CAVE AND KARST SCIENCE Vol. 24, No.2, August 1997
Transactions of the British Cave Research Association

The effects of decomposing animal remains on cave invertebrate communities

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Abstract: The deterioration and disarticulation of rat carcasses, exposed in caves at Creswell Crags near Worksop, Nottinghamshire, has been investigated over a five-year period, and the involvement of arthropods with the decomposing material examined. Following consumption of soft tissues by dipterous larvae, the fate of the remainder differs according to depth. Animals close to the cave entrance are likely to be mummified. Those deposited farther inside are first colonised by fungi and then attacked by diptera. Disarticulation and skeletalisation usually occur after 2-4 years, if scavengers are excluded. For several years, carrion provides a habitat for both cavernicolous and non-cavernicolous arthropods, the latter disrupting the threshold cave community. In the hypogean region, the over representation of some troglophilic species changes the community structure for at least two years after carcass deposition, although the non-cavernicolous arthropods soon disappear.

INTRODUCTION

Decomposition is responsible for over 95% of community metabolism in terrestrial ecosystems (Putman, 1983) and invertebrates play a vital role in this process. However, most early investigations (Steele, 1927; Duffield, 1937, and Kaufman 1937) concerned carrion and other materials exposed on the ground surface, as did work by Putman (1977). The most comprehensive study of arthropods associated with vertebrate remains (Payne et al, 1965 et seq.) concentrated on carrion decomposition above ground. However, Payne et al (1968) studied pigs buried in coffins. Five carcass stages, each with a specific microcommunity, were identified: fresh, inflation, deflation and decomposition, disintegration and skeletalisation. Carcass weight declined more slowly than on the surface and different organisms attacked the remains. Forty-eight arthropod species were recorded, 26 not implicated in above-ground decomposition.

Biospeleologists have used carrion as bait for cavernicolous arthropods (Peck, 1975). Arthropods attracted to carrion in caves may move or bury it, disturbing cave sediments (Macdonald, 1992) or disrupting archaeological deposits (Atkinson, 1957; Stein 1983). Oligochaete worms may also be responsible for such bioturbation (Thomas and Bottrell, 1992). However, exactly how animals decompose in caves, which are the most important British source of fossil vertebrates, and a key source of information on early humans is poorly understood. Many vertebrates live or over-winter in caves and some use them to cache or eat food (Andrews, 1990), while others simply fall in (Shipman, 1981). Inevitably, some will die there and little is known about how their remains are incorporated into cave deposits.

There are also important implications for an environment where lack of energy limits cave populations (Jefferson, 1976).

STUDY AREA

All work was carried out at Creswell Crags SSSI (SK535741), a Magnesian Limestone gorge on the Derbyshire and Nottinghamshire boundary, which is one of Britain's most important archaeological and paleontological sites (Fig. 1).

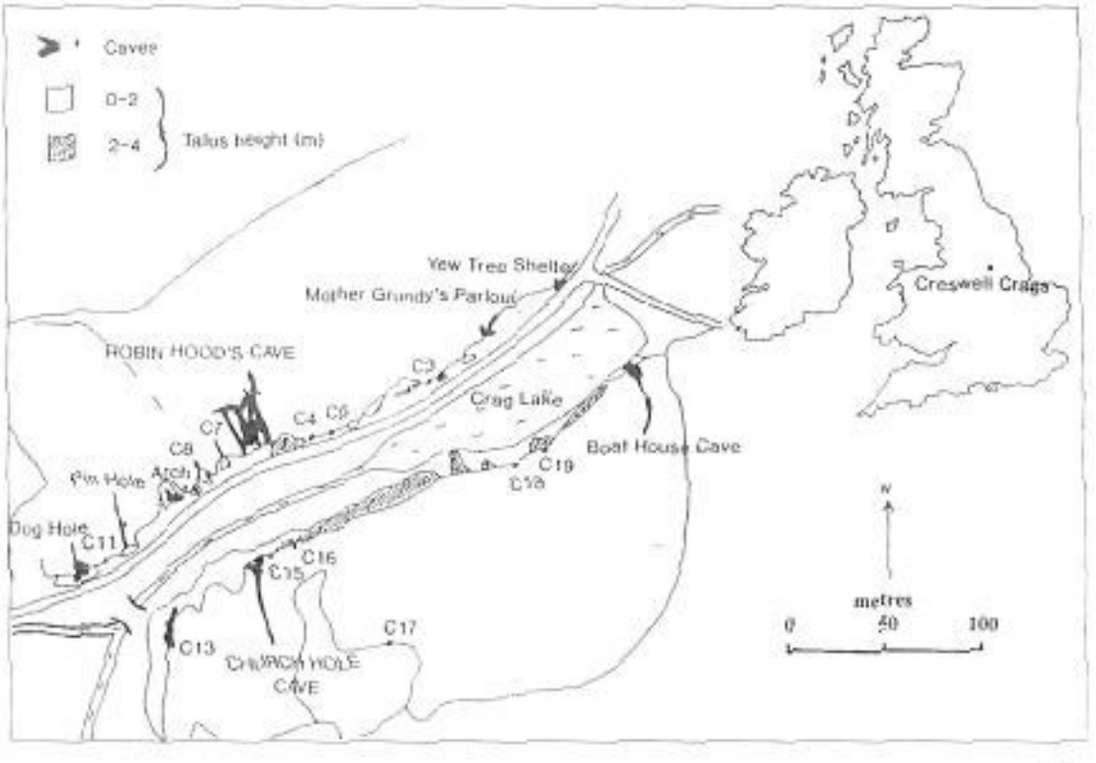

Figure 1. Creswell Crags SSSI, location of major caves.

