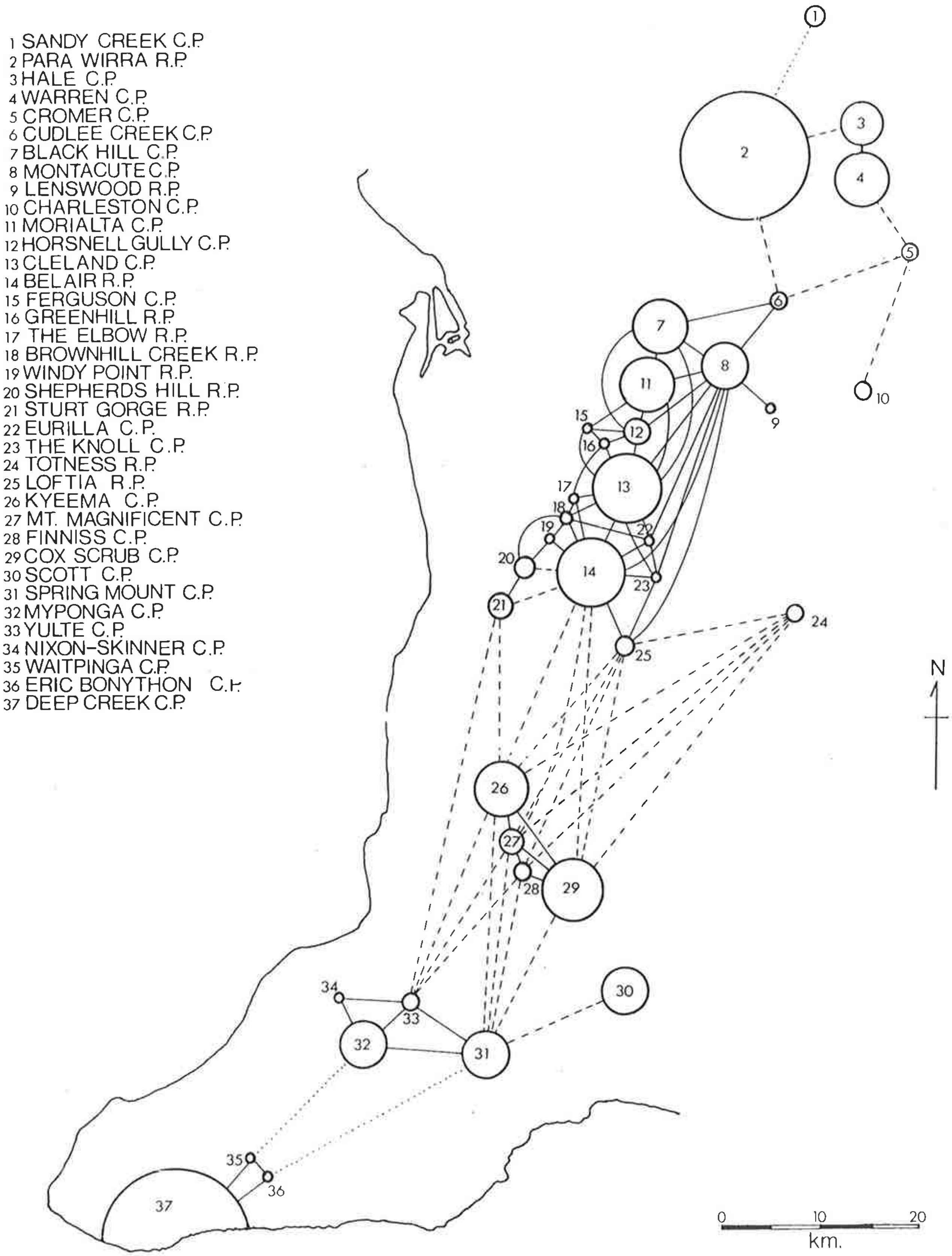
Mount Lofty Ranges Nature Reserve Network plus

1. Sandy Creek C.P.
2. Deep Creek C.P.
3. Waitpinga C.P.
and 4. Eric Bonython C.P.



Size of Nature Reserves
(ha.)

———	Corridors
— — — —	Corridors requiring roadside vegetation
....	Corridors added to network



1 SANDY CREEK C.P.
2 PARA WIRRA R.P.
3 HALE C.P.
4 WARREN C.P.
5 CROMER C.P.
6 CUDLEE CREEK C.P.
7 BLACK HILL C.P.
8 MONTACUTE C.P.
9 LENSWOOD R.P.
10 CHARLESTON C.P.
11 MORIALTA C.P.
12 HORSNELL GULLY C.P.
13 CLELAND C.P.
14 BELAIR R.P.
15 FERGUSON C.P.
16 GREENHILL R.P.
17 THE ELBOW R.P.
18 BROWNHILL CREEK R.P.
19 WINDY POINT R.P.
20 SHEPHERDS HILL R.P.
21 STURT GORGE R.P.
22 EURILLA C.P.
23 THE KNOLL C.P.
24 TOTNESS R.P.
25 LOFTIA R.P.
26 KYEEMA C.P.
27 MT. MAGNIFICENT C.P.
28 FINNISS C.P.
29 COX SCRUB C.P.
30 SCOTT C.P.
31 SPRING MOUNT C.P.
32 MYPONGA C.P.
33 YULTE C.P.
34 NIXON-SKINNER C.P.
35 WAITPINGA C.P.
36 ERIC BONYTHON C.P.
37 DEEP CREEK C.P.

four disconnected reserves to the network creates a situation of overall decreased network accessibility (due to the additional links required between Sandy Creek C.P. and Para Wirra R.P., Myponga C.P. [Reserve 32] and Waitpinga C.P. and Spring Mount C.P. [Reserve 31] and Eric Bonython C.P., [Fig. 34, Appendix J]) this can be offset by the inclusion of additional linkages within the network. For instance, the AAV for the extended network (Fig. 34) is 112.5 (Table 1), an increase of about 25 per cent over the original nature reserve network (Fig. 22). However, with the inclusion of only two new linkages (i.e., Cudlee Creek C.P.-Charleston C.P., Charleston C.P.-Totness R.P. [Reserve 24]) (Figure 35, Appendix K) the AAV can be reduced to 107.6 (Table 1) which, although still moderately high, is significantly less than the network minus these additional links (Fig. 34). The reduction results largely from the greater accessibility enjoyed by Charleston C.P.. With only two additional links the AV of Charleston C.P. is reduced from 167 to 109 (Table 1). Thus, by creating new linkages, once isolated nature reserves can be integrated with a network system and play a far greater role in overall conservation strategy.

Likewise, the subtraction of linkages can isolate once readily accessible reserves from a network or split the network into a number of smaller units. Those linkages that require roadside vegetation for their existence were differentiated from those which do not during the initial stages of the network analyses. Roadside vegetation, however, does have disadvantages for the movement of biota, as discussed in the opening chapter, and thus, for some species, it may not be utilized as biological corridors. If the linkages requiring roadside vegetation are removed from the original nature

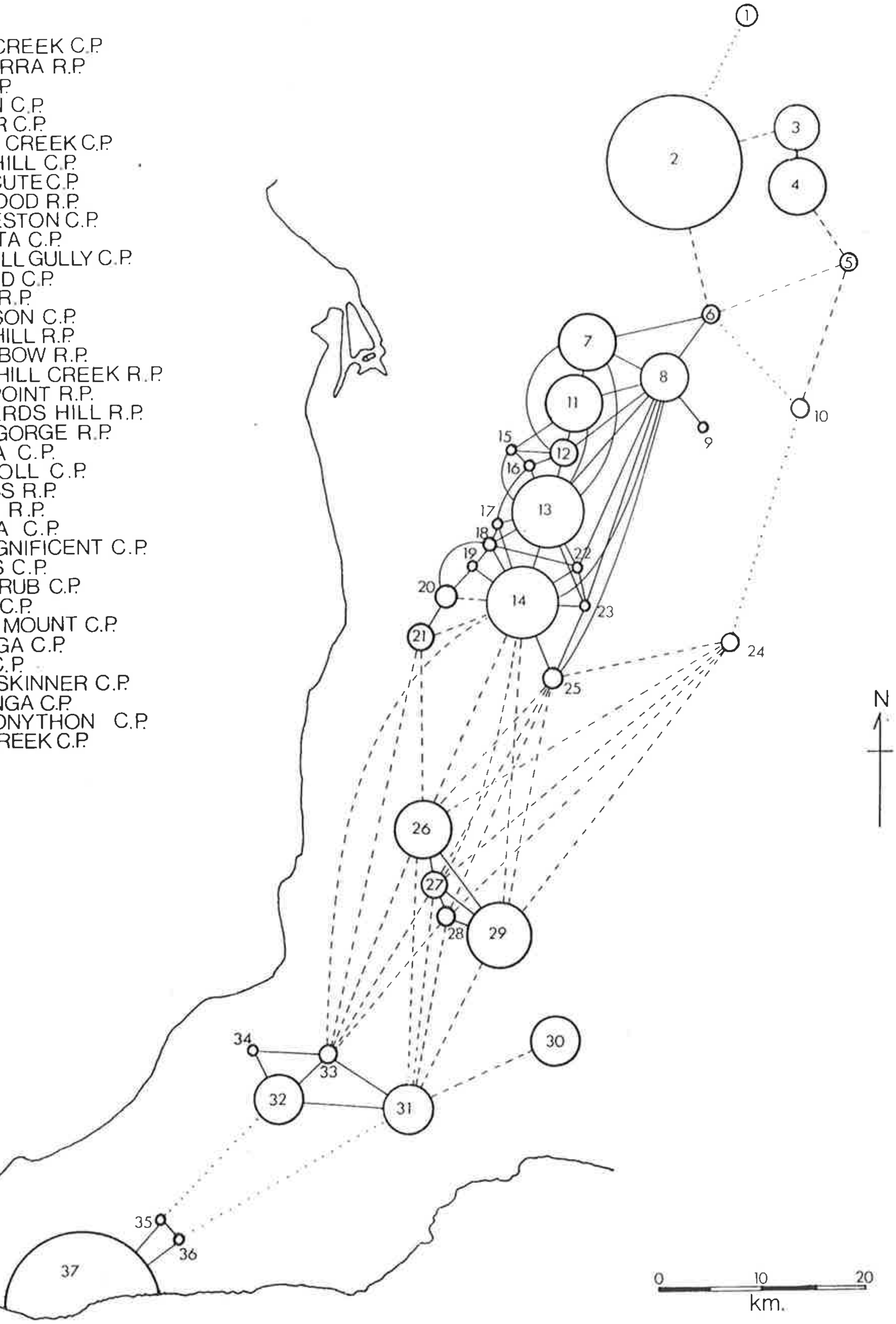
Figure 35

Mount Lofty Ranges Nature Reserve Network plus

1. Sandy Creek C.P.
2. Deep Creek C.P.
3. Waitpinga C.P.
4. Eric Bonython C.P.
5. Cudlee Creek C.P.-Charleston C.P. linkage

and 6. Charleston C.P.-Totness R.P. linkage

1 SANDY CREEK C.P.
2 PARA WIRRA R.P.
3 HALE C.P.
4 WARREN C.P.
5 CROMER C.P.
6 CUDLEE CREEK C.P.
7 BLACK HILL C.P.
8 MONTACUTE C.P.
9 LENSWOOD R.P.
10 CHARLESTON C.P.
11 MORIALTA C.P.
12 HORSNELL GULLY C.P.
13 CLELAND C.P.
14 BELAIR R.P.
15 FERGUSON C.P.
16 GREENHILL R.P.
17 THE ELBOW R.P.
18 BROWNHILL CREEK R.P.
19 WINDY POINT R.P.
20 SHEPHERDS HILL R.P.
21 STURT GORGE R.P.
22 EURILLA C.P.
23 THE KNOLL C.P.
24 TOTNESS R.P.
25 LOFTIA R.P.
26 KYEEMA C.P.
27 MT. MAGNIFICENT C.P.
28 FINNISS C.P.
29 COX SCRUB C.P.
30 SCOTT C.P.
31 SPRING MOUNT C.P.
32 MYPONGA C.P.
33 YULTE C.P.
34 NIXON-SKINNER C.P.
35 WAITPINGA C.P.
36 ERIC BONYTHON C.P.
37 DEEP CREEK C.P.



reserve network (Fig. 22), the network becomes fragmented into three subnetworks, in addition to the disconnected reserves to the north (Figure 36). Therefore, the removal of stretches of roadside vegetation from the Mount Lofty Ranges, both to the north and south of the central concentration of reserves, may cause fragmentation of the network and the resultant isolation of one or more reserves.

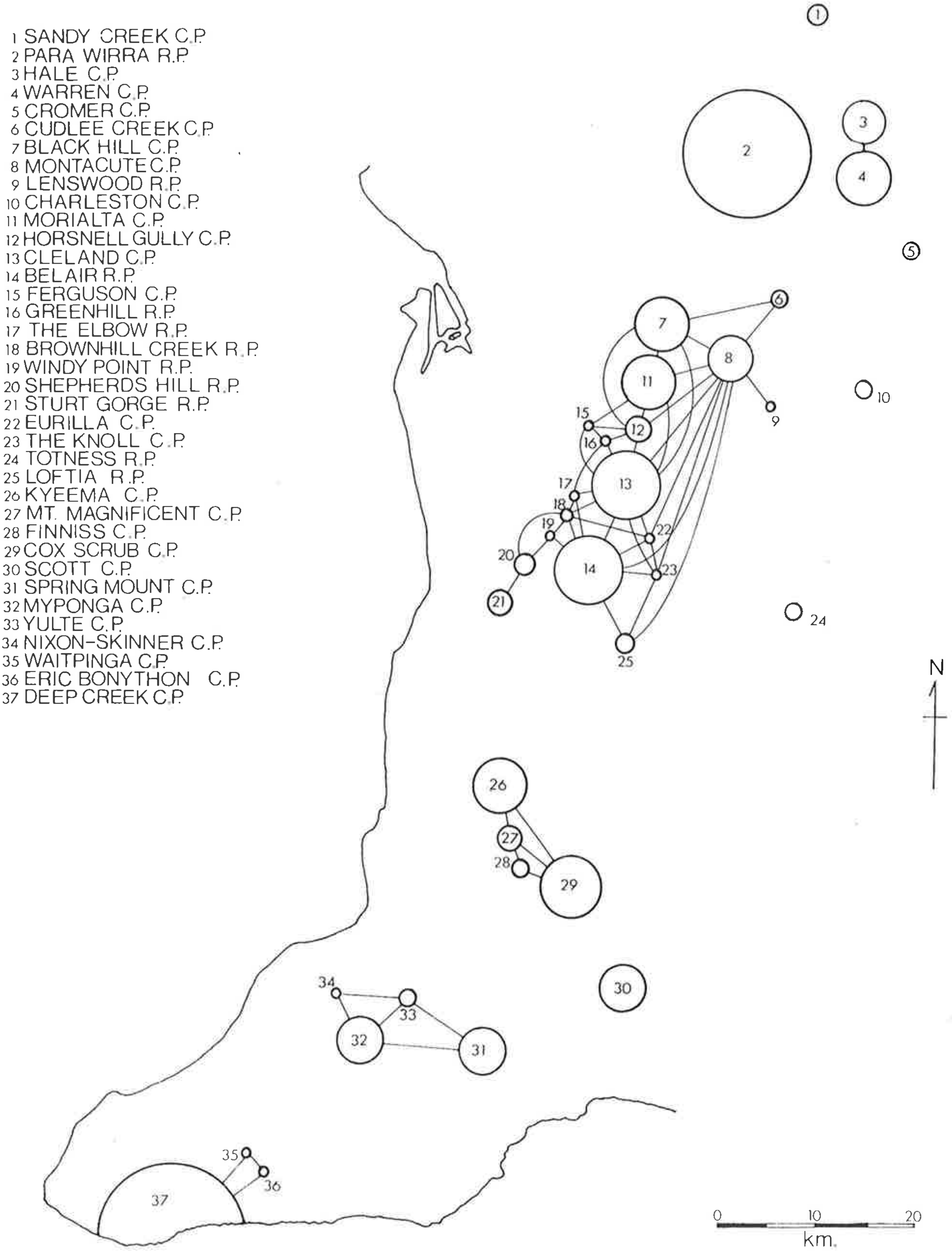
A similar situation occurs if the Recreation Parks are omitted from the Mount Lofty Ranges nature reserve network (Figure 37). Unlike Conservation Parks whose prime purpose is the conservation of biota, Recreation Parks are designated and managed primarily for public recreation in pleasant surroundings. Most Recreation Parks do contain stands of native vegetation, although these tend to be more disturbed than those which occur in Conservation Parks of equivalent size. If these stands of native vegetation were cleared for improved recreational facilities and the Recreation Parks were lost from the nature reserve network the effect on the network would be dramatic. The once continuous network would be split in two and effectively become two isolated smaller subnetworks (Fig. 37). The conservation potential of the Mount Lofty Ranges nature reserve system, therefore, would be severely reduced.

2. Linkage Weighting

To provide additional information about networks the links between nodes can be weighted for the Mount Lofty Ranges. First, a weight has been computed for the distance along the actual biological corridors between the reserves (Figure 38). Second, where a corridor exists between reserves, the actual distance along the corridor has been converted to direct distance and this has been used

Figure 36

Mount Lofty Ranges Nature Reserve Network minus roadside vegetation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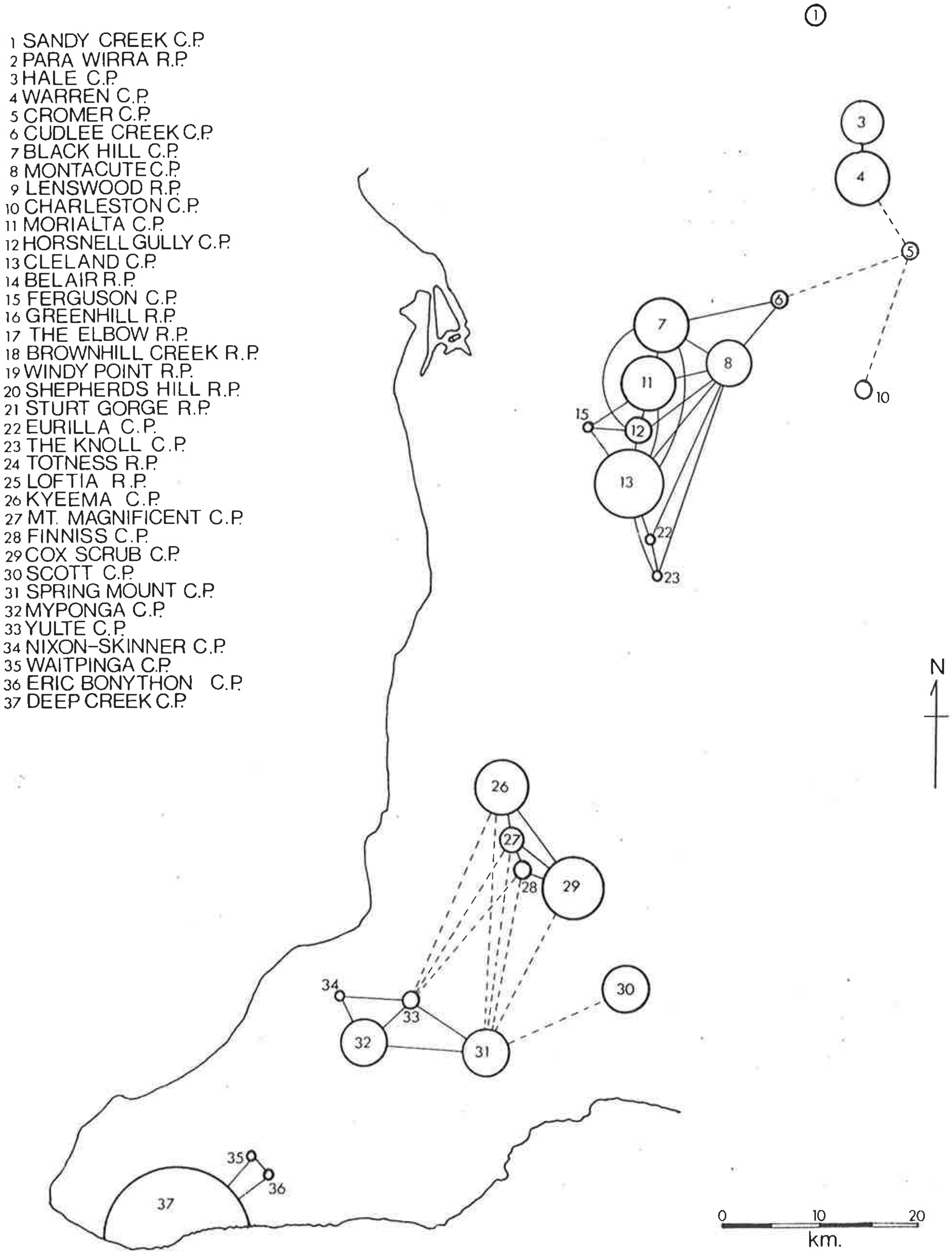
2 PARA WIRRA R.P.
3 HALE C.P.
4 WARREN C.P.
5 CROMER C.P.
6 CUDLEE CREEK C.P.
7 BLACK HILL C.P.
8 MONTACUTE C.P.
9 LENSWOOD R.P.
10 CHARLESTON C.P.
11 MORIALTA C.P.
12 HORSNELL GULLY C.P.
13 CLELAND C.P.
14 BELAIR R.P.
15 FERGUSON C.P.
16 GREENHILL R.P.
17 THE ELBOW R.P.
18 BROWNHILL CREEK R.P.
19 WINDY POINT R.P.
20 SHEPHERDS HILL R.P.
21 STURT GORGE R.P.
22 EURILLA C.P.
23 THE KNOLL C.P.
24 TOTNESS R.P.
25 LOFTIA R.P.
26 KYEEMA C.P.
27 MT. MAGNIFICENT C.P.
28 FINNISS C.P.
29 COX SCRUB C.P.
30 SCOTT C.P.
31 SPRING MOUNT C.P.
32 MYPONGA C.P.
33 YULTE C.P.
34 NIXON-SKINNER C.P.
35 WAITPINGA C.P.
36 ERIC BONYTHON C.P.
37 DEEP CREEK C.P.
N
0
10
20
km.

Figure 37

Mount Lofty Ranges nature reserve network minus Recreation Parks

i.e. 1. Para Wirra R.P.
2. Lenswood R.P.
3. Belair R.P.
4. Greenhill R.P.
5. The Elbow R.P.
6. Brownhill Ck. R.P.
7. Windy Point R.P.
8. Shepherds Hill R.P.
9. Sturt Gorge R.P.
10. Totness R.P.
11. Loftia R.P.


1 SANDY CREEK C.P.
2 PARA WIRRA R.P.
3 HALE C.P.
4 WARREN C.P.
5 CROMER C.P.
6 CUDLEE CREEK C.P.
7 BLACK HILL C.P.
8 MONTACUTE C.P.
9 LENSWOOD R.P.
10 CHARLESTON C.P.
11 MORIALTA C.P.
12 HORSNELL GULLY C.P.
13 CLELAND C.P.
14 BELAIR R.P.
15 FERGUSON C.P.
16 GREENHILL R.P.
17 THE ELBOW R.P.
18 BROWNHILL CREEK R.P.
19 WINDY POINT R.P.
20 SHEPHERDS HILL R.P.
21 STURT GORGE R.P.
22 EURILLA C.P.
23 THE KNOLL C.P.
24 TOTNESS R.P.
25 LOFTIA R.P.
26 KYEEMA C.P.
27 MT. MAGNIFICENT C.P.
28 FINNISS C.P.
29 COX SCRUB C.P.
30 SCOTT C.P.
31 SPRING MOUNT C.P.
32 MYPONGA C.P.
33 YULTE C.P.
34 NIXON-SKINNER C.P.
35 WAITPINGA C.P.
36 ERIC BONYTHON C.P.
37 DEEP CREEK C.P.
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3
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30
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36
37
0
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km.

Figure 38

Shortest-Path Matrix for Mount Lofty Ranges Nature Reserve network - corridor distance

Notes: Blank spaces on right-hand side of matrix are equivalent to zeros.

	SC	PW	H	W	Cr	CC	BH	Mon	Le	Ch	Mor	HG	Cl	B	Fe	G	TE	BC	WP	SH	SG	E	TK	T	Lo	K	MM	Fi	CS	S	SM	M	Y	NS	W	EB	DC
SC																																					
PW		0	54			148																															
H			0	4																																	
W				0	88																																
Cr					0	194				208																											
CC						0	138	88																													
BH							0	53			7	80	100																								
Mon								0	41		46	80	101	178								130	160		176												
Le									0																												
Ch										0																											
Mor											0	21	52		47																						
HG												0	16		20	26																					
Cl													0	43	30	4	6	32				5	30														
B														0			41	20	24	58	64	42	20		22	304	423		417				526				
Fe															0	10																					
G																0	20					56															
TE																	0	30																			
BC																		0	19	64																	
WP																			0	16																	
SH																				0	27																
SG																					0					400							623				
E																						0	34														
TK																							0														
T																								0	150	266	336	335	360								
Lo																									0	277	347	353	420								
K																										0	34		73		278		305				
MM																											0	4	27		242		259				
Fi																												0	14		244		260				
CS																													0		259						
S																														0	240						
SM																															0	73	68				
M																																0	45	36			
Y																																	0	39			
NS																																		0			
W																																					
EB																																					
DC																																					

as a weight (Fig. 39). The comparison of the two weighted values for a particular link indicates the effectiveness of the linkage between the reserves. A short, direct corridor between two reserves is of greater benefit for the movement of native biota than a longer, indirect corridor. In the binary format, of course, both types of linkage are given equal weighting. The weighted formats obviously give a clearer description of the Mount Lofty Ranges nature reserve network (Fig. 22) than that offered by the binary format.

