THE ECOLOGY AND LIFE HISTORY OF THE INTRODUCED MILLIPEDE, *Ommatoiulus moreletii* (LUCAS, 1860), IN SOUTH AUSTRALIA.

By

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SUMMARY

The millipede, Ommatoiulus moreletii (Iulidae), is indigenous to South-Western Europe. The species has been introduced to Australia where it is in large numbers and constitutes a severe nuisance.

The distribution of O. moreletii in Australia is increasing. Man is a major factor in the establishment of new outbreaks of the species. Individual outbreaks spread slowly but steadily (an expansion of up to 200 metres in radius per year).

The abundance of O. moreletii in Australia relative to its apparent rarity in South-Western Europe cannot be explained by differences in general climate. The variety of habitats colonized by O. moreletii in Australia is already wide and there is no reason to doubt that the species will continue to spread much further.

The life cycle of O. moreletii consists of an egg, pupoid and then a series of up to sixteen stadia. Males may mature at any moult from the eighth to the twelfth stadia, but most are mature by the tenth or eleventh. Maturation is more difficult to determine in females but seems similar to the males with respect to stadial age. O. moreletii therefore has more than one adult stadium.

O. moreletii is periodomorphic. That is, there are mature and "intercalary" (immature) forms of the adult male.

O. moreletii is probably capable of iteroparity (producing more than one brood). Iteroparity is however considered a rare occurrence in the field. Nests laid in the laboratory contain an average of 250 eggs.

Field studies were made of O. moreletii in an open grassland and a sclerophyllous woodland. Sampling of soil and litter collectively, litter by itself, pitfall trapping and visual assessment of activity gave data on the life history, abundance and activity of O. moreletii.

Females of O. moreletii matured their eggs in late summer - autumn. They mated and oviposited during autumn - winter. After 1 year, individuals were in the seventh, eighth or ninth stadium. After 2 years, the tenth or eleventh stadia were reached. In subsequent years, O. moreletii probably moulted twice per year (in spring and summer). In males, the summer moult was to the mature form (either from the juvenile or intercalary); the spring moult was to the intercalary form (from the mature). Thus intercalary males were present in spring - summer. For the remainder of the year, the adults were mature.

Maturation of adults was higher after a wet summer than after two dry summers. Maturation was more successful in the grassland than in the woodland. Production of young was much greater in the grassland.

Survival of females from the autumn breeding season to the subsequent spring was correlated (negatively) with their maturity in autumn. The advantage to O. moreletii of extended adult life in females after a poor breeding season is discussed with reference to Den Boer's (1968) concept of "spreading of risk". The advantage of periodomorphosis to this species is also discussed.

Active O. moreletii were most commonly seen and trapped in autumn. Day to day variations in activity were correlated with changes in temperature and moisture. Older stadia were more active than younger stadia.

During summer, O. moreletii aggregated in cool, moist sites (e.g. beneath tussocks of Lomandra fibrata (Liliaceae)) or burrowed underground. Behaviour of the species in gradients of temperature and humidity explained the aggregation in summer beneath the tussocks.

In a particularly hot, dry summer, mortality was demonstrated in the grassland but not in the cooler, moister woodland. A survey of the percentage water contents in O. moreletti during this particular summer gave no evidence of desiccation of the species in either habitat. This suggested

that high temperature was the important mortality factor. However, using a technique involving the appearance of the mid-gut, desiccation of O. moreletii was demonstrated in a later, milder summer and doubt was placed upon the earlier result.

O. moreletii developed resistance to high temperature and to desiccation at high temperature throughout summer. Mature males were less resistant to high temperatures and desiccation than females and juvenile males. Indirect evidence suggested that mature males were less resistant to desiccation at high temperature than intercalary males.

Two native species of millipede, Dimerogonus sp. (Cambalidae) and Australiosoma castaneum (Paradoxosomatidae), were found in the woodland but not in the grassland. The native species were rare relative to O. moreletii. They probably bred in late winter - spring. Juveniles of both native species were more susceptible to desiccation and high temperature than juveniles of O. moreletii. This is suggested as one reason for the differences in distribution and abundance of the three species.

Declaration

The work presented in this thesis is my own unless otherwise acknowledged, and has not previously been published or submitted to any university for the award of any degree.

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(Geoff Baker)

June 1976.

ACKNOWLEDGEMENTS

Professor Tom White (now at the University of the South Pacific) was first to recognize "the millipede" as a profitable avenue of ecological research. Tom stimulated me as an undergraduate student to undertake this present study. I thank him for many long discussions and his continued interest in my work.

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Mr. Bill King kindly allowed me the use of his property at Bridgewater. The National Trust of South Australia allowed me the use of Engelbrook Reserve. Ron Vincent, Bob and "Tobe" Armstrong of Bridgewater were invaluable for information and help in the field-work, as well as "refreshment" afterwards. Colin Wirth and Mr. R.E. Oswald of the Stirling District Council, Bill Anderson of the Keilor District Council, members of the Victorian Department of Agriculture and Neville Wanklyn of the "Port Lincoln Times" provided welcome assistance in my surveys of the distribution of O. moreletii in Australia. Dr. C.A.W. Jeekel (Amsterdam) identified O. moreletii, Dimerogonus sp. and A. castaneum for me. Dr. David Symon (Waite Institute) identified the plants at Bridgewater. Drs. J.M. Demange and J.P. Mauriès (Paris) provided the available information on O. moreletii in Europe. Dr. David Lee (South Australian Museum) identified H. feroniarum. Professor Carroll Williams (Harvard) assayed O. moreletii for juvenile hormone. Dr. Robin Bedding (C.S.I.R.O., Tasmania) assayed O. moreletii with Neoaplectana. Carol Crawford (Waite Institute) provided unpublished data on soil moistures. Marjorie and Robert Baker helped with the thesis' diagrams. I sincerely thank all these people.

Finally, I thank Nicole.

1. INTRODUCTION

In the past 20 years, there have been increasing numbers of complaints from various localities in South-Eastern Australia of hordes of millipedes invading houses, particularly during autumn and spring. The millipedes infest food, bedding and water, stain floors when squashed, stink, destroy backyard crops of tomatoes, melons, strawberries and potatoes and lower real estate values. In short, they are a revolting nuisance (see Figures 1.1 (a and b)).

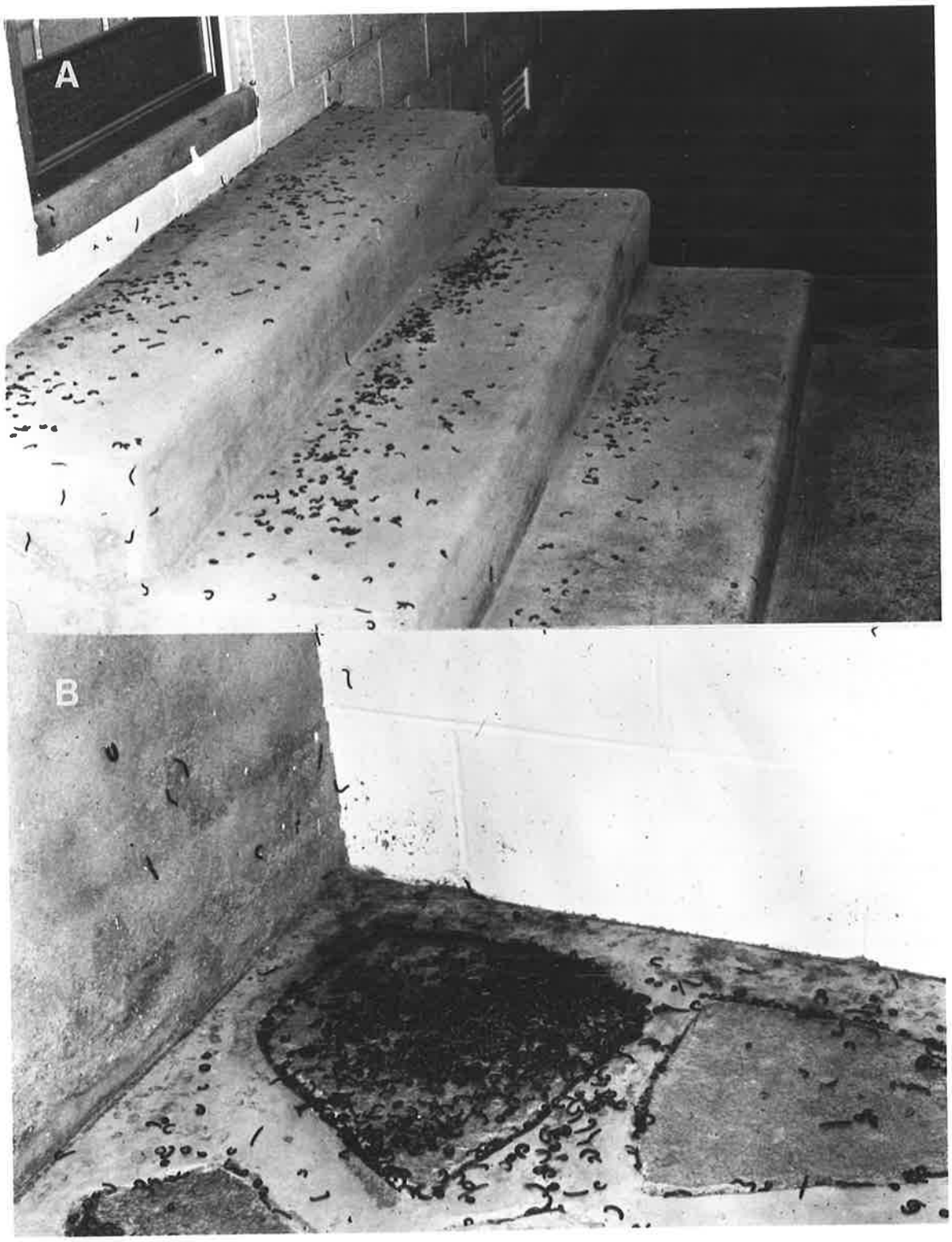
The millipedes concerned were identified as Ommatoiulus moreletii (Lucas, 1860) (Iulida, Iulidae) (see acknowledgements). The species has previously been referred to in the literature as Iulus moreleti, I. karschi, Schizophyllum moreleti, S. karschi and Archiulus moreleti (C.A.W. Jeekel and J.P. Mauriès, pers. comm.). O. moreletii is indigenous to South-Western Europe, in particular Portugal and Spain (Verhoeff, 1892 (a and b); Leonardi, 1898; Machado, 1946; Mauriès, 1964; Ceuca, 1974; Jeekel, Mauriès and J.M. Demange, pers. comm.). O. moreletii has never been reported in large numbers in South-Western Europe. It is to be assumed that the species is rare there. Demange (1970), Lohmander (1955), Attems (1933) and Brolemann (1896) reported O. moreletii present in large numbers at many sites in the Azores and Madeira. Apparently, O. moreletii was introduced to these islands (Jeekel, Mauriès and Demange, pers. comm.). O. moreletii was also introduced to South Africa (Jeekel, pers. comm.). Now it has reached Australia.

There are many reports in the literature of large numbers of millipedes being simply a nuisance (e.g. Cloudsley-Thompson, 1949; Morse, 1903; Brookes, 1919). There are also many reports of large numbers of millipedes being economic pests (e.g. Brade-Birks, 1930; Cloudsley-Thompson, 1950, 1968; Dunning, 1975; Baker, 1974; Pierrard and Biernaux, 1974). These high densities of millipedes have in general been the result of

FIGURE 1.1 The problem. O. moreletii photographed at Bridgewater, South Australia.

A. At night. O. moreletii is predominantly nocturnal

B. Various pesticides are sprayed around houses to kill O. moreletii and prevent them from coming inside. The result is smelling heaps of dead millipedes which stain concrete etc.


A
B

sporadic increases in the populations of native species. However, O'Neill and Reichle (1970, 1971) described the outbreaks of the introduced millipede, Oxidus gracilis, in Lenoir City, Tennessee. Their brief report is the only case in the literature that I can find of a study being made of the progress of an introduced millipede in its new habitat. During winter, O. gracilis was confined to moist stream beds. In spring and summer, the species invaded nearby urban areas but did not become established there.

The present study was undertaken to determine the distribution of O. moreletii in Australia, its rate of spread, its life history and the major factors in its environment which influenced its abundance and activity. Such a study, I hoped, would give the basic building blocks for future research into the control of the species.

Early impressions suggested that the life history and abundance of O. moreletii differed quite markedly in two separate habitats - an open grassland and a dry sclerophyllous woodland. Individuals seemed larger in size but smaller in number in the woodland. Two native species of millipede, Australiosoma castaneum Attems, 1944 (Polydesmida, Paradoxosomatidae) and Dimerogonus sp. (Spirostreptida, Cambalidae) were sympatric in the woodland with O. moreletii. Early impressions suggested the native species were very much rarer than O. moreletii. Studies were directed to explore these probable differences and to explain them as best as possible.

O. moreletii has a complex life history. The adaptive significances of certain features in the life history are evaluated in this study and discussed with reference to related findings on other species of millipede (Blower and Fairhurst, 1968; Blower, 1969 and Fairhurst, 1974).

2. DISTRIBUTION AND DISPERSAL

2.1 Distribution

The general areas where O. moreletii has become a pest in South-Eastern Australia are illustrated in Figure 2.1. Each general area is represented by the location (and date) where the species was first reported. I assume that the initial introduction of O. moreletii into Australia was at Port Lincoln, Eyre Peninsula, and that the more recent outbreaks of the species have stemmed from there.

(a) Eyre Peninsula

The distribution of O. moreletii on Eyre Peninsula was determined during January 1973 and January 1975. At these times, the species aggregated beneath loose stones and logs. A sampling technique was devised utilizing this behaviour. Stones and logs within a selected sampling area were turned over for up to 5 minutes until O. moreletii was found. If the species was not found after 5 minutes, it was scored as absent. 320 sites were sampled during the two visits to Eyre Peninsula. Sites were selected in the roadside vegetation where ample stones and logs were available. The sites where O. moreletii was found and where it was considered absent are shown in Figure 2.2. Local residents offered limited information on the history of O. moreletii on Eyre Peninsula. The "Port Lincoln Times" provided evidence for the presence of O. moreletii in certain areas of the Peninsula in the past.

O. moreletii was first reported as a pest on Eyre Peninsula at Port Lincoln and Coffin Bay in approximately 1953. Since then, the species has spread, particularly northwards. The more northerly and isolated outbreaks (e.g. in Cummins, Ungarra, Kapinnie and Yeelanna) were all reported more recently than 1970.

The northerly bias in the dispersal of O. moreletii on Eyre Peninsula

FIGURE 2.1 Distribution of major outbreak centres of *O. moreletii* in Australia. Dates of first complaints are given for each area.

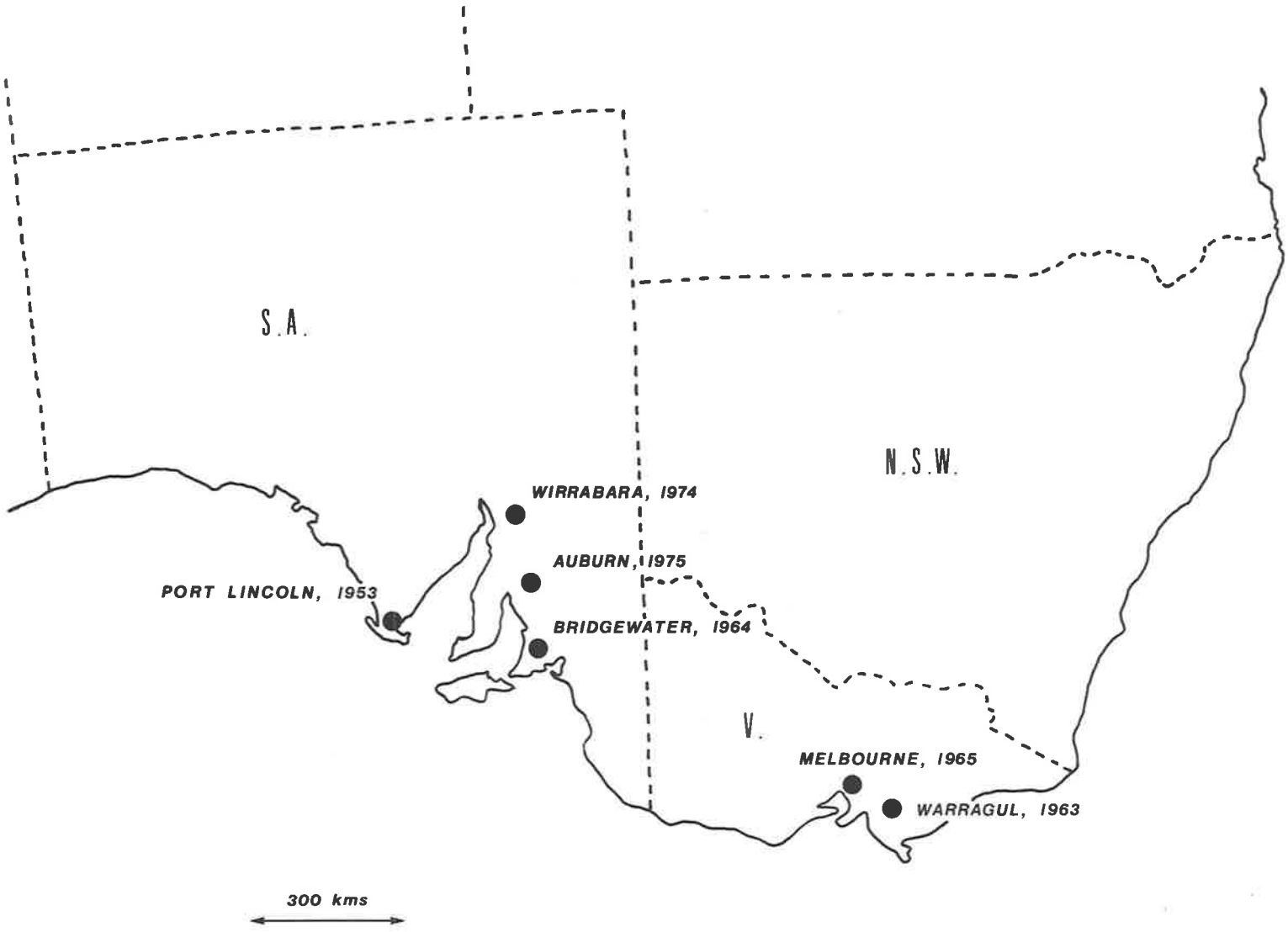
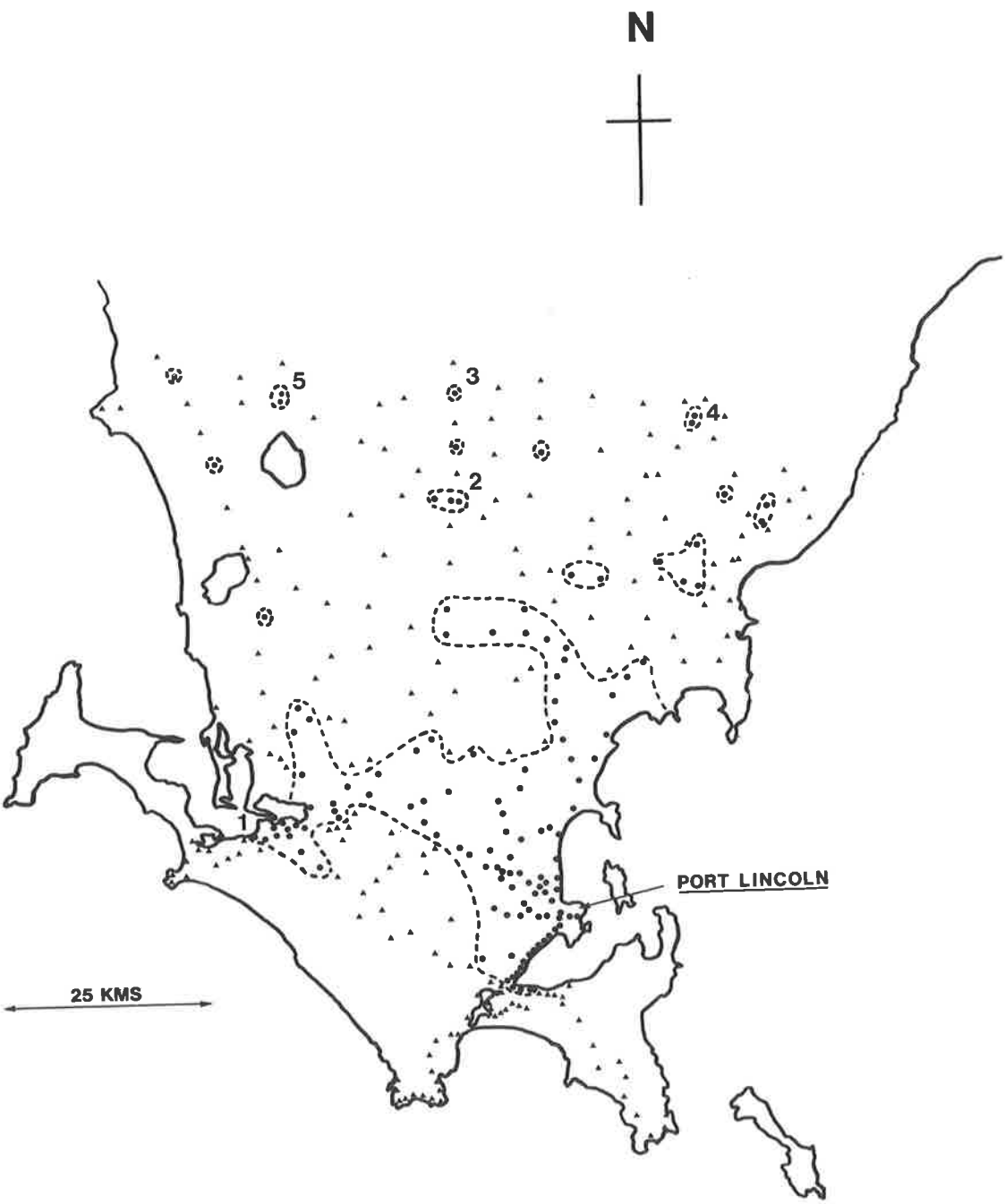

S.A.
N.S.W.
V.
WIRRABARA, 1974
AUBURN, 1975
PORT LINCOLN, 1953
BRIDGEWATER, 1964
MELBOURNE, 1965
WARRAGUL, 1963
300 kms

FIGURE 2.2 Distribution of O. moreletii on Eyre Peninsula, South Australia.
(● = O. moreletii was found, ▲ = O. moreletii was not found, 1 = Coffin Bay, 2 = Cummins, 3 = Yeelanna, 4 = Ungarra, 5 = Kapinnie).


N
5
3
4
2
1
PORT LINCOLN
25 KMS

is presumably related to man's activities, carrying and spreading the species by accident. Main roads and railways (see Figure 2.3) run north from Port Lincoln, but until only very recent years, very little traffic went south of the town. Whether O. moreletii will spread to colonize the as yet unoccupied areas between the recent and isolated northerly outbreaks in its distribution on the peninsula remains to be seen. The climate becomes progressively hotter and drier northwards and the distribution of the species may be checked there in future more so than it was near Port Lincoln.

The vegetation of Eyre Peninsula has been generally described as "shrubby-open scrub" (Williams, 1959 and Specht, 1970). A more detailed description has been given by Smith (1961). O. moreletii was found on Eyre Peninsula in mallee scrub (dominated by Eucalyptus flocktoniae, E. pileata, E. diversifolia and Melaleuca uncinata), mallee heath (E. incrassata and E. foecunda), sclerophyllous woodland (E. cladocalyx) and savannah woodland (E. camaldulensis, E. odorata, M. lanceolata and Casuarina stricta). Of course, much of Eyre Peninsula has been disturbed through agriculture and settlement. O. moreletii was found in both pastoral and urban areas.

The soils of Eyre Peninsula were also described by Smith (1961). O. moreletii was found on skeletal soils, podzolized soils, red-brown earths, solonized brown soils, Rendzinas and Terra Rossas (limestones) and even on coastal sand dunes.

(b) Mount Lofty Ranges

Several outbreaks of O. moreletii have been reported in Adelaide and the surrounding Mount Lofty Ranges during recent years. The first reported outbreak was in 1964 at Bridgewater (see Figure 2.4).

Those areas of the Mount Lofty Ranges in which O. moreletii has

FIGURE 2.3 Distribution of O. moreletii on Eyre Peninsula, South Australia in relation to main roads and railways.

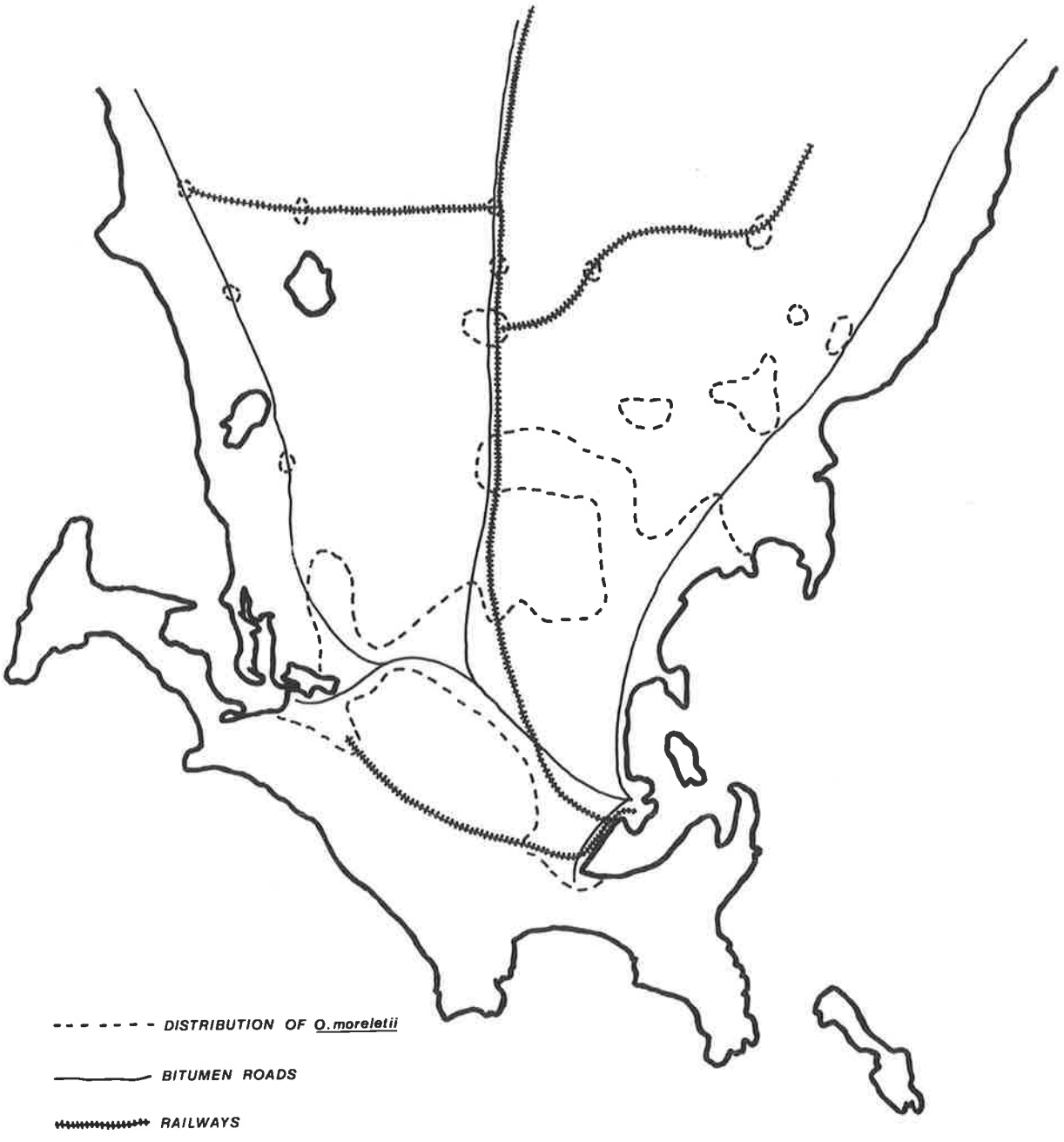
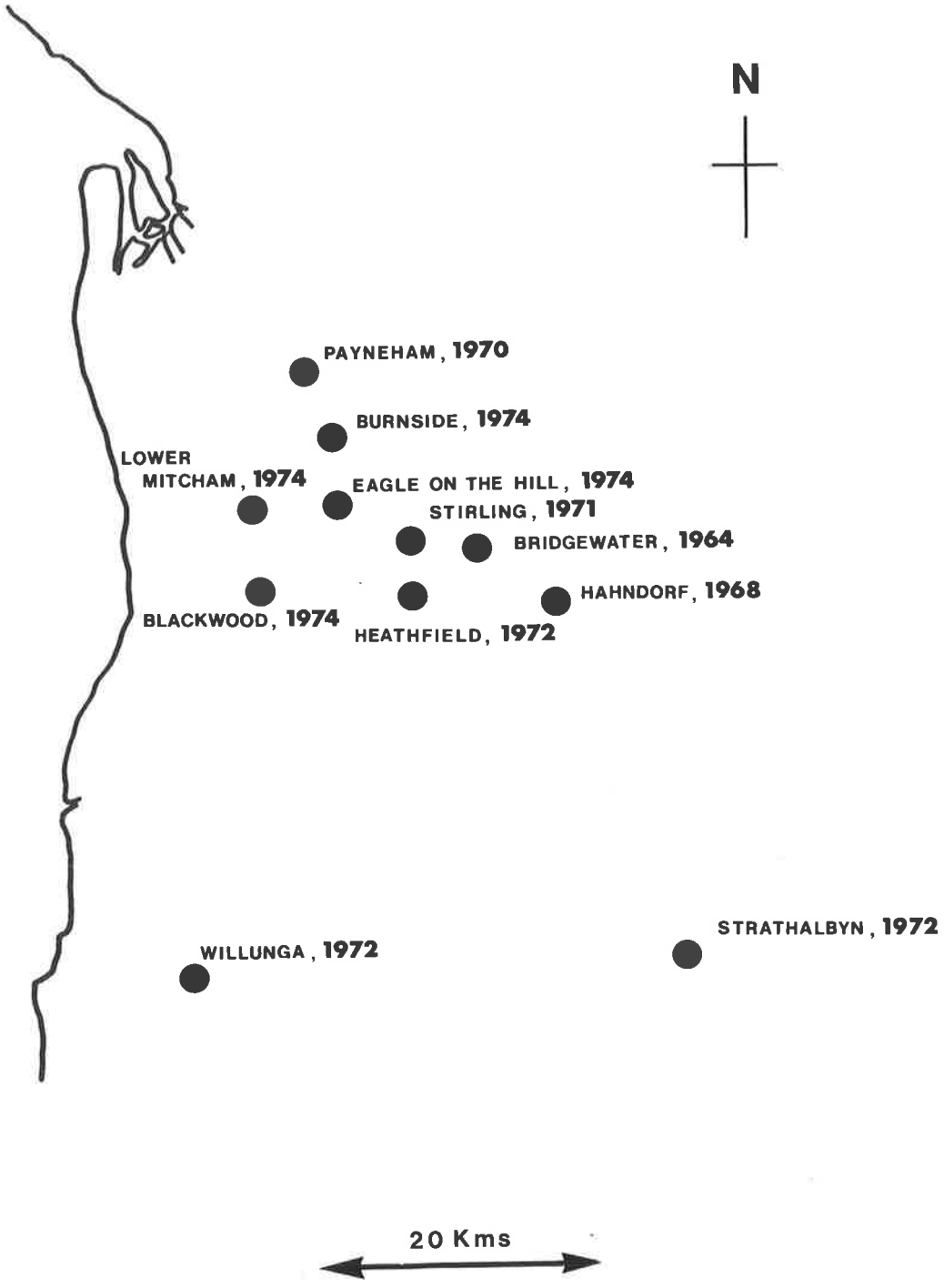

DISTRIBUTION OF O. moreletii
BITUMEN ROADS
RAILWAYS

FIGURE 2.4 Distribution of outbreaks of O. moreletii in Adelaide (Payneham, Burnside and Lower Mitcham) and the nearby Mt. Lofty Ranges. Dates indicate when each outbreak was first recorded.


N
PAYNEHAM, 1970
BURNSIDE, 1974
LOWER MITCHAM, 1974
EAGLE ON THE HILL, 1974
STIRLING, 1971
BRIDGEWATER, 1964
HAHNDORF, 1968
BLACKWOOD, 1974
HEATHFIELD, 1972
STRATHALBYN, 1972
WILLUNGA, 1972
20 Kms

been found and that are undisturbed are mostly dry sclerophyllous woodland (E. obliqua and E. baxteri). Such a habitat is described later for Bridgewater (see Section 4.3).

(c) Victoria

In recent years, the Victorian Department of Agriculture has recorded the locations where millipedes have been reported in large numbers. In the past ten years (particularly the last five), the numbers of reports have increased markedly. On some occasions specimens of the millipedes concerned have been kept, thus allowing identification.

Locations where the outbreaks have been confirmed to be O. moreletii are as follows (most are for suburban Melbourne or the near country areas):- Avondale Heights, St. Albans, Heathmont, Keilor, Balwyn, North Balwyn, Surrey Hills, Kew, Hawthorn, Warragul, Monbulk and Emerald. The earliest reports of O. moreletii in Victoria were at Warragul in 1963 and North Balwyn in 1965, but these complaints were minor compared with the storm of protest when in 1973 the species was in excessively high numbers at Avondale Heights.

Locations where millipedes have been reported in large numbers but as yet have not been confirmed as O. moreletii are given in Appendix A. Many of these locations are geographically very close to the known outbreaks of O. moreletii and it seems likely that several at least will prove to be of this same species.

As the outbreaks of O. moreletii in Victoria are mostly in suburban areas, the habitat is disturbed and variable.

(d) Climate

Appendix Tables 1 to 3 list general climatic data for locations at or near to where O. moreletii has been found, both in Australia, the Azores and Madeira and in Portugal and Spain. There are no obvious differences in climate between Portugal and Spain (where O. moreletii is presumably rare)

and other locations where the species is extremely numerous. An explanation of the abundance of O. moreletii in Australia in terms of general climate seems therefore unlikely.

2.2 Dispersal

Some indication of the rate of dispersal of O. moreletii in Australia is given by its present distribution (see Section 2.1 above). Now, the rates of expansion of three outbreaks of O. moreletii in the Mount Lofty Ranges will be described in greater detail.

(a) Bridgewater (1964 to 1972)

Discussions with local residents and records of pesticide distribution by the Stirling District Council enabled the history of the outbreak of O. moreletii at Bridgewater to be traced from 1964 (when the outbreak was first reported) to 1972. Figure 2.5 shows the approximate spread of the outbreak during this time (of course the spread can only be shown through residential areas). Figure 2.5 suggests an expansion in the radius of the outbreak of approximately 100 to 200 metres per year.

(b) Bridgewater, Stirling and Heathfield (1973 to 1975)

In July 1973, 1974 and 1975, the boundaries (or parts thereof) of the Bridgewater, Stirling and Heathfield outbreaks were determined*.

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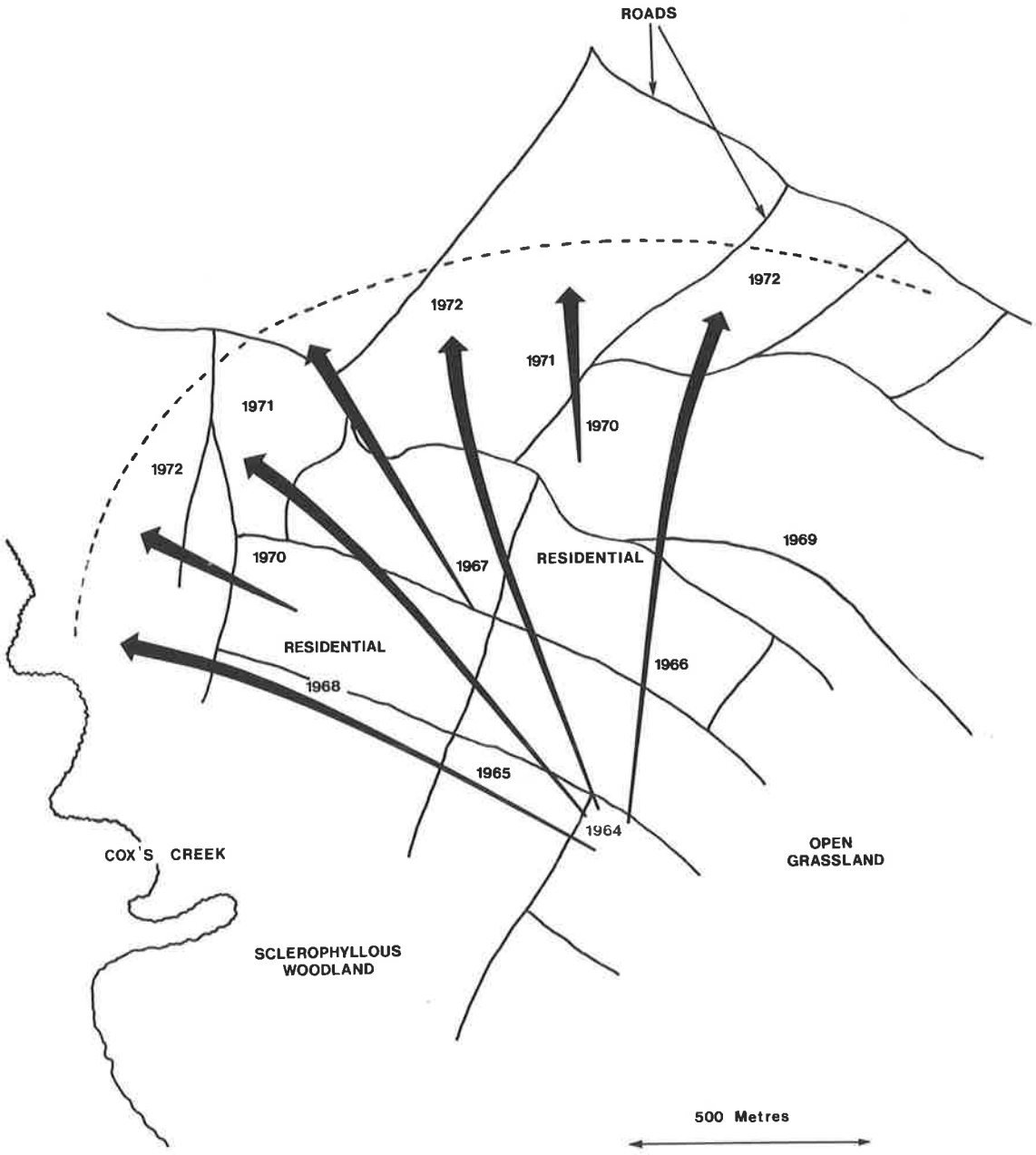
* The activity of O. moreletii (i.e. the numbers of the species moving about on the surface of the ground) is high during autumn (March to May), moderate during spring and summer (September to February) and low during winter (July and August) (see Section 4.59). I considered that plotting the boundary of an outbreak would be most representative for a particular year if done in winter. At this time, the boundary is most likely to be stationary.

FIGURE 2.5 Rate of spread of the outbreak of *O. moreletii* at Bridgewater prior to this study.


ROADS
1972
1972
1971
1971
1970
1972
1970
1969
1967
RESIDENTIAL
1966
RESIDENTIAL
1968
1965
1964
COX'S CREEK
OPEN
GRASSLAND
SCLEROPHYLLOUS
WOODLAND
500 Metres

Inaccessible terrain or lack of suitable sampling sites limited the plotting of the complete boundaries.

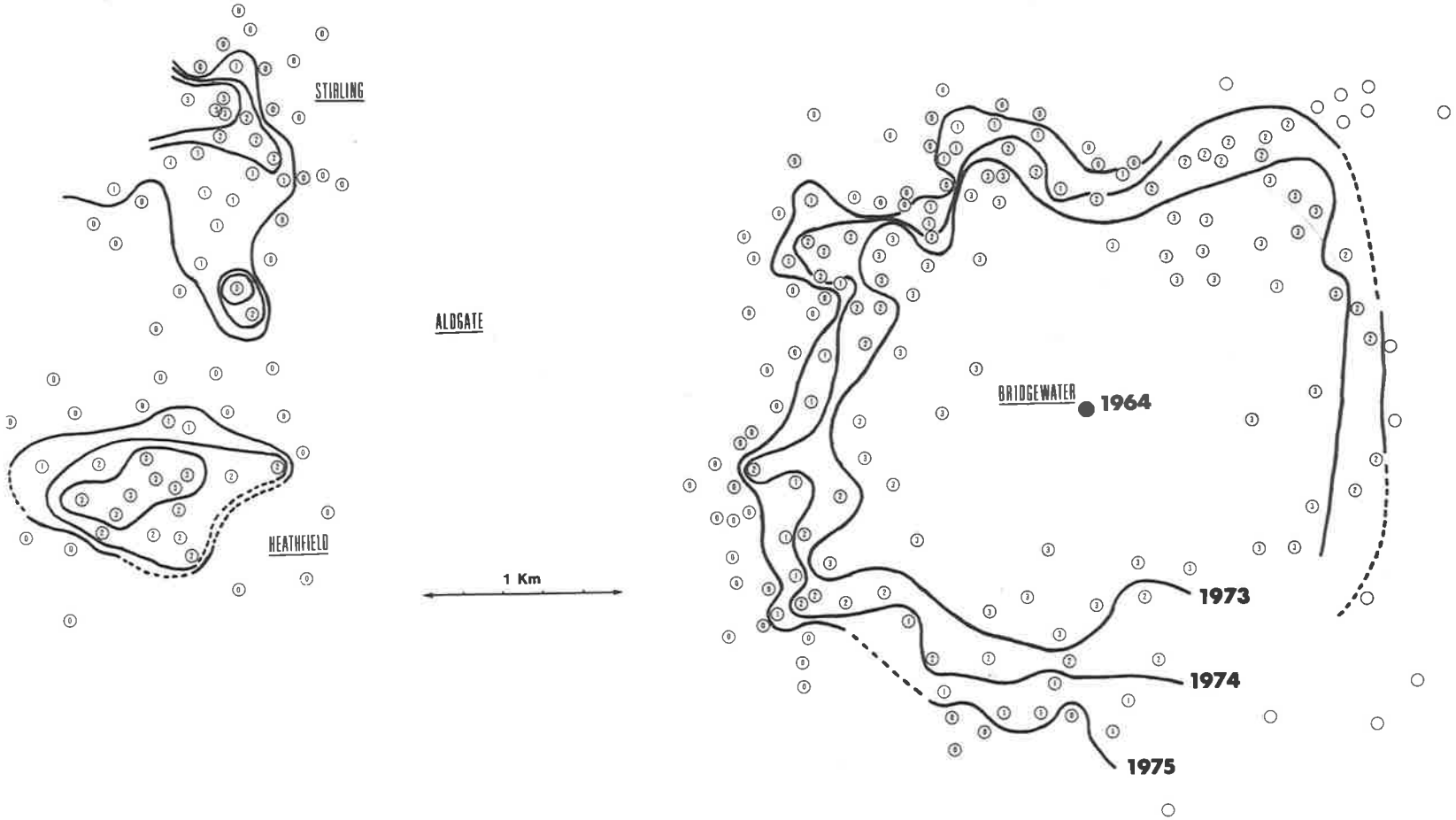
The method of determining the boundaries was as follows. In July 1973, 238 sampling sites were selected inside and outside of where initial observations suggested the boundaries of the three outbreaks would be. Sites outside the likely boundaries were extended a sufficient distance to allow the likely expansion of the populations to be followed during the next few years (based on knowledge of expansions prior to this study).

At each sampling site, a careful search was made in the leaf-litter and beneath loose stones, logs, bark etc. for O. moreletii. As soon as the species was found, searching was discontinued. If after 5 minutes, O. moreletii was not found, it was scored as absent.

The selections and spacings of sampling sites were dictated by the availabilities of sufficient litter in which to search for at least 5 minutes. Attempts were made however to keep sampling sites within a few hundred metres of their nearest neighbour. With the presence/absence data thus gained for each sampling site in 1973, a boundary could be drawn for each population. In July 1974, all those sampling sites where O. moreletii was not found in 1973 were again sampled in a similar way to that in 1973. Thus in 1974, presence/absence data again allowed a boundary to be drawn. The same was repeated in 1975. In 1975, 10 sampling sites which had been invaded by O. moreletii in 1974 were resampled to check the success of the invasion. In all cases O. moreletii was immediately found.

The positions of all the sampling sites and the boundaries that were drawn following each year's sampling are shown in Figure 2.6. The data suggest that the outbreaks are expanding at up to 200 metres per year; a figure comparable to that given earlier (see (a) above). Perhaps the rate of dispersal of O. moreletii through the residential parts of the

FIGURE 2.6 Rate of spread of the outbreaks of O. moreletii at Bridgewater, Stirling and Heathfield. Sampling sites are indicated (③ = O. moreletii found in 1973, ② = O. moreletii found in 1974, but not in 1973, ① = O. moreletii found in 1975, but not in 1973 or 1974, ⓪ = O. moreletii not found from 1973 to 1975, ◯= O. moreletii not found in 1973 or 1974 and site not sampled in 1975).


STIRLING
ALDGATE
HEATHFIELD
1 Km
BRIDGEWATER
1964
1973
1974
1975

three outbreaks was influenced by man. However dispersal through pastoral and wooded habitats appeared similar to that through residential areas and I consider the rate of spread depicted in Figures 2.5 and 2.6 to be indicative of the species' ability to disperse by itself.

It should be stressed here that I have measured the rates of dispersal of populations, not individuals. It is quite possible that up to 200 metres per year is not an accurate measure of an individual's movement per year. Perhaps individuals at the centres of outbreaks move quite different distances from individuals at the boundaries of outbreaks (e.g. due to resource availability). As a basis for future control of O. moreletii, I considered it more important to know the rate of dispersal of outbreaks than of individuals.

3. POST-EMBRYONIC DEVELOPMENT

3.1 General

From the egg of a millipede, a pupoid hatches which is legless, immobile and enclosed within a membrane. The pupoid then moults to a hexapod larva, the first in a series of instars or stadia. At each moult to an older stadium, the number of diplo-segments (referred to from now on simply as segments), and hence the size of the millipede, increases. The post-embryonic development of millipedes is anamorphic. In keeping with most authors (e.g. Blower and Gabbutt, 1964; Blower and Fairhurst, 1968; Blower, 1970; Blower and Miller, 1974 and Brookes, 1974) but unlike Pflugfelder (1932), Halkka (1958) and Rantala (1970), I will consider the hexapod larva to be the first stadium in post-embryonic life and not the pupoid.

In the Polydesmoidea and Nematophora, the increment in number of segments is constant between two given stadia. The stadia are therefore characterized by their numbers of segments. In addition, there is usually a fixed number of stadia in the life cycle, the last of which is the adult. In the Iuliformia (e.g. Iulidae and Blaniulidae) the increment in number of segments can be variable between two given stadia. Consequently there can be overlap between the numbers of segments of successive stadia. The numbers of juvenile stadia in species of the Iuliformia are generally similar to the numbers of juvenile stadia in the Polydesmoidea and Nematophora (seven and eight respectively). However in some Iuliformia the first mature stadium continues to moult - hence there may be a number of adult stadia.

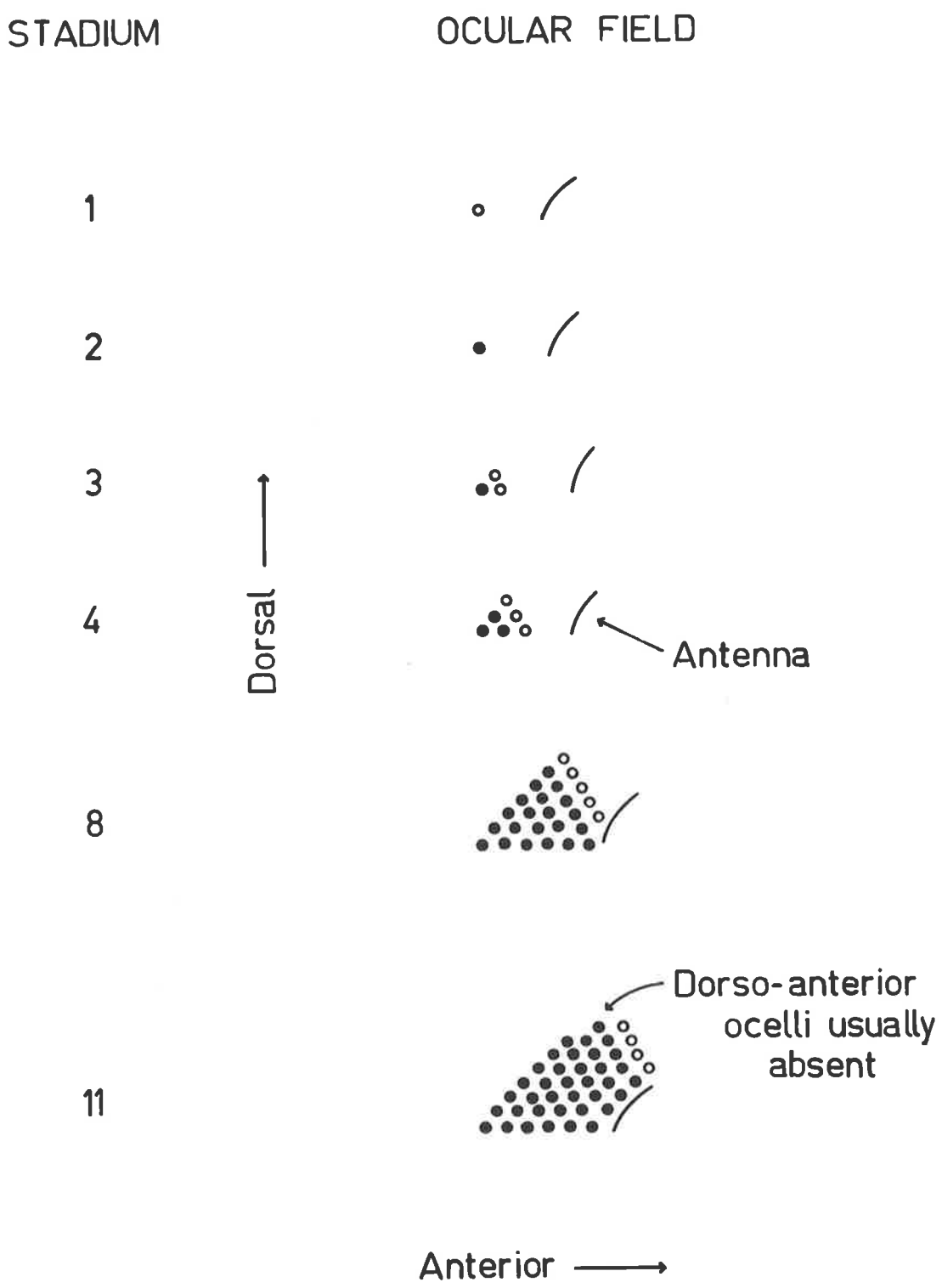
3.2 Characterizing the Stadia of O. moreletii

Previous authors have characterized the stadia in the life cycles of Iuliform millipedes by a variety of methods. Most commonly, the numbers

of podous and apodous segments have been used (e.g. Verhoeff, 1928; Blower and Gabbutt, 1964; Blower and Fairhurst, 1968; Blower, 1970; Blower and Miller, 1974; Brookes, 1974). For the early stadia, the numbers of segments are perfectly useful characters. Each stadium has a separate number or range of numbers of segments. However with increasing age, the numbers of segments in each stadium may overlap with the numbers found in other stadia (more so of course in some species than in others). Thus for the older stadia, individuals cannot always be aged precisely by their numbers of segments. Other methods that have been used to characterize stadia in the Iuliform millipedes include the number, colour and size of repugnatorial (defence) glands (Halkka, 1958; Brookes, 1963; 1974; Rantala, 1974), widths (Blower and Gabbutt, 1964; Blower and Fairhurst, 1968; Blower, 1970), lengths (Blower and Gabbutt, 1964; Blower and Fairhurst, 1968; Blower, 1970) and volumes and weights of the whole millipedes (Blower, 1970). These methods are also limited in their usefulness because of variabilities in the characters within stadia and, as a result, lack of discreteness between adjacent stadia, particularly the older ones.

By far the most exact technique for characterizing the stadia of Iuliform millipedes (and the easiest to measure) is that developed by Vachon (1947) and Saudray (1952) using the development of the ocular field. At each moult a new row of ocelli is added to the dorso-anterior edge of the ocular field (see Figure 3.1). By counting the number of rows of ocelli the stadium of the individual concerned can be determined precisely. Blower (1970), Blower and Fairhurst (1968), Brookes (1974) and Cotton and Miller (1974) have used this method successfully in characterizing the stadia of Iuliform millipedes. The method does however require that the growth of the ocular field during the life cycle is reasonably regular. Not all Iuliform millipedes fulfill this requirement and the method cannot

FIGURE 3.1 Development of ocelli in the ocular field of O. moreletii (o = ocelli added at moult to the present stadium, ● = ocelli added at earlier moults). Six or seven rows of ocelli were added before their growth was obstructed by the antennae. The dorso-anterior ocelli were usually missing in the older stadia. From the second stadium onwards, counting the number of rows of ocelli from bottom left to top right of the ocular field and adding one gave the stadium of the individual.


STADIUM
OCULAR FIELD
1
2
3
4
8
11
Dorsal
Antenna
Dorso-anterior ocelli usually absent
Anterior

be applied to them (e.g. Cylindroiulus latestriatus in Blower, 1970 and Blower and Fairhurst, 1968).

