PART 1

1.0 GENERAL INTRODUCTION

The past 30 years have seen a great increase in the number of ecological studies of reptiles, beginning with the work of Cagle (1953) and refined by Tinkle, so that today there is a vast literature available on the natural histories of many reptiles, particularly lizards. This accumulation of baseline data has allowed many researchers to propose and investigate previously untestable hypotheses. This trend is most evident in the northern hemisphere, North America in particular. In Australia, where the family Scincidae makes up approximately half of the total reptile fauna, of 250 known species (Cogger and Heatwole 1981) only nine have been the subjects of comprehensive ecological studies (Barwick 1965, Pengilley 1972), although other studies with different aims and thus more limited in scope have made significant contributions (Belmont 1977, Bustard 1970, Crome 1981, Davidge 1979, 1980, Hickman 1960, Joss and Minard in press, Murray 1980, Pianka 1969, Robertson 1976, 1981, Satrawaha 1980, Satrawaha and Bull 1981, Shearer 1979, Shine 1971, 1980b, 1983a, 1983b, Smyth 1968, 1974, Smyth and Smith 1974, Veron 1969a, 1969b, Wilhoft 1963a, 1963b, Wilhoft and Reiter 1963).

There are still many Australian scincid species about which little or nothing, is known. The genus Ctenotus fits into this category; although it is the Australian scincid genus with the greatest number of species (> 60; Greer 1979), few researchers have examined its ecology. Pianka (1969) examined the feeding and behaviour of 14 species of desert Ctenotus, Davidge (1979) and Murray (1980) examined some aspects of the ecology of C.lesueuri and C.fallens, while Way (1979) examined the reproductive biology of C.robustus. Further, within the genus Ctenotus, the species Ctenotus taeniolatus, although not the most widespread species of Ctenotus, has a range of significant size extending from northern Queensland to Victoria (Cogger 1979), where it is very evident

The past 30 years have seen a great increase in the number of ecological studies of reptiles, beginning with the work of Cagle (1953) and refined by Tinkle, so that today there is a vast literature available on the natural histories of many reptiles, particularly lizards. This accumulation of baseline data has allowed many researchers to propose and investigate previously untestable hypotheses. This trend is most evident in the northern hemisphere, North America in particular. In Australia, where the family Scincidae makes up approximately half of the total reptile fauna, of 250 known species (Cogger and Heatwole 1981) only nine have been the subjects of comprehensive ecological studies (Barwick 1965, Pengilley 1972), although other studies with different aims and thus more limited in scope have made significant contributions (Belmont 1977, Bustard 1970, Crome 1981, Davidge 1979, 1980, Hickman 1960, Joss and Minard in press, Murray 1980, Pianka 1969, Robertson 1976, 1981, Satrawaha 1980, Satrawaha and Bull 1981, Shearer 1979, Shine 1971, 1980b, 1983a, 1983b, Smyth 1968, 1974, Smyth and Smith 1974, Veron 1969a, 1969b, Wilhoft 1963a, 1963b, Wilhoft and Reiter 1963).

There are still many Australian scincid species about which little or nothing, is known. The genus Ctenotus fits into this category; although it is the Australian scincid genus with the greatest number of species (> 60; Greer 1979), few researchers have examined its ecology. Pianka (1969) examined the feeding and behaviour of 14 species of desert Ctenotus, Davidge (1979) and Murray (1980) examined some aspects of the ecology of C.lesueuri and C.fallens, while Way (1979) examined the reproductive biology of C.robustus. Further, within the genus Ctenotus, the species Ctenotus taeniolatus, although not the most widespread species of Ctenotus, has a range of significant size extending from northern Queensland to Victoria (Cogger 1979), where it is very evident often occurring in large numbers around centres of human population.

Hence, because of the paucity of comprehensive ecological studies on Australian reptiles and on skinks in particular, the first aim of the present study was to gather ecological information on C.taeniolatus and so bring knowledge of this species to a par with those occurring in Europe and north America. A secondary aim was to compare the ecology of C.taeniolatus with that which is known of other Australian skinks and so review Australian scincid ecology. To these ends, data were compiled using mark-recapture techniques, from behavioural observations and from comprehensive collections of large samples of lizards. These are presented in a section entitled 'Autecology of C.taeniolatus' in which habitat (Chapter 3), foods and feeding behaviour (Chapter 4), growth (Chapter 5), reproduction (Chapter 6) and energy storage (Chapter 7) are discussed.