The algorithm developed by Pape (1980) was used to calculate the shortest path distances between the nature reserves within the network for both forms of weighting. This algorithm also displays the route which gives the shortest path length. Thus, the distance required for either corridor or direct migration between any two reserves can readily be found.

A new measure of reserve accessibility was calculated by averaging the path lengths from each node to all other nodes. Table 2 gives the average path lengths for both the corridor and the direct lengths of each node. As expected, reserve accessibility is, to a large degree, correlated with geographic centrality. For instance, Cleland C.P., Belair R.P. and the neighbouring smaller reserves of Greenhill R.P., The Elbow R.P. and Brownhill Creek R.P. are the most accessible reserves with respect to both sets of data (Table 2). Montacute C.P. decreases in accessibility from the binary calculations due to its northern position in the network. The fact that the least accessible reserves, Scott C.P. and Charleston C.P., are the same for both the binary and weighted formats suggests that the results derived for reserve accessibility from the simpler binary operations are a reasonably accurate basis for planning decisions.

Figure 39

Shortest-Path Matrix for Mount Lofty Ranges Nature
Reserve network - direct distance

	SC	PW	H	W	Cr	CC	BH	Mon	Le	Ch	Mor	HG	Cl	B	Fe	G	TE	BC	WP	SH	SG	E	TK	T	Lo	K	MM	Fi	CS	S	SM	M	Y	NS	W	EB	DC
SC																																					
PW		0	48			123																															
H			0	4																																	
W				0	70																																
Cr					0	135				154																											
CC						0	95	58																													
BH							0	29			7	43	59																								
Mon								0	38		6	70	86	120								91	146		140												
Le									0																												
Ch										0																											
Mor											0	7	86		33																						
HG												0	16		20	20																					
Cl													0	34	14	4	6	29				5	30														
B														0			30	7	20	36	49	39	16		22	256	290		308				455				
Fe															0	10																					
G																0	10					9															
TE																	0	23																			
BC																		0	19	35																	
WP																			0	16																	
SH																				0	16																
SG																					0					249							410				
E																						0	28														
TK																							0		24												
T																								0	113	258	292	296	306								
Lo																									0	237	271	275	289								
K																										0	34		52		226		227				
MM																											0	4	18		192		209				
Fi																												0	14		192		210				
CS																													0		192						
S																														0	173						
SM																															0	72	43				
M																																0	34	28			
Y																																	0	33			
NS																																		0			
W																																					
EB																																					
DC																																					

TABLE 2

Average Total Path Lengths
for Mount Lofty Ranges nature reserves

Reserves	Aver. Path Length (kms)		Percent Difference
	Total Direct	Total Corridor	
SANDY CREEK CP	-	-	-
PARA WIRRA RP	375·9	451·5	83·3
HALE CP	413·4	493·7	83·7
WARREN CP	416·8	497·1	83·8
CROMER CP	383·9	488·7	78·5
CUDLEE CREEK CP	280·6	338·9	82·8
BLACK HILL CP	227·2	263·0	86·4
MONTACUTE CP	242·6	281·2	86·3
LENSWOOD RP	279·4	321·0	87·0
CHARLESTON CP	533·1	690·8	77·2
MORIALTA CP	227·4	256·8	88·5
HORSNELL G. CP	213·4	248·3	85·9
CLELAND CP	203·9	243·1	83·9
BELAIR RP	206·3	247·5	83·3
FERGUSON CP	211·1	253·0	83·4
GREENHILL RP	207·9	246·7	84·3
THE ELBOW RP	207·3	246·9	84·0
BROWNHILL CK. RP	207·0	249·3	83·0
WINDY POINT RP	216·5	259·2	83·5
SHEPHERDS H. RP	222·7	273·7	81·4
STURT GORGE RP	228·7	298·6	76·6
EURILLA CP	209·9	246·9	85·0
THE KNOLL CP	209·7	246·2	85·2
TOTNESS RP	294·8	355·6	82·9
LOFTIA RP	210·2	253·5	82·9
KYEEMA CP	320·5	380·4	84·2
MT. MAGN'ENT CP	340·7	401·6	84·8
FINNISS CP	343·7	401·7	85·6
COX SCRUB CP	355·4	415·2	85·6
SCOTT CP	645·9	808·3	79·9
SPRING MT. CP	478·3	575·8	83·1
MYPONGA CP	491·1	588·9	83·4
YULTE CP	459·7	549·3	83·7
NIXON-SKINNER CP	490·5	584·4	83·9
WAITPINGA CP	-	-	-
ERIC BONYTHON CP	-	-	-
DEEP CREEK CP	-	-	-

However, an important offshoot from the weighted format is that it is now possible to calculate how direct the corridors are that link a reserve with the remainder of the network by expressing average shortest path length as a per cent of average corridor path length. Since many linkages are used by most reserves the percentages should not be significantly different (Table 2). Most values, in fact, range between 83 per cent and 86 per cent. The differences result mainly from variations in the corridor length of the linkages adjoining a reserve and the following few links.

Sturt Gorge R.P. and Charleston C.P. have the least direct corridors. Less direct corridors usually consist of either roadside vegetation, only scattered remnants of native vegetation, or a combination of both. The reserves that are surrounded by large areas of native vegetation, such as Black Hill C.P., Morialta C.P. and Montacute C.P., show the least differences between the two types of path lengths (Table 2), since direct pathways between these reserves and nearby reserves are usually readily available.

3. Flow Characteristics

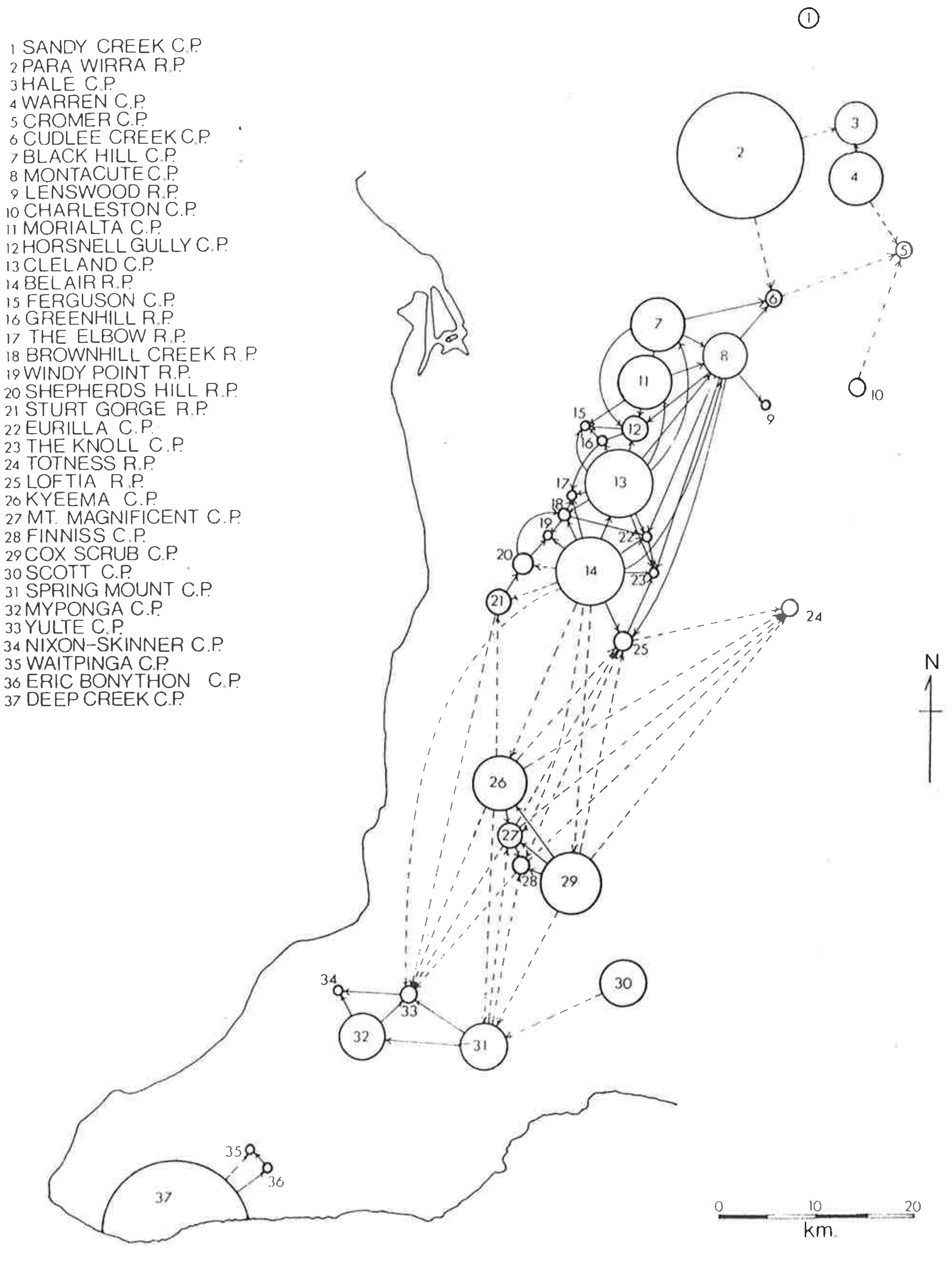
A large part of cartographic research within Human Geography is concerned with the characteristics of the flows between source and recipient areas. These flows may be between cities, a city and its hinterland, countries or trade areas. The interactions between nature reserves may be examined in a similar manner. The nature reserve network would then become a flow diagram expressing the rate of movement of the native species between the reserves. However, problems of flow measurement are far greater than those encountered in Human Geography. Nevertheless, some generalizations can be made about the possible rate of native species movement. Net flow will generally occur from a larger reserve to a smaller reserve, given that the larger reserve contains a greater number of species in accordance with the species-area relationship. This generalization is also in accordance with studies of Human Geography flow patterns (e.g., Zipf, 1946).

If this generalization is applied to the Mount Lofty Ranges nature reserve network a flow diagram showing source and recipient reserves is formed (Figure 40). A 'source reserve' is defined as a reserve which is connected only to reserves of smaller size; that is, there is a net outflow from the reserve. A 'recipient reserve' is one which is only connected to reserves of larger size and thus experiences a net inflow. Six source reserves were found: Para Wirra R.P., Warren C.P., Charleston C.P., Belair R.P., Scott C.P. and Deep Creek C.P. (Figure 40). Although most of these reserves are of sufficient size to cope with net outflow, Charleston C.P. and Scott C.P. are not only relatively small in size but also have been shown to be very isolated within the reserve network. This further questions their ability to act as viable conservation entities.

Ten recipient reserves were found and these are mainly the smaller reserves within the network (Figure 40). These recipient reserves include Cromer C.P., Lenswood R.P., Totness R.P. and Nixon-Skinner C.P.. Although small in size, these reserves may have a net inflow which would increase their conservation potential above what it would be if the reserves were totally isolated (i.e., Sandy Creek C.P.).

Figure <u>40</u>

Hypothesized flow diagram of the Mount Lofty Ranges nature reserve network


1 SANDY CREEK C.P.
2 PARA WIRRA R.P.
3 HALE C.P.
4 WARREN C.P.
5 CROMER C.P.
6 CUDLEE CREEK C.P.
7 BLACK HILL C.P.
8 MONTACUTE C.P.
9 LENSWOOD R.P.
10 CHARLESTON C.P.
11 MORIALTA C.P.
12 HORSNELL GULLY C.P.
13 CLELAND C.P.
14 BELAIR R.P.
15 FERGUSON C.P.
16 GREENHILL R.P.
17 THE ELBOW R.P.
18 BROWNHILL CREEK R.P.
19 WINDY POINT R.P.
20 SHEPHERDS HILL R.P.
21 STURT GORGE R.P.
22 EURILLA C.P.
23 THE KNOLL C.P.
24 TOTNESS R.P.
25 LOFTIA R.P.
26 KYEEMA C.P.
27 MT. MAGNIFICENT C.P.
28 FINNISS C.P.
29 COX SCRUB C.P.
30 SCOTT C.P.
31 SPRING MOUNT C.P.
32 MYPONGA C.P.
33 YULTE C.P.
34 NIXON-SKINNER C.P.
35 WAITPINGA C.P.
36 ERIC BONYTHON C.P.
37 DEEP CREEK C.P.
N
0
10
20
km

B. Application of Shape Analysis

1. Shape of Nature Reserves

The nature reserves of the Mount Lofty Ranges are similar in shape complexity to the political units measured by Blair and Biss (1967). Therefore, the technique devised by Blair and Biss (1967) should be equally applicable to the reserves. Indeed, the range of compactness values obtained for the reserves closely resembles that of the political units. Figures 41.1 to 41.37 present the shape analysis results for each of the 37 Conservation and Recreation Parks in the Mount Lofty Ranges. These results are also displayed in Table 3. The reserves which have the greatest compactness value are Lenswood R.P. (Fig. 41.9, Compactness = .9598), Cleland C.P. (Fig. 41.13, Comp. = .9473), Finniss C.P. (Fig. 41.28, Comp. = .9402), Nixon-Skinner C.P. (Fig. 41.34, Comp. = .9381) and Mt. Magnificent C.P. (Fig. 41.27, Comp. = .9306). Those reserves which have the lowest compactness values are Brownhill Creek R.P. (Fig. 41.18, Comp. = .4085), Eric Bonython C.P. (Fig. 41.36, Comp. = .4696), Windy Point R.P. (Fig. 41.19, Comp. = .4858) and Deep Creek C.P. (Fig. 41.37, Comp. = .5638) (Table 3).

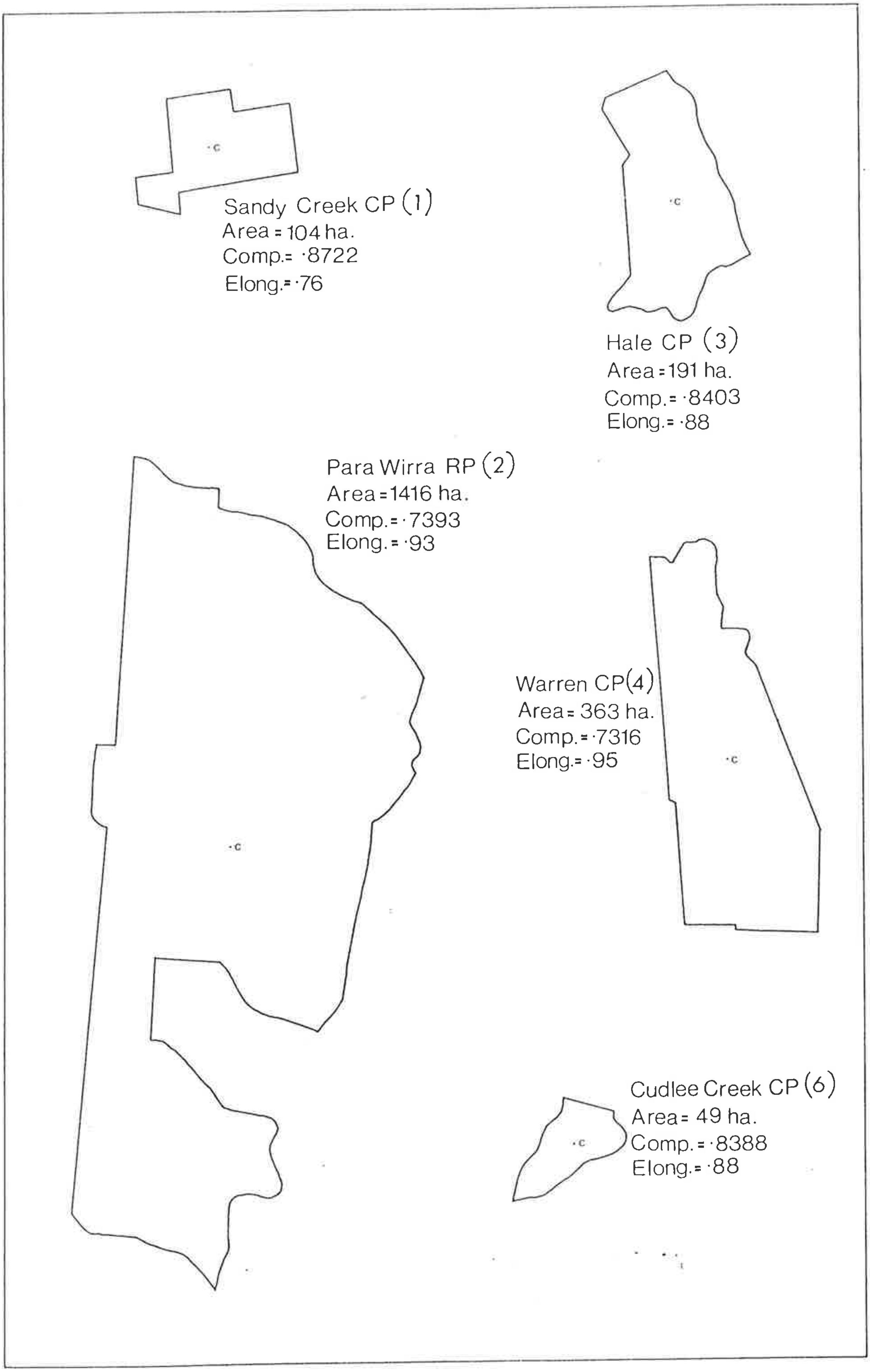
The biogeographical significance of the shape of nature reserves is obvious. Those reserves with high compactness values have a lower area-to-perimeter ratio and hence a larger 'core' for a given area, provided the area of the reserve is in fact above the threshold size to have a core. This corresponds to Diamond's sixth principle of reserve design which states that reserves should be as circular as possible to minimize dispersal distances within the reserve. It should also be noted that a more compact reserve also reduces peninsula effects, edge effects and disturbances from adjacent modified land.

Figure 41

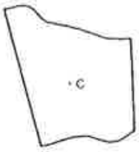
Area, Compactness and Elongation values for the Mount Lofty Ranges nature reserves

Notes: Compactness values are calculated to four decimal places whereas elongation values are calculated to two. The centroids of the reserve shapes (c) are also shown.

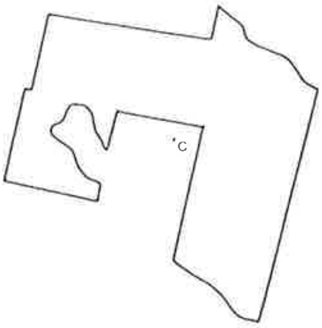
Reserve numbers are equivalent to those used in network analysis procedures.


Sandy Creek CP (1)
Area = 104 ha.
Comp.= ·8722
Elong.= ·76
Hale CP (3)
Area = 191 ha.
Comp.= ·8403
Elong.= ·88
Para Wirra RP (2)
Area = 1416 ha.
Comp.= ·7393
Elong.= ·93
Warren CP (4)
Area = 363 ha.
Comp.= ·7316
Elong.= ·95
Cudlee Creek CP (6)
Area = 49 ha.
Comp.= ·8388
Elong.= ·88
·c

Cromer CP (5)
Area = 44ha.
Comp. = ·9087
Elong. = ·78



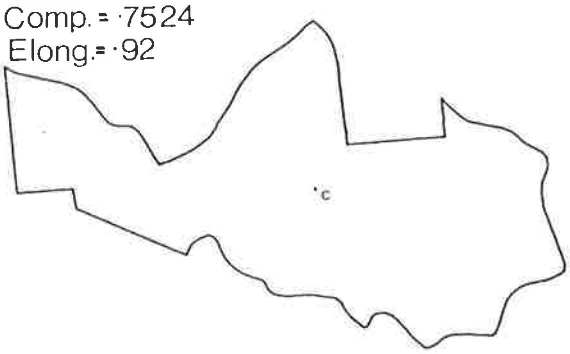
Charleston CP (10)
Area = 53ha.
Comp. = ·9300
Elong. = ·69



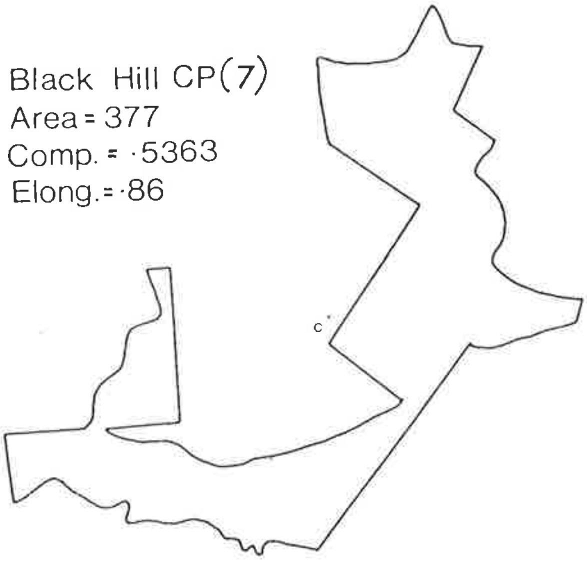
Montacute CP (8)
Area = 196 ha.
Comp. = ·7718
Elong. = ·72

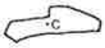
Lenswood RP (9)
Area = 17ha.
Comp. = ·9598
Elong. = ·66

Morialta CP (11)
Area = 374 ha.
Comp. = ·7524
Elong. = ·92

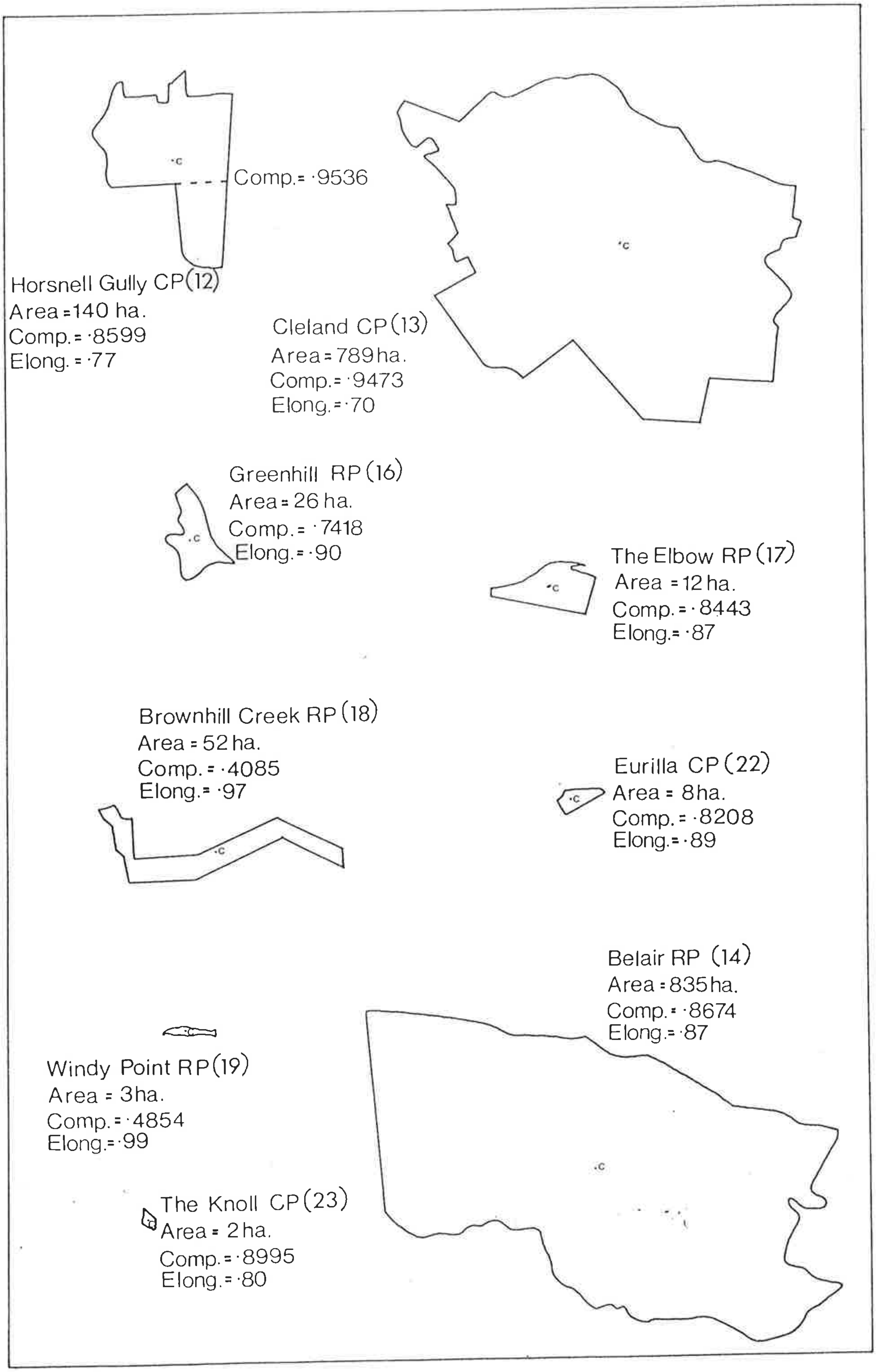


Black Hill CP (7)
Area = 377
Comp. = ·5363
Elong. = ·86



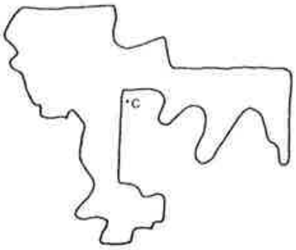


Ferguson CP (15)
Area = 8 ha.
Comp. = ·5763
Elong. = ·97

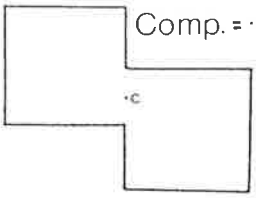

·c
Comp.= ·9536
Horsnell Gully CP(12)
Area =140 ha.
Comp.= ·8599
Elong. = ·77
·c
Cleland CP(13)
Area = 789 ha.
Comp.= ·9473
Elong.= ·70
Greenhill RP(16)
Area = 26 ha.
Comp. = ·7418
Elong.= ·90
·c
The Elbow RP(17)
Area = 12 ha.
Comp. = ·8443
Elong.= ·87
·c
Brownhill Creek RP(18)
Area = 52 ha.
Comp. = ·4085
Elong.= ·97
·c
Eurilla CP(22)
Area = 8 ha.
Comp. = ·8208
Elong.= ·89
·c
Belair RP (14)
Area = 835 ha.
Comp. = ·8674
Elong.= ·87
·c
Windy Point RP(19)
Area = 3 ha.
Comp.= ·4854
Elong.= ·99
The Knoll CP(23)
Area = 2 ha.
Comp.= ·8995
Elong.= ·80

