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A B S T R A C T S

HARVESTMEN OF THE SUB-ORDER LANIATORES FROM NEW ZEALAND CAVES. By R.R. Forster. Rec. Otago Mus. Zoology, 2, 1965 : 1 - 18.

This paper on cave-dwelling harvestmen from New Zealand confines itself to the sub-order Laniatores. The sub-order Palpatores and the spiders are to be the subject of later reports by the author. Ten species are recorded, nine of them new to science. Nine are restricted to the South Island, and a further four species noted in the paper, but not described, are also from this region. This indicates that the cave systems of Fiordland and the northwestern part of the South Island support the greatest bulk of New Zealand's true cave-dwelling endemics. Modifications shown by a number of the species include loss of pigment, and the tendency for the legs to become long and slender. An interesting character, apparently related to the modification of the legs, is the increase in the number of tarsal segments for the first two pairs of legs. Much emphasis is placed by specialists on the tarsal formula for the separation of genera in the sub-order Laniatores, and it is of considerable interest to find that this may be influenced so readily by adaptation to a different environment. All of the species recorded are placed in the two widespread New Zealand genera Hendea Roewer and Nuncia Loman. - A.M.R.

RECENT MAMMALIAN SUB-FOSSILS OF THE BASALT PLAINS OF VICTORIA. By N.A. Wakefield. Proc. Roy. Soc. Vict., 77, 1964 : 419 - 425.

This paper covers native mammals of species which have been known as living animals during European occupation of Australia. Details are given of eight Western Victorian sites which have yielded mammalian sub-fossils, and some corrections are made to previously published identifications of specimens. The sub-fossil sites are Tower Hill Beach, Bushfield and Skene Street Cave, all near Warrnambool; Mount Hamilton Lava Caves; Fern Cave, Lower Glenelg area; Byaduk Caves; "Natural Bridge," Mount Eccles; Gisborne Cave; and Swain's Cave, Mount Porndon. A table shows the species represented in each of these deposits and the approximate number of individuals of each species in the respective collections. Evidence is presented which suggests a post-Pleistocene period more arid than the present. Details are given of the virtual disappearance during the past century of the modern mammalian fauna of the basalt plains, particularly as regards members of the Macropodidae and the Muridae. Of the 42 species listed in the table, only 27 are known to survive in Victoria, and less still are known to occur now in the basalt areas. Of the 13 macropodids, no more than the three largest are known to frequent parts of this formation now, and none of the six pseudomid murids is known to survive there. - A.M.R.

MOVEMENTS OF RHAPHIDOPHORIDAE (ORTHOPTERA)

IN CAVES AT WAITOMO, NEW ZEALAND

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Summary

Cavernicolous Rhabdiphoridae are very active insects, in spite of their immobile appearance on the walls of caves. Movement is continuous to a greater or lesser degree throughout the 24 hour period of each day. Through marking a representative sample of the total adult population of two species of Rhabdiphoridae in limestone caves in New Zealand, it was shown that several different types of movement occurred; that home ranges had no well-defined limits; and that there was no evidence of territorial behaviour. The technique of marking Rhabdiphoridae is discussed in some detail.

Introduction

Over the years, experiments have been carried out in many countries by means of marking and recapturing insects. Of interest are the systems of Scott (1931), Swynnerton (1936), and O.W. Richards and Waloff (1954), used for studying large populations. Insects caught on a certain day were all given a similar paint mark in a particular position on the thorax. Recaptures were all marked again in another position, usually with a different coloured paint.

Gangwere, Chavin and Evans (1964) have recently proposed a "notch technique" for marking insects. Here v-shaped notches were cut into the pronotal margins of orthopterous insects. Notches have an advantage over the paint systems mentioned above in that they will persist through several larval ecdyses, as well as the adult stage. Paint was also used to supplement the notches, to facilitate easy recognition of recaptures. This method requires considerable handling of the specimens.

By individually marking, releasing and recapturing representative samples of two species of Rhabdiphoridae (subfamily Macropathinae) in the limestone caves at Waitomo, New Zealand, during 1955, information was obtained on their mating behaviour (A.M. Richards, 1961), distribution and

* This paper is derived from a study carried out while attached to Victoria University of Wellington, New Zealand, during the tenure of a New Zealand University Research Fund Fellowship.

daily movements, and their population fluctuations. For both species paint was used as the marking medium. The "notch technique" is not very practicable for the Saltatoria (grasshoppers, katydids, crickets, etc.) where the hind legs readily become detached from the bodies. Approximately 47% of the adult population of Gymnoplectron waitomoensis Richards in Aranui Cave, and 60% of Pallidoplectron turneri Richards in the Grotto of Waitomo Cave (Glow-worm Cave) were marked for study. Only adult insects were used, to avoid loss of paint spots due to periodic moulting of nymphs.

Marking Technique

Insects were marked on the dorsal surface of the thorax with a number of different coloured paints. In the caves it was very difficult to distinguish between green and blue, and between yellow and white, and these colours had to be intensified. The nitrocellulose lacquer used adhered very well to the chitinous exoskeleton, and was non-lethal to the insects. Aluminium paint was also used, and though it tended to clot, was quite successful. Recoveries from both types of paint were recorded up to four and a half months after marking.

In some cases a single drop of paint was placed on the centre of the pronotum, but with many insects additional spots were placed on the mesonotum and metanotum, allowing for the possibility of different colour combinations. Insulating wire and match sticks proved the most satisfactory instruments for application of the paint. Great care was needed to prevent paint touching the insects' permeable integumental membranes, as, if this happened, death ensued in less than a minute.

Early in 1955, all Gymnoplectron waitomoensis caught in Aranui Cave on any particular day were given the same coloured mark following the systems of Scott, Swynnerton, and O.W. Richards and Waloff. However, this method did not yield sufficient information at Waitomo, due to the comparatively small populations. Later, the insects were marked with additional individual colours and different colour combinations for specific identification, males and females being marked in pairs. This permitted compilation of more detailed and accurate information on their behaviour and movements.

In the Grotto of Waitomo Cave (Figure 1), the first 22 metres along the west wall of the Tunnel and the wall outside were divided into seven 3.7-metre quadrats, quadrat seven being farthest from the entrance, and quadrat one consisting of the wall just outside the cave (Figure 2). All Pallidoplectron turneri in each quadrat were marked with a different colour.

The insects were caught by hand on the walls of the caves, and, after being marked, were released again at the point of capture. Recoveries, and the exact positions where these insects were observed, were recorded on maps of the two cave areas, together with the date and time of sighting. Recoveries were not recaptured or remarked.