Different studies require different precision in characterizing animals into age groups. The present study required that the precise stadium of an individual could be determined. The numbers of segments, pairs of legs, pairs of defence glands, widths and lengths were either too variable or too indistinguishable (particularly in the older stadia), or too difficult to measure accurately to be used in characterizing the stadia of O. moreletii so that individuals could be classified precisely into stadia. The method used in this study to characterize the stadia of O. moreletii was that of Vachon (1947) and Saudray (1952). The pattern of development of the ocelli is outlined in Figure 3.1. Stadia 1 and 2 can be easily told apart by the number of pairs of legs that each has (3 and 7 respectively). Thereafter, the number of rows of ocelli + 1 equals the stadium. Sixteen stadia were identified for O. moreletii.

3.3 Differentiating the Sexes of O. moreletii

In very young Iuliform millipedes, the sexes cannot easily, if at all, be discriminated. However during juvenile development, the previously ambulatory legs on the seventh segment (assuming the collum to be the first segment) are modified in the male into developing gonopods (secondary sexual characters). In the female, the legs on the seventh segment remain ambulatory throughout life. Blower and Gabbutt (1964) reported that this sexual differentiation was normally first visible in the seventh stadium of Iulus scandinavius and Ophyiulus pilosus, sixth in Cylindroiulus punctatus and fifth in C. latestriatus. Halkka (1958) reported sexual differentiation in the fourth stadium of Ommatoiulus sabulosus. (Actually, Halkka reported the differentiation in the fifth

stadium, but since she referred to the pupoid as the first stadium, I have corrected for this).

In O. moreletii, the sixth stadium was the first and most common stadium in which males were differentiated from females by the modification of their legs on the seventh segment to developing gonopods. Tables 3.1 (a to f) give data collected at Bridgewater by various methods that will be outlined later (see Chapter 4). The data represent totals of individuals collected in each stadium. In all cases there are more females in the sixth stadium than there are males. However in the seventh and eighth stadia the numbers of each sex are more nearly equal. It seems likely therefore, that not all males differentiate in the sixth stadium but perhaps all do so by the seventh or eighth.

3.4 Development of Maturity in O. moreletii

Blower and Gabbutt (1964) collected O. pilosus and I. scandinavius in Devon and reported that for both species there were nine juvenile stadia. The tenth was the first and only adult stadium. Then, Blower (1970) and Blower and Miller (1974) later collected the same species at other sites in Britain and reported that maturity could be achieved in any of the ninth, tenth or eleventh stadia for the males and the tenth or eleventh stadia for the females in both species. The maturation of C. punctatus and C. latestriatus has similarly been found to be variable with respect to stadium. Some individuals of C. punctatus mature at the moult to the eighth stadium whilst others delay maturity to the ninth stadium. In C. latestriatus, maturation may occur at any one of the moults to the seventh, eighth or ninth stadia (Blower and Gabbutt, 1964). Blower and Fairhurst (1968) stated that maturation in the males of Tachypodoiulus niger (= T. albipes) could be achieved in either the seventh, eighth or

TABLES 3.1 (a and b)

Soil and litter sampling

Open grassland (November 1972 - April 1974)

(a) Tussocks of L. fibrata

	STADIA											
	6	7	8	9	10	11	12	13	14	15	16	Total
Females	964	1982	825	706	684	142	62	20	2			5387
Males	649	1910	913	994	628	180	48	11	3			5336
Juveniles	649	1910	874	896	269	10						4608
Adults			39	98	359	170	48	11	3			728
Mature			39	82	303	89	31	8	3			555
Intercalary				16	56	81	17	3				173
Total	1613	3892	1738	1700	1312	322	110	31	5			10723

(b) Pasture grasses

Females	370	366	394	72	122	103	40	8			1475
Males	310	382	379	105	184	93	23	7	1		1484
Juveniles	310	382	348	59	28	1					1118
Adults			31	46	156	92	23	7	1		356
Mature			31	45	149	65	13	7	1		311
Intercalary				1	7	27	10				45
Total	680	748	773	177	306	196	63	15	1		2959

TABLES 3.1 (c and d)

Pitfall Trapping (October 1972 - January 1974)

(c) Open grassland

	STADIA											
	6	7	8	9	10	11	12	13	14	15	16	Total
Females	199	217	116	155	869	1029	344	150	30	12	1	3122
Males	135	222	94	224	1608	803	255	59	15	3		3418
Juveniles	135	222	78	168	118	6						727
Adults			16	56	1490	797	255	59	15	3		2691
Mature			16	50	1445	676	207	50	13	3		2460
Intercalary				6	45	121	48	9	2			231
Total	334	439	210	379	2477	1832	599	209	45	15	1	6540

(d) Sclerophyllous Woodland

Females	19	7	23	53	161	337	362	205	73	14	1	1255
Males	7	3	19	39	159	99	79	30	3			438
Juveniles	7	3	19	30	9	1						69
Adults				9	150	98	79	30	3			369
Mature				8	142	85	77	29	3			344
Intercalary				1	8	13	2	1				25
Total	26	10	42	92	320	436	441	235	76	14	1	1693

TABLES 3.1 (e and f)

Litter Sampling (September 1974 - November 1975)

(e) Open grassland

	STADIA											
	6	7	8	9	10	11	12	13	14	15	16	Total
Females	72	31	110	343	483	257	29	3				1328
Males	69	40	126	359	406	153	12					1165
Juveniles	69	40	125	348	183	24						789
Adults			1	11	223	129	12					376
Mature			1	9	220	109	4					343
Intercalary				2	3	20	8					33
Total	141	71	236	702	889	410	41	3				2493

(f) Sclerophyllous Woodland

Females	11	25	157	210	316	347	121	31	9	1		1228
Males	5	32	159	207	297	133	12					845
Juveniles	5	32	159	198	76	13						483
Adults				9	221	120	12					362
Mature				9	219	91	4					323
Intercalary					2	29	8					39
Total	16	57	316	417	613	480	133	31	9	1		2073

ninth stadia. Sahli (1966), also working with males of T. niger, reported that maturation could occur in any stadium from the eighth to the eleventh. Halkka (1958) reported that the numbers of juvenile stadia were variable (8 to 10) in males of O. sabulosus, thus implying that maturation could occur at any of the moults to the ninth, tenth or eleventh stadia. Juveniles most commonly matured at the moult to the tenth stadium. (Again I have corrected Halkka's data and called the hexapod larva the first stadium). The literature therefore suggests that the maturation of Iulid millipedes is variable with respect to stadium.

Maturation of the male Iulid is typified by the full development of the gonopods on the seventh segment and the modification of the first pair of legs (previously ambulatory in the juvenile male) to secondary sexual characters. Blower and Gabbutt (1964) have described in detail the morphological changes that take place in the gonopods of I. scandinavius, O. pilosus, C. punctatus and C. latestriatus during maturation. Halkka (1958) gave a detailed description of the changes in the first pair of legs as well as the gonopods in O. sabulosus during maturation. The maturation of female Iulids is not as obvious as in the males, but is typified by a sudden increase in the size and hardness of the vulvae.

(a) Maturation in the Males of O. moreletii

Tables 3.1 (a to f) show the numbers of juvenile and adult males of O. moreletii collected in the various stadia. The data suggest, that like other Iulids, maturation of male O. moreletii is variable with respect to stadium, being possible in the eighth to twelfth stadia. Generally, most males are adults by the tenth or eleventh stadium.

(b) Maturation in the Females of O. moreletii

In April 1974, a number of females of O. moreletii in the seventh to fourteenth stadia were collected from Bridgewater. The vulvae in these

females were dissected out and assessed as either 1) obviously mature, 2) obviously juvenile or 3) intermediate, when it was not possible to classify the vulvae into one of the other categories with surety. Table 3.2 gives the resulting data. The results suggest that maturation of the females of O. moreletii is variable with respect to stadium, but has generally occurred by the tenth or eleventh stadium. During the breeding season, (autumn - early winter (see Sections 4.52 and 4.53)) mature eggs were occasionally found in individuals in the ninth stadium, but this was rare. More commonly, mature eggs were seen in the tenth and older stadia.

3.5 Periodomorphosis in O. moreletii

In not all Iulids, do the males continue to moult after reaching maturity (e.g. C. punctatus and C. latestriatus (Blower and Gabbutt, 1964)), but in those that do, the mature male does not moult directly to another mature male but rather to a "schalt" (Verhoeff, 1893) or "intercalary" (Blower and Fairhurst, 1968) male. In the intercalary male, the secondary sexual characters (gonopods on the seventh segment and the modified first pair of legs) regress and the animal is incapable of reproduction. Nevertheless, the functional characters are regained at the subsequent or later moults. Sahli (1958, 1961, 1966) and Halkka (1958) have shown with T. niger and O. sabulosus respectively that the intercalary male may moult once or more into another intercalary male before reverting to a mature form. After regaining its maturity, the adult male returns to the intercalary form at the next moult. This reversal of maturity and immaturity during the extended life of adult male Iulids was first recorded by Verhoeff (1923) with T. niger and termed "periodomorphosis". Halkka (1958) describes in detail the changes in the secondary sexual characters during periodomorphosis in O. sabulosus. She lists the species of Iulids, including O. moreletii and

TABLE 3.2

	VULVAE			
Stadium	Juvenile	Intermediate	Mature	Total
7	3			3
8	15	1		16
9	7	4	4	15
10		2	4	6
11		1	8	9
12			7	7
13			2	2
14			1	1

Females were collected from grassland at Bridgewater on 23/4/74.

Blaniulids in which periodomorphosis has been reported. There is as yet no evidence of an equivalent regression in the continued moulting of females of periodomorphic Iulids.

Verhoeff (1893, 1894) described periodomorphosis in O. moreletii, and both mature and intercalary males were found in this present study. Tables 3.1 (a to f) show the stadia in which mature and intercalary males were found. Later (see Section 4.54) it will become evident that, if intercalary males of O. moreletii do moult directly to produce further intercalary males, the phenomenon is rare - at least in the habitats sampled. More commonly, the sequence of moulting is from juvenile, to mature, to intercalary, to mature. Rarely does the sequence extend further.

Blower and Fairhurst (1968) suggested that the reason why mature male Iulids do not moult directly to mature males again "might be the mechanical difficulty of casting and remoulding the elaborate gonopod cuticle". Halkka (1958) drew attention to the similarities of periodomorphosis in millipedes and allied changes in the crab, Cambarus. Scudamore (1948) had indicated that reproductive hormones were responsible for the changes in the crabs and Halkka suggested that similar involvements might be found in millipedes.

A digression

Perhaps juvenile hormone, commonly known for its role in the control of metamorphosis and reproduction in insects (Engelmann, 1970; Wigglesworth, 1970; Gilbert and King, 1974) offers an explanation for periodomorphosis. Professor C.M. Williams assayed an ether extract of a mixture of both juvenile and adult O. moreletii for juvenile hormone for me. The method of assay is given in Appendix B. Juvenile hormone was present in O. moreletii.

Let us suppose that, due to the presence of juvenile hormone, the

juvenile form of the male O. moreletii is retained until the maturation moult, whereupon in the absence of the hormone maturity is attained - i.e. as in insects. Then in the mature animal, juvenile hormone is produced again during reproduction - i.e. as in insects. Now adult insects normally do not moult further (except e.g. the Thysanura); but O. moreletii does. At the first moult after maturation, the intercalary form is produced. Halkka (1958) described the intercalary males of Iulids as intermediary in form between the mature and juvenile males. One is tempted to ask, does the intercalary male of O. moreletii (and other Iulids) result because of juvenile hormone being produced in the mature stadium during reproduction and still being present at the time of subsequent moulting? In short, does the intercalary male represent a reversal of metamorphosis? In species where the intercalary male moults directly to another intercalary male is this explained by moulting (rapidly) in the continued presence of juvenile hormone?

Williams (pers. comm.) does not consider the above hypothesis likely. He believes metamorphosis cannot be reversed and that juvenile hormone is a status quo hormone (Williams and Kafatos, 1972). However, Willis (1974) cited evidence of adult insects being forced to moult in the presence of juvenile hormone - the results giving evidence of reversal of metamorphosis.

The above is a digression from the main theme of my thesis and I have not had time to develop my ideas or facts further. But I consider the possibility of juvenile hormone (or a closely related hormone) controlling the periodomorphosis of Iulids as an exciting avenue of research to be investigated.

3.6 Growth Increments in the Life Cycle of O. moreletii

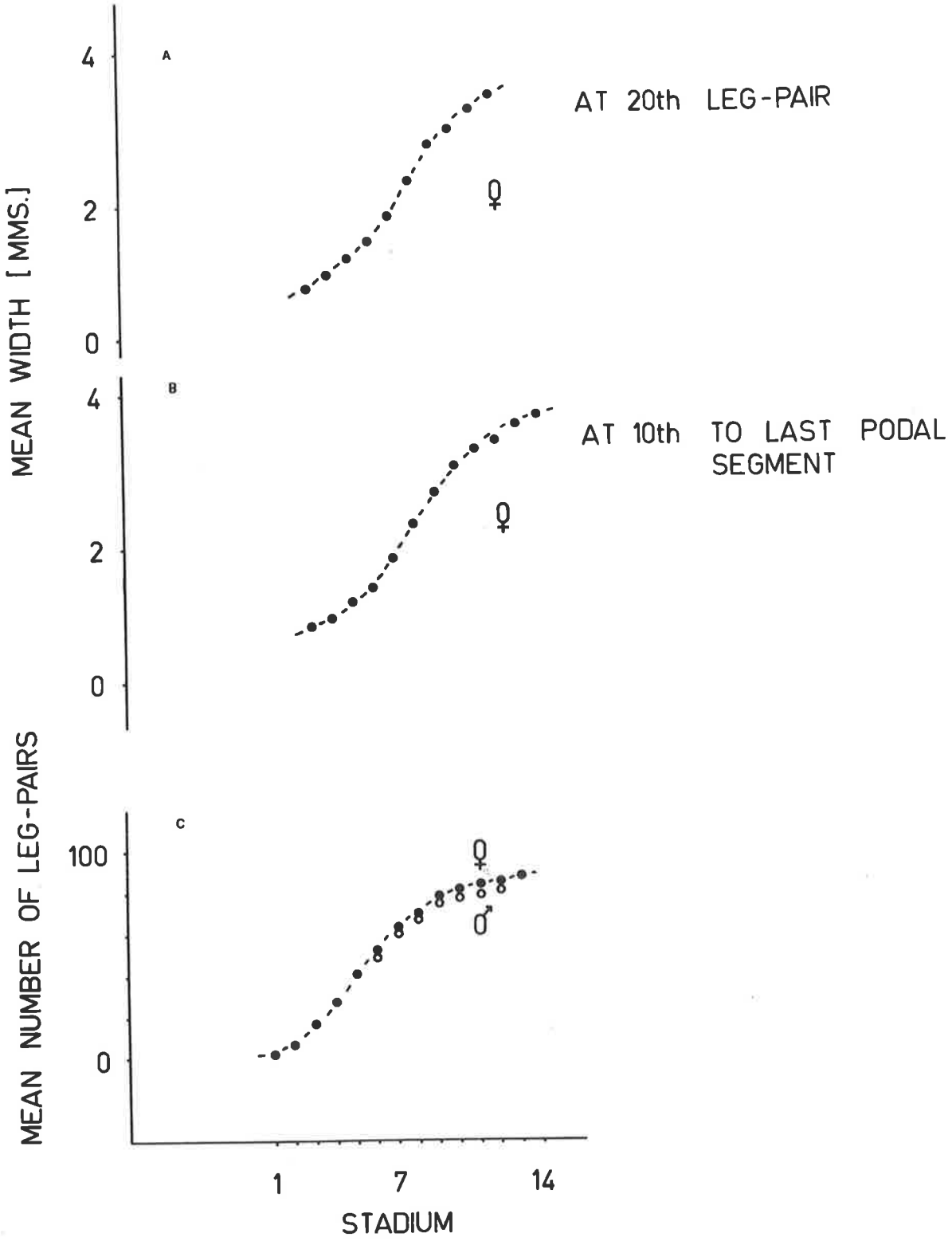
Blower and Gabbutt (1964) plotted the lengths and volumes of the

various female stadia of C. punctatus and C. latestriatus. They noted that the increase in size of the females fell off markedly after the first stadium in which maturity was possible. They suggested that this was "probably a consequence of the redirection of food material to the developing eggs". The same authors stated that a similar decrease in growth occurred in males - in this case "before the first mature stadium", but they gave no data. They argued that "sexual size and proportion differences are probably involved in addition to the redirection of food to the developing germ" when attempting to explain the earlier decrease in growth of the males compared with the females. Earlier in their paper, Blower and Gabbutt showed that the numbers of podous segments (and hence the numbers of pairs of legs) that were added at each moult also decreased after the first stadium in which maturity was possible in C. punctatus and C. latestriatus. Fairhurst (1968) working with T. niger and O. sabulosus also found a decrease in growth after maturity was reached.

Figure 3.2(c) shows the mean numbers of pairs of legs counted on at least 10 individuals of each sex in each stadium up to the thirteenth in O. moreletii. Maturity is usually reached by the tenth or eleventh stadium (see Section 3.4). The increment in numbers of pairs of legs decreases in the older stadia. The point where this decrease in growth begins (i.e. the point of inflexion in the curves) is well before maturity - at approximately the sixth stadium. However, the decrease is most marked in the tenth and older stadia.

The widths of the same individuals were also measured (at 2 points along the body) (see Figures 3.2 (a and b). This data draws essentially the same conclusions as that for the pairs of legs, except that the point at which a decrease in growth is noted is later - in approximately the eighth or ninth stadium.

FIGURE 3.2 Increase in size (width and number of pairs of legs) with stadial age.


MEAN WIDTH [MMS.]
4
2
0
A
AT 20th LEG-PAIR
♀
B
AT 10th TO LAST PODAL SEGMENT
MEAN NUMBER OF LEG-PAIRS
100
C
♂
1
7
14
STADIUM

3.7 Is O. moreletii Semelparous or Iteroparous?

The Iulids, I. scandinavius and O. pilosus are semelparous (Blower, 1969; Blower and Miller, 1974). That is, they produce only one brood during their life. On the other hand, the Iulids, C. punctatus, C. latestriatus and T. niger, and the Blaniulid, Proteroiulus fuscus are reported as iteroparous (Blower, 1969; Blower and Gabbut, 1964; Blower and Fairhurst, 1968; Blower and Miller, 1974; Cotton and Miller, 1974; Brookes, 1974). That is they are capable of producing more than one brood during their life.

The evidence for iteroparity in the above species is limited. Blower et al. have considered the continued moulting and survival of the adult females through more than one breeding season and "the very high percentage of successive female stadia carrying eggs in the breeding season" (Blower, pers. comm.) as indicative of iteroparity. The only reference I can find in the literature to more than one brood actually being reared from one female is that of Rantala (1974) with the parthenogenetic P. fuscus. Blower (pers. comm.) has obtained two broods separated by two months from the semelparous O. pilosus!

Females (≥ 10th stadium) of O. moreletii were collected from Bridgewater prior to and during the breeding season. Each female was placed with a mature male in a separate flower pot (see Figure 3.3a) in the laboratory under reduced light. Temperature varied between 10 and 25°C. Approximately 30% of the females (19/60) each laid one nest of eggs under these conditions. [The nests were usually laid within 7 cm of the surface of the soil. They were simply holes in the soil, excavated by the females and into which the eggs were laid. The eggs adhered to each other and were presumably cemented together.] Attempts were made to rear these females after they had reproduced in order to observe whether they would reproduce again. They were kept in the same flower pots. In all cases, the females died before reproducing again. Thus

FIGURE 3.3 (A & B) Flower pots used in investigations of iteroparity and fecundity. (① = clear, perforated plastic, ② = rubber band, ③ = pieces of potato, ④ earthenware flower pot, ⑤ = soil from beneath tussocks of Lomandra fibrata (Liliaceae), collected at Bridgewater, South Australia, ⑥ = plastic barrier, ⑦ = water.)

FIGURE 3.4 Diagrammatic representation of the development of the longitudinal, tubular ovary of O. moreletii.

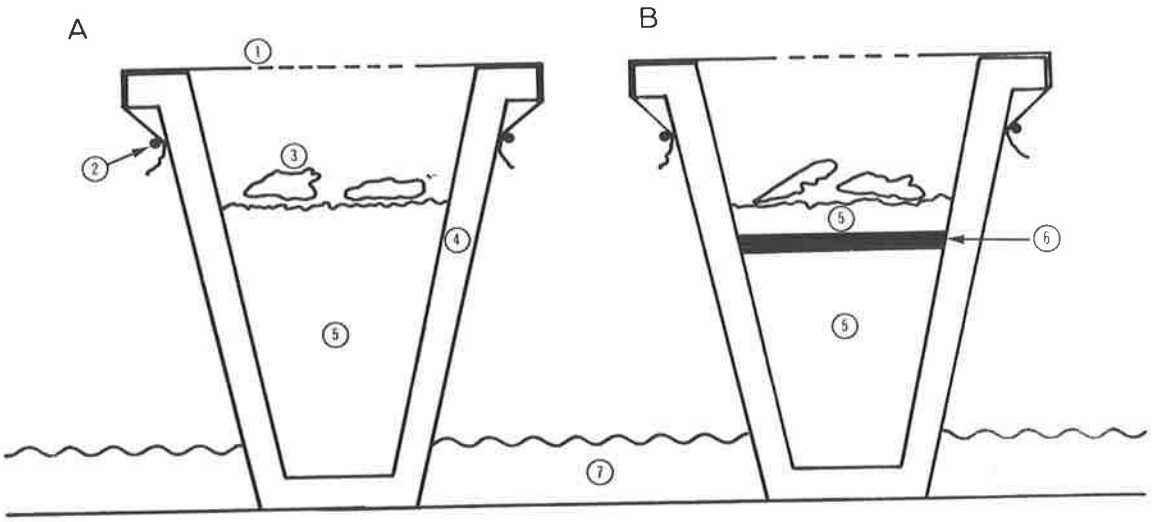
A. Small developing eggs.

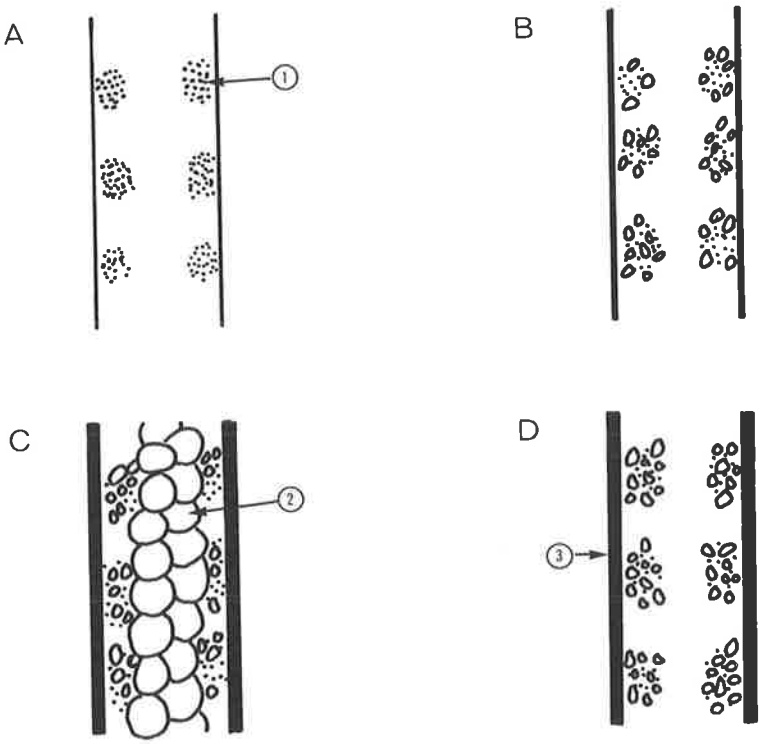
B. Large developing eggs.

C. Large mature eggs.

D. After oviposition.

(① = developing ovariole, ② = large mature eggs in the lumen of the ovary, ③ = wall of the ovary.)


A
B
1
2
3
4
5
6
7


A
B
C
D
1
2
3

iteroparity was not demonstrated (but not disproven either). Unfortunately, laboratory cultures of O. moreletii were consistently plagued by the deutonymphs of the mite, Histiostoma feroniarum, and by nematodes. The mites were ectoparasitic on O. moreletii, in many cases covering the anterior segments and head in very large numbers. The nematodes were in large numbers in and around the intersegmental membranes, again in the anterior parts of the body. Presumably, the mites and nematodes were detrimental to the survival of O. moreletii in culture.

Two of the limiting factors in studying the possibility of iteroparity in O. moreletii by the above method were 1) the space required to culture females individually under conditions suitable for oviposition, and 2) the small proportion of individuals that oviposited. As an alternative approach to the problem, the following experiment was devised. First consider the development of the gonads in female millipedes.

Millipedes have longitudinal, tubular ovaries which run ventral to the gut. In the young females of O. moreletii, the developing oocytes and associated structures are arranged segmentally on the inside of the wall of the ovary and tightly bound together in ovarioles (see Figure 3.4a). The walls of the ovary are thin and transparent. Upon maturation, the oocytes within each ovariole increase in size differentially and the closely-packed nature of the ovariole is lost (see Figure 3.4b). The walls of the ovary begin to thicken. Upon complete maturation one or more of the oocytes in each ovariole is chorionated and released into the lumen of the ovary. The lumen becomes packed tight with these mature eggs (see Figure 3.4c). Still present are the different sized undeveloped oocytes and associated bodies in the ovarioles. The wall of the ovary is now quite thick and opaque. At oviposition, the mature eggs pass forwards leaving behind a thick-walled ovary with the segmentally arranged remains of the ovarioles (see Figure 3.4d). Occasionally a few remnant mature

eggs may be seen.

Now, O. moreletii breeds only in autumn - early winter (see Sections 4.52 and 4.53). Further, it seems likely that the females lay only one clutch of eggs during a breeding season (see observations reported above on O. moreletii ovipositing in the laboratory). Data given in Section 4.53 demonstrate that all females present in the field during parts of summer have ovaries similar to those in Figure 3.4a. That is, they have compact ovarioles with small developing eggs. I would argue therefore, that if O. moreletii is iteroparous and survives from one breeding season to reproduce in subsequent seasons, then the ovaries must revert from being as in Figure 3.4d to become similar to those in Figure 3.4a during the non-breeding periods.

In very few invertebrates do the adults survive very long after final reproduction. Thus if O. moreletii is semelparous, I would expect there to be a measurable mortality soon after reproduction. Further, it is a matter of conjecture what the gonads might do after reproduction if O. moreletii is semelparous but it seems unlikely that they would revert from their state in Figure 3.4d to something similar to Figure 3.4a.

A further comment:- The breeding season of O. moreletii at Bridgewater is 3 to 4 months long (see Sections 4.52 and 4.53). I therefore suspected that individual females of O. moreletii would tolerate delays in oviposition, if they were imposed on them.

With the above considerations in mind, I argued that if during the breeding season laboratory populations of O. moreletii were set up in which oviposition was 1) allowed and 2) prevented, then given time,

a) If O. moreletii is semelparous, then higher mortalities of females would be expected when oviposition was allowed compared with when it was prevented. The ovaries should be full of mature eggs when oviposition was prevented. When oviposition was allowed it would not be

expected that the ovaries would revert to be similar to that in Figures 3.4a in those females which still survived after reproduction.

b) If O. moreletii is iteroparous, then no difference in mortality would be expected between females in either treatment (unless the conditions provided were too stressful for either group of females). The ovaries would be expected to be full of mature eggs in females where oviposition was prevented, but where oviposition was allowed, the ovaries would be expected to revert to a condition similar to that in Figure 3.4a.

The following experiment was designed to investigate the possibility of iteroparity in the females of O. moreletii. In addition, the experiment investigated the survival rates of males of O. moreletii when allowed to mate with females and when prevented.

Large numbers of adults of both sexes of O. moreletii were collected from Bridgewater on 29 and 30/3/75. Mating was first observed in the field for this particular breeding season on 28/3/75. The millipedes were added to either of two types of flower pot in the laboratory. The first type (FPI) was similar to that in Figure 3.3a. The second type (FPII) was again similar but had a plastic barrier placed 2 cm beneath the soil surface (see Figure 3.3b). The plastic barrier was intended to prevent the millipedes from burrowing into the soil - in particular to prevent the females from ovipositing. The surface soil in FPII dried out more than that in FPI. However the bases of all pots were immersed in 2 to 3 cm of water at all times and the sides of the flower pots remained equally moist. The millipedes in both types of pots showed no signs of desiccation (see Section 5.6). Copulations were seen frequently during the first 2 weeks in the pots.

In the experiment, there were 5 treatments (2 for FPI and 3 for FPII). There were 50 flower pots in all (20 of FPI and 30 of FPII). In

10 of the FPI pots, 20 females and 20 males were added to each. In the other 10 pots, 40 females only were added. In 10 of the FPII pots, 20 females and 20 males were added. In another 10 pots, 40 females were added, whilst in the remaining 10 pots, 40 males were added. The fifty pots were arranged at random in trays of water and maintained in reduced light at temperatures which varied from 11 to 22°C.

At intervals of 1 to 2 weeks, the soil was disturbed in each pot, the survival of the millipedes was checked and any nests of eggs that were present were removed. At the same time, fresh slices of potato were added to each pot for food.

On 14/7/75, the millipedes still alive in all the pots were killed in 70% alcohol. I had intended that the experiment would run for longer, but the infestations of mites and nematodes in the cultures were so bad that I feared with further time they would kill the millipedes. Perhaps if the soil and pots had been changed at each observation, the infestations of the mites and nematodes might not have been so bad.

All the females were dissected and their ovaries were assessed as either,

1) possessing mature eggs and thick ovarian walls (Figure 3.4c),

2) possessing small developing eggs and thin ovarian walls (Figure 3.4a),

or 3) otherwise. Unfortunately, I found it difficult quite often to assess a difference between females similar to Figures 3.4b and d. Thus these two categories have been summed under the term "otherwise".

The percentage of the females in each category given above was calculated for each pot. Since there were 10 pots in each treatment, an average percentage ($\bar{x} \pm$ S.E., n = 10) per pot was calculated for each treatment. The data are given in Table 3.3. Note that the percentages are

TABLE 3.3

(Mean ± S.E.)

Treatment	Mean Nos. of Nests per Female	Mean Percentage of Females with		
		Mature Eggs	Small Developing Eggs	Other-wise
FPI 20♀/20♂	0.38 ± 0.06	6.1±2.5	55.6±3.9	27.8±2.6
FPI 40♀	0.25 ± 0.06	29.0±6.3	28.5±4.4	23.8±2.7
FPII 20♀/20♂	0.02 ± 0.01	56.0±5.6	20.5±3.4	10.5±3.2
FPII 40♀	0	70.0±5.9	15.0±1.6	5.3±2.1

TABLE 3.4

% survival/flower pot in each treatment.

Treatment	Males	Females
FPI 20♀/20♂	72.2 ± 4.1	89.4 ± 2.8
FPI 40♀		81.3 ± 2.2
FPII 20♀/20♂	53.5 ± 7.3	87.0 ± 4.0
FPII 40♀		90.3 ± 4.3
FPII 40♂	68.9 ± 4.0	

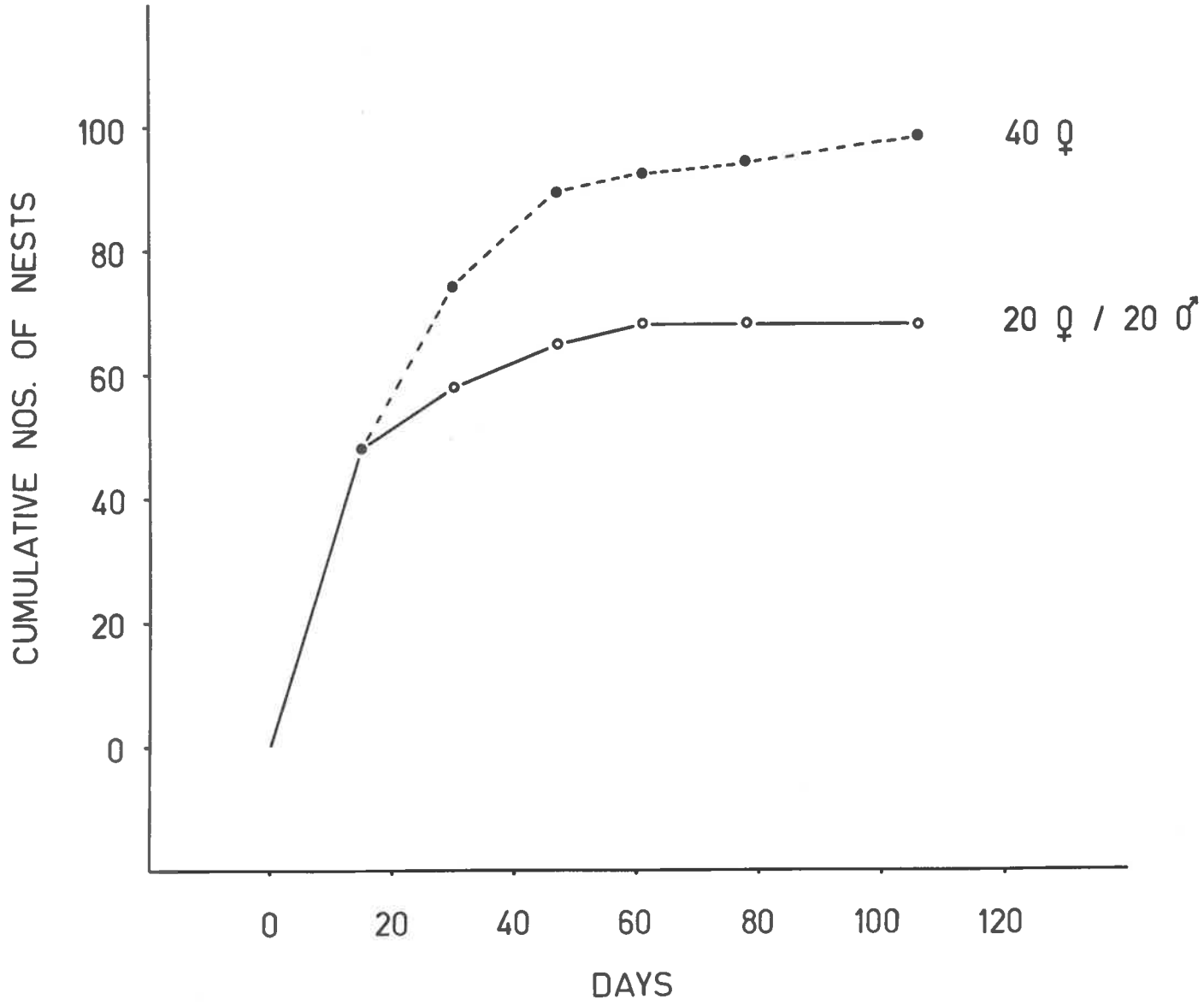
calculated on the total numbers of females initially placed in the pots and not on the numbers still living on 14/7/75. The numbers of nests laid per female per pot in each treatment are also given in Table 3.3. In Figure 3.5, the cumulative numbers of nests of eggs that were laid from 30/3/75 to 14/7/75 are given. Table 3.4 gives the percentage survivals of the males and females per pot for each treatment.

The data in Figure 3.5 show that most of the eggs were laid within 30 to 40 days of placing the millipedes in the pots. Thus the period of observation of post-reproductive survival was approximately 70 days (35 to 106). The results in Table 3.3 suggest that O. moreletii is probably iteroparous. Survival of females was similar irrespective of whether they had oviposited or not. Further, the majority of ovaries contained mature eggs when oviposition was prevented, but when oviposition was allowed very few females contained mature eggs and the majority (especially where males were provided) had small developing eggs and thin ovarian walls (i.e. as in Figure 3.4a).

With regard to the individual pots in the FPI treatments, no correlations were found between the survivals of the females (range 67.5 to 100%) and the numbers of nests produced (range .025 to .600 per female).

Rather higher numbers of nests were laid by the females without males in FPI pots than expected. As stated previously, the animals were collected from the field 1 and 2 days after mating was first observed. Mating was seen in the field for up to 10 to 12 weeks (see Section 4.51). I expected very few females to oviposit when cultured without males because I did not expect them to have mated before capture. However 98 nests were produced by the total of 400 females. Eggs from these nests hatched successfully. This result suggests that mating was occurring in the field prior to my observing it. The relatively high numbers of females with mature eggs (29.0% c.f. 6.1% in females provided with males) however might

FIGURE 3.5 Cumulative numbers of nests laid in flower pots by *O. moreletii*.


CUMULATIVE NOS. OF NESTS
100
80
60
40
20
0
0
20
40
60
80
100
120
DAYS
40 ♀
20 ♀ / 20 ♂

suggest that many of these females were not ovipositing because of the lack of males. On the other hand, the greater density of females (40 per pot c.f. 20 per pot where males were provided) might have inhibited oviposition in some females.

In many of the females in FPII pots, the mature eggs were split and obviously degenerating within the ovary. Whether this was due to the ill health of the female or was part of a natural resorption of unlaid eggs remains unknown.

In conclusion, the data given above by no means demonstrate that O. moreletii is iteroparous. They simply suggest that it is possible. Later (see Chapter 4), it will be argued from studies of field populations, that iteroparity is a rarity if indeed it occurs at all. Until individual females are reared successfully from one reproduction to another or until anatomical features (e.g. the equivalent of the mammalian corpora lutea) are found to indicate prior breeding, the question of whether O. moreletii is capable of iteroparity or not will remain unsolved.

The survivals of the males in the treatments were consistently lower than those of the females (see Table 3.4). There were no obvious differences in the survivals of males in the presence or absence of females. These findings will be discussed later (see Section 4.57).

3.8 Fecundity of O. moreletii

In March 1974, 120 females and 120 males were collected at Bridgewater and placed in 12 flower pots (10 of each sex in each) similar to those in Figure 3.3a. After 3 weeks the pots were inspected for nests of eggs. Twelve nests were laid by the 120 females. The numbers of eggs per nest ranged from 161 to 385 with a mean of 250.2.

In May 1974, 90 females in the ninth to 13th stadia were collected at Bridgewater. These females were killed in 70% alcohol and their widths at the 20th pair of legs and their ages were determined. Then the females were dissected and the numbers of mature eggs present were recorded for each.

In 45 of the females, mature eggs were found. The relationships between the numbers of eggs and the stadia and widths of the females are shown in Figures 3.6 (a and b).

Because the maturation of eggs takes time, many of the lower numbers of eggs found in some females are probably due to these females not yet developing all their eggs. Therefore it is probably unrealistic to average the numbers of eggs per female in order to obtain an average fecundity. Equally, it is probably unrealistic to average the numbers of eggs in females in each stadium or in size ranges (e.g. widths) in order to obtain an average fecundity per stadium or size range. Perhaps, the maximum numbers of eggs found in individuals in a sample taken during the breeding season reflect approximately the fecundity of the females. If so, the data suggest that the fecundity of O. moreletii is approximately 150 to 350 eggs per female - but this is a very rough estimate.

Although there was no obvious increase in fecundity with stadium there was an increase in fecundity with width ($r^*_{45} = +0.576$, $p < .05$). Presumably there were just not enough values for a relationship with stadium to be borne out.

The above two estimates of fecundity refer to females collected in a grassland at Bridgewater in autumn 1974. Of course, fecundity may vary according to the time during the breeding season when the estimates are made, vary from one year to the next, and vary from one habitat to

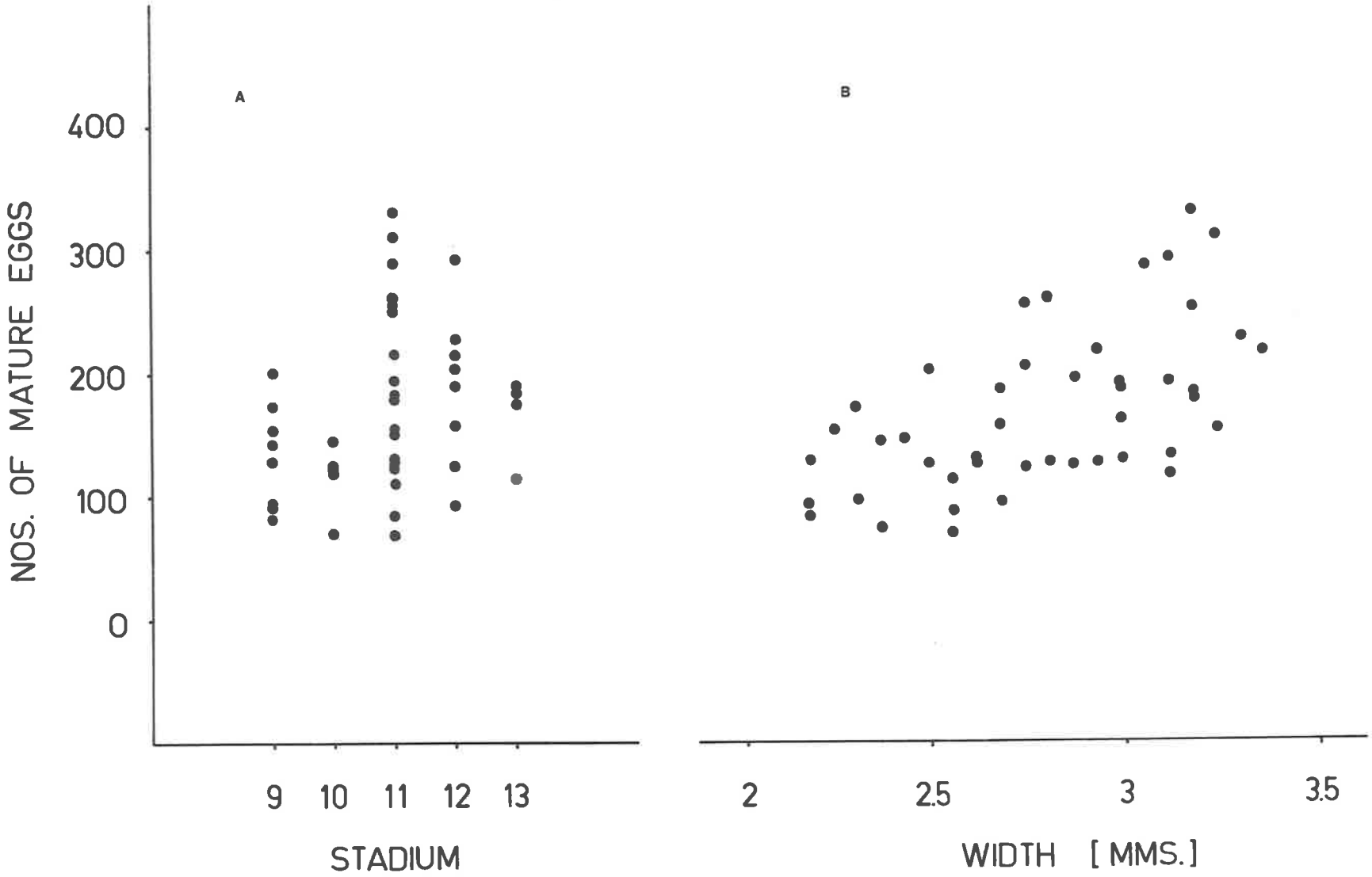
---

* The subscript 45 indicates the number of individuals used; the number of degrees of freedom for r are therefore 43.

FIGURE 3.6 Numbers of mature eggs counted in females of O. moreletii with respect to the female's:-

A. Age (stadium)

B. Size (width).


A
B
400
300
200
100
0
NOS. OF MATURE EGGS
9
10
11
12
13
STADIUM
2
2.5
3
3.5
WIDTH [MMS.]

another. Indeed, in collections made during autumn 1975 (see Chapter 4), females in the 10th and 11th stadium bore an average of 122.0 (range: 52 to 173) mature eggs per female in a grassland whilst at the same time 79.7 (range 17 to 204) mature eggs per female in a woodland.

The above estimates of fecundity of course refer only to one reproduction per female. If it is accepted that O. moreletii is capable of iteroparity, then the fecundity of some females may be two or more times the above figures.

3.9 Post-Embryonic Development of Australiosoma castaneum

Data on the post-embryonic development of Australiosoma castaneum was limited due to the rarity of the species in the study area, especially during summer. No attempts were made to culture the species in the laboratory. However, by considering the few specimens collected both casually and systematically during sampling for O. moreletii, the following statements can be made.

The final four stadia in the life cycle were collected. The numbers of podous segments (and apodous segments in brackets) in each of these stadia were 14(2) or 15(1), 16(1), 17(1) and 18(1) (adult). Since the number of apodous segments in one stadium equals the number of podous segments added at the next moult in millipedes, and since no A. castaneum were found with 14 podous and 1 apodous segments, I have included individuals with 14 and 15 podous segments in one stadium. If it is accepted that all Polydesmids have seven juvenile stadia (Blower and Gabbutt, 1964), then those individuals of A. castaneum with 14 or 15 podous segments are in the 5th stadium. A. castaneum has no ocelli and the repugnatorial (defence) glands are not obvious externally.

Juvenile males could be differentiated in the 5th stadium (Perhaps they can be differentiated earlier than that). The anterior pair of legs

on the seventh segment was already lost and replaced by the bulbous rudiments of the gonopods. The gonopods of the mature male are extremely large and complex. The first pair of legs in the male are always ambulatory.

A. castaneum like other Polydesmids (except perhaps Brachydesmus superus (Stephenson, 1961)) has only one adult stadium.

In May 1974, eleven adult females of A. castaneum were collected which contained large mature eggs in their ovaries. The range in numbers of mature eggs per female was 255 to 672 with a mean of 480.4.

3.10 Post-Embryonic Development of Dimerogonus sp.

Like A. castaneum, Dimerogonus sp. was difficult to find in the study area for much of the year. However, the species was found in moderate numbers during the wetter months beneath dense infestations of the introduced Chasmanthe aethiopica (Iridaceae)

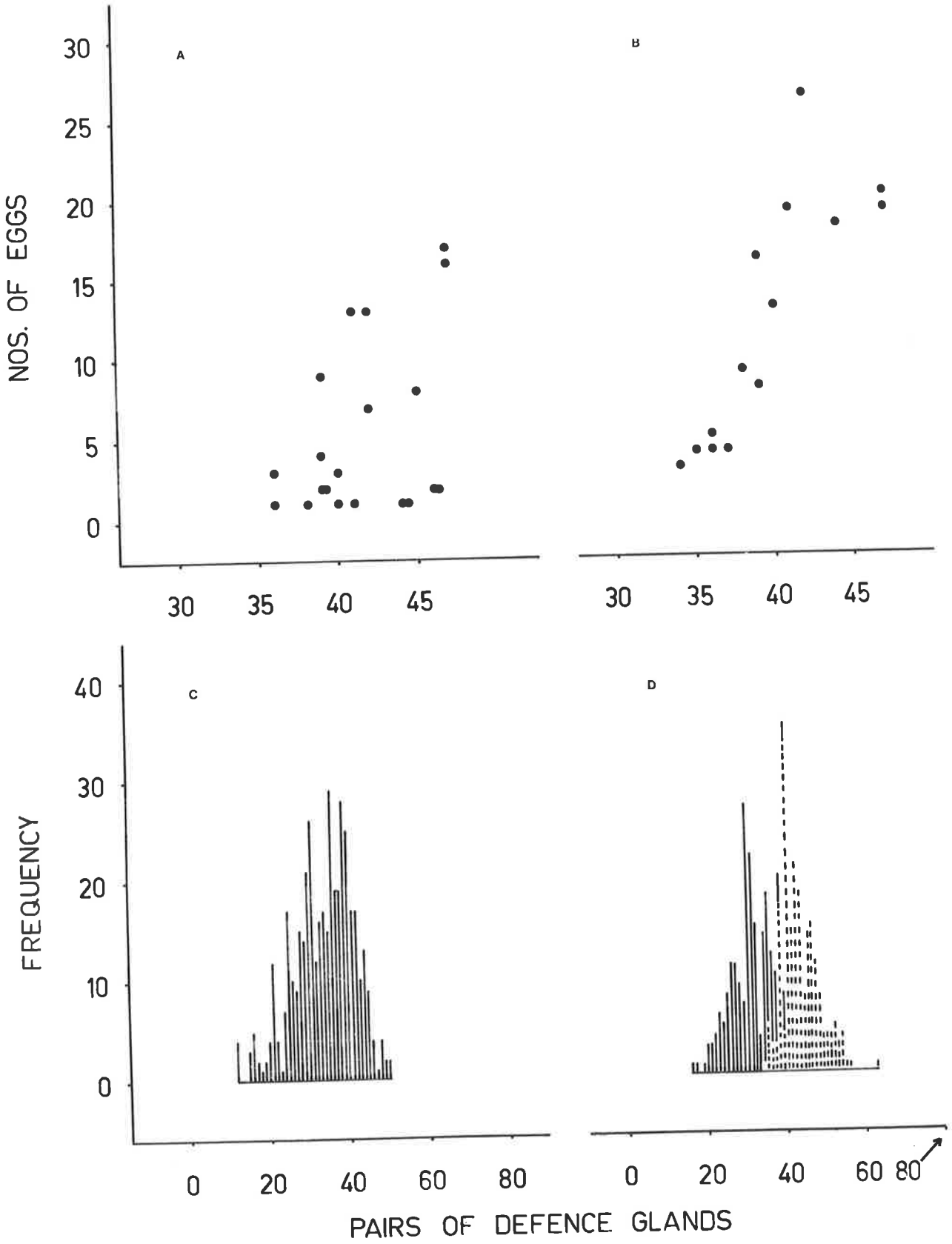
Dimerogonus sp. has ocelli but their development is too irregular to be useful in determining the stadia of individuals. Attempts were made to distinguish stadia by characterizing them by their numbers of segments, pairs of legs and pairs of repugnatorial glands. However there proved to be too much variation in these characters to be of use. Figures 3.7 (c and d) show the frequencies with which individuals with given numbers of pairs of repugnatorial glands were collected. The repugnatorial glands are very obvious externally in Dimercgonus sp. The lack of discreteness in the data that is necessary to characterize stadia is evident in Figures 3.7 (c and d).

Juvenile males of Dimerogonus sp. have ambulatory first pairs of legs. The gonopods on the seventh segment appear more advanced in juveniles of Dimerogonus sp. than they do in O. moreletii. At maturity, the first pair of legs of the male Dimerogonus sp. are modified. Both juvenile and mature males were found in the stages in the life cycle with 34 to 40 pairs of repugnatorial glands (see Figure 3.7d). This apparently

FIGURE 3.7(A) Numbers of mature eggs found in females of Dimerogonus sp. as a function of the numbers of pairs of repugnatorial glands of the females.

FIGURE 3.7(B) Numbers of mature and large developing eggs found in females of Dimerogonus sp. as a function of the numbers of pairs of repugnatorial glands of the females.

FIGURE 3.7(C and D) Numbers of females (C) and males (D) collected with given numbers of pairs of repugnatorial glands. The males are divided into juveniles (solid lines) and adults (dashes).


A
B
C
D
NOS. OF EGGS
FREQUENCY
PAIRS OF DEFENCE GLANDS
0
5
10
15
20
25
30
35
40
45
60
80

is the period of maturation of the males in Dimerogonus sp. The finding of mature males with up to 63 pairs of repugnatorial glands suggests that the males of Dimerogonus sp. moult after reaching maturity. However, no stages suggestive of intercalary males were found. Very few animals were collected during the drier months of the year and it is possible that intercalary males might be found then. Periodomorphosis has not yet been demonstrated in the Cambalidae, although Verhoeff (1943) suspected it.

Mature eggs were found in females with 34 and more pairs of repugnatorial glands. The mature eggs of Dimerogonus sp. are extremely large compared with those of A. castaneum and O. moreletii. All are to some degree ovoid:-

	Diameters (mm.)
Dimerogonus sp.	≃ 2.0 x 1.4
A. castaneum	≃ 0.6 x 0.5
O. moreletii	≃ 0.7 x 0.6

The chorion of the eggs in Dimerogonus sp. is soft compared with that of the other 2 species.

In June 1974 (five) and August 1975 (fifteen), 20 females of Dimerogonus sp. in which mature eggs were found were collected from Bridgewater. The range in numbers of mature eggs was 1 to 17. Given that the number of pairs of repugnatorial glands is a measure of size, the numbers of mature eggs in Dimerogonus sp. increase with size (see Figure 3.7a). In some cases, low numbers of mature eggs were recorded for large females. Probably, these females were collected before they had developed very many of their eggs (The prevalence of small developing eggs in these females suggested they had not already laid most of their eggs).

In June 1974, nine females were collected which had large developing eggs only. These are white and contrast with the yellow mature

eggs. The five females with mature eggs also had some large developing eggs. When for these fourteen females, the numbers of mature and large developing eggs were plotted against size a more marked relationship was found (see Figure 3.7b) because the influence of slow development in some of the large females was lessened.

4. LIFE HISTORY, ABUNDANCE AND ACTIVITY

4.1 Introduction

The work reported in this chapter was done primarily to determine the life history of O. moreletii in South-Eastern Australia. In addition to data on life history, some information was obtained on changes in the abundance and activity of the species. Further, limited information was gathered on the life histories of the two native species, Dimerogonus sp. and A. castaneum.

4.2 Literature Review

At the beginning of this chapter, I consider three aspects of the literature should be reviewed.

4.21 Maturation in Iuliform millipedes

The Iulids, I. scandinavius and C. punctatus normally take three years to mature and reproduce, whilst O. pilosus takes two years (Blower and Gabbutt, 1964; Blower 1970; Blower and Miller, 1974). The Blaniulids, I. varicornis and P. fuscus normally take two and three years respectively to reproduce (Brookes, 1974). However, in very warm weather, Brookes (1974) found that P. fuscus could reproduce after only two years.

By direct sampling of soil and litter, Blower and Gabbutt (1964) found that C. latestriatus took two years to mature and reproduce in a Devon oak wood. On sand dunes in Scotland, Cotton and Miller (1974) set pitfall traps and suggested that the males of C. latestriatus matured earlier there than in Devon, with respect to stadium. The maturity of the females on the other hand was delayed a stadium in Scotland. Deshmukh (p. 601 in Blower, 1974) stated that by direct sampling at the same site as Cotton and Miller (1974) used, he had shown that C. latestriatus matured after three years.

In T. niger, the time to maturity and reproduction is more complex.

