Small mammal deposits in archaeology:

a taphonomic investigation of *Tyto alba* (barn owl) nesting and roosting sites

James Philip Williams

Volume 1

Thesis submitted in fulfilment of the Degree of Doctor of Philosophy.

Department of Archaeology and Prehistory

University of Sheffield

February 2001

Dedicated to the many owls who have contributed countless pellets to this research, often without their permission, and also to the numerous small mammals who have given up their short lived lives to become part of this study.

Dedication Figure. One man and his owl.

Summary

Small mammals have often been utilised as indicators of past environments. Before palaeoecological assessments can be made, investigations into the origin and mode of deposition are carried out. Many small mammal accumulations are predator-derived, and in order to take account of predatory bias in these deposits, it is necessary to identify the predator. Several methodologies have catalogued patterns of bone modification from dietary waste of modern predators, for comparison with taphonomic features found on archaeological assemblages of small mammals. The majority of this research has concentrated only on the adult age range from these predators. However, data from owls have shown that younger individuals are often responsible for more extensive bone modification. To investigate this difference associated with the age of predators and bone modification, two modern *Tyto alba* roost samples and three modern *Tyto alba* nest samples were analysed to provide evidence of bone modification from adult and baby owls.

Significant differences were found between these two groups, with higher rates of bone digestion associated with the nest samples. To test whether these taphonomic patterns could be identified in archaeological deposits, small mammal assemblages from four archaeological sites (The Old Vicarage at Tadcaster, Filey Roman Signal Station, Fox Hole Cave and Carsington Pasture Cave) were analysed. At one of these sites, bone digestion matched that of the *Tyto alba* nest sites. Bone digestion at the other three sites was higher than that recorded in this study for either *Tyto alba* adults or their young. This study has shown that it is possible to recognise owl nests in the archaeological record, and concludes that analysis of these assemblages can elucidate not only the origin of specific predator deposits, but can also be used to investigate the nature of human occupation, usage and abandonment of these sites.

Small mammal deposits in archaeology: a taphonomic investigation of *Tyto alba* (barn owl) nesting and roosting sites.

Contents

Tables

Figures

Appendix tables

Appendix figures

Acknowledgements

I would like to begin by thanking all three of my supervisors, Professor Robin Dennell, Dr. Andrew Chamberlain and Professor Peter Andrews, who have offered genuine and considerable support throughout this research, and freely given guidance, advice and criticism wherever and whenever it has been needed. I must also thank them all for the speed with which they have always responded to questions, and demands for proof readings that have enabled me to complete this research within the time allocated. I would also like to thank the other members of the Department of Archaeology and Prehistory at Sheffield who have given their time and advice throughout the last three years, especially Dr. Pia Nystrom, Ms Pat Collins and Dr. Paul Buckland.

I would also like to thank Dr. Andrew Chamberlain, Dr. Keith Dobney and Ms Ros Westward for providing access to the archaeological small mammal deposits, and Professor Peter Andrews and Mr Colin Shawyer for the modern comparative roost and nest samples. I am also indebted to both Mr Derek Whiteley of Sheffield Museum and Ms Clem Fisher of Liverpool Museum for providing access to comparative collections for analysis of *Arvicola terrestris* (water vole) enamel structure. Furthermore, thanks are also extended to Dr. Patrick Ottaway and Mr. John Dilley and Dr. Derek Yalden for their advice on archaeological sites from which the small mammals were sampled.

My final thanks must go to those who have provided me with constant support throughout this process, and have had to read more about small mammals than they will have ever wanted to, my father Mr Phil Williams, and my wife and best friend, Ms Erika Petersen.

1.Introduction

1.1 Introduction

To understand fully the lives of human individuals and communities that are constructed from the analysis of material culture excavated from archaeological deposits, it is essential to consider the environment which they inhabited, and whether any changes to the nature of this environment may have affected their lives and actions. Within archaeology the study of these past environments has often been restricted to the analysis of a limited number of palaeoenvironmental indicators, such as plant macro- and micro-fossil evidence, pollen, terrestrial molluscs and coleopteran remains. Where the preservation of these remains is poor, due to soil conditions or the location of deposition, palaeoenvironmental considerations have been limited.

In many cases, the very conditions which lead to the low recovery of these 'traditional' types of evidence, tend to favour the preservation of the bones of both small and large mammals. The small mammals are particularly sensitive indicators of the environment and climate, and many species show a strong preference for specific habitats. When small mammals become incorporated within archaeological deposits, it is possible to apply this information to use small mammals as indicators of past environments. In spite of this, the role of small mammals as palaeoenvironmental indicators has rarely been studied by archaeozoologists, despite the importance given to this line of evidence by vertebrate palaeontologists.

However, before any environmental reconstructions can be carried out, there are a number of external factors to be considered. Small mammals rarely occur in archaeological deposits through any fault of their own, and they often appear within bone assemblages as a result of predator activity[1]. It is important to try to understand which predator was responsible for the deposit, as different predators have different

---

[1] In the majority of cases, the predatory origin of small mammal bones does not include humans as a possible predator, as unlike larger mammals, birds, fish and marine molluscs, these animals have a very low nutritional value, and the energy expended in catching them may be, in many cases more than that provided by their consumption. However, there are a small number of ethnographic examples of the exploitation of small mammals (Henshilwood 1997), and the role of small mammals in prehistoric human diets should not be entirely ruled out (Stahl 1982). This is further discussed in chapter two.

prey selection strategies and preferences. This may affect the prey species composition of the fossil assemblage, leading to the over- or under-representation of specific species, which may in turn bias any subsequent attempt to reconstruct the environment which these prey species represent.

It can therefore be seen that a palaeoenvironmental analysis of fossil microvertebrate assemblages has two principal tasks, the investigation into the factors determining the deposition of the small mammal material (taphonomy), and the environmental reconstruction based on the species contained within the deposit (palaeoecology).

1.2 Taphonomy

A fossil assemblage rarely contains the bones of animals in the location where they died, and it is often the case that these animals died as a result of predation rather than natural senescence. In many instances the bones of these animals may have been transported from their original point of deposition, and the remains may be fragmented either as a result of this movement, or through the destructive impact of predator activity. The potential for these bones to be buried and survive to be excavated and analysed is also affected by the nature of preservation accorded by the depositional environment.

In order to understand how these often fragmented remains represent the nature of the palaeocommunity or palaeoenvironment from which they came, it is necessary to reconstruct the chain of events that ultimately led to the discovery and excavation of the fossil material. The study of these events, which attempts to catalogue the life history of a specific fossil, or fossil assemblage is called taphonomy. This term was first coined by Efremov (1940), to describe the study of the 'laws of burial' affecting biological and zoological remains, and it covers both the pre-depositional and post-depositional history of these organisms. It takes as its starting premise the Laws of Uniformitarianism, and the concept of analogy, such that factors affecting the life and death of modern day organisms and their environment are applied, by analogy, to the study and understanding of these systems in the past. Although it was Efremov (1940) who first

used the term taphonomy, the analysis of the history of fossils and their deposition had been the subject of study as early as the nineteenth century, by researchers such as Rev. William Buckland and Charles Lyell (Lyman 1994: 13). For an in-depth review of the history of taphonomy see Lyman (1994: 12-41).

The following chart, adapted from Andrews (1990), summarises the various stages in the life and death of a fossil, where the study of taphonomy can shed light on the multitude of environmental (and cultural) agencies associated with the deposition and subsequent discovery of a fossil or fossil assemblage.

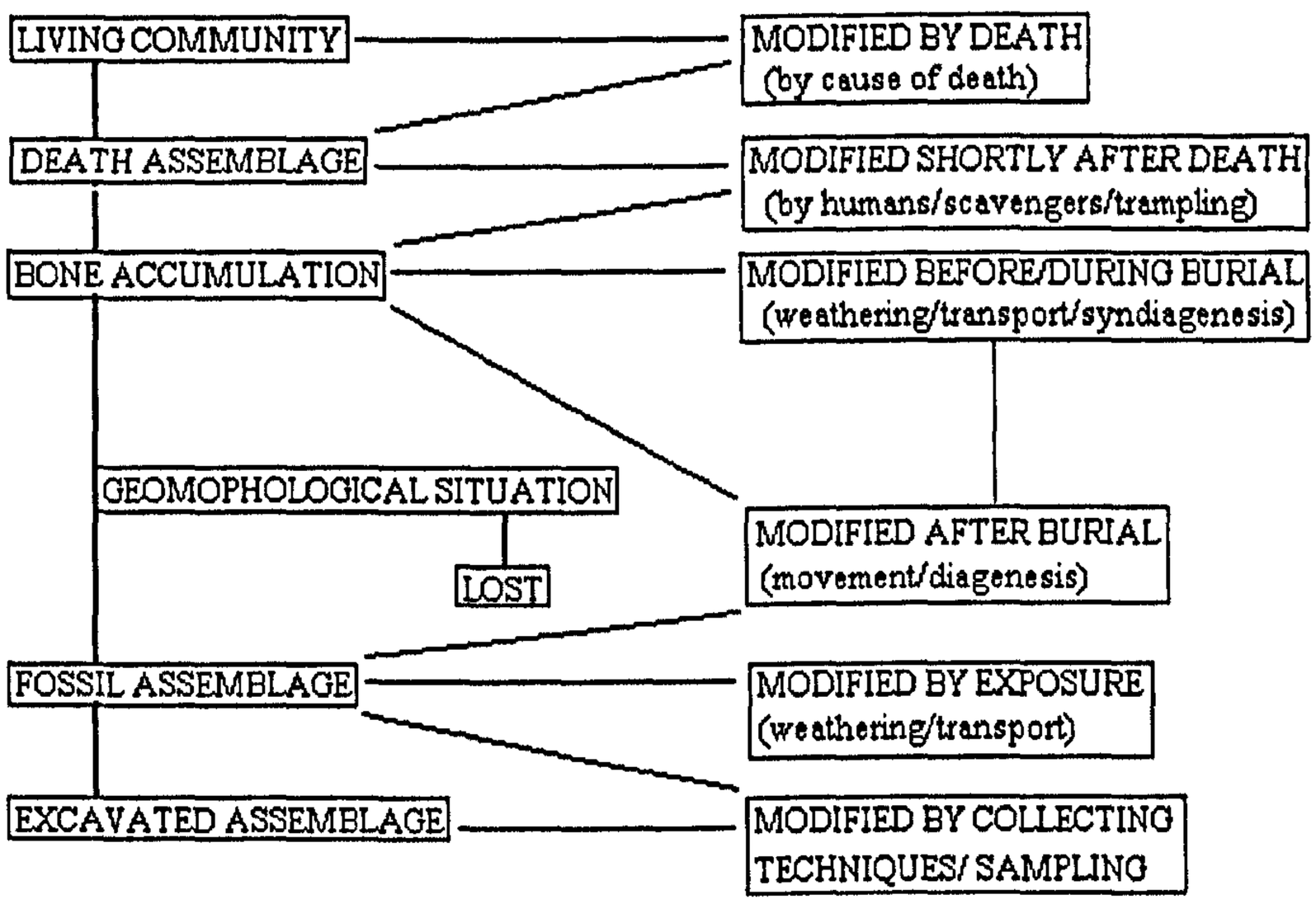


Figure 1. Diagram of the taphonomic stages involved in the accumulation of a fossil assemblage, after Andrews (1990).

In many cases, the techniques employed in small mammal taphonomy mirror those from the study of taphonomy as a whole. The principal difference is that small mammal taphonomy is concerned with only those mammals whose live body weight is under approximately 5kg; although most British small mammals weigh considerably less than this. Figure 1 above, shows all the stages in the formation and modification of fossil mammal bone assemblages, and these apply to small mammal assemblages as well as those containing larger mammals. Within this study, the research will concentrate on the first two aspects of this process, the living community and the death assemblage. Consideration will also be given to the problems encountered during excavation and

sampling, as well as problems with the analysis and interpretation of the deposits. However, only taphonomic methods applied to small mammals will be considered here. A critical review of the relationship of taphonomy to archaeology is provided by Gifford (1981). For a more wide-ranging review of vertebrate taphonomy, see Lyman (1994).

The next chapter (chapter two) reviews the subject of small mammal taphonomy, concentrating on the methodologies employed by various researchers to recognise the predatory origin and other possible modifying agents involved in the accumulation of microvertebrate assemblages. It concludes by considering how these modifying agents affect the composition of fossil assemblages, with specific reference to how an interpretation of a given environment can be biased by these processes.

As this research involves one specific predator, *Tyto alba* (barn owl), most of the analysis in this study concerns purely taphonomic issues of identifying and interpreting patterns of bone modification. The main interpretive tool in this analysis is the study of modern day owl species, and a summary of the biology and behaviour of *Tyto alba* is given in chapter three. The role of the predator is further analysed in chapter five, where predator / prey relationships are considered.

1.3 Palaeoecology

The previous section outlined the importance of taphonomic research to understanding the depositional history of fossils and fossil assemblages. However, taphonomy does not stand alone as a subject by its own account. It is in fact an integral part of the study of palaeontology and palaeoecology, and is to palaeontology what 'site formation processes' (Schiffer 1983), and 'middle-range theory' (Binford 1977) are to archaeology[2].

---

[2] I choose to make the distinction here between taphonomy in its original form, as applied to vertebrate (and invertebrate) palaeontology, and its appropriation by the archaeological community as a term to describe geological phenomena affecting the burial and preservation of artefactual remains. I make this distinction because I do not believe that methodologies signified by the term taphonomy provide an adequate investigative tool to analyse the complex nature of the role of human agency in the deposition of cultural remains. This human agency should not however be confused with that implied above (see figure 1) with reference to the excavation and recovery of fossil material, and the role that this process has in the overall modification of a fossil assemblage.

One of the main purposes of carrying out taphonomic research is to control for the events in the history of the fossil which would otherwise bias the interpretations made concerning the organism's placement within its original palaeocommunity, and hence how that community reflects the environment at the time of deposition. For small mammal assemblages, the most common form of modification of the fossil assemblages is the initial prey selection from the palaeocommunity. Different predators have different criteria and methods of selection of prey, and it is vital that taphonomic analysis is employed to identify these predators and then control for their effects.

Having identified the predator responsible for the accumulation, it is then possible to analyse to what extent the activities of that predator affect the prey species composition of the fossil assemblage. This is also done by comparison to modern day predator species, and details of *Tyto alba* hunting strategies are described in chapter three. In order to understand how the prey captured by, for example *Tyto alba*, reflects the composition of the environment from which is taken, it is also vital to understand the ecology of the small mammals themselves. A review of the habitats of the most common British small mammals is given in chapter four, and an analysis of the relationship between predator and prey is covered in chapter five. It is important to take into account all of these factors when producing a palaeontological reconstruction, the methods of which are described at the end of chapter five.

1.4 Other aspects of the study of microvertebrate fossil deposits

Despite the emphasis on taphonomy and palaeoecology, there are other areas in which the study of small mammals can inform archaeology and palaeontology. These are discussed briefly below, but do not feature with particular prominence in the rest of this research.

1.4.1 Occupation and abandonment

In Britain there are two species of rodent that live in close proximity to humans, *Mus domesticus* (house mouse) and *Rattus sp.* (rat)[3]. They occur in most urban environments, and many rural areas where shelter and food is available (Hinton 1931; Taylor 1991; Taylor *et al.* 1991). In places where their numbers are high, there will obviously be the chance that after natural death some of these animals become incorporated within archaeological deposits. This can be seen in the predominance of these two species in the small mammal faunal inventory from excavations at York (Buckland 1976; O'Connor 1988; O'Connor 1989; O'Connor 1991). In cases where the small mammal deposit is predator-derived, the species composition of this assemblage will be more mixed, and may contain species from a wider area than the limit of human habitation.

For a substantial small mammal assemblage to accumulate at a site through the activity of predators, it is likely that the site is not in constant usage by humans. This certainly applies to owls, and especially *Tyto alba* (barn owl), which will roost and nest in abandoned buildings in both towns and the countryside. Therefore, when large accumulations of small mammal bones are recovered from archaeological excavations within buildings or similar areas of occupation, it is reasonable to suggest that at the time of deposition the building was unoccupied, or only used occasionally (Dobney *et al.* 1996; Matthews and Hastorf 2000). This point will be further discussed in the concluding chapters, with reference to some of the small mammal deposits analysed in this study.

---

[3] At present in Britain the most common species of rat is *Rattus norvegicus* (common or brown rat). There have also been isolated finds of *Rattus rattus* (black or ship rat) from London and Avonmouth (Taylor 1991: 256). However, this has not always been the case, and until the beginning of the eighteenth century when *Rattus norvegicus* began its colonisation (Taylor 1991: 257), *Rattus rattus* was the only rat recorded in archaeological contexts from the time of its introduction during the Roman period (Rackham 1979; Yalden 1999: 125, 162).

1.4.2 Small mammal biostratigraphy

Small mammals have a rapid evolutionary turnover, with adaptations to new and changing environments giving archaeologists and palaeontologists the ability to reconstruct past environments on the basis of specific species' habitat requirements. This high rate of turnover offers evolutionary biologists the opportunity to study the various mechanisms that drive this change (Barnosky 1987), and more importantly for this study, also allows archaeologists to use the appearance and disappearance of certain species as a measure by which to date deposits, and periods within these deposits (Yalden 1982; Mayhew and Stuart 1986; Cuenca-Besco *et al.* 1997:187; Yalden 1999).

This approach to small mammal biostratigraphy will be utilised in this study to discuss the age of the four sites being analysed, and also to provide evidence of small mammal populations and introductions to Britain during the Holocene. It must however be recognised that the study of biostratigraphy is also dependant upon sound taphonomic research. This is aptly demonstrated by a number of anomalous discoveries in Holocene deposits from Britain and Ireland, where species have been found at times before their recorded introduction, or occur on islands which they have never colonised[4] (Kowalski 1990; Yalden 1992: 97; Yalden 1999: 67).

[4] The case of the 'Thatcham rabbit', a supposed Mesolithic rabbit (*Oryctolagus cuniculus*) is certainly intrusive (Yalden 1992:97), which is not surprising for a burrowing species! Small mammals may also be transported over large distances in the digestive tracts of predators (Kowalski 1990: 290), which has lead to the discovery of isolated examples of *Microtus agrestis* (field vole) in both Ireland (Savage 1966) and the Isle of Man (Corbet 1971), where the species has never been recorded in the wild.

1.5 Summary and aims

This study is principally concerned with taphonomy, specifically small mammal taphonomy. It is focussed on identifying the predator of microfaunal assemblages, which is essential before one can attempt to categorise the nature of the predator / prey interactions and produce a reconstruction of past environments. In this study, the specific predator under analysis is *Tyto alba* (barn owl).

Over the past twenty years a set of comparative criteria of bone modification by specific predators has been produced, through the study of pellet and faecal remains collected from modern avian and mammalian predators (Andrews 1990). These comparative data are then used to analyse the possible predatory origin of past faunas. In the case of owls, the majority of this modern data was collected for adult owls.

However, there is some evidence to suggest that young nesting owls produce greater amounts of bone modification than their parents (Andrews 1990: 32-33). This is probably an indication that the young owls 'make greater use of their food', digesting some of the bones as well as the flesh to optimise mineral intake during the early stages of their development (Raczynski and Ruprecht 1974: 8). To test whether it was possible to differentiate between the patterns of bone modification produced by adult owls and their young, three modern *Tyto alba* nest deposits were sampled and analysed, and compared with results from the analysis of two modern *Tyto alba* roost sites. These data were then used in the analysis of the predatory origin of deposits from four Holocene archaeological sites in Derbyshire and Yorkshire. The results of this research are given in chapter eight, and discussed in chapter nine.

2. Small mammal taphonomy; a review of the literature and methods.

2.1 Introduction

Not all excavated small mammal bones are accumulated as a result of the natural death of these animals, although examples of natural, accidental and catastrophic deaths of small mammals have been recorded in the archaeological and palaeontological record. However, the majority of microfaunal assemblages are likely to have been deposited by either avian or mammalian predators. Unfortunately, deposits within palaeontology and archaeology rarely contain both the accumulator and the accumulated; the predator and its prey (Andrews 1990: 27). It is therefore essential to employ a number of techniques to enable the identification of the depositional origin of these bones, to investigate the natural cause or predator responsible for the accumulation of small mammal bones.

Equally, after deposition, there are a number of environmental agencies that can alter the nature of the bone assemblage, through transportation, weathering and potential for preservation afforded by the location of deposition. It is important to recognise and differentiate between these various factors contributing to small mammal accumulations, as they may affect any palaeoecological reconstructions produced. It is for the very reason of ensuring correct palaeoecological reconstructions that vertebrate taphonomy is carried out, so that researchers can identify any possible biases that may affect the conclusions that they draw.

This chapter will focus on the methods used in recognising the various factors leading to the deposition of small mammals (predation, natural, accidental, and catastrophic death), and also give a brief overview of the other mechanisms responsible for the modification of small mammal bones and assemblages. The following chapters will review the role of both the predators and the prey, and their interaction, and also consider how the information gained from taphonomic and taxonomic analysis can be used in producing palaeoecological reconstructions.

2.2 Natural death assemblages

Small mammals do not live for a long time - usually about 1-2 years (Corbet and Harris 1991). Therefore, when these animals die, it is either of old age, disease, accident, catastrophe, or predation. However, although the small mammal population of Britain is approximately 240, 292, 000 individuals (Yalden 1999: 260), there are few occasions when one discovers dead small mammals on an every day basis. Even in cases where cyclical population fluctuations, and apparent mass deaths, have been recorded, the physical evidence of the dead often remains undiscovered (Chitty 1996: 8). Rates of decomposition of small mammals and weathering and destruction of their bones are discussed later (see Dodson 1973; Andrews 1995a), but it is clear that in most cases the carcasses of small mammals dying in open environments are likely to be destroyed. Even if predation is not the initial cause of death, consumption by carrion feeding species, both mammalian and avian, as well as insects, would also cause damage and potential loss of the skeletal information.

In most cases, in order for skeletal survival to take place, burial must be no more than a few months after death (Andrews 1995a). However there are a number of burial situations where small mammals are more likely to be preserved. These are pitfall traps, either natural or man-made shafts (Rackham 1982: 87; Yalden and Yalden 1989: 104; Yalden 1999: 163), or caves (Andrews 1990: 3; Behrensmeyer and Hook 1992: 62-63). There is evidence that quite large numbers of small mammals can accumulate in these locations, in relatively short periods of time (Armitage 1985), leading to potentially extensive small mammal deposits[5] (Guilday *et al.* 1964; Guilday *et al.* 1978).

In all cases one would expect the variety of small mammals to represent that which exists in the local area. The condition of the bone will vary according to the various depositional processes acting in each specific case, but it is likely that the skeleton should be relatively unbroken, and all the bones of the skeleton should be present. As no other agency is associated with the collection of these small mammals, the lack of predatory breakage or bone modification could be used to identify natural or accidental death (Andrews 1990: 4). Similarly, complete skeletons would be expected

[5] However, Yalden suggest that in most cases the number of individuals caught in pitfall traps is likely to be quite low (Yalden and Yalden 1989).

in cases where small mammals have died within their burrows, either during hibernation or through flooding or another natural disaster (Andrews 1990).

2.3 Identifying the predators

In Britain, and in most of the rest of the world, there are primarily two types of predator responsible for the death and accumulation of microfauna: mammals and birds. In some cases, reptiles can also be included (Fisher 1981; Andrews 1990: 4). This section will review some of the methods used in identifying these predators, and will be broken down into three sub-sections on the basis of specific methodologies. These are based on the analysis of both taxonomic and taphonomic characteristics of the bone assemblages.

The first sub-section will deal with cases where the identification of the predator has been based upon the species (taxonomic) composition and prey size. The second sub-section will review the contribution made by the analysis of skeletal element frequencies, and patterns of bone breakage. The final sub-section will deal with the assessment of bone modification through digestion of skeletal elements by the predators. A greater emphasis is placed on the role of avian predators throughout this review as they are associated with lower levels of bone modification. Very little data from mammalian predators are shown, as destruction of bones is often at a level exceeding that recovered from most archaeological sites.

It is worth emphasising that all of the methods outlined within this section can and do make a contribution to the analysis of small mammal deposits, and whilst criticism is given of certain methods, their applicability will be demonstrated in the methodology section, which will outline how the techniques of small mammal taphonomy have been applied to this study.

2.3.1 Identifying the predator through assumption and prey species composition

Before discussing the many studies that deal with methods aimed at identifying the predators responsible for the accumulation of small mammal remains through analysis of the skeletal remains, this section will detail a number of studies that have used either the assumption that owls are the most prolific accumulators of small mammals, or the composition of the prey remains, to suggest the origin of the deposit.

However, it is also interesting to note that one of the earliest researchers to consider the role of avian predators as accumulators of microvertebrate material, made the assumption that the likely accumulator was a hawk, and not an owl. This was Rev. William Buckland (1823), who writes of his discoveries at Pontnewydd Cave:

> *'In this earth I found the bones of various birds, of moles, water rats, mice and fish, and a few land snails ..... and their presence in this most inaccessible spot can only be explained by referring the bones [of birds, moles, rats and mice] to the agency of hawks, and the fish bones to that of sea gulls.'*
>
> (Buckland 1823: 63)

There are however, a greater number of authors who consider owls to be the most likely contributor to the accumulation of small mammal faunas in caves. This is a perspective that seems particularly prevalent in South African small mammal palaeontology, as many early researchers have commented on the probable origin of small mammal fossils coming from owl pellets (Broom 1948; Cooke 1952; Peabody 1954; Davis 1959). Other small mammal accumulators are rarely considered. This assumption is based on evidence of modern owl roosts in caves. It is suggested that since owls commonly used caves as nest or roost sites in the present, and vast accumulations of small mammal bones can build up at these sites, it is likely that given the correct circumstances, many of these bones could become part of future fossil deposits. The same has often been assumed for owls roosting in the past (Brain 1981: 118).

Avery (1982: 207-209) was one of the first South African researchers to have undertaken an analysis of some possible bone accumulators in South Africa. She ruled out diurnal raptors on the basis of the mainly nocturnal composition of the prey. Of the

owl species that could have contributed to small mammal accumulations in South Africa, the *Bubo* (eagle owl) species were considered to produce higher degrees of breakage (from the analysis of modern pellets) than was witnessed in either the archaeological deposits or modern *Tyto alba* (barn owl) pellets. Analysis of mammalian carnivores indicated that they too caused bone damage, and do not usually defecate in caves on a regular basis. That left only *Tyto alba* as a suitable accumulator of small mammal deposits (Avery 1982: 209; Avery 1990: 407). She also suggested that similarity in species composition between modern owl pellets and fossil rodent assemblages was further evidence of the role of *Tyto alba* as the accumulation agent. However, having carried out this analysis for one assemblage, Avery has not made any further attempt to carry out taphonomic analysis, and considers *Tyto alba* as the accumulation agent of all small mammal bones in caves. Brain (1981: 120) also suggests that *Tyto alba* is of greater significance in the accumulation of small mammal species than the *Bubo* species, but suggests that they should not be entirely ruled out.

Guilday et al. (1977: 7-8) suggest that small mammal bones excavated from Clark's Cave, Virginia, (USA), show similarity with recent owl pellet material, and that a number of carnivorous cliff and cave frequenting birds are responsible for the deposit: the 'variety of prey, nocturnal, diurnal, field, forest, vertebrate, invertebrate, argues for not one but probably many species of birds of prey' (Guilday *et al.* 1977: 15).

However, a comparison of the small mammal prey with modern carnivore diet data (Latham 1950) indicates that prey weight groups (i.e. Oryctolagus, Sciuridae, Muridae, Aves) from Clark's Cave are similar in composition to medium sized owls, such as *Tyto alba* (at the small end of medium) or *Asio flammeus* (short eared owl). The high percentage of prey representing 'field species' is also suggestive of one of these two owls in terms of dietary information, although species of woodland small mammals may indicate the presence of *Asio otus* (long-eared owl) as well (Guilday *et al.* 1977: 15).

Avery (1982) also suggests that the prey size of the fossil rodents in her sample indicates that some of the larger eagle owls are unlikely to have been responsible for the accumulations. This is confirmed by Brain (1981: 122-124) who has shown that both *Bubo capensis* (Cape eagle owl) and *Bubo lacteus* (giant eagle owl) regularly capture

much larger prey than *Tyto alba* or *Bubo africanus* (spotted eagle owl). Levinson (1982; 1983) reasons that as modern *Tyto alba* pellets contain small sized rodents, mainly murids, the bones of which are usually undamaged, then bones of similar compositions from breccias sampled at Makapansgat and Swartkrans, South Africa, must have been deposited by *Tyto alba* as opposed to any other South African owl species.

2.3.2 Identifying the predator using skeletal element frequency and bone breakage

Although the contribution of mammalian and avian predators to the collection of microvertebrate fossil remains had been alluded to in the past (Davis 1959; Brain 1981; Avery 1982, see previous section) these early studies contained little quantitative taphonomic analysis. Mellett (1974) compared modern carnivore scat material with microvertebrate remains recovered from Mesozoic and Tertiary deposits, and found them to be 'identical' in appearance. He suggested that all fluvial microvertebrate accumulations were due to deposition by carnivores ('mainly mammalian, but also including predacious fish, reptiles and birds' (Mellett 1974: 349)), and that the breakage witnessed on these bones was due to ingestive and digestive factors, and not to damage sustained as a result of stream transportation. Considerable, but unquantified bone breakage is also recorded by Mayhew (1977) in an analysis of the effects of predation by diurnal raptors on microfauna.

In 1979, Dodson and Wexlar published the first truly quantitative analysis of small mammal deposits, the *Taphonomic investigation of owl pellets*. In this study, pellets from three species of captive owls were analysed. The owl species were *Tyto alba*, *Bubo virginianus* (great horned owl) and *Otus asio* (Eastern screech owl). Each species was represented by at least three individuals from two different institutions (Dodson and Wexlar 1979: 276). Percentage presence and completeness was recorded for each of the major long bones (humerus, radius, ulna, pelvis, femur and tibia) as well as the scapula, skull and mandible. Percentage presence is expressed as a proportion of individual elements relative to the number of elements expected, twice that of the

minimum number of individuals (calculated from the most prevalent bone) in the case of the long bones. Percentage completeness is a record of the number of unbroken bones relative to the number recovered. Bone breakage was also recorded in greater detail, with each long bone being assessed as either intact, proximal, distal or shaft (Dodson and Wexlar 1979: 279).

The results indicated that there was a substantial difference in the amount of bone breakage, with O*tus asio* causing 80% breakage to the bones, compared to 65% for *Bubo virginianus* and only 30% for *Tyto alba.* This variation in the degree of breakage was related to the particular physiological factors and feeding habits of each owl. *Otus asio* is much smaller than the other two owls, and has to tear its prey to pieces before ingestion. During feeding observations, *Bubo virginianus* was witnessed moving the prey through its beak in a 'series of bites (during which the sound of breaking bones could be heard)' (Dodson and Wexlar 1979: 282). *Tyto alba* was witnessed separating the head from the body of its prey, however, both parts were swallowed whole, and very little breakage occurred (Dodson and Wexlar 1979: 183).

Analysis of the number of bones returned within the pellets, versus the expected number based on the minimum number of individuals (MNI) again indicated a difference between the three owls, most markedly between *Otus asio* and the other two owls: *Tyto alba* recorded the lowest loss of elements (Dodson and Wexlar 1979: 276). Skeletal element loss in owl pellets was also recorded by Raczynski and Ruprecht (1974), for three species of owl: *Tyto alba, Strix aluco* (tawny owl) and *Asio otus.* Skeletal element loss was highest in *Strix aluco* (51%), with *Asio otus* and *Tyto alba* scoring 46% and 34% respectively (Raczynski and Ruprecht 1974: 32).

Both of these studies were carried out on captive owls, where feeding and pellet production had been measured, and consequently, it was possible to calculate the percentage of bones that are not returned within the pellets analysed. There are a number of reasons for this. Raczynski and Ruprecht (1974) suggest that the main cause of this loss was the digestion of these elements whilst in the stomach of the owls. However it is possible that these elements were either retained in the stomach and ejected in pellets after the completion of the study, or digested after the ejection of one pellet and before the introduction of more food. A further compounding factor in

applying this data to archaeological and palaeontological deposits is that the artificial conditions produced in captivity may not reflect conditions in the wild, and consequently adversely affect the results produced.

This may be substantiated by the results obtained in similar analysis by Korth (1979) who studied owl pellets collected from the field, from roosts of *Tyto alba* and *Bubo virginianus*. He found little evidence of breakage (0% in *Tyto alba* sample) and very little incidence of digestion or erosion (Korth 1979: 240). Korth also found a high degree of element representation[6] within the pellets despite the fact that they were taken from the wild, and could have represented pellets ejected over a vast time period. This suggests that the degree of digestion or bone loss[7] in the samples of Raczynski and Ruprecht (1974) may also have been inflated by the use of mainly young birds in the experiments, as it is recognised that young birds digest more bones than the adults (Grimm and Whitehouse 1963; Raczynski and Ruprecht 1974: 33-34).

Korth (1979) also analysed microvertebrate prey remains from coyote scats. He discovered that the 'material consisted of sharply broken bone fragments' (Korth 1979: 247), similar in appearance to those described by Mellett (1974). However, despite the fragmentary nature of the assemblage, the mean bone loss was only 35.2%, lower than that recorded for any owl by Raczynski and Ruprecht (1974).

Working independently of Dodson and Wexlar, Andrews was also carrying out analysis of modern small mammal predator accumulations. In an attempt to identify the predator responsible for the accumulation of microfauna at Olduvai Gorge, Andrews analysed pellet material from a number of bird species: *Tyto alba, Nyctea scandiaca* (snowy owl), *Asio otus, Bubo africanus* (spotted eagle owl), *Bubo lacteus* (Verreaux eagle owl), *Strix aluco* (tawny owl), *Athene noctua* (little owl), *Buteo buteo* (common buzzard), *Falco tinnunculus* (Kestrel), *Falco peregrinus* (Peregrine), *Milvus milvus* (red kite) (Andrews 1983: 78). He also carried out the analysis of eight mammalian carnivores; *Vulpes vulpes* (red fox), *Canis latrans* (Coyote), *Otocyon megalotis* (bat-

---

[6] 73.9% for *Tyto alba*, 78.9% for *Bubo virginianus* (great horned owl), although these numbers are slightly deflated due to the inclusion of smaller elements such as the teeth and small fore- and hind-foot bones, which Korth acknowledges may have been overlooked during the recovery of the bones (Korth 1979: 246).

[7] Degree of digestion or bone loss in Raczynski and Ruprecht (1974), mean element representativeness in the samples of Korth (1979) and percentage presence in Dodson and Wexlar (1979) are the same measure. For comparison, the bone loss for Korth's data would be 26.1% for *Tyto alba* and 21.1% for *Bubo virginianus*.

eared fox), *Ichneumia albicauda* (white-tailed mongoose), *Genetta genetta* (small-spotted genet), *Meles meles* (badger), *Mustela vison* (American mink), and *Lutra lutra* (otter) (Andrews 1983: 79).

He compared the Olduvai FLKN1 L1-2 microfauna with the assemblages produced by extant African predators (*Tyto alba, Falco tinnunculus, Bubo lacteus, Otocyon megalotis, Ichneumia albicauda, Genetta genetta*) using bone element proportions[8] and bone breakage analysis (using similar categories to Dodson and Wexlar (1979)), as methods of comparison. He concluded that the low number of isolated teeth and high proportions of postcranial elements suggested that the assemblage could not have been produced by a diurnal raptor, such as the kestrel. Equally, the high degree of postcranial bone breakage indicated that it was unlikely that the accumulation agent was an owl. Further indications of mammalian predators could be seen in puncture or gnaw marks on the bones (Andrews 1990: 42). The Olduvai microfauna was most similar in appearance to the assemblages produced by small mammalian carnivores (Andrews 1983: 82-83), such as *Ichneumia albicauda* or *Genetta genetta*.

However, in a more wide-ranging review, Andrews and Evans (1983) suggest that the occurrence of such carnivore accumulations are rare within the fossil record. Where found, they are characterised by a high degree of bone breakage, and much higher rates of survival for postcranial bones than for cranial bones. They suggest instead (contrary to Mellett's scatological hypothesis[9]) that owls are of greater significance palaeontologically as accumulators of small mammal assemblages (Andrews and Evans 1983: 306).

Further experimental work was carried out by Hoffman (1988), who analysed pellets from seven owl species: *Bubo virginianus, Tyto alba, Otus asio, Strix varia* (barred owl), *Buteo jamaicensis* (red-tailed hawk), *Buteo lagopus* (rough-legged hawk) and *Falco sparverius* (sparrow-hawk). His results show similarity with those of Mayhew (1977), and Dodson and Wexlar (1979), although his results are perhaps slightly more rigorously tested. Hoffman fed 50 mice to each bird and analysed skeletal

---

[8] The same category of analysis used by Raczynski and Ruprecht (1974), Dodson and Wexlar (1979) and Korth (1979). Hereafter referred to as bone loss or skeletal element abundance.

[9] 'most or all microvertebrate fossil assemblages first passed into or through the digestive tract of carnivores' (Mellett 1974: 349).

element abundance in each species. Most of the bones were returned by *Bubo virginianus*, *Tyto alba,* and *Strix varia*, with lower results from *Otus asio* and still lower for the hawks (Hoffman 1988: 83). This is again related to feeding styles (as well as bone digestion) as *Otus asio* (screech owl) is small and has to break up its prey to feed. Hawks are recognised as being very destructive to bones, and often cause breakage when tearing the flesh from the bones. However, as these birds are targeting the flesh of their prey, they do not necessarily consume all of the bones (Andrews 1990: 38-39).

Similar results were obtained from analysis of skeletal element breakage, with low breakage in *Tyto alba* and *Strix varia*, intermediate breakage in *Bubo virginianus* and higher breakage from *Otus asio, Buteo jamaicensis, Buteo lagopus* and *Falco sparverius.* The results of these analyses were subjected to both Spearman's, and Kendall's Tau rank-order correlation to assess the degree of species specific patterns of both element representation and bone fragmentation, outlined above (Hoffman 1988).

Owl pellet taphonomy was also considered by Kusmer (1990) with an analysis of three owl species, *Tyto alba, Bubo virginianus* and *Asio flammeus*. She attempted to show that a specific taphonomic pattern could be recognised for owl accumulations. Using pellets collected from wild owls, she applied the same methods as those described above (Dodson and Wexlar 1979; Korth 1979; Andrews 1983; Andrews and Evans 1983; Hoffman 1988), and produced similar results. Comparing the owls sampled against mammalian carnivore data from Andrews and Evans (Andrews and Evans 1983) she found a statistically significant difference in the relative abundance of bones between the two groups of predators. Data on bone breakage was also fairly comparable with results obtained by Raczynski and Ruprecht, Dodson and Wexlar, and Hoffman (Raczynski and Ruprecht 1974; Dodson and Wexlar 1979; Hoffman 1988).

Another quantitative examination of bone breakage, following the methods of Dodson and Wexlar was carried out by Geering on a sample of pellets from *Tyto novaehollandiae castanops* (the Tasmanian sub-species of the chestnut-faced or masked owl). She found that breakage was generally low and mainly affected the most fragile bones, particularly the scapula and pelvis. The study also concluded that whilst breakage analysed from modern pellets may shed light on the origin of the predator, in

mixed and re-worked sub-fossil deposits, the possibility of post-depositional breakage could mask the identification of any breakage attributable to the owls (Geering 1990).

The most significant contribution to small mammal taphonomy was the publication of the book *Owls, Caves and Fossils*, by Andrews (1990). Not only did this book re-examine and evaluate the results of previous small mammal taphonomy literature, it also introduced a number of new methodologies and techniques. More than anything, its major contribution was to increase and refine the current knowledge of modern small mammal bone accumulators, and the quantitative methodologies needed for the analysis of microvertebrate fossil assemblages. Species used within this study were: *Tyto alba, Nyctea scandiaca, Asio otus, Asio flammeus, Bubo lacteus, Bubo africanus, Bubo bubo, Strix nebulosa* (great grey owl), *Strix aluco, Athene noctua, Falco tinnunculus, Circus cyaneus* (hen harrier), *Ichneumia albicauda, Genetta genetta, Otocyon megalotis, Canis latrans, Vulpes vulpes, Alopex lagopus* (arctic fox) and *Martes martes* (pine martin). Within this section, only the data on bone loss and breakage will be discussed.

Quantitative analysis of the degree of bone loss is given as the relative abundance, expressed as a proportion of a specific element against the number expected from the MNI of the prey. Graphs of the relative abundance of each major skeletal element allow the grouping of predator species to be prepared, based on the degree of bone loss. *Tyto alba* produced the lowest level of bone loss, with progressively higher bone loss recognised in *Bubo bubo, Strix aluco* and *Athene noctua* (Andrews 1990: 45-49). Further analysis of bone numbers was also quantified, in the form of postcranial / cranial proportions and also distal element loss. Both of these indexes assess and catalogue specific limb loss. Post-cranial / cranial proportions measures the difference between the number of crania returned in pellets and scats against the number of postcranial remains. The results show that there are a number of species where this ratio differs from the norm. For example, *Nyctea scandiaca, Vulpes vulpes, Ichneumia albicauda, Canis latrans* all have high proportions of postcrania, which may indicate some degree of selectivity, with decapitation of the prey and loss of the skull (Andrews 1990: 49). Distal element loss also provides some method of differentiating between the species sampled, with increased distal element loss in the diurnal raptors and

mammalian carnivores (Andrews 1990: 50). These results may also reflect differential feeding patterns between the different predator groups.

Postcranial breakage has been recognised in previous studies (Dodson and Wexlar 1979; Korth 1979; Andrews 1983; Andrews and Evans 1983; Hoffman 1988; Kusmer 1990) as a reliable method for distinguishing various predator species responsible for small mammal accumulations. Andrews (1990) collected breakage data for all eighteen species of predator within his study, for the humerus, ulna, femur and tibia. Each bone is recorded as either complete, proximal, shaft or distal. The analysis indicates that the predator species fall into at least three groups: all of the owls (group 1), except *Bubo africanus* and *Strix aluco* (group 2), and finally the diurnal raptors, *Athene noctua* and mammalian carnivores (group 3). A table summarising these results is shown in Appendix table 9, page 291. Group 1 predators produce only minor breakage, with over 80% of the bones complete. The degree of breakage for group 2 is slightly lower, between approximately 50 – 80 %. The degree of breakage in the last group is varied, from 0 - 50% of complete bones.

Cranial breakage, which was first catalogued by Andrews and Evans (1983) is refined and quantified within this study. It is divided into the breakage of maxillae, maxillary tooth loss, the breakage of mandible and mandibular tooth loss, and finally the loss of isolated teeth and breakage of teeth. The breakage of the skull is categorised by four different stages of breakage. These are shown in Figure 2, the letters in brackets refer to the image below. The first two categories are complete (A), with the third category representing a broken skull, with zygomatic intact (B), and the fourth category, a maxillary fragment lacking the maxillary (C), which includes the frontal and incisors.

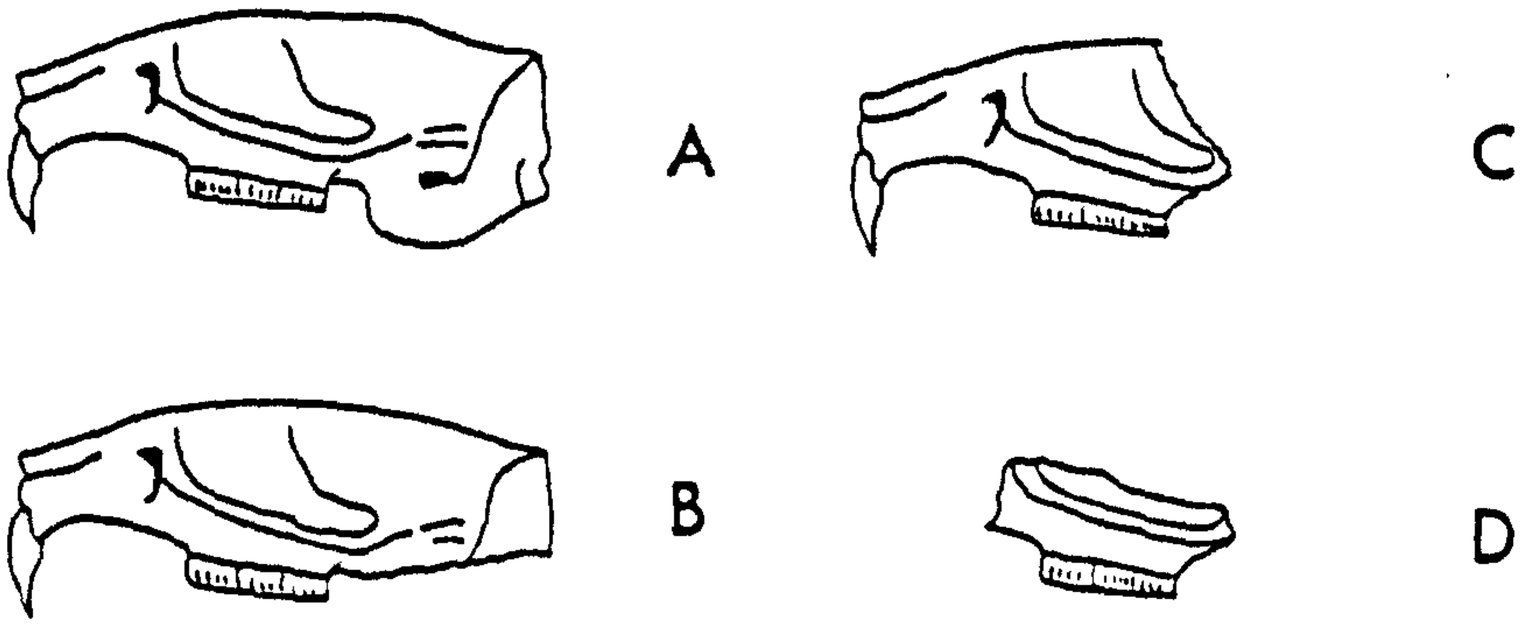


Figure 2. Categories of skull breakage, from Andrews (1990: 53).

Each complete skull is counted as having two maxillae, with isolated maxillae (containing only one side of the tooth row) counting as one (Andrews 1990: 53). As maxillary breakage is relatively high in mammalian carnivores, this should offer an easy method of distinguishing between owl deposits, and those of other predators, which have characteristically higher values of breakage. However, some of the owl species display moderately high rates of cranial breakage, for example *Asio flammeus, Bubo africanus* and *Bubo bubo* (all above 50% - less than 50% survival rate). Breakage by *Athene noctua, Falco tinnunculus* and *Circus cyaneus* all fall above 90% (only 10% survival rate), and there were no incidences of cranial survival in the analysis of mammalian carnivore scats.

Loss of maxillary teeth is also a measure of cranial breakage as the teeth become separated from the jaws. This is measured for both the incisors and the molars. It is a slightly unreliable method of quantification as some prey species are more susceptible to tooth loss than others. For example, the un-rooted teeth of Arvicolinae (voles and lemmings) are more likely to become detached from the jaws than the teeth of Murinae (mice and rats)[10] (Andrews 1990: 55). The same is true of mandibular tooth loss. Loss of isolated teeth also quantifies the extent of mandible and maxilla breakage, as the jaws are broken and teeth become detached. However this again highlights the difference between tooth loss in the prey species, as well as loss through sample process. Despite this, it is still possible to discern different patterns produced by specific predators

Mandible breakage is perhaps a better measure of breakage, as the mandible is stronger than the maxilla, and is a commonly preserved and easily recognised element in most microfaunal assemblages. There are four categories of mandible breakage, shown in Figure 3, overleaf, indicated by the letters in brackets. These are mandible complete (A), ascending ramus broken (B), ascending ramus missing (C), and inferior border broken (D) (Andrews 1990: 56).

---

[10] The sub-family names used throughout this study are taken from the *Handbook of British Mammals* (Corbet and Harris 1991).

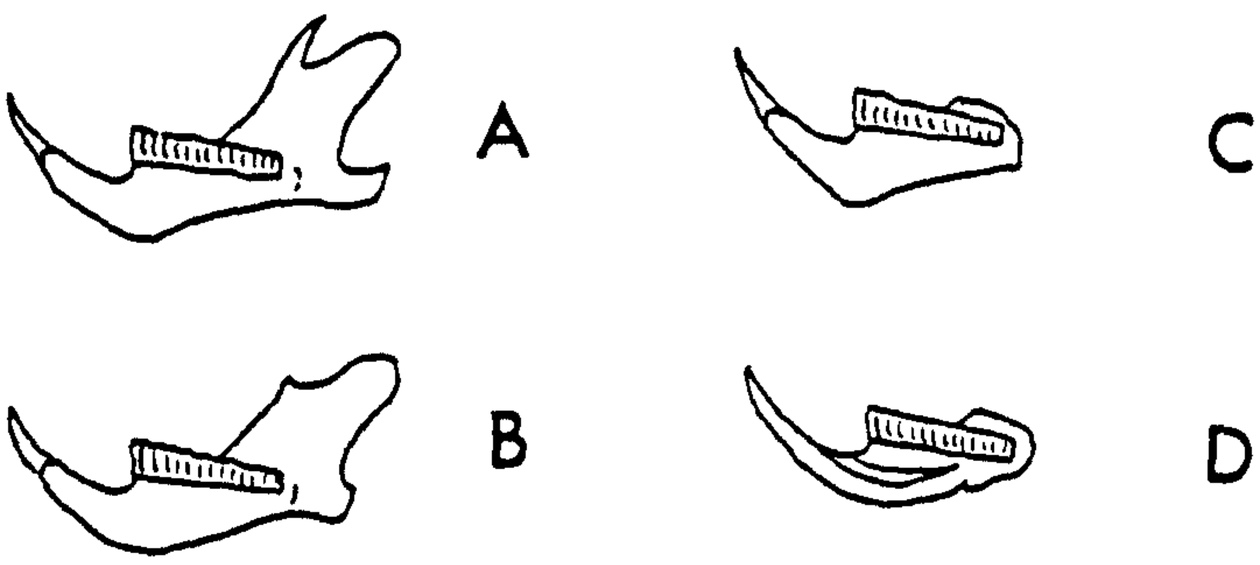


Figure 3. Categories of mandible breakage, from Andrews (1990: 56)

The groups produced by this analysis are similar to those for the maxillary breakage, with species such as *Tyto alba*, *Asio otus*, *Bubo lacteus* and *Strix nebulosa* producing very minimal modification. Greater damage is produced by *Asio flammeus*, *Bubo bubo* and *Strix aluco*, more extreme damage by the diurnal raptors and *Bubo africanus*, and finally complete destruction, with no mandible intact, characterising the mammalian carnivores (Andrews 1990: 56). The results of the cranial breakage analysis by Andrews are located in Appendix table 10, page 292. Further development of criteria for bone breakage has been advanced by Sanchez *et al* (1997) to deal with incidences of extreme fragmentation and destruction.

The methods of examination of bone breakage and skeletal element loss of Andrews (1990) are used within this project (see methodology section), and have been applied to a number of fossil assemblages (Andrews 1990; Fernandez-Jalvo and Andrews 1992; Fernandez-Jalvo 1995; Fernandez-Jalvo 1996). However, in all cases they have been used alongside other methods, such as digestion (see below). This is because element representation (relative abundances), and bone breakage data can be confused by later post-depositional effects, such as weathering, transportation, trampling and compaction (Hoffman 1988: 89; Andrews 1990: 64; Geering 1990: 141; Kusmer 1990; Fernandez-Jalvo 1996: 32-33). Skeletal element abundance and bone breakage can also be affected by excavation and sampling procedures. It is, however, possible to recognise and differentiate between modern breakage (associated with excavation, sieving) and more ancient breakage (pre-depositional predator breakage and post-depositional breakage from trampling, compaction or transportation), by examining the freshness of the bone breaks.

A more fundamental procedural problem is associated with the study of skeletal element abundances, as there is a potential for loss of these elements if the correct size sieve mesh is not used. This has been demonstrated by Shafter (1992: 133-135), who found that a sieve size of ¼ inch (used on some US rescue archaeology sites) led to the loss of nearly all small mammal elements. Experimental sieving tests carried out during research for an undergraduate dissertation (Williams 1997), have shown that using a sieve mesh size larger than 0.5 mm (approximately 1/16 inch) will lead to losses of particular bones. Losses of approximately 10% of bones, and 20% of isolated molars, (representing as many as 27 individuals) were reported when using a 1mm sieve rather than a 0.5 mm sieve (Williams 1997: 37), with particularly high losses recorded for ribs, vertebrae, podials and metapodials.

Recent research comparing interspecies variability in barn owl populations from North and South America has also demonstrated that the specific bone breakage patterns assumed for each predator species may be more variable than previously recorded (Saavedra and Simonetti 1998). They suggest that, at best, the patterns of bone breakage should be used to suggest categories of predators, such as owls, diurnal raptors or mammalian carnivores, and not predator species within these groups.

2.3.3 Identifying the predator through bone digestion

Whilst it has been shown that relative abundance and bone breakage do not always offer the most secure methods of assessing predator species responsible for small mammal assemblages (Andrews, pers. comm.; Andrews 1990; Fernandez-Jalvo 1996; Saavedra and Simonetti 1998), bone digestion is a more reliable indicator. 'It has been found ... that the corrosive effects of digestion on the bones and teeth in the predator's stomach are not duplicated by any other alteration process and so may be used to identify bone assemblages derived from predators' (Andrews 1990: 64). This was first recognised by Mayhew (1977), who analysed pellets from raptors and owls, and found a significant difference between the digestion and rounding of the bones from the raptor pellets as opposed to the owls. He suggested that on the basis of comparison with modern pellet remains, small mammal teeth excavated from the Cromerian freshwater deposits at West Runton were deposited by a diurnal raptor (Mayhew 1977: 31).

Mayhew (Mayhew 1977: 25) comments on the lack of digestion in the owl species used in his analysis, and a similar conclusion was drawn by Korth (1979: 240). Kusmer (1990) also comments on the low incidence of digestion, or erosion in her samples. However, these authors were using pellets from species of owls[11] that have now been shown (Andrews 1990) to digest bone only infrequently. Corrosion (or digestion) of the bone was also used as a category of bone alteration by Andrews and Evans (1983) in their analysis of mammalian carnivore deposits, although these data were not quantified to any great degree. Digestion and decalcification of small mammal teeth and bones was witnessed in experimental analysis of crocodiles, often leading to complete bone destruction (Fisher 1981), although in some cases teeth with no enamel are preserved and are attributed to crocodiles.

In his analysis of the Omo microfauna, Wesselman[12] (1984) considered that both diurnal and nocturnal bird species were responsible for the accumulation, as evidenced by the differential degree of enamel etching seen between the diurnal and nocturnal prey species (Wesselman 1984: 185). Bone digestion data was also collected by Geering

---

[11] Mayhew (1977) studies pellets from *Tyto alba*, *Asio flammeus* and *Asio otus*, Korth (1979) analysed pellets from *Tyto alba* and *Bubo virginianus*, and Kusmer (1990) studied pellets from *Tyto alba*, *Bubo virginianus* and *Asio flammeus*.

[12] Using criteria from Mellett (1974), Mayhew (1977) and Dodson and Wexlar (1979).

(1990) from modern pellets of *Tyto novaehollandiae castanops* (Tasmanian masked owl) for post-cranial elements. The data indicated that digestion varied according to the specific element, with a higher proportion of tibiae digested than mandibles. The study also investigated the link between digestion and age of prey and found that digestion was significantly more pronounced on un-fused juvenile and sub-adult bones than fused adult bones ("p"= 0.0001) (Geering 1990: 139).

As well as collecting data on bone breakage and element representation. Andrews (1990) has also collected a vast comparative data set of digestive modification to small mammal bones by the eighteen species of avian and mammalian predators previously listed[13]. He records digestion for three skeletal parts: molar, incisor, and postcranial digestion. For each of these groups, predator species are assigned to one of five specific categories, based on both the degree of digestion and the frequency of the skeletal elements (teeth or long bones) affected (Andrews 1990:65). The results of these analyses are displayed in Appendix table 11, page 293.

Whilst it has been shown that different predators produce a varied range of digestion, the type of prey caught will also affect the amount of digestion recorded. For example, Arvicolinae molars are more easily digested than Murinae, Gerbillinae (gerbil) or Cricetinae[14] (hamster) molars, as a result of their distinct shape. Arvicolinae molars are commonly digested on the corners of the salient angles of the teeth, leading to a rounding of the occlusal surface, where as Murinae molars are already more rounded in shape, and digestion appears to be less prevalent, and more difficult to detect (Andrews 1990). This differential is most visible in cases where low digestion prevails, (category 1 & 2 predators) and as a result, without recognition, could lead to bias in samples containing high proportions of a particular species. For example, a high proportion of the diet of *Tyto alba* in Britain is made up of Arvicolinae (Glue 1967; Glue 1970; Glue 1974; Andrews 1990: 96), whereas *Tyto alba affinis,* hunting in South Africa could be expected to capture a higher proportion of Murinae, Gerbillinae or Cricitinae species, (see Appendix table 12, data from Williams 1997; Coetzee 1972; Rautenbach 1978;

---

[13] Species used within this study were; *Tyto alba, Nyctea scandiaca, Asio otus, Asio flammeus, Bubo lacteus, Bubo africanus, Bubo bubo, Strix nebulosa, Strix aluco, Athene noctua, Falco tinnunculus, Circus cyaneus, Ichneumia albicauda, Genetta genetta, Otocyon megalotis, Canis latrans, Vulpes vulpes, Alopex lagopus* and *Martes martes.* (Andrews 1990).

[14] Of these Rodent sub-families only Arvicolinae and Murinae are present in Britain.

Brain 1981; Levinson 1983. Whilst this has implications for palaeoecological reconstructions (see next section), it could also, if unrecognised, lead to erroneous identification of the predator species. Andrews recognises this fact (1990: 65), but no attempt to quantify this problem is given.

Four species of owls are grouped in category 1 for molar digestion: *Tyto alba*, *Asio otus*, *Asio flammeus* and *Bubo lacteus*. This group is characterised by total molar digestion of 2% or less, [15] which is usually restricted to the salient angles of the teeth, producing a slight to moderate rounding of the occlusal surface (Andrews 1990: 65). The same degree of digestion, but at a higher frequency, is used to determine the next grouping, category 2. The three species, - *Nyctea scandiaca*, *Bubo africanus* and *Strix nebulosa* - all exhibit molar digestion rates between 4-5% of the total sample (Andrews 1990: 67).

The two owl species comprising category 3 (*Bubo bubo* and *Strix aluco*) produce significantly higher rates of digestion, up to 22% of the total sample, and when this digestion occurs, it is also extensive. The corners of Arvicolinae molars are much more rounded with the dentine exposed. This digestion also continues down the entire length of the salient angles, especially in the isolated teeth, which are no longer protected by the mandible (Andrews 1990: 67). Within this category it is also possible to detect digestion on Murinae and Cricetinae molars which show signs of surface pitting and partial enamel removal, but it is not as extensive as the damage seen on the microtine teeth.

Category 4 predators, - *Athene noctua*, *Falco tinnunculus* and *Falco peregrinus*, - exhibit even higher frequencies of digestion, over 50% of the total number of teeth. The extent of digestion is similar to category three predators (Andrews 1990: 67). Category 5 groups together those predators who digest teeth to such an extent that they are often unrecognisable, and with a frequency of almost 100%. These birds are *Circus cyaneus*, *Buteo buteo* and *Milvus milvus* (Andrews 1990: 67).

Whilst the category groupings for the birds based on molar digestion are readily discernable, and it is possible to identify 'species specific patterns of modification' (Andrews 1990: 64), digestion of molars by mammalian predators is far more variable,

---

[15] Although the *Tyto alba* sample shows 1% digestion, this includes data taken from a nest site. All of the data for *Tyto alba* adults shows no indication of digestion (Andrews 1990: 65).

both within and between species (Andrews 1990: 67). However, most species exhibit digestion comparable with the category 3-5 birds discussed above.

Incisor digestion appears to give similar results to the molar digestion, with species falling into roughly the same categories as before, see Appendix table 11. There are a few notable differences. In all cases the frequency of digestion is higher than on the molars. There is also less prey type differentiation, as both Arvicolinae and Murinae incisors are similar in size and shape. Soricid (shrew) incisors are not included within this section of Andrews' analysis (1990: 74). There also appears to be a higher incidence of upper incisor digestion (*in situ* incisors only) than lower incisors, which Andrews attributes to the greater degree of breakage of the maxilla (1990: 74). However, since owls often swallow their prey whole and head first (Bunn *et al.* 1982: 76), the greater incidence of maxillary incisor digestion could be a result of increased exposure of the upper teeth to the stomach acid at the base of the stomach, as the prey is digested. As this phenomenon of increased maxilla incisor digestion seems to exist in most of the owl species sampled, it does not significantly alter the results gained.

Incisor digestion is light for all category 1 predators, occurring with a frequency between 5-13%, on all parts of the teeth, and is occasionally heavier at the tips (Andrews 1990: 74). Digestion is slightly heavier for the category 2 predators, and occurs mostly at the tips, often exposing the dentine. Andrews suggests that this indicates a greater retention of the incisor in the jaws (1990: 75), as when only the incisor tips are digested, it can be assumed that the rest of the incisor is still protected by the maxilla. The frequency of incisor digestion exhibited by all category 2 predators ranges from 20-30%. The inclusion of *Strix nebulosa* within this category is as a result of the high frequency of digestion on incisors that it exhibits, even though the degree of digestion exhibited by this owl is more similar in form to the category 1 predators.

The degree and frequency of digestion are even higher in the samples from the category 3 predators, occurring on both the enamel and consequently exposed dentine, at a frequency between 50-70%. The category 4 predators exhibit extensive digestion of both enamel and dentine, with 'some teeth having all of the enamel removed' (Andrews 1990: 75). The frequency of this digestion is between 60-80%. Similarly high degrees of digestion are observed on the incisors from assemblages produced by the category 5

predators, where every tooth in the sample is digested (Andrews, 1990: 75). A summary of the molar and incisor digestion data for avian predators is given in the table below, taken from Andrews (1990: 75).

Digestion category	**Molar digestion**	**Incisor digestion**
1. digestion absent or minimal digestion. molars 0-3% incisors 8-13%	*Tyto alba* (barn owl), *Asio otus* (long-eared owl), *Asio flammeus* (short-eared owl), *Bubo lacteus* (Verreaux eagle owl).	*Tyto alba* (barn owl), *Asio flammeus* (short-eared owl) *Nyctea scandiaca* (snowy owl)
2. moderate digestion molars 4-6% incisors 20-30% (tips only)	*Nyctea scandiaca* (snowy owl), *Bubo africanus* (spotted eagle owl), *Strix nebulosa* (great grey owl).	*Asio otus* (long-eared owl), *Bubo lacteus* (Verreaux eagle owl), *Strix nebulosa* (great grey owl).
3. heavy digestion molars 18-22% incisors 50-70%	*Bubo bubo* (European eagle owl), *Strix aluco* (tawny owl).	*Bubo bubo* (European eagle owl), *Bubo africanus* (spotted eagle owl), *Strix aluco* (tawny owl), *Athene noctua* (little owl).
4. extreme digestion molars 50-70% incisors 60-80%	*Athene noctua* (little owl), *Falco tinnunculus* (kestrel), *Falco peregrinus* (peregrine).	*Falco tinnunculus* (kestrel), *Falco peregrinus* (peregrine).
5. extreme digestion molars 50-100% incisors 100% (dentine corroded)	*Circus cyaneus* (hen harrier), *Buteo buteo* (buzzard), *Milvus milvus* (red kite).	*Circus cyaneus* (hen harrier), *Buteo buteo* (buzzard).

Table 1. Summary of molar and incisor digestion, indicating categories of avian predator assigned on the basis of analysis of digestion, adapted from Andrews (1990).

These categories have been assigned on the basis of similarity of both the frequency and the extent of molar and incisor digestion. Within the initial analysis by Andrews (1990) no attempt was made to test the significance of these groupings. However, within this study these data have been tested using ANOVA. The results for both the molar and incisor digestion groups above indicate that these groups are significantly different from each other, and therefore represent discrete categories of predator modification.

Digestion variable	**"F"**	**"P"**
Total molar digestion	142.699	.000
Total incisor digestion	41.14	.000

Table 2. Results of One-Way ANOVA (analysis of variance) comparing total molar and total incisor digestion for the predator groups 1-4 (Andrews 1990).

The full results of this analysis are shown in Appendix notes - section 1, page 276, along with a more in depth discussion of sample size and group coherency.

As a further test of these groups, principal component analysis was carried out using the same data used above, and the plot of these principal components is shown below.

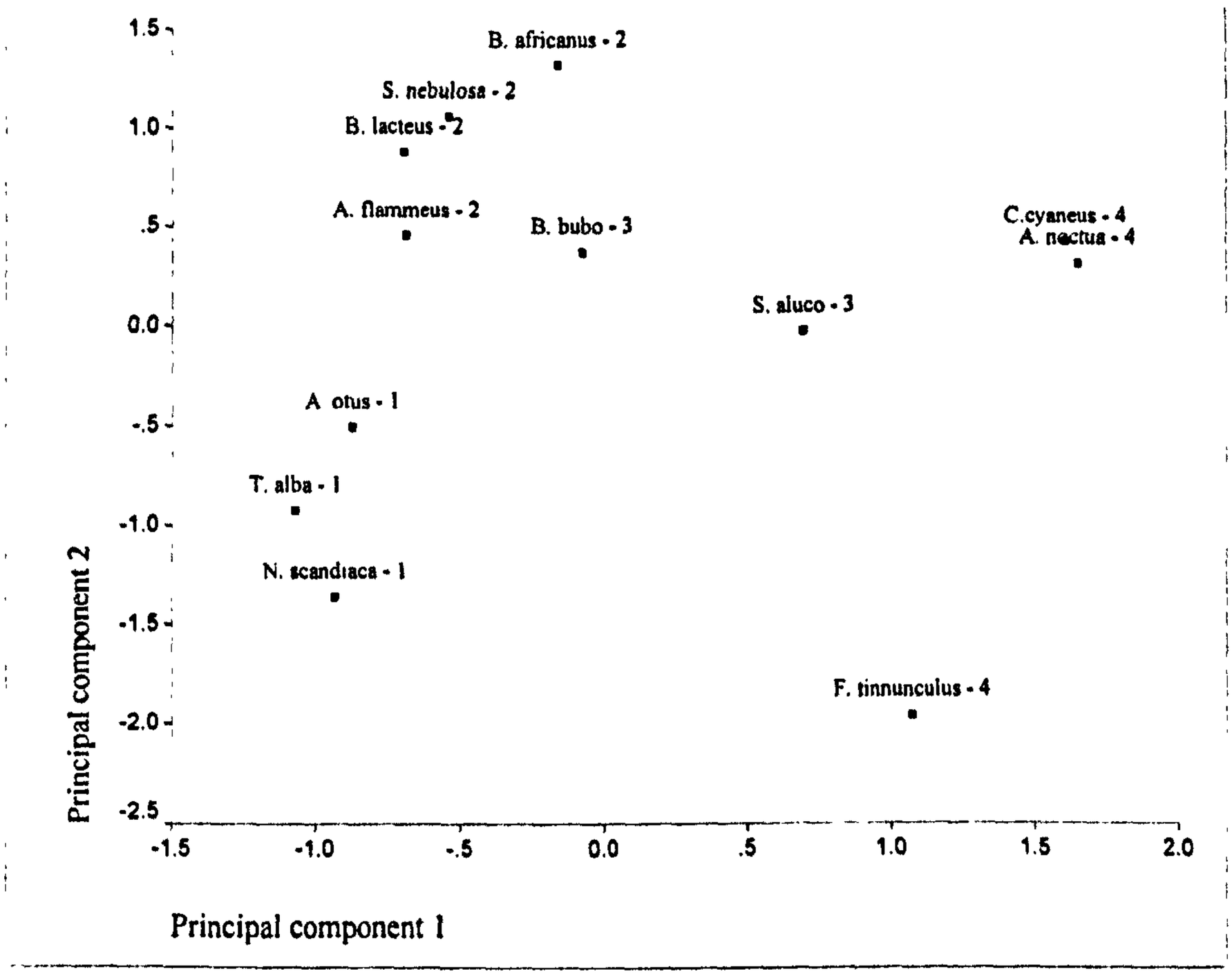


Figure 4. Principal component analysis of the categories of digestion, from Andrews (1990).

The principal component analysis graph (above) is a plot of the digestion recorded for different avian predator species. Principal component 1 (X axis) indicates the degree of digestion, and represents an increase in digestion from the left of the chart to the right. The second principal component (Y axis) represents the ratio of incisor digestion to molar digestion, with cases of higher incisor digestion plotted nearer the top of the chart.

This chart clearly demonstrates that there is a variation in digestion between category 1 & 2. The grouping of category 3 predators is not as well represented, but the bird species responsible for the highest degree of bone damage are grouped quite closely to the right of the chart, indicating higher degrees of digestion.

The categories of digestion initially described by Andrews (1990) have been further refined by Fernandez-Jalvo and Andrews (1992) with the introduction of a methodology to record the location of the digestion, and to categorise its extent. The new categories of digestion are based on the molars and incisors, and in each case digestion is broken down into sub-categories of light, moderate, heavy or extreme digestion. In the case of the incisors, the location of the digestion is recorded as either superficial (along the entire incisor) or tip (restricted to the incisor tips) (Fernandez-Jalvo and Andrews 1992: 412-417). Each of these sub-categories has been described and illustrated to show the variation between the different categories, and is reproduced in the methodology section, see Table 13 & Table 14, page 128 & 129. It was not possible to produce PCA of these more refined categories and sub-categories of digestion, as no raw data for digestion by predator species were available.

These more refined categories have made it easier to recognise particular predator patterns, and Fernandez-Jalvo & Andrews suggest that it is possible in the analysis of the small mammal faunas at Gran Dolina, Spain, 'to come to some fairly specific conclusions about their mode of accumulation' (1992: 423). These methodologies have also been employed in analysis of the adjacent site of Penal (Fernandez-Jalvo 1995), a re-evaluation of the small mammals from Dolina (Fernandez-Jalvo 1996), and an analysis of the small mammals at Olduvai Gorge (Fernandez-Jalvo *et al.* 1998), with great success in the identification of predator species.

Despite the detail with which small mammal digestion can now be assigned to predator species (see above), Hadly (1999), working on an accumulation of small mammal bones in Lamar Cave, Yellowstone National Park, does not carry out species specific taphonomic analysis of the bones. She states that the deposit represents an accumulation of bones collected by *Neotoma*[16] (wood rats), which she suggests are non-selective accumulators of material within their foraging radius. Within the modern study area several predators responsible for small mammal bone deposition have been identified, and it is suggested that an accumulation containing a random sample of the pellets and faecal material of these predators, (collected by wood rats), represents an

[16] Neotoma collect material found in their local environment to build middens. Materials include plants, wood, carnivore faeces, raptor pellets, as well as other objects, 'paper, shiny objects, string' etc (Wells 1976; Hadly 1999: 397).

reflection of the small mammals in the local environment (Hadly 1999). Taphonomic analysis of the bones suggests that both owl and diurnal raptor species are responsible for most of the small mammal deposition (Hadly 1999: 397).

Although all of the above cases have dealt with the identification of avian and mammalian predators responsible for small mammal accumulations, there is a collection agent that has not yet been mentioned. Whilst the idea of eating small mammals may not seem appealing to most people, this does not preclude the fact that small mammals may well have made up an important part of prehistoric diets (Stahl 1982; Simonetti and Cornejo 1991). Most studies dealing with small mammals in human diets have been based on coprolite and fossil coprolite analysis (Bryant 1974: 413; Reinhard 1988: 357-358), and very few studies have actually looked at the physical effects of consumption on a small mammal skeleton.

However, an intrepid analysis of the human digestive effects on a small mammal was carried out by Crandall and Stahl (1995). One of the authors ate the skinned, cooked and dissected remains of a shrew (*Blarina brevicauda*) and collected the bones once they had passed through his digestive tract. Skeletal element abundance, bone breakage and digestion were analysed, and the results indicate that the action of human digestion on small mammal bones is not dissimilar to that reported for other mammals by Andrews (1990). Bone survival was increased by the fact that the animal was swallowed without mastication, but most of the bones showed signs of damage and were severely weakened. It is likely that in most cases, small mammal bones consumed by humans are unlikely to survive into the archaeological record due to their fragile nature (Crandell and Stahl 1995:795).

Whilst the shrew species used in the above analysis was small enough to swallow whole, other species of small mammal are big enough to eat from the bone. Ethnographic observations of the preparation and consumption of one such species, *Bathyergus suillus* (Cape dune mole-rat), has indicated that there are specific patterns of burning associated with the cooking of this animal (Henshilwood 1997). Similar patterns of charring of the premaxilla, maxillary incisors and mandibular incisors from an assemblage of *Bathyergus suillus* from Blombos Cave, South Africa, suggest that these mammals were cooked and eaten in prehistory. Around 90% of the samples from

Blombos Cave show evidence of cranial burning indicating that the method of cooking may also have altered little over the years.

A final consideration in this section on digestion is the analysis of the bone chemistry of predator assemblages. Although the study of this subject is still in it infancy, there is evidence to suggest that the chemical composition of skeletal elements (bones and teeth) can be used to differentiate between different categories of predator, which is particularly important when dealing with sites where more than one predator may have been responsible for the accumulation of microvertebrate remains (Dauphin *et al.* 1997).

2.4 Other factors leading to bone modification

Whilst predators are often responsible for the modification of small mammal bones in archaeological and palaeontological assemblages, there are other factors responsible for the modification of these bones. These are important and need to be identified, so that they are not confused with the taphonomic signatures produced by predators. While early authors (e.g. Mellett 1974; Mayhew 1977; Andrews 1983; Andrews and Evans 1983) concentrated on the predatory origin of their deposits, more recent studies have included all aspects of bone modification (Andrews 1990; Fernandez-Jalvo and Andrews 1992; Andrews 1995a; Fernandez-Jalvo 1995; Fernandez-Jalvo 1996). Although these studies concentrate mainly on cave deposits, none of the bone modifications analysed in these papers has been identified on the bones from the two caves studied in the course of this project. Therefore, only passing remarks will be made.

For many years, Andrews (1990; 1995a) has been experimenting with bone modification, both in the analysis of weathering and trampling, as well as the physical effects of water transportation. Many of these methods are useful in documenting the history of specific fossils. For example, analysis of weathering will indicate if the bones were exposed to an open environment for a long period before burial, or whether the burial occurred shortly after deposition. In the case of small mammal bones, Andrews (1995a: 150) discovered that after exposure on a Welsh hillside for five years, most

bones showed signs of splitting, decalcification and collapse. However burial in either acid or alkali soils can still lead to some post-depositional bone modification (Fernandez-Jalvo and Andrews 1992: 411). Root action and high salinity can also lead to bone degradation, as can be seen Figure 5 below, showing a small sample of bones from a Pictish grave at Kilpheder, Orkney, (personal observation; see also Fernandez-Jalvo, 1992: 411).

Figure 5. Weathered bones from a Pictish grave, Kilpheder. Scale 10mm = 1mm.

Preservation is far better in caves, where there is often little modification from weathering (Andrews 1995a: 149), although there is evidence that insect and algal activity over a long period of time can cause some bone modification (Fernandez-Jalvo 1992; in Fernandez-Jalvo 1995). Although bones in and around caves are less likely to be weathered, and can in fact survive for long periods without burial (personal observation, see section on Carsington Pasture Cave), they are more susceptible to damage from trampling, sediment movement and collapse. These processes can lead to the destruction of the bone, and a potential loss of vital information.

Attritional damage and bone breakage is also caused by the action of water transportation, and abrasion from the streambed and sediment bed load. Studies by Korth (1979) and Andrews (1990) have both indicated (using data from tumbling experiments) patterns of wear that are characteristic of stream abrasion. Neither study

found any evidence of bone breakage during experiments with small grained material lasting over 300 hours, but Andrews (1990: 18) found that the addition of two larger rocks to the experiment lead to breakage of both long bones and crania within two hours.

2.5 Why do taphonomy ?

This chapter has introduced the concepts behind small mammal taphonomy, and the problems of trying to reconstruct the ways in which an assemblage of microvertebrate remains accumulated. This concluding section utilises this information, to show why it is necessary to carry out taphonomic research.

To recap, assemblages of small mammals are often produced by carnivorous birds or mammals. After they have digested their prey, there are a number of other environmental factors that may still affect the assemblage. All these categories of bone modification can, in some way or another, influence perception of the interpretation of the biocoenosis (living community) which these small mammals came from, and which ultimately, the archaeologist and palaeontologist are trying to reconstruct.

As was outlined at the beginning of this chapter, the goal of this taphonomic research is to identify these various processes of assemblage modification, so that they may be incorporated within the palaeoecological reconstruction, which is usually the final aim of this type of analysis. The following section will review three of these taphonomic problems and their association with palaeoecology, to highlight the need for, and importance of, detailed taphonomic research.

2.5.1 Taphonomic alteration by predation

2.5.1.1 Prey selection

Different predators sample different parts of the prey population (Brain 1981; Andrews 1990). Owls are generally nocturnal and their prey is therefore mainly nocturnal; raptors are more diurnal; and mammalian carnivores operate during both periods. Some predator species are generalists, and capture a wide variety of prey that accurately reflects the prey population. Others are more specialist feeders, which may select only parts of the prey populations, perhaps determined by prey frequency, size, weight or palatability. Anti-predatory behaviour may also be an influencing factor (Ylonen 1994), and some small mammal species are easier to capture than others (Pearson 1964; Taylor 1994).

The selection of prey may also be limited by habitat type and hunting method (Andrews 1990: 44). For example, *Strix aluco*, which captures mainly woodland species, prefers woodland habitats and hunts by sitting in a tree, then swooping down on its prey once it is in range. *Tyto alba*, on the other hand, takes predominately grassland species, reflecting the preferred habitats in which it hunts, by flying over the land in transects, until it locates its prey. Neither of the two birds would be able to use their specific hunting techniques in the other's habitat, a fact reflected by the abundance of habitat specific prey species in their diets. A summary of predator habitats and prey selection bias is given in Appendix table 13, page 295.

As well as possible taphonomic biases associated with the selection of prey, its transportation from one environment to another whilst being consumed must also be considered (Maas 1985). The result of these predator / prey biases is that, often, only certain parts of the total fauna will be sampled by specific predators, and that transportation could lead to the formation of allochthonous[17] deposits (Shotwell 1955).

---

[17] 'Allochthonous refers to remains that have been moved from the site of death and out of the original habitat' (Behrensmeyer and Hook 1992: 19).

2.5.1.2 Prey consumption and bone breakage

Variations in prey consumption also lead to variations in element and species frequency. For example, although most owls tend to swallow their prey whole, there are some cases of larger prey being broken into smaller pieces before being swallowed (Chitty 1938: 270; Lawrence 1997: 19), and some records indicating that on occasion, *Tyto alba* will consume only the head, and not the body of the prey, although this is viewed as a rare occurrence by Taylor (1994). However, Shotwell (1955: 331), proposed that similar mechanisms of selective feeding may have been responsible for the variation in cranial and postcranial elements of small mammals within the McKay Reservoir sample.

The method of prey consumption in diurnal raptors is different from owls. They do not swallow their prey whole, but pick it apart with their talons and beaks. This can cause high degrees of bone breakage, and element loss. There is also a potential for various parts of the skeleton to be left uneaten, once it has been stripped of meat (Andrews 1990: 39), also contributing to a loss of information. Most mammalian carnivores tend to eat all parts of their small mammal prey, but the chewing action (mastication) of the jaws causes an extreme amount of breakage, and many bones within carnivore scat material are often too damaged to identify (Maas 1985), or may have been entirely destroyed (Behrensmeyer 1975: 545). These various effects of consumption lead to further complications of the ecological information, which may already have been biased by predator prey selection.

A further factor to take into account is the variation in prey skeletal robustness. It is difficult to identify post cranial elements to species, but analysis of cranial elements (maxilla and mandible) indicates that certain prey species are more susceptible to cranial breakage than others (Denys *et al.* 1996: 111-114). This will be further investigated within this study for *Tyto alba* nest material, although it is recognised that there are a number of introduced and uncontrollable variables (such as breakage of bones by parents during feeding, and trampling of the disgorged pellet material in the nest) that may invalidate any comparisons.

2.5.1.3 Bone digestion

Bone digestion has been frequently used as a criteria for recognising predator species (Andrews 1990; Fernandez-Jalvo 1992; Fernandez-Jalvo 1995; Fernandez-Jalvo 1996), but whilst different predators are recognised as leaving characteristic levels, and frequencies, of digestion on teeth and long bones, they also appear to be destroying some bones altogether. This phenomenon has been reported in a number of studies (Raczynski and Ruprecht 1974; Dodson and Wexlar 1979; Lowe 1980; Andrews 1990; Saavedra and Simonetti 1998), and the results suggest that in some cases, the number of specific skeletal elements and even species is reduced, as prey is entirely digested by the owl. No reason is given to explain this occurrence, but it presumably represents the ability of specific predator species to produce pellets which do not contain all of the ingested bones. Those bones that are not contained within the pellet are then presumably digested after the pellet is ejected from the stomach[18].