Soon after the study commenced it became obvious that C.taeniolatus, unlike most other temperate lizards, possessed no abdominal fat bodies, storing the majority of its energy reserves within the tail, an organ which it appeared to autotomise readily. As Smyth and Smith (1974) and Robertson (1976, 1981) present similar results for Hemiergis peroni and H.decresiensis respectively, with Smyth and Smith (1974) suggesting that loss of the tail could drastically affect survival by reducing the ability of individuals to reproduce and overwinter, it was apparent that any study of the ecology of C.taeniolatus would not be complete without some discussion of the significance of autotomy. Accordingly, analyses and experiments were designed so that (i) the costs of reproduction and overwintering and (ii) the frequency and position of autotomy and its effects on reproduction and overwintering could be determined, and thence predictions made about the significance of the tail in the survival of

C.taeniolatus. The results of these are presented in Part 4, 'Significance of autotomy in C.taeniolatus', in Chapters 8, 9 and 10. Part 5 of this thesis presents an overall summary and conclusions. Finally, the thesis is arranged so that discussion sections of individual chapters present literature reviews and discussion of the results, while introductory sections describe only the aims of their respective sections, and so do not provide extensive treatments of the literature. Where published reviews were available, they were discussed and individual papers contained therein, although most were read by the author, were not individually treated except where they had special significance.

PART 2

2.0 GENERAL MATERIALS AND METHODS

2.1 STUDY AREA AND ENVIRONMENT

'The New England Region lies astride a particularly prominent section of the Eastern Highlands, the arc of ranges and tablelands that forms the eastern upland margin of the Australian continent, extending westward onto the level surface of the interior alluvial plains. It thus contains some of the highest country in Australia and a topography, as diverse as any Australian region of comparable size' (Walker 1977). For the purposes of this study only a small part of the New England Region, between Armidale and Tamworth was used (Fig. 1). This area has an elevation of between 800 to 1000 m with gentle to moderate slopes, except in the southern section in the Moonbi Ranges where slopes are steep (Walker 1977). The area is within the granite belt with soils of yellow and grey podzolic types (McGarity 1977).

The vegetation ranges from cleared paddocks of exotic and native grasses, through woodland of various degrees of openess, to dense uncleared eucalypt woodland in the Moonbi Ranges (Fig. 2).

The New England Region lies between two principal atmospheric zones which reflect the seasonal alteration of atmospheric circulation and rainfall regimes (Hobbs and Jackson 1977). The winds are mainly westerly and southwesterly in winter, and thus cold and dry, and easterly or maritime in summer, and thus warm and often unstable. The rain therefore falls predominantly in summer. Figure 3 shows the median monthly rainfall for Armidale (up to 1977) and the monthly rainfall for Laureldale (Rural Science Meteorological Station, 5 km from Armidale) for 1979-82, the years of this study. The rainfall figures for 1979-82 are much lower than previous records and in fact all agricultural districts in the New England Region have been declared drought areas since 1979. Figure 4 shows mean monthly maximum and minimum air temperature for Armidale (up to 1977). The New England Region has on average 200 frosts a year (Hobbs and Jackson 1977).

2.2 MONTHLY SAMPLING PROGRAM

Approximately 10 lizards of each sex were collected monthly from within the study area (Fig 1). Lizards were always collected in the early morning when they were inactive, usually within 4 hours of dawn. Lizards used for analysis of stomach contents were returned immediately to the laboratory where they were measured (snout-vent length, tail length), weighed and then killed with sodium pentobarbatone. Other lizards not used in stomach contents analysis were stored (not longer than 1 day) in the refrigerator (4 C) until dissection. After dissection reproductive organs were weighed and measured, and then either fixed in Bouin's fixative for later histological analysis or frozen for lipid extraction (Section 8.1.3). The alimentary canal was stored in 70% alcohol for later analysis (Section 4.2.1). Finally the carcasses were frozen for lipid analysis (Section 7.2.2).

In 1979 lizards were collected every month, while in 1980 and 1981 they were collected only at crucial times determined after analysis of the 1979 data, i.e. during the reproductive and pre-winter and post-winter periods.