Loftia RP (25)
Area = 91 ha.
Comp. = ·8295
Elong. = ·87

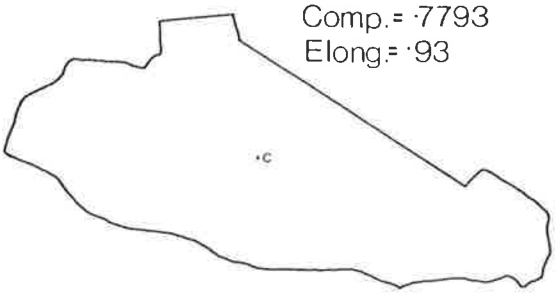
Sturt Gorge RP (21)
Area = 131 ha.
Comp. = ·7211
Elong. = ·70

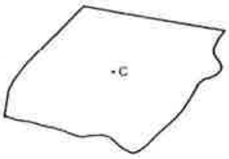


Shepherds Hill RP(20)
Area = 89 ha.
Comp. = ·8139
Elong. = ·89

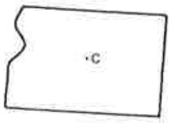


Kyeema CP(26)
Area = 349 ha.
Comp. = ·7793
Elong. = ·93





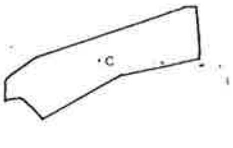
Mt. Magnificent CP(27)
Area = 90 ha.
Comp. = ·9306
Elong. = ·78

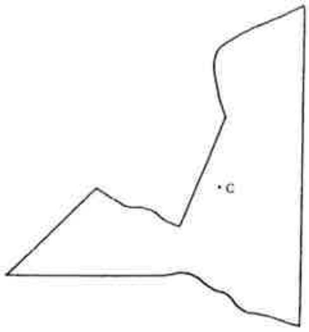


Finniss CP (28)
Area = 67ha.
Comp. = ·9402
Elong. = ·73

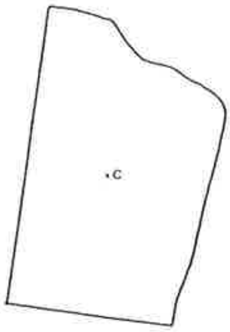
Nixon-Skinner CP (34)
Area = 8 ha.
Comp. = ·9381,
Elong. = ·46

Yulte CP (33)
Area = 42 ha
Comp. = ·6707. Elong. = ·97

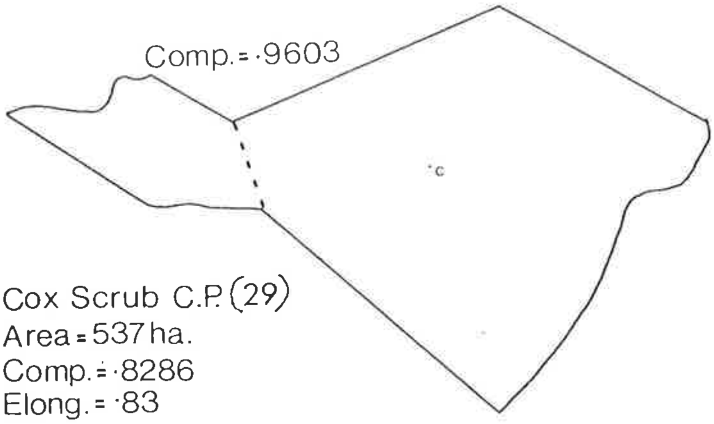




Myponga C.P.(32)
Area = 166 ha.
Comp. = ·7313
Elong. = ·76



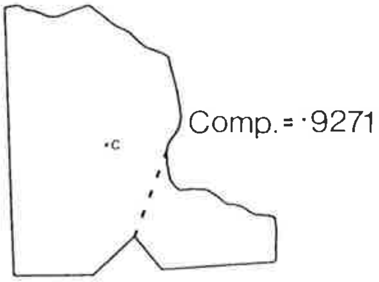
Scott C.P.(30)
Area = 209 ha.
Comp. = ·9276
Elong. = ·77



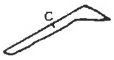
Cox Scrub C.P.(29)
Area = 537 ha.
Comp. = ·8286
Elong. = ·83

Waitpinga C.P.(35)
Area = 3 ha.
Comp. = ·9052
Elong. = ·83

Totness R.P. (24)
Area = 43 ha.
Comp. = ·7593
Elong. = ·93



Spring Mount C.P.(31)
Area = 199 ha.
Comp. = ·8773
Elong. = ·74



Eric Bonython C.P.(36)
Area = 6 ha.
Comp. = ·4696
Elong. = ·99

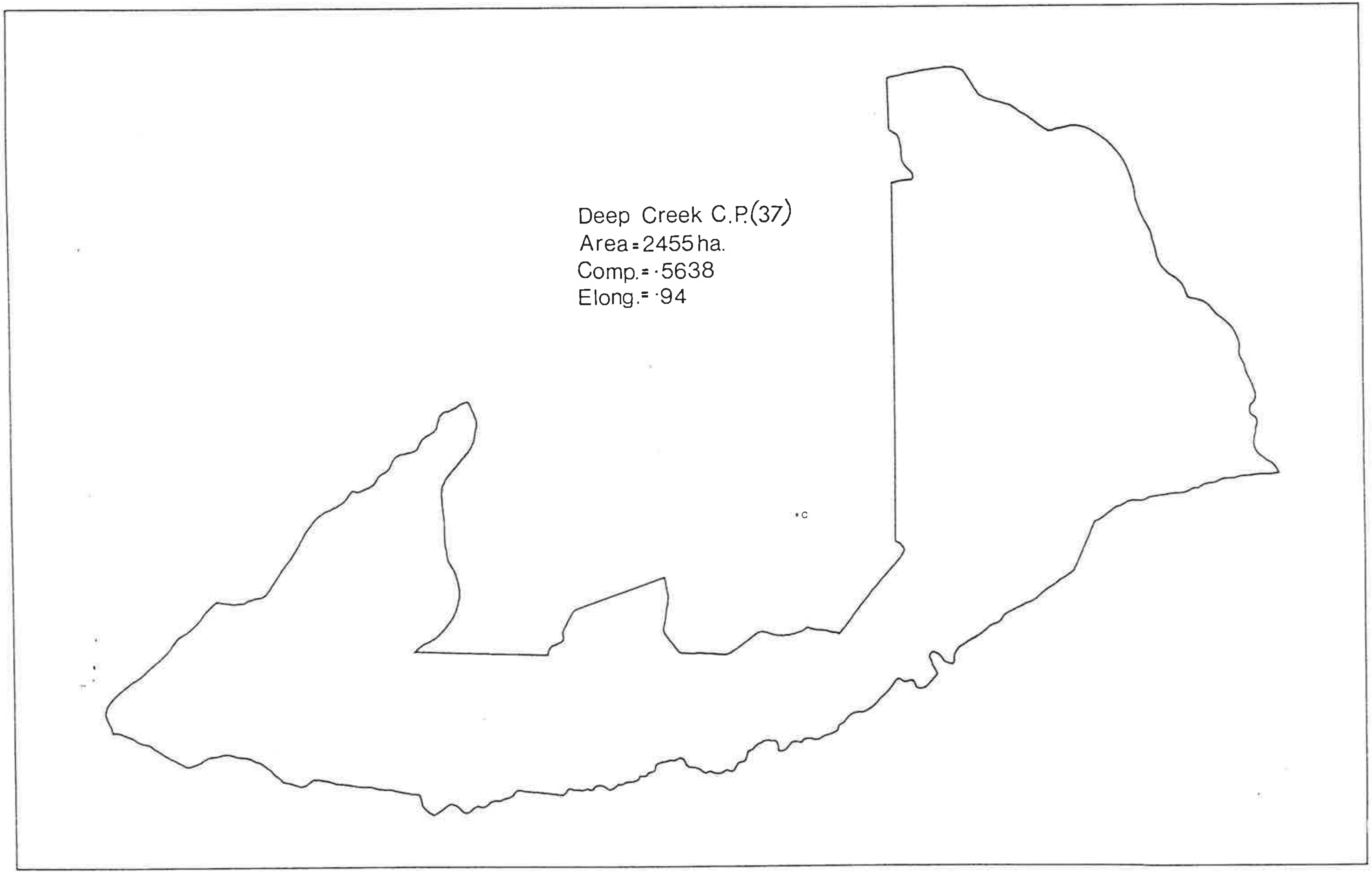

Deep Creek C.P.(37)
Area = 2455 ha.
Comp. = ·5638
Elong. = ·94
c

TABLE 3

Area, Compactness and Elongation Values
for the Mount Lofty Ranges nature reserves

Reserves	Area (ha)	Comp.	Elong.
SANDY CREEK CP	104	·8722	·76
PARA WIRRA RP	1416	·7393	·93
HALE CP	191	·8403	·88
WARREN CP	363	·7316	·95
CROMER CP	44	·9087	·78
CUDLEE CREEK CP	49	·8388	·88
BLACK HILL CP	377	·5363	·86
MONTACUTE CP	196	·7718	·72
LENSWOOD RP	17	·9598	·66
CHARLESTON CP	53	·9300	·69
MORIALTA CP	374	·7524	·92
HORSNELL G. CP	140	·8599	·77
CLELAND CP	789	·9473	·70
BELAIR RP	835	·8674	·87
FERGUSON CP	8	·5763	·97
GREENHILL RP	26	·7418	·90
THE ELBOW RP	12	·8443	·87
BROWNHILL CK. RP	52	·4085	·97
WINDY POINT RP	3	·4854	·99
SHEPHERDS H. RP	89	·8139	·89
STURT GORGE RP	131	·7211	·70
EURILLA CP	8	·8208	·89
THE KNOLL CP	2	·8995	·80
TOTNESS RP	43	·7593	·93
LOFTIA RP	91	·8295	·87
KYEEMA CP	349	·7793	·93
MT. MAGN'ENT CP	90	·9306	·78
FINNISS CP	67	·9402	·73
COX SCRUB CP	537	·8286	·83
SCOTT CP	209	·9276	·77
SPRING MT. CP	199	·8773	·74
MYPONGA CP	166	·7313	·76
YULTE CP	42	·6707	·97
NIXON-SKINNER CP	8	·9381	·46
WAITPINGA CP	3	·9052	·83
ERIC BONYTHON CP	6	·4696	·99
DEEP CREEK CP	2455	·5638	·94

These benefits of compactness, however, will not be forthcoming if reserve size is too small. Thus, reserves such as Nixon-Skinner C.P. (Fig. 41.34), Waitpinga C.P. (Fig. 41.35) and The Knoll C.P. (Fig. 41.23), although relatively compact in shape are nonetheless too small to buffer most forms of disturbance and create a core area. On the other hand, Cleland C.P. (Fig. 41.13) and to a lesser degree Cox Scrub C.P. (Fig. 41.29) have areas which may be of sufficient size to buffer disturbances and, combined with moderately high compactness values, may have the ability to create core areas of reasonable size.[1] This is dependent, though, on there being no internal disturbance factors operating within the reserves. This problem is evident in the Recreation Parks and some of the Conservation Parks that exist close to the Adelaide metropolis. The reserve most affected is Belair R.P. (Fig. 41.14) which, if it were in the relatively natural state of Cleland C.P., should be able to support a core area of native biota.

The compactness value of a number of reserves within the Mount Lofty Ranges are relatively low due to the existence of a 'peninsula'. A peninsula increases the elongation value for a reserve and thus decreases the reserve's degree of compactness. Three examples of peninsulas on nature reserves are Cox Scrub C.P. (Fig. 41.29), Spring Mount C.P. (Fig. 41.31) and Horsnell Gully C.P. (Fig. 41.12). In each case, the compactness value would be markedly increased with the exclusion of the peninsula. For instance, the compactness value of

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[1] Unfortunately, information is lacking, particularly in South Australia, about the critical size for a reserve to incorporate a core or 'wilderness' area. Therefore, the resulting conclusions are based on intuitive judgements of the reserve size required for the Mount Lofty Ranges. With further research into the critical size of nature reserves this problem could be overcome and more precise conclusions made.

Cox Scrub C.P. with the peninsula is .8286, but with the exclusion of the peninsula the compactness value rises to .9603.

On very small reserves the existence of a peninsula is probably inconsequential to reserve design. Likewise, on very large reserves which contain substantial core areas, the existence of a peninsula abutting a section of the reserve would be of only minor concern. However, the Mount Lofty Ranges contain no reserves of any great size. In fact, the average size of the reserves is only 258 hectares and this is due mainly to the presence of two reserves of moderately large size, namely Deep Creek C.P. (2455 ha.) and Para Wirra R.P. (1416 ha.). Thus, the existence of peninsulas is an important attribute of many of the reserves in the Mount Lofty Ranges. On the other hand, peninsulas may be part of an important linkage between two reserves, forming the initial stages of biological corridors. Peninsulas in these situations become important for network structure. Thus, to formulate an optimal design policy for nature reserves the two techniques devised for the analysis of biogeographic attirbutes of nature reserves should be united. This unison will be achieved in the next chapter of this thesis.

2. Additions to Existing Reserves

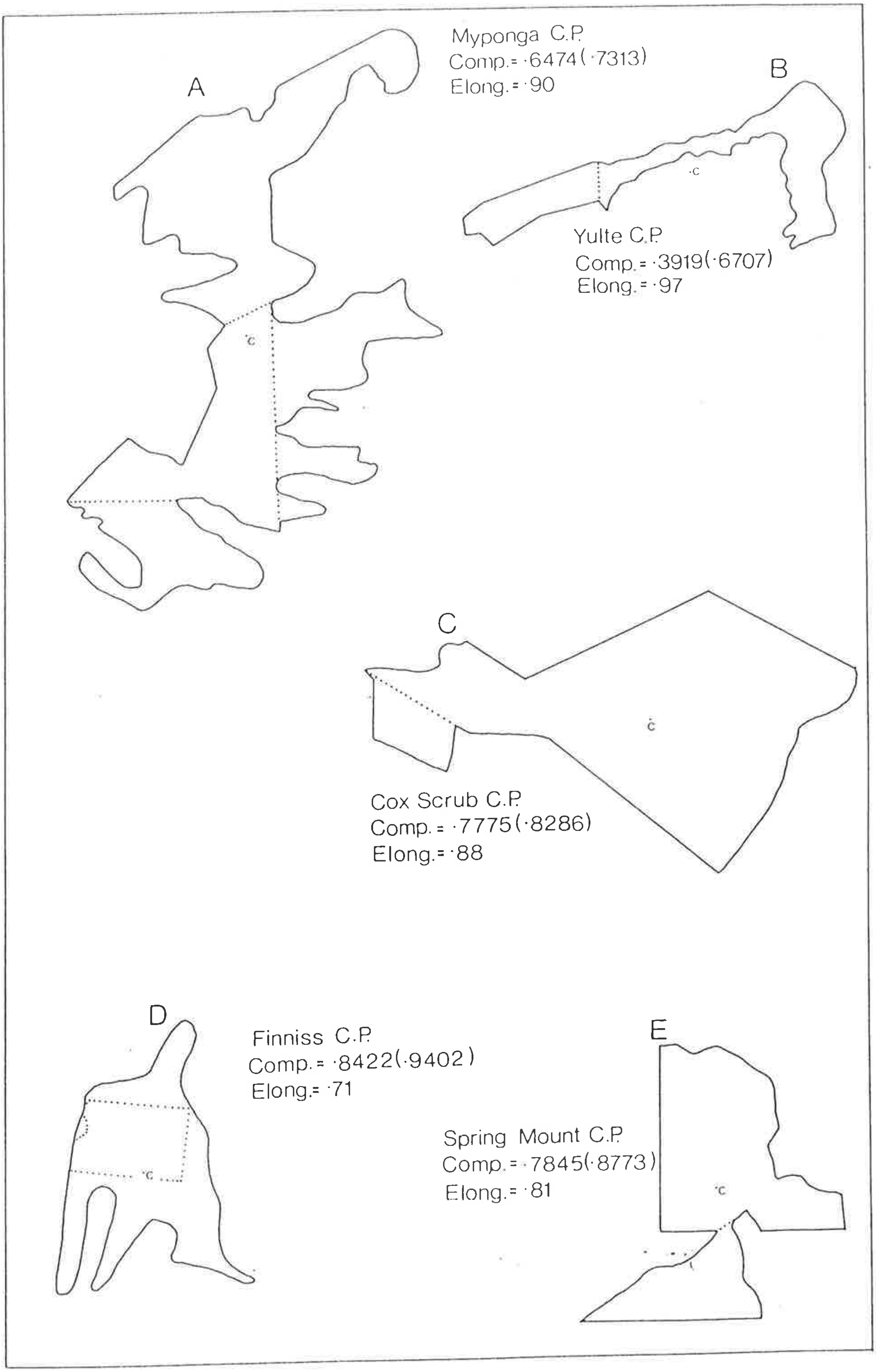
A significant proportion of the reserves in the Mount Lofty Ranges have patches of native vegetation adjoining sections of their boundaries. These patches of vegetation may effectively increase the area of a nature reserve for its biota, sometimes substantially. They also alter the shape parameters of nature reserves. The addition of contiguous patches of native vegetation to nature reserves may either increase or decrease their compactness values.

Figure 42A to O illustrates the effects of patch addition on many of the reserves in the Mount Lofty Ranges. The compactness value of most of these reserves is decreased by patch addition, some by quite notable amounts (i.e., Sturt Gorge R.P. [Fig. 42J], Cromer C.P. [Fig. 42N], Sandy Creek C.P. [Fig. 42L], Yulte C.P. [Fig. 42B]). However, a few reserves benefit by the addition of patches. These reserves are Cudlee Creek C.P. (Fig. 42M), Deep Creek C.P. (Fig. 42O), Loftia R.P. (Fig. 42H) and Para Wirra R.P. (Fig. 42K). Deep Creek C.P., in particular, increases in compactness from .5638 to .7301.

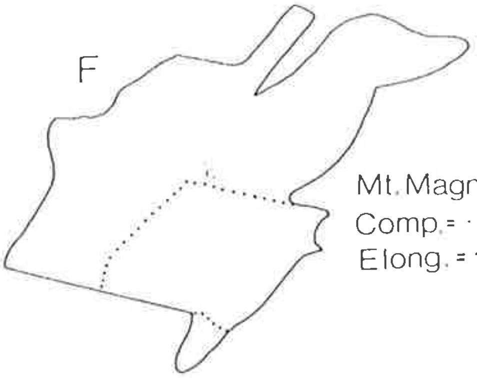
Public acquisition of additional reserve land is usually by the purchase of sections rather than of irregularly shaped vegetation patches. The compactness value of many of the reserves in the Mount Lofty Ranges can be significantly increased if particular sections are acquired. Figure 43A to H provides examples of this. In these examples only sections which contain remnant native vegetation were added. A few reserves, which are not included in these examples due to the lack of native vegetation in their adjoining sections, would have increased compactness if the adjoining sections were purchased (e.g., Cromer C.P., Yulte C.P., etc.). The reserves which benefit most from the acquisition of suitable adjoining sections are Black Hill C.P. (Fig. 43B), Montacute C.P. (Fig. 43E), Deep Creek C.P. (Fig. 43H) and Windy Point R.P. (Fig. 43C). These reserves, particularly the latter two, have high elongation values which decrease markedly with section addition. Montacute C.P. and Black Hill C.P. have complex geometric shapes which are simplified into neat, compact shapes by section addition. Some of the nature reserves have many adjoining sections which contain native vegetation remnants and, thus it is often necessary to choose among sections. As illustrated in Figure 44, poor

Figure 42

Compactness and Elongation values for select
Mount Lofty Ranges nature reserves plus
adjoining native vegetation

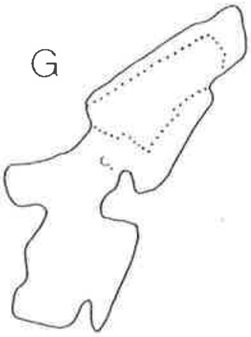

A
Myponga C.P.
Comp.= ·6474(·7313)
Elong.= ·90
c
B
Yulte C.P.
Comp.= ·3919(·6707)
Elong.= ·97
c
C
Cox Scrub C.P.
Comp.= ·7775(·8286)
Elong.= ·88
c
D
Finniss C.P.
Comp.= ·8422(·9402)
Elong.= ·71
c
E
Spring Mount C.P.
Comp.= ·7845(·8773)
Elong.= ·81
c

F



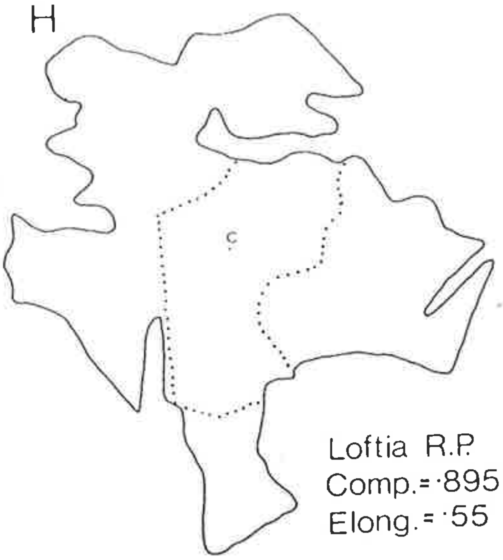
Mt. Magnificent C.P.
Comp. = ·8748 (·9306)
Elong. = ·81

G



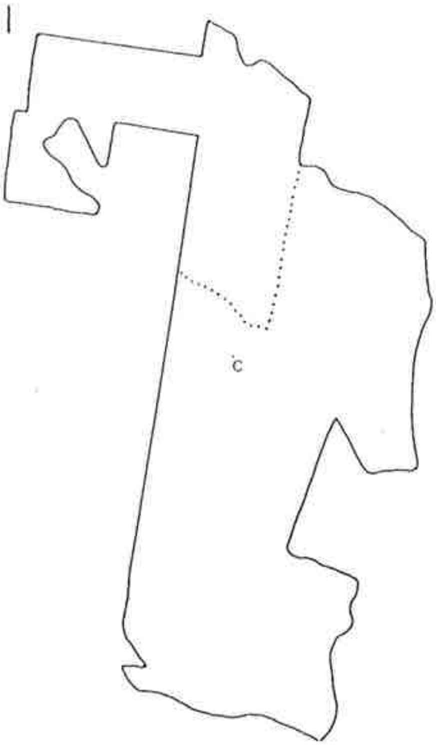
Totness C.P.
Comp. = ·6639 (·7593)
Elong. = ·95

H



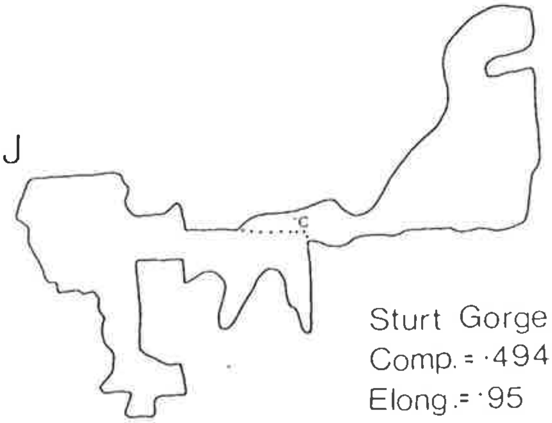
Loftia R.P.
Comp. = ·8955 (·8295)
Elong. = ·55

