THE DECOMPOSITION OF ANIMAL REMAINS IN CAVES

by

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DECLARATIONS

1 The observations presented in this study are, except where otherwise stated, entirely the work of the author.

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3 The author has attended conferences and programmes of study relevant to the present research.

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ABSTRACT

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Jemma Macdonald

The aim of this research, carried out at Creswell Crags, Derbyshire, was to investigate the decomposition of small mammal remains in temperate caves, with particular regard to the impact upon the cavernicolous invertebrate community and the cave sediments.

The carcasses of laboratory rats were deposited in the threshold, deep threshold and hypogean regions of two caves, on sediments of differing depths layered with markers to assess the extent of bioturbation. Carcasses were covered by wire mesh to exclude vertebrate scavengers. The physical condition of the carcasses, the succession of the carrion community and the diversity of the cavernicolous invertebrates were monitored for a minimum of one year. To investigate the effect of season on decomposition, experiments were begun in both summer and winter.

The processes of decomposition observed in this investigation differed considerably from those reported by other authors working on carrion deposited above ground or buried. This is especially true of the rate of carrion consumption by invertebrates which is strongly influenced by abiotic conditions. In the caves, carcasses persisted for much longer than on the surface. Carcasses in the threshold region were rapidly colonised by necrophagous Diptera, whilst the decomposition of those farther underground was initially microbial.

The diversity and evenness of the invertebrate community in the threshold region were disrupted by the influx of non-cavernicolous species. In the hypogean region, the over-representation of certain troglophilic species changed the structure of the invertebrate community.

These results have been incorporated into a descriptive model, which proposes decomposition pathways for small mammal carrion deposited in the threshold, deep threshold and hypogean region of shallow temperate caves.

The activity of arthropods, particulary dipterous larvae, was found to disrupt the sediment beneath carrion to a depth of at least 10 cm, which has implications for cave sediment stratigraphy.

A laboratory population of the staphylinid cave beetle *Quedius mesomelinus* was established to examine its life history and behaviour. It was concluded that the species shows a number of adaptations to cavernicolous life, including a K-selected reproductive strategy.

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CHAPTER ONE : INTRODUCTION

1.1 Aim of the project

The aim of this work was threefold: firstly to investigate the agencies responsible for the decomposition and burial of animal remains deposited in caves; secondly to determine the effects of decomposing material on the diversity of cavernicolous invertebrates; and thirdly to monitor the bioturbation of cave sediment caused by the presence of decomposing material.

The results of preliminary work (Terrell-Nield, 1985, 1988) demonstrated that the presence of decomposing animal material in caves has a profound effect upon the invertebrate community. It was also found that the processes which occur after a carcass had been deposited, during decomposition and subsequent burial in the sediment, were markedly different from those observed above ground.

A detailed study of post-depositional processes was therefore initiated to gather information for the construction of a model, integrating position in cave, substratum depth and invertebrate populations. The application of the model will be of use to workers discovering animal remains, whether ancient or modern, in deducing something of the abiotic conditions prevalent during the initial period of decomposition, as well as providing an insight into the ecology of the site of deposition.

The model is intended for use primarily by ecologists and palaeoecologists, but may also be germane to some areas of forensic science.

1.2 The decomposition of animal remains

An understanding of the processes of decomposition is extremely important to the study of energy flow and circulation of matter in the biosphere (Nabaglo, 1973). Decomposers are responsible for over 95% of community metabolism in terrestrial

ecosystems (Putman, 1983), and invertebrates perform a vital function in this recycling of nutrients and energy. The specific role of arthropods in the decomposition of organic matter has, however, received relatively little attention, leaf litter (Mason, 1977) and dung (Mohr, 1943) communities being the most intensively studied.

1.2.1 The role of invertebrates

The invertebrates attracted to decomposing animal material have long interested entomologists, and the twentieth century academic press is peppered with lists of species and anecdotal reports (Folsom, 1902; Steele, 1927; Duffield, 1937; Kaufmann, 1937; Moore, 1955; Disney, 1974). However, relatively little regard has been paid to the role of carrion-frequenting arthropods in the decomposition process or to the notion of carrion as a discrete ecological unit, in terms of the succession and community dynamics of the arthropod assemblage.

The concept of decomposition as a temporal sequence is not new. Mégnin (1884) distinguished eight stages in the decay of exposed human corpses, each identifiable by particular physical characteristics and odours, and accompanied by a distinct arthropod succession.

One of the first systematic investigations into the decomposition of animal remains was conducted by Illingworth (1927). He collected and identified the flies attracted to a dead cat, and a clear succession is apparent when the species are tabulated against time. It was not until the middle of this century though, that decomposition studies became more popular with entomologists and ecologists (Akopyan, 1953; Chapman & Sankey, 1955; Bornemissza, 1957; Reed, 1958; Walker, 1967).

Perhaps the most comprehensive study of the arthropods associated with vertebrate remains is that of Payne and his colleagues (Payne *et al*, 1965 *et seq*), who examined the decomposition of pigs (*Sus scrofa* Linnaeus). A total of 522 species from 151 families were collected from baby pig carcasses exposed in woodland during the summer. The best represented orders (78% of the total) were Coleoptera, Diptera, Hymenoptera and Araneida, with five families (the coleopterous Histeridae and Staphylinidae, and the dipterous Sarcophagidae, Calliphoridae and Muscidae) accounting for 26% of the fauna. Although 27 dipterous families were identified, only

the aforementioned three (46 species) actually fed on the carrion, and indeed these were primarily responsible for its consumption.

Payne found that insect activity was more influenced by temperature than any other environmental factor, and that in conditions of very high temperature and excessive moisture, decomposition was so rapid that some insect species either failed to colonise a carcass at all or were unable to complete their development (Payne, 1965).

Most workers studying carrion have followed Mégnin (1884) in attempting to define the decomposition process as a series of stages, each characterised by the physical appearance of a carcass. Bournemissza (1957) stresses, however, that "it is very difficult to determine accurately the beginning and end of each stage and the stages are therefore to a certain degree arbitrarily designated". Putman (1978a) also warns against the use of such a subjective and qualitative delineation of decomposition. He proposes that the external appearance of a carcass is not only affected by the stage of decay, but also by prevailing environmental conditions due to season, habitat and so on. Payne (1965) states that the arthropod succession is further influenced by the chemical and physical properties of the carrion, the type and rapidity of putrefaction, the time of day and the weather.

In spite of such criticisms, various authors have defined three (Fuller, 1934; Nabaglo, 1973), four (Reed, 1958; Johnson, 1975; Wasti, 1972; McKinnerney, 1978; Abell *et al*, 1982; Braack, 1981), five (Bornemissza, 1957), or six (Payne, 1965) stages in the decomposition of vertebrate remains. Braack (1981) suggests that this exercise is "an attempt to impose a standard series of clearly delimited stages of decomposition of carcasses". If this is so it would appear to be futile since individual workers modify the stages to such an extent as to preclude any sensible comparison between studies.

It was therefore decided that a more quantitative analysis should be used to describe the progress of carrion decay in this work. This can be achieved by plotting the relative weight loss of a carcass against time to illustrate decomposition as a decay curve. Thus the rate of decomposition in different situations can be compared, and more accurate predictions regarding the arthropod succession made. This method has been employed successfully in comparative studies investigating the effect of habitat

and season (Nabaglo, 1973; Putman, 1978a), and also to assess the differences in the decomposition process in carcasses exposed to and excluded from invertebrates (Payne, 1965).

Regardless of how the temporal progression of decomposition is measured and the validity of such measurements, it is undisputed that the arthropod assemblage associated with decaying animal remains demonstrates a clear successional pattern. The dominant insect orders are Diptera, Coleoptera and Hymenoptera, although only a few species of each occur frequently (Johnson, 1975).

Contrary to early assumptions, the arthropods collected from animal carcasses are not all necrophagous. Clark (1895) was among the first to observe that the Coleoptera associated with carrion were not necessarily feeding upon the remains, but were often predatory. Morley (1907) identified 113 species of beetle found on vertebrate carrion and attempted to divide them into four categories according to their habits. Morley's categories are somewhat unclear, however, and the classification of Easton (in Easton & Smith, 1970) is more useful. Easton also recognises four, slightly different, groups of arthropod, largely distinguished by their feeding habits:

* the genuine necrophagous insects and scavengers, mainly Diptera, which subsist on the carrion itself;
* the predators, mainly Coleoptera, which feed upon other carrion-frequenting arthropods;
* the omnivores, mainly Hymenoptera, which combine both carrion-feeding and predation;
* those arthropods merely seeking shelter, and not foraging.

Putman (1978b) maintains that very few species are positively associated with carrion, and even fewer directly involved in the consumption of the carcass. He further suggests that the only insects to devour significant quantities of material are the blowfly larvae.

Blowflies are the one group of carrion-frequenting arthropods to have received considerable attention in the academic press. They are the insects most readily associated with decaying organic remains, and their use as medico-legal indicators has

been examined (Nuorteva, 1967; O'Flynn, 1983) (Section 1.2.4).

Blowflies are also responsible for myiasis in sheep and cattle, which makes them an important group economically. Information about their behaviour, habitat preferences and life histories has led to the development of control methods which aim to reduce infection of livestock (Fuller, 1932). Details concerning seasonal abundance (Wardle, 1927), geographical distribution (Davies, 1990) and temperature range (Nicholson, 1934) are also important.

The blowflies are also an interesting group ecologically (Norris, 1965). Denno & Cothran (1975) investigated the niche relationships of a number of necrophagous fly species and concluded that a carcass was not treated as a homogenous resource, but exploited along seasonal, successional and carcass size gradients. Blowflies locate carrion extremely rapidly, sometimes within a few hours of death or deposition (Lane, 1975), and the distinct succession of species which follows is dependant upon a number of factors, including the type of carrion (Kuusela & Hanski, 1982), the ambient temperature (Deonier, 1940) and the amount of sunlight falling on the site (Lane, 1975).

Numerous studies have examined the nutritional requirements, competitive interactions and succession of the different species of blowfly (Mackerras, 1933; Denno & Cothran, 1975, 1976; Goddard & Lago, 1985). For further information, the reader is referred to the extensive research into the seasonal distribution, ecological succession, predators and parasites of blowflies by Fuller (1934).

Perhaps the best-known beetles associated with carrion are the sexton or burying beetles of the genus *Necrophorus* (Silphidae). These beetles are able to bury a small vertebrate carcass very rapidly by shifting the underlying sediment (Putman, 1983). Competition between individuals for a suitable carcass is fierce (Otronen, 1988), but once it is interred the female oviposits upon it, and the carcass then becomes an exclusive food source for the larvae (Milne & Milne, 1976). In some species, both male and female parents participate in the care of the larvae (Bartlett, 1988).

Burying beetles will only inter and oviposit upon carcasses which have not been heavily colonised by other species, such as blowflies, although the adults will themselves eat older carrion, as well as necrophagous dipterous larvae (Putman,

1983). Their ability to locate extremely fresh carrion is therefore vital, and has been the subject of much research (Shubeck, 1968; Conley, 1982; Eggert & Müller, 1989).

Although a number of beetles (for example, the staphylinids, *Aleochara* spp) are like *Necrophorus* in that they will eat both carrion and other insects, many of the coleopterous inhabitants of a carcass are purely predatory. The numbers of staphylinid and carabid beetles found on or near carrion increases significantly two to three days before blowfly larvae are due to migrate, and numbers remain high until all larvae have pupated (Putman, 1978b).

Unfortunately, the habits of many species regularly found on or near animal carcasses remain obscure. It is felt that the classifications of carrion-associated arthropods described by Morley (1907) and Easton (1966) are far from comprehensive, so throughout this work the species encountered have not only been identified, but also wherever possible reasons for their presence on vertebrate remains are proposed.

With the exception of Reed (1958) and McKinnerney (1978), most authors have declined to construct food webs for the carrion community they have studied, discouraged by the apparent complexity (Payne, 1965). However, it was felt that it would be possible to determine the trophic relationships of the species attracted to decomposing animal remains in caves due to the relative simplicity of the cavernicolous invertebrate community.

1.2.2 Decomposition in winter

The present work was carried out in caves which, even during the summer months, are notoriously cold and damp. It was therefore thought that the processes of decomposition and the arthropod succession observed may be more akin to those documented above ground during the winter rather than the summer. However, as most studies on the decomposition of carcasses in temperate regions have been carried out during the summer, the decay processes and the arthropods associated with carrion through the winter months are sparsely documented.

Putman (1978a) investigated the flow of energy and organic matter from decaying carcasses and concluded that, in temperate ecosystems, there are two major and distinct patterns of decomposition according to season. In summer and autumn when temperature and humidity are high, the early colonisation of carcasses by

blowflies leads to rapid decay with over 80% of all material decomposed. In the cold months, however, when temperature and humidity are low, decomposition is slow, and carcasses are liable to mummify. If this happens, then up to 85% of the original material may be preserved.

According to Johnson (1975), the time taken for complete decomposition of small mammal carcasses (squirrel, cat, opossum) varies between 35 days and eight months, depending on the time of year and environmental conditions. His results are summarised in Table 1.1, which also shows comparative figures from a similar study by Reed (1958).

Table 1.1: Duration (in days) of decomposition stages during different seasons (data from Johnson (1975) and Reed (1958)).

		Average duration of stage				
		Fresh	Bloat	Decay	Dry	Total
Johnson (1975)						
March - May		2	19	23	60	104
June - August		0.7	4	13	30	47.7
September - November		1.5	13	21	52	87.5
Reed (1958)						
Spring	Woods	4	7	26	90*	127
	Pasture	2.5	4.5	13	75*	95
Summer	Woods	0.9	3.5	11	50*	65.4
	Pasture	0.9	2.5	10	50*	63.4
Autumn	Woods	7	9	34	80*	130
	Pasture	2.5	11.5	21	80*	115
Winter	Woods	25	20	95	?	?
	Pasture	8	32	85	?	?

* Minimum duration

Johnson gives no figures for the winter period (December to February) because the stages of decomposition were unclear due to freezing and thawing of the carcasses, and the lack of associated arthropods. However he does state that in winter carcasses

underwent a "different" decomposition process. He attributes this to two factors: the decline in microbial activity due to reduced temperatures, and the absence of insects, particularly the Calliphoridae which, he says, do not breed during the colder months.

Reed (1958), however, observed that "Dipterous larvae, particularly those of Calliphoridae, were present in fairly large numbers throughout the winter", although these were generally found within the body cavity and not on the surface of a carcass.

As has been discussed, the Calliphoridae are a particularly important group in the decomposition of animal remains: Putman (1977) calculated that calliphorid larvae consume over 80% of available material of rodent carcasses during the summer. He further suggests that of all carrion-associated arthropods, only the Calliphoridae have any significant effect on the decomposition of a carcass in summer and autumn (Putman, 1978b).

However, there appears to be much contradiction in the literature about the activity of the Calliphoridae through the winter months. Putman (1978b) agrees with Johnson (1975), and states that in Britain blowflies are active only from the end of March to mid-October. Reed's (1958) observations were preceded by Walsh (1931), who reported the presence in baited traps of "necrophagous Dipterous larvae about half-grown (apparently those of *Calliphora*)" throughout the winter. Easton (1966) also found "enormous" numbers of dipterous, possibly blowfly, larvae on a dead fox in December, although Erzinçlioglu (1986) says that *Calliphora vomitoria* will not oviposit at or below 10 °C.

Various authors (Deonier, 1940; Nuorteva, 1967) have proposed temperature thresholds for different calliphorid species, below which they will not oviposit. These are, however, contentious, and Erzinçlioglu (1986) suggests that many of these thresholds need to be re-examined.

It has also been stated that most of the beetles commonly associated with carrion (ie Staphylinidae and Carabidae) are similarly inactive during the winter (Putman, 1978b). The findings of Walsh (1931) refute this assertion though. In an extensive survey of the British necrophagous Coleoptera throughout the year Walsh makes several important points:

* a considerable number of sarcophagous beetles are active all through the

year;

* these are almost entirely small species, the larger species probably hibernating during the winter;
* although the activity of the smaller species is reduced by low temperatures, some are on the move even during very cold weather;
* there is a considerable movement of these Coleoptera from place to place.

In the light of the paucity of knowledge concerning the arthropods associated with and responsible for the decomposition of animal remains during the winter months, it was decided that as part of this work parallel experiments would be carried out during the winter and the summer. The results of both investigations, as well as being important in their own right, can also be compared for a fuller understanding of the processes of decomposition in caves.

1.2.3 Decomposition underground

Work published on the decomposition of animal remains (Illingworth, 1927; Reed, 1958; Denno & Cothrane, 1975, 1976; Putman, 1977) has been predominantly concerned with carrion deposited above ground. However, a few reports exist which document the arthropod succession and the stages of decay associated with carcasses which have been shallowly buried in soil.

Interment of carcasses was initially seen as a means of limiting the blowfly population by preventing the infestation of dead cattle (Fuller, 1932). It was discovered, however, that the burial of carcasses is no impediment to the development of dipterous larvae, and bodies must be poisoned with sodium arsenite before interment to control the problem.

Like carrion found on the surface, buried carcasses go through characteristic sequences of decay. As part of an extensive study, Payne *et al* (1968) examined the decomposition and arthropod succession of pigs (*Sus scrofa* L.) buried in coffins in soil. Five distinct stages, each characterised by a specific microcommunity, were identified: fresh; inflation; deflation and decomposition; disintegration; and skeletonization.

However, the decomposition of a buried carcass, and the invertebrates

associated with it, may differ quite markedly from patterns observed above ground. In Payne's (1968) study, buried pigs were only reduced to approximately 20% of their original body weight, twice as much as carcasses deposited on the surface. A total of forty-eight arthropod species were found associated with the buried pigs, twenty-six of which were not implicated in the decomposition of carrion above ground.

In his work on the invertebrate fauna of the cadaver, Easton (in Easton & Smith, 1970) describes eight waves of insects involved in the decomposition of corpses above ground, but only four in that of buried corpses. Of the latter, the first wave consists of *Calliphora* (Calliphoridae) and Muscidae. These are followed in the succession by *Ophyra* (Muscidae), and after about a year Phoridae appear. The last stage, the Coleoptera, occurs during the second year.

Characteristic differences in the course and rate of decomposition can be observed which are related to depth of interment. Lundt (1964), investigating the arthropod colonisation of pieces of buried flesh found that when buried only shallowly, colonisation reached a maximum very quickly and then decreased rapidly. At greater depths the carrion dwellers appeared later, but remained for a much longer period.

Morovic-Budak (1965) also found minor differences in the decomposition of buried corpses due to the depth of interment, as well as the composition of the earth and the type of burial (without coffin, wooden or metal coffin, etc.). He also states that corpses buried in the warm summer months showed a higher initial rate of decomposition than those buried in the cold winter period.

The only published work found which compares the processes of decomposition on the surface with those in an underground environment (as opposed to a grave of some sort) was carried out in a forest in Poland (Nabaglo, 1973). The events following death in bank voles (*Clethrionomys glareolus* Schreber) both above ground and in their underground burrows are described (Table 1.2).

Three stages, preparatory, active and residual, were identified. The characteristics of the first two stages were identical in spring and summer (in both environments), although in each case the residual stage differed slightly. Carcasses were not observed during winter studies, and so no information is available on the decomposition processes in this season. The greatest variety of species was observed during the active stage.

Table 1.2: A summary of the decomposition of bank voles (*Clethrionomys glareolus* Schreber) in summer on the surface and in different seasons in underground burrows (Nabaglo, 1973).

Environment	Duration of stages			Proportion
	Preparatory	Active	Residual	remaining
Summer on surface	3	7	20	10%
Summer underground	6	18	30	10%
Spring underground	18	24	60+	15%
Winter underground	------ 3½ months ------			Bones, fur

Aside from this one study, however, the decomposition of animal remains in underground environments remains a neglected area of research. Biospeleologists have used carrion as bait to trap cavernicolous arthropods (Peck, 1975), and so have a working knowledge of some of the organisms likely to be involved in decomposition. However, there exists no systematic study of invertebrate succession on decomposing animal remains in caves, or on the role of individual species within this carrion community. This work aims to rectify this situation.

1.2.4 Forensic entomology

Keh (1985) defined forensic entomology as "the study of insects and other arthropods associated with certain suspected criminal events, for the purpose of uncovering information useful to an investigation". The earliest record of entomological techniques being used in a criminal inquiry comes from a thirteenth century Chinese manual of forensics (Keh, 1985). In the case in question, the victim was killed with a sickle. When the investigating officer ordered farmers to lay out their sickles in the sunshine, flies were attracted to one of the blades. The owner then confessed to the murder.

Entomological techniques have since been used to provide evidence in a number of criminal investigations. Nuorteva (1974) documents a case where dipterous

larvae found on a blood-stained shirt were reared and discovered to be the same species and age as larvae found in a nearby house. From the age of the larvae a date of oviposition was proposed, which coincided with the date of a knifing incident. This information gave detectives confirmation that the owner of the house was responsible.

In a rape case (Greenberg, 1985), it was found that the suspect owned a ski-mask similar to one worn during the assault, although he maintained that it had not been used since the previous winter. Upon closer examination of the mask, however, two cockleburs were found stuck to it. These contained larvae of the weevil *Rhodobaenus 13-punctatus* Illiger, a species which has a one-year life cycle, with summer larvae. The larvae do not overwinter, and could not possibly have survived in the cockleburs on the mask in a heated apartment for any length of time. This information led to the man's arrest, since the mask must have been used more recently than he had claimed.

Information about the fauna specifically associated with a cadaver has also been frequently used in forensic investigations. Such information may provide evidence concerning the time, place and manner of death, the time of burial, whether the body was moved, and the social status of the victim (by, for example, the presence of body lice) (Erzinçlioglu, 1989).

In some cases a knowledge of the appearance of a corpse after colonisation by particular arthropods may prevent incorrect interpretation of evidence (Erzinçlioglu, 1989). For example, the activity of dipterous larvae often produces small punctures in the skin which may be mistaken for bullet or buckshot wounds (Keh, 1985). Evans (1962), examining the mummified body of a woman, noticed that the hair was only 1 to 3 mm long, and the ends were clean cut as though the head had been shaved. It was later shown that this appearance was due to nothing more sinister than clothes moths.

In recent years entomology has been most commonly used to ascertain the time of death in murder victims (Lothe, 1964; Nuorteva, 1967; Greenberg, 1985; Erzinçlioglu, 1983). Although many other observations on the state of a corpse may give clues as to when death occurred (Medico-Legal Society, 1976), entomological techniques are particularly useful in cases when the body is in a fairly advanced state of decay.

One of the most well documented methods involves a thorough examination of the arthropod assemblage on a corpse at the time it is discovered. This information is then compared to known patterns of colonisation, and an estimation made regarding the timespan required for the corpse fauna to reach the stage of succession observed.

This technique was pioneered by Mégnin (1884), who was the first to examine the arthropod succession of human corpses. He was able to separate the decomposition of corpses which had lain exposed in the open air into eight stages, each characterised by a unique arthropod assemblage. Mégnin's work was augmented by Motter (1898) who, in an extensive study of 150 exhumed corpses, attempted to identify a similar pattern of colonisation relative to the period of interment. Motter became convinced, however, that to describe the decomposition of interred bodies as a series of stages was inapplicable, and no obvious arthropod succession was elucidated.

More recently though, Smith (in Easton & Smith, 1970) defined eight stages, characterised by the insect assemblage, in the decomposition of exposed corpses and four in that of buried ones. In the same paper, Easton outlines how observations on coleopteran succession have been employed to estimate the time of death of a number of exposed corpses.

This method is, however, subject to many variables. The species involved in decomposition depend upon the local fauna which is influenced by latitude, altitude, topography, surrounding vegetation, season and so on (Erzinçlioglu, 1983). Furthermore, the period of colonisation of many species, particularly the Diptera, is related to the development time. This is generally accelerated by high temperature and humidity and an ample supply of food and retarded by the reverse (Easton & Smith, 1970). Succession will thus proceed at varying rates according to environmental parameters. Erzinçlioglu (1983) also states that arthropods such as sphaerocerids and sepsids (Diptera), which are associated with the later stages of decomposition, may be found on relatively fresh corpses, further confusing the issue.

A more accurate method commonly used to estimate time of death requires knowledge of the life histories of certain necrophagous species. Central to this method are two observations: a) that the size and stage of development of larvae and pupae can be used to determine their age; and b) that certain species, particularly blowflies, only oviposit on very fresh carrion. Thus, if a corpse is found within the development

time of such species, examination of their immature stages can provide a good indication of the time elapsed since death.

Estimations of time of death calculated in this way are subject to relatively few sources of error. The most important variable involved is temperature, since this affects the rate of development. Although Lothe (1964) has criticised this method due to the "considerable difference between upper and lower limits of stages and delay [which] may occur before eggs are laid", it has been widely employed (Nuorteva, 1967; Greenberg, 1985; Goff & Odum, 1987).

Another important aspect of forensic science in which entomological techniques can prove useful is in determining whether a corpse has been moved. This could involve the transportation of a body many miles or just a few feet. The particular species of arthropod found on a corpse may give an indication of whether it has been moved from sunshine to shade, from a rural area to a city, from a different altitudinal zone, from woodland to open ground, and so on (Nuorteva, 1967).

In such cases, the distinctiveness of local faunas, which may confound attempts to determine time of death, is of great potential use (Erzinçlioglu, 1983). Greenberg (1985) cites a case where two bodies were found in a car. The age of the dipterous larvae led to the conclusion that the murders had occurred a day apart. It was further proved that one of the bodies had been transported north a considerable distance, since the species of fly involved was restricted to southern areas at that time of year.

Information concerning the life cycles, behaviour and faunal succession of arthropods associated with decaying remains has largely been elucidated from work carried out with animal carcasses (Walker, 1957; Wasti, 1972; Smith, 1975; Rotshild *et al*, 1977; Abell *et al*, 1982), although some decomposition studies have used human corpses (Lundt, 1964; Rodriguez & Bass, 1983; Galloway *et al*, 1989). The exposure of animal carcasses under carefully documented natural conditions may provide valuable information for the forensic entomologist (Erzinçlioglu, 1986), but the results of such experiments are not necessarily directly applicable to human corpses because of the specific features concerning the way in which a human body attracts arthropods (Nuorteva, 1967).

It is known that certain features of a carcass will affect the species of arthropod attracted to it. These include the size of the animal (Lane, 1975), its species (Abell *et*

al, 1982) and possibly the tissue chemistry (Walsh, 1933; Erzinçlioglu, 1986). With further regard to human remains, insects may be reluctant to oviposit upon bare (rather than fur-covered) skin (Bohart & Gressitt, 1951). Also, human cadavers are often clothed or wrapped (in blankets, paper, polythene etc.) which may attract or deter certain arthropods (Keh, 1985). The widespread modern usage of cosmetics, including deodorants and perfumes could also be important.

Thus, decomposition studies using animal carcasses can be applied only cautiously to forensic science. However, Erzinçlioglu (1986) believes that useful information, particularly about the early stages of decomposition, may be gleaned from experiments using small animal carcasses. He proposes that investigations into the faunal succession of animal carcasses in a variety of habitats and seasons, with environmental parameters as well as the physical condition of the carcasses being accurately measured, would be a "fruitful line of research" (Erzinçlioglu, 1986).

It is anticipated, therefore, that the results of this study may be useful to forensic entomologists examining corpses found in subterranean resting places, such as caves, mines and cellars. Details of the physical appearance and temperature of a carcass during decomposition underground will be documented, as well as information concerning the faunal succession of animal remains in temperate caves during summer and winter. It is anticipated, however, that the most important application to forensic science will be in determining whether remains have been moved after death, either into or out of an underground environment.

1.3 Taphonomy and bioturbation

The study of taphonomy, the events between the death of an organism and its subsequent deposition and fossilization (Efremov, 1940), has become increasingly important in the palaeoecological interpretation of fossil assemblages (Korth, 1979). By studying modern systems, taphonomists are able to make assumptions about the processes which dictate the condition, orientation, and selective preservation of fossil material.

Taphonomic studies are mostly concerned with bones (Armour-Chelu &

Andrews, 1991), although some have been conducted upon other elements, such as shells (Johnson, 1957). Different workers have, for example, focused upon the characteristic appearance and dispersal of owl pellets (Levinson, 1982), carnivore scats (Mellett, 1974), and of bones in water (Dodson, 1973). Extensive studies have been conducted to examine the gnaw damage, distribution and dispersal of bones caused by predators and scavengers (Haynes, 1982). Information of this nature can be used by ecologists in the interpretation of both fossil and modern bone assemblages.

The role of invertebrates in the dispersal of skeletal elements has received little attention, although it is known that their influence may be considerable. It has been reported, for example, that harvesting ants are capable of accumulating large numbers of microvertebrate bones in a characteristic pattern (Shipman & Walker, 1980). This is distinguishable from assemblages collected by avian or mammalian predators, and has important palaeoecological implications.

Korth (1979) stresses the importance of an understanding of the processes of decomposition in assessing the biases of preservation of a fossil assemblage. The direct comparison of living and fossil species has been widely and effectively used to study the palaeoecology of ancient ecosystems (Shotwell, 1955; Voorhies, 1974; Coe, 1976). Details concerning the habitat preference, diet, behaviour and so on of a living species can provide valuable information about the environment and habits of its ancestors. A comprehensive study of the activities of invertebrate decomposers and their effects upon the distribution and appearance of microvertebrate bones may, therefore, be applicable to the interpretation of fossil assemblages.

Animals which burrow will be particularly influential in the distribution, appearance and preservation of animal remains during decomposition. They may also be one of a number of factors which disrupt patterns of fossil assemblages and ancient artifacts already established in strata (Wood & Johnson, 1978).

The mixing of sediment by animals was termed faunalturbation by Thorpe (1949), and has since become widely known as bioturbation. The impact of burrowing animals on the environment has many ramifications and is well documented. Research is concerned with aspects such as erosion and landscape modification (Furness, 1991), soil fertility (Elmes, 1991), and effects on crops and other vegetation (Heth, 1991).

Bioturbation is also important to palaeontologists and archaeologists. Archaeologists in particular expect a certain degree of post-occupational disturbance of sites and are able to recognise certain indications of this phenomenon. Disruption caused by vertebrate burrowers, such as rabbits, moles and badgers, is easily identifiable, since the sediment which fills burrows often differs in texture or colour from that which is found in the surrounding area (Stein, 1983). However, the burrows of smaller animals are less easy to detect and are often overlooked. Many terrestrial invertebrates construct burrows and their activities may have a profound influence upon the distribution of objects within the substratum.

The ability of earthworms to bury objects through their activity in the soil was commented upon by Darwin (1883), but it was Atkinson (1957) who first realised the archaeological significance of this behaviour. The systematic transport of fine particles to the surface by earthworms causes objects to become incorporated into the sediment. Thus, upon excavation, certain artefacts may found far deeper than would be expected.

Considerable attention has been devoted to the significance of earthworm activity upon the dispersal of microvertebrate bones within the soil profile. Armour-Chelu and Andrews (in press) have conducted lengthy investigations to determine the extent to which various sizes of bone are incorporated into soil by earthworms. They also report characteristic damage to bones apparent upon excavation.

As a result of an examination of an Archaic shell midden, Stein (1983) suggests that the earthworm may be the "unexpected nemesis of archaeologists". The activity of earthworms not only causes the effective burial of fairly large objects, but also destroys stratification and obscures boundaries between the soil and areas such as ancient hearths or burial pits. The ingestion of sediment by earthworms alters the soil chemistry and removes important botanical evidence such as pollen and seeds, both of which may affect the interpretation of archaeological sites.

Although caves may be important archaeological sites (Section 1.5), most research into bioturbation by terrestrial invertebrates concerns the activities of earthworms (Stein, 1983; Armour-Chelu & Andrews, in press), which are not common cavernicoles. Papers devoted to the bioturbation of cave sediments are therefore rare, although Thomas & Bottrell (1992) have reported that oligochaete

worms are responsible for sediment bioturbation in a Derbyshire cave.

The archaeological significance of other burrowing invertebrate species, such as spiders, crickets and ants, while not expected to be as profound as that of the earthworm, has not been documented. The larvae of a number of decomposer species, most notably the Calliphoridae, show burrowing behaviour, and may thus contribute to the incorporation of microvertebrate bones into the sediment.

As part of this work, a method to assess bioturbation resulting from the activity of the arthropods associated with decomposing animal remains was included. This involved the incorporation of marker layers into the sediment below carcasses, on the principle that these layers would become obscure in the event of significant bioturbation.

Pollen and spores were chosen as markers to minimise modification of the sediment. Not only do both occur naturally in cave sediments, but pollen analytical techniques are widely used in conjunction with stratigraphical information such as is derived from cave deposits. Palynological techniques have been employed to provide both qualitative and quantitative evidence concerning the changing vegetation of an area over a period of time (Dimbleby, 1961; Hicks, 1971), and to date changes in the landscape such as landslides (Franks & Johnson, 1964) and the onset of erosion (Conway, 1954). Palynological investigations of cave sediments (Leroi-Gourhan, 1965; Van Zinderen Bakker, 1982) are not, however, common.

Pollen and spores may enter a cave by means one of a number of vectors, although it is likely that many are airborne. Van Campo & Leroi-Gourhan (1956) suggest that airborne pollen will be transported only about 10 m into a cave with no through-flow of air, and that the amount will decrease proportionally with increased distance from the entrance. In caves with more than one entrance and directional air movement, however, they discovered pollen and spores much further underground.

Subterranean streams may carry pollen and spores underground for up to 800 m (Peterson, 1976), and it has been suggested (Van Campo & Leroi-Gourhan, 1956) that seepage water may also be important, although there does not appear to be any firm evidence to support or refute this theory.

Animals are also important vectors. Unlike the random variety of pollen and spores transported by air and water, introduction by animals may be biased.

Burrowing bees, for example, are responsible for accumulations of millions of Compositae pollen grains in their nests (Van Zinderen Bakker, 1982). The presence of such concentrations of a particular type of pollen may lead to erroneous conclusions being drawn concerning the vegetation and climate of the area.

The variety of pollen brought into caves by vertebrates may be wider than initially supposed due to pollen from a number of species falling on vegetation subsequently ingested by animals (Thompson *et al*, 1980). Thus pollen and spores present in the gut contents of dead animals or in faeces need not necessarily be simply a reflection of the animal's diet.

Finally, the activity of humans is responsible for some of the pollen found in caves. Pollen will be brought in stuck to feet and clothing, and on vegetation for food and bedding (Van Campo & Leroi-Gourhan, 1956). Floral decorations and tributes for cave burials (Leroi-Gourhan, 1975) will also introduce pollen.

The relative contribution of the principle pathways for pollen and spore movement into the caves in which the present work was conducted has been extensively researched by Coles (1987). He concluded that airborne conveyance is the most important means of transporting pollen and spores into these caves under existing conditions. Further questions were raised by this work, however, concerning the post-depositional movement, degradation and alteration of pollen and spore assemblages in caves.

Several ways in which pollen and spores become incorporated into the cave sediment have been suggested. The most obvious is that the grains are entrapped during sediment deposition (Coles, 1987). They may also be washed down by water, although this is not usual in sandy sediments such as are found in the caves in question, because the grains tend to wash down as aggregates bound by organic material rather than individually (Dimbleby, 1961).

Other ways in which newly deposited pollen and spores become incorporated into cave sediment involve the movement of relatively large amounts of sediment and may lead to severe disruption of the strata. Causes of this could be "landslide"-like shifting of sediment due to roof-fall, excessive moisture, or earth tremors. Animal activities, such as digging and trampling, could also result in the destruction of intact deposits.

The latter phenomenon is the subject of this investigation. The activities of fly maggots and their predators are known to modify the soil structure in the vicinity of decomposing carcasses (Bornemissza, 1957). It is further proposed that the burrowing habits of certain species of invertebrate associated with decomposing animal remains in caves may cause sufficient bioturbation to obscure stratigraphy and confuse pollen and spore distribution within sediment.

1.4 Caves and their ecology

1.4.1 The cave environment

Of the vast number of subterranean systems present in karst landforms only a fraction are accessible to vertebrates, and even fewer have entrances large enough to admit exploring humans. Barr (1968) suggests that there might be 200,000 caves in North America, only ten percent of which are open to human penetration.

Howarth (1983) divides the interior of those caves which are open to the surface into four environmental zones: entrance, twilight, transition and deep cave (or dark). It is unclear as to the parameters used to define these zones, however, and the classification of land-area domains used by Jefferson (1976) is preferred: the surface of the planet, including all plants and bodies of water, is known as the epigean domain; the pro-epigean domain is the threshold of caves, from the entrance to the furthest point to which daylight penetrates; and the hypogean is the dark zone, including subterranean waters and sediments.

The hypogean domain in temperate regions is characterised by the following physical features which affect the survival of the organisms that live there:

* the relatively high (>90%) and constant relative humidity;
* the relatively low (6.7 - 12.8 °C) and constant temperature, which approximates the mean annual air temperature on the surface;
* the high CO_2 and low O_2 content of the atmosphere
* the lack of environmental cues;
* the absolute darkness.

High humidity is essential for many cavernicolous organisms, which have their origin in the endogean regions of the soil. The relative humidity regime, which has important implications for the evaporative rate, is considered to be more important to the distribution of cavernicoles than the temperature regime (Howarth, 1983).

Green plants are obviously precluded by the lack of available sunlight for photosynthesis. The darkness of the hypogean region thus indirectly prevents the survival of a whole host of animal species - not just those which are reliant upon vegetation for food, but also those which are specifically adapted to prey upon these herbivores.

Only by being equipped to tolerate these conditions are animals able to live and reproduce in this domain.

1.4.2 Biospeleology

Biospeleolgy, the biology of cavernicoles, is a relatively young science. It began in the middle of the last century in continental Europe, when the first study of cave fauna was published (Schiödte, 1849). North American caves received scant attention until the late 1880s (Packard, 1888, 1894), and although sporadic collections were made around the turn of the century, the systematic investigation of British cavernicoles did not begin until the late 1930s (Glennie & Hazleton, 1962). The lack of interest in North America and Britain was probably due to the paucity of cave faunas in these areas.

Species can be classified according to a system initially devised by Schiner (1854) and later added to by Racovitza (1907). Other classifications are described by Vandel (1965), but the Schiner-Racovitza system is the simplest and most widely used.

Three main groups of cavernicoles are defined: troglobites, troglophiles and trogloxenes. Species which are found nowhere but in caves, or obligate cavernicoles, are known as troglobites (*trogle* - cave, *bios* - life). These are the only true cave species and often show specific adaptations to their environment, such as loss of pigmentation. Troglophiles (*phileo* - love) are facultative cavernicoles and are able to live and breed in both epigean and hypogean environments. Other species, which spend part of their life cycle in the cave but forage and breed on the surface, are classed as habitual or accidental trogloxenes (*xenos* - guest); habitual if they are

frequent visitors, to hibernate for example, and accidental if they are merely carried in by air movement or floodwater.

If these definitions are strictly adhered to, however, animals which regularly enter the cave only to feed are not included in any category. Many species, such as woodlice and centipedes, belong to this group. For this work, therefore, the classification "habitual trogloxene" will be extended to include these.

Animals found widely distributed throughout both the hypogean and threshold regions of a cave are likely to be troglophiles. Troglobites are largely restricted to true hypogean regions, being unable to tolerate conditions in threshold areas, particularly the large fluctuations in temperature and relative humidity (and hence evaporative rate). The reverse is true for trogloxenes, which cannot survive the harsh conditions in the deep cave and so are generally found near entrances. Occasional individuals are carried further underground by air or water currents, but these do not live long.

Hypogean communities are strikingly simple compared to those on the surface and so cavernicolous ecosystem dynamics are relatively uncomplicated. The only primary producers present are chemosynthetic bacteria, the importance of which in the food web may be negligible (Barr, 1967). Most food enters a cave from the surface in the form of dead vegetation blown or washed in, or as the droppings and bodies of trogloxenes. Hence food availability, in terms of both amount and frequency, decreases with increasing depth and is a limiting factor on hypogean populations (Jefferson, 1976).

Hypogean communities, like other "island" fauna, thus illustrate two important characteristics: isolation due to abiotic conditions, and relative simplicity. Consequently, they afford ideal conditions for ecological studies (Culver, 1970a, 1970b; Poulson & Culver, 1969; McKinney, 1975; Peck, 1988). The simplest of these involve estimates of population densities (Johnson & Heath, 1976) and distribution (Busacca, 1975). Patterns of behaviour in cavernicoles, such as foraging strategies (Kane & Poulson, 1973, 1976), migration (Racovita, 1976) and colonisation (Humphreys, 1991) have been investigated. Comprehensive analyses of the biology (Humphreys *et al*, 1989), morphology (Van Zant *et al*, 1978) and genetics (Laing *et al*, 1976) of particular cave species are also familiar in the literature. The threshold

region of caves provides another unique environment, with more stable and sheltered conditions than the surface, but far greater accumulations of organic matter than the hypogean, including, in the shallow parts, green plants. As well as the expected detritus community, this region supports a comparatively diverse fauna known as the "parietal association" (Jeannel, 1926), and has received particular attention in recent years (Culver & Poulson, 1970; Peck, 1976; Jefferson, 1983).

In some caves the presence of localised populations of trogloxenes such as bats (Braack, 1989) or crickets (Peck, 1976) increases the nutrient availability of a particular area which may be fairly deep in the cave. Communities of specialised arthropods are concentrated in these areas, and peaks in numbers and diversity occur.

1.4.3 The colonisation of the hypogean domain

It is widely accepted that caves in temperate regions were first colonised by animals living in leaf litter or deep soil which were preadapted to the rigorous environment (Glennie and Hazleton, 1962; Vandel, 1965; Barr, 1968; Jefferson, 1976; Chapman, 1988; Holsinger, 1988). During the Pleistocene, when large areas of the earth's surface were covered by glaciers, the land just south of the ice fronts would have been inhabited by species which were adapted to constant low temperature and high humidity. As the climate got warmer and drier and the glaciers retreated, these animals would have been unable to survive and breed in the now-hostile epigean environment and so became increasingly troglophilic and isolated in caves. In this island-like environment evolution continued, culminating in the situation seen today of a large number of troglobite species with common ancestors belonging to a few taxonomic groups.

This explains why many troglobites in temperate areas are relicts, more closely related to long-extinct groups than to living epigean species.

A slightly different pattern is envisaged in tropical regions. Based upon observations in Hawaiian lava tubes, some of which are less than one hundred years old, Howarth (1981) proposed a theory of troglobite evolution in a stable climatic regime. He suggests that when lava tubes are formed, preadapted species move into the new ecological niches created and troglobites evolve from the speciation of this native fauna.

These two theories are based upon different mechanisms of evolution; episodic in the case of temperate regions and continual in the tropics. They both suggest that the evolution of troglobites involves an intermediate troglophile stage.

Troglobites may be characterised by a number of features, the most striking of which are the loss or reduction of eyes and of pigmentation. Theories concerning the mechanism of this so-called regressive evolution are controversial (Maguire, 1961; Chapman, 1988), and will not be discussed here. For more information on the colonisation of caves and the evolution of troglobites the reader is referred to the comprehensive reviews in Vandel (1965), Barr (1968), and Jefferson (1976).

1.5 History and importance of the experimental site - Creswell Crags

Creswell Crags (SK 535741), a magnesian limestone gorge on the border between Derbyshire and Nottinghamshire, is one of the most important archaeological and palaeontological centres in Britain. The area is a Site of Special Scientific Interest and contains a number of caves and fissures of various depths (Figure 1.1, overleaf).

The excavation of animal remains buried in cave sediments has always been important to palaeontology and, more recently, to palaeoecology (Bramwell, 1964; Gale *et al*, 1984). Caves are likely to be natural sediment traps and are also protected from most of the destructive elements to which surface sediments are exposed. The deep and comparatively undisturbed deposits recovered from caves provide extensive material of interest to archaeologists, palaeontologists, palaeoecologists, geologists and palynologists.

Over the past twelve decades the caves at Creswell have yielded a wealth of material from abundant late Pleistocene and early Flandrian deposits. Of particular significance is the extensive collection of Pleistocene remains, which has contributed immensely to knowledge of the fauna of the period. Also of interest is the evidence of Palaeolithic human occupation of the caves.

In 1876, when research into prehistory was still in its infancy, the Rev J Magens Mello began work on the caves at Creswell Crags, including both Robin Hood's and Church Hole. Over the next two decades Mello, aided at various times

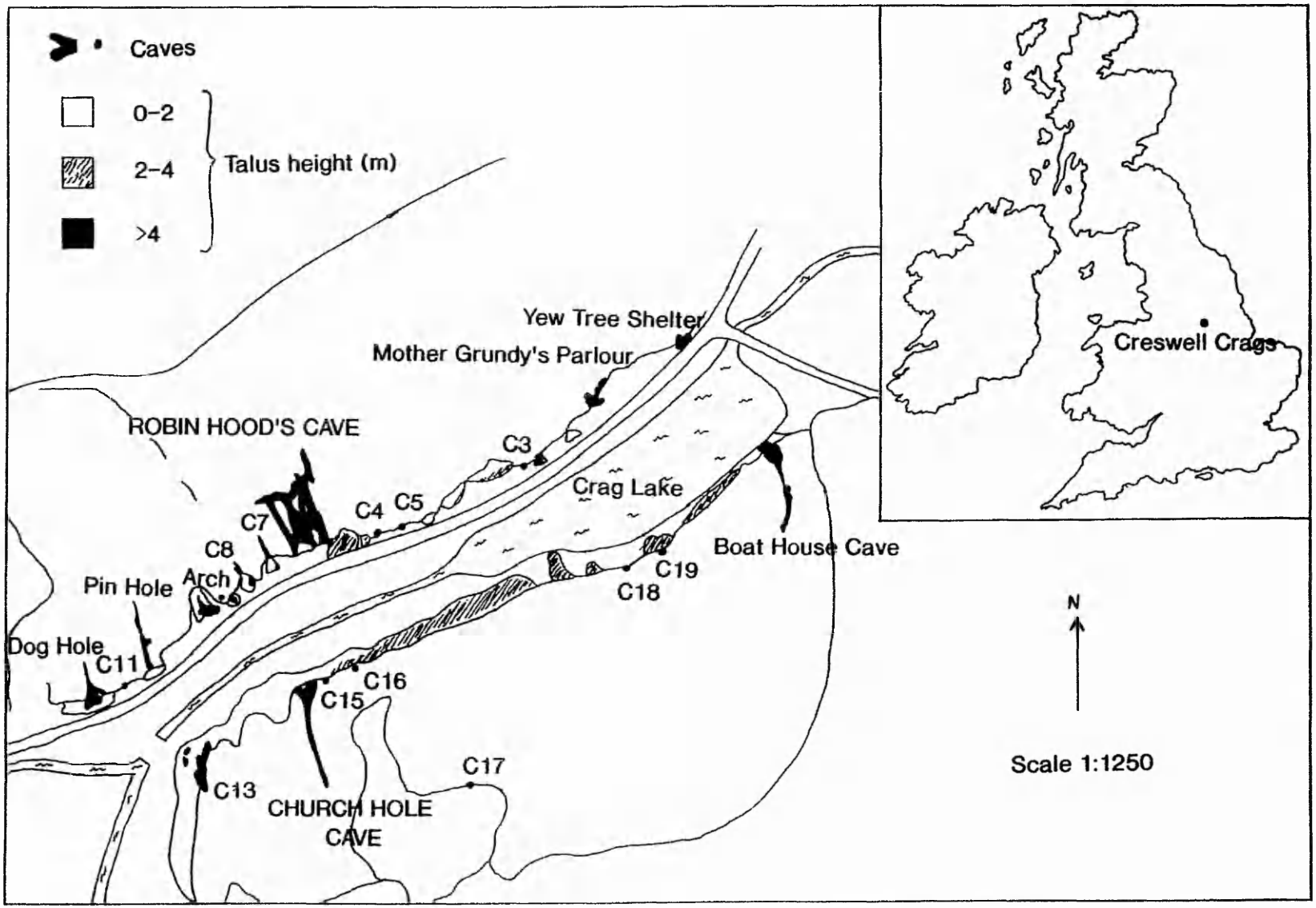


Figure 1.1: Map of Creswell Crags.

by fellow enthusiasts such as William Boyd Dawkins and Thomas Heath, conducted extensive excavations with spectacular results. In a single month Mello unearthed from Robin Hood's Cave not only "traces of the presence of man", but also bones from "some 15 or 16 species belonging to no fewer than 12 genera" (Mello, 1876). These included Irish elk, glutton, Arctic fox, hyaena, mammoth, cave lion, woolly rhino, brown bear, reindeer, bison, horse and urus. Conspicuous by their absence are records of findings of small vertebrate remains. Dawkins (1876) mentions hares, but only in the context of the diet of Palaeolithic Man.

The conclusions drawn by these early workers were that Robin Hood's Cave at least had served as a hyaena den for a considerable period, which explains the frequent occurrence of bones from large herbivores. Humans then took over residence, evidence of their occupation being found as charcoal fragments and numerous implements of antler, mammoth tooth, quartzite, ironstone, greenstone and flint (Dawkins, 1876).

By the end of the nineteenth century, the Victorians had completed their devastation of the site; scant regard for stratigraphy had destroyed many valuable deposits and the indiscriminate use of explosives had left large spoil heaps rich with the discarded bones of smaller animals.

The site was considered "worked out", and no more organised research was done until Armstrong began work in 1921. Unlike his predecessors, Armstrong painstakingly sieved all excavated sediment for small bones, and accurately recorded all finds (Armstrong, 1949). This period of activity ended with Armstrong's death in 1958.

About ten years later the excavation of the area outside the west entrance of Robin Hood's Cave was undertaken, and human bones and a well-defined hearth were discovered (Campbell, 1969).

More recent archaeological work at Creswell has been sponsored by Nottinghamshire and Derbyshire County Councils and the University of Sheffield, and has become a multi-disciplinary concern. Palaeoecological studies, including comprehensive surveys of flora and invertebrates, have been conducted, and especially relevant to this project is the work done by Coles (1987) on the palynology of cave sediments.

For comprehensive information about the archaeological, palaeontological, palaeoecological and ecological significance of Creswell Crags, the reader is referred to the excellent reviews in Jenkinson and Gilbertson (1984) and Briggs, Gilbertson and Jenkinson (1985), and to Cave Science (December 1989; volume 16 number 3), an issue of the journal of the British Cave Research Association almost entirely dedicated to contemporary work at Creswell.

Two caves, situated on opposite sides of the gorge at Creswell Crags were used in the present study: Robin Hood's Cave on the north side and Church Hole on the south (Figure 1.1, page 25).

Robin Hood's Cave is the most extensive system at Creswell. It consists of four main chambers (Figure 2.1) connected by a series of tunnels. This cave has been the site of numerous archaeological and ecological studies as described above. Terrell-Nield (1985) conducted an extensive survey of the cave fauna in 1983/4 and began preliminary work on animal decomposition underground (Terrell-Nield, 1988) in Church Hole Cave.

In the present study, three sites were used in each cave: one near the front of the cave, in the threshold region; one at the back, in the true hypogean domain; and an intermediate site, where visible light was just detectable, although environmental conditions such as temperature and relative humidity regimes, were more similar to those in the deep cave.

CHAPTER TWO : MATERIALS AND METHODS

2.1 Robin Hood's Cave

The main investigation was conducted in Robin Hood's Cave at Creswell Crags. The three sites used were 10 m (Front), 35 m (Frogpit) and 50 m (Back) from the nearest cave entrance. Figure 2.1 shows the position of the sites on a floorplan of the cave.

Pitfall traps were used to survey the cavernicolous invertebrate community. A previous study (Terrell-Nield, 1985) provided a baseline fauna for the cave, and continued trapping whilst the carcasses were *in situ* demonstrated the effects of decomposing animal material upon invertebrate diversity. Six pitfall traps, 3 cm high and 5.4 cm diameter, were positioned near the carcasses at each site. Each trap contained approximately 10 ml of pitfall fluid (50% ethylene glycol and 1% detergent in distilled water).

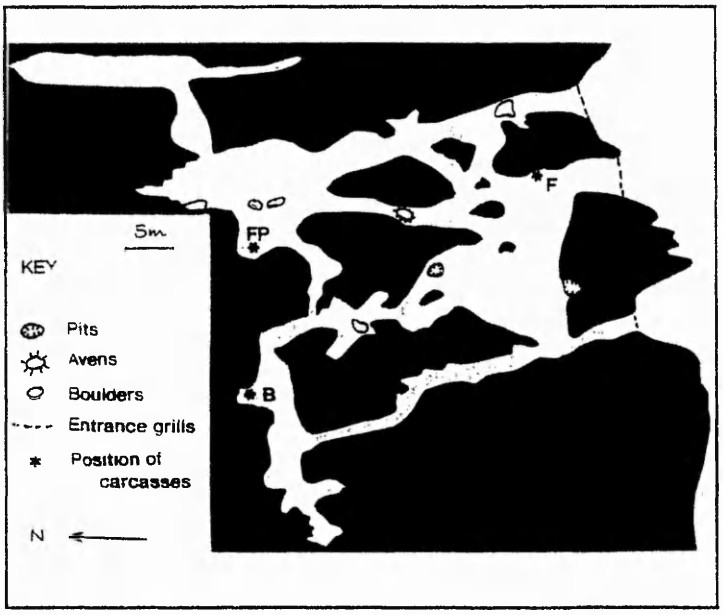


Figure 2.1: Floorplan of Robin Hood's Cave, Creswell Crags, showing the position of the carcasses.

During the baseline study and for the first year after the carcasses were deposited, traps were examined during the first or second week of every month. Following this, counts were made every second month (with one extra count in October 1989). Thus, pitfall traps were examined nineteen times during the experimental period.

The carcasses used were Sprague-Dawley rats killed by exposure to carbon dioxide. This method was employed in order to avoid bleeding (internal or otherwise) or contamination with anaesthetics, both of which may have affected the way in which the carcasses were colonised. (Ellison (1990) discovered that the succession observed on carcasses mutilated by vertebrate scavengers differed from that on intact carcasses, and Goff *et al* (1991) conducted experiments which showed that the presence of drugs in the tissue of a carcass influenced the development rate of certain colonising species.)

White rats were chosen because there was a plentiful supply of similar sized carcasses available. Many previous workers have used larger animals, such as cats (Illingworth, 1927), sheep (Deonier, 1940), dogs (Reed, 1958), pigs (Payne *et al*, 1965 *et seq*) and humans (Rodriguez & Bass, 1983) because "smaller carcasses (eg mice, rats and rabbits) do not last long enough to give a useful picture of the complete sequence of events occurring in a corpse" (Erzinçlioglu, 1986). However, preliminary work in the caves showed the rate of decomposition to be greatly reduced at lower temperatures and that distinct stages were obvious even in small carcasses.

The carcasses were deposited in the cave on 9th June, 1989 and left for two years. At the end of this time the remains were excavated. When designing the experimental set-up three factors had to be taken into account with regard to the placement and excavation of the remains in Robin Hood's Cave.

Firstly, since most of the cave floor is bare rock, and one aim of the experiment was to determine the effects of sediment depth on decomposition patterns, it was decided to place the carcasses on top of tanks containing cave sediment. This decision facilitated the other two problems: access during excavation and the desire to avoid disturbing the few remaining areas of natural sediment. The nature of the location - caves are cold, damp and dark - would have made *in situ* excavation difficult. Also two of the three sites were somewhat inaccessible which would have made it almost impossible to work with any accuracy. In addition, Robin Hood's

Cave is an English Heritage site, and as such is protected. There was then, no guarantee that permission would be granted for excavation work to take place.

The perspex tanks containing cave sediment were 32 x 22.5 cm and 20 cm deep, giving a maximum volume of 14.4 l (Figure 2.2). These could be removed for analysis at the end of the experiment. By using tanks in this way uniformity of sediment texture was guaranteed (by sieving), and depth could be varied. Different depths were achieved by partially filling the tanks with concrete which, in an attempt to make it as natural as possible, was made from water from the lake near the caves, cave sediment (which is very like red sand), and cement from a nearby quarry. Three depths were used: 5 cm, 10 cm and 15 cm.

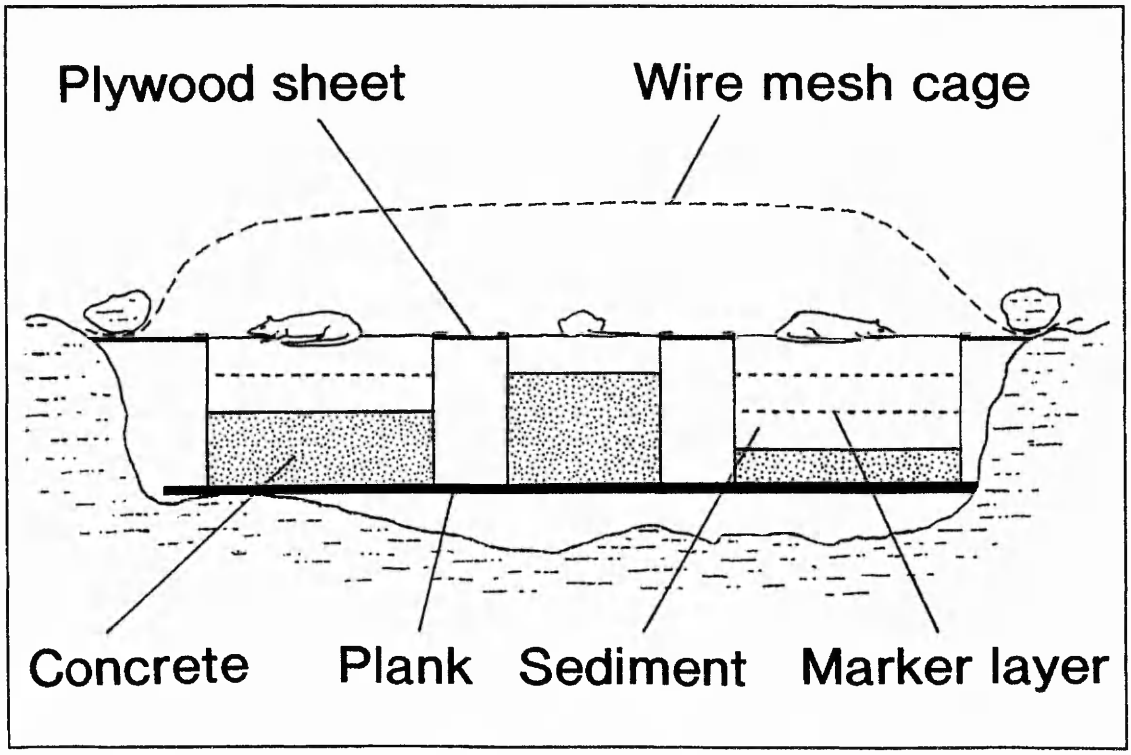


Figure 2.2: Tanks containing experimental rat carcasses *in situ*.

To monitor bioturbation, the sediments within the tanks into which the carcasses were placed were layered every 5 cm with a powder consisting of dried

Lycopodium spores, fresh pollen and polystyrene beads, mixed with talcum powder to make the marker layer more visible. The control tank at each site was also layered in the same way in order to measure the amount of sediment disturbance in the absence of decomposing material.

Lycopodium spores are commercially available, but the pollen had to be collected. This was done by drying and crushing the pollen sacs of honey bees (*Apis mellifera*) which had been caught as they returned to the hive.

The largest markers used were 1 mm diameter polystyrene beads, the same size as the largest particles in the sediment. Due to the inert composition of these beads no reaction could take place on their surface which might alter the sediment chemistry. They were also clearly visible in cave sediment with the naked eye, and readily available commercially.

The polystyrene beads were dyed different colours so that the different layers could be distinguished from one another. The dyes used were the haemocytological stains Oil Red O, Sudan Black and Crystal Violet. A number of stains were tested and these three chosen because they were easily distinguished from one another and also because they were adsorbed onto the surface of the beads and so reasonably permanent. This was important because of the high humidity in the cave and the high water content of the cave sediment. Additionally, bead colour had to be distinguishable after the extraction process. The stains were made up thus:

* **Oil Red O**: Oil Red O powder was dissolved in 99% isopropanol until a saturated solution was achieved.
* **Sudan Black**: Sudan Black powder was dissolved in 70% ethanol until a saturated solution was achieved.
* **Crystal Violet**: 2 g of Crystal Violet were dissolved in 20 cm^3 of 95% alcohol. This was in turn dissolved in 80 cm^3 of 1% aqueous ammonius oxalate using the minimum of heat, and filtered when cool.

So that the experimental rats could remain undisturbed two control rats were positioned on bare rock at each site. The experimental rats all weighed between 225 and 275 g while the control carcasses were slightly heavier at between 350 and 475 g.

The latter were used to record weight loss (using a spring balance) and temperature fluctuations in the carrion (by inserting a thermometer), as well as being periodically examined for invertebrates. Also measured regularly were ambient temperature and humidity (using a Casella digital thermohygrometer). Accurately positioned photographs were also taken of each carcass to survey post-depositional movement and to assess overall changes in appearance.

Six experimental tanks, two of each depth, were placed at each of the three sites. In order to ensure that the carcasses were accessible to flightless insects and other arthropods the tanks were lowered into holes cut into plywood sheets placed over pre-existing pits in the cave floor. A shallow layer of cave sediment was scattered over the plywood surround to give the appearance of continuation between the tanks, the plywood and the cave floor around the pit. The entire set-up was then covered with a dome made of wire netting to exclude vertebrate scavengers.

A control tank, prepared in the same way as the experimental ones but with no carcass, was also placed at each site.

For identification purposes, each carcass was allocated a number, experimental carcasses being ER/1 to ER/18, and control carcasses CR/1 to CR/6. ER/1 to ER/6, CR/1 and CR/2 were deposited in the Front chamber, ER/7 to ER/12, CR/3 and CR/4 in the Frogpit chamber, and ER/13 to ER/18, CR/5 and CR/6 in the Back chamber.

The remains of the experimental rats were removed, still within the tanks, after two years, on 30th April, 1991.

2.2 Church Hole Cave

Further investigations were carried out in Church Hole Cave, also at Creswell. Church Hole is a narrow fissure, approximately 44 m long, and sites were at 8 m (Front), 28 m (Middle) and 42 m (Back) from the entrance. Figure 2.3 (overleaf) shows the position of the sites on a floorplan of the cave.

Experiments in Church Hole were begun on 2nd February, 1990. Thus, results from this cave could be compared with those from Robin Hood's Cave (where carcasses were deposited in June), and any differences due to season identified.

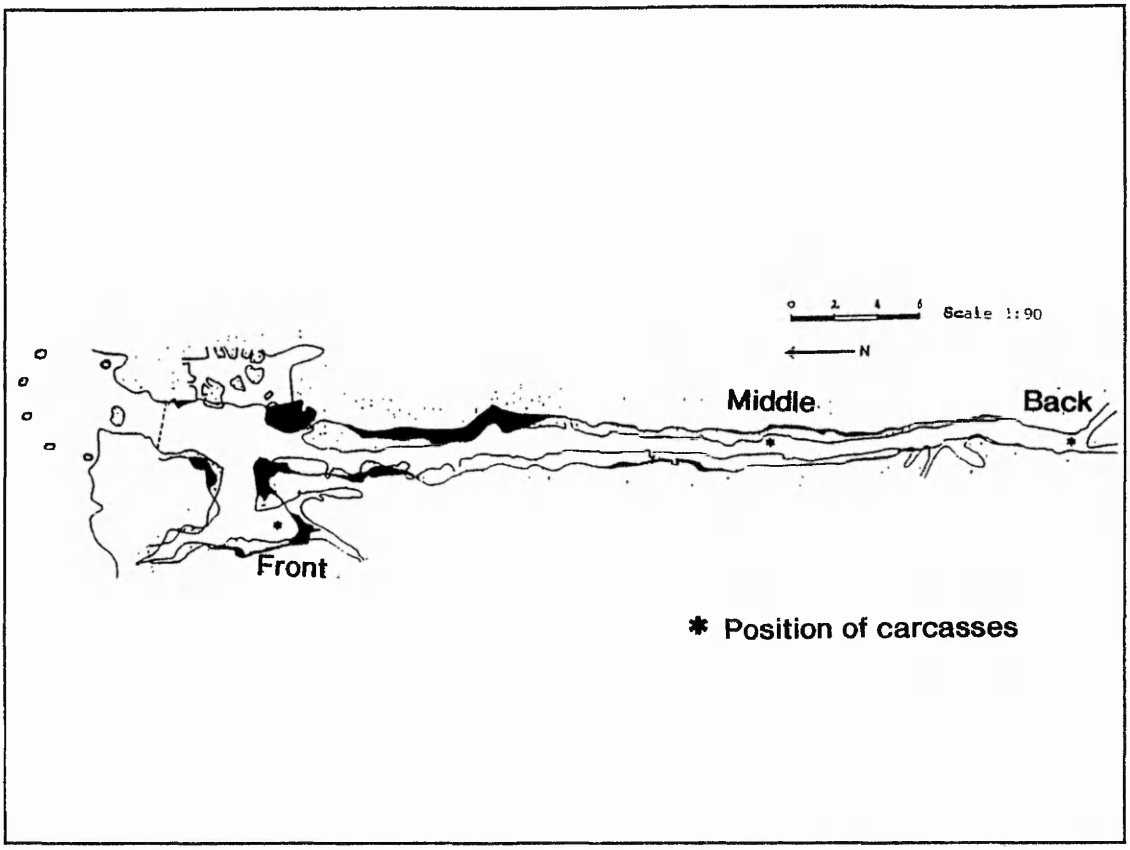


Figure 2.3: Floorplan of Church Hole Cave, Creswell Crags, showing the position of the carcasses.

Pitfall trapping had been continuous in this cave since 1986 and so a baseline species list had been established and changes in diversity were constantly monitored. Pitfall traps were situated at thirteen sites in the cave (every 4 m from the entrance, with two at 4 m), and were emptied once a month.

Just one tank was put at each site in Church Hole and although each was layered in the same way as those in Robin Hood's Cave, none of them contained concrete and so the sediment in each was approximately 20 cm deep. Due to a lack of suitable pits within Church Hole it was impossible to place the tanks flush with the cave floor. Instead, each tank was positioned touching the wall on one side and natural 'ramps' were constructed around the other three using rocks of various sizes from the cave. Regular readings of ambient temperature and humidity were taken, and an

accurate photographic record was kept.

The tanks were removed on 19th February, 1991 and returned to the laboratory for excavation.

2.3 Post-mortal movement

One further experiment was conducted in Robin Hood's Cave to assess the extent of post-mortal movement of carcasses (Figure 2.4). A plywood sheet approximately 1.5 x 1.5 m was placed on the ground in the Frogpit chamber.

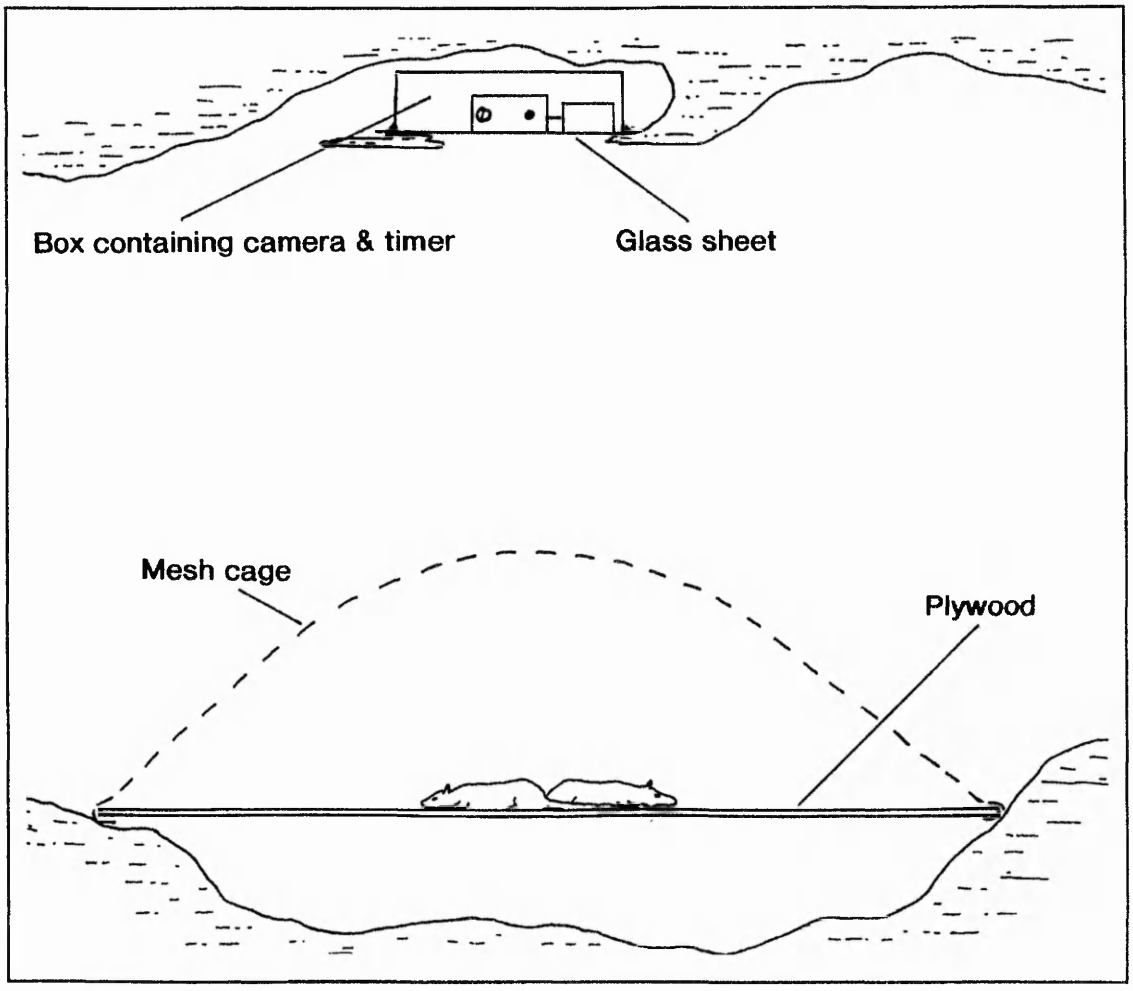


Figure 2.4: Apparatus to monitor post-mortal movement *in situ* (not to scale).

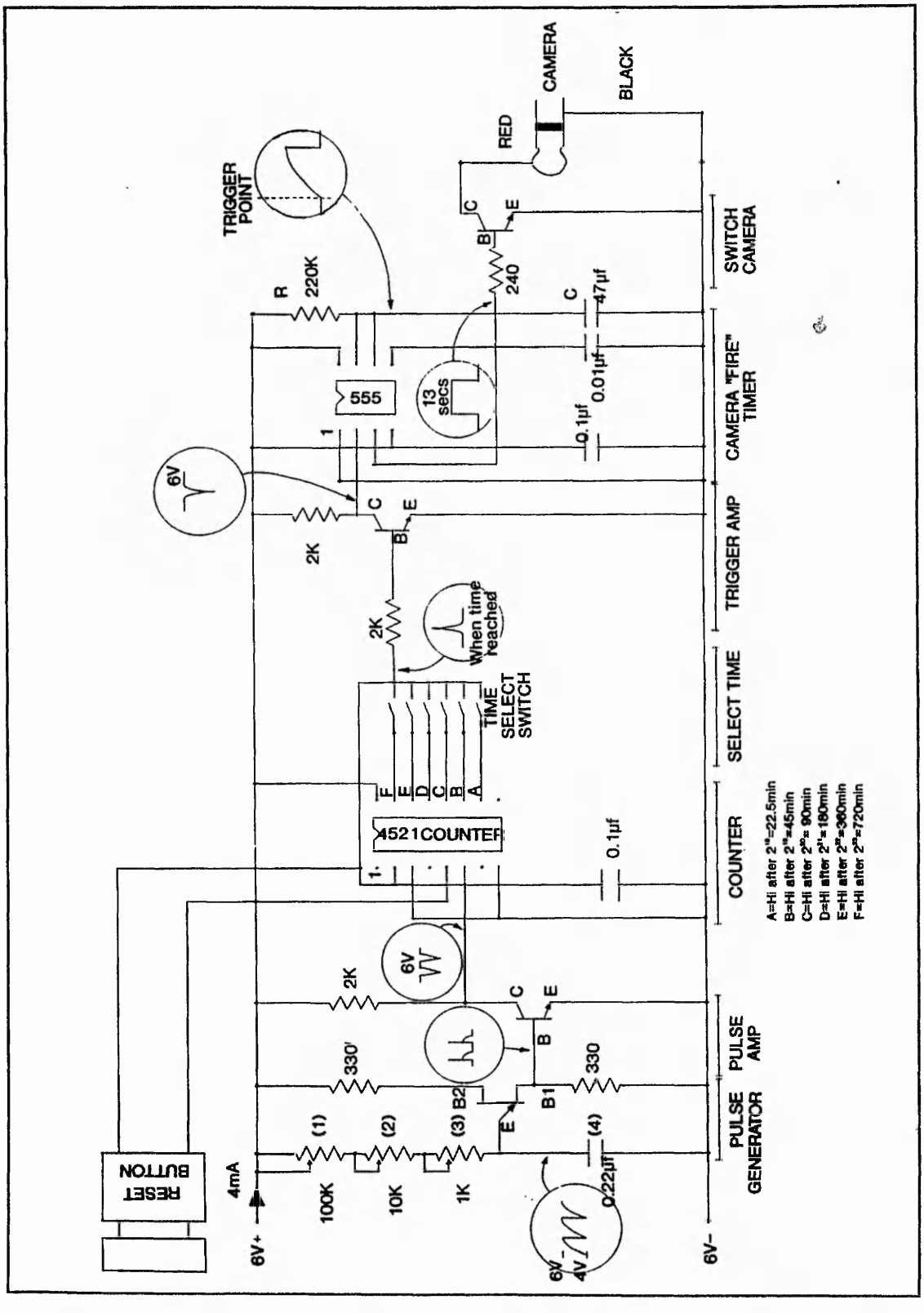


Figure 2.5: Circuit diagram of timer designed to trigger camera every 12 hours.

A grid consisting of 15 x 15 cm squares was drawn on the plywood, after which it was scattered with a shallow layer of cave sediment. Two rat carcasses, upon which *Calliphora vomitoria* had been allowed to oviposit outside the cave, were placed in the centre of the sheet, and a note made of their position in the grid. Finally, the apparatus was covered by a wire mesh dome to prevent interference by vertebrate scavengers.

Attached to the roof of the cave above the apparatus was a camera (Ricoh FF9D) which had been fitted with a timer (Figure 2.5, previous page). The shutter was triggered every twelve hours, and the series of photographs taken were to have been used in conjunction with personal observations to map the post-mortal movement of the two carcasses.

The experiment was begun in warm weather on 19th August, 1991 to coincide with a period of high calliphorid activity.

2.4 Bioturbation

To monitor bioturbation, three cores were taken from each of the experimental tanks in Robin Hood's Cave. This was done when the active stages of decomposition were judged to have ended, approximately six months after the experiment was begun. In each tank, one core was taken in the region of the head of the carcass, one in the region of the tail, and one from the edge of the tank, approximately 20 cm from the centre of the carcass. One core was taken from each control tank.

Cores were taken using 1.2 cm diameter plastic tubes, approximately 30 cm long marked with 1 cm graduations. These were pushed into the sediment to a depth of 5 cm, and removed carefully. The contents were extruded by means of a plunger. For tanks with more than 5 cm of sediment the process was repeated in the same borehole. Each core was separated into 1 cm sections and returned to the laboratory for analysis.

