The evolutionary history and palaeoecology of primate predation: *Macaca sylvanus* from Plio-Pleistocene Europe as a case study.

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ABSTRACT

In this article we briefly review primate interactions with predators throughout their evolutionary history. Like today, predators of past primates were taxonomically diverse, including crocodilians, aquatic mammals, hyaenids, raptors and other primates. There is strong evidence for felid predation of extinct primates, with most work undertaken on the African Plio-Pleistocene fossil record. Felid predation of Plio-Pleistocene primates from other areas, including Europe, is much less well understood so we explore co-occurrence and potential interaction between carnivorans (with particular reference to felids) and *Macaca sylvanus*, which was widespread and present in Europe from the late Miocene to the late Pleistocene. Over its tenure in the fossil record, *M. sylvanus* co-occurred with a diverse array of carnivorans, including canids and hyaenids, but medium-sized felids probably posed the most significant predation risk. It is likely, however, that human predation was a major factor contributing to macaque extinction in Europe.

Introduction

Felid-like mammals, the predator focus of the meeting that prompted this Special Issue, originated in the Oligocene, around 35 million years ago, but molecular data suggest that the modern family Felidae arose within the last 11 million years (Johnson et al., 2006). From a probable Asiatic origin, the Felidae spread relatively rapidly within the Old World and also colonised the New World before the end of the Miocene (Johnson et al. 2006). Felids are among the most prominent predators of modern primates (see references in this volume), and are viewed as being equally important predators in the past, particularly during the Plio-Pleistocene in Africa (Brain 1981, 1993; deRuiter and Berger 2000). The fossil record shows that primates have been subject to predation throughout their evolutionary history, and have interacted with a large group of potential and actual predators. Given that felid-like mammals evolved at least 20 million years after the origin of the first primates, other carnivores have also clearly played an important role in shaping primate responses to predation. Tooth marks on a *Notharctus* fossil roughly 50 million years old suggest that it was predated upon by a primitive carnivore from the genus *Vulpavus*, a member of the Miacidae, a family ancestral to modern Carnivora (Alexander 1992; Hart and Sussman 2005). A partial mandible of *Europolemur koenigswaldi*, found in a coprolite at the German Eocene site of Grube Messel (around 47 million years ago), indicates it probably fell prey to the aquatic mammal *Buxolestes piscator* (Franzen 1997). Also at Messel, another *E. koenigswaldi* specimen is likely to have been killed by being shaken in half by a crocodilian, with various skeletal elements, probably from a number of individuals, bearing crocodilian tooth marks (Franzen and Frey 1993).

Evidence from the fossil record shows that it was not just small primates that were victims of predators: there are numerous striking examples of predation on large-bodied primates, including hominins. Over 40 million years after the *E. koenigswaldi* specimen died at Messel, tooth marks indicate that another crocodilian fed on a foot and lower limb from Olduvai Gorge attributed to *Homo habilis* (Brochu et al. 2010). The early Miocene deposits of Rusinga and Mfangano Islands, East Africa, contain specimens assigned to *Proconsul*, *Dendropithecus* and *Limnopithecus* with bone modification and damage consistent with predation by creodonts and raptors (Jenkins 2011). The *Australopithecus africanus* juvenile from Taung, southern Africa, has the characteristic signatures of eagle predation, including puncture marks in the orbits (Berger 2006). Raptor predation is also implicated in the Plio-Pleistocene cercopithecid assemblage from the Humpata Plateau, Angola (Gilbert et al. 2009). Taphonomic analysis of the Chinese *Homo erectus* site Zhoukoudian suggests that it was a hyaena den, with the hominin fossils brought into the cave by the giant hyaenid *Pachycrocuta brevirostris* (Boaz et al. 2000; Boaz et al. 2004). Indeed, carnivore action has resulted in several highly significant fossil assemblages, including those at Swartkrans in southern Africa, where another juvenile hominin cranium, assigned to *Paranthropus robustus*, exhibits tooth marks that indicate it fell prey to a leopard (Brain 1981). In addition to preying on hominins, carnivorans at Swartkrans fed on cercopithecids (Brain 1993). Hominins were also predators of cercopithecids in the Plio-Pleistocene of Africa: bone breakage patterns provide good evidence for hominin butchery of *Theropithecus oswaldi* at the East African site of Olorgesailie (Shipman et al. 1981). This demonstrates that large primates in the past, like modern baboons (e.g. Willems and Hill 2009) and chimpanzees (e.g. Stanford 1995), were predators as well as prey.

Accurately estimating predation, as well as the relative importance of felids as predators, from the fossil record is very difficult. Predators may be the major accumulating agents of some fossil assemblages, and such taphonomic bias may lead to an over-estimate of the magnitude of predation on extinct primates. When correctly identified, tooth marks (and even cut marks left by hominins) on bone provide a good indication of consumption by carnivores but although it may be correct to assume in the majority of cases that they provide evidence of primary predation, it is also possible that they represent scavenged remains. In some instances, the predator species can be inferred from tooth marks, but a secure identification cannot always be made (Pickering et al. 2004). Certain predators, like sabre-toothed cats, may not leave any tooth marks on bone at all. Although predation on past species may be most accurately determined through examination of tooth marks on or breakage patterns of bones, such study is only possible when adequate fossil material is preserved. Many species are recognised in the fossil records of particular localities, sites and regions only through the presence of isolated teeth, which do not usually exhibit the characteristic signs of predation. Direct evidence for felid predation (and indeed, predation in general) on extinct primates around the world is thus patchy. This notwithstanding, we have two main aims in this article. The first is to give a brief review of what is known about past felid predation on primates around the world, focusing on the period since the modern Felidae arose. Necessarily given the sparse nature of the late Miocene primate fossil record in many regions of the world, our evidence primarily comes from the Pliocene and Pleistocene. Our second aim is to examine the European Pliocene and Pleistocene fossil record in more detail, using *Macaca sylvanus*, the Barbary macaque, as a case study to reconstruct past predation risk using synecological (community ecology) approaches.

PLIOCENE AND PLEISTOCENE SOUTH AMERICA

Several species of modern Neotropical cat, including the jaguar, the cougar, the ocelot, the jaguarundi and the margay, are known to be predators of extant atelid, cebid and callitrichid primates (reviewed in de Oliveira Calleia et al. 2009). It is therefore logical to assume that in South America, felids along with other modern predators such as raptors, snakes and mustelids (Cisneros-Heredia et al. 2005) preyed upon sympatric primates in the past. However, the Neotropical felid fossil record is sparse, with most specimens dated to the Pliocene and Pleistocene (Prevosti 2006). Several extant ocelot species are found in the South

American Pleistocene (Prevosti 2006) but given that the fossil record of primates (and indeed many potential predators) in the Neotropics is also poor, with patchy species occurrence records, it is difficult not only to reconstruct the relative importance of felids as predators of primates but also to examine how predator / prey interactions may have changed over time and differed across South America.

