STUDIES OF FACTORS WHICH DETERMINE THE DISTRIBUTIONS OF THREE SPECIES OF SOUTH AUSTRALIAN REPTILE TICKS.

by

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SUMMARY

Aponomma hydrosauri, Amblyomma albolimbatum and *Amblyomma limbatum* are ixodid ticks which parasitize a wide range of reptiles. The geographical distributions of the ticks are peculiar in that they abut but overlap very little along extensive boundaries, i.e., they are parapatric. In this study I searched for the factors which determined these distribution patterns. Examination of tick distribution maps revealed broad associations between the ranges of the ticks and climate or vegetation or both. But these associations were not consistent along the common boundaries of any pair of ticks. It was also evident that the distributions of the major host species were not delimiting tick boundaries.

The common boundary of *Ap. hydrosauri* and *Amb. limbatum* at Mt Mary was examined in more detail and associations found between changes in vegetation, climate weather, soil type and the ticks. Studies were made of the behaviour, development and seasonal activity of the ticks in the laboratory and field. The general biology of the major host in the Mt Mary area, the sleepy lizard, *Trachydrosaurus rugosus*, was also investigated, particularly the seasonal and diurnal activity of this skink.

These data alone, though necessary, are insufficient to uncover the mechanisms which maintain the boundary at Mt Mary. Laboratory and field experiments were conducted to test hypotheses proposed to account for the narrow zone of overlap between the species. The hypotheses were firstly that the tick species interact in such a way that each excludes colonizing ticks from its side of the boundary, or secondly that marked changes in some other environmental factor or factors make it impossible for colonizing ticks to survive across the boundary. A combination of both mechanisms might operate.

The experiments did not provide unequivocal support for either kind of hypothesis. These findings are coupled with data on the biology of the

ticks, their hosts, and the Mt Mary environment to model the mechanisms by which the degree of overlap between the ticks is kept small. It is hypothesized that *Ap. hydrosauri* is unable to live further north, in the Mt Mary area, because conditions become too dry for the non-parasitic stages. The reasons for *Amb. limbatum* not being found futher south are more difficult to uncover. The possibilities of this ticks' southern limit being due to winter cold or to interactions with *Ap. hydrosauri* are examined in detail.

The relevance of these findings to the other tick boundaries and the future of the Mt Mary boundary are discussed. Ideas are also presented on the possible ways in which the tick distribution patterns might have been determined by past changes in climate and sea level during the late Quaternary.

DECLARATION

This thesis contains no material which has been accepted for the award of any other degree or diploma in any university and, to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference is made in the text of the thesis.

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1.00 INTRODUCTION

Population biologists have long been intrigued by situations where the geographical distributions of two or more similar species, or forms, of organisms are allopatric but contiguous, or are generally allopatric with a relatively tiny area of sympatry. The study of these situations is contributing much to our understanding of ecology and evolution.

Smith (1955, 1965) coined the term 'parapatry' to cover distributions which were allopatric but 'in contact'. Vaughan (1967) and Key (1968) used 'parapatry' for distributions in which there was a narrow zone of overlap. Others have also used the term to include cases where there is a hybrid zone at the boundary (Bull 1973). I prefer this term, covering the three situations described, to the alternative 'contiguous allopatry'.

Parapatric distributions are quite common throughout the world (White 1978) and parapatric boundaries have been found between species or forms of animals from many taxonomic groups (e.g. mammals (Miller 1964), reptiles (Gorman and Hillman 1977), birds (Terborgh 1971), amphibians (Jaeger 1970), insects (Key and Balderson 1972) and crustaceans (Connell 1972)). In some cases the boundaries are between quite distinct species, which do not interbreed, in other cases hybrid zones are found where the populations contact.

It is thought that many parapatric boundaries arise from the secondary contact of formerly isolated populations. However some workers believe that parapatric boundaries may also, in some cases, be primary, and that the two populations may have differentiated by mechanisms which do not involve geographical separation (Bush 1975, White 1978). White (1978) describes three models of speciation which fall into this category; "clinal speciation", "area-effect speciation" and "stasipatric speciation".

Most explanations proferred to explain the existence of parapatric distributions fall into two categories (see Chapter 6). One is that the boundary between the two populations lies along a marked discontinuity in some environmental factor, or factors, for which the two populations have very different requirements. The discontinuity could be a major, readily observed one, i.e., an ecotone, or more subtle and cryptic. Its effect may be indirect - e.g., it may act on a third species (a predator, a competitor or a host) with which the two in question interact. The other kind of explanation is that the two populations interact in some way so that they cannot be sympatric. This interaction could be competitive, where at least one species is prevented from successfully colonizing the other's range by competitive interaction. The boundary then might be stable or moving. If stable it would be expected to coincide with an environmental discontinuity as described above (e.g., Miller 1964). If the boundary is moving (e.g., Crowell 1968), the animal whose range is being decreased may be moving towards extinction or to a stable situation as above. Another possible interaction giving rise to this type of distribution is that of two populations which give rise to unfit hybrids at their boundary which prevent successful immigration (e.g., Littlejohn et al., 1971).

Parapatric distributions might persist or be temporary. They might break down and the populations become sympatric. This could occur if some condition in the environment changes, or the organisms change so that the animals can survive within each other's range, or the cause of a competitive interaction is removed (these possibilities are not mutually exclusive). A parapatric distribution might also be disrupted by the two populations introgressing. There is as yet little evidence reported of either means of disruption of parapatric distributions in nature.

At a boundary where the parapatric distribution is determined by interactions between the populations there may be selection for characteristics different from those in allopatry. When this occurs the resultant change is called character displacement; see Grant (1972.6) for a review of this topic. The selection could be for character divergence, e.g. for increased premating isolation between the populations which would prevent the wastage of reproductive effort on unfit hybrids or for characteristics which reduce interspecific competition. On the other hand there might be selection for convergence of characters which would, for example, allow efficient division of the narrow zone of overlap by interspecific territoriality (Cody 1973).

It can be seen that the study of parapatric distributions involves consideration of a number of mechanisms important in determining the composition of animal communities.

Investigation of parapatric distributions should enable ecologists to assess the relative importance of the phenomena listed above in influencing the distribution and abundance of animals. One has only to consider the long and often bitter debate on the role and importance of interspecific competition in structuring communities to appreciate the importance of this prospect (Krebs 1978).

Michael Smyth (1973) observed that 3 species of ixodid ticks, *Aponomma hydrosauri*, *Amblyomma limbatum* and *Amblyomma albolimbatum*, distributed widely in Australia, had geographical distributions that 'abut but overlap very little along very long boundaries'. This observation led him to ask two questions. Firstly, why are the boundaries where they are? And secondly, why is there so little overlap?

Smyth studied data on the distributions of the three ticks from collections and collectors in many parts of Australia. In particular he made extensive collections in three areas of South Australia. They were the Cleve area, where *Amb. albolimbatum* and *Ap. hydrosauri* are parapatric, and the Pt. Pirie and Morgan regions where *Ap. hydrosauri* and *Amb. limbatum* meet. The ticks proved to be restricted to reptilian hosts but parasitized many species. There was no evidence that the distributions of the ticks were coincident with those of any particular hosts. There were, however, broad correlations with average annual rainfall and, in one case, soil type.

Nevertheless there was no rapid transition in obvious environmental features that was consistently associated with the common boundary between a pair of species.

Bull and Smyth (1973), studied the water balance of the ticks as "the ticks' distributions are at least broadly related to aridity". They hypothesized that a tick's ability to survive arid conditions would be correlated with the aridity of its range and that this ability might account for the positions of the boundaries between species. Their results were to some extent equivocal. Although *Ap. hydrosauri* showed a greater water loss than the two *Amblyomma* species, as expected from the more southerly range of the former, *Amb. albolimbatum*, which occurs south of *Amb. limbatum*, was the most resistant to desiccation!

The preliminary work by Michael Smyth and Michael Bull (Smyth 1973, Bull 1969, Bull and Smyth 1973) motivated the present enquiry into the factors which might bring about the parapatric distribution pattern of the ticks. The way in which this problem was tackled is outlined below.

Additional data on the distributions of the ticks were collected so that the distribution patterns could be examined closely. These data have been pooled with those of Michael Smyth and are to be found in Chapter 2 where the maps give a broad scale view of the situation. However, it was reasoned that factors responsible for the parapatric boundaries are best discovered by the close-up examination of such boundaries. The well-defined boundary between *Ap. hydrosauri* and *Amb. limbatum* east of Spencer Gulf seemed most appropriate for such work. A study area on this boundary was chosen at Mt. Mary, where it was known that ticks and their hosts were abundant and that the land had been subject to only minor interference by man (see Chapter 5). This tick boundary was also the closest to Adelaide and thus presented fewer logistic problems than the more distant alternatives. The ticks, *Ap. hydrosauri* and *Amb. limbatum*, were studied more closely than the third species, *Amb. albolimbatum*. However, it was immediately apparent that any consideration of the ultimate (historical and evolutionary) causes of the present distribution patterns must include consideration of this tick (see Chapter 7). There are parapatric boundaries between all three species and where *Amb. albolimbatum* is present in Western Australia the limits of distribution of the other ticks are in quite different positions from those in Eastern Australia where *Amb. albolimbatum* does not exist. Thus, relevant data on *Amb. albolimbatum* have been included in this study.

The interpretation of data on distributions requires knowledge of the general biology of the ticks, their life-cycles, behaviour, movements, etc. Indeed many studies of the factors which limit tick distributions have largely involvedstudies of their behaviour and physiological ecology (Arthur 1962). Information of this type is presented in Chapter 3.

A most important aspect of the ecology of these parasites is their dependence on various host species. In Chapter 4 the known hosts of the ticks are examined to see if they might, by their behaviour and/or distribution, influence the distribution of the ticks.

I pointed out above that, in general, two types of explanations are used for parapatric distributions. Chapters 5 and 6 describe tests of the following hypotheses as explanations for the parapatric boundary between *Ap. hydrosauri* and *Amb. limbatum* at Mt. Mary.

1. That the boundary lies along a discontinuity in some environmental factor or factors for which the species have different requirements.
2. That the two species interact in some way so that they cannot be sympatric.

In Chapter 5 the Mt. Mary study area is examined in detail. The boundary between *Ap. hydrosauri* and *Amb. limbatum* is explored to establish its position, whether or not it is stable and its relationship to the distribution of other environmental factors. In Chapter 6 information is presented on the experiments performed to test the hypotheses and models are presented to explain, in terms of present day(proximal)processes, the parapatric boundary at Mt. Mary.

The whole study is examined and discussed in Chapter 7. Here information on the ticks and their ecology is combined with information on past climates and sea levels in Australia in order to explore the ultimate (historical and evolutionary) causes of the present distributions.

2.00 THE GEOGRAPHICAL DISTRIBUTIONS OF THE TICKS

2.10 Introduction

Roberts (1970) made the first significant attempt to describe the ranges of these and other Australian ticks. Earlier workers had too few specimens to make other than fleeting comments on the subject (Ferguson 1925, Fielding 1926, Johnston 1932, Neumann 1899). Roberts noted that although members of the two genera, *Aponomma* and *Amblyomma*, are found throughout the world, *Ap. hydrosauri*, *Amb. albolimbatum* and *Amb. limbatum* seem to be confined to Australia and some of the islands on the continental shelf.

There is no evidence that Roberts detected the peculiar nature of the geographical distributions of the ticks, i.e., that they were parapatric (Roberts 1953, 1964, 1969, 1970). Smyth (1973) provides an explanation for this. He showed that a number of the records of the *Amblyommas*, used by Roberts, were probably incorrect. Roberts' data contained four records of *Amb. albolimbatum* from Victoria,while Ferguson (1925) and Fielding (1926) recorded it from New South Wales and Queensland. Smyth doubted that the tick occurred in eastern Australia. Examination of two of the Victorian collections showed one to be *Ap. hydrosauri* and the other to come from Western Australia. Fielding's identification was probably wrong (Roberts, 1964) and Ferguson's specimens have been lost. There was also a misleading record of *Amb. limbatum*, an inhabitant of arid and tropical regions, from King Island in the Bass Strait. Smyth found that the specimens, which in fact are the type specimens (Neumann 1906), were actually labelled "L'ile King." Smyth examined results of other collecting trips to the Bass Strait Islands and examined his own data on the range of *Amb. limbatum*. He decided that L'ile King could not be King Island in the Bass Strait. *Amb. postoculatum* Neumann had also been collected on L'ile King at the same time as the type specimens of *Amb. limbatum*. Roberts (1964) states that *Amb. postoculatum* has only been collected in the field once since, on Bernier Island off the coast of Western Australia where *Amb. limbatum* is also found. No one is sure where the original L'ile King is, but it is possible that it is Bernier Island or nearby.

Smyth during his study of the ticks examined specimens lodged with a number of museums and research institutions. These included the South Australian Museum, the Western Australian Museum, the National Museum of Victoria and the Waite Agricultural Institute. With these records plus the data he obtained from examining a variety of snakes and lizards, he drew up the distribution maps which are shown in his 1973 paper. He made extensive collections in three parts of South Australia:near Cleve, Pt.Pirie and Morgan, these being parapatric boundaries between *Amb. albolimbatum* and *Ap. hydrosauri* in the first area and between *Amb. limbatum* and *Ap. hydrosauri* in the other areas. He did not gather sufficient data to map a boundary between the two *Amblyommas*. I was given these records which consist of 433 record cards each detailing the ticks taken from an individual host. They have been used together with my own records, consisting of 1060 record cards, to map the geographical distributions of the ticks. The data recorded on the cards are shown in appendix I.

All the tick specimens Dr. Smyth and I collected in the field were taken from reptiles. The lizards and snakes were usually captured alive by hand or with noosing poles, often near or on roads. Sometimes snakes and lizards were found killed on roads, these were examined and any ticks attached were taken. Voucher specimens of ticks taken from reptiles in the field have been kept preserved in 70% alcohol.

Some of the tick specimens have been given to us by a variety of people. Care has to be taken in using such samples as in some instances the information gained may be misleading. Some people sent ticks that had been on reptiles, particularly sleepy lizards *Tr. rugosus*, kept as pets. Often these lizards which had been captured many miles away from their new home, may well have brought ticks with them, and might have picked up ticks in the new area or from other reptiles in the collection. Another potential danger concerns the use of bags in which herpetologists are wont to place captured specimens. A number of local biologists have regularly collected reptiles in various parts of Australia and have generously allowed their catch to be searched for parasites. It was soon evident that some of these collectors used the same bags on successive trips to different parts of the state. Further, it was found that ticks may detach from a host in such a bag and perhaps weeks later they can attach to the next occupant of the bag.

Other studies on tick distributions have been made easier by the development of techniques to obtain samples of unattached ticks in the field. These are discussed in more detail in Chapter 3 and include 'flagging' (Boardman 1944), carbon dioxide traps (Garcia 1962, 1965; Nosek and Kozuch, 1969), flotation methods (Salt and Hollick 1944) and the Tullgren funnel method (Wood 1965). Flagging involves dragging a cloth over pasture to which ticks, which live in the sward, attach, e.g. *Ixodes ricinus* (Milne 1945a). It proved inappropriate for the reptile ticks in that their micro-habitats off the hosts were quite different from those of pasture ticks like *I. ricinus* (see Chapter 3). The CO_2 trapping method relies upon the ticks being attracted to high CO_2 concentrations and moving along concentration gradients. In Chapter 3 I show that this does not happen with the three reptilian ticks. The flotation and funnel methods were also found to be useless for gathering distribution data.

It is perhaps as well, in one respect, that the ticks' behaviour is not influenced by CO_2 gradients. Earlier it was said that many of the ticks collected in the field were found on hosts near or on roads. McEnroe (1971) noted that the American dog tick *Dermacentor variabilis* was influenced by the CO_2 gradient produced by automobiles on roads! He stated that the adult tick distribution in America had been changed and that ticks along roadsides remained active for several weeks longer than those in adjacent open fields. It is unlikely that *Ap. hydrosauri* or either of the *Amblyommas* are similarly influenced.

In order to plot the distributions of related animals it is essential that they can be distinguished. These matters are discussed at length in Chapter 3. All stages of *Ap. hydrosauri* were readily distinguished from the other ticks. The *Amblyomma* adult ticks were easily distinguished but more difficulty was experienced with immature stages.

The distribution maps of the three ticks are presented below in 2.20 for Australia overall. Section 2.30 contains a description of the pattern in South Australia where data are most abundant. In this section correlations with climate and topography are examined and the distributions are discussed.

2.20 The Australia-wide distribution of the ticks.

The geographical distributions of the ticks in Australia and islands on the continental shelf are shown in figure 1. In this and the other maps in this chapter individual marks on the map represent ticks from one or more hosts. Thus the numbers of ticks represented by marks may vary greatly. Also in some areas too many tick infested reptiles have been caught to enable them all to be plotted.

Ap. hydrosauri has been collected extensively from reptiles in south eastern Australia, and Tasmania and the Bass Strait Islands. Smyth (1973) reported that Dr. M. Bull had found specimens of the tick near Albany and Bremer Bay in Western Australia. Dr. D. King of the Agriculture Protection Board in that state has kindly collected and sent to me many tick specimens from various western regions and we have examined specimens found attached to reptiles in the Western Australian Museum. Figure 2 shows the distribution of the ticks in Southern Western Australia which has resulted from these

Figure 1. Australia, showing the distribution of records of *Amb. albolimbatum, Amb. limbatum* and *Ap. hydrosauri*.

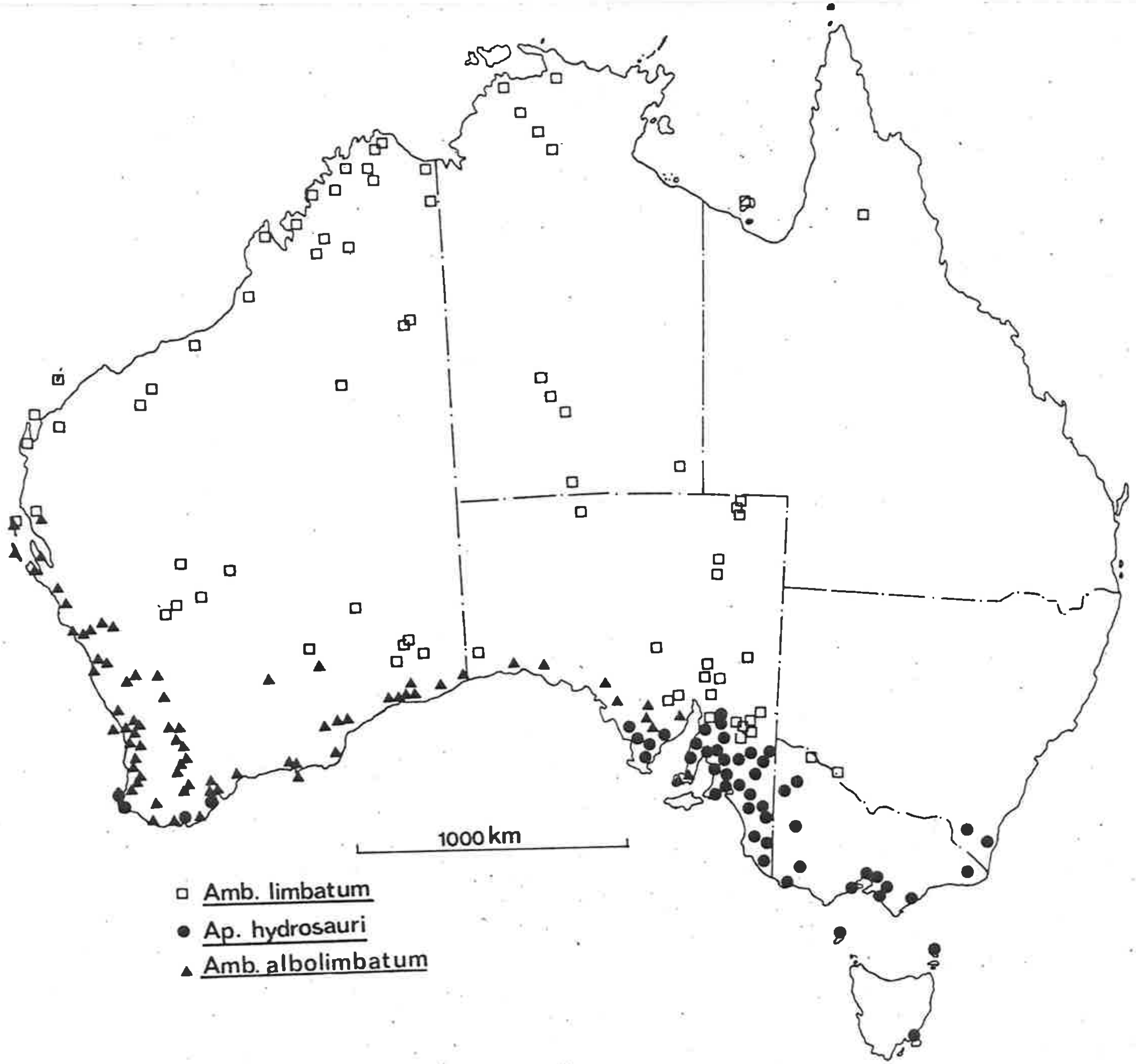
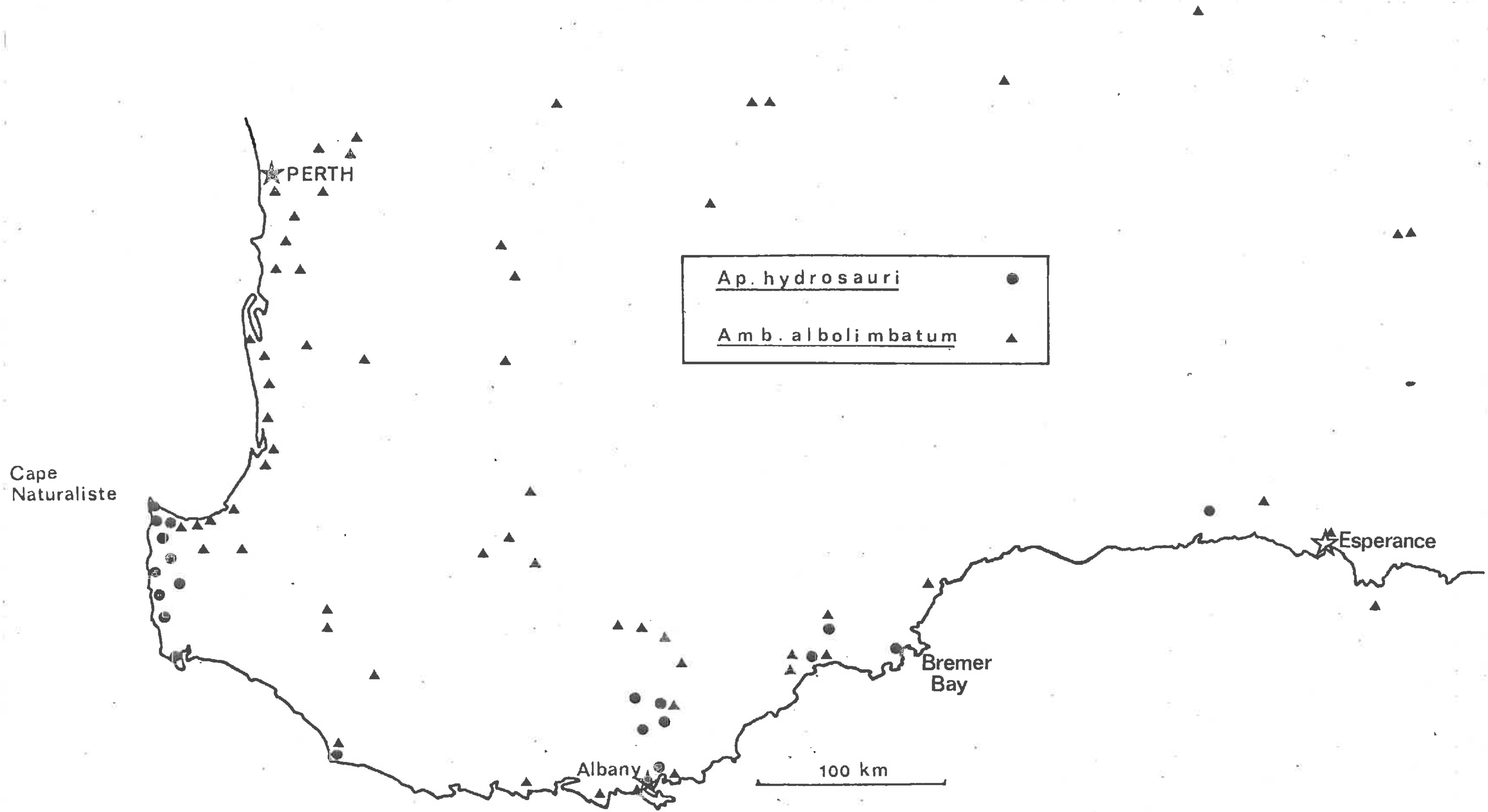

1000 km
□ Amb. limbatum
● Ap. hydrosauri
▲ Amb. albolimbatum

Figure 2. Part of Western Australia, showing the distribution of records of *Amb. albolimbatum* and *Ap. hydrosauri*.


Ap. hydrosauri ●
Amb. albolimbatum ▲
PERTH
Cape Naturaliste
Albany
Bremer Bay
Esperance
100 km

endeavours. It shows that there is a population of *Ap. hydrosauri* in the Capte Naturaliste area and that other specimens have been discovered near Albany, Bremer Bay and Esperance. It is not yet known if the latter occurrences represent one or more populations. The Western Australian collections reveal a similar pattern to that which exists in South Australia i.e. *Ap. hydrosauri* and *Amb. albolimbatum* are parapatric (see Sharrad and King 1979 in appendix 6).

Roberts (1970) also reported finding *Ap. hydrosauri* in Queensland infesting echidnas, *Tachyglossus aculeatus*, and other mammals. This tick, which certainly has different host preferences from the southern reptilian *Ap. hydrosauri*, seems to represent a quite isolated population. This matter is discussed further in Chapter 3.

Amb. albolimbatum is absent from south eastern Australia but occupies a considerable portion of south western Australia. *Amb. limbatum* is the most wide spread of the three species, being found in arid, semi arid and tropical regions and islands off the northern coast.

2.30 The Distribution in South Australia.

Figures 3, 4, 5 and 6 outline the present knowledge of the tick distributions in South Australia. Figure 3 gives the overall picture while figures 4, 5 and 6 concentrate on areas of interest.

The maps support the findings of Smyth (1973) that the tick distributions abut over long distances but overlap very little. This is most evident with the boundaries between *Amb. albolimbatum* and *Ap. hydrosauri* on Eyre Peninsula, and between *Amb. limbatum* and *Ap. hydrosauri* east of Spencer Gulf. The boundary between the two Ambolyommas on Eyre Peninsula has not been well defined. It may not be as clearly parapatric as the other two boundaries in that the ticks might occur together over a broader band or may not be in contact in some areas.

Figure 3. Part of South Australia, showing the distribution of records of *Amb. limbatum* *Amb. albolimbatum* and *Ap. hydrosauri*. Isohyets (mm) shown are taken from the Commonwealth Bureau of Meteorology (1968).

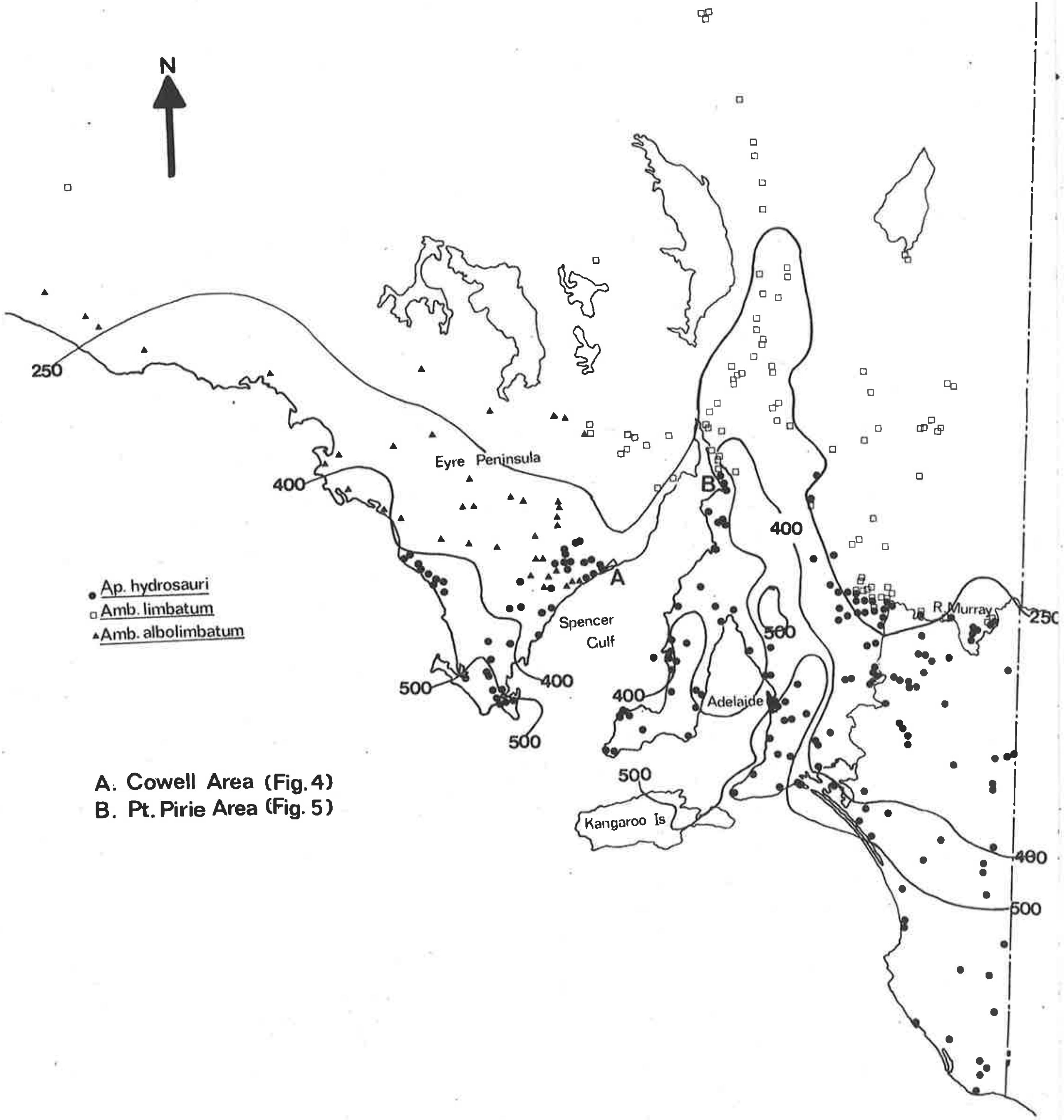

N
250
400
Eyre Peninsula
A
B
400
Spencer Gulf
Gulf
400
500
500
400
500
Adelaide
500
Kangaroo Is
R. Murray
250
400
500
● Ap. hydrosauri
□ Amb. limbatum
▲ Amb. albolimbatum
A. Cowell Area (Fig. 4)
B. Pt. Pirie Area (Fig. 5)

Figure 4. Part of Eyre Peninsula, South Australia; showing the distribution of records of *Amb. albolimbatum* and *Ap. hydrosauri*.

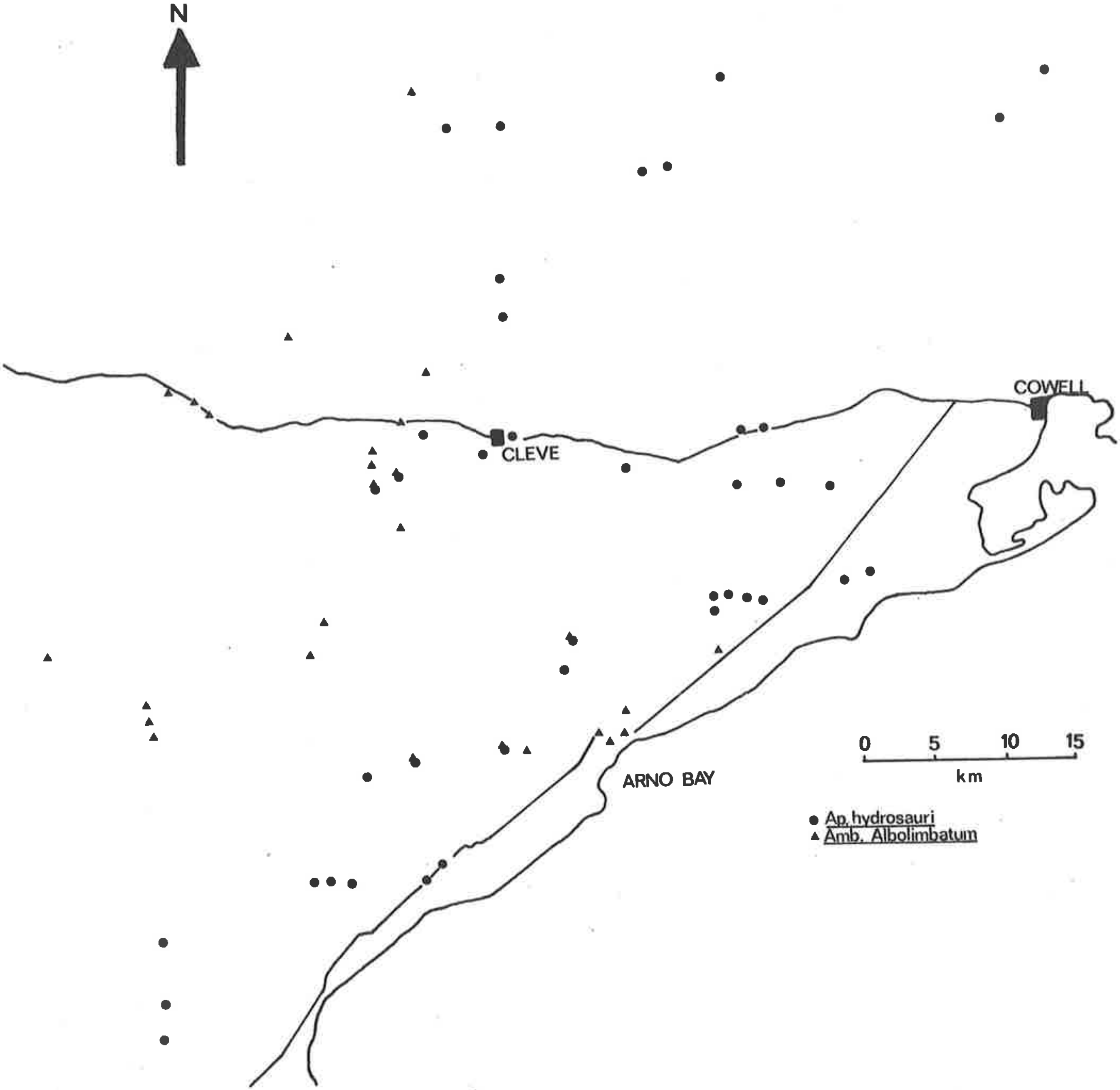

N
COWELL
CLEVE
ARNO BAY
0 5 10 15
km
● Ap. hydrosauri
▲ Amb. Albolimbatum

Figure 5. The Pt Pirie area of South Australia; showing the distribution of records of *Amb. limbatum* and *Ap. hydrosauri*.

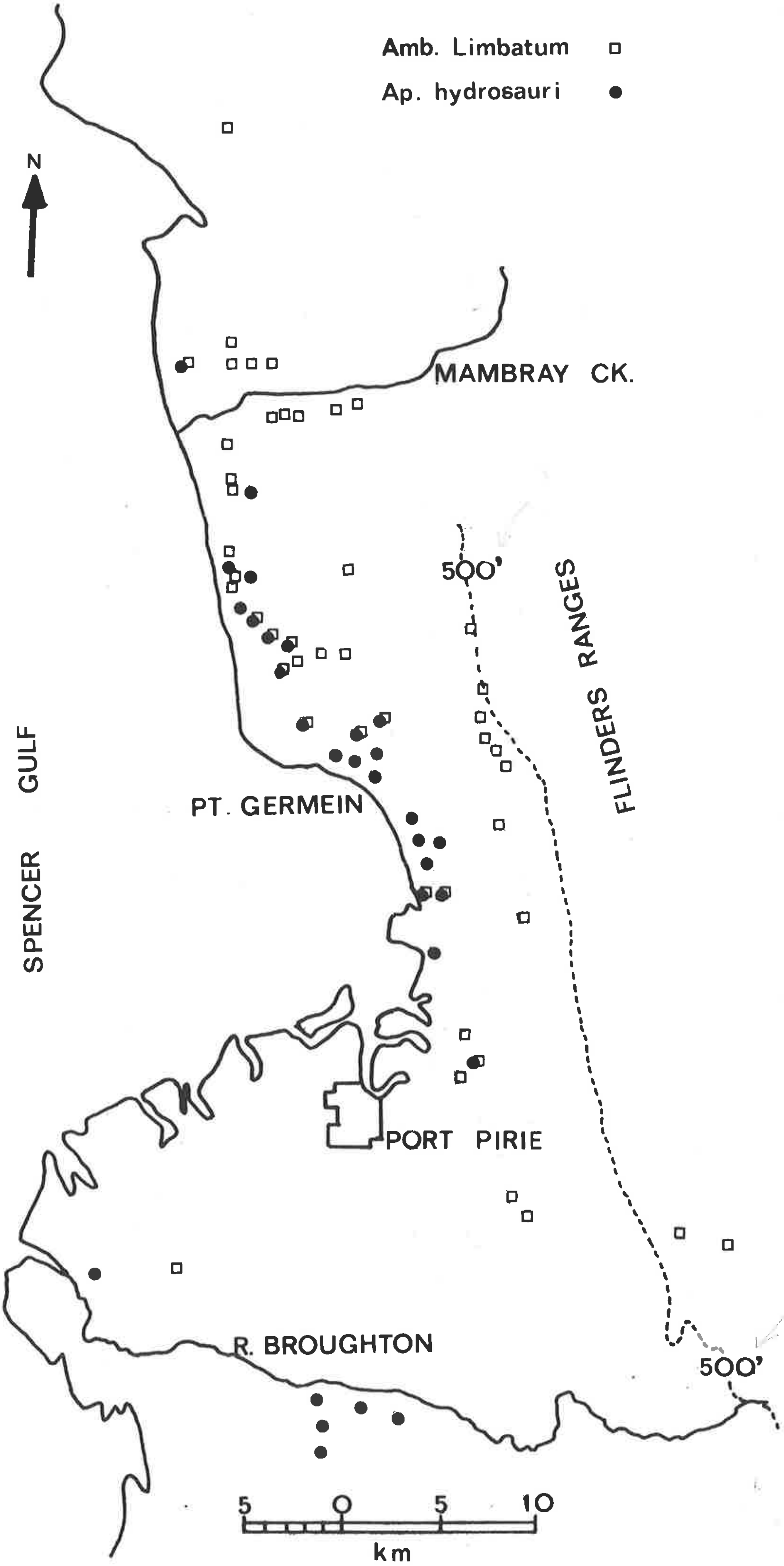
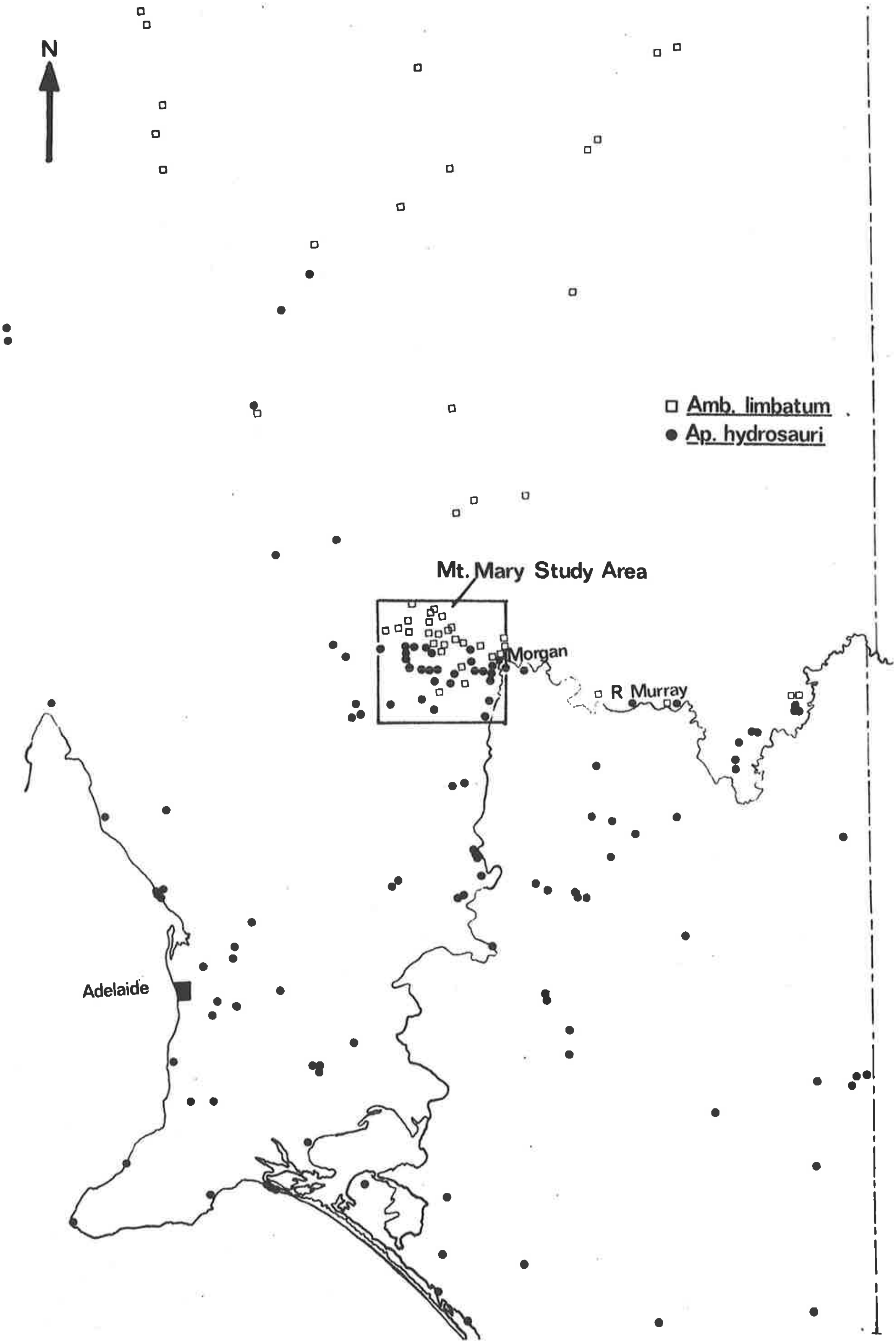

Amb. Limbatum □
Ap. hydrosauri ●
N
MAMBRAY CK.
500'
FLINDERS RANGES
SPENCER GULF
PT. GERMEIN
PORT PIRIE
R. BROUGHTON
500'
5
0
5
10
km

Figure 6. Part of eastern South Australia, showing the distribution of records of *Amb. limbatum* and *Ap. hydrosauri* and the location of the Mt.Mary study area.


N
□ Amb. limbatum
● Ap. hydrosauri
Mt. Mary Study Area
Morgan
R Murray
Adelaide

Another striking feature of the distributions shown on figure 3 is that there are no records of these ticks on Kangaroo Island. This large area, 150km x 60km, is only 10km from the mainland at the closest point and lies well within the climatic rnage of *Ap. hydrosauri*. Extensive collections have been made from reptiles on the island and it is unlikely that any species parasitizing them would have been missed. Another tick *Aponomma fimbriatum* is found there on goannas, *Varanus gouldii*, and also on the mainland where it is broadly sympatric with each of the other three ticks. In Chapter 4 the geographical distributions of the hosts are examined and it is shown that important hosts, particularly sleepy lizards, *Tr. rugosus*, are not found on Kangaroo Island. The sleepy lizard and *Ap. hydrosauri* are both found on the smaller Wardang Island in Spencer Gulf. Thus the problem of explaining the presence or absence of ticks on these offshore islands becomes, to some extent, the problem of explaining the presence or absence of their hosts. This involves a discussion of changes in climate and sea level in the past and how these may have influenced the ticks and their hosts. These matters are pursued in Chapter 8.

Smyth (1973) noted that the common boundaries between the tick species broadly correlated, in some areas, with average annual rainfall, vegetation and soils. He found, however, that these correlations were not consistent along the full length of the boundaries. Such general correlations have been demonstrated for a number of tick species in other continents. Russian workers have mapped the distributions and calculated indices of abundance for a number of tick species over a variety of habitats and vegetation types (Brovko 1966, Drozdova and Sapegina 1965, Popova, et al. 1966, Subotnik 1956). These studies, and others in North America (Semtner et al. 1971), in Scandinavia (Ohman 1961) and in southern Africa (Theiler 1964), clearly demonstrate correlations of this type, i.e. between the boundaries of tick species and climate and/or vegetation. The reason for such correlations was first clearly exposed by Milne (1944) in his study of the distribution of the sheep tick *Ixodes ricinus*, in the north of England. Ticks spend only part of their lives attached to hosts imbibing blood (see Chapter 3); the other part of their lives, and it may be the longer portion, is spent off the host in some microhabitat suitable for moulting or egglaying or awaiting a host. It is at this stage that they are most vulnerable to desiccation, starvation or extremes of temperature. The nature of the microhabitat of the tick off the host is thus crucial. Milne showed that *I. ricinus* required a thick mat of vegetation on the ground in which to develop off the host and in which to avoid desiccation. Such a microhabitat depends upon the vegetation type so *I. ricinus* cannot survive in habitats where the vegetation does not have these characteristics. However it must also be noted that, although the tick's microhabitat may possess appropriate structural qualities, it may experience weather that is too dry or too cold; thus the correlations between climate and tick boundaries. Subotnik (1956), for instance, showed that *Rhipicephalis sanguineus* in Russia had its geographical range restricted by the average monthly temperatures during cold months of the year and by relative humidity in the hot months. These two factors, temperature and humidity, are perhaps the most important climatic variables in influencing tick development, fecundity, behaviour and, thus, distribution (Arthur 1962). But it is the humidity and temperature in the tick microhabitat that is important, and this may vary within an area which receives uniform amounts of solar radiation and rainfall, with variations in soil type and vegetation type. Humidity and temperature vary with the seasons and, as Subotnick (1956) points out, the effects of either may only be important for part of the year. Therefore it is unlikely that tick boundaries would fall neatly along average annual isotherms or isohyets for the whole of their length.

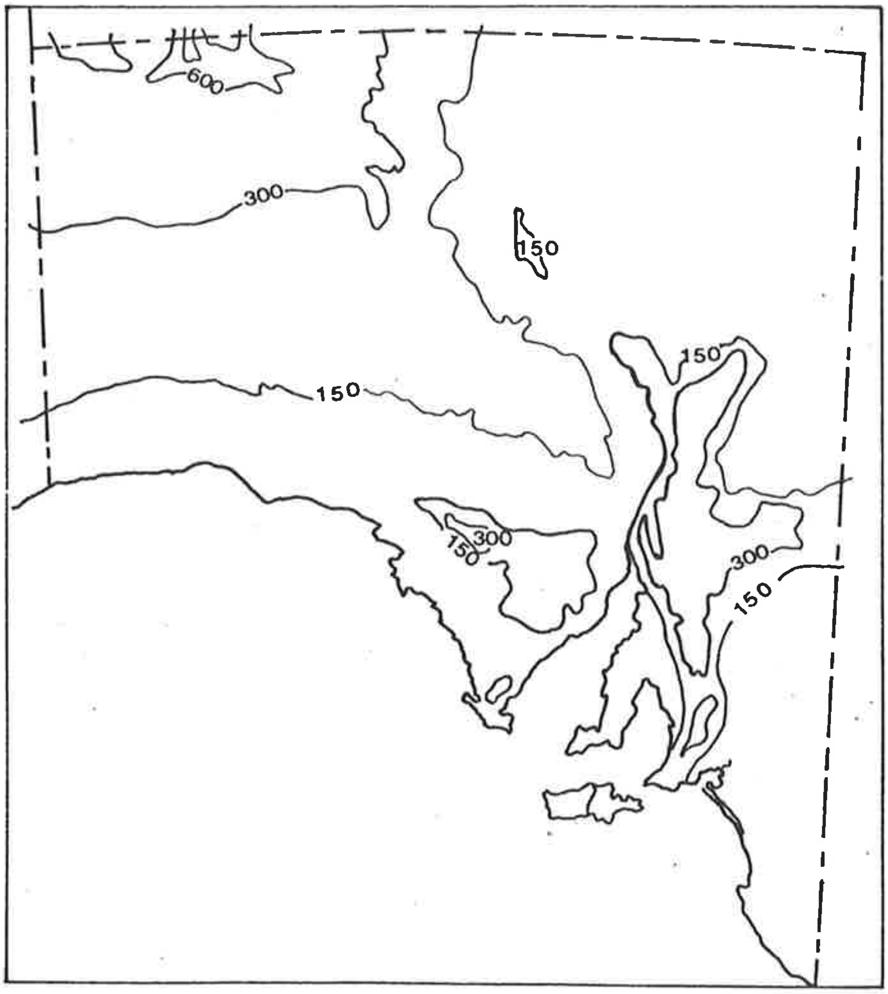
The climate of South Australia is of the type experienced in the Mediterranean region, in south western United States of America, southern and western South Africa and in Chile, i.e. winters are cool and wet while summers are hot and dry. Most of the State has irregular rainfall with great variation from year to year and a low average rainfall. The southern part of the state has regular winter rainfall - see the isohyets on figure 3. The 250mm isohyet serves as an approximate division between the two areas. Temperature and evaporation increase as one goes north - see figure 7. Both temperature and rainfall are influenced by the Mt.Lofty - Flinders Range system which runs north and south along the eastern side of the Gulfs (figures 3 and 7).

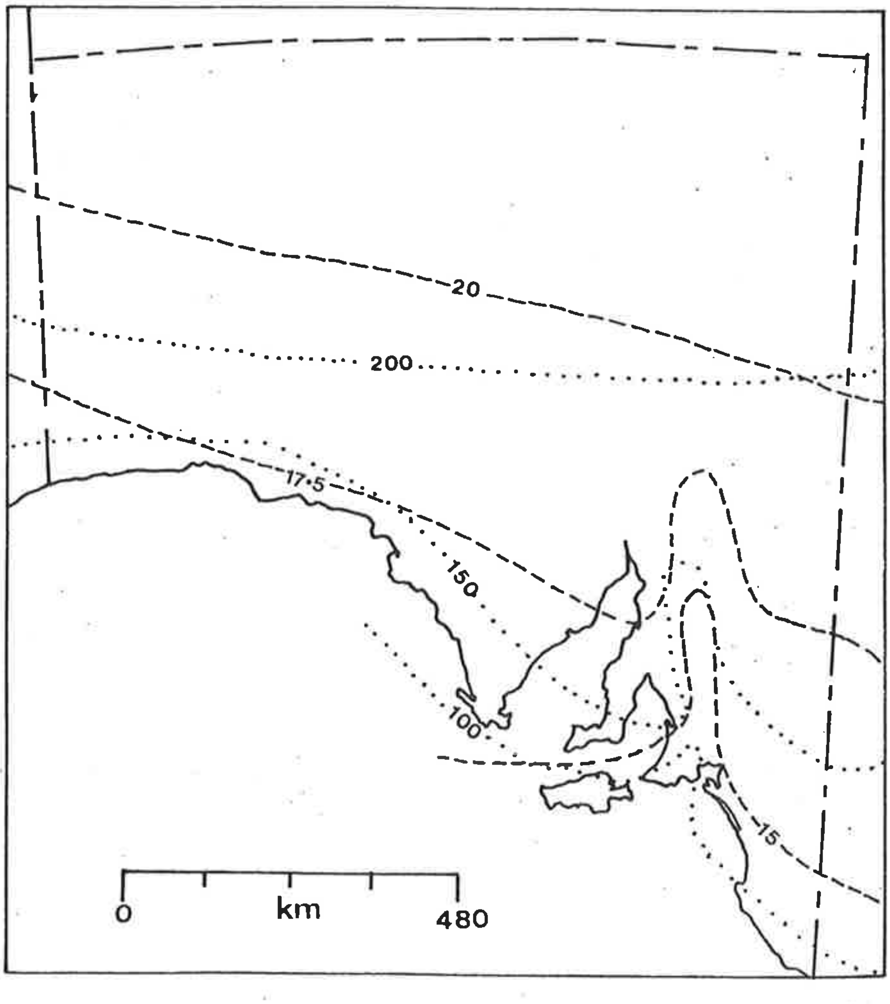
The boundary between *Ap. hydrosauri* and *Amb. limbatum* in South Australia runs for approximately 600km on the eastern side of Spencer Gulf. For most of its length it can be plotted accurately but there are too few records in the Lower Flinders Ranges and the Northern Mt.Lofty Ranges east of Pt Pirie to tell where it runs. Reptiles have proved elusive in that area. The boundary in the Pt Pirie area was examined closely by Smyth and later in the present study (see figure 5). Similarly the areas east of these Ranges were studied in some detail, see figure 6.

The boundary between *Ap. hydrosauri* and *Amb. limbatum* drops steeply southward on the eastern side of the Mt.Lofty Ranges, the rain shadow side. Along this north-south portion the boundary follows closely the 250mm isohyet (see figures 3 and 6). The boundary curves to run east-west just along the northern bank of the River Murray. For much of this distance *Ap. hydrosauri* extends a little north of the 250mm isohyet into regions where the average annual rainfall is less than 250mm. Smyth (1973) suggested that in the Mt Mary area the boundary corresponds closely with the transition from mallee scrub to plant associations more characteristic of arid areas.

Between the Mt.Lofty Ranges and Spencer Gulf *Ap. hydrosauri* extends furthes north along the coast, while inland *Amb. limbatum* is found. Smyth noted that in this area the former is in the area which receives the lower rainfall. However *Ap. hydrosauri* does not approach the 250mm isohyet which passes

Figure 7. South Australia, showing details of topographic relief —150— Contours (metres). Also showing - - -15- - - annual isotherms and ······100····· annual evaporation (cm), adapted from Specht (1972).


600
300
150
150
150
300
150
300
150


20
200
17·5
150
100
15
0
km
480

through Pt.Augusta to the north. These observations show that consideration of rainfall alone is inadequate in explaining the position of the boundary. It can be seen in figure 7 that the mean annual temperature and thus evaporation are much higher in this area than in the tick boundary region east of the Ranges. The *Ap. hydrosauri* in the coastal strip near Pt. Pirie are probably in a more humid region, as Smyth (1973) suggests, than further inland despite the higher rainfall in the latter area.

In the Flinders Range *Ap. hydrosauri* stops well south of the 250mm isohyet while *Amb. limbatum* extends further south of that isohyet there than elsewhere in the State. *Amb. limbatum* in this area experiences rainfall in excess of 350mm per annum. However, it is known that these areas of the Flinders Range which have high average annual rainfall receive rain less regularly than areas with similar averages further south (Kidson 1925). There would then be longer periods of low humidity in the southern Flinders Range than in more southerly areas.

On Eyre Peninsula, west of Spencer Gulf, all three species are found. (figure 3). *Amb. albolimbatum* extends in a narrow, coastal strip across the Great Australian Bight and occupies central Eyre Peninsula. It seems to be bounded to the north by the 200mm isohyet, which also marks the southern boundary of *Amb. limbatum* on Eyre Peninsula. There is in the southern part of the Peninsula an isolated population of *Ap. hydrosauri* which has a common boundary with *Amb. albolimbatum* just south of the 400mm isohyet.

Smyth (1973) detailed the eastern portion of this boundary in the Cleve area. Further collecting trips were made to the area during the present study; see figure 4. Here *Ap. hydrosauri* seems to push a narrow extension of its range north just inland of Arno Bay. This narrow projection broadens in the Cleve Cowell area. In the narrow section inland from Arno Bay *Ap. hydrosauri* and *Amb. albolimbatum* are found together, but in the broadened section further north there is a large area where only *Ap. hydrosauri* is found. There seem, as Smyth suggested, to be no obvious correlations between rainfall or humidity and the tick distributions in this area.

If the tick distributions on the eastern side of Spencer Gulf are contrasted with those on the west, the most obvious difference is the broad band of *Amb. albolimbatum* which separates *Amb. limbatum* and *Ap. hydrosauri* on the western side and the common boundary between these two ticks on the eastern side (figure 3). In Chapter 1 it was observed that parapatric distributions may result from competitive interactions between the species involved. The difference between the distributions of *Ap. hydrosauri* and *Amb. limbatum*, with and without *Amb. albolimbatum* being present, necessitates an examination of the hypothesis that the parapatric distributions of the ticks may have resulted from competitive interactions between them.

In summary, the analysis above has given rise to a number of observations and questions. The ticks do seem to have parapatric distributions, though more information is required on the boundary between the *Amblyommas*. The positions of the boundaries seem generally to correlate with climate, and in some areas with vegetation, i.e. the factors which influence the microhabitat of ticks off the host. The irregularities in the correlation between measured climatic factors and tick boundaries probably arise because the measured factors do not necessarily accurately mirror the actual conditions in the microhabitat of the tick, and because these conditions depend on the interaction of a number of factors. Another observation that can be made is that the difference in distributions between the areas with and without *Amb. albolimbatum* means that explanations of the parapatric boundaries by hypotheses which invoke interspecific competition must be seriously examined. Also, in attempting to model the manner in which the current distribution pattern arose one must account for the absence of ticks, and some of their hosts, from Kangaroo Island.

It was clear that there were two parapatric boundaries suitable for this study; the boundary between *Amb. albolimbatum* and *Ap. hydrosauri* on Eyre Peninsula and the boundary between *Ap. hydrosauri* and *Amb. limbatum* east of Spencer Gulf. Hypotheses erected in an attempt to explain the distributions needed testing at a tick boundary. It can be seen from figure 3 that the closest boundary to the Adelaide laboratories, where this study was based, is the one between *Ap. hydrosauri* and *Amb. limbatum* near Mt. Mary. This area was chosen not only for its proximity but because it was relatively sparsely populated by people, reptiles were known to be abundant there and it was well served by a grid of roads.

The discussion earlier in this chapter indicates that information is needed on the biology of the ticks, with precise details of their behaviour physiological capabilities and tolerances and of their hosts. These matters are examined in chapters 3 and 4. Data are given on all three species because, although the thrust of this work is to uncover the mechanism(s) involved in determining the boundary between *Ap. hydrosauri* and *Amb. limbatum*, the ecology of *Amb. albolimbatum* seems inexorably linked with that of the others, particularly when considering the ultimate causes of the distributions (see Chapter 8).

3.00 GENERAL BIOLOGY OF THE TICKS.

3.10 Introduction:

From ancient times to the present a number of tick species have attracted considerable attention from biologists in many parts of the world (Arthur 1962). This interest is due to the propensity of these species to attack humans and their domestic stock, often transmitting fatal or debilitating diseases. Accordingly there is a vast literature on the biology of many mammalian and avian ticks and the diseases that they transmit while ticks that prey on reptiles or other non-domesticated animals are, by comparison, little studied. The three ticks examined here have been exposed mainly to taxonomic investigations (Denny 1843, Koch 1844, Lucas 1861, Neumann 1899, 1906, 1911, Patton and Cragg 1913, Ferguson 1925, Fielding 1926, Robinson 1926, Johnston 1931, Tubb 1938, Seddon 1947, 1951, Roberts 1947, 1953, 1964, 1969, 1970). These concentrate on their morphological characteristics, particularly of the adults rather than immature stages, and only touch briefly, if at all, on other aspects of their biology. More detailed information on the life histories, physiology and ecology of the ticks is presented by Bull (1969), Bull and Smyth (1973) and Smyth (1973).

The three species have similar life histories of a type common to many of the Ixodidae (hard ticks) in that they are three-host ticks, see figure 8. This means that they pass through three distinct morphological stages in their life cycles; larvae (LL), which have six legs, and the nymphs (NN) and adults (♂♂ and ♀♀) with eight legs. Only in the adults is there apparent sexual dimorphism. At each of these three stages the ticks attach to reptilian hosts by inserting their mouthparts through the host's skin and imbibe large, slow meals of blood or other substances from the host over a period of time ranging from 5 days under some conditions to over two weeks under others. The remarkably extensible cuticles of the ticks allow them to increase greatly in volume and weight during the meal. Engorged larvae, nymphs and adult females detach from the host in the refuge (e.g. bush or burrow) it frequents and there find suitable crevices for moulting or, in the case of the female, for laying eggs (over 4,000 in some species). The adult male ticks do not engorge but frequently detach from the host and wander over its body in search of females with which they mate.

The taxonomy and identification of the ticks is discussed in detail below. Information is also presented on the life cycles of the ticks, their behaviour and physiology.

3.20 Taxonomy and Identification of the ticks.

In order to map the geographical distribution of a species, one must be able to identify the animal and distinguish it from other related species. Also, knowledge of the nomenclature applied to the organism by past workers is vital if their records are to be used. The task of distinguishing these tick species from one another is complicated by the existence within each species of four morphologically distinct types; larvae, nymphs, adult males and adult females. Below are reviews of the taxonomic literature on the three ticks and comments on the ease with which they can be separated from each other in the laboratory and in the field.

3.21 Aponomma hydrosauri (Denny)

Denny (1843) described an unknown number of female ticks collected in Tasmania from a *'Hydrosaurus gouldii'* (Roberts 1964). He named them

Ixodes hydrosauri. Roberts (1964) reported that he had searched unsuccessfully for these type specimens but was satisfied by Denny's 'brief and inadequate' description that they were of the species now called *Ap. hydrosauri*. It is also interesting to observe that Roberts (1953) deduced that the *'Hydrosaurus gouldii'* , of Denny, was the goanna *Varanus gouldii*.

and the other varanids are not believed to occur in Tasmania (see Chapter 4). Perhaps Denny, or the collector of the ticks, had confused a large skink with *Hydrosaurus gouldii*.

The tick suffered four name changes in the sixty years from 1843. Koch (1844) referred to the tick as *Amblyomma hydrosauri*. Lucas (1861) came upon specimens of the tick on *'Trachysaurus scaber'* and named them *Ixodes trachysauri*. The generic affinities of the tick were established by Neumann (1899) when he described the genus *Aponomma*. However he described the tick as two species *Ap. hydrosauri* and *Ap. trachysauri*, the latter from Lucas' type specimens.

Neumann (1906) then complicated the matter when he reported finding 1 ♂ and 5 ♀♀ ticks on an echidna, *Tachyglossus aculeatus*. These he identified as *Ap. concolor*, described by him in 1899, and he decided that this species was the same as the one named *Ap. hydrosauri*. The name *Ap. hydrosauri* was used to describe the echidna tick by Neumann (1906), Patton and Cragg (1913), Ferguson (1925), Fielding (1926), Seddon (1947), and Roberts (1947, 1953). The reptilian tick, to which this section is devoted, was called *Ap. trachysauri* by Patton and Cragg (1913), Ferguson (1925), Fielding (1926), Johnston (1932), Tubb (1938), Seddon (1947, 1951) and Roberts (1947, 1953).

Roberts (1953, 1964, 1970) resolved the matter. In his 1953 paper he referred to the echidna tick as *Ap. hydrosauri*, the reptilian tick as *Ap. trachysauri* and also described some Queensland specimens from echidnas and one from *Bos taurus* as *Ap. tachyglossi*. In the 1964 paper he described the mistake made by Neumann (1899, 1906), revealing that *Ap. concolor* was a parasite of echidnas and that *Ap. hydrosauri* and *Ap. trachysaur* were synonyms. He restored the name *Ap. hydrosauri* to the reptile tick and discarded *trachysauri*. The new species *Ap. tachyglossi* (Roberts 1953) was later said to be identical with *Ap. hydrosauri* (Roberts 1970).

This leaves *Ap. hydrusauri* as the tick with a southern Australian distribution where it parasitizes reptiles and an isolated population on echidnas near Rockhampton Qld. Dr. Smyth and I were loth to accept that the Qld. ticks were *Ap. hydrosauri*. The identification has, however, been confirmed by Drs. Roberts and Kemp of the C.S.I.R.O. Long Pocket Laboratories and Dr. Smyth (Kemp. Pers. Comm., Smyth, Pers. comm). The Qld. ticks are morphologically indistinguishable from the southern reptilian ticks. It would be interesting to pursue this matter further with mating trails and electrophoretic comparisons of the northern and southern populations.

Ap. hydrosauri ♂♂, ♀♀ and NN are readily distinguished in the field and laboratory from the other eight Australian *Aponommas*. *Ap. concolor*, which Neumann (1906) thought to be identical to the *Ap. hydrosauri* he viewed in 1899, has only been found on the echidna, *Tachyglossus aculeatus*, and never on reptiles. It is also morphologically distinct from *Ap. hydrosauri* at all stages of the life cycle excepting LL (Roberts 1953, 1970). *Ap. fimbriatum* is the only other member of the genus found on reptiles in South Australia. It is quite different in appearance from *Ap. hydrosauri* and is found on snakes and goannas.

Although the genus *Aponomma* is thought to be most closely related to *Amblyomma* (Neumann, 1906), their members are readily distinguished. At all stages of the life cycle *Amblyommas* have 'eyes' which *Aponommas* lack (the terminology is that used by Robinson (1926) and Roberts (1970)). Apart from this difference, there are great differences in body size and shape and ornamentation between *Ap. hydrosauri* and the two *Amblyommas*. (Roberts 1970).

3.22 *Amblyomma albolimbatum* Neumann
and *Ambylomma limbatum* Neumann

Neumann (1907) described *Amb. albolimbatum* from a *'Trachysaurus rugosus'* found in Western Australia. He had earlier (1899) classified ticks from 'Lile King' and 'Adelaide' as *Amb. limbatum.* Neither species has attracted such confusion in nomenclature as has *Ap. hydrosauri*, and later works which comment on them include Robinson (1926), Ferguson (1925), Johnston (1932), and Roberts (1953, 1964, 1969, 1970).

The ♀♀ of the two species and of one other, *Amb. moreliae*, L. Koch (1867), which does not appear to live in southern Australia, are said by Roberts (1953) to be difficult to distinguish. It can also be added that their NN and LL have proved well nigh impossible to separate. The ♂♂ present less of a problem (Roberts 1953) and fortunately these are the ones most often encountered in the field. *Amb. albolimbatum* ♂♂, and to a lesser degree, ♀♀, are usually distinguishable from the other species. There are rare specimens, however, which I have found difficult to so categorize. This occurred with specimens (vial No 153) collected near the boundary between *Amb. albolimbatum* and *Amb. limbatum* south of Iron Knob, South Australia. The ♂♂ collected appeared almost intermediate in morphology between *Amb. albolimbatum* and *Amb. limbatum!* It is not known if in fact the two species can or do hybridize. Sharrad and King (1979) report similar difficulties with a few such specimens from Western Australia (see appendix 6).

The most serious difficulty is in contrasting *Amb. limbatum* and *Amb. moreliae*. In fact Neumann (1899) suspected that *Amb. limbatum* might only be a variety of *moreliae*. Roberts (1964) reported that investigations convinced him that the 'two species may be readily distinguished'. Roberts (1970) described the ranges of the species and showed that they overlap. However, it seems that *Amb. moreliae* occurs mainly in eastern Australia, while *Amb. limbatum* is found in all mainland states. I have found no recognizable *Amb. moreliae* in South Australia during this study. However, I have obtained specimens from interstate and am confident that they, or at least the adults, can be distinguished from *Amb. limbatum*. More data are needed, though, on the geographical variation of the ticks, particularly in eastern Australia, before I can share Dr. Roberts' confidence that they are two distinct species.

Sharrad and King (1979) report the occurrence of very small *Amb. limbatum* from the north-west of Western Australia. The ♂♂ of these ticks are smaller than the minimum size listed by Roberts (1970).

I suggest that a thorough examination of *Amb. limbatum* from various parts of its huge range would reveal the existance of several distinct subspecies or species.

There are other *Amblyommas* closely related to the ones above. The first is an undescribed species first recognized by Dr. Smyth from specimens collected in the Flinders Ranges of South Australia (Smyth pers. comm.) I have collected a number of specimens since, and it proves easily recognizable due to its remarkable gold ornamentation. This species appears confined to large skinks, particularly *Egernia stokesii*, in the Flinders Ranges. The second was recently discovered among specimens from Western Australia (Sharrad and King 1979 appendix 6) and had parasitized a blue tongue lizard (*Tiliqua occipitalis*) near Derby.

3.23 The reliability of tick identification

In chapter 2 the method used to construct the distribution maps of the ticks is explained. The nature of the data collected in the field from tick infested reptiles is outlined in appendix 1. Ticks were identified in the laboratory using an Olympus SZ III stereo microscope and the keys of Roberts (1970). These keys require the observation and measurement of various morphological attributes of the ticks.

Some species are readily distinguished, or some stages are, and could even be sorted in the field with the aid of a hand lens. Others are more difficult to tell apart but may be confidently recognized in the laboratory with the aid of a microscope. Sometimes it is virtually impossible to assign specimens, particularly LL, to a particular species although one can recognize their generic affinities. In the following table (1) the above three categories are applied to the 3 ticks and *Amb. moreliae* (see 3.22).

Table 1

The ease with which the ticks can be differentiated from one another. F - readily and reliably distinguished even in the field. L - more difficult to distinguish but this has been done reliably in the laboratory with the aid of a microscope. X - where it has proved impossible to distinguish the ticks. NN = Nymphs. LL = Larvae.

		Aponomma hydrosauri	*Amblyomma albolimbatum*	*Amblyomma limbatum*
Amblyomma Albolimbatum	♀♀	F		
	♂♂	F		
	NN	F		
	LL	L		
Amblyomma limbatum	♀♀	F	L	
	♂♂	F	F	
	NN	F	X	
	LL	L	X	
Amblyomma Moreliae	♀♀	F	L	L
	♂♂	F	F	L
	NN	F	X	X
	LL	L	X	X

The table summarizes information discussed in 3.21 and 3.22 above. It can be seen that *Ap. hydrosauri* is readily distinguished from all the other ticks at all stages. It is also readily sorted from all other *Aponommas* except in the case of LL. It is within the genus *Amblyomma* that the difficulties lie. The three species listed above are only distinguishable as adults, particularly ♂♂. Fortunately *Amb. moreliae* has not been found in South Australia and is therefore unlikely to influence the reliability of the local distribution maps in Chapter 2. The more serious observation to make here is that although ♂♂ of *Amb.limbatum* and *Amb. albolimbatum* are usually quite distinct, some specimens have been found which are intermediate in morphology (see 3.22). This must be taken into account when consideration is made of the boundary between these two ticks.

3.30 Life Cycles of the Ticks.

The three ticks have life histories of a similar type in that they are all three host ticks (fig 8). However there is great scope for both temporal and spatial variation between them at each of the stages of the life cycle. The ticks might, for example, parasitize lizards at different times of the year or exhibit different patterns of seasonal and/or diurnal behaviour. They might seek different microhabitats in which to moult or lay eggs. Such differences in behaviour could mean that the ticks are exposed to quite different environmental conditions.

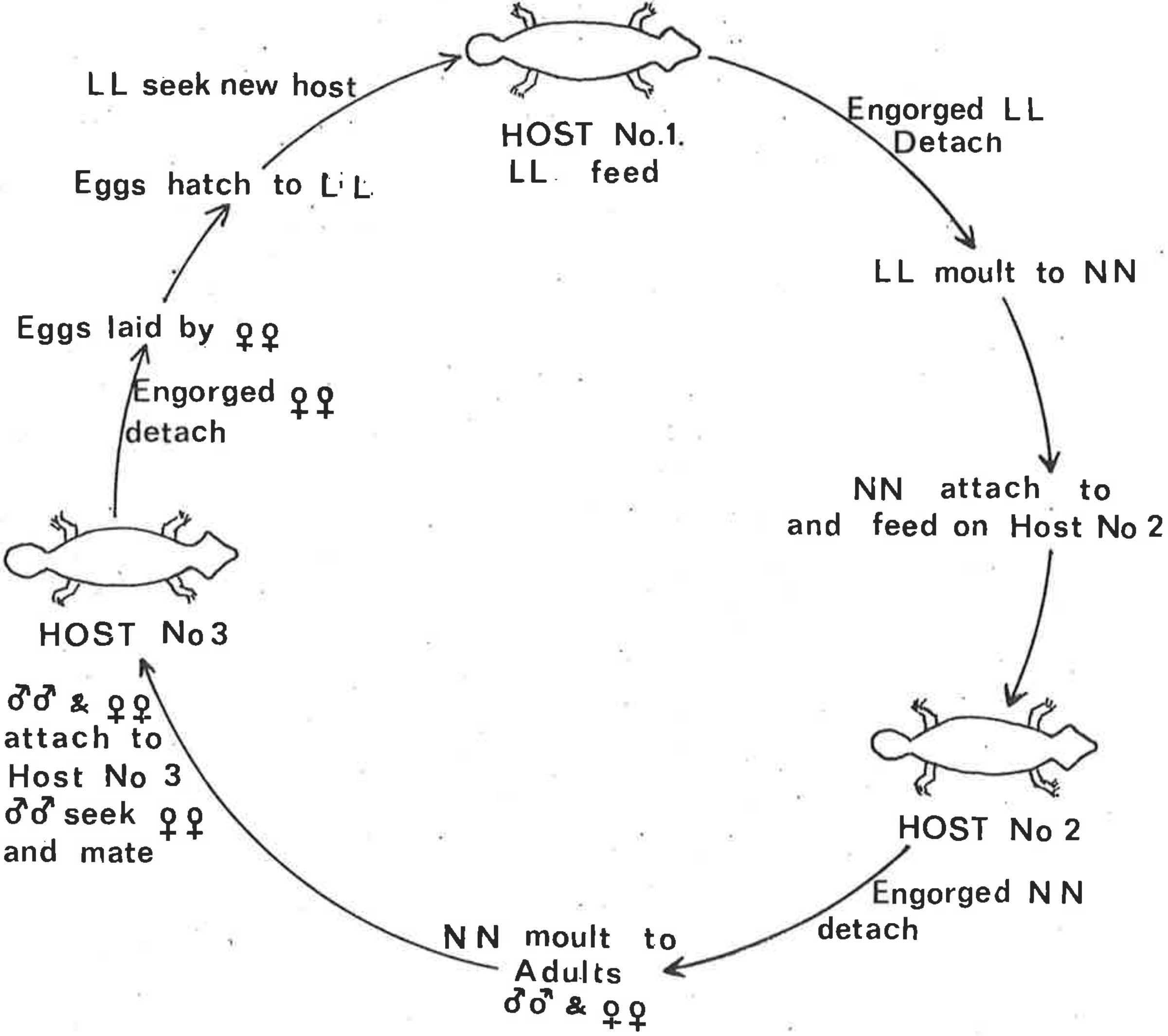
Apart from different behavioural reactions the ticks might also vary in their physiological capacities. Both areas have to be illuminated if the parapatric distributions of the ticks are to be understood. Bartholomew (1958) point out that to find out why a species lives in one area but not another area (nearby in this case) you need information on the physiological capacities of the animal, its behaviour and an understanding of the environment in the areas concerned.