LOWER SERIES

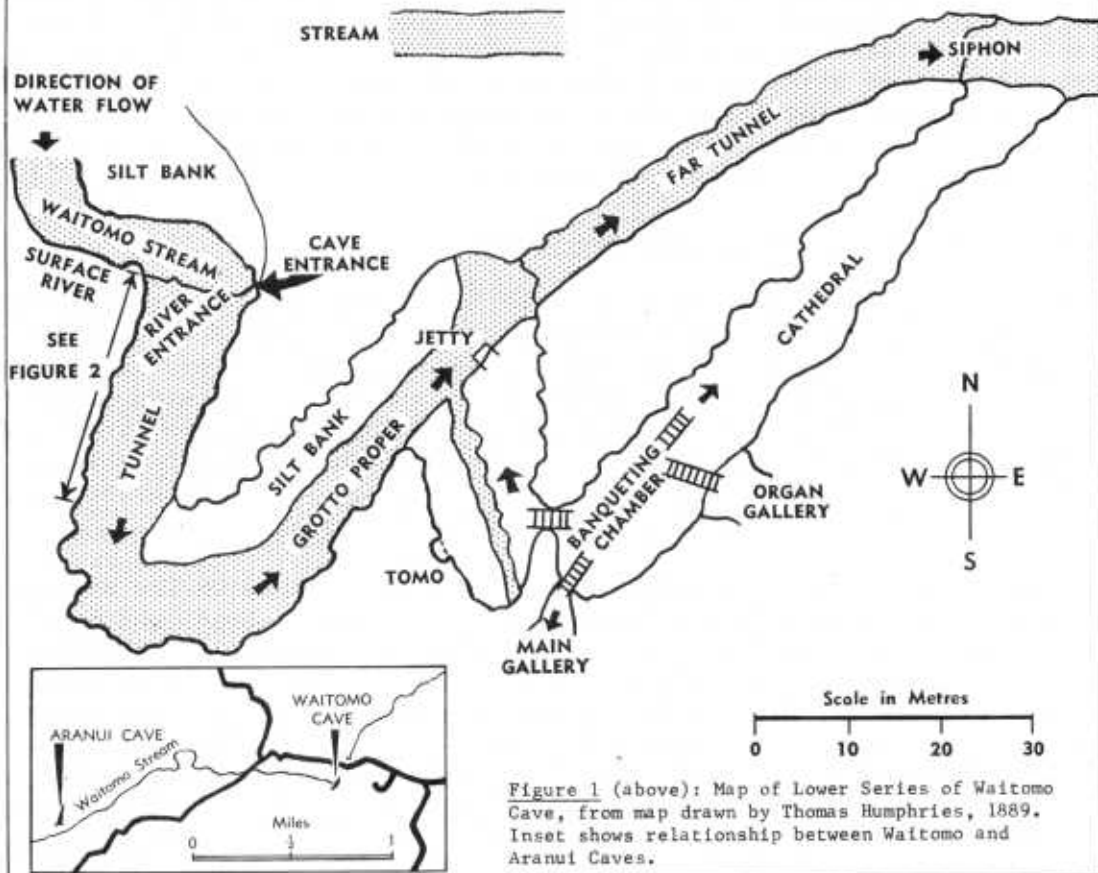


Figure 1 (above): Map of Lower Series of Waitomo Cave, from map drawn by Thomas Humphries, 1889. Inset shows relationship between Waitomo and Aranui Caves.

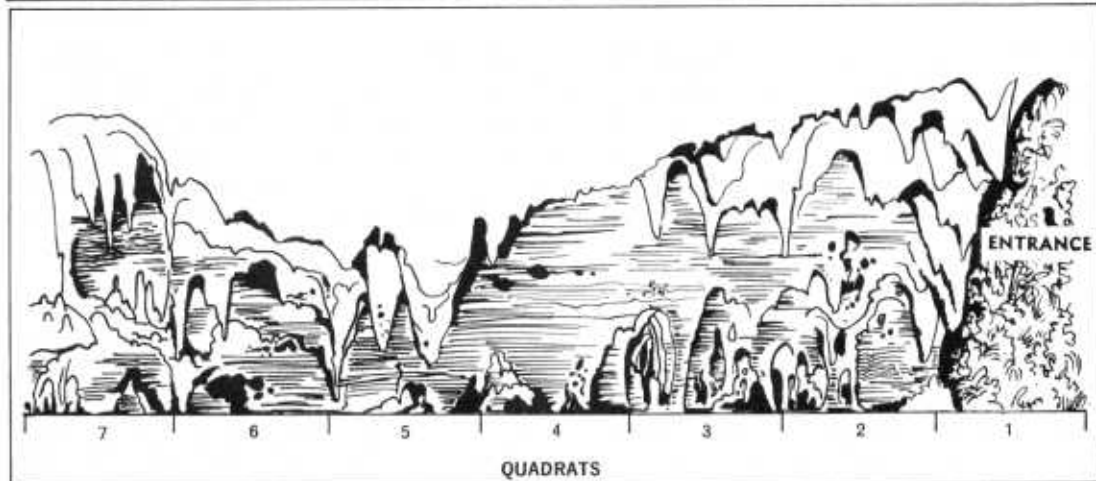


Figure 2: Part of west wall of Tunnel in Grotto, Waitomo Cave, showing seven 3.7-metre quadrats.

Individual marking of Rhabdophorids with different colour combinations of paint proved very successful. It yielded much interesting information which could not be obtained by other methods, and involved little handling of the insects. The daily activities of the insects could thus be observed with minimum disturbance. Admittedly the paint did not last indefinitely, but recoveries were obtained more than four and a half months after marking, allowing sufficient time for a number of observations and experiments to be carried out. It is realised, however, that this method might not be practicable when studying large numbers of insects.

The Environment in and around Waitomo Caves

The Waitomo Caves are found in part of the Te Kuiti limestone belt situated in the King Country, about 130 miles south of Auckland, in the North Island of New Zealand. This whole region is riddled with caves, but the Waitomo Caves are the best known, and have become one of the main tourist attractions of the country. The limestone is Tertiary in origin, and is considered to have been formed in the Oligocene Period, about 40 million years ago. It is estimated that the formation of the caves began about one million years ago (J.H. Richards, 1958; Laird, 1963).

Waitomo Cave consists of four separate caverns, each with its own system of passages. The Waitomo Stream flows through the lowest level which is known as the Grotto. The Grotto can be divided for convenience into four separate areas - the Far Tunnel, the Grotto Proper, the Stalactite Area and the Tunnel (Figure 1). Light from the exterior penetrates into the Grotto for about 21.7 metres along the Tunnel. On a sunny morning in 1955, the light intensity (measured with a Weston Photometer) along the west wall of the Tunnel ranged from 0.5 to 1 foot candle; along the east wall or on the stalactites of that side it varied from 1 to 1.5 f.c.; behind the stalactites it was 0.5 f.c.

The mean temperature in Waitomo Cave was 60.2°F (15.6°C) for summer, 57.4°F (13.7°C) for winter, and 57.1°F (13.7°C) for autumn and spring. As diurnal variation was almost absent, these results show that conditions were relatively stable throughout the year. The relative humidity ranged from 94% to 100%, but was usually 97% (Table 1). (Temperature and relative humidity were measured with an Assmann Psychrometer). (A.M. Richards, 1956 and 1960).

In contrast to Waitomo Cave, Aranui Cave is a simple cave system, consisting essentially of a winding, former river passage. In 1955, the light intensity 15.3 metres inside the cave on a sunny afternoon was 0.5 f.c. on the right wall, but zero on the left wall where most of the Rhabdophorids congregated. The mean temperature in Aranui Cave was 55.5°F (13.0°C) for summer, 55.1°F (12.8°C) for winter, and 54°F (12.2°C) for autumn and spring. The relative humidity ranged from 91% to 97%, and was usually 97%.

TABLE I - Mean Temperature and Relative Humidity Recordings in Grotto, Waitomo Cave, during 1955.

		Temp. °F		Relative
		Wet	Dry	Humidity
				%
Mid-day :	Summer	60	60	100
	Autumn & Spring	57	58	97
	Winter	55	56	97
Midnight :	Summer	59	60	97
	Autumn & Spring	56	57	97
	Winter	55	56	94

Movements

From February to October, 1955, 60 Gymnoplectron waitomoensis out of an estimated population of about 130 adults, were marked in the first 19 metres inside Aranui Cave. Many of the marked insects were not subsequently sighted. For the whole period 24.5% were recovered.

The total adult population of Pallidoplectron turneri in Waitomo Cave was estimated at about 500, the insects being spread throughout the Grotto and its two tunnels to a distance of 123 metres from the river entrance. The P. turneri were all closely associated with the stream, as they were confined to the lower parts of the walls. From February, 1955, to January, 1956, more than 300 of these insects were marked in the seven quadrats on the west wall of the tunnel, and 25.5% recovered.

Throughout the whole period, the total numbers of both species visible remained fairly constant. Obviously movement was taking place continuously, and the total cave populations were really much larger than could be observed on the walls of the two caves at any one time. Many of the insects passed in and out through tiny cracks and fissures in the limestone leading to inaccessible parts of the caves. The infrequency with which some marked individuals were recovered and others never seen again, may be attributed among other things to flaking off of paint, fluctuations in the populations due to movement, or death from marking.