PLIOCENE AND PLEISTOCENE AFRICA

Unsurprisingly, given the attention paid to hominin palaeocommunities, the biggest body of work on past predation of primates and modern felid evolution has been undertaken on the African Plio-Pleistocene fossil record. The Pliocene and Pleistocene fossil record of the felids in Africa is relatively rich with, for example, at least 14 felid species (out of 36 species of fossil Carnivora) identified in East Africa (Werdelin and Lewis 2005). Two of these felids, *Panthera leo* (the lion) and *Panthera pardus* (the leopard) are still represented in the modern East African fauna, and are predators of primates. Other taxa, including the members of the sabre-toothed cat radiation, are now extinct and without a modern analogue. Much of the palaeobiological and taphonomically-based research surrounding Plio-Pleistocene predation has been undertaken on southern African fossil communities, in which leopards and possibly lions were significant but not the only predators (Pickering et al. 2004). At Swartkrans Member 3, for example, there is evidence for hyaena, hominin and large canid predation, alongside felid activity (Pickering et al. 2004). Leopards are likely to have been responsible at Swartkrans Member 3 for collecting the smaller macromammals (Size Classes 1 and 2, under 84 kg) whilst the other predators were responsible for predation on the large mammals (Pickering et al. 2004). Thus, for primates including hominins, leopards would have been prominent predators. This is supported by stable isotope analysis of leopard teeth from Swartkrans Member 1, which also suggests that hominins and papionins may have been the prey of hyaenas and the sabre-toothed felid *Megantereon* (Lee-Thorp et al. 2000). Nonetheless, prey selection may not have remained static over time: isotope signatures from six leopards recovered from Swartkrans Member 2 indicate that they shifted their focus from C3 (browsing) prey to C4 (grazing) prey (Lee-Thorp et al. 2000). This suggests that hominins and C3-consuming papionins such as *Papio hamadryas* were less favoured by leopards in Member 2 times (Lee-Thorp et al. 2000), but does not automatically imply that leopards no longer hunted primates. Instead, the focus of their primate prey may have shifted away from the increasingly large-bodied hominins, with the isotope signatures reflecting the increase in open-habitat adapted papionins that occurred after 1.7 Ma in southern Africa, including the arrival of the C4-consuming *Theropithecus oswaldi* (Elton 2007). Isotope data also provide evidence of niche separation in the large felids at Swartkrans Member 1, with the ‘false’ sabre-toothed cat *Dinofelis* preying on C4 consumers. Association between *Dinofelis* and papionin remains at another southern African Plio-Pleistoce site, Bolt’s Farm, led to speculation that it was a specialised predator of baboons (Turner and Antón 1997). This cannot be supported or refuted on the basis of current evidence, but if it was preying on primates at Swartkrans

Member 1, it must have focused the majority of its attention on *Theropithecus oswaldi*, although the more likely scenario is that *Dinofelis* preyed upon the large grazing ungulates (Lee-Thorp et al. 2000).

PLIOCENE AND PLEISTOCENE ASIA

In Asia today, felids are highly significant predators of primates (Hart 2007), and again it can be assumed that where Asian primates co-existed with carnivorans, there would be predation. However, the hard evidence for this is poor. The fossil record of the Asian Plio-Pleistocene is generally less well-known than that from Africa, and there has been relatively little work on the community ecology and palaeoecology of Plio-Pleistocene Asian mammals, including carnivorans (Dennell et al. 2008). Felids are fairly cryptic in the Asian fossil record, and although the lack of lion and tiger fossils from the early Pleistocene may indicate their genuine absence in the faunal community, it is difficult to ascertain probable presence and distributions for many extinct Asian felids (Dennell et al. 2008). Nonetheless, there are some clues. *Panthera uncia* (snow leopard) has been recovered from early Pleistocene deposits in the Siwaliks, south Asia (Dennell et al. 2008). The large sabre-toothed cat *Megantereon* has also been found in the Siwaliks, (Dennell et al. 2008) as well as at other Pleistocene sites, including the *Homo erectus* locality at Zhoukoudian (Teilhard de Chardin 1939, cited in Martínez Navarro and Palmqvist 1995) and Dmanisi in Georgia (Martínez Navarro and Palmqvist 1995). Another large sabre-toothed cat, *Homotherium* is also found at early Pleistocene sites as far apart as China and Georgia, so despite its relatively poor fossil record in Asia may have been present across the continent (Dennell et al. 2008). In the Late Pleistocene many extant species are present in the fossil record, for example at Duoi U'Oi in northern Vietnam, where the mustelid *Arctonyx collaris*, the canid *Cuon alpinus*, the viverrids *Viverra* cf. *zibetha* and *Viverra* cf. *megaspila* and the felids *Neofelis* cf. *nebulosa*, *Panthera tigris* and *P. pardus* (Bacon et al. 2008). Given the patchy nature of the fossil record in Asia and the relative lack of direct evidence for predation, it is difficult to be precise about the behaviours of the different Asiatic carnivorans, especially for extinct animals with no modern analogue. Nonetheless, it is reasonable to assume that species found in the past that survive to the present would not have significantly altered their foraging strategies, although habitat shifts may have altered precise behaviours and interaction with prey species. For extinct species, and partly due to the study of likely dens with accumulation of carcasses that subsequently fossilised, such as at Zhoukoudian (discussed above; Boaz et al. 2000; Boaz et al. 2004), there is more evidence for the presence and activity of hyaenids in Asia than felids. There is thus much to discover about community ecology and the different roles of carnivorans including felids and it is yet unknown whether Asian hyaenids were significant hunters of prey or whether they scavenged kills made by cats (Dennell et al. 2008).

