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Effect of predation on prey abundance and survival in Plio-Pleistocene mammalian communities

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ABSTRACT

Question: Does predatory pressure affect the abundance and survival of prey species in extinct communities?

Data studied: Presence–absence data and body sizes of large mammals (partitioned into predators and prey) in Plio-Pleistocene Italian PaleoCommunities (PCOMs). *Transformed variables*: (1) Species' occupancy: number of presences/number of sites. (2) ADI: the index of disparity (ADI) reflects the relative abundance of a prey species in a PCOM. (3) Predatory pressure on a prey species: the proportion of predators in a given PCOM that are expected to feed on it. (4) Nestedness: the extent to which rare species occur only in the species-rich sites of a PCOM.

Search method: For each PCOM, the effect of preservation biases on species' occupancy was assessed by a nestedness analysis. The ADI was computed for each prey species in each PCOM. Predatory pressure was calculated for each prey species. We used linear regression to test the effect of predatory pressure on ADI. Non-parametric correlation was performed to determine the effect of ADI on species survival.

Results: Species prone to greater pressure appear at fewer sites than would be expected for their size alone. The relationship is limited to rare species only. Taphonomy does not explain this disparity. Abundant species survive longer than rare species.

Conclusion: Predation controls abundance and local survival of rare species. In contrast, it does not affect abundant species.

Keywords: Italian Quaternary, large carnivores, large herbivores, occupancy, predator–prey.

INTRODUCTION

The role of predation in extant large mammal communities has been of great interest since extensive field studies were carried out in the 1970s (e.g. Kruuk, 1972; Schaller, 1972; Mech, 1980). Predation is very important to ecologists interested in the study of community structure and stability (Abrams, 2000). Unfortunately, studies of species interactions in fossil assemblages are

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rather scarce. Indeed, data on predation are usually collected through observation of predators' behavioural attributes (such as prey detection and killing technique), which cannot fossilize. Indirect signals of predation in fossil communities come from studies of population demography. For instance, U- or L-shaped mortality profiles in prey populations help to clarify how predators select among prey age categories, even in extinct assemblages (see Steele, 2004, and references therein). Extensive research at the Venta Micena Pleistocene site (Arribas and Palmqvist, 1998; Palmqvist *et al.*, 1996, 2003) established, with great accuracy, the activity of predators and their influence on prey populations. A different means of ascertaining structure in extinct communities is guild analysis (Dayan and Simberloff, 1996; Lewis, 1997). Guild memberships are ascribed upon direct observation of osteological material (e.g. degree of hypsondonty, shape of the carnassial cusps, ratios between bone lengths to infer cursoriality, etc.). This approach relies heavily on direct comparisons with living species. Although very successful in many instances, it provides limited information about the evolutionary consequences of predation [here the term 'evolutionary' refers to the evolution of community structure, and not to the morphological change of species in the context of predator–prey co-evolution (e.g. Bakker, 1983; Vermeji, 1994)]. This is because guild analysis usually looks at the guild structure itself and not at prey responses (e.g. species abundance and long-term co-existence). Truly evolutionary studies of guild structure have been performed at a very large scale (i.e. larger than a community of interacting organisms), and have been intrinsically macro-evolutionary (e.g. Bakker, 1983; Werdelin, 1996; Van Valkenburgh, 1997). Because of this large scale, no reliable inferences about community-level species interactions between predators and their prey could be ascertained. An exception is the predator–prey ratio (Rosenzweig, 1995; Croft, 2006). The use of this ratio could be very informative from a macro-evolutionary perspective (Van Valkenburgh and Janis, 1993). However, since the predator–prey ratio addresses the effect of prey diversity on predators (and vice versa), it could be helpful to our understanding of the evolutionary consequences of predation, even at the community level. Nonetheless, the ratio does not take into account the population density of prey, a fundamental factor in interpreting predation dynamics (Abrams and Ginzburg, 2000).

The quantification of species density (abundance) in the fossil record is difficult. Damuth (1982) provided a theoretical model to calculate relative species abundance at fossil sites correcting NISP (number of identifiable specimens) data for the effect of species body size on preservation. Damuth's method was applied to (and is presumably only valid for) a single site.

There is good evidence that high-quality fossil records provide very precise indications of the abundance of fossil species relative to each other (Kidwell and Flessa, 1995; Hadly and Mauer, 2001; Kidwell and Holland, 2002; Barnosky *et al.*, 2004), although important limitations still require caution (Vermeji and Herbert, 2004). Alroy (1996, 2000) provided a direct link between multiple-site data sets and species abundance (at the regional scale) and demonstrated that species abundance could be ascertained from their occupancy (a measure of frequency of appearance across sites). Similarly, Jernvall and Fortelius (2004) examined occupancy (their 'locality coverage') in the NOW database and provided important indications as for the role of species occupancy in the evolution of trophic categories in large mammals. Raia *et al.* (2006a) studied the pattern of species occupancy in the Plio-Pleistocene Italian fossil record and its effect on species survival, and showed the close similarity in occupancy patterns between their PaleoCommunites (PCOMs) and extant mammalian communities. Here, we use PCOMs occupancy data as a proxy for relative species densities. These ranked abundance data were used to explore the effect of predation on prey density and survival in Plio-Pleistocene large mammal communities. The units of analysis are PCOMs. Raia *et al.* (2005, 2006b) identified nine PCOMs for the Italian peninsula. Here we include all but the oldest PCOM, thus our data set spans from 2.6 million to 300,000 years ago. Each PCOM includes data of species occurrences from various localities of presumably very similar age and statistically identical taxonomic composition (Raia *et al.*, 2005, 2006b). PCOMs behave as real sets of interacting organisms (large mammals) at a regional geographic scale (Italian peninsula). Therefore, we treated PCOMs as large ecosystems whose predator–prey dynamics can be explored at a regional scale.