2.3 MARK-RECAPTURE PROGRAM

A mark-recapture program was commenced in the Moonbi Ranges (Fig. 1) in April 1979. The Moonbi Ranges lie in the southern section of the study area and contain a relatively undisturbed habitat. The area is steep with an elevation of 800 m, and is characterised by the presence of large granite boulders and flat rocky expanses. Little clearing has taken place and the vegetation is eucalypt woodland (Eucalyptus melliodora, E.malacoxylon, E.caliginosa, Angophora floribunda) with the occasional Acacia nerifolia, and Callitris muelleri, around some of the rocky outcrops. There is an understorey of native grasses (Stipa sp. and Lomandra sp.) and shrubs (Bursaria spinosa, Clematis aristata, Olearia visidula and Cassinia quinquefolia). The climate is similar to that at the monitoring station near Armidale. Rainfall (Fig. 3) in 1979-82 was monitored by an adjacent landowner in a standard rainguage and was much lower than the averages recorded from Woolbrook (the nearest town at an equivalent elevation with a Meteorological Bureau monitoring station) except for some unseasonal winter rain in 1981. The area was classified as a drought area in 1979-82. Air temperatures were similar to those at Armidale with the maximum mean air temperature of the latter being only marginally higher than in the Moonbi study area (Fig. 4).

Lizards were captured in pit traps which consisted of a standard 10 litre plastic bucket, with a series of holes punched in the bottom to allow drainage, and two galvanised iron drift fences (Fig. 5). Soil and leaves were placed in the bottom to provide shelter from the sun in summer. Seventy-five traps were placed in a two hectare grid around a flattened granite outcrop, with a slope of 20 to 30 ° (Fig. 6). Pit traps were positioned at approximately 5 m intervals, with drift fences perpendicular to the rock outcrop. Maps were drawn with the aid of a theodolite.

Traps were opened for three days every month from April 1979 to May 1982, with the exception of the winter months of June and July each year. All lizards captured were marked by toeclipping, measured (snout-vent length, tail length and length to tail break), weighed, sexed (if possible by checking for presence or absence of the hemipenes) and then released at their point of capture. Traps were checked every day in the afternoon.

2.4 STATISTICAL PROCEDURES AND TERMINOLOGY

All statistical analyses are described in the relevant sections except for regression analysis. Simple linear, polynomial and multiple regressions were fitted using the Bar 3 computer package (Burr 1975) and presented so that the significance of all regression coefficients, the coefficient of determination, overall significance of the regression and the sample size were included as in the following example,

$$y = a^{*} + b^{*}.x_1 + c^{*}.x_2 + \ldots\ldots, R^2 = \ldots\ldots, P < \ldots\ldots, n = \ldots\ldots$$

Glossary of statistical terms

P	probability
*	significant at 0.05 level
**	significant at 0.01 level
***	significant at 0.001 level
****	significant at 0.0001 level
NS	not significant at the 0.05 level
n	sample size
R^2	coefficient of determination
SD	standard deviation

SS	sum of squares
DF	degrees of freedom
MS	SS/DF

Figure 1: Map of study area in New England Tablelands taken from Lea *et al*. (1977).