PLIO-PLEISTOCENE EUROPE

Plio-Pleistocene Europe had a diverse carnivoran fauna, including the felids *P. pardus, P. leo*, *Megantereon cultridens* (sabre-toothed cat), *Acinonyx pardinensis* (giant cheetah), *Panthera gombaszoegensis* (European jaguar), *Homotherium crenatidens* (European sabre-toothed cat), *Lynx spelea* (cave lynx), *Puma pardoides* (Owen's panther) and *Felis silvestris* (wildcat), as well as canids, hyaenids and mustelids, although not all these species were sympatric or even contemporaneous. The European Pliocene and Pleistocene primate fauna, extinct in the wild today, was less diverse than the carnivoran fauna, and comprised only monkeys: the cercopithecines *Macaca sylvanus* (including the Sardinian subspecies *M. s. majori*), *Theropithecus oswaldi*, *Paradolichopithecus arvernensis*, and the colobines *Dolichopithecus ruscinensis*, *Mesopithecus pentelicus* and *Me. monspessulanus*. Again, these species were not necessarily sympatric or contemporaneous. The focus of this study is *M. sylvanus*, the Barbary macaque, which today is endangered and survives only in marginal and relict areas of Morocco and Algeria plus a semi free-ranging population introduced in Gibraltar (Butynski et al. 2008). Found in Europe from the late Miocene to the late Pleistocene, *M. sylvanus* has been recovered from sites in England, the Netherlands, Germany, France, Austria, Italy, Spain and Greece. The fossil record of *Macaca* in Europe is dominated by teeth, with very few postcranial or even cranial specimens described. To our knowledge, there has been no taphonomic examination of either the fossil macaque material from Europe or the context of its deposition, and hence very little is known directly about predation pressure on European macaques. Given the small amount of material available for such study, we choose here to take an indirect, community ecological approach. We reconstruct predator-prey palaeoecology through examination of temporal and geographic species co-occurrence, also examining predator-prey ratios for Pliocene and Pleistocene sites where *Macaca* has been recovered. We thus focus on potential predation risk (the animals' perception of probability of an attack by a predator) rather than predation rate (the annual mortality in a population caused by predation directly) (cf. Hill and Dunbar 1998). This in turn may shed light on the evolutionary pressures influencing behaviours observed in modern *Macaca sylvanus*.

Materials and Methods

Localities, sample and taxonomic assessment

Fossil localities with accurate records of fossil *Macaca sylvanus* were extracted from the open-access NOW (Fortelius 2008) and Palaeobiology (http://paleodb.org/) databases (originally accessed on 14/05/2008 and verified in August 2012). For some Italian fossil localities (e.g. Valdarno, Tasso UF), database records were supplemented with additional mammal species lists from the literature (Palombo et al. 2003; Raia et al. 2006a). Fossil localities where the taxonomic attribution of *M. sylvanus* was uncertain (e.g. records listed as cf. *Macaca sylvanus* or *Macaca* sp.) were not included in analysis. Localities were also excluded when records of large mammals appeared incomplete (i.e. when the number of species was less than or equal to three). Twenty nine localities out of a possible total of 82 were therefore selected for inclusion in the analysis. These cover all Mediterranean regions (Spain, France, Italy, Turkey) together with Central and North Europe (Germany and one locality from United Kingdom). Minimum and maximum ages were recorded for each locality and mean age estimated (see Fig 1). Minimum and maximum ages were used to assign each locality to one of six time bins, comprising intervals of c. 500 ka, covering the whole Plio-Pleistocene. Those time bins correlate well with the classic biochronological units identified for Italy and applied elsewhere in Europe (Azzaroli 1983; Gliozzi et al. 1997; Rook and Martínez-Navarro 2009): 4.2-3.0 Ma (Early Villafranchian), 2.5-1.8 Ma (Middle Villafranchian), 2.1-1.7 Ma (early Late Villafranchian), 1.6-1.1 Ma (late Late Villafranchian), 1.0-0.4 (Galerian) Ma, 0.3-0.01 (Aurelian). By using time bins, the potential bias introduced by inaccurate clustering of fossil localities is avoided.

FIGURE 1 ABOUT HERE

For each fossil locality included in analysis, species lists for large mammals (excluding micromammals of the Orders Rodentia, Lagomorpha, Insectivora and Chiroptera) were downloaded to explore co-occurrences with mammalian predators as well as predator-prey ratios. Species lists and hence analyses were confined to mammals, as although raptors and reptiles could have preyed on fossil macaques their fossil record is patchy and exceedingly poor. The mammalian species list included Carnivora from the families Canidae, Felidae, Hyaenidae and Mustelidae with estimated body masses over five kilograms, all of which were potential predators of *Macaca sylvanus*. For all the fossil carnivoran species body mass estimates were based on regression equations (Van Valkenburgh 1990) using lower first molar length as presented in Meloro et al. (2007). The threshold between large and small carnivorans is usually considered to be seven kilograms (Van Valkenburgh 1985), but using carnivoran species above five kilograms allowed the inclusion of foxes (*Vulpes* sp.) and wildcats (*Felis silvestris*), both potential predators of juvenile macaques. However, because these smaller-bodied species were unlikely to pose a real threat to adult macaques, separate analyses including carnivorans between five and seven kilograms were undertaken. Although the relatively large mustelid species from the genus *Gulo* (wolverines) was included, smaller mustelids and viverrids (e.g. weasels, genets) were excluded because their fossil record is scant and it is unlikely that they represented a serious threat for even juvenile macaques. Bears were also excluded because all Plio-Pleistocene species are either omnivorous or herbivorous (Mazza and Rustioni 1994; Meloro 2011a), and were thus unlikely to be predators of monkeys. Only those carnivoran specimens identified to species level were included. Thus, *Canis* sp. from Eskisheir, *Panthera* sp. from Betfia 13, two records of *Felis* sp. (from Voigtstedt bei Sangerhausen, Lehmzone and Norfolk, England) and *Lynx* sp. from the Ubeidya formation were excluded, although the *Canis* sp. from Senéze was classified as *Canis senezensis* (cf. Rook 1993) and included in the sample.

When assessing co-occurrence in the fossil record it is essential to use the most up-to-date and accurate taxonomy, and ensure that taxonomic assignment is consistent across sites and over time. It is particularly important to ensure that synonymous species names (i.e. where the species is the same but has been given a different name at some point in the past or in a different region) are not treated as separate species. Thus, although the taxonomy of Plio-Pleistocene carnivorans is reasonably well understood and clarified in the databases used here, a detailed review was undertaken (Table 1). *Homotherium* has a very controversial taxonomy at species level and certain authors consider only the binomial *Homotherium latidens* as valid (Turner and Antón 1997). However, a more conservative taxonomy is used here, whereby *Homotherium crenatidens* is used for all the early-middle-late Villafranchian *Homotherium* spp. (Ficcarelli 1979), while *Homotherium latidens* is restricted to the middle Pleistocene (specimens from Mosbach, Norfolk, Valdemino and Voigtstedt bei Sangerhausen) (Antón and Galobart 1999; Antón et al. 2005). The decision to use this conservative scheme will influence co-occurrence analyses, as overall co-occurence between *M. sylvanus* and individual *Homotherium* species will be lower than if only a single taxon was recognised. The taxonomy of middle Pleistocene lynxes is also complex and poorly resolved but the taxonomy used here follows Testu (2006), who recognises only *Lynx spelaea* and *Lynx pardinus*. The taxonomy suggested by Testu (2006) is also followed for the Plio-Pleistocene dhole (genus *Cuon*), in which *Cuon stehlini* from L'Escale is better considered to be *Lycaon lycaonoides*. Following Martinez-Navarro and Rook (2003), all forms of *Canis* (*Xenocyon*) are considered here as *Lycaon*. Following the Palaeobiology Database, *Gulo schlosseri* is considered to be *Gulo gulo* and *Panthera schaubi* is instead classified as *Puma pardoides* (cf. Hemmer 2001; Hemmer et al. 2001).