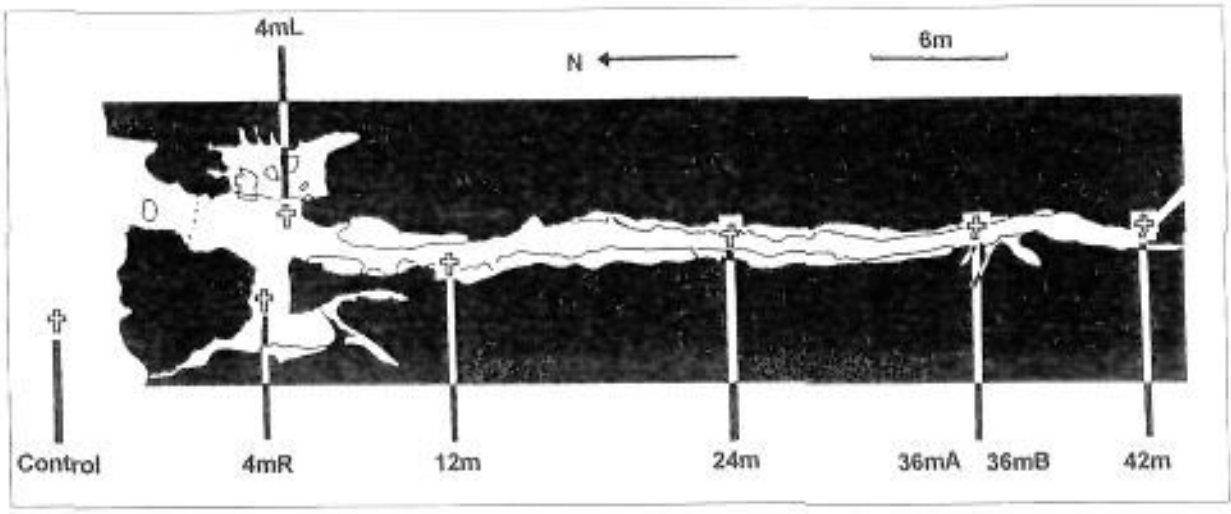

Figure 2. Church Hole Cave, Creswell Crags showing position of rat carcasses. For key see Fig 3

The caves at Creswell were first excavated by Mello (1876) and Dawkins (1876). The latter concluded that Robin Hood's Cave had served as a hyena den and provided human habitation. Work was also carried out by Armstrong (1949) and Campbell (1969). Investigations in the 1980s have been reviewed by Jenkinson and Gilbertson (1984) and Briggs et al (1985). Particular reference should be made to *Cave Science* (16, No. 3, 1989) largely dedicated to contemporary work at Creswell.

Two caves, situated on opposite sides of the gorge, were used in this study. Long term observations commenced in Church Hole Cave in 1986, with a second, shorter, study in Robin Hood's Cave in 1989.

Church Hole (Fig. 2) is situated in the North facing side of the gorge and is a linear, vadose canyon with a small side chamber 4 metres inside. The roof tapers from 3m high at the entrance to a 1m crawl at 32m, beyond which light does not penetrate. The cave terminates in a chamber backed by a vertical closed chimney at 42m.

Robin Hood's Cave (Fig. 3) on the South facing side of the gorge is the most extensive system at Creswell, consisting of four main chambers connected by a series of passages. The cave is mostly of phractic origin, with some vadose development. There are three current entrances and the maximum penetration into the cliff is 58m. Since the early 1980s the caves have been protected by metal grilles that deter casual visitors but allow access by invertebrates, small mammals and birds. A comprehensive survey of the invertebrates of Robin Hood's Cave was carried out by Terrell-Nield (1985).

METHODS

Church Hole Cave

On 23rd April 1986, five Sprague-Dawley (white) rats killed by exposure to carbon dioxide, were placed at 4, 12, 24, 36 and 42m into the cave (Fig. 2). A further three rats were positioned as controls outside. Each rat was covered by a dome of 1" gauge chicken wire secured by stones to deter scavengers, which may affect insect succession (Ellison, 1990).

Other investigators, mostly working above ground, have used cats (Illingworth, 1927), sheep (Deonier, 1940), pigs (Payne et al., 1965 et seq.) and humans (Rodriguez and Bass, 1983). Although small rodent carcasses rarely last long enough to illustrate the complete decomposition sequence (*Erzinclioglu, 1986*), previous observations on pheasants (Terrell-Nield, 1985) indicated that in caves small carcasses could provide sufficient information.

The rats were examined three times per month for three months and then monthly until October 1991, when most of the remains were vandalised. Each time the carcasses were described, photographed and weighed if possible. Fungal cover and dipteran activity were recorded on a 0-5 scale and insect specimens collected for identification. Temperature and humidity readings were taken at floor level at 4m intervals into the cave. Additional rats were placed at 4m and 36m in April 1987.

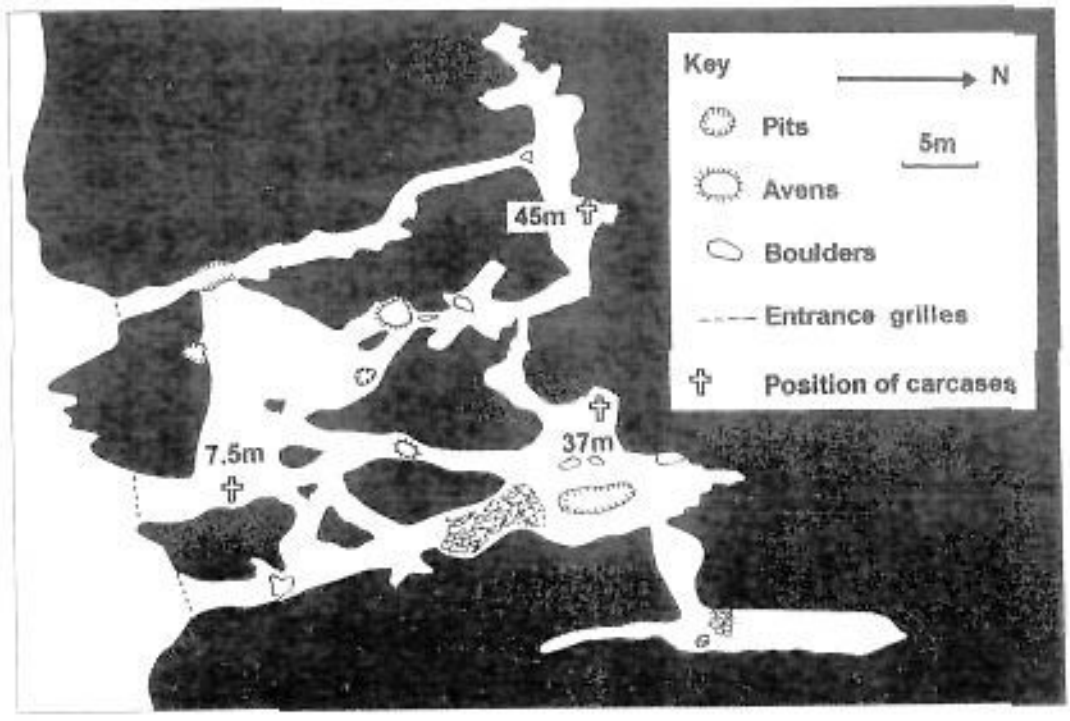

Figure 3. Robin Hood's Cave, Creswell Crags, showing position of rat carcasses

Robin Hood's Cave

On 9th June 1989, 24 rats were placed in the cave, eight each at 7.5, 37 and 45 metres from the entrance (Fig. 3), where holes in the cave floor allowed perspex tanks to be set level with the surface.