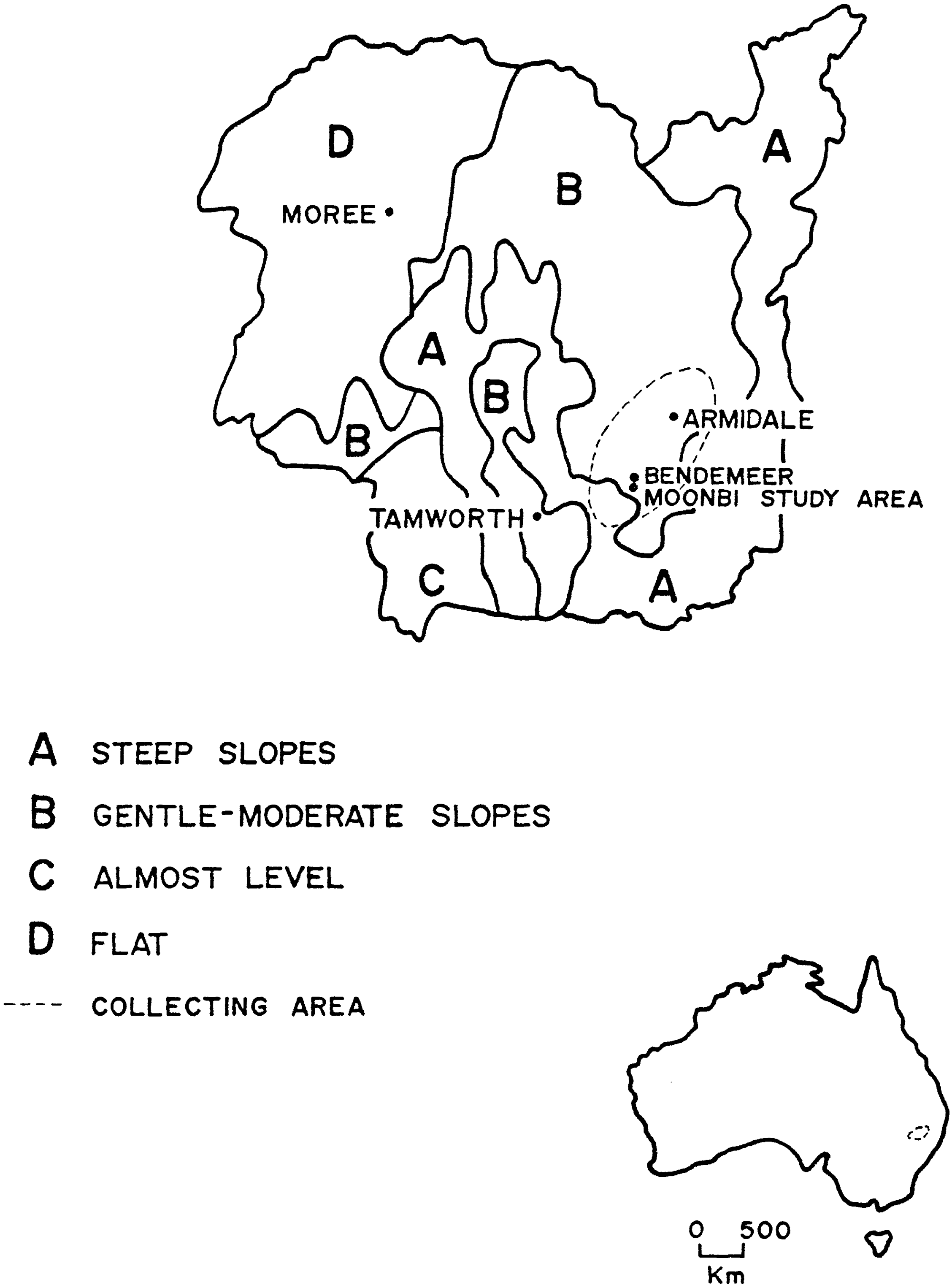
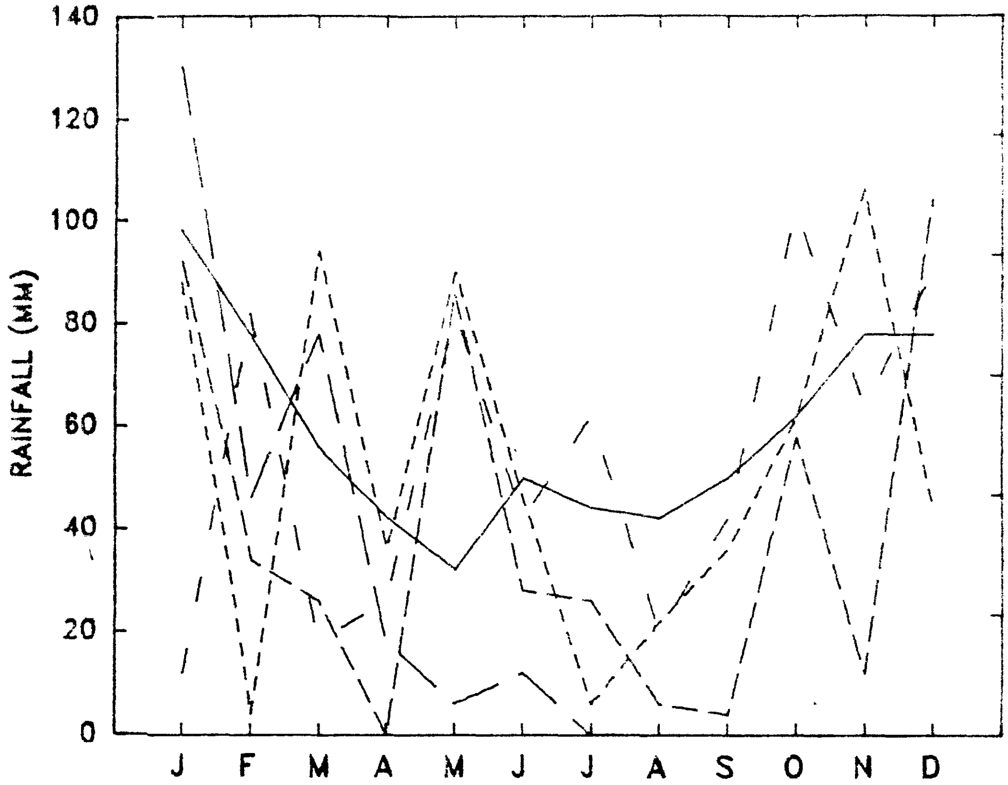