Observations showed that several different types of movement occurred among the Raphidophorids. These movements were all inter-related, and all of equal importance.

1. Gradual Movement

From observing marked G. waitomoensis and P. turneri, small movements within a confined area of 3.7 metres or less, and longer movements of up

to 160 metres were recorded. These movements were either towards the cave entrances, or deeper into the caves and in many cases were spread over a number of days.

Most G. waitomoensis confined themselves to the left wall and the first 19 metres inside Aranui Cave. Many of the crevices and depressions along this wall were often used for shelter. Some G. waitomoensis were always observed within about 30 cm of the same spot (Figure 3). Others repeatedly crossed from one wall to the other, or moved deeper into the cave. The furthest distance recorded in a single move was 44.4 metres (Figure 4), but, on the whole, distances travelled by each insect were small.

In the Grotto of Waitomo Cave, P. turneri were more active, and movements of well over 100 metres were recorded. Because of the shape of the Grotto with its wall indentations and silt banks, the actual distances travelled by some P. turneri were approximately double those measured in straight lines. Some insects repeatedly crossed from one wall to the other, probably by way of the ceiling near the entrance. Here the paucity of glow-worm larvae, Arachnocampa luminosa (Skuse), greatly reduced the danger of P. turneri becoming entangled in the long sticky fishing-lines (A.M. Richards, 1962). Other P. turneri, while feeding on floating debris, were passively carried considerable distances by the current of the Waitomo Stream. In March, 1955, two insects marked in quadrat seven were recovered after three days in quadrat one. Four days later, one was again observed outside the cave, while the other had returned to quadrat five. Nine days after being marked, one was still in quadrat five, while the other had moved a further distance of 16.9 metres inside the cave. Similar cases were observed on a number of occasions.

Although P. turneri were observed along the whole underground course of the Waitomo Stream, it was not known previously if they formed a single population, or a number of discrete units. Three insects were marked on the east wall of the Far Tunnel. Six days later one of these insects was recovered on the east wall of the Tunnel, 12 metres from the silt bank outside the river entrance. Two days after this, another was recovered on the same wall 3.7 metres from the entrance. Measured in straight lines, they had travelled 107.4 and 116 metres respectively. Allowing for the shape of the Grotto, these distances were approximately 150 and 160 metres from where last seen. They were the longest movements recorded for any Raphidio-phorid. This indicated that all the P. turneri belonged to one population.

2. Movements Due to Changing Light Intensity

At night a variable number of P. turneri always emerged from the river entrance to Waitomo Cave. A number of these insects were marked to study their movements. Of 46 insects marked 19 metres inside the cave, six were observed later outside on the moss and bryophyte. Of a further ten marked outside the cave, five were recovered 2 metres, and two more 6.2 metres

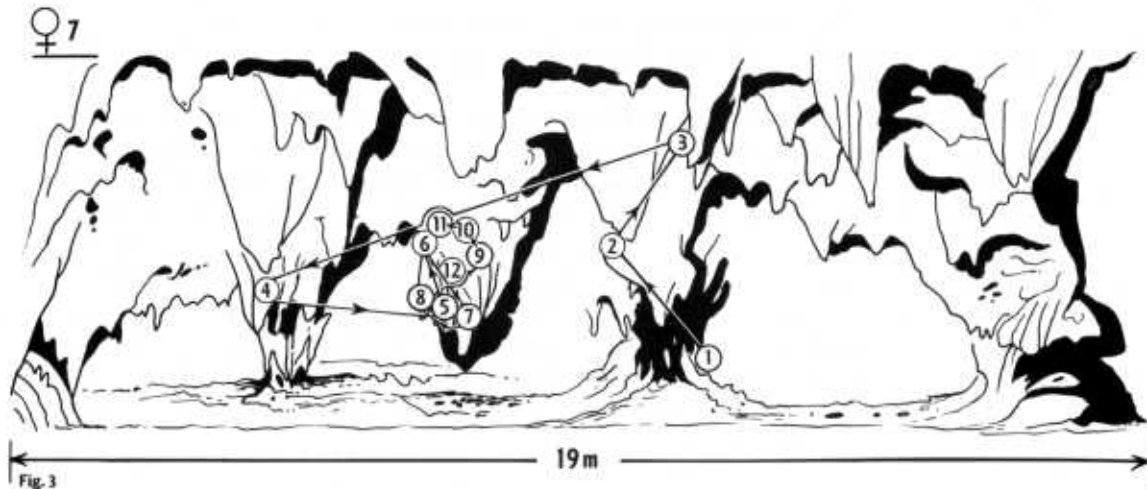


Fig. 3

Figure 3: Movements over left wall inside Aranui Cave of female *Gymnoplectron waitomense*. May to July, 1955. All observations were made between 2 - 4 p. m.

1. May 23. 2. May 24. 3. May 27. 4. May 31. 5. June 2. 6. June 4.
7. June 5. 8. June 6. 9. June 16. 10. June 18. 11. June 23. 12. July 3.

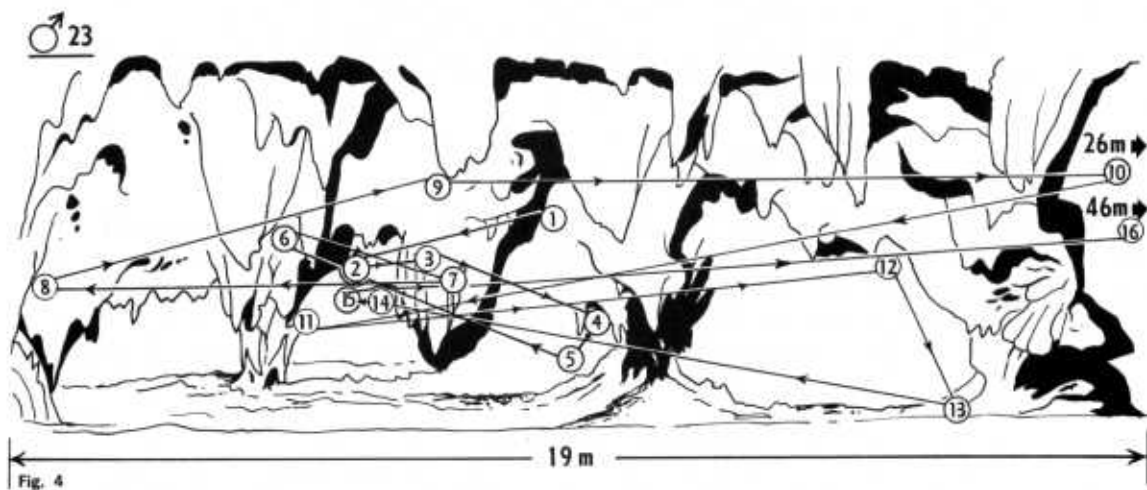


Fig. 4

Figure 4: Movements over both walls inside Aranui Cave of male *Gymnoplectron waitomense*. May to June, 1955. Station 15 is on right wall, all other stations on left wall. All observations except Nos. 8 and 15 were made between 2 - 4 p. m. No 8 was made between 9 - 10 p. m. and 16 between 10 - 11 a. m.

1. May 17. 2. May 18. 3. May 20. 4. May 23. 5. May 24. 6. May 26.
7. May 27. 8. May 27. 9. May 31. 10. June 2. 11. June 4. 12. June 5.
13. June 10. 14. June 18. 15. June 15. 16. June 21.

inside the entrance. This showed general movement of the population both towards the entrance, and back inside the cave.

From further observations on 300 marked insects, a definite behaviour pattern developed. Shortly before sunset the Rhabdiphorids commenced moving towards the cave entrance, and by an hour after sunset up to 110 to 160 insects could be observed outside if weather conditions were favourable. This was approximately 22% of the total adult population. If weather conditions were unfavourable, the largest aggregation was about four metres inside the entrance. By two and a half hours after sunset, most of the insects had returned inside, but in the preceding two hours period there was a steady stream of insects moving towards the entrance, and another stream returning. In most cases the insects outside rested on the walls without showing any signs of activity.