Each 320 x 225mm tank was filled with 50, 100 or 150mm of sieved cave earth, after partly filling the tanks with concrete made with cave sediment. This arrangement allowed the effects of sediment depth on decomposition to be examined (Macdonald and Terrell-Nield, 1991). At each site two control rats were placed on bare rock. All tanks were covered with chicken wire to exclude vertebrate scavengers.

Carcasses were examined each week for 7 weeks, then monthly until May 1991, after which the tanks were removed for excavation, a process described in Macdonald, (1992). On each visit the remains were photographed, weighed, insects collected and temperatures and humidities recorded.

The cave fauna was surveyed by pitfall traps, very efficient at catching invertebrates in caves (Peck, 1976). Six traps each containing 10ml of ethylene glycol-based preservative were set at each site and examined monthly for ten months before the rats were deposited, and then for the following two years.

RESULTS

Church Hole Cave

Temperatures and Humidities

The temperature profile of Church Hole (Fig. 4) typifies a well-ventilated cave, and follows the pattern described by Smithson (1982). The maximum temperatures decline with increasing depth, and the minimum temperatures rise gradually, reducing the range from 13°C at the entrance to 4°C at 42m. At the latter the average annual temperature was 8.3°C, almost the same as at 4m into the cave. However, its 95% confidence limits at +/-0.28°C were less than half that at the cave entrance (8.5°C +/- 0.65), where temperatures were much more variable.

Deeper in the cave the air is almost saturated (Fig. 5), especially in summer. The average humidity is slightly higher than reported for dry caves by Culver (1982), and the similar confidence limits (94.5% +/- 1.68 and 95.6% +/- 1.35) indicate little variation in range between the entrance and 42m.

State of rat carcasses

Decay followed the pattern described by Megnin (1884) and Payne et al. (1968). Although too small to show a "bloat" stage, wet and dry decay phases were evident, as was a putrefaction stage. To these can be added mummification, not usually seen above ground because of weathering and scavengers, except in cases of low temperature preservation (Doyle, 1996). The fate of the Church Hole Cave rats is illustrated in Table 1.

After a 3-10 day "fresh" phase (April 1986 was cold with temperatures of 10°C or less) each carcass began to putrefy, a stage varying from 7 days (controls) to 65 days in the deep cave. Carcasses were almost always colonised by sarcophagus diptera, especially *Calliphora vomitoria* (Tables 1, 2 and Fig. 8). This did not happen to rat 4R, which was buried by *Necrophorus humator* after 20 days. The controls and rat 4L were part stripped by these sexton beetles, but the sediment was too shallow for burial. Animals at 36 and 42m into the cave became breeding sites for *Heleomyza serrata*, which is regarded as a troglophilic dipteran (Jefferson, 1976).

Fungal colonisation (Fig. 6), which for carcasses more than 12m into the cave preceded dipteran colonisation, began with a grey-blue *Penicillium* species. This was followed by a basidiomycete (which never produced spores) and *Mucor haemalis*. Both are white, the former looking like loose cotton wool, the latter erect with typical *Mucor* sporangia. Fungi first appeared where the appendages and head touched the surface. Later, orange *Fusarium culmorum* and dark green *Aspergillus* species were observed. Fungi were visible on the carcasses throughout the experiment, eventually growing on exposed bones.

During *Calliphora* colonisation the fungi deteriorated, although when larvae left to pupate (often taking fur and tissues with them), the mycelia spread onto the surrounding sediment then degenerated. At 42m into the cave, the resting bodies of *Microascus* were observed, these black sclerotia persisting for several years.

The fate of carcasses depended on location. At the entrance, mummification occurred, the skin decomposed gradually over the years, accompanied by slow disarticulation. Farther into the cave, wet decay led to partial disarticulation after the first year (Table 1). Carcasses in wetter cave areas decomposed much more rapidly than in drier regions.

Disarticulation began as the tail bones and mandibles detached. Later, cervical vertebrae separated and the skull gradually moved away from the carcass. Eventually, major limb bones detached. Carcasses deposited between 12 and 36m were largely skeletalised by the fourth year, the

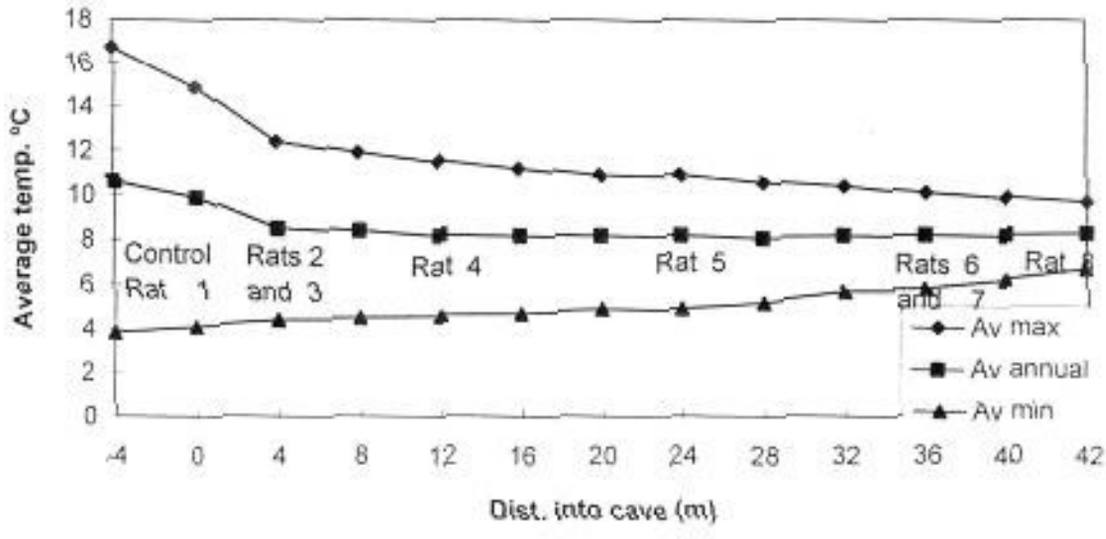

Figure 4. Church Hole Cave, ground temperatures 1986-1991

Days since deposit	Cont. rat	4 m left	4 m right	12 m rat	24 m rat	36 m a rat	36 m b rat	42 m rat
0	Fresh	Fresh	Fresh	Fresh	Fresh	Fresh	Fresh	Fresh
20	Rancid		Burial		Rancid			
40	Dry	Rancid	Buried	Rancid		Rancid	Rancid	Rancid
60	decay							
80				Wet				
100				decay	Wet	Wet	Wet	Fungal
120	Mumm	Dry			decay	decay	decay	decay
140	-ified	decay				Disart	Part	
160							disart	
180								Wet
200	Skin		Necro.					decay
300	decay		emerg.	Part	Part		Disart	
400	Scav.			disart	disart			
500		Mumm					Skin	Dry
600		-ified				Bone	decom	decay
700			Buried	Skin		and	and	and
800		Part		decay	Disart	skin	dry	skin
900		dis-			and	decay	decay	decay
1000		art		Dry	dry		Bone	
1200				decay	decay		decay	
1400			Spoil					Bone
1600		Dis-	heap	Dis-	Bone	Bones		decay
1800		art	flat	art	decay	spread		
2000		Scav.		Scav.				