The species oviposits in spring, the eggs hatch and the larvae develop to the fifth or sixth stadium by the next spring (Fairhurst, 1974). By the subsequent autumn, the millipedes are in the seventh or eighth stadium. Then by the following spring, when the millipedes are two years old, they are in the eighth or ninth stadium (Fairhurst, 1974). Fairhurst found that some of the males in the eighth stadium in autumn, eighteen months after oviposition, were mature and copulated. The function of this copulation, when oviposition occurred only in spring, remained obscure. Of the two year old males in the eighth stadium in spring, Fairhurst found only 2.5% were immature. He concluded that the majority of male T. niger matured after 2 years. However he noted that Sahli (1966) had found males of this same species maturing as late as the tenth stadium and added that maturation of male T. niger could take as long as three years. The eighth stadium in females of T. niger was immature, but the ninth was mature. Thus some females matured after two years, but others took a further year. The relative frequency of females in the eighth and ninth stadia after 2 years varied from one year to the next. Therefore the maturation and reproduction of different generations of females varied from two to three years.

Fairhurst (1974) set pitfall traps in four different habitats (sand dune, forest edge, young forest and old forest) to collect data on the development of maturity by O. sabulosus. He calculated the relative frequencies of the mature males in each stadium that he caught in each habitat. He assumed that a high frequency of mature males in a particular stadium indicated that maturity was common for that stadium. Fairhurst claimed that his catches in the sand dune suggested that most males matured there in the ninth stadium. That meant they were mature after two years. In addition, Fairhurst claimed a delay in the other three habitats in the achievement of maturity by the males, greatest delay being in the old forest where maturation was commonly at the eleventh stadium.

That meant, maturation was being delayed there a further year. However, the numbers of millipedes caught (in particular in the young and old forest) and on which Fairhurst based his conclusions were extremely small. His conclusions were not particularly convincing.

Fairhurst (1974) attempted to supplement his above findings by calculating the percentages of mature and juvenile males in the ninth stadium of O. sabulosus at each site. He found from his catches that very few males were immature in the ninth stadium in the sand dune, but relatively more were immature in the old forest, thus suggesting that maturity was delayed in the latter habitat. However, again Fairhurst's data suffered from lack of animals (e.g. a total of 9 males in the ninth stadium in the old forest) and was not convincing. In addition, although Fairhurst acknowledged that immature and mature males differed in their activities, he disregarded the possibility that their relative activities might be different in different habitats. Thus, using catches to compare the degrees of maturity in different habitats could be dangerous. Fairhurst did in fact take some "plot samples" to determine what was present as well as what was active, but he did this only in the old forest. He found very few males in the ninth stadium were mature in this habitat. It is important to take samples of what is present rather than active in all habitats to show that maturation varies from one to the other.

Fairhurst (1974) stated briefly that the maturation of the females of O. sabulosus followed similar trends to the males. He suggested that the females matured in three years in the sand dune and in four years in the forest. However, he gave virtually no data to substantiate this conclusion.

In attempting to explain variations in the development of maturity of O. sabulosus in the different habitats, Fairhurst (1974) first suggested that in the arid sand dune "the rules governing ..... the onset of

maturation may be strictly enforced". In the moist and "congenial" forest, "early maturation ..... may not be so vital". Secondly, Fairhurst suggested that the warmer temperatures in the sand dune might lead to a more rapid development of maturity compared with the cool forest. Thirdly, Fairhurst suggested that the variations in the development of maturity could be "a response to population pressure". I take this last suggestion of Fairhurst's to mean either 1) that the development of maturity by individuals could be influenced by the density of the population, or 2) that the movements of mature and immature individuals away from a population could be influenced differently by density. Thus the maturity of the remaining population would be a function of the previous density.

There is therefore some mention in the literature of variations in the development of maturity within Iuliform millipedes, although in some cases (e.g. Fairhurst 1974) such variation is not well demonstrated.

4.22 Seasonality of Mature and Intercalary Males in Periodomorphic Species

Halkka (1958) summarised the known seasonal occurrences of mature and intercalary males in periodomorphic millipedes. In the Mediterranean region, the mature males of several species (including O. moreletii and O. sabulosus) were found commonly in autumn. The intercalary males on the other hand were found commonly in the spring. Unfortunately, collections during summer and winter were too limited to give adequate data on the forms present then. Verhoeff (1940) in central Europe and Halkka (1958) in Finland both reported that mature males of O. sabulosus predominated during the summer months, but at other times of the year, the intercalary males were more common. The Blaniulid, Nopoiulus armatus, in central Europe showed a marked seasonality in mature and intercalary males, the former common in the breeding season, the latter in the inactive remainder

of the year (Verhoeff, 1939). Fairhurst (1968 - I have seen only his summary) referring to O. sabulosus and T. niger stated that the intercalary males "predominated outside the active season".

Verhoeff (1939) suggested a causal relationship between the occurrence of intercalary males of periodomorphic species during the inactive and unfavourable seasons of the year. Halkka (1958), whilst agreeing that the predominance of intercalary males coincided "with unfavourable seasons in a fair number of Diplopod species", was concerned that in certain species (e.g. T. niger, O. sabulosus, P. fuscus), both mature and intercalary (schalt) males could be found at all times of the year. She preferred to "emphasize the significance of the schalt stage as an intervening stage between two copulatory stages." In other words, she attributed little or no ecological importance to the intercalary male Halkka demonstrated that the intercalary males of O. sabulosus have active gonads. Fairhurst (1974 - in discussion) regarded the intercalary males of Iulids simply as "resting stages in which sperm is built up for the active copulatory stage".

4.23 Activity

There are many references in the literature (e.g. Brade-Birks, 1922; Cloudsley-Thompson, 1949, 1952) to the wanderings of millipedes on the surface of the ground. However there are few references in which the activities of millipedes have been rigorously studied. Barlow (1957, 1958) set pitfall traps in Holland for I. scandinavius, O. sabulosus, C. silvarum, C. frisius, Brachyiulus littoralis and P. denticulatus. The numbers caught in traps are functions of both 1) the abundance of stages in the life cycle that are capable of being active and 2) their activity. Barlow realised this but ignored abundance and equated activity with catch. Barlow found that O. sabulosus and P. denticulatus were most "active" during

summer, B. littoralis in spring and I. scandinavius, C. silvarum and C. frisius had peaks in "activity in spring and autumn. Barlow described the weather (temperature and precipitation) typical of the peaks and troughs in "activity" for each species. He attempted to correlate weather with the "activities" of the species. Only with C. frisius were significant correlations obtained (with temperature). Consistently, Barlow calculated higher correlation coefficients between "activity" and temperature compared with "activity" and precipitation. He concluded that temperature was more important in stimulating activity. Banerjee (1967a) set pitfall traps for C. punctatus, T. niger and P. angustus in England. He found for each species, the peaks in the numbers trapped were in spring. He was unable to correlate the numbers trapped with weather data. Several other authors (e.g. Blower and Fairhurst, 1968; Blower, 1970; Lewis, 1971 (a and b); Cotton and Miller, 1974) have described seasonal changes in catches of active millipedes.

Blower and Fairhurst (1968) found very few juveniles in collections of T. niger in a house. Blower (1970) trapped far more adults of I. scandinavius and T. niger than juveniles in a sycamore ash wood. Cotton and Miller (1974) trapped few juveniles of C. latestriatus in a sand dune although they strongly suspected that juveniles were reasonably abundant. This circumstantial evidence suggests that juvenile Iulids are less active than adults.

Fairhurst (1974) stated there was "evidence to suggest that there are distinct behavioural differences between immatures and adults" of O. sabulosus. I am unsure whether Fairhurst was referring to data in his present paper or to another source (perhaps Fairhurst (1968) of which I have read only the summary). If the former, his statement is unconvincing. A table in Fairhurst (1974) showed 44.5% (N = 9) (sic) of O. sabulosus taken in pitfall traps in an old forest were juvenile, whilst plot samples

in the same area showed 93.9% (N = 114) were juveniles. The numbers of individuals involved were very low, especially in the pitfall traps.

4.3 Habitat and Weather

Studies of O. moreletii were made primarily at Bridgewater in the Mt. Lofty Ranges, South Australia. At Bridgewater, two different habitats were studied - 1) an open grassland (see Figure 4.1) and 2) a dry sclerophyllous woodland (see Figure 4.2). The positions of the grassland and woodland within the outbreak of O. moreletii at Bridgewater are shown in Figure 2.5.

The dominant plants in the grassland were clovers (Trifolium subterraneum and T. campestre), wild oat (Avena fatua), barley grass (Hordeum leporinum), rye grass (Lolium rigidum), Yorkshire fog (Holcus lanatus); spear grass (Stipa sp.), silver grass (Vulpia myuros), dock (Rumex sp.), soft brome (Bromus mollis), rip-gut brome (B. diandrus) and Cape dandelion (Arctotheca calendula). Hereafter all these plants will be referred to collectively as pasture grasses.

Tussocks of Lomandra fibrata (Liliaceae) (see Figure 4.1) were common in the grassland, but their distribution was very patchy. Also common were bracken (Pteridium esculentum) and blackberry (Rubus fruticosus). The bracken and blackberry were slashed regularly during the period of study to check their spread.

Hereford steers grazed the grassland at a density of 0.40 steers/hectare. The grassland was consequently extremely undergrazed and plant growth was prolific.

The woodland (Engelbrook Reserve) was briefly described by Lee and Wood (1968) as "an area of dry sclerophyll woodland (Eucalyptus obliqua L'Herit - E. baxteri (Benth.) association) on a yellow podzolic soil". As well as the stringy-barks (E. obliqua and E. baxteri), the tree and shrub canopies of the woodland were dominated by Banksia marginata,

FIGURE 4.1 The open grassland at Bridgewater.

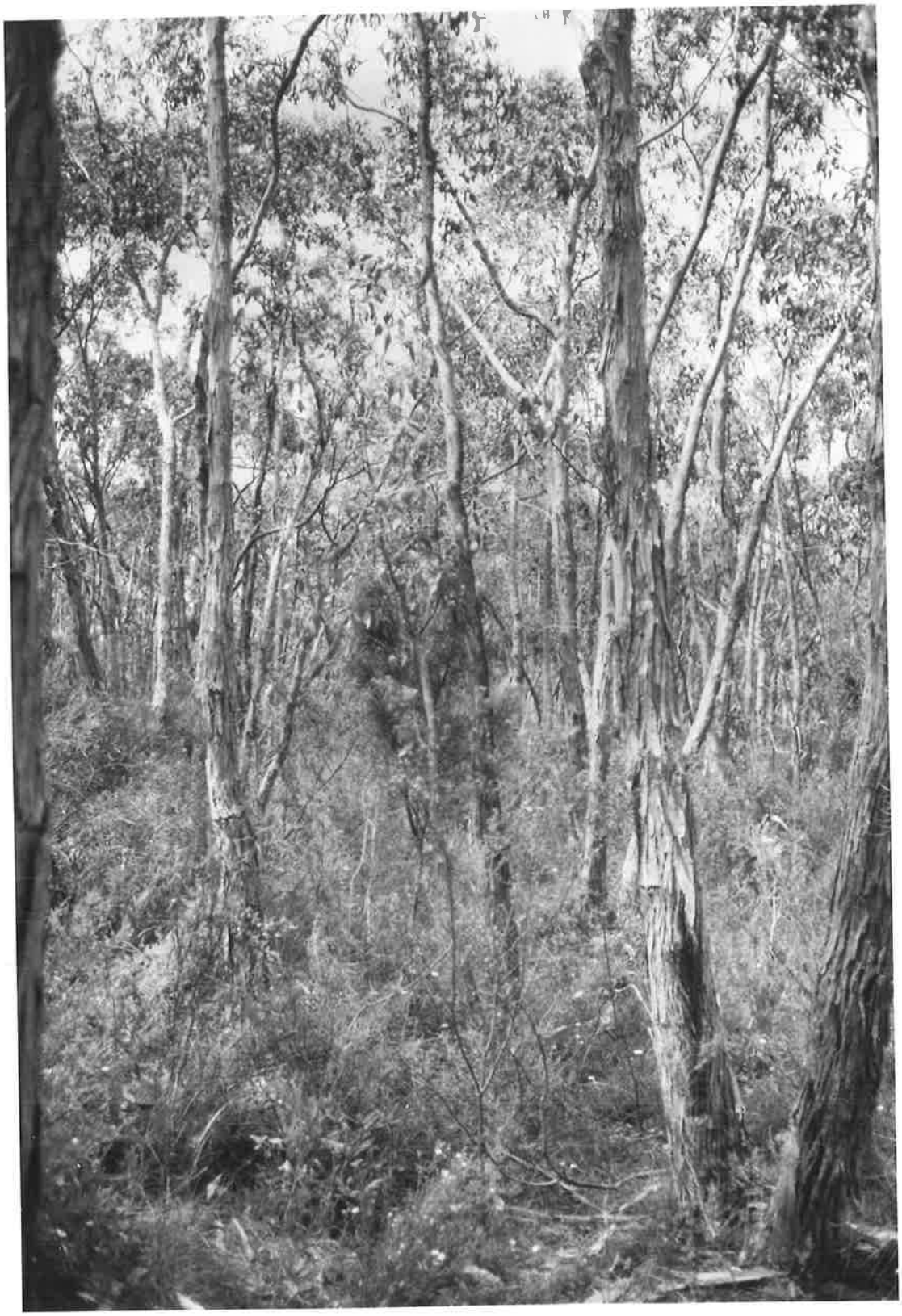
A. During winter - showing tussocks of *L. fibrata* and areas of pasture grasses.

B. During spring - early summer - showing the growth of pasture grasses at this time.


A


B

FIGURE 4.2 The dry sclerophyllous woodland at Bridgewater.



blackwood (Acacia melanoxylon), wattles (A. retinoides and A. gunnii needlebush (Hakea ulicina and H. rostrata), tea tree (Leptospermum pubescens) and broom (Cytisus sp.). Specht (1972) listed the many understorey plants normally associated with E. obliqua - E. baxteri alliances in the Mt. Lofty Ranges. Engelbrook Reserve appeared typical of Specht's description.

The closest reliable weather station to Bridgewater was at Stirling (5 km to the west). The average monthly rainfall and temperatures for Stirling are listed in Appendix Tables 1 to 3. The rainfall and the average maximum and minimum temperatures as recorded for each month at Stirling during the present study are given in Figures 4.3 (a & b). Stirling is slightly wetter and cooler than Bridgewater but the trends in weather are similar at both places.

Comparisons of Microclimate

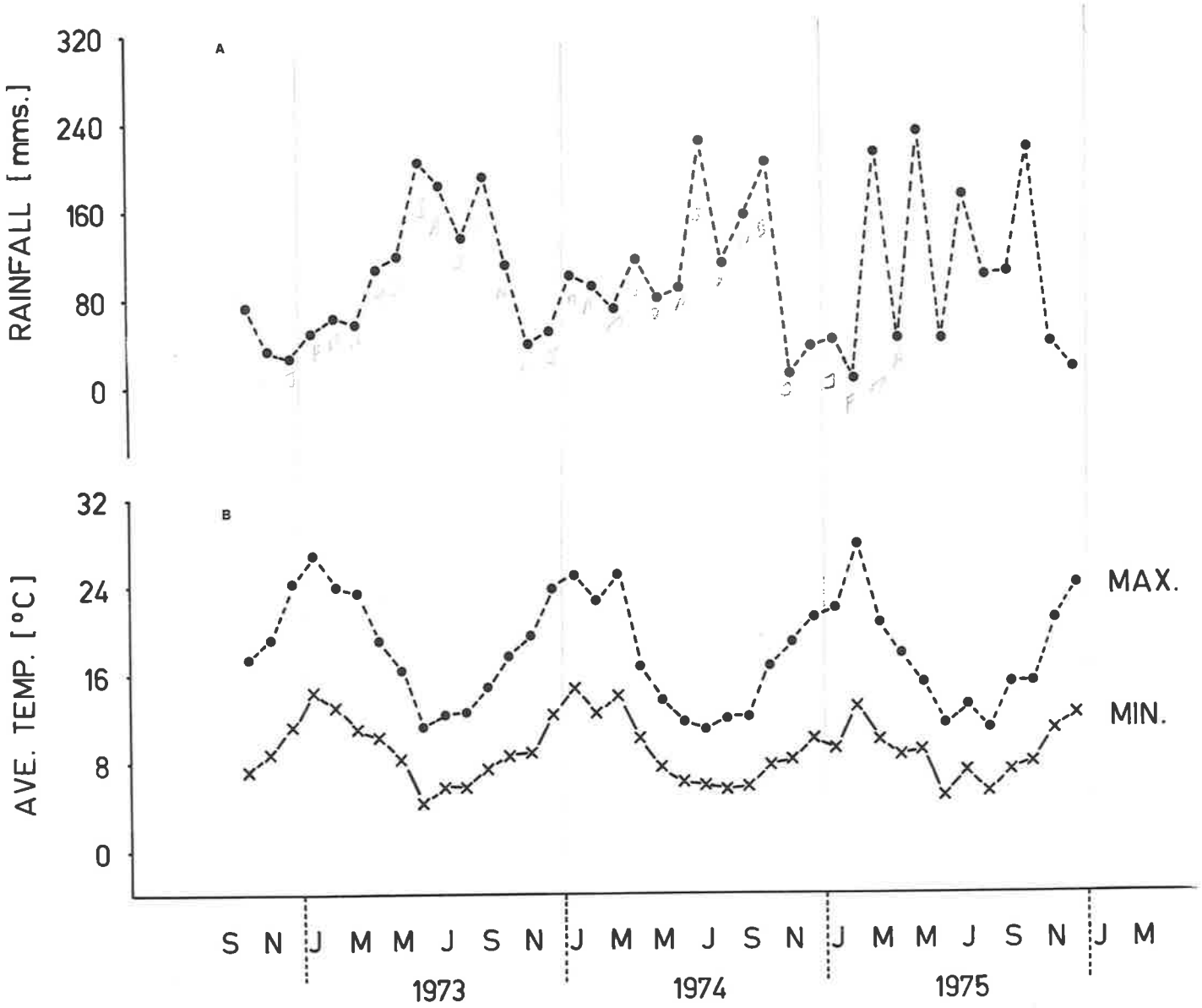
Sampling outlined in the next section (4.4) distinguishes grassland from woodland and pasture grasses from tussocks of L. fibrata. Here it is important to recognize differences in the microclimates of these different habitats.

On two days in mid-summer, the temperatures at the soil-litter interface at 10 sites in both the grassland (pasture grasses) and woodland were measured between 1.00 and 3.00 p.m. using an ordinary thermometer. Each site had a substantial (> 5 cm) layer of litter. The temperatures (°C) (mean and range) were as follows:-

	Grassland	Woodland
Day 1	33 (25-43)	21 (16-25)
Day 2	28 (26-30)	20 (16-28)

At half of these same sites, the relative humidity was measured at the soil-litter interface using a Lambrecht Hair Hygrometer. The humidities (%) (mean and range) were as follows:-

FIGURE 4.3 (a & b) Weather recorded at Stirling during the present study.


A
RAINFALL [mms.]
320
240
160
80
0
B
AVE. TEMP. [°C]
32
24
16
8
0
MAX.
MIN.
S N J M M J S N J M M J S N J M M J S N J M
1973
1974
1975

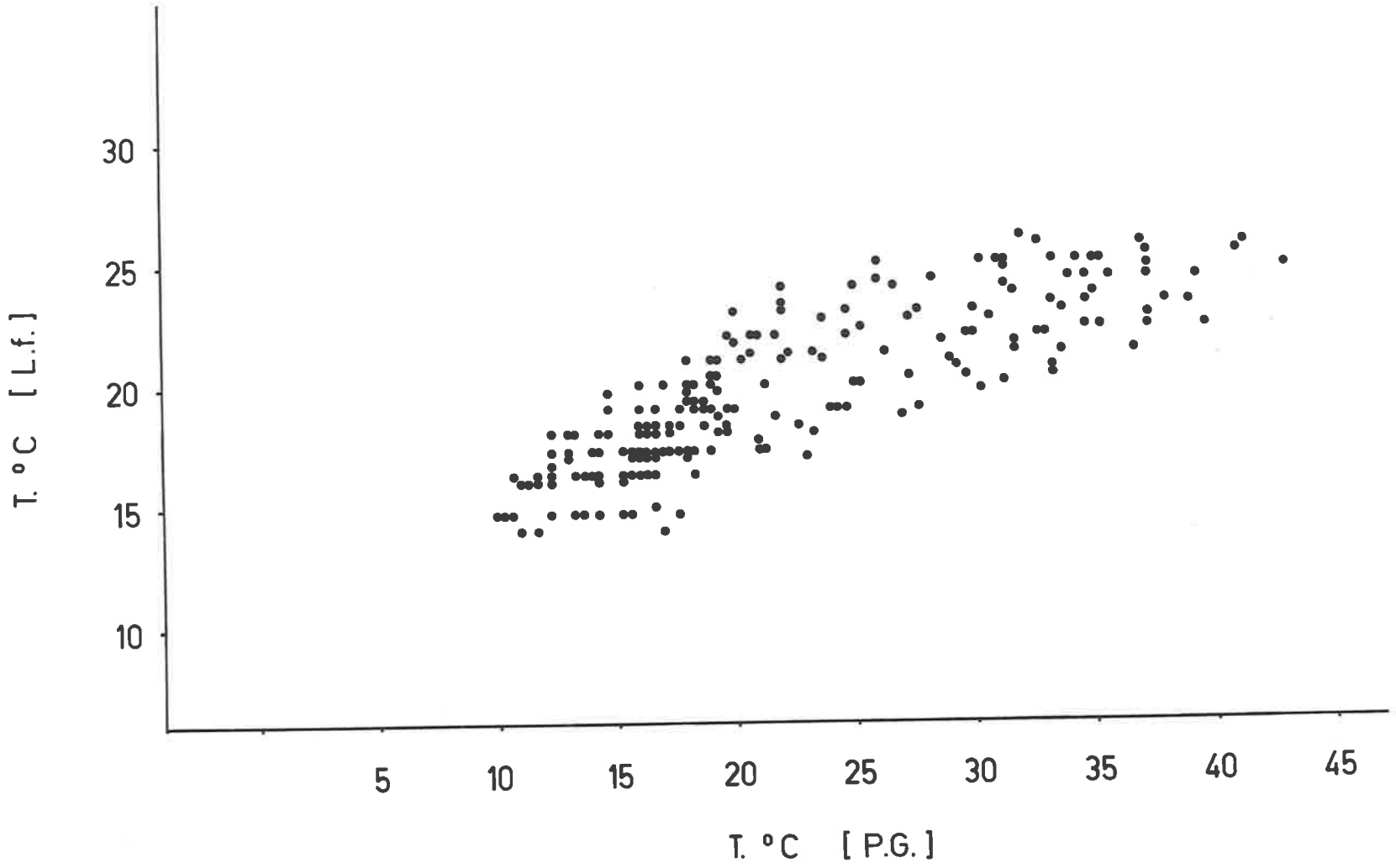
	Grassland	Woodland
Day 1	47 (45-51)	64 (61-68)
Day 2	55 (51-64)	63 (59-70)

These results suggest that the weather in the woodland was cooler and moister during mid-summer than it was in the grassland (as represented by the pasture grasses).

The top few cm of soil beneath the tussocks of L. fibrata in the grassland were moister than the soil beneath the pasture grasses during late summer. During a particularly arid period, samples of soil from beneath 5 tussocks and 5 adjacent areas of pasture grasses were collected, weighed, oven-dried, reweighed and the percentage water contents of each sample were calculated. The average percentage water content beneath the tussocks was 13.5 $\pm$ 2.0% ($\bar{x} \pm$ S.E.) and beneath the pasture grasses 4.6 $\pm$ 0.3%. The difference between the two was significant ($t = 4.49$, $p < .05$). Crawford (unpublished data) measured the pFs of these soils. The pF of a soil is a measure of the strength with which the water present is held by the soil. In short, the greater the pF, the less water is likely to be available to e.g. a millipede. Crawford found that the soil beneath the pasture grasses had a greater pF than that beneath the tussocks. This is added information to suggest that conditions beneath the tussocks were moister during summer than they were beneath the pasture grasses for O. moreletii. During winter, the reverse appeared to be the case. Probably rain was shed off the tussocks onto nearby pasture grasses, thus causing the soil below the tussock to remain drier during winter.

In late summer, thermistors (connected to a Grant Multipoint Temperature Recorder) were placed at the soil litter interface beneath 1) a tussock of L. fibrata (3 thermistors) and 2) the surrounding pasture grasses (3 thermistors). Every hour for 254 hours, temperatures were recorded. The simultaneous temperatures (averages of the three replicates) for each habitat are plotted in Figure 4.3(c). The data show that over the

FIGURE 4.3(c) Temperatures recorded at the same time beneath tussocks of L. fibrata and pasture grasses.


T. °C [L.f.]
30
25
20
15
10
5
10
15
20
25
30
35
40
45
T. °C [P.G.]

254 hours, the temperature varied from 10 to 43°C in the pasture grasses but from 15 to 26°C in the tussocks. Of particular importance here, is the fact that on hot days, the temperatures were cooler beneath the tussocks compared with those beneath the pasture grasses.

4.4 Methods of Sampling for Life History, Abundance and Activity

The life histories, abundances and activities of Iuliform millipedes have generally been studied in field populations by taking regular samples of soil and litter and extracting the millipedes in them using Tullgren funnels (e.g. Blower, 1970; Blower and Gabbutt, 1964; Blower and Miller, 1974; Brookes, 1974; Banerjee, 1967a). Pitfall traps have also been used (e.g. van der Drift, 1951; Barlow, 1957, 1958; Banerjee, 1967b, 1970a; Blower, 1970; Cotton and Miller, 1974) and occasionally hand-collections have given supplementary data (Blower and Miller, 1974; Banerjee, 1967a; Brookes, 1974). Blower and Fairhurst (1968) used collections of T. niger taken inside a house over several years to determine the species' life history and seasonal patterns of activity.

In the present study, data on the life history, abundance and activity of O. moreletii were obtained in several ways. These were,

a) Sampling of soil and litter in the grassland,

b) Sampling of litter by itself in the grassland and woodland,

c) Pitfall trapping in the grassland and woodland,

d) Visual assessment of activity and mating,

and e) Hand-collections (both at Bridgewater and at other outbreaks).

4.41 Sampling of Soil and Litter in the Grassland

As illustrated in Figure 4.1, the grassland can be divided essentially into two different micro-habitats - 1) pasture grasses and 2) tussocks of L. fibrata (hereafter referred to simply as tussocks). Both micro-habitats were sampled for O. moreletii as follows:-

In November 1972, 5 tussocks were dug up in the grassland. The border of a tussock is well-defined and therefore the tussock is easy to remove by itself. The soil and litter beneath each tussock were removed to a depth of approximately 10 cm below the soil-litter interface. No millipedes were found below this depth.

The surface area of the hole from which each tussock had been removed was measured by 1) placing a sheet of clear plastic over the hole and tracing its outline with a felt pen and 2) later in the laboratory placing the plastic "map" on a sheet of graph paper and calculating the area.

The samples of tussock, soil and litter were taken from the field in plastic bags and hand-sorted for millipedes in the laboratory.

At the same time as the tussock samples were taken, 5 samples from the pasture grasses were also taken. These were each $0.1m^2$ in area and approximately 5 cm in depth (below the soil-litter interface). No millipedes were found below this depth. The samples were placed in plastic bags and hand-sorted for millipedes in the laboratory.

The numbers of millipedes found in each sample (tussocks and pasture grasses) are given in Table 4.1 along with the surface areas for each sample. The results suggest that:-

1) During November, O. moreletii is more abundant in the tussocks than it is in equivalent areas of pasture grasses,

2) In a sampling program, two small (600 to 1,000 cm^2) tussocks and five samples of pasture grasses should yield sufficient O. moreletii for the age distributions of the populations in each habitat to be determined (i.e. at least 50 individuals for each habitat),

and 3) The relationship between the size of a tussock and the numbers of O. moreletii beneath it is probably not linear, but within the size range of tussock of 600 to 1,000 cm^2, the relationship can be assumed to be very nearly so. Thus, when the numbers of O. moreletii

TABLE 4.1

Numbers of *O. moreletii* collected in the grassland on 13/11/72

Sample	Area (cm^2)	Numbers of *O. moreletii*	Numbers of *O. moreletii* per cm^2
L. fibrata			
1	1400	243	0.174
2	1182	147	0.124
3	959	105	0.109
4	661	65	0.098
5	489	59	0.121
Pasture grasses			
1	1,000	32	.032
2	1,000	22	.022
3	1,000	16	.016
4	1,000	16	.016
5	1,000	6	.006

beneath such tussocks are expressed as the numbers of O. moreletii per cm^2, the abundances of O. moreletii beneath different tussocks (e.g. sampled on the one day or on different days) can be simply compared.

An area of 0.5 hectares was marked out in the grassland in which small tussocks were sufficient to be sampled adequately (L. fibrata occupied approximately 0.5% of the plot). This plot was surrounded on all sides by at least 50 metres of similar habitat.

At intervals of approximately five weeks from December 1972 until April 1974, collections of 2 small tussocks and 5 samples of pasture grass were taken at random coordinates within the plot. In the case of the tussocks, the closest suitable tussock to the random coordinate was selected. Additional samples were taken during October 1974 and January, May and October 1975.

The method of extracting the millipedes from the samples was changed early in the study. Instead of hand-sorting, the soil and litter from each sample were gently broken up and placed on individual tables (each 2,000 cm^2 in area). Each table stood over a tray (see Figure 4.4), the sides of which were either too smooth for the millipedes to gain a footing on, or had a barrier of adhesive tape attached which the millipedes could not traverse. The millipedes wandered out of the soil and litter, fell off the table and collected in the tray. The soil and litter were gently remixed and broken up every 48 hours. This mixing slowly dried the soil and litter out, preventing pockets of moisture occurring in which millipedes might linger. The mixing also agitated the remaining millipedes and enhanced their wanderings off the table.

The millipedes in the trays were collected every 24 hours and assessed for life history data - e.g. age, sex, maturity etc. The samples were extracted in a naturally-lit room in which the temperature varied throughout the year from 13 to 41°C. Each sample was extracted until

FIGURE 4.4A Pitfall trap, with rain shelter removed to one side.

FIGURE 4.4B Table and tray used in extraction of O. moreletii from soil and litter.


P.t.
A


B

4 days passed without any millipedes being found in the tray below it.

Casual observations made whilst remixing the soil and litter every 48 hours suggested this method of extraction was very efficient. In fact, when four tussocks (containing 5th and older stadia) were carefully hand-sorted for any remaining millipedes (dead or alive) after extraction was considered finished, only 1.0 to 1.6% of the total originally present (i.e. those extracted using the tables and trays plus those extracted by hand-sorting) were found.

The time required for extraction varied from one time of the year to another depending probably upon the moisture of the samples when collected, the conditions in the extraction room and the activity of the animals. Usually however, > 70% of the animals collected were extracted within the first four days.

The inactive stages in the life cycle (egg, pupoid and 1st stadium) were not extracted by the above method. The 2nd stadium was extracted but due to its small size and ease of damage on handling, numerical records were not kept of its presence. For these first four stages, only their presence was recorded for each sample.

On one occasion (August 1973) a large percentage of the millipedes were moulting at the time of sampling and thus were inactive (many were damaged too during collection). The extraction at this time was supplemented by hand-sorting those millipedes in moulting condition.

The dates of soil and litter sampling in the grassland, the numbers and the areas of the samples taken are given in Table 4.2.

4.42 Sampling of Litter by Itself in the Grassland and Woodland

In the woodland (Engelbrook Reserve), a hectare was marked out. On the 9th of each month from September 1974 to November 1975, 10 random

TABLE 4.2

Soil and Litter Sampling

Open Grassland

Sampling Occasion		Tussocks of L. fibrata		Method of Extraction
Sampling Code No.	Date	No. of tussocks	Area (cm^2)	
N 1	13/11/72	5	4691	Hand-sorted
D 2	20/12/72	2	1984	" "
D 3	20/12/72	1	637	Trays (see Fig. 4.4)
F 4	8/2/73	2	1377	" "
M 5	16/3/73	"	1490	" "
A 6	26/4/73	"	1935	" "
M 7	28/5/73	"	1551	" "
J 8	2/7/73	"	2127	" "
A 9	10/8/73	"	1992	" "
S10	10/9/73	"	1887	" "
O11	17/10/73	"	1549	" "
N12	22/11/73	"	1215	" "
J13	3/1/74	"	1708	" "
F14	7/2/74	"	1751	" "
M15	15/3/74	"	1295	" "
A16	23/4/74	"	1279	" "
O17	30/10/74	"	1228	" "
J18	23/1/75	"	1600	" "
M19	23/5/75	"	1224	" "
O20	6/10/75	"	1386	" "

On all sampling occasions, 5 samples of pasture grasses were collected. On 13/11/72 and 20/12/72 these samples were hand-sorted for O. moreletii. Thereafter, extraction was done using the trays shown in Figure 4.4.

coordinates within this plot were selected. At each coordinate a quadrat ($1m^2$) was placed on the ground. Then the millipedes present inside the quadrat and above the soil-litter interface were removed by hand. This method of sampling was more efficient for the larger rather than the smaller millipedes. However, only the 6th stadium and older individuals were included in subsequent analyses and careful researching of quadrats already sampled rarely revealed further millipedes in these stadia (In ten quadrats, the numbers of O. moreletii in the 6th and older stadia missed during initial sampling but found during researching were $\leq$ 8.3% of the total numbers found).

In the grassland, a plot 25 x 50 metres was marked out. The plot was devoid of tussocks; the closest tussock to the plot was approximately 100 metres distant. The plot had an easterly aspect, unlike the 0.5 hectare described in Section 4.31 which had a westerly aspect. On the 11th of each month from September 1974 to November 1975, 10 random coordinates within the plot were selected. At each coordinate a quadrat ($0.1m^2$) was marked out on the ground. Then the millipedes present within the quadrat and above the soil-litter interface were again removed by hand. [Preliminary observations suggested that O. moreletii was approximately 10x more abundant in the grassland than in the woodland. The size of the quadrat used in the woodland was 10x the size of that in the grassland. Thus similar numbers of millipedes were likely to be collected from both habitats].

The millipedes collected from the grassland and woodland were assessed as to age, sex and maturity.

4.43 Pitfall Trapping in the Grassland and Woodland

Sampling the soil and litter for millipedes showed what stages in the life cycle were present at different times of the year. The active

stages in the life cycle however were the ones that were the problem to the local residents. In order to show what stages were active at different times of the year, and also to show when the peaks of activity occurred, pitfall traps were set in the grassland and woodland.

The pitfall traps (see Figure 4.4) were made from glass jars (internal diameter of the rim 7 cm, internal depth 11 cm). The traps were set in the ground with the rim flush with the soil surface. In order to keep rain and leaves out of the traps, metal lids (10 x 10 cm) were set 2 to 3 cm above the rim of the jars. No provision however was made for flooding, and occasionally the traps did fill with water. The smooth glass walls of the jars were kept clean by wiping with a soft rag on inspection of the trap. When the traps were not being used, screw-on lids were put on the jars.

The traps were placed in the field in groups of four, each four arranged in a square with sides of 10 metres. Four trap-sites (Traps 1-16) were selected in the grassland and eight trap-sites (Traps 17-48) in the woodland. The four sites in the grassland were adjacent to the plot of 0.5 hectares used for the soil and litter sampling (two at the southern and two at the northern end of the plot, each pair separated by approximately 50 metres). The density of L. fibrata in the trapping areas was similar to that in the plot, varying between 0.38 and 3.92% of the total area. Measures of the density of L. fibrata were arrived at by 1) counting the numbers of tussocks within 5 metre radii of each trap, 2) assuming each tussock to be 800 cm^2 in area*, and hence 3) calculating the area occupied

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* The figure of 800 cm^2 for each tussock was arrived at by removing all 27 tussocks that were present in a nearby plot of 100m^2 and calculating the areas of each tussock individually (see Section 4.41 for method of calculating area). The average area of these tussocks was 802 cm^2.

by the plant.

The pitfall trapping was done during the period October 1972 to January 1974. In October - November 1972, the traps were open for 11 days whilst initial observations on the trapping design were made. Subsequently, the traps were normally open for 1 week in every 5 weeks. However, occasionally the traps were opened for 2 or 3 days when additional data on life history and activity were considered necessary. During the periods that the traps were open they were inspected each day at 9.00 a.m. (weather data were taken at 9.00 a.m. in Stirling) and the millipedes were removed and assessed as to age, sex and maturity.

The 24 hours between each inspection of each trap is called a trap-day. The dates of trapping and the corresponding numbers of effective trap-days in the grassland and woodland are given in Table 4.3. The variation in the number of trap-days from one sampling time to another is due to 1) the numbers of days of sampling and 2) the numbers of traps destroyed by flooding or other causes.

4.44 Visual Assessment of Activity and Mating

Throughout the study, the grassland and woodland at Bridgewater were visited many times - sometimes for the sampling already mentioned, at other times for collections of animals to use in experiments (see Chapters 5 and 6). In both habitats there were bare or nearly bare, paths which were regularly walked (approximately 100 metres long x 3 metres wide in the woodland, and approximately 50 metres long x 1 metre wide in the grassland). On each visit I recorded the numbers of active millipedes on these paths according to the following scheme:-

Numbers seen active	Classification
0	Nil
1 to 5	Few
6 to 25	Several
26 to 100	Many
> 100	Very Many

TABLE 4.3

Pitfall Trapping

Sampling Occasion		Number of Trap-Days	
Sampling Code No.	Date	Open Grassland	Sclerophyllous Woodland
O-N 1	28/10-7/11/72	132	308
D 2	11-18/12/72	110	224
J-F 3	29/1-5/2/73	96	214
F 4	13-15/2/73	32	64
M 5	5-12/3/73	112	224
M 6	18-21/3/73	48	96
A 7	9-16/4/73	112	224
M 8	3-6/5/73	48	96
M 9	14-21/5/73	112	224
J10	18-25/6/73	112	224
J11	23-30/7/73	109	224
A-S12	27/8-3/9/73	101	221
O13	1-8/10/73	112	224
N14	5-12/11/73	110	224
D15	10-13/12/73	48	96
J16	14-17/1/74	48	96
TOTALS		1442	2983

In addition, the number of mating couples seen on each path were recorded. Of course the times of day that the two habitats were visited throughout the study varied greatly, and since all the daily observations were pooled (see Table 4.9), the usefulness of the data is limited.

4.45 Hand-Collections and Miscellaneous Samples

Supplementary data on the life history of O. moreletii at Bridgewater was often obtained when hand-collections were taken for laboratory experiments. Hand-collections were also made at other outbreaks of O. moreletii. These collections were used to compare the life history of the species in different geographical areas.

Often the native species, Dimerogonus sp. and A. castaneum, were collected at the same time as O. moreletii and these animals were used to evaluate their own life histories.

4.5 Results of Sampling For Life History, Abundance and Activity

4.51 Mating

O. moreletii mated during autumn and early winter at Bridgewater. The peak in mating occurred in April and May (see Table 4.9 a & b). The earliest occasions each year when mating couples of O. moreletii were seen were 9/4/73, 17/4/74 and 28/3/75. The latest occasions were 19/6/73, 28/6/74 and 24/6/75.

4.52 Age Distributions

The age distributions of the individuals in the samples collected by the methods outlined in Section 4.4 are given in Tables 4.4 (a to f). The data in these tables have been partitioned into females, juveniles, mature and intercalary males in Appendix Tables 4.1 to 4.6.

Nests of eggs, pupoids and first stadia were found in the grassland from April to August, particularly in the soil beneath the tussocks. Very few nests were found in the soil beneath the pasture grasses. The development

TABLE 4.4(a)

Soil and Litter Sampling

Open Grassland

Tussocks of L. fibrata - Total

Sampling Code No.	STADIA															Total
	E	P	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	
N 1						5	28	8		14	362	145	36	13	6			617
D 2						11	102	168	3	16	721	575	70	13	1			1680
D 3						2	44	219	11	2	142	93	7	2				522
F 4						11	96	147	27	2	125	79	7		1			495
M 5							15	57	43	5	3	26	6	2				157
A 6	*							3	35	16	5	44	19	7	1	1		131
M 7	*	*	*					4	47	52	14	63	24	5				209
J 8	*	*	*					1	63	139	26	59	20	4				312
A 9	*	*	*	*	4	6	3		19	135	45	66	20	3	1			302
S 10				*	5	18	3	3	1	22	30	71	27	11	2			193
O 11					8	47	74	4		3	11	6	9	8				170
N 12						22	119	42			7	10	21	2	1			224
J 13							50	797	1989	95	46	29	22	18	8	2		3056
F 14							7	152	1410	185	43	14	16	5	1			1833
M 15								7	127	561	65	16	12	13	4	1		806
A 16	*							1	117	491	55	16	6	4	5	1		696
O 17						12	34	8		11	61	8						134
J 18							4	53	55	5	684	599	47	3	1			1451
M 19	*	*	*					1	8	17	7	57	19	2				111
O 20							1			1	3	7	17	4				33
TOTAL								1675	3955	1772	2455	1983	405	119	32	5		

N.B. The numbers of nests containing eggs, pupoids and first stadia were on all occasions extremely numerous. The data in this table are converted to numbers per 0.1 m^2 in Appendix Table 4.9.

TABLE 4.4(b)

Soil and Litter Sampling

Open Grassland

Pasture Grasses - Total

Sampling Code No.	STADIA															Total
	E	P	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	
N 1						1	6	4		1	29	39	7	3				90
D 2											5	7						12
D 3																		
F 4								3		1	9	4	2					19
M 5								12	16	2	4	21	15	1				71
A 6									4	6	4	37	24	5	2			82
M 7								2	1	3	3	32	25	4	2			72
J 8	*	*	*						2	15	4	37	23	9	2			92
A 9										4	6	28	20					58
S 10				*	180	173	5			4	12	12	9	6	1			402
O 11					38	70	108	5			18	14	16	1				270
N 12						25	350	598	40	1	21	31	26	15	1			1108
J 13								50	234	25	1	3	1	1	1			316
F 14								4	324	139	2	7	7	5	3			491
M 15							1	2	91	368	25	12	4	8	2	1		514
A 16	*								36	204	34	22	17	5	1			319
O 17							1	1		18	254	73	2					349
J 18								1	9	2	17	55	10	2				96
M 19	*	*						1	5	5	5	96	49	1	1			163
O 20							1			2	12	9	79	35	2			140
TOTAL								683	762	800	465	539	336	101	18	1		

N.B. The numbers of nests containing eggs, pupoids and first stadia were few in number (1 nest in July, 1973; 1 nest in April, 1974; and 2 nests in May, 1975).

TABLE 4.4(c)

Pitfall Trapping

Open Grassland - Total

Sampling Code No.		STADIA															Total
		2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	
O-N	1					2		3	134	146	98	70	30	7	3		493
D	2			1	9	54	31	4	94	239	33	13	4	1			483
J-F	3				4	5	4	2	43	93	21	6	2	2			182
F	4					1			1			1					3
M	5						6	2	3	59	78	14	7	1	1		171
M	6					2	5	2	2	86	65	17	4	2			185
A	7					1	4	47	32	768	551	149	66	17	4		1639
M	8						2	1	4	112	120	38	11	3	1		292
M	9						1	9	18	498	364	78	18	4	3		993
J	10							5	11	290	246	60	19	2			633
J	11							2	7	77	83	23	8	1			201
A-S	12		25	28	1			1	8	13	9	7	4	1			97
O	13	2	29	121	223	4		1	4	8	43	32	5	1			473
N	14		3	13	86	173	4	1	10	54	75	51	6		1	1	478
D	15				9	62	23	1		15	5	3	5				123
J	16				1	30	359	129	8	19	41	37	20	3	2		649
TOTALS		2	57	163	333	334	439	210	379	2477	1832	599	209	45	15	1	7095

TABLE 4.4(d)

Sclerophyllous Woodland - Total

Pitfall Trapping

Sampling Code	No.	STADIA 2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	Total
O-N	1				2		1	13	22	37	70	40	10	4			199
D	2		1		5	4		3	8	9	8	7	3	2			50
J-F	3			1	7	4		1	8	15	23	33	15	3	2		112
F	4									2	1	4	4	2			13
M	5					1	1		1	23	74	105	47	13			265
M	6					3	2		10	82	84	100	62	16	2	1	362
A	7					1			3	54	46	42	31	10	3		190
M	8					1				18	21	20	14	7			81
M	9						1		1	28	25	30	12	6	3		106
J	10								1	9	19	18	16	4			67
J	11						1			10	8	4	4	2			29
A-S	12		2				1	8	8	1	4	5	7	2			38
O	13				2			11	2	15	22	14	4	1	1		72
N	14			2	7	1		5	21	14	29	16	4	2	3		104
D	15				1	3	1	1	7	3	1	2	1	2			22
J	16				3	8	2				1	1	1				16
TOTALS			3	3	27	26	10	42	92	320	436	441	235	76	14	1	1726

TABLE 4.4(e)

Litter Sampling Sept. 1974 - Oct. 1975

Open Grassland - Total

Date	STADIUM										Total
	6	7	8	9	10	11	12	13	14	15	
11/9/74		2	41	81	5	1					130
11/10/74	1	1	50	328	47	4	1				432
11/11/74	7		1	175	140	7	1	1			332
11/12/74	3	4	2	35	142	14					200
11/1/75	12	29	2	21	196	14					274
11/2/75		5	1	1	19	4	1	1			32
11/3/75			1		38	55	2	1			97
11/4/75		13	47	8	120	116	3				307
12/5/75		17	69	8	84	80	3				261
11/6/75			2		41	27	3				73
11/7/75			2	2	21	10					35
11/8/75			4		16	7					27
11/9/75			13	17	3	13	1				47
11/10/75	1		1	19	2	27	8				58
11/11/75	117			7	15	31	18				188
TOTAL	141	71	236	702	889	410	41	3			2493

TABLE 4.4(f)

Litter Sampling Sept. 1974 - Oct. 1975

Sclerophyllous Woodland - Total

Date	STADIUM										Total
	6	7	8	9	10	11	12	13	14	15	
9/9/74	1	6	91	36	5	8	3	1	1		152
9/10/74	1	1	100	56	15	15	10	3			201
9/11/74	5		4	81	26	10	6	2	1		135
9/12/74	3	3	2	58	28	10	6	4	1		115
9/1/75	4	8		34	18	4		2			70
9/2/75		1				1	1				3
9/3/75					1	2	3	4	1		11
9/4/75	2	14	8	15	173	112	15	5	1		345
11/5/75		4	22	15	109	67	6	1	1	1	226
9/6/75		11	25	5	101	69	9	3			223
9/7/75		5	7	2	47	38	11	3	1		114
10/8/75		3	19		39	26	7		1		95
9/9/75			14	15	6	9	6				50
9/10/75			21	37	18	58	27				161
10/11/75		1	3	63	27	51	23	3	1		172
TOTAL	16	57	316	417	613	480	133	31	9	1	2073

through the life cycle of cohorts resulting from each autumn reproduction can be traced through the data shown in Tables 4.4 (a to f). This is especially so for the cohort produced in autumn 1973 which was extremely numerous.

The rate of moulting was high in the first year of growth. By the first summer, O. moreletii was in the 5th, 6th or 7th stadium. After 1 year, the millipedes reached the 7th, 8th or 9th stadium. After 2 years, they reached the 10th or 11th stadium. From the data presented in Tables 4.4 (a to f) it is not possible to follow clearly the development of O. moreletii in subsequent years. However, Tables 4.4 (b, e and f) indicate that in spring the 10th and 11th stadia moult to the 11th and 12th (refer in particular to the 1973 generation).

In Section 3.4, I indicated that by the 11th stadium (in both the woodland and grassland), the majority of males were adults. Later (see Section 4.54), I suggest that adult males moult twice per year - once in summer (January - February) and once in spring (August - September). The summer moult is to the mature form whilst the spring moult is to the intercalary form. Thus those males which are mature in the 9th stadium in autumn of a given year will be mature in the 11th and 13th stadia in the two subsequent years should they survive. Those that mature in the 10th stadium will later be mature in the 12th and 14th stadia in subsequent autumns. The males that do not mature until the 11th or 12th stadia will be mature in the 13th and 14th stadia respectively in the subsequent autumn. No 15th or 16th stadia males were ever found during the study.

The adult moulting of the females of O. moreletii cannot be followed so easily since different "forms" are not discernible in this sex. I can only suppose that, like the males, adult females moult twice a year. Indeed moulting adult females were most noticeable in the field during spring and summer - i.e. the same times as adult males.

The age distributions of O. moreletii taken in hand-collections

on Eyre Peninsula and in Melbourne at different times are given in Table 4.5. There are no obvious differences in the age distributions of O. moreletii at Bridgewater, Melbourne and on Eyre Peninsula, except perhaps the preponderance of the 9th stadium in Melbourne in April 1975. This will be referred to again later (see Sections 4.53 and 4.54).

4.53 Maturation in Females

For each sampling method at Bridgewater the percentages of females (9th stadium and older) with mature eggs (see Figure 3.4(c)) and those with small developing eggs (see Figure 3.4(a)) were calculated for each sampling occasion. These data are shown in Figures 4.5 and 4.6. Females carrying mature eggs were found from February to August with a peak in April, May and June. The graphs of the percentages of females with mature eggs followed similar courses for both grassland and woodland and there was no evidence to suggest that oviposition was delayed more in one habitat than the other.

During the summer prior to the breeding season, the majority of females carried small developing eggs. Maturation of the eggs appeared to be stimulated in January or February and was therefore correlated with high temperatures and low rainfall. In the spring (August and September) after the breeding season, the majority of females again had small developing eggs in their ovaries. This reversal was in part due to the recruitment of the next generation into the 9th and older stadia, the mortality of reproducing females during and after the breeding season and possibly the regression of the ovaries to the "small developing eggs" state in females which had been mature or maturing during the breeding season and had survived. During spring and summer, it was not possible to distinguish females which had reproduced or at least matured their eggs in autumn and winter, survived and regressed their ovaries to the "small developing eggs" state, from females which had not reproduced during the autumn and retained

TABLE 4.5

	STADIUM												Total
	4	5	6	7	8	9	10	11	12	13	14	15	
Eyre Peninsula													
Jan. 1973	2	24	7	-	16	459	255	22	1				786
Apr. 1973					1	19	130	80	28	3	1		262
Sept. 1973					5	6	33	83	17	2	2		148
May, 1974				1	36	28	93	129	105	16	1		409
Jan. 1975	5	207	1363	1812	62	606	428	22	19	12	2	2	4540
May, 1975				24	89	5	119	54	6	1			298
Melbourne													
Feb. 1975				2	10	47	29	10	1	1			100
Mar. 1975					4	3	14						21
Apr. 1975			1		6	75	108	234	152	4	3	1	584

The samples from Eyre Peninsula were mainly from near Port Lincoln (note the May, 1975 collection was from Coffin Bay).

The samples from Melbourne were from the suburb of Avondale Heights.

FIGURE 4.5 % of females with (a) mature eggs, and (b) small developing eggs collected during soil and litter sampling in the grassland (P.G. = pasture grasses; L.f. = L. fibrata).