TABLE 1 ABOUT HERE

Co-occurrence

Co-occurrence was estimated by recording the number of times each potential macaque predator was recorded in the same deposits as *M.sylvanus* during a specific time bin / interval (cf. species occupancy, Raia et al. 2006b). This approach avoids the potential bias introduced by species duration: co-occurrences will vary in each time interval but they will not be affected by species duration. Carnivore / macaque co-occurrence was also analysed at family level for each time interval and for the whole period of interest (4.2 – 0.1 Ma). A uniform distribution model of carnivore frequency assumes that all species at a given time interval have the same probability of co-occurrence with the Barbary macaque. However body size effects, whereby large carnivores are more likely to be preserved in the fossil record than small ones, may confound this assumption. This bias may be offset to a certain degree by considering likely abundance (n individuals / km^2) of particular species during life compared to their presence in the fossil record. Body size estimates (Table 1) are thus used to predict expected relative abundance (using equations devised by Silva and Downing 1995 that are different for species greater than and less than 100kg; see also Meloro and Clauss 2012).

Expected relative abundance for each species (i) is compared to the co-occurrence record by applying the following transformation factor (TF, cf. Meloro et al. 2007):

$$TF = \sum_{i=1}^{N} OC_i / \sum_{i=1}^{N} EO_i$$

where OC is the observed fossil co-occurrence and EO is the expected theoretical co-occurrence based on body mass estimates. Transformation Factors were computed separately for each time interval / bin. This enables each time bin to be treated as a single sampling unit unrelated to the other bins. The Transformation Factor (TF) allows species ecological abundance (n individuals / km^2) to be compared directly with species co-occurrences (expressed as frequency number of fossil sites). As an example, the Old World cheetah *Acinonyx pardinensis* co-occurs in the time bin 4.2.-3.0 Ma only once with the Barbary macaque. Consequently its observed co-occurrence is equal to 1. Based on its body mass, the relative number of individuals per km^2 of *A. pardinensis* should be 0.069 but this estimate (although ecologically realistic) is too low to be comparable with observed co-occurrence in the fossil record (equalling 1). By applying the transformation factor we obtain a value of 0.65 that could be interpreted as an ecological occurrence for that time interval. Interestingly, this species co-occurs with the macaque in four fossil localities during the successive time bin (2.5. – 1.8 Ma). For this time interval, its theoretical ecological occurrence is different (0.74) because a different transformation factor value was applied. Smaller carnivores were not included in this analysis because their record in each time interval is insufficient to allow computation of reliable theoretical estimates. A χ^2test was performed to compare the relative distribution of observed and expected (by body mass, corrected with the TF) co-occurrences at each time bin. It is worth noting that the TF does not account for differences of species density according to habitat, but only the fossil record itself (time bins with unequal number of sites). Meloro et al. (2007) demonstrated that the TF can be applied to quantify large mammal relative abundance based on their expected (by body mass) ecological densities. The application of TF to the Quaternary Italian palaeocommunity fossil record revealed higher densities of key prey species such as middle-sized ungulates while lower relative densities were recorded for smaller ungulates (Meloro et al. 2007).

Results

Twenty four Plio-Pleistocene large carnivore species co-occurred at least once with *Macaca sylvanus*. *Acinonyx pardinensis* exhibited the highest co-occurrence (n = 8) while the Eurasian dhole (*Cuon* spp.), *Canis senezensis*, *Lycaon lycaonoides*, *Lynx pardinus* and the wolverine *Gulo gulo* occurred only once alongside the Barbary macaque. Four smaller carnivoran species co-occurred with the Barbary macaque; the red fox (*Vulpes vulpes*) had the highest co-occurrence (n = 5), greater than the co-occurrence between wild cats and barbary macaques. Occurrences varied across the time period studied (Fig 2). Certain large carnivores (*Acinonyx pardinensis*, *Homotherium* spp., *Megantereon cultridens*, *Panthera* spp.) and the hyaenas (*Chasmaporthetes lunensis*, *Pliocrocuta*, *Pachycrocuta* and *Crocuta*) tended to have high co-occurrences during most time intervals. According to the χ^2 test (Table 2), some carnivores co-occurred with macaques more than expected by a theoretical (body mass) model in all time intervals except 1.6 – 1.1 Ma (the terminal Late Villafranchian) and 0.3- 0.1 Ma (the Galerian). Visual inspection of Figure 2 indicates that these species were felids and hyaenas, with many canids having greater theoretical than actual occurrences. At family level, *Macaca sylvanus* generally co-occurred more with large felids than with canids (Figures 2 and 3).

TABLE 2 AND FIGURES 2 – 4 AROUND HERE

Discussion

Macaca sylvanus fossils in Europe were found alongside a wide range of potential carnivoran predators, some of which, like the sabre-toothed cats, have no modern equivalent. Modern Barbary macaques in the wild and under semi-free ranging conditions produce alarm calls to warn against the approach of eagles (Mehlman 1984; Fooden 2007), snakes and domestic dogs (Fischer and Hammerschmidt 2002), although calls do not always result in escape behaviours (Fischer and Hammerschmidt 2001). The presence of alarm calls could indicate predation in the past significant enough to promote their initial evolution. Carnivorans, particularly felids, are our focus in this article but there is some evidence for possible co-occurrence of *Macaca sylvanus* and both birds of prey and snakes in the European record. Although the European Plio-Pleistocene bird record is limited (Mlíkovský 2009), there is evidence of *Aquila*, true eagles (Viret et al. 1954) at Saint-Vallier, a confirmed *M. sylvanus* site (Delson 2004). Modern observations indicate that the snakes most likely to prey on primates are the large constrictors such as pythons and boas although smaller venomous snakes may also kill and eat them (Headland and Greene 2011). The herpetological record of the European Plio-Pleistocene is generally less well known than that of the mammals, but again there is some circumstantial evidence that Barbary macaques may have been exposed to snakes. At the Spanish site of Sierra de Quibas, which has yielded *M. sylvanus* fossils, several poorly identified snake taxa have been recorded (Montoya et al. 2001), although by the Pleistocene, the Boidea (the family including the boa constrictors) were represented in Europe only by small forms similar to the modern sand boa (Holman 1998), unlikely to be a threat to adult and most juvenile macaques. It cannot be discounted that snake avoidance behaviours in the Barbary macaque were retained from a tropical ancestor exposed to snakes that actively preyed upon primates.