Key to terms:

Rancid:	with strong odour and active maggot colonisation
Scav:	scavenged (carcass removed via non-human or human activity)
Disart:	disarticulated, typically tail and/or neck vertebrae separated, followed by limb disarticulation
Necro:	Necrophorous investigator
Decom:	decomposing/decomposition

Table 1. Church Hole Cave, condition of rat carcasses, 1986-1991.

bones spread over a radius of 0.25m. The trunk region remained intact, although the vertebral column often separated. Exposed bones from the axial skeleton became brown and shiny after 2 - 3 years, but skulls remained white. Although the shallower carcasses were vandalised in 1991, the remains at 24 and 36m were untouched and still partly articulated in 1996. The rat buried by *Necrophorus* would require permission from English Nature for excavation.

Carcass weight provides a more quantitative assessment of decomposition (Fig. 7). Weight loss, due mainly to consumption by dipteran larvae, was very rapid for the controls and slower with increasing depth into the cave, but eventually carcasses averaged 27% of their fresh weight. Typically, a 230-250g rat was reduced to 56-74g, the weight of the skeleton and dried skin. These results agree with those of Nabaglo (1973) where bank voles took twice as long to decay in burrows as on the surface. The slower weight loss in the rats at 24 and 42m is similar to that of pig carcasses from which insects are excluded (Putman, 1983).

Invertebrate colonisation

Thirty-three species of invertebrates, all arthropods, were collected from the carcasses (Table 2). Although the number of colonising species decreased with increasing depth, the proportion of cavernicolous species increased. Some animals bred on the material, particularly flies such as *Megaselia brunneipennis* (Phoridae), which colonises dry carrion, and *Heleomyza serrata* (Heleomyzidae). The major carcass coloniser, however, was *Calliphora vomitoria* (blowflies, Calliphoridae). Dipteran colonisation is illustrated in Fig. 8, which shows that carcasses exposed deep in the cave were not colonised by blowflies until 40-50 days after deposition, maximum larval activity occurring later with increasing depth into the cave.

Collembola such as *Lepidocyrtus* spp were observed on carcass and cave floor fungi whilst other species, for example *Quedius mesomelinus* (Staphylinidae) were seen under the carcasses. Widespread in European

Group/Species	Cont	4L	4R	12 m	24 m	36 m a	36 m b	42 m
Acari, Mesostigmata	3	17						
Araneae, *Lepthyphantes* sp	8	6	60		21			
Isopoda, *Porcellio scaber*	3-13	19						
Oniscus asellus			23	15-36				
Diplura, *Campodea* sp					17			45
Insecta/Collembola								
Hypogastrura purpurea				11				
Lepidocyrtus cyaneus	7-11	4-15		5,49	5-11		13	4-5
L. curvicollis					6	6	19	20
Orchesella sp	10							
Insecta/Lepidoptera								
Hofmannophila sp		16			4			
Hofmannophila sp larvae		17						
Insecta/Diptera								
Bradysia brunnipes				15,29			29-30	
Sciaridae sp larvae						5		
Culex pipiens								33
Megaselia rufipes	3-10	2-33	16-28	1-40			38	
M. brunneipennis adults					15-38	2-52		2-38
M. brunneipennis larvae				3		4		5
Heleomyza sp adults		43	3	68	20-37	11	1-29	2-38
Heleomyza sp larvae							3-4	3-4
Sphaeroceridae				39				
Calliphora vomitoria adults	1							
Calliphora vomitoria larvae	1-2	2		2-3	2-4	3		
Insecta/Coleoptera								
Nebria brevicollis			39					
Pterostichus madidus								52
P. strenuus			39					
Necrophorus humator adults	1	2	3					
N. humator larvae			5-7					
Catops tristis		17						
Choleva glauca		3-21	1-3	1				
Alaeochara lanuignosa		2			19			
Acroton fungi				5				
Lesteva sp				6				
Tachyporus hypnorum	10							
Quedius mesomelinus adults		25	5-11	2-21	2-18	2,30	1-22	4-30
Q. mesomelinus larvae				4-7	2-21	6	6-20	1-8
Philonthus sp	2							
Oxytelus laqueatus		1						
Cryptophagus sp adults	7	7						
Cryptophagus sp larvae					8			
Atomaria sp		15	1					
Total species	11	16	10	13	11	6	6	8
- of which cavernicolous	2	4	3	6	6	5	6	7
Breeding on carcase	1	2	1	3	3	2	4	3
Feeding on carcase	4	7	2	6	4	4	3	2
Feeding on fungi	2	1	0	2	3	1	2	3

Table 2. Invertebrates associated with decomposing rats in Church Hole Cave, 1986-1991.
Numbers in the table refer to the time in months from deposition on which animals were observed.
Entries separated by a dash (-) indicate presence on all visits between the first and last indicated.

