

# Inconstancy in predator/prey ratios in Quaternary large mammal communities of Italy, with an appraisal of mechanisms

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## Abstract

Constancy in predator/prey ratio (PPR) is a controversial issue in ecological research. Published reports support both constancy and inconstancy of the ratio in animal communities. Only a few studies, however, specifically address its course through time. Here we study the course of predator/prey ratio in communities of large Plio-Pleistocene mammals in Italy. After controlling for taphonomic biases, we find strong support for PPR inconstancy through time. Extinction, dispersal events, and differences in body size trends between predators and their prey were found to affect the ratio, which was distributed almost bimodally. We suggest that this stepwise dynamic in PPR indicates changes in ecosystem functioning. Prey richness was controlled by predation when PPR was high and by resources when PPR was low.

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## Introduction

The question of constancy in predator/prey ratio (PPR) in animal communities is an old one in ecology that is still almost unresolved (Rosenzweig, 1995; Spencer et al., 1999; Croft, 2006). Arnold (1972) suggested that the number of predators follows the number of prey. Thus, the ratio should be constant. Some studies have supported constant PPRs across communities (Cohen, 1977; Jeffries and Lawton, 1985; Sugihara et al., 1989; Shoensly et al., 1991; Gaston et al., 1992; Warren and Gaston, 1992). Mithen and Lawton (1986) performed a computer-based experiment indicating PPRs are discrete, meaning that not all ratios are equally feasible. Inconsistent support for a constant ratio was reported by Simberloff (1976), and Valentine et al. (2002). More importantly, Wilson (1996) demonstrated that a constant ratio is expected by chance as one compares communities with different species diversities.

Studies of PPR in extinct mammal communities are much less common (but see Croft, 2006; Fortelius et al., 1996; Van Valkenburgh and Janis, 1993). Van Valkenburgh and Janis

(1993) analyzed patterns in PPR in Cenozoic large mammals from North America. They found evidence for strong variation in PPR through time. More specifically, Van Valkenburgh and Janis found that carnivore diversity did not increase at the same rate as herbivore diversity. They suggested that carnivores are less likely to share niche space and that this, in turn, would put a ceiling on their increase in number. In Van Valkenburgh and Janis' study, both the methods and the interpretation of results were based on the assumption that PPR reflects the effects of ecological interactions on species diversity in different trophic groups. It is worth mentioning that other authors have interpreted PPR differently. For instance, Gaston et al. (1992) noted that in most studies, the prey category often includes quarries for no predator. Consequently, they suggested using the term "non-predator" instead of "prey". Similar arguments persuaded Valentine et al. (2002) to use the expression "carnivorous to non-carnivorous" for their marine gastropods.

The spirit of our study is the same as that of Van Valkenburgh and Janis; we analyze the course of PPR through time in Plio-Pleistocene Italian large mammal communities. We present this study in two related parts. First, we show the results for the computation of PPRs and its validation, taking into account the influence of possible sampling biases. We then seek explanatory

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mechanisms for the inconstancy of PPR through time. In particular, we concentrate on the effect of body size trends (for carnivores and herbivores). Body size has an overwhelming importance in prey selection among mammals. Many studies have demonstrated a close correlation between predator and prey masses (Gittleman, 1985; Vezina, 1985; Carbone et al., 1999; Radloff and Du Toit, 2004). In modern mammalian communities, very large size (e.g. the size of hippos and elephants) helps limit predation risk. Rodriguez et al. (2004) have demonstrated that herbivores in Europe have grown larger (on average) since 1 Ma. In Italian paleocommunities, we found this size increase was asymmetrical across mammalian orders (i.e. it applied to herbivores but not to carnivores) and that it occurred some 1 Ma, consistent with the findings of Rodriguez et al. (2004). We suggest that this asymmetry negatively affected carnivore diversity, thereby lowering PPR since the late Early Pleistocene.

## Materials and methods

### Computing and validating PPRs

We computed predator/prey ratios for Italian paleocommunities (PCOMs) from the Late Pliocene to the Late Pleistocene (Table 1). A PCOM represents the large mammal community living in peninsular Italy at a given period during the Plio-Pleistocene (Raia et al., 2005, 2006b). Successive PCOMs replaced each other through time during the Plio-Quaternary. PCOMs were obtained by performing a bootstrapped cluster analysis on the presence/absence data matrix of fossil large mammal species per local assemblage (LA), then correcting for range through (Boltovskoy, 1988; Barry et al., 1995; Maas et al., 1995; Foote, 2000). A species missing in a given PCOM was considered present if it occurred in both the previous and the successive PCOMs.