Samples were treated using an adaptation of a technique designed to extract pollen from peat (Faegri and Iverson, 1964). Figure 2.6 (overleaf) is a flow diagram describing the extraction process. Samples from the control tanks were treated in the

same way as experimental samples.

Methylene blue is recommended to stain the pollen and *Lycopodium* for maximum contrast (the cave sediment from Creswell was reddish-orange).

Remove and record any bones, puparia etc. found in whole sample.

↓

Place 1 g of sample in centrifuge tube, and half fill tube with 20% KOH.

↓

Place tube in boiling water bath for 30 min to remove humified fraction.

↓

Filter contents through 100 nm nylon bolting cloth to remove larger particles and beads.

↓

Centrifuge filtrate at 550 G for 3 min.

↓

Tip off supernatant and resuspend in 2 ml distilled water. Add 0.8 ml 0.02% methylene blue. Centrifuge as before.

↓

Transfer 25 μl of sample and 20 μl glycerine albumen onto a microscope slide. Add cover slip.

↓

Examine slide immediately and record number of pollen grains and number of *Lycopodium* spores.

Figure 2.6: Extraction and quantification of markers

Methylene blue deteriorates rapidly, thus once it is added the remaining stages of the extraction process must be completed as quickly as possible.

Certain samples do not stain successfully with methylene blue, and as an alternative safranin may be used. This stains the pollen and spores red, which may make them more difficult to distinguish from the cave sediment.

2.5 Excavation of tanks

Upon removal from the caves, all experimental tanks were returned to the laboratory and kept in a cold room at a temperature of 10 ^{o}C until being excavated. This involved a number of stages. Firstly the surface of the sediment was surveyed to assess its topography. Next the surface was mapped to outline the position of the remains. Once this was done the decomposed carcass and/or any bones were removed, identified and bagged, and finally the sediment in the tank was excavated and examined layer by layer.

The surface was surveyed using the apparatus in Figure 2.7 (overleaf). The original level of the sediment (the height of the tank) was determined first and then, by moving the frame across the tank 2 cm at a time and manipulating the vertical probes, the difference between this reading and the actual level of the sediment was calculated.

In some cases the remains consisted of a more-or-less intact carcass, the bones being held together by dried out skin, fungal hyphae or connective tissue. When this was so, once the carcass had been removed, the area upon which it lay was surveyed again. In this way a picture was built up of the surface of the sediment with and without remains, and any depressions in the surface caused by the sinking of the carcass noted. In cases where the carcass had been reduced to bones which had to be removed individually, only the initial survey was carried out.

The sediment was removed in layers (spits) 1 cm deep. The exact three dimensional position of any bones within the sediment was plotted before they were identified and bagged. Once a complete layer had been removed the sediment was sieved and any dead invertebrates, puparia, etc. identified and counted.

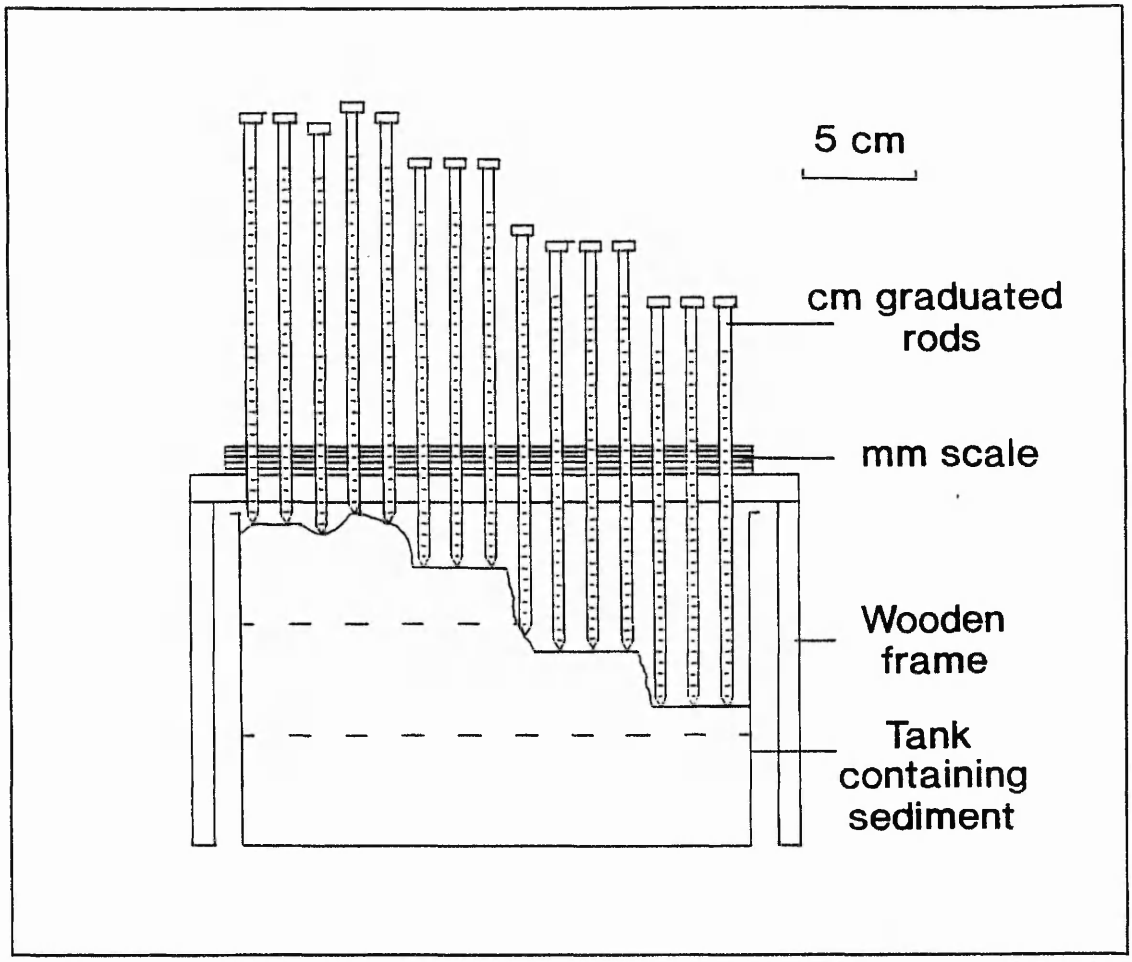


Figure 2.7: Apparatus used to measure depth of sediment during the excavation of the tanks.

One of the carcasses from the Front Chamber of Robin Hood's Cave was more closely examined to ascertain how much material had been removed from within the body cavity. The entire mummified carcass was soaked in a bath of 25% glycerol (by volume) for approximately 84 hours (method adapted from Evans, 1962), by which time the skin had softened and become pliable. It was then possible to pin the animal out in a dissecting tray and open up the abdomen from chin to anus.

CHAPTER THREE
RESULTS : ROBIN HOOD'S CAVE

Figure 3.0: The entrance to Robin Hood's Cave, Creswell Crags.

3.1 Abiotic conditions

Readings of temperature and relative humidity were taken regularly at each site, and the mean values for the period June 1989 to March 1991 are shown in Table 3.1, while Figure 3.1 (overleaf) shows the mean monthly ground level temperatures throughout the same period.

Table 3.1: Mean (±95% limits) temperature and relative humidity (RH) at ground level and 1 m above ground level at three sites in Robin Hood's Cave, (a) for the first three months after deposition, and (b) for the full two years of the experiment.

	Ground Level		1 m above Ground	
	Temp (^{O}C)	RH (%)	Temp (^{O}C)	RH (%)
(a) 90 days				
FRONT	13.2±0.4	89.7±3.1	15.9±0.9	76.4±4.3
FROGPIT	9.4±0.2	100.4±2.8	10.7±0.3	93.5±2.7
BACK	10.3±0.2	101.8±3.2	11.8±0.3	94.5±2.9
(b) 2 years				
FRONT	10.5±1.6	87.5±3.3	12.2±2.1	79.0±4.6
FROGPIT	8.7±0.6	95.7±3.4	9.6±0.7	90.4±2.9
BACK	9.9±0.4	99.4±2.6	11.2±0.5	93.0±2.2

The above figures show that over the two year period of the experiment, fluctuations in both temperature and relative humidity decreased with increasing depth. The temperature at ground level in both the Front and Back chambers was significantly higher than that in the Frogpit chamber ($t=3.61$, $p<0.05$ for Front and Frogpit; $t=9.29$, $p<0.001$ for Frogpit and Back). Although warmer on average, the temperature in the Front chamber was too variable to produce a significant comparison with the Back chamber.

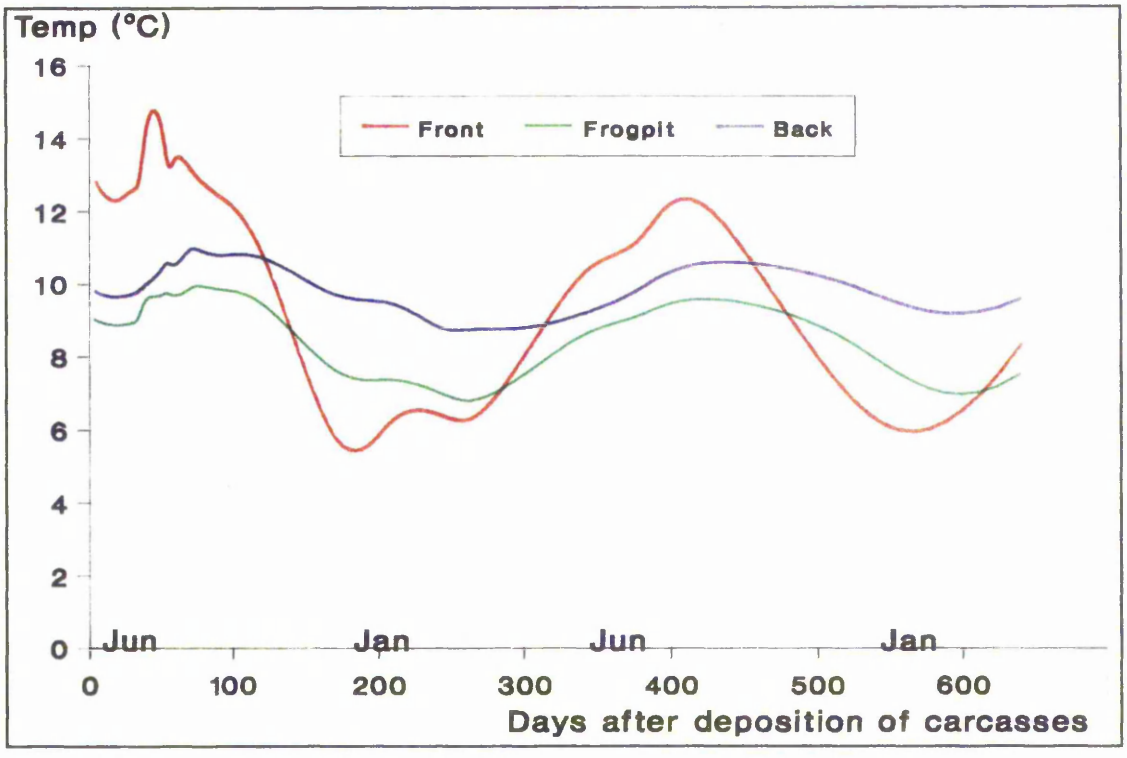


Figure 3.1: Monthly ground level temperature (mean) in the three chambers in Robin Hood's Cave during the two years of the experiment.

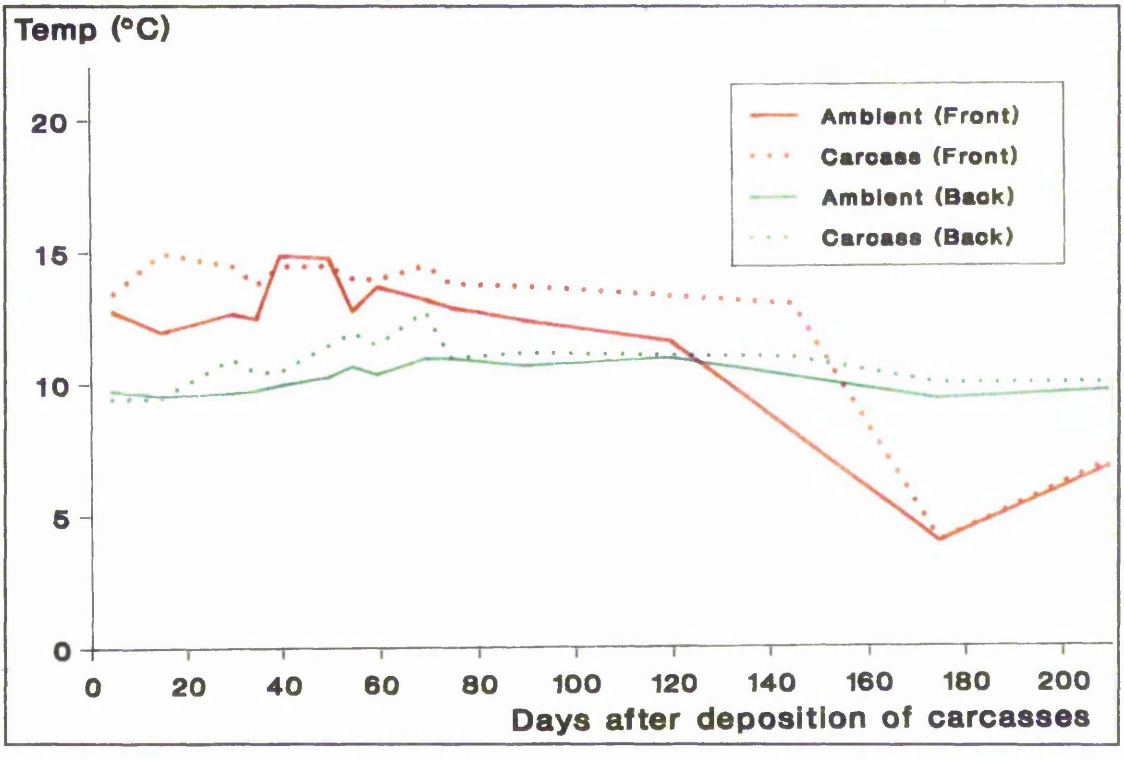


Figure 3.2: Comparison of carcass temperature with ambient temperature (at ground level) in the Front and Back chambers of Robin Hood's Cave.

Maximum/minimum thermometer readings show that the ground level temperature in the Frogpit chamber varied between 3 and 11 °C. In the Back chamber, however, there was far less fluctuation, with the temperature ranging between 7 and 11 °C at ground level.

As well as ambient temperature, carcass temperature was regularly recorded. The results of these readings for the first six months of the experiment from the Front and the Back chambers are presented in Figure 3.2 (previous page). This shows that carcass temperature was often higher than ambient temperature.

3.2 Fauna and fungi

Table 3.2 is a summary of all invertebrates found in Robin Hood's Cave during the course of this work, both before and after the carcasses were deposited.

Table 3.2: Species found in Robin Hood's Cave expressed as actual numbers (upper figure), and as a per cent of the total number of species found in that chamber (lower figure), before (Bline) and after (Exptl) carcasses were deposited.

	Front		Frogpit		Back	
	Bline	Exptl	Bline	Exptl	Bline	Exptl
Annelida	1 1.8					2 5.6
Acari	3 5.5	3 3.6	4 8.9	3 5.7	3 10.0	3 8.3
Chelonethi		1 1.2				
Opiliones		1 1.2	1 2.2		1 3.3	

continued.....

	Front		Frogpit		Back	
	Bline	Exptl	Bline	Exptl	Bline	Exptl
Araneidae	6 10.9	8 9.6	4 8.9	1 1.9	2 6.7	2 5.6
Isopoda	1 1.8					1 2.8
Chilopoda	2 3.6		1 2.2	1 1.9		1 2.8
Diplopoda	1 1.8	1 1.2	1 2.2		1 3.3	1 2.8
Diplura	1 1.8		1 2.2		1 3.3	
Collembola	10 18.2	5 6.0	8 17.8	7 13.2	8 26.7	7 19.4
Psocoptera		1 1.2	1 2.2			
Hemiptera	1 1.8	1 1.2				
Thysanoptera	1 1.8	3 3.6	1 2.2	1 1.9		
Mecoptera	1 1.8	1 1.2				
Lepidoptera	2 3.6	2 2.4		1 1.9		
Diptera	13 23.6	31 37.3	13 28.9	21 39.6	8 26.7	15 41.7
Siphonaptera					2 6.7	
Hymenoptera	2 3.6	8 9.6	1 2.2	4 7.5		
Coleoptera	10 18.2	18 21.7	9 20.0	14 26.4	4 13.3	4 11.1

The baseline fauna of Robin Hood's Cave comprised of 75 species whereas 117 were found in the two years after the carrion had been deposited, although only 34 species were found both before and after deposition. Full details of the baseline and the monthly pitfall catch during the experimental period can be found in Appendix 1.

Table 3.3 shows the number of species found in each chamber, and also the percentage of those which were also found in the other chambers.

Table 3.3: The distribution of species in the three chambers of Robin Hood's Cave, and the overlap between chambers.

	Total no of species found	Percentage of total also found in Front	Frogpit	Back	All
Baseline					
Front	55	100	56	36	36
Frogpit	45	69	100	53	49
Back	30	67	80	100	53
Experimental					
Front	83	100	36	26	21
Frogpit	53	57	100	42	34
Back	36	61	61	100	50

Both before and after deposition, most species found were restricted to one chamber only (40 before deposition, 79 after). Twenty species were found in all three chambers before the carrion was deposited, and eighteen after.

These figures show that those species found further into the cave were more likely to also be present elsewhere than those found near the entrance.

Changing temperatures were responsible for fluctuations in the baseline cavernicolous fauna (Figures 3.3 and 3.4, overleaf). The correlation between the number of species trapped and average ambient temperature is shown in Figure 3.3, and is especially significant in the Front and Frogpit chambers. The number of

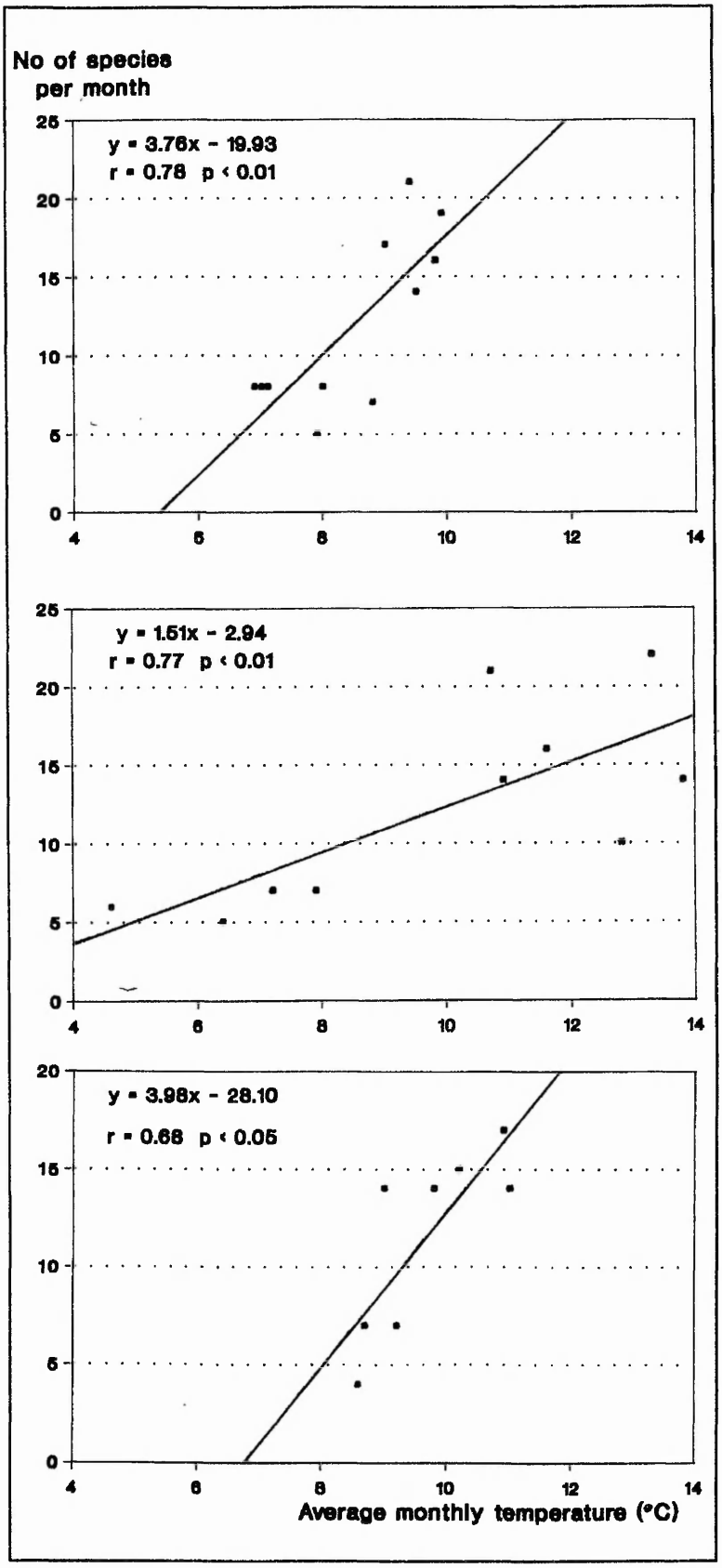


Figure 3.3: Baseline relationship between the number of species collected per month and the average ground level temperature for the preceeding four weeks, in:

(a) the Front chamber,

(b) the Frogpit chamber

(c) the Back chamber.

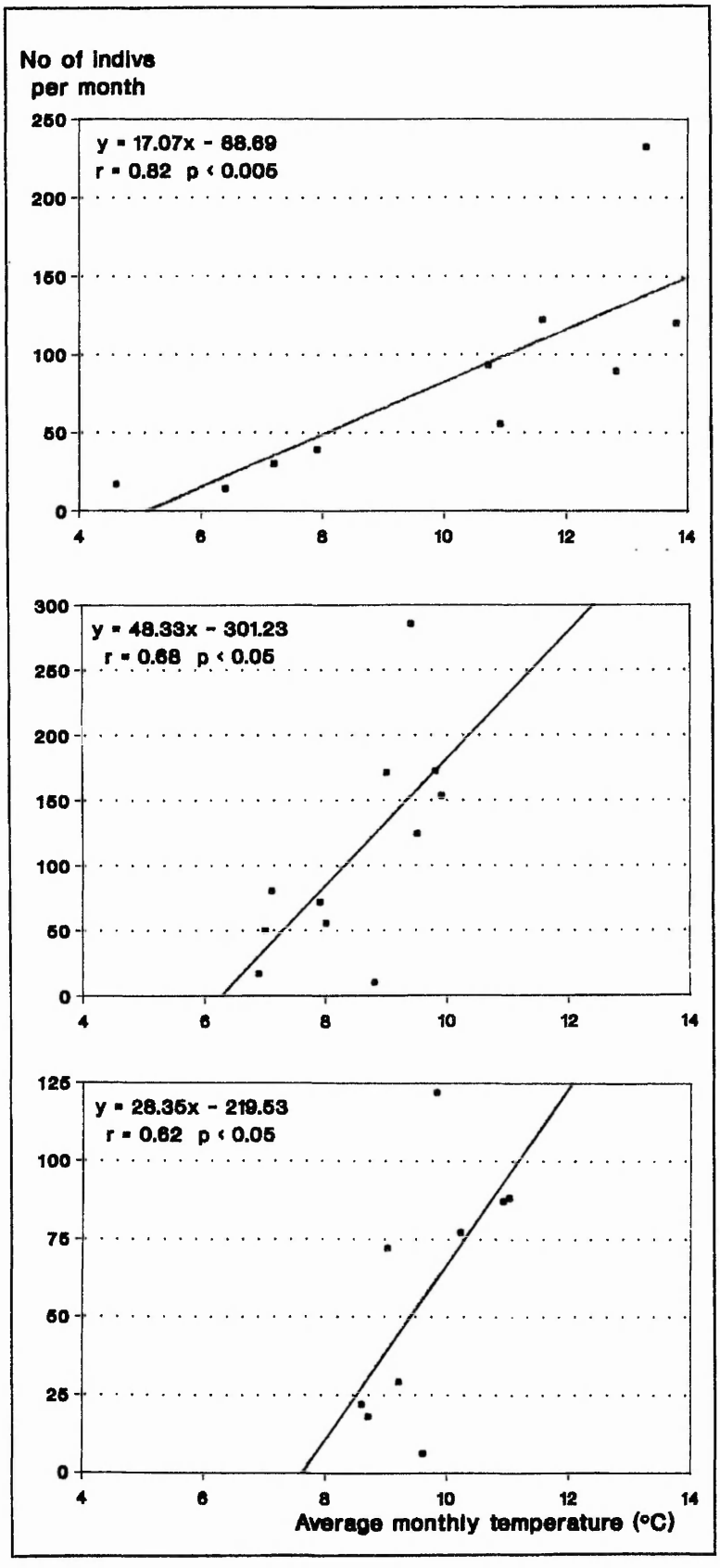


Figure 3.4: Baseline relationship between the number of individuals collected per month and the average ground level temperature for the preceeding four weeks, in:

(a) the Front chamber,

(b) the Frogpit chamber,

(c) the Back chamber.

individuals trapped in a month is also more strongly dependant upon temperature towards the entrance of the cave (Figure 3.4).

A number of fungal species were also involved in the decomposition of the carcasses, particulary at the back. It is thought that if carcasses were deposited far enough from the entrance then decomposition would be almost entirely microbial.

Table 3.4 lists a sample of the fungi isolated from the caves at Creswell during an investigation carried out by Terrell-Nield in 1984/5 (unpublished). These species are not necessarily restricted to the cave or the depth at which they are listed, and may be found closer to or further from the entrance in any of the caves at Creswell. Terrell-Nield (pers. comm.) found that the number of spores in both the air and the sediment decreased with increasing distance from the entrance of the cave.

Table 3.4: List of fungi isolated from Creswell caves.

KEY: P Pinhole Cave RH Robin Hood's Cave
B Boathouse Cave C7 Small, un-named cave between P & RH

Species	Depth (m)	Cave
Acremonium strictum	48	P
Alternaria alternaria	4	RH
Aspergillus aspherescens	36	P
Aspergillus niger	4	P
Aspergillus versicolor	44	P
Aureobasidium pullulans	12	RH
Aureobasidium sp	8	RH
Cladosporium (*cladosporoides*?)	12	P
Colletrichum sp (atypical)	12	C7
Fusarium culmorum	4	RH
Mortierella isabellina	46	P
Mortierella rathmanniana	12	RH
Mucor hiemalis	8	P

continued.....

Species	Depth (m)	Cave
Mucor sp	36	B
Paecilomyces lilacinus	44	P
Penicillium cyclopium	28	P
Penicillium granulosum	44	RH
Penicillium hirsutum	32	P
Penicillium mali	40	P
Penicillium (*melini*?)	31	RH
Penicillium piceum	20	P
Phoma exigua	20	P
Phoma herbarum	12	P
Phoma nebulosa	12	P
Phomopsis sp	8, 18	P
Sporobolomyces sp	28	RH
Stephanosporium cereale	28	P

Species identified by the Institute of Mycology, London.

It has been observed in this and previous decomposition studies at Creswell that the sequence of fungal succession is always the same, beginning with a greyish-blue *Penicillum* sp soon after deposition. This species first appeared on the heads of carcasses, and also grew on the parts touching the sediment, such as the underside of the belly. Two species of fungus were seen next, an unidentified Bacidiomycete and *Mucor* sp. Both are white, the former having the appearance of loose cotton-wool, while the latter is an erect species, which grows as a diffuse colony. Two other species appeared later; a yellowy orange *Fusarium* sp and a dark green *Aspergillus* sp. Although other fungi were seen on the carrion (the sclerotia of a species of *Microascus* were very common on the carcasses further into the cave), these five were the dominant species in the succession on all carcasses.

3.2.1 Front Chamber

Plates 1 to 4 (overleaf) show the physical appearance of ER/6, one of the carcasses deposited in the Front chamber, during the first four months of decomposition.

Plate 1: ER/6 after two weeks in the Front chamber of Robin Hood's Cave.

Plate 2: ER/6 after seven weeks in the Front chamber of Robin Hood's Cave.

Plate 3: ER/6 after ten weeks in the Front chamber of Robin Hood's Cave.

Plate 4: ER/6 after fifteen weeks in the Front chamber of Robin Hood's Cave.

The carcasses in the Front chamber were attacked very quickly by diptera. The most obvious of these were the blowflies (Calliphoridae), which came from outside the cave. All individuals collected were later identified as *Calliphora vomitoria*. Eggs were laid around the orifices of the carcasses. Between five and nine days after deposition the larvae began to hatch and burrow into the body cavity. The larval stage lasted for less than three weeks, during which time all the soft tissue on the carcasses was devoured (Plate 1). Much of the hair was shed and some transported up to 2.5 m by larvae leaving the carcasses to pupate (Plate 2). Figure 3.5 a (overleaf) shows that only one generation of *Calliphora* was evident.

Also associated with the carcasses during the first few months were the necrophagous *Triphleba antricola* and *Megaselia rufipes* (Diptera: Phoridae). The increase in numbers of *Triphleba* in December (Figure 3.5 a) indicates that this species may have bred on the carcasses, although no larvae or pupae were observed. There is no evidence of breeding in *Megaselia*, however.

Captures of other Diptera attracted to the carcasses in small numbers are represented in Figure 3.5 b (overleaf). These included the fungus gnats *Bradysia brunnipes* and *Lycoriella leucotricha* (Sciaridae), which are commonly found throughout the cave, as well as *Psycoda* sp (Psychodidae), *Anisopus fenestralis* (Anisopidae), *Saltella sphondylii* (Sepsidae), species of Mycetophilidae and Cecidomyiidae, and the predatory *Psylopus* spp (Dolichopodidae) and Empididae.

Individuals from the families Anthomyzidae, Drosophilidae, Tipulidae and Tabanidae were also found in the pitfall traps. It is unlikely, however, that their association with the carrion was anything more that accidental.

Figure 3.6 (page 54) represents the Coleoptera attracted to the carrion. The family Staphylinidae was represented by *Aleochara* spp, *Oxypoda opaca*, *Ocelea badia*, *Acrotona* spp, *Omalium excavatum* and *Oxytelus tetracharinatus*. *Choleva glauca* and *Catops tristis* (Cholevidae) were also present, as were *Cryptophagus* spp (Cryptophagidae) and *Cartodere ruficollis* (Lathridiidae).

Figure 3.7 (page 55) shows the occurrence of Lepidoptera and Hymenoptera in the pitfall traps. During the early stages two species of Lepidoptera from the families Pyralidae and Tineidae were attracted to the carcasses. Most of these were *Hofmannophila pseudospretella* (Tineidae), the brown house moth.

Figure 3.5: Numbers of individuals of Diptera trapped in the Front chamber of Robin Hood's Cave during the experiment in relation to the baseline: (a) *Calliphora vomitoria* (Calliphoridae), *Triphleba antricola* and *Megaselia rufipes* (Phoridae) (above), and (b) *Bradysia brunnipes*, *Lycoriella leucotricha* (Sciaridae) and other Diptera (below).

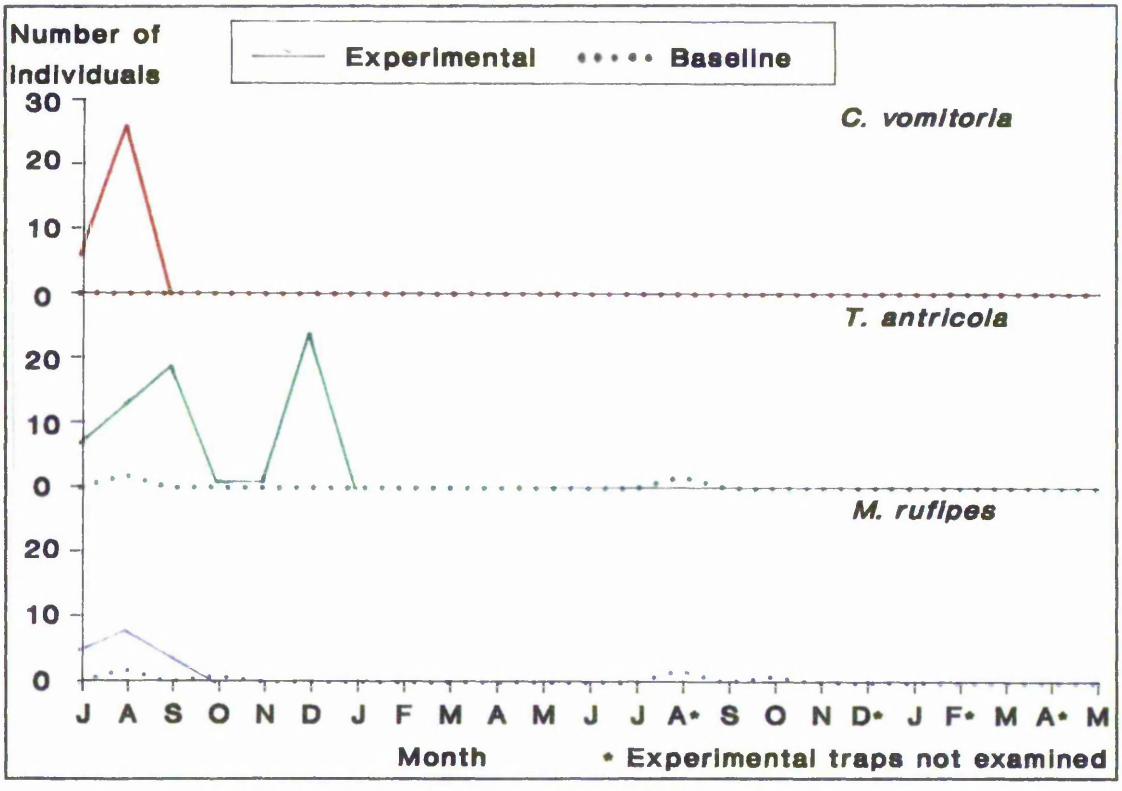


Figure 3.5 a

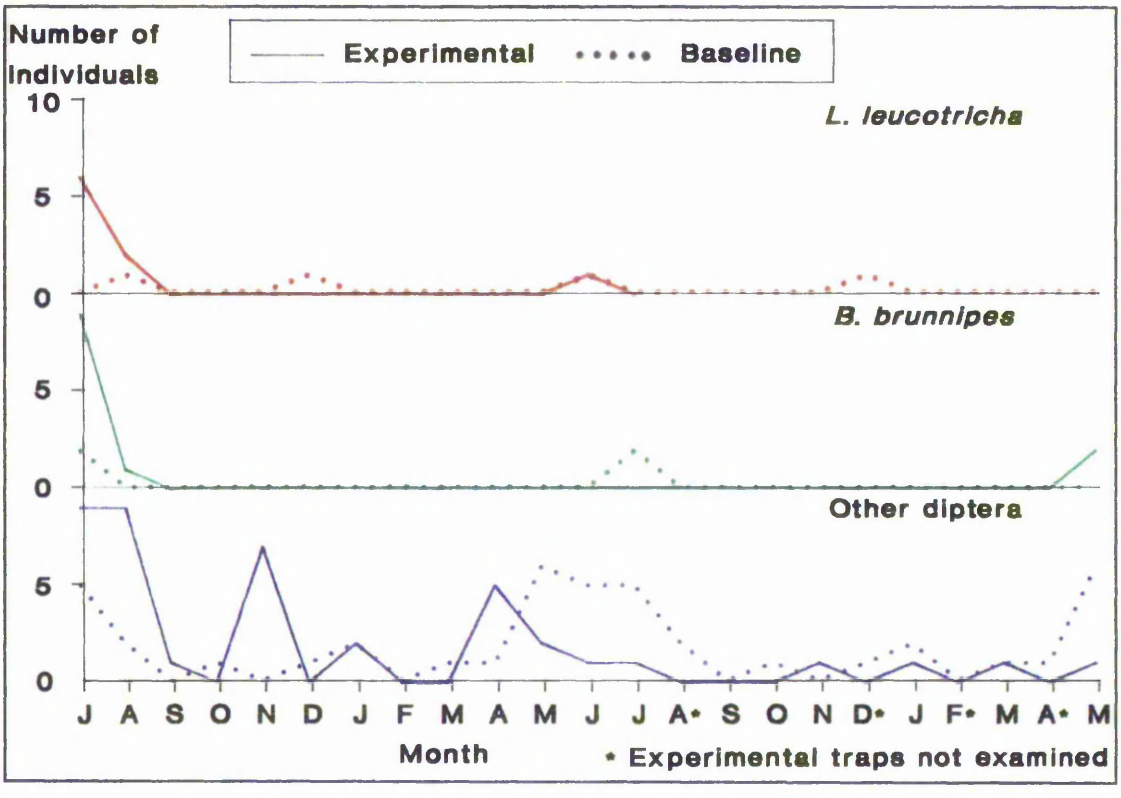


Figure 3.5 b

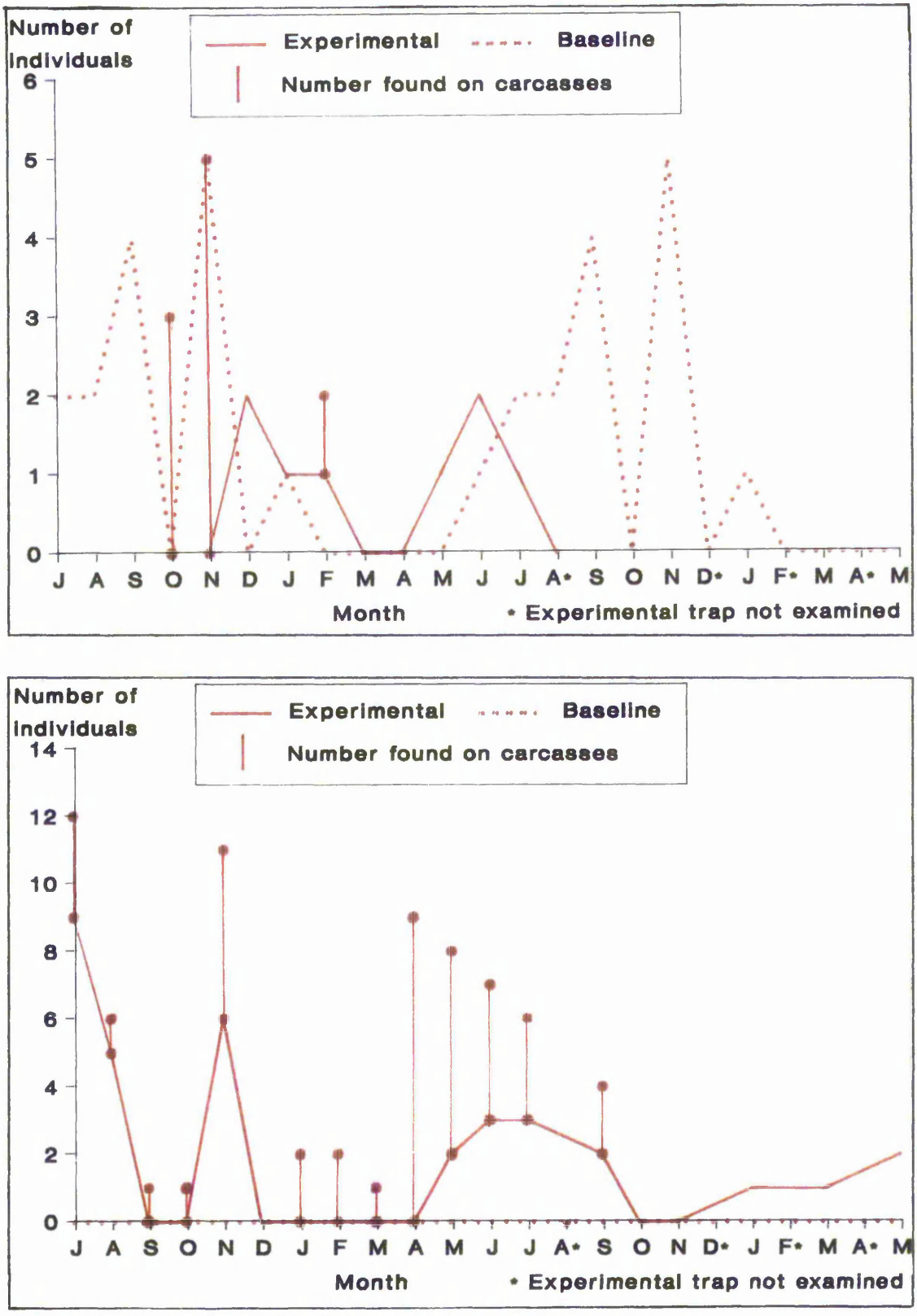


Figure 3.6: Numbers of individuals of Coleoptera trapped in the Front chamber of Robin Hood's Cave during the experiment in relation to the baseline:
(a) *Cryptophagus* spp (Cryptophagidae) (top) and (b) other Coleoptera (above).

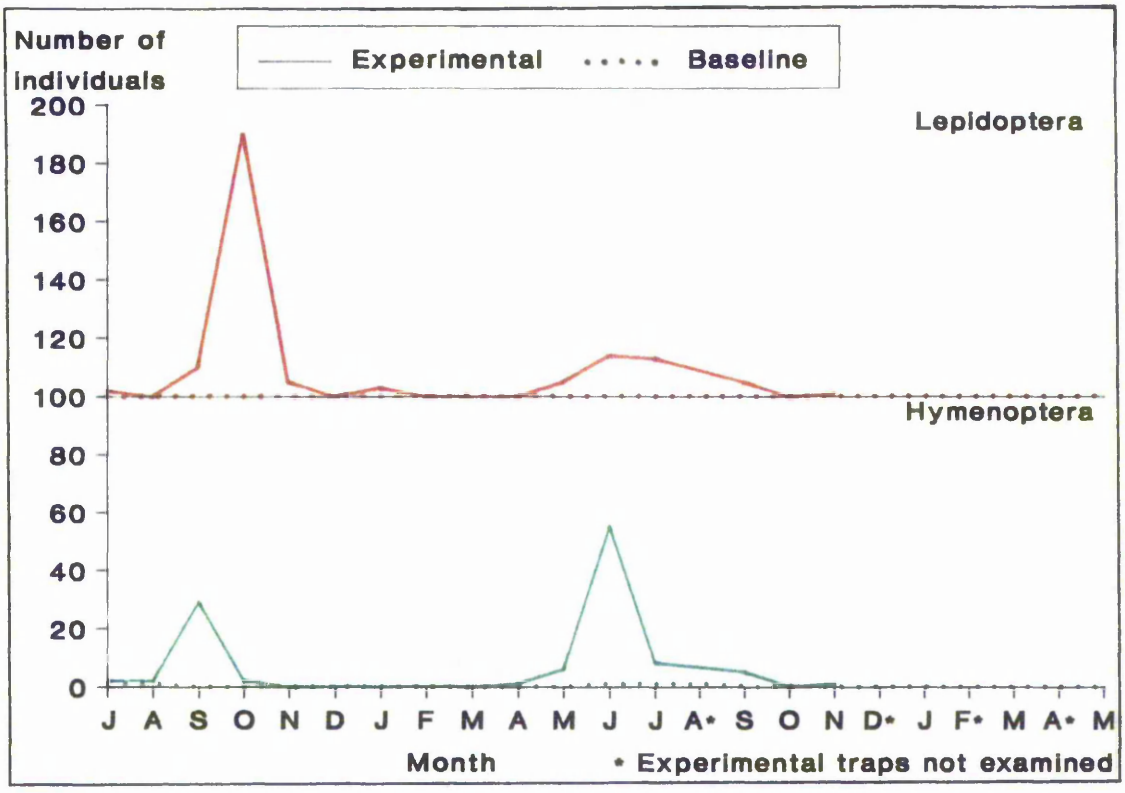


Figure 3.7: Numbers of individuals of Lepidoptera and Hymenoptera trapped in the Front chamber of Robin Hood's Cave during the experiment in relation to the baseline.

A number of adult Lepidoptera were found both in the pitfall traps and on or near the carcasses during July, and larvae hatched from August through to October, by which time the remains were completely mummified (Plates 3 & 4). After February of the next year there was no evidence of either adults or larvae until May when the adults reappeared. A few larvae were then found in September.

Associated with the Lepidoptera and also found in the vicinity of the carcasses at about the same time were a number of parasitic Hymenoptera. These included families such as Braconidae and Ichneumonidae, species of which parasitise lepidopteran larvae and pupae (Richards, 1977).

One non-cavernicolous species, *Thripia* sp (Thysanoptera: Thripidae) persisted in far greater numbers than would usually be expected (Figure 3.8, page 56). These, along with a number of mite species and the Collembola *Lepidocyrtus curvicollis* and

Figure 3.8: Numbers of individuals of the Tysanoptera *Thripia* sp (Thripidae) trapped in the Front chamber of Robin Hood's Cave during the experiment in relation to the baseline.

Figure 3.9: Numbers of individuals of the Collembola *Lepidocyrtus curvicollis*, *L. cyaneus* and *Pseudosinella alba* (Entomobryidae) trapped in the Front chamber of Robin Hood's Cave during the experiment in relation to the baseline.

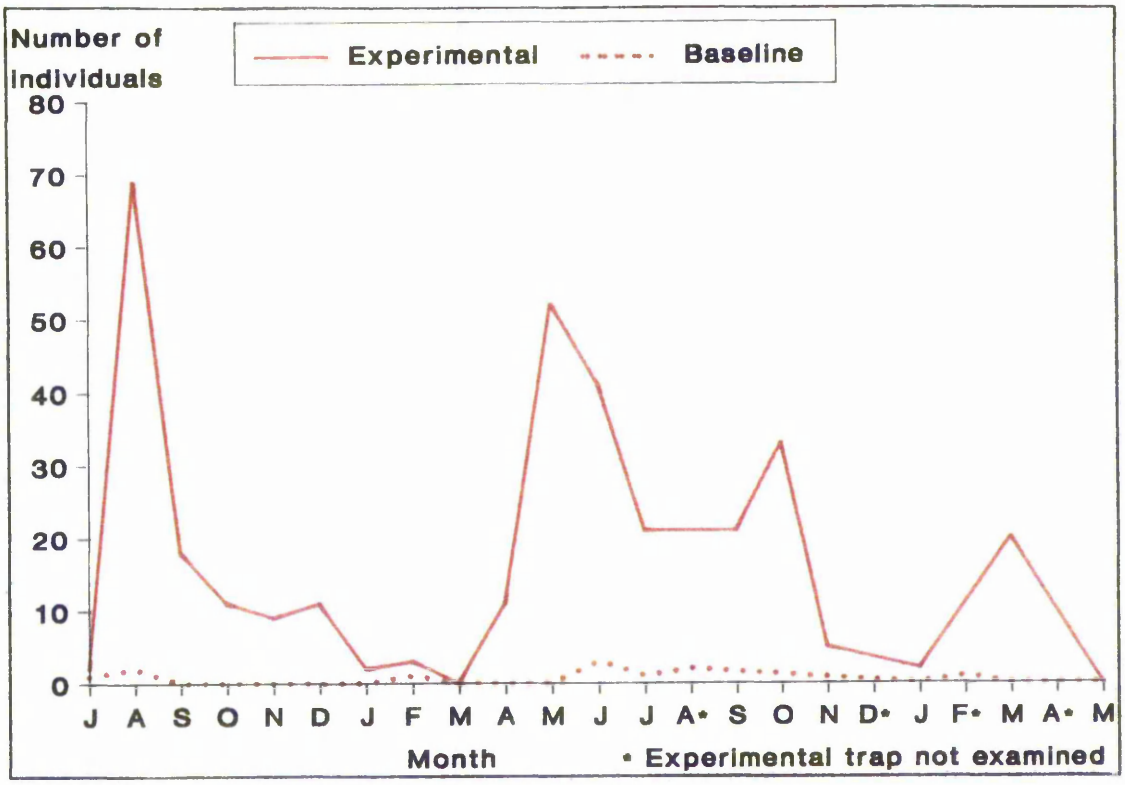


Figure 3.8

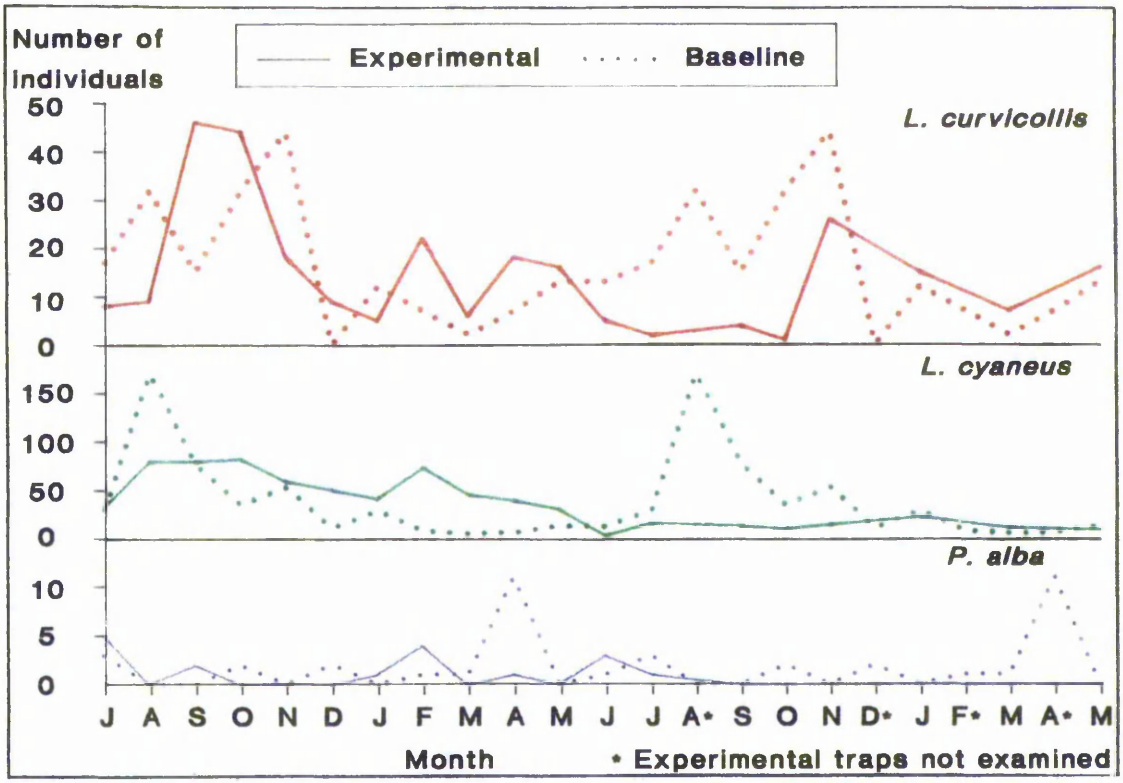


Figure 3.9

Figure 3.10: A comparison of the baseline fauna of the Front chamber in Robin Hood's Cave with that trapped during the experiment in terms of the numbers of individuals (a) and species (b), and the diversity (c) and evenness (d).

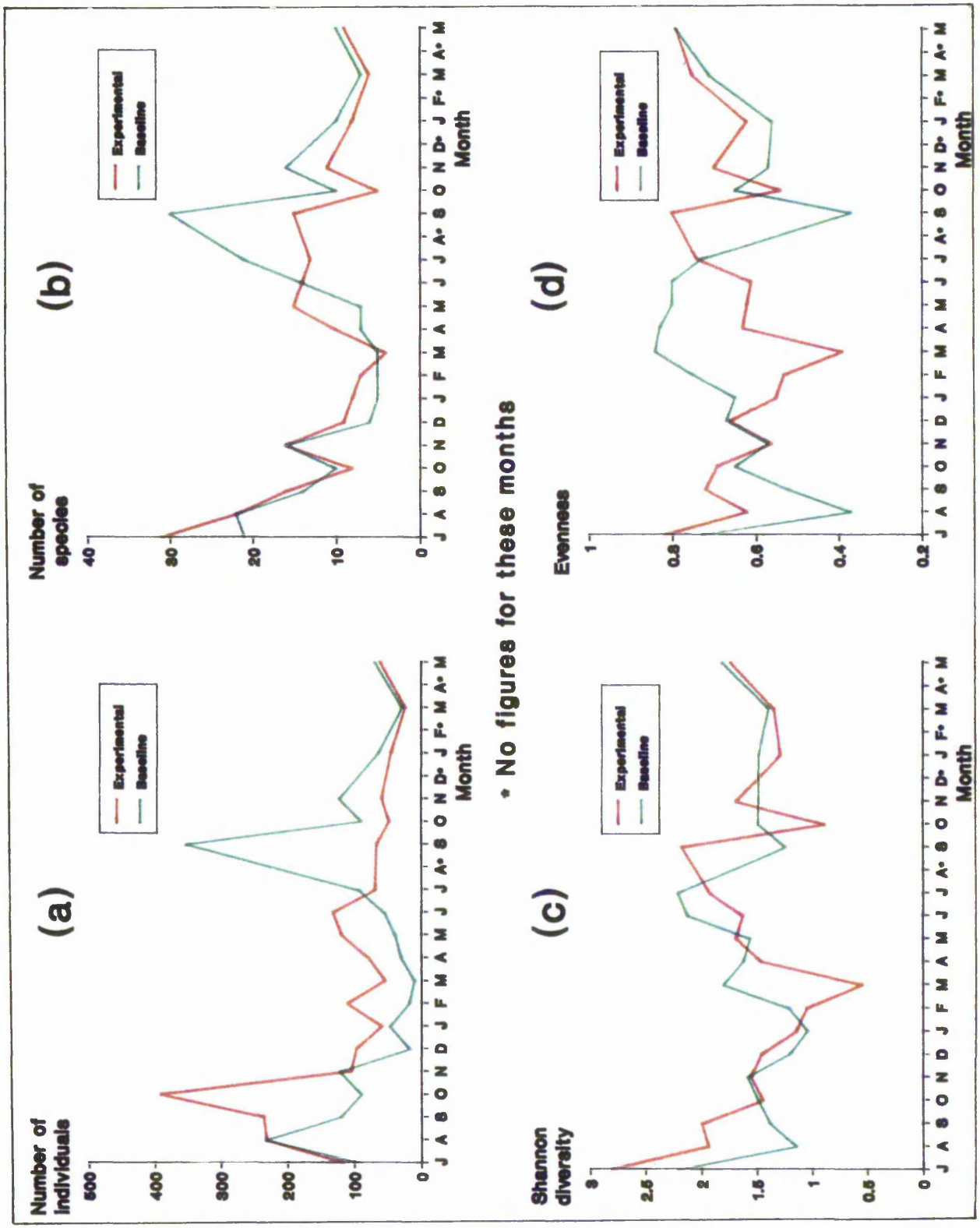

(a)
Number of individuals
Experimental
Baseline
Month
(b)
Number of species
Experimental
Baseline
Month
* No figures for these months
(c)
Shannon diversity
Experimental
Baseline
Month
(d)
Evenness
Experimental
Baseline
Month

Figure 3.10

L. cyaneus (Entomobryidae) (Figure 3.9, page 56), remained the dominant species associated with the carcasses in the Front chamber until approximately one year after deposition.

The numbers of individuals trapped each month are shown in Figure 3.10 a (previous page). These are higher than expected, particularly during the winter, for a period of one year after carcass deposition. Figure 3.10 b illustrates a similar pattern with regard to number of species. However, diversity (Figure 3.10 c) is depressed during decomposition due to the over-representation of a restricted number of species. Following this trend in diversity, evenness (Figure 3.10 d) is also disrupted.

3.2.2 Frogpit Chamber

Plates 5 to 8 (overleaf) show the physical appearance of ER/12, one of the carcasses deposited in the Frogpit chamber, during the first five months of decomposition.

The carcasses deposited in this chamber were also colonised within a relatively short period by *Calliphora vomitoria* (Plate 5). The first larvae were seen at the beginning of July (Figure 3.11, page 61). It is thought that these hatched from eggs laid by adults which had initially been attracted to the carcasses in the Front chamber. A few adults were also found in August, at a time corresponding to the emergence of the adults in the Front chamber. It is probable that the carrion in the Frogpit chamber was still attractive and that further eggs were laid by this generation.

The development time of *Calliphora* was longer in this chamber than in the Front chamber, and consequently adults did not begin to emerge until September. Only one generation completed development, since the carcasses were too old to be attractive by September (Plate 6). Almost three times as many *Calliphora* were caught in the pitfall traps in the Frogpit chamber as were at the Front.

Triphleba antricola and *Megaselia rufipes* also colonised the carcasses in the Frogpit chamber. An enormous number were attracted during the initial stages of decomposition when the carcasses were colonised by fungi. In the August pitfall trap collection (Figure 3.11 a) there were over 2000 more phorid individuals than would have been predicted for that time of year. The first larvae were seen during the second week of July, just after the first *Calliphora* eggs hatched, and the first pupae at the beginning of August.

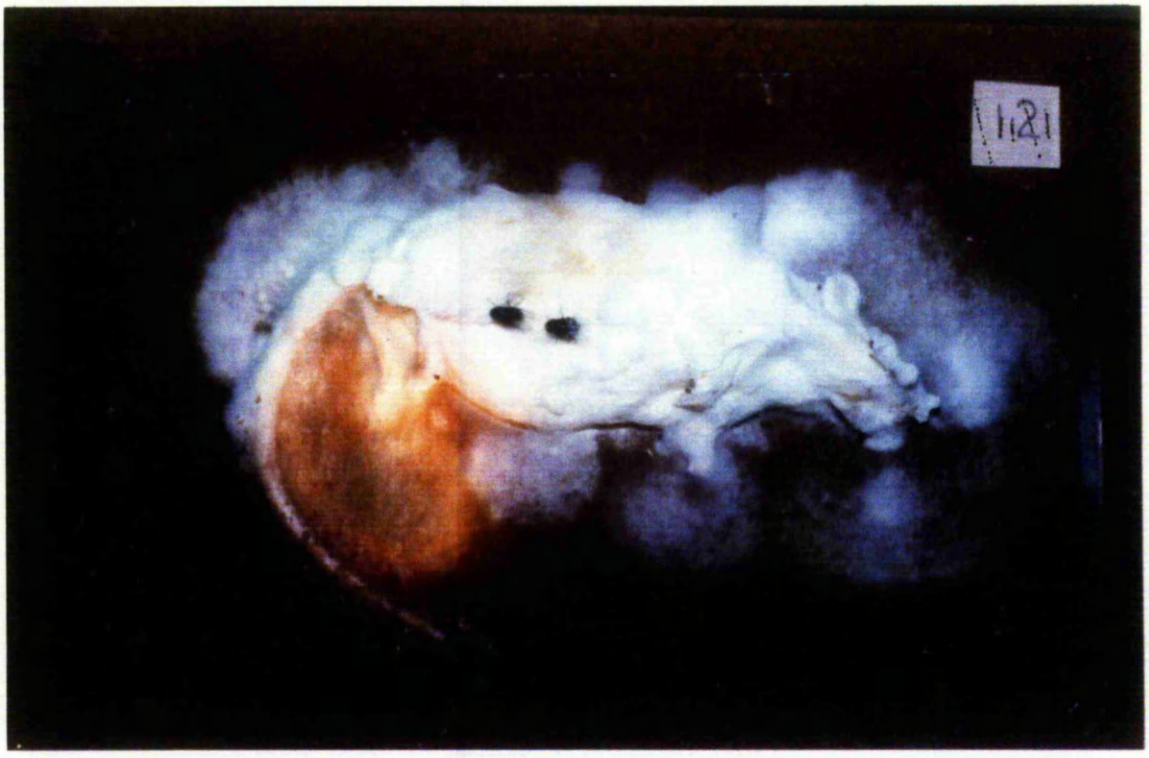


Plate 5: ER/12 after three weeks in the Frogpit chamber of Robin Hood's Cave.

Plate 6: ER/12 after twelve weeks in the Frogpit chamber of Robin Hood's Cave.

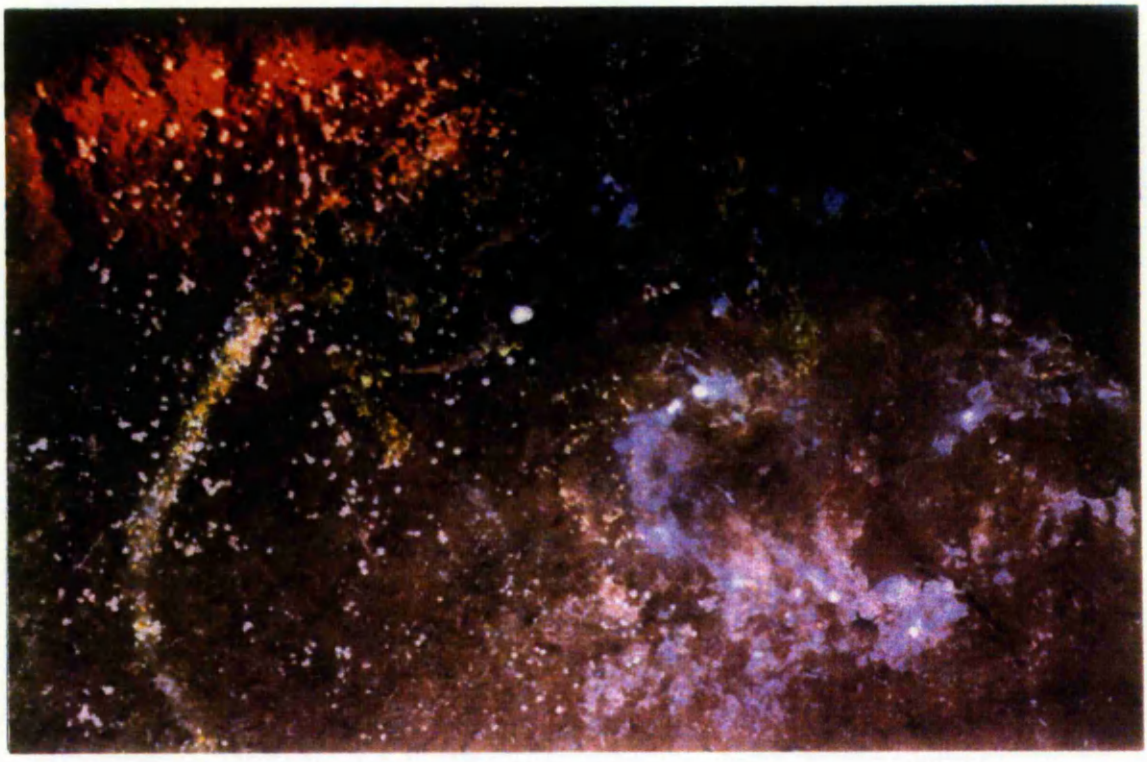


Plate 7: ER/12 after sixteen weeks in the Frogpit chamber of Robin Hood's Cave.

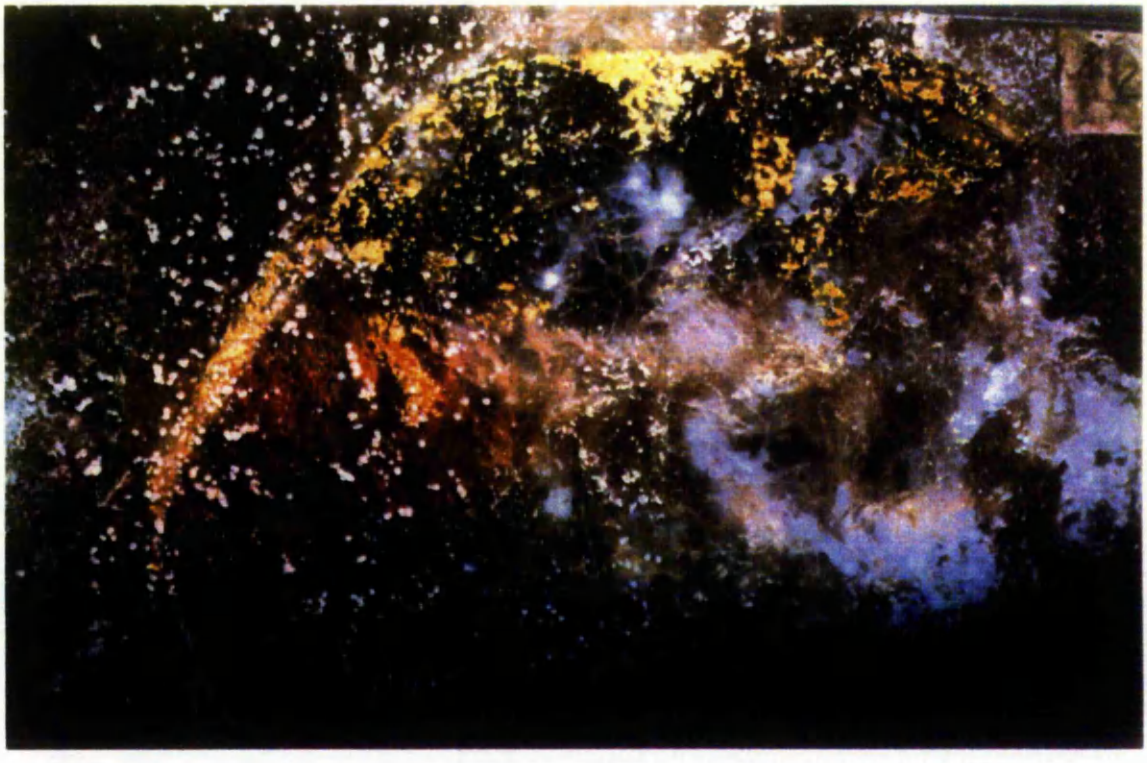


Plate 8: ER/12 after nineteen weeks in the Frogpit chamber of Robin Hood's Cave.

Figure 3.11: Numbers of individuals of Diptera trapped in the Frogpit chamber of Robin Hood's Cave during the experiment in relation to the baseline: (a) *Calliphora vomitoria* (Calliphoridae), *Triphleba antricola* and *Megaselia rufipes* (Phoridae) (above), and (b) *Bradysia brunnipes*, *Lycoriella leucotricha* (Sciaridae) and other Diptera (below).

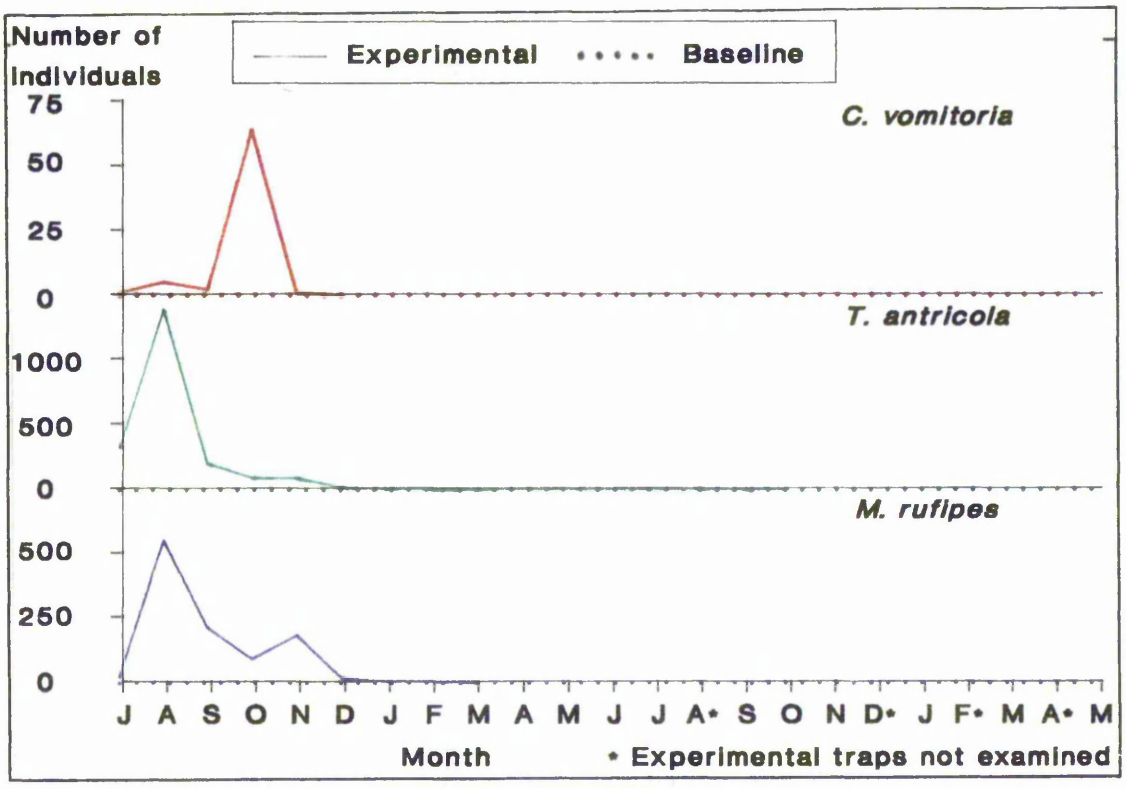


Figure 3.11 a

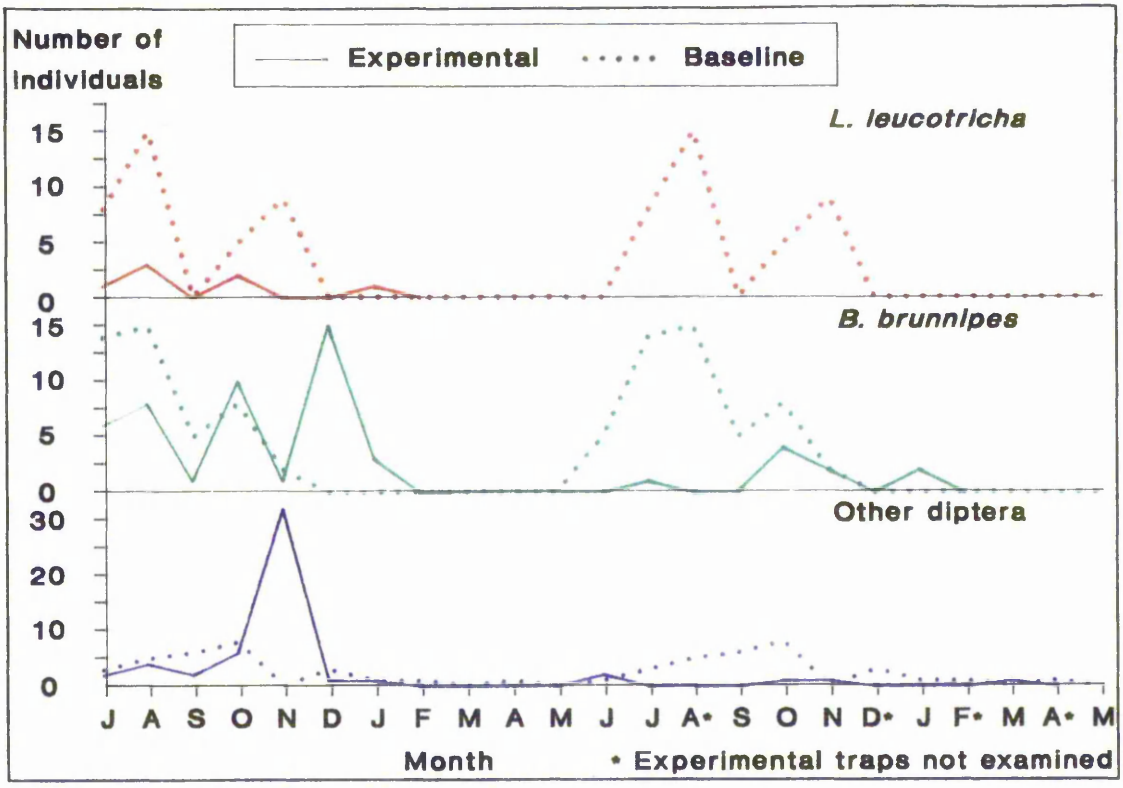


Figure 3.11 b

Evidence from the pitfall traps indicated that the number of adults that later emerged was disproportionately small, compared to the number that were initially attracted. By this time, however, the carcasses in this region were apparently decomposed to a much greater degree than were those at the Front. The hair turned brown and hair loss was more extensive. In some cases the skull, leg bones and vertebrae were clearly visible where the skin had been eaten away. It is probable, therefore, that the remains were no longer attractive to the phorids, leading to rapid dispersal. The absence of a second adult emergence peak supports this theory.

It is possible that a second species of *Megaselia* also bred on the carcasses, as indicated by the peak in November on Figure 3.11 b - blue bar (previous page). Other diptera, including Sphaeroceridae and troglophilic Heleomyzidae, were attracted to the carrion during the time of *Calliphora* and phorid infestation. These were not, however, found in large numbers (Figure 3.11 b), and there was no evidence of any breeding on the carcasses.

Once the initial stages of decomposition, characterised by substantial dipteran infestation and rapid removal of tissue, had been completed, the remains were colonised by several species of fungi (Plates 7 & 8). Associated with these were the fungus gnats *Lycoriella leucotricha* and *Bradysia brunnipes*. The latter was more numerous (Figure 3.11 b) and probably bred on the carcasses.

The succession continued with two more fungus-feeders: *Bessobia* sp (Coleoptera: Staphylinidae) utilised the carcasses in December and January (Figure 3.12 c, page 64) and then the populations of *Cryptophagus* spp (Coleoptera: Cryptophagidae), including that of the possible troglophile *Cryptophagus acutangulus*, began to increase (Figure 3.12 a, page 63).

Other Coleoptera associated with the remains (Figure 3.12 c) included *Choleva* and *Catops* spp (Cholevidae), and the staphylinids *Aleochara* spp, *Xylostiba monolicornis*, *Oxytelus tetracharinatus*, and *Quedius mesomelinus* (Figure 3.12 b, overleaf). This last species is a common troglophile and an important predator in the cave ecosystem; a comprehensive study of the life history and reproductive behaviour of *Quedius mesomelinus* was undertaken as part of this work (Chapter Seven). Although few individuals were caught in pitfall traps during the course of the experiment, many adults and larvae were found on and under the carcasses.