All of the above categories of taphonomic alteration by predation can lead to the modification of the community structure of the sampled fauna. However, as has been demonstrated, it is possible to predict and evaluate most of these taphonomic alterations by identifying the predator or predators responsible for the accumulation of the deposit.

The action of digestion on bones and teeth also affects the chemical composition of these skeletal elements (Denys *et al.* 1992). It is particularly important to bear this in mind, and if possible investigate the extent of this alteration, before attempting any chemical analysis of small mammal diet, and by extension behaviour and palaeoecology.

---

[18] Digestion of bones remaining in the stomach after pellet ejection is either caused by the remaining gastric juice or since it is suggested that after pellet ejection the pH of the stomach rises, then it is possible that the digestion is associated with increased preprandial stomach acidity before the next meal.

2.5.2 Taphonomic alteration by environmental factors

The following two sections deal with further modifications after deposition of the pellet or scat has occurred.

2.5.2.1 Bone breakage and loss

As has already been emphasised, bone breakage can offer some potential in the identification of predator species responsible for small mammal accumulations. However, external environmental agencies that also lead to bone breakage (such as trampling, sediment collapse and compaction, weathering, and in some cases transportation (Andrews 1990: 18)), could confuse these signatures. Moreover, this breakage often leads to loss of information, as bones either become destroyed, or too damaged to identify.

Whatever the post depositional cause of this breakage is, the end result is the same. Loss of bones means that information about the faunal composition of the community or region being studied, is altered. The ability to reconstruct these agents of attrition and damage, and identify the possible biases that they may produce, enables these aspects of post depositional history to be taken into account when analysing and reconstructing the faunal composition.

2.5.2.2 Transportation

Transportation is also responsible for the alteration of small mammal deposits. Experimental evidence suggests that transportation does not cause significant breakage to bones when transported with small sized clasts (Korth 1979; Andrews 1990). However, transportation still leads to the alteration of the composition of the deposit, as different sized bones have different fluvial properties and settling velocities (Voorhies 1969; Wolff 1973; Boaz and Behrensmeyer 1976; Dodson and Wexlar 1979; Korth 1979; Blob 1997). As species vary in size and weight, this action could be responsible for selectively winnowing out species of different weights, as well as mixing bones from different sources (Behrensmeyer 1975: 483).

The topography of an area of bone deposition can also alter the composition of the final assemblage. Owl pellets deposited on a mound have a tendency to roll down

slope (personal observation), and Levinson (1982) has shown that once a pellet has disintegrated (leaving only the bones), the cranial portions of the bones are more susceptible to rolling. This can lead to a disproportionate variation in the distribution of cranial and post cranial bones in various parts of the deposits.

The importance of investigating all aspects of transportation and bone breakage is aptly demonstrated by Dauphin *et al* (1994) in their analysis of microfaunal deposits from Tighenif (Algeria). In a study of the bone breakage and abundance of skeletal elements, and investigation of bone chemistry, they have shown that the species composition in many of the levels of this site is the result of taphonomic alteration of the initial assemblages by breakage and transportation rather than an indication of climate and environmental change. Further alterations to this thanatocene were also attributed to predator selectivity (Dauphin *et al.* 1994: 348).

2.5.3 Taphonomic alteration by sampling

Human, and animal agents, in the past may alter the nature of deposits by burrowing or digging into them. Such intrusions should be recognised in excavation, but failure to do so could lead to a bias in the sample. The excavator can also be viewed as a taphonomic agent, capable of producing biases in small mammal assemblages. The collection of samples over a wide area within each horizon will help to reduce the chances of encountering problems of localised sorting (as described above), and sampling in small depth units reduces problems associated with time resolution of deposits. However, the division of undifferentiated deposits into arbitrary sub-units (Avery 1981: 266) can lead to a taphonomic bias of species composition. Assuming different species proportions from these levels, of which the excavator may have little, or no knowledge of the rate of deposition, may well lead to erroneous palaeoecological conclusions. A well constructed dating program of these different sub-units can often help in this process (Hadly 1999)

Sieve mesh size is also important, as too large a mesh size will lead to the disproportionate recovery of larger bones, and an associated bias in skeletal element abundance (Wolff 1973; Shaffer 1992; Williams 1997). Although this loss of elements

may cause problems in using skeletal element abundances as a method of identifying predators responsible for the accumulation of the deposit, it has wider implications for the assessment of the palaeoecology as well. The loss of isolated teeth (which might occur more regularly in particular rodents after exposure to digestive juices (Andrews 1990)), and / or smaller species due to sieve size, would lead to the misrepresentation of the number of individuals of these species within a sample. Estimating this number of individuals within a sample is also difficult, as methods often over- or under-represent the numbers of individuals present (Gilinsky and Bennington 1994).

3. The Predators: Tytoninae and Striginae

3.1 Introduction

Strigidae (recent owls) are found in nearly every part of the world, comprising about 140 species (Lawrence 1997: 163-164). There are two sub-families of owls living today, the Tytoninae (*Tyto*, barn owls and grass owls, and *Phodilus,* bay owls) and the Striginae (the typical owls, e.g. *Strix*, wood owls, *Bubo*, eagle owls, etc) (Walker 1973: 27; Lawrence 1997: 36). They have a long history, dating back to at least the Palaeocene[19], where fossil forms represent both sub-families (Grossman and Hamlet 1964: 28; Voous 1988).

Most owls are nocturnal, although some exhibit more diurnal or crepuscular behaviours (Stonehouse 1973: 13). To enable them to hunt more efficiently at night, owls have very specialised vision, and increased auditory abilities. The physiology of an owl's eye is different from most birds. To facilitate improved sight, owls' eyes are much bigger than most birds, due to an increase in the number of retinal cells (Burton 1973b: 34). A further adaptation of the eye for night flight in owls is related to the ratio of rods to cones. The number of rods (which are more sensitive to low light) in the eye is much higher than in other birds, which have higher proportions of light sensitive cones (Lawrence 1997: 17). The placement of the eyes in the front of the head (as opposed to the side as is the case with most birds[20]) increases the amount of binocular vision, and as a result leads to greater depth perception (Burton 1973b: 35).

An additional aid to hunting is an owl's amazing hearing ability. Although the specialised eyes in owls means that they can hunt in almost complete darkness, operating at levels of light between one hundredth and one tenth lower than the minimum intensity required by man (Burton 1973b: 35), these levels of illumination are

---

[19] Many of the modern owl species first appear in the Miocene, which Grossman et al (1964: 31) suggest may be related to an increase in the number of seed bearing plants, and an associated rise in the small mammal populations that feed on them.

[20] On average an owl has a total field of vision of about 110°, compared with a pigeon (whose eyes are on the side of the head), which has a total field of vision of about 340° (Burton 1973b: 35).

sometimes absent on very dark nights[21] (Dice 1945). Increased ability to hunt by hearing is especially useful on these occasions. This is facilitated by a number of adaptations in ear, and cranial structure. The size of the ear is generally increased relative to other birds, with long vertical shafts nearly as long as the head (Burton 1973b: 35).

A further advantage is gained by the asymmetric placement of the ear-tuffs, with a 15% difference in planar position of the left and right ear-tuffs (Voous 1988: 13). This factor, as well as an increase in overall skull width (Burton 1973b), enables the bird to detect the precise position of its prey by sound alone. The owl calculates the difference in time (which is infinitesimal) it takes a sound to travel to each ear, and uses the difference to calculate distance. When a sound comes from straight ahead, the owl turns its head back and forth, so that the sound reaches the ears at different times (Lawrence 1997: 18-19).

Experiments with captive *Tyto alba* in an entirely blackened room found that the owl could catch its prey entirely by sound. Live mice were let loose in the room, and the owl caught them (or missed by 1°) by sound location alone (Payne 1971). Further studies with paper and string (replacing the live mice) indicated that the owl was not sensing the prey by some form of infra-red ability or smell[22].

Most owls hunt in the dark, so they are not usually visible to their prey. A further development to avoid detection is found in the wing morphology, which facilitates silent flight (Shawyer 1994: 51). The first primary feather on each wing has a serrated edge, rather than a smooth one, as is the case in most birds. During flight the serrations disrupt the flow of air over the wing and reduce the sound of turbulence (Lawrence 1997: 11). A low wing loading (caused by the difference in the relatively light weight of the bird compared to the wing area), also leads to quieter flight, as the greater wing size gives owls a more buoyant, gliding flight, with a reduced amount of noisy flapping (Burton 1973b: 39).

---

[21] Levels of light required by three owls (*Strix varia, Asio otus & Tyto alba*) from experimental data calculated from ability of owl to catch dead prey (mouse) in a darkened room (Dice 1945).

[22] Although Lawrence (1997) suggests that some owls use smell to capture their prey, this was not found to be, in the case of one *Tyto alba* used in experiments by Dice (1945), see footnote 21. The owl actually touched the prey with its wing, but was not able to smell it (Dice 1945).

3.2 Dict of owls

All owls are predatory birds, feeding on a wide range of prey from medium sized mammals such as small antelopes (Andrews 1990: 36), *Suricata suricatta* (suricate) and *Cynictis penicillata* (yellow mongoose) (Brain 1981: 124), in the case of *Bubo lacteus* [23] (Verreaux eagle owl), to small insects and moths, in the case of *Athene noctua* (little owl) (Ginn 1973: 166). The diet of the majority of owls however, is comprised of small mammals such as Murinae and Arvicolinae (Glue 1970; Brain 1981; Andrews 1990; Lawrence 1997).

Owls (and diurnal raptors) differ from most birds in that they produce pellets of undigested prey remains on a regular basis, normally at least once a day. Although many other bird species produce pellets [24] (Glue 1973: 193), their extent and frequency are much less than in owls. Pellet production occurs when, due to a lack of free acidity in the stomach, resistant materials, such as bones and fur, are not digested (Reed and Reed 1928). Furthermore, the high placement, and small size of the pyloric opening, does not allow these materials to pass into the intestinal regions of the owl (Grimm and Whitehouse 1963), and therefore they are formed into a pellet by the muscular action of the gizzard, and then retained in the proventriculus until stimulus for egestion is received (Smith and Richmond 1972).

The amount of undigested bone material within the pellets varies in different bird species. In the ornithological literature, it is suggested that this is a factor controlled by the pH level in the stomach of different predator species. This is a measure of hydrogen ion concentration in the stomach, and for optimum digestion (peptic activity) this should be at pH 2 or less (Farner 1960: 432). The pH value[25] of diurnal raptors (between 1.3 – 1.8) is much lower than that of owls (between 2.2 – 2.5) (Mikkola 1983: 32), and as a result leads to greater bone digestion (Duke *et al.* 1975: 656). It has also been suggested that the pH level in younger owls is lower (more acidic) than their parents (Grimm and Whitehouse 1963: 305; Raczynski and Ruprecht

---

[23] *Bubo lacteus* is known as the Verreaux eagle owl or the Giant eagle owl, see for example Brain (1981).
[24] Glue (1973:193) reports that a 1969 survey by the International Bird Pellet Study Group found that 330 species of birds, representing over 60 families produce pellets.
[25] The pH levels given by Mikkola (1983: 32) are similar to those of Duke et al. (1975). They are measures of the basal pH values. The pH values are lowest 4 hours before the meal (preprandial), and are found to rise after this point. Farner (1960) using data from Mennega (1938) quotes much high pH values for owls and hawks, as these measurement times were not regulated.

1974: 8), which almost certainly accounts for the higher rates of bone modification being investigated within this study.

However, recent laboratory experiments with fresh small mammal bones have also highlighted the importance of enzymatic activity in the digestion of these bones (Denys *et al.* 1995). In controlled analysis, bones were immersed in a solution of HCL (pH1) and microscopically studied. The bones were affected by this treatment, but not to the extent of that seen in predator assemblages. However, when a number of these already treated bones were then soaked in a buffered solution of protease (pronase) bone digestion was extreme, similar in appearance to category 4 and 5 predators. It is suggested therefore that whilst a difference may exist in the stomach acidity levels of various predators, enzymatic activity plays a more important role in the digestion of bones. It is further suggested that the longer the exposure to enzyme attack, the greater the digestion (Denys *et al.* 1995: 807), and the difference in digestion between hawks and owls may originate from the time of digestion (approximately 23 hours in Falconiforms, 10-13 hours in Strigiformes) rather than the pH of the gastric juices of these predators.

3.3 *Tyto alba* (barn owls)

3.3.1 General characteristics of *Tyto alba* behaviour and ecology

Tyto alba are the most geographically widespread species of owl in the world. Members of the 36 sub-species[26] of *Tyto alba* are found on all continents except Antarctica. Their distribution is mainly confined to tropical regions between latitudes 40° N and 40° S of the equator, with the exception of parts of Europe and the U.S.A. (Prestt and Wagstaffe 1973: 43) - see map below for details.

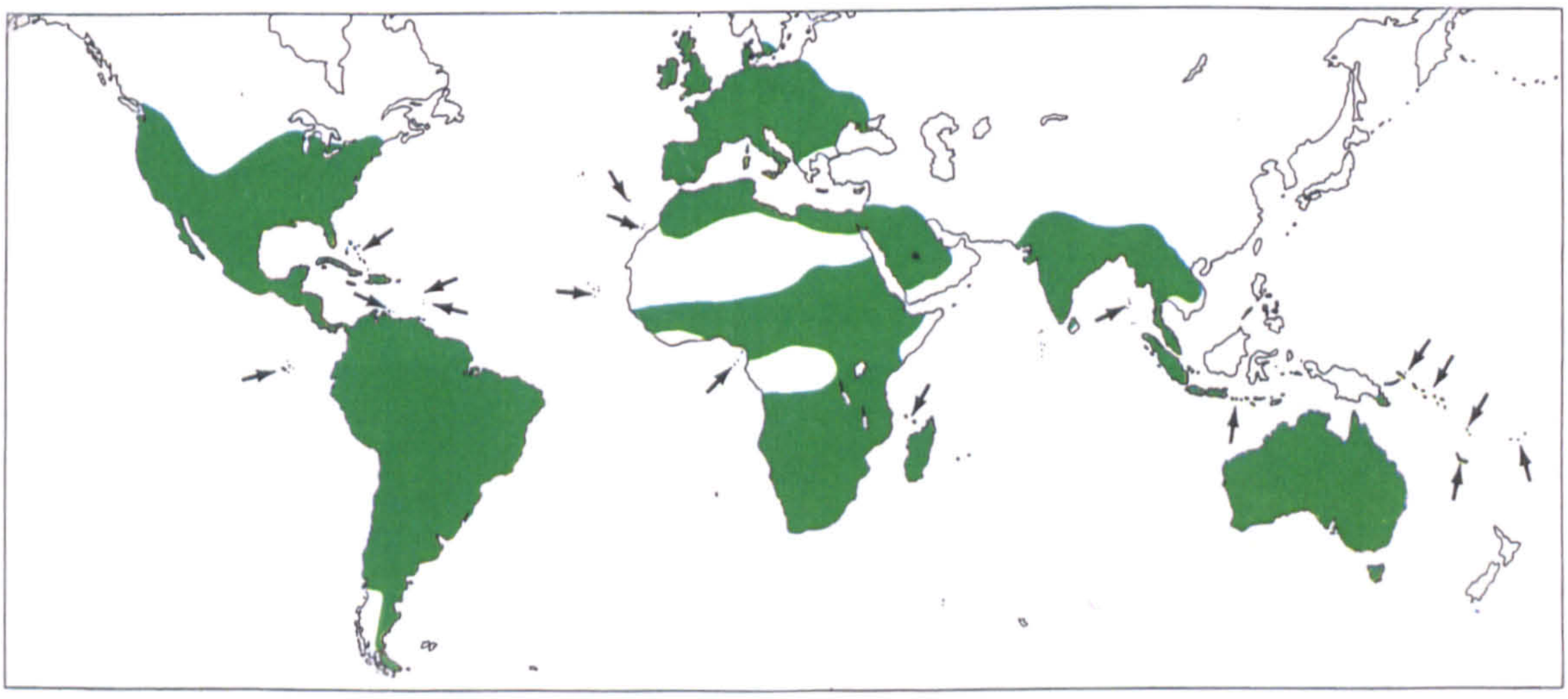


Figure 6. Distribution map of *Tyto alba* throughout the world, from Burton (1973a: 42).

[26] The precise number of sub-species of *Tyto alba* is a highly contested point. Some authors claim the total to be 36 (Taylor 1994: 24) others 35 (Bunn *et al.* 1982), 34 (Prestt and Wagstaffe 1973: 47) or 30 (König *et al.* 1999).

The Tytoninae are separated from the Striginae on the basis of a number of differences in skeletal structure[27] (Prestt and Wagstaffe 1973: 42; König *et al.* 1999: 193), by phylogenetic analysis[28], and also by the number, shape and structure of their chromosomes (Beltmann and de Boer 1984). The Tytoninae are typified by their heart-shaped face (Prestt and Wagstaffe 1973), although there is quite a wide variability between the different sub-species of *Tyto alba*, mainly in colour, size and habitat. The colour that most people associate with *Tyto alba* is orange-buff to yellowish brown body with a white breast (Prestt and Wagstaffe 1973: 43), although there are numerous variations in the different sub-species. The African sub species *Tyto alba affinis* has a much darker body, similar to the central and eastern European sub species *Tyto alba guttata* (Voous 1988: 10), while a number of the island forms are more orangey (Prestt and Wagstaffe 1973: 50-51).

Figure 7. The nominate race *Tyto alba alba*, showing heart-shaped face, orange-buff to yellowish brown body with a white breast

---

[27] The main skeletal characteristic used to separate Tytoninae (barn owls and bay owls) from Striginae (the typical owls) is the equal length of the inner and middle toes (König *et al.* 1999: 193). Other differences include the absence of indentations on the breast bone (Prestt and Wagstaffe 1973).

[28] Phylogenetic evidence, based on mutilocus protein electrophoresis (Randi *et al.* 1991), DNA-DNA hybridisation (Sibley and Ahlquist 1990), egg white protein electrophoresis (Sibley and Ahlquist 1972) and mitrochondial DNA (Wink and Heidrich 1999), indicates that Tytoninae diverged from Striginae early on in owl evolution, with both the Tytoninae and Striginae sharing a common ancestor. All of the above studies support the view that Tytoninae is the sister lineage of the Striginae (Randi *et al.* 1991: 299).

Size variability in *Tyto alba* is measured in wing length. A number of island races, for example *Tyto alba bargei* (Island of Caraçao), and *Tyto alba punctatissima* (James Island, Galapagos), are considerably smaller than *Tyto alba alba* (common barn owl, found in western Europe[29], and north Africa) (Prestt and Wagstaffe 1973). *Tyto alba affinis* (African barn owl) is only slightly bigger (approximately 2%), whilst at the other end of the scale, *Tyto alba pratincola* (American barn owl) has 20% longer wings than the nominate form. (Voous 1988). However, even larger species are known from the fossil record. *Tyto balearica*, found in Plio-Pleistocene deposits from Minorca, and Majorca, was 1.5 times the size of *Tyto alba alba* (common barn owl) (Mourer-Chauviré *et al.* 1980). Aside from the size differences between different sub-species, there is also considerable sexual dimorphism, with the average female weight being 362g, compared with 312g for the male (Mikkola 1983: 377).

Tyto alba is usually associated with areas of open woodland and grassland, and this is certainly the case in much of Europe and North America, where it inhabits a wide variety of open mosaic vegetation types (Voous 1988: 10). *Tyto alba affinis* shows similar habitat preferences, but is also found in more arid environments, such as the Sahara (Prestt and Wagstaffe 1973). Adaptations in island forms has lead to specialised habitat preferences, and some sub-species *Tyto alba* are located in more wooded, forest regions. As a consequence of this more restrictive habitat, these owls often have shorter wings (Taylor 1994: 21-22). *Tyto alba* is never found in tundra regions or high altitudes because of its low tolerance to cold (König *et al.* 1999: 193).

3.4 *Tyto alba alba* (barn owl) in Britain

The previous section concentrated on owls and barn owls across the world, introducing their general behaviour and ecology. Evidence of the differences in *Tyto alba* sub-species, in their size and habitat, indicates that in certain circumstances, gross generalisations about behaviour and the associated taphonomic conclusions that may be

[29] *Tyto alba alba,* the common or white-breasted barn owl is found in the 'British Isles ... Western France, Spain, Portugal, Italy and countries bordering the Mediterranean'(Prestt and Wagstaffe 1973: 43).

drawn, should be approached with care. Throughout the rest of this chapter, any reference to *Tyto alba* is to the sub-species *Tyto alba alba,* unless otherwise stated.

The following sections will provide an overview of *Tyto alba* in Britain. Information comes from a number of sources[30], mainly recently published books by Taylor (1994), Bunn *et al.* (1982), Shawyer (1994), and Walker (1993), and book chapters, such as those by Voous (1988), Prestt and Wagstaffe (1973), and Lawrence (1997). Information on diet is given by a vast number of authors, especially Glue (1967; 1970; 1974), and Taylor (1994).

3.4.1 Feeding

In Britain, *Tyto alba* is predominantly associated with areas of open grassland, farmland and woodland edges (Shawyer 1994: 35). The most important parts of these environments, for *Tyto alba*, are not the fields or woods themselves, but the areas of rough grassland adjacent to these areas. These habitats are home to numerous voles and shrews, which constitute most of the owl's diet.

Although most owls are nocturnal, *Tyto alba* will also hunt during dusk and dawn, and sometimes the day, if it is truly hungry, or if feeding young (Walker 1993). Hunger occurs quite quickly within *Tyto alba*, due mainly to their limited fat reserve, and most will die of starvation if they do not eat within 5 days (Voous 1988: 21). They need to eat at regular intervals[31] (Lawrence 1997), as they are inefficient feeders; nutrient efficiency was found to be 75% for *Tyto alba*, compared with 80% for *Strix aluco* (Ceska 1980; in Voous 1988).

The amount of prey that an owl captures is one of the factors leading to increased diurnal activity. Prey capture rates can vary for a number of reasons, prey availability being only one reason, which will be further discussed within the next chapter. The weather appears to play an important part in hunting activity (Lawrence

---

[30] A bibliography of all published works on owls produced in 1978, records 1100 books and articles about *Tyto alba*, over half of which deal with ecology (natural history, ecology per se, inter-specific relationships, roles of species in biological communities ecosystems etc) (Clark *et al.* 1978).

[31] It is suggested that when possible, *Tyto alba* will hunt at three specific points during the night; dusk, midnight and just before dawn (Lawrence 1997: 113).

1997: 19). *Tyto alba* do not like to hunt in heavy rain, so when it is rainy, they sit and wait it out (Mikkola 1983: 42).

However, the rain itself is not the only problem. In observations of *Tyto alba pratincola*, Walker (1993: 4) discovered that prey capture was much lower on rainy days and those succeeding them. Although there may be a number of different factors limiting the numbers of prey caught, it is most likely that the rain dampens the ground to the extent that the owl is no longer able to locate its prey by sound (Walker 1993: 6). As such, more time hunting during the day would be necessary. This may occur more in winter, when snow coverage leads to increased difficulty in hunting (Mikkola 1983: 43).

3.4.2 Hunting

Hunting usually takes place within a two – three kilometre radius of the roost or nest site, and often much closer, (Andrews 1990: 178) and although forays of up to 16km have been recorded (Brain 1981) this is thought to be rare. *Tyto alba* has a number of methods of hunting. In some cases, it sits on a perch, such as a fence post, watching for its prey. It has been suggested that this approach is most often used during winter, or periods of low prey availability, to conserve energy (Taylor 1994: 59). The technique more usually associated with *Tyto alba* is that of flight hunting. In fact, *Tyto alba* spends more time on the wing hunting than almost any other owl (Karalus and Eckert 1974: 14). The owl quarters[32] field margins, ditches and edges of woodland, looking and listening for its prey (König *et al.* 1999: 195). It usually flies between one and four metres above the ground (Bunn *et al.* 1982: 71). It hunts mostly with its ears, using eyes to avoid obstacles (Karalus and Eckert 1974: 14).

Once the prey has been located, the owl drops down to the ground, with its wings back and legs extended[33], sometimes conducting summersaults and other aerial manoeuvres to reach the prey (Mikkola 1983: 44-45). Several authors also claim that

---

[32] When an owl is said to quarter the land, it means that it flies back and forth over it.
[33] The long legs of *Tyto alba* enable it to capture its prey in long grass, its preferred habitat (Taylor 1994: 50).

shortly before it is about to strike its prey, the owl emits a screech[34] (Prestt and Wagstaffe 1973: 44). This sound (coming after the owl's silent flight) is supposed to scare the prey into a frozen pose; 'an instinctive protective reaction' (Karalus and Eckert 1974: 14). With its talons spread, the owl lands on top of the prey, and grasps its claws around it (Bunn *et al.* 1982: 71). Sometimes the action of being gripped by the claws will kill the prey (Bunn *et al.* 1982: 75). Otherwise, a bite to the neck is used to dispatch the small mammal (Shawyer 1994: 52). The prey is consumed either on the spot, or if the owl is feeding nesting chicks, carried back to the nest in the claws (Mikkola 1983: 46).

3.4.3 Roosts

Tyto alba will roost anywhere there is an abundance of prey (Lawrence 1997: 111), and many owls may occupy a roost site for a number of years. These sites can be divided into natural and man-made sites. The natural sites are those that are most likely to have been used in the past by owls before the development of buildings (Taylor 1994: 2). Natural sites often include trees (either inside hollows or within trees with thick foliage, such as spruce, pine or holly (Bunn *et al.* 1982: 58)), holes (natural or self made) in cliffs or river banks (Voous 1988: 10), abandoned burrows of badgers or similar sized mammals (Karalus and Eckert 1974: 16), rock fissures (Glue 1970: 55), or caves (Brain 1981; Levinson 1983; Shawyer 1994). Man-made sites include lofts and attics of buildings, church steeples, walls of mine shafts (Walker 1993: 12), disused barns, derelict mills, wells, cisterns, and even abandoned agricultural machinery (Voous 1988: 10).

In many cases, the roost site and the nest site are in the same location, or close together, and the female tends to stay at this site all year round (Voous 1988: 16). Generally, roosts are located above the ground, often on a tree branch, ledge, or in the case of manmade structures, a beam or railing. At these roost sites, the owl usually selects precisely the same spot to roost on all of the time, below which large

---

[34] This claim is refuted by Bunn *et al*, on the basis that this noise is never heard during observations of owls hunting during the day (Bunn *et al.* 1982: 72).

accumulations of pellets and droppings build up (Bunn *et al.* 1982: 57). If disturbed at a roost site, the owl will often fly off, usually alighting a short distance away (Prestt and Wagstaffe 1973: 44).

3.4.4 Nesting

Nest sites differ slightly in that they are usually more isolated and therefore provide greater security. They are situated on the ground, either on the floor of a belfry (Walker 1993), barn (usually the upper stories), in disused chimneys (Glue and Jordon 1988), on a cave floor (personal observation), or within a tree hollow (König *et al.* 1999: 195). More often than not, they are in extreme darkness (Voous 1988: 16). No 'structural' nests are built at these sites, and the eggs are laid directly on the floor, or onto a pile of pellets (Prestt and Wagstaffe 1973: 46). Eggs are laid over successive days, with incubation starting on the first day that an egg is laid. The average clutch size is about five, although up to 18 eggs have been recorded (Mikkola 1983: 51). The number of eggs laid each year is largely dependant upon the space available at the nest site. It is possible to lay a large clutch of eggs on the floor of a disused belfry, but only a few eggs are laid within the more confined space within a tree hollow (Walker 1993: 12).

The number of eggs may also be regulated by the availability of prey within a given area or year. Cyclical fluctuations of voles are strongly correlated with clutch size, and a reduced number of eggs are laid during years of decline in vole numbers (Taylor 1994: 163-164). These fluctuations are more marked in areas with only a limited number of prey species[35]. Although it is more common in more temperate climes, barn owls in Britain do sometimes lay two clutches of eggs during the year: one early in the season and one later after the first clutch have fledged (Taylor 1994).

Incubation takes approximately 33 days (Prestt and Wagstaffe 1973), a task carried out almost exclusively by the female[36] (Walker 1993). During this time, the male brings food to the female, and once the chicks have hatched, both of the parents

---

[35] Clutch size variations are less marked in North America, as the owls had a much more diverse diet, and often 'showed considerable year-to-year switching of prey species' (Taylor 1994: 164).

[36] 'Some days before laying the females lose their feathers in the belly region and develop a brood patch, as area of bare skin which becomes richly supplied with blood vessels' (Taylor 1994). This area is used to provide heat to the eggs.

are responsible for the hunting. The amount of prey that needs to be captured obviously varies with clutch size[37], but Walker recorded a pair of barn owls capturing 27 rodents in one night (Walker 1993: 4). After about four weeks, the young owls leave the confines of the nest, and walk about the nest area, returning for prey. By eight weeks, they have started to explore outside the nest, returning after short excursions (Bunn *et al.* 1982: 132). By the tenth week, they have left the nest, although they may still rely upon their parents to feed them until they become more independent, and are finally chased out of the area by the parents (usually the female), after about three months (König *et al.* 1999: 195). The range of dispersal is usually not great (between 3-4km), although some owls have been found up to 1600km from their original nest sites (Taylor 1994: 190-191).

The main purpose of this study was to explore the differences in taphonomic signatures between nesting and roosting barn owls, and it has been suggested that young owls are responsible for greater taphonomic alteration of bone than their parents (Andrews 1990: 33-35). Whilst this will be further discussed within much of the remainder of this study, it is also worth exploring if there is any difference in the prey represented in nest deposits, rather than at roost sites; i.e., if there is any evidence of prey species selectivity at nest sites.

When the baby owls are in the nest, it is their parents that do the hunting for them. There are few records of any difference in the dietary analysis of nest sites and roost sites, and following observational studies of adult owls returning to the nest with prey items, Taylor asserts that the prey brought to the nest is roughly the same as that consumed by the adults (1994: 85). While hunting, the owls will bring back most of the food items that they capture during the early parts of their flight, and feed only on very small prey, or after the baby owls have been fed, as hunting with the extra weight of the consumed prey will increase energy requirements (Taylor 1994: 85).

However, it would also seem profitable for the owl to bring larger prey items back to the nest (Taylor 1994: 77). This can be understood in terms of foraging efficiency, as more energy is expended in locating, capturing and delivering two small prey items, compared to one larger prey item. Therefore, if there are any noticeable

---

[37] In some cases, during bad weather, or low prey availability, the older chicks (and or parents) sometimes devour the youngest and weakest chicks (Bunn *et al.* 1982; Glue and Jordon 1988; Walker 1993).

differences in prey composition at the nest site, (and these maybe more of a result of other factors described previously, than those described within this specific section), then they are likely to be related to more energy efficient hunting, and therefore larger prey items (or those that are easier to capture) (Taylor 1994).

3.5 Conclusions

To what extent is the information outlined above useful to the understanding of *Tyto alba* as a contributor of small mammals to archaeological assemblages? What patterns are there that may help researchers get a better picture of their activities?

1) *Tyto alba* are not always nocturnal hunters, so it is not surprising that diurnal prey turns up in pellets. This should be remembered when considering the predator based on prey species alone (for example see Hadly 1999)

2) Roosting and nesting sites occur in many locations, and the opportunity for this material to enter the archaeological record is therefore high.

3) If one accepts that taphonomic signatures of *Tyto alba*, given by Andrews (1990), are truly representative of all *Tyto alba* in the present, and past, then analogies of hunting techniques and prey preferences can be applied *de facto* to these assemblages. One should however, consider the number of variations in the present sub-species of *Tyto alba*, that may lead to misleading results. For example, forest dwelling owl species, will be more likely to capture more forest dwelling small mammal species.

4) The hunting area of *Tyto alba* is mainly over grassland, and therefore much of the prey captured, will be representative of this type of environment. This relationship between habitat, small mammal species, and hunting strategy will be further explored in chapter 5.

4. The Prey: small mammal species in Britain

4.1 Introduction

> 'One of the first things with which an ecologist has to deal is the fact that each different kind of environment contains a characteristic set of animals'
>
> (Elton 1966: 5).

As small mammals are indicative of certain environments, it is necessary to investigate how accurately we can reconstruct these environments, using small mammal abundance data. By studying small mammal ecology, and understanding the life histories, population fluctuations, and habitat preferences of these species, it is possible to gain a better insight into the potential numbers of certain small mammal species within a landscape, and the concomitant relationship with the numbers of specific prey taken by *Tyto alba*.

This chapter will concentrate on the ecology of British Rodentia and Insectivora (rodents and insectivores), and how this ecology influences later taphonomic reconstructions. The previous chapter dealt with the ecology of owls, and in particular, *Tyto alba*. Chapter 5 will then combine the data from these two chapters, to show how the study of the ecology of both owls, and small mammals, is important to the understanding of small mammal assemblages within archaeology.

4.2 British small mammal species

Throughout the last two hundred years, the number of small mammal species in Britain has risen dramatically. The cause of this rise has been the taxonomic classification of many of these species, especially island faunas, into smaller sub-species, or individual species (Harrison Matthews 1982). However, this problem has now been resolved (Corbet 1961), and the total number of small mammal species commonly recognised in Britain are 23. These are divided between two orders, Insectivora and Rodentia. Other orders of small mammals, such as *Oryctolagus* and *Lepus* (rabbits and hares) are not considered in this review, as they above the size of the usual prey range of *Tyto alba.*

Within the order Insectivora, three families of terrestrial mammals are found in Britain, Erinaceidae, Talpidae and Soricidae, containing seven genera and species, which are shown in the table below.

Family	Genus	Species	Common name
Erinaceidae	*Erinaceus*	*europaeus*	European hedgehog
Talpidae	*Talpa*	*europaea*	Mole
Soricidae	*Sorex*	*araneus*	Common shrew
	Sorex	*minutus*	Pygmy shrew
	Neomys	*Fodiens*	Water shrew
	Crocidura	*sauveolens*	Lesser white-toothed shrew
	Crocidura	*russula*	Greater white-toothed shrew

Table 3. Species of the order Insectivora found in Britain, using data from Nowak (1999a) and Harrison Matthews (1982).

The last two species in Table 3, *Crocidura sauveolens* and *Crocidura russula*, only occur on the Scilly Isles and the Channel Isles (Harrison Matthews 1982: 20), and so will not be further considered here.

The order Rodentia is the largest order of mammals in the world, comprising over 1700 species (Corbet and Harris 1991: 176). In Britain these are represented by four families (five including the recently extinct[38] beaver, *Castor fiber*), containing 15 species. These are shown in the table below.

[38] The Beaver became extinct in Britain around AD 1200, although its numbers had been declining before this point (Harrison Matthews 1982: 25).

Family	Subfamily	Genus	Species	Common name
Sciuridae		*Sciurus*	*carolinensis*	Grey squirrel
		Sciurus	*vulgaris*	Red squirrel
Gliridae		*Muscardinus*	*avellanarius*	Common dormouse
		Glis	*glis*	Fat / edible dormouse
Myocastoridae		*Myocastor*	*coypus*	Coypu
Muridae	Arvicolinae (voles and lemmings)	*Clethrionomys*	*glareolus*	Bank vole
		Microtus	*agrestis*	Field vole
		Microtus	*arvalis*	Orkney & Guernsey voles
		Arvicola	*terrestris*	Water vole
	Murinae (mice and rats)	*Apodemus*	*sylvaticus*	Wood mouse
		Apodemus	*flavicollis*	Yellow necked mouse
		Micromys	*minutus*	Harvest mouse
		Mus	*domesticus*[39]	House mouse
		Rattus	*norvegicus*	Common (brown) rat
		Rattus	*rattus*	Ship (black) rat

Table 4. Species of the order Rodentia within Britain, data compiled from Corbet and Harris (1991) and Nowak (1999b).

Only twelve of the small mammal species in Table 3 and Table 4 are included in this review. They are all in the size range of under 500grams, and typically a great deal smaller, between 10-50g. Large rodents, such as the coypu are not included, as they are too large to become the prey of *Tyto alba*. Likewise, hedgehogs, moles, squirrels and dormice are excluded as they are rarely recovered as prey items from *Tyto alba* pellets (Glue 1974), or from archaeological assemblages; they are absent from all of the samples used in this analysis. The Orkney and Guernsey voles (*Microtus arvalis*) are also left out of further analysis as they occur in Holocene Britain only as introduced island faunas.[40]

Bats are not included in this study, as it is concerned only with terrestrial mammals. A further reason for the exclusion of bats is that they often roost in similar

---

[39] Formerly known as *Mus musculus*, the name was changed by the International Commission of Zoological Nomenclature in 1990 (Berry 1991: 239).

[40] *Microtus arvalis*, the common vole on the continent, is not found in mainland Britain. However a number of subspecies are found on islands. *Microtus arvalis orcadensis* occurs in Orkney: Mainland, Rousay, South Ronaldsay. *Microtus arvalis sandayensis* in Orkney: Sanday, Westray. *Microtus arvalis sarnius* occurs on Guernsey (Gorman 1991). None of these voles are represented in this study.

locations to the owls, and can become incorporated within the deposits because of natural death. It is also fairly difficult to distinguish between different species of bat on the basis of skeletal evidence alone (Yalden 1977). Finally, volant mammals and birds do not make good palaeoecological indicators. This is because flight enables them to range through different environments, and to die or become prey, in an environment that is ecologically different from their normal habitat.

4.3 Arvicolinae (Voles)

Arvicolinae (voles) are one of the most wide spread grassland small mammals throughout non-arid parts of the Holartic (Corbet and Harris 1991: 191). They are herbivorous, and primarily grazers, consuming high quantities of low quality plant material - mainly grasses (Gipps and Alibhai 1991: 206). This is facilitated by specially adapted molar teeth. They are high crowned (hypsodont), and continuously growing, so that as the grinding surface of the tooth is worn down, by the highly abrasive grass diet, it is then replaced (Corbet and Harris 1991: 191). This tooth growth is between 0.4 – 0.9 mm per week, which means that an entire molar tooth is replaced in 6-12 weeks (Stuart 1982: 36). *Clethrionomys glareolus* (bank vole) has a slightly different tooth morphology, in that the molar teeth develop roots[41] during life, which lengthen with age, rather than being continuously growing and rootless as is the case with most voles (Alibhai and Gipps 1991). By the time they reach old age, *Clethrionomys glareolus* teeth look more similar to the brachydont[42] molar teeth of mice and rats, than other voles.

Three vole species are included within this study; these are the *Microtus agrestis* (field vole), *Clethrionomys glareolus* (bank vole) and *Arvicola terrestris* (water vole).

---

[41] The development of roots is the primitive condition, which can be seen in the teeth of the fossil genera *Mimomys* and *Pliomys* (ancestral to *Microtus* and *Arvicola*) as well as *Clethrionomys*. However, through parallel evolution most of the microtine voles have developed teeth that are more hypsodont, and entirely unrooted (Stuart 1982).

[42] Brachydont – having short crowns, well developed roots and only narrow canals in roots.

4.3.1 *Microtus agrestis* (field vole)

Description: – *Microtus agrestis* is a small, greyish brown vole, with small ears and eyes, a short tail and blunt snout. Its colour varies from greyish to yellow brown. The mean length (head and body) of *Microtus agrestis* is between 102mm and 121mm, with slight sexual dimorphism; the males commonly have longer bodies. The weight of *Microtus agrestis* varies from 20.8g to 39.7g. Weight is also sexually dimorphic, with greater mean weights recorded for the males. The life span of *Microtus agrestis* is usually about 1 year, with very few adults surviving 2 winters (Gipps and Alibhai 1991).

Distribution: – This species is ubiquitous throughout mainland Britain. It is absent from Ireland, the Isle of Man, and most Atlantic islands (Yalden 1982; Gipps and Alibhai 1991).

Archaeological distribution: - *Microtus agrestis* is found in Britain with consistent regularity within Holocene archaeological deposits (Yalden 1982), and in a number of interglacial periods during the Pleistocene (Sutcliffe and Kowalski 1976; Yalden 1999).

Ecology: – *Microtus agrestis* lives mainly in rough grassland, including forestry plantations with lush areas of grass (Gipps and Alibhai 1991: 111), constructing runways within the grass. It is also found in scrub (Harrison Matthews 1982: 205), and other marginal habitats such as woodland, hedgerow, bog, dune and moorland (Gipps and Alibhai 1991). Unsurprisingly, the diet of *Microtus agrestis* comprises mainly grasses, stems and leaves. These voles are active through the day and night, due to their high food intake requirements[43]. It is possible that voles forage more in the daytime, during the winter, than the summer, as heat loss on cold winter nights would be higher than during the day (Taylor 1994: 73).

Population cycles play an important part in the regulation of vole numbers, and these cycles are particularly prevalent in *Microtus agrestis*. Seasonal variations in *Microtus agrestis* numbers are regulated by breeding, food and habitat availability, and

---

[43] Voles have to forage at constant intervals in order to secure high rates of food intake because of their high metabolic rate and energy expenditure (Taylor 1994: 73).

within any given year, numbers show marked variation. The lowest densities occur in spring, and tend to peak around autumn after the end of the breeding season (Taylor 1994: 67). Patterns of abundances also show longer term trends, usually indicated by a three to four year peak in numbers, followed by a population crash (Taylor 1994: 64). Despite the many years of scientific research dedicated to this subject, there is still no definite and easy answer as to the cause of these fluctuations (Chitty 1996: 19). The graph below, shows the extent of these three year fluctuations; in years of decline, vole abundance often reaches levels as low as 10% or less (Taylor 1994: 64).

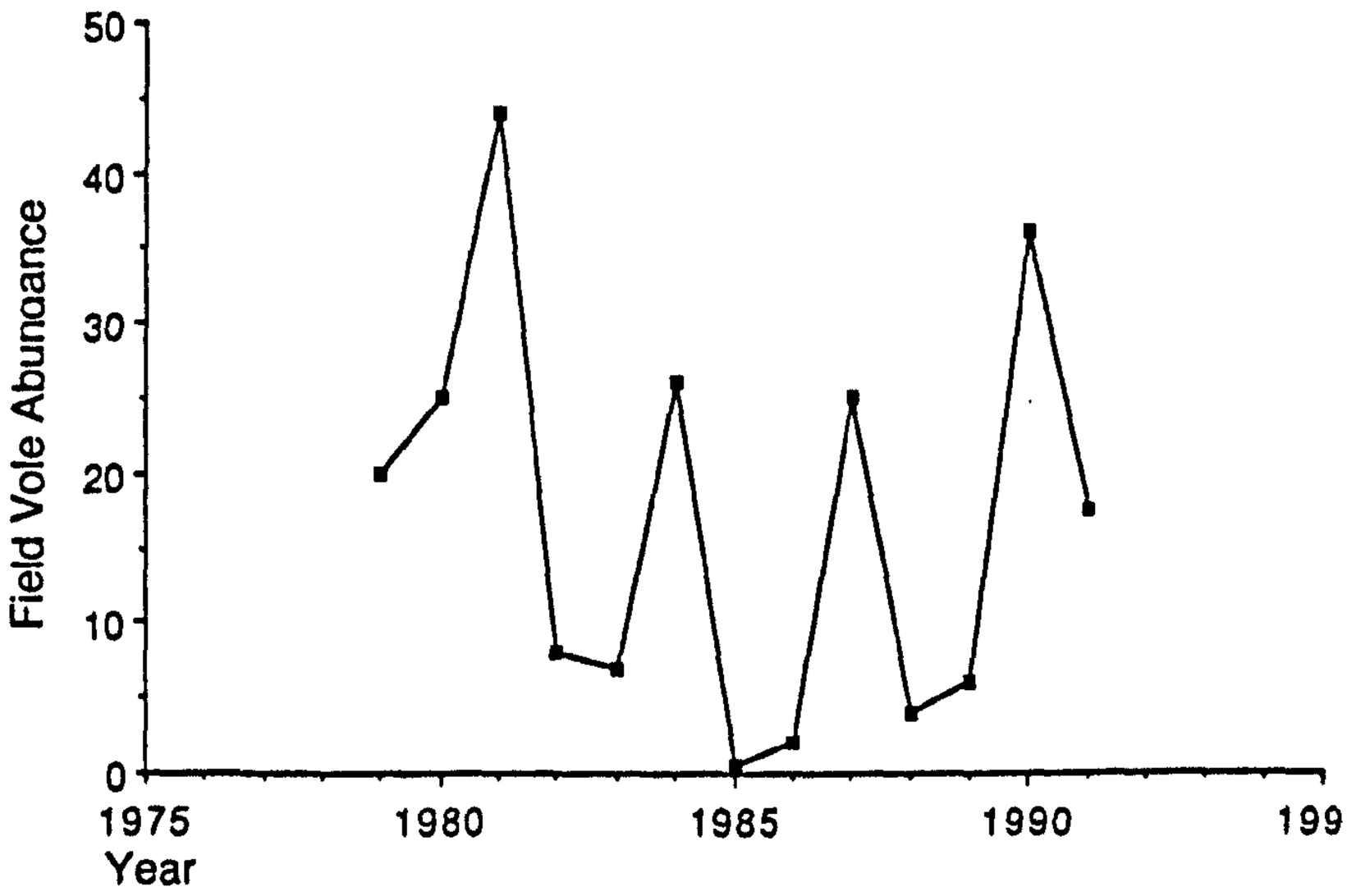


Figure 8. *Microtus agrestis* abundance from trapping data, indicating changes in numbers due to population fluctuations, from Taylor (1994: 64).

4.3.2 *Clethrionomys glareolus* (bank vole)

Description: – *Clethrionomys glareolus* is similar in appearance to *Microtus agrestis*, with a blunt nose and small ears and eyes, but with a longer tail and more prominent ears. Pelt colour is similar in young animals, but in adults it is characterised by a rich reddish brown colour on the upper side of the animal. It is approximately 90-110mm long (head and body), with a weight between 17-26g. Similar to *Microtus agrestis*, the males are usually heavier than the females (Alibhai and Gipps 1991).

Distribution: – *Clethrionomys glareolus* is distributed throughout Britain, and a limited number of islands. It is absent from the Isle of Man, Hebrides, Orkney and Shetland (Alibhai and Gipps 1991). It is also present in the south of Ireland, although this represents a very recent introduction, sometime around the 1960's (Smal and Fairley 1984).

Archaeological distribution: – *Clethrionomys glareolus* is present in interglacial deposits since the Cromerian (oxygen isotope stage 13) to the present (Yalden 1999: 24). It appears in Britain during the Mesolithic and its remains are found in all periods from this point onwards throughout the Holocene.

Ecology: – *Clethrionomys glareolus* lives mostly in woodland, scrub and hedgerows, in which it constructs runways and burrows (Harrison Matthews 1982: 26). It is also found in other habitats, including grassland, conifer stands and young deciduous plantations (Alibhai and Gipps 1991: 278), and occurs as the dominant rodent in trapping studies in fenland (Flowerdew *et al.* 1977). Throughout its range it feeds on a diet of seeds, fruit, leaves, fungi, and sometimes invertebrates (Hannson 1985). These food types are more commonly associated with woods rather than open fields. As *Clethrionomys glareolus* spends so much time foraging within woodlands and hedgerows, it is an uncommon prey item of *Tyto alba* (Taylor 1994: 32).

Population fluctuations are common for *Clethrionomys glareolus.* These fluctuations are not as predictably cyclical as those of *Microtus agrestis*, and both annual, and multi annual fluctuations have been recorded (Alibhai and Gibbs 1985: 278). Survival of young is low, with only 50% of juveniles reaching 4 months of age. Most animals that pass this hurdle live between a year and 18 months (Alibhai and Gipps 1991).

4.3.3 *Arvicola terrestris* (water vole)

Description: - *Arvicola terrestris* is the largest of the British vole species (Boyce 1991: 212). It is widely distributed throughout Europe and parts of Asia (Sutcliffe and Kowalski 1976: 105). It measures between 120-220mm, head and body length, with a tail length of approximately 65-125mm, and weighs between 70-250 grams[44] (Nowak 1999b: 1467). In analysis of archaeological deposits or owl pellets, it is easily recognised, as its molar teeth, (as well as the rest of the skeleton), are much bigger than the other vole species[45]. *Arvicola terrestris* do not usually live more than one winter, and weaning survival is low, with only 65% of some populations surviving to become adults (Woodroffe 1996: 16).

Distribution: – *Arvicola terrestris* is found throughout Britain, Wales and south eastern Scotland, at low altitudes. It is absent from Ireland, the Isle of Man and the Atlantic Islands, but is found on the Isle of Wight, Anglesey, Arran and on Eilean Gamhna and Eilean Creagach in Argyllshire (Boyce 1991: 214). As a consequence of the high ecological tolerance of *Arvicola terrestris*, it occurs in both glacial and interglacial deposits during the Pleistocene (Sutcliffe and Kowalski 1976: 105).

Archaeological distribution: – The present species, *Arvicola terrestris,* is present in Britain during the Holocene, from the Mesolithic onwards (Yalden 1999: 67). It first appears in the later parts of the Ipswichian (OIS 5) interglacial, while the earlier evolutionary form *Arvicola cantiana* is present from the Hoxnian until the beginning of the Ipswichian (Yalden 1999: 24).

Ecology: - *Arvicola terrestris* inhabits mainly lowland areas, in densely vegetated banks of streams and rivers (Boyce 1991: 212), canals, ponds and lakes (Glue 1974: 207). The depth of the water appears to be the key feature affecting habitat choice, and shallow water is usually avoided (Boyce 1991). *Arvicola terrestris* are semi-aquatic, able to

---

[44] Slightly heavier weights are reported by Woodroffe, with adult males ranging from 240-330g and females from 225-310g (Woodroffe 1996: 4).

[45] Molar row length of *Arvicola terrestris* is over 8mm, compared to less than 7mm in all other British vole species (Boyce 1991: 212).

swim in and under water. Their nests are often in the stream bank, with entrances placed above and below the water level (Woodroffe 1996). The diet of *Arvicola terrestris* is mainly aquatic plants, herbs, grasses, buds, roots and bulbs (Nowak 1999b: 1467). Aside from its waterside habitat preferences, *Arvicola terrestris* is tolerant of a wide range of climatic and vegetational conditions, occurring in taiga belt, deciduous forest, steppe and desert environments.

Although most present day *Arvicola terrestris* in Britain are restricted to a waterside habitat, non-aquatic populations of this species occur in Europe and some parts of Britain (Southern and Crowcroft 1956). Within these areas, they inhabit pastures and other grassland and agricultural environments, living in extensive tunnel systems. Their diet includes grasses and seeds, but they are also responsible for the destruction of a wide range of agricultural products and root systems (Woodroffe 1996).

It is possible that *Arvicola terrestris* had similar habitat preferences in Britain during prehistory[46]. Numbers of *Arvicola terrestris* within archaeological assemblages from the Neolithic or Bronze Age are much higher than from later periods, or modern owl pellets (Bramwell *et al.* 1990; Yalden 1999). In some cases, these sites are situated a long way from water (Jewell 1959), or *Arvicola terrestris* occur in such proliferation as to suggest that they were far more prevalent than is the case today[47]. A possible explanation for this is that *Arvicola terrestris* once inhabited environments in which they have now been out-competed by *Oryctolagus cuniculus*, or that changes in agriculture led to the land being used for grazing or arable farming, leading to a loss of the areas of long grass, once frequented by these voles[48] (Bramwell *et al.* 1990).

---

[46] A comparison of measurements of tooth size and pro-odonty in recent and fossil water voles (*Arvicola terrestris*) from Britain suggest that the fossil water voles (*Arvicola terrestris*) may have lived a more terrestrial life, as a high degree of pro-odonty may be related to using the teeth for digging (Montgomery 1975).

[47] *Arvicola terrestris* in Britain is a species in serious decline. Recently published data by the WWF indicates that it could become extinct in as little as three years (http://www.wwf-uk.org/news/news78.htm). The major reasons for this decline appear to be pollution, loss of habitat and predation, mainly by the recently introduced *Mustela vison* (American Mink) (Woodroffe 1996: 17). Analyses of *Tyto alba* pellets from Britain indicate that the *Arvicola terrestris* was not frequently captured, constituting only 0.2 % of total prey items (Glue 1974: 204).

[48] Loss of grassland habitats should also lead to a reduction in numbers of *Microtus agrestis*, and this has been shown to be the case in examples analysed from Ossum's Eyrie Cave, (Staffordshire), where declines in numbers of *Arvicola terrestris* and *Microtus agrestis* are recorded in the later periods of the excavation (Bramwell *et al.* 1990).

Although population fluctuations are rare in *Arvicola terrestris* in Britain, four to eight year population cycles have been recorded for the fossorial[49], non-aquatic forms on the continent (Woodroffe 1996: 14).

4.4 Murinae (Mice and Rats).

Compared with the Arvicolinae, the Murinae have longer tails, up to 80% of their body length. Their faces are more pointed and they have larger ears and eyes. The teeth are low crowned, and compared to the elongated form of Arvicolinae teeth, more rounded in form[50] (Corbet and Harris 1991: 218).

4.4.1 *Apodemus sylvaticus* (wood mouse).

Description: – *Apodemus sylvaticus* is dark brown in its upper parts, and white to pale grey on its underside. Size ranges from between 81-103mm, with slightly higher average sizes in males. *Apodemus sylvaticus* weights vary from 13-27g, again with slightly higher average weights recorded in males. Their life span does not usually exceed 2 years (Flowerdew 1991: 220-223).

Distribution: – *Apodemus sylvaticus* is found throughout Britain, Ireland and off-lying Islands (Harrison Matthews 1982: 27), although it is absent from mountainous areas (Flowerdew 1991: 223).

Archaeological distribution: – *Apodemus sylvaticus* is ideally suited to woodland environments that often established themselves during the interglacial periods of the Pleistocene. It occurs early in the Holocene at Mesolithic sites such as Dog Holes, and throughout the late periods, in both urban and rural settings (Yalden 1999).

---

[49] 'Burrowing', 'underground'.
[50] Mouse teeth are similar in shape to humans (compared with the elongated form of voles teeth, which are more similar to other grazing mammals such are horses and bovids).

Ecology: – *Apodemus sylvaticus* prefers habitats with cover, and these are mainly provided by woodlands and hedgerows (Harrison Matthews 1982: 27), but it is also found in arable land, grassland, heather, and dry stone walls (Flowerdew 1991: 224). Distribution and dispersal through these habitats is controlled in part by the amount of connecting hedgerows, linking fragments of woodland and other favourable habitats (Zhang and Usher 1991). Its diet varies seasonally, containing more nuts and fruit in autumn and winter (often partially from stored surplus), and more seeds (including recently drilled crops (Johnson 1993)), leaves and invertebrates during spring and summer (Hannson 1985: 147-150).

Population size does not appear to be influenced by cyclical population fluctuations in same way as voles. However, numbers do vary between seasons, with higher numbers over winter, with a spring decline and early summer lows. Yearly fluctuations are also recorded, and are density dependant; linked to the available seed crop during early autumn (Flowerdew 1985).

4.4.2 *Apodemus flavicollis* (yellow-necked mouse).

Description: – In colour, *Apodemus flavicollis* is very similar to the *Apodemus sylvaticus*. However, it has a yellow collar around its neck, and its tail is usually longer than the body. It is slightly larger than *Apodemus sylvaticus*; mean male length (head/body) is 103.8mm compared to 94.5mm for *Apodemus sylvaticus*. It is also approximately 1.5 times heavier (Montgomery 1991). Skeletally, it is hard to separate these two species, although upper incisor depth (Fielding 1966), and mandible length (Yalden 1992: 102), have been found to be useful methods of identification.

Distribution: - *Apodemus flavicollis* has a limited range in Britain, occurring only in central and southern parts of England and eastern Wales, with isolated records further north (for example Humberside). It is absent from Ireland, Scotland and most islands (Montgomery 1991: 230).

Archaeological distribution: - Formerly its range may have been slightly larger, a fact suggested by evidence of *Apodemus flavicollis* in Neolithic deposits in Dowel Cave, Roman deposits in Manchester, and in post-Roman layers of Ossum's Eyrie cave (Yalden 1992: 102), as well as Roman South Shields (Yalden 1999: 119). The limited distribution of this species may be due to the relative difficulties in identifying it, as in many cases *Apodemus sylvaticus* and *Apodemus flavicollis* are lumped together into one category of *Apodemus* sp., (Sutcliffe and Kowalski 1976; Yalden 1992: 100). Although *Apodemus flavicollis* is commonly associated with mature deciduous woodlands, there are no archaeological records of *Apodemus flavicollis* before the Neolithic, although it may have been present during parts of the Mesolithic (Yalden 1999: 119).

Ecology: – *Apodemus flavicollis* occurs in deciduous woodland, although it is also found in well established hedgerows (Kotzageorgis and Mason 1997), and other environments giving good cover and suitable forage (Montgomery 1991). Its diet is similar to *Apodemus sylvaticus*; nuts, fruit, leaves and seeds (Hannson 1985).

The population dynamics of *Apodemus flavicollis* are similar to *Apodemus sylvaticus*, although they show less evidence of density dependence with regard to population numbers. However, they do not ever reach high population numbers, and the very high winter population decline, may go some way to explaining why populations are often at a low density with limited distribution (Flowerdew 1985).

4.4.3 *Micromys minutus* (harvest mouse).

Description: - *Micromys minutus* is the smallest member of the order Rodentia[51] in the world (Alderton 1999: 9), only 50-70mm in size (head and body). It weighs only 6g[52] when fully adult (Harris and Trout 1991: 233). Its fur is more orangey than the other British Murinae (Harrison Matthews 1982: 28). It also has a particularly long tail, similar to body length, the tip of which is prehensile (Harris and Trout 1991: 233), enabling it to grip onto grass and crop stems.

---

[51] This does not include insectivores, such as *Sorex minutus* (pygmy shrew).
[52] Somewhat humorously described as 'just over four to the ounce' by Harrison Matthews (1982: 28).

Distribution: – *Micromys minutus* are found throughout much of central and southern England, with much more patchy distribution in Wales. Virtually absent from Scotland, although isolated populations do occur. Absent from Ireland, Isle of Man, Isle of Wight and Atlantic Islands (Harris and Trout 1991: 235).

Archaeological distribution: - The presence of *Micromys minutus* in the archaeological record, is limited to a number of sites from the Iron Age onwards (Yalden 1999: 127-128), although it is always a rare find (Harris and Trout 1991: 235). It is a rare prey item within modern owl pellets, and the lack of capture may be one reason for its lack of abundance in the fossil record (Harris and Trout 1991: 236).

Ecology: – *Micromys minutus* favours environments with tall grass, rough herbage or cereal crops[53] (Glue 1975; Harrison Matthews 1982: 28), rushes and reed beds (Harris and Trout 1991: 236; Yalden 1999: 127). During the summer they weave aerial nests on the stems of the monocotyledonous plants (Harris and Trout 1991: 237), and during the winter live in the leaf litter within these tall grass environments (Harrison Matthews 1982: 28). There may be some migration between favourable breeding grounds used in the summer (with a wide range of tall grasses to build nests in), and winter habitats, as some of the breeding grounds may be liable to winter flooding (Harris and Trout 1991: 236). Diet consists mainly of seeds, of grasses and crops, but also includes leaves, fruit, fungi and occasionally invertebrates (Harris and Trout 1991: 237).

---

[53]Although *Micromys minutus* in Britain has been associated with crops in the past, Glue, (1975) suggests that with changes in farming practices, *Micromys minutus* is no longer found with such regularity within crops.

4.4.4 *Mus domesticus* (house mouse).

Description: – *Mus domesticus* has dull greyish brown fur, which is slightly lighter on the underside. It is distinguishable from the other British Murinae by its wider head, and skeletally, the differences can be seen in the teeth. It has a head and body length of 65 –95mm, and a weight between 12-30 grams (Nowak 1991: 860). The upper incisor of *Mus domesticus* is notched, and the third molars are both small (Berry 1991: 239-241). The number of roots on the teeth (or alveolar spaces in the jaws) can also enable identification as the house mouse has fewer roots on the M^1 and the M_3.

Distribution: – *Mus domesticus* is ubiquitous in Britain, including most islands (Berry 1991: 243).

Archaeological distribution. – The most widely publicised date for the introduction of *Mus domesticus* into Britain is the Iron Age[54] (Berry 1991: 243) (Yalden 1999: 124) although Yalden also recognises one example from Bronze Age levels at Brean Down (1999: 124). Claims are also made within the subsequent sections of this study, for an equally early date, following the discovery of two *Mus domesticus* teeth from Fox Hole Cave (see chapter 7). However, small bones can easily become disturbed within deposits, and work their way down into lower levels, either through the action of earthworms (Armour-Chelu and Andrews 1994), animal burrows (Yalden 1999: 124), or actually burrow themselves down into the archaeological deposits, as is the case with the Thatcham rabbit (Yalden 1992: 97; pers.comm.).

Ecology: – *Mus domesticus* is commensal, and is regularly found within urban surroundings. However, it appears to be equally adapted to some more rural habitats as well, especially on arable land, and fields with good cover, although it avoids woodlands. It is commonly found around farm buildings and food storage facilities (Berry 1991: 243). In comparison with *Rattus rattus* the other commensal rodent in

---

[54] *Mus domesticus* is found at the Iron Age sites of Gussage All Saints, Danbury and Maiden Castle (Yalden 1999: 124).

Britain, *Mus domesticus* appears to spend less time in open environments, and more time within the safe confines of buildings (Ministry of Agriculture 1981: 91-92).

4.4.5 *Rattus* (rats).

Description: - There are two species of rat living in Britain during the Holocene, *Rattus norvegicus* (common or brown rat) and *Rattus rattus* (ship or black rat) (Taylor 1991; Taylor *et al.* 1991). They are similar in appearance, although *Rattus norvegicus,* the common rat is slightly bigger. They are both relatively large, with *Rattus norvegicus* measuring up to 280mm, while *Rattus rattus* measures only 240mm (Taylor *et al.* 1991: 248). The colouring of these two species is variable, although *Rattus norvegicus* usually has dark fur above with lighter under parts, compared to the more uniform, all over dark colouring of *Rattus rattus*. In both cases the fur is longer and shaggier than the other rodent species present in the British Isles (Taylor *et al.* 1991: 248-249).

Distribution: – The distribution status of these two rats in Britain changes through the Holocene. At present, *Rattus rattus* is virtually extinct in Britain, occurring occasionally in docks in London and Avonmouth (Taylor 1991: 256), with further isolated sightings in Goole (Delany 1985) and Cardiff (O'Connor pers. comm.). By comparison, *Rattus norvegicus* is found throughout most of the British Isles (except at high latitude), usually in association with humans, and often in urban areas (Taylor *et al.* 1991: 250).

Archaeological distribution: – *Rattus rattus* was first recorded in sealed stratified Roman deposits from a well in York (Rackham 1979; Yalden 1999: 125). It occurs at urban sites throughout the period, until early Anglo-Saxon times when its numbers dwindle. However, a resurgence in numbers occurs by the end of the ninth century (Yalden 1999: 162). It is recorded in Medieval contexts, where it is responsible as the host of the flea (*Xenopsylla cheopis*), which was the main vector for the bubonic

plague[55] of AD1348-1349 (Yalden 1999: 162). Its distribution was probably widespread until the beginning of the eighteenth century, when colonisation by *Rattus norvegicus* occurred (Taylor 1991: 257).

Ecology: – Both species are regarded as commensal, and to some extent their habitat is one in which they can forage for food, and food waste associated with human occupation. However, there is some variation, as *Rattus rattus* has a much more restricted distribution (in the recent past) within urban environments (Taylor 1991), whereas *Rattus norvegicus* has a greater habitat tolerance. It is found in 'association with farms, refuse tips, sewers, urban waterways and warehouses', although it is occasionally found in more rural environments, usually connected with crops or hedgerows (Taylor *et al.* 1991: 250).

4.5 Soricidae (shrews)

Soricidae are very different from the other British small mammal species considered above. They are characteristically smaller than most Rodentia. They have long narrow pointed noses and small ears and eyes (Corbet and Harris 1991: 49). However, the main difference is in the diet; Soricidae are carnivorous, or insectivorous (Harrison Matthews 1982: 19). This difference can be seen in the morphology of the teeth, which lack the grinding or bruising surfaces of the Muridae. Instead, the teeth are large (in proportion to skull), with high pointed cusps (Corbet and Harris 1991: 49). All of the British mainland Soricidae have red tipped teeth, by which they can be easily identified in owl pellets[56] (Yalden 1977).

Due to the similarity of distribution, and habitat of the three Soricidae in Britain, they will all be treated within this one section.

---

[55] *Yersinia (=Pasteurella) pestis.*

[56] The other British Soricidae, *Crocidura sauveolens* and *Crocidura russula* have white tipped teeth. They are found only in the Scilly and Channel Isles, and are therefore not considered within this review

Description: – The three species of Soricidae present in Britain differ in size, and the ranges of these data for each species are given in the table below.

Species	Head and Body length	Tail length	Weight
Sorex araneus	48-71mm	48-80mm	5-13g
Sorex minutus	40-55mm	32-46mm	2.3-5.5g
Neomys fodiens	61-72mm	45-77mm	9-16g

Table 5. Length and weight of the three species of Soricidae present in Britain, data from Churchfield (1990: 108).

Colouring is also variable between species. *Sorex araneus* has a brown back, with lighter grey flanks and a greyish underside (Churchfield 1991a: 52). *Sorex minutus* has slightly lighter fur (Harrison Matthews 1982: 19; Churchfield 1991b: 60). *Neomys fodiens* can be differentiated from the other British Soricidae by its black fur, with grey underside (Harrison Matthews 1982: 19; Churchfield 1991c: 64).

Distribution: – All three Soricidae are present throughout mainland Britain, although *Neomys fodiens* has a slightly patchy distribution in north Scotland. *Sorex minutus* has the widest distribution, and is found in Ireland, the Isle of Man, and most other islands, with the exception of only the Shetlands, Scilly Isles and Channel Islands (Churchfield 1991b: 61). Both *Sorex araneus* and *Neomys fodiens* are absent from Ireland, and most of the Atlantic islands (Churchfield 1991a: 53-54; Churchfield 1991c: 65). All three species are found throughout the Holocene (Churchfield 1991a: 54; Churchfield 1991b: 61; Churchfield 1991c: 65), as well as a number of interglacial periods during the Pleistocene (Yalden 1999: 24).

Ecology: - All of the Soricidae in this study conform to the common habitat preferences of all Soricidae, of moist environments, with an abundance of vegetation cover (Churchfield 1990: 4) although *Neomys fodiens* is more commonly found in association with water, beside streams, ponds and ditches (Churchfield 1990: 7). Soricidae are resistant to most climates, hot and cold, and have a wide distribution, from cold tundra to hot and moist rainforests (Churchfield 1990: 7). Their diet is almost exclusively composed of invertebrate prey, beetles, insects, spiders, worms and larvae (Churchfield

1994: 78), which they need to feed on almost constantly, to avoid starvation. Within Britain (and areas of similar climate), starvation will occur after two to three hours without food (Churchfield 1990: 23).

There is some evidence of dietary separation between the three species of Soricidae in mainland Britain. Diet of *Sorex araneus* contains large proportion of earthworms (Churchfield 1994: 79), whereas they are hardly ever recorded in the diet of *Sorex minutus* (Churchfield 1990: 91). The main prey items of *Sorex minutus* are, instead, spiders and beetles. *Neomys fodiens* takes a much high percentage of aquatic prey, mainly water slaters, shrimps, and fly larvae (Churchfield 1984: 222-226); although some terrestrial species, including beetles and earthworms are also caught (Churchfield 1990: 90; Churchfield 1994: 78). Unlike many Rodentia in Britain, food hoarding by Soricidae is rare, as the energy gained by hoarding small invertebrate prey, is negated by the high energy output expended in the process of building up a store (Churchfield 1990:127).

Survival of Soricidae is low, with few surviving longer than 13 months[57]. However, only half of the population survive the first two months of life, and only 20-30% of the original population number live long enough to breed (Churchfield 1980: 420). Fluctuations are seasonal in terms of numbers available for capture, with lower numbers during the winter months. Activity is also lower in these winter months, and movement around the home ranges is reduced, to a level usually half of that recorded for the summer (Churchfield 1980: 421). Movement into home ranges by nomadic Soricidae are only recorded in summer months (Pernetta 1977: 292), again suggesting higher summer numbers.

4.6 Analysis of small mammal population numbers

Small mammals have only limited home ranges, so for the most part, they are representative of the environment that they normally inhabit. There are notable exceptions to this however. *Microtus agrestis* are not exclusively restricted to fields, and *Apodemus sylvaticus* are also found in other habitats, especially where there is a

[57] *Neomys fodiens* has a slightly longer life span, up to 14-19 months (Churchfield 1990: 36).

good seed crop (Churchfield and Brown 1987), cereal crops, or recently sown fields (Johnson 1993) - where food is plentiful. These changing patterns of habitat usage may be seasonally affected, by food availability, and population numbers, or by dispersal of young into new territories.

To assess the number of small mammals within any given environment, it is necessary to carry out trapping experiments, as it is not possible to count small mammal number by visual identification alone, as is the case with large mammals. However, different trap types have a habit of capturing different types and frequencies of small mammals, and no one type of trap will capture all species, individuals, ages or sexes with equal probability. Some species are trap shy, whilst others more readily enter traps (Williams and Braun 1983: 841).

Problems of assessing the numbers of small mammals within any given biotic community are further compounded by changes in the numbers of small mammals. Very few animal populations remain the same over any amount of time, and often these populations are subject to marked fluctuations in numbers (Elton 1966: 127). These fluctuations can occur on a number of levels: seasonally (as a result of breeding), annually (as a response to an increase in food availability, leading to increased winter survival and larger spring breeding stock), or multi-annually (the reasons for which are still not known). Seasonal changes in numbers are common in most species, as the population increases during the breeding period. Mortality of the young is common, and during the autumn, those adults that survived the previous winter to breed, die. Winter numbers are low, and then begin to increase again the next year in spring. The availability of food can affect the amount of winter survival, and lead to larger numbers of individuals living until the spring, to breed. Conversely, reduced food availability may lead to limited breeding and a population reduction in some density dependant species.

Multi-annual population fluctuations are common in both Soricidae and Arvicolinae in Britain[58], occurring on a three to four year basis (Taylor 1994: 64). These cycles are sometimes widespread over large geographical regions, where peaks, or declines, of these species are recorded (Chitty 1996: 15). In other cases, areas that

---

[58] In fact cyclical fluctuations affect most species of Arvicolinae and Soricidae (Taylor 1994), as well as snowshoe hares (Chitty 1996).

are relatively close to each other may not be synchronised, with one area experiencing a decline in numbers, while relative abundances in the other areas are stable - only to be affected the next year (Taylor 1994: 65). In all cases, these fluctuations have the effect of changing the composition of the small mammal community being studied. These fluctuations will also affect the potential numbers of prey available to predators (Elton 1966: 139), such as *Tyto alba*, as will be discussed in the next chapter.

4.7 Summary

There are 23 species of small mammal in Britain today, 12 of which have been considered in detail within this review. They inhabit a number of different habitats, and the analysis of the community structure of these habitats indicates that there are certain gross generalisations about species and environment that can be made for these British small mammal species, shown in the following table. The next chapter seeks to explore to what extent these generalisations are applicable to studies of *Tyto alba* pellets, and whether the results of pellet analysis can be used to infer the environment around the area inhabited by the owls.

Species	Grassland	Woodland	Hedgerow	Riverside	Fen / bog	Urban
Sorex araneus	☑☑☑☑		☑			
Sorex minutus	☑☑☑☑		☑			
Neomys fodiens				☑☑☑☑		
Clethrionomys glareolus	☑	☑☑☑☑	☑☑☑		☑☑☑	
Microtus agrestis	☑☑☑☑	☑	☑		☑☑	
Arvicola terrestris				☑☑☑☑		
Apodemus sp.	☑	☑☑☑☑	☑☑☑		☑☑	☑
Micromys minutus	☑☑☑			☑	☑☑	
Mus domesticus	☑					☑☑☑☑
Rattus sp.	☑		☑	☑☑		☑☑☑☑

Table 6. Small mammal habitats, showing common occurrence (☑☑☑☑) through to rare (☑) or absent. Data from text.

It is recognised that there are many other possible habitats other than those listed above, however, these categories represent those environments that are most often sampled in small mammal trapping studies. Furthermore, some environment types have been excluded from the table as they can include many different aspects of the environments detailed above. For example, a moorland environment can contain riverside elements, areas of long un-grazed grassland, as well as areas of bracken and heather for which few trapping analysis exist. The information provided in the table gives the general habitat preference of the small mammal species, and it must be recognised that at any point in the environment where a number of these different habitat types are present, then a certain amount of cross-over into the edges of different environments will occur.

5. Predator / Prey relations and palaeoecology

5.1 Introduction

The preceding chapters have provided detailed background information on *Tyto alba* (barn owl) and its prey, because in a taphonomic analysis of small mammals, it is important to consider the role played by both the predator and the prey. Without an understanding of the nature of both small mammal and owl ecology, it is not possible to recognise how the prey species within the pellets represent the environment from which they were accumulated. To reconstruct small mammal environments based on the small mammal prey items in the pellets of *Tyto alba*, one must understand how this owl selects its prey.

There are a number of conflicting reports regarding the extent to which small mammals are good environmental indicators. Some authors believe that the number of small mammals contained within archaeological deposits, or owl pellets, are reflective of the numbers within the environment (Glue 1974; Avery 1982; Mikkola 1983; Avery 1991). However, it is possible that prey species abundance is more reflective of the specific hunting techniques of owls, and that the prey spectrum is a result of that selectivity, and may be partially caused by the owls operating an optimal foraging strategy[59] (Taylor 1994). The implicit question is therefore whether *Tyto alba* is a specialist hunter or a more generalist feeder, and to what extent its diet reflects the composition of the prey community.

---

[59] One would expect an optimally foraging owl to select the most profitable species to the exclusion of almost all others, and alter this strategy only when the optimal prey source becomes scarce, and therefore ceases to be profitable (Krebs 1978).

5.2 Diet

The diet of *Tyto alba* in Britain consists mainly of Arvicolinae, Murinae and Soricidae. These species constitute over 90% of the owl's diets in most European countries sampled (Mikkola 1983: 351). Other vertebrate and invertebrate prey makes up only a limited amount of total diet. In Britain[60], the most frequently captured small mammal is often *Microtus agrestis*, comprising approximately 40% of most prey assemblages. This can be seen in Table 7 below (species 8 = *Microtus agrestis*), derived from pellet analysis of 188 locations within Britain by Glue (1974)[61].

	1	2	3	5	6	7	8	16	17	18	Other	Total
Southwest England	10.9	0.4	0.8	0.2	0.2	4.8	49.6	24.0	6.0	2.1	0.8	**9539**
Southeast England	11.0	1.1	1.0	2.0	0.5	3.3	51.2	21.4	4.5	0.9	3.2	**7141**
Eastern England	9.6	1.1	3.0	6.3	0.2	3.8	45.5	21.9	3.3	1.0	4.2	**8182**
Midlands	9.6	0.8	0.6	1.2	< 0.1	5.8	44.0	28.9	3.9	1.2	3.9	**4793**
Northern England	6.9	0	0.4	0.4	0.1	3.4	48.8	31.8	5.7	1.1	1.4	**4350**
Wales	8.3	< 0.1	0.6	1.0	< 0.1	4.2	47.8	29.4	5.4	0.9	1.2	**4575**
Scotland	9.6	0	0.5	0.3	< 0.1	3.4	44.7	33.2	6.5	1.1	0.5	**7496**
Ireland and Isle of Man	64.3	-	8.5	7.8	-	-	-	-	15.2	-	3.2	**1735**
Combined regional results.	**11.8**	**0.5**	**1.4**	**2.0**	**0.2**	**3.9**	**45.8**	**25.6**	**5.4**	**1.2**	**2.2**	**47865**

Table 7. Regional analysis of 188 *Tyto alba* (barn owl) pellet samples expressed as percentages of the regional total (Glue 1974: 204). 1=*Apodemus sylvaticus*, 2= *Micromys minutus*, 3= *Mus domesticus*, 5= *Rattus norvegicus*, 6= *Arvicola terrestris*, 7= *Clethrionomys glareolus*, 8= *Microtus agrestis*, 16= *Sorex araneus*, 17= *Sorex minutus*, 18= *Neomys fodiens*.

[60] Voles are not found in Ireland, the Isle of Man or a number of the Scottish islands (Yalden 1982).

[61] Recently published data on *Tyto alba* diets from Britain (Love *et al.* 2000) indicates that there have been significant changes in the small mammal frequencies in owl diets compared to those published by Glue (1974). However, similar patterns exist and this latest survey has corroborated the predominance of *Microtus agrestis* within most diets, and whilst numbers of *Sorex araneus* have decreased, *Apodemus sylvaticus* numbers have increased (Love *et al.* 2000). Although this data is more up to date, the use of this data in this study is problematic, as in many cases the changes in frequencies of small mammals are likely to be the result of changes in agricultural practices, and reduction of small mammal habitats, rather then representing dietary changes reflecting *Tyto alba* behaviour. As the data on *Tyto alba* diets is included in this study to provide an analogous summary of owl and small mammal ecology for past environments, and these recent changes have almost certainly produced a landscape that is very different from any that may have existed in the past 10,000 years, only the results of the earlier survey by Glue are used here.

From the data in the table above (Table 7), there is clearly evidence that *Microtus agrestis* is a very frequent prey item in many *Tyto alba* diets. This is not unexpected given the fact that *Microtus agrestis* is one of, if not the most common rodent in the UK (Rogers Brambell 1958: 5; Glue 1974: 203). In addition, there is a strong correlation between the type of habitat hunted over by *Tyto alba*[62], and the habitats frequented by the *Microtus agrestis*[63], so such results are not surprising.

However, it is also important to highlight the variation that occurs in the numbers of prey species captured from specific environments within the general habitat favoured by *Tyto alba.* This is clearly demonstrated in Table 8 overleaf, where numbers of *Microtus agrestis* (commonly the dominant prey species) range between 10% to 78% of all prey items. This analysis also indicates that two other species of small mammal are caught with some regularity. These are *Sorex araneus* and *Apodemus sylvaticus*. *Sorex araneus* occupies nearly all habitats, especially those with dense low herbage, such as rank grassland, scrub, banks and hedges (Glue 1974: 203). It is usually the second most important species in the diet of *Tyto alba*. *Apodemus sylvaticus* is more commonly associated with woodland, but is also found at the edges of woodland, hedgerows, and sometimes grassland (Glue 1974: 205).

---

[62] Glue (Glue 1970) lists the variety of habitats in which *Tyto alba* are found as – 'pastoral, arable, and mixed farmland, upland pasture bordering on moorland, water-meadows, saltmarsh, heathland, open parkland and deciduous woodland, waste ground, young forestry plantations, open downland, disused sand and gravel quarries, commonland with bush scrub and rough grassland' (Glue 1970: 55).

[63] *Microtus agrestis* 'is the most abundant rodent of open country in mainland Britain' (Glue 1974: 203).

Environment	Site	1	2	3	5	6	7	8	16	17	Total
Rough grassland, scrubland	A	4.1	0.0	0.7	0.5	0.5	0.5	78.6	12.7	2.4	**416**
Rough grassland, scrubland	B	6.5	0.0	0.0	0.0	0.0	9.7	74.2	6.5	3.2	**62**
Small grazing fields nr. woodland	C	4.4	0.0	0.0	0.0	0.0	0.5	15.9	44.5	34.6	**182**
Small grazing fields nr. woodland	D	14.9	0.6	1.4	4.6	0.0	11.5	27.4	32.1	7.5	**504**
Mixed farming	E	16.4	0.3	0.1	9.6	0.6	0.6	56.5	14.7	1.3	**689**
Mixed farming	F	3.4	4.0	0.6	1.7	0.6	3.4	33.9	41.8	10.7	**177**
Mixed farming	G	5.3	1.7	2.3	1.7	0.7	2.7	36.9	36.5	12.3	**301**
Mixed farming	H	6.5	1.1	0.0	0.5	0.0	9.2	36.4	27.2	19.0	**184**
Mixed farming	I	5.3	0.0	31.6	31.6	0.0	21.1	10.5	0.0	0.0	**19**
Wet pastureland & water meadows	J	6.5	2.9	1.4	0.0	0.0	10.1	63.8	11.6	3.6	**138**
Wet pastureland & water meadows	K	19.6	3.2	4.6	1.3	0.0	13.4	41.0	10.2	6.7	**373**
Wet pastureland & water meadows	L	6.0	0.0	0.0	0.0	0.0	10.3	58.6	19.0	6.0	**116**
Wet pastureland & water meadows	M	12.5	1.9	0.0	3.4	0.4	2.3	57.2	17.4	4.9	**264**
Parkland	N	24.7	2.6	0.0	6.5	0.0	5.2	33.8	22.1	5.2	**77**
Total No. prey items		**393**	**42**	**44**	**125**	**10**	**192**	**1655**	**774**	**267**	**3502**
% of total prey		**11.2**	**1.2**	**1.3**	**3.6**	**0.3**	**5.5**	**47.3**	**22.1**	**7.6**	

Table 8. Prey of *Tyto alba* in different environments, numbers represent percentage relative abundance of species (Glue 1967). Sites - A = Nursling, B = Bayfield, C = Dennywood, D = Vagoul Park, E = Eling Hill, F = Ravenscroft Farm, G = Bagshot, H = Slapton, I = Church Melton, J = Cobham, K = Claremont, L = Longley, M = Flatford, N = Orwell Park]. 1=*Apodemus sylvaticus*, 2= *Micromys minutus*, 3= *Mus domesticus*, 5= *Rattus norvegicus*, 6= *Arvicola terrestris*, 7= *Clethrionomys glareolus*, 8= *Microtus agrestis*, 16= *Sorex araneus*, 17= *Sorex minutus*.