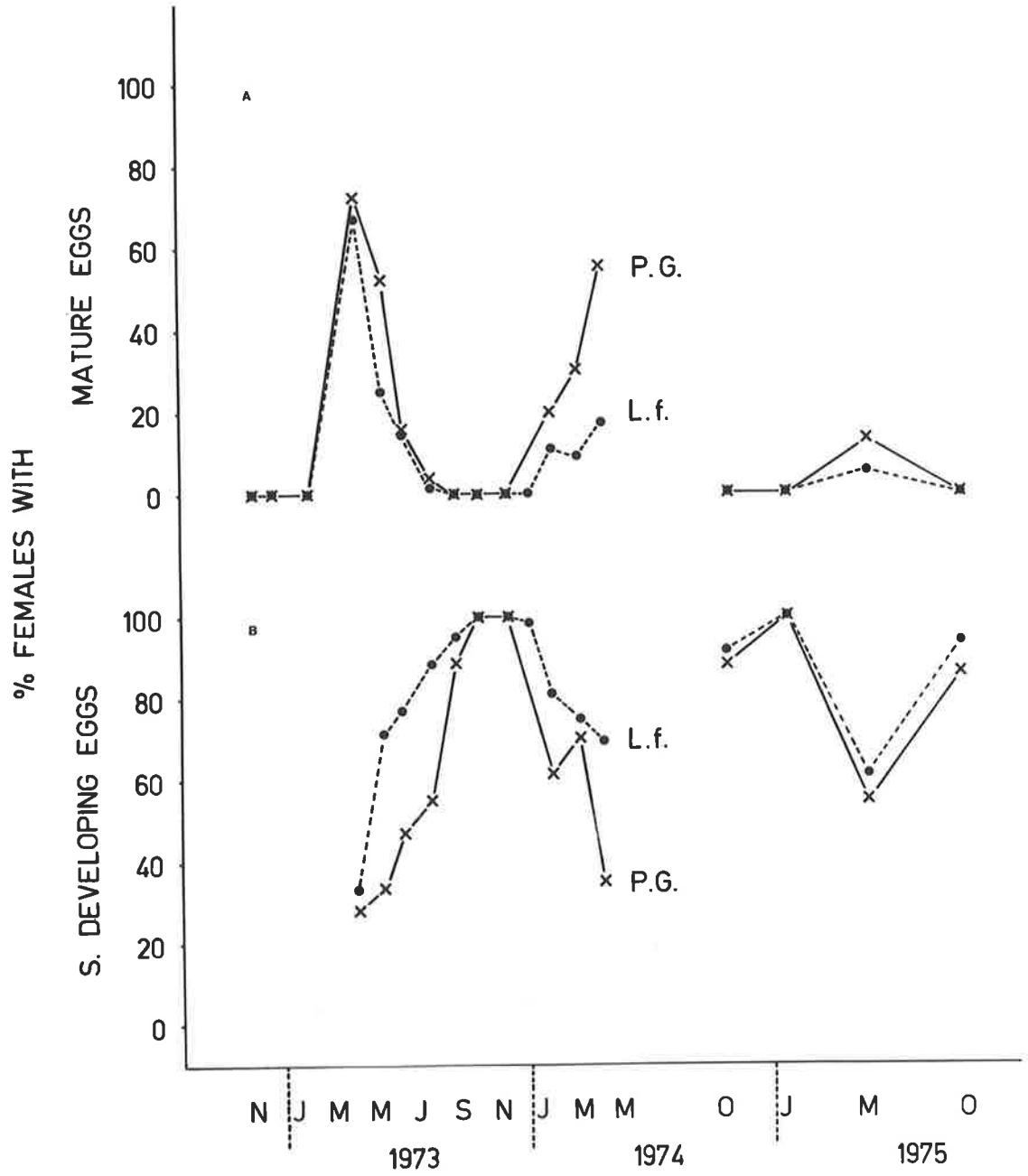
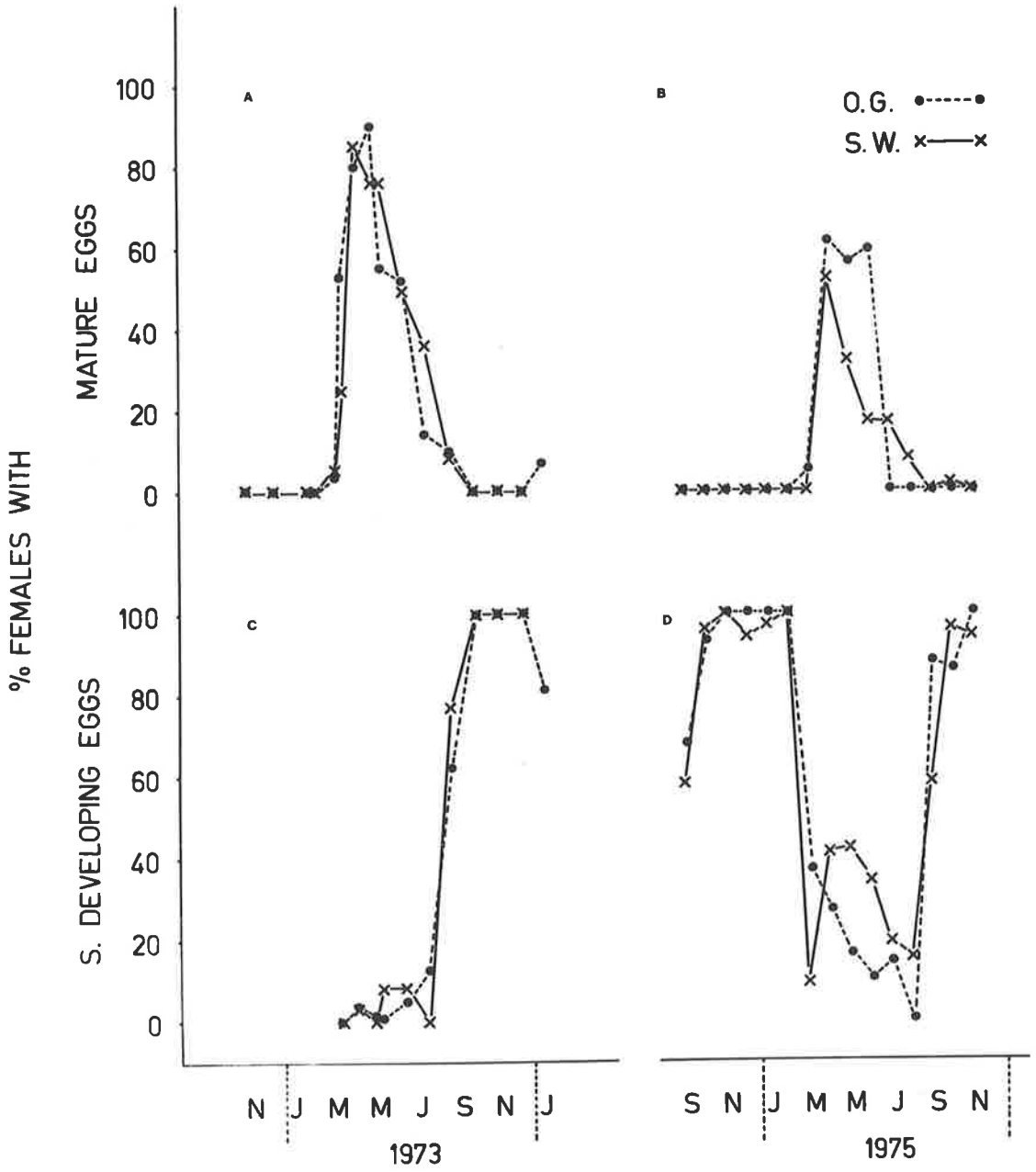

% FEMALES WITH
MATURE EGGS
S. DEVELOPING EGGS
A
B
100
80
60
40
20
0
P.G.
L.f.
L.f.
P.G.
N J M M J S N J M M O J M O
1973
1974
1975

FIGURE 4.6 % of females with (a & b) mature eggs, and (c & d) small developing eggs collected during (a & c) pitfall trapping, and (b & d) sampling of litter in the grassland (O.G.) and woodland (S.W.).


% FEMALES WITH
MATURE EGGS
S. DEVELOPING EGGS
100
80
60
40
20
0
A
B
C
D
O.G.
S.W.
N J M M J S N J
1973
S N J M M J S N
1975

small developing eggs throughout.

The percentages of females of O. moreletii carrying mature eggs in the hand-collections from Eyre Peninsula and Melbourne were as follows:-

Eyre Peninsula	%	N
Jan. 1973	0	334
Apr. 1973	32	127
Sept. 1973	0	111
May 1974	69	220
Jan. 1975	0	535
May 1975	78	91
Melbourne		
Feb. 1975	0	51
Mar. 1975	Too few females	
Apr. 1975	71	341

These data follow a similar pattern to that for Bridgewater, suggesting an autumn breeding season.

Of the 341 females collected in April 1975 in Melbourne, 63 were in the 9th stadium. Of these, 41% carried mature eggs. This was a far higher level of maturation than was ever seen in females in the 9th stadium from Bridgewater. For example, none of the females in the 9th stadium collected during autumn and winter 1975 at Bridgewater contained mature eggs. The results suggest earlier maturity with respect to stadium in Melbourne.

4.54 Maturation in Males

The sexes of O. moreletii are differentiated in the 6th stadium (see Section 3.3). Males older than the 5th stadium are then recognized as either juveniles, mature males or intercalary males. For simplicity here, the mature and intercalary males will be collectively called adults. For each sampling method used at Bridgewater the percentage of males in the

6th and older stadia that were adults were calculated from the data in Appendix Tables 4.1 to 4.6. These percentages are shown in Figures 4.7 and 4.8.

In spring and early summer, the populations of males were predominantly juveniles. In late summer (February), there was a maturation moult and the percentage of adults in the population increased. In spring (August to October), the percentage of adults decreased, due to mortality of the adults and recruitment of new juveniles into the sixth and subsequent stadia.

Within the adult males, the percentages of mature males as opposed to intercalary males were calculated for each sampling occasion using the data in Appendix Tables 4.1 to 4.4. These percentages are shown in Figures 4.7 and 4.8 for the samples of soil and litter and the pitfall trapping. The numbers of adult males in the litter by itself, particularly in summer, were too low to warrant similar graphs being drawn. Nevertheless, similar trends to those drawn in Figures 4.7 and 4.8 are evident in Appendix Tables 4.5 and 4.6.

In spring and early summer, the adult males were predominantly intercalary. In January and February the percentage of mature adults increased due to the maturation moults of the intercalaries and juveniles as described above. In spring (August to October), the percentages of mature adults decreased again when the "dematuration" moult to the intercalary form occurred.

Adult males of O. moreletii were commonly seen moulting in the field in spring and summer at the times when the changes described above occurred. They were rarely seen moulting at other times of the year. It seems most likely therefore that the adult males of O. moreletii only have 2 moults per year, moulting from the mature form to the intercalary form in spring and from intercalary to mature in summer. An intercalary to intercalary moult would seem rare, if it occurs at all.

FIGURE 4.7(a) % of males collected during soil and litter sampling in the grassland that were adults. (P.G. = pasture grasses; L.f. = L. fibrata).

FIGURE 4.7(b) % of adult males collected during soil and litter sampling in the grassland that were mature.

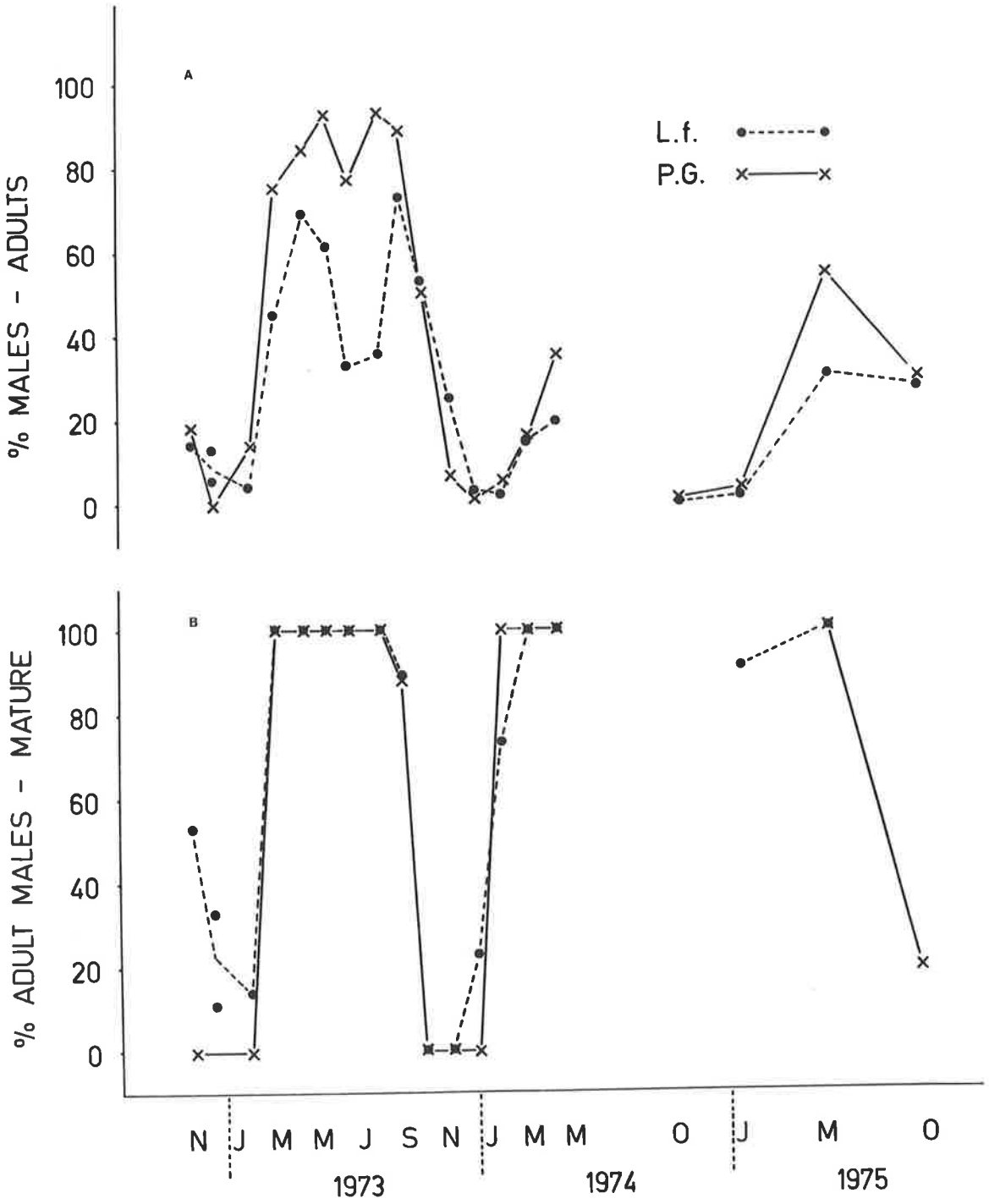
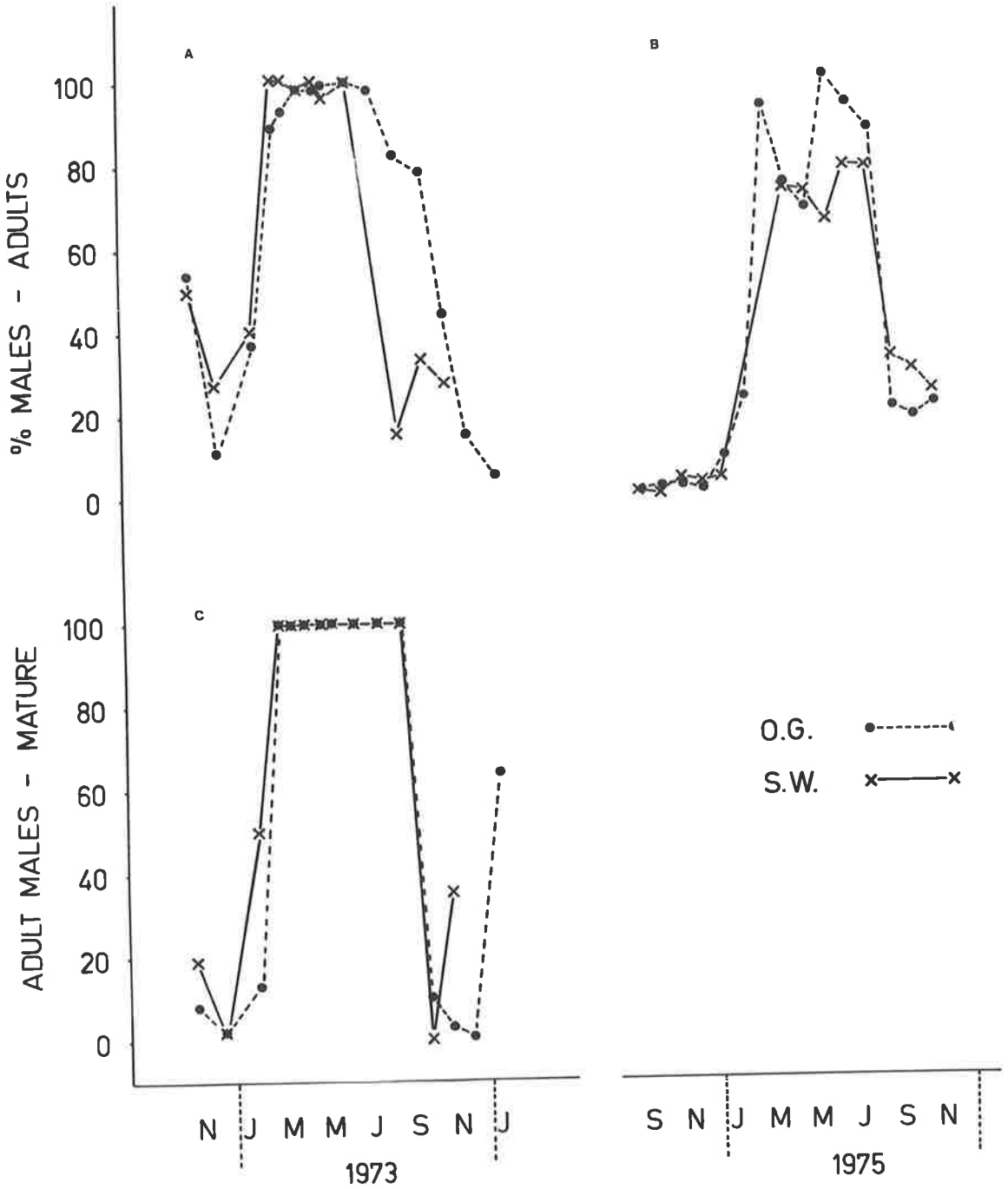

A
B
% MALES - ADULTS
% ADULT MALES - MATURE
100
80
60
40
20
0
L.f.
P.G.
N J M M J S N J M M O J M O
1973
1974
1975

FIGURE 4.8 (a & b) % of males collected during (a) pitfall trapping and (b) sampling of litter that were adults (O.G. = grassland, S.W. = woodland).

FIGURE 4.8 (c & d) % of adult males collected during (c) pitfall trapping and (d) sampling of litter that were mature.


A
B
C
% MALES - ADULTS
ADULT MALES - MATURE
100
80
60
40
20
0
O.G.
S.W.
N J M M J S N J
1973
S N J M M J S N
1975

The percentages of males of O. moreletii that were adults in the hand-collections from Eyre Peninsula and Melbourne were as follows:-

Eyre Peninsula	%	N
Jan. 1973	4	420
Apr. 1973	87	133
Sept. 1973	7	45
May 1974	92	168
Jan. 1975	0.5	1945
May 1975	62	149
Melbourne		
Feb. 1975	9	44
Mar. 1975	100	17
Apr. 1975	85	196

The percentages of the adult males that were mature were as follows:-

Eyre Peninsula	%	N
Jan. 1973	0	17
Apr. 1973	98	116
Sept. 1973	0	3
May 1974	99	155
Jan. 1975	0	9
May 1975	100	93
Melbourne		
Feb. 1975	50	4
Mar. 1975	100	17
Apr. 1975	100	167

The patterns in the above data for Eyre Peninsula and Melbourne are similar to those observed for Bridgewater.

Of the 196 males collected in April 1975 in Melbourne, 35 males

were in the 8th stadium. Of these, 29% were mature. On the other hand, of the 149 males collected in May 1975 on Eyre Peninsula, 41 males were in the 8th stadium and none were mature. Similarly, the maturity of males in the 8th stadium at Bridgewater in April and May 1975 was very low (see Appendix Tables 4.5 and 4.6). Of 49 males in the grassland, only one was mature; of 12 males in the woodland, none was mature. These observations suggest that the males of O. moreletii mature earlier (with respect to stadium) in Melbourne compared with Bridgewater and Eyre Peninsula.

In April 1974, following the wet 1973-4 summer at Bridgewater, 15% of the 110 males in the 8th stadium that were collected in the pasture grasses were mature (see Appendix Table 4.2). These males were only one year old (i.e. in the 1973 generation which can be traced through e.g. Tables 4.4 (a and b)).

4.55 Sex Ratios

For each sampling method, the percentages of males in the 6th and older stadia were calculated from the data in Appendix Tables 4.1 to 4.6. Firstly, the following data summarize the sex ratios calculated from the total numbers collected by the different sampling methods.

Methods and Site	♂%	N
Soil and Litter (tussocks)	50.4	12,401
" " " (pasture grasses)	50.1	3,705
Pitfall trapping (grassland)	52.3	6,540
" " (woodland)	25.9	1,693
Litter by itself (grassland)	46.7	2,493
" " " (woodland)	40.8	2,073

The striking facts in this data are the aberrant sex ratios in the samples from the woodland.

Secondly, the changes in the sex ratio with time throughout each sampling method are shown in Figures 4.9, 4.10 and 4.11. For most of the

FIGURE 4.9(a) Sex Ratio (% ♂) of millipedes collected during soil and litter sampling in the grassland (P.G. = pasture grasses, L.f. = L. fibrata).

FIGURE 4.9(b) Numbers of millipedes collected during soil and litter sampling in the grassland. Points for L. fibrata represent the means of two samples. Points for pasture grasses represent the means of five samples. Vertical lines represent ± 1 S.E.

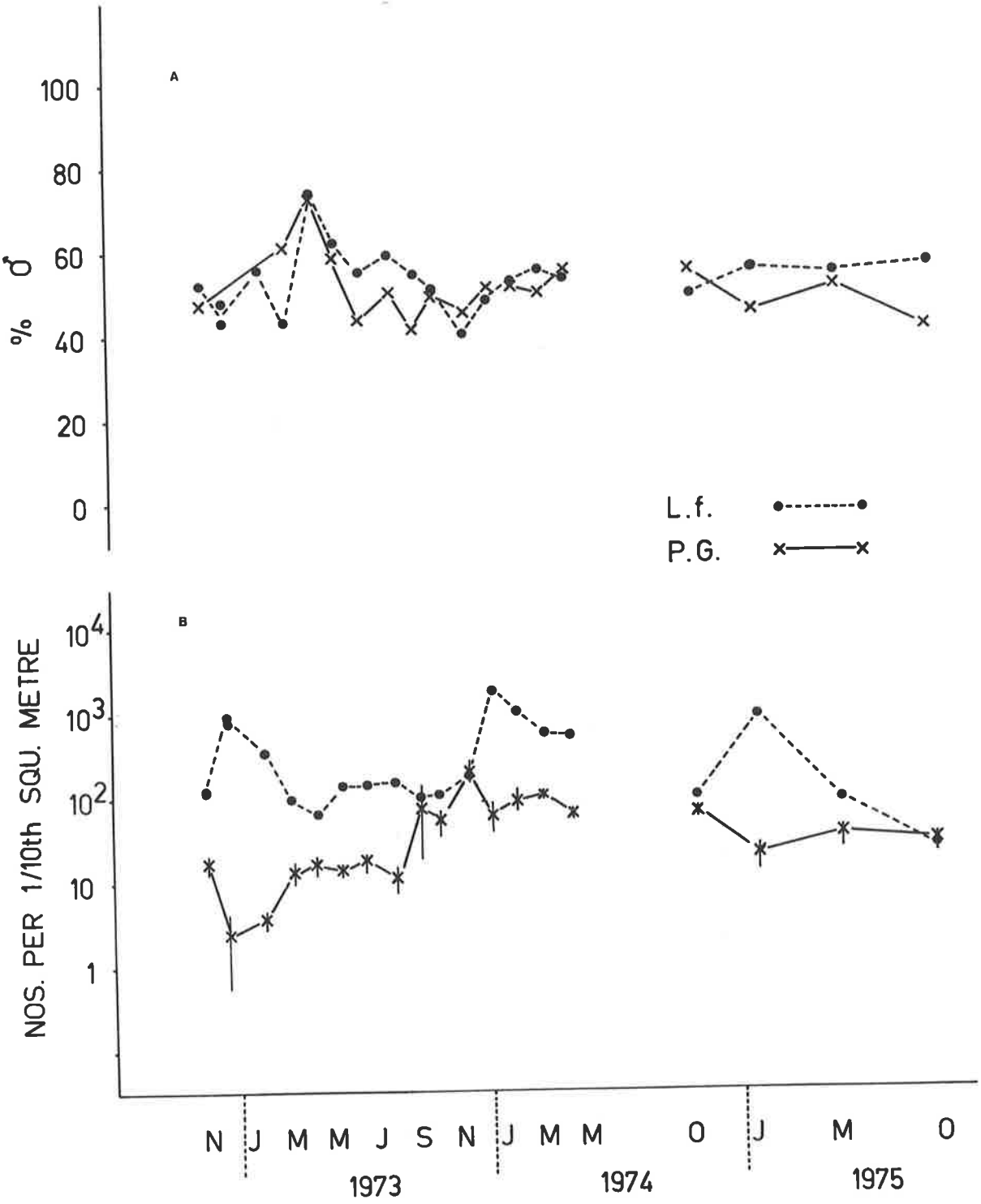

A
100
80
60
40
20
0
% ♂
L.f.
P.G.
B
10^4
10^3
10^2
10
1
NOS. PER 1/10th SQU. METRE
N J M M J S N J M M O J M O
1973
1974
1975

FIGURE 4.10(a) Sex Ratio (% ♂) of millipedes collected during sampling of litter in the grassland (O.G.) and woodland (S.W.)

FIGURE 4.10(b) Numbers of millipedes collected during sampling of litter in the grassland (●) and woodland (x). Points represent the means of 10 samples. Vertical lines represent ± 1 S.E. The o for November 1975 in the grassland represents the point on the graph when the 1975 generation are omitted from the data.

In spring 1974 both the grassland and woodland were dominated by juveniles in the 8th, 9th and 10th stadia (1973 generation). There was a large increase in the numbers of 9th and 10th stadia in the grassland from September to October 1974. This increase was probably due to the emergence of individuals from moulting beneath the ground. Whether these millipedes were produced within the area sampled or dispersed there from more productive areas during their previous 18 months of life is open to conjecture.

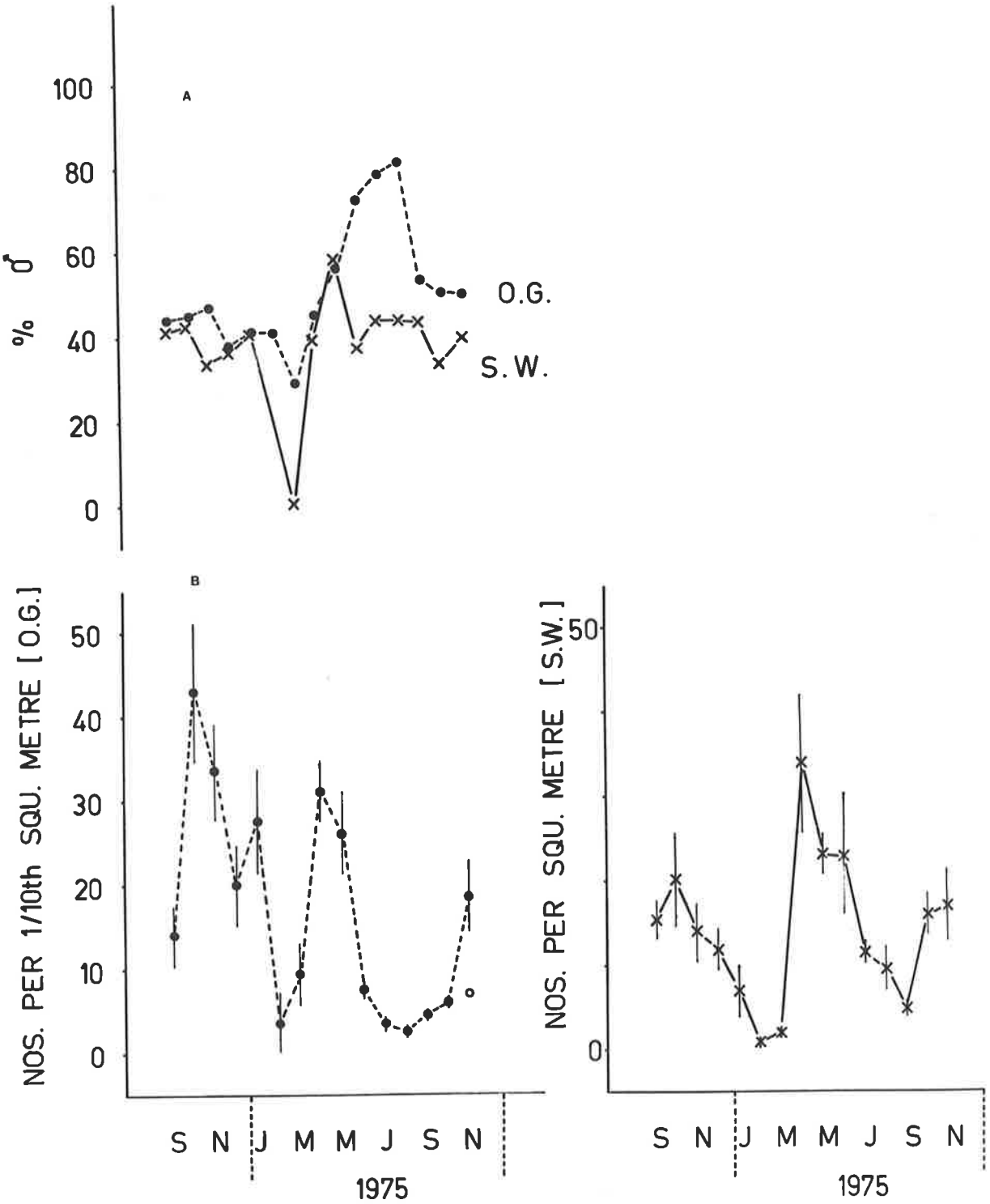
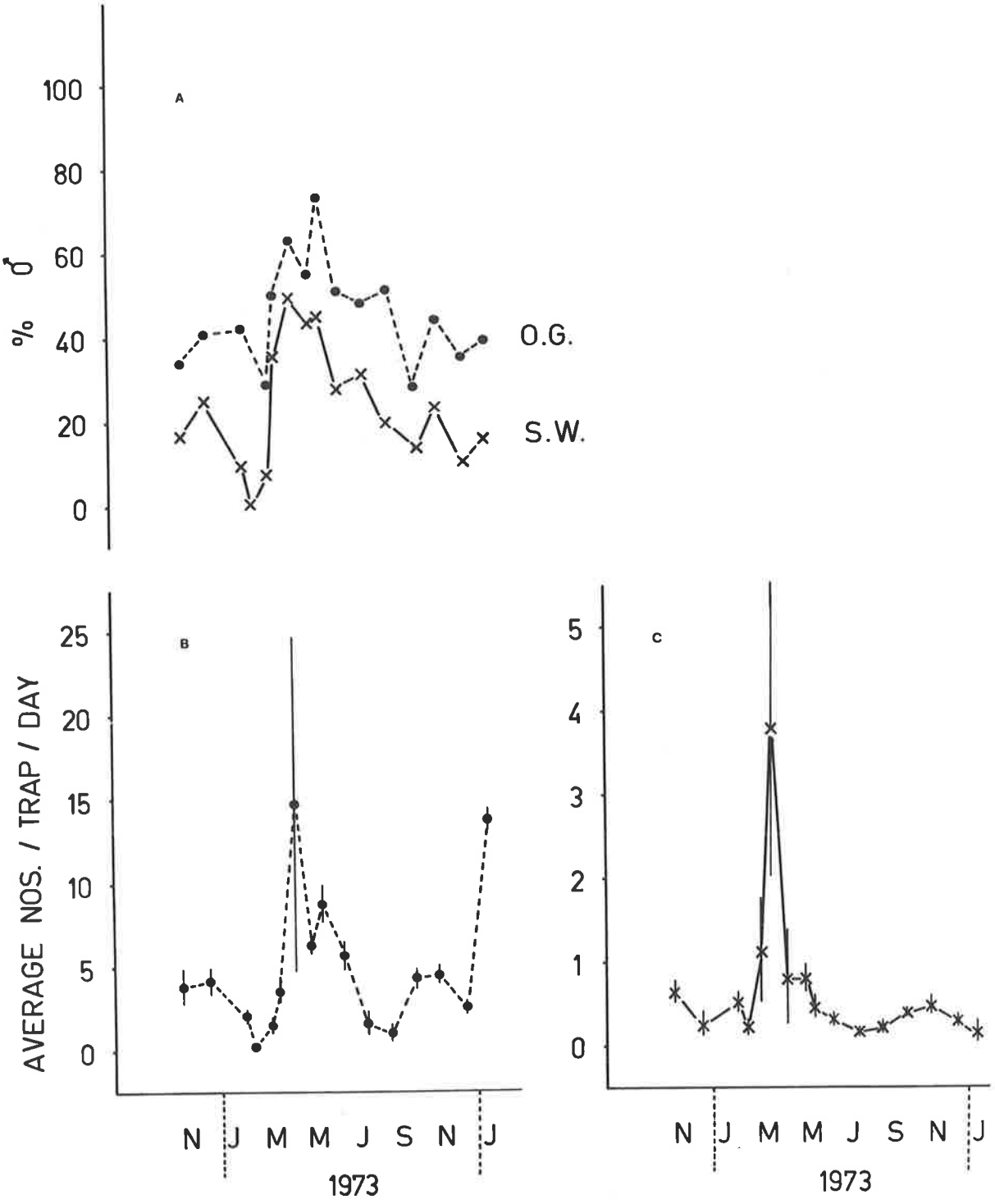

A
100
80
60
40
20
0
% ♂
O.G.
S.W.
B
NOS. PER 1/10th SQU. METRE [O.G.]
50
40
30
20
10
0
NOS. PER SQU. METRE [S.W.]
50
0
S N J M M J S N
1975
S N J M M J S N
1975

FIGURE 4.11(a) Sex Ratio (% ♂) of millipedes collected during pitfall trapping in the grassland (O.G.) and woodland (S.W.).

FIGURE 4.11(b) Numbers of millipedes collected during pitfall trapping in the grassland and woodland. Points represent average numbers collected per trap per day. Vertical lines represent $\pm$ 1 S.E.


A
100
80
60
40
20
0
% ♂
O.G.
S.W.
B
25
20
15
10
5
0
AVERAGE NOS. / TRAP / DAY
N J M M J S N J
1973
C
5
4
3
2
1
0
N J M M J S N J
1973

samples of soil and litter, the percentages of males varied little from 50%. There were no significant variations in the data presented in Figure 4.9(a). The data from the sampling of litter and the pitfall trapping (see Figures 4.10 and 4.11) suggested that 1) the percentages of males were consistently higher in the grassland compared with the woodland, and 2) in both habitats (particularly the woodland), the percentages of males were low during late summer and increased during autumn. The increase in percentage of males from March to May 1973 in the pitfall trapping was significant for both habitats (Grassland; $t_{12} = 7.52$, $p < .05$: Woodland; $t_{12} = 8.89$, $p < .05$. In this case the percentages of males for each of the 7 days of trapping were used to calculate the means and variances). The increase from March to May 1975 in the litter in the woodland was obvious. In the grassland over the same period, the increase was significant ($t_{11} = 3.59$, $p < .05$. Here the percentages of males for each of the samples taken (in which numbers were sufficient ($n > 10$) to calculate a meaningful value for the percentage of males present) were used to calculate the means and variances).

The sampling of the litter suggested that the percentages of males were much higher in the winter in the grassland than in the woodland. e.g.

	Grassland		Woodland	
	Nos. of ♂	Nos. of ♀	Nos. of ♂	Nos. of ♀
June	52	21	83	140
July	27	8	50	64
August	22	5	41	54

From the data in Appendix Tables 4.1 to 4.6, the sex ratios for each stadium were calculated using the total numbers collected by each sampling method. These sex ratios are given in Table 4.6. The data suggest that after the 9th stadium, 1) in both the woodland and the grassland, the ratio of males to females decreases with increased age, and 2) the decrease

TABLE 4.6

Sex ratios (♂ %) in the different stadia of *O. moreletii* collected at Bridgewater

	STADIUM				
	6 & 7	8 & 9	10 & 11	12 & 13	14 & 15
Pitfall Trapping					
Grassland	46.2	54.0	56.0	38.9	30.0
Woodland	27.8	43.3	34.1	16.1	3.3
Soil and Litter Sampling					
L. fibrata	46.4	58.2	46.8	41.7	
Pasture grasses	48.5	53.0	51.0	31.1	
Litter Sampling					
Grassland	51.4	51.7	43.0	27.3	
Woodland	50.7	49.9	39.3	7.3	0.0

is more marked in the woodland compared with the grassland.

4.56 Changes in Abundance Throughout Summer

Changes in the total numbers of O. moreletii collected in the samples of soil and litter are shown in Figure 4.9(b). The 1972-3 summer was hot and dry (see Figure 4.3). The numbers of O. moreletii decreased significantly in the pasture grasses from November to December 1972 ($t'_4 = 3.35^*$, $p < .05$). At the same time, the numbers of O. moreletii increased in the tussocks. The soil beneath the tussocks during summer remained cooler and moister than the soil beneath the pasture grasses. The population of O. moreletii present was mainly 5th, 6th and 7th stadia (juveniles in the 1972 generation) and 9th and 10th stadia (juveniles in the 1971 generation) (see Tables 3.4 (a and b) and Appendix Tables 4.1 and 4.2).

In autumn 1973, the numbers of O. moreletii beneath the tussocks decreased and the numbers increased significantly in the pasture grasses (e.g. February to April 1973; $t'_4 = 2.38$, $p < .05$). By this time, the 1972 generation were in the 6th, 7th and 8th stadia whilst the 1971 generation were in the 10th and 11th stadia. The data suggest that O. moreletii aggregated beneath the tussocks during summer and dispersed from it in autumn. The numbers of O. moreletii in the pasture grasses in autumn and early winter 1973 were similar to those observed prior to summer (November 1972), suggesting that survival over the summer was high.

The early summer of 1973-4 (December to early January) was dry. The remainder of the summer was abnormally wet. The numbers of O. moreletii

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* The variances of the two samples were significantly different. Therefore the degrees of freedom in the t test were = n - 1 and not = 2 (n - 1) (see Sokal and Rohlf (1969) p. 375). Hereafter t' (instead of t) will be used to indicate that the variances in a t test were significantly different.

increased beneath the tussocks from November 1973 to January 1974, suggesting aggregation. However, there was no obvious change in the numbers of O. moreletii in the pasture grass throughout the summer (Note: December 1973 to January 1974; $t'_4 = 1.91$, $p > .05$, therefore not a significant decrease). Survival was apparently high throughout the summer of 1973-4.

The summer of 1974-5 was dry. Early February was particularly hot and dry. The numbers of O. moreletii increased beneath the tussocks from October 1974 to January 1975 and decreased significantly ($t_8 = 3.84$, $p < .05$) in the pasture grasses at the same time. By May 1975, the numbers of O. moreletii had decreased beneath the tussocks but had not increased significantly in the pasture grasses ($t_8 = 1.16$, $p > .05$). Compared with 327 in the 9th and 10th stadia prior to the summer in the pasture grasses (October 1974), only 145 in the 10th and 11th stadia were found in May 1975. That is a survival of only 44% for the 1973 generation over the summer of 1974-5. The decrease in numbers was significant ($t_8 = 3.01$, $p < .05$). The 327 in the 9th and 10th stadia in October 1974 consisted of 152 females and 175 males. The 145 in the 10th and 11th stadia in May 1975 consisted of 72 females and 73 males. Survival of the sexes was therefore similar.

Changes in the total numbers of O. moreletii collected in the litter by itself are shown in Figure 4.10. Because the millipedes in the soil were not collected, statements concerning changes in the abundance of O. moreletii in toto in the grassland and woodland are therefore difficult to make from Figure 4.10. However, autumn and spring are times of the year when O. moreletii is most active above the surface of the ground (see Section 4.59). It seems reasonable to equate the numbers present in the litter at these times with the total numbers present in each habitat. Indeed when the soil beneath the samples taken in October 1974 and April 1975 was disturbed for the first few cm, very few millipedes were seen, suggesting that by far the majority of O. moreletii present then were in

the litter.

In both the grassland and woodland, the total numbers in autumn 1975 (April) were similar to those in spring 1974 (October) (see Figure 4.10). This at first suggested that survival over the summer of 1974-5 was high in both habitats. The data however deserve closer consideration.

In October 1974, the populations present were primarily in the 8th, 9th and 10th stadia (i.e. the 1973 generation) (see Tables 4.4 (e and f)). Any individuals in the 1974 generation were not sampled at this time because of their small size (see Section 4.42). In April 1975, the populations consisted of both the 1973 generation (now in the 10th and 11th stadia) and the 1974 generation (now in the 7th and 8th stadia and included in the sampling). Because the 1974 generation was not included in the population counts for October 1974, it cannot be included in the counts for April 1975 - if the two populations are to be compared. Only the data for the 1973 generation are relevant.

In October 1974, 42.5 $\pm$ 7.6 ($\bar{x}$ $\pm$ S.E.) O. moreletii in the 1973 generation were found in the grassland per sample of 0.1 m^2. In April 1975, 23.6 $\pm$ 3.0 per sample were found. This suggested a survival of only 56% throughout the summer (c.f. data given above for the sampling of soil and litter which suggested a survival of 44% throughout the summer of 1974-5). The drop in numbers was significant ($t'_9 = 2.30$, $p < .05$). The data in Appendix Tables 4.5 (a and b) suggest that the mortalities of both sexes in the 1973 generation were similar throughout this summer.

The data in Table 4.4(f) obviously give no evidence of mortality of the 1973 generation throughout the 1974-5 summer in the woodland.

In both the grassland and woodland, the numbers of O. moreletii in the litter decreased during the summer (see Figure 4.10). Presumably, O. moreletii moved underground in summer. Certainly, O. moreletii could be found reasonably commonly in the soil in summer. In late December 1972,

10 samples of both soil and litter were taken in the woodland. The samples were each 0.1 m^2 in area and were selected at random coordinates within a plot of 20 x 50 metres. The litter in each sample was first removed and placed in a plastic bag along with the millipedes present on the soil surface. Then the soil was removed to a depth of 10 cm (where possible) and placed in a separate bag. The depth of soil varied according to limitations arising from rocks, roots, etc. The millipedes were later removed from the samples by hand-sorting. The numbers of O. moreletii collected in the 10 samples were as follows.

	Male	Female	Total
Litter	2	9	11
Soil	13	5	18

The millipedes were predominantly in the 8th to 11th stadia. Although the data are limited and the soil samples were variable in size, the collections do suggest that many O. moreletii are found underground in summer.

4.57 Maturation and Subsequent Survival

The aim of this section is to describe 1) the degree of maturity achieved by O. moreletii during each breeding season (in particular the degree of maturity achieved by 2 year olds) and 2) the survival of O. moreletii (again in particular the 2 year olds) after each breeding season. Results from the sampling of 1) soil and litter and 2) litter by itself will be used primarily.

All but one of the 127 males recorded in the 10th and 11th stadia in the pasture grasses from autumn through winter (March to August) 1973 were mature. That is, virtually all the 1971 generation of males matured after 2 years. In April and May 1973, only 25% of the 40 females in the 10th and 11th stadia in the pasture grasses were carrying small developing

eggs. At the same time, 63% of the females in these stadia had mature eggs. The majority of females in the 1971 generation were therefore mature after 2 years also.

In passing, it should be noted here, that in April and May 1973, all but 6 of the 1634 males in the 10th and 11th stadia that were taken in the pitfall traps in the grassland were mature. (All but 2 of the 122 males in the same stadia trapped in the woodland at the same time were mature). Of the 779 females in these two stadia that were trapped in April and May in the grassland, 75% were carrying mature eggs, whilst only 3% were carrying small developing eggs. (The equivalent figures for the 70 females taken in the woodland were 80% and 6% respectively). These results suggest that the level of maturity in the active population during the 1973 breeding season was high.

The following table gives the numbers ($\bar{x} \pm$ S.E.) of the males (adults only) and females in the 1971 generation per sample of pasture grasses in autumn and spring 1973. Unfortunately, the data are too variable to demonstrate any mortality that might have occurred from autumn to spring.

	April	May
10th and 11th stadia ♂	8.8 ± 3.5	6.8 ± 2.1
" " " " ♀	3.4 ± 1.5	4.6 ± 0.7
	October	November
11th and 12th stadia ♂	1.6 ± 0.8	4.2 ± 0.4
" " " " ♀	1.8 ± 0.9	3.8 ± 1.9

Of the 39 O. moreletii collected in the pasture grasses in April 1974 in the 10th and 11th stadia, 14 were females and 25 were males. All the males were mature. Twelve of the 14 females were carrying mature eggs. No females had small developing eggs. Thus the maturation of the 1972 generation in 1974 was very successful.

Of the 34 O. moreletii in the 9th stadia collected in the pasture grasses in April 1974 and which almost certainly were only 1 year old (1973 generation), 14 were females and 20 were males. All the males were mature. Only one of the females carried mature eggs. The remainder had small developing eggs. Of the 204 eighth stadia present at this time, 110 were males of which 15% were mature. Therefore not only was the maturation of the 1972 generation successful in 1974, but even some of the 1973 generation, especially the males, matured.

In October 1974, only 1 female and 1 male (intercalary) were found in the pasture grass in the 11th and 12th stadia. This contrasted with the 14 females and 25 mature males in the 10th and 11th stadia in the previous April. Although the decrease from April to October was significant for the females ($t'_4 = 2.95$, $p < .05$), it was not for the males ($t'_4 = 2.11$, $p > .05$). The lack of significance for the males could be attributed to large variability between the samples taken in April. No adult males were found in the 9th and 10th stadia in October 1974. Therefore there was no evidence of any survival of the mature males in the 8th and 9th stadia in April 1974. Overall, the data suggest that survival of adults from autumn to spring 1974 was low.

There was no evidence of mortality of the 1973 generation (excluding the mature males mentioned above) from April to October 1974. Two hundred and thirty seven in the 7th, 8th and 9th stadia were found in April and 345 in the 8th, 9th and 10th stadia were found in October! Thus the factor killing the 1972 generation and the adults from the 1973 generation during April to October 1974 was not affecting the remainder of the 1973 generation. The survival of the 12th and 13th stadia past the autumn 1974 to spring 1974 appeared to be negligible (see Table 4.4b).

Of the 73 males collected in the pasture grasses (soil and litter) in May 1975 in the 10th and 11th stadia, only 43 (59%) were mature. Of the

72 females similarly collected, only 8 (11%) were carrying mature eggs. On the other hand, 55 (76%) were carrying small developing eggs. Similar percentages were found for the individuals beneath the tussocks (5% with mature eggs and 95% with small developing eggs). Thus for this breeding season (1975), maturation was poor compared with the two previous years.

In October 1975, 42 males and 72 females in the 11th and 12th stadia were collected in the samples of pasture grass. Of the 42 males, 27 were juveniles, 2 were mature and 13 were intercalary. There was no evidence of significant mortality of juvenile males from May to October 1975 (30 in May in the 10th and 11th stadia to the 27 in October) nor of females (72 to 72). Although mortality of the adult males during this time might have been suspected from the data (43 to 15) it was not demonstrated ($t'_4 = 1.82$, $p > .05$).

Turning now to the sampling of litter by itself, of the 400 O. moreletii in the 10th and 11th stadia collected in the grassland in April and May 1975, 201 were males of which only 11 were juveniles (i.e. 95% mature). Of the 199 females in these stadia, 119 (60%) were carrying mature eggs. Only 43 (22%) were carrying small developing eggs. Maturation was therefore successful for this (1975) breeding season, in this portion of the open grassland (c.f. soil and litter sampling). Of the 461 in the 10th and 11th stadia collected in the woodland in April and May 1975, 221 were males of which 35 were juveniles (i.e. 84% mature). Of the 240 females in these stadia, 113 (47%) were carrying mature eggs, whilst 102 (43%) were carrying small developing eggs. Maturation was therefore also successful in this habitat, but not as successful as in the grassland.

In April, May and June 1975, the first ten females from each habitat in the 10th and 11th stadia and which contained mature eggs were dissected and the mature eggs counted. The mean numbers and their ranges were as follows:-

	Grassland	Woodland
April	146 (115 - 173)	98 (64 - 204)
May	111 (76 - 159)	68 (38 - 119)
June	91 (52 - 148)	52 (17 - 92)

The above data further suggest that the maturation of the females was poorer in the woodland than in the grassland. The decrease in number of mature eggs per female from April to June perhaps reflected 1) the burrowing underground and ovipositing of the fecund females, and 2) poorer maturation of females that matured their eggs later in the breeding season.

In both the grassland and woodland, the numbers of the 1973 generation collected in spring 1975 (in the 11th and 12th stadia) were fewer than the numbers collected in the previous autumn (in the 10th and 11th stadia) (see Table 4.7). Large numbers of dead millipedes were seen on the surface of the ground in both habitats in winter 1975, indicating that heavy mortality had occurred. Assuming all the decrease in numbers to be due to mortality, the numbers collected in April and November were used to calculate the following percentage survivals from autumn to spring 1975.

1973 generation	Grassland	Woodland
Total	20.8	26.0
Females	18.3	33.5
Males	23.8	14.8
Adult males	19.6	16.8
Juvenile males	87.5	5.0

Notably, the survival of females was higher in the woodland than in the grassland whilst the survival of juvenile males was the reverse. The survival of adult males was poor and similar in both habitats.

In summary, the sampling of soil and litter in the grassland suggested that the maturation of O. moreletii in autumn (in particular the

TABLE 4.7

Average numbers ($\bar{x}$ + S.E.) of 1973 generation per sample taken in autumn (10th and 11th stadia) and spring (11th and 12th stadia), 1975. Note one sample in the grassland = 0.1 sq. metres, one sample in the woodland = 1.0 sq. metres.

GRASSLAND

		Autumn		Spring
TOTAL	Apr.	23.6 ± 3.0	Oct.	3.5 ± 0.7
	May	16.4 ± 2.0	Nov.	4.9 ± 1.2
FEMALES	Apr.	13.1 ± 1.5	Oct.	2.0 ± 0.6
	May	6.8 ± 0.5	Nov.	2.4 ± 0.7
MALES	Apr.	10.5 ± 1.9	Oct.	1.5 ± 0.3
	May	9.6 ± 1.7	Nov.	2.5 ± 0.6
AD. MALES	Apr.	9.7 ± 1.8	Oct.	0.6 ± 0.3
	May	9.3 ± 1.7	Nov.	1.9 ± 0.5
JUV. MALES	Apr.	0.8 ± 0.3	Oct.	0.9 ± 0.3
	May	0.3 ± 0.2	Nov.	0.7 ± 0.3

WOODLAND

		Autumn		Spring
TOTAL	Apr.	28.5 ± 7.1	Oct.	8.5 ± 1.0
	May	17.6 ± 2.0	Nov.	7.4 ± 2.0
FEMALES	Apr.	17.0 ± 5.1	Oct.	6.5 ± 1.0
	May	7.0 ± 1.0	Nov.	5.7 ± 1.6
MALES	Apr.	11.5 ± 2.7	Oct.	2.0 ± 0.5
	May	10.6 ± 1.6	Nov.	1.7 ± 0.6
AD. MALES	Apr.	9.5 ± 2.4	Oct.	1.5 ± 0.5
	May	9.1 ± 1.6	Nov.	1.6 ± 0.6
JUV. MALES	Apr.	2.0 ± 0.6	Oct.	0.5 ± 0.3
	May	1.5 ± 0.4	Nov.	0.1 ± 0.1

maturation of two year olds) was greatest in 1974, least in 1975 and intermediate in 1973. Survival of two year olds (in particular the females) from autumn to spring was greater in 1975 than in 1974. Survival of two year olds from autumn to spring 1973 was questionable due to variable data. The sampling of litter suggested that maturation of two year olds was greater in the grassland than in the woodland in autumn 1975. The subsequent survivals of these two year olds to spring 1975 was lower in the grassland than in the woodland for females, but the reverse for juvenile males.

4.58 Production of New Generations

(a) As measured over the first 6 months after the breeding season.

In autumn and winter 1973, large numbers of eggs were found beneath the tussocks. Few eggs were found beneath the pasture grasses (see Tables 4.4a and b). By spring 1973, large numbers of this new generation were in the pasture grasses as 4th, 5th or 6th stadia. At the same time, relatively few were found in the tussocks. Presumably O. moreletii dispersed from the tussocks into the pasture grasses once the active stages (> 1st stadium) in the life cycle were reached. Although eggs were common beneath the tussocks in the autumnsof 1974 and 1975, very few young were found either in the tussocks or in the pasture grasses in the following springs (compared with the 1973 generation).

The following table lists for April and May of each year the numbers of mature males and females carrying mature eggs in the five samples of soil and litter from the pasture grasses. The figures refer to all stadia (i.e. not just the 10ths and 11ths).

	Males		Females	
	April	May	April	May
1973	48	39	15	14
1974	62		19	
1975		44		10

The next table lists the mean (and range in) numbers of mature eggs in the females in the previous table:-

	April	May
1973	145 (90 - 302)	136 (65 - 217)
1974	140 (61 - 176)	
1975		58 (18 - 96)

The data above give no evidence to suggest that the greater production of young in 1973 compared with 1974 can be explained by 1) a greater abundance and 2) a higher fecundity of the breeding females during the former year's breeding season. Low production in 1975 however can probably be attributed, at least in part, to low abundance and fecundity of breeding females. Mature males were no more abundant in 1973 than in 1974 and 1975 and therefore do not help explain the differences in production between years.

Turning now to the samples taken of the litter by itself, juveniles in the 1975 generation were obvious in the grassland in the late winter and in spring. In November 1975, 117 were found in the 6th stadium. The 1975 generation was rarely seen in the woodland and by November none had been found in the 6th stadium.

The following table lists for April and May 1975 the numbers of mature males and females carrying mature eggs in the ten samples from both the grassland and woodland. The figures refer to all stadia (i.e. not just the 10ths and 11ths). The reader should remember that the samples taken in the grassland were 1/10th the area of those in the woodland.

	Males		Females	
	April	May	April	May
Grassland	102	99	82	40
Woodland	99	94	101	26

The greater production of young in the grassland compared with the woodland can probably be explained, at least in part, by the obviously greater abundance of breeding adults in the former habitat. Further, the differences in the fecundities of the females in the two habitats (e.g. see Section 4.57) could also help explain the differences in production.

(b) As measured over greater than 6 months after the breeding season.

If it is accepted that number of females with mature eggs in the pasture grasses in autumn (April and May) is an adequate estimate of the number of females that reproduced in a particular year, and if an average fecundity of 250 eggs is attributed to each female (see Section 3.8)*, then 3,625 eggs were produced as the 1973 generation by the females present per 5 samples of pasture grasses (i.e. 250 x 14.5). One year later, 274 millipedes belonging to the 1973 generation and in the 7th, 8th and 9th stadia were collected in 5 samples of pasture grasses (10th stadia were not included here but possibly could be). This suggests a survival of 7.6% to the 1st year. After 2 years, 145 of the 1973 generation were collected in the 10th and 11th stadia suggesting a survival of 4.0%. Of these 145, 72 were females.

Put differently, 14.5 females in 1973 produced 72 females which survived to 2 years old (i.e. 4.97 females per female). However only 8 (11%) of these 72 females had mature eggs after 2 years. Thus each breeding female in 1973 gave rise to only 0.55 females which were breeding in 1975. But after 2 1/2 years (spring 1975) there was no evidence of further

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* I have preferred here to use the number of eggs laid in a clutch in the laboratory as a measure of fecundity to the number of mature eggs found in females in the field at the time (approx. 140).

mortality of the 72 females. Those that survived to 3 years* and reproduced would have increased the replacement rate of 0.55 of the females breeding in autumn 1973.