A local assemblage is the list of species present at a given fossil site in a given stratigraphic interval (Raia et al., 2005, 2006b). By collecting data from several coeval sites, PCOMs have the advantage of including rare species and minimizing taphonomic biases (Raia et al., 2005, 2006a). Our large mammal data set includes 85 species and 602 occurrences in 71 LAs (mean = 8.47 species per site; see Raia et al., 2006b for further details). Local assemblages are distributed across 8 PCOMs (mean = 8.88 LAs per PCOM) ranging from 2.6 to 0.3 Ma.

Species were selected to represent interacting (in ecological terms) entities. In keeping with Van Valkenburgh (1988) we considered any land carnivore larger than 10 kg to be a large predator (see below for the calculation of body size). Cave bears (*U. spelaeus* and its very close relative *U. deningeri*) were excluded because isotopic analyses of dental enamel have indicated they fed exclusively on plant material (Stiner et al., 1998).

We ascribed to the “prey” category mammals belonging to the orders Artiodactyla, Perissodactyla and Proboscidea. Large carnivores usually feed on prey as large as and even larger than themselves (Gittleman, 1985; Vezina, 1985; Carbone et al., 1999). Consequently, the species we included probably had strong trophic interaction with each other, and much less with smaller species. Van Valkenburgh and Janis (1993) applied very similar criteria in their computation of PPRs in Eocene to Recent North American mammals, excluding any carnivore “... estimated to be smaller than the living grey fox (*Urocyon cinereoargenteus*).” Likewise, they excluded rodents and lagomorphs. We similarly excluded these small mammals because their fossil record is scarce and they often do not occur in the same fossil sites as larger mammals in the Italian record (Raia et al., 2005). Our criteria for species inclusion reduced our dataset to a total species diversity to 81 and occurrences to 589.

After PPRs were computed, we evaluated their reliability by tackling the problem of preservational bias with three different approaches. First, because carnivores are usually rarer in paleontological assemblages due to their high trophic level (Raia et al., 2005, 2006a) PPRs could have been artificially low in some instances. In particular, since PCOMs gather information on presence/absence data from fossil assemblages, those PCOMs including more local assemblages could contain more carnivore species by chance. To test for this potential bias, we regressed PPRs against the logarithm of the number of LAs in each PCOM.

A second test of PPR reliability was performed by applying rarefaction analysis (Sanders, 1968) to both carnivore and herbivore occurrence data. Although rarefaction on either the number of individuals or the number of identified specimens per assemblage is more appropriate, it is practically impossible here, given the inadequate data available for most local assemblages (Raia et al., 2005). This approach has been already applied by paleontologists to different taxa in multilocality

Table 1  
Distribution of predator and prey diversity (with the details for different orders), and predator/prey ratios (PPRs) for the paleocommunities (PCOMs)

PCOMs	Monopoli (2.6)	Late Villafranchian			Galerian	Galerian	Galerian	Aurelian
		Upper Valdarno (2)	V Chiana (1.5)	Pirro (1.2)	1 (0.9)	2 (0.6)	3 (0.45)	(0.3)
Number of Prey	16	14	13	13	15	17	17	19
Megaherbivores (>1000 kg)	4	3	4	4	6	7	6	7
ARTIO	11	10	8	8	8	9	10	11
PERIS	3	3	4	3	5	6	6	6
PROB	2	1	1	2	2	2	1	2
Number of predators	7	11	9	10	5	7	5	6
Predator/prey ratio (PPR)	0.438	0.786	0.692	0.769	0.333	0.412	0.294	0.316

Numbers in parentheses represent approximate age (Ma) of the PCOM.

datasets (Miller and Foote, 1996; Alroy, 1996; Marwick, 1998). Rarefaction was performed on the two PCOMs with the richest number of occurrences for carnivores and herbivores, Upper Valdarno and Aurelian PCOMs, respectively. If PPRs actually were inconstant, we expected either more carnivores or fewer herbivores than expected by rarefied estimates when PPR was high, and the converse when PPR was low. We argue that the use of rarefied estimates is a prudent approach given that low sample size, which is typical for terrestrial assemblages, should produce large confidence intervals in these analyses.