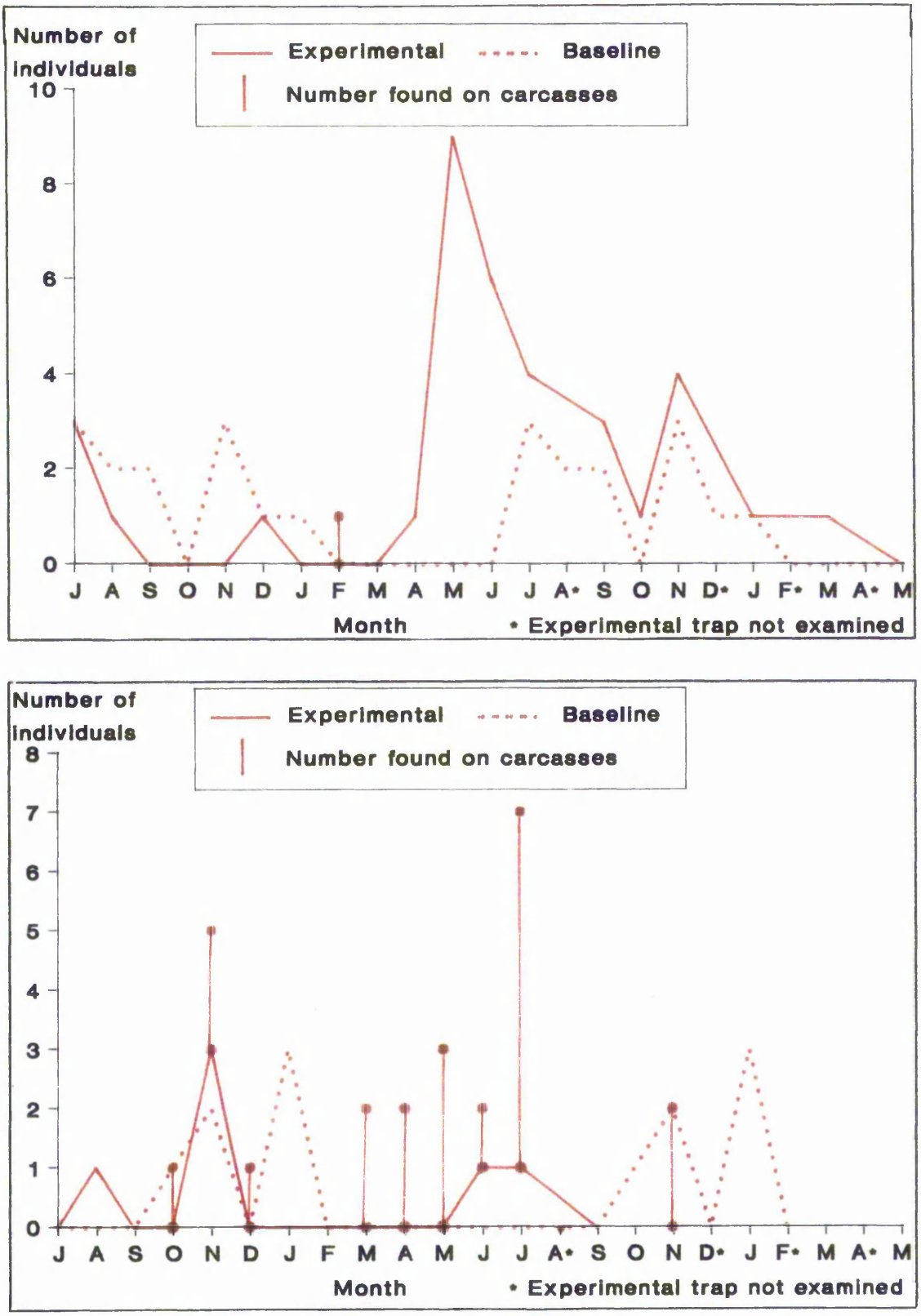


Figure 3.12: Numbers of individuals of Coleoptera trapped in the Frogpit chamber of Robin Hood's Cave during the experiment in relation to the baseline:
(a) *Cryptophagus* spp (Cryptophagidae) (top), and (b) *Quedius mesomelinus* (Staphylinidae) (above).

Figure 3.12: Numbers of individuals of Coleoptera other than Cryptophagidae and *Quedius* trapped in the Frogpit chamber of Robin Hood's Cave during the experiment in relation to the baseline.

Figure 3.13: Numbers of individuals of the Collembola *Lepidocyrtus curvicollis*, *L. cyaneus* and *Pseudosinella alba* (Entomobryidae) trapped in the Frogpit chamber of Robin Hood's Cave during the experiment in relation to the baseline.

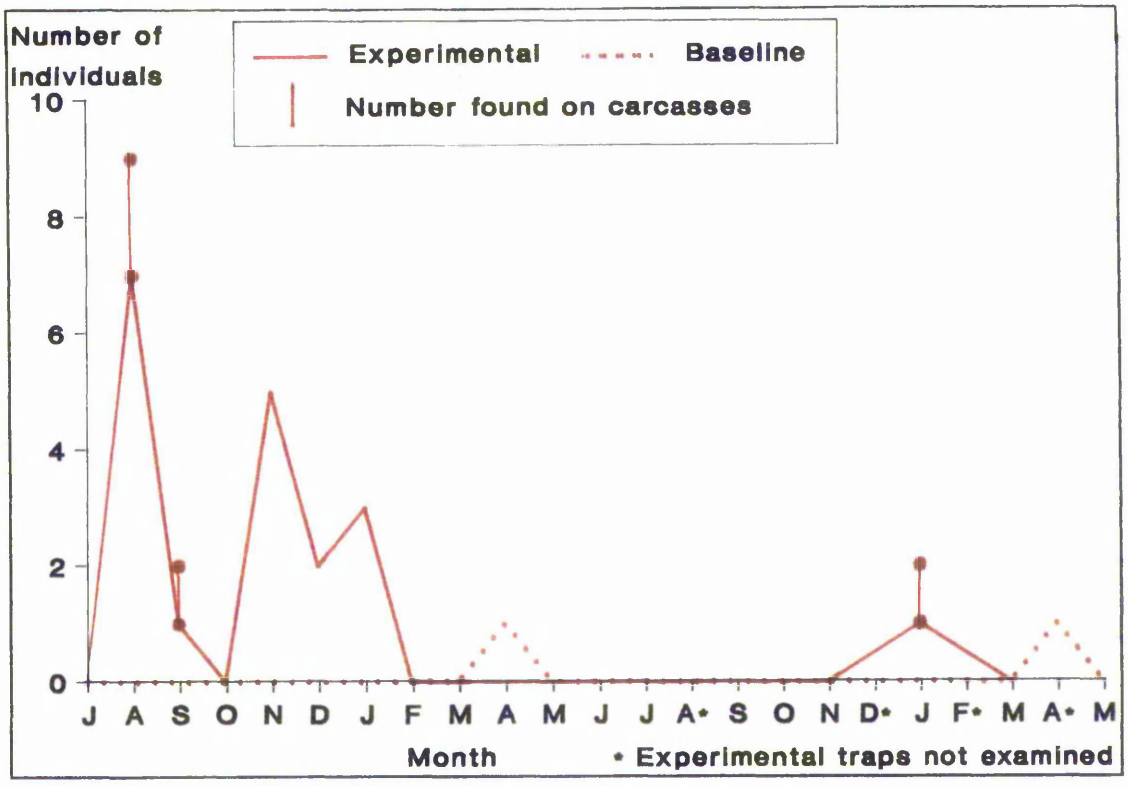


Figure 3.12 c

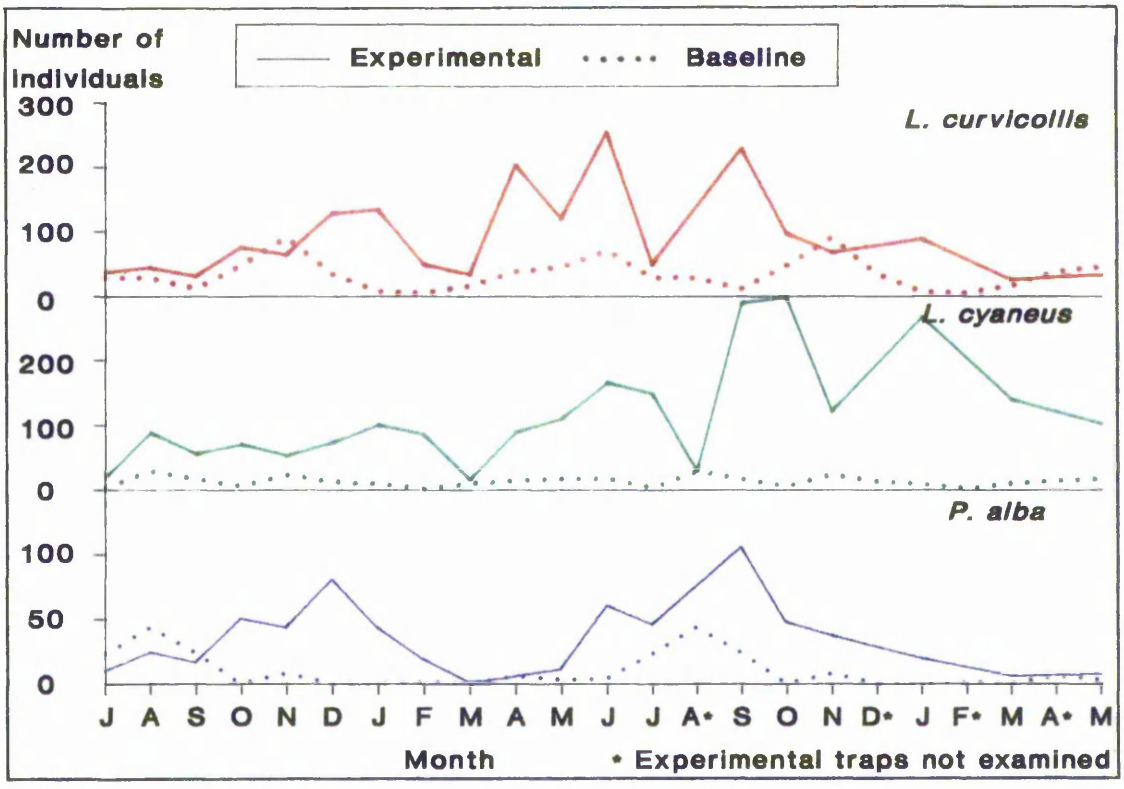


Figure 3.13

Figure 3.14: A comparison of the baseline fauna of the Frogpit chamber in Robin Hood's Cave with that trapped during the experiment in terms of the numbers of individuals (a) and species (b), and the diversity (c) and evenness (d).

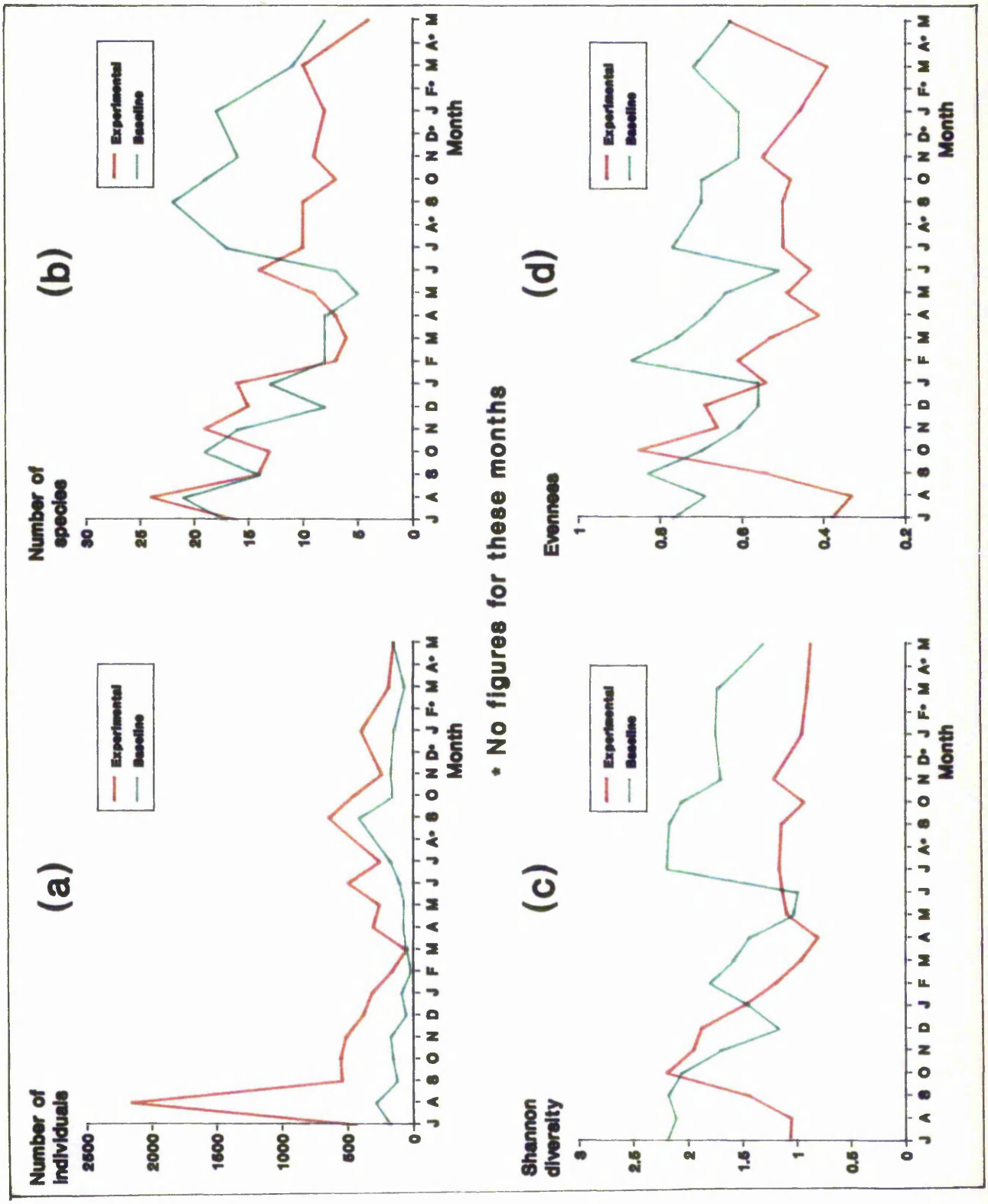

(a)
Number of individuals
2500
2000
1500
1000
500
0
Experimental
Baseline
J A S O N D J F M A M J J A S O N D J F M A M
Month
(b)
Number of species
30
25
20
15
10
5
0
Experimental
Baseline
J A S O N D J F M A M J J A S O N D J F M A M
Month
* No figures for these months
(c)
Shannon diversity
3
2.5
2
1.5
1
0.5
0
Experimental
Baseline
J A S O N D J F M A M J J A S O N D J F M A M
Month
(d)
Evenness
1
0.8
0.6
0.4
0.2
Experimental
Baseline
J A S O N D J F M A M J J A S O N D J F M A M
Month

Figure 3.14

Besides the Coleoptera, other species associated with the remains during the later stages of decomposition included a number of mite families and the Collembola *Lepidocyrtus curvicollis*, *L. cyaneus* and *Pseudosinella alba* (Entomobryidae). Population levels continued to be larger than expected until the end of the experiment (Figure 3.13, page 64).

Figure 3.14 a (previous page) illustrates the fluctuation in the numbers of invertebrates trapped in the Frogpit chamber. This shows that the presence of the carcasses led to a consistent elevation, particularly during the first year. The number of species found (Figure 3.14 b), however, was noticeably above the baseline only at certain times. These findings are reflected in the diversity (Figure 3.14 c) and evenness (Figure 3.14 d) of the region, which were generally lower than the baseline.

3.2.3 Back Chamber

At the back of the cave initial decomposition followed one of two distinct pathways: either microbial and dipteran, or microbial alone. Plates 9 to 12 (overleaf) show the physical appearance of ER/15 and ER/17, two of the carcasses deposited in the Frogpit chamber, during the first two months of decomposition. ER/15 was colonised by both fungi and by *Calliphora* during this time, whereas fungi only were present on ER/17. Plates 13 & 14 show ER/17 during later stages of decomposition, by which time all carcasses in the Back chamber were of a similar appearance.

Although there were large numbers of Phoridae present when the rats were colonised by fungus (Plates 9 & 11), the first sign of dipteran infestation was when four of the carcasses were located by *Calliphora vomitoria* approximately five weeks after deposition (Plate 10). *Calliphora* larvae were present from the middle of July until the end of August (Figure 3.15 a, page 70), by which time most had pupated. Adults began to emerge in September.

Although the extent of calliphorid attack was minimal, relatively large numbers of individuals were found in the pitfall traps and dead on the floor of the cave. This was probably because the adults were unable to find an exit.

The majority of larvae seen were phorids, which were present on all eight carcasses. They were first observed at about the same time as *Calliphora* larvae, but

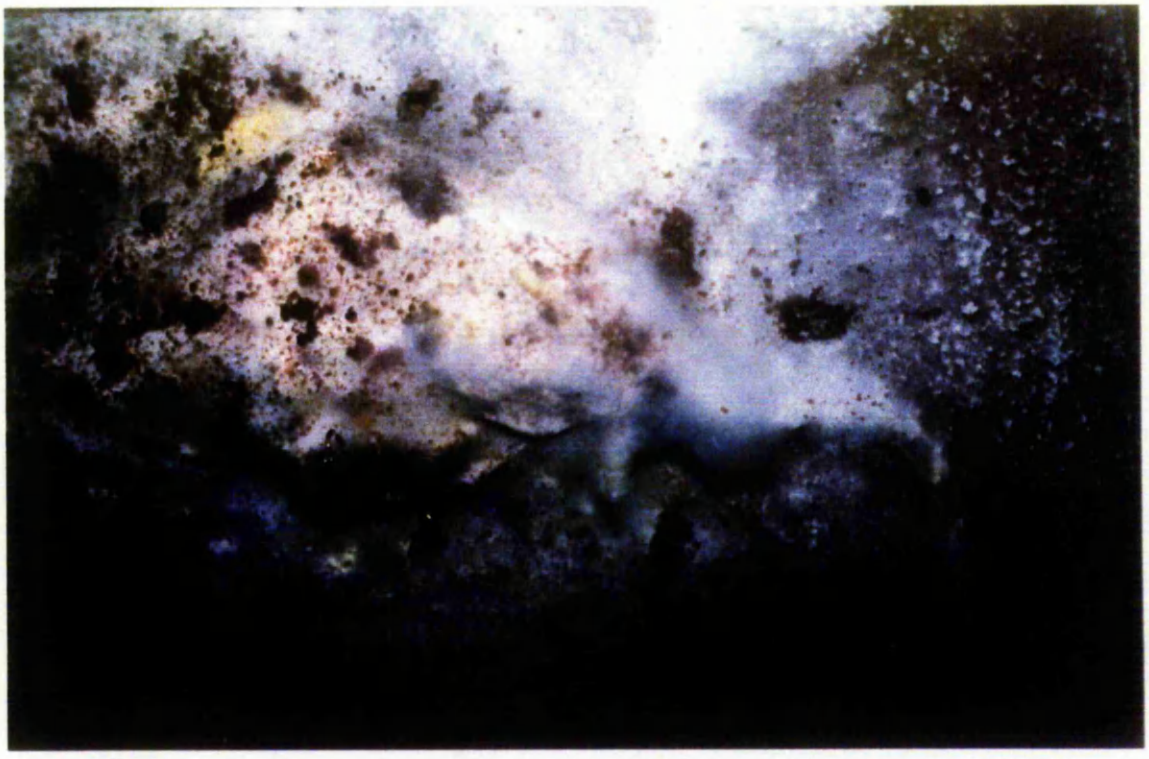


Plate 9: ER/15 after four weeks in the Back chamber of Robin Hood's Cave.

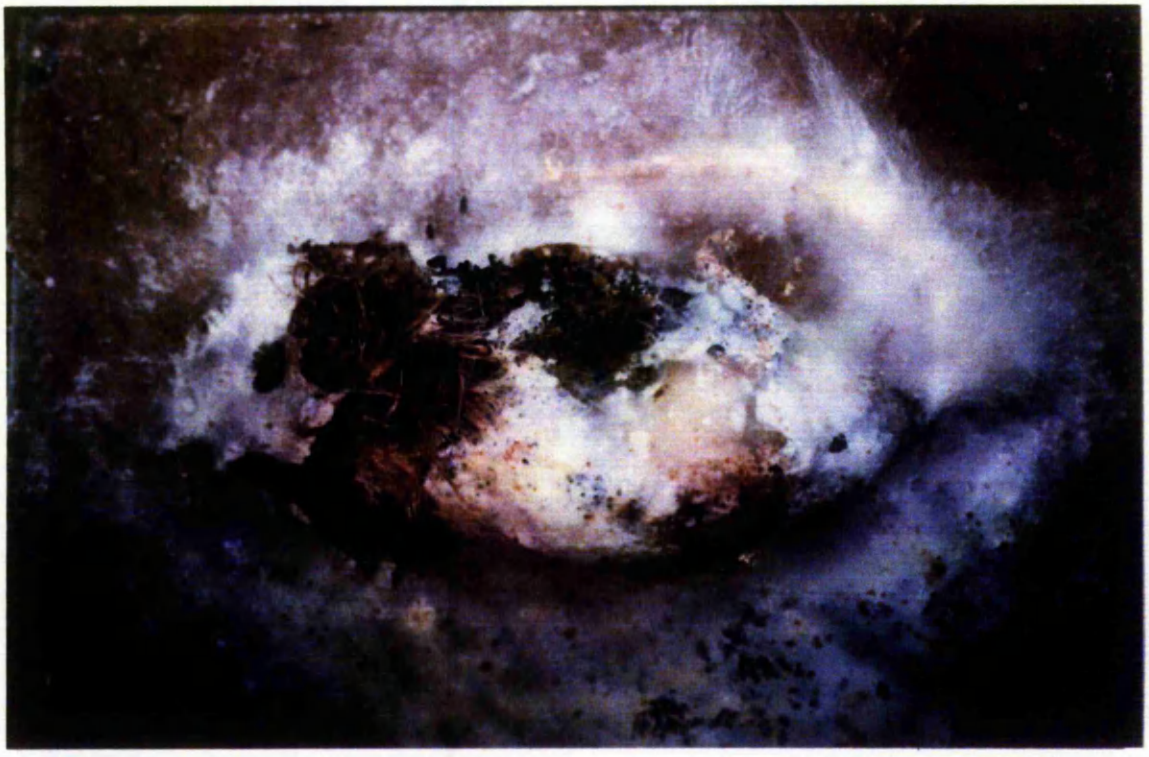


Plate 10: ER/15 after seven weeks in the Back chamber of Robin Hood's Cave.

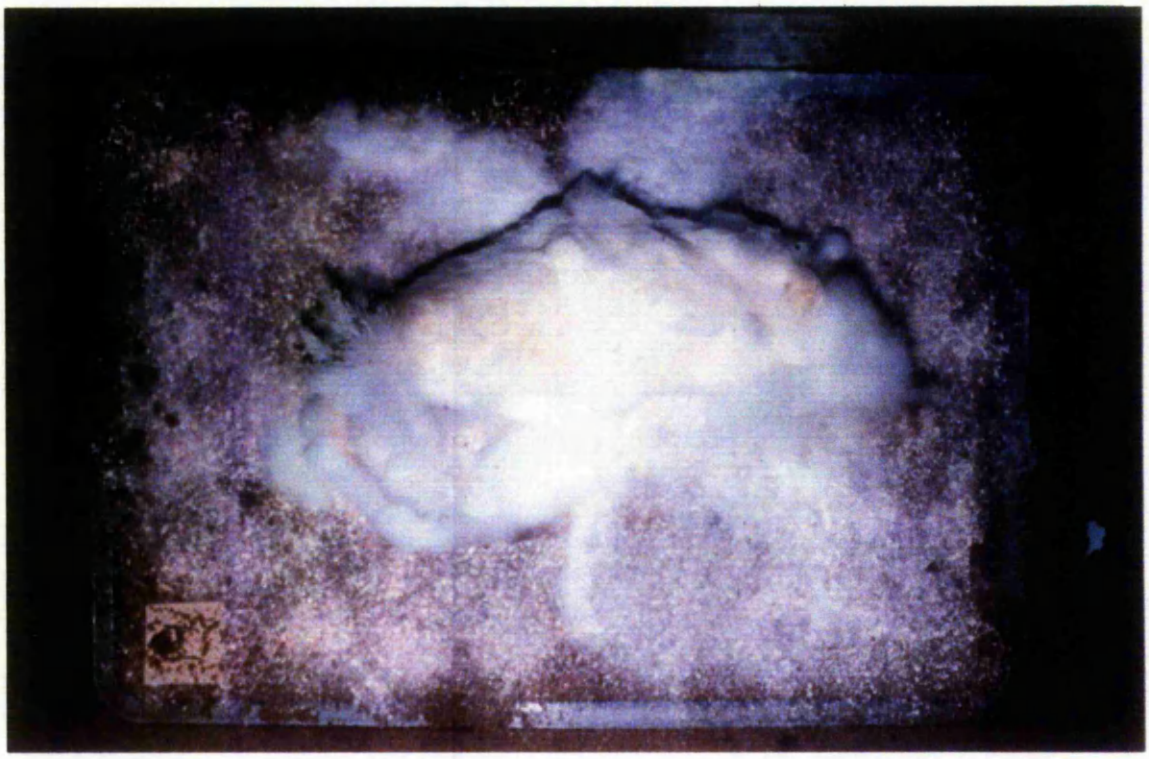


Plate 11: ER/17 after three weeks in the Back chamber of Robin Hood's Cave.

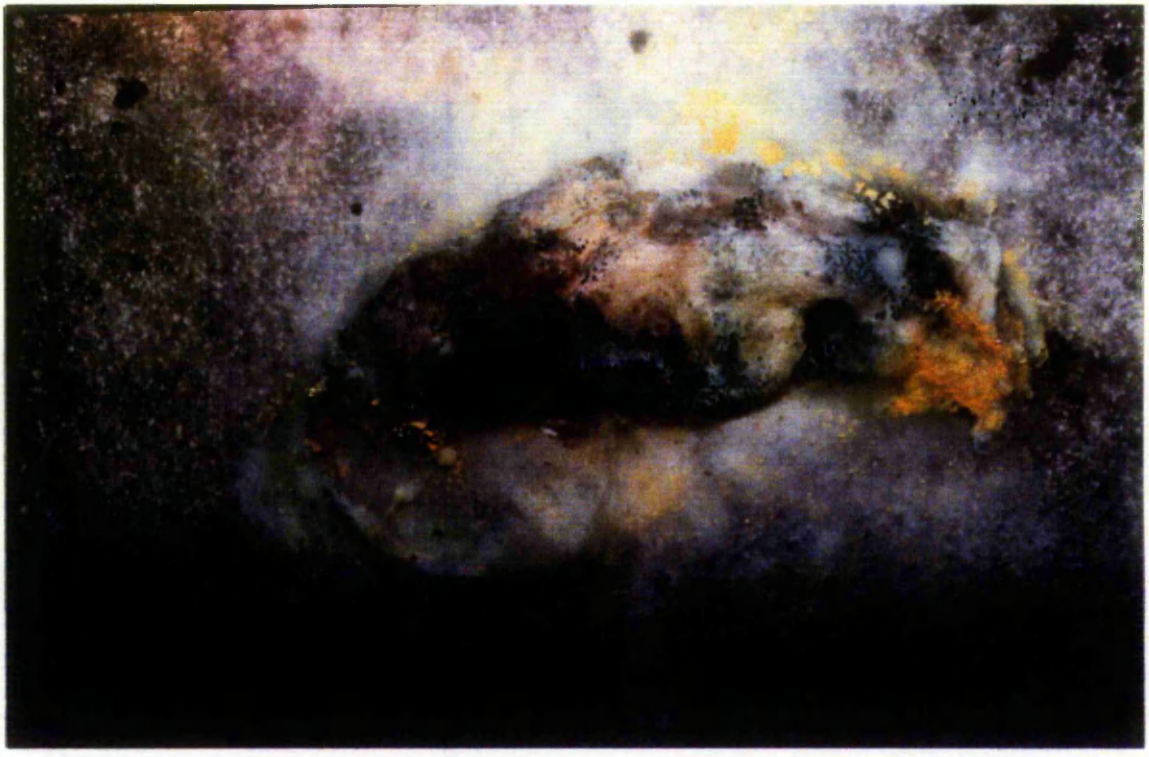


Plate 12: ER/17 after eight weeks in the Back chamber of Robin Hood's Cave.

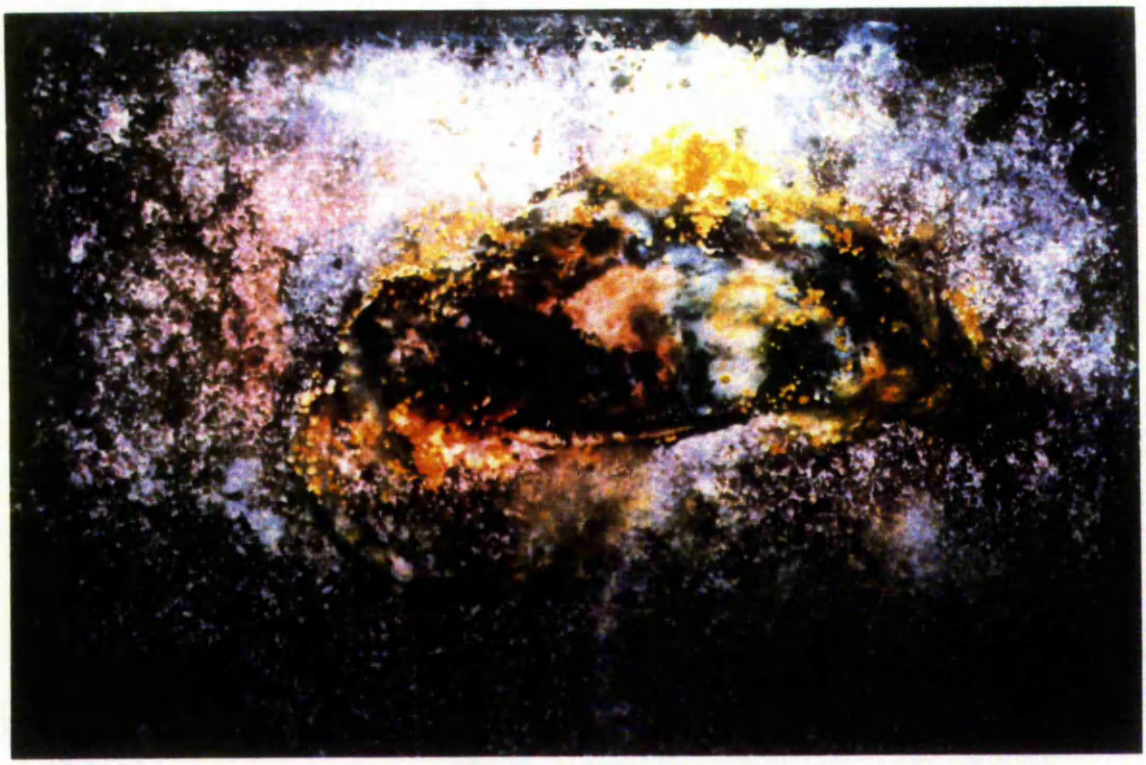


Plate 13: ER/17 after twelve weeks in the Back chamber of Robin Hood's Cave.

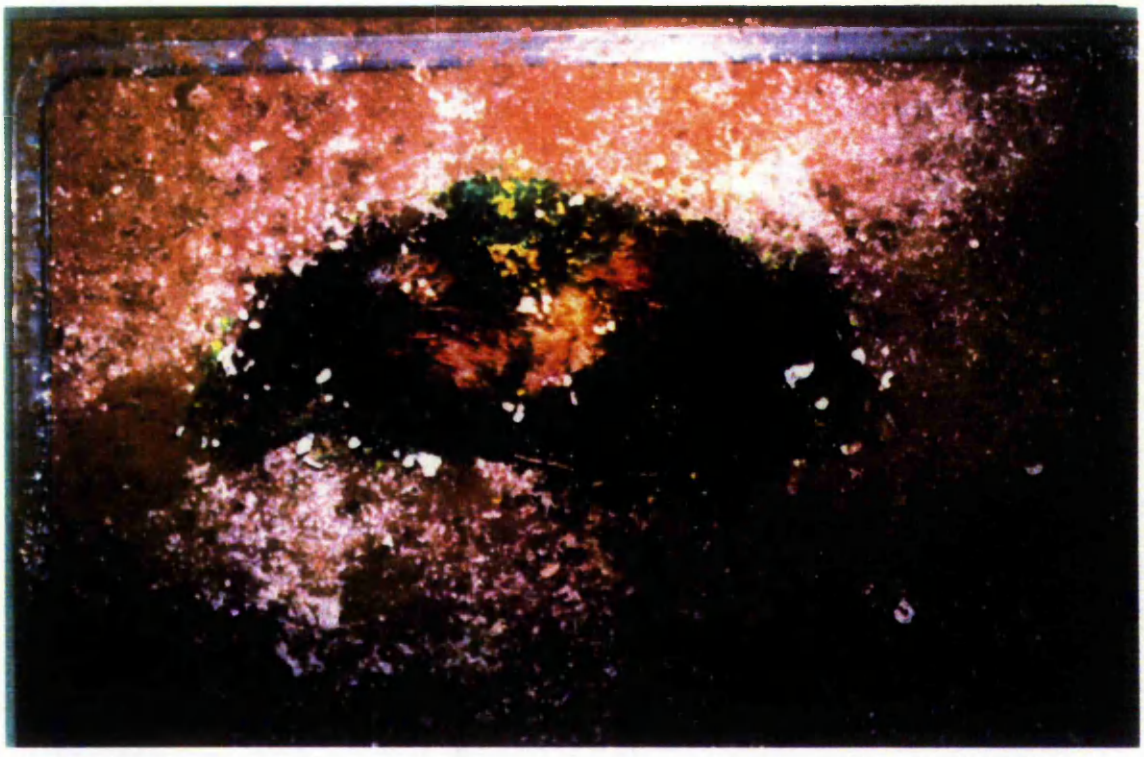


Plate 14: ER/17 after nineteen weeks in the Back chamber of Robin Hood's Cave.

Figure 3.15: Numbers of individuals of Diptera trapped in the Back chamber of Robin Hood's Cave during the experiment in relation to the baseline: (a) *Calliphora vomitoria* (Calliphoridae), *Triphleba antricola* and *Megaselia rufipes* (Phoridae) (above), and (b) *Bradysia brunnipes*, *Lycoriella leucotricha* (Sciaridae) and other Diptera (below).

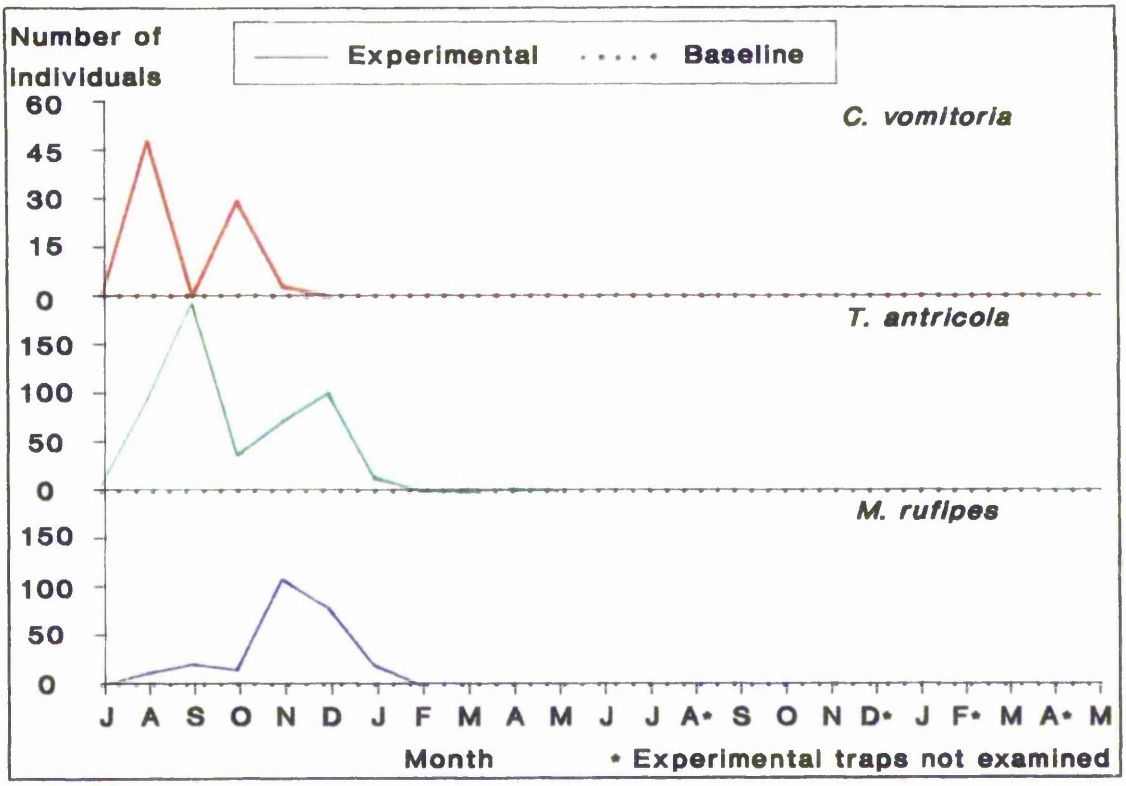


Figure 3.15 a

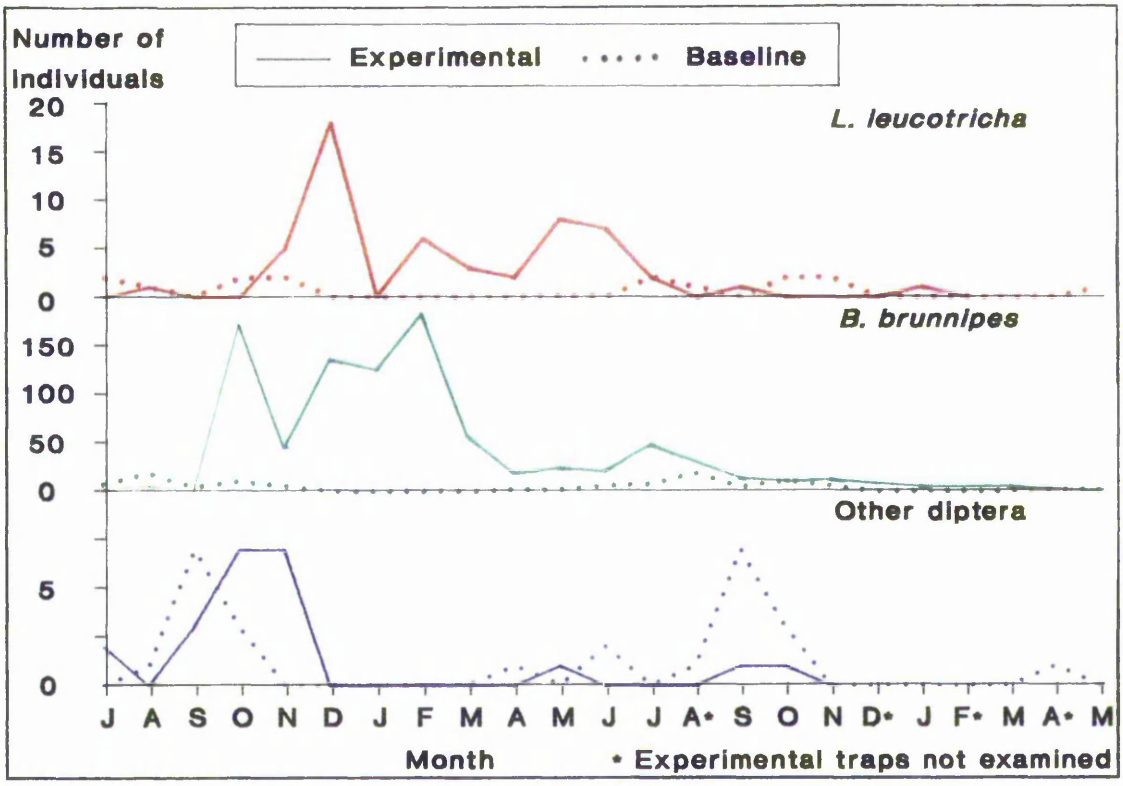


Figure 3.15 b

due to a shorter larval development time, adult *Triphleba* began to emerge at the end of August. At this time the carcasses were still a valuable resource since large scale consumption by *Calliphora* had not occurred (Plate 13). The peak in November and December (Figure 3.15 a) represents a second generation of *Triphleba*, from eggs laid on the carcasses while the *Calliphora* were pupating.

Although *Triphleba* and *Megaselia* apparently colonised the carcasses in the Frogpit chamber concurrently, in the Back chamber emerging adult *Megaselia* were not seen until October and November, at the time *Triphleba* was completing a second generation.

Larvae of the sciarid *Bradysia brunnipes* first appeared on the carcasses in mid-August and multiple generations were apparent; emerging in October, December, February, May, July and possibly during the second winter (Figure 3.15 b, page 70). As in the Frogpit chamber, *Bradysia* was more numerous than *Lycoriella*, which appears to have only produced one generation, which emerged in December. However, the presence of *Lycoriella* in numbers slightly above the baseline for the first six months of the following year suggests that a few individuals may have continued to breed on the carcasses.

Two other species of Diptera were attracted to the carcasses at the back of the cave: a mycetophilid during July, and a sphaerocerid in November (Figure 3.15 b).

Approximately six months after the carcasses were deposited, Coleoptera began to be attracted to the site. Although *Omalium* spp and *Cryptophagus acutangulus* were caught in pitfall traps (Figure 3.16 b, page 72), the majority of individuals were *Quedius mesomelinus*, and most of these were not trapped but found on, under and around the remains (Figure 3.16 a, page 72).

A thriving community including *Bradysia*, *Lycoriella*, *Quedius*, four species of Collembola (Figures 3.17 a and b, page 73) and a number of mite species was present for much of the second year. Also collected from the carcasses during this time were annelids (*Allolobophora caliginosa* (Lumbricidae) and *Enchytraeus* sp (Enchytraeidae)), crustacea (*Androniscus dentiger* (Isopoda: Trichoniscidae)) and millipedes (*Brachydesmus superus* (Diplopoda: Polydesmidae)).

The number of individuals trapped in the Back Chamber (Figure 3.18 a, page 74) was continuously higher than the baseline, with extremes during mid-winter and

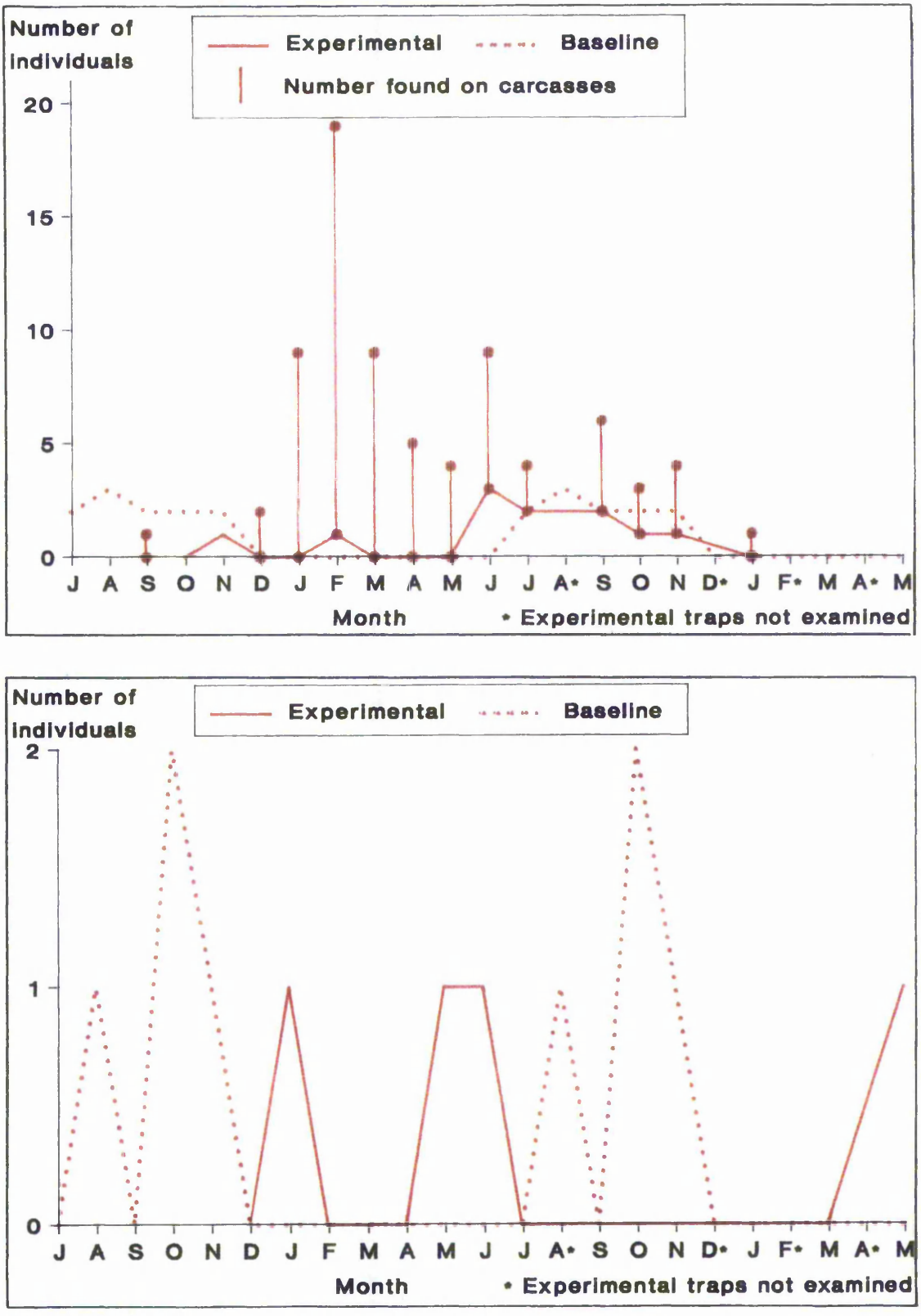


Figure 3.16: Numbers of individuals of Coleoptera trapped in the Back chamber of Robin Hood's Cave during the experiment in relation to the baseline:
(a) *Quedius mesomelinus* (Staphylinidae) (top), and (b) other Coleoptera (above).

Figure 3.17: Numbers of individuals of Collembola trapped at the Back site of Robin Hood's Cave during the experiment in relation to the baseline: (a) *Lepidocyrtus curvicollis* and *Pseudosinella alba* (Entomobryidae) (above), and (b) *Neelus* sp (Neelidae) and *Arrhopalites* sp (Sminthuridae) (below).

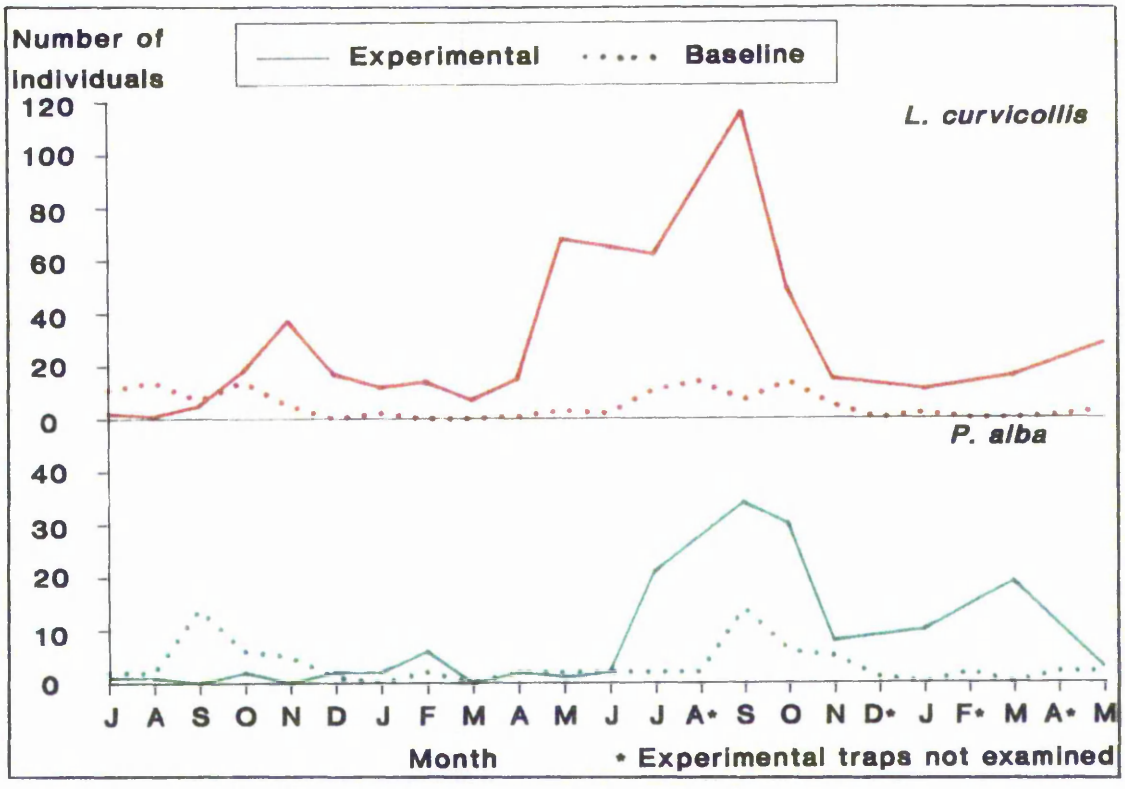


Figure 3.17 a

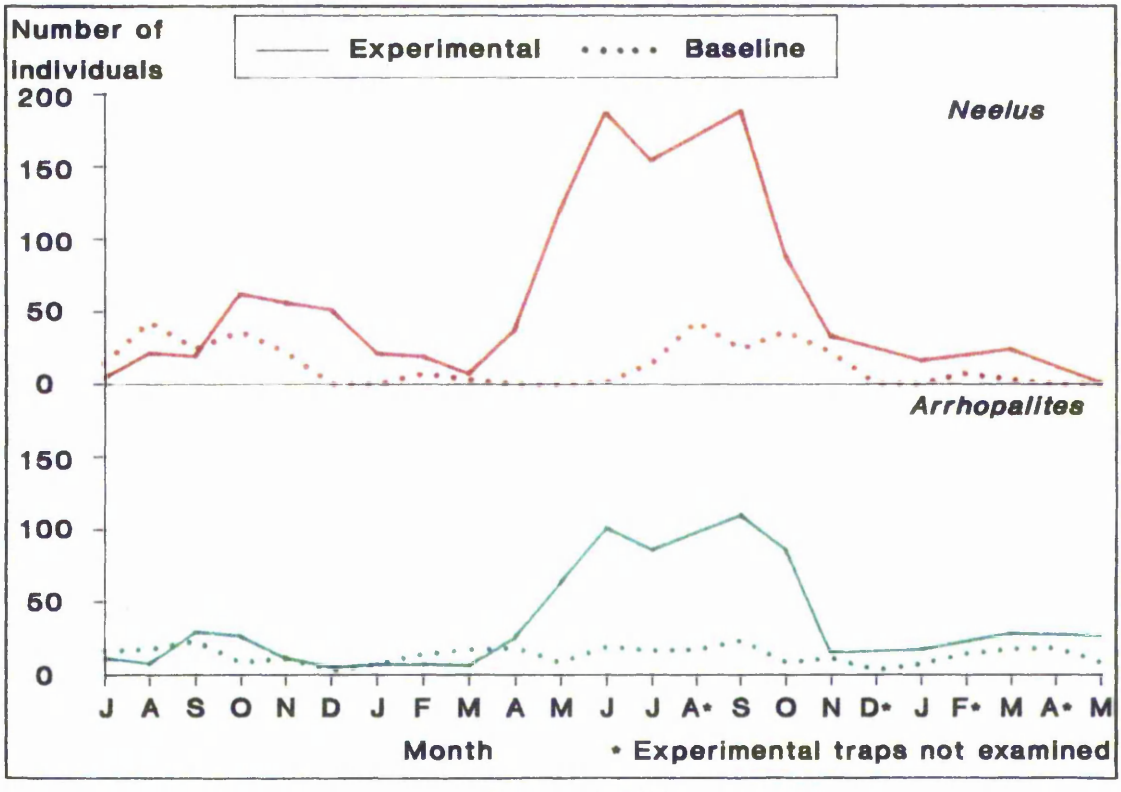


Figure 3.17 b

Figure 3.18: A comparison of the baseline fauna of the Back chamber in Robin Hood's Cave with that trapped during the experiment in terms of the numbers of individuals (a) and species (b), and the diversity (c) and evenness (d).

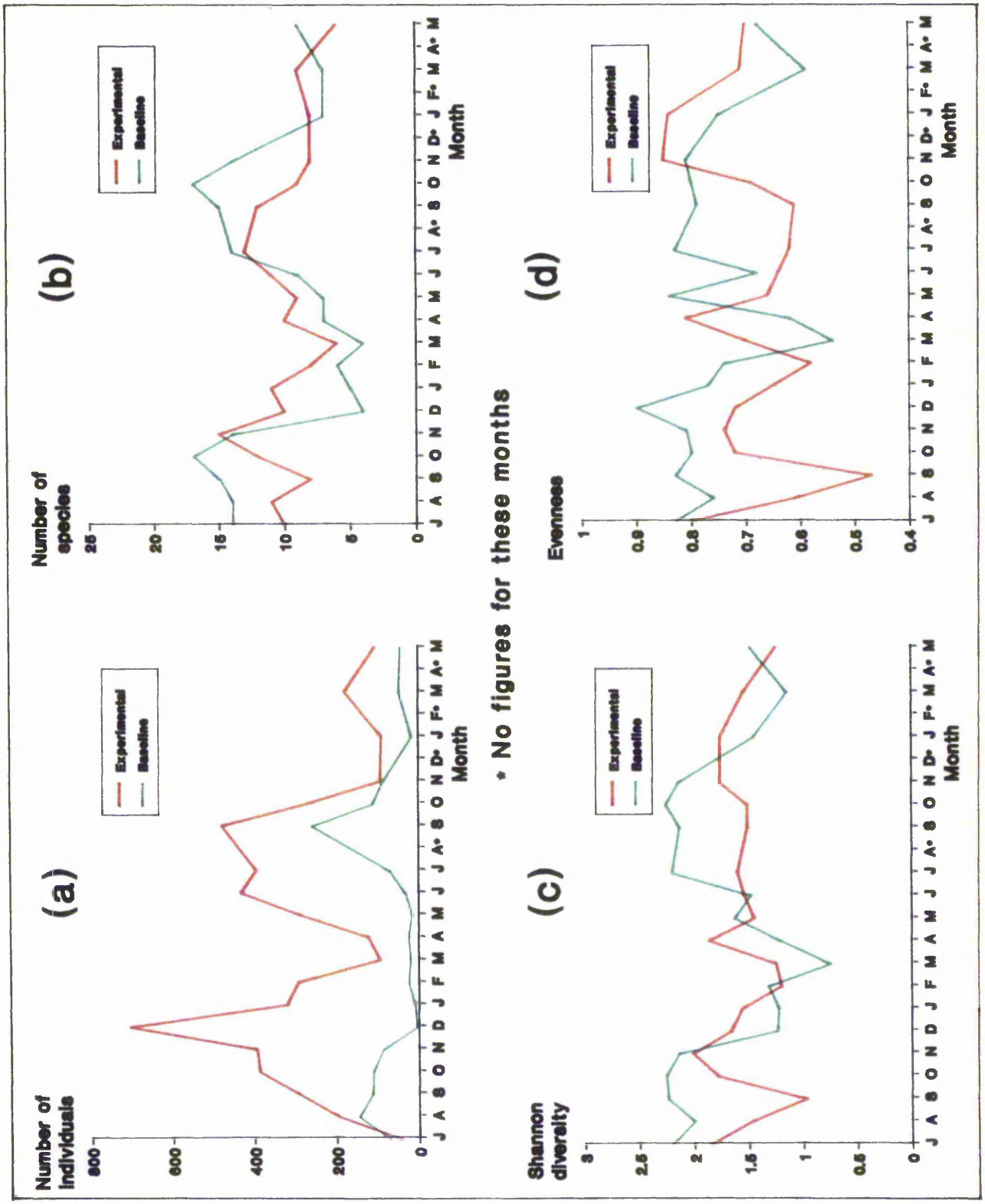

(a)
Number of individuals
Experimental
Baseline
Month
(b)
Number of species
Experimental
Baseline
Month
* No figures for these months
(c)
Shannon diversity
Experimental
Baseline
Month
(d)
Evenness
Experimental
Baseline
Month

Figure 3.18

mid-summer. In contrast, the number of species caught (Figure 3.18 b) did not increase until four months after deposition. After a year species richness dropped back to below baseline levels, where it remained except for a relatively small increase during the second winter. Consequently, diversity in the region followed a similar pattern (Figure 3.18 c), and evenness was generally much lower than the baseline (Figure 3.18 d).

3.3 Decay curves

Also measured on a regular basis were the weights of the control rats (CR/1 to CR/6). For each carcass, this was expressed as a percentage of the original weight and plotted against time to construct a decay curve (Figure 3.19).

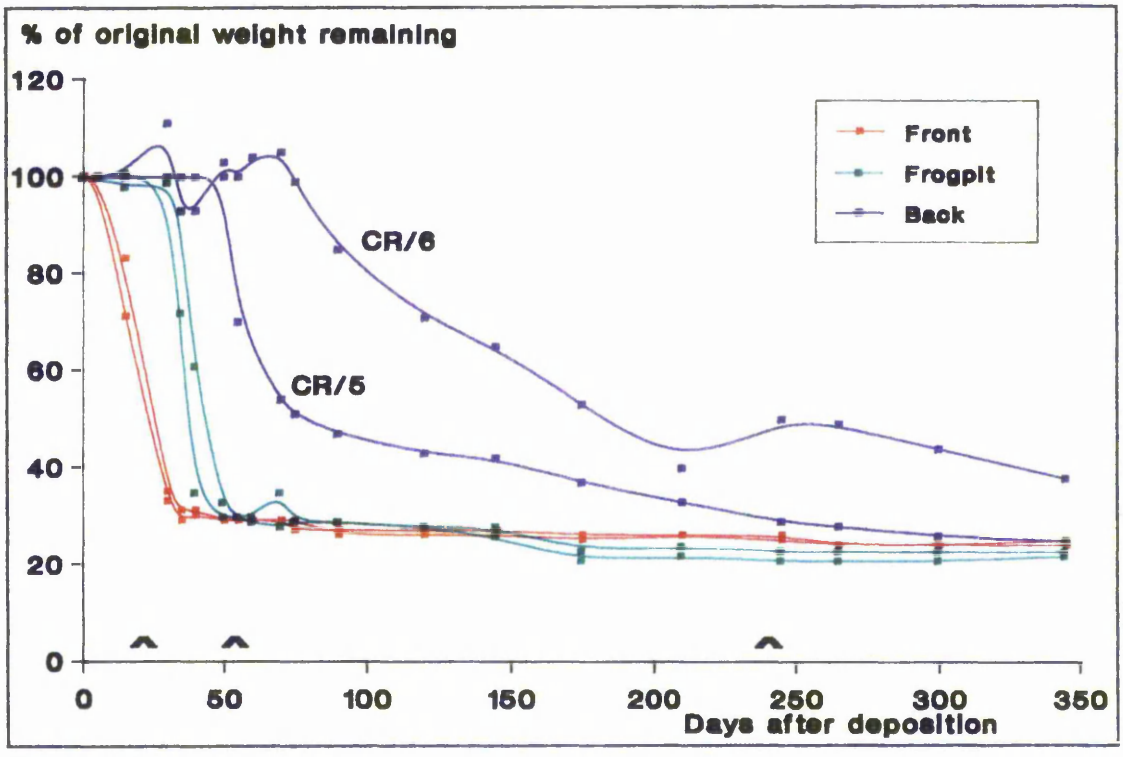


Figure 3.19: Decay curves of the carcasses in the three chambers of Robin Hood's Cave. (^ indicates heavy rainfall.)

In the event of heavy rain, water percolates down from the surface and drips from the roof of the cave at particular points. CR/6, which was situated in the Back chamber, was inadvertently placed in such an area and occasionally became saturated. This, and subsequent evaporation during dry spells, led to fluctuations in carcass weight. Periods of rainfall are apparent on the decay curve of CR/6 as periodic rapid increases in mass.

3.4 Excavation of tanks

3.4.1 Front tanks

The carcasses deposited in the Front Chamber mummified after only a few weeks (Section 3.2.1). When the tanks were removed from the cave, the dried out remains were all on the surface of the sediment and very little disarticulation or dispersal was evident (Figures 3.20, 3.21 and 3.22, overleaf). X-rays showed that the skeletons were intact within the parchment-like skin (Plate 15, page 80).

The only bones to become detached were the lower mandibles (ER/2, ER/3 and ER/5), and only in the case of ER/5 were these bones displaced to an appreciable degree (approximately 25 cm).

Each carcass was easily lifted off the surface, causing little or no disturbance. Only ER/3 was in any way incorporated into the sediment, part of its tail and lower mandibles being very lightly covered.

When one of the carcasses was dissected it was found that all the gut contents had been removed by decomposers, although the alimentary canal itself was intact. Some nervous tissue also remained, for example the sciatic nerves and the cervical ganglia. All muscle tissue and most connective tissue had been removed, although the cartilage between the vertebrae remained in place. The tail was untouched.

No appreciable pits or mounds were apparent in the sediment in any of the tanks, although a certain amount of disturbance had been caused by the dipteran larvae, leaving the surface uneven. During the time of the experiment the sediment in the tanks had dried out considerably and contracted in volume. This lead to sediment sinking at the edges of the tanks, but it is not thought that this affected the results.

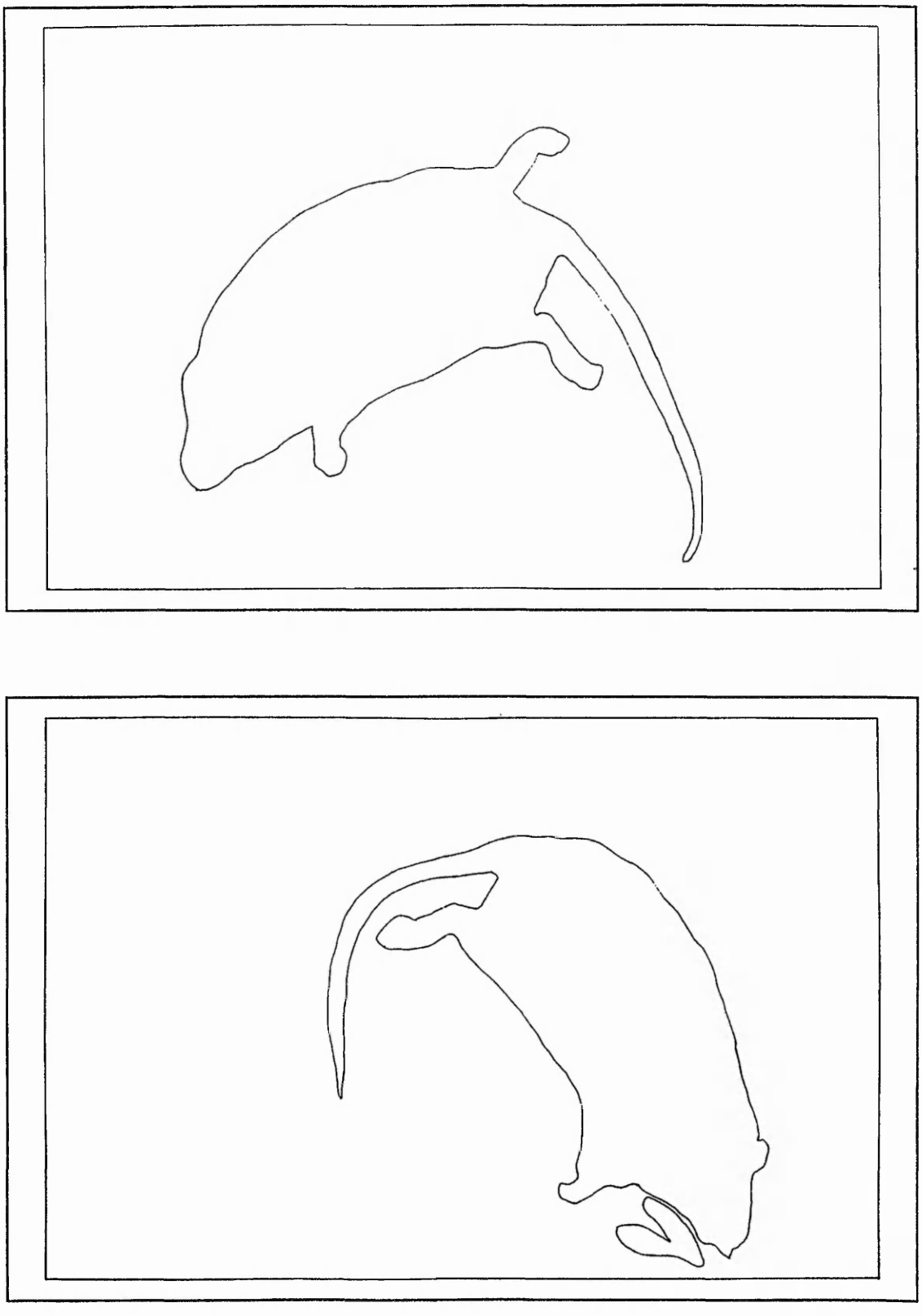


Figure 3.20: Final position of remains from the Front Chamber of Robin Hood's Cave: ER/1 (top) and ER/2 (above).

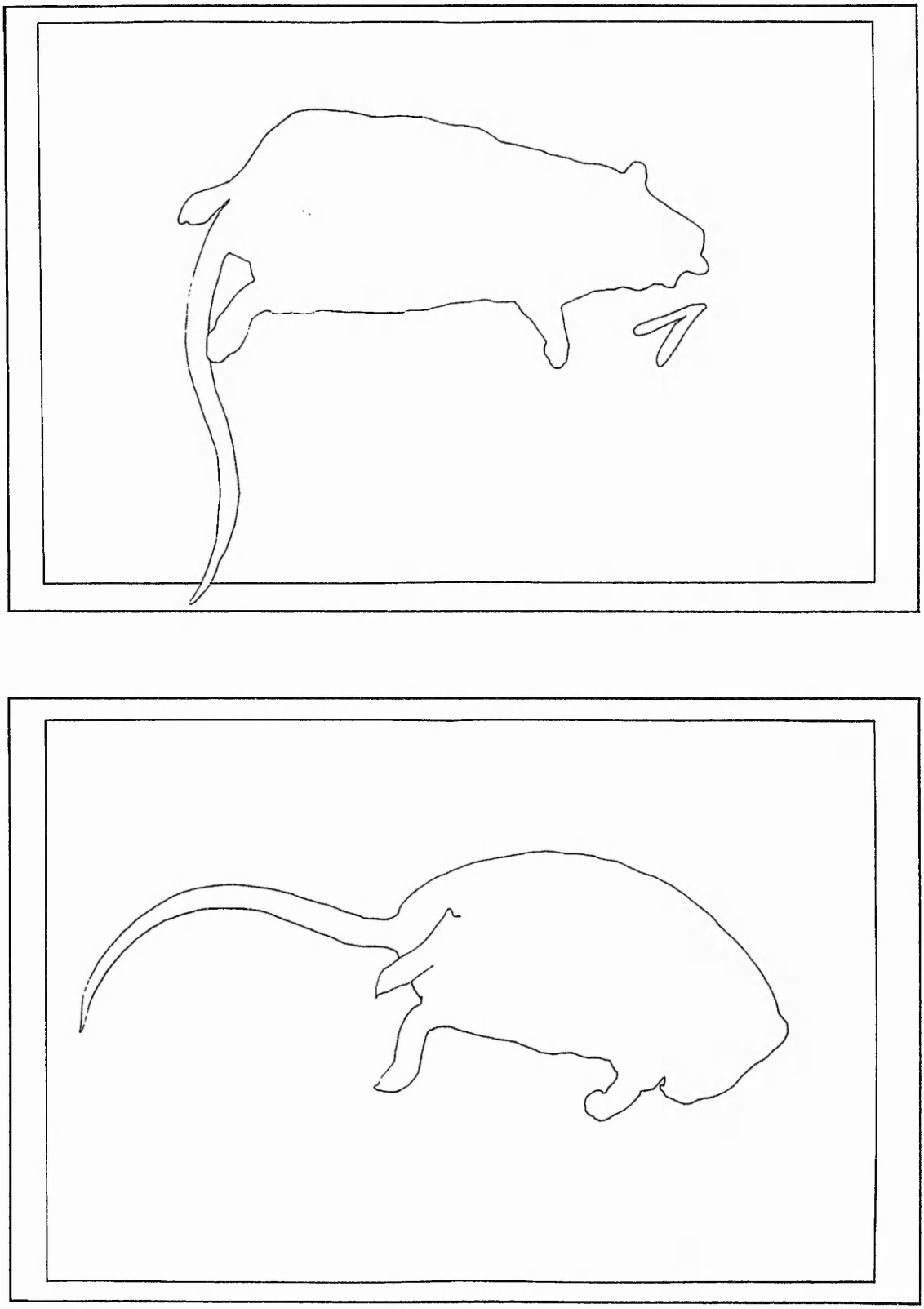


Figure 3.21: Final position of remains from the Front Chamber of Robin Hood's Cave: ER/3 (top) and ER/4 (above).

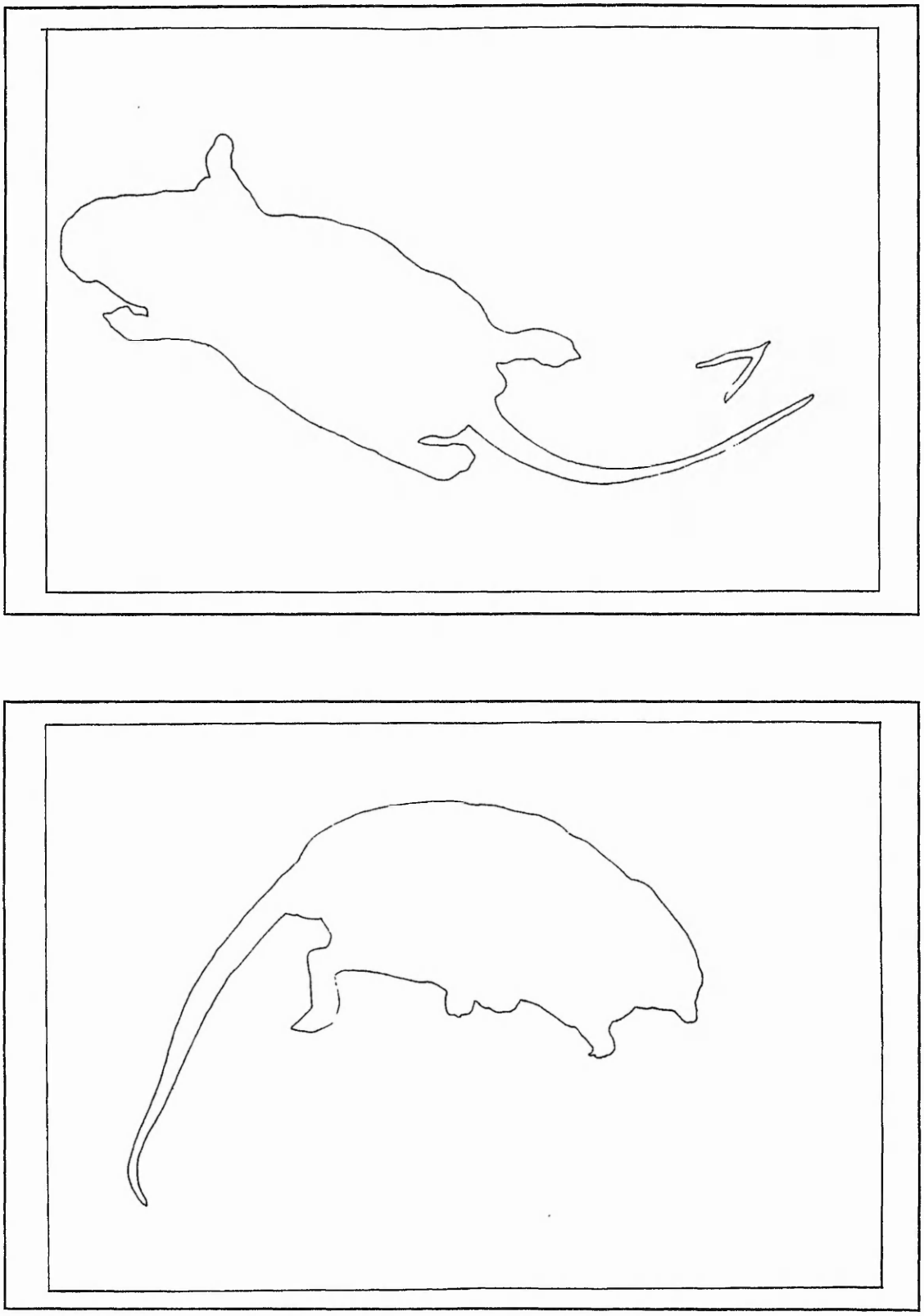


Figure 3.22: Final position of remains from the Front Chamber of Robin Hood's Cave: ER/5 (top) and ER/6 (above).

Plate 15: X-ray of one of the mummified rat carcasses from the Front chamber of Robin Hood's Cave.

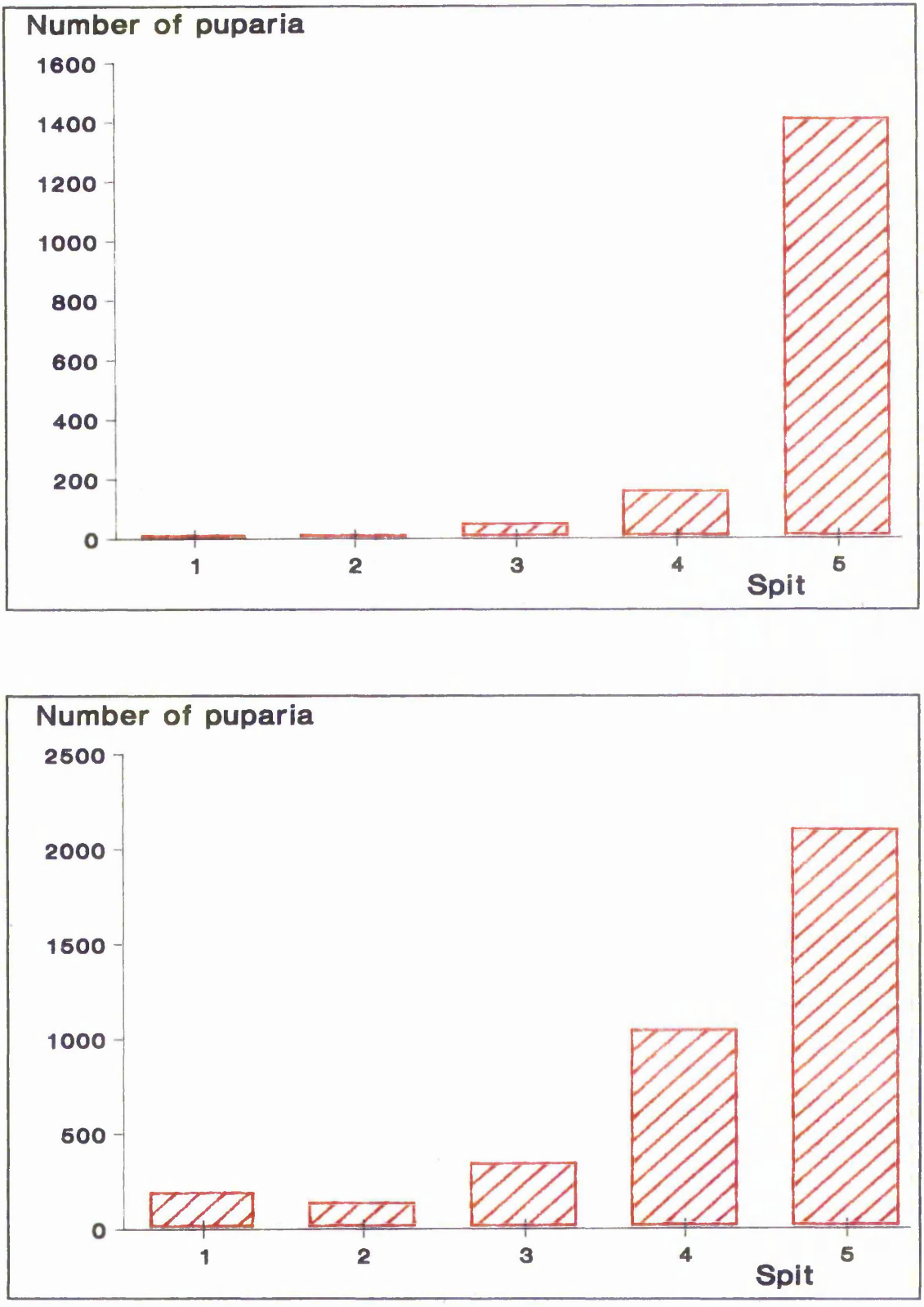


Figure 3.23: Distribution of puparia in the sediment beneath ER/3 (top) and ER/5 (above) from the Front Chamber of Robin Hood's Cave.