Similar behaviour was observed with a population of G. waitomoensis near the main entrance to Waitomo Cave, but no insects were observed outside Aranui Cave.

Thus rapidly changing light intensity initiated the development of a locomotor activity rhythm, and during this period there was noticeable movement towards cave entrances (A.M. Richards, in press). Moonlight and daylight raised the light intensity above the optimum tolerance of the insects, causing a marked decrease in their numbers and activity near cave entrances.

3. Movement in a Confined Area

By marking the P. turneri in each quadrat of Waitomo Cave a different colour, it was observed that on a number of occasions insects remained in the same quadrat for several days. Of particular interest was a group of 45 insects which stayed for 14 days in an embayment 21 metres from the entrance. Only a very limited food supply was available to them throughout this period.

As it is not necessary for insects to feed each day, there may be periods when Rhabdiphorids do not need to forage. Each night circadian rhythm effected about one third of the P. turneri population, but how frequently individual insects were effected is not known. The urge to oviposit would not explain this behaviour amongst certain females, because few eggs were laid on the west wall of the tunnel, and then only in areas outside the quadrats.

The G. waitomoensis in Aranui Cave were most frequently recovered round the second stalactite area, about 8 metres inside the entrance (Figure 3). This particularly applied to females, and in this case can be explained by the close proximity of the oviposition site. A plentiful food supply occurred throughout the entrance chamber. Round the electric lights

mosses and ferns had taken root, and among these plants, as well as in the crevices of the limestone walls, lived small spiders, mites and collembola. Basidiomycetes also grew on the duckboards. This food supplemented by cannibalism, made it unnecessary for the G. waitomoensis to forage over any great distance.

With both species there was no evidence of movement away from and back to the same area during the period the insects were under observation. The significance of this limited movement cannot as yet be fully explained.

4. Movements Concerned with Reproduction

With both species of Rhabdiphoridae the meeting of opposite sexes appeared to be entirely random, as the insects moved continuously over the walls of the caves. In Aranui Cave, G. waitomoensis males moved over a much greater area than females (Figure 5). In contrast, both male and female P. turneri moved freely throughout the whole Grotto. Both species were promiscuous in their behaviour, so that constant movement occurred throughout the breeding season.

Movements concerned with the selection of an area of mud in which to oviposit were of a more exacting type. Female G. waitomoensis with fresh mud on their ovipositors were most frequently seen in the second stalactite area on the left wall of Aranui Cave, this being close to the general site selected for oviposition. P. turneri females, however, moved throughout the whole Grotto. Some travelled distances of 43 metres or more from the area where last recorded, to the particular spots selected for oviposition. This greater movement may be attributed in part to the moister conditions in Waitomo Cave, which made more oviposition sites available. With both species the same sites were returned to on numerous occasions.

When a prospective site had been chosen, each female made a number of short, jerky, running movements with its maxillary palps extended anteriorly to explore the surface of the ground. Often many sites were rejected before a suitable one was selected, and the same procedure was repeated each time (A.M. Richards, 1961).

Home Range

Distances between points of recapture of individual adult G. waitomoensis were measured over a six weeks' period from May to July, 1955 (Figure 5). Females formed the least mobile units of the population. Ten females were recaptured a sufficient number of times after adequate intervals, to permit calculation of the greatest width of the home area. This ranged from 1.5 to 10.8 metres, with a mean of 5.5 metres. On the average, males moved about twice as far as females. Home ranges of from 3.25 to 43.4 metres, with a mean of 10.8 metres, were recorded for 16 males. Nymphs from fifth and sixth instars onwards moved in similar directions to the adults. They

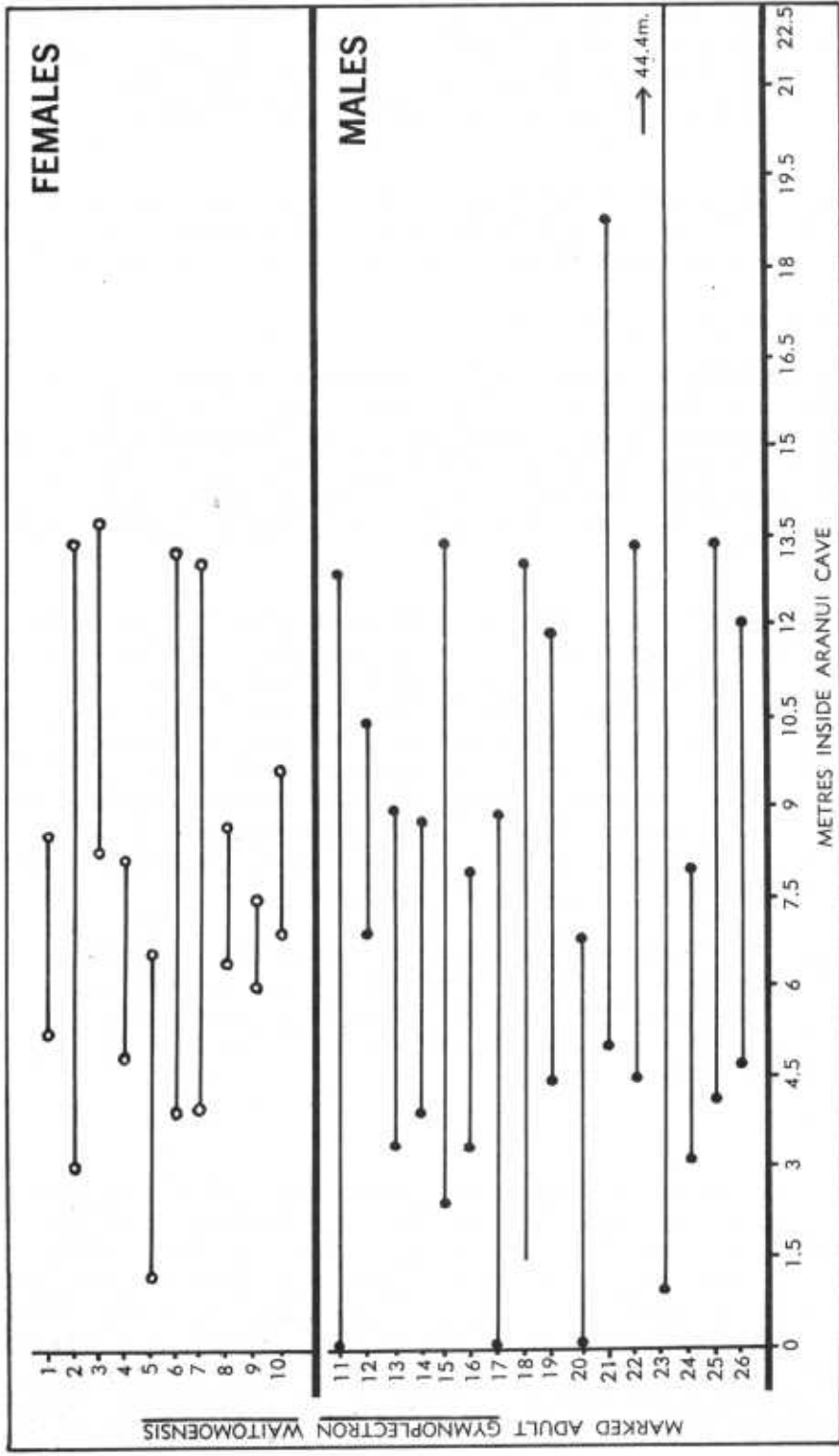


Figure 5: Maximum movements of individually marked *Gymnopletron waitomoensis* in Aranui Cave between May 17 and July 3, 1955.

were well spread out over the first 34 metres inside Aranui Cave, most being observed on the left wall.

Movements suggesting persistent use of an area occurred from within a space of one metre or less (Figure 3) to more than 43 metres (Figure 4). This suggests that home ranges have no well-defined limits, and the insects are influenced as much by food, sex urge, oviposition and environmental conditions as by familiarity with an area. No evidence of territorial behaviour, in the sense of defence of an area of occupancy, was observed.