3.31 Seasonal activity of the ticks.

It has been clearly demonstrated in a number of tick species that

Figure 8. A diagram of the life history of a three-host tick.

THE LIFE HISTORY OF A THREE-HOST TICK



LL – Larvae

NN – Nymphs

infestation of hosts is seasonal in nature. Milne (1945 a & b), who followed MacLeod (1939) in studying the sheep tick *Ixodes ricinus* in Scotland and northern England, called the period during which the ticks infected their hosts the season of 'tick activity'. "Activity" is a poor word to use here because ticks may be active without infesting a host. However I follow the lead of other workers and use it below. The sheep tick was shown to exhibit a pulse of "activity" during spring and in some areas during the autumn as well. A number of other three-host ticks have clearly defined seasonal "activity". Some, such as *Dermacentor reticulatus*, exhibit similar seasonal patterns to *I. ricinus* but others, such as *Rhipecephalus appendiculatus* do not (Arthur 1962). Two-host ticks, where LL do not detach before moulting to NN, may also exhibit seasonal variation in "activity". Pomerantzev and Matikashvich (1940) and Grobov (1946) noted that the "activity" of *Hyalomma rufipes* was confined to certain seasons. Arthur (1962) implies that one-host ticks, in which LL, NN and adults remain attached to the one host, do not seem to exhibit seasonal "activity". However Sutherst and Moorhouse (1972) show that the cattle tick, *Boophilus microplus*, is more abundant on cattle during some seasons of the year and in lower numbers at other times. There are some three-host ticks which have <u>no</u> apparent seasonal "activity", notably those that live in their hosts' burrows, e.g. *I. hexagonus* (Arthur 1962).

The seasonal "activity" of ticks may vary within the one species over its geographical range. MacLeod (1939) and Milne (1945 a) showed that in some areas of northern England *I. ricinus* was active in spring and autumn. Edwards and Arthur (1947) and Evans (1951) showed a similar pattern for *I. ricinus* in Wales, but Milne (1945 a) had shown that sheep ticks in parts of Scotland were only "active" during spring. Similar variation with geography has been shown for *Rhipecephalus appendiculatus* in Africa by Lounsbury (1904), Wilson (1953) and Matthyse (1954). Arthur (1962), in a review of the literature on this topic, pointed to comparable variations in *Hyalomma* *detritum* in Russia and *H. excavatum* in the Middle East. Some ticks exhibit the same seasonal pattern over their range but it is displaced in different areas. Gregson (1951) showed that *D. andersoni* in drier parts of British Columbia had a shorter "activity" season than those in wetter parts. Stampa and du Toit (1958) noted that in the Karoo paralysis tick, *I. rubicundus*, seasonal behaviour varied with altitude.

The above observations are consistent with the idea that climate has a great influence on tick development. MacLeod (1934) observed that relative humidity and temperature were the outstanding factors influencing the development of *I. ricinus*. It can be seen that these factors would vary with topography; thus populations of a tick species in different areas with, presumably, similar physiological capabilities may have their "activity" confined to different periods. There has been some debate, however, on just how factors such as temperature control the seasonal "activity" of ticks. MacLeod (1939) postulated that in the sheep tick unfed ticks were available in pasture for periods much longer than the "activity" season but that they were unable to invade a host at temperatures outside a range of 7.2 - 15.5°C: Milne (1945 a) and Lees and Milne (1951) rejected this hypothesis and showed that temperature controlled the development (egglaying, moulting etc.) of the ticks and thus the supply of unfed ticks. Thus in *I. ricinus* ticks are most "active" when the supply of unfed ticks is greatest. In other ticks though, it may well be that unfed ticks are available throughout the year but that they are only able to attach to hosts for a short period. This could be for a reason like that suggested by MacLeod above, or that the hosts' life histories imposed such a restriction.

A particular stage in the life cycle of a tick often has a pattern of "activity" different from other stages. Smith, Cole and Gouck (1946) determined the seasonal "activity" patterns for each of the instars of *D. variabilis* (American dog tick) by trapping rodent hosts and counting the attached ticks. They found that LL were most "active" early in spring, NN were "active" later in summer while adults parasitizing rodents slowly increased in numbers throughout spring and decreased again in summer. In this case the LL had over-wintered and during the warmer spring weather they quickly attached, engorged, detached and moulted to NN which formed the summer pulse. Similar differences between the "activity" of instars has been shown in a number of species including; *Amb. variegatum, H. exavatum, H. detritum, D. parumapertus, D. retuilatus, D. andersoni* and *I. ricinus* (Arthur 1962).

I mentioned above that characteristics of the host might also affect the "activity" of ticks. Some support for this occurring is supplied by investigations of ticks which have many hosts. Milne (1945 b) observed that *I. ricinus* infests different host species at different times. He particularly noticed differences between major infestations on sheep and on wild animals and birds. Randolph (1975) noticed that *I. trianguliceps* had different "activity" patterns on different species of small rodents.

Seasonal "activity" seems, from the above analysis, to be due to the requirements of the tick off the host to develop to the next stage of the life cycle and then to detect and invade a host without, in the meantime, succumbing to harsh environmental conditions. The microhabitat that the tick occupies during this time must represent a compromise between these requirements. For considerable periods, in some regions, climatic conditions completely prevent either further development or finding a host. Ticks in these conditions, when it is too cold or too dry, have been said to hibernate or aestivate (Gregson 1951, Arthur 1962), or to diapause (Razumova 1965, Doube 1975). It is evident that the onset and duration of diapause is under photoperiodic control in a number of ticks (Belozerov 1968, Doube 1975).

3.311 METHODS

A very few methods have been used to delimit the "activity" season of ticks. Often workers have counted numbers of ticks on hosts at regular intervals and calculated the average number per animal, as Milne (1945 a) did with *I. ricinus*. Boardman (1944) describes another method which has often been used since. Ticks which live in pasture sit on the tips of the vegetation when in search of a host and will attach to a cloth or blanket of cotton, flannel or wool if it is drawn past them. This technique, called 'flagging', was used by Milne and many later workers on other ticks and allows calculation of tick numbers/flag/man/hour (see Drozdova and Sapegina 1965). Another method arose from the discovery that many ticks will, when active, be attracted to higher than normal concentrations of CO_2, a way in which they detect potential host, particularly mammals. Garcia 1962, 1965, Miles 1968, Nosek and Kozuch (1969), Hair Hock, Barker and Semtner (1972) and Wilson, Kinger, Sauer and Hair (1972) describe how such ticks may be trapped and counted. If ticks move about on the ground they may also be caught on prepared sticky surfaces (Lees 1953).

In this investigation flagging proved useless. The ticks do not live in grassy pastures or climb to the grass tips to find a host. Off the host they live under bushes, bags or sheets of iron where the hosts take refuge. A dragged cloth would not pass near the ticks and they would not cling to it. Similarly the CO_2 trap technique does not work. The ticks are not stimulated by CO_2 gradients (see later). Information on seasonal "activity" was gained by catching reptiles whenever possible throughout the study and counting the numbers of each instar of each species attached - see appendix 1.

The examination above of the other studies on seasonal "activity" of ticks illuminates a number of possible pitfalls in using this technique. The seasonal activity of ticks might vary in timing on different hosts.

This problem is largely overcome as the vast bulk of tick infested reptiles caught were sleepy lizards *(Tr. rugosus)*. It was also noted above that the seasonal "activity" of ticks might vary over their range. Study of the data indicates that for *Amb. albolimbatum* and *Amb. limbatum* records are from quite small parts of their ranges and do not represent populations from widely different climatic regions. The bulk of the ticks collected is of *Ap. hydrosauri* and was taken from most parts of its range in South Australia - from Mt Mary which averages 225mm of rain per annum to areas of the Adelaide Hills with up to 1000mm per year.

There is a major difficulty in using data from captured reptiles to compile data on ticks' seasonal "activity". The reptilian hosts are difficult to capture during some seasons (see Chapter 4). During winter, lizards (which are ectotherms) are unlikely to move about in southern South Australia and remain in very cryptic refuges. Similarly during the hot dry months of late summer lizards like *Tr. rugosus* are seldom seen. This means that estimates of tick "activity" during those times are based on much smaller samples than in spring. In some cases below I have had to present combined data from two or more months because of this.

There are three ways in which the raw data from field collections can be presented to give an indication of seasonal "activity". Many workers in this field (see Arthur 1962) simply divide the number of ticks collected in a period of time by the number of hosts caught in that time to give the average number of ticks (LL, NN, ♂♂ or ♀♀) per host. Additional information can be gained by calculating the average number of ticks of a particular stage on hosts parasitized by that stage. Alternatively one can see if there is a seasonal change in the proportion of hosts infested with a particular stage out of the total number of hosts examined.

3.312 Aponomma hydrosauri

Figures 9, 10 and 11 present data collected on the seasonal "activity" of the ticks. To avoid problems discussed above, only records of numbers of ticks on *Tr. rugosus* have been used. Very low numbers of these lizards were found during Autumn and Winter months. Also, examination of the data revealed consistency within some seasons. So results for the months March and April have been pooled as have the numbers for May, June and July.

Figure 9 shows the overall average number of ticks per host obtained by dividing the total number of ticks of a particular stage by the total number of lizards recorded for that period. Figure 10 shows the proportion of the total number of hosts recorded during a period of the year that were found to be infested with a particular stage. The average numbers of ticks of a particular stage on lizards infested with that stage are shown in Figure 11.

Examination of these figures supports the comment of Bull (1969) that ticks are found on lizards throughout the year. However there is a distinct seasonal change in abundance on hosts. LL and NN are most abundant in spring and their numbers drop quickly in summer. It can be seen that the numbers of LL and NN on sleepy lizards increase sharply in August and peak in September - October. The numbers then drop sharply again during summer. In March - April there appears to be a slight increase in the numbers of immature stages on lizards (see figure 11) reminiscent of autumn pulses in tick "activity" discussed above in 3.31. However the number of hosts examined was very low, only 24, and the average numbers of ticks per host do not, on analysis, vary significantly from the other figures for summer and winter.

The spring figures for LL are underestimates of abundance on hosts. Some lizards collected during spring had very large numbers of LL attached and it was often too time consuming to count them all. These cases were

Figure 9. The seasonal activity of *Ap. hydrosauri*, showing the average number of ticks per host recorded per month. Due to low numbers of hosts in some months, data have been pooled for March and April and for May, June and July. The numbers of hosts on which ticks were counted are recorded at the bottom of the figure for each time period.

All the hosts were sleepy lizards, *Tr. rugosus*.

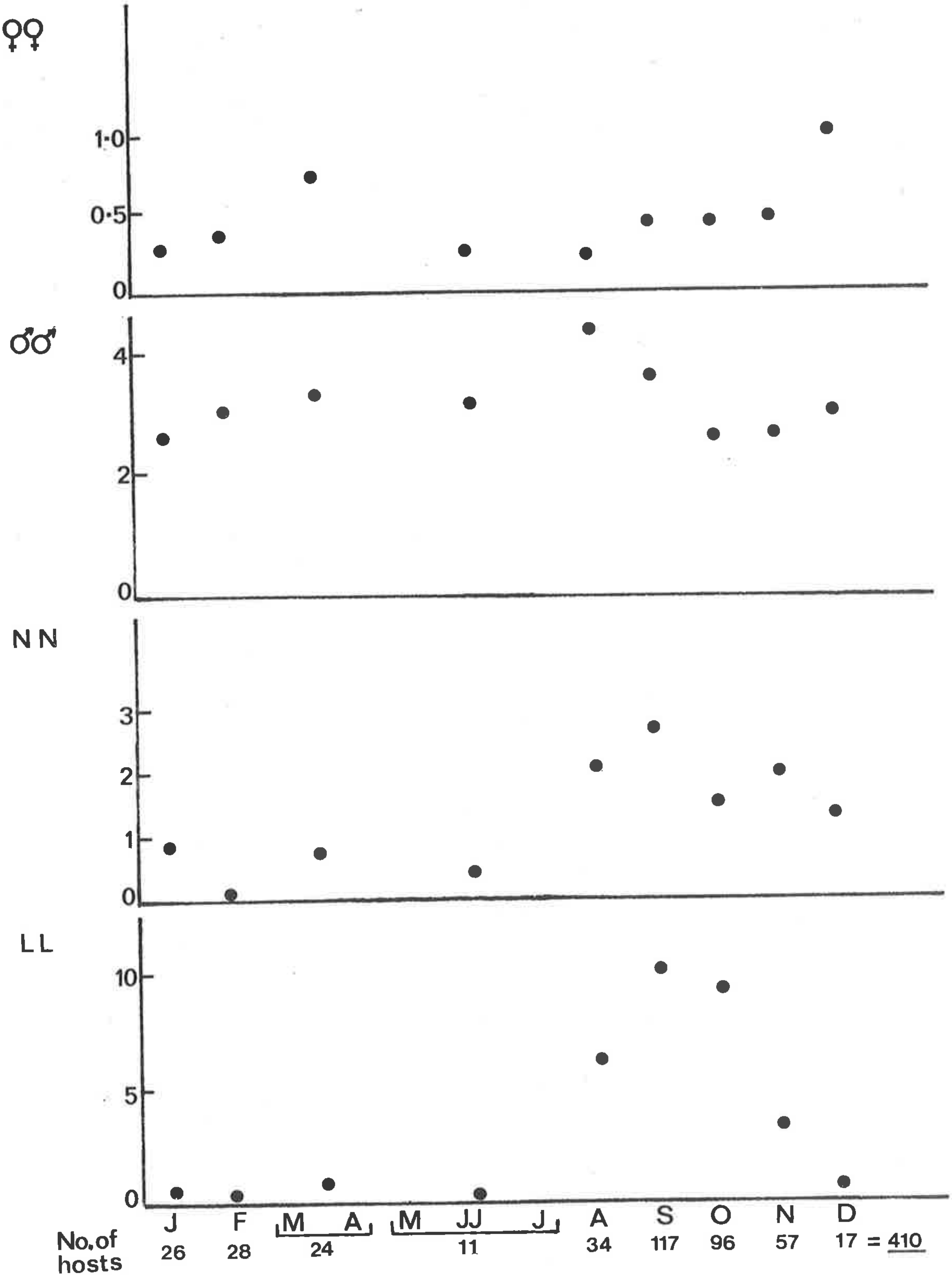

♀♀
1·0
0·5
0
♂♂
4
2
0
N N
3
2
1
0
L L
10
5
0
J
F
M
A
M
JJ
J
A
S
O
N
D
No. of hosts
26
28
24
11
34
117
96
57
17 = 410

Figure 10. The seasonal activity of *Ap. hydrosauri*, showing the proportion of tick infested hosts *(Tr. rugosus)* infested with a particular stage of the tick's lifecycle. Data are pooled for March and April and for May, June and July. The numbers of hosts on which ticks were counted are shown at the bottom of the figure for each time period.

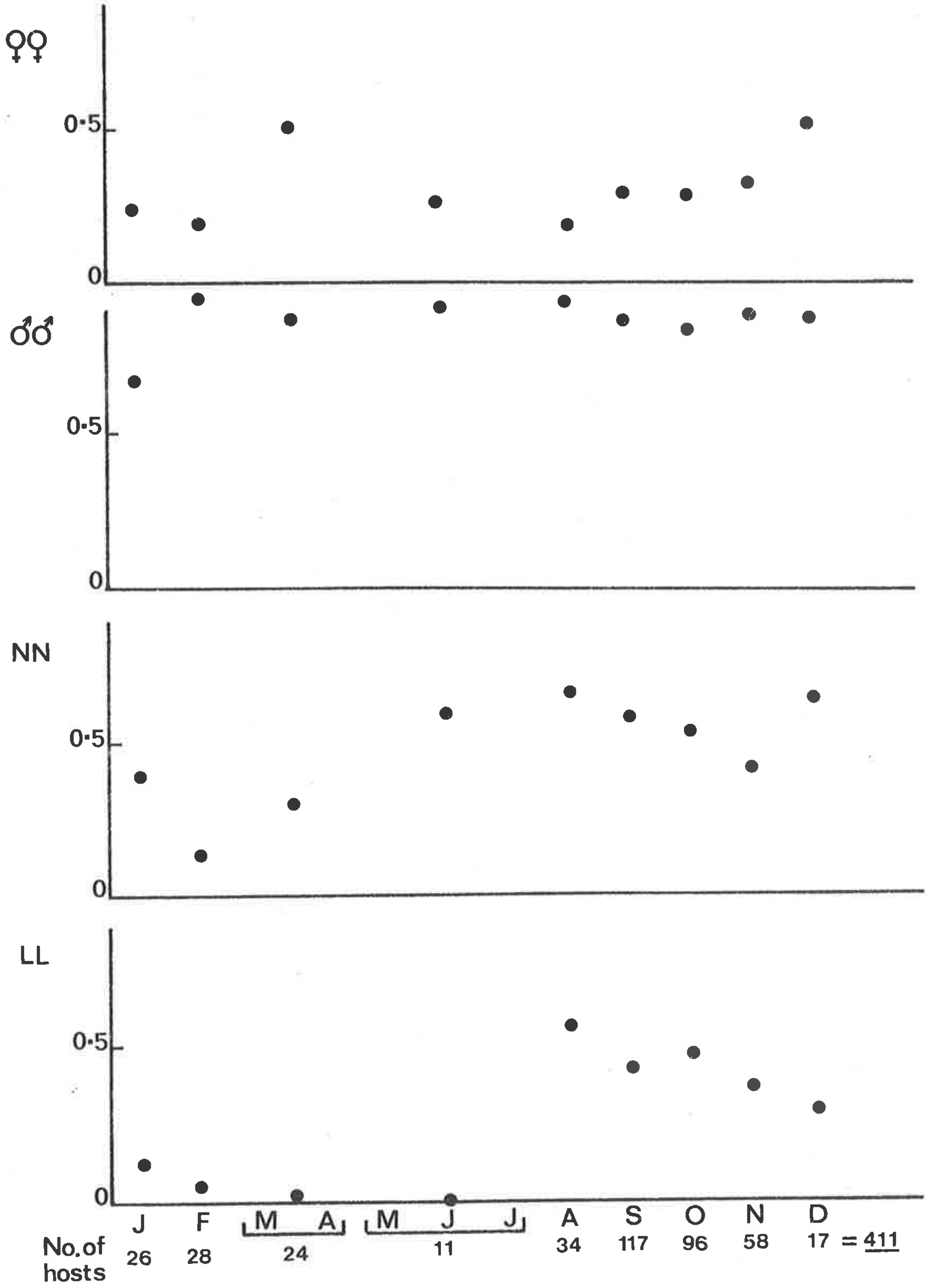
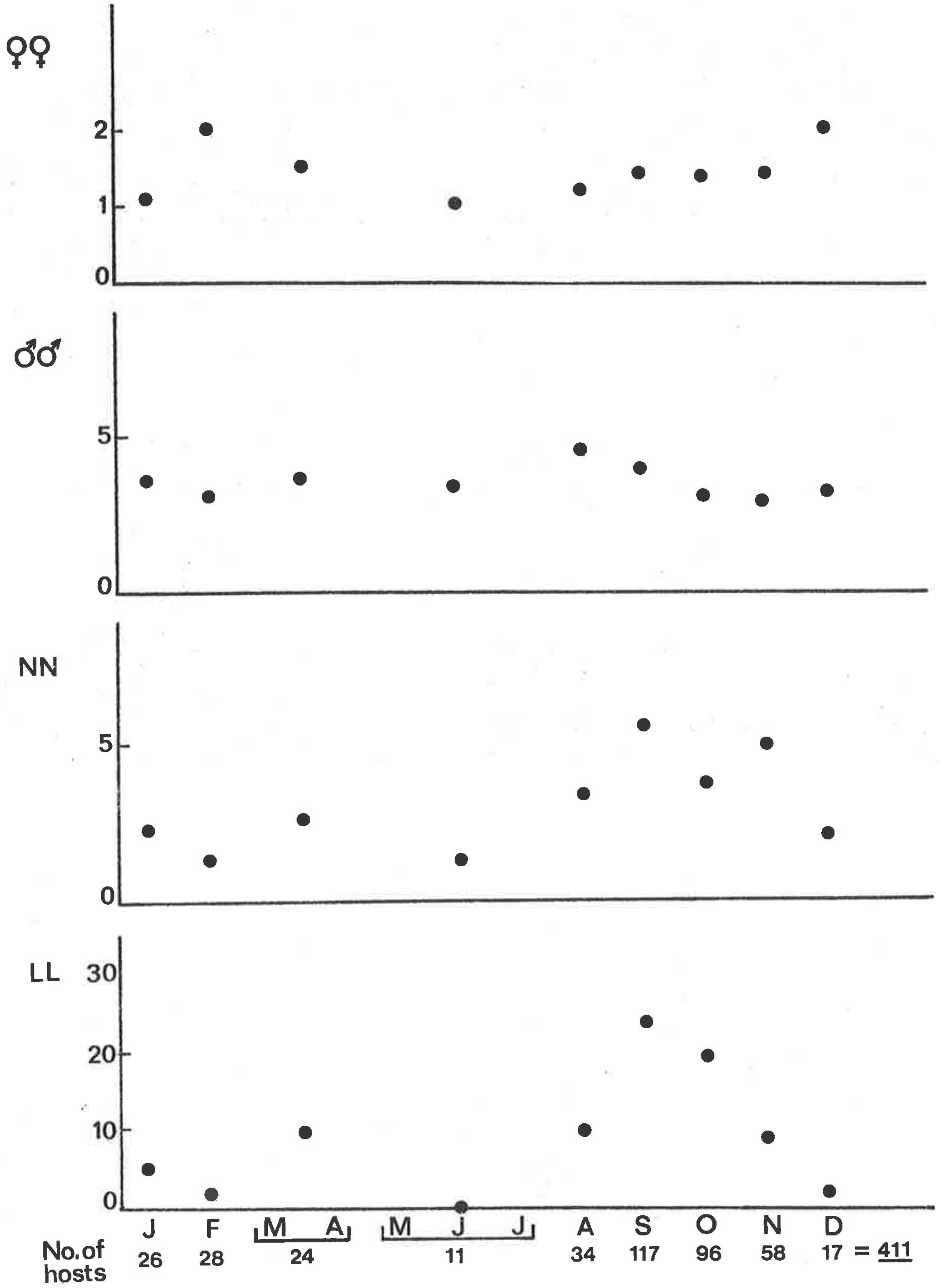

♀♀
0·5
0
♂♂
0·5
0
NN
0·5
0
LL
0·5
0
J
F
M
A
M
J
J
A
S
O
N
D
No. of hosts
26
28
24
11
34
117
96
58
17
= 411

Figure 11. The seasonal activity of *Ap. hydrosauri*, showing the average number of ticks of each stage parasitizing hosts (*Tr. rugosus*) that were infested with that stage.

Data are pooled for March and April, and for May, June and July. The numbers of hosts on which ticks were counted are shown at the bottom of the figure for each time period.



♀♀
2
1
0
♂♂
5
0
NN
5
0
LL
30
20
10
0
J
F
M A
M J J
A
S
O
N
D
No. of hosts
26
28
24
11
34
117
96
58
17 = 411

recorded as have 'many LL, greater than 100'; in fact some lizards had over 400 ticks attached to them. Only those records where accurate counts have been made are included. Thus the spring peaks in figures 9 and 11 should be higher.

It is apparent that the spring pulse in larval "activity" results from both an increase in the proportion of lizards infested by ticks (figure 10) and an increase in the number of LL infesting individual hosts. The same is probably true of NN, but the proportion of hosts infested with NN does not drop as dramatically in summer and winter as in the case of the LL. Also the spring pulse of "activity" seems relatively prolonged in NN; figure 11 shows high numbers per host continuing into November.

The adult ticks do not exhibit the same pattern of seasonal abundance on hosts as the immature stages. ♀ ticks may be found on hosts throughout the year. Numbers per host are as low during early spring as they are at any time of the year. The indication is that ♀♀ are less abundant in winter and their numbers pick up from mid spring through summer. ♂ *Ap. hydrosauri* are to be found attached to sleepy lizards throughout the year. There is a suggestion of a spring peak in "activity" in figure 9 but the averages for each month do not depart significantly from each other.

The seasonal "activity" pattern of the ticks may be explained by considering the effects of seasonal changes in temperature and humidity on the development of ticks off the host and on the ability of ticks to imbibe blood from hosts and detach. The hosts of *Ap. hydrosauri* are poikilothermic thus attached ticks experience quite different conditions as ambient temperatures change from season to season. So do detached ticks for they are also poikilothermic. Seasonal changes in humidity,however,would probably most greatly influence ticks off the host, as attached ticks have tapped a large supply of water.

During winter in southern South Australia temperatures decrease and humidity levels rise; most rain falls during winter (Aust. Bur. Met. 1975).

The average daily temperatures here do not fall below freezing point as they do during the winters experienced by some of the tick species mentioned in 3.31 above. The moderately cold conditions would certainly slow development of ticks off the host and also slow the feeding of attached ticks. Thus there would be few ticks moulted and ready to invade hosts, and few engorged ticks detaching. When temperatures increase during August both groups of ticks, attached and detached, would increase their activity. ♀♀ attached would quickly engorge, detach and lay eggs which would quickly hatch in the higher temperature regime. Detached, engorged ♀♀ which had been prevented, by low winter temperatures, from laying their eggs would do so. Unhatched eggs would begin to hatch rapidly. Thus there would be a spring pulse of LL.

LL are the most numerous stage of ticks. A ♀ *Ap. hydrosauri* may lay 3,000 eggs - see later. So the spring pulse of "activity" is marked. The LL can engorge, detach and moult within a month. Thus newly moulted NN are supplied later in spring. This probably explains why the "activity" peak of the NN extends further into November than the LL. Also the numbers of NN are lower than LL which probably reflects a high mortality rate after LL detach. Other NN are supplied early in spring as engorged LL might have over-wintered, prevented by low temperatures from moulting.

Another factor probably contributes to the high numbers of ticks attaching in spring. The hosts have been in refuges during winter (see Chapter 4 for details). During spring their activity is also at its greatest. The lizards would move about within their home ranges during the day and at night creep into refuges under bushes or logs. In Chapter 4 it is shown that lizards have a number of such refuges in their home range which they may use. During spring they are most likely to spend time in many of them whereas during winter most refuges would be empty of lizards. Thus ticks which stay in these refuges (see later) would have a much greater chance of encountering a host during spring.

During the summer the activity of lizards decreases (see Chapter 4) and it is possible that ticks have a lower chance of finding them. This could partly explain the decline in the proportion of hosts parasitized by ticks during summer.

♂ ticks are shown later in this chapter to remain unengorged on lizards for long periods of time perhaps a year or more seeking the opportunity to mate with ♀♀. This long stay tends to mask seasonal changes in numbers of new ticks attaching. It should also be remembered that adult ticks are relatively small in number compared with LL. ♀♀ are least often encountered in the field for this reason and because they do not stay very long on hosts, unlike the ♂♂.

Studies on a population of *Ap. hydrosauri* at Tickera (upper Yorke Peninsula) by Dr M. Bull and others have largely substantiated the pattern of infestation reported above (Bull pers. comm.). Weekly trips to this study area revealed a very marked pulse of larval infestation of sleepy lizards (*Tr. rugosus*) in the spring. This was followed by marked peaks of infestation of NN and adult ticks. These data show that, for the Tickera population, the seasonal pattern of infestation is more pronounced than my data suggest.

3.313 Amblyomma limbatum

Data on the seasonal "activity" of *Amb. limbatum* are presented in figures 12, 13 and 14. These were prepared and are presented in the same manner as that in 3.312 for *Ap. hydrosauri*. The records come from the Mt Mary boundary area and from areas just north of it. They may not be representative of populations in other parts of the State.

Figure 12. The seasonal of *Amb. limbatum*, showing the average number of ticks per host (*Tr. rugosus*) recorded over periods of two months. The numbers of hosts on which ticks were counted are shown at the bottom of the figure for each time period.

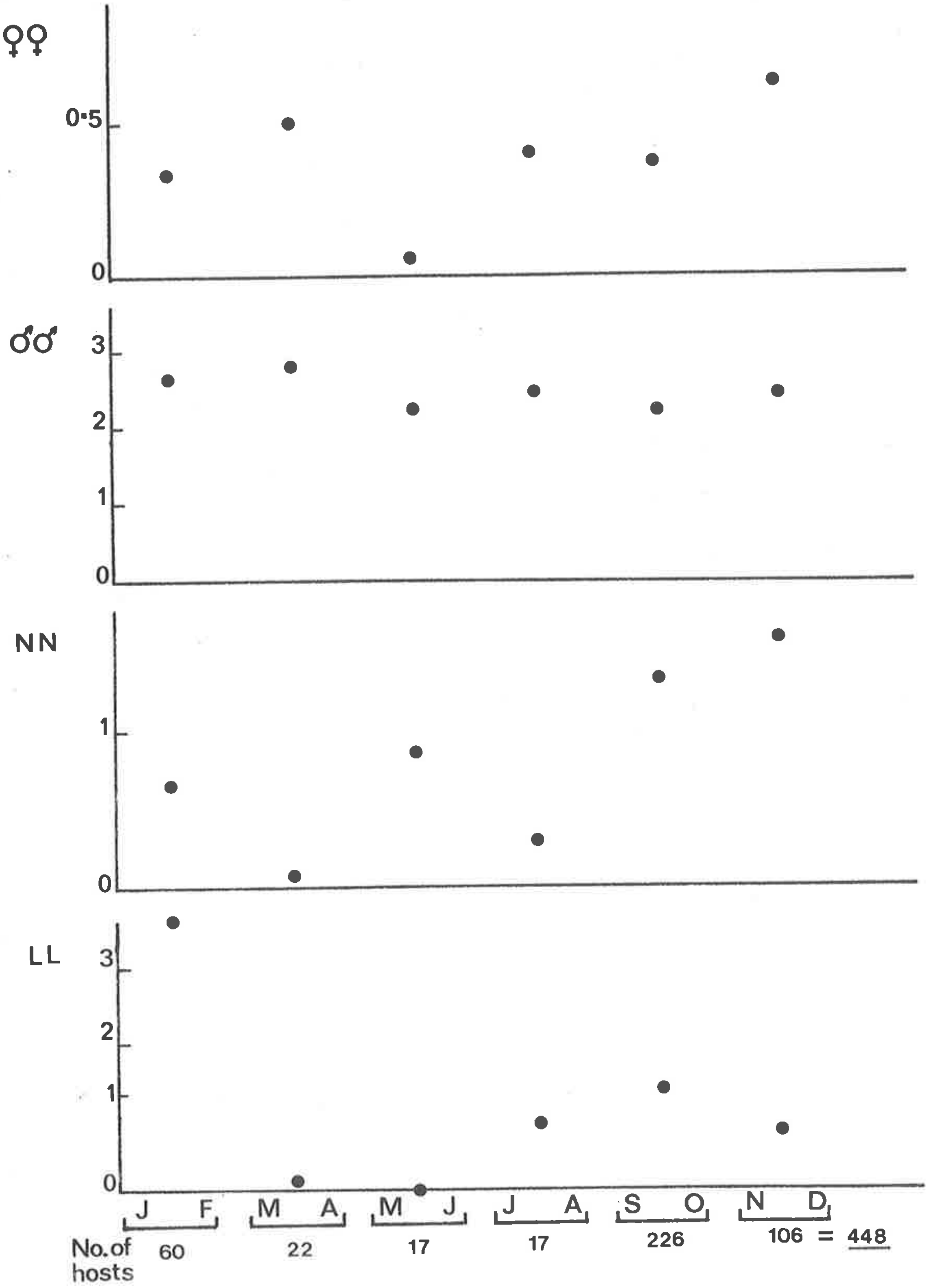

♀♀
0·5
0
♂♂
3
2
1
0
NN
1
0
LL
3
2
1
0
J F
M A
M J
J A
S O
N D
No. of hosts
60
22
17
17
226
106 = 448

Figure 13. The seasonal activity of *Amb. limbatum*, showing the proportion of tick infested hosts *(Tr. rugosus)* infested with a particular stage of the tick's life cycle. Data are presented for time periods of two months duration long.

The numbers of hosts on which ticks were counted are shown at the bottom of the figure for each time period.

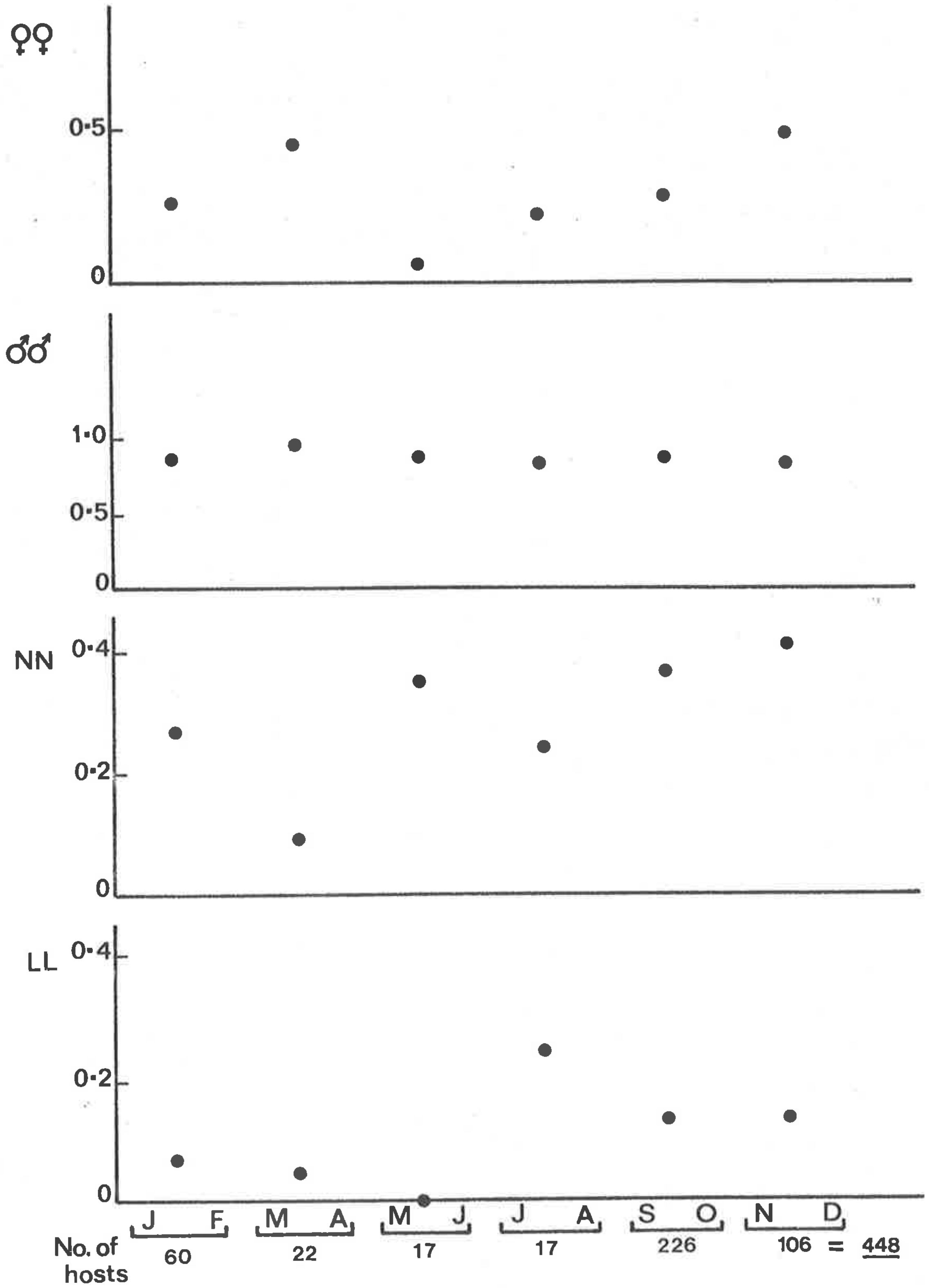
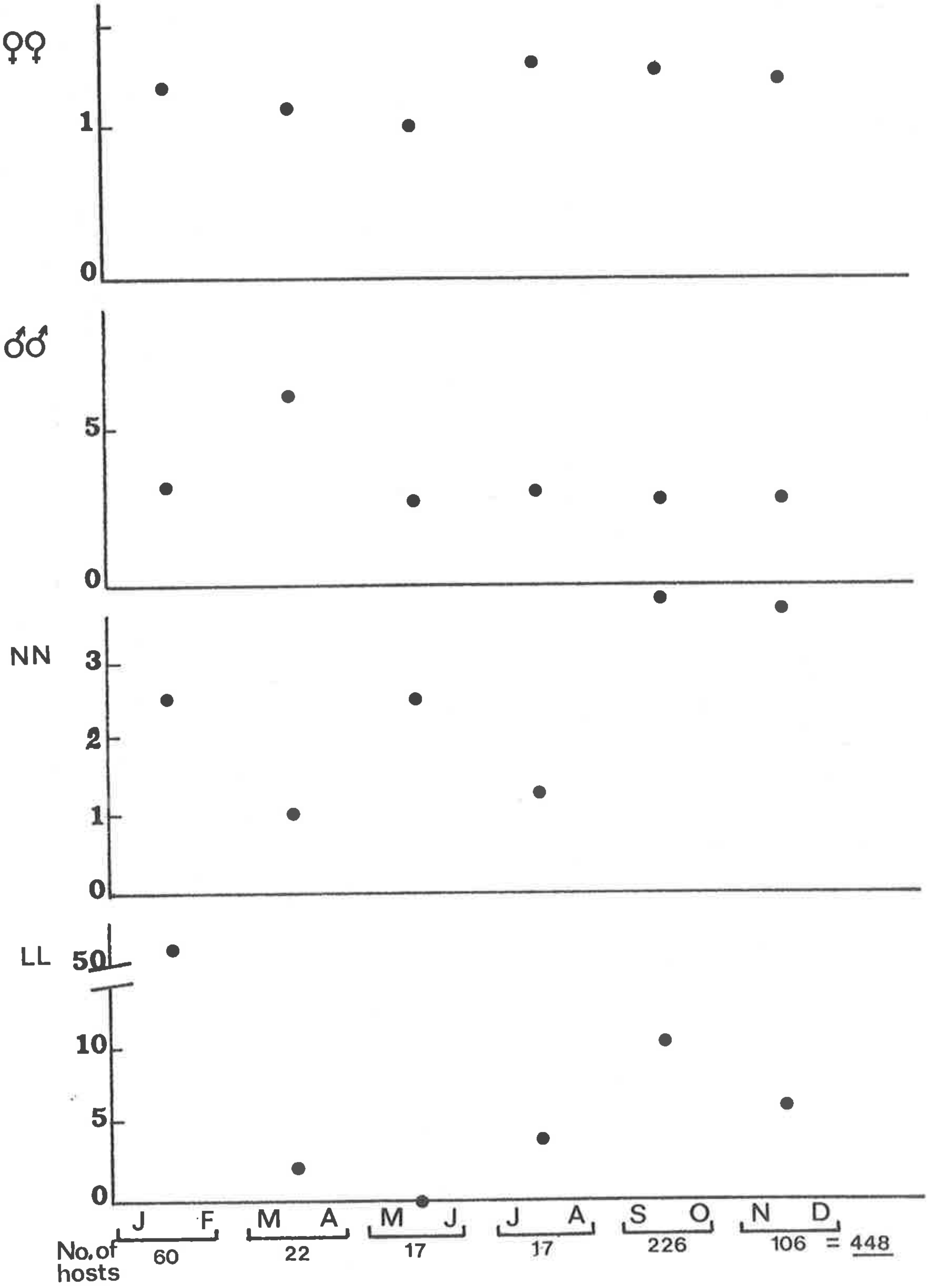

♀♀
0·5
0
♂♂
1·0
0·5
0
NN
0·4
0·2
0
LL
0·4
0·2
0
J F
M A
M J
J A
S O
N D
No. of hosts
60
22
17
17
226
106 = 448

Figure 14. The seasonal activity of *Amb. limbatum*, showing the average number of ticks of each stage parasitizing hosts *(Tr. rugosus)* that were infested with that stage.

Data are presented for periods of two months duration. The numbers of hosts on which ticks were counted are shown at the bottom of the figure for each time period.


♀♀
1
0
♂♂
5
0
NN
3
2
1
0
LL
50
10
5
0
J F
M A
M J
J A
S O
N D
No. of hosts
60
22
17
17
226
106
= 448

There does not seem to be as marked a pattern of seasonal "activity" in this tick as there is in *Ap. hydrosauri*. Part of the reason for this may lie in the difference in climate between areas south of the Mt Mary - Morgan area, where *Ap. hydrosauri* lives, and north of Mt Mary where *Amb. limbatum* is found. As one travels inland, north from Mt Mary, rainfall becomes less frequent and temperatures increase (see figures 3 and 7). This could mean that the development of *Amb. limbatum* is less influenced by low winter temperatures than is the case for *Ap. hydrosauri* to the south. The seasonal activity patterns of hosts might also change, with climate, from the type described in 3.312 above.

There is a suggestion in the figures that LL are more abundant and infest more lizards during spring and summer. The NN seem also to be more abundant in spring and summer. Adult *Amb. limbatum* seem to behave much like *Ap. hydrosauri* adults.

3.314 Amblyomma albolimbatum

There are insufficient records of these ticks to attempt the construction of graphs like those presented for the other species. The nearest *Amb. albolimbatum* population to Adelaide is 500km away in the Cleve area of Eyre Peninsula. Thus few collecting trips could be made and those that were conducted were timed so that lizards were likely to be active. Records are therefore only available for the spring months September, October and November. The results for the three months are pooled and presented in the table below.

Table 2

Spring abundance of *Amb. albolimbatum* in the Cleve area. Records of the numbers of these ticks infesting sleepy lizards *Tr. rugosus* during the months of September, October and November are used to show;

In column 1. The average number of ticks per host collected.

NN = Nymphs

LL = Larvae

In column 2. The proportion of the number of hosts collected that were infested with that stage.

In column 3. The average number of ticks of each stage parasitizing hosts which are infested with that stage.

The number of lizards recorded = 56.

	1.	2.	3.
♀♀	1.17	0.54	2.3
♂♂	4.25	0.96	4.41
NN	1.84	0.32	7.23
LL	7.69	0.29	29.89

The averages shown in table 2 are of the same order as the spring values for *Ap. hydrosauri* and *Amb. limbatum*. The relative abundance of the stages are similar and so are the proportions of hosts infested by the various stages. The numbers are a little higher than in the other species but it is not known if this is a significant difference. More data need to be collected.

One would expect *Amb. Albolimbatum* to have a similar pattern of seasonal activity to *Amb. limbatum*. The two ticks are very similar, mophologically, although the latter is smaller. If, as suggested in 3.313 above, the differences in seasonal activity between *Ap. hydrosauri* and *Amb. limbatum* are largely due to climatic differences which influence tick development and lizard activity, then *Amb. albolimbatum* might well have an intermediate type of pattern. This would mean that *Amb. albolimbatum* would have a more pronounced spring pulse of activity than *Amb. limbatum*. However more data need to be obtained to accurately test this hypothesis.

3.32 Frequency distributions of ticks on hosts.

Bull (1969) suggested that LL of *Ap. hydrosauri* tend to remain in aggregations after hatching, and thus lizards are likely to be infested either heavily or not at all. In this section the patterns of infestation are examined for each instar of *Ap. hydrosauri* and *Amb. limbatum* and this hypothesis is tested. The records used in 3.31 above are used for this purpose.

Figures 15 and 16 show the frequency with which particular numbers of *Ap. hydrosauri* were found on sleepy lizards *(Tr. rugosus)*. Figure 15 shows similar information for the immature stages. The records are from thoughout the year. It is evident that the ♂♂ are most often found on lizards while other stages are much less often to be found.

A similar pattern is shown in Figures 17 and 18 for *Amb. limbatum*. There are few data on *Amb. albolimbatum*, but those collected suggest, that the pattern is similar to that of the other ticks (see 3.314).

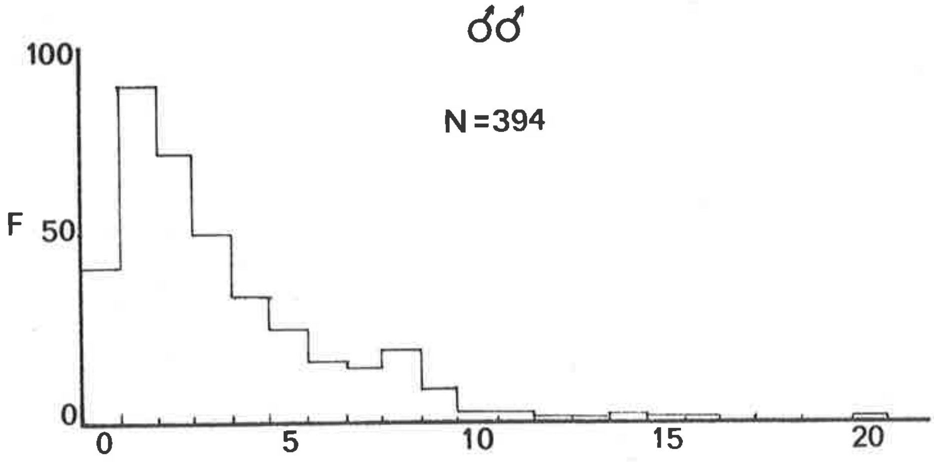
The figures suggest for both species that there may be some clumping of LL and perhaps NN on lizards, as Bull (1969) suggested. This can be tested. If ticks invaded hosts in a random fashion, i.e., hosts had equal chances of being parasitized, and the mean number of ticks per host was low, one would expect the observed frequencies of ticks per host to fit a Poisson distribution (Sokal and Rohlf 1969). The distribution of frequencies would depart from the Poisson distribution if clumping occurred.

In the tables below the observed frequencies of numbers of ticks on lizards are compared with Poisson distributions calculated from the sample means. See Sokal and Rohlf (1969, pp 85-95).

Figure 15. Frequency distributions of the number of adult *Ap. hydrosauri* (♂♂ and ♀♀) found on sleepy lizards, *Tr. rugosus*.

Lizards were searched for ticks throughout the year and the results pooled.

N = the number of records used to compile the frequency distribution.


♂♂
N =394
F
100
50
0
0
5
10
15
20

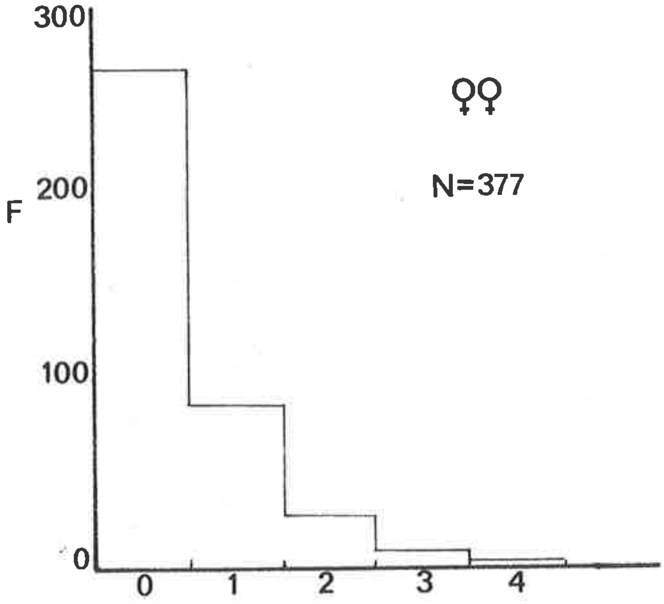
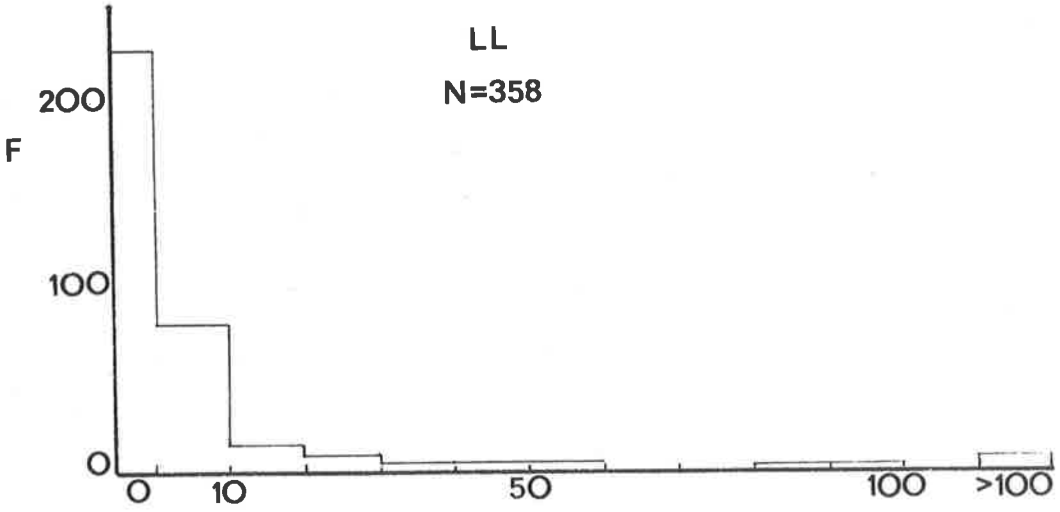

♀♀
N=377
F
300
200
100
0
0
1
2
3
4

Figure 16. Frequency distributions of the number of each immature stage of *Ap. hydrosauri* (NN and LL) found on sleepy lizards, *Tr. rugosus*.

N = the number of records used to compile the frequency distribution.


LL
N=358
F
200
100
0
0
10
50
100
>100

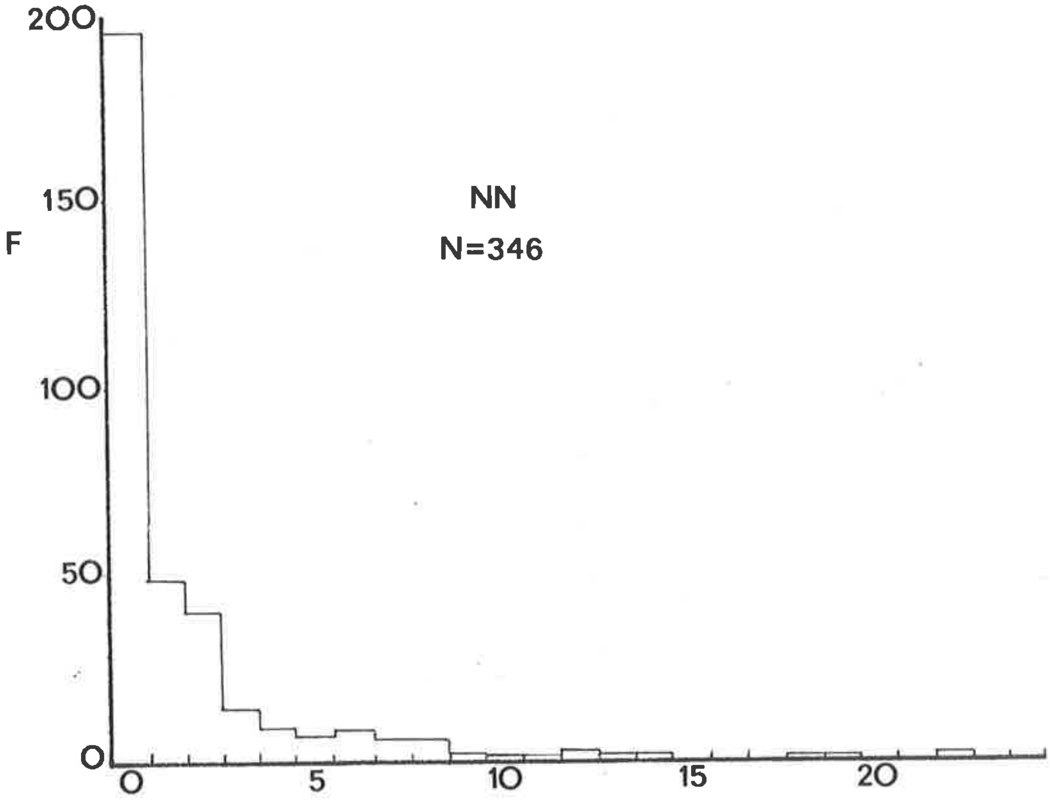
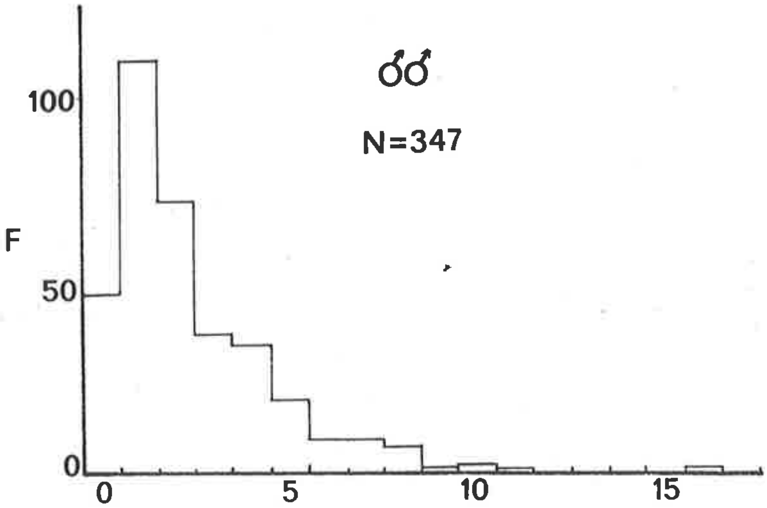

NN
N=346
F
200
150
100
50
0
0
5
10
15
20

Figure 17. Frequency distribution of the number of adult *Amb. limbatum* (♂♂ and ♀♀) found on sleepy lizards, *Tr. rugosus*.

N = the number of records used to compile the frequency distribution.


♂♂
N=347
F
100
50
0
0
5
10
15

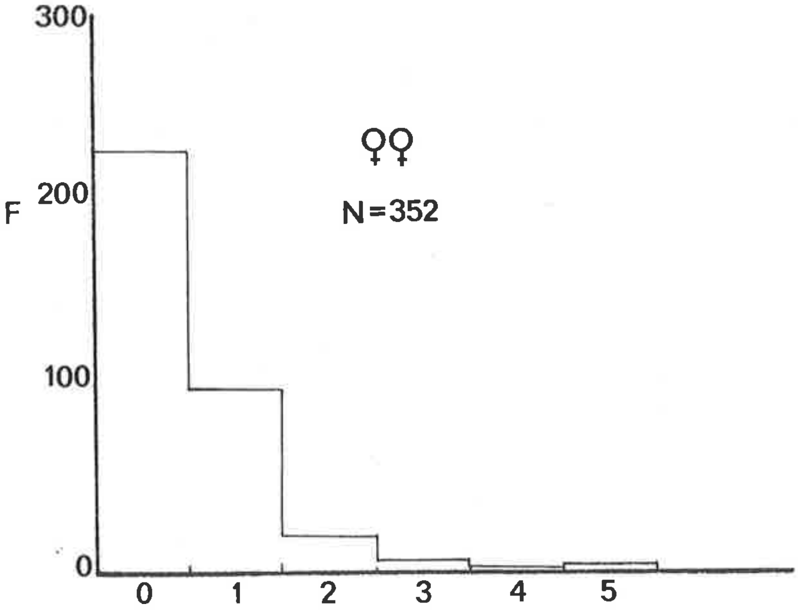
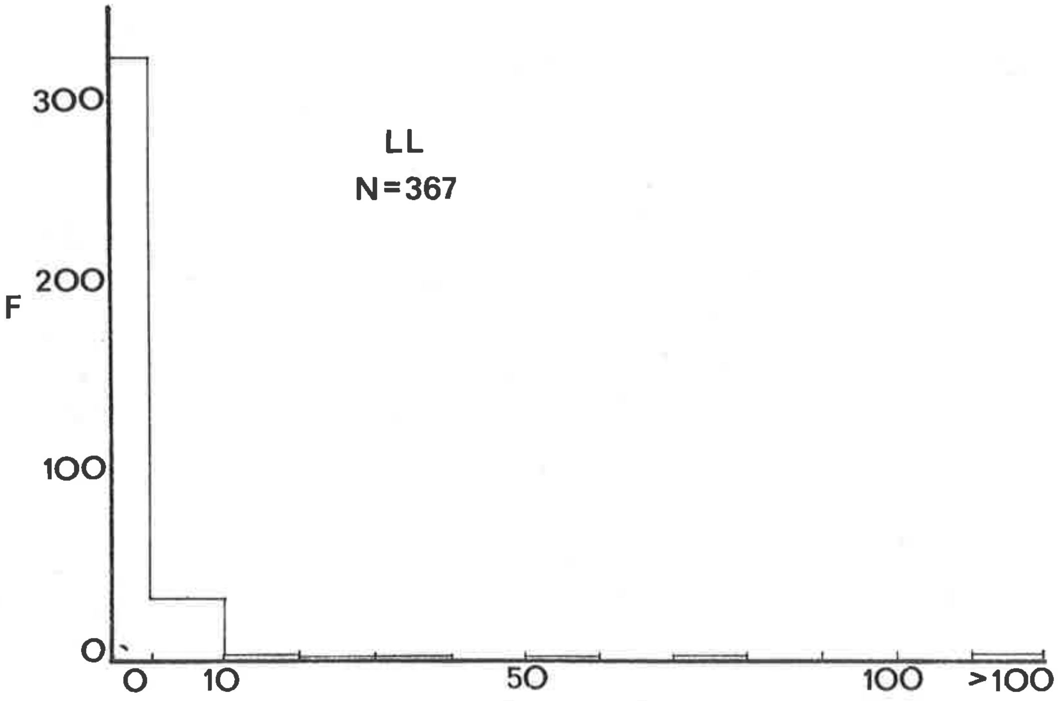

300
♀♀
N=352
F
200
100
0
0
1
2
3
4
5

Figure 18. Frequency distributions of the numbers of each immature stage of *Amb. limbatam* (NN and LL) found on sleepy lizards, *Tr. rugosus*.

N = the number of records to compile the frequency distribution.


300
200
F
100
0
LL
N=367
0
10
50
100
>100

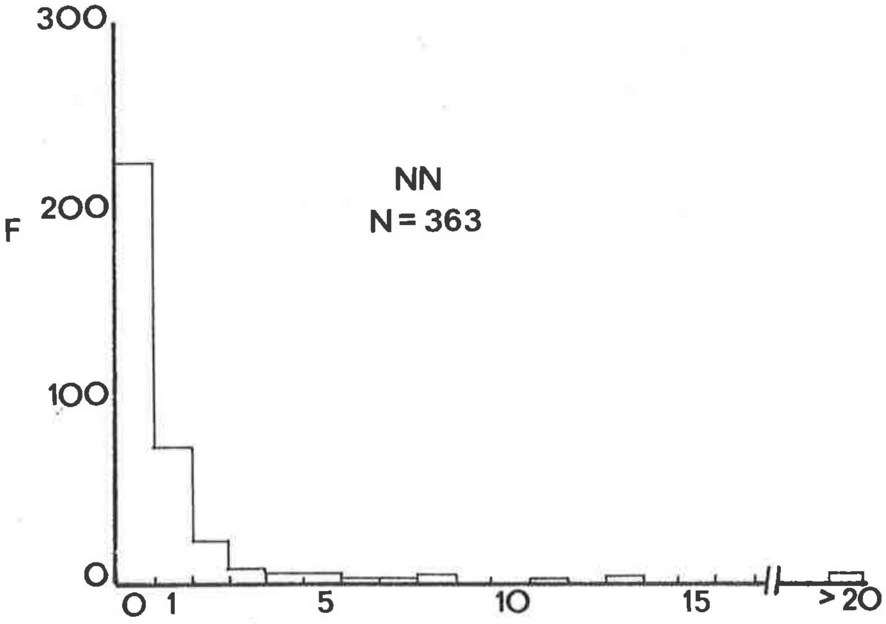

300
200
F
100
0
NN
N = 363
0
1
5
10
15
> 20

Table 3.

Ap. hydrosauri ♀♀ infesting 394 sleepy lizards *Tr. rugosus*

No. of ♀♀	Observed O	Poisson expected frequencies E	Deviation from expectation O-E
0	268	251.5	+
1	87	112.9	-
2	29)	)	
3	8) 39	) 29.6	+
4	2)	)	
Total	394	394.0	

$\bar{y}$ = 9.449 s^2 = 0.578 CD = 1.288

χ^2_1 = 10.0 (χ^2 .005(1) = 7.89

The coefficient of dispersion C D = $\frac{s^2}{\bar{y}}$ $\left(\frac{\text{sample variance}}{\text{Sample mean}} \right)$

In a Poisson distribution the variance is equal to the mean. Thus if C D ≃ 1 the agreement with a Poisson distribution is good. However a Chi-square test for goodness of fit of observed to expected frequencies was also performed (Sokal and Rohlf, 1969, p. 259). For this reason some of the frequencies have been lumped as no expected frequency should be less than 5 for the Chi-square test. As there are 3 classes of frequencies the degrees of freedom are maximally 3-1 = 2. However as the Poisson mean was estimated from the sample mean another degree of freedom must be removed, leaving 1.

It can be seen that, although the coefficient of dispersion is near 1 (1.288), the Chi-square tests leads to rejection of the null hypothesis that the observed frequencies of ♀♀ *Ap. hydrosauri* on *Tr. rugosus* follow a Poisson distribution ($p<.005$). Thus it seems that ♀♀ of this tick are not randomly distributed among lizards in nature, but are clumped. Similar analyses are performed below for other stages of *Ap. hydrosauri*.

Table 4

Ap. hydrosauri ♂♂ infesting 377 sleepy lizards, *Tr. rugosus.*

No. of ♂♂	Observed frequencies O		Poisson expected frequencies E		Deviation from expectation O-E
0	41		15.9		+
1	90		50.4		+
2	72		79.7		-
3	50		84.1		-
4	33		66.5		-
5	24		42.1		-
6	16		22.2		-
7	14		10.0		+
8	18				
9	8	37		6.1	+
10	2				
11	2				
12	1				
13	1				
14	2				
15	1				
16	1				
21	1				
Total	377		377.0		

$\bar{y}$ = 3.165 s^2 = 8.796 C D = 2.779

χ^2_1 = 269.8 (χ^2 .005$_{(7)}$ = 20.28)

It can be seen that clumping occurs in ♂♂ *Ap. hydrosauri.*

Table 5

Ap. hydrosauri NN infesting 346 sleepy lizards, *Tr. rugosus.*

No. of NN	Observed frequencies O		Poisson expected frequencies E		Deviation from expectation O-E
0	195		66.4		+
1	48		109.6		-
2	40		90.5		-
3	14		49.7		-
4	9		20.5		-
5	7	40		9.3	+
6	8				
7	6				
8	5				
9	2				
10	1				
11	2				
12	3				
13	2				
14	1				
18	1				
28	2				
Total	346		346.0		

$\bar{y} = 1.65$ $s^2 = 11.504$ C D = 6.972

$\chi^2_6 = 425.2$ ($\chi^2 .005(6) = 18.55$)

Similarly, observed frequencies of NN of *Ap. hydrosauri* do not fit a Poisson distribution.

Table 6

Ap. hydrosauri LL infesting 358 sleepy lizards, *Tr. rugosus*.

No. of LL	Observed frequencies O		Poisson expected frequencies E	Deviation from expectation. O-E
0	228		0.3	+
1-10	80		319.2	-
11-20	17		38.4	-
21-30	10	33	0.1	+
31-40	5			
41-50	5			
51-60	7			
81-90	1			
91-100	1			
111-120	1			
161-170	2			
231-240	1			
Total	358		358.0	

$\bar{y}$ = 7.123 s^2 = 476.886 C D = 66.950

χ^2 - huge P - very low

Of all the stages of *Ap. hydrosauri*, the LL seem most strongly clumped. This would be expected if LL remained together after hatching while awaiting hosts.

The same analysis was performed on *Amb. limbatum* infesting sleepy lizards, see below.

Table 7

Amb. limbatum ♀♀ infesting 352 sleepy lizards, *Tr. rugosus*.

No. of ♀♀	Observed frequencies O		Poisson expected frequencies E		Deviation from expectation O-E
0	227		219.6		+
1	97		103.6		-
2	20)	28	)	28.8	-
3	5)		)		
4	1)		)		
5	2)		)		
Total	352		352.0		

$\bar{y} = 0.472$ $s^2 = 0.597$ C D = 1.264

$\chi^2 = 0.692$ $(\chi^2{.05}_{(1)} = 3.84)$

In this case we must accept the null hypothesis that the observed frequencies follow a Poisson distribution.

Table 8

Amb. limbatum ♂♂ infesting 347 sleepy lizards, *Tr. rugosus*.

No. of ♂♂	Observed frequencies O		Poisson expected frequencies E		Deviation from expectation O-E
0	48		34.2		+
1	110		79.2		+
2	72		91.8		-
3	37		70.9		-
4	34		41.1		-
5	19		19.0		0
6	8	29		10.8	+
7	8				
8	6				
9	1				
10	2				
11	1				
16	1				
Total	347		347.0		

$\bar{y} = 2.317$ $s^2 = 4.644$ C D = 2-004

$\chi^2_5 = 73.9$ $(\chi^2 .005(5) = 16.75)$

The ♂♂ *Amb. limbatum* show clumping. The nature of the departures from the Poisson distribution are similar to those shown by *Ap. hydrosauri*.

Table 9

Amb. limbatum NN infesting 362 sleepy lizards, *Tr. rugosus*.

No. of NN	Observed frequencies O		Poisson expected frequencies E		Deviation from expectation O-E
0	228		88.7		+
1	74		124.8		-
2	23		87.7		-
3	9		41.1		-
4	7		14.4		-
5	7	21		5.3	+
6	1				
7	1				
8	3				
11	1				
13	3				
22	1				
28	1				
29	1				
42	1				
91	1				
Total	362		362.0		

$\bar{y}$ = 1.406 s^2 = 35.622 C D = 25.3356

χ^2_4 = 362.6 (χ^2.005 (4) = 14.86)

The *Amb. limbatum* NN also exhibit clumping.

Table 10

Amb. limbatum LL infesting 367 sleepy lizards, *Tr. rugosus*.

No. of LL	Observed frequencies O		Poisson expected frequencies E		Deviation from expectation O-E
0	323		18.3		+
1-10	32		348.6		-
11-20	2	12		0.1	+
21-30	1				
31-40	1				
51-60	1				
71-80	1				
100	6				
Total	367		367.0		

$\bar{y} = 2.997$ $s^2 \doteq 258.808$ C D = 86.356

χ^2 = huge P = very small

The LL of *Amb. limbatum* show marked clumping.

Apart from oo *Amb. limbatum*, all stages of both species show clumping. The nature of the clumping is consistent in that the numbers of lizards with no ticks or with many ticks are greater than expected. Such a pattern may be due to ticks only awaiting hosts in a few places in an area. These places are likely to be lizard refuge sites but probably not all such lizard shelters contain ticks. The pattern would also be produced if ticks were only available in individual sites for short periods of time and different lizards used the same refuges at different times. Such patterns of infestation would also result if lizards already infested with ticks were more attractive to additional ticks or if some lizards were either good or poor hosts for ticks.

The observed infestation patterns could be produced in other ways, however. Differences in infestation rates between areas within the sampled area, or differences in infestation rates at different times of the period sampled are such possibilities. Bull (1978 b) has since examined these matters carefully in a population of *Ap. hydrosauri* near Tickera on Yorke Peninsula. He found that adult ♂ and ♀ ticks showed geographical heterogeneity in their distribution patterns and that this can account for the observed non-random distribution of ♂♂ on lizards. The ♀♀ infested their hosts at random. The LL and NN both showed non-random distribution patterns. These patterns changed both with time and locality but even when these sources of variability were removed the analyses showed that the patterns retained a non-random (clumped) character.

Bull (1978 b) presents supporting evidence for his earlier hypothesis (Bull 1969), that ticks are clumped and that lizards are likely to be infested heavily or not at all. He cites unpublished data on tick aggregating behaviour (see 3.3414) and the behaviour of lizards to support this model. He suggests that lizards (*Tr. rugosus*) have overlapping home ranges which contain many refuge sites (for the lizard) and that these sites may only be occupied by one lizard at a time. The ticks detach from lizards in these sites and they don't venture from them. ♀ ticks lay their eggs in the refuge in which they detach and the resulting LL remain in an aggregation until a lizard enters and receives a massive infestation. The engorged LL detach in another (or the same) site later but within each site the ticks remain aggregated and tend to all infest a particular host together. In 3.3414 below further evidence is presented to show that unattached ticks do aggregate.

3.33 Tick Populations in Field Enclosures.

In 3.31 data on the seasonal dynamics of the ticks were presented. These data were obtained by sampling hosts at various times throughout the year and counting the ticks attached to them. This method is only partly satisfactory because the hosts are very difficult to find in autumn, winter and late summer. Thus samples of hosts (and ticks) were often too small to give a clear picture of tick infestation patterns. Other workers have found the method more successful when applied to ticks whose hosts are homeothermic (e.g., Clifford et al., 1976, MacLeod et al., 1977, Patrick and Hair, 1977 and Randolph, 1975).

In order to observe the ticks in nearly natural conditions throughout the year and thus help overcome this problem, enclosures were constructed in the field to house groups of lizards and their ticks. The opportunity was also taken to test the hypothesis that the ticks might exhibit interspecific competitive interactions. This latter aspect of the enclosure studies is discussed in detail in Chapter 6.

Enclosures were constructed near Pt.Gawler (40km north of Adelaide) on a property named Buckland Park. The site was selected for its isolation from interference and because ticks (i.e. *Ap. hydrosauri*) and their hosts were known to live there.

The area selected was 100 metres inland from the edge of the coastal salt-marsh. The substrate was a shallow layer of soil over deep shellgrit on which grew a low scrub dominated by *Olearia axillaris* and *Acacia ligulata*. Rabbits and cattle grazed in the same paddock.

Two enclosures were built during September 1970 and two more were erected in January 1972. Each enclosure was constructed from sheets of flat galvanized iron 60cm wide. The ends of the strips were riveted together to form a circular enclosure 10m in circumference. The bottom edge of the iron was buried 15cm under the soil surface leaving a wall 45cm high. The structure was secured by star pickets.

Enclosures were sited so that there were lizard refuges and adequate cover in each. This raised the concern that the enclosure might enclose ticks native to the area. To overcome this problem sleepy lizards were placed in the enclosures during the spring and summer and checked to see if they became infested. In each case it proved an unnecessary precaution.

Six similar enclosures were constructed in the Mt. Mary study area. These are described in Chapter 6.

3.331 Aponomma hydrosauri.

Enclosure 1 was chosen to house a population of *Ap. hydrosauri*.

Four lizards (*Tr. rugosus*) that had lived in the enclosure since the previous September were infested with LL on the 15th and 29th March 1971. The methods used to breed ticks in the laboratory and of infesting lizards are described in appendix 2. Each lizard received 400 LL. Approximately half had hatched from eggs laid in the laboratory by a ♀ collected at Pt. Gawler and half from a ♀ captured at the suburb of Tea Tree Gully about 16km north east of Adelaide. The eggs had hatched during late December 1970. The LL were kept in the dark at 25°C., 85% R H until used in March.

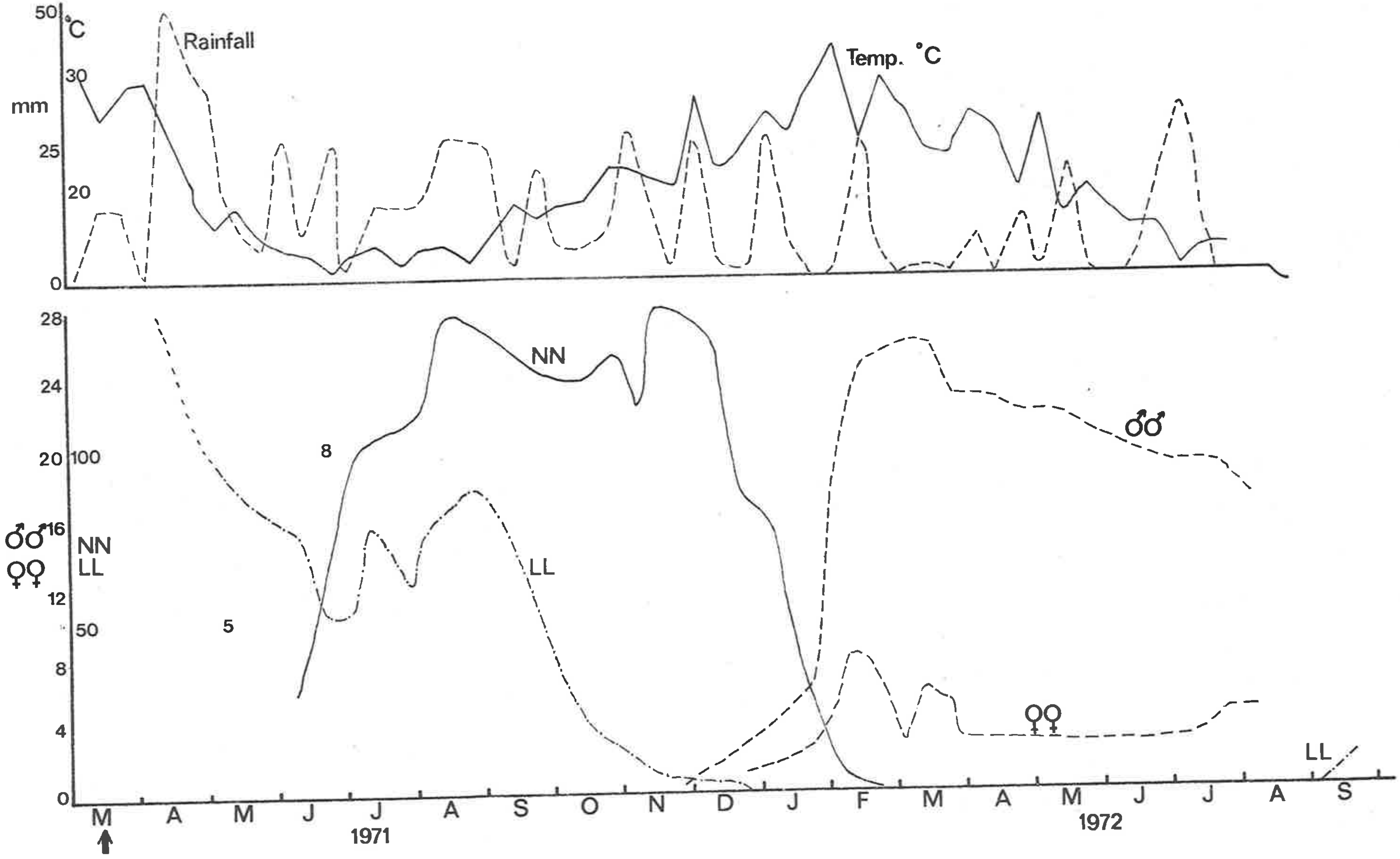
The infested lizards were placed in enclosure 1 on 30.3.1971. The enclosure was visited each week and the number of ticks on each host and their condition noted. It became apparent that the enclosures contained inadequate food supplies for the lizards. Their food supply had to be supplemented with tomatoes and minced steak each week during spring and summer. During winter when the lizards became inactive the weekly food provision was suspended.