The numbers of the three main prey species caught (*Microtus agrestis, Sorex araneus* and *Apodemus sylvaticus*) can be seen to fluctuate within the samples above, but to what extent do the differences in species numbers represent differences in habitat? In terms of reconstructing the environment from the action of a hunting owl, some questions must first be considered. How effectively does *Tyto alba* sample all aspects of the available small mammal fauna, and how much of that fauna is representative of specific environments? If *Sorex araneus* and *Microtus agrestis* are indicative of the presence of grassland, to what extent do the proportions of the other species caught (*Clethrionomys glareolus*, *Apodemus sylvaticus*, *Neomys fodiens*, *Arvicola terrestris*, etc), represent the particular habitats that these species are more likely to frequent?

As *Tyto alba* hunts over grassland, the main prey types captured should be grassland species. There are a number of possibilities to explain the presence of other species of prey within the diet of *Tyto alba*. Firstly, the capture of non-grassland species may occur during incursions by these prey species into grassland environments, due to dispersal, or for the exploitation of seasonally abundant foods. This would

account for the relatively low numbers of *Clethrionomys glareolus* within many *Tyto alba* diets (see for example Table 7), as these voles do not usually leave the confines of woodland or hedgerows to enter grasslands. Alternatively, the owl may be hunting over different parts of its range, including areas adjacent to those containing non-grassland species, and at these boundaries some cross-over of small mammal species is likely to occur. Finally, during periods of prey population crashes, habitat change (either environmental or anthropogenic), or adverse weather conditions, prey switching to other species and environments not normally exploited, maybe essential for an owl to survive.

5.3 Assessing proportions of species

There are a number of important factors to take into account when analysing pellet data, including the data reviewed in this chapter. Firstly, in any particular year or number of years, fluctuations in prey populations may lead to an increased (or reduced) number of specific species being recorded, and a number of studies have shown that both seasonal and multi-annual populations fluctuations can be identified from the analysis of *Tyto alba* pellets (Webster 1973; Taylor 1994: 43, see below). These population fluctuations have a knock-on effect as the number of other species taken by *Tyto alba* rises, a result of prey switching which frequently occurs during these periods (for example see differences in numbers of *Apodemus sylvaticus* and *Sorex araneus* in Table 7, and also Figure 9 below, (Taylor 1994: 43)).

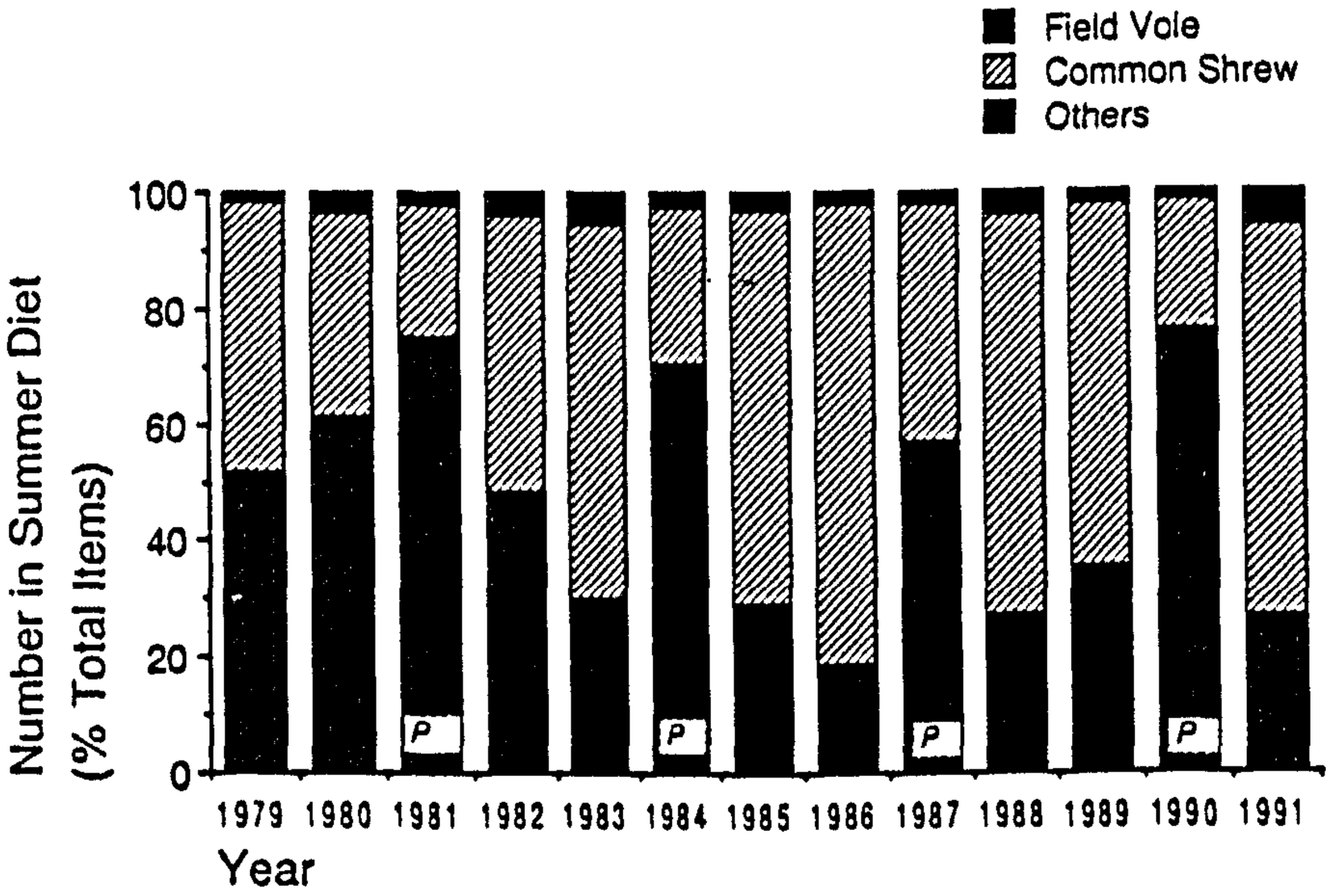


Figure 9. Prey fluctuations on Esk study area, Scotland, from Taylor (1994: 43). The "p" refers to years of peak vole population numbers based on trapping studies, see for example Figure 8, page 59.

Secondly, there is an underlying assumption that *Tyto alba* is a generalist feeder (Mikkola 1983), taking all of the prey in its range, in proportions equivalent to the numbers of those species. As has already been emphasised, the hunting habits of *Tyto alba* mean that its main prey primarily represents the type of habitat that it hunts over. The variability with which other (non-grassland) prey species are caught is therefore more likely to represent external factors affecting the hunting regimes of the owl, such as patterns of land management, weather, climate, prey density and availability, rather than being fully representative of dietary preference, or environmental diversity.

When considering the regularity with which *Microtus agrestis* is captured, it is also possible that an element of prey choice is motivated by prey size (Yom-Tov and Wool 1997) and ease of capture, rather than a random sampling of the prey within the environment. In terms of the ease with which certain species can be captured, spring and summer territorial fighting of Soricidae, and Arvicolinae, during the mating season (which often includes vocalisation), leads to increased capture, and an over-representation of males within the prey assemblage (Taylor 1994). However it is not nutritionally efficient for *Tyto alba* to hunt Soricidae, when Arvicolinae are available (Glue 1967: 178) and in areas where *Rattus* predominates, the obvious choice in terms of dietary efficiency, would be to hunt these species instead of the Arvicolinae.

5.4 Ecological and palaeoecological reconstruction

As was discussed in Chapter 2, an assemblage of small mammal bones can be affected by many different taphonomic occurrences. If, however, these are recognised, and the possible biases addressed, then it is possible to use microfaunal assemblages to produce a reconstruction of the palaeoecology. There are a variety of methods that can be used (Andrews 1995b), the most relevant of which will be covered here.

On the broadest levels, there are certain ecological rules about species diversity and environment type. Generally, there are a greater number of species and fewer individuals in more complex habitats, and more simple environments tend to have fewer species but more individuals (Krebs 1978; Andrews 1990; Avery 1992). Woodlands have greater species richness than grasslands, whereas grasslands have more individuals per species (Andrews and Evans 1979). Another indication of the general environment is the proportion of Murinae to Gerbillinae (Dauphin *et al.* 1994: 343; Fernandez-Jalvo *et al.* 1998). The ratio of abundance of these species can be used to indicate environmental types, as Murinae are predominantly woodland species, and Gerbillinae are usually found in grasslands.

Small mammals can also be very specific in their habitat preferences, and therefore are of great value in palaeoecological reconstruction. The method of 'taxonomic comparisons' uses simple comparison of fossil faunas with modern faunas

of the same species or taxa. The type of environment utilised by modern species is used as an analogy to suggest the most likely habitat occupied by the fossil species. It is a method used throughout most palaeoecological analysis (Andrews 1995b: 61) and is applied to many small mammal studies (Avery 1982; Avery 1990; Avery 1992; Alexeeva 1996; Khenzykhenova 1996; Vigne and Valladas 1996; Fernandez-Jalvo *et al.* 1998; Hadly 1999, to name but a few). Changes in proportions of species are often used to infer 'fluctuations in proportions of various types of vegetation' (Avery 1990: 407), and suggest periods of climatic change. However, the above methods rely upon the relative abundance of numbers of individuals per species, which may often occur as a result of taphonomic bias, and not necessarily reflect environmental or climatic variation (Van Kolfschoten 1995). Where these taphonomic biases affecting the species composition of a fauna are not taken into account, the validity of any palaeoecological and environmental reconstructions must be questioned (Andrews 1995b: 61).

The following two methods do not rely upon relative abundances, and as such give a more reliable indication of palaeoecology. The Taxonomic Habitat Index (THI) is a tally of the number of different species present, and not of the number of individuals within that species. It accounts for the fact that individual species of small mammals are not always so specific in their habitat preferences, and can often be found in a number of different environments and habitats. It comprises an index of species and that takes into account the diversity of habitat preferences. Each species is scored on habitat preferences, with a greater score given for the most prevalent habitat. An example of the taxonomic habitat index (THI) for *Microtus agrestis* and wood mouse is given below, from Andrews (1990: 167).

Species	Tundra Habitats	Boreal Forest	Deciduous Forest	Mediterranean Habitats	Steppe Habitats	Forest steppe	Arid habitats	Tropical habitats	Montane habitats
Microtus agrestis	.05	.4	.4	.05	-	-	-	-	.1
Apodemus sylvaticus	-	-	.2	.2	.2	.2	.2	-	-

Table 9. An example of THI scores for two British small mammals, from Andrews (1990: 167).

In cases where there are still living members of the same species as the fossil faunas under investigation, the THI score is produced on the basis of the modern species

habitat preferences. In the cases of extinct fossil faunas, the THI is calculated for the genus of that species, based on the average THI of the modern members of that genus. Individual THI scores for each species are then summed to give the total THI for the entire fauna (Andrews 1990; Fernandez-Jalvo *et al.* 1998).

However, all of the above studies of palaeoecology are bedevilled by the same problem, namely, that it is impossible to know the exact habitats of mammals in the past. Such habitats are merely recognised through uniformitarian analogy with present habitats. This problem affects the reconstruction of both habitats of extinct and extant mammals in the past (Andrews 1990; Andrews 1995b; Van Kolfschoten 1995: 81).

Very often there are no modern analogues of past environments (Semken 1988: 185), and evidence indicates that certain ancient environments may have been more ecologically diverse than present day analogues (Fernandez-Jalvo *et al.* 1998). Even extant mammals may have operated in different environments in the past. This is aptly demonstrated by the case of *Arvicola terrestris* in Britain, which inhabits predominantly waterside habitats at present (Woodroffe 1996), but appears to have been far more catholic in the past[64] (Jewell 1959; Bramwell *et al.* 1990; Yalden 1999).

The analysis of morphological characteristics is at least one method which does not suffer these problems of taxonomic and habitat change. Variations in skeletal traits are recognisable in small mammals, which relate to both feeding and movement within specific environments. Analysis of tooth shape (and wear) can often indicate type of diet (insectivorous, frugivorous, herbivorous), and therefore associated environment. Analysis of limb morphology can also differentiate between arboreal and terrestrial species (Andrews 1995b; Fernandez-Jalvo *et al.* 1998). It is also suggested that chemical analysis of diet, using isotope analysis may also shed light on small mammal environments (Wing *et al.* 1992; Gifford-Gonzalez pers. comm.). As in the case of small mammal taphonomy, the more methods that are used, the more accurate the conclusions will be, and in cases where there are other faunas available for study, the palaeoecological analysis of the entire community structure, and not just the small mammals will lead to greater accuracy. However, it must be remembered that the

---

[64] Evidence from Neolithic and Bronze Age archaeological sites indicates that *Arvicola terrestris* sometimes made up 50% of the small mammal fauna (Personal observation.; Jewell 1959; Bramwell *et al.* 1990; Yalden 1999), although today, it is rarely found in the pellets of owls, making up only 0.2% of the prey of *Tyto alba* in Britain (Glue 1974). For further discussion of this phenomenon see chapter 4.

taphonomic criteria applied here to small mammals also apply to the whole fauna, and there are certain members of the palaeocommunity that are more likely to be preserved than others (Shotwell 1955; Andrews and Evans 1979).

5.5 Conclusions

The propose of this review chapter was to summarise the data collected on owls and their small mammal prey to highlight the variability inherent in the study of the environment and palaeoecology, using microfaunal assemblages derived from owl pellets. Analysis of modern day owl pellet material from *Tyto alba* has shown that there are a number of specific points that are common to many of these assemblages. In most cases the assemblage is dominated by the most common species within the environment over which the owl hunts. For *Tyto alba* this environment is mainly grassland, and as a result the most common prey usually found in pellet assemblages is *Microtus agrestis*. When considering whether this owl operates an optimal foraging strategy, the evidence appears to suggest that *Tyto alba alba* is both a selective and generalist feeder, taking the most abundant and easy to catch species (*Microtus agrestis*) when this is available, and switching to other, less profitable species during periods of population decline. However, it must be recognised that there are many factors that control the numbers of each small mammal species in the environment, and the effect of these in any given time or place can considerably alter the prey assemblage.

Furthermore, the degree to which pellet derived deposits can be useful in the analysis of past environments, must to some degree be associated with the number of pellets which comprised that original deposit. The analysis of one pellet would not produce an effective summary of the local environment, as species richness would be low. An analysis of pellets from a depositional event lasting one year, would give a better indication of the variety of species contained within the region hunted over by the owl[65]. However, cyclical or seasonal population fluctuations could lead to a reduced

---

[65] It must also be recognised that only about half of the pellets produced by an owl are deposited at the roost site (Glue 1970). The rest are usually deposited at sometime during the evenings hunting, at a resting perch (Bunn *et al.* 1982). The picture is further complicated at nest sites, where many more pellets will be accumulated, representing many different owls, often adults and chicks.

number of certain species being recorded. A more profitable analysis would be one derived from an accumulation of pellets that represents a number of years of deposition, where the effect of any population fluctuations will be reduced by the sheer number of pellets represented within the sample.

However, there are few ways of accurately assessing the time taken to accumulate an archaeological deposit of small mammal bones, and whether, for example, a large accumulation of bones represents a number of concurrent years, or separate ones over a longer time period. One possible method would be to count the number of individuals, and assess whether it would be possible for that number to accumulate within a year. If more than one year's worth of pellets are represented, then it is possible to assume that some of the short term variations that could occur, will be reduced. Unfortunately, such a method relies upon the collection of all of the bones within the deposit, which is not always possible.

Despite these problems, a number of ecological parameters, based on the number of species, and their relative abundances, can provide vital information about the nature of specific habitats. Large numbers of *Sorex araneus* and *Microtus agrestis* within an assemblage, would be a good indicator of a grassland environment, and similarly, a high percentage of *Apodemus sylvaticus* and *Clethrionomys glareolus* would indicate the presence of areas of woodland. An assemblage of small mammal bones containing a number of *Neomys fodiens*, could be presumed to represent an environment through which water runs. These simple 'rules of thumb' could therefore be used to provide the basis of a limited environmental reconstruction from an assemblage of small mammal bones.

6. The sites and sampling methods

6.1 Introduction

The main aim of this study was to try to discover whether different taphonomic signatures are produced by *Tyto alba* chicks, compared with their adult counterparts. To carry out this research, material from two modern *Tyto alba* roost sites originally sampled by Andrews, were re-analysed for this study, for evidence of molar and incisor digestion. Data about prey species presence in *Tyto alba* pellets were provided from Glue (1967) and data on bone breakage for the adult owls came from Andrews (1990). This material was then analysed for patterns of bone modification, and these data used to compare patterns of bone breakage and digestion, with those from three modern *Tyto alba* nests. Finally, the modern nest data were used to investigate whether it was possible to recognise taphonomic signatures associated with *Tyto alba* nests within the archaeological record, using material from four archaeological sites from Holocene Britain. Within the results section, details of this analysis will first be given for the modern *Tyto alba* roost material, then the modern *Tyto alba* nest material, and finally the small mammal bones from the archaeological sites.

The modern comparative *Tyto alba* roost material was provided by Peter Andrews, from pellets, from Stratton in Norfolk and Rhulen in Wales, collected during his analysis for the book *Owls, Caves and Fossils* (1990). The *Tyto alba* nest material was collected from two sites in Lincolnshire, by Colin Shawyer, of the Hawk and Owl trust. In order to keep the location of the nests hidden, very little information about these sites has been made available for this study. The archaeological material in this study comes from four English sites, from various ages throughout the Holocene. In all cases there appeared to be some evidence that the small mammal assemblages could have been deposited by an owl, and might possibly have accumulated by *Tyto alba* as part of a nest. The sites are Fox Hole Cave, High Wheeldon, Derbyshire; Carsington Pasture Cave, Brassington, Derbyshire; Filey Roman Signal Station, Filey, North Yorkshire; and the Old Vicarage, Tadcaster, North Yorkshire. The locations of both the archaeological sites and owl pellet collection locations within Britain are shown on the map overleaf.

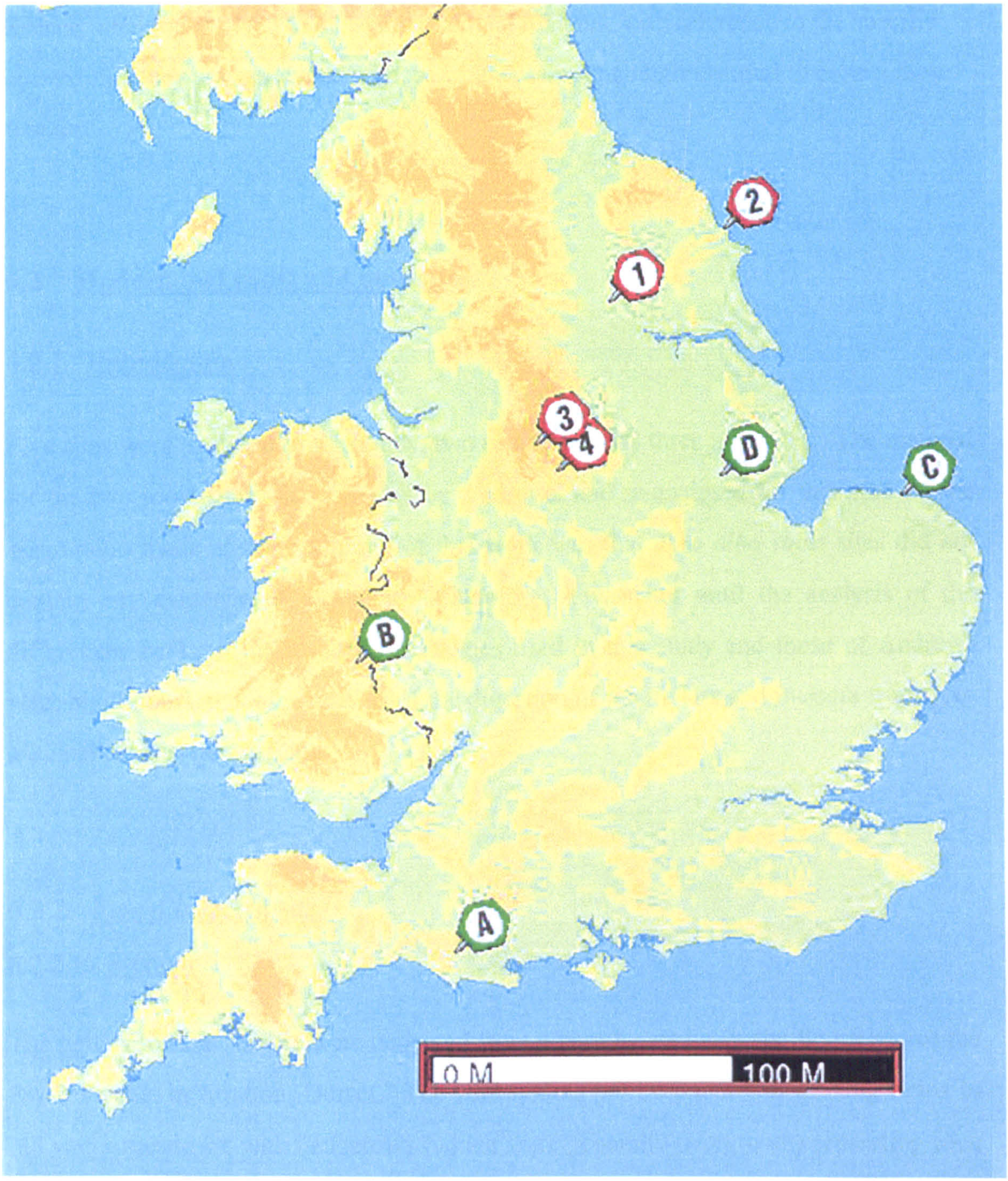


Figure 10. Map of United Kingdom, showing location of archaeological sites and owl roost and nest sites sampled in this study. A = Stratton, B = Rhulen, C = Salthouse, D = the approximate location of the two *Tyto alba* nests. 1 = Tadcaster, 2 = Filey, 3 = Fox Hole Cave, 4 = Carsington Pasture Cave.

Each site is discussed briefly below, with information given on location, excavation, date and a limited description of the archaeological and zoological material recovered. Special attention is given to the small mammal remains, with reference to the specific context that they are associated with, as well as sampling methods used to collect these remains.

6.2 Modern owl roost and nest sites

6.2.1 Introduction

Five sites were analysed in this study, two roost sites and three nest sites. The material for the two roost sites was collected by Andrews, and re-analysed for this study. The assumption made at the beginning of this work was that *Tyto alba* roost sites did not contain any evidence of digestion. Therefore, it was not until the analysis of the differences between the recording strategies used in this study and those of Andrews were highlighted, that any analysis of the digestion of the molars and incisors from *Tyto alba* pellets was investigated.

6.2.2 *Tyto alba* roost sites

6.2.2.1 Stratton

The pellets for this sample were collected from a barn located near the floodplain of the River Frome, in Stratton, Dorset. The surrounding environment was grazing fields in old water meadows, with hedgerows (which were generally overgrown) separating each of the fields. Areas of scrub were present along the river beds, and some woodland was present on the slopes away from the water meadows; there was also some new tree planting in the corners of fields and along the roads (Andrews pers.comm.).

6.2.2.2 Rhulen

The pellets for this sample were collected from near the village of Rhulen, Powys, Wales, 'ordinance survey sheet 148, map reference 141504' (Andrews and Armour-Chelu 1998). The environment of the area is mixed with 'areas of open moorland along the top of the hills, with heather, bilberry and bracken .... areas of rock scree and low cliffs in the south .... Several moorland pools. The lower slopes of the hills are fenced for rough grazing ' (Andrews and Armour-Chelu 1998). There are some trees scattered along generally overgrown hedge lines and some areas of scrub woodland in the valley bottoms. There are some areas of wet land, with impeded drainage, although there no real bogs or swamps (Andrews pers. comm.).

6.2.3 *Tyto alba* nest sites

The information, as well as the material, for the first two of these sites was provided by Colin Shawyer of The Hawk and Owl Trust. They are included verbatim below.

6.2.3.1 TF11 – 1999 breeding season

The material from this site comes from a location in Lincolnshire, within the 10km radius of the map reference TF11.

> 'The nest site in a triangular wooden nest box installed on a tree was occupied at the time the sample was taken and it represented a time-averaged sample from five years of continuous occupancy by barn owls. The surrounding habitat is largely arable but during the period represented by the sample, aggregate quarrying has advanced within 100 m of the site such that the arable / disturbed land is currently 50/50. Critically it is normally the micro-features of these habitats that contribute the majority of prey, notably grassland edge. The micro-features here are open ditches and drains, which I would estimate, are 5 km length within a 1 km radius of the nest. Average bank widths are 4 m.' (Shawyer pers.comm.)

6.2.3.2 ON2 – 1999 breeding season

The material from this site also comes from a location in Lincolnshire, in this case within a 10 km radius of map reference TF34.

> 'The nest site is a pole box and was not occupied at the time the sample was taken. However barn owls had bred in the box and would have left just before the box was visited. The sample represented a time-averaged sample from five years of continuous occupancy. The box is sited within a 1 acre conservation meadow created from grass seeding some seven years ago. The meadow forms part of a large sewage treatment works comprising "amenity grassland". The main navigable river adjoins the site and most of the hunting is believed to be conducted along the wide grassy flood banks which have a mixed grassland structure of rank tussocky grass and shorter mown grass to enable access along the tops of the banks. I would estimate 3-4 km of grassland of this type within a kilometre of the nest. The surrounding land is largely arable' (Shawyer pers.comm..)

6.2.3.3 Salthouse

This material comes from Peter Andrews, collected during the research for the book *Owls, Caves and Fossils* (1990). It represents a sample of a nest taken from a barn near Salthouse, located in the salt-flats of Norfolk (Andrews, pers.comm.).

6.3 The archaeological sites

6.3.1 The Old Vicarage, Tadcaster

6.3.1.1 The site

Restoration of the vicarage at Tadcaster, currently under the ownership of a local brewery, began in 1997 (and is still underway). At this time a number of archaeological analyses were undertaken, including the excavation of the deposits from the garderobe, located at the north end of the building. A garderobe is a pit (or long drop) toilet, which either opens out onto the exterior of the building, such as can be seen in the figure below from Peveril Castle, in Castleton, or confined within the building, as in the example from Tadcaster see Figure 16.

Figure 11. Garderobe from Peveril Castle, Castleton, Derbyshire.

Figure 12. The room containing the garderobe at the Old Vicarage, Tadcaster. The bucket marks the position of the rough location of the toilet.

The toilet was located on the first floor (Figure 12 above), with a drop below it to a hole, approximately one metre wide, set 2.5 metres below the ground floor surface (Figure 13 overleaf). Eight contexts were identified during the excavation of the garderobe, context 10 (the garderobe pit), and the remaining seven contexts representing the fill of this pit (contexts 11, 13, 14, 16, 17, 18, 19). The top three contexts were distinguishable on the basis of soil colour and compaction, as can be seen in Table 10, below. The lower contexts were arbitrarily designated and excavated 30-50cm spits, through a homogenous deposit as described for context 14, with the exception of the lowest deposit, context 19. The garderobe itself consisted of a stone lined square pit, one metre in width and approximately 2.5 metres deep (Dobney 1998). This pit

represents only the bottom of the deposit, which could have filled up to reach near the bottom of the first floor.

Figure 13. The pit, after excavation, into which waste from the toilet on the floor above would have fallen.

Context	Depth (cm)	Description
11	0-30	Extremely loose mid to light grey silt with abundant ash, charcoal and limestone fragments
13	30-70	Moderately loose mid to dark grey silt with abundant ash, charcoal and medium sized limestone fragments.
14	70-100	Moderately compacted mid grey clay-silt with abundant limestone and charcoal flecks and angular limestone fragments
16	100-150	Same as 014
17	150-200	Same as 014
18	200-230	Same as 014
19	230-245	Clean mid to light brown sand

Table 10. Description and depths of depositional contexts at Old Vicarage, Tadcaster, data from (Dobney 1998).

The lower levels of the garderobe deposit contained direct remains of dietary waste, as well as domestic and table refuse, suggesting a secondary use, as a convenient dump for waste material. Alongside the usual domestic animal remains (i.e. cattle, sheep, pig, chicken and goose) in these contexts, were the remains of a common porpoise. Whale, dolphin and porpoise meat is considered to be an indicator of high status during the high and late medieval periods, and its incorporation within this early post-medieval context suggests that the inhabitants of the Vicarage were fairly well off, with considerable social standing (Dobney 1998).

Alongside these indicators of diet and occupation, were also found numerous remains of small mammals and birds. It is suggested that these small mammal bones were incorporated within the deposits as a result of the nesting or roosting activity of owls. These owls were probably roosting or nesting directly above the garderobe within the rafters of the building, with material falling into the pit.

Figure 14. Rafters above the garderobe at Tadcaster, in approximately the same position of those which a roosting owl may have perched.

At this time it is likely that the site was only used periodically for human occupation, or completely abandoned. At some point in the mid 17th century the garderobe was

filled in with material brought in from elsewhere. These deposits contained the remains of vertebrates, plants, insects and numerous non-biological finds, such as iron work, window glass etc. Small mammals were also present in this context, suggesting that the infilling of the garderobe may have been associated with a period of abandonment (Dobney 1998). It is possible that around this time owls had roosting in the adjacent room (see figure below), and when the building was cleaned, this material was thrown directly into the garderobe, which as can be seen from the evidence of other domestic refuse (pottery, glass etc) was an activity practiced at the time. In either case, the occurrence of owl nests (or roosts) indicates that human activity at the time of the deposition of the small mammal remains may have been sporadic.

Figure 15. Room adjacent to the garderobe, looking back into the room containing the garderobe.

It is possible to place a date on these deposits, using the pottery from the garderobe. There were a total of 34 sherds recovered from contexts 11, 13, 16, 17, and 18. Most of the pottery dates from the middle of the 17th century, although some may have been of an earlier, 13th or 14th century date. However, it is likely that much of this deposit accumulated within a relatively short space of time, as there are number of examples of joining or same vessel sherds in different contexts. Two fragments of 17th century redware, one from context 11 and the other from context 13 join, and parts of the same post-medieval vessel were recorded in contexts 13, 16 and 17. Further evidence of a 17th century date comes from the clay pipes from context 11, dated to approximately AD 1650 (Dobney 1998).

6.3.1.2 Samples

The small mammal bones came from contexts 11, 17 and 18. These small mammal bones were recovered from environmental sampling of the deposits, as well as excavation. Ten litre samples were taken, one sample for context 11, four for contexts 17 and 18, all of which were processed through a 0.5mm sieve. For this study, all small mammal bones from these three contexts were studied and recorded.

6.3.1.3 Discussion

The garderobe deposits trace the history of occupation of this ecclesiastical site throughout the early post-medieval period, indicating periods of affluence and high status. However, there is also an indication that there were periods of time when the site was not in use, or possibly abandoned. The deposits containing small mammal remains are likely to represent these periods of abandonment, when the empty building offered suitable accommodation for a roosting or nesting owl. It has been suggested earlier (page 51), that a nesting owl requires greater security and isolation than a roosting owl, and if it were possible to identify specific taphonomic patterns indicative of nesting, it would be possible to suggest that a number of periods of abandonment, or discontinuous usage are indicated within the garderobe deposits containing small mammal bones.

Further evidence to suggest the presence of nesting owls was discovered within context 17, where the bones of a complete juvenile barn owl (*Tyto alba*), and some eggshell[66] were discovered. It is an obvious *a priori* assumption that these owl bones represent the agent of accumulation of the small mammal bones, although this is not an assumption that can be applied to all predator deposits. It is also possible that the eggshell may have been associated with the birth of this young owl, although it must be recognised that the garderobe was also used as a refuse pit for the house and therefore the eggshells may have entered as kitchen or table waste (Dobney 1998).

[66] Eggshell also present in context 18.

6.3.2 Filey Roman Signal Station, Carr Naze.

6.3.2.1 The site

The Roman signal station (NGR - TA 120810), at Carr Naze, Filey, North Yorkshire, was excavated in 1993 and 1994 by Patrick Ottaway of the York Archaeological Trust, to assess how much of the site remained intact, as heavy erosion of the promontory on which it was situated had occurred. Its location (and the projected location of the eroded areas) on the Carr Naze promontory can be seen in the map below.

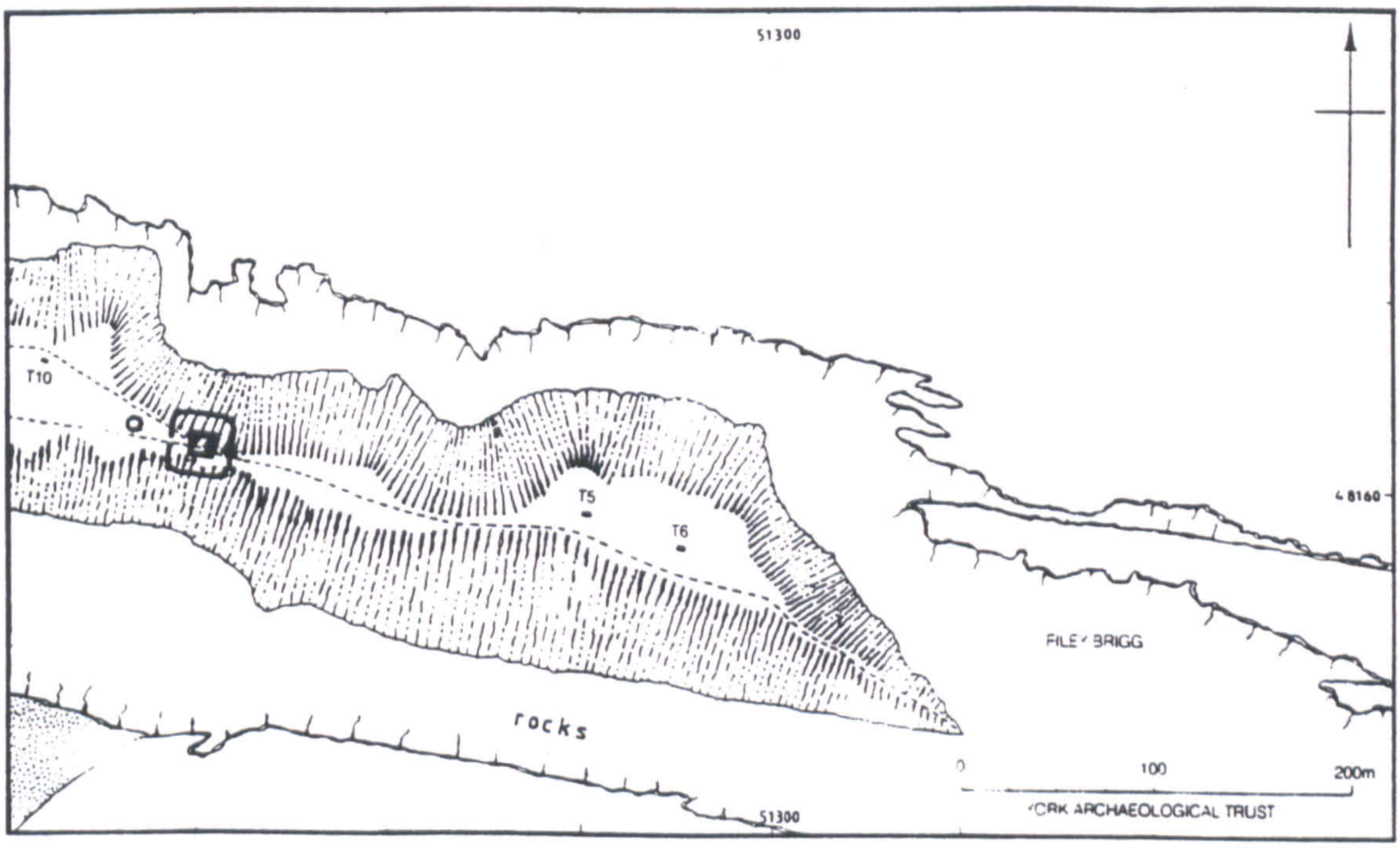


Figure 16. Location map showing the position of Filey Roman Signal Station on the Carr Naze Promontory.

The site dates to the end of the fourth century AD, and is one of a number of similar institutions along the coast of northern England (Dobney *et al.* 1996: 2). The other signal stations are located at Goldsborough (NGR – NZ 830150), Ravenscar (NGR – NZ 980010), and Scarborough (NGR – TA 050890) in North Yorkshire, and Huntcliffe (NGR – NZ 680210) in Cleveland (Green 2000). These coastal watch towers were up to 15 metres square, surrounded by a walled enclosure, and in most cases a ditch and rampart (Ottaway n.d.) (see Figure 17, page 99). It is likely that their purpose was to warn of any invasion from the sea (Dobney *et al.* 1996: 2).

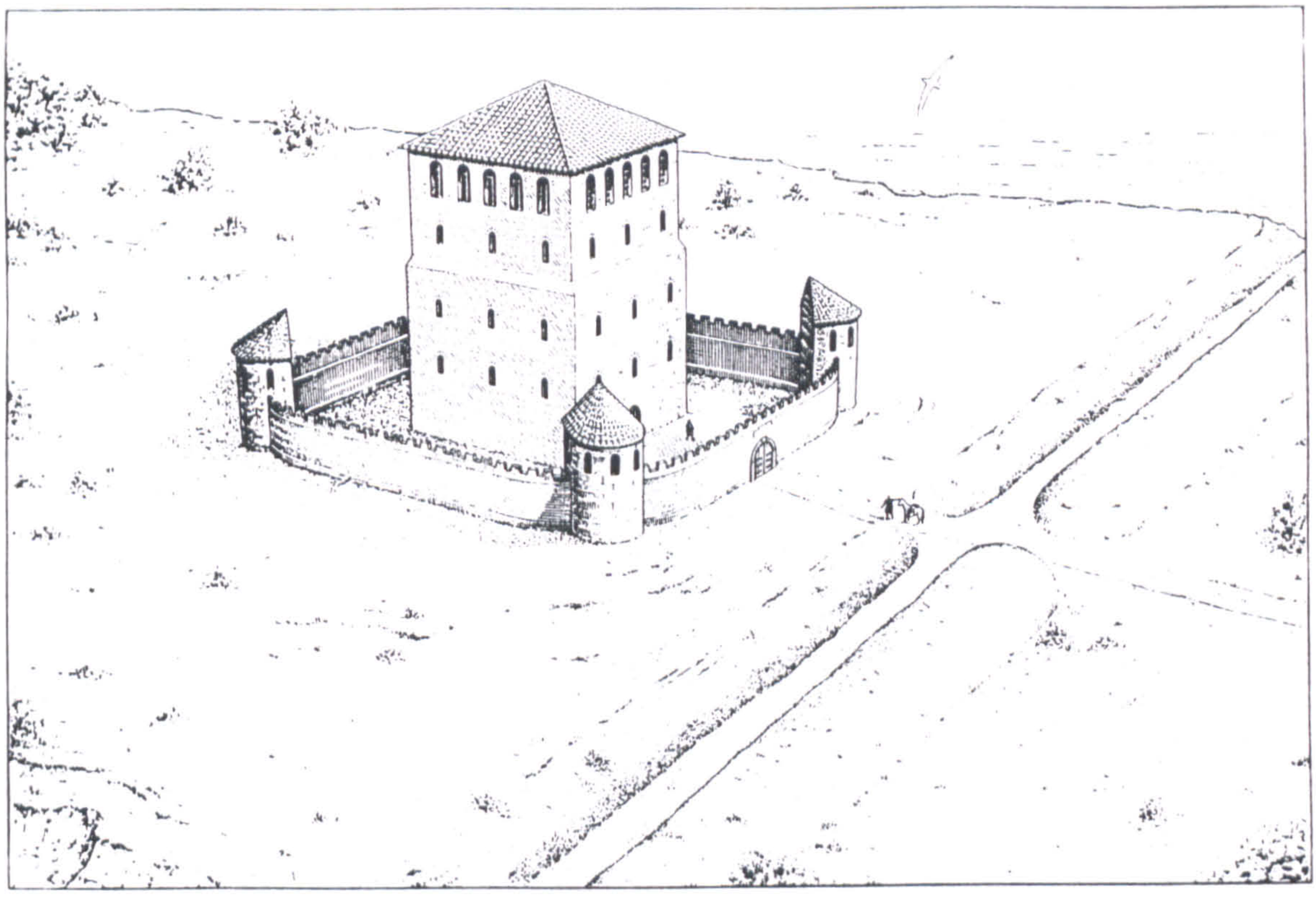


Figure 17. Possible reconstruction of a Roman Signal Station, provided by P. Ottaway.

6.3.2.2 Sampling

Forty-three samples were analysed from this site, representing six different contexts. In most cases, samples were taken from bulk samples recovered from 3-5 cm thick spits within the signal station courtyard, from contexts (spit numbers) 12024, 12025,12027 and 12028. Samples were also taken from well-defined contexts – 11038, 12022 (Dobney *et al.* 1996: 3). With the exception of 11038, all of these contexts came from trench 12 (Dobney *et al.* 1996: 19). Each bulk sample came from a minimum of 30 kg of sediment. This sediment was washed through 1mm and 0.5mm sieve mesh, dried and sorted (Dobney *et al.* 1996: 3). The location of trench 12 within the excavated signal station can be seen in the figure overleaf.

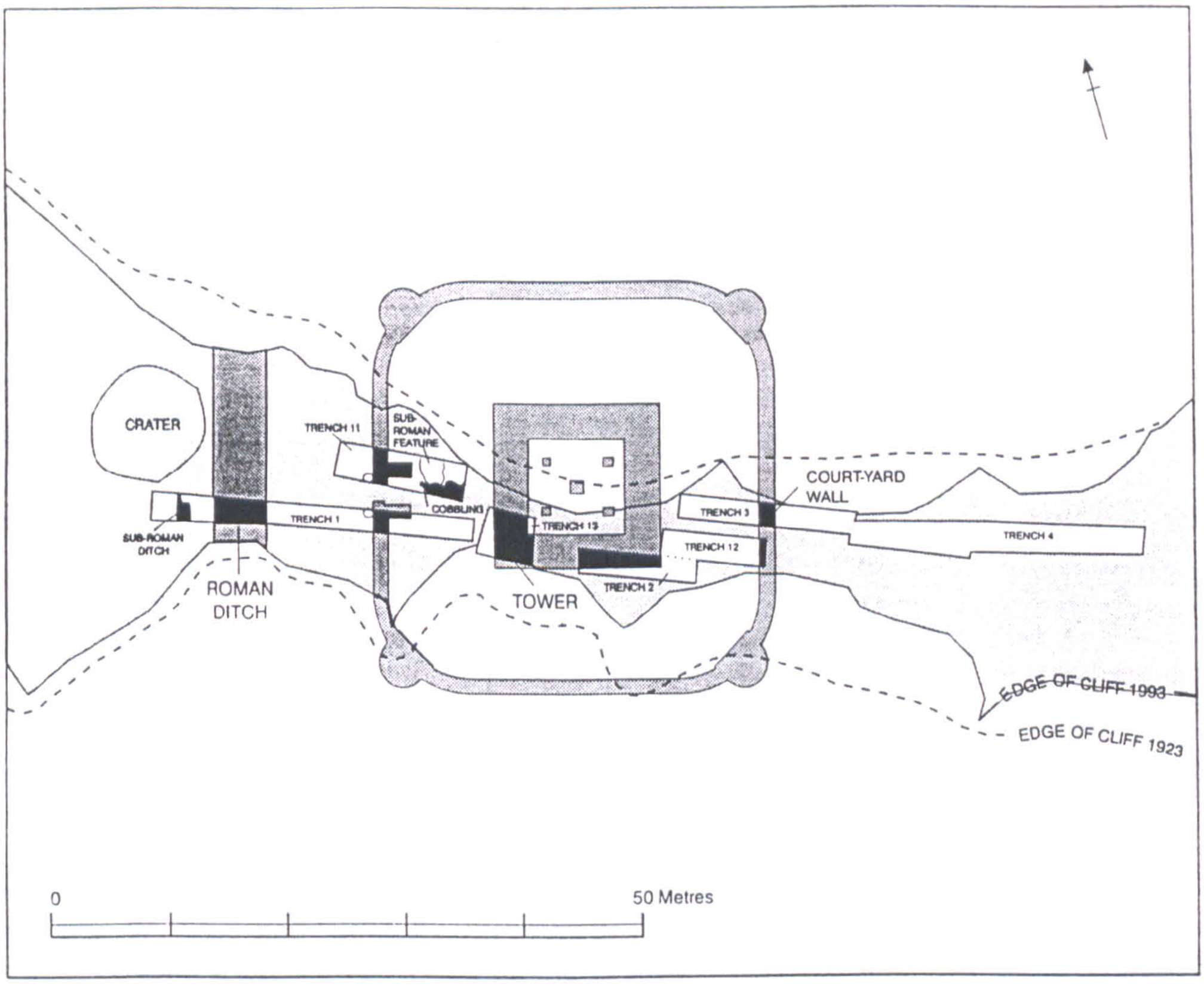


Figure 18. Plan of the excavation of Filey Roman Signal Station, drawing supplied by P. Ottaway.

6.3.2.3 Discussion

As can be seen in the section and photograph below, the sampled layers (highlighted in the section, dark brown layers in the photograph) represent some of the earliest activity at the site, although most of the material above these contexts built up after the abandonment of the signal station. The deposits containing small mammal bones were concentrated in the top layers of this occupation deposit, and are likely to represent the final stages of occupation and then abandonment of the complex (Dobney *et al.* 1996: 19-21).

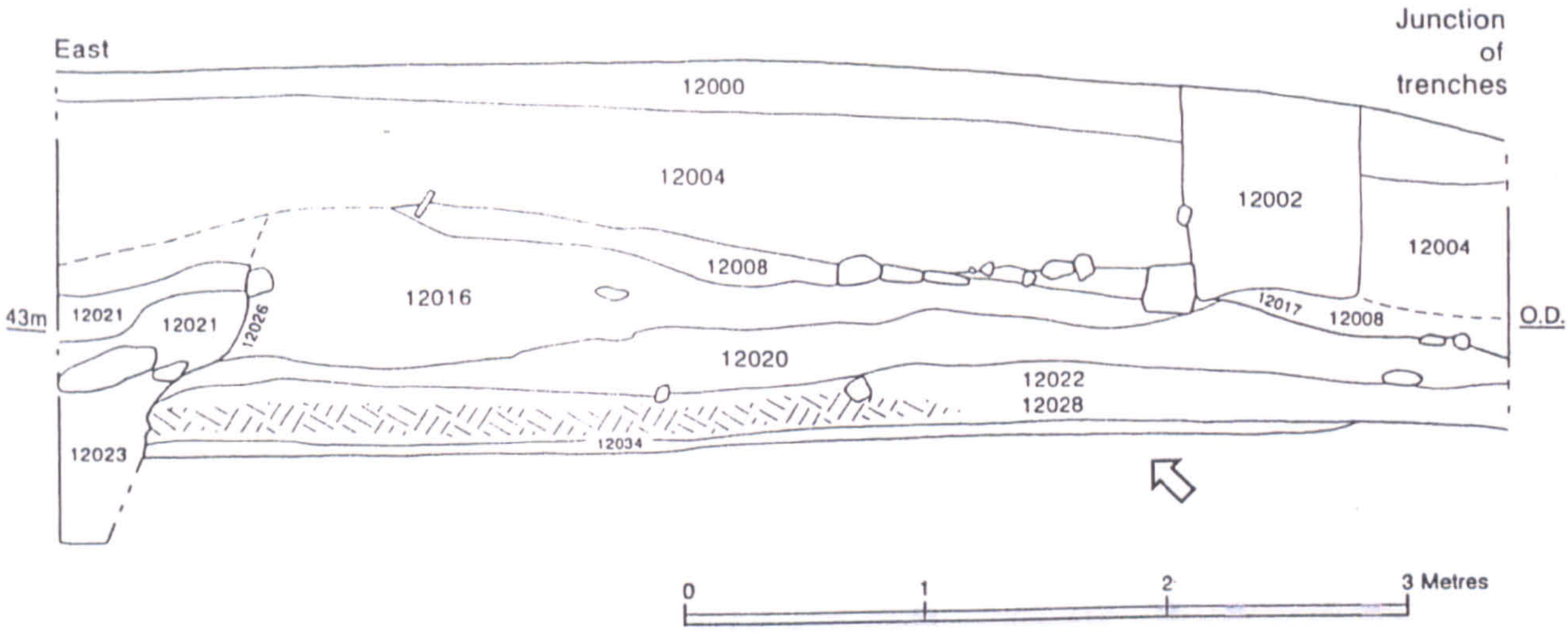


Figure 19. North facing section of trench 12, drawing provided by P. Ottaway.

Detail of cross-section through
the courtyard area at Filey:
1 = original ground level;
2 = Roman refuse deposits;
3 = ?medieval demolition rubble

Figure 20. Photograph of section of trench 12, from Ottaway (n.d.: 17).

Most of the small mammal bones were recovered from the top three contexts of this deposit, contexts 12022, 12024 and 12025, whilst only a few were represented within the lower layers, 12027 and 12028 (Dobney *et al.* 1996: 20). It is suggested that the origin of the small mammal remains is from owl pellets, either *Tyto alba* or A*sio otus* (Dobney *et al.* 1996: 17), and that these pellets accumulated either on the ground surface in times when the signal station was not in use, or had fallen from the tower, which was adjacent to the area of small mammal bone deposition, as can be seen in the site plan. Indeed, the fact the owls were using the signal station can be taken as evidence for abandonment (Dobney *et al.* 1996: 20).

Further suggestion for the role of owls as accumulators of the deposits came from studies of the small mammal species abundance, and comparison of these results with modern species abundances in the pellets of various avian predators (Dobney *et al.* 1996: 17), as well as evidence of bone modification (Dobney *et al.* 1996: 16). It is suggested that the predator was probably a 'roosting or nesting barn owl' (Dobney *et al.* 1996: 17), and that on the evidence of mild acid etching on some of the teeth and bones of the assemblage, it was perhaps more likely to represent a nesting site. The material for this site was therefore re-analysed in this study, to test this assertion.

6.3.3 Fox Hole Cave

6.3.3.1 The site

Fox Hole Cave, High Wheeldon, Derbyshire, (National Grid Reference [NGR] – SK 100663) is situated about one mile south of Earl Sterndale Village, see below, on the north facing side of High Wheeldon Hill, at an elevation of about 380m (Bramwell 1971: 1).

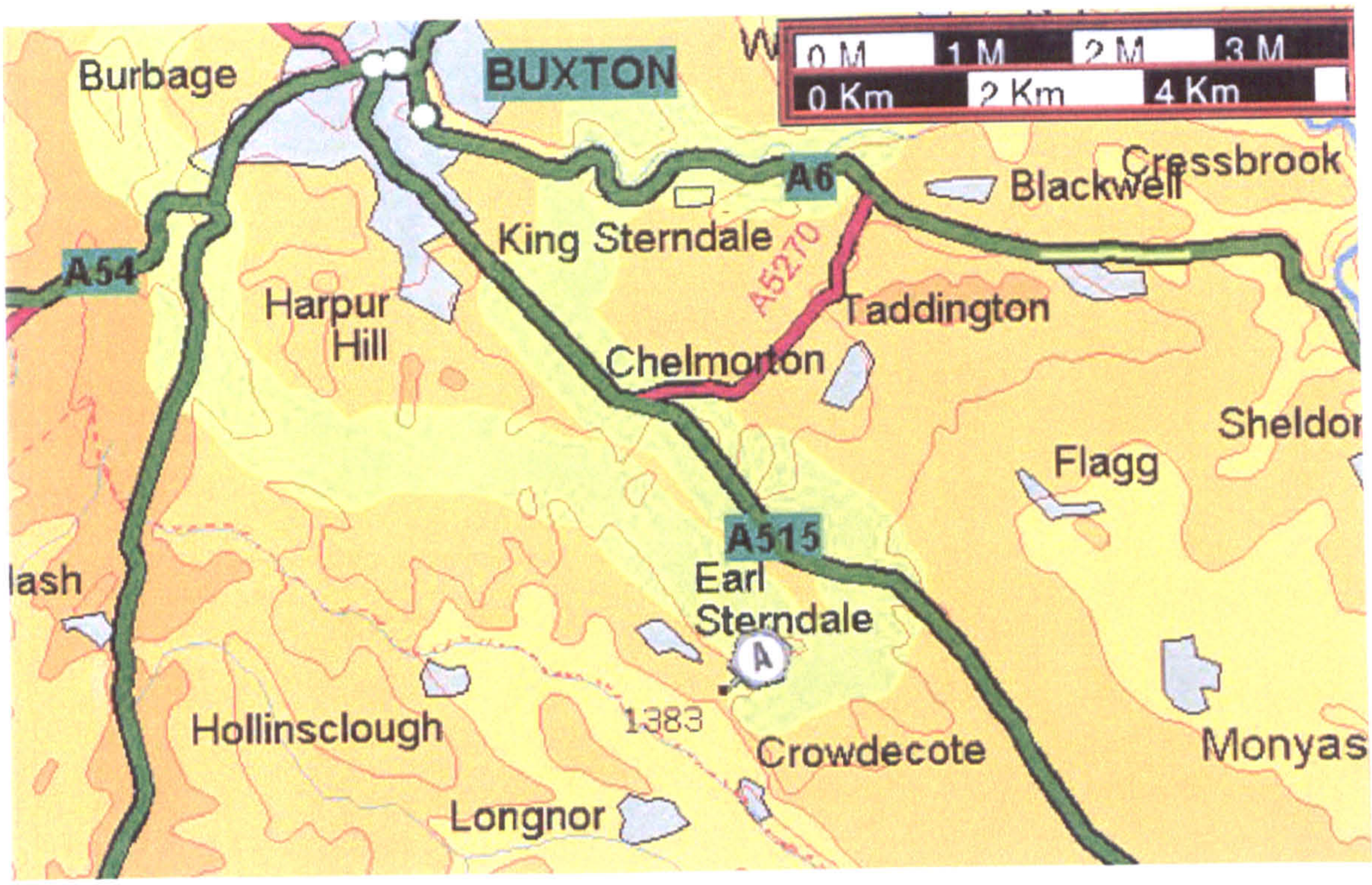


Figure 21. Location of Fox Hole Cave, marked A.

The cave was first excavated by S. G. B. Birks and B. S. Furneaux in 1928-1929[67] (Jackson and Piggott 1951: 72). More extensive excavations were carried out by the Peakland Archaeological Society between 1961 and 1981, although the majority of work took place during the period up to 1970. The material recovered from both excavations is now curated by Buxton Museum.

---

[67] The cave was discovered in 1928 when a lost dog was rescued by a thirteen year old boy (Jackson and Piggott 1951). To facilitate this rescue attempt, the entrance of the cave was enlarged, and was at this point that a number of archaeological finds were recovered, including human and animal remains as well as Peterborough Ware pottery (Bramwell 1971).

The cave can be described as a long tunnel extending about 70 metres into the hillside. Approximately 30 metres from the entrance of the cave, the tunnel opens up into a chamber, with three other passages radiating off from it (Jackson and Piggott 1951; Bramwell 1971). This is shown on the plan of the cave below.

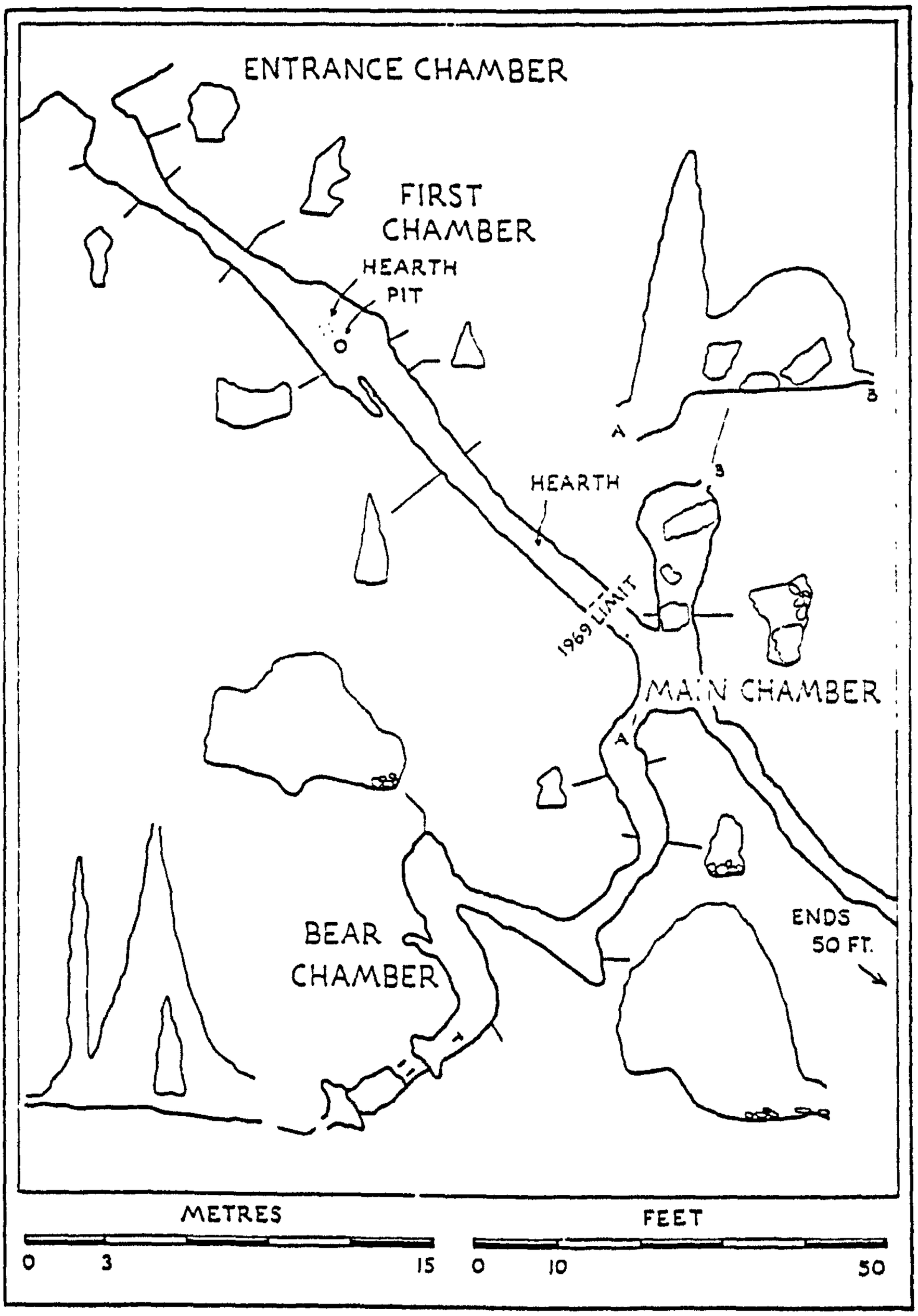


Figure 22. Plan of Fox Hole Cave, from Bramwell (1971).

Throughout much of the main passage, the deposits were about 1.6 metres deep, and followed a similar stratigraphy, a composite section of which is shown in the diagram, Figure 23, below.

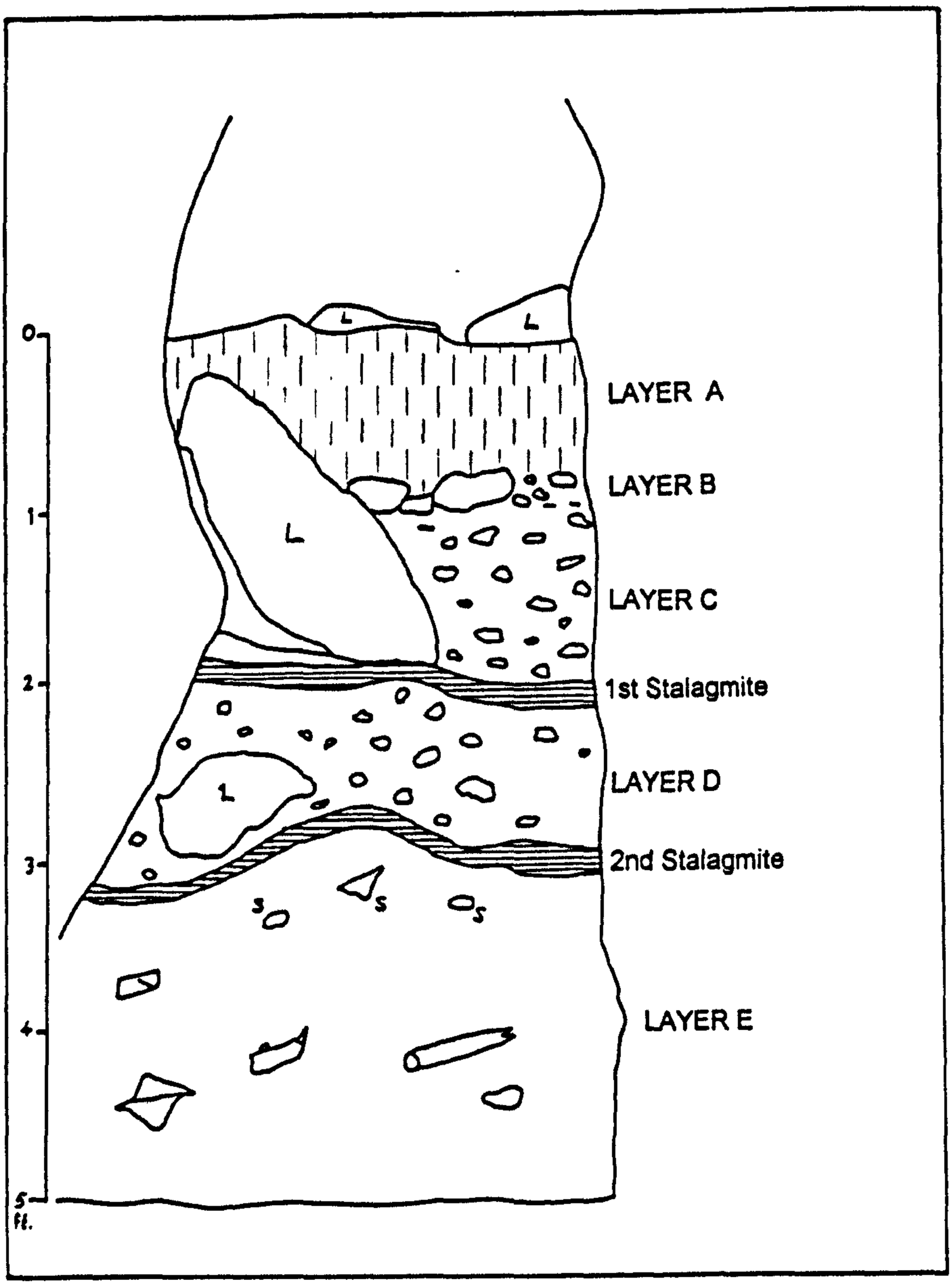


Figure 23. Composite section through Fox Hole Cave, after Bramwell (1971).

The deposits span dates from the Romano-British period back to the last glaciation. The majority of the Romano-British material was excavated from the entrance chamber during the earlier excavations, but also appeared in the top of layer A further back in the cave. Layer A was a dark brown silty mud, of a jelly-like consistency, which Bramwell suggested was formed during the early Iron Age, possibly associated with a deterioration in climate at the beginning of the sub-Atlantic phase, approximately

500BC (Bramwell 1971: 3). Below this layer was a cobbled limestone floor, from which numerous bones and 'Beaker age' artefacts were recovered, dating the horizon to the late Neolithic, early Bronze Age.

A clear delineation is made by Bramwell between the 'Beaker Folk' of layer B, and the earlier Neolithic Layer C1. This separation was made on the basis of pottery type, Beaker Ware in layer B and Peterborough Ware in Layer C, as well as by the construction of the cobbled floor at the base of layer B (Bramwell 1971: 3-6). Contamination between these layers was reduced by this cobbled floor, and attested to by the separation of pottery types[68].

Layer C1 (a mottled yellow clay) contained human remains, mixed in with a number of animal bones, and a few artefacts, such as a Peterborough Ware bowl, a small quantity of worked bone, and a Group VI greenstone polished axe-head (Bramwell 1971: 10). Radiocarbon evidence from this layer confirms the early Neolithic date for C1. Two human bones from layer C1 section VII were dated, one at 4230BC – 3800BC, the other 4500BC – 4050BC[69] (calibrated, 95.4% probability, OxCal version 3.5) (A. Chamberlain pers. comm.). Layer C2 contained no evidence of human occupation, or usage of the cave. The deposit was dominated by woodland type mammals, suggesting a landscape unaffected by human interaction. Layers D-F contained deposits dating from the Mesolithic through to the late upper Palaeolithic, during a period of glacial activity (Bramwell 1971: 12). Further description of these lower deposits can be found in Appendix table 14, page 296.

Pollen analysis was also carried out at this cave, from two horizons roughly contiguous with layers A and B. Sample A came from a 'thin layer of ... humic material ... approximately 2.5 cm above the cobbled floor horizon with its gritty clay and numerous rodent and amphibian remains.' Sample B came from 'a layer of jelly like humified material ... situated above a thin layer of clay with rodent and amphibian remains in a depression in the cobbled floor' (Shimwell 1971: 16).

The two samples were analysed by comparison to other pollen records from upland plateau sites around the Peak District. The two samples represent different

---

[68] No Beaker pottery was found in layer C1, and only a few sherds of Peterborough Ware were found in Layer B (Bramwell 1971: 6).

[69] The un-calibrated dates for the two human bones are 5185 ± 60 BP, and 5485 ± 75 BP (A. Chamberlain pers. comm..).

periods, sample A representing a period around 500 BC, in the early Sub-Atlantic period zone VIII, associated with heath formation of upland areas in the Peak District. Sample B is indicative of an earlier date, around 1200 – 600 BC. This sample contains a predominance of grass pollen, and indicates a more open environment. The origin of the pollen is unknown, although it is speculated that it represents either bedding material of a badger, or a food cache associated with the human usage of the cave (Shimwell 1971: 17-18).

The archaeological excavation was carried out by one person 'working at the face' (due to the confined space) whilst others sorted through the excavated material outside the cave. The deposits were excavated in units of approximately 90cm (3 ft), starting at the entrance of the cave, and extending back to the main chamber. Each unit was excavated in spits of between 5 – 10 cm deep, and material recorded from the unit and spit level (Bramwell n.d.). The excavation was very thorough, and great attention was paid to the retrieval of all finds, of which microfauna constituted a considerable percentage.

6.3.3.2 The samples

The three samples analysed in this study come from the early Bronze Age 'beaker layer', from a well defined and undisturbed layer which Bramwell suggests dates from between 1800 and 1600BC (Bramwell 1970). This layer also yielded finds of pottery and worked bone artefacts, as well as faunal remains including bear, deer and pig. The three samples all came from the curated material at Buxton Museum, and were selected for study on the basis of two criteria; the amount of small mammal remains, and an indication that the material came from a recognisable level, representing the 'beaker layer'.

These three samples are labelled –	Section 8B, layer B 6-9"
	B14, layer B
	A10 Beaker layer

They are recorded in the results section as Fox Hole - sample 1, Fox Hole – sample 2, and Fox Hole – sample 3 in the order as listed above.

Despite exhaustive searches through the archived material at Buxton Museum, it has not been possible to discover the precise location of these sampled deposits (or in fact any of the archaeological material from Fox Hole Cave, stored at Buxton Museum), as no overall plan for the site exists. However, the labels on the samples all suggest that they come from layer B or the Beaker layer (A10 - presumably the base of layer A, and the contact zone with layer B), and initial analysis also suggested that the small mammal species were all consistent with a deposit from Holocene Britain.

6.3.3.3 Discussion

An analysis of small mammals from Fox Hole was carried out by Bramwell (1970: 3-4) from material collected during the 1970 season of excavation, from the final section of the main passage. *Arvicola terrestris* and *Microtus agrestis* dominated the assemblage, constituting to almost half of the total small fauna. The rest of this sample comprised the remains of frogs and toads. The amounts are shown in Table 11 below.

Species	**Common name**	**Percentage**
Arvicola terrestris	Water vole	18.5
Microtus agrestis	Field vole	19.3
Clethrionomys glareolus	Bank vole	8.6
Apodemus sylvaticus	Wood mouse	2.6
Talpa europaea	Mole	1.5
Sorex araneus	Common shrew	2.4
Erinaceus europaeus	Hedgehog	.3
Plecotus auritus	Long-eared bat	.3
Rana & Bufo sp.	Frog & Toad	46.2
Anguis fragilis	Blindworm	.3

Table 11. Percentage of small fauna recovered from Fox Hole Cave, 1970 season, Bramwell (1970).

Bramwell suggests that the location of the deposit is outside of the daylight zone (the area at which humans can see light) and therefore it is unlikely that the small fauna has been accumulated by an avian predator, and instead suggests humans, badgers, foxes or cats as possible accumulation agents (Bramwell 1970: 3). However, as has been discussed in chapter 3 (page 41), an owl's vision is up to one hundred times more sensitive to light than humans are. Therefore the decision to sample deposits from Fox

Hole Cave was taken on the basis that they contained large amounts of microfauna, and that a narrow cave may have offered a suitable situation for a nesting barn owl. The reports from the excavation indicate that this cave was utilised by a number of different, episodic inhabitants, including humans, bears, foxes, badgers and cats. It is therefore likely that much of the accumulation in the cave could have a multitude of origins, which the fragmentary nature of the publications and archive material make it very difficult to uncover. Therefore, only the microfauna from this cave was analysed, to look for a possible avian predatory origin.

6.3.4 Carsington Pasture Cave

6.3.4.1 The site

The other cave site in this study is Carsington Pasture Cave, (NGR - SK 241536). It is located about 1 km southeast of the village of Brassington, on a limestone promontory; overlooking Carsington Reservoir (Chamberlain 1999), see figure below.

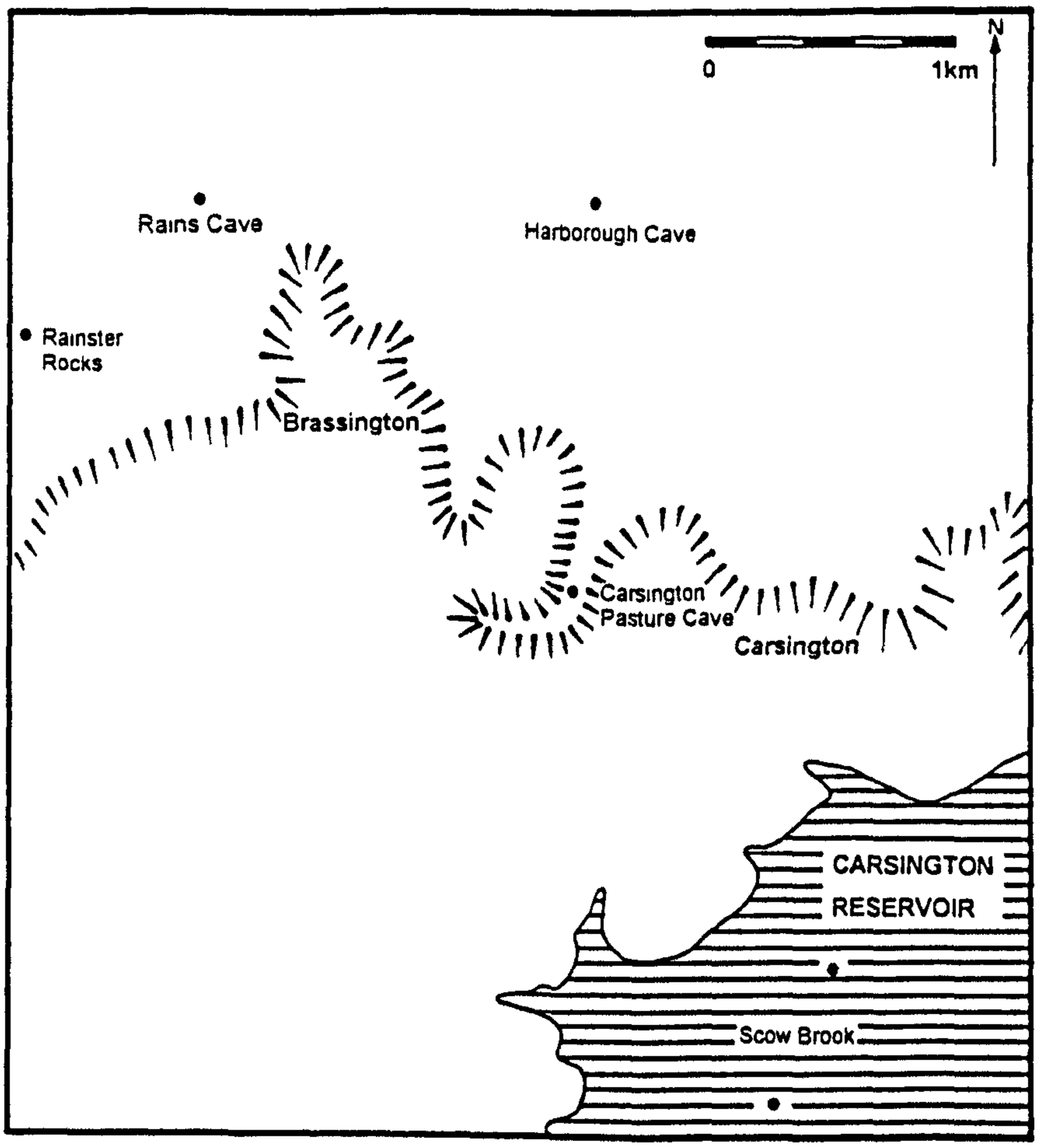


Figure 24. Location map, showing Carsington Pasture Cave, from Chamberlain (1999).

Although the location of this cave was well known, until 1998 the cave was only recognised as a small five-metre diameter chamber (Gill and Beck 1991). However, excavations by Pegasus caving club, revealed a further chamber, approximately 10 meters below the floor of the first chamber (entrance chamber) (Steans and Scothon 1998). Along the west wall of the second chamber, a number of human skulls had been placed, and throughout the rest of the chamber, more human remains and faunal deposits were clearly visible. A number of bones have been C14 dated to try to gain a better indication of the date of deposition of the human remains. A neonatal bone from

the second chamber (context 103) dates to 770BC – 400BC, whilst a human femur with cut-marks recovered approximately 30cm below the surface level of the 2nd chamber (context 314) yielded a date from 4500BC – 4050BC[70] (both dates calibrated, 95.4 % probability, OxCal version 3.5) (A. Chamberlain pers. comm.). The wide spread of these two dates indicates that the cave was in use for a long period as a locale for the deposition of human remains, which is consistent with other evidence from Britain which indicates that the use of caves as tombs is a phenomenon that is especially prevalent in the Neolithic and Bronze Age (Chamberlain 1996). Artefacts (including worked antler and stone) retrieved from the cave also suggest a similar date (Chamberlain 1999).

6.3.4.2 Sampling

After consultation with the County Archaeologist, it was decided that the best course of action was to begin a thorough archaeological excavation of the chamber, and remove the bones for scientific analysis, which would also preserve them from damage by cavers accessing the other parts of the cave. Therefore, in May 1998, Dr. Andrew Chamberlain and a team of students from Sheffield University, including myself, began a program of recording, documentation and excavation of all of the bones within this chamber. Every bone was allocated a three dimensional coordinate, plotted on a plan, and then removed. In the case of most of the human bones, these were also photographed as well. There appeared to be two discrete zones of deposition of the human remains, adults in the west of the cave, and children and neonates in the east (Chamberlain 1999). These are shown on the plan below, with open circles indicating neonates and closed circles indicating children and adults, (see figure below).

---

[70] Un-calibrated dates, neonatal bone (context 103) 2435 ± 55BP, the human bone with cut-marks (context 314) 3980 ± 60BP.

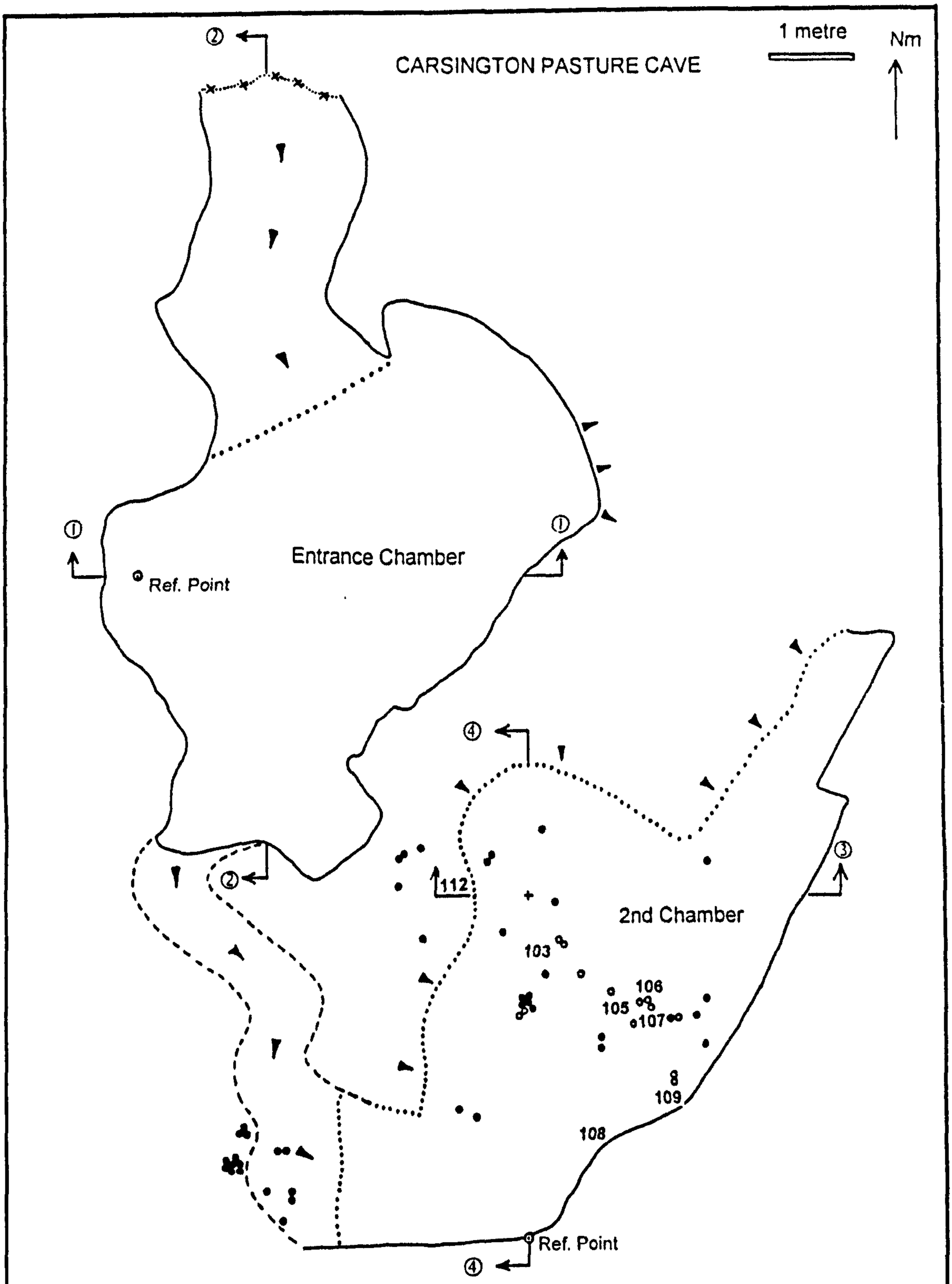


Figure 25. Plan of Carsington Pasture Cave, - open circles for remains of neonates and closed circles for remains of children and adults. Numbers indicate small mammal sampling locations, from Chamberlain (1999).

The bones were all on the surface of the floor of the second chamber, which had formed as the result of a collapsed boulder choke, sometime before the deposition of most of these bones. This is evidenced by the fact that few bones showed any sign of movement, or post deposition breakage. In the same area containing the neonate burials, there were also a number of discrete patches of small mammal bones (see figure below). These patches measured approximately 10-20cm in diameter, and were all situated in the southeast of the cave. They were located mainly on flat-topped boulders, although in some areas bones had fallen between boulders into lower parts of the boulder deposit.

Figure 26. One of the patches of small mammal bones from Carsington Pasture Cave, Photograph by A Chamberlain. Scale – arrow labelled 106 is 12cm in length

All of these small mammal deposits were bulk sampled and removed for further analysis. The bulk sampling was carried out as a total collection of the available bones, and all those bones that could be removed were, although some were lost because they had slipped down between the boulders. The samples that were used in this study are 103 and 109, which were located about a metre apart from each other, see Figure 25 on the previous page. Two different deposits from this cave were analysed in order to check that all of the small mammal bones had accumulated in the same fashion.

6.3.4.3 Discussion

As has been stated in the previous section, the small mammal bones had not undergone any transportation. In fact, they looked as if they had not been disturbed in any way. There were a vast number of bones and it is unlikely that this represents a natural death of all of these animals. In addition, there is no way that they have fallen into a pit fall trap, as the cave roof contains no evidence of a present or ancient fissure. One must therefore assume that the small mammal bones were deposited by some species of predator.