Our analysis indicated co-occurrence with canids throughout the Pleistocene, but at a lower level than either felids or hyaenas. This could be a taphonomic effect: the body masses of canids in our sample were considerably smaller than many of the hyaenas or felids and the theoretical models indicated that canids were less abundant than predicted. The possibility of taphonomic bias is reinforced by the fact that two other of the smaller ‘large’ (> 7kg) carnivorans, the Iberian lynx and the wolverine, also co-occur infrequently with *M. sylvanus* (which probably had body masses around 10kg (females) and 15kg (males) (sensu Fooden 2007)). These co-occurrences may also represent relative abundances during life: animals with greater abundance generally have a higher probability of being preserved in the fossil record, and this may explain why the red fox, which based on its modern populations was likely to maintain high numbers of individuals in the past, is so well represented in our sample despite having a small body mass. Observations of modern Barbary macaque behaviour and perceived predation risk (Fooden 2007) suggest that the fox was not a significant predator of the extinct European forms, however. Other canids represented in our sample, which co-occurred (albeit infrequently) with fossil macaques in Europe, may have been a threat. Feral dogs are a danger to several species of macaques across Asia (see for example Fooden 2000; Fooden and Aimi 2005; Fooden 2007). Indeed, although canids are generally less important predators of primates than felids, Asian canids seem to be much more likely than those elsewhere to take primates (Hart 2007). This notwithstanding, the dhole or Asiatic wild dog, present in Pleistocene Europe and today found in south and southeast Asia, seems to avoid taking langurs at several study areas across these regions (Karanth and Sunquist 1995; Andheria et al. 2007; Wang and Macdonald 2009). This is probably because the dhole focuses on hunting terrestrial prey, and langurs (even if they spend some time on the ground) can avoid capture through their arboreality (sensu Karanth and Sunquist 1995). For the more terrestrial Barbary macaque (Fooden 2007), predation risk from the dhole may have been higher than for more arboreal primates. However, the dynamics of canid predation on macaques requires further research, given that at least one study (in Tikjda Forest, Algeria) noted no predation at all on the macaque population, despite high numbers of jackals in the local area (Menard et al. 1986). This lack of predation may be because of the availability of domesticated herd animals that are easier to catch and have fewer social and cognitive mechanisms for predator avoidance (sensu Zuberbühler and Jenny 2002; Micheletta et al. 2012), but may also be related to the macaque ability to escape terrestrial predators by ascending trees.

There was a diverse hyaenid fauna in the European Pleistocene, reflected in our sample. Hyaenas are popularly viewed to be scavengers rather than primary predators, although research on the modern spotted hyaena (*Crocuta crocuta*) in Africa has demonstrated that they are efficient and frequent hunters (Hayward 2006). Hyaenas are important accumulating agents for fossil deposits, including some primates (Boaz et al. 2000; Boaz et al. 2004), but the predatory position of extinct species in their ecological communities is unclear (Dennell et al. 2008). Modern spotted hyaenas do hunt baboons from time to time, but it has been tentatively suggested that they are non-preferred prey in comparison to ungulates (Hayward 2006). Functional morphological research on *Chasmaporthetes lunensis* (the extinct running hyaena), that like *C. crocuta* co-occurred with the Barbary macaque in Europe, indicates that it was hunter specialising in large-sized ungulate prey that could also effectively consume whole carcasses (Antón et al. 2006; Meloro 2011a). Given this and the equivocal evidence for systematic hyaena predation on extinct and extant primates in general, it is possible that hyaenas did not actively seek macaques as prey. However, the behaviours of past animals, especially extinct species, are unlikely to have exactly replicated those of their closest living relatives, so the absence of direct taphonomic evidence means hyaenid predation on *M. sylvanus* in Europe cannot be discounted.

Felids, along with raptors, are often cited as the most significant predators of primates across the world (Hart 2007). Felid fossils were well-represented in our sample. One felid, the leopard (*Panthera pardus*) is well-known for its predation on primates, past and present. Until its massive decline in North Africa in modern times, it is likely that the leopard was a predator of the Barbary macaque (Fa 1986; Fooden 2007). To our knowledge, there have been no specific studies of *M. sylvanus* alarm calls in relation to leopard threats, but there is strong evidence for such calls in other macaque species (e.g. Coss et al. 2007). Given its co-occurrence with *M.sylvanus* at some European palaeontological sites, and also in line with its hunting behaviour across the Old World (Hart 2007), we can thus conclude with reasonable confidence that where the two species were sympatric in Pleistocene Europe, the leopard posed a significant predation risk. Co-occurrence in the fossil record does not imply sympatry per se, due to the effects of time and space averaging, but sympatry is more likely if particular species are found together over a long time period or at several different sites (Elton 2006). Macaques in Europe were thus likely to have been sympatric with a number of other large felids that are now extinct, including the giant cheetah (*Acinonyx pardinensis*), the European jaguar (*Panthera gombaszoegensis*) and several species of sabre-toothed cat.

The dynamics of carnivore guilds in the past as well as the present have been discussed extensively (e.g. Turner 1992; O'Regan and Reynolds 2009; Meloro 2011b, c), and it is likely that European Plio-Pleistocene felids employed an array of behavioural strategies such as different activity patterns (day versus night), preference towards different sizes of prey and exploitation of different habitats (arboreal versus terrestrial) to reduce competition. It is extremely challenging to reconstruct activity patterns, but consideration of the functional morphology and body masses of extinct felids can shed considerable light on habitat exploitation and probable prey preferences, and hence their likely predation risk to *Macaca sylvanus*. Predator size and prey selection are linked, with larger carnivorans that hunt individually generally selecting larger prey. This is evident in the tropical forests of India, for example, where tigers selected prey in excess of 175 kg and leopards took smaller prey, focusing on medium size classes (Karanth and Sunquist 1995). Interestingly, although leopards hunted langurs much more frequently than did tigers, langurs lay considerably below the preferred size range for both felids (Karanth and Sunquist 1995). This is an excellent example of opportunity, optimality and opportunism: prey may differ according to the habitat exploited (opportunity: leopards are more likely than tigers to prey upon arboreal animals) and - holding predation effort equal regardless of prey body mass - there are greater rewards for catching larger prey (optimality), although easy prey (such as monkeys ascending or descending trees at dusk and dawn (sensu Cheney et al. 2004) cannot be ignored (opportunism). It is likely therefore that the larger felids in Pleistocene Europe, including the lion and the sabre-toothed cats would not have preferentially hunted *M. sylvanus*. Indeed, the forelimb morphology of the sabre-toothed cats shows adaptations to grabbling large prey, presumably herbivores in the biggest size classes, with different species variously exploiting open and closed habitats (Lewis 1997; Turner and Antón 1997; Meloro 2011c). The Pleistocene lion has also been argued to be a large prey specialist (Meloro 2011a). However, it is highly probable that if the opportunity arose, these very large cats would take and consume Barbary macaques.