I

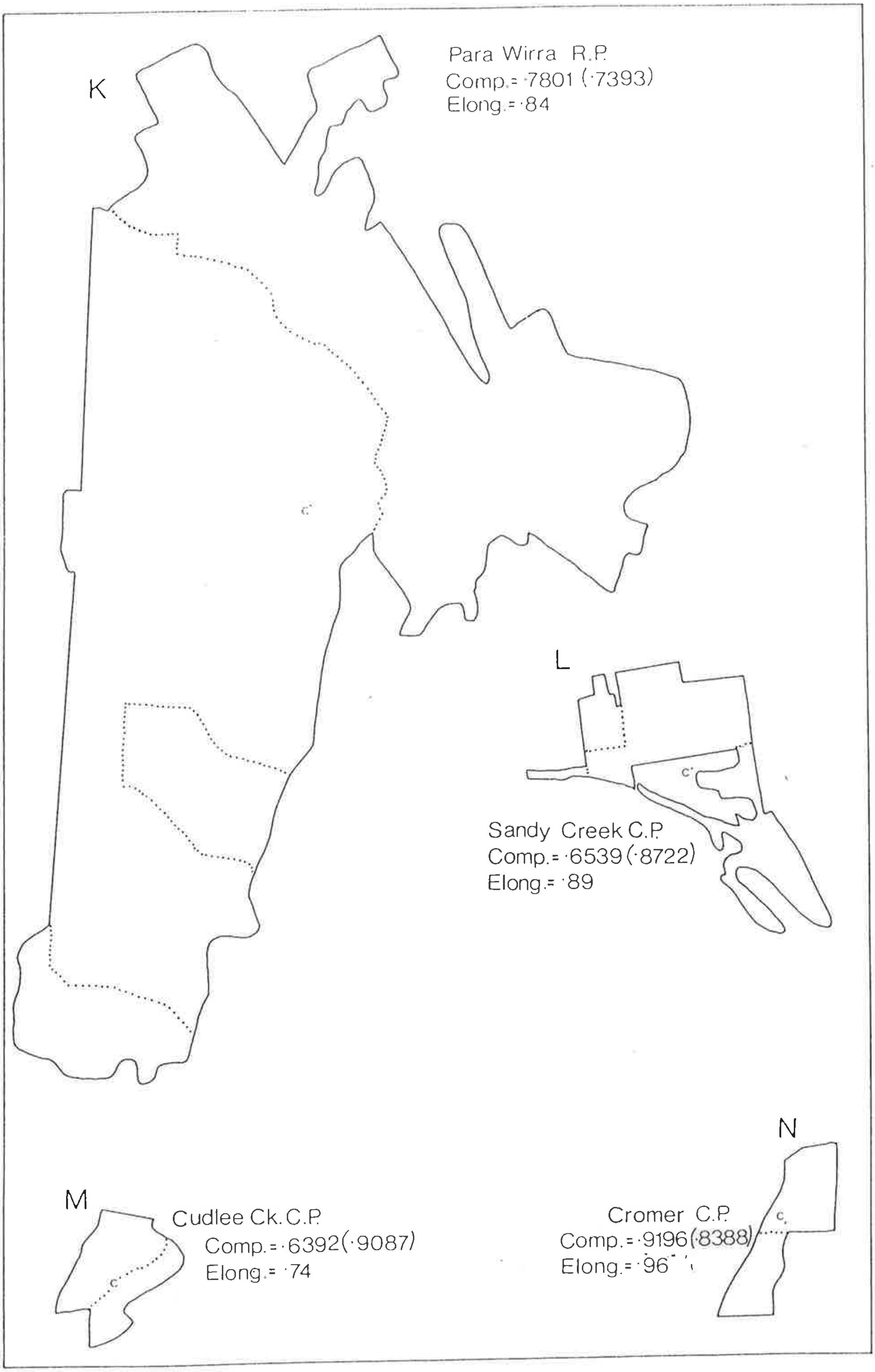


Montacute C.P.
Comp. = ·7310 (·7718)
Elong. = ·89

J



Sturt Gorge R.P.
Comp. = ·4948 (·7211)
Elong. = ·95


K
Para Wirra R.P.
Comp.= ·7801 (·7393)
Elong.= ·84
c
L
c
Sandy Creek C.P.
Comp.= ·6539 (·8722)
Elong.= ·89
M
Cudlee Ck. C.P.
Comp.= ·6392 (·9087)
Elong.= ·74
c
N
Cromer C.P.
c
Comp.= ·9196 (·8388)
Elong.= ·96

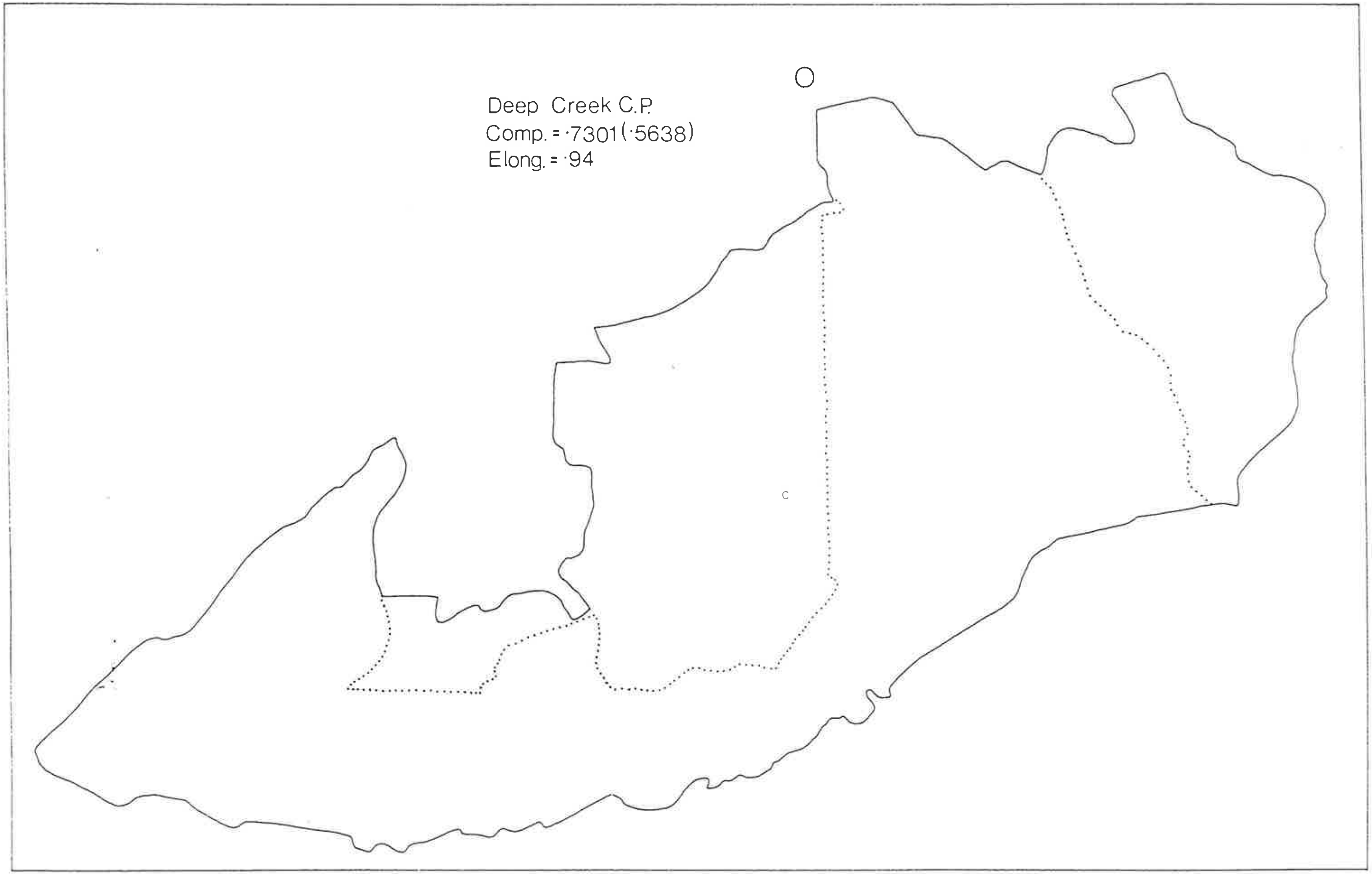
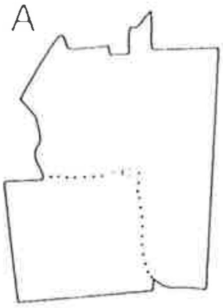

O
Deep Creek C.P.
Comp. = ·7301(·5638)
Elong. = ·94
C

Figure 43

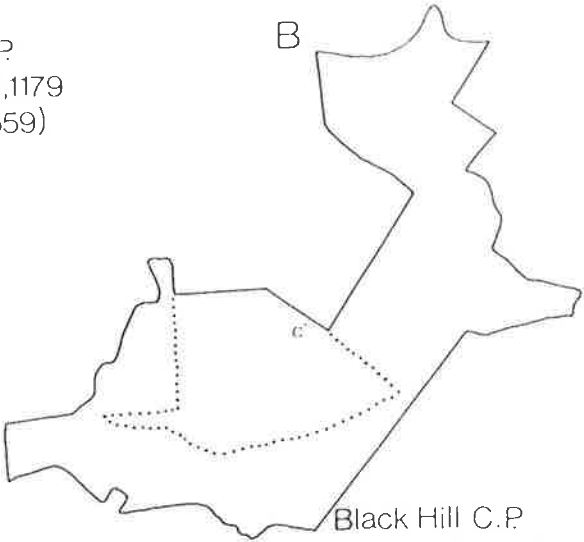
Compactness and Elongation values for select
Mount Lofty Ranges nature reserves plus
adjoining sections containing
native vegetation

A



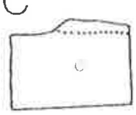
Horsnell Gully C.P.
plus Sections 1178,1179
Comp.= ·9496 (·8559)
Elong. = ·70

B



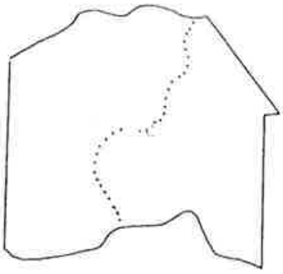
Black Hill C.P.
plus Sections 306,307
Comp. = ·7261 (·5763)
Elong. = ·87

C



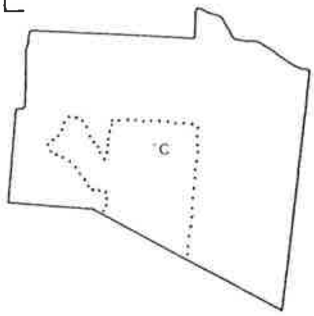
Windy Point R.P.
plus Section 1147
Comp = ·9492 (·4854)
Elong. = ·72

D



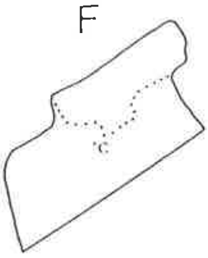
Loftia R.P.
plus Sections pt423,424
Comp.= ·9615 (·8295)
Elong. = ·48

E



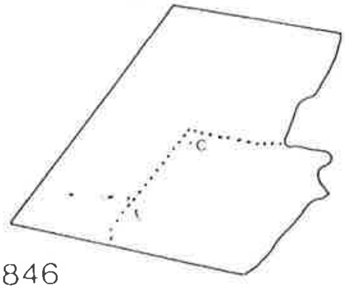
Montacute C.P.
plus Sections pt5544,pt5585,5588
Comp.= ·9396 (·7718)
Elong.= ·68

F

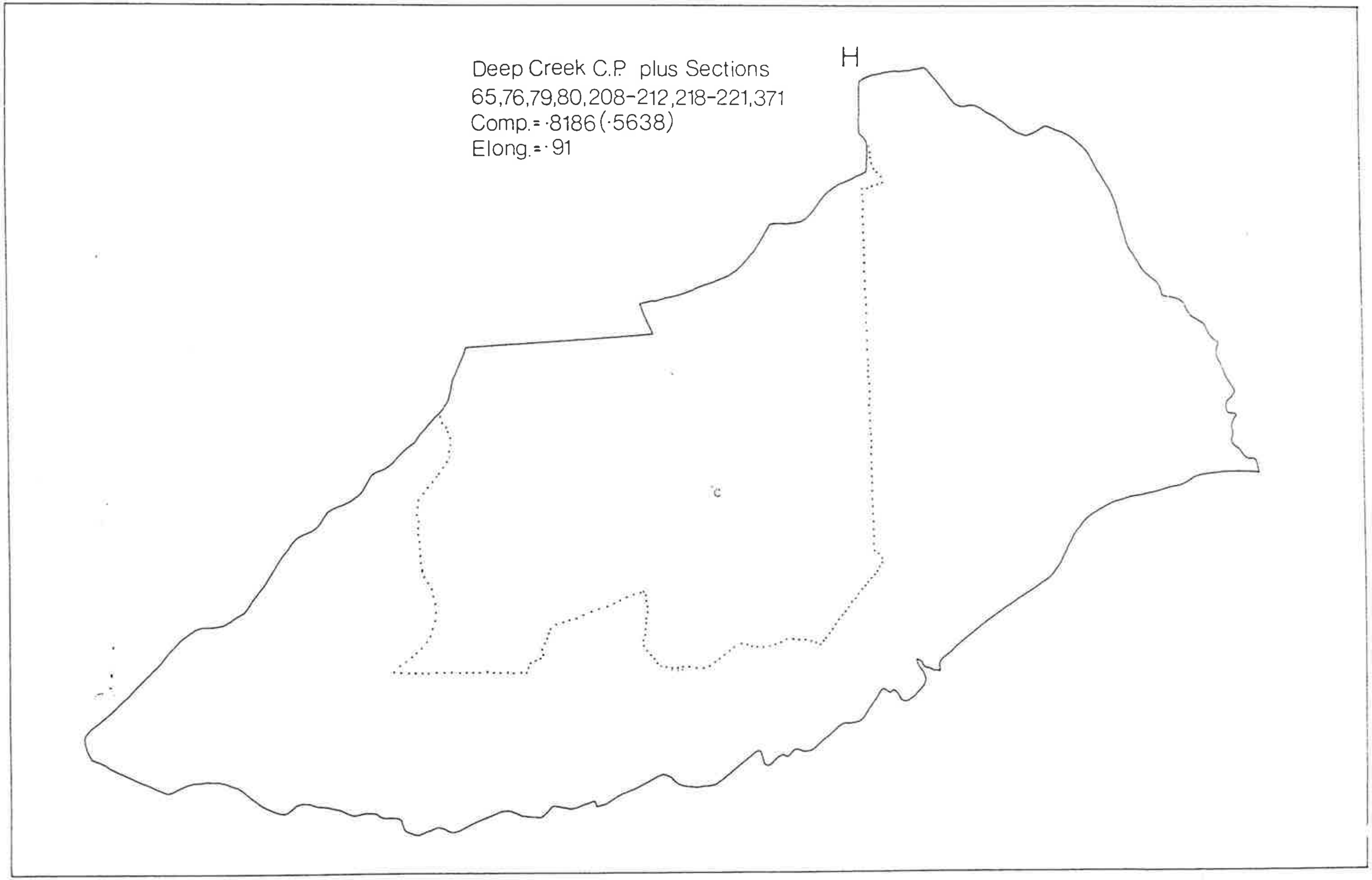


Totness R.P.
plus Sections pt.3822,pt.3824
Comp.= ·8516 (·7593)
Elong.= ·89

G



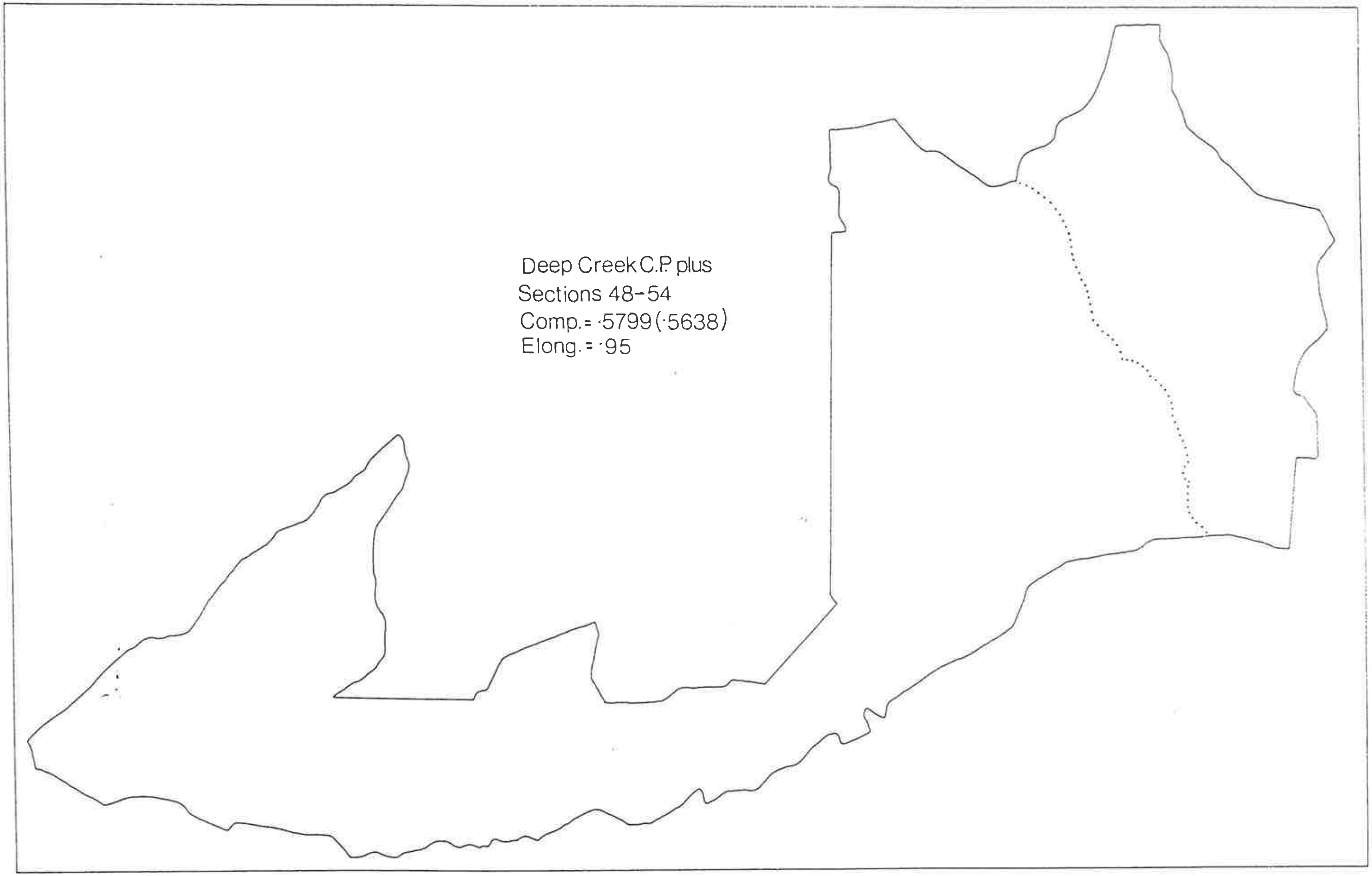
Mt.Magnificent C.P.
plus Sections 291,292,846
Comp.= ·9503 (·9306) Elong.= ·65



Deep Creek C.P. plus Sections
65,76,79,80,208-212,218-221,371
Comp. = ·8186 (·5638)
Elong. = ·91

Figure 44

Compactness value of Deep Creek C.P.
with different sections added



Deep Creek C.P plus
Sections 48-54
Comp.= ·5799(·5638)
Elong. = ·95

selection of sections may decrease or only marginally increase the compactness value of a reserve.

3. Centroids

In addition to compactness, elongation and area, the *centroid* of each nature reserve was computed. The centroid of a shape is the most accessible point for all points within the shape. Therefore, the centroid for complex, irregular shapes need not necessarily be within the shape itself. Optimally, in terms of a reserve's conservation potential, the centroid of the reserve shape should be within the core area of the reserve. For the more compact, regular reserve shapes this is often the case (e.g., Cleland C.P. [Fig. 41.13], Belair R.P. [Fig. 41.14], Mount Magnificent C.P. [Fig. 41.27], etc.). However, some reserve shapes have centroids outside the shape boundaries. These reserves are Montacute C.P. (41.8), Black Hill C.P. (Fig. 41.7), Sturt Gorge R.P. (Fig. 41.21) and Deep Creek C.P. (Fig. 41.37). Therefore, although these reserves are of reasonable size, their ability to hold interior species may be severely reduced due to the displacement of their centroids. Core areas are not located in the most accessible portion of the reserve (given by the centroid) and thus gene flow between interior populations may be decreased.

4. Archipelagos

One important attribute of the compactness index developed by Blair and Biss (1967) is that the index is capable of measuring the compactness of archipelago situations. Blair and Biss (1967) use the political units of Pakistan and the Philippines as examples of archipelagos. Groups of nature reserves, if the reserves are close together, can be considered as archipelagos within a reserve system. Inspection of Figure 22 reveals that numerous clusters of reserves do exist within the Mount Lofty Ranges nature reserve network. The reserves within these clusters may conceivably be considered as fragments of one larger unit, particularly if high internal connectivity exists. Such clusters include the Para Wirra R.P.-Hale C.P.-Warren C.P. archipelago (Figure 45), the Kyeema C.P.-Mt. Magnificent C.P.-Finniss C.P.-Cox Scrub C.P. archipelago (Figure 46), and the Nixon-Skinner C.P.-Myponga C.P.-Yulte C.P.-Spring Mount C.P. archipelago (Figure 47).

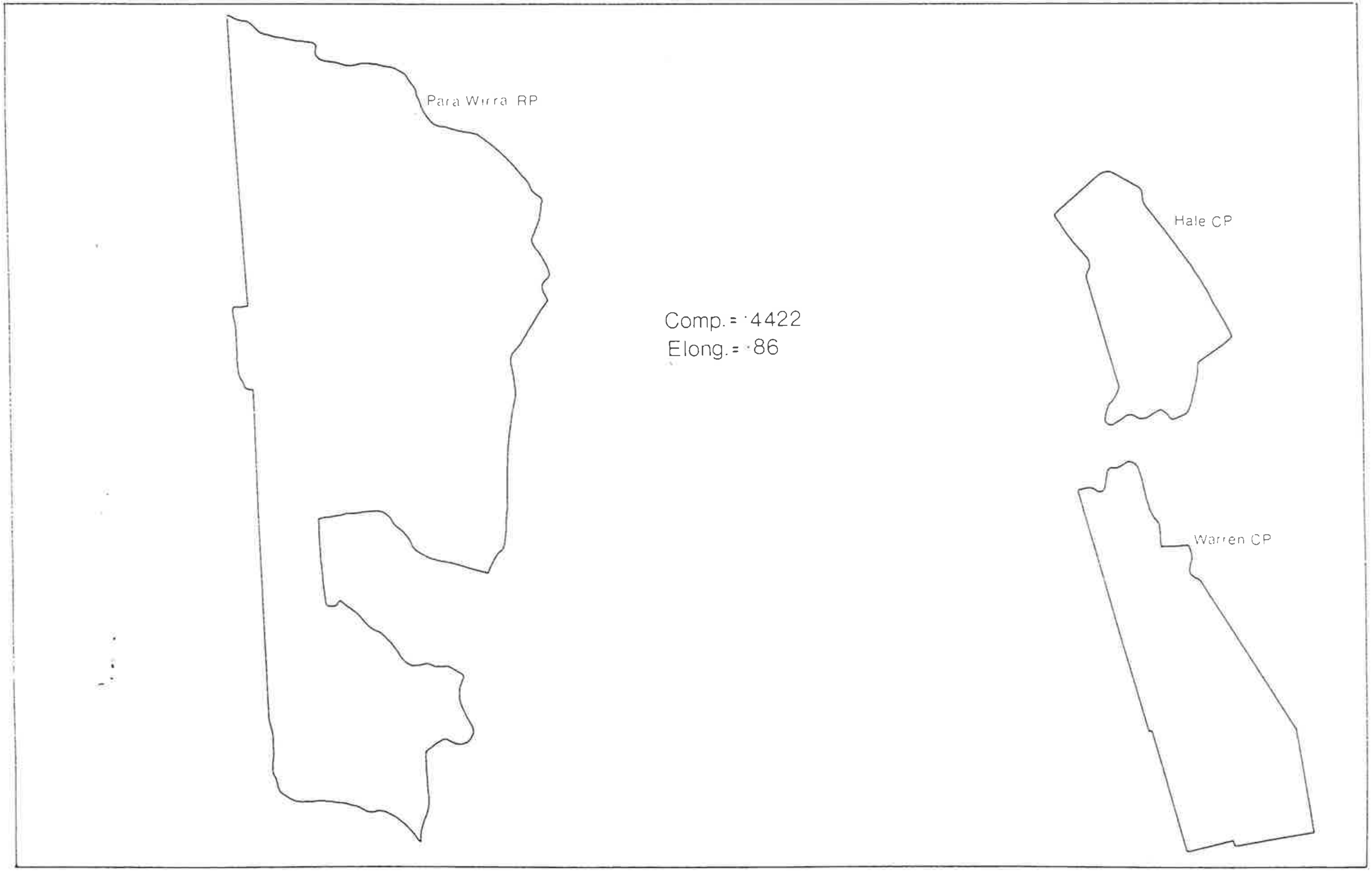
Compactness values for reserve archipelagos are generally lower than those for reserves of equal area. The compactness values for the reserve archipelagos listed above range from only .1902 for the Nixon-Skinner archipelago to .4422 for the Para Wirra archipelago. However, compactness values for the reserve archipelagos can be improved by the inclusion of the intervening patches of native vegetation. For example, in Figure 48, intervening patches of native vegetation have been added to the Nixon-Skinner archipelago. The resultant increase of the compactness value from .1902 to .4456 clearly indicates the importance of considering the intervening native vegetation patches in nature reserve design.