In Waitomo Cave, male and female P. turneri moved at random throughout the lower regions of the cave, so that it was not possible to estimate which sex was most active. Although part of the cave was divided into seven quadrats, no evidence of development of a homing instinct was recorded. Groups of insects in each quadrat were given a similar mark and their movements recorded. Table 2 shows daily distribution of marked P. turneri within the seven quadrats, out of a total of 150 insects previously marked in these quadrats. It illustrates clearly their random distribution over the wall of the Tunnel.

Discussion

In North America, Nicholas (1962) has recently studied the movements of the Rhabdiphorid Hadenoecus subterraneus (Scudder) (subfamily Ceuthophilinae) in Cathedral Cave, Mammoth Cave National Park, Kentucky. As at Waitomo, the cave was divided into a number of quadrats and the insects in each quadrat distinctively marked. Results from the 12 three-metre quadrats showed that, although one third of the total population from all quadrats left the cave each night to feed, 97% of all marked individuals recaptured were found in their home quadrats during daylight.

Comparable experiments in Waitomo Cave showed that Pallidoplectron turneri moved at random throughout the lower regions of the cave, some travelling considerable distances over several days. At no time was there any evidence of a homing instinct such as described by Nicholas. The author's and Nicholas' observations do agree that each night under favourable conditions about one third of the Rhabdiphorid population left the cave, but P. turneri were never observed to return to the same spot they had left a few hours earlier.

Although Gymnoplectron waitomoensis confined themselves to a much smaller area in Aranui Cave, there was still no evidence of a home range within well defined limits. No quadrats were marked out in this cave because of the limited area occupied by the insects. Individual marking of the insects showed that at certain times of the year G. waitomoensis were more active than at others. Distances travelled in March and April were quite small, but from May onwards there was much more movement over the first 19 metres inside the cave. This variation in activity is possibly associated with the reproductive cycle in this species. No evidence of it was observed with P. turneri.

TABLE 2 - Distribution of Marked Pallidoplectron turneri in Seven Quadrats on West Wall of Tunnel in Grotto, Waitomo Cave, January, 1956.

Quadrat	Total Marked Each Quadrat	Number of Marked Insects					Recovered January		
		15	16	20	21	22	23	24	
7	18 Yellow (Y)	1G	3W	1R	5W	3W	2G	2Y	
		1W	2Y	1G	1R	1Y	2W	3W	
		1Y	2G	2W	1G	1G		2G	
				2P	1Y	1B		1R	
				2Y	2Bk		1P		
6	6 Green (G)	2P	2G	2W	1P	1W	1Y		
		1Y	2P	1G	1R		1R		
			1W	1Y	1W				
			2Bk	2R					
			1B						
5	11 Pink (P)	3P	1Y	1W	1W	1W			
		1Y	1G		1R				
			3Bk		1Y	1Bk			
4	17 Blue (B)	1G	1W	2R	3R	1Y	1W	1Y	
		1R	1G	1Y	1Bk	1R	1P	1W	
		1Bk	1Y	1Bk			1Y		
			1Bk						
3	31 Red (R)	3R	1Y	5Bk	2W	4Y	2W	1Bk	
		1W	1P	1W	2Y	2W	1G	1Y	
		1Bk	1R		2R	1R	1Y		
			2W		1P	2Bk	1Bk		
			1G	5Bk					
2	30 Black (Bk)	1R	3R	1B	3W	1Y	1R		
		1B	4W		1P	1B			
		1Bk	1Bk		2Bk	1Bk			
1	37 White (W)	2W	2W	5W	6W	1P	3W	2W	
		1R	2Y	2B	1R	1G		1B	
		1P	1B	1R	2Bk	1Y		2Bk	
		2Bk	1Bk	1Bk		5W			
						1B			
						1R			
				2Bk					

Differences in the behaviour of North American Ceuthophilinae and New Zealand Macropathinae have already been noted (A.M. Richards, in press), and the presence or absence of a homing instinct is yet another difference. It would be of interest to study the homing behaviour of the European and Asiatic Rhabdophorinae, and to see to which of the other two subfamilies they show affinities.

Acknowledgments

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A B S T R A C T S

- A CAVE IN DOLERITE AT WAYATINAH, TASMANIA. By G.E. Hale and A. Spry. J. Geol. Soc. Aust., XI (2), 1964 : 213 - 216.

A cavity was found within solid Jurassic dolerite during tunneling operations for the Wayatinah hydro power scheme, Tasmania, in 1958. The cave (60ft by 30 ft by 17 ft) is 600 ft below the surface and 1,900 ft from the nearest valley wall. When first opened by blasting the cave was full of water, and about 120,000 gallons flowed out in 30 minutes, after this the cave was dry. Cavities of this size are rare in solid igneous rock, such as dolerite, which contains traces only of soluble minerals. The authors believe the most likely origin of the cave is that a mass of dolerite was converted into a mixture of calcite, limonite, zeolites and clay, and then movement of groundwater leached the soluble minerals out leaving a cavity. Groundwater later deposited calcite and clay on the walls and on blocks which had fallen from the roof. Some of the blocks had been wedged off the roof by the growth of calcite within flat-lying joints. - E.A.L.

- AGE AND ORIGIN OF THE GISBORNE CAVE. By E.D. Gill. Proc. Roy. Soc. Vict., 77, 1964 : 532 - 533.

The Gisborne Cave was formed during the Holocene Period, and is unusual in origin. It has been excavated in basaltic tuff which lies between bedrock of Upper Ordovician siltstone and a thick flow or flows of olivine basalt. The cave appears to have been dug out by fossorial animals. Wetting and drying effects and wind erosion have modified the entrance.- A.M.R.

BUNGONIA CAVES AND REJUVENATION

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Perhaps no Australian caves are set in more spectacular surroundings than those at Bungonia, at the threshold of the Southern Tablelands of New South Wales. After travelling about 20 miles southeast from Goulburn, over country which is not much more than undulating, even though this includes crossing a major river divide, one arrives without warning at Bungonia Lookdown on the edge of a plateau and stares down at the Shoalhaven River 1,400 feet below. From the nearby Adams Lookdown, an even more impressive view includes the saw-cut canyon of Bungonia Creek, with its almost vertical walls 800 feet high and the serrated arete of the Devils Staircase.

The magnificent scenery here, at Tallong, and at Bundanoon is, of course, the consequence of great rejuvenation of the Shoalhaven comparatively late in geological history. The special landforms at Bungonia itself are due to the same rejuvenation working headwards from the Shoalhaven up its tributary, Bungonia Creek, athwart the strike of a narrow belt of Silurian limestone, which dips so steeply that the river remained in it as it cut down from the plateau surface to the bottom of its gorge.

It is no accident that the deepest caves so far found on the mainland of Australia - Drum Cave (350 ft) and Argyle Pot (420 ft) - are here. The same features of geological structure and geomorphological history provide the explanation since in limestone country underground and surface features develop inter-dependently. It is not surprising, therefore, that the theme of the first geomorphological article devoted to Bungonia Caves should be the relationship between the caves and rejuvenation.

It is fitting that this paper, "The Origin of Bungonia Caves," by B.T. Pratt, in the Journal of the Mining and Geological Society of the University of New South Wales (Vol. 2, 1964 : 44 - 49), should be presented by a member of the University of N.S.W. Speleological Society. This Society, from its inception, has been very active at this caving locality. To say this is not to disparage the efforts there of the two older Sydney caving clubs (Sydney University Speleological Society and Sydney Speleological Society), the reputations of which are more closely associated with Jenolan Caves, nor to forget the name of Monsignor E.C. Favier, of Goulburn and Canberra, who was one of the first in the modern phase of Australian speleology to interest himself in the Bungonia area. Pratt's paper is a brief but stimulating one, which will now be summarised in terms of the geomorphological history it puts forward.