Finally, we tested whether the calculated PPRs could be a by-product of the computation of PCOMs themselves. Because we found that PPRs were distinctly higher during the Late Villafranchian Mammal Age, we looked *a posteriori* at the distribution of PPRs calculated for any single local assemblage. We explicitly tested the hypothesis that PPR values in Late Villafranchian local assemblages were higher than for all sites of a different age taken together.

Even given potential taphonomic biases, we did not expect to get biased results. Only a few large carnivore species living in Europe during the Plio-Pleistocene were absent from Italy (Turner, 1995). Range-through taxa account for only 8.4% of total occurrences in PCOMs (i.e. there are very few gaps in species occurrences; Raia et al., 2006b). Species diversity in our data set is very likely to be saturated and therefore “real” for both carnivores and herbivores (Raia et al., 2005) and PCOMs replicate living communities for other ecological features (e.g. occupancy frequency distribution; Raia et al., 2006a).

*Potential mechanisms*

To test the hypothesis that predator/prey body size ratio could have affected PPRs, we calculated the body sizes of the fossil species by applying regression equations published in Damuth and MacFadden (1990), Alberdi et al. (1995), and Christiansen (2004) (data available from the senior author). For each family, we selected the equations that minimized prediction error. We measured the difference in log<sub>10</sub> body size distribution of predators and prey (herbivore orders combined) at the 1st, 2nd, and 3rd quartile (body size differences at quartiles, BSDQ). The use of quartiles was meant to account for the correlation between body sizes of predators and prey, a “taxon free” approach. No attempt was made to ascribe any predator to specific prey. Proboscideans and hippos were excluded from BSDQ analyses because their extremely large body size (almost 3 tons) could have biased results. Moreover, their size estimates are less reliable because the small amount of variation in body mass among extant species makes prediction equations somewhat imprecise for these species. Regardless, this could not have biased our results because predation on such huge prey is accidental and extremely rare (Schaller, 1972; Kruuk, 1972; Ruggiero, 1991; Sinclair et al., 2003; Radloff and Du Toit, 2004). Rhinos are formidable prey as well but they were much smaller than elephants and hippos, and predation upon them could have been substantial. For instance, in a study on prey selection in the Venta Micena assemblage (Early Pleistocene, Spain)

Palmqvist et al. (1996) showed that predators had killed a proportion of juveniles of the rhino *Stephanorhinus etruscus* (33.3%), similar to what expected in the natural population. Conversely, juveniles of the hippo *Hippopotamus antiquus* (60.0%) and of the mammoth *Mammuthus meridionalis* (80.0%) were disproportionately selected for by predators. This indicates that adult rhinos were regularly killed by predators, but adult mammoth and hippo were not. It is worth noting that most of the species of the Venta Micena assemblage are present in our dataset.

BSDQ analysis could reveal the existence of different size trends between carnivores and their prey. Yet it could not account for possible alterations of actual prey number that these trends could have created. To test this hypothesis, which we name PPR asymmetry, we applied the model equations of Radloff and Du Toit (2004) to the two largest predators per PCOM, and counted the number of supposedly predation-free herbivores. Radloff and Du Toit (2004) performed a long-term field survey on East African savannah predators and calculated allometric equations to predict maximum prey size for a given predator size.

**Results**

*PPRs values and course*

The results of the PPR computation are shown in Table 1 and Figure 1. PPR is not affected by the number of local assemblages per PCOM ( $n=8$ ,  $r^2=0.003$ ,  $p=0.882$ ). It is evident that the three Late Villafranchian PCOMs (Upper Valdarno, V Chiana, and Pirro) had much higher PPRs. We verified this datum statistically with a resampling test. PPRs were shuffled among PCOMs. Then we drew three of them at random, and recorded the difference in mean PPR values between the three extracted ratios and the remaining. This procedure was repeated 1000 times (with replacement), thus

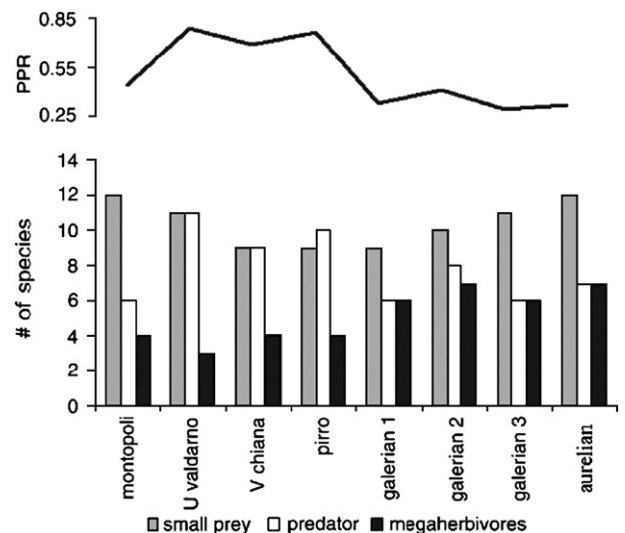


Figure 1. Predator/prey ratio (PPR) (solid line) compared with number of predators, number of smaller prey, number of megaherbivores (herbivores larger than 1000 kg, Owen Smith, 1990).