The felids of Pleistocene Europe had a wide range of body sizes, with some, like the various lynx species being relatively small. The modern Eurasian lynx is sympatric with macaques in several parts of Asia and where they come into contact, macaques are a prey species. This is illustrated most graphically by the predation of bobcats on transplanted Japanese macaques in the United States (Gouzoules et al. 1975). The giant cheetah and the European jaguar, which were larger than lynx but considerably smaller than lions and sabre-toothed cats, may have competed with the leopard for the same prey, including macaques. Although not identical in ecology or behaviour to their closest living relatives, the giant cheetah was cursorial and probably exploited open environments whereas the jaguar may have preferentially inhabited more forested areas (Turner and Antón 1997; Meloro 2011c). These two species have been found to co-occur at some Plio-Pleistocene sites, so in certain places these felids would have exerted considerable pressure on *M. sylvanus*. The same applies for the European leopard, whose observed co-occurrence with the Barbary macaque was relatively high during the interval between 1.0 and 0.4 Ma. Thus, in some places neither terrestrial nor aboreal habitats would present a safe option for retreat, and it can be concluded that medium-sized felids probably posed considerable risk to *M. sylvanus* in the European Plio-Pleistocene.

One potential predator of *M. sylvanus* has been disregarded so far in this article. With its dispersal from Africa, *Homo* joined the Eurasian carnivore guild (Turner 1992) and so became a potential predator of the Barbary macaque in Europe, and may also have significantly altered carnivore ecology more generally. Human activity has clearly influenced modern North African ecology and hence predation on *M. sylvanus*. Although the Barbary macaque and the Barbary leopard are sympatric in part of their modern ranges, which for the leopard is incredibly restricted (Henschel et al. 2008), anecdotal evidence suggests that the leopard today tends to hunt domestic livestock most successfully (Fa 1986). In contrast, the domestic dog is a significant predator of the modern Barbary macaque in North Africa (Butynski et al. 2008), and it is possible that at least some of this predation is directed by humans who view macaques as a threat to the forest due to their stripping and consumption of bark; it has been suggested that humans elicit anti-predator calls from modern Barbary macaques (Digweed et al. 2005). The bushmeat trade poses a dire threat to modern primates (Fa et al. 2002), and there is certainly evidence, described above, for hominin predation on African Pleistocene monkeys (Shipman et al. 1981). Given that *Homo* and *Macaca sylvanus* co-occur in the fossil record - for example, at the late Pleistocene site of Lezetxiki in the Basque region of Spain (Castaños et al. 2011) - it is highly likely that there was a predator-prey relationship between the two. *Homo neanderthalensis* has been described as a 'top level predator' (Richards et al. 2000), and although it and other Pleistocene humans would have preferentially exploited larger prey, macaques may have been important supplementary food resources for European hominins: research on marginalised modern human populations suggests that consumption of primate bushmeat is one response to a chronic lack of protein availability (Fa et al. 2003).

In conclusion, *M. sylvanus* has experienced profound synecological shifts over its evolutionary history, caused by turnover of other taxa, climate change and range shifts. The Barbary macaque, although clinging onto existence in modern times, has therefore proved to be tenacious and versatile in the face of extreme climatic, geographic and ecological variation, as well as potentially great predation pressure. This survival has been assisted by the ability, shared by many members of the genus, to adapt rapidly to changing conditions through relatively contracted life history events that allow for reasonably speedy reproduction and hence higher intrinsic rates of population growth (Jablonski et al. 2000). Nonetheless, the macaque went extinct in Europe during the late Pleistocene, as did the majority of European carnivorans (reviewed in O'Regan et al. 2002). These carnivoran and primate extinctions, likely to be uncorrelated and happening at different times, were probably the result of a complex web of ecological factors. The contraction of the spotted hyaena range out of Europe, for example, is seen not as a straightforward result of climate change but instead caused by interactions between climate and other factors such as human impact (Varela et al. 2010). Stochastic factors within small refugial populations may have resulted in the demise of the European jaguar (O'Regan et al. 2002). Given the paucity of the European macaque fossil record, it is unlikely to have been highly abundant in Europe at any time during the Pleistocene, and it is plausible that it, too, was subject to stochastic genetic factors in climate-induced refugia from which viable European populations could not re-emerge. Just as likely, given current evidence of human threats to primate survival, was that anthropogenic pressure, including direct predation, pushed small *M. sylvanus* populations, at the limits of their geographic range and ecological tolerance, to extinction in Europe.

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Species	**Common name**	**Family**	**Body mass (kg)**	**Notes on taxonomy**
Acinonyx pardinensis	Giant cheetah	Felidae	65	
Canis etruscus	Etruscan wolf	Canidae	21	
Canis lupus	Grey Wolf	Canidae	40	
Pliocrocuta perrieri	Perrier's hyaena	Hyaenidae	80	Synonymous with *Crocuta perrieri* from Sandalja 1, bei Pula and *Hyaena perrieri* from St. Vallier (Werdelin and Solounias 1991)
Chasmaporthetes lunensis	Hunting / running hyaena	Hyaenidae	76	
Panthera gombaszoegensis	European jaguar	Felidae	90	
Homotherium crenatidens	Sabre toothed cat	Felidae	231	Synonymous with *H. sainzelli* (2 occurrences in Seneze and St.Vallier) (Argant 2004)
Crocuta crocuta	Spotted hyaena	Hyaenidae	102	No synonymy, but subspecies were not considered as valid taxon name (e.g. *C. crocuta spelea*)
Homotherium latidens	Sabre toothed cat	Felidae	274	Synonymous with *H. moravicum* and *Homotherium* sp. from Mosbach and Norfolk (Reumer et al. 2003)
Lynx issiodorensis	Issoire Lynx	Felidae	22	
Lynx spelaea	Cave lynx	Felidae	23	Synonymous with *L.pardina* (from Vallonet), *L.pardina spelaea* (from Valdemino) (cfr. Testu 2006)
Megantereon cultridens	Dirk toothed cat	Felidae	63	Synonymous with *M. megantereon* (Sardella 1998; Palmqvist et al. 2007)
Pachycrocuta brevirostris	Giant hyaena	Hyaenidae	127	Synonymous with *Hyaena brevirostris* from Vallonet (Testu 2006)
Panthera leo	Lion	Felidae	183	
Panthera pardus	Leopard	Felidae	60	
Canis arnesi	Arno dog	Canidae	16	
Lycaon falconeri	Falconer's wild dog	Canidae	26	Synonymous with *Canis* (*Xenocyon*) *falconeri*
Lynx pardinus	Iberian lynx	Felidae	23	Only one record in Sierra de Quibas. No synonymy
Puma pardoides	Owen's panther	Felidae	45	Synonymous with *Panthera* and *Viretailurus schaubi* (Hemmer et al. 2004; Argant 2004)
Canis senezensis		Canidae	12	Recorded as *Canis* sp. from Seneze (Rook 1993)
Cuon alpinus	Dhole / Asiatic wild dog	Canidae	23	
Cuon priscus	Pleistocene dhole	Canidae	23	
Gulo gulo	Wolverine	Mustelidae	20	Synonymous with *G.schloesseri* of Mosbach (paleodb)
Lycaon lycaonoides	Pleistocene wild dog	Canidae	30	Synonymous with *Cuon stehlini* from L'Escale bed G (Testu 2006)
Nyctereutes megamastoides	Plio-Pleistocene racoon dog	Canidae	11	
Vulpes vulpes	Red fox	Canidae	8	
Vulpes alopecoides	-	Canidae	5	
Felis silvestris	Wildcat	Felidae	5	