Geomorphological History Suggested by Pratt

The Shoalhaven plateau is an erosion surface truncating folded Palaeozoic rocks, including the Silurian limestones, and on it were laid down ferruginous sandstones with the well known Cinnamomum flora, unfortunately poorly diagnostic as to age. Subsequently, basalt flows poured out over them. Following David (ed. Browne, 1950), these events are ascribed to the Lower Tertiary (Eocene-Oligocene). Very slight relief close to sea level is thought to have persisted into the Miocene, and during all this time phreatic solution is considered to have been taking place beneath the erosion surface in the limestones. Initially this solution might have reached deep, but gradually, before much in the way of caves developed, it came to be concentrated close to the surface and produced the "Series One Caves" - practically horizontal caves with wide, low passages within 100 feet of the surface, which are regarded as shallow phreatic in origin. In this way, Pratt elaborates the theory of Rhoades and Sinacori in relation to the erosional history of the area.

On the Shoalhaven plateau, lateritic profiles are found here and there, especially on the iron-rich basalts, and it is thought that the whole erosion surface was lateritised. Since lateritisation is generally regarded as having occurred in a zone of watertable oscillation, it implies that phreatic conditions persisted in the caves. However, Pratt thinks that at this time the caves were filled with red clay, remnants of which persist till today.

In Pliocene times, modest uplift is assumed to have taken place and to have caused shallow, broad valleys to develop, such as that of Bungonia Creek where the road to the Lookdown crosses it. This led to the emptying of the "Series One Caves," which were then subjected to vadose modification such as the fashioning of gutters in circular phreatic passages and the introduction of gravels.

There followed at the beginning of the Pleistocene, drastic uplift of the order of 2,000 feet of the whole region in the Kosciuskan tectonic movements. This uplift set in motion rejuvenation at the coast and a wave of erosion advanced up the Shoalhaven and eventually up Bungonia Creek to produce the deep V-shaped valley and gorge. These events had two consequences for the limestone hydrology and geomorphology. First, deep phreatic solution was initiated and fresh caves, chiefly vertically developed, were excavated below the "Series One Caves." Large, rounded tunnels were also fashioned as in Drum Cave, and rock spans and solution pockets are phreatic corrosional features surviving from this phase. These, called "Series Two Caves," carried cave development to a depth of 460 feet below the erosion surface level. Subsequently, river incision drained the "Series Two Caves," which became subject to a limited amount of vadose action; there is some in-washing of sand and gravel and some cutting of meandering passages at levels corresponding to halts in the incision of the gorge. However, rejuvenation

outpaced cave development, both phreatic and vadose, and Bungonia Creek now runs many hundreds of feet below the deepest cave levels.

In Recent times, vadose action in Bungonia Caves is thought to have declined since Pleistocene pluvial conditions were followed by an Early Recent arid phase.

A thorough assessment of this suggested history, which is of considerable theoretical interest, must await the publication of detailed plans and descriptions of individual caves, such as the one of Argyle Pot foreshadowed in Pratt's paper. The present reviewer, who has not descended the deep caves of the area, must confine himself to general comments.

Discussion

Bungonia Creek is referred to as "the base level of vadose action" in the area today. Whether this is true depends on the level of the lowest springs draining the caves. Obviously any evacuation going on below this level will not be vadose but phreatic of one sort or another. Springs are usually at the level of nearby rivers or close to them, in which case it would be legitimate to refer to the surface streams as the base level of vadose action within the nearby limestone. However, at Bungonia, the one big rising so far known (dug at so arduously, but so unrewardingly by the Sydney Speleological Society) is several hundred feet above the gorge bottom, with limestone along the same line of strike continuing below to river level. It is the level of spring outflow which acts as the base level of vadose action in that part of the limestone outcrop. Significantly, this level cannot be far below the bottom of the deep caves, though it is doubtful whether Argyle Pot and Drum Cave ever fed this particular rising because a strike belt of shales intervenes. Nevertheless, it could be that this rising marks the depth to which the limestone was opened up by solution before such development was outpaced by the rapid incision of Bungonia Creek in the limestone belt.

One of the most difficult parts to follow in the postulated history is the relationship of the "Series Two Caves" to the rejuvenation. It is not easy to see how the rejuvenation can be responsible for both the development of the phreatic system and its emptying. The limestone belt is so narrow that once a rejuvenation head reached back to the limestone it would rapidly cut right through it. Nor do we find much in the way of benches in the Bungonia Creek valley and gorge to suggest substantial halts in the vertical process of the incision. Together these facts suggest that there would be very little time for the development of a deep phreatic system before drainage ensued because of the presence of the gorge. At two points in Pratt's paper (namely, the correlation table and the second paragraph on page 47), there is the suggestion that uplift set in action the phreatic phases of the "Series Two Caves," and that it was later on that rejuvenation of the valleys actually reached the area and caused the emptying of

the caves, with subsequent vadose activity. In a large limestone mass like that of the classical holokarst of Yugoslavia where the limestone reaches to the coast and descends below sea-level, it is possible to conceive that uplift on its own could cause deep phreatic development inland in particular parts even before incised valleys reached back into those parts. However, such a sequence does not seem possible for the Bungonia area, which is a tiny limestone area completely surrounded by impervious rocks to great depths, i.e., it is a "karst barré" (Blanc, 1958). Here groundwater movements at any significant depth would not be affected until headward erosion began to impinge on the limestone outcrop. It is clear that further work is needed to establish a mechanism whereby rejuvenation can cause, in a short space of time, both deep and substantial phreatic development and the substitution of a vadose system for it.

The difficulty of dating the postulated history of the caves is rightly referred to in the paper. Despite this, there is a danger that the correlation table presented conveys far too great a sense of precision and certainty than is warranted in our present state of knowledge. It is true that this table adopts for the surface geological history the views to be found in the standard authorities, but these views remain very poorly based on evidence. It is scarcely an exaggeration to say that the ascription of the erosion surface and its lateritisation to the Miocene, the small uplift and the shallow valleys to the Pliocene, and the main uplift to the Pleistocene, has no better basis than that there are three happenings to be dated and there are three geological periods in which to put them.

We are faced with tremendous problems of dating cave history in the Eastern Highlands of New South Wales, and it is as well to admit our ignorance until radiometric rock dating and palynology have provided us with a better framework. Meanwhile, we should not confuse our efforts to understand caves by tying the sequences we establish for their internal history too precisely to an extremely shaky general geological chronology.

Included also in Pratt's correlation table is a very simple climatic history of a Pleistocene pluvial and an Early Recent arid phase to which the cave history at Bungonia is also linked. Soil studies (Walker, 1962a, b) suggest a much more complex sequence of drier and more humid phases than this in the area, though it would be wrong to suggest that this is thoroughly worked out. Little is known and there is very much to learn about Quaternary climatic history here. Even the customary assumption that the cold period of the Kosciusko glaciation was a wet period in the Southern Tablelands is now in question and the converse view that it was a drier time is being defended by R.W. Galloway (personal communication) in a forthcoming publication.

Pratt states that "generally rejuvenation has not been recognised as a mechanism of cave formation." Though it is not completely clear how far this remark is meant to extend, it is given a sweeping flavour by a reference following to Sweeting's work on the Craven District of England. It is

scarcely just to many writers in many parts of the world, who have discussed rejuvenation as a major factor in cave evolution. Indeed, perhaps no other external factor has been reckoned with in underground geomorphology so much as changing base levels and the incision of adjacent river valleys.

But Pratt is right in his view that recognition of the effects of rejuvenation may prove to be fundamental in establishing the age, origin and development of caves in southeastern New South Wales, though as he himself indicates, the further factor of climatic change must not be overlooked. In the Eastern Highlands of Australia as a whole, high plateaus with rejuvenated valleys of great depth are characteristic, and many of the small limestone areas flank these valleys or floor them. If this importance of rejuvenation has not yet appeared very prominently in the literature, this is simply because so little has been written about the geomorphology of the caves here, rather than because it was not apparent or was overlooked.