5. Remnant Native Vegetation Patches

In addition to the nature reserves in the Mount Lofty Ranges, numerous patches of unconserved native vegetation still exist. Many of these patches play important roles as parts of biological corridors between reserves. Some are of significant size (i.e., greater than 400 ha.) and may act as source areas for surrounding

Figure 45

Compactness and Elongation value for the
Para Wirra R.P.-Hale C.P.-
Warren C.P. archipelago



Para Wirra RP
Hale CP
Warren CP
Comp. = ·4422
Elong. = ·86

Figure 46

Compactness and Elongation value for the
Kyeema C.P.-Mt. Magnificent C.P.-
Finniss C.P.-Cox Scrub C.P.
archipelago

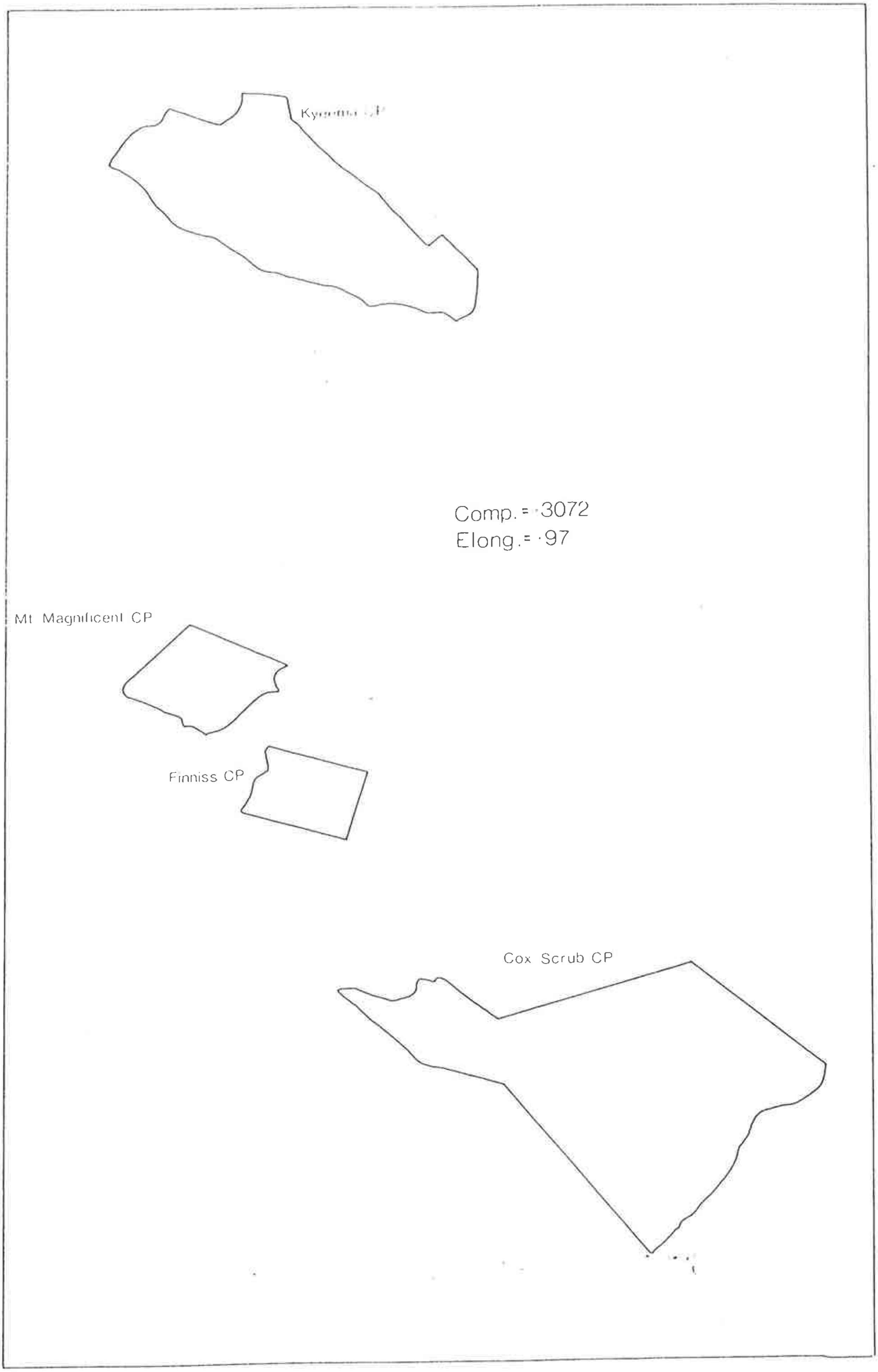

Kyeema CP
Comp. = ·3072
Elong. = ·97
Mt Magnificent CP
Finniss CP
Cox Scrub CP

Figure 47

Compactness and Elongation value for the
Nixon-Skinner C.P.-Myponga C.P.-
Yulte C.P.-Spring Mount C.P.
archipelago

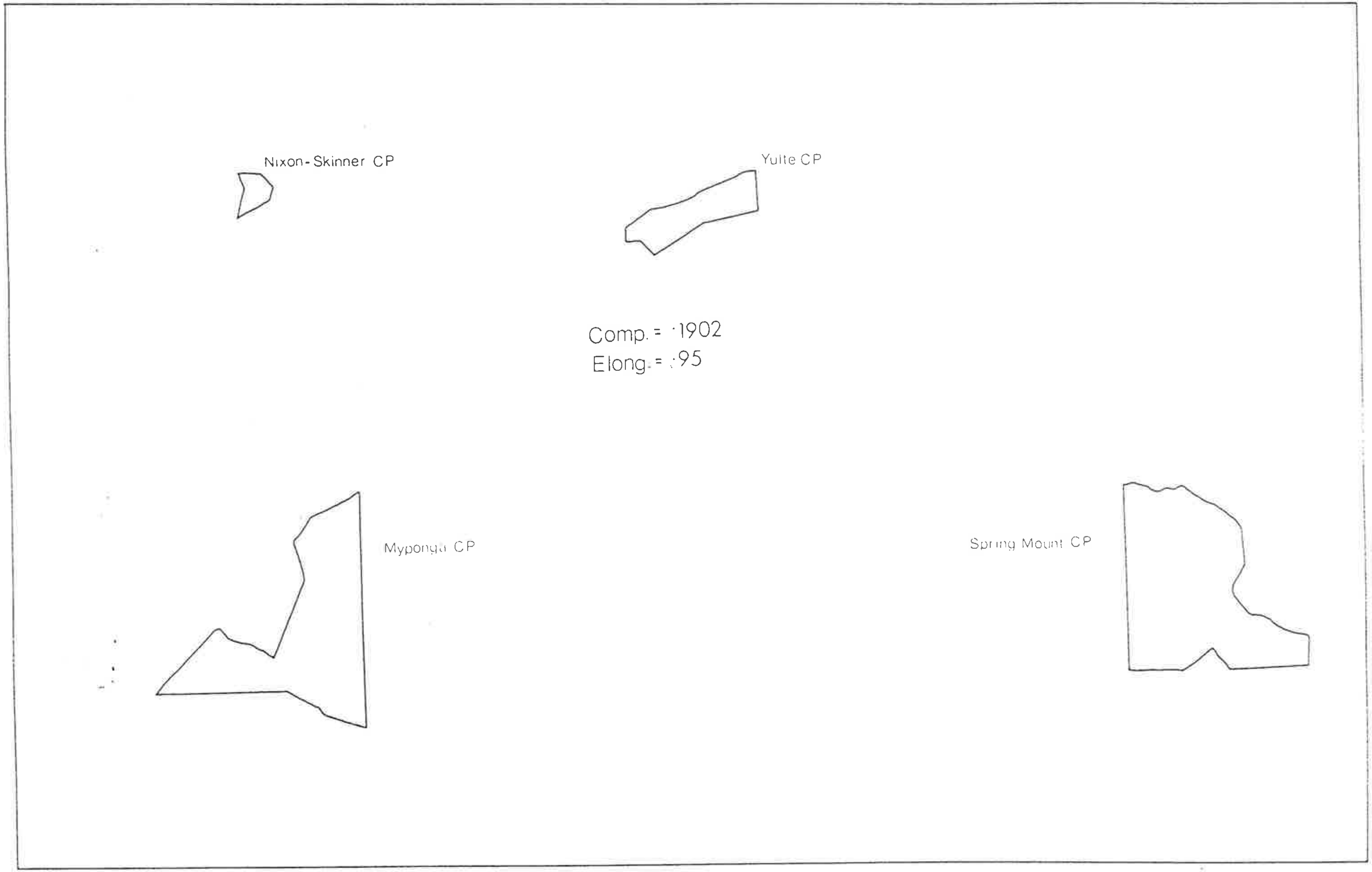
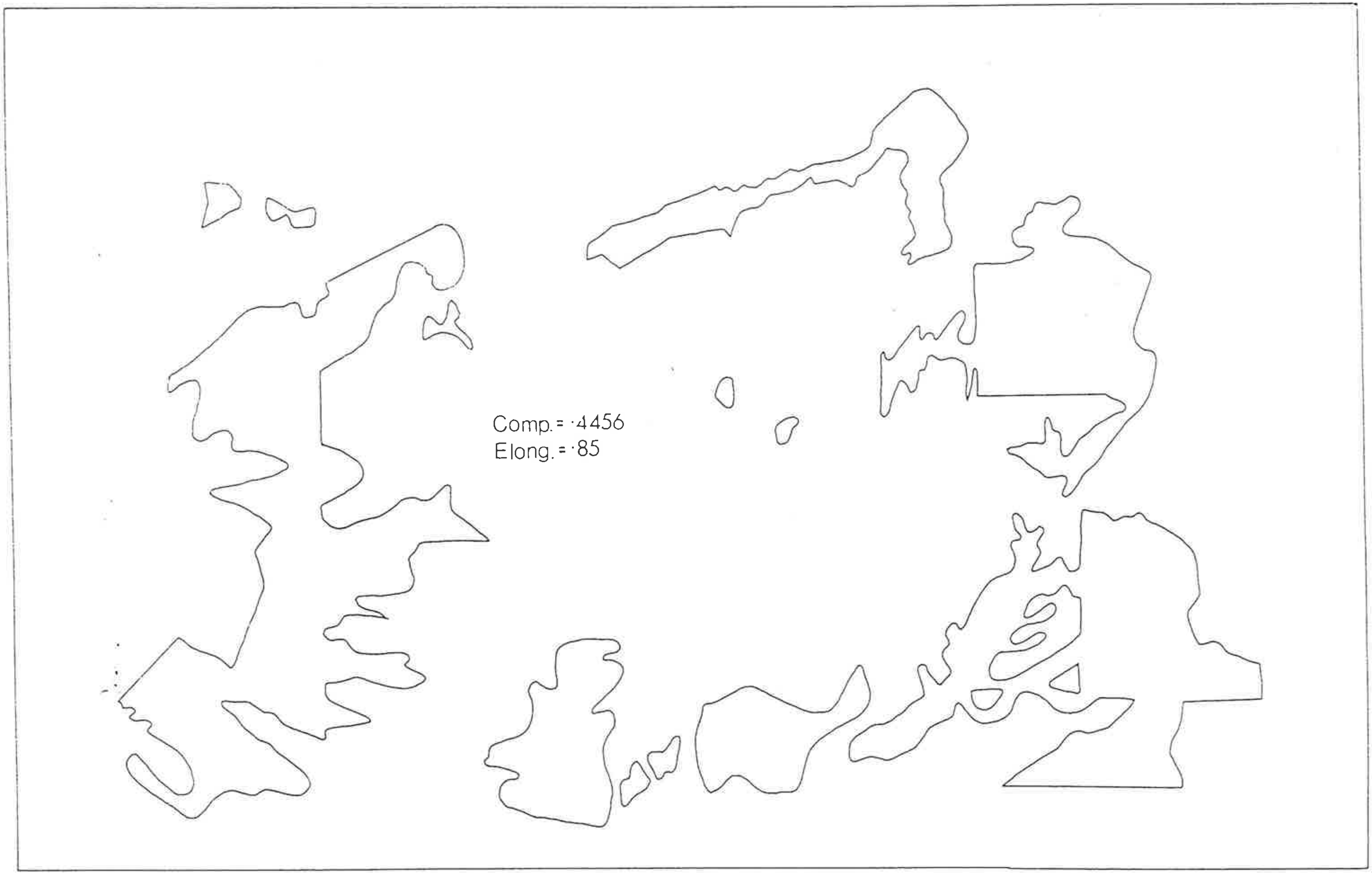

Nixon-Skinner CP
Yulte CP
Comp. = ·1902
Elong. = ·95
Myponga CP
Spring Mount CP

Figure 48

Compactness and Elongation value for the
Nixon-Skinner C.P.-Myponga C.P.-
Yulte C.P.-Spring Mount C.P.
archipelago plus intervening
native vegetation

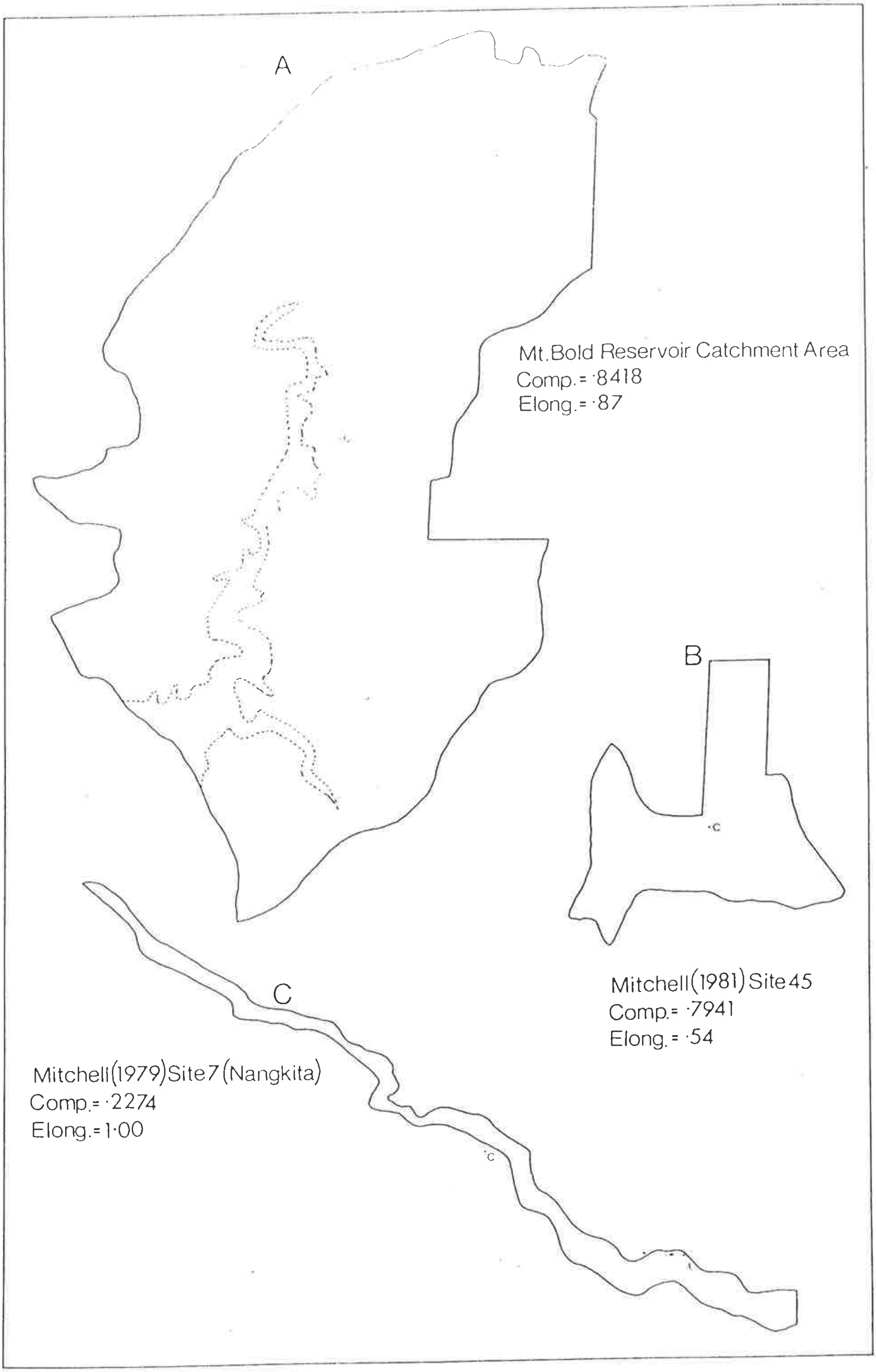

Comp. = ·4456
Elong. = ·85

smaller patches. Figure 49A to X illustrates some of the more prominant native vegetation patches within the Ranges that are not, at this time, managed for conservation purposes. The compactness and elongation values have been calculated for these patches. The compactness values range from only .2274 to .9453, although most of the patches have moderate values between .7500 and .8500. Thus, these vegetation patches may be important because of their size, compactness and juxtaposition. Only two patches are important with respect to all three of these attributes (Figures 49V and X). Five patches are important with respect to two of the three attributes (Figures 49A, F,K,N and U). Many of the patches, however, are not of any great importance with respect to any of the attributes (Figures 49B, C, G, H, I, M, Q, T and W). Of the two most significant patches, Figures 49V and X, the former is Woods and Forests land and part of the Mount Crawford-Kersbrook Forest district, while the latter is the catchment area of the Milbrook-Chain of Ponds reservoir and is managed by the Engineering and Water Supply Department.

Figure 49

Compactness and Elongation value and centroid of select native vegetation remnants within the Mount Lofty Ranges

Notes: The geographical location of these vegetation patches within the Mount Lofty Ranges is shown in Figure 21.

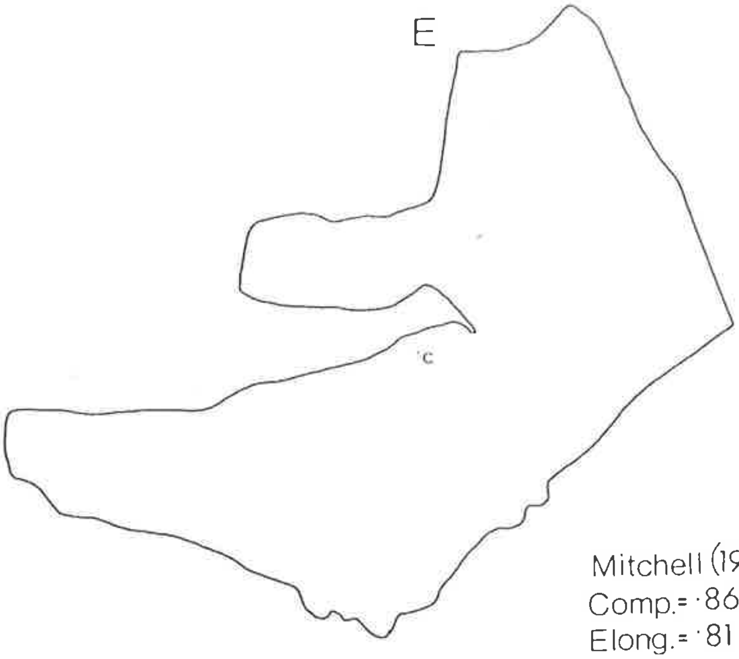


Mt.Bold Reservoir Catchment Area
Comp.= ·8418
Elong.= ·87

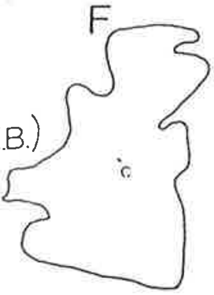
Mitchell(1981) Site 45
Comp.= ·7941
Elong.= ·54

Mitchell(1979) Site 7 (Nangkita)
Comp.= ·2274
Elong.= 1·00

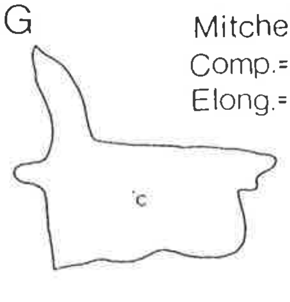
Mitchell (1979) Site 5 (Encounter Bay)
Comp. = ·3683
Elong. = ·99



Mitchell (1979) Site 7 (Wait.)
Comp. = ·8203
Elong. = ·84



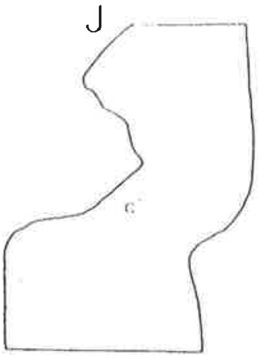
Mitchell (1979) Site 3 (E.B.)
Comp. = ·8694
Elong. = ·81



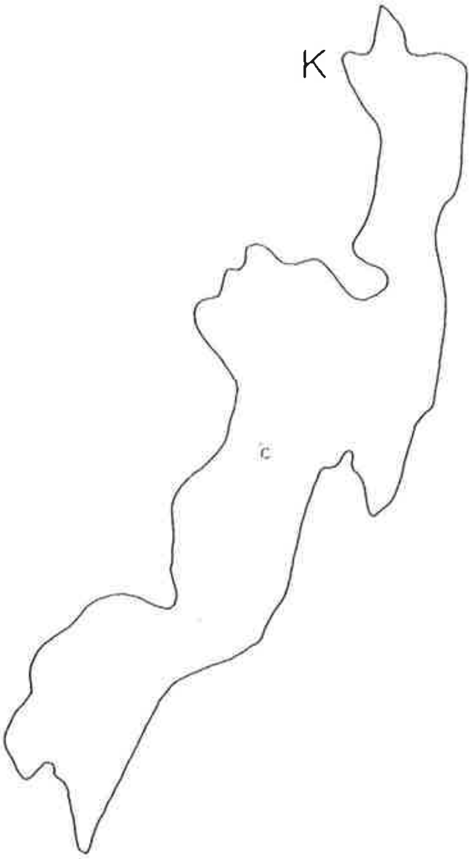
Mitchell (1979) Site 4 (E.B.)
Comp. = ·8443
Elong. = ·77

Mitchell (1981) Site 12
Comp. = ·8411
Elong. = ·90

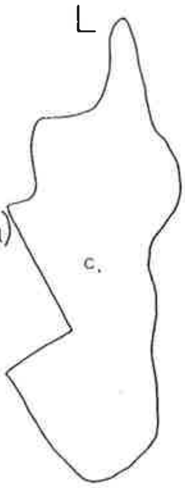
Mitchell (1981) Site 13
Comp. = ·7529
Elong. = ·64



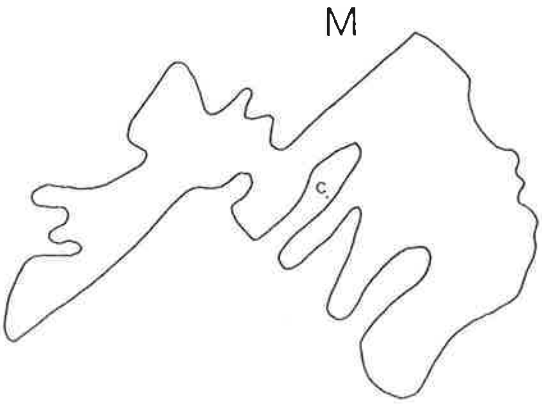
Mitchell (1981) Site 11
Comp. = ·8027
Elong. = ·88



Mitchell (1981) Site 38
Comp. = ·5733
Elong. = ·97

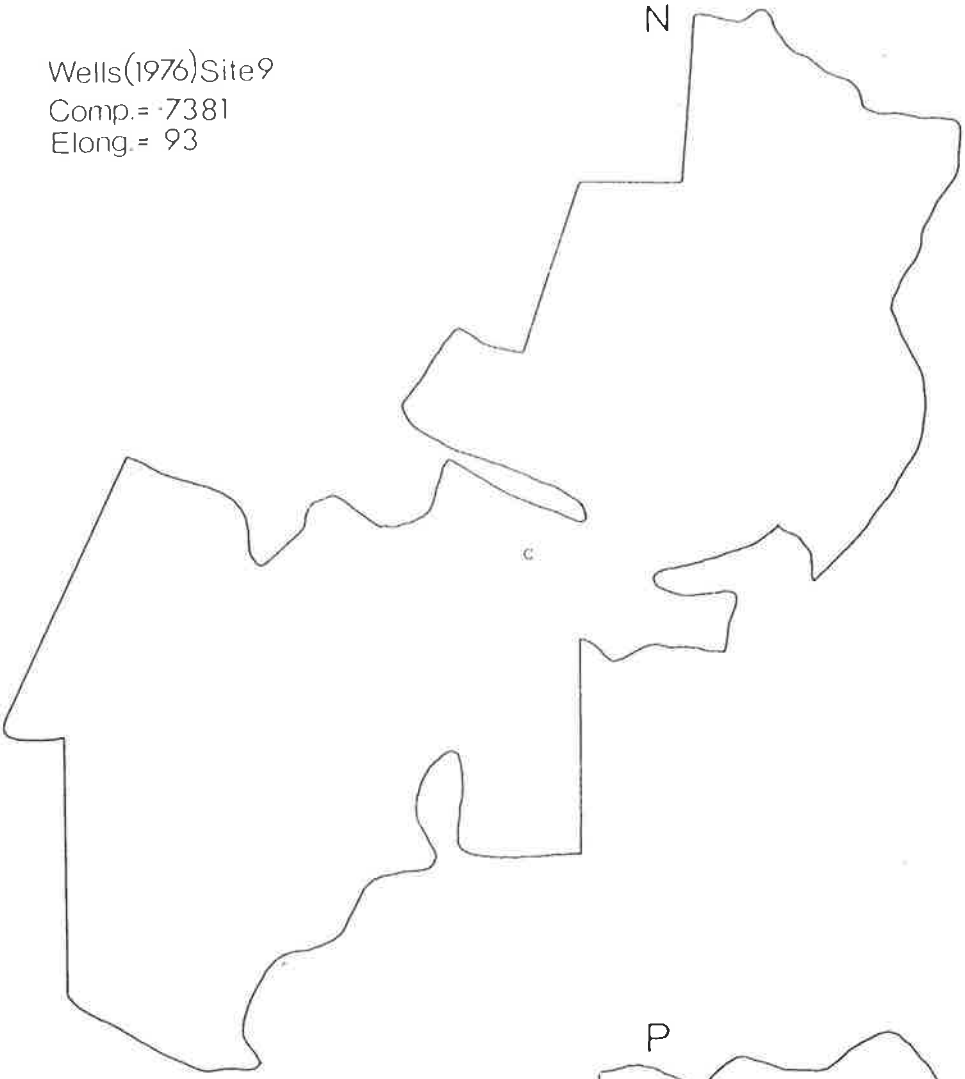


Mitchell (1979) Site 1 (Goolwa)
Comp. = ·7314
Elong. = ·94



Mitchell (1979) Site 2 (Wait.)
Comp. = ·6925
Elong. = ·81

N

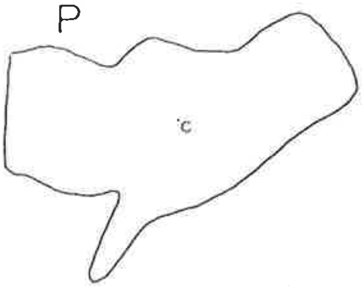


Wells(1976)Site9
Comp.= ·7381
Elong.= 93

O

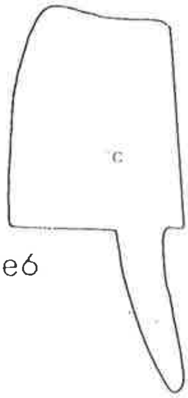
Mitchell(1981)Site4
Comp.= ·6966
Elong.= ·94