Table 1: Species used in this analysis with notes on taxonomy. Body mass estimates are from Meloro et al. (2007) and the NOW database.
Felids are marked in bold.

Ma	**X^2**	**df**	***P***
4.2-3.0	7.8693	3	0.049
2.5-1.8	120.27	10	<0.0001
2.1-1.7	40.616	8	<0.0001
1.6-1.1	3.1871	4	0.527
1.0-0.4	142.45	14	<0.0001
0.3-0.1	6.678	3	0.083

Table 2: Chi square test for each time interval comparing the observed carnivoran co-occurrences with *M.sylvanus* (corrected after applying transformation factor) with species abundance (n indiv / km^2) expected by their body mass.

FIGURE LEGENDS

Figure 1: Time interval of 29 selected macaque fossil localities.

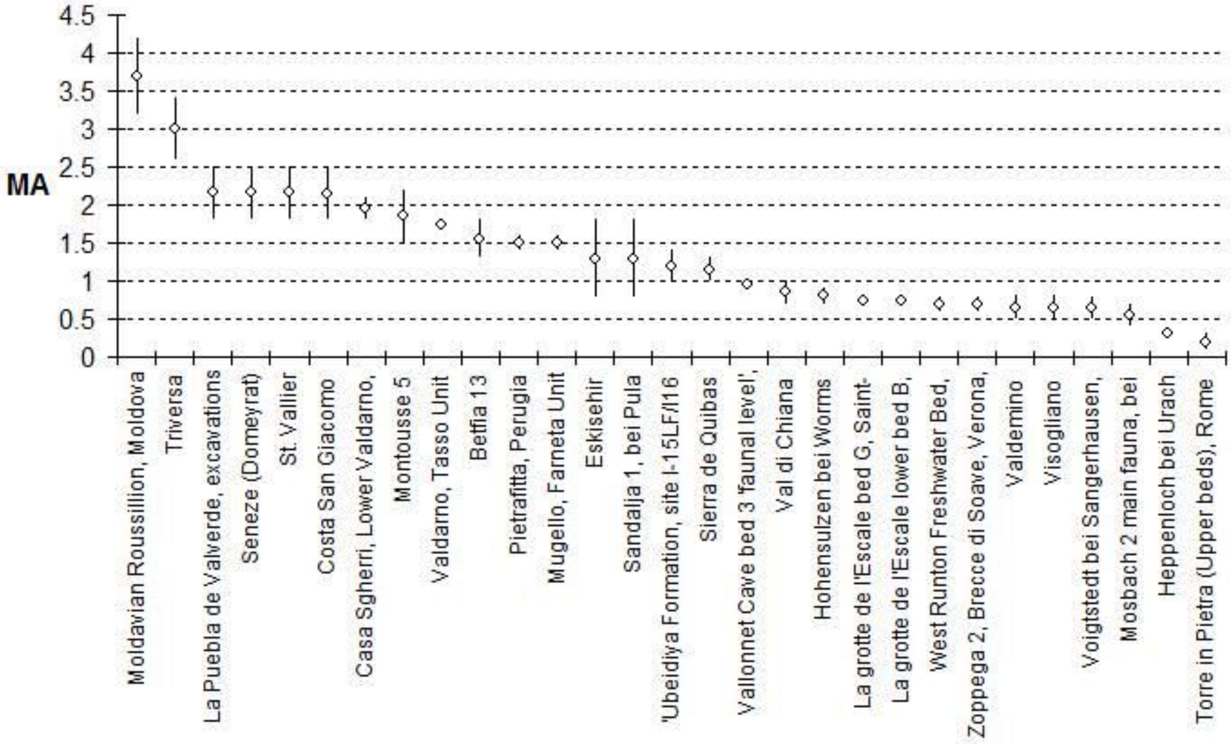

Figure 2: In black the observed co-occurrences of carnivorans with *Macaca sylvanus* (corrected after applying the transformation factor), in white the species abundance (n indiv / km^2) by their body mass