The LL quickly engorged, detached and moulted in the enclosures. The first NN on lizards were detected on 8.6.71. Figure 19 shows the numbers of LL and NN on the hosts. A number of LL, about 60, remained attached to the lizards during winter and detached during spring. The NN numbers increased rapidly during the cold months of June and July and then levelled off. NN numbers did not decrease until later in spring and early summer. The curves in figure 19 show the total number of ticks of each stage attached to the lizards in the enclosure, but they do not show how many of

Figure 19. The development of *Ap. hydrosauri* LL placed on 4 sleepy lizards, *Tr. rugosus,* in enclosure 1, at Buckland Park, Pt. Gawler. The data presented are weekly counts of the total numbers of ticks of each stage, LL, NN, ♂♂ or ♀♀, attached to the lizards. The months are shown on the bottom of the figure.

Also shown are rainfall and temperature graphs for that period. The temperature (°C) are ten-day average maxima obtained from the Bureau of Meteorology at Adelaide. The rainfall (mm) is that recorded for Two Wells, the nearest town 10km NE. The points plotted each show the total amount of rain that fell in a ten-day period.

↑ - marks the date on which the infested lizards were placed in the enclosure.



50
°C
Rainfall
30
mm
Temp. °C
25
20
0
28
24
20
100
♂♂
16
NN
LL
♀♀
12
50
8
4
0
8
5
NN
LL
♂♂
♀♀
LL
M
A
M
J
J
A
S
O
N
D
J
F
M
A
M
J
J
A
S
1971
1972

those ticks are new arrivals and how many are ready to detach, i.e. engorged. The time during which engorged NN were present is indicated by a bar graph at the top of the figure.

Figure 20 shows the incidence of engorged NN in the counts. NN scored as engorged probably detached quickly; marked individuals scored as engorged usually were gone in a week. It can be seen then that the curve of the total numbers of engorged and unengorged NN probably falls well short of the total number of individual NN that attached to the lizards. This applies particularly to the November section where many NN were engorging and detaching. The November peak in numbers is surprising. One would expect the curve to keep dropping with increasing rapidity from the end of October. Presumably a second wave of NN attached to the ticks at that time - enough in fact to more than replace those engorging and detaching.

Adult ticks appeared late in November, ♂♂ first, and three weeks later the ♀♀. Thus only eight months elapsed between the infestation of the hosts with LL and the adults attaching to lizards! There were always more ♂♂ on lizards than ♀♀. This was mostly due to the ♀ ticks engorging and detaching while fewer ♂♂ detached. Figure 21 shows the cumulative totals of ♂ and ♀ ticks attaching and detaching from the lizards. Ticks were marked with finger-nail polish and thus new arrivals on lizards could be recognized. During the nine month period 44 ♂♂ and 29 ♀♀ attached to the lizards. 25 ♂♂ and 19 ♀♀ left the hosts during that time. The ♂ ticks seemed also to invade the hosts earlier than the ♀♀.

The enclosures were, unfortunately, badly damaged by cattle or vandals during September 1972. However in the two visits before this happened, 5 LL were found attached to one of the lizards. Perhaps these were progeny of some of the ♀♀. The enclosures were repaired and two more lizards, free of ticks, were placed inside. During December to February they picked up 5 additional LL, which engorged, also 5 NN, 2 ♂♂ and 2 ♀♀. The enclosures were knocked down again and as the area was obviously becoming unsuitable and

Figure 20. The numbers of engorged and unengorged NN of *Ap. hydrosauri* attached to sleepy lizards, *Tr. rugosus*, in enclosure 1 at Buckland Park, Pt Gawler. The line labelled Total NN represents the total number of engorged and unengorged NN attached. The second-line represents the numbers of engorged NN. The space between the two thus shows the number of unengorged NN attached to the lizards.

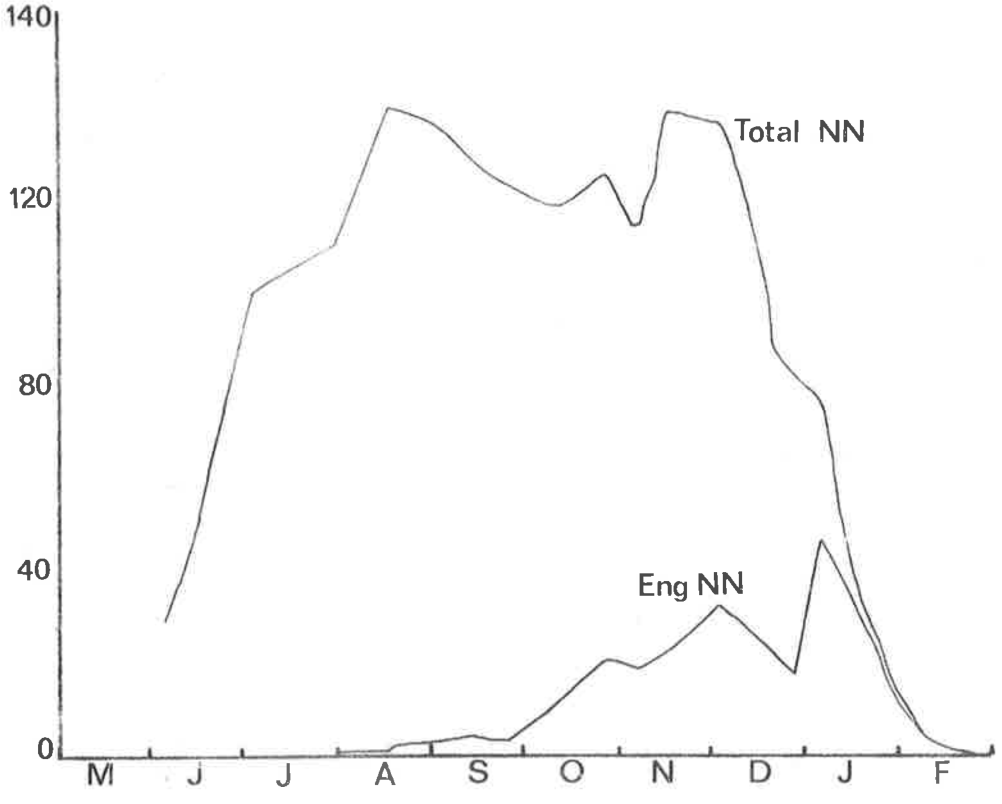
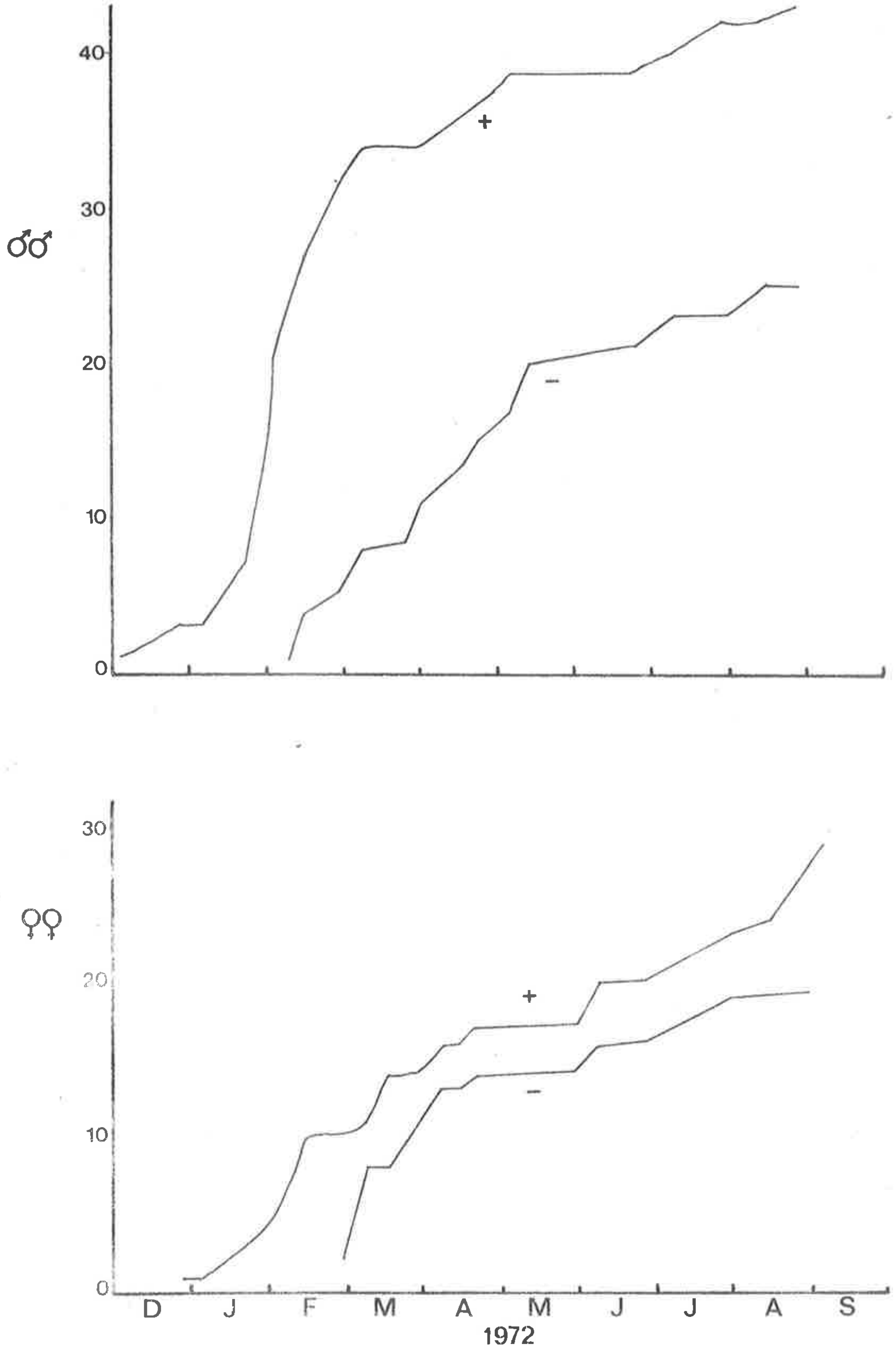

140
120
80
40
0
Total NN
Eng NN
M
J
J
A
S
O
N
D
J
F

Figure 21. Cumulative totals of *Ap. hydrosauri* ♂♂ and ♀♀ attaching (+) and detaching (-) from sleepy lizards, *Tr. rugosus*, in enclosure 1 at Buckland Park, Pt Gawler.


40
30
♂♂
20
10
0
+
−
30
♀♀
20
10
0
+
−
D
J
F
M
A
M
J
J
A
S
1972

local lizards, probably carrying ticks, had entered the enclosures, they were abandoned.

The results do show that the LL can engorge, detach and moult successfully during autumn. However LL left on hosts during the colder months of winter seem unable to engorge until spring. NN may attach in autumn, and some in spring, but those on lizards during winter fail to engorge until spring with a peak early in summer. In summer detached NN can quickly moult to give adults. Some of the ♀♀ can mate, engorge and detach that same summer. The data also suggest that newly hatched LL are not detected until the next spring. This last observation agrees with data in 3.312 on seasonal activity of *Ap. hydrosauri*.

The suggestion from these results is that the whole life cycle was turning once in 18 months. It should be remembered however that the ticks in the enclosure had their hosts confined with them. The hosts in natural conditions would be spaced out over greater areas - see the discussion of this in 3.312. Thus ticks in an enclosure would have a greater chance of encountering a host quickly when they were ready to attach. The rate of population development in an enclosure may well be a maximum value.

It must also be noted that the hosts were infested with LL during March, a time of the year when LL are not abundant on hosts in the field, although some infestations are found (see 3.31). This circumstance, a consequence of there being no laboratory stocks of the ticks or field caught ticks available at more suitable times, may have brought about a different mortality of ticks during the winter than might otherwise have been the case.

Another enclosure (no. 4) also had *Ap. hydrosauri* placed in it. In this case however the enclosure was divided into halves with 2 lizards in each, and *Amb. limbatum* were put in with the *Ap. hydrosauri*. This was one of a series of experiments to see if the ticks interacted in the field. That aspect of the experiment will be discussed in Chapter 6, but some aspects of the data are of use in exploring the seasonal "activity" of the tick.

Two lizards (*Tr. rugosus*), each infected with 200 LL of *Ap. hydrosauri* and 200 LL of *Amb. limbatum*, were placed in half of enclosure 4 - i.e. 4a. Two other *Tr. rugosus* were placed in enclosure 4b, one infected with 400 *Ap. hydrosauri* LL. The methods used were the same as for enclosure 1. The *Ap. hydrosauri* LL were progeny of a tick collected near the lizard enclosures at Pt. Gawler on 18.1.72.

As was the case in enclosure 1, the LL quickly engorged and most detached by mid-May. NN began attaching in the same month, the first being detected on the 4th of May. NN did not begin to engorge until July and August with most waiting until November. Adults were first detected late in November 1972.

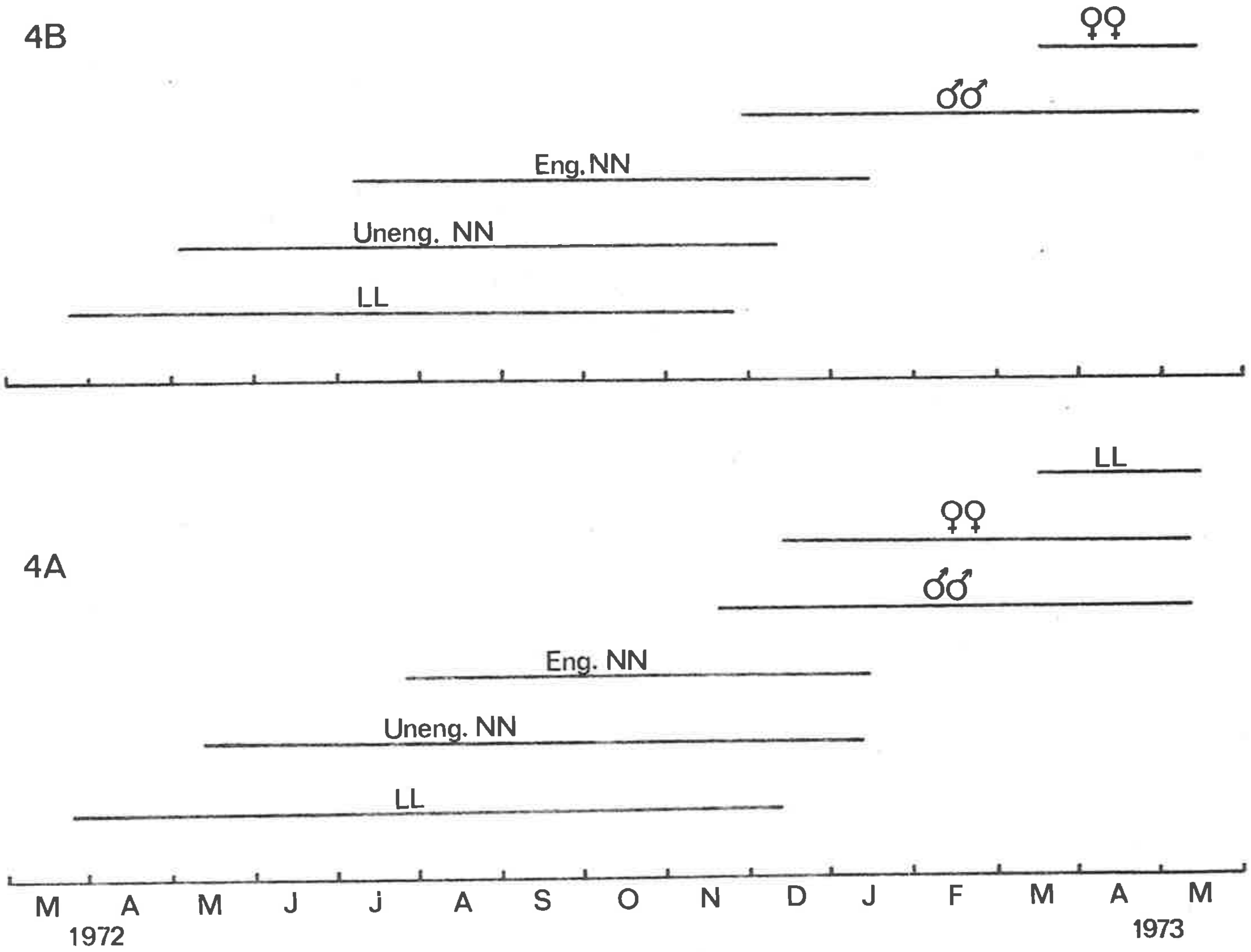
These changes are summarized in figure 22. Actual counts of the number of ticks on hosts are not presented because on a number of occasions lizards died and had to be replaced. The striking development took place in enclosure 4a. There, larvae appeared on 15.3.73, over 100 of them on a lizard. This means that the ticks had completed their life-cycle in 12 months! Again it must be emphasized that these ticks had a much greater chance of encountering a host than ticks in the wild.

Enclosure 4b showed similar development to 4a at first. But ♀♀ took longer to appear and no new LL were seen. All the enclosures were damaged, as explained above, and abandoned during 1973.

Six enclosures were built in the Mt. Mary study area. These were used to test hypotheses relating to the narrowness of the zone of overlap between *Ap. hydrosauri* and *Amb. limbatum*. Colonies of *Ap. hydrosauri* were put into two enclosures and mixed populations of the two species into two others. The nature of the experiments and the results are discussed in detail in Chapter 6. However the following points are pertinent here. The lizards (*Tr. rugosus*) in the enclosures were infested with LL and NN. In one enclosure the colony died out after a few adults appeared. In the other enclosures there was evidence that adult ticks mated, and ♀♀ engorged and

Figure 22. Development of *Ap. hydrosauri* populations in two separated halves of enclosure 4 at Buckland Park, Pt. Gawler. 400 LL of *Ap. hydrosauri* and 400 LL of *Amb. limbatum* were placed in each half of the enclosure, but only the results for the former are shown.

The figure shows the timings of the appearances and disappearances of the stages (LL, NN, ♂♂, ♀♀) in each half of the enclosure.


4B
♀♀
♂♂
Eng.NN
Uneng. NN
LL
LL
♀♀
4A
♂♂
Eng. NN
Uneng. NN
LL
M
A
M
J
J
A
S
O
N
D
J
F
M
A
M
1972
1973

detached. However, there was no sign of newly-hatched LL attaching to lizards. The results are not particularly helpful as the populations were established during spring and suffered one of the driest periods on record in that area.

Bull and Sharrad (1979) report these experiments and some performed by Michael Bull at Flinders University (see Appendix 5). Both sets of observations confirm the view that all activity stops during the cooler months (April-September), but for the rest of the year there were regular pulses of activity as successive stages in the life history predominated.

3.332 Amblyomma albolimbatum.

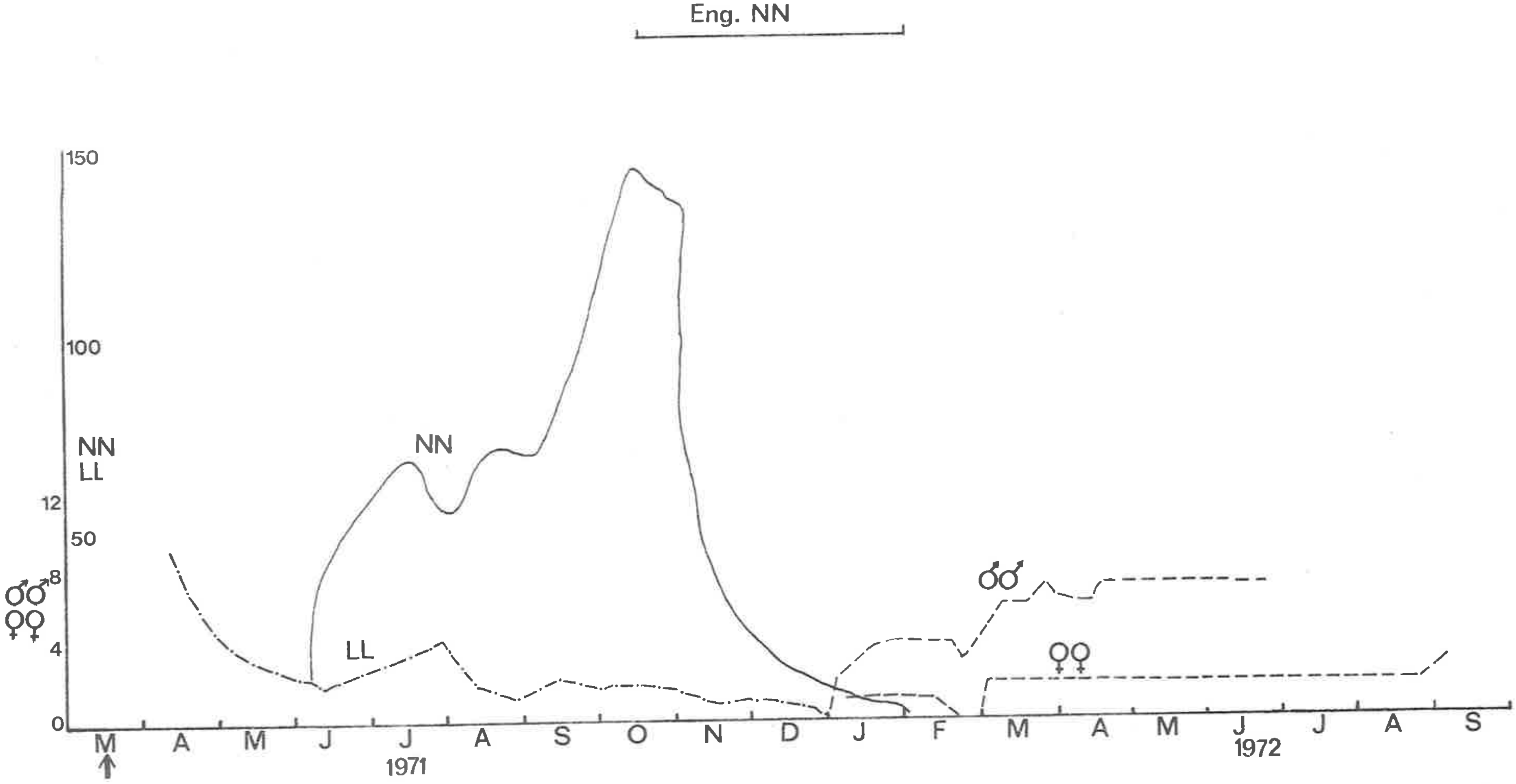
These ticks were placed in enclosure 2 at Pt. Gawler under identical conditions and at the same time as the *Ap. hydrosauri* in enclosure 1. Each of the 4 lizards was infested with 400 LL from 2 ♀♀ ticks (299 from each) captured near Arno Bay on Eyre Peninsula. They had laid their eggs in the laboratory during October 1970.

Figure 23 shows the results of the weekly counts of tick numbers on the lizards. The LL quickly engorged, detached and moulted. The NN began attaching to lizards at the same time as the other species in enclosure 1. Some LL persisted on lizards until December. The numbers of NN steadily increased to peak in mid October when the first engorged NN appeared. Just after that 2 lizards escaped from the pen. The now smaller graph shows that numbers dropped rapidly during November and December. Adults appeared early in January, some of the ♀♀ engorged and detached but no new LL appeared. This enclosure suffered the same fate as enclosure 1.

These ticks performed similarly to the *Ap. hydrosauri*. However, the time taken for NN to attach was longer - the curve in figure 21 rises much

Figure 23. The development of *Amb. albolimbatum* LL placed on 4 sleepy lizards, *Tr. rugosus,* in enclosure 2 at Buckland Park, Pt. Gawler. The figure is constructed from weekly counts of the total number of attached ticks of each stage (LL, NN, ♂♂, ♀♀) in the enclosure. The months are shown at the bottom of the figure. The time during which engorged NN were found on lizards is indicated at the top of the figure.

↑ - shows the date on which attached LL were placed in the enclosure.


Eng. NN
150
100
NN
LL
12
50
♂♂ 8
♀♀
4
0
NN
LL
♂♂
♀♀
M
A
M
J
J
A
S
O
N
D
J
F
M
A
M
J
J
A
S
1971
1972

less rapidly than that in figure 17. Also the NN took longer to begin engorging. It might be expected that *Amb. albolimbatum*, which lives in warmer, drier areas than *Ap. hydrosauri* on Eyre Peninsula, might have its rate of development more retarded by cold weather.

3.333 Amb. limbatum

Amb. limbatum LL attached to sleepy lizards were put in enclosures 3 and 4. Again the same methods were used here as those described above.

In enclosure 3 on 31.1.72 three lizards were released, each infested with 400 LL. The LL were progeny of a single ♀ collected 15km N of Mt. Mary during October 1971. The fate of the ticks is shown in figure 24.

It took less than six weeks for LL to engorge, detach and moult and for the NN to attach and begin engorging. Again it is evident that the cold weather stops attached NN from engorging. But in this case some adults, from the first moulting NN, attached by 20.4.72. This is only seven weeks after the LL attached! It should be noted that this enclosure was occupied two months earlier than enclosures 1 and 2 had been the year before.

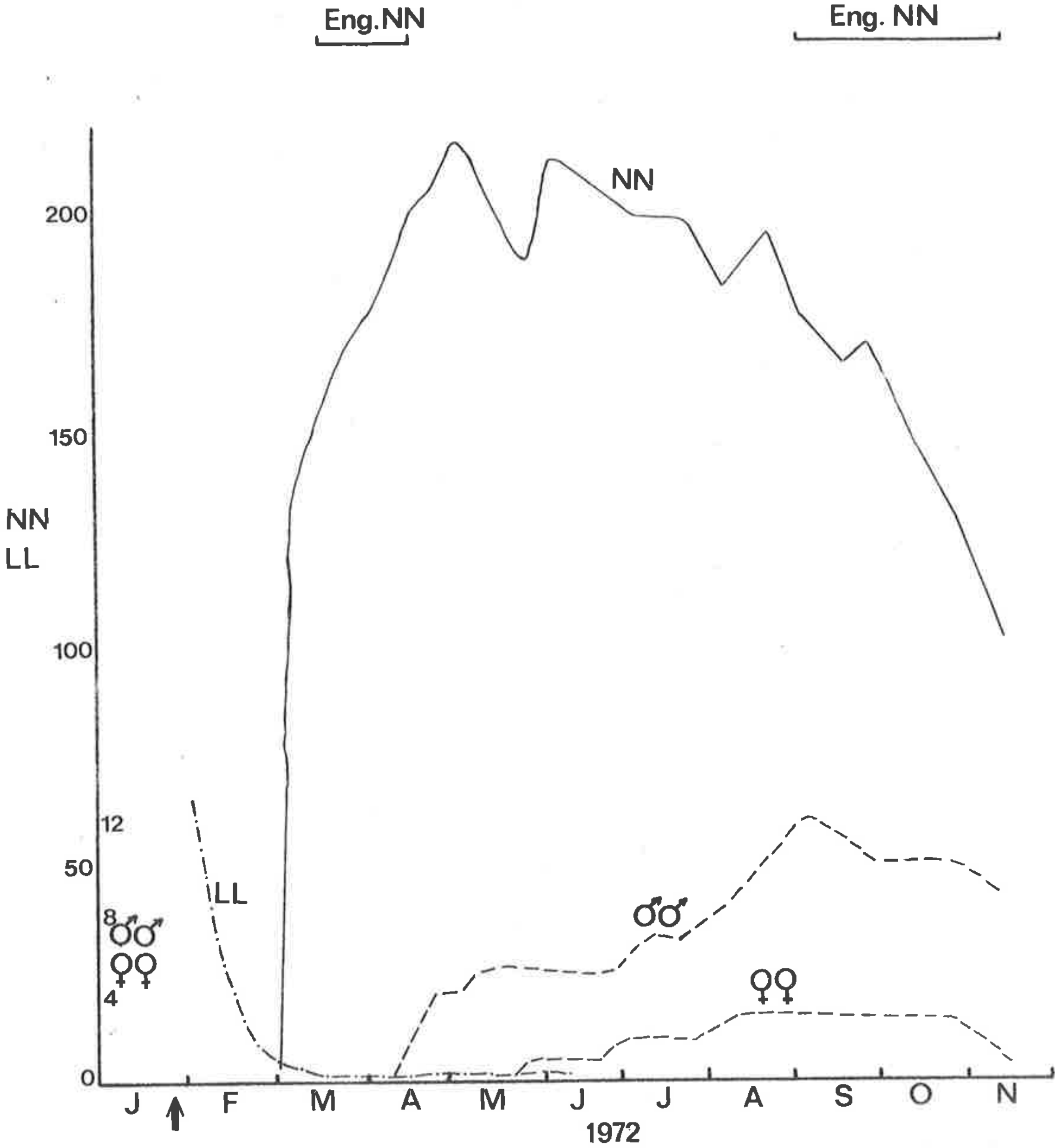
During September NN began engorging again - later than the *Ap. hydrosauri* NN in enclosure 4, see figure 22. The number of adults infesting lizards began to increase again in August (particularly the ♂♂). These can not have come from the second group of engorging NN. It seems that the cold weather may have also delayed moulting in NN that engorged during the autumn.

The *Amb. limbatum* apparently develop very quickly off and on hosts during warm periods but are slowed more than *Ap. hydrosauri* during cold weather.

Enclosure 3 results cease after November as a strange mortal illness began to infect lizards in that enclosure. Replacement lizards also died

Figure 24. The development of *Amb. limbatum* LL placed on 3 sleepy lizards, *Tr. rugosus*, in enclosure 3 at Buckland Park, Pt. Gawler. The figure is constructed from weekly counts of the total numbers of attached ticks of each state (LL, NN, ♂♂, ♀♀) in the enclosure. The months of the year are shown at the bottom of the figure. The times during which NN were found on lizards are indicated at the top of the figure.

↑ - shows the date on which the attached LL were placed in the enclosure.


Eng.NN
Eng. NN
NN
200
150
NN
LL
100
12
50
LL
8
♂♂
♀♀
4
♂♂
♀♀
0
J
F
M
A
M
J
J
A
S
O
N
1972

quickly. This situation was unique to enclosure 3.

Other *Amb. limbatum* LL were put into enclosure 4 with *Ap. hydrosauri* LL, see 3.331 above. They were placed in the enclosure on 22.3.72. When activity had slowed in enclosure 3 no *Amb. limbatum* NN or adults appeared in one half of the enclosure (4a). NN attached in 4b, three weeks later than *Ap. hydrosauri* NN but none engorged. It is impossible to say if this failure was due to cold weather or interaction with *Ap. hydrosauri* or some other unknown factor.

It seems that *Amb. limbatum*, which occurs in drier, warmer areas than at Pt. Gawler, and *Amb. albolimbatum*, are both slowed in development to a greater extent than is *Ap. hydrosauri* during cold periods. Another interesting outcome of these enclosure observations is that the development of the ticks is not only slowed in the microhabitat off the host during cold conditions but the attached ticks are also retarded. This is a more marked feature of the development of parasites in poikilothemic animals, and is not as evident in mammalian or avian ticks (Arthur, 1962).

3.34 Tick development and behaviour.

3.341 Tick development and behaviour off the host.

It has been shown above that the ticks live in two completely different environments during their life-cycles, off the host and attached to the host. When detached, the engorged ticks have to lay eggs, or moult and resist potential dangers of the environment. The newly moulted or hatched tick has the task of finding a host and invading it. In this section information gleaned on the behaviour of the ticks while off the host, and the rate at which they develop, is examined.

Ticks were collected during each spring and laboratory stocks established. The methods used in keeping these stocks are described in appendix 2. The information contained in this section was gained largely from the use of such stocks. *Amb. albolimbatum* laboratory stocks were derived from ♀ ticks caught in the Arno Bay - Cleve area. *Amb. limbatum* stocks were supplied from ticks captured in the Mt.Mary study area. *Ap. hydrosauri* were taken from Mt.Mary, from Pt.Gawler and Goolwa.

3.3411 The microhabitat of ticks off the host.

In a general discussion of seasonal 'activity' above (3.31) it was shown that in other tick species the nature of the microhabitat occupied by ticks while off the host is crucial. It is during this period that ticks are vulnerable to starvation and desiccation. Thus the selection of the site in which eggs are to incubate and ticks are to moult and await a host is critical. An engorged tick ready to detach could find such a site by detaching from the host in a suitable spot. This often involves timing the detachment to a particular period of the hosts' diurnal rhythms. For example, Kheisin and Lavrenenko (1956) found that *I. ricinus* engorged ♀♀ detached from cattle in pastures rather than in the cattle sheds into which cattle were driven at night. If the cattle were driven to pasture at night and into sheds during the day the ticks would still detach in the pasture. It appeared that the ticks responded to the diurnal activity rhythm of the hosts; and by doing so ensured that they fell into the most suitable microhabitats for egg-laying. Some ticks detach when their hosts are inactive in their burrow, e.g. *I. hexagonus* from hedgehogs (Arthur 1962).

The timing of detachment is important to engorged ticks because they are unable to move very far. This applies particularly to engorged ♀ ticks which are quite unable to climb slopes which approach the vertical as their bodies are bloated with blood. They must then, merely make minor adjustments to their position, perhaps pushing under leaves or bark.

Detachment in these ticks is discussed in 3.3424 below.

Bull (1969) describes how he attempted to find detached ticks in an outdoor enclosure which contained lizards and a large tick population. He sieved soil from in and near lizard shelter sites but failed to find any sign of the parasites. In the present study three techniques were used in an attempt to find ticks off the host. In each case the material collected was leaf litter and soil from near and in lizard refuges. Some samples were taken from the Pt. Gawler lizard enclosures and searched, as it was known that ticks were present.

The three methods used in an attempt to find ticks or eggs in the field were sieving, flotation extraction and funnel extraction. Sieving was carried out using a series of fine soil sieves. The flotation extraction technique involved placing coarsely sieved litter samples in water and another nonmiscable, liquid with a specific gravity less than that of water, e.g. benzene. The mixture was agitated and then allowed to stand. Remains of organisms would then be seen at the interface of the liquids. The apparatus and technique were of the conventional Salt and Hollick type, but including modifications described by Raw (1955). The funnel technique involved placing litter samples on a gauze platform over a funnel leading to a vial of preservative (70% alcohol) and positioning a heat source over the litter. Small living creatures able to move would then crawl away from the heat source and fall into the funnel. The apparatus and technique were based on that of Murphy (1958).

The only success in finding ticks by using these techniques was with samples from enclosures at Pt. Gawler. On 8.6.71 four samples were taken from enclosures 1 and 2 (see 3.33 above), which contained respectively populations of *Ap. hydrosauri* and *Amb. albolimbatum*. Soil and leaf litter samples, 12cm in circumference and 10cm deep were taken from the bottom of known lizard refuges in each enclosure and from areas around these sites. The flotation method described above yielded 2 engorged LL of *Amb. albolimbatum* from a lizard refuge in enclosure 2 and 1 unengorged N of *Ap. hydrosauri* from a similar site in enclosure 1. The ticks were all partly buried in loose soil and leaf litter within 1½cm of the surface. No ticks were found in other parts of the enclosures at Pt. Gawler. As these measures caused a major disturbance to the environment in the enclosures they were not tried in the Mt. Mary enclosures (see 6.30).

Soil samples (50 of them) were collected in the Mt. Mary study area from 4 sites on 21.11.71. These were cylinders (12cm x 10cm) of soil and leaf litter from, in the main, beneath bluebushes (*Kochia sedifolia*) in likely lizard refuges. Sieving and flotation (see above) failed to reveal any ticks. These attempts were discontinued as they were an unprofitable use of time.

However, in the laboratory data were gained on microhabitat selection by the ticks.

It had been observed, in the early stages of this study, that engorged LL, NN and ♀♀ of all three species could be obtained, from suitably infested hosts, if the lizards were placed in cages over trays on which there were sheets of paper (described in appendix 2). Usually the engorged tick, on detaching, would be found under the paper and only rarely were they found elsewhere. This observation suggested that, if given the opportunity, engorged ticks would crawl beneath objects in lizard refuges or into crevices.

In an attempt to observe microhabitat selection in engorged and in unfed ticks three types of apparatus were constructed. In each case 500ml beakers were used; one group of beakers contained sand covered with leaf litter and twigs, another contained filter paper evenly stacked on slivers of wood (2mm diam.), and a third group of beakers were filled, to a depth of 6cm, with 2cm diam. filter paper. Groups of engorged and unfed LL and NN of *Ap. hydrosauri* and *Amb. limbatum* were observed in each of these circumstances. At 25-29°C and in constant light, groups of 30 ticks of each category were observed for 3 hours, their positions recorded, and then observed again after 24 hours.

The engorged LL and NN in each case vanished into the loose litter or filter paper after a 1-2 hour period of wandering. They did not burrow into the sand. In filter paper tiers it was observed that the LL often sought the underside of objects and remained clinging upside down. Nearly all of the engorged LL and NN remained within 1cm of the surface.

Unfed LL and NN are more mobile than engorged ticks and appear to wander about more. However within 3 hours these also disappeared into the leaf litter or filter paper.

When stored in plastic vials (see appendix 2) unfed ticks of these species often clumped together at the top of the vial under the lid. In order to see if the ticks might climb when off the host, artificial plant stems were made. These were glass rods 6mm, 5mm and 2mm in diameter and were pushed through a cardboard base to give 'stems' 14cm, 7cm and 5cm tall. LL and NN of *Ap. hydrosauri* and *Amb. limbatum* were each observed on this artificial surface for 3 hours. The ticks tended to move in an apparently aimless fashion on the cardboard and from time to time encountered the 'stems'. Some ticks climbed the glass rods but most pushed their bodies into the tiny crevice between the base of the rod and the cardboard. *Ap. hydrosauri* did not cease to move while on the rods and always climbed down. A few *Amb. limbatum* LL and NN remained motionless 1-3 cm up the rods for the last 15 minutes of the observation period.

Trevor Petney (pers comm.) has begun a detailed study of the microhabitat of the ticks, off the host, in the Mt. Mary study area. He reports observing engorged *Ap. hydrosauri*LL climb down the gap between blue bush (*Kochia sedifolia*) stems and the surrounding soil. *Amb. limbatum* seem to behave in a similar fashion but some of these will climb up the stem of the bush a cm or so for periods of time.

In summary then the information presented here, the literature on other ticks, information on detachment in 3.354 and data in 3.32 suggest that these ticks choose moulting microhabitats and probably await hosts in crevices and under litter in the shelter or burrow used by their host. In 3.3414 below the movement of unfed ticks within the hosts' refuge and attachment are discussed.

3.3412 Egg Production and hatching

Ixodid ticks lay their eggs in one large batch unlike argasid ticks where ♀♀ may have several blood meals and lay several batches (Arthur 1962). The number of eggs laid by a single ixodid female varies greatly depending upon the size of the blood meal imbibed and the species of tick. Arthur (1962) reports a range among various species from 1 to 22; 891 eggs, the last figure achieved by *Amblyomma nuttalli*.

The preoviposition period of the ticks also varies. Hitchcock (1955) demonstrated that, in *Boophilus microplus*, temperature influenced the duration of this period. High temperatures resulted in very short preoviposition periods of as little as 2 days. Snow (1969) reported a similar effect in *Hyalomma anatolicim*. The duration of egglaying and hatching times of eggs are similarly influenced by temperatures. In fact it seems that temperature, rather than relative humidity, has a dominant influence on these developmental processes in ticks, e.g. see *Ixodes hexagonus* (Arthur, 1951) and *Dermacentor variabilis* (Smith et al 1946).

Some engorged ♀♀ are also influenced by photoperiod. Doube (1975) showed that ♀♀ of the kangaroo tick, *Ornithodoros gurneyi*, entered a reproductive diapause on being exposed to short photoperiods (e.g. 16 hours dark, 8 hours light). There is no evidence of diapause in *Ap. hydrosauri* or the two *Amblyomma* spp, although from time to time there were inexplicable delays in development of some ticks!

Methods used in weighing ticks and counting eggs are outlined in appendix 2.

Information of weights of engorged ♀♀, the numbers of eggs they lay, and preovipostion times are summarized below in table 11.

Table 11.

Egg production in the three ticks under constant conditions. Ranges shown are for temperatures between 20°C and 30°C at 85% RH. Means ($\bar{x}$) and standard errors of means (S E) are calculated from data on N ticks at 25-26°C, 85% RH.

	Ap. hydrosauri	*Amb. limbatum*	*Amb. albolimbatum*
Weights of engorged ♀♀ (Mgm)			
Range	367 - 716	206 - 746	
$\bar{x}$	577	537	-
SE	22.8	94.8	
N	18	5	
preoviposition times (days)			
Range	7 - 38	3 - 11	7 - 12
$\bar{x}$	26.6	6.17	8.2
SE	2.7	1.1	0.6
N	13	6	9
Number of eggs laid			
Range	989 - 2496	1522 - 5023	3018 - 4515
$\bar{x}$	1647	2785	3852
SE	115	790	160
N	14	5	9

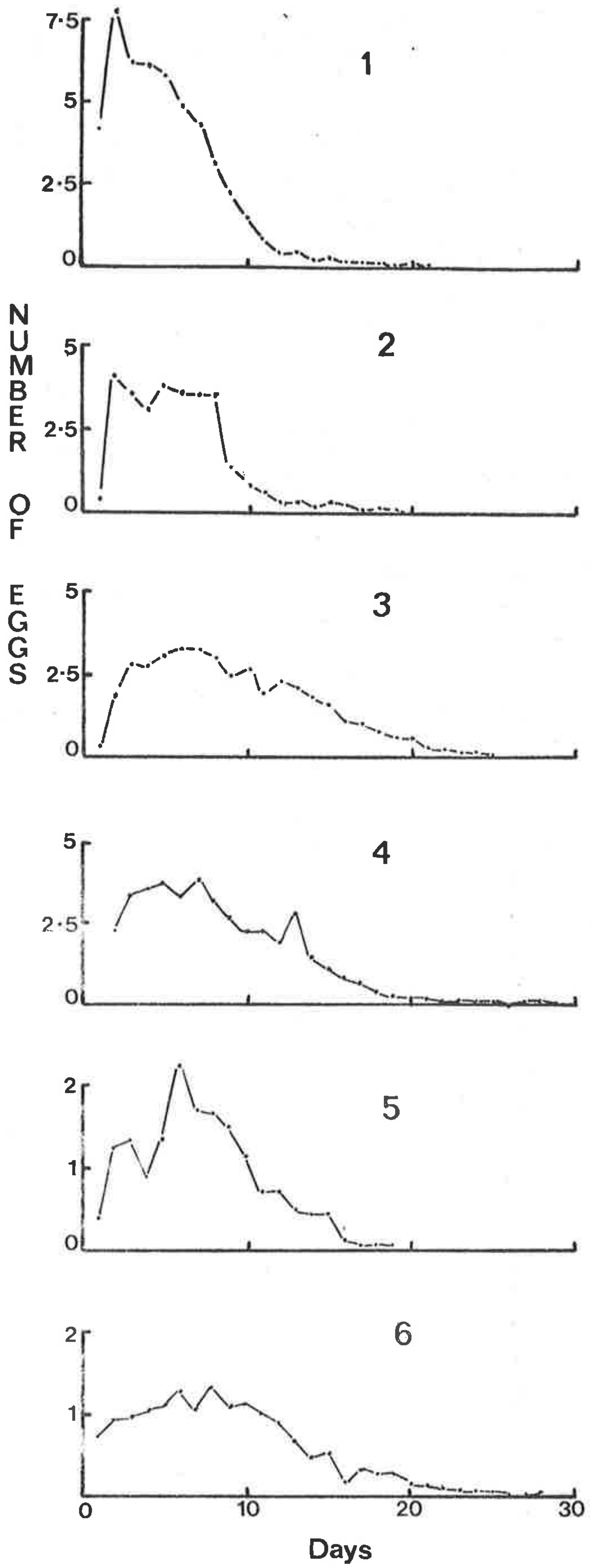
The table indicates that engorged *Ap. hydrosauri* ♀♀ are similar in weight to the *Amblyommas* but exhibit longer preoviposition times and lay fewer eggs. The pattern of egg laying in the three species is shown in figure 25 for selected specimens. In each case the rate of egg laying rapidly increased to reach a peak within a week. It then drops away and for a period the tick lays small numbers daily.

Increased ambient temperature seems to decrease the time taken for ♀♀ to lay their eggs. This is unusual of ticks (Arthur 1962, Hitchcock 1955 and Snow 1969). It is also evident that the number of eggs laid by a ♀ is

Figure 25. The pattern of egg laying in selected ♀♀ of *Ap. hydrosauri, Amb. albolimbatum* and *Amb. limbatum*. The number of eggs laid per day is grouped against time, in days, for 2♀♀ from each species. All had been kept at 85% RH and in the dark.

The graphs are:-

1. *Amb. limbatum* ♀ (M14/12) kept at a constant temperature of 30°C.
2. *Amb. limbatum* ♀ (M15/12) kept at a constant temperature of 30°C.
3. *Amb. albolimbatum* ♀ (BF1) kept at a constant temperature of 27°C.
4. *Amb. albolimbatum* ♀ (H1BF6) kept at a constant temperature of 27°C.
5. *Ap. hydrosauri* ♀ (SEII) kept at a constant temperature of 30°C.
6. *Ap. hydrosauri* ♀ (BPI) kept at a constant temperature of 27°C.


1
2
3
4
5
6
7·5
5
2·5
0
NUMBER OF EGGS
2
1
0
10
20
30
Days

positively correlated with her weight, see table 12 below. Similar results have been shown in other species, e.g. *Dermacentor variabilis* (Drummond et al., 1971).

Table 12

Weights on detachment (mgm) and number of eggs laid by 7 ♀♀ *Ap. hydrosauri* which detached in the laboratory from two *Tr. rugosus* collected near Millicent, S.A.

Lizard.	1	2	3	4	5	6	7
Weight	367	412	537	552	581	585	684
Eggs	989	1522	1616	1587	2222	2156	2496

Correlation coefficient R + 0.915, $P<0.01$

The eggs once laid stick to each other and to the substrate. They have each been coated with a waxy substance produced by the ♀♀ from Gene's organ. This coating no doubt assists the eggs to avoid desiccation (Lees and Beament 1948). Within a few days developing tick embryos are visible in the tiny (0.1 to 0.2 mgm) eggs.

The incubation period of the eggs is dependent upon the ambient temperature and also humidity. Low ambient temperatures increase the incubation period. This has been shown in several tick species, see MacLeod (1934), Arthur (1951, 1962), Randolph (1975). However MacLeod (1935) showed that *I. ricinus* eggs do not complete development below 80% RH! Arthur (1951) suggested a similar, critical value for *I. hexagonus*.

The precise effects of humidity and temperature on the incubation periods of the three species in the present study have not been adequately illuminated. Experience with laboratory stocks suggests that they will not hatch at low relative humidities and that there may be variation between the species of the type shown by Bull and Smyth (1973) when examining the water balance of the three ticks.

Bull (1969) attempted to discover the effects of temperature and humidity on the incubation period of *Ap. hydrosauri*. He placed lots of 100 eggs at 5 temperatures (36, 30, 25, 20, 15°C) and at 5 humidities (100, 75, 55, 36, 0% RH). At 36°C no ticks hatched at any humidity while at 0% RH similar results were obtained at all temperatures. Of 5 batches of eggs kept at 55% or 36% RH only one hatched (at 30°C). The eggs at 100% and 75% RH hatched at all temperatures, except 36°C, but took about 50 days at 20°C and more than 5 months at 15°C.

I made some observations on *Amb. limbatum* and found that eggs of this tick will not hatch at 0% RH.

Data on incubation times for tick eggs are presented in table 13. These are unpublished data from Dr. Smyth.

Table 13

Incubation periods for eggs from single females of *Ap. hydrosauri*, *Amb. albolimbatum* and *Amb. limbatum* kept at 25°C, in the dark at 85% RH. The ♀♀ ticks came respectively from Arno Bay, Cleve area and Whyalla. The range of times (days), means ($\overline{x}$) standard errors of the means (SE) and the numbers recorded (N) are shown.

	Ap. hydrosauri	*Amb. albolimbatum*	*Amb. limbatum*
Range	35 - 38	35 - 39	31 - 37
$\overline{x}$	36.52	37.18	34.42
SE	0.06	0.02	0.11
N	151	576	76

It can be seen that *Ap. hydrosauri* has an incubation period, at 25°C, midway between the two *Amblyommas*. At higher temperatures these incubation times decreased. *Amb. limbatum* LL have been seen to be hatched in less than 19 days at 32-34°C, 85% RH.

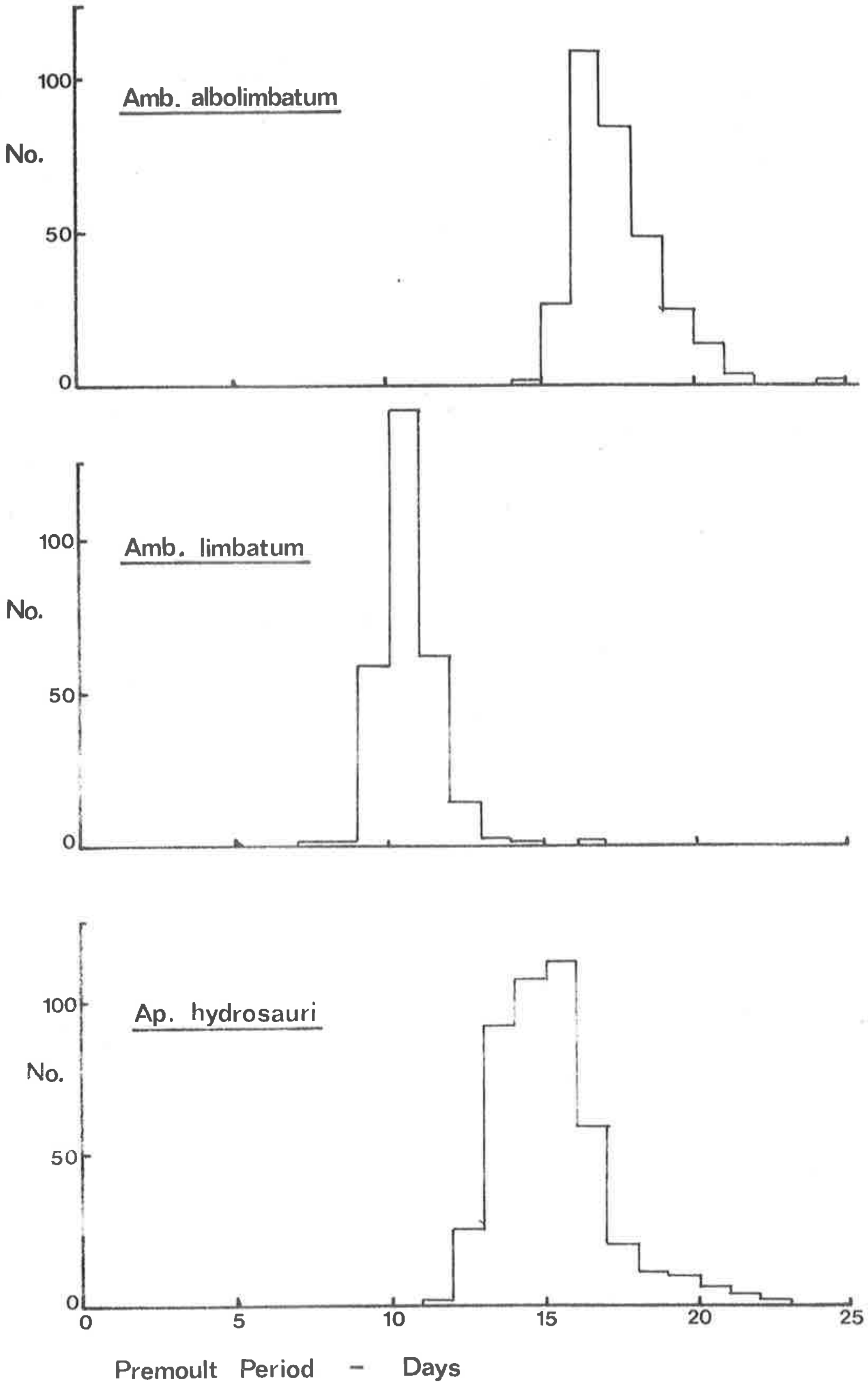
3.3413 Moulting

Three-host ticks moult twice;LL → NN and NN → adults. In this section data are presented on the time taken for the three ticks to moult after detaching from hosts, i.e. the pre-moult periods. The data were gathered by collecting detached and engorged LL and NN each day from sleepy lizards, *Tr. rugosus*, placing the ticks in vials (See appensix 2) which were deposited in desiccators and temperature cabinets. The time taken to moult was determined by examining the contents of the vials each day.

Figure 26 shows selected examples of the distribution of pre-moult periods of LL of the three species. Each graph represents an infestation by progeny of a single ♀ of a single host lizard. The engorged LL were kept at 25°C, in the dark at 85% RH. The figure suggests that *Amb. limbatum* LL moult more quickly than either of the other species. Also note that the distributions exhibit kurtosis in that they are skewed to the left. However, the calculationsof measures of kurtosis (Sokal and Rohlf 1962, p. 113) indicate that the departures from normality are not great and that the statistical calculations below are valid.

The graphs of NN pre-moult times are similar to those shown for LL, although the NN take longer to moult. Below in table 14 are shown data on pre-moult times for LL and NN under constant conditions.

Figure 26. Examples of the distribution of the pre-moult periods (in days) of LL of *Ap. hydrosauri*, *Amb. albolimbatum* and *Amb. limbatum* under constant conditions (27°C, dark, 85% RH).



Amb. albolimbatum
Amb. limbatum
Ap. hydrosauri
No.
100
50
0
0
5
10
15
20
25
Premoult Period - Days

Table 14

Pre-moult times, in days, of LL and NN of *Ap. hydrosauri*, *Amb. albolimbatum* and *Amb. limbatum*. The numbers counted (N) the ranges of times, the means ($\bar{x}$) and standard errors of means (SE) are shown. All ticks were kept at 25°C, in the dark, in 85% RH.

		Ap. hydrosauri	*Amb. albolimbatum*	*Amb. limbatum*
LL	N	452	315	281
	Range	11 - 22	14 - 24	7 - 16
	$\bar{x}$	14.72	17.0	10.2
	SE	0.09	0.08	0.06
NN	N	215	Not available	62
	Range	18 - 28		17 - 22
	$\bar{x}$	21.9		18.9
	SE	0.04		0.14

The pre-moult period is greatly influenced by temperature as would be expected (Arthur 1951, 1962, Cooney and Hays, 1972). Below, in table 15 are presented some unpublished data of Dr. Smyth which illustrate this.

Table 15

The pre-moult periods in days at 20°C, 25°C, 30°C (All at 85% RH, dark) of LL of *Ap. hydrosauri*, *Amb. albolimbatum* and *Amb. limbatum*, each from a single batch of eggs and one host individual.

	20°C	25°C	30°C
Ap. hydrosauri			
N	108	75	82
$\bar{x}$	31.03	18.61	12.65
SE	0.22	0.29	0.17
Range	26 - 38	15 - 27	10 - 20
Amb. albolimbatum			
N	318	309	318
$\bar{x}$	37.63	16.97	10.95
SE	0.16	0.08	0.05
Range	23 - 47	14 - 24	9 - 16
Amb. limbatum			
N	30	28	29
$\bar{x}$	32.23	13.86	8.90
SE	0.70	0.29	0.35
Range	23 - 39	11 - 16	7 - 17

A comparison of the values in the 25°C columnof table 15 with table 14 reveals intraspecific differences in pre-moult periods. Bull, Sharrad and Smyth (1977) examined the pre-moult period of one of the ticks, *Ap. hydrosauri*, in order to discover the nature of this variability (the paper is included below as appendix 4). We found that the pre-moult periods of LL and NN was not influenced by their engorgement weights or engorgement times. However, there were differences in pre-moult times between ticks from different individual hosts of the same species, perhaps this was due to differences in levels of resistance among the hosts. There were also differences observed between ticks from different localities, with the ticks from southern areas appearing to moult more rapidly than those from further north (see 3.60 for more information on geographical variation). The pre-moult periods of NN which subsequently became ♀♀ were longer than for those which moulted to ♂♂. It was also shown (Bull, Sharrad and Smyth 1977) that *Ap. hydrosauri* LL moulted significantly faster if they had fed on *Tr. rugosus* rather than on any of three other host species. *Tr. rugosus* is the most common, most heavily infested and most commonly infested host of *Ap. hydrosauri* (see also 4.22).

The variations in pre-moult periods described above do not appear to alter the general relationship between the species in that *Amb. limbatum* moults more quickly than *Amb. albolimbatum* which moults more quickly than *Ap. hydrosauri* at moderate to high temperatures (25-30°C). But at lower temperatures (20°C) *Ap. hydrosauri* is first to moult. These observations help explain the differences observed between the species in the field enclosures at Pt.Gawler (see 3.33).

Snow (1969) and Branagan (1973) have demonstrated that humidity seems relatively unimportant in influencing moulting. This is likely to be the case with these ticks. Indeed ticks left to moult under conditions where humidity was not controlled appeared to moult in the time expected at that temperature.

The pre-moult periods of these ticks are compared with those of other ticks in table 16.

Table 16

A comparison of pre-moult periods of other ticks which have been studied with *Ap. hydrosauri*, *Amb. albolimbatum* and *Amb. limbatum*. (+) means that the tick, the name of which appears at the top of the column, moults faster than the one in that row. (-) means it moults more slowly. (0) means that the times are about equal.

Species	*Ap. hydrosauri*	*Amb. albolimbatum*	*Amb. limbatum*
Dermacentor variabilis (Arthur 1962)	-	-	-
D. andersoni (Arthur 1962)	-	-	-
Haemaphysalis leporispalustris (Arthur 1962)	-	-	-
Hyalomma dromedarii (Feldman-Muhsam & Muhsam 1966)	0	+	+
H. anatolicum (Snow, 1969)	-	-	-
H savigny (Feldman-Muhsam, 1948)	-	-	-
Ixodes hexagonus (Arthur 1951)	+	+	+
Amblyomma tuberculatum (Cooney and Hays, 1972)	+	+	+
A. geomydae (Nadchatran, 1960)	+	+	+

The last two species listed are also reptilian ticks, and they take longer to moult than the three species in the present study. The other ticks parasitize mammals and generally moult faster.

3.3414 The behaviour of the ticks off the host and attachment

The newly-moulted or newly-hatched tick is unable at first to attach to a host (Arthur 1962). This is said to be due to the necessity for the newly exposed cuticle to be exposed to the air for a time before it hardens. The time before ticks attach is generally from a few days to four weeks (in *Amblyomma geomydae*, Nadchatran, 1960). In the three species studied here this period seems to be about one to two weeks at 25°C. It seems to be shorter in the *Amblyommas* and longer in *Ap. hydrosauri.*

The behavioural patterns of ticks off the host are adapted to prevent death by exposure to extremes of temperature or low humidities and to finding hosts. The sheep tick *I. ricinus* was first to have an extensive ethogram prepared. Lees (1948) summarized the information for this animal. Arthur (1962) discussed and reviewed the literature on tick behaviour.

The behaviour of ticks off hosts seems to be dominated by a few kineses and taxes stimulated by humidity, heat, touch, chemicals and light. Ticks possess, in the first tarsus on the anterior pair of legs, an organ called Haller's organ (Lees, 1948). This organ contains humidity sensors and chemo receptors (for odours). Also on ticks' legs are long sensory bristles which are both temperature and tactile receptors Wooley (1972). It is noticeable that ticks wave their fore-legs when disturbed or when moving about. This is called 'questing'. Some ticks have 'eyes'. *Amblyomma* spp do, but *Ap. hydrosauri* does not. Douglas (1943) reported that the eyes of *Dermacentor andersoni* are supplied with nerves and can detect light. Binnington (1972) also reported functional photoreceptors in a variety of ticks including eyeless ticks.

The investigation of sense organs of ticks has recently been aided by the development of scanning electron microscopy, e.g. Wooley (1972).

In general, unfed ticks seem to avoid prolonged exposure to low humidities, although they might have to so expose themselves from time to time in order to find a host (Arthur 1962). The response to humidity changes is determined by the physiological states of some ticks. Lees (1948) showed that if *I. ricinus* are placed in humidity choice chambers that they accumulate on the dry side for the first day but move to the other side after day 1. They also become less active as time goes by. Lees said that there were two reactions involved; the first was a taxis in which ticks avoided moist air, and the second a kinesis in which they avoided desiccation. Some ticks also avoid very high humidities (e.g.

Ornithodoros erraticus, El Ziady, 1958). The two reactions, above, of *I. ricinus* result in this tick moving up vegetation into dryer air and, after a time, down into the mat into wetter air. Thus it maximizes its chances of finding a host without desiccating too much.

The orientation of ticks and their degree of activity are thus influenced by humidity (Arthur, 1962). Bull (1969) showed that *Ap. hydrosauri* LL are more active at higher temperatures and relative humidities than at lower ones. This seems also to be true of *Amb. limbatum.* The ticks, which tend to clump while being stored in vials, also become active when they are (or a few of the group are) stimulated mechanically. Bull (1969) suggested that this might be a most significant instigator of activity in these reptilian ticks as in the case of the sand martin flea (Humphries 1969).

The phenomenon of clumping is found in all three species and, when considered with the observations on the non-random distribution of ticks on reptiles caught in the field (Bull 1969, 1978 b and 3.32 above), lend support to the hypothesis that they are similarly aggregated in reptile refuges in the field. There is now additional information on this matter. Petney and Bull (1979) have presented convincing evidence that NN of *Ap. hydrosauri* and *Amb. limbatum* produce a non-specific aggregation pheromone which attracts either species. Bull (1978) surmized that unfed LL remained clumped in the field, became active together on detecting a host and thus attached near each other.

Arthur (1962) reports that temperature and odour are very important stimuli in causing many ticks to attach to hosts. Lees (1948) showed that warm objects (37°C) are attractive to sheep ticks. Wilkinson (1953) reported that LL of the cattle tick *Boophilus microplus* are stimulated to 'quest' for a host partly by odours, air currents, vibration, interrupted light, warmth and moisture. High carbon dioxide concentrations near mammalian hosts seem important in mammalian ticks (Garcia, 1962).

The effect of CO_2 on ticks was tested in two ways with mixed groups of

Ap. hydrosauri and *Amb. limbatum* LL. In the first case the ticks were scattered randomly in a large tray containing a small block of 'dry ice' (frozen CO_2). This rapidly sublimed. The movements of the ticks were recorded but no movement towards the CO_2 source was noted. The experiment was repeated with similar results. In a second attempt CO_2 was allowed to leak slowly from a hose attached to a cylinder at room temperature into a tray containing LL. Again no response was observed.

The ticks do, however, respond to vibrations, sudden changes in air movement and mechanical disturbance, by questing. There is also a suggestion that they are attracted to objects warmer than ambient conditions. The 'odour' of the host may be important but CO_2 does not seem to be.

Although ticks may be activated by the stimuli listed above it is not believed that they move far to infest a host. Trevor Petney (pers. comm.) has been using radioactively labelled ticks to explore aspects of their behaviour in microhabitats off hosts at Mt Mary. He suggests that they are unlikely to move 1 metre from their crevice in order to attach to a host!

The attached LL, NN and ♀♀ become very firmly stuck to hosts. The reptilian ticks crawl under lizard scales, stick their mouthparts (which are long compared with other ticks) through the host's skin and secrete a 'cement' plug around them (Arthur 1962). ♂♂ do not attach as firmly as the others and can detach quickly and move about on the host.

3.342 Tick development and behaviour on the host.

While attached to a host, ticks experience a very different environment from that when detached. There is for example no longer danger of desiccation. The LL, NN and ♀♀ engorge with blood while the ♂♂ seek mates. The rates of development and behaviour of ticks on hosts are explored below.

3.3421 Engorgement.

When ixodid ticks attach to hosts they engorge in two stages (Arthur 1962). At first small amounts of host substances are imbibed and the tick's weight only increases a little. During this stage it is suggested (Lees 1952) that materials and energy gained from the small amounts ingested are used to prepare the tick for the second stage of engorgement. These preparations include synthesis of new compounds for the cuticle which must distend greatly in the second stage. Usually the second stage, in which the weight and volume of the tick increases many times, is shorter than the first stage. Kitaoka and Yajisma (1957) suggest that in *Boophilus candatus* engorgement can be divided into three such stages by considering changes in body length and weight.

The duration of engorgement may be prolonged by the physiological state of the host. Carrick and Bullough (1940) showed that *I. ricinus* took longer to engorge if attached to hibernating hedgehogs rather than active ones. The enclosure experiments reported in 3.33 show that engorgement of reptilian ticks may be greatly influenced by ambient temperature. The ambient temperature also influenced the poikilothermic hosts.

The duration of engorgement is measured from the time unfed ticks attach to a host to the time it detaches. Arthur (1962) in fact suggests that ticks might time engorgement so that it, and the subsequent detachment, occur during a suitable phase in the host's activity pattern.

The engorgement times of LL and NN are presented below for *Ap. hydrosauri* and *Amb. limbatum*. The ticks were placed on sleepy lizards, *Tr. rugosus*, in the manner described in appendix 2. The lizards in their cages (See appendix 2) were kept in a room with controlled light and temperature - both being supplied by heat lamps attached to a time switch. The temperatures varied from 18°C at night to 32°C during the day. The light:dark cycle was 12 hours light to 12 hours dark. The detached ticks were collected each day from trays under the lizards. The lizards were fed every other day.

Figure 27 gives the numbers of *Ap. hydrosauri* LL detaching from four lizards under the above conditions. Figure 28 shows similar graphs for *Amb. limbatum* LL. It is evident in both that some ticks detach, engorged, after only 8 days and that numbers detaching become high until about day 15 when only a few remain. Another striking feature of the graphs is that there is great variability between the different host individuals. Obviously some hosts are better for the LL than others, as each received the same number of ticks.

In figure 29 similar data are presented for NN of the two species. The times taken for the ticks to engorge and detach are similar to those for the LL.

Ap. hydrosauri LL weigh in the order of 0.1 to 0.2 mgm before engorgement. Engorged LL are much heavier, from 2.0 to 4 mgm, a tenfold increase. *Amb. albolimbatum* LL are of similar weight while *Amb. limbatum* are on average slightly lighter.

Engorged NN weights are distributed in a bimodal fashion see figure 30. In table 17 weights of NN of *Ap. hydrosauri* and *Amb. limbatum* are shown.

Table 17

Weights in mgms of NN of *Amb. limbatum* and *Ap. hydrosauri* from a number of hosts (*Tr. rugosus*). Values are shown for NN which subsequently moulted to give oo and those which gave rise to ♀♀ for each individual host. The figures for each tick species come from a single infestation of each individual host by NN which came from a single ♀.

Figure 27. The cumulative daily numbers of *Ap. hydrosauri* LL detaching, engorged, from each of four sleepy lizards, *Tr. rugosus*. Each lizard was infested with 400 LL which had hatched in the laboratory from two egg batches layed by field caught ♀♀.

The infested lizards were exposed to a 12h:12h, day:night, cycle and a daily temperature fluctuation from 18 to 32°C.

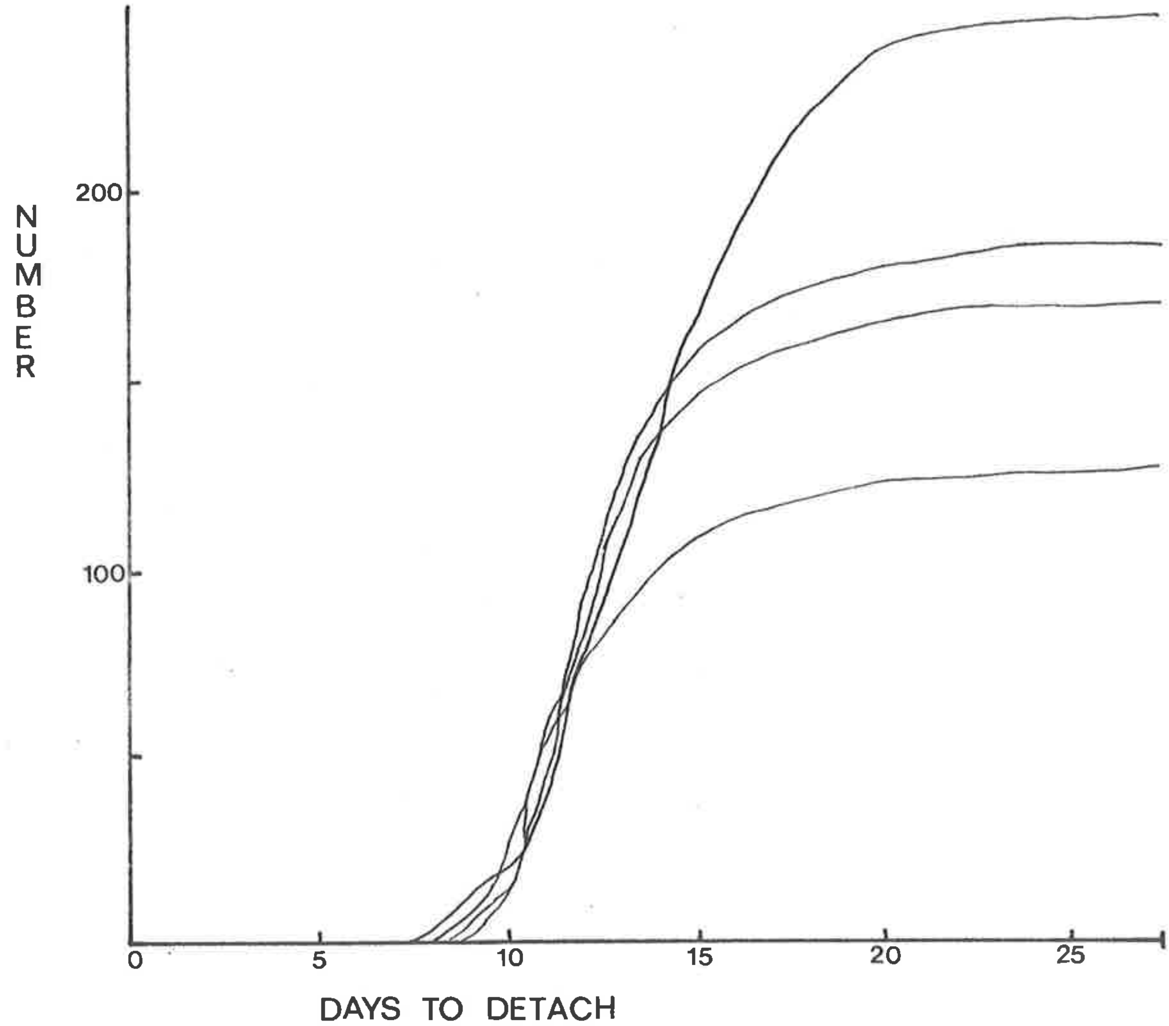

200
100
NUMBER
0
5
10
15
20
25
DAYS TO DETACH

Figure 28. The cumulative daily numbers of *Amb. limbatum* LL detaching, engorged, from each of four sleepy lizards, *Tr. rugosus*. Each lizard was infested with 400 LL which had hatched in the laboratory from eggs layed by a ♀ caught at Mt Mary.

The infested lizards were exposed to a 12:12, day:night, cycle and a daily temperature fluctuation from 18 to 32°C.

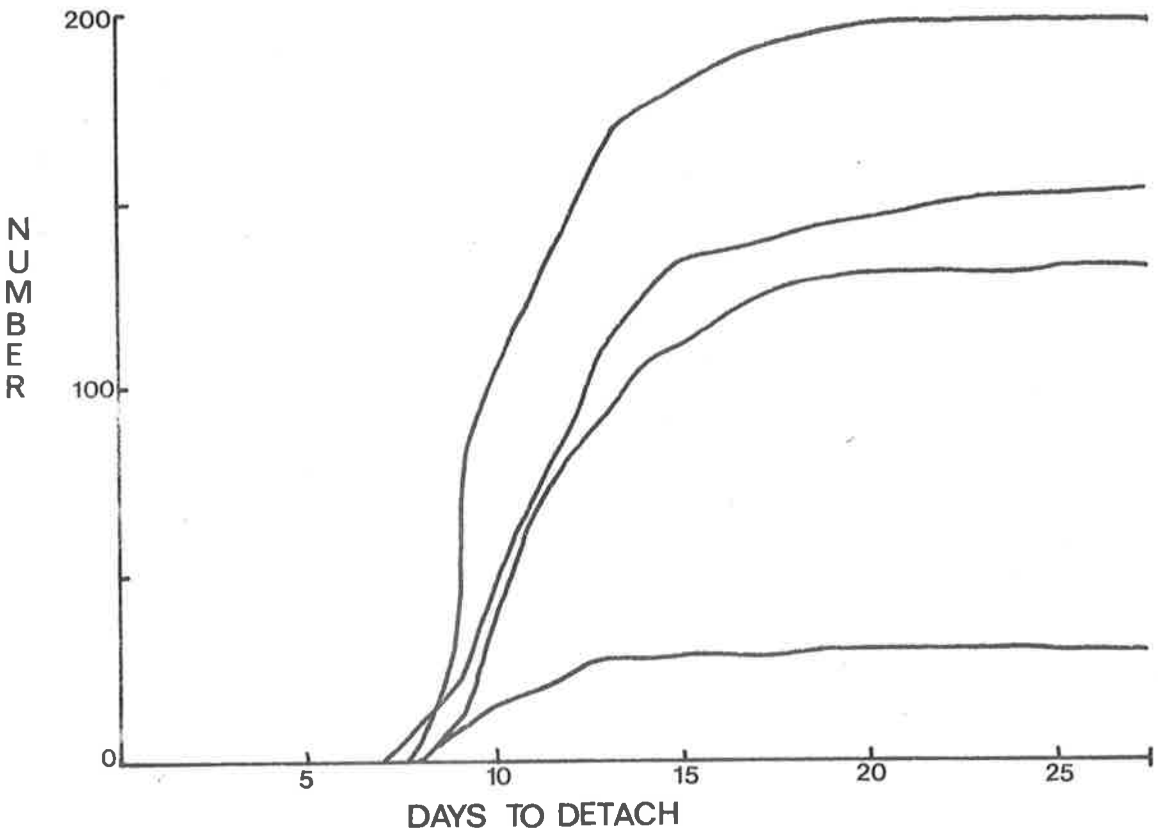

200
100
0
NUMBER
5
10
15
20
25
DAYS TO DETACH

Figure 29. The cumulative daily numbers of *Ap. hydrosauri* and *Amb. limbatum* NN detaching, engorged, from sleepy lizards, *Tr. rugosus*. Each lizard was infested with 80 NN which had developed in the laboratory from eggs layed by ♀♀ caught in the field.