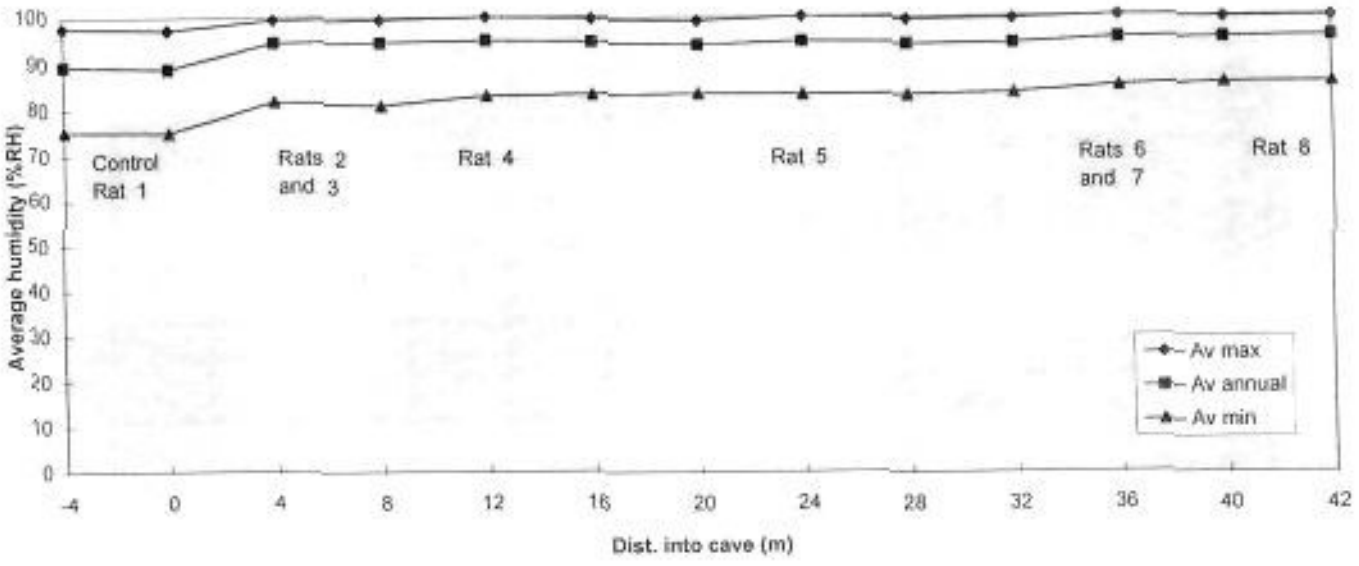

Figure 5. Church Hole Cave, ground humidities 1986-1991

caves (Hippa et al., 1985) and in the eastern United States (Peck, 1988), this predatory beetle feeds on dipteran larvae and Collembola (Turquin, 1983).

Robin Hood's Cave

Temperature and Humidity

The average temperature over the experimental period was 10.5°C (95% limits +/- 3.5°C) at 7.5m into the cave; warmer than, and more variable than Church Hole Cave at the same depth. At 37m, it was also slightly warmer at 8.7°C (+/- 1.3). Temperatures were also higher at the third site, 45m into the cave at 9.9°C (+/- 0.9).

The cave entrance was slightly less humid than Church Hole, at 87.5% (+/- 7.2%), but almost the same at 37m (95.7% +/- 7.4). Although the site at 45m was deeper than at Church Hole, the stagnant cave air here was almost saturated. All figures quoted are annual averages over the two-year study period.

Since carcasses were deposited in June, those at 7.5m experienced higher temperatures than in Church Hole, averaging 13 °C during the active decomposition phase. Carcasses exposed at 37 and 45m decayed at temperatures 1 °C higher than Church Hole for the first 90 days.

State of rat carcasses

The decomposition of the rats 7.5m into Robin Hood's Cave resembled that at 4m into Church Hole, although conditions were drier. *Calliphora vomitoria* larvae were seen 5 to 9 days after deposition and all soft tissues were consumed in the following three weeks. After this much of the hair was shed and moved up to 2.5m by dispersing larvae.

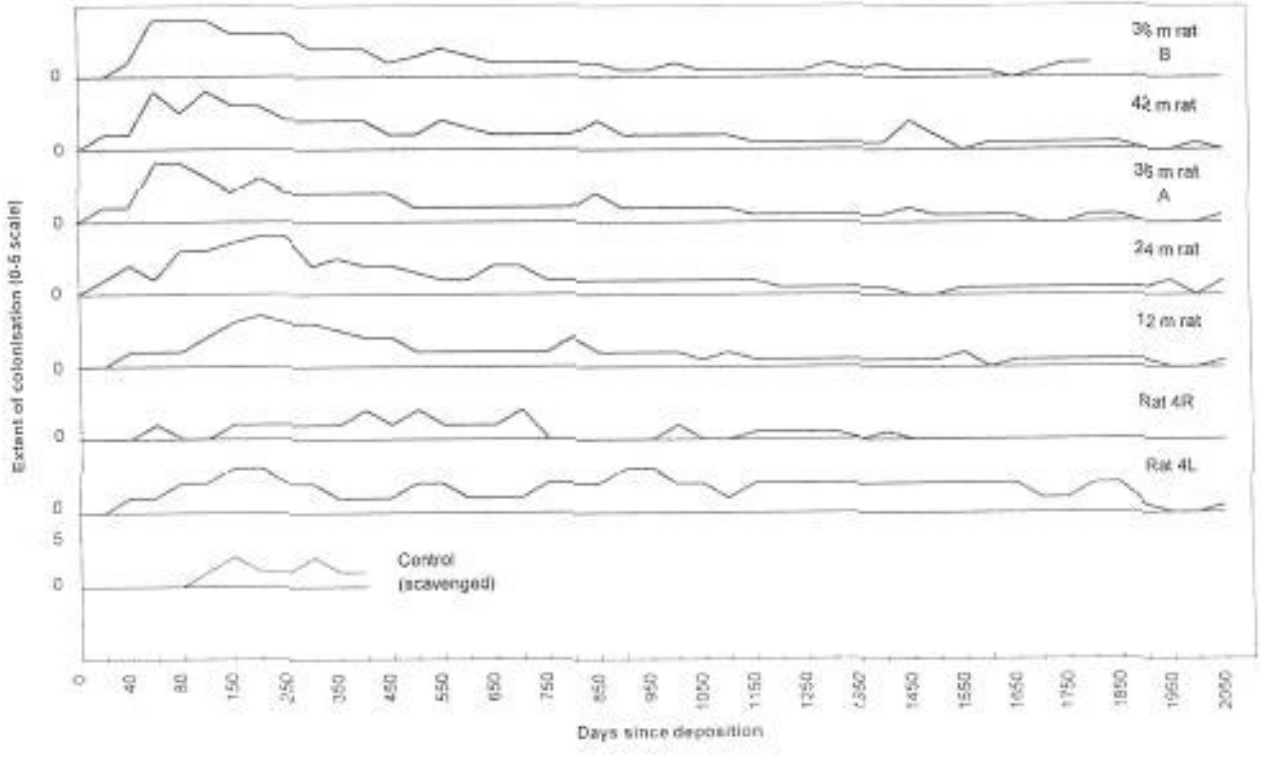

Figure 6. Church Hole Cave, fungal colonisation of rat carcasses. (0-5 scale)