MATERIALS AND METHODS

Estimators of predation and abundance

Our goal was to determine the influence of predation on prey density and survival in fossil large mammal communities. To do this, we had to translate ecological phenomena such as 'predation' and 'prey density' into operational measures applicable to our data. We estimated prey abundance with the abundance disparity index (ADI). This is the relative abundance of a prey species in a PCOM. The ADI is the difference between the expected number of individuals of a species based on its size (here named its 'theoretical abundance') and the number expected based on its occupancy (i.e. the fraction of sites where it occurs). This procedure benefits from the strong relationship between occupancy and abundance in modern communities. Clearly, the validity of this relationship in fossil communities needs to be demonstrated. We performed such a test by calculating PCOM nestedness. A PCOM is said to be nested if rare species occur only in its species-rich sites. Finally, predatory pressure on any specific prey was calculated as the proportion of predators in a given PCOM that are expected to feed on it.

The ADI was then regressed against predatory pressure to explore the effect of predation on prey density. The ADI (once the effect of predatory pressure was factored out) was also correlated with species duration.

Theoretical abundance

Each species has a 'theoretical abundance' related to its size. We reconstruct, only for prey species, the expected (theoretical) abundances in each PCOM. Species belonging to the orders Artiodactyla, Perissodactyla, and Proboscidaea were considered as prey. Most megaherbivores are rarely preyed upon by large carnivores in extant communities (Owen Smith, 1990), although such predation could have been substantial during the Plio-Pleistocene. For instance, the saber-toothed cat *Homotherium* spp. has been reported to have selected juvenile mammoths as prey (Turner and Antón, 1997).

In mammals, expected abundance scales roughly to the −0.75 power of body mass (Damuth, 1982, 1991; Calder, 1996). Although strong, this relationship is scale-dependent. If one includes only closely related species, the relationship may even reverse, because closely related species are involved in strong competitive interactions that usually favour larger forms. Inverse relationships have been reported for passerine birds (Nee *et al.*, 1991) and mammals (Damuth, 1991). Silva and Downing (1995) reported a non-linear relationship between body mass and expected abundance for mammalian herbivores and presented different equations for species < 100 kg and for species > 100 kg. We applied Silva and Downing's equations accordingly. Body size data for Plio-Pleistocene large mammals were computed by applying regression equations published in Damuth and MacFadden (1990), Alberdi *et al.* (1995), and Christiansen (2004). For each family, we selected equations so as to minimize prediction error. Body size estimates, together with regression equations used and data sources, are reported in the Appendix. The theoretical abundance is estimated as the number of individuals per square kilometre. Of course, population density depends also on local availability of resources (e.g. the abundance of modern elephants per unit area may vary by nearly an order of magnitude between semi-desert areas and wet savannas) and on the ability of individuals of one species to outcompete those of others at exploiting those resources. As stated above, PCOMs are not 'local' in their geographical spread. Interspecific variability in species abundance due to biological interactions is the datum examined in this study. Hence, the theoretical abundance distribution calculated by the body size–abundance relationship provides a reliable baseline to which deviations should be compared.

Species occupancy: an indicator of abundance

Departures from expected abundance were calculated by comparison with species occupancy (*sensu* Gaston and Blackburn, 2000). In the ecological literature, the close relationship between occupancy and abundance is well-supported (Brown, 1984; Hanski *et al.*, 1993; Gaston and Blackburn, 2000). Thus, occupancy provides a reference for comparing expected (by body size) abundances. Species with high occupancy (relative to the expected abundance) should be considered abundant. Conversely, species with low occupancy should be considered rare.

Species occupancy was calculated for each PCOM separately (Raia *et al.*, 2006a). In brief, as PCOMs include several local faunal assemblages, occupancy is the proportion of local faunal assemblages where a species is present in that PCOM. As occupancy is dimensionless, we transformed it according to a transformation factor (*TF*) to obtain a reference 'abundance' measure:

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

where EB is the expected (by body size allometry) abundance, OC is the actual occupancy, and N is the number of species. TF was calculated for each PCOM. Occupancy-based abundances (OA = number of individuals per square kilometre) were then calculated by multiplying the TF for real occupancy values. OA represents an abundance metric obtained directly from the fossil record. It can be compared with theoretical abundance resulting in the disparity index (ADI), which indicates the relative commonness (and rarity) of any species in each PCOM.

ADI: the disparity index

Deviations from theoretical abundance values indicate that few species are more abundant, and many more are less so. These differences are also reflected in the familiar right-skewed species occupancy frequency distribution. In fact, occupancy is closely related to abundance (Brown, 1984; Hanski *et al.*, 1993; Gaston and Blackburn, 2000). Thus, by looking at occupancy it is possible to obtain a good representation of abundance as well. Moreover, occupancy is much easier to calculate from the fossil record than abundance.

For this reason, an index of disparity (ADI) was computed to take into account the extent to which occupancy (in terms of species density) deviates from expected (by body size) abundance, assuming these two dimensions are as related in fossil data as they are in neontological data. The ADI was obtained by the subtraction of occupancy-based abundance (*OA*) from theoretical abundance (*EB*). The ADI gives negative values for species estimated to be rare and positive values for those estimated to be abundant.

Testing whether occupancy structure could be used to estimate abundances

As in most paleontological studies, taphonomic factors are relevant here. Taphonomic factors could alter the original occupancy structure. For instance, the density of leopard is usually low, given their hypercarnivorous behaviour (Schaller, 1972), but this species tends to accumulate prey bone remains at protected sites (e.g. karstic localities) used as lairs, where eventually the leopards die. Consequently, an over-representation of this species (and its favourite prey) can occur in the fossil record.