There are two options, a mammalian predator such as a fox or badger, or an avian predator, such as an owl. Diurnal raptors can be ruled out, as they would not venture this deep into the dark of a cave. Initial analysis of the species present within these discrete areas of small mammal bone, suggests that only the small mammals considered in chapter 4 were prey items of this predator. Deposits produced by foxes often contain other larger species, such as *Oryctolagus cuniculus* or *Lepus* sp., juvenile sheep (*Ovis*) and other carrion collected bones. None of these were found in association with the small mammal bones in Carsington Pasture Cave. Mammalian carnivores can also be identified by bone breakage, as they are often very destructive to small mammal bones. Whilst criticism has been made of bone breakage techniques in previous chapters (see for example, page 22), in this case they may be quite useful, as none of the bones show any signs of post-depositional movement or transportation; therefore any bone breakage is likely to be predator derived. Initial analysis suggests that the bones are too well preserved to have been deposited by a mammalian predator. However, this will not be treated as an implicit conclusion until a full taphonomic analysis has been carried out.

The evidence would therefore suggest that the most likely predator responsible for the deposit is an owl. The only owl species known to regularly inhabit caves in Britain is *Tyto alba*, although this rests upon the assumption that the deposit is Holocene in age. C14 dates have indicated that the human remains in the second chamber range in date from the Neolithic through to the beginning of the Iron Age, and although precise dates have not yet been established for the small mammal deposits, it is likely that the deposition of the human and small mammal remains are fairly

contemporary. An analysis of the small mammal species will also shed some light upon the possible date for their deposition. For example, the inclusion of *Mus domesticus* (house mouse) would tend to suggest a Holocene date, while *Dicrostonyx torquatus* (arctic lemming), *Lemmus lemmus* (Norway lemming) or *Microtus oeconomus* (northern vole), would suggest a much older date, during the Pleistocene. The survival of some of these species into the early Holocene in refuges such as the south west of England is however recognised (personal observation; Yalden 1999) and serves as a reminder of the need for the accurate assessment of all parts of an assemblage rather than just marker species.

If the predator was *Tyto alba*, then the evidence would also tend to suggest that it might have been nesting in the cave. There are a number of reasons for this. Firstly, the structure of the roof directly above the accumulations offer no place for an owl to perch on. This is important, because roosting *Tyto alba* usually perch above the ground. They are only found on the ground when nesting. Further evidence that attests to this hypothesis is the spread of small mammal bones. *Tyto alba* tend to perch in one place constantly, under which vast amounts of material will accumulate (Bunn et al 1982: 57). However, within a nest, once the chicks are old enough to wander around, pellet regurgitation can take place some distance away from the original nest site. This behaviour may be responsible for the spread of small mammal remains over such a large area.

Whatever the predatory origin of the deposit is, it is likely that this cave was only in periodic usage as a burial chamber, and perhaps not visited for any other reason. It would therefore make an ideal situation for a nest, roost or den - isolated and protected from much of the outside world. Although the cavers of Pegasus Caving Club may have rediscovered this cave through digging down through a tunnel of mud and clay, it is also likely that a different entrance to this second chamber was in use during the time that both the human and small mammal bones were deposited, possibly located in the current position of the boulder choke. Without an alternative entrance, it is unlikely that any owl would have ventured this far below ground and away from the light source, as no light is visible within this chamber naturally at the present time.

6.4 Sampling methods

In all cases the size of the archaeological samples used in this analysis were pre-ordained by the excavations from which they came. The analysis therefore looked at all of the small mammal (rodent and insectivore) bones from each of the sites described above, from the contexts available for study. Each context was analysed and recorded separately, to minimise mixing of samples. The material from Filey and Tadcaster, loaned by Keith Dobney of the York Faunal Remains Unit, was sampled in its entirety.

The specific sampling strategies for Fox Hole and Carsington Pasture Caves were outlined above, but will be reiterated here. Three samples were taken from the Fox Hole material stored at Buxton Museum. They were selected because they contained a large number of small mammal bones, and because they were well labelled, with the layer from which they were excavated.

It was hoped that all three of these samples would represent the 'Beaker' layer within the cave, which had been used in Bramwell's analysis of small mammal bones (Bramwell 1970). Pollen samples had also been taken from deposits within this cave (Shimwell 1971), and it was hoped that the small mammal evidence could be roughly correlated with the environmental evidence provided by these studies, especially the earlier of these two pollen samples, sample B. The two samples from Carsington Pasture Cave were chosen because they were some of the largest samples, and also were situated some distance from each other. This was felt to be important, to analyse the extent to which the accumulations represented one predator spread over a wide area, or a number of different predator deposits.

The samples from owl nest sites were chosen and collected by Colin Shawyer of the Hawk and Owl Trust. When these samples arrived in the laboratory for analysis, they constituted a considerable amount of bones and adherent fur. Random sub-samples were therefore taken from each of these two samples, representing approximately 500 grams of nest material, or one third of the total nest material.

7.Methodology

7.1 Introduction

Chapter 2 outlined the history of taphonomic research into small mammals, and reviewed the techniques used in these studies. In this chapter, the taphonomic techniques used in this study will be described, with reference to the information it was hoped that they would offer, and any drawbacks associated with each technique. Most of the methods outlined within Chapter 2 were used in the analysis of the small mammal assemblages within this study. For each deposit (with the exception of *Tyto alba* roost material), or small mammal assemblage, the number of bones was tallied, and recorded to skeletal element. Breakage data were collected for the cranial and post-cranial bones, and digestion was recorded for the molar and incisor teeth. Comparison was made between the modern *Tyto alba* roost material and the modern *Tyto alba* nest material. The material from the owl nests was then used to compare with the archaeological site data, to analyse the extent to which the small mammal assemblages from the archaeological sites may have been deposited as part of a *Tyto alba* nest.

7.2 Laboratory procedure

7.2.1 Washing

The samples from Fox Hole Cave, Tadcaster and Filey, as well as the samples from Stratton, Rhulen and Salthouse, were already washed and ready for analysis. The other samples, Carsington Pasture Cave, and the two comparative modern nest samples needed processing before analysis could be carried out. The samples from Carsington Pasture Cave were washed under gently running water in a series of sieves, the smallest with a 0.5mm mesh size, to remove all adherent mud and cave deposit. The samples were then left on a tray containing paper towels, until all the moisture had evaporated, and the bones were entirely dry.

The procedure for processing the small mammal bones from the nest sites was slightly different. The selected nest material was first washed in a mild antibacterial agent and commercial hand washing soap, and left to soak overnight. This reduced the acrid smell of the sample, and also acted to break down some of the materials binding the fur to the bones. This is also a very effective method for extracting bones from pellets. This soaked material was then washed in a sieve (smallest mesh size 0.5mm), and all visible bones extracted. The rest of the material left in the sieve was then turned out on to paper towels, and left until all of the fur and bones were dry.

7.2.2 Sorting

Initial sorting of all of the samples was necessary to remove elements that were not small mammal bones. These included the bones of birds, amphibians, and larger mammals, as well as stones, and in the case of the nest material, fur. This sorting was carried out with a pair of fine tweezers, using the naked eye. All small mammal material was selected, and the rest of the material bagged up as residue and saved. The samples were then sorted by body part: cranial, long bones (scapula, radius, ulna, humerus, pelvis, femur and tibia) and other parts (vertebrae, ribs, podials, metapodials and pes). To save time, only the cranial elements and the long bones were recorded, and the other parts bagged and saved. This decision was taken as very little information can be gained from the analysis of skeletal part representation, especially from elements as fragile as ribs and vertebrae, and as small as pes. The long bones were then recorded for both skeletal element representation , as well as breakage (see section below), and then saved. The cranial elements were sorted into species, and bagged for analysis.

7.2.3 Species identification

Identification of small mammal species was carried out using the upper and lower molar teeth, in the case of mice and voles, and the mandibles or maxillae for shrews, using dental charts in Lawrence and Brown (1967), Yalden (Yalden 1977) and Corbet

and Harris (1991). Further identification was made by reference to a comparative collection of small mammals at the Department of Archaeology and Prehistory, University of Sheffield. Each species that could occur within British small mammal deposits from the Holocene or late Pleistocene was given a code number, shown in Table 12 below.

Species	Common name	Numeric code
Apodemus sylvaticus	Wood mouse sp.	1
Micromys minutus	Harvest mouse	2
Mus domesticus	House mouse	3
Mus sp.	Mouse	4
Rattus sp	Rat	5
Arvicola terrestris	Water vole	6
Clethrionomys glareolus	Bank vole	7
Microtus agrestis	Field vole	8
Microtus arvalis	Common vole	9
Microtus gregalis	Narrow-skulled vole	10
Microtus oeconomus	Root vole	11
Microtine sp.	Vole	12
Lemmus lemmus	Norway lemming	13
Dicrostonyx torquatus	Arctic lemming	14
Neomys fodiens	Water shrew	15
Sorex araneus	Common shrew	16
Sorex minutus	Pygmy shrew	17
Soricidae sp.	Shrew	18
Talpa europaea	Mole	19
Rodentia	Rodent	20

Table 12. British small mammal species from the Holocene and late Pleistocene.

Species identification was not carried out on the long bones, which are difficult to assign accurately to species. They were therefore recorded within category 20, as rodent long bones (although this is slightly misleading as this category also includes shrew post-cranial bones).

Isolated incisors are difficult to assign to species, and they were also recorded as category 20, with two exceptions. Firstly, shrews do not have the same cranial physiology as rodents (mice and voles), and are not equipped with constantly growing incisors. In fact the occurrence of isolated shrew incisors in small mammal accumulations or pellets is rare. In addition, shrews were not used in digestion analysis due to this markedly different cranial physiology and tooth morphology. Secondly, due to the difference in size between *Arvicola terrestris*, and other vole and mouse species,

it was possible to identify both the cranial and post cranial elements of this species. As no effort was made to separate species in the identification of post-cranial breakage, the long bones of this species were recorded within category 20 in this part of the analysis. The isolated incisors of *Arvicola terrestris* were treated separately, in order to identify any patterns of digestion associated with a difference in size.

7.3 Techniques for recording small mammal bones

7.3.1 Skeletal element abundance

Each element was recorded on a specialised recording sheet (see Appendix table 15, page 297), with the cranial material identified to species, and the long bones and isolated incisors (except those of *Arvicola terrestris*) assigned to a category for all rodent (or small mammal) bones. The identification of the long bones (i.e. humerus, femur etc) was done with the naked eye. Species identification (and digestion) of the molars (and incisors) were carried out using a Carl Zeiss binocular microscope with x8 and x32 magnification.

7.3.2 Assessing the number of individuals

Many zooarchaeology reports use the NISP (number of identifiable specimens) as a method for quantifying bone assemblages. However, it is not appropriate to apply NISP to data used in this study, as certain elements were being deliberately selected against during the sorting procedure. The number of bones recorded on the first recording sheet (see Appendix table 15, page 297), is therefore just a count of the bones being used in the analysis, and does not offer a figure that can be said to represent all bones possibly recovered from the site. To measure the number of individuals in each sample, the MNI (minimum number of individuals) was calculated for each sample. It is taken here as implicit in applying MNI, that some under-representation of the sample size will occur (see Gilinsky and Bennington (1994) for criticism of this method, as well as Reitz and Wing (1999: 194-202) for further review).

The MNI for each sample was calculated from the most common, identifiable, molar tooth, mandible or maxillary fragment, for each species. This was usually the molar teeth, as they were often the best preserved elements found within small mammal assemblages. No attempt was made to match pairs of teeth or mandibles, and each species was assessed on the most prevalent molar tooth, mandible or maxilla (left or right) in each context. Therefore, the MNI represents the smallest number of each individual species needed to produce the material for each archaeological context (Shotwell 1955: 330). The MNI was not calculated for long bones, which are difficult to assign to species in most cases. Every effort was made to ensure that where broken bones could be matched with other fragments to make a complete bone, that one bone and not two were recorded.

7.3.3 Cranial and post-cranial breakage

Damage to the post-cranial and cranial elements was recorded following criteria developed by Andrews (1990), (discussed in chapter 2, page 22) and entered on specialised recording sheets (see Appendix table 16 page 298, and Appendix table 17 page 299). Wherever possible, cranial breakage was recorded to species, with isolated incisors allocated to a category of rodent (category 20). Molar and incisor breakage was not recorded in this study, and only whole molars or incisors were analysed for the MNI or digestion data.

Post-cranial breakage was not recorded to prey species, (due to the problems in assigning small mammal post-cranial material to species), and therefore, the results reflect the total post-cranial breakage for each context or sample. This was assessed for four long bones, humerus, ulna, femur and tibia, for which each bone was recorded as being either complete, or represented by a fragment from either the proximal, distal or mid shaft section of the bone. The radius, scapula and the pelvis were not included in the breakage analysis. The radius is a fairly weak and thin bone, and due to its slender shape, can sometimes pass through sieves with too large a mesh size. The scapula is a very weak bone, and is easily damaged even in owl pellets. The pelvis was not used as there are inherent weaknesses between the three constituent parts, pubis, ischium and

ilium. In juvenile prey, these bones are not fused, leading to greater incidence of breakage being recorded. The numbers recorded within the bone breakage analysis for each bone, may vary with those recorded within the skeletal element count, as bones are recorded for their breakage, and those that match (i.e. a proximal and distal section) are not treated as one bone as they are when recording the numbers of each bone, but the data entered for each breakage class.

Cranial breakage was recorded for all rodent species in each site and context. Insectivores were not used in this analysis, as due to a different cranial physiology, breakage and tooth loss was not comparable with the rodent species. By excluding the insectivore data from the analysis, it was hoped that certain species specific biases in the data could be avoided.

Results of cranial and post-cranial breakage for *Tyto alba* nest sites were compared with data for modern *Tyto alba* (Andrews 1990: 51-61). Results obtained from the analysis of the archaeological material was compared with the results from the analysis of the modern *Tyto alba* nests.

7.3.4 Digestion of teeth

The first stage in recording digestion was to decide what constituted digestion. Teeth from the comparative collection at Sheffield University (which were known to come from small mammals that had died a natural death, rather than at the 'hands' of a predator) were analysed to provide a record of the natural variation in small mammal tooth morphology. In most cases (except that of *Arvicola terrestris*), they showed no indication of bone modification, comparable to digestion described and pictured by Andrews (1990). Therefore the assumption was made that any teeth showing signs of bone modification, or digestion, could be recorded as such. Analysis of *Arvicola terrestris* molar teeth indicated that the surface morphology of the enamel was slightly different, and therefore a different approach was taken when analysing molar digestion in this species. This is described in detail in Appendix notes - section 2, page 276. However, this initial analysis of the comparative collection at Sheffield indicated that for every tooth analysed, a simple binary answer could be obtained, either digested or

not digested. It was assumed that this assumption should hold true whatever the degree of digestion visible on the tooth.

Data for digestion were collected for molar and incisor teeth, for murine and arvicoline small mammal species. This digestion was recorded for each species separately, so that any species specific digestion biases could be recognised. Digestion was not recorded for insectivores, as they have a different cranial morphology, and tooth structure. Isolated and *in situ* teeth (those teeth still retained within the jaw) were also recorded separately, and a distinction made between upper (maxillary) and lower (mandibular) *in situ* molars, and upper and lower *in situ* and isolated incisors. It was not always possible to ascertain the species identification for the isolated incisors, and the majority of these was recorded only as Rodentia, although where possible *Arvicola terrestris* incisors were recorded separately. Digestion data were therefore collected for a large number of variables.

For example, the data collected from one skull (maxilla and mandible) would represent four variables, (*in situ* maxillary and mandibular molars, and *in situ* maxillary and mandibular incisors), and seven variables, if half of the teeth fell out and were also recovered, (isolated molars, and isolated maxillary and mandibular incisors). Within the results and appendix sections, the terms 'maxillary' and 'mandibular' are often shortened to either 'max' and 'man', or upper and lower.

As has been suggested above, any modification of the teeth was analysed, and checked with criteria of digestion described and illustrated in Andrews (1990). Care was also taken to ensure that non-digestion related modification was not recorded as digestion, for example weathering or post-depositional enamel chipping. The characteristic patterns of digestion are slightly different between molars and incisors, and between different prey species.

Molar digestion was most visible on arvicoline molars, which were digested with an increased regularity over murine molars, because of the different tooth shape. The amount of digestion recorded for molar teeth is related to the relative acidity of the stomach of the specific predator responsible for the accumulation. In cases where stomach acidity is low, for example in *Tyto alba*, or *Nyctea scandiaca*, digestion of

arvicoline molars is restricted to the top of the teeth, leading to a rounding of the corners of the teeth, as can be seen below

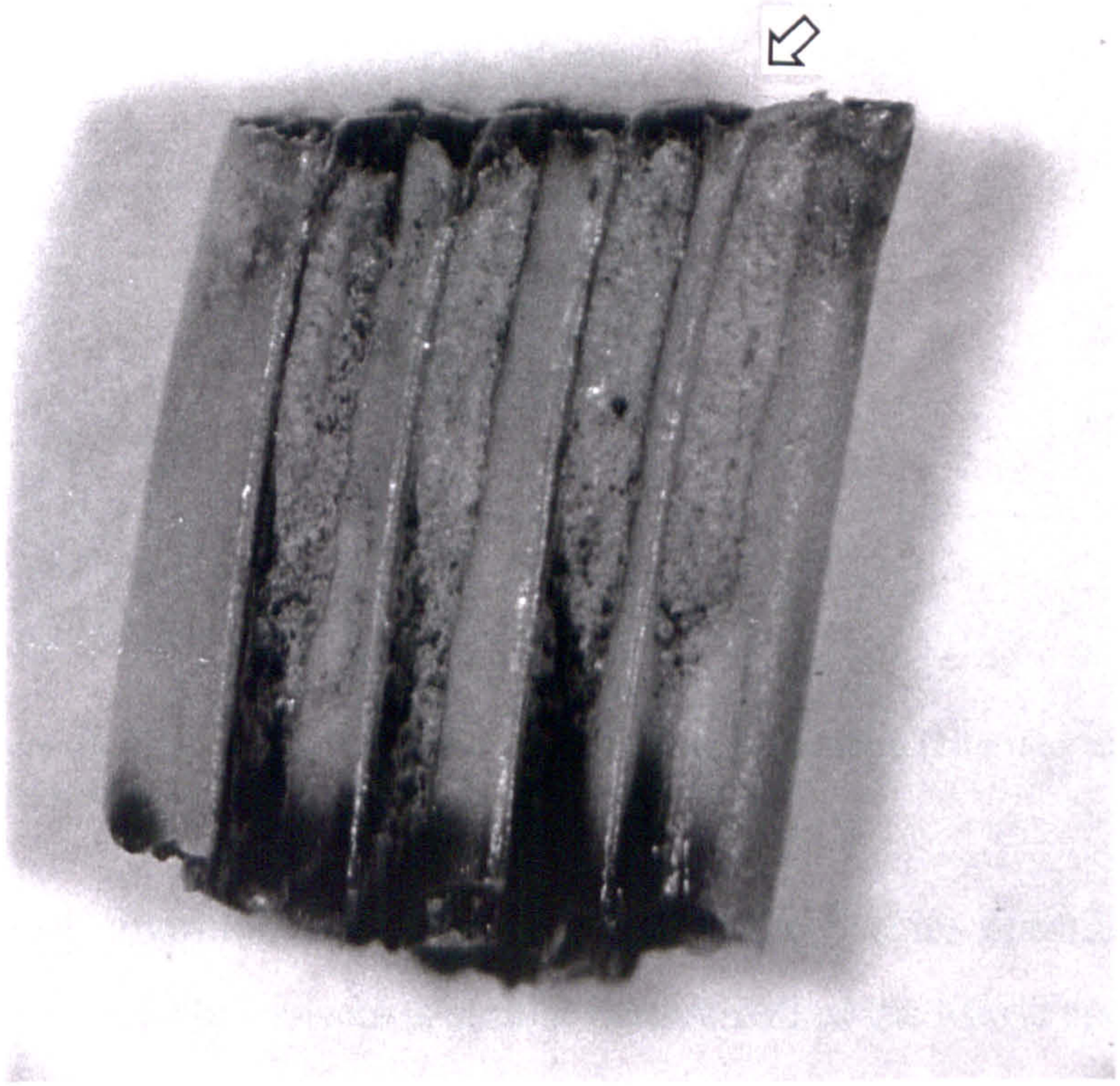


Figure 27. Digestion of arvicoline teeth (*Microtus agrestis*), showing rounding of occlusal surface of the teeth, see arrow. Scale 18mm = 1mm.

Levels of digestion that cause this limited rounding of arvicoline teeth, rarely leave any evidence on the teeth of Murinae. This is therefore an example of prey species specific digestion. In predators with higher levels of stomach acidity than *Tyto alba*, greater degrees of digestion are recorded. In these cases, the edges, (salient angles) of the teeth are often digested, in cases of heavy digestion, exposing the dentine below the enamel, see the figure below. This heavier digestion is also visible on murine teeth, with enamel penetration in extreme cases.

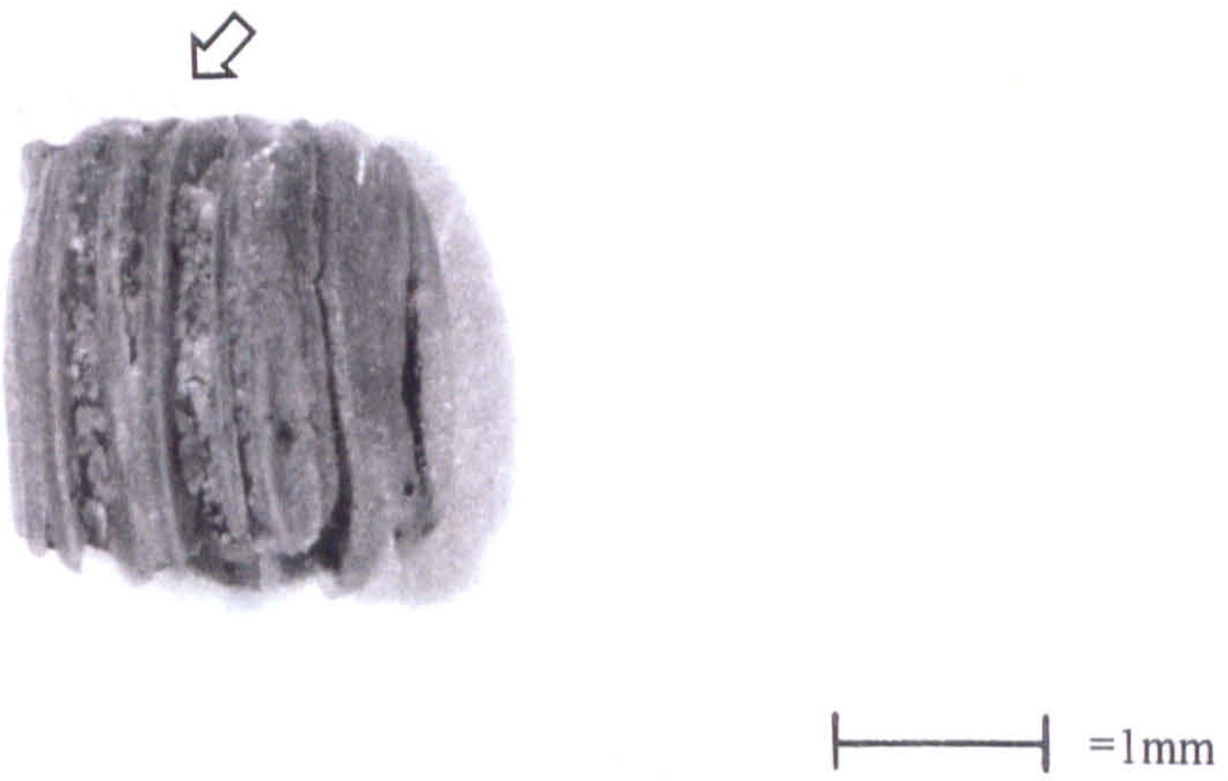


Figure 28. High levels of digestion of arvicoline molar teeth (*Microtus agrestis*), with dentine exposure of the salient angles, see arrow. Scale 14mm = 1mm.

Incisor digestion is not as affected by the species specific digestion, because the morphology of incisors is similar between all of the Murid species used in the analysis. The digestion is similar to the molars, in that different levels of digestion exist, also associated with levels of predator species stomach acidity. Low levels of digestion are visible as a light pitting of the enamel, which does not usually penetrate through to the dentine and also as a very gentle removal of the enamel exposing but not affecting small areas of the dentine.

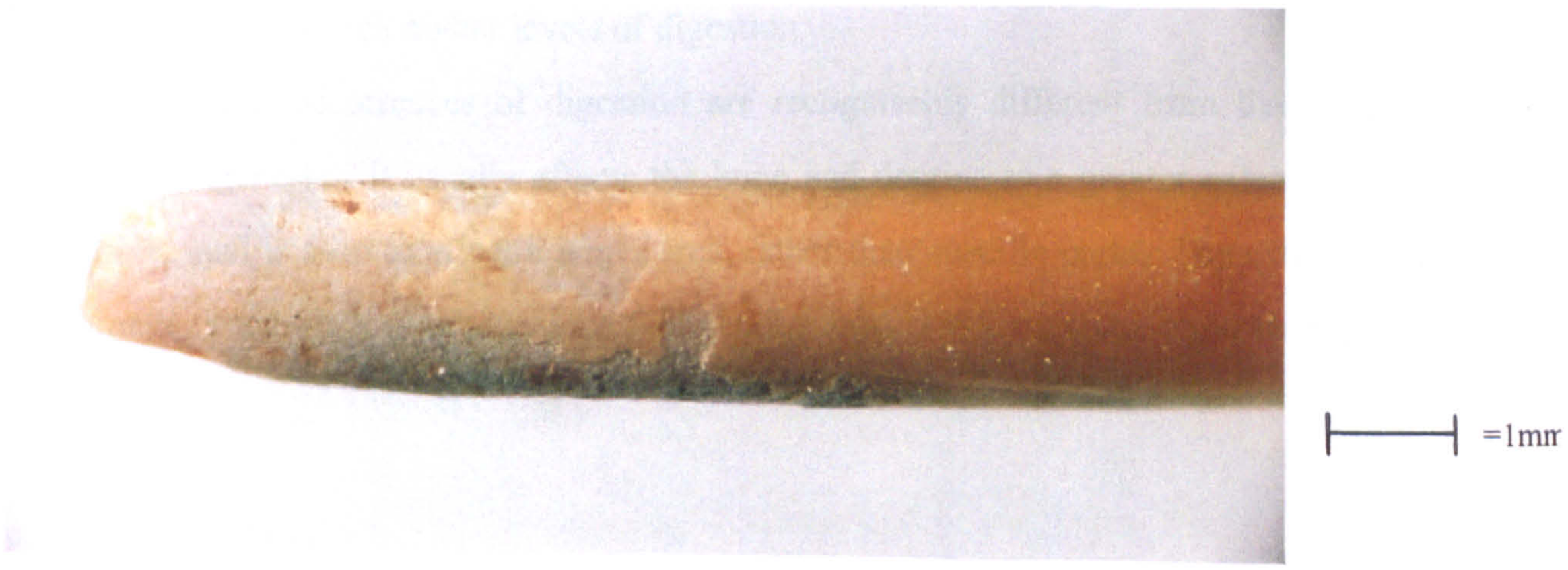


Figure 29. Example of light enamel digestion of the incisor. Scale 20mm = 1mm.

In some cases digestion is purely restricted to the incisor tips, reflecting the fact the incisor has been digested whilst still held within the jaw. This is still an indication that the degree of digestion was fairly light, as the rest of the tooth has not been digested. Higher levels of digestion affect the whole tooth, indicating that either the jaw was broken during ingestion, or that the bone surrounding and protecting the tooth has also been digested. In these cases, the enamel is usually penetrated, and the dentine digested, as can be seen below

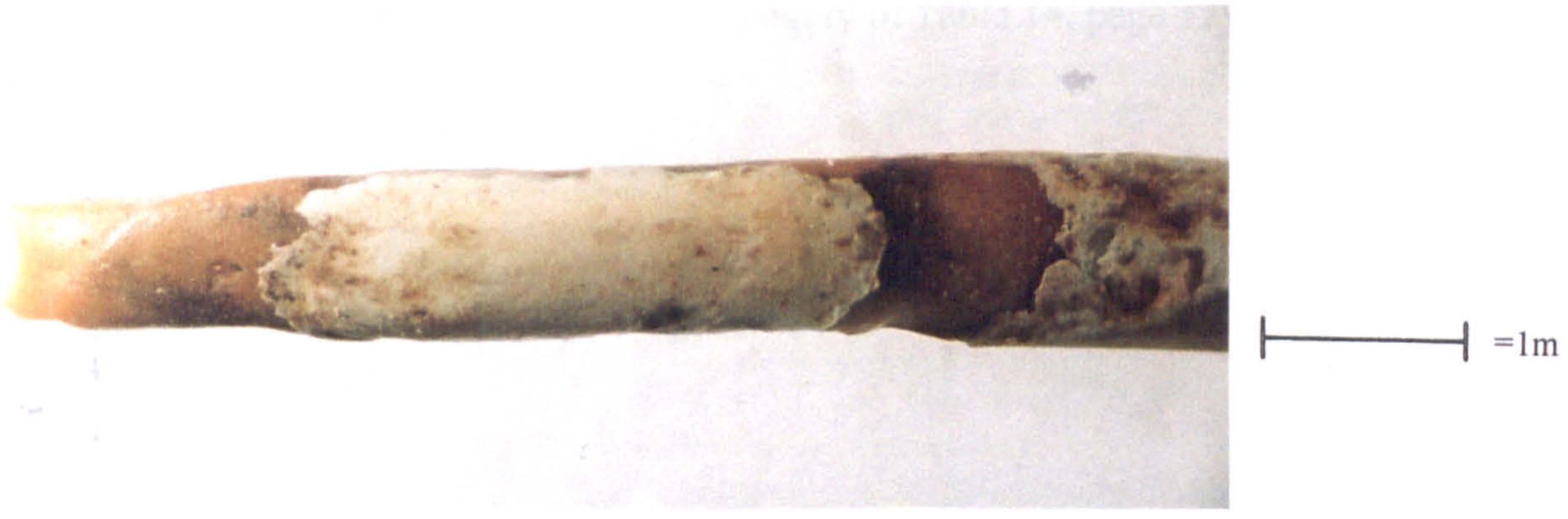


Figure 30. Higher levels of incisor digestion, showing enamel penetration and digestion of the dentine. Scale 15mm = 1mm.

It should however be pointed out that occasionally high levels of digestion can be recorded in predator species where this is not normally the case. It is most likely that this is caused by occasional stomach acidity increases, possibly as a result of weather changes (such as snow or rain), which impact on hunting ability and can therefore lead to hunger. However, an overall trend does appear to be present, that indicates that certain avian predator species are responsible for low levels of digestion, and others are responsible for much higher levels of digestion.

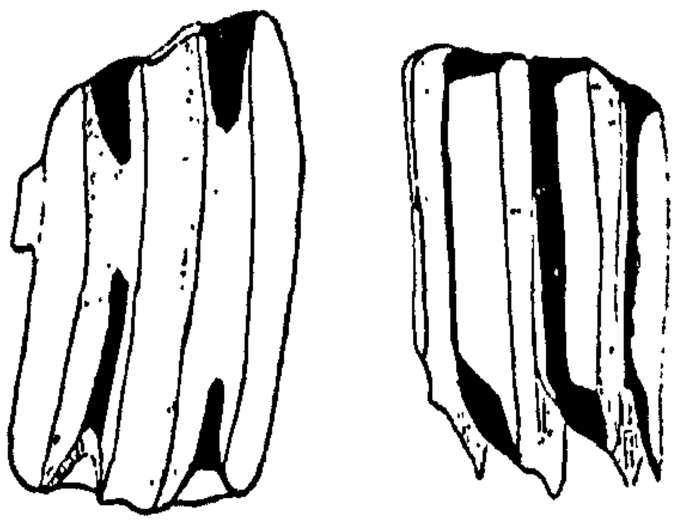
These occurrences of digestion are recognisably different from that of post-burial diagenesis. It usually effects the bone and dentine to a greater extent than the enamel, and is seen to effect a larger area, rather than specific parts. The extent of the damage is also light (Andrews 1990; Fernandez-Jalvo 1995; personal observation).

7.4 Recording the extent and frequency of digestion

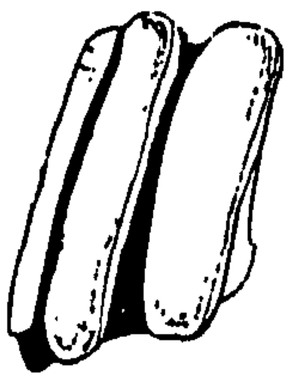
A further development of the methodology for recording digestion was developed by Fernandez-Jalvo (1992), and published by Fernandez-Jalvo and Andrews (1992). This methodology divided the extent of digestion into four categories for the incisors and molars, described as light, moderate, heavy and extreme. Whilst this type of information had been collected by Andrews, (1990), it has not been published as such a systematic method. Figures taken from Fernandez-Jalvo and Andrews (1992) are shown below, with the descriptions of each category for molar digestion in Table 13, page 128, and the descriptions for each incisor category in Table 14, page 129.

7.4.1 Molar digestion

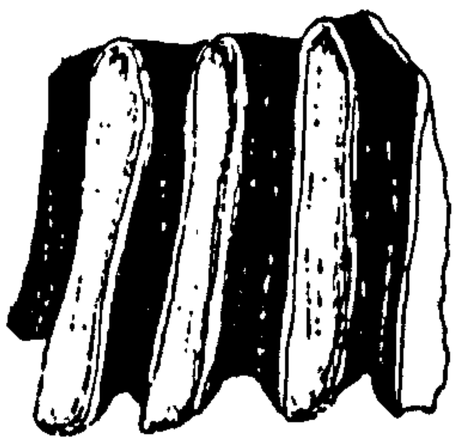
light



moderate



heavy



extreme

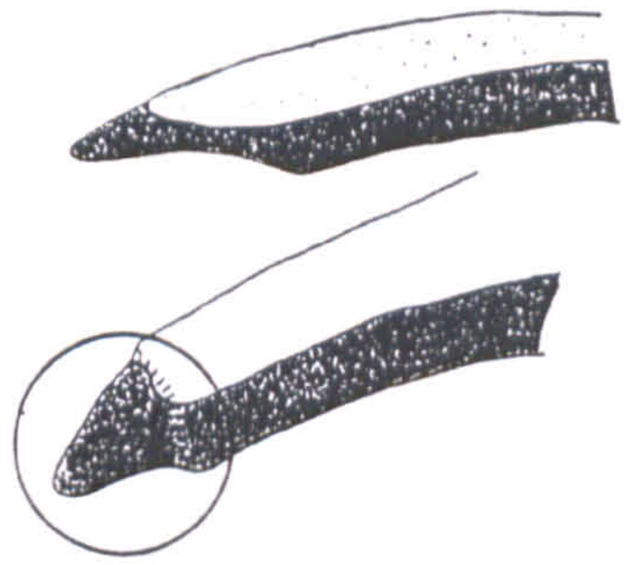
Figure 31. Categories of molar digestion, see Table 13 page 128 for description, from Fernandez-Jalvo and Andrews (1992)

Digestion category	Description
Light	Digestion in microtine molars is restricted to the occlusal corners of the salient angles of the teeth and does not penetrate below the alveolar margins. Also it does not usually penetrate through the enamel and into the dentine, so that the corners of the teeth are rounded and the salient angles flattened. Murids and cricetids have a smoother enamel and more rounded shape so that digestion is hard to identify. Insectivore molars do not show any signs of alteration.
Moderate	The enamel has been removed along half or the entire the length of the salient angles, leaving a smooth edge. Murids and cricetids show a pitted surface. No modification is observed on insectivore teeth.
Heavy	In microtine teeth, corners are strongly rounded with deeply penetrated salient angles and enamel extensively removed from the entire length of the salient angle and the dentine exposed and flattened. In murid and cricetid teeth, the surface is heavily pitted and the enamel partly removed along the edge of the wear facets. Similarly for insectivores, and on these and murids the dentine is not affected.
Extreme	The damage is so great that only rarely are the teeth identifiable. In microtines the damage of the enamel again extends along the salient angles but there is considerable digestion of the dentine, which undermines the enamel shell and causes it to collapse inwards along the length of the salient angles. This produces a characteristic curled appearance of the tooth and gaps in the dentine. Murids and cricetids show extreme digestion, with more of the enamel removed. In insectivore molars the enamel may be largely removed, leaving islands of cracked and scored enamel, or it may be entirely missing and the dentine hollowed out and etched so that only the bare outlines of the teeth remains.

Table 13. Description of digestion categories for molar teeth, from Fernandez-Jalvo and Andrews (1992)

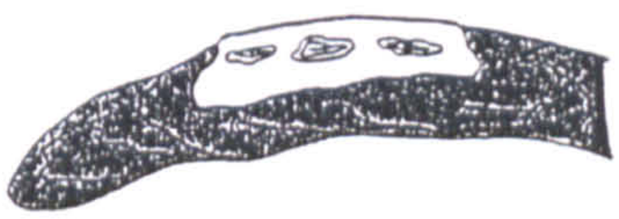
The rates of digestion recorded on the molar teeth conform to a scale of increasing amounts of digestion witnessed over the surface of the teeth. Light digestion is usually associated only with the salient angles at the tops of the teeth, and moderate (and heavier) digestion is recorded only when digestion has occurred on over half of the salient edges of the teeth. In most cases this digestion cannot occur unless the tooth has become detached from the jaw, indicating either that the digestive juices have loosened the teeth and they have fallen out (this is very often a prey species specific problem), or that the jaw has been either broken or digested.

7.4.2 Incisor digestion



light

moderate



heavy

extreme

Figure 32.Categories of incisor digestion, see table below for description, from Fernandez-Jalvo and Andrews (1992)

Digestion Category	**Description**
Light	Digestion affects the whole enamel surface showing slight to moderate pitting. In some cases digestion is concentrated at the tips of the incisors, where the enamel is totally removed, indicating digestion while the incisors are still retained in the jaws. The dentine may be slightly digested, producing a wavy outline.
Moderate	The surface of the enamel is more intensively affected, and the dentine is also modified with a wavy surface. Enamel remains along the length of the tooth, except sometimes when it is removed from the tip.
Heavy	Digestion occurs on both enamel and dentine, producing a wavy surface on the latter and reducing the enamel to small islands on the surface of the dentine. Sometimes the surface of the enamel is almost entirely eaten away, and the dentine can take on an appearance similar to the effects of weathering.
Extreme	Damage is extensive on both the enamel and the dentine, some teeth having all of the enamel removed, leaving a narrow and dentine core, while others also have much of the dentine removed so that the edges of the dentine, or of the enamel if still remaining, collapses in on itself. Where enamel remains on these teeth it is restricted to small islands separated by areas of dentine.

Table 14. Description of digestion categories for incisor teeth, from Fernandez-Jalvo and Andrews (1992)

Incisor digestion is more complex than molar digestion, as both the extent and frequency of the digestion can vary with different amounts of digestion. For light digestion, both the tips of the incisors, and in some cases the entire incisor surface can be affected. However, the extent of the digestion differs between these two areas, and between upper and lower incisors. All of the enamel may be removed from the incisor tip, leaving other areas unaffected, indicating that digestion occurred whilst the tooth was still held within the surrounding bone.

However, there is a difference in the amount of tooth protected by the jaw in the mandible compared with the maxilla. Three-quarters of the length of each incisor is protected within the jaws, however, these amounts are represented by different measurements on each tooth. Therefore, it is important to state what areas of each tooth are considered to be 'the tip' and what constitutes the rest of the surface. In the upper incisors, the tip is roughly one-fifth, to one-quarter of the tooth length. In the lower incisors, the tip is of a comparable size, but due to the greater length of the incisor, represents less of the actual length of the tooth. If digestion occurs to larger areas of the tooth than described above, it is recorded as surface digestion. This can occur either if the jaw bone is digested, and therefore no longer offers protection to the tooth below, or if the tooth becomes detached from the jaw.

In the category of light digestion, the amount of digestion recorded for the enamel surface is necessarily low, as indicated in the first section in Table 14, page 129, even if there are cases where the tips of these incisors show higher amounts of digestion.

Moderate digestion represents greater amounts of surface digestion, and also in some cases, modification of the incisor tips. In these cases, more of the dentine at the incisor tip is digested. The extent and frequency of digestion is greater than had occurred in the light digestion category. In cases where incisor digestion is heavy or extreme, digestion often occurs on most of the tooth, rather than specifically the tip, indicating digestion of the surrounding bone, or high rates of isolated teeth, as they have been loosened from the jaws. A scatterplot of isolated incisor tooth loss against incisor digestion (data from Andrews 1990) indicates a positive correlation between these two variables, as can be seen in the graph overleaf.

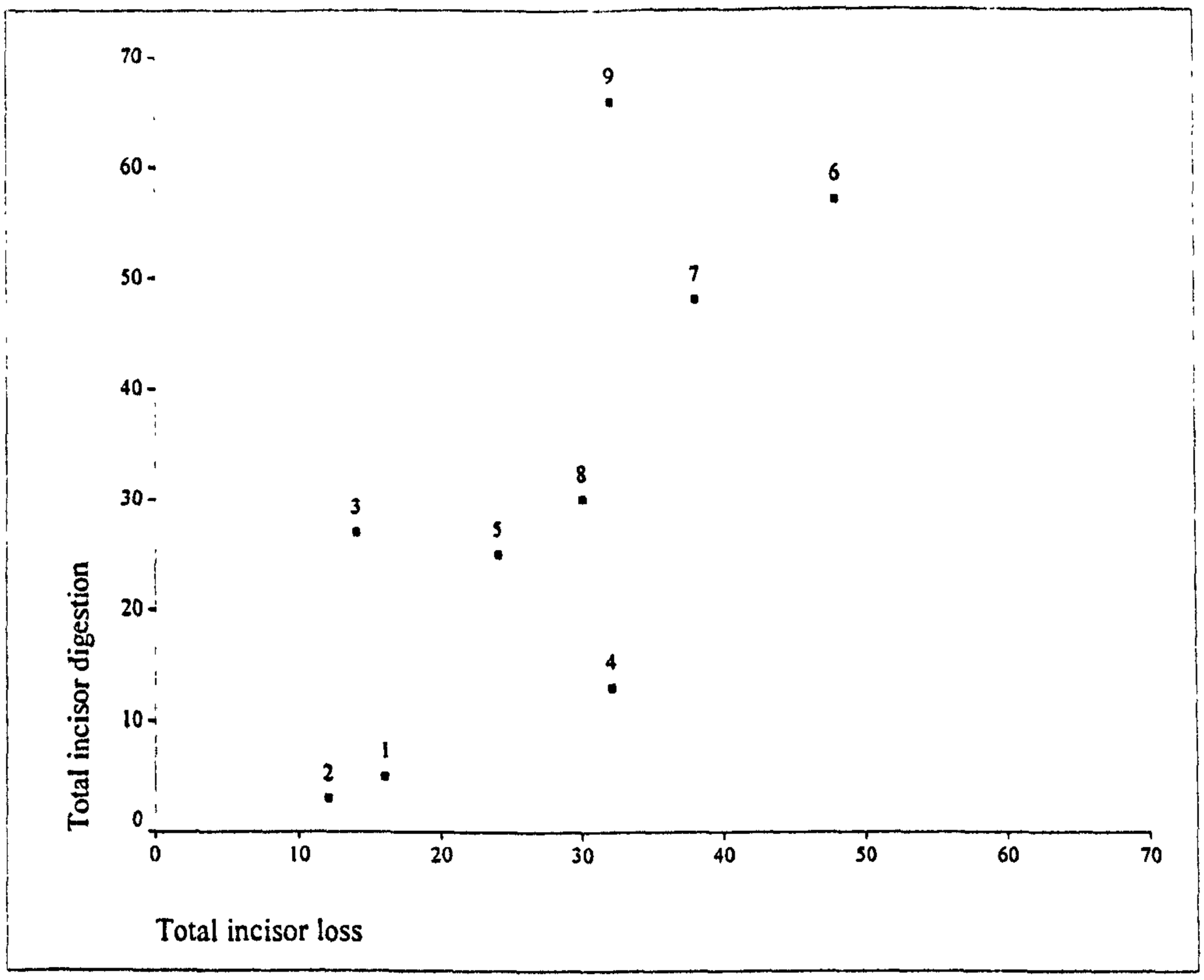


Figure 33. Scatterplot of total incisor loss against total incisor digestion, data from Andrews (1990) Legend: 1= *Tyto alba*; 2= *Nyctea scandiaca*; 3= *Asio otus*; 4= *Asio flammeus*; 5= *Bubo lacteus*; 6= *Bubo africanus*; 7=*Bubo bubo*; 8= *Strix nebulosa*; 9= *Strix aluco*; *Athene noctua* has not been included in this analysis because of the limited number of cases recorded.

These categories[71] for molar and incisor digestion are inherently arbitrary (Fernandez-Jalvo and Andrews 1992: 415), and the distinction between them is always going to be open to interpretation by different investigators. However, these categories are intended to indicate a general trend from low to high digestion. Whilst deposits may have a few teeth that fall into every category, in most cases the majority of the teeth recorded will fall clearly into only one of the four categories above, thereby indicating the likely predator origin of the deposit.

At all stages of the analysis in this study, these figures and descriptions were kept close to hand and constantly referred to, in order to ensure that digestion was recorded to the same criteria throughout the course of the analysis. Every tooth analysed was recorded on two recording sheets, specially designed for digestion recording, adapted from tables in Andrews (1990) and Fernandez-Jalvo and Andrews (1992), see Appendix table 18, page 300 and Appendix table 19, page 302.

---

[71] light, moderate, heavy and extreme.

7.5 Extra category of incisor digestion

A further category of incisor digestion was added to the four described above, as during initial analysis of incisors from the modern nest samples, a specific type of bone modification was discovered, that was not accounted for in the criteria of either Andrews (1990) or Fernandez-Jalvo and Andrews (1992). As it was an explicitly stated objective of this project, that all modification of the teeth would be recorded, a separate category was designed to record this new modification, since it was not felt to be appropriate to record it in any of the existing categories, as this would lead to the over-inflation of results. The new digestion was a very light form of digestion that could not be seen with the naked eye, and appeared as a very slight dulling of the enamel surface, often at the tips. Although no actual enamel loss could be seen, the shiny coating of the incisors was no longer visible, as is shown below

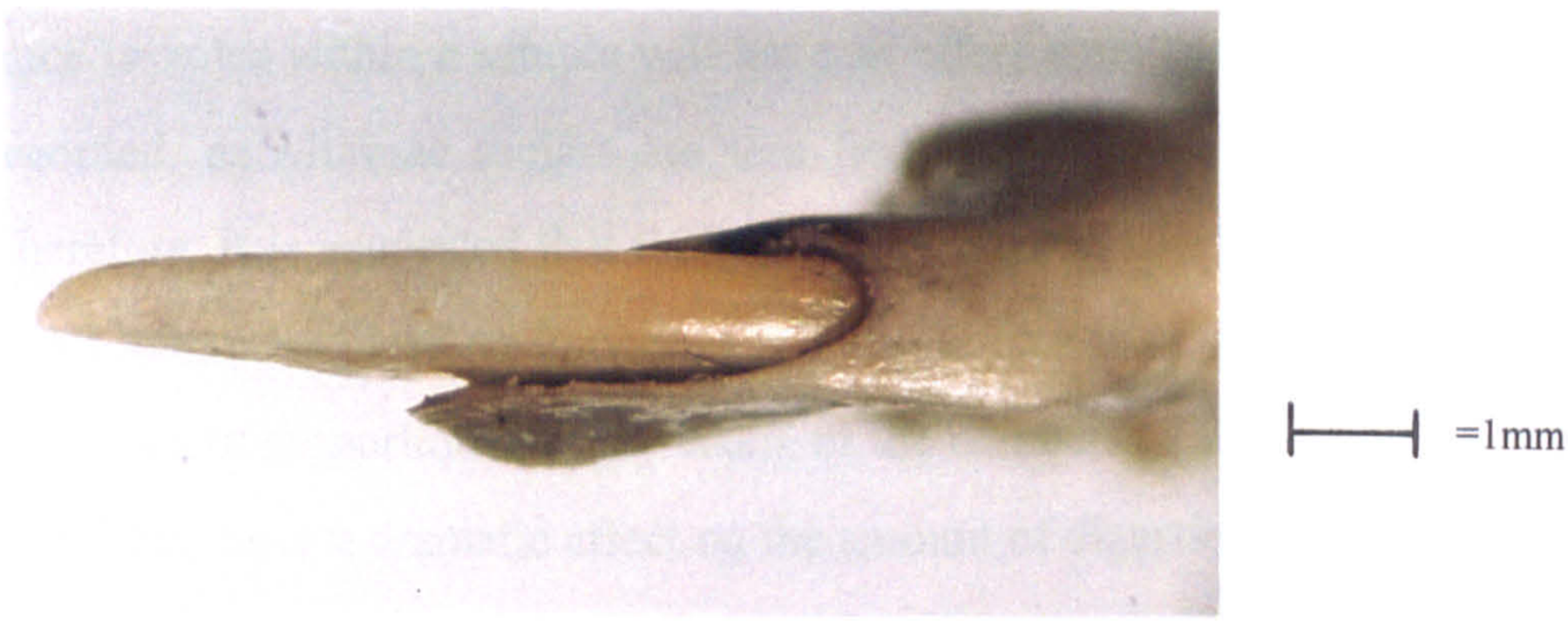


Figure 34. Example of very light digestion of incisor tip. Scale 10mm = 1mm.

It was possible that this modification was just a coating of dirt or dust, so every time this phenomenon was encountered, a dampened finger was wiped over the area of the incisor to check. No comparable category was recorded for molars. As this very light digestion was first noticed on the incisors from the modern nest deposits, it was felt that this category may give some aid in identifying barn owl nest deposits. Therefore, it was used in the analysis of both the nest material as well as the archaeological deposits.

It is clear that this is a product of direct predatory digestion rather than post-depositional diagenesis, as it was first encountered within the modern nest material, and is present in both the pellet material and that from archaeological sites.

7.6 Dealing with prey species specific digestion

One of the most important innovations used in this project was the recording of small mammal teeth to species, rather than lumping all of the teeth into the same category, as had been the case in previous analyses, see for example Andrews (1990), Fernandez-Jalvo and Andrews (1992) and Fernandez-Jalvo (1995; 1996; 1998). This problem was discussed in chapter 2 page 25, and was recognised by Andrews (1990: 65), although he made no attempt to quantify this problem.

Evidence from pellet analysis in both Britain and southern Africa indicates that it is common for the dominant prey species of a particular habitat to be captured with far greater regularity than other species, and for the proportions of the other species to rise or fall in response to the availability of the main prey species (Hanney 1963; Taylor 1994). This then has an impact upon the taphonomic analysis carried out on small mammals, especially analysis of molar digestion. For example, the proportion of mice to voles within a sample will have an effect upon the amount of molar digestion recorded, as Murinae molars are less frequently digested than Arvicolinae molars. Therefore, it is suggested that the number of specific species within an assemblage of small mammals plays an important role in the taphonomy of that deposits. Seasonal variations in proportions of prey taken, or the numbers of the most dominant prey type, could then have a dramatic affect on the amount of digestion in part of the sample; it is likely that more digestion will be recorded in a sample containing only vole species, than one containing mostly mice. Therefore all of the digestion and wherever possible breakage data, as well as the initial identification evidence, was recorded to species level. This meant that it would be possible to recognise the effect of a species bias during the analysis of the results.

Molar digestion was recorded for each prey species, and incisor digestion was recorded to species in the case of *in situ* incisors, and to a lumped category of all rodent (category 20) for isolated incisors, with the exception of *Arvicola terrestris* incisors, which were easily discernable from the other species. As has been stated earlier, insectivores were not used in this part of the analysis. A hypothetical example to illustrate this method is given in the table below, and the raw data can be found in Appendix table 20, page 303, and Appendix table 21, page 305.

Site	Hypo 1	Hypo 1	Hypo 1	Hypo 1	Hypo 1	Hypo 1	Hypo 1	Hypo 1	Hypo 1
Species code	**1**	**2**	**3**	**5**	**6**	**7**	**8**	**20**	**Total**
% Molar digestion	2%	2%	0	1%	11%	6%	8%	0	4%
% *In situ* incisor digestion	5%	7%	-	4%	22%	17%	19%	0	15%
% Isolated incisor digestion	-	-	-	-	33%	-	-	21%	24%

Table 15. Digestion data for hypothetical site 1, recorded for each species. For species codes see Table 12, page 119.

The data in the table above shows the percentage of total molar digestion, total *in situ* incisor digestion, and total isolated incisor digestion. It demonstrates that certain species are more often digested than others, and this can have the effect of increasing the digestion in the sample, on the basis of the species present and their relative abundance. If comparison is to be made with other samples that do not have the same species composition, then it is possible that biases will occur. To reduce this chance of bias, it is possible to standardise this variability.

This variability is most visible in the molar teeth, due to the markedly different physiology between the species sampled. For example, Murinae (in the example above - *Apodemus sylvaticus, Micromys minutus, Mus domesticus* and *Rattus sp.*) molar teeth are less often digested than Arvicolinae teeth (in the example above - *Microtus agrestis, Clethrionomys glareolus* and *Arvicola terrestris*). Although this species specific digestion is mainly associated with the molar teeth, the standardisation is applied to all digestion data collected in this research. One reason for this is it may even out inconsistencies associated with size, in *Arvicola terrestris* for example. The methodology for this standardisation is located in Appendix notes - section 3, page 281.

7.7 Correlation of results with other studies

As has been stated throughout this chapter, the data collected within this study will be analysed in two ways. Firstly, the data from the modern *Tyto alba* nest material will be compared with data for modern adult *Tyto alba*, to indicate to what degree nest material differs from that collected from roost sites. Secondly, the data from the small mammals sampled from archaeological sites will then be compared with the modern nest material, to look for evidence of similarity, assessing the possibility of a *Tyto alba* nest origin for these archaeological deposits.

All of these criteria are internally consistent and have been checked for any evidence of intra-observer error (see next section). Therefore, any interpretations made between the nest material and the archaeological material analysed within this study are going to be made using exactly the same criteria. However, this is not the case when comparing the results of this study to other, previous research. Firstly, a number of new methodologies have been employed within this study, for example, prey species standardisation, that would not translate to other studies. Secondly, very detailed levels of digestion have been recorded in this study, (for example, very light digestion), that would have to be ignored in comparisons with past research. Finally, due to the complexity of the analysis of molar and incisor digestion, it is possible that variations in recording techniques exist between this study and other previously published analysis, (for example Andrews 1990; Fernandez-Jalvo and Andrews 1992; Fernandez-Jalvo 1995; Fernandez-Jalvo 1996; Fernandez-Jalvo *et al.* 1998).

To test this assumption, a number of samples used by Andrews, in his initial study (published Andrews 1990) were re-analysed. The three samples came from, 1) material from two *Tyto alba* roosts (Stratton, Norfolk and Rhulen, Wales), 2) a *Tyto alba* nest (Salthouse, Norfolk, U.K.), and 3) from a collection of *Bubo bubo* pellets (Oster Malma, Sweden). As all of the criteria for measuring bone breakage are easily replicable, the analysis concentrated only on the analysis of molar and incisor digestion.

It was suggested, (Andrews, pers. comm.), that this analysis would indicate the extent to which results from digestion analyses used in this study, could be compared with results from his original analysis (Andrews 1990). If less digestion was recorded

in this study, then it would suggest that certain cases of digestion may have been overlooked. If more digestion was recorded in this study, it would suggest that digestion had been recorded at a greater detail than in previous studies.

With reference to this last point, Andrews also notes (Andrews, pers. comm.), that in his original analysis, very limited digestion may not have been recorded, as when compared to the frequency and variability of those predators with much higher rates of digestion (category 3-5), such differences appeared slight. Furthermore, in samples containing these heavier rates of digestion, very light modification may have been over-looked (Andrews, pers. comm.).

In all three samples, higher rates of digestion were recorded within this study than had been recorded by Andrews, with consistently greater differences for the incisor digestion than the molar digestion (an average of 6% compared to 18%). This indicates that digestion is being recorded at a more detailed level within this study than may have been the case in the past. It also means that only limited reference can be made between the results of this study and those of previous researchers, without this variability being recognised and accounted for. Where comparisons between data from this study are to be made with data from previous studies, such as Andrews (1990), the variability of the results of the above analysis will be clearly demonstrated.

The results of this analysis are located in Appendix notes - section 4, page 283.

7.8 Accuracy tests

7.8.1 Inter-observer error

The analysis of previously published material as outlined in the last section also provided a useful comparison as a form of inter-observer error testing. This was probably the most effective method to use for the analysis of digestion, as it is not a simple technique to master, and therefore having a colleague who is unfamiliar with the method carry out an inter-observer error study, would not be particularly conclusive.

However, an inter-observer error study was carried out as a test for the sampling procedure. An undergraduate student was employed to sort through the residue material left over from sorting one of the samples from a *Tyto alba* nest site, to ensure that all of the bones had been removed for study. A total of 2436 identifiable bones (teeth and long bones) were recovered from nest material from site ON2, during the initial sorting procedure. The residue from this sorting was the material that was re-sorted. A total of 17 bones were found, representing three species. Ten cranial items, and seven post-cranial bones were found. In only one of the species recorded, did the addition of these bones affect the MNI, raising it by one.

7.8.2 Intra-observer error

As barn owls nest only once a year, it is only possible to sample the nest material after a nest site has been occupied. As already stated, the samples were taken while the birds were still in the nest, and therefore the deposits represent material from very young birds. Unfortunately, it was not possible to time the collection of these deposits so that the owl nest sites could be analysed first. Therefore, the archaeological material was analysed first.

As has been discussed above, following analysis of the nest material, a new category of digestion (very light) was discovered and recorded. As this category of very light digestion appeared to be diagnostic of *Tyto alba* nest sites, it was felt that it would be judicious to reanalyse all of the archaeological samples to look for this category of digestion. Although this category of digestion was only recorded on the

incisors, this appeared to be an appropriate time to re-analyse all of the molar and incisor digestion in the archaeological samples, as an intra-observer error exercise. This was essential, as some of the original analysis had been carried out over a year previously.

The intra-observer error analysis was carried out at the same time as an analysis of very light incisor digestion. In only one sample were the results of the incidence of digestion found to be dramatically different. However, this difference was as a result of one of the contexts being missed in the first analysis. In all of the other samples, results were found to vary by either one or two teeth, or not at all. As the results indicated such similarity, it was not considered necessary to keep a record of them, especially since the re-analysis had taken place over four weeks, during which time, the same methodology had been used.

7.9 Methods of data analysis

Half of the analysis in this study concentrated on material recovered from *Tyto alba* nests, and this material was used as the main interpretive tool by which the archaeological deposits are compared. The analysis followed roughly that used by Andrews (1990), with results obtained and interpreted for similarity to the comparative material for four categories of analysis. These were post-cranial breakage, cranial breakage, molar digestion, and incisor digestion.

The data for the post-cranial breakage for each site was converted into percentage scores, for each of the bones used in the analysis. This is compared with the amount of breakage from the nest material, and other predator assemblages listed in Andrews (1990: 51), and reproduced in Appendix table 9, page 291. A similar procedure was used in the analysis and interpretation of the results of the cranial breakage data. A concise version of the comparative results for cranial breakage from Andrews (1990: 54-57) is reproduced in Appendix table 10, page 292.

The data for molar and incisor digestion from the archaeological sites was compared directly with the data obtained from the analysis of the comparative *Tyto*

alba nest sites used in this study[72]. As has been discussed above, digestion was recorded for a large number of variables. Individually, the results for these variables can be quite irregular, and sometimes widely different, even between the same predator species from different locations. The variables that collate these data, for example, 'total molar digestion', are more similar, and often correlate well between sites, and the same predator species.

However, some of these variables are highly inter-dependent (for example see footnote[73]) and only six of these variables actually contain unique digestion data. They are, *in situ* molar digestion, isolated molar digestion, *in situ* lower and *in situ* upper incisor digestion, and isolated lower and isolated upper incisor digestion. Other variables used in the analysis of digestion are ones that group together the results of these six variables. They are total molar digestion, total *in situ* incisor digestion, total isolated incisor digestion, total upper incisor digestion, total lower incisor digestion and total incisor digestion. All of these grouping variables can be used to investigate and analyse certain trends and patterns within the data, often providing explanations for apparent similarities or variability that may occur at a more basic level of analysis. To make comparisons of digestion between sites, the 'raw' digestion data from these categories was also standardised, to reduce the effects of prey species variability.

Digestion was compared using not only the percentage of digestion recorded but also data collected regarding the extent and frequency of this digestion. These categories indicate the location of the digestion, either at the tips, or along the entire incisor surface, as well as the amount of this digestion, recorded as very light, light, moderate, heavy or extreme. This data was also used to assist in the identification of the predator species, because, as mentioned above, digestion restricted to the incisor tips, and light in nature, indicates the presence of low amounts of digestion, commonly associated with species such as *Tyto alba*.

---

[72] Although only two *Tyto alba* nest sites were originally analysed as part of this study, material from a third nest (Salthouse, Norfolk) was also studied, for comparison of digestion recording techniques with data from Andrews (1990). Although the results of this analysis are not exactly comparable with the data recorded by Andrews (1990: 33), when compared with the other two nest sites used in this study, the results show a striking similarity. This will be further discussed in the results chapter.

[73] Categories of digestion such as 'total molar digestion', are dependant upon the results of the '*in situ* molar digestion' and the 'isolated molar digestion', and are not therefore, a unique category of digestion, but a combination of two other, previously recorded measures.

For the results and analysis of the material, Microsoft EXCEL was used as a data base, to record the results of the taphonomic and taxonomic investigations. These data, especially that recorded for the percentage of digestion, was used to produce histograms. Microsoft EXCEL was also used to calculate the prey species standardisation. The other computer program used to analyse the digestion data was SPSS. This program was used to calculate correlation (Pearson's), ANOVA analysis of variance, and principal component analysis (PCA). Scatterplots were produced in SPSS from the PCA data, as well as data recorded for total molar and incisor digestion.

8.Results

8.1 Introduction

This chapter will review the results for each of the sites analysed, starting with the modern *Tyto alba* roost and nest sites, followed by the four archaeological sites. For each site, information will be given on species present, MNI of species and site, bone breakage, molar digestion and incisor digestion.

8.2 The roost sites

Data of skeletal element count, species and MNI were not recorded for the two *Tyto alba* roost sites. Similarly, bone breakage data were not collected, as they were also already published by Andrews (1990) and are located in Appendix table 9, page 291, and Appendix table 10, page 292. However it was essential to collect data for molar and incisor digestion as different recording techniques were being used in this analysis when compared with original methodology used by Andrews (1990). As discussed in the methodology chapter, the extent of digestion as well as the frequency was recorded for the molars and incisors, and a further category of very light digestion was added for incisor digestion.

However, this category of digestion was not found to be equally prevalent across all of the sites (roosts, nests and archaeological) sampled, and during the analysis it was discovered that this variability masked the general results of incisor digestion. For example, the total incisor digestion for nest sites ON2 and TF11 was very similar when very light digestion was excluded, but differed considerably when included. As the results of molar digestion indicated a strong similarity in the rates of digestion between these two sites, it was therefore felt that it was the variability in the category of very light digestion that was affecting the results. Therefore the results of this analysis were not included within the main results section, but will be discussed in the discussion chapter. Consequently, the frequency and extent of incisor digestion discussed below, and shown in the appendix tables indicated within each section are the values without the very light incisor digestion category.

8.2.1 Stratton

8.2.1.1 Stratton – Molar digestion

Source - Appendix table 22, page 306

Molar digestion in this sample was low, and out of 923 molars recovered, only 15 showed any signs of digestion, representing only 2% of the sample. There was a slight difference between isolated and *in situ* molar digestion, with higher digestion recorded for the isolated molars (3%) compared with the *in situ* molars (1%). The majority of the digestion was light in nature, 13 molars representing 87% of all digested molars. The remaining two teeth exhibited slightly higher degrees of digestion, but comprised only 13% of all of the digested molars. Digestion affected the molar teeth of only two species of small mammal, *Microtus agrestis* and *Clethrionomys glareolus*. An example of this digestion is shown in the figure below.

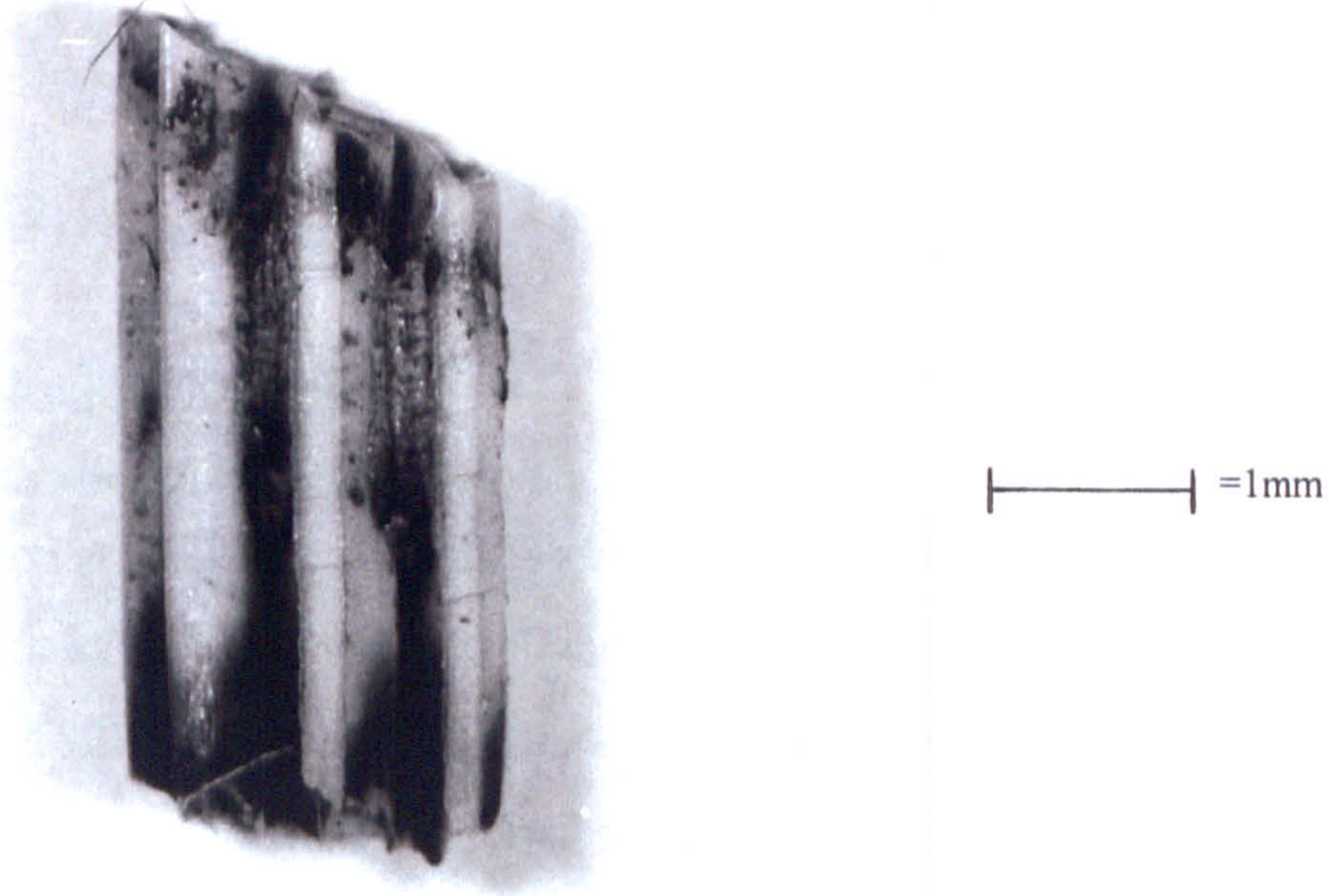


Figure 35. Molar digestion from a *Tyto alba* pellet, collected at Stratton, showing light digestion and a rounding of the occlusal surface. Scale 18mm = 1mm.

8.2.1.2 Stratton – Incisor digestion

Source - Appendix table 23, page 308.

A total of 350 incisors were recovered from this sample, of which 13% (47 incisors) were digested. As a result of the low levels of cranial breakage associated with *Tyto alba* pellets, most of the incisors were still retained within the jaws, 304 *in situ* incisors compared with 46 isolated incisors. An almost equal proportion of both lower and upper *in situ* incisors were digested, 12% and 16% respectively. The digestion was restricted solely to the incisor tip, and light in extent. As only 46 isolated incisors were recovered, the results of the percentage of digestion are less reliable because of the small sample size. Only one out of 23 lower isolated incisors was digested (exhibiting moderate digestion), and 4 out of 23 upper incisors were digested (exhibiting light digestion). Overall, 11% of the lower incisors and 16% of upper incisors were digested. Almost all of this digestion was light and restricted to the tips (98% of all digested incisors) with only 2% of the digested incisors recorded as moderately digested.

8.2.2 Rhulen

8.2.2.1 Rhulen – Molar digestion

Source - Appendix table 24, page 309

Molar digestion at Rhulen was slightly higher than at Stratton, totalling 3% of all molar teeth. However, the total number of molar teeth in this sample was lower (376 compared with 923), and it is possible that this 1% difference in digestion is a product of sample size. Of the twelve digested molars in this sample, seven were *in situ* molars, and the remaining five were isolated molars. Proportionately, the percentage of digested teeth was higher for the isolated molars (5% digested) than the *in situ* teeth (2% digested), and this is probably associated with the higher levels of stomach acidity to which the isolated teeth were subjected, compared with the more protected *in situ* molars. The extent of digestion was the same for all of the digested molars, represented by a slight rounding of the corners of the occlusal surface, recorded as light digestion.

8.2.2.2 Rhulen – Incisor digestion

Source - Appendix table 25, page 311.

A total of 105 incisors were recovered from this sample, which is slightly too few to draw any concrete conclusions. There are a number of variables where the number of incisors recorded was less than ten, and as a result of this difference in sample size, some of the percentage figures for incisor digestion were un-naturally inflated. Out of the sample of 105 incisors, 24 were digested, representing 23% of all incisors. Rates of *in situ* incisor digestion varied, with 28% of lower incisors and 18% of upper incisors digested, with a total of 22% of all *in situ* incisors digested. There were only seven isolated incisors within this sample, and as a result the percentage digestion for the isolated incisors was variable, with 0% digestion for lower incisors and 33% for upper incisors. In total, 23% of incisors were digested, representing 27% lower incisors and 20% upper incisors. Overall, the extent of digestion was mainly light (88%), with 12% of moderate digestion represented by only three incisors. The figure below shows one of these digested incisors.

Figure 36. Incisor digestion from Rhulen, showing light digestion of the tips of the incisors, penetrating to, but not affecting the dentine. Scale 10mm = 1mm.

8.2.3 Similarities and differences between the two *Tyto alba* roost sites

Source - Appendix table 26, page 312, and Appendix table 27, page 314.

The most important conclusion to draw from these two samples is that whilst published data suggest that there is no evidence of digestion from *Tyto alba* roost (pellets) samples, the results outlined above do not agree with this finding. However, the amount of molar digestion is exceedingly small, with only 27 out of 1299 molars (2%) showing any evidence of digestion. Equally importantly, the extent of this digestion was light on 93% of these digested molars. The difference between the digestion rates for these two sites was minimal, with only 1% of total molars digested, a result which stays unchanged even after standardisation to account for prey species variability. The graph showing the percentage digestion for the molars from the two sites, and the combined score for both sites is shown below.

Graph of standardised values of molar digestion for *Tyto alba* roost sites.

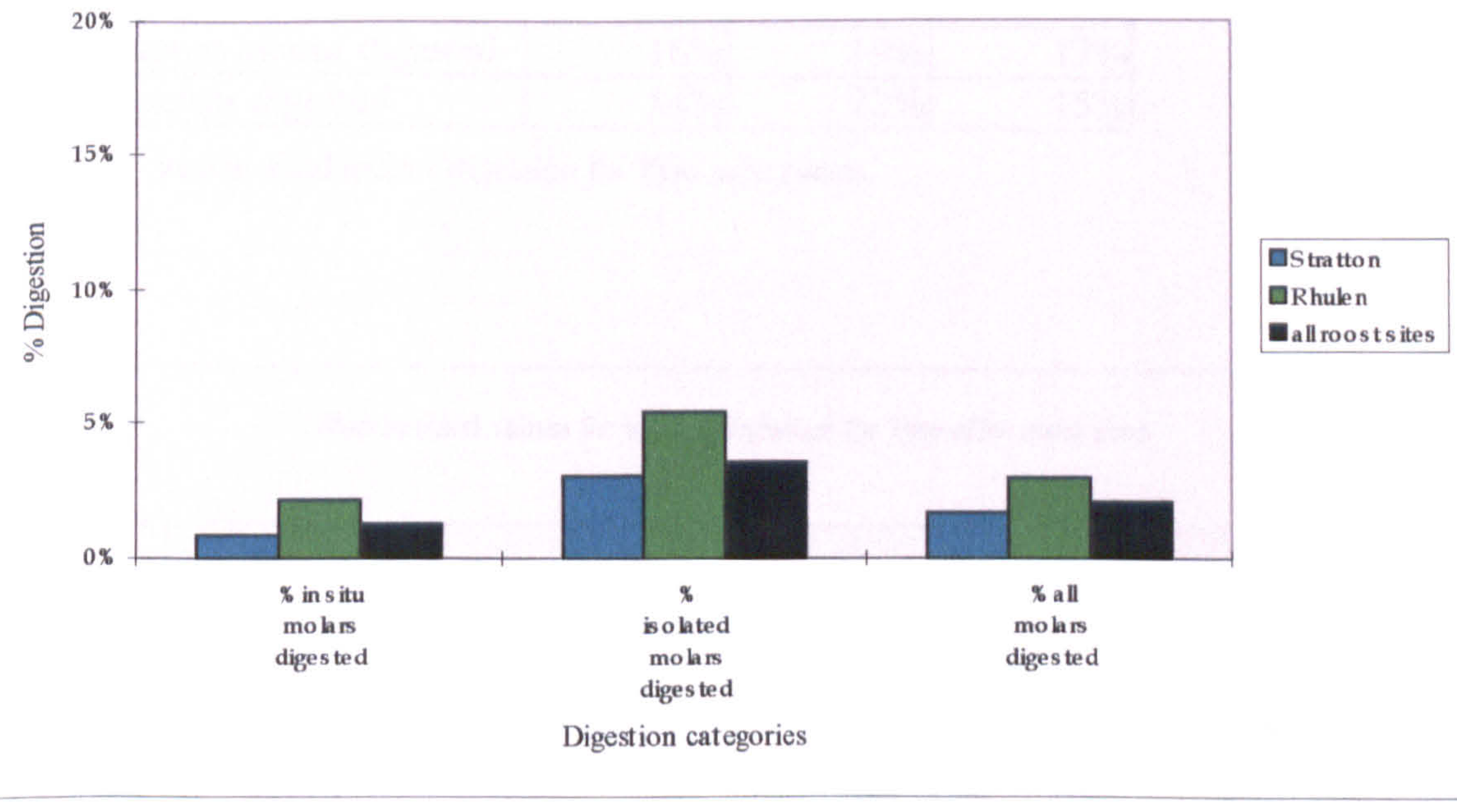


Figure 37. Graph showing standardised molar digestion rates for *Tyto alba* roost sites.

The frequency of incisor digestion was higher than that recorded for the molar teeth, with 15% of all incisors[74] showing some signs of digestion. A further example of this digestion at Rhulen in shown overleaf.

[74] 15% of total incisor digestion after prey species standardisation.

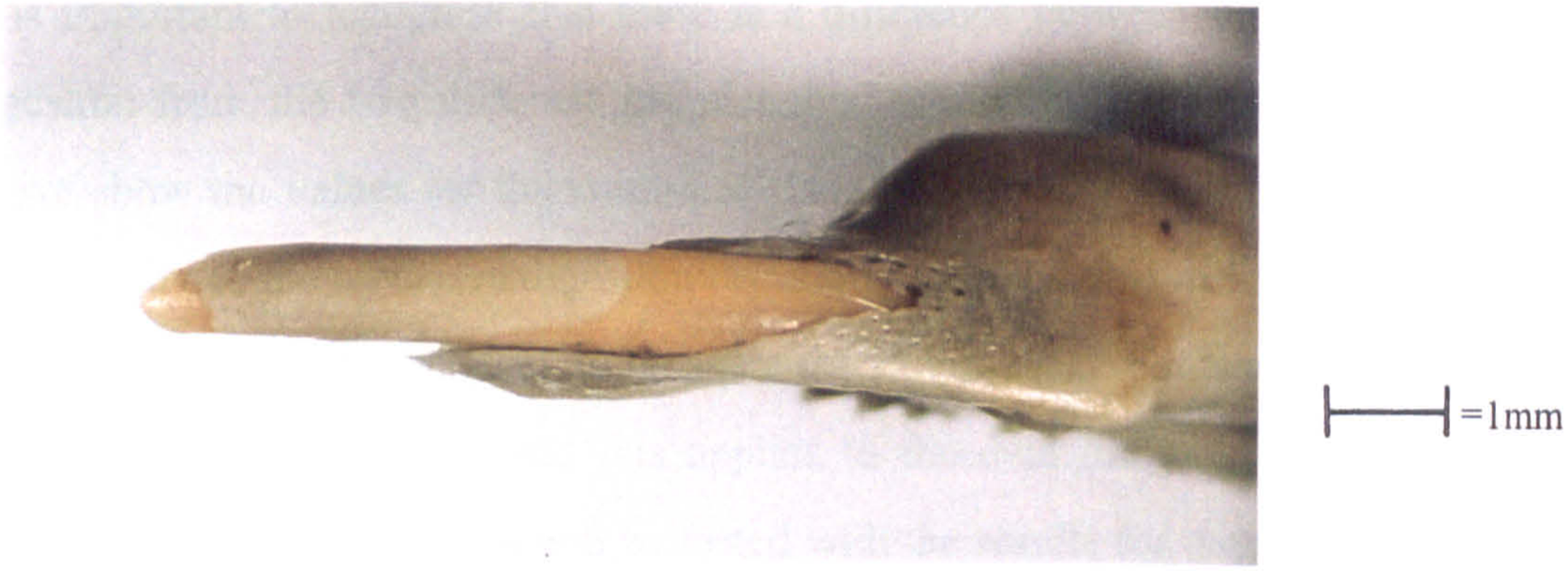


Figure 38. Digested *Microtus agrestis* incisor from Rhulen. Scale 10mm = 1mm.

Most of this digestion was light in nature (94%), and was only restricted to the incisor tips. There was also more variability in the digestion between the two sites (even after standardisation), as can be seen in Table 16 and Figure 39, below.

	Stratton	Rhulen	All roost
% total lower incisor digested	11%	25%	14%
% total upper incisor digested	16%	19%	17%
% total incisor digested	14%	22%	15%

Table 16. Standardised incisor digestion for *Tyto alba* roosts.

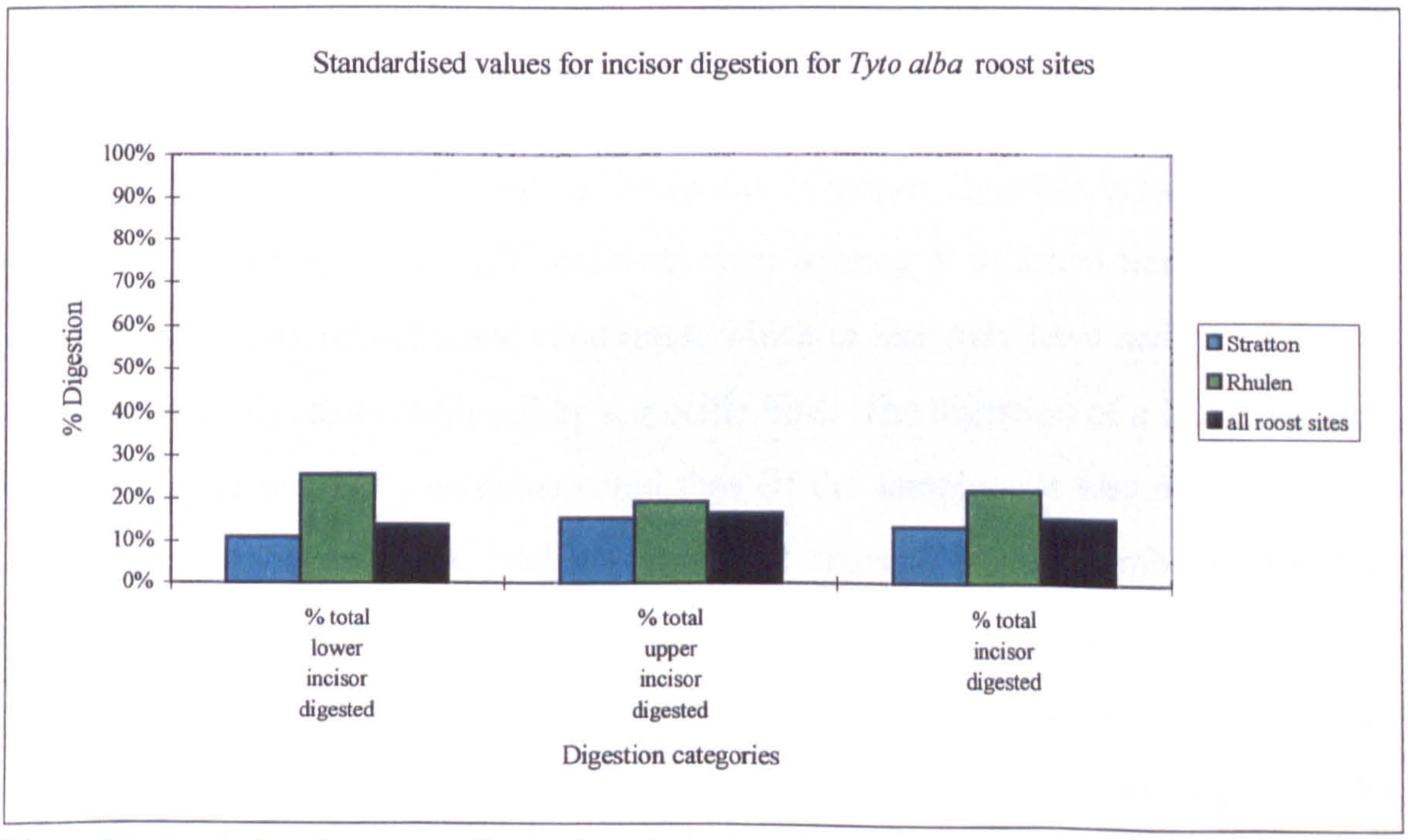


Figure 39. Graph showing standardised values for incisor digestion for *Tyto alba* roost sites.