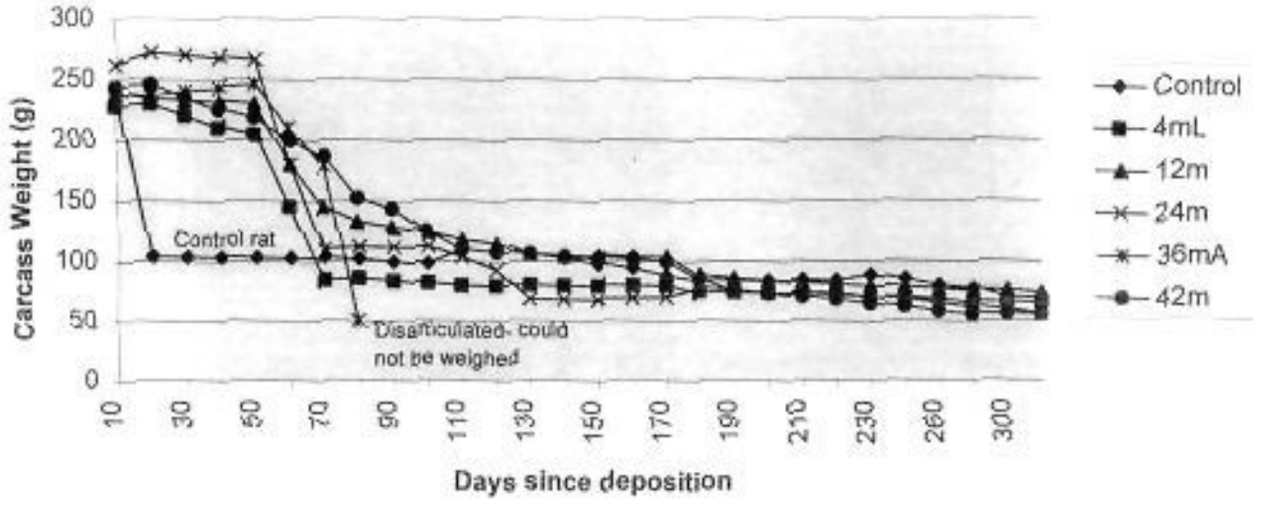

Figure 7 Church Hole Cave, weight loss of rat carcasses during first year

The carcasses attracted many other insects, but there was no burial by *Necrophorus*. Later, the remains were attacked by moths, especially *Hofmannophila pseudospretella* (Tineidae), the brown house moth, but the end point was always mummification. All carcasses remained intact and stabilised at 20-25% of their original weight.

At 37m fungal colonisation was rapidly followed by enormous numbers of phorid flies mainly *Triphleba antricola* and *Megaselia rufipes*. The carcasses were then colonised by *Calliphora vomitoria*. In the first two months, carcass weights reduced by 75%. After larval dispersal, fungal decomposition attracted the troglophilic gnats *Lycoriella leucotrica* and *Bradysia brunnipes*, the latter breeding on the carcasses. Finally, dry decay occurred and the carcasses were colonised by staphylinid beetles such as *Quedius mesomelinus* and *Bessobia* sp. and *Cryptophagus acutangulus* (Cryptophagidae). After two years the remains were largely skeletalised, partly or totally disarticulated, but unburied, with sporing colonies of *Fusarium*, *Microascus* and *Aspergillus*.

At 45m, initial decomposition was fungal and dipteran. Some carcasses were colonised by basidiomycetes and then by *Calliphora vomitoria*. All attracted Phoridae, the same species as at 37m predominating. This colonisation began after 6 weeks and lasted for 5 months. It was followed by the sciarid flies *Bradysia brunnipes* and *Lycoriella leucotrica*, the former breeding on the slowly decaying carcasses. The remaining decomposition was fungal, with a thriving community of mostly troglophilic arthropods. After two years, carcass weight stabilised at 25-30%; all rats were partly or totally skeletalised, disarticulated and covered with a layer of sclerotia from *Microascus*. Minor bones were jumbled, but in half of the carcasses the axial skeleton was intact.

Effects of carcasses on cave invertebrates

Table 3 shows the results of pitfall trapping before and during the decay process and the percentage of species gained, lost or unchanged. Species richness increased at all sites as sarcophagus insects were attracted into the cave. The 7.5m site gained 55 species during the experiment (50% of the total), but lost only 15. At 37m the gain was 32 species, and at 45m 18 species were added, but 11 lost (22% of the total).

Before carcass deposition, species richness declined by almost 50% from the cave entrance to the hypogean region, as observed in 1983-84 (Terrell-Nield, 1985). This pattern persisted during the first year of

	Baseline (10 months)			Experimental year 1			Experimental year 2		
Depth (m)	7.5	37	45	7.5	37	45	7.5	37	45
Total species	49	40	28	59	47	29	39	24	23
Total individ	637	1000	442	1431	5108	2718	691	3251	2447

Species/Depth	7.5 m	37 m	45 m
% Gained	50	42	37
% Lost	13	30	22
% Unchanged	37	28	41

Note: At 7.5m, 22 of species gained were associated with carrion, including 13 diptera. At 37m, 12 species gained were carrion-associated (11 diptera). At 45m, of the 12 carrion-associated species gained, 10 were dipterans.

Table 3 Species richness, numbers of individuals and community change of arthropods trapped in Robin Hood's Cave before and after carcass deposition

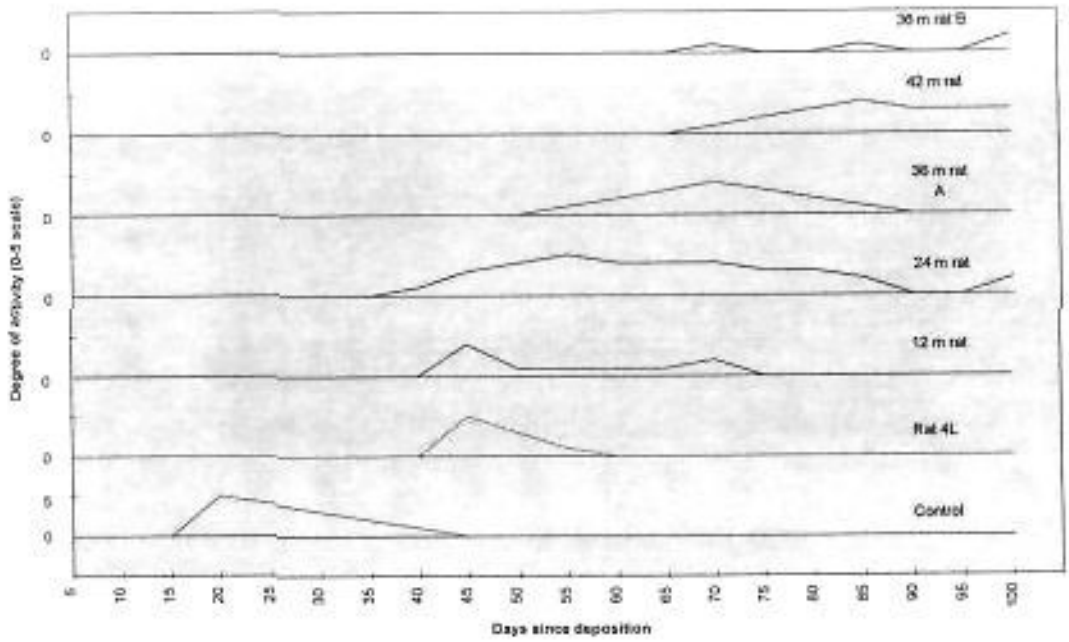

Figure 8. Church Hole Cave, extent of maggot activity in rat carcasses, (0-5 scale).