The infested lizards were exposed to a 12h:12h, day:night, cycle and a daily temperature fluctuation from 18 to 32°C.

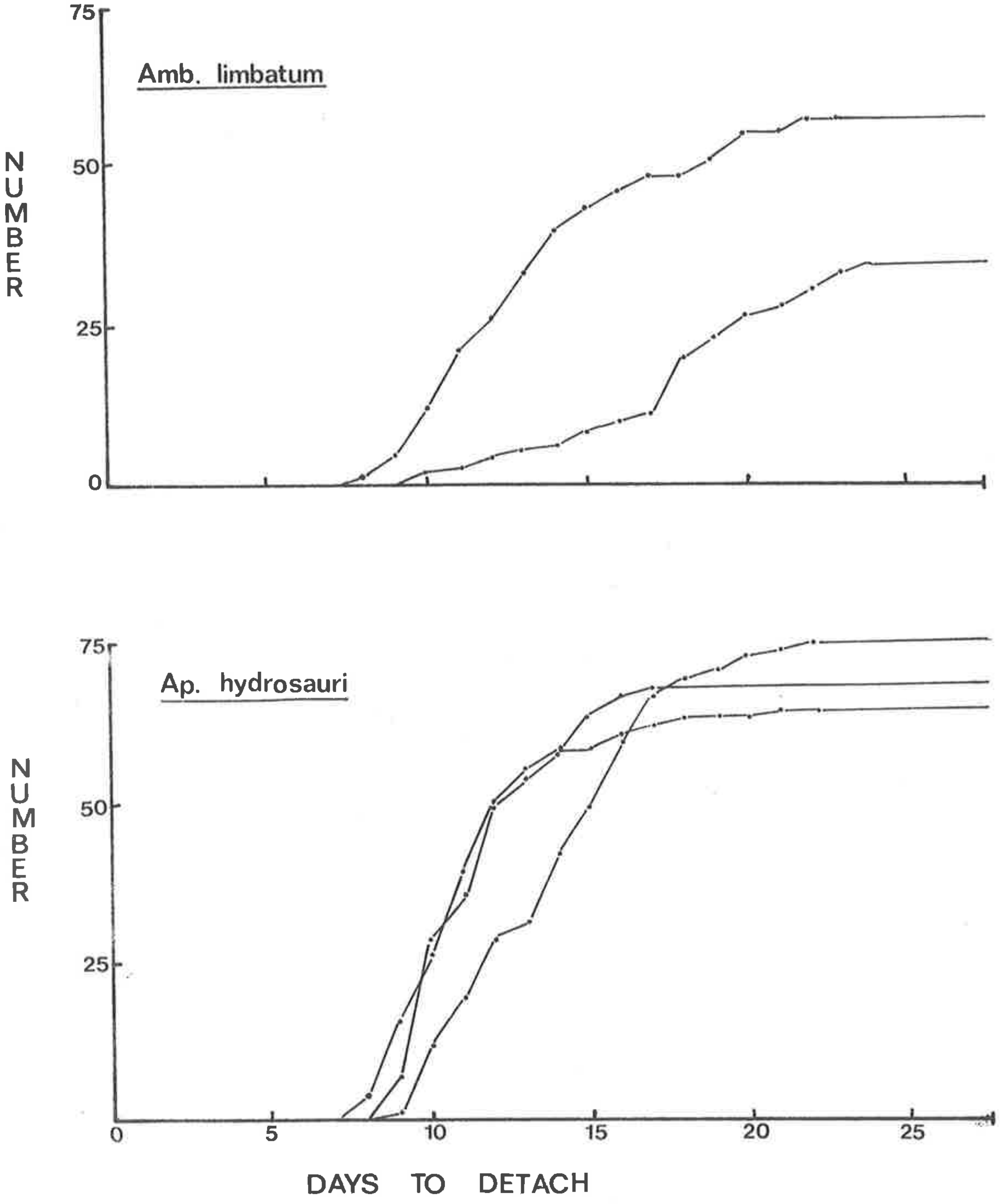
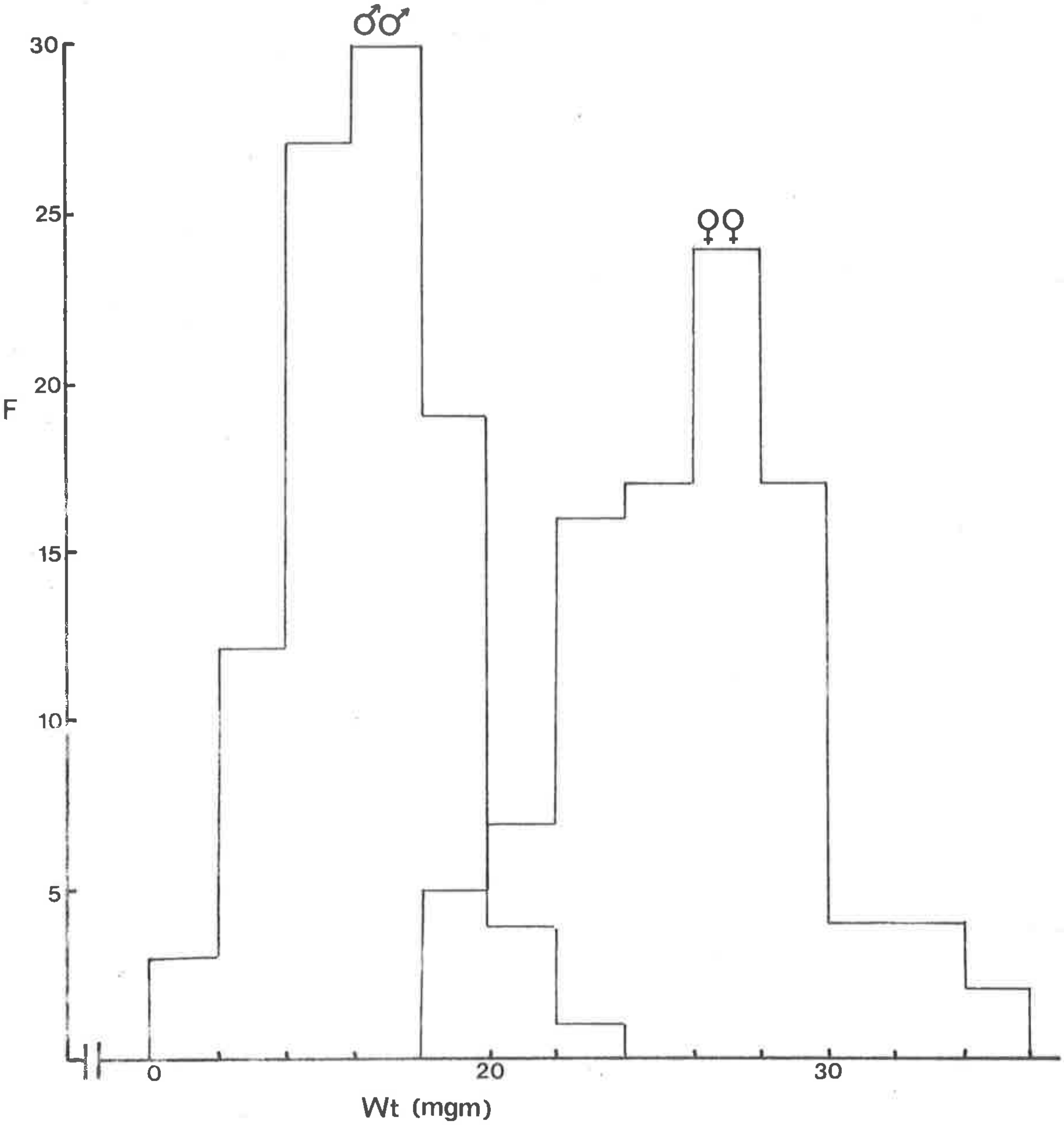

Amb. limbatum
Ap. hydrosauri
NUMBER
NUMBER
0
25
50
75
0
5
10
15
20
25
DAYS TO DETACH

Figure 30. Frequency distributions of weights (mgm) of engorged NN of *Ap. hydrosauri*, showing separate graphs for those NN which subsequently moulted to ♂♂ and those which moulted to ♀♀.

♂♂
♀♀
30
25
20
15
10
5
F
0
20
30
Wt (mgm)

		Amb. limbatum		*Ap. hydrosauri*	
	Sex of NN	♂♂	♀♀	♂♂	♀♀
Host 1.	N	35	12	28	30
	$\bar{x}$	16.6	28.92	16.6	27.1
	SE	0.36	1.03	0.48	0.66
Host 2.	N	8	12	29	33
	$\bar{x}$	15.9	28.36	17.46	28.73
	SE	0.57	1.04	0.33	0.70
Host 3.	N	6	4	33	34
	$\bar{x}$	14.22	26.97	14.73	23.69
	SE	0.79	2.28	0.29	0.66
Host 4.	N	3	5	12	31
	$\bar{x}$	14.91	27.17	15.73	25.69
	SE	1.61	2.86	0.50	0.51

The weight of engorged, detached LL and NN (see table 17 above) varies from host to host. It also varies over the period of engorgement, i.e., ticks which detach first tend to be lighter (and ♂♂) while ticks which detach later tend to be heavier (and ♀♀) (Smyth, pers. comm.).

The ticks engorge faster at higher ambient temperatures (Smyth, pers. comm.). And it seems that the *Amblyomma* spp are more retarded by cold conditions than *Ap. hydrosauri* (see 3.33).

The engorgement of ♀♀ has not been well documented. Weights of engorged ♀♀, however, were presented in table 11 (3.3412) above. The ♂♂ do not engorge or attach as firmly as the ♀♀. However they do imbibe some blood probably, as Bull (1969), suggests, to provide energy for roaming in search of ♀♀. It has been demonstrated in some ticks that mating is necessary before ♀♀ will engorge, e.g. *Dermacentor variabilis* (Pappas and Oliver 1971).

It is evident that ♀♀ may take along time to begin engorging, or may not engorge at all. Nine lizards (*Tr. rugosus*) were infested with ♂♂ and ♀♀ *Ap. hydrosauri* and *Amb. limbatum* (3 lizards per species) and regularly checked for two months - only 1 ♀ *Ap. hydrosauri* engorged. On repeating this procedure 2 ♀♀ *Amb. limbatum* engorged in 2 months. However on other occasions ♀ *Ap. hydrosauri* have engorged and detached in 25 days.

3.3422 Mating

It was noted early in the present study that mating occurs on the host in these ticks. ♂ and ♀ ticks were observed copulating on field caught lizards and in some cases ♀♀ were found with signs of spermatophores at their genital openings. However Michael Smyth (pers. comm.) reported seeing what appeared to be copulation between a ♂ and unengorged ♀ *Ap. hydrosauri* off the host.

In Chapter 6 I detail experiments in which attempts were made to have the three species mate in the laboratory. These met with little success. However our knowledge of the mating behaviour of the ticks has been greatly expanded recently by the work done by Ross Andrews a PHD student at Flinders University.

Ross Andrews has been able, after very long and laborious trial and error, to observe many matings both on and off hosts. He has confirmed the observations of Michael Smyth (pers. comm.) and Michael Bull (pers. comm.) and my observations that ♀♀ ticks do not move much on the host whereas ♂♂ do. The ♂♂ may move about considerably at night, particularly early in the dark phase, and have been observed mating with or attaching to the host near ♀♀ (Andrews pers. comm.). Mating has often been observed in ticks off the host. In some ticks the ♀♀ release pheromones which attract ♂♂ to them (Burger, Dukes and Chow 1971). There is some evidence that ♀♀ of these ticks also release pheromones of this type. There is no evidence that ♀♀ actively seek out mates themselves - unlike *Amb. maculatum* on cattle where ♀♀ may move in search of ♂♂ (Gladney 1971).

In order to successfully copulate with a ♀ the ♂ tick has to locate her (the possibility of pheromones being involved is mentioned above), climb beneath the ♀ (who is probably firmly attached to the host), cling to her upside down and insert his mouthparts into the vaginal opening. This involves a series of stereotyped positional movements by both ticks (Andrews pers. comm.)

These complex behaviour sequences might be important as pre-mating isolating mechanisms as it appears that the pheromone which attracts the ♂ to a ♀ may not be species specific. A critical point in this sequence is a movement by the ♀ which allows the ♂ to get beneath her into the mating position. Ross Andrews reports seeing instances where ♀♀ have clamped their ventral surfaces close to the hosts' body and thus excluded active ♂♂. In Chapter 6 the possibility of interspecific mating is discussed as a mechanism which, it has been hypothesized, determine the parapatric nature of the tick distributions.

Observations in the laboratory and on ticks in field enclosures suggest that in these ticks, as in many species (Arthur 1962), mating must precede final engorgement of the ♀.

3.3423 Detachment

It was shown in 3.3411 that the timing of detachment in ticks is of importance in selecting microhabitats off the host. It would seem likely that the reptile ticks would detach in host refuges. Bull (1969) tested the influence of light:dark cycles and temperature on the timing of detachment in the ticks. He showed that LL of *Ap. hydrosauri* detached most readily in the dark and when it was warm. It is not clear, however, whether these stimuli act directly on the tick or whether the tick reacts to changes in the host.

3.343 Summary of Tick development

The data presented on the ticks in 3.341 and 3.342 above give some indication of the duration of the various stages of their life cycles. These are summarized in table 18 below. The times given are measures and estimates described in more detail in 3.341 and 3.342.

Table 18

The duration of the various stages of the life cycles of *Ap. hydrosauri*, *Amb. albolimbatum* and *Amb. limbatum* in days under constant conditions at 25-27°C and 85% RH. The figures are average ones or estimates. Estimates for which there is little supporting data are placed in brackets ( ).

Stage	*Ap. hydrosauri*	*Amb. Albolimbatum*	*Amb. limbatum*
LL Time before attaching	(15)	(15)	(12)
Time to engorge and detach	14	(14)	14
Time to moult	15	17	10
NN Time before attaching	(20)	(20)	(20)
Time to engorge and detach	14	(14)	14
Time to moult	22	(23)	19
♀♀ Time before attachment	(20)	(20)	(20)
Time before detachment	25	(25)	(25)
Preoviposition time	27	6	8
Time for eggs to hatch	37	37	34
TOTAL	209	191	176

In nature temperatures and humidities do not remain constant. However the ones chosen above are well within the ranges experienced by the ticks (Aust. Bur. Met., 1975). The rates of development, shown in table 18, are probably rarely achieved outside laboratories. However if the data for the *Amb. limbatum* population at Buckland Park (3.33) are examined it can be seen that in 70 days after lizards were infested with LL the first adults appeared. Table 18 gives 97 days for this development at 25°C. This perhaps indicates that the estimates of the time before ticks attach after moulting are too high and that brief exposures to higher temperatures had a marked influence.

It should also be noted that the field situation includes extra time in that ticks do not find hosts immediately. In fact at high humidities ticks may live many months without food.

A number of other workers have presented similar life history tables for other ticks (e.g. Arthur and Snow, 1968, Murray and Vestjens 1967, Nadchatran 1960). However, none was researched under the same conditions as the present study.

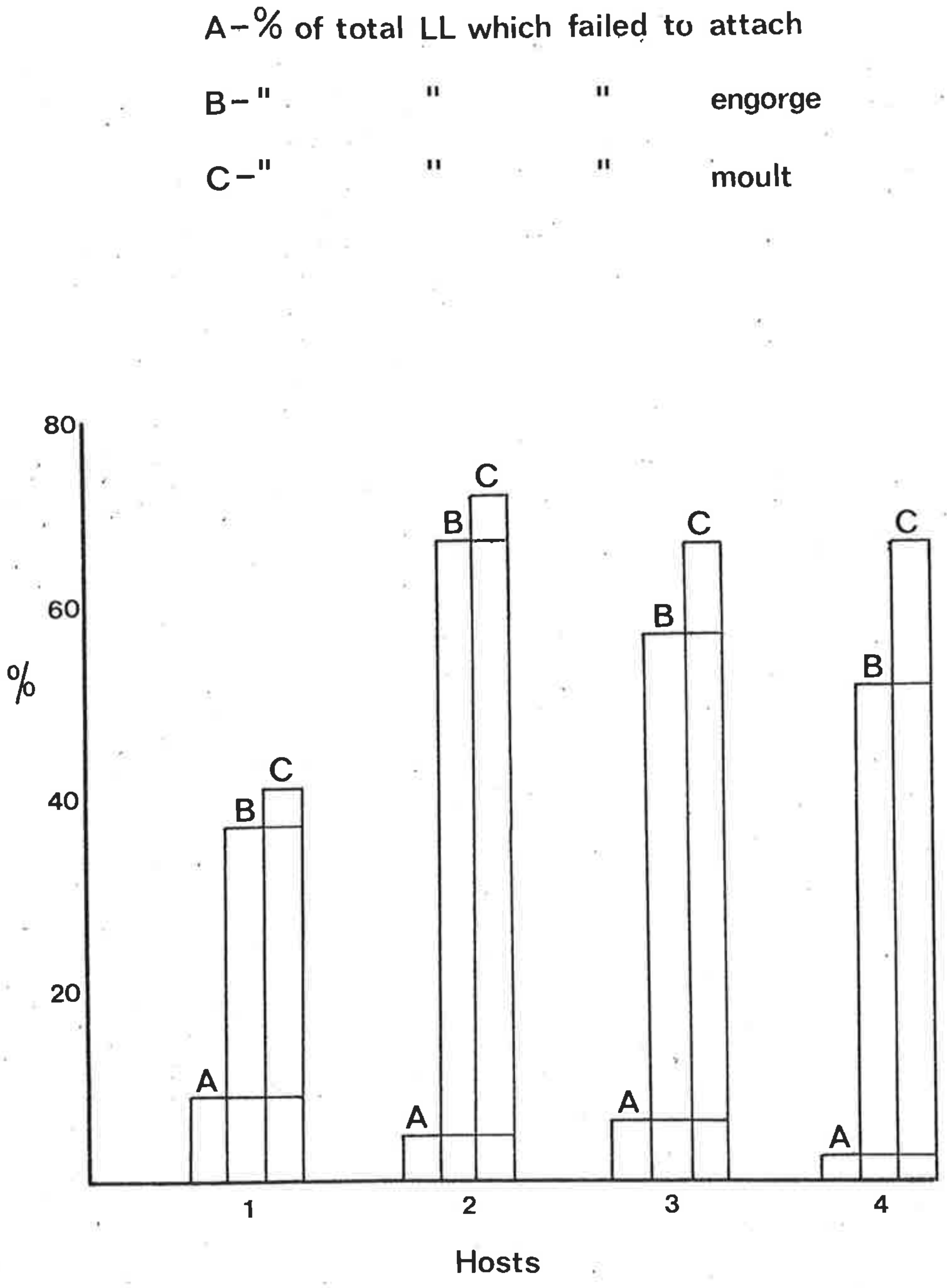
Work of various researchers on the ecology of ticks indicates that ticks are most likely to die when detached and awaiting a host (Giurgis 1971, Owen 1975, Randolph 1975, Theiler 1964). This mortality must be high, for ticks lay many eggs and yet relatively few adults are seen attached to hosts.

In the laboratory, records were kept of the proportion of ticks which died during particular stages of their life cycles. Figures 31 and 32 show the percentage of LL of *Ap. hydrosauri* and *Amb. limbatum* which failed to attach, to engorge and to moult in a particular experiment. The conditions were the same as those described in 3.3421 above. It can be seen that under optimum laboratory conditions ticks are more likely to succeed at attaching and moulting than at engorging. In the field, however, ticks have to moult and then await hosts and may die before one happens by. The Pt Gawler enclosure experiments (see 3.33) show that, even under circumstances where hosts are readily available, many ticks fail to survive the period between detaching and attaching.

Figure 31. The percentages of *Ap. hydrosauri* LL which failed to attach, to engorge and to moult on each of four sleepy lizards, *Tr. rugosus*. Each lizard had been infested with 400 LL.

The infested lizards were exposed to a 12:12, day:night, cycle and a daily temperature fluctuation from 18 to 32°C.

The detached LL were kept at 27°C, and 85% RH.

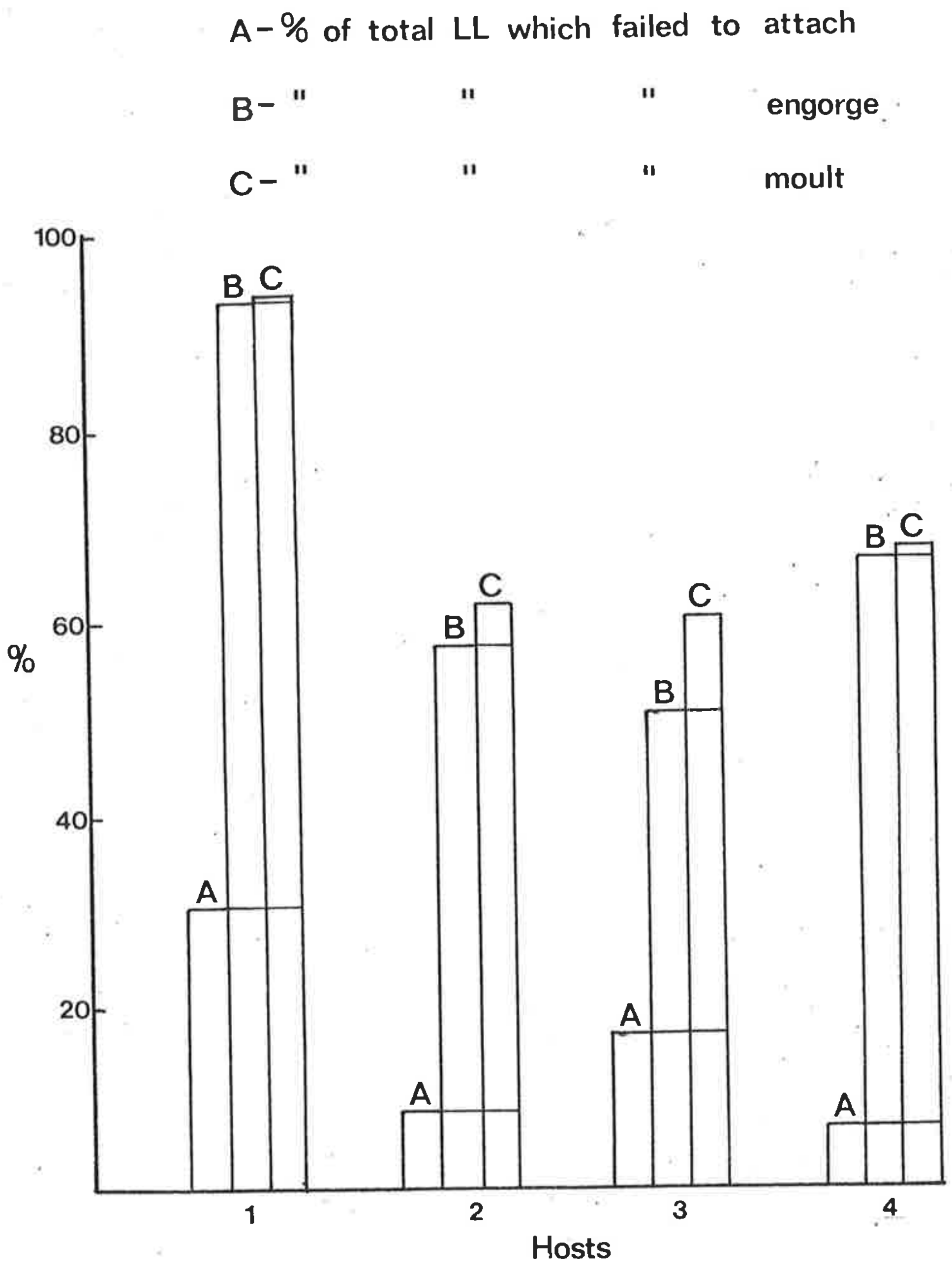


A–% of total LL which failed to attach
B–" " " engorge
C–" " " moult
80
60
40
20
%
A
B
C
1
2
3
4
Hosts

Figure 32. The percentages of *Amb. limbatum* LL which failed to attach, to engorge and to moult on each of four sleepy lizards, *Tr. rugosus*. Each lizard had been infested with 400 LL.

The infested lizards were exposed to a 12:12, day:night, cycle and a daily temperature fluctuation from 18 to 32°C.

The detached LL were kept at 27°C, and 85% RH.


A- % of total LL which failed to attach
B- " " " engorge
C- " " " moult
100
80
60
40
20
%
A
B
C
1
2
3
4
Hosts

3.40 Water Balance

Bull (1969) and Bull and Smyth (1973) describe their investigations on the water balance of the three ticks. They chose this aspect of tick physiology because of the apparent correlation between the distributions of the ticks and some parameters of climate. While seeing these parameters as but one group of factors possibly determining the distributions they believed them to be likely ones. If the boundaries were determined by the climate they reasoned that the responses or tolerances of the ticks to climatic conditions, particularly their capacity to survive arid conditions, would vary. Further, they deduced that the ability of the ticks to withstand dehydration should be illuminated. As attached ticks can make up water lost through evaporation by imbibing fluids from hosts, Bull and Smyth concentrated on the water balance of unengorged, unattached ticks.

Bull and Smyth (1973) report three approaches to measuring the ability of the ticks to withstand arid conditions. They measured 'the rate of evaporative water loss at normal temperatures'. This loss, they suggest, is from two sources; loss through the (almost) waterproof monolayer of wax molecules on the surface of the cuticles of the ticks (see Beament 1965) and water lost during respiration. The structure and waterproofing properties of the wax monolayer are markedly disrupted if its temperature reaches and passes a certain critical point. Lees (1947) and Hafez et al (1970b) had observed that 'ticks from hotter, drier habitats usually have higher critical temperatures (Bull and Smyth 1973). Their second approach was to measure the critical temperatures of the ticks. The third approach involved discovering the humidity range within which the ticks could absorb water from the atmosphere. The relative humidity value above which a tick can gain water from the atmosphere and below which it cannot, is called the equilibrium humidity.

They found that *Ap. hydrosauri*, despite being the largest of the three species, lost water more quickly than the *Amblyomma* spp. *Amb. albolimbatum*, though larger than its congener, lost water at a similar rate. When survival times in dry air were compared, *Amb. albolimbatum* lived longest and *Ap. hydrosauri* died most quickly.

Amb. limbatum had the highest mean critical temperature (53.9 ± 0.63°C). Critical temperatures were only measured in adult ticks.

The estimates of the equilibrium humidities of the ticks were very similar, i.e. in the range 81 to 83% RH. There was a suggestion that *Amb. limbatum* might absorb water from air at slightly lower humidities within this range than the other ticks.

Bull and Smyth (1973) briefly reported preliminary experiments to find the site of water intake in the ticks. They found that by blocking the mouthparts of a tick with wax they could prevent water intake, at 91% RH, whereas blocking the spiracles or the anus did not. It was not clear whether wax on the mouthparts stopped water intake there or elsewhere.

The information obtained by Bull and Smyth enabled them to suggest that the northern limit of the distribution of *Ap. hydrosauri* might be due to its inability to survive long exposure to dry conditions. But the reasons for the southern limit of the two *Amblyomma* spp. remained obscure. Their results indicated that *Amb. albolimbatum* was best able to survive dry periods and yet it is found south of *Amb. limbatum*!

The research of Bull and Smyth indicates that an understanding of the ticks' resistance to desiccation is insufficient to account for their distributions, except for the observations on the northern boundaries of *Ap. hydrosauri*. It is evident that knowledge is needed of the factors which influence the ticks in the field, particularly at the boundaries.

Indeed such studies, of physiological ecology under laboratory conditions, have been criticised as being only able to show that an animal can live where it does, not why it doesnt live in other areas (Bartholomew 1958).

In this case data on differences in the physiological capabilities of the ticks do not, by themselves, help us decide which factors are primarily responsible for the distributions.

3.50 Predators and pathogens

Predators may influence the distribution of animals. Kitching and Ebling (1967) clearly demonstrated such an interaction in the Lough Ine area of Ireland. A mussel (*Myticlus edulis*) though common along the coast was absent from sheltered waters. Kitching and Ebling showed that this distribution was due to species of crabs which were able to eat adult mussels and were common on more-protected shores.

It is known that ticks have a number of predators, parasites and pathogens. Petrishcheva and Zhmayeva (1949) examined the stomach contents of birds which they observed on the backs of spotted reindeer in the southern Siknota - Alin mountains. The birds, magpies, *Cyanopica cyana pallescens* and *Pica pica Eucoptera*, each contained from 3 to 30 ticks, with representatives of eight different genera. In fact, Petrishcheva and Zhmayeva noted that every type of tick known to exist in the area was represented in the stomachs of the magpies and of starlings. Amadon (1967) reported observing birds remove ticks from lizards. He describes the removal of *Amb. d. darwini* from marine iguanas by Galapagos finches.

Ticks are also attached by species of wasps. Doube and Heath (1975) noted that an encyrtid wasp, *Hunterellus* sp., parasitized engorged LL and NN of *Haemaphysalis bancrofti* and NN of *H. bremneri*, *Ixodes holocyclus* and *I. tasmani* in Queensland. Oliver (1964) had also reported finding wasps attacking engorged NN of *I. tasmani*. It is apparent that some ticks, at least in laboratories, may be attacked by fungi (Randolph 1975). Ants are also known to kill and eat ticks. Harris and Burns (1972) described how the lone-star tick (*Amb. americanum*) was predated upon by the five-ant. Ticks are also likely to be preyed upon by insectivorous rodents and predaceous mites.

Healey (1973, cited in Healey 1979) used precipitating antisera for the serological identification of the predators of *Ixodes ricinus*. He suggested (Healey 1979) that bredation by spiders, harvestmen, centipedes and beetles, all of which may attack *I. ricinus*, played a "subordinate role" in restricting the spatial distribution of the tick. Factors such as relative humidity and availability of hosts (sheep in that case) were found to be more important.

I have not observed any grooming of sleepy lizards by birds. Sometimes, however, one sees attached to lizards mouthparts of ticks with bodies missing. Such occurrences are rare. In the laboratory sleepy lizards, *Tr. rugosus*, will bite engorged ♀ ticks off other lizards caged with them. They also eat any engorged ticks which detach and remain within reach. This is not known to happen in the field. In field enclosures, lizards bore engorging ♀♀ for many days at a time and there was no evidence that other lizards ate these ticks.

Oliver (1964) and Doube and Heath (1975) found evidence of parasitizm by wasps of engorged NN by keeping detached NN from wild caught hosts in the laboratory. The wasps lay eggs in the NN which hatch, devour the contents of the ticks and bore a hole in the cuticle through which the tiny adult wasps egress. Many hundreds of engorged LL, NN and ♀♀ of the three species have been kept in the laboratory and none showed signs of such parasitizm.

Observations on laboratory and field populations also failed to produce evidence of other predators. However, in laboratory stocks in vials, it was noticed that types of mould would sometimes destroy ticks or their eggs.

3.60 Geographical Variation

Thomas (1968) showed that *Haemaphysalis leporispalustris*, a rabbit tick found in North America, exhibits variation in morphology across its range. He analysed six morphological characteristics and uncovered correlations between some changes in morphology and geographical position. In *Rhipicephalus* *sanguineus* analysis of morphological variability shows that it is probably a complex of species (Paperna and Giladi, 1974). Apart from variation in morphology with geography the seasonal activity and rates of development of ticks may show similar trends (see 3.30).

There is morphological variation within each of the three species. Roberts (1970) notes that there is variability in size and ornamentation of the ticks. In South Australia, *Ap. hydrosauri* appears to vary in size across its range. The populations in the northern parts of its distribution seem to contain larger members than those farther south. Table 19 shows measurements of scutum sizes in adult ticks from various parts of the state.

Table 19

Scutum widths in mm of ♂♂ *Ap. hydrosauri* from various localities in South Australia.

Locality (latitude)	Number of ticks	Mean (mm)	SE of mean
Cleve (33.7°)	26	3.88	0.033
Mt Mary (34°)	40	4.08	0.026
Renmark (34.2°)	10	3.90	0.039
Maggea (34.5°)	10	3.86	0.039
Central Yorke Pen. (34.5°)	27	3.88	0.037
Cambrai (34.6°)	12	3.96	0.053
Pt Gawler (34.7°)	44	3.86	0.025
Lower Yorke Pen. (35°)	12	3.82	0.082
Pinnaroo (35.3°)	10	3.88	0.04
Meningie (35.7°)	13	3.67	0.064
Mia Mia Flat (36.5°)	31	3.72	0.041
Cape Northumberland (38°)	13	3.08	0.056

The results of the analysis of variance are shown in table 20 (Sokal and Rohlf, 1969).

Table 20

One-way analysis of variance of scutum widths of ♂♂ *Ap. hydrosauri* from various localities shown in table 19.

Source of variation	d.f.	s.s.	M.S.	F_s	P
among groups	11	11.71	1.06	30.29	$p<0.01$
Within groups	236	8.31	.035		
TOTAL	247	20.02			

Table 20 shows that there is a significant added variance component among areas for width of scutum in ♂♂ *Ap. hydrosauri*. Similar measures have not been made of ticks from laboratory stocks originating in the different areas.

There is also evidence that ticks from different areas might moult at different rates when kept under the same conditions (Bull, Sharrad and Smyth 1977 - appendix 4).

The evidence above suggest that caution must be used in using results from one local population of a tick to explain happenings in another local population within the species. Ehrlich and Raven (1969) in fact suggest that gene flow between local populations is so low that they (local populations), and not the biological species, are the 'real' units of nature.

Bull and Sara (1976) report studies of esterase polymorphisms in *Ap. hydrosauri* . These data were preliminary but support the hypothesis that gene flow between different local populations of this tick is low. These studies, involving electrophoretic techniques, are proceeding with ticks from many parts of the range of *Ap. hydrosauri* being tested.

4.00 HOSTS

4.10 Introduction

The geographical distributions of parasites and diseases are limited by the distributions of their hosts. Similarly one might expect there to be a relationship between abundance of parasites and diseases and abundance of hosts.

If a parasite is host specific,or if, say, the adult stage of its life cycle is, then the geographical distribution of the parasite cannot exceed that of the host.

The tick *Amblyomma tuberculatum* is one such parasite whose distribution seems to be largely determined by the distribution of its one host the gopher tortoise *Gopherus polyphemus* (Cooney 1968, 1972). The distribution of a parasite may, however, be smaller than that of the hosts. In some parts of the host's range,other factors, such as predators of the parasite or adverse aspects of the microhabitat of the non-parasitic stages, might impose distributional limits. Changes of host abundance across its range might also effect the parasite's distribution. Mohr (1961A) showed that the infestation rate of rabbits by *Haemaphysalis leporispalustris* decreases with increased spacing of the hosts. There may also be a particular host abundance below which the parasite will not persist. If the host's distribution is disjunct, the parasite may be absent from some populations if one of the above factors is operating or has been important in the past. This might have occurred with *Aponomma aurignans*, a wombat tick whose hosts have disjunct populations. Roberts (1970) remarked that this tick is not found on Queensland populations of wombats. It also seems absent from the isolated population of *Lasiorhinus latifrons* near Blanchetown, South Australia (R.T. Wells pers comm).

Distributions of parasites that infest a wide range of hosts might not be limited by the distribution of any one of them. The *Ixodes ricinus* species group seems to belong in this category (Arthur, 1962). On the other hand, a parasite might have a wide range of hosts but some, or one, may be more important, in this regard, than the others. The ubiquitous *Rhipicephalus sanguineus* appears to belong in this category (Roberts 1970). It can parasitize a number of mammals but does best on the domestic dog, and its distribution largely matches that of the dog. However, low temperatures also seem to restrict the range of this tick (Subotnick 1956).

Smyth (1973) showed that *Ap. hydrosauri, Amb. albolimbatum* and *Amb. limbatum* parasitized at least 31 species of reptiles. He said that four host species were used by all 3 ticks. They were a dragon, *Amphibolurus barbatus,* two skinks, (the blue tongue *Tiliqua occipitalis* and the sleepy lizard *Trachydosaurus rugosus*), and the brown snake *Pseudonaja textilis.* Two hosts had shared 2 tick species each: *Noetchis sp.* (tiger snakes) parasitized by *Ap. hydrosauri* and *Amb. albolimbatum* and the goanna *Varanus gouldii* with *Ap. hydrosauri* and *Amb. limbatum.* Although the ticks had a number of hosts in common, Smyth suggested that they "might not have the same host preferences or requirements." A preferred host for a particular tick would possess physiological and behavioural characteristics most likely to enable <u>that</u> tick to complete its life cycle.

If the ticks do have different host preferences, then the distribution and abundance of the hosts must be examined, particularly across the tick boundaries. It may be that changes in the behaviour of the hosts are also important. The seasonal and diurnal activity patterns of a poikolothermic host species might change over its geographic range in response to changes in climate. Also, the activity pattern might change at the boundary with a change in food type or some other environmental factor.

In 4.2 the known host species are listed and an attempt made to assess their relative importance as hosts of the ticks. The geographical distributions of the hosts are contrasted in 4.3 with the tick distributions described in Chapter 2. This information is used with findings from 4.2 to see if it is possible to maintain the hypothesis that the tick boundaries are determined by host distributions.

The host species which emerges as the most important South Australian host of the three ticks is examined more closely in 4.4. Here aspects of the host's behaviour are illuminated and suggestions made of the way in which they might affect the ticks' distribution and abundance. Finally in 4.5 the information contained in this chapter, and thus the overall importance of the hosts in influencing the tick distribution, is discussed.

4.20 Host species and their relative importance.

4.21 Host Species.

The known reptilian host species of the three ticks are shown in table 21. The data given are those published by Roberts (1969, 1970) and Smyth (1973), plus other information collected during this study. The table also shows the number of animals of each species recorded as being parasitized in my records and in Smyth's.

Roberts (1970) lists *Ap. hydrosauri* as parasitizing *Bos taurus, Equis caballus* and *Tachyglossus aculeatus*, as well as reptiles. The first two seem to be very rare occurrences and can be disregarded in this treatment. The case of the echidna *(T. aculeatus)* is different. There seems little doubt that there is a population of ticks on echidnas in Queensland near Rockhampton (see chapters 2 and 3). Roberts (1970) noted that this northern form of *Ap. hydrosauri* differed in host preference from southern populations. Apart from the above cases, *Ap. hydrosauri* is a parasite of reptiles. The two *Amblyommas* have only been found on reptiles - except for one ♂

Table 21

A list of known reptilian hosts of *Ap. hydrosauri*, *Amb. albolimbatum* and *Amb. limbatum*, showing for each host species the number found parasitized by each tick species.

HOST		*Ap. hydrosauri*	*Amb. albolimbatum*	*Amb. limbatum*	Total parasitized
Chelonia					
Chelodina longicollis		*			
Pseudemydura umbrina			*		
Sauria					
Agamidae					
Amphibolurus barbatus	X	19	N	31	> 50
" *cristatus*	X	-	-	2	2
" *decresii*	X	-	-	1	1
" *diemensis*		*			
" *fionii*	X	-	-	† 2 †	2
" *ornatus*			N		
" *pictus*	X	-	-	4	4
Moloch horridus		-	1	-	1
Gekkonidae					
Gehyra variegata	X	-	-	† 1 †	1
Gymnodactylus milii	X	-	-	1	1
Scincidae					
Egernia margaretae personata	X	-	-	1	1
" *multiscutata*	X	-	1	-	1
" *whitei*	X	1	-	-	1
Leiolopisma metallicum	X	1	-	-	1
Tiliqua multifasciata		-	† 1 †	† 1 †	2
" *nigrolutea*	X	16	-	-	16
" *occipitalis*	X	3	4	N	>7
" *scincoides*	X	6	-	-	6
Trachydosaurus rugosus	X	696	327	410	1433
Varanidae					
Varanus acanthurus		-	-	*	
" *giganteus*	X	-	-	2	2
" *glebopalma*		-	-	† 2 †	2
" *gouldii*	X	N	-	49	> 49
" *glauerti*		-	-	† 1 †	1
" *timorensis*		-	-	† 1 †	1
" *timorensis scalaris*		-	-	† 1 †	1
Ophidae					
Boidae					
Aspidites sp		-	-	*	
Liasis olivaceus		-	-	*	
Morelia spilotes		-	1	*	1

HOST		*Ap. hydrosauri*	*Amb. albolimbatum*	*Amb. limbatum*	Total parasitized
Elapiade					
Acanthophis antarcticus	X	2	-	-	2
Austrelaps superbus	X	3	-	-	3
Drysdalia coronoides		*			
Notechis sp		*	*		
Notechis ater			1		1
Pseudechis australia	X				
Pseudonaja nuchalis	X				
" *textilis*	X	2	*	4	> 6

N number not known but recorded by Smyth (1973).

* These records are from Roberts (1969, 1970) and have not been replicated in the present study or by Smyth (1973).

†...† A new host record.

X This reptile is a host of ticks in South Australia.

Amb. limbatum which attached to me.

4.22 The relative importance of the reptile species as hosts.

Some reptiles that appear in table 21 are probably rarely parasitized by the ticks - a very small proportion of a tick population would depend on them. Others are more heavily parasitized and a large proportion of the ticks feed on them. The second group is the one which is of interest in that such hosts are most likely to influence the distribution of the ticks.

The relative importance of hosts in this context can be assessed if we know, for each host species, the average number of ticks per host and the proportion of the host population infested. The relative abundances of the different host species are also important in this assessment. The task of determining which hosts are more important for consideration here may be made more difficult if it transpires that juvenile and adult stages of the ticks have different host preferences.

Some idea of the relative importance of host species can be gained by examining field collection records of specimens I collected, or had given to me, and those of Michael Smyth (see appendix 1). There are a number of potential hazards in utilizing these data. Many people who collected ticks for us only recorded the occasions when they found tick infested hosts and did not record and report specimens which were searched and found free of ticks. The proportion of members of that host population parasitized is thus impossible to obtain accurately from the records. Another problem is that some hosts are faster, more cryptic or more dangerous than others and so appear less often in the records. This means that there is a difficulty in calculating accurately the relative abundance of hosts. It is apparent that some collectors are more skilled and/or experienced than others and are likely to find more ticks on a host. This applies particularly to unengorged LL and NN which are often quite difficult to detect.

Despite the above shortcomings of the records, it is possible to obtain some notion of the role of the various hosts. Table 22 shows, for the most important host species, the average number of ticks per host, calculated from the pooled records.

Some animals listed in table 21 as hosts have not been included in Table 22. These are considered as being of minor importance as hosts and as having a negligible role in influencing the distribution of the ticks. Some are excluded because there are too few records of them to analyse. They are listed below with reasons for such categorization.

Chelodina longicollis is a long-necked tortoise found in or near rivers and permanent streams in south-eastern Australia (Worrell 1963). Roberts (1964, 1970) reported that *Ap. hydrosauri* has been found on this chelonian but I have no record of such an association despite examining ten tortoise specimens. I suspect that it is not a common host of *Ap. hydrosauri*, a view which Roberts (1964, 1970) appears to have held also. Also, the tortoise has a very restricted range in South Australia.

Pseudemydura umbrina is a rare West Australian tortoise which lives in swampy areas near Perth (Worrell 1963). *Amb. albolimbatum* was recorded on this animal by Roberts (1964, 1970). The very restricted range of *P. umbrina* rules it out from further consideration.

Amphibolurus cristatus is found in southern central Australia from Pt. Augusta west to within 300km of Perth (Pianka 1972). I have collected six of these dragons, from an area 28km south west of Pt. Augusta; one of these had a single ♂ *Amb. limbatum* attached. Smyth (1973) also recorded a single occurrence of this tick on *A. cristatus*. *Amphibolurus diemensis* was recorded as a new host for *Ap. hydrosauri* by Roberts (1970). The collection was made in Tasmania. Although *A. diemensis* is also found in the Victorian highlands and into the Blue Mountains of New South Wales, there are no records of ticks infesting it on the mainland. *Amphibolurus ornatus* has

Table 22

The degree of infestation of the major hosts by *Ap. hydrosauri*, *Amb. albolimbatum* and *Amb. limbatum*.

N - recorded as hosts by Smyth (1973) but numbers not known.

1 - The proportion of hosts recorded which were infested with a particular stage.

2 - The average number of ticks, of a particular stage, on hosts infested with that stage.

HOST		Ap. hydrosauri				Amb. albolimbatum				Amb. limbatum			
		LL	NN	♂♂	♀♀	LL	NN	♂♂	♀♀	LL	NN	♂♂	♀♀
Amphibolurus barbatus	1.	0.53	0.32	0.37	0.21		N			0.23	0.48	0.71	0.29
	2.	4.75	1.5	2.0	1.75					1.71	2.64	2.05	1.11
Amphibolurus pictus	1.									0	0.5	0.75	0.25
	2.									0	1.0	2.0	2.0
Tiliqua nigrolutea	1.	0.15	0.46	0.92	0.54		-				-		
	2.	1.0	2.0	4.58	1.29		-				-		
Tiliqua occipitalis	1.	0.33	1.0	0	0	0.5	0	1.0	0.5		N		
	2.	2.0	2.0	0	0	1.0	0	3.5	2.0				
Tiliqua scincoides	1.	0	0.25	1.0	0.25		-				-		
	2.	0	N	1.25	2.0								
Trachydosaurus	1.	0.30	0.40	0.88	0.30	0.13	0.23	0.89	0.59	0.10	0.33	0.87	0.34
rugosus	2.	13.52	3.40	3.43	1.47	22.62	4.83	4.58	2.45	14.63	3.67	2.81	1.39
Varanus gouldii	1.		N					-		0.14	0.32	0.95	0.5
	2.									1.0	5.86	2.67	1.64
Pseudonaja textilis	1.	0.5	0.5	0.5	0.5		N			0.5	0.75	0.75	0.75
	2.	3.0	2.0	3.0	1.0					1.5	4.0	22	9

a restricted distribution in Western Australia (Cogger 1975). Specimens of *Amb. albolimbatum* were collected from this agamid by P. Baverstock but its restricted range rules it out as an important host. *Amphibolurus decresii* is recorded in Smyth (1973) as a host of *Amb. limbatum*, and Smyth cites Roberts (1969, 1970) as the authority. I have been unable to find such a reference in Roberts' papers. A search of Smyth's records showed that he collected from an *A. descresii* four LL which he identified as *Amb. limbatum.* The identification is doubtful, however, as other ticks which I have collected since from *A.descresii* in that area of the Flinders Ranges have proved to be of an undescribed species of *Amblyomma* whose larvae are indistinguishable from those of *Amb. limbatum* (see section 3.22).

Amphibolurus fionii has only twice been found to carry ticks; both were collected near Woomera and both carried NN of *Amb. limbatum.* Many other specimens of this dragon have been collected by colleagues in the Zoology Department but no others were infested. This suggests that *A. fionii* is rarely parasitized. *Moloch horridus* is recorded by Smyth (1973) as a host of *Amb. albolimbatum.* There is one record in his files of a *M. horridus* with a single ♂ attached. I have examined other individuals of this species and failed to find ticks. *Gymnodactylus milii* only appears once in the collection records where a N of *Amb. limbatum* was found on one. Many other *G. millii* have been collected by colleagues; none was found to bear ticks. *Gehyra variegata* is certainly a very infrequent host of ticks. A larva of *Amb. limbatum* was found on one by M. King who, in the course of his research, examined hundreds of these geckos. *Egernia margaretae personata* is said by Smyth (1973) to be parasitized by *Amb. limbatum.* A search of his records and tick collection failed to reveal the specimen and confirm this identification.

Egernia multiscutata has been collected many times by colleagues and one individual had attached a larva, probably of *Amb. albolimbatum.*

Egernia whitei has been collected as frequently as *E. multiscutata* and Smyth

(1973) records it as a host of *Ap. hydrosauri*. The record and specimen have not been found but it is evident that this skink is, like the two previously mentioned, a very infrequent tick host. *Leiolopisma metallicum*, a small common skink, was once found by Smyth to bear a larva of *Ap. hydrosauri*, but it is obviously a relatively unimportant host.

Varanus acanthurus is found only in northern Australia and is reported by Roberts (1969, 1970) to be a host of *Amb. limbatum*. *Varanus timorensis, V. timorensis sealaris, V. glauerti* and *V. glebopalma* are new host records for *Amb. limbatum*. They all have distributions restricted to the far north (Cogger 1975) of Australia and are therefore not significant in this study.

Varanus giganteus, the largest Australian lizard, has its own tick *Amb. calabyi* (Roberts 1970) but I have received *Amb. limbatum* from two specimens. *V. giganteus* is found only in central and western Australia in rocky areas.

Liasis olivaceus, found in northern Australia, is reported by Roberts (1969, 1970) as a host of *Amb. limbatum*.

Aspidites spp.(either *As. melanocphalus* or *As. ramsayi*) are also pythons, and Roberts found *Amb. limbatum* on them. They do not appear in our records.

Morelia spilotes hosts at least two of the ticks, *Amb. albolimbatum* and *Amb. limbatum*. Smyth found a ♀ of the former on a specimen from Western Australia.

Acanthophis antarcticus has a southern distribution (Cogger 1975) but only two specimens appear in the records. Both were hosts of *Ap. hydrosauri*; there were six ♂♂ on the two snakes.

Pseudonaja nuchalis was named *Demansia nuchalis* by Smyth (1973) who had a record of it as host of *Amb. limbatum*.

Austrelaps superbus and *Drysdalia coronoides*, called respectively *Denisonia superba* and *Denisonia coronoides* by Smyth (1973), are said by Roberts (1973) to be hosts of *Ap. hydrosauri*.

Notechis spp. (tiger snakes) are recorded by Roberts (1970), Smyth and myself as hosts of *Ap. hydrosauri* and *Amb. albolimbatum*, but records are few.

Pseudechis australis has an inland distribution, and I have found *Amb. limbatum* on it, but records are few.

Table 22 lists eight hosts which seem to be more important than the ones listed above. *Trachydosaurus rugosus* is the one most often encountered in most parts of South Australia (see numbers in table 21). Next in numbers captured come *Amphibolurus barbatus, Varanus gouldii* and *Tiliqua nigrolutea.*

It is evident that *Trachydosaurus rugosus* is a major host not only because it seems abundant, but as all stages of each of the ticks parasitize it relatively heavily. It is particularly noticeable that the other hosts are less likely to bear LL and when they do they have fewer.

Amphibolurus barbatus is another widespread species which seems to be suitable to each tick, though we do not know how many *Amb. albolimbatum* were found by Smyth on this dragon. In some areas of its range, however, *A. barbatus* is less often found to bear ticks than in other areas and also less often than *Tr. rugosus* (see section 5.34).
In the Mt. Mary study, for instance, only 27% of *A. barbatus* examined were infested, while 85% of *Tr. rugosus* had ticks (see section 5.34). Yet 8 *A. Barbatus* caught during two successive springs (26.8.72 and 18.9.73) (50km E. of Adelaide) were heavily infested with *Ap. hydrosauri* LL and NN.

Amphibolurus pictus is less important than its congener even though it has a wide range. Approximately 50 specimens of *A. pictus* caught in areas where *Ap. hydrosauri* is common were not parasitized. It is a host of *Amb. limbatum* in central South Australia and may be of importance to that tick as it is an abundant lizard. Larger collections need to be made to assess more closely its importance.

Tiliqua nigrolutea and *Tiliqua scincoides* may be important hosts of *Ap. hydrosauri* particularly in areas where *Tr. rugosus* is rare or absent. The numbers of ticks recorded on these skinks do not match those for the same tick on *Tr. rugosus.*

Tiliqua occipitalis hosts all of the ticks, though the number of *Amb. limbatum* recorded is not known. In this case more samples are needed before accurate assessment can be made. However a number of these lizards and of *Ti. scincoides* have been examined during the study and most proved tick-free.

Varanus gouldii is recorded as a host of *Ap. hydrosauri* and yet I have examined over 40 specimens collected by D. King, in areas in which the tick occurs, and found none attached. The same is not true of *V. gouldii* from further north which are often attacked by *Amb. limbatum*. Another tick *Ap. fimbriatum* is common on these goannas.

The snake *Pseudonaja textilis* appears rarely in our records as it is dangerous and hard to catch. But all stages of *Ap. hydrosauri* and *Amb. limbatum* attach to it and it also hosts *Amb. albolimbatum*; ♀♀ and NN have been found thus far. Though these snakes are not as abundant as *Tr. rugosus* they may be an important host of the ticks.

4.30 The Geographical Distributions of the Hosts.

The Australia-wide distributions of the major hosts are shown in figures 33 and 34. These were compiled from data supplied in Worrell (1963), Rawlinson (1966, 1974) and Pianka (1972), and subsequently checked against Cogger (1975).

The South Australian distributions are shown in figures 35 - 41. These are compiled from Smyth's and my records, and from South Australian Museum records made available to me by T. Houston. In some cases the contribution is overwhelmingly from my records (e.g. *Tr. rugosus*), while in others they come largely from the Museum records (e.g. *P. textilis*).

It can be seen that in no case does the limit of a host's geographical distribution coincide with a tick boundary. Some hosts occur on both sides of such boundaries and are parasitized by ticks on either side e.g. *Tr. rugosus, A. barbatus, P. textilis, T. occipitalis*. *A. pictus* also exists in all three tick areas but is only infested by *Amb. limbatum*. *V. gouldii* similarly

Figure 33. The Australia-wide distributions of:

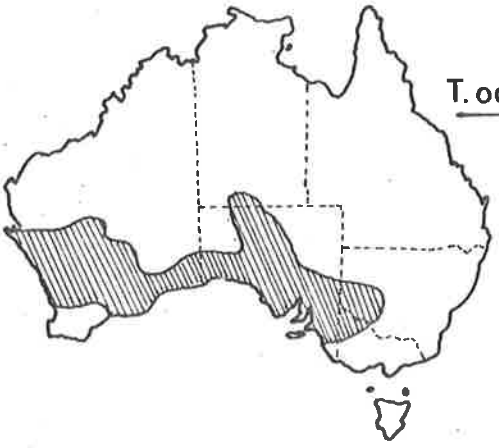
Tiliqua nigrolutea

Tiliqua occipitalis

Tiliqua scincoides, and

Trachydosaurus rugosus

T. nigrolutea



T. occipitalis

T. scincoides

T. rugosus

Figure 34. The Australia-wide distributions of:

Amphibolurus barbatus

Amphibolurus pictus

Varanus gouldii, and

Pseudonaja textilis

A. barbatus

A. pictus

V. gouldii

P. textilis

Figure 35. The distribution of *Amphibolurus barbatus* in South Australia.

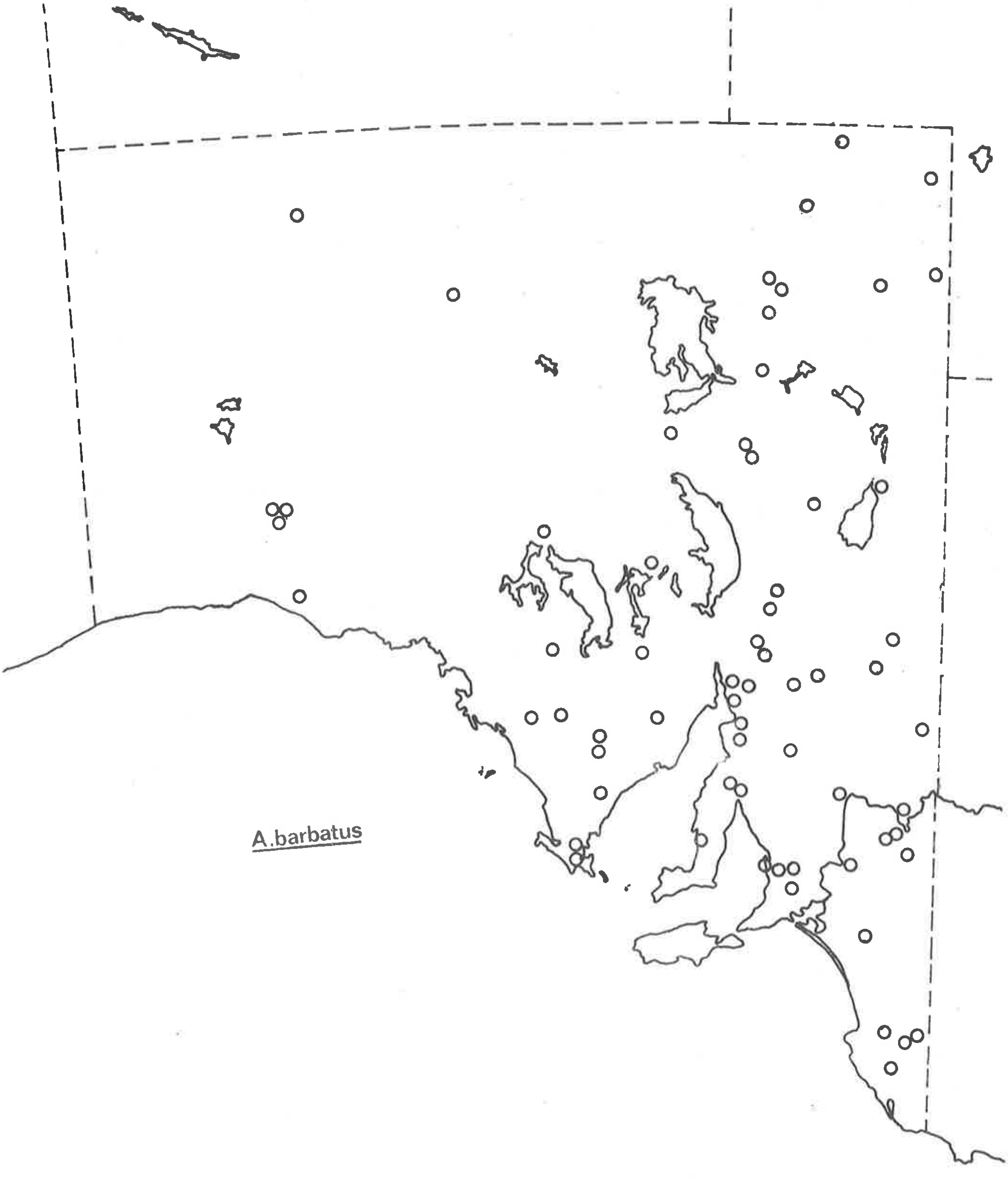
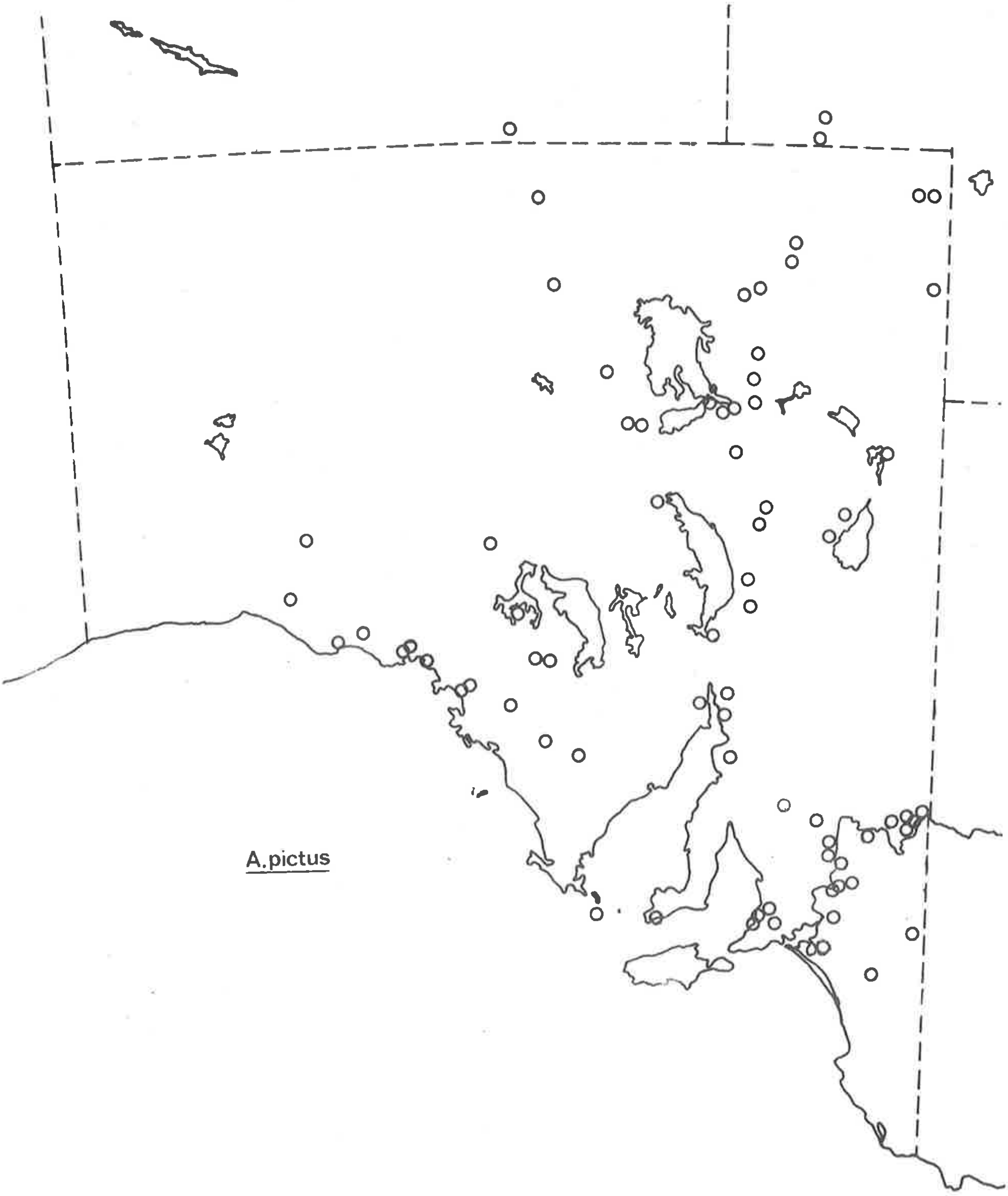

A.barbatus

Figure 36. The distribution of *Amphibolurus pictus* in South Australia.



A.pictus

Figure 37. The distributions of *Tiliqua nigrolutea* and *Tiliqua occipitalis* in South Australia.

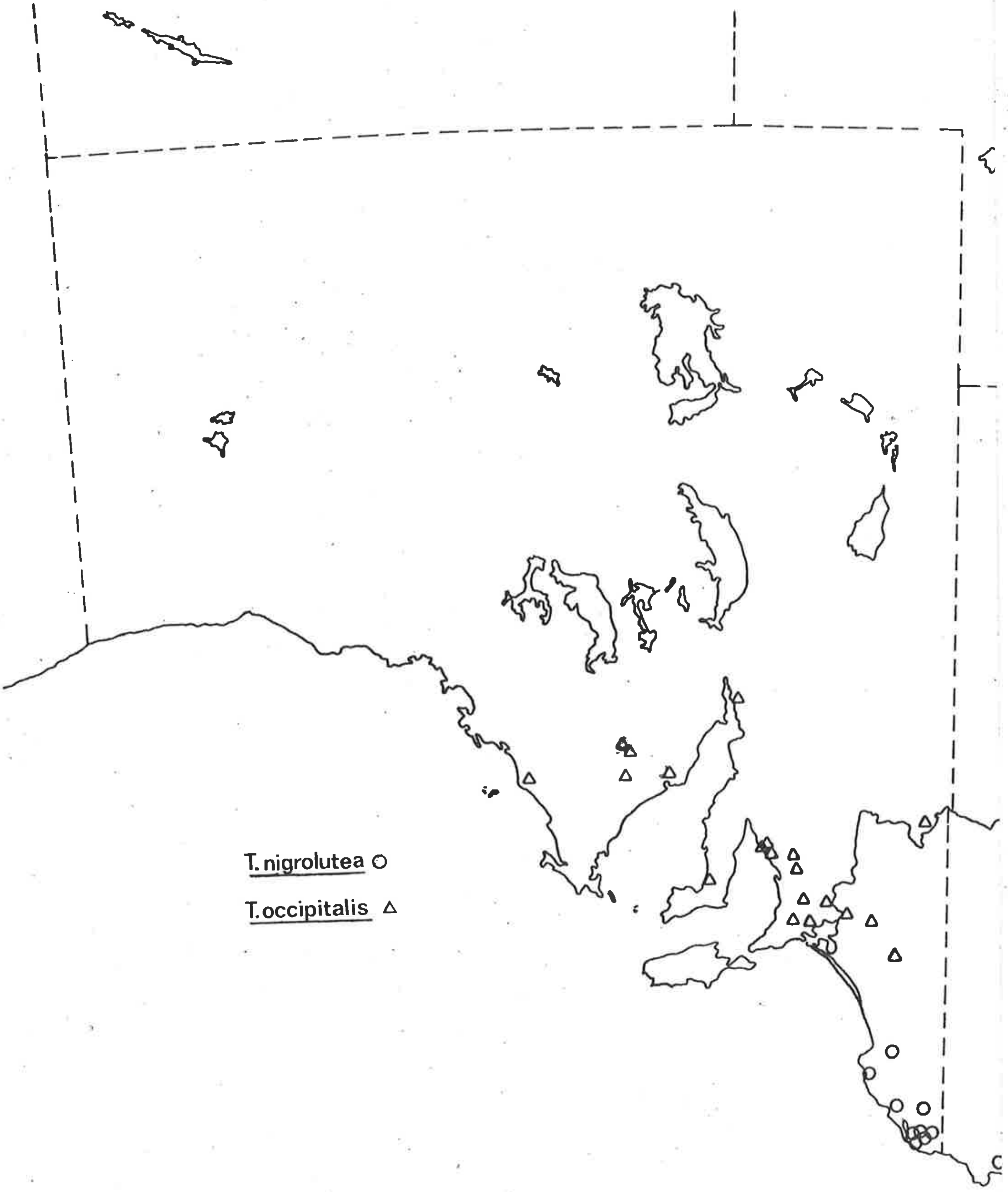
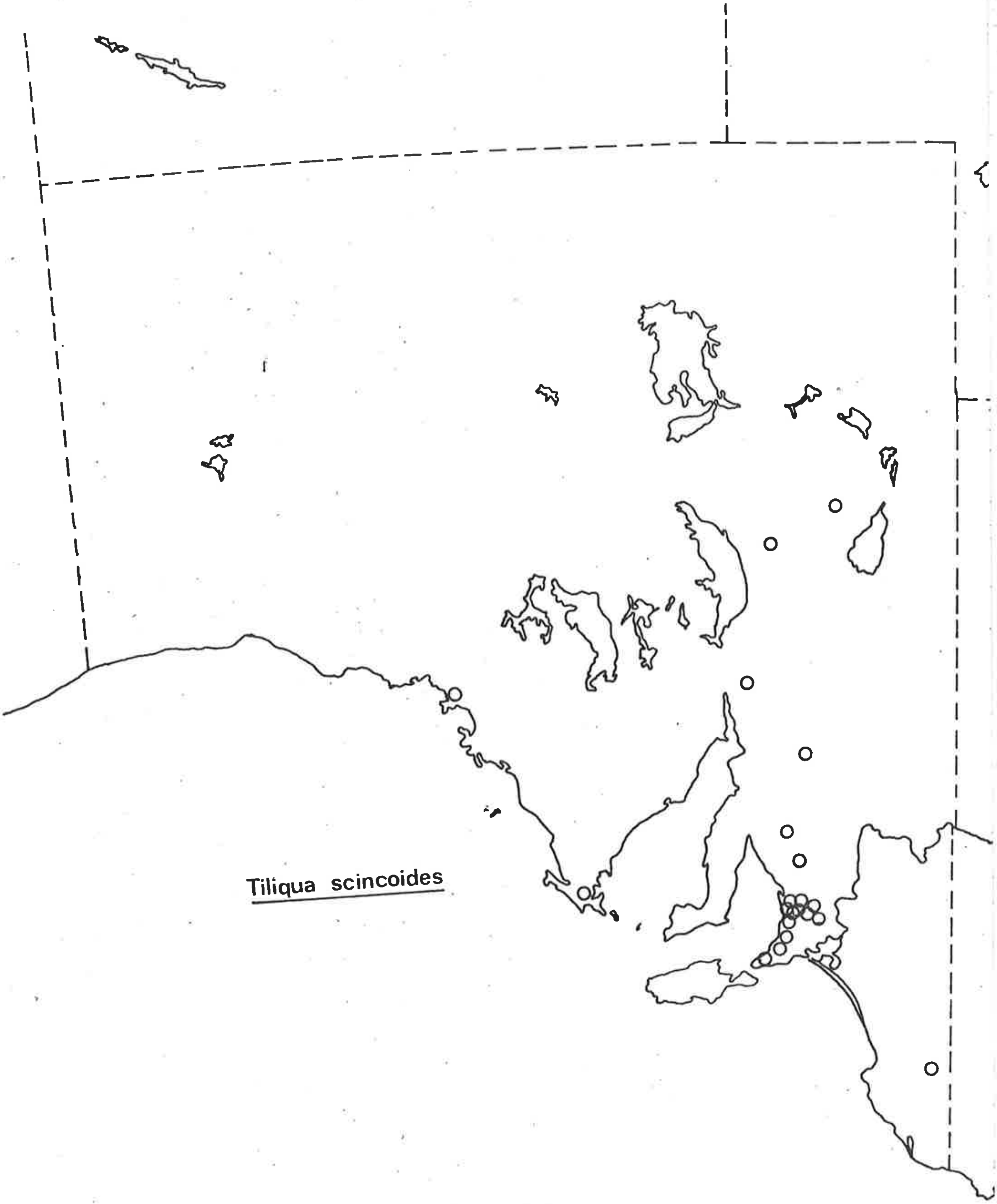

T. nigrolutea ○
T. occipitalis △

Figure 38. The distribution of *Tiliqua scincoides* in South Australia.



Tiliqua scincoides

Figure 39. The distribution of *Trachydosaurus rugosus* in South Australia.

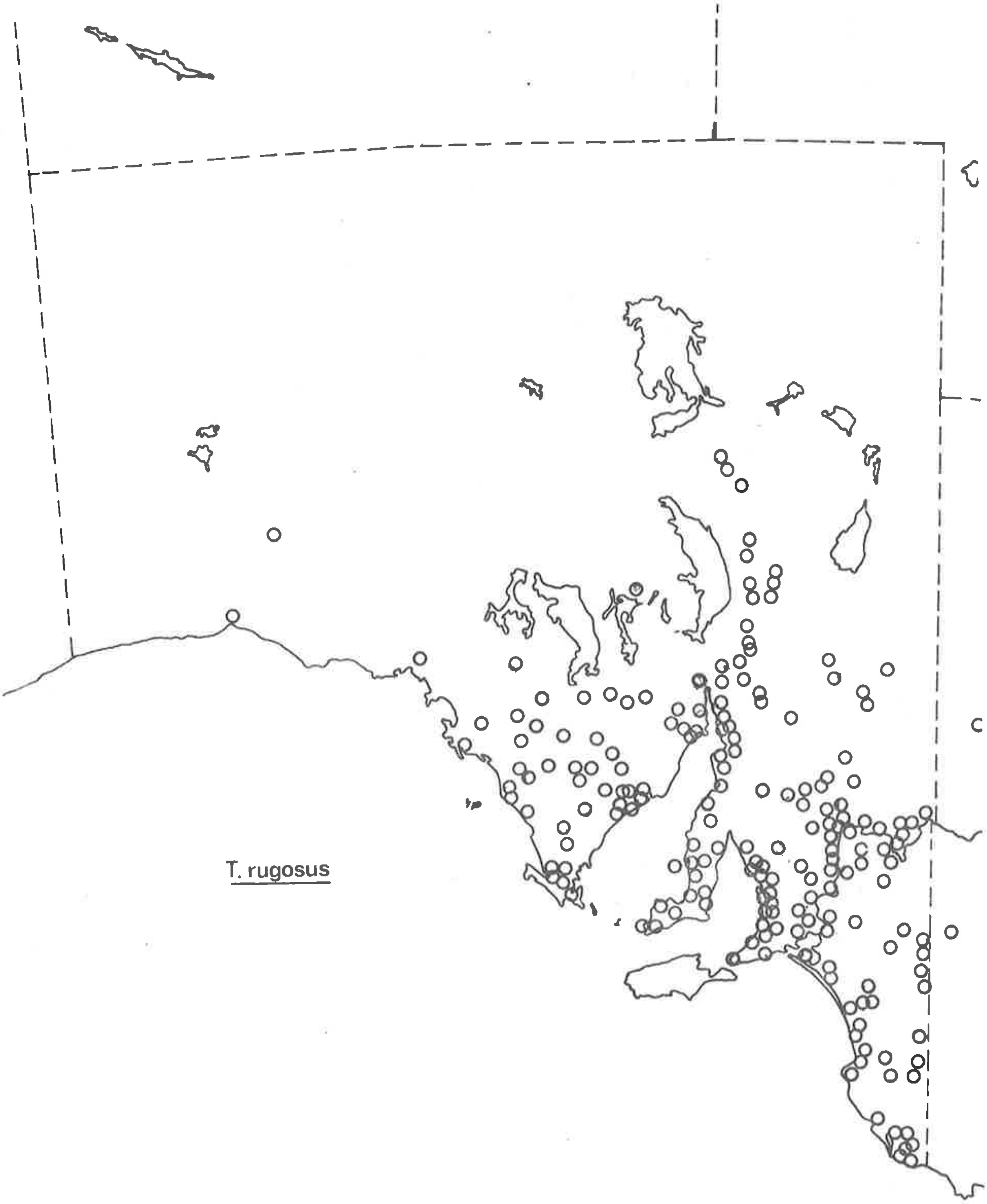

T. rugosus

Figure 40. The distribution of *Varanus gouldii* in South Australia.