Besides carnivores, selective agents include humans, birds of prey, woodrats, water transport, and other biostratinomic phenomena, diagenetic conditions, and species abundance (Behrensmeyer and Hill, 1988; Martin, 1999; Barnosky, 2004). If taphonomic agents act pervasively across sites, they are likely to alter the original species occupancy structure by removing abundant species from some fossil assemblages, and disproportionately favour the occurrence of other, rare, species. If taphonomic agents are not as pervasive or occur idiosyncratically across sites, their effect on occupancy structure might be considered negligible. In the latter case, abundant species are likely to occur in most sites within a paleocommunity (here a PCOM), whereas rare species will most probably occur in sites yielding more remains (hence more species; Fig. 1). A sample of sites where rare species occur only in the species-rich sites is said to be 'nested'. Nestedness derives from passive sampling, selective colonization–extinction dynamics or habitat nestedness (Atmar and Patterson 1993; Patterson, 1999). Colonization–extinction dynamics could nest assemblages because only highly vagile species may colonize species-poor assemblages (e.g. distant islands in an archipelago), while extinction-prone species readily vanish from all but the larger biota. Eventually, if habitats are themselves nested, nestedness at the species level occurs as an epiphenomenon. Colonization–extinction dynamics and habitat nestedness within PCOMs cannot affect the fossil assemblages, since species-poor fossil sites do not support fewer species. They are just sites where the fossilization of a large part of the biota was unlikely. In a fossil assemblage, nestedness should then be due to passive sampling because the preferential collection of the most abundant species affects species occurrences (Fig. 1). In contrast, the variation in taphonomic conditions across sites should disrupt the nested pattern. In a special case, if a particular taphonomic selector dominates over all sites, the species occurrences could be significantly nested unless the original abundance structure is completely distorted. Fortunately, this is unlikely to occur and easy to control. To our knowledge, no PCOM presents this situation.

We used the nestedness calculator (Atmar and Patterson, 1998) to determine if PCOMs were significantly nested. Only significantly nested PCOMs were included in the analyses.

Abundance	BW		a	a	a	a	a	a	a	a
decreasing abundance ↓	40	1	x	x	x	x	x	x	x	x
	70	2	x	x	x	x	x	x	x	
	80	3	x	x	x	x	x	x		
	60	4	x	x	x	x	x			
	90	5	x	x	x	x				
	10	6	x	x	x					
	30	7	x	x						
	50	8	x							

(a) T = 0.01° P = 0.00009

Abundance	BW		a	l	s	l	a	s	c	a
decreasing abundance ↓	40	1	x		x		x	x		x
	70	2	x	x	x	x	x			
	80	3	x	x	x	x	x		x	
	60	4	x	x	x	x	x		x	
	90	5	x	x		x				
	10	6	x	x		x				
	30	7	x		x			x		
	50	8	x	x	x			x		

(b) T = 25.38° P = 0.105

Fig. 1. In a perfectly nested cluster of sites (a), the matrix temperature is extremely low and packing is very unlikely to occur by chance. In (b) we provide a very simple example of how different taphonomic factors could alter matrix nestedness. Sites labelled 'a' refer to attritional assemblages where species occurrences mainly depend on their abundance. Sites labelled 'l' are those where the occurrence of large species is favoured. 's' denotes sites where small species are likely to occur given a different taphonomic sorting. Finally, a third taphonomic selector applies to site 'c', which represents the den of a carnivore selecting prey of 60–80 units of body weight (BW). Where attritional factors prevail, matrix temperature is lower and the original abundance structure is represented.

Predatory pressure

The predatory pressure on a given prey is proportional to the number of predators actually preying upon it (Sinclair *et al.*, 2003). Living large carnivores, especially if social, usually kill species larger than themselves (Gittleman, 1985). Previous paleoecological studies support this widely held view also for extinct species (Turner and Antón, 1997; Palmqvist *et al.*, 2003). Mathematical relationships between predator size and the size of their prey were calculated by Vezina (1985) and Carbone *et al.* (1999).

Radloff and Du Toit (2004) recalculated this same relationship including large mammals of African savannahs only. Given the taxonomic similarity between Radloff and Du Toit's model system and ours, we applied their equations. We considered a large predator to be any carnivore whose estimated body mass was greater than 21.5 kg. This threshold has been chosen because carnivores heavier than 21.5 kg are obligate vertebrate meat-eaters, since they cannot subsist on a diet exclusively based on non-vertebrate meat (Carbone *et al.*, 1999). Furthermore, the exclusion of smaller species avoids the bias due to under-representation of fossil remains. It is thus conceivable that the species we included fed mostly on large herbivores. Bears were also excluded because most of them were strictly herbivore (e.g. *Ursus deningeri* and *Ursus spelaeus*) (Bocherens *et al.*, 1994; Stiner *et al.*, 1998) and no living bear except the polar bear is strictly a vertebrate meat-eater (Gittleman, 1985). Moreover, no hypercarnivorous bears (such as short-faced bears of the genus *Arctodus*) occur in the Italian Plio-Pleistocene faunas.

For each PCOM, we calculated the prey range size that any carnivore could have included in its diet by applying equations in Radloff and Du Toit (2004). These equations were extended to extinct saber-tooth cats even if their feeding behaviour was likely different from any living relative. Palmqvist *et al.* (2003) reported that these predators probably fed on prey larger than modern felids. We are confident of our approach since we obtained the same result by applying both Radloff and Du Toit's (2004) formulas. Thus, we calculated the number of predators that fed on any specific prey in each PCOM, and divided it by the total number of predators. This allows the comparison of predatory pressure across PCOMs comprising different predator diversities. Accordingly, our measure of predatory pressure can be defined as the proportion of predators, in a given PCOM, expected to feed on any specific prey. To avoid biases due to the inaccuracy of the fossil record, we have used data corrected according to range-through (Barry *et al.*, 1995; Maas *et al.*, 1995; Foote, 2000).