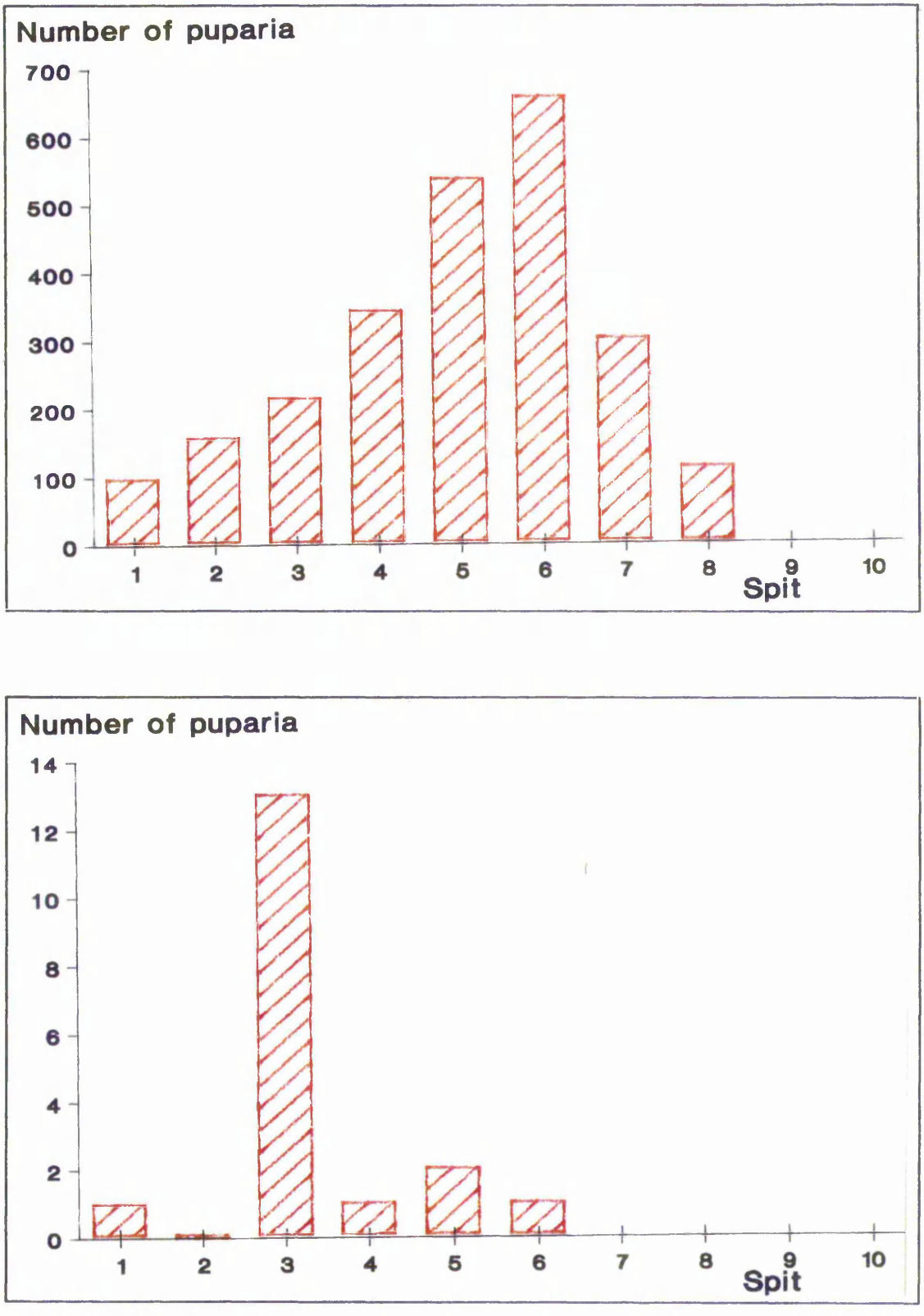


Figure 3.24: Distribution of puparia in the sediment beneath ER/2 (top) and ER/4 (above) from the Front Chamber of Robin Hood's Cave.

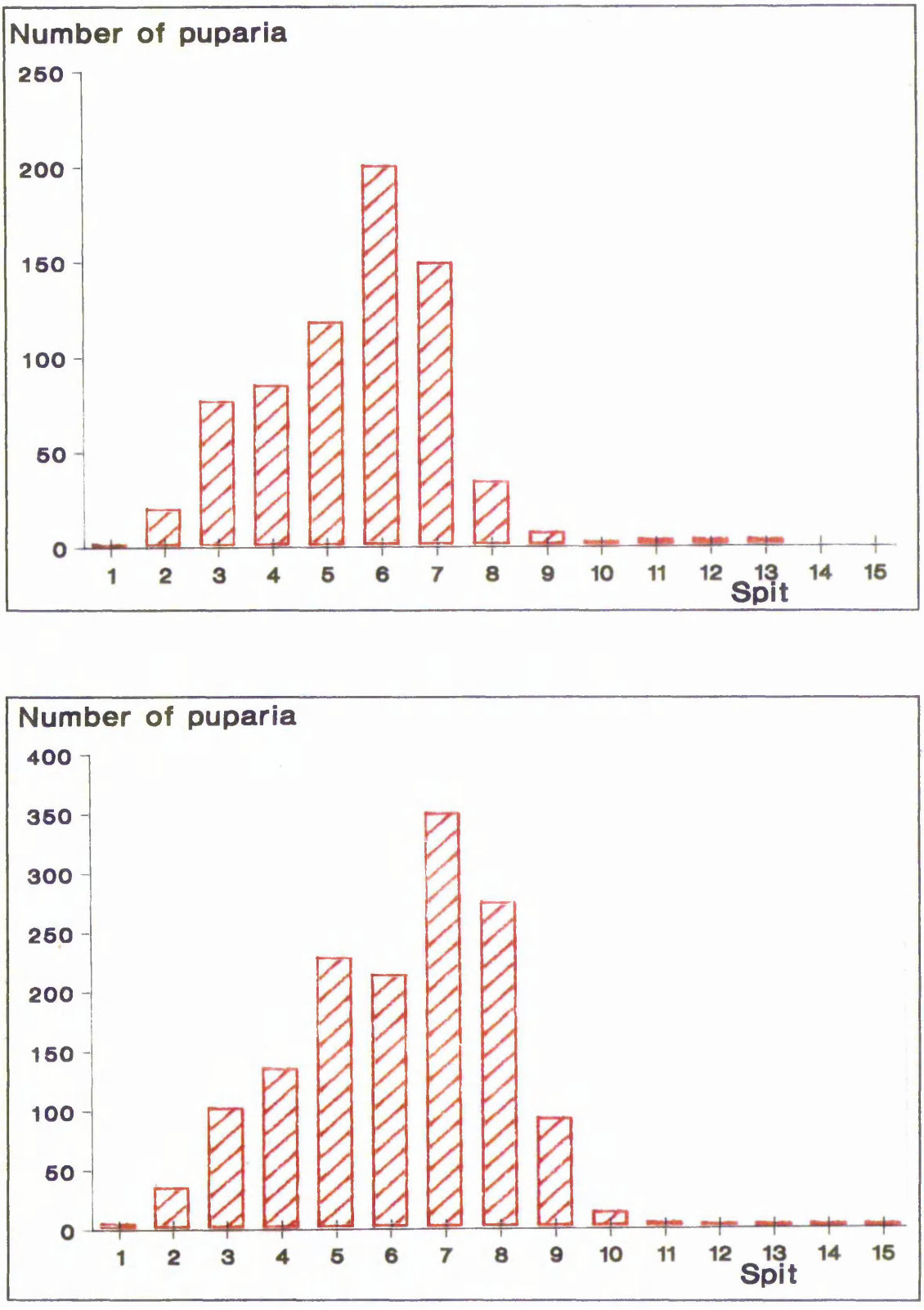


Figure 3.25: Distribution of puparia in the sediment beneath ER/1 (top) and ER/6 (above) from the Front Chamber of Robin Hood's Cave.

During the excavation of the tanks, a large number of empty *Calliphora vomitoria* puparia were found, as well as dead larvae and adults. Figures 3.23, 3.24 and 3.25 (previous pages) show the distribution of the puparia in the tanks.

A comparison of these figures demonstrates that there is a preferred depth to which the larvae burrow to pupate. Since this is between 4 and 8 cm, most of the puparia in Tanks 3 and 5 (Figure 3.23) were found at maximum depth. The number of puparia removed from the tanks varied between 18 and 3796. However, the tank containing 18 puparia was anomalous. A comparable number of larvae infested the carcasses in all tanks, but very few pupated in Tank 4.

Although it was thought that at least one other species of Diptera colonised the carcasses (ie *Triphleba antricola* - Section 3.2.1), the only evidence of this is from the pitfall trap results. No puparia were found.

3.4.2 Frogpit tanks

The remains in the tanks removed from the Frogpit showed the highest degree of decomposition, disarticulation and dispersal. In all cases most of the skeleton was exposed although relatively intact (Plates 16, 17 & 18, overleaf). Certain groups of bones were commonly displaced, including the lower mandibles, the neck and tail vertebrae, the ribs and the sternum. ER/11 showed the most disturbance; one femur and half of the pelvic girdle was found on the surface of the adjacent tank.

The majority of bone movement occurred across the surface, and little material was incorporated into the sediment. In some cases (ER/11 and ER/12), post-mortal movement had led to carcasses settling very close to the edges of tanks. The sediment in the tanks had contracted due to drying, and some bones from ER/11 had slipped down between the wall of the tank and the now-sloping sediment to a depth of up to 7 cm (Figure 3.27, page 88). Further drying out led to more sediment falling on top of these bones effectively burying them. Thus, four vertebrae were found at a depth of 4 - 5 cm, and a rib was found flat against the side of the tank, pointing diagonally upwards and spanning the sixth and seventh centimetre spits. The bones were all vertically below the area they would have occupied on the surface.

Some bones from ER/11 were genuinely incorporated into the sediment. Six tiny bones, thought to be phalanges, were found in the first centimetre spit below the

Plate 16: Final position of remains from the Frogpit chamber of Robin Hood's Cave: ER/7 (top) and ER/8 (above).

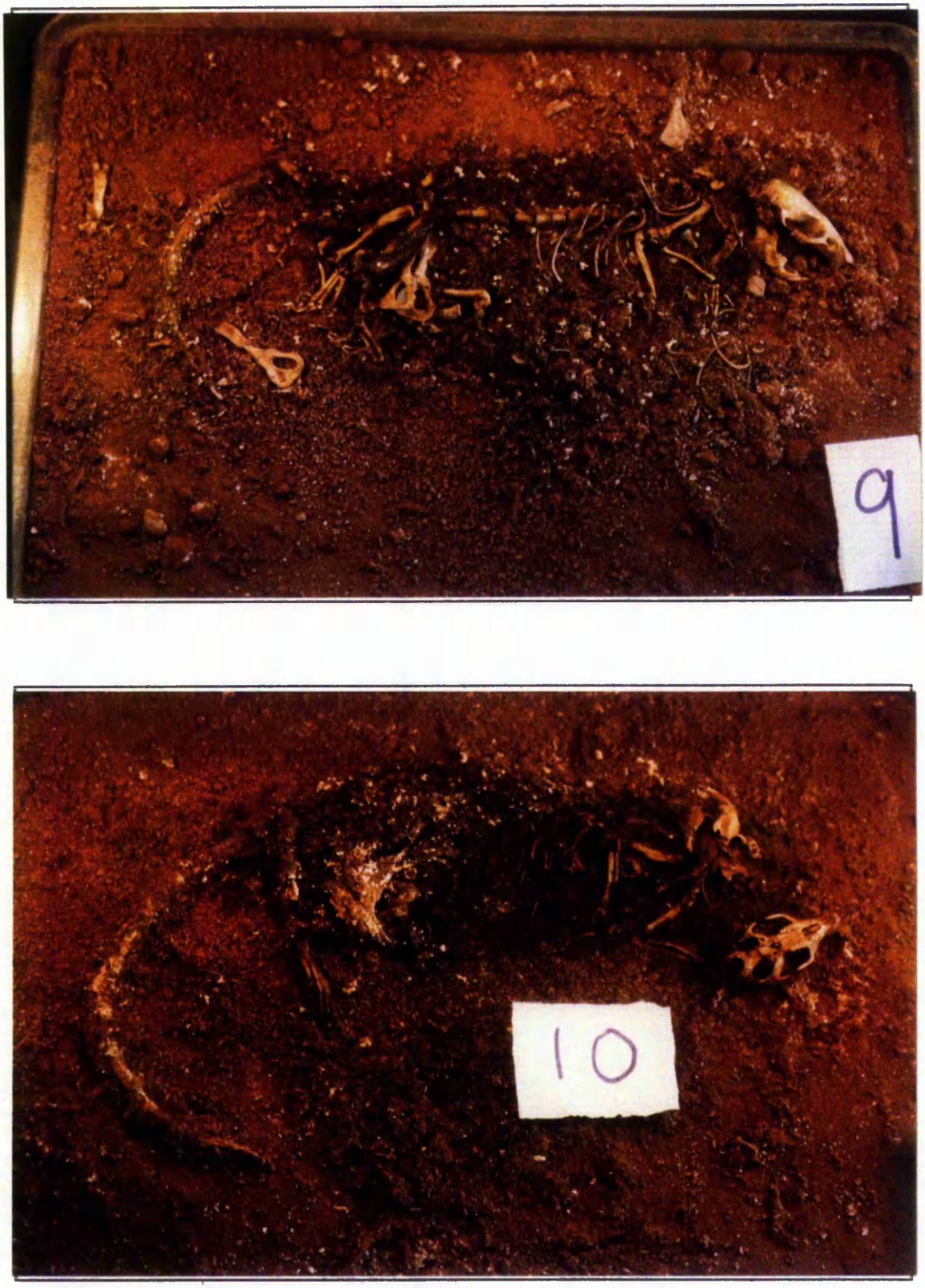


Plate 17: Final position of remains from the Frogpit chamber of Robin Hood's Cave: ER/9 (top) and ER/10 (above).

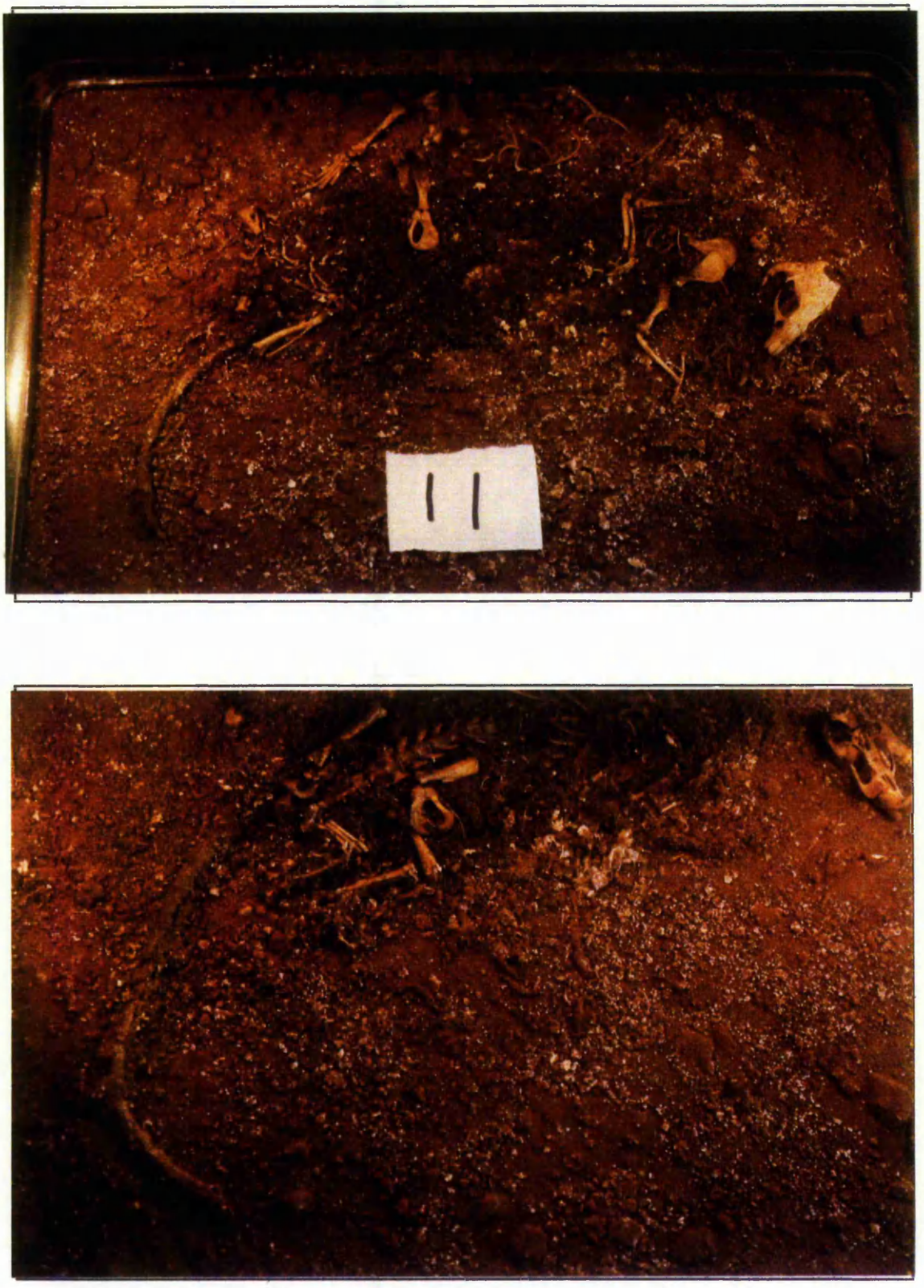


Plate 18: Final position of remains from the Frogpit chamber of Robin Hood's Cave: ER/11 (top) and ER/12 (above).

area from which the front foreleg was removed. These were the only bones considered to have been buried by the activities of invertebrates.

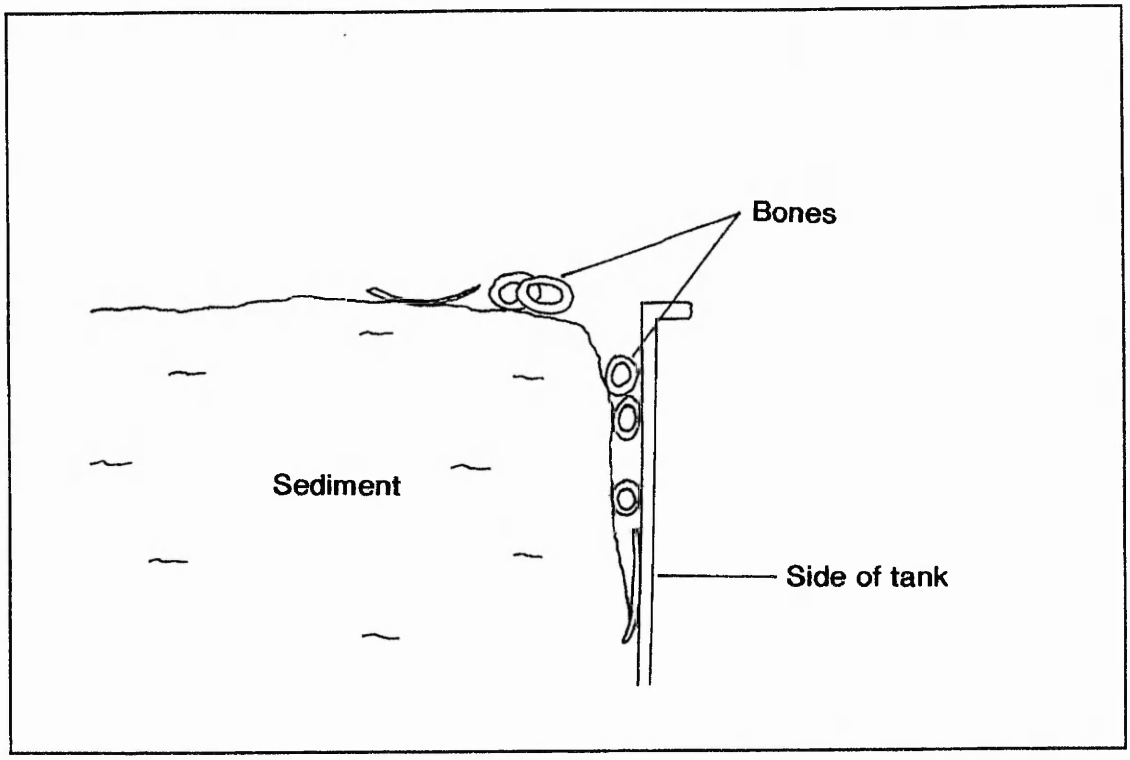
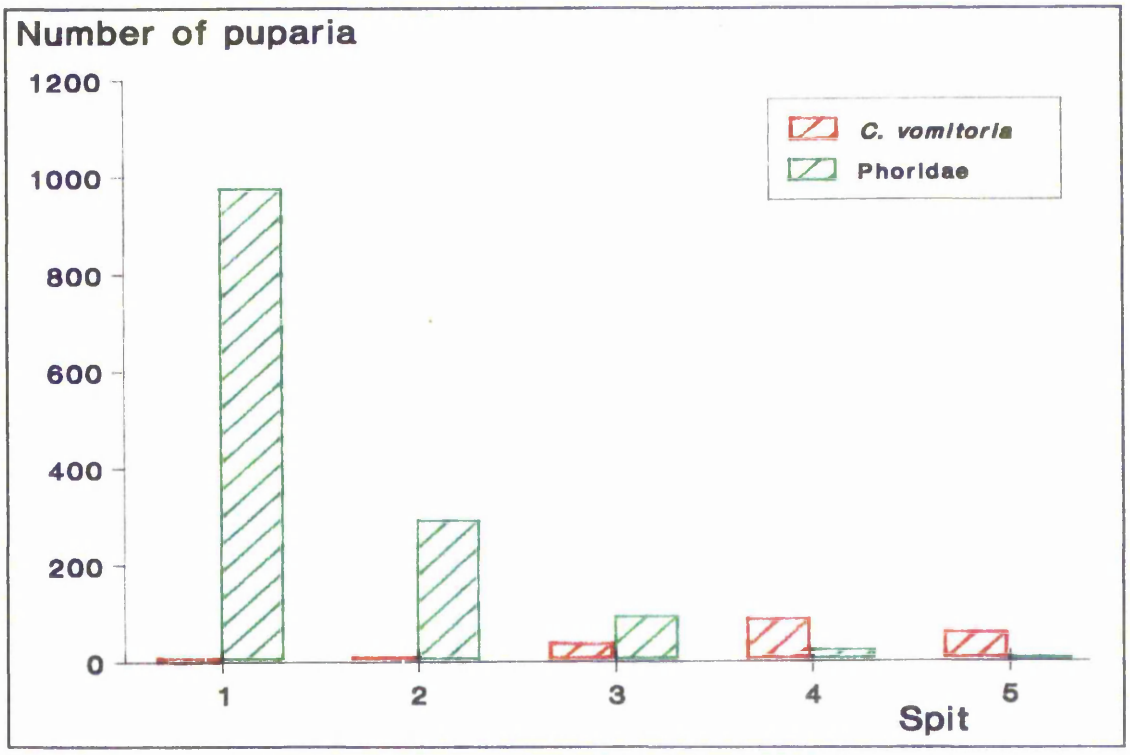


Figure 3.27: Position of bones from ER/11.

In all cases, some skeletal elements were found underneath others (and hence are not visible on the photographs). These were not incorporated in the substratum but were in that position because of the way the carcass had collapsed.

When the tanks from the Frogpit were excavated a large number of dipteran remains were discovered. Many empty phorid puparia were found, as were dead *Calliphora vomitoria* larvae, adults and empty puparia. Dead heleomyzid adults were found in the top centimetre spit under ER/11, and in the seventh centimetre spit of the tank containing ER/8. The empty puparia of two other dipteran species were also found, but unfortunately were too decomposed to be identified.

Figures 3.28, 3.29 and 3.30 (overleaf) show the distribution of *Calliphora* and



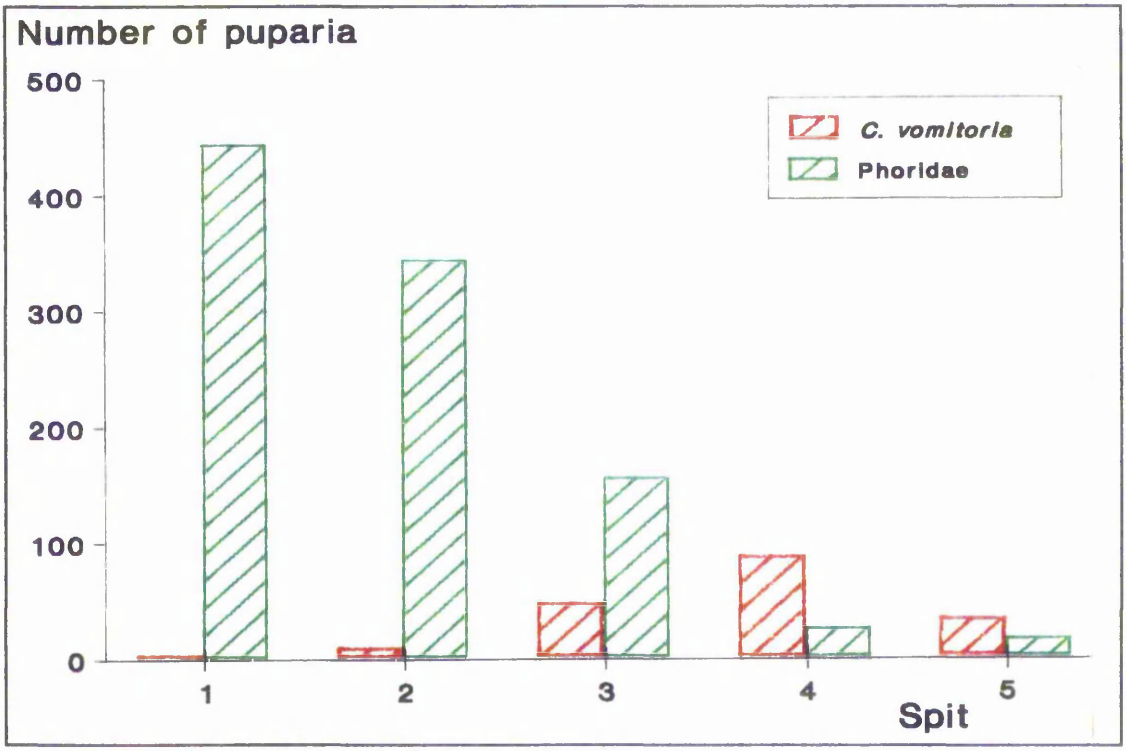


Figure 3.28: Distribution of puparia in the sediment beneath ER/7 (top) and ER/10 (above) from the Frogpit Chamber of Robin Hood's Cave.

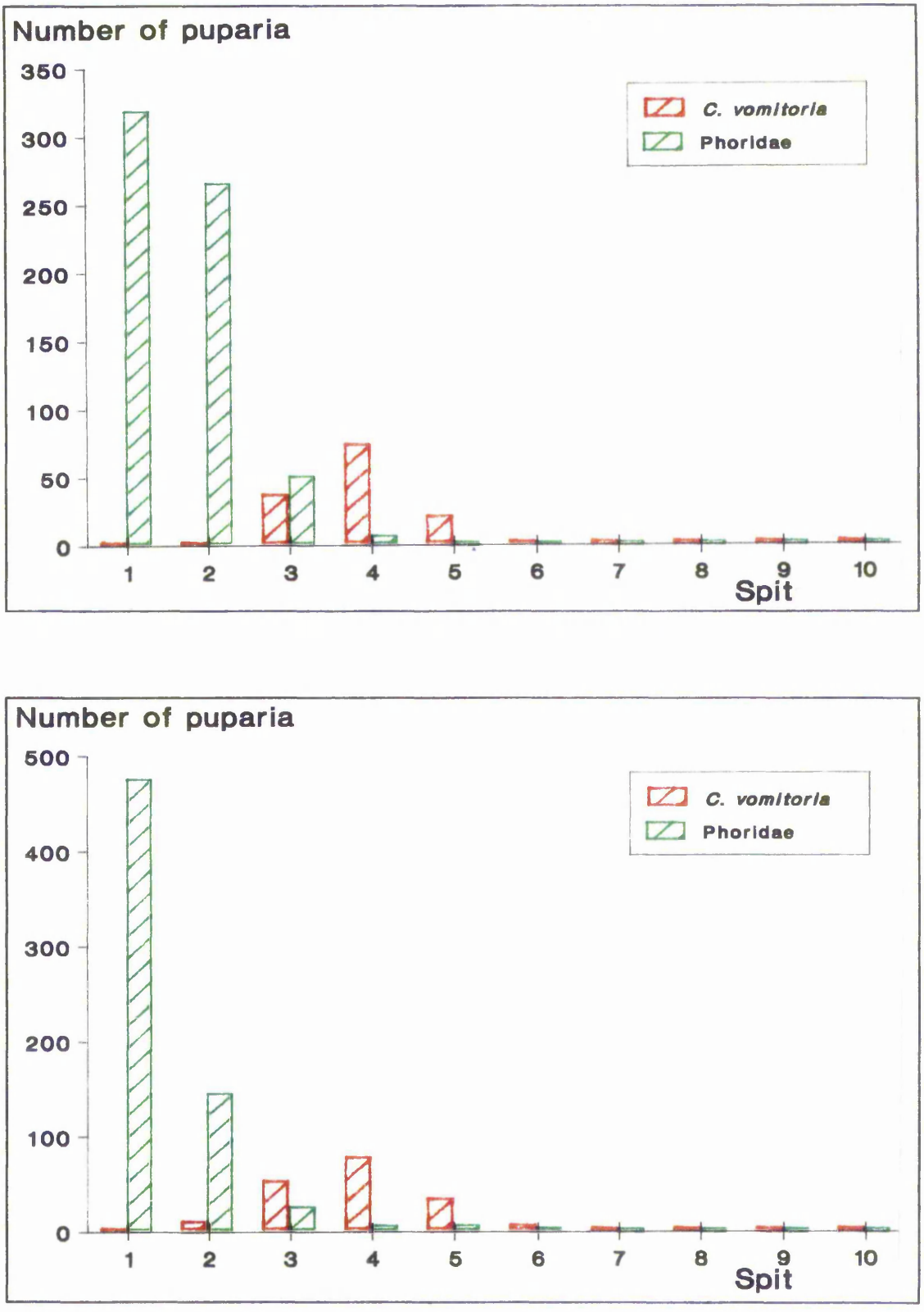
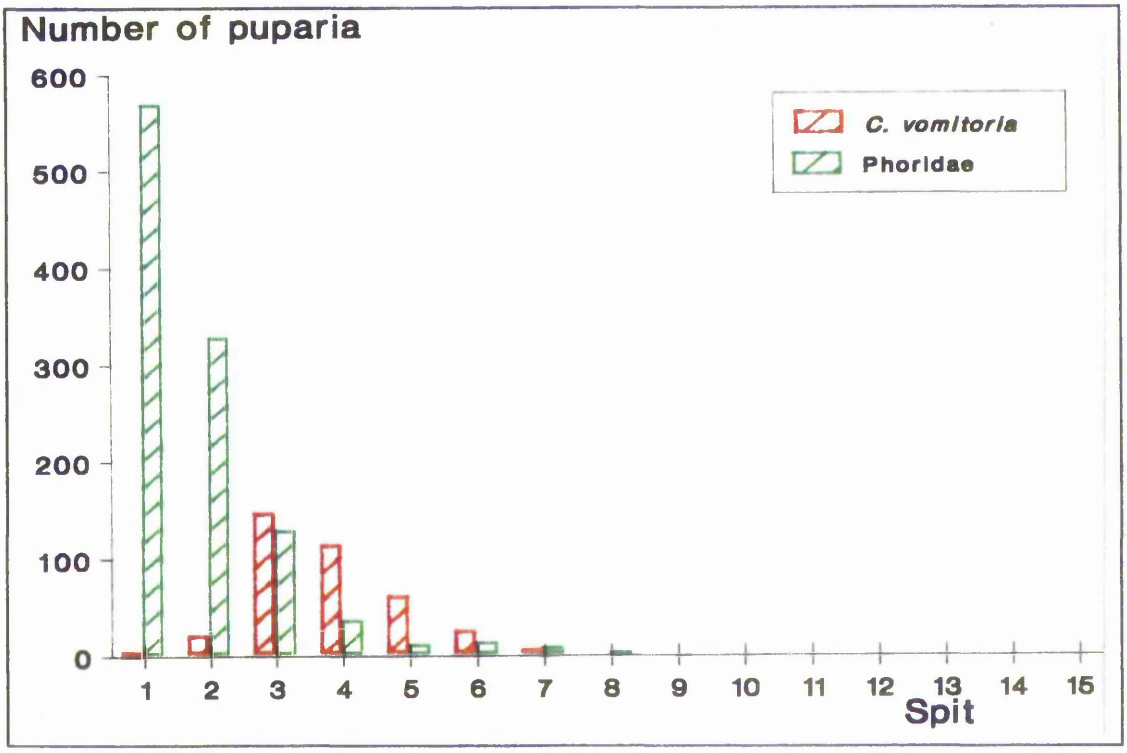


Figure 3.29: Distribution of puparia in the sediment beneath ER/9 (top) and ER/12 (above) from the Frogpit Chamber of Robin Hood's Cave.



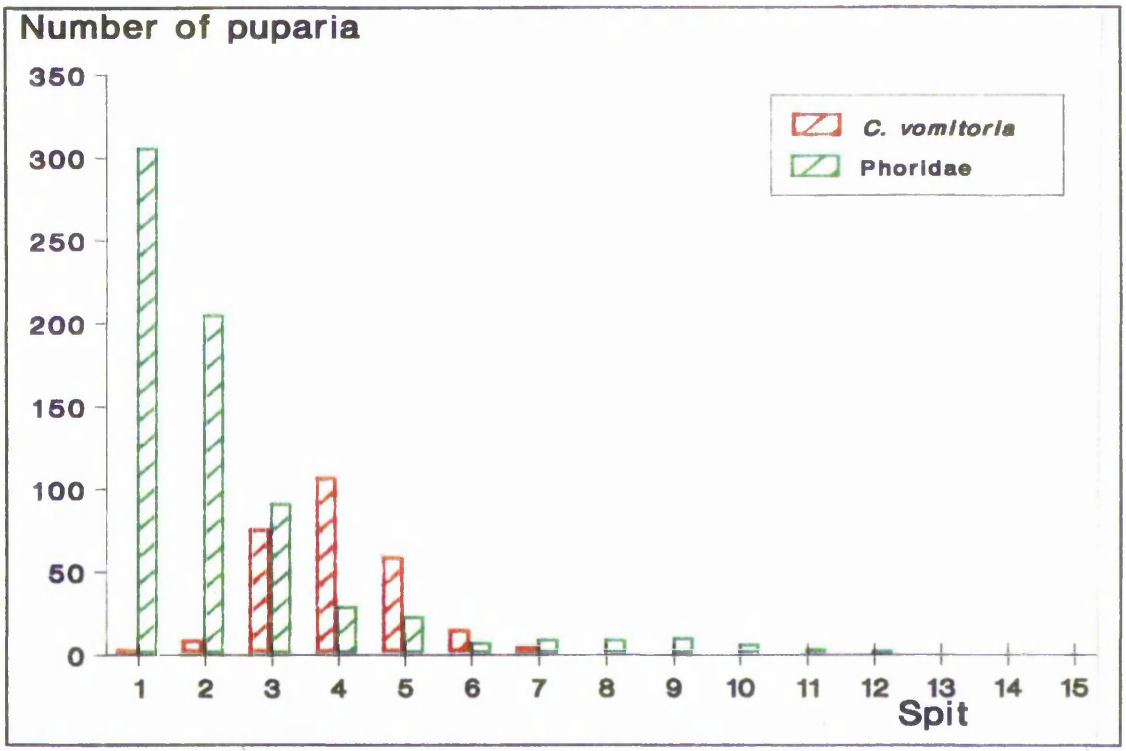


Figure 3.30: Distribution of puparia in the sediment beneath ER/8 (top) and ER/11 (above) from the Frogpit Chamber of Robin Hood's Cave.

phorid puparia within the tanks. In each case, most *Calliphora* had pupated at between 3 and 5 cm, none being found more than 8 cm below the surface. In contrast, the majority of phorid puparia were removed from the first two centimetre spits.

3.4.3 Back tanks

All the carcasses removed from the Back Chamber were covered in fungal hyphae and sclerotia. In some cases hyphae held the bones together in a discrete unit. This could be removed almost whole, and any bones remaining on the sediment plotted and bagged separately (Plate 19, overleaf). Other carcasses had all the detritus carefully scraped and brushed off before being removed from the tank piece by piece (Plates 20, 21 & 22).

Relatively little dispersal across the surface of the sediment was apparent except in the tank containing ER/14 (Plate 22). As in the tanks removed from the Frogpit chamber, certain parts of the remains were hidden underneath others, although not buried. When ER/17 was cleaned, however, a pit approximately 7 cm deep was discovered. A number of bones from the carcass were found in this, although none were actually incorporated into the substratum.

Upon excavation, empty phorid and *Calliphora* puparia were found in the tanks containing ER/13, ER/14 and ER/15, but just those of the phorid species in the remaining tanks. The distribution of dipteran puparia is illustrated in Figures 3.31, 3.32 and 3.33 (overleaf). *Calliphora* puparia were found in the top 7 cm with a peak at 4 cm. Phorid puparia predominated in the top 2 cm whether or not *Calliphora* was present.

Plate 19: Final position of remains from Back chamber of Robin Hood's Cave: ER/18 removed (top) and remains (above)

Plate 20: Final position of remains from Back chamber of Robin Hood's Cave: ER 15 *in situ* (top) and cleaned (above)

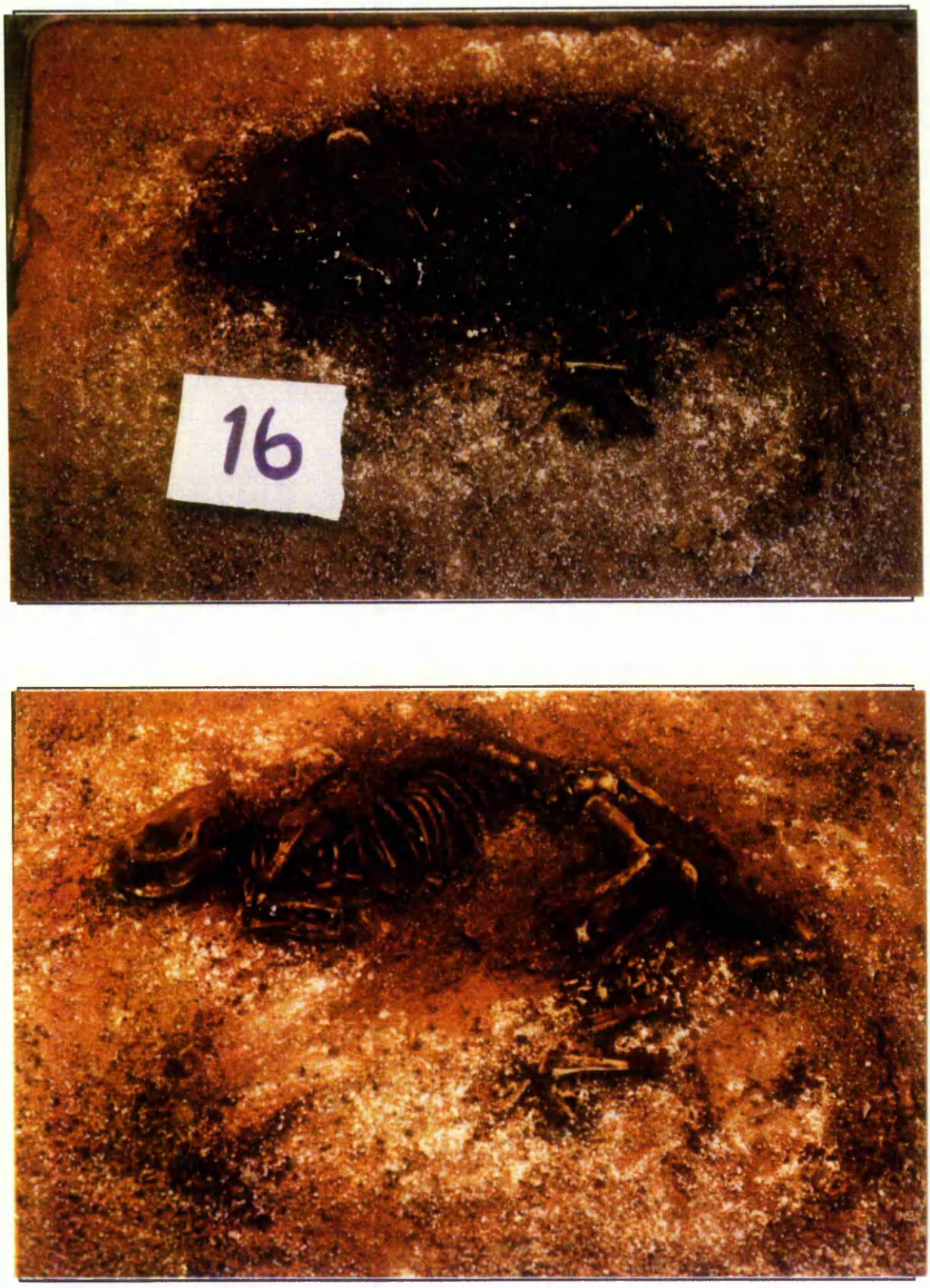


Plate 21: Final position of remains from Back chamber of Robin Hood's Cave: ER/16 *in situ* (top) and cleaned (above)

Plate 22: Final position of remains from Back chamber of Robin Hood's Cave: ER/13 (top) and ER/14 (above)

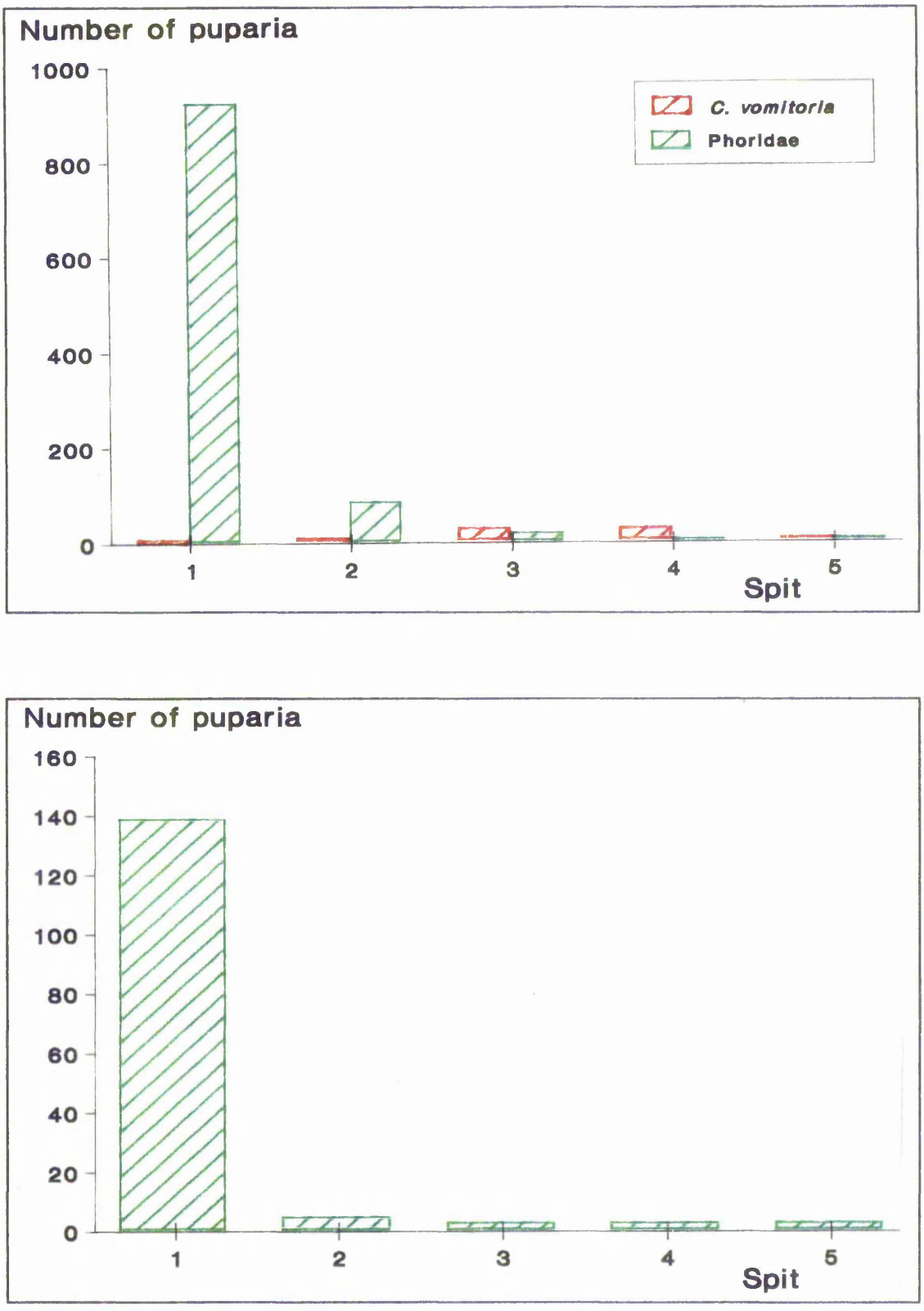


Figure 3.31: Distribution of puparia in the sediment beneath ER/15 (top) and ER/16 (above) from the Back Chamber of Robin Hood's Cave.

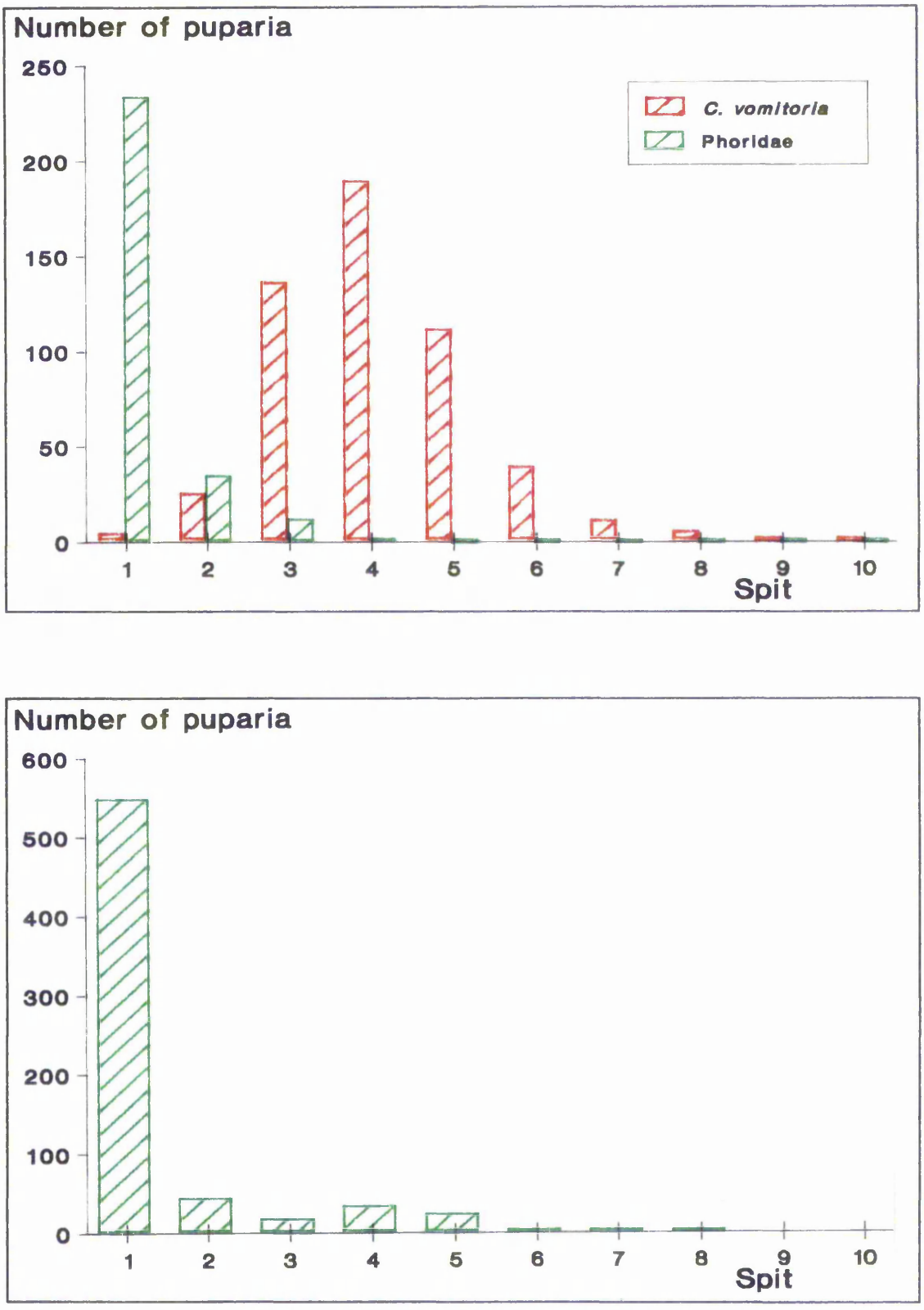


Figure 3.32: Distribution of puparia in the sediment beneath ER/14 (top) and ER/18 (above) from the Back Chamber of Robin Hood's Cave.

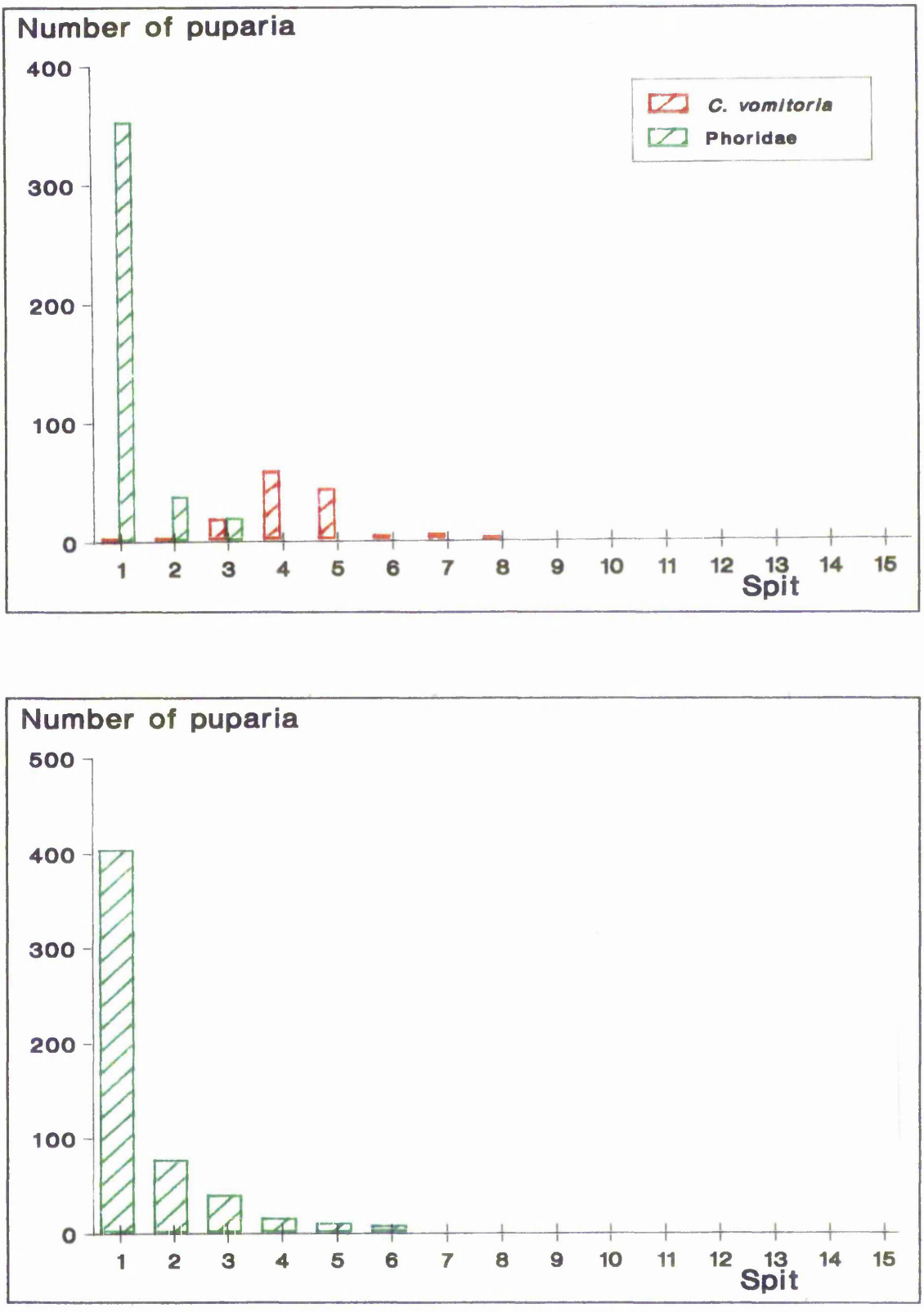


Figure 3.33: Distribution of puparia in the sediment beneath ER/13 (a) and ER/17 (b) from the Back Chamber of Robin Hood's Cave.

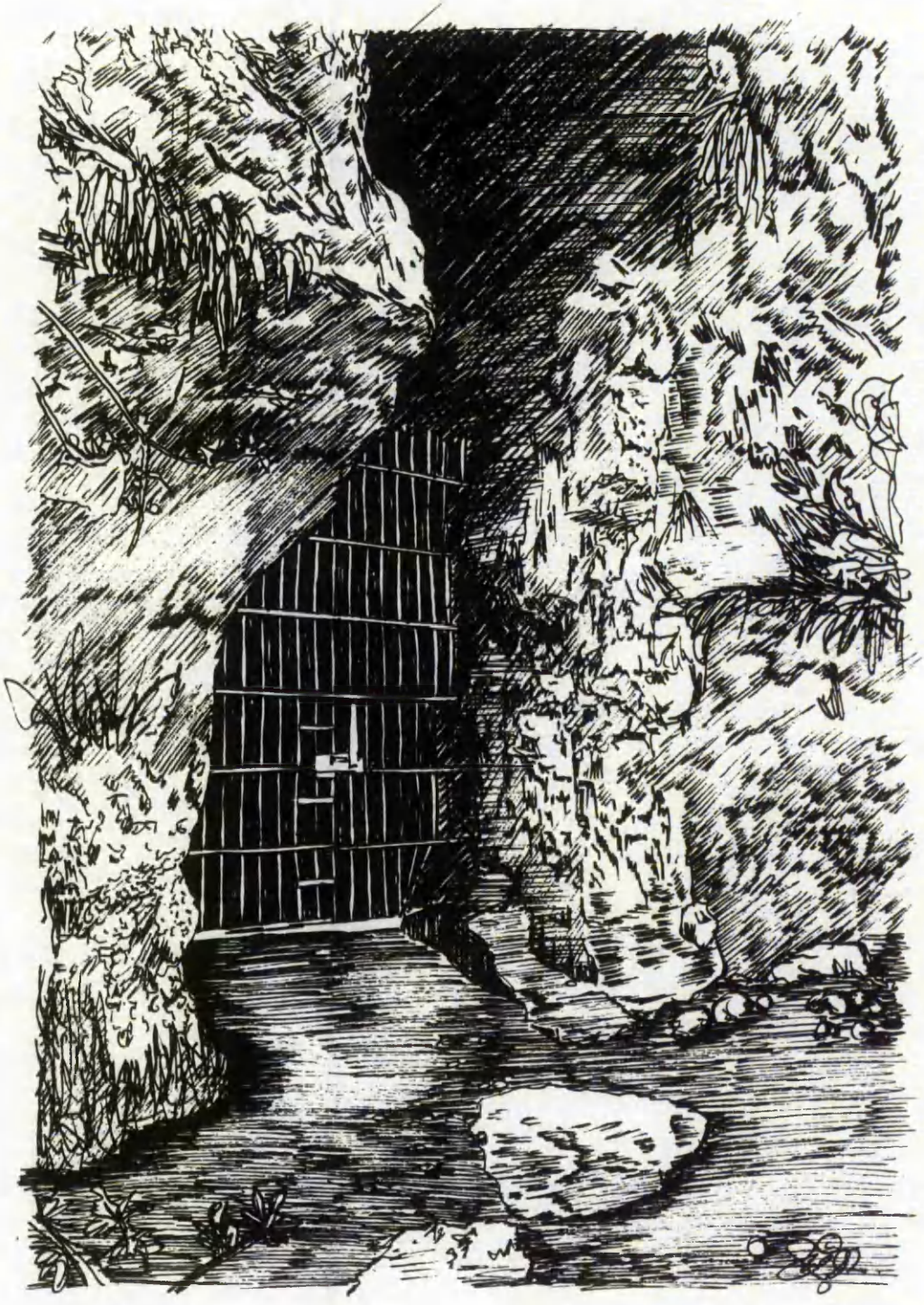


Figure 4.0: The entrance to Church Hole Cave, Creswell Crags.

4.1 Abiotic conditions

As in Robin Hood's Cave, the processes of decomposition observed in the carcasses in Church Hole varied in relation to the distance from the entrance. Once again, readings of ambient temperature and relative humidity at each site (Figure 4.1) show that temperatures 42 m from the cave entrance (Back site) were generally higher than those 28 m from the entrance (Middle site), and that the front of the cave was the most variable region.

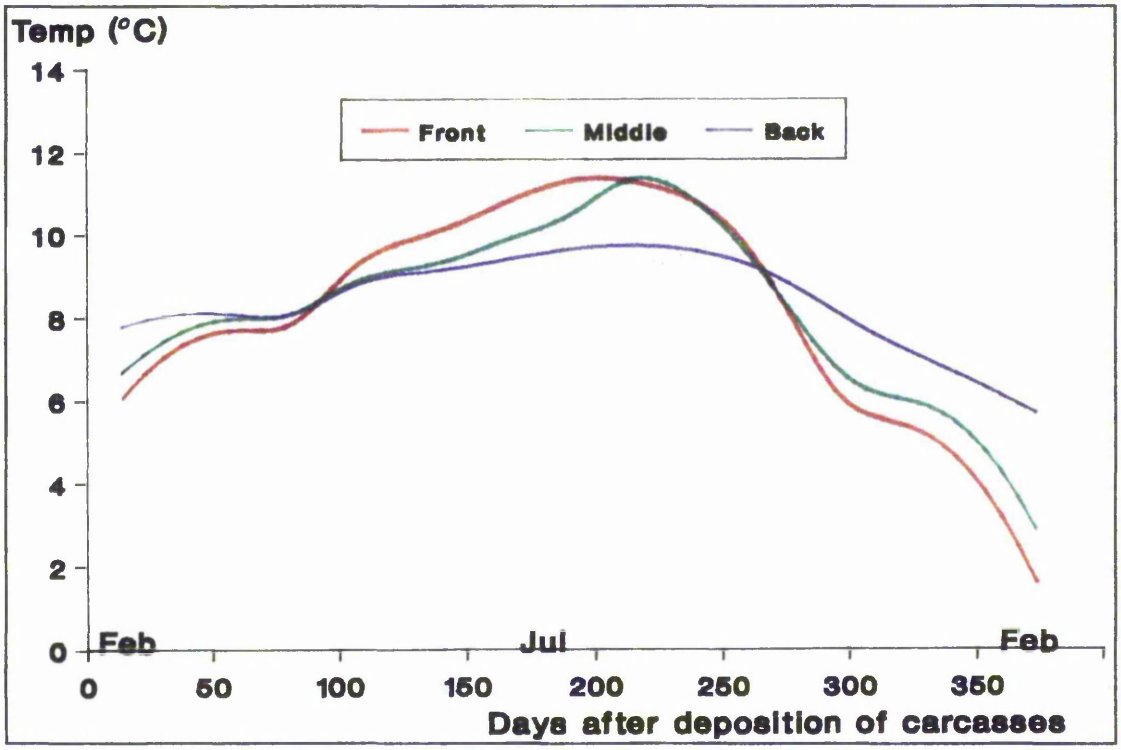


Figure 4.1: Monthly ground level temperature (mean) at the three sites in Church Hole Cave during the year of the experiment.

However, the overall yearly differences in temperature measured at the three sites in Church Hole Cave (Table 4.1) are not statistically significant.

Table 4.1: Mean (±95% limits) temperature and relative humidity at ground level at the three sites in Church Hole Cave, (a) for the first three months after deposition, and (b) for the full year of the experiment.

	FRONT	MIDDLE	BACK
(a) 90 days			
TEMP (°C)	7.1±0.9	7.5±0.5	7.9±0.3
RH (%)	93.7±3.8	91.3±2.8	93.0±1.7
(b) 1 year			
TEMP (°C)	7.9±1.9	8.0±1.6	8.3±0.8
RH (%)	94.2±4.2	92.8±4.2	92.9±3.9

4.2 Fauna and fungi

Table 4.2 is a summary of all species found in Church Hole Cave during the course of this work, both before and after the carcasses were deposited.

Table 4.2: Species found in Church Hole Cave expressed as actual numbers (upper figure), and as a per cent of the total number of species found at that site (lower figure), before (Bline) and after (Exptl) carcasses were deposited.

	Front		Middle		Back	
	Bline	Exptl	Bline	Exptl	Bline	Exptl
Mollusca	1 4.2					
Acari	3 12.5	3 15.8	3 17.6	4 21.1	3 15.8	3 18.8
Araneida	1 4.2		1 5.9	1 5.3	1 6.7	1 6.3

continued.....

	Front		Middle		Back	
	Bline	Exptl	Bline	Exptl	Bline	Exptl
Isopoda	1 4.2					
Diplura			1 5.9	1 5.3	1 6.7	1 6.3
Collembola	5 20.8	5 26.3	5 29.4	6 31.6	5 33.3	6 37.5
Thysanoptera	1 4.2	2 10.5		1 5.3		
Diptera	6 25.0	5 26.3	6 35.3	5 26.3	4 26.4	4 25.0
Hymenoptera	2 8.3	3 15.8				
Coleoptera	4 16.7	1 5.3	1 5.9	1 5.3	1 6.7	1 6.3

The baseline fauna of Church Hole Cave comprised of 32 species whereas only 28 were found during the experimental period. 20 species were found both before and after deposition. Full details of the baseline and of the monthly pitfall catch during the experimental period can be found in Appendix 2.

Table 4.3 (page 106) shows the number of species found at each site, and also the percentage of those which were also found at the other sites. Both before and after deposition, proportionally fewer species (17 before, 10 after) were present at one site only than was the case in Robin Hood's Cave. Nine species were found at all three sites before the carrion was deposited, and eight after.

The figures in Table 4.3 show that, as in Robin Hood's Cave, those species found further into the cave were more likely to also be present elsewhere than those found near the entrance.

Figures 4.2 and 4.3 (overleaf) show that fluctuations in the baseline cavernicolous fauna in Church Hole Cave were related to temperature as they were in

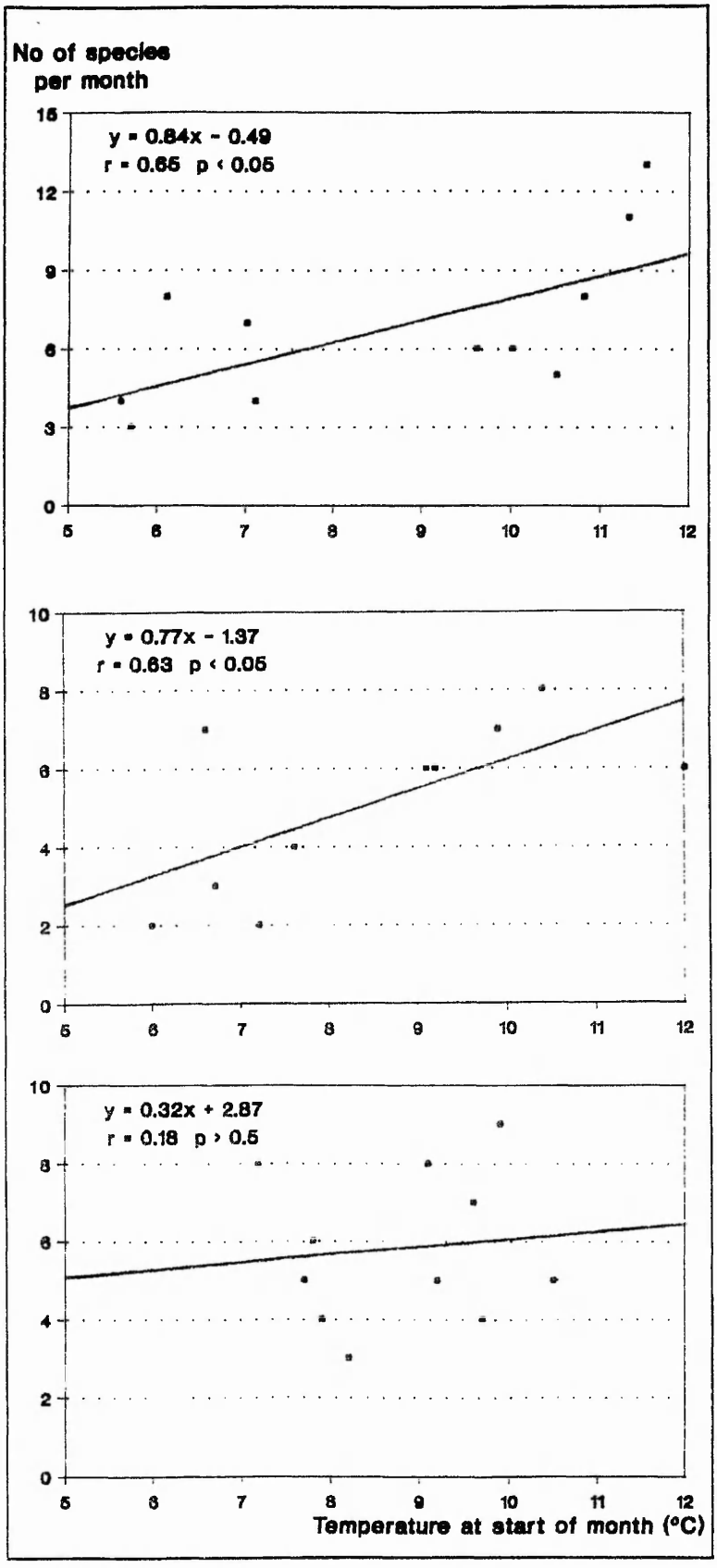


Figure 4.2: Baseline relationship between the number of species collected per month and the average ground level temperature at the beginning of the month, at:

(a) the Front site,

(b) the Middle site,

(c) the Back site.

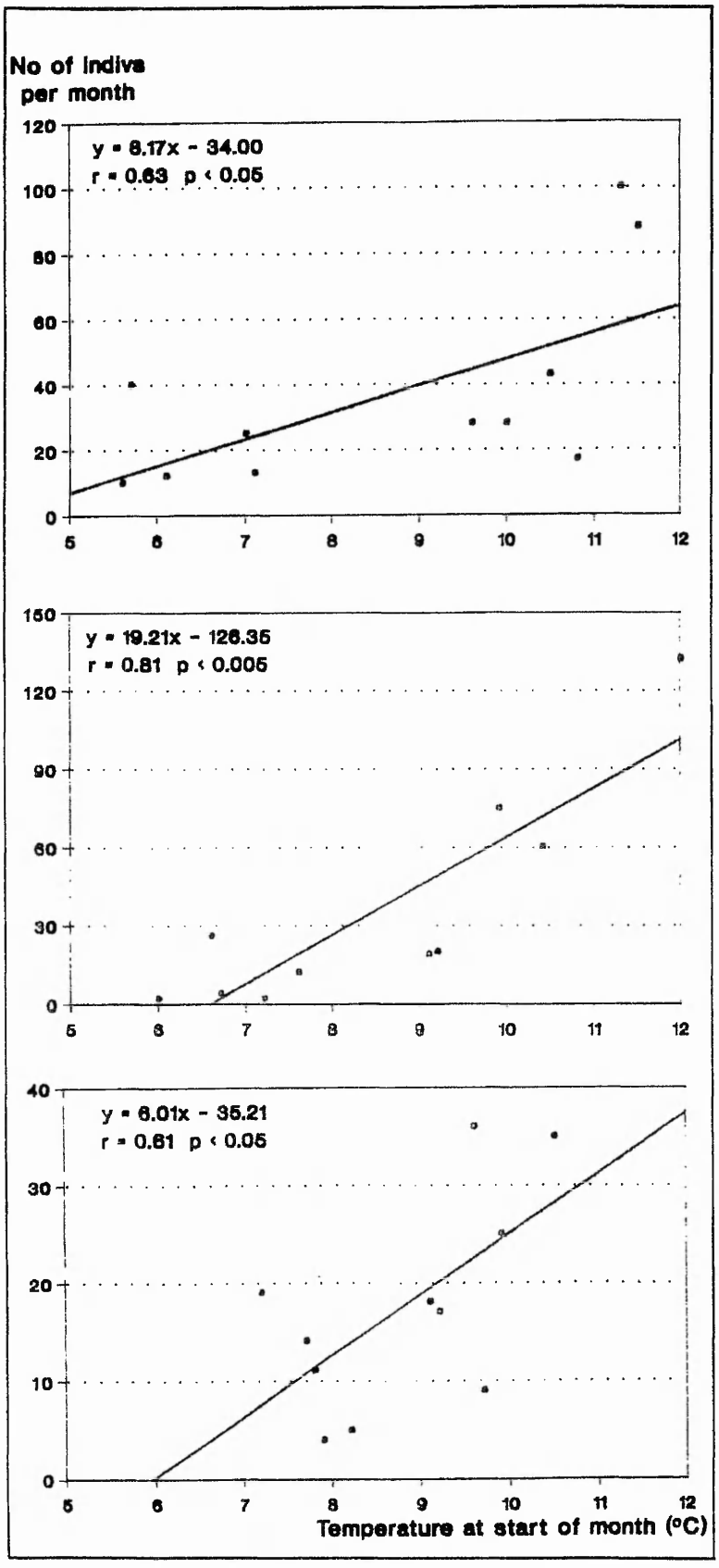


Figure 4.3: Baseline relationship between the number of individuals collected per month and the average ground level temperature at the beginning of the month, at:

(a) the Front site,

(b) the Middle site,

(c) the Back site.

Table 4.3: The distribution of species in the three chambers of Church Hole Cave, and the overlap between sites.

	Total no of species found	Percentage also found in Front	Middle	Back	All
Baseline					
Front	24	100	42	38	38
Middle	17	59	100	82	53
Back	15	60	93	100	60
Experimental					
Front	19	100	58	53	42
Middle	19	58	100	68	42
Back	15	63	81	100	50

Robin Hood's Cave. The correlation between the number of species trapped and average ambient temperature is shown in Figure 4.2, and is only significant at the Front and Middle sites. However, the number of individuals trapped in a month was significantly related to temperature at all three sites (Figure 4.3), and especially strongly at the Middle site.

4.2.1 Front Site

Plates 23 and 24 (overleaf) show the physical appearance of the carcass deposited at the Front site, during the first four months of decomposition.

The carcass remained unchanged for over six weeks, after which a bluish fungus, possibly a species of *Penicillum*, appeared around the eyes and mouth. This gradually spread across the head (Plate 23) and was then also found on the underside of the legs. During the period of the experiment a number of different fungi colonised the carcass, closely resembling the succession observed in Robin Hood's Cave (Section 3.2).

No invertebrates were seen until forty six days after deposition, when a few Collembola, probably *Lepidocyrtus* spp, were observed apparently feeding on the

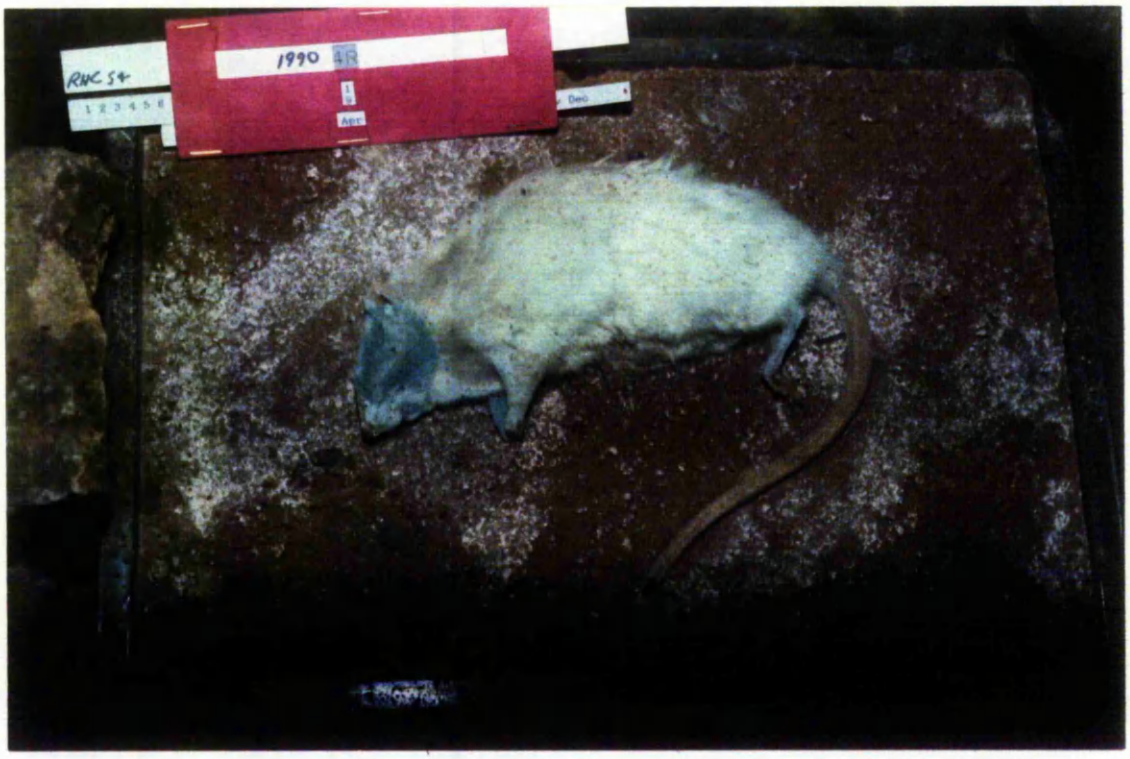


Plate 23: Carcass after eleven weeks at the Front site of Church Hole Cave.

Plate 24: Carcass after four months at the Front site of Church Hole Cave.

fungus.