D
MOREE
B
A
A
B
B
ARMIDALE
BENDEMEER
MOONBI STUDY AREA
TAMWORTH
C
A
A STEEP SLOPES
B GENTLE-MODERATE SLOPES
C ALMOST LEVEL
D FLAT
---- COLLECTING AREA
0 500
Km

Figure 2: Habitat, cleared paddocks and rocky outcrops (upper) and uncleared eucalypt woodland (lower) of the New England Tablelands.

Figure 3: Rainfall records from Laureldale Meteorological Station (upper) and Moonbi (lower), median monthly rainfall for Bendemeer taken from Hobbs and Jackson (1977). Rainfall for 1979 is represented by--------, 1980 by---- , 1981 by — — —, 1982 by —— —, and mean montly rainfall by ———. Months are represented by their first initial.


140
120
100
80
60
40
20
0
RAINFALL (MM)
J
F
M
A
M
J
J
A
S
O
N
D

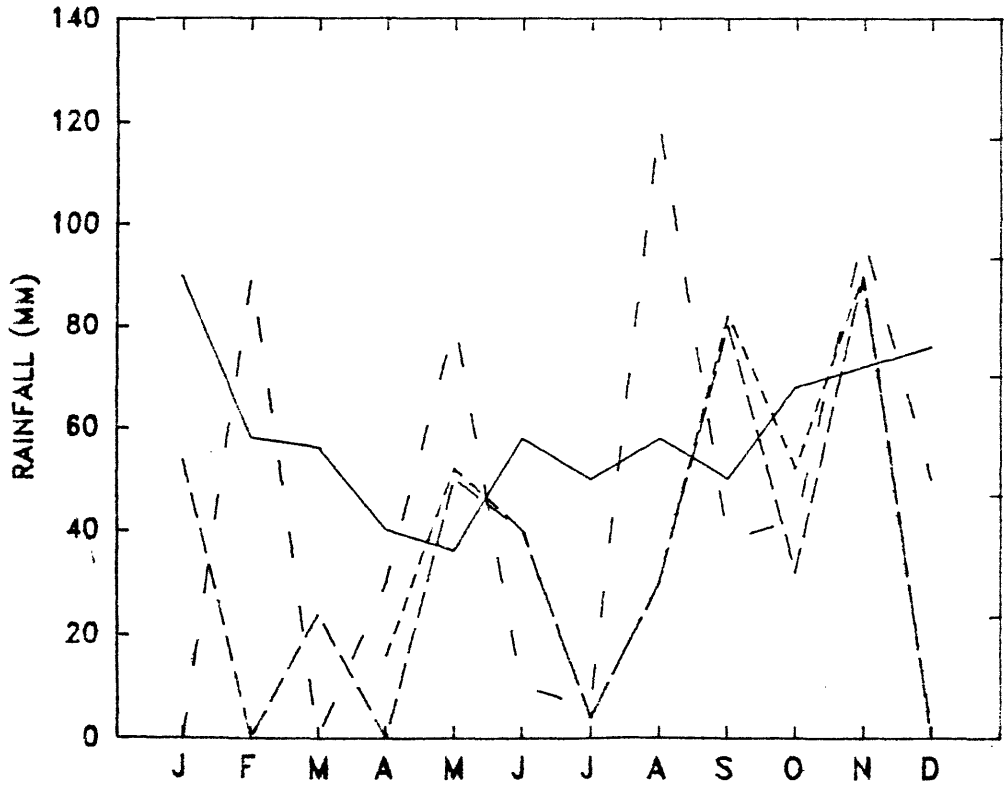
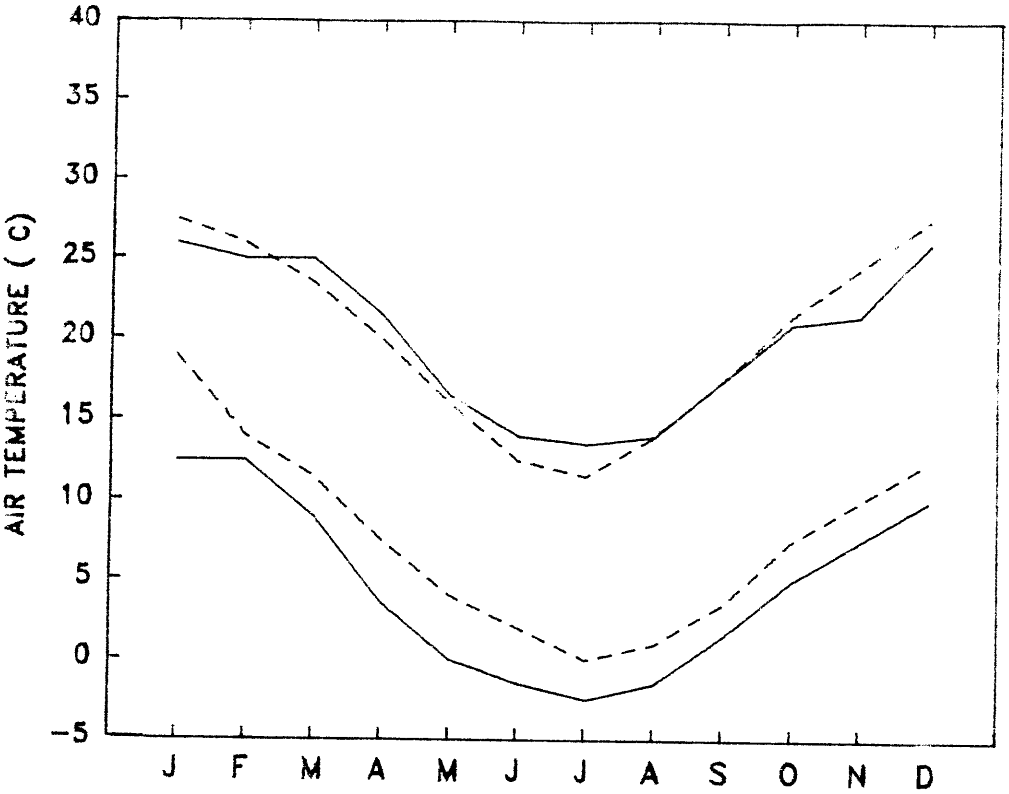
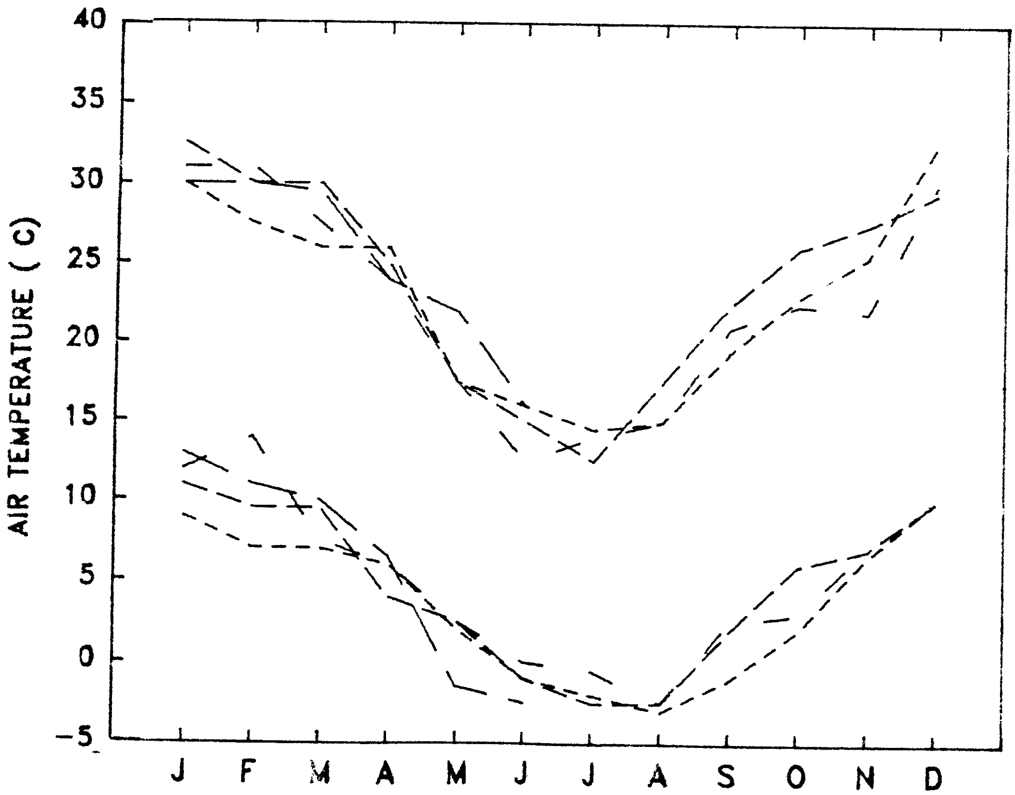