4.59 Activity

The numbers of O. moreletii per trap for each trapping day are given in Appendix Tables 4.7 (a and b) for both the grassland and the woodland. These data were averaged for each sampling "week" and the resulting values of the average numbers of O. moreletii per trap per day are given in Figure 4.11. There was no evidence in the data to suggest a relation between the numbers trapped and the day of the "week". An alternative method of expressing the numbers trapped in each sampling "week" would have been to calculate the average numbers per trap-day (e.g. where usually n, the number of trap-days in the "week" equals 7 x 16 = 132 in the grassland and 7 x 32 = 224 in the woodland). However, the basic data (i.e. the numbers of O. moreletii in each trap-day) were not always normally distributed within a trapping day or "week". Cumbersome transformations of the data would have been necessary in order to calculate

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* In April and May 1976, an additional 10 samples of pasture grass were taken. From these samples, 166 O. moreletii were extracted in the 12th and 13th stadia (1973 generation). This abundance of the 1973 generation suggests a survival to 3 years of age of 2.3%. Of the 166 in the 12th and 13th stadia, 106 were females - of which 79 contained mature eggs. Thus although 14.5 females breeding in 1973 only produced 8 females which bred in 1975, they produced 39.5 which bred in 1976 (All values here refer to numbers of females per 5 samples of pasture grass). The continued survival of the offspring from 1975 to 1976 raised the replacement rate per female from 0.55 to 3.28.

standard errors and present the data in a similar form to that in Figure 4.11.

From Figure 4.11 it is obvious that peaks in the numbers trapped occurred in autumn in both habitats sampled. Prior knowledge of the life history of O. moreletii (see Section 4.52) suggests that the increases in the numbers trapped during autumn represent increases in activity and not abundance. The large variation in the data for April, 1973 from the grassland was due to an exceptional number of millipedes being caught on just one day (75.4 ± 8.4 ($\bar{x}$ ± S.E.)). Large numbers of O. moreletii (predominantly 7th and 8th stadia) were also trapped in the grassland in January 1974 when for this time of year, 1) conditions were exceptionally moist and 2) O. moreletii was exceptionally abundant in the pasture grasses.

From data presented earlier (see Sections 4.53 and 4.54) and later (see Sections 5.4 and 6.3), it is obvious that the physiology of O. moreletii can change markedly over a period of a few weeks (e.g. the maturity of the gonads, resistances to extremes in temperature and humidity). In addition, structural variables in the habitat such as the amount of cover by grass can change markedly. It is therefore unrealistic to attempt to correlate the activity of O. moreletii (as measured by the numbers trapped and corrected for changes in abundance if need be) with prevailing weather by using the data from different sampling "weeks" in one analysis. However for trapping days within a sampling "week" it is more reasonable to assume that the physiology of the population and the structural variables in the habitat are constant and that correlations of daily activity with weather will be realistic. Moreover, within one sampling week, except for exceptional circumstances, it can be assumed that abundance does not change significantly.

Attempts were made to obtain correlations between the numbers of O. moreletii trapped within "weeks" in both the grassland and woodland and the available meteorological data from Stirling (e.g. rainfall,

relative humidity, saturation deficit, maximum and minimum temperatures). Rarely was a significant correlation obtained, presumably because of the often poor relationships between the prevailing weather as measured at Stirling and the environment on the soil-surface at Bridgewater (moisture in particular).

Table 4.8 lists the numbers of O. moreletii trapped and the associated weather data for the trapping "weeks" during October-November 1972 and April and June 1973. Although correlations proved elusive, (see above) the data in Table 4.8 strongly suggest that the activity of O. moreletii is influenced by both moisture and temperature. Under dry conditions (e.g. 27-30/10/72 and 9-14/4/73) activity was inhibited although on occasions temperatures appeared to be suitable. Under moist conditions (e.g. 30/10-4/11/72, 14-16/4/73 and 18-25/6/73), activity was stimulated and correlated with temperature.

The frequencies with which nil, few, several, many and very many active O. moreletii were seen on the paths in the grassland and woodland during the different months of the year are given in Table 4.9 (a and b). It is obvious that the abundance of active millipedes on the paths was most marked during autumn and to a lesser extent spring in both habitats. However on several days in summer, large numbers of active millipedes were seen. These occasions were all in association with heavy rainfall on the days in question or on days just prior to them. Never were millipedes seen active on the paths in July or August.

For March, April, July and November 1973 and January 1974 (i.e. representative seasons of the year), the age distributions of the active populations (those trapped) and the populations present (those extracted from samples of pasture grass) in the grassland were compared by taking the ratio of the numbers active to the numbers present for each stadium. These ratios, calculated from the data in Tables 4.4 (b and c) and Appendix Tables 4.2 and 4.3 are expressed in Figure 4.12 and Appendix Table

TABLE 4.8

Numbers of O. moreletii trapped and associated weather.

Date	Average Nos./Trap		Weather for the 24 Hours		Rain In Past 7 Days	Days Since Last Rain
	Grassland	Woodland	Min. Temp. °C	Rainfall (mms)	(mms)	
27-28/10/72	0.500	0.357	6	0	0	12
28-29	0.417	0.929	11	0	0	13
29-30	0.500	0.393	14	0	0	14
30-31	8.417	0.929	9	3	3	0
31-1/11/72	5.000	0.571	7	0	3	1
1-2	7.250	1.321	12	2	5	0
2-3	2.583	0.536	7	2	7	0
3-4	9.750	1.250	8	2	9	0
4-5	3.167	0.429	6	0	9	1
5-6	2.583	0.214	7	0	9	2
6-7	1.500	0.179	5	0	6	3
9-10/4/73	4.875	0.094	7	0	1	5
10-11	2.750	0.125	10	0	1	6
11-12	4.438	0.031	12	0	0	7
12-13	2.875	0.156	13	0	0	8
13-14	3.063	0.094	15	0	0	9
14-15	9.063	1.656	13	10	10	0
15-16	75.375	3.781	9	1	11	0
18-19/6/73	4.625	0.125	4	0	28	5
19-20	5.563	0.219	6	1	28	0
20-21	10.125	0.531	10	7	15	0
21-22	4.438	0.219	2	2	10	0
22-23	6.000	0.344	7	0	10	1
23-24	4.813	0.344	7	2	12	0
24-25	4.000	0.313	5	7	19	0

TABLE 4.9

Numbers of visits to Bridgewater throughout the year and the frequencies of observations of mating and different numbers of active millipedes seen on the ground during such visits.

(a) Open Grassland

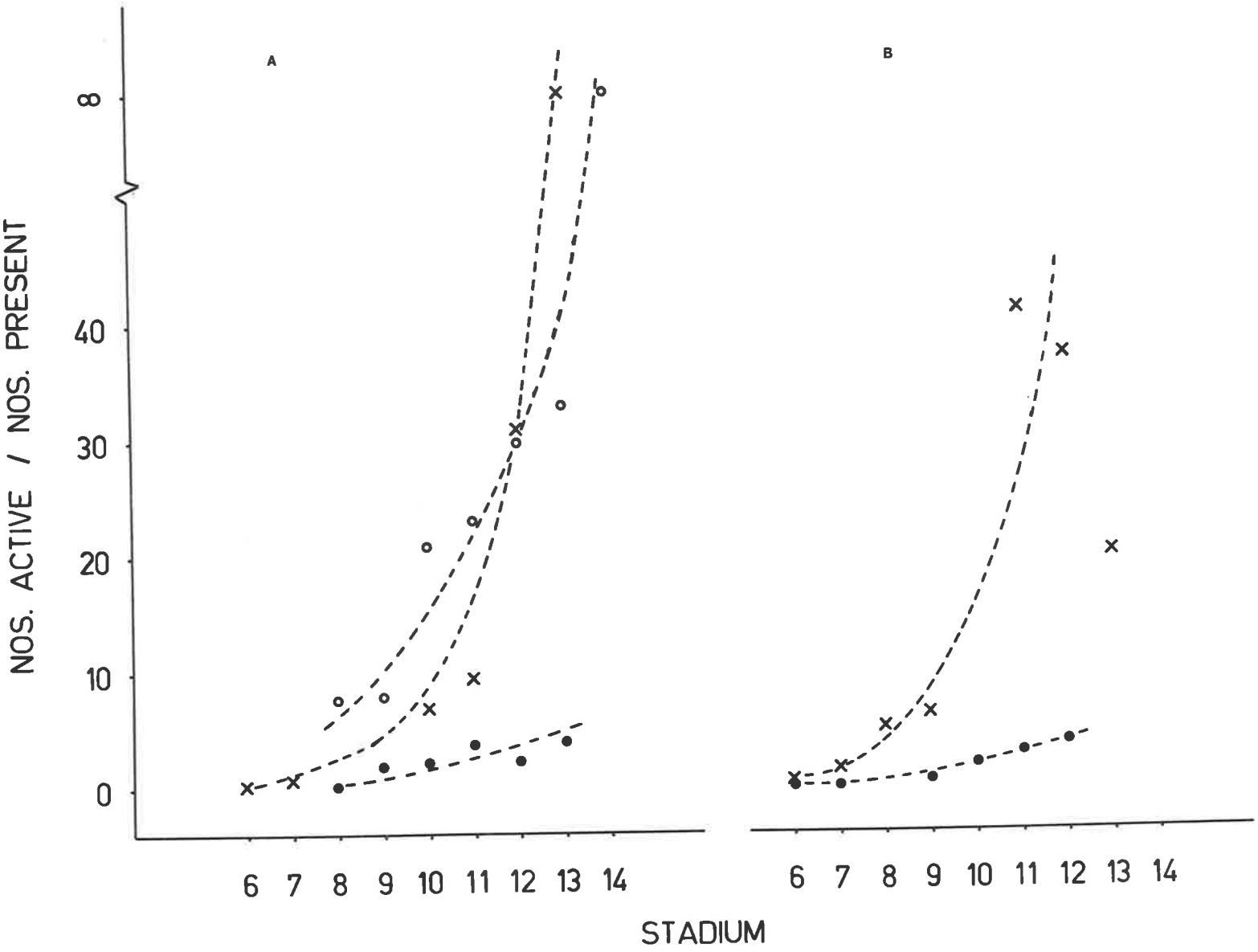
	Month											
	J	F	M	A	M	J	J	A	S	O	N	D
Number of Visits	19	23	32	23	36	11	13	12	11	23	15	15
Number of Visits when mating seen			2	16	14	3						
Number of Visits when												
1) Very many active	4	1	4	1								
2) Many active	3	1	7	5	1					4	3	1
3) Several active	2	2	3	8	2					3	1	2
4) Few active	1	9	10	6	13	2			3	10	4	2
5) Nil active	9	10	8	3	20	9	13	12	8	6	7	10

(b) Sclerophyllous Woodland

	Month											
	J	F	M	A	M	J	J	A	S	O	N	D
Number of Visits	10	10	20	16	23	13	20	11	9	20	15	10
Number of Visits when mating seen				4	1							
Number of Visits when												
1) Very many active			5	2								
2) Many active	1	1	5	3								
3) Several active	2		3	4	2					5	1	1
4) Few active	4	4	4	4	8				3	9	9	2
5) Nil active	3	5	3	3	13	13	20	11	6	6	5	7

(Data from 9/10/72 to 7/11/75)

FIGURE 4.12 (a & b) The numbers of millipedes active/numbers present in each stadium in the grassland during certain months. Lines fitted by eye (Figure 4.12(a); x = March 1973, o = April 1973, ⊙ = July 1973: Figure 4.12(b); ● = November 1973, x = January 1974).


A
B
NOS. ACTIVE / NOS. PRESENT
8
40
30
20
10
0
6 7 8 9 10 11 12 13 14
6 7 8 9 10 11 12 13 14
STADIUM

4.8. Actually, the pitfall traps were not set within the 0.5 hectare plot that was sampled for pasture grass, but rather in areas adjacent to it. Since there was no obvious difference in habitat between the areas sampled (see Section 4.43), I have considered them one and the same.

Consistently, the older stadia were more active (i.e. more were trapped considering how many were present) than the younger stadia. Although the data in Figure 4.12 perhaps suggest increases in activity within the older stadia (10th and older) with increased stadial age, the data in Appendix Table 4.8, where males and females are treated separately, suggest no such increases.

4.510 Life Histories of the Native Species, Australiosoma castaneum and Dimerogonus sp.

A. castaneum and Dimerogonus sp. were never found in any samples (soil and litter, litter by itself, pitfall trapping and hand-collections) taken in the grassland and I conclude that neither species occurs there, or they are extremely rare. However, several A. castaneum were found on the fire-break bordering the grassland during late winter and spring. They had presumably dispersed there from nearby woodland.

The numbers of A. castaneum collected in the woodland by pitfall trapping and in the samples of litter are given in Tables 4.10 (a and b) where they are arranged according to stadium and sex. The hand-collections of A. castaneum that were made during the period 4/9/72 to 11/11/75 have been arranged in Table 4.11 according to the month of the year in which they were found. Of course the intensity of hand-collections varied greatly throughout the year, and therefore the data in Table 4.11 should only be regarded qualitatively.

Only the last three stadia (two juvenile stadia and the adults) of A. castaneum were found commonly. Perhaps this reflected an inefficiency in sampling for the younger stadia, but more likely it reflected greater

TABLE 4.10(a)

Numbers of Australiosoma castaneum collected during pitfall trapping*

Sampling Code	No.	Numbers of podous segments					Females with large mature eggs
		Unknown	14 & 15	16	17	18	
O-N	1			6(2)	1(1)		
D	2						
J-F	3						
F	4						
M	5						
M	6				1(1)		
A	7						
M	8						
M	9						
J	10					1(1)	
J	11					5(3)	1
A-S	12			1(1)			
O	13			1(1)	2(2)	2(-)	2
N	14	1	1(1)	6(4)	5(2)		
D	15				1(-)		
J	16				4(2)	1(-)	
TOTAL		1	1(1)	14(8)	14(8)	9(4)	3

* The numbers of males in each age group (determined by the number of podous segments) is indicated in brackets for each sampling occasion.

TABLE 4.10(b)

Numbers of *Australiosoma castaneum* collected during litter sampling*

Date	Numbers of podous segments				Females with large mature eggs
	14 & 15	16	17	18	
9/9/74		4(1)	2(1)	3(-)	3
9/10/74		3(3)		1(-)	
9/11/74			2(1)		
9/12/74			6(2)		
9/1/75			1(1)		
9/2/75					
9/3/75					
9/4/75		1(-)		2(-)	1
9/5/75				2(1)	1
9/6/75				2(1)	1
9/7/75	1(1)			2(-)	2
9/8/75	1(-)			1(1)	
9/9/75					
9/10/75		6(4)	2(-)		
10/11/75			2(1)		
TOTAL	2(1)	14(8)	15(6)	13(3)	8

* The numbers of males in each age group (determined by the number of podous segments) is indicated in brackets for each sampling occasion.

TABLE 4.11

Numbers of *Australiosoma castaneum* taken in hand-collections from 4/9/72 to 11/11/75*

Month of the Year	Numbers of podous segments					Females with large mature eggs
	14	15	16	17	18	
January					1(1)	
February						
March					5(5)	
April**					39(29)	6
May**	3(-)				57(31)	10
June		3(-)		1(-)	19(14)	3
July**	2(1)	7(3)	18(6)	3(2)	65(45)	18
August				1(1)	27(12)	13
September		1(1)	64(31)	2(2)	18(8)	6
October	1(-)		83(48)	6(4)	4(1)	3
November						
December						
TOTAL	6(1)	11(4)	165(85)	13(9)	235(146)	59

* The numbers of males in each age group (determined by the number of podous segments) is indicated in brackets for each sampling occasion.

** Mating couples observed in the field.

surface activity of the last three stadia. Blower (1970) and Lewis (1971a) have commented on the predominant surface activity of only the last few stadia in the life cycles of Polydesmid millipedes.

A. castaneum was present in the litter from late winter to spring (July to November) in the second to last and last juvenile stadia. It seems likely that A. castaneum passes the summer in the last juvenile stadium emerging as the adult in the subsequent autumn and winter. Adults were present from March to October. Adult males predominated during autumn and winter, whilst females were more common during spring (see Table 4.11). Mating was observed in the field from April to July. Presumably oviposition occurred in spring, but no nests of eggs were found.

Juveniles of A. castaneum were aggregated in their dispersion in the litter. Usually when one juvenile was found, 10 or 20 others of the same stadium were also found within a tenth of a square metre. These aggregates of juvenile A. castaneum could not be described as "swarms" (see Lewis, 1971(b); Fryer, 1957 and Toye, 1967 for descriptions of swarms of other Polydesmids). Probably, the aggregates represented "family groups" as described by Blower (1969).

Little can be said of the life history of Dimerogonus sp. because of its rarity (see Table 4.12). However hand-collections of the species were made from July to October, particularly beneath the introduced Chasmanthe aethiopica (see Section 3.10). The available data suggest 1) that the species is most active in winter and spring and 2) that reproduction occurs at this time (mature males were present and the females were carrying mature eggs).

The apparent winter-spring breeding seasons of A. castaneum and Dimerogonus sp. were in marked contrast to the autumn breeding season of O. moreletii.

TABLE 4.12

Numbers of *Dimerogonus* sp. collected during pitfall trapping

Sampling Code	No.	Juvenile Males	Adult Males	Females
O-N	1	1		
D	2			
J-F	3			
F	4			
M	5			1
M	6			1
A	7			
M	8			
M	9			
J	10			
J	11			1
A-S	12			1
O	13		2	2
N	14		1	3
D	15			
J	16			
TOTAL		1	3	9

Only 2 *Dimerogonus* sp. were collected in the sampling of litter (1 adult male on 9/9/74 and 1 female (with large mature eggs) on 9/6/75).

4.6 Discussion

No provisions were made in this study to measure emigrations from and immigrations into the areas studied. It is possible therefore that the changes (or lack thereof) in the numbers in and structures (e.g. age distributions, sex ratios etc.) of the populations of O. moreletii referred to in the preceding pages were explainable in terms of emigration and immigration. However, I consider this unlikely. The study areas used were surrounded on all sides by large areas of similar habitats (see Section 4.4). It is hard to imagine emigration from or immigration into the study areas without reciprocal movements in the surrounding areas.

Mating and Oviposition

Metschnikoff (1874 - cited by Halkka, 1958) reported that O. moreletii oviposited in Madeira in autumn. At Bridgewater, O. moreletii mated and oviposited during autumn and winter. Nests of eggs, pupoids and first stadia were very common in the soil beneath the tussocks of L. fibrata, but were rare in the soil beneath the pasture grasses. This difference in the abundance of the inactive stages in the two micro-habitats probably reflected 1) a preference for oviposition sites by females, and/or 2) higher mortalities of the very young beneath the pasture grasses compared with beneath the tussocks. The young of O. moreletii (eggs to third stadia) were very susceptible to excess water in laboratory cultures. They were trapped by films and droplets of water. The soil in which the nests were found beneath the tussocks remained drier than that beneath the pasture grasses during the wetter months of the year and perhaps more suitable for the survival of the very young.

Development and Maturation

After 1 year, O. moreletii was in the 7th, 8th or 9th stadium. After 2 years, the 10th or 11th stadia were reached. In subsequent years,

O. moreletii probably moulted only twice per year, in spring and summer. The environmental cue that triggered moulting in the older O. moreletii remains unknown. The moult in summer coincided with the hottest and driest time of the year (perhaps the most opportune time for the millipedes to be underground moulting - c.f. O'Neill, 1969(a)), but the cue for the moulting may have operated well before this time. Similarly, the cue for the spring moult may have occurred well before spring. Perhaps, changes in day length, temperature or moisture could be investigated as the possible cues for the two moults.

Brookes (1974) found that the juveniles of the Blaniulid, Proteroiulus fuscus, developed more rapidly in Britain in an open and warm plot of elm than they did in a shaded and cool plot of larch and spruce. In addition, Brookes found that the juveniles of P. fuscus developed more rapidly in Britain than in Finland (Rantala, 1970). Fairhurst (1974) outlined variations in the rates of development of juveniles of the Iulids, T. niger and O. sabulosus in different habitats. Banerjee (1970b) reared juveniles of the Polydesmid, Polydesmus angustus, in the laboratory under various regimes of food and weather and found different rates of development to adulthood. There was however no evidence in the present study to suggest that the rates of stadial growth of juveniles of O. moreletii were markedly different in the different habitats studied nor in different years in the one habitat (the grassland at Bridgewater).

In the present study, there was evidence of large differences in the development of maturity of both sexes of O. moreletii, both between different habitats and between different years in the one habitat. Maturation of individuals at 1 (in particular the males), 2 or 3 years of age was inferred from field sampling. Data from the sampling of the litter suggested that maturation was more successful in the grassland than in the woodland in autumn 1975. Data from the sampling of the soil and litter suggested that maturation in the grassland was unsuccessful in autumn 1975,

successful in autumn 1974 and intermediate in autumn 1973. Collections made in Melbourne in autumn 1975 suggested that maturation was more successful there than at Bridgewater or on Eyre Peninsula at the same time.

Since 1) Melbourne received a higher rainfall than Bridgewater and Eyre Peninsula during the summer of 1974-5 and 2) conditions at Bridgewater were very moist in the summer of 1973-4 but dry in the summers of 1972-3 and 1974-5 (especially in February 1975), there was some evidence to suggest that the degree of maturation in a particular autumn and the aridity of the previous summer were correlated. Moister conditions may have allowed greater feeding prior to the breeding season.

Although the climate at the soil surface was moister in the woodland in mid-summer (see Section 4.3), the litter in the woodland did appear to dry out more quickly in spring-early summer than the litter in the grassland. Growth of the pasture grasses in the grassland in early summer was prolific and the soil surface remained cool and damp. Perhaps additional feeding during early summer (allowed by moister conditions then) explained the higher maturation in the grassland. On the other hand, perhaps the quantity and quality of food was greater in the grassland than in the woodland and this was reflected by the different degrees of maturation in the two habitats.

In the grassland, the sampling of soil and litter was done on a westerly slope in a habitat of both tussocks and pasture grasses, whilst the sampling of the litter was done on an easterly slope in a habitat of "pure" pasture grasses. The sampling on the westerly slope suggested that maturation of the 1973 generation was unsuccessful in 1975. Intriguingly, the sampling on the easterly slope suggested the opposite; maturation of of the 1973 generation was successful in 1975. I can give no explanation for this difference. Perhaps there was a difference in micro-climate, soil or food type, etc. between the sites which explained the results - but such a difference was not obvious.

Maturation and Subsequent Survival

There was a negative correlation between the degree of maturation of a particular generation of females and its subsequent survival. Within the grassland, the sampling of the soil and litter suggested that maturation was successful in 1974 and survival of females to spring was low. Maturation was unsuccessful in 1975 and survival was high. The sampling of litter suggested that maturation in the grassland was successful in 1975 and survival was low, whilst maturation in the woodland was relatively unsuccessful and survival relatively higher. The possible advantage to O. moreletii of a continued survival of females after a poor breeding season is discussed in Chapter 7.

The survivals of mature males from autumn to spring were generally low. The numbers of juvenile males in the same stadia as the mature males were usually too few to calculate their survivals and compare them with the mature males. However, limited data from the sampling of soil and litter and litter by itself in the grassland showed no evidence of mortality of the juvenile males in the 1973 generation from autumn to spring 1975. On the other hand, the sampling of litter in the woodland suggested poor survival of juvenile males from autumn to spring 1975. I can give no explanation for this difference between habitats - except perhaps that the numbers of individuals in the samples were low and variable.

When the sex ratios of the total O. moreletii collected in the grassland and woodland were compared (see Table 4.6) it was noticeable 1) that in both habitats the percentage of males decreased with stadial age, especially after the 10th and 11th stadia, and 2) that this decrease in the percentage of males was more marked in the woodland than in the grassland. Table 4.6 seems best explained by a higher survival of older females than older males, especially in the woodland. If the poor survival of juvenile males in the woodland is real, this would also help explain the data.

Production of Young

The production of young in the plot in the grassland where samples of soil and litter were taken was very high in 1973 but low in 1974 and 1975. Variations in the numbers of breeding adults present in each year and variations in the fecundities of females could not explain the difference in production between 1973 and 1974, but could, at least in part, help explain the difference between 1973 and 1975. Other possible explanations for the differences in production between years were 1) if the availability of sites of oviposition varied between years, and 2) if the mortality of the very young stages in the life-cycle differed in the winter months of each year. Further, the sampling of litter suggested that the production of young was much higher in the grassland in 1975 compared with the woodland at the same time. Again differences in the numbers of breeding adults and the fecundities of females could, at least in part, help explain the differences in production. Of course, differences in 1) the availabilities of sites of oviposition (although there was no evidence in Figure 4.6 (a and b) to suggest delays in oviposition in the woodland relative to the grassland) and 2) survivals of the very young might also explain the differences in production. Further, the lower abundance of adults in the woodland may have given lower probabilities of females copulating successfully with males. Production may therefore have been lower in the woodland.

Seasonality of Mature and Intercalary Males

In South-Eastern Australia, the intercalary males of O. moreletii predominated in spring to mid-summer whilst the mature males were present at other times of the year. This seasonality in the form of the adult male was in agreement with the limited data for O. moreletii and other periodomorphic millipedes in the region of the Mediterranean (see Section 4.22). Is the seasonality in the form of the adult male of O. moreletii

of adaptive advantage? This question is discussed further in Chapter 7.

Behaviour and Survival During Summer

O. moreletii aggregated in cool, moist sites (e.g. beneath tussocks) or burrowed underground during summer. During the summer of 1974-5, when the weather was particularly hot and dry, significant mortality was demonstrated (but only in the grassland and not in the woodland). Mortalities of the sexes (in the 9th to 11th stadia) were similar on this occasion. Extremes in desiccation and/or high temperature might be considered responsible for this behaviour and mortality of O. moreletii in summer. The likelihood of this is pursued in the following two chapters.

Changes in Sex Ratios

Barlow (1957) trapped in a variety of habitats in Holland. The females of C. silvarum and O. sabulosus were collected in a slightly wider variety of habitats than the males. Barlow suggested that the females of these species were "slightly less restricted ecologically than males".

The sex ratios (percentage of males) in the populations of O. moreletii present and active in the litter in both the woodland and grassland were low in late summer but increased in autumn. Considering in particular the data from the sampling of litter in the woodland, there was no evidence to suggest changes in abundance throughout the summer of either sex. The low sex ratios in late summer would seem best explained by greater burrowing underground by males compared with females. Are the males less tolerant of aridity and high temperature than the females? Experiments reported in the next two chapters suggest 1) that mature males are less resistant (i.e. less able to survive exposure) to high temperature and desiccation than females, and 2) that males show a more rapid preference for moisture in a gradient of humidity than do females.

The sampling of litter suggested that the sex ratios were much

higher in the winter in the grassland than in the woodland. With the aid of Appendix Tables 4.5 and 4.6 this is attributable to 1) earlier mortality in winter of females relative to males in the grassland compared with the woodland, and/or 2) greater predominance of females underground in winter in the grassland compared with the woodland.

Activity

In the present study, active O. moreletii were most commonly seen and trapped in autumn, to a lesser extent in spring, occasionally in summer and rarely in winter. Day to day variations in activity were correlated with changes in temperature and moisture. Results strongly suggested that the activity of older stadia was greater than that of younger stadia (c.f. studies discussed in Section 4.23).

Native Species

A. castaneum and Dimerogonus sp. were not found in the grassland. They were found in the woodland, but they were rare there relative to O. moreletii. The possibility that this confinement and relative rarity of the native species in the cooler and moister woodland was due to poor tolerance of extremes in desiccation and/or high temperature is pursued in the following two chapters.

5. WATER RELATIONSHIPS

5.1 Introduction

Millipedes are generally regarded as being dependent upon cool, moist conditions for their survival (e.g. Cloudsley-Thompson, 1958). The summers at Bridgewater are usually hot and dry. However, O. moreletii is extremely abundant there. Furthermore, until the summer of 1974-5, no mortality of O. moreletii was demonstrated at Bridgewater during summer. Admittedly, the summer of 1973-4 was very wet and perhaps mortality over this summer might not have been expected to be high. But the summer of 1972-3 was hot and dry and I found my inability to demonstrate mortality over this summer surprising.

The experiments reported in this chapter and in the following one investigate the resistance of O. moreletii to hot and dry conditions (i.e. the ability of the species to survive exposure to high temperatures and low humidities). The majority of the work was done throughout the very hot and dry summer of 1974-5, when the reader will recall, significant mortality was in fact measured at Bridgewater.

In addition to the above, two specific questions were asked. Firstly, the native species, A. castaneum and Dimerogonus sp., were confined to the cool moist woodland where they were rarer than O. moreletii. Could this difference in the abundances of the three species be attributed to differences in their water and temperature dependencies? Secondly, O. moreletii aggregated in the grassland beneath tussocks of L. fibrata during summer. Was this behaviour explainable in terms of preferences of the species for certain temperatures and/or humidities?

5.2 Literature Review

The abilities of millipedes to survive when desiccated have been studied by several authors (Barlow, 1957; Toye, 1966, 1967, 1975; Causey,

1943; Stewart and Woodring, 1973; Haacker, 1968; O'Neill, 1969 (a and b)). Differences in survival between males and females were demonstrated in several species by Barlow (1957) and Haacker (1968), notably in O. sabulosus. The females were more resistant to desiccation than the males. In addition, Barlow (1957) showed seasonal changes in resistance. O. sabulosus survived longest during the summer months (its period of activity).

Several authors (Barlow, 1957; Toye, 1966, 1967, 1975; Cloudsley-Thompson, 1950, 1954, 1959; Causey, 1943; Perttunen, 1953; Edney, 1951; Dwarakanath and Job, 1965 (a and b); Crawford, 1972; Stewart and Woodring, 1973; O'Neill, 1969b) measured the rates of water loss of millipedes under dry conditions. Perttunen (1953) demonstrated that the males of O. sabulosus lost water more rapidly than the females. He further showed with O. sabulosus that the rate of water loss when desiccated varied seasonally, being lowest during summer.

Barlow (1957), Dowdy (1968), Toye (1966), Cloudsley-Thompson (1951), Young (1958), Shelford (1913), Haacker (1968) and Perttunen (1953, 1955 (a and b)) studied the preferences of millipedes when placed in gradients of relative humidity. Perttunen (1953) was unable to demonstrate a difference in the preferences of the sexes of O. sabulosus, unless they were first desiccated. Then the males showed a stronger preference for the moist end of a gradient than the females. Barlow (1957) demonstrated a stronger preference for moisture by males than females of O. sabulosus without prior desiccation. Both Perttunen and Barlow showed seasonal changes in the humidity preferences of O. sabulosus. Generally, the millipedes preferred the dry end of a gradient in summer but the moist end in winter. Perttunen (1955b) elaborated on this behaviour by showing that during summer, females of O. sabulosus near the surface of the ground preferred dry conditions whilst those deep in the soil and about to reproduce preferred moist conditions. Perttunen (1955b) suggested these results indicated "a reversal

of the humidity reaction in the females just before egg-laying".

5.3 Resistance to Desiccation at a Moderate Temperature (20°C)

Unless stated otherwise, the individuals of O. moreletii used in the experiments in this and subsequent sections were ≥ 8th stadium and were collected from the grassland in areas of pasture grass adjacent to the plot used for sampling of litter. No intentional bias was shown in collecting the millipedes, save that they were in the litter, alive and ≥ 8th stadium. The animals collected were therefore regarded as representative of the populations present at the time. The animals were normally maintained in the laboratory in moist humus for 2 days before beginning the experiments. All experiments were kept in darkness.

Experiment 1

In April and November 1975, males and females of O. moreletii were collected and their resistances to desiccation (at 20°C) were measured. On each occasion, the millipedes were placed at random in groups of 25 in each of 30 containers as shown in Figure 5.1(b) (sexes were not separated). Fifteen of the containers were kept over fused $CaCl_2$ (relative humidity < 5%) in large air-tight canisters. The other 15 containers were kept over distilled water in similar canisters. At intervals of 2 days, the dead millipedes were removed and aged and sexed. Death was assessed by using the antennal reflex (see O'Neill, 1969).

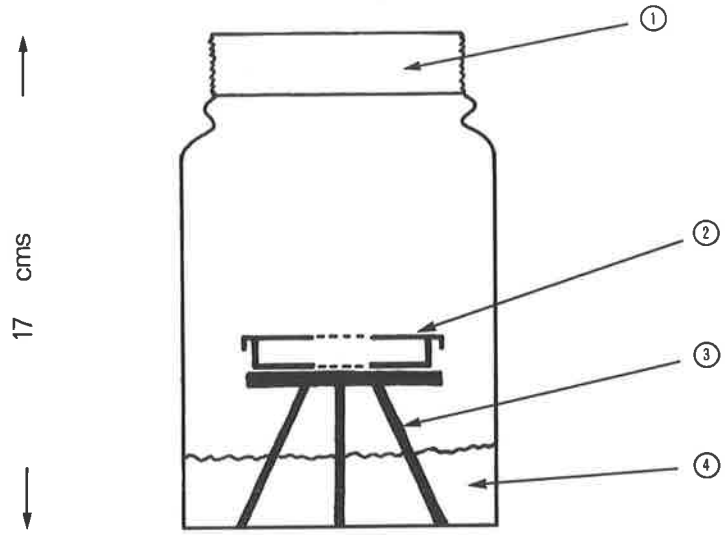
The cumulative mortalities of the adult males (mature and intercalary), juvenile males and females under the dry conditions are shown in Figure 5.2. The mortalities of the millipedes over distilled water were negligible during the experiments (3 died in the April experiment and 5 in November).

At both times of year, O. moreletii was obviously very resistant to desiccation at moderate temperatures. The results for April 1975 show

FIGURE 5.1(a) Glass jars used in probit analyses (① = screw on lid, ② = plastic container with gauze vents, ③ = tripod, ④ = water or fused $CaCl_2$).

FIGURE 5.1(b) Container used in experiments on resistance to high temperature and desiccation (⑤ = gauze).

A



B

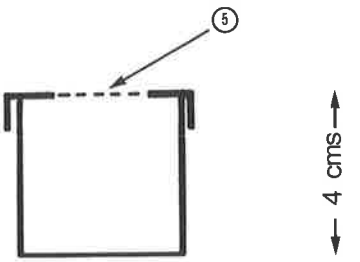
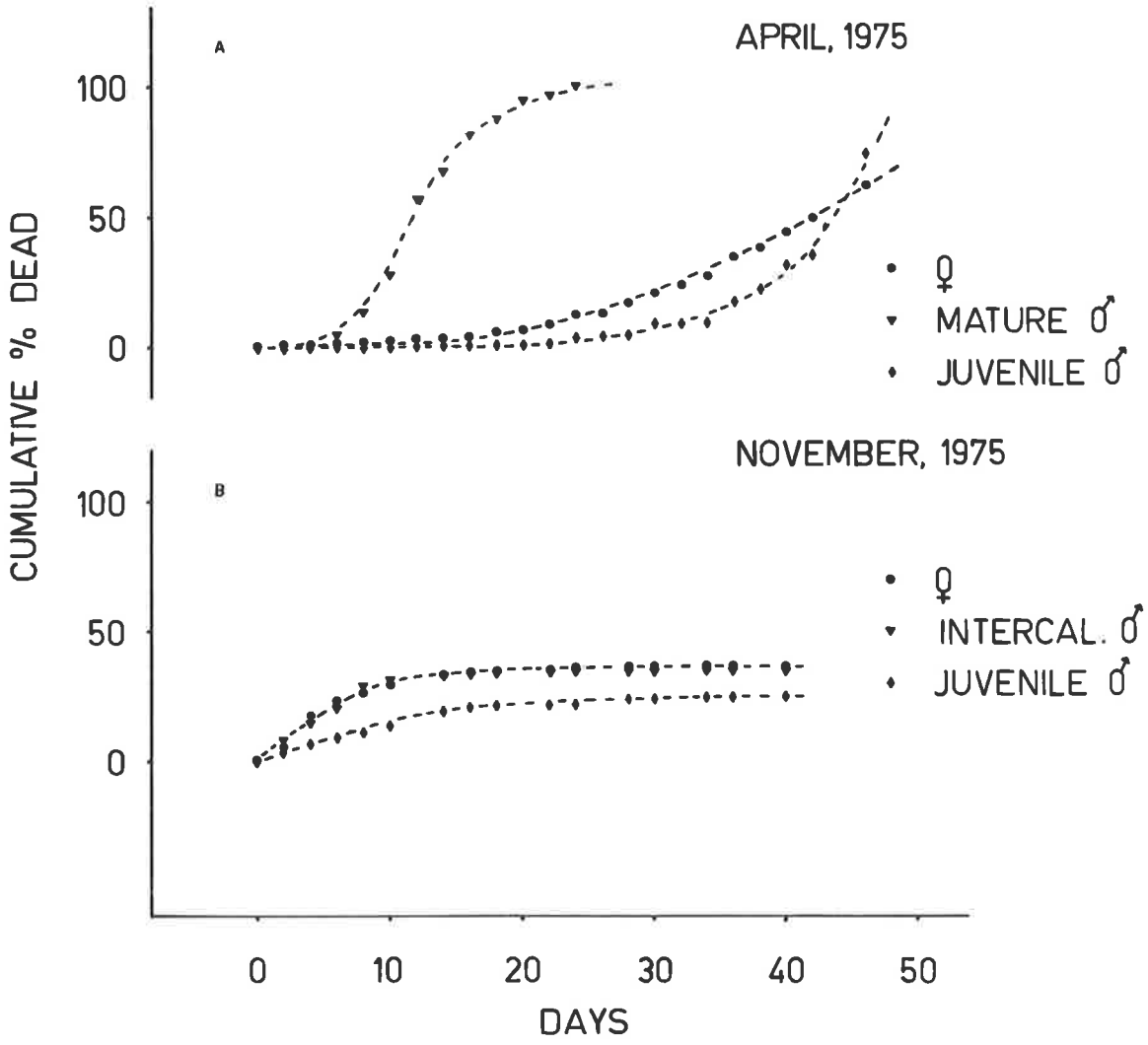


FIGURE 5.2 Numbers (expressed as cumulative %) of O. moreletii dying at 20°C, < 5% R.H.

	Numbers of animals used
April 1975	
Females	216
Juvenile Males	23
Mature Males	135
November 1975	
Females	224
Juvenile Males	75
Intercalary Males	76

[Occasionally the reader will notice small discrepancies between the numbers of animals claimed to have been used in the text and actual numbers in results (expressed in the tables and graphs). These discrepancies were brought about by omitting from the results, 1) animals damaged during handling in the experiments, 2) unsuitable animals that had been included in experiments unintentionally (e.g. the occasional 7th stadium when only ≥ 8th stadium were intended), and 3) animals for which insufficient data were obtained (e.g. intercalary males were often rare in samples taken in the field for laboratory experiments).]


A
APRIL, 1975
100
50
0
♀
MATURE ♂
JUVENILE ♂
B
NOVEMBER, 1975
100
50
0
♀
INTERCAL. ♂
JUVENILE ♂
CUMULATIVE % DEAD
0
10
20
30
40
50
DAYS

that the mature males were less resistant to desiccation than the females and juvenile males. There was no appreciable difference in the resistances of females and juvenile males. The results for November 1975 suggested little difference between the resistances of intercalary males, juvenile males and females. The curves for November 1975 were different in shape from those for April 1975. Those few that died in November, died early in the experiment. Early mortality was rare in April.

Experiment 2 (a and b). Comparisons of species

The resistances to desiccation (at 20°C) of O. moreletii, A. castaneum and Dimerogonus sp. were compared in June and September 1975 using essentially the same experiment as that reported above. However, the animals were collected in the woodland and they were added to the containers in groups of 10 rather than 25.

In June, the O. moreletii used were ≥ 7th stadium, the Dimerogonus sp. had 10-54 pairs of repugnatorial glands and the A. castaneum were adults. In September, the O. moreletii were ≥ 8th stadium, the Dimerogonus sp. had ≥ 43 pairs of repugnatorial glands and the A. castaneum were adults and juveniles (16 podous segments).

The mortalities of each species are given in Tables 5.1 and 5.2. On all occasions the mortalities over distilled water were negligible (≤ 4 dead individuals for each species). A. castaneum was very susceptible to desiccation. Dimerogonus sp. and O. moreletii were more resistant. The juveniles of Dimerogonus sp. were less resistant than the adults. In contrast, the juveniles of O. moreletii were more resistant than the adults, especially the adult males (which were all mature). The juveniles of Dimerogonus sp. were less resistant than the juveniles of O. moreletii. For short exposures, the adults of Dimerogonus sp. were more resistant than the adults of O. moreletii.

TABLE 5.1

Numbers Dying at 20°C; < 5% R.H. - (June, 1975)

	Days of Exposure										Still Alive	Total Used
	2	4	6	8	10	12	14	16	18	20		
O. moreletii												
Adult ♀	1	1	2	-	3	-	-	1	-	-	46	54
Adult ♂	5	1	2	4	6	3	2	2	3	1	10	39
Juvenile ♀	-	-	-	-	-	-	-	-	-	-	17	17
Juvenile ♂	-	-	-	-	-	-	-	-	-	-	20	20
A. castaneum												
Adult ♀	1	7	3	-	-	-	-	-	-	-	0	11
Adult ♂	4	6	1	1	-	-	-	-	-	-	0	12
Dimerogonus sp.												
Adult ♀	-	-	-	-	-	2	5	9	17	26	31	90
Adult ♂	-	-	-	1	-	-	1	7	9	26	32	76
Juvenile ♀	1	4	2	3	7	11	27	21	6	7	0	89
Juvenile ♂	1	1	-	-	6	15	17	20	11	8	8	87

O. moreletii: adult females taken as ≥ 9th stadium

Dimerogonus: adult females taken as ≥ 34 pairs of repugnatorial glands.

TABLE 5.2

Numbers Dying at 20°C; < 5% R.H. - (September, 1975)

	Days of Exposure										Still Alive	Total Used
	2	4	6	8	10	12	14	16	18	20		
O. moreletii												
Adult ♀	-	2	1	2	1	-	-	-	-	-	80	86
Adult ♂	3	1	-	-	3	-	-	-	-	-	10	17
Juvenile ♀	-	-	-	-	-	-	-	-	-	-	9	9
Juvenile ♂	-	-	-	-	-	-	-	-	-	-	16	16
A. castaneum												
Adult ♀	4	3	-	-	-	-	-	-	-	-	0	7
Adult ♂	3	1	-	-	-	-	-	-	-	-	0	4
Juvenile ♀	21	11	-	-	-	-	-	-	-	-	0	32
Juvenile ♂	15	13	-	-	-	-	-	-	-	-	0	28
Dimerogonus sp.												
Adult ♀	-	-	-	-	-	-	-	-	1	2	8	11
Adult ♂	-	-	-	-	-	-	-	1	3	3	2	9

5.4 Resistance to Desiccation at High Temperature (35°C) by O. moreletii

The experiments in this section measured and compared the resistances of males and females of O. moreletii to desiccation at high temperature at different times of the year.

Experiment 1. A Useful Temperature

In November 1974, males and females of O. moreletii were collected from the field. They were placed in containers (as in Figure 5.1b) in groups of 25 (again the sexes were not separated). Some of the containers were placed in canisters with fused $CaCl_2$, others in canisters with distilled water. At least one canister with fused $CaCl_2$ and one with distilled water was kept at each of 5 constant temperatures (20, 25, 30, 35 and 45°C). The numbers of millipedes used are indicated in Table 5.3.

The survivals of the millipedes were checked every 2 days in the 20, 25, 30 and 35°C treatments. The 45°C treatments were observed only once (after 1 1/2 hours) when all the millipedes were dead. At each checking of the treatments, the dead animals were removed and sexed. After 14 days, the experiment was terminated and the remaining animals were sexed.

The percentage survivals in each treatment after 14 days are given in Table 5.3. For the 35°C, < 5% R.H. treatment, the times for 50% mortality for both sexes were approximately 6 days.

The results of this first experiment suggested it would be practical to measure the resistance of O. moreletii to desiccation at high temperature at different times of the year at 35°C when < 5% R.H. was used. At this temperature, a proportion of the mortality observed would be due to the effect of high temperature alone, the remainder to desiccation.

Experiment 2. Resistances at different times of the year

In October and November 1974, February, March and April (twice) 1975, large numbers of O. moreletii were collected from the grassland and

TABLE 5.3

Treatment	Initial Numbers		% Survivals After 14 Days	
	♂	♀	♂	♀
20°C, 100% R.H.	38	62	100.0	100.0
25°C, 100% R.H.	136	232	97.1	98.7
30°C, 100% R.H.	123	244	96.9	98.4
35°C, 100% R.H.	130	245	49.2	49.0
45°C, 100% R.H.	28	72	all dead after 1½ hours	
20°C, < 5% R.H.	36	64	97.2	98.4
25°C, < 5% R.H.	138	230	97.2	98.7
30°C < 5% R.H.	130	238	99.2	97.5
35°C < 5% R.H.	29	71	0.0	0.0
45°C < 5% R.H.	34	66	all dead after 1½ hours	

treated on each occasion as in Section 5.3, Experiment 1, except that those millipedes kept over fused $CaCl_2$ were maintained at 35°C rather than at 20°C.

The cumulative mortalities at 35°C, < 5% R.H. of the females, juvenile and mature males collected on each occasion are shown in Figure 5.3. Unfortunately, intercalary males were too few in number to warrant similar curves being drawn for them. Approximate $L.D._{50}$s were read from the graphs in Figure 5.3 and are given in Table 5.4. In all cases, mortalities in the controls (20°C, over distilled water) were negligible (≤ 4 dead individuals).

The results suggested that 1) the resistances to desiccation at high temperature of females, juvenile and mature males varied seasonally, being greatest during summer and least during the cooler and wetter months, and 2) the resistances of mature males were consistently lower than those of females and juvenile males. There were no indications in the basic data of differences in resistance between younger and older stadia.

In November 1975, intercalary males were more common in the grassland than they were in the 1974-5 summer. The above experiment was repeated then to obtain a measure of the resistance of the intercalary males to desiccation at high temperature. The results are given in Figure 5.4 and Table 5.4. The results suggested no differences in the resistances of females, juvenile and intercalary males at this time of year.

Experiment 3. Probit Analysis

The correct method for measuring and comparing resistances is the probit analysis (Finney, 1947). However, probit analysis requires prior knowledge of approximate $L.D._{50}$s (such as provided in Experiment 2 above) before it can be done with any efficiency. Within the scope of the present study it was not practicable to do both Experiment 2 and probit

FIGURE 5.3 Numbers (expressed as cumulative %) of O. moreletii dying at 35°C, < 5% R.H.

	Numbers of animals used		
	Females	Juvenile Males	Mature Males
1. October 1974	244	131	
2. November 1974	266	109	
3. February 1975	197	113	53
4. March 1975	263	43	69
5. April ① 1975	211	5	157
6. April ② 1975	178	18	174

(Lines fitted by eye).

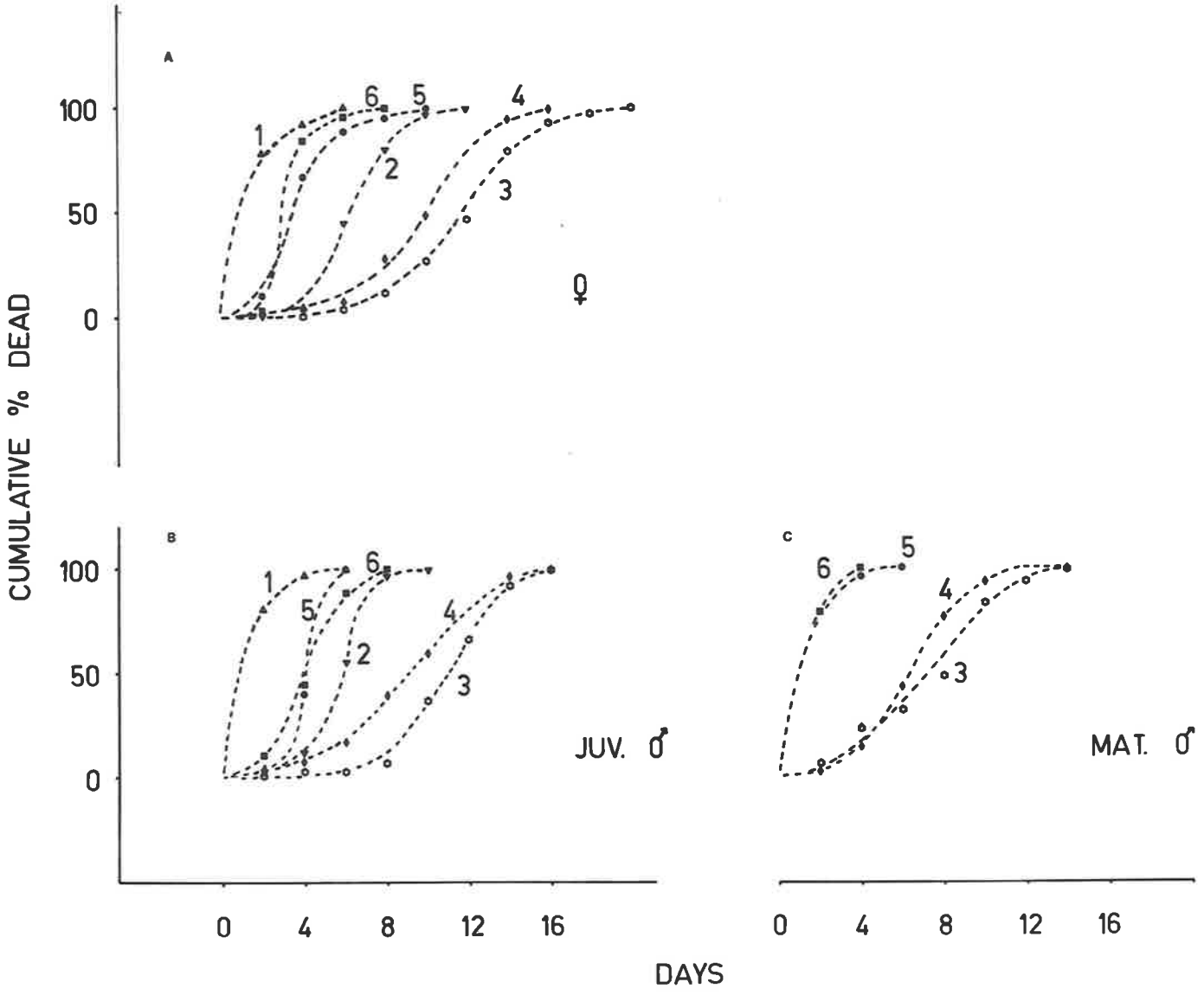

A
B
C
100
50
0
CUMULATIVE % DEAD
1
2
3
4
5
6
♀
JUV. ♂
MAT. ♂
0
4
8
12
16
DAYS

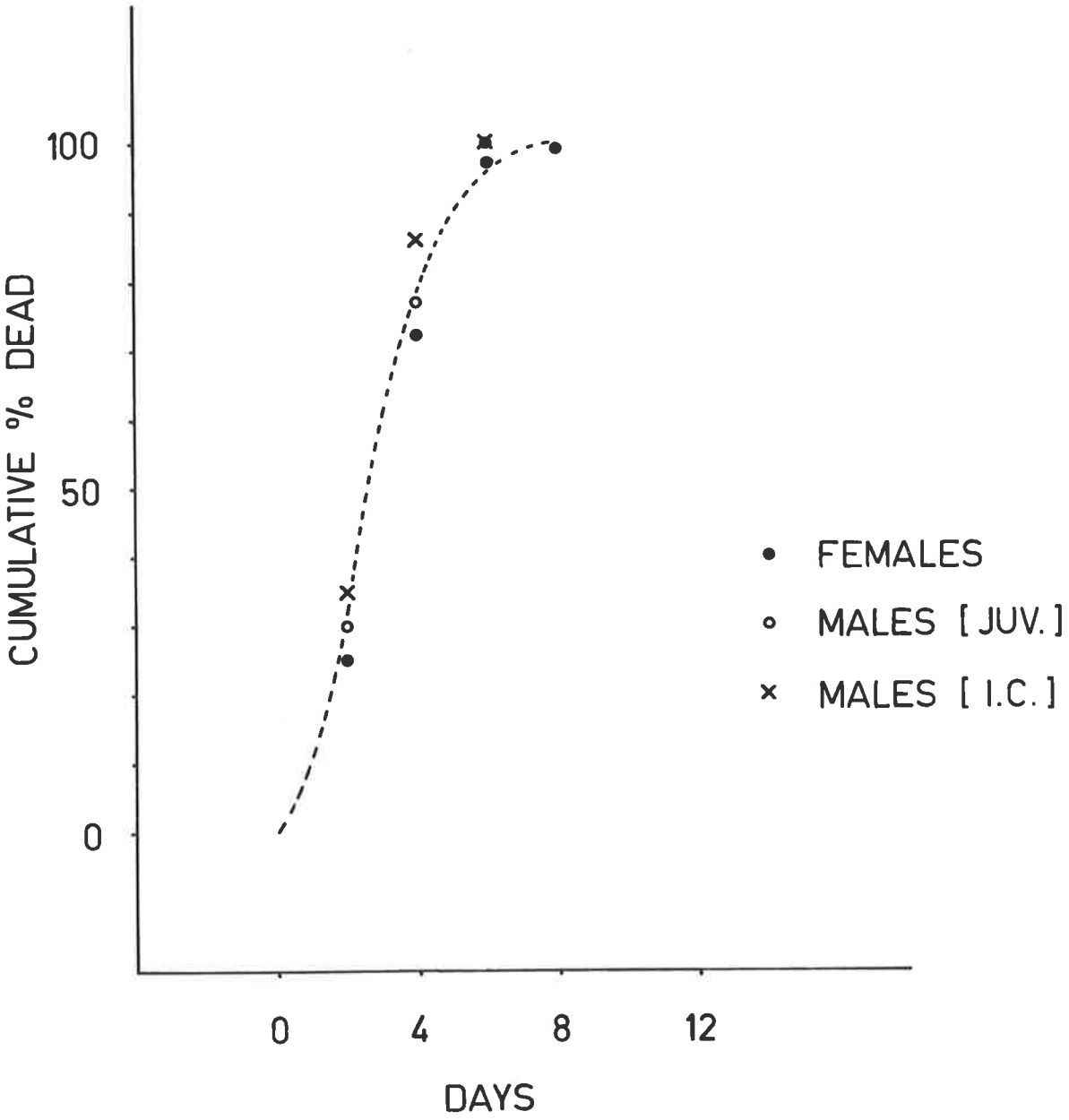
TABLE 5.4

$L.D._{50}$s at 35°C; < 5% R.H. (Days).