P



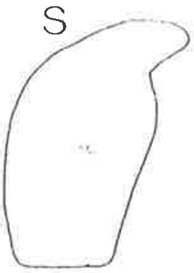
Mitchell(1981)Site26
Comp. = ·8566
Elong. = ·85

Q

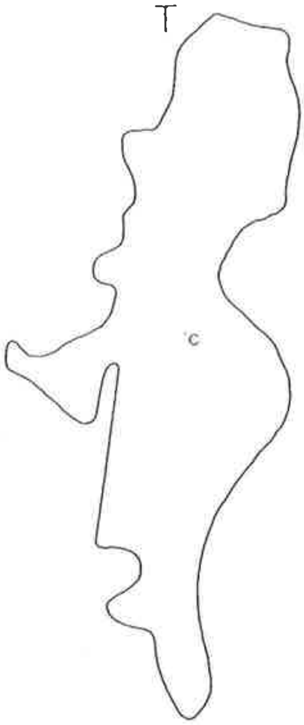


Wells(1976)Site6
Comp.= ·8098
Elong.= ·87

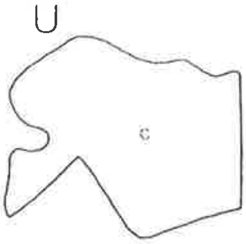
Wells (1976) Site 2
Comp. = ·8876
Elong. = ·78



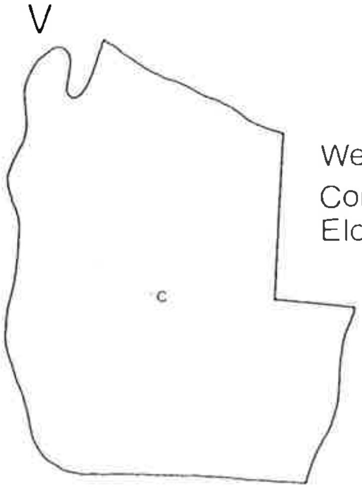
Wells (1976) Site 17
Comp. = ·8891
Elong. = ·85



Mitchell (1981) Site 15
Comp. = ·6666
Elong. = ·96

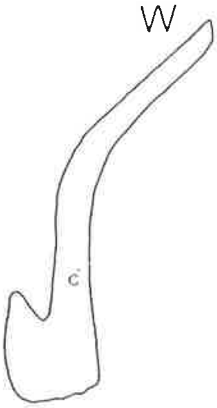


Mitchell (1981) Site 7
Comp. = ·9300
Elong. = ·69



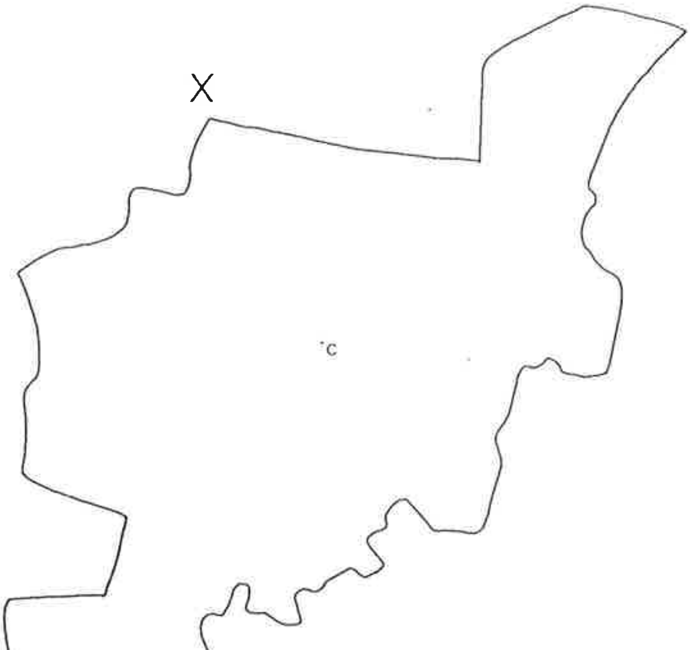
Wells (1976) Site 10
Comp. = ·9453
Elong. = ·73

W



Wells (1976) Site 13
Comp. = ·4329
Elong. = ·98

X



Wells (1976) Site 14
Comp. = ·8731
Elong. = ·83

V. THE MOUNT LOFTY RANGES : DISCUSSION AND RECOMMENDATIONS

This chapter will use the results of the analyses presented in the previous chapter to develop a conservation policy for the Mount Lofty Ranges. It was clearly demonstrated by network analysis procedures that a few reserves are highly significant with respect to connectivity within the Mount Lofty Ranges nature reserve network. These reserves are Montacute C.P., Cleland C.P., Belair R.P. and Loftia R.P.. High connectivity resulted from geographic centrality of these reserves within the network and the relatively large amount of remnant native vegetation that still occurs contiguous to them.

Other reserves were discovered to be isolated either within the network (i.e., Lenswood R.P., Charleston C.P., Scott C.P.) or with respect to the total network (i.e., Deep Creek C.P., Sandy Creek C.P., Eric Bonythen C.P., Waitpinga C.P.). Most of these reserves are geographically isolated from the main concentration of nature reserves that occurs along the western spine of the Ranges and thus are connected to fewer neighbouring reserves. In addition, far more clearing of native vegetation has occurred away from the western spine due to the change in the Range's geomorphological character from steep, rugged slopes to moderate, rolling slopes, thus allowing their greater exploitation by past and present agricultural methods. The reserves in these areas are basically isolated remnants and may function as habitat islands, whereas those on the western spine are representative portions of a moderately extensive vegetation unit. Unfortunately, apart from Deep Creek C.P. which is 2455 ha. in extent, the isolated reserves are generally quite small and their average size is just above 63 ha. (excluding Deep Creek C.P.). Thus, even though these reserves may at the present time contain a reasonable number of native species, due to their small size and isolation the process of species loss or relaxation may be quite rapid. In just a few decades these reserves may only contain exotic species plus a few native species with high competitive powers. Therefore, the value of these reserves as Conservation Parks may be greatly diminished in the near future.

On the other hand, the small reserves on the western spine (e.g., Eurilla C.P., Ferguson C.P., Greenhill R.P., The Knoll C.P., Windy Point R.P., etc.) are in a different situation. These reserves are either contiguous to or nearby moderately large stands of native vegetation, including the larger nature reserves of Cleland C.P., Belair R.P. and Morialta C.P., which may act as source areas for the smaller reserves. The small isolated reserves have no such immediate source areas. However, continuing residential expansion is beginning to erode the existing linkages between many of the reserves close to the Adelaide metropolis. For instance, this is already evident around The Knoll C.P., Ferguson C.P. and Belair R.P.. Residential development forms a more formidable barrier to native species movement than most other forms of land modification and thus, even though reserves may be less than one kilometre apart, the presence of an intervening residential development may effectively block any possible movement by native species between two reserves. Important linkages may be broken and once highly connected reserves may become isolated.

The viability of many reserves within the Mount Lofty Ranges is dependent upon the existence of a single linkage or the presence of an adjacent larger, unconserved vegetation patch. Thus, some vegetation patches are crucial to the continued integrity of the

Mount Lofty Ranges nature reserve network. For example, the biological corridors linking the two nature reserves, Totness R.P. and Scott C.P., with the remainder of the network are both reliant upon the presence of a single vegetation patch; that is, no other routes are available apart from the ones passing through these patches. These vegetation patches, Unit K (Fig. 49K) and Unit L (Fig. 49L), if removed, would isolate these two reserves from the network.

Other remnant vegetation patches play an even more important role in maintaining the network structure and the possibility of inter-reserve exchange of native species. Units N (Fig. 49N), V (Fig. 49V) and X (Fig. 49X) form an important linkage between the northern reserves (e.g., Para Wirra R.P., Hale C.P., etc.) and the central concentration of reserves along the western spine. It should be noted that these three patches are publically owned and managed by the Woods and Forests Department (Units N and V) and the Engineering and Water Supply Department (Unit X). These patches, therefore, enjoy relatively more protection than many which are privately owned. This is also the case with the Mount Bold Reservoir Catchment Area (Fig. 49A) which is an important component of the linkages that unite the central concentration of reserves with those in the southern portion of the network (e.g., Kyeema C.P., Yulte C.P., etc.). The removal of any of these four vegetation patches would create weak links between the three sections of the network. Extra importance would then fall upon Cromer C.P. and Totness R.P. as cutpoints between the sections. These reserves, however, are both small in size and are relatively isolated from the central concentration of reserves. This is in contrast to the four vegetation patches which are all much larger and close to other nearby large vegetation patches.

The size of a vegetation patch or habitat island is an important biogeographic principle for conservation. Thus, any additions that can be made to existing nature reserves can only have positive benefits. However, in the opening chapter it was demonstrated that reserve shape is also an important biogeographic principle. Thus, to fully optimize the benefits for conservation from the acquisition of contiguous vegetation patches to existing reserves, attention must be given to the subsequent changes in reserve shape. Greater benefit will accrue from the addition of a vegetation patch which increases reserve compactness than one which decreases reserve compactness, given that both units are of equal size.

The examples given in Figures 42A to O are a clear illustration of how the acquisition of different parcels of adjoining vegetation patches can have contrasting effects on reserve compactness. Attention should be focused on those vegetation patches which have the greatest effect in increasing reserve compactness. Thus, the vegetation patches adjoining Deep Creek C.P. (Fig. 42O), Cudlee Creek C.P. (Fig. 42M) and Para Wirra R.P. (Fig. 42K) are important in aiding the continued survival of the native species within the reserves by creating increased core area and minimizing detrimental perimeter effects and disturbance factors. This is particularly important for the nature reserves in the Mount Lofty Ranges where the continued invasion of exotic species into many reserves from adjacent modified land has left relatively few undisturbed native areas for the preservation of interior species. Such invasions are particularly evident along disturbance lines within the reserves of the Hill-Face Zone (McLoughlin, 1967).

The economic and planning benefits that can be gained from increasing rather than decreasing reserve compactness may also be of importance in a park management policy. Increased compactness means a lower perimeter-to-area ratio and thus costs of fencing the reserve or the management of any form of buffer zone is subsequently decreased.

Figures 43A to H have been analysed to aid in the possible process of land acquisition (or subsidization) where whole sections are more likely to be purchased than the irregular shapes of the remnant vegetation patches. The same factors now apply as with the vegetation patches in terms of the need to increase reserve compactness. The purchase of suitable sections, in fact, can have marked effects on reserve compactness as illustrated in Figures (43E to H). Sections need not even be entirely covered by native vegetation, for if left relatively undisturbed from grazing and other similar pressures natural regrowth will occur. This regrowth can be assisted by the planting of native species (Gray, 1977), although this need not be of the order described by Schwerdtfeger (1979). Planting should preferably take into account the ecological needs of the individual species, rather than the present standard parkland nature of restoration, to ensure a greater likelihood of success.

The centroid of reserve shape should ideally be within the core area (e.g., Cleland C.P., Mt. Magnificent C.P., etc.). If this does not already occur, it can be achieved by the addition of adjoining native vegetation patches (or sections) that increase reserve compactness. The additions proposed to Horsnell Gully C.P.

(Fig. 43A), Loftia R.P. (Fig. 43D), Montacute C.P. (Fig. 43E) and Deep Creek C.P. (Fig 43H), in particular, alter reserve shape significantly so that the centroid becomes located in the core area.

A. Recommendations

In a seminar conducted by the Adelaide University Department of Adult Education (AUDAE) in 1969, it was stated by a representative of a residents committee from the Mount Lofty Ranges that *"if more* [reserves] *must be established they should be further afield such as the reserve at Monarto South, surrounded by wide open flat farmland, easily accessible for fire-fighting units and no threat to neighbouring properties"* (Whitelock, 1969, 129). This statement could hardly be further from any form of sound conservation policy for the Mount Lofty Ranges. Where then should efforts be channelled to maximize the benefits for conservation activities within the Ranges?

The nature reserve network created for the Ranges has been demonstrated to be of a fairly complex nature with a total of 86 linkages connecting the 37 reserves, although only 33 reserves (83 linkages) are contained in the main network. Some reserves and linkages were found to be crucial to the structural integrity of the network and therefore to the conservation potential of the Ranges in general. The reserves in question were Belair R.P., Cleland C.P., Loftia R.P. and Montacute C.P.. These reserves should, therefore, be 'developed' to maximize their ability to conserve their present native biota. For Montacute C.P. and Loftia R.P., in particular, adjoining stands of native vegetation, or those sections containing these stands, could well be added to these reserves not only to increase their size but also their compactness (i.e., Figs. 42I and H).

This should be of very high priority, for if these reserves are allowed to degrade as conservation units or are lost through private acquisition the integrity of the Mount Lofty Ranges nature reserve system becomes increasingly threatened (i.e., Figures 25-8, 30). On the other hand, some reserves can be lost without harming the network at all (i.e., Sandy Creek C.P., Charleston C.P., Scott C.P.) (Figure 29). Thus, if in the future, pressures force the deletion of one or more reserves within the Ranges then these reserves, in terms of their overall contribution to the Mount Lofty Ranges nature reserve network, are the most expendable, although few people would wish any reserves to be lost.

It has been stated that any additions to reserves should, if possible, increase reserve compactness. It was discovered that Cudlee Creek C.P., Deep Creek C.P. and Para Wirra R.P. benefitted most from the selected additions of adjacent stands of native vegetation. Deep Creek C.P., in particular, being isolated from the main network and thus out of the reach of most forms of propagules, is almost an independent unit and therefore conservation efforts should be directed mainly towards preserving what species remain. This can most effectively be achieved by increasing reserve size and compactness. Remnant vegetation patches are available for this purpose and these have been shown in Figure 42O. Not only is the available patch relatively extensive, but there are also no significant disturbances, such as dwellings or roads, present.

This compares with the possible addition to Cudlee Creek C.P. where the presence of an adjoining patch of vegetation also enables an increase in compactness (i.e., Fig. 42M). However, not only is the additional area small, thus still keeping the total area small, but there is also a major road dividing the reserve and the vegetation patch. This disturbance factor will greatly diminish the benefits that might otherwise have been gained with the addition of this patch to Cudlee Creek C.P..

Fortunately for conservation purposes most of the least compact nature reserves within the Mount Lofty Ranges are of very small size, Deep Creek C.P. being the major exception. The other three least compact reserves, Brownhill Creek R.P. (Fig. 41.18), Eric Bonython C.P. (Fig. 41.36) and Windy Point R.P. (Fig. 41.19), are so small as to allow most forms of environmental disturbance to penetrate to all areas of the reserves, regardless of how compact they are. This problem, therefore, also applies to all of the smaller reserves within the Ranges which, without continued management and control, could hardly be expected to fulfill any significant conservation objectives.

One reserve which should be the focus of conservation attention within the Mount Lofty Ranges is Montacute C.P. (Fig. 41.8). This reserve is one of the most accessible within the nature reserve network and thus may play a very important role in facilitating gene flow through the network. However, Montacute C.P. is relatively small, only 196 ha., and is considerably less compact than is desirable for a conservation park. Nevertheless, with the addition of only three relatively small sections (i.e., Pt.5544, Pt.5585, 5588; Fig. 43E) the reserve's compactness is increased from 0.7718 to 0.9396. In addition, the centroid of the new reserve shape is centrally placed (Fig. 43E), whereas the centroid of the present reserve shape is located outside the reserve boundary (Fig. 41.8). The addition of these sections would not only greatly enhance the conservation potential of Montacute C.P. itself, but would also benefit the conservation potential of the whole of the Mount Lofty Ranges nature reserve network.

The question now arises of the importance placed on conservation within the eleven Recreation Parks in the Mount Lofty Ranges. It has already been demonstrated that the Recreation Parks play a major role in maintaining a linkage between species in the central and southern reserves (Fig. 37). At present the Recreation Parks contain some remnant areas of modified to semi-natural bush. However, with the growing recreational needs of the expanding metropolitan area greater stress will no doubt be placed on the Recreation Parks, particularly Para Wirra R.P. and Belair R.P., to cater for these needs. Nevertheless, it is important that the native vegetation remaining within these reserves be kept for the benefit of the Ranges conservation viability as a whole. Any expansion of reserve facilities should be on reserve land that has already been modified or additional land should be purchased contiguous to the reserves.

Significant conservation benefits can be gained by treating concentrations or groups of reserves as a single planning unit. This not only applies to the Mount Lofty Ranges nature reserve network as a whole but also to the smaller archipelagos of nature reserves and intervening vegetation patches which it contains. Four concentrations of reserves were found within the network, three of which are illustrated in Figures 45, 46 and 47. The fourth concentration is the largest and consists of the central group of reserves along the western spine of the Ranges (e.g., Black Hill C.P., Cleland C.P., Shepherds Hill R.P., etc.). If the intervening vegetation patches are included in the planning decisions for a reserve archipelago (i.e., Fig. 48) then the constituent reserves may be effectively united to form one larger unit. This may be particularly important if the archipelago contains a rare, endangered or habitat specializing species.

Of the native vegetation patches between the nature reserves only those in reservoir land seem to be safe from possible clearance or major disturbance. However, one attribute of reservoir land, in terms of its conservation potential, is that it often lacks a significant core area. This area is generally used for water storage which can take up a large proportion of the reservoir catchment area. Not only does the water flood potential interior habitats, but it also creates a significant barrier to movement for many species. On the other hand, reservoir land may also create important havens for waterfowl and other aquatic species. Plant communities which are flood tolerant may also proliferate along reservoir margins and various annual species may only occur on the areas exposed by the retreat of water during the drier months. Thus, reservoir lands provide an important variety of environmental conditions which could increase the native species diversity of a region. Gill (1977) has discussed aspects of the promotion of nature conservation and other compatible uses for reservoir margin areas.[1]

One patch of native vegetation has consistently figures as important with respect to the biogeographic principles studied.

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[1] Unfortunately, the policy within South Australian reservoir lands is for the reservoir margins within the flood range to be cleared, thus eliminating most of this important habitat.

This unit, Unit V (Figure 49V), is owned by the Woods and Forests Department and thus may be in some danger of being cleared for future exotic timber production. Unit V is not only relatively large for a unit of remnant vegetation within the Mount Lofty Ranges (i.e., 500 ha.) but is also very compact with a value of 0.9453. Therefore, its conservation potential is very high. Unit V is also extremely important as part of the major linkage connecting the northern and central reserve concentrations and thus may be crucial in maintaining the present level of gene flow through the Ranges. Wells (1976) has also ranked this unit highly in terms of both scientific and social factors, particularly with respect to uniqueness and degree of preservation of the habitat and constituent species. Internal disturbance is confined to walking tracks, although other disturbances are present along parts of the perimeter of the vegetation patch (Wells, 1976). Nevertheless, due to the size and compactness of the patch it is unlikely that these disturbances will have any real effect on the patch's overall conservation viability. Other vegetation patches which have been demonstrated to be of importance to the conservation potential of the Mount Lofty Ranges in general are shown in Figures 49F, K, N and U, although every remaining patch of native vegetation within the Ranges has a role to play in the protection of the native species.

Nature conservation planning within the Mount Lofty Ranges can no longer be of an ad hoc nature, goals have to be set and a co-ordinated planning policy needs to be developed in order to achieve these goals. Specht and Cleland (1961, 1963) and Specht (1972) have already set a goal of the preservation of formations and endangered species within South Australia. Specht and Cleland (1961, 1964) recommend that reserves should be established to ensure that *"every major plant formation and, if possible, every species within its boundaries is preserved for posterity"*. However, this policy alone is not sufficient to guarantee the survival of the native biota. Island Biogeography Theory has demonstrated that small, isolated patches of vegetation in a sea of modified land are likely to undergo a natural process of relaxation of the endemic species. Thus, even though an endangered community may be temporarily saved from clearance or other forms of destruction by the designation of a nature reserve, its continued survival is dependent on the constructive application of island biogeographic principles in reserve management operations.

Fortunately the National Parks and Wildlife Service (NPWS) of South Australia has begun to recognise that a large percentage of their nature reserves are a size which may well be insufficient to ensure the long-term survival of the native biota and that increased concentration in *off-park conservation activity* is required. The NPWS views off-part conservation activity not only as a means of enhancing long-term genetic viability, but also as a means of enabling and encouraging landowners to contribute to conservation programmes.

However, a policy of the NPWS is that current land acquisitions should consolidate existing reserves rather than create new reserves. The consolidation of existing reserves at the moment is merely intended to increase reserve size. However, it is most unlikely that increasing the size of most of the nature reserves in the Mount Lofty Ranges and similar areas will produce reserves of sufficient extent to independently preserve the native species that they contain. On the other hand, if increased reserve size is matched by increased reserve compactness, these reserves may become far more viable.

If inter-reserve connectivity is also encouraged through the presence of biological corridors then many small reserves may well be united to form a single larger unit well beyond the minimum area required for the preservation of even the most mobile native species. Within the one larger unit or network, the larger nature reserves, forested reservoir margins, and other large areas of native vegetation may act as 'hot spots' for the native species in times of increased stress or as focal points for the re-establishment of nearby failed agricultural or forestry land. For instance, during bushfires the existence of biological corridors leading to alternative suitable habitats for the fleeing native biota may be vital not only for their successful evacuation (Caldicott, 1977), but may also aid in the re-establishment of the denuded area by the native species. The Ash Wednesday fire of 1980 in the Mount Lofty Ranges clearly illustrated that even the moderate sized reserves are far below the minimum dynamic area postulated by Pickett and Thompson (1978). Thus, unless the native species of a reserve have available migration paths, for both emigration and immigration, a single large disturbance could render that reserve biologically pauperate.

However, the intervening vegetation patches that form the biological corridors for inter-reserve movement have their own inherent conservation problems. These patches are often subject to scrub grazing, timber collection and other similar pressures from the rural community (Caldicott, 1974). Similarly, the remaining roadside vegetation in the Ranges is also under a variety of pressures which would not be found to the same extent within nature reserves. Since the nature reserves and the larger vegetation patches are the only remaining habitats which afford a reasonable degree of protection for interior species, these areas should be left as large and as compact as possible.

For instance, if some form of development is necessary to 'up-grade' a nature reserve by the construction of dwellings or tourist facilities then these disturbances should at least be placed along the peripheral regions of the reserve (NCSSA, 1972). Better still, additional areas should be added to a reserve for such facilities. However, if the facilities have to be placed within the existing boundaries of a reserve they should be placed on peninsula areas (if a suitable peninsula area is available) for this would then minimize the impact on the reserve's conservation viability, particularly if the reserve is of reasonable size. All efforts should be directed towards the discouragement of any form of disturbance in the core or 'wilderness' areas of reserves.

Although the rate of vegetation clearance in the Mount Lofty Ranges has dropped markedly over the past few decades, due mostly to the fact that there is now little arable land remaining that has not been cleared, the rate of detrimental disturbance is rapidly increasing. Whereas the remaining stands of native vegetation were once interrupted mainly by agricultural or grazing land with few major roads and settlements, the growth of rapid transportation has meant increased and wider road construction and the growth of rural commuter settlements (e.g., Bridgewater, Stirling, etc.). Improved farming techniques with insecticides and fertilizers have also caused increased disturbances on the remaining vegetation. These changes can only mean greater pressures and handicaps for the surviving native biota in the Mount Lofty Ranges, particularly if no form of direct planning control is forthcoming.

Many conservationists and rural planners have put forward plans for the continued survival of the Mount Lofty Ranges as an important conservation and recreation area. One of the most notable suggestions is to dedicate the whole of the Ranges as a national park in the same form as those existing in the United Kingdom (e.g., Caldicott, 1974; Nature Conservation Society of South Australia [NCSSA], 1972). Within the proposed large national park, significant areas could be designated by the titles Landscape Preserve, Scenic Preserve or Conservation Area (NCSSA, 1972). Smaller national parks have also been recommended for the Para Wirra-Mount Crawford district (Wells, 1976), and the Hill-Face Zone and the Deep Creek region (NCSSA, 1972). The theme of these recommendations is that there should be more control and monitoring of the human and physical processes operating within the Ranges by some centralized public body. This body would then be given the power to control all planning decisions within the Ranges and would be able to block any proposed diversions from the body's objectives. This presumably would include the power to block any proposed clearance of remnant native vegetation. Without this protection the remaining native vegetation that exists on private land is in constant danger of being cleared.

A policy of retaining as much of this remnant native vegetation as possible is required through either land acquisition or subsidization. The NPWS is presently undergoing a policy of land subsidization by means of the Vegetation Retention Scheme whereby landowners receive incentives, such as a reduction in local government rates and/or a subsidy to fence the area of native vegetation in question, and on-going management assistance and advice. Significantly, one of the criteria for selection of possible subsidized areas is that the area of native vegetation may act as a *"last refuge for birds or animals, or a connecting 'corridor' of native plants providing natural cover between parks and other heavily vegetated areas"* (S.A. Department of Environment and Planning, 1981, 7).