140
120
100
80
60
40
20
0
RAINFALL (MM)
J
F
M
A
M
J
J
A
S
O
N
D

Figure 4: Mean monthly air temperatures recorded by Meteorological stations at Armidale and Woolbrook (upper), and for Laureldale (lower). In upper figure intact lines represent Armidale and dashes lines represent Woolbrook. In lower figure 1979 is represented by ------ , 1980 by – – – –, 1981 by — — —, 1982 by ——— ——— . Months are represented by their first initial.

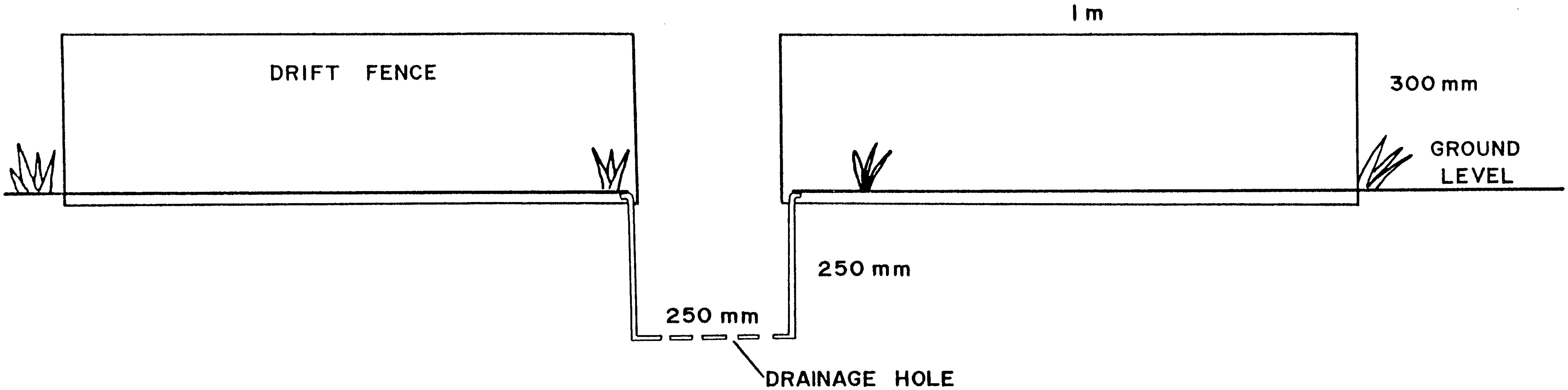


40
35