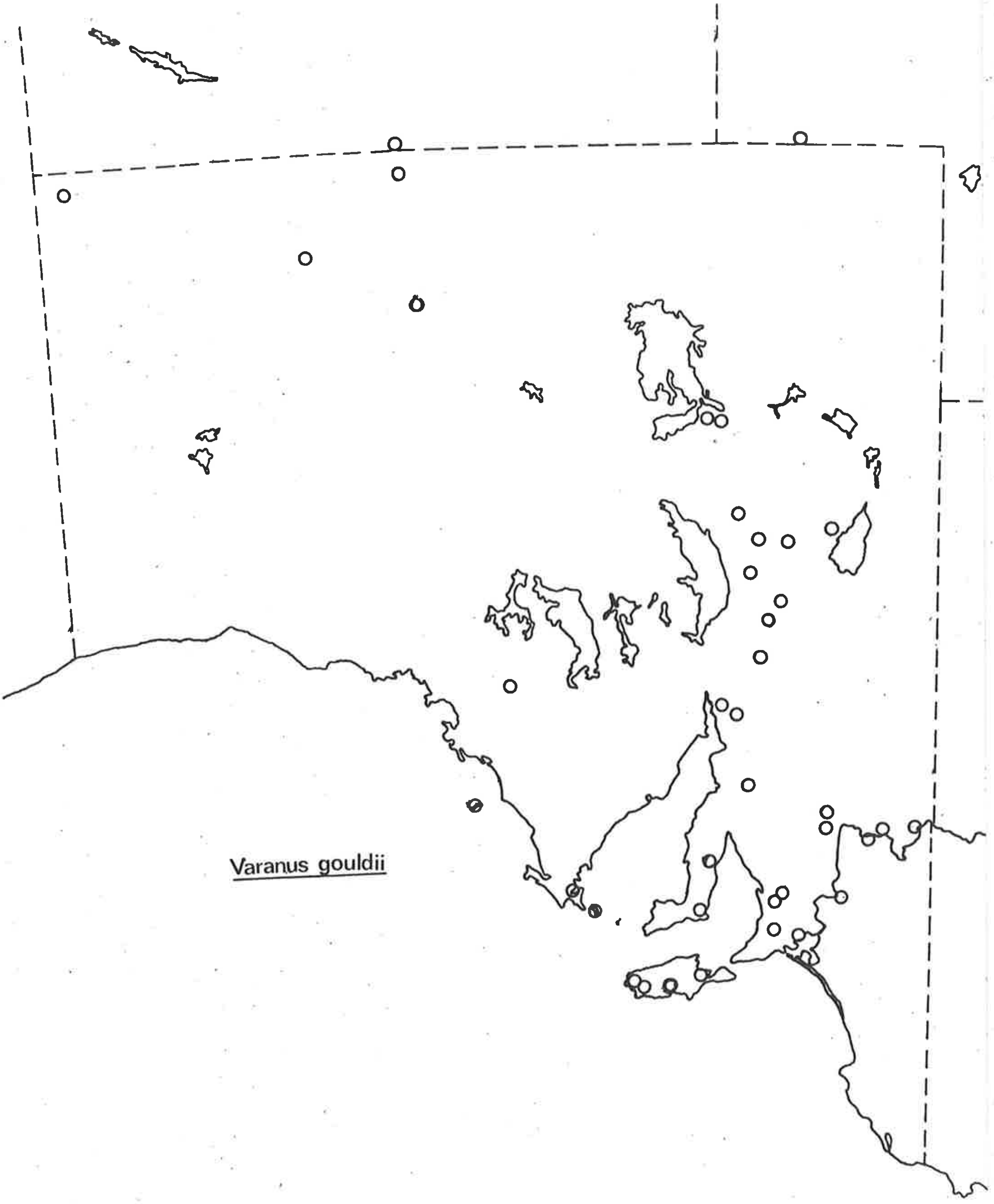
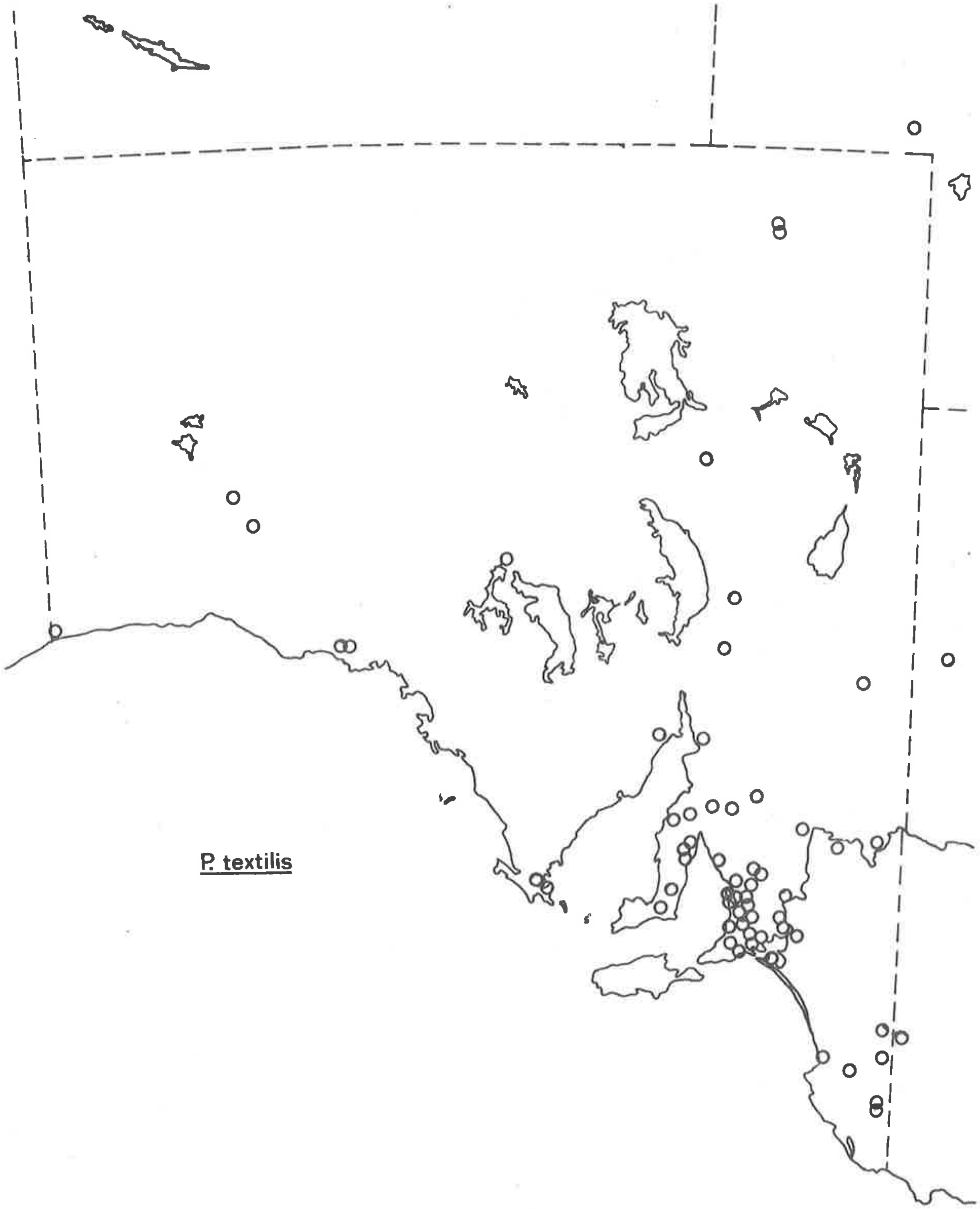

Varanus gouldii

Figure 41. The distribution of *Pseudonaja textilis* in South Australia.



P. textilis

is widespread and obviously a common host of *Amb. limbatum,* but rarely of *Ap. hydrosauri*. *T. scincoides*, on the other hand, is a host of *Ap. hydrosauri* but not of the *Amblyommas* (in our records), though these skinks have been collected from those areas. *T. nigrolutea* has a range well contained within that of *Ap. hydrosauri*.

A. barbatus is really a species complex consisting of a number of forms (Cogger 1975). However, examination of the South Australian Museum records does not reveal a correlation between the distribution of any form and a tick distribution. Similarly *V. gouldii* is said by taxonomists (Worrell 1963, Cogger 1975) to consist of three subspecies; *V. gouldii gouldii* from northern and eastern Australia, *V. g. flavirufus* from arid Central areas and *V.g. rosenbergi* which exists on Kangaroo Island, southern Eyre and Fleureau Peninsulas. *V.g. gouldii* is the subspecies which ranges on both sides of the tick boundaries.

In South Australia, *Tr. rugosus*, followed by *A. barbatus* and *P. textilis*, seem to be most important as hosts. They are not present on Kangaroo Island, where *Ap.hydrosauri* is absent - though *V. gouldii* and *Notechis ater* are on the Island. But the distribution maps, compared with those of the ticks, reveal that on Tasmania *Tr. rugosus, A. barbatus* and *P. textilis* are also absent but *Ap. hydrosauri* is there on *T. nigrolutea* and possibly *T. casuarina, Notechis ater, Austrelaps superbus* and *Drysdalia coronoides*. *T. nigrolutea* is found in areas of southern Victoria and Tasmania from which *Tr. rugosus* is absent and may well replace it in importance as a host of *Ap. hydrosauri* in those areas.

4.40 General Biology of the Sleepy Lizard Trachydosaurus rugosus (Gray)

This skink is a very important host to each of the ticks in South Australia, is easy to capture in large numbers, is easy to handle and keep in captivity, and in each of these considerations ranks above the other hosts; thus it has received most attention during this study. The other important hosts are compared with *Tr. rugosus* in 4.50 below.

There has been some disagreement among workers on the generic status of the lizard. Some maintain that it is so similar to lizards of the genus *Tiliqua* That it should be included in that genus. This argument has been based on morphological considerations including examination of prepared skeletal material (Mitchell 1950) and of chromosomes (King 1972). Others continue to allocate the lizard to the genus *Trachydosaurus* (Merters 1958, Bull and Smyth 1973, Smyth 1973, Cogger 1975). I have followed the latter course in this study.

Tr. rugosus shows variation in size, colour and body shape across its extensive range. In South Australia sleepy lizards from southern areas are smaller than lizards from further north. For instance the mean weights of groups of adult lizards collected during spring at Goolwa and Mt. Mary were 421 ± 6.59g and 685.3 ± 43.3g respectively (means ± S.D.). Lizards from southern areas are often darker in appearance, with greyish scales in bands on a background of almost black scales. Lizards from Mt. Mary are generally lighter in colour, with yellow and brown scales and no distinct banding pattern. Some lizards collected in areas further north (e.g. near Lake Eyre) are very light in colour. There is also variation in body shape, including sexual dimorphism in which males often have broader heads than females. Lizards from Western Australia, for example, have distinctly different heads and tails from South Australian specimens.

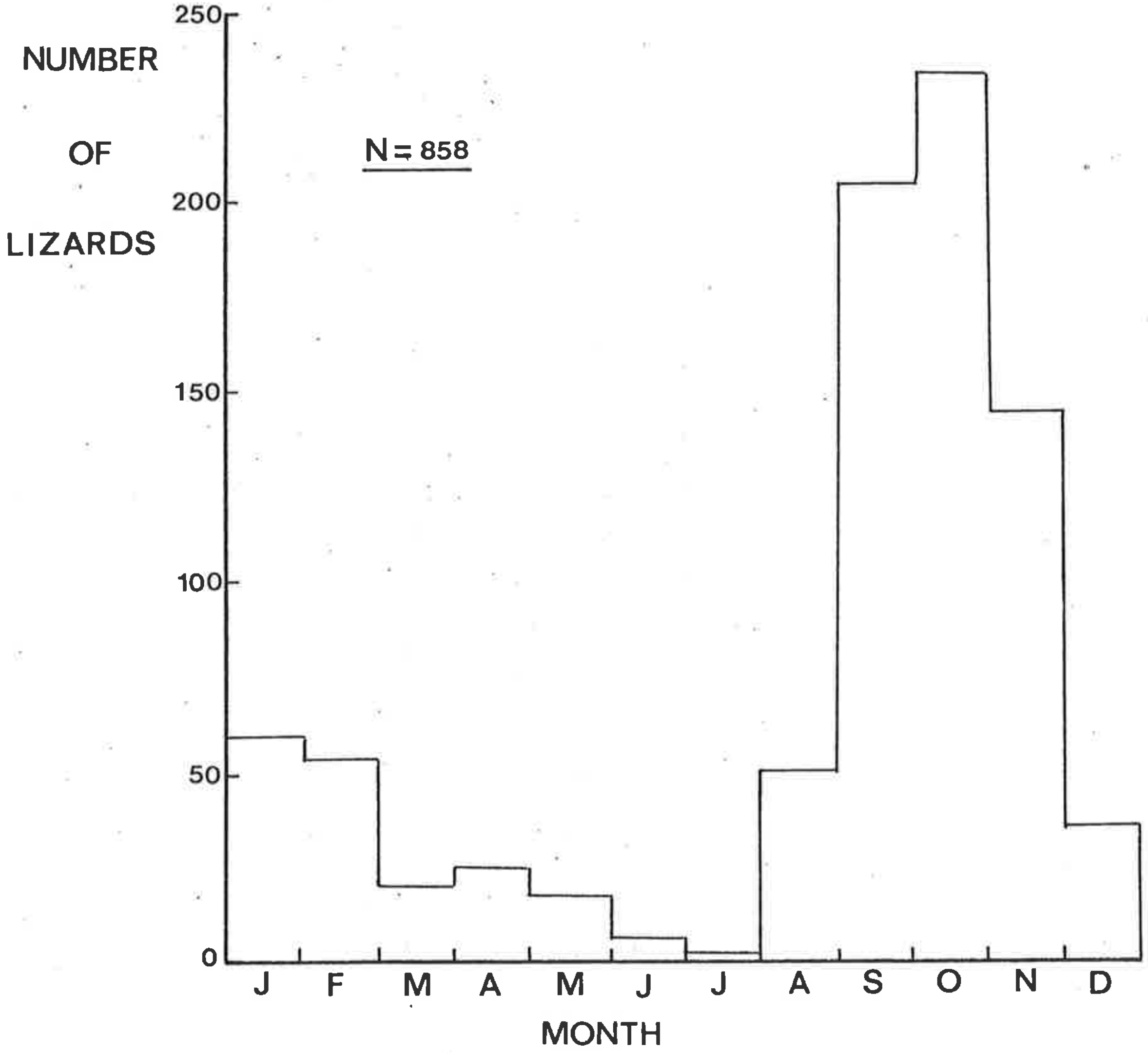
Sleepy lizards are omnivores. They eat a wide range of green herbage, flowers and fruit,particularly during spring. During this season they are often seen on road verges eating succulent herbage. It is evident that herbage forms a large part of their diet at this time as indicated by the faeces which they void on being picked up. They also eat any snails and insects that are slow enough to be captured. In the Mt.Mary area beetles form a large part of their diets during summer.

The food ingested by sleepy lizards supplies sufficient water and they do not need a supply of drinking water. At times they take in with their food a high salt load, particularly those which live on coastal dunes. Braysher (1971) has shown that they possess a nasal salt gland which enables them to rid themselves of high salt loads.

The activity of sleepy lizards varies from season to season so that they are often seen walking about at some times but remain hidden from view at others. This variability is to be expected of an ectotherm in a region where there is a marked difference in average ambient temperatures between the seasons. An appreciation of the marked change can be gained from figure 42 in which the numbers of sleepy lizards captured per month are plotted. Ideally in such graphs the effort per month expended in searching for lizards should be the same and comparable areas should be searched each month. This is not true of the data in figure 42. These data were compiled from field collection data which were mainly gained by driving along country roads in areas south of the 200mm isohyet and catching lizards that crossed. During the spring, when many lizards were about, it was often impossible to process captured beasts fast enough to catch all seen crossing roads. Thus the spring numbers are underestimates. During winter and summer, when fewer lizards were about, I have been forced to go to areas and search off roads in lizard refuge sites. This means that the low figures in these seasons are overestimates of lizard numbers - not a true indication of activity. So the seasonal variation is more dramatic than that shown.

Spring, when average temperatures increase and vegetation grows fastest,

Figure 42. The number of sleepy lizards, *Tr. rugosus*, captured per month during this study.


NUMBER
OF
LIZARDS
N = 858
250
200
150
100
50
0
J
F
M
A
M
J
J
A
S
O
N
D
MONTH

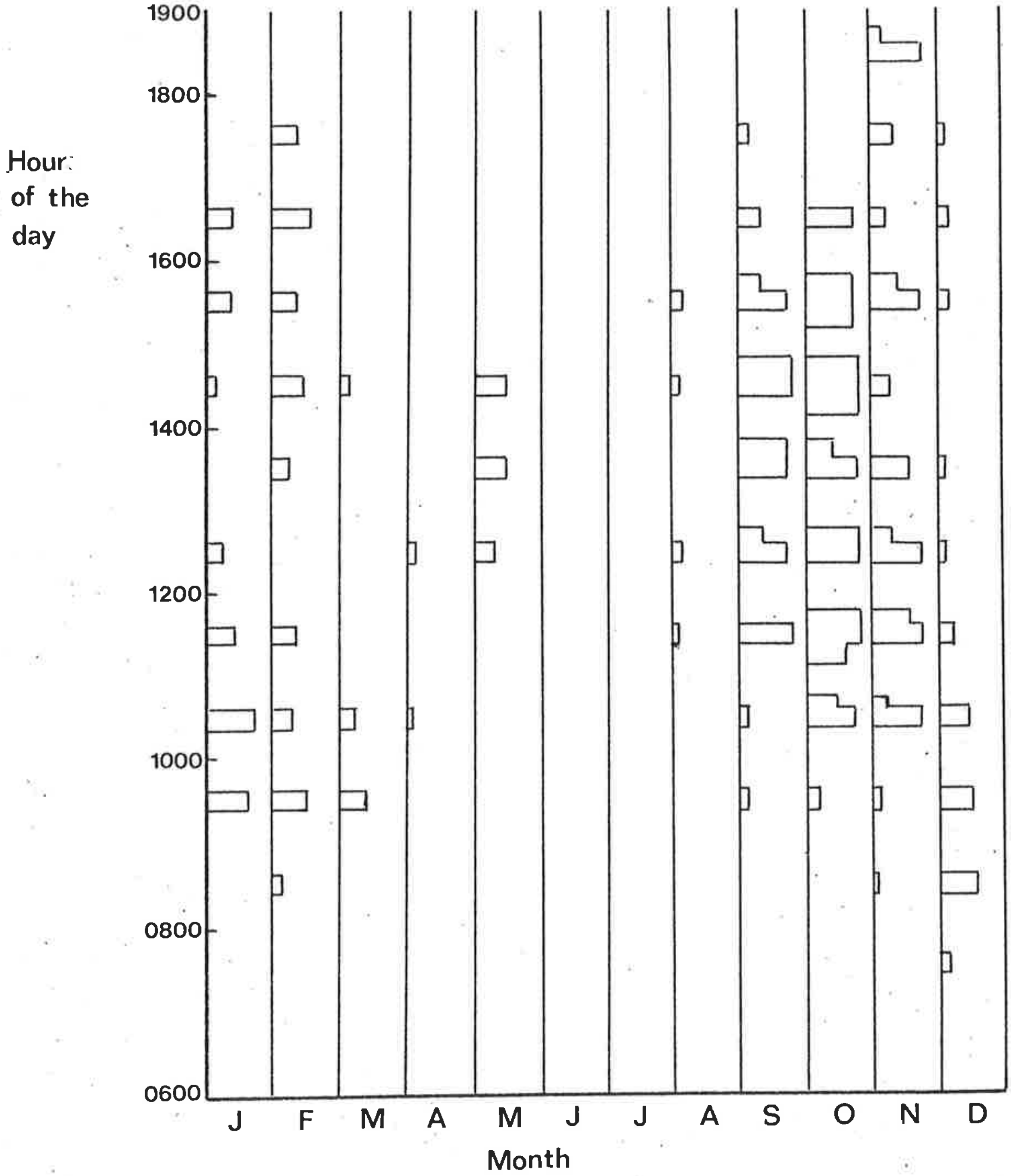
is the period of maximum lizard activity in the southern part of South Australia which experiences a mediterranean weather pattern. In these areas most sleepy lizards are seen during late August through to November. They often move around in pairs and apparently copulate in the early spring. During a warm day lizards may be seen for most of the daylight hours except early morning and twilight; see figure 43.

As conditions become dry during summer, sleepy lizards are seen less often and very rarely during the heat of the day. In some areas, though, they may be seen, very active, for brief periods during and after thunder storms when it is wet and warm. In the Mt. Mary area, where such storms are common in February - March, there is often a burst of activity though not as pronounced as in spring. Winter in southern South Australia heralds a complete disappearance of the lizards and they do not re-appear until spring.

I mentioned above that the seasonal pattern in daily activity might be different in different regions of the state which experience other weather patterns. In areas like Mt. Mary where rainfall is infrequent and variable, such changes were noticeable over the course of the study. There was always a spring burst of lizard activity but the duration of this period and the summer and autumn activities of the lizards were variable. The lizards seemed active when it was warm enough and there was green herbage or moisture about. On hot days when there was moist food available they might be active in the mornings and sometimes late in the afternoon but be absent during the hotter parts of the day.

Sleepy lizards thermoregulate, largely by behavioural means (Warburg 1965). They, like other heliotherms (basking reptiles), use the energy in solar radiation to increase their body temperatures and by moving between shaded and unshaded areas they can keep their body temperatures within a preferred range. An active lizard, under favourable conditions, can maintain its body temperature within narrow limits. If conditions are not favourable and there is insufficient sunlight to allow the lizard achieve its preferred

Figure 43. Seasonal changes in the activity of sleepy lizards, *Tr. rugosus*, showing the relative numbers caught during each hour of the day for each month. The area of each box represents the number of lizards caught during that hour of the day for that month.


1900
1800
1600
1400
1200
1000
0800
0600
Hours of the day
J
F
M
A
M
J
J
A
S
O
N
D
Month

body temperature, it may not emerge from its shelter. Indeed sleepy lizards will not emerge when ambient temperatures are low (see below).

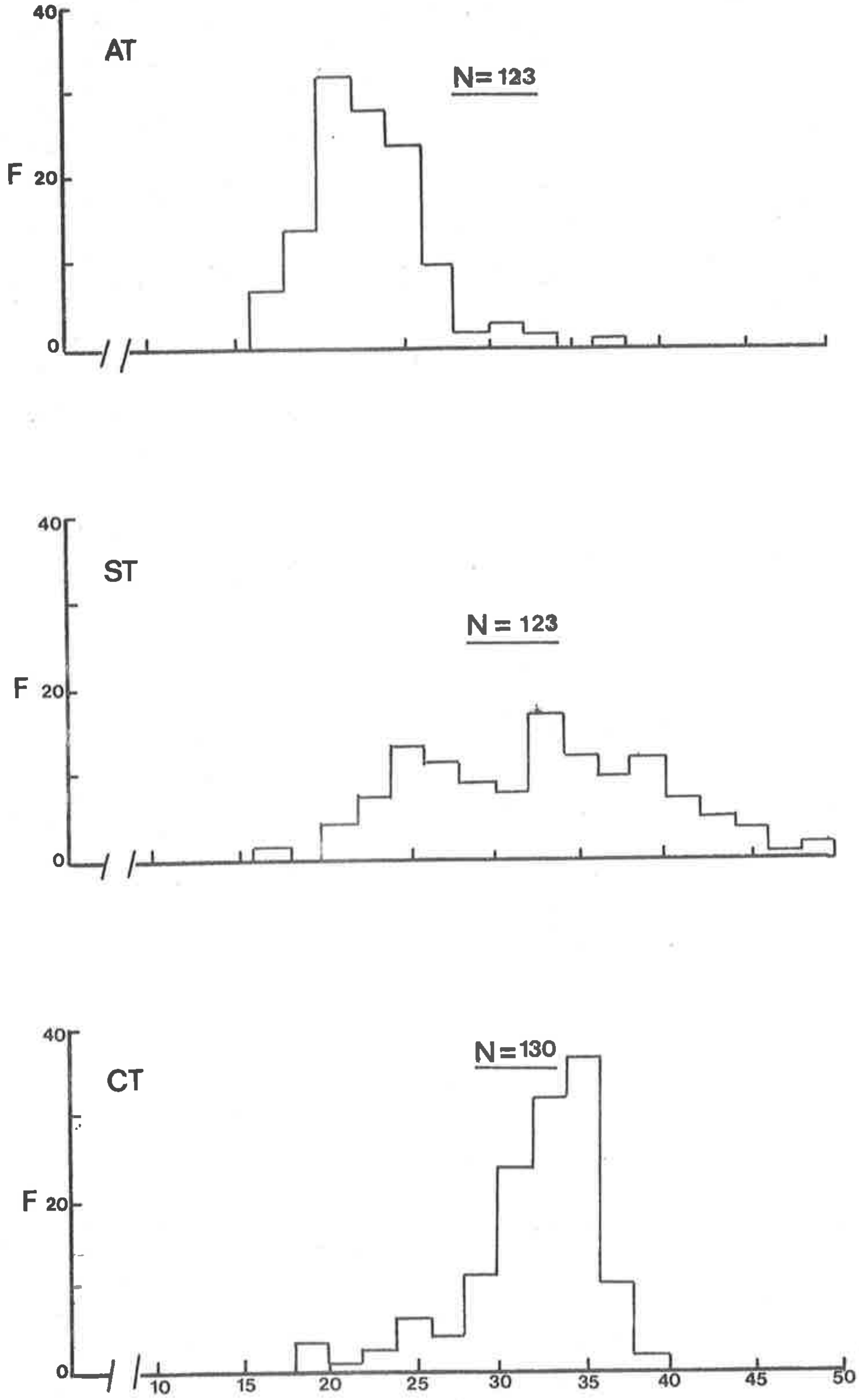
Some idea of the range of body temperatures of active lizards and the preferred range can be gained by measuring cloacal temperatures (CT) of specimens caught in the field (Bradshaw and Main 1968). This was done throughout the study using a WESCO (0-50°C) thermometer. Air temperatures (with the thermometer shaded) and soil temperatures (unshaded) were also taken. These data are presented in figure 44.

Figure 44 shows that sleepy lizards are rarely active when the air temperature is above 30°C, a figure often reached during summer days, or when the air temperature is below 16°C, a temperature not attained on many winter days. It also appears that active sleepy lizards are most likely to have CT's in the range 30 - 36°C. Very few lizards are found with CT's above this range, though a number are active at lower temperatures. A number of those at lower temperatures would probably have been basking in order to heat up and attain optimum activity.

The diurnal activity pattern of a lizard is not necessarily determined only by fluctuations in ambient temperature. It has been demonstrated in a number of diurnal lizard species that there may be an internal diurnal rhythm of activity and individuals may emerge or increase activity before temperatures begin to rise (Cloudsley - Thompson 1965, Heath 1962).

Cloudsley - Thompson (1965) suggests that some lizards might emerge from night time refuges when light levels increase early in the day. Changes in light levels at dawn might act as zeitgebers for diurnal activity rhythms of some lizards (Henzel 1972). It is evident that sleepy lizards are quickly driven to seek refuge on hot days. Some species may emerge again at dusk (Cloudsley - Thompson 1965, Henzell 1972). Some lizards allow their body temperatures to rise with increasing ambient temperatures until their CT's are higher than those observed in sleepy lizards (Cowles and Bogert 1944, Bradshaw and Main 1968).

Figure 44. Frequency distributions of cloacal temperatures (CT) of active sleepy lizards, *Tr. rugosus*, captured in the field and of soil temperatures (ST) (unshaded) at the capture site and of air temperature (AT) (with the thermometer shaded).


40
AT
N= 123
F 20
0
40
ST
N = 123
F 20
0
40
CT
N=130
F 20
0
10
15
20
25
30
35
40
45
50

Henzell (1972) showed that in *Egernia* spp., the duration of exposure (activity) decreased with dehydration. Dennis King and I were able to show a similar situation with sleepy lizards (King and Sharrad, unpublished paper). We placed 6 *Tr. rugosus* in 6 enclosures (2 metres x 50cm) and monitored CT's, air temperatures and soil temperatures with a chart recorder (using the same techniques as Henzell 1972). The enclosures each had a refuge at one end and a heat source at the other end. The heat lamps and lights were automatically controlled to give a 12/12 hour, day/night cycle. CT's were recorded once a minute for 4 weeks. The lizards exhibited marked diurnal patterns of behaviour, emerging from the refuges soon after the lights switched on and quickly reaching and maintaining a preferred CT of about 32-34°C by moving to and from the hot areas of the enclosures. During the last 2 weeks of the study, 3 of the lizards were deprived food and water while the others were fed and had water ad. lib. The starved lizards appeared to restrict the time spent active and thus reduced the time spent with high CT's.

The vagility of ticks is likely to depend largely on the movement of hosts. Thus a study of the distance moved by lizards was undertaken. Small radio transmitters (weight = 55gms) were constructed in the fashion described by Green (1969). These transmitters produced a series of pulses which could be detected at 30 to 50 metres on portable radio receivers. The transmitters were stuck, with epoxy resin, onto small aluminium plates (7 x 2½cm). These were taped and glued onto the tail of the lizard to be followed.

Four lizards in the Mt. Mary study area were fitted with radios and released. Table 23 summarizes the results of these studies. Home range areas were calculated using the convex polygon method described by Southwood (1966). It can be seen that these areas are much smaller than those predicted using the formula of Turner et al., (1969) which is based on the weight of individual lizards. Their formual is:

$$A = 171.4\ W^{0.95}$$

where W = weight in grams of the lizard

A = area in square metres.

Table 23

Area of home ranges of *Tr. rugosus* in the Mt.Mary study area.

Lizard	Weight (grams)	Period	Number of captures	Area - by convex polygon (m^2)	Estimated area Turner et al. (m^2)
M 43	658	24/11/71- 19/ 3/72	11	5,066	81,910
M 74	750	26/11/71- 19/ 1/72	7	3,429	92,320
M 91	558	14/ 1/72- 26/ 5/72	5	1,525	69,708
M 92	579	14/ 1/72- 26/ 5/72	5	5,281	72,190

Saint Girons and Saint Girons (1959,cited by Turner et al. 1969) noted that herbivorous lizards would have much smaller home ranges than carnivorous lizards.

M. Bull subsequently attempted to accurately measure the disposal of ticks within a population of *Ap. hydrosauri* near Tickera on Yorke Peninsula (Bull 1978 a). He marked, released and recaptured sleepy lizards and also fixed radios to 14 lizards. He suggests that sleepy lizards' home ranges in that area are between 2,000 and 5,000m^2 in size and overlap extensively. The opportunities for tick dispersal are thus quite limited. Bull (1978 a) calculates that this probably amounts to 800m or less during a tick's life, if one assumes that the tick relies entirely on the host for such dispersal (see 3.3411).

The Mt.Mary study also showed that the lizards use a number of different shelters in their home ranges. These shelters varied from bushes (e.g. *Kochia sedifolia*) to old tree stumps or hollow logs. It was also evident that the home ranges of lizards overlap.

However, the investigations at Mt.Mary were only of adult lizards and only for summer and autumn months. It is possible that lizards move further during spring - although this would seem unnecessary as food is then more abundant. Also, the movements of juvenile lizards are not known.

Female sleepy lizards bear live young, usually twins. These are most often seen new born, during April. If female lizards are captured during early autumn they readily give birth in the laboratory. The young which resulted ranged in weight from 55 to 85g.

The recorded birth dates of young *Tr. rugosus* are given in table 24.

Table 24

Birth dates of 12 *Tr. rugosus*.

Number	Date In the week	Particulars
1.) 2.)	23/3 - 30/3/1972	These were born in enclosure 2 at Pt.Gawler
3.) 4.)	9/4/72	From a female collected in the South East of South Australia
5.	13/4/72	From a second female lizard collected with the one above.
6.) 7.)	13/4/72	From a female captured near Mt. Mary
8.	19/4/72	From same female as No. 5.
9.) 10.)	19/4/72	From a third female from the South East
11.	26/4/72	From a female captured near Mt.Mary
12.	7/5/72	From the same female as No. 11.

It may be that young lizards move much more than adults. They would, however, be unlikely to pick up ticks until spring (see 3.31).

4.50 Discussion

It is evident that there is no correlation between the limits of the distributions of host species and the positions of the parapatric tick boundaries. The non-occurrence of ticks on Kangaroo Island, however, might be a result of an inadequate supply of suitable host species.

The behaviour and biology of a host species at a boundary may be important, even if it is found on both sides of that boundary. It could be that the choice of shelter or burrows by the host changes across the boundary. This would influence the microhabitat of ticks off the host. The hosts' activity both diurnal and seasonal may change across the boundary in response, for example, to different vegetation types. Such differences across a boundary could result in ticks on one side being more likely to find a host. The density of hosts might change across the boundary. It may be that one tick is able to survive at lower host densities than the other but cannot survive interspecific competition at higher host densities. Hosts by their movement disperse ticks. Such movement would be one factor which would tend to disrupt a parapatric boundary. The other possibility that must be considered is that if interspecific competition does take place between the ticks, it probably does so on the hosts.

Tr. rugosus, a most important host in much of South Australia, is found in high numbers on both sides of all the tick boundaries. The seasonal "activity" of the ticks and their behaviour is correlated with that of this reptile. One would expect from the data on home ranges (in 4.40) that the ticks would have very low vagility. One would also expect that the availability of potential microhabitats to ticks in the boundary areas would be dependent on the behaviour of this lizard.

Other reptiles do carry ticks. Some, e.g. *V. gouldii*, occupy different shelters and may have larger home ranges (Green 1969, King pers.com.). Some, e.g. *A. barbatus*, might be active at higher temperatures during summer (Bradshaw and Main 1968). Some, e.g. *T. nigrolutea*, are probably active at lower temperatures. But in general they exhibit similar seasonal and diurnal changes in behaviour to those shown by sleepy lizards, and they appear to be quantitatively minor hosts (sect. 4.22).

It is apparent that there is much to learn about the hosts of the ticks. More information on the relative importance of different host species would be useful, but detailed investigation of *Tr. rugosus* would seem to be more profitable. Not enough is known of the movements of these lizards at a tick boundary or how far or how often they move ticks across such a region. We know that some sleepy lizards are better hosts than others but do not understand the reasons for this; why such variability exists, its extent or how a particular host might itself vary in this way with time and/or experience of infestation. The relationship between host density and the survival of ticks is another unexplored area.

5.00 THE PARAPATRIC BOUNDARY BETWEEN APONOMMA HYDROSAURI AND AMBLYOMMA LIMBATUM AT MT MARY.

5.10 Introduction

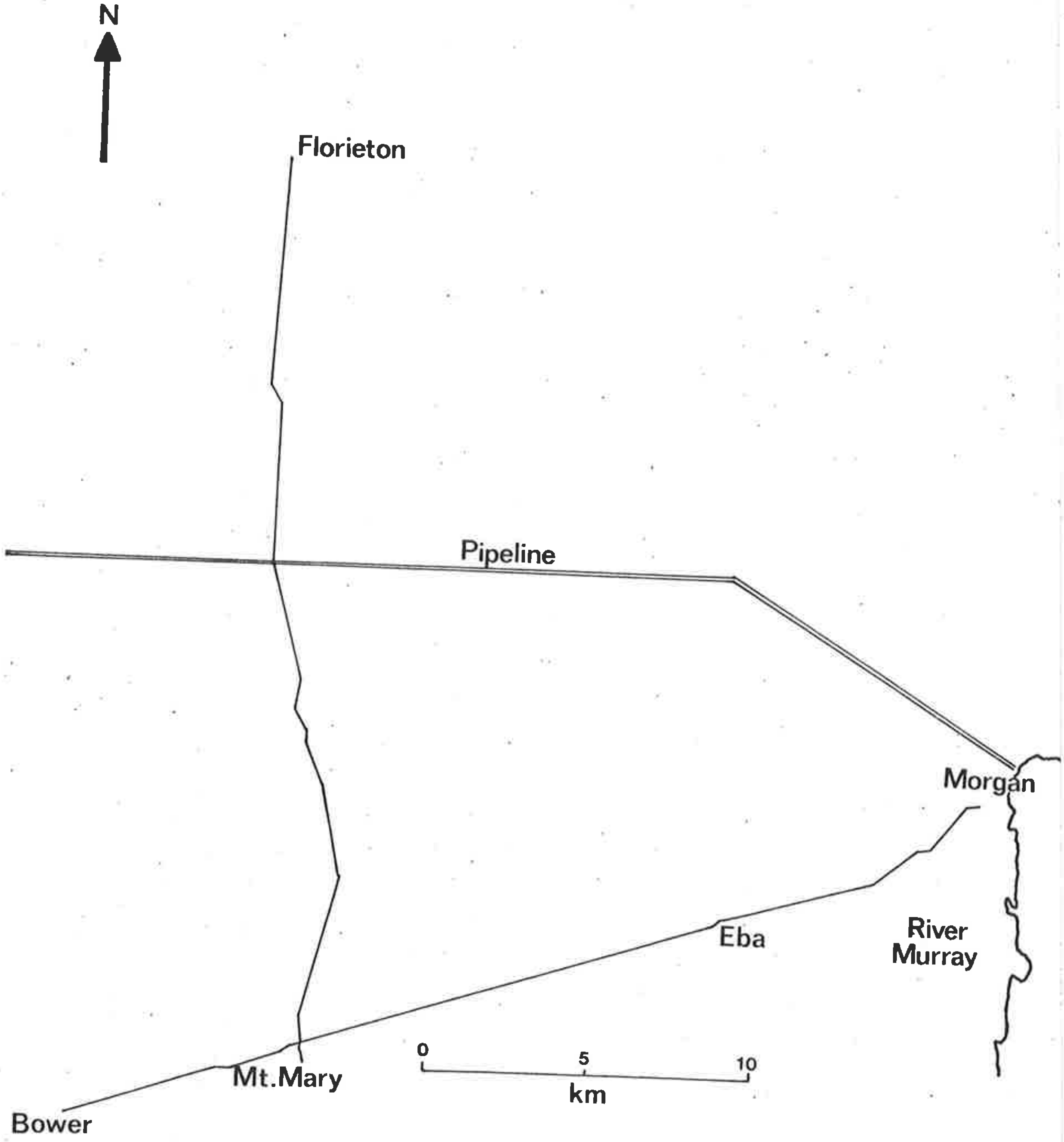
In section 2.30 the need for, and the selection of, the Mt Mary study area were discussed. The study area is 120 km north east of Adelaide bounded in the east by the River Murray and in the west by the eastern slopes of the Mt Lofty Ranges (see Fig. 6). The area studied most intensively includes the towns of Bower, Mt Mary and Morgan, the former railway siding of Eba and the undeveloped townsite of Florieton (see Fig. 45). It is divided by a major highway from Adelaide passing through Bower, Mt Mary, Eba and Morgan. The Morgan-Whyalla pipeline runs east-west through the centre of the area studied. A network of minor, unsealed roads forms a grid pattern over the region.

In this chapter the distributions of the two tick species are examined in detail. The topography, vegetation, soils and weather of the study area are then analysed and patterns which emerge are compared with the distributions of the ticks.

5.20 The distribution of ticks in the study area.

Tick collecting expeditions to the Mt Mary area began in August 1971 and continued at regular intervals (usually monthly) until December 1973. Thereafter fewer such trips were made. Reptiles were collected when seen, usually crossing roads; they were examined for ticks, the location recorded to the nearest 0.1 km and data recorded as described in appendix 1. Apart from lizards required for experiments, those examined were marked and released. The methods of marking reptiles are described in appendix 3. See also comments on mapping tick distributions in 2.10

Figure 45. The Mt Mary Study Area.


N
Florieton
Pipeline
Morgan
River Murray
Eba
Mt.Mary
Bower
0
5
10
km

Ticks had often to be taken from lizards and brought to the laboratory for identification using the keys of Roberts (1970).

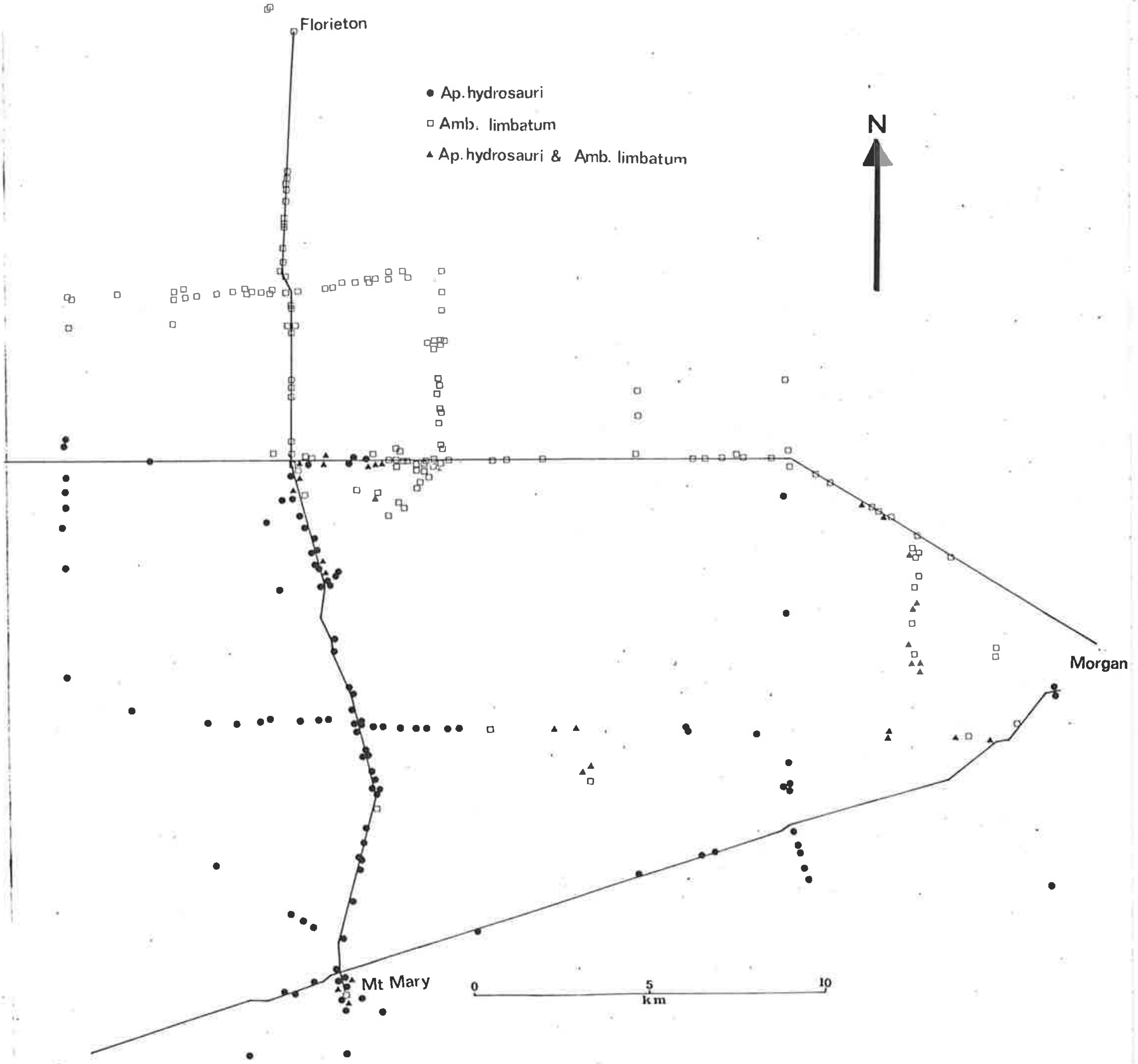
Tick species other than *Ap. hydrosauri* and *Amb. limbatum* were sometimes found on reptiles in the area. Six *Tr. rugosus* bore single specimens of the kangaroo tick, *Ornithodoros gurneyi*, which apparently lives further south than Browning (1962) suggests. This tick has also been found on sleepy lizards from Western Australia. Two goannas, *Varanus gouldii*, were found to be parasitized by *Ap. fimbriatum*. But *O. gurneyi* and *Ap. fimbriatum* were obviously rare compared with *Ap. hydrosauri* and *Amb. limbatum*, which were found on more than four hundred reptiles.

The distributions of the two major reptilian ticks are shown in figure 46. Refer also to figure 6 in Chapter 2 to see this portion of the tick boundary relative to the rest of South Australia. Most records come from the area between Mt Mary and Florieton, particularly near the pipeline. The central area of the map, between the highway and the pipeline and from the Mt Mary - Florieton road to about 10 km west of Morgan, has relatively few records. This central zone is poorly served by tracks and largely covered by scrub. It proved difficult to find lizards there. In other parts of the study area too many records were obtained to fit on the map, e.g. along the pipeline 2-4 km east of the Mt Mary - Florieton road.

In the areas north of Bower and Mt Mary, and near the pipeline, the boundary between the ticks is clear. The boundary zone where either species may be found is up to 3 km wide and runs east-west on the western side of the Mt Mary - Florieton road but curves south on the eastern side of the road. It is unclear whether or not there is a continuous tongue of *Amb. limbatum* all the way to Mt Mary, although it seems likely. Further east in the centre of the study area a broad band of *Ap. hydrosauri* extends north of the highway and just reaches the pipeline. However further west the boundary plunges south again.

The distributional data collected in the present study support the observations made by Smyth (1973). Many of the gaps in Smyth's map have

Figure 46. Records of *Ap. hydrosauri* and *Amb. limbatum* in the Mt Mary area.


Florieton
● Ap. hydrosauri
□ Amb. limbatum
▲ Ap. hydrosauri & Amb. limbatum
N
Morgan
Mt Mary
0
5
10
km

been filled in and it appears that the zone of overlap (the area in which both spp. are found) is as narrow as he suggested. In addition the distributions of the ticks are the same as those shown by Smyth. There is no evidence, from comparing the present map with that of Smyth (1973), or from comparing data from different years in the present study, which indicates any movement of the boundary. Indeed Bull (1978 a) shows that the vagility of *Ap. hydrosauri* is probably very low, so that it would be unlikely to detect movement of the boundary.

Examination of the boundary on the western side of the Mt Mary - Florieton road reveals that in this area no reptiles have been found bearing both species. In fact there is no sign of overlap between the ticks. Few lizards have been caught in this region, and those that have been usually bear no ticks. The density of lizards in the area is discussed later; in parts of the area it may be too low to support a tick population.

The distribution of adult lizards (*Tr. rugosus*) found which did not bear ticks is shown in Fig. 47. The probable positions of the distribution limits of the ticks are also shown. Although there are a number of records of uninfested lizards east of the Mt Mary - Florieton road, it should be noted that these constitute only a low percentage of those found.

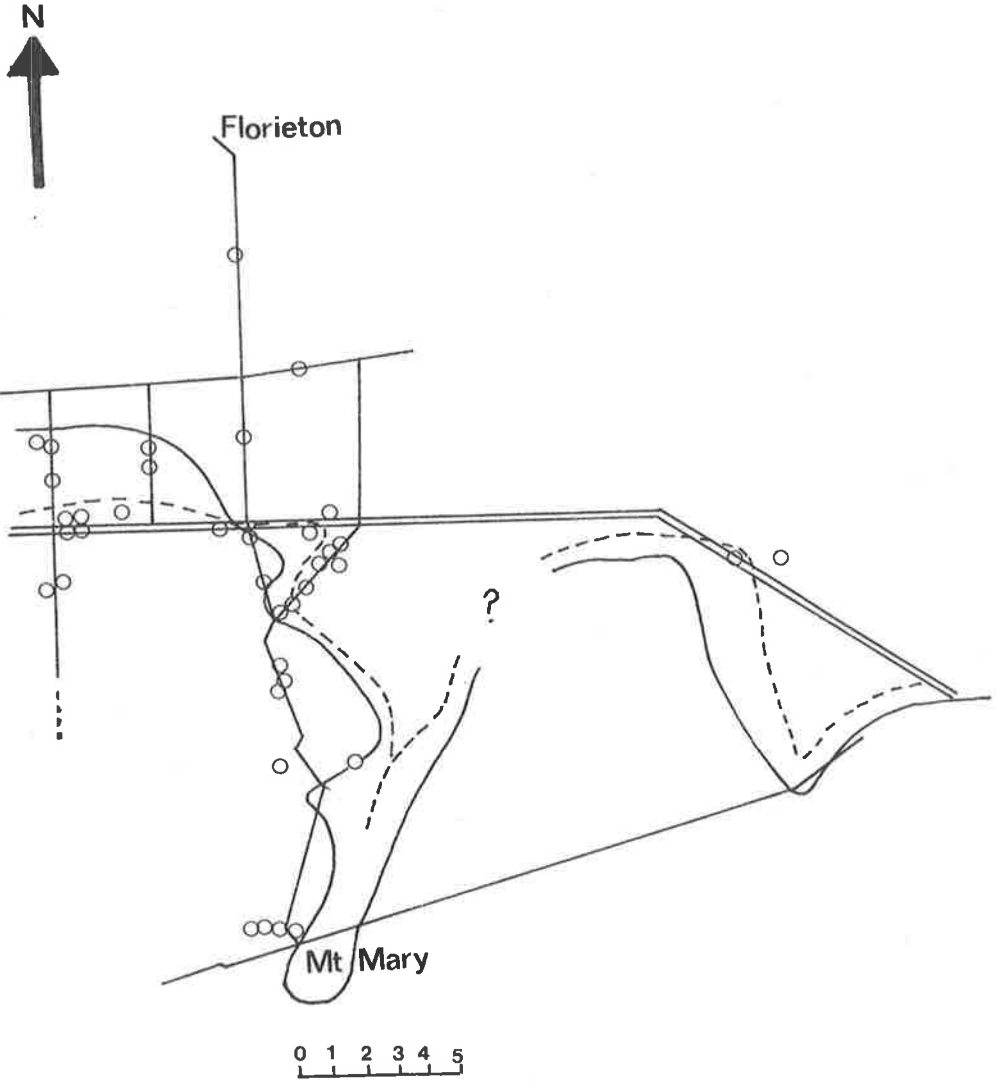
5.30 Biotic and Abiotic characteristics of the Mt Mary Study Area.

In this section the Mt Mary area is examined to see if there are any obvious correlations between the tick distribution above and environmental parameters (I am using the term "correlation" here to mean a correspondence or coincidence).

5.31 Topography

Figure 48 is a contour map of the study area. The contours were

Figure 47. The distribution limits of *Ap. hydrosauri* and *Amb. limbatum* in the Mt Mary area. Also shown are the records of unparasitized sleepy lizards, *Tr. rugosus*.

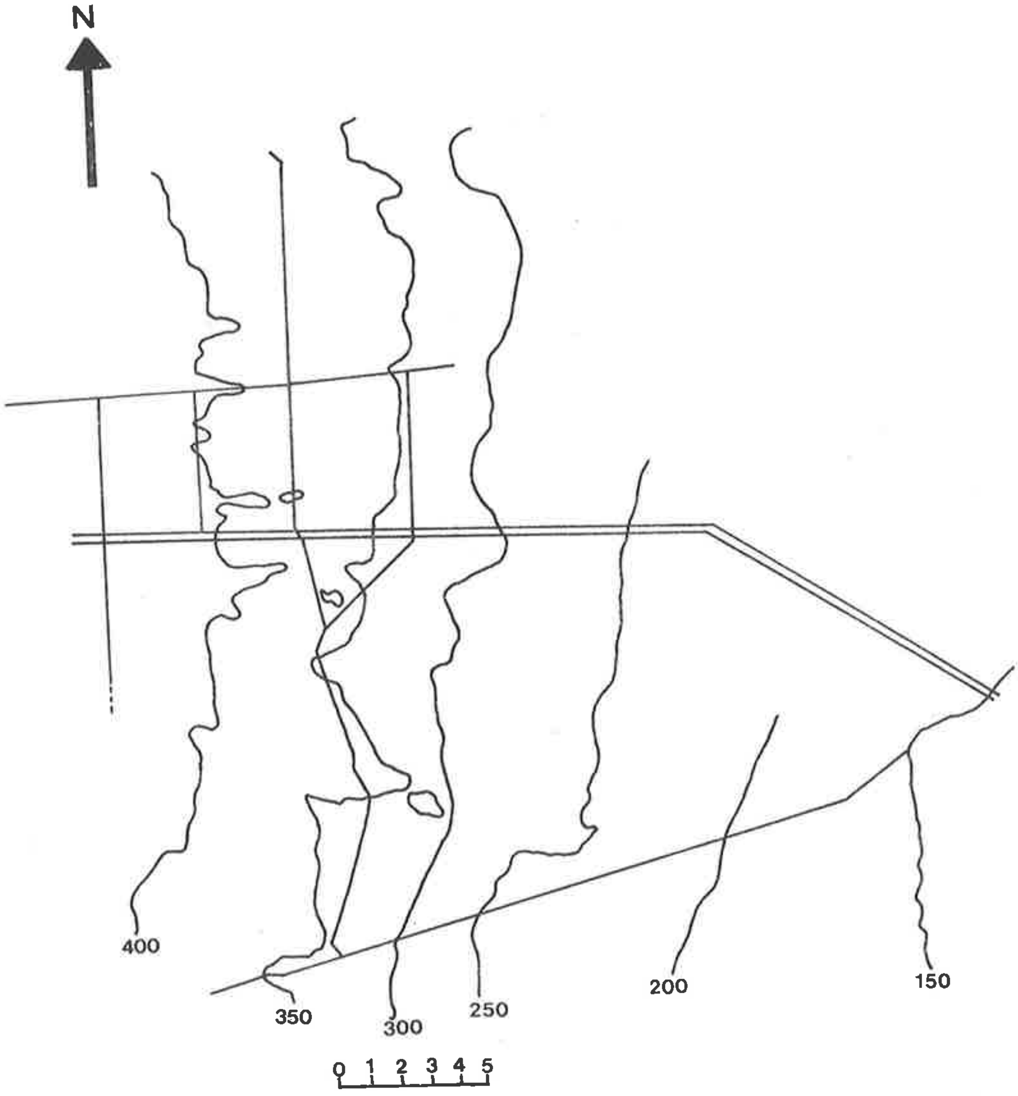


Distribution limit of Amb limbatum ————

Distribution limit of Ap hydrosauri - - - - - - -

Unparasitized lizards ○

Figure 48. Mt Mary topography. Contours (ft) are shown.


N
400
350
300
250
200
150
0 1 2 3 4 5

obtained from Edition 1-AAS series R502 (1:250,000) maps - SI54-5, SI54-9, SI54-10 and from S.A. Lands Dept. sheets 771 zone 6 and 781 zone 6. The map shows a general, gradual decrease in altitude from west to east. There are gentle undulations in the landscape but no marked highlands.

Some areas are quite swampy after rain. The Burra Creek curves around the northern boundary of the study area and into the River Murray 4 km east of Morgan. The Creek rarely flows but after rain consists of a series of swampy lakes. Other areas also become swamps during rain. One large area is on the Mt Mary - Florieton road,2-4 km north of the pipeline. The Mt Mary town-site is just south of another swampy area. These swamps persist for some weeks after rain and attract large populations of water birds.

There seems to be no evident association between the tick boundary and topography.

5.32 Vegetation.

In 2.30 above it was noted that many instances have been reported of broad correlations between vegetation boundaries and the limits of tick distributions. (Brovko 1966, Drozdova and Sapegina 1965, Ohman 1961, Popova et al 1966, Semtner et al 1971, Subotnick 1956, Theiler 1964). Smyth (1973) also suggested a correlation between vegetation type and the tick distributions - this originated from observations and collections made prior to 1970. It was therefore necessary to examine the distribution of vegetation types in the area.

Boehm (1940) had listed many of the vascular plants in the Mt Mary area, but it was Jessup (1948) who first recognized and mapped plant associations. Jessup's maps were evidently compiled by motoring through the area and noting the approximate position of vegetation boundaries. It seemed that his maps overlooked minor convolutions in the boundaries. The vegetation maps in Specht (1972) also show broad changes and not enough detail for the purposes of this study.

A central area (see figure 49) was chosen in which to study vegetation in detail. This region seemed to contain all vegetation types. Samples were taken of 55 different plants from this central area, and these were identified by M.C.R. Sharrad using the keys in Black (1943-57);see table 24. Pressed, dried voucher specimens were attached to a clipboard for field use.

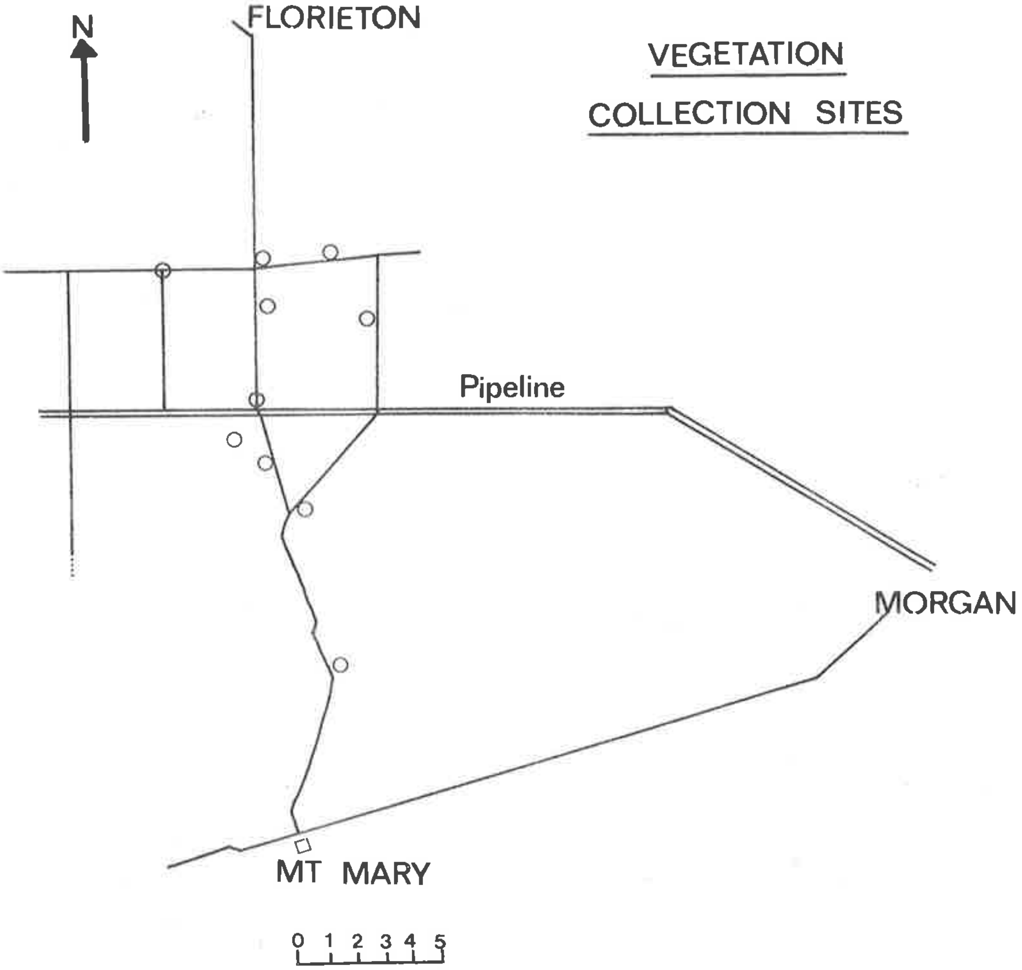
The presence or absence of each of the 55 plants was recorded in 100 quadrats in the same central area. The optimum quadrat size and shape was found (see Greig-Smith 1964 pp 27-29) to be 20 metres diameter and round. The allocation of quadrats was restricted in that I ensured that they were distributed on both sides of what appeared to be the vegetation boundary. The data on presence and absence of plants in the quadrats were analysed to see which species were positively or negatively associated (see Greig-Smith 1964 Chapt 4).

The results are analysed in figures 50 and 51.

The mallee scrub comprises one of the association groupings. There are two other recognizable groupings in the area; *Casuarina cristata* scrub, and more open grassland with a few scattered trees of *Myoporum platycarpum*. Some plant species are, of course, found in all areas while others are less cosmopolitan.

Armed with these data I mapped vegetation throughout the study area. This was achieved in two ways. The first involved driving along all the navigable tracks stopping every 200 metres and recording the plants seen - a technique used by Connor (1966). The second involved aerial photography and photo-interpretation. Black and white photographs from the S.A. Lands Department were useful to determine where scrub boundaries went between roads. However these photographs did not enable recognition of vegetation types. It was therefore

Figure 49. Sites at which samples were collected for identification during a survey of the vegetation in a central region of the Mt Mary study area.



VEGETATION
COLLECTION SITES

Figure 50. The results of 2 x 2 contingency table tests for association between pairs of plant species in a central region of the Mt Mary study area. 55 species were included in the survey but only those that were adequately represented in the data are shown.

+	significant positive association
-	significant negative association

Plant sp

Plant sp

	1	5	7	10	18	22	26A	26B	31	35	40	41	43	47	48	49	51	53	54	55
1																				
5																				
7																				
10																				
18																				
22				−																
26A	+			−																
26B					−															
31				+	+															
35				+					−											
40				−	−	+	+													
41				−		+	+				+									
43				−		+	+	+			+	+								
47		−				+							+							
48		+		+		−			−				−	−						
49				−		+					−									
51		+				−					−	−	−	−	+					
53										+										
54					+			−										+		
55	+			−			+	+	−		+		+							

Figure 51. Patterns of association between plant species in a central region of the Mt Mary study area. Significant positive associations (at the 1% level) are shown by the continuous lines while significant negative associations (at the 1% level) are shown by the broken lines.

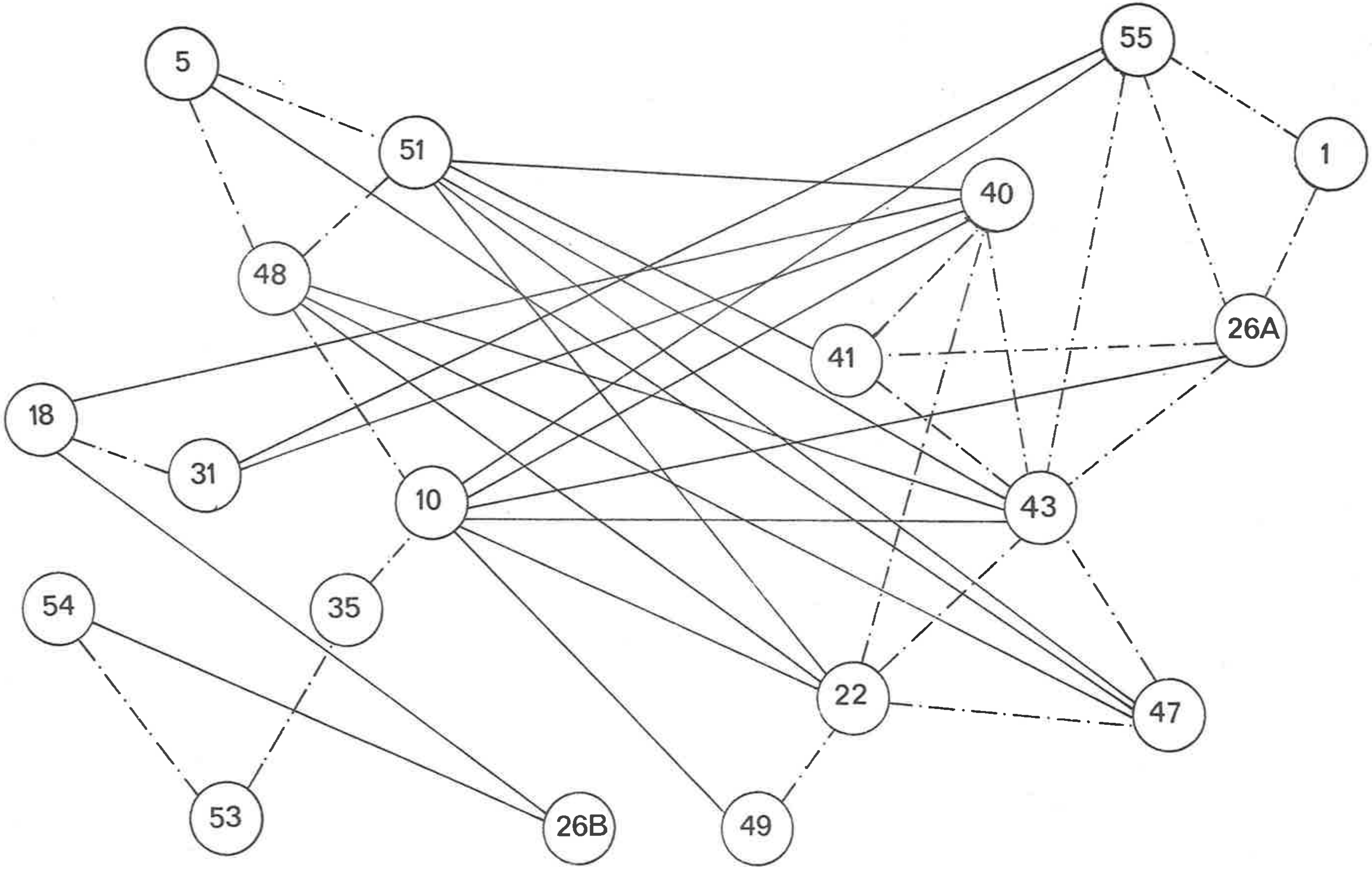

5
51
48
18
31
10
35
54
53
26B
49
22
47
43
41
40
55
1
26A

Table 24

A list of plants collected in the Mt Mary Study Area.

1. *Kochia sedifolia* (Blue Bush)
2. *Lycium australe*
3. *Oxalis corniculata*
4. *Brachyscome gramineae*
5. *Scaevola spinescens*
6. *Chenopodium cristatum*
7. *Bassia ventricosa*
8. *Kochia brevifolia*
9. *Salsola kali*
10. *Atriplex rhagodioides*
11. *Velleia paradoxa*
12. *Olearia ciliata*
13. *Prostanthera striatiflora*
14. *Heliotropium europaeum*
15. *Solanum esuriale*
16. *Muehlenbeckia cunninghami*
17. *Calotis multicaulis*
18. *Nicotiana goodspeedii*
19. *Eremophila surrulata*
20. *Enchylaena tomentosa*
21. *Atriplex rhagodioides (♀)*
22. *Bassia paradoxa*
23. *Wahlenbergia sieberi*
24. *Geijera linearifolia*
25. *Goodenia subintegra*
26. *Zygophyllum sp.*
27. *Eremophila sturtii*
28. *Eremophila oppositifolia*
29. *Blenodia trisecta*
30. *Brachyscome ciliaris*
31. *Elachanthus pusillus*
32. *Carrichtera annua*
33. *Salsola kali*
34. *Verbena officinalis*
35. *Sisymbrium erysimoides*
36. *Sisymbrium orientale*
37. *Atriplex campanulata*
38. *Zygophyllum apiculatum*
39. *Zygophyllum aurantiacum*
40. *Kochia lanosa*
41. *Rhagodia crassifolia*
42. *Kochia (ciliata?)*
43. *Eucalyptus oleosa (var glauca?)*
44. *Eucalyptus oleosa*
45. *Eucalyptus gracilis*
46. *Eucalyptus calycogona*
47. *Anthocercis anisantha*
48. *Exocarpus aphyllus*
49. *Acacia euthycarpa*
50. *Atriplex spongiosa*
51. *Casuarina cristata*
52. *Atriplex rhagodioides*
53. *Myoporum platycarpum*
54. *Lycium australe*
55. *Atriplex sp*

decided to photograph the area from the air using colour films.

A metal frame was designed to hold two single-lens reflex, 35mm cameras. This frame was attached to a single engined Cessna aircraft which had one door removed. The project was carried out jointly with J.D. Roberts who was studying frogs in the area. A pilot from Rossair flew us over the study area following a predetermined grid pattern at an altitude of 3,050 metres. The photographs, on Kodak Ektachrome X film, were taken at regular, predetermined intervals so that successive ones would overlap.

The photographs were used with the data discussed above to compile a vegetation map, see figure 52. Some parts of the study area had been extensively cleared - particularly near Mt Mary. It was sometimes difficult to determine what the original vegetation had been, however it was possible to map the general distribution pattern.

North of the pipeline there are extensive open areas but these are not due to the action of man.

Vegetation does not occur in neat readily delimited parcels. There is some overlap and some interdigitation where major plant communities meet. It was noticeable in the area north of Mt Mary near the pipeline that, where vegetation overlap occurred, mallee scrub was found on the ridges and plants characteristic of the other communities grew in the valleys along drainage lines. This division probably reflected a change in substrate, see 5.33 below.

If the boundary of the mallee scrub is compared with the tick boundary, some association is evident, see figure 53. *Amb. limbatum* are rarely found inside the mallee region. However *Ap. hydrosauri* extends out from the mallee 2 to 4 km in places.

If the change in vegetation were responsible for the tick boundary it might achieve this effect in a number of ways. Perhaps the nature of the vegetation influences the availability and suitability of microhabitats for ticks off the host. Perhaps the vegetation might indirectly influence the

Figure 52. A vegetation map of the Mt Mary study area showing the distribution of Mallee scrub.

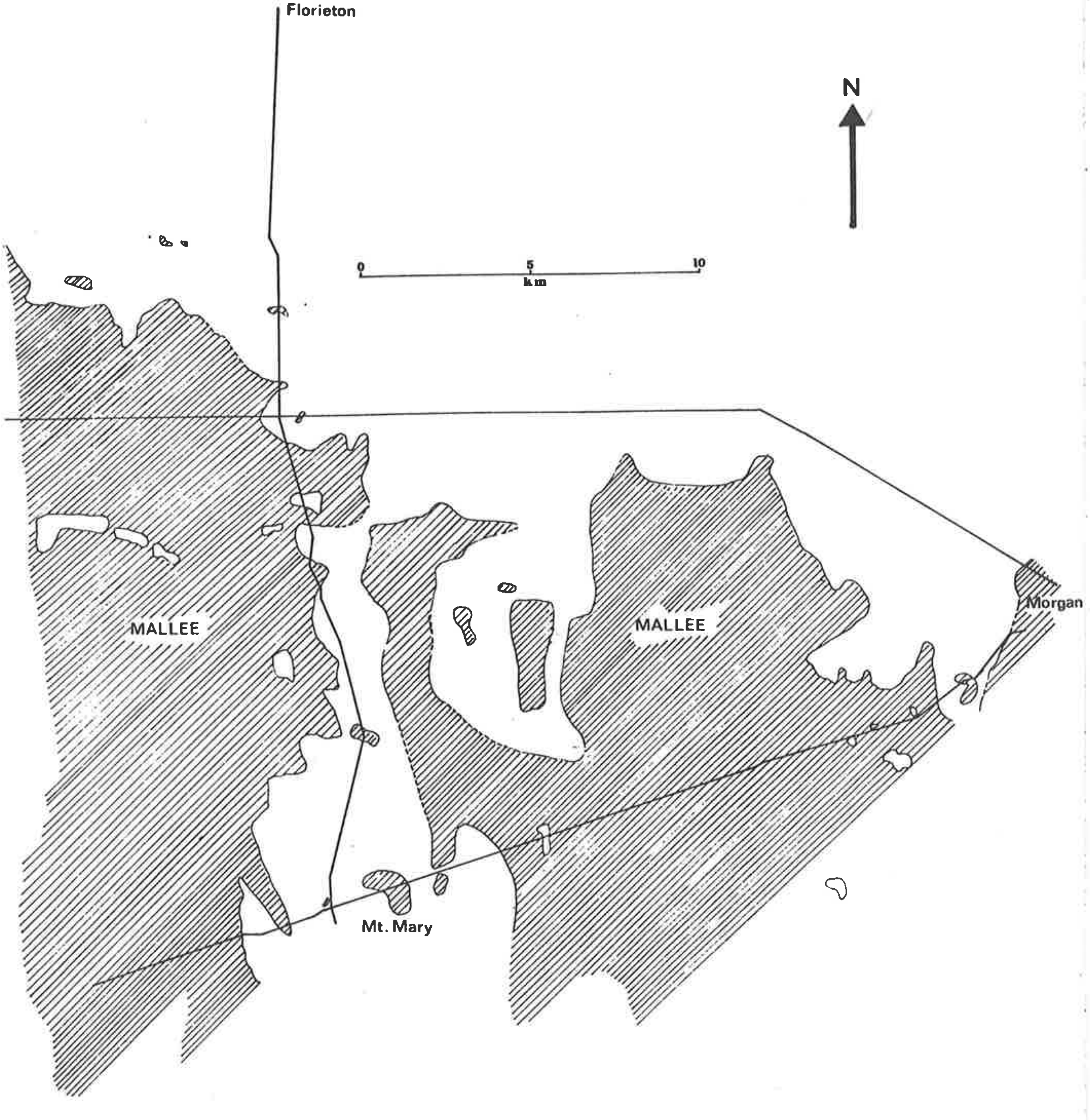
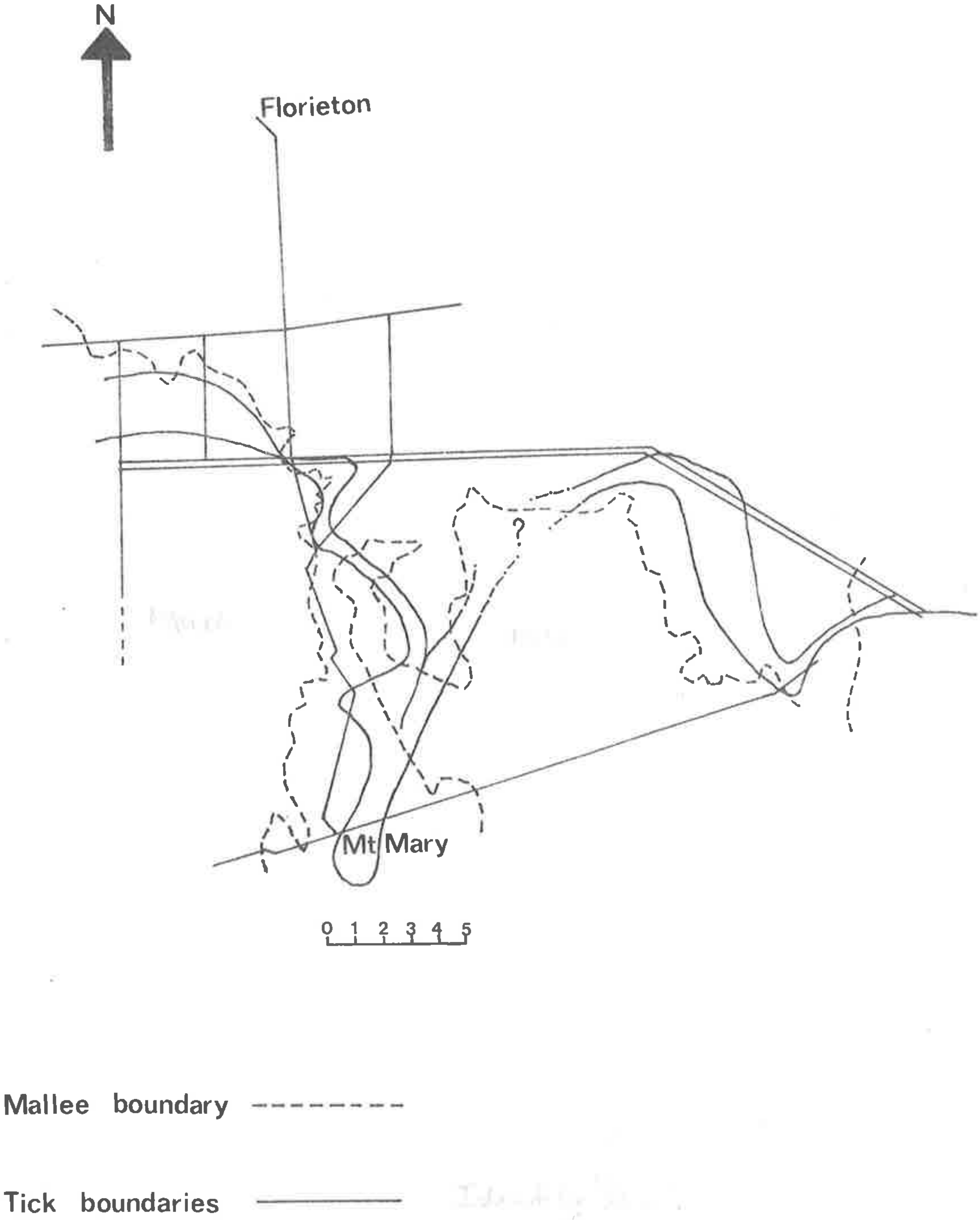

Florieton
N
0
5
10
km
MALLEE
MALLEE
Morgan
Mt. Mary

Figure 53. The positions of the tick distributional limits (*Ap. hydrosauri* and *Amb. limbatum*) and the boundary of the Mallee scrub.