In May, fifteen weeks after deposition, three *Aleochara languinosa* (Coleoptera: Staphylinidae) were found on the carcass. The dominant invertebrate species in the area was by that time the cave spider, *Meta menardi*, there being approximately ten to twelve adults in the small area around the tank in which the rat had been placed. There were none actually on the carcass though, and no indication of what the beetles or the spiders were feeding upon.

There was, however, a strong smell in the vicinity of the carcass, suggesting that decomposition was fairly advanced, and about a month later, a large amount of fur from the rat was noted on the surrounding sediment (Plate 24). Both suggested the presence of dipterous larvae, although none were actually seen without disturbing the carcass.

Further evidence of dipteran colonisation of the carcass came in July (during the 25th week after deposition), when a number of adult *Calliphora vomitoria* (Diptera: Calliphoridae) were seen in the area around the carcass. No empty puparia were found, however, although there were a few exit holes in the sediment upon which the carcass was lain, like those seen in the tanks in Robin Hood's Cave.

Two weeks later, by which time all the *Calliphora* had dispersed, phorid puparia were seen near the carcass.

By the end of August the carcass was mummified. The continuing presence of tiny amounts of fungus on the skin supported a small population of Collembola, but other than these, no more invertebrates were seen for the rest of the experiment.

Figures 4.4 and 4.5 (overleaf) show the fluctuations in the numbers of mites and *Lepidocyrtus* spp (Collembola: Entomobryidae) pitfall trapped during the period of the experiment. These were the only groups trapped at the Front site in any number.

The species richness and the number of individuals caught before and after deposition of the carcass at the front of Church Hole Cave are shown in Figure 4.6 a and b (page 110). In both cases, the figures during the experimental period are generally equal to or lower than the baseline. A similar depression can also be seen in the graphs of species diversity and equitability (Figure 4.6 c and d).

Figure 4.4: Numbers of individuals of Acari trapped at the Front site of Church Hole Cave during the experiment in relation to the baseline. (* No figures for baseline as trap was disturbed.)

Figure 4.5: Numbers of individuals of the Collembola *Lepidocyrtus curvicollis* and *L. cyaneus* (Entomobryidae) trapped at the Front site of Church Hole Cave during the experiment in relation to the baseline. (* No figures for baseline as trap was disturbed.)

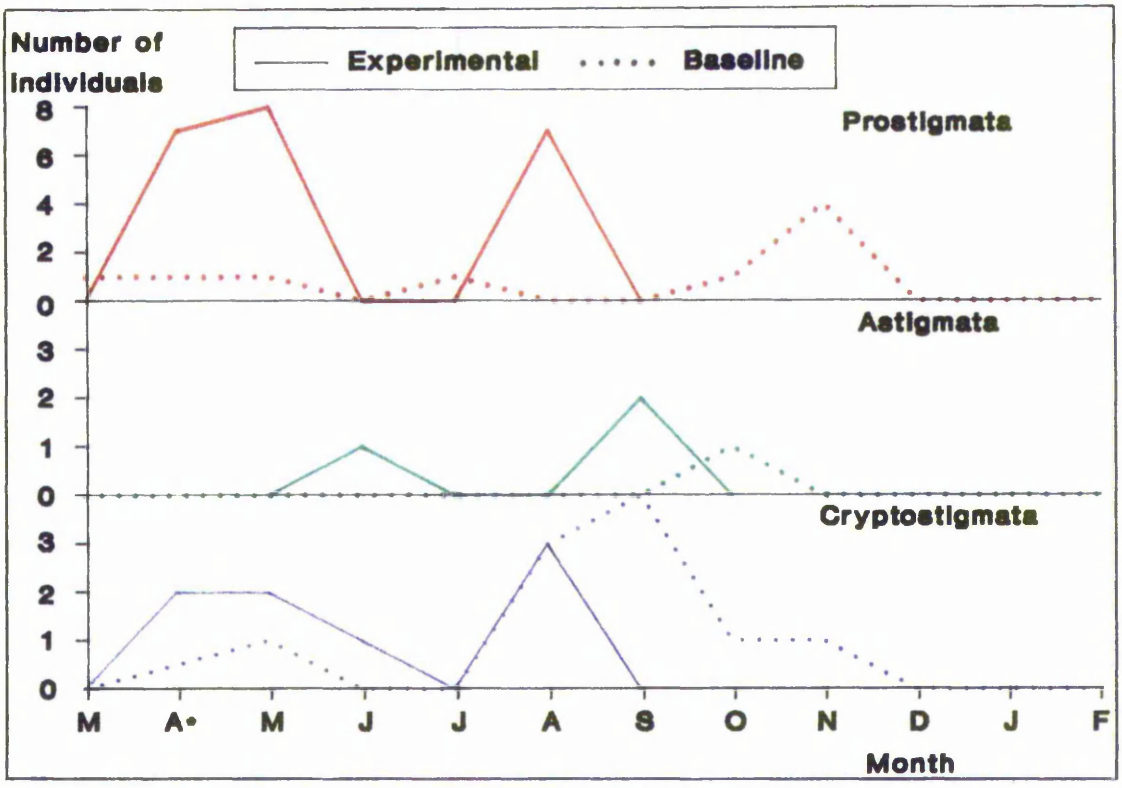


Figure 4.4

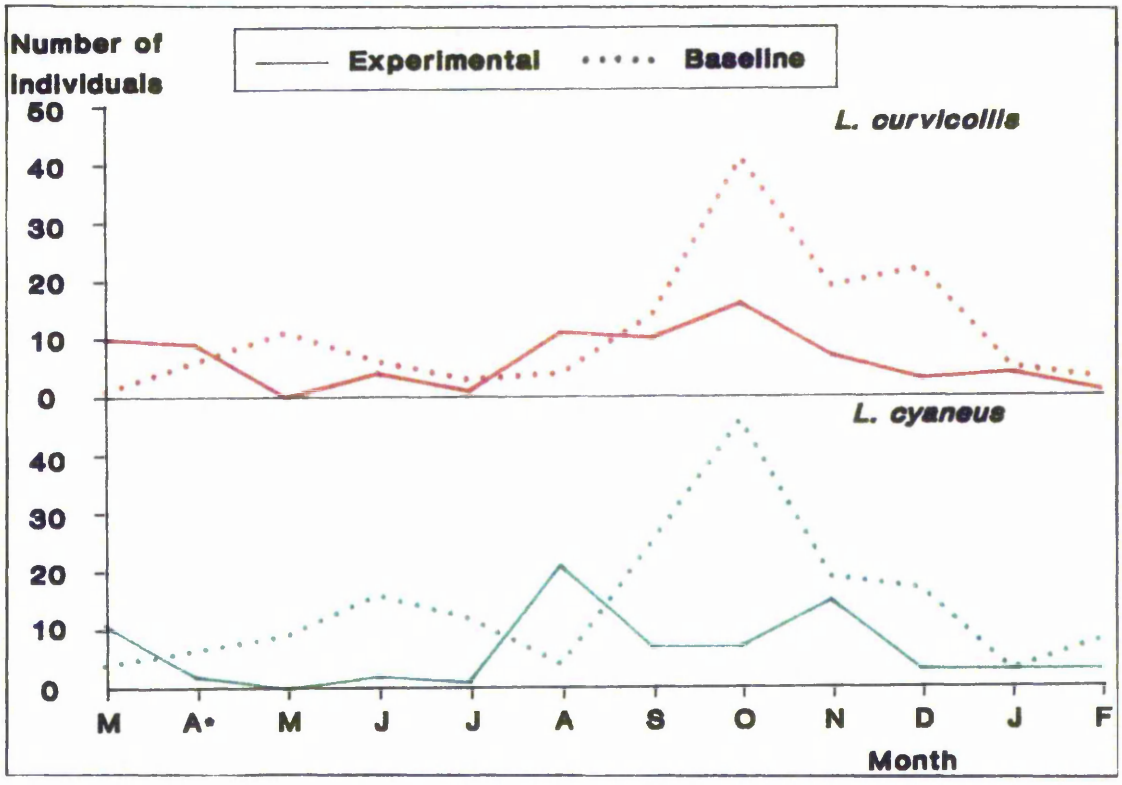


Figure 4.5

Figure 4.6: A comparison of the baseline fauna of the Front site in Church Hole Cave with that trapped during the experiment in terms of the numbers of individuals (a) and species (b), and the diversity (c) and evenness (d). (* No figures for baseline as trap was disturbed.)

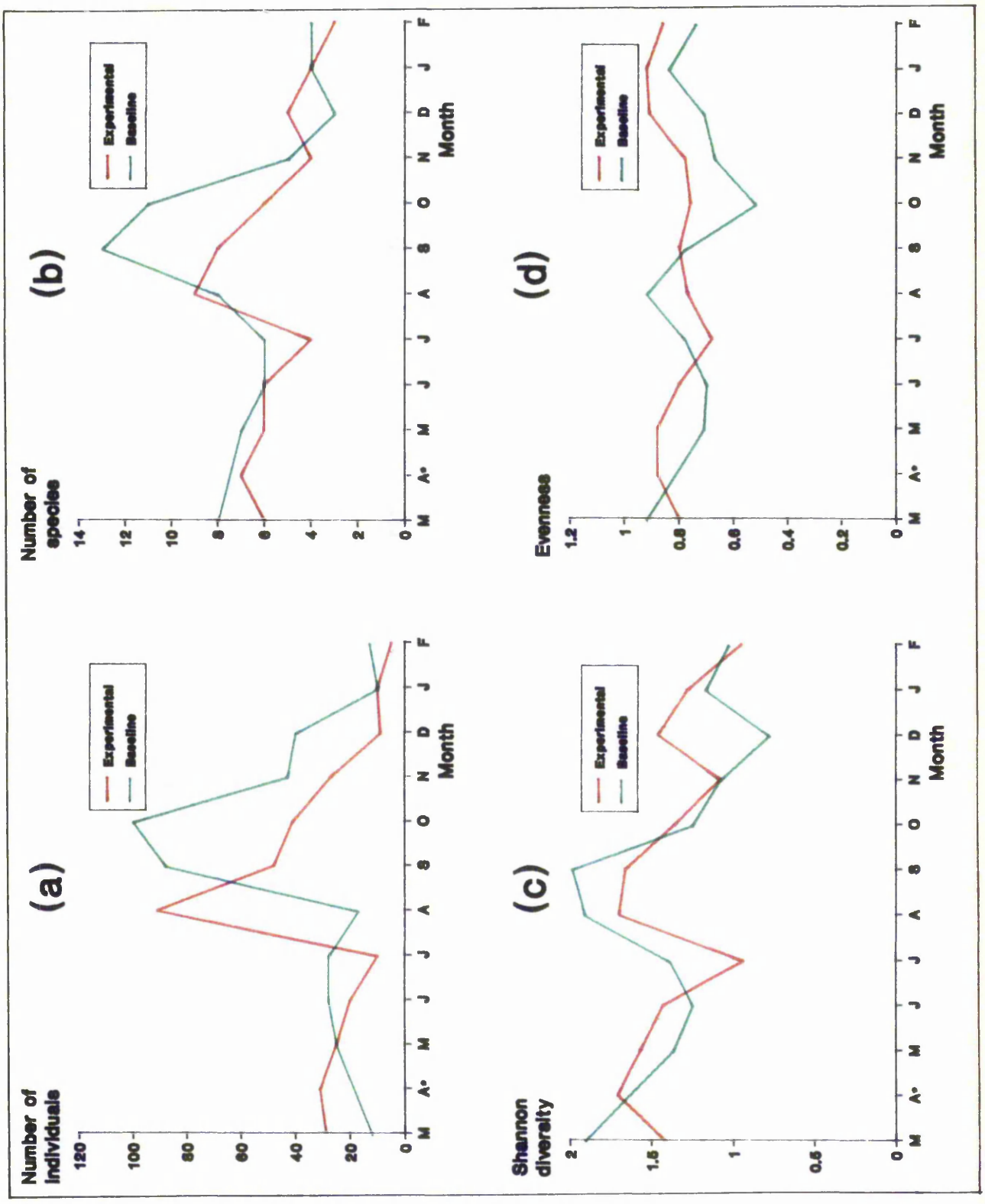

(a)
Number of individuals
Experimental
Baseline
Month
(b)
Number of species
(c)
Shannon diversity
(d)
Evenness
M A S O N D J F M A M J J A S O N D J F

Figure 4.6

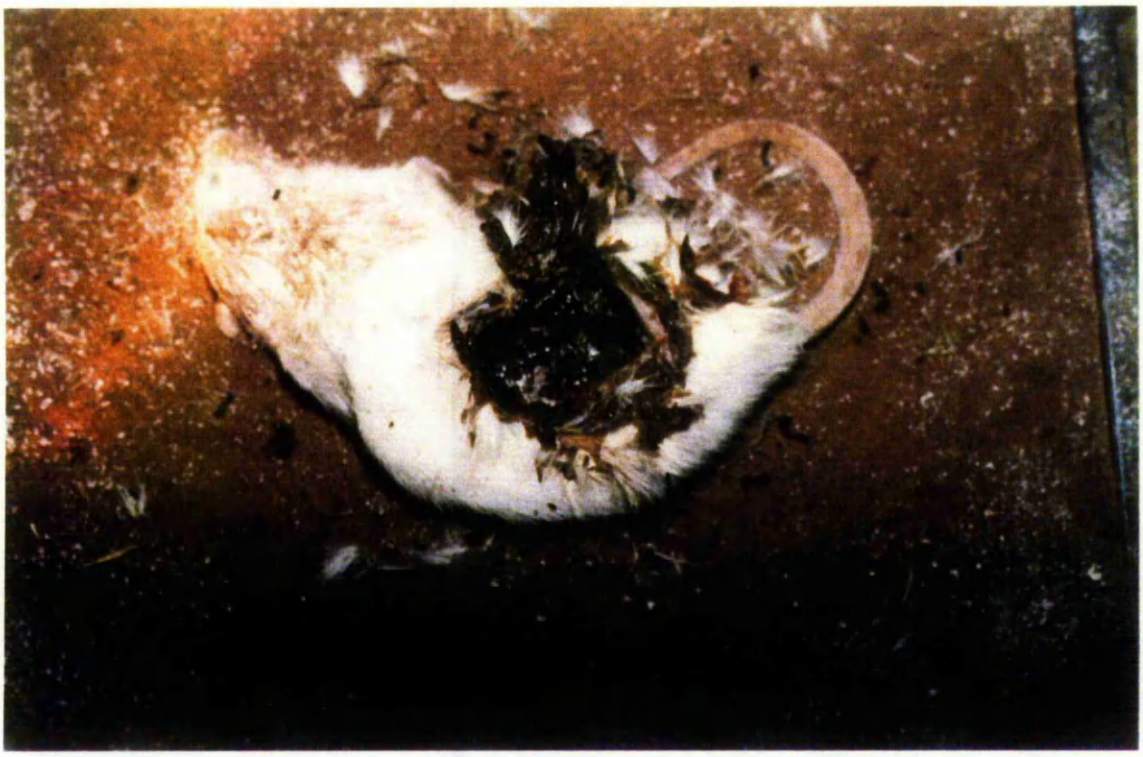


Plate 25: Carcass after ten weeks at the Middle site of Church Hole Cave.

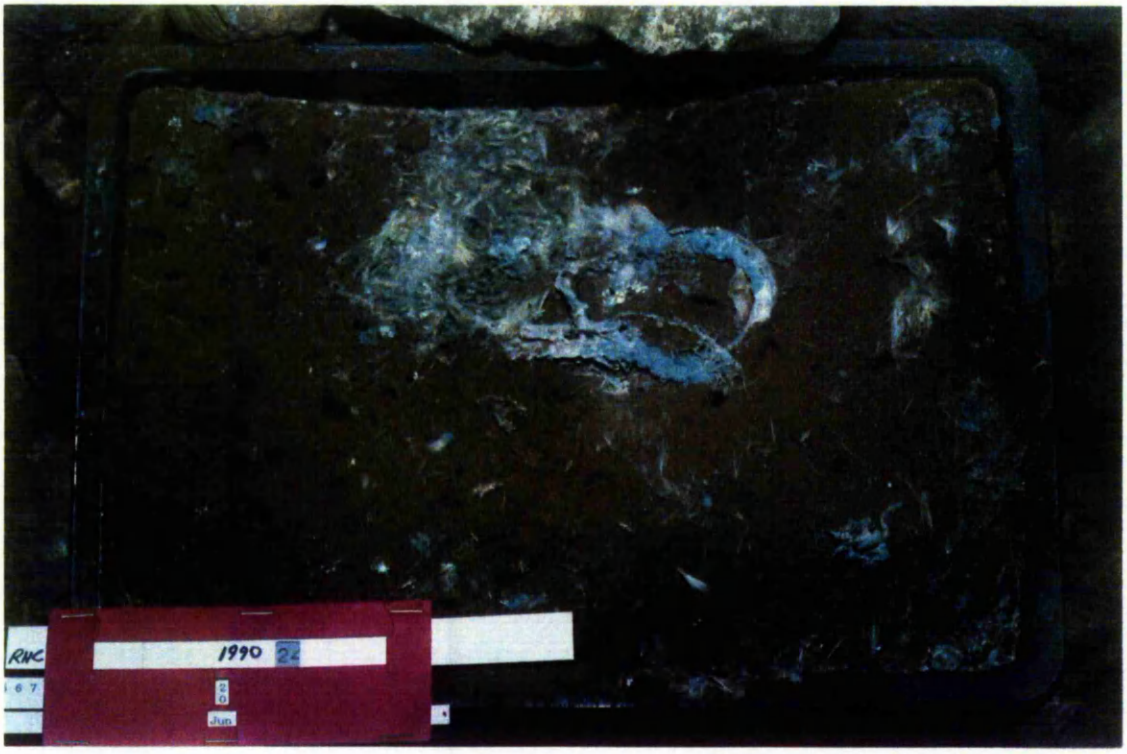


Plate 26: Carcass after four months at the Middle site of Church Hole Cave.

4.2.2 Middle Site

Plates 25 and 26 (previous page) show the physical appearance of the carcass at the Middle site during the first four months of decomposition.

Approximately five weeks after deposition, the carcass was colonised by the blue fungus seen later on the front rat. This was first seen on the parts of the head in contact with the sediment, and also on the eye. Microbial succession proceeded much as on the front carcass and those in Robin Hood's cave over the next five weeks. A distinct odour indicated that there may have also been some dipterous activity, although no larvae were seen. The only invertebrate to be found associated with the carcass was *Cryptophagus pilosus* (Coleoptera: Cryptophagidae), a fungus feeder.

At the beginning of April, about ten weeks after deposition, an unknown species of animal found the carcass and consumed much of the abdominal skin and organs (Plate 25). A considerable volume of sediment had been pushed out of the tank which, along with scratch marks and droppings on the sediment around the rat, suggested a small vertebrate scavenger had been responsible.

Two of the droppings were removed and found to contain the following material: beetle elytra and other insect fragments; fungal fruiting bodies and sclerotia; rat hair; a polystyrene bead; and a piece of plant material.

For the rest of April and the first two weeks of May this scavenger paid repeated visits to the carcass and consumed most of the edible parts. The remains became covered with loose sediment. The blue fungus seen earlier colonised some of the exposed parts, namely the fur and skin, and the only recognisable feature was the tail.

No other evidence of activity was seen during this time, but at the beginning of June exit holes similar to those found in the sediment in the tank at the Front site were found around the carcass (Plate 26). These suggested that the rat had been colonised by *Calliphora vomitoria*, a theory supported by the presence of adults of this species on the walls of the cave nearby.

The exposed parts of the carcass, mostly just bones by this time, supported small colonies of fungi, but no further invertebrate activity was apparent until November, when a single larva of *Hofmannophila pseudospretella* (Lepidoptera: Tineidae) was collected. Nothing more was seen until the end of the experiment.

Figure 4.7: Numbers of individuals of Collembola trapped at the Front site of Church Hole Cave during the experiment in relation to the baseline: (a) *Lepidocyrtus curvicollis* and *L. cyaneus* (Entomobryidae) (above), and (b) *Neelus* sp (Neelidae) and *Arrhopalites* sp (Sminthuridae) (below). (* No figures for baseline as trap was disturbed.)

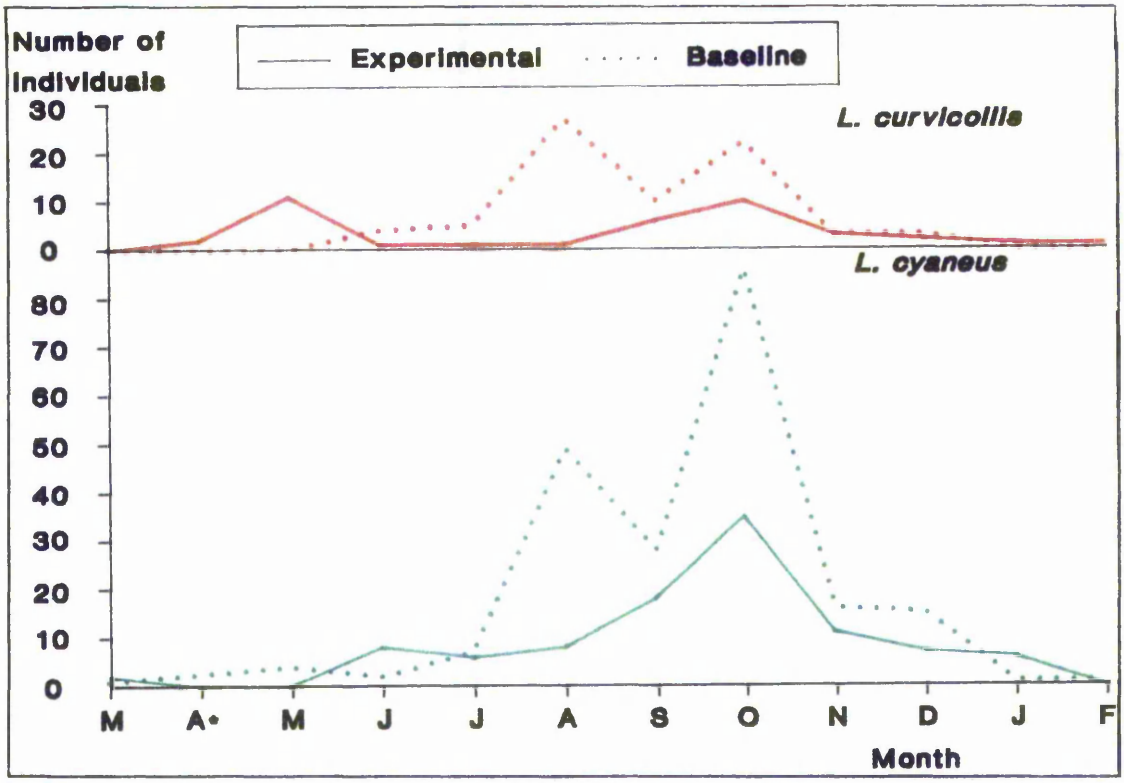


Figure 4.7 a

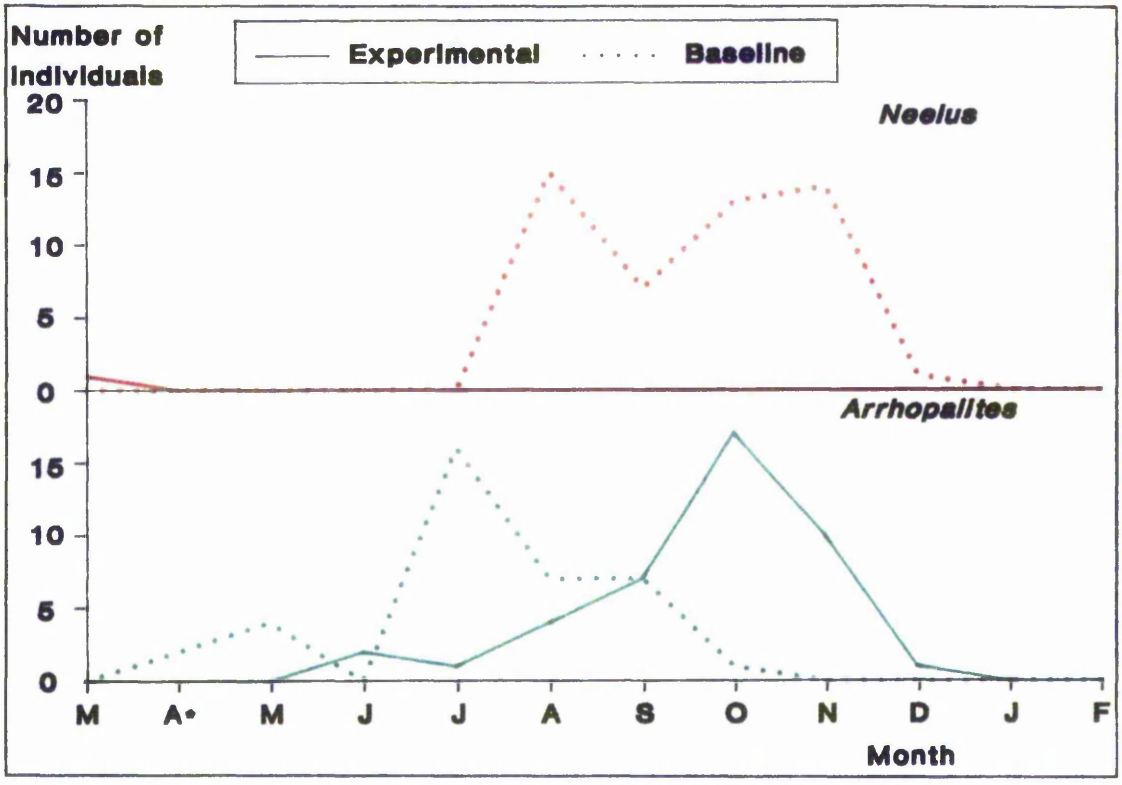


Figure 4.7 b

Figure 4.8: Numbers of individuals of Acari trapped at the Middle site of Church Hole Cave during the experiment in relation to the baseline. (* No figures for baseline as trap was disturbed.)

Figure 4.9: Numbers of individuals of the *Cryptophagus acutangulus* (Coleoptera: Cryptophagidae) trapped at the Middle site of Church Hole Cave during the experiment in relation to the baseline. (* No figures for baseline as trap was disturbed.)

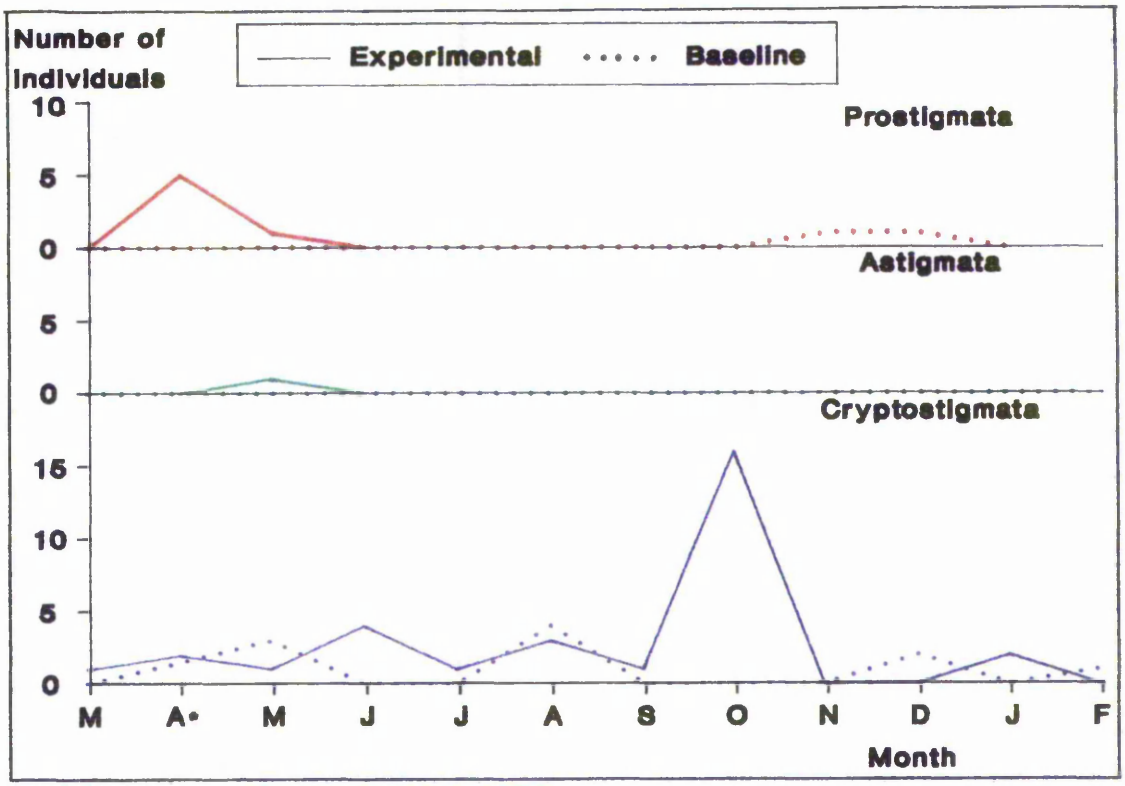


Figure 4.8

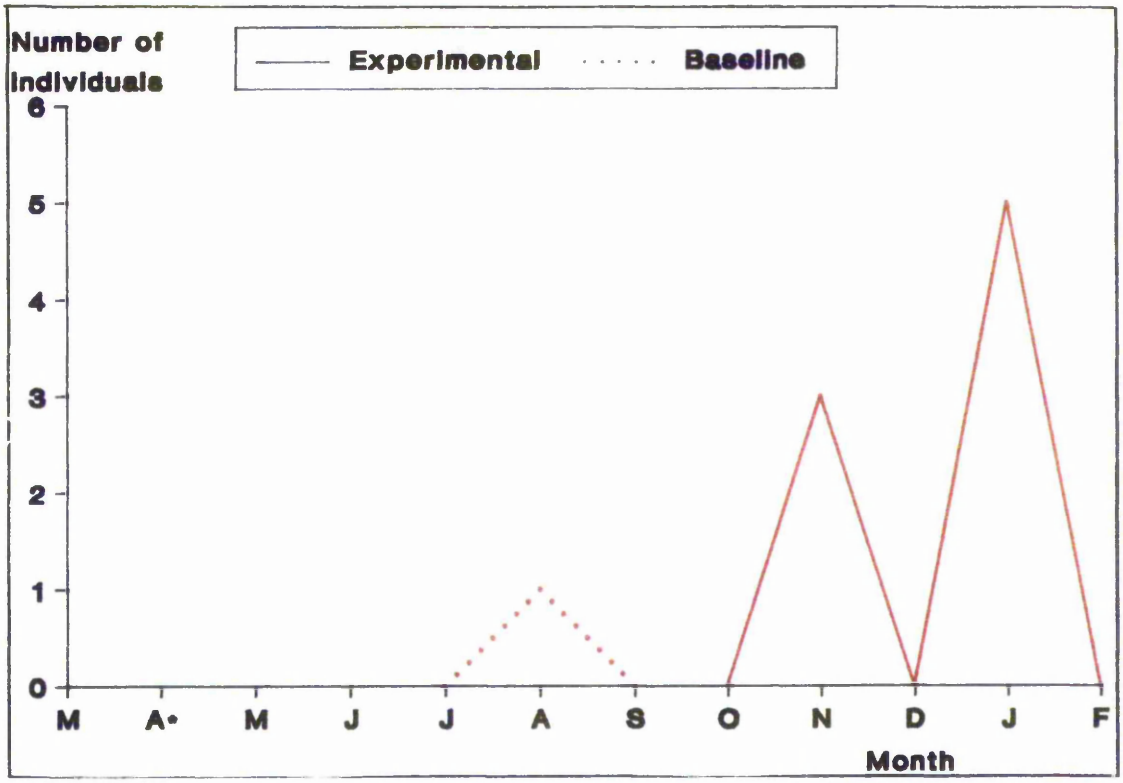


Figure 4.9

Figure 4.10: A comparison of the baseline fauna of the Middle site in Church Hole Cave with that trapped during the experiment in terms of the numbers of individuals (a) and species (b), and the diversity (c) and evenness (d). (* No figures for baseline as trap was disturbed.)

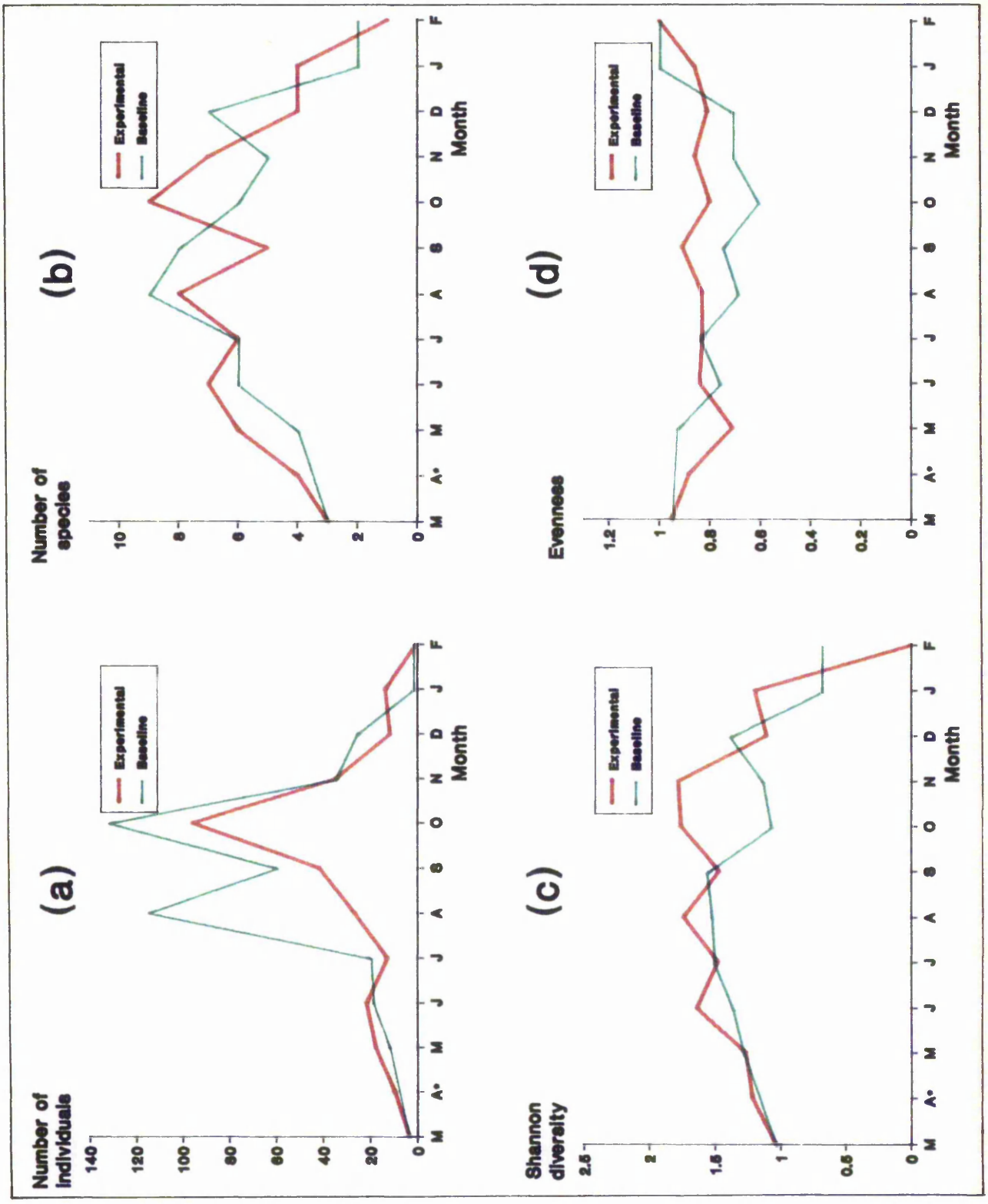

(a)
Number of individuals
Experimental
Baseline
Month
(b)
Number of species
Experimental
Baseline
Month
(c)
Shannon diversity
Experimental
Baseline
Month
(d)
Evenness
Experimental
Baseline
Month

Figure 4.10

As at the Front site, the only groups present in any numbers were Collembola (Figure 4.7, page 113), and mites (Figure 4.8, page 114). Populations of all four species of Collembola were much lower than the baseline throughout the experimental period. The mite population differed noticeably from the baseline only in October, when cryptostigmatid mites were more abundant than expected.

During the latter part of the year, *Cryptophagus acutangulus* (Coleoptera: Cryptophagidae) was found associated with the carrion (Figure 4.9, page 114). Larvae, as well as adults, were trapped, suggesting that the species was breeding on the carcass.

The fluctuations in the numbers of species and individuals caught in the pitfall trap at the Middle site are illustrated in Figure 4.10 a and b (previous page). As at the Front site, numbers caught during the experimental period did not generally vary greatly from the baseline, although lower numbers of individuals were trapped during August of the experimental year than would have been predicted. Consequently, neither species diversity or equitability show any large deviations from the baseline (Figure 4.10 c and d).

4.2.3 Back Site

Plates 27 and 28 (overleaf) show the physical appearance of the carcass at the Back site during the first four months of decomposition.

The carcass was initially colonised by a white pin-mould type fungus, probably a species of *Mucor*, approximately four weeks after deposition. The normal microbial succession then followed at a rapid rate, reaching an advanced stage during the following fortnight.

Unlike the other two carcasses in Church Hole, a number of invertebrates were found on the back rat during the initial weeks after deposition. These were all troglophilic species, and included the cryptophagid beetle *Cryptophagus acutangulus*, and flies from the families Phoridae and Heleomyzidae. No eggs or larvae were found, however, and no indirect evidence of their presence (such as shed hair (from the carcass) or exit holes) was noted.

Approximately fifteen weeks after deposition this carcass was also located and almost entirely consumed by whatever attacked the middle rat. Although the head and

Plate 27: Carcass after eleven weeks at the Back site of Church Hole Cave.

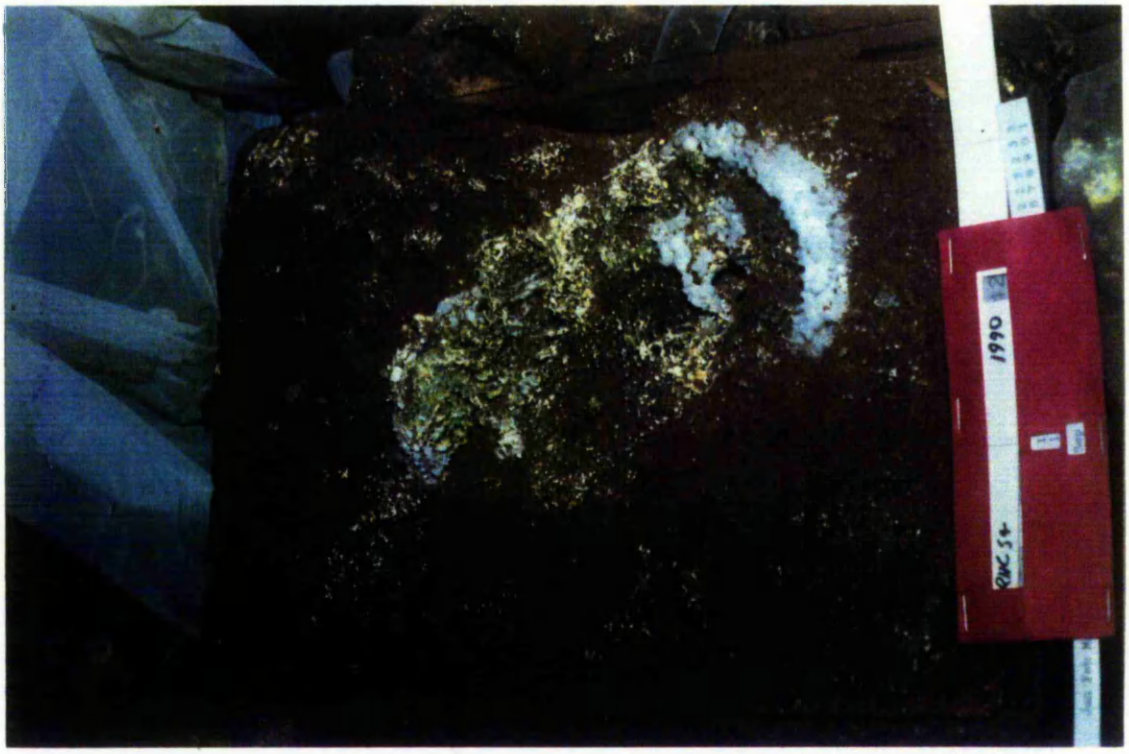


Plate 28: Carcass after four months at the Back site of Church Hole Cave.

tail were virtually untouched, the rest of the body was reduced to an essentially intact skeleton, part of which was shallowly buried in the sediment. Some skin fragments and hair were present on the surface.

The carcass remained more or less unchanged over the remaining weeks, becoming slightly more interred (Plate 28). The only invertebrates to be seen on the carrion were phorids, although very few were found in the pitfall trap. Phorid puparia were also found on the surrounding sediment.

In contrast to the Front and Middle sites, the presence of the carcass at the back of the cave was accompanied by larger than normal populations of three species of Collembola, particularly during the latter part of the year (Figure 4.12, overleaf). Also caught in the pitfall trap at this time was *Cryptophagus acutangulus* (Figure 4.11).

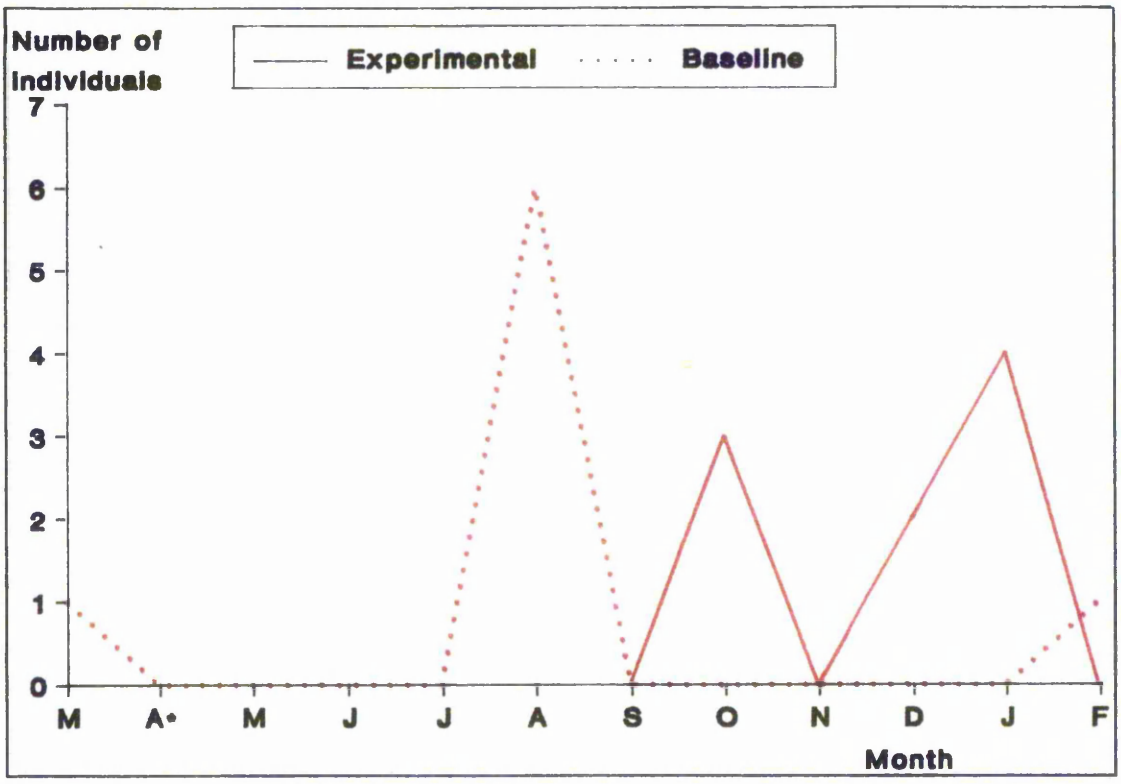


Figure 4.11: Numbers of individuals of *Cryptophagus acutangulus* (Coleoptera: Cryptophagidae) trapped at the Back site of Church Hole Cave during the experiment in relation to the baseline. (* No figures for baseline as trap was disturbed.)

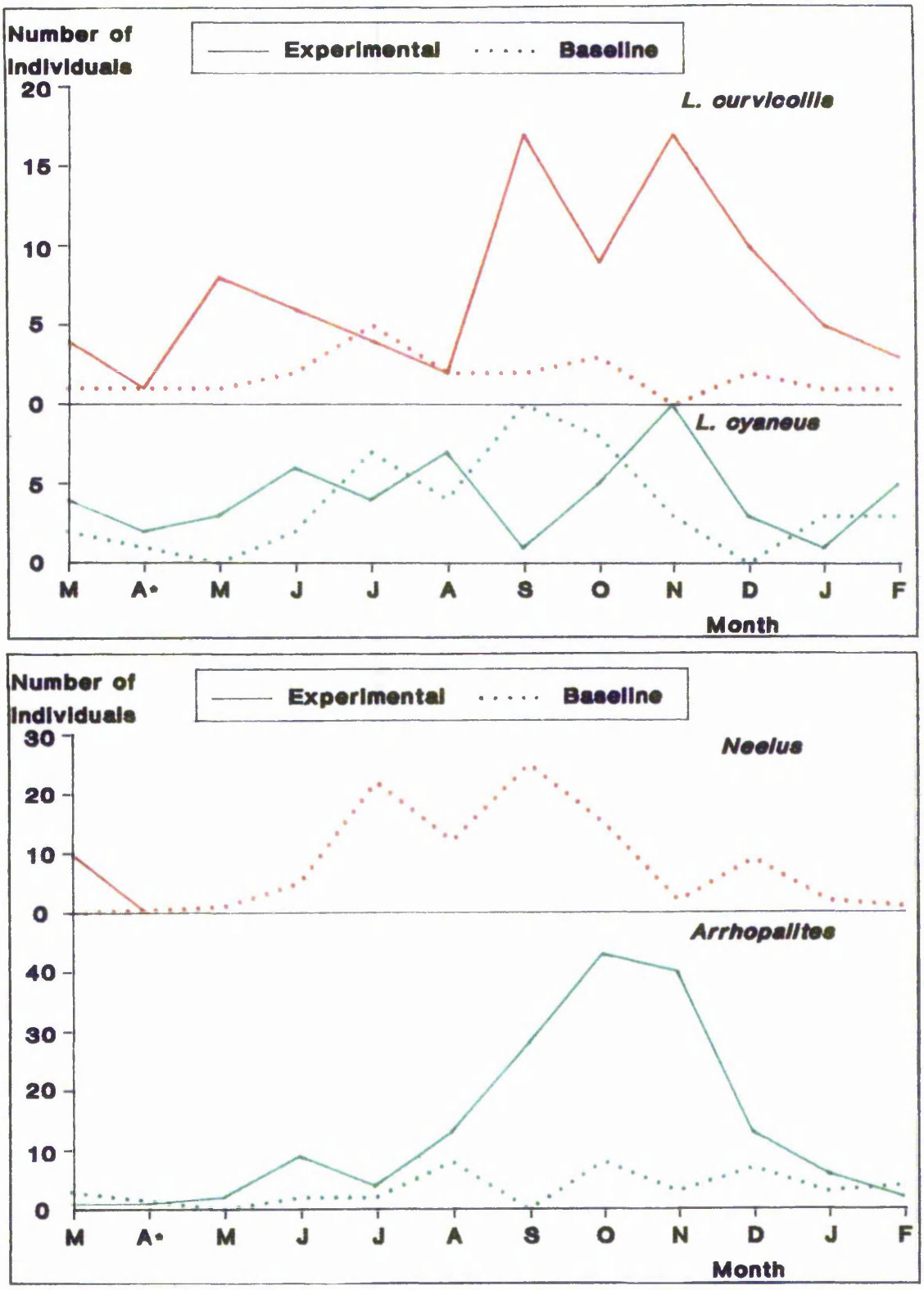


Figure 4.12: Numbers of individuals of Collembola trapped at the Back site of Church Hole Cave during the experiment in relation to the baseline:
(a) *Lepidocyrtus curvicollis* and *L. cyaneus* (Entomobryidae) and (b) *Neelus* sp (Neelidae) and *Arrhopalites* sp (Sminthuridae). (* No figures for baseline as trap was disturbed.

Figure 4.13: A comparison of the baseline fauna of the Back site in Church Hole Cave with that trapped during the experiment in terms of the numbers of individuals (a) and species (b), and the diversity (c) and evenness (d). (* No figures for baseline as trap was disturbed.)

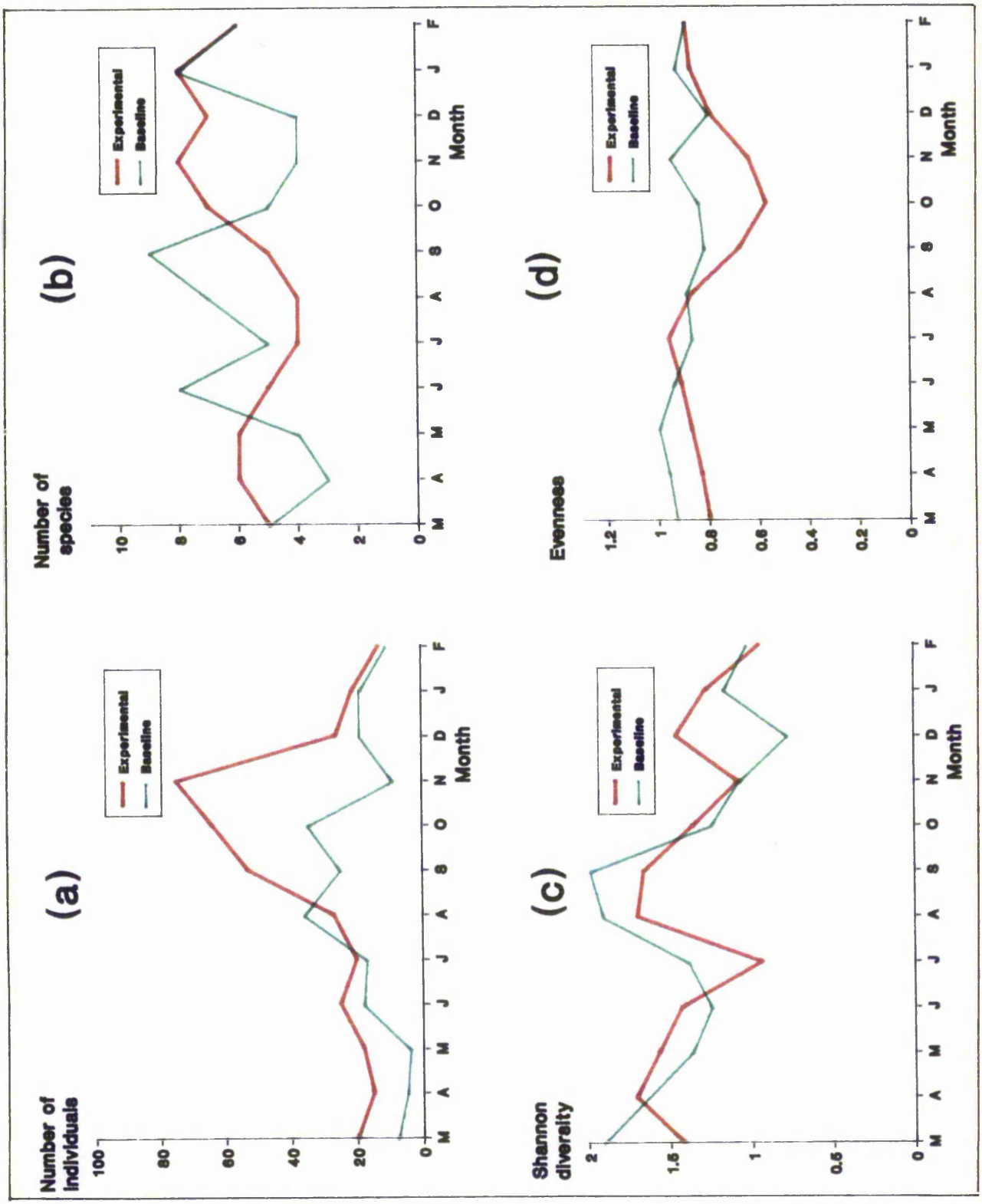

(a)
Number of individuals
Experimental
Baseline
Month
(b)
Number of species
Experimental
Baseline
Month
(c)
Shannon diversity
Experimental
Baseline
Month
(d)
Evenness
Experimental
Baseline
Month

Figure 4.13

Overall changes in the pitfall catches, the species diversity and the equitability are illustrated in Figure 4.13 (previous page). More deviation from the baseline is apparent at this site than was seen at the Front or Middle sites.

4.3 Excavation of tanks

4.3.1 Front tank

The carcass from the front of Church Hole Cave was fairly intact (Plate 29, overleaf). It had been mummified, but by the time it was excavated, much of the skin had been decomposed, and what remained was held together by fungal hyphae.

The carcass was uninterred, except for part of the tail which was lightly covered with sediment.

On the surface of the tank were found a large number of empty puparia and dead adults of the brown house moth (Lepidoptera: Tineidae).

The carcass was lifted off the sediment in one piece, and excavation of the tank revealed over 300 dead *Calliphora* larvae in the first two spits, and many empty *Calliphora* puparia, mostly in Spits 2 to 12 (Figure 4.14, overleaf).

Also present in the top four spits were a few smooth orange puparia about half the size of the *Calliphora* puparia. Unfortunately, these were all empty, and identification was impossible. They were, however, very similar to some found in tanks from the Frogpit chamber of Robin Hood's Cave which were too decomposed to be identified (Section 3.4.2).

4.3.2 Middle tank

The remains of the carcass deposited at the Middle site were not excavated. The tank had been taken to Sheffield University and attempts made to x-ray it to determine the exact position of the bones. This unfortunately proved impossible. However, the tank was left at Sheffield for some time and was used by archaeology students in a coring exercise.

Initially this was not considered a problem, but when the time came to excavate the tank and the coring tubes were removed, the core-holes collapsed in on

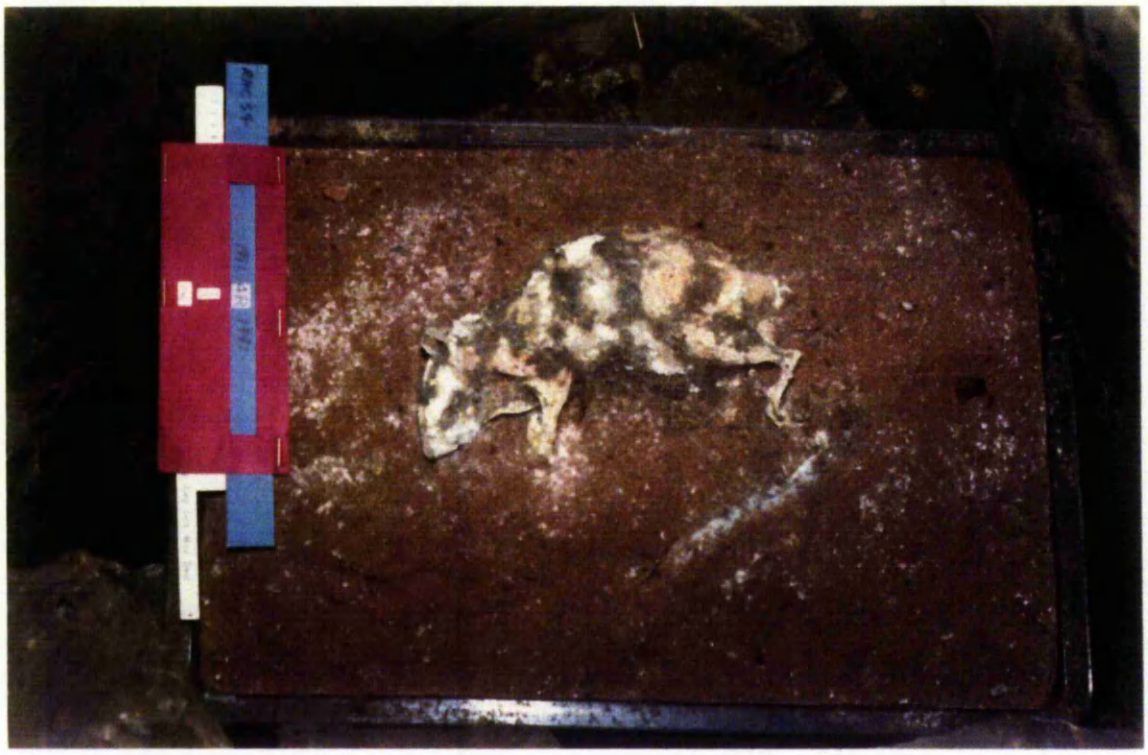


Plate 29: Final position of the remains from the Front site in Church Hole Cave.

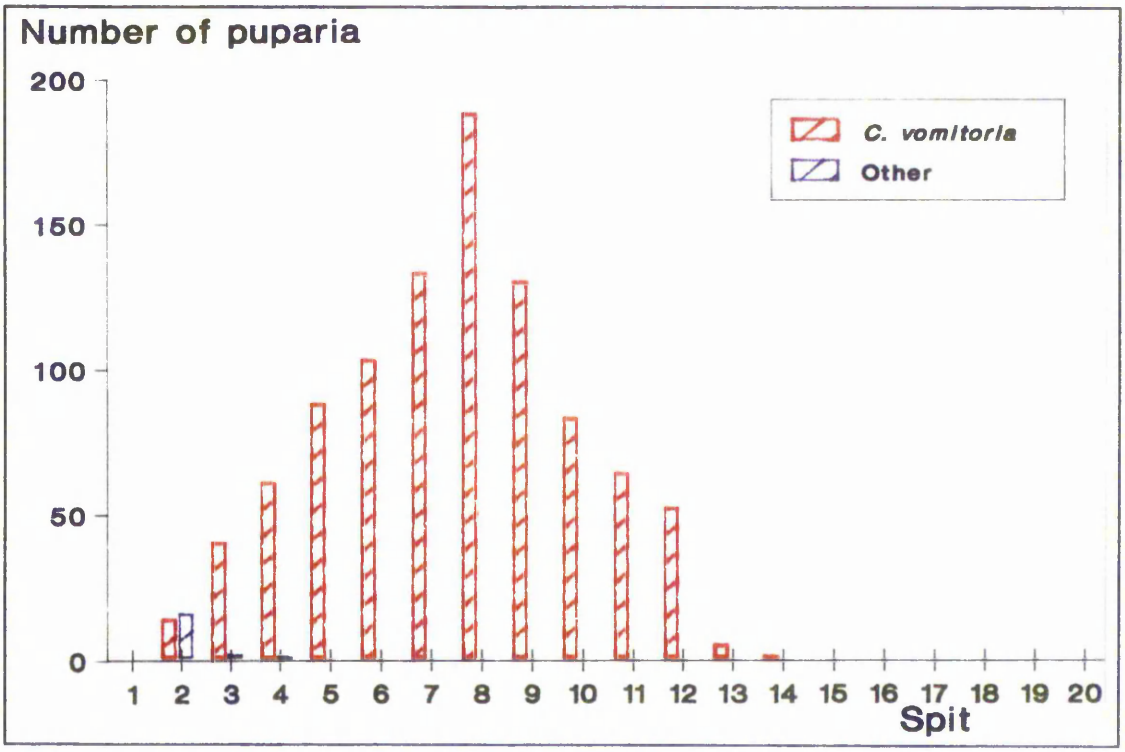


Figure 4.14: Distribution of puparia in the sediment in the tank from the Front Site of Church Hole Cave.

themselves. This was partly because the sediment was extremely dry, and also because the surface was uneven due to the activity of the scavenger which had disturbed both the carcass and the sediment in the tank (Section 4.2.2).

Thus the integrity of the strata within the tank was destroyed, with sediment, bones, invertebrate material and markers from the surface falling to the bottom of the tank. It would have been impossible to determine to what extent any disturbance in the sediment was due to bioturbation rather than this anthropogenic disruption, so it was decided not to excavate this tank.

4.3.3 Back tank

The carcass from the back of Church Hole Cave (Plate 30, overleaf) was in a similar state to that from the Middle site before it was disturbed.

The surface of the sediment in the tank was very uneven, and the remains of the rat were lying partially buried in a hollow. Most of the skin and soft tissue had been consumed, but the bones were held together by the remaining connective tissue and fungal hyphae. Thus the skeleton was fairly intact and was removed almost whole. Although some of the smaller bones had become disarticulated, no noticeable displacement of these had occurred, and none were found interred deeper than the rest of the remains (a maximum of 1 cm).

Also found in the sediment were a few dead *Calliphora* larvae in the top layer (but no puparia), and three empty phorid puparia (Figure 4.15, overleaf). The majority of empty puparia found were the smooth orange ones also seen in the tank from the Front site. These were present in the first eight spits, with the largest number (44) in Spit 4.

Plate 30: Final position of remains from the Back site in Church Hole Cave.

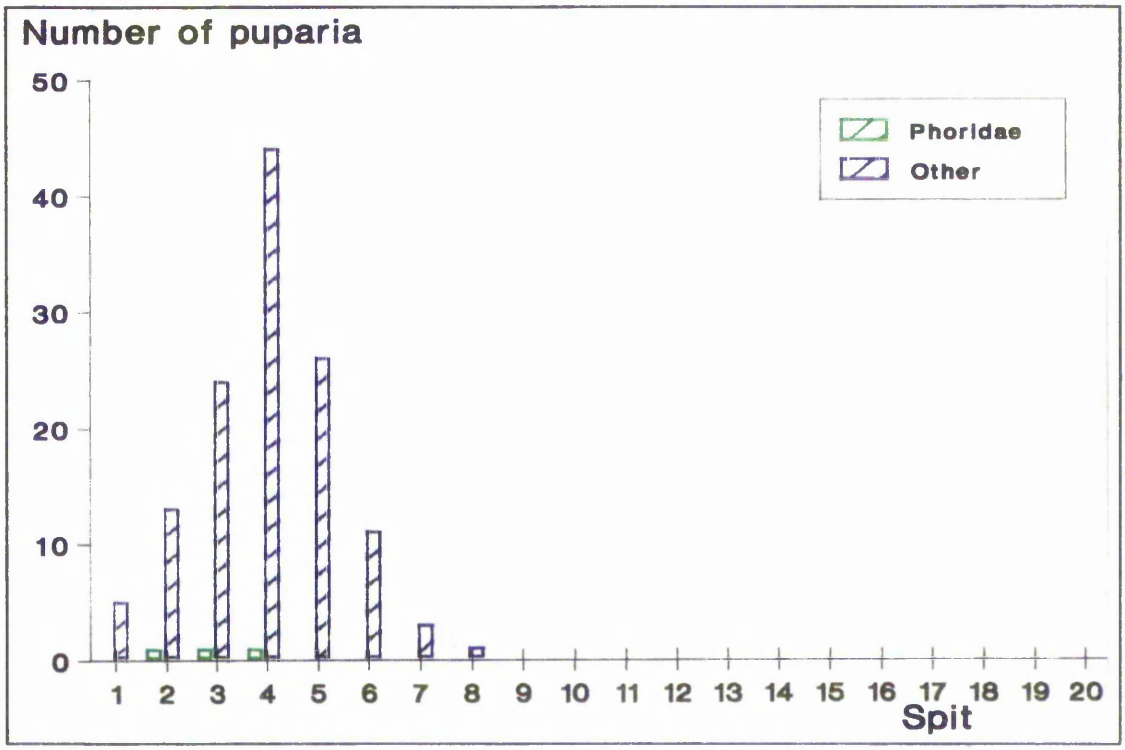


Figure 4.15: Distribution of puparia in the sediment in the tank from the Back Site of Church Hole Cave.

CHAPTER FIVE: RESULTS
TAPHONOMY AND BIOTURBATION

5.1 Post-mortal movement

The experimental carcasses in the Front and Frogpit chamber were considerably displaced (up to 40 cm) during the initial stages of decomposition, although the carcasses in the Back chamber underwent no noticeable post-mortal movement. Plate 31 shows how ER/4 was found on the sediment next to ER/5, its original position being above and to the left of the number 4 in the top left corner of the photograph. The trail of shed hair shows clearly the direction from which it came.

This photograph was taken on July 5th, 1989, almost four weeks after the carcasses had been deposited. The carcasses in the Front chamber were all heavily

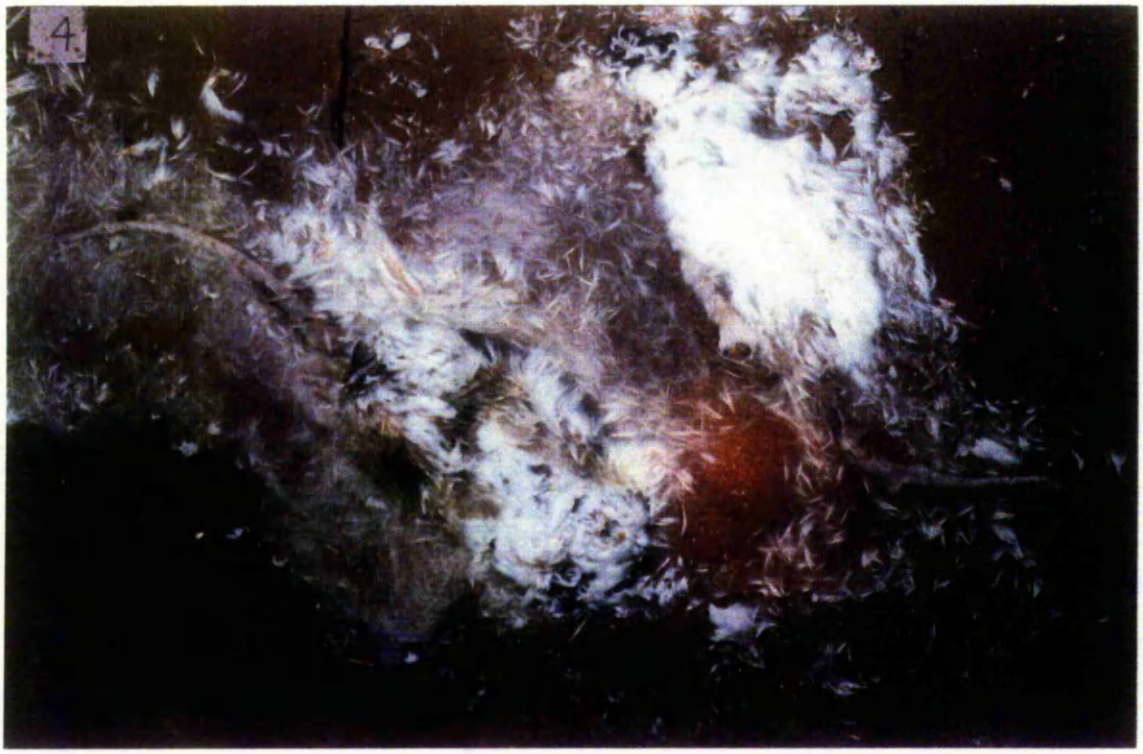


Plate 31: Position of ER/4 and ER/5 following displacement.

infested with dipterous larvae at this time, although on the previous visit, six days earlier, no dipterous activity had been evident and it had been assumed that the mature larvae had begun to burrow.

In the Frogpit chamber too, carcasses underwent post-mortal movement. Figure 5.1 shows the position of the carcasses on July 19th, 1989, almost six weeks after deposition.

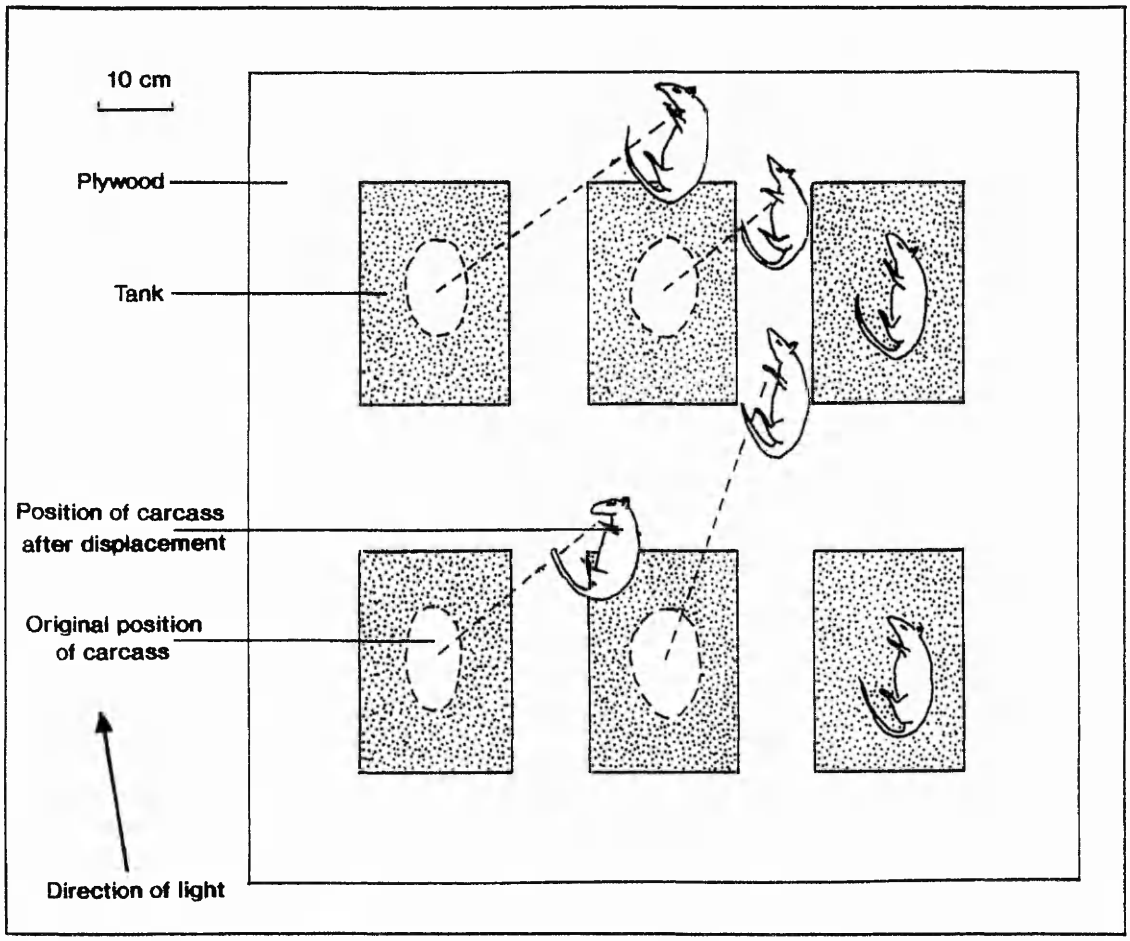


Figure 5.1: Positions of carcasses in the Frogpit chamber of Robin Hood's Cave following displacement.

The direction and distance moved by each carcass is indicated. As in the Front chamber, very few dipterous larvae had been seen on the carcasses on the previous

visit.

The degree of displacement observed in the Front and Frogpit chambers was unexpected, and so not accurately recorded. Thus, a further experiment was designed to investigate this phenomenon more thoroughly: to monitor any movement using time-lapse photography, and to elucidate the agencies responsible, by frequent examination of carcasses. This experiment was conducted in the Frogpit chamber during the following summer (Section 2.3).

Unfortunately excessive condensation on the glass through which the photographs were taken prevented accurate autofocussing by the camera, so there were no photographic results.

Despite this it was decided to continue the experiment, and the site was visited weekly for visual observations. During the first six weeks the carcasses decayed as expected (Section 3.2). Both were heavily infested with *Calliphora vomitoria* larvae, which began to migrate across the plywood sheet in all directions three weeks after deposition. By the sixth week there were about half as many larvae present on the carcasses as there were in the third week.

No post-mortal movement occurred until the seventh week (Figure 5.2 b, overleaf), by which time very few colonising larvae remained. Both carcasses were displaced in approximately the same direction and by similar distances.

The site was visited for another three weeks during which no further movement occurred. After this time most of the soft tissue had been devoured and, in contrast to what had been observed in the Frogpit chamber during the previous experiment (Section 3.2.2), the carcasses were dry, inflexible and apparently devoid of larvae. By this stage, it was felt that the experiment was over, and no further visits were made to the site.

However, one more visit was paid to the cave approximately six weeks later, to dismantle the apparatus. It was then found that one of the carcasses had been further displaced (Figure 5.2 c). The second carcass was lodged at the edge of the board with its claws hooked around the wire mesh, which would have prevented any further movement. There was no evidence of any invertebrate activity.

The two carcasses used in this experiment showed movement in the same direction as the experimental carcasses in the Front chamber, ie towards the light.

However, the experimental carcasses in the Frogpit chamber all moved in the opposite direction, away from the light.

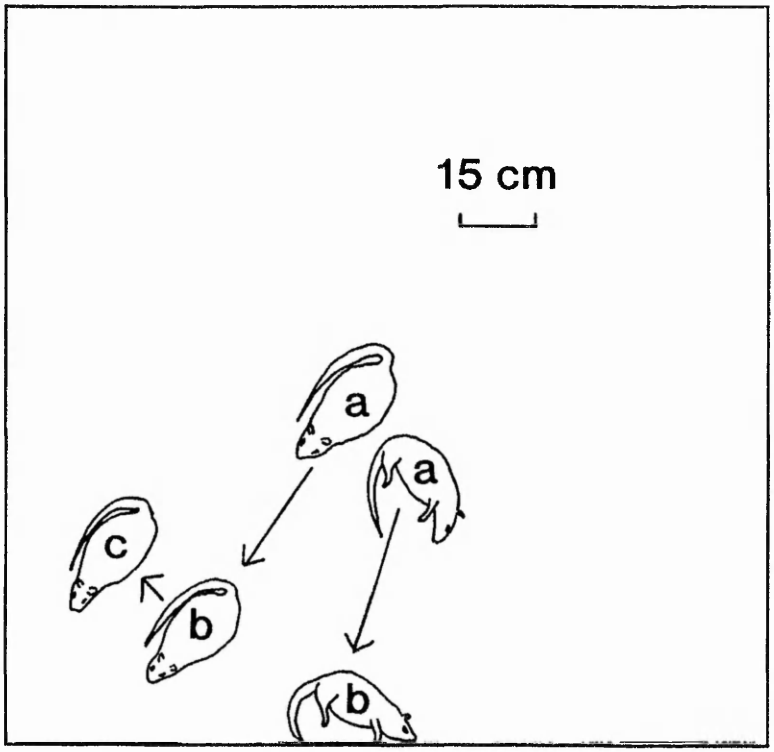


Figure 5.2: Positions of the two carcasses on the plywood sheet during the post-mortal movement experiment, at the beginning of the experiment (a), after seven weeks (b), and after sixteen weeks (c).

5.2 Bioturbation

During the initial stages of decomposition in both Robin Hood's Cave and Church Hole Cave, the sediment beneath the carcasses was considerably disturbed by arthropods. Particularly instrumental were the *Calliphora* larvae; empty puparia were found at the bottom of even the deepest tanks (15 cm deep) (Section 3.4). However, other insects are also known to burrow. For example, mature larvea of the cavernicolous staphylinid beetle, *Quedius mesomelinus*, construct underground

pupation chambers (Plate 32).