30
25
20
15
10
5
0
-5
AIR TEMPERATURE (C)
J F M A M J J A S O N D



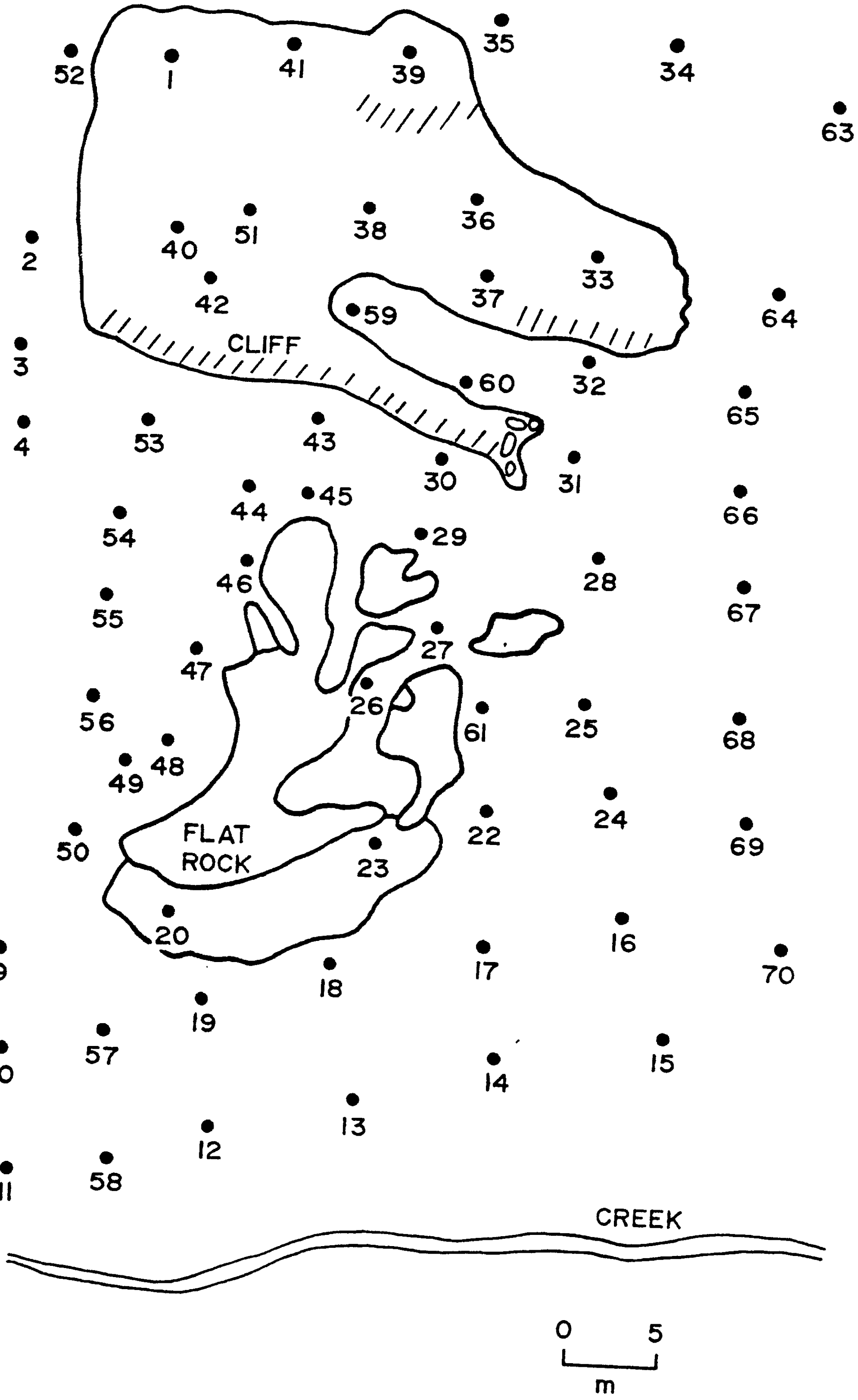
40
35
30
25
20
15
10
5
0
-5
AIR TEMPERATURE (C)
J F M A M J J A S O N D

Figure 5: Construction of pit trap and drift fence.



DRIFT FENCE
1 m
300 mm
GROUND LEVEL
250 mm
250 mm
DRAINAGE HOLE

Figure 6: Moonbi study area with numbers representing location of pit traps.


CLIFF
FLAT ROCK
CREEK
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
63
64
65
66
67
68
69
70
0 5
m