N
Florieton
?
Mt Mary
0 1 2 3 4 5
Mallee boundary
Tick boundaries

ticks via the hosts. Changes in vegetation might influence the abundance of lizards through their requirements for food and/or shelter. Different vegetation types might also remain succulent for different periods of time during the year and thus influence the activity of herbivorous reptiles.

Other species, which in turn influence the ticks or their hosts, might be confined to one vegetation type and thus to one side of the boundary. Perhaps a predator of the ticks is influenced in this way - although I have not uncovered any predators of the ticks.

Despite the correlation, tick distribution and vegetation might not be causally related. It may well be that they are both due to the action of other factors; e.g. climate or soil type.

5.33 Soils

One would suspect the abrupt transition from mallee plant communities to the more arid communities near Mt Mary to be due to changes in weather or soil type or both. Specht (1972) points out the close association between soil type and plant communities in South Australia.

Boehm (1940) noted that the area near Bower and Mt Mary was characterized by "chocolate-brown loam" soils "with nodular travertine limestone". He observed that flat areas had similar soil without the limestone nodules. Jessup (1948) made similar general comments on the region.

Examination was made of the work of Northcote (1960, 1968) and Stephens (1962) and of soil samples and soil profiles in the area. The predominant soil was a brown calcareous earth categorized as solonized brown soil by Stephens (1962) and as Gc1.12 and Gc1.22 by Northcote (1968). In some areas there were patches of crusty loams with red clay beneath; Dr 1.13 and Dr 1.33 (Northcote 1968). There were deposits of kunkar particularly on ridges where soil was shallow. In drainage lines alluvial, kunkar free clays and silts had accumulated. The soils in the northern parts of the area tended to contain less kunkar and to have a higher clay content.

It was evident that the mallee scrub was confined to brown solonized soil which was often shallow with kunkar deposits. The other plant associations, of which *Myoporum platycarpum* and *Casuarina cristata* were dominant members, were found in soils with fewer kunkar deposits and higher clay content.

Thus the soil type, vegetation type and tick boundaries are to a considerable degree coincident. The soil type might well be important not only in influencing vegetation as pointed out in 5.32 above but directly influencing the characteristics of the ticks' microhabitats when off the host.

5.34 Weather

Ticks and, in this case, their hosts are poikilothermic. Both are greatly influenced by changes in temperature and humidity (see Chapters 3 and 4). The possibility had to be explored that weather, acting directly on ticks or through their hosts, might cause the parapatric distribution.

The Mt Mary area receives an average annual rainfall of less than 250mm per year. The monthly averages are much less predictable than in wetter areas to the south and west but most rain falls during the winter months.

Rainfall records were obtained from the Bureau of Meteorology in Adelaide for Morgan, Bower and Sutherlands and from 3 homesteads in the study area. The locations of these and average annual rainfall over the last 10 years (up to 1973) is shown in figure 54. In figures 55, 56 and 57 rainfall records are graphed for these stations from 1967 to 1973.

It can be seen that there are few differences between the areas. All have low average rainfall of uncertain timing. Some years, e.g. 1967 and 1972, were drought years with little rain, and the rain that did fall was

Figure 54. Towns and homesteads from which rainfall records were obtained. The average yearly rainfall from 1963-1972 (m.m.) is shown for each site.

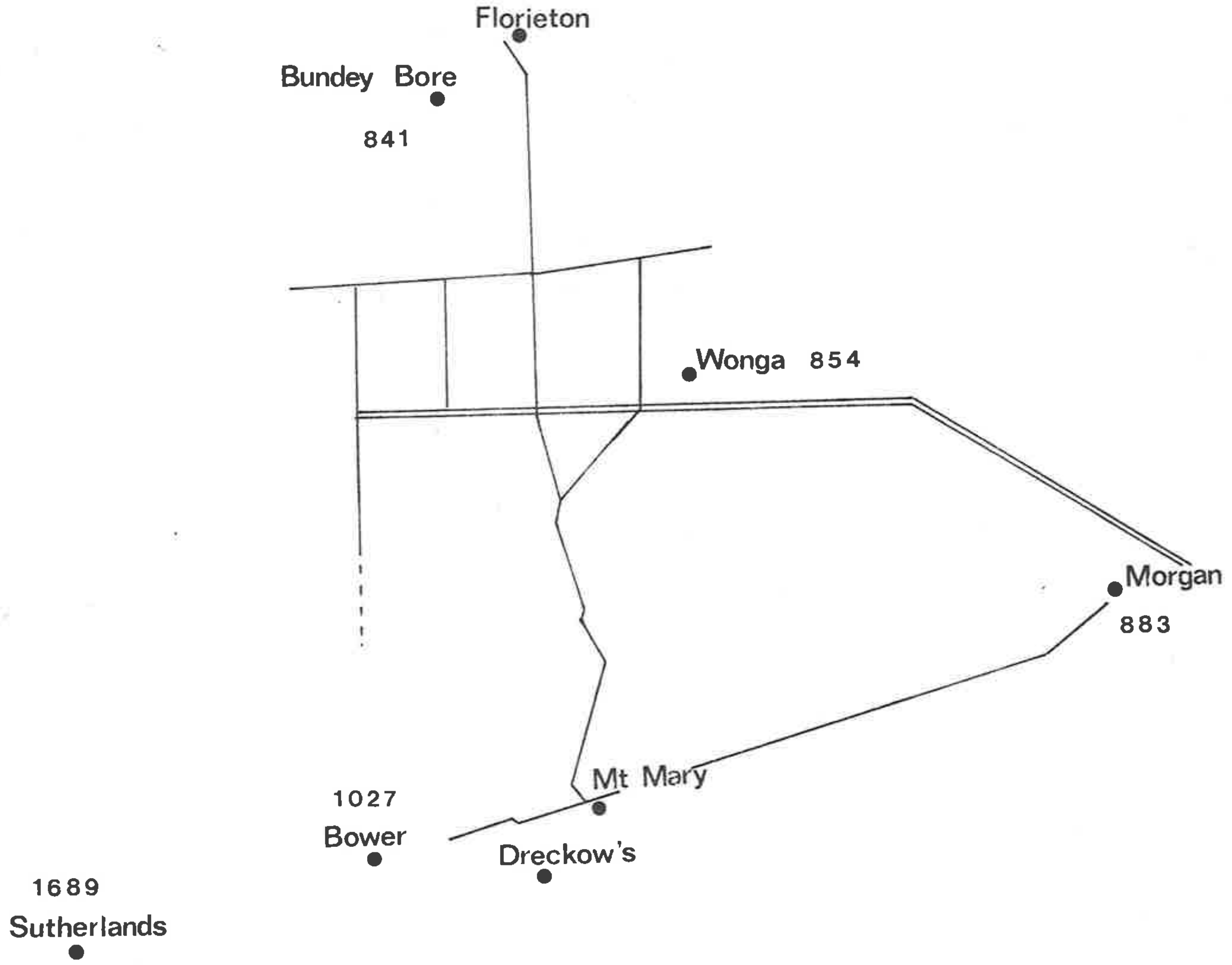

Florieton
Bundey Bore
841
Wonga 854
Morgan
883
Mt Mary
1027
Bower
Dreckow's
1689
Sutherlands

Figure 55. Rainfall records for Morgan and Bower, 1967-1973. Each point represents the total rainfall over a 4-week period.

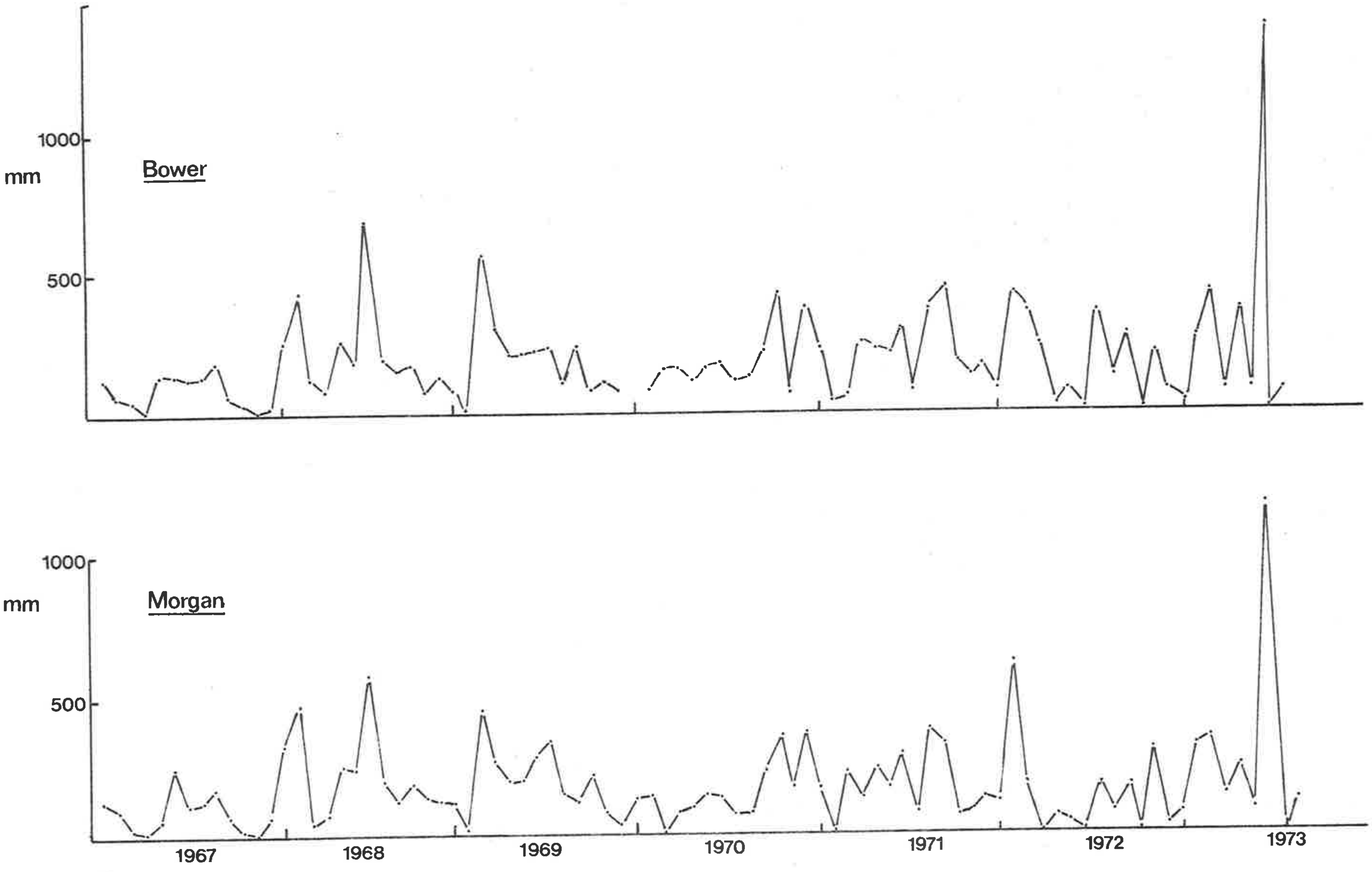

1000
mm
Bower
500
1000
mm
Morgan
500
1967
1968
1969
1970
1971
1972
1973

Figure 56. Rainfall records for 'Wonga' and Dreckow's homesteads (see fig. 53). Each point represents the total rainfall over a 4-week period.

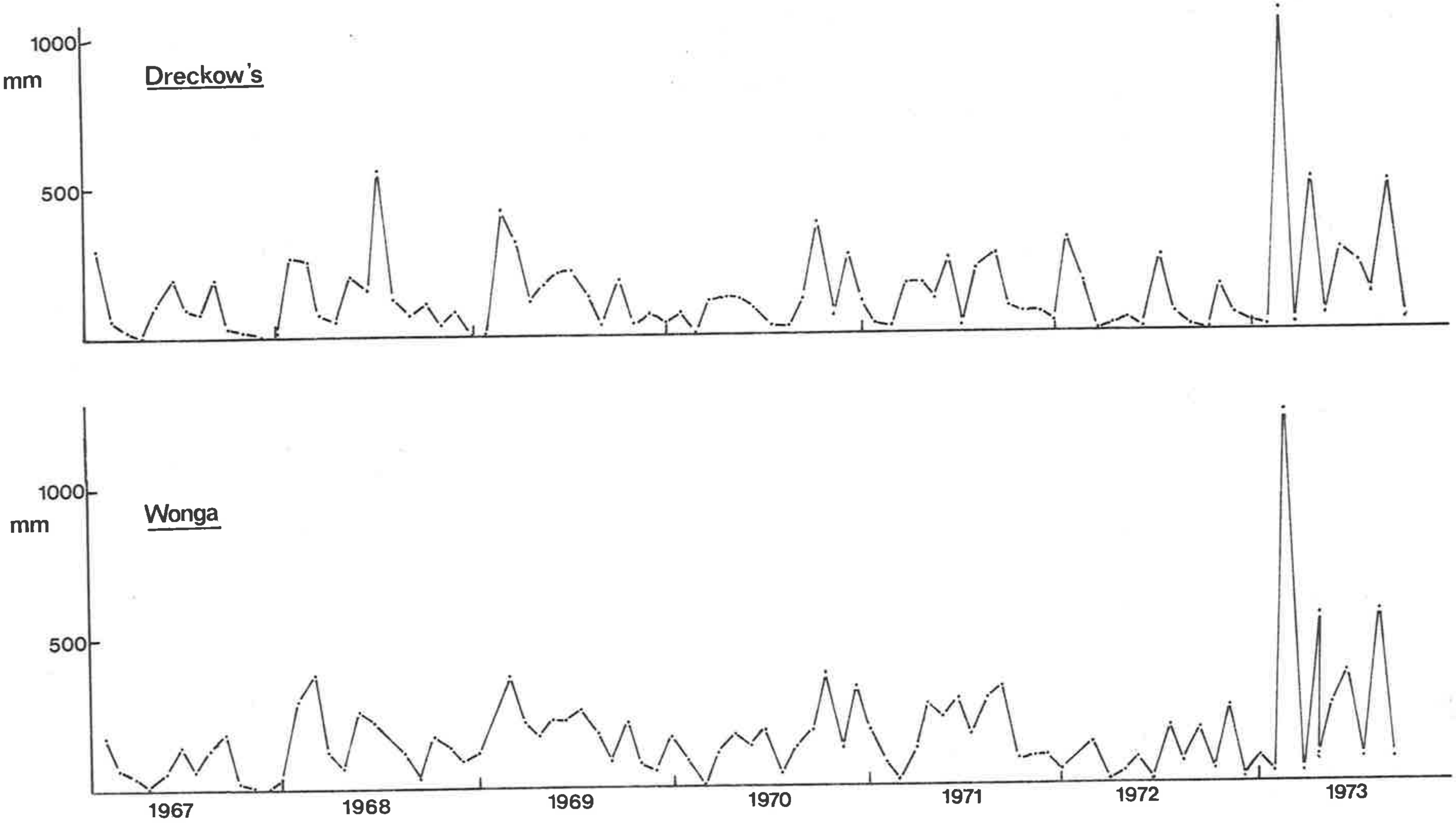
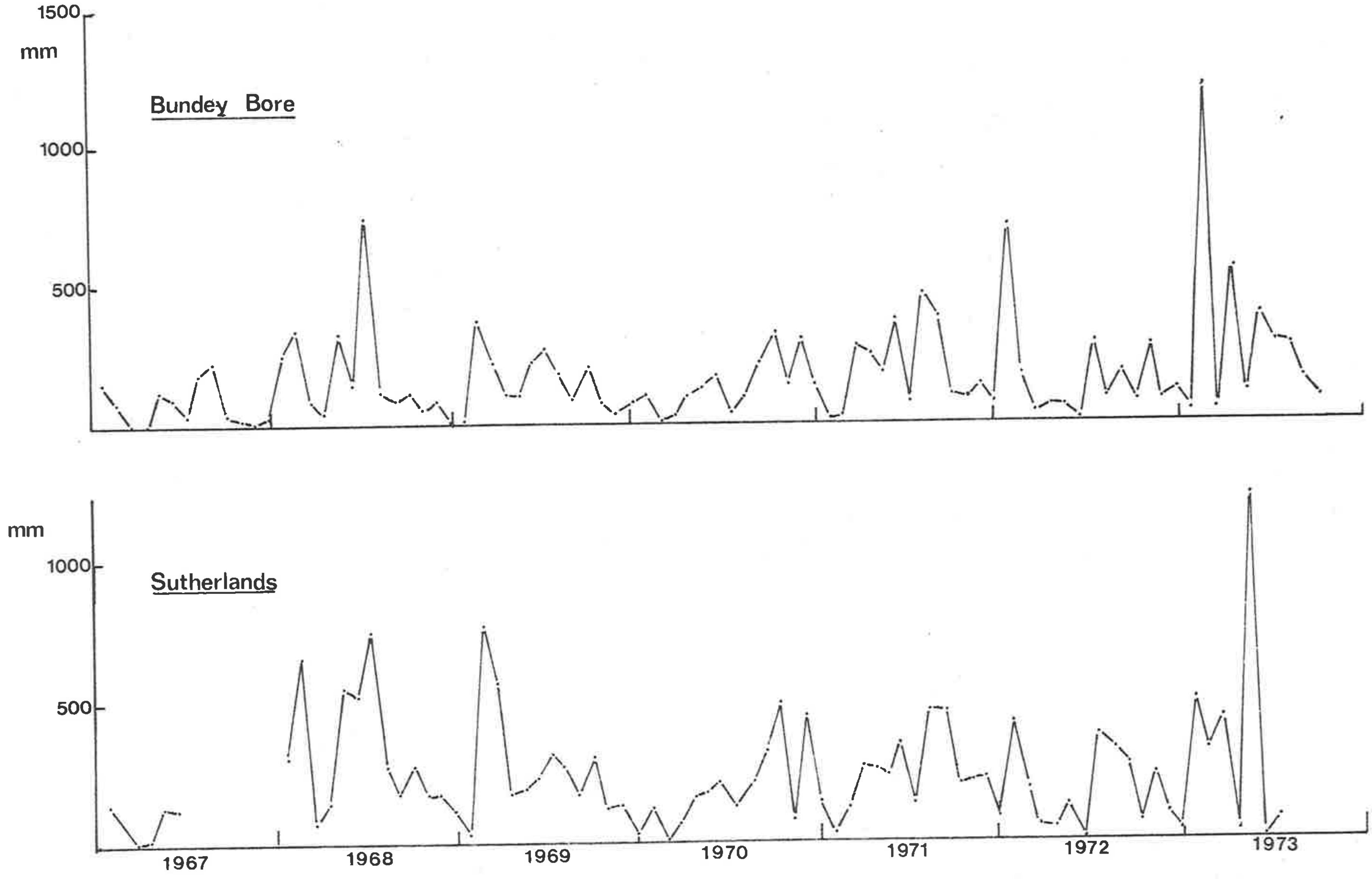

1000
mm
Dreckow's
500
1000
mm
Wonga
500
1967
1968
1969
1970
1971
1972
1973

Figure 57. Rainfall records for Bundey Bore and Sutherlands (see fig. 53). Each point represents the total rainfall over a 4-week period.


1500
mm
Bundey Bore
1000
500
mm
1000
Sutherlands
500
1967
1968
1969
1970
1971
1972
1973

too widely scattered to sustain vegetation growth. There does not seem to be a marked drop in rainfall at the tick boundary, but there is a gradual decrease from west to east.

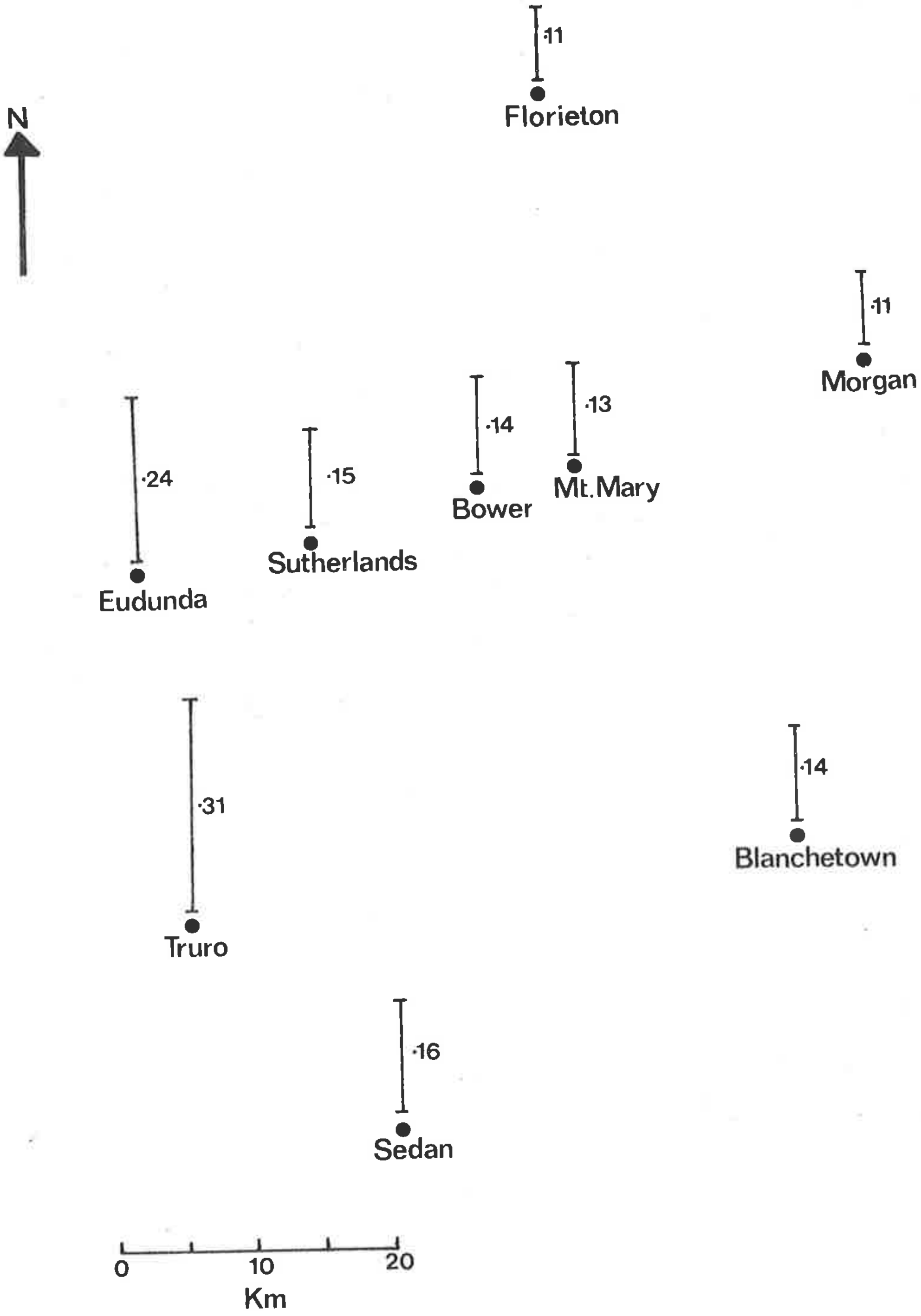
However the rainfall alone does not give a good indication of moisture in the soil, vegetation or air. Evapotranspiration must also be taken into account. Trumble (1948) measured evaporation from free water surfaces in various parts of South Australia and then estimated evaporation in other areas of the state. The rate of evaporation from a free water surface would usually be greater than evapotranspiration. Trumble suggests that the latter is from a fifth to one-half of the former. He also estimated the percentage drought frequency of these areas, i.e., "the number of years in a hundred in which the season of continuously effective rainfall is less than 5 months". Under this system 95% of years at Morgan are classified as drought years. Sutherlands, to the west of Mt Mary, had 67% drought year frequency. This system is designed to indicate the suitability of areas for agriculture. However it does give a measure of the relative aridity of different areas.

It seemed that the ratio of mean annual rainfall (R) to mean evaporation (E) may serve as a measure of the "aridity" of different sites. Accordingly I used the data of Trumble (1948) and these are shown in figure 58. In this figure values for Florieton, Bower and Mt Mary do not appear in Trumble (1948) but have been estimated.

It can be seen that *Ap. hydrosauri* lives in areas where R/E is less than .13. Florieton and Morgan have similar R/E values yet *Ap. hydrosauri* survives near Morgan but not near Florieton! It seems that raw data on annual rainfall and evaporation are unenlightening by themselves.

Morgan and Florieton have similar R/E values, in fact Florieton's may be slightly higher - records were kept of rainfall at the latter from 1888 to 1915 and it had slightly more rain than Morgan. However Morgan is near the River Murray and this might result in slightly higher humidities nearby.

Figure 58. Ratios of mean annual rainfall (R) to mean evaporation (E) in the Mt Mary area and surrounding sites. The height of the bars represent the size of the ratio.


·11
Florieton
N
·11
Morgan
·14
·13
·24
·15
Bower
Mt.Mary
Sutherlands
Eudunda
·14
·31
Blanchetown
Truro
·16
Sedan
0
10
20
Km

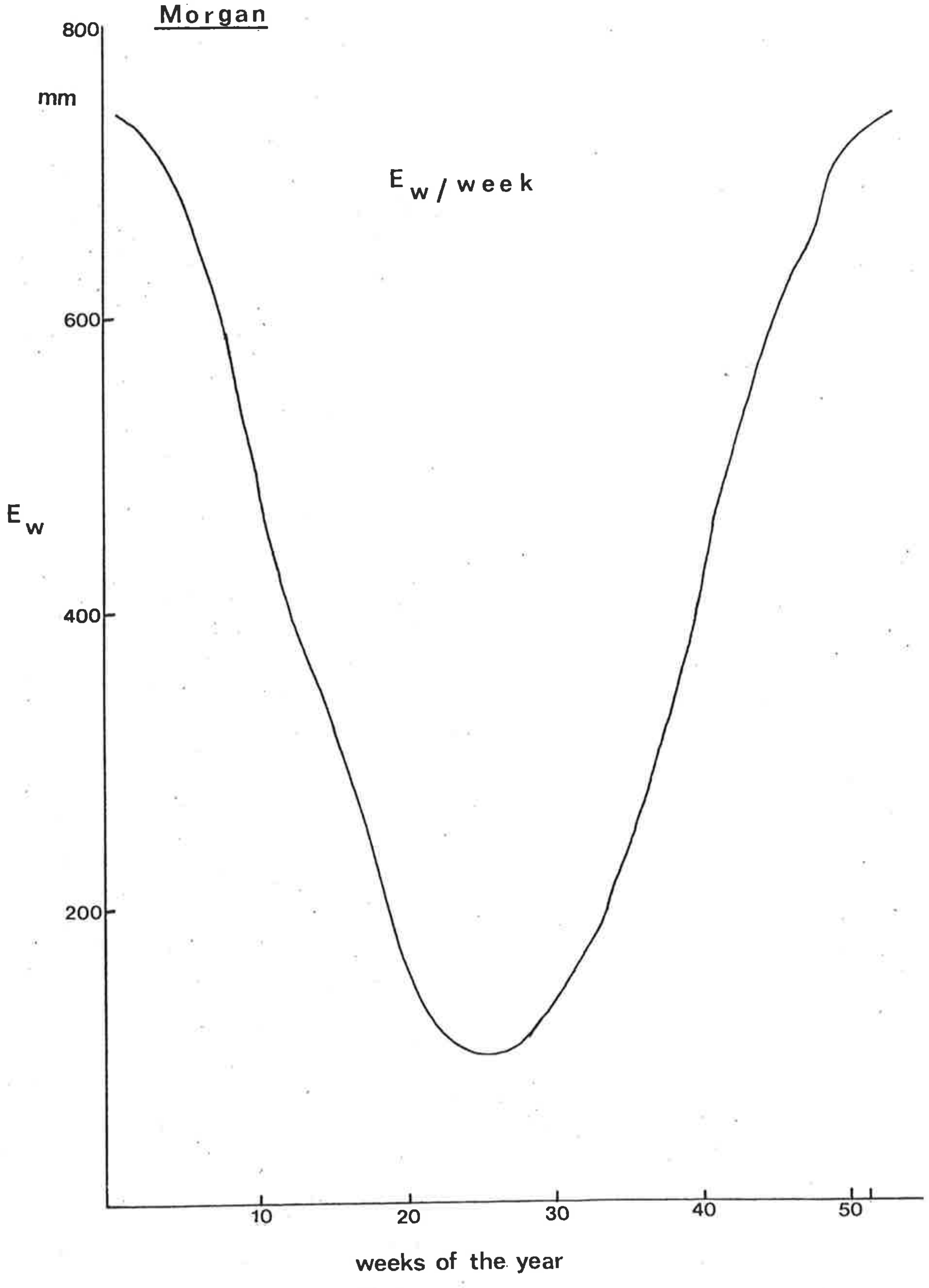
Slatyer (1960 a and b, 1962) and Specht (1972) show that soil types influence the amount of surface runoff, penetration by water and evaporation in an area. Some soils are relatively impermeable while others allow rapid and deep penetration by water. Some soils have a greater water holding capacity than others. Thus, although two areas might have similar annual rainfall and evaporation, the microhabitats of organisms on or near the soil might vary greatly in humidity. The soils in the study area are discussed in 5.33.

It must also be noted that in the Mt Mary area rainfall and evaporation vary from month to month and rainfall fluctuates from year to year. Evaporation seems to fluctuate throughout the year in a more regular fashion. Figure 59 shows evaporation values for Morgan (from Trumble 1948).

Rayson (1957) and Specht (1972) discuss variations in rainfall, evaporation and humidity with microtopography. Values for these quantities may vary between different sides and on the tops of ridges or dunes. Perhaps local changes in microtopography might influence humidity at the boundary.

In 3.40 the ability of the ticks to obtain water from the air was discussed. At relative humidities of 82-85% and above, *Ap. hydrosauri* and *Amb. limbatum* can, at normal temperatures, more than match evaporative water loss by this method. If relative humidity falls below 80% they lose water and will in time die, *Ap. hydrosauri* being more prone to death in these circumstances than *Amb. limbatum*. Might it be then that in the study area the northern limit of *Ap. hydrosauri* is set by such a change in humidity? If evaporation increases and rainfall decreases steadily across the area and soil and vegetation types change rapidly, then the humidity of most of the ticks' moulting microhabitats on the northern side of the boundary might be too low for too long. This change might prevent the tick from living north of the boundary or from successfully competing with *Amb. limbatum* in that area. See Chapter 7 for further discussion. The

Figure 59. The distribution of estimates of weekly evaporation, Ew, from a free water surface at Morgan (from Trumble 1948).


Morgan
800
mm
E w / week
600
E w
400
200
10
20
30
40
50
weeks of the year

above meteorological data from the Mt Mary area are not precise enough to allow close examination of this hypothesis.

Osborn et al. (1935) published data on the Koonamore vegetation reserve which is 200km north of Mt Mary but has similar weather - about 25mm a year less rain. They showed that in every month of the year there is some time in which relative humidity, in a Stephenson screen, exceeds 80% - even in February this happens for an average of 3.9 hours per day! Ticks off the host are buried in leaf litter or in cracks in the soil (see 3.3411) which are fluctuating in moisture content between rains and the air around them fluctuates in relative humidity with temperature. It is evident that measures of tick resistance to desiccation under constant laboratory conditions do not reflect all aspects of the real situation but they enable us to say that the air around the ticks at some times of the day enables them to imbibe more water than they lose and vice versa. They are subject also to changing temperatures and are continually, though slowly, using up energy reserves.

Osborn et al. (1935) point out that semi-arid regions of South Australia experience two well-marked seasons, a cold season from April to September and a hot season from October to March. At Koonamore the mean monthly maxima during the hot season ranged from 26° to 33°C and during the cold season from 15° to 21°C. During the night temperatures drop markedly. The mean diurnal range at Koonamore was 16.7°C. Soil temperatures would fluctuate more widely than the air temperatures. During summer soil temperatures at Mt Mary often exceed 50°C (in direct sunlight) and 35°C (in the shade). Thus ticks in their microhabitats off the host might experience fluctuations in temperature different from those observed in air temperature.

5.35 Hosts.

Boehm (1943) listed reptile species found in the Mt Mary area. He listed all the species which I have found and examined in the area, plus a snal which has not been found during the present study. It is the carpet snake

"Python spilotes" (Morelia spilotes) which Boehm recorded as being rare. Painted dragons, *Amphibolurus pictus*, occur in the study area and though they bear ticks in some parts of the State they do not at Mt Mary.

The records of tick infestations on reptile species in the Mt Mary study area are summarized in table 24.

Table 24.

Species of reptiles found to bear ticks in the Mt Mary study area showing the numbers caught and the numbers bearing each tick species.

Host species	Total No. Caught	No. carrying *Ap. hydrosauri*	No. carrying *Amb. limbatum*	No. not carrying either tick spp.	No. carrying both tick spp.
Tr. rugosus (sleepy lizards)	426	160	241	69	44
A. barbatus (Bearded dragons)	33	2	7	24	-
V. gouldii (Goannas)	6	-	1	5	-
Pseudonaja sp (Brown snakes)	2	-	2	-	-

There is no doubt that *Tr. rugosus* is the most abundant host at Mt Mary (see also 4.22). Bearded dragons and goannas are seldom parasitized. Brown snakes, though more cryptic than sleepy lizards, seem to be in much lower numbers.

There are a number of ways in which hosts could act as factors causing the parapatric boundaries or as factors tending to disrupt them (see 4.50). Accordingly changes in host abundance, refuge sites and behaviour were searched for across the boundary area.

The sleepy lizards were most often found to shelter under low spreading bushes such as the blue bush (*Kochia sedifolia*). These bushes were found on both sides of the boundary and did not appear to differ consistently in size or shape. The soil in which they grew did vary, however, see 5.33 above.

Lizard density does vary across the study area. In 5.20 above attention was drawn to the lack of lizards in certain areas. Most lizards were caught by driving along tracks until they were seen, active, crossing the road. It was therefore possible to use these capture records to compute indices of relative abundance. As high numbers of lizards were only found in spring and summer only these data are useful. The numbers of lizards caught per kilometre per trip on sections of road were calculated. Only trips over a road on a day when lizards were active were counted and then only after the first had been observed.

Figure 60 shows the roads used in this study. Table 25 shows the relative abundance indices of *Tr. rugosus* on the numbered roads.

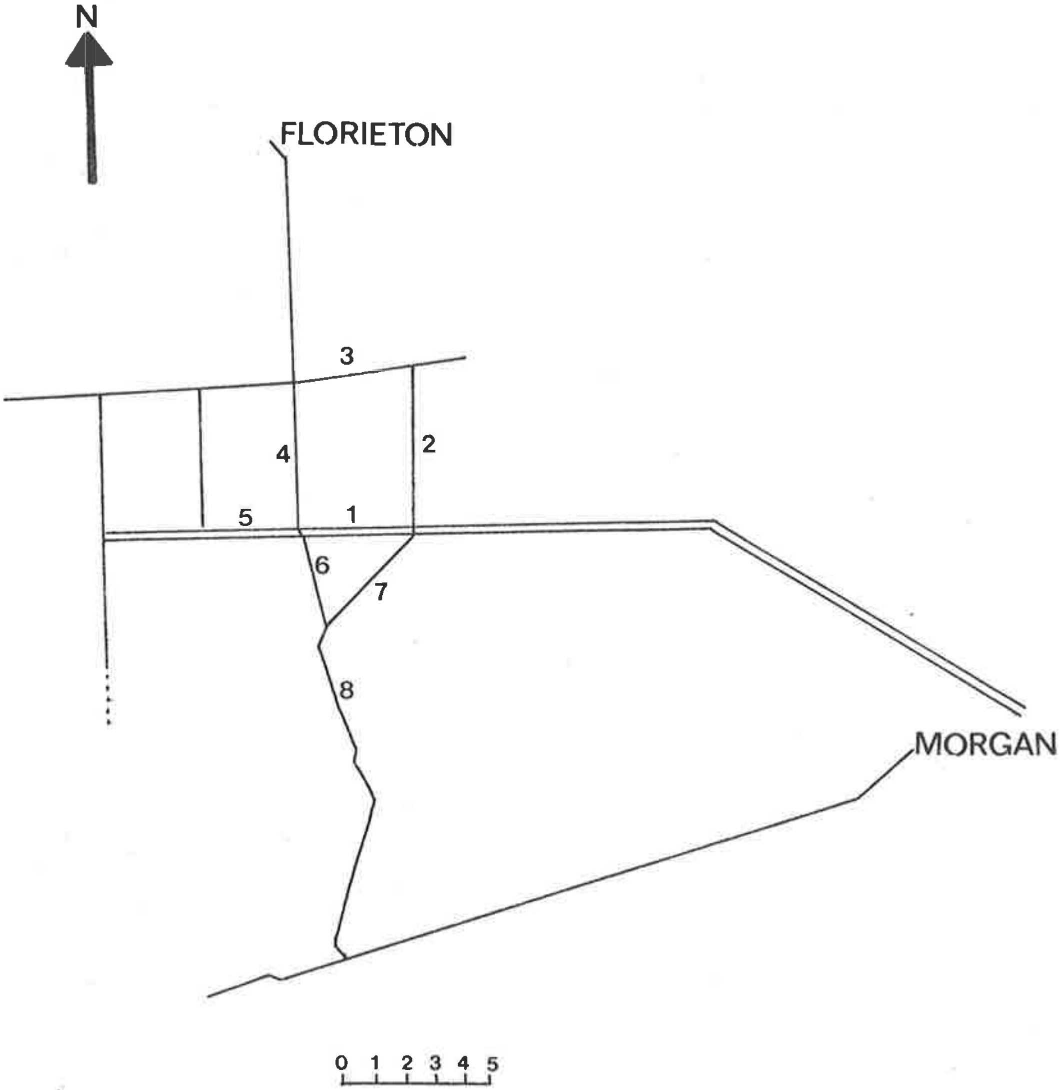
Table 25

The numbers of *Tr. rugosus* caught per kilometer per trip on the roads shown in figure 60.

Road No.	Spring-Summer 1971/1972	Spring-Summer 1972/1973	Spring-Summer 1973/1974
1	0.52	0.32	0.10
2	0.16	0.18	0.06
3	0.27	0.17	0
4	0	0.03	0.21
5	0	0.05	0
6	0.32	0.17	0
7	0.11	0.20	0.25
8	0.21	0.05	0.13

There are difficulties associated with using these data, because it is very difficult to time trips so that lizards have equal chances of being active on each occasion, and the activity of the lizards also varies throughout the day. However some indications from table 25 are probably reliable. The general decrease in numbers seen during 1972 and 1973 was

Figure 60. Roads (numbered 1 to 8) in the Mt Mary study area on which estimates were made of the relative abundance of sleepy lizards, *Tr. rugosus*.


N
FLORIETON
3
4
2
5
1
6
7
8
MORGAN
0 1 2 3 4 5

most marked. This was partly due to increased ground cover by herbage after rains in early 1973. The drought of 1972 might also have caused numbers to decrease. The heavy flooding rains of 1973 inundated large tracts of land and this probably caused lizards to disperse. Also during drier years lizards may clump along roads, which have relatively good growth of herbage on the verges, and then disperse after rains when food is more abundant and widespread.

The other observation to make on the capture data is that they suggest that the relative densities of lizards in two different areas may change from season to season. Thus it was impossible, in view of these fluctuations, to say whether host densities were on average greater on one side of the tick boundary than on the other.

Attempts to count the numbers of sleepy lizards in sectors of paddocks were made. There was great variability in such counts as the lizards are most cryptic while in shelters but quite apparent when active or basking. It appeared though that in some areas there were at least 15 lizards per hectare.

In 4.40 data were presented on the movements of sleepy lizards. It was suggested that they do not move very far but occupy a small home range. Juvenile lizards possibly move greater distances and adults must do so after floods at Mt Mary. Lizards caught and released in the study area were marked (see appendix 3) so that they could be individually recognized on recapture. However only five lizards were recaptured. Four were recaptured one year after the first capture and were within 200 metres of that spot. The fifth had moved almost 2.5 km in two years. This beast had been first taken in an area that was subsequently inundated with water during heavy rains.

There was no evidence gathered during the study at Mt Mary which suggests a change in lizard behaviour across the boundary although I observed and compared activity on both sides.

5.40 Discussion.

The boundary between the tick species does lie along an ecotone, the transition from mallee scrub on solonized brown soil with kunkar to more arid woodland and savannah where soils contain less kunkar and more clay. The climate varies more gradually across the study area becoming drier as one goes north and east. But the discovery of these correlations between environmental changes and the tick boundary does not uncover the factors which determine the position of the parapatric boundaries or the narrowness of the zone of overlap. These observations do not make more or less credible the hypotheses that the parapatric nature of the ticks' distribution is the result of interspecific interactions between the ticks or that each finds conditions unsuitable on the other side of the boundary because of a change or changes in some environmental factor or factors.

Ap. hydrosauri may well have its northern boundary determined by its inability to withstand arid conditions or to compete with *Amb. limbatum* in such conditions. This depends upon changes in weather and soil type, which result in humidity of the ticks' microhabitat off the host falling below 80% (RH) for too long. As the ticks have low vagility, such conditions need not occur every season but perhaps only every few years. I did not detect movement of the boundary during the study. If animals of high vagility were in such a situation then the distribution limit should fluctuate in an area with variable weather.

It is more difficult to postulate a factor which might prevent *Amb. limbatum* from surviving further south. It is difficult to believe that increased moisture would kill the tick - in fact the soils south of Mt Mary are more permeable to water. In the first season of study it seemed that there were fewer hosts south of the boundary and that this might halt the tick. But in subsequent seasons the numbers of lizards seemed to fluctuate and destroy the apparent difference. Longer periods of cold weather might retard development of *Amb. limbatum* much more than *Ap. hydrosauri* - indeed the Pt Gawler enclosure observations (in sect. 3.3) support this idea. However, the data above do not suggest that temperatures would change so markedly at Mt Mary.

To resolve these problems and test the hypotheses it was necessary to design and carry out experiments in the laboratory and field. These are described in chapter 6.

6.00 TESTING THE HYPOTHESES

6.10 Introduction

The data gathered in the present study, and those of Bull (1970), Smyth (1973) and Bull and Smyth (1973), show that the distributions of the three ticks are generally parapatric with very little overlap, and that their common boundaries seem to lie along ecotones. Certainly these observations are accurate for the boundary between *Ap. hydrosauri* and *Amb. limbatum* at Mt. Mary. In order to uncover the reasons for the small degree of overlap between the ticks along their long boundaries, it was necessary to design and perform the experiments described in this chapter.

In chapter 1 it was noted that two sorts of hypotheses can be advanced to explain the distributions of the ticks or of other pairs of organisms with similar parapatric distributions. One of the hypotheses is that the ticks interact in some way to exclude each other. The other hypothesis is that environmental changes, other than the presence of the other tick, across the boundary make it impossible for each tick to survive on the other side.

If the second hypothesis is correct and competitive interactions between the tick species are not involved, then the distribution limits of the ticks might be determined by other species of organisms or by physical and chemical factors. If other species are involved they might be, for example, hosts (see 4.50) or predators, pathogens or parasites (see 3.50). Physical and chemical factors have been shown to limit the geographical range of many tick species (see 2.30). Krebs (1978, p.20) points out that in studying these abiotic factors ecologists' major "conceptual tool" is Liebigs' Law of the Minimum, namely that - "the distribution of a species will be controlled by the environmental factor for which the organism has the narrowest range of adaptability or control". This "Law" is of course a simplification, since several factors may interact. Such studies require that data be accumulated on the tolerances of organisms to a range of environmental variables. Some such data are presented in Chapter 3 but more are presented below. However to test the hypothesis adequately and to explore fully the causal factors involved in determining distribution limits, experimental manipulation of organisms in the field is essential. Such a test is described in 6.30 below. Theories which involve the suggestion of interspecific interactions leading to one species excluding another have been the focus of considerable debate, and at times acrimony, among ecologists. The first hypothesis, above, belongs to this category. It appears appropriate then to briefly review this area of ecological theory, i.e., the "competitive exclusion principle" - that "complete competitors cannot coexist" (Hardin 1960).

The development of theory in this area has progressed through four phases. The first phase involved observations on natural populations of organisms and attempts to construct general principles from them. Another development came from attempts to model mathematically the growth of populations and interactions between populations. These models, or aspects of them, were tested in a series of controlled experiments in laboratories. The fourth phase, which met success many years later, has involved experimentation on natural populations in the field.

A number of biologists had, during the late nineteenth and early twentieth centuries, made observations on the relationships between similar species of organisms, and to different degrees anticipated the idea of competitive exclusion. These biologists included Darwin, Grinnell and Monard (Krebs 1978). These ideas were forcefully expressed by Gause (1934) who suggested that two similar species living in the same area rarely occupy similar niches. He used the term niche in the manner defined by Elton (1927, p. 63) to mean an animal's "place in the biotic environment, its relations to food and enemies". Gause suggested that the reason for species not sharing niches was that they compete; through this process they displace each other until each is in possession of "peculiar kinds of food and modes of life in which it has an advantage over its competitor".

Lotka (1925, 1932) and Volterra (1926, 1931) independently derived equations which were extensions of the Verhulst-Pearl logistic equation and from which they concluded that two species of animals cannot exist in the same area utilizing the same resource indefinitely. Gause (1934) used these equations in formulating his hypothesis (see above) that if two species are to coexist they must occupy different niches. Gause (1935) reported a number of laboratory experiments which it was claimed confirmed the competitive exclusion hypothesis. Other workers also performed similar experiments with mixed populations of various small laboratory organisms and reported support for the hypothesis (e.g. Crombie 1945, and Park et al. 1941).

A number of controversial issues arose from this hypothesis and many disagreed with its importance. It was noted by some that many closely-related species are sympatric (Krebs 1978). Others criticised the Lotka-Volterra equations as being too far removed from reality. For instance the equations have rates of population growth and coefficients of competition which are constant, whereas in nature these factors do vary (Pianka 1974). Andrewartha and Birch (1954) were strong critics of the competitive exclusion principle, which was then called Gause's hypothesis, and detailed the shortcomings of the equations. They and others also strongly criticised the laboratory experiments of Gause and his successors. These criticisms were reviewed by Miller (1967) who noted that the proponents of the competitive exclusion principle overlooked the importance of the many experiments in which species did coexist.

Another problem associated with this controversy was in defining "niche". I have mentioned the definition of Elton (1927) which concerned the "role" of a species; however others (e.g. Grinnell 1917, in Udvardy 1959) saw niche as a subdivision of habitat. Later Hutchinson (1958) presented his famous concept of niche as an N-dimensional hypervolume. Hutchinson's niche possesses so many possible parameters that it is impossible for two species or even two individuals to occupy precisely the same niche. This had been deduced earlier. Gilbert et al. (1952) noted that no two species could be ecologically identical. They, and others (see Miller 1967), noted a consequent weakness in the arguments of the proponents of competitive exclusion. If similar species coexist, then the principle requires that they occupy different niches. When such species are examined long enough, differences in niche are found. Whilst this may be upheld as evidence confirming the principle, it is inevitable, given that they are different species. Thus, critics argue that the principle is trite (Cole 1960).

Andrewartha and Birch (1954) were concerned about the term "competition" as its popular use was not compatible with its technical, ecological meaning. They also doubted that competition was as important and widespread in nature as some had supposed. Birch (1957) later defined competition:

> "competition occurs when a number of organisms utilize common resources that are in short supply; or, if the resources are not in short supply, competition occurs when the organisms seeking that resource nevertheless harm one another in the process."

This definition incorporates two types of competition, "exploitation" and "interference".

The competitive exclusion principle thus attracted severe criticism and almost blind acceptance. Cole (1960) saw it as a "trite maxim", while others saw it as a central tenet of ecological theory (Hutchinson and Deevey 1949). Many of the arguments concerned semantics and the usefulness of apparently untestable theories and over-simplified models. Pianka (1974) suggests that ecologists now should examine closely-related species to see how much ecological overlap they can tolerate.

Field studies have shown that competitive exclusion can occur. In particular it has been demonstrated that parapatric distributions with little overlap may be due to competitive interactions. Connell (1961) demonstrated with a series of field experiments that two species of barnacles which occupied abutting areas in intertidal zones competed for space on rocks. *Balanus balanoides* excluded *Chthamalus stellatus* from a particular region by crushing or undercutting the smaller, slower-growing *Chthamalus* while growing. Others have provided similar demonstrations of competition between species, e.g. Jaeger (1970, 1971) with salamanders, and see Grant (1972) for a review of interspecific competition in rodents.

Smyth (1973) points out that in the documented cases of competitive exclusion, the form of competition is usually direct physical interference and aggression, e.g. Miller (1964). It is difficult to see how the ticks in this study could so interfere with each other, or how they could compete through exploitation. Ticks off the host are, it seems, dispersed in numerous aggregations in lizard shelters and the available microhabitats for detached ticks can hardly be in short supply. It is also unlikely (see Chapter 3) that feeding sites on lizards are in short supply. At low lizard densities there might be a relative shortage of hosts but seldom an absolute shortage (see Andrewartha and Browning 1961 for definitions of these types of shortage). Smyth (1973) suggested that the ticks might, somehow, adversely influence one another through the host's immunological system. Bull (1969) advanced the hypothesis that the ticks might compete for mates at the boundary. Colonizing ♀ ticks would be most likely to meet ♂♂ of the other species. Now if these ♂♂ mated with such ♀♀ or were attracted to them and thus blocked them from conspecific males, colonization across the boundary would be inhibited. But would it be stopped?

The above discussion of the development of theories concerned with competitive exclusion and previous comments on the range of other possible causes of the parapatric distributions show that ultimately one must test hypotheses experimentally. This chapter describes detailed experiments designed to determine whether the narrow zone of overlap between *Ap. hydrosauri* and *Amb. limbatum* could be due to interspecific competition (the first hypothesis) or to other factors (the second hypothesis). If *Ap. hydrosauri* and *Amb. limbatum* do compete on hosts for attachment sites, or in some other way, then ticks in mixed batches on lizards should differ in development rates or mortality from ticks in single species groups. In the following experiments in the laboratory and field these parameters were compared for mixed and unmixed batches of ticks. If the second hypothesis is correct then the development rates or mortality of the ticks should vary when exposed to the variable involved. If it is a physical or chemical factor, such as temperature or humidity, then the different tolerances of the ticks should readily be uncovered by exposing them to a range of such conditions in the laboratory. The identification of the causal factor, however, requires observations and experiments to test the hypotheses in the field.

6.20 Laboratory Experiments

The ticks readily survive and pass through their life cycles in the laboratory (see 3.343), although some difficulty was found in inducing them to mate. It was therefore possible to test in conctrolled conditions the hypothesis that they compete. All the experiments reported here were conducted in a room in which the temperature and light were controlled by airconditioning and 250 watt heat lamps. The lights were switched on and off by a time switch which was set to a 12 hours dark:12 hours light cycle. Room temperature cycled from 32^{o}C (day) to 18^{o}C (night). Lizards, *Tr. rugosus*, were housed in cages on trays as shown in appendix 2. The room was visited once each day during the experiments and the lizards were fed on every second day. Engorged ticks, taken from the trays beneath the lizards, were stored in controlled-temperature cabinets at $25^{o}C$ in the dark at 85% RH. On each day ticks from an individual lizard were put into one vial - thus ticks from mixed batches were also mixed in vials.

It was possible that the ticks might respond differently to lizards which had previously experienced them than to lizards which had been parasitized by another species. Thus each experimental group included lizards which came from different sides of the boundary at Mt.Mary. Thus of the 12 lizards used in each experiment, 6 had had prior experience of *Ap. hydrosauri* and 6 had had prior experience of *Amb. limbatum*. The lizards were deticked before the experiment began. Table 26 summarizes the design of the experiment.

Table 26

The design of laboratory experiments to test the hypothesis that *Ap. hydrosauri* and *Amb. limbatum* compete. Each lizard was infested with an equal number of ticks, H - *Ap. hydrosauri* or L - *Amb. limbatum*

		Groupings		
		A (control)	B (control)	C (mixed)
Host's previous exposure to ticks	*Amb. limbatum*	2H/lizard	2L/lizard	H+L/lizard
	Ap. hydrosauri	2H/lizard	2L/lizard	H+L/lizard

Experiments were begun by infesting 12 healthy adult lizards, 4 in each group of which 2 were former hosts of *Amb. limbatum* and 2 were former hosts of *Ap. hydrosauri*. The success of ticks and the rates of development could be compared between the groups for each species and between the hosts within groups. Table 27 summarizes the variables which could be observed to make the comparison; note that not all variables were used in every experiment.

Table 27

Possible Measurements of the development of the ticks of each species in order to compare control and experimental groups.

(1) The proportion of ticks which fail to attach to the host.
(2) The proportion of ticks which fail to engorge and detach.
(3) The time taken for ticks to engorge and detach.
(4) The weights of engorged ticks.
(5) The time taken for ticks to moult.
(6) The proportion of ticks which fail to moult.

The first experiment was performed with LL. Each lizard was infested with 400 LL - a high but not uncommon number to be found on lizards in the field. In the mixed species group, lizards were also infested with 400 LL 200 from each species. The *Ap. hydrosauri* LL comprised equal proportions of the progeny of two ♀♀, one from Buckland Park collected on 18/1/72 and one from the Cleve area, collected on 29/11/71. The *Amb. limbatum* LL were all progeny of a ♀ from Mt. Mary, collected on 25/1/72.

The lizards were placed in individual calico bags and vials of counted LL were emptied into bags with them on 13/4/72. On 16/4/72 the lizards were placed in their numbered cages which were randomly located in two rows in the experiment room.

The LL left in the bags were counted. These were scored as failing to attach as were the few unengorged ticks which appeared in the lizard trays on the first three days (17/4/72 - 19/4/72). The numbers of LL which failed to attach were compared for each species between control and mixed groups, and between groups of lizards which had experienced different hosts. As the mixed group lizards received only half as many LL of a particular species as the control group lizards, the numbers in the former group were doubled in order to make the comparisons.

Why not [illegible] the [illegible] [illegible]?

These data were analysed using two-way analysis of variance - see Sokal and Rohlf (1969,chapter 11). The raw data and the two-way anova are shown in tables 28 and 29.

Table 28

Differences in the numbers of out of 400 *Ap. hydrosauri* LL that failed to attach to each of 8 sleepy lizards, *Tr. rugosus*. The data are classified in two ways, by prior host experience of ticks (of *Amb. limbatum* (Li) vs experience of *Ap. hydrosauri* (Hy))and presence or absence of *Amb. limbatum* LL (mixed vs control).

	Hosts	
	Hy	Li
Control	33 18	24 10
Mixed	26 44	24 18

Completed anova

Source of variation	df	SS	MS	F	
Between rows	1	91.12	91.12	0.93	NS
Between columns	1	253.12	253.12	2.6	NS
Interaction	1	15.13	15.13	0.15	NS
Error	4	390.5	97.63		
Total	7	749.87			

Table 29

Differences in the numbers out of 400 *Amb. limbatum* LL that failed to attach to each of 8 sleepy lizards, *Tr. rugosus*. The data are classified in two ways, by prior host experience of ticks (of *Ap. hydrosauri* (Hy) vs experience of *Amb. limbatum* (Li)) and presence or absence of *Ap. hydrosauri* LL (mixed vs control).

	Hy	Li
Control	79 31	43 52
Mixed	114 122	24 22

Completed anova

Source of variation	df	SS	MS	F	
Between rows	1	742.12	742.12	2.42	NS
Between columns	1	5253.12	5253.12	17.13	**
Interaction	1	3827.13	3827.13	12.48	**
Error	4	1226.5	306.63		
Total	7	11048.87			

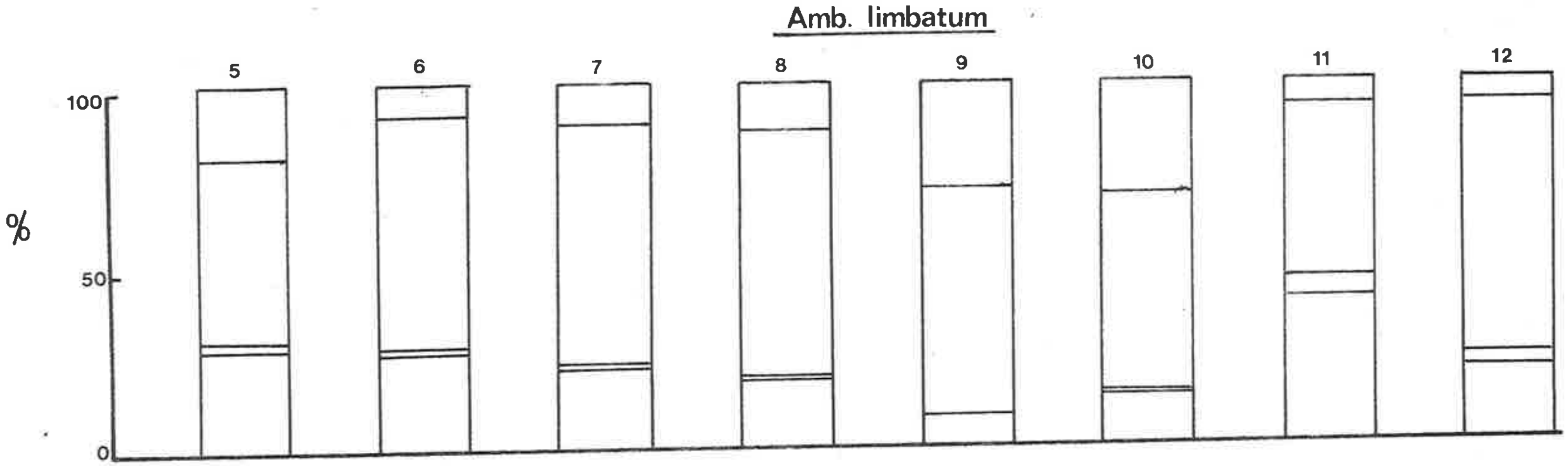
Table 28 shows no significant variation in failure to attach by *Ap. hydrosauri* LL, no matter what prior experience the hosts had had of ticks nor whether *Amb. limbatum* LL were present or not. However table 29 shows two significant sources of variation. Significantly more *Amb. limbatum* LL failed to attach to hosts that had previously been exposed to *Ap. hydrosauri* than to hosts that had borne *Amb. limbatum* LL. This result, if repeatable, suggests that the ticks might interact via the host! However there was a significant interaction component in the table. This implies that pure infestations (control) are more likely to attach than those in mixed infestations onto lizards that have experienced *Ap. hydrosauri*, and that the opposite relationship holds on lizards previously exposed to *Amb. limbatum*.

In the same experiment similar analyses were performed on the percentages of attached ticks which engorged and detached and the percentages of engorged ticks which succeeded in moulting. Most ticks detached in 20 days but some lingered until 50 days - see section 3.3421 for patterns of detachment. The *Amb. limbatum* moulted more rapidly than the *Ap. hydrosauri* - see section 3.3413 for the description of moulting times. The percentages of ticks which passed through the various stages are represented for each host in figures 61 and 62.

In order to perform the two-way analyses of variance on these data it was necessary to perform an arc-sine transformation (Sokal and Rohlf 1969 p 386). This was required because percentages are not distributed normally and have variances related to their means. The data in tables 28 and 29, though not percentages, are not completely compatible with the assumption of normality. But the assumption of normality seemed approximately true,and Sokal and Rohlf (1969, p 377) indicate that departures have little influence on anova.

Summaries of the analyses on the data graphed in figures 61 and 62 are shown in table 30.

Figure 61. The percentages of LL in the first experiment which attached, engorged and detached on 12 sleepy lizards *Tr. rugosus* (numbered) and the numbers which then moulted. Lizards 1 to 4 were each infested with 400 *Ap. hydrosauri* LL. Lizards 5 to 8 were each infested with 400 *Amb. limbatum* LL. Lizards 9 to 12 each received 200 LL of each species.


Amb. limbatum
5
6
7
8
9
10
11
12
100
50
0
%

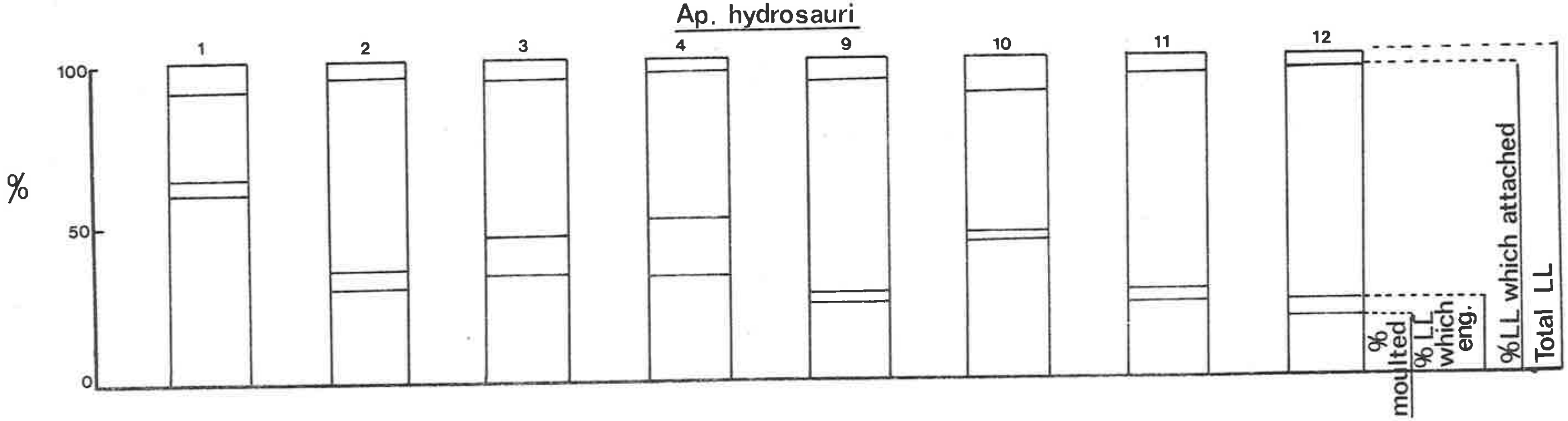
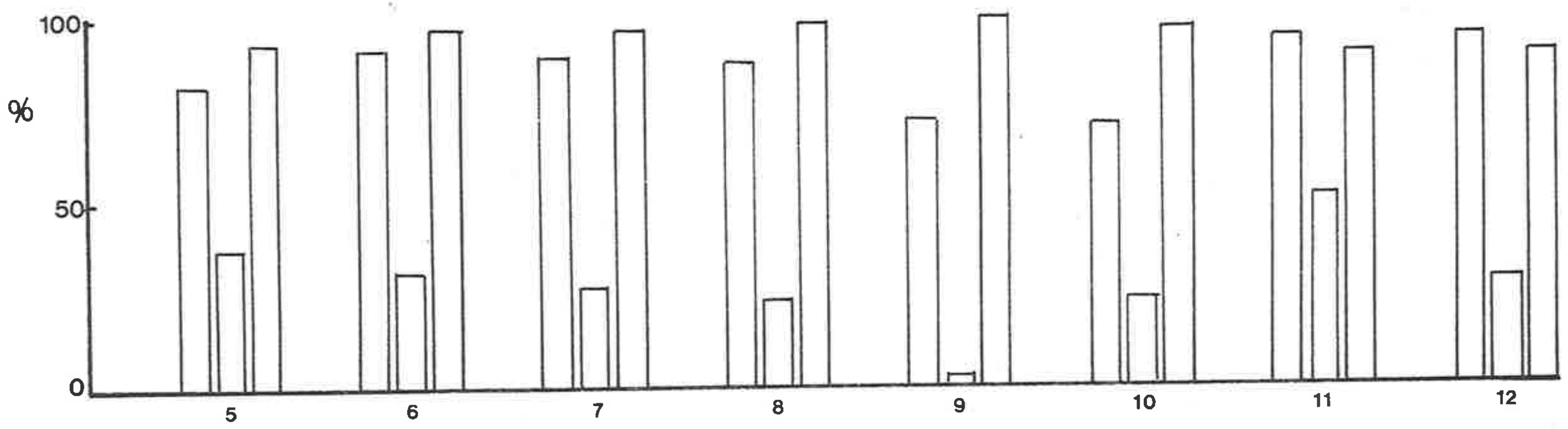
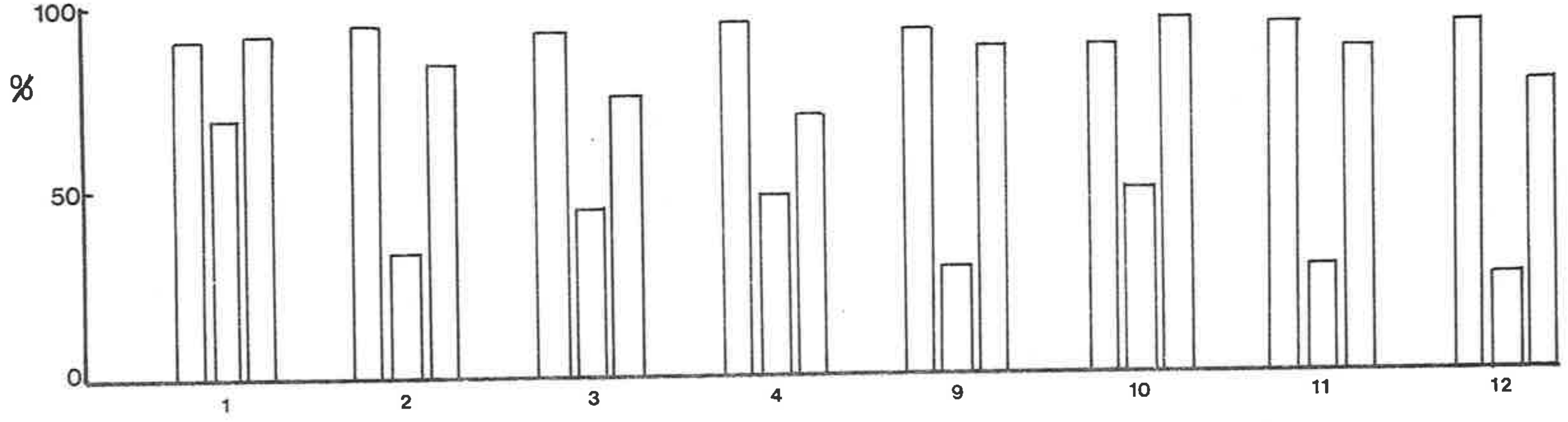

Ap. hydrosauri
1
2
3
4
9
10
11
12
100
50
0
%
% moulted
% LL which eng.
%LL which attached
Total LL

Figure 62. Percentages of LL in the first experiment completing parts of their life cycle on each of 12 hosts - as described in figure 60. The group of bar graphs for each host shows (from left to right): The percentage of LL which attached to the host, the second bar shows the percentage of the attached LL which engorged and detached, the third bar shows the percentage of the detached LL which moulted.



Amb limbatum



Ap hydrosauri

Table 30

Summary of two-way analyses of variance on :-

1. the percentages of attached LL that engorged and detached, and on
2. the percentages of engorged LL that failed to moult.

The percentages shown in the table required arc-sine transformation for analysis.

Hy - host had had prior experience of *Ap. hydrosauri*.

Li - host had had prior experience of *Amb. limbatum*.

C - control group of LL.

M - mixed group of LL.

Ap. hydrosauri

1.

	Hy	Li
C	68.4 34.6	45.7 49.2
M	28.3 50.0	28.2 24.1

Control vs mixed	NS
Host prior experience	NS
Interaction	NS

2.

	Hy	Li
C	7.1 15.2	23.7 30.8
M	10.9 3.8	12.1 20.9

Control vs mixed	NS
Host prior experience	$F_{(1,4)} = 8.89$ * $.01<p<.025$
Interaction	NS

Amb. limbatum

1.

	Hy	Li
C	36.7 29.3	25.2 22.4
M	9.8 21.6	48.4 25.9

Control vs mixed	NS
Host prior experience	NS
Interaction	NS

(cont. on p 120)

Table 30 (Cont'd.)

2.

	Hy	Li
C	6.1 2.6	3.1 2.1
M	11.0 3.3	10.1 11.0

Control vs mixed	NS
Host prior experience	NS
Interaction	NS

The single significant component in table 30 concerns the influence of the prior experience of hosts on the mortality of *Ap. hydrosauri* LL moulting to NN. In fact a significantly higher percentage failed to moult that had engorged on lizards which had experienced *Amb. limbatum* previously!

The time taken for the LL to moult was also measured. In this case LL in the mixed group engorged and lived in vials with the other species. The mean times to moult of control groups were compared with mean times for mixed groups. These data are presented in table 31 below. The comparison of means is that described in Bailey (1959, p 35).

Table 31

A comparison of mean times to moult (in days) of *Amb. limbatum* and *Ap. hydrosauri* LL from control and mixed groups. The means ($\bar{x}$) are of the data pooled for each group. Standard errors of means (SE) and sample sizes (N) are also shown. Comparison of means as in Bailey (1959, p 35).

Ap. hydrosauri

	Control	Mixed	Comparison of means
$\bar{x}$	14.57	14.37	d = 0.96 NS
SE	0.08	0.19	
N	425	86	

Amb. limbatum

	Control	Mixed	Comparison of means
$\bar{x}$	10.05	10.53	d = 3.69 * $p<.001$
SE	0.05	0.11	
N	258	129	

Here again there was a significant result in that *Amb. limbatum* LL took longer to moult in the presence of *Ap. hydrosauri*. It was also found that *Amb. limbatum* LL took longer to moult if they had engorged on lizards which had prior experience of *Amb. limbatum*. The mean time to moult for *Amb. limbatum* LL from lizards that experienced *Amb. limbatum* was 10.42 ± 0.10 (days), and the mean time for those from lizards formerly hosts of *Ap. hydrosauri* was 9.96 ± 0.05 (days). Comparison of means gave $d = 3.8$ ($P<0.001$).

The results of this experiment suggest that the ticks might interact in some way possibly via the host. The experiment was repeated.

The second competition experiment was designed in the same way and performed under the same conditions as the first experiment.

The *Ap. hydrosauri* LL were progeny of 2 ♀♀ collected at Pt.Gawler which detached on 31/3/72 and 1/4/72. The *Amb. limbatum* LL were from 2 ♀♀ collected at Mt.Mary during December 1971. The LL hatched during February 1972. The proportions of ticks completing stages of development are shown in figures 63 and 64. One of the lizards in the *Ap. hydrosauri* control group died soon after the experiment began.

As in the previous experiment, two-way analyses of variance were performed on the data for *Amb. limbatum* LL, see table 32.

Figure 63. The percentages of LL in the second experiment which attached, engorged and detached from 12 sleepy lizards, *Tr. rugosus*, (numbered) and the numbers which then moulted. Lizards 1 to 4 were each infested with 400 *Ap. hydrosauri* LL. Lizards 5 to 8 were each infested with 400 *Amb. limbatum* LL. Lizards 9 to 12 each received 200 LL of each species.