Table 1  
Molecular targets in cerebral ischemia

PCOM	Carnivore number of occurrences	Herbivore number of occurrences	$S_{\text{carnivores}}$	$S_{\text{herbivores}}$	$S_{\text{carnivores}}$ (exp.)	$S_{\text{herbivores}}$ (exp.)	95% CI <sub>carnivores</sub>	95% CI <sub>herbivores</sub>
Monopoli	7	36	7	16	5.25	13.5	3.5–7.0	10.6–16.3
U Valdarno	51	88	11	14*	–	17.5	–	15.4–19.4
V Chiana	9	31	9*	13	6.18	12.7	4.3–8.1	9.9–15.6
Pirro	12	34	10*	13	7.28	13.2	5.2–9.3	10.3–16.0
Galerian 1	5	29	5	15	4.11	12.4	2.7–5.5	9.6–15.3
Galerian 2	9	31	7	17*	6.18	12.7	4.3–8.1	9.9–15.6
Galerian 3	8	38	5	17*	5.74	13.7	3.9–7.6	10.9–16.6
Aurelian	24	138	6*	19	9.6	–	7.8–11.3	–

Occurrence data used to calculate rarefaction curves are indicated in grey. Significant deviations from rarefied estimates are marked with an asterisk.

generating a sample of 1000 mean differences. The null hypothesis is that PPR mean differences as large as between Late Villafranchian and other PCOMs occur more than 5% of the time in random samples. The resampling test indicates that the null hypothesis should be rejected ( $p=0.014$ ). Consistent with the PPR computation result, the rarefaction curve indicates carnivore species to be higher than the 95% confidence interval (CI) in V Chiana and Pirro PCOMs and lower than 95% CI in Aurelian PCOM (Table 2). As for herbivores, rarefaction indicates there were significantly more species than expected in Galerian 2 and Galerian 3 PCOMs and fewer than expected in U Valdarno PCOMs (Table 2). Taken together, all significant deviations agree with predictions for inconstant PPR (binomial test,  $n=6$ ,  $p=0.016$ ). Deviations from rarefied estimates were non-significant only for Montopoli and Galerian 1 PCOMs. Interestingly, Montopoli PCOM precedes Late Villafranchian whose PPRs were very high, and its carnivore diversity (7) coincides with the CI upper limit. Galerian 1 was the earliest with a low PPR and its herbivore diversity was very close to the upper CI limit (15.3, Table 2). Therefore, even these PCOMs indicate a switch from low to high PPRs and vice versa. The analysis of PPR at the LA level confirms that higher PPR in Late Villafranchian was not an artifact of PCOMs computation (Mann–Whitney  $U=367$ ;  $n=71$ ;  $p=0.011$ ) (Fig. 2).

#### Body size trends and their effect on predation structure

In our data, prey have grown larger since the Galerian (some 1 Ma), in agreement with Rodriguez et al. (2004). Interestingly, the size of the smallest prey follows a bell-shaped trajectory peaking at latest Villafranchian (Pirro PCOM, the lower limit in “prey” size distribution in Fig. 3). Small-sized prey were remarkably absent during Late Villafranchian. Apart from the deer *Pseudodama* (body weight=88–111 kg) there were no artiodactyls smaller than 200 kg (Fig. 3) during this mammal age. Post-Villafranchian artiodactyl mean body size decreased, although some species (e.g. the bovids *Hemibos galerianus* and *Bos primigenius*) approached  $10^3$  kg. Conversely, perissodactyl body size increased during Galerian and Aurelian PCOMs. Rhino diversity decreased to one species (*S. etruscus*, body weight=1345 kg) during the early Late Villafranchian. Galerian and Aurelian PCOMs had at least two rhinos occurring together. The smaller of them (*S. hundsheimensis*) was larger than *S. etruscus*. Furthermore, it is well known that Galerian and Aurelian horses were remarkably large (Alberdi et al., 1995).