Date	Females	Juvenile Males	Mature Males	Intercalary Males
October 1974	1	1		
November 1974	6	6		
February 1975	12	11	8	
March 1975	10	9	6	
April (1) 1975	4	4	1	
April (2) 1975	3	4	1	
November 1975	3	3		3

FIGURE 5.4 Numbers (expressed as cumulative %) of O. moreletii dying at 20°C, < 5% R.H.

	Numbers of animals used
November 1975	
Females	228
Juvenile Males	76
Intercalary Males	71


100
50
0
CUMULATIVE % DEAD
0
4
8
12
DAYS
FEMALES
MALES [JUV.]
MALES [I.C.]

analyses throughout the summer to measure the resistances of O. moreletii. But in late October 1975, the resistances of both females and juvenile males were measured using probit analyses. The procedure was as follows.

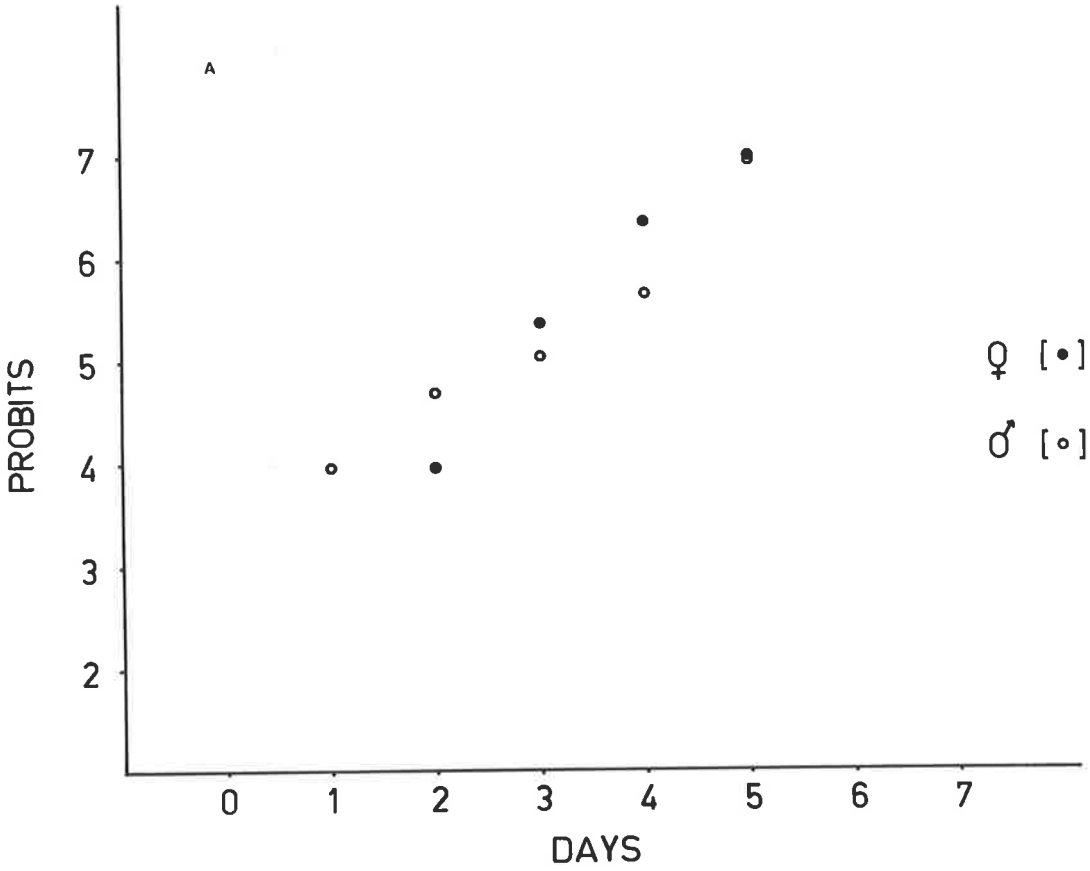
Fourty three containers (see Figure 5.1a) were made from plastic petri dishes. Fourty millipedes of the one sex were added to each container. Nineteen containers held males; the other 24 containers held females. Each container was placed in a glass jar as shown in Figure 5.1. Initially, 4 containers (2 of each sex) were placed in jars containing distilled water and kept at 20°C. The remaining containers were placed in jars containing fused $CaCl_2$ (i.e. < 5% R.H.) and kept at 35°C. At intervals of 24 hours over a period of 6 days, two or more of the containers for each sex were transferred from their hot and dry jars to fresh jars containing distilled water and kept at 20°C. On the 6th day, when one container for each sex still remained in jars at 35°C, < 5% R.H., the millipedes in each container were removed and their survival assessed. The numbers of O. moreletii used per exposure to 35°C, < 5% R.H. and the numbers that died are given in Appendix Table 5.1. Figure 5.5(a) illustrates the data transformed to probits.

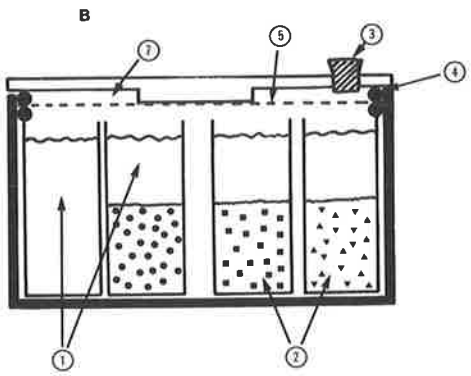
The $L.D._{50}$s at 35°C, < 5% R.H. were calculated for both sexes using the approximate method of Finney (1947). The provisional probit lines were $Y = 2.90 + 0.77x$ for the males and $Y = 2.25 + 0.98x$ for the females. The $L.D._{50}$s and their fiducial limits at the 5% probability level were 2.73 $\pm$ 0.43 days for the males and 2.81 $\pm$ 0.27 days for the females. There was no evidence to suggest a significant difference between the resistances of the males and females.

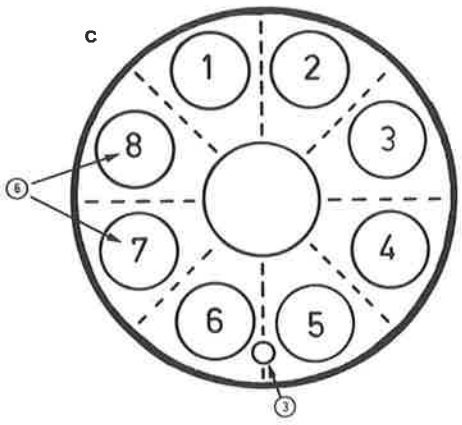
There were reasonably close agreements between the $L.D._{50}$s calculated here and those approximated in Experiment 2 at a similar time of year (November 1975). It seems permissible therefore to accept the $L.D._{50}$s given in Experiment 2 as reasonably accurate estimates of the resistance of O. moreletii.

FIGURE 5.5(a) Probit analysis of resistance to desiccation at high temperature (35°C, < 5% R.H.)

FIGURE 5.5(b & c) Apparatus used to create a humidity gradient. (① = saturated solutions, ② = excess salt, ③ = hole through which animals were added to the apparatus, ④ = rubber tubing, ⑤ = gauze, ⑥ = containers holding different saturated solutions (1 & 2 were distilled water, 3 & 8 saturated KCl, 4 & 7 saturated NaCl and 5 & 6 saturated $Ca(NO_3)_2$), ⑦ = chamber in which millipedes moved around.


A
PROBITS
7
6
5
4
3
2
0
1
2
3
4
5
6
7
DAYS
♀ [•]
♂ [∘]


B
SIDE VIEW


C
1
2
3
4
5
6
7
8
TOP VIEW

Experiment 4. A Comparison of the Rates of Water Loss by Females and Juvenile Males of O. moreletii when desiccated

In December 1974, 60 females and 60 juvenile males of O. moreletii in the 9th and older stadia were collected from the grassland. They were starved in the dark at 20°C over distilled water for 2 days. The starvation reduced defaecation later in the experiment. After the 2 days, each millipede was placed in a container (see Figure 5.1b) by itself. Twenty containers with males and twenty with females were then placed in canisters at each of 1) 35°C, < 5% R.H., 2) 20°C, 100% R.H. and 3) 35°C, 100% R.H. After 24 hours, each millipede was reweighed and assessed as alive or dead. Then each individual was dried at 105°C for 48 hours and its dry weight determined. The few faeces that were produced during the 24 hours were included in the above weighings.

After the 24 hours, only 10 of the 20 females and 8 of the 20 males were alive at 35°C, < 5% R.H. All the animals were alive at 20°C, 100% R.H. and 35°C, 100% R.H. It seems reasonable to attribute the deaths in the 35°C, < 5% R.H. to desiccation. (In passing, it should perhaps be pointed out here that the survivals under hot, dry conditions in the present experiment were much lower than those reported in Section 5.4, Experiment 2 for a similar time of year. This difference might be attributed to the animals in the present experiment being 1) kept individually rather than in groups, and/or 2) starved rather than fed during the 2 days prior to the experiment.)

I assumed that during the 24 hours exposure to each treatment, the dry weights of the millipedes did not change and that changes in weight over this period reflected changes in water content. I further assumed that all volatiles given off when the millipedes were dried at 105°C were water. I then calculated the percentage of the initial water in the animals that was lost over the 24 hours. This data is given in Table 5.5 for each treatment. The data suggest that both sexes of O. moreletii lost similar proportions

TABLE 5.5

% of initial water lost by individuals

after 24 hours ($\bar{x} \pm$ S.E.)

	FEMALES		MALES	
	Alive after 24 hours	Dead after 24 hours	Alive after 24 hours	Dead after 24 hours
20°C, 100% R.H.	2.4 ± 0.5		1.6 ± 0.4	
35°C, 100% R.H.	4.2 ± 0.6		7.3 ± 0.5	
35°C, < 5% R.H.	47.8 ± 1.3	80.6 ± 3.6	47.0 ± 2.1	80.0 ± 3.9

of their initial water when they were desiccated. Those animals which died during the 24 hours exposure lost almost twice the amount of water as those that survived.

No significant differences in the small rates of water loss were found between the sexes at 20°C, 100% R.H. ($t = 1.25$, $p > .05$), but there were significant differences at 35°C, 100% R.H. ($t = 3.97$, $p < .05$). Both sexes had elevated rates of water loss at the higher temperatures (males, $t = 8.91$, $p < .05$; females, $t = 2.31$, $p < .05$).

The initial percentage water contents (100x weight of water/fresh weight) were calculated for the individuals exposed to 35°C, < 5% R.H. For those that survived 24 hours exposure the average initial water contents were 77.7 $\pm$ 0.6% (males) and 78.0 $\pm$ 0.6% (females). For those that died during the 24 hours, the figures were 73.9 $\pm$ 0.8% (males) and 76.3 $\pm$ 1.1% (females). For the males, the two figures were significantly different ($t = 3.9$, $p < .05$) suggesting that males with low water contents were more likely to die when desiccated. For the females however, there was no such significant difference ($t = 1.37$, $p > .05$).

5.5 Humidity Preferences of O. moreletii

During 1974 and 1975, the humidity preferences of the males and females of O. moreletii (9th stadium and older) were measured on 6 days from October to December, 6 days from January to February, 6 days in early March and 6 days from May to August using apparatus as shown in Figure 5.5 (b and c) (c.f. Barlow, 1957) to create a gradient of humidity. From October to February the males were all juveniles; from March to August they were all mature. Six replicates of the apparatus were used on each day (three for each sex). They were kept in a dark room at 20 to 23°C. Four different solutions were added to the eight sections in each apparatus. The

solutions used, their respective sections and the approximate humidities they gave in the air above them were as follows.

Solution	Section	Relative Humidity (%)
Distilled water	1 and 2	100
Saturated KCl	3 and 8	85
Saturated NaCl	4 and 7	75
Saturated $Ca(NO_3)_2$	5 and 6	55

Each solution had excess solute added. The humidities were checked with cobalt thiocyanate papers. The humidities existed within 2 hours and up to 24 hours after setting the solutions up.

On an additional 6 days (February and December) controls were run in which no gradient was created in the apparatus. Distilled water was placed in all sections. The males used were all juveniles.

The millipedes were collected from the litter in the pasture grass at Bridgewater in the morning. Immediately on returning to the laboratory, 10 individuals were added between the 5th and 6th section of each of the 6 replicates. The gradient of humidity was established 2 hours before the addition of the millipedes. At 1, 2, 3, 4, 5 and 21 hours after addition, the numbers of millipedes in each section of each replicate were recorded.

For simplicity, I will only consider here the data recorded at the 1st, 5th and 21st hours. For each of these times, the frequencies of O. moreletii in the different sections of the three replicates on each day within a given time of year (e.g. October to December, January to February etc.) were summed for each sex. The resulting total frequencies are given in Table 5.6 (a to c). Significant variation within the data was tested for using χ^2.

Conclusions:-

1) After 1 hour, neither sex showed a preference in the controls.

TABLE 5.6

Frequencies recorded in humidity gradient.

(a) 1 hr Readings		SECTIONS 5 & 6 (55%)	4 & 7 (75%)	3 & 8 (85%)	1 & 2 (100%)	χ^2_3	Prob.
Controls	♂	34	41	55	50	5.8	>.05
	♀	42	35	52	51	4.3	>.05
Oct.-Dec.	♂	37	37	45	61	8.5	<.05
	♀	50	42	43	45	0.8	>.05
Jan.-Feb.	♂	39	40	41	50	2.3	>.05
	♀	47	33	32	58	10.8	<.05
Early Mar.	♂	30	40	40	70	20.0	<.05
	♀	36	60	33	61	15.7	<.05
May-Aug.	♂	25	29	47	79	40.4	<.05
	♀	43	46	36	55	4.1	>.05

TABLE 5.6

		SECTIONS 5 & 6 (55%)	4 & 7 (75%)	3 & 8 (85%)	1 & 2 (100%)	χ^2_3	Prob.
(b) 5 hr Readings							
Controls	♂	41	45	50	44	0.9	>.05
	♀	40	47	54	39	3.2	>.05
Oct.-Dec.	♂	36	45	41	58	5.9	>.05
	♀	47	46	37	50	2.1	>.05
Jan.-Feb.	♂	32	38	39	71	20.7	<.05
	♀	40	38	42	60	6.8	>.05
Early Mar.	♂	28	35	57	60	16.8	<.05
	♀	37	52	28	63	16.1	<.05
May-Aug.	♂	36	43	38	63	10.2	<.05
	♀	28	42	34	76	30.6	<.05
(c) 21 hr Readings							
Controls	♂	52	30	54	44	7.9	<.05
	♀	27	55	51	47	10.3	<.05
Oct.-Dec.	♂	19	29	46	86	58.1	<.05
	♀	23	41	44	72	27.3	<.05
Jan.-Feb.	♂	19	28	31	102	98.0	<.05
	♀	24	19	26	111	129.6	<.05
Early Mar.	♂	16	26	33	105	109.9	<.05
	♀	25	15	22	118	159.1	<.05
May-Aug.	♂	19	28	15	118	159.9	<.05
	♀	15	18	14	133	229.6	<.05

Throughout the year, the males consistently showed a preference for the moist end of the gradient of humidity, although this preference was not always significant (e.g. January to February). For the females, there was no evidence to suggest a preference for the moist end of the gradient after 1 hour.

2) After 5 hours, again neither sex showed a preference in the controls. Throughout the year, both sexes (especially the males) showed a preference for the moist end, although again this was not always significant (e.g. the males in October to December).

3) After 21 hours, both sexes showed obvious preferences for the moist end of the gradient throughout the year. Although significant variation was detected in the controls for 21 hours, it seems reasonable in view of the data in Table 5.6(c) to dismiss this as unimportant. (The values of χ^2 for the controls were negligible compared with those for the experimental gradients).

Overall, the results suggest that both sexes of O. moreletii prefer moist conditions throughout the year, the males being quicker than the females to express this preference.

5.6 Desiccation in Field Populations of O. moreletii

(a) Percentage water content

I expected that the water content of O. moreletii would be high during winter when conditions were moist. In addition, I expected that if O. moreletii was desiccated in summer, its water content would be lower then compared with that in winter. If O. moreletii was not desiccated during summer, I expected that the water content then would be similar to that in winter.

Once per month, from October 1974 to October 1975, males and females of O. moreletii were collected from the litter in the woodland and the

grassland (only from pasture grasses and not from beneath L. fibrata). Collections were made in areas adjacent to those used in the sampling of litter in both habitats. Normally, 50 individuals of each sex in each habitat were collected, but on occasion numbers were lower when collecting was difficult. The millipedes were all 9th stadium or older and alive.

In the laboratory, fresh weights were recorded for each millipede. Then the millipedes were dried at 105°C for 48 hours and their dry weights determined. The percentage water contents were calculated for each individual, assuming all volatiles to be water.

The results of this survey of percentage water contents are given in Figure 5.6. The standard errors and the numbers of individuals used to calculate the means in Figure 5.6 are given in Appendix Table 5.2. The results were not as I expected. They suggested that the percentage water contents of both sexes in both habitats were higher during summer than they were in winter. At first glance this implied that O. moreletii was desiccated more in winter than in summer! However a complication arose in the data as follows.

The dry weights of millipedes collected in the field of course vary throughout the year. Their age distributions change, they increase in size and hence weight, they feed more at certain times of the year than at others, they deposit fat, they develop eggs and then oviposit. A survey such as that reported above assumes that these variations in the dry weight do not influence the values of percentage water content that are obtained. That is, it assumes there is no relationship between dry weight and percentage water content, such that variations in dry weight will alter the value of percentage water content irrespective of whether desiccation has occurred.

In fact there was a relationship between the dry weight of O. moreletii and its percentage water content. Figure 5.7(a) illustrates as an example this relationship for both sexes collected during the sampling from the

FIGURE 5.6 (a & b) % water contents of O. moreletii collected in the grassland (O.G.) and woodland (S.W.) throughout the year.

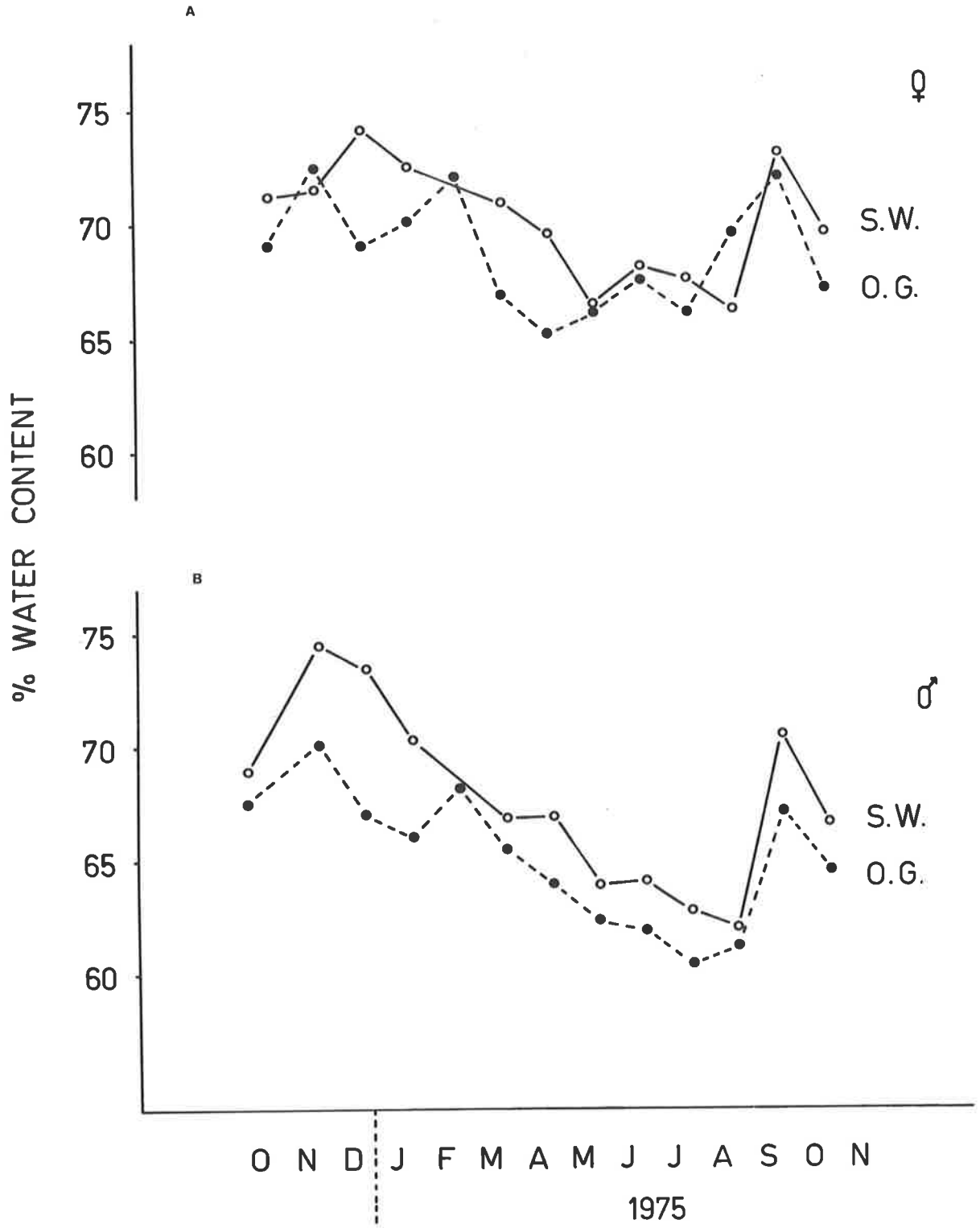
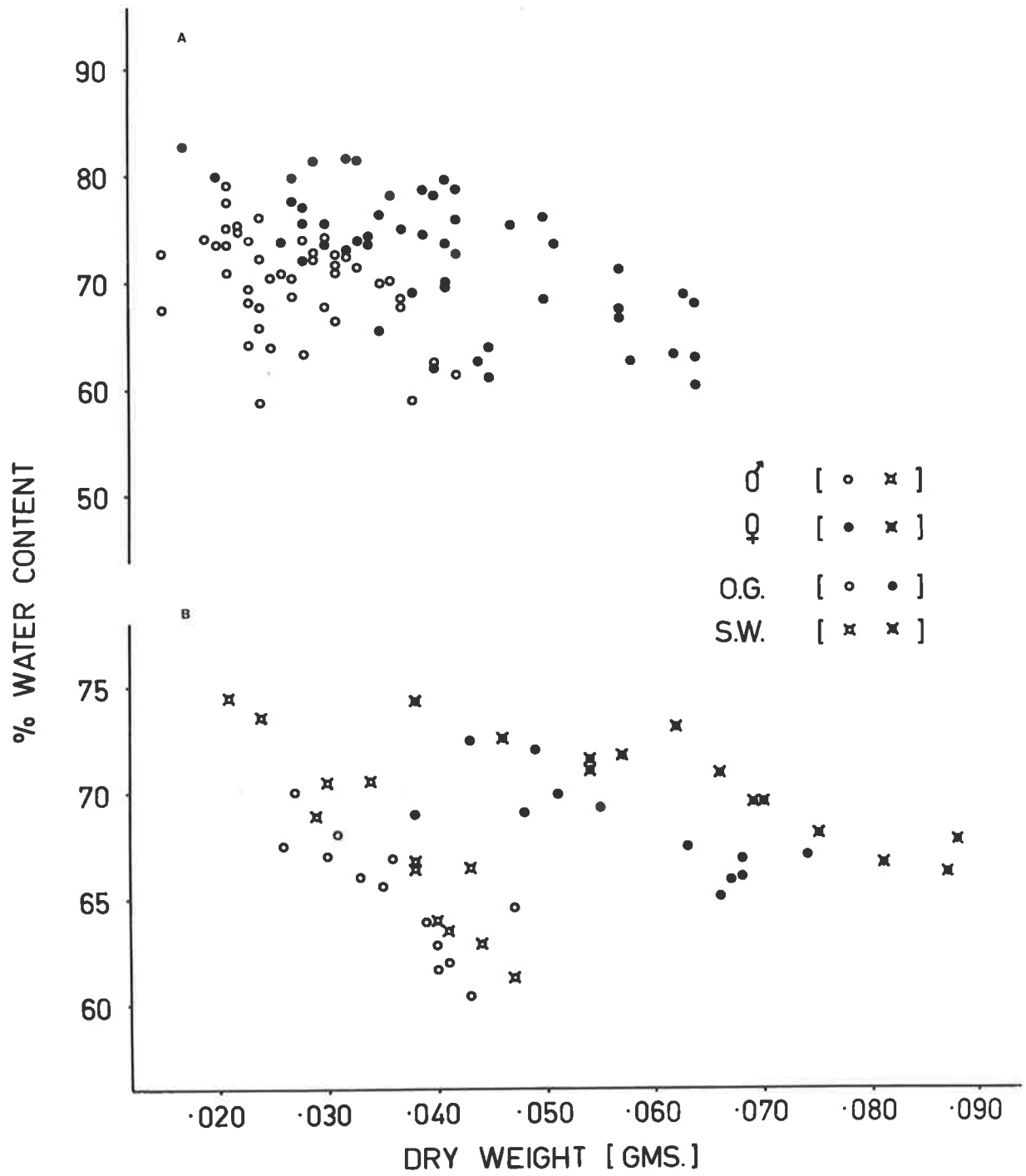

A
75
70
65
60
♀
S.W.
O.G.
% WATER CONTENT
B
75
70
65
60
♂
S.W.
O.G.
O N D J F M A M J J A S O N
1975

FIGURE 5.7 % water contents of animals collected in the grassland (O.G.) and woodland (S.W.) as a function of dry weights.

(a) Individuals collected in November 1974 (♀, $r_{50} = -0.552$, $p < .01$; ♂, $r_{47} = -0.435$, $p < .01$).

(b) Monthly means from October 1974 to October 1975.


A
B
90
80
70
60
50
75
70
65
60
% WATER CONTENT
♂ [○ ✕]
♀ [● ✕]
O.G. [○ ●]
S.W. [✕ ✕]
·020
·030
·040
·050
·060
·070
·080
·090
DRY WEIGHT [GMS.]

grassland in November 1974 (females $r_{50} = -0.552$, $p < .01$; males $r_{47} = -0.435$, $p < .01$). The actual relationship may be hyperbolic rather than linear. In August 1975, a large number of males and females of O. moreletii ranging from young juveniles (7th stadium) to adults (12th stadium) were collected from the woodland. Their percentage water contents were measured and are plotted as a function of dry weight in Figure 5.8.

The finding of the above relationship raised doubt as to whether the seasonal variations in percentage water content illustrated in Figure 5.6 were due to desiccation or simply due to variations in the dry weights of the millipedes collected. This doubt was further aggravated when the mean dry weights for each sample (see Appendix Table 5.3) were plotted against the corresponding mean percentage water contents and obvious correlations were obtained (see Figure 5.7b).

There are complicated methods of eliminating the interaction between dry weight and water content from the data expressed in Figure 5.6. A simple approach was however taken here. The smallest (by dry weight) ten individuals of each sex in each sample from May, June and July 1975 were isolated from the remainder of the data and their percentage water contents and dry weights ($\bar{x} \pm$ S.E.) were calculated. The dry weights are given in Appendix Table 5.4. The percentage water contents were as follows.

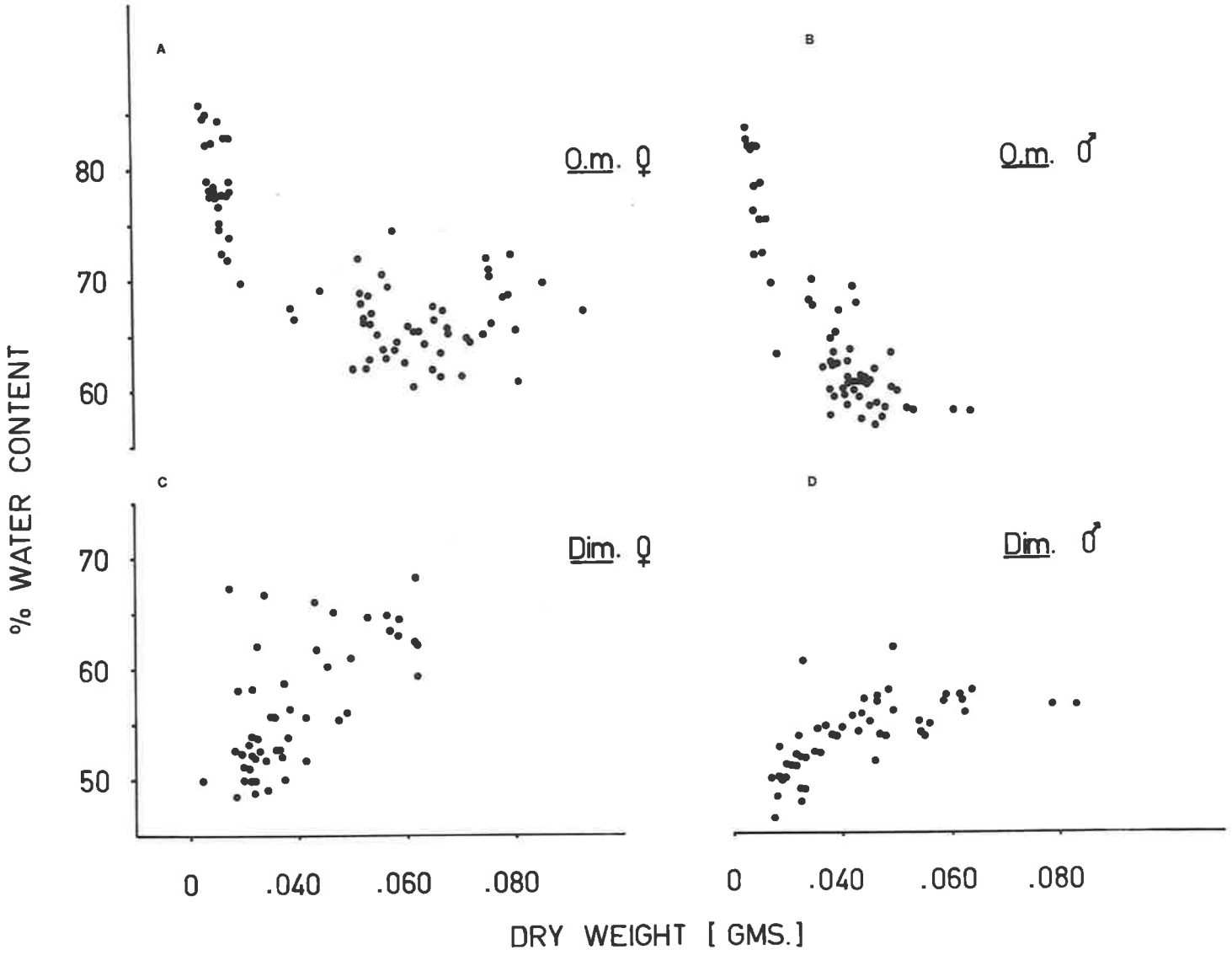
	May	June	July
Grassland			
♂	64.2 ± 0.9	61.4 ± 0.8	60.2 ± 0.5
♀	68.5 ± 0.7	68.4 ± 1.4	66.0 ± 0.8
Woodland			
♂	64.9 ± 0.7	64.8 ± 0.8	63.2 ± 1.0
♀	68.0 ± 0.9	66.8 ± 0.7	67.5 ± 0.9

The dry weights of these individuals were in most cases similar to those collected in summer (compare Appendix Tables 5.3 and 5.4). However

FIGURE 5.8 % water contents of millipedes collected in the woodland in August 1975 as a function of dry weight.

(a & b) O. moreletii

(c & d) Dimerogonus sp.


A
B
C
D
O.m. ♀
O.m. ♂
Dim. ♀
Dim. ♂
80
70
60
70
60
50
% WATER CONTENT
0
.040
.060
.080
0
.040
.060
.080
DRY WEIGHT [GMS.]

the percentage water contents for May, June and July were still smaller than those measured in summer (compare the data above with Appendix Table 5.2). There was therefore no evidence to suggest by way of percentage water content that O. moreletii was more desiccated in summer (1974-5) than in winter (1975).

(b) Appearance of the mid-gut

Obviously the measurement of percentage water content as an indicator of desiccation in field populations is awkward. Not only is there the problem of the dry weight - water content interaction but also there is the necessity of having to return the animals quickly to the laboratory, weigh them, dry them and weigh them again. Fortunately, Bridgewater was only 21 km from the Waite Institute and this was possible in the present study. However often field sites are much further away (e.g. Eyre Peninsula) and ready access to laboratory facilities is not possible. Further, even if laboratory facilities are close, time is not always available to assess desiccation by laboratory weighings when arid weather prevails. A simple and quick method for assessing desiccation in the field is desirable.

A quick method for detecting desiccation was devised using the appearance of the mid-gut and evidence for desiccation of O. moreletii during summer was again looked for in the field - this time in the summer of 1975-6.

Preliminary observations suggested that when O. moreletii was kept in dry containers in the laboratory, the mid-gut became filled with bubbles of gas. This bubbling intensified with time until the whole mid-gut was one "big bubble". Then the gut disintegrated and the animal died.

The most likely cause of this bubbling seemed to be either starvation or desiccation. Much gas is formed in the human alimentary canal during starvation (Keys et al., 1950; Canter and Reynolds, 1957; Calloway, 1968). Perhaps the same applied in O. moreletii. On the other hand, perhaps during desiccation, water was absorbed from the gut into the body tissues or was

lost from the mouth and/or anus. Gas could have entered the gut passively or the animal may have produced the gas to serve a function, perhaps to maintain the internal pressure of the body cavity.

The preliminary observations of the bubbling of the mid-gut were made by cutting off the head and tail of the millipede with scissors and then, with forceps, gripping the hind-gut and pulling the intact gut out posteriorly. Initially, I thought that starvation emptied the gut and then the bubbles were formed as the gut was removed. However guts were removed by the same method but under water and the bubbles were still observed. In addition, bubbles were present in the mid-gut when millipedes were dissected in wax under alcohol. In these cases, the middle segments of the millipedes were dissected away leaving the gut intact from head to tail. Thus the bubbles were not artifacts formed by removal of the gut from the body. They were present in the animal beforehand.

The following two experiments investigated the possibility that bubbling of the mid-gut of O. moreletii might be a useful indicator of desiccation.

Experiment 1

In September 1975, many O. moreletii were collected from the grassland at Bridgewater. They were in the 8th and older stadia. They were maintained overnight at 20°C in the dark in moist humus. They were then grouped into 22 lots of 50 at random. Two lots were selected at random and the appearance of the mid-gut in each animal was assessed as either "normal" or "bubbled". Bubbling of the mid-gut is obvious when it occurs, but as a demarcation point, > 2 small bubbles in the mid-gut was taken as "bubbled" whilst ≤ 2 small bubbles was taken as "normal". The gut was removed for assessment by cutting off the head and tail and pulling it out as described above.

Figure 3.3b but without the soil and food). Of these 20 pots, 10 were taken at random and placed in trays with 2 to 3 cm of water. The other 10 pots were placed in dry trays. The humidities in the flower pots were measured using cobalt thiocyanate papers. In the dry pots the relative humidity was approx. 50% whilst in the wet pots it was approx. 95%. The pots were maintained in the dark at 20°C.

After 3 days, the individuals still surviving in 5 wet and 5 dry pots were observed as to the appearance of their mid-guts. After 6 days, the individuals in the remaining 5 wet and 5 dry pots were also observed. The results are given in Table 5.7. Note the sexes of the individuals were not determined until after their gut appearance had been observed - hence sex ratios in the various pots differed somewhat.

Experiment 2

Many O. moreletii were collected from the grassland in October 1975 and were maintained in moist humus for 2 days in the dark at 20°C (They were again in the 8th and older stadia). Then these millipedes were arranged randomly in 16 lots of 50. Initially 2 lots of 50 were assessed for bubbled or normal mid-guts. The remaining 14 lots of 50 O. moreletii were placed in dry flower pots similar to those in Experiment 1. The pots were kept in the dark at 20°C.

After 2 days, the individuals in 2 pots were assessed for the appearance of their mid-guts and sexed; 7 pots were transferred to trays with 2 to 3 cm of water in them, and 5 pots were retained under dry conditions. After 12 hours in the wet trays, 2 pots were assessed for the appearance of their mid-guts. After 11 days as wet pots the remaining 5 pots that had been transferred from dry pots after 2 days were also assessed, as were the 5 pots that had been dry from the beginning of the experiment (i.e. 13 days). The results are given in Table 5.7.

The results of Experiments 1 and 2 suggest that desiccation induces

TABLE 5.7

Experiment 1	MALE				FEMALE			
	Total	Bubbled	Normal	Dead	Total	Bubbled	Normal	Dead
Initial (2 pots)	49	2	47	-	51	1	50	-
3 days Wet (5 pots)	83	10	71	2	167	16	145	6
3 days Dry (5 pots)	83	81	1	1	167	155	5	7
6 days Wet (5 pots)	104	25	77	2	146	30	111	5
6 days Dry (5 pots)	110	104	-	6	140	135	5	-
Experiment 2								
Initial (2 pots)	39	4	35	-	61	6	55	-
2 days Dry (2 pots)	23	21	2	-	77	65	12	-
2 days Dry to 12 hrs Wet (2 pots)	35	22	13	-	65	44	21	-
2 days Dry to 11 Days Wet (5 pots)	95	8	85	2	155	31	121	3
13 days Dry (5 pots)	92	90	2	-	158	151	-	7

bubbling of the mid-gut in both sexes of O. moreletii, and that this can be reversed by transferring the animals from desiccated to moist conditions. The results suggest that bubbling of the mid-guts in field populations would indicate that desiccation was occurring. Of course, other environmental factors might also induce bubbling. But it is difficult to imagine what they might be. Animals which have been kept at high temperatures (35°C) and moist conditions (see Section 6.3) have shown no signs of bubbling in their mid-guts. From the above results, starvation does not seem important (since bubbling can be reversed whilst starvation continues).

Observations in the field

At various times throughout the summer of 1975-6, O. moreletii present in the litter in the pasture grass at Bridgewater were assessed for bubbling of their mid-guts. The dates and numbers of animals assessed are given in Table 5.8 along with the percentages of the populations with bubbled mid-guts. Samples were deliberately taken after periods of dry or wet weather. These are designated as D and W respectively in Table 5.8. The results suggest that O. moreletii is desiccated during dry weather in the grassland in summer. No measurements of abundance were taken whilst the appearances of the mid-gut were being assessed, but experience in previous years (see Section 4.56) and visual assessment of populations present at the time suggested little if any mortality occurred then. Therefore, the low percentage of animals with bubbled guts after the wet periods of the summer probably reflect recovery from desiccation.

5.7 Discussion

The significances of the more important findings reported in this chapter in the ecologies of the three species are discussed in Chapter 7, together with findings from Chapter 6 concerning temperature relationships.

TABLE 5.8

DATE	MALE N	MALE % Bubbled	FEMALE N	FEMALE % Bubbled
November, 1975 (D)	50	0.0	50	0.0
December, 1975 (D)	13	0.0	70	5.7
January, 1976 (D)	32	6.3	148	11.5
January, 1976 (D)	22	63.6	108	47.2
February, 1976 (W)	24	0.0	159	1.3
February, 1976 (W)	28	0.0	148	1.4

(Samples taken from the litter in the open grassland (pasture grasses). Animals in the 9th and older stadia).

The water contents of O. moreletii were higher in summer than in winter. The resistance of O. moreletii to desiccation at high temperature was also higher in summer than in cooler and moister months. Perhaps there is a causal relationship between water content and resistance. i.e. Perhaps the greater the water content, the greater the resistance. A short experiment (see Section 5.4, Experiment 4) supported this suggestion, at least for juvenile males. Those males that survived desiccation at high temperature for 24 hours had higher percentage water contents initially than those that died. A problem here however is knowing whether the amount of water in an animal is the actual determinant of that animal's ability to survive or is simply correlated with it. Barlow (1957) found a correlation between longevity and initial water content when O. sabulosus, C. silvarum and I. scandinavius were desiccated, but he considered the relationship was too variable to be causal. He suggested that differences in longevity were due to differences in the "permeability of the cuticle". Perhaps seasonal changes in the physiology and/or behaviour of O. moreletii explain the changes noted in water content and resistance, there being no causal relationship between the latter two.

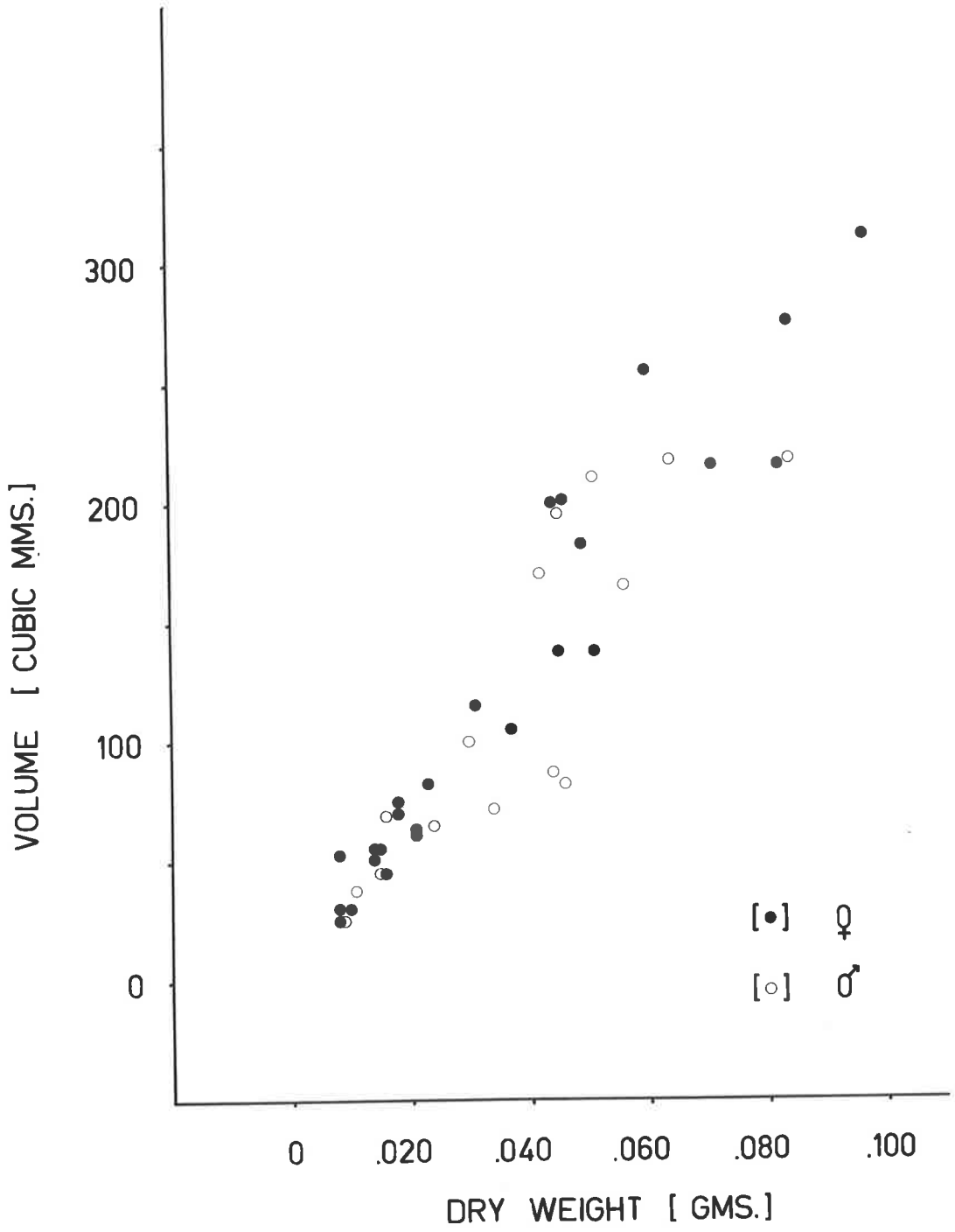
It should be pointed out here that much (perhaps all) of the seasonal variation in resistance to desiccation at high temperature noted for O. moreletii in the present study can be attributed to changes in resistance to high temperature only (see Section 6.3). Unfortunately, time did not allow enough simultaneous measurements of resistance to 1) high temperature and 2) desiccation at high temperature to enable corrections for temperature to be made and thus assess whether resistance to desiccation in its own right varies seasonally. However the limited data given in Figure 5.2 do suggest that the resistance to desiccation does vary seasonally.

As a general principle for insects, Buxton (1932) stated that the

larger the animal, the less its percentage water content. This, he argued, was the result of an increase in the proportion of the total weight contributed by cuticle in larger animals. Barlow (1957) could show no correlation between "body weight" (presumably fresh weight) and the "proportion of dry matter to water" for O. sabulosus, C. silvarum and I. scandinavius. Barlow implied that these millipedes were not in keeping with Buxton's principle. For O. moreletii, the percentage water content did decrease with size. Dry weight and water content were negatively correlated (see Section 5.6). Dry weight is positively correlated with size (see Figure 5.9). The fact that the relationship between water content and size appears hyperbolic (see Figures 5.8 a and b) may explain Barlow's results. If he used only very large animals, similar relationships to that in O. moreletii would have been hard to demonstrate.

At the same time as O. moreletii were collected to give the data in Figures 5.8 (a and b), large numbers of juvenile and adult Dimerogonus sp. were also collected at the same site. The percentage water contents of these animals as a function of their dry weights are given in Figures 5.8 (c and d). The difference between species is striking. In O. moreletii juveniles have higher water contents than adults. In Dimerogonus sp. the reverse is the case. Obviously within Dimerogonus sp., Buxton's principle is not obeyed. I can give no reason for the differences between species. However perhaps it is relevant here to mention the work of Vannier (1975) on the collembolan, Tomocerus minor. The relationship between dry weight and percentage water content in T. minor is hyperbolic, but variable. At certain times of the year, the smaller individuals have higher water contents than the larger individuals, whilst at other times, the situation is reversed. Perhaps comment on the differences between species shown in Figure 5.8 should be deferred until more is known of the relationships between size and water content for other times of the year.

FIGURE 5.9 Volume of O. moreletii as a function of dry weight.


VOLUME [CUBIC MMS.]
300
200
100
0
0
.020
.040
.060
.080
.100
DRY WEIGHT [GMS.]
[•] ♀
[○] ♂

5.8 Summary

At moderate temperature (20°C), O. moreletii was very resistant to desiccation. Mature males were less resistant than females and juvenile males. The resistances of intercalary males, juvenile males and females were similar.

Both juveniles and adults of A. castaneum were much less resistant to desiccation at 20°C than the equivalent stages in the life cycle of O. moreletii. The juveniles of Dimerogonus sp. were less resistant than the juveniles of O. moreletii. For short exposures at least, the adults of Dimerogonus sp. were more resistant to desiccation than the adults of O. moreletii.

The resistance of O. moreletii to desiccation at high temperature (35°C) changed substantially throughout the year, being greatest in the drier and hotter and least in the cooler and wetter months. There was no evidence of a difference between the resistances of females, juvenile and intercalary males. There was however evidence to suggest that the resistance of mature males was lower than that of the females and juvenile males.

Throughout the year, both sexes of O. moreletii showed a preference for the moist end of a gradient of humidity after 21 hours exposure to it. Generally, the males showed this preference more rapidly than the females.

Using percentage water content as an indicator of desiccation, no evidence was obtained of O. moreletii being desiccated in the litter in either the grassland or the woodland in the summer of 1974-5. Then a technique using the appearance of the mid-gut was developed to detect desiccation. Using this technique, desiccated millipedes were found in the litter in the grassland in dry weather in the summer of 1975-6.

6. TEMPERATURE RELATIONSHIPS

6.1 Introduction

The experiments reported in this chapter 1) investigated the resistances to high temperature (i.e. the abilities to survive exposure to high temperature) and the temperature preferences of the males and females of O. moreletii at different times of the year, and 2) compared the resistances to high temperature of O. moreletii, A. castaneum and Dimerogonus sp. The reasons for doing these experiments are outlined in Section 5.1.

6.2 Literature Review

Barlow (1957), Causey (1943) and Haacker (1968) studied the resistances to high temperature of several species of millipede. Their techniques were to increase the ambient temperature slowly until the animals died, thus recording lethal temperatures. These temperatures were generally between 36 and 43°C under moist conditions. Haacker and Barlow recorded lethal temperatures of 40 to 42°C for O. sabulosus. No differences were recorded for males and females. Barlow also exposed small numbers of three species to various constant temperatures (5 to 30°C) for 42 days. For O. sabulosus, he found negligible mortality for both sexes at all temperatures.

Several authors (Cloudsley-Thompson, 1951, 1954; Barlow, 1957; Haacker, 1968; Dowdy, 1968; Toye, 1966; Gromysz-Kalkowska, 1967) have measured the temperature preferences of millipedes under moist conditions. Haacker (1968) gave the preference of O. sabulosus as approximately 26 to 32°C. Barlow (1957) measured the preferences of O. sabulosus at different times of the year in a 5 to 30°C gradient. He stated that O. sabulosus "showed no definite preference and indicated only a tendency to avoid the highest temperatures in the range". Barlow further stated that for O.

sabulosus there was "a narrowing of the selected temperature range and a consequent increase in the intensity of selection during the winter months", but his data were very variable and his conclusion is difficult to accept. Barlow suggested that the "intensities of selection" of the males were higher than the females during winter. It is to be presumed that adults were used for the tests.

6.3 Resistance to High Temperature

The designs of the following experiments were essentially the same as those reported in Section 5.3. Where the designs differed, the differences are indicated. Results in Section 5.4, Experiment 1 suggested 35°C was a suitable high temperature at which to measure resistance.

Experiment 1. Resistances at different times of the year

Large numbers of O. moreletii were collected from the grassland in September and November 1974, February, March and April (twice) 1975. They were maintained over distilled water at temperatures of either 35°C or 20°C. At intervals of 2 days, the dead millipedes were removed and aged and sexed.

The cumulative mortalities at 35°C are shown in Figure 6.1 for each sampling occasion. In all cases, mortalities at 20°C (controls) were negligible (≤ 5 dead individuals) and have been ignored. The data suggest that the resistance to high temperature changes throughout the year, being highest during the warmer months and lowest during the cooler months.

Approximate $L.D._{50}$s were read from the graphs in Figure 6.1 and are given in Table 6.1. The data suggest that the mature males are less resistant to high temperature than the juvenile males, in particular during the late summer to early autumn. The data suggest little or no difference in resistance between females and juvenile males (Also there was no evidence in the results to suggest differences in resistance between stadia in either

FIGURE 6.1 Numbers (expressed as cumulative %) of O. moreletii dying at 35°C, 100% R.H.

	Numbers of animals used		
	Females	Juvenile Males	Mature Males
1. September 1974	250	145	
2. November 1974	245	130	
3. February 1975	193	154	27
4. March 1975	236	38	100
5. April ① 1975	216	17	136
6. April ② 1975	199	21	149

(Lines fitted by eye).

(The data for February 1975 are limited because the experiment was terminated by a laboratory fire!)

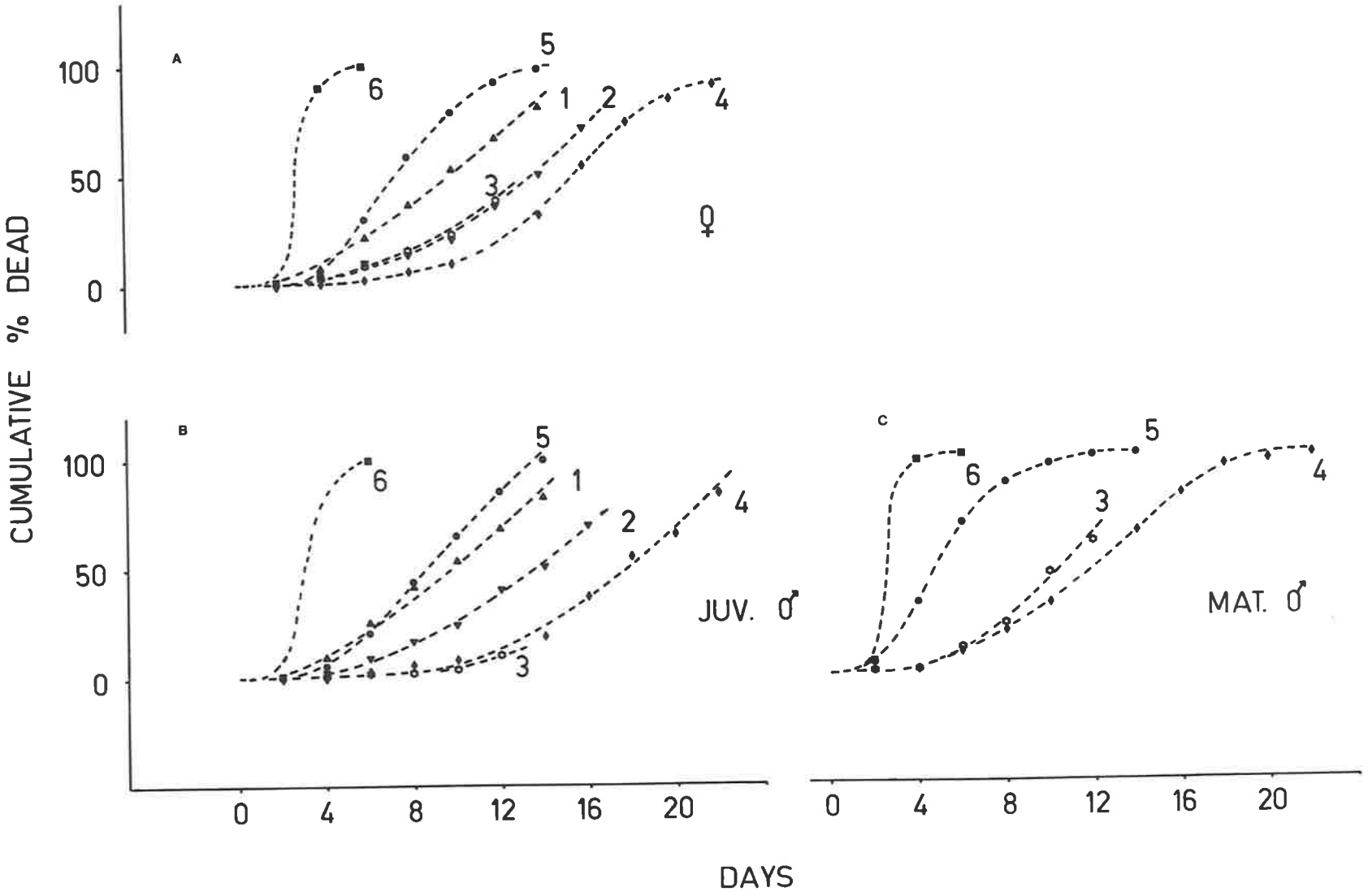

A
B
C
100
50
0
CUMULATIVE % DEAD
6
5
1
2
3
4
♀
JUV. ♂
MAT. ♂
0
4
8
12
16
20
DAYS

TABLE 6.1

$L.D._{50}$s at 35°C; 100% R.H. (Days)

Date	Females	Juvenile Males	Mature Males
September 1974	10	9	
November 1974	14	14	
February 1975	>12	≫12	11
March 1975	16	18	12
April (1) 1975	7	9	5
April (2) 1975	3	3	3

sex). Unfortunately intercalary males were too rare in the collections used in the experiments to warrant their mortalities being calculated.