deposition, but the total number of individuals more than doubled at the front of the cave, increased five-fold at 37m and by six times at 45m. Numbers in the cave threshold decreased almost to the baseline in the second year. There was less decrease in the middle and little at the back.

If population sizes increase much more than species numbers, a measure of diversity such as Shannon-Weaver's H (which takes into account the proportional abundance of each species) will show a decline (Rickleffs, 1996). Fig. 9 shows that the deeper cave regions were particularly affected, since most additional individuals came from a small number of species. This also affects the Evenness, which reaches a maximum of 1.0 when all species are equally present (Odum, 1971). Again, the cave entrance was little affected but the central part of the cave showed a marked decline.

The main species responsible for diversity changes are listed in Table 4. The major introductions are thrips such as Aelolothripidae (known to breed in decomposing material) and the sarcophagus flies *Calliphora* and *Megaselia*. The ichneumonids and braconids are parasites of dipteran and lepidopteran larvae. None of the new species persisted into the second year, although more species were added.

Twenty pre-existing species were strongly affected by the experiment, 14 positively, 6 negatively. The largest increases were seen in the Phoridae, but Brown House moths (*Hoffmanophilia* spp) which attack skins and fur, also increased substantially. Many more thrips and predatory mites (Mesostigmata) were seen, but the latter are commensal on the phorid *Triphleba*. Some fungus feeders such as Collembola, Mycetophilidae and Cecidomyidae increased, the first much more so in year 2. *Cryptophagus ruficornis*, which feeds on dry, mouldy material was stimulated, but the troglophilic *C. acutangulus* declined in numbers.

DISCUSSION

Decomposition is vital to ecosystem energy flow, especially in habitats *without primary producers*. These studies indicate that animal remains deposited even shallowly in caves decompose differently from those on the surface. Differences in decay are attributable to the cave environment and the difficulty of access to the carrion by non-cavernicolous species. The caves at Creswell are relatively shallow, with only a few troglobitic species (Terrell-Nield, 1985), so many of the arthropods involved in decay were epigeal.

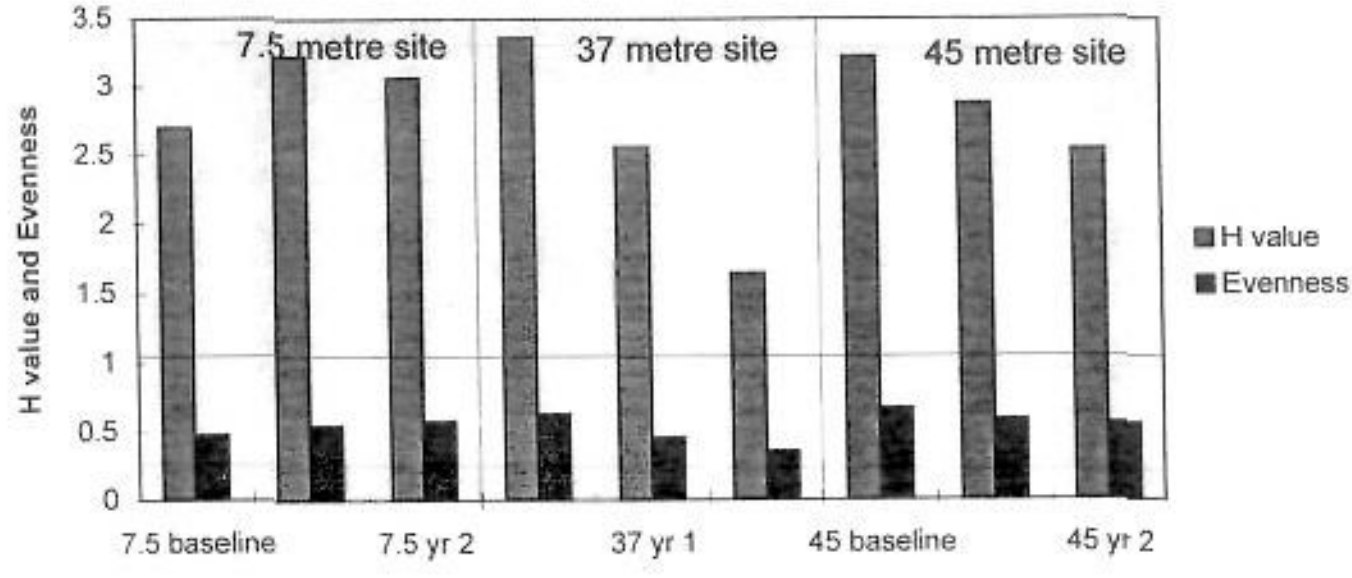

Figure 9. Robin Hood's Cave, effects of decomposing rats on arthropod diversity during the first two years.