The body size difference between the largest predators and largest prey were smaller in Late Villafranchian PCOMs than in others (see Fig. 3). To test for the reliability of this result, we shuffled BSDQs (without replacement) among PCOMs. With

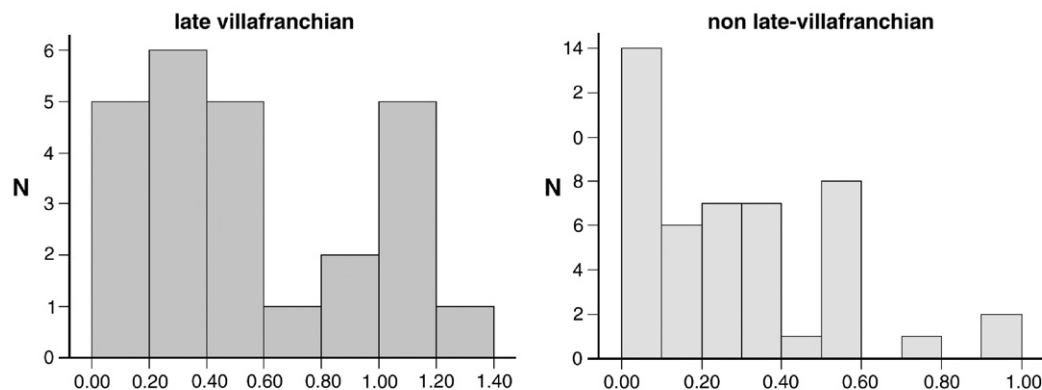


Figure 2. Predator/prey ratios computed for the local assemblages. Local assemblages have been partitioned into Late Villafranchian and Non Late Villafranchian.

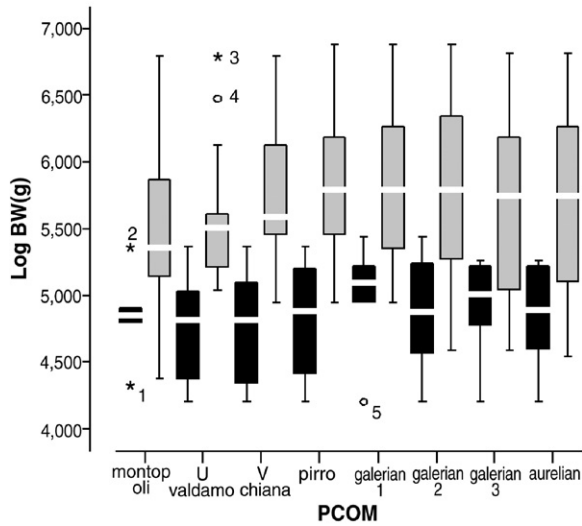


Figure 3. Body size trend for different trophic groups. Black box, carnivores; grey box, herbivores. Box length represents the interquartile range of the body size distribution. The white horizontal band represents the median value. Circles are outliers (values 1.5 to 3 box lengths outside the box). Stars represent extreme cases (values more than 3 box lengths outside the box). (1) *Canis etruscus*, (2) *Homotherium cranatidens*, (3) *Mammuthus meridionalis*, (4) *Hippopotamus antiquus*, (5) *Canis arnensis*.

each repetition, three PCOMs (at random) were considered to be “Late Villafranchian”, the others “Non-Late Villafranchian”. Mean BSDQs between “Late Villafranchian” and “Non-Late Villafranchian” were then computed. BSDQs at the 3rd quartile was significantly smaller during Late Villafranchian (resampling test, without replacement,  $n=1000$ ,  $p_{one\ tailed}=0.039$ ). Interestingly, the opposite trend occurred at the first quartile ( $n=1000$ ,  $p_{one\ tailed}=0.018$ ). At the second quartile, there was no significant variation ( $n=1000$ ,  $p=0.156$ ). In sum, during Late Villafranchian herbivores were more similar in body size to each other than in other PCOMs.

The application of equations for maximum prey size indicates that PPR asymmetry does apply (Table 3). The number of herbivores exceeding maximum prey size (calculated on the largest predator mass) was significantly higher during Late-Villafranchian (resampling test, with replacement  $n=1000$ ,  $p=0.019$ ). The same applies for the second largest predator (resampling test, with replacement  $n=1000$ ,  $p<0.001$ ). This

indicates that a significantly higher proportion of ungulate species were available to predators during Late Villafranchian.