Since one of the most important effects of predation is the alteration of prey abundance (Sih *et al.*, 1985; Mills and Shenk, 1992; Sinclair *et al.*, 2003), we performed a linear regression analysis (Zar, 1984) of the ADI (non-transformed, dependent variable) on predatory pressure (independent variable) to determine if this relationship is also consistent at the macro-ecological scale. Next, we took the residuals to factor out the effect of predatory pressure and to study the distribution of prey abundance *per se*. Finally, we examined the effect of mean abundance (the average residuals) on species survival, by correlating it against the number of PCOMs each species survived. Indeed, this procedure is rather conservative because species occupancy is not constant throughout a species' life but is low at a species' appearance, then rises before declining again towards its extinction (Raia *et al.*, 2006a). Thus, by taking the average of species abundance we include periods of very low abundance.

RESULTS

Five of eight (62.5%) PCOMs exhibit a nested pattern of presence–absence. Four (50%) show significant nestedness at the 0.01 level. Twenty-three of 32 (71.9%) species-poor local faunal assemblages have significantly more common species than expected by chance. This figure becomes 17 of 25 (68%) when significantly nested PCOMs are analysed separately. This means that, in general, species abundance was primarily responsible for species presence at sites and not for PCOM nestedness only. The lack of nestedness in V Chiana and Galerian 2 is probably caused by the high number of range-through taxa (respectively 6 and 4 range-through do not occur in any site, hence they could not contribute to nestedness). The case for Montopoli PCOM is more enigmatic. That PCOM is preceded by a period (middle Pliocene) when there are few fossil remains (Raia *et al.*, 2005). Hence, the Montopoli PCOM taxonomic list could be somewhat less accurate than the others.

Predatory pressure has a significant negative effect on the ADI ($b = -1.304$; $R^2 = 0.341$; $F_{1,74} = 37.712$; $P < 0.0001$) (Fig. 2). This result holds when PCOMs are analysed separately (Table 1). This means that prey with lower predatory pressure had higher than expected abundances, in striking accord with similar studies carried out on extant communities (Sinclair *et al.*, 2003). Prey such as mammoths and large rhinos had much lower probability to be preyed upon. On the other hand, medium-sized ungulates had higher predatory pressures. However, there is a significant variation in ADI values between similar-sized

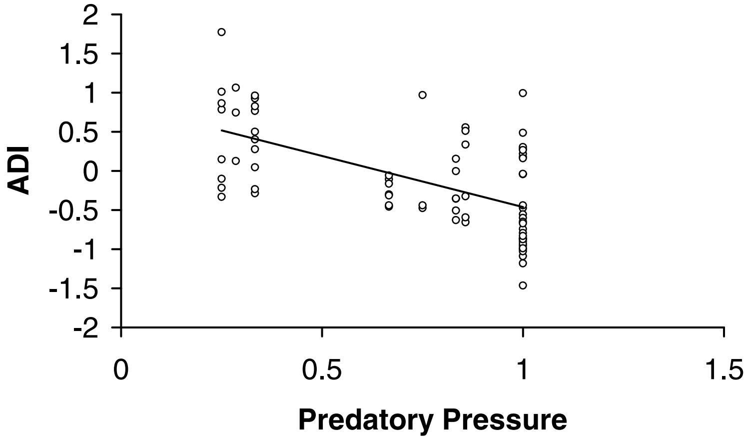


Fig. 2. Linear regression calculated for ADI on predatory pressure.

Table 1. Linear regression performed for each PCOM with ADI as the dependent variable and predatory pressure as the independent variable

	n	SS Res	d.f. Res	Slope	Intercept	*F*	*P*
Up Valdarno	14	3.967	12	−1.490	1.121	6.789	0.023
Pirro	13	1.810	11	−1.285	0.862	9.479	0.010
Galerian 1	15	0.464	13	−1.655	0.840	31.839	0.005
Galerian 3	14	3.175	12	−0.889	0.678	4.266	0.061
Aurelian	19	9.824	17	−1.258	0.822	6.272	0.023

species. Indeed, the relationship between the ADI and predatory pressure becomes non-significant when only species with an ADI > 0.5 are included ($b = -0.331$; $R^2 = 0.085$; $F_{1,13} = 1.202$; $P = 0.293$). Thus, a high predatory pressure affects prey abundance only in rare species.

Rank/abundance diagrams performed on residuals (Fig. 3) show a stepwise switch from abundant to rare species. The species *Equus stenonis*, *Pseudodama* spp., *Sus strozzii*, *Leptobos* spp., and *Eucladoceros* spp. were overly abundant (and conceivably profitable prey) in Late Villafranchian ecosystems. *Cervus elaphus*, *Bison schoetensacki*, and to a lesser extent *Dama* spp., *Equus ferus*, and *Bos primigenius* played the same role in the Galerian–Aurelian PCOMs. Prey abundance–frequency distribution in PCOMs thus replicates living East Africa ecosystems, where wildebeest (*Connochaetes taurinus*), zebras (*Equus burchelli*), and Thomson's gazelle (*Gazella thomsoni*) are key prey for any large predator (Kruuk, 1972; Schaller, 1972; Creel and Creel, 2002) and other antelopes are much rarer.