It is important to recognise that there is a difference between the results for incisor digestion from the two different samples, and whilst the third columns in the graph above show the values for the combined data from both of these sites, indicating that the majority of the increased digestion occurred at Rhulen, this difference should not be totally dismissed. It is difficult to measure the significance of this relationship within a sample of two roost sites, and this applies to the data for molar digestion as well. However, these relationships will be tested with the results for the nest sites within the nest section.

One possible reason for the difference in the results of incisor digestion between sites may be sample size, as percentage differences are increased by samples with low numbers of bones. Interestingly, sample size can also affect the number of species represented in the samples, as the species richness of the sample increases as the sample size rises. This is aptly demonstrated by a comparison between the two *Tyto alba* roost sites, as shown in the table below.

Site	No of molars and incisors	No of species represented
Stratton	1273	6
Rhulen	481	3

Table 17. Comparison between species richness and sample size, using the example of two *Tyto alba* nest sites, Stratton and Rhulen.

A further reason for the difference in the results of incisor digestion between these two sites may be that these two different owls were hunting at different times of the year and subject to different climatic conditions, which in turn may have had an impact on the amount of digestion produced by a specific bird. The digestion of a few extra teeth due to adverse weather conditions could then (if the sample size was not sufficiently large) considerably raise the total percentage of digested teeth. Combining the data from the two sites therefore has the effect of smoothing out these seasonal or individual variations, but also hides the natural variation inherent within the two samples, which should be taken into consideration when using the data for incisor digestion for comparison with other samples.

Overall, the results of the analysis of molar digestion are marginally higher than those of Andrews (1990), whilst the results of the incisor digestion appear to be much higher. This difference reflects the variation in recording techniques, and the degree to which light amounts of digestion were recorded here. In this study, all deviation from the natural state of the teeth was recorded as digested, except where the origin of this modification was clearly post-depositional. The results of Andrews' analyses were determined more by the presence of specific criteria for specific predator groups, and digestion was not recorded in his analysis at such a detailed level as that used here.

8.3 The nest sites

8.3.1 TF11- Lincolnshire

8.3.1.1 TF11 - Skeletal element count, species and MNI

Source - Appendix table 28, page 315.

The modern nest material from TF11 contained 1207 identifiable bones (identifiable bones used here to mean molar and incisor teeth, maxillae and mandibles - or fragments containing alveolar spaces - and long bones), representing a minimum of 58 individuals, based on the most prevalent molar tooth for each species. Out of the total number of bones, 511 were post-cranial elements and 696 were cranial elements (mandible, maxilla, molars and incisors). *Apodemus sylvaticus* and *Microtus agrestis* dominated the sample, with a MNI for each species of 26% and 41% of the species total respectively. The species present at this site, the MNI[75] and the percentage of the MNI for the sample are given in Table 18, below.

Species	Species code	MNI	%MNI
Apodemus sylvaticus	1	15	26%
Micromys minutus	2	1	2%
Mus domesticus	3	1	2%
Rattus sp.	5	1	2%
Arvicola terrestris	6	2	3%
Clethrionomys glareolus	7	3	5%
Microtus agrestis	8	24	41%
Sorex araneus	16	8	14%
Sorex minutus	17	3	5%

Table 18. TF11, species present and MNI.

8.3.1.2 TF11 - Bone breakage

Source - Appendix table 29, page 316, and Appendix table 30, page 317.

Post-cranial breakage in this sample is low, with between 89% – 94% of the major bones (humerus, ulna, femur and tibia), still complete, although only 25% of scapulae were complete.

---

[75] The species data (specifically the MNI and % MNI) for the *Tyto alba* nest sites (TF11 and ON2) and the archaeological sites were collected using different criteria than those used to analyse the two roost samples (Stratton and Rhulen), for which species information was only collected during the analysis of digestion in order to save time in the analysis.

The cranial breakage recorded for this site indicates higher degrees of breakage, especially on the maxilla, where only 34% of the sample was recorded as complete. Maxillary molar loss was low (33%), indicating retention of many of the molars within the jaws, but incisor loss was much higher (69%), perhaps indicating greater breakage of the frontal area of the maxilla, where the frontal region had separated from the maxilla along the suture lines. This was more prevalent in the Murinae species than the Arvicolinae. Mandibular breakage was limited, affecting only about a third of the total number of mandibles, and only 7% of the sample was seriously damaged (missing ascending ramus or inferior border). As a result of this limited mandible breakage, restricted mainly to the back of the mandible, incisor loss was very low, only 6%. Molar loss was higher, although not extensive, affecting Murinae prey species more than Arvicolinae, and totalling 36% for the whole assemblage.

The loss of isolated molars and incisors was below 100%, indicating that more mandibles and maxillae had been recovered than isolated teeth. This also suggests that teeth are being lost either as a result of digestion by the owl, or as a result of sampling a limited amount of the total nest site. Approximately 60% of the isolated molars were present, and 80% of the incisors, indicating fairly consistent recovery within the laboratory, and suggesting that very few, or no teeth were lost as a result of sieving and sorting.

8.3.1.3 TF11 - Molar digestion

Source - Appendix table 31, page 318.

Molar digestion in this sample was low, with only 12% of all molars, (45 out of a total of 372 molars) showing signs of digestion. Of the digested teeth, 91% were lightly digested, displaying a slight rounding of the occlusal surface, with the other 9% (representing only 1% of the entire sample) moderately digested. Digestion was slightly higher for the isolated teeth than those still retained within the jaws (16% compared to 11%), and more of the moderate digestion was recorded on the isolated teeth, than the *in situ* teeth. Seven prey species were represented in this sample, but molar digestion only affected two of these species, *Microtus agrestis* and *Clethrionomys glareolus*. The molars from these two species represented approximately two-thirds of the total number of molars within the sample.

8.3.1.4 TF11 - Incisor digestion

Source - Appendix table 32, page 320.

Incisor digestion was higher in frequency than molar digestion in this sample, with 38% of the 168 incisors recorded as digested. Much of this digestion was light (73% in total) and mainly restricted to the tips of the incisors. *In situ* maxillary incisor digestion only affected the very tips of the incisor, and the majority of the *in situ* mandibular incisor digestion was also restricted to the tips. However, 7% of the *in situ* mandibular digestion was recorded as affecting the incisor surface, indicating digestion of the tooth projecting from the mandible, and in some cases, that usually held within the mandible. The digestion in these areas ranged from light (4 % of *in situ* mandibular incisors), to heavy (1% of *in situ* mandibular incisors). The frequency of digestion for lower and upper *in situ* incisors ranged between 32% for mandibular incisors, and 50% for maxillary incisors. There was no difference in the incidence of incisor digestion between different small mammal species.

The digestion of isolated incisors was again mainly light and restricted to the tips. There were only 7 isolated mandibular incisors, 29% of which were digested. Out of 39 maxillary isolated incisors, 44% were digested (76% recorded as light digestion). There were 4 isolated maxillary incisors where digestion was recorded for the surface as well as the tips, indicating perhaps greater exposure to digestive acids. Comparing the digestion rates for the lower and upper incisors, indicates a difference in digestion between these two regions with 32% of lower incisors digested, compared with 46% of upper incisors

An analysis of all of the digestion for each species indicates that, with few exceptions, the digestion was restricted to the tips and light in nature, and did not show any signs of being prey species specific. With most species, as well as the total combined result, the percentage rate of light digestion was very similar, with 73% of light digestion recorded for the total digestion for the sample.

8.3.2 ON2 – Lincolnshire

8.3.2.1 ON2 - Skeletal element count, species and MNI

Source - Appendix table 33, page 321.

A total of 2436 identifiable bones were recorded for this sample, of which 1144 are post cranial bones and 1292 are cranial bones. Eight species were represented in this sample (see Table 19 below), comprising a total MNI of 113, based on the most prevalent molar tooth, or mandible for each species. Similar to TF11, the sample was dominated by *Apodemus sylvaticus* and *Microtus agrestis,* totalling 31% and 42 % of the sample respectively.

Species	Species code	MNI	%MNI
Apodemus sylvaticus	1	35	31%
Micromys minutus	2	1	1%
Mus domesticus	3	4	4%
Rattus sp.	5	1	1%
Clethrionomys glareolus	7	4	4%
Microtus agrestis	8	48	42%
Sorex araneus	16	15	13%
Sorex minutus	17	5	4%

Table 19. ON2, species present and MNI.

8.3.2.2 ON2 - Bone breakage

Source - Appendix table 34, page 322, and Appendix table 35, page 323.

Post-cranial breakage was low in this sample, and similar to TF11, completeness was between 87% and 95% for the long bones, and 23% for the scapula.

Cranial breakage was also similar in appearance to TF11, with only 41% of maxillae surviving intact. Maxillary molar loss was low (33%) whilst incisor loss was again high (55%) with similar species specific losses occurring in the murine species (72% incisor loss for *Apodemus sylvaticus* compared with only 29% incisor loss in *Microtus agrestis*). Less than half (46%) of the total number of mandibles survived intact, however, breakage was limited to the ascending ramus, and only 7% of the total mandibles showed signs of more extensive damage. Mandibular tooth loss was similar in frequency to TF11, with 34% molar loss, and 5% incisor loss. The majority of the

molar loss occurred in the murine prey species. The percentage of isolated incisors indicated that recovery of these teeth was high, with 77% of the teeth missing from the mandibles and maxilla recovered. However, recovery of molar teeth was much lower (34%), suggesting lost teeth were subject to digestion, or not sampled from the nest sites.

8.3.2.3 ON2 – Molar digestion

Source - Appendix table 36, page 324.

Molar digestion was low in frequency (11%) and mainly light in nature. It affected the teeth of *Apodemus sylvaticus*, *Clethrionomys glareolus* and *Microtus agrestis*, although the majority of digested teeth (83%) were from *Microtus agrestis*. Frequency of digestion was similar to the results for TF11, with 10% of *in situ* molars digested and 17% of isolated molars digested, and the total percentage of digestion was 11% for all molars. Most of that digestion was light in nature (90%), with 67 out of a total of 682 molars lightly digested, 7 molars moderately digested, and 1 molar heavily digested (representing only 1% of all digested molars).

8.3.2.4 ON2 – Incisor digestion

Source - Appendix table 37, page 326.

A total of 266 incisors were analysed from this site, of which 38% were digested. Out of the *in situ* incisors, 29% of the mandibular incisors were digested and 38% of the maxillary incisors. In both cases the digestion was mainly light (a total of 63% of all *in situ* digested incisors). The *in situ* maxillary incisor digestion was mainly restricted to the tips (80%), whilst the mandibular incisor digestion was more varied, 57% at the tips and 43% on the incisor surface.

The isolated incisors were more frequently digested, with 78% of the mandibular incisors digested and 58% of the maxillary incisors digested. Of the 7 digested mandibular incisors, the majority of the digestion was moderate or heavy (86%), the remaining 14% lightly digested. An increase in the incidence of light digestion was recorded for the upper isolated incisors, although the majority of digestion was still moderate, heavy or extreme, 56% compared with 44%. The incidence of higher rates of digestion is not surprising within the isolated incisors, as

they will have been subjected to a greater amount of stomach acidity. A comparison between the lower and upper incisors indicates lower rates of digestion for the lower incisors (32%), compared with the upper incisors (47%)

When all of the digestion data was analysed, it indicated that much of the digestion at this site was restricted to the incisor tips, and light in nature, representing 43% of all digested incisors in the sample. A further 21% of teeth were more heavily digested at the tips, 15% moderate, 6% heavy. The rest of the digested teeth exhibited digestion which affected a larger portion of the tooth, 13% surface light, 10% surface moderate, 12% surface heavy and 1% surface extreme.

8.3.3 Salthouse – Norfolk

8.3.3.1 Introduction

The site of Salthouse was not part of the initial study, but was used in a comparison with analysis carried out by Andrews (1990) (see chapter/section 7.7, page 135). As only digestion data was recorded for that part of the analysis, no skeletal element count, species data or MNI is available for this sample. Similarly, bone breakage data was not collected. However, some of these results can be found in Andrews (1990: 33), discussed below.

Whilst the results of the analysis of this sample for reference between this study and that of Andrews (1990), did show a number of differences, this site was included within this section, as the results of molar and incisor digestion were similar to that of the other two nest sites TF11 and ON2.

8.3.3.2 Salthouse - Skeletal element count, and bone breakage

Source - Appendix table 38, page 327, Appendix table 39, page 328, and Appendix table 40, page 329.

The table of skeletal elements from Andrews (1990: 33) does not match with data collected within this study; however, a count of the major elements indicates that the Salthouse nest site contains a smaller number of bones than either of the other two sites, although there was a difference in the recording of molars and incisors. In this study all molars and incisors were sided and counted, whereas the data from Andrews only tallies the isolated teeth, and not those still held within the jaws.

Post-cranial bone breakage in this sample was, however, recorded using the same criteria, and this indicated that all of the four bones sampled were not usually subjected to high levels of breakage, with completeness between 78% - 96%.

Analysis of the data for cranial breakage, indicated that cranial breakage was higher, with only 51% of maxilla surviving intact. However, the breakage was not severe, as molar and incisor loss was not extensive: 17 % and 42% respectively (this high maxillary incisor loss is not unusual, as incisors detach within the frontal bone, following weaknesses in suture lines). Mandible breakage was also limited and although 57% of the mandibles were recorded as complete, only 2% had broken

inferior borders (a measure of increased breakage). This limited breakage was also suggested by the mandibular tooth loss: 11% for molars, and 2% for incisors. Retrieval of isolated incisor teeth was also relatively high in this sample (92%), although only 46% of isolated molars were recovered. However, this is not surprising in a sample from a nest, where only part of the deposit was sampled, and where some teeth may have been digested completely within the owls' stomachs.

8.3.3.3 Salthouse - Molar digestion and species

Source - Appendix table 41, page 330.

Whilst the analysis of skeletal elements and bone breakage is taken from data in Andrews (1990:33), the data for molar and incisor digestion has been collected for this study. A total of 367 molars were used in this analysis, representing five species: *Apodemus sylvaticus*, *Rattus sp.*, *Arvicola terrestris*, *Clethrionomys glareolus* and *Microtus agrestis*. Molar digestion was low within this sample, with only 13% of all molars recorded as digested, representing 48 teeth (from a total of 367). Most of this digestion was light in nature (83% of digested teeth), with 13% moderately digested (6 teeth), and 4% heavily digested (two teeth). The frequency of digestion was higher for isolated molars (29%) than for *in situ* molars (12%), but also represented different sample sizes: 24 isolated molars, compared with 343 *in situ* molars. Prey species variability in digestion was again evident, as only *Microtus agrestis* molars showed any indication of digestion.

8.3.3.4 Salthouse – Incisor digestion

Source - Appendix table 42, page 332.

A total of 142 incisors were used in this analysis, of which 30% were recorded as digested. Of the digested incisors, 86% were lightly digested, whilst the remaining 14% were recorded as more heavily digested. Most of the digestion (91%) occurred at the incisor tips. Most of the incisors were still held within the jaws, 117 *in situ* incisors, compared to 25 isolated incisors, however, digestion was higher for the isolated incisors than the *in situ* incisors, 56% (isolated) compared to 25% (*in situ*). Digestion was also higher for upper incisors than lower incisors, 45% and 21% respectively.

8.3.4 Similarities and differences between the three *Tyto alba* nest sites

8.3.4.1 Introduction

The data from the three nest sites described above constitutes the main comparative material for analogous studies with the small mammal data from the archaeological sites. Before comparison with the archaeological site data, it is necessary to compare the results of the three nest site analyses, to check for similarity of the results. Within this section, the results from the analysis of the nest material are also compared with those of the roost sites, to ensure that the expected differences are present and testable.

8.3.4.2 Skeletal element count, species and MNI

A comparison of the number of species of the nest sites (see Figure 40, below) indicates a similar prey preference, suggesting there was little prey species variability between these two sites, and as a result, few prey species-specific taphonomic biases. Species data from Salthouse could not be included in these comparisons, as although it was recorded, it was not collected using the same criteria. As well as displaying a similarity between the two nest sites, the results shown in the graph below, are also similar to those recorded for the diet of *Tyto alba* in Britain, as shown in Table 7, page 76, (data from Glue (1974: 204)). Both data sets indicate a dietary preference for *Microtus agrestis*, *Apodemus sylvaticus* and *Sorex araneus*, although the two nest sites contain higher numbers of *Apodemus sylvaticus*, and lower numbers of *Sorex araneus* than that indicated for *Tyto alba* diets by Glue (1974).

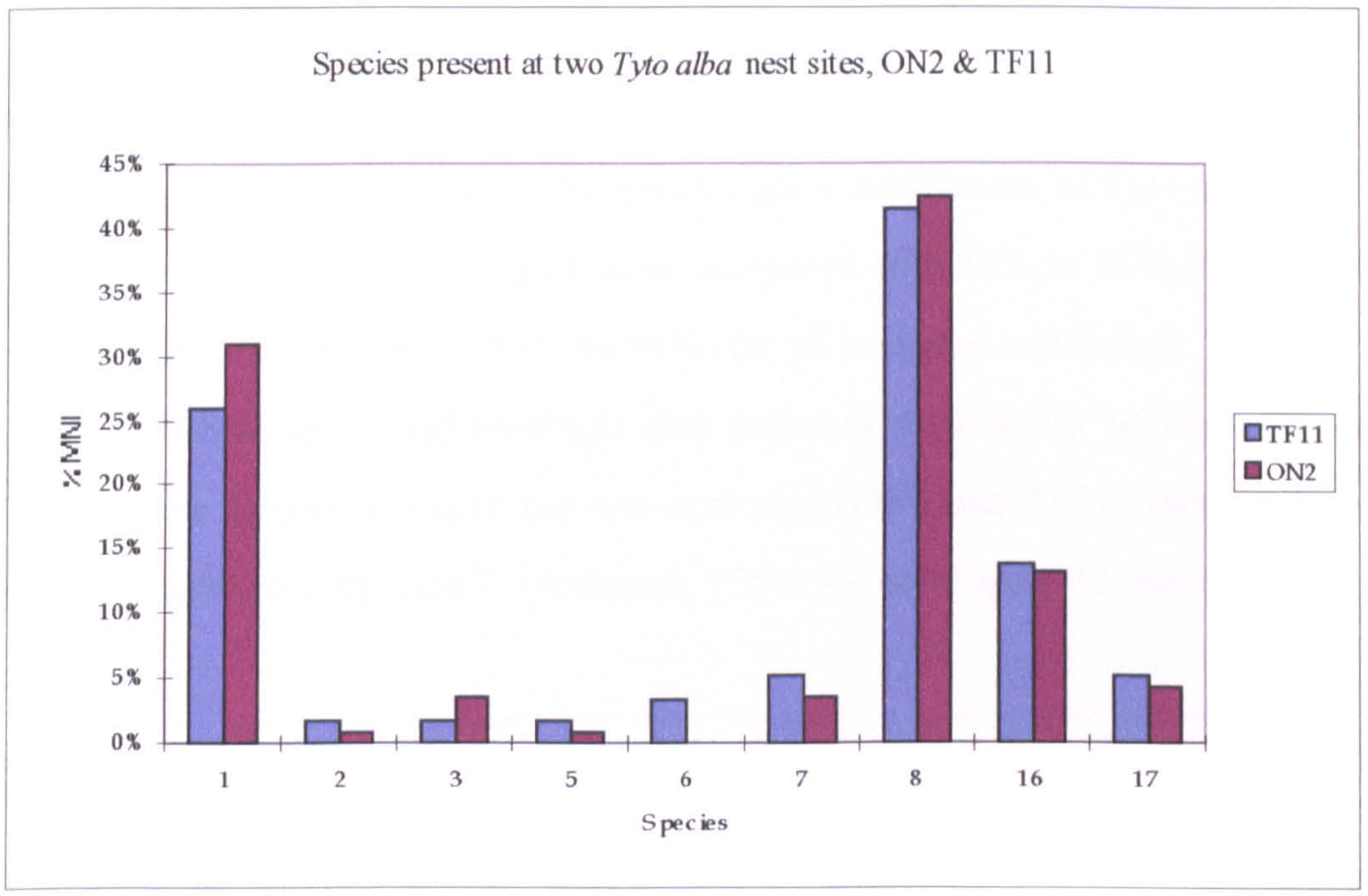


Figure 40. Percentage MNI of prey species at two *Tyto alba* nest sites, ON2 & TF11.

8.3.4.3 Bone breakage

Comparison between the data for post-cranial breakage for the three sites, indicates similar results, with the majority of bones unaffected by breakage.

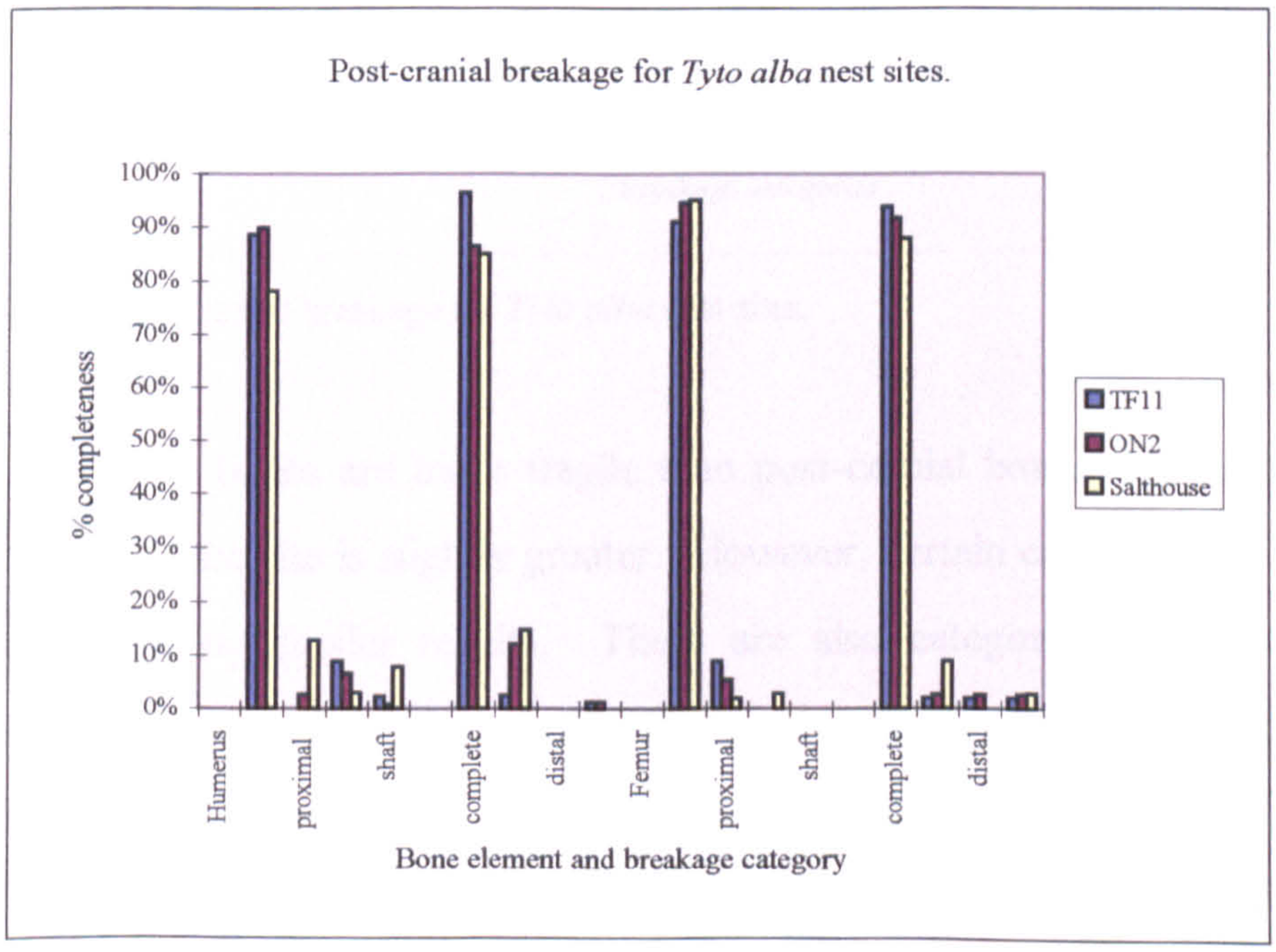


Figure 41. Post-cranial breakage for *Tyto alba* nest sites.

Compared to the results for adult *Tyto alba* (non-nest deposits) from Andrews (1990), breakage was slightly higher in the nest sites, for a graph of roost and nest breakage see Appendix figure 5, page 442. The percentage completeness of *Tyto alba* roost sample ranges from 97% to 99% completeness, compared with 78% to 96% for *Tyto alba* nests (taken as individual sites) or 86% to 94% (for all nest sites combined).

Analysis of cranial breakage also indicates a similarity between the nest sites. Comparison is made between the two nest sites (ON2 and TF11) used in this study, as well as data from Salthouse[76], (Andrews, 1990: 33, see Figure 42, below).

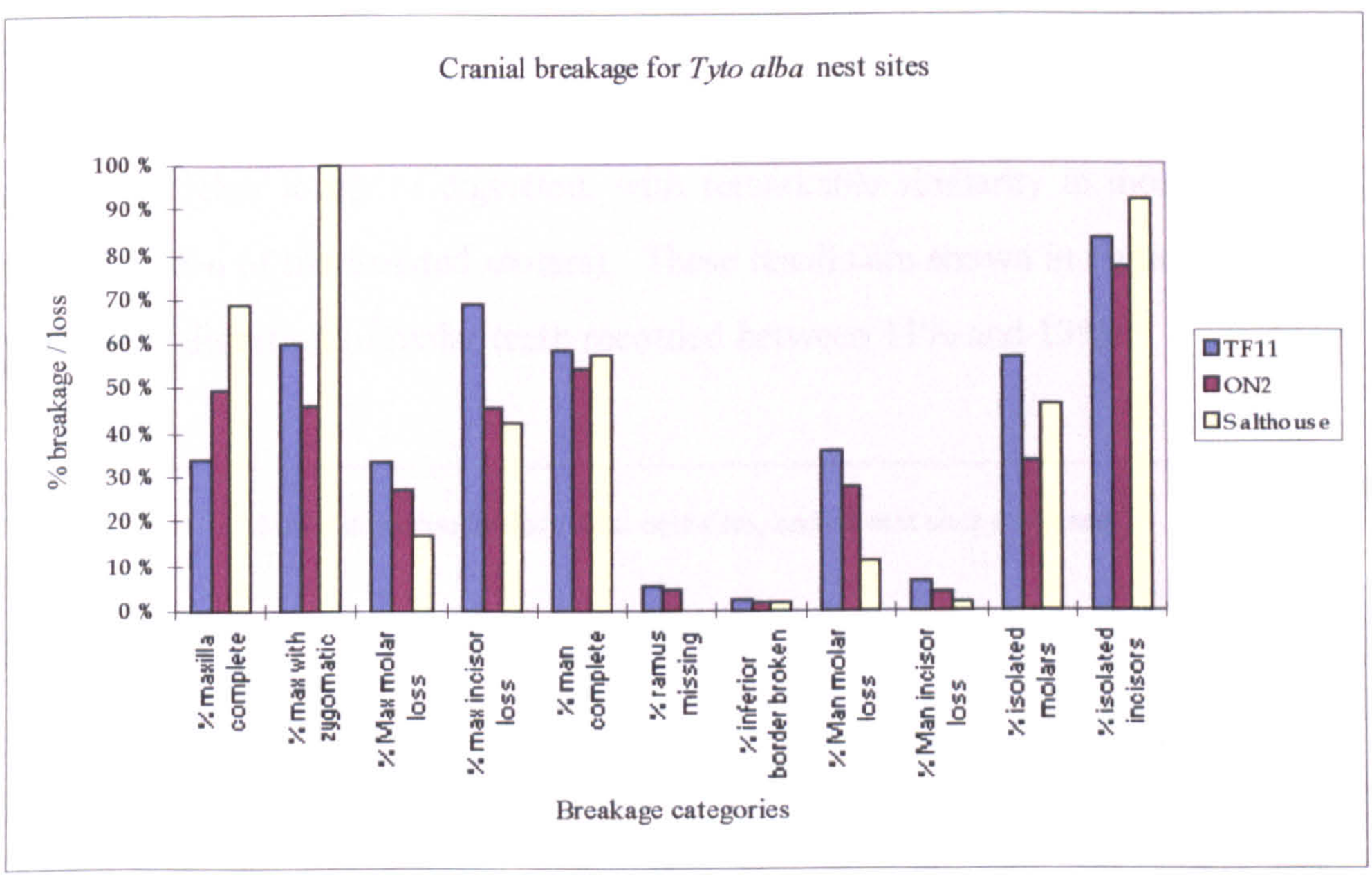


Figure 42. Cranial breakage for *Tyto alba* nest sites.

As cranial bones are more fragile than post-cranial bones, the variability between the data for each site is slightly greater. However, certain categories of breakage stand out as indicating similar results. These are also categories that are less prey species specific, and attributable to bones that are less likely to be severely broken, such as the mandible. For example, mandible completeness is similar in all of the samples, as is the amount of inferior border loss, indicating that mandible breakage is not severe within *Tyto alba* nest deposits. There is also a greater similarity between the results from TF11 and ON2, than with the material from Salthouse. A comparison with data

[76] The published Salthouse data contains no entry for % ramus missing (see Andrews 1990: 33).

for *Tyto alba* roost material (see Appendix figure 6, page 443) again indicates the variability of the results. However, a trend towards better preservation (less breakage) of bones in *Tyto alba* roost sample is visible in most of the categories.

8.3.4.4 Molar digestion

In his analysis of digestion of small mammal teeth by adult *Tyto alba*, Andrews (1990: 33) records that there is no evidence of digestion of either molars or incisors. However, analysis earlier in this chapter has shown that using the recording criteria developed in this study, there is evidence of molar and incisor digestion in *Tyto alba* pellets. For the molar teeth, the frequency of this digestion was extremely low, only 2-3% of the samples analysed. Data for digestion of molars from *Tyto alba* nest sites indicates higher levels of digestion, with remarkable similarity in most variables (with the exception of the isolated molars). These results are shown in Figure 43 below, with the rate of digestion of molar teeth recorded between 11% and 13%.

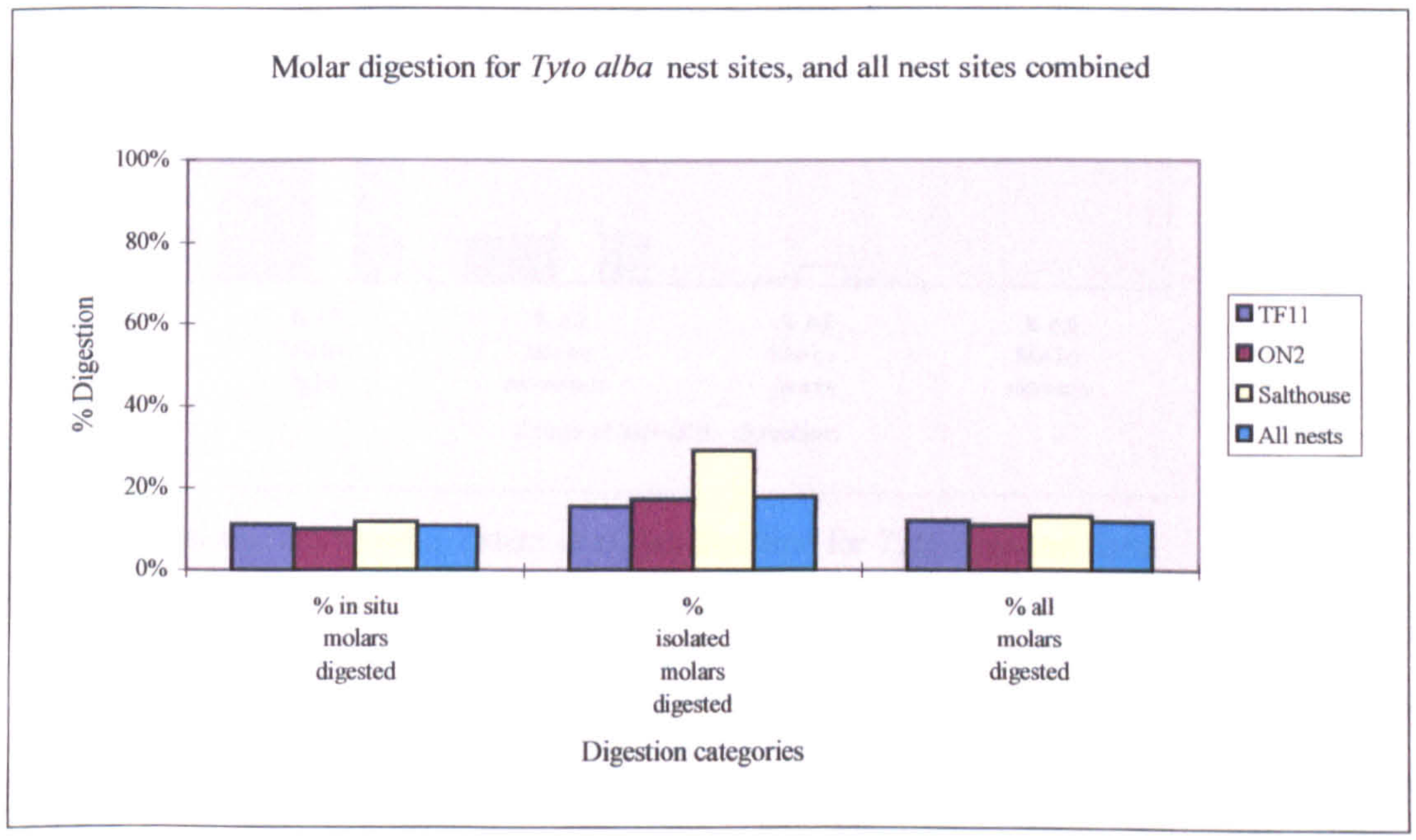


Figure 43. Molar digestion for *Tyto alba* nest sites.

The higher rates of digestion of isolated molars between the sites appears to be linked to the variability of maxilla and mandible breakage, and subsequent tooth loss and digestion in different owls. In this case, the amount of cranial breakage in the Salthouse sample (which has higher values for isolated molar digestion) is actually the

lowest of the three nest sites. Subsequently, tooth loss is also low. Because of this, there are fewer isolated teeth in the sample (only 24, compared to 90 and 93 for the other two sites), and therefore a small fluctuation in the amount of digestion can produce quite a large percentage difference. Evidence for the small size of the Salthouse isolated molar sample, and its effects on the other data, can be seen in the results of all molars digested (column 3 Figure 43), and also the value for the all the sites combined for isolated molar digestion (column 2, Figure 43)

The strength of the digestion is also similar between the three sites, with most of the digested molars recorded as lightly digested, as can be seen in Figure 44, below.

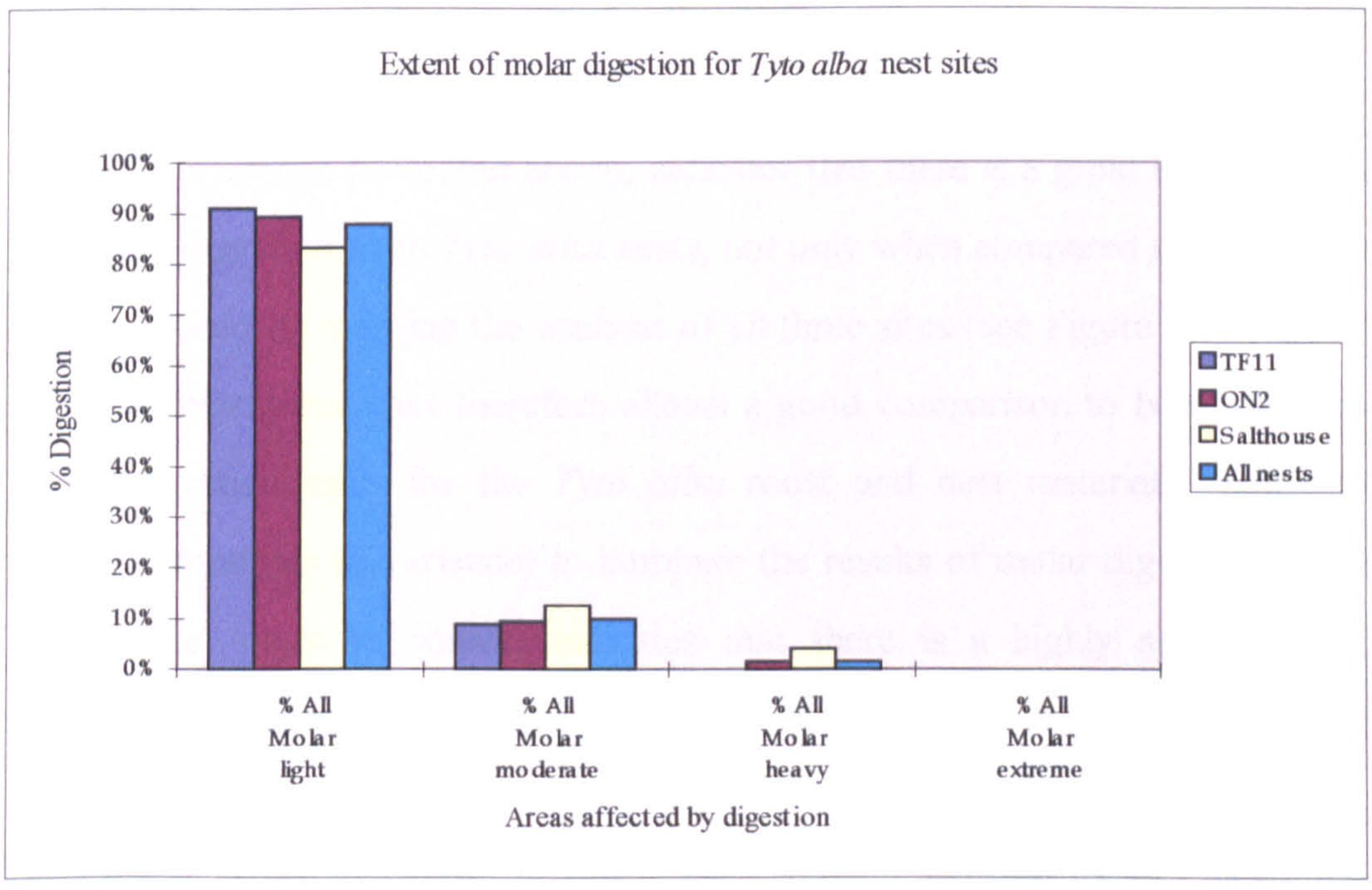


Figure 44. Histogram showing extent of molar digestion for *Tyto alba* nest sites.

Standardised values for the molar digestion from *Tyto alba* nests also indicates that there is little difference between the three sites, even when specific prey species are considered, as was suggested by the data in Figure 40, which indicated that there was little difference in the prey species recovered at each site.

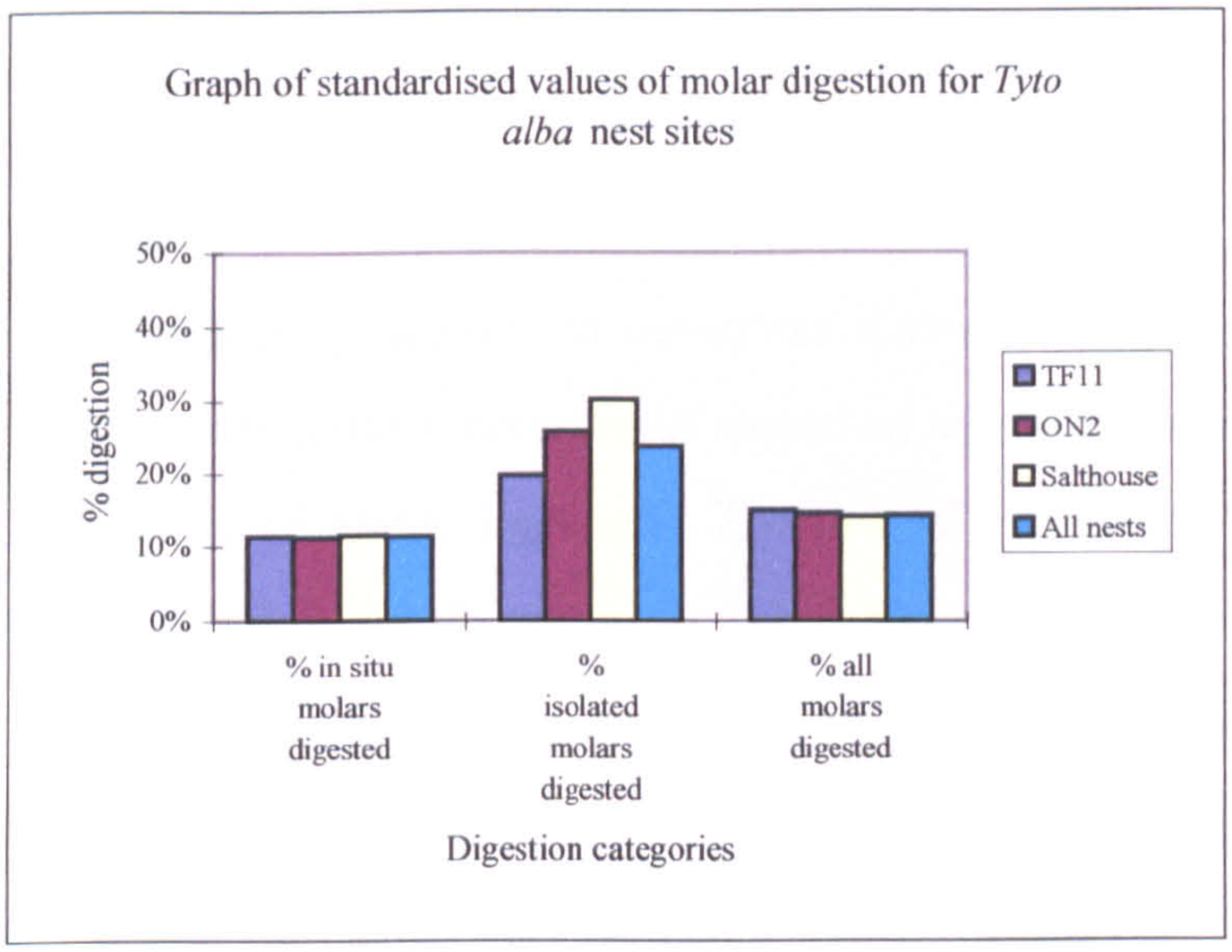


Figure 45. Standardised values of molar digestion for *Tyto alba* nest sites.

All of the evidence presented above, indicates that there is a great similarity in the data for molar digestion from *Tyto alba* nests, not only when compared to each other, but to data produced by merging the analysis of all three sites (see Figure 43). This similarity between these three sites therefore allows a good comparison to be made between the molar digestion rates for the *Tyto alba* roost and nest material. Using One-Way ANOVA (analysis of variance) to compare the results of molar digestion for these two groups (i.e. nests vs roosts) indicates that there is a highly significant difference between the frequency of molar digestion associated with roost sites, compared with nest sites. The table below gives the "F" value and significance ("P") for three variables of molar digestion; *in situ* molar digestion, isolated molar digestion and total molar digestion.

Digestion variable	**"F"**	**"P"**
In situ molar digestion	136.458	.001
Isolated molar digestion	8.874	.059
Total molar digestion	129.960	.001

Table 20. Results of One-Way ANOVA (analysis of variance) comparing molar digestion from *Tyto alba* roosts and nests.

As ANOVA compares variation both within and between the different groups, this analysis indicates that not only is there a significant difference in the frequency of molar digestion between the roost and nest sites, but that the results within each group are significantly similar to constitute discrete groupings for both the nests and the roosts. This gives a measure of statistical significance to the similarities visible in the histograms of molar digestion. The low "F" value and low significance recorded for the 'isolated molar digestion' in Table 20, indicate that this category of analysis is too highly variable to use as a measure of either within group similarity or between group difference for the nest and roost sites. This is most likely due to the fact that any difference in the number of isolated molars digested will increase the percentage of these digested teeth at an increased rate to that recorded for the in situ teeth, as there are fewer isolated molars compared with in situ molars.

An analysis of the extent of molar digestion does not indicate such clear results, as can be seen in the table below. The table only includes data for two variables, molar digestion light and molar digestion moderate, as most of the results for the other two available variables (molar digestion heavy and molar digestion extreme) contained no entries.

Digestion variable	**"F"**	**"P"**
Molar digestion light	.862	.422
Molar digestion moderate	.476	.540

Table 21. Results of One-Way ANOVA (analysis of variance) comparing the extent of molar digestion from *Tyto alba* roosts and nests.

The results of this analysis indicate that there is no significant difference between the two groups, and that the variability of the results of both the nest and roost sites indicate greater similarity between the groups than difference. This is indicated by the low "F" value and high "P" value in the table above. The result of this is that there is no significant difference in the extent of molar digestion between *Tyto alba* roost and nest samples, and therefore the only difference between these two groups is the frequency of digestion, which is statistically significant.

8.3.4.5 Incisor digestion

The histogram below (Figure 46) shows the frequency of combined incisor digestion data for *Tyto alba* roosts and nests. It indicates that there is a clear difference in the amount of digestion recorded for each of these groups.

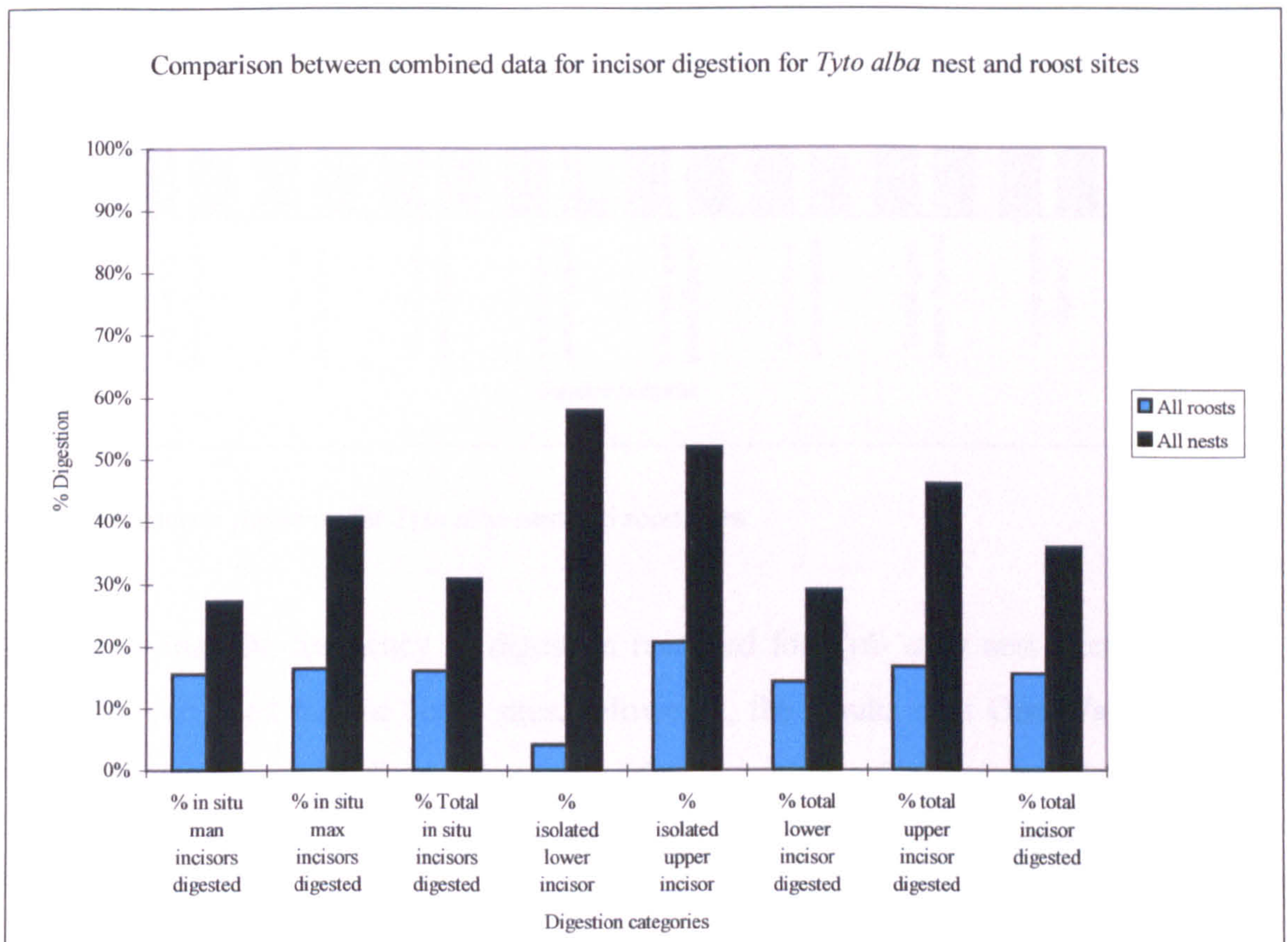


Figure 46. Histogram showing the comparison between combined incisor digestion data for *Tyto alba* roost and nest sites.

However, unlike the results for molar digestion, the data used to produce these combined groups are somewhat more variable. In most of the categories, higher frequencies of digestion were recorded for Rhulen than were recorded for Stratton (see Figure 39, page 146). Similarly, the incisor digestion recorded for ON2 and TF11, was higher than that recorded for Salthouse. This variability for the nest sites can be seen in the histogram below.

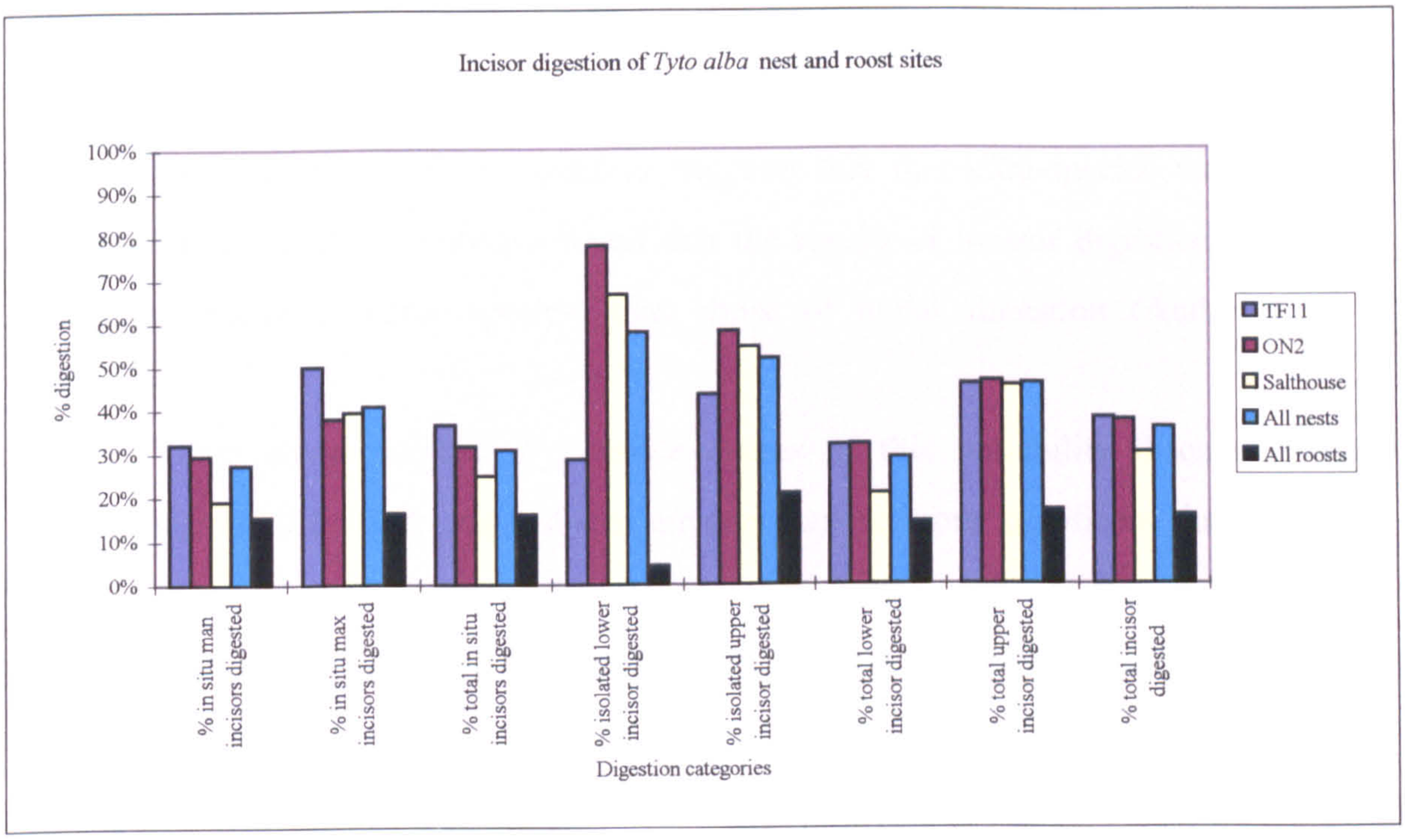


Figure 47. Incisor digestion for *Tyto alba* nest and roost sites.

It is clear that the frequency of digestion recorded for *Tyto alba* nest sites is greater than that recorded for the roost sites. However, the results of a One-Way ANOVA analysis of variance indicate that with the exception of the upper incisors, the differences within and between these two groups (roosts vs nests) are often too variable for the results of incisor digestion to be given any degree of statistical significance in comparative analysis.

Digestion variable	**"F"**	**"P"**
Lower incisor digestion	1.848	.267
Upper incisor digestion	366.971	.000
Total incisor digestion	14.367	.032

Table 22. Results of One-Way ANOVA (analysis of variance) comparing incisor digestion from *Tyto alba* roosts and nests.

The similarity of the nest sites for upper incisor digestion indicates that there is some statistically significant evidence that the nests sites represent a coherent group.

However, this similarity is not present in the other two categories of analysis, and there is a 8% difference in the frequency of total incisor digestion between TF11 and ON2 (38%) and Salthouse (30%). Andrews suggests that this intra-species variability is surprising, given that he always found that the results of incisor digestion were less variable (within predator species) than those of molar digestion (Andrews pers. comm.).

There are a number of possible causes of this variability discussed here, although it is difficult to suggest that anyone may be more significant than another. One possible cause of this variability (compared with the results of Andrews) is that the exact origin of the nest samples is not known, nor the age of the chicks at which the sample was either deposited or collected. It is difficult to evaluate critically what affect these variables may have had on the amount of incisor digestion. Also, as the nest deposit is likely to be a composite of both adult and baby owls (and over time, adult and juvenile owls), then some of the variability may be the result of the intermixing of pellet material from these differently aged individuals. However, it may also be the case that, the level of detail used in this study to differentiate between bone modification features on incisors, was recorded to such a detailed degree that some of the more basic trends recorded by Andrews have been obscured.

The data for the extent of digestion for the roost sites indicated that most of the digestion (94%) was light and restricted to the incisor tips. The results of the nest sites are more variable, with greater amounts of moderate and heavy digestion recorded, affecting the entire surface as well as just the tips. This is shown in the histogram below.

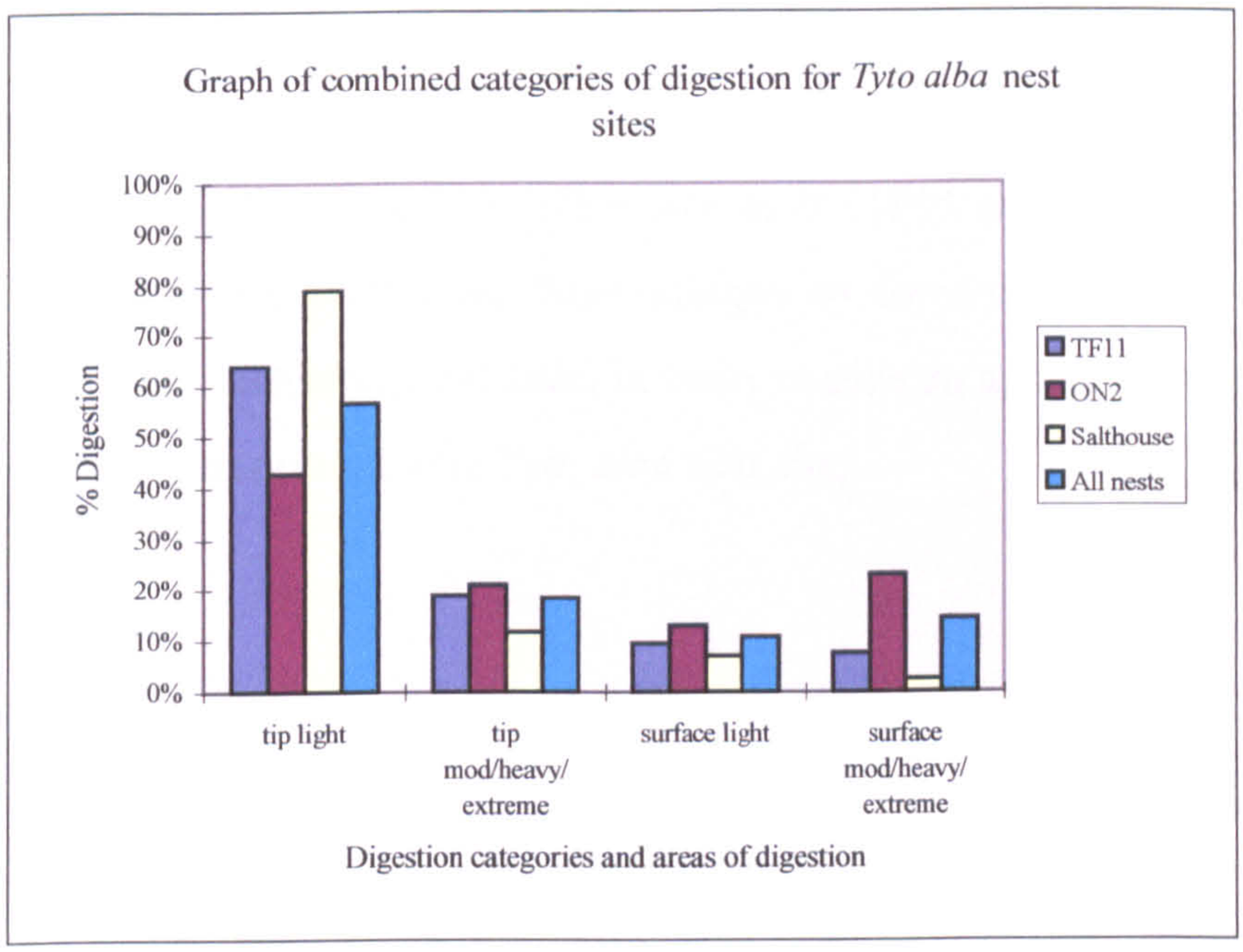


Figure 48. Graph of combined categories of the extent of incisor digestion from *Tyto alba* nest sites.

Although there appears to be similarities between these three nest sites, indicating that most of the digestion was restricted to the tips of the incisors and light in extent, there is also a clear trend indicating the most extensive digestion for ON2 with the least digestion for Salthouse. This confirms the possibility that the material from Salthouse may well represent a palimpsest of both roost and nest material, categorised by a lower frequency of digestion, restricted mainly to the incisor tips and light in nature.

As a result of the differences in the extent of digestion between these three nest sites, when these data is compared with the roost material using ANOVA, the high degree of variability within and between these two groups produces results that indicate there is no evidence of group coherency.

Digestion variable	**"F"**	**"P"**
Incisor tip light	4.914	.113
Incisor tip moderate / heavy / extreme	3.310	.166
Incisor surface light	18.021	.024
Incisor surface moderate / heavy / extreme	1.862	.266

Table 23. Results of One-Way ANOVA (analysis of variance) comparing the extent of incisor digestion from *Tyto alba* roosts and nests.

Given the fact that the results of molar digestion indicate a similarity between the three nests, it would seem inappropriate to dismiss the difference in the incisor digestion between Salthouse and the other two nests (TF11 and ON2). Therefore, the data from the three nest sites have been merged to form one data set to compare with the individual archaeological sites, in order to give an approximation of the level of incisor digestion associated with *Tyto alba* nest sites.

8.3.5 Conclusions

The purpose of comparing the data from the three nest sites was to identify how similar these results were, and whether they represented a specific set of taphonomic patterns that were different from those associated with pellets collected from *Tyto alba* roost sites. If this were possible, could these results be used to identify (by analogy), archaeological material accumulated from *Tyto alba* nesting activity ?

The summary information for bone breakage indicated that post-cranial breakage was similar for all three nest sites and generally higher than that recorded for the roost sites. This similarity was also matched by some of the variables used in the analysis of cranial breakage and tooth loss. Most of the variability in the cranial breakage data is the result of the inherent weakness of the maxilla, and the fact that this breakage can then lead to differential levels of molar and incisor tooth loss. To reduce the amount of data used in comparisons (and because of the similarity of the data), the results of the three nests sites were combined to produce one composite data set from *Tyto alba* nest bone breakage. However, cranial breakage was also higher in the nest sites than the roost sites.

Although these results would tend to indicate that bone breakage could provide a suitable taphonomic criteria for differentiating nest and roost sites, this breakage (especially the breakage of the maxilla), can be caused, and / or affected, by other post-depositional agencies, making it a less reliable indicator of the predatory origin of archaeological deposits (Fernandez-Jalvo 1996). As recognised by Andrews (1990: 64), molar and incisor digestion analysis is not hampered by these problems, as the patterns

of digestion caused by predatory birds and animals are not replicated by any post-depositional agency.

The results of the analysis of molar digestion for the three nest sites are very similar, especially after standardisation, and when the results for *in situ* and isolated molars are combined. This conclusion was also backed up by the results of the One-way ANOVA analysis of variance. The extent of molar digestion also yielded results that appear to be similar when compared between the three nest sites. However, the analysis of variance for these variables indicated that there was little difference between the results obtained for the roost and nest sites. As the data for molar digestion for the three nests was so similar, it has been combined into one data set to make comparison with the individual archaeological sites.

Similarly the results for the incisor digestion have also been combined into one data set for comparison with the individual archaeological sites. One reason for combining these sometimes variable data together for comparison with the archaeological sites, is that despite the variability indicated by the ANOVA analysis of variance, evidence provided by a scatterplot of molar and incisor digestion indicates that the data for the roost sites, and the three nest sites group fairly decisively. The variables used in this analysis were total molar digestion and total incisor digestion.

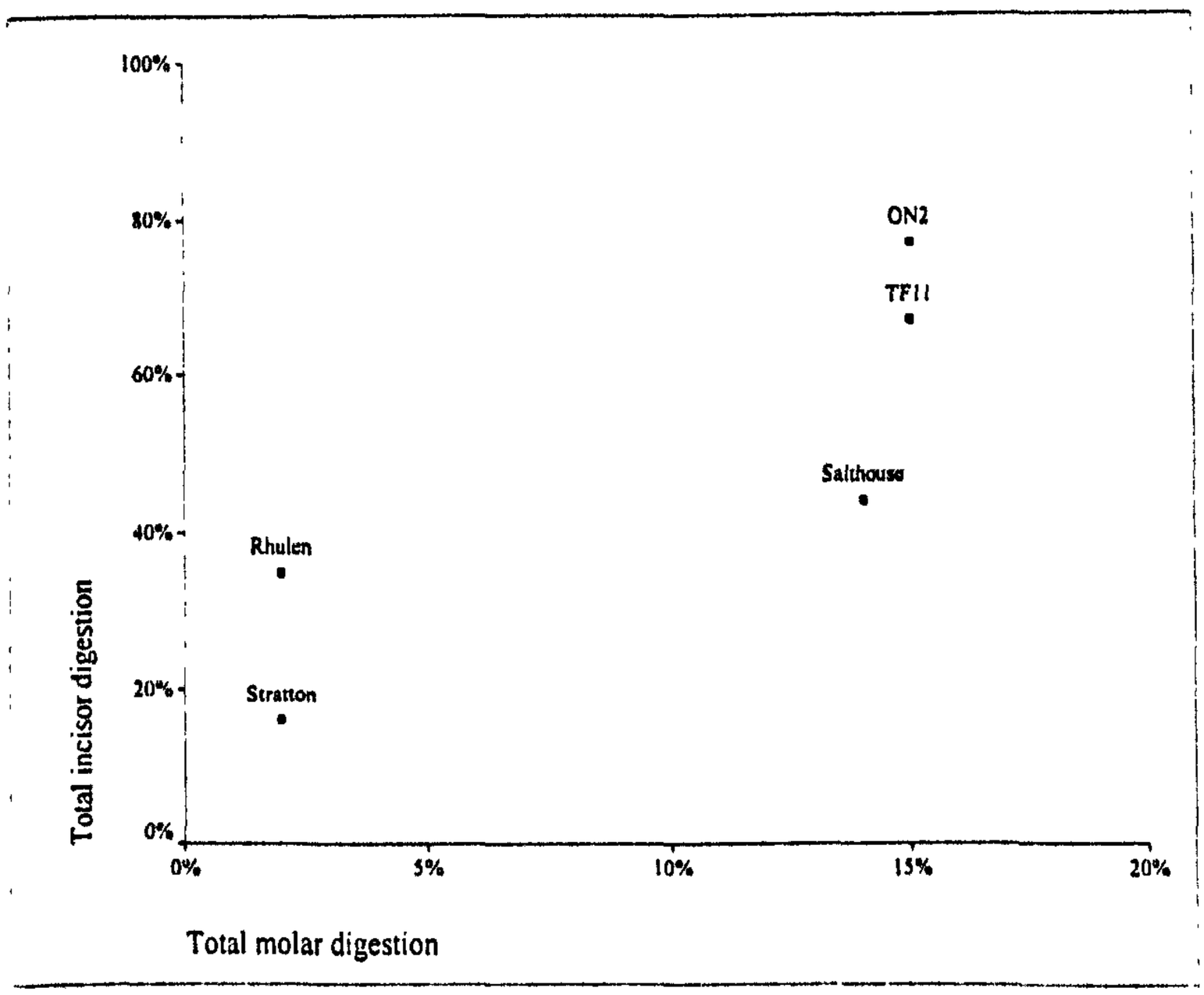


Figure 49. Scatterplot of molar and incisor digestion for *Tyto alba* roost and nest sites.

As can be seen in the diagram above, the two roost sites Rhulen and Stratton are quite closely grouped, as are the two nest sites TF11 and ON2. The third nest site Salthouse, falls outside of this second group, although at a similar distance as that which is exhibited by the two roost sites, and only on the y axis (incisor digestion). It is possible therefore that this site represents a mixture of materials common two both groups, indicating that these bones may have been accumulated by both adult and baby owls.

8.4 Archaeological sites

In the previous section, the analysis of the nest and roost sites used the difference between these two groups as a gauge of the variation in results. Having demonstrated that there is a clear difference between the *Tyto alba* roost and nest samples, data from the four individual archaeological sites will be compared with data from the *Tyto alba* nests. Further analysis will also utilise comparisons with the *Tyto alba* roost sites, as well as between the other archaeological sites. The majority of the quantitative analysis will be based around the molar and incisor digestion, but analyses of skeletal element representation and bone breakage are also important for fully understanding any small mammal assemblage.

8.4.1 The Old Vicarage, Tadcaster (OVT)

Three samples were taken from deposits at Tadcaster. They will be considered individually and also together, as some of the samples are small, and by merging them together, some of the effects of sample size may be reduced.

8.4.1.1 OVT - Skeletal element count, species and MNI

Context 11 - Source - Appendix table 43, page 333.

The sample from context 11 contained 873 identifiable bones, representing a minimum of 52 individuals. Out of the total number of bones, 427 were cranial elements, the remaining 446 bones were post-cranial bones. The sample was dominated by *Apodemus sylvaticus*, *Microtus agrestis* and *Sorex araneus*, each accounting for approximately 20-30% of the species. The other species present were *Mus domesticus*, *Arvicola terrestris*, *Clethrionomys glareolus* and *Sorex minutus*. One molar was recorded as microtine sp. (species: 12), indicating that it was not possible to identify it to species level. The species present in this context, the MNI and the percentage of the MNI for the sample are given in Table 24, below.

Species	Species code	MNI	%MNI
Apodemus sylvaticus	1	12	23%
Mus domesticus	3	4	8%
Arvicola terrestris	6	1	2%
Clethrionomys glareolus	7	4	8%
Microtus agrestis	8	15	29%
Microtus sp.	12	1	2%
Sorex araneus	16	14	27%
Sorex minutus	17	1	2%

Table 24. OVT context 11, species present and MNI.

Context 17 - Source - Appendix table 44, page 334.

Context 17 was a smaller sample, containing a total of only 181 bones, and representing a minimum of 14 individuals. Of the total number of bones, 85 were cranial elements, and 96 post cranial elements. The sample size was too small to give any significance to the range of prey species, which represented five species, *Apodemus sylvaticus*, *Clethrionomys glareolus*, *Microtus agrestis*, *Sorex araneus* and *Sorex minutus*, which are shown in Table 25, below.

Species	Species code	MNI	%MNI
Apodemus sylvaticus	1	6	43%
Clethrionomys glareolus	7	1	7%
Microtus agrestis	8	2	14%
Sorex araneus	16	3	21%
Sorex minutus	17	2	14%

Table 25. OVT context 17, species present and MNI.

Context 18 - Source - Appendix table 45, page 335.

A total of 608 bones were recorded for this sample, representing a minimum of 39 individuals. Out of the total number of bones, 293 were cranial elements, the remaining 314 post-cranial elements. *Apodemus sylvaticus*, *Microtus agrestis* and *Sorex araneus* dominated the sample, as can be seen in Table 26, below.

Species	Species code	MNI	%MNI
Apodemus sylvaticus	1	11	28%
Mus domesticus	3	2	5%
Mus/Apodemus	4	1	3%
Arvicola terrestris	6	2	5%
Clethrionomys glareolus	7	2	5%
Microtus agrestis	8	9	23%
Sorex araneus	16	12	31%

Table 26. OVT context 18, species present and MNI.

All contexts - Source - Appendix table 46, page 336.

When all of the three contexts described above were combined, they produced a total of 1629 bones, of which 723 were cranial elements and 906 were post-cranial elements. The minimum number of individuals recorded for this composite data set, was lower than the sum of that recorded for the sites individually, with only 97 individuals recorded, compared with 105 for the sum of the three contexts. This fact indicates the importance of treating these contexts separately.

Species	Species code	MNI	%MNI
Apodemus sylvaticus	1	29	30%
Mus domesticus	3	6	6%
Mus/Apodemus	4	1	1%
Arvicola terrestris	6	2	2%
Clethrionomys glareolus	7	3	3%
Microtus agrestis	8	24	25%
Microtus/Clethrionomys	12	1	1%
Sorex araneus	16	29	30%
Sorex minutus	17	2	2%

Table 27. OVT all contexts, species present and MNI.

The species present and their percentage presence was similar to those recorded for *Tyto alba* (Glue 1974), with the sample dominated by *Apodemus sylvaticus*, *Microtus agrestis* and *Sorex araneus*, although the percentage presence of *Microtus agrestis* was slightly lower than usual.

8.4.1.2 OVT - Bone breakage

Context 11 - Source - post-cranial breakage - Appendix table 47, page 337; cranial breakage – Appendix table 51, page 341.

Post-cranial breakage in this sample was low, with between 88% and 98% of bones recovered complete. These results are similar to those of *Tyto alba* nest material.

Cranial breakage was higher, with only 23% of maxilla and 35% of mandibles complete. The maxilla sustained greater levels of damage (probably due to its inherent weakness), and only 22 out of 80 maxillae still retained the zygomatic (28% of the sample). Mandible breakage was moderate, 22% of all mandibles missing their ascending ramus. This indicates that mandible breakage results are slightly higher than those of *Tyto alba* nest material, although there is a similarity in the results of inferior border breakage, affecting only 3% of the mandibles.

Context 17 - Source – post-cranial breakage - Appendix table 48, page 338; cranial breakage - Appendix table 52, page 342.

Post-cranial breakage in this sample was also low, with the percentage of completeness ranging from 70% - 94%. Some of this variability was the result of the small sample size exaggerating the percentage scores.

Cranial breakage in this sample was moderate, with 33% of complete maxilla and 67% of maxilla with zygomatic, indicating that two-thirds of the damage was only slight. Mandible breakage was also moderately low, and although only 13% of all mandibles were complete, only 20 % (three mandibles) were missing their ascending ramus. Three mandibles also had broken inferior borders, again representing 20% of the sample. Tooth loss was higher in this sample than context 11, averaging between 50% to 70%, although mandible tooth loss was only 7% (one tooth). With such a small sample it is difficult to compare breakage with data from *Tyto alba* nest sites.

Context 18 - Source – post-cranial breakage - Appendix table 49, page 339; cranial breakage - Appendix table 53, page 343.

Post-cranial breakage in this sample was higher than the other two contexts, and also displayed a pattern suggesting that hind-limbs were broken with greater frequency than fore-limbs. The results are displayed in Table 28, below.

Long bone	% completeness
Humerus	90%
Ulna	93%
Femur	76%
Tibia	54%

Table 28. OVT context 18, post-cranial breakage.

Cranial breakage in this sample was high, with only 7% of maxilla complete, and only 19% with zygomatic. Mandible breakage was also quite high, with only 26% of mandibles complete, and 40% missing the ascending ramus. Tooth loss was also high, between 50% and 70%, for maxilla molar and incisor loss, and mandible molar loss. In the other two contexts, as well as *Tyto alba* nest material, mandibular incisor loss was low (under 10%), but in this sample, it was 33%. Overall this sample exhibited much higher breakage than has so far been quantified in the results section, and this increased breakage was also confirmed by the results of the recovery of isolated incisors. In *Tyto alba* nest material fewer incisors were recovered than mandibles and maxillae, indicating that tooth loss and subsequent tooth destruction was greater than the destruction of the skull. In these cases, a percentage score of less than 100% was recorded. A result of over 100% (as recorded in this context) indicated that due to damage to the cranial bones (mandible or maxilla), more isolated incisors had been recovered, than jaws to fit them into.

All contexts - Source – post-cranial breakage - Appendix table 50, page 340; cranial breakage - Appendix table 54, page 344.

The results for all three contexts have been merged to form one composite data set for OVT. The data for all of the contexts and the composite data set (OVT ALL) are shown below (Figure 50). Plotting all of the contexts together has eliminated some of the variability associated with small sample size, but still indicates higher levels of breakage of the hind-limb bones; 87% completeness for the femur and 76% completeness for the tibia, compared with 91% completeness for the humerus and 93% completeness for the ulna. Overall, there appears to be slightly more breakage

associated with context 18 than context 11[77], which may well be caused by compression and compaction of a stratigraphically lower deposit, which also contained a high frequency of large angular rock clasts.

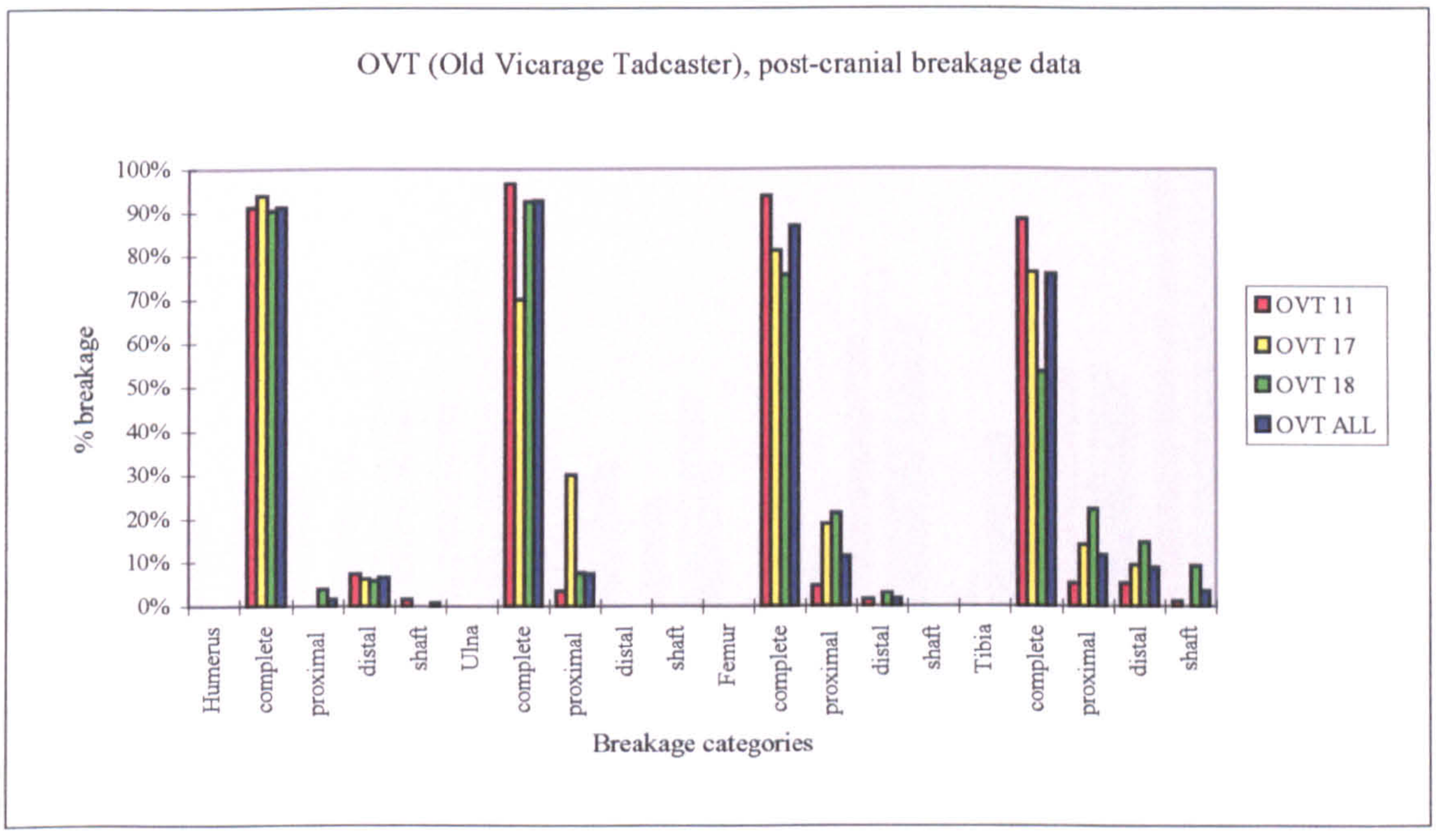


Figure 50. OVT all contexts, post-cranial breakage.

More variability was recorded in the cranial breakage categories than the post-cranial categories, due to both the inherent weakness of the cranial bones, and the small sample size of some of the contexts. Treating all of the data as one sample indicated that breakage was high, with only 19% of the maxilla surviving intact, and only 27% maintaining the zygomatic. Mandible completeness was also low (29%), although only 28% of the mandibles were missing the ascending ramus and only 12 % had broken inferior borders. Maxillary tooth loss was moderate, 41% molar loss and 48% incisor loss, and molar loss was also moderately high for the mandible (54%), although incisor loss was only 12%. An analysis of isolated teeth indicated that only half of the molars lost were recovered, but that more incisors were recovered than maxillae or mandibles, attesting to relatively high levels of cranial breakage. The results for the composite data (OVT ALL), as well as the three contexts (OVT 11, OVT 17 & OVT 18) are shown below.

[77] Context 17 contains too few bones on which to base concrete conclusions.

As was the case with the post-cranial breakage, high frequencies of damage were usually associated with the stratigraphically lower contexts (17 & 18).