**Discussion**

We found evidence for PPR inconstancy through time, consistent with previous investigations of the same issue (Van Valkenburgh and Janis, 1993). In particular, Late Villafranchian PCOMs show significantly higher PPRs. Potential biases in the fossil record do not alter the PPR computation, thus indicating that PPR inconstancy was genuine.

The analysis of body size trends indicates that herbivores, but not carnivores, have become larger since the Galerian. Significantly fewer prey were large enough to avoid predation during the Late Villafranchian. The hypothesis we therefore propose to account for inconstant PPRs deals with this disparity between carnivore and herbivore body size evolution. It often has been noted that Pleistocene herbivores grew huge (e.g. Geist, 1971). In fact, during the Middle to Late Pleistocene, odd-toed ungulates grew toward the huge size of *Stephanorhinus kirchbergensis*, *S. hemitoechus*, *S. hundsheimensis* and the woolly rhino, *Coelodonta antiquitatis* (not included here). These beasts were more than 2 tons in body weight. Artiodactyls approached the size class of megaherbivores (1000 kg) with the auroch *Bos primigenius*, and *Hemibos galerianus*. BSDQs data indicate post-Villafranchian predators were unable to grow this large. Galerian predators of Europe were, in fact, not much larger than modern ones, perhaps with the exception of the cave hyena, *Crocota crocuta spelaea* (Klein, 1986; Klein and Scott, 1989), and the cave bear, *Ursus spelaeus* (Christiansen, 1999) which was exclusively herbivorous (Bocherens et al., 1994; Stiner et al., 1998). Most of the adult Galerian and Aurelian large herbivores (other than mammoths, elephants and hippos) probably avoided predation. This is at least true for rhinos which were much larger and more diverse in post-Villafranchian faunas.

Megaherbivores can monopolize a large proportion of ecosystem resources (Owen-Smith, 1987, 1990; Fritz et al., 2002; Cristoffer and Peres, 2003). Consequently, perceived productivity for both carnivores and their prey drops where megaherbivores are abundant (Cristoffer and Peres, 2003). This decreases the population abundances of smaller herbivores (Fritz et al., 2002). Because carnivores are much rarer than most

Table 3  
Largest predators per paleocommunity (PCOM) and number of prey outside their maximum prey-size target

PCOM	Largest predator	Mass (kg)	Max prey Mass (kg)	Number of prey >max	Second largest predator	Mass (kg)	Max prey mass (kg)	Number of prey >max
Montopoli	<i>Homotherium crenatidens</i>	231	1909	3	<i>Pachycrocuta perrieri</i>	80	406	5
U Valdarno	<i>Homotherium crenatidens</i>	231	1909	2	<i>Pachycrocuta brevirostris</i>	127	797	3
V Chiana	<i>Homotherium crenatidens</i>	231	1909	2	<i>Ursus etruscus</i>	160	1117	4
Pirro	<i>Homotherium crenatidens</i>	231	1909	3	<i>Ursus sp.</i>	166	1179	4
Galerian 1	<i>Homotherium latidens</i>	274	2450	3	<i>Ursus sp.</i>	166	1179	5
Galerian 2	<i>Homotherium latidens</i>	274	2450	4	<i>Panthera leo</i>	183	1359	6
Galerian 3	<i>Panthera leo</i>	183	1359	5	<i>Ursus arctos</i>	167	1189	5
Aurelian	<i>Panthera leo</i>	183	1359	6	<i>Ursus arctos</i>	167	1189	5

Differences between Late-Villafranchian PCOMs and others are highly significant. Largest predator: resampling test, with replacement  $n=1000$ ,  $p=0.019$ . Second largest predator: resampling test, with replacement  $n=1000$ ,  $p<0.001$ .