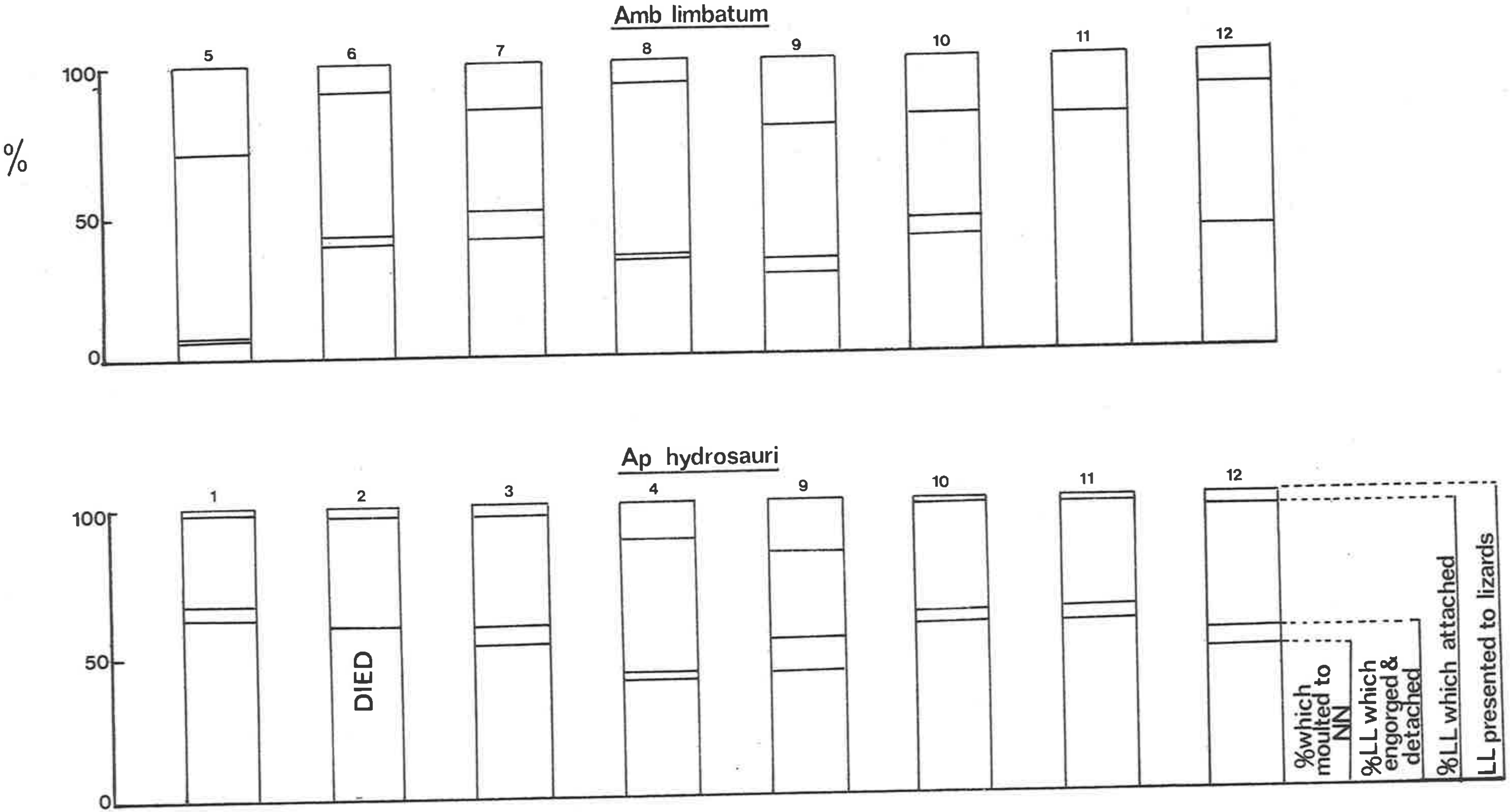
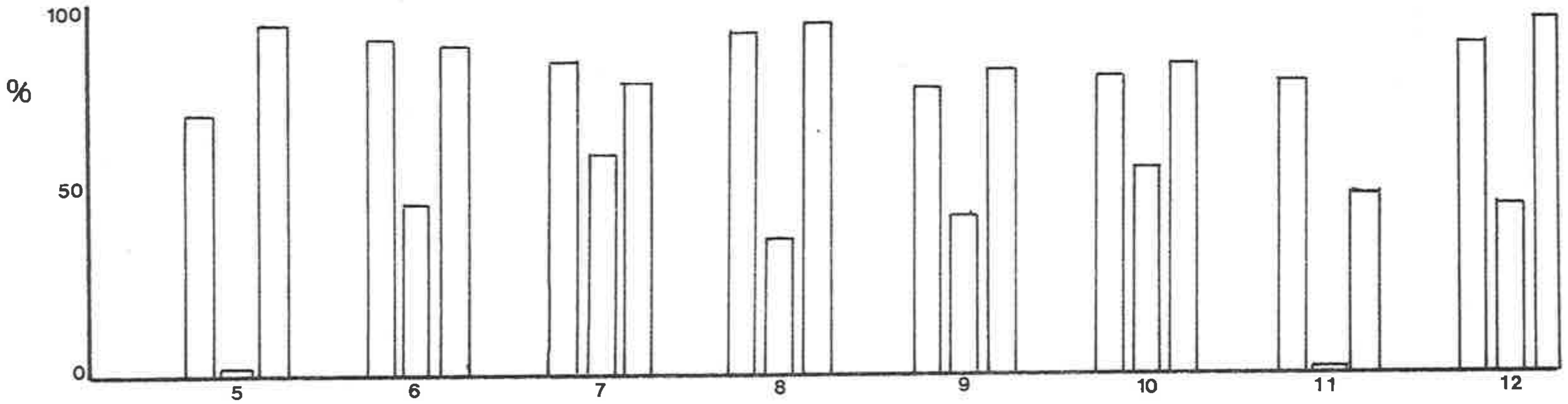
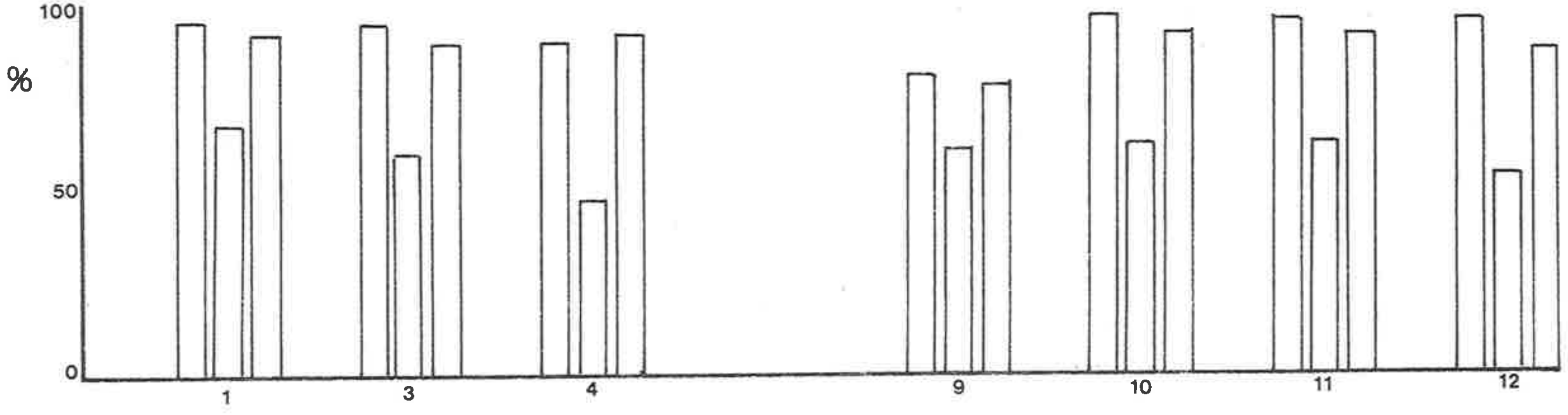

Amb limbatum
%
100
50
0
5
6
7
8
9
10
11
12
Ap hydrosauri
100
50
0
1
2
3
4
9
10
11
12
DIED
%which moulted to NN
%LL which engorged & detached
%LL which attached
LL presented to lizards

Figure 64. Percentages of LL in the second experiment completing parts of their life cycles on each of 12 hosts - as described in figure 63. The group of bargraphs for each host shows (from left to right): The percentage of LL which attached to the host, the percentage of the attached LL which engorged and detached, and the percentage of the detached LL which moulted.



Amb limbatum



Ap hydrosauri

Table 32

Summary of two-way analyses of variance on data *Amb. limbatum* LL, in a second experiment of design shown in table 26.

1. The number of LL that did not attach.
2. The percentages of attached LL that engorged and detached.
3. The percentages of engorged LL that failed to moult.

The percentages shown required arc-sine transformation for the analysis.

Hy - host had had prior experience of *Ap. hydrosauri*

Li - host had had prior experience of *Amb. limbatum*

C - control group of LL

M - mixed group of LL

1.

	Hy	Li
C	115 63	33 26
M	88 76	72 38

Control vs mixed NS
Host prior experience $F_{(1,4)} = 7.38$ * $.025<P< .05$
Interaction NS

2.

	Hy	Li
C	9.8 59.7	46.6 36.4
M	42.3 1.2	56.1 46.4

Control vs mixed NS
Host prior experience NS
Interaction NS

3.

	Hy	Li
C	4.3 20.3	9.1 3.8
M	17.0 50.0	14.1 1.2

Control vs mixed NS
Host prior experience NS
Interaction NS

The single significant source of variation in table 32 concerns the numbers of LL which failed to attach. In this case, as in table 29, the *Amb. limbatum* LL did not attach as readily to lizards previously exposed to *Ap. hydrosauri*. The other data in table 32, for engorging and moulting, show a similar pattern but the differences were not significant.

It was evident that there were no significant differences between control and mixed groups for *Ap. hydrosauri* LL, see table 33 (the data for the lizard that died are excluded).

Table 33

Summary of data on *Ap. hydrosauri* LL, in a second experiment of design shown in table 26.

1. The numbers of LL that did not attach.
2. The percentages of attached LL that engorged and detached
3. The percentages of engorged LL that failed to moult.

C - control group of LL (3 lizards)

M - mixed group of LL (4 lizards)

Hy- host had had prior experience of *Ap. hydrosauri*

Li- host had had prior experience of *Amb. limbatum*

1.

	Hy	Li
C	8 11	42
M	66 8	4 10

2.

	Hy	Li
C	68.9 60.1	47.8
M	63.5 64.3	63.1 55.9

3.

	Hy	Li
C	7.1 9.1	6.5
M	20.6 7.0	5.6 7.0

A similar experiment was performed using NN of the two species. Again 12 lizards were used, half having previously experienced each species, in

3 groups - two control and one mixed group. The NN had been raised in the laboratory from wild captured ♀♀. 80 NN were put on each lizard (*Tr. rugosus*), thus in the mixed group, a lizard had 40 NN of each species.

The numbers of NN which failed to attach are shown in table 34.

Table 34

Summary of the numbers of NN that failed to attach to hosts, *Tr. rugosus*.

Hy - host had had prior experience of *Ap. hydrosauri*
Li - host had had prior experience of *Amb. limbatum*
C - control group of NN
M - mixed group of NN

Ap. hydrosauri

	Hy	Li
C	6 2	2 4
M	4 0	0 2

Amb. limbatum

	Hy	Li
C	32 7	48 24
M	18 32	0 6

It soon became apparent that the numbers of ticks per host were too high or that the lizards had contracted a fatal disease. 6 lizards died before the experiment was 24 days old. One of these died after only 12 days. Half of those that died belonged to the *Ap. hydrosauri* control group and half belonged to the mixed group. These deaths ruled out further, meaningful analysis of the results.

The results in table 34 however do not reveal any differences in attachment due to prior experience of the host. There is a suggestion though that the NN attached more readily in the mixed group!

It can be seen in each of the experiments above that there were considerable differences between individual hosts. These differences and the low numbers of lizards per treatment require one to be cautious when interpreting the results; see discussion 6.40. The numbers of lizards, though low (12 per experiment), represented close to a maximum feasible number as 4800 LL (in the first experiments) of equivalent age etc., had to be gathered for the experiments and each experiment entailed daily attention for up to 80 days.

Observations were also made on adult ticks which had moulted in the laboratory from NN used in the previous experiment. It was possible that they might interact by inhibiting attachment of the other species in some way or that the ♂♂ might compete for mates in the fashion suggested by Bull (1969) - see 6.10 above. Accordingly ♂♂ and ♀♀ of both species were gathered and divided into 6 groups. The same experimental room was used as in the experiments reported above. 12 lizards were selected from an outdoor enclosure that contained both tick species. The allocation of ticks to lizards is shown in table 35.

Table 35

Design of an experiment on interactions between adults on hosts, showing the allocation of adult ticks, *Ap. hydrosauri* and *Amb. limbatum* to 12 *Tr. rugosus* on 25/6/73. The lizards were numbered 1 to 12.

Hy - *Ap. hydrosauri*
Li - *Amb. limbatum*

	Hy ♀♀ (4/lizard)	Li ♀♀ (4/lizard)
Hy ♂♂ (6/lizard)	1. 2.	7. 8.
Li ♂♂ (6/lizard)	3. 4.	9. 10.
Hy ♂♂ Li ♂♂ (3 of each/lizard)	5. 6.	11. 12.

The lizards and ticks were placed in calico bags on 25/6/73 and removed on 3/7/73. The numbers of ticks left in the bags and on the lizards were counted. These data are shown in table 36.

Table 36

The numbers of adult ticks found attached to lizards on 3/7/73. Maximum possible numbers are shown in brackets.

Hy - *Ap. hydrosauri*
Li - *Amb. limbatum*

	Hy ♀♀		Li ♀♀	
	♀♀	♂♂	♀♀	♂♂
Hy ♂♂	7 (8)	12 (12)	6 (8)	2 (12)
Li ♂♂	4 (8)	10 (12)	8 (8)	12 (12)
Hy ♂♂ Li ♂♂	5 (8)	2(6)(Hy) 6(6)(Li)	4 (8)	2(6)(Hy) 5(6)(Li)

There were differences between the groups. But as the number of ticks available was low the differences were not significant.

The ticks were left attached to the lizards for a month and observations made on the movements of ♂♂ relative to ♀♀ on the hosts. At that time it was thought that ♀ ticks of these species attracted ♂♂ to them by releasing pheromones. It was also observed that ♂♂ often attach near the ♀♀ before mating which, it was hypothesized, involved a second stimulus. However it is now known that ♂♂ are very active on lizards at night and may mate with a ♀ and then attach again some distance away (Bull pers. comm.). So, although changes in ♂ position were observed, it was not known where they had wandered or what they had done.

Only one ♀ engorged, an *Ap. hydrosauri* from lizard No. 5 - in the mixed group. No mating was observed.

The results in table 36, if the differences were real, can be explained in two ways: Firstly, that *Ap. hydrosauri* ♂♂ are more likely to attach to a host if *Ap. hydrosauri* ♀♀ are present, and/or secondly, that *Ap. hydrosauri* ♂♂ are inhibited from attaching when *Amb. limbatum* ♀♀ or ♂♂ are present. An experiment was designed to test these hypotheses. It consisted of three treatments. In one, only *Ap. hydrosauri* ♂♂ were put on a group of hosts. In a second, *Ap. hydrosauri* ♂♂ and ♀♀ were placed on hosts. The third treatment consisted of putting *Amb. limbatum* ♀♀ on hosts with *Ap. hydrosauri* ♂♂. If the first hypothesis, above, were correct, the numbers of ♂♂ attaching in the three treatments should be ranked as 2>1≈3. If the second hypothesis was correct then the ranking should be 3<1≈2. If both hypotheses had some truth we might expect the ranking 2>1>3. Only 36 ♂♂ and 6 ♀♀ from each species were available and 2 lizards were used in each of the groups.

No ♂♂ attached in any group! Such experiments are very difficult to perform as it takes a considerable portion of a year to breed adults and then one only obtains low numbers.

In addition to the experiments performed in the laboratory to test the competition hypothesis, observations were made and experiments conducted which are pertinent to the hypothesis that changes in physical and chemical characteristics (in the ticks' microhabitats) across the tick boundary might bring about the parapatric distribution. Some of these were reported in Chapter 3 where the effects of such factors (particularly temperature and humidity) on rates of development are analysed. Bull and Smyth (1973) also looked at some of these matters when they examined water balance in the ticks (see 3.40).

Summarised in this section are observations on the survival of different stages of the ticks in the laboratory under a variety of environmental conditions. These observations show differences between the ticks but do not, of course, finally indicate which factors are crucial in the field. Ultimately, hypotheses concerning distribution limits must be tested in nature.

Bull and Smyth (1973) demonstrated that NN of the two *Amblyomma* species seemed able to withstand desiccation better than *Ap. hydrosauri*. It is likely, they suggest, that the relative differences between the species are similar at all developmental stages. It is important that this assumption be tested because in other tick species the evidence from both laboratory and field work, indicates that eggs and LL often suffer much greater mortality, while off the host, than NN or adults (Branagan 1973, Milne 1945 a, Randolph 1975).

Experiments were designed to test the effects of desiccation on various stages of *Ap. hydrosauri* and *Amb. limbatum*. Ticks were offspring of ♀♀ caught in the Mt. Mary study area while attached to sleepy lizards (*Tr. rugosus*). These ♀♀ engorged, detached and laid eggs in the laboratory and the offspring were later taken through their lifecycles as outlined in appendix 2.

Very low relative humidities (close to 0%RH) were obtained in sealed glass desiccators over a layer of silica gel (see Winston and Bates 1962). Temperatures were regulated in a Gallenkamp cooled incubator. Ticks used in the experiment were counted into groups (the sizes of which are detailed below) and kept in small (4cm) glass tubes with gauze-covered ends, to allow free movement of air and water-vapour in and out.

Groups of ticks were exposed to desiccation (0% RH) for different lengths of time while control groups remained in similar desiccators at 85% RH (over a saturated solution of KCl - see Winston and Bates 1962). This method enables an estimate of the 'dose' of desiccation (i.e., the time of exposure to 0% RH) required to kill half of the tick population (the LD 50) - see Andrewartha (1970), chapter 6, for a discussion of this method.

A series of attempts were made to estimate the LD 50's of desiccation for LL and NN of *Ap. hydrosauri* and *Amb. limbatum*. In each case, preliminary observations were made on ticks at 0% RH in order to estimate approximately the time over which the experiment needed to be run. 6 treatments were used in each experiment. In each treatment there were 40 ticks per tube. The percentage mortality in each tube was measured at the end of the experiment. Table 37 shows how such experiments were set up and the data analysed. The particular experiment shown involved *Ap. hydrosauri* LL; in experiments with *Amb. limbatum* LL or NN or NN of the former species, the time of exposure to desiccation was longer. The method followed is that explained by Andrewarth (1970), pp 229-231.

Table 37

The death-rate in samples of *Ap. hydrosauri* LL exposed for various periods to 0% RH at 27°C.

Days at 0% RH	No. of LL	No. Dead	Proportion Dead	Estimate of Proportion killed by desiccation	Emprical Probit
0	40	1	.025	0	
2	40	6	.150	.128	3.86
4	40	10	.250	.231	4.26
6	40	21	.525	.513	5.03
8	40	28	.700	.692	5.50
10	40	29	.725	.718	5.58

LD50≃6.3 days

LD50 values were estimated by converting percentage mortalities to probits (see Fisher and Yates 1948), plotting these against log days and fitting lines of best fit by eye. These experiments were repeated many times for LL and NN of the two species. The results are summarised in table 38 below, where LD50's are shown - to the nearest day.

Table 38

LD50 estimates of exposure to desiccation (in days at 0% RH and 27°C) for LL and NN of *Ap. hydrosauri* and *Amb. limbatum*. Each estimate is for a particular experiment of the type outlined in table 37.

Tick species		LD50 estimates (days)
Ap. hydrosauri	LL	4, 8, 6
Ap. hydrosauri	NN	15, 13, 17, 15
Amb. limbatum	LL	6, 12, 12
Amb. limbatum	NN	25, 21, 18, 20

The data suggest that there are appreciable differences between the two tick species. It must be pointed out though that there were a number of shortcomings in these experiments. Firstly it was impossible to ensure that the environment within the desiccators remained at 0% RH as they had to be opened from time to time so that samples could be transferred from 0% RH to 85% RH. Sometimes in moving desiccators some tubes had KCl solution splashed on them. Such accidents resulted in some samples having to be left out of the analyses.

Bull and Smyth (1973) observed that the survival time at 0% RH of NN varied with temperature. They estimated that the mean survival time for *Ap. hydrosauri* was 27.3 days at 20°C, 20.5 days at 25°C and 10.2 days at 30°C. *Amb. limbatum* survived for 34.2 days at 20°C, 27.8 days at 25°C and 18.8 days at 30°C. It is clear that increased ambient temperature decreases the time a tick can survive at low humidities.

If ticks are kept in the laboratory, at RH = 85%, for some time, then they succumb more quickly when exposed to very low humidities. In one such experiment, where results were very variable, the LD50 of desiccation for *Ap. hydrosauri* LL, which had hatched 5 months before, was between 20 and 35 hours. It is evident that the slow loss of energy reserves in unfed ticks reduces their resistance to periods of desiccation.

Bull (1969) and Bull and Smyth (1973) also demonstrated that the ticks lost water less rapidly at higher relative humidities. When they measured the percentage weight change at a variety of humidities they found that there was an 'equilibrium humidity' above which the ticks could gain water from the atmosphere. These equilibrium humidities were about 82% and it was impossible to separate the tick species on this criterion. I have kept unfed LL, NN and adults of *Amb. limbatum* and *Ap. hydrosauri* alive at RH = 85% for over a year!

Attempts have also been made to illuminate the relationship between survival of eggs and different temperature - humidity regimes. This is a more difficult task because one cannot observe when eggs die. The observer must wait to see if the eggs hatch, or place batches of eggs in the harsh conditions for varying times and then back in suitable (control) conditions to see if they will hatch.

Bull (1969) attempted to discover the tolerances of eggs to a variety of temperatures and humidities (see 3.3412). Eggs of *Ap. hydrosauri* were divided into groups of 100 eggs, placed in desiccators containing saturated salt solutions so that appropriate relative humidities could be obtained, the desiccators were put in temperature cabinets (constantly dark). The time taken for the eggs to hatch was assessed. No eggs hatched at 0% RH at any temperature (15, 20, 30^{o}C) and no eggs hatched at 36^{o}C at any relative humidity (100%, 75%, 55%). I attempted a similar experiment with *Amb. limbatum* eggs. Four batches each of 100 eggs failed to hatch when kept at 0% RH at 15°C, 25°C, 30°C or 35°C. Eggs did hatch at 35% RH at 25°C and 30°C while eggs at 15°C did not hatch in 4 months and eventually were attacked by a fungus.

Bull and Smyth (1973), in pondering the possible reasons for *Amb. limbatum* not occuring south of the 250mm isohyet in southern Australia; suggested that these ticks while off the host might be susceptable to drowning in the wetter southern regions. I decided to measure LD50's of exposure to complete immersion in water of LL and NN of *Amb. limbatum* and *Ap. hydrosauri*. However preliminary experiments with 40 LL and NN of each species immersed in sealed 500ml containers filled with water showed that either species can survive for more than 6 days when immersed. It was clear then that the ticks could survive long periods immersed in water - as is the case with other tick species (Murray and Vestjens 1967 and Sutherst 1971).

6.30 Field Experiments.

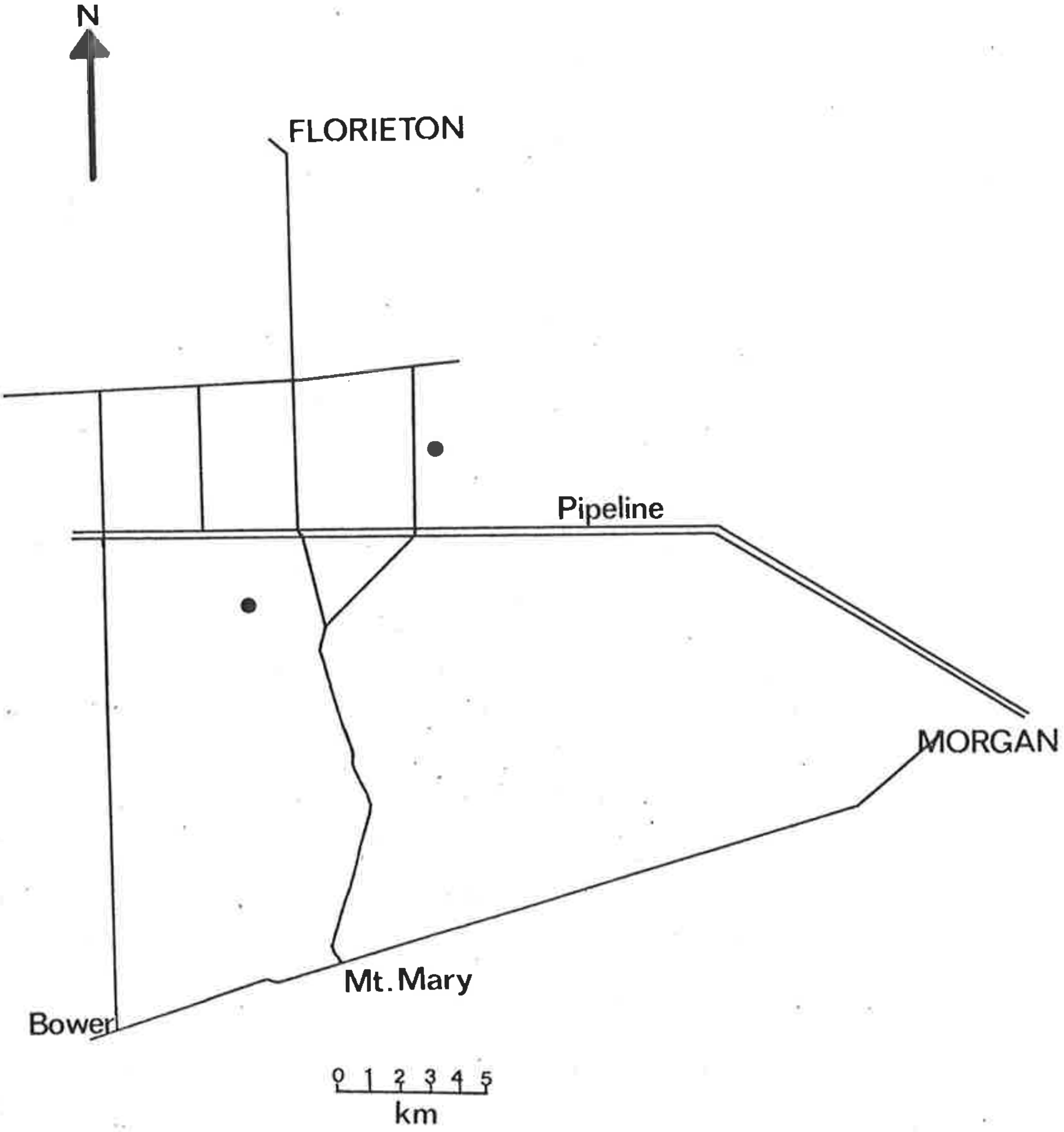
In 3.33 I described the construction and use of lizard enclosures in the field to maintain populations of ticks. Also in that section are described experiments at Pt Gawler in such enclosures. Enclosure 3 at Pt. Gawler (see 3.331 and 3.333) contained a pure colony of *Amb. limbatum*. This arose from LL placed in the enclosure attached to hosts (*Tr. rugosus*) on 31/1/72. Mixed batches of ticks were placed in the two separated halves of enclosure 4 on 22/3/72. In one half (4a), two sleepy lizards, each infested with 200 LL of each species,were released. In the other half (4b) two other lizards, one infested with 400 LL of one species and one infested with 400 LL of the other species were released. One would expect then, if ticks compete on the host, that those in 4b would do better than those in 4a for a time until NN emerged. In fact only *Ap. hydrosauri* did well (see 3.331) and they completed more of their life-cycle in 4a than in 4b! There is no evidence of interspecific competition there. However the *Amb. limbatum* performed poorly in both 4a and 4b, much worse than in enclosure 3. But this could be due to the earlier start of enclosure 3, during warmer weather. Again there is no strong evidence here for competition.

The obvious place in which to test the two hypotheses, which attempt to explain the narrow zone of overlap between the ticks, was at such a boundary at Mt. Mary.

Two groups each of three enclosures were sited as shown in figure 65. One group (the *Casuarina* enclosures) was in "typical" *Amb. limbatum* habitat 3 km north east of the boundary,and the other (the mallee enclosures) in "typical" *Ap. hydrosauri* habitat 1½ km SW of the boundary. The enclosures were 45.7 metres in diameter, circular, made of chicken wire, the walls were 0.75 metres high with the top bent inwards and the bottom dug into the

Figure 65. The location of groups of enclosures in the central region of the Mt. Mary study area. The two sites are shown by solid dots; the south western one contains the Mallee enclosures and the north eastern site contains the Casuarina enclosures.

The pattern of stocking of enclosures is shown below the map.



ALLOCATION OF TICK SPECIES TO ENCLOSURES

Ap hydrosauri (A)	zone of overlap	Amb limbatum (B)
Mallee enclosures		Casuarina enclosures
1 A		1 B
2 A/B		2 A/B
3 B		3 A

the ground 10cm.

The experiments were designed to test both hypotheses; see figure 65. Enclosure 1 in each area was stocked with ticks found in the area - a control. Enclosure 2 contained both species - if competition occurred it should be evident in that one. Enclosure 3 contained ticks from the other side of the boundary. These last ticks should do better than conspecifics in the second enclosure if competition occurs. If environmental factors also play a part they should not do as well as conspecifics in enclosure 1 on the "correct" side of the boundary. But if other environmental factors are entirely responsible for the boundary and interactions between ticks are not, then both groups of colonizing ticks should do poorly. The possible outcomes are summarized in table 39 below.

Table 39

Predicted outcomes of enclosure experiments in terms of tick survival on both sides of the boundary.

	Tick's own side	Opposite side
Pure	1.	3.
Mixed spp.	2.	4.

If the "competition hypothesis" is correct then

$$3 = 1 > 2 = 4$$

If the "other environmental factors hypothesis" is correct then

$$1 = 2 > 3 = 4$$

If both operate then

$$1 > 2 > 3 > 4$$

Ticks used:-

NN - 480 of each species. These had been kept at 15-20°C, 85% RH in the laboratory for 5 months.

LL - 480 of each species. These had been kept in the laboratory for 6 months at 15-20°C, 85% RH.

Lizards used:- 24 lizards were used, collected in the Mt.Mary area, 12 from the *Ap. hydrosauri* side and 12 from the *Amb. limbatum* side of the boundary.

In each enclosure there were 4 lizards - these had been placed in the enclosures before the spring of 1972 to see if there were any wild ticks present; none were detected. Two lizards in each enclosure, one with prior experience of *Ap. hydrosauri* and one with prior experience of *Amb. limbatum* were infested with 60 NN each. The other two lizards, of similar prior experience to the other pair, were infested with 60 LL each. In the mixed enclosures (No. 2) the 60 ticks per lizard contained equal numbers of both species.

The lizards were placed individually in bags with their ticks on 24/10/72 and released into the enclosures on 26/10/72.

The LL and NN quickly engorged and detached. On 20/12/72 lizards were infested with more LL (200 per lizard). On that day it was observed in some enclosures that adult ticks had appeared. The numbers are summarized in table 40 below.

Table 40

Numbers of ♂ and ♀ ticks that were found on lizards in each enclosure at Mt. Mary on 20/12/72.

Mallee enclosures

	Ap. hydrosauri		*Amb. limbatum*	
	♀♀	♂♂	♀♀	♂♂
Enclosure 1	7	9	-	-
Enclosure 2	9	12	1	1
Enclosure 3	-	-	0	0

Casuarina enclosures

	Ap. hydrosauri		*Amb. limbatum*	
	♀♀	♂♂	♀♀	♂♂
Enclosure 1	-	-	0	0
Enclosure 2	2	5	1	0
Enclosure 3	4	6	-	-

A surprising aspect of these data is that *Amb. limbatum* adults have not appeared and yet in other experiments this tick developed quickly, see 3.333 and 3.343. The only adult *Amb. limbatum* to appear were in the mixed enclosures. In fact the results for this tick support neither hypothesis - though the numbers are very low.

Ap. hydrosauri developed very quickly. They did very well in the mixed enclosures. It must be remembered that these were infested with only half as many of a species as the control enclosures and to compare control and mixed enclosures for this tick the numbers shown in table 40 should be doubled, see table 41.

Table 41

The numbers of adult (♂♂ and ♀♀ numbers summed) *Ap. hydrosauri* which appeared in enclosures on 20/12/72, with numbers in mixed enclosures adjusted (doubled) to allow for differences in initial numbers.

	Mallee enclosures	Casuarina enclosures
control	16	10
mixed	42	14

The results do not support the competition hypothesis, but do suggest that the ticks develop more readily on their own side of the boundary. However caution must be exercised in interpreting these results as the number of enclosures used was small and although attempts were made to make them equivalent, they may have differed markedly even in the same area in their quality as tick development sites.

The summer of 1972/73 was very dry and hot and it seems that the extra 200 LL per lizard in these conditions was too much for the lizards. Most died in the next month and it is doubtful that many of the LL engorged and detached. When this was discovered on 31/1/73 12 more lizards were obtained, deticked and 2 placed in each enclosure to provide food for any unattached ticks. Table 42 summarizes the numbers of ticks which then attached.

Table 42

Numbers of ticks (NN, ♂♂ and ♀♀) that attached to lizards placed in enclosures on 8/2/73.

	Ap. hydrosauri			*Amb. limbatum*		
	NN	♂♂	♀♀	NN	♂♂	♀♀
Mallee enclosures						
Enclosure 1	1	0	0	-	-	-
2	7	7	3	9	10	2
3	-	-	-	16	2	1
Casuarina enclosure						
Enclosure 1	-	-	-	30	8	3
2	4	10	6	7	12	6
3	12	12	4	-	-	-

Again the ticks did better in the mixed enclosures - the numbers shown above in enclosures No. 2 should be doubled in order to compare with control enclosures; see table 43 below.

Table 43

The numbers of adult (♂♂ + ♀♀) ticks which appeared in the enclosures attached to lizards after 8/2/73. The numbers in the mixed enclosures have been adjusted (doubled).

Ap. hydrosauri

	Mallee enclosures	Casuarina enclosures
control	0	16
mixed	20	32

Amb. limbatum

	Mallee enclosures	Casuarina enclosures
control	3	11
mixed	24	36

Ap. hydrosauri has done better on the *Amb. limbatum* side of the boundary while *Amb. limbatum* have developed more readily on their own side of the boundary, despite the dry year which might, perhaps have been expected to make the Casuarina side more harsh for both species.

The lizards in the enclosures were examined throughout 1973 and until August in 1974. However no LL appeared although a number of ♀♀ engorged and detached. This might have been due to the enclosures being poorly sited and not providing suitable microhabitats for egglaying or hatching. Even if a few LL hatched they might have been confronted with hosts that had high resistance to ticks due to their prolonged, enforced contact with these parasites.

It was noted that ♀♀ in the mixed enclosures did engorge and detach, suggesting that they probably had mated - see 3.3422. ♂♂ were often seen attached near or beneath ♀♀ on these lizards but these alliances were always between conspecifics.

With some species of ticks it has proved possible to study the survival of non-parasitic stages by exposing large numbers of ticks to field conditions at different times of the year. Snowball (1957) was able to do this with the cattle tick *Boophilus microplus* in southern Queensland. Each week he placed freshly detached, engorged ♀♀ into small cylinders, partly made of gauze, and deposited these into holes bored in the ground. He then noted the fate of the ♀♀, their eggs and LL. Harley (1966) performed similar experiments with *B. microplus* in climatically dissimilar areas of northern Queensland as did McCulloch and Lewis (1968) in the north coast area of New South Wales. These experiments enabled the researchers to assess the effects of seasonal and geographical variations in climate on the survival of the ticks while off the host.

Such studies may well be of great value in resolving the problems of survival of *Ap. hydrosauri* and *Amb. limbatum* while off the host on either side of the boundary.

I have begun such experiments and so too has Trevor Petney. There are however, some major difficulties in producing results as complete as those obtained for the cattle tick, *B. microplus*. The first problem is that we have been unable to breed or capture enough engorged ♀ ticks to expose them to the environment at or near the boundary. We obtain so few ♀♀ that it is important that they all be placed in optimal conditions for egg production so that other research programmes on these ticks can proceed. Therefore the affects of the field environment on oviposition are beyond our reach, at the moment. Another major problem involves the vagaries of the environment at the tick boundary (see 5.34) which require that a study of the survival of non-parasitic stages should proceed for some years. Indeed Harley (1966) investigated survival in the field over a 5-year period.

Trevor Petney (pers. comm.) has begun such experiments in the Mt.Mary study area. He has left NN of both species in plastic vials in sites on both sides of the tick boundary and measured the time it takes for the ticks to die. His data are preliminary, but it is apparent that in all the various microhabitats used on either side of the boundary, *Amb. limbatum* NN live longer than *Ap. hydrosauri* NN (Petney pers. comm.). It was also noticeable that some positions chosen for leaving tick vials afforded the ticks greater chances of survival than others. When vials were sheltered by vegetation or leaf litter the ticks inside survived longer than those in more exposed sites.

I have also made observations on the survival of non-parasitic stages of the two tick species. These experiments have involved engorged and unengorged LL and NN and unengorged adults. In all cases the ticks were offspring of ticks caught in the Mt.Mary study area, from within 5km of the Mt.Mary-Florieton road/pipeline junction (see Fig. 47, Chapter 5).

Ticks were placed in 5ml plastic vials with perforated caps. These were placed in the soil so that the top of the cap was at ground level. The use of a perforated cap was to simulate a degree of cover over the ticks while allowing air movement. The evidence presented in 3.3411 below indicates that the ticks do, normally, take cover in crevices or beneath loose material in lizard refuge sites. The sites chosen were sheltered from direct sunlight and close to the base of Blue bushes (*Kochia sedifolia*).

Two areas were chosen in the Mt.Mary study area, one on each side of the tick boundary. The locations of these can be judged from Fig. 65. The "southern" site was in mallee scrub, 2km E of the "mallee enclosures"; while the "northern" site was 1½km NW of the "Casuarina enclosures".

Groups of ticks were deposited in these sites on two occasions, during winter and spring. Each vial contained 5 ticks, all of the same species and developmental stage. The first batch of ticks, engorged LL and NN, were released on 31st June 1979. The results are summarised in table 44.

Table 44

The fate of engorged LL and NN of *Ap. hydrosauri* and *Amb. limbatum* left in vials at two sites in the Mt. Mary study area. One site was north of and one south of the tick boundary. Ticks were placed in the area on two occasions (31st July and 13th October 1979). The numbers represent the ticks alive at the time; those in brackets indicate the number which moulted but were found dead.

Northern Site.

Week		*Ap. hydrosauri* eng LL		eng NN		*Amb. limbatum* eng LL	
0	31 July	30		15		30	
7	17 Sept.	4(19)		10(4)		17(11)	
11	13 Oct.	0	20	1(13)	8	2(26)	15
15	14 Nov.	0	0(14)	0	3(2)	0	5(6)

Southern Site.

Week		*Ap. hydrosauri* eng LL		eng NN		*Amb. limbatum* eng LL	
0	31 July	30		15		30	
7	17 Sept.	2(24)		8(2)		14(12)	
11	13 Oct.	0	20	3(7)	8	3(23)	15
15	14 Nov.	0	0(17)	0	1(2)	0	7(5)

These data do not show any marked difference between the two sites chosen in either species. *Amb. limbatum* engorged LL seem to moult, and the unfed NN live longer, during winter-spring, than do those of *Ap. hydrosauri*. It is interesting to note that most ticks moulted successfully. These experiments are, however, too small in scope (as pointed out earlier) to test adequately the survival of the ticks on either side of the boundary. To do this in an appropriate fashion, many more ticks need to be left in a greater variety of microhabitats over a number of seasons.

6.40 Discussion

I shall first consider the impact of the data presented in this chapter on the hypothesis that interspecific interactions might cause the parapatric boundary between *Ap. hydrosauri* and *Amb. limbatum*, and then examine the 'alternative' that the boundary is caused by factors other than interspecific interactions, most likely by aspects of 'weather' (Andrewartha 1970). Note that the 'alternatives' are not mutually exclusive.

In the laboratory experiments there were four occasions when it appeared that there might be negative interspecific interactions between the ticks. On one occasion significantly fewer *Ap. hydrosauri* LL moulted, after engorging on lizards with prior experience of *Amb. limbatum*, than moulted after engorging on lizards which had experienced *Ap. hydrosauri*. On two occasions significantly fewer *Amb. limbatum* LL attached to lizards that had experienced *Ap. hydrosauri* than attached to lizards with prior experience of *Amb. limbatum*. There was also an interaction component in that the presence of *Ap. hydrosauri* accentuated this failure to attach. On another occasion *Amb. limbatum* LL took longer to moult in a mixed group than in a control group. However, these LL moulted faster if they had engorged on lizards with prior experience of *Ap. hydrosauri*.

It is very difficult to visualize a mechanism that would cause a host parasitized by one species of tick to be more resistant to another species of tick than are the hosts of that second species. One would expect the immunological responses of a host to be greater toward a tick it had experienced. Of course it is possible that an immunological response by the host is sufficiently generalized to inhibit both species; the hosts which yielded significant results may, by chance, have been individuals with a greater degree of response (to either tick).

There are a number of points to consider in interpreting these results. The hosts were caught in the field as adults. It is therefore impossible to say how many ticks had infested them and what effect this had on their resistance, behavioural and/or physiological, to infestation. Such differences are important as only low numbers of hosts can be used in each treatment due to the labour involved in these experiments. Ideally one would breed lizards in the laboratory and keep them free of ticks for such experiments. This was tried, but young sleepy lizards are prone to premature death in captivity.

It must also be noted that of many tests that were performed only a few proved to be significant. One would expect a few such results in accepting or rejecting hypotheses at the 5% level of probability. Miller (1967), in a criticism of early laboratory experiments on competition, observed that one should be careful in accepting a few such results as good evidence for interspecific interactions.

The ticks used had been reared in the laboratory. The influence of exposure to abnormal, constant conditions on the ticks is not understood. Also, these experimental animals were progeny of few ♀♀, and thus do not reflect a broad range of genetic types.

The enclosure experiments did not indicate any sign of competition between the ticks. In fact ticks in mixed enclosures developed more readily than those in control groups. As the number of ticks of a particular species put into a mixed enclosure was half that put into a control enclosure, this result is consistent with the hypothesis that intraspecific competition, takes place in each species.

Amb. limbatum appeared to develop more readily in its own area than across the boundary. This supports the alternative hypothesis that environmental factors other than competition are involved. However, in the mallee enclosures, *Ap. hydrosauri* did poorly in its control enclosure. This hypothesis is inadequately tested in enclosures, as ticks do not have to wait long before finding a host.

Evidently there are problems associated with the siting of enclosures. Some enclosures were probably less adequate than others for ticks - and for lizards - even though the two 3 enclosures in each area were placed in apparently similar sites. This could be overcome by using larger enclosures or more enclosures. The former is difficult as the lizards are, at times, difficult to find even in a small enclosure. The use of more enclosures is only limited by the labour involved.

Another problem of small enclosures is that only a small number of hosts can be used in each. Thus, differences in host resistance to ticks may introduce large variability into the results.

It might also be that the interspecific interaction sought is only evident during certain seasons or under peculiar circumstances. A short study cannot hope to experience all these possibilities.

The laboratory experiments reported above, which tested the tolerances of ticks to a variety of environmental conditions, do show that there are marked physiological differences between the species. *Amb. limbatum* LL, NN and adults can withstand desiccation and starvation for longer periods of time than can *Ap. hydrosauri* - particularly during the warmer months of the year. It is reasonable to suggest that the northern limit of the range of *Ap. hydrosauri*, east of Spencer Gulf, may be determined by conditions becoming too arid for it to survive long enough while off the host.

It is more difficult to uncover tenable suggestions for the factors which might limit the distribution of *Amb. limbatum*. The experiments reported above do not allow us to eliminate the hypothesis of interspecific interactions with any degree of confidence. However, that hypothesis is only very weakly supported. It may perhaps be rejected after further work, and the answer be found to lie in the physiological ecology of the tick. It appears likely, from the data presently available, that the marked retardation of its development at low temperatures will prove to be a significant factor in fixing the southern limit to the range of *Amb. limbatum*.

Thus the experiments reported here do not give convincing support for either hypothesis. These experiments would have been capable only of demonstrating a powerful interspecific interaction (c.f. Connell 1961), or of detecting strong and consistent effects of components of the environment other than the other tick species (such as differences in 'weather'). One positive result from the experiments is that it is now quite clear that we are dealing with subtle processes. Certain simple, essentially deterministic versions of the hypothesis are now untenable. It is clear that an explanation for the parapatric boundary will have to take account of variability between years, between microhabitats, between hosts, and probably between ticks. I think it is clear that the testing of the several hypotheses must depend upon long-term manipulation of tick populations at a boundary; but it is now possible to refine their design - and to justify the expense of using more replicates and longer time periods. Each tick species should be transplanted into the range of the other, to simulate colonization, using the general type of design outlined in Figure 65. Then careful observations should be made of the survival of parasitic and non-parasitic stages during a number of seasons. Numbers of replicates should be large enough to provide an understanding of variability between hosts, between microhabitats and between ticks.

7.00 DISCUSSION

The present maintenance of the distributions.

The geographical distributions of *Ap. hydrosauri* and *Amb. limbatum* east of Spencer Gulf are parapatric, as are those of *Ap. hydrosauri* and *Amb. albolimbatum* to the west of that gulf. The distributions of the *Amblyomma* spp. may well abut in a similar fashion but evidence for this is not as strong as in the other cases (see Chapter 2). There is a broad association between the distributions of the three ticks and climate. There seems to be no such association between the geographical distributions of host species and those of the ticks (see Chapter 4).

Studies in the Mt. Mary (study) area revealed that the parapatric boundary of *Ap. hydrosauri*and *Amb. limbatum* is associated with a marked change in vegetation and soils (an ecotone), and a more gradual change in climate (see Chapter 5). There are no apparent consistent differences in host species, numbers or behaviour, across the boundary. *Tr. rugosus*, the sleepy lizard, is by far the most abundant and frequently infested host at Mt. Mary, on both sides of the boundary.

If a tick were transported across the boundary from one side to the other it would experience two types of change. Firstly, on attaching to a host on the other side of the boundary the tick would probably be exposed to ticks of the other species, and the host would probably have been infested on a number of earlier occasions by ticks of the other species. The hypothesis that the parapatric boundary might arise from interspecific interactions during such situations was discussed in Chapters 1 and 6 above. Secondly, upon detaching from the host the tick would find a microhabitat, in which to lay eggs or moult and wait for a host, which differed in humidity and, to some extent, temperature, from those available on the other side of the boundary. There would also be some differences between faunas of the leaf litter layers under bushes on either side of the boundary. In these respects, of course, there is also considerable variability within the range of each tick species. The hypothesis that factors in this second category might cause the parapatric boundary between two tick species was also discussed above (see Chapters 1 and 6).

The extent of overlap between the tick species at the parapatric boundary depends upon:

(i) how frequently and how far ticks are transported across the boundary,

(ii) how well these colonists withstand the changed conditions on and off hosts, and

(iii) how markedly environmental conditions change across the boundary.

The ticks exhibit low vagility. When detached and engorged they are incapable of moving very far. After moulting or hatching they seem to wait in reptile shelters for a host; see the discussions of these matters in 3.32 and 3.341. They would be moved only short distances when attached, as their hosts have small home ranges; see 4.40. The home ranges of their most important host, the sleepy lizard (*Tr. rugosus*), do overlap (see 4.40), so there is a chance that a tick might, on successive attachments, move more than the width of a home range. Bull (1978 a) estimated that overlapping lizard home ranges, in the Tickera area of Yorke Peninsula, provided "limited opportunities for dispersal of up to 800m during a ticks' life", in a population of *Ap. hydrosauri*. The home ranges of lizards at Mt.Mary may be a little larger than those at Tickera, but it is unlikely that ticks at the boundary zone have more than a slight chance of being moved further than those at Tickera. It is possible, though, that lizards in the Mt.Mary area are forced to move further after heavy rains (see 5.35), which cause some regions to be completely flooded for many days. Such flooding seems only to occur at intervals of some years (there have been two such periods between 1970 and 1978), but might result in a few ticks being moved up to 1km or so more than would normally be expected.

Both the ticks and their hosts are poikilotherms and this also restricts the vagility of the ticks. The activity and development of the parasites and their hosts are restricted by low temperatures during some seasons of the year, and the activity of the hosts is also restricted during the hot summer months. When hosts are most active, during spring (4.40), the ticks engorge and detach rapidly (3.3421), and thus spend only a short time attached. This behaviour would reduce the chances of them being transported very far. Actually, many ticks do not find a host; thus large numbers are needed for successful colonization. One would expect ectoparasites that remain attached to homeothermic animals for long periods to have a much higher vagility than these ticks.

It is evident then that ticks at a parapatric boundary are likely to be moved only small distances into the territory of the other species and, of course, stand a similar chance of being moved a small distance in another direction. However, although the movement of ticks across the boundary is small, it does occur. Thus, this low vagility must be coupled with factors which cause colonizing ticks to die out on crossing the boundary in order to produce the small degree of overlap reported above (see Chapter 2 and 5.20). These factors were examined in Chapter 6 to see if the two tick species interacted in some way, or if changes in another environmental factor or factors caused the boundary. The data presented in that Chapter did not clearly demonstrate that either occurred during the study.

In the experiments where ticks, of both species, and lizards were released in enclosures on both sides of the Mt. Mary boundary, *Ap. hydrosauri* adults survived quite well for a year on the "wrong" side of the boundary in the presence of *Amb. limbatum* or alone. *Amb. limbatum* showed more signs of being disadvantaged by transportation across the boundary. But there is some doubt that the site chosen on that side was a good one for either species. In the experiment where LL and NN were left to see how they survived on both sides of the boundary, *Amb. limbatum* seemed to be able to survive desiccation and starvation for longer periods than *Ap. hydrosauri* in both areas - as was expected from experiments in the laboratory. In laboratory competition experiments there was more evidence, though not convincing (see 6.40), that *Amb. limbatum* was adversely influenced when it attempted to attach to lizards which had formerly borne *Ap. hydrosauri*.

Bull and Smyth (1973) suggest that the northern limit of the range of *Ap. hydrosauri* is set by its tolerance (or intolerance) of dry conditions. This hypothesis remains the most acceptable and plausible; see 6.40. The reasons for the southern limit of *Amb. limbatum* are more difficult to unravel. The suggestion by Bull and Smyth (1973) that the tick seeks the most moist microhabitats when off the host, and that in wetter areas it might therefore drown, is unlikely to be true. In the Mt.Mary area, the soils south of the boundary tend to be more permeable to water; see 5.33. When heavy rains did occur during the study, water was more often seen forming swamps in the *Amb. limbatum* areas north of the boundary. In addition, the experiments described in 6.30, in which both species were immersed in water, showed that the ticks can survive many days under water.

Amb. limbatum is influenced more adversely by cold conditions than is *Ap. hydrosauri*. It is shown in Chapter 3 that the rate of development (moulting and hatching) of this tick is faster than that of *Ap. hydrosauri* at high temperatures (>25°C), but it is markedly lower in colder conditions. It may be that *Amb. limbatum* is unable to survive in southern regions because ambient temperatures are too low for too long. It has been suggested that the cattle tick, *Boophilus microplus*, is obstructed by winter cold from further southward migration in northern New South Wales (McCullock and Lewis 1968), but this was only demonstrated by long-term field experimentation.

If the distributional limit of a species of tick ~~was~~ were determined by some component of weather, then it would be reasonable to expect that at the limit there would be a zone in which the tick might live in seasons when the weather is favourable (c.f. the hypothetical map of the distribution of *Austroicetes cruciata* in Andrewartha and Birch 1954). Indeed, the transplant experiments described in Chapter 6 suggest that this may be the case with *Ap. hydrosauri* and *Amb. limbatum*. The portion of this zone occupied would depend upon the vagility of the tick and the temporal and spatial fluctuations in weather at the edge of the tick's distribution. If the distributions of these ticks are determined by such factors, it is a remarkable coincidence that their distribution limits correspond so precisely and with such limited overlap. It might also be predicted that, even at an ecotone (e.g., Mt. Mary), the extent of overlap might vary with fluctuations in weather from year to year.

Bull (1969) noted that the parapatric boundaries of some other pairs of closely-related species of animals were determined by biological barriers due to hybrid sterility. An example of this is described by Littlejohn et al., (1971) in frog species. Such a mechanism relies upon colonizing ♀♀ being most likely to meet ♂♂ of the other species, and on the progeny of inter-specific matings being infertile. Colonization is thus swamped and a hybrid zone separates the species. Some ticks do mate with ticks of other species, in some cases with ticks of different genera (Balashov 1972, Ermoshkevich 1956, Kalyagin 1967). However, no such occurrences have been observed between these reptile ticks, although many mixed batches of adults have been observed; see 3.3422, 6.20 and 6.30. I suspect, then, that the "Bull hypothesis" is inappropriate for *Ap. hydrosauri* and *Amb. limbatum*.

In summary, it seems that the boundary at Mt. Mary is not determined by any one factor. The northern limit of *Ap. hydrosauri* is most likely determined by its ability to tolerate low humidities when off the host. The change in humidity of tick microhabitats across the boundary would result from changes in vegetation and soils which accentuate gradual changes of climate across the area. *Amb. limbatum* may be stopped from further movement south either by interaction with *Ap. hydrosauri* via host resistance, or by a change in some other, unidentified, environmental factor, possibly cold conditions. If it transpired that *Amb. limbatum* is influenced by *Ap. hydrosauri*, then this would be the first evidence of such phenomena in ectoparasites - few such studies have been made, and they have ruled out interspecific competition (Ryckman and Ryckman 1967). Examples of intra-specific competition in ticks are, however, well known (Sutherst et al., 1973). The overlap zone is particularly narrow in these ticks because of their low vagility (see above), as in the wingless grasshoppers described by White (1968).

If the tick boundary at Mt.Mary is determined in the way suggested above, what is its future? It seems that the tick boundary is stable, as Bull (1969) suggests. The ecotone itself, which probably influences at least *Ap. hydrosauri*, is similarly stable. Both the ecotone and the tick boundary would change if there were large fluctuations in climate of the type that have occurred a number of times in the Quaternary i.e. the succession of glacial and interglacial periods (Rawlinson 1974). If the vegetation were much changed, e.g. by man, or the numbers of hosts were to fall too low, then the distribution limits of the two species might move apart, leaving an unoccupied zone between them. Minor changes in the weather from year to year, or decade to decade, would be unlikely to change the position of the boundary, but ~~it~~ they might have a small effect on the degree of overlap between the distributions of the ticks.

The vegetation change associated with the tick boundary at Mt.Mary is not typical of the rest of the boundary between these two ticks. In fact, the edge of the mallee scrub, which marks the tick boundary at Mt.Mary, curves north of the tick boundary to the east of Morgan (Specht 1972). However, soil types and the floral composition of the scrub change in this area. Thus the relationship between micro-environmental conditions and the vegetation, which holds at Mt.Mary, may not apply to the east. It is thus probable that the relationship between humidity or other micro-environmental variables and the tick distributions still holds along the whole of the boundary.

Much less is known about the boundaries the ticks share with *Amb. ambolimbatum*. If it is shown that the two *Amblyommas* do have a common boundary with little overlap, the hypothesis of Bull (1969), referred to above, may well deserve further consideration. I mentioned in 3.22 that some ticks of intermediate appearance were taken from near a boundary between the two species.

The Ultimate Causes of the Distributions

Among the most difficult questions about the tick distributions are those which concern the past and how such patterns arose. I have shown, in Chapter 2, that the geographical ranges of the ticks are broadly associated with climate, as are the distributions of their hosts. It can be assumed that marked long-term changes in climatic conditions would lead to changes in the ranges of the tick species and their reptilian hosts. An understanding of past changes in climate is, therefore, essential if previous patterns of tick distribution, and how and when these patterns have fluctuated, are to be understood.

It is believed that during the Tertiary, Australia was warmer and wetter than it is today (Gentilli 1961), and that since then there has been a general cooling and drying. There were major climatic fluctuations in Australia (and elsewhere) during the last 2 million years (the Quaternary). During the Pleistocene, the first epoch of the Quaternary which lasted from 2 million years B.P. (before present) to 10,000 years B.P., there were five worldwide glaciations (Ericson and Wollin 1968). These periods, the Nebraskan (the earliest), Kansan, Illinoian, Early Wisconsin and late Wisconsin (the most recent), were characterised by a global lowering of surface temperatures and a large increase in the proportion of the world's water bound in ice. The latter led to large eustatic lowering of sea levels. In the most recent glaciation, the late Wisconsin, the sea level dropped to 132-150 metres below the present level about 20,000-18,000 years B.P. (Jennings 1971). Thus, for a time, many islands on the Australian continental shelf, including Tasmania (Davies 1974), were part of the mainland. These major changes in climate and geography probably brought about fluctuations in the distributions of the ticks.

There seems to be some broad agreement among authors in this field about the timing and extent of sealevel changes and the fluctuations in land temperature (see Rawlinson 1974). The main uncertainties are about the rainfall. Galloway (1965 a, b) suggested that the glacial periods in Australia were accompanied by cold and dry conditions. This notion ran counter to the widespread theory, at the time, that the glacial periods were pluvial periods (Main et al., 1958, and Link 1967). These opposing ideas are still subject to some debate, but climatic sequences recently investigated in alluvial deposits in south eastern Australia (Bowler 1970, Bowler and Hamada 1971, and Dodson 1974 a, b) indicate that during the late Wisconsin glaciation conditions were relatively arid. Wyrwoll (1979) suggests that south western Australia was similarly affected.

Gentilli (1961) and Galloway (1971) observed that making interpretations of broad climatic changes in the past is fraught with pitfalls. They suggest, for instance, that there may have been a large number of fluctuations of climate that were experienced quite differently in different parts of the continent. However, the recent studies mentioned above indicate that there were some major climatic changes which were widespread in southern Australia (Bowler 1976, Wyrwoll 1979). More data are needed, though, particularly from south western and central southern Australia.

Figure 66 shows how climate and sea level may have fluctuated during the late Quaternary in south eastern Australia.

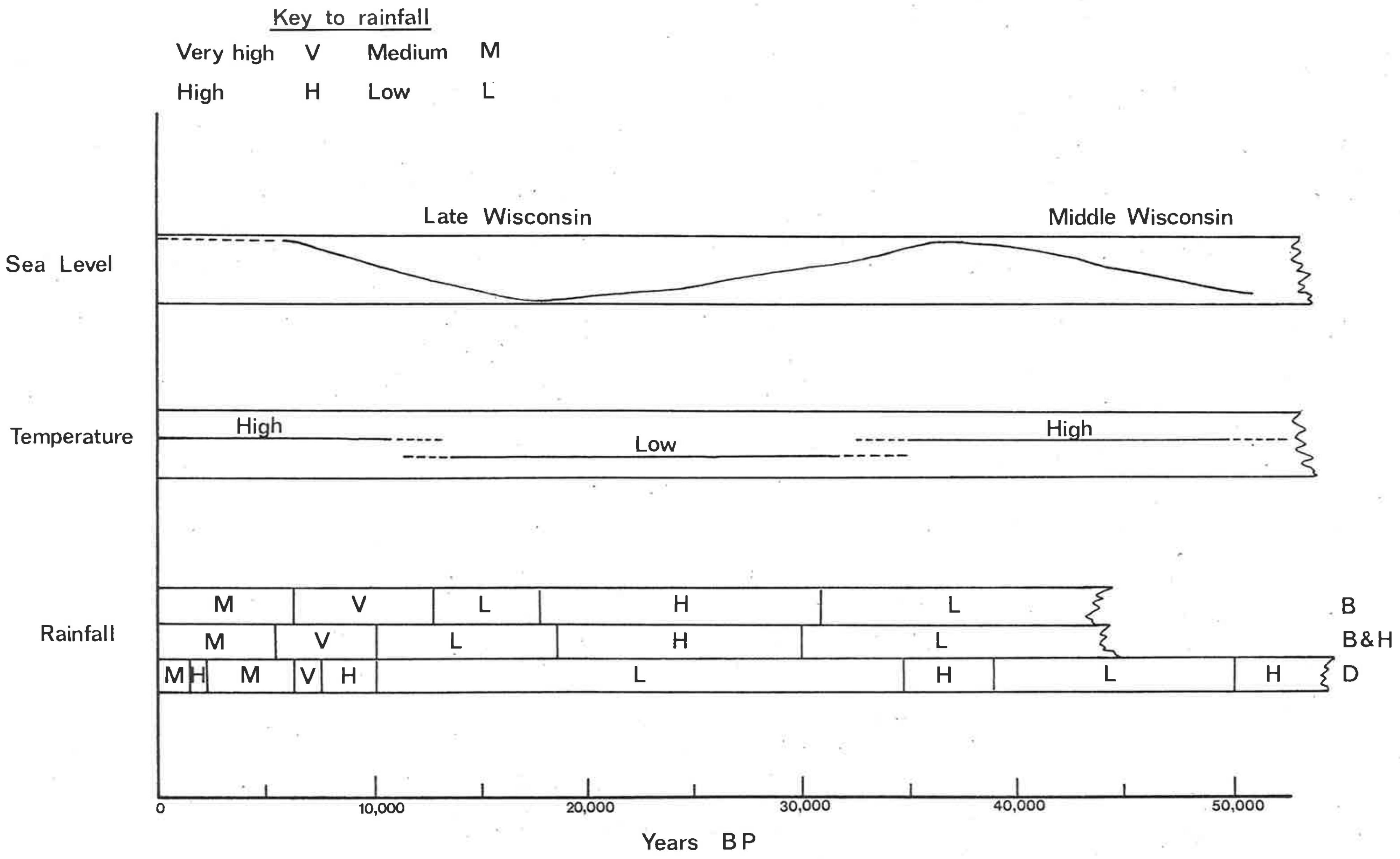
Sutherland (1971) points out that southern Australia has been relatively stable since the early Cainozoic. Thus, given accurate information on the timing of sea level changes and the depth of water between islands and the

Figure 66. Probable changes in sea level, surface temperature and rainfall in south eastern Australia during the late Quaternary. The sea levels and temperatures are based on those used by Rawlinson (1974). The rainfall data are those of

Bowler (1970) - 'B',

Bowler and Hamada (1971) - 'B + H', and

Dodson (1974 a & b) - 'D'


Key to rainfall
Very high V
Medium M
High H
Low L
Late Wisconsin
Middle Wisconsin
Sea Level
Temperature
High
Low
High
Rainfall
M
V
L
H
L
B
M
V
L
H
L
B&H
M
H
M
V
H
L
H
L
H
D
0
10,000
20,000
30,000
40,000
50,000
Years BP

mainland, it is possible to estimate the periods during which such islands were joined to the mainland. Rawlinson (1974) has calculated the time of isolation of a number of islands from south eastern Australia in this manner. Main (1961) and Abbott (1978) have made similar estimates concerning islands in western Australia. Main (1961) noted that if an animal occurs on an offshore island one can assume that it occurred on the adjacent mainland when the island-mainland link was broken. Table 45 lists some of the islands on which the ticks have been found with an estimate of their time of isolation. The geographical positions of these islands are shown in Figure 67. These data give a glimpse of past geographical distributions of the ticks.

Table 45

Australian Islands mentioned in the text with estimated times of most recent isolation from the mainland based on Abbott (1978) and Rawlinson (1974). Tick species found on the islands are shown as:- *Aponomma hydrosauri* = H, *Amblyomma albolimbatum* = A and *Amb. limbatum* = L. The location of the islands are shown on Figure 67.

Island	Time of isolation (years before present)	Tick species
1. Tasmania	12,750	H
2. West Wallabi Is.	12,000	A
3. Mondrain Is.	12,000	A
4. Kangaroo Is.	10,000	None
5. Bernier Is.	8,000	A & L
6. Rottnest Is.	7,000	A
7. Dirk Hartog Is.	6,000	A
8. Wardang Is.	5,000	H

Ap. hydrosauri is found on the Bass Strait Islands (between Tasmania and the mainland) and on Tasmania. This suggests that this tick lived in south eastern Australia about 13,000 years B.P., as it does now. *Tr. rugosus*, a major host of *Ap. hydrosauri*, has not been found in Tasmania or in parts of southern Victoria (see 4.30) but *Tiliqua nigrolutea* does occur in these

Figure 67. Australia, showing the locations of the islands listed in table 45.


5
7
2
6
3
8
4
1
1000 km

places and apparently enables the tick to live further south than *Tr. rugosus*. *Ap. hydrosauri* and both of these skinks are absent from Kangaroo Island, off South Australia, which was probably isolated from the mainland about 10,000 years B.P. (Rawlinson 1974), i.e., nearly 3,000 years after Tasmania. Presumably neither skink was on the adjacent shore at the time the link was severed. The climate may well have been too cold for *Tr. rugosus*, which even today does not inhabitat the colder regions of Victoria. It is difficult, however, to explain the absence of *Ti. nigrolutea* (a Bassian species) from that area 10,000 years ago. It seems unlikely that either of these skinks was isolated on Kangaroo Island and then became locally extinct, as the island is much larger than others on which they live and it seems to have appropriate weather. *Ap. hydrosauri* and *Tr. rugosus* are found on Wardang Island off central Yorke Peninsula. This island is close to the shore and has probably been connected to the mainland as recently as 5,000 years ago.

Amb. albolimbatum is found on a number of islands in southern Western Australia (see table 45). These were isolated by rising seas from about 12,000 years B.P. (West Wallabi) to 6,000 years B.P. (Dirk Hartog). Evidently *Amb. albolimbatum* was in much the same regions of south western Australia then as it is now. It is interesting to note that both *Amb. albolimbatum* and *Amb. limbatum* have been found on Bernier Island (isolated 8,000 years B.P.), and that this island ? is very close to the present distribution limits of the two ticks on the adjacent mainland. The co-existence on the island, and the similarity between past and present distributions of these ticks, suggest that the boundary between them is relatively stable. It is not known how they are distributed on the island.

Amb. limbatum has been identified in collections from islands off north western Australia (see Sharrad and King 1979 - appendix 6). These are well within the geographical limits of the tick on the mainland.

Many southern Australian plants and animals have disjunct east-west distributions with eastern and western forms being separated by the

Nullarbor Plain. A number of workers have attempted to explain these present distributions, and the phylogenetic relationships of the disjunct groups, by postulating that successive migrations of organisms have taken place across the Nullarbor Plain when conditions have been favourable, and that these conditions have been interspersed by periods of aridity (Main et al. 1958, Keast 1961, Kluge 1967). Often such writers believed that the glacial periods were pluvial periods - a view now questioned (see Figure 66).

Ap. hydrosauri is found in three quite separate regions on the mainland, south western Australia, Eyre Peninsula and south eastern Australia. This distribution is most simply explained if it is postulated that formerly the Species tick occupied a band from east to west across the continent. This would only be possible if the factor or factors which presently determine the northern limit of its range were changed. If the northern limit of its distribution is largely determined by climate, as I suggest earlier in this discussion, then this would involve lower temperatures and/or greater precipitation. Figure 66 shows that there was probably a period of higher rainfall about 6,000 years B.P. It is unlikely, in my view, that this relatively minor and brief period would have been sufficient to link the south western Australia and Eyre Peninsula populations. Wyrwoll (1979) also notes that there is some evidence that the Nullarbor Plain has had much the same climate during the last 10,000 years. The populations separated by Spencer Gulf in South Australia would seem to be more likely to be brought together by such conditions. However, it is probable that during the last glaciation (between 12,000 and 26,000 years B.P.) the species? ticks and their hosts lived further north. I have mentioned above that many workers now consider this period to have been relatively arid, although Bowler (1970) and Bowler and Hamada (1971) consider that the early part of the glaciation may have been wet (see Figure 66). The period before 12,000 years B.P. is the most recent time when it appears likely the *Ap. hydrosauri* populations were linked. However, this scheme is partly disturbed by consideration of *Amb. albolimbatum*. It seems likely that this tick originated in south western Australia, where it now lives north of *Ap. hydrosauri*, on *Tr. rugosus*. *Amb. albolimbatum* extends across the Great Australian Bight into Eyre Peninsula but has not crossed the top of Spencer Gulf! This is perplexing as *Ap. hydrosauri* has done so. One possibility is that *Ap. hydrosauri* spread across the continent well before the other tick, and that the spread of *Amb. albolimbatum* has been more recent, after the northern Spencer Gulf area became too arid for either species. It is also perplexing that *Amb. albolimbatum* crossed the head of the Bight (and still occurs there) but has not penetrated the top of Spencer Gulf - for the former region seems to be as arid as the latter (see the isohyets shown in Fig. 3, Chapter 2). This observation points again to the possible complexity of the factors which limit the distributions of the ticks.

Amb. limbatum seems well adapted to life in arid and tropical conditions, and survives well on goannas which are most abundant in those regions. Bull (1969) suggests that this tick probably spread from north western Australia. There seems no reason to suggest other than a northern origin for this species.

The parapatric distributions of the ticks have only been partly explained. Further work is needed. The most important experiments required are those which involve long-term, controlled transportation of ticks at a boundary (as outlined in 6.40) - i.e., artificial colonizations. In addition the hypothesis that the ticks might interact, and in this way limit the distribution of one or both species at a boundary, requires further critical testing (see Chapter 6).

The answers to problems in ecology are seldom quickly found; indeed Andrewartha and Birch (1954, p 10) note that some of the best studies in population ecology have entailed routine data collection for 10 to 15 years! This will clearly be the case with the present problem largely because of the variability in the organisms and in the relevant components of their environments. This variability, described in the present study, is likely to form an essential part of the answer to the problem and as such cannot be ignored but must be measured. To measure the variability between animals or between different habitats, in a region where rainfall varies from year to year, requires the use of many animals, many replicates and long-term studies.

The multiplicity of questions to answer, and the long-term nature of the investigations, require the ecologist to choose carefully the most important questions and to design critical experiments, with the aim of rejecting, not merely supporting hypotheses. Despite their difficulty and cost, I consider that field experiments are an important part of this endeavour. Only in this way can models of nature, such as the competitive exclusion principle, be kept in the realm of testable scientific theory rather than mere conjecture.

Appendix 1

The nature of data collected in the field.

All reptiles captured in the field were examined for ticks and, unless they were in the Mt.Mary study area or the ticks were wanted alive, any found were removed with watchmakers No. 5 forceps. The specimens were placed in 2ml plastic vials of 70% alcohol, labelled and brought back to the laboratory. In the laboratory each tick was examined under an Olympus SZ III stereo microscope and identified using the keys in Roberts (1970).

The following data was collected during these procedures and stored on 4½" x 6" Invicta Sorter Cards (No 200). The information was written on the cards and also coded by punching out gaps in the numbered sides of the cards.

Data stored:

1. Host species.
2. The date.
3. Where the host was found, to the nearest 100 metres.
4. Time.
5. Notes on the behaviour of the host.
6. The cloacal temperature of the host plus soil temperature. and air temperature.
7. The species of ticks found.
8. The numbers of each stage found.
9. The position of each tick on the host - shown with a diagram.
10. General notes on the habitat.

Appendix 2

Keeping ticks in the laboratory.

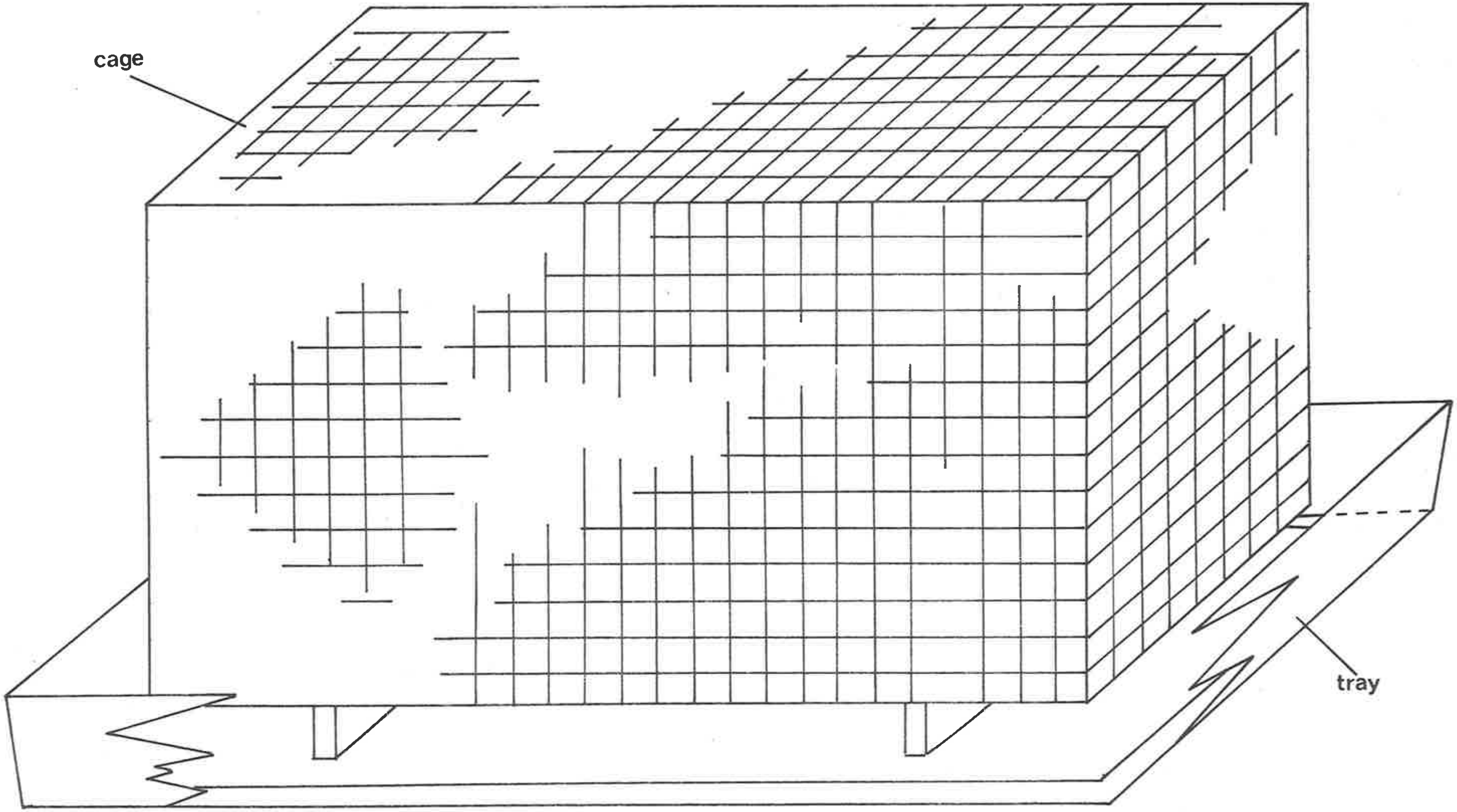
During this study, and those of Drs. Bull and Smyth methods were developed for keeping the ticks in the laboratory and for enabling them to complete their life cycles. Laboratory stocks have been kept for more than 2 generations and these organisms used in numerous laboratory experiments some of which are reported here.

Ticks were brought into the laboratory attached to hosts, usually *Tr. rugosus,* the sleepy lizard. The lizards were placed individually in bird cages with wire mesh floors large enough to allow passage of the largest engorged female tick. The occupied cages were placed folded paper in white plastic butchers trays, see figure 68.

Engorged ticks on detaching from hosts fell into the trays and took refuge under the paper. The tray contents were checked each day, the ticks removed and paper changed. Engorged ticks were picked up, with watchmakers No 5 forceps and placed in plastic vials which had perforated lids. Usually all the engorged LL or NN from a host were kept in the same vial, engorged ♀♀ however were put in larger vials.

Engorged ticks require appropriate temperatures in order to moult or lay eggs and also survive best if kept a moderately high relative humidity. Plastic vials containing ticks were kept in glass desiccators over various saturated salt solutions in constant temperature cabinets. Relative humidity of air in closed containers containing saturated salt solutions are given by Winston and Bates (1960). It was found that a sat. KCl solution provided optimum conditions for tick development. This solution has over it a RH of 85% at 25°C. Laboratory stocks of ticks not being used in experiments were kept at 27°C if it was desirable for them to moult quickly, or for ♀ to lay eggs quickly. If the ticks were not required for some time they were kept at lower temperatures (e.g. 20°C) which slowed development.

Figure 68. A diagram of a lizard cage (40cm long x 30cm x 30cm) on a tick catching tray (50cm x 35cm x 15cm).