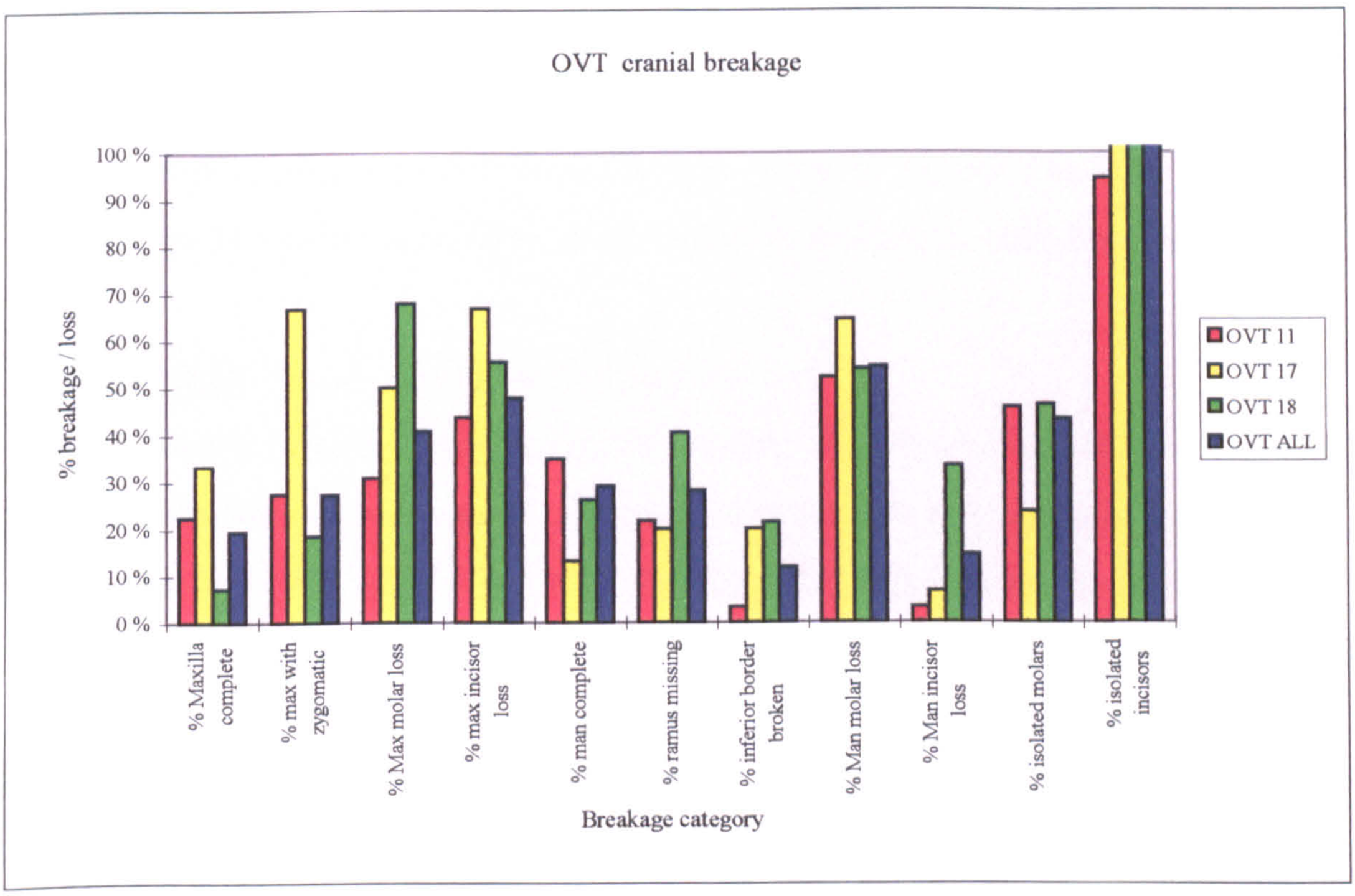


Figure 51. OVT all contexts, cranial breakage.

8.4.1.3 OVT - Molar digestion

Context 11 - Source - Appendix table 55, page 345.

A total of 230 molars were analysed from this sample, of which 8% were digested. Lower levels of digestion were recorded for *in situ* molars (4%) than isolated molars (16%). Of the 19 molars that were digested in this context, 12 were recorded as lightly digested, and only one molar was moderately digested - less than 1% of the total sample. In general, digestion was light in this sample, and low in frequency, with a slightly higher percentage of light digestion than was recorded for *Tyto alba* nest sites, (95% light digestion compared with 88%)

Context 17 - Source - Appendix table 56, page 346.

This sample was the smallest of the three contexts and contained only 37 molar teeth, none of which showed any sign of digestion. Over two-thirds of these teeth were *Apodemus sylvaticus*, which are less likely to be affected by low levels of digestion. One can conclude either that this sample was too small to contain enough teeth to sample those that may have been digested, or that it was not *Tyto alba* nest material. Analysis of incisor digestion from this context should help to elucidate this situation.

Context 18 - Source - Appendix table 57, page 347.

This sample contained more molars than context 17, and out of a total of 126 teeth, 12% were digested, representing 8% of *in situ* molars and 16% of isolated molars. Most of the digestion was light (93% of the digested teeth), although one murine tooth was so extremely digested that it was not possible to identify it to species. However, this tooth represented less than 1% of the total number of teeth, and was a rare occurrence in a deposit where digestion was low in frequency and light in nature, the results very similar to *Tyto alba* nest data.

All contexts - Source - Appendix table 58, page 348.

There was some variability in the results from these three contexts, much of it caused by small sample size, and some caused by prey species specific biases. *In situ* digestion ranged between 0% and 8%, with the total for the combined contexts only 5%. There are slightly higher values for isolated molar digestion, ranging between 0% and 16%, with a combined value of 15%. Combining these two data sets, there was an overall molar digestion rate at Tadcaster of 9%. These values are similar to those of *Tyto alba* nest sites, as shown below.

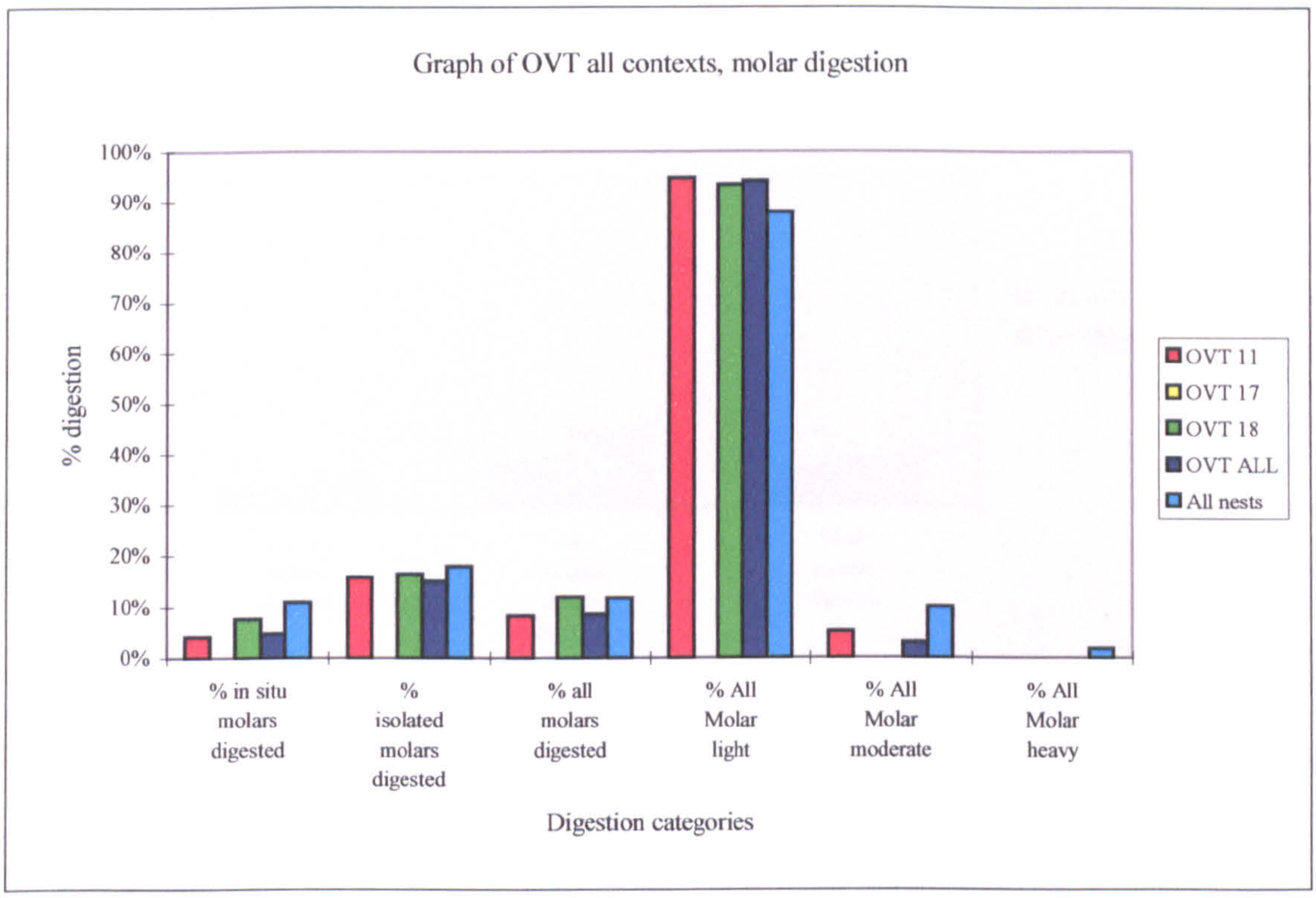


Figure 52. OVT all contexts, and *Tyto alba* nest sites, molar digestion.

The extent of digestion was also low, with most of the digested molars only lightly digested, between 93% and 95% of digested teeth.

The frequency of digestion was slightly lower than *Tyto alba* nest material, and some of that difference was related to the number of prey species. Therefore the data for all three contexts at Tadcaster were merged and standardised. Compared with the standardised values for *Tyto alba* nest sites, the overall molar digestion rate at Tadcaster was 12% compared to 14%.

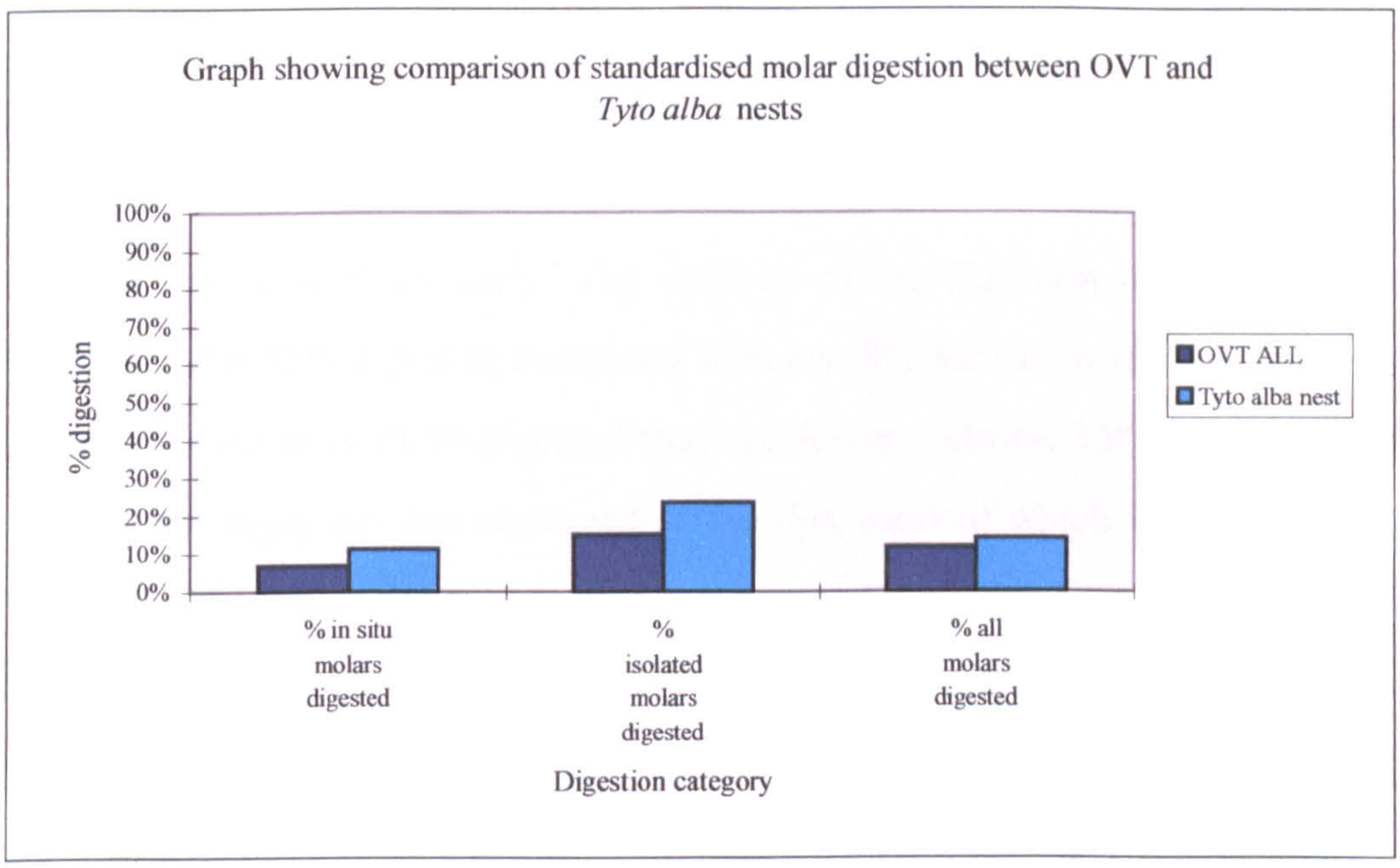


Figure 53. Standardised molar digestion between OVT and *Tyto alba* nests.

8.4.1.4 OVT - Incisor digestion

Context 11 - Source - Appendix table 59, page 350.

A total of 106 incisors were recovered from this context, of which 28 incisors were digested, representing 26% of the incisors. There were more *in situ* incisors than isolated incisors, 69 compared with 37. The rate of digestion was however higher for the isolated teeth, 35% for isolated incisors, 22% for *in situ* incisors. Digestion was also higher for the upper incisors compared with the lower incisors. Out of the 28 digested incisors, 82% were lightly digested at the tips, with a further 14% lightly digested along the incisor surface. One tooth (4%) exhibited moderate digestion on the incisor surface.

Context 17 - Source - Appendix table 60, page 352.

Only 21 incisors were recovered from this context, less than the number digested in context 11. Out of these 21 incisors, 5 were digested, (24%). The proportion of *in situ* to isolated incisors was roughly even, with 9 *in situ* incisors and 12 isolated incisors. The rate of digestion was higher for the isolated incisors, and most of this digestion was attributable to the upper (maxillary) incisors. All of the digestion was light in extent, and mainly restricted to the incisor tips.

Context 18 - Source - Appendix table 61, page 354.

A total of 73 incisors were recorded for this context, of which 20 or 27% were digested. *In situ* incisors made up about a third of the incisors (26) with the remaining 47 recorded as isolated incisors. The majority of the digestion occurred on the isolated incisors, with 38% digested compared with just 8% for the *in situ* incisors. Overall, the upper incisors were more digested than the lower incisors, 35% and 21% respectively. 90% of the digestion was restricted to the tips, most of which was light in extent (75% tip light, 15% tip moderate.

All contexts - Source - Appendix table 62, page 356.

An analysis of the incisor digestion data for Tadcaster indicated that there was a level of variability between the three contexts for the *in situ* and isolated incisor digestion categories, similar to that discussed earlier for *Tyto alba* nest data. One of the main problems associated with this site was the small sample size of some of the contexts, with some variables containing less than ten teeth (for a histogram depicting this variability see Appendix figure 7, page 444).

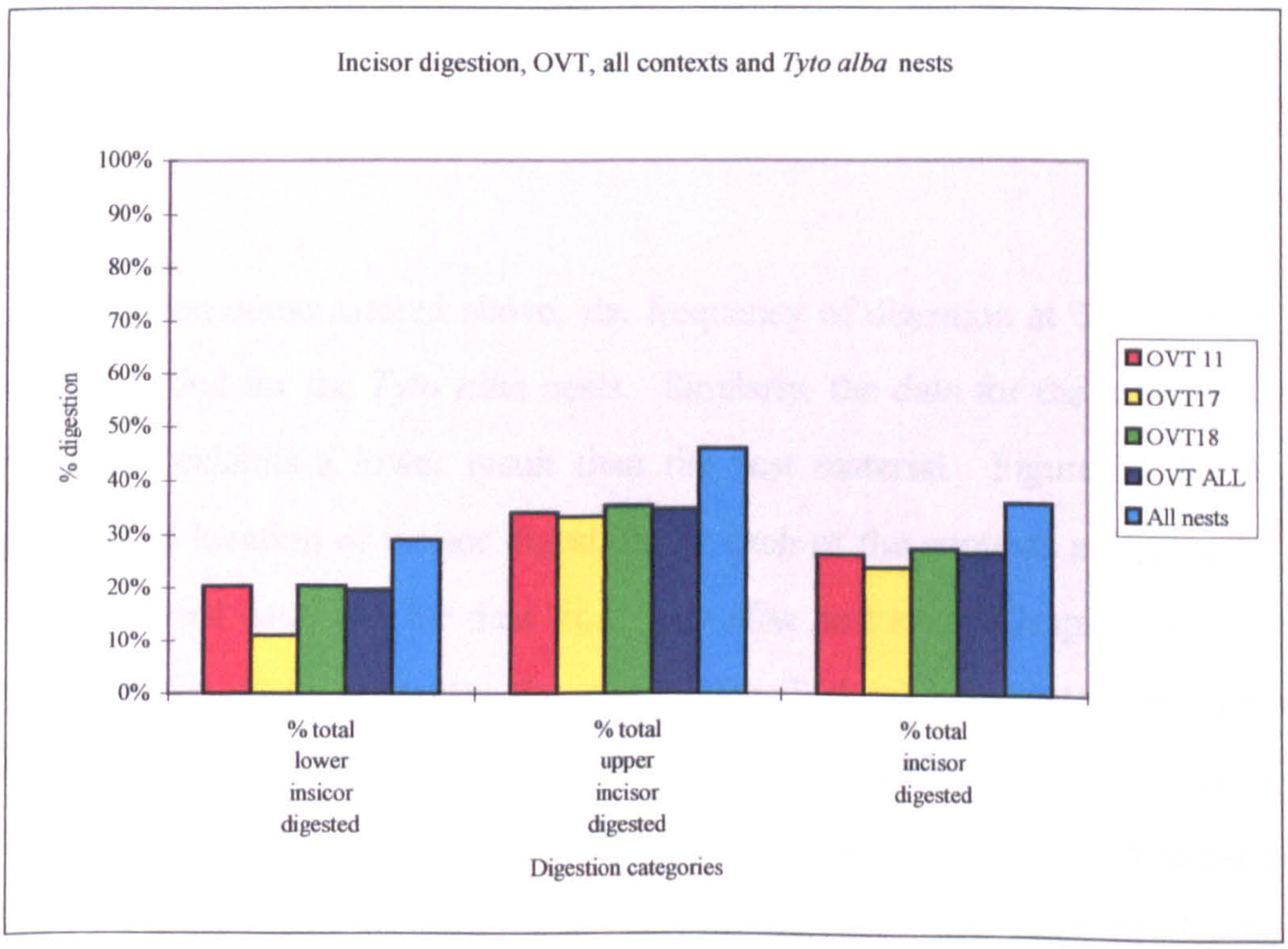


Figure 54. Incisor digestion for OVT and *Tyto alba* nest sites.

However, an analysis of the three summary variables indicates quite a similarity between these three contexts, as can be seen in the histogram above. As the results exhibit such strong similarity for the frequency of digestion, the three contexts were merged to form one data set, for comparison with data from the roost and nest sites, (see Figure 55, below, data after standardisation). The results indicate that the frequency of incisor digestion is slightly lower at Tadcaster than the data for the owl nest material, but higher than that recorded for the *Tyto alba* roost material.

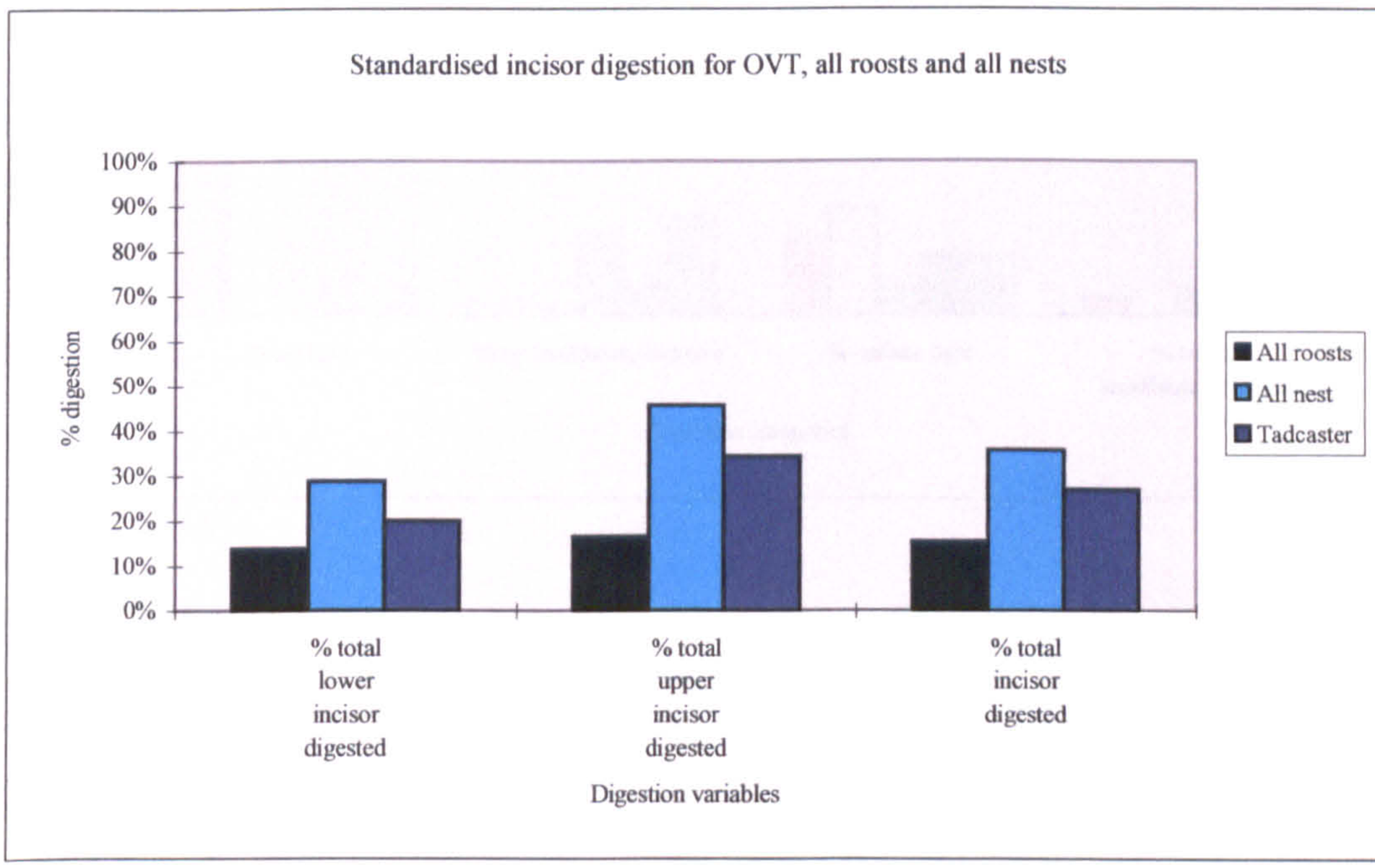


Figure 55. Standardised incisor digestion for OVT and *Tyto alba* roost and nest sites

As has been demonstrated above, the frequency of digestion at Tadcaster is lower than that recorded for the *Tyto alba* nests. Similarly, the data for the extent and location of digestion exhibits a lower result than the nest material. Figure 56 below shows the extent and location of incisor digestion for each of the contexts at Tadcaster, as well as the combined data, and the data from *Tyto alba* nest sites. Despite the slight variability between the three contexts, the results for Tadcaster indicate that the location of digestion is more restricted to the incisor tips at this site, than is the case for the *Tyto alba* nest deposits. Equally, the extent of digestion is lighter at Tadcaster, with less moderate, heavy and extreme digestion recorded than at the nests, (Tadcaster 91% light

digestion, 9% moderate/ heavy/ extreme digestion, All nests 67% light digestion, 33% moderate/ heavy/ extreme digestion).

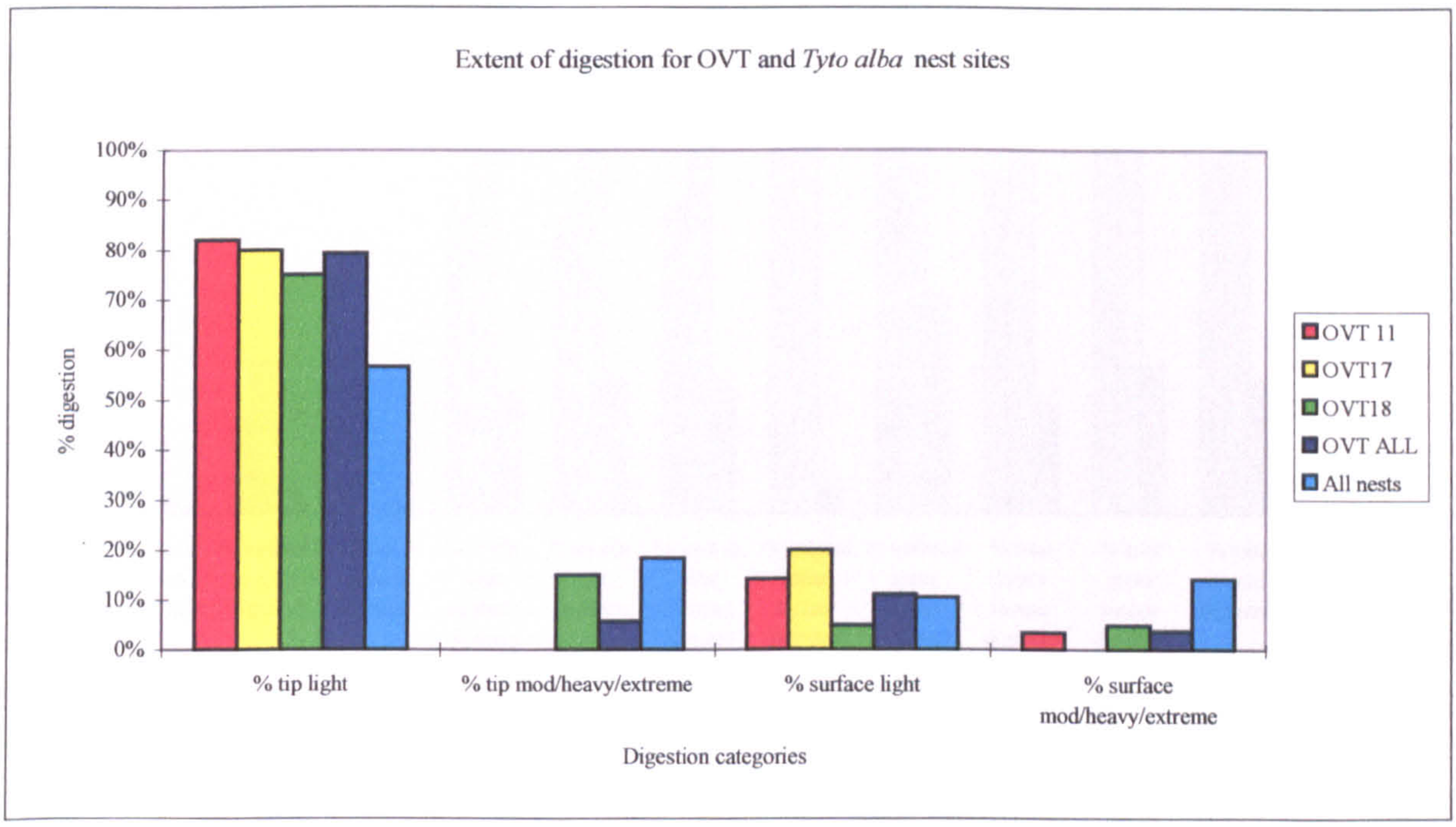


Figure 56. Histogram showing extent and location of incisor digestion for OVT all contexts and *Tyto alba* nest sites.

8.4.1.5 OVT - Conclusions

Most of the analyses indicate that the contexts sampled from the Old Vicarage at Tadcaster bear similar taphonomic signatures to *Tyto alba* nests analysed in this study. In general, the bone breakage was slightly higher at this site than in *Tyto alba* nest material. Too much significance should not be attached to this, as post-depositional breakage could also affect this analysis, and the bones from the basal deposits are more damaged than those from the upper levels of the excavation. Overall, the frequency of digestion at Tadcaster was slightly lower than *Tyto alba* nest data, but higher than that of the *Tyto alba* roost material, as can be seen in the following histogram.

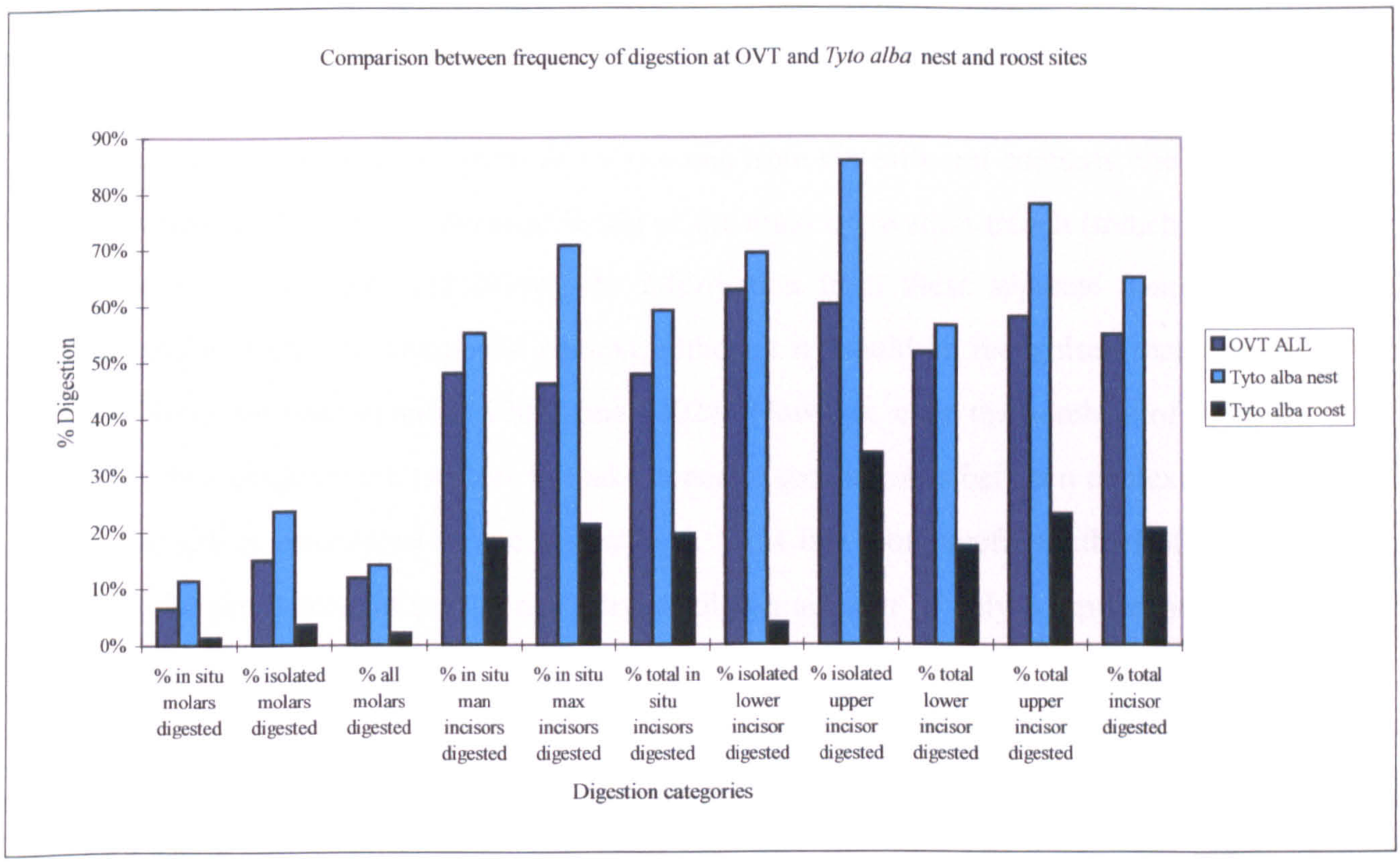


Figure 57. Histogram showing frequency of digestion for OVT compared to *Tyto alba* nest and roost sites.

However, the frequency of molar digestion varies between those contexts at the top, and those at the base of this deposit, and the molar digestion for context 18 is in fact very similar to that recorded for the *Tyto alba* nests. The lower levels of molar digestion recorded in the later context (11) are perhaps suggestive of the fact that some mixing of pellet remains of adult and young birds has occurred, with a resultant reduction in the overall level of digestion recorded on the molar teeth. This trend is not recorded in the results of the frequency of incisor digestion, however, an analysis of the extent of digestion indicated that greater levels of digestion were recorded for context 18 than context 11. This further suggests its similarity to the *Tyto alba* nest material, and the conclusion that context 11 contains a combination of small mammal bones from the pellet material of both adults and their chicks.

8.4.2 Filey Roman Signal Station

The small mammal bones from this site come from six different contexts, the majority of which are from the uppermost levels of the main excavation trench (trench 12), and therefore, as is discussed below, the information from these separate contexts was merged to form one composite context, although it should be recognised that most of the bones are from contexts 12022 and 12024. However, even the numbers of bones in these two contexts are too low to make concrete comparisons between contexts, so the entire site is considered as one assemblage. This is a more useful method of analysis than the production of results that vary wildly on account of only a limited number of bones in each category.

8.4.2.1 Filey - Skeletal element count, species and MNI

All contexts - Source - Appendix table 63, page 357, and Appendix table 64, page 358.

A total of 652 small mammal bones were recovered from 6 contexts at Filey, representing over 27 separate samples. As some of these individual samples contained only a limited number of bones, the information for each sample was merged with that for each context, although species data were recorded for each sample and context (see Appendix table 102, starting at page 406). It is recognised that this technique could have the effect of reducing the minimum number of individuals recorded, as bones from spatially different areas of each context are merged together. However, it is equally likely that calculating the MNI for each sample rather than context, could lead to an inflation of the MNI, as bones of the same individual may be distributed in spatially distinct areas of the same context, and thus fall into different sample zones. The minimum number of individuals for each species, and context are displayed in Table 29, below.

Species	Species code	MNI 11038	MNI 12022	MNI 12024	MNI 12025	MNI 12027	MNI 12028	MNI per species	% MNI
Apodemus sylvaticus	1		3	1				4	8%
Arvicola terrestris	6		1		1			2	4%
Microtus agrestis	8	2	12	7	5	2	1	29	61%
Sorex araneus	16	1	5	3	1			10	21%
Sorex minutus	17			1				1	2%
Talpa europaea	19		1	1				2	4%
MNI per context		3	22	13	7	2	1	48	

Table 29. Filey all contexts, species and MNI.

The table above demonstrates that the main species recovered at Filey were *Microtus agrestis* and *Sorex araneus*, similar to results for *Tyto alba* in Britain (Glue 1974). The majority of bones were recovered from only two contexts (12022 and 10204), containing 350 and 214 identifiable bones respectively, the remaining 88 bones from the other four contexts.

8.4.2.2 Filey - Bone breakage

All contexts - Source - Appendix table 65, page 359, and Appendix table 66, page 360.

As discussed above, the limited number of bones at this site has lead to the information being treated as one sample for the whole site. Data for post-cranial breakage are calculated for each context and also for all of the data. Because of the low number of bones in many of the contexts, the results vary with between 0% and 100% of bones recorded as complete for individual contexts, and 33% and 64% for all of the data combined. The results indicate that there is a much greater amount of post-cranial bone breakage at Filey than has been recorded for *Tyto alba* nest material. However, it is also likely that much of this breakage is the result of post-depositional trampling, and possibly excavation and recovery.

Results for cranial breakage also indicate a high degree of breakage, again possibly related to post-depositional agencies. Only 27% of the maxilla survived intact, and because of this breakage, tooth loss was also quite high: 58% for maxillary molars, 91% for incisors. Mandibular breakage was also extensive, with very few mandibles recorded as complete. Many had broken or missing ascending rami, and about one third

also had broken inferior borders. Molar tooth loss was again quite high (60%), and incisor loss was only moderate (28%), although this is high compared to the results of *Tyto alba* nest material, which is approximately 5%. Recovery of isolated teeth was high within this sample, and the results for both molar and incisor recovery were above 100%, indicating that more teeth than jaws were recovered, either as a result of dispersal of remains outside of the area of excavation, or fragmentation and loss of some of the mandibles and maxillae.

8.4.2.3 Filey - Molar digestion

All contexts - Source - Appendix table 67, page 361.

As a result of the small sample sizes for this site, molar digestion was calculated for each context and for the all the data as well. *In situ* molar digestion ranged between 0% and 100%, for the individual contexts, with an overall result of 18% of molars digested for all of the contexts, representing 3 out of 17 teeth. The limited numbers of *in situ* teeth also indicate that there was a high degree of breakage at this site. The frequency of digestion of isolated teeth was high, ranging between 25% and 100% for the individual contexts, with 43% of all of the teeth digested when all the contexts were combined to form one data set. Taking all of the teeth (both *in situ* and isolated) as one category, 39% of all molars were digested. The diversity of these results are shown in Appendix figure 9, page 446.

Compared to the results for *Tyto alba* nest sites, this frequency of digestion is high, however, analysis of the extent of digestion indicates that it is nearly exactly the same as that recorded for the nest sites. The majority of digestion (89%) was light in nature, restricted to the tops of the molars and causing a rounding of the occlusal surface. Only 9% of the digestion was moderate, and only 2% recorded as heavy. These results are shown below, in Figure 58.

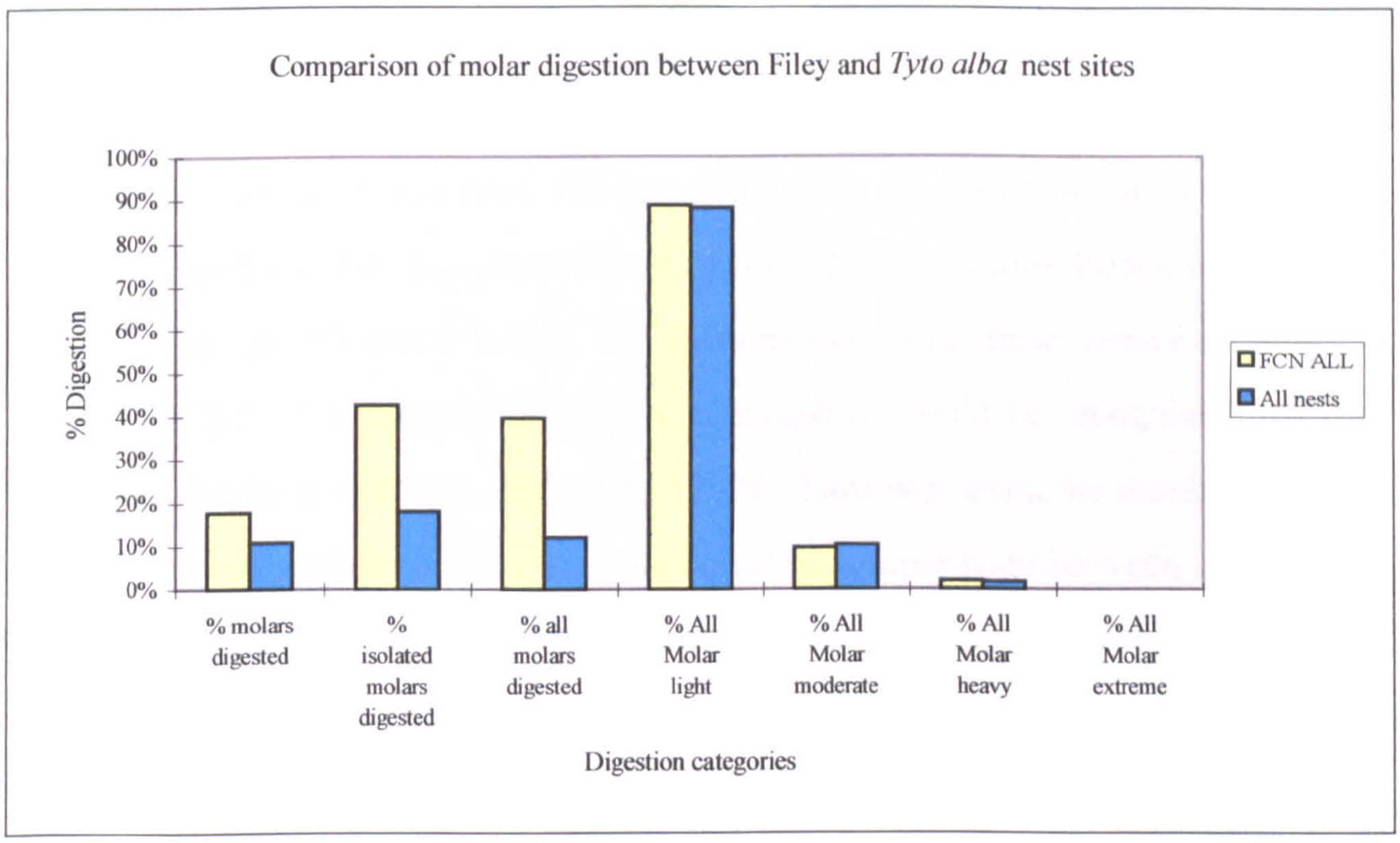


Figure 58. Histogram showing comparison of molar digestion between Filey and *Tyto alba* nest material.

When these results were standardised, the digestion rate for *in situ* molars was increased (from 18% to 26%), although the total digestion rate was unaffected, and remained at 39%.

8.4.2.4 Filey – Incisor digestion

All contexts - Source - Appendix table 68, page 363.

As has been explained above, the analysis of the bones from this site has been hampered by the small sample size of some of the contexts. This is certainly the case with the analysis of incisor digestion, and as a result, there is a great deal of variability between the results of incisor digestion from different contexts, as can be seen in the graph below.

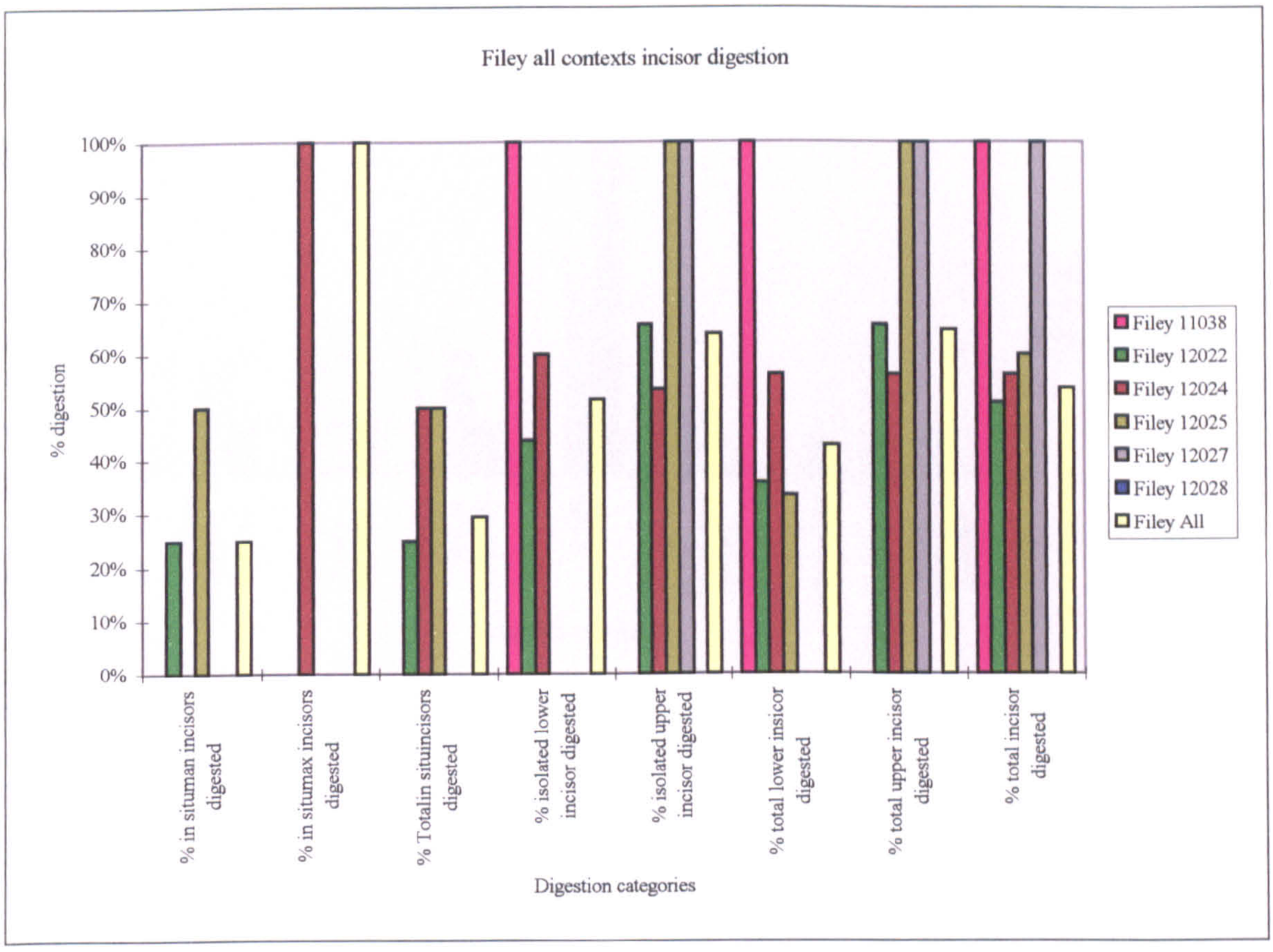


Figure 59. Filey all contexts incisor digestion.

It is difficult to assess whether all of this variation is caused by the problem of sample size, or whether any of this variability is representative of different predator activity. However, out of the six contexts sampled at this site, only two of them contained more than 5 incisors. These were contexts 12022 and 12024, and therefore a combined total for all of the contexts at the site is based almost entirely on the results from these two contexts, the results of which are certainly less variable than the other contexts.

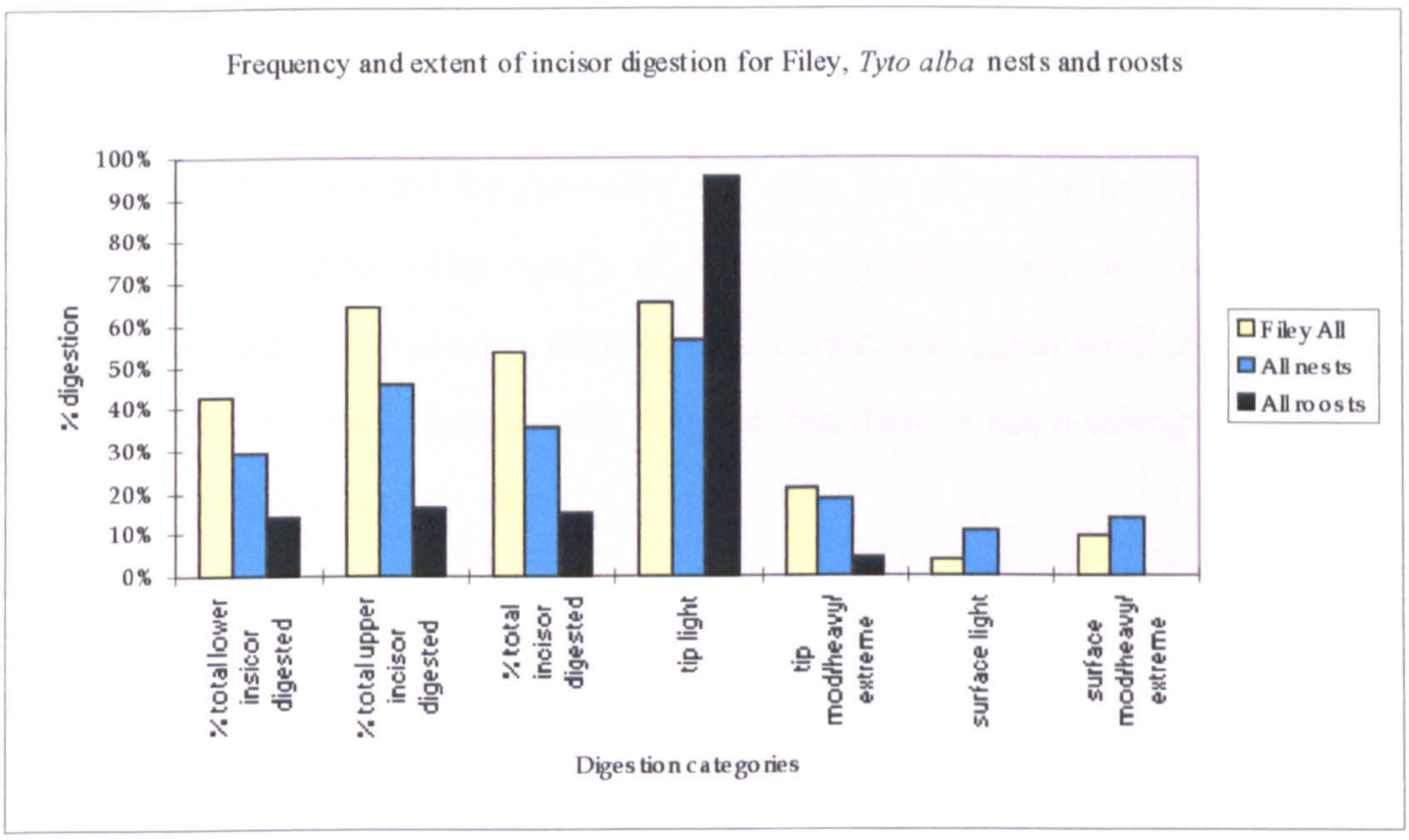


Figure 60. Incisor digestion for Filey and *Tyto alba* roost and nest sites.

Analysis of the incisor digestion at Filey indicates that in frequency it was slightly higher than that recorded for *Tyto alba* nest sites. There was however, a similarity in the extent of digestion; the digestion at Filey was slightly less severe than *Tyto alba* nest material, and concentrated to a greater extent at the tips of the incisors.

8.4.2.5 Filey – Conclusions

Analysis of the results of taphonomic enquiry of the small mammal deposits at Filey Roman Signal Station, Carr Naze, indicate that there are similarities and differences between this material and that recovered from *Tyto alba* nest sites. Firstly, the species recovered and their frequency is similar to that recorded for *Tyto alba* in Britain, and not dissimilar to the results gathered for this study. However, analysis of bone breakage from this site indicate that many more bones are broken than usually recorded for *Tyto alba* nest sites. As has been discussed earlier, the usefulness of bone breakage analysis in the assessment of predatory origins of small mammal deposits is, to some extent, dependant upon the post-depositional history of the material, as well as any possible pre-depositional predatory modification. As the deposit originated in a courtyard complex, it is perhaps not surprising that some trampling, and therefore damage, may have been sustained.

Analysis of the digestion of the molars and incisors also indicates some similarities with *Tyto alba* nest results. Although the frequency of molar digestion was significantly higher than that recorded for *Tyto alba* nest sites, the extent of digestion and its strength were well correlated. The results of incisor digestion were less well matched, with greater frequency of digestion, although the extent was again similar to that recorded at the nest sites. Overall, these results suggest that there is not a strong similarity between this site and *Tyto alba* nest sites.

8.4.3 Fox Hole Cave, High Wheeldon, Derbyshire

The deposits from Fox Hole cave were selected as they were all labelled in such a way as to suggest that they were from the same depositional horizon. As there is only a limited amount published about this site, these were the only indications as to the origin of the bones. The three samples had already been sorted from the large bone and other cave material, and contained only small mammal and amphibian bones, of which only the former were used within this study.

8.4.3.1 Fox Hole - Skeletal element count, species and MNI

Sample 1 - source - Appendix table 69, page 364.

A total of 509 small mammal bones were analysed from this sample, representing only three species: *Arvicola terrestris*, *Clethrionomys glareolus*, and *Microtus agrestis*. A bias in favour of the larger *Arvicola terrestris*, comprising 62% of all bones in this sample, may have arisen during excavation, or may reflect real numbers present in the deposit. Given the often very reliable excavation strategy of Bramwell (Yalden pers. comm.), the latter may be more likely, especially given the fact that this trend is in fact reversed in sample 3. The species and the percentage MNI is given in Table 30, below.

Species	Species code	MNI	%MNI
Arvicola terrestris	6	26	61%
Clethrionomys glareolus	7	1	2%
Microtus agrestis	8	16	37%

Table 30. Fox Hole sample 1, species present and MNI.

Sample 2 - Source -Appendix table 70, page 365.

This was the smallest of the three samples with only 464 bones recovered. There were four species in this sample, which was dominated by *Microtus agrestis* and *Arvicola terrestris*. The species present and MNI are given in Table 31, below.

Species	Species code	MNI	%MNI
Apodemus sylvaticus	1	2	6%
Arvicola terrestris	6	11	36%
Clethrionomys glareolus	7	1	3%
Microtus agrestis	8	17	55%

Table 31. Fox Hole sample 2, species present and MNI.

Sample 3 - Source - Appendix table 71, page 366.

This was the largest sample from Fox Hole, containing 1928 bones, just under twice as many bones as the sum of the two other samples[78]. Six species were represented in this sample, with the numbers of each species shown in Table 32, below. As discussed above, there was a reversal of the number of *Arvicola terrestris* and *Microtus agrestis* compared with sample 1, with twice as many *Microtus agrestis* as *Arvicola terrestris*.

Species	Species code	MNI	%MNI
Apodemus sylvaticus	1	4	3%
Mus domesticus	3	1	1%
Arvicola terrestris	6	33	25%
Clethrionomys glareolus	7	12	9%
Microtus agrestis	8	77	59%
Sorex araneus	16	4	3%

Table 32. Fox Hole sample 3, species present and MNI.

It is also interesting to note that an increase in species diversity was recorded for this sample, which may well be associated with sample size, suggesting that in order to record some of the rarer species it is important to select as large a sample as possible. One of the rarer species that was found in this sample was *Mus domesticus*, which is almost certainly one of, if not the earliest recorded example of this species in the British Isles (Yalden, 1999; pers. comm.).

[78] There were 1928 bones in sample 3, compared with 973 bones for the sum of samples 1 and 2 – twice this figure is 1946 bones.

8.4.3.2 Fox Hole - Bone breakage

Post-cranial breakage - Source - Appendix table 75, page 370, see also Appendix table 72, page 367, Appendix table 73, page 368, and Appendix table 74, page 369.

Cranial breakage - Source - Appendix table 79, page 374, see also Appendix table 76, page 371, Appendix table 77, page 372, and Appendix table 78, page 373.

The recovery of post-cranial bones from these three samples was relatively low, and in part was due to the high degree of fragmentation of these bones. It was not, however, possible to ascertain whether this breakage was pre- or post-depositional, representing either the destructive nature of the predator, or the potential for breakage from trampling, compaction and excavation that has been discussed earlier. Due to the variability that occurred as a result of this small sample size, the post-cranial breakage analysis from Fox Hole was considered only from the composite of all three of the samples. Similarly, results of the cranial breakage analysis are also best considered for the site as a whole rather than the separate samples, again a result of the high levels of breakage recorded for this site.

Post-cranial bone breakage was very high at Fox Hole, with only 9% to 18% of bones recorded as complete. A consistent pattern throughout all three samples indicated higher recovery (or preservation) of distal elements for the humerus and tibia, and high figures for the recovery of proximal elements of the ulna and femur. This pattern does not fit any current predator pattern of bone breakage (Andrews 1990), and is perhaps more an indication of the relative strengths and weaknesses of the various bones.

Cranial breakage was also high at this site, and none of the maxillae or mandibles were recorded as complete. In fact all of the maxillae were missing the zygomatic process, and breakage of the mandibles was also very severe, with 91% recorded with missing ascending ramii. The breakage of the inferior border was also high (65%). The result of this breakage was that only around half of the molar teeth were still retained within the jaws, and in the case of the maxillae, 82% of the incisors were also missing. Mandible incisor loss was lower, only 48%, although this is a large figure for this category of analysis. A final confirmation of the high degree of fragmentation at this site is given in the record of the percentage of isolated teeth recovered. Figures for both molar and incisor recovery were above 100%, and

therefore indicate that more isolated teeth were recovered than the jaws from which they originated, which presumably were too damaged to be recognised and recovered.

8.4.3.3 Fox Hole - Molar digestion

Sample 1 - Source - Appendix table 80, page 375.

A total of 237 molars were recovered from this sample, of which 42% were digested. Only three species were represented, *Arvicola terrestris, Clethrionomys glareolus* and *Microtus agrestis*, with the majority of the teeth coming from *Arvicola terrestris* (78% of the sample) and the fewest from *Clethrionomys glareolus* (2% of the sample). Only 49 *in situ* teeth were recorded, compared with 188 isolated molars, attesting to a relatively high degree of cranial breakage. Most of the digestion in the sample was light (84%) with only 14% moderate digestion and 1% heavy (one tooth).

Sample 2 - Source - Appendix table 81, page 376.

Only 209 molars were recovered form this sample, of which 38% (80 teeth) were digested. Four species were recorded, *Apodemus sylvaticus, Arvicola terrestris, Clethrionomys glareolus* and *Microtus agrestis* with the assemblage again dominated by *Arvicola terrestris* and *Microtus agrestis* (93% of the sample). The majority of the teeth were again isolated molars, (177 teeth, compared with only 32 *in situ* molars). Higher frequencies of digestion were recorded on these isolated molars than the *in situ* molars. Most of the digestion in this sample was light (94%) with only 6% moderate digestion.

Sample 3 - Source - Appendix table 82, page 377.

This was the largest of the three samples, with 1039 molars recorded, of which 36% were digested. It is interesting that a sample five times the size of sample 2, the level of digestion is almost the same. In this sample, five species were recorded, the same four as above, as well as *Mus domesticus.* The difference between *in situ* and isolated molars was very pronounced in this sample, with only 23 *in situ* molars, compared with 1018 isolated teeth. However, in contrast to sample 2, higher frequencies of digestion

were recorded for the *in situ* molars than the isolated teeth. The majority of the digestion was light (85%) with 10% moderate and 5% heavy digestion.

All samples - Source - Appendix table 83, page 378

In the previous section on bone breakage, the amount of cranial breakage at Fox Hole was discussed, and it was suggested that the high degree of breakage led to an increase in isolated molars, and a loss of *in situ* molars. This has been demonstrated in the last section detailing the molar digestion from three samples. This high degree of breakage has lead to a high variability of results for *in situ* molar digestion (see Figure 61, below), as the analysis is limited by too few bones within the analysis. Even after standardisation (see Figure 62, page 197), the results for this category of digestion were highly variable, indicating that the difference in prey captured was not entirely responsible for the results, although it will be noted in comparison between the Figure 61 and Figure 62, that the amount of digestion is significantly reduced in this category following standardisation.

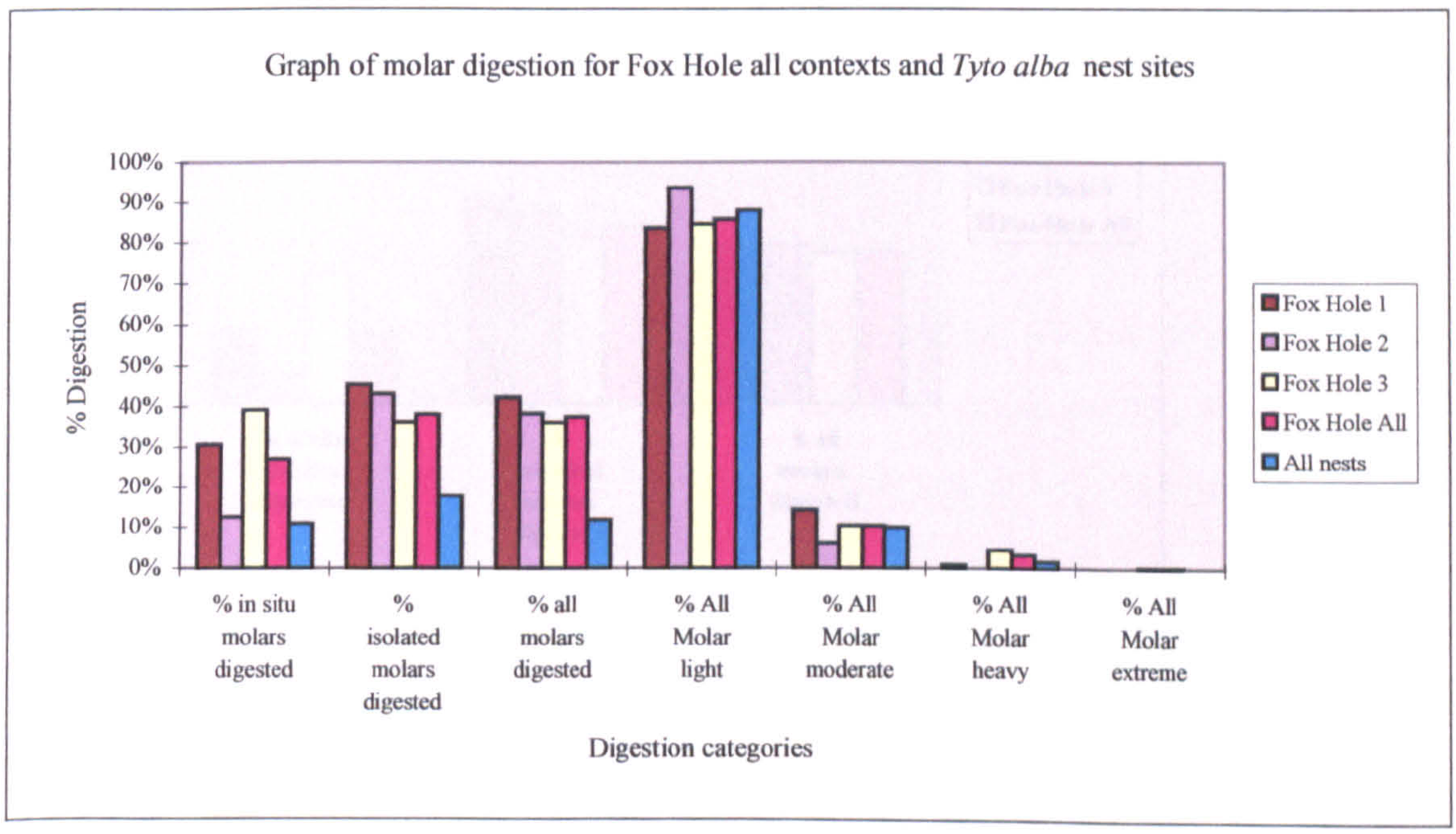


Figure 61. Molar digestion for Fox Hole, all contexts, and *Tyto alba* nest sites.

As there were a large number of isolated molars, compared to *in situ* molars, these results were less variable, and the results obtained for isolated molar, and total molars

digestion were very similar. As a result, only total molars will be discussed here, as the differences between the samples were even less variable. It should be pointed out that it may seem like an attempt is being made to search only for similarities in the data and not differences, and that the possibility that different deposits could have been accumulated by different predators is being overlooked in order to create homogeneity of results. However, what is being suggested is in fact mirrored by the results of standardising prey species digestion from these three sites, shown in Figure 62, below. Before standardisation, the amount of total molar digestion varied between the three samples from 36% to 42%, and afterwards only between 32% and 33%. A further indication of the similarity of these three contexts comes from the analysis of the extent of digestion, shown in Figure 61, above. This graph indicates that the majority of the digestion (between 84% and 94%) was of a light nature.

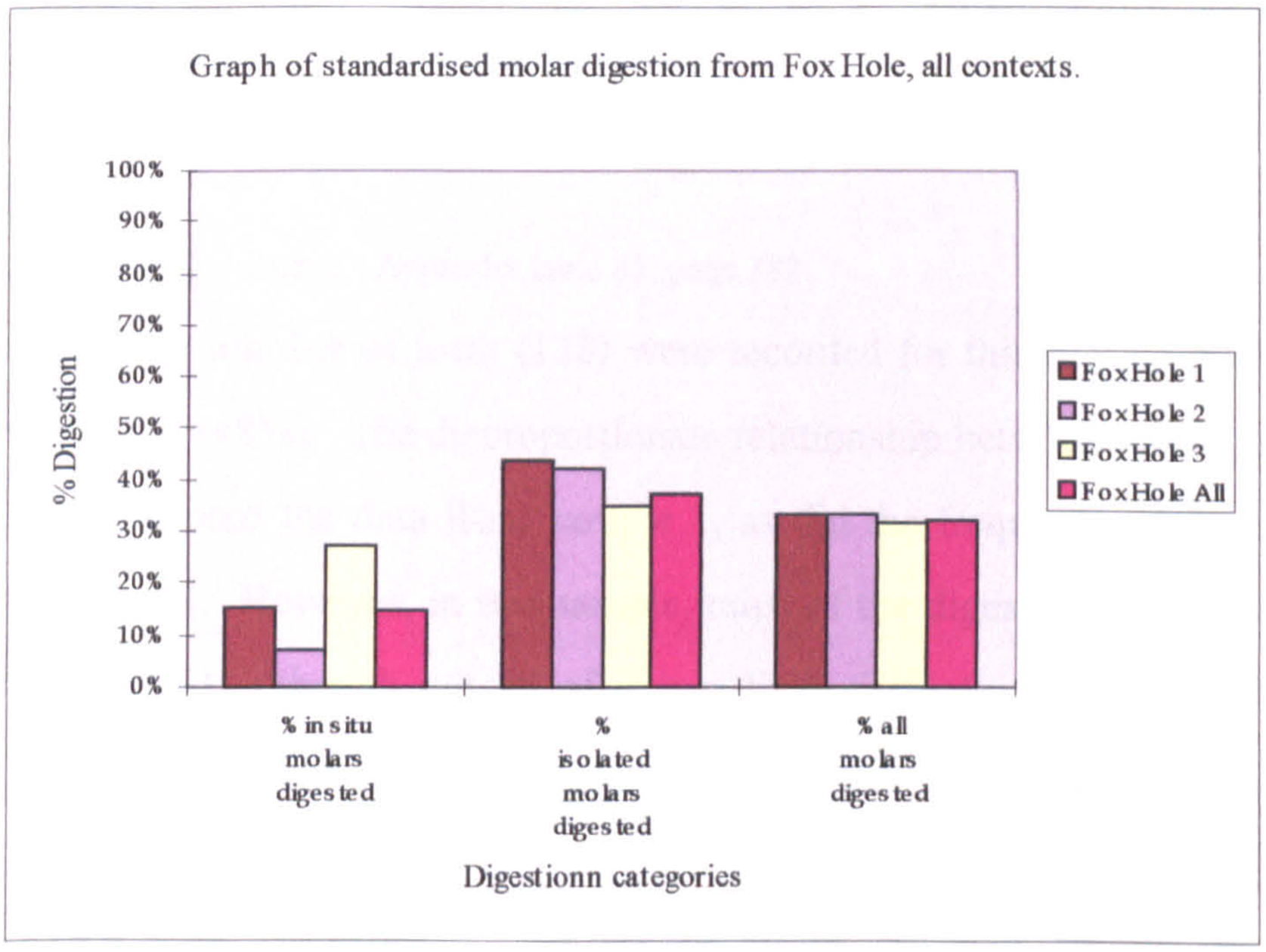


Figure 62. Standardised molar digestion for Fox Hole, all contexts.

The effect of prey standardisation[79] is fairly dramatic for the category of total molar digestion, indicating that the difference in molar digestion between the three samples occurred as a result of differential digestion of prey species. The standardisation of the

[79] For prey standardisation method see Appendix notes - section 3, page 281.

results calculates the difference between the amount of digestion for each prey species in each context or site (the sample), compared to the data for all of the analysis of this study (the population).

8.4.3.4 Fox Hole - Incisor digestion

Sample 1 - Source - Appendix table 84, page 380.

A total of 125 incisors were recovered from this sample, half of which were digested. As was the case with the molars, the majority of the incisors were isolated, with a higher frequency of digestion than the *in situ* incisors. Only 11 *in situ* incisors were recorded, all of which were mandibular. The extent of digestion in this sample was quite varied, with only 44% of incisors lightly digested at the tips, and 15% lightly digested along the surface. The remaining 41% of digestion was moderate or heavy, and divided equally between the tips and the incisor surface.

Sample 2 - Source - Appendix table 85, page 382.

A similar number of teeth (128) were recorded for this sample, with a similar level of digestion (48%). The disproportionate relationship between *in situ* and isolated incisors also mirrored the data from sample 1, as did the frequency of digestion for these two categories. However, in this sample, most of the digestion was restricted to the incisor tips (82%), although not all of it was light (21% tip moderate, 7% tip heavy). The remaining 18% of digestion was recorded on the incisor surface, 5% light, 7% moderate and 7% heavy.

Sample 3 - Source - Appendix table 86, page 384.

The largest of the three samples, with 509 incisors recovered, of which only 42% were digested. This sample, although the largest, contained the smallest number of *in situ* incisors, in this case just one. The remaining 508 teeth were isolated incisors. As no digestion was recorded for the *in situ* incisor, the frequency of digestion for the isolated incisors was considerable higher, 38% isolated lower incisors and 45% isolated upper

incisors. Although the frequency of digestion is lower in this sample, compared to sample 2, the extent and location of digestion is very similar, with around 80% of the digestion restricted to the tips (65% tip light, 15% tip moderate) with the remaining 20 % on the surface of the incisors (10 surface light, 6% surface moderate, 4% surface heavy).

All samples - Source - Appendix table 87, page 386.

None of the maxillae from the three samples contained any *in situ* incisors, and only 28 *in situ* mandibular incisors were recovered. The results of the incisor digestion was therefore separated into only three categories: total lower, total upper and total incisor digestion. The results of upper and lower isolated incisor digestion are not discussed here, as these teeth constitute nearly all of the teeth under analysis, and the three summary categories used enables the inclusions of the *in situ* teeth in more meaningful analysis.

Digestion of incisors was quite high for this site, between 42% and 50% (see figure below), and for the most part, these figures do not change considerably following standardisation. In about 60% of these cases, the digestion was restricted to the incisor tips and was light in nature.

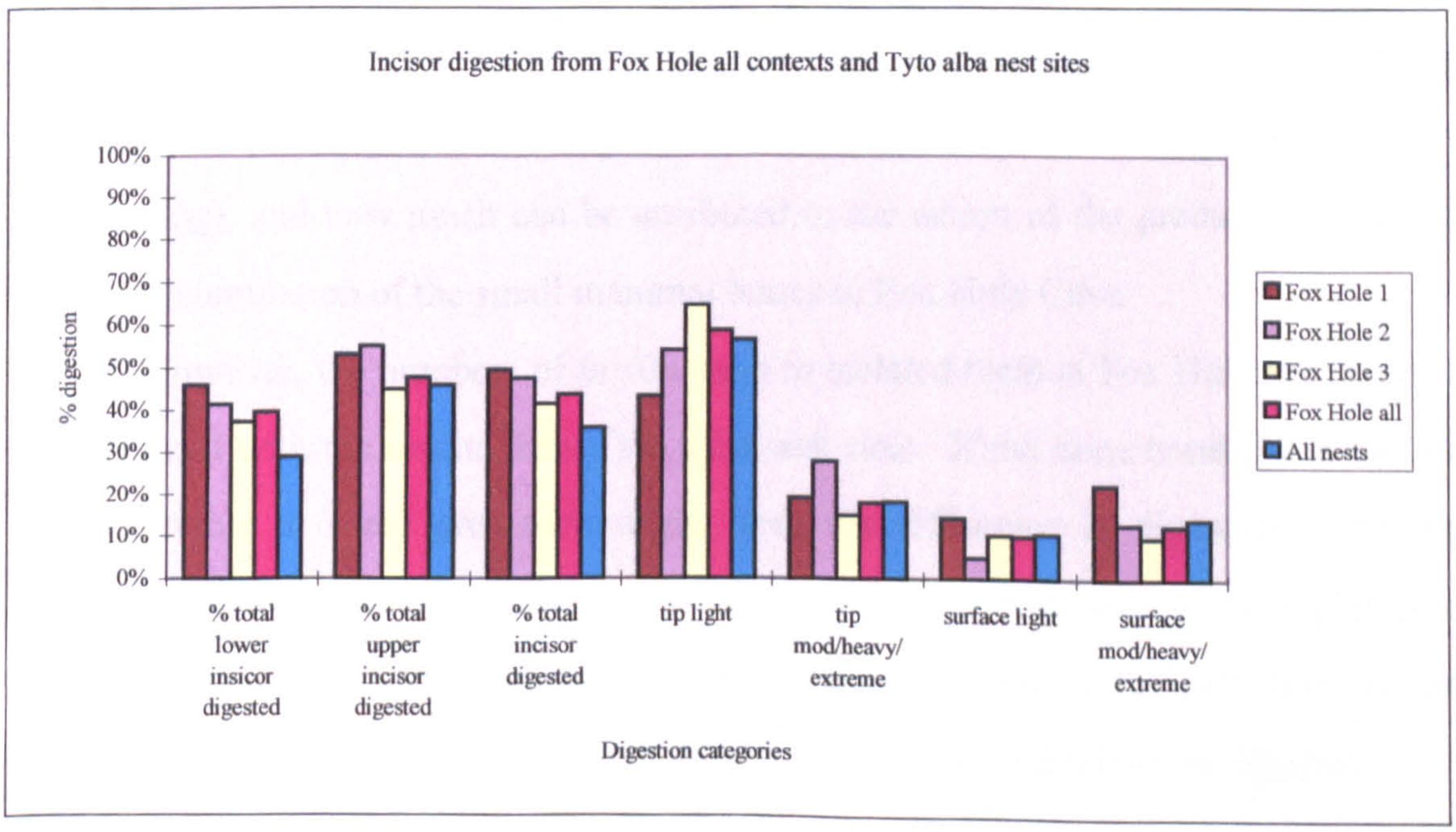


Figure 63. Graph of incisor digestion for Fox Hole, all contexts and *Tyto alba* nest sites.

As can be seen in the histogram above, there is clearly evidence of some variability in the results of incisor digestion from the three contexts sampled. However, it is possible that much of this variability is the result of problems associated with sample size. Samples 1 and 2 contain only 125 and 128 incisors respectively, compared with sample 3, which contains 509 incisors, twice the amount of the other two samples combined (125 + 128 =253, multiplied by 2 = 506). It is therefore not possible to comment on whether the higher levels of digestion in the first two samples are a result of different predatory origin, as only a limited number of teeth in each sample represent those exhibiting both the higher frequency and extent of digestion.

When the deposit is analysed as a single combined data set, the above analysis indicates that it is similar to the *Tyto alba* nest material. The frequency of digestion is slightly higher at Fox Hole (44% compared with 36%), however the extent and location of digestion exhibits strong similarities, characterised by digestion mainly restricted to the tips and light in extent, but with other teeth showing signs of higher levels of digestion on the tips and along the entire incisor surface.

8.4.3.5 Fox Hole - Conclusions

The bones from this site were extremely fragmented, with few cranial or post-cranial bones surviving intact. As a result of these high levels of cranial breakage, there was an over-representation of isolated teeth in these samples, and far fewer *in situ* teeth, than recorded for *Tyto alba* nest sites. It is difficult to assess how much of this breakage was the result of post-depositional diagenetic forces (including the subsequent excavation and sieving), and how much can be attributed to the action of the predator responsible for the accumulation of the small mammal bones in Fox Hole Cave.

However, the numbers of *in situ* teeth to isolated teeth at Fox Hole are inversely proportional with the results from *Tyto alba* nest sites. If the bone breakage at this site is attributable to some predatory origin, then the difference in digestion, especially molar digestion, between Fox Hole and the *Tyto alba* nest material may be explained as a consequence of increased exposure to the digestive stomach juices by more isolated teeth, therefore increasing the numbers of teeth that are more likely to be digested.

At a site like Fox Hole, where the archaeological record indicates that there have been a wide range of mammal species inhabiting or brought into the cave, one must also consider that it is possible that some of the small mammal bones at Fox Hole may have a different predatory origin to others, from the same stratigraphic unit, area of the cave, or even small sample. It is difficult with the approach taken within this work to fully assess whether this was the case at Fox Hole. Further consideration of this problem will be given in the next chapter, although the results outlined above indicate a fairly high degree of uniformity throughout these three samples.

8.4.4 Carsington Pasture Cave (CPC)

Two samples were used for the analysis of small mammal bones from this site, context 103 and context 109.

8.4.4.1 CPC – Skeletal element count, species and MNI

Context 103 - Source - Appendix table 88, page 387.

A total of 766 bones were recorded from context 103, of which 584 were cranial bones, and 192 were post-cranial elements. The samples from Tadcaster and the three *Tyto alba* nest sites contained high numbers of *Apodemus sylvaticus*, *Microtus agrestis* and *Sorex araneus*. This sample is dominated by *Arvicola terrestris* and *Microtus agrestis*, with *Arvicola terrestris* occurring in far higher numbers than it occurs in the pellets of *Tyto alba* (or in fact any British owl) in the present time. The small *Micromys minutus* mandible (species 2) attests to high recovery rate of even the smallest species present. The species present in this context, the MNI and percentage of the MNI for the sample are given in Table 33, below.

Species	Species code	MNI	%MNI
Apodemus sylvaticus	1	2	4%
Micromys minutus	2	1	2%
Arvicola terrestris	6	20	42%
Clethrionomys glareolus	7	1	2%
Microtus agrestis	8	24	50%

Table 33. CPC context 103, species present and MNI.

Context 109 - Source - Appendix table 89, page 388.

A total of 1673 identifiable bones were recovered from this context, 1279 cranial bones and 394 post cranial bones. Again the species present were dominated by *Arvicola terrestris* and *Microtus agrestis*, with no Soricidae species recovered. The occurrence of two molars of *Mus domesticus* within this deposit, which, (by association with the human remains and artefacts), is likely to date to the Bronze Age, is a very early date

for this species in Britain. The species present in this context, the MNI and percentage of the MNI for the sample are shown below in Table 34.

Species	Species code	MNI	%MNI
Apodemus sylvaticus	1	13	15%
Mus domesticus	3	1	1%
Arvicola terrestris	6	28	31%
Microtus agrestis	8	47	53%

Table 34. CPC context 109, species present and MNI.

8.4.4.2 CPC – Bone breakage

Context 103 - Source - post-cranial breakage - Appendix table 90, page 389; cranial breakage - Appendix table 92, page 391.

Post-cranial breakage was high in this sample, with only 32% completeness for the humerus, and as little as 17% for the femur. There does not appear to be any significant pattern to this breakage, as most of the breakage to the femur and ulna has caused the loss of the distal end of the bones, whereas the breakage location was evenly distributed in the breakage analysis of the humerus and tibia.

Cranial breakage was also high in this sample, affecting both the maxilla and the mandible. Only 6% of the maxilla are complete (2 out of 34), with just 11% with the zygomatic. As a result of this extensive breakage, maxillary molar and incisor tooth loss was also high, 81% and 94 % respectively. None of the mandibles was recorded as complete, and most (90%) were missing the ascending ramus. A further indication of the severity of breakage was the inferior border breakage, which affected almost half of the sample (45%). The effect of this breakage was again high tooth loss, with 93% of the molars missing from the mandible, and 45% of the incisors missing. Loss of mandibles and maxillae through breakage was also likely to have occurred in this context, as the total number of isolated teeth (both molars and incisors) was higher than the number missing from the maxilla and mandibles. This was indicated by percentage values above 100% for isolated teeth, 145% for molars, and 243% for the incisors.

Context 109 - Source - post-cranial breakage - Appendix table 91, page 390; cranial breakage - Appendix table 93, page 392.

Post-cranial breakage for context 109 was similar to context 103, with percentage completeness only 30% for the humerus, whilst the lowest value was 19% for the femur. The location of breakage also followed the same pattern as context 103, with high distal element loss for the ulna and femur, and more evenly distributed breakage for the humerus and tibia.

Cranial breakage was also high in this sample, with maxilla breakage even higher than that recorded for context 103. None of the 75 recorded maxillae were complete and only 3% still had the zygomatic attached. Not unexpectedly, the tooth loss from the maxilla was also high, with 70% loss of molars and 97% incisor loss. Mandible breakage was also similar to context 103, with only 1% of mandibles surviving undamaged. The majority of the rest (86%) were missing the ascending ramus, and 49% had broken inferior borders. Tooth loss was also high, with 75% loss of molars and 96 % loss of incisors. Destruction of some of the mandibles and maxillae was evidenced by the high values for isolated molars and incisors, 138% and 203% respectively.

8.4.4.3 CPC – Molar digestion

Context 103 - Source - Appendix table 94, page 393.