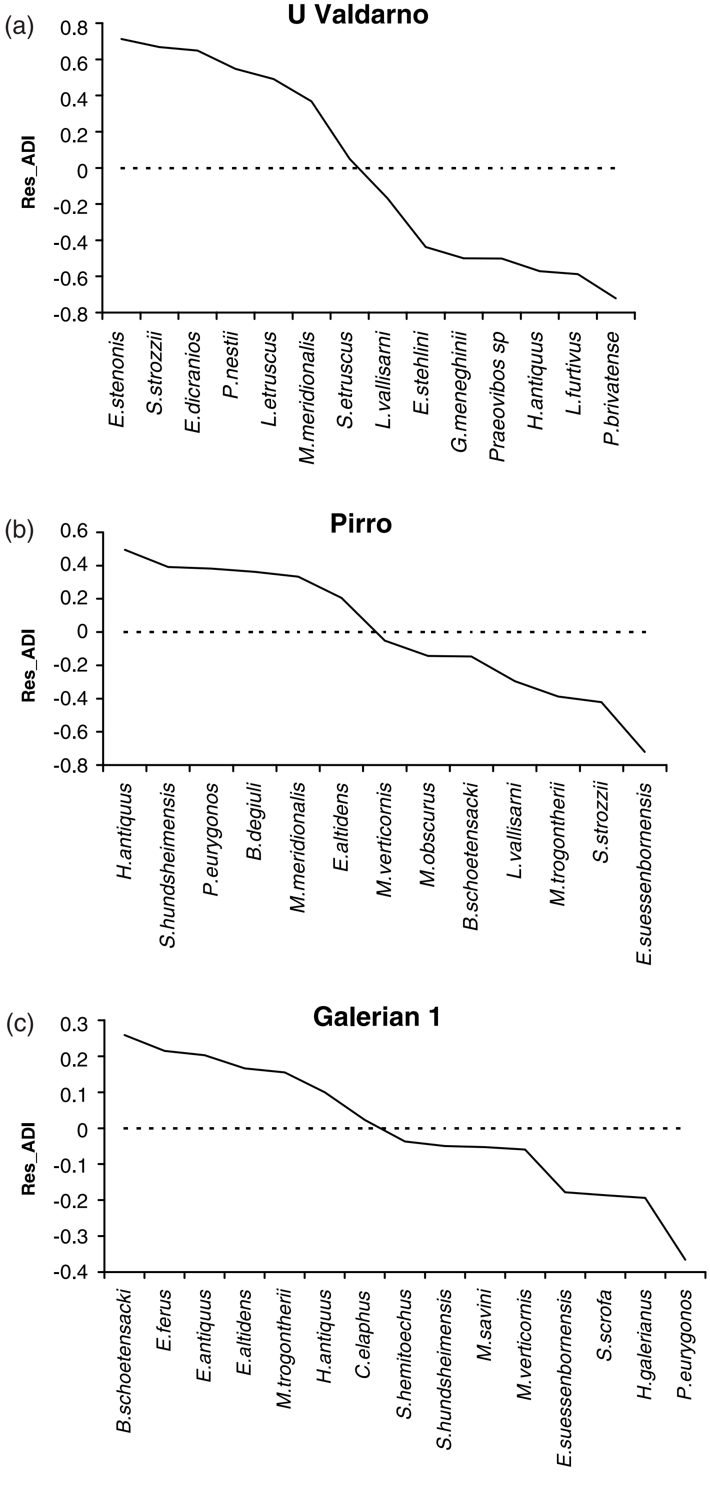
We found a positive non-parametric relationship between average ADI residuals and the number of PCOMs that species were able to survive ($N = 44$, Spearman $\rho = 0.369$; $P = 0.014$).

DISCUSSION

After factoring out the effect of predatory pressure, the distribution of species abundances in PCOMs replicates that in living communities (Fig. 2). Species were either rare or common, and common species tended to survive longer. It is possible that the positive relationship between survival and abundance reflects higher extinction risk in rare species.

Although megaherbivores are often very abundant and little threatened by predators, they are probably over-represented in PCOMs. Obvious taphonomic factors make megaherbivore bones the most durable and easy to classify. On the other hand, megaherbivores provide the largest contribution to total biomass in living ecosystems (Owen Smith, 1990). We suspect that megaherbivores were very abundant in Plio-Pleistocene Italian ecosystems, even if the actual figure was somewhat lower than we got. We obtained high ADI values for megaherbivores after controlling for predatory pressure (Fig. 3). This is expected since megaherbivores are little influenced by predators (Owen Smith, 1990; Sinclair *et al.*, 2003). However, the saber-tooth cat *Homotherium serum* was considered a predator highly specialized in killing young elephants (Turner and Antón, 1997). A similar behaviour has been supposed also for its European counterpart *Homotherium latidens* (Palmqvist *et al.*, 2003). Instead, Antón *et al.* (2005) argued that this feature should be implausible considering the locomotion of such large predator. In studying the taphonomy of the Vallonet site (upper Pliocene, France), Echassoux (2004) found no evidence of predation on early Pleistocene proboscideans or rhinos in spite of the presence of *Homotherium crenatidens*. Only minor emphasis is given to rhinos as prey in living ecosystems (Kruuk, 1972; Schaller, 1972). At Venta Micena, the small rhino *Stephanorhinus etruscus* could have been actively selected by the giant hyena *Pachycrocuta brevirostris* and *Homotherium latidens* (Palmqvist *et al.*, 1996; Arribas and Palmqvist, 1998) but less so at Vallonet (Echassoux, 2004).