For instance, at Yarrangobilly, N.S.W., although certain outflow caves such as River Cave and Coppermine Cave have active levels adjusted to the present course of the Yarrangobilly River, withal possessing higher abandoned levels, there are many former outflow caves opening into the gorge at various heights above the river. These include Trickett's Cave, Castle Cave, the Glories, Jersey and Jellabanan. There can be no doubt about the importance of rejuvenation here.

North of Yarrangobilly at Cooleman Plain, N.S.W., most of the caves are found within the part that has been effected by the vigorous rejuvenation advancing up Cave Creek from the deep valley of the Goodradigbee River. The big rising of the Blue Waterholes drains caves as yet unentered and in all probability water-filled, which have functionally replaced the Cooleman-Right Cooleman cave system. The latter comprises two former outflow caves, which have gone out of action through a further small incision of the creek. This downcutting was probably accompanied by the removal of more of the impervious cover of Blue Waterhole Beds from above the Cooleman Limestone, thus permitting a rising further downstream. Downstream, late incision has been responsible for the replacement of the upper dry passage of Barbers Cave by the lower active one, which crosses the former twice.

Again at Wombeyan, it is most likely that the replacement of the high dry caves, such as the Wollondilly and Figtree Caves, by the lower active systems of the River and Junction Caves, is an accompaniment of incision by the main river.

However, it would be wrong to think that rejuvenation has not been appreciated previously in southeastern Australia. Sweeting (1960) has related the Buchan Caves, Victoria, to the river terraces there, the product of the halting progress of rejuvenation. River incision is closely involved in the history of the Wee Jasper, N.S.W., caves which have been discussed in some detail in this Journal, though the relationship is different in the

two cases concerned, namely Dip Cave and the Punchbowl-Signature system (Jennings, 1963, 1964).

If we turn to the classic cave area of New South Wales, Jenolan, it is true that no reference to rejuvenation is to be found in the more recent account of Dunlop (1952), but inspection of Trickett's survey republished there suggests that this has affected cave development. If we turn to Süssmilch and Stone (1915), the link is stated explicitly: "the various cave levels representing successive levels of the stream channels as they cut their way downwards from the tableland surface." It is true that this older paper was written in terms solely of vadose action, which at that time dominated speleological literature, and today a detailed interpretation might be different. Yet the recognition of the importance of rejuvenation is there.

Nevertheless, it is true that at none of these localities has major rejuvenation left its impress so markedly on cave development as at Bungonia. Nor have any caves elsewhere in New South Wales been attributed to an ancient phase of planation earlier than the rejuvenation of the valleys. We are grateful to Pratt's contribution for drawing our attention to these points.

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BAT EROSION IN AUSTRALIAN LIMESTONE CAVES

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Summary

The clustering areas of bent-winged bats in limestone caves are frequently stained and etched. This staining is very intense, and covers large areas at breeding caves present in Palaeozoic limestones. Erosion of limestone is very conspicuous in these caves. Staining is not intense at breeding caves in Tertiary limestones, but a combination of chemical and mechanical erosion may, in part, account for the depth of dome pits in which the bats cluster. Certain caves that are characterised by extensive guano deposits and by conspicuously eroded and/or stained limestone, but which are currently without large colonies of bats, may represent ancestral breeding caves.

Introduction

King-Webster and Kenny (1958) have suggested that the jostling of clustering bats might abrade soft limestone and thereby play a role in cave formation. They attribute the presence of many "bell-shaped cavities" upon the ceilings of three Trinidad bat caves to such mechanical erosion. Hooper (1958) and Jennings (1964) consider, however, that abrasion by bats would probably be of little significance in determining the size and shape of such ceiling pockets, and they follow Bretz (1942) in interpreting them as solution holes formed beneath the watertable.

The possibility of chemical erosion by bat urine or by "chemically active gases rising from the guano pile" is raised by Jennings (1963) to explain the "pronounced irregular corrosion" found in portions of the Dip Cave, Wee Jasper, N.S.W.

Frequent observations in the limestone caves of northeastern New South Wales since 1960, and more limited examination of bat caves in South Australia, Victoria, and southern New South Wales, indicate that chemical erosion of the type suggested by Jennings (1963) may have been significant at a number of roosts of the bent-winged bat, Miniopterus schreibersi (Kuhl).

The Limestones

The cave areas considered in this paper are those at Naracoorte (South Australia), Warrnambool and Nowa Nowa (Victoria), Wee Jasper, Kempsey and

Ashford (N.S.W.), and Riverton and Glen Lyon (N.S.W.-Q'ld. border). (See Figure 1). The caves in the Riverton-Glen Lyon area are frequently referred to as the Texas Caves.

Two major time sequences are represented by the limestone deposits in which these caves occur. Those at Naracoorte and Nowa Nowa are in soft, friable Tertiary limestone deposits, whereas all others are in hard rock of Palaeozoic origin. It is noteworthy that there is a marked structural difference between the limestones of the Kempsey area (Yessabah Limestone belt) and the sequence of the northwestern slopes (N.S.W.) that outcrops at Ashford, Riverton and Glen Lyon. The Yessabah Limestone is rich in fossil material (Brachiopods, crinoids, etc.) with the fossils projecting from the roof and walls in many of the caves. Jennings (1964) describes a similar condition for the Punchbowl-Signature system at Wee Jasper. In the Yessabah Limestones the original fossil material has apparently been replaced by silicious compounds. Chemical solution has eroded these more slowly than the carbonates of the bedrock in which they lie (J. Lindsay, personal communication). The remarkably white limestones of the northwestern slopes are very poor in fossil material.

The Nature of Erosion

The clustering points of M. schreibersi in roosts are often darkly stained and may be partly etched. This staining and etching is thought to represent a chemical reaction of bat urine, excreta, and perhaps gases from the guano, with the rock substrate of the roosts. In limestone, the reaction is presumably slightly erosive in its action and leaves a black deposit upon the rock. However, the intensity of staining and the extent of erosion is highly variable between roosts.

In the Yessabah Limestone belt a small inner chamber of Carrai Bat Cave has had a long history of occupation by bats, for a large mound of guano has accumulated beneath the small dome where the bats cluster. A few thousand bats are present in this chamber through late summer and autumn, and again in spring. Staining of the ceiling is patchy, and nowhere intense, while erosion of the rock is only evidenced by slight etching. These characteristics are representative of many roosts currently supporting well established colonies other than maternity colonies.

Maternity colonies of M. schreibersi are present through the spring and summer months at special breeding caves. Observations on erosion at breeding caves have been made at Riverton Cave, Willi Willi Bat Cave (Yessabah Limestone), Church Cave (Wee Jasper Limestone), Naracoorte Bat Cave, Lake Gilliar Guano Cave (Warrnambool), and Nargun's Cave (Nowa Nowa).