Experiment 2. Probit Analysis

In early October 1974, a probit analysis was done to measure the resistances of males (juveniles) and females of O. moreletii when exposed to 35°C and 100% R.H. The experimental design differed from that in Section 5.4, Experiment 3 as follows:-

1) The two treatments used were 20°C and 35°C, but in both cases distilled water was placed in the bottom of the jars,

and 2) Transfers from the first treatment to the second were at intervals of 2 days rather than 1.

The numbers of millipedes used and the numbers surviving at each exposure to 35°C are given in Appendix Table 6.1. Figure 6.2(a) illustrates the data transformed to probits.

The $L.D._{50}$s at 35°C were calculated for both sexes using the approximate method of Finney (1947). The provisional probit lines were $Y = 3.23 + 0.19x$ for the males and $Y = 3.32 + 0.19x$ for the females. $L.D._{50}$s and their fiducial limits at the 5% probability level were 9.32 ± 1.27 days for the males and 8.84 ± 0.92 days for the females. There was no evidence to suggest a significant difference between the resistances of the males and females.

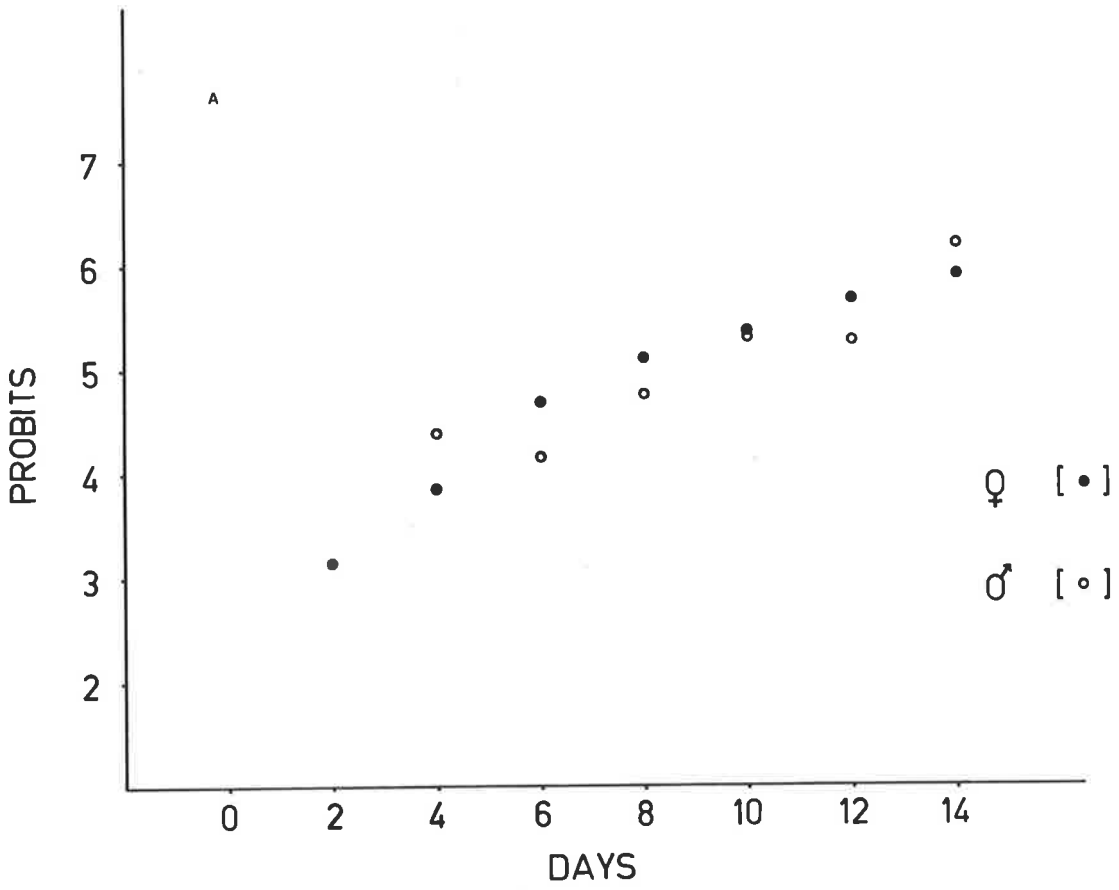
There were reasonably close agreements between the $L.D._{50}$s calculated here and those approximated in Experiment 1 at a similar time of year (September 1974). It seems permissible therefore to accept the $L.D._{50}$s given in Experiment 1 as reasonably accurate estimates of the resistance of O. moreletii.

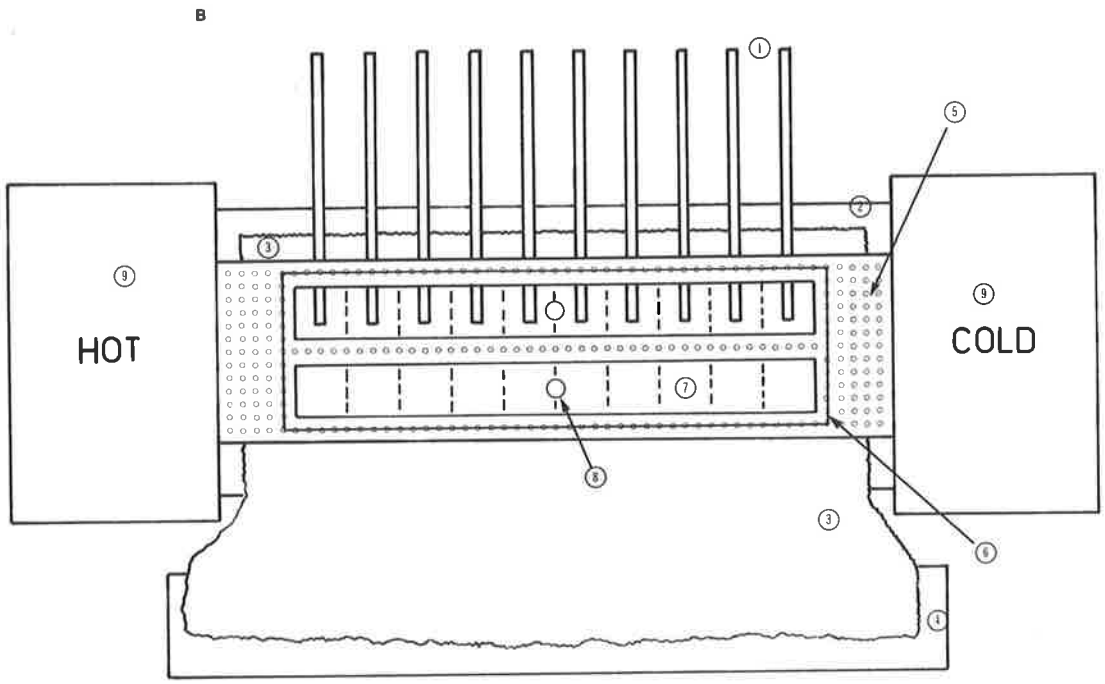
Experiment 3 (a and b). Comparisons of Species

In June 1975, O. moreletii ($\geq$ 7th stadium) and Dimerogonus sp. (17 to 50 pairs of repugantorial glands) were collected from the woodland.

FIGURE 6.2(a) Probit analysis of resistance to high temperature (35°C, 100% R.H.).

FIGURE 6.2(b) Apparatus used to create a temperature gradient (top view). (① = thermometers, ② = aluminium base of gradient, ③ = paper towelling, ④ = water reservoir, ⑤ = polysterene foam walls of gradient, ⑥ = perspex roof of gradient, ⑦ = chamber in which millipedes moved around, ⑧ = hole through which animals were added, ⑨ = hot and cold water baths).


A
PROBITS
7
6
5
4
3
2
0
2
4
6
8
10
12
14
DAYS
♀ [•]
♂ [∘]


B
HOT
COLD
1
2
3
4
5
6
7
8
9

Their resistances to high temperature were tested by essentially the same method as described in Section 5.3, Experiment 2, except that exposures to 35°C over distilled water were used rather than exposures to 20°C over fused $CaCl_2$. The mortalities at 35°C are given in Table 6.2. The mortalities at 20°C (controls) were negligible (1 O. moreletii and 3 Dimerogonus sp. died) and have been ignored.

In October 1975, a similar experiment was conducted to compare O. moreletii and A. castaneum. The animals were again collected in the woodland. The O. moreletii were ≥ 8th stadium. The A. castaneum were juveniles (16 podous segments). Their mortalities at 35°C are given in Table 6.3. Again the mortalities at 20°C were negligible (2 O. moreletii and no A. castaneum died).

The results of both these experiments suggest that O. moreletii is more resistant to high temperature than the two native species, especially A. castaneum.

6.4 Temperature Preferences of O. moreletii

During 1974 and 1975, the temperature preferences of the males and females of O. moreletii (≥ 9th stadium) were measured on 6 days from October to December, 6 days from January to February, 6 days in early March and 9 days from May to August using the apparatus shown in Figure 6.2 (b). From October to February, the males used were all juveniles; from March to August they were all mature. On 3 days in January, warm water at 60°C and ice and salt were used at either end of the apparatus to create the gradient of temperature. On all other days, warm water at 40°C and ice and salt were used. In addition to the above, controls were run on 6 days (3 in February and 3 in May) in which no gradient was created in the apparatus. The males used then were juvenile in February and mature in May.

The millipedes were collected from the litter in the pasture grass

TABLE 6.2

Numbers Dying at 35°C; 100% R.H.

- (June, 1975).

	Days of Exposure						Still Alive	Total Used
	2	4	6	8	10	12		
O. moreletii								
Adult ♀	6	23	13	5	4	-	0	51
Adult ♂	8	15	12	9	3	1	0	48
Juvenile ♀	1	8	6	3	3	-	0	21
Juvenile ♂	6	5	2	1	1	-	0	15
Dimerogonus sp.								
Adult ♀	31	19	-	-	-	-	0	50
Adult ♂	12	18	2	1	-	-	0	33
Juvenile ♀	16	17	-	-	-	-	0	33
Juvenile ♂	19	13	-	-	-	-	0	32

For the females of *Dimerogonus* sp., $\geq$ 34 pairs of repugnatorial glands in an individual was taken to indicate an adult whilst $<$ 34 pairs was defined as a juvenile. For the females of *O. moreletii*, $\geq$ 9th stadium was taken as an adult, $<$ 9th stadium as a juvenile (see Chapter 3).

TABLE 6.3

Numbers Dying at 35°C; 100% R.H.

- (October, 1975)

	Days of Exposure					Still Alive	Total Used
	2	4	6	8	10		
O. moreletii							
Adult ♀	8	17	15	11	5	18	74
Adult ♂	3	3	1	1	1	1	10
Juvenile ♀	-	-	-	4	1	10	15
Juvenile ♂	1	4	2	8	4	15	34
A. castaneum							
Juvenile ♀	36	-	-	-	-	0	36
Juvenile ♂	53	-	-	-	-	0	53

(The adult males here were intercalary)

at Bridgewater in the morning. Immediately on returning to the laboratory, 20 males were added to one chamber of the apparatus and 20 females to the other. The chamber to which each sex was added was decided by the toss of a coin and therefore varied from one day to another. The millipedes were added at the mid-point of the apparatus. The gradient of temperature was established 2 hours before the addition of the millipedes. At 1, 2, 3, 4 and 5 hours after addition, the temperatures and the numbers of millipedes in each section were recorded. The apparatus was kept in a dark room at 20 to 23°C. Relative humidities throughout the apparatus were checked (whilst gradients of temperature were operating) using cobalt thiocyanate papers. In all sections, the relative humidities were approx. 100%.

For a given time of year (e.g. October to November, January to February etc.) there were no obvious changes in the positions of the animals in the gradients from the 1st to the 5th hour. Therefore for simplicity, I will consider here only the data recorded at the 5th hour.

The frequencies of males and females in each section of the apparatus at the 5th hour on each day at a given time of the year were summed. Then these summed frequencies for each section were expressed as percentages of the total numbers in all sections. The resulting data are given in Table 6.4 along with the average temperatures recorded in each section of the apparatus at the same time.

When there was no gradient of temperature in the apparatus (i.e. controls), both sexes of O. moreletii showed obvious preferences for sections 1 and 10. There were no differences in the behaviours of the sexes. Toye (1966) observed a similar "end-effect" in three species of Nigerian millipedes (Spirostreptus assiniensis, Habrodesmus falx and Oxydesmus sp.) and attributed it to thigmo-kinesis. When there was a gradient, both sexes of O. moreletii avoided the coolest and warmest sections (otherwise the numbers in sections 1 and 10 would have been much

TABLE 6.4

Frequencies and temperatures recorded in temperature gradient

(a) Frequency (as a % of N, the total numbers used).

		SECTION										
		1	2	3	4	5	6	7	8	9	10	N
Controls	♂	44	7	3	1	3	3	1	2	8	29	120
	♀	43	7	7	6	3	3	3	3	4	22	120
Oct.-Dec.	♂	28	41	17	1	1	1	1	6	1	4	120
	♀	13	38	23	6	3	4	1	3	3	7	120
Jan.	♂	2	42	38	7	2	0	2	0	3	5	60
(60°C-ice)	♀	0	28	48	10	5	2	0	2	5	0	60
Jan.-Feb.	♂	20	32	13	5	2	3	2	5	5	13	60
(40°C-ice)	♀	7	30	27	3	7	4	3	7	2	10	60
Early Mar.	♂	13	38	8	8	3	3	5	5	5	13	120
	♀	14	32	23	5	2	3	1	4	3	13	120
May-Aug.	♂	29	29	17	3	6	2	3	3	4	4	180
	♀	15	17	16	11	16	7	4	3	4	7	180

(b) Temperature (°C)

	1	2	3	4	5	6	7	8	9	10
Controls	19.9	19.7	19.9	20.2	20.2	20.1	19.9	19.7	19.7	19.6
Oct.-Dec.	25.2	22.3	21.5	20.4	19.5	18.3	17.7	16.7	14.9	11.9
Jan. (60°C)	30.5	25.3	23.3	22.1	20.9	19.5	19.1	18.0	16.2	13.5
Jan.-Feb. (40°C)	26.5	23.1	21.9	21.2	20.7	19.1	19.0	18.0	15.2	13.9
Early Mar.	27.0	24.5	23.7	23.0	22.4	20.9	20.9	19.6	17.5	15.2
May-Aug.	25.5	23.1	21.6	20.4	19.8	18.3	17.9	16.4	14.8	12.1

greater than those in the other sections).

Overall the data in Table 6.4 suggest that both sexes preferred temperatures between 20 to 25°C throughout the year.

6.5 Summary

The resistance to high temperature of O. moreletii collected from the litter in the grassland changed substantially throughout the year, being greatest in the warmer and least in the cooler months. There was no evidence of a difference between the resistances of females and juvenile males. There was evidence however to suggest that the resistance of mature males was lower than that of juvenile males.

Juveniles of A. castaneum and juveniles and adults of Dimerogonus sp. were less resistant to high temperature than equivalent stages in the life cycle of O. moreletii.

Both sexes of O. moreletii showed preferences of 20-25°C throughout the year.

The significances of the above facts in the ecologies of the three species are discussed in Chapter 7, together with findings from Chapter 5 concerning water relationships.

7. DISCUSSION

The life history of a species is an adaptive character. "The life history of organisms ..... represents a series of selective compromises to a suite of environmental variables. Components of any life history, such as clutch size, age at maturity, and body size, constitute a life history "strategy", implying a suite of adaptive responses over evolutionary time, without any teleological implications" (Wilbur et al., 1974).

In some species, the life history selected for has included semelparity (only one clutch per female), short generation time and high fecundity (e.g. most insects). In other species, iteroparity (more than one clutch per female), long generation time and low fecundity have evolved (e.g. most birds and mammals). Some species on the other hand have evolved iteroparity with long generation time but high fecundity (e.g. oak trees). Further, some species have very flexible or opportunistic life histories in which generation time varies greatly (e.g. many parasites and desert plants). Recent attempts to explain the evolution of the many different types of life histories have been dominated by the concepts of 1) r- and K-selection, and 2) optimum allocation of available energy amongst growth, maintenance and reproduction (e.g. see MacArthur, 1962; Cody, 1966; Williams, 1966; MacArthur and Wilson, 1967; Pianka, 1970, 1972; Gadgil and Bossert, 1970; Gadgil and Solbrig, 1972; Hairston et al., 1970 and Schaffer, 1974, but see Wilbur et al., 1974; Southwood et al., 1974; Tinkle and Hadley, 1975; Vinegar 1975 and Demetrius, 1975 for criticisms of the limitations of these concepts). Two "optional" components in a life history and the selective advantages they can convey are of most relevance in this thesis. They are 1) iteroparity, and 2) flexibility in the timing of reproduction.

Cole (1954) recognized the often very limited advantage that iteroparity held over semelparity in contributing to a species' intrinsic rate of natural increase (or innate capacity for increase, r_m (Andrewartha

and Birch 1954)). It should be noted here however that the smaller the replacement rate (or effective litter size) and the longer the generation time relative to the time between breeding seasons, the greater is the contribution of iteroparity to r_m. Murphy (1968) asked, that if iteroparity contributed very little to r_m, then what other selective advantages might it convey. He suggested that iteroparity might be an evolutionary response to uncertain survival of juveniles coupled with relatively stable survival of adults. He than went further and recognized the benefits to semelparous species of individuals reproducing at different ages "though all die after a single reproduction". He recognized that such flexibility in the reproduction of semelparous species was a method of achieving the same benefit he had attributed to iteroparity - namely the ability to reproduce over a number of seasons and so counter the effects of uncertain survival of the young in each generation.

Laughlin (1965) reached a similar conclusion to that of Murphy. Also stimulated by Cole (1954), Laughlin wondered at the selective advantages of "old mothers" and why they remained in a population at all. He concluded, "Perhaps older mothers have other selective advantages - increased power of survival for instance - which could, in conjunction with their (normally unimportant) reproductive ability, help a population through a particularly nasty catastrophe". Laughlin however drew no distinction between iteroparous and semelparous mothers.

Both Murphy (1968) and Laughlin (1965) are in keeping with the concept of spreading of risk developed by den Boer (1968). Briefly, den Boer considered every species to be at risk of extinction due to fluctuations in its numbers brought about by changes in its environment. He suggested that if the influential factors in the environment were many and varied rather than few and if the species itself was variable in make-up rather than stereotyped, then the overall effect would be to dampen or spread the

risk of extinction and stabilize population numbers. Reddingius and den Boer (1970) demonstrated this did happen in a stochastic model. Den Boer (1968) gave examples of how certain species spread their risk of extinction by citing cases of variability both within the species concerned (spreading of risk by phenotypic variation and in time) and within their environment (spreading of risk in space and in relations with other species). Spreading of risk in time is of most relevance to the present thesis. Den Boer (1968) realised that variation in the timing of reproduction could lead to the spreading of risk in time. Thus I conclude, both semelparous and iteroparous species which can spread the breeding of one generation over a number of seasons effectively spread their risk of extinction in time.

Blower and Fairhurst (1968) and Blower (1969) considered the possible adaptive advantages that iteroparity might have for Iulid millipedes. Initially, Blower and Fairhurst (1968) assumed that iteroparity had a negligible effect on r_m and suggested that extended adult life and iteroparity facilitated dispersal. Later, Blower (1969) noted in the conclusions of Cole (1954) that iteroparity did influence r_m significantly if the replacement rate was low. Blower (1969) compared the iteroparous cylindroiulines, C. punctatus and C. latestriatus, with the semelparous iulines, O. pilosus and I. scandinavius, and noted that the numbers of eggs per clutch were smaller in the iteroparous species. On these limited grounds it appeared that iteroparity might be an adaptation to cover a low replacement rate. However, Blower (1969) also noted that the iteroparous schizophylline, T. niger, lays comparable numbers of eggs per clutch to the semelparous iulines. Thus from the point of view of fecundity, there was little evidence to suggest lower replacement rates by the iteroparous species.

Blower (1969) (1970) found that the iteroparous species were more

aggregated in their dispersion than the semelparous species. Hence he argued that successful dispersal of individuals was less likely in the former species. Blower (1969) hypothesized that extension of adult life and iteroparity aided aggregated species in dispersing to their special requirements. Blower pointed out that this hypothesis of extended life and iteroparity adapting a species to the hazards of dispersal fitted the earlier comment of Cole (see above) that iteroparity was useful when the replacement rate was low. "The greater the difficulties of effective dispersal the lower the effective replacement rate" (Blower, 1969).

The dispersions of the Polydesmids, P. angustus and P. denticulatus are very aggregated, but the species are semelparous (Blower, 1969, 1970). These species oviposit over a longer period of time than the Iulids and Blower (1969) suggested that extended breeding seasons were an alternative to iteroparity in facilitating dispersal.

The arguments put forward by Blower and Fairhurst (1968) and Blower (1969) are severely limited by the fact that nobody has yet shown that "iteroparous" Iulids are indeed iteroparous (see Section 3.7). There is a possibility that they may in fact be semelparous.

Turning to the present study, laboratory evidence (see Chapter 3) suggested that iteroparity was possible in O. moreletii. However evidence from populations in the field (see Chapter 4) suggested that iteroparity was uncommon if it did occur at all. Low survival of females followed breeding seasons when maturation was successful (e.g. after a wet summer or in the grassland) whilst high survival followed breeding seasons when maturation was poor (e.g. after a hot, dry summer or in the woodland). I cannot see iteroparity as an important component in the life history strategy of O. moreletii. I do however see the species' ability to extend life following a poor breeding season as important.

Murdoch (1966 a and b) found with the carabid Agonum fuliginosum that the survival of adult females from one breeding season to the next was inversely related to the reproductive rate in the first season. Thus females that laid few eggs in the first season stood a better chance of surviving to the next season to continue breeding than did females which reproduced heavily initially. Murdoch indicated the obvious stabilizing effect this had on population numbers. The species was insured against a poor breeding season (e.g. brought about by drought). Sutton (1968) working with the wood-louse Trichoniscus pusillus (the breeding of which was also inhibited by drought) reached similar conclusions to those of Murdoch. The survival of T. pusillus was high until successful breeding occurred and then it declined rapidly. Mortality depended "upon breeding history rather than age". Sutton again recognized the stabilizing effect such a flexible life history had on population numbers. I consider the strategy in the life history of O. moreletii to be very much the same as that of A. fuliginosum and T. pusillus. The flexibilities of the life histories of the three species are examples of spreading of risk in time.

I do not disagree with Blower and Fairhurst (1968) and Blower (1969). Provided their Iulids are iteroparous, their hypotheses are workable. Blower and Fairhurst's (1968) hypothesis that extended adult life and iteroparity facilitate dispersal can be viewed through den Boer's (1968) spreading of risk in space. The wider the distribution of a species the less is the risk of its extinction. Blower's (1969) hypothesis of extended adult life and iteroparity compensating for a low replacement rate brought about by unsuccessful dispersal to aggregated resources stands by itself. But there seems no objection in viewing iteroparity in millipedes as a means of spreading of risk in time as well. In this case, iteroparity would be an insurance against poor survival of the young in one or more generations (c.f. Murphy, 1968). In the case I have argued for O. moreletii,

extended life with probably only semelparity is an insurance against poor production of the young in the first place.

Blower and Fairhurst (1968) saw periodomorphosis (the extended life of adult males) as a complicated means of maintaining a reasonable sex ratio in the adult stadia. They noted that in T. niger, periodomorphosis increased the sex ratio (% males) by 5 to 7%. Blower and Fairhurst argued that an even sex ratio would be of particular advantage in vagile (i.e. very active and dispersive) species.

I agree that periodomorphosis also increases the sex ratio in O. moreletii, but I emphasize again the concept of spreading of risk. Very few mature males of O. moreletii survived through winter to become intercalary males in spring in the populations studied at Bridgewater (see Appendix Tables 4.1 to 4.6). The continued survival of these males to become mature at the next breeding season contributed very little to the sex-ratio (as Blower and Fairhurst (1968) showed for T. niger). However, if for some reason, maturation of new adults was very poor in a particular breeding season, then the contribution of the old males might be more important (hence spreading of risk).

That O. moreletii should die after reproducing but survive if reproduction is inhibited is not surprising. Reproduction is a metabolically exhausting process. Those animals which contribute a major portion of their available energy to reproduction (either through development of the gonads or locomotory activity) become more susceptible to mortality factors. Alternatively, reproduction may stimulate "aging" and rapid death (see Rockstein and Miquel, 1973).

Does the intercalary male represent an adaptation in the life cycle or is it a hormonal "mistake"? The seasonality of the intercalary and mature forms in O. moreletii (the intercalary form predominating in summer) suggests an adaptation. Further, there is indirect evidence (see Section 5.4) to suggest that the intercalary form is more resistant to desiccation

at high temperature than the mature form. During spring, the resistance of intercalary males is similar to that of juvenile males and females. During autumn, the resistance of mature males is less than that of juvenile males and females. Unfortunately the mature and intercalary forms do not occur simultaneously in the field in sufficient numbers to allow a direct comparison of their resistances. In addition, when they do co-exist (spring and summer), they have quite different recent histories. One form is old, the other newly moulted. Comparisons at such times would not be very meaningful. Comparisons of the relative resistances of the two forms can therefore only be indirect. But perhaps the intercalary form is physiologically more resistant, perhaps behaviourally (e.g. less active and therefore less exposed to extremes in climate) and therefore an adaptation that enables the males to survive the summer. On the other hand, perhaps the intercalary male represents an adaptation to slow down physiological aging (Rockstein and Miquel, 1973). Perhaps decreased activity as an intercalary male allows metabolic reserves to be used by the mature male during the breeding season. But perhaps a hormonal explanation (see Section 3.5) is simply involved.

Why does O. moreletii continue to moult in the older stadia? Growth seems an unlikely motive. Increase in size decreases markedly after the point at which maturity is usually reached (see Section 3.6). Energy is presumably devoted to reproduction and dispersal rather than growth. That the gonads develop in older animals is obvious and greater activity in older stadia was demonstrated in Section 4.59. Perhaps moulting is a necessary repair process. The cuticle is no doubt abraded during active periods and perhaps it has to be renewed to allow continued survival. On the other hand, perhaps moulting is simply unavoidable because there is no mechanism present in the animal to terminate it.

O. moreletii aggregated beneath tussocks of L. fibrata or burrowed

underground during summer in the grassland. The top-soil beneath the tussocks remained moist during summer and dry during winter relative to that beneath the surrounding pasture grasses. The temperatures beneath the tussocks never exceeded 26°C during a 10 day period in summer, but reached 43°C beneath the surrounding pasture grass over the same period. In laboratory experiments, both males and females showed preferences for 100% R.H. and temperatures between 20 and 25°C throughout the year. The aggregation of O. moreletii beneath the tussocks in summer seems well explained by the behaviour of the species in the laboratory.

At Bridgewater, mortality of O. moreletii during summer was demonstrated only during the very hot and dry summer of 1974-5. At this time, mortality was measured in the open grassland but not in the cooler and moister woodland. Large numbers of dead O. moreletii were seen in January 1973 and 1975 on Eyre Peninsula. Eyre Peninsula is hotter and drier than Bridgewater. It was impossible to tell how long the millipedes on Eyre Peninsula had been dead, but it seemed reasonable to assume that death was recent. The dead millipedes were commonly aggregated beneath loose stones and were still"intact". These observations suggest that O. moreletii is killed during hot and dry summers.

Whilst mortality of O. moreletii was demonstrated in the grassland during the summer of 1974-5, measurement of water contents gave no evidence to suggest that the millipedes present at the time were being desiccated. It might be concluded therefore, that if the mortality is attributed to the extreme weather during this particular summer, that the high temperature rather than the aridity was the mortality factor*. A severe limitation

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* Indeed laboratory experiments demonstrated that O. moreletii was particularly susceptible to short exposures to high temperatures (45°C); temperatures that were approached in the litter when measurements were taken (see Section 4.3).

here however is that the water contents were measured only at intervals of 1 month. If death due to desiccation was rapid, and recovery of lost water by survivors was prompt, then this survey of water contents may not have been sufficient to indicate any desiccation in the field. Indeed, desiccation was demonstrated in the milder summer of 1975-6, using the appearance of the mid-gut as an indicator. (The millipedes appeared to recover from this desiccation in 1975-6). In future studies, I suggest that the influence of desiccation on field populations of O. moreletii be monitored using this more practical method of the appearance of the mid-gut.

O. moreletii developed resistance to 1) high temperature and 2) desiccation at high temperature throughout summer. This finding at first glance implied that millipedes in the field at the height of summer were more able to survive hot, dry weather than those millipedes in early and late summer. A caution should be issued here though. Resistance in this study was measured under a sudden change in surroudings from 20° to 35°C and approx. 100% to < 5% R.H. In the field, changes in weather are slower than those that I imposed. Time for acclimation therefore exists in the field. Baldwin (1954) demonstrated with Dahlbominus fuscipennis that very brief periods of acclimation could change an animal's resistance to an extreme in weather quite markedly. How closely my measurements of resistance in O. moreletii actually reflect ability to survive in the field therefore require further study with respect to acclimation before they can be regarded as indicative. Likewise, the comparisons I have made between sexes, adults and juveniles, native species and O. moreletii are all subject to knowledge of the influence of acclimation. For this reason, I stress that my findings (and those of others cited in the literature) on resistance to extremes of weather are limited.

Why is O. moreletii far more abundant in the grassland than in the woodland? Survival of older stadia throughout summer and females

throughout winter was higher in the woodland than in the grassland. Reasons for the difference in abundance between the two habitats must therefore be sought in the production and survival of the young. I have already indicated (see Section 4.6) possible reasons for production differing in the two habitats. It would be a thesis in itself to elucidate the factors influencing the survivals of the young in both habitats.

Why are A. castaneum and Dimerogonus sp. only found in the woodland, whilst O. moreletii is found in the grassland as well? Why is O. moreletii so much more abundant in the woodland compared with A. castaneum and Dimerogonus sp.? O. moreletii breeds in autumn-winter, the native species in late winter-spring. The very young of O. moreletii therefore develop in winter-spring; the very young of the native species develop in summer. Do the extremes of summer take a greater toll on the young of the native species, than the extremes of winter take on the young of O. moreletii? Does summer kill more of the native species than O. moreletii? Limited evidence suggested that the juveniles of the native species were less resistant to desiccation than the young of O. moreletii. No difference in resistance was demonstrated between the adults of O. moreletii and Dimerogonus sp. Both the young and adults of O. moreletii were more resistant to high temperature than those of the native species. But all these comparisons were made in winter and spring. Ideally they should have been made in summer. However the rarity of the native species in summer made this impossible.

Alternatively, are sites for oviposition scarcer in the woodland for the natives - hence the different abundances of the three species in the woodland? Are predators, parasites or diseases more influential on the native species? Is suitable food scarce for them? What is so special about Chasmanthe aethiopica that Dimerogonus sp. is much more common beneath it than elsewhere? There are many questions to be answered, but sampling

problems with rare animals which "disappear" in summer will make finding the answers difficult.

To be successful in its new environment, an invading species has to find a niche. The niche it finds might be vacant or occupied. If it is occupied then the invader has to compete with the occupant. The question immediately arises, is O. moreletii competing with either A. castaneum or Dimerogonus sp. for the same niche in the woodland at Bridgewater? Will O. moreletii replace either species or will it simply add an extra species to the fauna? Is O. moreletii competing with species other than a millipede?

Superficially it seems unlikely that O. moreletii competes for oviposition sites with the native species, if in fact the same sites are used. Separate breeding seasons suggest this. The gut contents of all three species suggest that none is a specific feeder. Soil particles and a variety of plant debris were found in their guts. The amount of litter in the woodland during the study suggested that food was abundant and I consider it unlikely that the three species compete for this resource at present. Competition for shelters over summer or for moulting sites are unknown entities.

As well as the influence of O. moreletii on the native fauna, the effect of the species on the decomposition of litter and soil formation should be investigated. The invasion of such large numbers of this scavenger must influence the rate of turnover of soil nutrients.

In most successful introductions, the numbers of individuals arriving in new environments are far less than the maximum numbers that can exist there (the carrying capacities of these environments). With time, each introduced species increases in numbers towards the carrying capacity. In some cases, if the "ecological resistance" (Elton, 1958), to the invader is low, the carrying capacity is exceeded, resources (in particular food) are over-exploited and numbers then decrease dramatically. Caughley (1970)

described the progress of the introduced Himalayan thar (Hemitragus jemlahicus) in New Zealand. Caughley suggested this ungulate erupted in numbers after introduction and exhausted its food, declined in numbers and then became relatively stable at an abundance lower than the initial eruption. Drawing upon an earlier model of Riney (1964), Caughley suggested that "the same sequence of events occurs in areas to which the animals disperse. At the dispersal front density is increasing; further back into the range the density is at a peak; and nearer the point of liberation the population attains relative stability at a lower density. These zones move outward from the centre like the expanding wave generated by a stone thrown into a lake. The sequence following liberation (or introduction by dispersal) can, by hypothesis, be observed both at one point over a range of time, and at one time over a range of distance."

Whether O. moreletii has or will reach the carrying capacities in its new habitats in Australia, and whether it will surpass these capacities, exhaust its resources and decrease in numbers as was noted for the thar remains to be seen. But if an overall drop in numbers of O. moreletii due to exhaustion of resources is to happen in Australia, then it will probably take a long time. O. moreletii has now been in large numbers in parts of Eyre Peninsula for over 20 years. There is no obvious evidence either on Eyre Peninsula or at Bridgewater to suggest a lower abundance of O. moreletii near the origin of the outbreak compared with more peripheral areas.

The expansion of individual outbreaks of O. moreletii in Australia is slow but steady (approx. 100 to 200 metres per year). The numbers of outbreaks have increased markedly in recent years as man has dispersed the species to new habitats. A variety of habitats have already been colonized in large numbers (e.g. arid habitats such as at Cummins on Eyre Peninsula, grassland and woodland in temperate habitats such as at Bridgewater where rainfall is seasonal, urban areas in again temperate habitats such as in

Melbourne where rainfall is however not markedly seasonal etc.). The variety of habitats in which O. moreletii is very successful is extended even further if the Azores and Madeira are also considered (see Appendix Tables 1 to 3). There seems no reason to doubt that given time, O. moreletii will invade much of Australia in large numbers.

The agricultural importance of O. moreletii in South-Eastern Australia has not yet been evaluated. On Eyre Peninsula, O. moreletii is a minor pest in cereal crops (e.g. barley and wheat) where it infests stored grain. Several graziers in the Mt. Lofty Ranges claim that O. moreletii fouls pasture and deters the feeding of sheep and cattle. However this has yet to be demonstrated convincingly. O. moreletii destroys back-yard crops of fruit and vegetables (e.g. strawberries, melons, potatoes, tomatoes etc.) but as yet has not reached areas where such crops are grown commercially. If andwhen the species does reach such areas, perhaps its current status as a "nuisance pest" will be broadened.

There are no obvious differences in climate between Portugal and Spain (where O. moreletii is presumably rare) and other locations where the species is extremely numerous (see Appendix Tables 1 to 3). An explanation of the super-abundance of O. moreletii in Australia in terms of general climate seems therefore unlikely. However, the microclimate on the surface of the ground in the different areas might be substantially different (e.g. due to quantity of leaf litter, texture of the soil etc.). On the other hand, perhaps quantity or quality of food explains the differences in abundance between South-Western Europe and Australia, the Azores and Madeira. Perhaps a biological factor such as a predator, parasite, virus or other disease is involved. There are numerous possibilities - which should be investigated (see Appendix C).

Throughout this study, I have confined myself to determining the distribution and rate of spread of O. moreletii in Australia, the life

history of the species, changes in its abundance and activity throughout the year, and two factors that are important in the survival of the older stadia in the life cycle - namely 1) the degree of maturation in a particular breeding season and 2) the extremity of the weather during summer. A fellow student once grumbled to me that a Ph.D. was an exercise in generating loose ends. This thesis has generated its fair share. Those that I consider most worthy of pursuing, I have indicated in this discussion.

APPENDIX A.

Locations in Victoria where millipedes have been reported in large numbers but as yet have not been confirmed as *O. moreletii*.

Park Orchards, Warburton, Lower Templestowe, East Ringwood, Mitcham, Donvale, Nunawading, Montrose, Mt. Evelyn, Tarwin Lower, Venus Bay, Werribee, Sassafras, Scoresby, Belgrave, North Geelong, North Ballarat, Mt. Dandenong, Mt. Eliza, Seville, West Brunswick, Wonga Park, Studley Park, Montmorency, Box Hill, East Warhoe, Caulfield, East Malvern, Heidelberg, Brighton, Rye and Hexham.

APPENDIX B

Assay of O. moreletii for Juvenile Hormone

Approximately 100 O. moreletii were collected from the field in January 1974. They were of various ages ranging from the fifth to the twelfth stadium. The millipedes were homogenized together in diethyl ether, the solid material filtered off and the ether evaporated. The remaining mixture was sent to Professor C.M. Williams, Harvard University who assayed it for juvenile hormone.

His reply:-

"The extract was taken up in about 15 ml hexane and filtered twice through a small column of alumina of activity IV, capped with anhydrous sodium sulfate. The hexane was removed using a rotary evaporator and the residual 50 µl of amber-colored oil was dissolved in 200 µl cyclohexane.

The latter solution was assayed by topical application onto head-ligated fourth-instar larvae of the tobacco hornworm, Manduca sexta, as described by Truman et al., 1973 (J. Insect Physiology 19: 195-203).

I am pleased to report that a weak but definitely positive assay for JH activity was obtained in all animals that received a topical application of 0.5 to 2 µl of the cyclohexane solution. If we assign a specific gravity of one to the oil, these volumes correspond to 125 to 500 µg of the crude extract".

APPENDIX C

Neoaplectana spp. (Nematoda) have proved successful in the biological control of the wood-wasp, Sirex noctilio (Hymenoptera, Siricidae) Dr. R. Bedding of C.S.I.R.O. (Hobart, Tasmania), suggested that Neoaplectana might well be a parasite that would efficiently control O. moreletii. He infected large numbers of O. moreletii with nematodes, but found no significant mortality within realistic dosage levels.

TABLE 1

Average Monthly Rainfall (mm.)

	J	F	M	A	M	J	J	A	S	O	N	D	Annual
Portugal													
Melgaço	113	122	141	77	87	54	20	42	60	109	156	175	1156
Oporto	159	112	147	86	87	41	20	26	51	105	148	168	1151
Coimbra	132	95	131	76	76	38	13	18	48	87	105	142	961
Faro	70	52	72	31	21	5	1	1	17	51	65	67	453
Spain													
Zaragoza	17	17	27	34	49	36	15	19	30	34	28	31	337
Açores													
Angra Do Heroismo	143	131	150	77	70	49	43	44	98	126	143	112	1186
Horta	125	105	122	69	70	48	32	44	81	110	109	113	1028
Ponta Delgada	120	100	105	67	62	42	27	29	81	103	120	102	958
Santa Cruz	181	159	163	108	84	71	58	78	112	119	139	158	1430
Santa Maria	108	80	79	49	49	28	22	38	44	77	105	57	736
Madeira													
Areiro	336	240	274	184	102	20	18	30	140	308	452	358	2460
Funchal	64	74	80	34	18	6	2	2	26	76	90	84	548
Australia													
Stirling	39	37	43	96	143	183	161	156	124	99	61	48	1190
Strathalbyn	21	21	24	39	56	59	64	60	53	43	29	25	494
Pt. Lincoln	14	15	19	37	57	75	78	67	49	35	23	18	487
Cleve	15	24	19	31	41	47	44	49	42	36	28	22	398
Pt. Pirie	18	19	18	29	39	41	33	36	34	31	23	21	342
Melbourne	48	49	53	59	57	50	49	49	59	67	59	58	657

TABLE 2

Average Daily Maximum Temperature (°C)

	J	F	M	A	M	J	J	A	S	O	N	D	Annual
Portugal													
Melgaço	11.6	12.9	15.9	18.5	20.9	24.2	27.4	26.7	24.1	20.3	14.9	11.8	19.1
Oporto	13.2	14.2	16.3	18.4	19.6	22.6	24.7	25.0	23.7	20.8	16.7	13.7	19.1
Coimbra	14.0	15.7	18.2	20.9	22.5	26.1	28.9	29.3	27.2	23.0	17.8	14.4	21.5
Faro	15.3	16.1	17.5	19.7	21.9	25.2	28.2	28.2	25.7	22.4	18.9	16.2	21.3
Spain													
Zaragoza	9.9	12.5	16.6	19.3	22.6	27.4	30.8	30.0	26.5	20.3	14.3	10.1	20.0
Açores													
Angra Do Heroismo	15.9	15.7	15.8	16.8	18.4	21.0	23.3	24.4	23.2	20.8	18.3	16.8	19.2
Horta	16.6	16.6	16.8	17.8	19.5	22.2	24.8	26.2	24.6	21.8	19.2	17.6	20.3
Ponta Delgada	17.2	17.1	17.4	18.3	19.9	22.4	24.7	25.9	24.8	22.4	19.8	18.2	20.7
Santa Cruz	16.8	16.6	16.8	17.6	19.2	22.0	24.4	26.0	24.4	21.8	19.3	18.0	20.2
Santa Maria	16.6	16.6	17.0	17.8	19.8	22.0	24.1	25.2	24.6	22.2	19.4	17.5	20.2
Madeira													
Areiro	8.9	8.9	9.4	10.6	11.7	15.6	18.9	18.9	16.1	13.3	11.1	8.9	12.8
Funchal	18.9	18.3	18.9	19.4	20.6	22.2	23.9	24.4	24.4	23.3	21.7	19.4	21.1
Australia													
Stirling	24.9	24.4	22.6	18.1	14.4	11.7	10.6	11.7	14.4	17.0	19.9	22.5	17.7
Strathalbyn	27.5	27.1	25.4	21.7	18.2	15.4	14.6	15.7	18.2	21.0	24.0	26.1	21.2
Pt. Lincoln	25.0	24.7	23.7	21.3	18.6	16.4	15.7	16.3	18.1	19.8	21.5	23.3	20.4
Cleve	28.2	26.8	25.7	22.1	18.6	15.9	14.9	16.2	19.0	21.8	24.4	26.5	21.7
Pt. Pirie	31.8	31.4	29.5	24.6	20.2	17.1	16.3	17.8	21.3	24.5	27.6	29.9	24.3
Melbourne	25.8	25.6	23.8	20.1	16.4	13.9	13.2	14.8	17.1	19.5	21.8	24.1	19.7

TABLE 3.

Average Daily Minimum Temperature (°C)

	J	F	M	A	M	J	J	A	S	O	N	D	Annual
Portugal													
Melgaço	4.2	4.7	6.8	7.9	10.4	13.1	14.8	14.4	13.4	10.2	7.2	4.9	9.3
Oporto	4.7	5.0	7.5	8.8	10.8	13.4	14.6	14.6	13.6	10.8	7.8	5.4	9.8
Coimbra	5.4	5.8	8.2	9.3	11.0	13.6	14.9	15.0	14.1	11.7	8.7	6.1	10.3
Faro	9.0	9.5	11.1	12.5	14.4	17.5	19.5	19.9	18.6	15.7	12.6	9.8	14.2
Spain													
Zaragoza	2.2	3.3	5.8	8.2	11.4	15.2	17.5	17.4	15.2	10.5	6.1	3.4	9.7
Açores													
Angra Do Heroismo	11.9	11.6	11.5	12.1	13.5	15.9	17.6	18.7	18.0	16.1	14.3	12.9	14.5
Horta	12.2	12.0	11.8	12.6	14.0	16.3	18.4	19.5	18.6	16.6	14.6	13.3	15.0
Ponta Delgada	11.5	11.3	11.5	11.9	13.1	15.2	17.0	18.0	17.3	15.7	13.8	12.4	14.1
Santa Cruz	12.3	12.2	12.0	12.9	14.4	16.8	19.1	20.3	19.1	17.1	14.9	13.6	15.4
Santa Maria	12.1	11.7	12.1	12.4	14.2	16.3	18.2	19.2	18.5	17.0	14.6	13.1	14.9
Madeira													
Areiro	2.8	3.3	3.3	4.4	5.0	8.3	10.6	11.1	9.4	7.8	6.1	3.9	6.7
Funchal	13.3	13.3	13.3	14.4	15.6	17.2	18.9	19.4	19.4	18.3	16.1	14.4	16.1
Australia													
Stirling	11.6	11.8	10.7	8.9	6.9	5.4	4.7	4.8	5.9	7.2	8.7	10.3	8.1
Strathalbyn	13.2	13.3	11.9	9.9	8.1	6.5	5.8	5.9	6.9	8.4	10.2	12.0	9.3
Pt. Lincoln	15.3	15.6	14.9	12.9	10.9	9.3	8.5	8.3	9.2	10.6	12.2	13.9	11.8
Cleve	15.4	15.6	14.9	12.1	9.6	7.9	6.8	7.1	8.3	9.9	11.8	13.7	11.1
Pt. Pirie	17.1	17.3	15.7	12.7	10.2	8.2	7.4	7.8	9.4	11.6	13.8	15.8	12.3
Melbourne	13.9	14.2	12.8	10.5	8.3	6.6	5.7	6.4	7.6	9.2	10.8	12.5	9.9

APPENDIX TABLE 4.1(a)

Soil and Litter Sampling - Open Grassland

Tussocks of L. fibrata - Females

Sampling Code No.		STADIA											
		6	7	8	9	10	11	12	13	14	15	16	Total
N	1	7		1	132	107	21	8	4				280
D	2	123	2	6	336	379	34	9					889
D	3	121	8	1	51	61	4	1					247
F	4	80	14	1	28	42	4						169
M	5	44	26	3	1	3	3	2					82
A	6	1	15	9		2	3	2	1	1			34
M	7	4	27	26	7	8	8	1					81
J	8	1	17	75	21	19	5	2					140
A	9		6	55	30	14	11	2					118
S	10	3		9	18	18	12	10	2				72
O	11	4		2	5	2	3	4					20
N	12	25			5	4	14	1	1				50
J	13	462	1048	46	9	16	5	8	7	1			1602
F	14	85	707	91	15	3	7	3					911
M	15	3	53	258	28	3	7	7	2				361
A	16	1	59	242	20	3	1	2	3				331
O	17	4		5	30	6							45
J	18	28	35	2	189	349	44	2	1				650
M	19		4	8	1	28	10						51
O	20				3	2	6	3					14
TOTAL		996	2021	840	929	1069	202	67	21	2			6147

APPENDIX TABLE 4.1(b)

Soil and Litter Sampling - Open Grassland

Tussocks of L. fibrata - Males

Sampling Code No.		STADIA											
		6	7	8	9	10	11	12	13	14	15	16	Total
N	1	1		13	230	38	15	5	2				304
D	2	45	1	10	385	196	36	4	1				678
D	3	98	3	1	91	32	3	1					229
F	4	67	13	1	97	37	3		1				219
M	5	13	17	2	2	23	3						60
A	6	2	20	7	5	42	16	5					97
M	7		20	26	7	55	16	4					128
J	8		46	64	5	40	15	2					172
A	9		13	80	15	52	9	1	1				171
S	10		1	13	12	53	15	1					95
O	11			1	6	4	6	4					21
N	12	17			2	6	7	1					33
J	13	335	941	49	37	13	17	10	1	1			1404
F	14	67	703	94	28	11	9	2	1				915
M	15	4	74	303	37	13	5	6	2	1			445
A	16		58	249	35	13	5	2	2	1			365
O	17	4		6	31	2							43
J	18	25	20	3	495	250	3	1					797
M	19	1	4	9	6	29	9	2					60
O	20			1		5	11	1					18
TOTAL		679	1934	932	1526	914	203	52	11	3			6254

APPENDIX TABLE 4.1(c)

Soil and Litter Sampling - Open Grassland

Tussocks of L. fibrata - Juvenile Males

Sampling Code No.		STADIA										
		6	7	8	9	10	11	12	13	14	15	16	Total
N	1	1		13	226	20							260
D	2	45	1	10	377	153	4						590
D	3	98	3	1	89	26							217
F	4	67	13	1	95	34	1						211
M	5	13	17	2		1							33
A	6	2	20	7	1								30
M	7		20	25	3	3							51
J	8		46	64		4	2						116
A	9		13	80	11	2							106
S	10		1	13	10	1	1						26
O	11			1	5	3	1						10
N	12	17			2	6							25
J	13	335	941	49	37	11							1373
F	14	67	703	93	28	5	1						897
M	15	4	74	282	9								369
A	16		58	233	3								294
O	17	4		6	31	2							43
J	18	25	20	3	495	241	1	1					786
M	19	1	4	9	5	18	2						39
O	20			1		5	11	1					18
TOTAL		679	1934	893	1427	535	24	2					5494

APPENDIX TABLE 4.1(d)

Soil and Litter Sampling - Open Grassland

Tussocks of L. fibrata - Mature Males

Sampling Code No.	STADIA 6	7	8	9	10	11	12	13	14	15	16	Total
N 1				1	12	5	3	2				23
D 2					5	1	1					7
D 3					2	1	1					4
F 4					1							1
M 5				2	22	3						27
A 6				4	42	16	5					67
M 7			1	4	52	16	4					77
J 8				5	36	13	2					56
A 9				4	50	9	1	1				65
S 10				2	48	10	1					61
O 11												0
N 12												0
J 13					1	1	3	1	1			7
F 14			1		6	4	2					13
M 15			21	28	13	5	6	2	1			76
A 16			16	32	13	5	2	2	1			71
O 17												0
J 18					8	2						10
M 19				1	11	7	2					21
O 20						2						2
TOTAL			39	83	322	100	33	8	3			588

APPENDIX TABLE 4.1(e)

Soil and Litter Sampling - Open Grassland

Tussocks of L. fibrata - Intercalary Males

Sampling Code No.	STADIA 6	7	8	9	10	11	12	13	14	15	16	Total
N 1				3	6	10	2					21
D 2				8	38	31	3	1				81
D 3				2	4	2						8
F 4				2	2	2		1				7
M 5												0
A 6												0
M 7												0
J 8												0
A 9												0
S 10					4	4						8
O 11				1	1	5	4					11
N 12						7	1					8
J 13					1	16	7					24
F 14						4		1				5
M 15												0
A 16												0
O 17												0
J 18					1							1
M 19												0
O 20						2	1					3
TOTAL				16	57	83	18	3				177

APPENDIX TABLE 4.2(a)

Soil and Litter Sampling - Open Grassland

Pasture Grasses - Females

Sampling Code No.		STADIA 6	7	8	9	10	11	12	13	14	15	16	Total
N	1	3			7	27	5	2					44
D	2				2	6							8
D	3												
F	4	1			3	1							5
M	5	9	9	1	1	1	6	1					28
A	6		3	1	1	4	13	2	1				25
M	7			3	1	10	13	3					30
J	8			10	2	15	17	7	2				53
A	9			3	3	11	13						30
S	10			2	8	6	4	5	1				26
O	11	3			10	6	8	1					28
N	12	330	21		7	21	12	7	1				399
J	13	22	116	13		2		1	1				155
F	14	2	155	70	2	5	1	2					237
M	15		48	197	11	1	3	4	1				265
A	16		14	94	14	6	8	5	1				142
O	17	1		4	107	45	1						158
J	18		5	1	6	31	8	2					53
M	19	1	1	3	2	44	28	1	1				81
O	20				6	3	44	28	2				83
TOTAL		372	372	402	193	245	184	71	11				1850

APPENDIX TABLE 4.2(b)

Soil and Litter Sampling - Open Grassland

Pasture Grasses - Males

Sampling Code No.		STADIA 6	7	8	9	10	11	12	13	14	15	16	Total
N	1	1		1	22	12	2	1					39
D	2				3	1							4
D	3												
F	4	2		1	6	3	2						14
M	5	3	7	1	3	20	9						43
A	6		1	5	3	33	11	3	1				57
M	7	2	1		2	22	12	1	2				42
J	8		2	5	2	22	6	2					39
A	9			1	3	17	7						28
S	10			2	4	6	5	1					18
O	11	2			8	8	8						26
N	12	268	19	1	14	10	14	8					334
J	13	28	118	12	1	1	1						161
F	14	2	169	69		2	6	3	3				254
M	15	2	43	171	14	11	1	4	1	1			248
A	16		22	110	20	16	9						177
O	17			14	147	28	1						190
J	18	1	4	1	11	24	2						43
M	19		4	2	3	52	21						82
O	20			2	6	6	35	7					56
TOTAL		311	390	398	272	294	152	30	7	1			1855