In contrast to megaherbivores, smaller prey could have played key roles for predators. In line with our results, Palmqvist *et al.* (2003) and Turner and Anton (1997) reported a possible selection by the large canid *Lycaon falconeri* and the dirk toothed cat *Megantereon cultridens* on *Equus stenonis*. Medium-sized artiodactyls (e.g. *Pseudodama* spp., *Eucladoceros* spp.) could have been equally important. Echassoux (2004) reported selection by


(a)
U Valdarno
Res_ADI
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
E.stenonis
S.strozzii
E.dicranios
P.nestii
L.etruscus
M.meridionalis
S.etruscus
L.vallisarni
E.stehlini
G.meneghinii
Praeovibos sp
H.antiquus
L.furtivus
P.brivatense
(b)
Pirro
Res_ADI
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
H.antiquus
S.hundsheimensis
P.eurygonos
B.degiuli
M.meridionalis
E.altidens
M.verticornis
M.obscurus
B.schoetensacki
L.vallisarni
M.trogontherii
S.strozzii
E.suessenbornensis
(c)
Galerian 1
Res_ADI
0.3
0.2
0.1
0
-0.1
-0.2
-0.3
-0.4
B.schoetensacki
E.ferus
E.antiquus
E.altidens
M.trogontherii
H.antiquus
C.elaphus
S.hemitoechus
S.hundsheimensis
M.savini
M.verticornis
E.suessenbornensis
S.scrofa
H.galerianus
P.eurygonos

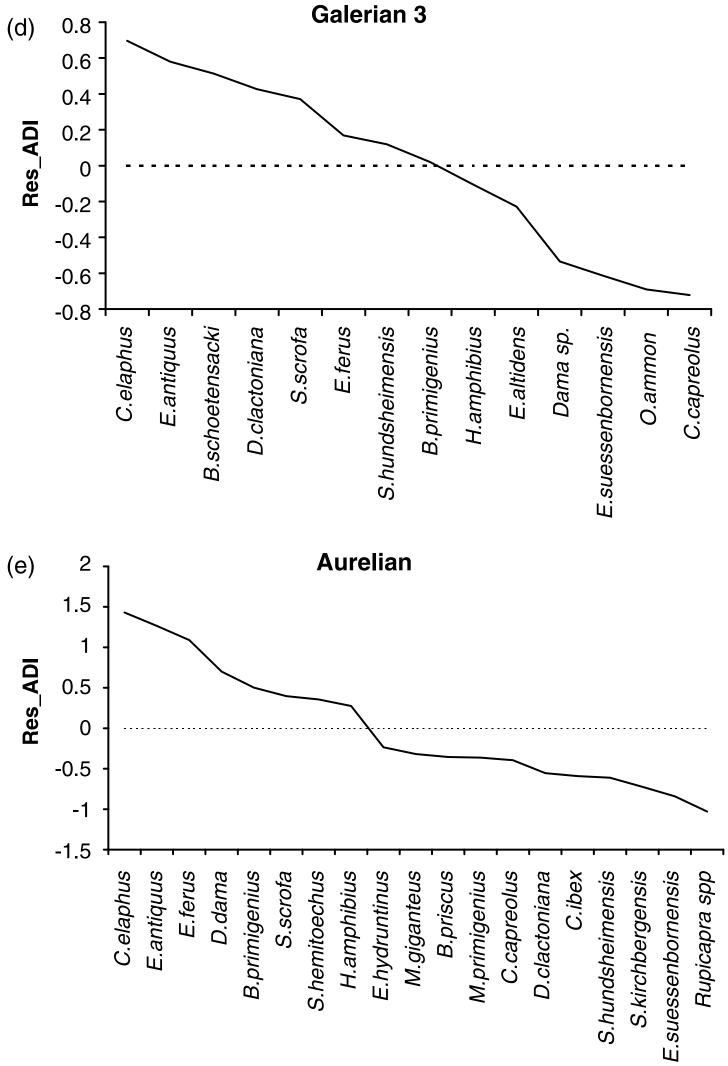


Fig. 3. Rank/abundance diagrams per PCOM. Residuals are from the linear regression of ADI against predatory pressure. (a, b) Villafranchian PCOMs; (c, d) Galerian PCOMs; (e) Aurelian PCOM.

predators (e.g. *Lycaon lycaonoides*) on *Pseudodama nestii* and Valli (2004) provided significant evidence for predator selection on *Croizetoceros ramosus* in St. Vallier.

In the early Galerian, many key prey species vanished, while some Villafranchian predators (*Homotherium latidens*, *Pachycrocuta brevirostris*, *Panthera gombaszoegensis*) persisted. These predators switched to new dominant prey species: the red deer (*Cervus elaphus*), horses *Equus* spp., and *Bison schoetensacki*. The appearance of pantherine cats did not affect prey rank abundance, as was the case later with the spotted hyena (*Crocuta crocuta*) and the grey wolf (*Canis lupus*).

The importance of the bison for the Pleistocene lion is supported by some taphonomic observations made on a frozen Pleistocene bison in Alaska (Turner and Antón, 1997). However, this single case should be validated for European localities.

All these reports on prey selection are in line with our results. Taken together, they are consistent with the fact that abundant prey populations are controlled by resources, whereas rare prey are predator-controlled (see Sinclair, 1985, for an example on large mammals). They also probably suggest that ecological attributes such as species commonness could well have surpassed the geopolitical frontiers of Italy. This is expected since species abundant in some places tend to be widespread (Brown, 1984; Hanski *et al.*, 1993; Gaston and Blackburn, 2000).

Since the middle Pleistocene, there has been an addition of ever-increasing importance to the predator guild: humans. Some observations at the Isernia La Pineta site (here included in the PCOM Galerian 2) underlined that *Bison schoetensacki* was especially abundant and on some bones there is evidence of human activity (Anconetani and Peretto, 1996). Similarly, red deer could have been hunted by humans (Steele, 2004). We need more accurate data to establish the relative importance of human hunting on Middle to Late Pleistocene prey guilds (but see Palombo and Mussi, 2001).