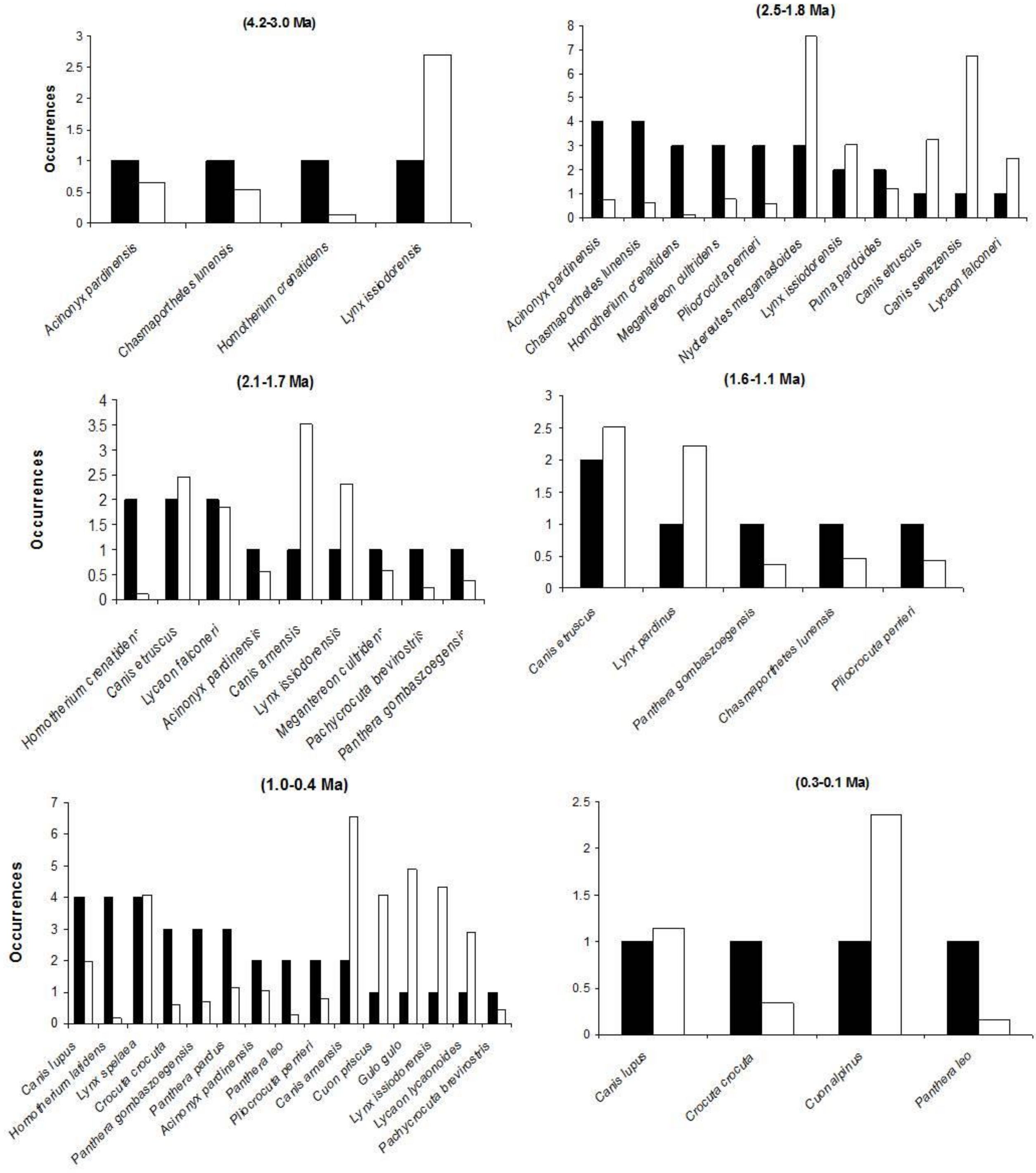

Figure 3: Co-occurrence of fossil macaque with large carnivorans quantified at family level.

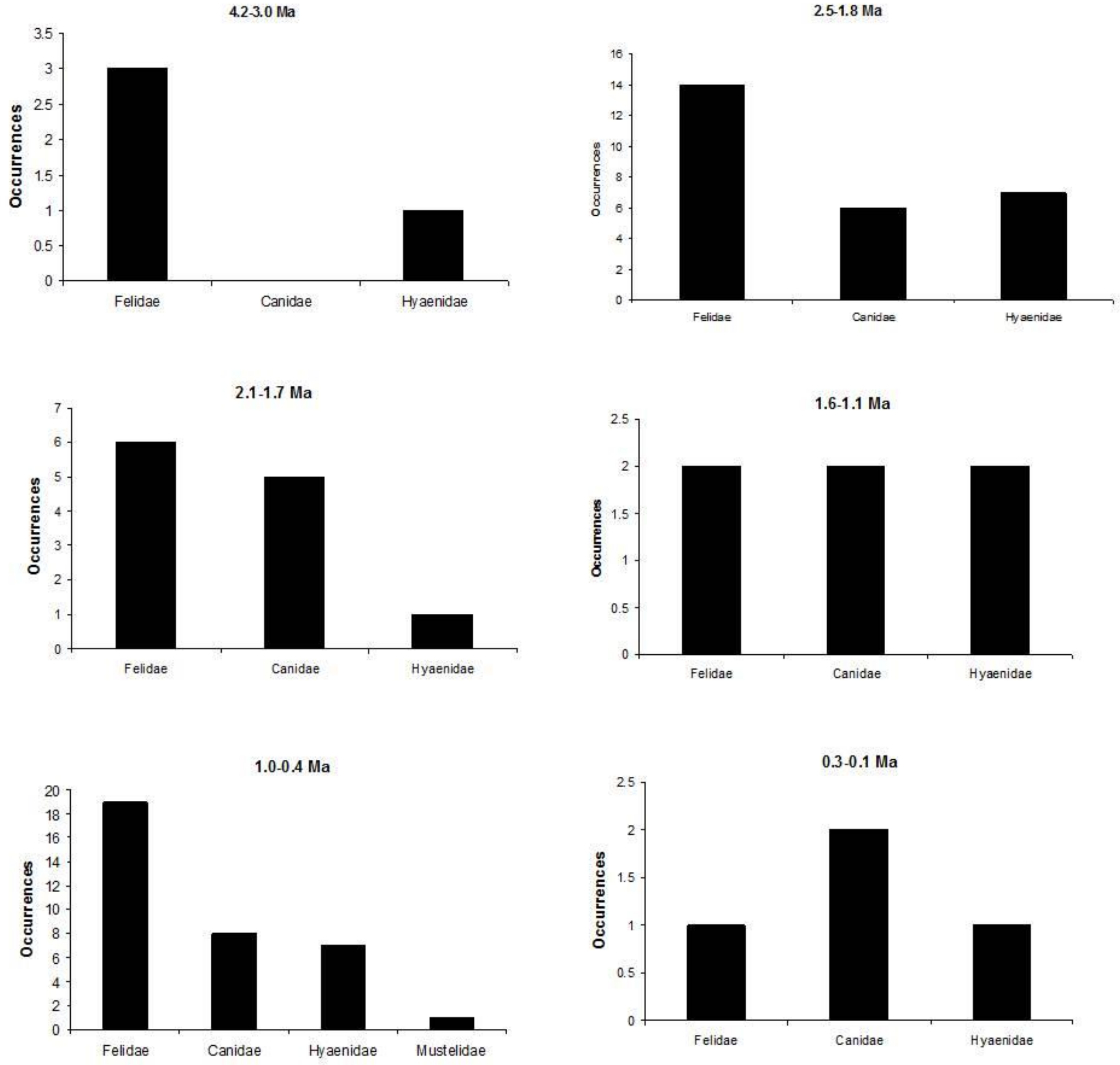

Figure 4: Overall carnivore co-occurrences for large and small carnivores.