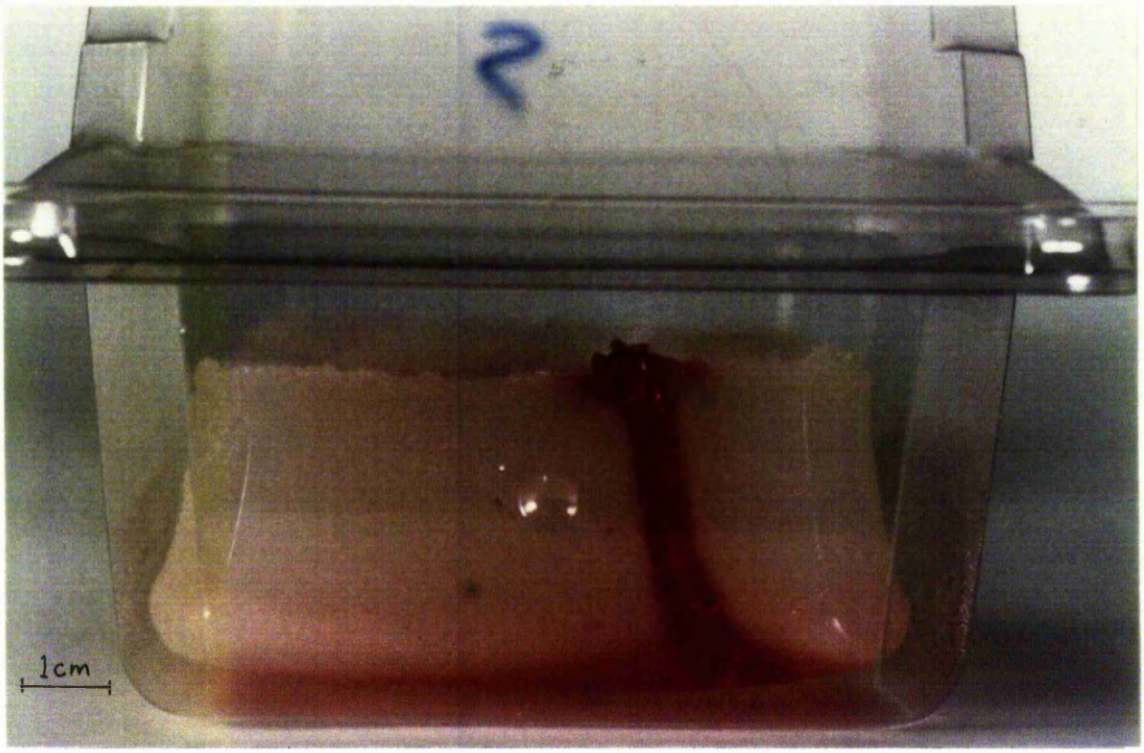


Plate 32: Tunnel and pupation chamber constructed in agar by a stage III larva of the staphylinid beetle *Quedius mesomelinus* (the red colouring is latex which was poured into the burrow).

No cores were taken from the tanks in Church Hole cave, because the activity of the vertebrate scavenger in Church Hole Cave had caused very obvious disturbance, making further analysis of these sediments unnecessary. Also, the analysis of samples was lengthy and it was felt that the results from Robin Hood's Cave provided sufficient evidence of bioturbation.

Results are presented from the shallow (5 cm) tanks in the Frogpit chamber, and the deepest (15 cm) tanks in the Frogpit and Back chambers. Unfortunately it proved impossible to core the tanks at the front of the cave because the sediment was too dry.

When the sediment samples collected were analysed (Section 2.4) it was found that there was no significant movement of the beads through the sediment, and that the adapted extraction process did not successfully extract pollen from cave sediment. *Lycopodium* spores, however, were easily detected once the sediment samples had been treated, so graphs were constructed of percent (log) *Lycopodium* against depth to indicate the degree of bioturbation through the core.

Firstly, the samples from the control tanks were analysed to give an indication of the amount of disturbance caused by experimental error. (The light, airborne spores were present in the control samples mainly due to the unavoidable contamination of the sediment during preparation of the tanks.) For each control tank, this was expressed as the mean number of spores present in the samples which did not contain marker layers.

Before the results from the experimental tanks were analysed, the mean number of spores calculated from the corresponding control tank was subtracted from the number found in each experimental sample to give a true representation of the distribution of *Lycopodium* within a core.

For experimental samples containing no spores, the per cent (log) was, obviously, 0, and these samples were not used in the calculations for those containing one or more spores, the per cent (log) of which was calculated using the following equation:

$$\%(\log) = \frac{\log s_x}{\sum_{x=1}^{n} \log s_x} x100$$

where: n = number of samples containing one or more spores

s_x = number of Lycopodium spores in sample x

For the cores from tanks containing sediment to a depth of 5 cm (Figure 5.3, page 130), the per cent (log) of spores in a sample was expressed as a proportion of the number of spores in the whole core, since all spores originated from one marker layer (on the surface of the sediment).

In the tanks containing deeper sediment (Figures 5.4, to 5.7, pages 132 to 135), unequal numbers of spores were present in the three original marker layers. If the per cent (log) of spores in the samples had been expressed as a proportion of the number of spores in the whole core, certain samples may have produced artificially high or low results due to extremely high or low numbers of spores being present in a particular marker layer. To overcome this, an estimate was made of the probable origin of the spores in each sample (ie upper, middle or lower marker layer), and the number of spores in a sample was then expressed as per cent (log) of the number of spores originating from the same marker layer.

Example 1: The core from the sediment in the region of the head of ER/7 was separated into 1 cm samples, which were found to contain 476, 56, 2, 18, and 0 *Lycopodium* spores (after the subtraction of the average number in the control samples). The per cent (log) of spores in the second sample was calculated thus:

$$\%(\log) = \frac{\log 56}{\log 476 + \log 56 + \log 2 + \log 18} x100 = 29$$

The distribution of *Lycopodium* spores in the tanks containing sediment 5 cm deep is shown in Figure 5.3 (overleaf). Both tanks were in the Frogpit chamber of Robin Hood's Cave. The distribution of *Lycopodium* spores in the sediment indicates considerable bioturbation.

Example 2: The core from the sediment in the region of the head of ER/8 was separated into fifteen samples, which were found to contain 2268, 62, 0, 0, 121, 568, 0, 41, 0, 522, 1341, 45, 0, 0 and 0 *Lycopodium* spores (after subtraction of the average number in the control samples). Marker layers were evident in the first, sixth and eleventh samples. It was estimated that spores in the first and second samples originated from the upper marker layer, those in the fifth, sixth and eighth samples from the middle marker layer, and those in the tenth, eleventh and twelfth samples from the lower marker layer. The per cent (log) of spores in the fifth sample

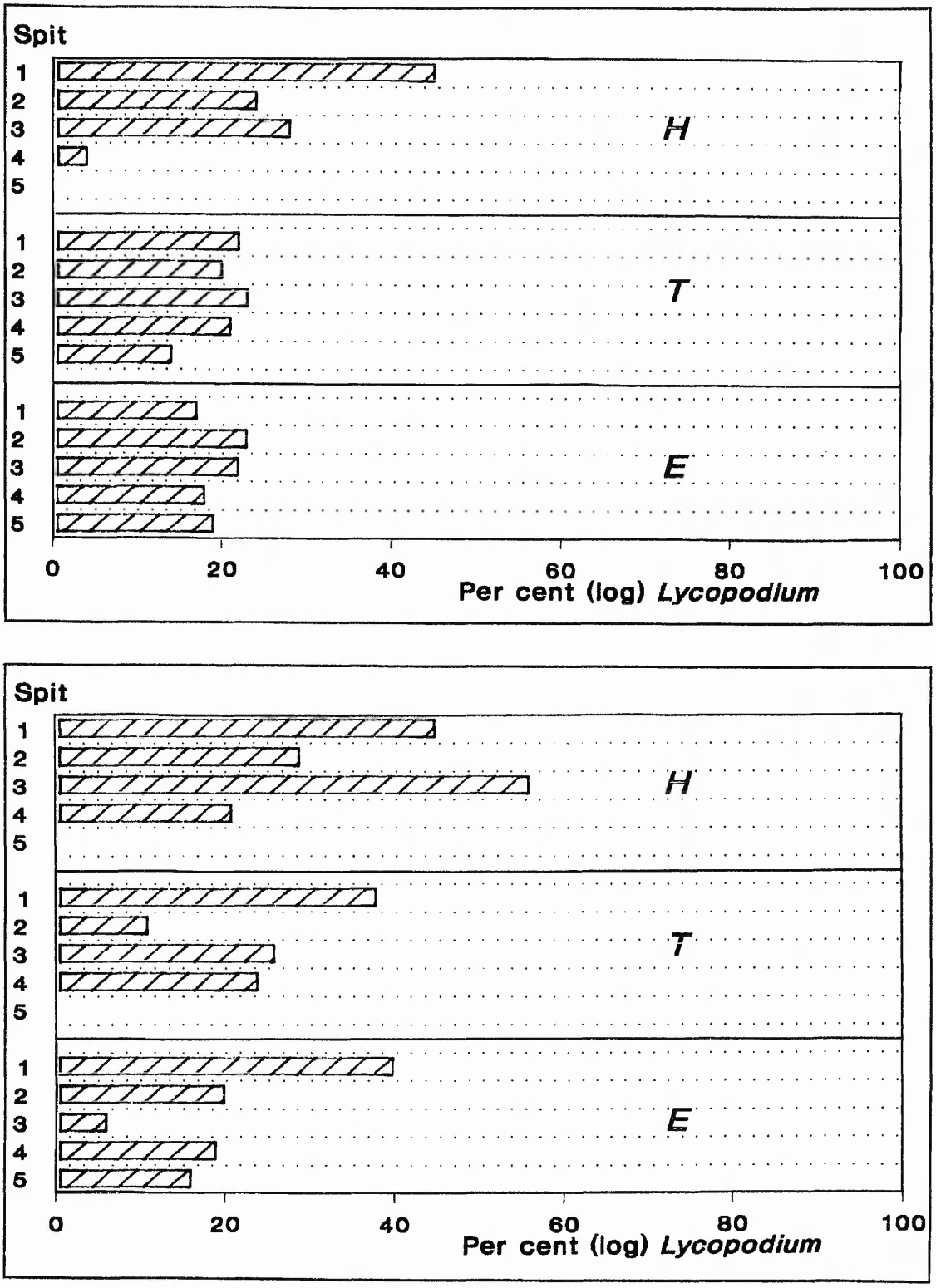


Figure 5.3: Distribution (logarithmic) of *Lycopodium* spores in the sediment beneath was (a) ER/7 and (b) ER/10 in relation to depth. Sediment was 5 cm deep, and cores were taken from the region of the head of each carcass (*H*), the tail region (*T*), and from the edge of the tanks (*E*).

calculated thus:

$$\%(\log) = \frac{\log 121}{\log 121 + \log 568 + \log 41} x100 = 32$$

Figures 5.4 to 5.7 (overleaf) show the distribution of spores in the deeper tanks. Tanks containing ER/8 and ER/11 were in the Frogpit chamber of Robin Hood's Cave. Little disturbance of the sediment is evident in the tail region of the tank containing ER/11, although in other areas of this tank, and in the tank containing ER/8, the distribution of spores illustrates that mixing occured throughout the sediment.

Results from the tanks in the Back chamber (those containing ER/13 and ER/17) show that, while some mixing had occured in the sediment beneath ER/13, the *Lycopodium* spores in the other tank were clumped in or around the marker layers, indicating a less bioturbation.

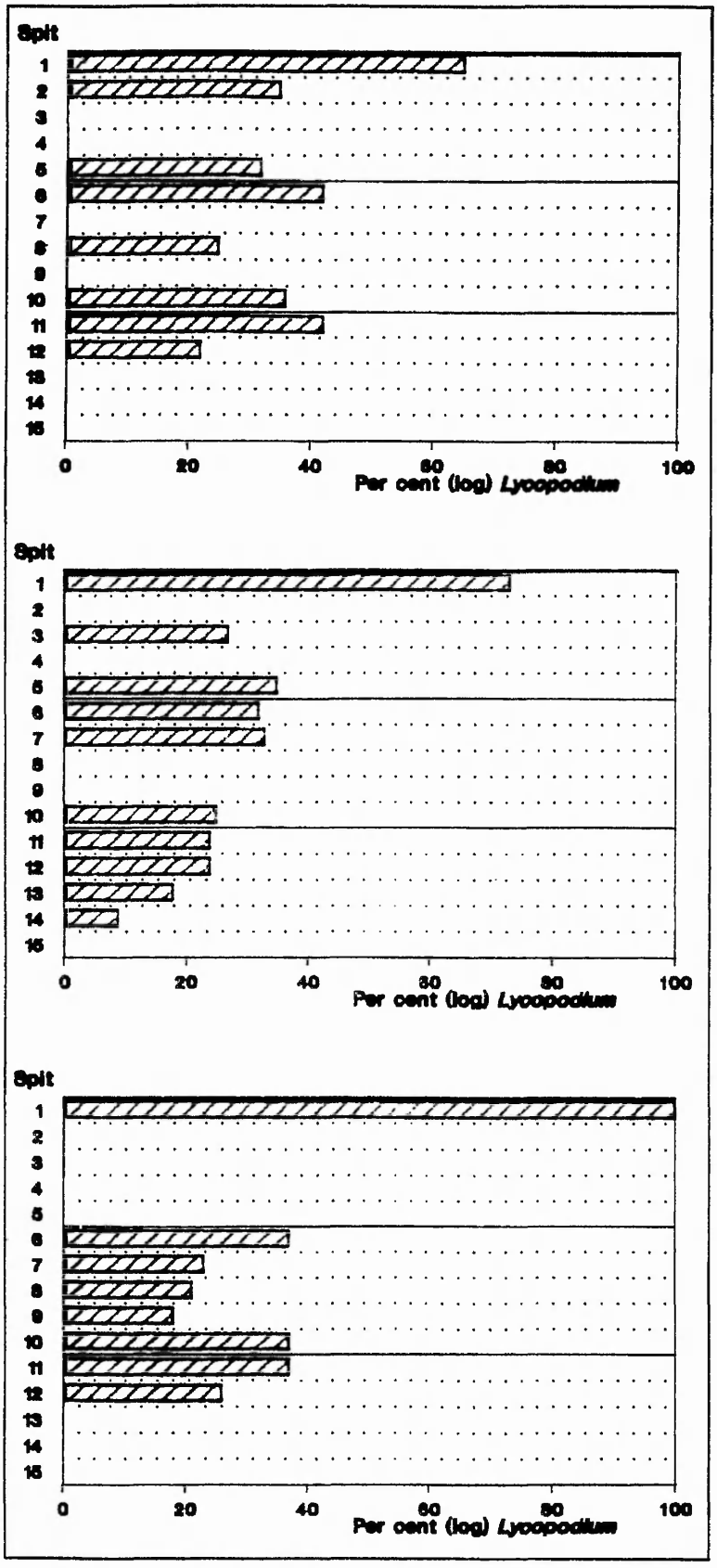


Figure 5.4: Distribution (logarithmic) of *Lycopodium* spores in the sediment beneath ER/8 in relation to depth. The sediment was 15 cm deep, and cores were taken from (a) the region of the head of the carcass

— Original positions of marker layers

(b) the region of the tail of the carcass

(c) the edge of the tank.

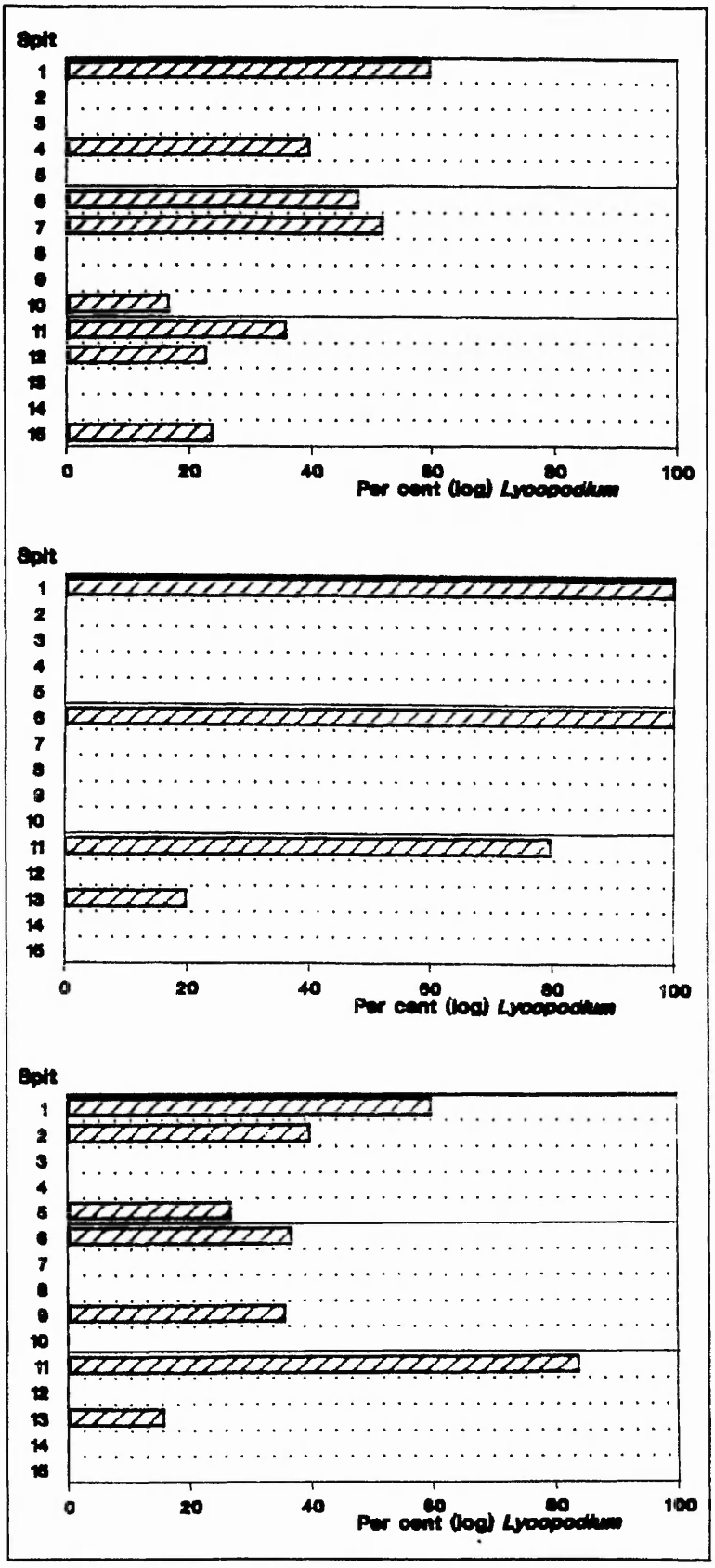


Figure 5.5: Distribution (logarithmic) of *Lycopodium* spores in the sediment beneath ER/11 in relation to depth. The sediment was 15 cm deep, and cores were taken from (a) the region of the head of the carcass

— Original positions of marker layers

(b) the region of the tail of the carcass

(c) the edge of the tank.

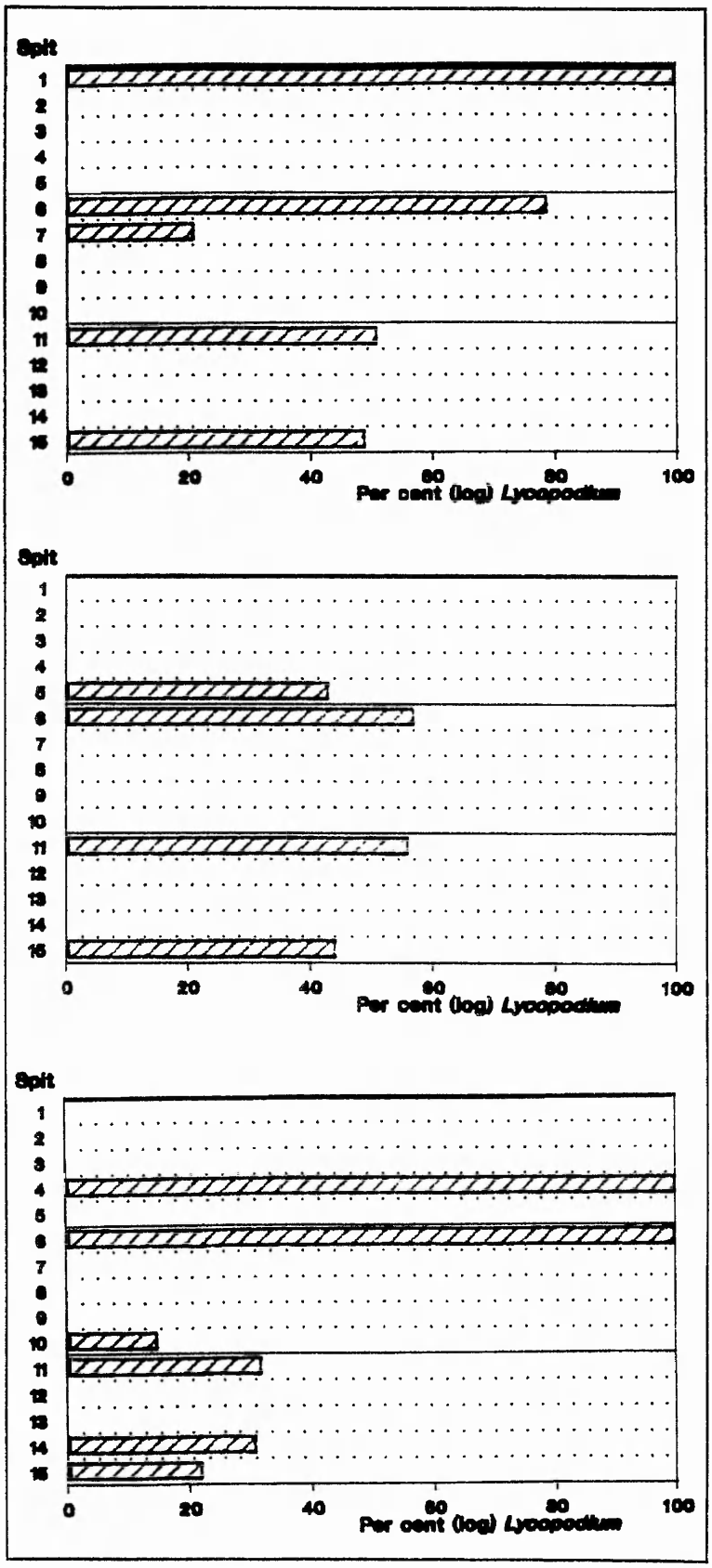


Figure 5.6: Distribution (logarithmic) of *Lycopodium* spores in the sediment beneath ER/13 in relation to depth. The sediment was 15 cm deep, and cores were taken from (a) the region of the head of the carcass

— Original positions of marker layers

(b) the region of the tail of the carcass

(c) the edge of the tank.

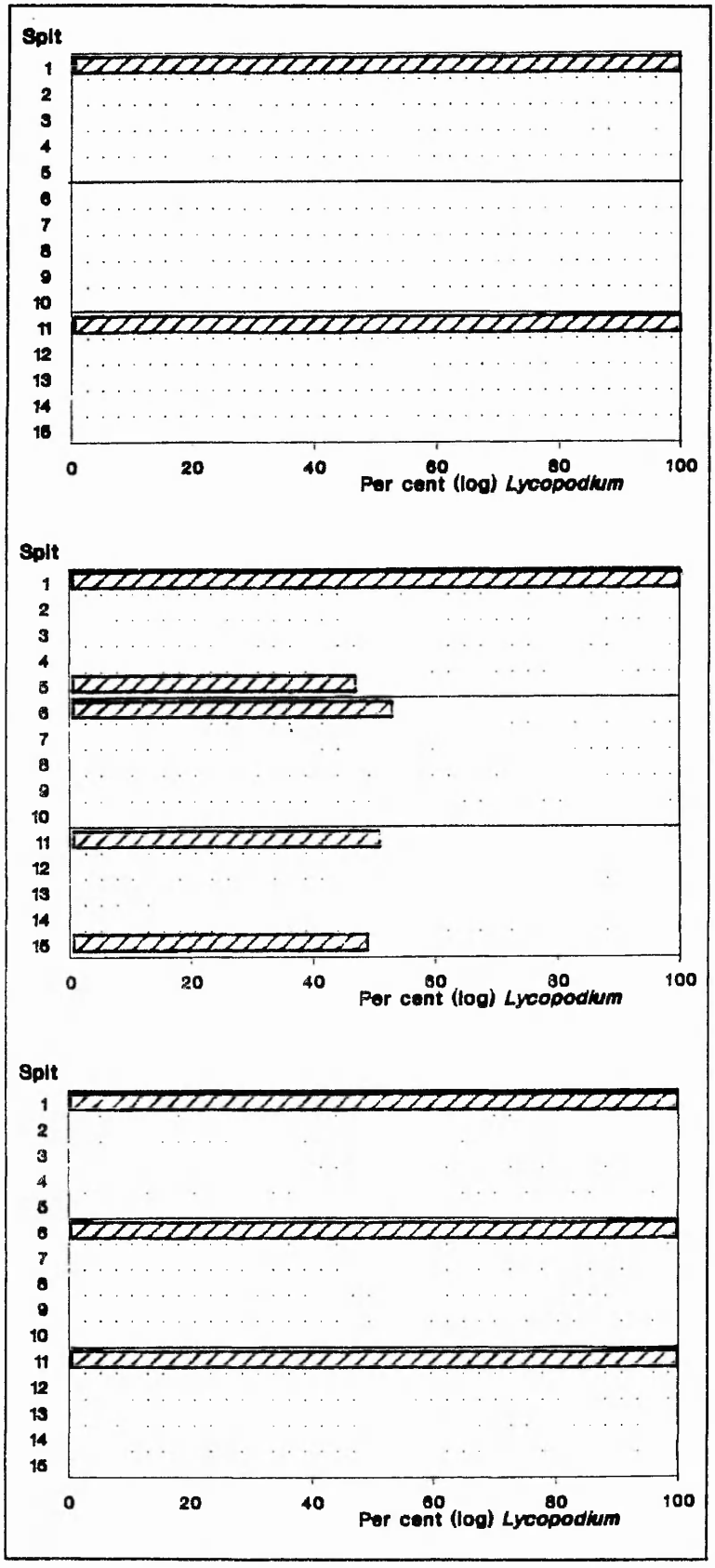


Figure 5.7: Distribution (logarithmic) of *Lycopodium* spores in the sediment beneath ER/17 in relation to depth. The sediment was 15 cm deep, and cores were taken from (a) the region of the head of the carcass

— Original positions of marker layers

(b) the region of the tail of the carcass

(c) the edge of the tank.

CHAPTER SIX : DISCUSSION

The decomposition of dead organic matter is a vital process in the flow of energy and nutrients within any ecosystem. In caves, due to the absence of primary producers, the efficient breakdown of such material is particularly important to the cavernicolous community.

The results of the present work indicate not only that the processes of decomposition in an underground environment differ considerably from those observed on the surface, but also that these differences are more marked in carcasses deposited deep underground than in those near a cave entrance.

6.1 The decomposition of the carcasses in Robin Hood's Cave

6.1.1 Abiotic conditions

The processes of decomposition observed in Robin Hood's Cave were largely governed by three features of the faunal succession on the carcasses:

* the species involved
* the numbers involved
* the length of time each species was associated with the carrion

All three varied according to abiotic conditions, which led to dissimilar patterns of decay in the different regions of the cave.

Certain invertebrates which are normally associated with carrion were absent from the carcasses in the cave. Some were possibly precluded by the low light intensity. The actual physical distance underground of the carcasses in the Back chamber almost certainly accounted for their failure to attract all but those species most efficient at carrion-location. However, particularly important in limiting the faunal diversity in the cave were the relative humidity and temperature regimes. Both

are involved in governing the evaporative rate, which must remain low if arthropods are to avoid desiccation.

In the Back chamber relative humidity was consistently high for the duration of the experiment (Table 3.1). Further toward the entrance of the cave, relative humidity became progressively lower and more variable. Fluctuations in humidity were largely a result of air currents flowing through the shallow regions of the cave. The entrances of caves "breathe" (Barr, 1968), because of the density gradient between cooler and warmer air. Thus in summer, denser cool air flows out of the cave, while in winter the reverse occurs. Air movement on the surface (wind) also creates drafts in the shallower regions of the cave.

In the Front chamber, the prevailing high temperature during the first weeks after deposition of the carcasses led to their rapid location and consumption by blowflies. After the larvae pupated, however, temperature and humidity conditions led to the mummification of the remains.

Mummification rarely occurs in this country and may take several months to reach completion (Medico-Legal Society, 1976). References in the literature to cases of mummification are not common, but it is generally suggested that the phenomenon occurs in cold dry conditions, and only when a carcass is for some reason not colonised by arthropods.

Dalquest & Coln (1987), upon discovering the mummified remains of a woodrat being used as a bird's nest, speculated that the carcass had been protected from insects because of high altitude and cold weather, causing it to become freeze-dried. Johnson (1975) and Putman (1978a) both observed mummification only in winter. The shape of carcasses did not change radically (Johnson, 1975) and up to 85% of material was preserved (Putman, 1978a).

The conditions at the front of the cave were not at all like those described by these authors - all carcasses were heavily infested by *Calliphora* and supported a fairly diverse community of associated species. The site was sheltered, relatively warm (during those first weeks), and humidity was never particularly low.

A similar situation has been documented by Evans (1962). The mummified body of a woman was discovered in a cupboard, along with numerous flies stuck to a flypaper, dead moths and spiders, and pupal cases all over the body. When the body

was examined internally, it was found to be in a comparable state to that of the mummified rat carcass examined in this work (Section 3.9.1). Evans attributes the absence of much of the soft tissue to dipterous activity.

The Medico-Legal Society (1976) states also that mummification occurs "in warm dry surroundings, especially where there is air movement", conditions similar to those at the front of the cave.

The mummification of the remains at the front of the cave led to the near cessation of the decomposition process because the carcasses became too dry for most fungi and invertebrates. Species which would have been expected later in the succession were unable to colonise the remains, and both fungi and arthropods were extremely limited during the second year of the experiment. A corresponding situation may be observed on the surface, when fluctuating humidity levels result in an initial rapid rate of decomposition being diminished by desiccation of the remains (Nabaglo, 1973).

Nabaglo (1973) also investigated the conditions governing the decomposition of dead bank voles in their burrows. He found that the rate of decay underground was more uniform than it was on the surface, and continued for much longer. Nabaglo attributed this to the consistently high relative humidity in the burrows which prevented the carcasses from drying out. This situation was observed in the Back chamber of the cave, where the carcasses remained moist for the duration of the experiment.

In the Frogpit chamber, however, the rate of decomposition (Figure 3.19) was more akin to that at the front of the cave. The carrion in the Frogpit chamber never became desiccated and thus continued to support a number of species, even after dipterous activity had virtually exhausted the carcasses. The remaining material (mostly bones, skin and hair) was decomposed only very slowly.

In the Front chamber then, the faunal succession on the carcasses, and hence the decomposition rate, was dictated to a certain degree by the changes in the physical state of the carrion caused by fluctuating humidity levels. In the deeper regions of the cave, where humidity levels never became low enough to curtail decomposition, other factors, governing the activity of micro-organisms and invertebrates, were more important regulators of the decay rate.

One of the most critical of these is temperature. The rate of development of the micro-organisms which are involved in the early stages of decomposition is temperature dependant (Nabaglo, 1973). The activity of these bacteria and fungi, which is curtailed by low temperatures (Deonier, 1940), results in the onset of putrefaction, signs of which are discoloration, bloating and breakdown of connective tissue (Lothe, 1964). Blowflies will only oviposit upon carcasses showing such signs, since putrefaction is an essential part of the preparation of carrion for larger necrophages (Nabaglo, 1973). Low temperatures in the Frogpit and Back chambers resulted in long intervals between deposition and dipteran infestation of the carcasses in these regions. This can be at least partially attributed to a reduction in microbial activity leading to a diminished rate of putrefaction.

Temperature also limits the distribution, dispersal and development of many of the invertebrate species involved in decomposition, most notably the blowflies. The low temperature in the cave may have precluded some species of blowfly, since all have a threshold temperature below which females will not oviposit (Nuorteva *et al*, 1967). (The distribution and dispersal of various blowflies is discussed more fully later in this work.)

The effect of temperature upon the development of the immature stages of invertebrates is an important factor governing the progress of succession and hence decomposition. The rates of development of various necrophagous species have been studied in relation to temperature (Erzinçlioglu, 1983), and the results of such studies are particularly important to forensic entomologists (Easton & Smith, 1970; Greenberg, 1985; Keh, 1985).

Three species of necrophagous Diptera were involved in the decomposition of the carcasses in this work. In the Front chamber, *Calliphora vomitoria* far outnumbered any other species, while in the Frogpit chamber, *Calliphora* larvae co-existed with those of *Triphleba antricola* and *Megaselia rufipes* on all carcasses. Some of the carcasses in the Back chamber were colonised by the phorids only, and some supported small populations of *Calliphora* as well.

At the front of the cave, the larval development of *Calliphora* took approximately three weeks. Deeper underground, higher levels of humidity would have decreased this period (Putman, 1978a), but this was masked by the effect of the

much lower temperatures, resulting in a net increase in development time to over four weeks. Although both temperature and humidity were slightly higher in the Back chamber than in the Frogpit chamber, this difference was apparently insufficient to affect the development of *Calliphora*.

Although a few adult phorids were caught in the pitfall traps in the Front chamber, no larvae or pupae were seen at any time. In contrast, large numbers colonised the carcasses in the Frogpit chamber. The first pupae were noticed about five weeks after the larvae hatched. In the Back chamber, where the population densities of all three species were much lower, phorid larvae began to pupate just three weeks after hatching.

The slow development of the phorids in the Frogpit chamber may have been due to the cooler drier atmosphere there compared with the Back chamber. It is probable, though, that the high inter- and intra-specific competition for resources in the Frogpit chamber was largely responsible.

The readings of air temperature in the vicinity of the carcasses only provided an indication of the temperature conditions in the carrion itself. Reed (1958) monitored the temperature of dog carcasses during decomposition, and found that between 10 and 25 °C carcass temperature was generally lower than ambient. Though the air temperature in the cave during the initial period following deposition generally fell within these limits, carcass temperatures consistently exceeded ambient. The difference was not, however, of sufficient magnitude to negate the influence of the ambient temperatures in the three regions on the development time of the dipterous larvae.

Microbial activity alone did not produce a significant amount of heat, since elevated carcass temperatures were only recorded during the period of dipteran infestation. Previous authors have reported similar findings in exposed carcasses (Reed, 1958; Wasti, 1972), and Deonier (1940) says that "although bacteria may have been responsible for some of the heat generated during larval development, heat from bacterial decomposition alone was not perceptible".

The high temperature of decomposing carrion can therefore be attributed to the metabolic activity of dipterous larvae. Provided conditions are favourable for oviposition, the hatched larvae will generate sufficient heat within a carcass to ensure

continued development, even when ambient temperatures are as low as was recorded from the cave (Deonier, 1940). This explains why, when prevailing conditions are unfavourable, such as during winter, larvae hatching from eggs laid during warmer spells are able to complete their development.

Deonier (1940) concluded that small carcasses do not usually develop or maintain temperatures significantly above ambient, which may explain why the differences in temperature recorded during this work are not nearly as large as those reported by other authors (Deonier, 1940; Reed, 1958). It may, however, be more sensible to compare carcass temperature with that of the underlying soil, since the thermal capacity of a carcass is more akin to that of the soil than of the atmosphere. This method has been used successfully (Payne, 1965), and differences are generally more significant than those between carcass and air temperature (Wasti, 1972). Abell *et al* (1982) report that while temperatures recorded from reptile carcasses do not exceed ambient, during dipteran infestation they are consistently higher than that of the soil.

It has been suggested that the pattern of differences over time between carcass temperature and that of the underlying soil may be used as an aid to forensic scientists attempting to determine time since death (Payne, 1965). However, it is not felt that this work could be similarly useful, since the difference between carcass and air temperatures recorded were not of significant magnitude. No obvious pattern common to all regions can be discerned either, although further investigation, recording the temperature of sediment rather than air, and involving regular and more frequent monitoring, may provide valuable information.

6.1.2 Fauna and fungi

Before the carcasses were deposited, the species richness in Robin Hood's Cave was strongly correlated with temperature (Figure 3.3), which showed seasonal variations in all three chambers. The number of individuals trapped was also related to temperature (Figure 3.4). There are several reasons for these relationships:

* surface activity increases with increasing temperature, making individuals more likely to fall into pitfall traps;

* many non-cavernicoles enter the cave as their surface populations become active during their reproductive and dispersive phases which generally occur during the warmer months of the year;
* seasonal reproductive cycles in the cavernicolous invertebrates lead to large numbers of juveniles during the warmer months of the year;
* troglophilic and troglobitic species tend to be found more frequently towards the front of the cave during the summer.

Fluctuations in the baseline fauna of all three chambers of Robin Hood's Cave are therefore strongly seasonal. However, large non-seasonal variations were recorded in the cavernicolous community during the course of the experiment, which were caused by the experimental manipulation of the cave environment, ie the presence of the carcasses.

The invertebrates found in the cave (Table 3.2 and Appendix 1) were there for a number of reasons. Some are commonly found underground (troglobites, troglophiles and habitual trogloxenes), others ventured into the cave due to the presence of the carcasses which provided a concentrated food source, and the remainder were accidentals.

With reference to Glennie and Hazleton (1962), Vandel (1965), Jefferson (1976, 1983), Peck (1976, 1988), Hazleton (1977), Hippa *et al* (1985) and Terrell-Nield (1985, 1986) the following is a brief outline of the status within the cave of some of the more common animals. The important groups are discussed in more detail later in this chapter.

Both families of annelid found have been previously reported from caves. *Enchytraeus bucholzi* (Enchytraeidae) is a troglophile, and many members of the Lumbricidae are potential troglophiles, entering caves accidentally and remaining if conditions are suitable.

Of the arachnids, all mites (Acari) found in the cave can be classed as troglophiles. The pseudoscorpion *Chthonius ischnoceles* (Chelonethi: Chthoniidae) has been found in a number of caves and is probably troglophilic. About a sixth of all known pseudoscorpions are cavernicolous. Harvestmen are likely to be habitual trogloxenes, using the cave for shelter and possibly feeding there, but not breeding.

Mitostoma chrysomelas, however, may be troglophilic.

The spiders *Nesticus cellulanus* (Nesticidae) and *Meta menardi* (Metidae) are troglophiles commonly found around the entrance, and *Lepthyphantes pallidus* (Linyphiidae) has also been reported as a threshold troglophile. In Robin Hood's Cave, however, all three species have been collected much deeper in the cave. The only troglobitic spider found was the linyphiid *Porrhomma egeria*.

Terrestrial isopods are classed as threshold trogloxenes, although *Androniscus dentiger* (Trichoniscidae), which is often found much further underground, is a potential troglophile.

Lithobiidae (Chilopoda) frequently visit caves in search of prey. The diplopods *Polymicrodon polydesmoides* (Craspedosomatidae) and *Brachydesmus superus* (Polydesmidae) are common troglophiles closely related to species which are troglobitic in Europe. Other millipedes found are threshold troglophiles which venture further underground if conditions are suitable.

Diplura and Collembola (Insecta: Apterygota) are soil and leaf litter inhabitants which are ideally suited to the hypogean environment. Most are able to breed in the cave provided there is sufficient food, and certain species of *Onychiurus* (Onychiuridae) are troglobites. Collembola are fungus-feeders and are preyed upon by numerous invertebrate predators. Thus, much of the nutrient and energy transfer between trophic levels in the cave involves this important group.

The Psocoptera, Hemiptera, Thysanoptera and Mecoptera are all usually considered accidental trogloxenes. In this study, however, large numbers of *Thripia* sp (Thripidae) were found in the threshold region, suggesting a positive move into the cave.

A number of Lepidoptera are habitual trogloxenes, entering the cave to shelter, hibernate or feed. In this study the Tineidae found were breeding in the cave, and are therefore troglophilic in suitable conditions.

Many dipteran species are common trogloxenes. Female *Culex pipiens* (Culicidae) are often found hibernating in large numbers, as are *Trichocera* spp (Trichoceridae). In some areas the sphaerocerid *Crumomyia nigra* enters caves in swarms. *Psychoda* sp (Psychodidae) and Tipulidae are frequent threshold dwellers and the fungus gnats (Phoridae and Mycetophilidae) are also common near the entrance.

Heleomyzidae are familiar cavernicoles, and are generally classed as habitual trogloxenes, since no previous evidence has been found of their breeding underground.

In this study the most important dipterous groups were the sciarids, phorids and calliphorids. *Bradysia* spp (Sciaridae) are common troglophiles, and *Lycoriella leucotricha* (Sciaridae) also breeds in the caves at Creswell. *Triphleba antricola* and *Megaselia rufipes* (Phoridae), are frequent cavernicoles, breeding in dry carrion. Perhaps unexpectedly, *Calliphora erythrocephala* and *C. vomitoria* (Calliphoridae) are quite often found deep in caves.

The two fleas (Siphonaptera) found in the Back chamber would have been carried in on vertebrate hosts (Ichnopsyllidae are bat fleas).

Ichneumonids and other parasitic Hymenoptera have been reported from the threshold regions of caves, and have been observed hibernating in Robin Hood's Cave. A large number of species were attracted in during this study due to the presence of hosts.

The Coleoptera are the best represented group of cavernicolous insects. *Leptinus testaceus* (Leptinidae), the cholevids *Catops* spp, *Choleva glauca* and *C. oblonga* and the staphylinids *Omalium excavatum* and *Quedius mesomelinus* are all considered troglophilic. *Cryptophagus acutangulus* (Cryptophagidae) can probably be added to this list. Many Coleoptera are known to forage but not breed in caves. These include predatory staphylinids and others, such as *Bessobia* sp (Staphylinidae) and the cryptophagids, which are fungus feeders. Some, like *Meligethes aeneus* (Nitidulidae), the pollen beetle, are accidentals.

Whilst the community in a cave will comprise species from all of the Schiner-Racovitza categories (Racovitza, 1907), under normal conditions it is the activity of the troglophiles and troglobites which has most effect on the energy flow. Trogloxenes and accidentals contribute to the nutrient cycle in the form of droppings, and obviously affect nutrient levels considerably should they die whilst underground, but they do not usually remove energy by consumption. The large number of trogloxene species found feeding in the caves in this study slightly alters this situation.

When a significant nutrient source in the form of animal carcasses was deposited in the cave the effect of visiting species upon the structure of the cavernicolous community was profound. The number of individuals of species classed

as "feeding trogloxenes" increased dramatically, as did the number of new species found regularly. These entered the cave for a variety of reasons and sometimes appeared to be in direct competition with the cavernicolous community for resources.

The most obvious non-cavernicole was *Calliphora vomitoria*, which was directly involved in the consumption of carrion. It is unusual to find a species not generally supposed to be troglophilic breeding so far underground. Erzinçlioglu (1983) reports that *Calliphora* spp will colonise carcasses in very dark places, although they will not oviposit at night. The latter is probably due to an endogenous circadian rhythm, since *Calliphora vomitoria* was able to lay eggs in the total darkness of the Back chamber.

Calliphora spp will also oviposit at much lower temperatures than other blowflies (Deonier, 1940).

Although a number of different blowfly larvae are often found on a single carcass, those colonising small carcasses, as used in this study, are commonly restricted to only one species (Putman, 1983). However, it is widely accepted that *Calliphora vomitoria* is universally absent from small animal carrion (Davies, 1990), and that its frequent occurrence in dead sheep confirms that the species is confined to large carcasses (Hennig, 1950; Nuorteva & Skaren, 1960). Many studies have neglected the importance of this species due to their use, generally on grounds of convenience, of small animals as bait (Suenaga, 1959a, 1959b; Denno & Cothran, 1976; Goddard & Lago, 1985; Putman, 1977).

C. vomitoria is also considered an upland species, while in lowland areas *C. vicina* is generally more common (Davies, 1990).

The presence of *C. vomitoria* on the carrion in the cave therefore appears to be anomalous, since the carcasses used were small (225 - 475 g) and Creswell is not an upland site. However, the area around the caves at Creswell is wooded, and it is known that *C. vomitoria* predominates over *C. vicina* in woodland even in lowland regions (Davies, 1990). Additionally, the population of *C. vomitoria* at Creswell may be artificially high due to other decomposition studies in the area.

C. vomitoria is also more likely to oviposit in shade (Wardle, 1927), and is active at far lower temperatures than other calliphorids, the minimum threshold being less than 2 °C (Deonier, 1940). Thus, the species is the best adapted for colonisation

of carrion deposited in the conditions found in the caves.

The findings of this study therefore prove that *C. vomitoria* is not necessarily restricted to large carcasses and confirm the presence of the species in lowland areas. Furthermore these observations imply that *C. vomitoria* is probably excluded from otherwise suitable habitats by other, competitively dominant necrophagous Diptera.

Calliphora larvae were found on the carcasses in the Front chamber only a few days after deposition. The carrion-locating methods employed by blowflies, while obviously very efficient, remain somewhat obscure. Mackerras (1933) suggests that blowflies will lay eggs on a variety of materials which are not necessarily suitable larval environments, and that oviposition is a reflex reaction to a tactile stimulus.

It seems generally accepted though, that olfactory mechanisms are important, since blowfly eggs are not usually found until a carcass shows some signs of putrefaction (Deonier, 1940), which is accompanied by a distinct odour. It is thought that the activities of micro-organisms, which lead to putrefaction, are essential in the preparation of carrion for larger necrophages (Nabaglo, 1973). However, blowfly eggs have been recorded on carcasses prior to the onset of microbial decomposition (Lothe, 1964), sometimes within minutes of death (Putman, 1983), on fresh meat, and even on live animals (Norris, 1965).

In the present work it seems likely that it was the smell from the carrion which attracted *Calliphora*, particularly in the deeper regions of the cave. Although the carcasses in the Front chamber were not especially malodorous when first colonised, no larvae were seen on the carrion in the deeper regions until much later, when putrefaction was well underway. However, the odour from these carcasses was not discernible outside, due to the direction of airflow through the cave. It is thought that *Calliphora* colonising the carcasses in the Frogpit chamber were initially attracted to those at the front, and that once in the cave, they then followed the smell deeper underground.

At this time the odour from the carcasses in the Back chamber could only be detected locally, and it is likely that the individuals which later ventured through to the back of the cave were the offspring of those from the front which had been attracted into the Frogpit chamber. A small tunnel connects this chamber to the back of the cave (Figure 2.1), and by the time the adults in the Front chamber emerged a strong

smell emanated from the mouth of this tunnel into the Frogpit chamber. It is assumed then, that this was the route used to gain access to the Back site.

These observations suggest that had there been no decomposing material near the entrance of the cave, *Calliphora* may have been absent from the Frogpit chamber. Furthermore, it is almost certain that blowflies would not have detected the carcasses at the back of the cave without already having colonised those in the Frogpit chamber. This "island hopping" from one discrete unit of carrion to another obviously has important implications for a predictive model.

In the Front and Frogpit chambers, considerable intraspecific competition existed between the *Calliphora* larvae on the carrion. The first adults to arrive at a carcass oviposited around the orifices, from where the newly-hatched larvae had easy access to the body cavity and organs. According to Lane (1975), this can confer a competitive advantage over individuals hatching later. Larval competition was evident in the number of dead larvae which were found in the upper layers of sediment when the tanks were excavated (Section 3.4), suggesting that the carcasses were exhausted before all larvae had accumulated sufficient resources to undergo pupation.

Another indication of larval competition is the body size of newly emerged adults (Davies, 1990). In the Front and Frogpit chambers it was observed that the later emerging adults were smaller, which implies that the larvae had progressively less food. In contrast, all *Calliphora* adults seen in the Back chamber, where competition was not as strong, were much larger than average.

It is also probable that the development of the reproductive organs in females is dependant on adequate larval nutrition, although this is apparently not the case in males (Mackerras, 1933).

In the Front chamber, the *Calliphora* larvae consumed approximately 70% of the total body weight of the control rats, and the remains subsequently mummified. It is thought that when the adults emerged they dispersed rapidly as the mummifying carcasses were no longer attractive oviposition sites (Johnson, 1975; Putman, 1978b). This explains why relatively few were caught in the pitfall traps: most did not remain in the area for long but emerged, dried and flew out of the cave. Light from the cave entrance penetrates as far as the Front site and the adult flies are positively phototactic.

Many more *Calliphora* were found in the pitfall traps in the Frogpit chamber.

This was not a reflection of the numbers of larvae colonising the carcasses, which were no higher than in the Front chamber, but rather the behaviour of the adult blowflies. Although the carcasses were no longer attractive, and light from the entrance was just visible in this chamber, the newly emerged adults were very lethargic due to the low temperature and did not disperse. They were found on the floor, rocks and walls in the vicinity of the carcasses for some time after emerging and were thus more likely to fall into a trap than if they had flown out immediately as had those in the Front chamber.

In the Back chamber, both the original *Calliphora* adults which laid the eggs and the emerging offspring were dramatically disabled by the lower temperature and total darkness. As well as being extremely sluggish, they appeared disorientated due to a lack of environmental cues, such as temperature or light intensity gradients, which would have enabled them to locate the exit.

Calliphorids are generally accepted to be primary Diptera (Mégnin, 1884; Fuller, 1932; Payne, 1965) colonising only relatively fresh carrion. In the present study, however, *C. vomitoria* larvae were found on carcasses which were in a fairly advanced state of decay, apparently competing for food and space with secondary species (the troglophilic phorids *Triphleba antricola* and *Megaselia rufipes*). In the Front chamber, the rapid depletion of resources by *Calliphora* and the subsequent mummification of the carcasses effectively precluded colonisation by these phorids, which are known to prefer carcasses in the butyric fermentation and dry decay stages (Johnson, 1975). It is possible, however, that a very small population of *Triphleba* was supported by the mummified carrion in the Front chamber long after calliphorid colonisation (Section 3.2.1).

Further underground, *Calliphora*, *Triphleba* and *Megaselia* co-existed. In the Frogpit chamber, this led to high inter- as well as intra-specific larval competition, manifest as high larval mortality in *Calliphora* (Section 3.4), and slow development in the phorids (Section 6.1.1). In the Back chamber colonisation by *Calliphora* was minimal possibly because by the time the species reached the back of the cave, the carcasses were in a suitable state for phorids. Thus, although competition apparently had little effect on the carrion community in this region, *Calliphora* may have been excluded to some extent by the Phoridae, in a situation the reverse of that in the Front

chamber.

Calliphoridae and Phoridae were the only necrophagous families of Diptera represented on the carrion in the cave. Others, such as Muscidae which are common secondary species (Chapman & Sankey, 1955; Illingworth, 1927; Payne, 1965), were universally absent from the carcasses in the cave. Although the environment within the cave (Section 1.4.1) obviously precludes some of these, the presence of others, particularly those common on buried carrion, would perhaps still be expected.

A particular species may be missing for a number of reasons. In some, it is the larvae of the species, rather than the adults, which are found underground. *Muscina pabulorum* (Muscidae), for example, which Lundt (1964) found to be the dominant species on flesh buried in the upper layers of the soil (2.5 to 10 cm deep), lay their eggs on the surface and leave the larvae to burrow and find the carrion. Obviously this strategy would be less effective for locating carrion deposited in caves.

Other secondary Diptera, such as some sphaerocerids, were present in the cave, but may have been unable to colonise the carcasses due to competitive exclusion by *Triphleba* and *Megaselia*, species which are better adapted to a cavernicolous existence.

The burial of carcasses in soil sometimes leads to a similar discriminatory effect against secondary species. Fuller (1932) implies that this may be at least partially due to the lack of predatory beetles associated with buried carrion. This results in very high population densities of primary Diptera, which consequently exclude secondary species. A comparable situation almost certainly occurred in the shallower regions of the cave where there was a relative paucity of predatory Coleoptera during the period of Dipteran infestation. Thus, populations of *Calliphora* at least were able to reach very high densities, resulting in the rapid exhaustion of resources and exclusion of other dipterous species.

This theory is supported by the views of Paine (1966), who believes that "local species diversity is directly related to the efficiency with which predators prevent the monopolization of the major environmental requisites by one species".

Despite the predominance of *Calliphora*, *Triphleba* and *Megaselia* during the active stages of decomposition, other species were able to exploit the carrion both at this time and later. These subsisted upon parts of the carcasses not consumed by the

three dominant species, and were not necessarily common cavernicoles. Such species included astigmatid mites which eat skin and were found throughout the cave. In the Front and Frogpit chambers *Anisopus fenestralis* (Diptera: Anisopidae) fed upon the liquids oozing from the carrion, while in the Back chamber this role was filled by *Enchytraeus* sp (Annelida: Enchytraeidae).

Hofmannophila pseudospretella (Lepidoptera: Tineidae), the brown house moth, although absent from the deep cave, was an important member of the carrion community in the shallower regions. This species was one of the few able to colonise the mummified remains in the Front chamber, and was a seasonal visitor, breeding on the carcasses during the two summers of the experiment.

Adult tineids do not feed, but the larvae are frequently found on dried plant and animal material, being among the few insects able to digest the keratin of hair and feathers (Chinery, 1976). The larvae of *H. pseudospretalla* are very sensitive to desiccation, and can only develop normally in areas of high humidity. They are thus ideally adapted to a cavernicolous environment, although they are more often found in damp rooms and cellars (Mourier *et al*, 1977). The species has also been previously reported from the dry remains of carrion (Payne & King, 1969) and from human corpses (Forbes, 1942).

Thripia sp (Thysanoptera: Thripidae) are normally associated with living plant material since, like aphids, most thrips feed by piercing plant cells and drawing sap. A number of tree roots penetrate the roof of the cave in places, and the few individual thrips present in the baseline fauna were probably associated with these. However, some species are said to live on fungi and decaying material (Chinery, 1976). The presence of thrips in the Front chamber in such high numbers during the entire two years of the experiment may give support to this theory.

Some species found would have been associated not with the carrion *per se*, but rather with the fungus growing on it. These include the Collembola, Diptera from the families Mycetophilidae, Sciaridae, Cecidomyiidae and Dryomyzidae, and some beetles (all the cryptophagids and the staphylinids *Bessobia* and *Omalium* spp).

The sciarids *Bradysia brunnipes* and *Lycoriella leucotricha* were the most successful fungus feeding dipteran colonisers in spite of potential competition from other, non-cave, species. They were frequently found colonising the same carcasses in

Robin Hood's Cave, and it is probable that these two species, which differ considerably in body size, can co-exist by foraging on different species of fungus. Similar methods of resource compartmentalisation may be employed by the different species of Collembola and Cryptophagidae associated with the fungus on the carcasses. The presence on carrion of a number of congeneric species is common, although they tend to be separated by temporal distribution and habitat preference (Kentner & Streit, 1990).

Parasites are found in all communities and the carrion community is no exception. Non-cavernicolous parasite species were attracted into the Front and Frogpit chambers by the presence of hosts. Ichneumonid, and particulary braconid, Hymenoptera are parasitic upon Lepidoptera, and were found only when tineid moths were associated with the carrion. The other Hymenoptera found in the cave were mainly parasites of Lepidoptera or Diptera (Richards, 1977). It has been suggested (Easton & Smith, 1970) that some Hymenoptera associated with carrion are necrophagous or predacious, although evidence of neither was seen during the present study.

In view of the dipteran presence on the carcasses, it was expected that at least one species of Hymenoptera known to parasitise dipterous eggs and/or larvae would also be present in large numbers. This was not the case, however, which may be another reason for the high population densities of the three dominant dipterous species discussed earlier.

The most frequently encountered parasite in this investigation was a gamasid mite. This was found in large numbers as an ectoparasite of *Triphleba antricola* and *Megaselia rufipes*, individuals of which sometimes carried as many as ten or eleven gamasids.

The remaining group of species attracted to the carrion were the predators. These were predominantly staphylinid beetles, notably *Quedius mesomelinus* (Chapter 7), although spiders, harvestmen and predatory flies, such as empids and dolichopodids, were found in small numbers.

The dipterous larvae and the Collembola would have been the main prey for these species, although the thrips provided a concentrated source of food for predatory staphylinids present in the Front chamber after July 1990.

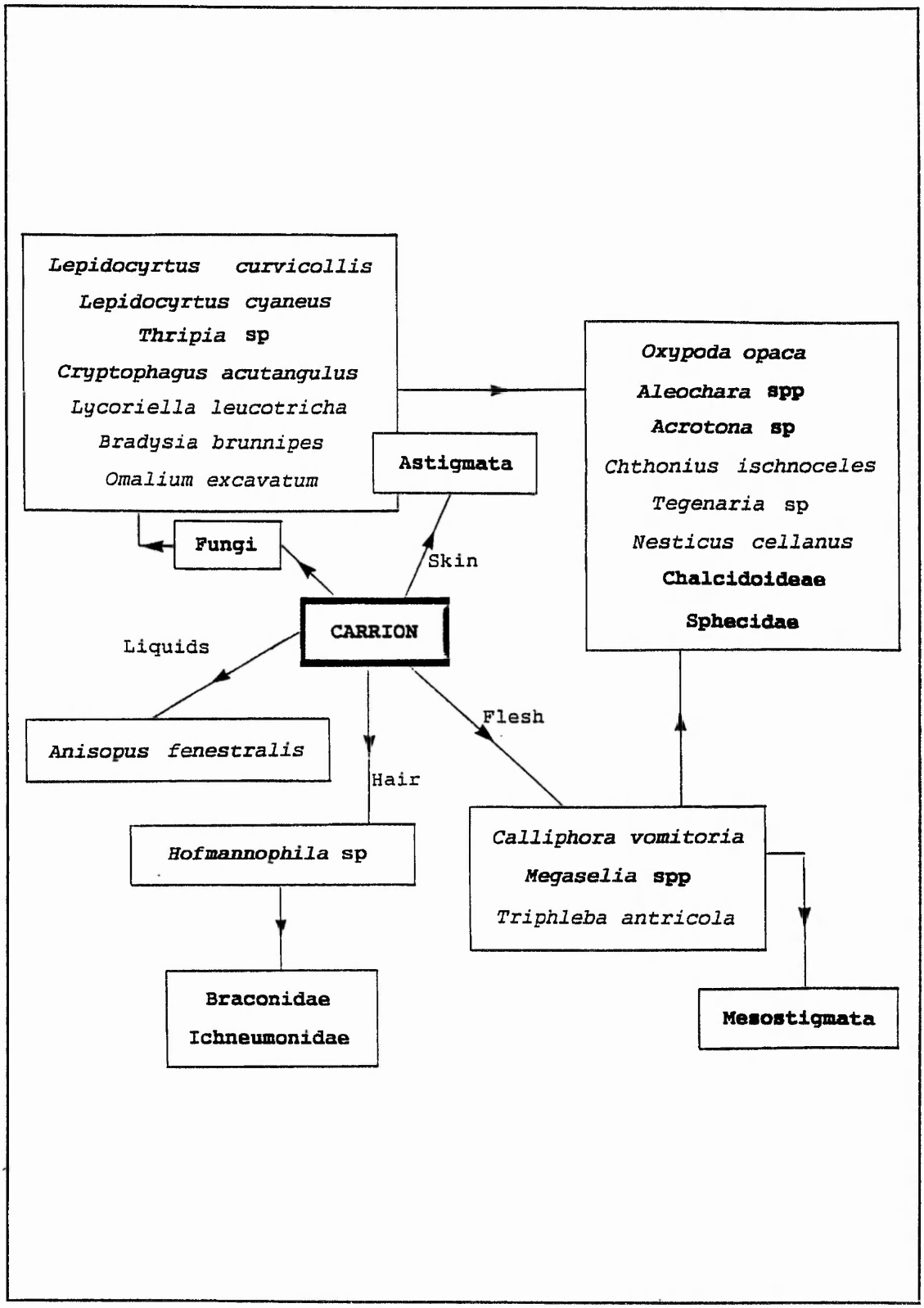


Figure 6.1: The trophic relationships within the carrion community in the threshold region.

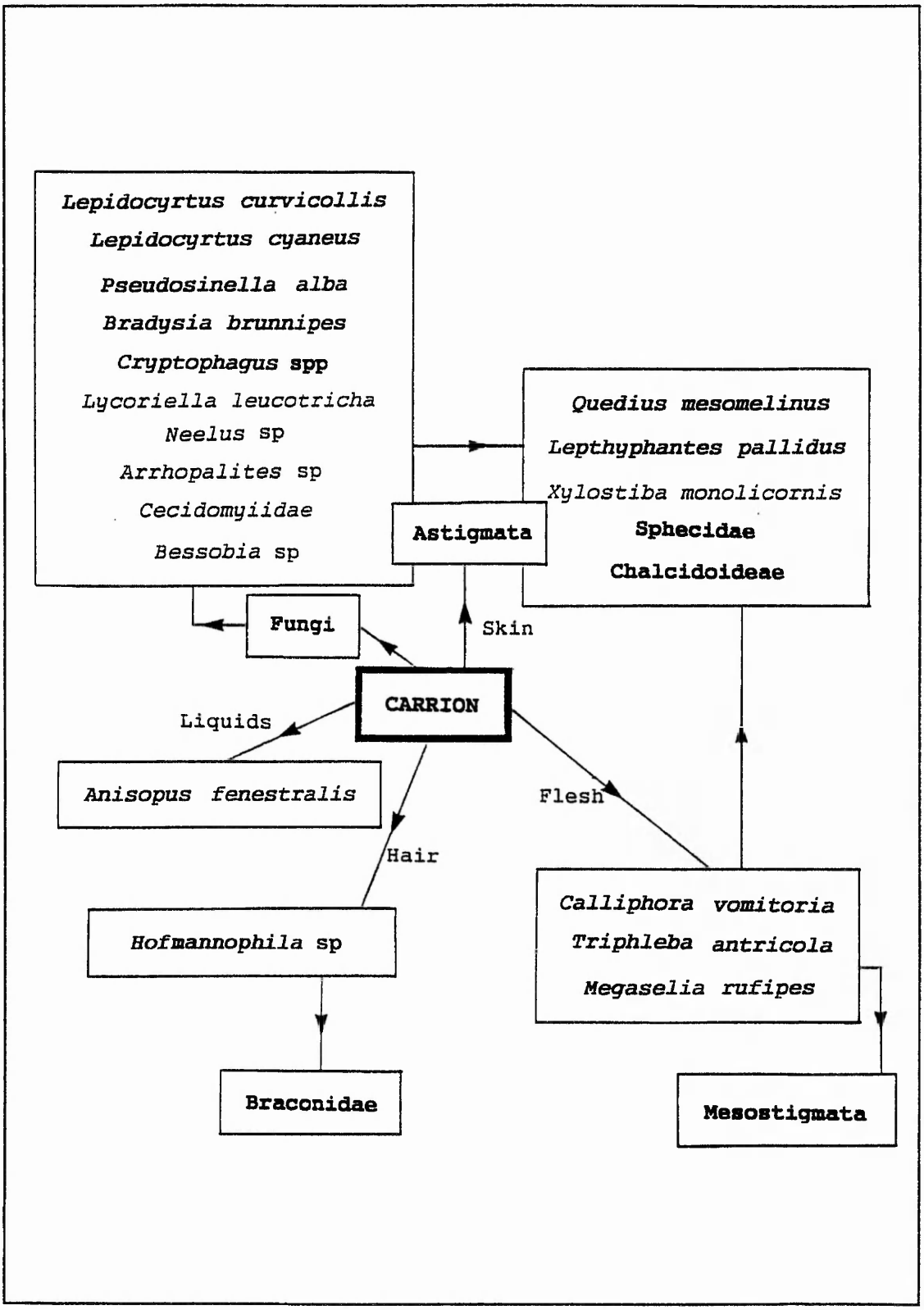


Figure 6.2: The trophic relationships within the carrion community in the deep threshold region.

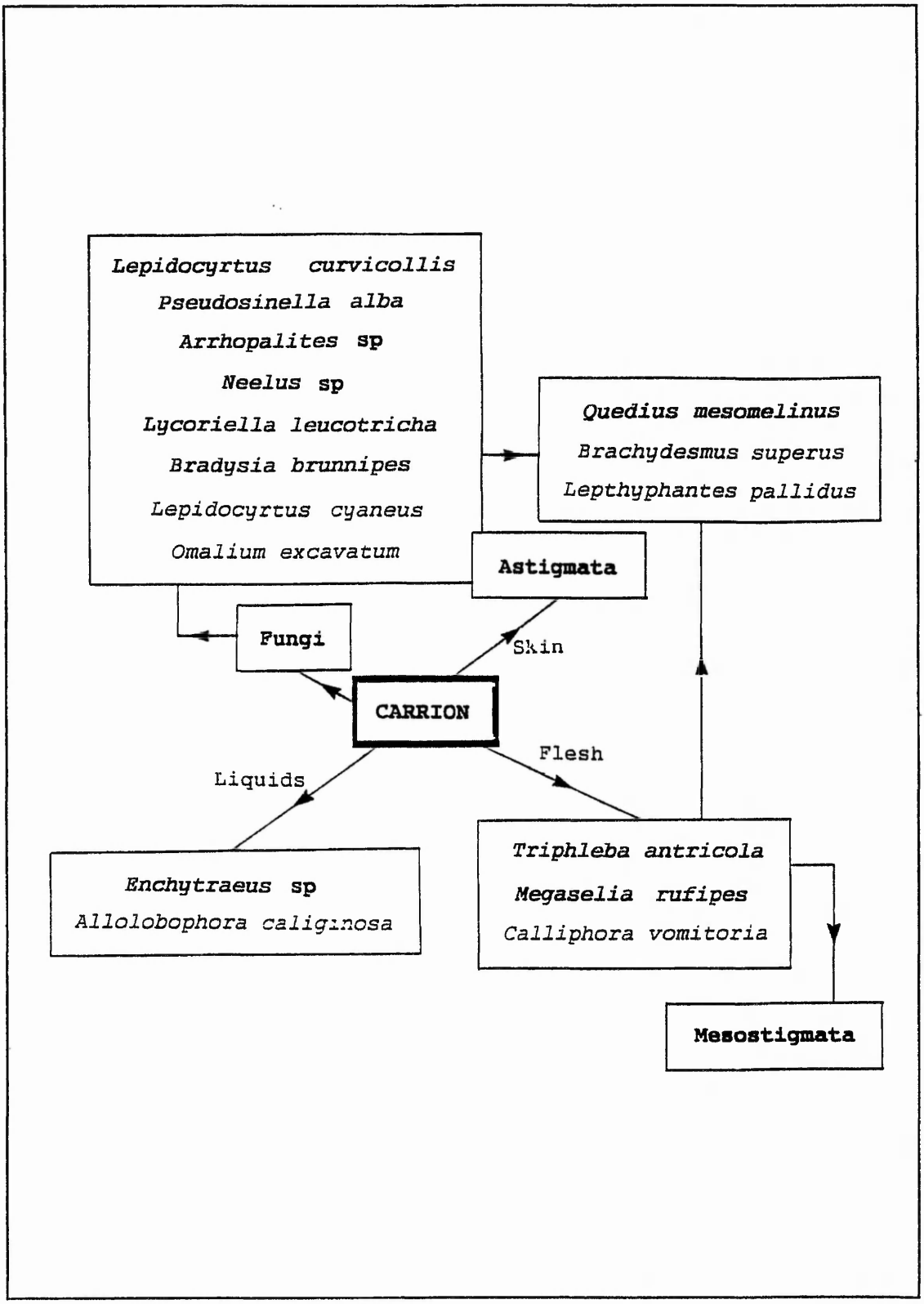


Figure 6.3: The trophic relationships within the carrion community in the hypogean region.

Something of the structure of the food webs based upon the animal carcasses deposited at the three sites in Robin Hood's Cave can be seen in Figures 6.1, 6.2 and 6.3 (previous pages).

6.1.3 Decay curves

The rate of consumption of a carcass, known as carrion removal (Payne, 1965), is a very important aspect of any decomposition study, and can be quantitatively expressed as a decay curve. This is constructed by plotting the relative amount of carrion remaining against time, as in Figure 3.19.

Excluding the data from CR/6, which will be considered separately, the decay curves from all three chambers are similar. They are sigmoidal and can be described as in Figure 6.4. The initial flat section corresponds to the period before dipteran infestation. Had any reduction in weight occurred during this time it would have been due to microbial activity. The slope of the curve represents the decay of the carcass

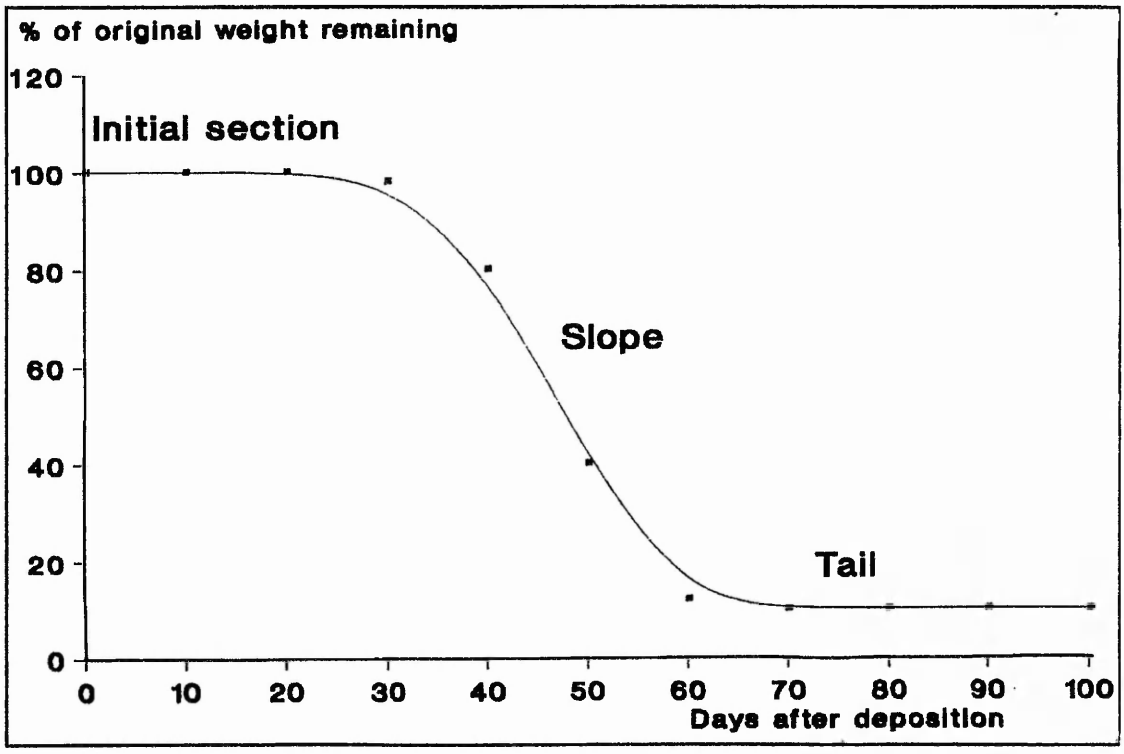


Figure 6.4: A typical decay curve.

during dipteran infestation. Reduction in mass is due to the consumption of the flesh by dipterous larvae, with the gradient of the slope indicating the rate of carrion removal. The decay of the carcass remains (hair, skin, bones, etc.) after all necrophagous diptera have pupated is represented by the tail of the curve.

The decay of the carcasses in the Front chamber began almost immediately after deposition. This was due to consumption of the flesh by *Calliphora vomitoria* larvae, which reduced the carcasses to 30% of their original weight in 35 days (between the 6th and 41st day after deposition). Carrion removal effectively ceased after the *Calliphora* pupated, and the relatively small loss in weight after this time was largely due to the presence of mites and Lepidoptera, which gradually consumed the remaining skin and hair.

In the Frogpit chamber a similar situation was seen, the main difference being the time before carrion removal began (the length of the initial section on the curves). This is an indication of the time taken by *Calliphora* to locate the carcasses. Other species, ie *Triphleba antricola* and *Megaselia rufipes*, also played a major role in the decomposition of the carrion in this chamber. The slope of the decay curves show that the rate of carrion removal during dipteran infestation was higher in the presence of these three species than in was when carcasses were colonised by *Calliphora* only (in the Front chamber). In the Frogpit chamber carcasses were reduced to 30% of their original weight in just 26 days (between the 29th and the 55th day after deposition).

The decay curve of CR/5 shows a similar pattern to those of CR/3 and CR/4 (from the Frogpit chamber) in that a relatively long initial period is followed by rapid carrion removal upon infestation by *Calliphora*. CR/5 was reduced to 46% of its original weight by *Calliphora*, *Megaselia* and *Triphleba* larvae between the 48th and the 69th day after deposition.

In the Front and Frogpit chambers, carcasses were so heavily infested with *Calliphora* that they were exhausted by one generation. Not all carcasses in the Back chamber were colonised by *Calliphora* though, and those that were supported relatively small populations. Thus less carrion was consumed by the blowfly larvae, and sufficient edible material apparently remained when these larvae pupated to support a second generation.

However, when the adults emerged the carcasses had reached the butyric fermentation stage, and were no longer attractive oviposition sites for *Calliphora*, although *Triphleba* and *Megaselia* were able to continue to colonise the carrion in this condition. The decay curve of CR/5 reflects this change in the invertebrate community: the gradient of the slope becomes less steep, indicating a reduction in the rate of carrion removal.

Thus, in the Frogpit chamber, where *Calliphora* was dominant throughout the entire period of dipteran infestation, 70% of material was consumed in less than a month, while equivalent carrion removal in the Back chamber, where blowflies played a more minor role, took approximately six months (from the 48th to the 243rd day after deposition in CR/5).

Considering now the decay curve of CR/6, most of the initial fluctuations in weight can be accounted for by changes in the moisture content of the fur of the rat due to water dripping onto it from the roof of the cave. CR/6 was only minimally colonised by Diptera, most of the decomposition being microbial. This is reflected in the very gradual rate of carrion removal shown in the decay curve of this carcass; 35% of material remained even after two years.

All carcasses were colonised by fungi prior to dipteran infestation, although no reduction in the weight of carrion due to microbial activity during this time is evident in the decay curves. In the Front chamber, this was because *Calliphora* larvae hatched and began to consume the carcasses before fungal colonies were sufficiently established to effect any significant decomposition. In the deeper regions of the cave it is possible that low temperatures resulted in enough of a reduction in activity to appreciably lengthen the period before significant microbial decomposition commenced, by which time *Calliphora* had again located the carcasses.

In Figure 6.5 (overleaf) comparable decay curves are illustrated from data taken from Nabaglo's (1973) study of bank voles (*Clethrionomys glareolus* Schreber), and Payne's (Payne, 1965; Payne *et al*, 1968) work with baby pigs (*Sus scrofa* Linnaeus). These show that the decay of the rats in the cave during the first 50 days of this study was markedly different from that of carcasses which had been exposed on the surface. Furthermore, the pattern of carrion removal observed was also different from that of baby pigs which had been buried in a shallow grave.