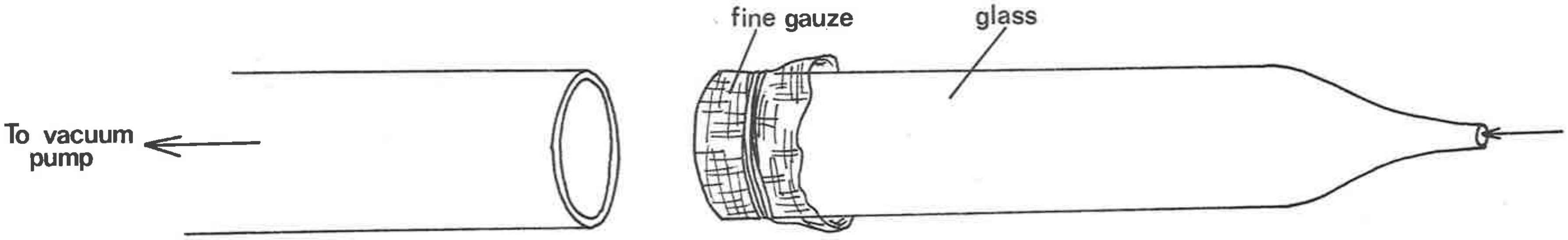

cage
tray

It was sometimes necessary to count eggs and to place batches of them in separate vials. A ♀ tick may lay 4,000 of these tiny, round sticky wax coated objects. To count them a binocular, stereo microscope was used (Olympus SZ III)and they were handled with fine dissecting needles.

Unengorged LL or NN are quite small and active. It was often necessary to count batches of them, newly hatched or moulted, which might number hundreds per vial. I developed a quick, accurate technique. Pasteur pippettes were made from glass tubing and fine gauze placed over the large end and secured with a rubber band (see figure 69). The device was then attached to a vacuum pump on a laboratory tap which meant that air was sucked through it. To count a group of ticks one would sprinkle them onto a sheet of white paper and suck them into the device where they would collect on the gauze. When the desired number had been counted and collected the device was disconnected and the very tip of the fine end placed at the edge of a bunsen burner flame which quickly sealed it and left the ticks unharmed. The device could then be stored in a desiccator in the same way as plastic vials.

Often it was necessary to infect lizards with known numbers of ticks of a particular stage. They could be counted in the manner described above. The lizard to be infested was first checked thoroughly for ticks and then placed in a clean, washed, calico lizard bag. Ticks, in the tick counting devices, were brought to the lizard, the rubber bands holding the gauze cut, and the ticks sprinkled onto the prospective host. The bag containing ticks and lizard was sealed with stout rubber bands and placed in a quiet, dark warm (25°C) container. The bag was left undisturbed for at least 24 hours and often 48 hours. The number of ticks attached and those remaining in the bag could then be counted.

Figure 69. A device for handling, collecting and counting large numbers of ticks in the laboratory.


fine gauze
glass
To vacuum pump

Appendix 3

Marking sleepy lizards *Trachydosaurus rugosus*

During this study it was necessary to mark and release lizards in the Mt Mary study area, and to mark lizards used in field and laboratory experiments so that individuals could be distinguished.

Each lizard was marked in two ways. Firstly, circular spots of scarlet finger-nail polish were applied to the dorsal surface of the lizard. These were put onto one or more of four regions on the lizard; on the head (H), Tail (T), the anterior part of the back (BF) or on the posterior part of the back (BH). The colour marking could then be easily recorded, e.g. a lizard with 3 spots on the head and 1 on the tail would be H3, T1. The second marking technique involved toe clipping. The toes on one foot were numbered 1 to 5 from near the body working out. The feet were coded; RF - right front (looking at the dorsal surface of the lizard), LF - left front, RH - right hind, LH - left hind. Thus a lizard with the middle toe on the right front foot and the first toe of left hind foot missing would be RF3, LH1.

It was necessary to use both methods as fingernail polish sloughed off with skin when lizards moulted and lizards also lost toes in the field.

Appendix 4

The following is a copy of:

Bull, C.M., Sharrad, R.D. & Smyth, M. (1977).

The pre-molt period of larvae and nymths of the Australian reptile tick *Aponomma hydrosauri*. Acarologia, 19(4): 593-600.

THE PRE-MOLT PERIOD OF LARVAE AND NYMPHS OF THE AUSTRALIAN REPTILE TICK *APONOMMA HYDROSAURI*

BY

M. Bull [1], R. D. Sharrad [2,3] and M. Smyth [2,4]

Résumé

Dans les infestations simples, la période moyenne qui précède la mue variait pour les larves engorgées d'*Aponomma hydrosauri* à 25°C de 15 à 24 jours, et pour les nymphes engorgées de 20 à 33 jours. La période diminuait à mesure que la température montait, mais n'était influencée ni par la durée de l'engorgement, ni par son poids final. Il fallait plus de temps aux nymphes qui devenaient femelles qu'à celles qui devenaient mâles. Des différences se sont manifestées dans la durée de la période moyenne d'avant la mue, entre les infestations sur hôtes d'une seule espèce, les infestations sur hôtes de différentes espèces, et les infestations sur hôtes pris dans de différentes régions de l'Australie du Sud.

Summary

Within single infestations the mean pre-molt period for engorged larvae of *Aponomma hydrosauri* at 25°C varied from 15 to 24 days, and for engorged nymphs from 20 to 33 days. The period decreased with increasing temperature but was not influenced by engorgement time or engorgement weight. Nymphs turning to females took longer than those turning to males. Differences were detected in the mean pre-molt periods from infestations on different individual hosts of the same species, from infestations on different host species, and from infestations of stocks from different localities within South Australia.

Introduction

In our investigations of the ecology of the Australian reptile tick *Aponomma hydrosauri* (Bull and Sara, 1976 ; Bull and Smyth, 1973 ; Sharrad, 1976 ; Smyth, 1973) information was needed about the life cycle. While the timing of different phases of the life cycle is well known for many tick species (Arthur, 1962), there are few descriptions in the literature for reptile ticks (Nadchatran, 1960 ; Cooney and Hays, 1972), and even fewer for species of the genus *Aponomma*.

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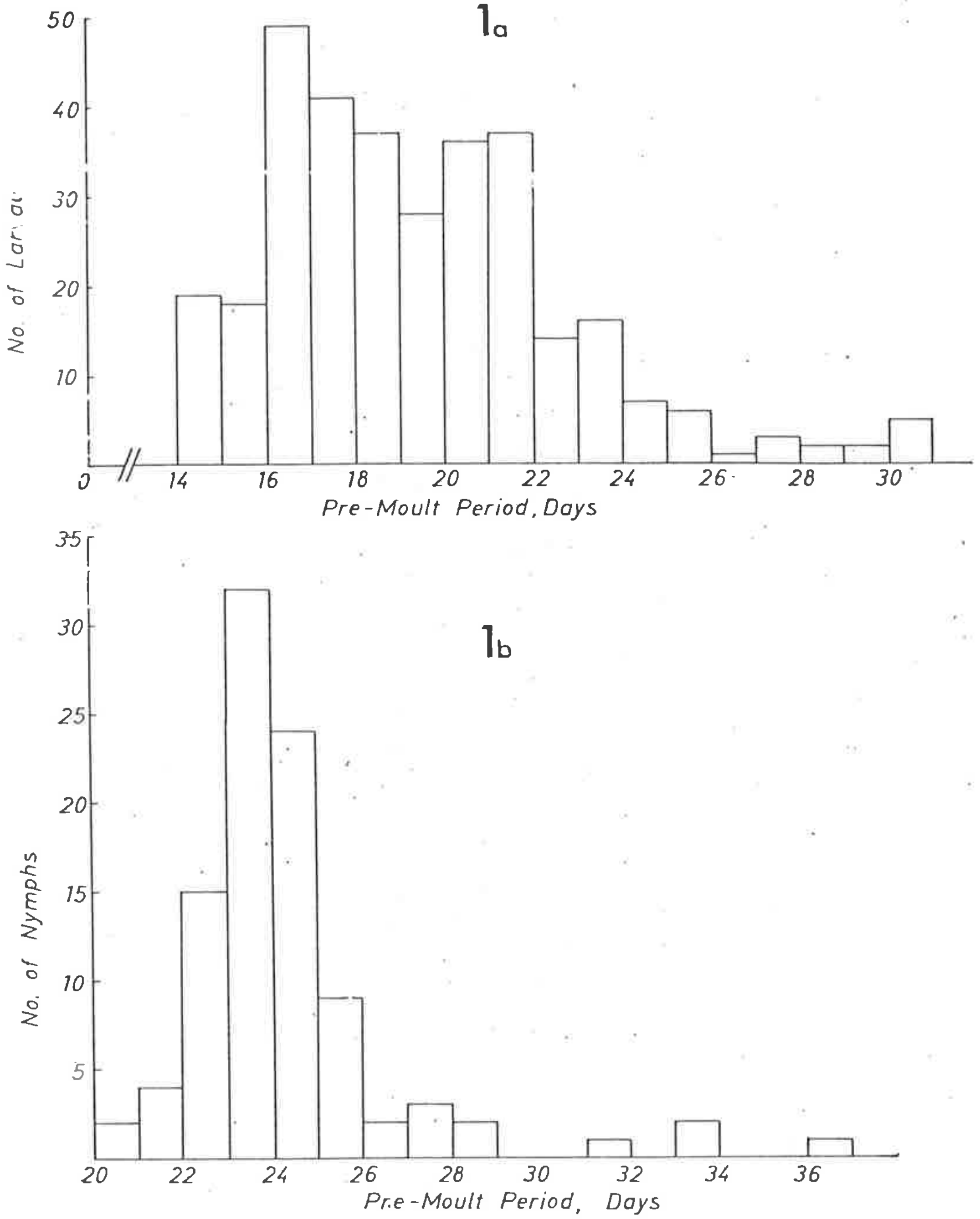

Fig. 1 : a) The distribution of pre-molt periods of 321 larvae from the Tickera laboratory stock from a single host infestation ; b) The distribution of pre-molt periods of 97 nymphs from the Port Lincoln laboratory stock from a single host infestation.

In this paper we describe measurements of the pre-molt period of *A. hydrosauri*, that is the time taken from detachment of engorged larvae and nymphs to their molting to the next stage.

MATERIALS AND METHODS

Ticks used were either from laboratory stocks, or from natural infestations of field caught hosts. Unless otherwise indicated the host used was the sleepy lizard *Trachydosaurus rugosus*. As they detached from their hosts engorged larvae and nymphs were placed in 3 ml ventilated plastic tubes. These were stored in glass desiccators above saturated solutions of salts chosen from the table of WINSTON and BATES (1950) to provide a relative humidity of 85 % within the desiccator. In most cases the ticks were kept at 25°C over saturated KCl. Daily checks were made to record the time taken by each tick to molt.

RESULTS

Typically, from a single infestation, there is wide variation between individual ticks in the time between detachment from the host and molting (fig. 1). The mean pre-molt period for 32 single infestations of larvae kept at 85 % relative humidity and 25°C ranged from 15.0 to 24.2 days. In the same conditions the mean pre-molt period for 17 single infestations of nymphs ranged from 20.2 to 33.0 days.

To test the effect of temperature, larvae, originating from the eggs of a single female, were attached to a single host, and when they detached were divided into three groups and kept at 20°, 25° and 30°C, respectively. TABLE 1 shows the pronounced decrease in the pre-molt period with increased temperature.

TABLE 1

Mean pre-molt periods in days of larvae from a single infestation kept at three different temperatures.

TEMPERATURE	20°	25°	30°
No. of engorged larvae	108	75	82
Mean pre-molt period	31.03	18.61	12.65
s.e. of mean	0.22	0.29	0.17

Other data for both nymphs and larvae consistently support this observation, although it is not always possible to separate the effects of temperature from other potential sources of variability.

In two experiments the time taken to engorge on the host, and the final engorgement weight at detachment were recorded for each tick. For 961 larvae from seven hosts there was no consistent relationship between the pre-molt period and either the engorgement time or the engorgement weight. Nor was there any such relationship in 230 female nymphs or in 191 male nymphs from eight hosts.

In each infestation the mean pre-molt period of nymphs turning to females was longer than that of nymphs turning to males (TABLE 2). Over eight hosts the difference between sexes was statistically significant ($F = 5.35$, $p < .02$).

TABLE 2

The mean pre-molt periods ($\bar{x}$) in days of larvae and nymphs from individual infestations of genetically homogeneous groups of ticks engorged on several hosts. Engorged ticks kept at 25°C.

EXPERIMENT	STAGE						
74-1	larvae	(Lizard	B	D	E		
		(Infest. density	50	250	250		
		($\bar{x}$	17.44	17.79	18.20		
		(s.e. of mean	0.48	0.21	0.26		
74-2	larvae	(Lizard	F	C	G		
		(Infest. density	900	200	200		
		($\bar{x}$	16.90	17.37	17.52		
		(s.e. of mean	0.08	0.17	0.35		
74-3	nymphs	Lizard	1	2	3		
		Infest. density	120	30	120		
		$\bar{x}$ ♂	26.61	24.58	24.44		
		s.e. of mean	0.92	0.61	0.36		
		$\bar{x}$ ♀	26.20	25.51	25.58		
		s.e. of mean	0.41	0.42	0.54		
74-4	nymphs	Lizard	G	H	J	K	L
		Infest. density	230	230	50	50	50
		$\bar{x}$ ♂	24.74	27.74	24.50	26.56	24.75
		s.e. of mean	0.61	2.17	1.50	2.81	1.37
		$\bar{x}$ ♀	28.60	32.33	31.31	37.14	42.29
		s.e. of mean	0.38	3.91	4.40	4.85	6.51

In TABLE 2 each of the four experiments involved infesting a number of lizards with ticks originating from eggs of a single female. Despite the presumed genetic homogeneity of the ticks, there is considerable heterogeneity between hosts in the mean pre-molt period of ticks. For instance in the third experiment nymphs from the first lizard had a significantly longer mean pre-molt period than those from the other two ($F = 3.66$, $p < .05$). Initial infestation densities varied between hosts in these experiments, but the mean pre-molt periods were not related to density in any predictable way.

TABLE 2 also shows differences between the tick stocks used in the different experiments. A further analysis comparing the mean pre-molt period of a number of our laboratory stocks

TABLE 3

Mean pre-molt period ($\bar{x}$) in days of larvae and nymphs at 25°C from different populations in South Australia. For each locality the latitude is shown, as well as the number of *T. rugosus* hosts used, the number of engorged ticks detaching from those hosts and the mean of standard error of the pre-molt periods for those ticks.

POPULATION	LATITUDE (°S)	ORIGIN OF TICKS	NO. OF HOSTS	LARVAE			NO. OF HOSTS	NYMPHS		
				N	$\bar{x}$	s.e.		N	$\bar{x}$	s.e.
Tickera	33° 44'	Lab Stock	2	378	20.20	0.18				
Tickera	33° 44'	Field	12	824	20.34	0.33	12	79	24.82	0.36
Middle Beach	34° 19'	Lab Stock	1	75	18.61	0.30				
Pt. Gawler	34° 30'	Field	4	198	23.39	0.50				
Pt. Gawler	34° 30'	Lab Stock					4	215	21.35	0.15
Pt. Lincoln	34° 44'	Lab Stock	4	236	17.93	0.18	3	197	25.53	0.26
Halidon	34° 44'	Lab Stock	3	725	17.06	0.08	5	218	29.71	1.24
Coobowie	35° 10'	Lab Stock	2	134	15.63	0.17				
Goolwa	35° 30'	Field	6	452	19.62	0.16	6	57	24.53	0.43
Carpenter Rocks	37° 55'	Lab Stock	2	437	17.82	0.20				

TABLE 4

Mean pre-molt period ($\bar{x}$) in days of larvae at 25°C from a single egg batch which have engorged on different host species. In each case a t-test is used to test the significance of the difference between the larvae on the new host species and the pooled sample from *T. rugosus*

HOST SPECIES		HOST 1	HOST 2	HOST 3
T. rugosus	No. of larvae	50	76	61
	$\bar{x}$ (s.e.)	16.44 (0.23)	16.13 (0.24)	16.43 (0.21)
A. barbatus	N	11	31	
	$\bar{x}$ (s.e.)	20.46 (1.17)	16.87 (0.35)	
	t (signif)	6.72 ($p < .001$)	1.56 (n.s.)	
V. gouldii	N	3	20	
	$\bar{x}$ (s.e.)	16.33 (0.33)	17.60 (0.31)	
	t (signif)	0.02 (n.s.)	3.05 ($p < .005$)	
T. scincoides	N	19	7	
	$\bar{x}$ (s.e.)	18.84 (0.71)	17.86 (0.88)	
	t (signif)	5.31 ($p < .001$)	2.17 ($p < .05$)	

(TABLE 3) shows significant differences between different collecting localities within South Australia. There appears to be a trend for the populations from more southern latitudes (Port Lincoln, Carpenters Rock, Coobowie) to have shorter larval pre-molt periods at 25°C.

In another experiment larvae from a single batch of eggs were divided into nine groups of 150. These were used to infest three *T. rugosus*, two bearded dragon lizards (*Amphibolurus barbatus*), two sand goannas (*Varanus gouldii*) and two southern blue tongue lizards (*Tiliqua scincoides*). The pre-molt period at 25°C of engorged larvae from these nine hosts are shown in TABLE 4.

While the sample sizes were not large for the other host species (due to the low success of larval attachment) the results suggest that larvae feeding on *T. rugosus* had significantly shorter pre-molt periods.

DISCUSSION

The mean pre-molt period of larvae of *A. hydrosauri* at 25°C varied from 15 to 24 days, and for nymphs it varied from 20 to 33 days. These values are usually longer than those reported for other ixodid ticks from mammals (ARTHUR, 1951 ; ARTHUR, 1962 ; FELDMAN-MUHSAM, 1948 ; FELDMAN-MUHSAM and MUHSAM, 1966 ; RANDOLPH, 1975 ; SNOW, 1969), but they are shorter than those reported for two other reptile ticks. It should be noted that in these latter two cases, the report on *Amblyomma geomydae* (NADCHATRAN, 1960) does not specify the conditions used, and the study on *Amblyomma tuberculatum* (COONEY and HAYS, 1972) involves the use of a mammal for the experimental infestation. This makes direct comparisons difficult. If *A. hydrosauri* is representative of the genus *Aponomma*, then no major changes from other genera have occurred in the timing of the molt.

Field observations have indicated that most of the engorgement and detachment activity of this species takes place during the spring and summer months (September-March). Measurements of climatic conditions in lizard refuge sites during this period show that 25°C is within the range of temperature most engorged and detached ticks would experience. The laboratory measurements of pre-molt period at 25°C should provide an estimate of the time taken in natural populations.

There are several factors which can cause variation in the pre-molt period. Changes in the relative humidity of the environment of the detached tick were not investigated. It has been shown in other studies (SNOW, 1969 ; BRANAGAN, 1973) that humidity levels have little influence over the rates of tick development. Temperature on the other hand has a major influence. Increasing the temperature leads to a shortening of the pre-molt period. This result has been reported for a number of other species (e. g. ARTHUR, 1951 ; COONEY and HAYS, 1972 ; SNOW, 1969).

The time taken to engorge and the final engorgement weight do not appear to influence the pre-molt period of nymphs or larvae of *A. hydrosauri*. This is opposite to the positive correlation between engorgement weight and pre-molt period reported by HAJJAR (1972) for nymphs of two species of *Hyalomma*.

Where sexual differences in pre-molt period were observed in *A. hydrosauri* the nymphs changing to females took longest. Differences between sexes have been previously reported although the faster sex is different in different species (HAJJAR, 1972 ; FELDMAN-MUHSAM and MUHSAM, 1966).

The variability in pre-molt periods between ticks engorging on different hosts of the same species may result from different hosts having different levels of resistance. WAGLAND (1975) showed that the rate of development of *Boophilus microplus* is retarded when it is feeding on cattle with induced resistance.

A. hydrosauri larvae have a shorter pre-molt period when they have engorged on *T. rugosus* than when feeding on any of three alternative reptile hosts. The species has been collected attached to a large number of reptile species (ROBERTS, 1970 ; SMYTH, 1973). However our personal field observations suggest that the sleepy lizard *T. rugosus* is the most common host species, the most commonly infested host species and the host species with the highest densities of infestation. Perhaps *A. hydrosauri* has adapted its development processes to *T. rugosus*, and it cannot develop as fast after feeding on different host species. A similar effect was shown by FELDMAN-MUHSAM and MUHSAM (1966) for *Hyalomma dromedarii*, and BRANAGAN (1974) suggests that some host species are less suitable than others for the feeding of *Rhipicephalus appendiculatus*.

There have only been few studies on variability between populations of a single species of tick (THOMAS, 1968 ; GREGSON, 1971 ; PAPERNA and GILADI, 1974 ; BULL and SARA, 1976), but it is to be expected from other animal and plant studies that *A. hydrosauri* will show genetic differences between populations, reflecting local adaptations. The variation in the pre-molt period between populations may be one such case.

ACKNOWLEDGEMENTS

Beverley Jones and David MARTIN provided technical assistance at various stages of the investigation.

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Appendix 5

The following is a copy of:

Bull, C.M. & Sharrad, R.D. (1980). The population structure of an Australian reptile tick, *Aponomma hydrosauri* (Acari: Ixodidae). II. Seasonal dynamics in experimental enclosures. J. Aust. Entomol. Soc., (in press).

This paper reports, in part, on the data discussed in 3.33. It also presents additional information which is referred to in 3.312.

SEASONAL ACTIVITY OF THE REPTILE TICK, *APONOMMA HYDROSAURI* (DENNY) (ACARI:IXODIDAE) IN EXPERIMENTAL ENCLOSURES

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Abstract

In two enclosures near Adelaide, South Australia, the reptile tick, *Aponomma hydrosauri*, was reared on the lizard *Trachydosaurus rugosus*. Ticks went through one and three complete life cycles in 18 and 26 months, respectively. Feeding activity continued six months of the year but activity stopped during the cooler months of April to September.

Introduction

A knowledge of the changes in abundance in different seasons is important in the study of any population. In populations of the Australian reptile tick, *Aponomma hydrosauri* (Denny) (Acari:Ixodidae), we have studied dispersal and genetic structure (Bull and Sara 1976), the non-random patterns of host infestation (Sharrad 1977, Bull 1978), and the geographic distribution, which abuts with but does not overlap those of other reptile ticks in South Australia (Smyth 1973, Bull and Smyth 1973, Sharrad 1977). We needed information about seasonal changes in the tick population to incorporate into models which might be used to explain our previous observations.

In most studies of tick populations the host populations are randomly sampled throughout the year and the seasonal dynamics recorded from these samples (Randolph 1975, Clifford *et al.*, 1976, MacLeod *et al.*, 1977, Patrick and Hair 1977). For *A. hydrosauri* this approach is inadequate because large samples of the hosts are available only in spring and early summer (Sharrad 1977). Further, with infestation patterns being heterogeneous between individual hosts (Bull 1978), small host samples may give biased estimates of infestation levels in the whole host population at the time of the sample. To overcome this problem we enclosed small sub-samples of the host population and scored the numbers of ticks attached to each host on each sampling date. In this way the entire population of attached ticks in one area could be monitored.

This paper reports the seasonal changes in infestation of *A. hydrosauri* observed on enclosed populations of the sleepy lizard *Trachydosaurus rugosus* Grey.

Materials and Methods

Enclosures were constructed from sheets of flat galvanised iron, formed into a circle, with the bottom edge of the iron buried 15 cm under the soil surface and the walls supported by steel or wooden stakes. The first enclosure (10 m circumference; 45 cm wall height) was built near Pt. Gawler (40 km north of Adelaide, South Australia) in Sept. 1970, on grazed open grassland with a low scrub dominated by *Olearia axillaris* and *Acacia ligulata*. In Jan. 1975 a second enclosure (20 m circumference; 75 cm wall height) was built on the southern edge of the Flinders University campus (10 km south of Adelaide), an unused area of grassland and olive bushes (*Olea europea*).

The sleepy lizard *T. rugosus* is the most common host for all three stages of *A. hydrosauri* (Roberts 1970, Smyth 1973, Sharrad 1977). At both experimental sites *T. rugosus* occurred naturally, and were commonly infested with *A. hydrosauri*. Both experiments were started at a time when engorged females were laying eggs in natural populations.

In the first experiment four tick free *T. rugosus* were each exposed in the laboratory to 400 unfed larval *A. hydrosauri*, and then introduced into the enclosure on 30th March, 1971. This experiment ended on 15th Sept. 1972 when the enclosure was found destroyed by vandals or strong cows. The second experiment started on 29th Jan. 1975 with three *T. rugosus* each previously exposed in the laboratory to 200 unfed larval ticks. The number of lizards in the enclosure varied from three to six during this second experiment and occasional dead or missing lizards were replaced within a week. Observations were continued until 2nd May, 1977.

Both enclosures included low bush and grass clump refuge sites for lizards as well as sheets of corrugated iron. They were visited each week to record the number and instar of *A. hydrosauri* attached to each host and the proportions of these that were engorging.

Results

The total number of ticks of each instar that were attached to lizards in each enclosure at each observation time are shown in Fig. 1 and Fig. 2. The percentages of attached larvae and nymphs which were engorging at each observation date during the second experiment are shown in Fig. 3. Mean monthly maximum and minimum temperatures for Adelaide (Fig. 4) indicate the prevailing climatic conditions.

The two experiments showed similar seasonal changes in the pattern of abundance of each instar. In the first experiment, of 18 months, the tick population developed through one complete life cycle from larvae to adults and then to the next generation of larvae. (Fig. 1). The larvae which were initially attached to the lizards engorged and detached during autumn (up to May 1971). Some more larvae attached during the winter and early spring (July - Sept. 1971). Presumeably these had been present in the enclosure before the experiment. Over the same period (June - Sept. 1971) nymphs attached. From Sept. 1971 to Jan. 1972 the number of attached larvae declined because they were engorging and detaching from their hosts. By Jan. 1972 no larvae were left on the lizards and no new larvae attached until the following spring (Sept. 1972). The attached nymphs also engorged and detached during spring and summer (Sept. 1971 - Feb. 1972) until none were left on the lizards by the end of Feb. 1972. After the nymphs had started to detach adult ticks appeared on the lizards for the first time (Dec. 1971). Females engorged and detached during summer and autumn (Feb. - May 1972). The larvae which were probably the progeny of these females, first attached to the lizards in the following spring (Aug. - Sept. 1972).

The second experiment was followed for 26 months and by the end of this time there appeared to be some generation overlap in the tick population. There were some changes in the lizard population which had major consequences on the size of the attached tick population. Most significant were the theft of all lizards on 19th May, 1976 the death on 4th Feb. 1976 of a lizard which was the host of 78 adult ticks, and the loss on 22nd Feb. 1976 of a lizard with 262 larvae attached. These losses did not affect information concerning attachment and detachment activity.

Many of the larvae initially attached to the lizards in this experiment Fig. 2,3) engorged and detached during the summer and autumn (Feb-March 1975). The first nymphs attached to the lizards in early autumn (March-May 1975), but most remained without engorging until the following spring (Oct 1975). Some larvae also remained attached but unengorged during the winter. Larval numbers increased again from Aug. 1975. Larval engorgement became increasingly frequent after Oct 1975 and until mid-summer (Dec. 1975) by when all attached larvae had dropped from their hosts. Nymphs started to engorge in spring (October 1975) and continued to have a high engorgement rate until late summer (Feb. 1976) when they had also all detached.

Meanwhile, following nymph engorgement and detachment in spring, adults started to attach to lizards during summer and autumn (Jan-March 1976). Adult numbers declined in April 1976 partly from a high detachment rate of mated, engorged females, but also because of predation on attached ticks, probably by mice.

The second generation of larvae in the enclosure started to attach in autumn (Feb-May 1976). Some of these engorged and detached quickly and nymphs appeared on the hosts in late autumn (April-May 1976). In the 1976 winter, after April, attached larvae and nymphs did not engorge and only a few new ticks attached. Then in mid August there was a large increase in attached larvae, although subsequent engorgement and detachment of larvae only became common in late spring (Nov. 1976). Shortly after this the number of attaching nymphs increased (Dec. 1976). Larvae continued to engorge and detach until none were left on the hosts in mid summer (Jan. 1977). Nymphs continued to engorge and detach until the end of March 1977, by when their numbers on the hosts had also declined.

The adult ticks present in low numbers on lizards in the late winter (July -August 1976) must still have been of the first generation. (No second generation nymphs had yet detached). Their detachment and egg laying in spring (Oct.-Nov. 1976) would have contributed to the increase in larvae at this time. Those larvae were still part of the second generation. Second generation adults were probably attaching in early summer (Nov.-Dec. 1976) after early nymph detachments. They probably made up a major fraction of the rising numbers of adults attaching and engorging in late summer and autumn (Jan-April 1977). At least some of the larvae which appeared in increasing numbers in summer and autumn (Jan-April 1977) and the increased numbers of nymphs (March-April 1977) would have been of the third generation in the enclosure.

Observations in the second experiment were stopped in May 1977. All lizards were removed from the enclosure by August 1977. In February 1978 three further lizards were put into the enclosure and within one week they had become infested with 291 larvae, four nymphs, 11 males and 11 females.

Discussion

In the enclosures the tick populations had an active phase of attachment and engorgement during the warmer months (generally October to March) when there was rapid progress through the life cycle. For instance ticks which were larvae in spring 1976 developed to adults and their progeny reached the nymphs stage by autumn 1977. The populations also had an inactive phase in the cooler months (generally April to September) when tick development stopped temporarily. During this time attachment and engorgement were infrequent. Some ticks spent the non-feeding winter period attached to their hosts. Many larvae and nymphs did this during the 1971 and 1975 winters, only starting engorgement in the following springs. Other ticks spent the winter off the host. When all lizards were stolen in May 1976, only a few ticks attached to the replacement lizards over the following winter. The many larvae which attached in the next spring most have overwintered on the ground, either as eggs or unfed larvae.

Although a winter diapause has been found in some tick species (Belozerov and Lamanova 1967, Immler 1973), it is more likely that *A. hydrosauri* development is controlled by temperature through its influence on host behaviour. In the enclosures weekly records showed that the lizards moved very little during the winter, staying for long periods in single refuge sites. There was little opportunity for ticks waiting elsewhere in the enclosures to contact the host and attach. Furthermore hosts overwintering in refuge sites would have low body temperatures and metabolic rates. Ticks may require some minimum host temperature or rate of blood circulation before feeding is possible. Reptile ticks have seasonal constraints on development which may not be experienced by ticks which feed on homeotherms.

A. hydrosauri can also spend long periods off their hosts during the active season. The population in the enclosure survived the 1977-1978 summer without any hosts to feed on for most of that period. The persistence of a population does not depend on the immediate availability of hosts, even in the period of the year when ticks are most active. The time that ticks can survive without hosts in the field would be influenced by the availability of suitable micro-habitat In laboratory conditions unfed ticks can be kept alive for up to two years.

The experimental enclosures probably represented ideal conditions for the growth of tick populations because of the density of lizards with enforced small ranges of activity. This would increase the chance of a tick quickly finding its next host and could speed the passage through the life cycle and allow more generations per year than in a natural population with fewer lizards.

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FIG. 1 Numbers of *A. hydrosauri* larvae (open circles), nymphs (closed circles), females (open triangles) and males (closed triangles) attached to lizards during the first experiment, from April 1971 to Sept. 1972.

FIG. 2 Numbers of *A. hydrosauri* larvae (open circles), nymphs (closed circles), females (open triangles) and males (closed triangles) attached to lizards during the second experiment, from Feb. 1975 to April 1977.

FIG. 3 Percentage of attached *A. hydrosauri* larvae (open circles) and nymphs (closed circles) engorging on lizards in the second experiment. The arrows and the numbers above them indicate when engorged females detached, and how many did so.

FIG. 4 Monthly average maximum (open circles) and minimum (closed circles) temperature for Adelaide; from: Australia:Bureau of Meteorology (1975).

FIG 1

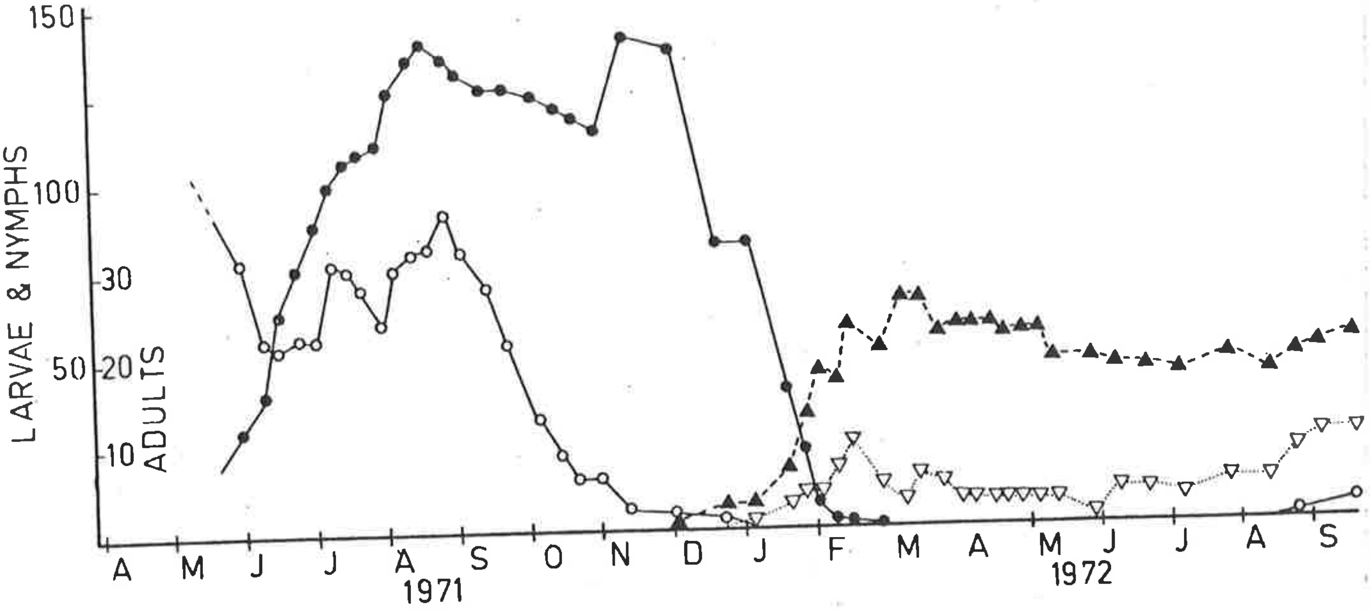
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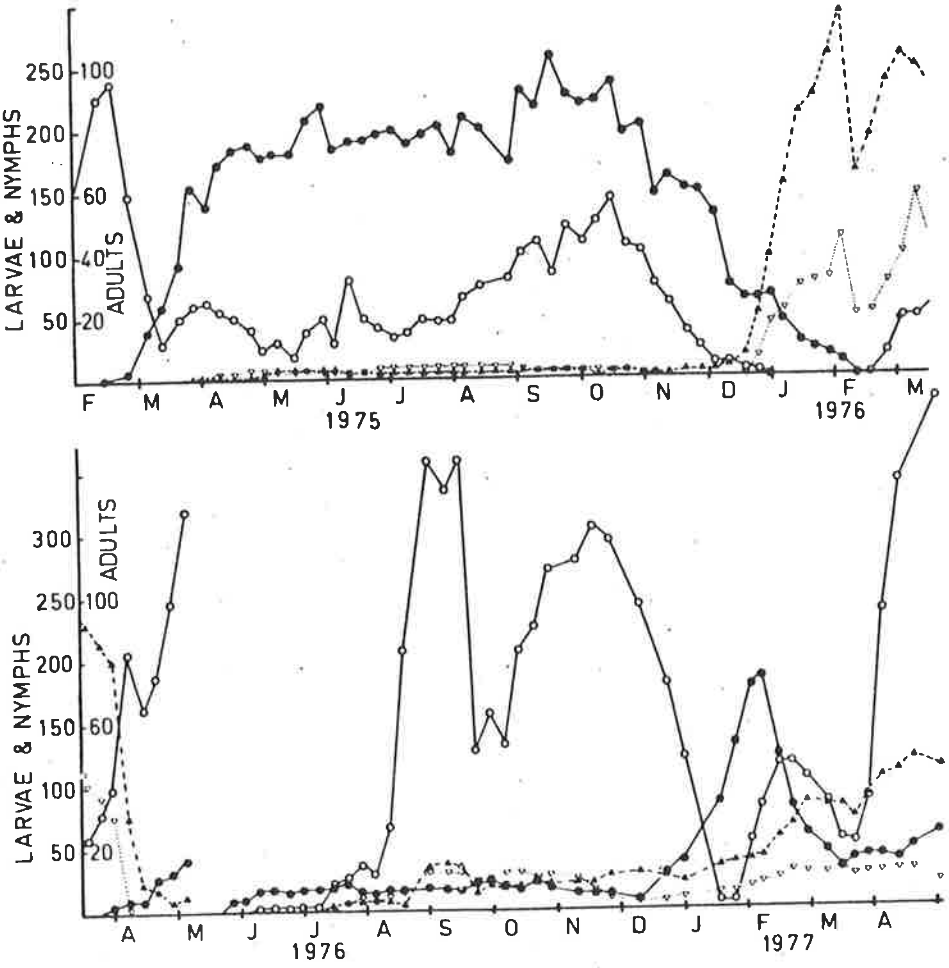
FIG 2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LARVAE & NYMPHS
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ADULTS
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FIG 3

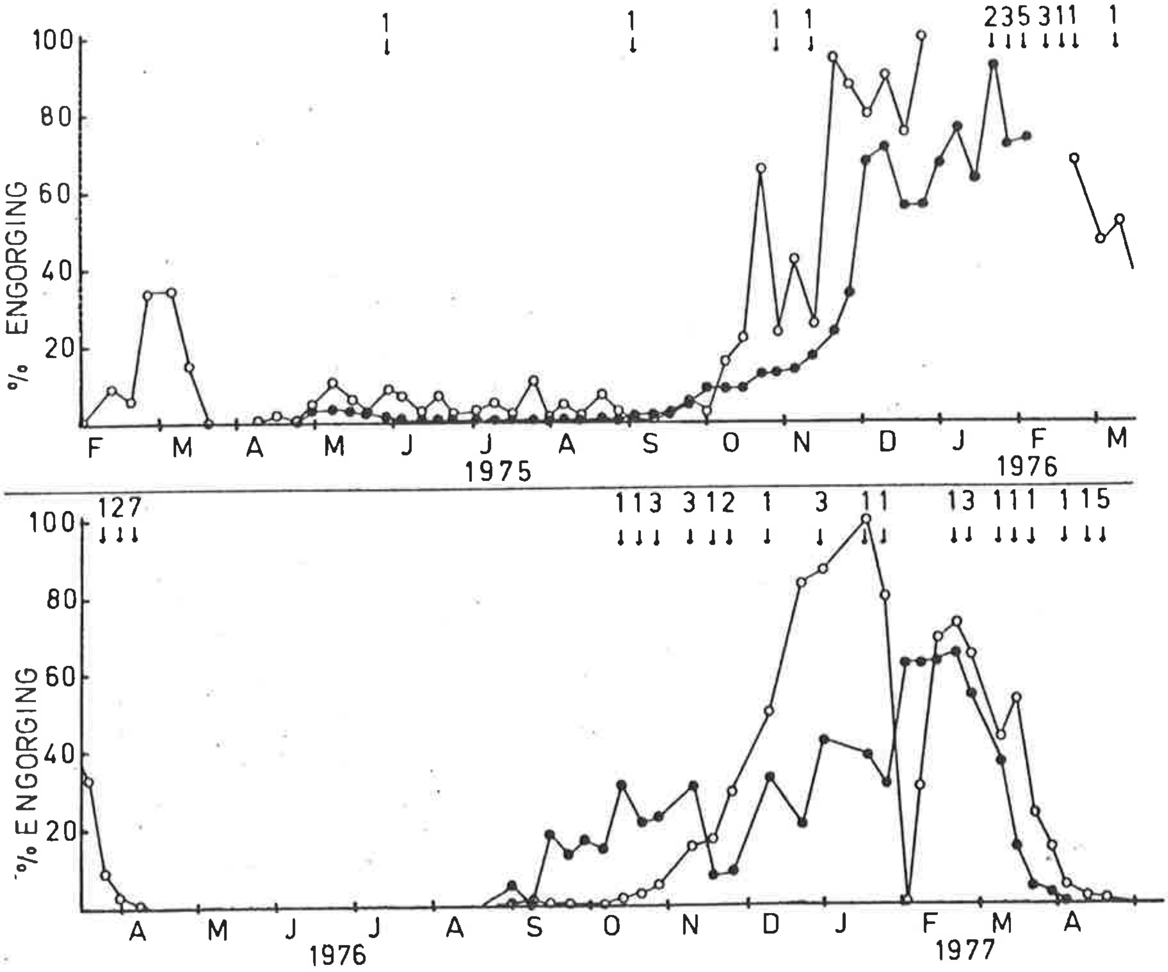
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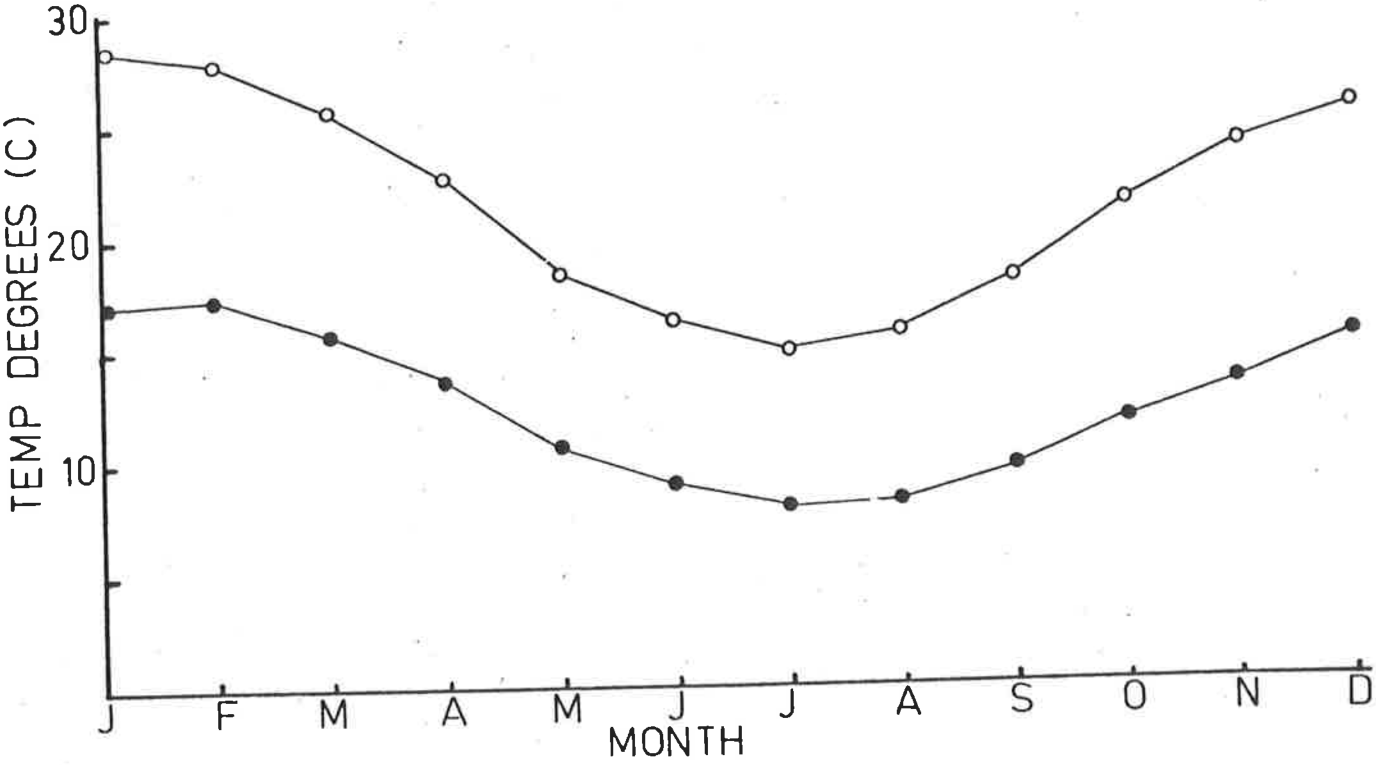
FIG 4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TEMP DEGREES (C)
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Appendix 6.

The following is a draft copy of:

Sharrad, R.D. & King, D.R. (1980). The geographical distribution of reptile ticks in western Australia. Submitted to Aust. J. Zool.

The information provided in this paper is referred to extensively in Chapter 2.

THE GEOGRAPHICAL DISTRIBUTION OF REPTILE TICKS IN WESTERN AUSTRALIA

by

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ABSTRACT

In a study of ticks which parasitize reptiles in the western half of Australia, eight species were identified including two undescribed ticks. The data confirm that three species, *Amblyomma albolimbatum, Amb. limbatum* and *Aponomma hydrosauri*, have distributions which abut with very little overlap (i.e. they are parapatric). *Ap. fimbriatum* is sympatric with *Amb. albolimbatum* and *Ap. hydrosauri*. The other ticks identified, *Ap. sp. nov., Amb. sp. nov., Amb. calabyi* and *Ornithodorus gurneyi*, were not found in sufficient numbers to allow mapping of their distributions.

Data are also presented on the hosts of the ticks and on the occurrence of ticks on islands off the Western Australian coast.

I. INTRODUCTION

Smyth (1973) made a detailed study of the geographical distributions of three species of reptile ticks, *Aponomma hydrosauri, Amblyomma albolimbatum* and *Amblyomma limbatum,* in South Australia. He found that wherever any two of the three species contact they abut and overlap very little along long boundaries, i.e. they are parapatric. In some cases the boundaries are associated with marked ecotones (Sharrad, 1979) and it may be hypothesized that the distributions of the ticks are limited at these because in a very short distance environmental conditions become inimical. However, Smyth's (1973) observation that west of Spencer Gulf, where all three species are present, *Ap. hydrosauri* and *Amb. limbatum* are separated by a broad band of *Amb. albolimbatum* while east of Spencer Gulf where *Amb. albolimbatum* does not occur these two species are in contact, gives some support to the hypothesis that the boundaries may be the results of some interaction(s) between the species.

The ticks are distributed widely in Australia and all three occur in the western half of the continent. We addressed ourselves to discovering whether parapatry is the general condition for these ticks and to the examination of related species to see if similar patterns exist.

II. MATERIALS AND METHODS:

The data used to compile the maps and tables below come from three sources.

1. Live lizards and snakes from known localities were examined for ticks which were removed and preserved in 70% alcohol, as voucher specimens. Ticks were identified by the taxonomic keys of Roberts (1969, 1970). In some cases it was virtually impossible to assign specimens, particularly larvae and sometimes nymphs, to a particular species although one could recognize their generic affinities. Where the ticks on a host were thus only partly classified they were listed under the generic label as an undetermined species. These should not be confused with two

species which we recognized as undescribed species - these have been classified as "sp. nov.".

2. Ticks found attached to reptiles preserved in the Western Australian Museum's collection, were examined and identified. They have been placed in the Arachnology collection of the Western Australian Museum.

3. Earlier distribution data had been compiled by Smyth (1973).

III. RESULTS:

Eight tick species were identified including two undescribed, but readily distinguishable, ticks one an *Aponomma* and the other an *Amblyomma*. These ticks and the hosts which they had parasitized are shown in Table 1.

The geographical distributions of *Amb. albolimbatum* and *Amb. limbatum* are shown in Figure 1. *Amb. limbatum* occurs widely in semi-arid, arid and tropical Australia while *Amb. albolimbatum* is confined to the south-west. The tick's distributions do not overlap, however, there is insufficient data to confirm that they contact.

TABLE 1

A list of ticks and their reptilian hosts recorded from Western Australia

TICK SPP HOST SPP	Amblyomma albolimbatum	Amb. calabyi	Amb. limbatum	Amb. sp?	Amb. sp. nov.	Aponomma fimbriatum	Ap. hydrosauri	Ap. sp. nov.	Ornithodorus gurneyi
Agamidae									
Moloch horridus	1								
Chlamydosaurus kingii				1					
Scincidae									
Egernia multiscutata	1								
Tiliqua multifasciata	1		1						
T. occipitales	2								
T. rugosa	228		10				83		2
T. scincoides			6		1				
Varanidae									
Varanus acanthurus			7						
V. glebopalma			2	1				6	
V. gouldii		1	16			28			
V. panoptes			1						
V. pilbarensis				1					
V. semiremex mitchelli			2						
V. timorensis			4						
V. timorensis glauerti			2					2	
V. timorensis orientalis			1						
V. timorensis scalaris			1						
V. tristis			3			1			
V. tristis centralis			1						
V. tristis orientalis			4						

TICK SPP HOST SPP	Amblyomma albolimbatum	Amb. calabyi	Amb. limbatum	Amb. sp?	Amb. sp. nov.	Aponomma fimbriatum	Ap. hydrosauri	Ap. sp. nov.	Ornithodorus gurneyi
Boidae									
Aspidites melanocephalus			1			1			
A. ramsayi						1			
Liasis childreni			2						
L. olivaceus				2					
Python spilotes	2		1						
Colubridae									
Boida irregularis			13						
Dendrelaphis punctualatus			7	5					
Elapidae									
Acanthophis antarcticus			2						
Demansia affinis						1			
D. nuchalis						1			
Notechis ater	1					1			
Pseudechis australis			4	1					

Ap. hydrosauri occupies only small portions of the south-western corner of Western Australia. Figure 2 shows that there are at least two and possibly more disjunct populations of the tick surrounded by the more widely spread *Amb. albolimbatum*. These species are parapatric in the Cape Naturaliste area (Figure 3) and are probably similarly related in the Albany-Bremer Bay areas.

Figure 4 contains distribution data on *Ap. fimbriatum* and *Ap. sp. nov.* which are the only ticks, other than those above, which were found in sufficient numbers to enable analysis. *Ap. fimbriatum* is common on snakes and goannas in the south west and is sympatric with *Ap. hydrosauri* and *Amb. albolimbatum*. *Ap. sp. nov.* is probably restricted to two goanna species in the north west and is sympatric with *Amb. limbatum* but much more restricted in range.

Ticks have been identified from hosts found on islands off the western coast of Australia. Table 2 lists these and the time of separation of some of these islands from the mainland as this gives minimum times for the occurrence of the ticks on the adjacent mainland.

IV. DISCUSSION:

(a) Factors which may limit the range of ticks

The distributions of tick species have often been shown to correlate broadly with vegetation and soil type. This pattern has been noted in many parts of the World; in Russia (Brovko, 1966; Drozdova and Sapegina, 1965; Popova et al, 1966; Subotnik, 1956), in North America (Semtner et al, 1971), in Scandinavia (Ohman, 1961) and in South Africa (Theiler, 1964). The reason for such correlations was clearly demonstrated by Milne (1944) in a study of the sheep tick, *Ixodes ricinus*, in the north of England. He showed that the nature of the microhabitat of the tick while off the host was crucial in that it was at this stage, of their life cycle, that they were most vulnerable to dessication, starvation or extremes of temperature. The two factors, temperature and humidity, are perhaps the most important climatic factors influencing tick development and, thus, distribution (Arthur, 1962). These factors may vary with variations in soil type and vegetation thus the correlation with tick distribution limits.

The area under consideration is huge and is subject to widely different climatic conditions. The south western corner of Australia has an extreme Mediterranean climate characterized by cool wet winters and hot very dry summers. Summer ambient temperatures frequently exceed 40°C in much of this area and little or no effective rainfall is recorded from December to April in most years (Australia: Bureau of Meteorology, 1975). Much of the central region of Western Australia is arid and has low and irregular rainfall with great variation from year to year. Winter temperatures are generally low and summer temperatures are often very high (Australia: Bureau of Meteorology, 1975). North western Australia has a monsoonal pattern of rainfall with a pronounced "wet season" from November to April, when temperatures and rainfall are both high, and a relatively mild "dry season" during the remainder of the year. The annual isotherms and annual evaporation for the western half of Australia are shown in Figure 5, and rainfall isohytes are shown in Figures 1-3.

TABLE 2

The Occurrence of Reptile Ticks On Islands Off Western Australia

The numbers in brackets are the approximate times (in years before present) that these islands have been separated from the mainland. These data are from Abbott (1978).

ISLAND	TICK SPECIES	HOSTS
Barrow	Amblyomma limbatum	Varanus acanthurus
Bernier (8,000)	Amblyomma albolimbatum	Tiliqua rugosa
	Amblyomma limbatum	Varanus gouldii
Boongaroo (Prince Frederick Harbour)	Aponomma sp. nov.	Varanus glebopalma
Byam Martin (Bonaparte Arch.)	Aponomma sp. nov.	Varanus glebopalma
Dirk Hartog (6,000)	Amblyomma albolimbatum	Tiliqua rugosa
Dorre	Amblyomma albolimbatum	Tiliqua rugosa
Heywood (largest) (Bonaparte Arch.)	Aponomma sp. nov.	Varanus timorensis glauerti
Koolan	Aponomma sp. nov.	Varanus glebopalma

ISLAND	TICK SPECIES	HOSTS
Lowendal	Amblyomma limbatum	Not known
Mondrain (Recherche Arch.) (12,000)	Amblyomma albolimbatum	Tiliqua rugosa
North Twin Peaks (Recherche Arch.)	Amblyomma albolimbatum	Tiliqua rugosa
Rottnest (7,000)	Amblyomma albolimbatum	Tiliqua rugosa
Sir Graham Moore (Bonaparte Arch.)	Amblyomma limbatum	Varanus acanthurus
South Mation	Amblyomma limbatum	Varanus acanthurus
South West Osborne	Amblyomma limbatum	Varanus timorensis glauerti
West Wallabi (12,000)	Amblyomma albolimbatum	Python spilotes

Apart fron changes in climatic factors (temperature and humidity) other factors in the environment of a tick might limit its range. These might include the availability of suitable hosts. Ultimately the distribution of ticks is limited by that of their hosts however, some ticks infest a number of species so that the range of the parasite might exceed the range of a particular host species.

In the case of ticks with parapatric boundaries the possibility that interspecific interactions might be important in determining the position of the boundary and the degree of overlap, must be considered. However, no such mechanism has yet been uncovered in these animals.

(b) DISTRIBUTION PATTERNS:

(i) *Aponomma hydrosauri*

There are two striking features of the distribution of this tick in south western Australia (Figs. 2 and 3). The first is that it and *Amb. albolimbatum* are parapatric as they are on Eyre Peninsula in South Australia (Smyth, 1973). The second feature is that it is confined to small areas of higher average rainfall than those in which it occurs in south eastern Australia (Smyth, 1973). It is pertinent here to note that Bull and Smyth (1973) show that *Ap. hydrosauri* is less able to withstand desiccation than *Amb. albolimbatum*. This physiological limitation and the fact that the summers in south western Australia are relatively long and dry, compared with the south east (Australia: Bureau of Meteorology, 1975), may well be important in limiting the size of these relict *Ap. hydrosauri* populations. However, the marked parapatric boundary of this tick with *Amb. albolimbatum* requires that the possibility be considered of competitive interactions playing a role in determining the present distribution.

(ii) *Amblyomma albolimbatum* and *Amblyomma limbatum*

The distributions of *Amb. limbatum* and *Amb. albolimbatum* in western Australia are generally in agreement with those reported by Smyth (1973) for this region. *Amb. albolimbatum* forms parapatric boundaries with *Ap. hydrosauri* and may also with *Amb. limbatum* but additional data are necessary to confirm this. Bull and Smyth (1973) demonstrated that *Amb. albolimbatum* is in many ways more resistant to long periods of desiccation than *Amb. limbatum*. This observation seems at odds with the observed geographical range of the ticks in that *Amb. limbatum* occupies regions which are apparently more arid. However, we do not know whether or not the boundary between the ticks is stationary.

(iii) *Aponomma fimbriatum*

It is intriguing to note that this tick appears to be absent from the north western portion of Australia. It does inhabit the north east of Australia and parts of the Northern Territory (Roberts, 1970). This gap in its range is unlikely to be due to a scarcity of appropriate hosts as in the south west, *Ap. fimbriatum* infests snakes and a goanna (*Varanus gouldii*) which also occur in the northern areas.

(iv) *Aponomma sp. nov.*

This tick has been found only on *V. glebopalma* and *V. timorensis glauerti* and seems to be restricted to the Kimberly region of Western Australia and northern parts of Northern Territory where these occur.

(v) *Amblyomma sp. nov., Amblyomma calabyi* and *Ornithodorx gurneyi*

Few specimens of these species have been found and no accurate account can be given of their distributions. *Amb. sp. nov.* has been found only once; attached to a blue-tongue lizard, *Tiliqua scincoides*, near Derby. *Amb. calabyi* may well be wide spread in central Australia and had previously only been reported from *Varanus giganteus*. It has now been collected from *V. gouldii*. *O. gurneyi* is primarily a mammal tick although it has previously been found on *T. rugosa* (Sharrad, 1979).

(c) PAST DISTRIBUTIONS OF THE TICKS:

The existence of at least two (possibly more) apparently separate populations of *Ap. hydrosauri* in south western Australia and their extensive distribution in south eastern Australia (including Tasmania) suggests that the distribution was much more extensive in the past. Whether the diminished distribution of the species has resulted from changes in sea-level and submergence of parts of their former range and/or from unsuccessful competition with *Amb. albolimbatum* can not be determined.

The present distribution of *Amb. albolimbatum* is most readily explained if it is considered that this species originated in south western Australia and has subsequently spread eastwards to Eyre Peninsula (as suggested by Bull, 1969). The fact that it does not occur in the south east of Australia and that it occurs north of *Ap. hydrosauri* in the south west suggest that *Ap. hydrosauri* occupied a southern band of Australia stretching from east to west before *Amb. albolimbatum* began to spread towards the east.

The relationship between the morphologically similar but distinct species *Amb. albolimbatum* and *Amb. limbatum* is of potential interest to evolutionary researchers. The ticks are found on islands off the coast whose time of separation from the mainland can be assessed, and on at least one such island (Bernier Island) both species occur. Thus some idea may be gained of past movements, if any, of the boundary between the ticks. If the boundary between them proves to be truly parapatric, it will be of interest to determine whether it is an example of primary or secondary contact and whether these closely related ticks hybridize.

(d) INTRA SPECIFIC VARIATION:

Our investigations revealed considerable morphological variability within species. This was particularly noticeable in *Amb. limbatum* where the degree of body ornamentation, body size and shape of ticks varied between locations.

In some areas of the north west, specimens of this species were very small when compared to southern ticks and the size range of adult males lay outside that described by Roberts (1970). In addition, some ticks, eventually designated as *Amb. limbatum*, closely resembled *Amb. moreliae*. We anticipate that a close investigation of *Amb. limbatum* and its close relatives may result in the identification of a number of readily distinguished sub species or species.

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Fig. 1 Records of *Amb. albolimbatum* (○) and *Amb. limbatum* (■) in western Australia.

Rainfall isohyets are also shown (—— 200mm ——).

Fig. 2 Records of *Amb. albolimbatum* (▲) and *Ap. hydrosauri* (●) in south western Australia.

Rainfall isohyets are also shown (—— 200mm ——).

Fig. 3 Records of *Amb. albolimbatum* (○) and *Ap. hydrosauri* (●) in the Cape Naturaliste area of south western Australia.

Fig. 4 Records of *Ap. fimbriatum* (■), *Ap. sp. nov.* (●), *Amb. sp. nov.* (◉) and *Amb. calabyi* (▲) in western Australia.

Fig. 5 The average annual isotherms (----°C-----) and average annual evaporation (——mm——) in western Australia.

FIG. 1

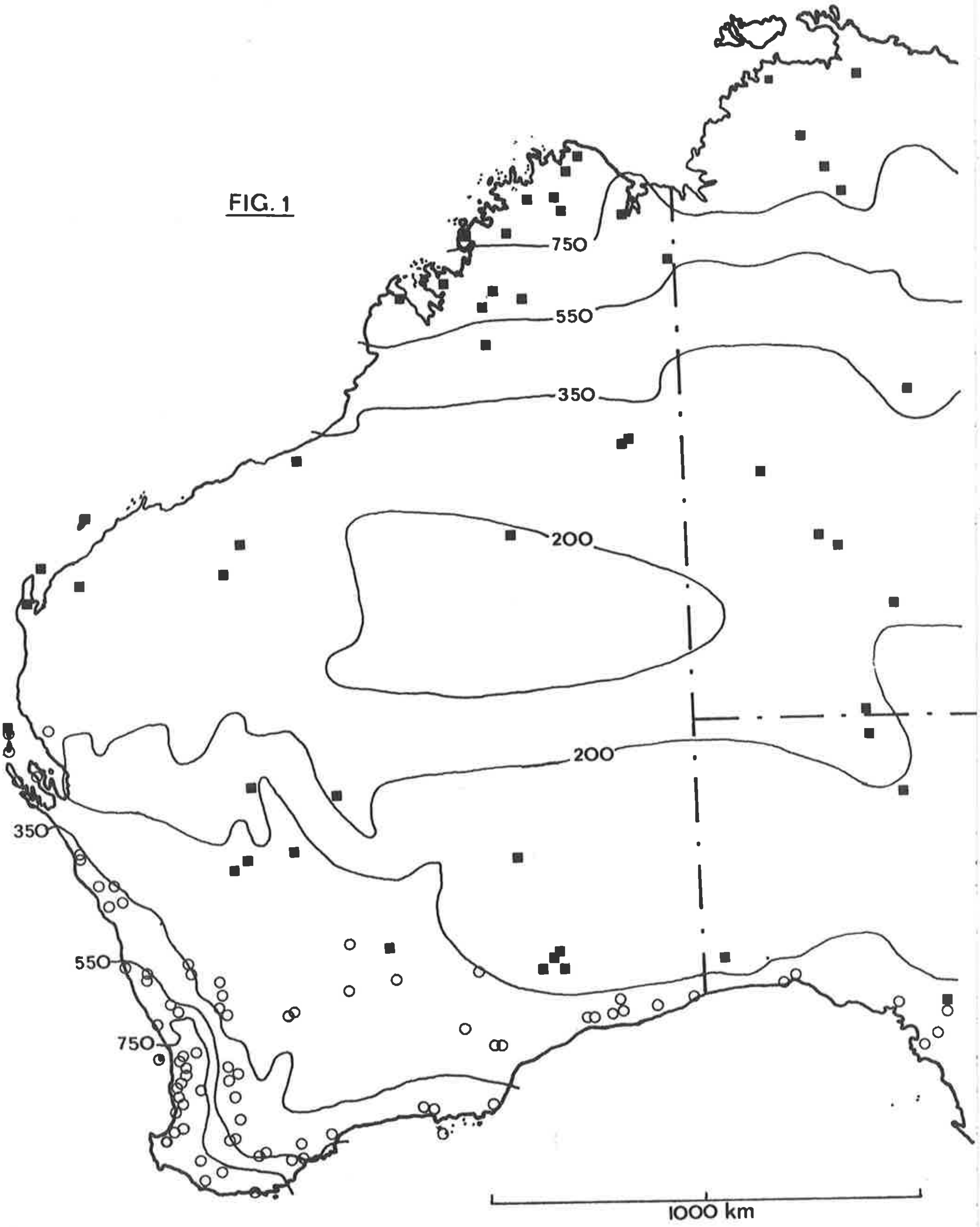


FIG. 2

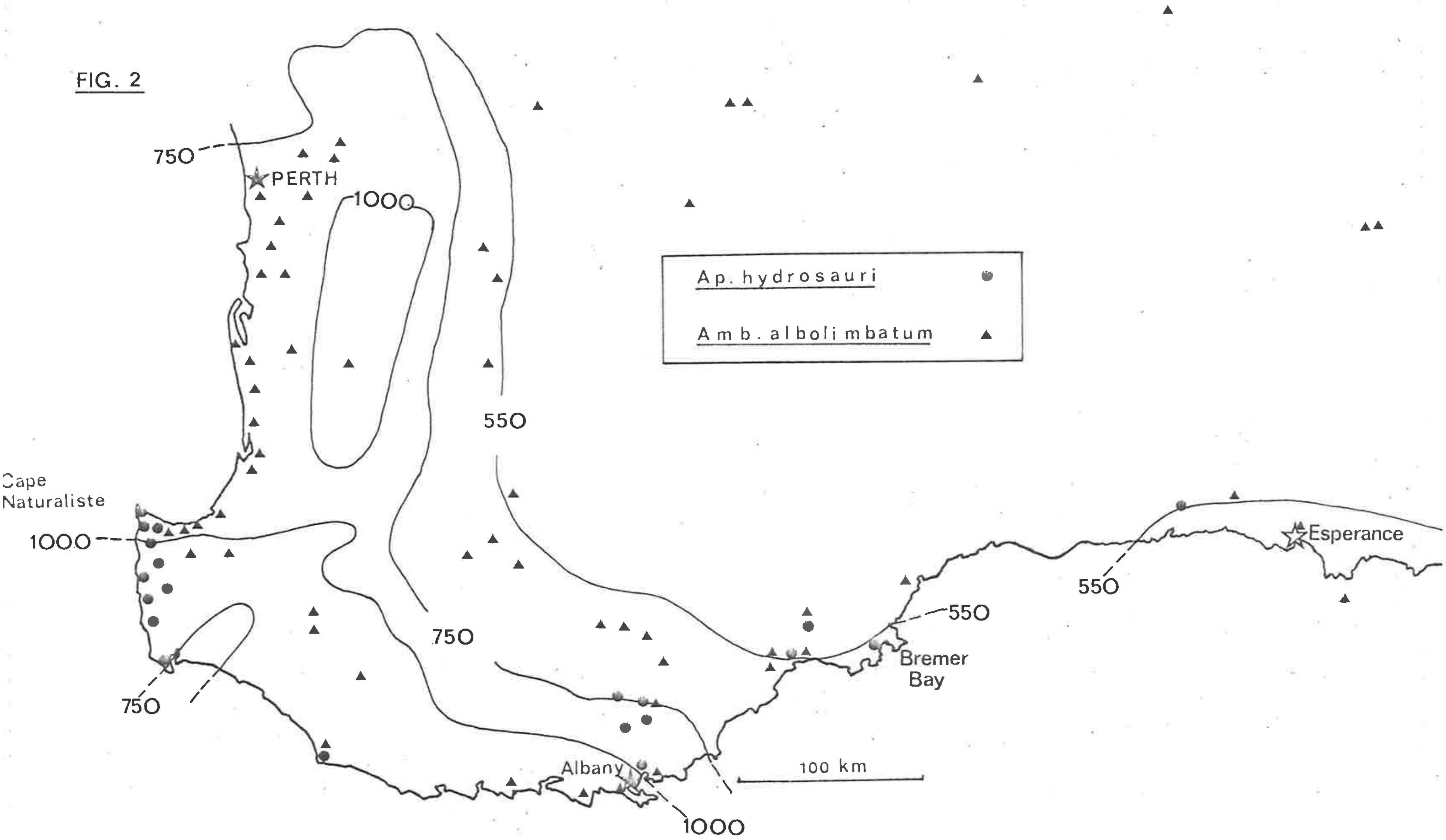

Ap. hydrosauri ●
Amb. alboli mbatum ▲
PERTH
Cape
Naturaliste
Albany
Bremer
Bay
Esperance
750
1000
550
750
1000
750
550
550
1000
100 km

FIG. 3

FIG. 4

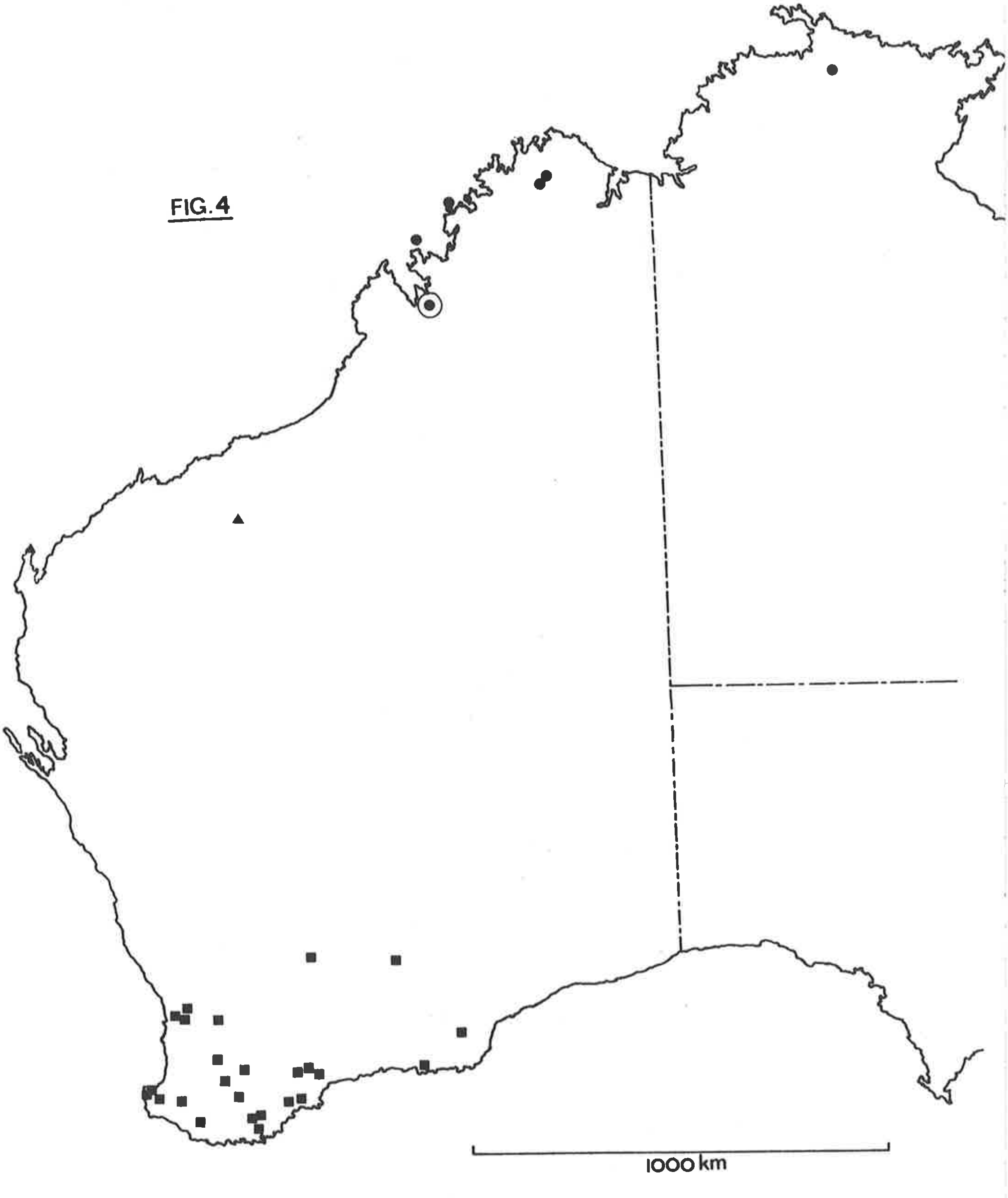
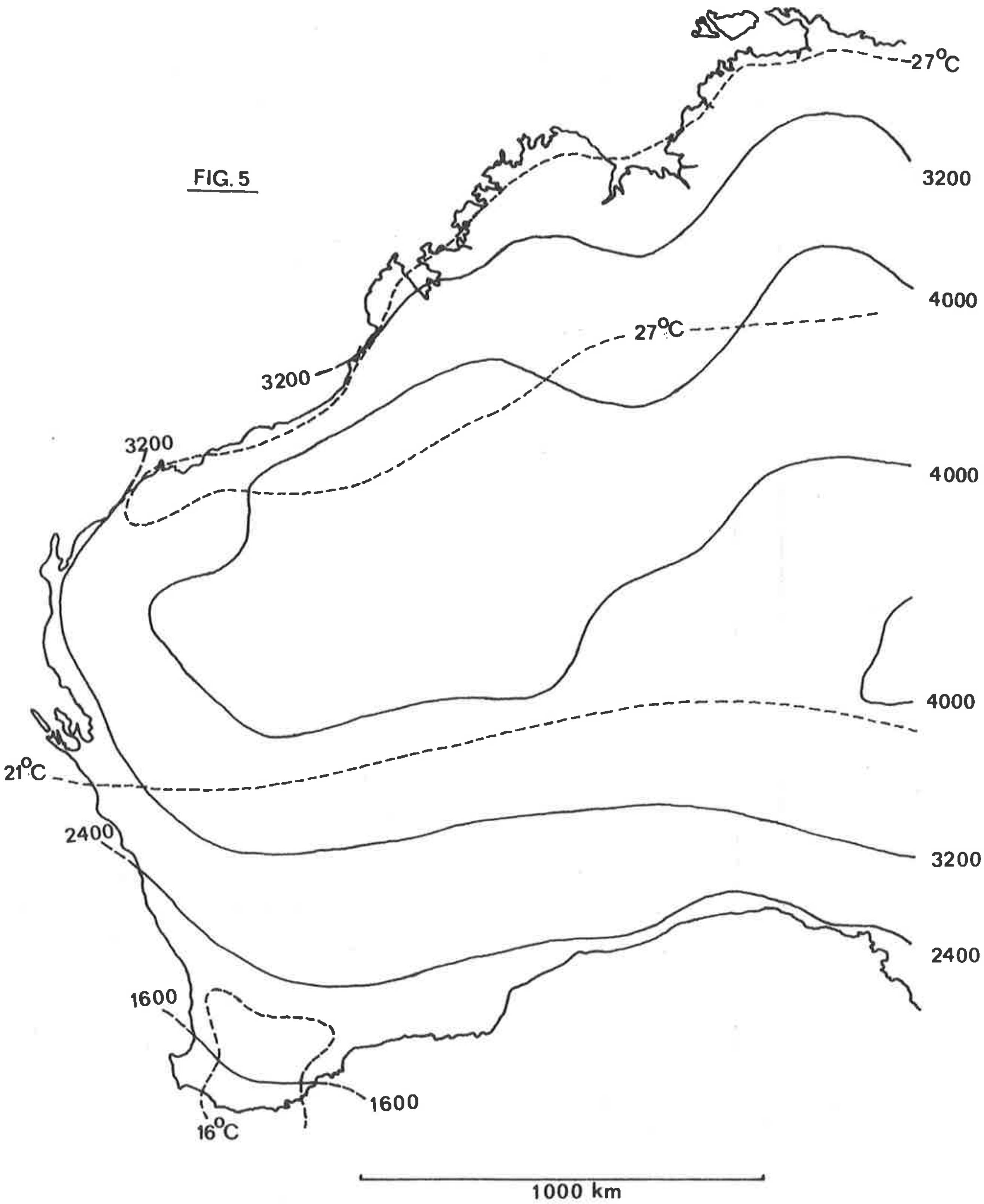


FIG. 5


27°C
3200
4000
27°C
3200
3200
4000
4000
21°C
3200
2400
2400
1600
1600
16°C
1000 km

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