The formulation of the Vegetation Retential Scheme has enabled a degree of government control over many of the remaining larger patches of privately owned native vegetation. Thus, even though money is not readily available for the purchase of those vegetation patches that are of importance as part of corridors or as significant refuges, these patches can now at least be protected against future clearing.

The NPWS is now beginning to use island biogeogrpahic principles in its assessment of habitat patches. For example, the most recent Mount Lofty Ranges report (Mitchell, Prizibilla and Dendy, 1981) has used a number of biogeographic principles in the evaluation of native vegetation patches. This is in contrast to the earlier Mount Lofty Ranges reports by Wells (1976) and Lampray and Mitchell (1979) who only took into account basic scientific (e.g., uniqueness of stand, degree of modification, etc.) and social criteria (e.g., aesthetic value, accessibility to nearby population, etc.) in their rankings of native vegetation patches.

In the report by Mitchell, Prizibilla and Dendy (1981) mention was made of: a) the size of the patch; b) the patch as a percent of the total scrub within 2.5 kilometres radius from the centre of patch; and c) the proximity of the patch to a nearby nature reserve (i.e., contiguous or non-contiguous). A large patch (i.e., greater than 100 ha.) which contained greater than 50 per cent of the total scrub cover and was contiguous to a nature reserve received the highest total weighting. The only obvious problem with this procedure is that an isolated patch with little or no surrounding native vegetation in the 2.5 kilometre radius would receive the highest rating, whereas in biogeographical terms such a patch would be of least value. Nevertheless, the report attempted to understand the importance of biogeographic principles in nature conservation planning, or at least those three listed above. If island biogeography principles can be properly applied, then the future conservation potential of the Mount Lofty Ranges appears much brighter.

B. Summary of Recommendations

a. Nature reserve policy for the Mount Lofty Ranges should take into account the reserve system as a whole rather than treating each individual reserve as an independent unit.

b. An off-park conservation policy is necessary to complement a nature reserve policy to achieve maximum benefits from any conservation programme.

c. All remaining vegetation patches within a region play a role in maintaining native species diversity.

d. The size and compactness of Montacute C.P. need to be increased so that maximum use can be made of the reserve's high accessibility in the Mount Lofty Ranges nature reserve network.

e. The compactness of Deep Creek C.P. needs to be increased. This can best be done by the addition of the adjoining sections, indicated in Figure 430, containing native vegetation.

f. Of the remaining reserves Cleland C.P. and Belair R.P. have proven to be important with respect to size, accessibility and compactness. It is important that the remaining vegetation within Belair R.P. be conserved to maintain accessibility through the network.

g. Although the present policy of the National Parks and Wildlife Service is to create no new reserves, attention should be paid to Unit V as an important conservation patch within the Ranges.

h. Additions to all reserves should be aimed at increasing reserve compactness as well as size.

i. Where groups of reserves occur on both a regional and local scale, maximum conservation benefits will accrue if the groups of reserves are managed as one unit.

j. Where corridors of native vegetation occur between two reserves they should at least be maintained and, if possible, encouraged through revegetation.

k. Corridors could be created, if they do not already exist, between reserves of similar ecological characteristics.

l. It is imperative that species ranges be studied within the Mount Lofty Ranges so that an effective conservation policy can be formulated for a species or community.

VI. CONCLUSIONS

The techniques developed in this study have relied heavily on Island Biogeography Theory for the measurement of the biogeographic attributes of nature reserves. Island Biogeography Theory, as it applies to both true islands and habitat islands, was examined in the first chapter. It was discovered that the theory, as developed by MacArthur and Wilson (1963, 1967), Preston (1962) and others, is based upon two premises. The first of these is the species-area relationship whereby there is a positive relationship between the number of species of a given taxon on an island and the area of that island. This relationship was found to hold in a large number of studies (e.g., Darlington, 1957; McLaren, 1979; Robbins, 1979; Wilson, 1961; etc.), although some studies demonstrated slight complications (e.g., Heatwole, 1975; Whitehead and Jones, 1969, etc.) and a few demonstrated no obvious relationship (e.g., Levenson, 1976; etc.). However, these discrepancies were usually due to some form of interference by man. Thus, the notion that a substantial increase in island area will produce some form of increase in species numbers has generally been accepted within biogeographic circles. Likewise, a large decrease in island area will produce a decrease in species numbers for a given taxon. The exact reasons for this relationship are still being debated. However, the five reasons offered by Diamond (1975a) appear intuitively appealing, although these need not necessarily be complete and, indeed, it is doubtful whether they are since Diamond's work concentrated almost exclusively on avifauna.

The second premise is that each island, whether true or habitat, has some balance or equilibrium between immigration and extinction rates which at least partially explains an island's biotic diversity.

The immigration rate for an island depends mainly on: a) the size of the source pool; b) the distance of the island from the source pool; c) the number of species already present on the island and, to a lesser extent; d) the size of the island. The extinction rate depends mainly on: a) the size of the island and; b) the number of species on the island. The immigration rate will decrease if (a) decreases, (b) decreases, (c) increases and, (d) decreases. The extinction rate will decrease if (a) increases and (b) decreases. The two most important factors stressed in the equilibrium model are the size and degree of isolation of an island.

The effects of reduction in the size of an island on the endemic biota has been a major topic within Island Biogeography research. The works of Diamond (1972, 1975a), Terborgh (1974, 1975) and Willis (1974) are particularly evident within this field. Even though all of these studies have their faults and limitations there is little doubt that a reasonable decrease in the area of an island will produce a relaxation of the endemic biota to a lower level in general accordance with the equilibrium theory and the species-area relationship. Whether a new equilibrium is reached or, subsequently, if turnover exists at this new equilibrium, is still very much debatable. However, species loss generally occurs with reduced island area. Importantly, the rate of extinction of species is not equal and certain life forms consistently disappear first. Therefore, conservation efforts need to be aimed at conserving those species that are most susceptible to area reduction and habitat loss. The application of Island Biogeography Theory to nature conservation planning can directly assist in this goal.

Probably the most important attribute of Island Biogeography

Theory is its predictive powers and it is these predictive powers that have become most useful for many conservationists and environmental planners. The application of Island Biogeography Theory to nature conservation planning has also introduced a dynamic element into what was previously, and still is in some countries, a static and site centred planning policy. The theory has shown that to maintain or increase the species diversity for a given habitat island the extinction rate for the habitat island should be decreased and the immigration rate increased. To achieve these objectives certain design principles for a habitat island or nature reserve have been developed by Diamond (1975b) and Diamond and May (1976), and these were illustrated in Figure 9. The principles are based around the size and shape of an individual nature reserve and its geographic juxtaposition.

Planning for reserve size is very straightforward, with increasing reserve size being of increasing importance for conservation. However, difficulty is encountered when attempting to assess the relative benefits for conservation of different reserve shapes and geographic positionings, particularly when complex intervening environments of inhospitable modified terrain interspersed with stepping-stone islands and biological corridors are encountered. Techniques are required that can assess the relative merits of varying reserve shape and positioning, especially when the optimal situations described by Diamond (1975) are unlikely to be met. The importance of finding measures of these reserve attributes has been demonstrated by Kent and Smart (1981). Kent and Smart (1981), using multivariate analysis techniques, have found that the number of higher plant species in remnant forest woodlots in two areas of lowland Britain is related more to the fragmentation characteristics of the sites (i.e., size of sites, inter-site distance) than to their habitat characteristics. Kent and Smart (1981) came to the important conclusion that the assessment of fragmentation is as important as the collection of habitat and species data.

Accessibility and shape analyses have long played an important part in Human Geography and a large variety of techniques of varying complexity have been developed to assess these properties. The simpler techniques (e.g., Kanksky, 1963; Pounds, 1963; Chorley and Haggett, 1965) offer little to a comprehensive planning policy. However, the more complex techniques for both shape (e.g., Blair and Biss, 1967) and accessibility measurement (e.g., Taaffee and Gauthier, 1973) provide important information based on a relatively large number of the inherent properties of a unit.

Accessibility analysis has previously been confined to the analysis of network structures that include transport, information and other similar network structures (e.g., Garrison, 1968; Hay, 1973; Reed, 1970; etc.). Thus, to utilize this form of analysis for nature reserve design, the reserves need to be transformed into a network. This is quite readily achieved by equating the nature reserves and intervening biological corridors with nodes and linkages respectively. With the network now constructed (e.g., Figure 22) the relatively powerful measures derived for accessibility analysis can be applied. Taaffee and Gauthier's (1973) technique can calculate the most accessible, or the least isolated nodes within a network. The technique also allows experimentation by adding or subtracting nodes or even by altering network configuration. Changes in accessibility can be examined at both the nodal level and the level of the total network.

The application of the shape measure derived by Blair and Biss (1967) provides equally important information for a nature reserve planning policy that relies at least partially on Island Biogeography Theory. Diamond (1975b) has stated that the optimal shape of a nature reserve is circular. However, sections are very rarely, if ever, circular and thus nature reserves are consistently of some other shape. For instance, if a comparison between an elongated or fragmented nature reserve were required, there has been no method for planners to judge which shape provides the greatest compactness, apart from the often inaccurate use of visual inspection. Therefore, what is required is a measure which can calculate the degree of compactness of a reserve or patch of native vegetation and is able to rank varying shapes, regardless of their complexity, with respect to their compactness. This is precisely what the Blair and Biss (1967) technique does.

Both of these techniques provide means of accurately measuring a number of biogeographic attributes of nature reserves which had previously been only qualitatively examined. For the first time all the principles devised by Diamond (1975b) can be included in actual planning decisions even when the optimal conditions are unlikely to be satisfied.

An important criticism of techniques that attempt to place relative values on individual sites or habitat patches is that they inevitably produce a list of elite sites within a region (e.g., Wells, 1976). Conservation activity then becomes focused on such sites, which may be few in number and only occupy a very small proportion of a region's total area. This results in the neglect of the majority of sites with less obvious scientific value which, taken as a whole, represent an important habitat resource (Kent and Smart, 1981). Placing conservation efforts entirely on designated nature reserves is equally unfounded in any form of conservation policy. An important feature of the proposed techniques is that they do expand conservation efforts from the nature reserves to the overall spatial distribution of remnant vegetation (Kent and Smart, 1981).

With growing public interest in nature conservation and increasing pressure for revegetation schemes from many conservation groups in the developed countries, it is important that efforts should reap maximum benefits for the preservation of the native biota. Revegetation should be aimed at either increasing species movement between reserves through the construction or improvement of biological corridors or improving the conservation potential of the existing nature reserves by increasing their size and compactness. The techniques proposed can demonstrate where such revegetation schemes can be of maximum use.

Many techniques developed for the analysis of biogeographic properties of vegetation (e.g., Specht, 1972) or rural landscapes (e.g., Kent and Smart, 1981) have inherent problems whenever any comparison between areas is attempted. The techniques or measures are usually based on the characteristics of the area studied by the authors and may not apply in areas of dissimilar characteristics. The compactness indix developed for the analysis of reserve shape is readily applicable to any individual reserve, habitat island and archipelago situation. The only limitation is that a recognisable boundary must be present so that a shape can be defined. However, limitations do apply more to the comparison of network accessibilities between two or more nature reserve networks. These limitations concern the extent of the networks in question which should be reasonably similar in size and number of nodes for a meaningful comparison to ensue.

In this present study Taaffee and Gauthier's (1973) method of network analysis has already proven to be useful for archipelago planning of a group of nature reserves and their intervening vegetation patches. In addition, a most practical and informative use for the network analysis technique of measuring accessibility would be in the scientific study or conservation of individual species. Ecologists have long tried to measure the effects of isolation and fragmentation on a species, yet no effective measure of isolation had been developed for their purposes, particularly on mainland areas. Thus, instead of nature reserves, concentrations of a species and areas of suitable intervening habitat could be mapped to give a similar network as that created for the nature reserves within the Mount Lofty Ranges. This automatically negates two problems which were evident for the nature reserve network. First, the nature reserve network had all forms of modified land considered unsuitable for species survival or movement. However, with an individual species, whose habitat requirements are known, a far more accurate network can be drawn when considering isolation effects. Second, the problem encountered of gap-size between stepping-stone islands or within biological corridors becomes less of a difficulty with an individual species whose critical distances may already be known or at least intuitively judged.

Both of these features, however, rely upon a relatively detailed knowledge of the habitat requirements and movement patterns of the species in question which at present, at least in Australia, is relatively scarce. This is certainly an area of research where biogeographers in particular could well concentrate their efforts (e.g., Keynes, 1981). Once these features are known for a species and the consequent network drawn, an effective conservation policy can easily be developed to minimize extinction loss and maximize the interaction between the concentrations of a species. Isolated concentrations can be discovered and a policy of revegetation can be initiated to increase their accessibility with the remainder of the network, or to increase the size and compactness of a concentration by creating a buffer area of suitable habitat. In fact, the techniques proposed for both accessibility and shape analysis would be invaluable for a conservation policy aimed at maintaining the survival of a rare or endangered species.

Simberloff and Abele (1976, 286) have strongly criticized the current application of Island Biogeography Theory to the design of nature reserves as being based on *"limited and insufficient validated theory and on field studies of taxa which may be idiosyncratic."* This criticism does have some foundation and was discussed in the opening chapter of the present study. Certainly more research is required to ascertain the accuracy of the established relationships developed by MacArthur and Wilson (1967) and Preston (1962). However, many of the broad generalizations have been consistently verified and the realization of these generalizations by nature reserve planners could only improve their current design policies. For instance, in the opening speech to a seminar held at the University of Adelaide in 1969, Sir Mark Oliphant stated:

> *"The British scientific journal 'Nature', has pointed out in its editorial for 14th June, 1969, that there is a very real danger that the natural reaction of governments will be to ask for further information, for more research, and thereby shelve the awkward problem. While the ideal method for dealing with every question of environmental deterioration, or of pollution of air, river, lake or sea, is not yet known, there is enough knowledge to make an energetic beginning, expecting to make some mistakes, but to profit by them."* (Oliphant, 1969, 11)

This is precisely the position of environmental planners with respect to the application of Island Biogeography Theory to the design of nature reserves. If future research demonstrates that another set of principles may be more beneficial to nature reserve design then the role of Island Biogeography Theory may well diminish. However, until then Island Biogeography Theory does, at the very least, give direction to the somewhat disparate nature of reserve management at present. Suddenly nature reserves become part of a purposeful whole rather than isolated entities with only marginal integrational significance.

VII. APPENDICES

APPENDIX A

Accessibility Matrix for Mount Lofty Ranges Nature Reserve Network

	SC	PW	H	W	Cr	CC	BH	Mon	Le	Ch	Mor	HG	Cl	B	Fe	G	TE	BC	WP	SH	SG	E	TK	T	Lo	K	MM	Fi	CS	S	SM	M	Y	NS	W	EB	DC
SC																																					
PW		0	1	2	2	1	2	2	3	3	3	3	3	3	4	4	4	4	4	4	4	3	3	4	3	4	4	4	4	6	5	5	4	5			
H			0	1	2	2	3	3	4	3	4	4	4	4	5	5	5	5	5	5	5	4	4	5	4	5	5	5	5	7	6	6	5	6			
W				0	1	2	3	3	4	2	4	4	4	4	5	5	5	5	5	5	5	4	4	5	4	5	5	5	5	7	6	6	5	6			
Cr					0	1	2	2	3	1	3	3	3	3	4	4	4	4	4	4	4	3	3	4	3	4	4	4	4	6	5	5	4	5			
CC						0	1	1	2	2	2	2	2	2	3	3	3	3	3	3	3	2	2	3	2	3	3	3	3	5	4	4	3	4			
BH							0	1	2	3	1	1	1	2	2	2	2	2	3	3	3	2	2	3	2	3	3	3	3	5	4	4	3	4			
Mon								0	1	3	1	1	1	1	2	2	2	2	2	2	2	1	1	2	1	2	2	2	2	4	3	3	2	3			
Le									0	4	2	2	2	3	3	3	3	3	3	3	3	2	2	3	2	3	3	3	3	5	4	4	3	4			
Ch										0	4	4	4	4	5	5	5	5	5	5	5	4	4	5	4	5	5	5	5	7	6	6	5	6			
Mor											0	1	1	2	1	2	2	2	3	3	3	2	2	3	3	3	3	3	3	5	4	4	3	4			
HG												0	1	2	1	1	2	2	2	2	2	2	2	3	2	2	2	3	2	4	3	3	2	3			
Cl													0	1	1	1	1	1	2	2	2	1	1	3	2	2	2	3	2	4	3	3	2	3			
B														0	2	2	1	1	1	1	1	1	1	2	1	1	1	2	1	3	2	2	1	2			
Fe															0	1	2	2	3	3	3	2	2	4	3	3	3	4	3	5	4	4	3	4			
G																0	1	2	3	3	3	2	2	4	3	3	3	4	3	5	4	4	3	4			
TE																	0	1	2	2	2	2	2	3	2	2	2	3	2	4	3	3	2	3			
BC																		0	1	1	2	2	2	3	2	2	2	3	2	4	3	3	2	3			
WP																			0	1	2	2	2	3	2	2	2	3	2	4	3	3	2	3			
SH																				0	1	2	2	3	2	2	2	3	2	4	3	3	2	3			
SG																					0	2	2	2	2	1	2	2	2	3	2	2	1	2			
E																						0	1	3	2	2	2	3	2	4	3	3	2	3			
TK																							0	2	1	2	2	2	2	4	3	3	2	3			
T																								0	1	1	1	1	1	3	2	3	2	3			
Lo																									0	1	1	1	1	3	2	3	2	3			
K																										0	1	2	1	2	1	2	1	2			
MM																											0	1	1	2	1	2	1	2			
Fi																												0	1	2	1	2	1	2			
CS																													0	2	1	2	2	3			
S																														0	1	2	2	3			
SM																															0	1	1	2			
M																																0	1	1			
Y																																	0	1			
NS																																		0			
W																																					
EB																																					
DC																																					

APPENDIX B

Accessibility Matrix for Mount Lofty Ranges Nature Reserve Network minus Montacute C.P.

	SC	PW	H	W	Cr	CC	BH	Ch	Mor	HG	Cl	B	Fe	G	TE	BC	WP	SH	SG	E	TK	T	Lo	K	MM	Fi	CS	S	SM	M	Y	NS	W	EB	DC
SC																																			
PW		0	1	2	2	1	2	3	3	3	3	4	4	4	4	4	5	5	5	4	4	6	5	5	5	6	5	7	6	6	5	6			
H			0	1	2	2	3	3	4	4	4	5	5	5	5	5	6	6	6	5	5	7	6	6	6	7	6	8	7	7	6	7			
W				0	1	2	3	2	4	4	4	5	5	5	5	5	6	6	6	5	5	7	6	6	6	7	6	8	7	7	6	7			
Cr					0	1	2	1	3	3	3	4	4	4	4	4	5	5	5	4	4	6	5	5	5	6	5	7	6	6	5	6			
CC						0	1	2	2	2	2	3	3	3	3	3	4	4	4	3	3	5	4	4	4	5	4	6	5	5	4	5			
BH							0	3	1	1	1	2	2	2	2	2	3	3	3	2	2	4	3	3	3	4	3	5	4	4	3	4			
Ch								0	4	4	4	5	5	5	5	5	6	6	6	5	5	7	6	6	6	7	6	8	7	7	6	7			
Mor									0	1	1	2	1	2	2	2	3	3	3	2	2	4	3	3	3	4	3	5	4	4	3	4			
HG										0	1	2	1	1	2	2	2	2	2	2	2	3	2	2	2	3	2	4	3	3	2	3			
Cl											0	1	1	1	1	1	2	2	2	1	1	3	2	2	2	3	2	4	3	3	2	3			
B												0	2	2	1	1	1	1	1	1	1	2	1	1	1	2	1	3	2	2	1	2			
Fe													0	1	2	2	3	3	3	2	2	4	3	3	3	4	3	5	4	4	3	4			
G														0	1	2	3	3	3	2	2	4	3	3	3	4	3	5	4	4	3	4			
TE															0	1	2	2	2	2	2	3	2	2	2	3	2	4	3	3	2	3			
BC																0	1	1	2	2	2	3	2	2	2	3	2	4	3	3	2	3			
WP																	0	1	2	2	2	3	2	2	2	3	2	4	3	3	2	3			
SH																		0	1	2	2	3	2	2	2	3	2	4	3	3	2	3			
SG																			0	2	2	2	2	1	2	2	2	3	2	2	1	2			
E																				0	1	3	2	2	2	3	2	4	3	3	2	3			
TK																					0	2	1	2	2	2	2	4	3	3	2	3			
T																						0	1	1	1	1	1	3	2	3	2	3			
Lo																							0	1	1	1	1	3	2	3	2	3			
K																								0	1	2	1	2	1	2	1	2			
MM																									0	1	1	2	1	2	1	2			
Fi																										0	1	2	1	2	1	2			
CS																											0	2	1	2	2	3			
S																												0	1	2	2	3			
SM																													0	1	1	2			
M																														0	1	1			
Y																															0	1			
NS																																0			
W																																			
EB																																			
DC																																			

APPENDIX C

Accessibility Matrix for Mount Lofty Ranges Nature Reserve Network minus Belair R.P. and Montacute C.P.

	SC	PW	H	W	Cr	CC	BH	Ch	Mor	HG	Cl	Fe	G	TE	BC	WP	SH	SG	E	TK	T	Lo	K	MM	Fi	CS	S	SM	M	Y	NS	W	EB	DC
SC																																		
PW		0	1	2	2	1	2	3	3	3	3	4	4	4	4	5	5	6	4	4	6	5	6	6	6	6	8	7	8	7	8			
H			0	1	2	2	3	3	4	4	4	5	5	5	5	6	6	7	5	5	7	6	7	7	7	7	9	8	9	8	9			
W				0	1	2	3	2	4	4	4	5	5	5	5	6	6	7	5	5	7	6	7	7	7	7	9	8	9	8	9			
Cr					0	1	2	1	3	3	3	4	4	4	4	5	5	6	4	4	6	5	6	6	6	6	8	7	8	7	8			
CC						0	1	2	2	2	2	3	3	3	3	4	4	5	3	3	5	4	5	5	5	5	7	6	7	6	7			
BH							0	3	1	1	1	2	2	2	2	3	3	4	2	2	4	3	4	4	4	4	6	5	6	5	6			
Ch								0	4	4	4	5	5	5	5	6	6	7	5	5	7	6	7	7	7	7	9	8	9	8	9			
Mor									0	1	1	1	2	2	2	2	2	4	2	2	4	3	4	4	4	4	6	5	6	5	6			
HG										0	1	1	1	2	2	2	2	4	2	2	4	3	4	4	4	4	6	5	6	5	6			
Cl											0	1	1	1	1	2	2	3	1	1	3	2	3	3	3	3	5	4	5	4	5			
Fe												0	1	2	2	3	3	4	2	2	4	3	4	4	4	4	6	5	6	5	6			
G													0	1	2	3	3	4	2	2	4	3	4	4	4	4	6	5	6	5	6			
TE														0	1	2	2	3	2	2	4	3	4	4	4	4	6	5	5	4	5			
BC															0	1	1	2	2	2	4	3	3	4	4	4	5	4	4	3	4			
WP																0	1	2	3	3	4	3	4	4	4	4	5	4	4	3	4			
SH																	0	1	3	3	3	3	2	3	3	3	4	3	3	2	3			
SG																		0	4	3	2	2	1	2	2	2	3	2	2	1	2			
E																			0	1	3	2	3	3	3	3	5	4	5	4	5			
TK																				0	1	2	2	2	2	2	4	3	4	3	4			
T																					0	1	1	1	1	1	3	2	3	2	3			
Lo																						0	1	1	1	1	3	2	3	2	3			
K																							0	1	2	1	2	1	2	1	2			
MM																								0	2	1	2	1	2	1	2			
Fi																									0	1	2	1	2	1	2			
CS																										0	2	1	2	2	3			
S																											0	1	2	2	3			
SM																												0	1	1	2			
M																													0	1	1			
Y																														0	1			
NS																															0			
W																																		
EB																																		
DC																																		

APPENDIX D

Accessibility Matrix for Mount Lofty Ranges Nature Reserve Network minus Belair R.P., Montacute C.P. and Cleland C.P.

SC PW H W Cr CC BH Ch Mor HG Fe G TE BC WP SH SG E TK T Lo K MM Fi CS S SM M Y NS W EB DC

SC PW H W Cr CC BH Ch Mor HG Fe G TE BC WP SH SG E TK T Lo K MM Fi CS S SM M Y NS W EB DC

0	1	2	2	1	2	3	3	3	4	4	5	6	7	7	8	7	8	10	9	9	10	10	10	11	10	10	9	10
	0	1	2	2	3	3	4	4	5	5	6	7	8	8	9	8	9	11	10	10	11	11	11	12	11	11	10	11
		0	1	2	3	2	4	4	5	5	6	7	8	8	9	8	9	11	10	10	11	11	11	12	11	11	10	11
			0	1	2	1	3	3	4	4	5	6	7	7	8	7	8	10	9	9	10	10	10	11	10	10	9	10
				0	1	2	2	2	3	3	4	5	6	6	7	6	7	9	8	8	9	9	9	10	9	9	8	9
					0	2	1	1	2	2	3	4	5	5	6	5	6	8	7	7	8	8	8	9	8	8	7	8
						0	4	4	5	5	6	7	8	8	9	8	9	11	10	10	11	11	11	12	11	11	10	11
							0	1	1	2	3	4	5	5	6	5	6	8	7	7	8	8	8	9	8	8	7	8
								0	1	1	2	3	4	4	5	4	5	7	6	6	7	7	7	8	7	7	6	7
									0	1	2	3	4	4	5	4	5	7	6	6	7	7	7	8	7	7	6	7
										0	1	2	3	3	4	3	4	6	5	5	6	6	6	7	6	6	5	6
											0	1	2	2	3	2	3	5	4	4	5	5	5	6	5	5	4	5
												0	1	1	2	1	2	4	3	3	4	4	4	5	4	4	3	4
													0	1	2	2	3	4	4	3	4	4	4	5	4	4	3	4
														0	1	2	3	3	3	2	3	3	3	4	3	3	2	3
															0	3	3	2	2	1	2	2	2	3	2	2	1	2
																0	2	3	2	3	3	3	3	5	4	5	4	5
																	0	2	1	2	2	2	2	4	3	4	3	4
																		0	1	1	1	1	1	3	2	3	2	3
																			0	1	1	1	1	3	2	3	2	3
																				0	1	2	1	2	1	2	1	2
																					0	1	1	2	1	2	1	2
																						0	1	2	1	2	1	2
																							0	2	1	2	2	3
																								0	1	2	2	3
																									0	1	1	2
																										0	1	1
																											0	1
																												0

APPENDIX E

Accessibility Matrix for Mount Lofty Ranges Nature Reserve Network minus Lenswood R.P., Charleston C.P. and Scott C.P.