Sinclair (1985) argued that predation is more effective than competition in shaping African ungulate communities. We have no direct measure of exploitative competition and cannot infer its influence on the composition of Plio-Pleistocene communities here. Yet, although not evident, interspecific competition could have been related to predation via superabundant prey. Indeed, very common species increase the effect of predation on rare species by sustaining high numbers of predators. This effect, called 'apparent competition', has been widely studied in extant animal communities (Holt and Lawton, 1994; Holt *et al.*, 1994). Predation and apparent competition likely influence the positive relationship between abundance and species survival by removing rare species. A similar detrimental effect of predation was reported by Schoener *et al.* (2001). Moreover, our findings support the widely held belief that population abundance is a critical factor in species survival (Jernvall and Fortelius, 2004; Raia *et al.*, 2006a). Sinclair *et al.* (2003) argued that medium-sized ungulates suffer very high predatory pressure due to concurrent kills by several predators. In keeping with the latter study, we found that predatory pressure has a negative influence on prey abundance. Importantly, some species were able to overcome the negative impact of predators by being high in numbers.

CONCLUSION

During the Plio-Pleistocene, medium-sized herbivores had a key role as prey. Some of them were unable to grow very high in numbers and this seemingly doomed them to extinction. Larger Perissodactyls and Proboscideans were probably resources-controlled and much less prone to predation. Usually, they reached very high abundance, in line with the pivotal role for ecosystem functioning already suggested for them elsewhere (Owen Smith, 1990). Overall, the structure of prey abundance in PCOMs is very similar to living communities. This similarity adds further confidence to the use of PCOMs in evolutionary ecology studies.

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APPENDIX

Body size estimates for large mammals of the Plio-Pleistocene of Italy

Species	Weight (kg)	Log W (g)	Data source	Equation used
Acynonix pardinensis	65.7	4.818	Ficcarelli (1979)	Van Valkenburgh (1990); M_1 length in felids
Anancus arvernensis	3500	6.544	Guerin (2004)	Average of estimates for best equations in Christiansen (2004, Table 7)
Bison degiuli	667	5.824	Masini (1988)	Janis (1990); SLML for bovids
Bison priscus	687	5.837	Sala (1986)	Scott (1990); various equations for the limb elements. Average estimate
Bison schoetensacki	624	5.795	Sala (1986)	Janis (1990); TLML for bovids
Bos primigenius	939	5.973	Sala (1986)	Janis (1990); TLML for bovids
Canis arnensis	16	4.204	Rook (1993)	Van Valkenburgh (1990); M_1 length in canids
Canis etruscus	21	4.322	Rook (1993)	Van Valkenburgh (1990); M_1 length in canids
Canis lupus	40	4.602	Own	Van Valkenburgh (1990); M_1 length in canids
Capra ibex	150	5.176	Bartolomei and Sala (1972)	Janis (1990); TLML for bovids
Capreolus capreolus	39	4.591	Own	Janis (1990); SLML for cervids
Cervalces gallicus	412	5.615	Azzaroli (1981)	Scott (1990); various equations for the limb elements. Average estimate
Cervus elaphus	187	5.272	Abbazzi and Masini (1996)	Janis (1990); SLML for cervids
Chasmaportetes lunensis	76	4.881	Bebi (1998)	Van Valkenburgh (1990); M_1 length in all carnivores
Crocuta crocuta	102	5.009	Bebi (1998)	Van Valkenburgh (1990); M_1 length in all carnivores
Croizetoceros ramosus	47	4.672	De Giuli and Heintz (1974)	Janis (1990); SLML for cervids
Dama clactoniana	110	5.041	Di Stefano (1994)	Janis (1990); SLML for cervids
Dama dama	65	4.813	Di Stefano (1994)	Janis (1990); SLML for cervids
Dama sp.	65	4.813	Di Stefano (1994)	Janis (1990); SLML for cervids
Elephas antiquus	6499	6.813	Average of estimates for best equations in Christiansen (2004, Table 7)	
Equus livenzovensis	389	5.590	Size estimate as in Alberdi *et al.* (1995)	
Equus altidens	532	5.726	Azzaroli (1999)	Alberdi *et al.* (1995); various equations for the metapodials. Average estimate
Equus ferus	563	5.751	Size estimate as in Alberdi *et al.* (1995)	
Equus hydruntinus	210	5.322	Size estimate as in Alberdi *et al.* (1995)	
Equus stehlini	321	5.507	Size estimate as in Alberdi *et al.* (1995)	
Equus stenonis	409	5.612	Size estimate as in Alberdi *et al.* (1995)	
Equus suessenbornensis	820	5.914	Size estimate as in Alberdi *et al.* (1995)	