APPENDIX TABLE 4.2(c)

Soil and Litter Sampling - Open Grassland

Pasture Grasses - Juvenile Males

Sampling Code No.		STADIA 6	7	8	9	10	11	12	13	14	15	16	Total
N	1	1		1	21	9							32
D	2				3	1							4
D	3												
F	4	2		1	6	3							12
M	5	3	7	1									11
A	6		1	5	3								9
M	7	2	1										3
J	8		2	5	1	1							9
A	9			1	1								2
S	10			2									2
O	11	2			8	3							13
N	12	268	19	1	14	10	1						313
J	13	28	118	12	1	1							160
F	14	2	169	67									238
M	15	2	43	159	1								205
A	16		22	93									115
O	17			14	147	28							189
J	18	1	4	1	11	24	1						42
M	19		4	1	3	27	3						38
O	20			2	6	5	24	3					40
TOTAL		311	390	366	226	112	29	3					1437

APPENDIX TABLE 4.2(d)

Soil and Litter Sampling - Open Grassland

Pasture Grasses - Mature Males

Sampling Code No.		STADIA 6	7	8	9	10	11	12	13	14	15	16	Total
N	1												0
D	2												0
D	3												
F	4												0
M	5				3	20	9						32
A	6					33	11	3	1				48
M	7				2	22	12	1	2				39
J	8				1	21	6	2					30
A	9				2	17	7						26
S	10				4	6	4						14
O	11					1							1
N	12												0
J	13												0
F	14			2		2	6	3	3				16
M	15			12	13	11	1	4	1	1			43
A	16			17	20	16	9						62
O	17												0
J	18						1						1
M	19			1		25	18						44
O	20					1	2						3
TOTAL				32	45	175	86	13	7	1			359

APPENDIX TABLE 4.2(e)

Soil and Litter Sampling - Open Grassland

Pasture Grasses - Intercalary Males

Sampling Code No.		STADIA											
		6	7	8	9	10	11	12	13	14	15	16	Total
N	1				1	3	2	1					7
D	2												0
D	3												
F	4						2						2
M	5												0
A	6												0
M	7												0
J	8												0
A	9												0
S	10						1	1					2
O	11					4	8						12
N	12						13	8					21
J	13						1						1
F	14												0
M	15												0
A	16												0
O	17						1						1
J	18												0
M	19												0
O	20						9	4					13
TOTAL					1	7	37	14					59

APPENDIX TABLE 4.3(a)

Pitfall Trapping
Open Grassland - Females

Sampling Code No.		STADIA 6	7	8	9	10	11	12	13	14	15	16	Total
O-N	1			1	73	106	58	55	24	5	3		325
D	2	28	16	1	24	173	23	8	4	1			278
J-F	3	4	1	1	24	58	10	1	1	2			102
F	4	1						1					2
M	5		3	1	2	28	69	12	6		1		122
M	6	2	3		1	30	43	12	3				94
A	7	1	1	27	8	173	269	68	45	11	3		606
M	8				1	24	80	18	6	1	1		131
M	9		1	2		71	162	29	9	3	1		278
J	10			1	2	102	162	30	13	1			311
J	11			1	5	24	58	12	5	1			106
A-S	12				6	2	5	5	2	1			21
O	13	2			1	7	28	27	5	1			71
N	14	99		1	3	43	25	34	4		1	1	211
D	15	43	12			12	2	1	4				74
J	16	19	180	80	5	16	35	31	19	3	2		390
TOTALS		199	217	116	155	869	1029	344	150	30	12	1	3122

APPENDIX TABLE 4.3(b)

Pitfall Trapping
Open Grassland - Males

Sampling Code No.		STADIA 6	7	8	9	10	11	12	13	14	15	16	Total
O-N	1	2		2	61	40	40	15	6	2			168
D	2	26	15	3	70	66	10	5					195
J-F	3	1	3	1	19	35	11	5	1				76
F	4				1								1
M	5		3	1	1	31	9	2	1	1			49
M	6		2	2	1	56	22	5	1	2			91
A	7		3	20	24	595	282	81	21	6	1		1033
M	8		2	1	3	88	40	20	5	2			161
M	9			7	18	427	202	49	9	1	2		715
J	10			4	9	188	84	30	6	1			322
J	11			1	2	53	25	11	3				95
A-S	12			1	2	11	4	2	2				22
O	13	2		1	3	1	15	5					27
N	14	74	4		7	11	50	17	2				165
D	15	19	11	1		3	3	2	1				40
J	16	11	179	49	3	3	6	6	1				258
TOTALS		135	222	94	224	1608	803	255	59	15	3		3418

APPENDIX TABLE 4.3(c)

Pitfall Trapping
Open Grassland - Juvenile Males

Sampling Code No.		STADIA 6	7	8	9	10	11	12	13	14	15	16	Total
O-N	1	2		2	57	16	1						78
D	2	26	15	3	69	58	2						173
J-F	3	1	3	1	18	24	1						48
F	4				1								1
M	5		3	1	1								5
M	6		2	2	1	1							6
A	7		3	14	6	5	1						29
M	8		2	1									3
M	9			1									1
J	10												0
J	11			1	1								2
A-S	12			1	1	2							4
O	13	2		1	3								6
N	14	74	4		7	6	1						92
D	15	19	11	1		3							34
J	16	11	179	49	3	3							245
TOTALS		135	222	78	168	118	6						727

APPENDIX TABLE 4.3(d)

Pitfall Trapping
Open Grassland - Mature Males

Sampling Code No.		STADIA 6	7	8	9	10	11	12	13	14	15	16	Total
O-N	1					1	3	1	1				6
D	2												0
J-F	3					2	1	1					4
F	4												0
M	5					31	9	2	1	1			44
M	6					55	22	5	1	2			85
A	7			6	18	590	281	81	21	6	1		1004
M	8				3	88	40	20	5	2			158
M	9			6	18	427	202	49	9	1	2		714
J	10			4	9	188	84	30	6	1			322
J	11				1	53	25	11	3				93
A-S	12				1	9	4	2	2				18
O	13						2						2
N	14					1	1						2
D	15												0
J	16						2	5	1				8
TOTALS				16	50	1445	676	207	50	13	3		2460

APPENDIX TABLE 4.3(e)

Pitfall Trapping
Open Grassland - Intercalary Males

Sampling Code No.		STADIA										
		6	7	8	9	10	11	12	13	14	15	16	Total
O-N	1				4	23	36	14	5	2			84
D	2				1	8	8	5					22
J-F	3				1	9	9	4	1				24
F	4												0
M	5												0
M	6												0
A	7												0
M	8												0
M	9												0
J	10												0
J	11												0
A-S	12												0
O	13					1	13	5					19
N	14					4	48	17	2				71
D	15						3	2	1				6
J	16						4	1					5
TOTALS					6	45	121	48	9	2			231

APPENDIX TABLE 4.4(a)

Pitfall Trapping
Sclerophyllous Woodland - Females

Sampling Code No.		STADIA											
		6	7	8	9	10	11	12	13	14	15	16	Total
O-N	1		1	6	15	28	63	38	10	4			165
D	2	3		2	3	7	7	7	2	2			33
J-F	3	1		1	5	13	22	32	15	3	2		94
F	4					2	1	4	4	2			13
M	5	1	1		1	18	71	96	45	13			246
M	6	3	2		3	39	51	73	49	15	2	1	238
A	7				1	11	21	28	25	9	3		98
M	8	1				3	13	10	13	6			46
M	9					7	15	20	9	6	3		60
J	10					4	15	13	13	4			49
J	11		1			2	7	4	4	2			20
A-S	12			3	8	1	4	5	6	2			29
O	13			8	1	14	19	13	4	1	1		61
N	14			2	11	9	26	16	4	2	3		73
D	15	3	1	1	5	3	1	2	1	2			19
J	16	7	1				1	1	1				11
TOTALS		19	7	23	53	161	337	362	205	73	14	1	1255

APPENDIX TABLE 4.4(b)

Pitfall Trapping
Sclerophyllous Woodland - Males

Sampling Code No.		STADIA											
		6	7	8	9	10	11	12	13	14	15	16	Total
O-N	1			7	7	9	7	2					32
D	2	1		1	5	2	1		1				11
J-F	3	3			3	2	1	1					10
F	4												0
M	5					5	3	9	2				19
M	6				7	43	33	27	13	1			124
A	7	1			2	43	25	14	6	1			92
M	8					15	8	10	1	1			35
M	9		1		1	21	10	10	3				46
J	10				1	5	4	5	3				18
J	11					8	1						9
A-S	12		1	5					1				7
O	13			3	1	1	3	1					9
N	14	1		3	10	5	3						22
D	15				2								2
J	16	1	1										2
TOTAL		7	3	19	39	159	99	79	30	3			438

APPENDIX TABLE 4.4(c)

Pitfall Trapping
Sclerophyllous Woodland - Juvenile Males

Sampling Code No.		STADIA 6	7	8	9	10	11	12	13	14	15	16	Total
O-N	1			7	7	2							16
D	2	1		1	5	1							8
J-F	3	3			2	1							6
F	4												0
M	5												0
M	6				2								2
A	7	1			1	1							3
M	8												0
M	9		1			1							2
J	10												0
J	11												0
A-S	12		1	5									6
O	13			3	1	1	1						6
N	14	1		3	10	2							16
D	15				2								2
J	16	1	1										2
TOTALS		7	3	19	30	9	1						69

APPENDIX TABLE 4.4(d)

Pitfall Trapping
Sclerophyllous Woodland - Mature Males

Sampling Code No.		STADIA 6	7	8	9	10	11	12	13	14	15	16	Total
O-N	1					2		1					3
D	2												0
J-F	3					1		1					2
F	4												0
M	5					5	3	9	2				19
M	6				5	43	33	27	13	1			122
A	7				1	42	25	14	6	1			89
M	8					15	8	10	1	1			35
M	9				1	20	10	10	3				44
J	10				1	5	4	5	3				18
J	11					8	1						9
A-S	12								1				1
O	13												0
N	14					1	1						2
D	15												0
J	16												0
TOTALS					8	142	85	77	29	3			344

APPENDIX TABLE 4.4(e)

Pitfall Trapping

Sclerophyllous Woodland - Intercalary Males

Sampling Code No.		STADIA											
		6	7	8	9	10	11	12	13	14	15	16	Total
O-N	1					5	7	1					13
D	2					1	1		1				3
J-F	3				1		1						2
F	4												0
M	5												0
M	6												0
A	7												0
M	8												0
M	9												0
J	10												0
J	11												0
A-S	12												0
O	13						2	1					3
N	14					2	2						4
D	15												0
J	16												0
TOTALS					1	8	13	2	1				25

APPENDIX TABLE 4.5(a)

Litter Sampling

Open Grassland - Females

Date	STADIA										
	6	7	8	9	10	11	12	13	14	15	Total
11/9/74			14	55	3	1					73
11/10/74		1	18	175	40	3	1				238
11/11/74	2			64	103	6	1	1			177
11/12/74	2	1		17	92	13					125
11/1/75	10	15		8	117	11					161
11/2/75		3			11	3	1	1			19
11/3/75			1		21	44	2	1			69
11/4/75		6	28	4	48	83	1				170
12/5/75		5	39	2	25	43	2				116
11/6/75			2		7	10	2				21
11/7/75			1		3	4					8
11/8/75			2			3					5
11/9/75			5	8	1	7	1				22
11/10/75				8	1	14	6				29
11/11/75	58			2	11	12	12				95
TOTAL	72	31	110	343	483	257	29	3			1328

APPENDIX TABLE 4.5(b)

Litter Sampling

Open Grassland - Males

Date	STADIA										
	6	7	8	9	10	11	12	13	14	15	Total
11/9/74		2	27	26	2						57
11/10/74	1		32	153	7	1					194
11/11/74	5		1	111	37	1					155
11/12/74	1	3	2	18	50	1					75
11/1/75	2	14	2	13	79	3					113
11/2/75		2	1	1	8	1					13
11/3/75		-			17	11					28
11/4/75		7	19	4	72	33	2				137
12/5/75		12	30	6	59	37	1				145
11/6/75					34	17	1				52
11/7/75			1	2	18	6					27
11/8/75			2		16	4					22
11/9/75			8	9	2	6					25
11/10/75	1		1	11	1	13	2				29
11/11/75	59			5	4	19	6				93
TOTAL	69	40	126	359	406	153	12				1165

APPENDIX TABLE 4.5(c)

Litter Sampling

Open Grassland - Juvenile Males

Date	STADIA										
	6	7	8	9	10	11	12	13	14	15	Total
11/9/74		2	27	26	1						56
11/10/74	1		32	152	5						190
11/11/74	5		1	110	36						152
11/12/74	1	3	2	18	49	1					74
11/1/75	2	14	2	13	71	1					103
11/2/75		2	1	1	6						10
11/3/75					2						2
11/4/75		7	19	1	7	1					35
12/5/75		12	29	2		3					46
11/6/75											0
11/7/75			1	1							2
11/8/75			2		1						3
11/9/75			8	8	1	3					20
11/10/75	1		1	11	1	9					24
11/11/75	59			5	3	6					73
TOTAL	69	40	125	348	183	24					789

APPENDIX TABLE 4.5(d)

Litter Sampling

Open Grassland - Mature Males

Date	STADIA										
	6	7	8	9	10	11	12	13	14	15	Total
11/9/74					1						1
11/10/74											0
11/11/74											0
11/12/74					1						1
11/1/75					8	1					9
11/2/75					2	1					3
11/3/75					15	11					26
11/4/75				3	65	32	2				102
12/5/75			1	4	59	34	1				99
11/6/75					34	17	1				52
11/7/75				1	18	6					25
11/8/75					15	4					19
11/9/75				1	1	3					5
11/10/75											0
11/11/75					1						1
TOTAL			1	9	220	109	4				343

APPENDIX TABLE 4.5(e)

Litter Sampling

Open Grassland - Intercalary Males

Date	STADIA										
	6	7	8	9	10	11	12	13	14	15	Total
11/9/74											0
11/10/74				1	2	1					4
11/11/74				1	1	1					3
11/12/74											0
11/1/75						1					1
11/2/75											0
11/3/75											0
11/4/75											0
12/5/75											0
11/6/75											0
11/7/75											0
11/8/75											0
11/9/75											0
11/10/75						4	2				6
11/11/75						13	6				19
TOTAL				2	3	20	8				33

APPENDIX TABLE 4.6(a)

Litter Sampling

Sclerophyllous Woodland - Females

Date	STADIA											
	6	7	8	9	10	11	12	13	14	15	16	Total
9/9/74		3	41	29	4	8	3	1	1			90
9/10/74	1	1	42	34	12	13	10	3				116
9/11/74	2		2	45	23	9	6	2	1			90
9/12/74	3	2		27	21	9	6	4	1			73
9/1/75	4	4		12	17	3		2				42
9/2/75						1	1					2
9/3/75					1	2	3	4	1			11
9/4/75	1	8	6	6	91	79	14	5	1			211
11/5/75		1	12	4	33	37	5	1	1	1		95
9/6/75		2	17	1	54	55	8	3				140
9/7/75		3	4	1	14	27	11	3	1			64
10/8/75		1	13		14	19	6		1			54
9/9/75			4	10	3	5	6					28
9/10/75			16	16	10	44	21					107
10/11/75				25	19	36	21	3	1			105
TOTAL	11	25	157	210	316	347	121	31	9	1		1228

APPENDIX TABLE 4.6(b)

Litter Sampling

Sclerophyllous Woodland - Males

Date	STADIA											
	6	7	8	9	10	11	12	13	14	15	16	Total
9/9/74	1	3	50	7	1							62
9/10/74			58	22	3	2						85
9/11/74	3		2	36	3	1						45
9/12/74		1	2	31	7	1						42
9/1/75		4		22	1	1						28
9/2/75		1										1
9/3/75												0
9/4/75	1	6	2	9	82	33	1					134
11/5/75		3	10	11	76	30	1					131
9/6/75		9	8	4	47	14	1					83
9/7/75		2	3	1	33	11						50
10/8/75		2	6		25	7	1					41
9/9/75			10	5	3	4						22
9/10/75			5	21	8	14	6					54
10/11/75		1	3	38	8	15	2					67
TOTAL	5	32	159	207	297	133	12					845

APPENDIX TABLE 4.6(c)

Litter Sampling

Sclerophyllous Woodland - Juvenile Males

Date	STADIA											
	6	7	8	9	10	11	12	13	14	15	16	Total
9/9/74	1	3	50	6	1							61
9/10/74			58	22	3	2						85
9/11/74	3		2	36	2							43
9/12/74		1	2	31	7							41
9/1/75		4		22	1							27
9/2/75		1										1
9/3/75												0
9/4/75	1	6	2	6	19	1						35
11/5/75		3	10	9	12	3						37
9/6/75		9	8	2	9	1						29
9/7/75		2	3		6							11
10/8/75		2	6		1							9
9/9/75			10	5								15
9/10/75			5	21	7	5						38
10/11/75		1	3	38	8	1						51
TOTAL	5	32	159	198	76	13						483

APPENDIX TABLE 4.6(d)

Litter Sampling

Sclerophyllous Woodland - Mature Males

Date	STADIA											
	6	7	8	9	10	11	12	13	14	15	16	Total
9/9/74				1								1
9/10/74												0
9/11/74												0
9/12/74												0
9/1/75												0
9/2/75												0
9/3/75												0
9/4/75				3	63	32	1					99
11/5/75				2	64	27	1					94
9/6/75				2	38	13	1					54
9/7/75				1	27	11						39
10/8/75					24	7	1					32
9/9/75					3	1						4
9/10/75												0
10/11/75												0
TOTAL				9	219	91	4					323

APPENDIX TABLE 4.6(e)

Litter Sampling

Sclerophyllous Woodland - Intercalary Males

Date	STADIA											
	6	7	8	9	10	11	12	13	14	15	16	Total
9/9/74												0
9/10/74					1	1						2
9/11/74												0
9/12/74						1						1
9/1/75						1						1
9/2/75												0
9/3/75												0
9/4/75												0
11/5/75												0
9/6/75												0
9/7/75												0
10/8/75												0
9/9/75						3						3
9/10/75					1	9	6					16
10/11/75						14	2					16
TOTAL					2	29	8					39

APPENDIX TABLE 4.7(a)

Pitfall Trapping

Date	Average Numbers/Trap		Date	Average Numbers/Trap	
	Grassland	Woodland		Grassland	Woodland
27-28/10/72	0.500	0.357	13-14/2/73	0.063	0.281
20-29	0.417	0.929	14-15	0.125	0.125
29-30	0.500	0.393			
30-31	8.417	0.929	5-6/3/73	0.625	0.125
31-1/11	5.000	0.571	6-7	0.563	0.375
1-2	7.250	1.321	7-8	1.000	4.719
2-3	2.583	0.536	8-9	1.438	1.281
3-4	9.750	1.250	9-10	1.813	0.750
4-5	3.167	0.429	10-11	3.500	0.281
5-6	2.583	0.214	11-12	1.750	0.750
6-7	1.500	0.179			
			18-19/3/73	2.688	7.188
11-12/12/72	4.938	0.000	19-20	4.375	2.000
12-13	2.125	0.031	20-21	4.500	2.125
13-14	7.250	0.031			
14-15	5.688	0.000	9-10/4/73	4.875	0.094
15-16	2.813	0.000	10-11	2.750	0.125
16-17	0.667	0.094	11-12	4.438	0.031
17-18	7.200	1.406	12-13	2.875	0.156
			13-14	3.063	0.094
29/1/-30/1/73	-	0.318	14-15	9.063	1.656
30-31	2.500	0.844	15-16	75.375	3.781
31-1/2/73	3.125	0.313			
1-2	3.188	0.406	3-4/5/73	5.625	0.813
2-3	1.063	0.250	4-5	6.625	1.125
3-4	0.563	0.594	5-6	6.000	0.594
4-5	0.938	0.875			

APPENDIX TABLE 4.7(b)

Pitfall Trapping

Date	Average Numbers/Trap		Date	Average Numbers/Trap	
	Grassland	Woodland		Grassland	Woodland
14-15/5/73	12.625	1.406	31/8-1/9/73	0.438	0.313
15-16	11.813	0.500	1-2	2.571	0.276
16-17	12.563	0.531	2-3	3.214	0.094
17-18	7.500	0.188			
18-19	6.688	0.156	1-2/10/73	1.313	0.219
19-20	4.875	0.219	2-3	4.188	0.344
20-21	6.000	0.313	3-4	6.313	0.156
			4-5	4.875	0.125
18-19/6/73	4.625	0.125	5-6	2.563	0.656
19-20	5.563	0.219	6-7	4.313	0.313
20-21	10.125	0.531	7-8	6.000	0.438
21-22	4.438	0.219			
22-23	6.000	0.344	5-6/11/73	1.813	0.406
23-24	4.813	0.344	6-7	4.125	0.250
24-25	4.000	0.313	7-8	5.938	0.406
			8-9	7.875	0.313
23-24/7/73	2.125	0.156	9-10	3.125	0.250
24-25	2.938	0.281	10-11	3.500	0.250
25-26	2.214	0.188	11-12	4.000	1.375
26-27	1.267	0.063			
27-28	0.750	0.063	10-11/12/73	2.250	0.406
28-29	1.625	0.000	11-12	2.375	0.156
29-30	2.000	0.156	12-13	3.063	0.125
27/8-28/8/73	0.125	0.344	14-15/1/74	11.875	0.063
28-29	0.625	0.063	15-16	14.875	0.406
29-30	0.750	0.063	16-17	13.813	0.031
30-31	0.313	0.063			

APPENDIX TABLE 4.8

Numbers of O. moreletii taken in pitfall traps in the grassland/Numbers of O. moreletii collected in samples of pasture grass at the same time.

	STADIUM									
	6	7	8	9	10	11	12	13	14	15
Total										
Mar. 73	0.17	0.69			6.90	9.53	31.00	∞		
Apr. 73			7.83	8.00	20.76	22.96	29.80	33.00	∞	
Jul. 73			0.13	1.75	2.08	3.61	2.56	4.00		
Nov. 73	0.29	0.10		0.48	1.74	2.88	3.40			
Jan. 74	0.60	1.53	5.16		6.33	41.00	37.00	20.00		
Females										
Mar. 73	0.22	0.67			58.00	18.67	24.00			
Apr. 73			27.00		43.25	20.69	34.00	45.00	∞	
Jul. 73			0.10		1.60	3.41	1.71			
Nov. 73	0.30	0.00		0.43	2.05	2.08	4.86			
Jan. 74	0.86	1.55	6.15		8.00	∞	31.00	19.00		
Males										
Mar. 73		0.71			4.35	3.44				
Apr. 73			4.00	8.00	18.03	25.64	27.00	21.00		
Jul. 73					2.41	4.17	5.50			
Nov. 73	0.28	0.21		0.50	1.10	3.57	2.13			
Jan. 74	0.42	1.52	4.08							
Juv. Males										
Mar. 73										
Apr. 73			2.80							
Jul. 73										
Nov. 73	0.28	0.21		0.50	0.6					
Jan. 74	0.42	1.52	4.08							
Mat. Males										
Mar. 73					4.30	3.44				
Apr. 73					17.88	25.55	27.00	21.00		
Jul. 73					2.52	4.17	5.50			
Nov. 73										
Jan. 74										

APPENDIX TABLE 4.9

Soil and Litter Sampling

Open Grassland

Tussocks of L. fibrata
Data in Table 4.4(a) corrected to numbers of O. moreletii per 0.1m² of tussock on each sampling occasion.

		STADIA																
		E	P	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	Total
N	1						1	6	2		3	77	31	8	3	1				132
D	2						6	52	85	2	8	364	290	35	7	1				850
D	3						3	69	342	17	3	222	145	11	3					815
F	4						8	70	107	20	1	91	57	5		1				360
M	5							10	38	29	3	2	17	4	1					104
A	6	*							2	18	8	3	23	10	4	1	1			70
M	7	*	*	*					3	30	34	9	41	15	3					135
J	8	*	*	*						30	65	12	28	9	2					146
A	9	*	*	*	*	2	3	2		10	68	23	33	10	2	1				154
S	10				*	3	10	2	2	1	12	16	38	14	6	1				105
O	11					5	30	48	3		2	7	4	6	5					110
N	12						18	98	34			6	8	17	2	1				184
J	13							29	466	1163	56	27	17	13	11	5	1			1788
F	14							4	87	806	106	25	8	9	3	1				1049
M	15								5	98	432	50	12	9	10	3	1			620
A	16	*							1	91	384	43	13	5	3	4	1			545
O	17						10	28	7	9	50	7								111
J	18							3	33	34	3	428	374	29	2	1				907
M	19	*	*	*					1	7	14	6	47	16	2					93
O	20							1			1	2	5	12	3					24

APPENDIX TABLE 5.1

Results of Probit Analysis as reported in Section 5.4, Experiment 3.

O. moreletii males

x	n	r	p (c = .075)	Emp. Prob.
0	80	6	0	
1	160	34	.148	3.96
2	160	67	.372	4.67
3	120	65	.505	5.01
4	120	90	.730	5.61
5	80	78	.973	6.93
6	40	40	1.000	

O. moreletii females

x	n	r	p (c = .041)	Emp. Prob.
0	80	5	} 0	
1	160	3		
2	160	29	.146	3.95
3	240	157	.639	5.36
4	200	182	.906	6.32
5	80	78	.974	6.94
6	40	40	1.000	

Where; x = duration of exposure, n = number of millipedes in each treatment, r = number that died, p = proportion dead (corrected by Abbott's formula), Emp. Prob. = Empirical Probit.

APPENDIX TABLE 5.2

% Water Contents of *O. moreletii*

Collected at Bridgewater.

($\bar{x}$ ± S.E.) (N)

Dates	Males		Females	
	Grassland	Woodland	Grassland	Woodland
24/10/74	67.6 ± 0.6 (50)	68.8 ± 0.6 (28)	68.9 ± 0.7 (50)	71.2 ± 0.5 (50)
24/11/74	70.0 ± 0.7 (47)	74.4 ± 0.9 (23)	72.3 ± 0.9 (50)	71.4 ± 0.9 (48)
24/12/74	66.8 ± 0.4 (50)	73.6 ± 0.5 (5)	69.0 ± 0.5 (50)	74.2 ± 1.5 (19)
24/1/75	66.0 ± 0.5 (37)	70.2 ± 0.8 (12)	69.9 ± 0.7 (50)	72.4 ± 0.6 (37)
26/2/75	68.2 ± 0.7 (40)		71.9 ± 0.6 (50)	
24/3/75	65.6 ± 0.4 (49)	66.7 ± 0.5 (49)	66.7 ± 0.5 (50)	70.7 ± 0.4 (50)
24/4/75	63.8 ± 0.3 (50)	66.7 ± 0.4 (50)	65.1 ± 0.5 (50)	69.6 ± 0.5 (50)
26/5/75	62.7 ± 0.3 (50)	63.7 ± 0.4 (43)	66.1 ± 0.4 (49)	66.7 ± 0.4 (50)
24/6/75	61.7 ± 0.3 (49)	64.1 ± 0.3 (49)	67.3 ± 0.4 (50)	68.0 ± 0.3 (50)
25/7/75	60.3 ± 0.3 (50)	62.7 ± 0.3 (50)	65.8 ± 0.3 (50)	67.6 ± 0.4 (50)
25/8/75	61.9 ± 0.5 (50)	61.2 ± 0.5 (46)	69.3 ± 0.8 (39)	66.2 ± 0.5 (50)
24/9/75	67.1 ± 0.8 (33)	70.4 ± 1.1 (16)	71.8 ± 0.6 (50)	73.1 ± 0.7 (50)
24/10/75	64.6 ± 0.7 (34)	66.6 ± 0.7 (27)	67.0 ± 0.6 (49)	69.5 ± 0.6 (50)

APPENDIX TABLE 5.3

Dry Weights (gms) of *O. moreletii*
Collected at Bridgewater ($\bar{x}$ (S.E.))

Dates	Males		Females	
	Grassland	Woodland	Grassland	Woodland
24/10/74	.026 (.001)	.029 (.002)	.038 (.002)	.054 (.003)
24/11/74	.027 (.001)	.021 (.002)	.043 (.003)	.054 (.004)
24/12/74	.030 (.001)	.024 (.002)	.048 (.003)	.038 (.004)
24/1/75	.036 (.001)	.030 (.002)	.051 (.002)	.046 (.002)
26/2/75	.031 (.001)		.049 (.002)	
24/3/75	.035 (.001)	.038 (.001)	.068 (.003)	.066 (.003)
24/4/75	.039 (.001)	.038 (.001)	.066 (.002)	.069 (.003)
26/5/75	.040 (.001)	.041 (.001)	.068 (.002)	.081 (.004)
24/6/75	.040 (.001)	.040 (.001)	.063 (.002)	.075 (.004)
25/7/75	.043 (.001)	.044 (.001)	.067 (.002)	.088 (.003)
25/8/75	.042 (.001)	.047 (.002)	.055 (.003)	.087 (.003)
24/9/75	.036 (.002)	.034 (.003)	.057 (.002)	.062 (.004)
24/10/75	.047 (.002)	.043 (.002)	.074 (.003)	.070 (.003)

APPENDIX TABLE 5.4

Dry weights (gms) of *O. moreletii*
Collected at Bridgewater ($\bar{x} \pm$ S.E.)

	May, 1975	June, 1975	July, 1975
Pasture Grass			
♂	.032 (.001)	.030 (.001)	.033 (.001)
♀	.049 (.001)	.047 (.001)	.050 (.001)
Sclerophyllous Woodland			
♂	.033 (.001)	.030 (.002)	.033 (.001)
♀	.051 (.002)	.051 (.001)	.061 (.002)

APPENDIX TABLE 6.1

Results of Probit Analysis as reported in

Section 6.3, Experiment 2.

O. moreletii males

x	n	r	p (c = .038)	Emp. Prob.
0	120	5	} 0	
2	120	4		
4	120	35	.264	4.37
6	120	27	.194	4.14
8	120	50	.394	4.73
10	120	77	.628	5.33
12	120	74	.602	5.26
14	120	106	.878	6.17

O. moreletii females

x	n	r	p (c = 0)	Emp. Prob.
0	120	0	0	
2	120	4	.033	3.16
4	120	15	.125	3.85
6	120	45	.375	4.68
8	120	64	.533	5.08
10	120	77	.642	5.36
12	120	89	.742	5.65
14	120	97	.808	5.87

Where; x = duration of exposure, n = number of millipedes in each treatment, r = number that died, p = proportion dead (corrected by Abbott's formula), Emp. Prob. = Empirical Probit.

9. BIBLIOGRAPHY

ANDREWARTHA, H.G. and BIRCH, L.C. (1954). "The Distribution and Abundance of Animals".
Univ. Chicago Press, Chicago.

ATTEMS, C. (1933). Voyage de MM. L. Chopard et A. Méquignon aux Açores Myriapodes.
Annls. Soc. ent. Fr. 102: 23-4.

BALDWIN, W.F. (1954). Acclimation and lethal high temperatures for a parasitic insect.
Can. J. Zool. 32: 157-71.

BAKER, A.N. (1974). Some aspects of the economic importance of millipedes.
Symp. zool. Soc. Lond. No. 32: 621-8.

BANERJEE, B. (1967a). Diurnal and seasonal variations in the activity of the millipedes Cylindoiulus punctatus (Leach), Tachypodoiulus niger (Leach) and Polydesmus angustus Latzel.
Oikos 18: 141-4.

BANERJEE, B. (1967b). Seasonal changes in the distribution of the millipede Cylindroiulus punctatus (Leach) in decaying logs and soil.
J. Anim. Ecol. 36: 171-7.

BANERJEE, B. (1970a). A mathematical model on sampling diplopods using pitfall traps.
Oecologia 4: 102-5.

BANERJEE, B. (1970b). Effects of unmixed and mixed leaf litter of three species of plants on the development and growth of Polydesmus angustus Latzel.
Experientia 36: 1403-4.

BARLOW, C.A. (1957). A factorial analysis of distribution in three species of diplopods.
Tijdschr. Ent. 100: 349-426.

BARLOW, C.A. (1958). Distribution and seasonal activity in three species of diplopods.
Archs néerl. Zool. 13: 108-33.

BLOWER, J.G. (1969). Age-structures of millipede populations in relation to activity and dispersion.
Syst. Ass. Publs. No. 8: 209-16.

BLOWER, J.G. (1970). The millipedes of a Cheshire wood.
J. Zool., Lond. 160: 455-96.

BLOWER, J.G. (1974) (ed.) Myriapoda.
Symp. zool. Soc. Lond. No. 32: 524 pp.

BLOWER, J.G. and FAIRHURST, C.P. (1968). Notes on the life-history and ecology of Tachypodoiulus niger (Diplopoda, Iulidae) in Britain.
J. Zool., Lond. 156: 257-71.

BLOWER, J.G. and GABBUTT, P.D. (1964). Studies on the millipedes of a Devon oak wood.
Proc. zool. Soc. Lond. 143: 143-76.

BLOWER, J.G. and MILLER, P.F. (1974). The life-cycle and ecology of Ophyiulus pilosus (Newport) in Britain.
Symp. zool. Soc. Lond. No. 32: 503-25.

BRADE-BIRKS, S.G. (1922). Notes on Myriapoda - XXVII. Wandering millipedes.
Ann. Mag. nat. Hist. (9) 9: 208-12.

BRADE-BIRKS, S.G. (1930). Notes on Myriapoda - XXXIII. The economic status of Diplopoda, Chilopoda and their allies. Part II.
Jl S. - east. agric. Coll. Wye No. 27: 103-46.

BRÖLEMANN, H. (1896). Myriapodes provenant des campagnes scientifiques de 1'Hirondelle et de la Princesse Alice.
Bull. Soc. zool. Fr. 21: 198-205.

BROOKES, C.H. (1963). Some aspects of the life histories and ecology of Proteroiulus fuscus (Am Stein) and Isobates varicornis (Koch) with information on other blaniulid millipedes.
Ph.D. Thesis. University of Manchester.

BROOKES, C.H. (1974). The life cycle of Proteroiulus fuscus (Am Stein) and Isobates varicornis (Koch) with notes on the anamorphosis of Blaniulidae.
Symp. zool. Soc. Lond. No. 32: 485-501.

BROOKS, F.E. (1919). A migrating army of millipedes.
J. econ. Ent. 12: 462-4.

BUXTON, P.A. (1932). Terrestrial insects and the humidity of the environment.
Biol. Rev. 7: 275-320.

CALLOWAY, D.H. (1968). Gas in the alimentary canal. In: "Handbook of Physiology". Vol. 5. Section 6. Alimentary Canal. pp 2839-59.
Amer. Physiol. Soc. Wash.

CANTOR, M.O. and REYNOLDS, R.P. (1957). "Gastro-intestinal obstruction".
Williams and Wilkins, Baltimore.

CAUGHLEY, G. (1970). Eruption of ungulate populations, with emphasis on Himalayan thar in New Zealand.
Ecology 51: 53-72.

CAUSEY, N.B. (1943). Studies on the life history and the ecology of the Hothouse millipede, Orthomorpha gracilis (C.L. Koch 1847).
Am. Midl. Nat. 29: 670-82.

CEUCA, T. (1974). Alcuni Diplopodi epigei della fauna di Spagna raccolti dal Dr. Guiseppe Osella.
Mem. Mus. Civ. Stor. Nat. Verona 20: 507-28.

CLOUDSLEY-THOMPSON, J.L. (1949). The significance of migration in Myriapods.
Ann. Mag. nat. Hist. (12) 2: 947-62.

CLOUDSLEY-THOMPSON, J.L. (1950). Economics of the "Spotted Snake-Millipede", Blaniulus guttulatus (Bosc.).
Ann. Mag. nat. Hist. (12) 3: 1047-57.

CLOUDSLEY-THOMPSON, J.L. (1951). On the responses to environmental stimuli, and the sensory physiology of millipedes (Diplopoda).
Proc. zool. Soc. Lond. 121: 253-277.

CLOUDSLEY-THOMPSON, J.L. (1952). The behaviour of centipedes and millipedes 1. Responses to environmental stimuli.
Ann. Mag. nat. Hist. (12) 5: 417-34.

CLOUDSLEY-THOMPSON, J.L. (1954). Problems of dispersal in some terrestrial arthropods.
Advanc. Sci. 11: 73-5.

CLOUDSLEY-THOMPSON, J.L. (1958). "Spiders, scorpions, centipedes and mites".
Pergamon Press, London.

CLOUDSLEY-THOMPSON, J.L. (1959). Studies in diurnal rhythms IX. The water-relations of some nocturnal tropical arthropods.
Entomologia exp. appl. 2: 249-56.

CODY, M.L. (1966). A general theory of clutch size.
Evolution 20: 174-84.

COLE, L.C. (1954). The population consequences of life history phenomena.
Q. Rev. Biol. 29: 103-37.

COTTON, M.J. and MILLER, P.F. (1974). A population of Cylindroiulus latestriatus (Curtis) on sand dunes.
Symp. zool. Soc. Lond. No. 32: 589-602.

CRAWFORD, C.S. (1972). Water relations in a desert millipede Orthoporous ornatus (Girard) (Spirostreptidae).
Comp. Biochem. Physiol. 42A: 521-35.

DEMANGE, J.M. (1970). Myriapodes diplopodes de Madère et des Açores.
Bol. Mus. Munic. Funchal 25: 5-43.

DEMETRIUS, L. (1975). Reproductive strategies and natural selection.
Am. Nat. 109: 243-9.

DEN BOER, P.J. (1968). Spreading of risk and stabilization of animal numbers.
Acta biotheor. 18: 165-94.

DESHMUKH, I.K. (1974). In: Blower, J.G. (ed.)
Symp. zool. Soc. Lond. No. 32: p. 601.

DOWDY, W.W. (1968). An ecological study of some millipedes in two central Missouri communities.
Ann. entomol. Soc. Am. 61: 1059-63.

DUNNING, R.A. (1975). Arthropod pest damage to sugar beet in England and Wales, 1947-74.
Rothamsted Experimental Station Report for 1974, Part 2: 171-85.

DWARAKANATH, S.K. and JOB, S.V. (1965a). Studies on transpiration in millipedes I. Spirostreptus asthenes Poc., from a tropical jungle near Madurai.
Proc. Indian. Acad. Sci. 61: 142-6.

DWARAKANATH, S.K. and JOB, S.V. (1965b). Studies on transpiration in millipedes II. Respiration and water loss in Spirostreptus asthenes.
Proc. Indian. Acad. Sci. 62: 224-8.

EDNEY, E.B. (1951). The evaporation of water from woodlice and the millipede Glomeris.
J. exp. Biol. 28: 91-115.

ELTON, C.S. (1958). "The ecology of invasions by animals and plants".
Methuen, London.

ENGELMANN, F. (1970). "The physiology of insect reproduction".
Pergamon Press, New York.

FAIRHURST, C.P. (1968). Life cycles and activity patterns in schizophylline millipedes.
Ph.D. Thesis. University of Manchester.

FAIRHURST, C.P. (1974). The adaptive significance of variations in the life cycles of schizophylline millipedes.
Symp. zool. Soc. Lond. No. 32: 575-87.

FINNEY, D.J. (1947). "Probit analysis; a statistical treatment of the sigmoid response curve".
University Press, Cambridge.

FRYER, G. (1957). Observations on some African millipedes.
Ann. Mag. nat. Hist. (12) 10: 47-51.

GADGIL, M. and BOSSERT, W.H. (1970). Life historical consequences of natural selection.
Am. Nat. 104: 1-24.

GADGIL, M. and SOLBRIG, O.T. (1972). The concept of r- and K-selection: Evidence from wild flowers and some theoretical considerations.
Am. Nat. 106: 14-31.

GILBERT, L.I. and KING, D.S. (1974). Physiology of growth and development: Endocrine aspects. In: Rockstein, M. (ed.). "The physiology of Insecta".
Academic Press, New York.

GROMYSZ-KALKOWSKA, K. (1967). Minimum, maximum and preferred temperature in Orthomorpha gracilis. C.L. Koch (Diplopoda).
Folia Biol. Krakow 15: 101-15.

HAACKER, U. (1968). Deskriptive, experimentelle und vergleichende Untersuchungen zur Autökologie rhein-mainischer Diplopoden.
Oecologia 1: 87-129.

HAIRSTON, N.G., TINKLE, D.W. and WILBUR, H.M. (1970). Natural selection and the parameters of population growth.
J. Wildl. Mgmt. 34: 681-90.

HALKKA, R. (1958). Life history of Schizophyllum sabulosum (L.) (Diplopoda, Iulidae).
Ann. Zool. Soc. Zool. Bot. Fenn. "Vanamo" 19: 1-72.

KEYS, A., BROŽEK, J., HENSCHEL, A., MICKELSEN, O. and TAYLOR, H.L. (1950). "The biology of Human Starvation".
University of Minnesota Press, Minneapolis.

LAUGHLIN, R. (1965). Capacity for increase: a useful population statistic.
J. Anim. Ecol. 34: 77-91.

LEE, K.E. and WOOD, T.G. (1968). Preliminary studies of the role of Nasutitermes exitiosus (Hill) in the cycling of organic matter in a yellow podzolic soil under dry sclerophyll forest in South Australia.
9th, Intern. Congr. Soil Sc. Trans. 2: 11-18.

LEONARDI, G. (1898). Alcuni Miriapodi del Portogallo.
Atti della Società Veneto-Trentina di Scienze Naturali Ser. II Volume III.

LEWIS, J.G.E. (1971a). The life history and ecology of the millipede Tymbodesmus falcatus (Polydesmida:Gomphodesmidae) in northern Nigeria with notes on Sphenodesmus sheribongensis.
J. Zool., Lond. 164: 551-63.

LEWIS, J.G.E. (1971b). The life history and ecology of three paradoxosomatid millipedes (Diplopoda:Polydesmida) in northern Nigeria.
J. Zool., Lond. 165: 431-52.

LOHMANDER, H. (1955). Die Arthropodenfauna von Madeira nach den Ergebnissen der Reise von Prof. Dr. O. Lundblad Juli - August 1935.
Ark. Zool. 9: 1-65.

MACARTHUR, R.H. (1962). Some generalized theorems of natural selection.
Proc. natn. Acad. Sci. U.S.A. 48: 1893-7.

MACARTHUR, R.H. and WILSON, E.O. (1967). "The theory of island biogeography".
Princeton University Press, Princeton.

MACHADO, A. (1946). Contribuição para o conhecimento dos Miriápodes de Portugal.
Brotéria (Sér. Ciênc. Naturais), Porto 15: (42) (1): 5-37.

MAURIES, J.P. (1964). Sur quelques Diplopodes de la peninsule iberique (2e note).
Bull. Soc. Hist. nat. Toulouse 99: 425-43.

METSCHNIKOFF, E. (1874). Embryologie der doppelfüssigen Myriapoden (Chilognatha).
Z. wiss. Zool. 24: 253-83.

MORSE, M. (1903). Unusual abundance of a Myriapod, Parajulus pennsylvanicus (Brandt).
Science 18: 59-60.

MURDOCH, W.W. (1966a). Aspects of the population dynamics of some marsh Carabidae.
J. Anim. Ecol. 35: 127-56.

MURDOCH, W.W. (1966b). Population stability and life history phenomena.
Am. Nat. 100: 5-11.

MURPHY, G.I. (1968). Pattern in life history and the environment.
Am. Nat. 102: 391-403.

O'NEILL, R.V. (1967). Behaviour of Narceus americanus (Diplopoda) on slopes and its ecological significance.
Am. Midl. Nat. 77: 535-9.

O'NEILL, R.V. (1969a). Adaptive responses to desiccation in the millipede, Narceus americanus (Beauvois).
Am. Midl. Nat. 81: 578-83.

O'NEILL, R.V. (1969b). Comparative desiccation tolerance in seven species of millipedes.
Am. Midl. Nat. 82: 182-7.

O'NEILL, R.V. and REICHLE, D.E. (1970). Urban infestation by the millipede, Oxidus gracilis (Koch).
J. Tenn. Acad. Sci. 45: 114-5.

O'NEILL, R.V. and REICHLE, D.E. (1971). Analysis of a millipede population outbreak.
Oak Ridge National Laboratory Report ORNL - 4634: 50-51.

PEITSALMI, M. (1974). Vertical orientation and aggregations of Proteroiulus fuscus (Am Stein) (Diplopoda, Blaniulidae).
Symp. zool. Soc. Lond. No. 32: 471-83.

PERTTUNEN, V. (1953). Reactions of diplopods to the relative humidity of the air. Investigations on Orthomorpha gracilis, Iulus terrestris and Schizophyllum sabulosum.
Ann. Zool. Soc. Zool. Bot. Fenn. "Vanamo" 16: 1-69.

PERTTUNEN, V. (1955a). The effect of antennectomy on the humidity reactions of normal and desiccated specimens of Schizophyllum sabulosum L. (Diplopoda, Iulidae).
Ann. Ent. Fenn. 21: 157-62.

PERTTUNEN, V. (1955b). The reversal of the humidity reaction at the onset of the egg-laying period in the diplopod Schizophyllum sabulosum.
Arch. Soc. Zool. Bot. Fenn. "Vanamo" Suppl. 9: 231-4.

PFLUGFELDER, O. (1932). Über den Mechanismus der Segmentbildung bei der Embryonalentwicklung und Anamorphose von Platyrrhacus amauros Attems.
Z. wiss. Zool. 140: 650-723.

PIANKA, E.R. (1970). On r- and K-selection.
Am. Nat. 104: 592-7.

PIANKA, E.R. (1972). r and K selection or b and d selection?
Am. Nat. 106: 581-8.

PIERRARD, G. and BIERNAUX, J. (1974). Note à propos des Diplopodes nuisibles aux cultures tempérées et tropicales.
Symp. zool. Soc. Lond. No. 32: 629-43.

RANTALA, M. (1970). Anamorphosis and periodomorphosis of Proteroiulus fuscus (Am Stein) (Diplopoda, Blaniulidae).
Bull. Mus. natn. Hist. nat., Paris (2) 41: Suppl. no. 2: 122-8.

RANTALA, M. (1974). Sex ratio and periodomorphosis of Proteroiulus fuscus (Am Stein) (Diplopoda, Blaniulidae).
Symp. zool. Soc. Lond. No. 32: 463-9.

REDDINGIUS, J. and DEN BOER, P.J. (1970). Simulation experiments illustrating stabilization of animal numbers by spreading of risk.
Oecologia 5: 240-84.

RINEY, T. (1964). The impact of introductions of large herbivores on the tropical environment.
IUCN Publications new series No. 4: 261-73.

ROCKSTEIN, M. and MIQUEL, J. (1973). Aging in insects. In: Rockstein, M. (ed.) "The physiology of Insecta".
Academic Press, New York. 2cnd Edition. Volume I. pp 371-478.

SAHLI, F. (1958). Données sur le développement post-embryonnaire du Diplopode Tachypodoiulus albipes C.L. Koch.
C.r. hebd. Séanc. Acad. Sci., Paris 246: 2037-9.

SAHLI, F. (1961). La succession des différentes formes mâles au cours de la périodomorphose chez le Diplopode Tachypodoiulus albipes C.L. Koch.
C.r. hebd. Séanc. Acad. Sci., Paris 253: 3094-5.

SAHLI, F. (1966). Contribution à l' étude de la périodomorphose et du system neurosecreteur des diplopodes Iulides.
Thèse Sc. Dijon N 94: 226 pp.

SAUDRAY, Y. (1952). Développement post-embryonnaire d'un Iulide indigène Cylindroiulus (Aneuloboiulus) silvarum Meinert.
Archs Zool. exp. gen. 89: 1-14.

SCHAFFER, W.M. (1974). Optimal reproductive effort in fluctuating environments.
Am. Nat. 108: 783-90.

SCUDAMORE, H.H. (1948). Factors influencing molting and the sexual cycles in the crayfish.
Biol. Bull. 95: 229-37.

SHELFORD, V.E. (1913). The reactions of certain animals to gradients of evaporating power of the air. A study in experimental ecology.
Biol. Bull. 25: 79-120.

SMITH, D.F. (1961). The ecology and land use of lower Eyre Peninsula, South Australia.
M.Sc. Thesis, University of Adelaide.

SOKAL, R.R. and ROHLF, F.J. (1969). "Biometry. The principles and practice of statistics in biological research".
W.H. Freeman & Co., San Francisco.

SOUTHWOOD, T.R.E., MAY, R.M., HASSELL, M.P. and CONWAY, G.R. (1974). Ecological strategies and population parameters.
Am. Nat. 108: 791-804.

SPECHT, R.L. (1970). Vegetation In Leeper, G.W. (ed.) "The Australian Environment" Melb. Univ. Press, Melbourne, pp. 44-67.

SPECHT, R.L. (1972). "The Vegetation of South Australia".
Adel. Govt. Pr., Adelaide.

STEPHENSON, J.W. (1961). The biology of Brachydesmus superus (Latz.) Diplopoda.
Ann. Mag. nat. Hist. (13) 3: 311-9.

STEWART, T.C. and WOODRING, J.P. (1973). Anatomical and physiological studies of water balance in the millipedes Pachydesmus crassicutis (Polydesmida) and Orthoporus texicolens (Spirobolida).
Comp. Biochem. Physiol. 44A: 735-50.

SUTTON, S.L. (1968). The population dynamics of Trichoniscus pusillus and Philoscia muscorum (Crustacea, Oniscoidea) in limestone grassland.
J. Anim. Ecol. 37: 425-44.

TINKLE, D.W. and HADLEY, N.F. (1975). Lizard reproductive effort: caloric estimates and comments on its evolution.
Ecology 56: 427-34.

TOYE, S.A. (1966). The reactions of three species of Nigerian millipedes (Spirostreptus assiniensis, Oxydesmus sp., and Habrodesmus falx) to light, humidity and temperature.
Entomologia exp. appl. 9: 468-83.

TOYE, S.A. (1967). Observations on the biology of three species of Nigerian millipedes.
J. Zool., Lond. 152: 67-78.

TOYE, S.A. (1975). The ecology and behaviour of Prepodesmus ornatus Peters and Afolabina yoruba Hoffman (Polydesmida:Prepodesmidae).
Nigerian J. Entomol. 1: 81-110.

TRUMAN, J.W., RIDDIFORD, L.M. and SAFRANEK, L. (1973). Hormonal control of cuticle coloration in the tobacco hornworm, Manduca sexta: basis of an ultrasensitive bioassay for juvenile hormone.
J. Ihsect Physiol. 19: 195-203.

VACHON, M. (1947). Contribution à l'étude de développement post-embryonnaire de Pachybolus ligulatus Voges. Les etapes de la croissance.
Annls Sci. nat. Zool. 9: 109-21.

VAN DER DRIFT, J. (1951). Analysis of the animal community on a beech forest floor.
Tijdschr. Ent. 94: 1-168.

VANNIER, G. (1975). Les trois cas de figure de la relation teneur en eau corporelle-poids sec mis en évidence chez un Insecte Collembole au cours du cycle annuel.
C.r. hebd. Séanc. Acad. Sci., Paris 280: 117-20.

VERHOEFF, K.W. (1892a). Neue Diplopoden der palaarktischen Region.
Zool. Anz. 15: 377-87.

VERHOEFF, K.W. (1892b). Neue Diplopoden der paläarktischen Region.
Zool. Anz. 15: 389-91.

VERHOEFF, K.W. (1893a). Über ein neues Stadium in der Entwicklung von Juliden-Männchen.
Zool. Anz. 16: 20-26.

VERHOEFF, K.W. (1893b). Neue Diplopoden der portugiesischen Fauna.
Zool. Anz. 16: 156-9.

VERHOEFF, K.W. (1894). Beitrage zur Anatomie und Systematik der Juliden.
Verh. zool.-bot. Ges. Wien. 44: 137-62.

VERHOEFF, K.W. (1923a). Periodomorphose.
Zool. Anz. 56: 233-8.

VERHOEFF, K.W. (1923b). Periodomorphose.
Zool. Anz. 56: 241-54.

VERHOEFF, K.W. (1928). Diplopoden. In: Bronn, H.G. (ed.)
Klassen und Ordnungen des Tierreiches 5(2): 1-1072.

VERHOEFF, K.W. (1933). Wachstum und Lebensverlängerung bei Blaniuliden und über die Periodomorphose.
Z. Morph. Ökol. Tiere 27: 732-48.

VERHOEFF, K.W. (1939). Wachstum und Lebensverlängerung bei Blaniuliden und über die Periodomorphose.
Z. Morph. Ökol. Tiere 36: 21-40.

VERHOEFF, K.W. (1940). Uber einige Diplopoden, Chilo- und Isopoden der Insel Ischia.
Zool. Anz. 131: 271-87.

VERHOEFF, K.W. (1943). Zur Kenntnis der Cambaliden und über einige neue australische Formen derselben.
Zool. Anz. 145: 27-45.

VINEGAR, M.B. (1975). Demography of the striped plateau lizard, Scleroporus virgatus.
Ecology 56: 171-82.

WIGGLESWORTH, V.B. (1970). "Insect hormones".
W.H. Freeman & Co., San Francisco.

WILBUR, H.M., TINKLE, D.W. and COLLINS, J.P. (1974). Environmental certainty, tophic level, and resource availability in life history evolution.
Am. Nat. 108: 805-17.

WILLIAMS, C.M. and KAFATOS, F.C. (1972). Theoretical aspects of the action of juvenile hormone. In: Menn, J.J. and Beroza, M. (eds.) "Insect juvenile hormones chemistry and action".
Academic Press, New York. pp 29-41.

WILLIAMS, G.C. (1966). Natural selection, the costs of reproduction and a refinement of Lack's principle.
Am. Nat. 100: 687-92.

WILLIAMS, R.J. (1959). In: Leeper, G.W. (1970) (ed.), "The Australian Environment".
Melb. Univ. Press, Melbourne. Figure 32.

WILLIS, J.H. (1974). Morphogenetic action of insect hormones.
A Rev. Ent. 19: 97-115.

YOUNG, F.N. (1958). A large aggregation of larva millipedes Zinaria butleri (McNeill) in Brown County, Indiana.
Proc. Indiana Acad. Sci. 67: 171-2.