As a result of the high degree of cranial breakage described in the last section, the number of *in situ* teeth recovered was low, and therefore the *in situ* molars comprise only 10% of the total number of teeth in this sample. Half of these teeth were digested (54%), of which 75% were lightly digested, the remainder moderately digested. Half of the isolated teeth were also digested (50%) of which 89% were lightly digested while the remaining 11% were moderately digested. In total, 87% of all the digested molars are lightly digested, the remaining 13% moderately digested.

Context 109 - Source - Appendix table 95, page 394.

The number of *in situ* molars in this sample was also low, only 21% of all of the molars. Of these *in situ* molars, 36% are digested, 91% of which was light digestion. A high

frequency of the isolated molars are digested (56%) although the extent of digestion was almost the same (83% light digestion). In total, 52% of all of the molars were digested, of which 84% of these digested teeth were lightly digested.

Both contexts - Source - Appendix table 96, page 395.

Analysis of molar digestion from both of the two contexts from Carsington Pasture Cave indicates that they were relatively similar, with only a 1% difference in total molar digestion between these two contexts, (see Figure 64 below). The extent of the digestion was also similar, with 87% of light digestion recorded for context 103, and 84% for context 109. As both of the samples come from the same cave, only a few metres from each other, this similarity indicates that they may have the same predatory origin.

Comparison of molar digestion between CPC contexts 103 and 109, and *Tyto alba* nest sites

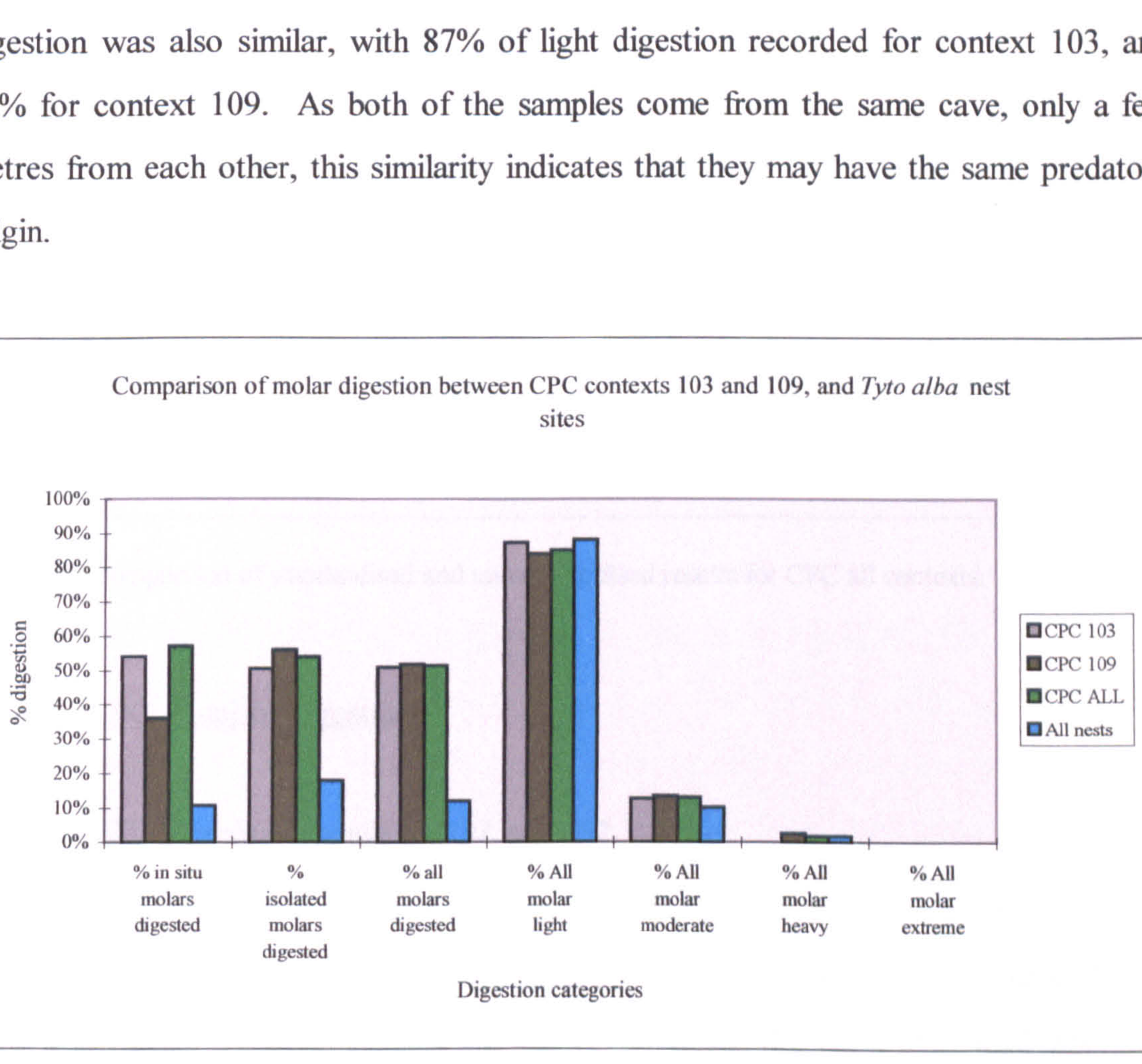


Figure 64. Comparison of molar digestion from CPC, contexts 103 and 109 and *Tyto alba* nest sites.

A comparison of the data from Carsington Pasture Cave with that from *Tyto alba* nests indicates that there was a much greater frequency of digestion at this site, but that the extent of the digestion was very similar, with the majority of the digestion recorded as light. Standardising the results for molar digestion has some effect on the frequency of digestion, as the prey species variability associated with the large numbers of *Arvicola*

terrestris within these two contexts was reduced. However, although the differences were great for *in situ* teeth (43% digestion compared with 57%), the difference for all molars was only slight (47% compared to 52%). These results are shown in Figure 65, below.

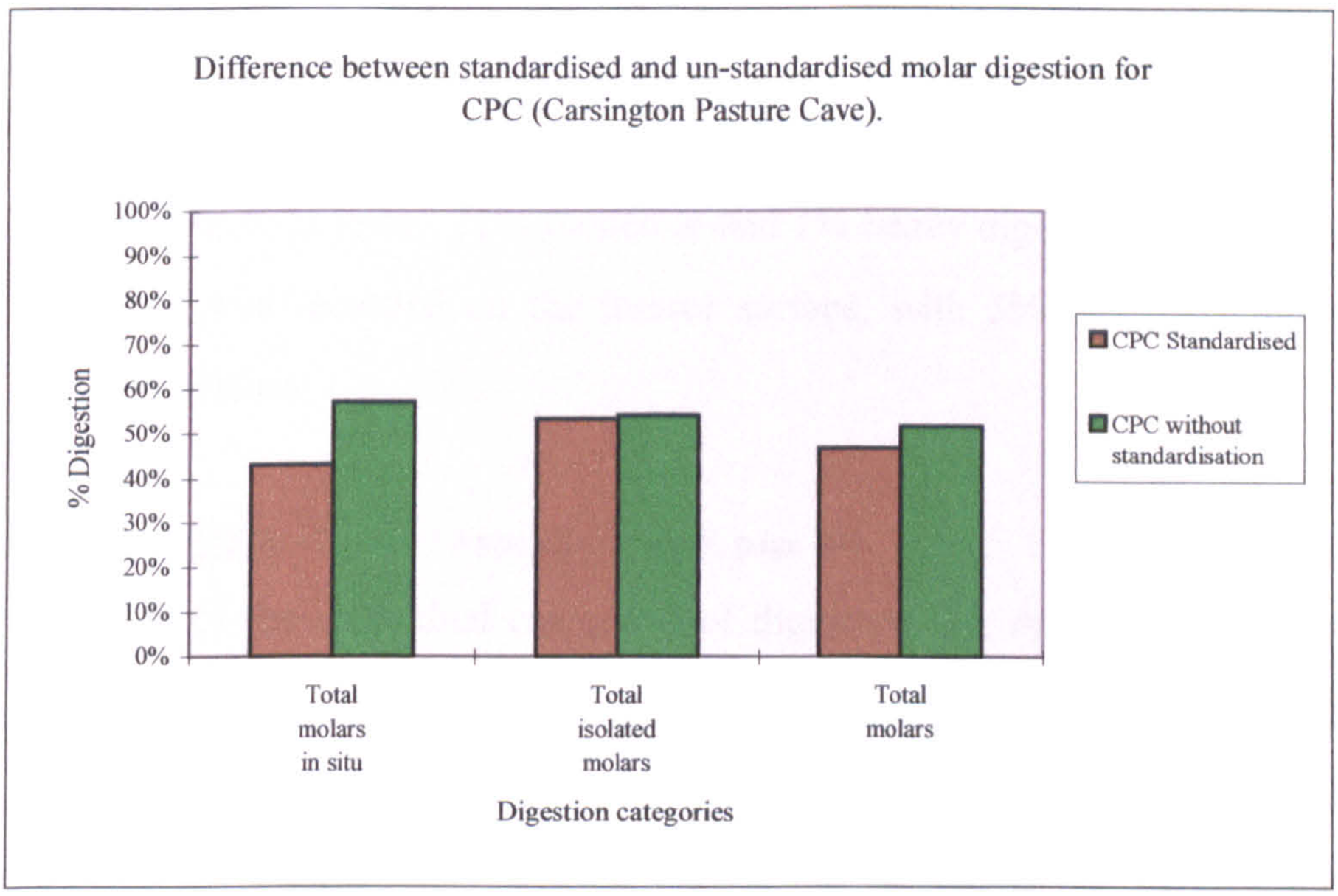


Figure 65. Comparison of standardised and un-standardised results for CPC all contexts.

8.4.4.4 CPC – Incisor digestion

Context 103 - Source - Appendix table 97, page 397.

A total of 176 incisors were recovered from this, the smaller of the two contexts. Out of this total, 59% of the incisors showed signs of digestion. As was the case with Fox Hole, most of the teeth analysed were isolated incisors (153 teeth compared with only 23 *in situ* incisors). The frequency of digestion was roughly even between these two categories, and there was little evidence of preferential digestion of the upper incisors over the lower ones, as had been the case at other sites. Most of the digestion was restricted to the incisor tips (84%) of which 55% was light and 29% moderate. The remaining 16% of digestion affected the incisor surface, with 12% light, 2% moderate and 2% heavy digestion.

Context 109 - Source - Appendix table 98, page 399.

Almost twice as many incisors were recovered from this context compared to context 103, of which an equal amount (60%) were digested. Similarly, most of the teeth were isolated incisors (304 teeth compared with 40 *in situ* incisors). Higher frequencies of digestion were recorded for the *in situ* incisors, however, this is possibly a result of inflation due to the small sample size. Similar amounts of digestion were recorded for the upper and lower incisors. Digestion was again restricted mainly to the incisor tips (89%) with 67% light, 21% moderate and 1% heavy digestion. The remaining 11% of digestion was recorded on the incisor surface, with 5% light, 5% moderate and 1% heavy digestion.

Both contexts - Source - Appendix table 99, page 401.

Analysis of the individual categories of digestion (i.e. *in situ* and isolated mandibular and maxillary incisor digestion) indicates some variability between the two contexts[80], as can be seen in Appendix Figure 8, page 445. However, as has been explained earlier, much of this variation was related to the level of cranial breakage for the site, and the limited number of bones recorded for the *in situ* incisors. As can be seen in Figure 66 below, this variability was reduced in the composite categories. The frequency of digestion was higher at Carsington Pasture Cave than for *Tyto alba* nest sites, with approximately 60% of the incisors showing an indication of digestion. Analysis of this data after standardisation indicates that there was little difference between the standardised and non-standardised results for the incisor digestion.

[80] The majority of the variability in these individual digestion variables occurs in the *in situ* incisors, whereas the results of the isolated incisor digestion are very similar.

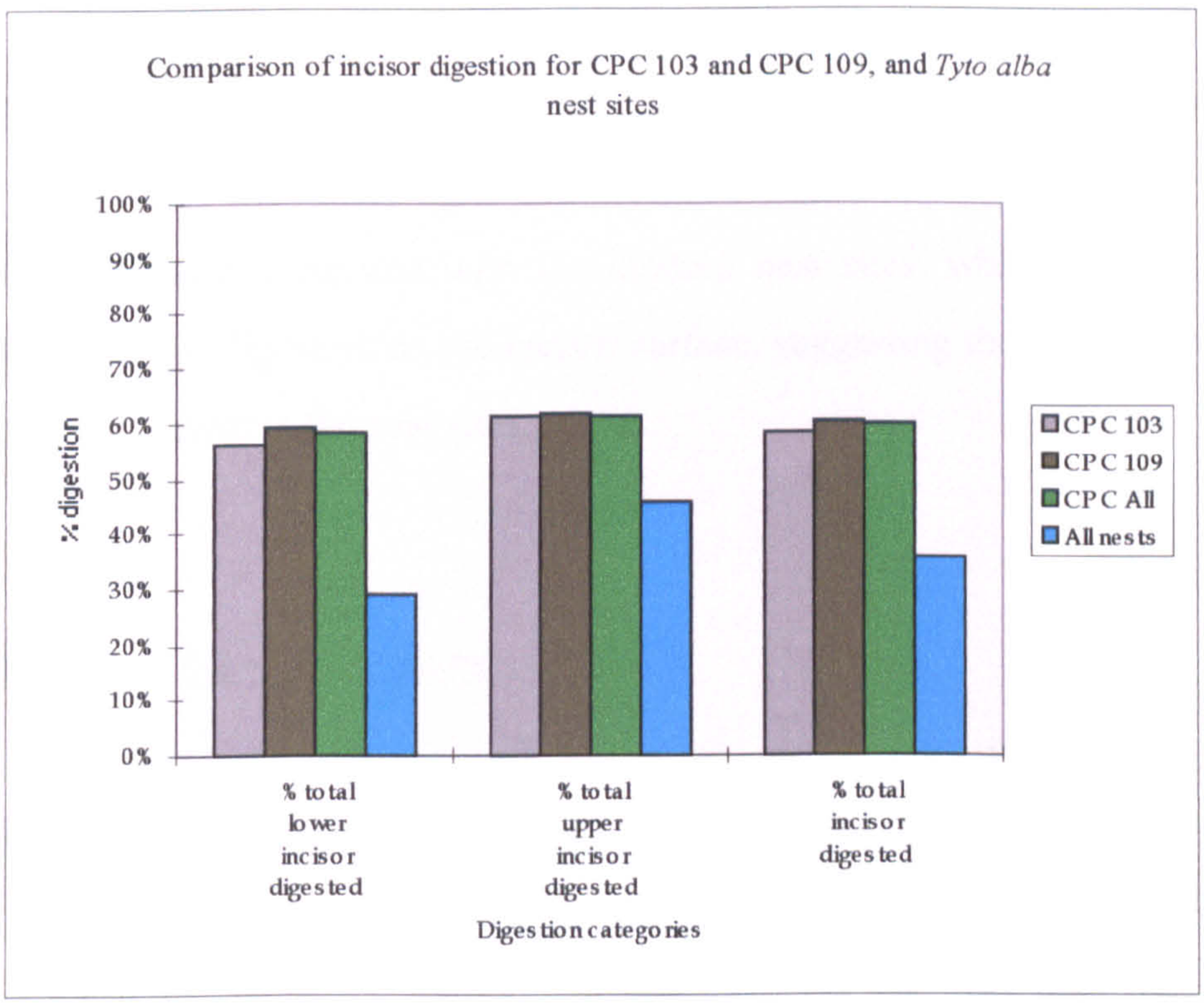


Figure 66. Incisor digestion for CPC 103 and CPC 109 and *Tyto alba* nest sites.

Approximately 60% of this digestion was light and restricted to the tips, similar to the results for *Tyto alba* nest sites, as can be seen in Figure 67, below.

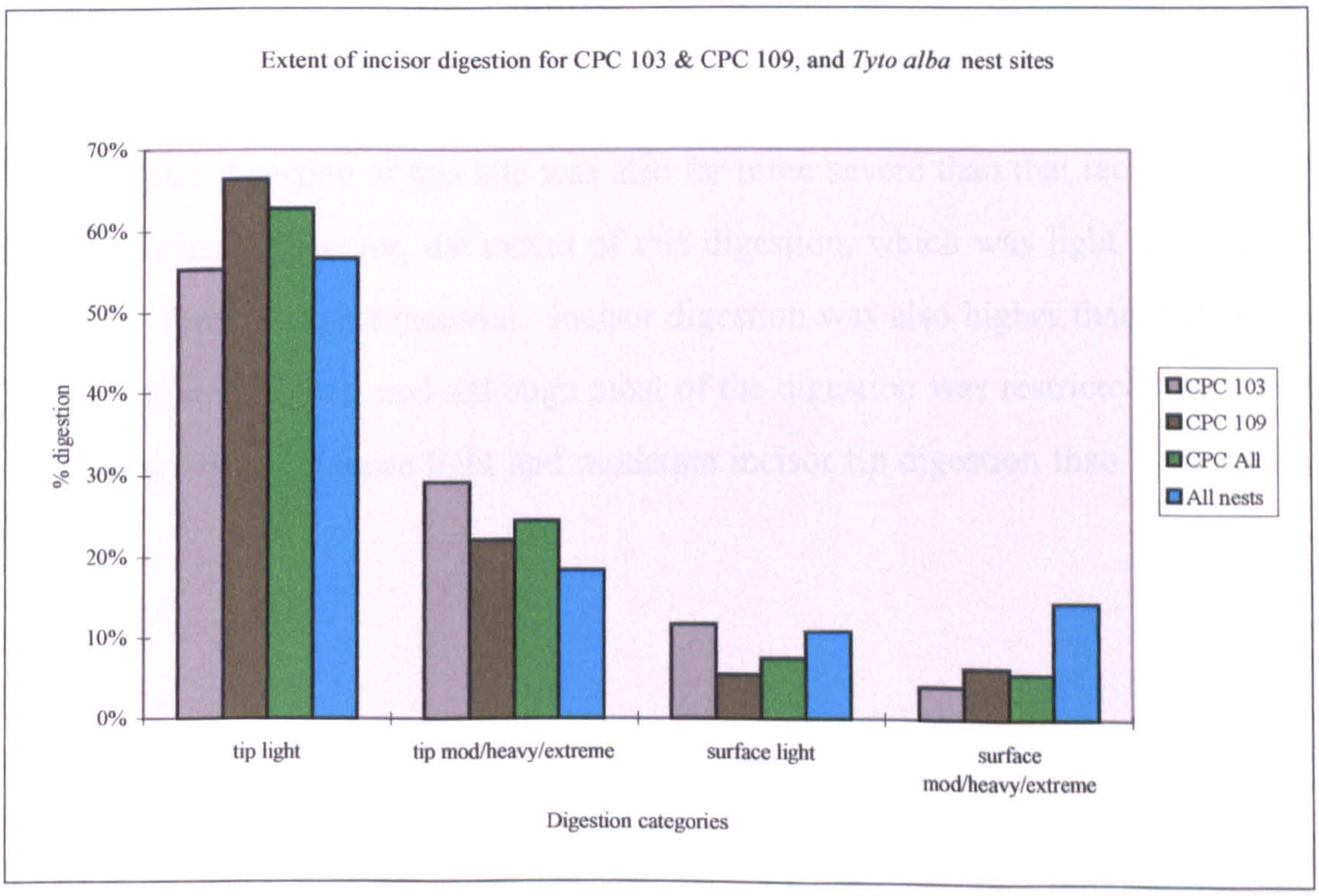


Figure 67. Comparison in extent of digestion between CPC contexts 103 and 109, and *Tyto alba* nest sites.

Closer analysis of these categories recording the extent of the digestion indicates slight differences between the digestion at Carsington Pasture Cave and that of *Tyto alba* nest sites. There was more light and moderate digestion at the incisor tips at Carsington Pasture Cave, compared with the modern nest sites, which in general had a greater incidence of digestion on the incisor surface, suggesting that the extent of digestion was slightly greater at the nest sites.

8.4.4.5 CPC – Conclusions

Analysis of the various taphonomic characteristics of the small mammals from Carsington Pasture Cave indicates that both bone breakage, and molar and incisor digestion were similar between the two contexts. Bone breakage, both cranial and post-cranial, was far more severe than that recorded for *Tyto alba* nest sites, and as the deposit from this cave has been shown to have remained where it was deposited, it is possible to rule out transportation or compression by overlying sediment as a mechanism for the bone breakage. The location of these deposits, resting on top of, and between the rocks of a collapsed boulder choke, however, suggest that it is possible that some of this damage may be attributed to trampling, either by other inhabitants and users of the cave, or by the accumulation agent themselves.

Molar digestion at this site was also far more severe than that recorded for *Tyto alba* nest sites. However, the extent of this digestion, which was light in nature, was similar to *Tyto alba* nest material. Incisor digestion was also higher than that recorded for *Tyto alba* nest sites, and although most of the digestion was restricted to the tips, it was characterised by more light and moderate incisor tip digestion than *Tyto alba* nest data.

9. Interpretation and Discussion

9.1 Introduction

The aim of this study was to carry out a taphonomic analysis of owl pellets, to add further to the accumulated knowledge reviewed within chapter 2. Previous reports on the degree of breakage and digestion for owl species (and especially *Tyto alba*) had concentrated on data mainly collected from adult birds. However, some authors also suggested that the rates of digestion and breakage were higher in young and baby owls (Raczynski and Ruprecht 1974; Andrews 1990). If this were the case, and high rates of digestion, not normally associated with *Tyto alba* were recognised, it is possible that this could lead to interpretations that deposits containing this degree of digestion had been deposited by a predator other than *Tyto alba*.

If such a difference does exist, and is quantifiably and significantly different from the adult *Tyto alba*, then it is important to realise that these results may have important implications for past and future small mammal taphonomies. To address these questions, an analysis of three *Tyto alba* nest sites was undertaken, and the data compared with that of two *Tyto alba* roost sites, and small mammal assemblages from four archaeological sites spanning the British Holocene. From the results, it is possible to draw a number of conclusions about both the taphonomy of *Tyto alba* nest material, and to make some suggestions about the four archaeological sites analysed within this study.

9.2 Data analysis techniques

For each site with more than one context, as well as the nests and the roosts, the data were displayed using both the data for the individual sites and also the sum of all of these contexts / samples combined, to give a total for this data set. This then could be used to indicate the variation in the amount of digestion in each context for example, from the combined result. In cases such as the incisor digestion for the nest sites, where both the mean and the individual scores were the same, this indicates a marked similarity between the samples analysed. In other cases, there was a marked variance between these individual data and the combined result. However, for most of these cases, the mean was closer to one of the samples than the others, and very often this was the sample with the largest number of recorded cases. This allows analysis of the problems of sample size to be explored, indicating where this variability may have resulted from samples with too few values in some of the variables, as was the case of Tadcaster and Fox Hole, where one or two of the contexts contained the majority of the sampled material.

In the case of Fox Hole, the results from the three contexts all gave similar results, that did not have too much effect on the data analysis techniques, especially when considering molar or incisor digestion. However, for Tadcaster it was more applicable to use the result of the combined data than the individual contexts when comparing these data with other sites, as the variability caused by low numbers of cases was reduced. It is however, important to fully analyse these different samples to ensure that the variability is the result of small sample size, rather than the possibility that the deposit has had multiple accumulators within different contexts. For example, at Tadcaster, context 17 was perhaps more similar to data for the *Tyto alba* roosts and context 11 and context 18 more similar to the *Tyto alba* nests. As the numbers of bones recorded for some of the these contexts was so low, the three contexts were merged together to form one data set. Similarly, all of the contexts from Filey were merged into one data set. The rest of the deposits, either roost, nest or archaeological site are used in the analysis in their original form.

9.3 Analysis of the digestion data

Within the last chapter, the results for the four archaeological sites were compared almost exclusively to those of the *Tyto alba* nest sites. The main reason for this was that the three nest sites constituted the main reference for bone breakage and digestion collected for this study. Furthermore, having demonstrated that there was a difference in the frequency of digestion recorded at *Tyto alba* roost and nest sites, it was not essential to include the data for both of these groups in all of the analyses. In the following section it is possible to compare the data from all of the sites together using both bi-variate and multivariate approaches, in order to shed light on the nature of the assemblages from the roosts, nests and archaeological sites. To add an extra dimension to the analysis, the results of the data collected for *Bubo bubo* (European eagle owl) have also been used to give a comparison with a bird which exhibits higher degrees of digestion than *Tyto alba* (Andrews 1990). For data on molar and incisor digestion for *Bubo bubo* see Appendix table 107, page 439, and Appendix table 108, page 441.

9.3.1 Frequency of digestion

One of the most informative methods of comparison is a scatterplot of the two most informative variables. In all cases the variables that have shown the greatest consistency and those that encompass the highest number of cases are 'total molar digestion' and 'total incisor digestion'.

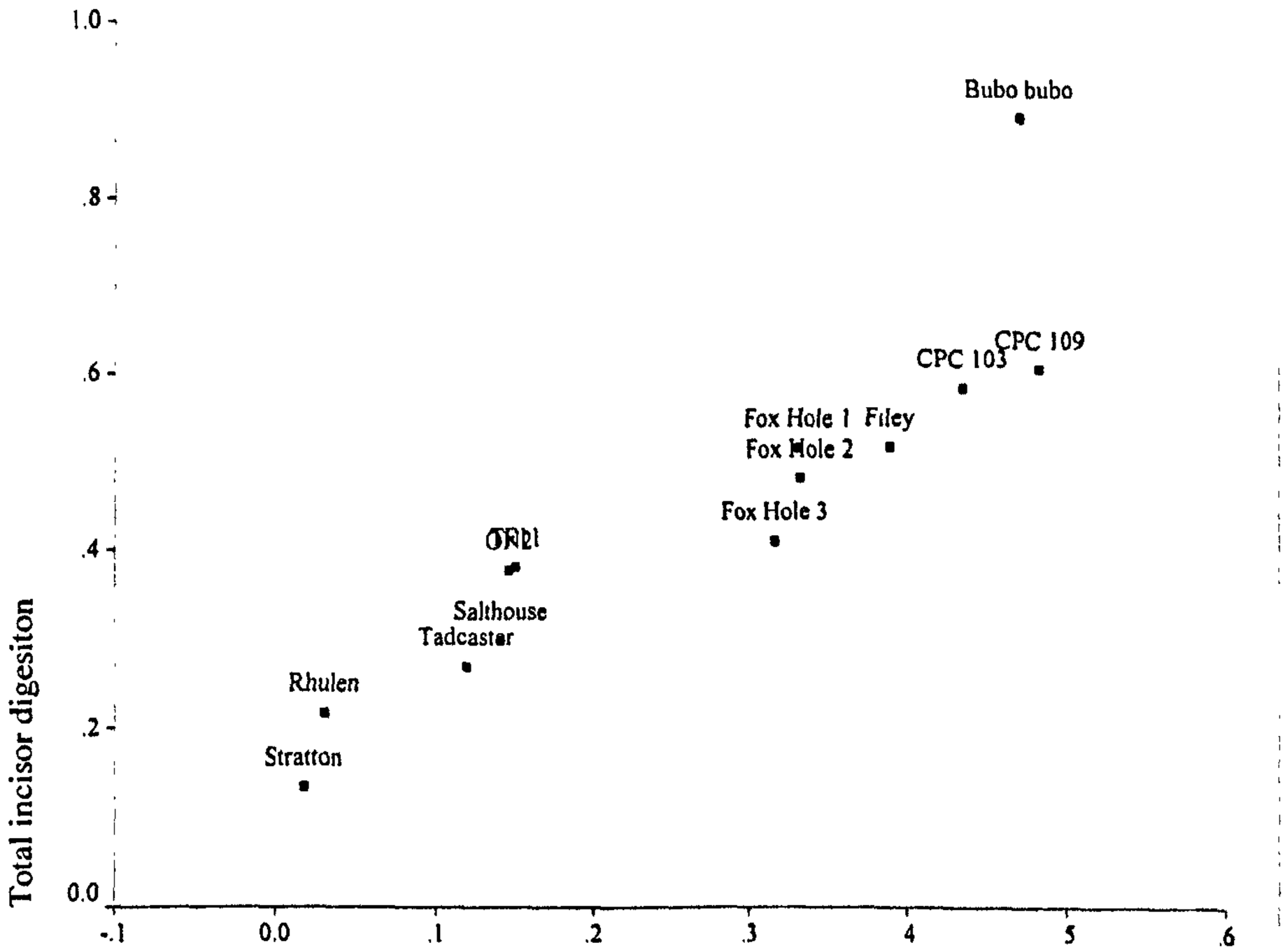


Figure 68. Scatterplot of molar digestion and incisor digestion.

As can be seen in the above diagram, the sites cluster into a number of clearly discrete groups. At the bottom left are the owls and archaeological sites that exhibit the least digestion, with increasing digestion on both the molars and incisors to the top right of the picture. Molar digestion increases from left to right and incisor digestion from bottom to top. There is a positive correlation between molar and incisor digestion, r = .908, Sig. = .000[81]. This graph displays only the frequency of digestion, and not the extent, which will be discussed later.

[81] Pearson's correlation, two tailed significance.

There are four clear groups indicated on the graph above:

1. roosts (Stratton and Rhulen)
2. nests (TF11, ON2 and Salthouse) and Tadcaster
3. Fox Hole, Filey and Carsington Pasture Cave (CPC 103 & CPC 109)
4. *Bubo bubo.*

The first group, comprising the roost sites have very similar results for molar digestion, but the two sites are separated by a higher level of incisor digestion at Rhulen. Similarity in molar digestion is also a significant feature in the second group, the nests and Tadcaster. This group could in effect be divided into two groups, TF11 and ON2 (1), and Salthouse and Tadcaster (2). As has been suggested in the previous chapter, the digestion of both the molars and incisors at Salthouse and Tadcaster is slightly lower than that of the other two nest sites, and it is likely that these sites represent an admixture of material derived from both adult and baby owls. This is further confirmed by their placement within this diagram, positioned between the roost and nest sites.

If this roost and nest data are analysed using ANOVA, the differences between these two groups are also corroborated. For example when molar digestion is considered, the most parsimonious grouping is roosts (group 1), and TF11, ON2, Salthouse and Tadcaster (group 2) – "F"= 108.112, "P" = .000'. Equally, splitting these sites into three groups for molar digestion, (roost (group 1) nests - TF11 & ON2 - (group 2) and Salthouse and Tadcaster (group 3)) also produces significant results – "F" = 86.513, "P" = .002. However, no significant results are obtained if the roosts, Salthouse and Tadcaster are grouped together (group 1) against the nests - TF11 and ON2 - (group 2) – "F" = 2.361, "P" = .199, indicating the results of Salthouse and Tadcaster are closer to the nest sites, than the roosts. None of the three analyses produces significant results for the analysis of total incisor digestion. This is not entirely surprising as whilst molar digestion in the graph above (x axis) is divided into a number of discrete groups, the incisor digestion is represented by an almost straight line of steadily increasing values.

When the above data are analysed with the data from the archaeological sites and *Bubo bubo* added to the ANOVA analysis, the results are more significant for both

the molar and incisor digestion variables. The groups used in this analysis are as follows:

1. Stratton and Rhulen.
2. TF11, ON2, Salthouse and Tadcaster
3. Fox Hole (samples 1, 2 & 3) and Filey
4. Carsington Pasture Cave (CPC 103 & CPC 109)
5. *Bubo bubo.*

The table below shows the "F" and "P" values for the variables used in this analysis.

Variable	**"F"**	**"P"**
In situ molar digestion	8.273	.006
Isolated molar digestion	37.575	.000
Total molar digestion	130.717	.000
Lower incisor digestion	30.112	.000
Upper incisor digestion	32.759	.000
Total incisor digestion	43.018	.000

Table 35. ANOVA analysis of variance of standardised molar and incisor digestion.

The results above represent the groupings that produce the highest "F" and lowest "P" values. However, there are a number of variations in these groups that also produce significant results, but with lower "F" values. These include designating the nests, roosts and Tadcaster to one group, the archaeological sites to a second with *Bubo bubo* in a third. Further variations include placing Carsington Pasture Cave with Fox Hole and Filey, and splitting the group with the nests, into two, one with ON2 and TF11, the other representing Salthouse and Tadcaster.

The ANOVA test calculates the difference between the variation within groups compared to between groups. The high "F" values and low significance "P" values, indicate that there is greater variation between data used to form the groups than within the groups themselves. A plot produced from the principal component analysis (PCA) of these results also indicates similar conclusions, as can be seen below.

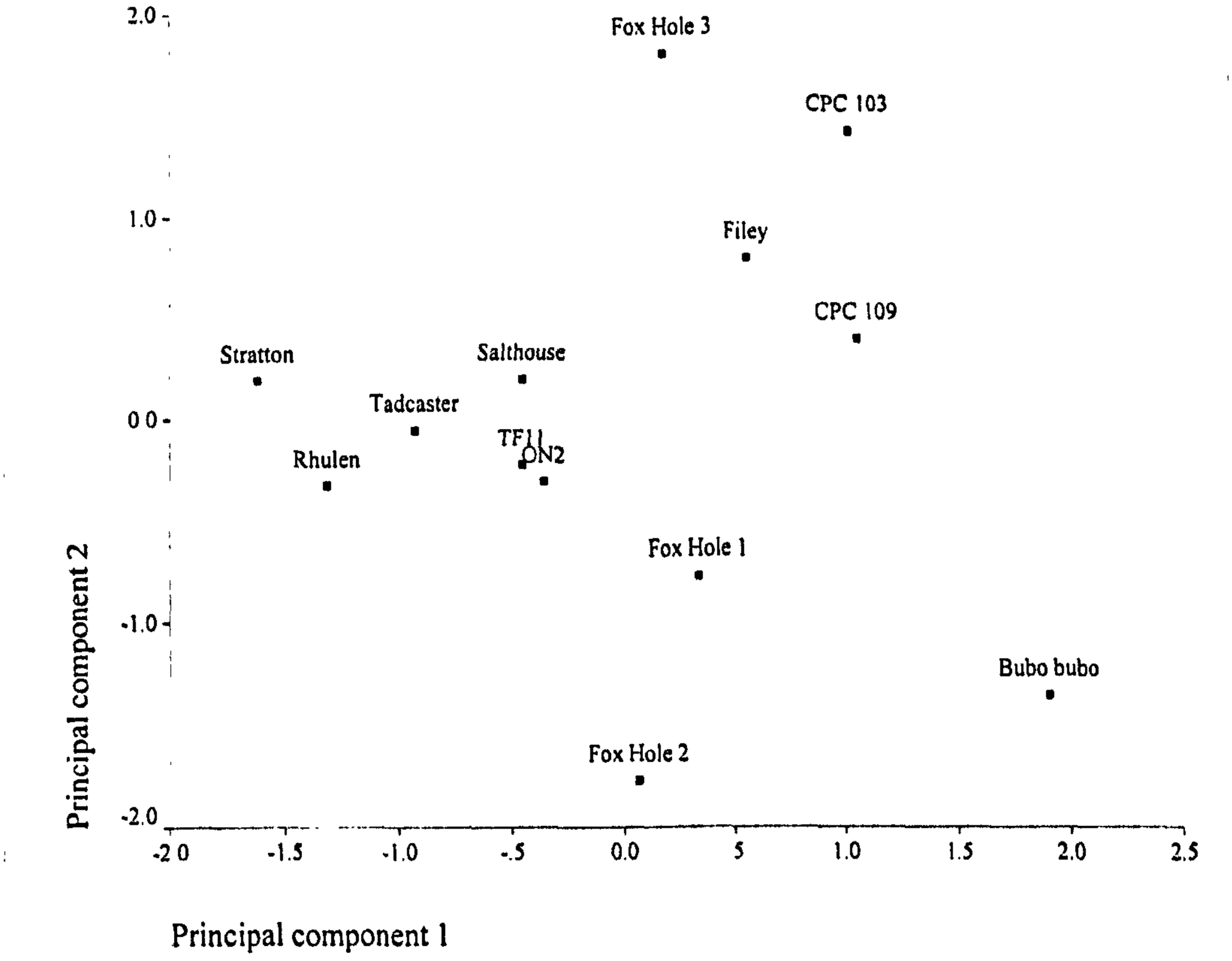


Figure 69. Principal component plot of *in situ* and isolated molar, and lower and upper incisor digestion.

The difference in the grouping between the scatterplot of molar and incisor digestion and this principal component plot, is a product of sampling different variables for the PCA, (in situ and isolated molar, and upper and lower molar digestion) namely those variables that are combined in the categories of total molar and incisor digestion. As a result, the variability of these other categories is more visible. The first principal component which accounts for 89% of the variance between the samples, is situated on the x axis in the plot above. This component corresponds to the frequency of digestion in the samples. In the plot it can be seen that the lowest digestion is found at Stratton and the highest with *Bubo bubo* (EEO).

The second principal component, which accounts for only 6% of the variation and gives the diagram the vertical variation (y axis) represents the variability in the ratio of molar and incisor digestion. It is also possible that this component is picking up variation in sample size more than any clear patterns produced by the predators responsible for the accumulation of the assemblage.

9.3.2 Extent of digestion

Principal component analysis was also carried out on the data collected for the extent of digestion. Unlike the data for the frequency of digestion, there were no summary variables, such as total molar digestion and total incisor digestion, for which bi-variate plots and analysis could be sought. It was therefore essential to utilise multivariate statistical methods to analysis this data. The PCA plot of this analysis (which has not been standardised for prey species biases) is shown below. From this plot, and the data that were used to produce it, it is possible to discern certain patterns associated with the extent of digestion at these sites.

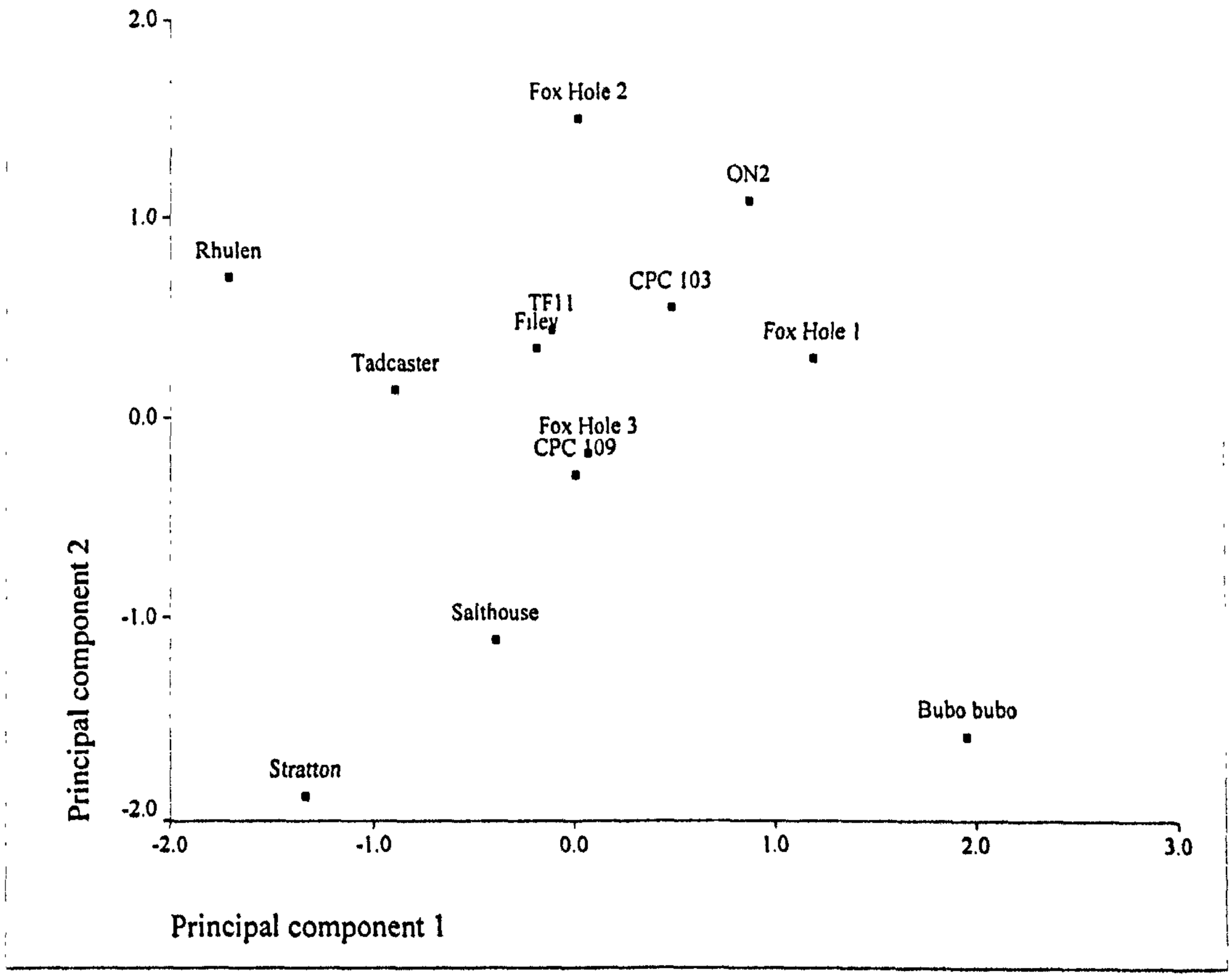


Figure 70. Scatterplot of the extent of digestion.

It is clear from the diagram above that none of the sites sampled in this study have the same extent of digestion as *Bubo bubo*, which includes far greater levels of moderate, heavy and extreme digestion. It is also important to point out that this first PCA plot is not in any way associated with the data on the frequency of digestion. In this analysis,

two potential data sets are being sampled, the extent of digestion on the molars, and the extent of digestion on the incisors. For each of these two categories, four variables were recorded. A percentage was calculated for the amount of digestion associated with each of these variables, based on the total recorded for each set of four variables. The extent of digestion therefore is sampling the location of the digestion irregardless of its frequency, so 50% of the digestion can be located at the incisor tips for a site which has 10% incisor digestion or 100% incisor digestion. The variables recorded were:

Molars – molar digestion light, molar digestion moderate, molar digestion heavy and molar digestion extreme.

Incisors – incisor tip light, incisor tip moderate, incisor tip heavy, incisor tip extreme, incisor surface light, incisor surface moderate, incisor tip heavy, incisor tip extreme.

Only the first two variables for the molar digestion were used, as the remaining two variables often contained no data. The incisor digestion categories were grouped into four variables to reduce the effect of sample size biases, that could have occurred if all eight variables were used. These four variables were: incisor tip light, incisor tip moderate/heavy/extreme, incisor surface light, incisor surface moderate/heavy/extreme.

9.3.3 Frequency and extent of digestion

It is possible to combine the results from the analysis of the frequency and also the extent of digestion to produce a PCA plot. This is done by using weighted values for the extent of digestion. In the last analysis of the extent of digestion, the percentage values represented the amount of digestion for that variable, divided by the total number of teeth, minus the number of undigested teeth. For example:

$$\textbf{\% molar light} = \frac{\text{N° of lightly digested molars}}{\text{total digestion molars}} = D^a$$

$$\nearrow$$

$$\text{(total molars – number of undigested teeth)}$$

In this analysis, the number of un-digested teeth (for example molars) is not subtracted, and the results therefore represent the percentage of digestion for all teeth (D^b), rather than a percentage figure of only the digested teeth (D^a). This is demonstrated in the example of *Tyto alba* and *Bubo bubo* incisors below.

	% digested teeth	% digestion for all teeth	% digested teeth	% digestion for all teeth
Incisors	*Tyto alba* (D^a)	*Tyto alba*, weighted (D^b)	*Bubo bubo* (D^a)	*Bubo bubo*, weighted (D^b)
% tip light	94%	15%	44%	40%
% tip mod/heavy/extreme	6%	1%	21%	19%
% surface light	0%	0%	13%	11%
% surface mod/heavy/extreme	0%	0%	22%	19%

Table 36. Example of weighted and un-weighted extent of incisor digestion using *Tyto alba* and *Bubo bubo* incisors.

The data for the extent of molar and incisor digestion for each site were converted in this fashion and used in principal component analysis (variables same as previous page). To extract all of the potential variation from the data, the principal components were rotated using Direct Oblimin rotation (an oblique - non orthogonal - method of rotation). This allowed for inter-correlated factors to be recognised and used in the construction of the PCA plot. This is born out by comparing the rotated and un-rotated PCA plots, discussed in Appendix notes - section 5, page 286.

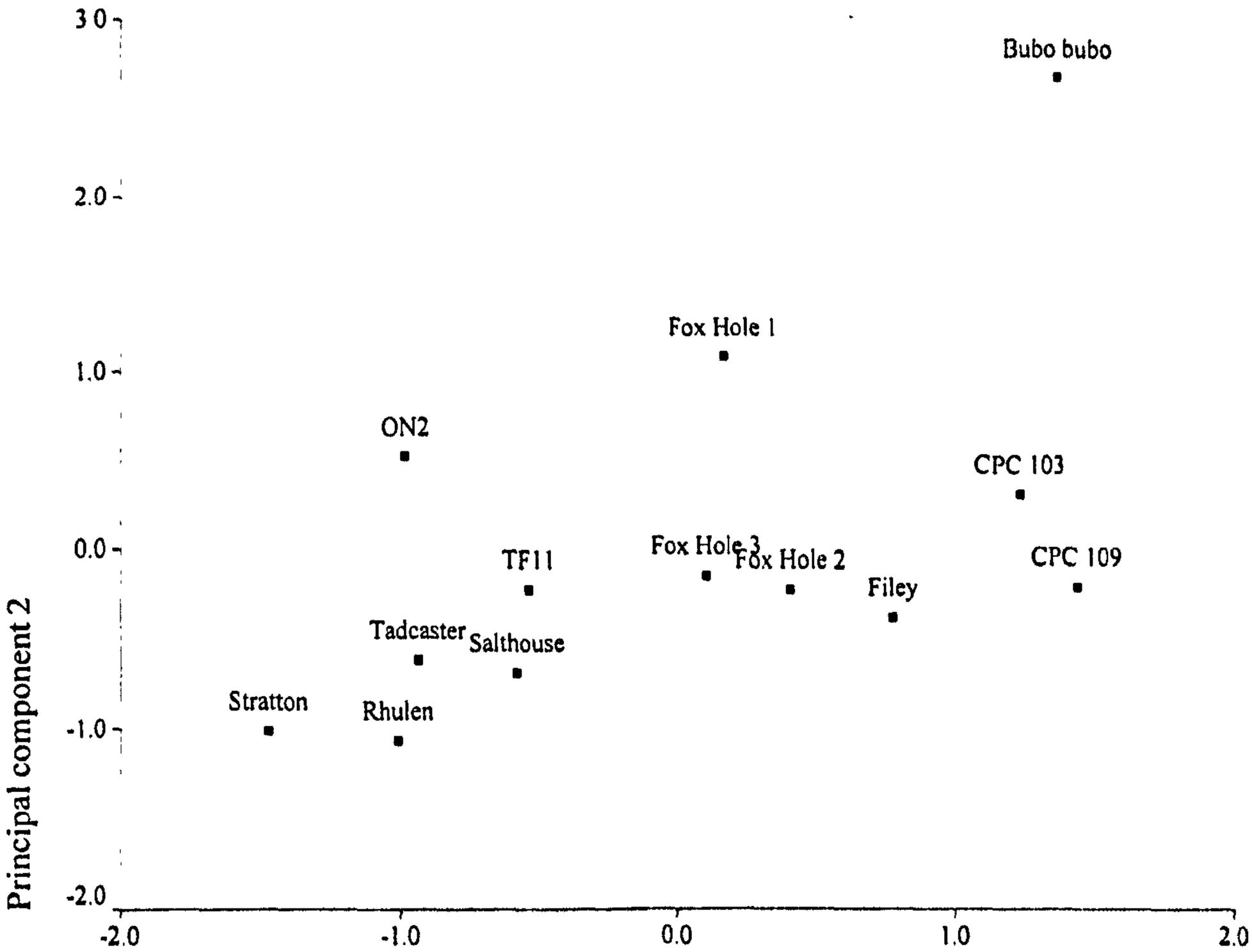


Figure 71. PCA plot of weighted extent of digestion, direct-oblimin rotation.

The PCA plot demonstrates that there is a difference between the weighted extent of digestion for the sites sampled here. The x axis, (principal component 1) accounts for 75% of the variance between the samples, and accounts for the frequency of digestion, mainly comprised from the digestion data from the molar light and incisor tip light categories. A further 15% of the variance is represented by principal component 2, which accounts for the distribution of the digestion across the various categories of the extent of incisor digestion. The highest values for the second principal component represent the sites with high values for incisor surface digestion, and the lowest values for the sites with only limited incisor surface digestion. The remaining 10% of variation is made up by the remaining 4, unselected components. On both the x and y axis, the principal components indicate a general trend of high digestion at the positive end of the component plot, to the right of the plot on the x axis and the top of the plot on the y axis.

This plot is also similar in shape and composition to the scatterplot of molar and incisor digestion discussed at the beginning of this chapter. The main differences are associated with the placement of three sites, ON2, Fox Hole 1 and *Bubo bubo.* The remaining ten cases exhibit similar placement, and grouping as shown in the aforementioned scatterplot. The principal reason for this difference is that these three sites exhibit much higher levels of incisor surface digestion than the other sites, and it is this variation that has been reproduced as the second principal component in the rotated PCA plot. The variables used to produce the PCA plot were also subjected to ANOVA, with different identified groups than in previous analysis, to take account of the variation shown in the PCA plot. As can be seen below, half of these variables produced significant results, with relatively high "F" values. The groups used in the analysis were:

1) Stratton, Rhulen, TF11, Salthouse and Tadcaster.
2) ON2.
3) Filey, Fox Hole 2 and Fox Hole 3.
4) Fox Hole 1.
5) CPC 103 and CPC 109.
6) *Bubo bubo.*

Only one other permutation of these cases provided significant results (1 – Stratton, Rhulen, TF11, ON2, Salthouse, and Tadcaster; 2 – Filey, Fox Hole 1,2,& 3, and CPC 103 &109; 3 - *Bubo bubo*), although with lower "F" and "P" values.

Digestion category	**"F"**	**"P"**
Molar light	44.056	.000
Molar mod/heavy/extreme	68.523	.000
Incisor tip light	6.070	.017
Incisor tip mod/heavy/extreme	7.920	.008
Incisor surface light	5.383	.024
Incisor surface mod/heavy/extreme	51.089	.000

Table 37. ANOVA analysis of variance of the extent of digestion.

The conclusion that can be drawn from this analysis is that the variability of results (for some variables), of the *Tyto alba* roost and nest sites (including Tadcaster, but excluding ON2) is lower compared to groups containing Filey, Fox Hole, Carsington Pasture Cave, and *Bubo bubo,* using data for the weighted extent of digestion. Equally, there is also some similarity, although not as significant, if ON2 is included in the group along with the other *Tyto alba* roost and nest sites.

9.3.4 Very light digestion

During the analysis of the *Tyto alba* nest sites ON2 and TF11, a very light category of digestion was recognised, and because it was felt that this could be indicative of *Tyto alba* nest deposits, this digestion was recorded along side the other data on digestion, for each pellet assemblage and archaeological site. However, in the initial analysis of the data for incisor digestion it was discovered that as this category of digestion was so variable that it reduced the similarity of the results of incisor digestion from each site. It was therefore removed from the main analysis, and will considered separately below. The data are in Appendix table 100, and Appendix table 101, from page 402.

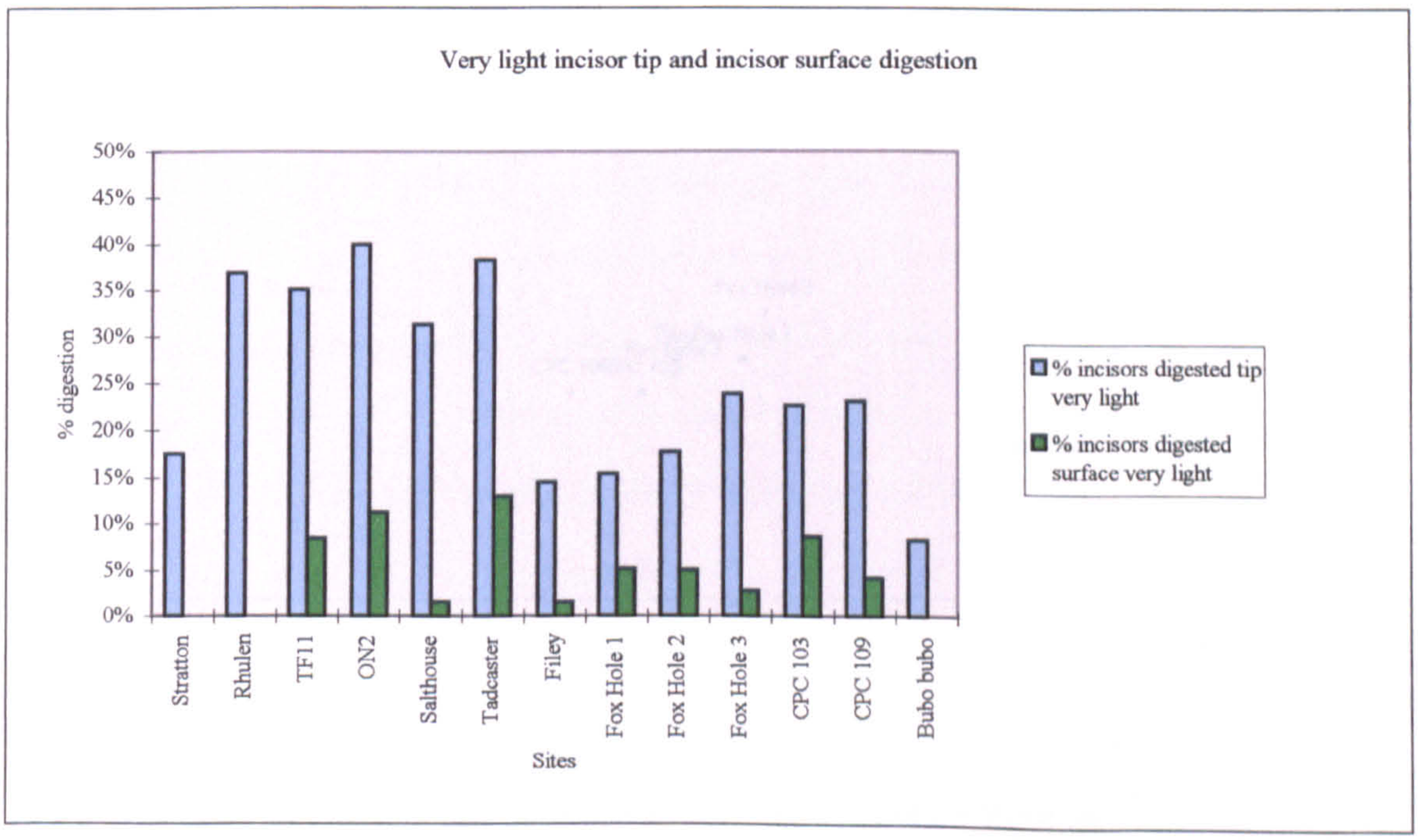


Figure 72. Comparison between very light incisor tip and incisor surface digestion.

There is a clear indication that the majority of this very light digestion is associated with the *Tyto alba* nest sites (as well as one roost site Rhulen). The percentage figures for digestion represent the % of very light digestion out of all of the digested teeth. The most very light incisor digestion occurs at the incisor tips, and can be seen as the first step in the process of digestion, where the enamel surface has not yet been penetrated down to the dentine, but has had the upper surface modified so that the incisor no longer retains it's shiny appearance.

The highest frequency of this very light digestion was found at ON2, whilst the lowest in the *Bubo bubo* assemblage. Equally, a low frequency of incisor tip digestion was recorded at the roost site of Stratton, but not at Rhulen. Neither of the two roost sites showed any evidence of very light incisor surface digestion, and this was also absent from the results of *Bubo bubo.*

To enable a clearer visualisation of the results, a scatterplot has been produced, showing very light incisor tip digestion against total incisor digestion. The total incisor digestion category does not contain data for very light digestion.

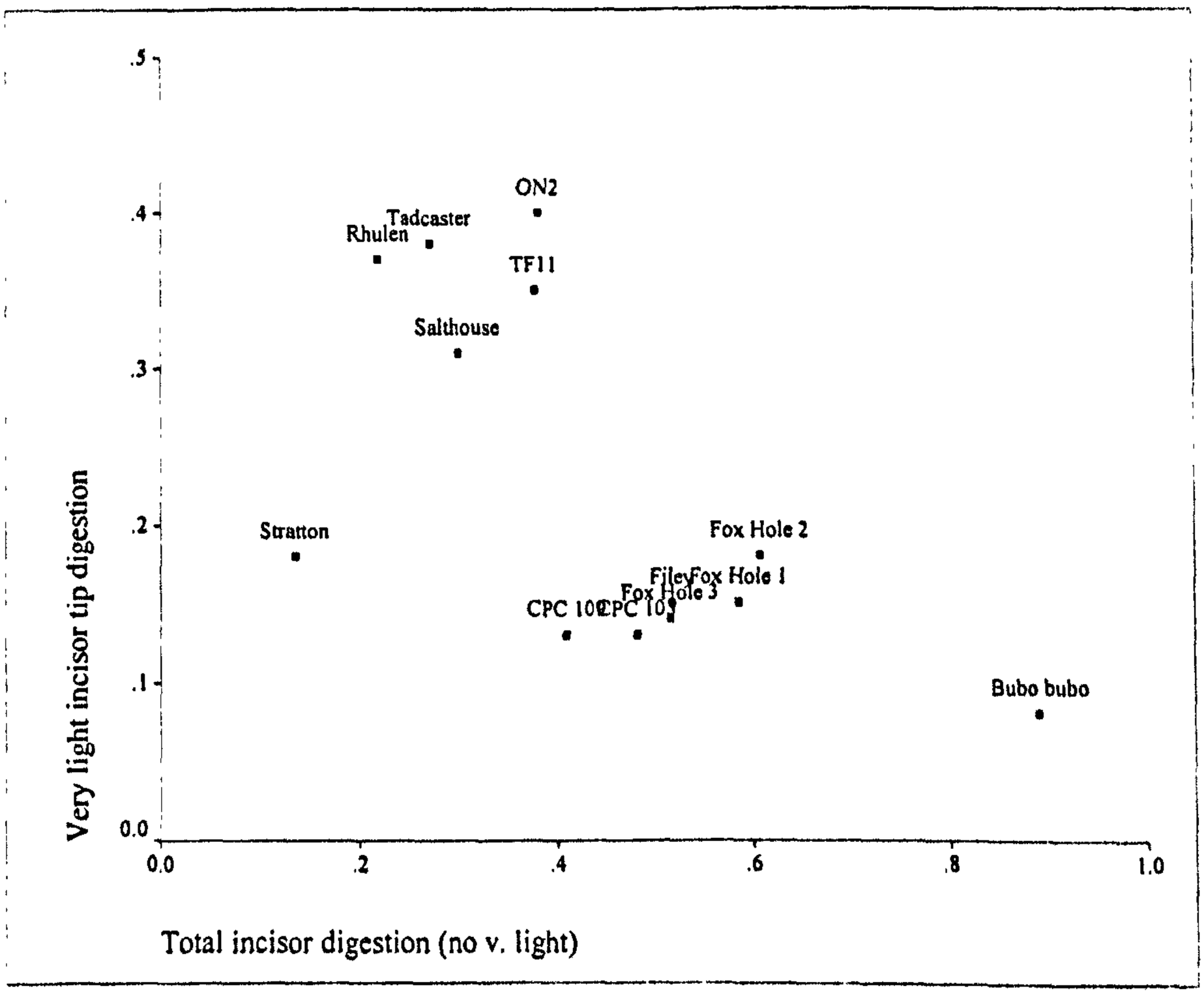


Figure 73. Scatterplot of total incisor digestion and very light incisor tip digestion.

This scatterplot shows that the amount of very light digestion was significantly high at the nest sites, Tadcaster and Rhulen, when compared to the other archaeological sites, and especially *Bubo bubo.* The low levels of very light incisor digestion at Stratton are also mirrored in the low levels of all incisor digestion at this site, 14% compared with 22% at Rhulen. However, when this difference is considered in term of the number of teeth digested, then the difference is only a matter of a few extra digested teeth.

By plotting the amount of very light incisor digestion against the total incisor digestion it is also possible to see that there is a significant drop off in the frequency of very light digestion as total incisor digestion increases. This indicates that at sites with higher frequencies of digestion, the extent of that digestion is often higher, with less very light digestion, as those teeth that may have been very lightly digested have been more extensively affected. This negative correlation is also supported by Pearson's correlation, r= -.631, "P" = 0.021 (significant at 0.05 level – two tailed test).

9.3.5 Summary of digestion analysis

As can be seen from the analysis of the digestion data, there are a number of significant points that have been identified and tested in this chapter, which are reiterated below.

- There is a difference in the frequency of incisor and molar digestion between the roost sites (Stratton and Rhulen) and nest sites (ON2 and TF11).
- Higher frequencies of digestion are recorded at the nest sites.
- Two sites were identified (Salthouse and Tadcaster) that exhibited frequencies of digestion that fell between the data for roost and nests, suggesting that they represented an admixture of both of these two accumulations.
- The frequency of molar digestion for the three other archaeological sites (Fox Hole, Filey and Carsington Pasture Cave) was at least twice as high as that recorded for the roost or nest sites.
- The frequency of incisor digestion for these three sites did not exhibit such a marked increase, but was higher in all cases.

- The data for *Bubo bubo*, (added to the analysis for comparison as a species with higher digestion) indicated higher levels of molar digestion than all but Carsington Pasture Cave, and considerably higher frequencies of incisor digestion than any other site or pellet assemblage.
- Data on the extent of digestion indicated that there was a similarity between the roost and nest sites when compared with the other data.
- Within this analysis three sites (ON2, Fox Hole 1 and *Bubo bubo*) stood out as exhibiting higher levels of incisor surface digestion, relative to the other sites with which they shared similar results on the frequency of digestion.
- At no site was the frequency or extent of digestion as severe as that recorded for *Bubo bubo.*
- The very light digestion occurs mainly in the nest sites, and also Tadcaster and Rhulen.
- There is a significant negative correlation between very light incisor digestion and total incisor digestion, indicating that as total incisor digestion increases, the incidence of very light incisor digestion decreases.

9.4 Breakage – post or pre depositional

9.4.1 Introduction

Analysis of the breakage of post-cranial bones was used as a criteria to recognise predatory origin in a number of early taphonomic studies (Dodson and Wexlar 1979; Korth 1979), and a detailed account of bone breakage criteria was given by Andrews (1990). However, it has been shown that there is a level of inter-species variability in the results of this analysis[82] (Saavedra and Simonetti 1998), whilst Andrews (1990: 64) and Fernandez Jalvo (1996) also point out that post-depositional agencies can mask the predatory origin as a result of further breakage. The extent to which this category provides a useful methodology is therefore dependant upon the depositional history of the deposit, and if this is known, it may be possible to utilise this category of analysis.

In this study the range of breakage recorded from different sites has fluctuated by often large amounts, and in many cases cranial breakage has been much higher than post-cranial breakage. As there are many possible non-predatory agencies that can cause bone breakage, the post-depositional histories of each of the sites will first be considered, before any analysis of the breakage data for these sites takes place.

9.4.2 Bone breakage for *Tyto alba* nest sites

As indicated in the last chapter, bone breakage at the three nest sites sampled in this analysis was slightly higher than that recorded for the adult *Tyto alba* roost deposits. For the most part this breakage differed by only 5-10% from the roost samples, and is likely to represent either trampling or prey dissection activity associated with nesting behaviour by both the adult and baby birds. The breakage resulting from this trampling is limited in the samples taken from nest boxes, as the accumulation of fur and bones from previous occupations acts as a cushion against high levels of bone breakage.

---

[82] An analysis of the results of the study by Saavedra and Simonetti (1998) indicate that the variation for post-cranial breakage is between 88% and 94% of complete elements. For the purpose of this study, these results are still well within the variation recorded for the owl species by Andrews (1990). It is also difficult to make direct comparisons between these two studies, as the post-cranial elements were all grouped into one category by Saavedra and Simonetti, which will have had the affect of masking the differences in weakness of specific bones, that are more liable to be affected by breakage.

9.4.3 Evidence of the origin of bone breakage for the archaeological sites

There is certainly one site in this study where one may assume that little post-depositional movement and therefore modification, has occurred. At Carsington Pasture Cave, it is likely that the bones have remained where they were deposited, and it is certain that very few of them have moved from this original position. Equally, as they were discovered on the surface, sediment compaction is also unlikely to have had an affect upon the bones. However, these bones are extremely damaged, and bear no resemblance to the published bone breakage criteria for owls.

Therefore, either the breakage occurred before deposition, or the breakage is the result of severe trampling. If the breakage is pre-depositional, it would indicate that either the depositional agent was a mammalian carnivore, or that the small mammals were being dissected before being eaten, which does occur when parents are feeding their chicks. However, there is no other evidence that the bones at this site have been deposited by a mammalian carnivore, as the amount of digestion does not match the intensity of that recorded for these predators.

Equally there is no evidence of characteristic carnivore damage, such as gnawing and bite marks, usually associated with these assemblages, and whilst the breakage at this site is high, it does not reach the intensities usually recorded for these animals. Analysis of the prey species represented in these two contexts also indicates that the predator responsible is not likely to be a mammalian carnivore, as larger prey species, such as *Lepus* (hare) and a wide range of bird species, commonly found in the diet of canids, mustelids and felids (Andrews 1990: 206-209) are absent[83]. Therefore, it is likely that the breakage is a result of trampling by the owls (or other animals coming into the cave), on a hard and rugged surface, which has led to far greater fragmentation than is found at the nest sites sampled in this study.

The other site where it is possible that little post-depositional breakage has occurred is Tadcaster. At this site around half of the material comes from the upper levels of a garderobe, where sediment compaction, movement or trampling by large animals is unlikely to have been an issue. As a result, very few of the post-cranial

---

[83] It is however recognised that absence of evidence is not evidence of absence.

bones have been severely broken, and the pattern of bone modification is very similar to that recorded for *Tyto alba* nest sites. The amount of damage recorded for these sites is only slightly greater than recorded by Andrews (1990) for the *Tyto alba* pellet material (from adult owls), and probably represents breakage that has occurred either as a result of dissection of the prey by the adults for feeding to the young chicks, or as a result of trampling in the nest site. There was slightly more breakage from the contexts at the base of the deposit (17 and 18) probably caused by compaction and the inclusion of large angular clasts within this part of the garderobe.

Post-cranial bone breakage is also high at the other two sites, and again it is suggested that the origin of this breakage is post-depositional, and in both cases the result of trampling and sediment compaction. The area excavated at Filey was the courtyard, where even occasional usage would result in bone breakage though trampling, and the material from Fox Hole came from the central passage of the cave, a thoroughfare that would have been in repeated usage by the numerous inhabitants and visitors (human and animal) to the cave. As has been suggested with the deposits from the nest boxes, even limited trampling can lead to bone breakage. Therefore, trampling by larger animals than owls is likely to lead to much higher levels of bone breakage. This is demonstrated in Table 38 below.

The table shows the percentage bone breakage of an excavated sample of small mammal bones (from a *Tyto alba roost*) taken from a loose sandy deposit from the surface of Rainbow Cave in South Africa, where footprints in the excavated area attested to recent visits to the cave by humans, small ungulates, baboons and monkeys (Williams 1997). These data is compared with that of adult *Tyto alba*, and *Tyto alba* nest material, data from Andrews (1990) and this study. As can be seen in this table, even the action of trampling in soft sediment can lead to breakage of the long bones. In more compact samples the amount of bone breakage through trampling could be even higher.

	Tyto alba roosts	TF11	ON2	Salthouse	Rainbow Cave
Humerus					
complete	99%	89%	90%	78%	90%
proximal	0%	0%	3%	13%	1%
distal	0%	9%	7%	3%	1%
shaft	1%	2%	1%	8%	8%
Ulna					
complete	97%	96%	87%	85%	66%
proximal	3%	2%	12%	15%	33%
distal	0%	0%	0%	0%	0%
shaft	0%	1%	1%	0%	1%
Femur					
complete	97%	91%	95%	95%	84%
proximal	1%	9%	5%	2%	16%
distal	2%	0%	0%	3%	0%
shaft	0%	0%	0%	0%	0%
Tibia					
complete	98%	94%	92%	88%	80%
proximal	1%	2%	3%	9%	8%
distal	1%	2%	3%	0%	0%
shaft	0%	2%	3%	3%	12%

Table 38. Comparison of post-cranial breakage for *Tyto alba* roosts (Andrews 1990), *Tyto alba* nests (this study) and a trampled deposit Rainbow Cave, South Africa (Williams 1997).

9.4.4 Summary of bone breakage data

In this study, the amount of bone breakage recorded at the *Tyto alba* nest sites, and four archaeological sites has been compared with *Tyto alba* roost data collected by Andrews (1990). For each archaeological site, the possibility that the breakage is a result of post-depositional breakage has also been investigated and is displayed in the table below.

Site	**Pre- or post-depositional breakage**	**Cause of breakage**
Tadcaster	Post-depositional	Limited amount, similar to that recorded for *Tyto alba* nest sites.
Filey	Post-depositional	Relatively high, associated with trampling of archaeological deposit.
Carsington Pasture Cave	Post-depositional	High levels of breakage, however no evidence of mammalian predatory origin, sediment transportation or compaction, or trampling by large animals. Also likely to represent trampling by nesting bird, but on hard deposit, with nothing to cushion the bones.
Fox Hole	Post-depositional	Evidence of both sediment compaction and trampling, with evidence for many different mammal species utilising the cave at various times.

Table 39. Origin of the bone breakage at the archaeological sites.

9.5 Location of material collected, and analysis of the suitability of the site as nest

Three *Tyto alba* nest sites were analysed to produce a set of taphonomic criteria that could be used to recognise *Tyto alba* nest material in archaeological deposits. These archaeological deposits were selected for this study on the basis of a number of criteria that suggested that they had the potential to have been deposited as *Tyto alba* nest material. This information is re-capped below as a prelude to an examination if the possible predatory origin of these deposits

9.5.1 The Old Vicarage, Tadcaster

The material from this site came from a deposit excavated during the course of building work. The deposit came from an abandoned structure, a common roosting and nesting site used by *Tyto alba*. The initial analysis of the site had suggested that the location of the deposit and the nature of the small mammal assemblage suggested that it was possible that this site represented a *Tyto alba* nest site. The most suggestive piece of evidence recovered from this site was the discovery of a complete juvenile owl, identified as *Tyto alba*, within context 17 (Dobney 1998).

9.5.2 Roman Signal Station, Filey

The material from Filey Roman signal station was investigated as the report of the biological remains from the site contained an appraisal of the small mammal remains, with an analysis of the digestion of the incisors and molars (Dobney *et al.* 1996). The amount of digestion was higher than had been recorded by Andrews (1990) for *Tyto alba* pellet deposits, although still within the range of a category one or two predator. It was therefore possible that this deposit had been accumulated as part of a *Tyto alba* nest deposit. The location of this assemblage, within an abandoned building complex, also suggested that it could have provided an ideal location for nesting owls.

9.5.3 Fox Hole Cave, High Wheeldon

One of the remarkable things about this site is the sheer numbers of small mammal bones excavated from the cave, and the care that was taken at the time of excavation to recover as much bone and archaeological material as possible. It was felt that the high concentration of small mammal bones within such a confined location could indicate a prolonged usage of the cave by a nesting or roosting owl. In the most detailed of his analyses of the small mammals from this site, Bramwell suggests that it is unlikely that the deposit could have been produced by an owl because much of the area of accumulation was outside of the daylight zone of the cave (Bramwell 1971). However, there is clearly a difference in the light sensitivity of human eyes compared with those of an owl, and it is possible that the area of deposition was suitably light for a nesting owl. Equally, the location deep within the cave will also have provided some protection against unwanted intrusions.

9.5.4 Carsington Pasture Cave, Brassington

The issue of the penetration of light into the depths of the cave is also an issue to consider with the small mammal accumulation at Carsington Pasture Cave. However, it is not as easy to test this theory as the original entrance into the cave, used by whoever accumulated the small mammal remains is no longer visible. However, the location of the deposit deep within the cave would certainly have afforded protection and privacy for the occupants. When the shape of the cave structure is considered, then it is possible to differentiate between the options of an owl roost or nest. There are no ledges for the owl to have been roosting on (perching) in the roof, which is only approx 1-1.5 metres above the cave floor.

As the deposit was distributed across an area of about three metres in length, it is possible that it could represent a number of different nests. However, it could be the result of only one period of nesting activity, with the spread of pellets representing the movements of the young owls away from the central nest areas to separate areas of the cave. This has been recorded to take place about four weeks after hatching, when the

chicks have developed the ability to 'walk' around (Walker 1973: 9; Voous 1988: 17). It was also considered that the sheer mass of small mammal material, its relatively well preserved nature, and undisturbed nature could only have resulted from an owl nest.

Due to the policy of total collection operated during the excavation of this cave, it is likely that most of the bones deposited at this site have been recovered. Therefore the number of individuals present should shed some light on the length of time the cave was utilised. From the numbers present it is suggested that this site was only occupied for a few years at the most, or used very intermittently over a longer period of time.

9.6 Possible predatory origin of the archaeological sites

The principle aim of this investigation was to ascertain whether it was possible to differentiate between the taphonomic signatures produced by adult and baby owls. This has been clearly demonstrated throughout the last two chapters. The second aim of this study was to investigate whether these taphonomic signatures could be recognised in the archaeological record, using material from four archaeological sites, which as has been demonstrated above, were thought to have been accumulated as the result of *Tyto alba* nesting activity. It is important therefore to reiterate that the aim was to investigate whether the small mammals at these sites could have been deposited as part of a *Tyto alba* nest. At sites where the data did not match that collected for *Tyto alba* nests, it was not the purpose of this research to identify the predator (beyond all reasonable doubt) of these assemblages.

It was also not possible to identify the predatory origin of the archaeological sites if they did not match the data for *Tyto alba* nest or roost deposits. This was because this investigation had used slightly different methods of analysis to previous studies on small mammal taphonomy (see for example Andrews 1990; Fernandez-Jalvo and Andrews 1992; Fernandez-Jalvo 1995; Fernandez-Jalvo 1996; Fernandez-Jalvo *et al.* 1998), and comparisons using data collected on the frequency and extent of digestion was not comparable to that used in these previous studies. This difference in recording techniques had arisen because it was necessary to catalogue all digestion, however light, in this study, in order to differentiate between the nest and roost sites.

There are however a number of points of comparison that can be made between the data in this study, and that collected by Andrews (1990). At all of the sites, the digestion is heavier than that recorded for *Tyto alba* (roosts or nests), and lighter than *Bubo bubo.* Therefore, using the scale of digestion produced by Andrews (1990: 75), it is possible that the small mammal bones at these sites could have been accumulated by any predator with a higher frequency of digestion than *Tyto alba* and a lower frequency than *Bubo bubo.* In Britain, during the Holocene, this would only include *Asio otus* and *Asio flammeus*, and as demonstrated above, *Tyto alba* nest deposits.

The evidence given in this section is drawn from a number of different sources, the most obvious being the analysis of molar and incisor digestion discussed at the beginning of this chapter. However, further evidence on bone breakage and location will also be discussed in order to shed light on the possible predatory origin of the four archaeological deposits.

9.6.1 Sites which exhibit similar taphonomic signatures to *Tyto alba* nest deposits.

The evidence from Tadcaster has perhaps the strongest indications out of the four sites of *Tyto alba* nesting activity. In analysis of the frequency and extent of digestion, this site appears to bear a strong resemblance with the *Tyto alba* nest sites. Slightly lower frequencies of digestion were recorded in some instances, which suggests that the deposit may represent an admixture of material from both nest and roost accumulations, or young and adult owls. However, the results clearly indicate that the majority of the material is representative of *Tyto alba* nest deposits. The recovery of the complete skeleton of a juvenile owl from context 17 provides direct *prima facie* evidence of this conclusion. The location of the assemblage, within an abandoned building is also suggestive of *Tyto alba* behaviour.

9.6.2 Sites which do not exhibit similar taphonomic signatures as *Tyto alba* nest deposits.

The remaining three sites exhibit higher frequencies of molar and incisor digestion than recorded for the *Tyto alba* nest deposits. It would therefore seem likely that they were deposited by a different predator, possibly either *Asio otus or Asio flammeus.* However, in the case of Fox Hole Cave and Carsington Pasture Cave, this also seems unlikely, as neither of these owls are renowned for troglodyte activity. Analysis of the depositional conditions of these two sites indicates that the material could not have filtered into the cave from outside; the bones were recovered in a similar location to where they were deposited.

At Filey it is possible that the agent of accumulation was either *Asio otus* or *Asio flammeus*. Both owls exhibit higher frequencies of digestion than *Tyto alba*. Out of these two owls, it is *Asio flammeus* that is more commonly associated with open ground, and as a result exhibits a prey preference more similar to prey range of small mammals recovered from this site. *Asio otus* is more commonly associated with woodland habitats. It is possible that the abandonment of the signal station afforded a suitable location for *Asio flammeus*, either for roosting or nesting.

The predatory origin of the two cave deposits is difficult to assess given the current scope of this project. At both of these sites the frequency and extent of digestion is too low to have been the result of a mammalian predator, and it is therefore only possible for these sites to have been deposited by an owl. It is clear that the frequency of molar and incisor digestion at these two sites is considerably higher than that recorded for *Tyto alba*, and at Carsington Pasture Cave, the molar digestion exhibits a similar frequency as that recorded for *Bubo bubo.* However, with the exception of Fox Hole 1, most of the extent of the digestion recorded for these two sites is only slightly higher than the average for the nest sites, and with lower frequencies of more extreme cases of incisor digestion than the nest site ON2. The increase in frequency of digestion is not matched by an increase in the extent of digestion, and it is this that is the significant difference between these sites and the data for *Bubo bubo*

It is possible that at Fox Hole, the small mammal bones could represent a palimpsest of many different predators, with undigested molars representing *Tyto alba*

and the remaining bones deposited by a predator with higher frequencies of digestion. However, given the relatively limited extent of digestion recorded on the incisors from this site (compared with more destructive mammalian predators also recorded at Fox Hole) this seems unlikely. This explanation certainly does not fit the evidence collected during the excavation of Carsington Pasture Cave, where the lack of cave deposit would make it possible to recognise patterns associated with multiple predators.

As the frequency and extent of digestion implicate an owl as the most likely predator at these two sites, and as *Tyto alba* is the only owl present in the British Holocene that would make use of caves for roosting and nesting, it is possible that the small mammals from Fox Hole and Carsington Pasture caves represent *Tyto alba* accumulations. What is puzzling however, is the much higher frequency of digestion recorded for these two sites, compared to the data collected for the *Tyto alba* nest sites, such as TF11 and ON2.

One of the outstanding facts relating to these two sites is the presence of *Arvicola terrestris,* occurring in higher frequencies than any recorded predator assemblage studied in this project. It is possible that the increase in number of this species at these two sites has also lead to an increase in the frequency of digestion, possible in order to cope with larger meals, or due to prey dissection, each chick only receiving portions of the kill.

It is also possible that the increase on digestion at these two sites, may indicate a period where prey was relatively scarce, and therefore chicks were fed less than they required. This would have the effect that any food consumed would be more heavily digested in order to receive the maximum nutrients from each meal. A final consideration is that the digestion varies at nest sites, as a result of the specific age of the chicks, and the samples analysed in this study may represent periods where the chicks require less nutrients for growth, and therefore do not produce such higher frequencies of digestion.

However, without further research to answer these questions, it is difficult to clearly assess the predatory origin of these two sites. The environmental reconstruction of these sites will therefore take this consideration into account.

9.7 Species richness of the archaeological deposits.

Although the main thrust of this study is primarily taphonomic, in order to indicate how the taphonomic analysis carried out in this study relates to the wider subject areas of archaeology and palaeoecology, an environmental reconstruction will be produced for each of the archaeological sites studied. However, before it is possible to analyse the species range and frequencies from these sites, it is essential that investigation of species richness from the sites and their individual contexts is performed, in order to assess to what extent the numbers of different species are affected by the size of the sample.

Site	N° of bones	N° of species
OVT 17	181	5
Fox Hole 2	464	4
Fox Hole 1	509	3
OVT 18	608	6
CPC 103	766	5
Filey	871	6
OVT 11	877	7
TF11	1207	9
CPC 109	1673	5
Fox Hole 3	1928	6
ON2	2436	8

Table 40. Comparison between the number of bones (based on initial skeletal element count) and number of species present, listed in ascending order for number of bones.

The analysis of these results indicates that whilst there is a correlation between sample size and species richness, it is neither a very strong correlation nor very significant:

$r = .487$, "P"= .129 (Pearson's correlation, two-tailed significance).

These results are also displayed in the scatterplot below.