a) Major families and species added (+) (represented by more than one individual)						
Depth	7.5m		37m		45m	
Group/Species	Year 1	Year 2	Year 1	Year 2	Year 1	Year 2
Arachnida						
Chthonius ischnocheles		+				
Tegenaria sp		+				
Myriapoda						
Brachydesmus superus						+
Insecta/Thysanoptera						
Acolothripidae (2spp)	+		+			
Insecta/Diptera						
Psylopus sp (2spp)	+					
Trichosa absurda			+			
Megaselia bifida			+		+	
Calliphora vomitoria	+		+		+	
Insecta/Hymenoptera						
Ichneumonidae (1sp)	+					
Braconidae (1sp)	+					
Pteromalidae (1sp)			+			
Insecta/Coleoptera						
Alaeochara lanuignosa	+					
Oxypoda opaca		+				
Xylostiba monolicornis			+			
Bessobia sp			+			
Omalium excavatum	+					
b) Pre-existing species with more than a 5-fold change over baseline (- = decline, bracketed = lost)						
Arachnida						
Astigmata (Acari, 1sp)	x 8					
Prostigmata (Acari, 1sp)			x - 11	x - 10		
Mesostigmata (Acari, 1sp)	x 24		x 7		x 31	
Cryptostigmata (Acari, 1sp)	(x -2)		(x - 2)		(x -10)	
Porhomma egeria (Araneae)					x -5	
Insecta/Collembola						
Hypogastrura purpurea					(x -6)	
Onychiurus sp						x 7
Lepidocyrtus cyaneus			x 5			x 15
L. curvicollis						x 11
Pseudosinella alba						x 5
Neelus sp	(x -25)		x -9	x -30		
Arrhopalites pygmaeus	(x -13)			x -25		
Insecta/Thysanoptera						
Thripia sp	x 21	x 35				
Insecta/Lepidoptera						
Hoffmanophilia pseudospretella	x 110	x 41				
Insecta/Diptera						
Bradysia brunnipes	x 5				x 22	x 5
Lycoriella leucotrica					x 8	x 5
Triphleba antricola	x 35		x 2130		x 546	
Megaselia rufipes	x 9		x 1099			
Insecta/Coleoptera						
Cryptophagus acutangulus			(- 1)			
C. ruficornis				x 15		

Table 4 Species turnover in Robin Hood's Cave during carcass deposition

Air temperature is critical in controlling decomposition, since carcass temperature determines the rate of bacterial and fungal development (Nabaglo, 1973). Environmental temperature also affects the metabolism of colonising and associated invertebrates, dipteran larvae developing more slowly at lower temperatures. Just as important, however, are temperature and humidity variation in the cave threshold.

Cave passageways "breathe" (Barr, 1968), because of the density gradient between cooler and warmer air. In summer, denser cool air flows out of the caves, taking with it the odour of decay that will attract necrophagous insects. In both caves, relative humidity became progressively lower and more variable towards the entrance. Here, drying airflows can create an environment lethal to cavernicoles adapted to high humidities (Chapman, 1993), but which provides suitable conditions for mummification before or after dipteran evisceration. The Medico-Legal Society (1976) commented that mummification is likely in warm dry surroundings, especially with air movement.

Desiccation of the remains significantly slows down decomposition because the body becomes too dry to sustain most fungi and insects. It is important for the long-term integrity of the carcass that disarticulation is largely prevented by the encasing and shrunken skin. If the remains are subsequently buried, the skeleton should remain substantially intact even if the skin is decomposed. These events are more likely in the cave entrance, and may be observed above ground in dry conditions.

In the mid part of the caves, decomposition was more complete. Even in dry passages, the humidity of cave air rarely falls below 80% (Culver, 1982). Although these caves have no running and little standing water, continuous drips and limited air circulation often produce summer humidities of 100%. Under these conditions there were clear stages of fungal colonisation, dipteran consumption and wet decay, followed by dry decay. Disarticulation occurred as cartilage and connective tissue were decomposed, but rats deposited close together decayed at different rates, emphasising the importance of local microclimates. Under these conditions, rats lost substantial parts of their skeletons in 2-5 years.

Decomposition in the deepest part of the caves was primarily fungal. Insects initially played a lesser role, leading to relatively gentle decay, especially where carcasses were colonised by Phoridae and Heleomyzidae. The end point was a partly disarticulated but complete skeleton covered in a mass of resting fungal stages. Fungal decay in the hypogean region is thus particularly important for both decomposition and invertebrate populations. This supports findings by Dickson and Kirk (1976) that the abundance of cave-limited invertebrates correlated with the abundance of micro-fungi.

For an animal that dies in a cave, or is carried in by a predator, the extent of consumption by non-cavernicoles will depend on its location. Close to the entrance, dipterans will predominate, but even here carcasses lose weight more slowly than outside, since flies may take longer to find them. The slower weight loss may also be a consequence of lower shade temperatures, which reduce the metabolism of fly larvae.

Flies dispersing from a carcass normally move towards light which will take them to habitats where more oviposition chances are likely. However, in both caves there was a "chain" of carrion. The emergence pattern is akin to an "island effect" where animals disperse along an archipelago. This may explain blowfly colonisation of rats at 45m in Robin Hood's Cave. In contrast, the second rat at 36m in Church Hole Cave attracted only Phoridae and Heleomyzidae. This animal was deposited one year after the first and there was no chain of fresh carrion to lead blowflies to it.

There have been few observations of *Heleomyza* breeding in caves, and several authors doubt that this happens (Hazelton, 1977, Chapman, 1993). In the present study, *Heleomyza serrata* emerged from pupae taken from carcasses at 36 and 45m. However, the larval populations were small.

Later stages of decomposition attracted other diptera, particularly those associated with fungi. Sciaridae were the most prominent group, including cavernicolous species such as *Bradysia* and *Lycoriella*. Associated with the dry decay stage were larvae of the Brown House moth, *Hofmannophila pseudospretella*, as well as detritivorous beetles such as Cryptophagus. The carcasses also attracted predators, especially the cavernicolous staphylinid *Quedius mesomelinus*. All stages of the beetle were found under or near the carcasses, the carrion having an important effect on its population.

Other beetles such as Necrophoridae attack only very fresh carrion. They will not breed if there is insufficient sediment for interment. Burial may result in a fully intact skeleton since scavengers do not break up the carcass and there is less chance of weathering or trampling dispersing the remains (Andrews, 1990). Digging may also disrupt sediment stratigraphy, inserting remains in levels to which they do not belong. This post-mortum movement must be considered when interpreting excavated remains (Jenkinson and Gilbertson, 1984).

Decomposing remains thus attracted cavernicolous and non-cavernicolous arthropods from several trophic levels. The main effect was to modify significantly the threshold fauna by the addition of new species and the stimulation of existing ones. Few new species persisted beyond the first year, being closely associated with the earlier stages of decomposition, so this cave region began to return to its previous state. The introduction of non-cavernicolous species into the hypogean regions reduced diversity, but most of the decrease was due to population increase in pre-existing species, an effect still detectable after two years.

The deep cave is a vulnerable, energy-poor environment. The addition of only small amounts of carrion may have profound effects that persist beyond the active decay stage. It is therefore important to consider the effects on cave communities of deliberate or accidental introduction of carrion or any other putrescible material, and take into account carcass location when interpreting animal remains discovered therein.

ACKNOWLEDGEMENTS

This work was funded in part by a grant from the Science and Engineering Research Council (SERC), and carried out with the permission and assistance of Creswell Heritage Trust.

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