APPENDIX—*Continued*

Species	Weight (kg)	Log W (g)	Data source	Equation used
Eucladoceros dicranios	253	5.403	Azzaroli and Mazza (1992)	Janis (1990); SLML for cervids
Eucladoceros falconeri	218	5.338	Spaan (1992)	Janis (1990); SLML for cervids
Eucladoceros teguliensis	238	5.377	Spaan (1992)	Janis (1990); SLML for cervids
Gallogoral meneghinii	165	5.217	Duvernois and Guerin (1989)	Janis (1990); TLML for bovids
Gazella borbonica	24	4.380	De Giuli and Heintz (1974)	Janis (1990); TLML for bovids
Gazellospira torticornis	288	5.459	Duvernois and Guerin (1989)	Janis (1990); TLML for bovids
Hemibos galerianus	939	5.973	Assumed the same weight as with *B. primigenius*	
Hemitragus bonali	156	5.193	Crégut-Bonnoure (1989)	Janis (1990); TLML for bovids
Hemitragus sp.	156	5.193	Assumed the same weight as with *H. bonali*	
Hippopotamus amphibius	2495	6.397	Mazza (1995)	Janis (1990); SUML for all ungulates
Hippopotamus antiquus	2973	6.473	Mazza (1995)	Janis (1990); SUML for all ungulates
Homotherium crenatidens	231	5.364	Sardella (1993)	Van Valkenburgh (1990); M_1 length in all felids
Homotherium latidens	274	5.438	Sardella (1993)	Van Valkenburgh (1990); M_1 length in all felids
Hyaena prisca	76	4.881	Bebi (1998)	Van Valkenburgh (1990); M_1 length in all carnivores
Leptobos etruscus	400	5.602	Masini (1988)	Janis (1990); TLML for bovids
Leptobos furtivus	138	5.140	Masini (1988)	Janis (1990); TLML for bovids
Leptobos stenometopon	146	5.164	Masini (1988)	Janis (1990); TLML for bovids
Leptobos vallisarni	378	5.577	Masini (1988)	Janis (1990); TLML for bovids
Lycaon falconeri	26	4.415	Rook (1993)	Van Valkenburgh (1990); M_1 length in all canids
Lynx issiodorensis	22	4.342	Ficcarelli and Torre (1967)	Van Valkenburgh (1990); M_1 length in all felids
Lynx pardina spelaea	23	4.362	Ficcarelli and Torre (1967)	Van Valkenburgh (1990); M_1 length in all felids
Mammut borsoni	7162	6.855	Tsoukala (2000)	Average of various estimates for equations in Christiansen (2004)
Mammuthus meridionalis	6254	6.796	Average of estimates for best equations in Christiansen (2004, Table 7)	
Mammuthus primigenius	4283	6.632	Average of estimates for best equations in Christiansen (2004, Table 7)	
Mammuthus trogontherii	7544	6.878	Maglio (1973)	Body size calculated by extrapolation. Upper dentition was compared with that of *M. meridionalis* and the cube of the average ratio was taken. The resulting value was then multiplied by the weight of *M. meridionalis*
Megaceroides obscurus	289	5.461	Azzaroli and Mazza (1993)	Janis (1990); SUML for cervids
Megaceroides solilhacus	247	5.393	Abbazzi and Masini (1996)	Janis (1990); SLML for cervids

Megaceroides verticornis	213	5.328	Caloi and Palombo (1980)	Janis (1990); SLML for cervids
Megaloceros giganteus	388	5.589	Caloi and Palombo (1980)	Janis (1990); SLML for cervids
Megaloceros savini	242	5.384	Caloi and Palombo (1980)	Janis (1990); SLML for cervids
Megantereon cultridens	63	4.799	Sardella (2003)	Van Valkenburgh (1990); M_1 length in all felids
Megantereon whitei	55	4.740	Sardella (2003)	Van Valkenburgh (1990); M_1 length in all felids
Ovis ammon	54	4.732		Janis (1990); TLML for bovids
Pachycrocuta brevirostris	127	5.104	Bebi (1998)	Van Valkenburgh (1990); M_1 length in all carnivores
Pachycrocuta perrieri	80	4.903	Bebi (1998)	Van Valkenburgh (1990); M_1 length in all carnivores
Panthera gombaszoegensis	90	4.954	Shaub (1949)	Van Valkenburgh (1990); M_1 length in all carnivores
Panthera leo	183	5.262	Piccoli *et al.* (1979)	Van Valkenburgh (1990); M_1 length in all carnivores
Panthera pardus	60	4.778	Piccoli *et al.* (1979)	Van Valkenburgh (1990); M_1 length in all carnivores
Praeovibos sp	327	5.515	De Giuli and Masini (1983)	Scott (1990); various equations for the limb elements. Average estimate
Procamptoceras brivatense	108	5.033	Duvernois and Guerin (1989)	Janis (1990); TLML for bovids
Pseudodama eurygonos	88	4.944	De Giuli *et al.* (1986)	Janis (1990); LMRL for cervids
Pseudodama lyra	71	4.851	Spaan (1992)	Janis (1990); SLML for cervids
Pseudodama nestii	114	5.057	Leonardi and Petronio (1976)	Janis (1990); SLML for cervids
Rupicapra spp	35	4.544	Own	Janis (1990); TLML for bovids
Stephanorhinus etruscus	1345	6.129	Fortelius *et al.* (1993)	Janis (1990); TLML for perissodactyls and hyraxes
Stephanorhinus hemitoechus	2191	6.341	Fortelius *et al.* (1993)	Janis (1990); TLML for perissodactyls and hyraxes
Stephanorhinus hundsheimensis	1534	6.186	Fortelius *et al.* (1993)	Janis (1990); TLML for perissodactyls and hyraxes
Stephanorhinus jeanvireti	2283	6.358	Guerin (1980)	Janis (1990); TLML for perissodactyls and hyraxes
Stephanorhinus kirchbergensis	2828	6.452	Guerin (1980)	Janis (1990); TLML for perissodactyls and hyraxes
Sus arvernensis	114	5.057	Azzaroli (1966)	Janis (1990); SUML for all ungulates
Sus scrofa	90	4.954	Own	Janis (1990); SUML for all ungulates
Sus strozzii	266	5.425	Koufos (1986)	Janis (1990); SUML for all ungulates
Tapirus arvernensis	153	5.185	Rustioni (1992)	Janis (1990); LMRL for perissodactyls and hyraxes
Ursus arctos	167	5.223	Capasso Barbato *et al.* (1993)	Van Valkenburgh (1990); SKL length in ursids
Ursus deningeri	275	5.439	Assumed to be the same weight as with *U. spelaeus*	
Ursus etruscus	160	5.204	Own, IGF11568	Van Valkenburgh (1990); SKL length in ursids
Ursus minimus	104	5.017	Own, IGF906	Van Valkenburgh (1990); SKL length in ursids
Ursus sp.	160	5.204	Assumed to be the same weight as with *U. etruscus*	
Ursus spelaeus	275	5.439	Capasso Barbato *et al.* (1993)	Van Valkenburgh (1990); SKL length in ursids

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