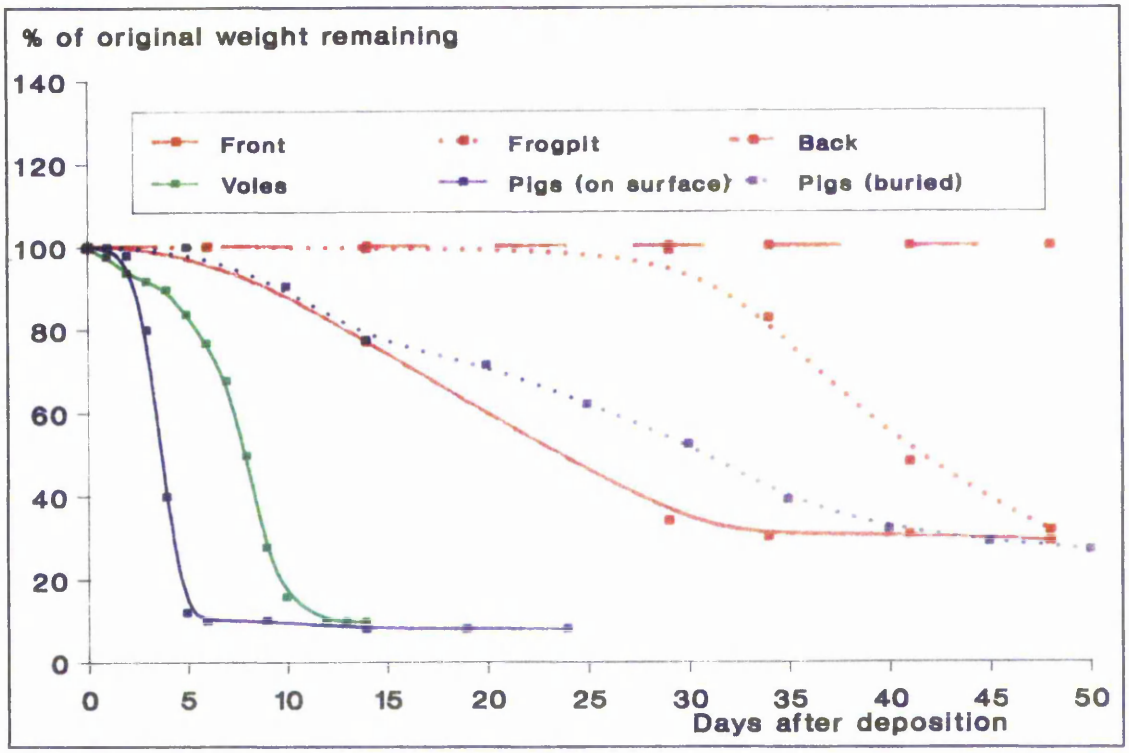


Figure 6.5: Patterns of carrion removal in the carcasses in the three chambers of Robin Hood's Cave, in bank voles (*Clethrionomys glareolus* Schreber) (Nabaglo, 1973), and baby pigs (*Sus scrofa* Linnaeus) (Payne, 1965) on the surface, and in buried pigs (Payne *et al*, 1968).

It has been suggested that in similar conditions small carcasses decompose significantly faster than large ones (Erzinçlioglu, 1986). A comparison of the decay curves constructed by Payne (1965) and Nabaglo (1973) (using data from experiments conducted at similar temperatures) refutes this implication, since voles are far smaller than baby pigs. In the absence of further comparative data it is impossible to state categorically the relationship between size of carcass and decay rate.

However, as has been discussed (Section 6.1.3), it is accepted that the decay rate in similar conditions is dependant upon the invertebrate succession and those species involved, which may in turn be specific to carcass size (Denno & Cothran, 1975; Lane, 1975) and species (Kuusela & Hanski, 1982). Therefore, sensible comparisons between the decomposition of dissimilar sized carcasses in different

conditions can be made, provided that the processes of decomposition are described according to the activity of the specific arthropods involved.

Thus, it can been seen (Figure 6.5) that regardless of carcass size, the entire decay process occurs much faster on the surface, where carcasses are reduced by 90% in a matter of days, than it does in the cave. Decomposition proceeds so quickly in exposed carcasses that the initial flat section of the decay curve is barely apparent, and the gradient of the slope is extremely steep, indicating rapid carrion removal.

In contrast, the decomposition of buried pigs involved a much more gradual and uniform rate of carrion removal. The decay curves constructed from the carcasses in both the Front and Frogpit chambers show a noticeably steeper gradient than that of buried pigs, although the onset of carrion removal is later in the Frogpit chamber. In the Back chamber carrion removal had not commenced, even seven weeks after deposition.

Figure 6.6 (overleaf) shows that the pattern of carrion removal in the Front and Frogpit chambers is much more akin to that measured in dead voles in underground burrows (Nabaglo, 1973) although the time taken for Diptera to locate the carcasses varies. The gradients of the slopes indicate that the rate of carcass consumption during dipteran infestation in the Front chamber is comparable with that of voles in their burrows in spring, whereas in the cooler Frogpit chamber the pattern is more similar to that of voles in their burrows in summer. Referring back to the decay curve of CR/5 in Figure 3.19, it can be seen that the gradient of the first part of this slope is comparable to that of the Frogpit chamber carcasses.

These findings imply that in the colder, deeper areas of the cave, carrion removal during at least the initial stage of dipteran infestation is more rapid than it is near the entrance. This seems surprising, since one would expect the rate of carrion removal in the cave to be positively related to temperature as it is above ground (Johnson, 1975; Putman 1978a; Reed, 1958), and in the shallow burrows of the voles (Nabaglo, 1973).

However, if the invertebrates encountered in the latter studies are scrutinised, it can be seen that the decomposition of a carcass is slower at reduced temperatures because fewer species of Diptera are active in significant numbers. This has two implications; firstly the carcass will remain undetected by primary species for a longer

Figure 6.6: Patterns of carrion removal in the carcasses in the three chambers of Robin Hood's Cave (this study), and in bank voles (Clethrionomys glareolus Schreber) in their underground burrows (Nabaglo, 1973).

Figure 6.7: Patterns of carrion removal in the carcasses in the Back chamber of Robin Hood's Cave (this study), in buried pigs (Sus scrofa Linnaeus) (Payne *et al*, 1968), and in baby pigs on the surface but protected from arthropods (Payne, 1965).

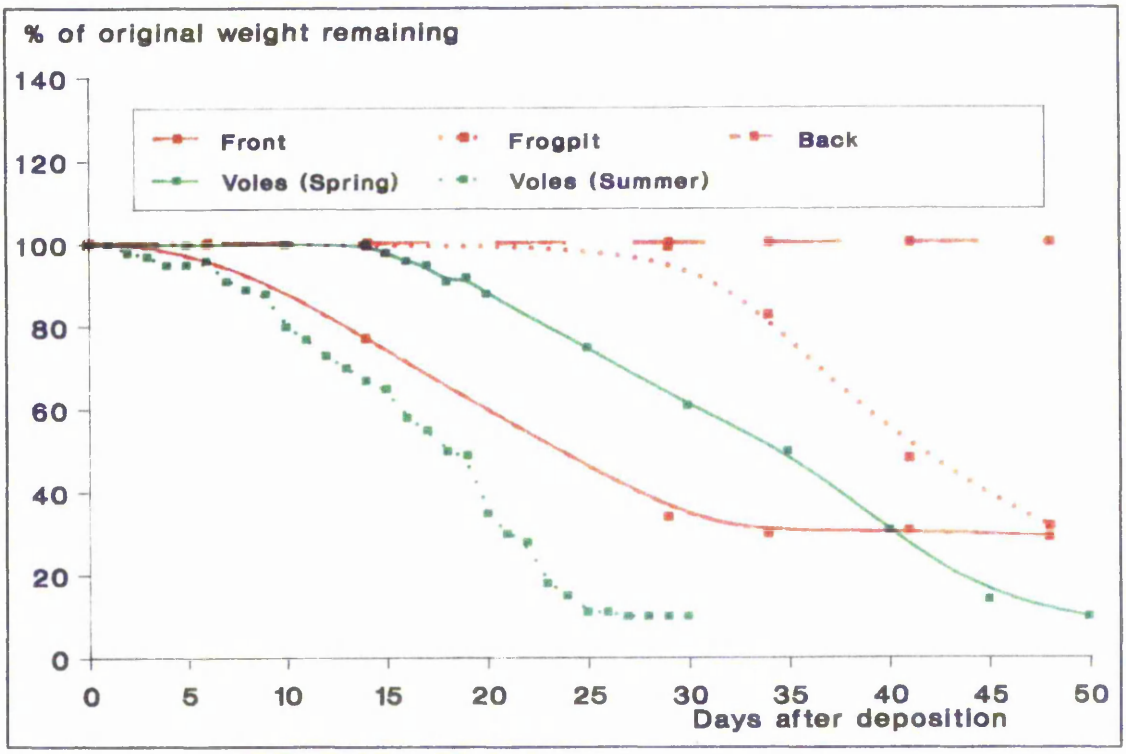


Figure 6.6

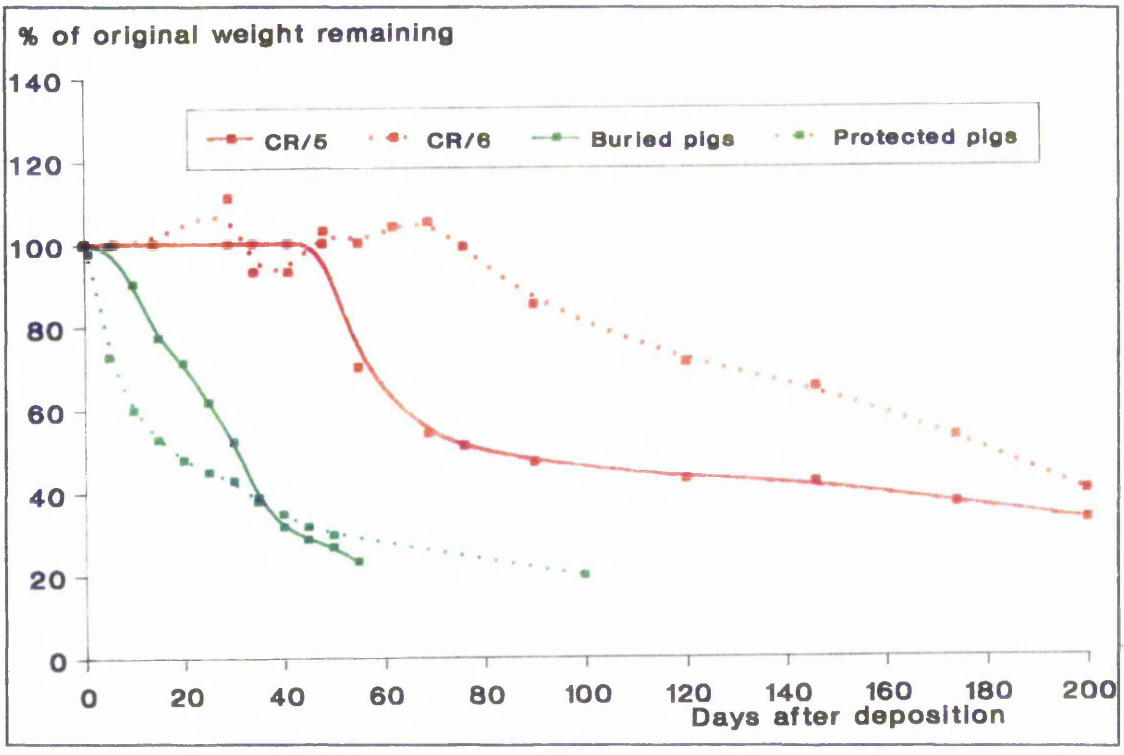


Figure 6.7

period (hence a longer initial section on a decay curve). Secondly fewer ovipositing females, and consequently larvae, will be present which, combined with a reduction in microbial activity due to reduced temperature, results in the more gradual consumption of carrion, possibly involving several generations.

In the cave there were actually more species of necrophagous Diptera active in significant numbers in the colder areas, due to the presence of the cavernicolous Phoridae which were largely absent from the carcasses in the Front chamber.

So, lower temperatures in the Frogpit and Back chambers led to a reduction in microbial activity and thus slowed the process of putrefaction. This, combined with a reduction in blowfly activity, delayed location of the carcasses deeper in the cave by primary Diptera. However, once these carcasses were located, the combined activities of blowflies and the troglophilic secondary species resulted in a more rapid rate of carcass consumption during dipteran infestation. In the Front and Frogpit chambers, carrion removal effectively ceased with the pupation of the blowfly larvae, while in the Back chamber sufficient material remained at that point to support the phorids, and consumption continued at a reduced rate.

The overall shape of the decay curve of CR/5 (Figure 6.7, previous page) is analogous to that of buried pigs (Payne *et al*, 1968). In both cases primary species of Diptera had limited access to the carcasses, much more so than in the other regions of the cave or in the vole burrows (which were relatively shallow). The slope of the buried pig curve is slightly less steep during initial dipteran infestation than is that of the CR/5 curve. This is because burial also restricted access by secondary Diptera, whereas these were well represented in the cave.

The decay of CR/6 appears to be more similar to that of carrion protected from arthropods (Payne, 1965). Both curves show a gradual decrease in mass, with no "slope" phase due to the rapid consumption of material by large numbers of dipterous larvae. The decay of CR/6 is even slower than that of protected pigs, because low temperatures in the deep cave led to a reduction in microbial activity.

The true weight of CR/6 was periodically masked by fluctuating amounts of water absorbed in the fur. Had CR/6 remained dry, evidence of microbial activity may have been manifest much sooner (the decrease in mass measured between soakings indicates that decomposition may have commenced by this time).

6.2 A comparison between summer and winter decomposition in caves

The carcasses at the Middle and Back sites in Church Hole Cave were largely consumed and interred by a vertebrate scavenger (Section 4.2). This dramatically affected the progress of decomposition, and led to the absence of many invertebrate species which were expected to colonise the remains. The interment and consumption of the carrion also led to an extended pattern of invertebrate succession. Those species found were present in greatly reduced numbers and much later than would have been predicted, even allowing for seasonal variations.

Similar findings are reported by Ellison (1990), who studied the effect of scavenger mutilation on insect succession in carrion. He found that the stages of decay of impala were clearly different in carcasses which had been fed upon by large mammalian scavengers when compared with those in unmutilated carcasses.

Since the succession on the carcasses in the deeper regions of Church Hole Cave was affected by similar mutilation, while the microbial and invertebrate colonisation of the carcasses in Robin Hood's Cave was uninterrupted (Section 3.2), a strict comparison between winter and summer decomposition can only be made for carcasses deposited in the threshold region. Nevertheless, before being mutilated, the carcasses deposited in Church Hole demonstrated markedly different patterns of early decomposition from those at comparative depths in Robin Hood's Cave. These differences can be attributed to season, since the baseline cavernicolous fauna and the annual mean temperature and humidity are similar in both caves.

The effects of season were manifest in the rate of decomposition (monitored by the physical appearance of the carcasses), which is governed by prevailing temperatures and the activities of the carrion community.

The local abiotic conditions have been shown to influence the processes of decomposition in a number of ways (Section 6.1.1). Temperature is particularly important, since it affects both microbial activity and the distribution, dispersal and development of invertebrates.

Figures 3.1 and 4.1 show that the temperature in Church Hole was much lower than in Robin Hood's Cave during the initial period after deposition. Consequently, the decomposition of the carcasses in the former was far slower than in the latter.

This was mainly because the lower temperatures in Church Hole affected microbial succession and the rate of development of *Calliphora vomitoria* colonising the carrion.

Additionally, during the first three months of the investigations, the temperature at the back of Church Hole was conspicuously higher than that at the front, whereas the reverse was true in Robin Hood's Cave. This is reflected in the progress of decomposition of the carcasses in the two caves during this period, which is summarised in Table 6.1.

Table 6.1: A comparison of the initial stages of decomposition in caves during summer and winter.

Stage of decomposition	Region of cave	Time since deposition	
		Summer (RHC)	Winter (CHC)
First fungus	Threshold	5-9 days	6 weeks
	Deep threshold	9-13 days	4 weeks
	Hypogean	9-13 days	3 weeks
Hair shed due to activity of *Calliphora* larvae	Threshold	9-13 days	4 months
	Deep threshold	5-6 weeks	2 months*
	Hypogean	6-7 weeks	Not seen
Emergence of adult *Calliphora*	Threshold	6-7 weeks	5½ months
	Deep threshold	3 months	4 months
	Hypogean	3½ months	Not seen

* Calliphora eggs must have been laid on the carcass at the Middle site of Church Hole Cave before it was interred by a scavenger two months after deposition.

Certain similarities do exist between the summer and winter studies. In both seasons, the carcasses deposited at the front of the caves mummified. The abiotic

conditions necessary for this phenomenon have been discussed (Section 6.1.1), and were similar in both cases at Creswell. The carcass deposited in the winter remained damp and fungus-covered for a much longer period, and mummification was not completed until six months after deposition. In contrast, the carcasses deposited in the summer were completely dried out after only two months. In both cases, though, mummification occurred during July and August, when local conditions were relatively warm and dry.

The results from Church Hole Cave confirm theories concerning the effect of temperature on microbial and invertebrate activity (Section 6.1.1), and were entirely in line with expectations based upon knowledge of winter decomposition above ground (Section 1.2.2).

As has been discussed (Chapter 3 and Section 6.1.2) initial decomposition in Robin Hood's Cave was microbial, but most of the carcasses were located within five weeks by *Calliphora vomitoria*. This commenced a period of dipteran infestation which resulted in the consumption of the edible parts of the carcasses. Following pupation of the dipterous larvae, a number of other invertebrates became associated with the carcasses, and microbial succession continued.

Observations from Church Hole (Chapter 5 and Table 6.1) suggest that the initial decomposition of carcasses deposited during the winter occurs at a much slower rate and is largely microbial. The fungal succession on the carcass in the front of the cave began later and proceeded more slowly than on those deeper underground. This was a result of lower temperatures near to the entrance of the cave, which had the effect of "refrigerating" the carcass at the Front site, thus retarding microbial development.

The baseline fauna in Church Hole Cave was, like that in Robin Hood's Cave, subject to seasonal fluctuations (Figures 4.2 and 4.3). In the winter, when the carcasses were deposited, only a limited number of species were active (Section 6.1.2). Thus, dipteran infestation did not occur until later in the year, when temperatures were higher, by which time the carcasses were relatively old. Furthermore, one of the dominant necrophagous species in Robin Hood's Cave, *Calliphora vomitoria*, colonised the carcasses in Church Hole only minimally, and was confined to the front and middle of this cave.

Adult *Calliphora* emerged from the carcass at the Middle site sooner than from that at the front of the cave, which suggests that the former was colonised before the latter. Initially this seems surprising, since the reverse was observed in Robin Hood's Cave. However, the slightly higher temperature at the Middle site led to the more rapid putrefaction of this carcass, due to increased microbial activity. This carcass became malodorous sooner, and it was presumably more attractive to *Calliphora* than that at the front of the cave, which had not yet begun to smell. In addition, air flows out of the cave along the main passage at this time of year (Smithson, 1982). This carried the smell from the carcass at the Middle site out of the cave entrance. The Front site was a side chamber (Figure 2.3), and the smell from the carcass was only perceptible locally.

It is assumed that Diptera were first attracted to the carcass at the front of the cave about twelve weeks after deposition, when the local population of *Meta menardi*, the cave spider, increased noticeably. This species migrates seasonally within the cave, moving toward the front as the surface temperature rises, so it is to be expected that more individuals would be found in the threshold region at this time. The density of individuals and webs (which are constructed across holes or dips in the cave wall and roof) implies that an additional factor was involved, possibly the presence of a concentrated food source. As it is known that *Meta* feed upon flying insects it would appear that they were attracted to Diptera associated with the carrion, although no evidence of such was seen directly during this period. It is possible, however, that either *Calliphora* or troglophilic Phoridae were present in the area.

Calliphora was absent from the back of Church Hole Cave. It is thought that this was because the carcass there was interred and largely consumed by a vertebrate scavenger before it was located by *Calliphora*. However, other species of Diptera, notably the phorids *Triphleba antricola* and *Megaselia rufipes*, colonised this carcass.

Also attracted to the carrion in Church Hole Cave were members of the Heleomyzidae, some of which are known as cave flies. Individuals were found on and around the carcasses throughout the experiment, and it is thought that the "other" empty puparia found in the tanks in both Church Hole and Robin Hood's Cave (Sections 3.4 and 4.3) may have been those of a heleomyzid species. The presence of apparently newly emerged dead adults in the sediment in some of the tanks supports

this theory.

Cavernicolous heleomyzids are generally classed as habitual trogloxenes (Hazleton, 1977), although Jefferson (1976) says that *Scoliocentra villosa* and *Heleomyza serrata* at least "seem to be well established in caves and are presumably troglophiles". Busacca (1975) also suggests that heleomyzids may breed underground on "bat guano, decaying organic matter, and dead bats". He produces no evidence of this however, since when he searched such material for heleomyzid larvae he found none.

The present work may thus provide the first firm evidence, albeit indirect, that at least some species of Heleomyzidae do breed on carrion and are troglophilic. It is not known, however, whether adults and larvae are necrophagous, predatory or feed on the fungus found on decaying organic material.

The presence of Heleomyzidae on the carcasses in Church Hole, along with the troglophilic Cryptophagidae, Phoridae, Collembola and Acari indicate that in winter the invertebrate community associated with carrion consists of a greater proportion of cavernicolous species than it does in summer. This is particularly true at the back of the cave. In summer, trogloxenes play a more important role in the decomposition of animal remains in caves.

6.3 Taphonomy and bioturbation

6.3.1 Post-mortal movement

Accounts of the post-depositional movement of archaeological artefacts and of individual skeletal elements are fairly commonplace (Johnson, 1957; Shipman & Walker, 1980; Stein, 1983). However, there are no reports of the movement of entire carcasses under dry conditions as observed in the present work.

The displacement of the experimental carcasses during the initial stages of the main investigation (Section 5.1) was attributed to the activity of dipterous larvae. Upon reaching maturity, blowfly larvae are known to travel considerable distances from a carcass before pupating, presumably to avoid predators which are attracted to carrion because of the high prey concentration (Cragg, 1955). In both the Front and

Frogpit chambers of Robin Hood's Cave, post-mortal movement occurred when *Calliphora vomitoria* larvae would have begun to migrate from the carcasses to burrow and pupate. Thus, there seemed a simple reason for the displacement observed: the combined activity of hundreds of larvae had moved the carcasses across the sediment.

However, there was some doubt that larvae could generate sufficient energy to move something as large as a carcass, unless all moved at the same time and in the same direction.

It is felt that the theory is still plausible, since it is known that all the larvae (of which there were some thousands) would have reached maturity concurrently, simply because they all hatched at the same time and developed under nearly identical conditions. Therefore they would have dispersed from the carcass *en masse*. In addition, by the time movement occurred, the carcasses were only about a third of their original weight of about 250 g (Figure 3.19). It is not inconceivable that the activity of the larvae could lift a carcass of this mass slightly away from the sediment, thus reducing friction and facilitating movement.

More evidence for the theory comes from the carcasses which were not moved. None of the carcasses in the Back chamber (which were only minimally colonised by blowfly larvae) showed any displacement at all. Neither did two of the carcasses in the Frogpit chamber which, although colonised by a comparable number of larvae, appeared relatively less decomposed (and thus heavier) and more intact at the time the others were displaced.

It is also probable that all migrating larvae moved in the same direction. No larvae were observed on the surface of the carcasses immediately prior to the time of displacement. At the time it was assumed that they had already burrowed to pupate, but now it is felt that it was because the blowfly larvae were all deep inside the carcasses. This situation is maintained by negative phototaxis if there is sufficient light, and suggests that when they migrate from a carcass, the direction in which the larvae travel will be non-random and negatively phototactic.

In the Front chamber, where daylight cues were strong because of the proximity of the cave entrance, all the carcasses were moved towards the light whereas in the Frogpit chamber, carcasses were all displaced diagonally away from the direction of the cave entrance. These findings appear to be contradictory if it is

assumed that larval migration is directed by a phototactic response. However, light cues in the Frogpit chamber are minimal, and the carcasses were positioned such that a low wall was between them and the light source. Thus, although visible light is just detectable in this chamber, the carcasses themselves were effectively in complete darkness, which suggests that the behaviour of migrating larvae is not governed solely by directional light cues.

Upon closer examination of the photographs taken of the carcasses at this time, it was noted that all carcasses were displaced in the direction in which their spine was facing - towards the entrance of the cave in the Front chamber (Plate 31), and further into the cave in the Frogpit chamber (Figure 5.1). This implies that larval migration, and thus post-mortal movement, may be dictated by the orientation of the carcass.

Experiments conducted after this work was completed (Terrell-Nield, pers. comm.) supported this theory by demonstrating that the migration of blowfly larvae from carrion usually occurs at night, that it is non-random even in the absence of light, and that it may indeed be influenced by the original position of the carcass.

Further evidence to support the theory that it was the migrating larvae which caused the movement of the carcasses was found when the tanks were excavated. Surprisingly few empty *Calliphora* puparia were found in the tank containing ER/4, even though the numbers of larvae seen on the carcass (and of those found dead upon excavation) were comparable with others in the same chamber (Section 3.4.1). Plate 8, however, shows that ER/4 was moved across the sediment until it was adjacent to ER/5, which was not so far displaced. In the sediment in the tank which had contained ER/5 were found over twice as many empty *Calliphora* puparia as expected (3796 as opposed to an average of 1668 for all six tanks).

ER/1 had also been displaced such that it came to rest partly in its own tank and partly in that of ER/2. The former was found to contain less than average numbers of empty puparia and the latter more.

These findings imply that when the mature larvae migrated, they carried the carcass with them, and most had burrowed to pupate by the time the carcasses were moved back to their original position by the author.

The distribution of empty *Calliphora* puparia between the tanks from the Frogpit chamber was found to be fairly even, suggesting that the carcasses were

moved back before the larvae burrowed. This is in line with knowledge about the development time of *Calliphora* (Section 6.1.1) in the two chambers.

Thus, the physiology and behaviour of blowfly larvae mentioned indicate that the theory proposed for the post-mortal movement of the experimental carcasses in the Front and Frogpit chambers of Robin Hood's Cave is credible.

Unfortunately, attempts to confirm this theory proved inconclusive (Section 5.1). Although the distance and direction of carcass displacement were comparable to those observed the previous year, movement occurred much later after deposition in this second investigation, long after most larvae had apparently left the carcasses.

There are several possible explanations for this. The carcasses in the original experiment were placed on relatively deep sediment (Section 2.1), whereas the two used in the second investigation were simply laid on a piece of plywood sprinkled with a shallow covering (Section 2.3). Less force was required to shift them, especially since the platform may have been sloping slightly.

Firstly, it is possible that even after seven weeks there were sufficient larvae remaining to effect displacement in these more favourable circumstances, and carcasses had not been moved by the activity of the earlier migrating larvae because they were still too heavy. However, the carcasses changed very little between the time most of the larvae migrated and the time when displacement was observed, and it is unlikely that the few remaining larvae could have been solely responsible for the movement.

Secondly, in a nearby quarry, blasting is carried out daily, and the shock waves from the explosions can be felt quite definitely throughout Robin Hood's Cave. These may have been partly responsible for the movement of the carcasses on the board, which was positioned (Figure 2.4) such that vibrations were magnified. If the platform had been sloping, lateral movement of the carcasses would have been facilitated.

Finally, the possibility of human intervention cannot be ruled out. Although the caves at Creswell are closed to the public, break-ins do occur, and evidence of such unwelcome visitors was found during the course of the experiment. It was felt at the time that the equipment had not been tampered with, since the mesh cage (Figure 2.4) was undisturbed. Also, the initial movement of the carcasses (Figure 5.2 b) was in the direction and to the degree expected from previous observations (Section 5.1).

It is possible, however, that someone who knew about the experiment decided to "improve" the results.

6.3.2 Bioturbation

As well as displacing the carcasses, the arthropods involved in the decomposition process caused considerable disruption to the underlying sediment. Had the sediment remained undisturbed during the course of the investigation, all of the *Lycopodium* spores extracted from the cores (Section 2.1), would have been found in the samples which contained the marked layers (the first sample of the 5 cm cores and the first, sixth and eleventh samples of the 15 cm cores). None would have been present in the other samples after any movement which had occurred in the control tanks had been accounted for. This was clearly not the case (Section 5.2).

Other authors investigating decomposing animal remains have made passing references to sediment disruption due to the activity of the carrion fauna. Easton (1966), for example, reports that a "small hollow" developed under a dead fox he was monitoring.

Bournemissza (1957) conducted an extensive study on the effects of carrion on the soil fauna, which he concluded were profound and long-lasting. This was particularly significant in the upper layers of the soil immediately beneath decomposing carcasses, although the fauna was changed to a depth of 14 cm, and to at least 10 cm away from the carrion. Bournemissza does not specifically consider the implications of his findings with regard to sediment disturbance, although it is probable that such changes in fauna would affect the rate and degree of bioturbation of soil around a carcass.

During the investigations conducted in both Robin Hood's Cave and Church Hole Cave, dipterous larvae colonising the carcasses caused significant disruption to the sediment. *Calliphora* spp larvae are known to burrow to a depth of about 5 cm prior to pupation (Norris, 1965). When the adult flies emerge they then dig their way back up to the surface, causing further disruption within the sediment, and leaving the distinct exit holes apparent on some of the photographs (Plates 2 & 26).

When the tanks were excavated large numbers of empty pupal cases were found (Sections 3.4 and 4.3). These were often from *Calliphora vomitoria*, although those

of other species, including the phorids *Megaselia rufipes* and *Triphleba antricola*, were present. Of the Diptera, *Calliphora* undoubtedly caused most bioturbation, since the larvae are considerably bigger than the other species found, and were present in large numbers relatively deep in the sediment (Figures 3.23 & 3.29 a). It is thus not surprising that those cores taken from tanks containing carcasses minimally colonised by *Calliphora* (Figure 5.6), or not at all (Figure 5.7), provided little evidence of bioturbation.

In this study, the *Calliphora* larvae burrowed far deeper than has previously been reported, probably because of the sandy sediment around the carcasses. It was seen that the drier the sediment, the deeper the larvae burrowed: in the Front chamber (where the sediment was driest) the preferred depth was 5-8 cm, in comparison with 3-5 cm in the other areas.

Some Coleoptera also show burrowing behaviour. Payne (1965) noticed an abundance of excavations and tunnels in soil beneath carrion due to the activities of predatory histerid, staphylinid and carabid beetles.

In the present study, the cave beetle, *Quedius mesomelinus* (Staphylinidae), was the dominant coleopteran species associated with the carrion. A population of these was kept in the laboratory (Chapter Seven), and the mature larvae were seen to construct underground chambers in which to pupate (Plate 32). The adults are also active burrowers, causing considerable disruption of the substratum. Turquin (1983) suggests that *Quedius* burrows create minute biotopes, providing niches for new species which possibly alter the sediment even further.

The results of the *Lycopodium* extractions show that in the shallow (5 cm) tanks, significant bioturbation occurs in the presence of decomposing material throughout the sediment (Figure 5.3). This was expected, since large numbers of empty *Calliphora* puparia were found in these relatively small volumes of sediment.

In the deeper (15 cm) tanks, the disturbance was found to be less uniform (Figures 5.4 to 5.7), particularly in the absence of *Calliphora*, with a greater proportion of the spores persisting in the marker layers. In the tank which contained ER/13 (Figure 5.6), no spores were extracted from the top layer in the region of the tail of the carcass. This suggests that something may have eaten them. In contrast, the marker layers in the tank which contained ER/17 (Figure 5.7) were virtually

intact. Since ER/17 was not colonised by *Calliphora*, this indicates that neither phorids nor fungal hyphae significantly disturbed the sediment.

Some of the experimental findings remain puzzling. At the edge of the tank which contained ER/13 (Figure 5.6 c), the top marker layer seems to have shifted to the 4th spit. Figures 5.6 a, b and c and 5.7 b all show spores present in the very bottom spit, although no puparia were found this deep in these tanks.

Initially it was assumed that this was a consequence of the sampling method, and that the end of the tube used to core the sediment had pushed spores down the column. However, if this were the case, spores would have been found in the last spit of every core, which obviously was not so.

The method used was entirely new though, and it is probable that human error was the source of these inexplicable findings. Nevertheless, encouraging results were obtained from this investigation, the main drawback being the time taken to analyse the samples. Furthermore, the information gleaned from the excavation of the tanks (Section 3.4), a much less time-consuming exercise, led to the same conclusions. However, the advantage of using marker layers should not be underestimated. This provides opportunities for taking repeated samples over an extended time period without the need to disturb the carcass or terminate the decomposition process.

In spite of the evidence of significant bioturbation of the cave sediment in the vicinity of decomposing carrion, the excavation of the tanks was somewhat disappointing in that the activities of the invertebrate carrion community were ineffectual in the incorporation of the remains into the substratum.

Of the insects, only *Necrophorus* spp, the burying beetles, are known for their ability to inter animal remains (Putman, 1983). These beetles have previously buried small mammal carcasses in the threshold regions of the caves at Creswell (Terrell-Nield, pers. comm.), although none visited the carrion deposited in the present study. There are a number of reasons for this. *Necrophorus* will only utilise fresh carrion free from other arthropods (Kentner & Streit, 1990), and so would have been excluded from the carcasses at the front of Robin Hood's Cave by the rapid colonisation by blowflies. The carcasses deposited in the deeper regions of the two caves were probably too far underground for burying beetles, which are not troglophilic, to locate soon enough. Their absence from the front of Church Hole Cave was because this

experiment was begun in the winter, when *Necrophorus* are not active (Putman, 1978b, 1983).

A combination of factors prevented the interment of the remains by the invertebrate carrion community in the caves. One of these was the physical condition of the carcasses. At the front of the cave, apart from a few holes, the skin of the carcasses remained intact throughout the period of *Calliphora* infestation, and subsequently mummified with all the bones still within. Further into the cave, although much of the skin decomposed, the skeletons were largely held together by the remaining connective tissue and fungal hyphae. Thus it was effectively impossible for the individual bones to become interred by the activity of the dipterous larvae because the skeletons were still largely intact.

Furthermore, in the Frogpit and Back chambers, liquids which leeched from the carcasses during the initial stages of decomposition combined with the upper layers of the sediment to form a hard crust, similar to that seen in studies above ground (Bournemissza, 1957). While larvae evidently were able to penetrate this, it would have been impossible for inanimate objects, such as bones, to become interred by being covered with loose sediment shifted around by invertebrates.

Finally, although a number of the invertebrates associated with the carrion in the caves were seen to burrow into the sediment, it is possible that their activities were not conducive to the interment of bones on the surface because of their method of burrowing. Those invertebrates, such as burying beetles and earthworms, which are known to be instrumental in incorporating surface objects into the substratum actually excavate the sediment and bring material up to the surface from below. Thus any bones or artefacts become covered with sediment and consequently buried. In contrast, the dipterous larvae and the Coleoptera which were seen to burrow in the caves did so simply by pushing their way through the loosely packed sediment. This involved no turnover of material, and no sediment was transported up to the surface to cover the bones.

The persistence of animal remains on the surface in caves has been noticed by at least one other author. In a study of the taphonomy of microvertebrate bones, Levinson (1982) monitored the fate of owl pellets deposited on a cave floor. A number of invertebrates found in the present work, such as beetles, tineid moths,

parasitic wasps, pseudoscorpions and mites, were also attracted to the owl pellets, although dipterous larvae were absent. Levinson also concludes that interment is not readily effected by the arthropods attracted to the remains. He further suggests that vertebrate trampling, water and the topography of the cave floor are more important factors influencing the dispersal of bones, and that their incorporation into the sediment occurs only over a long period, even then being due to physical rather than biological methods.

In spite of the absence of any significant interment, some of the observations made during the experiments in Robin Hood's Cave may provide useful information for palaeontologists and palaeoecologists. In some cases, particularly in the Front and Frogpit chambers, individual bones, such as lower mandibles, ribs, vertebrae, and in one case part of the pelvic girdle, were found up to 25 cm away from the main carcass. It is likely that these isolated bones will become incorporated into the sediment at different rates from those still attached to the main skeleton. Thus bones from a single carcass could be found at different depths in the substratum, providing misleading evidence in the event of their later excavation, since it may appear that they originated from a number of animals, over a protracted time period.

As well as vertebrate remains, the presence of insect fragments in the substratum can give insight into the ecology of past environments (Shotwell, 1955). In the presence of carrion, the distribution of dipterous puparia and adult flies in the stratigraphy of cave sediment is widespread due to the deep burrowing behaviour of the mature larvae. If a similar distribution was observed in ancient sediment, it may appear that a species was present locally for a longer period than it actually was, and also that the species was very common throughout this period. Thus, the palaeoecological interpretation of deposits containing insect fragments, particularly from the Diptera, must be treated with caution if vertebrate remains are also present.

The results of the present work also have important implications for palynological investigations of sediments upon which decomposing carcasses may have lain. The degree of bioturbation beneath carrion was found to be particularly significant in shallow sediment. Such disturbance could obviously produce misleading results in palynological investigations, in which pollen stratigraphy is used to map the patterns of temporal distribution of local vegetation.

Evidence of the disruptive activity of large animals is often obvious to workers examining ancient deposits. For example, sediment filling rabbit burrows may differ in colour or texture from that in nearby areas (Stein, 1983). However, the tiny burrows made by Diptera and Coleoptera around a carcass are practically undetectable, even after only a short period of time, and may go unnoticed by palynologists.

The distribution of dipterous fragments within the stratigraphy provide important evidence regarding the extent of possible bioturbation within a sediment column. Examination of a section through an ancient deposit may reveal a band of sediment containing dipterous fragments. Since these are an indication of past bioturbation, palynological evidence from this particular band will obviously be treated with caution, although it may be assumed that the sediment above and below it is undisturbed. However, this may not be so, since the distribution of *Lycopodium* spores within the tanks in this study indicated that bioturbation occurred in some cases throughout the sediment, even in areas where no evidence of dipterous activity was found. Thus, layers of sediment at least 2 cm above and below any concentration of dipterous fragments should also be assumed to have been disturbed.

6.4 Conclusions and model

The results of this investigation suggest that small mammal carcasses deposited in temperate caves demonstrate characteristic patterns of decomposition, which are strongly influenced by distance underground and by season, and which differ conspicuously from decomposition processes observed in carrion exposed on the surface. Above ground, carrion decomposes rapidly, largely as a result of the activities of necrophagous arthropods. In the hypogean domain, decaying remains persist for a much longer period, and microbial decomposition is important. The initial decomposition of carrion deposited in the threshold region of caves is more akin to that observed above ground, although mummification is common, and may be inevitable.

A distinctive invertebrate community, comprising both cavernicolous and non-cavernicolous species, was associated with decomposing animal remains in all regions

of the caves. The species composition of this arthropod assemblage changes in a predictable successional pattern which is related to the distance underground and to season. The representation of troglophiles in the carrion community is proportionally larger in the hypogean region, particularly in winter.

The effect of decomposing animal remains on the cavernicolous invertebrate community is profound. In the threshold region large numbers of non-cavernicolous species are attracted to fresh carcasses deposited in the summer, although very few are present in the carrion community which is subsequently established. However, the over-representation of some of these species, such as *Calliphora vomitoria*, and later *Hofmannophila pseudospretalla* and *Thripia* sp, leads to a depression in local invertebrate diversity and equitability. In contrast, the presence of fresh carrion in the threshold region in winter attracts very few invertebrates, none of which were necrophagous in this study. Carrion removal does not commence until much later in the year, when surface species, such as *Calliphora*, become active.

In the deep threshold region, the carrion community includes both cavernicolous and non-cavernicolous invertebrates. Again, very large populations of a few species are associated with carcasses deposited in the summer, although this far underground troglophilic species, such as Phoridae, were better represented in the caves at Creswell. In the winter, decomposition is largely microbial until location of the carrion by surface species.

In the present work, the majority of invertebrates found on the carcasses in the hypogean region in both winter and summer were cavernicolous species. These included troglophilic Phoridae, Sciaridae and Heleomyzidae, and later the staphylinid cave beetle *Quedius mesomelinus*.

The results of this work have been incorporated into a model (Figure 6.8), which proposes decomposition pathways for small mammal carrion deposited in the threshold, deep threshold and hypogean region of shallow temperate caves. Included are the dominant species in the succession on carrion, the changes to the physical appearance of a carcass, an indication of the rate of carrion removal and the state of the remains after one year.

This information may be of interest to other ecologists investigating decomposition processes, and to biospeleologists studying cavernicolous community

dynamics. Additionally, the pattern of invertebrate colonisation under different conditions is of potential use to forensic scientists, and possibly palaeoecologists.

Palaeoecologists may also find relevant the results of the work carried out on the bioturbation of sediments by invertebrate decomposers. The presence of a virtually intact skeleton within an ancient deposit may be seen as evidence that little disturbance to the sediment has occurred. The absence of characteristic patterns of carnivore breakage and gnaw damage on the bones may further support this assumption. However, this study demonstrates that although a skeleton found in the threshold region of a cave may be intact and unmarked, considerable bioturbation of the sediment immediately beneath it may have occurred, due to the burrowing behaviour of members of the invertebrate carrion community.

Figure 6.8 - Explanatory notes

Figure 6.8 maps changes in the dominant species of the carrion community over one year in the three cave regions at Creswell, in summer and winter. In summer, (Chapter 3), carcasses were deposited upon sediment of varying depth. This did not affect the fungal or invertebrate communities associated with the remains.

Except where indicated, all species bred on the carrion. For details of trophic relationships, refer to Figures 6.1 to 6.3.

The species are listed in the order in which they appeared upon the carcasses. Some were present for a short period, others for much longer. For further details refer to Chapters 3 and 4.

The initial fungal succession on all carcasses is listed. Except in the threshold regions, where very few fungi were seen after the onset of dipteran infestation, this succession continued after pupation of *C. vomitoria*.

KEY

* *Meta menardi* were present in large numbers in the vicinity of the carrion, although none were present on the carcass itself.

A Adults only present; no evidence of larvae.

\+ Estimated oviposition time.

70% Per cent of original carcass weight remaining at that time.

SPECIES AFFILIATIONS

Enchytraeus sp (Oligochaeta: Enchytraeidae)

Meta menardi (Araneida: Metidae)

Brachydesmus superus (Diplopoda: Polydesmidae)

Thripia sp (Thysanoptera: Thripidae)

Hofmannophila psuedospretella (Lepidoptera: Tineidae)

Sciaridae (Diptera) - *Bradysia brunnipes* & *Lycoriella leucotricha*

Phoridae (Diptera) - *Triphleba antricola* & *Megaselia rufipes*

Calliphora vomitoria (Diptera: Calliphoridae)

Aleochara spp & *Quedius mesomelinus* (Coleoptera: Staphylinidae)

Cryptophagus spp (Coleoptera: Cryptophagidae)

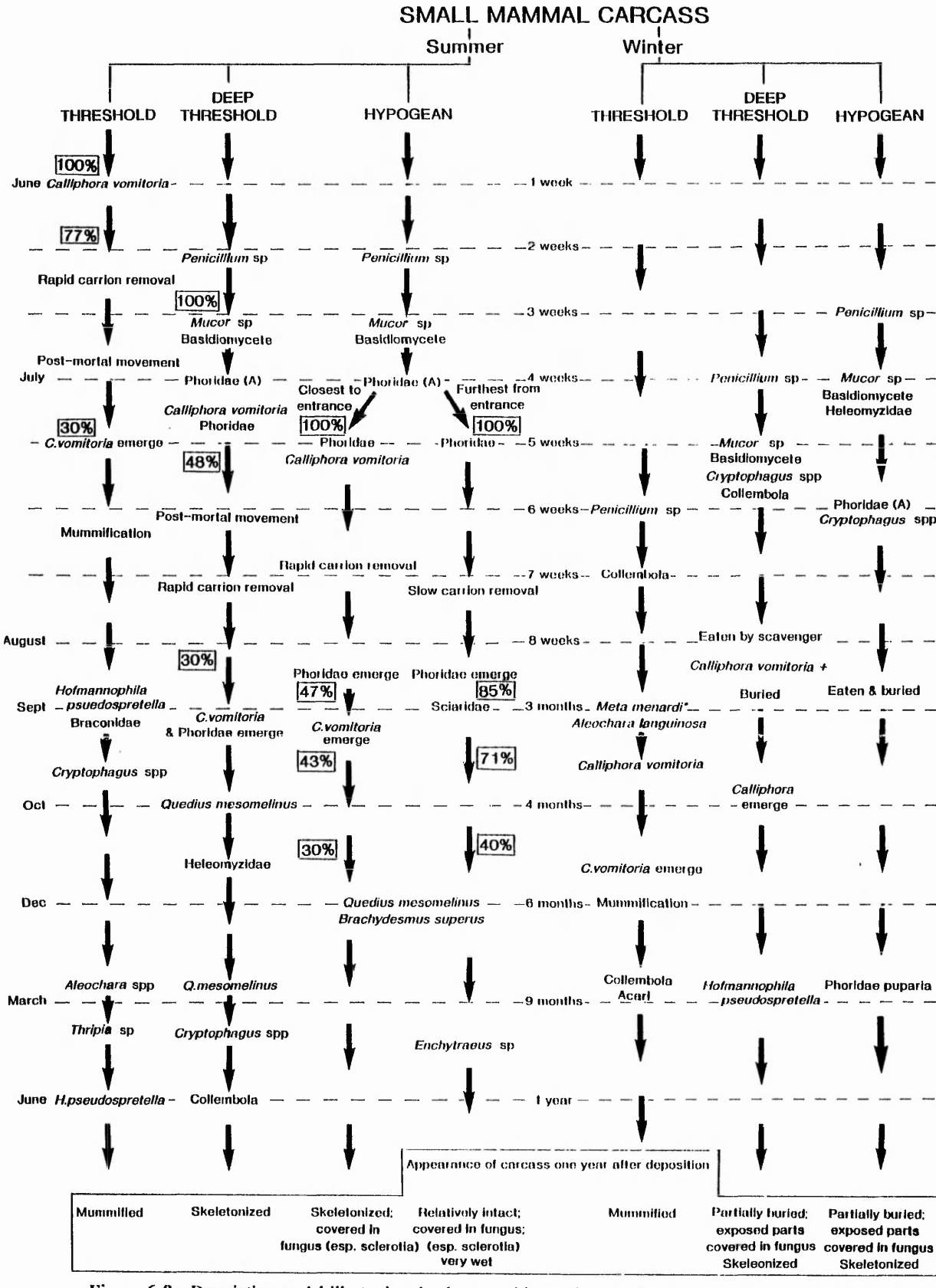


Figure 6.8: Descriptive model illustrating the decomposition pathways of carcasses in the three regions of the caves at Creswell in summer and winter. The model gives details of succession of the dominant species associated with the carrion, and of physical changes to the carcasses. The rate of decay of carcasses deposited in summer is indicated by percentage values, which represent the proportion of the original weight remaining (see also Explanatory notes, page 180).

CHAPTER SEVEN : THE BIOLOGY OF *QUEDIUS MESOMELINUS* (COLEOPTERA : STAPHYLINIDAE)

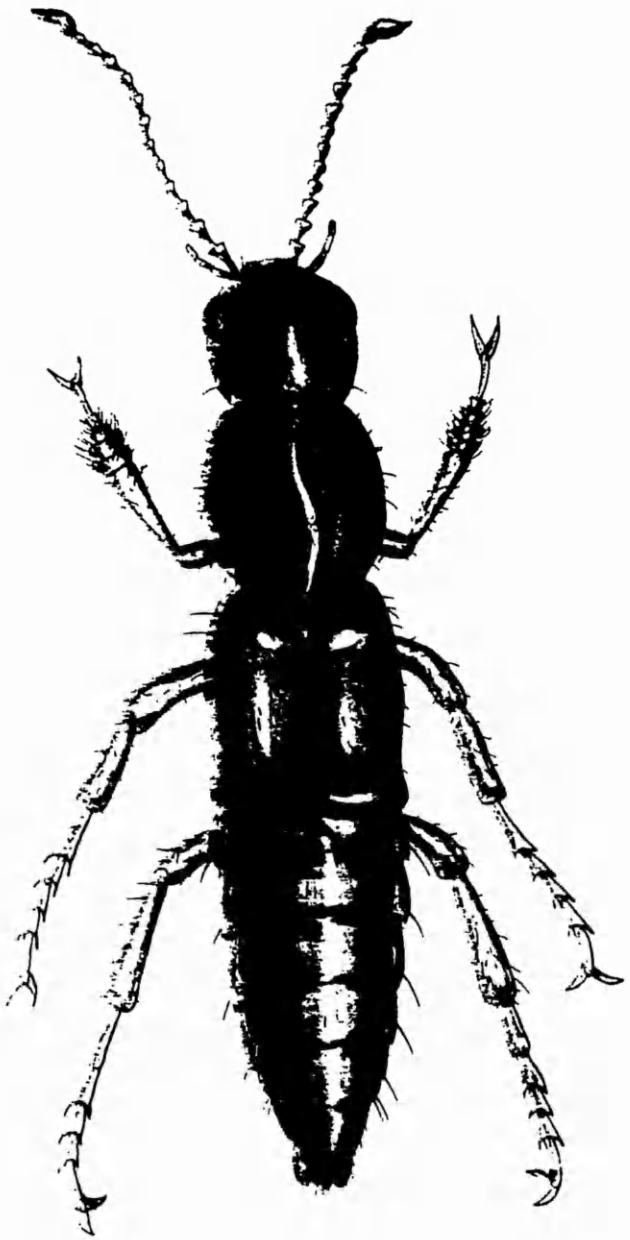


Figure 7.0: The external appearance of the adult cave beetle, *Quedius mesomelinus* (Coleoptera: Staphylinidae)

7.1 Introduction

The staphylinid beetle *Quedius mesomelinus* Marsham is described by Joy (1976) as approximately 8-11 mm long and entirely black and glabrous. The eyes, which are small for a staphylinid, occupy about one third of the side of the head. A full description of the larvae can be found in Kasule (1970b). Figure 7.0 shows the external appearance of the adult and Plate 33 (below), the stage II larva.

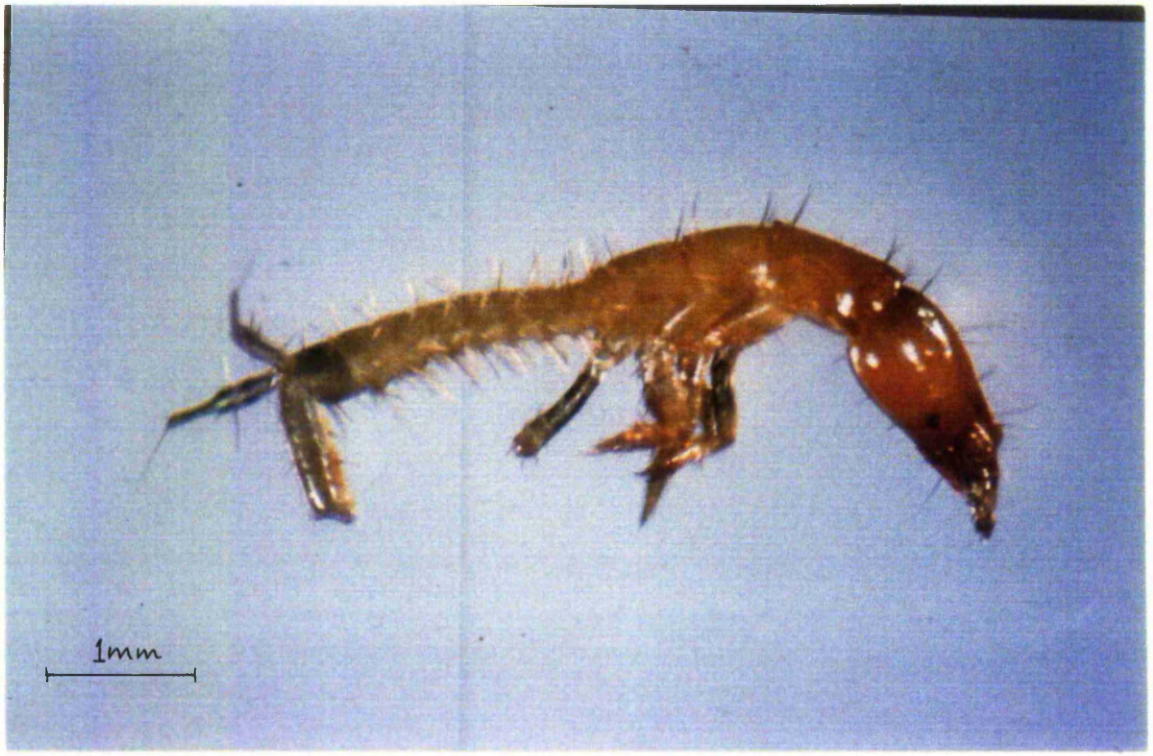


Plate 33: The external appearance of the stage II larva of *Quedius mesomelinus* (Coleoptera: Staphylinidae).

Kasule (1970b) comments that *Q. mesomelinus* is a "common cave species, but usually (found) in decaying vegetable matter; occasionally in birds' nests". It is reported as a frequent cavernicole by Vandel (1965). As well as being locally common, it is a widespread species; its status as a troglophile is well known all over

Europe (Hazleton, 1977). Hippa *et al* (1985) found it to be the most abundant coleopteran species in Scandinavian caves, and Jeannell (1926) quotes its presence in hypogean areas of Jura and the Alps. *Q. mesomelinus* has also been reported from both North and South America (Falcoz, 1914). Peck (1988) comments that since being introduced into the United States, the species has become prevalent in many eastern caves.

The species is known to be an important predator in underground habitats (Turquin, 1983), and in the caves at Creswell it was originally thought to feed on the dipteran larvae which colonise decaying carcasses. Turquin also suggests that *Q. mesomelinus* preys upon certain species of Collembola, which may explain why individuals have been found on carcasses in Robin Hood's Cave long after all dipteran infestation has apparently ceased (Sections 3.3 and 3.4).

Barr (1968), in his comprehensive paper on the evolution of troglobites, suggests that cavernicolous adaptations include increase in egg size and decrease in egg number, and population regulation via longer life span, infrequent reproduction and perhaps density-dependant cannibalism. He also maintains that reproduction is probably more or less seasonal in most troglobites. These characteristics were thus of particular interest in this study.

A laboratory population was established to study the life history and behaviour of *Q. mesomelinus* in an attempt to find out more about the annual activity and larval stages, and to discover within the population any adaptations to a hypogean existance.

7.2 Methods

Twenty-five *Quedius mesomelinus* adults were removed from beneath rat carcasses deposited the previous year in Church Hole Cave. These were transferred individually onto discs of filter paper on non-nutrient agar in plastic petri dishes. Each petri dish also contained a glass microscope slide balanced on the inverted bowl part of a plastic spoon to provide the beetles with a dry surface on which to move. The petri dishes were kept in the dark in a 10 °C incubator in the laboratory.

The beetles were fed approximately every 7-10 days on mealworms (*Tenebrio*

molitor larvae). Each time they were fed excess moisture was wiped from the inside of the lid of the petri dish, and any dead mealworms removed. The dish was also searched for eggs. If fungal growth had occurred on the dead mealworms and spread excessively onto the agar, the beetle was transferred into a fresh dish.

Any eggs laid were transferred onto non-nutrient agar in clean petri dishes until hatching, when the newly-emerged *Q. mesomelinus* larvae were moved into seperate petri dishes containing non-nutrient agar. Both eggs and larvae were kept at 10^{o}C in the dark. Larvae were fed small mealworms at the same time as the adults.

Each time a larval *Q. mesomelinus* was fed a note was made of the date, how much food had been taken since the last feeding and the developmental stage reached (eg LII, pupa, etc.). If ecdysis had occurred since the last feeding the shed skin was removed and the length and width of the head capsule measured (Figure 7.1).

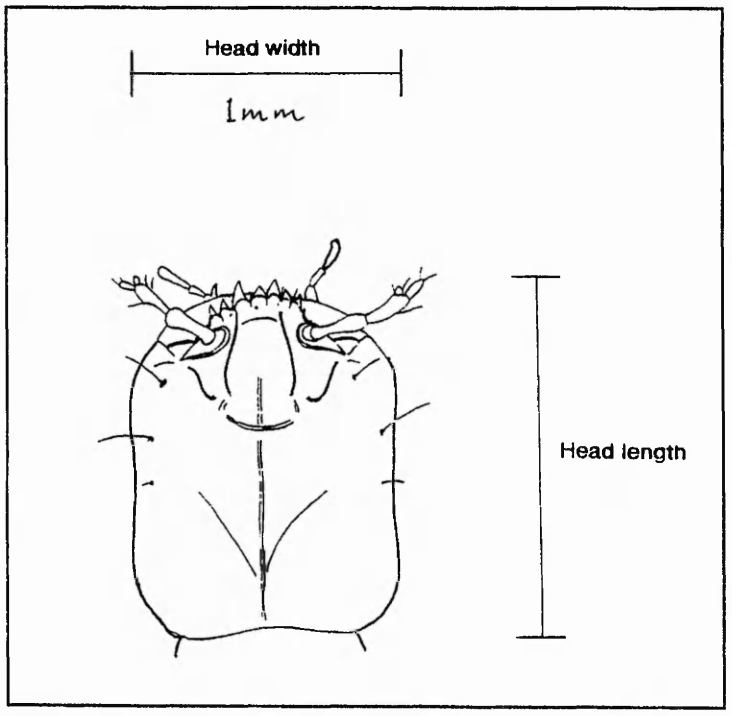


Figure 7.1: Head capsule of stage III larva of *Quedius mesomelinus* (Coleoptera: Staphylinidae), showing the two measurements made.

Also measured was the head width and total length of the pupa. It was at the pupal stage that the beetles were sexed. This was done by examining the region between the

cerci (Figure 7.2). It had been thought that adult beetles could be sexed by measuring the width of the front tarsi (Stanley, 1987). This, however, proved to be an unreliable indicator.

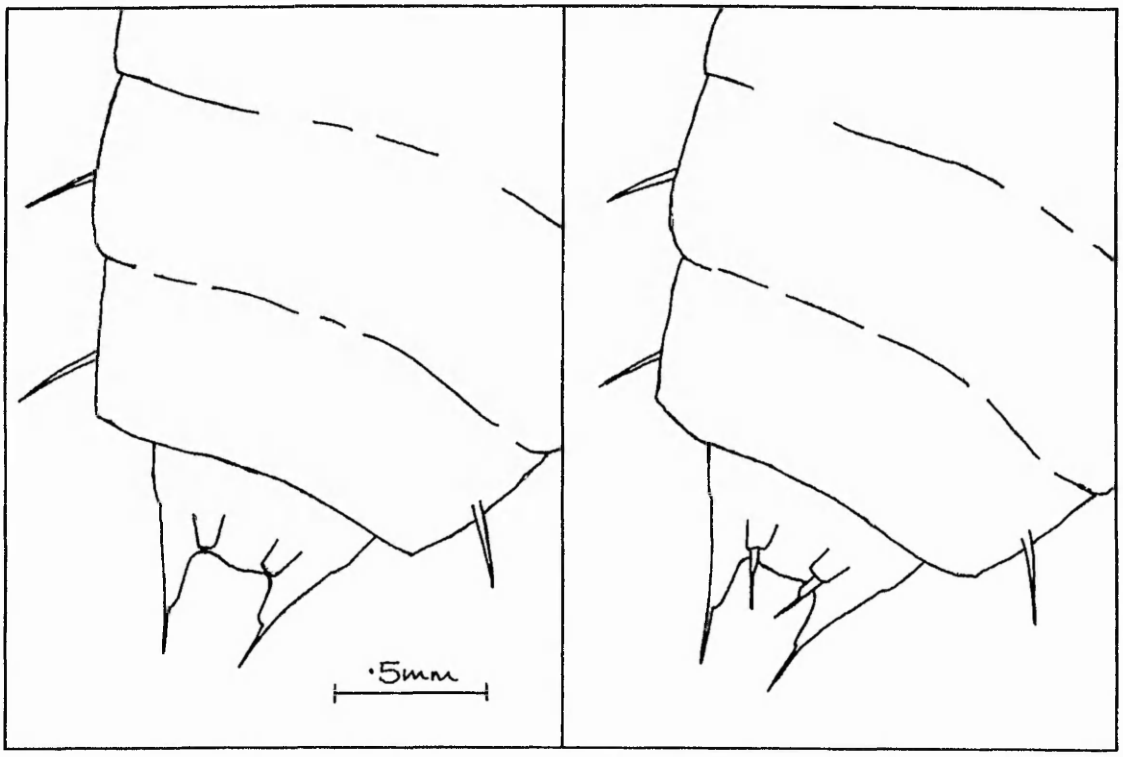


Figure 7.2: The terminal cerci of male (left) and female (right) *Quedius mesomelinus* (Coleoptera: Staphylinidae) puparia.

Once the offspring of the *Q. mesomelinus* from the cave had matured some of them were paired so that a breeding population could be established.

Experiments were also carried out whereby, immediately after being paired, beetles were kept for periods of time at high (20 °C) or low (10 °C) temperatures, so that their breeding behaviour and fecundity could be compared.

7.3 Results

Quedius mesomelinus eggs are cream, semi-transparent, ovoid (approxiamtely 1.25 x 0.85 mm in size) and have a leathery texture, being flexible rather than hard shelled. They have an even surface microsculpture of tiny, regularly spaced pits. Although eggs were found in all areas of the petri dish, they were usually buried about 1 mm into the agar, often just under the edge of the filter paper floor.

Figure 7.3 (overleaf) was drawn from data taken from females who were allowed to mate regularly. In this situation the proportion of fertile eggs produced fluctuated from 44% to 68% depending on the time of year. A higher proportion of eggs laid in spring and summer were viable.

When seperated from their mates female *Q. mesomelinus* continued to lay eggs until their death, as much as 20 months later. The proportion of these eggs which hatched dropped with increased time but not significantly so (Figure 7.4, overleaf).

The average number of eggs laid in a lifetime by the 13 F1 females was 30.46 (S.D.=23.65), and the average proportion that hatched was 54.94% (range = 0 - 80%). It was found that, unless removed to a seperate petri dishimmediately, newly hatched larvae would readily eat one another.

When kept at higher temperatures females apparently started laying eggs sooner after being paired (48.6 $\pm$ 60.29 days, n=6) than females kept at lower temperatures (104.0 $\pm$ 189.90 days, n=5). A Wilcoxon Rank Test was not significant at the p=0.05 level (T=27), therefore the null hypothesis (that there is no difference between the means) cannot be rejected. This implies that females kept at higher temperatures do not start laying eggs significantly earlier than females kept at lower temperatures, but these results are based upon very small sample sizes.

Although there was no difference in the number of eggs laid by the two sets of females, 67% (range = 60 - 80%) of eggs from females kept 20 °C hatched, in comparison to 41% (range = 0 - 75%) of those from females kept at 10 °C. However, a Wilcoxon Rank Test (T=21) showed no significant effect.

The results of the larval head capsule measurements are illustrated in Figures 7.5 and 7.6 (page nn). It can be seen that both the head width and the head length fall into well defined boundaries for each larval stage.

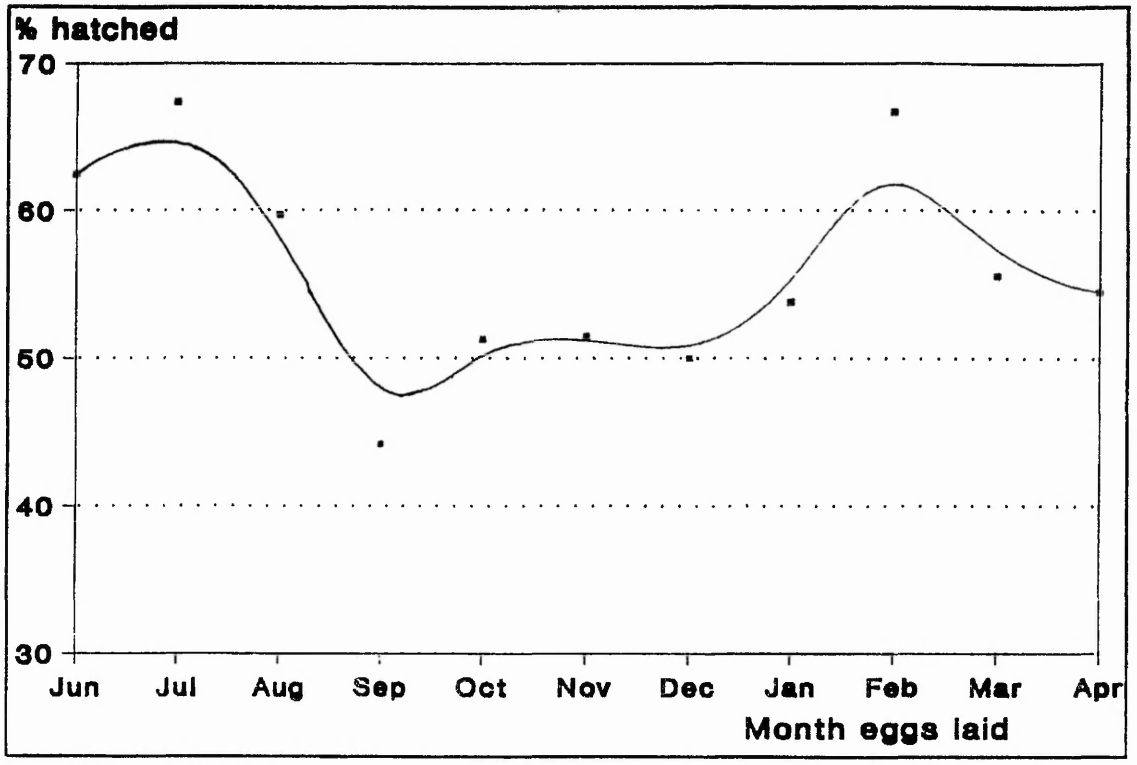


Figure 7.3: Relationship between the viability of *Quedius mesomelinus* eggs and the month of oviposition.

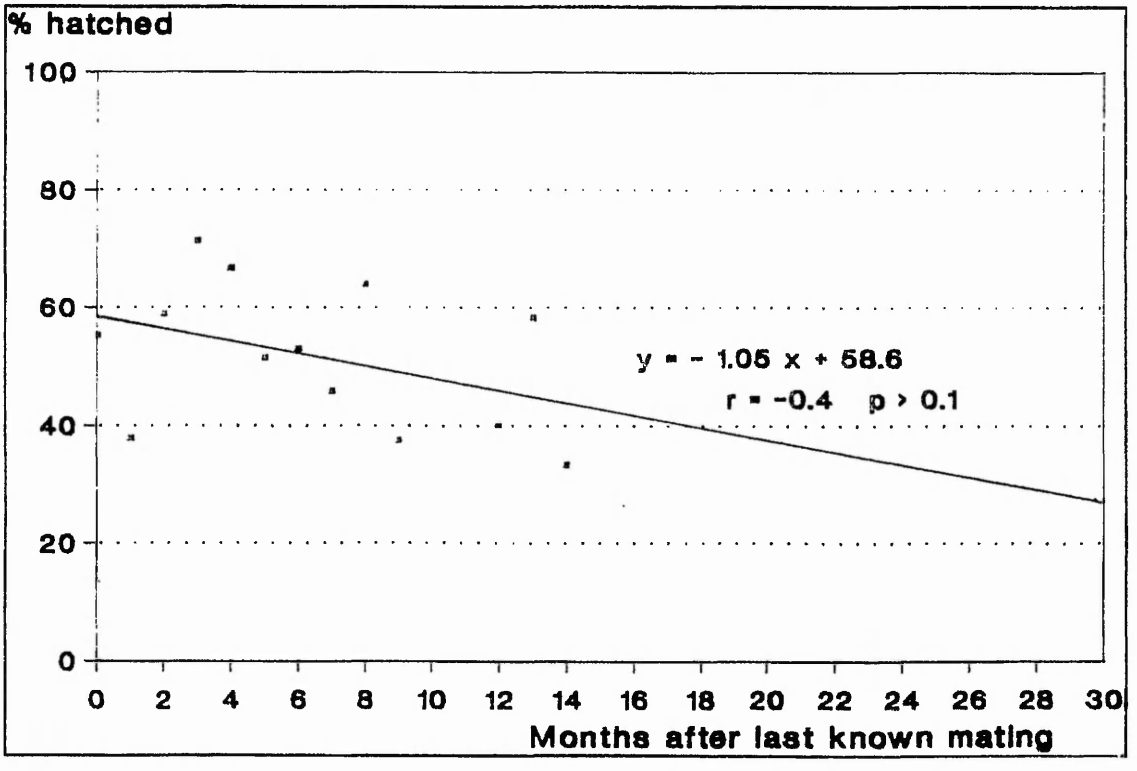


Figure 7.4: Decline in viability of *Quedius mesomelinus* eggs with increased delay between mating and oviposition.

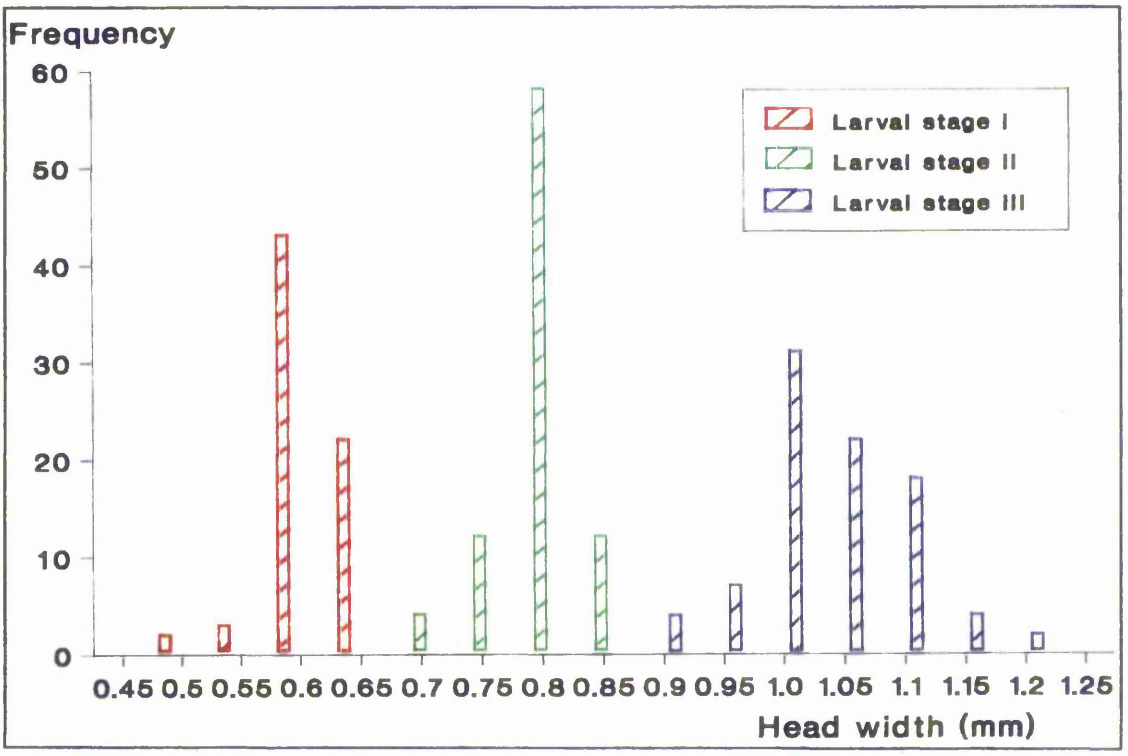


Figure 7.5: Head capsule widths of the three larval stages of *Quedius mesomelinus* (Coleoptera: Staphylinidae).

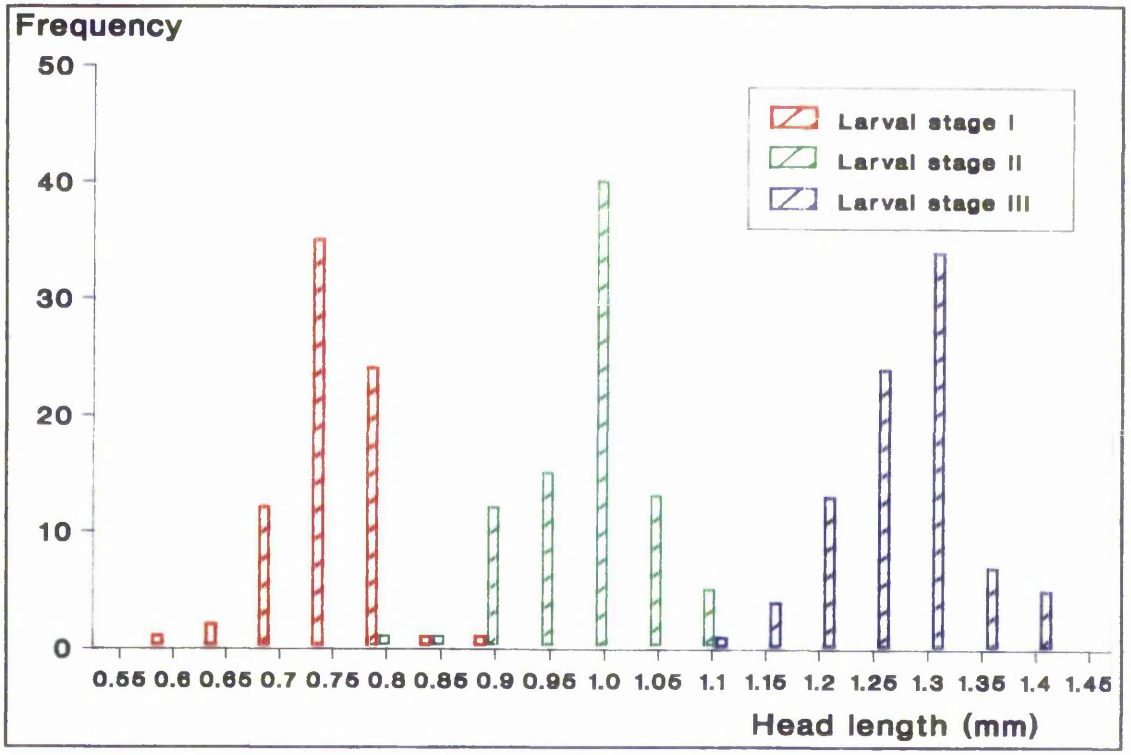


Figure 7.6: Head capsule lengths of the three larval stages of *Quedius mesomelinus* (Coleoptera: Staphylinidae).

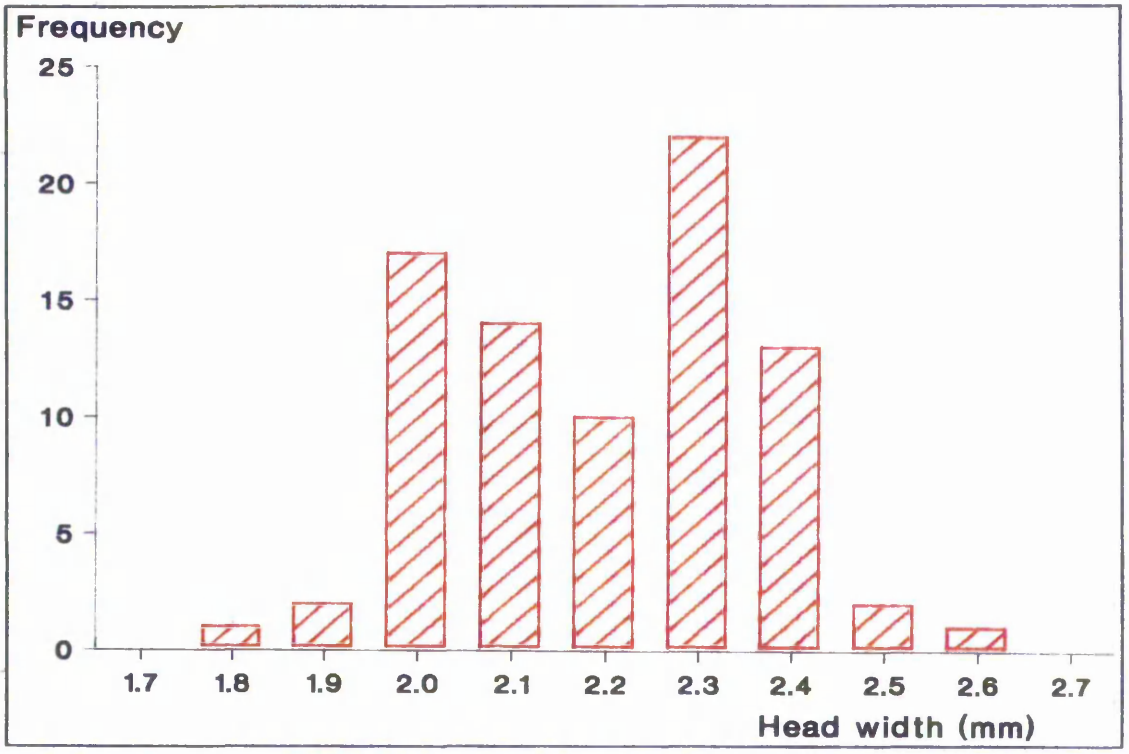


Figure 7.7: Head widths of *Quedius mesomelinus* (Coleoptera: Staphylinidae) puparia.

