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Taphonomy for taxonomists: Implications of predation in small mammal studies

Yolanda Fernández-Jalvo [a], [*], Peter Andrews [b], [c], Christiane Denys [d], Carmen Sesé [a], Emmanuelle Stoetzel [e], Dolores Marin-Monfort [a], Dolores Pesquero [a]

[a] Museo Nacional de Ciencias Naturales (CSIC), José Gutiérrez Abascal 2, 28006, Madrid, Spain
[b] The Natural History Museum, Cromwell Road, London, SW7 5BD, UK
[c] Blandford Museum, Bere's Yard, Blandford, DT11 7AZ, Dorset, UK
[d] Muséum national d'Histoire naturelle - CNRS, UMR 7205 ISYEB, 55,rue Buffon, 75005, Paris, France
[e] Muséum national d'Histoire naturelle - CNRS, UMR 7194 HNHP, Musée de l'Homme - Palais de Chaillot, 17 place du Trocadéro, 75016, Paris, France

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ABSTRACT

Predation is one of the most recurrent sources of bone accumulations. The influence of predation is widely studied for large mammal sites where humans, acting as predators, produce bone accumulations similar to carnivore accumulations. Similarly, small mammal fossil sites are mainly occupation levels of predators (nests or dens). In both cases, investigations of past events can be compared with present day equivalents or proxies. Chewing marks are sometimes present on large mammal predator accumulations, but digestion traits are the most direct indication of predation, and evidence for this is always present in small mammal (prey) fossil assemblages. Digestion grades and frequency indicates predator type and this is well established since the publication of Andrews (1990). The identification of the predator provides invaluable information for accurate interpretation of the palaeoenvironment. Traditionally, palaeoenvironmental interpretations are obtained from the taxonomic species identified in the site, but rather than providing direct interpretations of the surrounding palaeoenvironment, this procedure actually describes the dietary preferences of the predators and the type of occupation (nests, marking territory, dens, etc). This paper reviews the identification of traits produced by predators on arvicolins, murins and soricids using a method that may be used equally by taxonomists and taphonomists. It aims to provide the "tools" for taxonomists to identify the predator based on their methodology, which is examining the occlusal surfaces of teeth rather than their lateral aspects. This will greatly benefit both the work of taphonomists and taxonomists to recognize signs of predation and the improvement of subsequent palaeoecological interpretations of past organisms and sites by identifying both the prey and the predator.

1. Introduction

Small mammals (rodents, bats, shrews, hedgehogs, hares) represent around 80% of mammal species richness, and this gives them a special role in palaeoecology. Relative abundance of microfaunal skeletal elements is often greater than that of large mammal fossils, and species richness of small mammals may easily be double that of large mammals. In addition, fossil small mammals are good palaeoecological indicators because they are highly dependent on vegetation cover, they have a more limited territory than large mammals (they do not migrate on long distances) and their species richness correlates highly with vegetation species richness (Andrews & O'Brien, 2000, 2010).

Predation is the main factor accumulating small mammal assemblages both in modern and in fossil sites (Andrews, 1990; Fernández-Jalvo and Andrews, 1992; Sanchez et al., 1997; Mondini, 2002; Gómez, 2005, 2007; Verzi et al., 2008; Stoetzel et al., 2010; Lloveras et al., 2013; Matthews et al., 2005, 2006). Predation of small mammals may be recognized by the presence of digestion on their teeth and skeleton, shown by the pioneering

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[*] Corresponding author.
E-mail addresses: yfj@mncn.csic.es (Y. Fernández-Jalvo), pjandrews@uwclub.net (P. Andrews), denys@mnhn.fr (C. Denys), c.sese@mncn.csic.es (C. Sesé), stoetzel@mnhn.fr (E. Stoetzel), dores@mncn.csic.es (D. Marin-Monfort), mcnpf503@mncn.csic.es (D. Pesquero).

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studies of Mellet (1974), Mayhew (1977) and Andrews (1990), together with recent studies (Fernández-Jalvo, 1995; Fernández-Jalvo et al., 1998; Sanchez et al., 1997; Stoetzel et al., 2011; Montalvo et al., 2007, 2011; Lloveras et al., 2008c, 2014). Tooth marks are rare on micromammal bone, for damage inflicted by mammalian predators during ingestion (unless the size of the prey is large, e.g. rabbit), and subsequent digestion of the ingested bones are often so extensive as to obliterate evidence of tooth marks (Andrews, 1990).

Mikkola (1983) published an extensive description of the diets of European owls. In addition, species of raptors and small carnivores were being investigated to extend palaeontological implications due to predation by Dodson and Wexlar (1979), Korth (1979) Andrews and Evans (1983), Andrews (1990). These authors demonstrated that predator digestion produces different grades and intensities of preservation (e.g. anatomical element survival, breakage, digestion, postcranial vs. cranial element preservation) of their prey assemblages. They also show how predation affects interpretations of palaeoecological and palaeolandscape interpretations (Fernández-Jalvo et al., 1998; Scott et al., 1996; Stoetzel et al., 2011), highlighting the great range of predators which are the main producers of small mammal assemblages.