of their prey (Spencer, 2000) they should suffer the highest risk of extinction by the reduction in available productivity. Consequently, the extinction of some carnivores relaxes predatory pressure on smaller prey (Sinclair et al., 2003). We argue that both these factors decrease PPR. These theoretical arguments perfectly fit the data provided here. When mega-herbivores diversified at the beginning of the Galerian mammal age, carnivore diversity was halved within 2–300 Ka. That is, the reduction in available prey (but not in total prey number) resulted in a reduction in predators (see Table 1, and Fig. 3). Consistent with this, we calculated a significant negative relationship between megaherbivore number and predator number (Pearson  $r = -0.791$ ,  $p = 0.019$ ; Spearman  $\rho = -0.719$ ,  $p = 0.044$ ). A decrease in carnivore diversity coinciding with an increase in megaherbivore diversity was already reported by Fortelius et al. (1996), dealing with a larger geographical scale (Europe) and a different period (late Miocene). Consistent with our findings, PPR decreased at that time (Fortelius et al., 1996). Interestingly, even if the largest artiodactyls grew huge after Late Villafranchian, the median size for this group progressively decreased from the Galerian onward. The appearance of some small to medium sized artiodactyls such as the roe deer (*Capreolus capreolus*), fallow deer (*Dama dama*), ibex (*Capra ibex*), wild sheep (*Ovis ammon*), and chamois (*Rupicapra rupicapra*) explains this pattern. These newcomers seemingly were residing in the smallest size class once occupied by species such as *Gazella borbonica* and *Croizetoceros ramosus* that became underrepresented during Late Villafranchian (that is 1 myr ca; the highest median values for artiodactyl body size occur in V Chiana, Pirro and Galerian 1 PCOMs). This is not an artifact of preservation (i.e. of some PCOMs failing to sample the smallest and/or least abundant species because of taphonomic biases) because the numerous Late Villafranchian carnivores were, on average, as small as or even smaller than the smallest herbivores from any other PCOM. Furthermore, these carnivores certainly were less abundant than many of those small herbivores (Raia et al., 2006a). In fact, this paucity of smaller artiodactyls during Late Villafranchian is expected (Sinclair et al., 2003) because of the intense predation that the numerous carnivores put on them. It is possible that the abundant Late Villafranchian carnivores could have driven some medium-sized artiodactyls to extinction. Beyond raw numbers, some simple considerations of species biology are consistent with our interpretation. The numerous Late Villafranchian predators probably coexisted because of their high trophic specialization, since they include two machairodont cats, the cheetah *Acinonyx pardinensis*, the running hyena *Chasmaportetes lunensis* and the giant hyena *Pachycrocuta brevirostris* along with three different canids. The latter typically are omnivores and thus could subsist on food other than large mammal prey, thereby increasing total perceived productivity for the carnivore group taken as a whole. In other PCOMs, either canids were rare (Montopoli) or there were other less specialized predators (i.e. pantherine cats, cave hyena; from the Galerian onward). In modern faunas, carnivore-dominated assemblages tend to be filled with non-specialized, even omnivorous carnivores (e.g. Kuril Islands: Hoekstra and

Table 4

Summary characteristics of both predators and prey under different regimes of predator/prey ratio (PPR)

		High PPR	Low PPR
Predators	Predators number	Relatively high	Relatively low
	Generalist predators	Few	Many
	Specialist predators	Many	Few
Prey	Prey number	Relatively low	Relatively high
	Megaherbivores	Few	Many
	Small herbivores	Few	Many

Fagan, 1998). Further, as we noted above, smaller prey reappeared beginning in the Early Galerian.

PPR asymmetry is not the only factor affecting PPR inconstancy. For instance, some 7–8 herbivore species would need to be removed from Galerian faunas to drop their PPRs to Villafranchian levels. Clearly, no Italian Plio-Pleistocene paleocommunity had this many predation-free herbivores. Even if this were the case, the resulting diversity would have been some 30% lower in these communities. This is not plausible because large mammal diversity did not change significantly during the Plio-Pleistocene period (Raia et al., 2005). Therefore, some additional factors should have affected PPR patterns. We envision a dispersal event as one such a factor. Plio-Pleistocene large mammals of Italy were primarily Eurasian immigrants. Only four of 85 large mammal taxa are suspected to have originated in the Italian peninsula (Kotsakis et al., 2002; Raia et al., 2005). Most species colonized from the outside in massive immigration episodes (“dispersal events” Azzaroli, 1983; Azzaroli et al., 1988; Koenigswald and Werdelin, 1992). Carnivores are better than herbivores at dispersing (Sutherland et al., 2000; Kelt and Van Vuren, 2001; Bowman et al., 2002; Gaston, 2003). Consistent with patterns in PPR, carnivore diversity increased sharply at the onset of Late Villafranchian (the “Wolf-event” Azzaroli, 1983; Koenigswald and Werdelin, 1992; Rook and Torre, 1996). Some seven new carnivore species appeared at Upper Valdarno PCOM (the highest number of first appearance among carnivores). Carnivore diversity decreased again during early Galerian, when seven local extinctions occurred. At the same time, herbivore diversity rose again (Fig. 1) and PPR decreased. The Wolf Event entailed an increase in predatory pressure on smaller herbivores (see Sinclair et al., 2003 for a discussion on body size and predatory pressure in large mammal communities). Most small artiodactyls went extinct at that time and PPR reached a very high level (see Table 4 for a definition). One million years later the diversification of megaherbivores reduced PPR back to the previous (low) values.