	SC	PW	H	W	Cr	CC	BH	Mon	Mor	HG	Cl	B	Fe	G	TE	BC	WP	SH	SG	E	TK	T	Lo	K	MM	Fi	CS	SM	M	Y	NS	W	EB	DC
SC																																		
PW		0	1	2	2	1	2	2	3	3	3	3	4	4	4	4	4	4	4	3	3	4	3	4	4	4	4	5	5	4	5			
H			0	1	2	2	3	3	4	4	4	4	5	5	5	5	5	5	5	4	4	5	4	5	5	5	5	6	6	5	6			
W				0	1	2	3	3	4	4	4	4	5	5	5	5	5	5	5	4	4	5	4	5	5	5	5	6	6	5	6			
Cr					0	1	2	2	3	3	3	3	4	4	4	4	4	4	4	3	3	4	3	4	4	4	4	5	5	4	5			
CC						0	1	1	2	2	2	2	3	3	3	3	3	3	3	2	2	3	2	3	3	3	3	4	4	3	4			
BH							0	1	1	1	1	2	2	2	2	2	3	3	3	2	2	3	2	3	3	3	3	4	4	3	4			
Mon								0	1	1	1	1	2	2	2	2	2	2	2	1	1	2	1	2	2	2	2	3	3	2	3			
Mor									0	1	1	2	1	2	2	2	3	3	3	2	2	3	2	3	3	3	3	4	4	3	4			
HG										0	1	2	1	1	2	2	2	2	2	2	2	3	2	2	2	3	2	3	3	2	3			
Cl											0	1	1	1	1	1	2	2	2	1	1	3	2	2	2	3	2	3	3	2	3			
B												0	2	2	1	1	1	1	1	1	1	2	1	1	1	2	1	2	2	1	2			
Fe													0	1	2	2	3	3	3	2	2	4	3	3	3	4	3	4	4	3	4			
G														0	1	2	3	3	3	2	2	4	3	3	3	4	3	4	4	3	4			
TE															0	1	2	2	2	2	2	3	2	2	2	3	2	3	3	2	3			
BC																0	1	1	2	2	2	3	2	2	2	3	2	3	3	2	3			
WP																	0	1	2	2	2	3	2	2	2	3	2	3	3	2	3			
SH																		0	1	2	2	3	2	2	2	3	2	3	3	2	3			
SG																			0	2	2	2	2	1	2	2	2	2	2	1	2			
E																				0	1	3	2	2	2	3	2	3	3	2	3			
TK																					0	2	1	2	2	2	2	3	3	2	3			
T																						0	1	1	1	1	1	2	3	2	3			
Lo																							0	1	1	1	1	2	3	2	3			
K																								0	1	2	1	1	2	1	2			
MM																									0	1	1	1	2	1	2			
Fi																										0	1	1	2	2	2			
CS																											0	1	2	2	3			
SM																												0	1	1	2			
M																													0	1	1			
Y																														0	1			
NS																															0			
W																																		
EB																																		
DC																																		

APPENDIX F

Accessibility Matrix for Mount Lofty Ranges Nature Reserve Network minus Belair R.P., Montacute C.P., Cleland C.P. and Loftia R.P.

	SC	PW	H	W	Cr	CC	BH	Ch	Mor	HG	Fe	G	TE	BC	WP	SH	SG	E	TK	T	K	MM	Fi	CS	S	SM	M	Y	NS	W	EB	DC
SC																																
PW		0	1	2	2	1	2	3	3	3	4	4	5	6	7	7	8	7	8	10	9	10	10	10	11	10	10	9	10			
H			0	1	2	2	3	3	4	4	5	5	6	7	8	8	9	8	9	11	10	11	11	11	12	11	11	10	11			
W				0	1	2	3	2	4	4	5	5	6	7	8	8	9	8	9	11	10	11	11	11	12	11	11	10	11			
Cr					0	1	2	1	3	3	4	4	5	6	7	7	8	7	8	10	9	10	10	10	11	10	10	9	10			
CC						0	1	2	2	2	3	3	4	5	6	6	7	6	7	9	8	9	9	9	10	9	9	8	9			
BH							0	3	1	1	2	2	3	4	5	5	6	5	6	8	7	8	8	8	9	8	8	7	8			
Ch								0	4	4	5	5	6	7	8	8	9	8	9	11	10	11	11	11	12	11	11	10	11			
Mor									0	1	1	2	3	4	5	5	6	5	6	8	7	8	8	8	9	8	8	7	8			
HG										0	1	1	2	3	4	4	5	4	5	7	6	7	7	7	8	7	7	6	7			
Fe											0	1	2	3	4	4	5	4	5	7	6	7	7	7	8	7	7	6	7			
G												0	1	2	3	3	4	3	4	6	5	6	6	6	7	6	6	5	6			
TE													0	1	2	2	3	2	3	5	4	5	5	5	6	5	5	4	5			
BC														0	1	1	2	1	2	4	3	4	4	4	5	4	4	3	4			
WP															0	1	2	2	3	4	3	4	4	4	5	4	4	3	4			
SH																0	1	2	3	3	2	3	3	3	4	3	3	2	3			
SG																	0	3	4	2	1	2	2	2	3	2	2	1	2			
E																		0	1	5	4	5	5	5	6	5	5	4	5			
TK																			0	6	5	6	6	6	7	6	6	5	6			
T																				0	1	1	1	1	3	2	3	2	3			
K																					0	1	2	1	2	1	2	1	2			
MM																						0	1	1	2	1	2	1	2			
Fi																							0	1	2	1	2	1	2			
CS																								0	2	1	2	2	3			
S																									0	1	2	2	3			
SM																										0	1	1	2			
M																											0	1	1			
Y																												0	1			
NS																													0			
W																																
EB																																
DC																																

APPENDIX G

Accessibility Matrix for Mount Lofty Ranges Nature Reserve Network minus Belair R.P., Montacute C.P., Cleland C.P. and the Brownhill Ck. R.P. - Eurilla C.P. Linkage

	SC	PW	H	W	Cr	CC	BH	Ch	Mor	HG	Fe	G	TE	BC	WP	SH	SG	E	TK	T	Lo	K	MM	Fi	CS	S	SM	M	Y	NS	W	EB	DC
SC																																	
PW		0	1	2	2	1	2	3	3	3	4	4	5	6	7	7	8	12	11	10	10	9	10	10	10	11	10	10	9	10			
H			0	1	2	2	3	3	4	4	5	5	6	7	8	8	9	13	12	11	11	10	11	11	11	12	11	11	10	11			
W				0	1	2	3	2	4	4	5	5	6	7	8	8	9	13	12	11	11	10	11	11	11	12	11	11	10	11			
Cr					0	1	2	1	3	3	4	4	5	6	7	7	8	12	11	10	10	9	10	10	10	11	10	10	9	10			
CC						0	1	2	2	2	3	3	4	5	6	6	7	11	10	9	9	8	9	9	9	10	9	9	8	9			
BH							0	3	1	1	2	2	3	4	5	5	6	10	9	8	8	7	8	8	8	9	8	8	7	8			
Ch								0	4	4	5	5	6	7	8	8	9	13	12	11	11	10	11	11	11	12	11	11	10	11			
Mor									0	1	1	2	3	4	5	5	6	10	9	8	8	7	8	8	8	9	8	8	7	8			
HG										0	1	1	2	3	4	4	5	9	8	7	7	6	7	7	7	8	7	7	6	7			
Fe											0	1	2	3	4	4	5	9	8	7	7	6	7	7	7	8	7	7	6	7			
G												0	1	2	3	3	4	8	7	6	6	5	6	6	6	7	6	6	5	6			
TE													0	1	2	2	3	7	6	5	5	4	5	5	5	6	5	5	4	5			
BC														0	1	1	2	6	5	4	4	3	4	4	4	5	4	4	3	4			
WP															0	1	2	6	5	4	4	3	4	4	4	5	4	4	3	4			
SH																0	1	5	4	3	3	2	3	3	3	4	3	3	2	3			
SG																	0	4	3	2	2	1	2	2	2	3	2	2	1	2			
E																		0	1	3	2	3	3	3	3	5	4	5	4	5			
TK																			0	2	1	2	2	2	2	4	3	4	3	4			
T																				0	1	1	1	1	1	3	2	3	2	3			
Lo																					0	1	1	1	1	3	2	3	2	3			
K																						0	1	2	1	2	1	2	1	2			
MM																							0	1	1	2	1	2	1	2			
Fi																								0	1	2	1	2	1	2			
CS																									0	2	1	2	2	3			
S																										0	1	2	2	3			
SM																											0	1	1	2			
M																												0	1	1			
Y																													0	1			
NS																														0			
W																																	
EB																																	
DC																																	

APPENDIX H

Accessibility Matrix for Mount Lofty Ranges Nature Reserve Network plus *P. radiata* Plantations

	SC	PW	H	W	Cr	CC	BH	Mon	Le	Ch	Mor	HG	Cl	B	Fe	G	TE	BC	WP	SH	SG	E	TK	T	Lo	K	MM	Fi	CS	S	SM	M	Y	NS	W	EB	DC
SC																																					
PW		0	1	1	2	1	1	1	2	2	2	2	2	2	3	3	3	3	3	3	3	2	2	3	2	3	3	3	3	5	4	4	3	4			
H			0	1	1	2	2	2	3	2	3	3	3	3	4	4	4	4	4	4	4	3	3	4	3	4	4	4	4	6	5	5	4	5			
W				0	1	2	2	2	3	2	3	3	3	3	4	4	4	4	4	4	4	3	3	4	3	4	4	4	4	6	5	5	4	5			
Cr					0	1	2	2	2	1	3	3	3	3	4	4	4	4	4	4	4	3	3	4	3	4	4	4	4	6	5	5	4	5			
CC						0	1	1	1	1	2	2	2	2	3	3	3	3	3	3	3	2	2	3	2	3	3	3	3	5	4	4	3	4			
BH							0	1	2	2	1	1	1	2	2	2	2	2	3	3	3	2	2	3	2	3	3	3	3	5	4	4	3	4			
Mon								0	1	1	1	1	1	1	2	2	2	2	2	2	2	1	1	2	1	2	2	2	2	4	3	3	2	3			
Le									0	1	1	1	1	2	2	2	2	2	3	3	3	1	2	3	2	3	3	3	3	5	4	4	3	4			
Ch										0	2	2	2	2	3	3	3	3	3	3	3	2	2	3	2	3	3	3	3	5	4	4	3	4			
Mor											0	1	1	2	1	2	2	2	3	3	3	2	2	3	2	3	3	3	3	5	4	4	3	4			
HG												0	1	2	1	1	2	2	2	2	2	2	2	3	2	2	2	3	2	4	3	3	2	3			
Cl													0	1	1	1	1	1	2	2	2	1	1	3	2	2	2	3	2	4	3	3	2	3			
B														0	2	2	1	1	1	1	1	1	1	2	1	1	1	2	1	3	2	2	1	2			
Fe															0	1	2	2	3	3	3	2	2	4	3	3	3	4	3	5	4	4	3	4			
G																0	1	2	3	3	3	2	2	4	3	3	3	4	3	5	4	4	3	4			
TE																	0	1	2	2	2	2	2	3	2	2	2	3	2	4	3	3	2	3			
BC																		0	1	1	2	2	2	3	2	2	2	3	2	4	3	3	2	3			
WP																			0	1	2	2	2	3	2	2	2	3	2	4	3	3	2	3			
SH																				0	1	2	2	3	2	2	2	3	2	4	3	3	2	3			
SG																					0	2	2	2	2	1	2	2	2	3	2	2	1	2			
E																						0	1	3	2	2	2	3	2	4	3	3	2	3			
TK																							0	2	1	2	2	2	2	4	3	3	2	3			
T																								0	1	1	1	1	1	3	2	3	2	3			
Lo																									0	1	1	1	1	3	3	3	2	3			
K																										0	1	2	1	2	1	2	1	2			
MM																											0	1	1	2	1	2	1	2			
Fi																												0	1	2	1	2	1	2			
CS																													0	2	1	2	2	3			
S																														0	1	2	2	3			
SM																															0	1	1	2			
M																																0	1	1			
Y																																	0	1			
NS																																		0			
W																																					
EB																																					
DC																																					

APPENDIX I

Accessibility Matrix for Mount Lofty Ranges Nature Reserve Network plus Mt. Bold Reservoir Catchment Area

	SC	PW	H	W	Cr	CC	BH	Mon	Le	Ch	Mor	HG	Cl	B	Fe	G	TE	BC	WP	SH	SG	E	TK	T	Lo	MB	K	MM	Fi	CS	S	SM	M	Y	NS	W	EB	DC
SC																																						
PW		0	1	2	2	1	2	2	3	3	3	3	3	3	4	4	4	4	4	4	4	3	3	4	3	4	5	5	5	5	6	5	5	4	5			
H			0	1	2	2	3	3	4	3	4	4	4	4	5	5	5	5	5	5	5	4	4	5	4	5	6	6	6	6	7	6	6	5	6			
W				0	1	2	3	3	4	2	4	4	4	4	5	5	5	5	5	5	5	4	4	5	4	5	6	6	6	6	7	6	6	5	6			
Cr					0	1	2	2	3	1	3	3	3	3	4	4	4	4	4	4	4	3	3	4	3	4	5	5	5	5	6	5	5	4	5			
CC						0	1	1	2	2	2	2	2	2	3	3	3	3	3	3	3	2	2	3	2	3	4	4	4	4	5	4	4	3	4			
BH							0	1	2	3	1	1	1	2	2	2	2	2	3	3	3	2	2	3	2	3	4	4	4	4	5	4	4	3	4			
Mon								0	1	3	1	1	1	1	2	2	2	2	2	2	2	1	1	2	1	2	3	3	3	3	4	3	3	2	3			
Le									0	4	2	2	2	2	3	3	3	3	3	3	3	2	2	3	2	3	4	4	4	4	5	4	4	3	4			
Ch										0	4	4	4	4	5	5	5	5	5	5	5	4	4	5	4	5	6	6	6	6	7	6	6	5	6			
Mor											0	1	1	2	1	2	2	2	3	3	3	2	2	3	2	3	4	4	4	4	5	4	4	3	4			
HG												0	1	2	1	1	2	2	2	2	2	2	2	3	2	2	3	3	3	4	4	3	3	2	3			
Cl													0	1	1	1	1	1	2	2	2	1	1	3	2	2	3	3	3	4	4	3	3	2	3			
B														0	2	2	1	1	1	1	1	1	1	2	1	1	2	2	2	2	3	2	2	1	2			
Fe															0	1	2	2	3	3	3	2	2	4	3	3	4	4	4	5	5	4	4	3	4			
G																0	1	2	3	3	3	2	2	4	3	3	4	4	4	5	5	4	4	3	4			
TE																	0	1	2	2	2	2	2	3	2	2	3	3	3	3	4	3	3	2	3			
BC																		0	1	1	2	2	2	3	2	2	3	3	3	3	4	3	3	2	3			
WP																			0	1	2	2	2	3	2	2	3	3	3	3	4	3	3	2	3			
SH																				0	1	2	2	3	2	2	2	3	3	3	4	3	3	2	3			
SG																					0	2	2	2	2	2	1	2	2	2	3	2	2	1	2			
E																						0	1	3	2	2	3	3	3	4	4	3	3	2	3			
TK																							0	2	1	2	3	3	3	3	4	3	3	2	3			
T																								0	1	1	1	1	1	1	3	2	3	2	3			
Lo																									0	1	2	2	2	2	4	3	3	2	3			
MB																										0	1	1	1	1	3	2	3	2	3			
K																											0	1	2	1	2	1	2	1	2			
MM																												0	1	1	2	1	2	1	2			
Fi																													0	1	2	1	2	1	2			
CS																														0	2	1	2	2	3			
S																															0	1	2	2	3			
SM																																0	1	1	2			
M																																	0	1	1			
Y																																		0	1			
NS																																			0			
W																																						
EB																																						
DC																																						

APPENDIX J

Accessibility Matrix for Mount Lofty Ranges Nature Reserve Network plus Sandy Creek C.P., Deep Creek C.P., Waitpinga C.P. and Eric Bonython C.P.

	SC	PW	H	W	Cr	CC	BH	Mon	Le	Ch	Mor	HG	Cl	B	Fe	G	TE	BC	WP	SH	SG	E	TK	T	Lo	K	MM	Fi	CS	S	SM	M	Y	NS	W	EB	DC
SC	0	1	2	3	3	2	3	3	4	4	4	4	4	4	5	5	5	5	5	5	5	4	4	5	4	5	5	5	5	7	6	6	5	6	7	7	8
PW		0	1	2	2	1	2	2	3	3	3	3	3	3	4	4	4	4	4	4	4	3	3	4	3	4	4	4	4	6	5	5	4	5	6	6	7
H			0	1	2	2	3	3	4	3	4	4	4	4	5	5	5	5	5	5	5	4	4	5	4	5	5	5	5	7	6	6	5	6	7	7	8
W				0	1	2	3	3	4	2	4	4	4	4	5	5	5	5	5	5	5	4	4	5	4	5	5	5	5	7	6	6	5	6	7	7	8
Cr					0	1	2	2	3	1	3	3	3	3	4	4	4	4	4	4	4	3	3	4	3	4	4	4	4	6	5	5	4	5	6	6	7
CC						0	1	1	2	2	2	2	2	2	3	3	3	3	3	3	3	2	2	3	2	3	3	3	3	5	4	4	3	4	5	5	6
BH							0	1	2	3	1	1	1	2	2	2	2	2	3	3	3	2	2	3	2	3	3	3	3	5	4	4	3	4	5	5	6
Mon								0	1	3	1	1	1	1	2	2	2	2	2	2	2	1	1	2	1	2	2	2	2	4	3	3	2	3	4	4	5
Le									0	4	2	2	2	2	3	3	3	3	3	3	3	2	2	3	2	3	3	3	3	5	4	4	3	4	5	5	6
Ch										0	4	4	4	4	5	5	5	5	5	5	5	4	4	5	4	5	5	5	5	7	6	6	5	6	7	7	8
Mor											0	1	1	2	1	2	2	2	3	3	3	2	2	3	2	3	3	3	3	5	4	4	3	4	5	5	6
HG												0	1	2	1	1	2	2	2	2	2	2	2	3	2	2	2	3	2	4	3	3	2	3	4	4	5
Cl													0	1	1	1	1	1	2	2	2	1	1	3	2	2	2	3	2	4	3	3	2	3	4	4	5
B														0	2	2	1	1	1	1	1	1	1	2	1	1	1	2	1	3	2	2	1	2	3	3	4
Fe															0	1	2	2	3	3	3	2	2	4	3	3	3	4	3	5	4	4	3	4	5	5	6
G																0	1	2	3	3	3	2	2	4	3	3	3	4	3	5	4	4	3	4	5	5	6
TE																	0	1	2	2	2	2	2	3	2	2	2	3	2	4	3	3	2	3	4	4	5
BC																		0	1	1	2	1	2	3	2	2	2	3	2	4	3	3	2	3	4	4	5
WP																			0	1	2	2	2	3	2	2	2	3	2	4	3	3	2	3	4	4	5
SH																				0	1	2	2	3	2	2	2	3	2	4	3	3	2	3	4	4	5
SG																					0	2	2	2	2	1	2	2	2	3	2	2	1	2	3	3	4
E																						0	1	3	2	2	2	3	2	4	3	3	2	3	4	4	5
TK																							0	2	1	2	2	2	2	4	3	3	2	3	4	4	5
T																								0	1	1	1	1	1	3	2	3	2	3	4	3	4
Lo																									0	1	1	1	1	3	2	3	2	3	4	3	4
K																										0	1	1	1	2	1	2	1	2	3	2	3
MM																											0	1	1	2	1	2	1	2	3	2	3
Fi																												0	1	2	1	2	1	2	3	2	3
CS																													0	2	1	2	2	3	3	2	3
S																														0	1	2	2	3	3	2	3
SM																															0	1	1	2	2	1	2
M																																0	1	1	1	2	2
Y																																	0	1	2	2	3
NS																																		0	2	3	3
W																																			0	1	1
EB																																				0	1
DC																																					0

APPENDIX K

Accessibility Matrix for Mount Lofty Ranges Nature Reserve Network plus Sandy Creek C.P., Deep Creek C.P., Waitpinga C.P., Eric Bonython C.P., the Cudlee Ck. C.P. - Charleston C.P. Linkage and the Charleston C.P. - Totness R.P. Linkage

	SC	PW	H	W	C	CC	BH	Mon	Le	Ch	Mor	HG	Cl	B	Fe	G	TE	BC	WP	SH	SG	E	TK	T	Lo	K	MM	Fi	CS	S	SM	M	Y	NS	W	EB	DC
SC	0	1	2	3	3	2	3	3	4	3	4	4	4	4	5	5	5	5	5	5	5	4	4	4	4	5	5	5	5	7	6	6	5	6	7	7	8
PW		0	1	2	2	1	2	2	3	2	3	3	3	3	4	4	4	4	4	4	4	3	3	3	3	4	4	4	4	6	5	5	4	5	6	6	7
H			0	1	2	2	3	3	4	3	4	4	4	4	5	5	5	5	5	5	5	4	4	4	4	5	5	5	5	7	6	6	5	6	7	7	8
W				0	1	2	3	3	3	2	4	4	4	4	5	5	5	5	5	5	5	4	4	3	4	4	4	4	4	6	5	6	5	6	6	6	7
Cr					0	1	2	2	3	1	3	3	3	3	4	4	4	4	4	4	4	3	3	2	3	3	3	3	3	5	4	5	4	5	5	5	6
CC						0	1	1	2	1	2	2	2	2	3	3	3	3	3	3	3	2	2	2	2	3	3	3	3	5	4	4	3	4	5	5	6
BH							0	1	2	2	1	1	1	2	2	2	2	2	3	3	3	2	2	2	2	3	3	3	3	5	4	4	3	4	5	5	6
Mon								0	1	2	1	1	1	1	2	2	2	2	2	2	2	1	1	2	1	2	2	2	2	4	3	3	2	3	4	4	5
Le									0	3	2	2	2	2	3	3	3	3	3	3	3	2	2	3	2	3	3	3	3	5	4	4	3	4	5	5	6
Ch										0	3	3	3	3	4	4	4	4	4	4	3	3	3	1	2	2	2	2	2	4	3	4	3	4	5	5	6
Mor											0	1	1	2	1	2	2	2	3	3	3	2	2	3	2	3	3	3	3	5	4	4	3	4	5	5	6
HG												0	1	2	1	1	2	2	2	2	2	2	2	3	2	2	2	3	2	4	3	3	2	3	4	4	5
Cl													0	1	1	1	1	1	2	2	2	1	1	3	2	2	2	3	2	4	3	3	2	3	4	4	5
B														0	2	2	1	1	1	1	1	1	1	2	1	1	1	2	1	3	2	2	1	2	3	3	4
Fe															0	1	2	2	3	3	3	2	2	4	3	3	3	4	3	5	4	4	3	4	5	5	6
G																0	1	2	3	3	3	2	2	4	3	3	3	4	3	5	4	4	3	4	5	5	6
TE																	0	1	2	2	2	2	2	3	2	2	2	3	2	4	3	3	2	3	4	4	5
BC																		0	1	1	2	1	2	3	2	2	2	3	2	4	3	3	2	3	4	4	5
WP																			0	1	2	2	2	3	2	2	2	3	2	4	3	3	2	3	4	4	5
SH																				0	1	2	2	3	2	2	2	3	2	4	3	3	2	3	4	4	5
SG																					0	2	2	2	2	1	2	2	2	3	2	2	1	2	3	3	4
E																						0	1	3	2	2	2	3	2	4	3	3	2	3	4	4	5
TK																							0	2	1	2	2	2	2	3	3	3	2	3	4	4	5
T																								0	1	1	1	1	1	3	2	3	2	3	4	3	4
Lo																									0	1	1	1	1	3	2	3	2	3	4	3	4
K																										0	1	1	1	2	1	2	1	2	3	2	3
MM																											0	1	1	2	1	2	1	2	3	2	3
Fi																												0	1	2	1	2	1	2	3	2	3
CS																													0	2	1	2	2	3	3	2	3
S																														0	1	2	2	3	3	2	3
SM																															0	1	1	2	2	1	2
M																																0	1	1	1	2	2
Y																																	0	1	2	2	3
NS																																		0	2	3	3
W																																			0	1	1
EB																																				0	1
DC																																					0

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