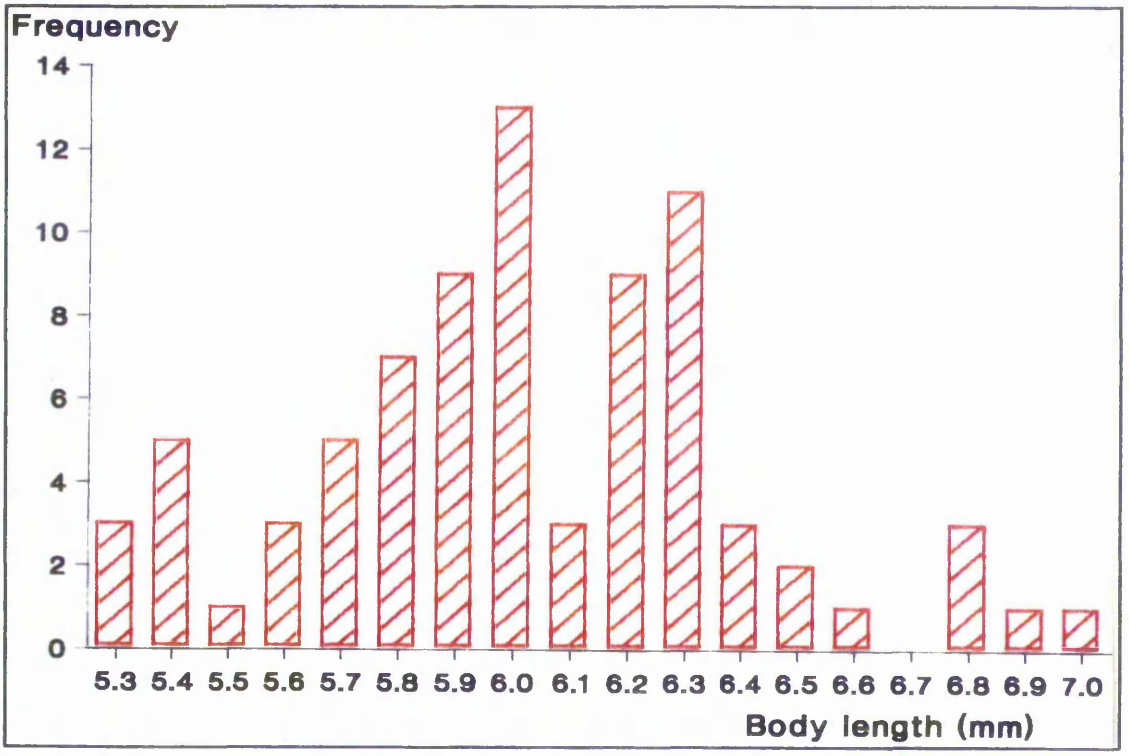


Figure 7.8: Total body lengths of *Quedius mesomelinus* (Coleoptera: Staphylinidae) puparia.

Statistical tests show that the stages are significantly different from one another for both parameters ($p > 99\%$).

Figures 7.7 and 7.8 (previous page) show the results of the measurements of head width and total body length taken from the pupae.

A summary of this data is presented in Table 7.1, which also shows the duration of each larval stage. It is apparent that the duration of the LIII stage is the most variable, with the other stages, particularly the pupal stage, being much more uniform.

Table 7.1: Average head width, head length and duration ($\pm$ 1.96 SD) of each larval stage of *Quedius mesomelinus* (Coleoptera: Staphylinidae).

	Egg	LI	LII	LIII	Pupa
Head Width (mm)		0.6±0.1	0.8±0.1	1.0±0.1	
Head Length (mm)		0.8±0.1	1.0±0.1	1.3±0.1	
Duration (days)	21±20	25±20	31±24	85±53	42±10

Further information on the demographic structure of the *Q. mesomelinus* population is shown in Figure 7.9 (overleaf), which demonstrates the changes throughout the year.

Q. mesomelinus lays eggs from late April through to late February of the following year, although the majority of eggs are laid during May and June. The first larval instar occurs predominantly during the summer, but stage I larvae were present from the middle of May to the beginning of March. Stage II larvae were found from July until January, although one or two individuals spent February, March and most of April as stage II larvae. These individuals are seen as stage III larvae during June and July. Most larvae, however, spent some time between August and the following May in stage III. The pupal stage was largely restricted to the period between March and mid-July.

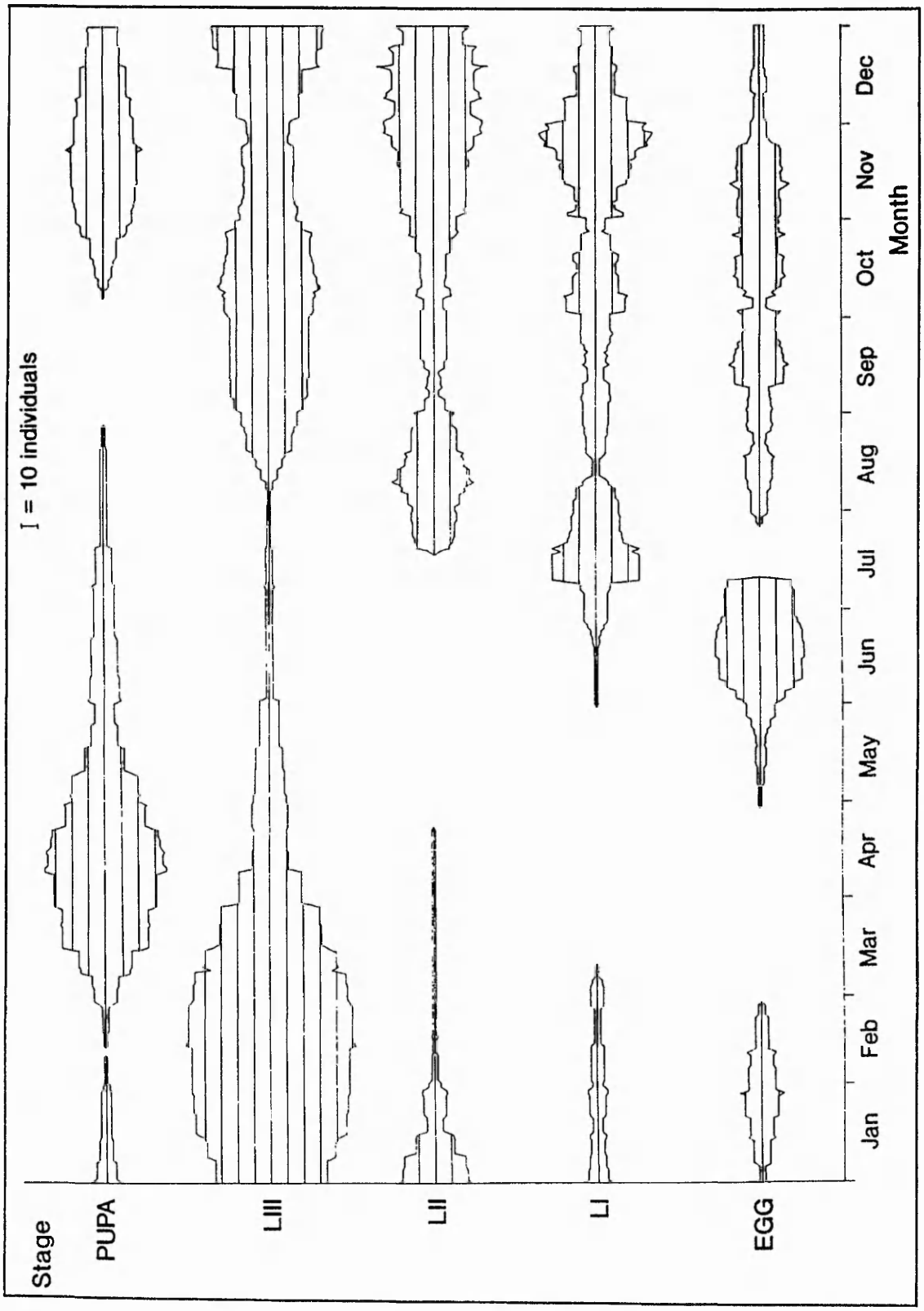


Figure 7.9: Annual demographic structure of a population of *Quedius mesomelinus* (Coleoptera: Staphylinidae) kept in an incubator at 10 °C (data collected from July 1987 to June 1989).

7.4 Discussion

7.4.1 Annual Activity and Larval Stages

The population arising from *Quedius mesomelinus* collected from Church Hole Cave and kept at 10 °C laid eggs in the early summer, completed its larval development from midsummer to late winter, and pupated in the spring. Table 7.2 compares this life history with other staphylinid species in the same size range.

Table 7.2: Annual patterns of *Quedius mesomelinus* compared with other staphylinids.

Species	Eggs laid	Larvae found	Reference
Q. mesomelinus	Early summer	Summer-spring	This study
Q. molochinus	Summer/autumn	Winter/spring	Kasule, 1970b
Q. fuliginosus	Early summer	Summer	" "
Q. lateralis	Summer/autumn	Winter/spring	Frank, 1968
Q. picipes	Summer/autumn	Winter/spring	" "
Q. fumatus	Summer/autumn	All year	" "
Othius punctulatus	Winter	Jan-Sept	Kasule, 1970a
Philonthus decorus	Spring/summer	Summer	Brunsting, 1981
Staphylinus aenocephalus		Early summer	Nield, 1976

Evidence from *Q. mesomelinus* trapped in Robin Hood's Cave (Stanley, 1987) largely supports this annual pattern. The majority of stage II larvae were caught between July and December, while stage III larvae were most abundant from August to February.

Thus, *Q. mesomelinus* differs from most other *Quedius* species studied in that it lays eggs earlier in the year and then takes much longer to complete its development. Certain aspects of the life history seem to be more allied to less closely related staphylinids, such as *Philonthus decorus*, which lays eggs at the same time as

Q. mesomelinus, but which generally has a shorter period of development, pupating in the autumn and overwintering as an adult in hibernation (Brunsting, 1981). This pattern is seen in those *Q. mesomelinus* individuals which reach larval stage III early, although no evidence of hibernation has been found.

From Figure 7.9 it is apparent that *Q. mesomelinus* generally spend January and February, the coldest and leanest months of the year (Figures 3.1 and 4.1), as stage III larvae and the spring as pupae. The timing of egg laying, hatching and duration of early larval stages appear to make little difference to this pattern, as larvae will simply lengthen or shorten the time spent in stage III in order to pass the beginning of the year in this stage and pupate in the spring. Larvae which reach stage III early, ie in late summer/autumn, will spend a very short period of time in this stage in order to pupate during the early winter and emerge as adults before the coldest time of the year.

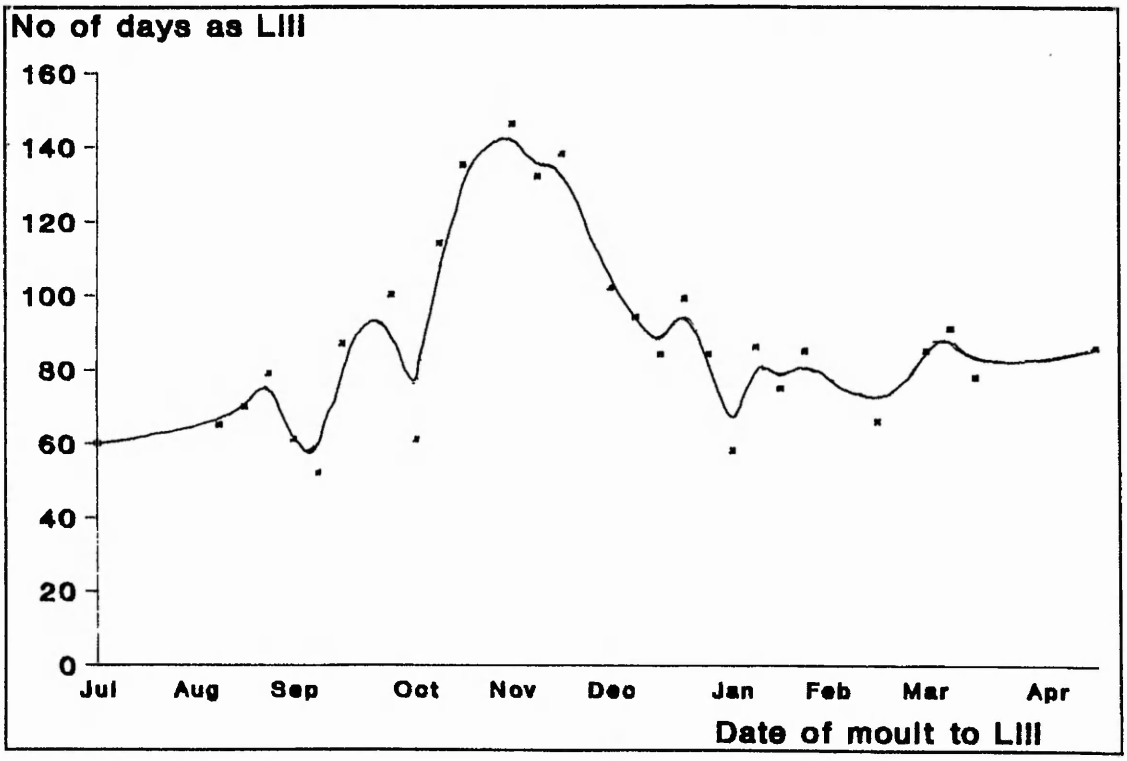


Figure 7.10: Relationship between the date of moult to LIII and the time spent in that instar by *Quedius mesomelinus* (Coleoptera: Staphylinidae).

Similar strategies are adopted by other coleoptera, for example, *Staphylinus olens* (Staphylinidae) (Nield, 1976), and *Nebria brevicollis* (Carabidae) (Penney, 1966).It is likely, however, that rather than it being advantageous to spend winter as an LIII, it is extremely disadvantageous to spend it as a newly emerged adult. All the energy resourses built up in the LIII are used during metamorphosis while the animal is in the pupal stage. When the young adult emerges it needs to rebuild those enery resourses reasonably quickly, something which would obviously be difficult during the early part of the year as the availability of food is greatly reduced (Chapter 3). The minimal variation observed in the timing of the pupal stage (Table 7.1) implies that it is not possible for the animal to simply lengthen or shorten the time spent as a pupa in order to emerge as an adult at the optimal time of the year, as do some Lepidoptera (Chapman, 1971). However, the animal is able to alter the duration of the third larval stage in this way, and seems to do so to ensure it does not pupate at such a time as to emerge in an unfavourable season, ie January or February.

Observations upon the captured *Q. mesomelinus* showed that for some time (up to a number of weeks) before pupation, stage III larvae stopped eating and appeared to be in a 'resting' phase. Thus, once sufficient energy reserves have been built up for metamorphosis, a partial diapause is entered until pupation. This behaviour is seen in a number of other species, e.g. *S. olens* (Nield, 1976) and, in the case of *Q. mesomelinus*, may have adapted in response to the paucity of the cave environment at this time of the year.

This is obviously not the whole picture, however, or all *Q. mesomelinus* would overwinter in the pupal stage when no food is required, and emerge in the spring.

It is possible, therefore, that there is a critical temperature, below which *Q. mesomelinus* cannot survive. Should the temperature in some regions of the cave drop below this limit, adults and larvae are capable of moving further underground where it is generally warmer during the winter months (Figures 3.1 and 4.1). Pupae obviously do not have this option, so it would be advantageous to minimize the chances of spending the cold months in this vulnerable state by ensuring that pupation occurs either before or after this period. Figure 7.9 shows that one or two individuals did spend January and February as pupae; these animals may have died if in the wild.

7.4.2 Cavernicolous Adaptations

The adult of *Quedius mesomelinus* does not show any obvious adaptations specific to cave life. It is darkly pigmented, relatively large and an active predator. Its eyes, although smaller that other *Quedius* species (Joy, 1976) are still fairly big.

Like other Staphylininae, *Q. mesomelinus* larvae have four ocelli on each side of the head, and have a lightly pigmented body. The only adaptation which appears to be genuinely advantageous to a cavernicolous existance is the appearance of the setae on the abdomen (Figure 7.11).

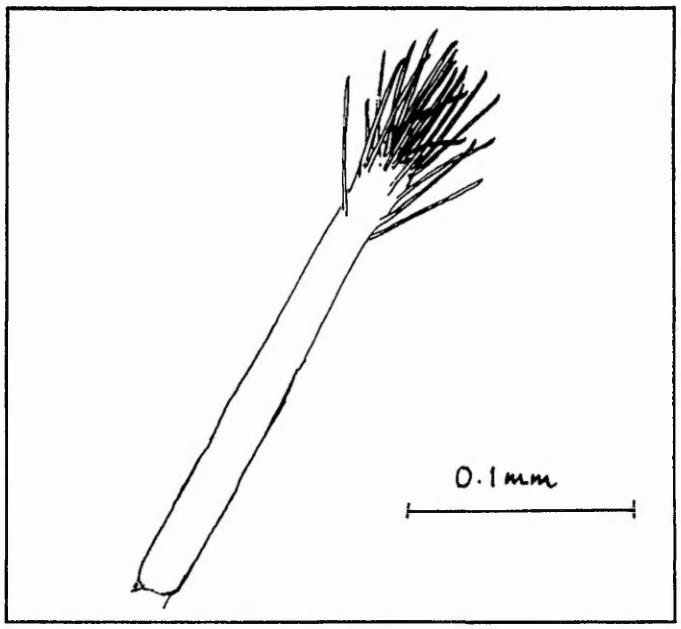


Figure 7.11: Appearance of the specially adapted setae found on the abdomen of the larvae of *Quedius mesomelinus* (Coleoptera: Staphylinidae). (After Stanley, 1987.)

These setae are also found on other *Quedius* spp larvae and are probably proprioreceptors. In *Q. mesomelinus* they are expanded terminally and frayed, possibly making them more sensitive to air movement or low frequency sound. This would obviously be useful in caves, where sight becomes obsolete. This feature is seen in other *Quedius* species, for example, *Q. brevis* and *Q. puncticollis*, which live in dark habitats, such as wasps' and ants' nests (Joy, 1976).

Figure 7.12 (overleaf) shows the development pattern of *Q. mesomelinus*, with comparative data for two other staphylinds, *Staphylinus olens* and *Creophilus*

maxillosus. Although sharing similar food preferences, both *S. olens* and *C. maxillosus* are larger than *Q. mesomelinus*, and would be expected to take longer to complete their development.

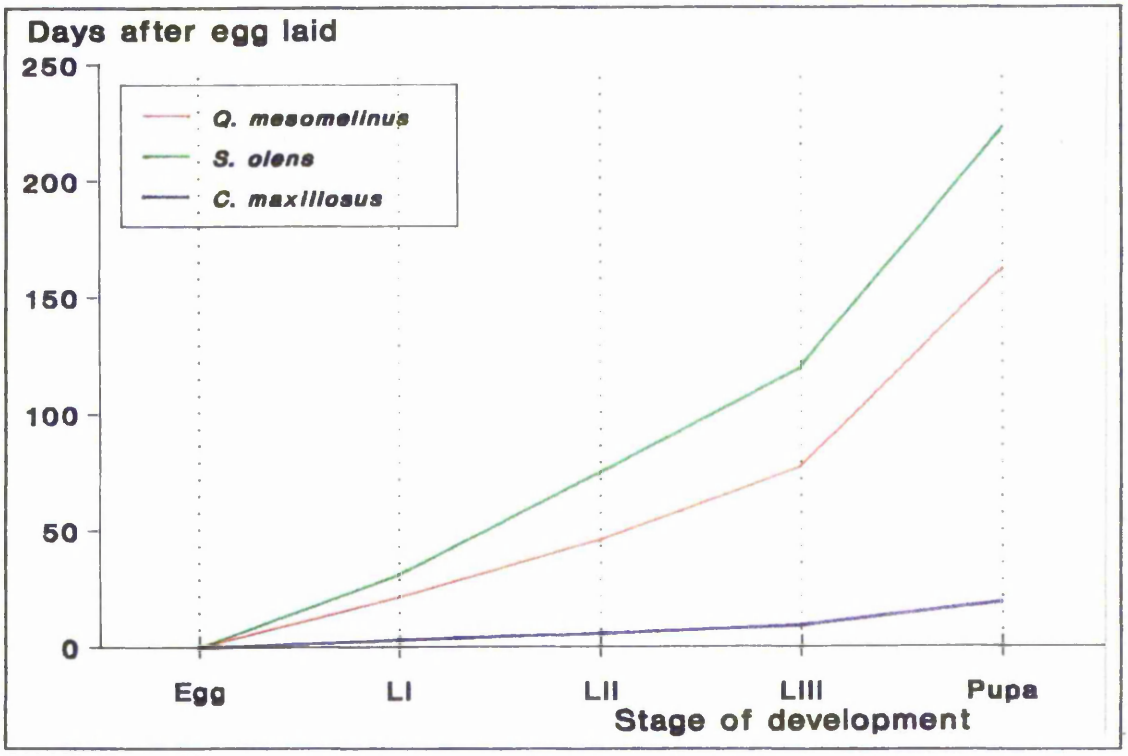


Figure 7.12: Development patterns of the staphylinid beetles *Quedius mesomelinus* (this study), *Staphylinus olens* (Nield, 1976) and *Creophilus maxillosus* (Dajoz & Caussanel, 1968).

It can be seen from the information in Figure 7.12, however, that the development time for *C. maxillosus* appears to be very short. This is likely to be a result of the temperature regime in which the experimental animals were kept while this data was collected. Dajoz & Caussanel (1968) kept their population at 25 °C, whereas the *Q. mesomelinus* in this study were kept at a temperature approximating the average cave temperature of 10 °C. The much larger *S. olens*, also kept at approximately 10 °C, showed a similar pattern to that of *Q. mesomelinus*.

Thus the apparently slow development time, rather than being a genetic adaptation to cave life, is more likely to be a result of a cavernicolous existance, since the lower summer temperatures encountered in temperate caves would slow down biological processes and thus retard development during these months. It would be interesting to determine if the rate of development is wholly temperature controlled or whether there is a degree of genetic influence. For this, equivalent figures for populations of *Q. mesomelinus* captured from open-air habitats and reared under different temperature regimes, and also for cavernicolous populations reared at normal external temperatures would be needed. Although the experiments which were carried out (Section 7.4.1) produced inconclusive results, promising trends were observed which suggested temperature can have an effect upon breeding behaviour and success.

Nield (1976), working with *Staphylinus olens*, suggests that external factors, such as changes in temperature or day length, may trigger pupation. Since the laboratory population of *Q. mesomelinus* was kept at constant temperature (10 °C) and in constant darkness, triggers for ecdysis, pupation, emergence and egg-laying must be largely internal. This adaptation in *Q. mesomelinus* would aid its cavernicolous existance.

However, the offspring of those animals which spent a long time as stage III larvae began to drift, suggesting that internal triggers need to be re-set after a generation. Seasonal temperature fluctuations in a cave of this size should provide the necessary stimulus to affect this. This is analogous to rhythm-setting by temperature in constant light conditions (Chapman, 1971). For animals in deep caves, however, no such external triggers are evident, and internal 'clocks' must wholly govern life cycles.

The ability of females to retain viable sperm for long periods after mating would aid the survival of any cavernicolous animal. Unless they are habitual bat roosts, caves are relatively energy-poor, and populations are expected to be small and widely distributed. The chances, therefore, of one *Q. mesomelinus* encountering another of the opposite sex on a regular basis are small. The ability to fertilize eggs with sperm which has been stored for at least 18 months means that mating need only occur once in a lifetime.

When studying *S. olens*, Nield (1976) noticed that after mating the females laid

viable eggs in the autumn, but then egg- laying ceased. Eggs which were laid the following spring were non-fertile. He suggests that to produce fertile eggs in the spring, *S. olens* would need to mate continuously through winter or have a spring mating. Alternatively, some sperm storage may occur, but not enough is transferred in one mating to fertilize eggs the following spring. Obviously, in an underground, nutrient-poor habitat such as a cave, the strategy observed in *S. olens* is inferior to the long-term storage of sperm carried out by *Q. mesomelinus*.

It would seem that the cave environment, with its low energy input and intermittent food sources, would support species favouring 'scramble' or r-selection (Putman, 1983). One of the characteristics of this is the production of large numbers of relatively short-lived offspring. When compared with other staphylinids, however, it can be shown that *Q. mesomelinus* does not do this: female *Q. mesomelinus* lay an average of 28 eggs in a lifetime, and live for at least two seasons; female *S. olens* lay between 150 and 200 eggs per season (Lincoln, 1961); and female *C. maxillosus* produce approximately 185 eggs per season (Dajoz & Caussanel, 1968).

This can perhaps be explained by looking more carefully at the cave environment. Apart from apparently fluctuating food availability the cave is a fairly stable habitat, with almost constant temperature and relative humidity away from the entrance. Because of the low temperatures and the relative paucity of species, nutrient sources are generally long lasting and utilised in some way by a large proportion of the species present. Thus, a carcass will be colonised for some time by a number of different species, although each individual species may not utilise it for long. As *Q. mesomelinus* is known to take a variety of prey, an animal carcass, with its succession of different colonisers, will support the beetle for much longer than it will other species which are more selective feeders.

So, while species such as *Triphleba antricola* (Diptera: Phoridae) will be r-selected to exploit a short-lived food source (the flesh of dead animals), *Q. mesomelinus* shows a K-selected reproductive strategy.

Barr (1968) lists seven features which he concludes are later adaptations in troglobite evolution. Of these the cavernicolous population of *Q. mesomelinus* which was studied shows at least four: infrequent reproduction, larval cannibalism, decrease in egg number and long life span, in relation to other staphylinids. Without

conducting a comparative study of a non-cavernicolous population, however, it is impossible to determine whether these have evolved in response to the selective pressures of the cave environment or whether they are in fact pre-adaptations.

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APPENDIX ONE : FAUNA
ROBIN HOOD'S CAVE

The following is a complete list of all species found in Robin Hood's Cave both before and after the carcasses were deposited. The three chambers, Front, Frogpit and Back, are 10, 35 and 50 m respectively from the entrance to the cave.

KEY:

- \- Present in Baseline only
- \+ Present only after deposition of carcasses
- * Present both in Baseline and after deposition of carcasses
- # Present on carcasses only (not found in traps)

	Front	Frogpit	Back
Annelida:			
Lumbricidae			
Allolobophora caliginosa			+
Enchytraeidae			
Enchytraeus sp			#
sp indet	-		
Arachnida:			
Acari			
Sp indet (larva)		-	
Prostigmata	+	*	+
Astigmata	*	*	*
Mesostigmata	*	*	*
Cryptostigmata	-	-	-
Chelonethi			
Chthonius ischnoceles	+		

continued.....

	Front	Frogpit	Back
Opiliones			
Phalangidae			
Opilio parientinus	+		
Mitostoma chrysomelas		-	-
Araneida			
sp indet (juvenile)	+		
Dictynidae			
Ciniflo sp	*		
Lycosidae			
Lycosa agrison	-		
Agelenidae			
Tegenaria sp	+		
Nesticidae			
Nesticus cellulanus	+		
Metidae			
Meta menardi	-	-	
Argiopidae			
Araneus sp	-		
Linyphiidae			
Prosopotheca sp		-	
Porrhomma egeria	*	-	*
Lepthyphantes sp (Gp I)	+		
Lepthyphantes leprosus	+		
Lepthyphantes obscurus	+		
Lepthyphantes pallidus	*	*	*
Crustacea:			
Isopoda			
Trichoniscidae			
Androniscus dentiger			+

continued.....

	Front	Frogpit	Back
Oniscidae			
Oniscus asellus	-		
Myriapoda:			
Chilopoda			
Lithobiidae			
Lithobius variegatus	-		+
Lithobius forficatus		+	
Lithobius dubosqui	-		
Lithobius crassius		-	
Diplopoda			
Craspedosomatidae			
Polymicrodon polydesmoides		-	-
Polydesmidae			
Brachydesmus superus			+
Polydesmus sp	-		
Iulidae			
sp indet	+		
Insecta:			
Diplura			
Campodea sp	-	-	-
Collembola			
Hypogastruridae			
Hypogastrura purpurescens	*	*	*
Onychiuridae			
Onychiurus sp	-	*	*
Isotomidae			
Isotoma sp	-	-	-
Entomobryidae			
Entomobrya sp	-		
Lepidocyrtus sp	-		

continued.....

	Front	Frogpit	Back
Entomobryidae (cont)			
Lepidocyrtus curvicollis	*	*	*
Lepidocyrtus cyaneus	*	*	*
Pseudosinella alba	*	*	*
Neelidae			
Neelus sp	*	*	*
Sminthuridae			
Arrhopalites sp	-	*	*
Psocoptera			
Psyllopsocidae			
sp indet	+	-	
Hemiptera			
Aphididae			
Aphis sp	*		
Thysanoptera			
Thripidae			
Thripia sp	*	*	
Aeolothripidae			
sp 1 indet	+		
sp 2 indet	+		
Mecoptera			
Panorpa sp	*		
Lepidoptera			
Pyralidae			
sp indet	*		
Tineidae			
Hofmannophila pseudospretella	*	+	
Diptera			
sp indet (pupa)	-		

continued.....

	Front	Frogpit	Back
Tipulidae			
Tipula sp	*	-	
sp 1 indet	+		
sp 2 indet			+
Anisopodidae			
Anisopus fenestralis	*	+	
Mycetophilidae			
Macrocera maculata	+		
sp 1 indet	-	-	
sp 2 indet			-
sp 3 indet		-	-
sp 4 indet	-	-	-
sp 5 indet			+
sp 6 indet	+	+	+
sp 7 indet	+		+
sp 8 indet		+	
Sciaridae			
sp indet (larva)	-		
Lycoriella leucotricha	*	*	*
Bradysia brunnipes	*	*	*
Trichosia absurda	+	+	
Cecidomyiidae			
sp 1 indet	*	-	
sp 2 indet			*
sp 3 indet	+		
sp 4 indet	+		
Psychodidae			
Psychoda sp	*	-	
Culicidae			
Culex sp	*	-	

continued.....

	Front	Frogpit	Back
Tabanidae			
sp indet	+		
Empididae			
Empis sp	*		
sp indet		+	
Dolichopodidae			
Psylopus sp	+		
Psylopus longulus	+		
sp indet	+		
Phoridae			
Triphleba antricola	*	*	+
Megaselia rufipes	+	+	+
Megaselia brunneipennis	+	+	+
Megaselia bifida		+	+
Megaselia sp 1 indet	*	*	*
Megaselia sp 2 indet	+	+	
Megaselia sp 3 indet	+		
Megaselia sp 4 indet	+		+
Megaselia sp 5 indet	+		
Anthomyzidae			
sp indet	+		
Calliphoridae			
Calliphora vomitora	+	+	+
Dryomyzidae			
sp indet		+	
Heleomyzidae			
sp 1 indet		-	
sp 2 indet		*	
sp 3 indet		+	
sp 4 indet		+	

continued.....

	Front	Frogpit	Back
Sepsidae			
Saltella sphondylii	+		
Sphaeroceridae			
Limnosina silvatica		+	
Leptocera fontinalis		+	
sp 1 indet			*
sp 2 indet		+	
Drosophilidae			
sp indet	+		
Siphonaptera			
Leptosyllidae			
sp indet			-
Ichnopsyllidae			
sp indet			-
Hymenoptera			
Ichneumonidae			
sp indet	+		
Braconidae			
sp 1 indet	+	+	
sp 2 indet	+	+	
sp 3 indet	+		
Mymaridae			
sp indet	-		
Chalcidoidea			
sp indet	+		
Torymidae			
sp indet	+		
Pteromalidae			
sp indet		+	

continued.....

	Front	Frogpit	Back
Proctotrupidae			
sp indet		-	
Sphecidae			
sp indet	+	+	
Eupelmidae			
sp indet	-		
Ceraphronidae			
sp indet	+		
Coleoptera			
Carabidae			
Pterostichus madidus		-	
Pterostichus melanarus	-		
Staphylinidae			
Aleochara spadicea	+		
Aleochara languinosa	+		
Aleochara villosa		+	
Aleochara cuniculorum		+	
Aleochara moerens	+		
Oxypoda opaca	+		
Ocalea badia	#		
Calodera uliginosa	+		
Bessobia sp		+	
Acrotona clientula	+		
Acrotona sp	+	+	
Tachyporinae sp indet (larva)		-	
Omalium excavatum	+		+
Omalium tricolor			+
Xylostiba monolicornis		+	
Quedius mesomelinus	-	*	*
Oxytelus tetracharinatus	+	+	

continued.....

	Front	Frogpit	Back
Leptinidae			
Leptinus testaceus			-
Cholevidae			
Choleva jeanneli		+	
Choleva angustata		-	-
Choleva oblonga		#	
Choleva glauca	+	-	
Catops chrysomeloides		+	
Catops tristis	+		
Cryptophagidae			
Cryptophagus acutangulus	*	*	*
Cryptophagus ruficornis	*	*	
Cryptophagus dentatus	+	+	
Cryptophagus distinguendus	-	+	
Cryptophagus badidus	-		
Cryptophagus pilosis	-		
Crypotphagus saginatus	-	-	
Cryptophagus sutatus	-	-	
Lathridiidae			
Cartodere ruficollis	+		
Holoparamecus caularum	#		
Salpingidae			
Rhinosimus planirostris	-		
Nitidulidae			
Meligethus aeneus	+		

The following is a complete list of the number of individuals of each species caught in the pitfall traps in each chamber before the carcasses were deposited. Pitfall traps were emptied during the first or second week of each month.

December - January

Group/species	Front	Frogpit	Back
Acari sp indet (larva)		3	
Prostigmata		57	
Porrhomma egeria			1
Lepthyphantes pallidus		1	
Onychiurus sp		2	
Lepidocyrtus curvicollis	12	7	2
L. cyaneus	29	9	
Neelus sp		3	
Arrhopalites sp			7
Thripia sp		1	
Psychoda sp	3		
Culex sp		1	
Megaselia sp 1 indet	2		
Heleomyzidae sp 1 indet		1	
Leptosyllidae sp indet			1
Ichnopsyllidae sp indet			1
Tachyporinae sp indet (larva)		1	
Quedius mesomelinus (LI)		3	
Cryptophagus acutangulus	1		
C. ruficornis		1	

January - February

Group/species	Front	Frogpit	Back
Mesostigmata		1	2
Mitostoma chrysomelas			1

continued.....

Group/species	Front	Frogpit	Back
Hypogastrura purpurescens		1	
Lepidocyrtus curvicollis	7	5	
L. cyaneas	8	2	1
Pseudosinella alba	1	1	2
Neelus sp			7
Arrhopalites sp		5	14
Thripia sp	1		
Diptera sp indet (pupa)	1		
Psychoda sp		1	
Triphleba antricola		1	

February - March

Group/species	Front	Frogpit	Back
Astigmata			1
Mesostigmata		1	1
Hypogastrura purpurescens		2	
Lepidocyrtus curvicollis	2	16	
L. cyaneus	5	10	
Pseudosinella alba	1		
Neelus sp		3	3
Arrhopalites sp		16	17
Sciaridae sp indet (larva)	1		
Culex sp		1	
Megaselia sp 1 indet	1		
Proctotrupidae sp indet		1	

March - April

Group/species	Front	Frogpit	Back
Porrhomma egeria			2
Lepthyphantes pallidus		2	

continued.....

Group/species	Front	Frogpit	Back
Hypogastrura purpurescens	2	1	
Lepidocyrtus sp	2		
L. curvicollis	7	38	1
L. cyaneus	6	14	
Pseudosinella alba	11	6	2
Arrhopalites sp		17	18
Thripia sp	1		
Bradysia brunnipes			2
Megaselia sp 1 indet	1	1	1
Leptinus testaceus			1
Choleva glauca		1	

April - May

Group/species	Front	Frogpit	Back
Mesostigmata			1
Hypogastrura purpurescens	6	3	
Lepidocyrtus curvicollis	13	45	3
L. cyaneus	13	17	
Pseudosinella alba		3	2
Arrhopalites sp		3	8
Panorpa sp	1		
Mycetophilidae sp 1 indet	1		
Lycoriella leucotricha			1
Bradysia brunnipes			2
Psychoda sp	2		
Megaselia sp 1 indet	3		
Leptinus testaceus			1

continued.....

May - June

Group/species	Front	Frogpit	Back
Astigmata	2		
Mesostigmata	2		
Lepthyphantes pallidus		1	
Campodea sp			1
Hypogastrura purpurescens	12		
Lepidocyrtus curvicollis	13	71	2
L. cyaneus	12	17	1
Pseudosinella alba	1	4	2
Neelus sp			1
Arrhopalites sp		2	19
Thripia sp	3		
Pyralidae sp indet	1		
Anisopus fenestralis	3		
Mycetophilidae sp 1 indet	2		
Mycetophilidae sp 2 indet			1
Mycetophilidae sp 3 indet			1
Lycoriella leucotricha	1		
Bradysia brunnipes		5	6
Heleomyzidae sp 2 indet		1	
Eupelmidae sp indet	1		
Quedius mesomelinus	1		
Cryptophagus ruficornis	1		

June - July

Group/species	Front	Frogpit	Back
Astigmata	1		
Mesostigmata	2	3	2
Cryptostigmata	3	2	8
Mitostoma crysomelas		1	

continued.....

Group/species	Front	Frogpit	Back
Ciniflo sp	1		
Porrhomma egeria	2		2
Lepthyphantes pallidus	1	2	1
Polymicrodon sp		2	1
Hypogastrura purpurescens		5	1
Isotoma sp	1		
Lepidocyrtus curvicollis	17	28	11
L. cyaneus	30	3	2
Pseudosinella alba	3	23	2
Neelus sp	17	43	14
Arrhopalites sp	3	30	16
Thripia sp	1		
Tipula sp		1	
Mycetophilidae sp 1 indet	1		
Mycetophilidae sp 4 indet	2	1	
Lycoriella leucotricha		8	2
Bradysia brunnipes	2	14	8
Cecidomyiidae sp 1 indet	1	2	
Empis sp	1		
Mymaridae	1		
Pterostichus melanarus	1		
Quedius mesomelinus			2
Cryptophagus acutangulus	2	3	

July - August

Group/species	Front	Frogpit	Back
Enchytraeidae	1		
Astigmata	1	2	
Mesostigmata	2	3	7
Cryptostigmata	2	2	32

continued.....

Group/species	Front	Frogpit	Back
Mitostoma chrysomelas		1	
Araneus sp	1		
Prosopotheca sp		1	
Porrhomma egeria		2	1
Lepthyphantes pallidus	2	1	
Lithobius variegatus	1		
Polydesmus sp	1		
Hypogastrura purpurescens			3
Lepidocyrtus curvicollis	32	28	14
L. cyaneus	170	29	3
Pseudosinella alba		44	2
Neelus sp		87	43
Arrhopalites sp	4	44	17
Aphis sp	1		
Thripia sp	2		
Hofmannophila pseudospretella	1		
Tipula sp	2	1	
Mycetophilidae sp 4 indet	2	5	
Lycoriella leucotricha	1	15	1
Bradysia brunnipes		15	19
Cecidomyiidae sp 2 indet			1
Culex sp		1	
Triphleba antricola	2		
Megaselia rufipes	2	1	
Pterostichus madidus		1	
Quedius mesomelinus			3
Cryptophagus acutangulus	1	1	1
C. sutatus	1	1	
Rhinosimus planirostris	1		

August - September

Group/species	Front	Frogpit	Back
Mesostigmata	2	4	4
Cryptostigmata	3	4	11
Porrhomma egeria		1	1
Lepthyphantes pallidus		5	
Lithobius dubosqui	1		
Campodea sp	1		
Hypogastrura purpurescens	1		2
Onychiurus sp			2
Isotoma sp			1
Entomobrya sp	1		
Lepidocyrtus curvicollis	15	12	7
L. cyaneus	77	17	2
Pseudosinella alba		24	14
Neelus sp	8	12	24
Arrhopalites sp	6	31	23
Psyllopsocidae sp indet		1	
Mycetophilidae sp 1 indet		1	
Mycetophilidae sp 2 indet			2
Mycetophilidae sp 4 indet		5	5
Bradysia brunnipes		5	5
Quedius mesomelinus			2
Cryptophagus acutangulus	2	2	
C. distinguendus	1		
C. badidus	1		
Rhinosimus planirostris	1		

September - October

Group/species	Front	Frogpit	Back
Astigmata		1	

continued.....

Group/species	Front	Frogpit	Back
Prostigmata		2	
Mesostigmata	1	5	3
Cryptostigmata	2	2	14
Lycosa agrison	1		
Porrhomma egeria		2	
Lepthyphantes pallidus		3	1
Polymicrodon sp			2
Hypogastrura purpurescens		1	5
Onychiurus sp			4
Isotoma sp		1	
Lepidocyrtus curvicollis	32	47	14
L. cyaneus	35	6	
Pseudosinella alba	2		6
Neelus sp	10	43	36
Arrhopalites sp	4	17	8
Mycetophilidae sp 3 indet		1	
Mycetophilidae sp 4 indet	1	7	2
Lycoriella leucotricha		5	2
Bradysia brunnipes		8	11
Culex sp		1	
Megaselia rufipes	1		
Sphaeroceridae sp 1			1
Quedius mesomelinus		1	2
Choleva angustata		1	1
Cryptophagus acutangulus			1

October - November

Group/species	Front	Frogpit	Back
Mesostigmata	3	2	2
Cryptostigmata	3	1	21

continued.....

Group/species	Front	Frogpit	Back
Ciniflo sp	1		
Meta menardi	1		
Porrhomma egeria			1
Lepthyphantes pallidus		1	
Oniscus asellus	2		
Lithobius crassius		1	
Campodea sp	2	2	1
Hypogastrura purpurescens	2	2	8
Onychiurus sp	1		
Lepidocyrtus curvicollis	44	91	5
L. cyaneus	53	23	1
Pseudosinella alba		8	5
Neelus sp	3	18	22
Arrhopalites sp		7	11
Lycoriella leucotricha		9	2
Bradysia brunnipes		2	6
Culex sp	1		
Quedius mesomelinus	1	2	2
Cryptophagus acutuangulus	2	2	1
C. pilosis	1		
C. saginatus	2	1	

November - December

Group/species	Front	Frogpit	Back
Mesostigmata	1	1	1
Meta menardi		1	
Porrhomma egeria			1
Lepidocyrtus curvicollis		34	
L. cyaneus	11	13	
Pseudosinella alba	2		1

continued.....

Group/species	Front	Frogpit	Back
Neelus sp		1	
Arrhopalites sp			3
Mycetophilidae sp 1 indet	1		
Lycoriella leucotricha	1		
Psychoda sp		3	
Culex sp	1		
Megaselia sp 1 indet		1	
Cryptophagus acutangulus		1	

Below is a complete list of the number of individuals of each species caught in the pitfall traps in each chamber during the time of the experiment. The rat carcasses were deposited on 9th June 1989 and removed on 30th April 1991. Pitfall traps were emptied during the first week of each month. (Parasites found on Phoridae (Diptera) were all Gamasidae (Acari).)

June - July 1989

Group/species	Front	Frogpit	Back
Astigmata	1		
Ciniflo sp (shed skin only)	1		
Lepthyphantes pallidus		3	1
Androniscus dentiger			1
Hypogastrura purpurescens	3		
Onychiurus sp		1	
Lepidocyrtus curvicollis	8	37	2
L. cyaneus	31	19	1
Pseudosinella alba	5	10	1
Neelus sp			14
Arrhopalites sp		3	11
Aphis sp	1		
Thripia sp	2	1	

continued.....

Group/species	Front	Frogpit	Back
Aeolothripidae sp 1 indet	2		
Aeolothripidae sp 2 indet	1		
Panorpa sp	1		
Pyralidae sp indet	1		
Hofmannophila pseudospretella	2		
Tipula sp	1		
Tipulidae sp 1 indet	1		
Anisopus fenestralis	2		
Mycetophilidae sp 5 indet			2
Lycoriella leucotricha	6	1	
Bradysia brunnipes	9	6	4
Psychoda sp	1		
Tabanidae sp indet	1		
Empididae sp indet		1	
Empis sp	1		
Psylopus sp	1		
Psylopus longulus	2		
Triphleba antricola			
0 parasites	6	300	7
1 parasite	1	17	
2 parasites		5	
3 parasites		2	
4 parasites		1	
Megaselia rufipes	5	24	
Megaselia sp 1 indet	1		
Anthomyzidae sp indet	1		
Calliphora vomitoria			
adult	3	1	
pupa	1		
larva	2		

continued.....

Group/species	Front	Frogpit	Back
Saltella sphondylii	1		
Limnosina silvatica		1	
Chalcidoidae sp indet	2		
Omalium excavatum	9		
Cryptophagus acutangulus		1	
C. ruficornis		2	

July - August 1989

Group/species	Front	Frogpit	Back
Nesticus cellanus (juvenile)	2		
Porrhomma egeria			1
Lithobius forficatus		1	
Lepidocyrtus curvicollis	9	44	1
L. cyaneus	79	88	
Pseudosinella alba		25	1
Neelus sp		1	21
Arrhopalites sp		20	7
Psyllopsocidae sp indet	1		
Thripia sp	69		
Aeolothripidae sp 1 indet	4		
Pyralidae sp indet	1		
Hofmannophila pseudospretella		3	
Tipulidae sp 2 indet			1
Macrocera maculata	1		
Lycoriella leucotricha	2	3	1
Bradysia brunnipes	1	8	6
Cecidomyiidae sp 1 indet	6		
Cecidomyiidae sp 3 indet	1		
Dolichopodidae sp indet	1		

continued.....

Group/species	Front	Frogpit	Back
Phoridae sp indet			
larva			1
pupa			1
Triphleba antricola			
0 parasites	8	1138	86
1 parasite	4	155	6
2 parasites		44	
3 parasites	1	26	1
4 parasites		17	
5 parasites		5	
6 parasites		2	
7 parasites		2	
8 parasites		1	
9 parasites			1
10 parasites		1	
Megaselia rufipes			
0 parasites	8	554	12
3 parasites		1	
Megaselia sp 2 indet		1	
Calliphora vomitoria			
adult	23	5	
larva	3		48
Heleomyzidae sp 3 indet		1	
Leptocera fontinalis		1	
Sphaeroceridae sp 2 indet		1	
Drosophilidae sp indet	1		
Chalcidoidea sp indet	1		
Pteromalidae sp indet		2	
Ceraphronidae sp indet	1		
Aleochara spadicea	1		

continued.....

Group/species	Front	Frogpit	Back
Aleochara cuniculorum		1	
Acrotona clientula	2		
Xylostiba monolicornis		3	
Quedius mesomelinus		1	
Oxytelus tetracharinatus	1		
Choleva jeanneli		1	
Catops chrysomeloides		1	
C. tristis		1	
Cryptophagus ruficornis		1	

August - September 1989

Group/species	Front	Frogpit	Back
Prostigmata	5		
Astigmata	3		
Mesostigmata	30		
Araneae sp indet (juvenile)	1		
Porrhomma egeria	1		
Lepthyphantes pallidus		1	
Lepidocyrtus curvicollis	46	31	5
L. cyaneus	79	56	
Pseudosinella alba	2	17	
Neelus sp		2	19
Arrhopalites sp		12	29
Thripia sp	18	1	
Aeleothripidae sp 1 indet	1		
Hofmannophila pseudospretella (larva)		10	
Mycetophilidae sp 5 indet			2
Bradysia brunnipes		1	1
Triphleba antricola			
0 parasites	5	174	189

continued.....

Group/species	Front	Frogpit	Back
Triphleba antricola			
1 parasite	19	20	
2 parasites		7	3
3 parasites		1	1
4 parasites		1	
Megaselia rufipes	4	214	21
Megaselia sp 1 indet	1	1	
Megaselia brunneipennis		1	1
Calliphora vomitoria		2	
Ichneumonidae sp indet	27		
Braconidae sp 1 indet	2		
Oxytelus tetracharinatus		1	

September - October 1989

Group/species	Front	Frogpit	Back
Mesostigmata	160	48	18
Lepthyphantes obscurus	1		
Lepidocyrtus curvicollis	44	75	18
L. cyaneus	82	70	
Pseudosinella alba		52	2
Neelus sp		7	62
Arrhopalites sp		32	26
Thripia sp	11		
Hofmannophila pseudospretella (larva)	90		
Mycetophilidae sp 6 indet		1	1
Mycetophilidae sp 7 indet			1
Lycoriella leucotricha		2	
Bradysia brunnipes		10	172
Phoridae sp indet (pupa)			1

continued.....

Group/species	Front	Frogpit	Back
Triphleba antricola			
0 parasites	1	81	28
1 parasite		9	6
2 parasites		2	1
3 parasites		1	1
4 parasites			1
Megaselia rufipes			
0 parasites		89	13
1 parasite		3	1
2 parasites			1
Megaselia sp 1 indet		5	
Megaselia bifida			5
Calliphora vomitoria		64	29
Ichneumonoidae sp indet	2		

October - November 1989

Group/species	Front	Frogpit	Back
Prostigmata			2
Mesostigmata	1	10	41
Lepthyphantes pallidus		1	
Lepidocyrtus curvicollis	18	64	37
L. cyaneus	59	53	3
Pseudosinella alba		44	
Neelus sp		6	56
Arrhopalites sp		2	11
Thripia sp	9		
Hofmannophila pseudospretella (larva)	5		
Mycetophilidae sp 8 indet		1	
Lycoriella leucotricha			5
Bradysia brunnipes		1	45

continued.....

Group/species	Front	Frogpit	Back
Trichosia absurda		1	
Phoridae sp indet (pupa)			2
Triphleba antricola			
0 parasites		59	30
1 parasite		23	21
2 parasites		6	10
3 parasites		1	2
4 parasites		1	4
5 parasites			1
6 parasites			2
7 parasites			1
9 parasites			1
Megaselia rufipes			
0 parasites		176	81
1 parasite		8	19
2 parasites			4
3 parasites			3
4 parasites			1
6 parasites			1
Megaselia sp 1 indet	2	30	2
Megaselia sp 2 indet	1		
Megaselia sp 3 indet	1		
Megaselia sp 4 indet	1		4
Megaselia sp 5 indet	1		
Megaselia brunneipennis	1		
Calliphora vomitoria		1	3
Dryomyzidae sp indet		1	
Sphaeroceridae sp 1 indet			1
Braconidae sp 1 indet		14	
Aleochara lanuginosa	1		

continued.....

Group/species	Front	Frogpit	Back
Aleochara villosa		1	
A. moerens	2		
Xylostiba monolicornis		4	
Quedius mesomelinus			
adult		2	1
LIII		1	
Catops tristus	1		
Cartodere ruficollis	1		

November - December 1989

Group/species	Front	Frogpit	Back
Prostigmata		1	
Astigmata	18		
Mesostigmata	1	21	287
Lepthyphantes pallidus		2	
Hypogastrura purpurescens	1	1	
Onychiurus sp			2
Lepidocyrtus curvicollis	9	128	17
L. cyaneus	50	73	
Pseudosinella alba		81	2
Neelus sp			51
Arrhopalites sp		3	5
Thripia sp	11		
Lycoriella leucotricha			18
Bradysia brunnipes		15	136
Triphleba antricola			
0 parasites	21	7	19
1 parasite		3	25
2 parasites		1	19
3 parasites	1	2	6

continued.....

Group/species	Front	Frogpit	Back
Triphleba antricola			
4 parasites	1	1	12
5 parasites		2	10
6 parasites			2
7 parasites		1	5
8 parasites		1	3
9 parasites			2
10 parasites			4
11 parasites	1		
Megaselia rufipes			
0 parasites		13	27
1 parasite		4	28
2 parasites		2	16
3 parasites			6
4 parasites			2
Megaselia bifida		2	
Braconidae sp 1 indet		10	
Bessobia sp		2	
Cryptophagus acutangulus	1		
C. ruficornis	1	1	

December 1989 - January 1990

Group/species	Front	Frogpit	Back
Prostigmata		3	2
Astigmata	3	1	3
Mesostigmata		5	113
Lepthyphantes pallidus		1	
Hypogastrura purpurescens		1	
Onychiurus sp		1	
Lepidocyrtus curvicollis	5	134	12

continued.....

Group/species	Front	Frogpit	Back
Lepidocyrtus cyaneus	41	100	
Pseudosinella alba	1	44	2
Neelus sp			21
Arrhopalites sp			7
Thripia sp	2		
Hofmannophila pseudospretella (larva)	3		
Bradysia brunnipes		3	125
Lycoriella leucotricha		1	
Trichosia absurda		1	
Triphleba antricola			
0 parasites			2
1 parasite		2	8
3 parasites		2	
4 parasites		1	1
5 parasites		1	
6 parasites		2	
7 parasites			1
8 parasites			1
12 parasites			1
Megaselia rufipes			
0 parasites		2	8
1 parasite		2	5
2 parasites			5
3 parasites			1
4 parasites		1	1
Megaselia sp 1 indet	2		
Bessobia sp		3	
Omalium tricolor			1
Cryptophagus acutangulus	1		

January - February 1990

Group/species	Front	Frogpit	Back
Astigmata	5		
Mesostigmata		2	55
Lepthyphantes pallidus		1	
Lepidocyrtus curvicollis	22	49	14
L. cyaneus	73	85	
Pseudosinella alba	4	19	6
Neelus sp			19
Arrhopalites sp			7
Thripia sp	3		
Lycoriella leucotricha			6
Bradysia brunnipes			183
Triphleba antricola		1	
Megaselia rufipes			
0 parasites		3	
1 parasite		3	
Calodera uliginosa	1		
Quedius mesomelinus			1
Cryptophagus acutangulus	1		

February - March 1990

Group/species	Front	Frogpit	Back
Prostigmata		1	
Mesostigmata			13
Hypogastrura purpurescens	1	1	
Lepidocyrtus curvicollis	6	33	7
L. cyaneus	45	16	
Pseudosinella alba		1	
Neelus sp			7
Arrhopalites sp			6

continued.....

Group/species	Front	Frogpit	Back
Aeolothripidae sp 1 indet	1		
Lycoriella leucotricha			3
Bradysia brunnipes			57
Sphecidae sp indet		1	

March - April 1990

Group/species	Front	Frogpit	Back
Prostigmata		1	6
Astigmata		1	
Mesostigmata	2	2	12
Lepthyphantes leprosus	1		
Hypogastrura purpurescens	1		
Onychiurus sp			2
Lepidocyrtus curvicollis	18	203	15
L. cyaneus	39	89	
Pseudosinella alba	1	6	2
Neelus sp			37
Arrhopalites sp			25
Thripia sp	11		
Anisopus fenestralis	1		
Lycoriella leucotricha			2
Bradysia brunnipes			19
Trichosia absurda	1		
Triphleba antricola			
2 parasites			1
Megaselia sp 1 indet	3		
Cryptophagus ruficornis		1	

April - May 1990

Group/species	Front	Frogpit	Back
Prostigmata			1
Mesostigmata	1		
Chthonius ischnoceles	1		
Nesticus cellanus	2		
Hypogastrura purpurescens		1	
Lepidocyrtus curvicollis	15	120	68
L. cyaneus	30	109	
Pseudosinella alba		13	1
Neelus sp			120
Arrhopalites sp		1	63
Thripia sp	52		
Hofmannophila pseudospretella	5	1	
Mycetophilidae sp 6 indet	1		
Lycoriella leucotricha			8
Bradysia brunnipes			24
Culex sp	1		
Megaselia sp 1 indet	1		1
Braconidae sp 2 indet	2		
Sphecidae sp indet	4		
Acrotona sp	1		
Omalium excavatum			3
Choleva glauca	1		
Cryptophagus acutangulus		1	
C. ruficornis		4	
C. dentatus	1	4	

May - June 1990

Group/species	Front	Frogpit	Back
Prostigmata			41

continued.....

Group/species	Front	Frogpit	Back
Mesostigmata		1	1
Tegenaria sp	1		
Lepthyphantes sp (Gp I)	1		
Hypogastrura purpurescens		2	
Onychiurus sp			2
Lepidocyrtus curvicollis	5	254	65
L. cyaneus	3	165	
Pseudosinella alba	3	61	2
Neelus sp			187
Arrhopalites sp			101
Thripia sp	41		
Aeolothripidae sp 1 indet	1		
Hofmannophila pseudospretella	14	1	
Anisopus fenestralis		1	
Lycoriella leucotricha	1		7
Bradysia brunnipes			21
Cecidomyiidae sp 4 indet	1		
Heleomyzidae sp 2 indet		1	
Braconidae sp 1 indet	55		
Braconidae sp 2 indet		1	
Oxypoda opaca	2		
Acrotona sp	1		
Omalium excavatum			1
Quedius mesomelinus			
adult		1	1
LI			1
LIII			1
Cryptophagus acutangulus	2	1	
C. ruficornis		3	
C. dentatus		1	
C. distinguendus		1	

June - July 1990

Group/species	Front	Frogpit	Back
Prostigmata	1	2	1
Astigmata			2
Mesostigmata			1
Hypogastrura purpurescens		1	1
Onychiurus sp			1
Lepidocyrtus curvicollis	2	49	72
L. cyaneus	16	147	3
Pseudosinella alba	1	46	21
Neelus sp			154
Arrhopalites sp		1	86
Thripia sp	21		
Hofmannophila pseudospretella	13		
Mycetophilidae sp 7 indet	1		
Lycoriella leucotricha			2
Bradysia brunnipes		1	48
Braconidae sp 1 indet	6		
Braconidae sp 2 indet		1	
Torymidae sp indet	2		
Oxypoda opaca	1		
Acrotona sp	2		
Quedius mesomelinus		1	2
Cryptophagus acutangulus	1		
C. dentatus		4	
Meligethes aeneus	1		

July - September 1990

Group/species	Front	Frogpit	Back
Astigmata	2	2	
Mesostigmata	2		2

continued.....

Group/species	Front	Frogpit	Back
Chthonius ischnoceles	2		
Opilio parientinus	1		
Lepthyphantes pallidus	3	2	1
Brachydesmus superus			3
Iulidae sp indet	1		
Hypogastrura purpurescens	1		
Onychiurus sp			4
Lepidocyrtus curvicollis	4	229	116
L. cyaneus	13	289	
Pseudinella alba		106	37
Neelus sp		1	188
Arrhopalites sp		3	110
Thripia sp	21		
Aeolothripidae sp 1 indet	1		
Hofmannophila pseudospretella			
adult	3		
larva	5		
Lycoriella leucotricha			1
Bradysia brunnipes			14
Cecidomyiidae sp 2 indet			1
Triphleba antricola		2	
Braconidae sp 1 indet	2		
Braconidae sp 2 indet	3		
Acrotona sp	2		
Quedius mesomelinus			2
Cryptophagus dentatus		2	
C. ruficornis		1	

September - October 1990

Group/species	Front	Frogpit	Back
Prostigmata		1	
Mesostigmata	2		
Tegenaria sp	1		
Lepthyphantes pallidus			2
Lithobius variegatus			1
Lepidocyrtus curvicollis	1	97	49
L. cyaneus	10	298	
Pseudosinella alba		48	30
Neelus sp			88
Arrhopalites sp			86
Thripia sp	33		
Bradysia brunnipes		4	11
Megaselia sp 1 indet		1	
Megaselia bifida			1
Quedius mesomelinus			1
Cryptophagus ruficornis		1	

October - November 1990

Group/species	Front	Frogpit	Back
Prostigmata	2		4
Mesostigmata	4	1	
Lepthyphantes pallidus		2	
Hypogastrura purpurescens	2	1	
Onychiurus sp			4
Lepidocyrtus curvicollis	26	68	15
L. cyaneus	14	121	
Pseudosinella alba		38	8
Neelus sp	1		33
Arrhopalites sp			15

continued.....

Group/species	Front	Frogpit	Back
Thripia sp	5		
Aeolothripidae sp 1 indet	1		
Hofmannophila pseudospretella	1		
Bradysia brunnipes		2	12
Megaselia sp 1 indet	1	1	
Braconidae sp 3 indet	1		
Quedius mesomelinus			1
Cryptophagus ruficornis		4	

November 1990 - January 1991

Group/species	Front	Frogpit	Back
Prostigmata	1		28
Astigmata	1		
Mesostigmata	1	10	
Allolobophora caliginosa			1
Lepidocyrtus curvicollis	15	88	11
L. cyaneus	22	267	
Pseudosinella alba		20	10
Neelus sp		4	16
Arrhopalites sp			17
Thripia sp	2		
Psychoda sp	1		
Lycoriella leucotricha			1
Bradysia brunnipes		2	5
Oxypoda opaca	1		
Acrotona sp		1	
Cryptophagus ruficornis		1	

January - March 1991

Group/species	Front	Frogpit	Back
Prostigmata		2	84
Mesostigmata	1	6	1
Lepthyphantes pallidus		1	1
Hypogastrura purpurescens		1	
Onychiurus sp			1
Lepidocyrtus curvicollis	7	25	16
L. cyaneus	11	139	
Pseudosinella alba		6	18
Neelus sp			24
Arrhopalites sp		1	28
Thripia sp	2		
Bradysia brunnipes			5
Megaselia sp 1 indet	1		
Heleomyzidae sp 4 indet		1	
Oxypoda opaca	1		
Cryptophagus acutangulus		1	

March - May 1991

Group/species	Front	Frogpit	Back
Prostigmata			46
Astigmata	1		
Mesostigmata	7	5	
Hypogastrura purpurescens	2		
Lepidocyrtus curvicollis	16	33	28
L. cyaneus	9	101	
Pseudosinella alba		8	3
Neelus sp			1
Arrhopalites sp			26
Thripia sp	20		

continued.....

Group/species	Front	Frogpit	Back
Bradysia brunnipes	2		
Megaselia sp 1 indet	1		
Oxypoda opaca	2		
Cryptophagus acutangulus			1

APPENDIX TWO : FAUNA
CHURCH HOLE CAVE

Below is a complete list of all species found in Church Hole Cave both before and after the carcasses were deposited. The three sites, Front, Middle and Back, are 8, 28 and 40 m respectively from the entrance to the cave.

KEY:

- \- Present in Baseline only
- \+ Present only after deposition of carcasses
- * Present both in Baseline and after deposition of carcasses
- \# Present on carcasses only (not found in traps)

	Front	Frogpit	Back
Mollusca:			
Pyramidula rupertris	-		
Arachnida:			
Acari			
Sp indet (L)	+		
Prostigmata	*	*	*
Astigmata	*	+	
Mesostigmata		*	+
Cryptostigmata	*	*	*
Araneae			
Linyphiidae			
Centromerus prudens	-		
Lepthyphantes pallidus		*	*

continued.....

	Front	Frogpit	Back
Crustacea:			
Isopoda			
Oniscidae			
Oniscus asellus	-		
Insecta:			
Diplura			
Campodea sp		*	*
Collembola			
Hypogastruridae			
Hypogastrura purpurescens	*	*	*
Entomobryidae			
Lepidocyrtus sp	+	+	+
Lepidocyrtus curvicollis	*	*	*
Lepidocyrtus cyaneus	*	*	*
Tomoceros sp	-		
Neelidae			
Neelus sp		*	*
Sminthuridae			
Arrhopalites sp	*	*	*
Thysanoptera			
Thripidae			
Thripia sp	*	+	
Aeolothripidae			
sp 1 indet	+		
Diptera			
Trichoceridae			
Trichocera sp		-	
Anisopodidae			
Anisopus fenestralis		-	

continued.....

	Front	Frogpit	Back
Sciaridae			
Lycoriella leucotricha	-	*	*
Bradysia brunnipes		-	*
Cecidomyiidae			
Cecidomyia sp	-	+	
Psychodidae			
Psychoda sp	*	-	
Phoridae			
Triphleba antricola			-
Megaselia rufipes	*	*	*
Megaselia sp 1 indet	+	+	
Megaselia sp 2 indet	+		+
Heleomyzidae			
sp 1 indet	*		
Sphaeroceridae			
sp 1 indet	-	+	
Hymenoptera			
Braconidae			
sp 1 indet	+		
Mymaridae			
sp indet	-		
Pteromalidae			
sp indet	+		
Proctotrupidae			
sp indet	*		
Coleoptera			
Staphylinidae			
Proteinus sp	-		
Trogophloeus pusillus	-		

continued.....

	Front	Frogpit	Back
Cholevidae			
Catops fuliginosus	*		
Cryptophagidae			
Cryptophagus acutangulus	-	*	*

Below is a complete list of the number of individuals of each species caught in the pitfall trap at each site before the carcasses were deposited. Pitfall traps were emptied around the middle of each month.

December - January

Group/species	Front	Frogpit	Back
Pyramidula rupestris	1		
Cryptostigmata			4
Lepthyphantes pallidus			1
Leipdocyrtus curvicollis	5		1
L. cyaneus	3	1	3
Neelus sp			2
Arrhopalites sp			3
Lycoriella leucotricha			1
Psychoda sp		1	
Sphaeroceridae sp indet	1		

January - February

Group/species	Front	Frogpit	Back
Cryptostigmata		1	1
Lepidocyrtus curvicollis	3		1
L. cyaneus	8	1	3
Neelus sp			1
Arrhopalites sp	1		4
Cryptophagus acutangulus	1		1

February - March

Group/species	Front	Frogpit	Back
Prostigmata	1		
Mesostigmata		2	
Cryptostigmata	1		1
Lepidocyrtus curvicollis	1		1
L. cyaneus	4	1	2
Tomoceros sp	1		
Neelus sp		1	
Arrhopalites sp			3
Thripia sp	2		
Psychoda sp	1		
Cryptophagus acutangulus			1

March - April

Group/species	Front	Frogpit	Back
Mesostigmata		1	
Cryptostigmata			2
Hypogastrura purpurescens	1		
Lepidocyrtus cyaneus		1	2
Triphleba antricola			1

April - May

Group/species	Front	Frogpit	Back
Prostigmata	1		1
Cryptostigmata	1	3	
Lepthyphantes pallidus			1
Centromerus prudens	1		
Hypogastrura purpurescens	1		
Lepidocyrtus curvicollis	11		1
L. cyaneus	9	4	

continued.....

Group/species	Front	Frogpit	Back
Neelus sp			1
Arrhopalites sp		4	
Trichocera sp		1	
Lycoriella leucotricha	1		

May - June

Group/species	Front	Frogpit	Back
Prostigmata			2
Mesostigmata			1
Cryptostigmata			3
Campodea sp		1	
Hypogastrura purpurescens	1		
Lepidocyrtus curvicollis	6	4	2
L. cyaneus	16	2	2
Neelus sp			5
Arrhopalites sp			2
Anisopus fenestralis		1	
Lycoriella leucotricha	1		
Bradysia brunnipes		1	1
Cecidomyia sp	1		
Trogophloeus pusillus	3		

June - July

Group/species	Front	Frogpit	Back
Prostigmata	1		
Lepidocyrtus curvicollis	3	5	5
L. cyaneus	12	7	7
Neelus sp			2
Arrhopalites sp			2
Trichocera sp		1	

continued.....

Group/species	Front	Frogpit	Back
Cecidomyia sp	1		
Bradysia brunnipes		1	
Lycoriella leucotricha	1		
Megaselia rufipes		5	
Heleomyza sp	1		
Sphaeroceridae sp indet	2		
Proctotrupidae sp indet	9		

July - August

Group/species	Front	Frogpit	Back
Mesostigmata		1	
Cryptostigmata	3	4	
Hypogastrura purpurescens	2		
Lepidocyrtus curvicollis	4	27	2
L. cyaneus	4	49	4
Neelus sp		15	12
Arrhopalites sp	1	16	8
Thripia sp	1		
Psychoda sp		1	
Bradysia brunnipes			2
Cecidomyia sp	1		
Catops fuliginosus	1		
Cryptophagus acutangulus		1	6

August - September

Group/species	Front	Frogpit	Back
Mesostigmata			1
Cryptostigmata	4	1	
Oniscus asellus	1		
Campodea sp			1

continued.....

Group/species	Front	Frogpit	Back
Hypogastrura purpurescens			5
Lepidocyrtus curvicollis	14	10	2
L. cyaneus	25	28	10
Neelus sp	1	7	2
Arrhopalites sp	2	7	
Thripia sp	14		
Lycoriella leucotricha		1	
Bradysia brunnipes			1
Cecidomyia sp	1		
Triphleba antricola			2
Megaselia rufipes	10	5	1
Sphaeroceridae sp indet	1		

September - October

Group/species	Front	Frogpit	Back
Prosigmata	1		
Astigmata	1		
Cryptostigmata	1	3	
Lepthyphantes pallidus		1	
Lepidocyrtus curvicollis	41	22	3
L. cyaneus	46	86	8
Neelus sp		13	15
Arrhopalites sp		7	8
Thripia sp	4		
Cecidomyia sp	1		
Megaselia rufipes	1		1
Sphaeroceridae sp indet	1		
Mymaridae	1		
Proteinus sp	2		

October - November

Group/species	Front	Frogpit	Back
Prostigmata	3	1	
Mesostigmata			1
Cryptostigmata	1		
Hypogastrura purpurescens	1		
Lepidocyrtus curvicollis	19	3	
L. cyaneus	19	16	3
Neelus sp		14	2
Arrhopalites sp		1	3

November - December

Group/species	Front	Frogpit	Back
Prostigmata		1	
Mesostigmata		1	
Cryptostigmata		2	1
Hypogastrura purpurescens		3	
Lepidocyrtus curvicollis	22	3	2
L. cyaneus	17	15	
Neelus sp		1	9
Arrhoplaites sp			7
Thripia sp	1		

Below is a complete list of the number of individuals of each species caught in the pitfall traps at each site during the time of the experiment. The rat carcasses were deposited on 2nd February 1990 and removed on 19th February 1991. Pitfall traps were emptied around the middle of each month.

February - March 1990

Group/species	Front	Frogpit	Back
Mesostigmata	2		
Cryptostigmata		1	1
Centromerus prudens	1		
Lepidocyrtus curvicollis	10		4
yL. cyaneus	11	2	4
Neelus sp		1	10
Arrhopalites sp			1
Thripia sp	1		
Proctrotrupidae sp indet	4		

March - April 1990

Group/species	Front	Frogpit	Back
Prostigmata	7	5	7
Cryptostigmata	2	2	3
Lepidocyrtus sp	6		1
L. curvicollis	9	2	1
L. cyaneus			2
Arrhopalites sp			1
Aeolothripidae sp indet	5		
Megaselia sp 1 indet	1	1	
Catops fuliginosus	1		

April - May 1990

Group/species	Front	Frogpit	Back
Acari sp indet (L)	8		
Prostigmata	8	2	
Astigmata		1	
Cryptostigmata	2	1	2
Mesostigmata		1	
Hypogastrura purpurescens	3		
Lepidocyrtus sp		2	2
L. curvicollis		11	8
L. cyaneus			3
Arrhopalites sp			2
Thripia sp	1		
Aeolothripidae sp indet	3		
Megaselia sp 2 indet			1

May - June 1990

Group/species	Front	Frogpit	Back
Astigmata	1		
Cryptostigmata	1	4	2
Campodea sp		1	
Lepidocyrtus sp	10	6	2
L. curvicollis	4	1	6
L. cyaneus	2	8	6
Arrhopalites sp		2	9
Aeolothripidae sp indet	2		
Lycoriella leucotricha		1	

June - July 1990

Group/species	Front	Frogpit	Back
Cryptostigmata		1	

continued.....

Group/species	Front	Frogpit	Back
Lepidocyrtus sp	7	3	8
L. curvicollis	1	1	4
L. cyaneus	1	6	4
Arrhopalites sp		1	4
Thripia sp	1		
Sphaeroceridae sp indet		1	

July - August 1990

Group/species	Front	Frogpit	Back
Prostigmata	7		
Cryptostigmata	3	3	
Campodea sp		1	
Hypogastrura purpurescens	1		
Lepidocyrtus sp	33	8	5
L. curvicollis	11	1	2
L. cyaneus	21	8	7
Arrhopalites sp		4	13
Aeolothripidae sp indet	13		
Cecidomyiidae sp 1 indet		1	
Megaselia rufipes	1	1	
Pteromalidae sp indet	1		

August - September 1990

Group/species	Front	Frogpit	Back
Astigmata	2		
Cryptostigmata			1
Campodea sp		6	
Hypogastrura purpurescens	1		
Lepidocyrtus sp	19		6
L. curvicollis	10	6	17

continued.....

Group/species	Front	Frogpit	Back
L. cyaneus	7	18	1
Arrhopalites sp	1	7	28
Thripia sp	6		
Aeolothripidae sp indet	2		
Megaselia rufipes		5	

September - October 1990

Group/species	Front	Frogpit	Back
Cryptostigmata		16	1
Lepthyphantes pallidus		1	
Campodea sp		2	
Hypogastrura purpurescens	2		
Lepidocyrtus sp	14	9	4
L. curvicollis	16	10	9
L. cyaneus	7	35	5
Arrhopalites sp		17	43
Thripia sp	1	2	
Lycoriella leucotricha			1
Megaselia sp 2 indet			1
Braconidae sp indet	1		
Cryptophagus acutangulus (L)		3	

October - November 1990

Group/species	Front	Frogpit	Back
Cryptostigmata			2
Lepthyphantes pallidus			1
Campodea sp		3	
Hypogastrura purpurescens	4		1
Lepidocyrtus sp	1	3	3
L. curvicollis	7	3	17

continued.....

Group/species	Front	Frogpit	Back
L. cyaneus	15	11	10
Arrhopalites sp		10	40
Bradysia brunnipes			1
Megaselia rufipes		2	
Cryptophagus acutangulus			
adult		2	
larva		1	

November - December 1990

Group/species	Front	Frogpit	Back
Onychiurus sp			2
Hypogastrura purpurescens	1		
Lepidocyrtus sp	1	2	
L. curvicollis	3	2	10
L. cyaneus	3	7	3
Arrhopalites sp		1	13
Megaselia rufipes			1
Megaselia sp 2 indet	1		
Cryptophagus acutangulus			2

December 1990 - January 1991

Group/species	Front	Frogpit	Back
Cryptostigmata		2	1
Centromerus prudens			1
Campodea sp			1
Lepidocyrtus sp	2		2
L. curvicollis	4	1	5
L. cyaneus	3	6	1
Arrhopalites sp			6
Heleomyza sp indet	1		
Cryptophagus acutangulus		5	4

January - February 1991

Group/species	Front	Frogpit	Back
Mesostigmata			1
Cryptostigmata			1
Lepidocyrtus curvicollis	1	1	3
L. cyaneus	3		5
Arrhopalites sp			2
Psychoda sp	1		
Cryptophagus acutangulus			1