## Conclusion

Geist (1998, 2000) argued that end-Pleistocene large mammal communities were either predator-limited (in North America) or food-limited (in Eurasia). These arguments extend an attribute of prey populations to whole communities. That is, prey can be either predator-limited or food-limited (Kruuk, 1972; Schaller, 1972; Sinclair, 1985, 2000; Sinclair et al., 2003).

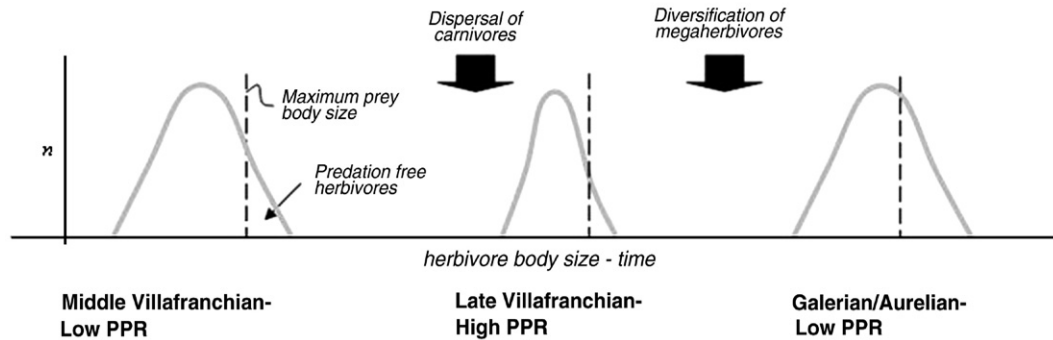


Figure 4. Schematic depiction of causal mechanisms affecting PPR course. Grey solid line represents the distribution of herbivore body masses. The distribution becomes narrow after the dispersal event named Wolf Event (2 My BP ca.), when carnivore diversity increases abruptly. The vertical broken line represents the mass of the largest prey carnivores could have seized.

Van Valkenburgh and Janis (1993) found one of Geist's predator-limited faunas, the North American Late Pleistocene large mammal community, to have particularly high PPR. Consistent with Geist's suggestion, we found that PPR in Plio-Pleistocene Italian mammalian communities fits a two-stage model (Table 4). High PPR stand coincides with a dispersal event involving a high number of incoming carnivores (Fig. 4). Some medium-sized herbivores declined soon thereafter, perhaps because of the high predatory pressure from new carnivores. PPR declined to the low stand when megaherbivores became more numerous at some 1 Ma (Fig. 4). It is possible that the two distinct PPR stages we found are merely special cases of alternative ecosystem stable states (Shröder et al., 2005).

It is difficult to say to what extent these results can be generalized. Van Valkenburgh and Janis (1993) found inconstant ratios in Cenozoic North American mammals. The time span and the area they considered are larger than ours by one order of magnitude. Even more importantly, diversity was inconstant in their data, and they relied on different diversification rates between carnivores and herbivores to explain PPR inconstancy.

Given the very nature of this study, we could not take into account the potentially important influence of "ecological" parameters (e.g. productivity change, climate-driven disturbance) which could not be measured in the fossil communities. Interestingly, Croft (2006) found marsupial communities to show unusually low PPRs, suggesting that species taxonomic identity could be equally important. Unfortunately, any information on productivity and/or humidity in past ecosystems is circumstantial at best. Indeed, productivity proved to be difficult to infer and hence mostly unpredictable (e.g. Janis, 1984, Janis et al., 2000, 2004; Guthrie, 2001). Another obvious factor to take into account is predator functional response (Abrams, 2000; Abrams and Ginzburg, 2000). PPR calculation does not include prey abundance, yet carnivores often select for the most abundant prey. Differences in evenness among prey populations could have compensated for extinction risk in the rarest prey species via disproportionate selection on the most abundant prey (Abrams and Matsuda, 1996; Fortelius et al., 1996).

This study provides evidence for community-level mechanisms controlling diversity at different but strongly interacting

trophic levels. We propose a conceptual model to explain these mechanisms and hope that further studies will test the generality of both the inconstancy in PPR and the mechanisms that we suggest underlie this inconstancy.

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