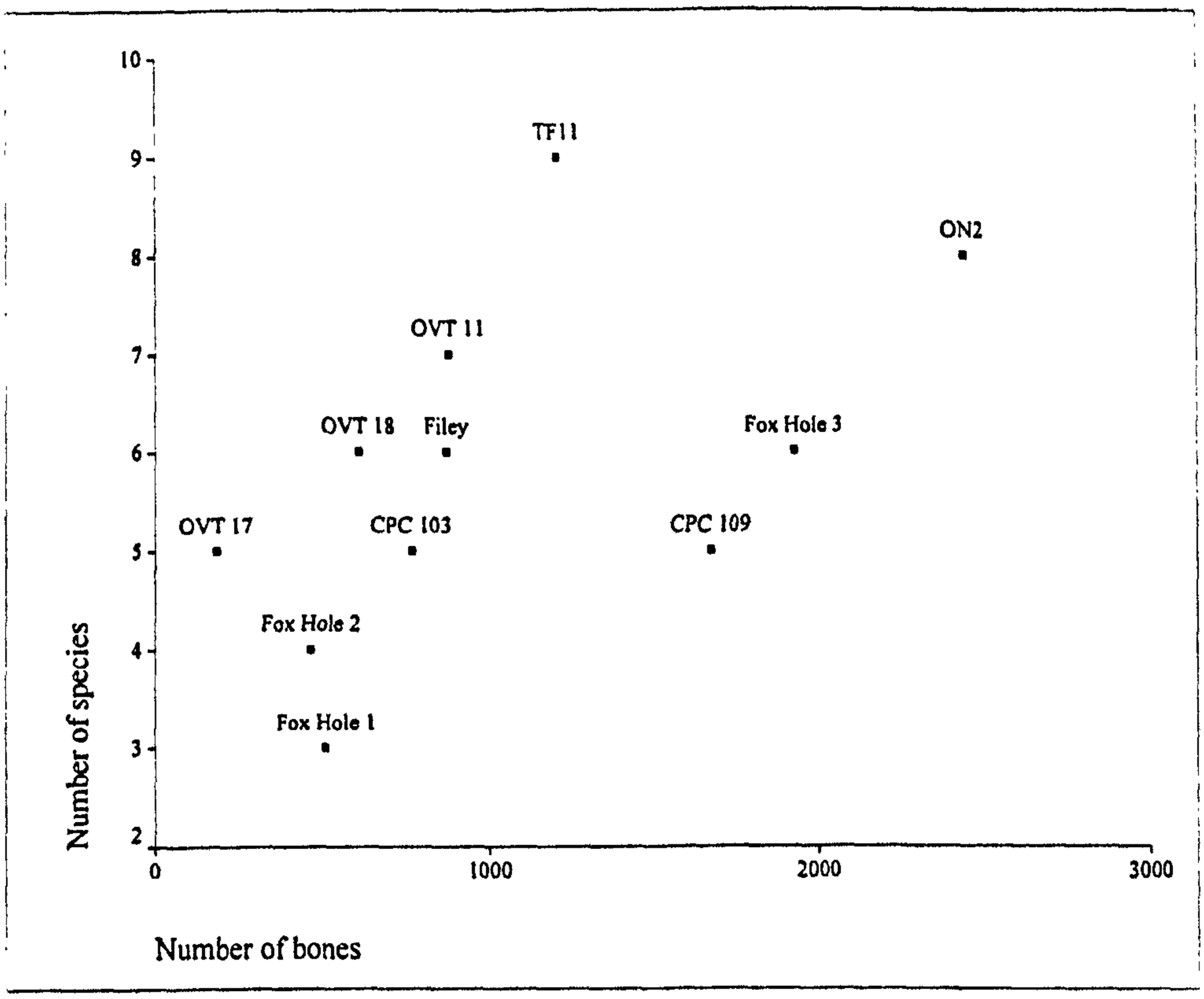


Figure 74. Comparison between number of bones and number of species, indicating species richness.

From the evidence presented above, it is clear that when species richness is considered for all of the sites, it is not a significant issue with regards to making accurate palaeoecological conclusions. Andrews suggests that the expected relationship between species richness and sample size is probably exponential rather than a straight line, and as a general rule of thumb, when there is in excess of one hundred individuals in any assemblage or sample, then the curve has generally flattened off, and the addition of other individuals is unlikely to increase the range of species (Andrews pers. comm.). There are however some sites where species numbers are lower than would be predicted if there was a clear correlation between species richness and sample size, and these sites will be considered individually within next section.

9.8 Environmental reconstructions of the archaeological sites.

As has been expressed earlier in this study, the main purpose of this research was to investigate the differences in taphonomic signatures produced by adult and baby owls, specifically *Tyto alba.* As such these enquiries are predominately methodological, and the following section examining the environmental reconstructions of the small mammal material from the archaeological sites, is included in order to demonstrate why such taphonomic investigations are important to the overall analysis of a small mammal assemblage. The production of these palaeoecologies is not therefore the principal goal of this analysis, but only a subsidiary part of it.

9.8.1 The Old Vicarage, Tadcaster.

This is the only site out of the four investigated in this study for which the taphonomic signatures can be matched closely with those recorded for *Tyto alba* nest deposits, and to some extent (if one considers the individual contexts, specifically context 17) *Tyto alba* roost sites. As a result, any attempt to reconstruct the environment around this site, can draw upon the evidence for prey selectivity discussed in chapter 5.

If one compares the number of different species within three contexts, it is clear that there is a relationship between the number of bones in the sample and the number of different species. Sample 11 which contains the most bones, had a higher species richness than sample 18, which in turn had a higher species richness than sample 17 (which contains the least bones), suggesting a link between species richness and sample size for this site.

Sample	Sample size	No of species
11	877	7
17	118	5
18	608	6

Table 41. Table of relationship between species richness and sample size for Tadcaster samples 11, 17 and 18.

As this data indicates that some of the difference in the species present within specific contexts may be a result of sample size rather than a change in environment around the site, what interpretations can be made about the number of these species within the three samples from Tadcaster?

Graph showing proportions of species in each context sampled at Tadcaster.

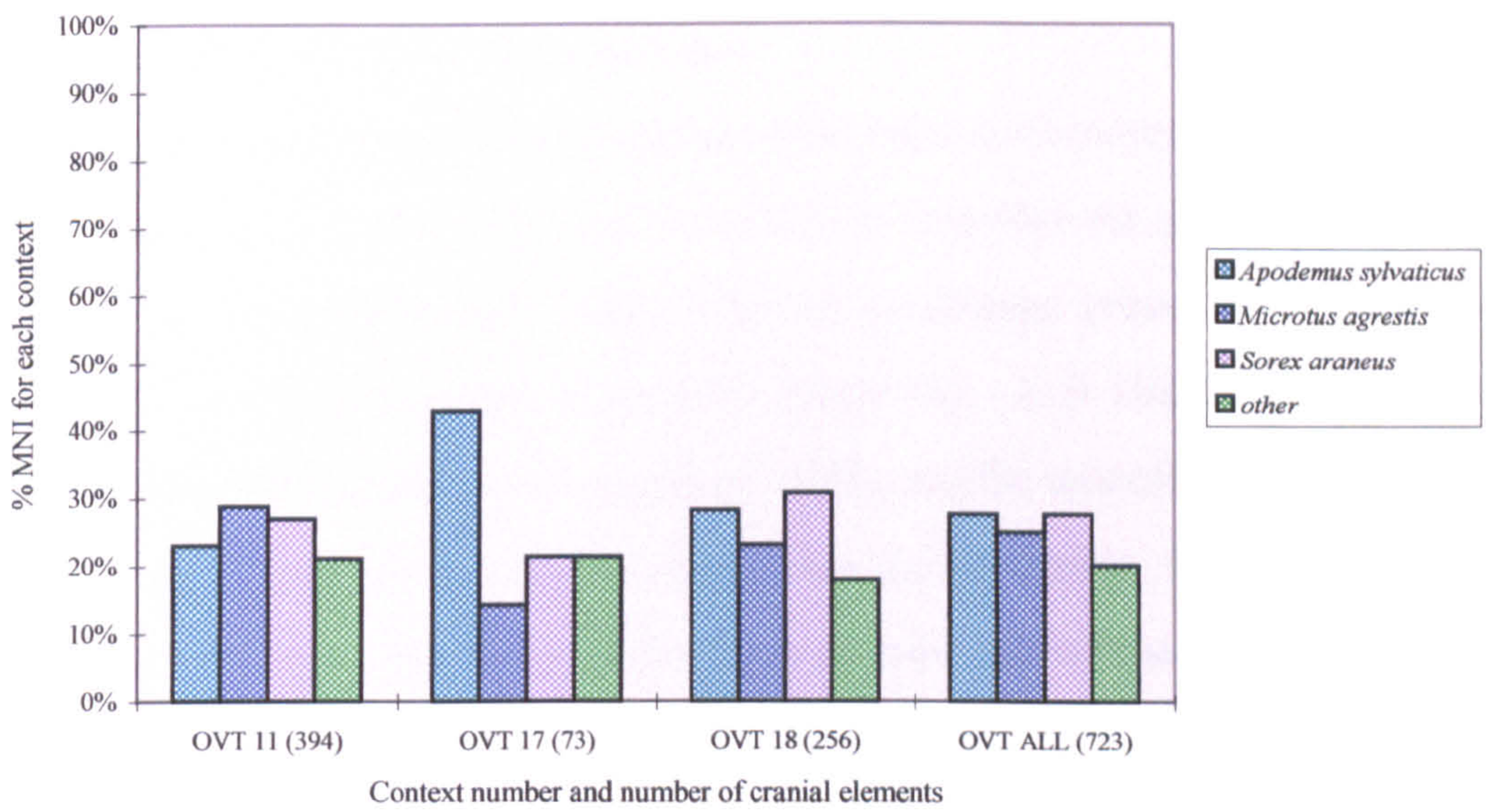


Figure 75. Species present from individual contexts at Tadcaster, data from pages 171 and 172.

In all three contexts around 85% of the total MNI is made up by *Apodemus sylvaticus, Microtus agrestis* and *Sorex araneus*. The high percentage of *Apodemus sylvaticus* recorded for context 17 is almost certainly a function of small sample size. However, analysis of the remaining two contexts, 11 and 18, indicate high numbers of both *Sorex araneus,* and *Apodemus sylvaticus* when compared to the normally higher numbers recorded for *Microtus agrestis* within *Tyto alba* diets (Glue 1970; Glue 1973).

There is also a change in the numbers of *Microtus agrestis* in these three contexts, with 29% of the total number of species in context 11, 23% in context 18, and only 14% in context 17 (although the MNI of context 17 was very small, with only 12 individuals recorded). This difference could indicate a change in the distribution of small mammal species around this site, either as a result of population fluctuations in the small mammal community, or changes in the local environment.

Overall, the proportions of *Apodemus sylvaticus* recorded at this site are higher than usually associated with *Tyto alba,* and it might therefore be reasonable to suggest that there is a high proportion of woodland environment around this site. However, this may also be an indication of prey switching in response to low numbers of *Microtus agrestis.* This may be confirmed by the presence in high frequencies of the species most often switched to, *Apodemus sylvaticus* and *Sorex araneus.* The other species of small mammal recorded at this site do not increase significantly above the abundance usually recorded for *Tyto alba* derived assemblages.

When considering the composition of the local environment, with an assemblage as small as this, it is probably most beneficial to consider the presence of species as indicators of the environment, rather than the percentage presence of these species, which are most likely a result of predator selectivity. It is also possible that as this deposit accumulated quite quickly (Dobney 1998), and the assemblage represents only a short period of deposition, not necessarily into the garderobe, from where the bones excavated. Until the time it took to fill the garderobe can be discovered it is difficult to assess whether the abundance of certain species at this site represents environmental changes or population fluctuations in particular species.

A total of seven species were present at this site. Apart from the three species mentioned already, the deposit also contained *Mus domesticus, Arvicola terrestris, Clethrionomys glareolus,* and *Sorex minutus.* The environment suggested by the presence of these species is fairly mixed, with both abundant grassland – indicated by the occurrence of *Microtus agrestis* (Gipps and Alibhai 1991: 111), *Sorex araneus* and *Sorex minutus* (Churchfield 1990: 4) - and woodland – suggested by the presence of *Apodemus sylvaticus* (Harrison Matthews 1982: 27) and *Clethrionomys glareolus* (Harrison Matthews 1982: 26). The existence of water near the site is also suggested by *Arvicola terrestris* (Glue 1974: 204; Boyce 1991: 212), most probably a stream or river.

This high incidence of *Apodemus sylvaticus* could also indicate the tendency of this species to use hedgerows as a means of dispersal (Zhang and Usher 1991), a behaviour also observed in *Clethrionomys glareolus* (Harrison Matthews 1982: 26). The high capture rate of this species may also represent incursions into agricultural land, in search of food, particularly grain (Flowerdew 1991: 224; Johnson 1993). The

presence of the commensal *Mus domesticus* is not surprising given the location of the site (within an urban setting), but is clearly a prey item, rather than an intrusive occurrence, as digestion of the molars and incisors of this species occurs in both of the contexts from which it has been recovered.

9.8.2 Roman Signal Station, Filey.

The following table shows the MNI and percentage frequency of the species recorded at Filey, from all contexts combined.

Species	MNI	% MNI
Apodemus sylvaticus	4	8%
Arvicola terrestris	2	4%
Microtus agrestis	29	61%
Sorex araneus	10	21%
Sorex minutus	1	2%
Talpa europaea	2	4%

Table 42. Filey, species MNI and % MNI for all contexts combined.

With the exception of *Talpa europaea,* the species listed above were identified using cranial remains only. No identification was attempted using the post cranial remains. Post-cranial identification was carried out by Dobney *et al* (1996: A26-27) and tentative identification have made for at least one individual *Micromys minutus* and at least two *Neomys fodiens.* A limited number of bird species are also identified, as well as amphibian and reptile remains (Dobney *et al.* 1996: A 18-19). It is suggested that these species may also have been accumulated by an owl (Dobney *et al.* 1996: 17).

The high frequency of *Microtus agrestis* at this site suggests that the sample is likely to have been accumulated by either *Tyto alba,* or one of the eared owls, either *Asio otus* or *Asio flammeus,* which all exhibit high numbers of this species in their prey assemblages (Glue 1974; Mikkola 1983; Andrews 1990). Although these three owls do not hunt over exactly the same territory, they show signs of a similar prey bias, (as vole

specialists) then the effect this bias has upon the palaeoecological reconstruction can be taken into account, even though it is not possible to directly identify the predator.

The environment suggested by the range of species recorded at Filey, is fairly mixed, with a number of different habitats represented. The presence of *Microtus agrestis, Sorex araneus* and *Sorex minutus* indicates areas of rough grassland and scrub (Churchfield 1990; Gipps and Alibhai 1991), and the occurrence of both *Arvicola terrestris* and *Neomys fodiens* (identified from post-cranial remains by Dobney *et al* (1996)) indicate the presence of water close to the site (Glue 1974; Churchfield 1990: 7; Boyce 1991). It is difficult to assess the importance of *Apodemus sylvaticus* within this assemblage for indicating the presence of woodland (Harrison Matthews 1982: 27), as it is likely that the deposit was accumulated by a vole specialist, and therefore low numbers are to be expected (Andrews 1990). However, it would suggest that some woodland was present in the vicinity of the site. The identification of an individual *Micromys minutus* from this site, could be taken to indicate the presence of agricultural land - cereal crops - (Glue 1975), tall grass and rough herbage (Harrison Matthews 1982: 28), or rushes and reed beds (Harris and Trout 1991: 236; Yalden 1999: 127) in the vicinity of the site.

9.8.3 Fox Hole Cave, High Wheeldon.

The three samples from Fox Hole Cave all come from the same horizon within the cave, and presumably represent a similar date of deposition, and from the analysis of taphonomic criteria were deposited by a similar accumulator, although it is not possible to ascertain the precise predatory origin of these bones. For the purpose of producing an environmental reconstruction the three contexts will therefore be merged into one dataset. This seems appropriate as it is possible that the differences in species numbers are the result of sample size dictating species richness. As the location of the three samples within the cave cannot be precisely ascertained, it is also possible that the representation of species within each context has resulted from the sampling of only part of a number of different small mammal assemblages. It is also impossible to rule

out the fact that larger small mammals, for example *Arvicola terrestris,* were sampled preferentially during the excavation and sampling procedure.

A total of six species were recovered from this site, representing at least 205 individuals. The number of each species present and their relative abundance is shown in Table 43 below.

Species	MNI	% MNI
Apodemus sylvaticus	6	3%
Mus domesticus	1	<1%
Arvicola terrestris	70	34%
Clethrionomys glareolus	14	7%
Microtus agrestis	110	54%
Sorex araneus	4	2%

Table 43. Fox Hole Cave, MNI and % MNI for combined contexts.

The most noticeable aspect of this assemblage is the high numbers of *Arvicola terrestris* recorded, occurring in a far greater concentration than is found in any present day predator accumulation. However, numbers of *Microtus agrestis* are also high, recorded with a similar frequency to pellet studies of *Tyto alba* and *Asio otus* (Andrews 1990). The environment around the site at Fox Hole during the accumulation of these faunas is likely to have included a predominance of grassland areas, indicated by the presence of *Microtus agrestis* (Gipps and Alibhai 1991) and *Sorex araneus* (Churchfield 1990). This correlates well with the second of the two pollen samples taken from Fox Hole Cave, sample B, which Shimwell suggests represents an open environment with abundant grassland (Shimwell 1971).

The other indicator of a relatively open grassland environment is possibly *Arvicola terrestris.* This species occurs in high frequencies in many Neolithic and Bronze Age deposits (Yalden 1999), some of them are located a long way from water (Jewell 1959). It has been suggested that it is only in recent times that *Arvicola terrestris* has become purely associated with waterside habitats, and in the past it lived a more terrestrial life (Montgomery 1975), most likely in grassland environments (Bramwell *et al.* 1990). This habitat preference is also found in non-aquatic forms of *Arvicola terrestris* in Continental Europe.

The presence of both *Apodemus sylvaticus* and *Clethrionomys glareolus* indicate that there were probably areas of woodland close to the site. The final species from this site is *Mus domesticus*, and if the dates given for the samples are correct, this find represents one of the earliest records of this species in Britain (Yalden 1999).

As it was not possible to suggest an exact predatory origin for these deposits, it is not possible to use this information to indicate how the abundance of species at this site may have resulted from predator selection. However, the relatively high numbers of *Arvicola terrestris* suggest that it is possible that large prey items were targeted. If this site was an owl nest, this would seem to fit in with models of optimal foraging theory, which would predict that larger prey items would be selected and brought back to the nest, rather than a number of smaller prey species (Taylor 1994: 77).

9.8.4 Carsington Pasture Cave, Brassington.

The small mammals from the two contexts from Carsington Pasture Cave were located very close together within the cave, and there is no reason to believe that they were not both deposited by the same predator, and probably within a short period of time of each other, or even simultaneously. The species numbers recorded for these two contexts will therefore be merged for the palaeoecological analysis. These species and their relative abundances are shown in the table below.

Species	MNI	% MNI
Apodemus sylvaticus	15	11%
Micromys minutus	1	<1%
Mus domesticus	1	<1%
Arvicola terrestris	48	35%
Clethrionomys glareolus	1	<1%
Microtus agrestis	71	52%

Table 44. Carsington Pasture Cave, species MNI and %MNI.

The abundance of species at Carsington Pasture Cave is similar to those recorded at Fox Hole Cave, and it is likely that these two assemblages were deposited at a similar period

of time. It is also possible that the abundance of these species indicates similar environments at both of these sites.

The environment suggested by the small mammal species recorded at Carsington Pasture Cave is one with abundant grassland areas (*Microtus agrestis* and *Arvicola terrestris*), as well as evidence of some woodland (*Apodemus sylvaticus* and *Clethrionomys glareolus*). The presence of the small *Micromys minutus* is also indicative of areas of grassland, indicating areas of tall grass, or possibly reed beds (Harris and Trout 1991; Yalden 1999). It is also interesting to note the presence of *Mus domesticus* at this site, which is likely to date to the Bronze Age, as it is yet another early record of this species in Britain.

As with Fox Hole Cave, the lack of exact identification of the predator responsible for the accumulation of these samples means that it is not possible to fully investigate any prey selectivity on the part of the predator. However, it is also possible that this site could have accumulated as a result of owl nesting activity, and therefore the suggestions concerning optimal foraging theory discussed for Fox Hole Cave, could also apply to this deposit.

10. Conclusions

10.1 Summary review

It has been emphasised throughout this study that evidence from experiments with captive birds suggests that younger owls digest higher proportions of the bones of small mammals than their parents (Grimm and Whitehouse 1963; Raczynski and Ruprecht 1974). A limited test of this hypothesis was carried out by Andrews (1990: 33-34) in a comparison of *Tyto alba* pellets collected from a roost and a nest site. The principal aim of this current study was to investigate whether this difference previously recorded for adult and nesting owls, could be accurately characterised, and also whether it was possible to use this information to investigate the predatory origin of four British Holocene archaeological deposits containing small mammal bones.

This study has shown that it is possible to differentiate between *Tyto alba* roost and nest deposits. In some cases, it also possible to recognise these characteristic taphonomic signatures in small mammal deposits collected from four British Holocene archaeological sites in Derbyshire and North Yorkshire. At one of these sites, the Old Vicarage at Tadcaster, a clear association could be made with the digestion data collected for modern *Tyto alba* nest sites, suggesting a similar predatory origin for the Tadcaster deposit.

At the other three sites (Filey, Fox Hole and Carsington Pasture Cave) the frequency of molar and incisor digestion was higher than that recorded for the modern *Tyto alba* material. However, the extent of this digestion for these three sites was mainly light, with few instances of moderate, heavy or extreme digestion. It is therefore likely that these deposits were accumulated by a category one or two predator (Andrews 1990), which for Britain include *Tyto alba, Asio otus* and *Asio flammeus.*

As this frequency of digestion is only slightly higher than that recorded for the *Tyto alba* nests in this study it possible that the difference is a result of variability in the sampling of both the nest deposits and the archaeological material. The two nest deposits represent sub-samples from the nest sites, and it is possible that there are times during the development of the young owls, where the levels of digestion are higher than those described in this research. If this is the case, then it is also a possibility that the

archaeological deposits analysed in this study, which are all with the exception of Tadcaster sub-samples, may represent this period of increased digestive activity. However, it is also possible that these higher frequencies are associated with other factors affecting these predators, that may result from adaptations to external environmental influences rather than any physiological condition. This is further discussed below.

Comment was also made on the environment at the time of deposition for the four sites, and where possible, the conclusions about the predatory origin of these deposits was also considered in this analysis, to investigate the extent to which the relative abundance of the species recorded at these sites represented the environment at the time, rather than any predatory preference.

10.2 The taphonomy of the provisioning of the young.

The review of previous studies of small mammal taphonomy presented in chapter two demonstrated that most of these researchers had concentrated on the role of only adult predators when collecting modern day pellet or scat material for comparison with microvertebrate fossil deposits. As a result, a major time period in the predator's lives was not considered, and therefore any contribution they may have made to the fossil record during this time, will have gone unrecognised. As nesting activity (in any owl or diurnal raptor species) involves a long period of sedentary occupation of the nest site, there is a heightened potential for a large number of bones to accumulate in that location. This is especially important when considering that the ejection of pellets by an adult owl will not always occur at a roost site, and in some species no preference is shown for the continued use of one particular site. For these species, pellets collected at the nest may provide the only opportunity to sample a large accumulation of pellets and therefore prey remains (Glue 1973: 194).

This has important implications for zoologists trying to reconstruct the prey range of specific predators. If more of the pellets are ejected at the nest, do these sites contain a more accurate measure of the prey caught, or do they also contain inherent biases that must be considered, as can be seen in the pellets deposited at roost sites by

the adult owls? Outside of the nesting period, an average of two pellets a day are cast. For *Tyto alba* most of the prey remains are contained within the larger pellet ejected at the daytime roost site, whilst the rest are usually cast in a smaller pellet at resting points during the evening's hunting activity (Glue 1973: 194). Therefore, the pellets from the roost site do not contain all of the prey consumed. It is difficult to assess to what extent the absence of the prey deposited during the evening hunting period would effect the analysis of the prey species abundance of the roost pellets, especially if these are compared with other roost material.

At the nest site, the pellets should contain all of the prey brought to the chicks by their parents. As was suggested in chapter 3, the prey remains at the nest were roughly similar to that consumed by the parents, although it would be more energy efficient for the owls to bring back larger prey items to the nest. However, it must also be considered that not all prey fed to the young owls may be returned in pellets, and in experiments with captive young owls, Raczynski and Ruprecht (1974) reported an 8.2% loss of prey individuals for *Tyto alba.*

Investigating the difference between the nest and roost site has important implications for the study of the predator / prey relationships between owls (and other raptors) and small mammals, and may provide essential methodological data on small mammal collection agents that can be used by palaeoecologists and archaeologists trying to reconstruct past environments. However, this information must also be viewed with reference to the provisioning of the young, and the study of juveniles, both within the archaeological and palaeontological record. Very little taphonomic data has been collected on the role of juvenile predators, with the notable exception of Brain (1981), who collected taphonomic data on food procurement and breeding lairs for both *Crocuta sp.* (hyena) and *Panthera pardus* (leopard). It would seem that the study of all of the parts of a predator population is essential, if taphonomic patterns are to be accurately collected. This is especially important if, as has been shown from this study, a difference in the physiology or behaviour in the young, leads to the production of different patterns of bone modification.

10.3 Palaeoecology and the small mammal species identified in this research

The essential aspects of the palaeoecology of the four archaeological sites has been discussed in the last chapter, and it is only the problems associated with these reconstructions that this section will discuss. Out of the four sites, it was only possible to provide an accurate palaeoecological reconstruction for one site, Tadcaster, where the taphonomic analysis of the small mammal bones had enabled a definitive identification of the predatory origin of this deposit. At the other three sites where it was not possible to identify the predator, only limited environmental information could be provided on the presence of the prey species, and not their relative abundance.

However, the aim of this study was not to identify the predator at these sites, but only to investigate whether they may have been accumulated as part of a *Tyto alba* nest. Where the taphonomic signatures did not match those collected for comparison in this study, it was not possible to correlate precisely the results with previous authors' analyses of bone digestion, as different criteria were used in this research.

Of the eleven species of small mammal identified in this study, there are two for which further comment could be made. Firstly, in the palaeoecological analysis of both Carsington Pasture and Fox Hole caves, the presence of *Arvicola terrestris* was taken as an indication of grassland, and in particular upland pasture, rather than the waterside habitat now favoured by this species. It has been suggested by many authors (Jewell 1959; Montgomery 1975; Bramwell *et al.* 1990) that this was the preferred habitat of this species until sometime around the Roman period, when probably as a result of changing patterns of land use, and competition for this environment with other grass browsers, such as cattle and sheep, *Arvicola terrestris* may have been forced to seek different and maybe new habitats (Bramwell *et al.* 1990). This problem is likely to have been exacerbated after the Norman Conquest following the introduction of *Oryctolagus cuniculus* (rabbit).

These factors appear to have had a dramatic effect on population numbers, and there is a noticeable drop in the occurrence of *Arvicola terrestris* in archaeological deposits starting at the end of the Roman period (Yalden 1999). However, there is also a reduction in the number of sites located in these same upland locations after the Roman period, so part of this extreme drop in numbers maybe due to sampling error.

Aside from the reduction in recorded occurrence of this species in rural locations, there is little concrete evidence for habitat change, and this is an area where further research, into the habits of both the terrestrial, and more aquatic forms of this species would be highly desirable. For this reason, it is suggested that any discussion of past environment (both within and outside of this research) based on the possible habitat preference of *Arvicola terrestris* are treated with caution.

The large numbers of *Arvicola terrestris* found at Fox Hole and Carsington Pasture Cave are mirrored by similar discoveries at many other upland sites in the Peak District from the Neolithic and Bronze Age (Bateman 1861; Stubbs 1926a; Stubbs 1926b; Jewell 1959; Bramwell *et al.* 1990), adding further weight to the suggestion that this species may have had different habitat requirements in the past. However, as has been discussed throughout this research, there are certain aspects of predator derived deposits that must be addressed before it is possible to consider the past ecology of the small mammal species being analysed.

One of the most interesting questions concerning *Arvicola terrestris* is whether the high proportion of these species recovered from archaeological sites indicates their concentration in the environment, or is a result of specific exploitation by *Tyto alba.* Such high numbers perhaps attest to the possibilities of large scale population fluctuations, on the scale of that recorded for some of the vole species, including the fossorial water vole in Eastern Europe (Southern and Crowcroft 1956), and suggest that a link may exist between these fluctuating populations and their possible predators, which in the cases outlined above may be *Tyto alba.*

The mechanisms that control and influence these small mammal population cycles are still not fully understood despite many years of research (Chitty 1996), although it has recently been suggested that different prey and predator related factors may be responsible for controlling these fluctuations in different small mammal species (Turchin *et al.* 2000). If the high numbers of *Arvicola terrestris* recovered from the two cave sites are indicative of fluctuating small mammal populations, and if this seasonal resource is being exploited by *Tyto alba,* then the high numbers of these voles may not be an indication of a constant population figure, but reflect a dynamic and constantly changing interaction between predator and prey. A follow on from this point is that

during a period of peak density of these voles, the number of owls would also increase, and when vole populations then declined, it would be necessary for these owls to engage in prey switching to avoid death themselves.

This necessity for prey switching (particularly during periods when both *Arvicola terrestris* and *Microtus agrestis* numbers may have been in decline) may offer a possible suggestion as to the often large numbers of amphibian bones also found in association with some small mammal assemblages, for example Fox Hole Cave. As a final consideration of this point, if owls did not adapt to the need to diversify their prey range during vole declines, then they would die. It has been suggested in the last chapter that the deposits of small mammals at Carsington Pasture Cave represent only a short accumulation period, which could indicate that the cave was once again in human usage, and/or that the practice of utilising caves as ritual loci was discontinued and the tomb sealed. However, it is also possible that those owls using the cave for nesting purposes failed to react to the changing nature of their prey, and it was no longer ecologically practical to nest in the area.

The other small mammal species of particular interest is *Mus domesticus*. This species was recovered from all four archaeological sites, but it is its occurrence in Bronze Age deposits at both Fox Hole and Carsington Pasture Cave (where the deposition of the small mammal remains may date from the Neolithic to the Iron Age) that is interesting, as these are early dates for this species (see dates for introduction in Yalden 1999). *Mus domesticus* is usually considered to be a purely commensal species, and studies of mice from farms have indicated that they exhibit very low rates of dispersal from colonised buildings (Ministry of Agriculture 1981: 91-92). This is in contrast to *Rattus norvegicus* which is often far more active, especially in food orientated movements, and appears to be able to adapt to live in hedgerows near farms, visiting farm buildings only for food (Taylor 1978). *Mus domesticus* is therefore more likely to be captured in close proximity to farm buildings, and if these isolated farmhouses can be seen here as a broad analogy to the isolated settlements of the Bronze Age, then the implications are that some type of human settlement may have been located within the area covered by an owl's hunting range, close to the two cave sites. This is confirmed by current thinking on the nature of land use and patterns of

habitation in the Peak District during the Bronze Age (Barnatt 1999; Edmonds pers. comm.). As the introduction of *Mus domesticus* must have occurred by sea from Europe, its appearance in the Peak District indicates that it has probably made most of the journey from the coast with the assistance of humans, which are its main vector for dispersal (Brothwell 1981), and this may therefore have important implications for understanding human population movements, and networks of trade and the storage and distribution of arable food crops.

10.4 New techniques in the analysis of microvertebrate assemblages.

Before discussing the need for any further methodological development of the study of small mammals, it is worth emphasising the substantial progress has been made in this research. Firstly, it has been shown that the use of principal component analysis (PCA) can shed substantial light on the analysis of taphonomic data, especially that relating to the digestion of molars and incisors. The use of this technique to test the coherence of Andrews (1990) predator groups (see chapter 2) and the further analysis of these groups using ANOVA (analysis of variance) has indicated that these associations can be afforded a high degree of statistical significance. Furthermore, the application of PCA to the results of this current study, has indicated that it provides an effective interpretive tool for assessing the origin of predator deposits.

Secondly, during the analysis of the digestion data, two other important improvements have also enabled more detailed analysis to be carried out. The first of these new techniques was the use of a prey standardisation calculation, to attempt to reduce the variability of molar digestion results associated with different small mammal prey. This problem, resulting from the difference in tooth morphology between Murinae and Arvicolinae which leads to a greater susceptibility to digestion of arvicoline molars, had been commented on by Andrews (1990: 65). Hopefully, the use of this calculation has reduced this problem, as has been aptly demonstrated in the previous chapters. The other important development was the use of the data recording the extent of digestion, and its incorporation within the analysis of both the modern owl nest and pellet material, as well as the archaeological assemblages. Only by recording

separately the extent of the digestion has it been possible to differentiate between incidences of high frequencies of digestion (for example Carsington Pasture Cave), and more highly destructive digestion seen in category 3-5 predators, such as *Bubo bubo.* Again, the use of PCA and ANOVA in the analysis of this data has enabled further understanding, visualisation and characterisation of each of the sampled assemblages to be accurately detailed.

10.5 Potential for further development of the methods of small mammal taphonomy and palaeoecology.

All of the analysis of small mammal palaeoecology carried out in this study has concentrated on comparisons of species recorded from archaeological deposits (and by extension *Tyto alba* pellets and nest deposits) with the preferred and recorded environment of British small mammals. However, in order to make accurate reconstructions of these environments, there are problems associated with prey selection, and seasonal and yearly variability in prey abundance to first be considered, some of which cannot always be addressed.

A more profitable method of analysis of predator-derived microfaunal assemblages would be to compare the species composition of the archaeological assemblage with composition of species from the same modern day predator from known environments. It is not possible to apply such an approach at the present because no comparative modern data has been collected that catalogues the environment of the predator and the abundance of the prey within the predator's diet. However, the methodology of such an approach is relatively simple, and outlined below using the example of *Tyto alba* as the accumulating predator.

Firstly, a collection of pellets from *Tyto alba* should be made from a number of different environments, over a period of approximately 6-10 years. Using pellets collected over a long period of time, rather than from just one or two years, will reduce the chance of encountering any prey species population fluctuations. Therefore, the numbers of small mammals represented in pellets, should be roughly reflective of the numbers of small mammals regularly caught, within a given area hunted over by an owl.

The second part of this method relies on information gathered about the environments from which the pellets have been collected. By recording the amount of trees, grassland, hedgerow, and pasture, within each environment, it would then be possible to derive an understanding of how prey species represented in the pellets of *Tyto alba*, represented the type of environment from which they have been caught. It is therefore unnecessary to consider the abundance of certain species (due to predator specialisation) as a bias to the understanding the biotic composition of the environment. The species composition of specific small mammal deposits can then be analysed against collections of known owl pellets from specific owl species and environments, to produce the most likely environmental reconstruction, based on the relative abundance of all prey species within the deposit. It must however be realised that past environments do not always have present day equivalents, and this point is aptly demonstrated in results comparing small mammal prey from *Tyto alba* diets over the last thirty years, where changes in agricultural practices have dramatically affected the abundance of particular small mammals and habitat types (Love *et al.* 2000).

10.5.1 Identifying roost and nest deposits.

This study has concentrated on differentiating between the taphonomic signatures associated with *Tyto alba* nest and roost deposits. The presence of microscopic features such as pitting and digestion of the bone and tooth enamel have been taken as indicators of predatory activity. In archaeological assemblages the presence of these features could be taken to indicate that the small mammals were accumulated as part of a predator assemblage. However, when dealing with *Tyto alba* roost material, which is characterised by very low frequencies of digestion, it is not always possible to be totally certain as to the origin of the deposit, and the absence of any bone modification through digestion is often taken as *a priori* evidence that the depositional agent was *Tyto alba*.

Although most of the archaeological assemblages analysed in this study contain numerous small mammal bones, there are occasions when excavations will only discover a limited amount of microfaunal material. As a result of small sample size, the chances of encountering infrequent incidences of digestion are that much lower, and it

may therefore not be possible to even ascertain whether the small mammals represent a natural death or predator assemblage. Furthermore, given the fact that current excavation practice tends to favour minimum intervention and partial excavation, the chance that only part of a specific deposit will be sampled is increased.

After deposition, there are very few instances or environments where the fur from the owl pellets will be preserved. This is because the fur is less resistant to decay than the bones. However, this decay is also intensified by the action of insects, for example the Tineidae (Lepidoptera) and Dermestidae (Coleoptera) (Smith 1986), which are capable of digesting the keratin of hair and feathers (Chinery 1993: 236). In the analysis of modern owl pellets it is not unusual to encounter at least one of these insects (personal observation.; Sutton and Beaumont 1989: 95), for example *Tineola bisselliella* (common clothes moth), and it is suggested that owl pellets and birds nests may be the prehistoric origin of this family of insects (Tineidae), now more usually associated with human habitation (Hickin 1974:71-72). Further analysis of this relationship between owl pellets or nest material, and the insects and mites found in pellet and scat accumulations (c.f. Woodroffe 1953), would certainly aid in the identification of predator activity at sites where preservation of insect remains occurred.

10.5.2 Abandonment of archaeological sites and evidence for multiple use and multiple occupancy.

One of the principal differences between nest and roost sites utilised by *Tyto alba* is that nest sites tend to be more isolated and secluded, providing greater security and protection. When disturbed at a roost site, the owl can take flight, often alighting only a short distance away (Prestt and Wagstaffe 1973), but if constantly disturbed may find a new roosting location. It is not possible to do this with a nest full of eggs or small chicks, and therefore nest sites are chosen carefully to avoid disturbance. At present these nest sites are often found in secluded parts of abandoned or rarely used buildings (Prestt and Wagstaffe 1973: 44; Walker 1993), and it is likely that similar habits existed in the past.

This would appear to have been the case at all of the archaeological sites sampled in this study. The two most recent sites (Tadcaster and Filey), both associated with man-made structures, were certainly abandoned when the small mammal assemblages accumulated, and these bones were then incorporated into the final phases of these sites. The area in Carsington Pasture Cave was also not in constant human usage, and would therefore have provided a well sheltered location for a nesting owl. There is evidence that a number of other animals may have utilised this site from the late Pleistocene and throughout part of the Holocene (Chamberlain 1999), but given the low number of both predator and prey species recovered from this site, it was only ever used intermittently.

The final site, Fox Hole Cave was probably in more constant usage, not only as a locale for human burial, but may also have been used for shelter and occupation (Bramwell 1971). The range of animals recovered from the site also indicates that many different predator species may have been contributing to the accumulation of the deposits (Bramwell 1971; Shimwell 1971), and it is possible that some of the small mammal bones excavated from this site (although not those studied here) may have been accumulated by a predator other than an owl. However, the recovery of probable owl nest derived deposits does indicate that there were periods when the cave was not habituated by any of these other depositional agents.

10.6 Small mammals and the treatment of the dead in the late Neolithic and Bronze Age.

As part of the investigation into the multiple occupancy of the sites sampled in this analysis, consideration is given in this section to the association of the small mammal bones and human remains excavated at Carsington Pasture cave. Until such times as radiocarbon dates are available to ascertain the precise date of the Carsington Pasture Cave small mammal bones, one can only work within the framework of given archaeological practice. When the bones were sampled from the cave, it was difficult to determine the precise relationship between the human neonatal bones and the small mammal bones. In some cases, the small mammal bones were on top of the neonatal

bones, and in other cases below them, and any slight disturbance of these bones would have only helped to further confuse any previously visible pattern.

However, what is certain is that there is an association between the area of the cave in which small mammal bones were located, and the area where neonatal bones were also discovered. Furthermore, there was also a segregation in the placement of bodies within the cave, between the adult and juvenile members of the community (located along the north-west wall) and the neonatal bones, recovered from the south-eastern portion of the cave (Chamberlain 1999). The association of small mammal and neonatal bones, either deliberate or accidental, raises some interesting questions. Either the neonatal bones were placed in an area of the cave where there was an abundance of small mammal bones, or the predator responsible for the deposition of the small mammal bones deposited the material in an area of the cave where human neonatal bones had been deposited.

When considering the first of these options, that the neonatal bones were deliberately (or accidentally) placed in an area of the cave containing small mammal bones, one must also consider the possibility that this area still contained the regurgitated fur of these small mammals as well the bones recovered in the excavation. This fur (if present) would have distinguished this area of the cave, both in terms of texture and colour, from the rest of the cave. However it is also possible that the small mammal bones were deposited in an area of the cave previously used for the deposition of neonatal bones, and that any specific and formal association is purely accidental.

It seems that these two possibilities are more realistic than the conclusions drawn by Stubbs (1926b), who suggested that both human and small mammal bones had been introduced together into archaeological deposits, as part of the burial ritual. In his analysis of the small mammal bones from Bronze Age barrows, he claimed that those individuals involved in the burial practice had deliberately captured and interned large numbers of *Arvicola terrestris*, which as a species were elevated to some high position of ritual worship!

If it could be shown that the deposition of the small mammal bones pre-dates that of the human neonatal bones[84], then the prospect that a link exists between these two deposits, must be given some consideration. Such a conclusion is however only appropriate to the analysis of this deposit, and no attempt is made, or suggested here, that the occurrence of the remains of small mammals and humans in other contexts should be interpreted within the same light. In most cases, notably the barrows of the Peak District, it is far more likely that during the construction of these monuments, they were utilised by mammalian and avian predators as lairs, roosts or nests.

[84] It is recognised that dating of the human bones from this cave, as with many Neolithic and Bronze Age funerary deposits, would only give a date of death, and not necessarily that of the deposition of the remains in the cave, which could have occurred any time after death (Edmonds 1999).

10.7 Of mice and men: studying small mammals from archaeological deposits

This study has shown that there is a difference in the taphonomic signatures associated with *Tyto alba* roost and nest sites. In and of itself this conclusion has important implications for the study of small mammal taphonomy. Particularly, it has highlighted an imbalance in much of the taphonomic literature, where little or no attention has been paid to the investigation and understanding of the early life of predators, and the implications that their actions may have for the interpretation of the archaeological and palaeontological record.

Within the discipline of small mammal taphonomy these conclusions should not be seen to supersede previous research but to provide a useful and essential adjunct to the study of microfaunal assemblages. This research is also particularly significant for studying small mammals in archaeological deposits if one considers that nesting is a period of guaranteed sedentism during the life cycle of a predator, and therefore significant assemblages of the diet of that predator can accumulate at a site. It is these assemblages that can then be used to study the environment at the time of deposition, and the identification of the predator responsible for these deposits enables more accurate reconstructions of these environments to be made.

Apart from the taphonomic and palaeoecological significance of this analysis that has been discussed above, this research has also highlighted other issues associated with small mammal deposits, and specifically predator derived nest deposits, that can contribute to how archaeologists interpret microfaunal remains. In particular, the apparent association between the abandonment or intermittent use of occupation sites and the use of these locations by animals, in this case nesting owls, can be used as an interpretive tool not only during the Holocene as demonstrated in this study, but at any time that humans have made use of building materials and other parts of the physical environment, to provide shelter and accommodation.

11. References

Alderton, D. 1999. *Rodents of the World.* London: Blandford.

Alexeeva, N. 1996. Pleistocene small mammals of Tologoi (Western Transbaikalia, Siberia). *Acta Zoologica Cracoviensia* **39** : 57-60.

Alibhai, S. K. and Gibbs, J. H. W. 1985. The populations dynamics of bank voles. In, J. R. Flowerdew, J. Gurnell and J. J. W. Gibbs, (Eds.) *The Ecology of Woodland Rodents. Bank Voles and Mice. Symposia of the Zoological Society of London.* pp. 277-313. London: Academic Press.

Alibhai, S. K. and Gipps, J. H. W. 1991. Bank vole *Clethrionomys glareous.* In, G. B. Corbet and S. Harris, (Eds.) *Handbook of British Mammals.* Third edition. pp. 192-203. Oxford: Blackwell Scientific Publications.

Andrews, P. 1983. Small mammal diversity at Olduvai Gorge. In, J. C. Brook and C.Grigson, (Eds.) *Animals and Archaeology Vol. 1 Hunters and their prey.* pp. 77-85. Oxford: British Archaeological Reports, International Series.

Andrews, P. 1990. *Owls, Caves and Fossils.* Chicago: Chicago University Press.

Andrews, P. 1995a. Experiments in taphonomy. *Journal of Archaeological Science* **22** : 147-153.

Andrews, P. 1995b. Mammals as palaeoecological indicators. *Acta Zoologica Cracoviensia* **38** : 59-72.

Andrews, P. and Armour-Chelu, M. 1998. Taphonomic observation on a surface bone assemblage in a temperate environment. *Bull. Soc. géol. France* **169** (3): 433-442.

Andrews, P. and Evans, E. M. N. 1979. The environment of *Ramapithicus* in Africa. *Paleobiology* **5** : 22-30.

Andrews, P. and Evans, E. M. N. 1983. Small mammal bone accumulations produced by mammalian carnivores. *Paleobiology* **9** : 289-307.

Armitage, P. L. 1985. Small mammal fauna in late mediaeval towns. *Biologist* **32** : 65-71.

Armour-Chelu, M. and Andrews, P. 1994. Some effects of bioturbation by earthworms (Oligochaeta) on archaeological sites. *Journal of Archaeological Science* **21** : 433-443.

Avery, D. M. 1981. Holocene micromammalian faunas from the Northern Cape Province, South Africa. *South African Journal of Science* **77** : 265-273.

Avery, D. M. 1982. Micromammals as palaeoenvironmental indicators and an interpretation of the late Quaternary in the Southern Cape Province, South Africa. *Annals of the South African Museum* **85** (2): 183-374.

Avery, D. M. 1990. Holocene climatic change in Southern Africa: the contribution of micromammals to its study. *South African Journal of Science* **86** : 407-412.

Avery, D. M. 1991. Micromammals, owls and vegetation change in the Eastern Cape Midlands, South Africa, during the last millenium. *Journal of Arid Environments* **20** : 357-369.

Avery, D. M. 1992. The environment of early modern humans at Border Cave, South Africa: micromammalian evidence. *Palaeogeography, Palaeoclimatology, Palaeoecology* **91** : 71-87.

Barnatt, J. 1999. Peak District farming and ritual in the Bronze Age. *Derbyshire Archaeological Journal* **127** : 19-78.

Barnosky, A. D. 1987. Punctuated equilibrium and phyletic gradualism: some facts from the Quaternary mammalian record. In, H. H. Grenoways, (Ed.) *Current Mammaology*. pp. 109-147. London: Plenum Press.

Bateman, T. 1861. *Ten years' diggings in Celtic and Saxon grave hills, in the counties of Derbyshire, Stafford, and York, from 1843 to 1858*. London: George Allen.

Behrensmeyer, A. K. 1975. The taphonomy and paleoecology of Plio-Pleistocene vertebrate assemblages east of Lake Rudolf, Kenya. *Bulletin of the Museum of Comparative Zoology* **146** : 473-578.

Behrensmeyer, A. K. and Hook, R. W. 1992. Paleoenvironmental contexts and taphonomic modes. In, A.K. Behrensmeyer, J.D. Damuth, W.A. Dimichele, R. Potts, H. Sues and S. L. Wing., (Eds.) *Terrestrial Ecosystems Through Time. Evolutionary Paleoecology of Terrestrial Plants and Animals*. Chicago: Chicago University Press.

Beltmann, R. H. R. and de Boer, L. E. M. 1984. A karyological study of 55 species of birds, including karyotypes of 39 species new to cytology. *Genetica* **65** : 39-82.

Berry, R. J. 1991. House mouse *Mus domesticus*. In, G. B. Corbet and S. Harris, (Eds.) *Handbook of British Mammals*. Third edition. pp. 239-247. Oxford: Blackwell Scientific Publications.

Binford, L. R. 1977. General introduction. In, L. R. Binford, (Ed.) *For theory building in archaeology: essays on faunal remains, aquatic resources, spatial analysis and systematic modeling*. pp. 1-10. London: Academic Press.

Blob, R. W. 1997. Relative hydrodynamic dispersal potentials of soft-shelled turtle elements: Implications for interpreting skeletal sorting in assemblages of non-mammalian terrestrial vertebrates. *Palaios* **12** : 151-164.

Boaz, N. T. and Behrensmeyer, A. K. 1976. Hominid taphonomy: transport of human skeletal parts in an artificial fluviatile environment. *American Journal of Physical Anthropology* **45** : 53-60.

Boyce, C. C. K. 1991. Water vole *Arvicola terrestris*. In, G. B. Corbet. and S. Harris, (Eds.) *Handbook of British Mammals*. Third edition. pp. 212-218. Oxford: Blackwell Scientific Publications.

Brain, C. K. 1981. *The Hunters or the Hunted*. Chicago: Chicago University Press.

Bramwell, D. 1970. Fox Hole Cave Report for 1970 Season. *Peakland Archaeological Society Bulletin* **26** : 1-13.

Bramwell, D. 1971. Excavations at Fox Hole Cave, High Wheeldon, 1961-1970. *Derbyshire Archaeological Journal* **91** : 1-19.

Bramwell, D. n.d. Peakland Archaeological Society excavation notebooks. *Unpublished, curated by Buxton Museum, Derbyshire*.

Bramwell, D., Yalden, D. W. and Yalden, P. E. 1990. Ossum's Eyrie Cave: an archaeological contribution to the recent history of vertebrates in Britain. *Zoological Journal of the Linnean Society* **98** : 1-25.

Broom, R. 1948. Some South African Pliocene and Pleistocene mammals. *Annals of the Transvaal Museum* **21** : 1-38.

Brothwell, D. 1981. The Pleistocene and Holocene archaeology of the house mouse and related species. In, R. J. Berry, (Ed.) *Biology of the house mouse*. pp. 1-11. London: Academic Press.

Bryant, V. M. J. 1974. Prehistoric diet in southwest Texas: the coprolite evidence. *American Antiquity* **39** : 407-420.

Buckland, P. C. 1976. *The environmental evidence from the Church Street Roman sewer system*. The Archaeology of York 14/1 London: Council for British Archaeology.

Buckland, W. 1823. *Reliquiae diluvianae; or observations of the organic remains contained in caves, fissures and diluvial gravel, and on other geological phenomenon, attesting to the action of an universal deluge.* London: John Murray.

Bunn, D. S., Warburton, A. B. and Wilson, R. D. S. 1982. *The Barn Owl.* Vermillion, South Dakota: Buteo Books.

Burton, J. A., Ed. 1973a. *Owls of the World.* London: Peter Lowe.

Burton, P. 1973b. What makes an owl. In, J. A. Burton, (Ed.) *Owls of the World.* pp. 34-40. London: Peter Lowe.

Ceska, V. 1980. Untersuchungen zu nährungsverbrauch, nährungsnützung und energiehaushalt bei Eulen (Investigation on food consumption and energy budget in owls). *Journal für Ornithologie.* **121** : 186-199 [In German with English summary].

Chamberlain, A. T. 1996. More dating evidence for human remains in British caves. *Antiquity* **70** : 950-953.

Chamberlain, A. T. 1999. Carsington Pasture Cave, Brassington, Derbyshire: a Prehistoric Burial Site. *Cave Archaeology and Palaeontology Research Archive (CAPRA)* **1** : available at - http://www.shef.ac.uk/~capra/1/carsing.html.

Chamberlain, A. T. 2001. Radiocarbon Dates from Carsington Pasture Cave, Brassington, Derbyshire. *Cave Archaeology and Palaeontology Research Archive (CAPRA)* **3** : available at - http://www.shef.ac.uk/~capra/3/carsdates.html.

Chinery, M. 1993. *Insects of Britain and Northern Europe. 3rd edition.* London: Harper Collins.

Chitty, D. 1938. A laboratory study of pellet formation in the short-eared owl. *Proceedings of the Zoological Society of London* **108 A** : 267-287.

Chitty, D. 1996. *Do lemmings commit suicide? Beautiful hypotheses and ugly facts.* Oxford: Oxford University Press.

Churchfield, S. 1980. Population dynamics and seasonal fluctuations in numbers of the common shrew in Britain. *Acta Theriologica* **25** : 415-424.

Churchfield, S. 1984. Dietary separation in three species of shrew inhabiting watercress beds. *Journal of Zoology, London* **204** : 211-228.

Churchfield, S. 1990. *The Natural History of Shrews*. New York: Cornell University Press.

Churchfield, S. 1991a. Common shrew *Sorex areneus*. In, G. B. Corbet and S. Harris, (Eds.) *Handbook of British Mammals*. Third edition. pp. 51-58. Oxford: Blackwell Scientific Publications.

Churchfield, S. 1991b. Pygmy shrew *Sorex minutus*. In, G. B. Corbet and S. Harris, (Eds.) *Handbook of British Mammals*. Third edition. pp. 60-64. Oxford: Blackwell Scientific Publications.

Churchfield, S. 1991c. Water shrew *Neomys fodiens*. In, G. B. Corbet and S. Harris, (Eds.) *Handbook of British Mammals*. Third edition. pp. 64-68. Oxford: Blackwell Scientific Publications.

Churchfield, S. 1994. Foraging strategies of shrews, and the evidence from field studies. In, J. F. Merritt, G. L. Kirkland and R. K. Rose, (Eds.) *Advances in the Biology of Shrews. Carnegie Museum of Natural History Special Publication No 18.* pp. 77-87. Pittsburgh: The Carnegie Museum of Natural History.

Churchfield, S. and Brown, V. K. 1987. The trophic impact of small mammals in successional grasslands. *Biological Journal of the Linnean Society* **31** : 273-290.

Clark, R. J., Smith, D. G. and Kelso, L. H. 1978. *Working bibliography of owls of the world, with summaries of current taxonomy and distribution status.* Washington: National Wildlife Federation.

Coetzee, C. G. 1972. The identification of southern African small mammal remains in owl pellets. *Cimbebasia* **A** (2): 53-64.

Cooke, H. B. S. 1952. Mammals, apemen and Stone Age men in southern Africa. *South African Archaeology Bulletin* 7 : 59-69.

Corbet, G. B. 1961. Origin of the British insular races of small mammals and Lasitanian fauna. *Nature* **161** : 1037-1040.

Corbet, G. B. 1971. Provisional distribution map of British mammals. *Mammal review* **1** : 95-142.

Corbet, G. B. and Harris, S., Eds. 1991. *Handbook of British Mammals*. Oxford: Blackwell Scientific Publications.

Crandell, B. D. and Stahl, P. W. 1995. Human digestive effects on a micromammalian skeleton. *Journal of Archaeological Science* **22** : 789-797.

Cuenca-Besco, G., Conesa, C. L., Canudo, J. I. and Arsuaga, J. L. 1997. Small mammals from Simos de los Huesos. *Journal of Human Evolution* **33** : 175-190.

Dauphin, Y., Denys, C. and Kowalski, K. 1997. Analysis of accumulations of rodent remains: Role of chemical composition of skeletal elements. *Neues Jahrbuch fur Geologie und Palaontologie Abhandlungen* **203** (3): 295-315.

Dauphin, Y., Kowalski, C. and Denys, C. 1994. Assemblage data and bone and teeth modifications as an aid to palaeoenvironmental interpretations of the open-air Pleistocene site of Tighenif (Algeria). *Quaternary Research* **42** : 340-349.

Davis, D. H. S. 1959. The barn owl's contribution to ecology and palaeoecology. *Ostrich Supplement* **3** : 144-153.

Delany, M. J. (Ed.) 1985. *Yorkshire Mammals*. Bradford: University of Bradford.

Denys, C., Dauphin, Y., Rzebik-Kowalska, B. and Kowalski, K. 1996. Taphonomic study of Algerian owl pellet assemblages and differential preservation of some palaeontological implications. *Acta Zoologica Cracoviensia* **39** : 103-116.

Denys, C., Fernandez-Jalvo, F. and Dauphin, Y. 1995. Experimental taphonomy: preliminary results of the digestion of micromammalian bones in the laboratory. *Comptes Rendus hebdomadaires de l'Académie des Sciences de Paris* **321** (2a): 803-809.

Denys, C., Kowalski, K. and Dauphin, Y. 1992. Mechanical and chemical alterations of skeletal tissues in a recent Saharian accumulation of feaces from *Vulpes rueppelli* (Carnivora, Mammalia). *Acta Zoologica Cracoviensia* **32** (2): 265-283.

Dice, L. R. 1945. Minimum intensities of illumination underwhich owls can find dead prey by sight. *American Naturalist* **79** : 384-416.

Dobney, K. 1998. Statement of potential of the biological assemblage from the garderobe of The Old Vicarage, Tadcaster. Environmental Archaeology Unit, University of York, (unpublished report).

Dobney, K., Jaques, D., Carrott, J., Hail, A., Issitt, M. and Large, F. 1996. Biological remains from excavations at Carr Naze, Filey, N. Yorkshire: Technical Report. Reports from the Environmental Archaeology Unit, Report **96/26**.

Dodson, P. and Wexlar, D. 1979. Taphonomic investigation of owl pellets. *Paleobiology* **5** : 275-284.

Duke, G. E., Jegers, A. A., Loff, G. and Evanson, O. A. 1975. Gastric juice of some raptors. *Comparative Biochemistry and Physiology A - Physiology* **50** : 649-656.

Edmonds, M. 1999. *Ancestral Geographies of the Neolithic: Landscape, Monuments and Memory.* London: Routledge.

Efremov, I. A. 1940. Taphonomy: a new branch of paleontology. *Pan-American Geologist* **74** : 81-93.

Elton, C. 1966. *Animal Ecology.* London: Methuen & Co.

Farner, D. S. 1960. Digestion and the digestive system. In, J. A. Marshall, (Ed.) *Biology and Comparative Physiology of Birds.* pp. 411-467. New York: Academic Press.

Fernandez-Jalvo, Y. 1992. Tafonomia de microvertebrados del Complejo carstico de Atapuerca (Burgos), Doctoral Thesis. Universidad Complutense de Madrid, Spain.

Fernandez-Jalvo, Y. 1995. Small mammal taphonomy at La Trinchera de Atapuerca (Burgos, Spain). A remarkable example of taphonomic criteria used for stratigraphic correlations and palaeoenvironmental interpretations. *Palaeogeography, Palaeoclimatology, Palaeoecology* **114** : 167-195.

Fernandez-Jalvo, Y. 1996. Small mammal taphonomy and the Middle Pleistocene environments of Dolina, Northern Spain. *Quaternary International* **33** : 21-34.

Fernandez-Jalvo, Y. and Andrews, P. 1992. Small mammal taphonomy of Gran Dolina, Atapuerca (Burgos), Spain. *Journal of Archaeological Science* **19** : 407-428.

Fernandez-Jalvo, Y., Denys, C., Andrews, P., Williams, T., Dauphin, Y. and Humphrey, L. 1998. Taphonomy and Palaeoecology of Olduvai Bed-1 (Pleistocene, Tanzania). *Journal of Human Evolution* **34** : 137-172.

Fielding, D. C. 1966. The identification of skulls of two British species of *Apodemus*. *Journal of Zoology* **150** : 498-500.

Fisher, D. C. 1981. Crocodilian scatology, microvertebrate concentrations, and enamelless teeth. *Paleobiology* **7** : 262-275.

Flowerdew, J. R. 1985. The population dynamics of wood mice and yellow-necked mice. In, J. R. Flowerdew, J. Gurnell and J. H. W. Gibbs, (Eds.) *The Ecology of Woodland Rodents. Bank Voles and Mice. Symposia of the Zoological Society of London. Vol. 55.* pp. 315-338. London: Academic Press.

Flowerdew, J. R. 1991. Wood mouse *Apodemus sylvaticus*. In, G. B. Corbet. and S. Harris, (Eds.) *Handbook of British Mammals*. Third edition. pp. 200-229. Oxford: Blackwell Scientific Publications.

Flowerdew, J. R., Hall, S. J. G. and Clevedon Brown, J. 1977. Small rodents, their habitats, and the effects of flooding at Wicken Fen, Cambridgeshire. *Journal of Zoology, London* **182** : 323-342.

Geering, K. 1990. A taphonomic analysis of recent masked owl (*Tyto novaehollandiae castanops*) pellets from Tasmania. In, S.Solomon, I. Davidson and D. Watson, (Eds.) *Problem solving in taphonomy, archaeological and palaeontological studies for Europe, Africa and Oceania.*. Queensland: Tempus.

Gifford, D. P. 1981. Taphonomy and paleoecology: a critical review of archaeology's sister disciplines. In, M. B. Schiffer, (Ed.) *Advances in Archaeological Methods and Theory*. pp. 365-438. New York: Academic Press.

Gilinsky, N. L. and Bennington, J. B. 1994. Estimating numbers of whole individuals from collections of body parts: a taphonomic limitation of the paleontological record. *Paleobiology* **20** : 245-258.

Gill, D. W. and Beck, J. S. 1991. *Caves of the Peak District*. Clapham: Dalesman.

Ginn, H. 1973. Little, Pygmy and Elf owls. In, J. A. Burton, (Ed.) *Owls of the World*. pp. 164-185. London: Peter Lowe.

Gipps, J. H. W. and Alibhai, S. K. 1991. Field vole *Microtus agrestris*. In, G. B. Corbet and S. Harris, (Eds.) *Handbook of British Mammals*. Third edition. pp. 203-208. Oxford: Blackwell Scientific Publications.

Glue, D. E. 1967. Prey taken by the barn owl in England and Wales. *Bird Study* **14** : 169-183.

Glue, D. E. 1970. Avian predator pellets analysis and the mammalogist. *Mammal Review* **1** : 53-62.

Glue, D. E. 1973. Owl Pellets. In, J. A. Burton, (Ed.) *Owls of the World*. pp. 193-196. London: Peter Lowe.

Glue, D. E. 1974. Food of the Barn owl in Britain and Ireland. *Bird Study* **21** : 200-210.

Glue, D. E. 1975. Harvest mice as Barn owl prey in the British Isles. *Mammal Review* **5** : 9-12.

Glue, D. E. and Jordon, R. 1988. Early 20th Century Barn owl *Tyto alba* diet in Hampshire. *Hampshire Bird Report* : 79-81.

Gorman, M. L. 1991. Orkney and Guernsey Voles *Microtus arvarlis*. In, G. B. Corbet and S. Harris, (Eds.) *Handbook of British Mammals*. Third edition. pp. 208-211. Oxford: Blackwell Scientific Publications.

Green, P. 2000. A gazetteer of Roman military sites in Britain, northern England. http://www.morgue.demon.co.uk/Pages/Gazetteer/ENGN.HTM.

Grimm, R. J. and Whitehouse, W. M. 1963. Pellet formation in a Great-horned owl. A roentgenigraphic study. *The Auk* **80** : 301-306.

Grossman, M. L. and Hamlet, J. 1964. *Birds of Prey of the World.* New York: Clarkson. N. Potter.

Guilday, J. E., Hamilton, H. W., Anderson, E. and Parmalee, P. W. 1978. The Baker Bluff Cave deposit, Tennessee and the Late Pleistocene faunal gradient. *Bulletin of the Carnegie Museum of Natural History* **11** : 1-67.

Guilday, J. E., Martin, P. S. and McCrady, A. D. 1964. New Paris No.4: A Pleistocene cave deposit in Bedford County, Pennsylvania. *Bulletin of the National Speleological Society* **26** : 121-194.

Guilday, J. E., Parmalee, P. W. and Hamilton, H. W. 1977. The Clark's Cave bone deposit and the Late Pleistocene paleoecology of the Central Appalachian Mountains of Virginia. *Bulletin of the Carnegie Museum of Natural History* **2** : 1-88.

Hadly, E. A. 1999. Fidelity of terrestrial vertebrate fossils to a modern ecosystem. *Palaeogeography, Palaeoclimatology, Palaeoecology* **149** : 398-409.

Hanney, P. 1963. Observations upon the food of the Barn owl (*Tyto alba*) in Southern Nyasaland, with a method of ascertaining population dynamics of rodent prey. *Annals and Magazine of Natural History* **65** : 305-313.

Hannson, L. 1985. Food of bank voles, wood mice and yellow necked mice. In, J. R. Flowerdew, J. Gurnell and J. J. W. Gibbs, (Eds.) *The Ecology of Woodland Rodents. Bank Voles and Mice. Symposia of the Zoological Society of London. Vol. 55.* pp. 141-168. London: Academic Press.

Harris, S. and Trout, R. C. 1991. Harvest mouse *Micromys minutus*. In, G. B. Corbet and S. Harris, (Eds.) *Handbook of British Mammals*. Third edition. pp. 233-239. Oxford: Blackwell Scientific Publications.

Harrison Matthews, L. 1982. *Mammals in the British Isles.* London: Collins.

Henshilwood, C. S. 1997. Identifying the collector: evidence for human processing of the Cape dune mole-rat, *Bathyergus suillus*, from Blombos Cave, Southern Cape, South Africa. *Journal of Archaeological Science* **24** : 659-662.

Hickin, N. E. 1974. *Household insect pests. 2nd edition.* London: Associated Business Programmes Ltd.

Hinton, M. A. C. 1931. *Rats and mice as enemies of mankind (Third edition).* London: British Museum Natural History.

Hoffman, R. 1988. The contribution of raptorial birds to patterning in small mammal assemblages. *Paleobiology* **14** : 81-90.

Jackson, J. W. and Piggott, S. 1951. Peterborough (Neolithic B) pottery from High Wheeldon Cave, Earl Sterndale. *Derbyshire Archaeological Journal* **24** : 72-77.

Jewell, P. A. 1959. Small mammals of the Bronze Age. *Bulletin of the Mammal Society* **51** : 9-11.

Johnson, P. N. 1993. Sugarbeet, mice and barn owls. *The Raptor* **4** : 60-62.

Karalus, K. E. and Eckert, A. W. 1974. *The Owls of North America.* New York.: Doubleday.

Khenzykhenova, F. 1996. Late Pleistocene small mammals from the Baikal region (Russia). *Acta Zoologica Cracoviensia* **39** : 229-234.

König, C., Friedhelm, W. and Becking, J. 1999. *Owls. A Guide to the Owls of the World.* London: Yale University Press.

Korth, W. W. 1979. Taphonomy of microvertebrate fossil assemblages. *Annals of the Carnegie Museum* **48** : 235-285.

Kotzageorgis, G. C. and Mason, C. F. 1997. Small mammal populations in relation to hedgerow structure in an arable landscape. *Journal of Zoology, London* **242** : 425-434.

Kowalski, K. 1990. Some problems with the taphonomy of small mammals. In, O. F. a. W.-D. Heinrich, (Ed.) *International symposium evolution, phylogeny and biostratigraphy of Arvicolids (Rodentia, Mammalia).* pp. 285-295. Prague: Geological Survey.

Krebs, C. J. 1978. *Ecology.* Second Edition. New York: Harper & Row.

Krebs, J. R. 1978. Optimal foraging: decision rules for predation. In, J. R. Krebs and N. B. Davies, (Eds.) *Behavioural Ecology: An evolutionary approach.* pp. 23-63. London: Blackwell Scientific Publications.

Kusmer, K. D. 1990. Taphonomy of owl pellet deposition. *Journal of Paleontology* **64** : 629-637.

Latham, R. M. 1950. *The food of predaceous animals in Northeastern United States. Final report.* Harrisburg: Pennsylvania Game Commission.

Lawrence, M. J. and Brown, K. W. 1967. *Mammals of Britain: Their Tracks, Trails & Signs.* London: Blandford Press.

Lawrence, R. W. 1997. *Owls: The Silent Fliers.* New York: Firefly Books.

Levinson, M. 1982. Taphonomy of micovertebrates - From owl pellets to cave breccia. *Annals of the Transvaal Museum* **33** : 115-121.

Levinson, M. 1983. An assessment of small rodents as environmental indicatiors, with reference to palaeoecological reconstructions of the Makapansgat and Swartkrans hominid sites, Unpublished PhD Thesis. University of Witwatersrand, Johannesburg, South Africa.

Love, R. A., Webbon, C., Glue, D. and Harris, S. 2000. Changes in the food of British Barn Owls (*Tyto alba*) between 1974 and 1997. *Mammal Review* **30** (2): 107-129.

Lyman, R. L. 1994. *Vertebrate Taphonomy.* Cambridge: Cambridge University Press.

Maas, M. C. 1985. Taphonomy of a Late Eocene microvertebrate locality, Wind River Basin, Wyoming (U.S.A.). *Palaeogeography, Palaeoclimatology, Palaeoecology* **52** : 123-142.

Matthews, W. and Hastorf, C. 2000. Integrating archaeological science. In, I. Hodder, (Ed.) *Towards reflexive method in archaeology*. pp. 37-50. Cambridge: McDonald Institute for Archaeological Research.

Mayhew, D. F. 1977. Avian predators as accumulators of fossil mammal material. *Boreas* **6** : 25-31.

Mayhew, D. F. and Stuart, A. J. 1986. Stratigraphic and taxonomic revision of the fossil vole remains (Rodentia, Microtinae) from the Lower Pleistocene deposits of Eastern England. *Philosophical Transactions of the Royal Society, London* **B 312** : 431-485.

Mellett, J. S. 1974. Scatological origin of microvertebrate fossil accumulations. *Science* **185** : 349-350.

Mennega, A. M. W. 1938. Waterstofionenconcentratie en vertering in de maag van eenige vertebraten, PhD Dissertation, Rijks-Universiteit, Utrecht.

Mikkola, H. 1983. *Owls of Europe*. Vermillion, South Dakota: Buteo Books.

Ministry of Agriculture, F. a. F. 1981. *Pest infestation control laboratory report 1977-1979*. London: HMSO.

Montgomery, W. I. 1975. On the relationship between sub-fossil and recent British Water voles. *Mammal Review* **5** : 23-29.

Montgomery, W. I. 1991. Yellow-necked mouse *Apodemus flavicollis*. In, G. B. Corbet and S. Harris, (Eds.) *Handbook of British Mammals*. Third edition. pp. 229-233. Oxford: Blackwell Scientific Publications.

Mourer-Chauviré, C., Alcover, J. A., Moya, S. and Pons, J. 1980. Une nouvelle forme insulaire d'effraie géante *Tyto balearica* n. sp., du Plio-Pleistocene des Baléares. *Géobios* **13** : 803-811.

Nowak, R. M. 1991. *Walker's Mammals of the World*. Volume 2. Fifth Edition. London: John Hopkins University Press.

Nowak, R. M. 1999a. *Walker's Mammals of the World*. Volume 1. Sixth Edition. Baltimore: John Hopkins University Press.

Nowak, R. M. 1999b. *Walker's Mammals of the World*. Volume 2. Sixth Edition. Baltimore: John Hopkins University Press.

O'Connor, T. P. 1988. *Bones for the General Accident site, Tanner Row*. The Archaeology of York 15/2 London: Council for British Archaeology.

O'Connor, T. P. 1989. *Bones from Anglo-Scandinavian levels at 16-22 Coppergate*. The Archaeology of York 15/3 London: Council for British Archaeology.

O'Connor, T. P. 1991. *Bones from 46-54 Fishergate*. The Archaeology of York 15/4 London: Council for British archaeology.

Ottaway, P. n.d. *Romans on the Yorkshire coast*. York: York Archaeological Trust Publication.

Payne, R. S. 1971. Acoustic location of prey by Barn Owls (*Tyto alba*). *Journal of Experimental Biology* **54** : 535-573.

Peabody, F. E. 1954. Travertines and cave deposits of the Kaap Escarpment of South Africa, and the type locality of *Astralopithicus africanus* Dart. *Bulletin of the Geological Society of America* **65** : 671-706.

Pearson, O. P. 1964. Carnivore - mouse predation: an example of its intensity and bioenergetics. *Journal of Mammalogy* **45** : 177-188.

Pernetta, J. C. 1977. Population ecology of British shrews in grassland. *Acta Theriologica* **22** : 279-296.

Prestt, I. and Wagstaffe, R. 1973. Barn and Bay owls. In, J. A. Burton, (Ed.) *Owls of the World.* pp. 42-60. London: Peter Lowe.

Rackham, D. J. 1982. The smaller mammals in urban environments: their recording and interpretation from archaeological deposits. In, A. R. Hall. and H. K. Kenward, (Eds.) *Environmental archaeology in the urban context.* pp. 86-93. London: The Council for British Archaeology.

Rackham, J. 1979. *Rattus rattus*: the introduction of the black rat into Britain. *Antiquity* **53** : 112-120.

Raczynski, J. and Ruprecht, A. C. 1974. The effects of digestion on the osteological composition of owl pellets. *Acta Ornithologica* **14** : 1-12.

Randi, E., Fusco, G., Lorenzini, R. and Spine, F. 1991. Allozyme divergence and phylogenetic relationships within the Strigiforms. *The Condor* **93** : 295-301.

Rautenbach, I. L. 1978. Ecological distribution of the mammals of the Transvaal. *Annals of the Transvaal Museum* **31** : 131-157.

Reed, C. I. and Reed, B. P. 1928. The mechanism of pellet formation in the Great Horned Owl (*Bubo virginianus*). *Science* **68** : 359-360.

Reinhard, K. J. 1988. Cultural ecology of prehistoric parasitism on the Colorado plateau as evidenced by coprology. *American Journal of Physical Anthropology* **77** : 355-366.

Reitz, E. J. and Wing, E. S. 1999. *Zooarchaeology.* Cambridge: Cambridge University Press.

Rogers Brambell, F. W. 1958. Voles and Field Mice. *Forestry Commision Leaflet* **44** : 1-11.

Saavedra, B. and Simonetti, J. A. 1998. Small mammal taphonomy: intraspecific bone assemblage comparison between South and North American barn owl *Tyto alba* populations. *Journal of Archaeological Science* **25** : 165-170.

Sanchez, V., Denys, C. and Fernandez-Jalvo, Y. 1997. Origine et formation des accumulations de microvertébrés de la couche 1a du site su Monte di Tuda (Corse, Holocène). Contribution à l'étude taphonomique des micromammifères. *Geodiversitas* **19** (1): 129-157.

Savage, R. J. G. 1966. Irish Pleistocene mammals. *Irish Naturalists' Journal* **15** : 117-130.

Schiffer, M. B. 1983. Toward the identification of formation processes. *American Antiquity* **48** (4): 675-706.

Semken, H. A. J. 1988. Environmental interpretations of the "disharmonious" Late Wisconsinan biome of Southeastern North America. In, R. S. Laub., N. G. Miller, and

D. W. Steadman., (Eds.) *Late Pleistocene and Early Holocene Paleoecology and Archeology of the Eastern Great Lakes Region. Bulletin of the Buffalo Society of Natural Sciences.*. New York: Buffalo.

Shaffer, B. S. 1992. Quarter-inch screening: Understanding biases in recovery of vertebrate faunal remains. *American Antiquity* **57** : 129-136.

Shawyer, C. 1994. *The Barn Owl.* London: Hamlyn.

Shimwell, D. W. 1971. Pollen analysis from two horizons in Fox Hole Cave. *Derbyshire Archaeological Journal* **91** : 16-18.

Shotwell, J. A. 1955. An approach to the paleoecology of mammals. *Ecology* **36** : 327-337.

Sibley, C. G. and Ahlquist, J. E. 1972. A comparative study of non-passerine birds. *Peabondy Museum of Natural History Yale University Bulletin* **39** : 1-276.

Sibley, C. G. and Ahlquist, J. E. 1990. *Phylogeny and Classification of Birds.* London: Yale University Press.

Simonetti, J. A. and Cornejo, L. E. 1991. Archaeological evidence of rodent consumption in central Chile. *Latin American Antiquity* **2** : 92-96.

Smal, C. M. and Fairley, J. S. 1984. The spread of the bank vole *Clethrionomys glareous* in Ireland. *Mammal Review* **14** : 71-78.

Smith, C. R. and Richmond, M. E. 1972. Factors influencing pellet egestion and gastric pH in the Barn owl. *The Wilson Bulletin* **84** : 179-186.

Smith, K. G. V. 1986. *A Manual of Forensic Entomology.* London: British Museum (Natural History).

Southern, H. N. and Crowcroft, W. P. 1956. Terrestrial habitats of the water vole (*Arvicola amphibius*). *Proceedings of the Zoological Society London* **126** : 166-167.

Stahl, P. W. 1982. On small mammal remains in archaeological contexts. *American Antiquity* **47** : 822-829.

Steans, A. and Scothon, M. 1998. With a little skullduggery. *Descent* **145** : 34.

Stonehouse, B. 1973. Introduction. In, J. A. Burton., (Ed.) *Owls of the World.* pp. 13-16. London: Peter Lowe.

Stuart, A. J. 1982. *Pleistocene Rodents in the British Isles.* London: Longman.

Stubbs, F. J. 1926a. The water vole in relation to prehistoric man. *The Naturalist* **832** : 141-144.

Stubbs, F. J. 1926b. The water vole in relation to prehistoric man (cont.). *The Naturalist* **833** : 177-180.

Sutcliffe, A. J. and Kowalski, K. 1976. Pleistocene Rodents of the British Isles. *Bulletin of the British Museum (Natural History) Geology* **27** : 31-147.

Sutton, S. L. and Beaumont, H. E., Eds. 1989. *Butterflies and Moths of Yorkshire.* Doncaster: Yorkshire Naturalists Union.

Taylor, I. 1994. *Barn Owls: predator - prey relationships and conservation.* Cambridge: Cambridge University Press.

Taylor, K. D. 1978. Range movement and activity of common rats (*Rattus norvegicus*) on agricultural land. *Journal of Applied Ecology* **15** : 663-677.

Taylor, K. D. 1991. Ship rat *Rattus rattus*. In, G. B. Corbet and S. Harris, (Eds.) *Handbook of British Mammals*. Third edition. pp. 255-259. Oxford: Blackwell Scientific Publications.

Taylor, K. D., Fenn, M. G. and Macdonald, D. W. 1991. Common rat *Rattus norvegicus*. In, G. B. Corbet and S. Harris, (Eds.) *Handbook of British Mammals*. Third edition. pp. 248-255. Oxford: Blackwell Scientific Publications.

Turchin, P., Oksanen, L., Ekerholm, T., Oksanen, T. and Henttonen, H. 2000. Are lemmings prey or predators? *Nature* **405** : 562-565.

Van Kolfschoten, T. 1995. On the application of fossil mammals to the reconstruction of the palaeoenvironment of northwestern Europe. *Acta Zoologica Cracoviensia* **38** : 73-84.

Vigne, J. and Valladas, H. 1996. Small mammal fossil assemblages as indicators of environmental change in Northern Corsica during the last 2500 years. *Journal of Archaeological Science* **23** : 199-215.

Voorhies, M. R. 1969. Taphonomy and population dynamics of an early Pliocene vertebrate fauna, Knox County, Nebraska. *University of Wyoming Contributions to Geology, Special Paper* **1** : 1-69.

Voous, K. H. 1988. *Owls of the Northern Hemisphere*. London: Collins.

Walker, C. A. 1973. The origins of owls. In, J. A. Burton, (Ed.) *Owls of the World*. pp. 27-33. London: Peter Lowe.

Walker, L. W. 1993. *The Book of Owls*. Texas: University of Texas Press. 1st Published 1974. New York: Knopf.

Wells, P. V. 1976. Macrofossil analysis of wood rat (*Neotoma*) middens as a key to the Quaternary history of arid America. *Quaternary Research* **6** : 233-248.

Wesselman, H. B. 1984. *The Omo Micromammals*. Contributions to Vertebrate Evolution 7 London: Karger.

Williams, D. F. and Braun, S. E. 1983. Comparison of pitfall and conventional traps for sampling small mammal populations. *Journal of Wildlife Management* **47** : 841-845.

Williams, J. P. 1997. What is the contribution of small mammals to our understanding of palaeoecology, how is this relevant to archaeology, and how can taphonomic studies aid in that interpretation? Department of Archaeology and Prehistory, University of Sheffield. Undergraduate Dissertation.

Wing, S. L., Sues, H., Potts, R., DiMichele, W. A. and Behrensmeyer, A. K. 1992. Evolutionary Paleoecology. In, A. K. Behrensmeyer, J. D. Damuth, W. A. Dimichele, R. Potts, H. Sues and S. L. Wing, (Eds.) *Terrestrial Ecosystems Through Time. Evolutionary Paleoecology of Terrestrial Plants and Animals*. Chicago: Chicago University Press.

Wink, M. and Heidrich, P. 1999. Molecular Evolution and Systematics of the Owls (Strigiforms). In, C. König, F. Weick and J. Becking, (Eds.) *Owls. A Guide to the Owls of the World*. London: Yale University Press.

Wolff, R. G. 1973. Hydrodynamic sorting and ecology of a Pleistocene mammalian assemblage from California (U.S.A.). *Palaeogeography, Palaeoclimatology, Palaeoecology* **13** : 91-101.

Woodroffe, G. 1996. *The Water Vole*. London: The Mammal Society.

Woodroffe, G. E. 1953. An ecological study of the insects and mites in the nests of certain birds in Britain. *Bulletin of Entomological Research* **44** : 739-772.

Yalden, D. W. 1977. *The Identification of Remains in Owl Pellets*. : Mammal Society.

Yalden, D. W. 1982. When did the mammal fauna of the British Isles arrive? *Mammal Review* **12** : 1-57.

Yalden, D. W. 1992. Changing distribution and status of small mammals in Britain. *Mammal Review* **22** : 97-106.

Yalden, D. W. 1999. *The History of British Mammals*. London: T & AD Poyser Natural History.

Yalden, P. E. and Yalden, D. W. 1989. Small vertebrates. In, P. Ashbee, M. Bell and E. Proudfoot, (Eds.) *Wilsford shaft: excavations 1960-2*. pp. 103-105. London: Historic Buildings & Monuments Commission for England.

Ylonen, H. 1994. Vole cycles and antipredatory behaviour. *Tree* **9** : 426-430.

Yom-Tov, Y. and Wool, D. 1997. Do the contents of Barn owl pellets accurately represent the proportions of prey species in the field? *The Condor* **99** : 972-976.

Zhang, Z. and Usher, M. B. 1991. Dispersal of wood mice and bank voles in an agricultural landscape. *Acta Theriologica* **36** : 239-245.