Predation is a complex ecological process occurring at the level of ecosystem and is based on predator-prey relationships. Two factors are important here, first ‘density dependence’ (Allee, 1931; Begon et al., 1990; Sidorovich et al., 2011) of prey according to population fluctuations, and second, the trophic preferences of the predator. The size ratio of the predator/prey relationship, diurnal or nocturnal hunting behaviour, and hunting strategy and territory size are all factors that may vary from one predator to another (summary in Andrews, 1990). The species composition of prey remains may or may not be an indicator of predator species, and in any case it cannot be relied on. Breakage may be influenced by post-depositional factors and anatomical element survival patterns, both of which may obscure breakage resulting from predation.

The distinction and identification of the predator(s) helps to better identify the nature and origin of the assemblage, the source of the fossil specimens and potential spatial-time mixtures during the initial stages of site formation. Palaeoecological studies based on small mammals need to take these factors into account when comparing fossil species (prey assemblages selected by predator's preferences and deposited in the predator's habitats) with their modern equivalents (ecological studies of living specimens in their own habitat), both with individual species comparisons and at the community level, for example through multivariate statistical analysis, indices focused on frequency percentages, taxonomic weighting of the fauna relative to their living relatives, or ratios of frequencies of key-taxa. On the other hand, past biomes may represent habitats with no modern counterpart (Fernández-Jalvo et al., 1998, 2011).

Differences in habitat due to predator-prey behaviours have to be taken into account during habitat reconstruction. For example, the small mammal, amphibian and squamate faunas recovered from Pleistocene deposits at Azokh cave (Southern Caucasus) are mostly species or genera found today in semi-arid environments, but the evidence from the local flora and large mammals preserved in the cave indicates that the local environment was deciduous woodland. Such apparent contradiction based on taxonomic identifications is due to different sources of predation. Large mammals were mainly predated by humans in the surroundings (Marin-Monfort et al., 2016) and local flora was the most available woods collected from the nearby habitats in the mountain slope (Allué, 2016). Taphonomic analysis of the small mammals showed that small mammals were the prey assemblage of *Bubo bubo* (Andrews et al., 2016). Amphibians and squamates showed signs of digestion (Blain, 2016) indicating the source could also be these eagle owls. The inference was that *Bubo bubo* was roosting close to or inside the cave, which was in a wooded valley, but it was hunting several kilometres away in the adjoining open country, as modern eagle owls do, in this case the lowland arid zone (Andrews et al., 2016).

In other example, the combination of taxonomic, taphonomic and palaeoecological studies at the open air site of Olduvai Bed I (Fernández-Jalvo et al., 1998) differentiated taphonomic effects on the fauna from real environmental and ecological changes. A change in the taxonomic richness and composition of the faunas at the base of Bed I site FLKNN (richer in murins) and those from upper Bed I site FLKN (richer in gerbillins) was previously proposed by Jaeger (1976) to be indication of a drastic climatic change which could actually be linked to the first appearance of representatives of the genus *Homo* (*Homo habilis*). Fernández-Jalvo et al. (1998) showed that the FLKNN faunas were accumulated by predators with light categories of digestion (with FLKNN2 most possibly be *Tyto alba*). The small mammal faunas following the sequence of Bed I (FLKN6-4) were probably the prey of mammalian carnivores, and these are better adapted to detect and hunt burrowers, such as *Gerbillus* and *Gerbilliscus (Tatera).* These rodents are usually found in arid environments or in environments with sandy and soft soils, but their abundance in upper Bed I may be an artefact of predation rather than indicating these environments. Unit FLKN4, apart from mammalian carnivores, showed also the influence of a nocturnal raptor (likely *Bubo lacteus*), and different rodent species could be distinguished to have been hunted by each predator on the basis of the category of digestion. The change from murin-dominated faunas at FLKNN to more gerbillin-dominated faunas at FLKN6 to 4 was attributed to change in predator instead of a climatic change. On the other hand, the faunas from the top of upper Bed I, sites FLKN3 to 1, which showed the highest Gerbillinae/Murinae ratios, but low species richness, were accumulated by two nocturnal owls that normally have prey assemblages with high species richness, *Bubo lacteus* and *Bubo africanus* respectively, and the low species richness in these levels is anomalous and inconsistent with these owl's behaviour. This indicates that the low species richness at FLKN 3-1 is due to the predator and not a postdepositional artefact (i.e. reworking or time-averaging), and together with the high Gerbillinae/Murinae ratio shows that the palaeoecological trend towards aridity at the top of Bed I could be generated by climate change, with a marked shift from woodland vegetation (FLKNN and FLKN6-4) to a more open woodland or wooded grassland. Identical indications were obtained from large mammals, based on taxon-free analysis of bovid postcrania (Plummer and Bishop, 1994).

The aims of this article are firstly to provide a simplified method adapted from original taphonomic protocols in order to enable taxonomists to recognize signs of predation and, therefore, the influence of predation in a fossil assemblage; and secondly to obtain a better approach of the predator's diagnosis, which bone remains may not be fossilized at the site. Digestion patterns were described and illustrated in Andrews (1990) in most micromammal groups on dental lateral views, using SEM pictures. Each category of digestion in voles was sketched in Fernández-Jalvo and Andrews (1992) together with descriptions of digestion in murids and soricids. We focus now on the description and images of digestion and dental elements based on the views that are most frequently analyzed, stored and figured by taxonomists, here illustrated with images taken under the binocular light microscope. We aim to describe key features to facilitate the identification of the intensity and grades of digestion recorded on fossils which are diagnostic of predator action that, in some cases indicate the predator's identity at species level or, in some others, a general indication of the natural group's category. Some examples, from modern and fossil sites,