At Riverton Cave the roof of the outer portion of the cave, used by the maternity colony, is darkly stained over areas of several square yards. Pitting of the limestone is not very conspicuous. Much of the roof of the

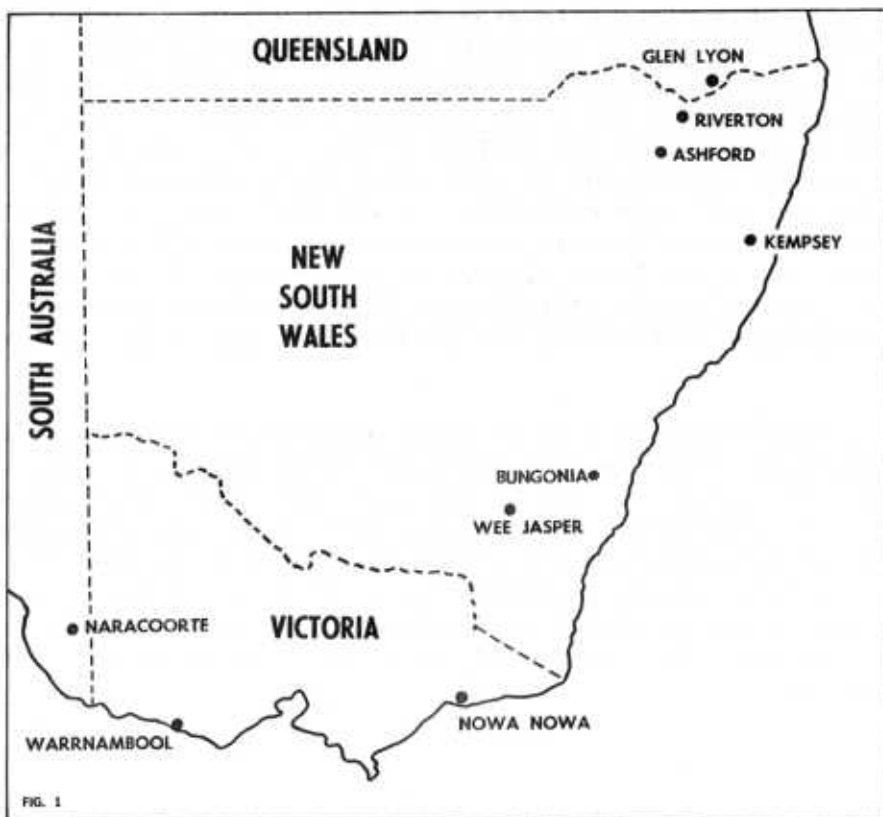


FIG. 1

Willi Willi Bat Cave is very darkly stained, and the walls of the chamber are quite spongy so that handfuls can be broken away without difficulty. The chamber is in an advanced stage of decay with limestone blocks scattered over the floor. In the areas where the young cluster, the limestone has completely fallen away so that the roof is formed of a mudstone strata overlying the limestone. Similar large areas of densely stained and pitted limestone occur at Church Cave.

In contrast to these breeding caves in Palaeozoic limestone, the breeding caves found in Tertiary limestone are not characterised by extensive areas of intensely stained rock. At Naracoorte Bat Cave and Lake Gilliar Guano Cave very deep domes are present in the ceiling and these appear to be regularly used by clustering bats. The limestone walls of Naracoorte Bat Cave and Nargun's Cave are extremely soft and rotted.

Extensive erosion and staining is also evident at a number of caves that do not currently support large colonies of bats but which, on the basis of guano deposits, have been important roosts in the past. Thus, the inner portion of the Riverton Cave is characterised by extremely extensive

guano deposits and, more particularly, by intensely stained and deeply pitted limestone. This pitting is especially evident in a series of deep fissures in the roof and on a prominent stalagmite below these. Viator Cave (Glen Lyon area) comprises a single large chamber with two moderately large openings in the roof and a few entrances at lower points. At one end of the chamber the height of the system drops to about eight feet. Here the roof is uniformly black and is characterised by several deeply eroded fissures. Guano deposits are extensive through the cave, but do not represent recent accumulation. Intense staining over large areas occur at Glen Lyon River Cave and in an inner chamber of the Ashford system which, currently, is seldom used by M. schreibersi. Eroded ceiling fissures are conspicuous at Glen Lyon River Cave, but ceiling erosion is less evident at Ashford.

Connecting with the main cave at Willi Willi is a relatively small and enclosed chamber. Much of the roof and walls of this chamber show a similar eroded surface to the rock in the breeding chamber, but while intense staining is evident on some areas, it appears that most of the previously stained surfaces have fallen away from the limestone. Sections of the wall that are still stained project beyond unstained areas. There is a suggestion of previous intense staining within an enclosed chamber of Yessabah Bat Cave and there is unstained ceiling pitting in a deep recess of one of the other Willi Willi caves.

Discussion

Several factors could contribute to the intensity and nature of the chemical reaction upon limestone. The nature of the erosion could be a function of the structure of the limestone itself. Thus the absence of extensive areas of very blackly stained rock in the breeding caves at Naracoorte, Warrnambool and Nowa Nowa might mean that abrasion of these soft Tertiary limestones continually removes any deposit that is formed. The deep ceiling domes, conspicuous at Naracoorte and Warrnambool, may well have been exaggerated by a combination of chemical and mechanical erosion. Abrasion does not appear to have been significant in the Palaeozoic limestones. The different characteristics of eroded surfaces at Willi Willi and the northwestern localities (Riverton, Viator, Glen Lyon River Cave) could be correlated with the difference in limestone structure.

Chemical erosion would be influenced by the actual volume of urine, or of active gases, contacting the rock. This would be a function of the number of bats present at the roost, the interval of time present and the season.

Thus, increased erosion would be expected at roosts supporting large colonies, particularly where those colonies were present for relatively long periods of time at a season when the bats were actively feeding. Contact of urine with limestone depends upon the manner in which bats urinate.

Twente (1955) has suggested that bats awaken during hibernation due to the irritation of a full bladder and refers to urination while in flight. M. schreibersi frequently urinate after they fly from clusters, but it is possible that this is simply a consequence of the bats having been disturbed. I have observed solitary males urinate while hanging from the ceiling and on these occasions the penis was turned forwards and the urine directed downwards. It is known, however, that some urine is left on the ceiling after clusters of adult bats disperse. The relative quantity of urine contacting rock would be greatest for large clusters, especially where these remain upon the roof for long periods of time. High temperatures, too, might accelerate the chemical reaction.

The largest colonies of M. schreibersi occur in breeding caves where from spring to autumn the bats are actively feeding and therefore voiding body wastes fairly liberally. In addition, breeding caves are characterised by large masses of non-flying young that remain upon the roof almost continually for three months, and also by high temperatures (Dwyer, 1963). Thus, the intensity of chemical reaction on limestone, and consequently the development of bat-stained and eroded surfaces, should be greatest at caves supporting maternity colonies. The habit of juveniles of frequently clustering in ceiling fissures would tend to increase the relative quantity of urine contacting the rock and thereby would accentuate erosion or staining in such sites. Thus, it follows that roosts showing similar erosion to that found at breeding caves, and also having extensive guano deposits, but which are not presently being used as significant bat roosts, may represent ancestral breeding caves. This suggestion is particularly supported by the condition of the inner portion of the Riverton Cave. The intensity of staining and the accumulated guano show that this portion of the cave has had a longer history of occupation by bats than the outer portions. The restricted access to the inner portion of the cave is reminiscent of that found at the Willi Willi and Bungonia (N.S.W.) breeding caves of M. schreibersi. At the Willi Willi and Bungonia caves, the restricted access is interpreted to facilitate maintenance of high temperatures necessary for development of young (Dwyer, 1963). It is feasible, therefore, that the inner portion of Riverton Cave served as a breeding site at a time when cave temperatures were cooler, or when fewer bats were available to warm the system. A similar interpretation can be placed upon the condition described by Jennings (1963) for the Dip Cave at Wee Jasper.

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WESTERN AUSTRALIAN MUSEUM CAVE RESEARCH CENTRE

Strong's Cave, near Boranup, in the Augusta-Margaret River region of the southwest of Western Australia, has been leased from the Crown by the Western Australian Museum to establish a cave research centre. Initial interest centres on extinct marsupial remains which have been found from time to time in a stream bed in the cave (see Cook, D.L. 1963 : The Fossil Vertebrate Fauna of Strong's Cave, Boranup, Western Australia. W. Aust. Nat., 8 : 153 - 162). It is now thought that some of this transported material may come from an old cave floor deposit at a relatively high level in the main entrance chamber, and it is proposed to conduct systematic excavation in this deposit and in other likely-looking deposits.

It is hoped that other kinds of investigations, perhaps by institutions other than the Museum, may be conducted in Strong's Cave, and that it may come eventually to serve similar ends in Western Australia to those served by the William Pengelly Cave Research Centre in Devon.

In preparation for long-continued studies in the cave, work on the entrance has recently been begun by joint parties from the Western Australian Museum and the Western Australian Speleological Group.

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